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

Mateusz Antczak [Corresp., 1] , Adam Bodzioch [2]

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

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

Corresponding Author: Mateusz Antczak
Email address: mateusz.antczak@amu.edu.pl

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

Methods. To analyse the observed diversity in the temnospondyl *Metoposaurus krasiejowensis* from Late Triassic deposits in Krasiejów (Opole Voivodeship, Poland), the characteristics of the ornamentation (such as grooves, ridges, tubercules) of 25 clavicles and 13 skulls were observed on macro- and microscales, including the use of a scanning electron microscope for high magnification. The different ornamentation patterns found in these bones have been used for taxonomical and ecological studies of inter- vs intraspecific variation.

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

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

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3 **Mateusz Antczak[1], Adam Biodzioch[2]**

4 [1] Institute of Geology, Adam Mickiewicz University of Poznań, Poznań, Poland
5
6 [2] Department of Biosystematics, University of Opole, Opole, Poland

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18 **Results.** Two distinct types of ornamentation (fine, regular and sparse, or coarse, irregular and dense)

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20 dimorphism in *Metoposaurus krasiejowensis*.

21 **Discussion.** Analogies with modern Anura and Urodela, along to previous studies on temnospondyls

22 amphibians and the geology of the Krasiejów site suggest that the differences found are rather

23 intraspecific and may suggest ecological adaptations. Sexual dimorphism and ontogeny cannot be

24 undoubtedly excluded, but ecological variation between populations of different environments or

25 facultative neoteny (paedomorphism) in part of the population (with types of ornamentations being

26 adaptations to a more aquatic or a more terrestrial lifestyle) are the most plausible explanations.

Introduction

29 The fossil assemblage from the Late Triassic deposits in Krasiejów (SW Poland, near the city of Opole) is

30 a unique discovery. Excavations carried out since 2000 have revealed new data concerning the evolution

31   of terrestrial Triassic faunas. In Krasiejów, although the remains of several groups of fish and archosaurs

32   were also found (e.g. Dzik & Sulej, 2007, 2016; Brussatte et al., 2009; Piechowski & Dzik, 2010; Sulej,

33   2010; Skrzycki, 2015; Antczak, 2016; Dzik & Sulej, 2016; Antczak & Bodzioch, 2018), fossils of large

34   temnospondyl amphibians described as *Metoposaurus krasiejowensis* (Sulej, 2002; species name revised

35   by Brusatte et al., 2015) were the most abundant.

36   Despite many years of study, new data are still being collected and some aspects of the anatomy and

37   ecology of extinct animals are being reinterpreted (e. g. Konietzko-Meier & Klein, 2013; Konietzko-Meier

38   & Sander, 2013; Gruntmejer, Konietzko-Meier & Bodzioch, 2016; Konietzko-Meier et al., 2018), along

39   with the age of bone accumulations in Krasiejów (Lucas, 2015; Szulc, Racki & Jewuła, 2015) and their

40   origin (Bodzioch & Kowal-Linka, 2012). One aspect not described in detail is the morphology of

41   metoposaurid dermal bone ornamentation, which was assumed to be randomly variable (Sulej, 2007) or

42   similar in all representatives of the species, as suggested by Witzmann et al. (2010). The aim of this

43   paper is to describe in detail, on macro- and microscales, the ornamentation of metoposaurid clavicles

44   and skull bones, in order to examine its variation and to test whether or not it is the same in all

45   specimens. A thorough probe of skeletal elements from one site shows that differences between

46   specimens are not random.

Material and methods

49   The size, number, shape, placement, and other features of the ornamentation elements of

50   metoposaurid clavicles (and as a remark: skull bones) were analysed. The material derived from the

51   'Trias' site at Krasiejów (SW Poland; Fig. 1). The fine-grained (mudstones and claystones) Late Triassic

52   (Carnian, according to Dzik & Sulej, 2007; Lucas, 2015; Norian, according to Szulc, 2005; 2007; Szulc,

53   Racki & Jewuła, 2015) deposits can be divided into three units (e.g. Gruszka & Zieliński, 2008), in which

54   two bone-bearing horizons occur. The lower horizon, the product of a mudflow deposition that probably

55   occurred during a heavy rainy season, is especially abundant in fossils, including *Metoposaurus*

56   *krasiejowensis*. The upper horizon was described within massive claystones covering palaeochannels of

57   low-energy meandering river. Within the upper horizon remains of *Silesaurus* and *Polonosuchus* were

58   found (Dzik & Sulej, 2007).

59   To test the diversity of dermal bone ornamentation in metoposaurids from Krasiejów, 25 clavicles

60   (UOPB1152–1176) and 13 skulls (working numbers counting from the excavation site: UO/PP01–20)

61   were analysed in detail (Tables 1–3). Morphometric measurements for 21 skulls were also taken (Table

62   4). The clavicles were removed during the excavation and are held in the Opole University collection,

63   while the skulls were present *in situ* in the palaeontological pavilion (also part of Opole University) at the

64   digging site in Krasiejów; one of them is housed in the Faculty of Geographical and Geological Sciences

65   Museum of Earth at the Adam Mickiewicz University in Poznań (uam/mz/586). As an outgroup skull and

66   clavicle of *Cyclotosaurus* (ZPAL/AbIII/397) from Museum of evolution in Warsaw were examined.

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

68

69   The characteristics of the polygonal and radial structure of clavicles were described, using over 20

70   features, including some of the 12 used by Witzmann et al. (2010). Observations are shown in Table 1,

71   which groups similar features and assigns them numerical values.

72   Observations were made macroscopically and microscopically using an Olympus SZ61 binocular

73   microscope, a Zeiss SteREO microscope, and a DIGEYE digital microscope.

74   Fragments of 10 clavicles were analysed using a Hitachi S-3000N Scanning Electron Microscope. Samples

75   were taken from the same parts of the clavicles: radial ornamentation in the posterior region of the

76   bone, several centimetres behind the ossification centre. Samples were sprayed with gold and palladium

77   and observed under a high vacuum at the Institute of Plant Protection – National Research Institute in

78   Poznań. One sample was observed using a Hitachi S-3700N at the SEM-EDS Laboratory of Faculty of

79   Geographical and Geological Science of Adam Mickiewicz University in Poznań.

80   Selected macroscopic features of skull bones were described only as a result of the fact that the

81   presentation of bones *in situ* makes it impossible to describe micro- or sub-microscopic features. Not all

82   such features were described. Dermal bone ornamentation can be divided into radial ornamentation,

83   composed of parallel or radial ridges without transverse ridges, and polygonal ornamentation,

84   composed of short ridges connected to form polygons. The vertices of the polygons are called nodal

85   points. The polygonal sculpture area is the ossification centre, the part of the bone that ossifies first.

86   Near the ossification centre is an anterior appendix. Polygons may be hexagonal, pentagonal,

87   rectangular, or irregular in shape. Polygons joined by means of a missing ridge are called multipolygons

88   (Fig. 2). All measured features are listed in Table 1. SEM observations included features of the surface of

89   the ridges, such as the number of foramina and degree of ridge roughness (Fig. 3). The possible relative

90   individual ages of the clavicle specimens were determined using the method based on ornament

91   development, presented by Witzmann et al. (2010) and improved by Zalecka (2012).

92   For testing the significance of described variation statistical test were used. At first Shapiro-Wilk test for

93   testing normality of the data, then respectively test F, test T and test U. Test F was used if both

94   compared samples had normal distribution. Test F was used for testing the variance. If the difference

95 between variances were not significant, test T was used. If the variances were significantly different, or

96 samples not had normal distribution, test U was used. If the final test gave the p-value (probability

97 value) less than 0.05 it means that samples are significantly different.

Observations

Diagnosis: Clavicles

100 Clavicles of metoposaurids from Krasiejów showed diversity in ornamentation, having fine, regular and

101 sparse, or coarse, irregular and dense sculpture. After this observation, the clavicles ornamentation was

102 examined in greater detail.

103 Some of the analysed features show random variation or none; however, most are distributed

104 bimodally. Therefore, in every specimen one or the other set of characteristics occur, and two types of

105 ornamentation can be distinguished (Tc1 and Tc2).

106 **Specimens classified as type 1 (Tc1)** are characterised by more regular ornamentation of the clavicles:

107 the borders of the ossification centre (polygonal sculpture) are easily recognised, the polygonal

108 sculpture field has a square shape, and the ornamentation is fine and sparse, moreover, nodal points are

109 more pronounced, being broader and higher than the ridges that connect them, ridges are usually

110 narrow, hexagons with a low level of size diversity dominate, multipolygons are rare, clavicles, even

111 when large, are relatively thin; the anterior process of the clavicle is usually flat and small (Fig. 2); while

112 specimens classified as **type 2 (Tc2)** posses less regular ornamentation: the borders of the ossification

113 centre (polygonal sculpture) are difficult to recognise, the polygonal sculpture field is characterised by a

114 rectangular shape (elongated posteriorly), and the ornamentation is thicker and denser, moreover,

115 nodal points are only slightly broader and higher than the ridges that connect them, ridges are wide or

116 narrow, often rounded, polygons are more often pentagonal or irregular, multipolygons are frequent,

117 clavicles are relatively thick, independently of their size or age, and the anterior process is usually round

118 in cross section and expanded (Fig. 2).

119 Both types of *Metoposaurus* dermal bones ornamentation are however distinct from *Cyclotosaurus*

120 sculpture (Sulej & Majer, 2005). *Cyclotosaurus* can be characterised by relatively large and rhomboidal

121 polygons (sometimes elongated pentagons). Radial ornament is very sparse (spaces between ridges are

122 wide). Ossification centre is large and posses distinct borders, but the polygon number is low (25).

123 Clavicle is thick. Ridges are round and thick (ZPAL/AbIII/397, personal observation).

124

125   The distribution of certain characteristics according to the relative individual age or type assignment is

126   presented in figures 3–7. All plots show bimodal distribution of the parameters, which are independent

127   of estimated relative individual age of specimens. UOPB1165 (Fig. 2) specimen not fitting any of this

128   types might be the representative of a different taxon, although it was the most incomplete specimen,

129   which may affect the result of its description. Some features were not described for this specimen i. e.

130   borders and shape of the ossification centre or radial ridges character (Table 1). Estimated size of the

131   complete specimen is small, but the ossification degree is high. Its possible assignment to species other

132   than *M. krasiejowensis* would be difficult without other findings.

133   In table 5, the results of conducted statistical test are presented – F and T or U, dependent on the data

134   distribution. Considering described types as different groups, quantitative and qualitative data shows

135   that they differ significantly ($\alpha = 0.05$).

136

Micro/nanoscale

138   Two types can also be distinguished according to the micromorphology of the ornamentation ridges and

139   bone structure in cross-section. Clavicles assigned to type 1 do not possess striations (or striations, if

140   present, are barely visible and sparse) and possess a low number of small capillary foramina at the

141   slopes of the ridges (less than 7 per 100 μm^2). Usually they also have less than one foramen per 1 mm of

142   ridge length and no distinct bumps or roughness at the top of the ridge (Figs. 8–9, Table 2). In cross-

143   section they possess growth marks in close proximity within poorly vascularised upper cortex (Fig. 8).

144   Clavicles assigned to type 2 possess striations on the ridges and a greater number of small foramina

145   (more than 7 per 100 μm^2). Usually they also have more than one foramen per 1 mm of ridge length and

146   distinct bumps and roughness at the top of the ridge (Figs. 8–9, Table 2). In cross-section they possess

147   growth marks separated by well-vascularised zones (Fig. 9). This difference in histological patterns is

148   analogous to different growth strategies described for the example of long bones (Teschner, Sander &

149   Konietzko-Meier, 2017).

150

151

152   **Remarks on other dermal bones**

153   *Skulls*

154   Bimodal differences were found also in skulls (Table 3), which have been divided in the Ts1 and Ts2

155   types. The main characteristic of ornamentation of ossifying centers resembles either Tc1 (large,

156   hexagonal, sparse polygons, almost no multipolygons; 6 specimens; Ts1) or Tc2 (small, irregular and

157   dense polygons with common multipolygons; 7 specimens; Ts2). There is also a visible difference in the

158   spatial distribution of polygonal and radial ornamentations between Ts1 and Ts2 (Fig. 10). In the first

159   type, radial pattern covers large areas of the skulls roof in their both preorbital and postorbital

160   (postfrontal, postorbital, supratemporal bones) parts, while in the second it occupies much smaller

161   areas.

162   An important fact is that the skulls classified as Ts2 are relatively small (averaging 28 cm in length) in

163   contrast to Ts1 skulls (averaging 35 cm in length). However, this was not a rule. Among analysed skulls

164   were two 35 cm in length (UO/PP04, 35 cm; UO/PP18, 35.4 cm) with different ornamentation types (Fig.

165   10, Tables 3, 4).

166

167   **Discussion**

168   *Reasons for the observed variation in dermal bone ornamentation*

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

170   species diversity, ontogenetic diversity, sexual dimorphism and individual variation, different habitats of

171   two populations or facultative neoteny.

172   1. **Species diversity.** Given that no differences were found in axial and appendicular skeleton

173   characteristics – all analysis described metoposaurid material as one species, *M. krasiejowensis*

174   (i. e. Gądek, 2012; Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander, 2013; Teschner,

175   Konietzko-Meier & Sander, 2017) or in dermal bone measurements, it is also unlikely that the

176   described differences in the analysed material represent differences between two species.

177   Shape and ornamentation pattern of the clavicles (both described types) is strongly distinct from

178   *M. algavrensis or Cyclotosaurus intermedius* (Figs. 4–6) (Sulej & Majer, 2005; Brusatte et al.,

179   2015). Only the distinct character of the UOPB1165 specimen observed on the bivariate plots of

180   countable features might suggests that this specimen does not belong to the same species. The

181   occurrence of some other taxon is possible because of the redeposited character of the fossils.

182   Moreover, in skulls (both types – Ts1 and Ts2), the prepineal part of the parietals is short and

183   the expansion angle of the sutures separating the parietal from the supratemporal vary

184   between 19 and 26º which is characteristic of *M. krasiejowensis* instead of *M. diagnosticus*

185   (longer prepineal part and parietal expansion angle being around 13º) (Sulej, 2002) (Fig. 11).

186   Also relatively narrow shape of the skulls and shape of the sutures (i. e. between frontals and

187   narials or parietals) is typical of *M. krasiejowensis*, being distinct from *M. diagnosticus*, *M.*

188   *algavrensis* (Brusatte et al., 2015) (Fig. 11) or *Cyclotosaurus* (ZPAL/AbIII/397). According to this

189   all skull specimens belong to *Metoposaurus krasiejowensis*. As only one species (*M.*

190   *krasiejowensis*) can be described considering skulls, and only this species was described in

191   Krasiejów during over 15 years of studying metoposaurid material, it seems justified to consider

192   all of the clavicles as belonging to *M. krasiejowensis*. With possibly one exception – UOPB1165.

193   2. **Ontogenetic diversity.** According to Witzmann et al. (2010), all described specimens belongs to

194   adult individuals, as they all can be assigned to the last stage of sculpture development

195   (Witzmann et al., 2010: fig. 6E). Although singular features may be connected with the age of

196   the specimen, the method of determination of relative age for clavicles (youngest, intermediate,

197   and oldest stages) based on the number of partition walls within the radial ornament shows that

198   most of the analysed features, along with bone thickness, are not connected in this way. The

199   youngest specimens possessed no partition walls between radial ridges. An intermediate stage

200   was represented by specimens with developing partition walls within radial ornaments, and the

201   oldest specimens possessed many well-developed partition walls between radial ridges.

202   Additionally, clavicles described as the oldest stage, are the largest ones (UOPB1152 ~19,5cm x

203   9,7cm, UOPB1164 ~20cm x 9cm), while the youngest are usually of small size (UOPB1166 ~12cm

204   x 6cm, UOPB1171 ~ 10cm x 5cm).

205   Unfortunately the histology of dermal bones cannot be used to determine the exact individual

206   age, as different cross sections of the same bone reveals different stage of remodelling and

207   counting the growth marks is unreliable (Gruntmejer, personal communication; Konietzko-Meier

208   et al., 2018; Figs. 8–9). The diversity of skull sizes assigned to different types also argues against

209   ontogenetic diversity. Relatively small skulls possess more polygonal (adult; Witzmann et al.,

210   2010) ornament than the largest skulls. In addition, there are no differences in the ratio of skull

211   portions according to size; whereas in the metoposaurids, in the younger specimens, the orbits

212   are placed further back on the skull relative to its length (Davidow-Henry, 1989), i.e. the area

213   between orbits grew faster in temnospondyls than the orbits themselves. Polygon

214   characteristics also indicate the adult stage in all skull specimens. Rinehart et al. (2008) and

215   Lucas et al. (2010) also suggest that all individuals are adults. Sulej (2002) suggests that size of
216   the clavicle depends on the age and recognized several clavicles of different size as an
217   ontogenetic sequence. Nevertheless, this ontogeny cannot be used to explain ornamentation
218   variety, as the two types of sculpture occur in both small and large specimens. The
219   differentiation is also not the same as in the Rotten Hill, where age differences were proposed
220   (Lucas et al., 2016). There are no size classes that can be correlated with sculpture variety in
221   clavicles. In skulls, specimens assigned to type 2 are usually smaller, with exception of UO/PP18
222   (Table 4, Fig. 12, 13).

223   3.   **Sexual dimorphism.** In the described material there is lack of dimorphism in the shape of the
224   skulls (Urban & Berman, 2007), clavicles or dentition (Kupfer, 2007). The location of clavicles
225   (under the skin and on the ventral side of the body) and discussed function of the
226   ornamentation excludes its role as 'display structures' in mating rituals (Kupfer, 2007) in
227   contrast to i. e. *Zatrachys serratus* were spinescence and shape of the skull (rostrum) were
228   considered as sexual dimorphism (Urban & Berman, 2007). Different growth strategy seen in
229   clavicles (Figs. 8–9), skulls (Gruntmejer, personal communication) and long bones (Teschner,
230   Sander & Konietzko-Meier, 2017) ('seasonal' growth marks separated by vascularised zones or
231   slower growth with growth marks in close proximity within poorly vascularised bone) rather do
232   not indicate different sexes, but was ecologically controlled.

233   4.   **Individual variation.** The existence of two distinct ornamentation types with no intermediate
234   patterns (Fig. 3–7) may support different ecological adaptations (see below) rather than
235   individual variation as the only reason of diversity.

236   5.   **Different habitats**. Morphology of the dermal sculpture and vascularisation are not separable.
237   Regularity of the ornamentation reflects the mode of life of temnospondyls to a certain degree.
238   The coarser ornament, more pronounced ridges and irregularity is characteristic of rather
239   terrestrial taxa (i. e. *Seymouria, Eryops*, see: Witzmann et al., 2010) – T2, while irregular
240   sculpture represents rather aquatic animals (Witzmann et al., 2010) – T1. The variety seen
241   within *M. krasiejowensis* allows expanding this conclusion, showing that the ecological
242   difference (listed features) can be observed within one species.

243   Metamorphosis is a hormonally induced and controlled process; thus, its results might be
244   morphologically unequal even in closely-related taxa (Fritzsch, 1990; Norris, 1999) or within taxa
245   (Rafiński & Babik, 2000; Pogodziński, Hermaniuk & Stępniak, 2015). Because of this and the fact that
246   amphibians, as animals very closely connected with the environment, are phenotypically plastic

247 (examples below), the morphological diversity of the analysed material may be a result of differences

248 between ecologically separated populations (geographic separation). Ecological separation of animals

249 which remains are deposited in one bone-bed is possible, because of the bone-bed character (material

250 partially redeposited, possibly from distant area, and partially local). Redeposition from different

251 environments is suggested by the variant infill succession in the pore system and trace elements

252 contents in the individual remains (Bodzioch & Kowal-Linka, 2012; Bodzioch, 2015). The more aquatic

253 population might have lived at a different site – fossils are redeposited and material might be

254 transported even from Variscian Upland according to isotopic analysis of Konieczna, Belka & Dopieralska

255 (2015). Thus, geographical separation is a probable explanation, because the different ecological

256 character of specimens might suggest that the two populations did not interbreed with each other. Time

257 separation is also plausible. Some clavicles can be reworked more than once, being removed from older

258 level than those which provided the skulls, which often seem to have a better preservation.

259 The more terrestrial population probably lived at the site, where environment resembles modern Gilgai

260 relief of Texas or Australia (Szulc, Racki & Jewuła, 2015) while more aquatic populations lived at some

261 distance in larger reservoir(s).

262 Although the presence of some large skulls with no abrasion or weathering does not support transport

263 from a distant area, a brief transport however is plausible as the teeth in the mandibles and upper jaws

264 are usually lost (Lucas et al., 2010).

265 Other possibility is temporal diversity – gradually changing conditions of environment parallel with

266 amphibian morphology/behaviour adaptation, however some intermediate ornamentation patterns

267 should have been noticed in that case – see 'individual variation'.

268   6. **Facultative neoteny (paedomorphism).** Explanation assuming the same environmental

269   differences between described morphotypes, but within a single population.

270   The Late Triassic Krasiejów environmental conditions (dry and rainy season with possible

271   periodic lack of food) may have even contributed to the formation of a neotenic population

272   (Duellman & Trueb, 1986; Safi et al., 2004; Frobisch & Schoch, 2009). However, evidence of

273   larval structures (i.e. branchial ossicles) in adult metoposaurids from Krasiejów is lacking.

274   Nevertheless, facultative neoteny is possible (Motyl, 2008), as shown by the more radial

275   (juvenile) sculpture on the large skulls of Ts1 (Witzmann et al. 2010). Facultative neoteny can be

276   observed in several extant taxa i. e. *Ambystoma talpoideum* with aquatic paedomorphic adults

277   and terrestrial metamorphic adults (Whiteman, Krenz & Semlitsch, 2005). Breeding between

278   such morphs is less common than within morphs, because paedomorphic adults begin to breed

279   earlier (Krenz & Sever, 1995; Whiteman & Semlitsch, 2005). In this case *M. Krasiejowensis* Type
280   2 (Tc2, Ts2) reflects metamorphic adults that transform into somewhat terrestrial, while Type 1
281   (Tc1, Ts1) reflects (partially) paedomorphic aquatic adults. This is possible because larval
282   development is dependent on the environmental conditions. In Late Triassic Krasiejów dry and
283   rainy seasons occurred which is known thanks to the versicolor nature of claystone and faunal
284   composition with i. e. dipnoans (Szulc, 2005; 2007; Skrzycki, 2015). Associated with these
285   changes in water-level, food availability, living space, and competition (Ghioca-Robrecht, Smith
286   & Densmore, 2009) may have influenced the preferred lifestyle. Metamorphosis into terrestrial
287   or paedomorphic aquatic form is in this case the response to the individual expected success in
288   the environment (Wilbur & Collins, 1973; Whiteman, 1994; Michimae & Wakahara, 2002)
289   controlled by endocrine signals (Pfennig, 1992). Facultative neoteny in metoposaurids may
290   occur in a single population (no geographical separation is needed) – spatial separation of
291   morphs may occur instead, with the paedomorphic concentrating in deeper habitats (Whiteman
292   & Semlitsch, 2005).

293

294   *Ornamentation and lifestyle*

295   The environmental differentiation is the most likely explanation regardless of whether caused by
296   facultative neoteny or existence of two ecological types. Thus, described ornamentation types reflect
297   more aquatic (Type 1) and more terrestrial (Type 2) morph of *Metoposaurus krasiejowensis*. In modern
298   limbless serpentine amphibians (Gymnophonia: Apoda) and lizard-like salamanders (Caudata: Urodela),
299   larvae resemble miniature adult specimens. Metamorphosis is gradual and there is little reorganisation
300   of body plan (Zug, 1993). In fossil amphibians, body plan reorganisation was also minimal and rather
301   gradual (Boy, 1974, 1988, 1990; Schoch, 2002, 2004), although its rate (trajectory: Schoch 2010) might
302   differ between taxa depending on their habitat (Schoch, 2009). This is also the cause that there are no
303   other features suggesting more aquatic or more terrestrial lifestyle. Such changes, like differences in
304   lateral line morphology, require more 'evolutionary effort', while changes in ornamentation are
305   probably fast, reversible and do not require genetic changes (Rafiński & Babik, 2000; Babik & Rafiński,
306   2000).

307   Typically aquatic taxa are characterised by slow changes (low trajectory), sometimes with incomplete
308   ossification of the pelvic region and limbs (last stages of ontogenetic trajectory). Terrestrial taxa are
309   characterised by faster metamorphosis (high trajectory, with particular phases condensed within a short

310   period of time), including final phases (limb ossification) enabling locomotion on land. The trajectory of

311   semi-aquatic taxa lies between the two above-mentioned types.

312   This is an example of heterochrony. The length and composition of the temnospondyl ontogenetic

313   trajectory is ecologically controlled (Schoch, 2010). Metamorphosis in this case might be described as

314   extreme heterochrony, because many phases are condensed within a short time span (Alberch, 1989).

315   Ontogenetic trajectory and the morphology of adult specimens and their sizes may differ between

316   various environments inhabited by representatives of the same taxon (Schoch, 2010). There are several

317   examples of such diversity, such as differences observed in the length of the hind limbs of modern frogs

318   (Schmidt, 1938; Dubois, 1982; Emerson, 1986; Emerson, Travis & Blouin, 1988; Rafiński & Babik, 2000)

319   and the morphology of extinct temnospondyls: the ontogenetic rate and dentition of *Apaeton* (Schoch,

320   1995); the size of *Micromelerpeton* (Boy & Suess, 2000; Schoch, 2010); the morphology of

321   *Sclerocephalus* (Schoch, 2010); the branchiosaurids (Werneburg, 1991, 2002; Werneburg, Ronchi &

322   Schneider, 2007); and the plasticity of the plagiosaurid *Gerrothorax* (Schoch & Witzmann, 2012; Sanchez

323   & Schoch, 2013). Polyphenism (environmentally controlled polymorphism) exists in a wide range of

324   extant taxa (Roff, 1996) in adults (Whiteman, Krenz & Semlitsch, 2005) and tadpoles (Collins & Cheek,

325   1983; Pfennig, 1990; 1992; Walls, Belanger & Blaustein, 1993; Nyman, Wilinson & Hutcherson, 1993;

326   Michimae & Wakahara, 2002; Pfennig & McGee, 2010).

327   Dimorphism in bone characteristics of metoposaurids from Krasiejów can be seen in dermal bones as

328   well as in non-dermal skeletal elements from Krasiejów. Two types connected with growth trajectory

329   were seen in histological observations of metoposaur skulls (Gruntmejer, personal communication),

330   humeri (Teschner, Sander & Konietzko-Meier, 2017), and the morphology of femora (Konietzko-Meier &

331   Klein, 2013).

332   New facts about metoposaurids from Krasiejów show that they were not fully aquatic animals. 3D

333   computational biomechanics analysis of the skull of *Metoposaurus* show that it was capable of biting

334   prey in the same manner as semi-aquatic and terrestrial animals like *Cyclotosaurus* or modern crocodiles

335   (Gruntmejer, Konietzko-Meier & Bodzioch, 2016; Fortuny, Marcé-Nogué & Konietzko-Meier, 2017;

336   Konietzko-Meier et al., 2018).

337   The described diversity is consistent with the experiment of Schoch (1995) and the results of Werneburg

338   (2002) and Schoch (2010). One of the *Metoposaurus* ornamentation types from Krasiejów (T2) thus

339   represents a more terrestrial form (associated with the more variable and unstable environment of a

340   river or a small lake or the metamorphic adult form of facultative neotenic population), while the other

341   represents forms more closely related to water (a large lake habitat or partially paedomorphic aquatic

342 adults) (T1) (ecological populations – as stated by Witzmann et al., 2010; but described as species-

343 specific; neoteny as described by Whiteman, Krenz & Semlitsch, 2005).

344 The adaptations in T2 favouring a more terrestrial lifestyle are:

    a) The increased mechanical strength of the bones (Rinehart & Lucas, 2013) (coarser, denser,

345   irregular sculpture, thicker clavicles);

347   b) Protection from a greater number of blood vessels, improving thermoregulation (Gądek, 2012)

348   (denser sculpture, more numerous polygons and radial rows, more numerous microforamina);

349   c) Stronger integration of bone and skin, which is thicker in terrestrial amphibians and exfoliates

350   (Zug, 1993; Schoch, 2001) (coarser, denser sculpture, microstriations);

351   d) Stronger connection of the pectoral girdle elements and, potentially, limbs (expanded anterior

352   projection of the clavicle);

353   e) Faster growth revealed by histological structure (growth marks separated by zones of highly

354   vascularised bone).

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

356   f) Faster (at younger age) metamorphosis revealed by smaller skulls;

357   g) The length of limb bones not correlated with individual age (Teschner, Sander & Konietzko-

358   Meier, 2017) or a slender or robust femur (Konietzko-Meier & Klein, 2013); 10% elongation of

359   limbs in Anura distinctly increases migration capabilities (Pogodziński, Hermaniuk & Stępniak,

360   2015; Pogodziński, personal communication).

361 The dimorphic character of clavicles described herein and the two growth patterns of dermal and long

362 bones (humeri) (Teschner, Sander & Konietzko-Meier, 2017) suggest that the ontogeny of specimens

363 assigned to *Metoposaurus krasiejowensis* could have proceeded via a different growth rate and time

364 span of metamorphosis, caused by differing environmental conditions. The similar number of specimens

365 from both populations (Tc1/Tc2 – 44%/56% and Ts1/Ts2 – 53%/47%) suggests stable populations.

366 Apart from dermal bone ornamentation, the degree of ossification and variation in skull sizes divides

367 metoposaurids into two groups. Smaller skulls occur in the more terrestrial type, as in *Micromelerpeton*

368 from Germany, where smaller specimens represent an unstable lake environment (Boy & Sues, 2000).

369 The described type T2 reflects a more terrestrial or riparian habitat, where environmental conditions are

370 variable and amphibians are forced to change their dwellings more often (migration between

371 watercourses or 'stream-type' small, drying lakes; Werneburg, Ronchi & Schneider, 2007). It does not

372 mean that 'more terrestrial/stream' metoposaurids moved efficiently on land. Modern salamanders can

373 migrate between rivers and lakes by 'pond-hopping' (Zug, 1993). The first type reflects a more stable

374 habitat, possibly a large lake, where animals are not forced to migrate ('pond-type'; Werneburg, 2007).

375 Geological, sedimentological, and other analysis of the Krasiejów site shows that both of these habitats

376 – episodic rivers and ponds at the excavation site and a large reservoir in close proximity – may have

377 occurred there (redeposited charophytes and Unionidae bivalves; Szulc, 2005; 2007), and that

378 conditions changed over time (Dzik & Sulej, 2007; Gruszka & Zieliński, 2008; Bodzioch & Kowal-Linka,

379 2012). Differences in dermal bone ornamentation constitute an adaptive answer to changes in the

380 environment (temperature, water level, food availability) over time or to geographical differentiation of

381 habitats, i. e. faster metamorphosis (at smaller size) as an answer to higher temperatures; or

382 metamorphosis into terrestrial adult vs. transformation into aquatic paedomorphic individuals.

383 Rapid changes in the ornamentation morphology in one population (or part of the population, when

384 weather conditions favour such solution) are possible because they are the effects of hormonally

385 induced metamorphosis. The water temperature in which larvae live strongly affects ectothermic

386 animals. The growth of amphibians and larval development both depend on external environmental

387 factors. At higher temperatures, not only metabolic rate but also development rate increases (Motyl,

388 2008). Low temperatures reduce development rates to a greater extent than they reduce growth rate,

389 as a result of which amphibians metamorphose after achieving larger size (Wilbur & Collins, 1973) (Ts1

390 skulls are usually larger than Ts2 skulls). Prey abundance might exert some influence as well (Motyl,

391 2008), but probably not as much (Blouin & Loeb, 1990).

392 The Krasiejów ecosystem changed over time. The Late Triassic climate favoured evolution of freshwater

393 environments. In Krasiejów, small periodic reservoirs, probably also inhabited (as in the environments of

394 the Saar-Nahe Basin), occurred along with larger more stable ones (Szulc, 2005; 2007; Gruszka &

395 Zieliński, 2008; Szulc, Racki & Jewuła, 2015). Small reservoirs (and potentially with higher temperature)

396 or periodic rivers forced earlier metamorphosis, dwelling on land, or migration between lakes and

397 watercourses. On the other hand, larger lakes or the proximity of a large reservoir enabled the

398 development of a fully aquatic (Szulc, 2005), possible neotenic population.

399 Large reservoirs, stable over long periods of time, enable the development of a fully aquatic (neotenic?)

400 ecotype T1 (Tc1, Ts1), reducing the need to dwell on land by virtue of providing:

401 • enough room for numerous large specimens;

402 • shelter from mainland carnivores;

403 • stable, invariable conditions;

404 • potential lower temperatures.

405   The ontogenetic trajectories of the two metoposaurid ecotypes from Krasiejów cannot differ on a large

406   scale, because they are assigned to the same semi-aquatic species. However, between types there was

407   clearly some deflection into a more aquatic or more terrestrial form. In the case of a more terrestrial

408   (stream-type) ecomorph, the trajectory would be more condensed (Schoch, 2001).

409

410   According to the described observations, it is possible to introduce an argument about the function of

411   temnospondyl ornamentation into the discussion. There are several hypotheses as to the function of the

412   ornamentation, which may have been:

413   1.   mechanical strengthening of the bone (Coldiron, 1974; Rinehart & Lucas, 2013);

414   2.   water-loss reduction (Seibert , Lillywhite & Wassersug, 1974);

415   3.   integration of the bone and skin (Romer, 1947; Bossy & Milner, 1998);

416   4.   improvement of dermal respiration (Bystrow, 1947);

417   5.   thermoregulation (Seidel, 1979; Grigg & Seebacher, 2001);

418   6.   acting as a metamorphosis marker (Boy & Suess, 2000);

419   7.   buffering of acidosis and lactic acid build-up in tissues due to anaerobic activity (Janis et al.,

420   2012).

421   The microstructural observations described in this manuscript support two hypotheses. Ornamentation

422   increases the surface area of the bone (Rinehart & Lucas, 2013) and thus improves its thermoregulatory

423   abilities and probably its integration with the skin, as histological thin sections show many Sharpey's

424   fibres residing deep in the ridges (Gądek, 2012). Moreover SEM photographs presented herein show

425   more or less numerous striations (skin and bone contact) and vascular foramina.

426   The hypothesis put forward by Janis et al. (2012) of dermal bone ornamentation developed in primitive

427   tetrapods for the purpose of buffering acidosis and lactic acid build-up in their tissues due to anaerobic

428   activity is also plausible. This would enable the amphibians to spend longer times on land and thus

429   better exploit the terrestrial environment. This statement is in agreement with a study by Witzmann et

430   al. (2010), who stated that terrestrial forms (according to species or population) show more pronounced

431   sculpture than aquatic forms.

432

Summary

434   The diversity of metoposaurid material from the 'Trias' site at Krasiejów (SW Poland) includes the

435   character of ornamentation of clavicles and remarks of the ornamentation of skulls (although

436   histological character suggests that all types of bones possess two types of bone growth). Similar

437 differences in dermal bone ornamentation in Temnospondyli were cited as ecologically dependent by
438 Witzmann et al. (2010); however, these differences were assigned to particular taxa. Detailed analyses
439 of large probe from one species shows that ecologically induced ornamentation differences can be
440 observed within one species (from a single site).

441 Except for UOPB1165 specimen the taxonomical variety of the material was excluded. Observed
442 differences in polygon shape, area, sculpture density, regularity and others (Table 1, Table 6) could be
443 the result of individual, ontogenetic, sexual or ecological variation. Although some sort of sexual
444 dimorphism or ontogenetic changes cannot be excluded, the most probable explanation for the
445 described variation is ecological difference between two populations as stated by Witzmann et al.
446 (2010); or existence of facultative neotenic population. Described ornamentation types within one semi-
447 aquatic species possess characteristic of either more-terrestrial or more-aquatic taxa. Some ontogenetic
448 differences can be observed in both populations but they can be described separately in both
449 populations with the smallest (youngest) specimens having low number of ramifications and partition
450 walls within radial ornamentation and the largest (oldest) having high number of ramifications and
451 partition walls.

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

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

469   The isotopic (or REE) analysis in the future may confirm the most probable explanation for

470   metoposaurid ornamentation diversity and will provide valuable insight into the mechanism between it.

471   More information about possible ornamentation character diversity can be obtained in the future

472   considering distribution of shape (geometric morphometrics), possibly in all of the Metoposauridae.

473

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480
481

483 **Literature**

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

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

488 **Antczak, M., Bodzioch, A. 2018.** Diversity of fish scales in Late Triassic deposits of Krasiejów (SW
489 Poland). *Paleontological Research,* **22(1)**: 91–100.

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

492 **Blouin, M. S., Loeb M. L. G. 1990**. Effects of environmentally induced development-rate variation of
493 the head and limb morphology in the green tree frog, *Hyla cinerea. The American Naturalists,* **138(3)**:
494 717–728.

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

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

500 **Bossy, K. A., Milner, A. C. 1998.** Order Nectridea Miall 1875. In: Wellnhofer, P. (eds.). *Handbuch der*
501 *paläoherpetologie*, 1. München: Verlag Dr. Friedrich Pfeil: 73–131.

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

504 **Boy, J. A. 1988**. Über einige Vertrteter der Eryopoidea (Amphibia: Temnospondyli) aus dem
505 europäischen Rotliegend (? höchstes Karbon-Perm). 1. *Sclerocephalus. Paläontologische Zeitschrift,* **62**:
506 107–132.

507 **Boy, J. A. 1990**. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem
508 europäischen Rotliegend (?höchstesKarbon – Perm). 3. *Onchiodon. Paläontologische Zeitschrift*, **64**:287–
509 312.

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

513 **Brusatte, S. L., Butler, R. J., Sulej, T., Niedźwiecki, G. 2009.** The taxonomy and anatomy of
514 rauisuchian from the Late Triassic of Germany and Poland. *Acta Palaeontologica Polonica,* **54(2)**: 221–
515 230.

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

519   **Bystrow, A. P. 1947.** Hydrophilous and xerophilous labyrinthodonts. *Acta Zoologica* (Stockholm), **28**:
520   137190–274164.

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

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

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

528   **Dubois, A., 1982**. Notes sur les grenouilles brunes (groupe de Ranatemporaria) I. Introduction. *Alytes*, **1**:
529   56–70.

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

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

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

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

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

540   **Fortuny, J., Marcé-Nogué, J., Konietzko-Meier, D. 2017.** Feeding biomechanics of Late Triassic
541   metoposaurids (Amphibia: Temnospondyli): a 3D finite analysis approach. *Journal of anatomy,* **DOI**:
542   10.1111/joa.12605

543   **Fritzsch, B. 1990.** The evolution of metamorphosis in amphibians. *Journal of Neurobiology,* **21**: 1011–
544   1021.

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

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

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

551 **Grigg, G., Seebacher, F. 2001.** Crocodilian thermal relations. In: Grigg, G. C., Seebacher, F., Franklin,
552 C.E., (eds.). *Crocodilian biology and evolution*, Chipping Norton: Surrey Beatty: 297–309.

553 **Gruntmejer, K., Konietzko-Meier, D., Bodzioch, A. 2016**. Cranial bone histology of *Metoposaurus*
554 *krasiejowensis* (Amphibia, Temnospondyli) from the Late Triassic of Poland. *PeerJ,* 4:e2685; DOI:
555 10.7717/peerj.2685.

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

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

561 **Konieczna, N., Belka, Z., Dopieralska, J., 2015.** Nd and Sr isotopic evidence for provenance of clastic
562 material of the Upper Triassic rocks of Silesia, Poland. *Annales Societatis Geologorum Poloniae*, **85**:
563 675–684.

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

567 **Konietzko-Meier, D., Sander, P. M. 2013.** Long bone histology of *Metoposaurus diagnosticus*
568 (Temnospondyli) from the Late Triassic of Krasiejów (Poland) and its palaeobiological implicatios.
569 *Journal of Palaeontology,* **33**: 1003−1018.

570 **Konietzko-Meier, D, Gruntmejer, K., Marcé-Nogué, J., Bodzioch, A., Fortuny, J. 2018**. Merging
571 cranial histology and 3D-computational biomechanics: a review of the feeding ecology of a Late Triassic
572 temnospondyl amphibian. *PeerJ,* 6:e4426; **DOI**: 10.7717/peerj.4426
573
574 **Krenz, J. D, Sever, D. M. 1995.** Mating and oviposition in paedomorphic *Ambystoma talpoideum*
575 precedes the arrival of terrestrial males. *Journal of Herpetology*, **51**: 387–393.

576 **Kupfer, A. 2007.** Sexual size dimorphism in amphibians: an overview. Chapter 5. In: Fairbairn, D. J.,
577 Blanckenhorn, In. U., Szekely, T. (eds.). *Sex, size and gender roles: evolutionary studies of sexual size*
578 *dimorphism,*, Oxford University Press:50–59.
579
580 **Lucas, S. G. 2015.** Age and correlation of Late Triassic tetrapods from southern Poland. *Annales*
581 *Societatis Geologorum Poloniae*, **85**: 627–635.
582
583 **Lucas, S. G., Rinehart, L. F., Krainer, K., Spielmann, A., Heckert, A. B. 2010.** Taphonomy of the Lay
584 amphibian quarry: A Late Triassic bonebed in New Mexico, USA. *Palaeogeography, Palaeoecology,*
585 *Palaeoclimatology,* **298**: 388–398.

586

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

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

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

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

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

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

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

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

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

605 **Pogodziński, D., Hermaniuk, A., Stępniak, K. 2015.** Phenotypic variability of the moor frog (Rana
606 arvalis) in populations from Podlasie and Wielkopolska. *IVth Student Herpetological Conference,*
607 *Abstractbook*: 1–2.

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

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

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

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

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

619   **Safi, R., Bertrands, S., Marchand, O., Duffraisse, M., Luze, A., Vanacker, J., Maraninchi, M.,**
620   **Margotat, A., Demeneix, B., Laudet, V. 2004**. The axolotl (*Ambystoma mexicanum*), a neotenic
621   amphibian, express functional thyroid hormone receptors. *Endochrynology*, **154**: 760–722.

622   **Sanchez, S., Schoch, R. R. 2013**. Bone histology reveals a high environmental and metabolic plasticity
623   as a successful evolutionary strategy in a long-lived homeostatic Triassic temnospondyl. *Evolutionary*
624   *Biology*, **DOI**: 10.1007/s11692-013-9238-3.

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

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

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

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

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

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

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

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

640   **Seidel, M. R. 1979.** The osteoderms of the American Alligator and their functional significance.
641   *Herpetologica*, **35**: 375–380.
642
643   **Seibert, E. A., Lillywhite, H. B., Wassersug, R. J. 1974.** Cranial co-ossification in frogs: relationship to
644   rate of evaporite water loss. *Physiological Zoology,* **47**: 261–265.
645
646   **Skrzycki, P. 2015.** New species of lungfish (Sarcopterygii, Dipnoi) from the Late Triassic Krasiejów site
647   in Poland, with remarks on the ontogeny of Triassic dipnoan tooth plates. *Journal of Vertebrate*
648   *Palaeontology*, **35(5)**, **DOI**: 10.1080/02724634.2015.964357.

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

651   **Sulej, T. 2007.** Osteology, variability, and evolution of *Metoposaurus*, a temnospondyl from the Late
652   Triassic of Poland. *Palaeontologia Polonica,* **64**: 29–139.

653 **Sulej, T. 2010.** The skull of an early Late Triassic aetosaur and the evolution of the stagonolepidid
654 archosaurian reptiles. *Zoological Journal of the Linnean Society,* **158(4)**: 860–881.

655 **Sulej, T., Majer, D. 2005**. The temnospondyl amphibian *Cyclotosaurus* from the Upper Triassic of
656 Poland. *Palaeontology*, **48(1)**: 157–170.

657 **Szulc, J. 2005.** Sedimentary environments of the vertebrate−bearing Norian deposits from Krasiejów,
658 Upper Silesia (Poland). *Hallesches Jahrbuch für geowissenschaften Reihe B*, **19**: 161–170.

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

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

664 **Teschner E. M., Sander, P., Konietzko-Meier, D. 2017.** Variability of growth pattern observed in
665 *Metoposaurus krasiejowensis* humeri and its biological meaning. *Journal of Iberian Geology*, **DOI**:
666 10.1007/s41513-017-0038-y.

667 **Urban, D. S., Berman, M. 2007.** First occurrence of the Late Paleozoic amphibian *Zatrachys serratus*
668 (Temnospondyli, Zatrachydidae) in the eastern United States. *Annals of Carnegie Museum*, **76**: 157–164.

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

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

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

676 **Werneburg, R., Ronchi, A., Schneider, J. W. 2007.** The Early Permian branchiosaurids (Amphibia) of
677 Sardinia (Italy): systematic palaeontology, palaeoecology, biostratigraphy and palaeobiogeographic
678 problems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**: 383–404.

679 **Wilbur, H. M., Collins, J. P. 1973.** Ecological Aspects of Amphibian Metamorphosis: Nonnormal
680 distributions of competitive ability reflect selection for facultative metamorphosis. *Science*, **182(4119)**:
681 1305–1314.

682 **Witzmann, F., Henning, S., Muller, J., Kardjilov N. 2010**. Sculpture and vascularization of dermal
683 bones, and the implications for the physiology of basal tetrapods. *Zoological Journal of Linnean Society,*
684 **160**: 302–340.

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

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

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

692 **Zalecka K. 2012**. Międzyobojczyk *Metoposaurus diagnosticus krasiejowensis* (Amphibia,
693 Temnospondyli) ze stanowiska dokumentacyjnego 'Trias' w Krasiejowie. [Interclavicle of *Metoposaurus*
694 *diagnosticus krasiejowensis* (Amphibia, Temnospondyli) from 'Trias' site in Krasiejów. Unpublished
695 Master Thesis. Opole University: 1–81.

696 **Zug, G. R. 1993.** *Herpetology. An introductory biology of amphibians and reptiles*. Academic Press
697 Limited, London. ISBN 0-12-782620-3: 1 –527.
698

699 **Figure captions**

700 Figure 1: Localization and geological map of Krasiejów (after Bodzioch & Kowal-Linka, 2012).
701
702 Figure 2: Clavicles ornamentation character.
703 (A) Basic ornamentation features explanation. (B) Clavicle assigned to ornamentation type 2
704 (Tc2). (C) Clavicle assigned to ornamentation type 1 (Tc1). (D) UOBP1165, partially incomplete
705 specimen, not fitting to the described types (C, Figs. 4–6).
706
707 Figure 3: Thickness of the bone in particular types and ontogenetic stages.
708 Measurements made at the border of polygonal and radial ornamentation areas.
709
710 Figure 4: Ratio of the bone width and amount of radial ridges.
711 Measurement taken 2.5 cm, from ossification centre.
712 (A) Considering appointed types, showing two subsets within metoposaurid data. (B)
713 Considering individual age, showing no subsets within metoposaurid data.
714
715
716 Figure 5: Ratio of polygon number and surface.
717 (A) Considering appointed types, showing two subsets within metoposaurid data. (B)
718 Considering individual age, showing no subsets within metoposaurid data.
719
720 Figure 6: Ratio of multipolygon and all polygon numbers.
721 (A) Considering appointed types, showing two subsets within metoposaurid data. (B)
722 Considering individual age, showing no subsets within metoposaurid data.
723
724 Figure 7: Percentage of hexagonal, pentagonal and other polygons.

725   (A) Considering appointed types, showing two subsets within metoposaurid data. (B)
726   Considering individual age, showing no subsets within metoposaurid data.
727

728   Figure 8: SEM (SE) and histological observations of clavicle radial ridges for Tc1.
729   (A–B) UOPB1152. (C–D) UOPB1161. (E) UOPB1160. (F) UOPB1167. (G) UOPB1170.
730

731   Figure 9: SEM (SE) and histological observations of clavicle radial ridges for Tc2.
732   (A–B) uam/kng/02. (C–D) UOBP1157. (E–F) UOPB1163. (G) UOPB1172. (H) UOPB1158. (I)
733   UOPB1163.
734

735   Figure 10: Types of skulls ornamentation of metoposaurids from Krasiejów (*M. krasiejowensis*,
736   as explained at Fig. 11). Blue area represents surface covered with radial ornamentation. (A)
737   UO/PP20. (B) UO/PP13. (C) UO/PP08. (D) UO/PP09. (E) Ts2 skull. (F) Ts1 skull. Scale bar 5
738   cm.
739

740   Figure 11: Comparison of analyzed skull material (examples) with reconstructions of
741   *Metoposaurus diagnosticus*, *M. krasiejowensis* and *M. algavrensis* skulls.
742   (A) *M. algavrensis*. (B) *M. krasiejowensis*. (C) *M. algavrensis*. (D) UO/PP02 (Ts2). (E)
743   UO/PP09 (Ts1). (F) UO/PP13 (Ts1). (G) UO/PP04 (Ts1). A–C after Brusatte et al., 2015.
744

745   Figure 12: Skull measurements.
746

747   Figure 13: Ontogenetic stages in clavicles. Arrows show partition walls and ramifications within
748   radial ridges.
749   (A–C) Ornamentation type 2 (Tc2) from possibly the youngest specimen to the oldest one. (D–F)
750   Ornamentation type 1 (Tc1) from possibly the youngest specimen to the oldest one. (A)
751   UOPB1155. (B) UOPB1168. (C)UOPB1164. (D)UOPB1171. (E) UOPB1166. (F)UOPB1152.
752

754 **Tables**

755

756

757 Types numerical codes:

758

759

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

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Figure 1

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

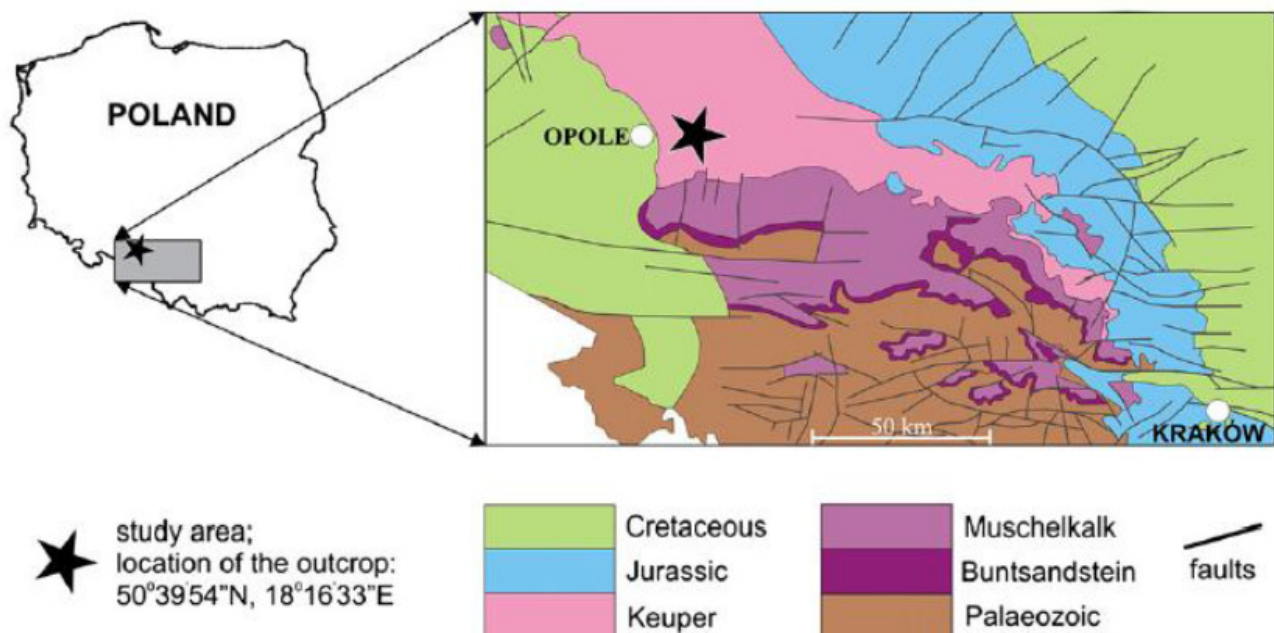



Figure 2

Clavicles ornamentation character.

(A) Basic ornamentation features explanation. (B) Clavicle assigned to ornamentation type 2 (Tc2). (C) Clavicle assigned to ornamentation type 1 (Tc1). (D) UOBP1165, partially incomplete specimen, not fitting to the described types (C, Figs. 4–6).

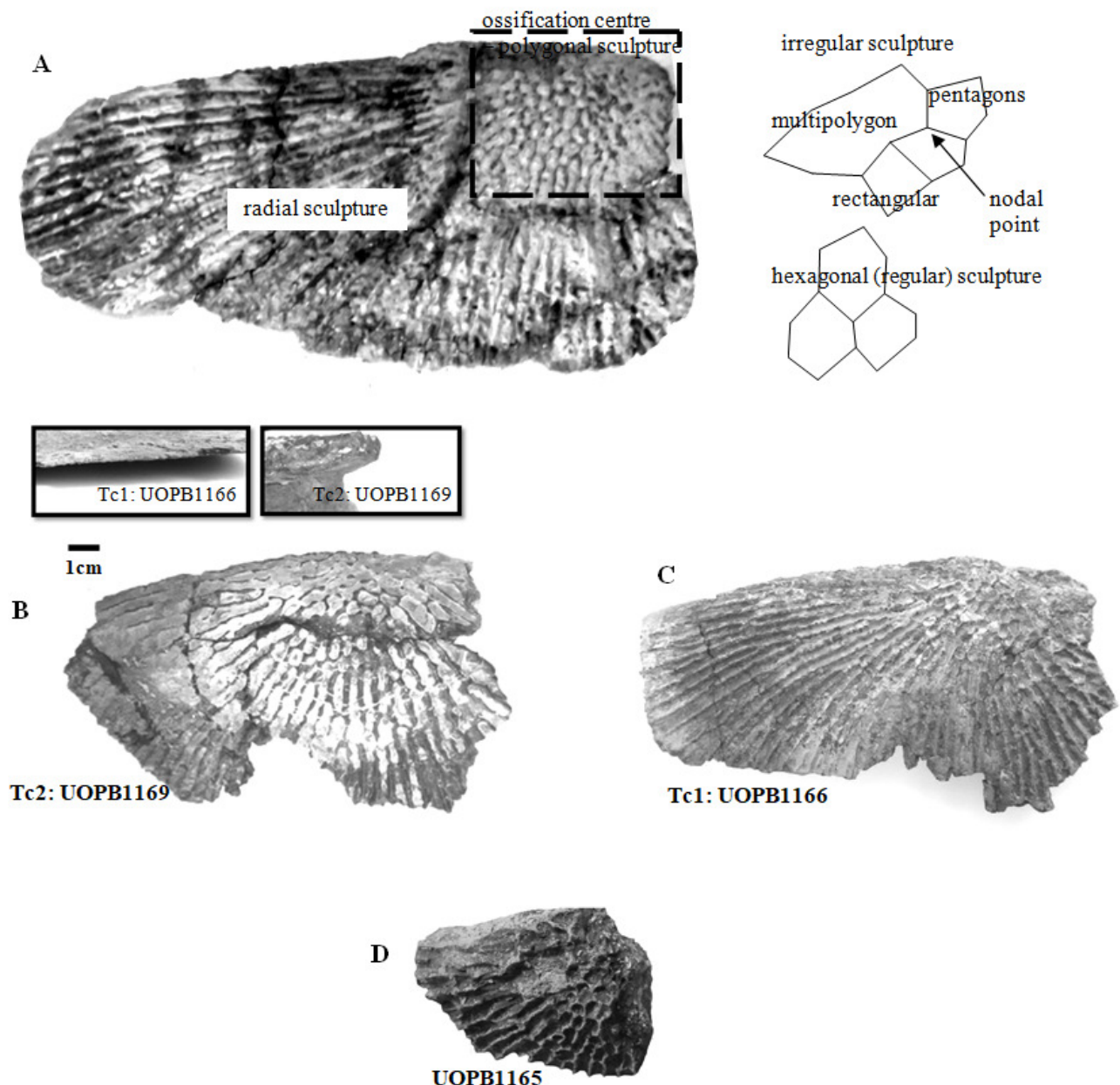



Figure 3

Thickness of the bone in particular types and ontogenetic stages.

Measurements made at the border of polygonal and radial ornamentation areas.

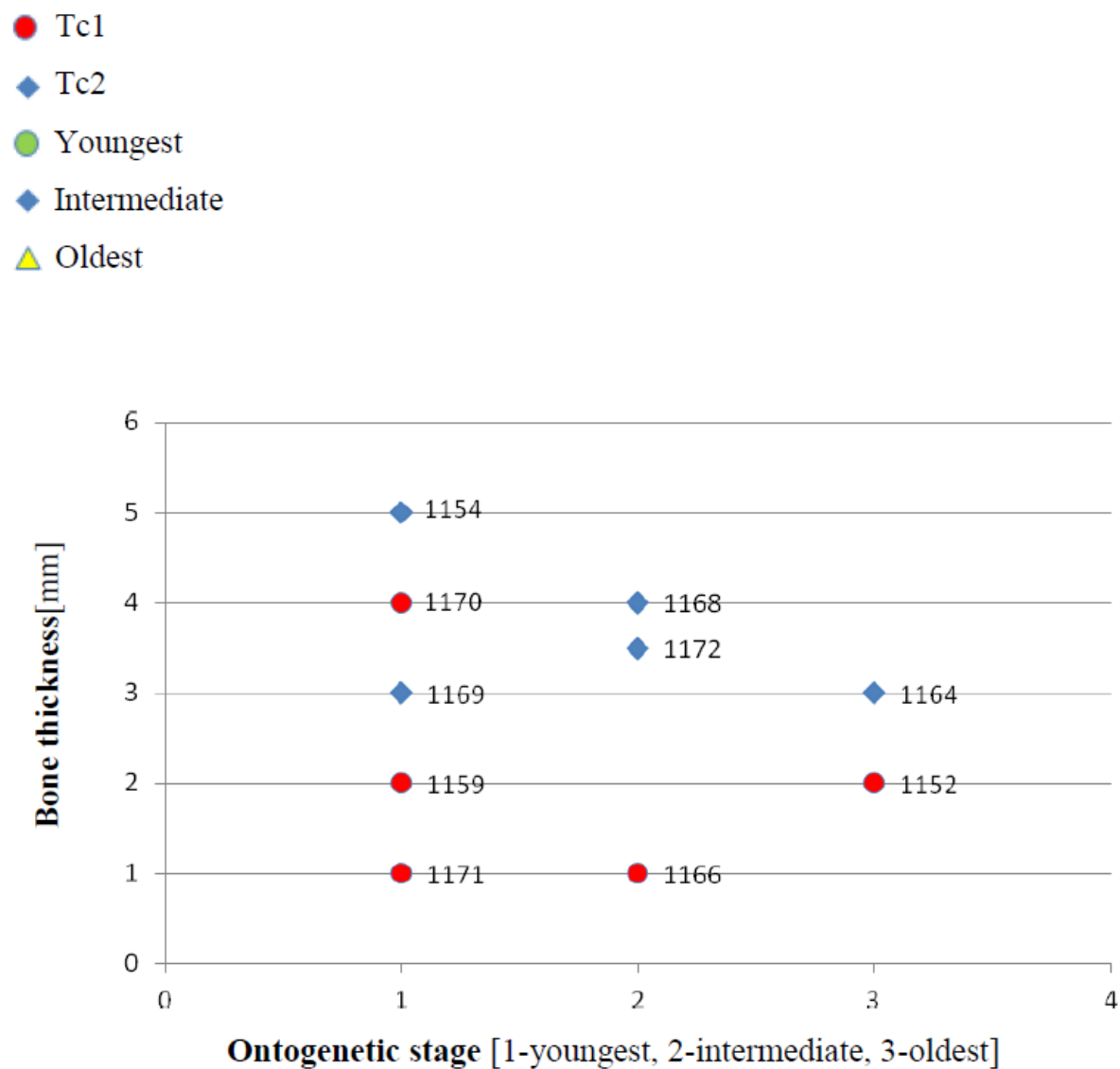



Figure 4

Ratio of the bone width and amount of radial ridges.

Measurement taken 2.5 cm, from ossification centre. (A) Considering appointed types, showing two subsets within metoposaurid data. (B) Considering individual age, showing no subsets within metoposaurid data.

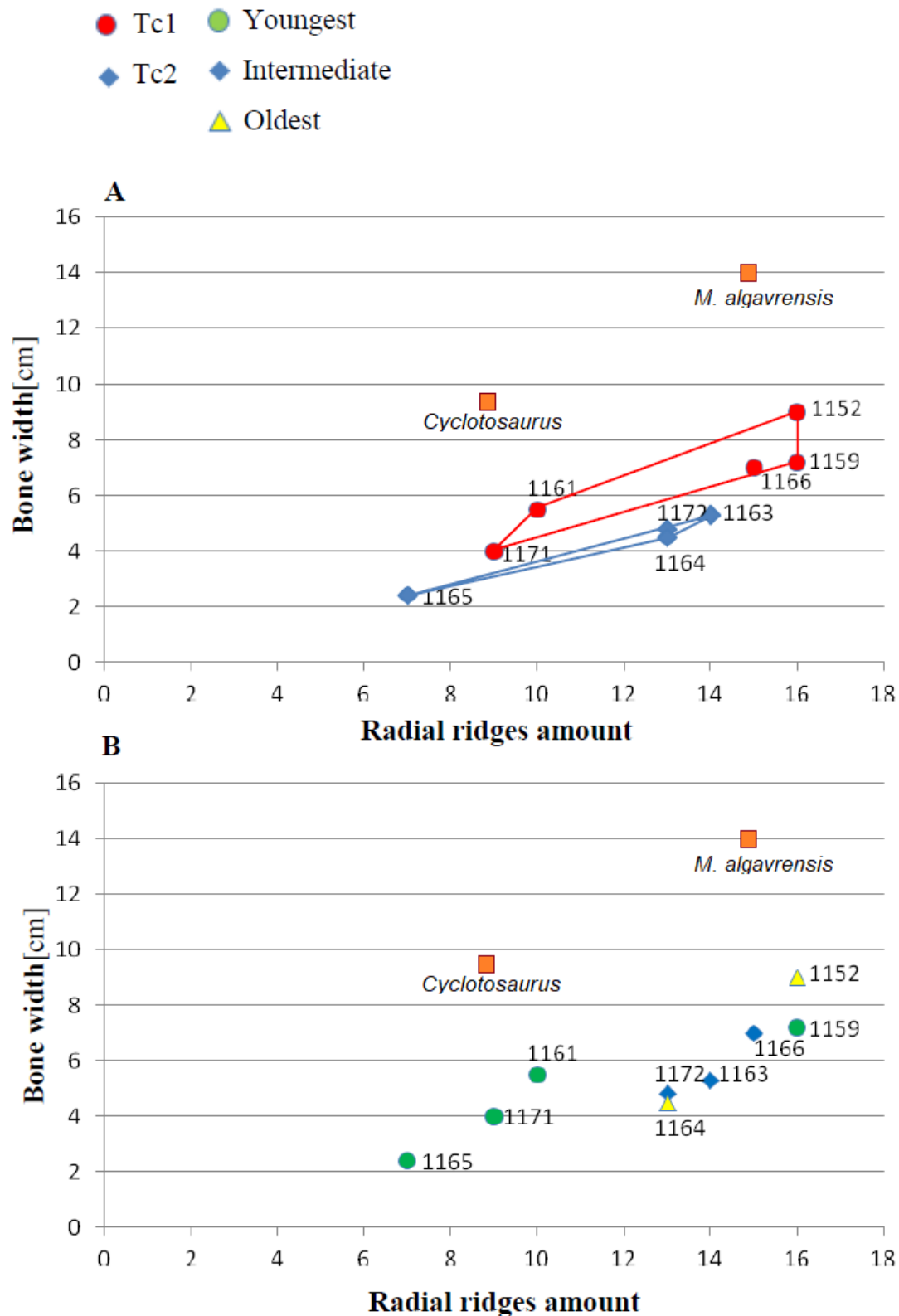



Figure 5

Ratio of polygon number and surface.

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

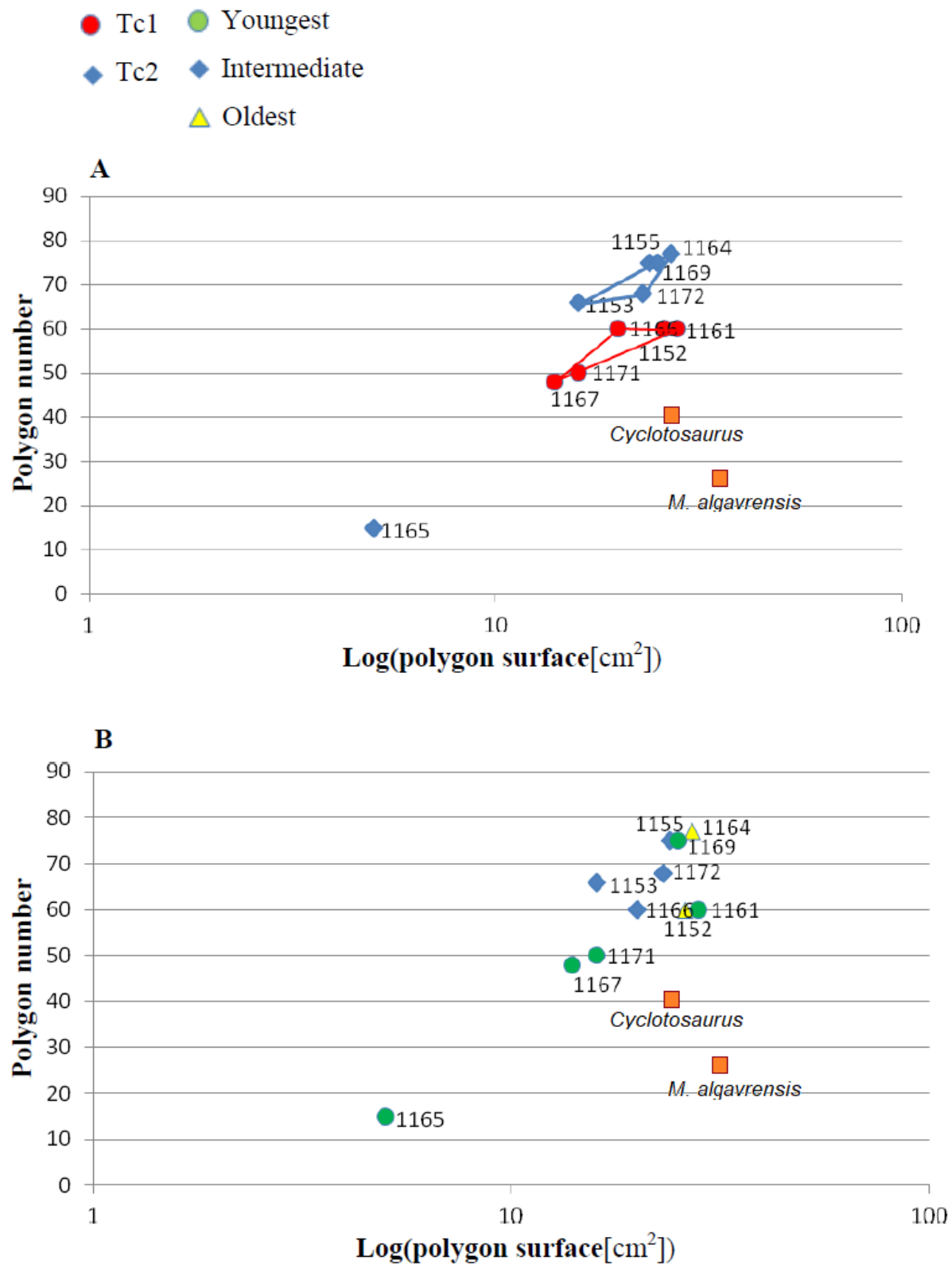



Figure 6

Ratio of multipolygon and all polygon numbers.

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

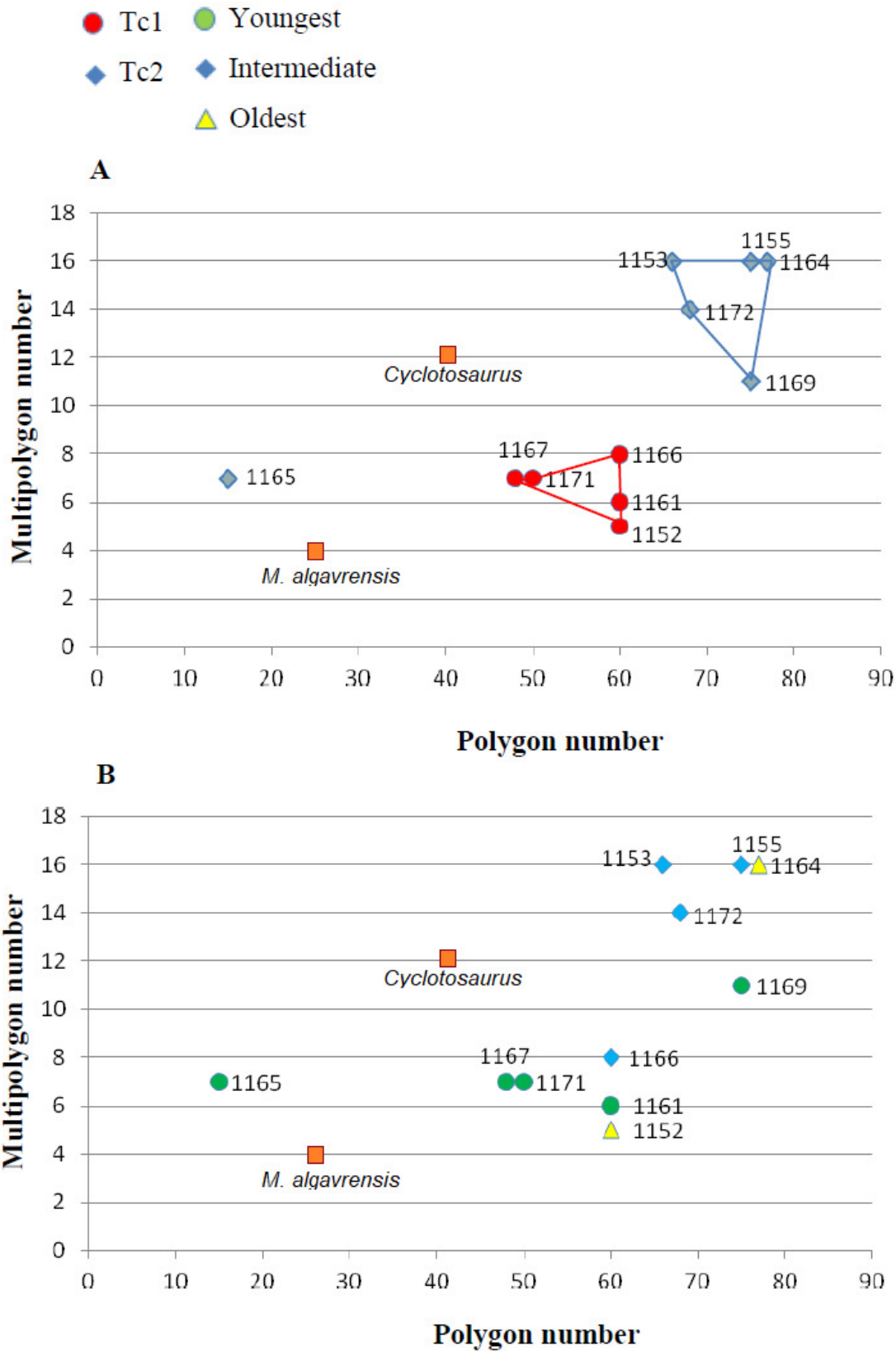



Figure 7

Percentage of hexagonal, pentagonal and other polygons.

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

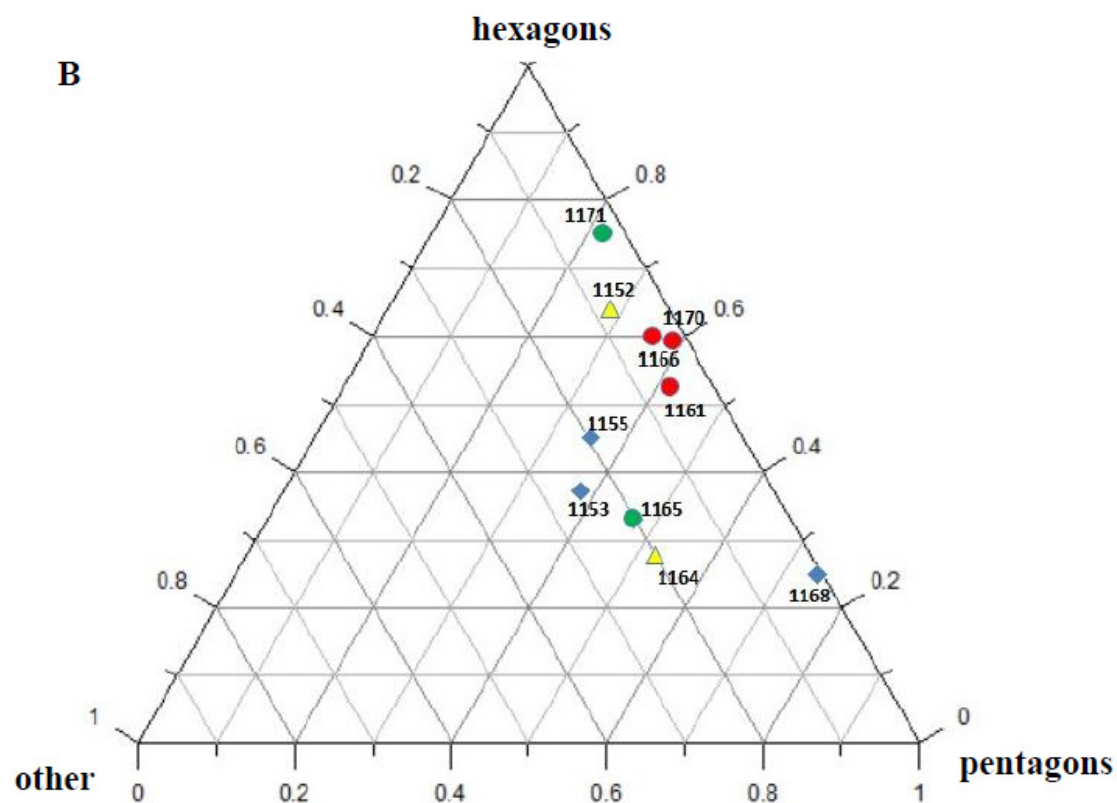
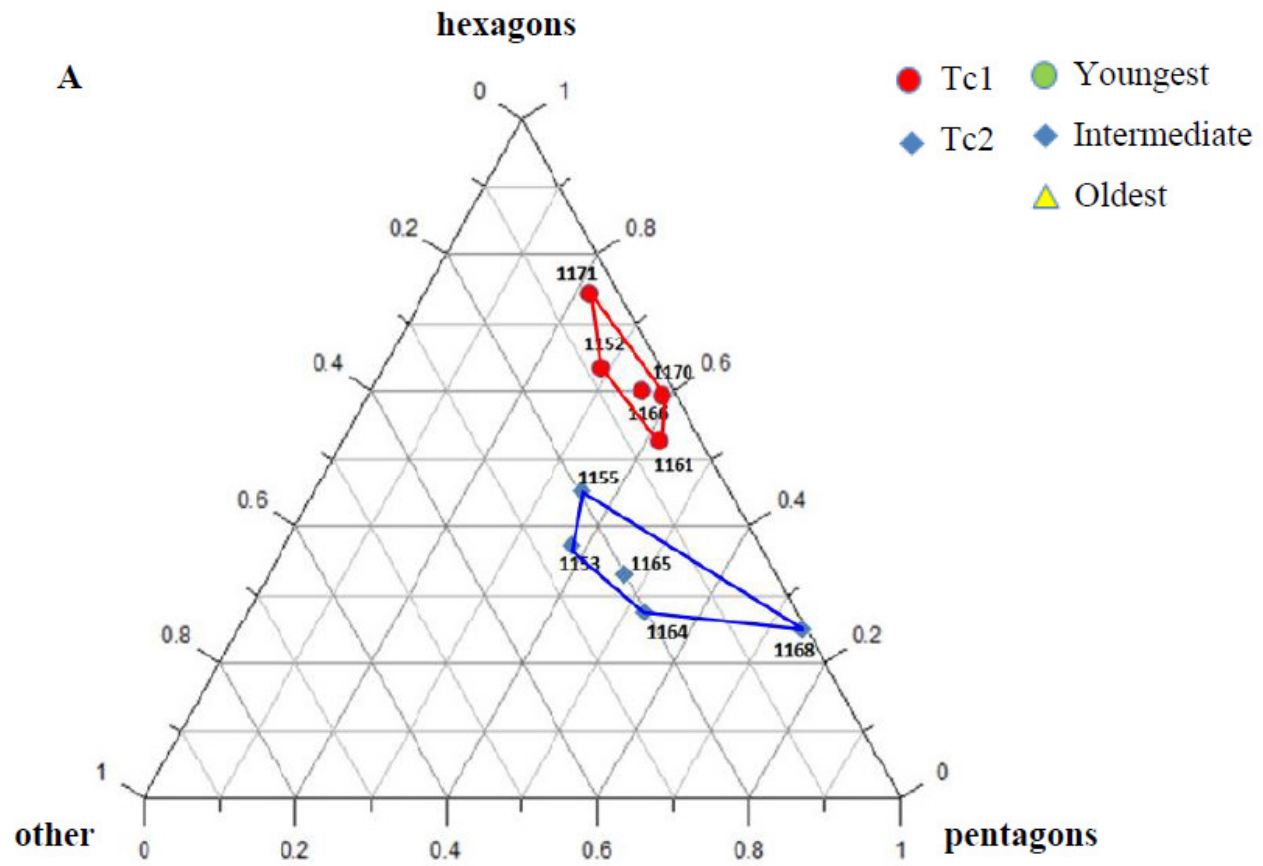



Figure 8

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

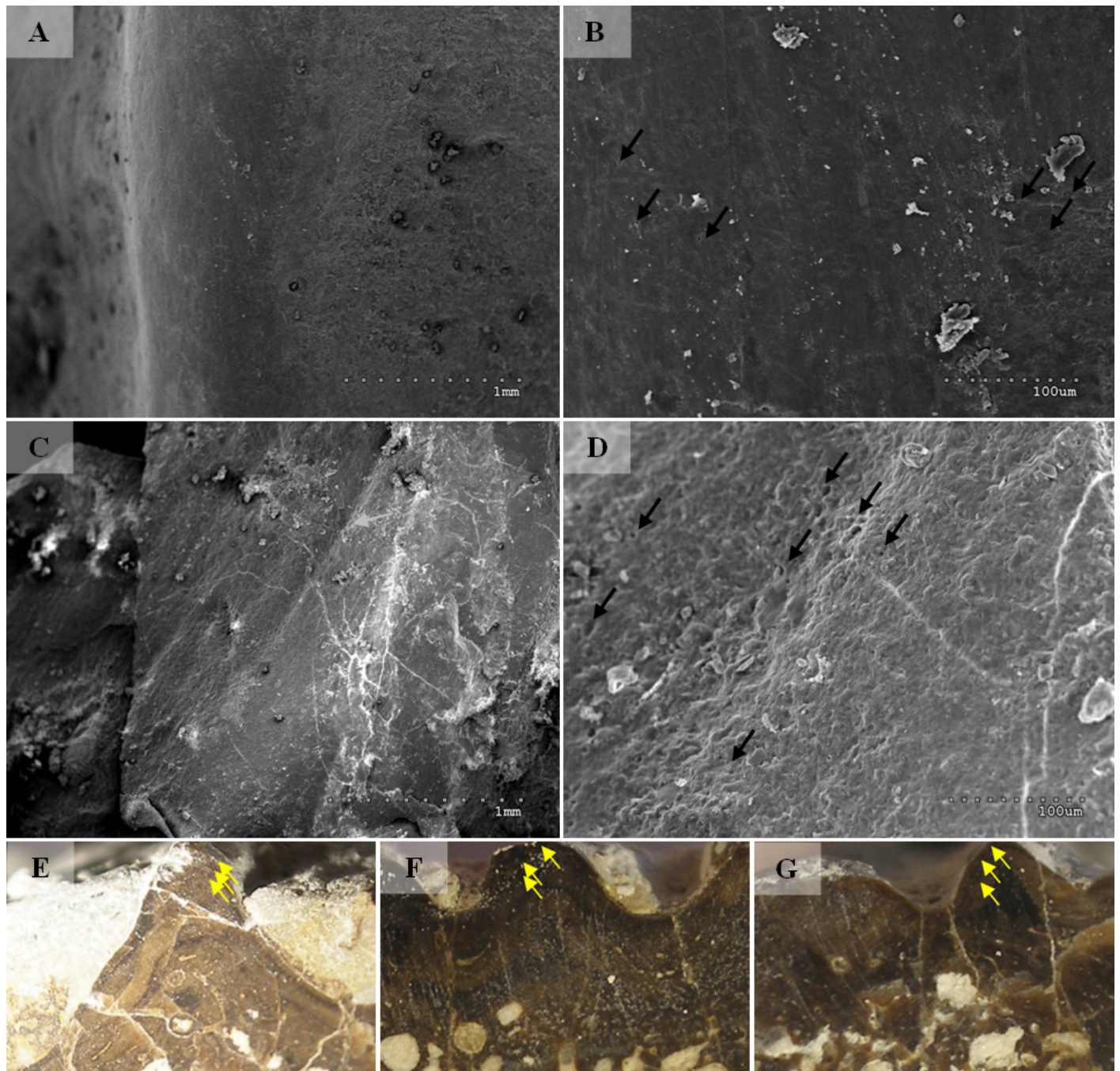
(A–B) UOPB1152. (C–D) UOPB1161. (E) UOPB1160. (F) UOPB1167. (G) UOPB1170.

sharp edge ↘
foramen ↙
striations and bumps ◪
growth marks ↗
zones (vascularised bone) ↗

Figure 9

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

(A–B) uam/kng/02. (C–D) UOBP1157. (E–F) UOPB1163. (G) UOPB1172. (H) UOPB1158. (I) UOPB1163.

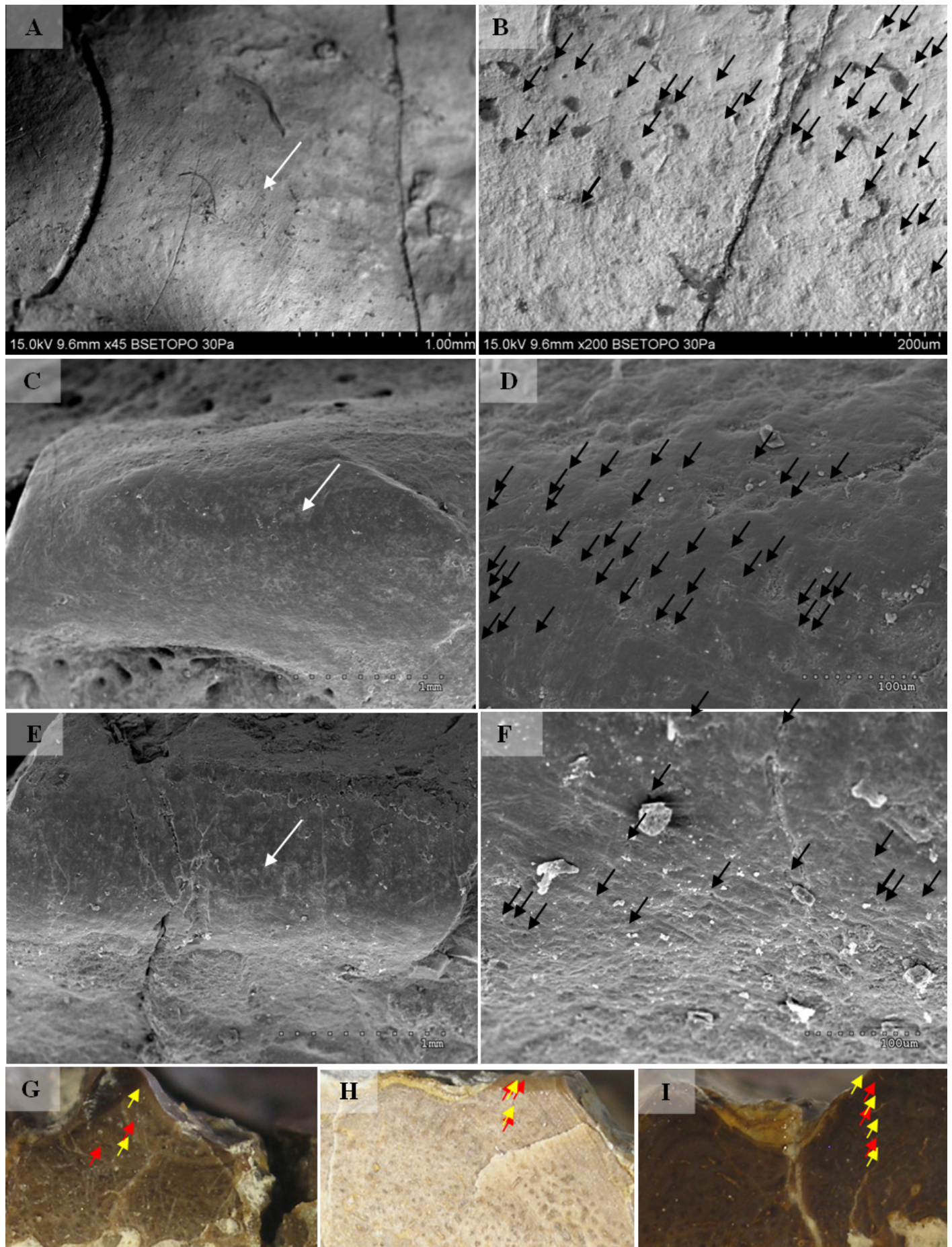



Figure 10

Types of skulls ornamentation of metoposaurids from Krasiejów (*M. krasiejowensis*, as explained at Fig. 11).

Blue area represents surface covered with radial ornamentation. (A) UO/PP20. (B) UO/PP13.
(C) UO/PP08. (D) UO/PP09. (E) Ts2 skull. (F) Ts1 skull. Scale bar 5 cm.

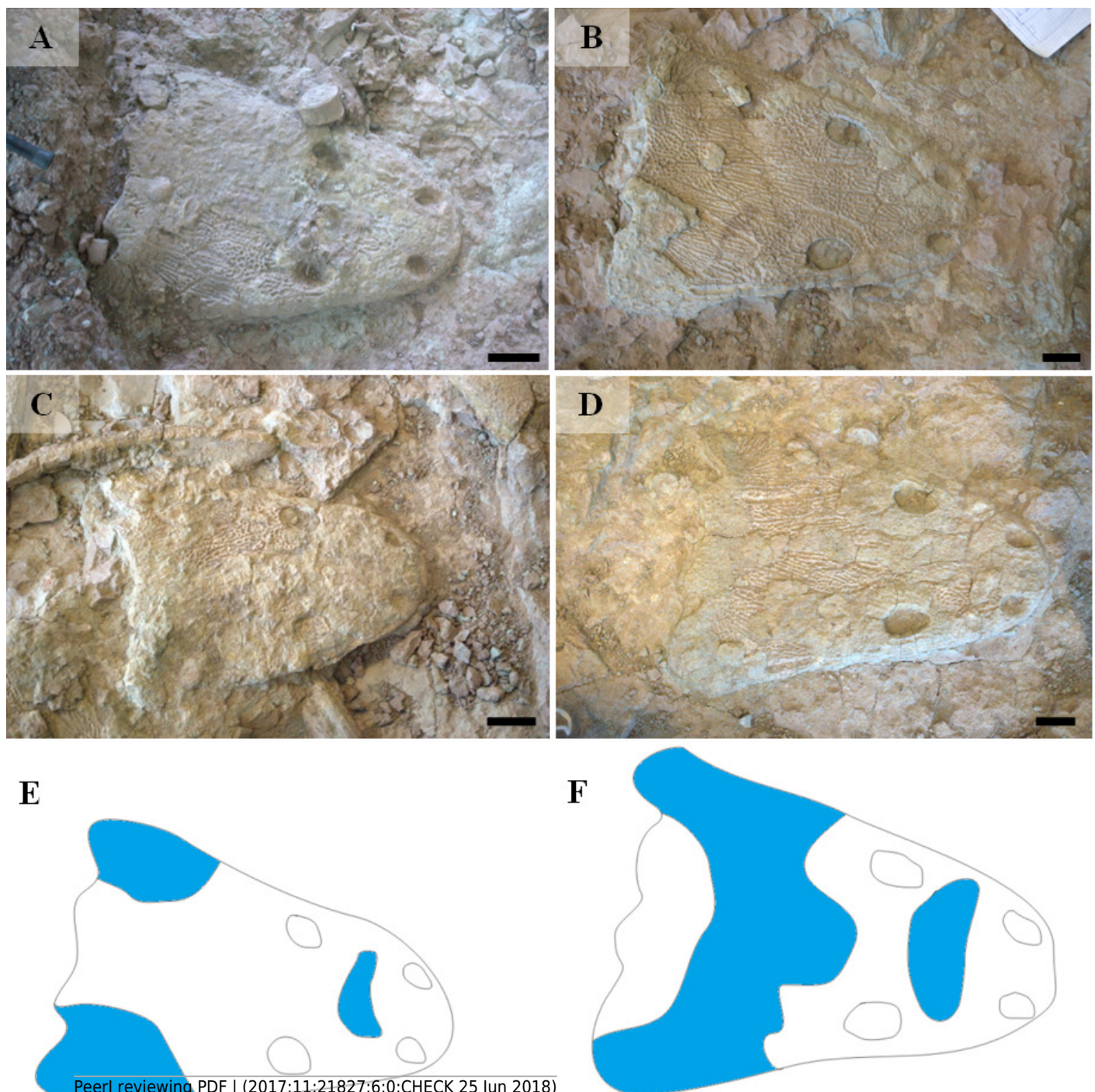



Figure 11

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

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

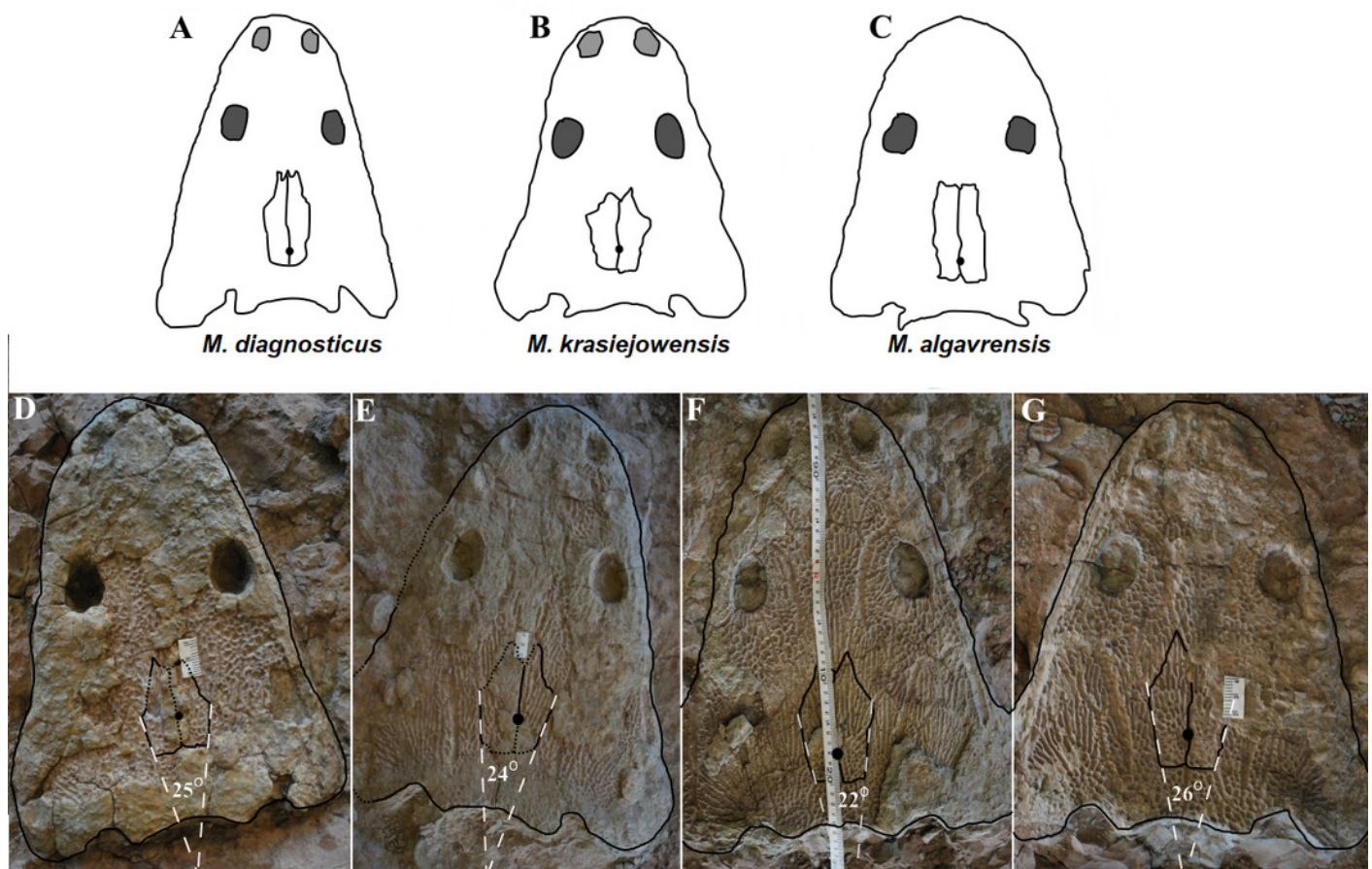



Figure 12

Skull measurements.

A) Skull roof. B) Palate.

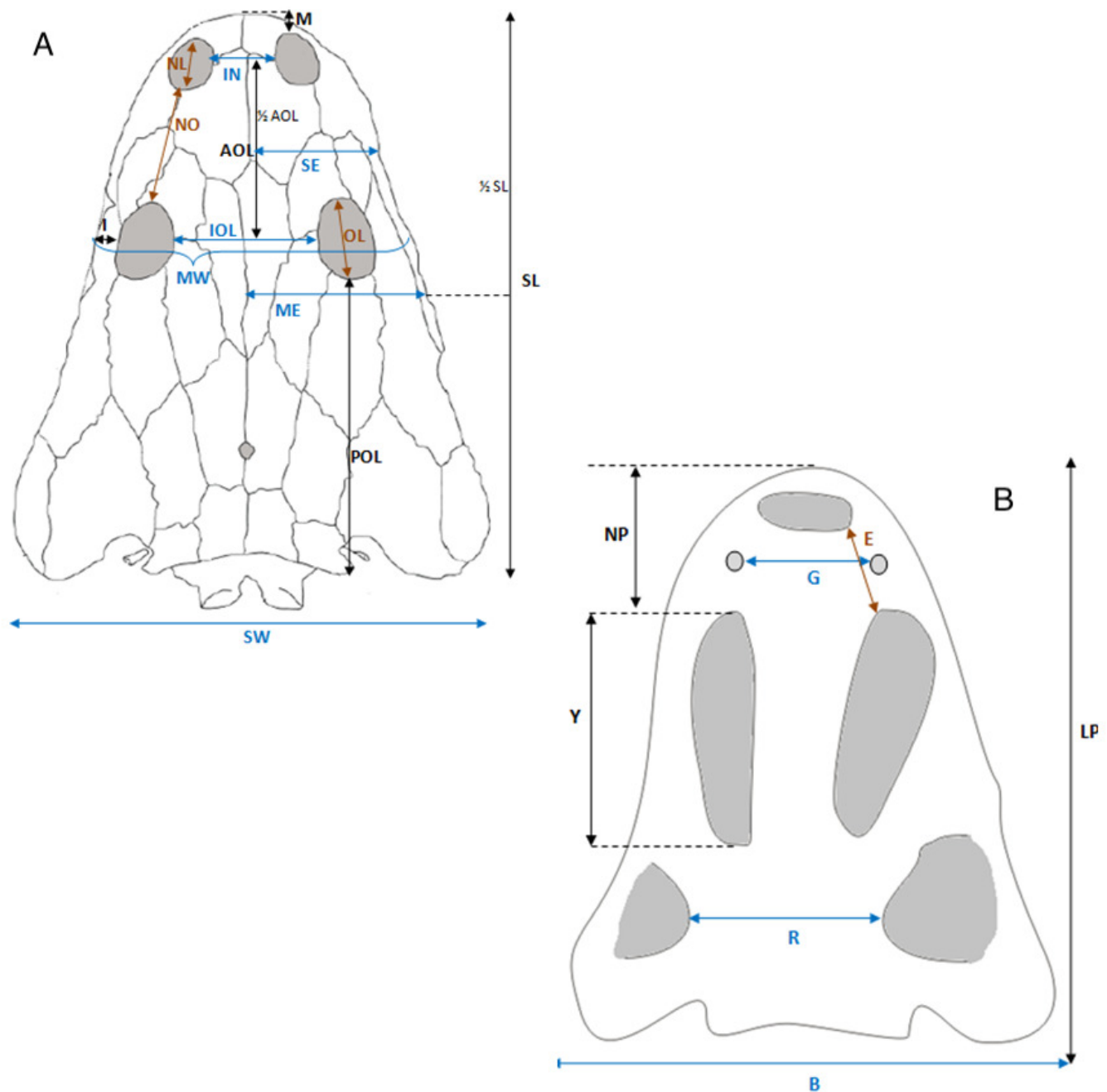
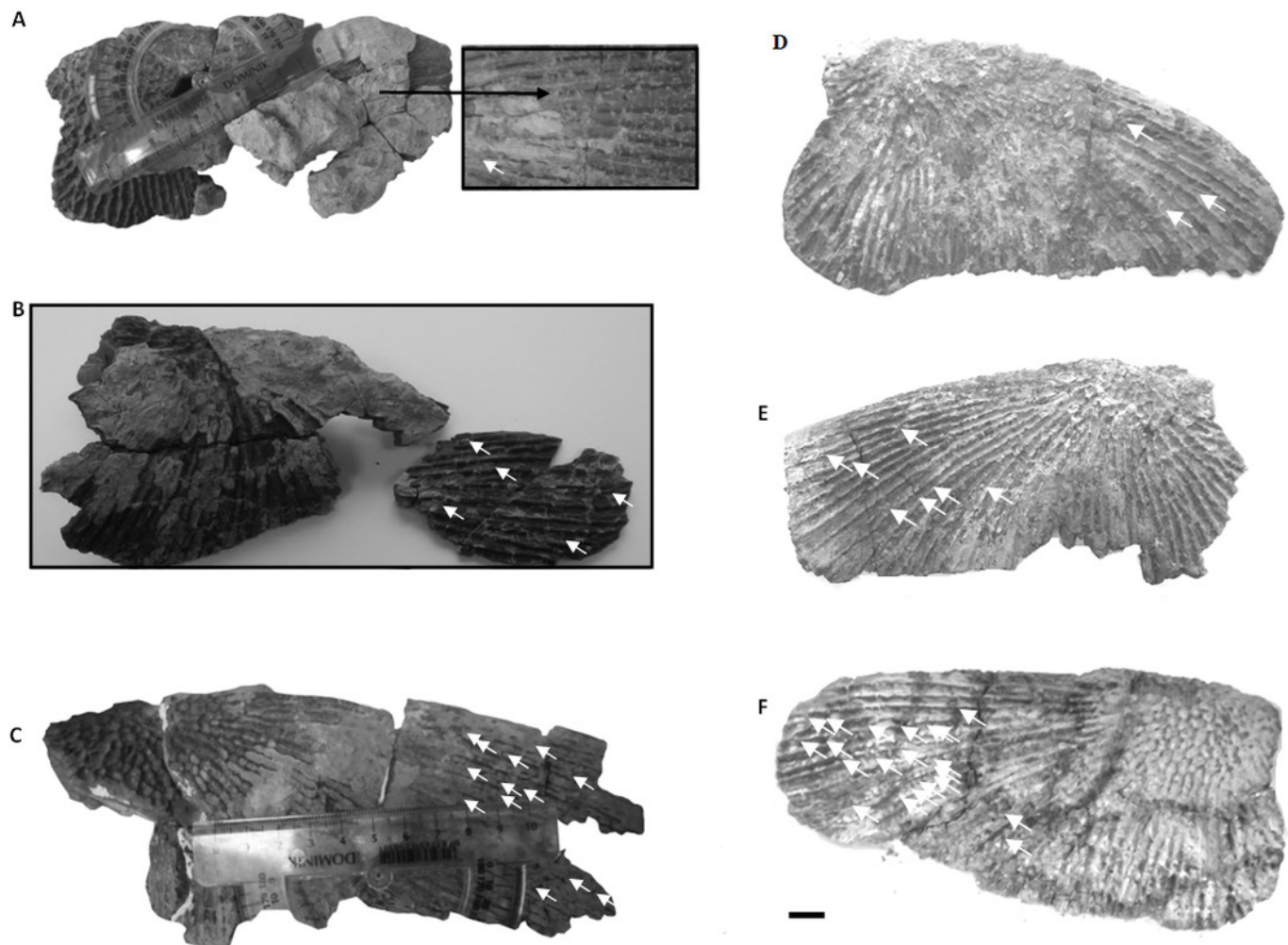



Figure 13

Ontogenetic stages in clavicles.

Arrows show partition walls and ramifications within radial ridges. (A–C) Ornamentation type 2 (Tc2) from possibly the youngest specimen to the oldest one. (D–F) Ornamentation type 1 (Tc1) from possibly the youngest specimen to the oldest one. (A) UOPB1155. (B) UOPB1168. (C) UOPB1164. (D) UOPB1171. (E) UOPB1166. (F) UOPB1152.

Clavicles ornamentation

	Zpal AbIII 397	UOPB 1152	UOPB 1153	UOPB 1154	UOPB 1155	UOPB 1156	UOPB 1157	UOPB 1158	UOPB 1159	UOPB 1160	UOPB 1161	UOPB 1162	UOPB 1163	UOPB 1164	UOPB 1165	UOPB 1166	UOPB 1167	UOPB 1168	UOPB 1169	UOPB 1170	UOPB 1171	UOPB 1172	UOPB 1173	UOPB 1174	UOPB 1175	UOPB 1176
Cycl		T1	T2	T2	T2	T2	T2	T1	T1	T1	T1	T1	T2	T2	T2	T1	T1	T2	T2	T1	T1	T2	T1	T1	T2	T1
Age (Zalecka 2012): juvenile (J), intermediate (I), adult (A)		A	I	J	J				J	J/I				A	J/I	I	J	I	J	J	I	I	I	I	A	J
Regular (1), irregular (2)	1	1	2	2	2	2	2	1		1	1	1		2	2	1	1	2	2	1	1	2	1	1	2	1
Very fine (0), fine (1), coarse (2), very coarse (3)	3	1	1	2	2	2	2	1	1	1	1	2	2	1	2	1	0	2	2	0	1	2	1	1	2	1
Very sparse (0), sparse (1), dense (2)	0	1	2	2	2	1	2	1	1	1	1	1		2	2	1	2	2	2	2	1	1	2	1	2	1
Av. polygon diameter/av. ridge width [<4 (1), >4 (2), >6 (3)]	3	2	1		1	1	1	2		2	2	2		1	1	2	1		1	1	1	1				
Distinct borders of polygonal field (1), borders partially hard to recognize (2), hard to recognize (3)	3	1	2		3				1	1	1			3		1	1		2	1	1	3	1		3	1
Ridge quantity/bone width [measurement 2,5cm from polygon border]: >2,3 (2), <2,3 (1), <2 (0)	0	1	2	2					1		1	1		2	2	1		2	2	1	1					
Nodal points slightly wider than ridges (1); some nodal points distinctly wider than ridges (2); nodal points distinctly wider than ridges (3) [Witzmann et al. 2010]	3	3	2	1	1	1	1	3		3	3	2		2	2	3	3	1	1	3	3	1	1	3	1	3
Ridges edged (1); round or edged (2); round (3) [Witzmann et al. 2010]	3	1	2	3	3	3	2	1	2	2	2	2	3	2		1	1	3	3	2	2	2	2			
Deep polygons (1), deep or shallow polygons (2); shallow polygons (3)	1	1	1	3	3	3	3	1		1	1	2		2	1	1	1	2			1	2				

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Polygon shape:>50% hexagons (1), <50% hexagons (2), >50% quadrangle (3)	3	1	2	2	2	2	2	1	1	1	1	2	2	1	1	2	2	1	2	2	1	1	2	1
Polygon size: usually small (1), usually large (2), very large (3) [large: >0,4mm diameter].	3	1	2	2	2	2	2	1	1	1	1	2	1	1	1	2	2	2	1	2	1	1	2	1
Multipolygons: several or none (1), numerous(2) [more than 11]	1	1	2	2	2	1	2	1	1	1	1	2	2	1	1	2	2	1	1	2	1	1	2	1
Polygon field shape: square (1), rectangular (2), elongated (3)	3	1	2		2			1		1		2		1	1		2		1	2	1			1
Ridge height: lower than nodal points (1), almost equal to nodal points (2)		1	2	2	2	2	2	1	1	1	2	2	2	1	1	2	1	2	1	1	2	1		2
Ossification degree: low (1), high (thick bones) (2)	2	1	2	2	2	2			1	1	2	1		2	2	1	2	2	2	2	1	2	2	1
Anterior clavicle projection: small and flat (1), round and expanded (2), more than 45 deg. (3)	3	1	2	2	2	2			1	1			2	2		1	2	2	2	1	2	2		
More ramificatios: opening (1), closing (2)		1	1	1	1		2						1											
Shape of the radial ridges: undulated (1), straight (2)	2	2	2	2	2			2			2	2	2	2										
Ridge surface (macroscale): bumps (1), large cuts (2), small cuts (3)		1	2	2	3		2	3	3	3	3		1											
Ridge width<half of the polygon diameter: yes (1), no (2) (Witzmann et al. 2010)		1	1		2	1	1	1		1	1		1	1										
Radial ridges constrictions and height differences: distinct (1), not distinct (2)		1	1	2	2	2		1	1	1	2	1	1	1	1	2	2	2			2	1		
Shape of the clavicle (angle) > 100º (1), < 100º (2)	2	1		2	2				1				2			1			1			2		

SEM observations of the clavicles.

1 Table 2. 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 $1/1$mm of length]	x	x	v	v	x	v	v	v	x	v	x

Skulls ornamentation characteristcs.

1   Table 3. Skulls ornamentation.

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

Skull measurements [in cm].

1 Table 4. Skull measurements [in cm].

	UO/P P01	UO/P P02	UO/P P03	UO/P P04	UO/P P05	UO/P P06	UO/P P07	UO/P P08	UO/P P09	UO/P P10	UO/P P11	UO/P P12	UO/P P13	UO/P P14	UO/P P15	UO/P P16	UO/P P17	UO/P P18	UO/P P19	UO/P P20
Skull roof																				
SL	25,2	28,4		35		34		28,8	43,1			28	42,7	28,5		30,3	34,1	35,4	32,7	33
SW	21	24,5		28,6		31		~23	36,8			~25,8	37	26,7		26,5	~26	27,2	28,6	~29
IN						5		4,7	6			~4,5	6	~4				4,4	4,1	5
IOL	7,5	7,6		9,1		8,4		8,5	12			7,8	12,1	8		9	9	8,8	9	9
AOL	10					14,2		13	13,5			9,4	13,7	8,9		10	10,3	11,1	10,1	10,5
POL	16,8	16		18,3		14,9		15,9	25,8			16,4	21,4	13,8		18,4	19,2	17,9	17,4	18
SE	5	7,2				6,8		6,2	10			6,4	10,7	8,1		8,2	8,5	8,8	7,5	8,3
ME	7	8,5		9,6		8,8		9	11,5				13,8	9,8		11	11,6	11	9,7	11,5
NL						2,6		2,1	3,6				3,9			3,1	3,2	3,4	~2,8	2,2
I (L)	2	2		1,7		1,6		1,8	2,5			1,8	2,3	1,9		2	1,9	2,3	2,3	2
I (P)	2	2		2,2		2,2		2,2	3			2	3	1,9		1,9	2,3	2	2	2,7
M		4,3				3,9		3	4				3	3,1			4	3,8	3,4	4,2
NO	6,1	6,3		7,9		7,4			9,8			6,5	9	6,7		6,4	7,2	7,5	7,4	7,5
LO	2,8	4		4,6		4		3,7	5,6			3,9	5,6	36		4	4	4,6	4,3	3,4
MW		16		19,4		18,6		18	24			15,7	23,5	17,2		19	19,1	19	18,5	19
Palate																				
LP			30		30,3					32,1	33,4				30					
NP.			9,9		10										7,9					
Y			15,4		15,1		14			14	16				14,7					
R			10,6		11,2		11,4			14,1	13,2				11,6					
B			23,5		~27		20,4			26,7	29				~24					
O															4,4					
E			6												4,4					
G			4,6																	

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Statistical tests.

1   Table 5. Statistical tests.

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

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

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

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