Species discrimination of the Late Triassic temnospondyl amphibian *Metoposaurus diagnosticus*

TOMASZ SULEJ

Sulej, T. 2002. Species discrimination of the Late Triassic temnospondyl amphibian *Metoposaurus diagnosticus*. *Acta Palaeontologica Polonica* 47 (3): 535–546.

Re-investigation of the skull roof in *Metoposaurus diagnosticus* from the German Middle Keuper revealed that in contrast to previous opinions, the lacrimal bone in this species enters the orbital margin. The same pattern is demonstrated by the skulls of a newly discovered metoposaur from the Keuper of Krasiejów in Poland. The difference in the shape of the parietal between the population from Krasiejów and the type population of *Metoposaurus diagnosticus* enables the discrimination of two separate subspecies within *Metoposaurus diagnosticus*. For the specimens from the Late Carnian of Drawno Beds at Krasiejów, Poland and its lateral equivalents Lehrberg Beds at Stuttgart-Sonnenberg and Kieselsandstein at Fichtenberg, Germany, a new chronosubspecies *Metoposaurus diagnosticus krasiejowensis* is erected. The new subspecies differs from the older nominal subspecies *M. diagnosticus diagnosticus* in having a shorter and wider prepineal part of the parietal. If one accepts that the nominal subspecies is the ancestor of *M. krasiejowensis* the change in the shape of the parietal would be a reversal of the trend towards elongating postorbital part of the skull observed in ancestors of the metoposaurids. It seems that the skull development in ontogeny changed after the anterior shift of the orbits occurred in the phylogenetic history of the metoposaurids. The difference in ornamentation of the interclavicle between European *Metoposaurus* and North American genera is corroborated by Polish material.

Key words: Amphibia, Temnospondyli, Metoposauridae, *Metoposaurus*, Triassic, Poland.

Tomasz Sulej [sulej@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

Metoposaurids are Late Triassic temnospondyl amphibians characterized by anteriorly located orbits and cylindrical intercentra. They are known from many localities in North America, Africa, Europe, and India (Fraas 1913; Chowdhury 1965; Hunt 1993; Dutuit 1978; Sengupta 1992; Jalil 1996). The earliest species is known from the Late Carnian (Schilfsandstein) of Germany, and the latest one from the Early Norian of Arizona, New Mexico, and Texas (Hunt 1989). The first named metoposaurid was *Metopias diagnosticus*, described by Meyer (1842). Fraas (1889) published a more extensive description of the species, based on additional material. Because *Metopias* was preoccupied by a coleopteran genus, Lydekker (1890) erected the name *Metoposaurus*. A detailed history of the study on metoposaurids was presented by Hunt (1993).

A new Central European locality containing metoposaurs has been recently discovered at Krasiejów in the Opole Silesia, Poland (Dzik et al. 2000). The fossil-bearing level corresponds to Drawno Beds and is probably coeval with the Lehrberg Beds in the western part of Germanic Basin. The material from Krasiejów shed new light on the metoposaurid morphology that was used to discriminate the taxa within this family.

Until recently, the taxonomy of the Metoposauridae was based mainly on the position of the lacrimal, as well as on the shape and pattern of the sculpture of clavicles and interclavicles (Colbert and Imbrie 1956; Hunt 1993). Along with studies on the new metoposaurid materials from Krasiejów (see Dzik et al. 2000 for a preliminary report; Dzik 2001), I examined the specimens housed in Staatlisches Museum für Naturkunde in Stuttgart. Earlier views on morphology of the lacrimal, as a feature of taxonomic value (Fraas 1889; Hunt 1993), have not been confirmed. The purpose of this paper is to present a new interpretation of cranial characters of the holotype of *Metoposaurus diagnosticus* and to compare the metoposaurids from various European localities. Detailed description of the skull and postcranial skeleton of new metoposaurids from Krasiejów will be published at a later date.

Institutional abbreviations.—NHM, Natural History Museum, London; PMJ-P, Phyletisches Museum Jena, Jena; SMNS, Staatlisches Museum für Naturkunde, Stuttgart; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; WT, West Texas State collection; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Material

The data presented in this paper are based on material from several localities in Germany and one locality in Poland. The first specimen, the original of Meyer (1842), catalogued as

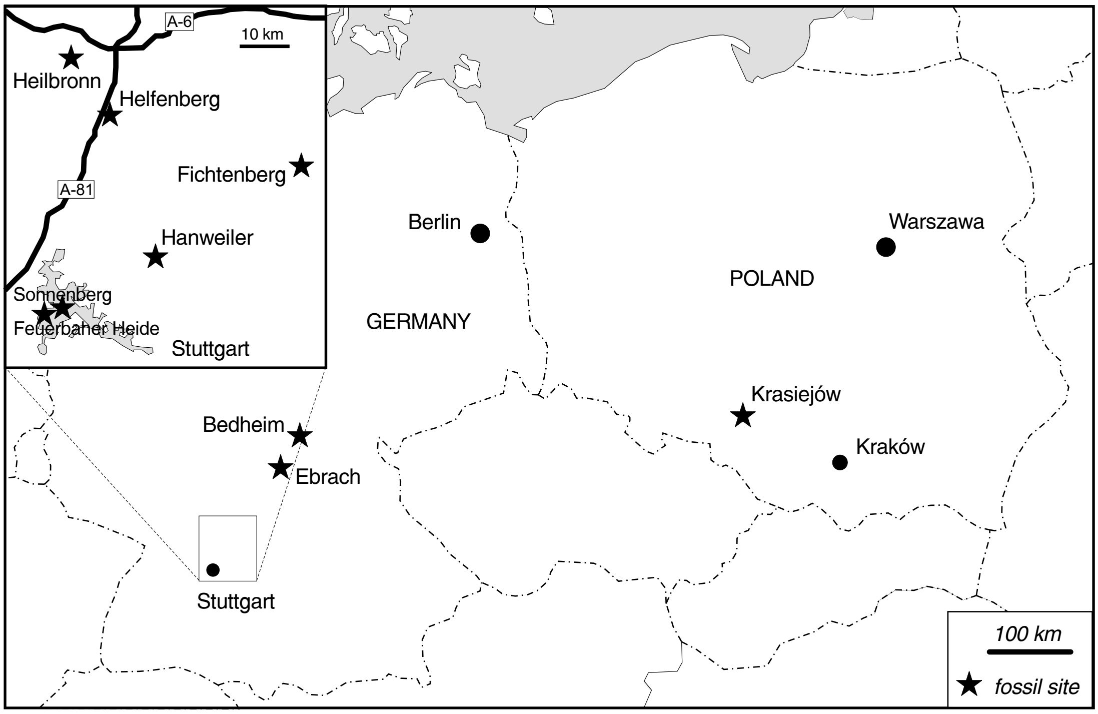

Fig. 1. Metoposaurid-bearing localities in Central Europe.

SMNS 10825 from Baden-Württemberg, was found in the early nineteenth century. Numerous fossils from Poland studied herein, from Krasiejów in the Opole Silesia, have been excavated there since 1993 (Dzik et al. 2000). At this new locality, which is still being excaveted, metoposaurids occur in marly clays as disarticulated or partially articulated bones. However, completely articulated skeletons of phytosaurs were found at this locality, and finding of articulated metoposaurid specimens in future appears possible. So far only one articulated specimen of *Metoposaurus diagnosticus* from Hanweiler Germany in the SMNS collection (without number) is available.

I examined the following specimens (grouped below according to the local lithostratigraphic units of the Middle Keuper from which they were collected):

Schilfsandstein: SMNS 10825—an almost complete skull with articulated jaws, from Feuerbacher Heide (Fig. 1), the holotype of *Metoposaurus diagnosticus* Meyer, 1842. SMNS without number—a skull articulated with pectoral girdle and partial vertebral column from Hanweiler, described as *Metoposaurus diagnosticus* by Fraas (1889). SMNS 4943—an incomplete skull in sandstone from Feuerbacher Heide labeled *Metoposaurus diagnosticus*. SMNS 1010—an almost complete skull roof with a fragment of the left ramus of the lower jaw preserved in sandstone; in the skull, only the ventral side of its roof is visible; same locality and labeling.

Rote Wand (Untere Bunte Mergel): SMNS 56633—a complete small skull (17.5 cm long) embedded in plastic (only the skull roof can be seen) from A.88 NE Helfenberg (Seegis 1997), labelled *Metoposaurus diagnosticus*.

Lehrberg Beds: SMNS 11423—an impression of a part of the interclavicle, from Stuttgart, district “Stadt Stuttgart” in the area of Sonnenberg street, described as *Metoposaurus stuttgartiensis* by Fraas (1889).

Kieselsandstein: SMNS 80573—an impression of the part of a skull roof in sandstone, from NW of Fichtenberg, labeled *Metoposaurus* sp. indet.

The collection from Krasiejów in Poland consists of complete skulls ZPAL Ab III 10, 116, 358, 681, 682, 683, 684, and 689; almost complete skulls ZPAL Ab III 3, 4, 11, and 318; postorbital parts of skulls ZPAL Ab III 6; a preorbital skull fragment ZPAL Ab III 13 and 537. The dermal elements of the shoulder girdle include incomplete interclavicles ZPAL Ab III 90, 91, 92, 117, 122, and 314; a complete interclavicle ZPAL Ab III 317; incomplete clavicles ZPAL Ab III 72, 87, and 143; and almost complete clavicles ZPAL Ab III 306 and 333.

Comparison of European and North American metoposaurids

In Europe, metoposaurids occur in the Middle Keuper (Late Carnian) strata beginning from the Schilfsandstein (Fraas 1889) up to the Blasensandstein (Kuhn 1932). Several species were erected for specimens from Germany: *Metoposaurus diagnosticus* Fraas, 1889 from the Schilfsandstein, *M. stuttgartiensis* Fraas, 1913 from the Lehrberg Beds, and *M. heimi* Kuhn, 1932 from the Blasensandstein (see Table 1). Although Hunt (1993) and Schoch and Milner (2000) classified *M. stuttgartiensis* and *M. heimi* as indeterminate metoposaurids, I follow Colbert and Imbrie (1956) in recognizing

Table. 1. Synonymy of species belonging to the Metoposauridae discussed in the text.

First description	Colbert and Imbrie 1956	Chowdhury 1965	Hunt 1993	This paper
Metoposaurus diagnosticus Meyer, 1842	*Metoposaurus diagnosticus* Meyer, 1842; Keuper, central Europe	*Metoposaurus diagnosticus* Meyer, 1842; Keuper, central Europe	*Metoposaurus diagnosticus* Meyer, 1842 in part: *Buettneria perfecta* Case, 1922	*Metoposaurus diagnosticus* Meyer, 1842
Metoposaurus stuttgartiensis Fraas, 1913			Metoposauridae indet.	
Metoposaurus heimi Kuhn, 1932			Metoposauridae indet	
Metoposaurus santaecrucis Koken, 1913			Family ?Metoposauridae	*Nomen dubium*
Trigonosternum latum Schmidt, 1931		*Nomen dubium*	Temnospondyli ndet	
Calamops paludosus Sinclair, 1917	*Eupelor durus* Cope, 1866; Newark Group, Pennsylvania, New Jersey	*Metoposaurus durus* (Cope, 1866); Newark Group, North America	Temnospondyli indet.	?
Buettneria major Branson and Mehl, 1929	*Eupelor fraasi fraasi* (Lucas, 1904); Chinle Formation, Arizona, New Mexico, Utah	*Metoposaurus fraasi fraasi* (Lucas, 1904); Chinle Formation, North America	*Buettneria perfecta* Case, 1922	*Buettneria perfecta* Case, 1922
Kalamoiketor pinkleyi Branson and Mehl, 1929			?*Apachesaurus gregorii* Hunt, 1993	?*Apachesaurus gregorii* Hunt, 1993
Metoposaurus fraasi Lucas, 1904			Metoposauridae indet.	?
Metoposaurus jonesi Case, 1920	*Eupelor fraasi jonesi* (Case, 1922); Dockum Formation, Texas	—	Metoposauridae indet.	?
Buettneria bakeri Case, 1931		*Metoposaurus fraasi jonesi* (Case, 1922); Dockum Formation, North America	*Metoposaurus bakeri* (Case, 1931)	*Buettneria bakeri* Case, 1931
Buettneria perfecta Case, 1922 *Buettneria howardiensis* Sawin, 1945			*Buettneria perfecta* Case, 1922	*Buettneria perfecta* Case, 1922
		Metoposaurus maleriensis Chowdhury, 1965; Maleri Formation, India		
Borborophagus wyomingensis Branson and Mehl, 1929 *Koskinonodon princeps* Branson and Mehl, 1929	*Eupelor browni* (Branson, 1905); Popo Agie Formation, Wyoming	*Metoposaurus browni* (Branson, 1905); Popo Agie Formation, North America		
Anaschisma sp. (in part: Gregory, 1980)			*Apachesaurus* sp. Hunt, 1993	*Apachesaurus* sp. Hunt, 1993
Anaschisma brachygnatha Branson, 1905			Metoposauridae indet.	?
Anaschisma browni Branson, 1905			Metoposauridae indet.	?
Dictyocephalus elegans Leidy, 1856	*Dictyocephalus elegans* Leidy, 1856; Newark Group, North Carolina	*Nomen dubium*	Temnospondyli indet.	?
Metoposaurus ouazzoui Dutuit, 1976; Argana Formation, Morocco			*Dutuitosaurus ouazzoui* (Dutuit, 1976); Argana Formation, Morocco	*Dutuitosaurus ouazzoui* (Dutuit, 1976); Argana Formation, Morocco
Metoposaurus azerouali Dutuit, 1976; Argana Formation, Morocco			Metoposauridae indet.	?
Metoposaurus lyazidi Dutuit, 1976; Argana Formation, Morocco			*Arganasaurus lyazidi* (Dutuit, 1976); Argana Formation, Morocco	*Arganasaurus lyazidi* (Dutuit, 1976); Argana Formation, Morocco

them as *M. diagnosticus* (see below). Hunt (1993) assigned the skull of *Metoposaurus diagnosticus* from Schilfsandstein, stored in NHM, to *Buettneria perfecta,* but arguments against this are presented below. There are few reports on metoposaurids from Europe outside Germany: "*Metopias*" *diagnosticus* for fossils from the Rhaetic Penarth Group of Aust Cliff, England (Miall 1875, cited after Hunt 1993) which are probably lost, and "*Metopias*" *santaecrucis* Koken, 1913 from the upper Raibl beds, Austria. I agree with Hunt (1993) and Schoch and Milner (2000) who questioned this affiliation and considered the species a *nomen dubium*.

It follows that all the identifiable metoposaurid remains from Europe may belong to a single species—*Metoposaurus diagnosticus*. The unusually good state of preservation of the fossils from Krasiejów enables a more detailed comparison of the European and American materials.

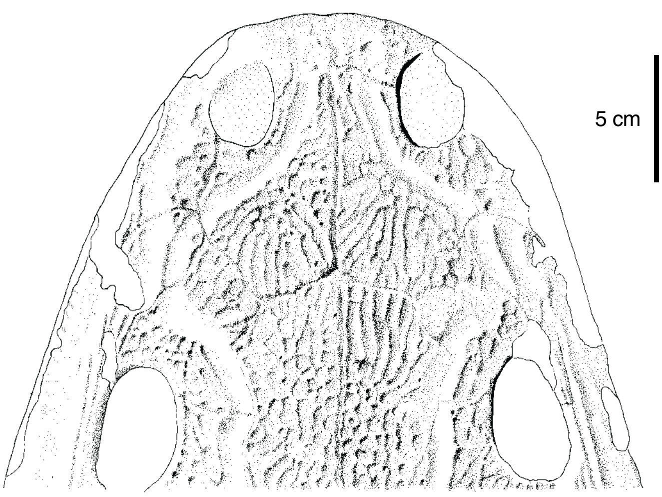

Fig. 2. *Metoposaurus diagnosticus diagnosticus* Meyer, 1842. The anterior part of the skull SMNS 10825, the holotype. Schilfsandstein at Feuerbacher Heide near Stuttgart.

Colbert and Imbrie (1956) reviewed data on the American species and compared them with European metoposaurids. They recognized four species from America (Table 1). Hunt (1993) proposed a different approach and recognized three species: *Buettneria perfecta* Case, 1922 from the locality Sand Creek, Crosby County, Texas; *Buettneria bakeri* Case, 1931 from the Camp Springs Member of the Dockum Formation, Texas; and a new species *Apachesaurus gregorii* Hunt, 1993 from a locality in Quay County, New Mexico. They differ primarily in the position of the lacrimal, as far as the skull roof pattern is concerned. In all the papers on the taxonomy of the Metoposauridae, this feature has been recognized as important.

The lacrimal.—It has been generally believed that within the Metoposauridae the species differ in the relative position of the lacrimal with respect to the orbit. Fraas (1889) described *Metoposaurus diagnosticus* as having the lacrimal excluded from the orbital margin. The skulls of *M. diagnosticus* from Stuttgart and Ebrach housed at SMNS show that the shape and position of the lacrimal as interpreted by Fraas (1889) are not accurate. The new well-preserved metoposaurid material from Krasiejów discussed here helps to determine the actual condition of this character.

In the holotype of *M. diagnosticus* SMNS 10825, the sutures of the lacrimal are only partly visible (Fig. 2). The sutures of the lacrimal with the prefrontal, the nasal, and partially with the maxilla are well preserved on both sides of the skull. On the left side, the lateral border of the prefrontal reaches the orbital margin in its anterolateral quarter. The preservation of the bones (lacrimal or/and jugal), which contact with the prefrontal at this border, is poor. The lacrimal-jugal suture is not recognizable, so it remains unknown whether it reaches the prefrontal or the orbital margin. On the right side, the margin of the prefrontal is preserved, but its termination at the orbital margin is not visible. On this side the lacrimal-jugal suture is visible as an indistinct furrow, which runs at a low angle to the margin of the orbit, as in other skulls from Germany and Krasiejów. The lacrimal contributes a little less than a quarter to the orbital margin (Figs. 2, 3). It is longer than it is wide and extends anteromedially. The anterior part of the lacrimal is sutured to the nasal and the maxilla, and is wider than the posterior part of the bone. Its posterior tip is spindle-shaped with the external edge contacting the jugal.

In SMNS 80573, an impression of the right lacrimal is visible on the left side. The sutures with the prefrontal, the nasal, and the jugal are preserved in negative relief as narrow, continuous grooves. The edge of the impression probably corresponds to the lacrimal-maxilla suture. The lacrimal-jugal suture runs at a low angle to the margin of the orbit. The lacrimal-prefrontal suture reaches the orbital margin in its most anterior part. Posteromedial border of the lacrimal contributes to significant part of the anterolateral quarter of the orbital margin.

On the left side of SMNS 56633 the lacrimal is poorly preserved; on the right side its sutures with the prefrontal, the nasal, and partially with the jugal are visible. The lacrimal-jugal suture runs at a low angle to the margin of the orbit. Only the termination of the lacrimal-prefrontal suture on the orbital margin is preserved. The lacrimal contributes to a small part of the anterolateral quarter of the orbital margin.The almost complete skull of a metoposaurid from Feuerbacher Heide, Schilfsandstein, housed in the Natural History

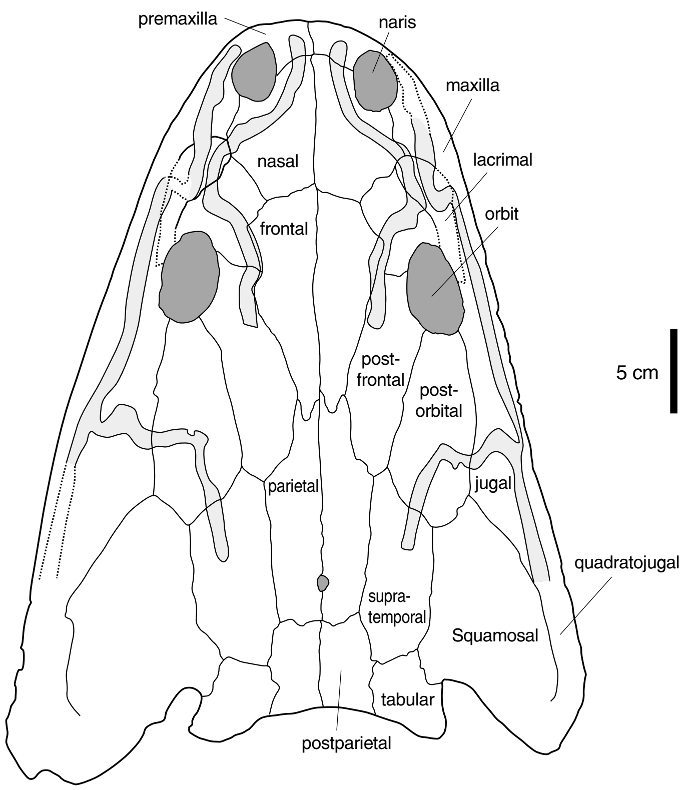

Fig. 3. *Metoposaurus diagnosticus diagnosticus* Meyer, 1842. The dorsal view of the skull SMNS 10825, the holotype. Note the shape of the lacrimal. Schilfsandstein at Feuerbacher Heide near Stuttgart.

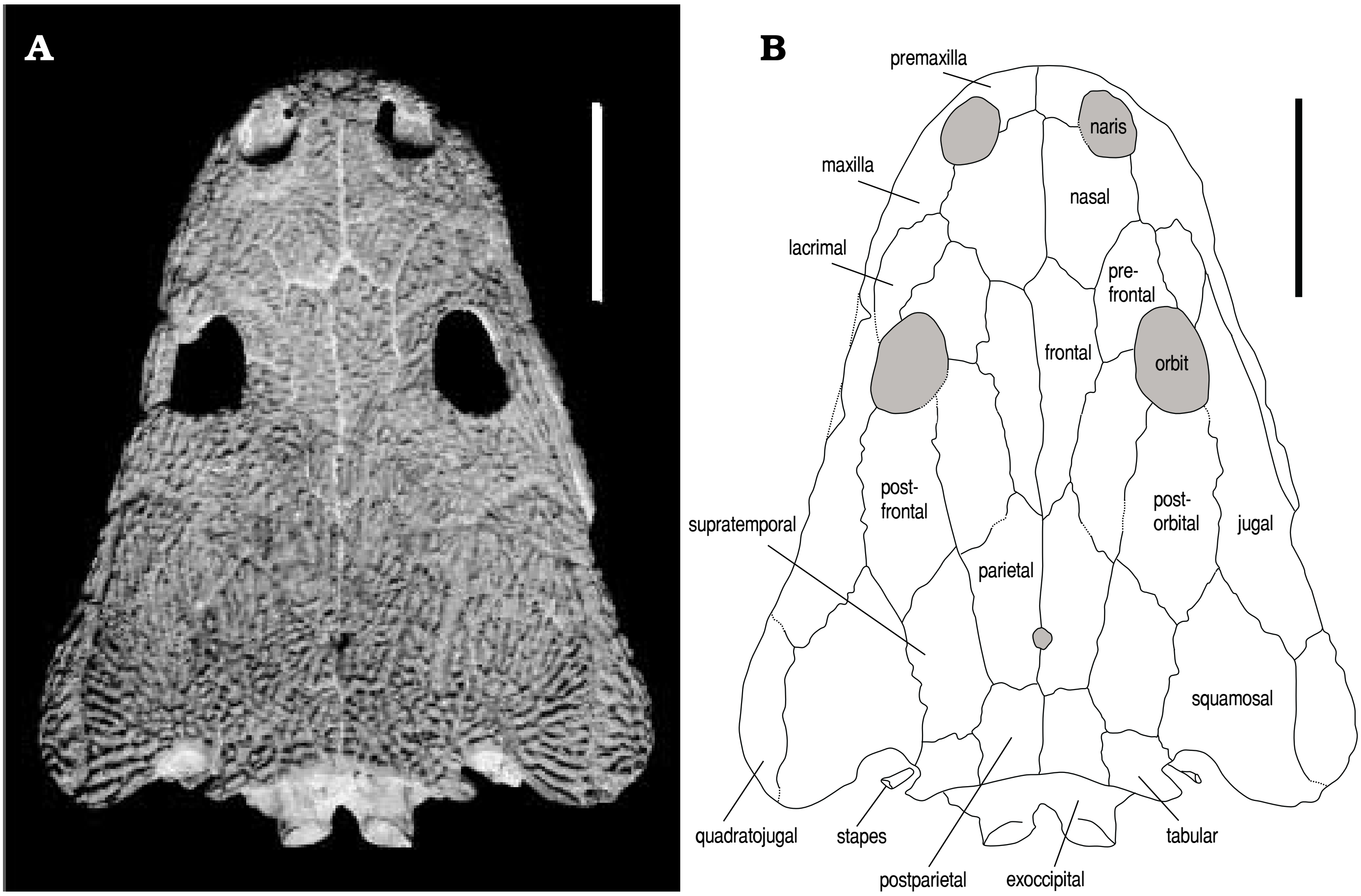

Fig. 4. *Metoposaurus diagnosticus krasiejowensis* subsp. nov. **A**. The skull roof ZPAL Ab III 358, the holotype. **B**. Explanatory drawing of the same. Drawno Beds at Krasiejów. Scale bars 10 cm.

Museum, London (Watson 1919) was identified by Lyddeker (1890) as *M. diagnosticus*. I have not had an opportunity to examine this specimen (NHM 37938), but its photograph published by Hunt (1993) shows that the lacrimal enters the orbit. Hunt (1993) identified it as *Buettneria perfecta* based on this feature considered by him to be diagnostic for the genus. Schoch and Milner (2000) attributed it to *Metoposaurus* sp., but they questioned the origin of this skull. In fact, the shape and position of the lacrimal is the same as in the holotype of *M. diagnosticus*.

In the material from Krasiejów, the lacrimal is visible in ZPAL Ab III 11, 13, 358, 682, 684, and 688. The shape of the lacrimal is presented in Fig. 4. The variability of this feature is low and the specimens do not differ in this respect from the holotype of *Metoposaurus diagnosticus*.

These data on the morphology of the lacrimal of *Metoposaurus diagnosticus* challenge the opinions presented by earlier authors. Fraas (1889) wrote that in *M. diagnosticus* the lacrimal is completely excluded from the edge of the orbit, and that plate of the lacrimal is wider than long and resembles in form and size the lacrimal of *Cyclotosaurus*. The skulls of metoposaurids studied by Fraas were poorly preserved and it is possible that he might have based his interpretation of the shape of the lacrimal largely on his knowledge of the much better preserved cyclotosaur fossils.

New evidence obtained from both the holotype of *M. diagnosticus* and the metoposaur skulls from Krasiejów, along with previously known data on the pattern of the lacrimal in the specimen SNMS 37 probably from the Schilfsandstein, indicate that in all European metoposaurs the lacrimal enters the orbital margin. They do not differ in this respect from the populations of *Buettneria perfecta* Case, 1922 (*sensu* Hunt 1993) from North America. This feature distinguishes all these populations from *Buettneria bakeri* Case, 1931 and *Apachesaurus gregorii* Hunt, 1993 of North America, and from *Dutuitosaurus ouazzoui* (Dutuit, 1976) and *Arganasaurus lyazidi* (Dutuit, 1976) from Morocco (Hunt 1993); their lacrimal is excluded from the orbital margin. The new data on the lacrimal topography in European *Metoposaurus* appear to invalidate Hunt's conclusions about the generic status of American *B. bakeri*, as well as his attribution of the skull SMNS 37 from the British Museum collection to *Buettneria.* In this light, the actual generic status of the Indian *Metoposaurus maleriensis*, also assigned by Hunt to *Buettneria*, remains open to question.

The clavicle.—Colbert and Imbrie (1956) pointed out the ex-

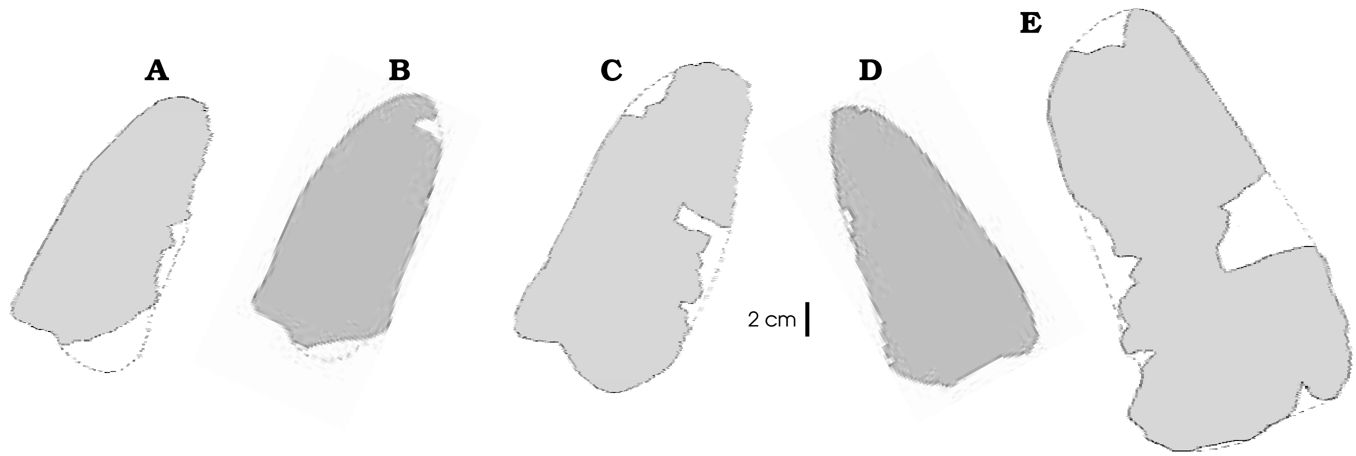

Fig. 5. *Metoposaurus diagnosticus krasiejowensis* subsp. nov. Contours of the clavicle plates (in ventral view) restored in natural position (anterior is up). **A**. ZPAL Ab III 306. **B**. ZPAL Ab III 72. **C**. ZPAL Ab III 333. **D**. ZPAL Ab III 143. **E**. ZPAL Ab III 87.

tent of contact of the clavicles as a feature differentiating the Old World species from the North American ones. My studies on the material from Krasiejów and a comparison with the morphology of the clavicles of *Buettneria bakeri* (Case 1931) challenge this conclusion. The only complete clavicles of *Metoposaurus diagnosticus* from Germany belong to the articulated unnumbered specimen from SMNS described by Fraas (1889). The clavicles touch each other at their anterior part. The contact line is long and straight, begining at the anterior part of the clavicle and ending where the clavicles separate from each other and a sculptured area of the interclavicle begins. Such a long medial contact is quite exceptional among the Metoposauridae.

Unfortunately, articulated shoulder girdles are very rare and any assessment of the patterns of clavicular median contact may be made only indirectly, based on the shape of the clavicle plate. The clavicles from Krasiejów show a great degree of variation (Figs. 5). Specimens ZPAL Ab III 143 have their medial edges almost straight (long medial contact) and the anterior parts of the plate are relatively narrow. In ZPAL Ab III 87 and 333, the anterior part is relatively wide, while in ZPAL Ab III 306 the anterior part of the medial edge is concave. Accordingly, the contact of the clavicle with its counterpart in the specimens from Krasiejów in most cases appears to be rather short (Fig. 6).

Hunt (1993) and Long and Murry (1995) recognized the long and straight contact of clavicles in *M. diagnosticus* as diagnostic for this species. However, the metoposaurids from North America exhibit a great diversity of the shape of the clavicle plate. For instance, the shape of the contact of the posterior part of the clavicle plate with the interclavicle is very variable in *Buettneria bakeri* (Case 1932: pls. IV–VII). This contact may be a straight line as in UMMP 13912, or the medial edge of posterior part may have a swelling. This cannot be an expression of sexual dimorphism as there are transitions between these extremes. Additionally the shape of the anterior part of the clavicle plate is variable in *B. bakeri*. It may end very sharply, as in the clavicle UMMP 13895, which is rather narrow or it may be obtuse and much wider (UMMP 13903). The lateral edge of the clavicle may also vary. It can be straight (UMMP 13824), or curved as in UMMP 13895 (Case 1932). Such diversity appears to characterize all the species of the Metoposauridae.

Colbert and Imbrie (1956: fig. 11) presented clavicle plates of three species of metoposaurs that differ from one another. The authors indicated this as the difference between *M. diagnosticus* and the American species. The first has “lines of contact” with clavicles of the opposite side, whereas the second has “points of contact”. Although the difference is obvious, Colbert and Imbrie (1956) did not recognize it as diagnostic, probably in the light of the extensive variability of this feature in other metoposaurids. It seems that the reconstruction of the pectoral girdle of cf. *Metoposaurus diagnosticus* with a short contact of clavicles presented by Werneburg (1990) is accurate for the European metoposaurids. Five clavicles studied from Krasiejów show that the contact with their counterparts differs from that proposed for *M. diagnosticus* by earlier authors. There are two morphological variants of the anterior part of the clavicle plate, narrow and wide (Fig. 5). However, the sample is still too small to allow anything more than to note that the shape of the clavicle plate is variable in the material from Krasiejów, and short contact is more common, as in other genera of Metoposauridae. The extent of variation in the German subspecies remains unknown (although, on general grounds, the shorter contact is supposed to be more common). This indicates that the shape of the anterior part of the clavicle plate cannot be used to distinguish the European and American species.

The interclavicle.—Among the metoposaurids, the interclavicle has two kinds of ornamentation on the ventral side. The middle of the bone is covered with rounded and hexagonal depressions, and the rest of sculptured area is covered with radial grooves. The shape of the sculpture of the inter-

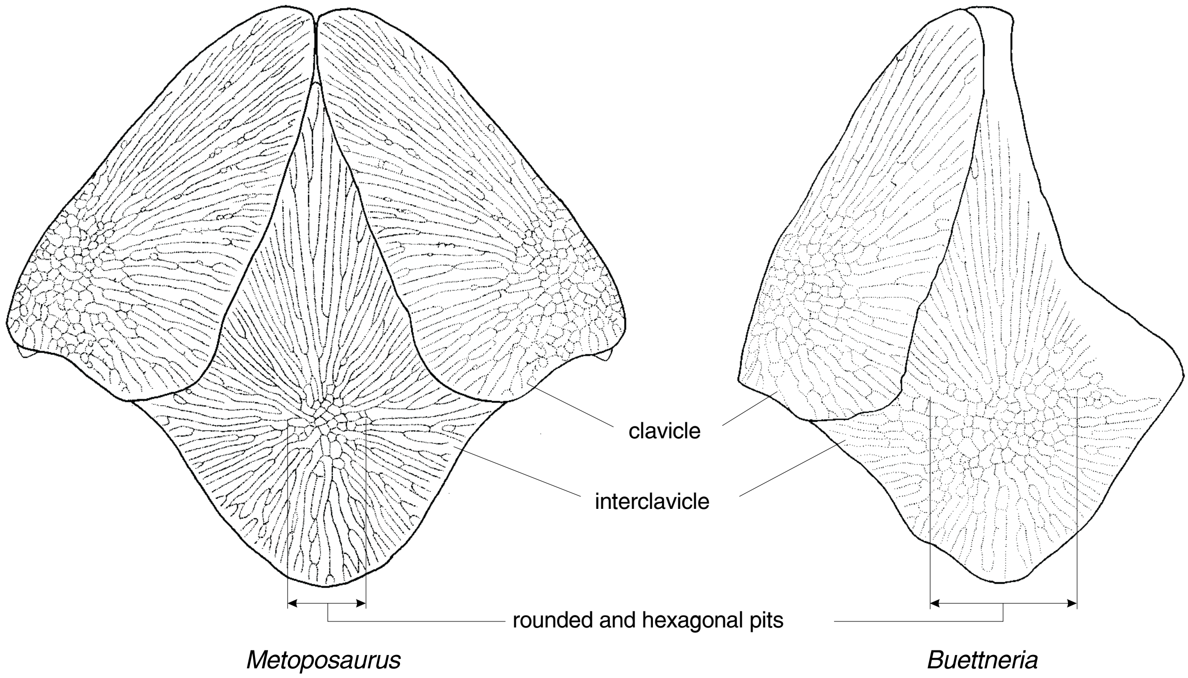

Fig. 6. The reconstructions of pectoral girdle of *Metoposaurus* from Europe (based on Ab III 333 clacivula and Ab III 317 inter clavicula) and *Buettneria* (without the left clavicle; based on Hunt 1993: fig. 9B, WT uncatalogued) from North America and India. Comparison of patterns of the sculpture of interclavicles, and position of the clavicles.

clavicle was used to separate the Old World metoposaurids from those of the New World; Colbert and Imbrie (1956: 428) stated: "[…] In *Metoposaurus* of Europe there is a very small area of rounded or hexagonal depressions at the very middle of the interclavicle, and from this area long grooves radiate laterally to all edges of the bone. In American metoposaurs, on the other hand, the area of rounded pits is of considerable extent, and the development of long grooves extending radially to the edges of the bone is correspondingly reduced". Hunt (1993), and Long and Murry (1995) acknowledged that this character distinguishes *Metoposaurus* from the American species *Buettneria* and *Apachesaurus*. This agrees with my observations on the material from Krasiejów and Germany (Figs. 6–8).

The interclavicles from Germany and Poland come from various horizons. Specimens from Poland were found in one horizon at Krasiejów (coeval with the Lehrberg Beds) and as their variability is continuous, they must belong to a single species. The interclavicles from Germany come from the Schilfsandstein, the Lehrberg Beds, and the Blasensandstein and were determined as *Metoposaurus diagnosticus* (Colbert and Imbrie 1956; Kuhn 1936; Werneburg 1990, 1991). The interclavicles from Poland and Germany belong to the same species.

The course of the lateral line grooves in the skull.—In all photographs of *M. diagnosticus* presented by Fraas (1889) the supraorbital groove ends on the postfrontal. Additionally, Moodie (1908) described *M. diagnosticus* with such morphology of these grooves. However, Colbert and Imbrie (1956) illustrated *M. diagnosticus* with the supraorbital groove connected with postorbital groove. Milner (1994) used this feature to recognize *Metoposaurus* as the oldest grade of the family. The material from Poland and studies of the German metoposaurids show that in *Metoposaurus diagnosticus* the supraorbital groove actually ends on the postfrontal (Fig. 3) and does not contact the postorbital groove.

Case (1922) claimed that a continuous lateral-line loop behind the orbits is present in *Buettneria perfecta*. However in many published photographs (for instance, Hunt 1993: figs. 7 and 8) and drawings (Sawin 1945: figs. 2 and 3), the grooves discussed are typically disconnected in this species. According to Moodie (1908), in *Anaschizma browni* (Metoposauridae indet. of Hunt 1993) the presence of such a loop depends on the age of the individual. Of the two skulls studied by him, only the larger one shows a connection between the supraorbital and postorbital grooves. Such a connection of grooves occurs in many temnospondyls and it seems that the American materials require revision in this respect.

Possible interrelationships of European metoposaurs

Because some species from North America have a closed loop of the lateral line grooves around the orbits, this may be a feature distinguishing European metoposaurids from some American ones. The lateral line grooves, ornamentation of the interclavicle, and position of the lacrimal are the same in

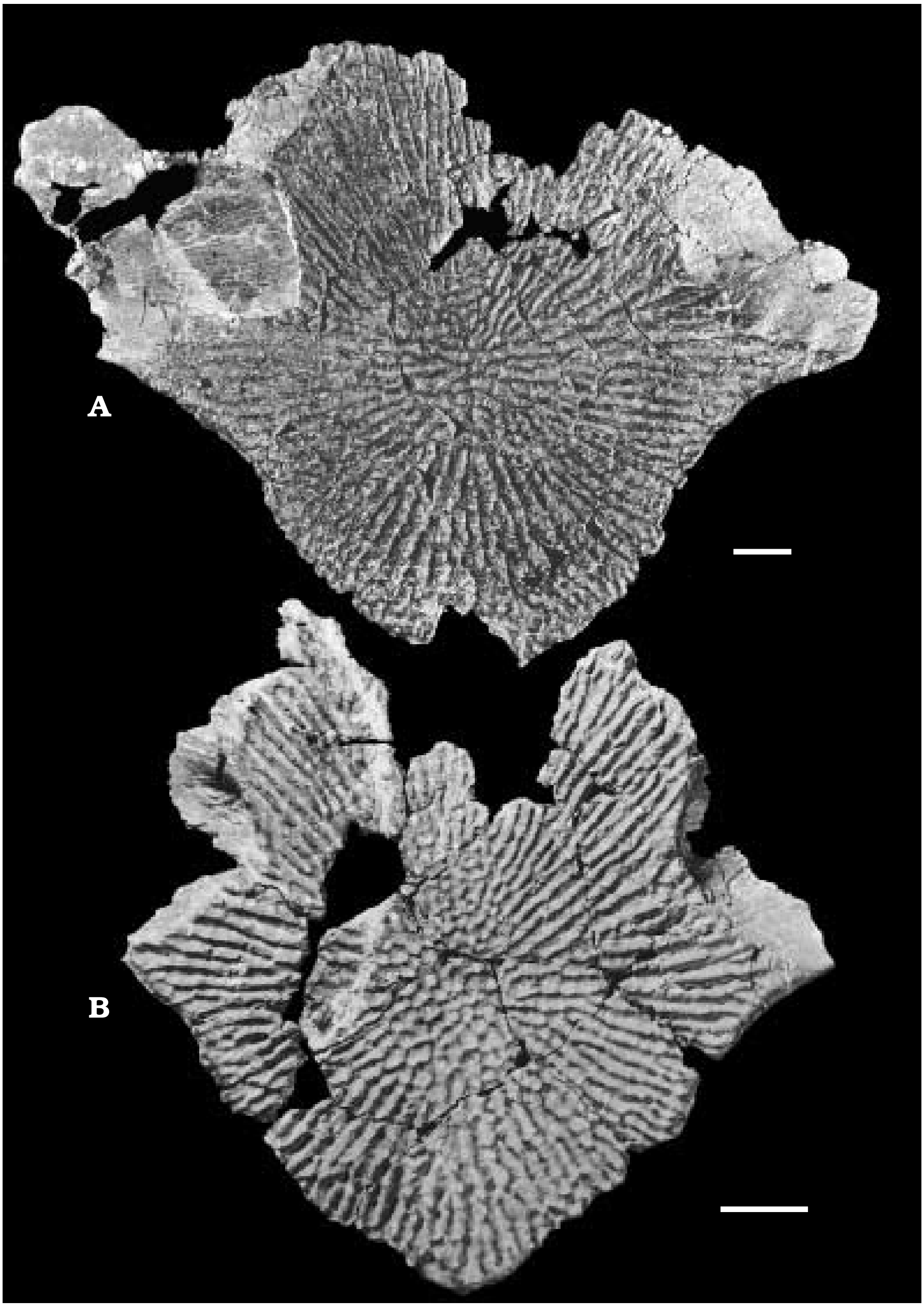

Fig. 7. *Metoposaurus diagnosticus krasiejowensis* subsp. nov. Ventral side of the interclavicle. **A**. ZPAL Ab III 92. **B**. ZPAL Ab III 90 Drawno Beds at Krasiejów. In both specimens, the small area with pitted ornament is visible. In this respect the European metoposaurids differ from those from North America. Scale bars 2 cm.

all populations from Europe, but there are still some differences with respect to at least one character of the skull dermal roof between the populations from Germany and Poland. As was mentioned above, the metoposaurids from the German Keuper are known from the stratigraphic interval spanning the Schilfsandstein, Rote Wand, Lehrberg Beds, and Kieselsandstein with its equivalents, whereas Polish finds come from the level correlated by Dzik et al. (2000) with the Lehrberg Beds. The only difference detectable at the present state of knowledge is the shape of the parietals. Possible implications of this difference are discussed below.

The parietal.—Populations of metoposaurids from Germanic Basin show differences in the expansion angle of the

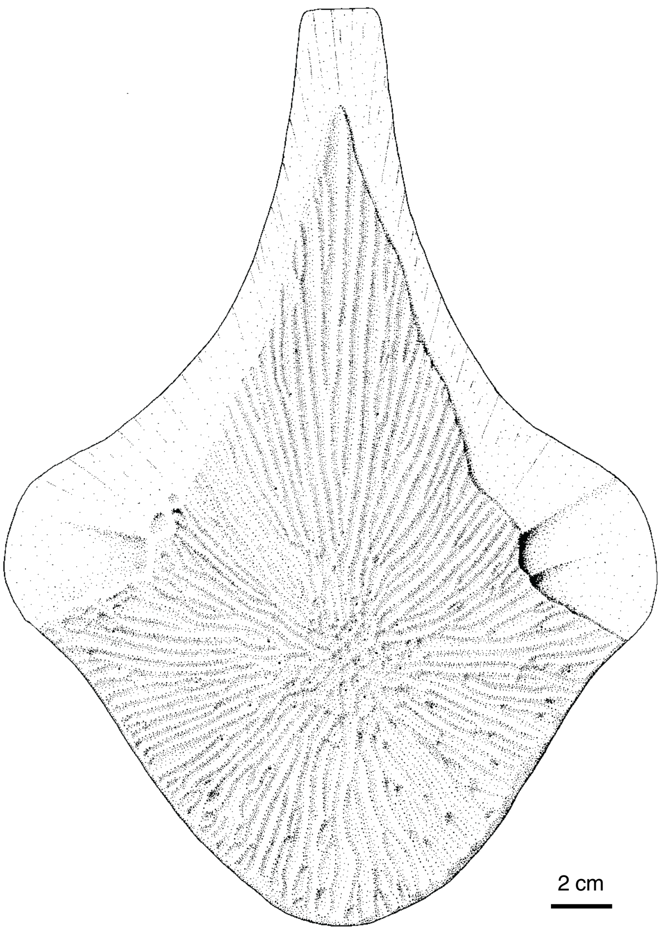

Fig. 8. Reconstruction of the interclavicle of *Metoposaurus diagnosticus krasiejowensis* subsp. nov. in ventral view. The drawing based on ZPAL Ab III 317.

sutures separating the parietal from the supratemporals (from now on called “the angle of the parietal”) and in the length of the prepineal part of the parietal.

The values of the parietal angle cluster in two groups (Figs. 9 and 10). In skulls from Würtembergs (Schilfsandstein, Rote Wand and Kieselsandstein) the mean value of the angle is 12°42’ (standard deviation 3°30’), while for those from Krasiejów it is 22°30’ (standard deviation 2°18’). This feature probably does not change during ontogeny, as there is no correspondence with developmental stages, as indicated by the width of skulls. The length of the parietal of the skull from Kieselsandstein is similar to those from Krasiejów in that they have shorter parietals than the populations from Schilfsandstein and Rote Wand (Fig. 10B). It seems that the length of the parietal is more important (as will be explained below) in distinguishing the European metoposaurs and discrimination of their two populations (Fig. 10A). Older population contains the skulls from Schilfsandstein and Rote Wand. They have mean values of the parietal angle of 12°48’ (standard deviation 3°54’), while those from Krasiejów and Kieselsandstein 21°48’ (standard deviation 3°30’). The skull from Blasensandstein (equivalent of Kieselsandstein) at Ebrach, which Kuhn (1932) labeled *M. heimi*, was not included into this comparison, because I had no opportunity to study it.

Developmental interpretation.—In temnospondyls the skulls of adult specimens have two kinds of ornamentation of the dermal bones (Säve-Söderbergh 1937). There are isometric pits and grooves. The isometric pits cover the whole skull roof in juvenile individuals (Warren and Hutchinson 1988) and only some parts in adults. In advanced trematosauroids (*sensu* Schoch and Milner 2000) grooves occur in adults mainly in two zones, between the orbits and nares and behind the orbits. The grooves develop during ontogeny in zones where bones grow extensively in length. The proportions between preorbital and postorbital zones of intense growth changed during the evolution of the group. Along the phylogenetic lineage from the platystegids to metoposaurids (Schoch and Milner 2000), the postorbital zone increases whereas the preorbital zone decreases, resulting in a shift of orbits towards the tip of the snout. The prepineal part of the parietal contributes to the postorbital zone (Fig. 11). The observed differences in the development of this part of the skull

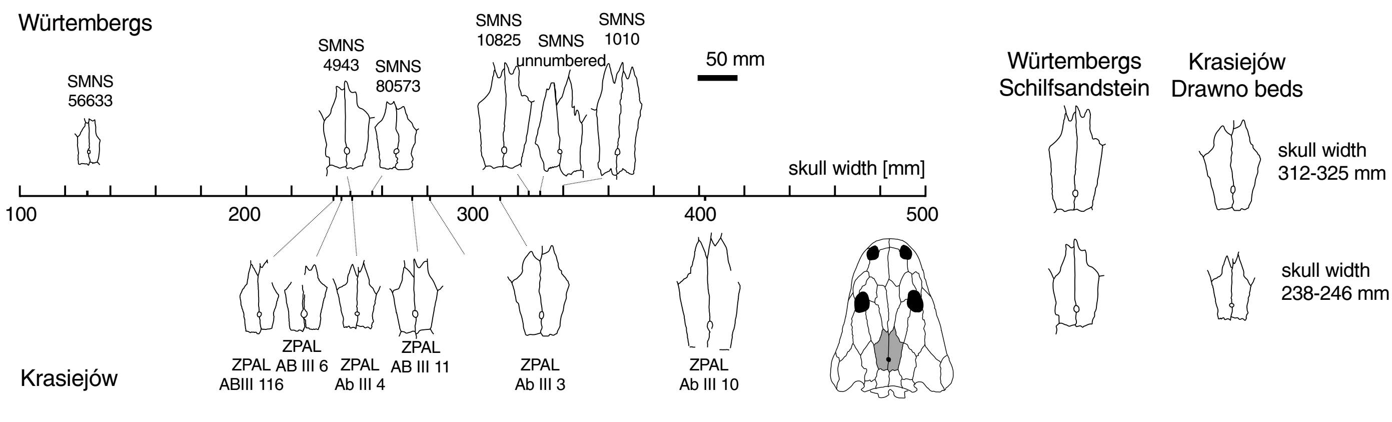

Fig. 9. Shapes of parietals in specimens of *Metoposaurus diagnosticus diagnosticus* (from Würtembergs) and *Metoposaurus diagnosticus krasiejowensis* subsp. nov. (from Krasiejów). The bones are according to the skull width as an indication of ontogenetic advancement. On the right are shown the parietals from skulls of similar width.

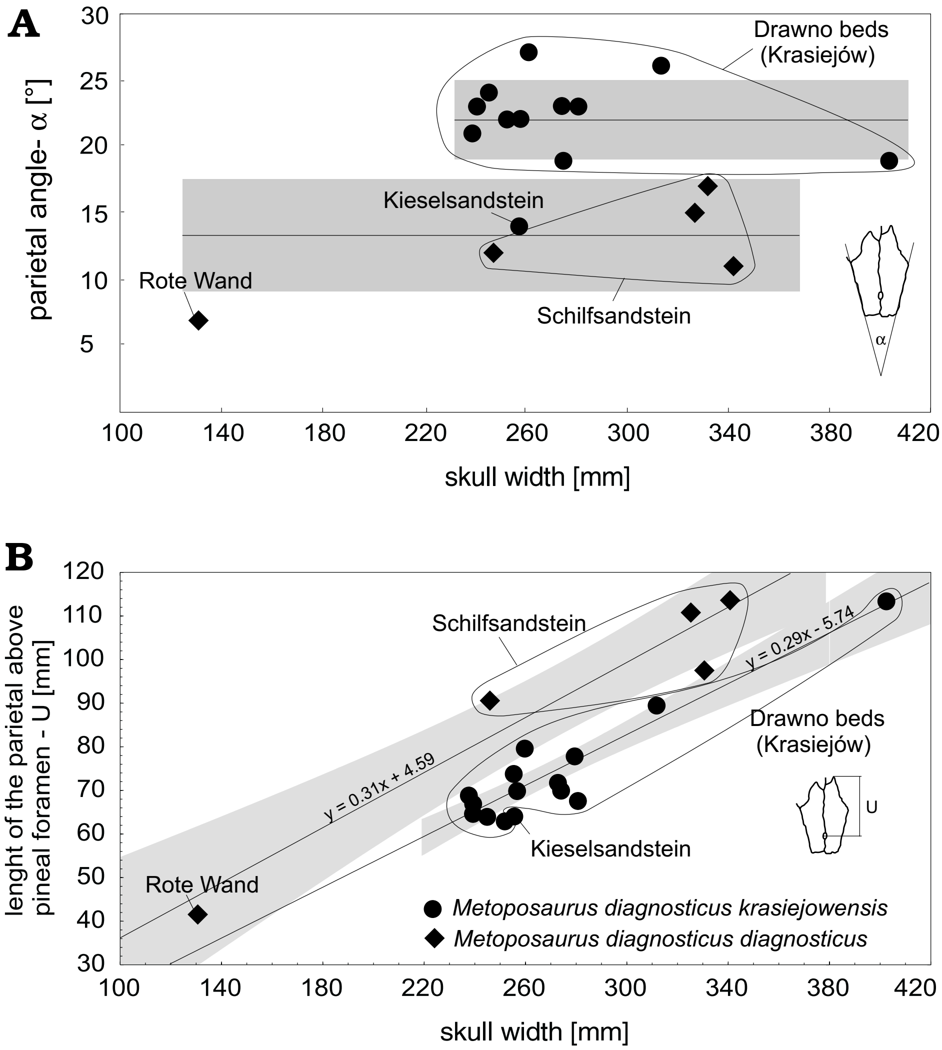

Fig. 10. Scatterplots of the angle of forward widening of the parietal (**A**) and length of the prepineal part of the parietal (**B**) against values for skull width for specimens of *Metoposaurus diagnosticus diagnosticus* (diamonds) and *Metoposaurus diagnosticus krasiejowensis* (dots). For skulls SMNS 4943 and SMNS 80573 the width was extrapolated from the distance between the orbit and otic notch according to the proportions of other skulls from Germany.

in European metoposaurids may express the evolution of this pattern. These changes probably affected the whole skull, but the material from Germany is too fragmentary to determine this with certainty.

The origin of such distinction within the European metoposaurids is not clear. The difference in the value of parietal angle separates the populations from the western and eastern parts of the Germanic Basin and may require a biogeographic explanation. However, the differences in the length of this bone indicate a change that reflects chronological variation rather than spatial variation. The younger population from Krasiejów and Kieselsandstein has shorter prepineal part of the parietal and a wider anterior part (greater parietal angle). This may indicate that, in comparison to their ancestors from the Schilfsandstein and Rote Wand, postorbital zone of extensive growth developed more in width than in length. This would be a reversal of the earlier trend to elongate the postorbital part of the skull observed in phylogenetic history of the metoposaurids. It appears that the ontogeny of the skull changed after the anterior shift of the orbits occurred in the group's evolution.

The difference between the population from Krasiejów and the type population of *Metoposaurus diagnosticus* is so great that standard deviations from the mean do not overlap (Fig. 10). This enables the discrimination of two separate subspecies within the species *Metoposaurus diagnosticus*. The material from Germany is too scarce to clarify if these were temporal subspecies or geographical races. The choice between these interpretations depends on one skull from the Kieselsandstein. It seems that the temporal explanation is methodologically more parsimonious, because the introduction of geographical races would require the identification of geographical barrier that separated the ranges of the subspecies.

Conclusions and diagnosis of the new taxon

Only one species of the stereospondyl family Metoposauridae is known from the Middle Keuper of Central Eu-

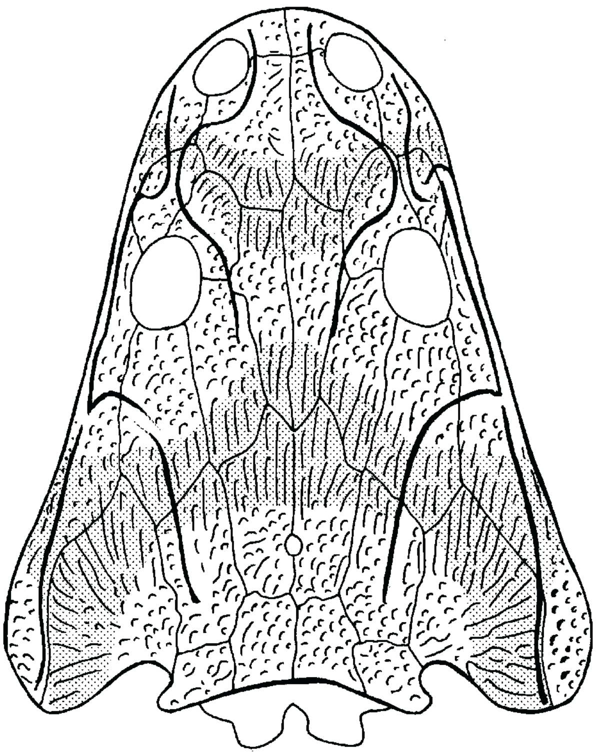

Fig. 11. *Metoposaurus diagnosticus krasiejowensis* subsp. nov. Schematic presentation of the distribution of zones of intense growth (shaded).

rope, *Metoposaurus diagnosticus*. It had the lacrimal entering the orbit, the supraorbital groove terminating on the postfrontal, and a rather small area with pitted ornament in the middle of the interclavicle. It is possible to distinguish two subspecies, one geologically older, occurring in the Schilfsandstein and Rote Wand, and the other, occurring in the Kieselsandstein, Lehrberg Beds and their equivalent Drawno Beds. They differ mostly in the degree of elongation of the prepineal zone of the parietals. A new subspecies *Metoposaurus diagnosticus krasiejowensis* is proposed for the younger subspecies.

Temnospondyli Zittel, 1888
Stereospondyli Fraas, 1889
Family Metoposauridae Watson, 1919
Genus *Metoposaurus* Lydekker, 1890

Metopias Miall, 1875.
Buettneria in part: Hunt 1993; Hunt 1993: 78–79, fig. 8.

Revised diagnosis.—*Metoposaurus* differs from *Apachesaurus* Hunt, 1993; *Arganasaurus* Hunt, 1993; *Dutuitosaurus* Hunt, 1993; and *Buettneria bakeri* Case, 1931 in the position of the lacrimal which enters the orbital margin. It differs from *Buettneria* Case, 1922 and *Apachesaurus* Hunt, 1993 in the smaller area with sculpture formed by the isometric pits of the interclavicle. It is a monotypic genus with a single species *Metoposaurus diagnosticus* represented by two subspecies.

Metoposaurus diagnosticus von Meyer, 1842

Metoposaurus stuttgartiensis Fraas, 1913.
Metoposaurus heimi Kuhn, 1932.
Buettneria perfecta in part: Hunt 1993; Hunt 1993: 78–79, fig. 8.

Metoposaurus diagnosticus krasiejowensis subsp. nov.

Holotype: ZPAL Ab III 358, Fig. 4.

Type locality: Krasiejów, Opole Silesia, Poland.

Type horizon: Late Carnian, probably Drawno Beds coeval to the Lehrberg Beds of Germany.

Diagnosis.—The new subspecies differs from the nominal *Metoposaurus diagnosticus diagnosticus* in the much shorter prepineal part of the parietal and in the higher value of the expansion angle of the sutures separating the parietal from the supratemporal. The mean value for the angle is 21.81 (standard deviation 3.51), in contrast with the mean value 12.81 (standard deviation 3.91) in the nominal subspecies. Ontogenetically, the length of the parietal follows the regression formula $y = 0.29x - 5.74$ in the new subspecies, in contrast with $y = 0.31x + 4.59$ in the nominal subspecies (y, length of prepineal part of parietal; x, skull width).

Etymology.—From the name of the village Krasiejów, the type locality.

Refered specimens.—Drawno beds (Krasiejów) all studied materials specimens, Lehrberg beds (Stuttgart) SMNS 11423, and Kieselsandstein (Fichtenberg) SMNS 80573.

Acknowledgements

I would like to thank Jerzy Dzik for discussions about metoposaurid morphology and for his great help in preparing the text. I thank Magdalena Borsuk-Białynicka and Mieczysław Wolsan for comments on an earlier version of the text and Christine Janis for linguistic help. I am grateful to Rupert Wild (Stuttgart) for providing access to specimens in the SMNS collection and for information concerning the localities. Excavation in Krasiejów was sponsored by grants KBN 6PO4D 072 19 (to M. Borsuk-Białynicka) and Górażdże Cement SA.

References

Case, E.C. 1922. New reptiles and stegocephalians from Upper Triassic of western Texas. *Carnegie Institution of Washington Publications* 321: 1–84.

Case, E.C. 1931. Description of a new species of *Buettneria* with a discussion of brain case. *Contribution from the Museum of Paleontology, University of Michigan* 3: 187–206.

Case, E.C. 1932. A collection of stegocephalians from Scurre County, Texas. *Contributions from the Museum of Paleontology, University of Michigan* 4: 227– 274.

Chowdhury, T.R. 1965. A new metoposauroid amphibian from the Upper Triassic Maleri Formation of Central India. *Philosophical Transactions of the Royal Society London B* 250: 1–52.

Colbert, E.H. and Imbrie, J. 1956. Triassic metoposaurid amphibians. *Bulletin of the American Museum of Natural History* 110: 403–452.

Dutuit, J.M. 1976. Introduction à l'étude paléontologique du Trias continental marocain. Description des premiers Stegocephales recueillis dans le couloir d'Argana (Atlas occidental). *Memoires du Museum National d'Histoire naturelle, Paris. Series C* 36: 1–253.

Dutuit, J.M. 1978. Descripion de quelques fragments osseux provenant de la région de Folakara (Trias supérieur Malagache). *Bulletin de Museum Nationale d'Histoire naturelle, Paris. Series III* 516: 79–89.

Dzik, J., Sulej, T., Kaim, A., and Niedźwiedzki, R. 2000. Późnotriasowe cmentarzysko kręgowców lądowych w Krasiejowie na Śląsku Opolskim. *Przegląd Geologiczny* 48: 226–235.

Dzik, J. 2001. A new *Paleorhinus* fauna in the Early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 21: 625–627.

Fraas, E. 1889. Die Labyrinthodonten aus der Schwäbischen Trias. *Palaeontographica* 36: 1–158.

Fraas, E. 1913. Neue Labyrinthodonten aus der Schwäbischen Tias. *Palaeontographica* 60: 275–294.

Hunt, A.P. 1989. Comments on the taxonomy of North American metoposaurs and a preliminary phylogenetic analysis of the family Metoposauridae. *In*: S.G. Lucas and A.P. Hunt (eds.), *Dawn of the Age of Dinosaurs in the American Southwest*, 293–300. New Mexico Museum of Natural History, Albuquerque.

Hunt, A.P. 1993. Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from Western North America. *In*: M. Morales (eds.), Aspects of Mesozoic Geology and Paleontology of the Colorado Plateau. *Museum of Northern Arizona Bulletin* 59: 67–97.

Jalil, N.E. 1996. Les Vertébrés permiens et triasiques de la Formation d'Argana (Haut Atlas occidental): liste faunique préliminaire et implications stratigaphiques. *In*: F. Medina (eds.), *Le Permien et le Trias du Maroc: état des connaissance*, 227–250. Editions Pumag, Marrakech.

Koken, E. 1913. Beiträge zur Kenntnis der Schichten von Heiligenkreuz (Abteital, Südtirol). *Abhandlungen der Kaiserlich-Koniglichen Geologischen Reichsanstalt* 16: 1–44.

Kuhn, O. 1932. Labyrinthodonten und Parasuchier aus dem mittleren Keuper von Ebrach in Oberfranken. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. Abteilung B* 69: 94–144.

Kuhn, O. 1936. Weitere Parasuchier und Labyrinthodonten aus dem Blasensandstein des Mittleren Keuper von Ebrach. *Palaeontographica, Abteilung A* 83: 61–98.

Long, R.A. and Murry, P.A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *Bulletin of the New Mexico Museum of Natural History and Science* 4: 1–254.

Lydekker, R. 1890. *Catalogue of the fossil Reptilia and Amphibia in the British Museum of Natural History.* Part IV. 295 pp. British Museum of Natural History, London.

Meyer, E. 1842. Labyrinthodonten-Genera. *Neues Jahrbuch für Mineralogie, Geographie, Geologie, Paläeontologie* 1842: 301–304.

Miall, L.C. 1875. Report of the committee on the structure and classification of the labyrinthodonts. *Report of the Meeting of the British Association for the Advancement of Science* 44: 149–192

Milner, A.R. 1994. Late Triassic and Jurassic amphibians: fossil record and phylogeny. *In*: N.C. Fraser and H.D. Sues (eds.), *In the Shadow of Dinosaurs, Early Mesozoic Tetrapods*, 5–22. Cambridge University Press, Cambridge.

Moodie, R.L. 1908. The lateral line system in extinct Amphibia. *Journal of Morphology* 19: 511–541.

Sawin, H.J. 1945. Amphibians from the Dockum Triassic of Howard County, Texas. *University of Texas Publication* 4401: 361–399.

Säve-Söderbergh, G.1937. On the dermal skulls of *Lyrocephalus*, *Aphaneramma*, and *Benthosuchus*, Labyrinthodonts from the Triassic of Spitsbergen and N. Russia. *Bulletin of the Geological Institute of Upsala* 27: 189–208.

Schoch, R.R. and Milner, A.R. 2000. Stereospondyli. *Handbuch der Paläoherpetologie*, teil 3B. 170 pp. Verlag Dr. Friedrich Pfeil, München.

Seegis, D. 1997. *Die Lehrbergschichten im Mittleren Keuper von Süddeutschland Stratigraphie, Petrographie, Paläontologie, Genese*. 336 pp. Verlag Manfred Hennecke, Ramshalden.

Sengupta, D. P. 1992. *Metoposaurus maleriensis* Roy Chowdhury from the Tiki Formation of Son-Mahanadi Valley of Central India. *Indian Journal of Geology* 64: 300–305.

Warren, A.A. and Hutchinson, M.N. 1988. A new capitosaurid amphibian from the Early Triassic od Queensland, and the ontogeny of the capitosaur skull. *Palaeontology* 31: 857–876.

Watson, D.M.S. 1919. The structure, evolution and origin of the Amphibia —The Orders Rhachitomi and Stereospondyli. *Philosophical Transactions of the Royal Society of London*, *Series B* 209: 1–73.

Werneburg, R. 1990. Metoposaurier (Amphibia) aus dem Unteren Keuper (Obertrias) Thüringens. *Veröffentlichung Naturhistorisches Museum Schleusingen* 5: 31–38.

Werneburg, R. 1991. Kurze Beiträge. *Veröffentlichung Naturhistorisches Museum Schleusingen* 6: 100–112.

Zittel, K.A. 1888. *Handbuch der Paläeontologie. Abteilung 1. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves).* 900 pp. Oldenbourg, München.