

Ornamentation of dermal bones of *Metoposaurus krasiejowensis* and its ecological implications

Mateusz Antczak¹ and Adam Bodzioch^{2,3}

¹Institute of Geology, Adam Mickiewicz University, Poznań, Poland

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

³European Centre of Palaeontology, University of Opole, Opole, Poland

Corresponding author:

Mateusz Antczak¹

Email address: mateusz.antczak@amu.edu.pl

too short: one more sentence explaining why amphibians are better suited than other animal groups and what is meant with "environmental analysis"

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, tubercles, etc.) including the use of a scanning electron microscope for high 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.

better
"..., such as
grooves, ..."

"temnospondyls" or "temnospondyl amphibians" or "Temnospondyli"

italic font required

The abstract should more explicitly state (in 1-2 sentences)

(a) what the main difference between these ornamentation types is or represents
(b) why differences in ecology are the best explanation for the observed variation

INTRODUCTION

The fossil assemblage from the Late Triassic of Krasiejów is a unique discovery. Excavations carried out since 2000 have revealed a unique set of terrestrial Triassic faunas. In Krasiejów, alluvial deposits were also found (e.g. Dzik et al., 2000; Dzik and Sulej, 2007, 2016; Brusa 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 micro-scales, 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

but no statistical tests in the stricter sense are applied, so this phrase might be misleading

?diversification = evolution that leads to a higher diversity

the 'Trias' site at Krasiejów (SW Poland; Fig. 1), where a very rich accumulation of fossil remains was found. The fine-grained (mudstones and claystones) Late Triassic (Carnian, according to Norian, according to Szulc, 2005; 2007; Szulc, Racki and Jewuła, 2015) deposits (e.g. Gruszka and Zieliński, 2008), in which two bone-bearing horizons are 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/IP01–20), and several interclavicles (UOBSO1–3) were removed during the excavation and are stored in the Opole University collection. Morphometric measurements 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).



and interpretation drawings of all the basis for the comparison of measurements should be part of supplementary material

This idea by Zalecka (2012) should not be taken as granted, rather unreliable evidence for ontogenetic stages - in comparison with e.g. histological evidence.

the number of foramina and degree of ridge roughness. The possible relative

vice 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).

PCA \neq factor analysis, both are (distinct) methods for multivariate data analysis

Analysis (PCA) was conducted using PAST. PCA, one of several statistical methods for factor analysis, A set of data consisting of N observations, where each is interpreted as a cloud of N points in a K-dimensional space.

Similar results (points in the diagram) are connected via convex hulls into subsets.

What is similar?... This appears to be a rather arbitrary/ non-reproducible way of (unsupervised) classification.

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).

would take that as a hypothesis, but not a reliable one

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).

you may put PCA results in a table

The Principal Component Analysis Charts presented below were created for a correlation matrix following transformation of the data using the equation $B = (A - \text{mean})/\text{standard deviation}$, 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).

one data point is not enough to illustrate the distribution of these two reference species

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 striae (barely visible and sparse) and possess a small number of small cap ridges (less than 7 per 100 μm^2). Usually they also have less than one and no distinct bumps or roughness at the top of the ridge (Fig. 10,

include all points that belong to the same group in the convex hulls to get a more realistic representation of the variance

132 2 possess striations on the ridges and a greater number of small foramina (more than 7 per 100 μm^2).
133 Usually they also have more than one foramen per 1 mm of ridge length and distinct bumps and roughness
134 at the top of the ridge (Fig. 10, Table 5).

135 **Remarks on the dermal bones**

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

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

- 145 • seven (7) possessed thick, irregular, usually small polygons, covering a large part of the surface of
146 the skull; the radial ornamentation of these skulls was sparse in the postorbital part of the skull;
147 multipolygons were frequent. These are features of T2 described in the clavicles.
- 148 • six (6) possessed larger, regular polygons, which covered a smaller part of the surface of the skull;
149 radial ornamentation was common in the postorbital part of the skull (parietals, supratemporals,
frontals, postorbitals). These are features of T1 described in the clavicles.

(3) skulls were largely covered with sediment, and thus cannot be attributed to either of the types.

It is a fact that the skulls classified as T2 were relatively small (averaging 28 cm in length) in comparison to T1 skulls (averaging 35 cm in length). However, this was not a rule. Among analysed skulls there were also small (28 cm in length (UO/JP04, 35 cm; UO/JP18, 35.4 cm) with different ornamentation types (Fig. 13, 14).

157 **DISCUSSION**

158 **Possible solutions**

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

160 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
161 material represent differences between two species (Opole University Collection, Sulej, 2002).

162 **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, Drózdziel (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).

171 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).

172 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.

173 5. **The differentiation between populations.** Caused by the different environmental and metamorphic conditions resulting from the different habitats of the population.

Why stratigraphic or geographic separation? How likely is that?
Don't these specimens come from the same locality or even from the same horizon/bedding plane?
...the co-occurrence arguably contradicts the assignment to separate populations of the same species

process; thus, its results might be morphologically (Morris, 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 Schmidler, 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 metoposaurus 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).

But isn't that a type of "ontogenetic diversity" ... same species, but different growth trajectories?

Is there any indication that some of the studied dermal bones belong to the same individuals as some of the studied long bones?

But how can you tell which femora and dermal bones belong together?
T2 has been described as a type of clavicle and the assignment of other disarticulated bones to this type appears to be arbitrary.

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

239 The dimorphic character of the dermal bones described herein and the two growth patterns of long bones
240 (humeri) discovered by Teschner and Konietzko-Meier (2015) suggests that the ontogeny of specimens
241 assign to *Metoposaurus krasiejowensis* could have proceeded via a different growth rate and time span of
242 metamorphosis, caused by differing environmental conditions. The similar number of specimens from
243 both populations (M1/M2 – 44percent/56percent for clavicles and 53percent/47percent for skulls) suggests

244 stable populations. Apart from dermal bone ornamentation, the degree of ossification and variation in
245 skull sizes divides metoposaurids into two groups. Smaller skulls in the more terrestrial type, as in

unconvincing:
How can two "stable
populations" of the same
species occur together in the
same environment without
interbreeding?
What does "population"
mean in this context?

helerpeton from Germany, represent an unstable lake environment (Boy and Suess, 2000). The
type reflects a more terrestrial or riparian habitat, where environmental conditions are variable
phibians are forced to change their dwellings more often (migration between watercourses or
'type' small, drying lakes; Wernerburg, Ronchi and Schneider, 2007). It does not mean that 'more
al/stream' metoposaurids moved efficiently on land. Modern salamanders can migrate between
and lakes by 'pond-hopping' (Zug, 1993). The first type reflects a more stable habitat, possibly
lake, where animals are not forced to migrate ('pond-type'; Wernerburg, 2007). Geological,
ntological, and other analysis of the Krasiejów site shows that both of these habitats – episodic
nd ponds at the excavation site and a large reservoir in close proximity – may have occurred there
sited charophytes and Unionidae bivalves; Szulc 2005, 2007), and that conditions changed over

256 time (Dzik and Sulej, 2007; Gruszka and Zieliński, 2008; Bodzioch and Kowal-Linka, 2012). Differences
257 in dermal bone ornamentation constitute an adaptative answer to changes in the environment over time or
258 to geographical differentiation of habitats. Rapid changes in the morphology of ornamentation in one
259 population are possible because they are the effects of hormonally induced metamorphosis. The water
260 temperature in which larvae live strongly affects ectothermic animals. The growth of amphibians and
261 larval development both depend on external environmental factors. At higher temperatures, not only
262 metabolic rate but also development rate increases (Motyl, 2008). Low temperatures reduce development
263 rates to a greater extent than they reduce growth rate, as a result of which amphibians metamorphose
264 after achieving larger size (Wilbur and Collins, 1973) (T1 skulls are usually larger than T2 skulls). Prey
265 abundance might exert some influence as well (Motyl, 2008), but probably not as much (Blouin and
266 Loeb, 1990). The Krasiejów ecosystem changed over time. The late Triassic climate favoured evolution
267 of freshwater environments. In Krasiejów, small periodic reservoirs, probably also inhabited (as in
268 the environments of the Saar-Nahe Basin), occurred along with large stable ones (Szulc, 2005; 2007;
269 Gruszka and Zieliński, 2008; Szulc, Racki and Jewuła, 2015). Small reservoirs (and potentially higher
270 temperature) or periodic rivers forced earlier metamorphosis, dwelling on land, or migration between
271 lakes and watercourses. On the other hand, large lakes or the proximity of a large reservoir enabled the
272 development of a fully aquatic population (Szulc, 2005). As already mentioned, ecomorphs may also
273 reflect changes over time. A primary large reservoir in which an aquatic population lives (Dzik and Sulej,
274 2007) dries out slowly, inducing gradual changes in the amphibian population from aquatic ecomorphs to
275 more terrestrial ones. Metoposaurids adapted to unstable conditions; however, they still needed water for
276 reproduction and to prevent hyperthermia. When a reservoir finally dried out (barite, carbonate concretes;
277 Gruszka and Zieliński, 2008; Bodzioch and Kowal-Linka, 2012) amphibians hibernated in the sediment
278 to survive the drought period (Konietzko-Meier and Sander, 2013). More aquatic population would have
279 lived at different site - fossils are redeposited and material might be transported even from variscian
280 upland according to isotopic analysis of Konieczna, Belka and Dopieralska (2015). Large reservoirs,
281 stable over long periods of time, enable the development of a fully aquatic ecotype (T1), reducing the
282 need to dwell on land by virtue of providing:

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

287 These conditions may have even contributed to the formation of a neotenic population (Duellman and
288 Trueb, 1986; Safi et al., 2004; Frobisch and Schoch, 2009). However, evidence of larval structures (i.e.
289 branchial ossicles) in adult metoposaurids from Krasiejów is lacking. Nevertheless, facultative neoteny is
290 possible (Motyl, 2008), as shown by the more radial (juvenile) sculpture on the large skulls of ecotype

but their is weak to no evidence for ecomorphotypes in other temnospondyl species that can be clearly distinguished by their ornamentation patterns

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 ontogenetic curves for the described eco(morpho)types (Fig. 14).

Ornament function

According to the described observations, the temnospondyl ornamentation into the vascular surface appears first in the ontogeny, 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 strengthening 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.

This point of the discussion does not consider much the sample/specimens of *M. krasiejowensis*, nor the main point of the paper, i.e. distinction of two morphotypes. ... could be reduced

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.

[syntax]

should be formulated
more carefully ...
i.e. as speculation

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Table. 1. Clavicles ornamentation.

		U'OPB 1152	U'OPB 1153	U'OPB 1154	U'OPB 1155	U'OPB 1156	U'OPB 1157	U'OPB 1158	U'OPB 1159	U'OPB 1160	U'OPB 1161	U'OPB 1162	U'OPB 1163	U'OPB 1164	U'OPB 1165	U'OPB 1166	U'OPB 1167	U'OPB 1168	U'OPB 1169	U'OPB 1170	U'OPB 1171	U'OPB 1172	U'OPB 1173	U'OPB 1174	U'OPB 1175	U'OPB 1176
		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	J	I	I	I	I	A	J
Ornamentation main features	Regular (1), irregular (2)	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)	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)	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)]	2	1		1	1	1	2		2	2	2		1	1	2	1		1	1	1	1				
Features of different types	Distinct borders of polygonal field (1), borders partially hard to recognize (2), hard to recognize (3)	1	2		3		3	1		1	1	1		3	3	1	1		2	1	1	3	1		3	1
	Ridge quantity/bone width [pomiar ok. 2,5cm od poligonów]: >2,3 (2), <2,3 (1), <2 (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	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]	1	2	3	3	3	2	1	2	2	2	2	3	2	2	1	1	3	3	2	2	2	2			
	Deep polygons (1); deep or shallow polygons (2); shallow polygons (3)	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)	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: >6mm diameter]	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	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)	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)	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)	1	2	2	2	2				1	1			2	2	1	1	2	2	2	1	2	2			
Features with no trends (individual, ontogenetic variety, interspecific characters or taphonomy)	Opening ramification	9	10	3	6			4	2		4	3		9	5											
	Closing ramification	10	4		3			2	0		1			4	1											
	More ramification: 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											
	Radial ridges/polygon ratio	0,38	0,28		0,4							0,33		0,29												
	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											
	Unornamented regions	No	No	No	No	No	No	No	No	No	No	No	No	No	No											
Features with no trends (individual, ontogenetic variety, interspecific characters or taphonomy)	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° (1), < 100° (2)	1		2	2						1			2		1		1			2					

Table. 2. Skulls ornamentation.

		UO/JP01	UO/JP02	UO/JP04	UO/JP06	UO/JP08	UO/JP09	UO/JP12	UO/JP13	UO/JP14	UO/JP16	UO/JP17	UO/JP18	UO/JP20	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 density	Sparse (1), dense (2)		2	1		2	1	2	1	x	2	x	2	2	1

Table. 3. Interclavicles ornamentation.

sculpture description		UOBS 00656	UOBS 02448	UOBS 02452	UOBS 02480	UOBS 02465
Polygon number	<40 [1], > 40 [2]	1	1	2	2	2
Polygon shape	hexagons moslty [1], pentagons mostly [2]	1	1	2	2	2
Bone width/radial ridges number	<2,5 [1], >2,5 [2]	1	1	2	1	2
Multipolygons	none or few [1], numerous [2]	1	1	2	2	2
Sculpture density	low [1], high [2]	1	1	2	2	2
Sculpture character	regular [1], irregular [2]	1	1	1/2	2	2
Polygon area borders	visible [1], hard to recognize [2]	1	1	2	2	2
age		I	A	I/A	J/I	J
morphometry						
P/R				1,06	1	
A/R		2,13		2,35	1,95	
A/P			2	2,2	1,95	
V/H				1,61	1,48	

Table. 4. Skulls measurments.

	UOP01	UOP02	UOP03	UOP04	UOP05	UOP06	UOP07	UOP08	UOP09	UOP10	UOP11	UOP12	UOP13	UOP14	UOP15	UOP16	UOP17	UOP18	UOP19	UOP20
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
IL(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
IP(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
LO	2,8	4		4,6		4		3,7	5,6			3,9	5,6	3,6			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																				
E				6														4,4		
G				4,6														4,4		

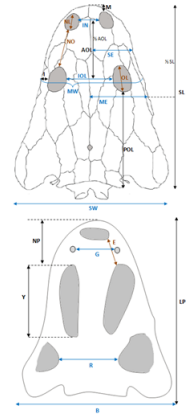


Table. 5. SEM observations.

	UOPB 1152	UOPB 1153	UOPB 1155	UOPB 1157	UOPB 1160	UOPB 1161	UOPB 1163	UOPB 1164	UOPB 1167	UOPB 1168	UOPB 1169
Roughness [v - distinct x - not distinct]	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 than 1/1 mm of length x - less than 1/1mm of length]	x	x	v	v	x	v	v	v	x	v	x

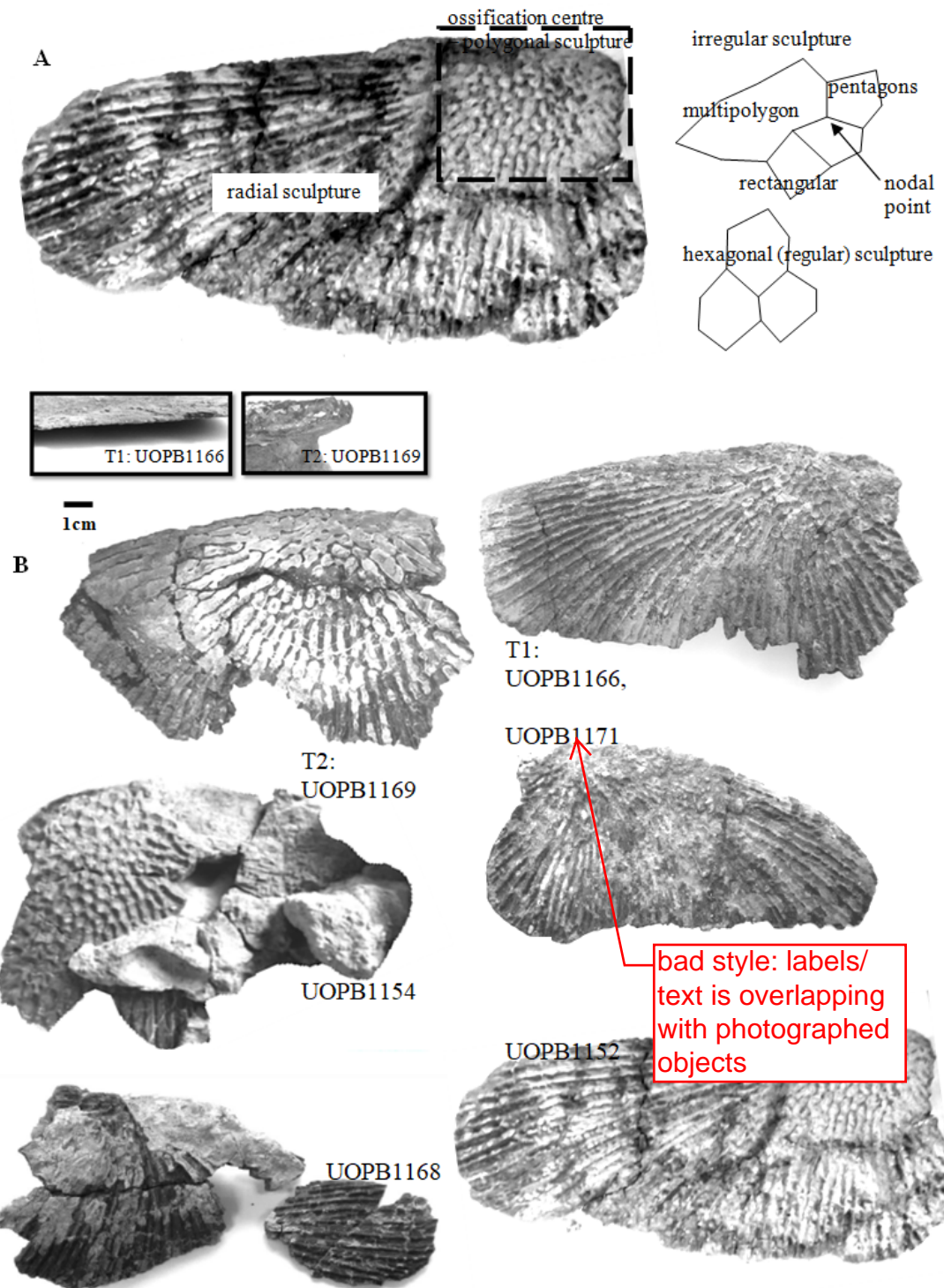


Figure 2. Figure 2. Basic ornamentation features explanation (A). Clavicles assigned to two types of ornamentation (B).

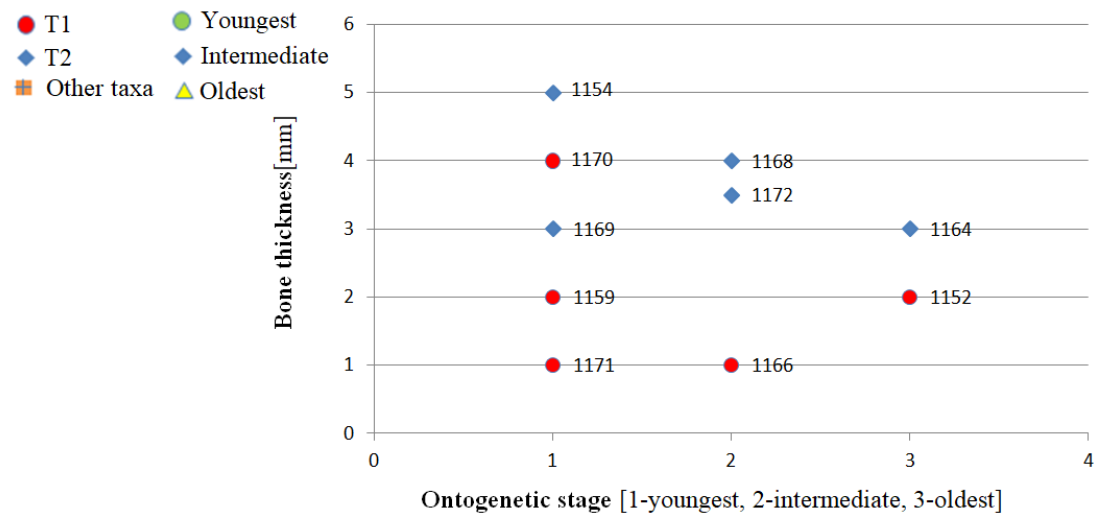


Figure 3. Thickness of the bone in particular types and ontogenetic stages. Measurements made at the border of polygonal and radial ornamentation areas.

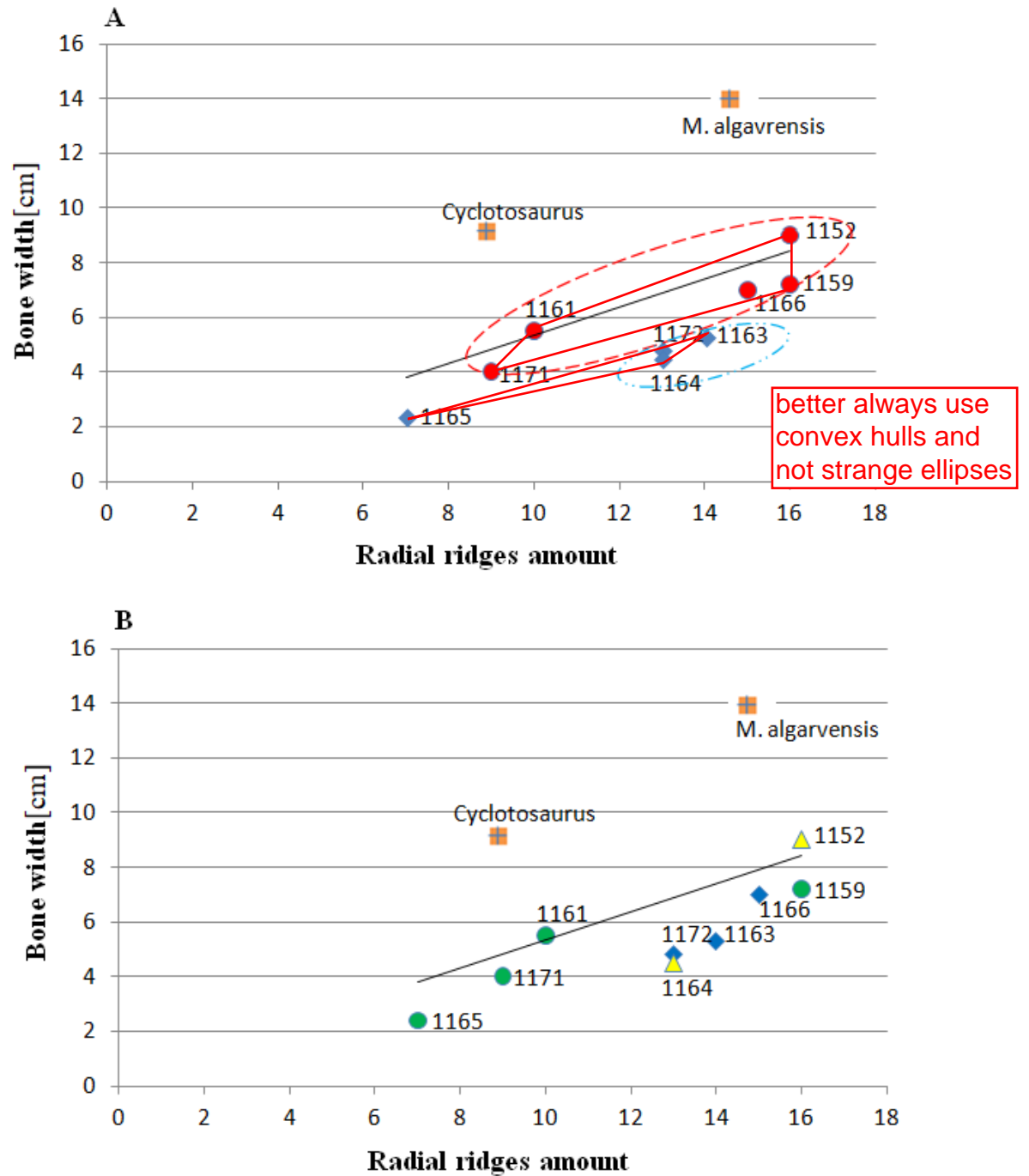


Figure 4. Ratio of the bone width and amount of radial ridges (measurement taken 2,5 cm from ossification center). A: Considering appointed types, showing two subsets within metoposaurid data (ellipses on the chart). B: Considering individual age, showing no subsets within metoposaurid data.

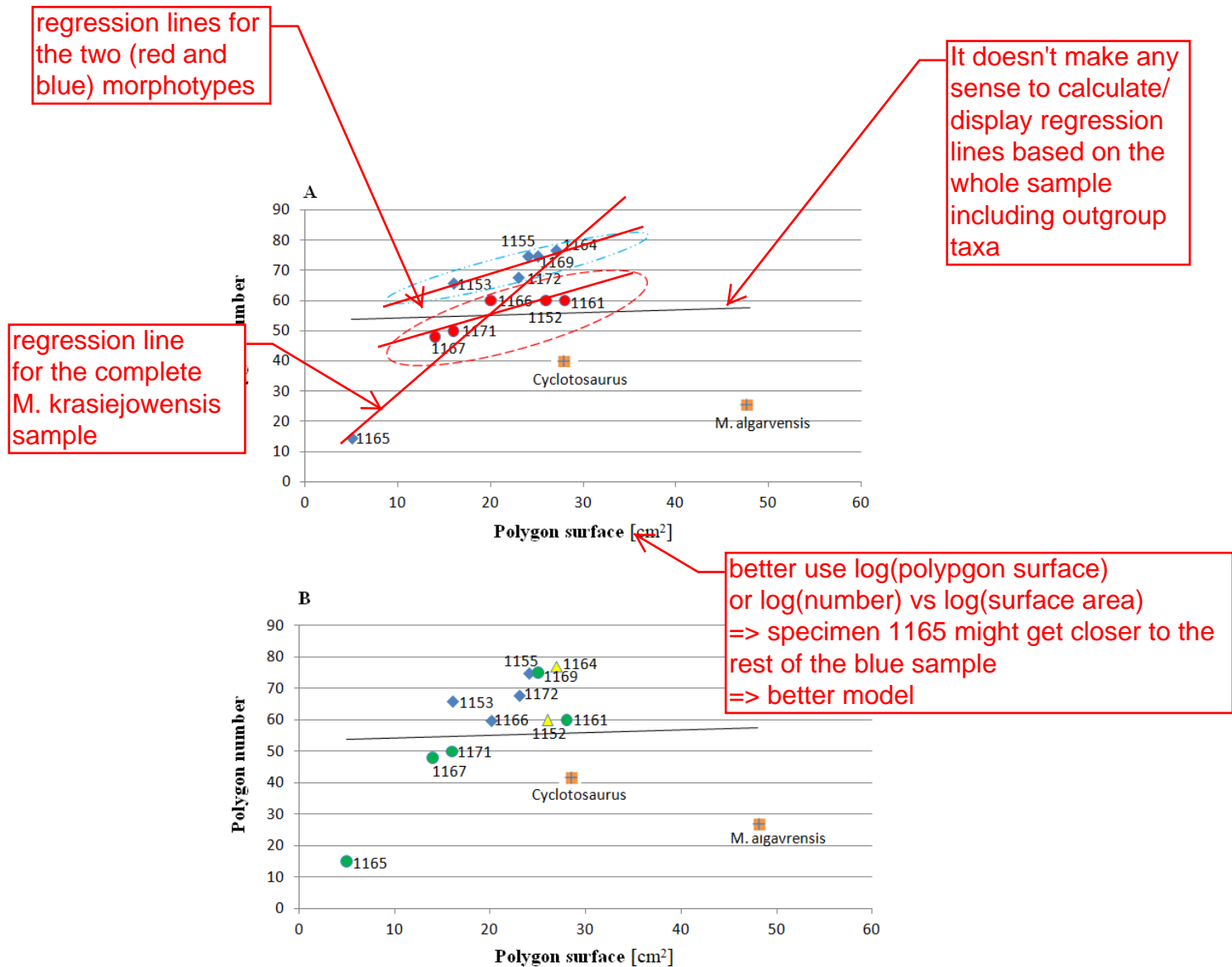


Figure 5. Ratio of polygon number and surface. A: Considering appointed types, showing two subsets within metoposaurid data (elipses on the chart). B: Considering individual age, showing no subsets within metoposaurid data.

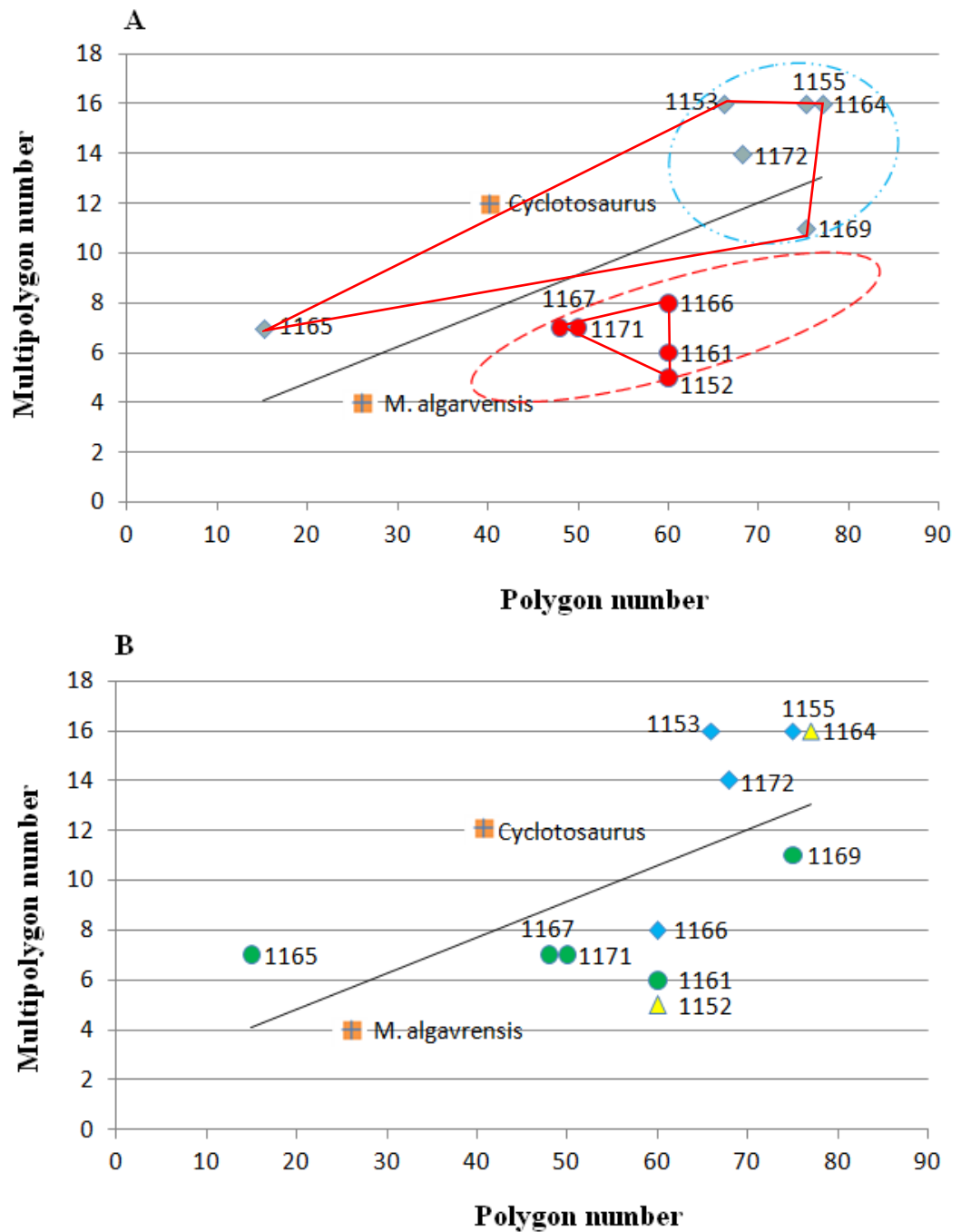


Figure 6. Ratio of multipolygon and all polygons number. A: Considering appointed types, showing two subsets within metoposaurid data (elipses on the chart). B: Considering individual age, showing no subsets within metoposaurid data.

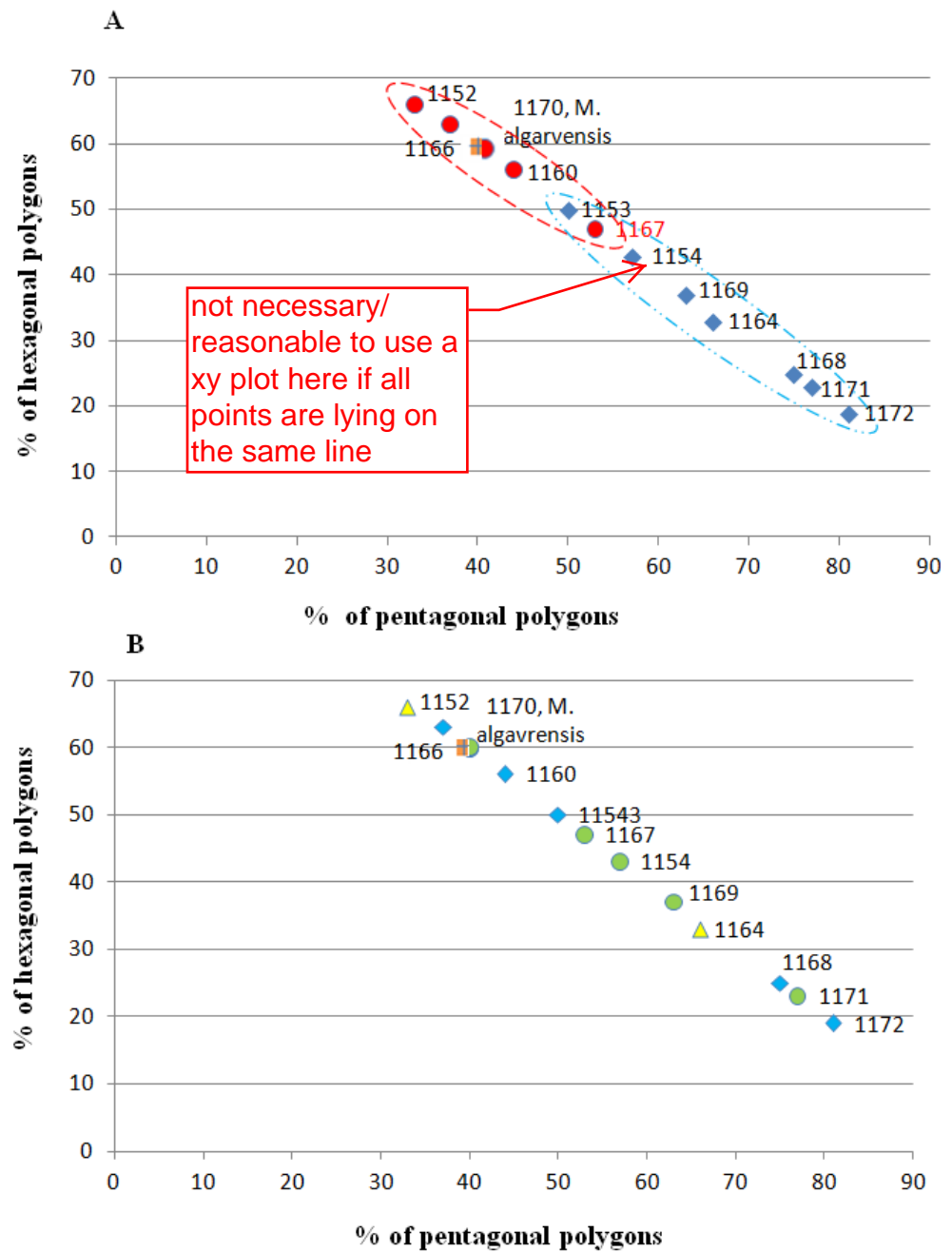


Figure 7. Percentage of hexagonal and pentagonal polygons. A: Considering appointed types, showing two subsets within metoposaurid data (ellipses on the chart). B: Considering individual age, showing no subsets within metoposaurid data.

rather unnecessary figure - would be sufficient to put that in a table

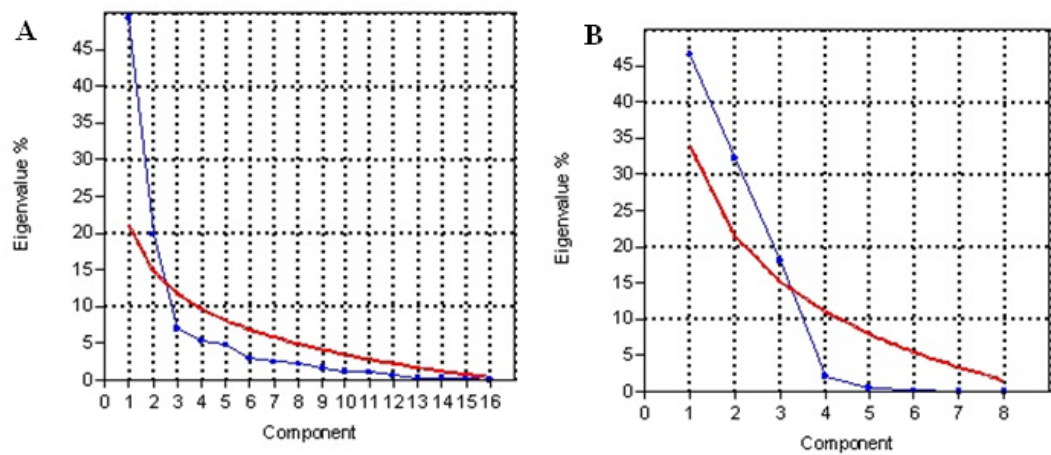


Figure 8. Importance of particular components in the variation: nominal (A) and countable data (B).

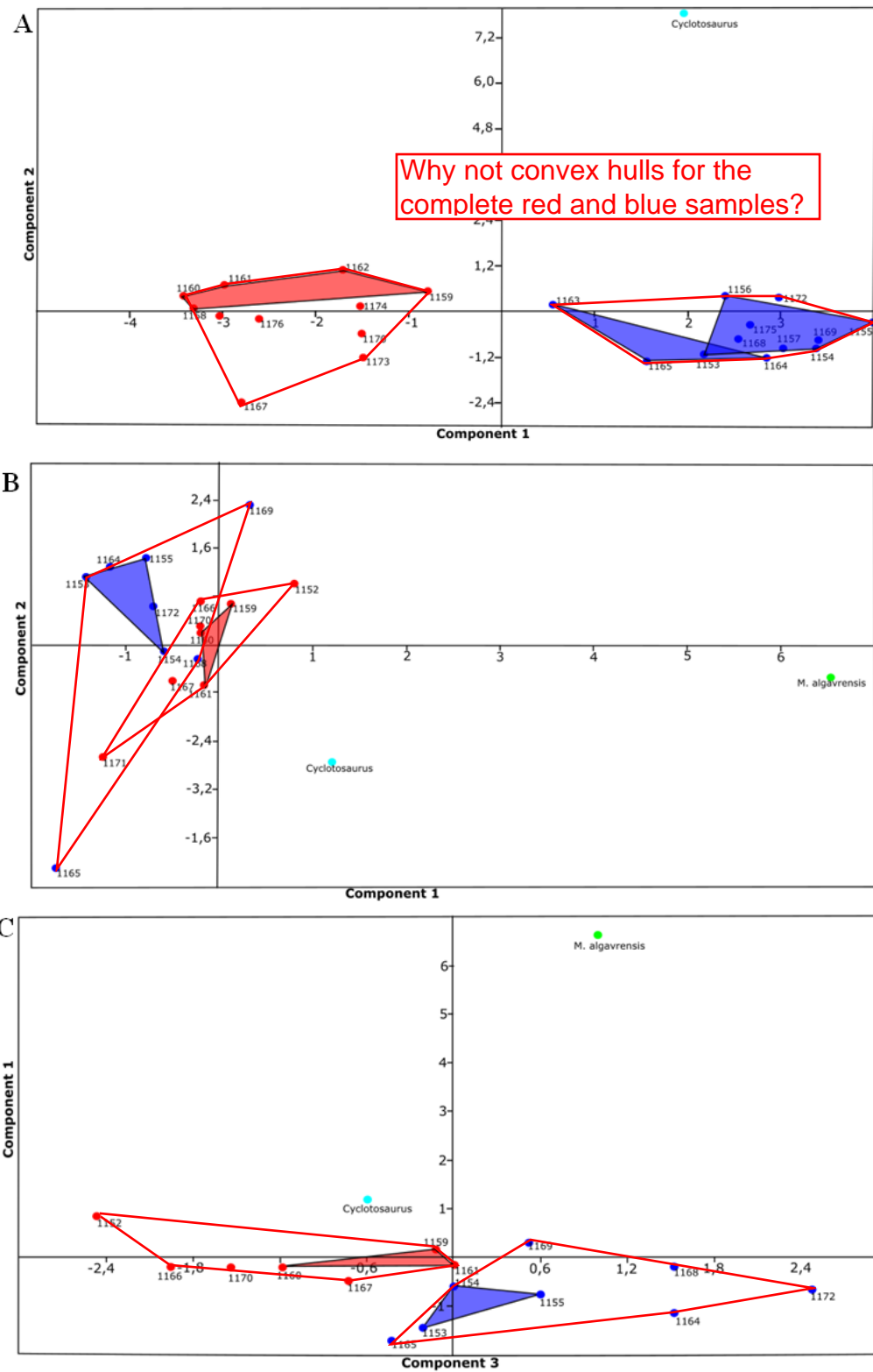


Figure 9. PCA for transformed data. Nominal – Table 1 (A) and countable (number of polygons, ridges, polygon area surface, ratio of penta- and hexagons) data (B, C).

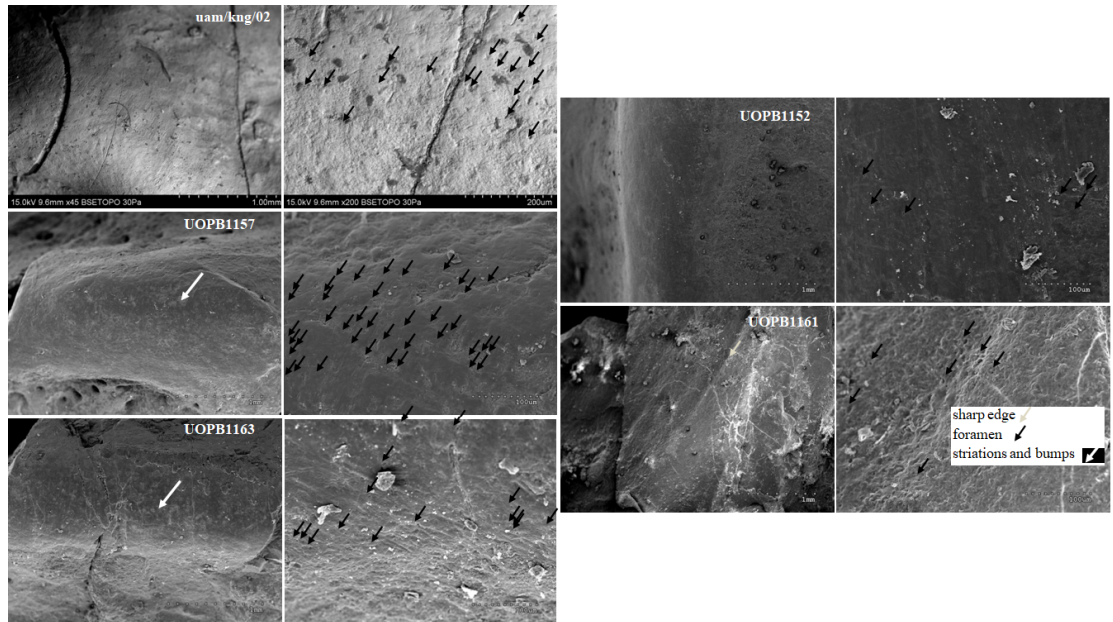


Figure 10. SEM (SE) observations of clavicle radial ridges.

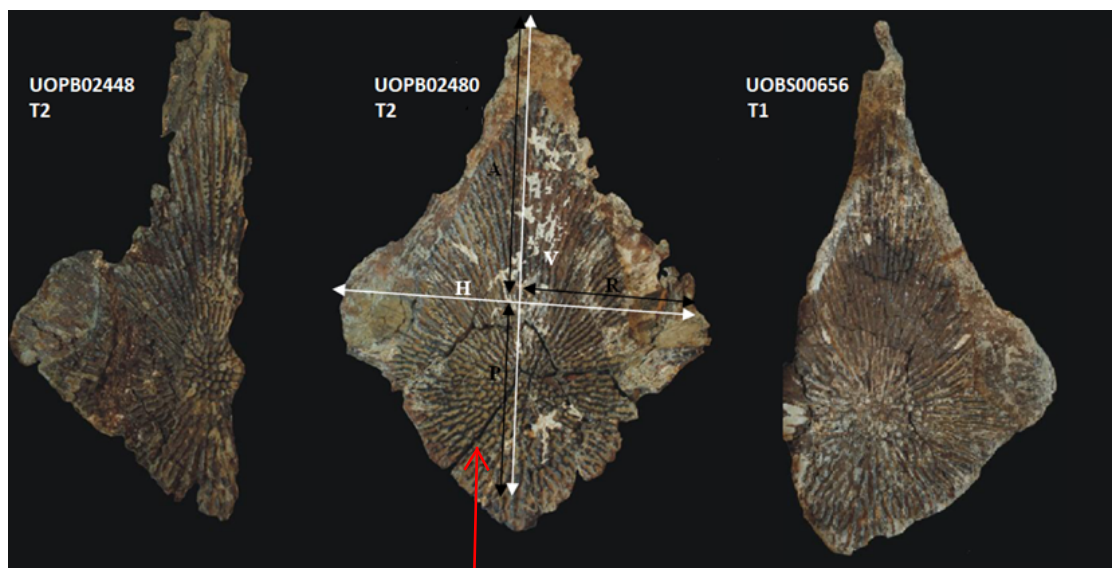


Figure 11. *Metoposaurus krasiejowensis* interclavicles.

arrows accidentally shifted -
please correct that

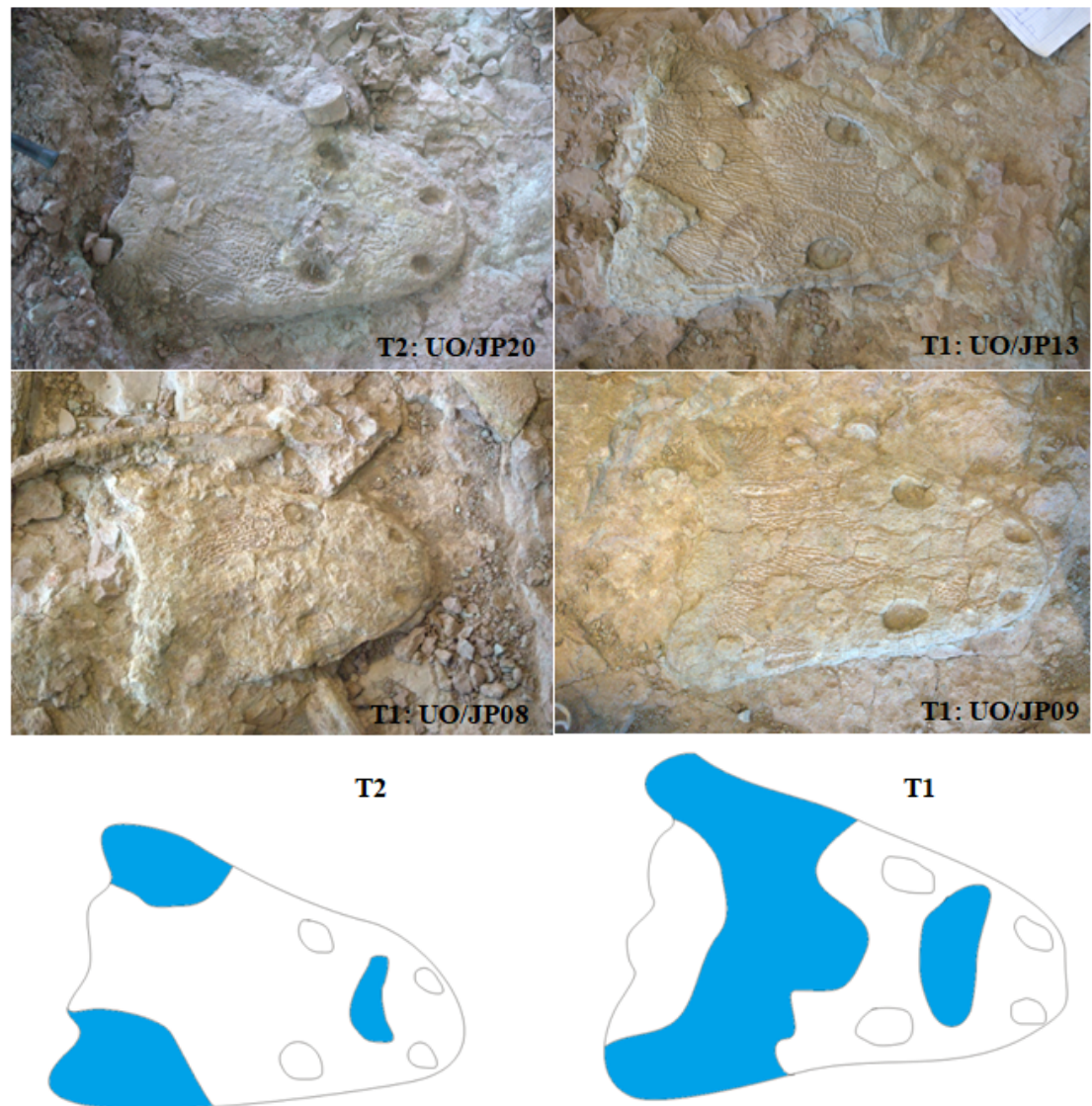


Figure 12. Types of skulls ornamentation of metoposaurids from Krasiejów. Blue area represents surface covered with radial ornamentation.

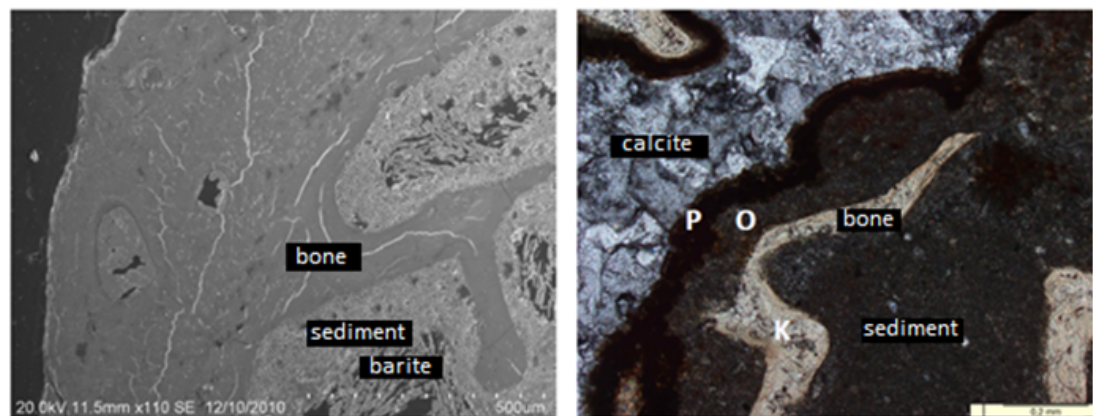
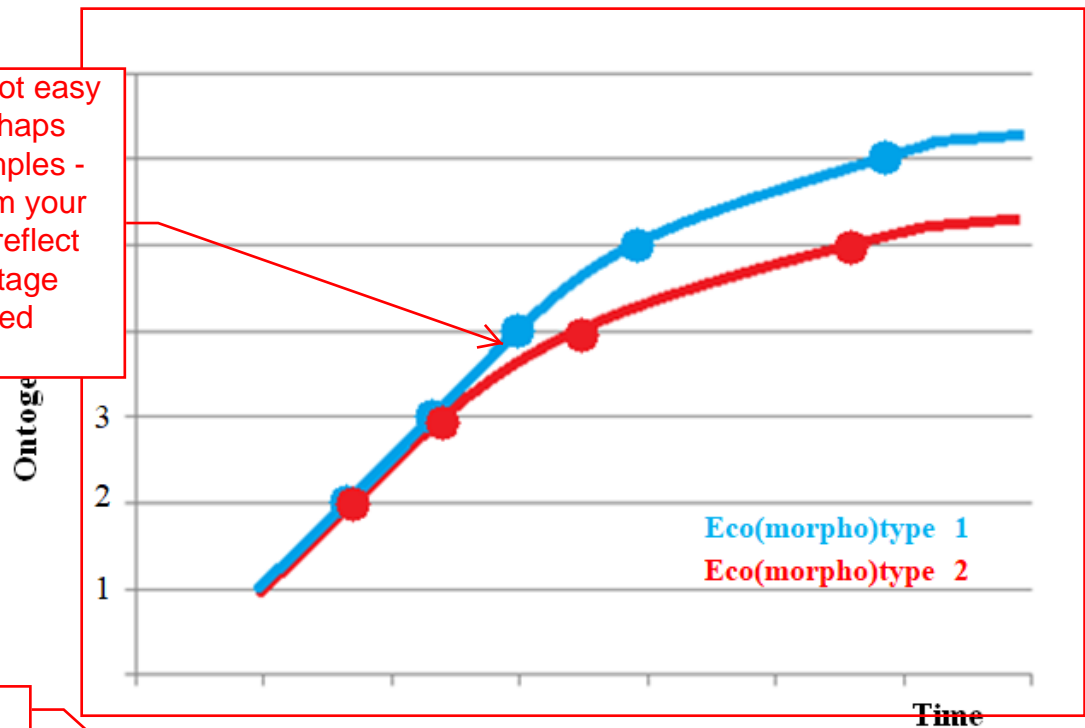


Figure 13. Different fossilization character of *Metoposaurus krasiejowensis* bones: sediment and barite infills (semi-terrestrial deposition) (A) and sediment and calcite infills (aquatic deposition) (B).

These models are not easy to comprehend: Perhaps you give could examples - which specimen from your sample is meant to reflect which ontogenetic stage (1-6) of the blue or red curve?



Hypothetical ontogenetic trajectories...

Figure 14. Hypothetical ontogenetic trajectory of *Metoposaurus krasiejowensis* eco(morpho)types. Ontogenetic phases: 1 – ossification of dermal bones, 2 – initial polygonal sculpture, 3 – juvenile sculpture, 4 – adult sculpture, 5 – initial limb ossification, 6 – full limb ossification.

better call it 'morphotype' if you have got no independent control for 'ecology' as a factor (e.g. specimens from two distinct sites)