

Morphology and ontogeny of the humerus of the Triassic temnospondyl amphibian *Metoposaurus diagnosticus*

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With 10 figures and 2 tables

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Abstract: A morphology of 22 humeri of *Metoposaurus diagnosticus* from Late Triassic assemblage of Krasiejów (Poland) reveals general metoposauroid conditions, being well-ossified with well-developed processes and wide, flattened ends. These characteristics do not occur in the humerus referred to as *M. diagnosticus* by FRAAS, proving the improper identification of this specimen. In contrast to other metoposauroid species' humeri, they exhibit a smaller degree of torsion of the ends, unrelated to absolute size. Together with the unscrewed head shape, oblique position of the *condylus radialis*, less prominent *processus supinatorius* and *crista deltopectoralis*, these indicate a paddle function of the forelimbs and therefore imply a fully aquatic mode of life for *M. diagnosticus*.

Key words: morphology, aquatic, ontogeny, growth, *Metoposaurus diagnosticus*.

1. Introduction

Metoposaurus diagnosticus krasiejoviensis is the most abundant metoposauroid amphibian of the Krasiejów site, an assemblage of aquatic and terrestrial animals, located in southern Poland and dated on Keuper (Late Triassic) (DZIK et al. 2000). The Metoposauridae are a family of large aquatic temnospondyl amphibians, widespread in the Upper Triassic over much of the world and characterized by anteriorly located orbits and cylindrical intercentra. The metoposauroid humerus has been described and characterized in several descriptions of metoposauroid species (FRAAS 1889; CASE 1931, 1932; SAWIN 1945; CHOWDHURY 1965; DUTUIT 1976; SENGUPTA 2002). In general, lower tetrapod humeri have not been regarded as taxonomically useful, and consequently are seldom characterized in detail in the literature. There are only a few significant papers, mostly from the first half of

the twentieth century, with comparative description of the humeri of primitive tetrapods (MINER 1925; ROMER 1922; NILSSON 1939) or interpretations of the evolution of the humerus (WATSON 1917; GREGORY 1949). Only OLSEN (1951) has discussed variation in a sample of 23 humeri of *Buettneria perfecta*. The few works on primitive humerus morphology have used varying morphological terminology, usually based on extrapolation from the better-known reptile humeral anatomy.

The *M. diagnosticus* humerus has not been described. Admittedly, FRAAS (1889: pl. 11, fig. 9) described a separately-found humerus from the locality “Feuerbacher Heide” within the township of Stuttgart (Schilfsandstein, now Stuttgart Formation) as a single bone belonging to *M. diagnosticus*. And also, in Krasiejów none of the articulated humeri had been found. However, very abundant remains of *M. diagnosticus* and scarce remains of *Cyclotosaurus inter-*

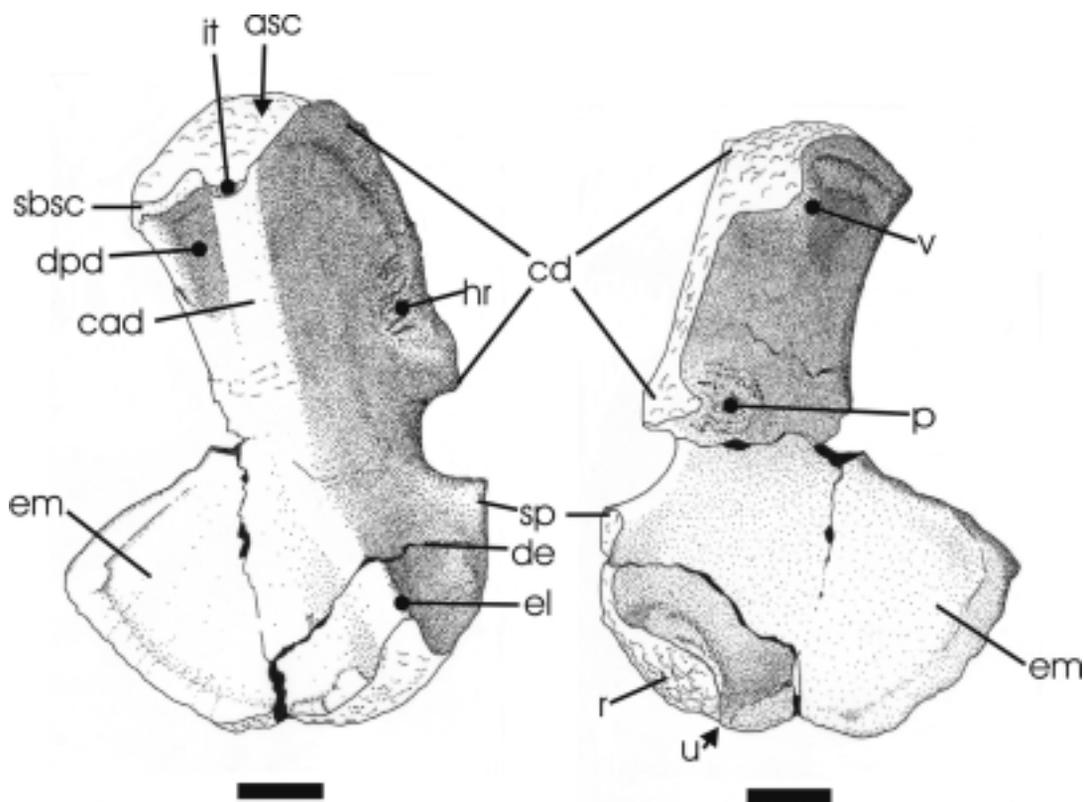


Fig. 1. Right humerus of *Metoposaurus diagnosticus* ZPAL III 816 in **A** – dorsal and **B** – ventral view. Abbreviations: asc – facies articularis scapulocoracoidea; cad – crista adductore; cd – crista deltopectoralis; de – depressio epicondylaris; dpd – depressio postero-dorsale; el – epicondylus lateralis; em – epicondylus medialis; hr – tuberositas humero-radialis; I – incisura cranialis*; lpl – linea postero-lateralis; lt – processus latissimi; p – tuberculum pectorale; r – condylus radialis; sbsc – processus subcoracoscapularis; sp – processus supinatorius; u – facies articularis ulnaris; v – tuberculum ventrale. – Scale bar equals 1 cm.

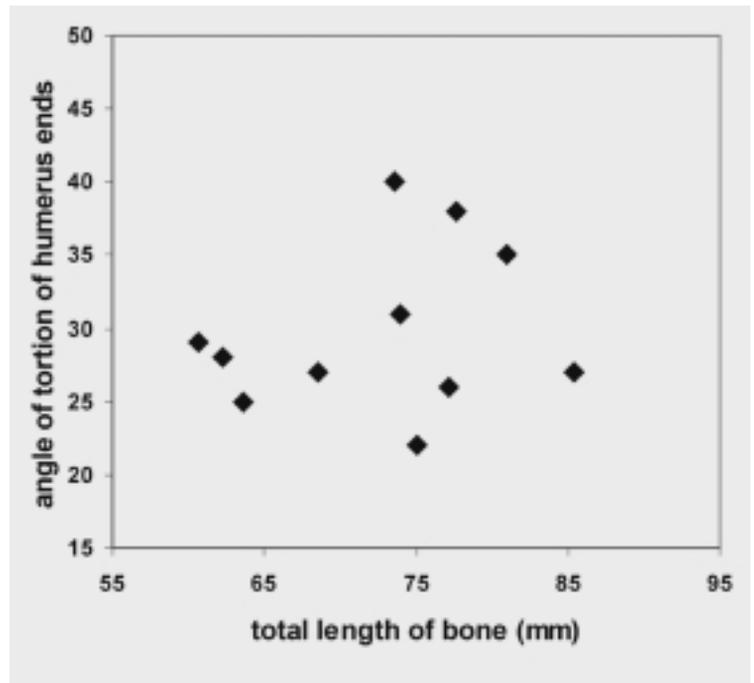
medius, the only other known temnospondyl amphibian, clearly suggest that numerous amphibian humeri studied in this work belong to *M. diagnosticus*. Additional confirmation of proper taxonomical determinations of studied humeri proves WARREN & SNELL'S (1991) revision of Mesozoic Temnospondyl amphibians' humeri, which reveals the significant difference between well-ossified metoposauroid humeri with pronounced processes and the poorly-ossified, narrow-ended humeri of other aquatic Mesozoic Temnospondyl amphibians. In addition, the striking similarity of the studied humeri to specimens of other metoposauroid species (which cannot be confirmed in the case of FRAAS' 1889 specimen) confirms that they are rightly classified as belonging to species other than *M. diagnosticus*.

This study aims to describe the morphology and ontogeny of the humerus of *Metoposaurus diagnosticus* based on a new sample of specimens.

2. Materials and methods

This study is based on 22 humeri of the *Metoposaurus diagnosticus* (9 left bones and 13 right bones) from the Keuper claystone (Late Triassic) of Krasiejów in southern Poland (DZIK et al. 2000). All the material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw. Measurements were taken using calipers with 170 mm range and to a precision of 0.1 mm. The degree of proximal to distal end rotation was measured using the long axis of the humeral head and the plane of the *entepicondyle*

Fig. 2. Comparison of humerus twist to total length of bone.



as referents. Only well-preserved and slightly cracked bones were measured. In order to determine the growth rate, the length of the bone, width of the shaft, width of the proximal end, width of the distal end, length of the *crista deltopectoralis* and twist of the bone (following KLEMBARA et al. 2001) were measured. The ratios of the bone length to shaft width and bone length to distal end width were calculated. Comparison of *Metoposaurus diagnosticus* humeri with those of other species' humeri was undertaken on the basis of observation, description of characters and numerical data.

Recent revisions of the taxa of Metoposauridae family caused changes to the internal systematics of this family. I followed HUNT'S (1993) and SENGUPTA'S (2002) systematics in my work.

3. Results and discussion

3.1. Functional morphology

The short and robust humerus of *Metoposaurus diagnosticus* (Fig. 1) with a poorly-defined shaft reflects the shorter contractile ranges of its respective muscles or group of muscles. It reveals an adaptation to resist bending moments imposed by muscle force converging towards the humerus from various directions, being in tetrahedral shape with twisting flattened

proximal and distal ends common to most primitive tetrapods (GREGORY 1949). Contrary to the constant degree of twist of bone ends in other metoposaur species: 45° – *M. howardensis*, 50° – *B. perfecta*, *B. maleriensis* and *M. ouazzoui* (SAWIN 1945; OLSEN 1951; CHOWDHURY 1965; DUTUIT 1976), the studied humeri reveal striking variations in the divergence of the planes of the bone ends, from 22° to 40° that show no consistent relation to growth (Fig. 2). Such a large scattering of the proximo-distal angle in this species may be a result of low selective pressures on the forelimb performance. The low degree of twist in forelimb bones confirms the fully aquatic mode of *Metoposaurus diagnosticus* (DE FAUW 1989). The surface of the humerus is slightly pitted or smooth with fine striae diverging from the centre of the shaft to both ends. The unfinished ends of the humerus reveal the areas which remained as cartilage in the living animal. Striped proximal articular surfaces are convex but not spirally warped as in the terrestrial labyrinthodont *Eryops* (Fig. 3a), indicating limitation of twisting movements and permitting only rolling movements of the humerus in the shoulder joint (GREGORY 1949; RACKOFF 1980). Situated beneath, on the anterior edge of the proximal part of bone, the well-developed L-shaped *crista deltopectoralis* reveals general metoposauroid patterns (see also Table 1). It never lost the cartilage connection with the upper

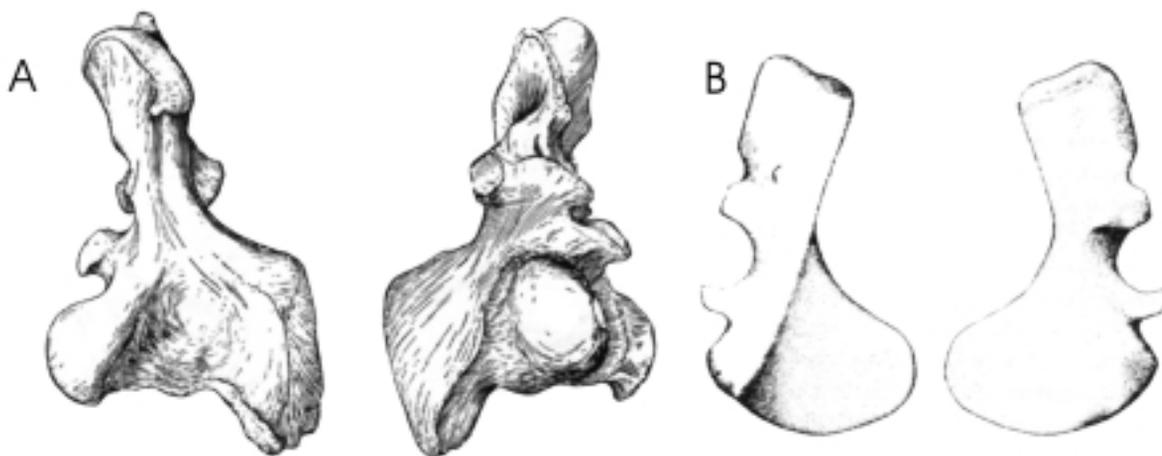


Fig. 3. A – Humerus of *Eryops* (GREGORY, 1949); B – humerus of *Lydekkerina huxleyi* (PAWLEY & WARREN, 2005).

articular surface that occurs in terrestrial forms like the Permo-Carboniferous *Eryops* (GREGORY, 1949) and lower Triassic *Lydekkerina huxleyi* (PAWLEY & WARREN, 2005). Similar conditions can be noted for the *processus supinatorius*, which in *M. diagnosticus* forms a continuous surface with flattened distal end.

In the abovementioned terrestrial forms, it is separated by deep notch from ectepi- to entepicondylus (Fig. 3). These clearly suggest the aquatic condition of the *M. diagnosticus* humerus. The *tuberositas humero-radialis* located in the nearby *crista deltopectoralis* is comprised of rows of ridges set perpendicularly to

Table 2. Measurements of humerus of *Metoposaurus diagnosticus*.

	length of bone	distal width	shaft width	proximal width	twist of bone	length of crista delt.
ZPAL III 804	–	–	24.2	33.2	–	35.3
ZPAL III 822	59.8	–	20.2	28.0	–	23.0
ZPAL III 817	60.7	37.0	20.0	27.1	30	29.1
ZPAL III 815	62.2	–	21.0	24.0	28	28.0
ZPAL III 812	63.6	40.5	20.5	26.5	25	27.8
ZPAL III 821	67.9	–	22.0	–	–	–
ZPAL III 814	68.6	41.4	20.6	34.2	27	26.0
ZPAL III 508	69.5	47.4	23.4	–	–	–
ZPAL III 819	69.5	46.5	22.2	34.0	–	30.1
ZPAL III 806	72.0	45.2	22.2	–	–	–
ZPAL III 330	73.6	50.4	23.9	35.0	40	30.3
ZPAL III 809	74.0	45.7	22.7	–	31	–
ZPAL III 803	74.4	48.0	24.4	36.5	–	29.5
ZPAL III 823	75.0	–	22.1	35.5	22	33.1
ZPAL III 818	76.8	52.1	24.3	34.6	–	36.4
ZPAL III 810	77.2	48.5	24.0	34.0	26	34.0
ZPAL III 805	77.7	49.6	25.2	31.0	38	33.9
ZPAL III 820	77.8	49.4	22.5	–	–	–
ZPAL III 816	81.0	55.3	26.0	–	35	–
ZPAL III 824	85.4	56.0	24.8	39.1	27	37.3
ZPAL III 801	107.4	–	–	51.0	–	52.2
ZPAL III 830	107.5	70.0	32.6	49.2	–	48.0

Fig. 4. Growth series of the right humeri of *Metoposaurus diagnosticus* in dorsal (top) and ventral (bottom) views. The specimen numbers from left to right ZPAL AbIII 817, ZPAL AbIII 806, ZPAL AbIII 803, ZPAL AbIII 818, ZPAL AbIII 810, ZPAL AbIII 816, ZPAL AbIII 824, ZPAL AbIII 830.

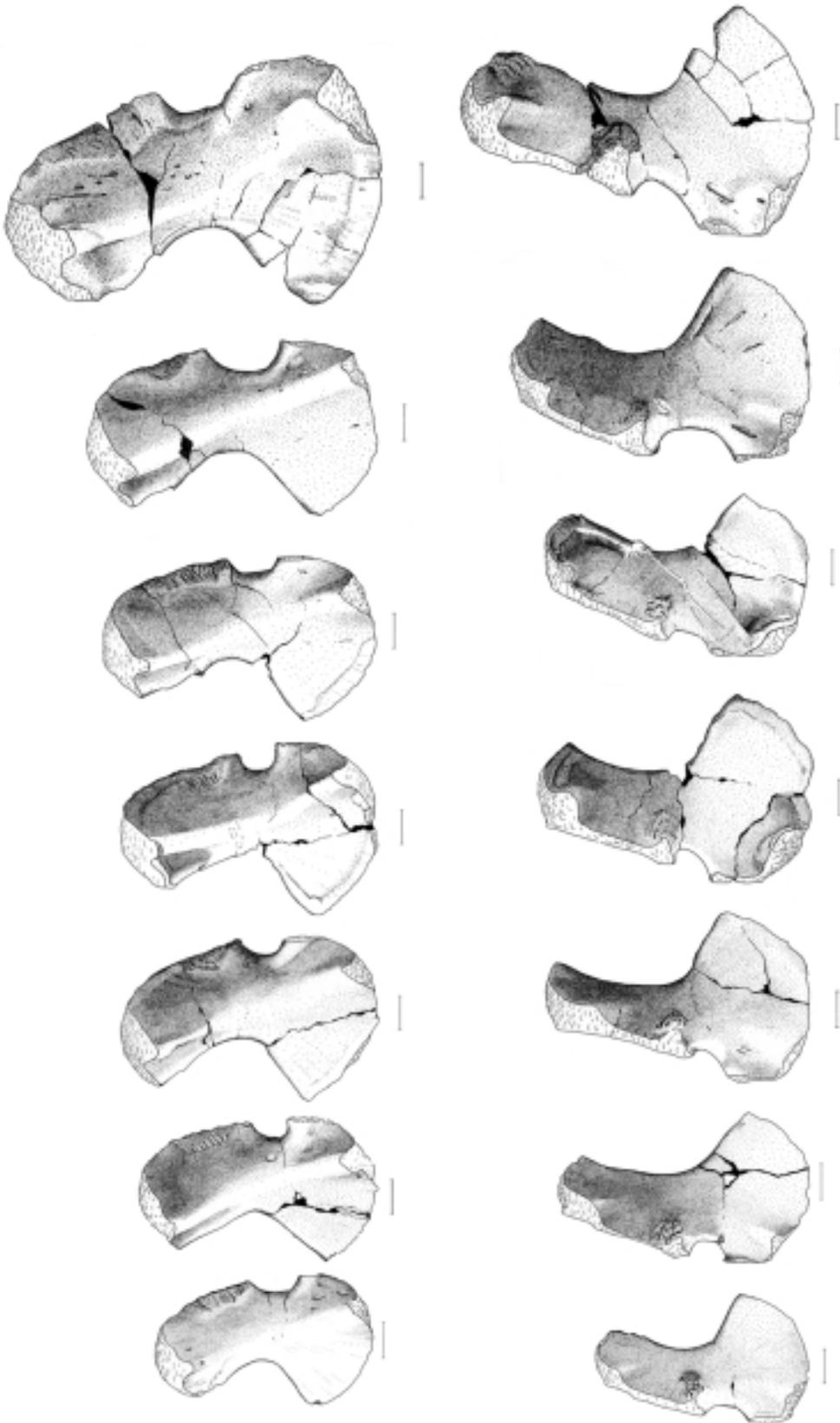


Fig. 4 (Legend see p. 354)

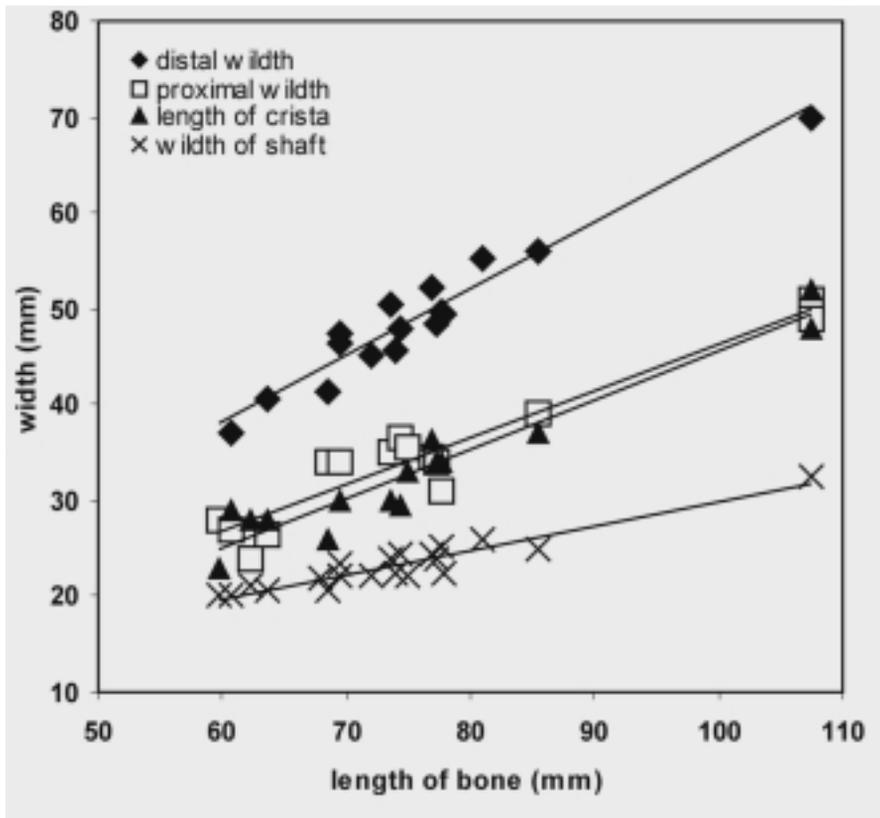


Fig. 5. Ratios of distal width, proximal width, shaft width and length of supinator process to bone length.

the anterior edge. The *processus latissimi*, *crista adductore* and *processus subcoracoscapularis* are visible on the proximal dorsal side, and *processus supinatorius*, *epicondylus lateralis* and large *epicondylus medialis* are visible on distal dorsal (deltoid-supinator-ectepicondyle) side.

The ventral (pectoral) surface bears *tuberculum pectorale* encompassing the shorter ramus of *crista deltopectoralis*, and *tuberculum ventrale* located over. On the distal part of ventral side, the round *condylus radialis* together with *processus supinatorius* and *epicondylus medialis* is seen. The rounded shape of *condylus radialis* suggests the possibility of pronation-supination (rotation) movements of forearm in some degree at least. The curvature of the *condylus radialis* on ventral surfaces indicates the flexed position of forearm. However, the flexion is not as evident as in terrestrial forms (GREGORY 1949; RACKOFF 1980). The more flat and fully distal facet for the ulna limits the flexion. The oblique axis of the elbow flexion developed for effective slow paddling (RACKOFF 1980). Thus, the angle of twist and rotation of distal elements in the arm of *M. diagnosticus* may

suggest that the forearms could be used as some kind of paddles during a slow swim.

3.2. Ontogeny, growth and proportions

The studied humeri belonged to animals at different stages of growth (from 59.8 to 107.5 mm) (Table 2). The absolute size does not necessarily reflect the age of the animal but may in fact be the result of the abundance or scarcity of environmental resources influencing growth (STEYER 2000). The smallest bones are characterized by smooth surfaces (Fig. 4), weakly developed processes, crests and tuberositas, with the exception of the longer ramus of the *processus supinatorius*, *crista deltopectoralis* and *epicondylus medialis*, which are well-defined. The *processus latissimi*, *processus subcoracoscapularis* and *epicondylus lateralis*, somewhat less distinct in small forms, grows to become prominent and well-developed. Tubercle surfaces are covered by sparse pits in small humeri; but in larger bones these pits become more numerous, creating a rugose surface. Small bones have all articular surfaces depressed

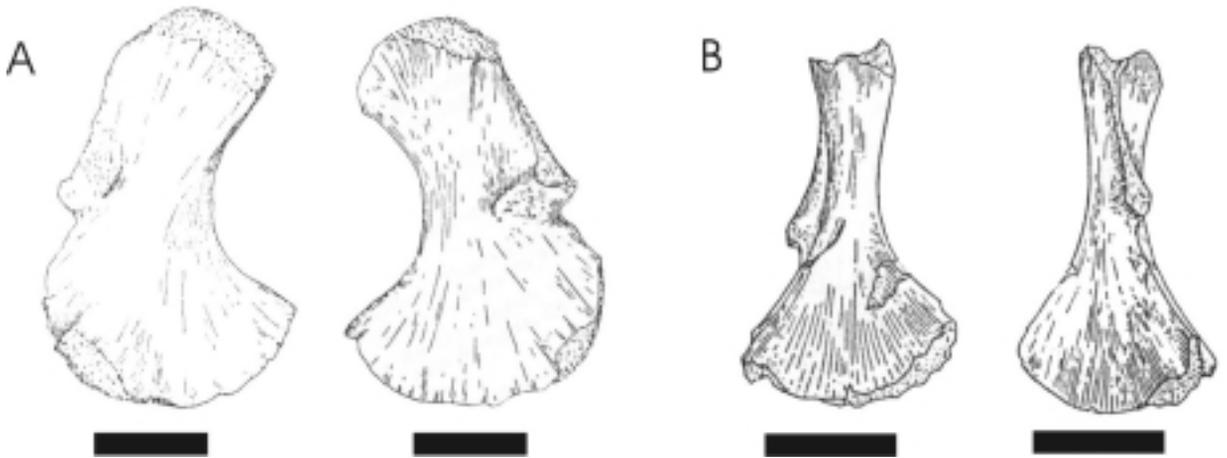


Fig. 6. A – Humerus of *Buettneria perfecta* (CASE 1931); B – humerus of *Buettneria perfecta* (CASE 1932). – Scale bar equals 2 cm.



Fig. 7. Humeri of *Metoposaurus ouazzoui* (DUTUIT, 1976). – Scale bar equals 2 cm.

and roughened similar to the unfinished cartilaginous surfaces of crests and processes, with the exception of the articular surfaces of the *facies articularis scapulocoracoidea*. Depressed articular and unfinished bone surfaces indicate substantial cartilage structure in the living animal. This is characteristic of the bones of juvenile vertebrates, and particularly aquatic forms. During bone growth, the cartilaginous surfaces of the *facies articularis scapulocoracoidea*

and *epicondylus lateralis* become embossed, suggesting a reduction of cartilage thickness.

All structures become more developed with size increase, and the concavities between them become deeper. Enlargement and rounding of the *condylus radialis*, together with expansion of the caudal ventral surface, results in an increased surface for radius articulation. In the biggest bones the origins for the muscles are well-formed and visible. The edges of the

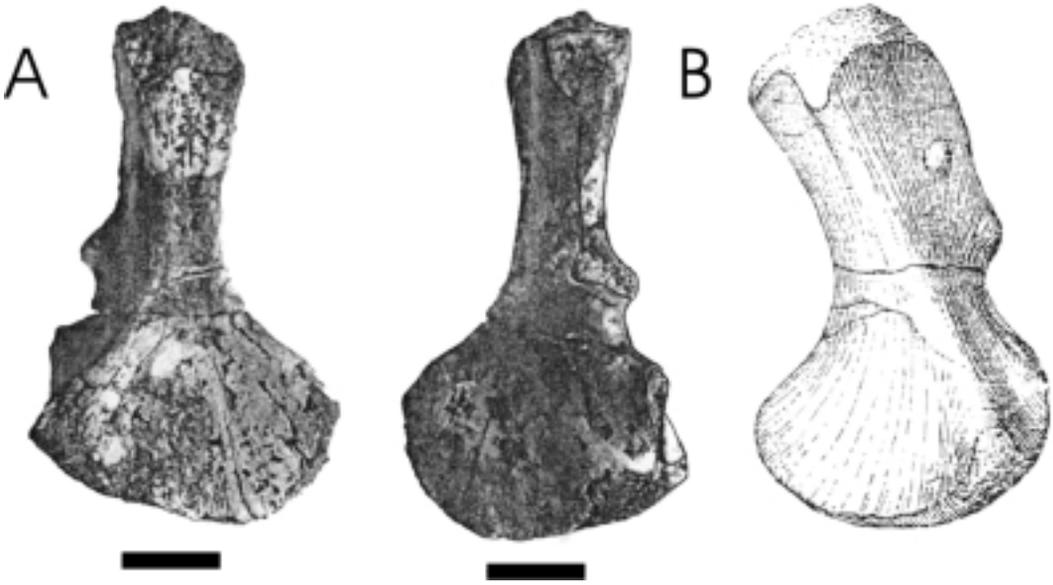


Fig. 8. A – Humerus of *Buettneria maleriensis*; B – humerus of *Buettneria perfecta* (OLSEN 1951). – Scale bar equals 2 cm.

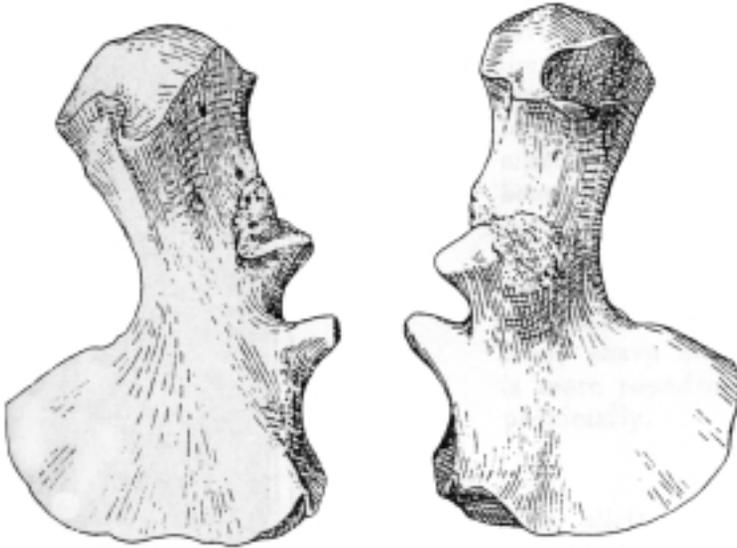


Fig. 9. Humerus of *Metoposaurus howardensis* (SAWIN, 1945). – Bone length equals 118.5 mm.

proximal and distal ends thicken to create a larger area for cartilaginous articular surfaces.

Proportional growth characterizes all bone structure ($y = ax + b$; a = rate of the change of width with respect to length, and b = the intercept of the line). However, each structure may grow at a different rate (Fig. 5). The fastest rate of growth occurs in the width of the distal end of the humerus, which formed the area for the attachments of flexor muscles (on the

epicondylus medialis) and extensor muscles (*epicondylus lateralis*) of the zeugopodium. Bone shafts are characterized by the slowest growth.

4. Comparisons

WARREN & SNELL (1991), in their analysis of the postcranial skeleton of Mesozoic Temnospondyl amphibians, pointed out that the humeri of all Mesozoic

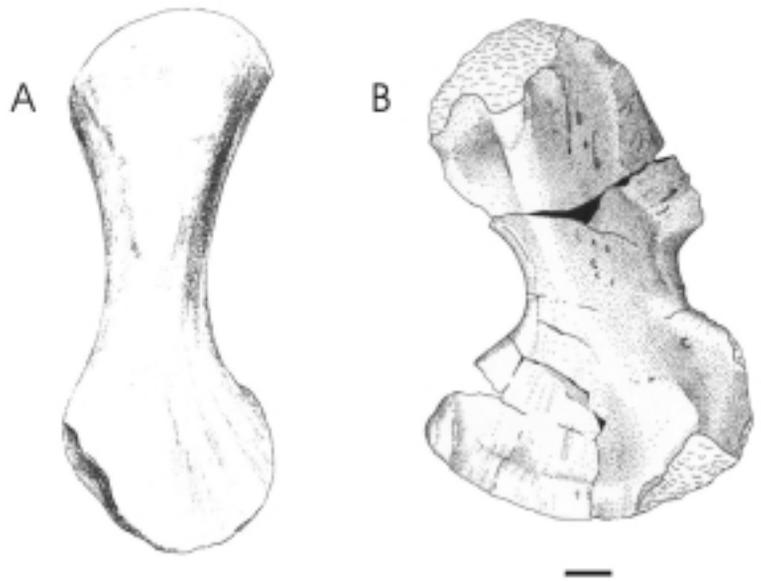


Fig. 10. **A** – Humerus of *Metoposaurus diagnosticus* (FRAAS, 1889); **B** – humerus of *Metoposaurus diagnosticus* from Krasiejow (ZPAL AbIII 830). – Scale bar equals 1 cm.

families except the Metoposauridae possess poorly-developed proximal and distal ends and underdeveloped muscle insertions. The Metoposauroid humerus stands out from the rest of the Mesozoic Temnospondyl taxa humeri by having quite well-ossified proximal and distal ends and protruded muscle insertion. All humeri of compared species agree with the pattern determined by WARREN & SNELL (1991). Nevertheless, they show some interfamilial variation. The studied humeri show an intermediate pattern in those of *Buettneria perfecta* (CASE 1931, 1932). The small *Buettneria perfecta* humeri described by CASE (1931, 1932) are somewhat less ossified, shorter, and have less-developed tuberositas than the studied ones in size comparison (Fig. 6). The middle-sized (about 75 mm long) *M. ouazzoui* humeri (DUTUIT 1976) show a somewhat different pattern of ossification of the *entepicondylus*, *processus supinatorius* and *crista deltopectoralis*, causing the significant differences between the humeri of both species (Fig. 7). However, the larger *M. ouazzoui* humeri (over 110 mm long) are approximate in shape to those of *M. diagnosticus*. The *Buettneria perfecta* humerus described by OLSEN (1951) is more congruent in shape, process and crest condition and proportion to the *M. diagnosticus* ones (Fig. 8b). Likewise, the *B. maleriensis* (Fig. 8a) (SENGUPTA 2002) very closely resemble the shape (however, measured around 90 mm, it is somewhat more slender than the studied humeri). *M. howardensis* (SAWIN, 1945) shows the most outstanding shape

(Fig. 9). Measuring 118.5 mm, it has more robust tuberositas and processes, and the separation of the prominent *processus supinatorius* from the radius' articular surface is well-defined. Likewise, the *crista deltopectoralis* is separated from the cartilage of the proximal articular surface (*facies articularis scapulocoracoidea*). Comparisons of this material with published descriptions of other taxa suggests that the humerus of *Metoposaurus diagnosticus* can be diagnosed by the presence of a well-developed *crista deltopectoralis* connected to the *facies articularis scapulocoracoidea*. The well-developed *processus supinatorius* retains a connection with the *condylus radialis* via a cartilaginous unfinished surface, but lacks a *depressio posteriole* (DUTUIT 1976). The two former features are clearly related to the presumed aquatic life-style of this taxon in contrast to the humerus of the terrestrial *Eryops* (CASE 1911; GREGORY 1949), in which these structures are separated. The unfinished end of the *epiconylus medialis* is always rounded.

Comparisons of the Krasiejów humeri with humerus bone described by FRAAS (1889) manifest the clear differences. In contrast to the Krasiejów humeri, the humerus referred to *Metoposaurus diagnosticus* by FRAAS (1889) differs substantially from others attributed to this family. Its flattened ends are relatively narrower (Fig. 10), the shaft is more clearly defined from the ends and more slender, and its crests and processes barely distinct despite its size (length of

110 mm). This is slightly greater than the length of the largest humerus of the Krasiejów metoposaurs. In FRAAS' (1889) specimen, distal width to humerus length amounts to 45% and the shaft width to the bone length is 23% in contrast to the Krasiejów material where the ratios are 60-68% and 29-34% respectively. WARREN & SNELL (1991) noted these small changes in shape and proportion during humerus growth in Triassic temnospondyls. Hence, such conspicuous differences must reflect phylogenetic rather than ontogenetic variation. The only other described humerus from the Feuerbacher Heide locality belonged to *Mastodontosaurus giganteus*. It is long with narrow ends, in general view more similar to FRAAS' *Metoposaurus* humerus. Such similarity suggests that the humerus described as metoposauroid more probably may have belonged to one of the remaining three *Mastodontosaurus* or one *Cyclotosaurus* species found from the Feuerbacher Heide locality.

5. Conclusions

The studied humeri reveal characteristics typical of metoposauroid humeri, such as good ossification, wide, flattened ends and well-developed *processus supinatorius*, and *crista deltopectoralis*. The low degree of bone twist, the shape of the humeral head (that allows only for rolling movements), the oblique position of the *condylus radialis* and the narrow ulna articulation indicates the paddle usage of forelimb. Although metoposauroid humeri have never been used for species-level diagnoses, comparison with other members of the family suggests that they may operate diagnostically at the family level. Lack of metoposauroid characters excludes the FRAAS' (1889) specimen from the *M. diagnosticus* species and even from the Metoposauridae. It requires a revision and new identification. Further study of the elements of proximal and distal limb and vertebrae may well contribute significant data about the locomotion of metoposaurids as well as about their evolution.

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Appendix

Table 1. Revised terminology of the humerus of Temnospondyli, with new terms asterisked (*).

extremitas proximalis	facies articularis scapulocoracoidea ¹
	tuberculum ventrale ²
	processus subcoracoscapularis ³
	crista adductore ⁴
	depressio postero-dorsale ⁵
	processus latissimi ⁶
	linea postero-lateralis ⁷
	crista deltopectoralis ⁸
	tuberositas humeroradialis ⁹
	tuberculum pectorale ¹⁰
corpus humeri	
	incisura cranialis*
extremitas distalis	
	condylus radialis ¹¹
	facies articularis ulnaris
	epicondylus medialis, entepicondylus ¹²
	epicondylus lateralis, ectepicondylus ¹³
	depressio epicondylaris ¹⁴
	processus supinatorius ¹⁵

¹ Commonly referred to as caput humeri (NILSON 1939; GREGORY 1949). However, this term is misleading because the temnospondyls (and many other non-mammals) do not have any structure comparable to the mammalian caput humeri that is proximally defined by a column.

² Synonym: eminentia coracobrachialis brevis (NILSON 1939).

³ Based on ROMER (1922, 1956).

^{4,5,10} Following DUTUIT (1976).

⁶ An abbreviation of processus latissimi dorsi (MINER 1925; NILSON 1939).

⁷ Based on NILSSON (1939). Synonym: bord posterior (DUTUIT 1976).

⁸ Synonym: eminentia deltopectoralis (NILSON 1939).

⁹ Based on ROMER (1956: fig. 163).

¹¹ Based on NILSSON (1939). Synonyms: radial tuberosity (CASE 1931), epicondylus radialis (BYSTROW 1938).

¹² Synonyms: entepicondylar process CASE (1931), CHOWDHURY (1965), epicondylus ulnaris (BYSTROW & EFREMOV 1940).

¹³ Synonyms: ectepicondylar process (CASE 1931), extensor crest HOLMES (1977), crista radialis (BYSTROW & EFREMOV 1940), radial column (SCHOCH 1999).

¹⁴ Gouttiere ectepicondylenne (DUTUIT 1976).

¹⁵ Following the majority of authors (MINER 1925; SAWIN 1945; NILSON 1939; GREGORY 1949; DUTUIT 1976; WARREN & SNELL 1991; SENGUPTA 1995; SCHOCH 1999; KLEMBARA 2000). Synonyms: crista supinatoria (ROMER 1922, 1956; HOWIE 1970), epicondylus radialis (BYSTROW & EFREMOV 1940).