

OSTEOLOGY, VARIABILITY, AND EVOLUTION OF *METOPOSAURUS*, A TEMNOSPONDYL FROM THE LATE TRIASSIC OF POLAND

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A new reconstruction of the whole skeleton of the Carnian temnospondyl *Metoposaurus diagnosticus krasiejowensis* is presented with a detailed description of skeletal elements and their variability. The rigid construction of the vertebral column and limb articulations suggest that the metoposaurs used their limbs as flippers and swam by symmetrical and simultaneous movements of the limbs, like the plesiosaurs. The dentigerous ossicles are for the first time identified in metoposaurs. The Meckelian cartilage allowed for rotation of the mandible rami while opening the mouth. The osteological variability of *Metoposaurus* reveals allometry in growth of adult specimens. A possible role of natural selection in controlling the decrease of the variability during ontogeny of the metoposaur is inferred. Close relationship of the Metoposauridae and the Brachyopoidea is supported, contrary to their alleged trematosaurid origin. Two evolutionary lineages of the metoposaurids are distinguished based on metrics of cranial and postcranial elements. In the lineages with the lacrimal excluded from orbital margin, there is a tendency to decrease the depth of the otic notch and to decrease body-size. In the lineage in which the lacrimal forms part of the orbit margins, there is a tendency to elongation of the posterior part of the interclavicle and to diminish the central area with polygonal pits of the interclavicle. The decrease in ossification of the braincase, and gracilization of the humerus, scapula, and fibula may be an adaptation to the aquatic life. These changes were connected with the neotenuous origin of the metoposaurids. Both lineages evolved mostly by extension of the ontogeny, possibly reactivating silenced developmental programmes.

Key words: Metoposauridae, ontogeny, allometry, anatomy, autecology, locomotion, canalization.

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INTRODUCTION

Metoposaurids are Late Triassic temnospondyl amphibians characterised 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). Questionable materials were reported also from Madagascar (Dutuit 1978) and China (Yang 1978). The first named metoposaurid was *Metopias diagnosticus* Meyer, 1842, described in detail by Fraas (1889). Because the name *Metopias* was pre-occupied by a coleopteran genus, Lydekker (1890) replaced it with *Metoposaurus*. A history of studies on the metoposaurids was presented by Hunt (1993).

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; Sulej 2002). However, the metoposaurid populations exhibit much variability of this character as well as the morphology of postcranial bones. More detailed research suggests phylogenetically important differences between them. There is also a possibility to identify ecological background of the differences, as assemblages of species co-occurring with metoposaurids in these localities are markedly different. All this calls for more re-

search on variability of metoposaurids. Commonly the papers concerning temnospondyl amphibians concentrate on the taxonomy or phylogeny, and ontogeny is rarely discussed. In principle, the key to understanding factors controlling variability of fossil amphibians should be looked for in biology of their Recent closest relatives. Indeed, the frogs and salamanders are model subjects of research on genetic and environmental aspects of population variability. It is well established that hybridization is frequently involved (Berger 1973). The pattern of gene exchange was extensively studied also in its geographic dimension (Szymura and Barton 1991). Unfortunately, the morphological variability of Recent amphibians has been described mostly with respect to those traits that are unlikely to be identified in the fossil material. For instance, Simons and Brainerd (1999) showed considerable variation of the fiber angle and even the number of layers in the hypaxial musculature of salamanders. The large variation of the first transverse processes and ribs in recent *Ascaphus* was described by Ritland (1955). Trueb *et al.* (2000) presented ontogeny and osteological description of *Pipa*.

In the lack of comparable data on large, strongly ossified early amphibians, the ontogeny of externally similar reptiles may offer a useful analogy. The variability of theropod dinosaur *Tyrannosaurus* was recently described by Carr and Williamson (2004). Farlow and Elsey (2004) showed that the mid-thigh circumference of the intact hind limb of *Alligator* is strictly correlated with the transverse dimensions of the proximal and distal articular surfaces of the femur. According to them, this correlation may be used to estimate the transverse dimensions of the intact hind limb in extinct crocodile-like archosaurs. Their studies showed that the regression value may be representative for a species. This idea is tested in this paper in respect to *Metoposaurus*. An opportunity to address the problem of variation of characters assumed to be of diagnostic value in the metoposaurids emerged recently.

In 2000–2002, the Institute of Paleobiology organised palaeontological excavations at Krasiejów near Opole, southern Poland. Among the remains of plants, insects, crustaceans, fishes, reptiles and amphibians, the excavations yielded a great number of bones of *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002. This collection permits a study of the osteological variability as well as identification of morphological features stable enough to be used in phylogenetic analyses. Along with studies on the new metoposaurid materials from Krasiejów, the specimens housed in Staatliches Museum für Naturkunde in Stuttgart, Muséum National d'Historie Naturelle in Paris and Museum of Geology in Calcutta were examined. Recognition of the variability of the features and its range is particularly important for the taxonomy of temnospondyls, because they are usually known from single specimens. The knowledge of their population variability is poor and therefore its refining is important. The latest paper of Pawley and Warren (2006) about morphology and ontogeny of the appendicular skeleton of *Eryops megacephalus* is exceptional. The study on the metoposaurs from Krasiejów may offer a standard of variation also for other temnospondyl families.

The Krasiejów material represents a sample from a time-averaged metoposaurid population, with many generations of organisms mixed within a single stratigraphic horizon. A time-averaged sample of a taxon should be somewhat more variable than a single-generation sample, because variability of a population living in variable conditions are present in this case. In extreme cases of long-term averaging, evolutionary changes may also be involved. To investigate these issues, Bush *et al.* (2002) estimated the variability of six modern, single-generation samples of bivalve. They showed that the modern and the fossil (Pleistocene) samples had different range of variability, but these ranges were virtually identical. Morphology of bivalves studied by them was quite stable over hundreds to many thousands of years that passed as the assemblages accumulated. This means that the variability of the fossil samples can be used to estimate single-generation variability. It seems that the geologically relatively short period of accumulation of the metoposaurids from Krasiejów allows for a study of their variability on similar terms as in a living population.

The great number of *Metoposaurus* bones from Krasiejów allows to identify differences in the range of the variability of particular traits. It seems large enough to show morphological changes in ontogeny and differences in the range of variability between various regions of the skull and elements of the skeleton. There are skull parameters, which have a narrow range of variability, and stabilizing selection probably controlled these parameters because of their functional importance. Also measuring a great number of the limb bones may allow to establish the pattern of their variability and then to speculate on their locomotory function.

Institutional abbreviations. — ISIA, Indian Statistical Institute, Calcutta; MNHN, Muséum National d'Historie Naturelle, Paris; SMNS, Staatliches Museum für Naturkunde, Stuttgart; TMM, Texas Memorial Museum, Austin; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

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GEOLOGICAL SETTING

Metoposaurus comprises the majority of large-size fossils at Krasiejów. Most of the fossils from this locality occur in one of two horizons. In the lower horizon, bones of *Metoposaurus* (Sulej 2002) and the phytosaur *Paleorhinus* (Dzik *et al.* 2000) predominate, followed by the aetosaur *Stagonolepis* (Dzik 2001) and the temnospondyl *Cyclotosaurus* (Majer 2002; Sulej and Majer 2005). The upper horizon is dominated by *Stagonolepis* and the dinosauromorph *Silesaurus* (Dzik 2003). Between these horizons, a small accumulation of bones of the rauisuchian *Teratosaurus* (Sulej 2005) and *Silesaurus* have also been found.

Bones classified as *Metoposaurus diagnosticus krasiejowensis* (Sulej 2002) have been collected from both the lower (where they are abundant) and upper (where they are very rare) horizons. Apart from reptiles and amphibians, there are undescribed fishes, pterosaurs? and coleopterans. There are many microfossils of the charophytes (Zatoń *et al.* 2005; Zatoń and Piechota 2003) and conchostracans (Olempska 2004), whereas the ostracods are rare (Olempska 2001).

At the Krasiejów clay pit the marly mudstone is exposed to a depth of 14 m. The strata probably correspond to the subsurface Drawno beds and the Lehrberg Beds of Baden-Württemberg (Dzik 2001). The correlation with the Lehrberg Beds was recently questioned by Milner and Schoch (2004) on the basis of new interpretation of the age of the skull of *Metoposaurus diagnosticus diagnosticus*. Szulc (2005), based on lithology, dated the Krasiejów deposits as Norian. This problem will be discussed in the chapter on geochronology.

PRESERVATION AND TAPHONOMY

The bones occur at Krasiejów in calcareous concretions or just in marly clay. Specimens from the concretions are three-dimensionally preserved; however, the concretion may cover only a part of the whole element. Partial skulls are not uncommon. In contrast, the specimens found in the clay usually are crushed and deformed. The skull bones may be separated along the sutures and loose parts of the skull are then slightly displaced. Isolated skull bones with well-preserved sutured margins are rare. Postcranial bones are usually disarticulated. Elements of the vertebral column or limbs have been rarely found in association.

The *Metoposaurus* specimens from the lower horizon were deposited probably on the bottom of a lake as partially decayed cadavers. This is suggested by the common association of skulls with mandibles and bones of the pectoral girdle. Winnowing was frequent and many disarticulated bones occur in lenticular intercala-

tions of calcareous grainstone. The clavicles usually occur with their convex side down, indicating deposition from suspension. Closed shells of unionid bivalves co-occur, which probably died from suffocation under the load of dysaerobic mud.

MATERIAL AND METHODS

Detailed description of excavation methods in Krasiejów was presented by Dzik (2003). While removing the rock matrix in the field and in the laboratory, the specimens were impregnated with dilute cyanoacrylic glue, if it was necessary. The specimens preserved in the claystone or mudstone demanded only cleaning in water. Those one covered by limestone crust were cleaned mechanically and brushed with dilute formic acid. After washing in water to remove calcium formate they were dried and impregnated with dilute cyanoacrylic glue. The procedure was repeated up to the desired result.

For taking photographs, small specimens were coated with ammonium chloride. Large specimens as the skulls, mandibles, clavicles and interclavicles were covered with white washable paint, using the aerograph.

The Krasiejów material of *Metoposaurus diagnosticus krasiejowensis* yielded complete skulls (51 specimens), pieces of the skull smaller than the half (38), vertebrae (about 450), rami of the mandible (28), clavicles (37), interclavicles (39), scapulae (20), cleithra (16), humeri (36), radii (9), ulnae (4), ilia (27), ischia (13), femora (24), tibiae (13), and fibulae (10). The 66 skulls were measured using 28 parameters (Fig. 75, Appendix 1) to describe the ontogeny and variability of the species.

Taphonomy of the locality suggests that the fossil assemblage was accumulated in soft, semi-liquid sediment and that specimens were subsequently flattened in result of dehydration of the mud (Dzik *et al.* 2000). This situation concerns especially specimens preserved in clay. Those that are preserved in concretions are deformed only slightly. Deformation of the bones oblique to their axes calls for caution in interpretation of measurements. The height and width of the skull are the most sensitive parameters. For this reason comparisons are based mostly on the length of skulls that have not changed in result of the sediment compaction. Among the parameters related with the width of the skull, the interorbital width seems to be the less distorted, because this part of the skull is flat.

OSTEOLOGY

Numerous specimens of *Metoposaurus diagnosticus krasiejowensis* from Krasiejów add new information to earlier descriptions. The holotype specimen (ZPAL AbIII/358) is well preserved entirely in calcareous concretion and suggests that the skull of *M. diagnosticus diagnosticus* was reconstructed too flat by Fraas (1889). Part of the palate of a single skull is covered by denticulous ossicles as in the *Cyclotosaurus* (Sulej and Majer 2005) where a shagreen of denticles was preserved.

Morphology and variability of each bone of *Metoposaurus diagnosticus krasiejowensis* is described below and compared with published evidence on homologous bones in other temnospondyls.

SKULL

The skull roof comprises dermal bones with a distinctive sculpture. Generally, the sculpture of the central area of these bones consists of isomeric pits that gradually elongate to the edges of the bone and in the regions of fast growth the sculpture consists of long grooves. The differences in the sculpture of dermal bones of different metoposaurids species were already discussed by other authors (Branson and Mehl 1929; Colbert and Imbrie 1956) and some of them proposed them as important in taxonomy. In the very rich material from Krasiejów, the large variability of the depth and shape of ridges is observed. It clearly shows that these characters cannot be used as diagnostic features.

Premaxilla. — It forms the tip of the snout that is well ossified. Strong tooth arcades and the olfactory passages are located in close proximity to each other. The premaxilla supports the median roofing series by not a very broad suture with the nasal. The premaxilla consists of three branches: the dental shelf, which forms the tooth-bearing anterior margin of the skull, the alary process (Schoch 1999) that connects the skull roof with its margin, and the vomeral process, which connects the dental shelf to the vomer (Fig. 1).

The dental shelf is ventrally flat and in larger specimens widens medially. The first teeth are the largest. Further posterolaterally, towards the maxilla, tooth size decreases markedly, and 18 to 20 teeth are present (Fig. 2). All tooth crowns are bent lingually. The posterior surface of the premaxilla behind the dentary shelf is concave transversely and the vomeral process is above the dentary shelf. The anterior surface of the dentary shelf is unsculptured.

The vomeral process is a posteromedial outgrowth of the premaxilla that separates the anterior palatal vacuities. The premaxillae form substantial part of the margins of these vacuities. The vomeral process is flat dorsally. On the ventral surface, it bears fossa subrostralis media, which has a rugose surface. The fossa subrostralis was also described, for instance, in *Trematosuchus sobeyi* Haughton, 1915 (Shishkin and Welman 1994) and *Dvinosaurus egregius* Shishkin, 1968 (Shishkin 1973).

The alary process forms the anterior margin of the naris. On the dorsal side, it is covered by the weakly developed sculpture and bears the supraorbital canal of the lateral line. The alary process is ventrally convex and bears (together with nasal) small shallow pits for the symphyseal tusks of the mandible.

On the suture between premaxillae, there is an inter-rostral fenestra (Wilson 1941), which in some skulls is weakly defined. Its size is not correlated with the size of the skull.

Nasal. — The nasals occupy the space between the prefrontals and frontals posteriorly (Fig. 1). Laterally they contact the lacrimals, anterolaterally the maxillae, and anteriorly the premaxillae. A length of the suture of the right nasal and left frontal is very variable; in 3% of the skulls there is no suture. Also, the suture of the nasal with the lacrimal is present in not all skulls. In 11% of the studied skulls, at least one nasal does not form this suture. It is connected with the relation of the anterior top of the lacrimal and the prefrontal. In most skulls from Krasiejów, the anterior top of the lacrimal is closer to the nares than to the top of the prefrontal; however, in 4% the top of the prefrontal is closer, and in 11% ($n = 72$; left and right bones were counted) both bones have tops at the same level.

The shape of the nasal is that of a rectangle which widens in its middle. The sculpturing of the nasal is divided into two unequal areas by the wide supraorbital canal. The radially arranged ridges have their centre at the margin of the canal. The central area of the bone bears the polygonal pits.

The anterolateral sculptured region also bears a network of small, polygonal pits, but the size of this region is variable, in the ZPAL AbIII/894 being very small (Fig. 4F), in ZPAL AbIII/1192 very large, but it is not connected with the size of the skull. The supraorbital canal forms a broad, shallow groove, which has a largely smooth surface. It becomes wider at the contact with the maxilla and the lacrimal. Ventrally, the nasal is generally flat but anteriorly is weakly convex in transverse section.

Frontal. — It is the longest bone of the medial skull series. It contacts the nasal anteriorly, the prefrontal along its anterolateral margin, the postfrontal posterolaterally, and the parietals posteriorly. It is in the shape of an elongated rectangle. The central area of the frontal bears polygonal pits. In the anterior and posterior parts the sculpture is dominated by long ridges. In the largest skull of *Dutuitosaurus ouazzoui* Hunt, 1993 (MNHN XIII/36/66) the long ridges are present also laterally from the centre of ossification. The presence of the ridges laterally to the centre of the frontal differentiates *Dutuitosaurus* from *M. diagnosticus*, but it is visible only in large skulls. The supraorbital canal forms a shallow groove at the contact of the frontal with the prefrontal and postfrontal.

The ventral surface of the frontal forms a plane and is smooth, with the exception of a trace, left in the midline of the skull, of the attachment site of the braincase (Fig. 2). The trace of the braincase has the shape of an elongated prominence. It is placed in the posterior part of the frontal, although the weakly developed ridges begin in the centre of an anterior part of the bone.

Parietal. — It contacts the following bones: the frontal anteriorly, the postfrontal anterolaterally, the supratemporal laterally, and the postparietal posteriorly. The position of the pineal foramen is in the posterior fourth of the parietal. This position results from the strong elongation of the postorbital zones of intense growth (Moody 1908; Sulej 2002), demonstrated by long ridges. Polygonal pits dominate the sculpture of the part behind the pineal foramen.

Ventrally, the parietal forms the orbitotemporal crest (Shishkin 1973; Damiani and Jeannot 2002) that is an elongation of the attachment site of the braincase on the frontal. In the posterior part, it expands laterally at the pineal foramen. Anteriorly to the pineal foramen, there is a shallow trough in the capital crest.

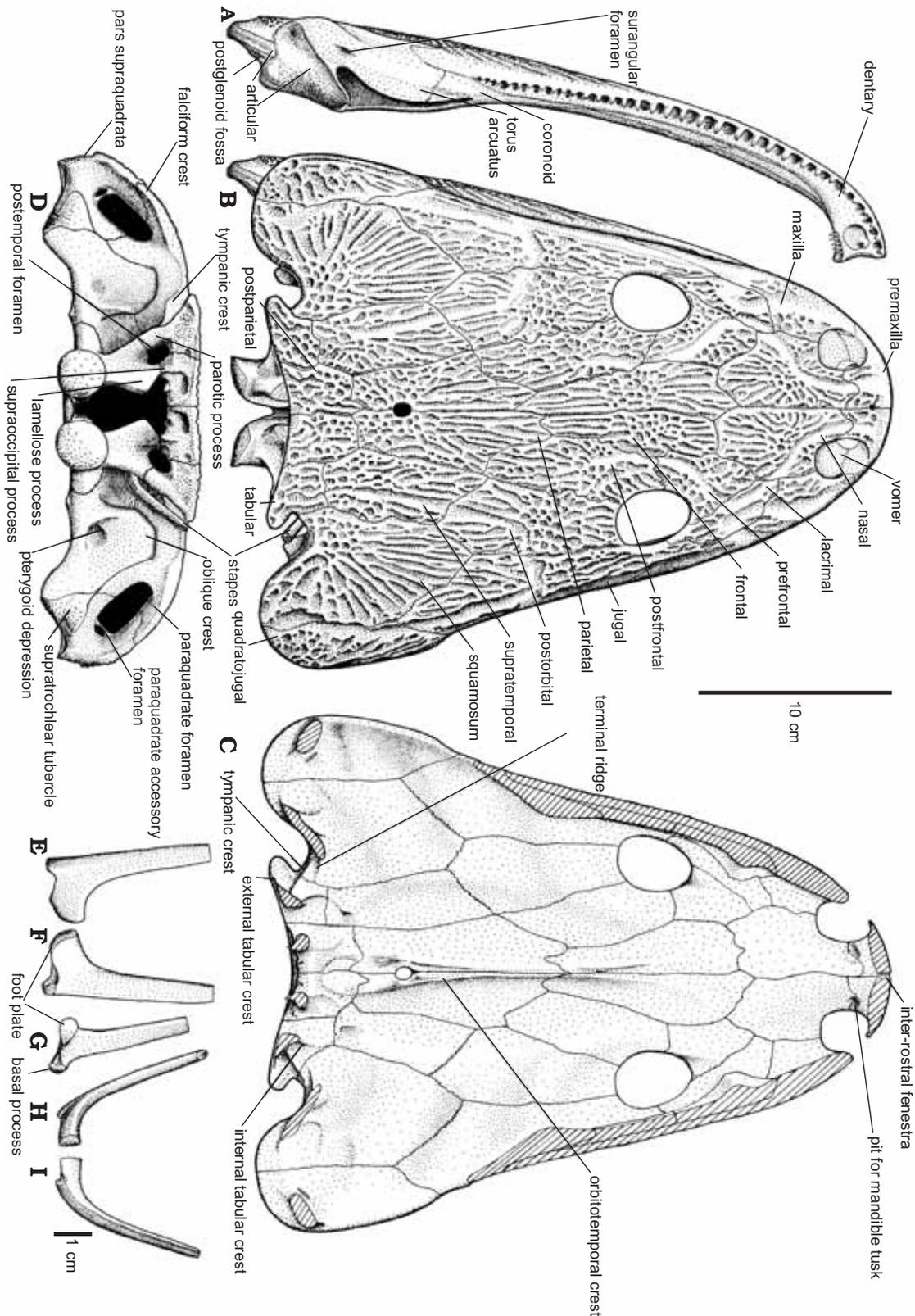


Fig. 1. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of the skull, mandible and stapes. A. Mandible in dorsal view. B. Skull roof in dorsal view with left mandible and right stapes in articulation. C. Skull roof in ventral view (without palate). D. Skull in occipital view. E. Stapes in anteromedial view. F. Stapes in posterolateral view. G. Stapes in anteromedial view. H. Stapes in posteromedial view. I. Stapes in anterolateral view. The reconstruction of the skull is based mainly on ZPAL AbIII/358 and ZPAL AbIII/1191, the mandible on ZPAL AbIII/41, the stapes on ZPAL AbIII/11 and ZPAL Ab III/358.

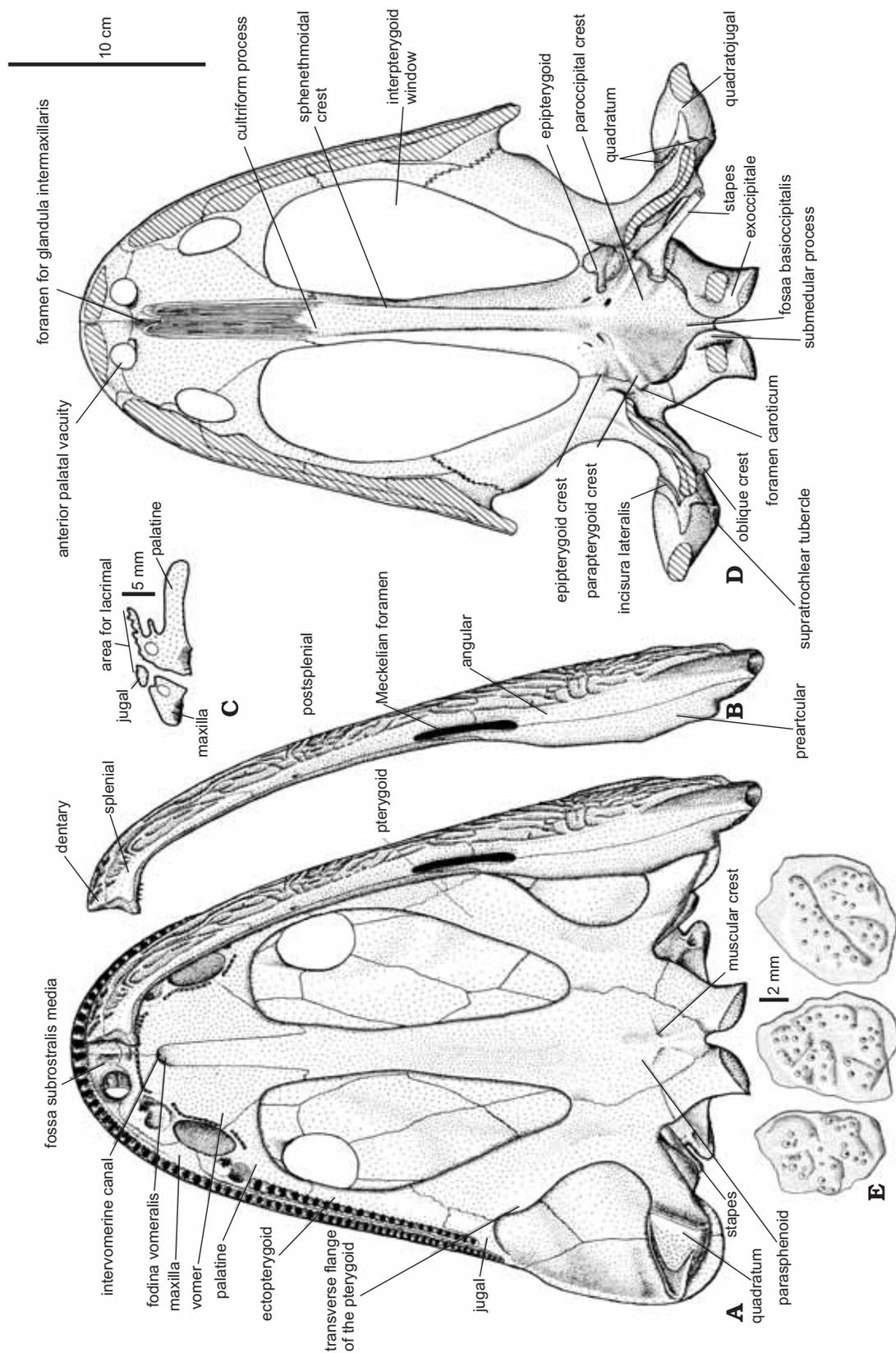


Fig. 2. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of the skull, mandible and dentigerous ossicles. **A.** Skull in ventral view with left ramus of mandible and right stapes articulated. **B.** Mandible in ventral view. **C.** Cross-section through palate of ZPAL AbIII/1706. **D.** Skull palate in dorsal view, left epipterygoid removed. **E.** Dentigerous ossicles in ventral view. Reconstruction of the dentigerous ossicles based on ZPAL AbIII/1675/1 (see also Fig. 1).

The orbitotemporal crest of *Metoposaurus diagnosticus krasiejowensis* is similar to that of *Bathignathus poikilops* Damiani et Jeannot, 2002 from the Middle Triassic of Karoo (Damiani and Jeannot 2002). The trematosaurids and capitosaurids have much different ventral side of the pineal foramen. In *Trematosaurus thuringiensis* Werneburg, 1993, it has a reversed T shape (Werneburg 1993). In *Cyclotosaurus* and *Benthosuchus sushkini* Efremov, 1929 (Bystrow and Efremov 1940), this region is completely smooth.

Metoposaurus diagnosticus krasiejowensis has a shorter prepineal region of the parietal than *M. diagnosticus diagnosticus*, and the expansion angle of the suture separating the parietal from the supratemporal has a lower value (Sulej 2002). *Buettneria howardensis*, *B. perfecta*, and *M. maleriensis* have the parietal similar as *M. diagnosticus diagnosticus*.

Postparietal. — It forms the posteromedial edge of the skull roof, connecting it to the exoccipital by means of a slender descending outgrowth, the supraoccipital process. The roofing part is roughly rectangular in outline and expands laterally in contact with the tabular. The shape of that contact is very variable. In most of the skulls, it is oblique to midline, but in a few cases it is parallel. The dermal sculpturing consists of equally sized polygonal pits. In largest skulls, there are elongated pits in the anterior part.

The posterior margin of the skull roof is clearly concave in dorsal view; it bears the sculpture up to the posterior edge or there is a smooth slope that widens medially. The occipital part of the postparietal is very well ossified and slopes posteroventrally, being markedly thickened medially. Its entire occipital area is roughened, with a marked pit near the sagittal suture. The shape of this pit is variable. Generally, it is shallow but in some skulls it is very deep and then the sagittal suture near the pit is prominent.

Ventrally, the columna verticalis (exoccipital) firmly connects the rather short supraoccipital process. The process in cross-section has the shape of curved drop in small and average-size skulls and it is oval in large skulls (e.g., ZPAL AbIII/17). The anterior ridge of the supraoccipital process extends far to the anterior part of the ventral side of the bone. In the largest skulls, the supraoccipital process bears the suture of the postparietal with tabular anteroventrally. In smaller skulls, this suture is placed laterally from the supraoccipital process. In the posterior part, medially to supraoccipital process a distinctive prominence is developed, which is very massive in the largest skulls. On its top (in ventral view), there is a small sharp-ended ridge, which is oblique to the midline in ventral view (Figs 2, 4G). It exists in all examined skulls of *M. diagnosticus krasiejowensis* and was not earlier reported in any other metoposaurid, although it was also identified in *Dutuitosaurus*. In the anterior part of the ventral surface of the postparietal, the elongation of the traces of the braincase from the parietal is visible.

Lacrimal. — It contacts the nasal medially, the maxilla laterally, the prefrontal posteromedially, and the jugal posteriorly. Medially, it forms the part of the orbital rim, although in ZPAL AbIII/1665 the left lacrimal and in ZPAL AbIII/893 the right one is separated from the orbit margin (see also Fig. 12). The usual situation in which the lacrimal forms a part of the orbital rim was observed in 53 studied skulls.

The lacrimal bears the supraorbital and a part of the infraorbital canal of the lateral line system (Fig. 5A). The infraorbital canal curves in sigmoid fashion to give the lacrimal flexure. Most of the dorsal surface of the lacrimal is dominated by the impressions of these canals, so that only a small area in the posterior part is sculptured in elongated pits. Ventrally, the lacrimal contacts a short column of the palatine, which tightly connects the palatine tusk region to the roof (Fig. 2C).

The lacrimal of *M. diagnosticus krasiejowensis* is very similar to that of *M. diagnosticus diagnosticus* and *M. maleriensis*.

Prefrontal. — It contacts following bones: the nasal anteriorly, the lacrimal anterolaterally, the frontal medially, and the postfrontal posteriorly. The supraorbital canal runs through the centre of the bone. The prefrontal is sculptured in polygonal pits, only the largest skulls have the elongated pits in the anterior part of the bone. The ventral side of the prefrontal is smooth, with exception of a shallow depression anteriorly to the orbit.

Postfrontal. — It contacts the prefrontal anteriorly, the frontal medially, the parietal and supratemporal posteriorly, and the postorbital laterally. The suture with the supratemporal is not present in some specimens. In 27% of 41 studied skulls, at least right or left postfrontal/supratemporal suture is lacking (Figs 5, 9, 12–15). The postfrontal forms posteromedial border of the orbits. The shape of the postfrontal is that of an elongated rectangle with pointed ends. It bears the ending of the supraorbital canal. The anterior area of the

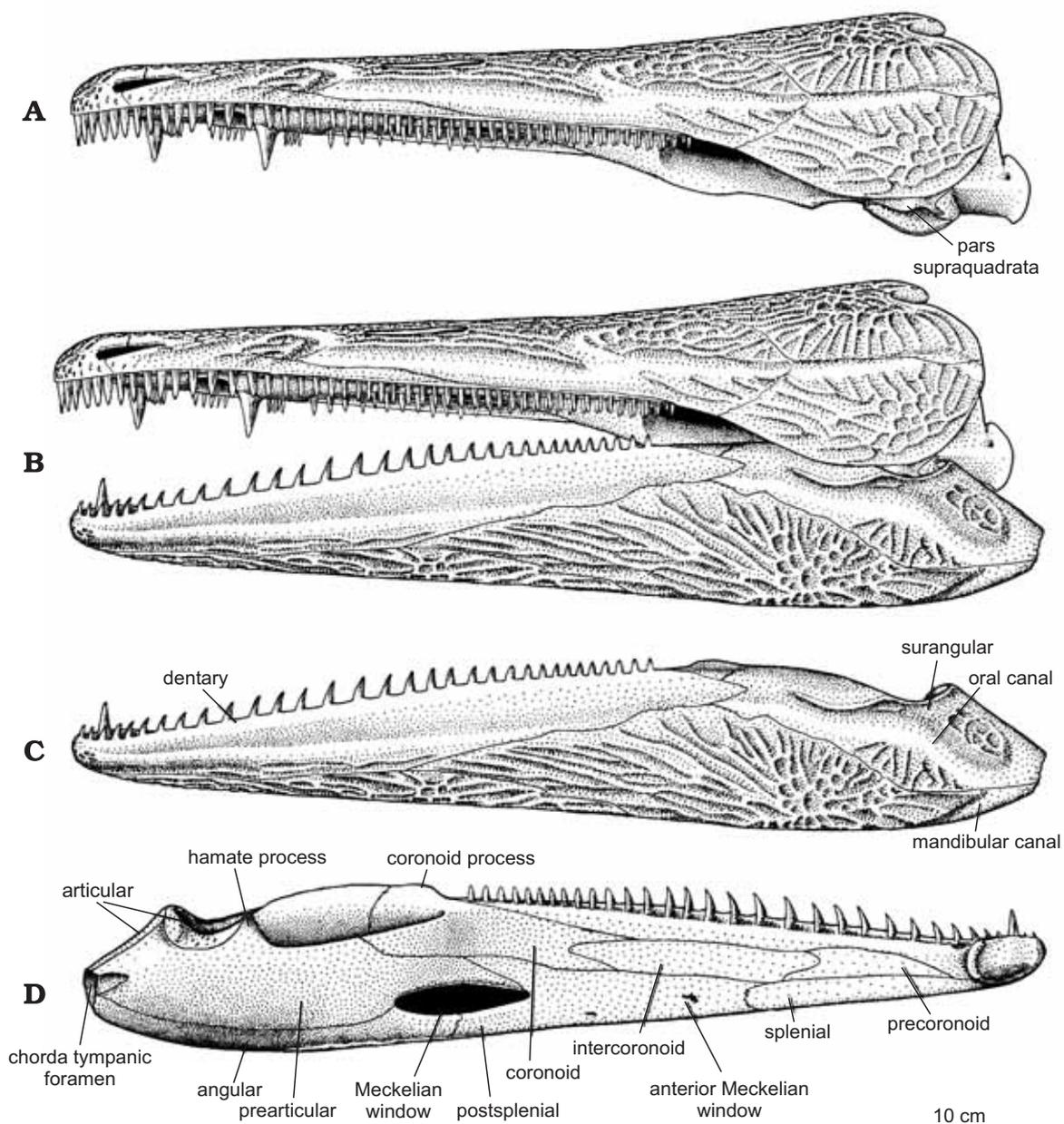


Fig. 3. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of the skull and mandible. **A.** Skull in lateral view. **B.** Same with articulated mandible. **C.** Mandible in lateral view. **D.** Mandible in medial view (see also Fig. 1).

bone bears polygonal pits. The posterior part of the postfrontal forms the postorbital zone of intense growth and is sculptured in long ridges. The ventral side is smooth with shallow depression in the posteromedial part.

Postorbital. — It contacts the jugal laterally, the squamosal and supratemporal posteriorly, and the postfrontal medially. In a few cases, there is a contact with the parietal. The bone forms the posterior border of the orbit. The shape of the postorbital is that of an elongated rectangle with pointed posterior termination. It bears the temporal canal and polygonal pits in its central area. The sculpturing of the remaining areas is arranged radially, consisting of long ridges. On ventral side, a transverse slope is developed in its centre and almost sagittal slope in the posterior part near the parietal.

Supratemporal. — It contacts the tabular posteriorly, the squamosal laterally, the parietal and postparietal medially. The supratemporal has the elongated parallelogram shape. The dermal sculpture consists of polygons in the central and posterior part, and radially arranged grooves in anterior part. The temporal ca-

nal terminates slightly posteriorly to the centre of the bone. On the ventral side, the element bears a sagittal slope, which curves medially in its posterior part. In this area, there is a prominence, which is directed to the ascending lamella of the pterygoid. In the most posterior part, there is a prominent opening for veins.

Tabular. — The element contacts the squamosal anteromedial to the otic notch, the supratemporal anteriorly and the postparietal medially. The posterolateral corner forms the tabular horn. The ventral side bears a ventromedially directed process, the parotic process, which is generally blade-like in cross-section, but in the largest skull ZPAL AbIII/17, it is oval. The tabular meets the exoccipital in a broad, serrated suture. Medially, the parotic process frames the posttemporal foramen, which is variable in shape. Generally, it is oval. In small skulls, the oval is set horizontally and in large ones vertically.

The tabular horn is supported by the external tabular crest, which connects it with parotic process. The base of the parotic process terminates dorsally in internal tabular crest anteriorly and high tympanic crest posterolaterally (Bystrow and Efremov 1940). The whole occipital area is very roughened. The tabular horn markedly widened in ontogeny, whereas the width of the otic notch increased only slightly (Fig. 18).

Maxilla. — It forms a large, completely dentigerous shelf bearing 83 to 107 teeth. The first teeth are large, and tooth size decreases markedly further posteriorly. The tooth bases are characteristically anteroposteriorly compressed, giving flattened anterior and posterior surfaces. The crowns of anterior teeth are only very slightly bent medially, and are flattened lateromedially. The posterior teeth have the crowns of conical shape.

The maxilla makes a well-defined contribution to the skull roof, especially anteriorly to the lacrimal, where it contacts the nasal (Fig. 1). Only this part bears the sculpture consisting of irregular polygons. Anteriorly, the maxilla contacts the premaxilla and borders the naris posterolaterally. The element bears the infraorbital canal.

Posteriorly, for most of its length the maxilla is narrow and rather thin, with a convex lateral surface and a dorsally flattened dental shelf. The dental shelf is remarkably thin, and posteriorly forms a sheet covered by the jugal.

On the ventral side, the maxilla contacts the ectopterygoid, palatine and vomer. In the choanal region, the maxilla is slightly broadening medially on the palatal side where it borders the choana. The margin of the choana is variable. In most skulls, it is weakly distinguished and rounded, but in a few cases it is more solid and sharply outlined.

Jugal. — It has a concave curved lateral margin that slopes toward the maxilla. Anteriorly, it borders the orbit and contacts the lacrimal. The jugal bears the infraorbital canal on its entire length and the temporal canal in its middle part. The sculpture consists of polygonal pits in the centre of the bone and elongated ridges in the anterior and posterior parts. Ventrally, the roofing part of the jugal is generally flat. Only in the central part, there is a weak prominence, which forms a support of the contact of the palatine ramus of the pterygoid with the skull roof.

On its ventral side, the jugal wedges in between the maxilla and the palatine (and the ectopterygoid, respectively), and further posteriorly it forms a medially directed ventral process that contacts the palatine ramus of the pterygoid and joins the palate with the roof. The dentigerous, rather thin-walled maxilla and ectopterygoid are framed by this ventral process, and it has a well-defined, ventrally rectangular face on the palatal side.

Squamosal. — It forms the anterior margin of the otic notch. The sculpturing of the squamosal is arranged radially from the otic notch, and the polygons tend to increase in length from that area. The posterolateral corner of the element bears the termination of the infraorbital canal. The posterior rim of the squamosals extends strongly posteriorly and with the quadratojugal it forms the falciform crest.

On the ventral side, the roofing part of the squamosal is slightly roughened in several areas, especially posteriorly near the apex of the strongly convex elevated region. The posteriorly sloping occipital portion is formed by the lamina descendens of the squamosal, which is thin-walled and overlaps the pterygoid and quadratojugal dorsally. Between the sutures with these elements, the lamina descendens forms the margin of the very large paraquadrate foramen. It is as large as in *Trimerorhachis* (Case 1935).

Medially, the base of the lamina descendens terminates forming the terminal ridge, which was described in *Benthosuchus* by Bystrow and Efremov (1940) as the linea terminalis.

Quadratojugal. — The cheek is the most vertical region in the skull roof, a part that is largely formed by the quadratojugal. This element framed laterally the subtemporal window. It forms the posterolateral corner

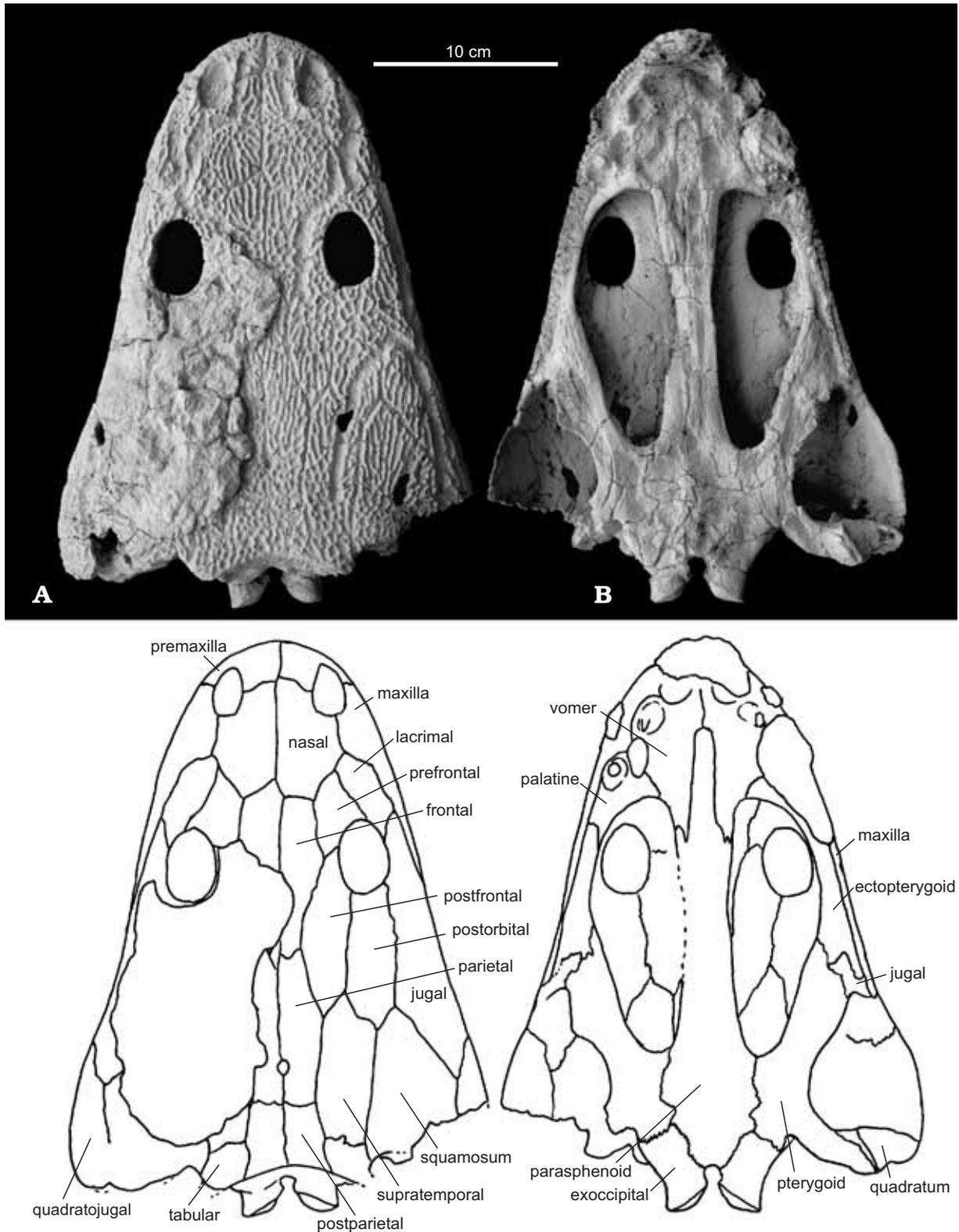


Fig. 4. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Small skull ZPAL AbIII/1683 in dorsal (A) and ventral (B) views.

of the skull roof and integrates the quadrate into the framework of the palate, cheek, and occiput. The element forms a slight convexity in the lateral border of the skull. This convexity is visible in lateral and dorsal views. The occipital components consist of three branches: the posterior, anterior and ventral processes. The poste-

rior and anterior processes overlay the quadrate from respective sides. The ventral process is very thin and narrow. It underlies the quadrate and occurs between the ventral area of the quadrate condyle and the supratrochlear tubercle (described in *Benthosuchus* by Bystrow and Efremov 1940).

The base of the anterior process and the ventral process forms the ventrally directed pars supraquadrata, which is sharply terminated ventrally. Pars supraquadrata was described by Shishkin (1987) for *Plagiosternum paraboliciceps* Shishkin, 1986 and *P. danilowi* Shishkin, 1986. Its ventral edge is C shaped (in ventral view) with belly of C directed laterally. Its edge is broken in most specimens, because of its prominent and sharp edge. Between the ventral edge of the pars supraquadrata and the quadratum is deep groove that was probably filled by cartilage. In the largest skull it is smaller, because of the quadrate is more ossified. There is a question about the function of the ventral edge of the pars supraquadrata. It could be a part of the glenoid surface or it could have limited the glenoid laterally. The counterpart structures of the mandible do not resolve this problem.

Medially to the pars supraquadrata, the quadratojugal forms a small foramen, probably the paraquadrata accessory foramen, which was not identified in metoposaurids earlier. It occurs in the lateral end of the quadrate foramen and is well visible in specimens ZPAL AbIII/1716, AbIII/503/1, AbIII/537, AbIII/1679, and AbIII/1727. The vertical wall that forms the medial margin of the paraquadrata foramen may be situated more medially and then is visible in occipital view of the skull, or more laterally and then it is not visible in occipital view, e.g., in ZPAL AbIII/537. But in specimens ZPAL AbIII/11, AbIII/652, AbIII/1165, and AbIII/1680 there is no trace of the medial wall forming the paraquadrata accessory foramen. In other specimens, this region is not well visible. Shishkin (1973: fig. 23) showed two foramina in this region of the skull of *Dvinosaurus egregius* and *Benthosuchus sushkini*. But in these species both foramina occur in the quadratojugal. There is a possibility that the larger is homologous to the paraquadrata foramen and the smaller to the paraquadrata accessory foremen.

The sculpturing is of similar type as that of the squamosal, and the centre of divergence is at the ventral margin of the roofing portion of the bone. The quadratojugal bears the infraorbital canal on the suture with the squamosal. The ventral side is roughened in several areas. The subtemporal window is completely bordered laterally by this bone, which is convex in lateral and dorsal views.

Orbits and nares. — The shape of the orbital window is oval, slightly flattened laterally in some cases. The rim of the orbits is unsculptured and generally vertical. Only its anterior part is oblique ventrally. The right orbit is generally situated slightly more anteriorly than the left one. It is not connected with diagenetic distortion and was probably normal asymmetry for the population.

The nares of *Metoposaurus diagnosticus krasiejowensis* are relatively large and occur close to the margin of the skull. They are widely separated. The variability of the width of distance between the nares is much larger than the variability of the length and the width of the orbits (Fig. 19). The outline of the naris is also variable. Its shape varies from longitudinally oval to triangular or trapezoid (ZPAL AbIII/1192). In many specimens, the anterolateral margin of the naris is only slightly exposed on the premaxillary. There is no septomaxilla. The anterior palatal vacuity is set under the medial margin of the naris and is tunnelling it. The length of both the orbits and nares increased in ontogeny (Fig. 19).

Vomer. — The ventral snout region is dominated by the vomers. The vomer bears a pair of tusks and an almost continuous row of small “circum-vomerine” teeth (Fig. 2). The bone contacts the premaxilla anteriorly, the maxilla laterally, the palatine posterolaterally, and the cultriform process (parasphenoid) medially and dorsally. The latter contact is established by a broad posteromedial process (processus parasphenoidalis) that forms a frame into which the cultriform process is set in firmly.

The symphyseal tusks of the dentary are partly framed by the anteromedial fenestral process and the anterolateral subnarial process of the vomer. The former contacts the vomeral process of the premaxilla, whereas the latter binds the vomer tightly to the medial wall of the premaxillary and maxillary dental shelves. The vomer forms the anterior and medial rim of the choana and the anteromedial rim of the interpterygoid window.

The parasphenoid separates the vomers in the midline up to the dentigerous region at its anterior rim, where the vomers meet each other in a tight suture. The exposed area of the cultriform process forms anteriorly a deep incline, which terminates forming a foramen in the palate. The incline and foramen form the fodina vomeralis. It was described in not closely related *Mastodonsaurus giganteus* Jaeger, 1828 (Schoch 1999) and in *Vanastega plurimidens* Damiani *et* Kitching, 2003 (Damiani and Kitching 2003).

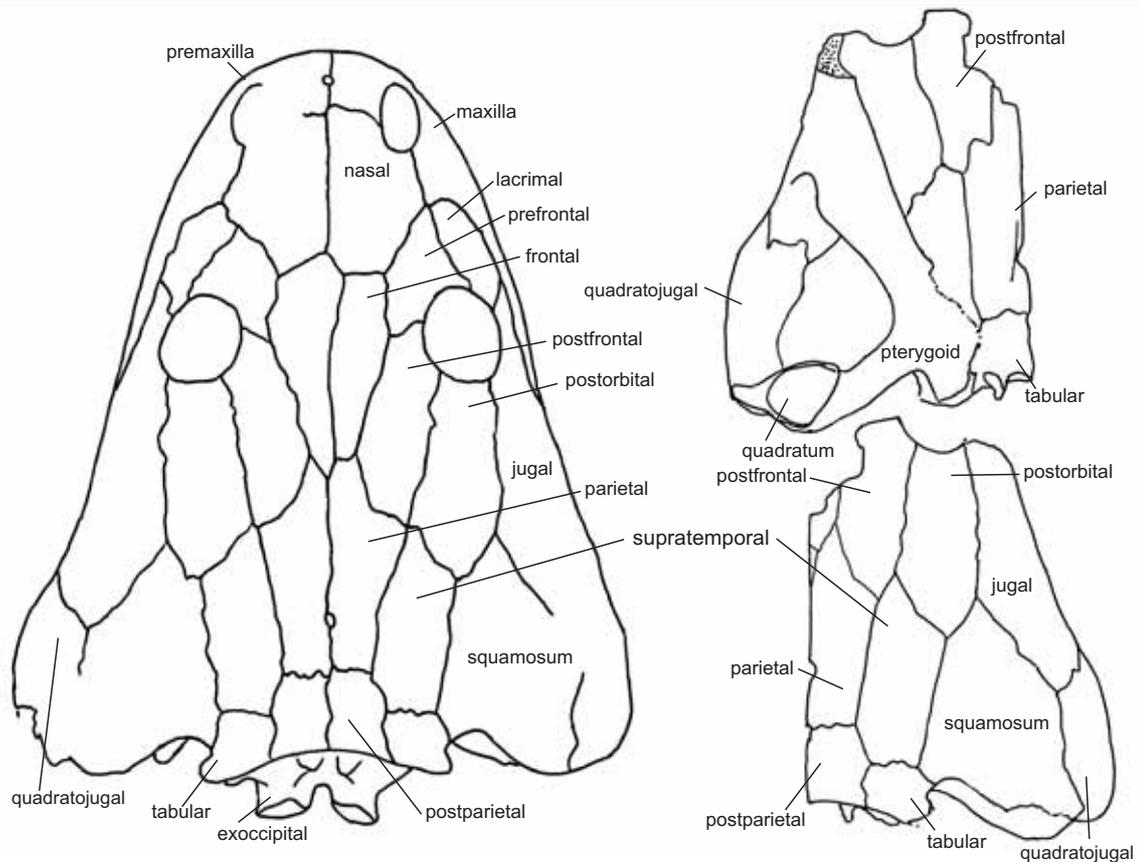
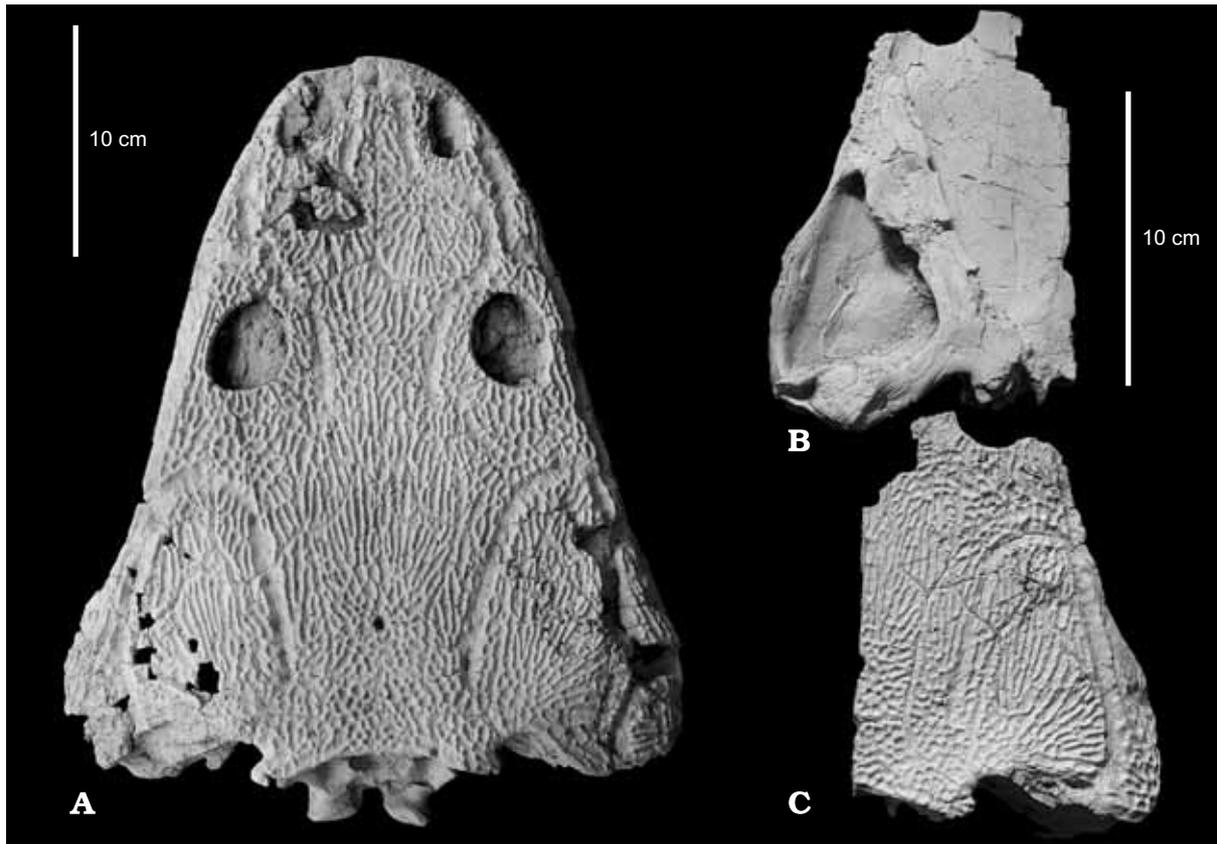


Fig. 5. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. A. Small skull ZPAL AbIII/682 in dorsal view. B, C. Fragment of the smallest skull ZPAL AbIII/1007 in ventral (B) and dorsal (C) views.

The cultriform process overlaps the medial border of the vomer dorsally. On the suture of the fenestral process, there is a deep funnel on the dorsal side (Fig. 2). It was described in *Buettneria perfecta* Case, 1922 (Wilson 1941) as the foramen for glandula intermaxillaris. In *B. perfecta*, Wilson (1941) described numerous tubules around the foramen that are absent in *Metoposaurus diagnosticus krasiejowensis*. However, on the bottom of the foramen for glandula intermaxillaris, there is an anteriorly directed tunnel in the vomers, which exits anteriorly to the transverse row of “circum-vomerine” teeth. The fodina vomeralis might be a passage for veins of the glandula intermaxillaris.

The dorsal and ventral surfaces of the vomer are generally flat and smooth. Anteriorly, the vomer forms a small vertical lamina directed dorsally on the medial margin of the anterior palatal vacuity that probably laterally limits a symphyseal tusk of the dentary. This structure was not described in other species, probably because of its poor preservation.

The vomerine tusks pair is situated on the elevation at the anterolateral corner of the vomer. The tusks were oriented vertically and they have a shape of straight cone. In most cases, there is a single tusk in the socket, but in a few cases there are two and sometimes even three tusks. The vomerine and palatal tusks are of the same size.

The “circum-vomerine” tooth arcade consists of a transverse row of 9–12 small teeth (dentes post-fenestrales), and the parachoanal tooth row situated on the margin of the choana. It consists of 15–25 small teeth (dentes parachoanales). The teeth are small, posteriorly and medially curved.

Parasphenoid. — It is divided into the basal plate and the cultriform process. The former is an elongated trapezoidal plate, which floors the hindbrain and auditory capsules and firmly connects the pterygoids and exoccipitals. Its thickness increases markedly towards the extensive sutures with the latter two bone pairs. The cultriform process is a wide and strut-like in ventral view. It connects the basal plate with the vomers.

The ventral surface of the basal plates may be smooth or slightly sculptured by transverse and oblique ridges (Fig. 10) but never as strongly as in *Buettneria howardensis* Sawin, 1945 (Sawin 1945). It forms a shallow bowl that continues for a short distance onto the base of the cultriform process. Laterally to this bowl, there is a small prominence on the anterior part of the suture with the pterygoid. Between the bowl and the muscular crest (crista muscularis), there is a medial prominence. The muscular crest may be very distinctive or only slightly developed, in a few cases even barely visible. According to Damiani (2001), the muscular crest extending laterally on the pterygoid is unique for *Cherninia megarhina* (Chernin *et* Cosgriff, 1975). In the metoposaurid material, the large variability in its shape is seen. Generally, it is present only on the parasphenoid but in a few cases it is extended on the pterygoid (*e.g.*, in ZPAL AbIII/11). Posteriorly, the basal plate terminates as a thin and narrow blade between the sutures with the exoccipitals.

The dorsal side of the basal plate has a smooth surface. It bears a complex system of crests and depressions, which are, from posterior to anterior: the medial basioccipital fossa, the paired paroccipital crests, the paired parapterygoid crests, and the paired epipterygoid crests. The paroccipital crest may be very weakly developed. Through the parapterygoid crest, the tunnel for the internal carotid artery runs. This artery enters anteriorly to the pterygoid/exoccipital suture. The tunnel extends anteromedially and opens fairly close to midline as a round foramen or trough. The palatine ramus of the carotid interna artery exits anteriorly to this foramen (Bystrow and Efremov 1940). The system is very similar to that in *Metoposaurus maleriensis* and *Buettneria perfecta*. At the lateral termination of parapterygoid crest the stapes articulates with the parasphenoid. This articulation is visible in ZPAL AbIII/1165, AbIII/1517, and AbIII/1679. In the specimens with the stapes unpreserved, the trace of this contact is invisible. The epipterygoid crest was marked in the figures of *B. perfecta* by Wilson (1941) but he did not name it. The epipterygoid crest bears the anterior edge of the epipterygoid.

The cultriform process is wide and forms the largest part of the medial border of the interpterygoid window. The ventral side of the cultriform process is anteriorly flat and becomes gradually posteriorly slightly concave. On the dorsal surfaces, it bears the paired and very prominent sphenethmoidal crest. The sphenethmoid was attached to them as it is preserved in *D. ouazzoui* (Dutuit 1976). The sphenethmoidal crest terminates anteriorly at the place where cultriform process sutures the vomers. The anterior part of the cultriform process is very wide and is dorsally covered by numerous small sagittal ridges. In this part, it overlaps the vomers. Before termination, it bifurcates and forms borders of trough, which run from the fodina vomeralis to the foramen for the glandula intermaxillaris.

The minimum width of the cultriform process, which forms the margin of the interpterygoid windows, is very variable (Fig. 19A). The width of the anterior part of the cultriform process is also very variable. In three

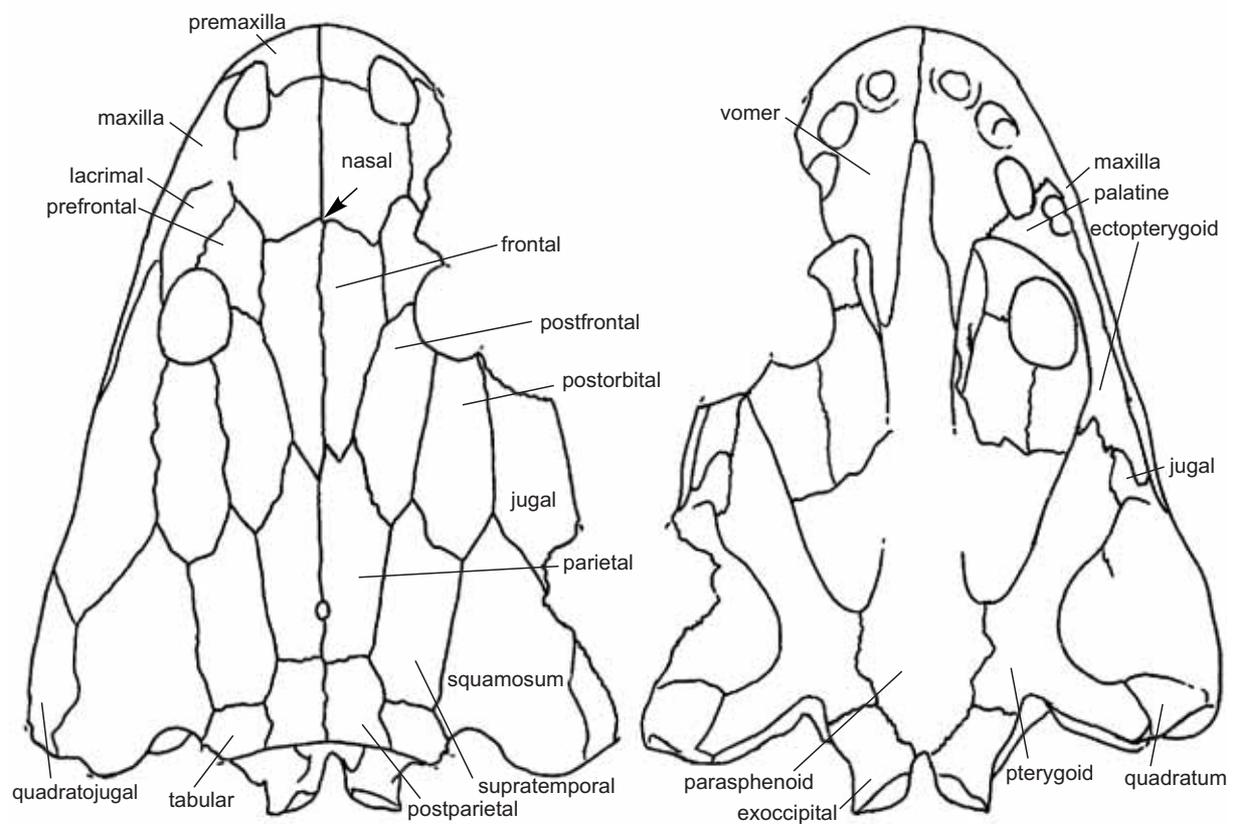
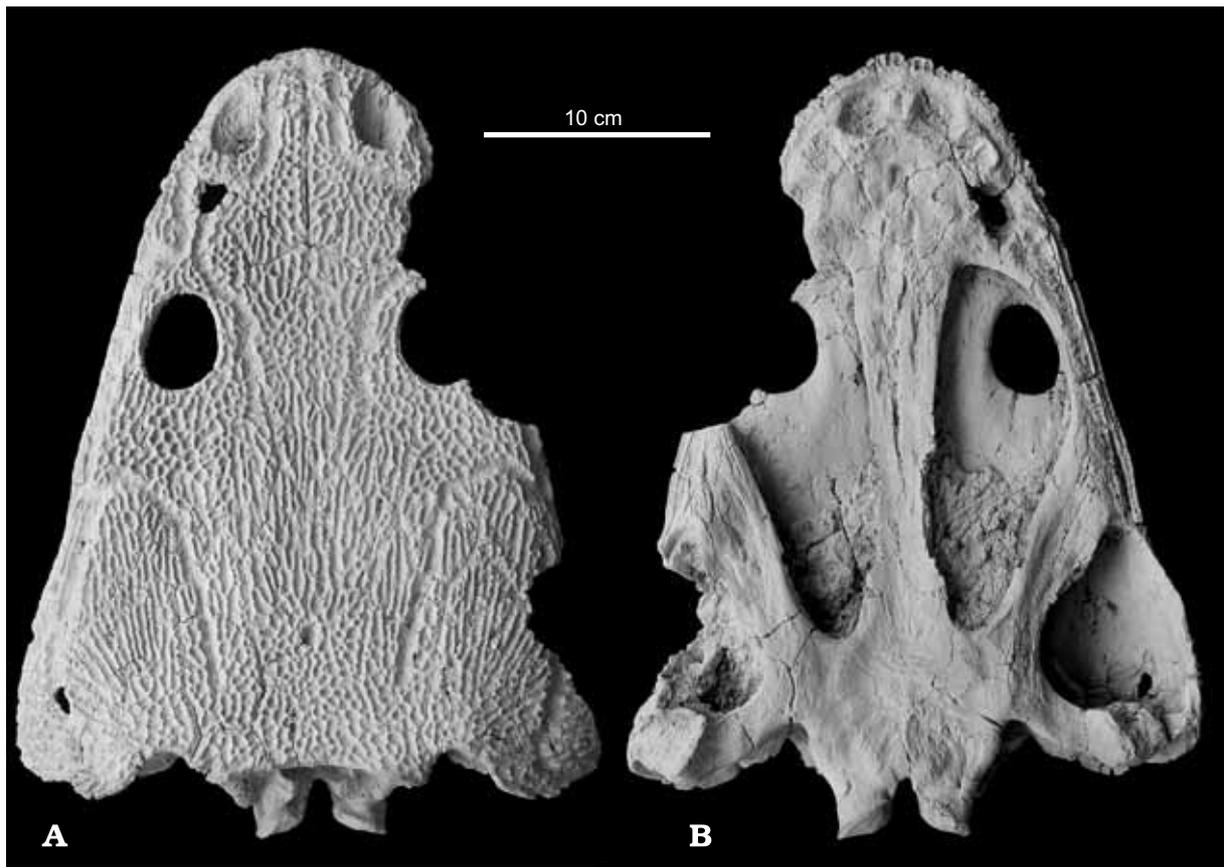


Fig. 6. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Skull ZPAL AbIII/1514 with very short right-nasal left-frontal suture (arrow), in dorsal (A) and ventral (B) views.

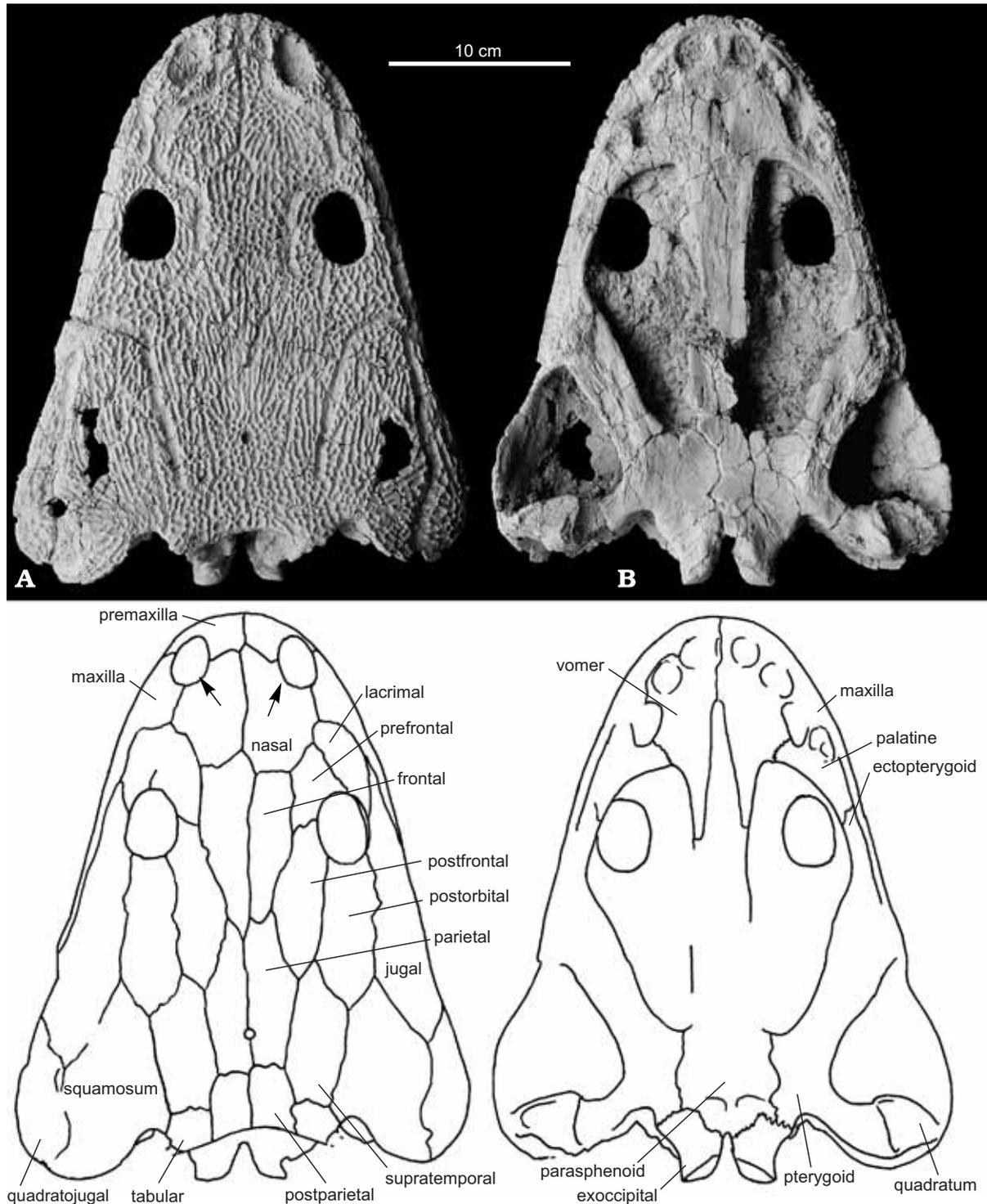


Fig. 7. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Skull ZPAL AbIII/1682, in dorsal (A) and ventral (B) views. Note oval nares (arrowed).

specimens of *Metoposaurus diagnosticus diagnosticus* (SMNS 10825, SMNS 4943, SMNS 5143), the cultriform process is wider than usual in *M. d. krasiejowensis*, but because of great variability of this character in the population from Krasiejów it seems that this difference is not important taxonomically.

Palatine. — The interpterygoid vacuities are laterally framed by the palatine and ectopterygoid. The palatine connects the maxilla laterally, the vomer anteromedially, the ectopterygoid posteriorly, and the lacrimal

dorsally. The palatine bears two tooth arcades and a pair of tusks. The posterior tooth row that continues from the tusks has 8–12 teeth. Their size decreases gradually posteriorly. The parachoanal tooth row consists of 6–9 tiny teeth. The base of the palatal tusk pair is situated posterolateral to the choana. Their lateral wall is elevated above the level of the maxilla surfaces.

Medially to the tusk pair, the palatine is very wide, forming the complete anterior rim of the interpterygoid window. Dorsally, the palatine contacts the lacrimal by a dorsomedially directed blade that meets the lacrimal in a horizontal, flat suture (Figs 1, 5C). This contact was observed in *Benthosuchus* (Bystrow and Efremov 1940), *Mastodonsaurus* (Schoch 1999), and *Cyclotosaurus* (Sulej and Majer 2005). In specimen ZPAL AbIII/1706 (Fig. 5C) preserved in concretion, the palatine forms an additional horizontal thin shelf between the main body of the bone and the shelf that underlies the lacrimal. A similar structure was not observed in other specimens from Krasiejów and the meaning and variability of this character is unknown.

Ectopterygoid. — This element is rather thin, especially in its posterior part. It is longer than the palatine, and forms the smaller part of the interior tooth arcade. The ectopterygoid bears in between 30 and 36 teeth size-decreasing posteriorly. In small skulls, the first tooth of the ectopterygoid is set obliquely to the palatine row (Konietzko-Meier and Wawro 2007). In the larger skulls the continuity of both tooth rows is smooth. The ectopterygoid contacts the maxilla laterally, the palatine anteriorly, the pterygoid posteromedially and the jugal dorsally and posteromedially. It is excluded from the subtemporal window by a large ventral process of the jugal. The ectopterygoid in cross-section is oblique ventromedially. Its slope is continued by the lateral termination of the ventral surface of the palatal ramus of the pterygoid.

Pterygoid. — In all stereospondyls, which have the fused basiptyergoid joint, the rigidity of the skull depends on the pterygoid (Schoch 1999). The pterygoid connects the upper jaws with the quadrate condyles, the cheek region, the occipital condyles, and the floor of the braincase. It consists of four rays: the palatine ramus, the basiptyergoid ramus, the quadrate ramus, and the lamina ascendens, which is a dorsal sheet-like prolongation of the latter.

The largest and most strengthened ramus is the palatine branch, that connects the basal plate of parasphenoid with the jugal, and ectopterygoid. It is stout, markedly widened and never sculptured, in contrary to *Buettneria howardensis* (Sawin 1945: fig. 3).

The palatine ramus is directed parasagittally and widens anteriorly. Its narrowest part occurs at the connection with the basiptyergoid ramus. The palatine branch is flattened anteriorly in cross-section. On the posterior border in its anterior part, it forms the prominent transverse flange (Damiani 2001) directed ventrally. It is very distinctive in all metoposaurids. Dorsally, the palatine ramus bears a slightly marked trough, which is curved posteriorly in the place where it contacts basiptyergoid ramus. The minimum width of the ramus was measured and it is only slightly variable; it has the standard deviation two times smaller than the width of the cultriform process (Fig. 19).

The basiptyergoid ramus is short. It contacts the parasphenoid. On ventral side, the basiptyergoid ramus bears a small prominence, which continues on the palatine ramus. It was not described in other metoposaurids species. On the dorsal side, the basiptyergoid ramus bears the large conical recess. It is well visible in the small skull ZPAL AbIII/36. In this specimen, the conical recess is directed medially, contrary to dorsomedial direction in *Benthosuchus* (Bystrow and Efremov 1940). In the large specimen ZPAL AbIII/17, the pterygoid, the footplate for epiptyergoid, and epiptyergoid are fused into single element and the conical recess is covered by the epiptyergoid.

At the suture with exoccipital, the basiptyergoid ramus bears a vertical wall that probably underlies the lateroventral border of the otic region. Posteriorly the wall continues on the exoccipital. At the base of this wall, both bones contact the parasphenoid. In *Benthosuchus* and *Mastodonsaurus*, this structure was called recessus tympanicus and probably is situated on exoccipitals, not on the pterygoid (Schoch 1999; Bystrow and Efremov 1940). It seems that the recessus tympanicus occurs in *Eryosuchus* (“*Parotosuchus*”) (Howie 1970: fig. 5A), but it is not well visible on the figure if it is on the exoccipital or the pterygoid.

The quadrate ramus is relatively short and stout. It is directed posterolaterally. The ventral surface of the ramus is laterally strongly curved downward to the quadrate. The suture with the quadrate is very long and reaches far dorsally because of the large supratrochlear tubercle, which is well visible in occipital view.

The lamina ascendens is an extended dorsal outgrowth of the quadrate ramus. It is a highly elaborate structure of remarkable thickness. The lamina ascendens contacts with the quadratojugal laterally. Dorsally,

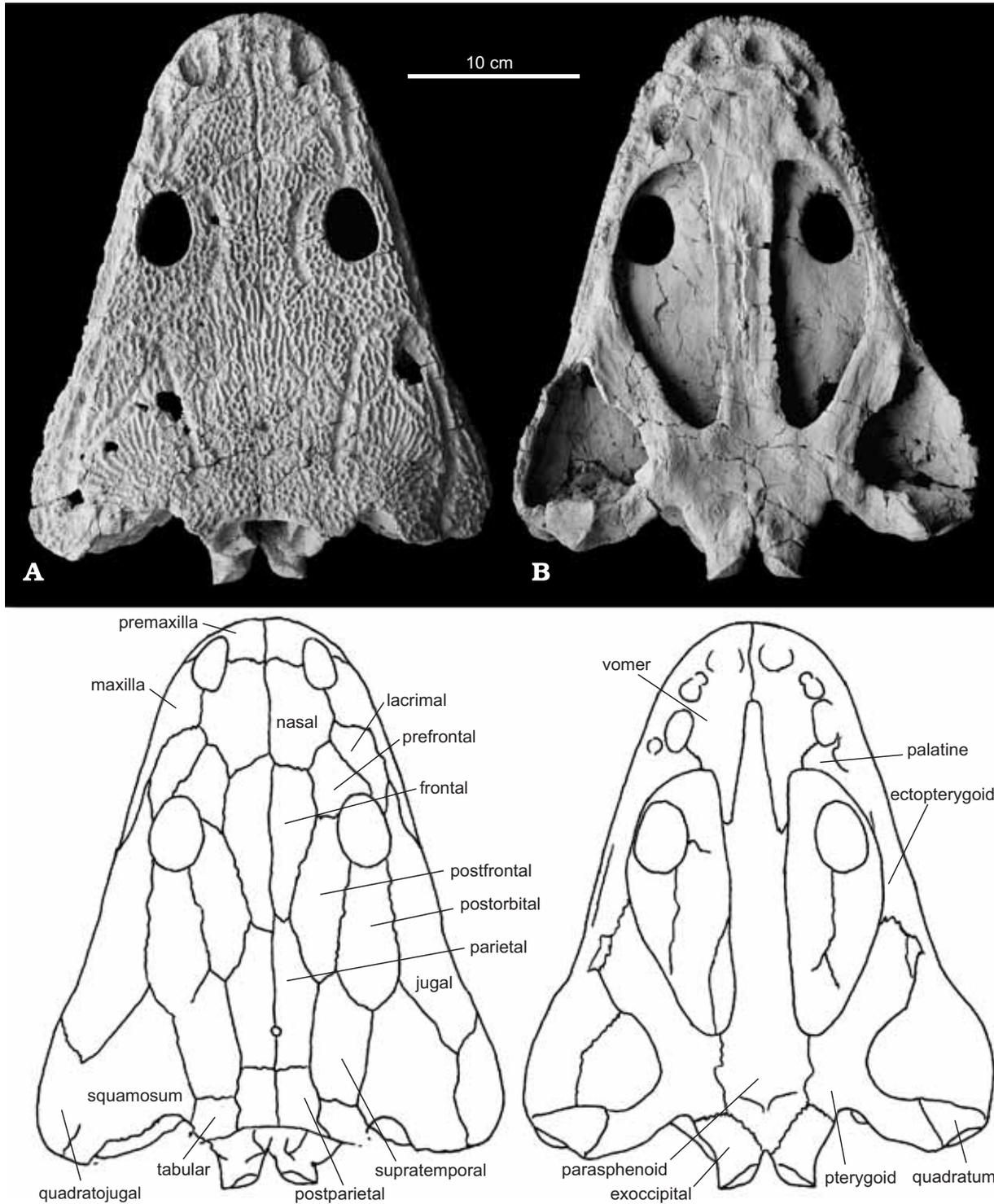


Fig. 8. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Skull ZPAL AbIII/894, in dorsal (A) and ventral (B) views. Note the anterolateral region of nasal with a small network of polygonal pits.

it unites the squamosal by complete fusion with the descending flange of this element, hence entirely closing the occipital surface anterior to the inferred columellar cavity. The suture with the squamosal in occipital view is covered by the oblique crest. The oblique crest is a subvertical, well-ossified blade that is grown out of the dorsal portion of the lamina ascendens of the pterygoid. Its posterior face may be roughened. The lateral edge of the oblique crest is very short, in opposite to medial edge, which reaches ventrally far to the

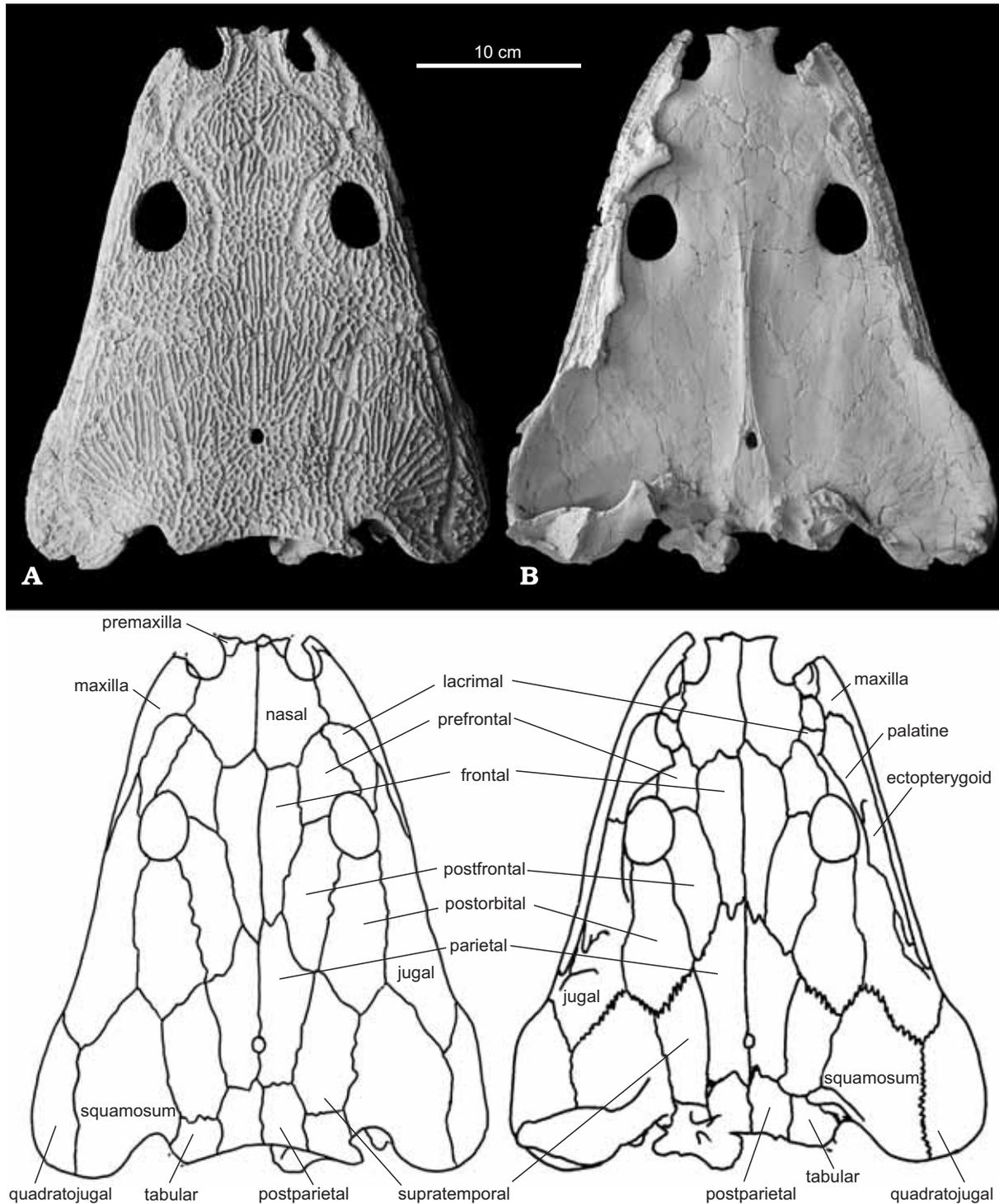


Fig. 9. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. The skull roof ZPAL AbIII/1191 with removed palate, in dorsal (A) and ventral (B) views.

basipterygoid ramus of the pterygoid. Below the oblique crest on the posterior side, there is a deep round recess, the pterygoid depression sinus pterygoidei. It was described only in metoposaurids as sinus pterygoidei by Dutuit (1976) for *Dutuitosaurus*.

Epipterygoid. — It consists of the large basal plate and the dorsal process. Its structure is simpler than in *Mastodonsaurus*, where it consists of six processes (Schoch 1999). The basal plate ventrally bears two rugose surfaces, but the way the epipterygoid contacts the pterygoid is unclear; there are many possible con-



Fig. 10. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. The palate of the skull ZPAL AbIII/1191, in dorsal (A) and ventral (B) views.

figurations. In the largest skull, the entire ventral surface is fused with the pterygoid and it is impossible to localise the proper suture. A medial edge of the basal plate is roughened, and probably contacts with a cartilaginous element of the braincase. Dorsally, it bears many vascular foramina. Posteriorly, the basal plate contacts the lamina ascendens of the pterygoid. The round anterior and lateral edges are slightly roughened. The dorsal process is long and narrow similar to *Paracyclotosaurus* (“*Parotosuchus*”) (Mukherejee and Sengupta 1998) and *Lyrocephaliscus* (Mazin and Janvier 1983).

Quadrate. — Its main body is formed by the trochlea quadrati set in a frame formed by the quadrate ramus of the pterygoid, the lamina descendens of the squamosum and the processes of the quadratojugal (Figs 1, 2). The trochlea consists of two triangular surfaces, the ventral and posterior, which are separated by the posteroventral process of the quadratojugal. The ventral surface is slightly convex sagittally and concave transversely. In the small skulls, the ventral part of the trochlea fills over half of the glenoid area, the rest was probably cartilaginous. In the large skulls, the quadrate is very ossified and fills larger part of the glenoid area. The posterior part of the trochlea is more or less rounded, convex and its surface is always rugose. The quadrate forms additional contact surface with cartilage on the anterior side of the quadrate ramus, which is called *incisura lateralis* (Bystrow and Efremov 1940). It is surrounded by the pterygoid medially, the squamosum dorsally and the quadratojugal laterally (Fig. 2).

The quadrate differs strongly from that of the capitosaurids because of the presence of the triangular posterior part of the trochlea, supratrochlear tubercle, and the almost flat surface of the glenoid. The presence of the supratrochlear tubercle, which was probably the part of the glenoid, differentiates the metoposaurids from most of other stereospondyls. According to Shishkin (1973), it is the tuberculum hyoideum to which the hyomandibulare was primarily articulated. It was described in *Stenocephalosaurus* (Howie 1970; Schoch

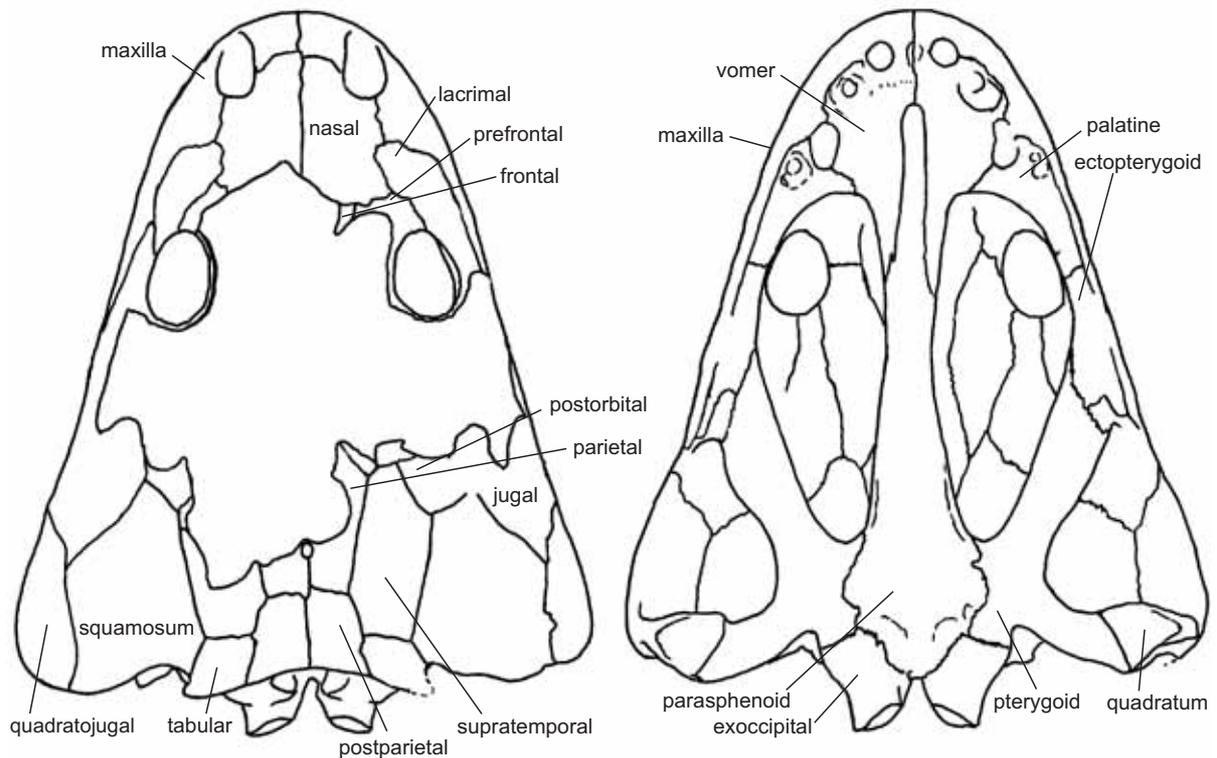
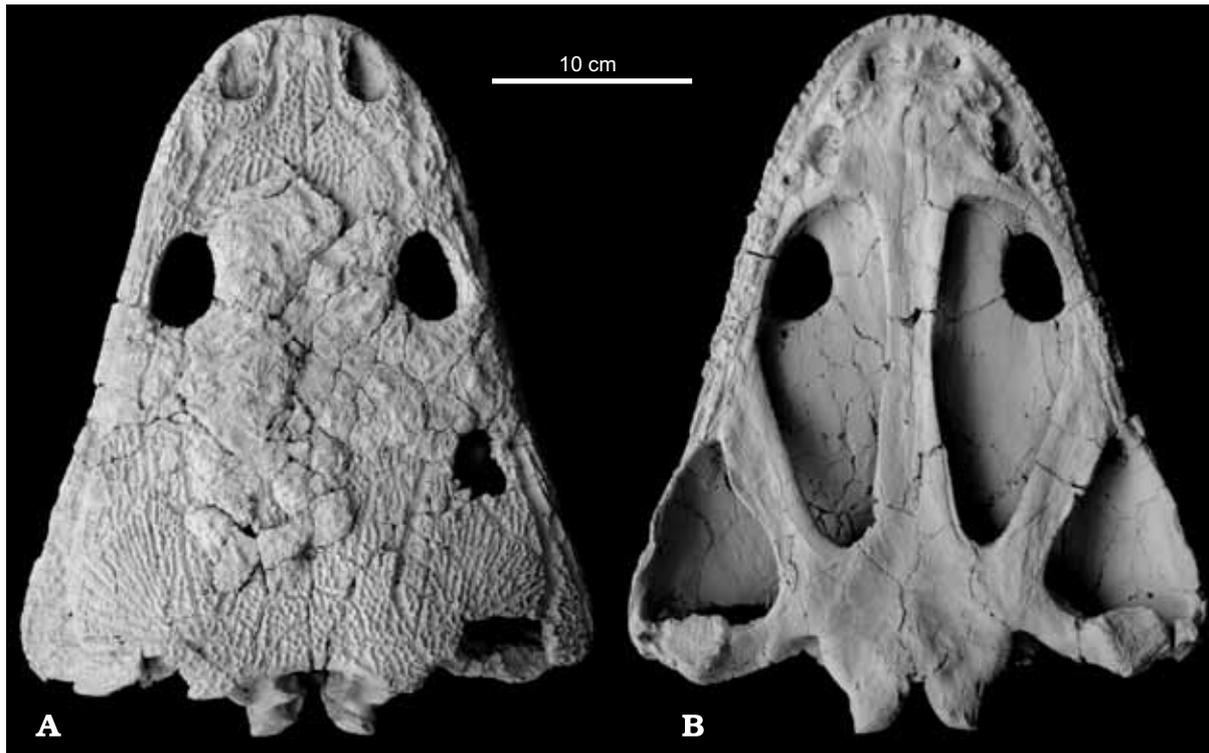


Fig. 11. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Skull ZPAL AbIII/1674, in dorsal (A) and ventral (B) views.

and Milner 2000), *Dvinosaurus* (Shishkin 1973), *Benthosuchus* (Bystrow and Efremov 1940), *Eryosuchus* (“*Parotosuchus*”) *pronus* (Howie 1970), and in *Eolydekkerina* (Shishkin *et al.* 1996). The triangular shape of the quadrate (in ventral view) is similar to *Dvinosaurus* (Shishkin 1973) and different from the rectangular quadrate of most capitosauroids.

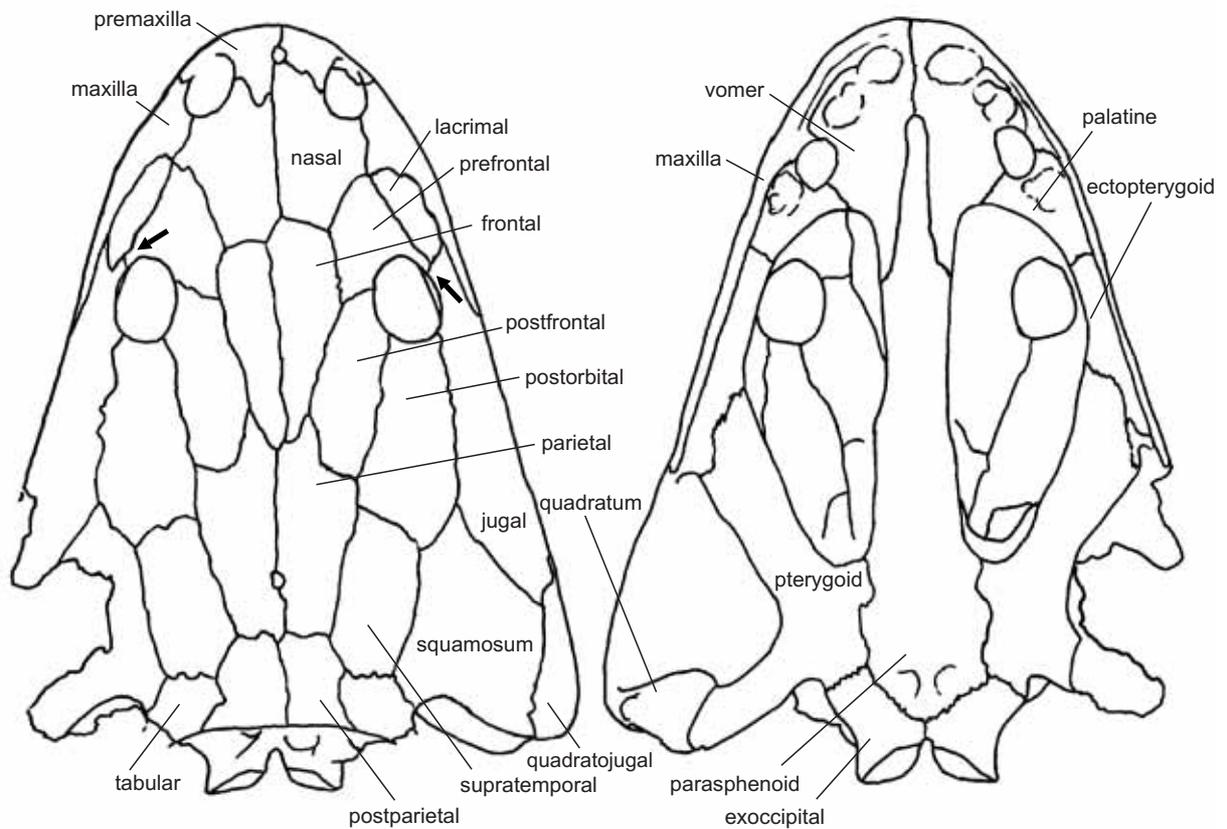
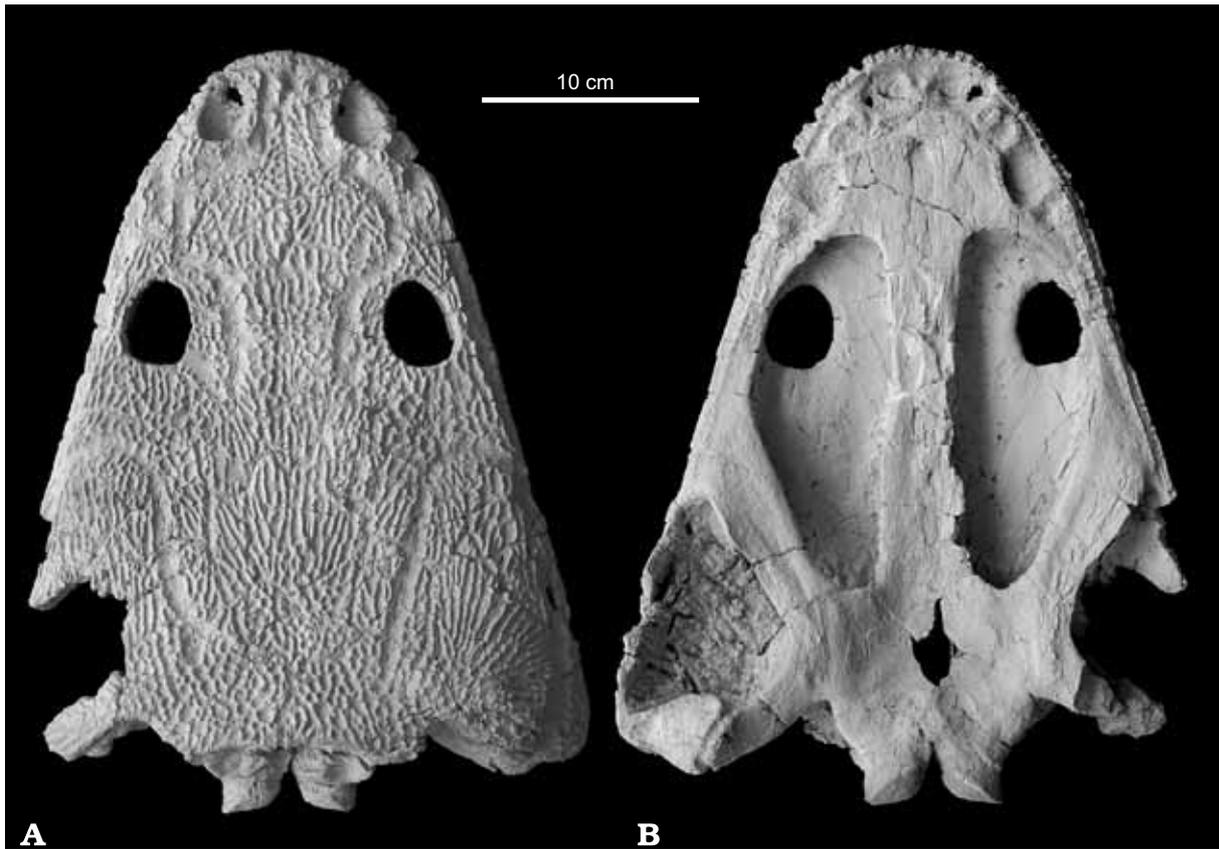


Fig. 12. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Skull ZPAL AbIII/681, in dorsal (A) and ventral (B) views. Note lacrimals excluded from orbital margin (arrowed).

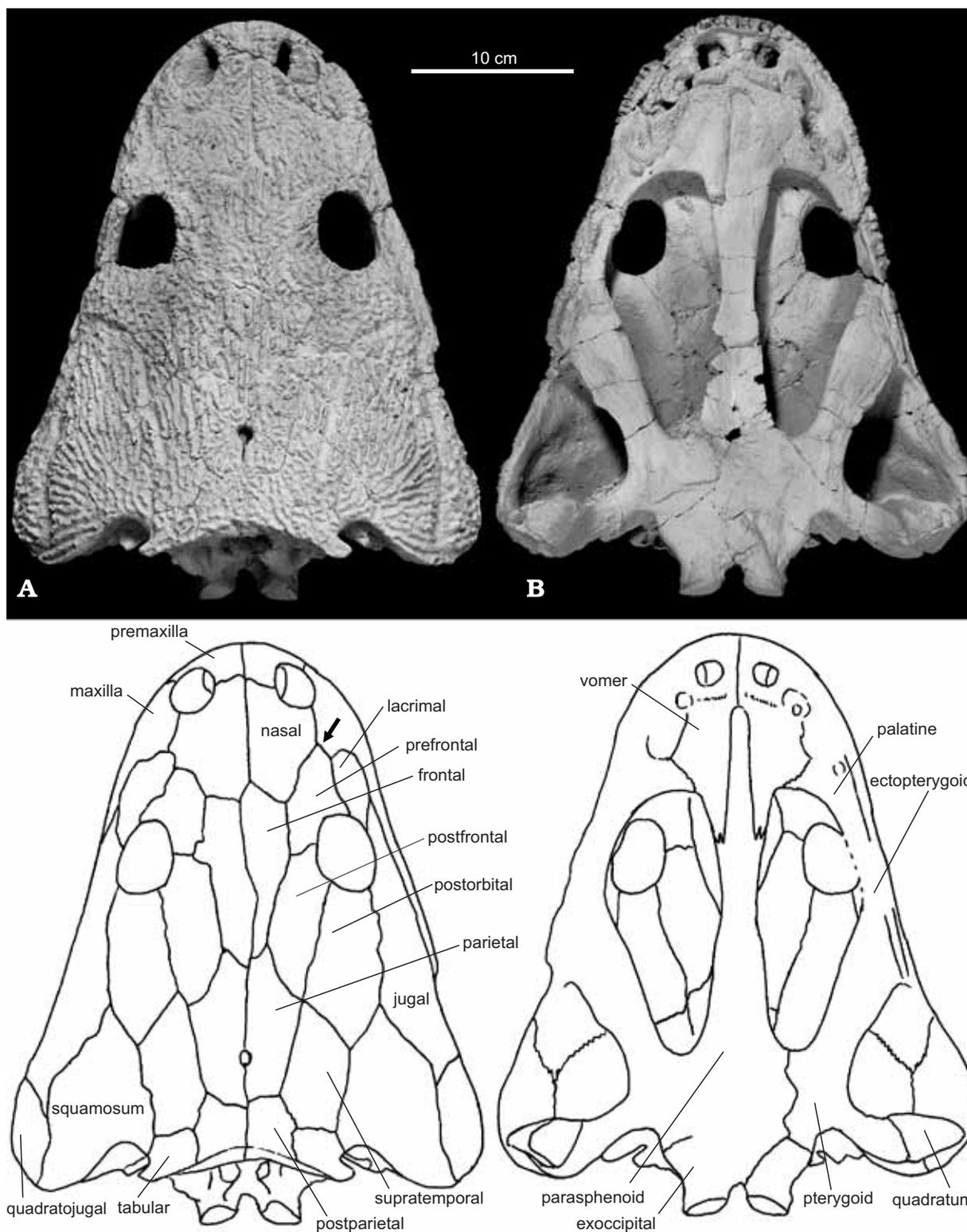


Fig. 13. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Skull ZPAL AbIII/358, the holotype, in dorsal (A) and ventral (B) views. Note anteriorly elongated right prefrontal (arrowed)

The main glenoid area is oblique in occipital view, it was exposed ventrolaterally, in contrast to most capitosaurians. It seems that during the opening of the mouth the mandible rami was curved ventrolaterally (Fig. 21A).

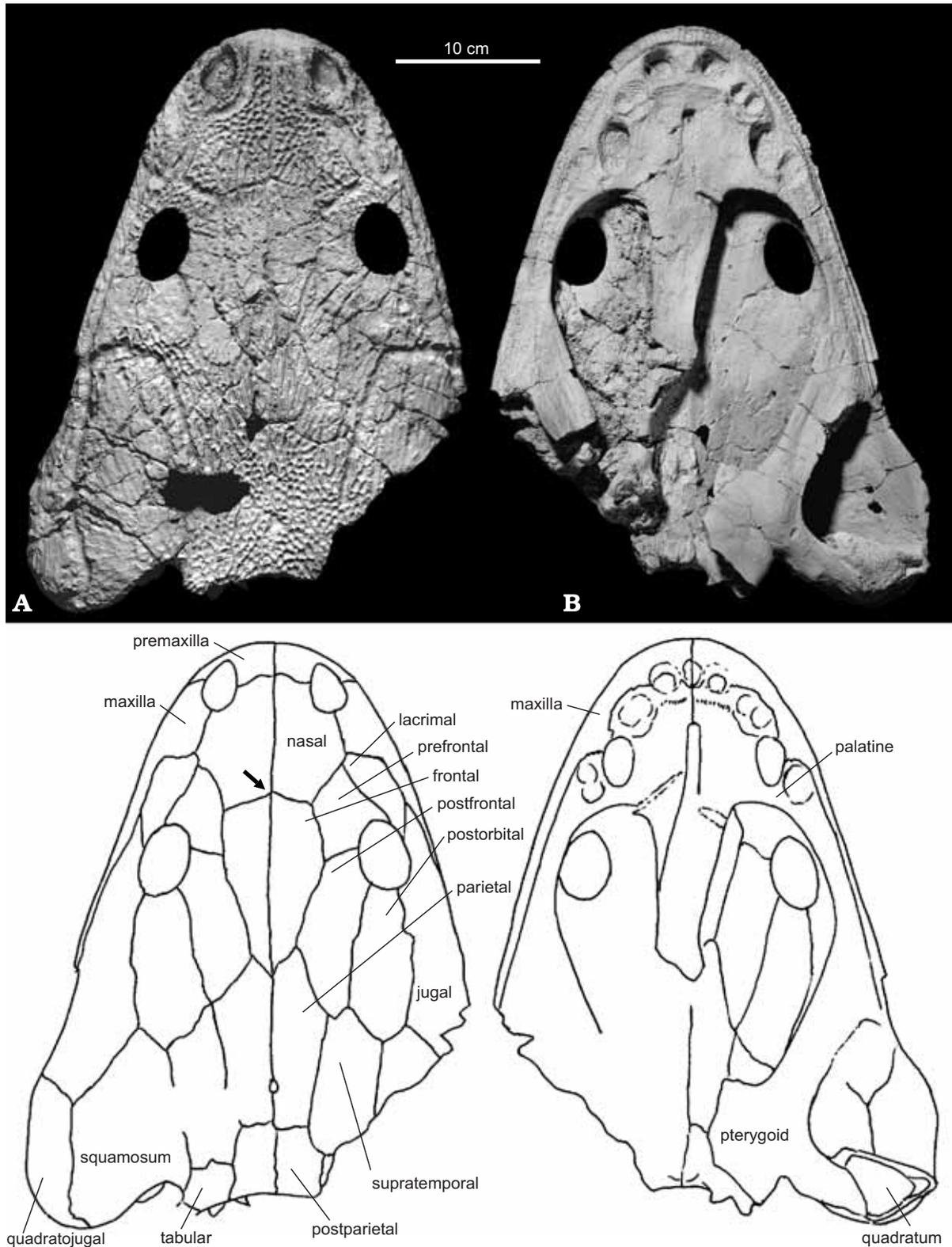


Fig. 14. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Skull ZPAL AbIII/3, in dorsal (A) and ventral (B) views. Note the common anterior top of left and right frontals (arrowed).

Sphenethmoid. — The braincase is not ossified in *Metoposaurus diagnosticus krasiejowensis*. The opisthotic is preserved only in *Dutuitosaurus ouazzoui* and in *Buettneria perfecta*. In *Dutuitosaurus* also the sphenethmoid is preserved. In all metoposaurids, unfinished edges of the exoccipitals strongly indicate the

presence of a cartilaginous basioccipital. It is not possible to demarcate the anterior limit of the basioccipital region. The otic process and basisphenoid were probably cartilaginous and are not preserved.

The sphenethmoid is an unpaired structure in the capitosaurids. In *Dutuitosaurus*, it was described as two blades lying on the cultriform process of the parasphenoid. In the *Metoposaurus diagnosticus krasiejowensis*, it is usually not preserved, only specimen ZPAL AbIII/160 has a blade that may be considered as a part of the sphenethmoid. The very thin and rather short blade lies under the pineal foramen, obviously not in articulation. It is much smaller than in *Dutuitosaurus* and only with difficulties may be considered the sphenethmoid.

Although the otic region was entirely cartilaginous, its position is indicated by a shallow depression on each side of the parasphenoid anterolateral to the basioccipital region. The original position of the main basioccipital body was between the exoccipital condyle facets as in *Trimerorhachis insignis* (Schoch 1999). In metoposaurids, it was cartilaginous and probably attached to roughened medial surface of the submedular process of the exoccipital and covered the basal plate of parasphenoid (basioccipital fossa). Anteriorly, it was probably restricted to the area framed by the paroccipital crest.

Supraoccipital region. — It was cartilaginous as in most temnospondyls. Bystrow and Efremov (1940) described the medial process of columna verticalis of the exoccipital as the lamellose process that supported the cartilaginous supraoccipital. The lamellose process is very massive in metoposaurids and its dorsal surface is rugose. It seems that it is the trace of the contact of the exoccipital with cartilaginous supraoccipital. Dutuit (1976) described the lamellose process as ossified supraoccipitalis but there are not any sutures between the exoccipital and the lamellose process elements and they form an evident unit.

Stapes. — Some Krasiejów specimens of *Metoposaurus diagnosticus krasiejowensis* have the stapes preserved in articulation (Fig. 15), in others it is disarticulated but exceptionally well-preserved.

The stapes is long and slender (Fig. 1). It consists of an elongated shaft (stylus columellae), which ends abruptly at the distal end and has a bifurcating proximal termination. The shaft of the stapes is flattened anteroposteriorly with the sharp anterior edge. In most specimens, it is compressed by the compaction and the groove on the posterior surface is visible. But well-preserved specimens show that originally it was drop shaped in cross-section. The shaft is smooth. The distal end is oval and its surface is roughened suggesting a cartilaginous continuation.

The proximal portion consists of two heads, which are asymmetric in shape, size and inclination towards the proper shaft: a ventral proximal head (processus basalis or basal process) and a dorsal proximal head (caput columellae or footplate). The latter is much larger and more distinctly inclined towards the long axis of the shaft. Its proximal end has the shape of a drop and is concave and roughened. A similar heads morphology was described for *Mastodonsaurus* (Schoch 1999).

The basal process is well preserved in ZPAL AbIII/11. Its head is reniform. The basal process is supported by two walls that run toward it from the base of the proximal head. In specimens ZPAL AbIII/1517, AbIII/1679, and AbIII/1392, the basal process lays on the lateral edge of the parapterygoid crest of the parasphenoid. It is a probable position of articulation. This connection is not as complicated as Schoch (1999) described for *Mastodonsaurus*. It is more similar to *Benthosuchus*, although the stapes of *Metoposaurus* from Krasiejów is more regularly shaped (Bystrow and Efremov 1940). A similar stapes was described for *Buettneria howardensis* by Sawin (1945). It seems that the stapes of *Dutuitosaurus* are different than in *Metoposaurus diagnosticus krasiejowensis* in the details but they are worse preserved. In many specimens from Krasiejów, the stylus columellae of the stapes lay on the oblique crest of the pterygoid. This position is probably the result of postmortem dislocation of the stapes.

Exoccipital. — The exoccipital is a very strongly ossified element in all metoposaurids. It is basically five-rayed represented by anterodorsally directed columna verticalis, which bifurcates and contacts the supraoccipital process of the postparietal, and parotic process of the tabular (after Bystrow and Efremov 1940). The columna verticalis medially bears the lamellose process. The subtympanic process contacts the pterygoid, and the condylus occipitalis. Ventromedially to the columna verticalis, there is the submedular process that forms a horizontal shaft directed medially (Fig. 5). The occipital condyles are round or oval and strongly concave vertically and horizontally. They are situated posteriorly to the quadrate condyles. In occipital view, they are situated slightly above them.

The lamellose process in metoposaurids is very large in comparison to the columna verticalis. The opposite situation is in *Benthosuchus*. The columna verticalis sometimes bears additionally a small processus

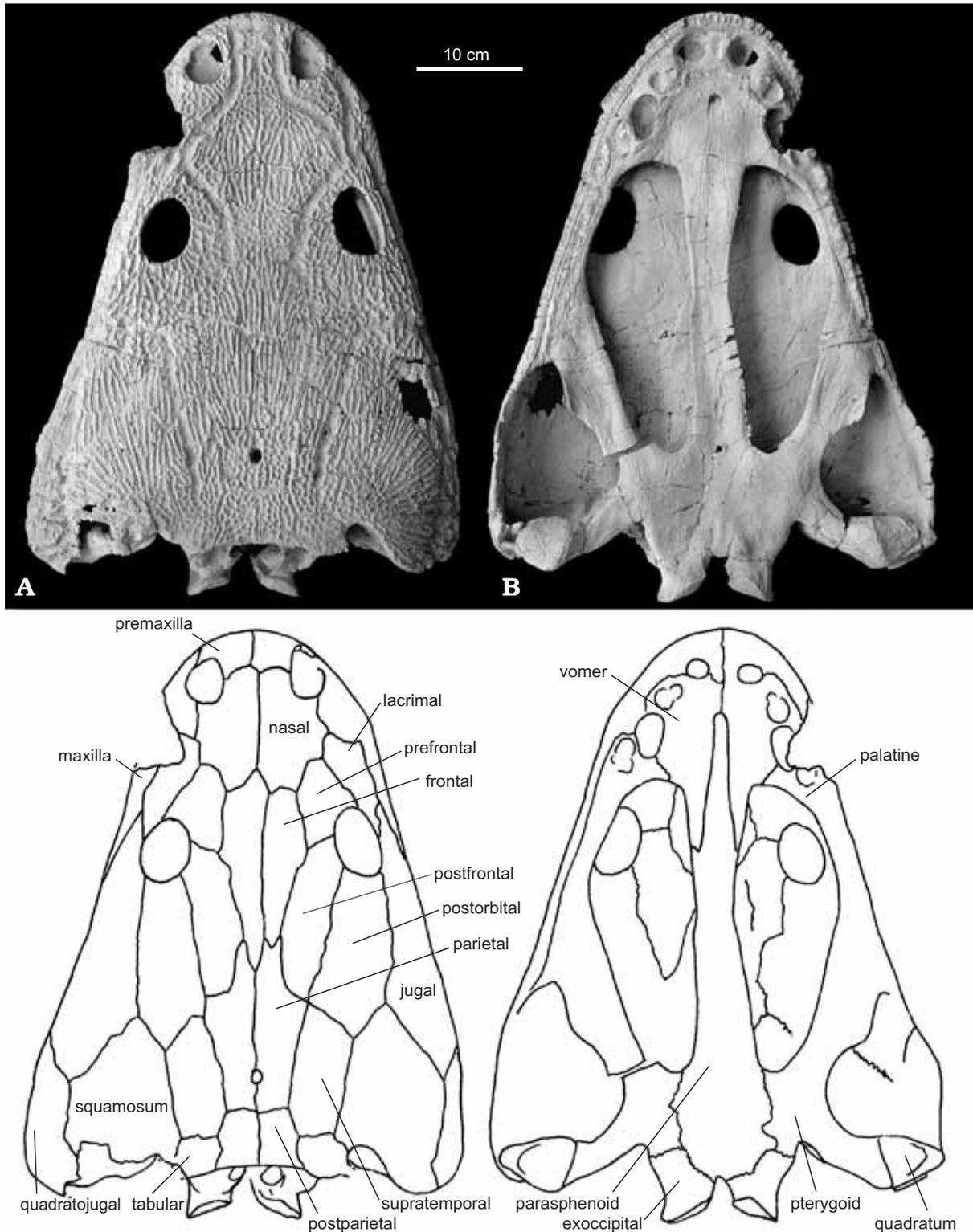


Fig. 15. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. The largest skull ZPAL AbIII/1192, in dorsal (A) and ventral (B) views.

directed anterodorsally. The submedular process is very large. It bears the surface to contact the cartilaginous basioccipital. It continues into the lateral edge of braincase on the subtympanic process and farther on the pterygoid. The subtympanic process is very massive and forms a very strong suture with the pterygoid.



Fig. 16. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. The skulls in occipital view (not to scale).
 A. ZPAL AbIII/358. B. ZPAL AbIII/1517. C. ZPAL AbIII/1674. D. ZPAL AbIII/894.

The metoposaurid exoccipital encloses two narrow channels. The larger and more dorsal of them traditionally is interpreted as a canal for cerebral nerve X (Dutuit 1976) or hypoglossal nerve (Sawin 1945), but both of them run toward the inside of the bone and seem to be for veins. The X nerve laid probably on the subtympenic process anteriorly to columna verticalis. The exoccipitals form lateral edges of the foramen magnum. It is large and high, with a keyhole-shaped outline. It is bordered laterally by strong columnae verticals and the massive lamellose process. The foramen magnum is roofed by the postparietals and floored by the parasphenoid.

Dentigerous ossicles. — Numerous dentigerous ossicles are preserved (Fig. 2) in specimen ZPAL AbIII/1675/1, in the sediment under the vomer. They seem to be unordered and only some of them contact the vomer. Similar ossicles are described in *Sclerocephalus haeuseri* Goldfuss, 1847 from the Early Permian of Germany by Boy (1988), in *Balanerpeton woodi* Milner *et* Sequeira, 1994 from the Viséan of Scotland

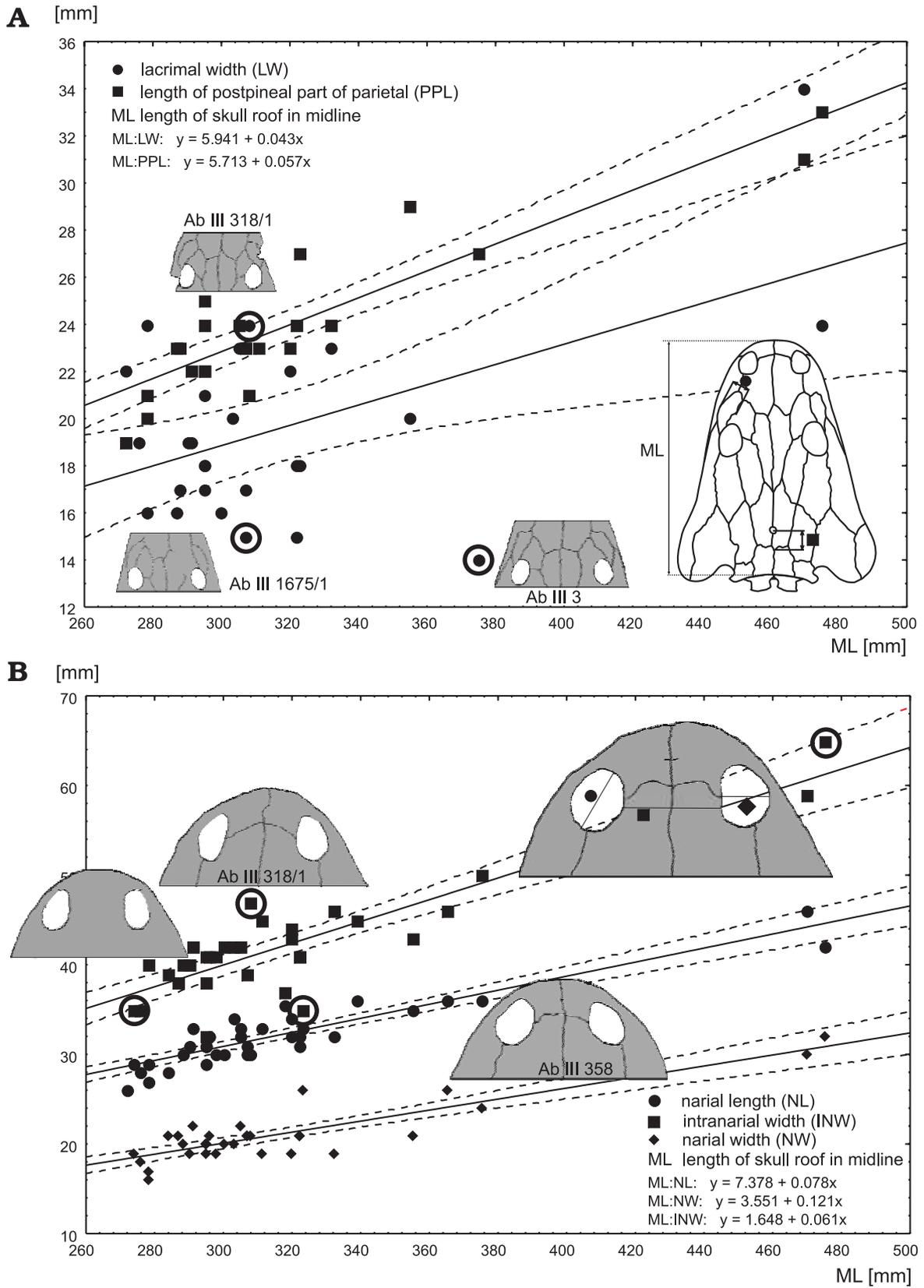


Fig. 17. Scatter-plots showing variability of some skull parameters in *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002. **A.** Width of lacrimal and length of the postpineal region of parietal. **B.** Width between nares, length and width of nares. Note two times larger standard deviation of width of the lacrimal than length of the postpineal region, and distance between the nares than their length and width. Dashed lines show standard deviation. For discussion see p. 115.

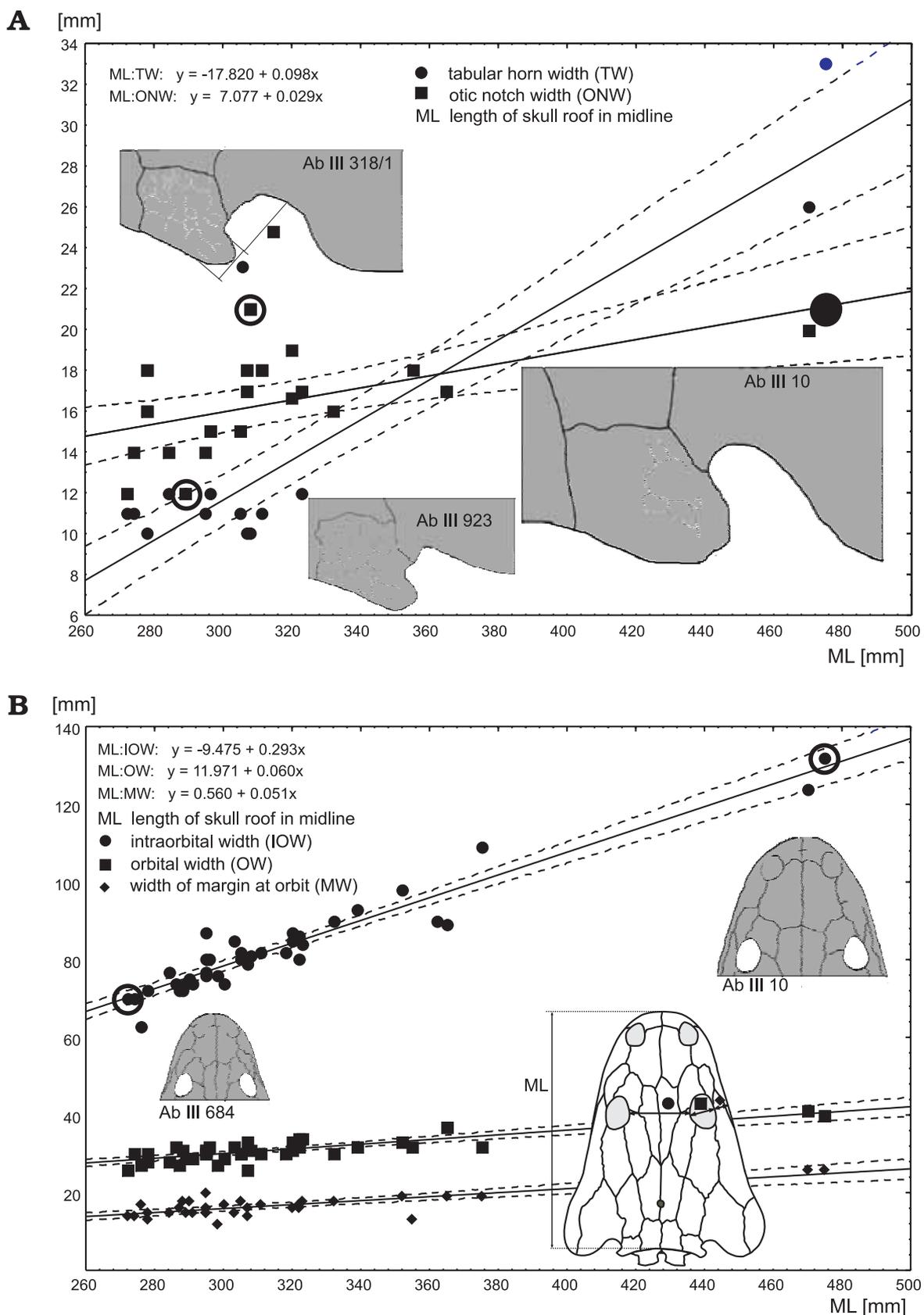


Fig. 18. Scatter-plot showing differences in growth rates of cranial parts in *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002. **A.** Width of otic notch and tabular horn. **B.** Width of orbits and skull roof between orbits and width of lateral margin of skull at level of orbits. Dashed lines show standard deviation. For discussion see p. 115.

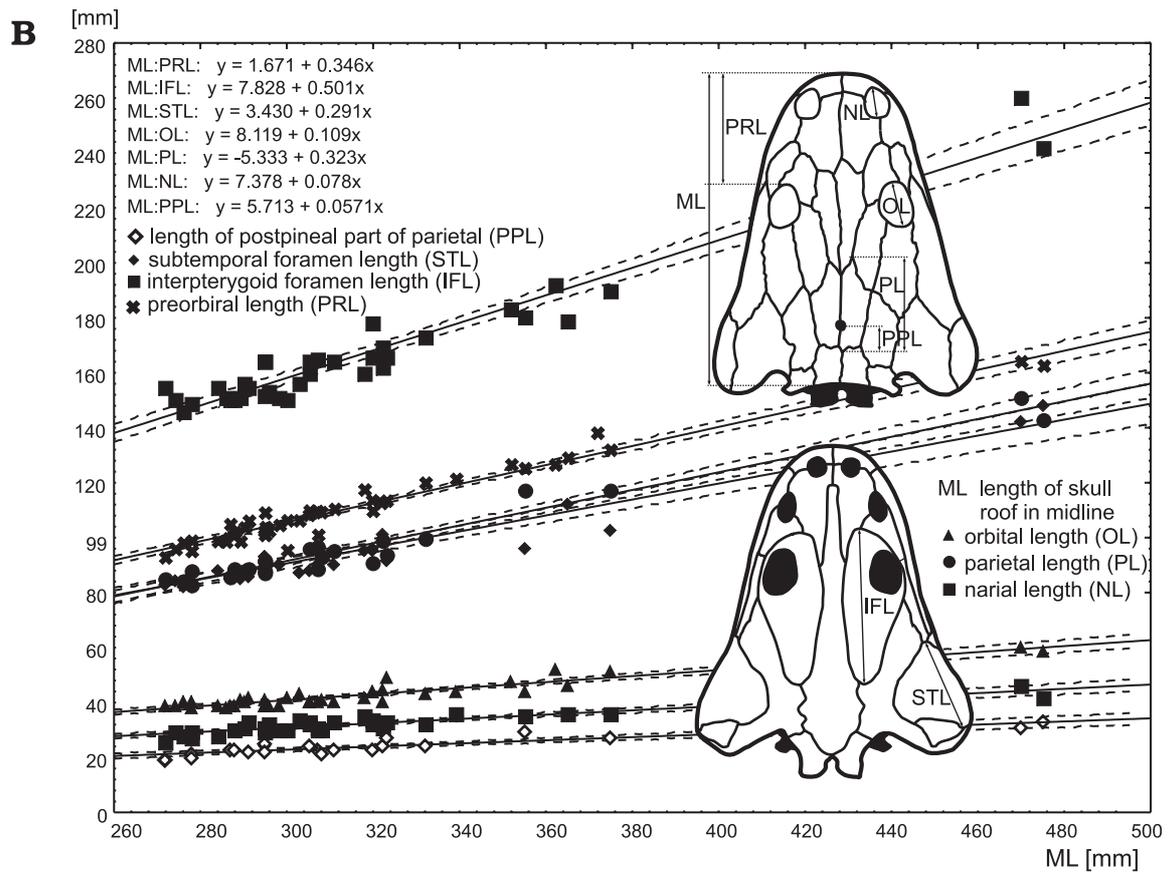
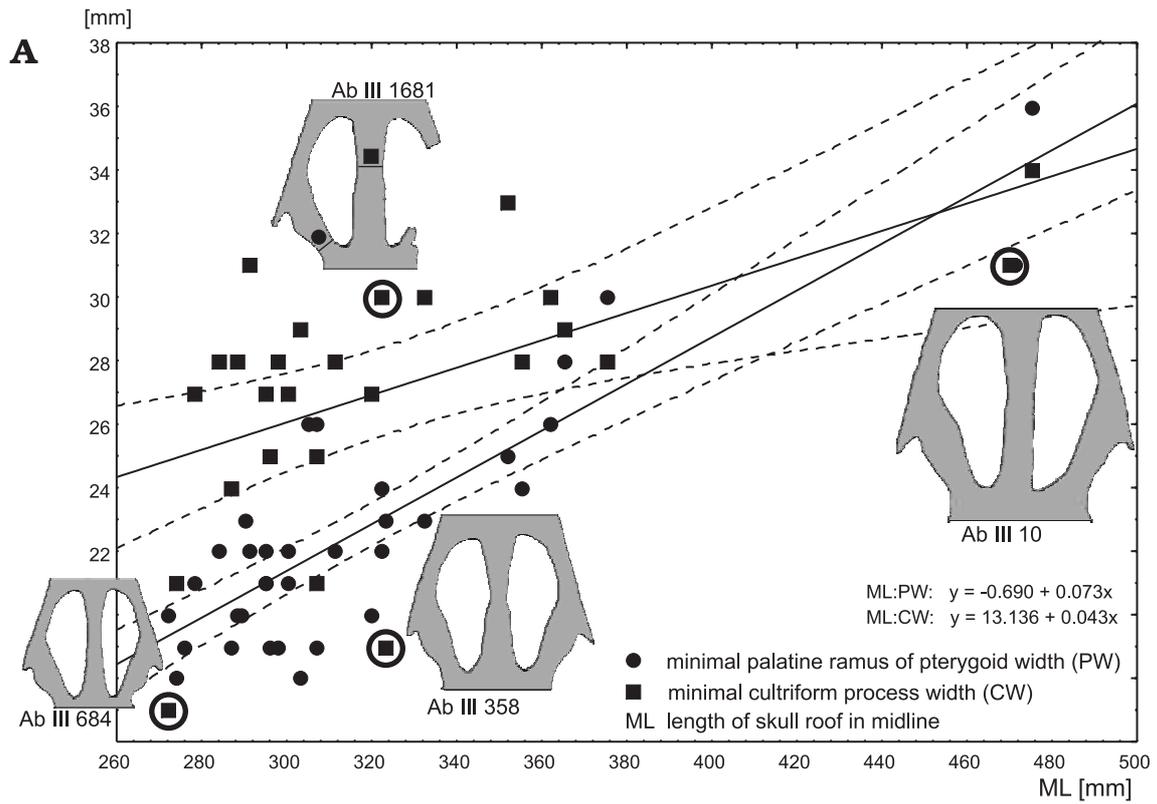


Fig. 19. Scatter-plots showing variability and differences in rate of ontogenetic growth of some skull parameters in *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002. **A.** Width of cultriform process and of palatal ramus of pteryoid. **B.** Growth rates of various skull parameters. Dashed lines show standard deviation. For discussion see p. 115.

(Milner and Sequeira 1994), in *Apateon dracyiensis* Boy, 1972 from the Early Permian of Thuringian Forest (Werneburg 2001), and in *Trematolestes hadgorni* Schoch, 2006 from the Mid Triassic of Baden-Württemberg. They probably ossified in the skin and filled the interpterygoid vacuity as reconstructed in *Sclerocephalus* by Schoch and Milner (2000) and *Trematolestes* (Schoch 2006).

MANDIBLE

General structure. — The metoposaurid mandible was studied in detail by Romer (1947) and Jupp and Warren (1986). The Krasiejów material agrees in most aspects with other metoposaurid mandibles, but reveals a great deal of new information (Figs 1A, 2B, 20, 21). The extended symphysis is formed by the dentary and splenial. There was a paired cartilaginous mentomandibular connecting the rami of the mandibles. The symphysis bears the continuous marginal tooth row, a pair of large tusks on each side and row of teeth posterior to the tusks. The glenoid foramen is typical for metoposaurids, although in some specimens the whole glenoid and part of the postglenoid area is ossified. The jaw has two large openings, the lingually situated Meckelian window and dorsally situated adductor window. In *Metoposaurus diagnosticus krasiejowensis*, like in most metoposaurids, the prearticular forms a part of the glenoid area, the hamate process is remarkably high. The glenoid region consists of two slopes of the medial sagittal ridge. The medial slope is much larger and extends far anterodorsally to form the hamate process by participation of the prearticular. Posteriorly, it forms horizontal surface to contact with the supratrochlear tubercle of the quadratum.

Similarly to *Mastodonsaurus*, the *Metoposaurs* from Krasiejów does not support the concept of two types of postglenoid area proposed by Jupp and Warren (1986) for the temnospondyls. Indeed, *M. diagnosticus krasiejowensis* shares similarities with both types, although there are also characters that differentiate it from both types. It is similar to the type I in that the posterior extremity of surangular forms an arcadian process, chorda tympanic foramen is located on the prearticular at the suture with the articular, and the arcadian groove is present. It is similar to type II in that the angular and prearticular participate in the postglenoid area, the articular is surrounded by the surangular, and the prearticular, if ossified, is exposed dorsolingually in most of the specimens.

The surangular forms the most posterior extremity of the postglenoid area. In the concept of Jupp and Warren (1986), the marginalis canal (mandibular in their terminology) is prominent in the type I, and the dentary canal (oral) is prominent in the type II. In *M. diagnosticus krasiejowensis*, both canals are present and their contribution is equal (Fig. 3C).

The concave and roughened surface of the symphysis suggests the presence of the cartilage between the ramus and probably it was the mentomandibular. Schoch (1999) proposed for *Mastodonsaurus* a loose articulation of the two jaw rami. The opposite situation is in *Cyclotosaurus intermedius* (Sulej and Majer 2005) that has large and flat surface of the symphysis with the track of the suture. In articulated specimens of *Cyclotosaurus* from Krasiejów, it is visible that the two rami are strongly united.

The ventral border of the mandible is unusually straight in *M. diagnosticus krasiejowensis*. It might indicate that these animals laid the head on a ground while lying on the bottom. The flat skull roof and low and straight mandible gives an enormously flat head.

Surangular. — It wedges in between the dentary and angular, then frames the glenoid area of the articular anteriorly and labially, and further backwards it forms the labial part of the postglenoid area (Fig. 1A). Anteriorly, the surangular builds the complete labial margin of the adductor window and forms a part of the adductor chamber, as well. The top of the labial wall of the adductor chamber forms torus arcuatus (Bystrow and Efremov 1940), which has widened and slightly concave border. Contrary to *Mastodonsaurus*, the surangular forms only a part of the torus arcuatus. The coronoid forms its anterior part. The torus arcuatus is covered by numerous parallel stripes and ridges suggesting insertion of musculature. The shape of the torus arcuatus is very variable, the lingual edge may be flat like in ZPAL AbIII/1693 or may form a vertical wall like in ZPAL AbIII/41 (Fig. 20). The surangular meets the coronoid in a broad, serrated suture. The suture with the dentary runs on the labial side ventral to the torus arcuatus. A long posterior lappet of the dentary overlaps an elongate depression of the surangular.

The labial side of the surangular is characterised by sculpturing which consists of short grooves. It bears the dentary canal and articular canal; however, there is no accesorius canal like in *Benthosuchus* and *Mastodonsaurus* (Bystrow and Efremov 1940; Schoch 1999). The dorsal surface of the postglenoid area has

a deep groove aligned to the long axis of the mandible, the postglenoid fossa (Schoch 1999). The postglenoid fossa varies considerably in the width and the depth, but is always straight. In most cases, the surangular is divided from the prearticular by more or less ossified articular, but in ZPAL AbIII/647 the articular is covered by the surangular and the prearticular.

In contrast to chigutisaurids (Sengupta 1995; Warren 1981; Warren *et al.* 1997; Warren and Black 1985), the surangular forms the medial plate similarly to *Cyclotosaurus* (Sulej and Majer 2005) and *Eryosuchus* (“*Parotosuchus*”) (Howie 1970). In *Plagioscutum* (Shishkin 1987) the surangular forms a small lateral prominence. In *M. diagnosticus krasiejowensis*, the medial plate formed by surangular extends very deeply ventrally.

The surangular forms most of the labial part of the jaw articulation. Lingual to the glenoid the surangular forms the wide, generally flat (in the largest mandible ZPAL AbIII/1693 there is prominent ridge on the labial edge) and horizontal surface with a distinctive groove, in which there is a surangular foramen (Shishkin *et al.* 2004) for neurovasculature.

Angular. — It is one of the major ossifications in the posterior half of the mandible, forming the lateral wall and bottom of the adductor chamber. The angular is wedged in labially between the surangular, dentary, and the postsplenial and lingually between the prearticular, surangular, and the articular (if ossified). The entire element is relatively tall (Fig. 3C). Its lingual surface is smooth. The sculpturing starts abruptly exactly at the turning point towards the ventral side. Ventrally, it bears the mandibular canal (sulcus marginalis) in the postglenoid region. The labial side is covered by sculpturing. The sculpture consists of long radial rays of ridges that converge towards a small area slightly posterior to half of the bone.

The dentary is overlapped along its contact to the angular. The sulcus is covered with ridges and at the margin of the angular the dentary ascends abruptly and can be recognised by its smoothness. Anteroventrally, the angular is overgrown by a thin lappet of the sculptured postsplenial. Posteriorly, the angular forms the ventral keel up to the posterior end of the postglenoid area in contrast to the Platystegidae, Almasauridae, Benthosuchidae, Lonchorynchinae, and Trematosaurinae, where the angular is much shorter posteriorly (Schoch and Milner 2000). In this area, the angular supports the articular, if ossified. Lingually, the angular forms a straight suture with the prearticular and it builds the posteroventral margin of the Meckelian window.

Postsplenial. — It forms the ventral keel of the mandible in its middle. It extends dorsally on labial (slightly) and lingual sides (Fig. 3C, D). On the lingual side, it extends almost to the half of the mandible height and contacts the angular and prearticular posteriorly, the coronoid and intercoronoid dorsally, and the splenial anteriorly. It forms the anteroventral margin of the Meckelian window and bears the anterior Meckelian foramen. Labially, the postsplenial contacts the angular, the dentary dorsally, and the splenial anteriorly. The surface of this part is intensely sculptured by irregular pits and grooves.

Splenial. — The shallow splenial aligns to the postsplenial anteriorly and participates in shaping of the symphyseal region (Fig. 3C, D). It forms the ventral margin of the symphysis that is strongly concave in ventral view. It contacts the postsplenial posteriorly, the intercoronoid and precoronoid dorsally on the lingual side, and the dentary anterodorsally. The lingual side of the splenial is smooth. The sculpturing on the labial side is weaker than that of the postsplenial. It mainly consists of shallow pits and short grooves.

Articular. — It forms the jaw articulation (Fig. 1A). In the small specimens, the articular is not preserved (ZPAL AbIII/399 and AbIII/501). In the most numerous medium size specimens, it is partly preserved. In these specimens, only the posterior part of the glenoid is ossified. It forms a tubercle, described as the postglenoid ridge by Jupp and Warren (1986). This tubercle probably contacted the supratrochlear tubercle of the skull. The fact that this part of the articular firstly ossified suggests that the connection between these elements was very loaded, that happened only at wide opening of the mouth. It suggests that metoposaurids opened the mouth with large force, which opposed against a resistance of water.

In a few cases, entire articular is preserved, which is not related to size of the mandible. In these specimens, the articular extends anteriorly up to the termination of the hamate process. When the glenoid area is entirely ossified, the articular forms a posterior spine that produces the dorsal margin of the postglenoid area. A posterior tongue of the articular extends posteriorly between the surangular and the prearticular along the dorsal surface of the retroarticular process, which differentiates brachyopid, plagiosaurid (Hellrung 2003) and metoposaurid mandibles from those of other Triassic temnospondyls (Warren 1981). It suggests the

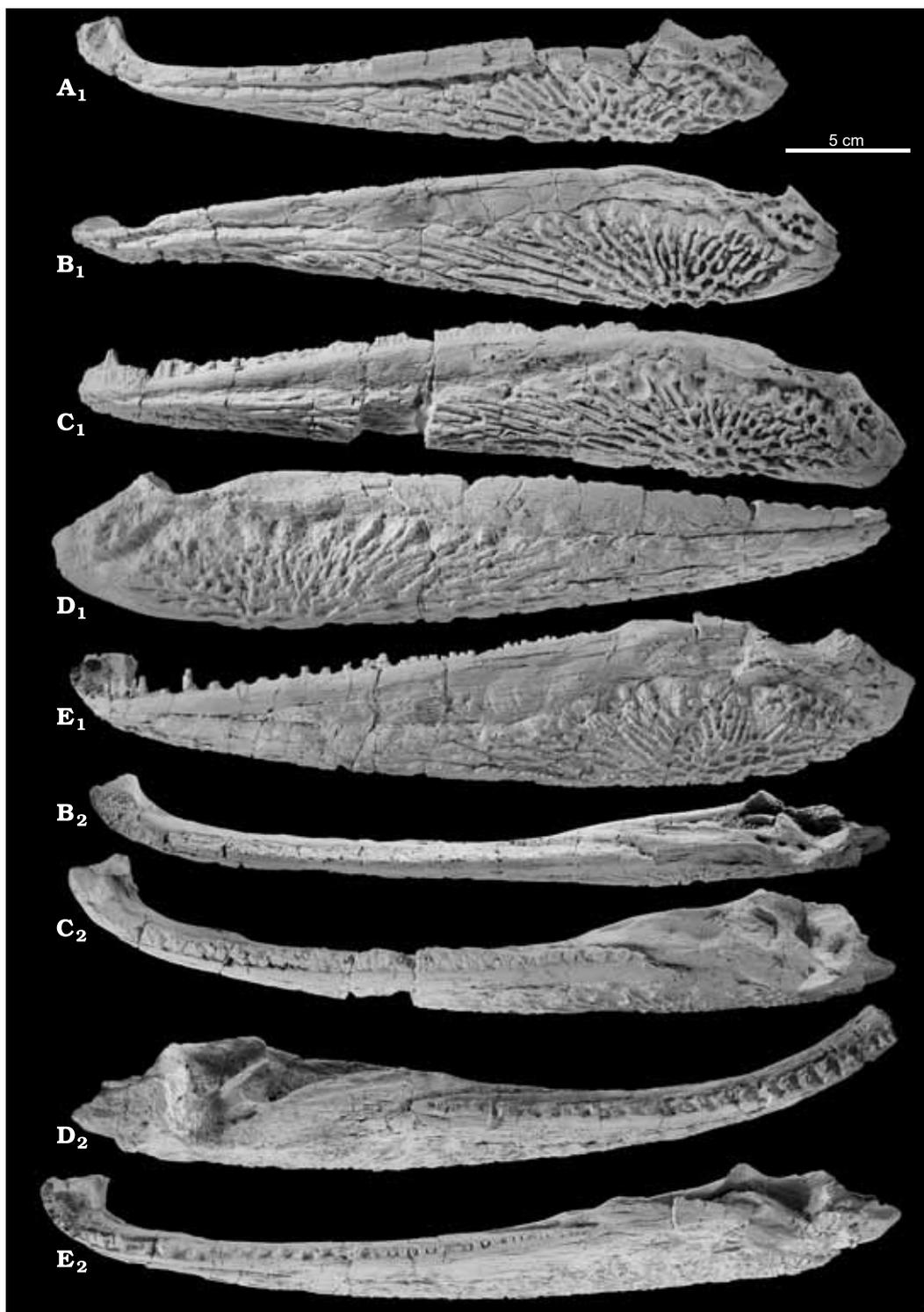
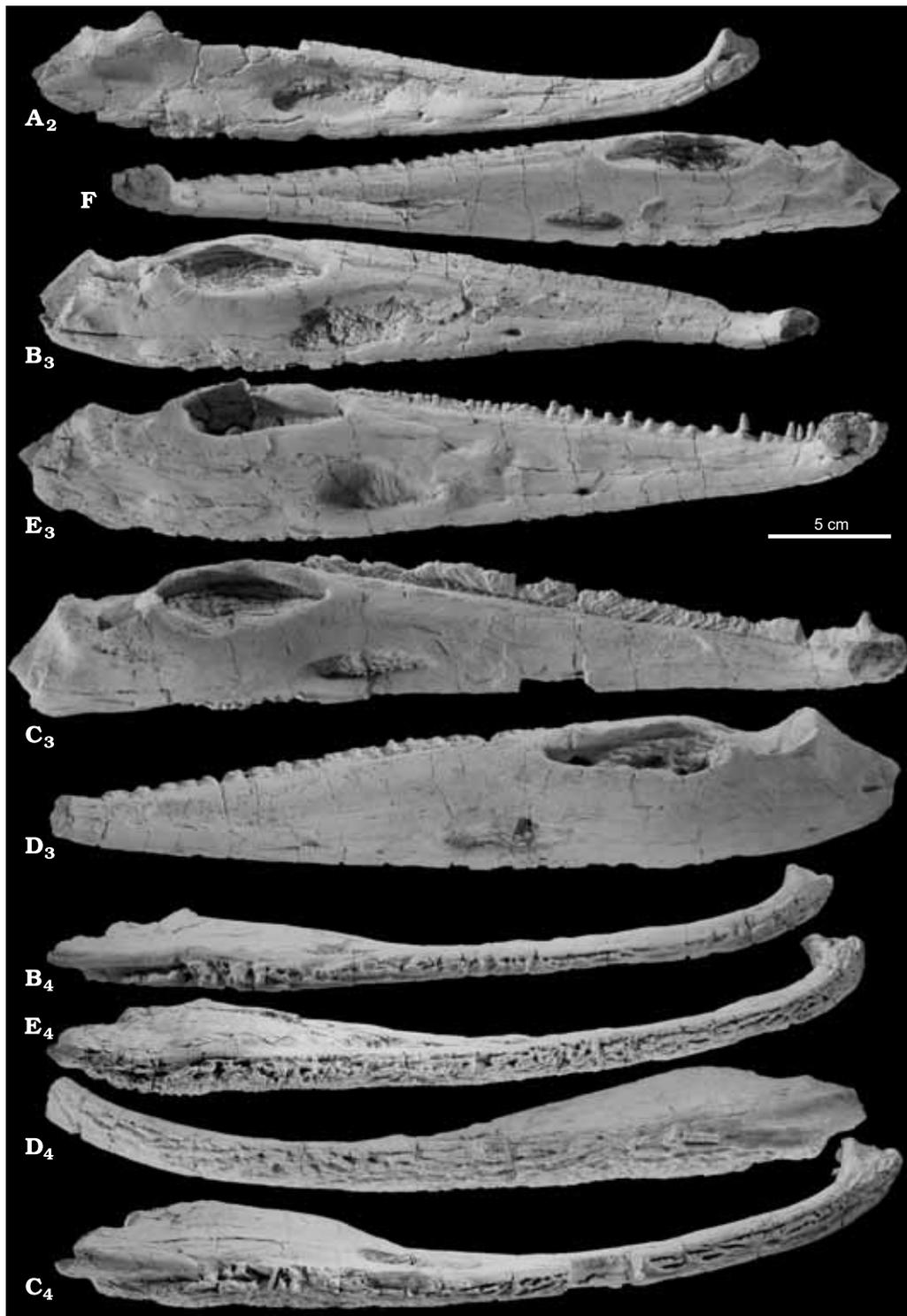


Fig. 20. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of mandibles. **A.** ZPAL AbIII/501, in labial (A₁) and lingual (A₂) views. **B.** ZPAL AbIII/399, in labial (B₁), dorsal (B₂), lingual (B₃), and ventral (B₄) views. **C.** ZPAL AbIII/41, in labial (C₁), dorsal (C₂), lingual (C₃), and ventral (C₄) views. **D.** ZPAL AbIII/51, in labial (D₁), dorsal (D₂), lingual (D₃), and ventral (D₄) views. **E.** ZPAL AbIII/1663, in labial (E₁), dorsal (E₂), lingual (E₃), and ventral (E₄) views. **F.** ZPAL AbIII/1678, in lingual view.

close relationship between these groups. The posterior part of the articular extends ventrally to the angular. In a few cases, the dorsal edge of the postglenoid part of the articular is covered by both the surangular and prearticular, which contact each other.



Prearticular. — It is the largest element of the lingual side of the mandible. The prearticular contacts the angular ventrally, the coronoid anterodorsally and forms the frame for the lingual side of the articular. In a few cases, it contacts the surangular in the postglenoid area. It does not contact the intercoronoid, as it does in *Mastodonsaurus* (Schoch 1999) and *Cyclotosaurus* (Sulej and Majer 2005).

The prearticular forms the hamate process that is relatively high. In natural position of the mandible (Fig. 3C, D), it is not visible in labial view. The hamate process bordered the glenoid area anterolingually. In the largest specimens, the top of the hamate process is roughened. In the small and medium-size specimens, the

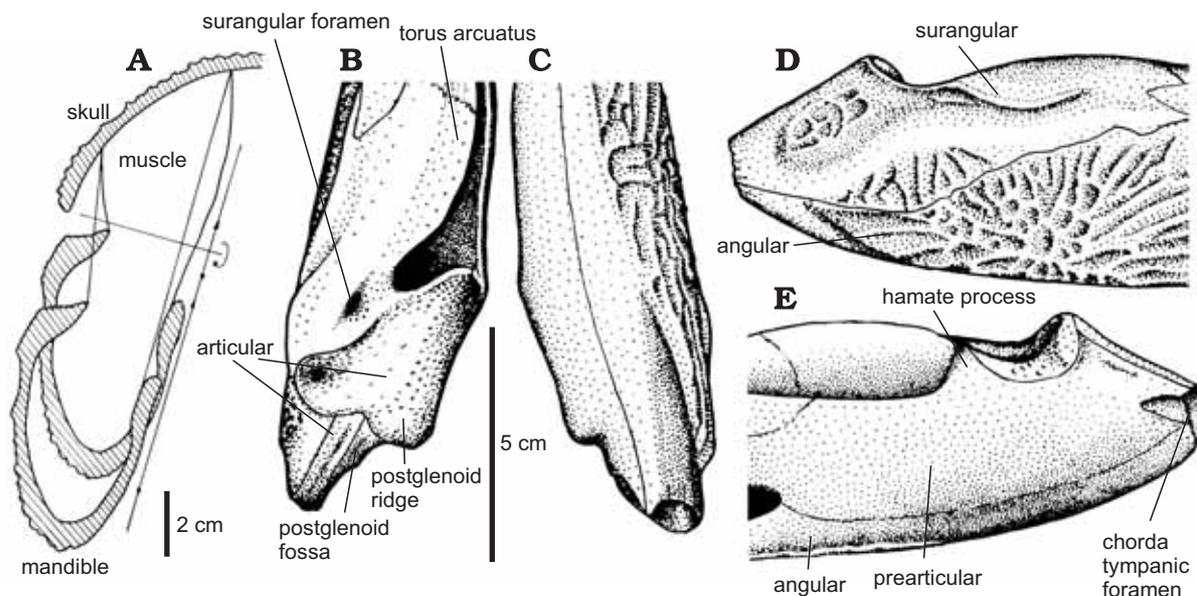


Fig. 21. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. **A**. Lateroventral curve of rami of mandible in cross-section. **B–E**. Retroarticular region, in dorsal (**B**), ventral (**C**), lateral (**D**), and medial (**E**) views.

prearticular sharply terminates dorsally in the contact with the articular, but in large specimens (ZPAL AbIII/191 and AbIII/1693) it forms a horizontal shelf, which is a small part of the glenoid area.

At the posterior end, the prearticular forms large chorda tympanic foramen margin, which is open posteriorly (Fig. 21). Usually, it is open dorsally and the prearticular forms its labial border that is high and roughened. The lingual border forms the edge of the prearticular. The shape of the chorda tympanic foramen is much variable, it may be vertical fissure like in ZPAL AbIII/41 or horizontal fissure like in ZPAL AbIII/1693. The very large posterior extension of the prearticular is very rare. It occurs in *Cyclotosaurus intermedius* (Sulej and Majer 2005). Anteriorly, the prearticular forms a narrow wedge overlapping the postsplenial and bordering the Meckelian window.

Coronoid. — The coronoid contributes to the formation of the bulges of the torus arcuatus that frame the adductor window on both sides of its front. It contacts the dentary anterodorsally, the surangular posteriorly, the intercoronoid anteriorly, and the prearticular and postsplenial ventrally (Figs 1A, 3D). The suture with the dentary runs in a narrow groove lingually to the teeth row of the dentary. In the middle part of this suture, the coronoid forms ridge extends up beyond the dentary. As in advanced temnospondyls, the coronoid does not bear any teeth. The posterior dorsal surface of the coronoid forms the large roughened prominence at the suture with the surangular invisible in labial view. It is a part of the coronoid process and is particularly developed in the largest specimens.

Intercoronoid. — It is entirely confined to the lingual side and forms a rectangle that is posteriorly sharpened (Fig. 3D). It contacts the coronoid posteriorly, the dentary dorsally, the precoronoid anteriorly, and the splenial and postsplenial ventrally. Its surface is smooth. The only exception is its dorsal margin that is thickened like in coronoid and forms a roughened ridge at the suture with dentary. It overlaps the dentary and it is overlapped by the postsplenial.

Precoronoid. — It is the most anterior, and the smallest element of the coronoid series (Fig. 3D). It wedges in between the splenial and dentary anteriorly and closes up to the intercoronoid posteriorly. At the anterodorsal edge of the element there is a slightly raised area with an irregular surface.

Dentary. — It forms the tooth arcade of the lower jaw. The dentary bears 71 to 75 teeth. This is a broad strip of bone set in the framework formed by the coronoids, angular and splenials (Figs 1A, 3C, D). Posteriorly, it contacts the surangular. The dentary forms the broad labial unit that underlies the angular and splenials. Its labial surface consists of the dorsal belt that is smooth and the ventral belt that is sculptured. The

ventral belt overlaps a part of the dorsal one in the middle part of the bone and there is a distinctive fissure between them. The sculpture of the ventral belt consists of long ridges and irregular pits in anterior part. The dentary thickens markedly as it bends into the transverse plane at the symphyseal region. The teeth diminish in size, and the tooth sockets attain a more rounded, short-oval shape, which is different from the predominant shape in the rest of the arcade. On the curve from dorsal surface to lingual, the dentary bears a short row of 8–10 teeth that are directed posteriorly, almost horizontally. It is similar to that of *Eryosuchus*, *Parotosuchus*, *Wellesaurus*, and *Kupferzellia* (Schoch and Milner 2000). In a few cases, there is no tooth arcade (e.g., in ZPAL AbIII/970/1). The tusk pair is situated between the main tooth arcade and the small symphyseal teeth. The tusks are relatively small. They match the anterior palatal foramina of the skull.

The shape of the symphysis area is very characteristic. It consists of the predominantly roughened medial surface and smooth anterior and posterior ridges that in largest specimens are distinctive. The roughened surface is oblique ventrolaterally up to the small foramen for a vein. The ventral concavity of the symphysis is formed by the splenial. The concave and composed symphysis suggests the presence of the mentomandibular cartilage.

Meckelian cartilage. — The shape of the symphysis in *Metoposaurus diagnosticus krasiejowensis* and the roughened surface of the most symphyseal area (Fig. 3D) shows that the Meckelian cartilage remained unossified between the rami of the mandible. It suggests that the connection was elastic. The mandibles are disarticulated in majority of metoposaurid specimens even if otherwise they are articulated, except for one specimen of *Arganasaurus lyazidi* (Dutuit 1976) from the Argana Formation, MNHN XIX\8\66, but the connection of the rami has not been cleaned.

In articulated specimens of *Metoposaurus diagnosticus krasiejowensis*, in which the mandible and skull from the same individual are preserved, usually one ramus is articulated with the skull and its counterpart is lying near the skull. After the mandible tusks are fit into the anterior palatal vacuities, which are widely separated, a space remains between mandibles rami to be filled with an additional element.

Mandibular fenestrae. — The adductor musculature is inserted into the adductor cavity (Schoch 1999: *cavitas adductoris*), the high chamber that opens as a window. According to Schoch (1999), in capitosaurids, both walls of that chamber (labial and lingual) were high. In *Metoposaurus diagnosticus krasiejowensis*, the labial wall is much higher than lingual, similarly to the Trematosauridae. In contrast to *Mastodonsaurus*, the adductor window opens slightly lingually because the torus arcuatus is strongly sloped lingually (Fig. 21A) and the prearticular is much lower than the angular. In dorsal view, it is visible in anterior and medial part as the very narrow fissure.

It seems that lingual opening of the adductor cavity was connected with the oblique axis of the mandible rami motion. The mandible ramus during the opening of the mouth was ventrally bent (Fig. 21A), in relation to its position when the mouth was closed. During the closing of the mouth the mandible was pulled to its normal position by the adductor musculature and the lingual opening of the adductor window supported this pulling.

The Meckelian foramen is the lingual opening of the adductor chamber (Schoch 1999). Usually, it is three-fourths of the length of the adductor window but in ZPAL AbIII/1678 it is shorter than half of that length, which shows that the length of the Meckelian foramen is variable. Generally, it is narrow anteriorly and wide posteriorly.

VERTEBRAL COLUMN

The intercentra of cervical and thoracic vertebrae are fully ossified. The neural arches are fused with intercentrum only in the atlas and axis. The pleurocentra are not preserved and there is no evidence that they were present as cartilages. Eleven sections of vertebral column of the vertebrae can be distinguished along the column. The atlas, axis and cervical vertebrae third and fourth are characteristic and similar to those in stereospondyls. The dorsal and caudal intercentra are distinguished mainly on the basis of both size and number of parapophyses. To classify thoracic intercentra, the shape of the anterior surface of the intercentrum was used. In the caudal intercentra, the shape of the basis of the chevron appears to be the most characteristic. However this differentiation is not precise, because in some specimens the left side of one type and the right side of the following one are almost identical.

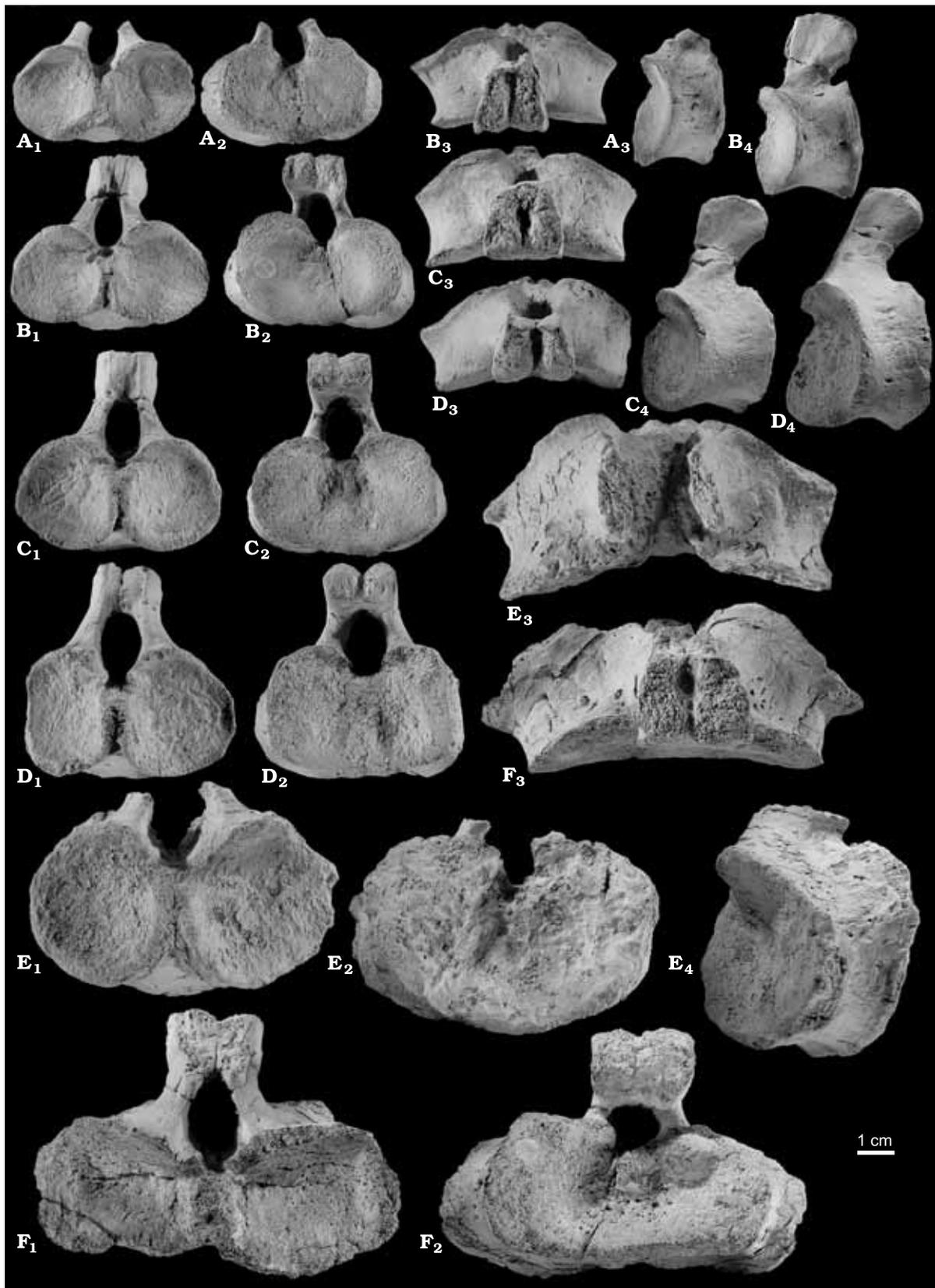


Fig. 22. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of atlases. Specimens ZPAL AbIII/1063/1 (A), ZPAL AbIII/629 (B), ZPAL AbIII/1702 (C), ZPAL AbIII/168 (D), ZPAL AbIII/104 (E), and ZPAL AbIII/888/2 (F), respectively in anterior (A₁, B₁, C₁, D₁, E₁, F₁), posterior (A₂, B₂, C₂, D₂, E₂, F₂), dorsal (B₃, C₃, D₃, E₃, F₃), and lateral (A₃, B₄, C₄, D₄, E₄) views.

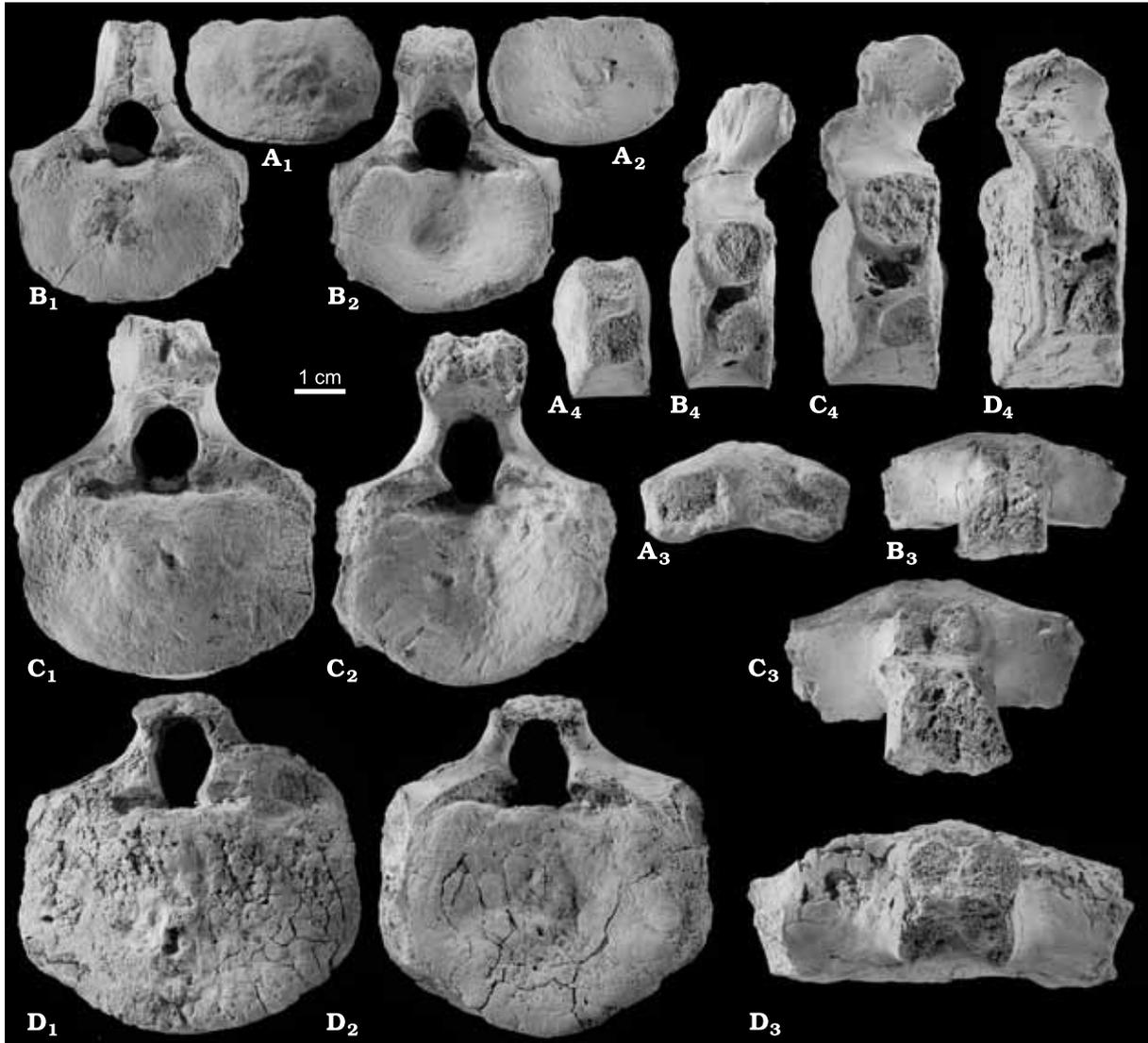


Fig. 23. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of axes. Specimens ZPAL AbIII/1703 (A), ZPAL AbIII/319 (B), ZPAL AbIII/1704 (C), and ZPAL AbIII/989/1 (D), respectively in anterior (A₁, B₁, C₁, D₁), posterior (A₂, B₂, C₂, D₂), dorsal (A₃, B₃, C₃, D₃), and lateral (A₄, B₄, C₄, D₄) views.

The small thoracic intercentra and all caudals have a very large chordal canal that is not overgrown and forms a trough on their dorsal surface. In medium and large-sized thoracic vertebrae, the chordal canal is overgrown and becomes in ontogeny.

The general tendency in changing shape and position of the parapophyses is their shift narrower upward (up to the sacral region) and then downward (in the caudal vertebrae) in contrast to *Mastodonsaurus*, in which the parapophyses shift ventrally from the cervical to caudal region (Huene 1922; Schoch 1999). In *Metoposaurus diagnosticus krasiejowensis*, the parapophyses become shorter posteriorly and in presacral intercentra their anterior and posterior parts are on two neighbouring centra. A similar situation was described in the plagiosaurids (Shishkin 1987, 1989; Hellrung 2003). The thoracic neural arches differ in position of the prezygapophyses and in the shape of transverse processes and diapophyses. The intercentra of all the cervical vertebrae are fused with the neural arches. These neural arches are low and fairly broad (Figs 22, 32).

Atlas. — The anterior surface of the intercentrum of the atlas is bilobed and forms an articulation facet for the occipital condyles (Figs 22, 32). The facets are round in anterior view. At the connection of the facets, in their ventral part, a prominent ridge occurs. It is much larger than in *Mastodonsaurus*. The condyles fit

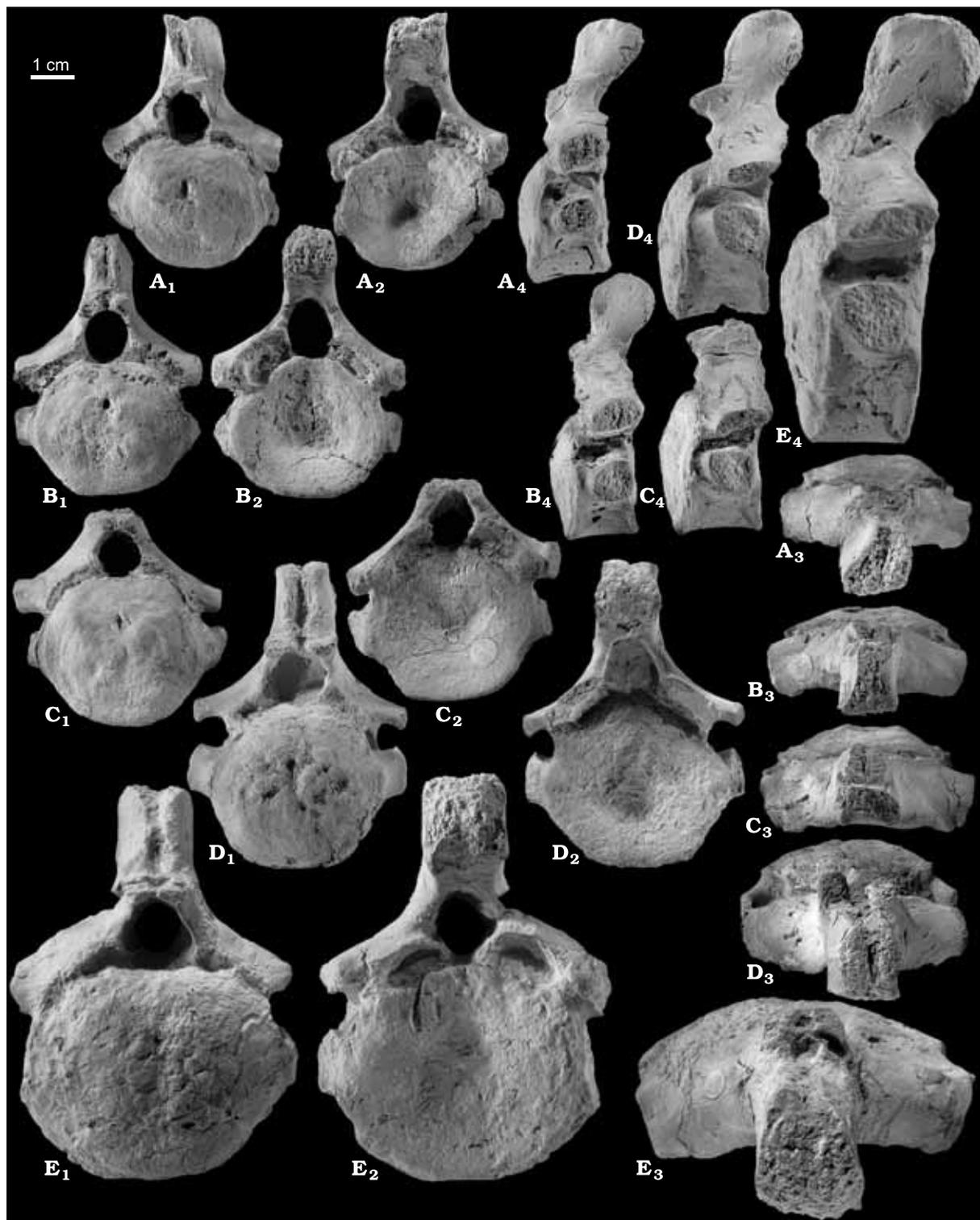


Fig. 24. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of third and fourth intercentra. Specimens ZPAL AbIII/1621/1 (A), ZPAL AbIII/1615 (B), ZPAL AbIII/1659/2 (C), ZPAL AbIII/169 (D), and ZPAL AbIII/175 (E), respectively in anterior (A₁, B₁, C₁, D₁, E₁), posterior (A₂, B₂, C₂, D₂, E₂), dorsal (A₃, B₃, C₃, D₃, E₃), and lateral (A₄, B₄, C₄, D₄, E₄) views.

tightly the atlas. The atlas is wider and longer than the next vertebrae, as in the capitosaurids (Schoch 1999). It lacks diapophyses or parapophyses. The posterior side is strongly concave, forming a single, transversely elongated oval.

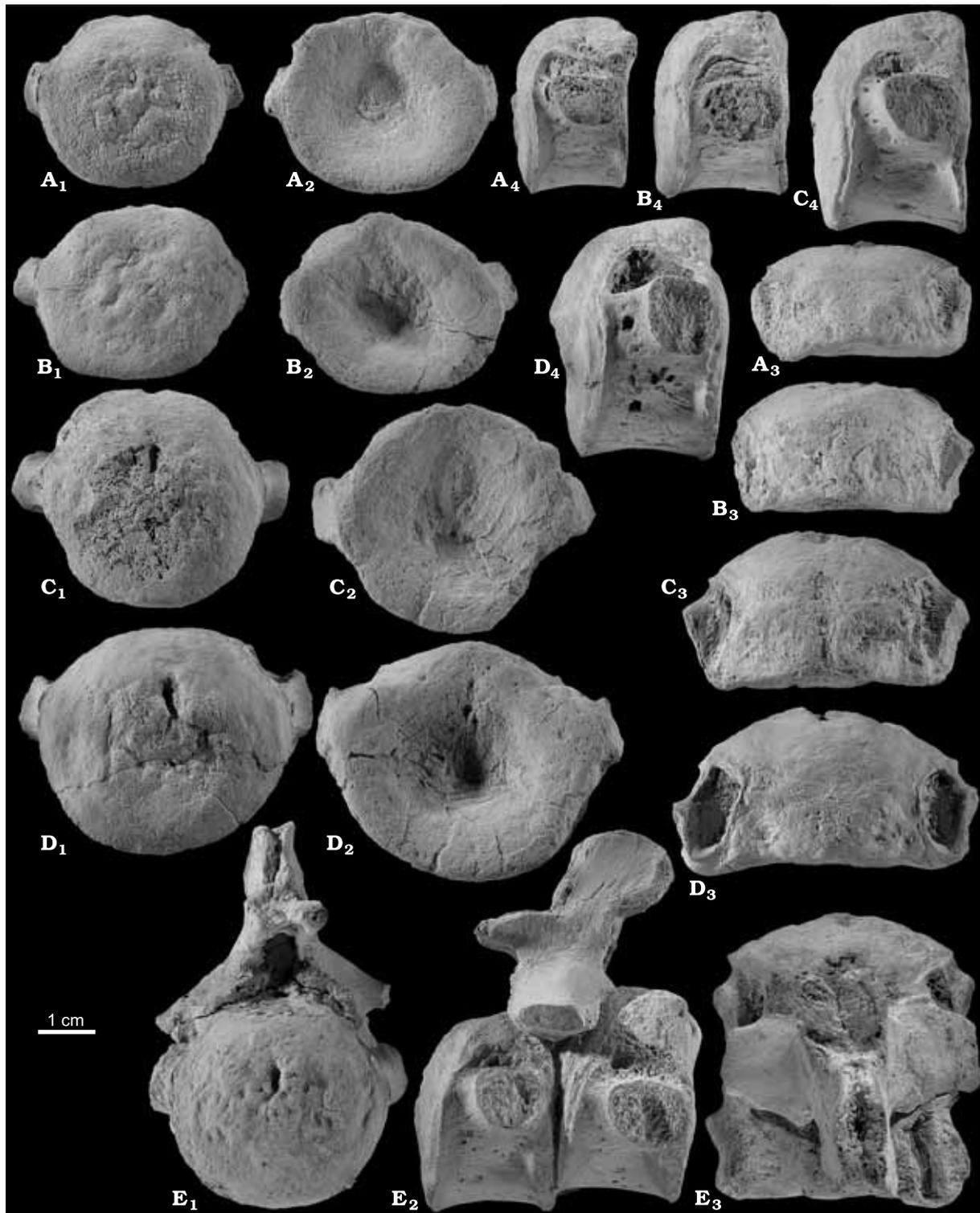


Fig. 25. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of postcervical intercentra. Specimens ZPAL AbIII/1707 (A), ZPAL AbIII/1136/1 (B), ZPAL AbIII/881/5 (C), ZPAL AbIII/320 (D), and ZPAL AbIII/1710 (E), respectively in anterior (A₁, B₁, C₁, D₁, E₁), posterior (A₂, B₂, C₂, D₂, E₂), dorsal (A₃, B₃, C₃, D₃), and lateral (A₄, B₄, C₄, D₄, E₃) views.

The neural arch is lower than that of the axis. It is permanently fused with the intercentrum, unlike *Mastodonsaurus*, where they were found separately. The lateral vertical ridges on the anterior surface of the neural arch are variable: in ZPAL AbIII/1033/1 they are prominent, in ZPAL AbIII/168 they are small. There

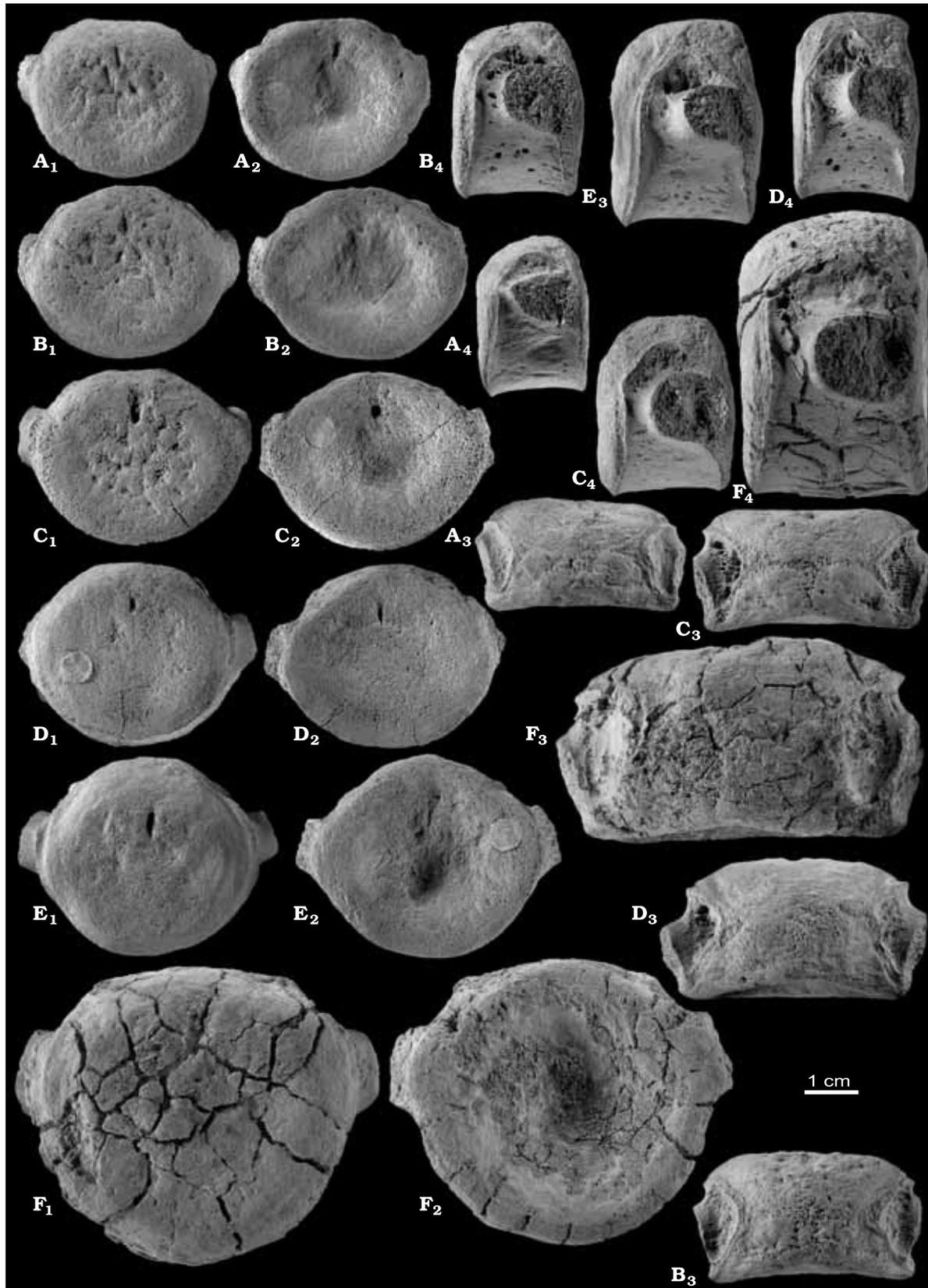


Fig. 26. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of anterior dorsal intercentra. Specimens ZPAL AbIII/1127/2 (A), ZPAL AbIII/1601/2 (B), ZPAL AbIII/942/2 (C), ZPAL AbIII/952/2 (D), ZPAL AbIII/936/2 (E), and ZPAL AbIII/1650/26 (F), respectively in anterior (A₁, B₁, C₁, D₁, E₁, F₁), posterior (A₂, B₂, C₂, D₂, E₂, F₂), dorsal (A₃, B₃, C₃, D₃, F₃), and lateral (A₄, B₄, C₄, D₄, E₃, F₄) views.

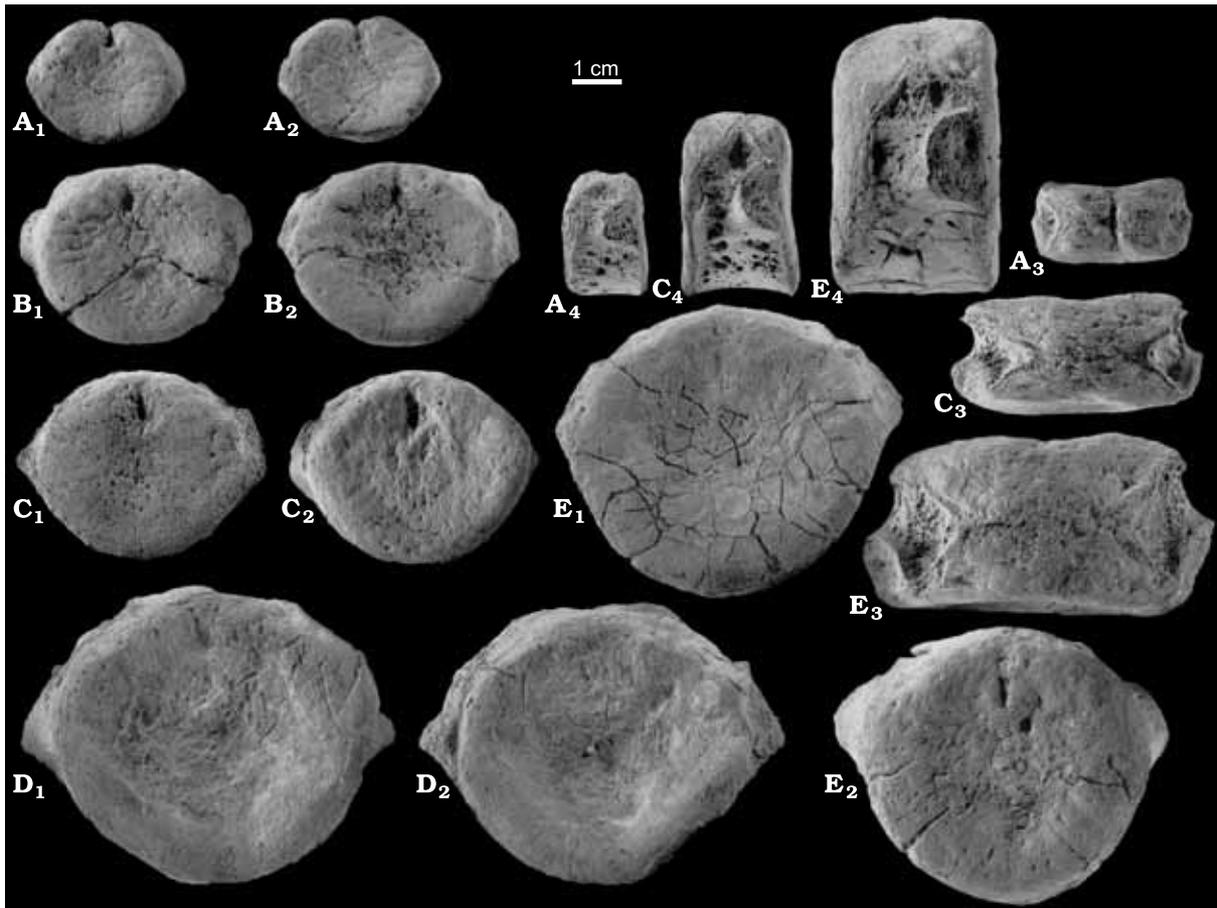


Fig. 27. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of mid-dorsal intercentra. Specimens ZPAL AbIII/1650/8 (A), ZPAL AbIII/1706 (B), ZPAL AbIII/933/3 (C), ZPAL AbIII/1701 (D), and ZPAL AbIII/1705 (E), respectively in anterior (A₁, B₁, C₁, D₁, E₁), posterior (A₂, B₂, C₂, D₂, E₂), dorsal (A₃, B₃, C₃, D₃), and lateral (A₄, B₄, C₄, D₄, E₄) views.

is a characteristic sharp edge between the anterior smooth and dorsal roughened surface of the neural arches. The dorsal surface is trapezoid in dorsal view with a marked medial trough. The posterior surface of the dorsal part is roughened and forms an articulation for the prezygapophyses of axis, unlike *Mastodonsaurus*, which has a smooth posterior surface of the neural arch (Schoch 1999).

Axis. — The anterior surface is convex, forming a transversely elongated oval with vertical lateral edges that make it similar to rectangle (Fig. 23). The posterior surface is convex and more rounded. In ventral view, the anterior edge is convex and the posterior edge is straight or concave, *e.g.* in ZPAL AbIII/1043/1. In the axis, third and fourth vertebrae, the apophyses are closely set and aligned laterally in a horizontal line, contrary to *Mastodonsaurus* in which they are aligned laterally in a vertical line.

The neural arch is closely fused with the intercentrum, except for the smallest specimens (see Fig. 23A). It is higher than that of the atlas but lower than that of the third vertebra (Fig. 32). The anterior surface of the spine process bears medial roughened trough like all the following types of neural arches. The diapophysis is round and larger than the oval parapophysis. The parapophysis becomes smaller in ontogeny. In specimen ZPAL AbIII/607, the left parapophysis is missing. The prezygapophyses are flat and oblique interiorly. The diapophyses and parapophyses are generally very short, but in ZPAL AbIII/630 they are quite prominent.

Third and fourth vertebrae. — The intercentrum is fused with the neural arch and both diapophysis and parapophysis are closely set and aligned in a vertical line (Fig. 24). The anterior surface of the intercentrum is convex and oval or round. Its posterior surface is also oval or round and concave. Probably, the more rounded intercentra represent the fourth vertebra.

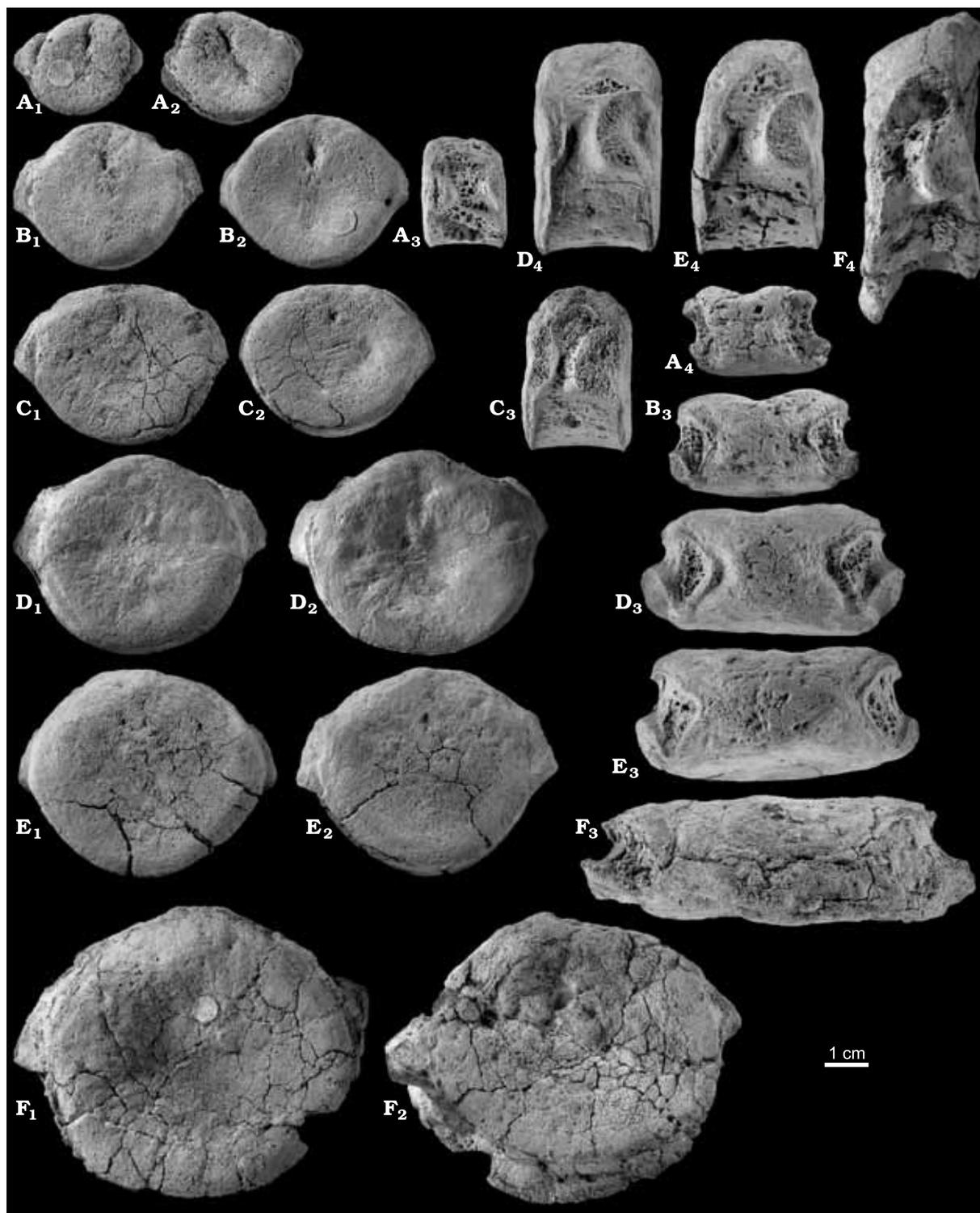


Fig. 28. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of the presacral intercentra. Specimens ZPAL AbIII/1651/1 (A), ZPAL AbIII/960/1 (B), ZPAL AbIII/992/3 (C), ZPAL AbIII/323 (D), ZPAL AbIII/171 (E), ZPAL AbIII/1024 (F), respectively in anterior (A₁, B₁, C₁, D₁, E₁, F₁), posterior (A₂, B₂, C₂, D₂, E₂, F₂), dorsal (A₃, B₃, D₃, E₃, F₃), and lateral (A₄, B₄, C₃, D₄, E₄, F₄) views.

The neural arch is fused with the intercentrum, except the smallest specimens, but not so closely as in atlas and axis. The prezygapophyses are flat in anterior view. In the third vertebrae, the parapophysis and diapophysis are of similar size, and both are rounded. In the fourth vertebra, the parapophysis is larger and

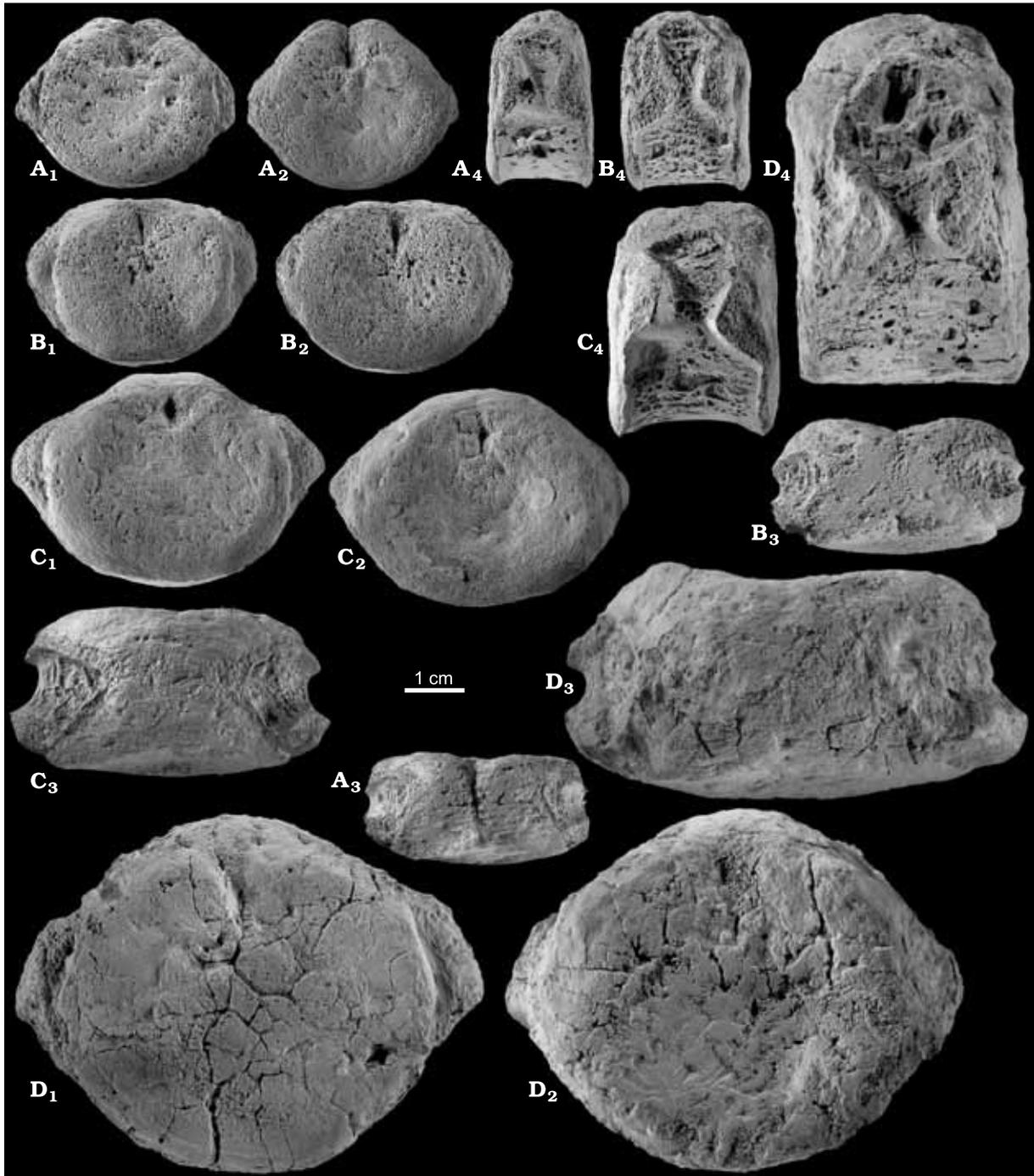
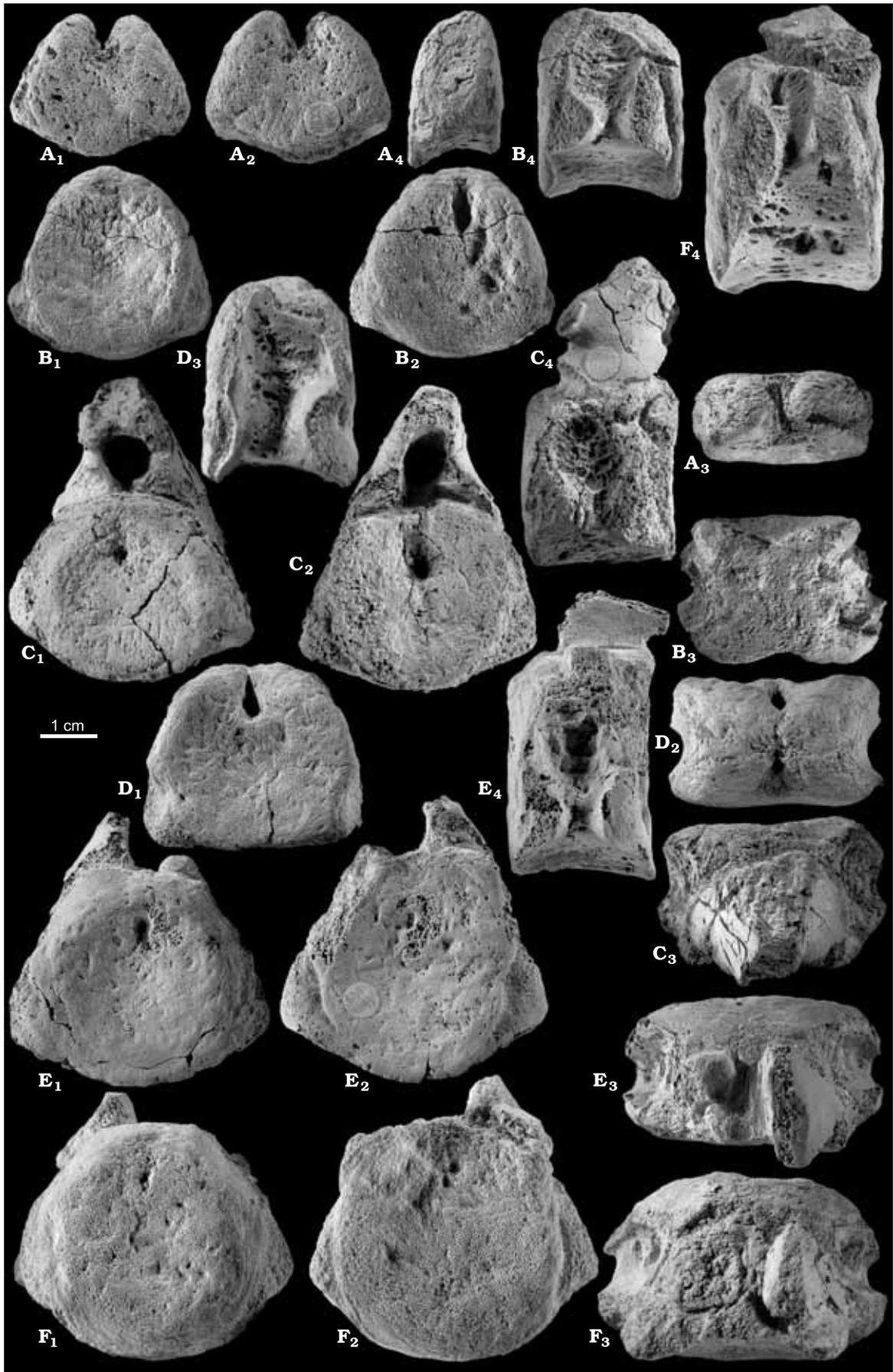


Fig. 29. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of perisacral intercentra. Specimens ZPAL AbIII/1030/1 (A), ZPAL AbIII/1718 (B), ZPAL AbIII/172 (C), and ZPAL AbIII/1715 (D), respectively in anterior (A₁, B₁, C₁, D₁), posterior (A₂, B₂, C₂, D₂), dorsal (A₃, B₃, C₃, D₃), and lateral (A₄, B₄, C₄, D₄) views.

diapophysis is flat. In the corresponding vertebrae of *Mastodonsaurus*, the diapophyses and parapophyses are also flat but they are set vertically, whereas in *M. diagnosticus krasiejowensis* horizontally, as in ZPAL AbIII/1710.

Post-cervical vertebrae. — The parapophysis of these intercentra is large and longer (Fig. 25) than half of the length of the latera of intercentrum (Schoch 1999). The anterior surface and ventral edge are convex in ventral view. The intercentrum is cylindrical with concave posterior area.



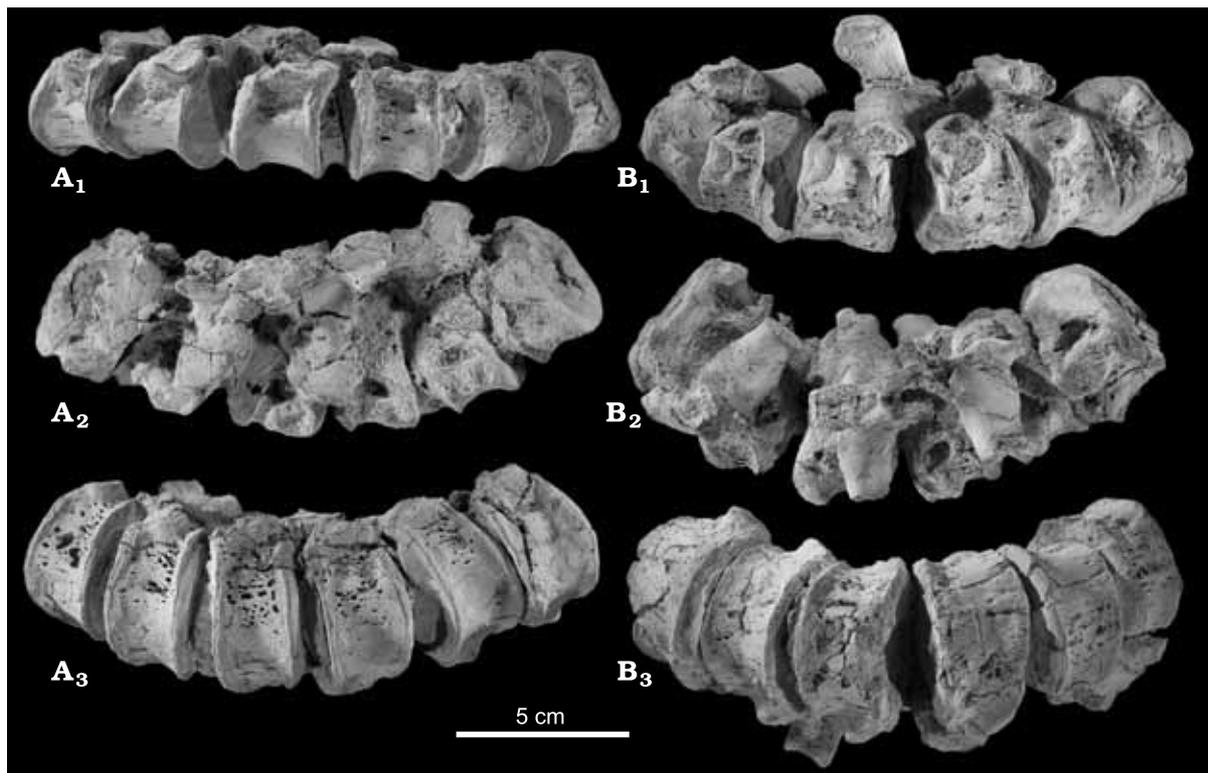


Fig. 31. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2003 from Krasiejów. Articulated postcervical and anterior dorsal vertebrae. Specimens ZPAL AbIII/1132/1 (A) and ZPAL AbIII/1133/1 (B), respectively in lateral (A₁, B₁), dorsal (A₂, B₂), and ventral (A₃, B₃) views.

The thoracic vertebrae are not fused with the neural arches and their classification concerns only the intercentra, but two types of neural arches connected with the thoracic vertebrae can be distinguished. The post-cervical neural arches (Fig. 32) have the prezygapophyses flat in anterior view (ZPAL AbIII/1132/1) whereas the diapophyses are wide and divided from the intercentrum articulation surface by smooth area. The transverse process is trapezoidal in dorsal view with oblique anterior and posterior edges. The spine process has a slightly elongated posteriorly dorsal part, as it is visible in ZPAL AbIII/1710.

Anterior dorsal vertebrae. — The parapophysis is large and longer than half the length of the latera, like in the previous type, but the anterior surface is flat and its edge is straight in ventral view (Figs 26, 32). The intercentrum is cylindrical, with concave posterior area. In the articulated specimen ZPAL AbIII/1132/1, there are at least six post-cervical and anterodorsal intercentra. The articulated neural arches of post-cervical vertebrae have the prezygapophyses flat, whereas in the anterodorsal vertebrae they are oblique in anterior view.

The neural arches of the anterodorsal vertebrae are characteristic, with almost vertical, oblique prezygapophyses in anterior view, the diapophysis is narrow and separated from the intercentrum articulation surface. The surface bears tubercle in its lateral part. The transverse processes are similar to those in the post-cervical vertebrae, they are trapezoid in dorsal view, with oblique anterior and posterior edges. The spine process has a slightly elongated posteriorly dorsal part in ZPAL AbIII/1053/1, AbIII/1612/1, and AbIII/1611/2.

The variability of the post-cervical and anterodorsal intercentra concerns the shape and size of the parapophysis. It may be slightly longer than half of the length or almost as long as the latera (Schoch 1999) in its ventral length. The shape of the parapophysis may be circular or more subtriangular.

← Fig. 30. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of postsacral intercentra. Specimens ZPAL AbIII/1068/1 (A), ZPAL AbIII/1714 (B), ZPAL AbIII/174 (C), ZPAL AbIII/1650/13 (D), ZPAL AbIII/644 (E), and ZPAL AbIII/1711 (F), respectively in anterior (A₁, B₁, C₁, D₁, E₁, F₁), posterior (A₂, B₂, C₂, E₂, F₂), dorsal (A₃, B₃, C₃, D₂, E₃, F₃), and lateral (A₄, B₄, C₄, D₃, E₄, F₄) views. B₄, C₄, F₄ reversed.

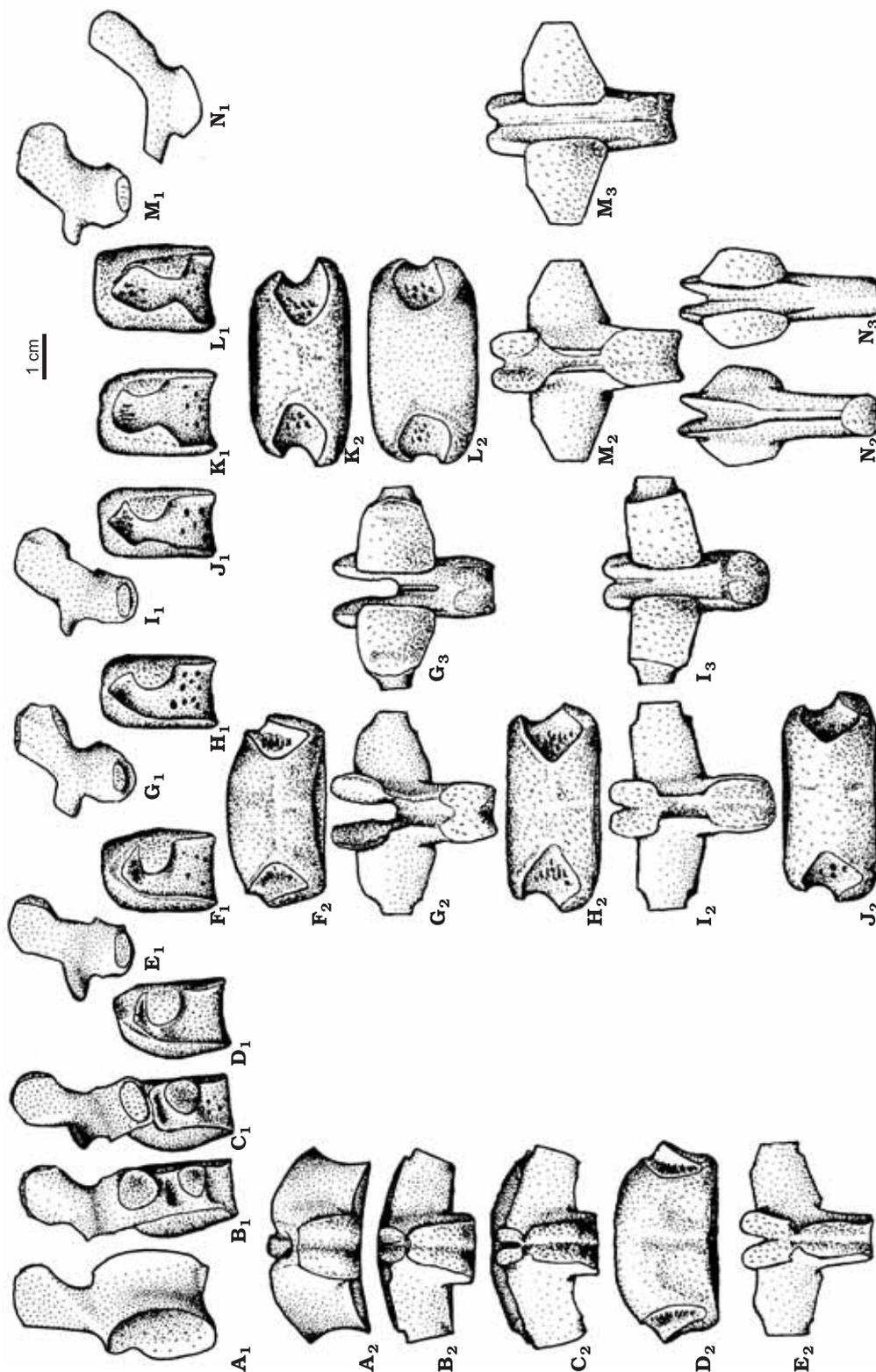


Fig. 32. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of neural arches and intercentra. A. Atlas based on ZPAL Ab/III/1702. B. Axis, Ab/III/319. C. Third and fourth intercentrum, Ab/III/1615. D. Post cervical intercentrum, Ab/III/881/5. E. Postcervical neural arch, Ab/III/1710. F. Anterodorsal intercentrum, Ab/III/936/2. G. Anteriodorsal neural arch, Ab/III/1612/2. H. Mid-dorsal intercentrum, Ab/III/1071. I. Dorsal neural arch, Ab/III/1030/2. J. Presacral intercentrum, Ab/III/323. K. perisacral intercentrum, Ab/III/172. L. postsacral intercentrum, Ab/III/1714. M. postsacral neural arch, Ab/III/1708. N. Antericaudal neural arch, Ab/III/1709. Vertebrae in lateral (A₁, B₁, C₁, D₁, E₁, F₁, G₁, H₁, I₁, J₁, K₁, L₁, M₁, N₁), dorsal (A₂, B₂, C₂, E₂, F₂, G₂, H₂, I₂, J₂, K₂, L₂, M₂, N₂), and ventral (G₃, I₃, M₃, N₃) views, respectively.

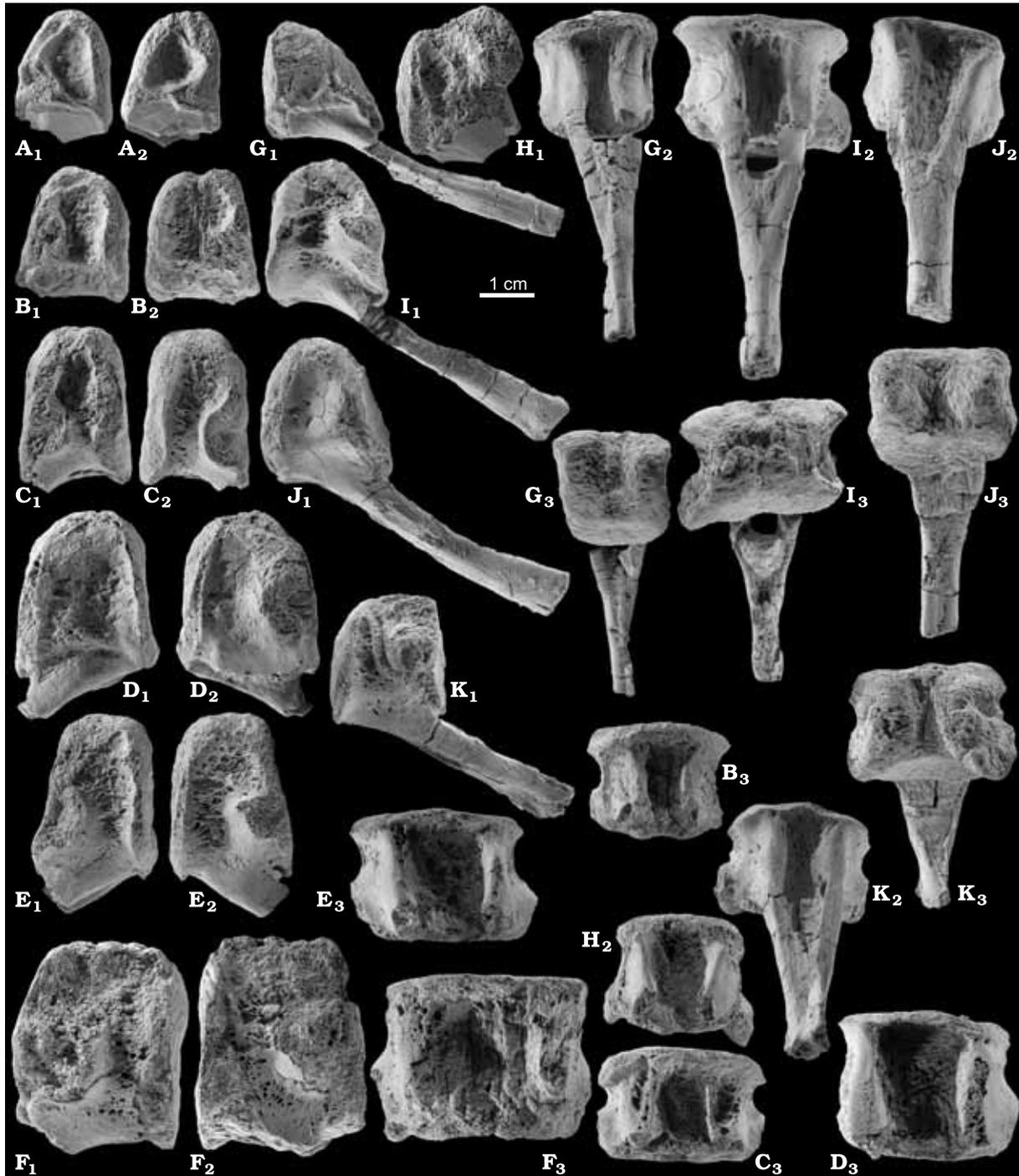


Fig. 33. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of anterior caudal intercentra. Specimens ZPAL AbIII/1700 (A), ZPAL AbIII/892/2 (B), ZPAL AbIII/1697 (C), ZPAL AbIII/1698 (D), ZPAL AbIII/176 (E), ZPAL AbIII/942/1 (F), ZPAL AbIII/1654 (G), ZPAL AbIII/1699 (H), ZPAL AbIII/1189 (I), ZPAL AbIII/458/4 (J), ZPAL AbIII/1619 (K), respectively in right side (A₁, B₁, C₁, D₁, E₁, F₁), left side (A₂, B₂, C₂, E₂, F₂, G₁, I₁, J₁, K₁ reversed), ventral (B₃, C₃, D₃, E₂, F₃, G₂, H₂, I₂, J₂, K₂), and dorsal (G₃, I₃, J₃, K₃) views.

Mid-dorsal vertebrae. — The parapophysis is shorter than half of the length of the latera. The intercentrum has flat or slightly concave anterior and posterior surfaces (Fig. 27). In specimen ZPAL AbIII/1133/1, the neural arches are articulated with the intercentra of this type and they have slightly oblique prezygapophyses.

The neural arch has rectangular transverse processes. The prezygapophyses are slightly oblique in anterior view, transitional between their horizontal orientation in the third and fourth vertebrae and almost verti-



Fig. 34. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of posterior caudal intercentra with chevrons (A–H) and caudal neural arches (I–K). Specimens ZPAL AbIII/182 (A), ZPAL AbIII/1653 (B), ZPAL AbIII/1154/1 (C), ZPAL AbIII/1088 (D), ZPAL AbIII/1622/1 (E), ZPAL AbIII/1659/1 (F), ZPAL AbIII/1657/1 (G), ZPAL AbIII/1701 (H), ZPAL AbIII/1196/3 (I), ZPAL AbIII/1659/1 (J), ZPAL AbIII/866/1 (K), respectively in lateral (A₁, B₁, C₁, D₁, E₁, F₁, G₁, I₁, J₁, K₁), ventral (A₂, B₂, C₂, E₂, F₂, G₁, I₁, J₁, K₁ reversed), ventral (B₃, C₃, D₃, E₂, F₃, G₂, I₂, J₂, K₂), and dorsal (A₃, B₃, C₃, D₃, E₃, F₃, G₃, H₂, I₃, J₃, K₃) views; B₁, C₁, F₁, K₁ reversed.

cal in the post-cervical vertebrae. The surface of articulation with the anterodorsal intercentrum is trapezoidal and flat. The diapophysis is wider than in the anterodorsal vertebrae. They probably occur in all dorsal intercentra except for the post-cervical and anterodorsal vertebrae. Typical neural arch of this type is represented by ZPAL AbIII/1030/2

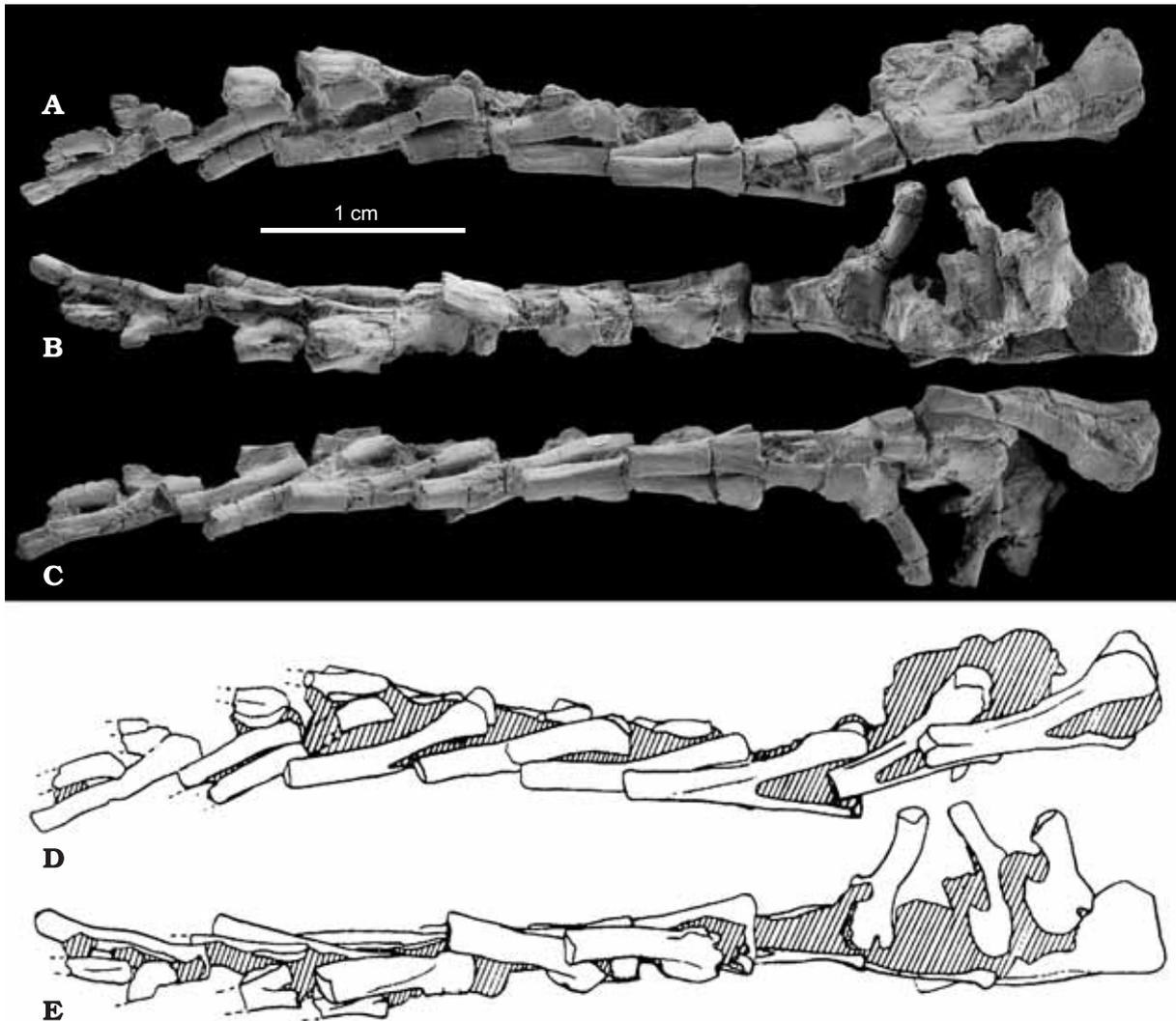


Fig. 35. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Articulated caudal vertebrae ZPALAbIII/1189. A. Lateral view. B. Dorsal view. C. Ventral view. D, E. Explanatory drawing in lateral and dorsal views, respectively.

Presacral vertebrae. — This type has a small and very short anterior parapophysis. The intercentrum has slightly concave anterior and posterior surfaces, but the posterior facet of articulation is more concave (Fig. 28). The posterior parapophysis is short. In this and subsequent types, the posterior parapophysis does not pass continuously into the posterior facet of articulation of the intercentra but there is a sharp notch at the connection of the medial edge of the parapophysis and the posterior facet of articulation. In *Dutuitosaurus*, the first presacral vertebra is 18th (15th thoracic; Dutuit 1976).

Perisacral vertebrae. — The typical intercentrum bears both parapophyses of the same size (Fig. 29) and has slightly concave anterior and posterior surfaces. The posterior parapophysis is much shorter and the anterior one larger than in presacral vertebra. The shape and height of both parapophyses is variable, it may be semicircular or triangular. They may be very close to each other or rather far from each other.

In *Dutuitosaurus*, there are four (personal observations) or three (Dutuit 1976) vertebrae of this type. According to Dutuit (1976), the vertebrae near 23rd vertebra are sacral. This variation is similar to that in modern salamanders where the number of dorsal vertebrae varies from 14 to 21 (Litvinchuk and Borkin 2003).

Postsacral vertebrae. — The caudal vertebrae are very variable, in some specimens the left and right sides are much different, but three types can be distinguished. The anterior and posterior parapophyses of postsacral vertebrae are of similar size and occur very close to each other, in some cases they are even con-

nected (Fig. 30). The most characteristic feature of this type is a very low position of both parapophyses and almost flat or flat ventral surface of the intercentrum. In anterior view, the shape of articular surface is oval, like in anteriorly located vertebrae, but the main axis of the oval is vertical instead of horizontal in anteriorly located vertebrae. In a few cases, the posterodorsal edge of the centrum forms a prominent ridge, often connected with the fused neural arch.

The neural arch was set over the intercentrum, not between them as it is in the case of the thoracic vertebrae. The spine process of the neural arch is long and increases in length posteriorward; prezygapophyses are small. The base of neural arch is trapezoidal in dorsal view and shortening toward the tail. The diapophyses are fused with the intercentrum. The representative specimen is ZPAL AbIII/1708. The relatively vertical centra and the neural arches articulated over the centrum suggest that this part of the vertebral column curved mainly horizontally together with the tail.

Anterior caudal vertebrae. — The chevrons are fused with the intercentrum that is more or less trapezoidal in lateral view (Figs 33, 36). Beginning from this position to the end of the tail the notch for the chordal canal becomes larger and larger. Only in very large specimens, it is overgrown but still distinct. The intercentra bear a small and vertically elongated or large and rounded parapophyses. In a few cases, only a small anterior parapophysis is visible or is missing. The anterior facet of the intercentrum is convex, flat or concave, whereas the posterior facet is always concave. The base of chevrons is generally developed on the anterior part of ventral surface of the intercentrum, but in a few cases at the posterior edge. The neural arches are transitional between those in perisacral and caudal vertebrae, as can be seen in ZPAL AbIII/1709 (Fig. 33).

Posterior caudal vertebrae. — These intercentra differ from the previous ones as they are triangular in lateral view (Figs 34–36). The base of the chevron may form prominent ridges protruding behind the intercentrum in anterior view or the ridges may also be low.

Small specimens of this type are very low. They do not bear the latera, and entire surface of the intercentrum is roughened. The base of the chevron forms most of the lateral surface of the vertebra. In ZPAL AbIII/1189, almost the whole tail is articulated. It is slightly compressed but the long neural arches and chevrons that form the caudal fin are well visible. In this type of the vertebrae, the neural arch does not have any diapophysis. The spine process becomes longer and slender up to the few latest vertebrae, whereas the base becomes shorter and more vertical in anterior view.

Ribs. — Numerous ribs were found associated with disarticulated specimens during the Krasiejów excavations. There is a large sample of isolated ribs; many of them are well-preserved and fairly complete.

Among the presacral vertebrae, there are at least nine different rib types (Figs 38, 39). Their sequence in the trunk is problematic, but may be ascertained on the basis of homology with ribs of *Metoposaurus diagnosticus diagnosticus* (Fraas 1889) and *Dutuitosaurus ouazzoui* (Dutuit 1976). This is uncertain because the changes in ontogeny overlap with the differences between subsequent ribs. All ribs have heads with surfaces for cartilaginous attachment and their life position is very difficult to restore. The distinction of rib types is made according to (1) morphology of the head region, (2) presence and expression of uncinatous process, (3) length, and (4) morphology of the distal end.

Rib type A: Capitulum and tuberculum are distinct, both almost round, and of similar size (Figs 38A, 39A). There are clearly two proximal heads, which are separated by a well-established groove. The shafts of the capitular and tubercular heads are divided by a furrow on the anterior and posterior side. The straight tuberculum shaft bears a crest on the anterior side that, behind the bending point of the rib, forms a vertical blade directed slightly posteriorly. The capitulum shaft is curved anteriorly. It forms an oblique blade with a sharp edge, which is perpendicular to the blade. This rib type is represented by specimens ZPAL AbIII/1519, AbIII/1520, and AbIII/1054.

It is similar to the cervical rib (articulated with second vertebra) described by Dutuit (1976) from articulated specimen MNHN XII/12/65 of *Dutuitosaurus ouazzoui*. The same kind of rib was shown by Case (UMMP 1932) as a “possible rib” (UMMP 13788) of *Buettneria perfecta*. Similarly as in the material of *D. ouazzoui*, there is no specimen with preserved complete distal part.

Rib type B: Only heads of these ribs are preserved. The capitulum and tuberculum are closely set, both oval, and of similar size or with larger the tuberculum. Their facets are perpendicular to each other. The capital groove is very small. The short furrow separating capitulum from tuberculum is represented only on the

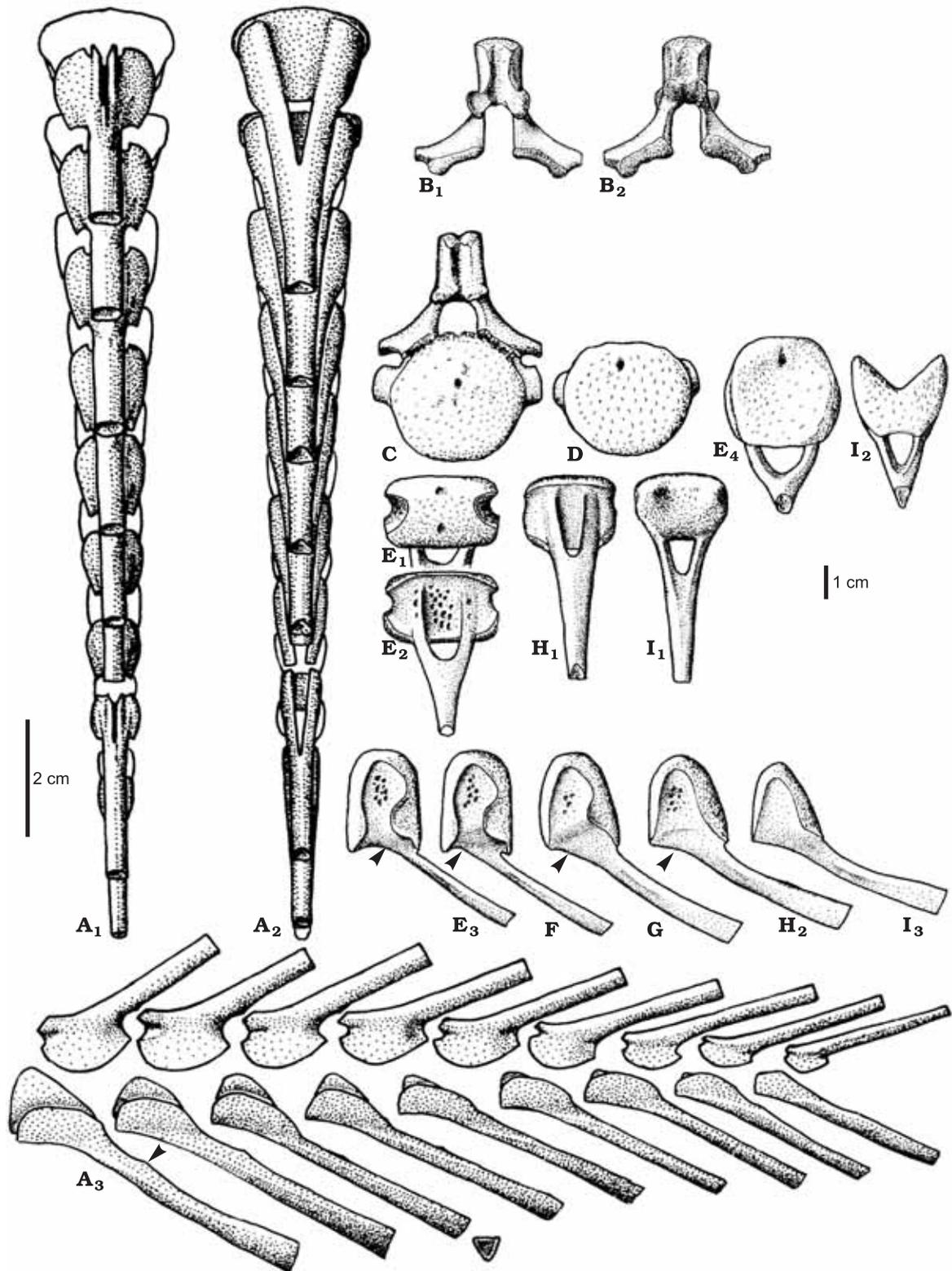
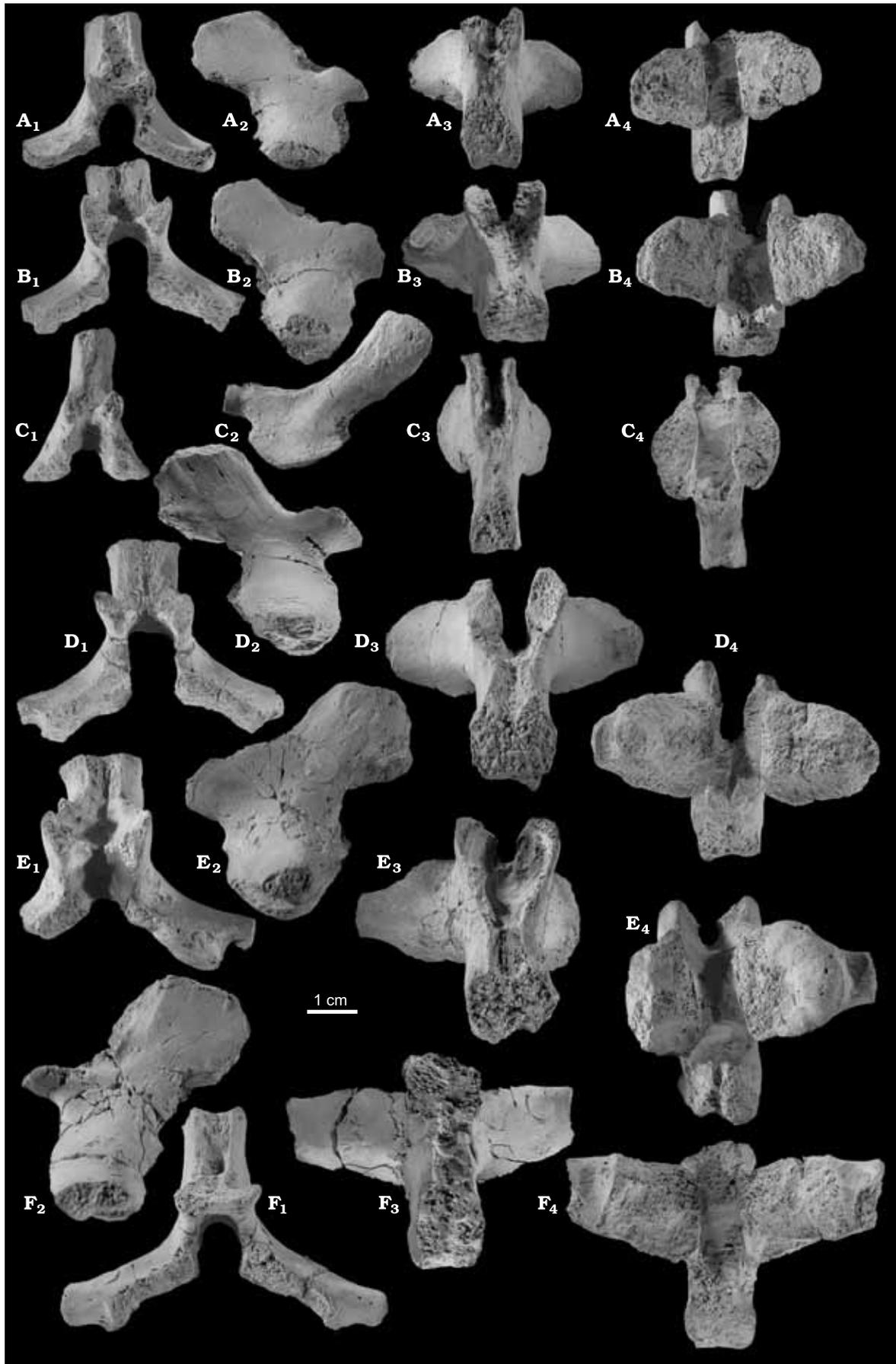


Fig. 36. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of neural arches and intercentra. A. Part of caudal fin based on ZPAL Ab/III/1189. B. Postsacral neural arch, ZPAL AbIII/1708. C. Third and fourth intercentrum, ZPAL AbIII/169. D. Anterodorsal intercentrum ZPAL AbIII/942/2. E. Anterior caudal intercentrum with chevron, ZPAL AbIII/1697. F. The same, ZPAL AbIII/176. G. The same, ZPAL AbIII/456/4. H. Posterior caudal intercentrum with chevron, ZPAL AbIII/1659/1. I. The same ZPAL AbIII/1154/1. Respectively in dorsal (A₁, E₁, I₁), ventral (A₂, E₂, H₁), ventral (A₃, E₃, F, G, H₂, I₃), anterior (B₁, C, D) posterior (B₂, E₄, I₂).



posterior side of the rib. This type is represented by specimens ZPAL AbIII/1065/2, AbIII/1521, AbIII/1523, and AbIII/1522. The heads of type B seem to correspond to third cervical rib of *D. ouazzoui* (Dutuit 1976).

Rib type C: This rib type has uncinat process and narrow medial column (Fig. 39B). The proximal end is wide and flat with tuberculum and capitulum merged. Some ribs of this type have the proximal head oval and flat, some of them have the faces bent. Only a few ribs have the faces with a slight furrow between shafts of tuberculum and capitulum, but the merging of the heads is not connected with ontogeny. The distal part is bent, so it is almost horizontal in posterolateral view. The distal end is flat, while in cross-section it has the shape of comma. The rib bends almost in the middle but closer to the proximal end. The medial column is round in cross-section or oval in larger specimens. The length of the uncinat process is very variable. The distal end in lateral view can be straight as in ZPAL AbIII/1046/3 (Fig. 39B) or curved, as in ZPAL AbIII/1115. Surfaces of the ends are rotated to each other, about 45°.

This type is represented by specimens ZPAL AbIII/1041, AbIII/1046/3, AbIII/1082/2, AbIII/1037, AbIII/1152/1, AbIII/1155/2, AbIII/864/2, AbIII/1114/2, AbIII/306, AbIII/1116, and AbIII/1146/6. The rib types C–E correspond to the 5–10th vertebrae of *Dutuitosaurus*, but this species have uncinat plate instead of the uncinat process of *M. diagnosticus krasiejowensis*, *Buettneria howardensis* (TMM 31100-237; Sawin 1945: fig. 7), and *M. maleriensis* (Sengupta 2002). The thoracic ribs of *D. ouazzoui* and *M. maleriensis* (Sengupta 2002) have the tuberculum and capitulum connected by a narrow extension. In the types D–F of *M. d. krasiejowensis*, they are totally merged.

Rib type D: This rib type has one or two uncinat processes and narrow medial column (Fig. 28C). The proximal end is the same as in previous type. The distal end is very flat. The distal part behind the uncinat process strongly widens towards the end as in *Buettneria howardensis* (TMM 31100-237; Sawin 1945: fig. 7). It is vertical in posterolateral view. The rib bends almost in its middle, closer to proximal head. The medial column in the bending place is oval. The length of the uncinat process is very variable. This type is represented by specimens ZPAL AbIII/1070, AbIII/1158/3, AbIII/365, AbIII/1140, AbIII/1089/2, AbIII/1537, AbIII/972, AbIII/1145/8, and AbIII/1141.

Rib type E: There are only two specimens of this type, both are relatively large. They have additional crest on the dorsal area of the column (Fig. 39D). The crest begins in the middle of the distal portion and runs through the bending medial shaft and ends as a posterior edge of the distal part in lateral view, these ribs had the proximal head oval, expressed by merged tuberculum and capitulum, and flat in anterior view. This type is represented by specimens ZPAL AbIII/1003 and AbIII/1123.

Rib type F: In this rib type, the distal portion is straight, and is slenderer than in previous type. It has a less distinctive crest than in previous type. The proximal head is wide and its facet is oval or slightly slender in the middle (Fig. 39E). This type is represented by specimens ZPAL AbIII/1154/3, AbIII/1545, AbIII/1038, and AbIII/1538. Type F corresponds to the ribs articulated to 11–18 vertebrae of *Dutuitosaurus*.

Rib type G: The architecture is similar to the previous type. It differs in the longer, arched and slender distal portion. The crest is present only in the middle of the shaft (Fig. 39F). This type is represented by specimens ZPAL AbIII/1149, AbIII/938/3, AbIII/1051, and AbIII/1080. It seems that types G–I were not in detail described by Dutuit (1976) for *Dutuitosaurus*.

Rib type H: In this type, the proximal facet has triangular shape (Fig. 39G). The lower part of this facet probably relates to capitulum and is wider than the upper part. The proximal part is wide. The distal part has the same width like in the middle of the shaft, where it slightly bends. This type is represented by specimens ZPAL AbIII/1139/4, AbIII/1001, AbIII/313, AbIII/1106, AbIII/1117, AbIII/1023/5, and AbIII/980/3.

Rib type I: In this type, the ribs are shorter than in type H and the proximal head has tuberculum and capitulum difficult to recognise (Fig. 39H). It has the shape of rotated b. The larger, probably distal part (belly of b) is strongly bent laterally. There are some large proximal fragments with a very massive distal part and relatively smaller ventral part (stick of b). The stylus is narrow and straight or only weakly curved. This type is represented by specimens ZPAL AbIII/1030/3, AbIII/1687, AbIII/1043/2, AbIII/1083/3, AbIII/1108/2, AbIII/987/2, AbIII/862/4, AbIII/860/3, AbIII/1144, and AbIII/1540.

← Fig. 37. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Well-preserved neural arches. Postsacral type ZPAL AbIII/1708 (A), anterodorsal type, ZPAL AbIII/1053/1 (B), anterior caudal type ZPAL AbIII/1709 (C), anterodorsal type, ZPAL AbIII/1612/1 (D), anterior caudal type, ZPAL AbIII/1611/2 (E), and mid-dorsal type ZPAL AbIII/1030/2 (F), respectively in anterior (A₁, B₁, C₁, D₁, E₁, F₁), lateral (A₂, B₂, C₂, D₂, E₂, F₂), dorsal (A₃, B₃, C₃, D₃, E₃, F₃), and ventral (A₄, B₄, C₄, D₄, E₄, F₄) views, .

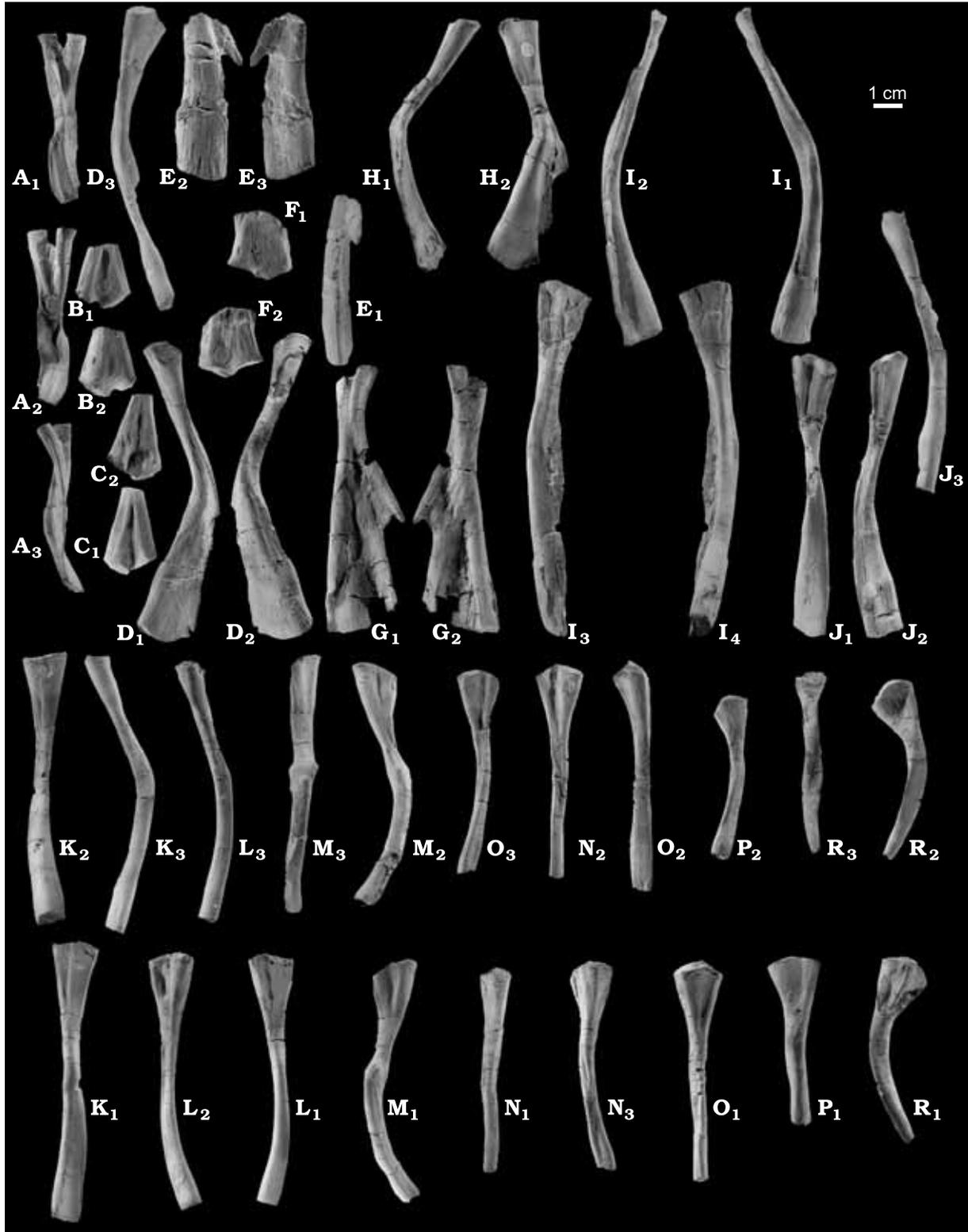


Fig. 38. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów, ribs. **A.** Type A, ZPAL AbIII/1519. **B.** Type B, ZPAL AbIII/1523. **C.** Type B, ZPAL AbIII/1522. **D.** Type C, ZPAL AbIII/1115. **E.** Type C, ZPAL AbIII/1155/2. **F.** Type B, ZPAL AbIII/1521. **G.** Type D, ZPAL AbIII/1089/2. **H.** Type D, ZPAL AbIII/1537. **I.** Type E, ZPAL AbIII/1003. **J.** Type F, ZPAL AbIII/1154/3. **K.** Type F, ZPAL AbIII/1038. **L.** Type G, ZPAL AbIII/1149. **M.** Type G, ZPAL AbIII/1051. **N.** Type H, ZPAL AbIII/1139/4. **O.** Type I, ZPAL AbIII/1030/3. **P.** Type I, ZPAL AbIII/1687. **R.** Type J, ZPAL AbIII/1518. Respectively in anterior (A₁, B₁, C₁, F₂, H₁, I₁, J₁, K₃, L₃, M₂, N₂, O₁, P₁, R₁), posterior (A₂, B₂, C₂, D₃, E₁, F₁, O₂, R₂), dorsal (A₃, D₁, J₃, M₃, N₁, O₃, P₂, R₃), ventral (D₂, E₄, F₄), lateral (E₂, G₂, H₂, J₂, K₁, L₁, M₁, N₁), and medial (E₃, G₁, I₄, K₃, L₂, N₃) views.

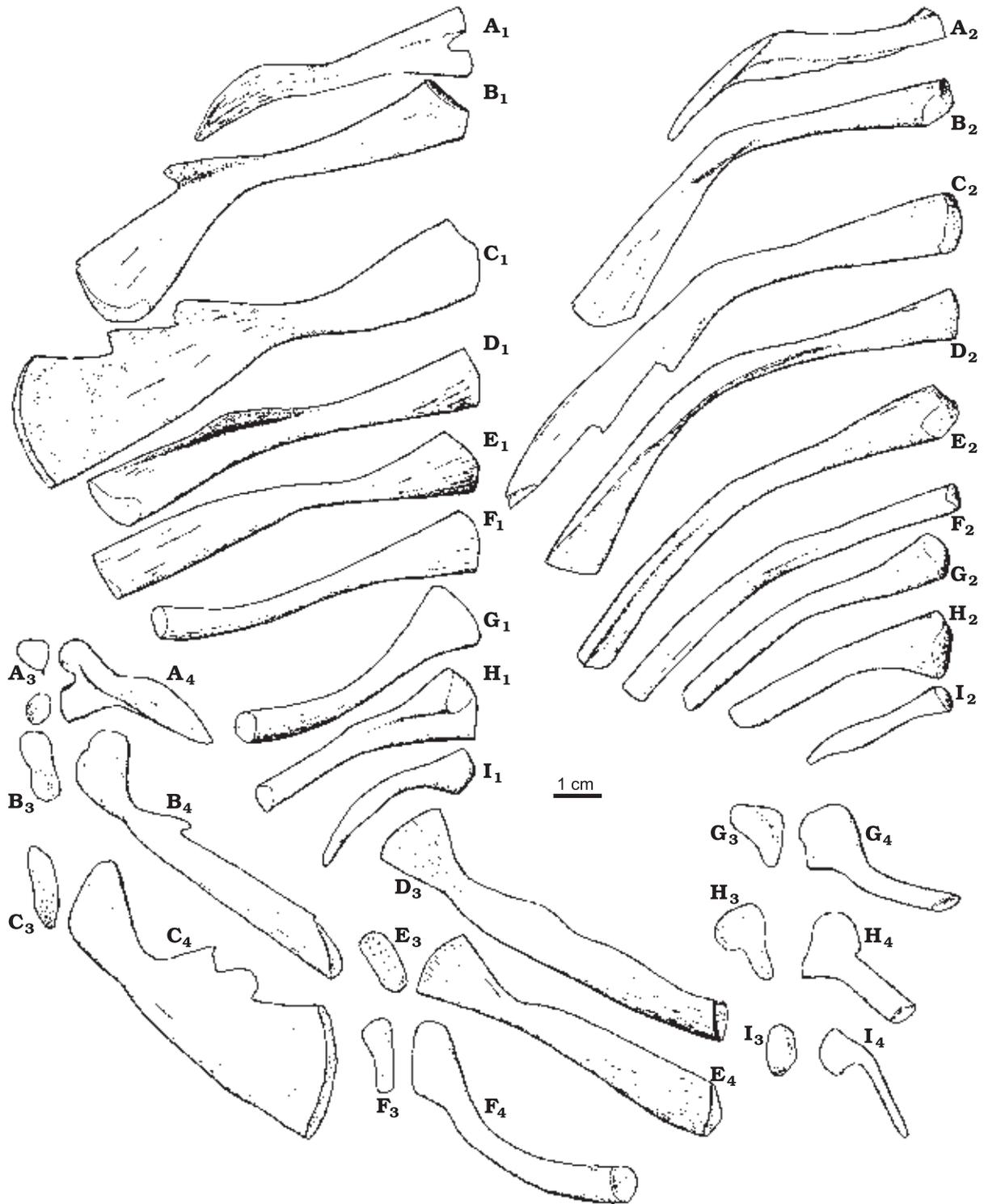


Fig. 39. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of ribs. A. Type A based on ZPAL AbIII/1519. B. Type C, ZPAL AbIII/1115. C. Type D, ZPAL AbIII/365. D. Type E, ZPAL AbIII/1003. E. Type F, ZPAL AbIII/1154/3. F. Type G, ZPAL AbIII/1149. G. Type H, ZPAL AbIII/1139/4. H. Type I, ZPAL Ab/III/1687. I. Type J, ZPAL Ab/III/1518. Respectively in posterior (A₁, B₁, C₁, D₁, E₁, F₁, G₁, H₁, I₁, J₁), lateral (A₂, B₂, C₂, D₂, E₂, F₂), dorsal (A₃, B₃, C₃, D₃, E₃, F₃), and ventral (A₄, B₄, C₄, D₄, E₄, F₄) views.

Rib type J: These are probably antero-caudal ribs that are rather short and strongly curved (Fig. 39I). The whole stylus or only the middle part is flat. The proximal head is oval and massive. The complete rib ZPAL AbIII/1518 has the stylus flat and wide in the middle and narrowing at the tip. This type is represented by

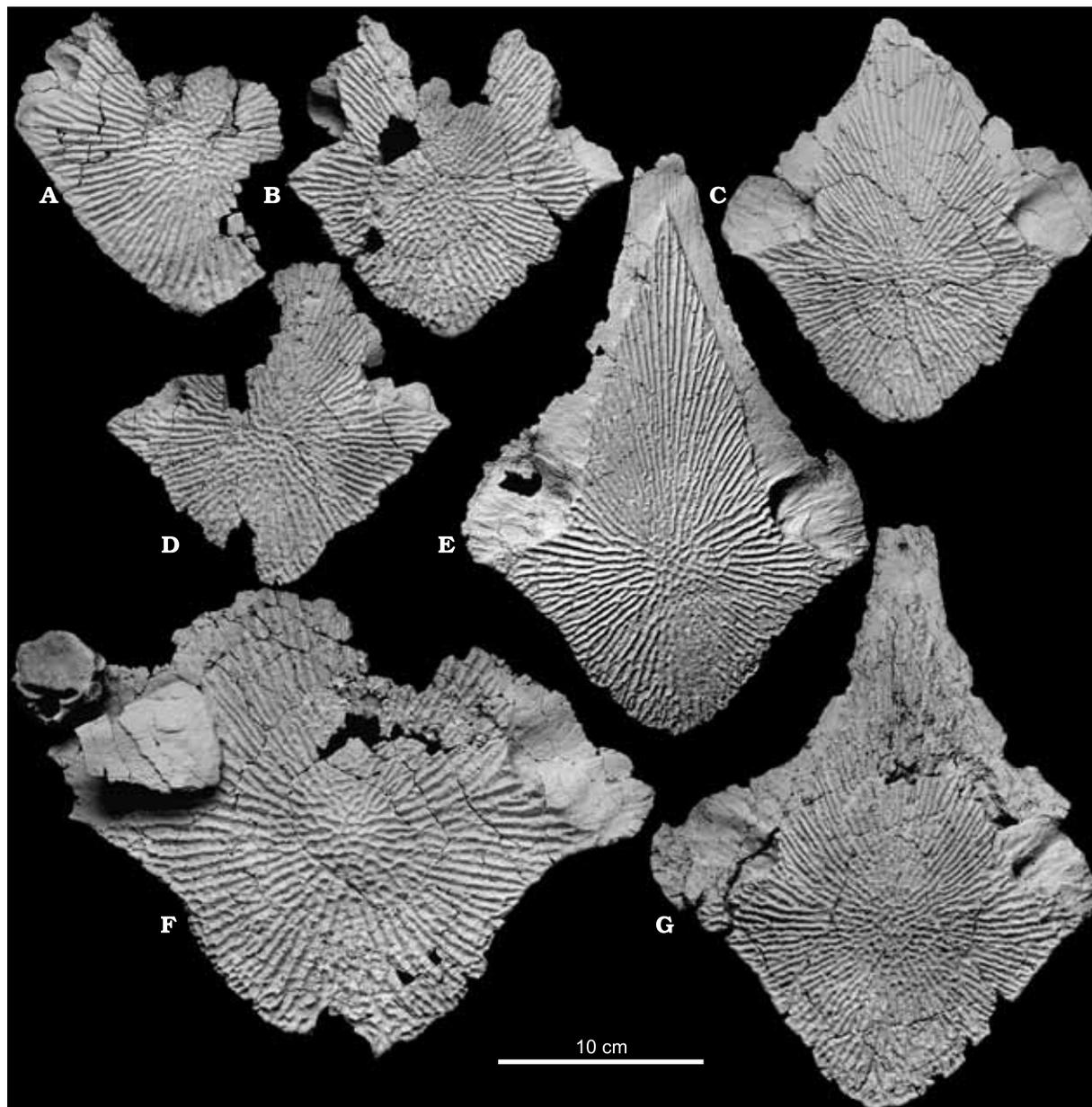


Fig. 40. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of interclavicles in ventral view. Specimens ZPAL Ab/III/1696 (A), ZPAL AbIII/90 (B), ZPAL AbIII/314 (C), ZPAL AbIII/1526 (D), ZPAL AbIII/1195 (E), ZPAL AbIII/92 (F), and ZPAL AbIII/347 (G).

specimens ZPAL AbIII/1518, AbIII/970/4, AbIII/1060/4, AbIII/1564, and AbIII/1541. Type J corresponds to the caudal ribs of *Dutuitosaurus*.

SHOULDER GIRDLE

Interclavicle. — According to Schoch (1999) the interclavicle of the Capitosauridae are the most massive and extended among all the temnospondyls. They are really the most extended, especially antero-posteriorly, but the metoposaurids have a much more massive interclavicle than the capitosaurids. *Metoposaurus maleriensis*, for instance, has the medium-size interclavicle almost 2 cm thick at approximately 25 cm width. Although the *Metoposaurus diagnosticus krasiejowensis* interclavicle is not as massive as that of *M. maleriensis*, but it is much thicker than interclavicle of *Cyclotosaurus intermedius* from the same locality.

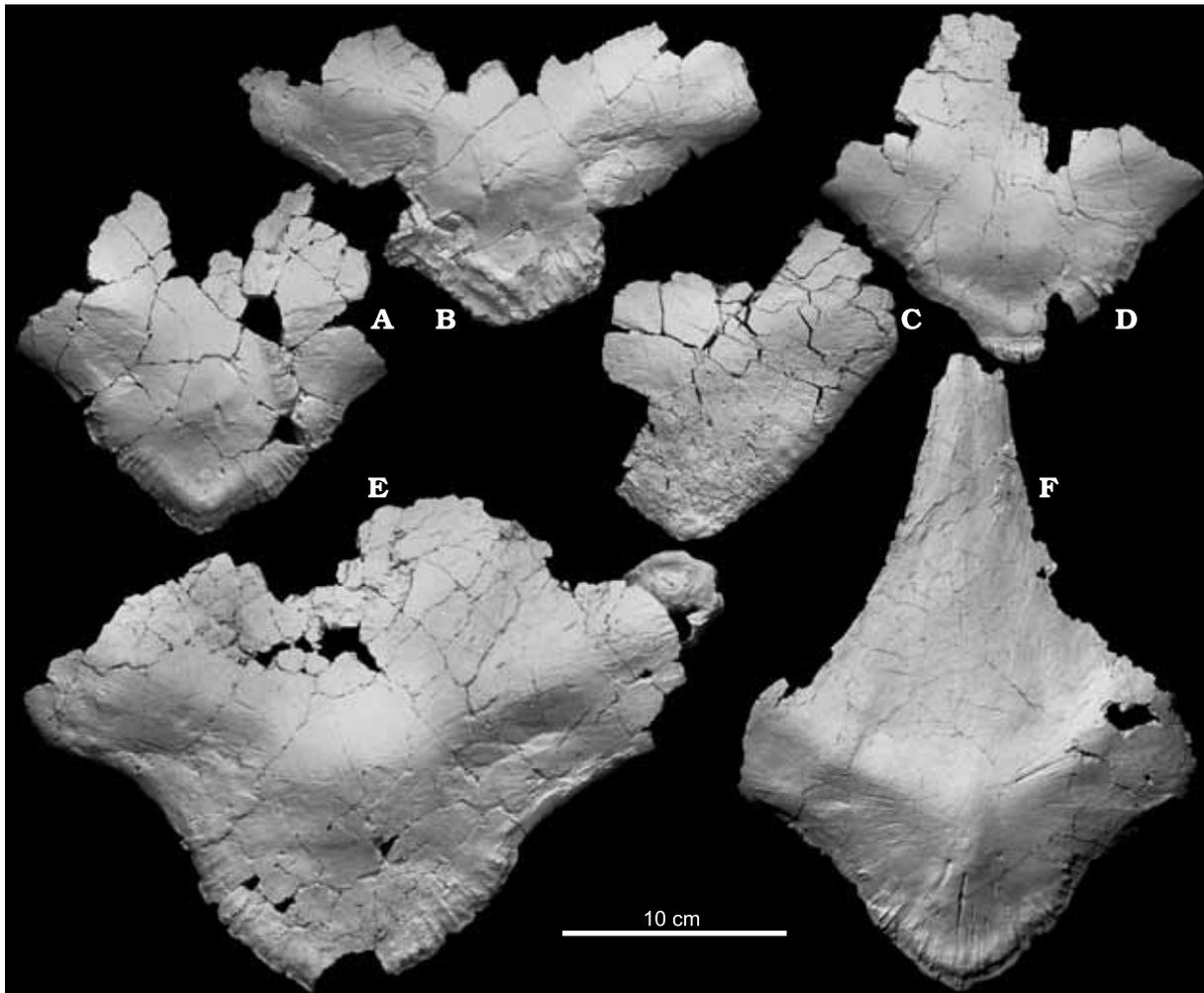


Fig. 41. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of interclavicles in dorsal view. A. ZPAL AbIII/90. B. ZPAL AbIII/1252. C. ZPAL AbIII/1696. D. ZPAL AbIII/1526. E. AbIII/92. F. ZPAL AbIII/1195.

The posterolateral edges of the interclavicle show a great variety of shapes (Figs 40, 41). In specimen ZPAL AbIII/1696, they are convex. In the specimen ZPAL AbIII/347, they are straight, but more usually they are more or less concave. Its extreme case can be seen in the largest interclavicle from Krasiejów, ZPAL AbIII/92.

The clavicles overlap the interclavicle in the posterior part of the lateral wings, whereas they abut against the lateral rim of the anterior portion of the latter. This connection is very variable. Some interclavicles have a strong inclination for clavicle, some have the connection almost straight. There is continuity between these extremes.

The ornament is generally very clear and strongly developed through the ventral face of the element. A few specimens have extremely shallow sculpture. It encompasses polygons in the centre. These polygons become rapidly elongate, especially anteriorly and posteriorly. The central pitted area is relatively small, similar to *Metoposaurus diagnosticus diagnosticus*. The ventral surface of the lateral wings is generally smooth. There are a few specimens with slight ridges.

The dorsal surface of the interclavicle is mostly smooth. Only the posterior edge is sculptured with numerous ridges. At the centre, there is central projection (eminentia centralis) that anteriorly bifurcates into clavicular bar directed anterolaterally (trabecula clavicularis; Bystrow and Efremov 1940). Posteriorly to them, in a few cases (it is well visible in ZPAL AbIII/1632/1), a large triangular area occurs that is slightly roughened and lowered (Figs 41A, B, 42). It seems that these are traces of an insertion of muscles. It could be also an articulation with coracoid, but it seems to be situated too far medially.

The interclavicles of *Metoposaurus diagnosticus krasiejowensis* and *M. maleriensis* were measured. For other known metoposaurid populations the measurements were taken from illustrates (Sawin 1945; Case 1932). Case (1922) suggested that *B. perfecta* has the posterior part of the interclavicle shorter than

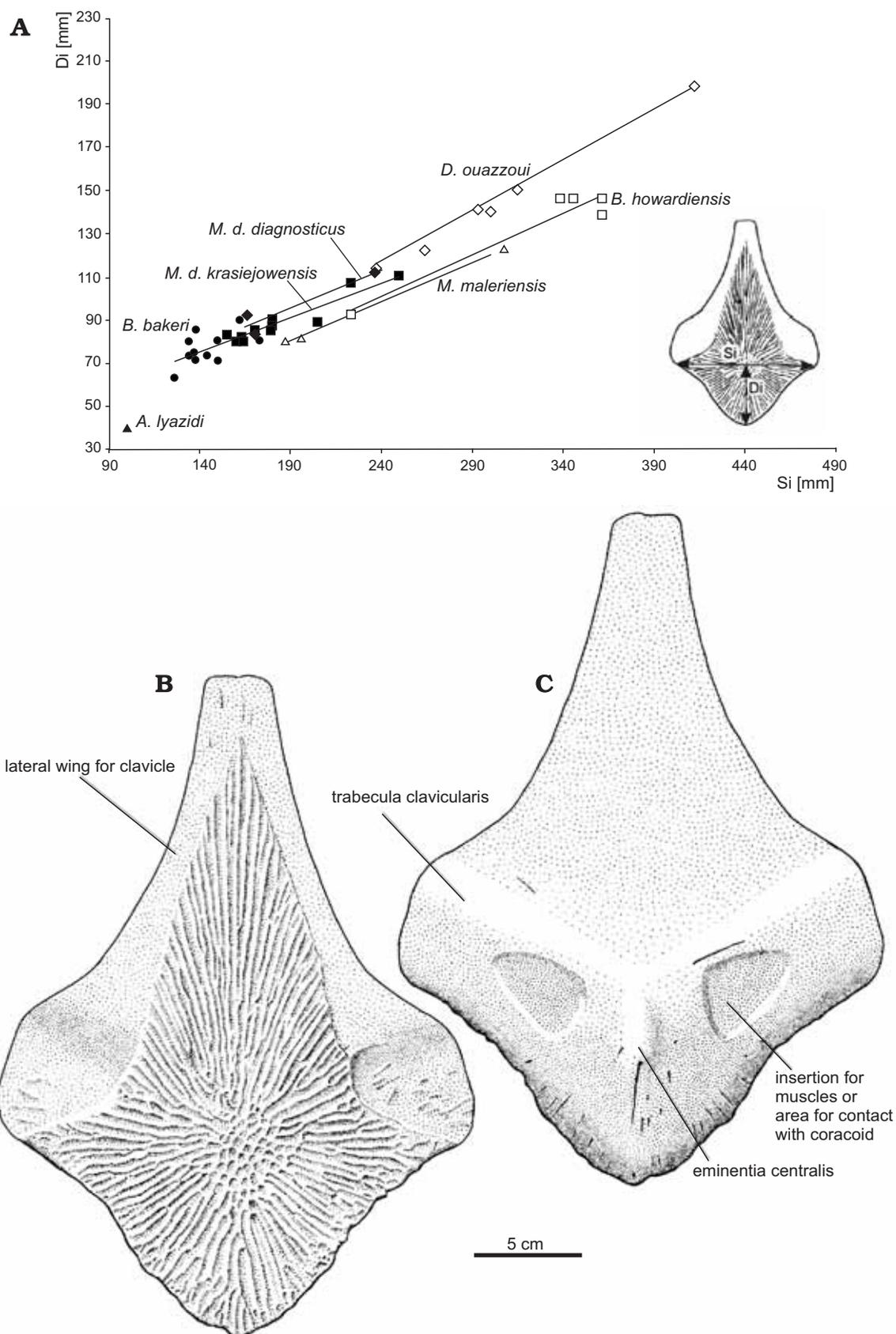


Fig. 42. **A.** Scatter-plot showing the differences in interclavicle proportions among the metoposaurids. **B, C.** Reconstruction of interclavicle of *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 based mainly on ZPAL AbIII/1195 and ZPAL AbIII/90, in ventral (**B**) and dorsal (**C**) views.

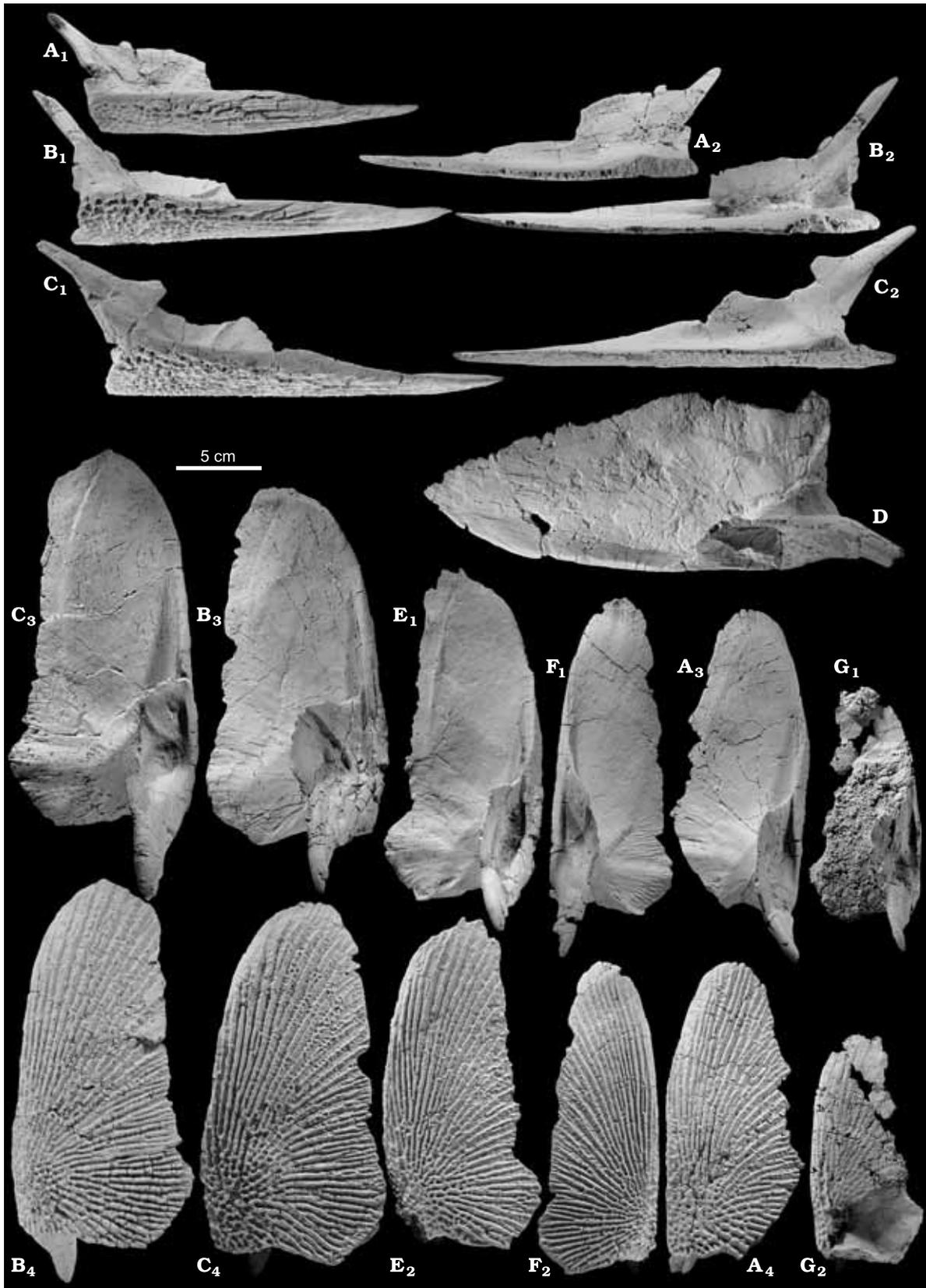


Fig. 43. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of clavicles. Specimens ZPAL AbIII/306 (A), ZPAL AbIII/1677 (B), ZPAL AbIII/1670 (C), ZPAL AbIII/1691 (D), ZPAL AbIII/1578 (E), ZPAL AbIII/1602 (F), and ZPAL AbIII/1131 (G), respectively in lateral (A₁, B₁, C₁), medial (A₂, B₂, C₂), dorsal (A₃, B₃, C₃, D, E₁, F₁, G₁), and ventral (A₄, B₄, C₄, E₂, F₂, G₂) views.

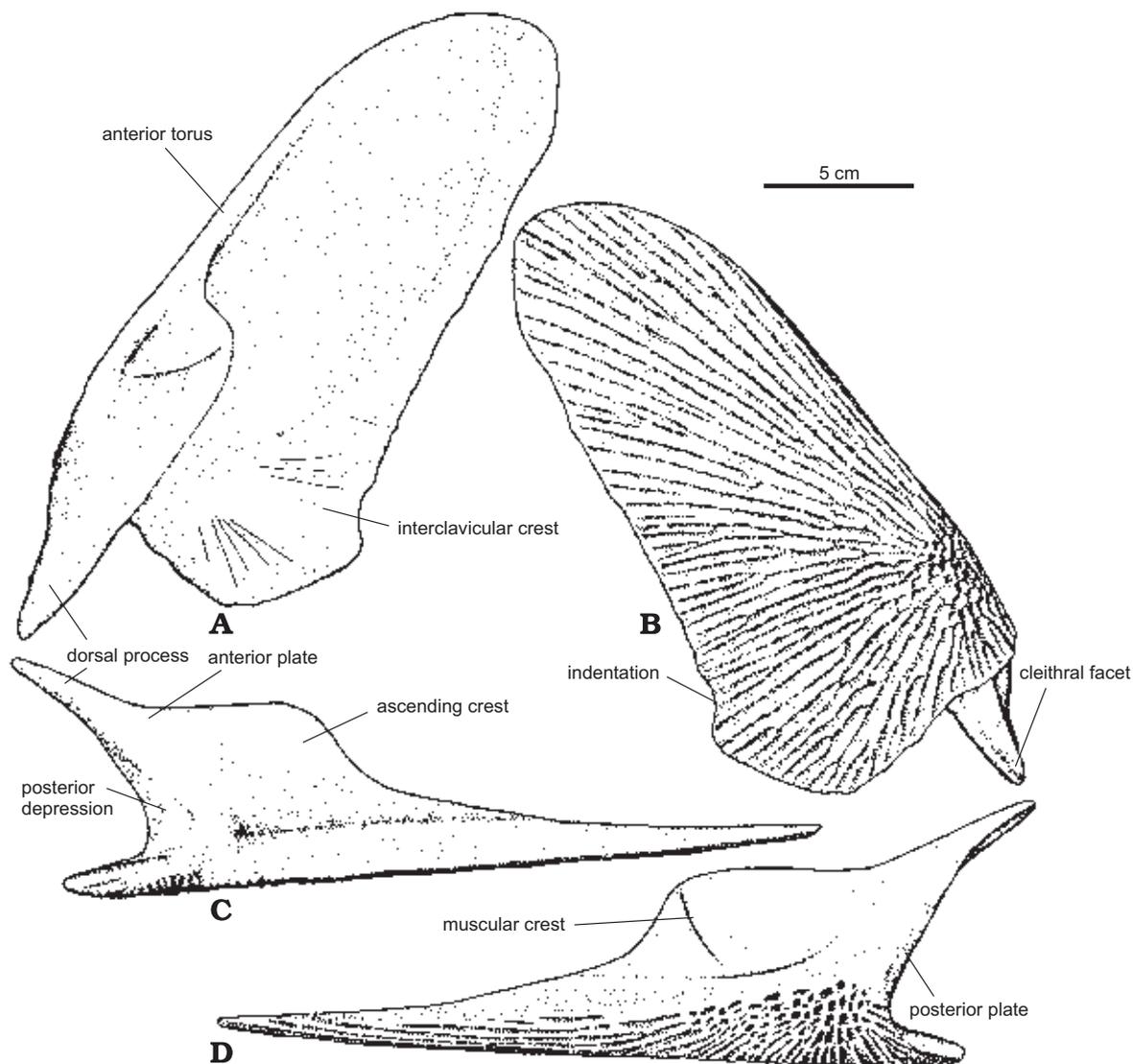


Fig. 44. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of clavicle based mainly on specimens ZPAL AbIII/1670 and AbIII/1677, in dorsal (A), ventral (B), medial (C), and lateral (D) views.

Metoposaurus. It seems that the most diagnostic is the relation of the length of the posterior part (Di) to the width of the sculptured area (Si) proposed also by Wernerburg (1990) (see also Fig. 42). The data are too limited to conduct statistical analysis and only the scatter-plot is presented. Despite sparse data points it seems that the length of the posterior part of the interclavicle is different in these populations. The shortest posterior part can be observed in *M. maleriensis* and the longest in *Dutuitosaurus ouazzoui*.

Clavicle. — The clavicles are sagittally elongated, generally slender and strongly ossified plates. Their medial and anteromedial shields underlie the lateral wings of the interclavicle to a large degree, and postero-medially directly connect the interclavicle with their own ornamentation. This part of the plate is very thick and forms apparent interclavicular crest (Shishkin 1987), its dorsal sculpture consist of radiate ridges. The area of a contact with the interclavicle is slightly depressed in respect to the rest of the dorsal area (Figs 43, 44). An indentation occurs in the medial border of its posterior part. Generally, it is very well developed, although in a few cases difficult to recognise. According to Warren and Marsicano (2000), such indentation on the medial edge of the clavicular plate is common for all brachyopids. It was demonstrated in *Batrachosuchus* (Brachyopidae) and *Compsocerops* (Chigutisauridae) and this character occurs “elsewhere in temnospondyls, for instance in plagiosaurs” (Warren and Marsicano 2000: p. 476); however, it appears that the Trematosauridae and Capitosauroida *sensu* Schoch and Milner (2000) do not have this indentation.



Fig. 45. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of scapulae. Specimens ZPAL AbIII/1058/2 (A), ZPAL AbIII/1555 (B), ZPAL AbIII/951/2 (C), ZPAL AbIII/1600 (D), ZPAL AbIII/1073/5 (E), ZPAL AbIII/1114/1 (F), ZPAL AbIII/1554 (G), and ZPAL AbIII/1595 (H), respectively in medial (A₁, B₁, C₁, D₁, E₁, F₁, G₁, H₁), and lateral (A₂, B₂, C₂, D₂, E₂, F₂, G₂, H₂) views.

The strongest portion of the clavicle is the base of the ascending process. The dorsal process is well ossified. Its dorsal part forms a stylet-like spike that partially underlies the base of the cleithrum. The dorsal process is generally at 45° to the plate of clavicle in lateral view, although in a few cases it is sloped more horizontally. In posterior view, it is at almost straight angle to the plate. Posteriorly the dorsal process is sup-



Fig. 46. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of scapulae. Specimens ZPAL AbIII/1555 (A), ZPAL AbIII/1600 (B), and ZPAL AbIII/1114/1 (C), respectively in posterior (A₁, B₁, C₁), ventral (A₂, B₂, C₂), anterior (A₃, B₃, C₃), and dorsal (A₄, B₄, C₄) views.

ported by the posterior plate (Shishkin 1987). The lateral side of the edge of the posterior plate is roughened and in ZPAL AbIII/1713 it bears an additional lamina. The posterior plate runs continuously into the dorsal part of the dorsal process and, like the latter, it is posteriorly roughened. This roughened area contacted the cleithrum. The anterior plate of the dorsal process forms a very high and thin ascending crest.

The muscular depression (fossa muscularis) of the ascending crest bears the ridge (thickened central rib of Yates and Warren 2000). The size of the ridge is very variable. Usually, it is distinct but in a few cases only slightly marked. The muscular depression was probably an insertion of the cleidomastoideus muscle (Watson 1958; Howie 1970; Sulej and Majer 2005). At the medial side of the base of the ascending crest, a very wide and shallow ridge supports the crest. It was described in *Eryosuchus* (“*Parotosuchus*”) *pronus* by Howie (1970) as “centre”, and by Dutuit (1976) as “eminence transverse”. At the lateral side of the base of the ascending crest, a deep trough is present. It forms ventral surface of the prescapular cavity (Damiani 2001). The lateral edge of the clavicular plate may form the anterior ridge (torus anterior), which is the lateral edge of the trough. The anterior ridge may be pointed or round. The trough may run to the anterior termination of the ascending crest or it may terminate before. In that case, the ascending crest smoothly passes into anterior ridge. The presence of the trough is the main character that distinguishes the metoposaurids clavicle from that of *Cyclotosaurus intermedius* found in the same locality.

The ventral area of the clavicle is sculptured in the way typical for metoposaurids. The sculpture consists of the polygonal pits in the posterolateral part of the clavicle and the ridges radiate posteromedially, medially, and anteriorly. Generally, they run towards the anterior edge of the plate, but in a few cases they terminate before, leaving a smooth marginal area.

Although there are no specimens of well articulated clavicles, it seems that the clavicles meet in variable ways. The shape of the clavicle margin, which contacts counterpart clavicle, is variable (Sulej 2000). When it is straight, the contact was extensive as it is visible in *Metoposaurus diagnosticus diagnosticus*; when it is curved or the edge is serrated, the clavicles probably did not stay in contact. The clavicle plate has proportions similar to the juvenile clavicles of *Benthosuchus* (Bystrow and Efremov 1940).

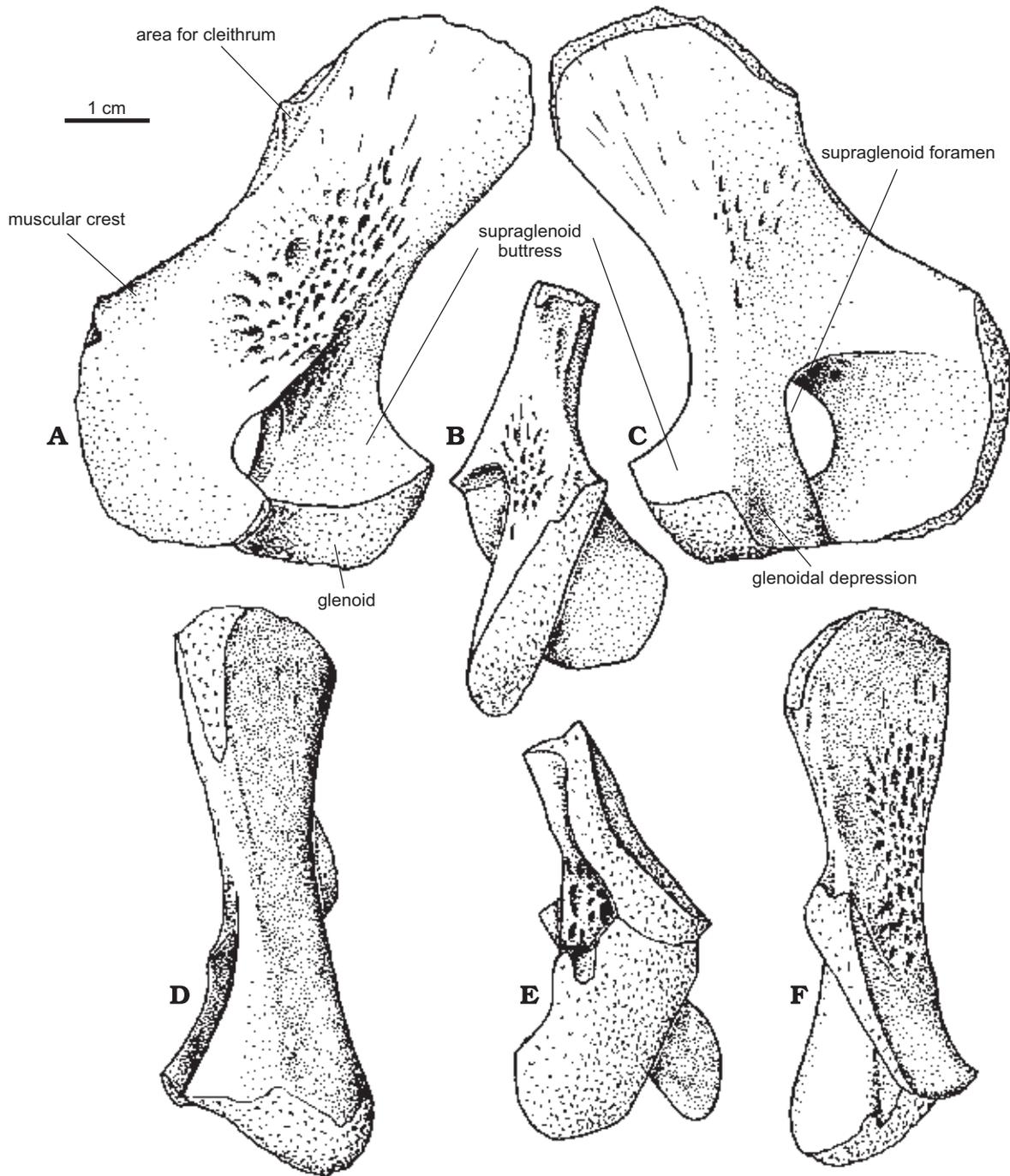


Fig. 47. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of scapula based mainly on ZPAL AbIII/1554, in lateral (A), dorsal (B), medial (C), posterior (D), ventral (E), and anterior (F) views.

Scapula — The scapula of *Metoposaurus diagnosticus krasiejowensis* is well ossified. The coracoid must have been cartilaginous even in the late developmental stages because numerous large scapula were found, and there were no coracoids. The coracoid is preserved in *Buettneria perfecta*, *Dutuitosaurus ouazzoui*, and probably in *Metoposaurus diagnosticus diagnosticus* (Huene 1922: fig. 36, and personal observation). In *M. maleriensis*, it is not well preserved but it seems that a part of ossified coracoid is present in specimens ISIA90 and ISIA92 (Sengupta 2002 and personal observation). No observation is available for other species.

The morphology of the scapula is similar throughout the temnospondyls and basal tetrapods. It consists of the upper blade that bifurcates in the middle into the blade that contacts coracoid and the shaft that extends



Fig. 48. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of cleithra. Specimens ZPAL AbIII/1012/9 (A), ZPAL AbIII/303 (B), ZPAL AbIII/156 (C), ZPAL AbIII/1058/3 (D), ZPAL AbIII/994/6 (E), ZPAL AbIII/1068/5 (F), and ZPAL AbIII/159 (G), respectively in medial (A₁, B₁, C₁, D₁, E₁, F₁, G₁), lateral (A₂, B₂, D₂, E₂, F₂, G₂), posterior (A₃, B₃, E₃, F₃), and anterior (A₄, B₄, E₄, F₄) views.

ventrally to form the glenoid facet (Figs 45–47). Between the ventral shaft and blade there is the supraglenoid foramen, which is open ventrally in small specimens. In the smallest ones, the ventral blade is much shorter than the shaft with glenoid facet. The supraglenoid foramen is oval with almost vertical longer axis. It is situated posterodorsally to the upper edge of the glenoid facet. The position of the supracoracoid foramen is ambiguous. In the large scapula ZPAL AbIII/1554, the fissure that may be interpreted as the part of the supracoracoid foramen is present. It is situated at the posterior corner of the glenoid facet. This position is similar to that in other metoposaurids. In the ZPAL AbIII/1595, such a fissure is situated on the ventral edge, but the meaning of it is unclear.

Most of the surface of the scapula is smooth or with a fine striation, with exceptions of well-defined area, ornamented with very deep large pits at the medial part of the scapula blade on the lateral side. Such ornamentation is absent in the capitosaurids (*e.g.*, *Cyclotosaurus* and *Mastodonsaurus*). It might be due to pedomorphic origin of the metoposaurids. A muscle attachments occur (1) on the dorsal part of its medial side, (2) on the upper and lateral margins of the supraglenoid foramen, and (3) on the posteriolateral edge of the scapula.

The glenoid is directed posterolaterally and slightly ventrally. Usually, it is rectangular but there is a great variety of its shape. The glenoidal depression may be well developed, as in ZPAL AbIII/1084/1 or absent,

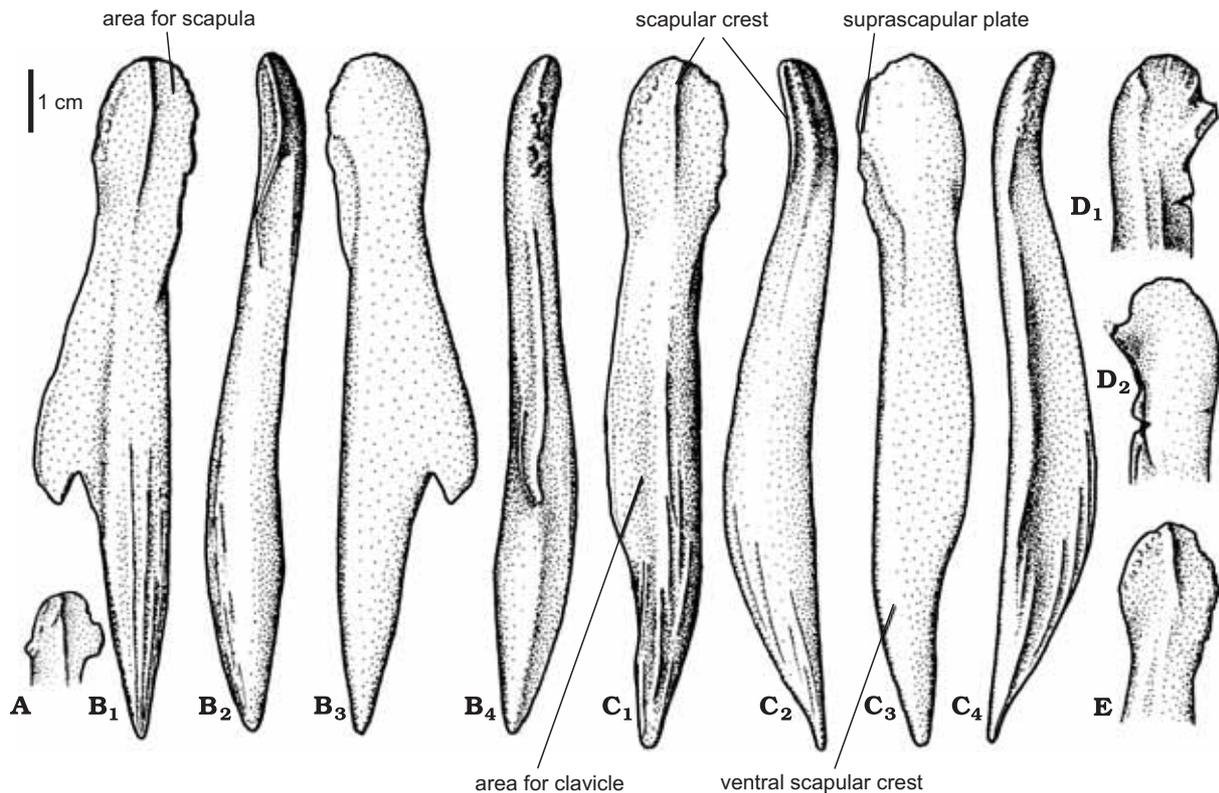


Fig. 49. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstructions of various morphologies of cleithra. Based on specimens: ZPAL Ab/III/1728 (A), ZPAL Ab/III/1012/9 (B), ZPAL Ab/III/303 (C), ZPAL Ab/III/311 (D), and ZPAL Ab/III/1058/3 (E), in medial (A, B₁, C₁, D₁, E), posterior (B₂, C₂, D₂, F₂, G₂), lateral (B₃, C₃), and anterior (B₄, C₄) views.

then the anterior surface of the glenoid shaft may be flat, as in ZPAL Ab/III/1595. The glenoid facet in small specimens is flat but very convex in large ones.

The medial side of the scapula bears a ridge, which widens both dorsally, and ventrally. Anteriorly and dorsally, the margins of the scapula are not completely ossified, as indicated by its roughened and flat or concave surface. The medial part of the anterior margin is smooth and varies in length. The anterior margin is curved in sigmoid fashion if viewed dorsally. The area for cleithrum is situated at the contact of the medial smooth anterior edge with the dorsal roughened edge. Its surface is rugose and reflects the shape of the area for scapula on the cleithrum.

The glenoid facet of *Buettneria howardensis* is directed lateroventrally. In *Dutuitosaurus*, it is directed posterolaterally and only slightly ventrally. The posterior edge of the scapula of *Dutuitosaurus* is markedly concave in lateral view, much more than in *M. diagnosticus krasiejowensis*. It may be connected with ossification of the coracoid and probably larger ossification of the glenoid; however, it seems that these are generic differences rather than related to degrees of ossifications. *M. maleriensis* is similar in these aspects to *M. diagnosticus krasiejowensis*.

In the *B. howardensis*, only very large scapulocoracoids are preserved, the scapula is almost two times larger than in the largest specimens of *M. diagnosticus krasiejowensis*. But in *Dutuitosaurus* the scapulocoracoid of the size similar to that of the scapula of *M. diagnosticus krasiejowensis* has the coracoid ossified. It seems the ossification of the coracoid or its lack is not related to size as it is in the case of *Dutuitosaurus*. The presence of the coracoid together with the scapula may be useful in defining genera or species.

Cleithrum. — It has a stout and well-ossified shaft and the most dorsally situated head (Figs 37, 38). The external surface of the shaft is smooth and convex. The internal facet bears a concave area for clavicle and a convex area for scapula. Both are prominently rugose, especially in the ventral part. It seems that the area for clavicle tightly fits the dorsal process of the clavicle. The head bears a distinct scapular crest, and the suprascapular plate (suprascapularis lamina) is covered with many small nodes.



Fig. 50. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of humeri. Specimens ZPAL AbIII/817 (A), ZPAL AbIII/814 (B), ZPAL AbIII/815 (C), ZPAL AbIII/816 (D), ZPAL AbIII/330 (E), ZPAL AbIII/1542 (F), ZPAL AbIII/830 (G), respectively in ventral (A₁, B₁, C₁, D₁, E₁, F₁, G₁), anterior (A₂, C₂, E₂, G₂), dorsal (A₃, B₂, C₃, D₂, E₃, F₂, G₃), and posterior (A₄, B₃, C₄, D₃, E₄, F₃, G₄) views.

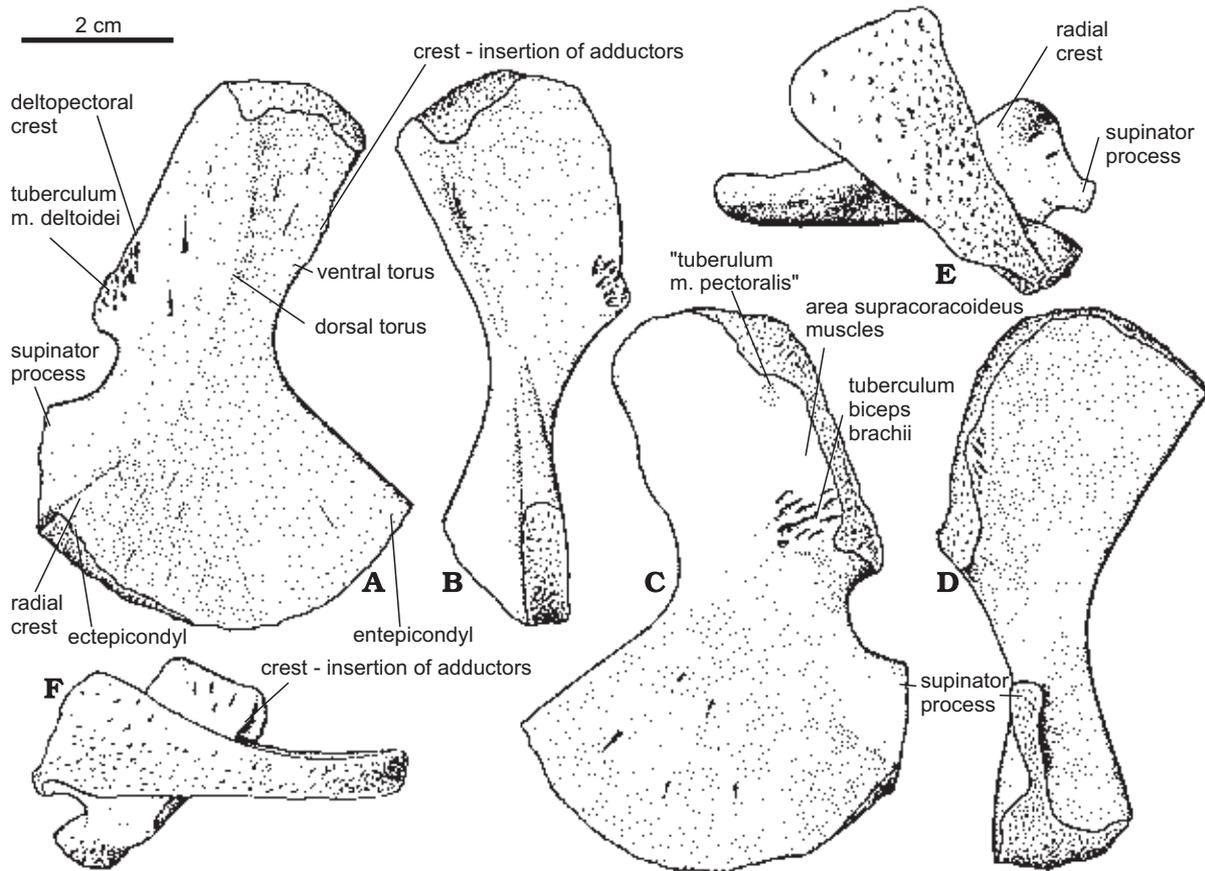


Fig. 51. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of humerus based on ZPAL AbIII/330, in ventral (A), posterior (B), ventral (C), anterior (D), proximal (E), and distal (F) views.

The shape of the head and the anterior margin of the area for clavicle is very variable. The anterior margin of the area for clavicle may form an extended shelf as in ZPAL AbIII/1036/9, or the shelf may form additional shaft directed ventrally, as in ZPAL AbIII/1012/9. The suprascapular plate may form a large process as in ZPAL AbIII/159, or various prominences, as in ZPAL AbIII/311. The shape and proportions of the cleithrum in *M. diagnosticus krasiejowensis* are similar to that of *Metoposaurus maleriensis*, *Buettneria perfecta*, and *Dutuitosaurus*.

Humerus. — The general structure of the humerus is similar in most basal tetrapods (Miner 1925; Romer 1957; Jarvik 1980). It is short, markedly widened at both ends and forms a tetrahedron. In temnospondyls, the humerus differs from that of most anthracosaurs (Romer 1957), *Ichthyostega* (Jarvik 1996), and microsaur (Carroll and Gaskill 1978) in showing clear torsion (Schoch 1999). The humeri of metoposaurids are well known and follow this pattern, but they are wider than the humeri of capitosaurids (e.g., *Cyclotosaurus*, *Mastodonsaurus*) and have much shorter anterior edge of the shaft.

The humerus of *Metoposaurus diagnosticus krasiejowensis* is typical for the metoposaurids. It has a short and slender shaft, a wide head, and a pronounced ectepicondyl (Figs 50, 51). The base of radial condyle forms a small prominence on its ventral side. The radial crest continues from the ectepicondyl to the proximal head. The supinator process is thin and rather short. The anterior margin of the humerus is unusually short and concave, but its length is variable. The entepicondyl is thicker than supinator process.

Dorsally, the proximal head is very thick with the wide dorsal surface that bears, on the ventral torus, a crest for insertion of the adductor muscles (Dutuit 1976). The crest forms a short additional ridge. The head has a very long trace of cartilaginous part on its medial and ventral sides. Generally, it becomes narrower posteroventrally, but there are two prominences on the ventral side. More apparent is the deltopectoral process with a rugose insertion of the grand pectoral muscle (Dutuit 1976) or biceps brachii (Ochev 1972). At the middle of the long trace of cartilage, there is a prominence, which has a variable size and shape. It may be

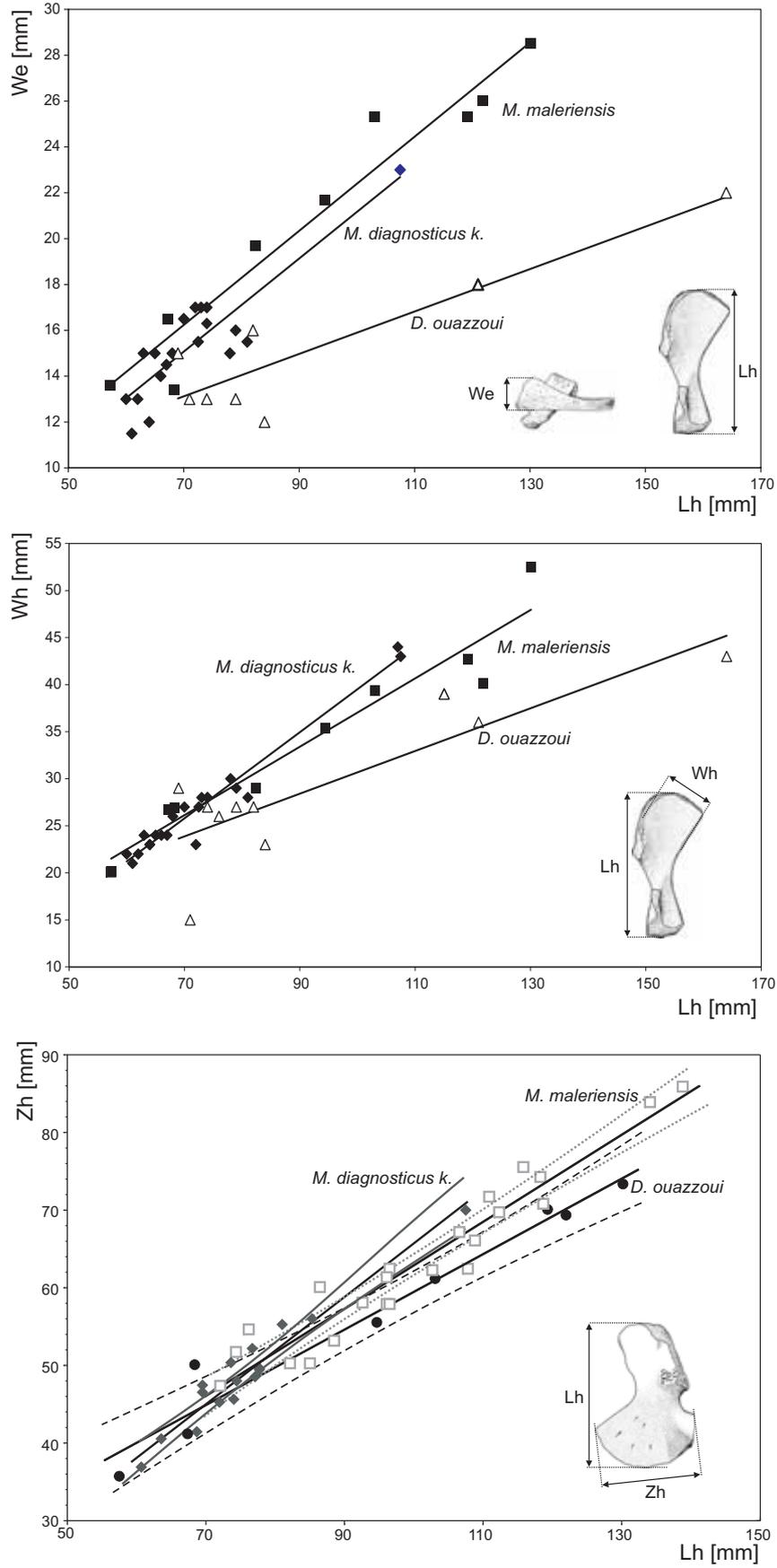


Fig. 52. Scatter-plots showing differences of proportion of humerus in metoposaurids.

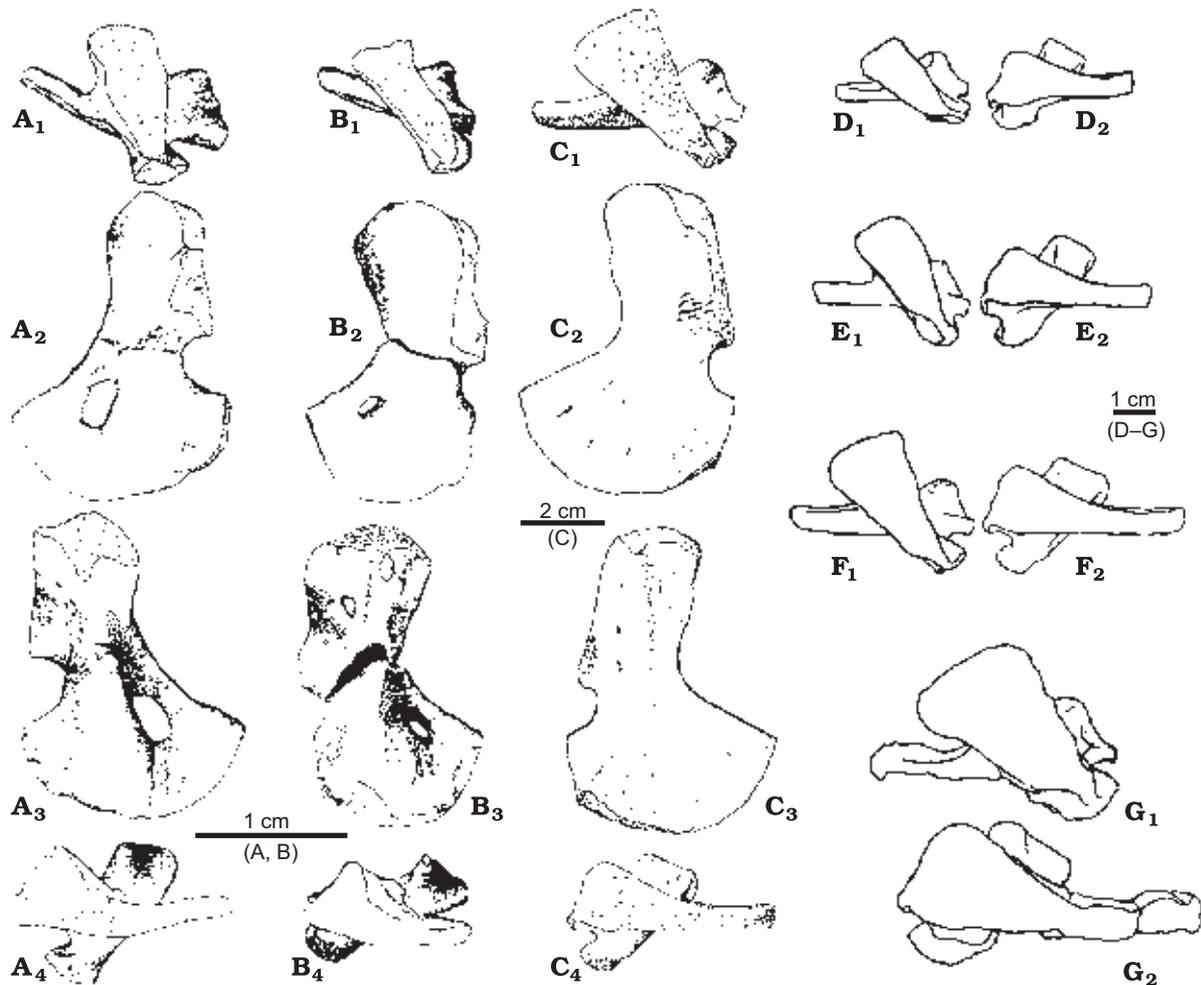


Fig. 53. Similarity of humeri of *Metoposaurus*, *Seymouria*, and *Discosauriscus*, both latter from Klembara *et al.* (2001). **A.** *Seymouria sanjuanensis*. **B.** *Discosauriscus austriacus*. **C–G.** *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002. On the right, variability of humerus heads from Krasiejów. **E.** ZPAL AbIII/817. **F.** AbIII/1542. **G.** AbIII/830. Respectively in proximal (A₁, B₁, C₁, D₁, E₁, F₁, G₁), ventral (A₂, B₂, C₂), dorsal (A₃, B₃, C₃), and distal (A₄, B₄, C₄, D₂, E₂, F₂, G₂) views.

only slightly developed with a narrow base or its base may be very wide and markedly high. In the largest specimen, it forms a large surface on the anteroventral side of the head. According to Ochev (1972), this is the “tuberculum m. pectoralis”. It may also be interpreted as a termination of the main area, which contacts glenoid, similar to *Mastodonsaurus*, where the proximal and posteroventral parts of the glenoid facet are not fused.

Supracoracoideus muscles occupy the area between the deltopectoral process and “tuberculum m. pectoralis” (Ochev 1972). In the specimens from Krasiejów, it is smooth. The dorsal side of the ventral edge of the head, proximally to the deltopectoral process, bears a rugose area, which according to Dutuit (1976) and Ochev (1972) is the insertion of the deltoid muscle.

The area of the insertion of the pectoral muscle is very large already in small specimens. Later in ontogeny, it increases only slightly but it becomes more convex up to forming a high prominence in the largest specimens. In contrast, the ventral part of the ectepicondyl is indistinct in small specimens but very large in the largest ones.

The posterior edge of the proximal head (ventral torus) and the posterior edge of the distal head forms an angle in ventral view, which may be almost right, as in ZPAL AbIII/330, or much obtuse as in ZPAL AbIII/815. The roughened connection of the supinator process and ectepicondyl has a variable width or may vanish as in ZPAL AbIII/1126, where the supinator process is divided from the ectepicondyl by the smooth bone area.

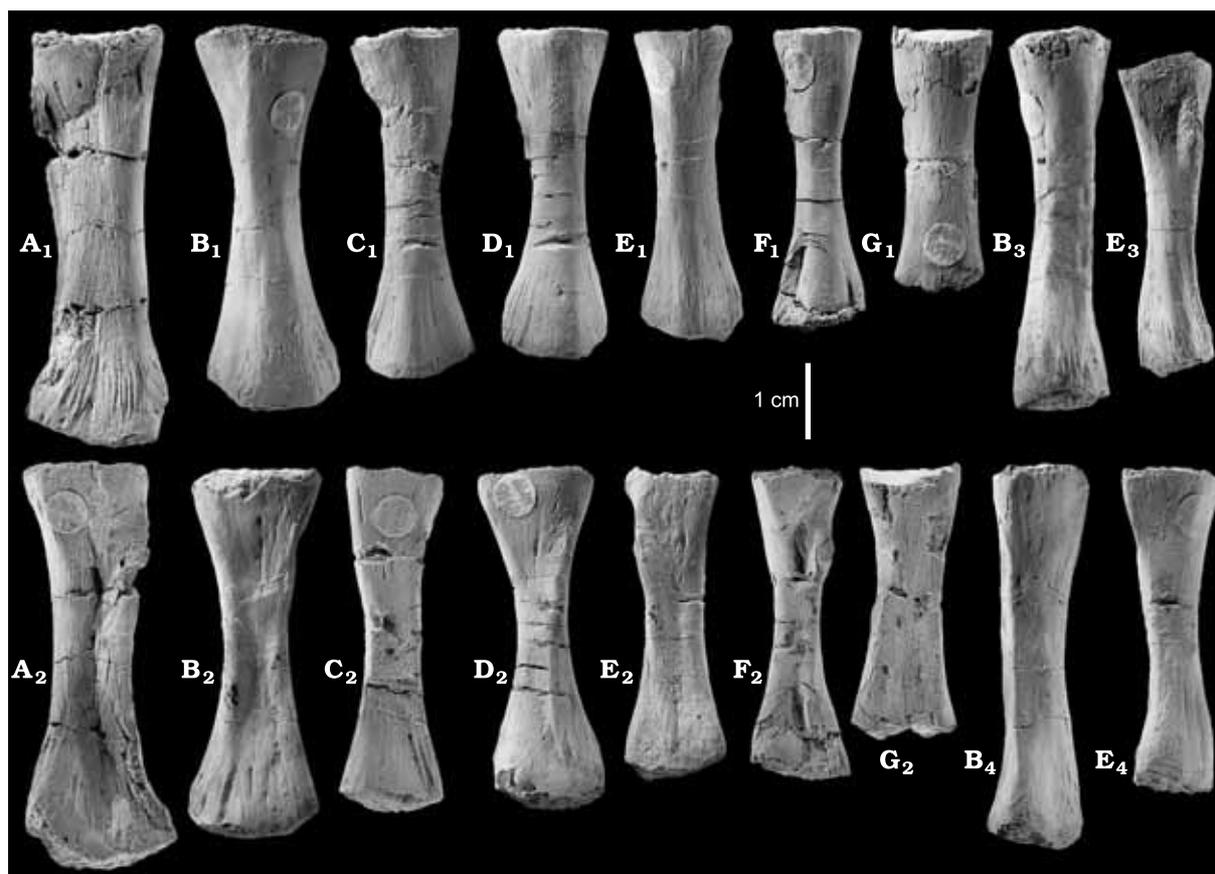


Fig. 54. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of radii. Specimens ZPAL AbIII/1056/4 (A), ZPAL AbIII/1590 (B), ZPAL AbIII/1027/1 (C), ZPAL AbIII/956/1 (D), ZPAL AbIII/950/6 (E), ZPAL AbIII/975/9 (F), and ZPAL AbIII/1157/2 (G), respectively in lateral (A₁, B₁, C₁, D₁, E₁, F₁, G₁), medial (A₂, B₂, C₂, D₂, E₂, F₂, G₂), anterior (B₃, E₃), and posterior (B₄, E₄) views.

Some parameters of the humeri of three metoposaurids populations were measured. It seems that the most diagnostic features are the width of the ectepicondyl and the proximal head. The scatter-plots show that the populations of *M. diagnosticus krasiejowensis* and *M. maleriensis* are closer to each other than to the population of *Dutuitosaurus* (Fig. 52). Probably the other basal metoposaurids were similar to *Dutuitosaurus* also in these aspects. Sawin (1945) showed that the humeri of the *B. howardensis* have the very large supinator process, similar to that of *Eryops*. In general, shapes of the humeri of *M. maleriensis*, *Dutuitosaurus*, and *M. diagnosticus krasiejowensis* are almost identical to the juvenile humerus of *Seymouria sanjuanensis* and *Discosaurus austriacus* (Klembara *et al.* 2001). The main difference is that these species have the entepicondyl foramen (Fig. 53). Except for some differences, the humerus is more similar to that of the seymouriamorphs than to larger specimens of *Benthosuchus*, or other capitosaur (*Eryosuchus pronus*, *Mastodonsaurus*, *Cyclotosaurus*) or *Compsoceros cosgriffi* (personal observation). The similarity to juvenile specimens of the anthracosaurs suggests that metoposaurids have a strongly paedomorphic humerus.

Radius. — The medial surface is flat, and bears a ridge on its distal portion already described in *Dutuitosaurus* by Dutuit (1976) as “gouttière longitudinale interne”. A similar ridge was illustrated in *Eryosuchus garjainowi* Ochev, 1966 (Ochev 1972). The anterior ridge of the medial surface in its proximal part forms the “tubercule antero-superieur” (Dutuit 1976), present also in *Eryosuchus*. The mentioned “gouttière” and “tubercule” are well visible in ZPAL AbIII/950/6, AbIII/956/1, and AbIII/1587/1, but in other specimens they are not developed (Figs 54, 55).

The radius has different but variable proximal and distal ends. The proximal end is almost round with a rectangular anteromedial edge. The proximal head is triangular with the posterior apex more shaped than the anterior one. General shape of the radius is very similar to the radius of *Eryosuchus*. The lateral surface of the

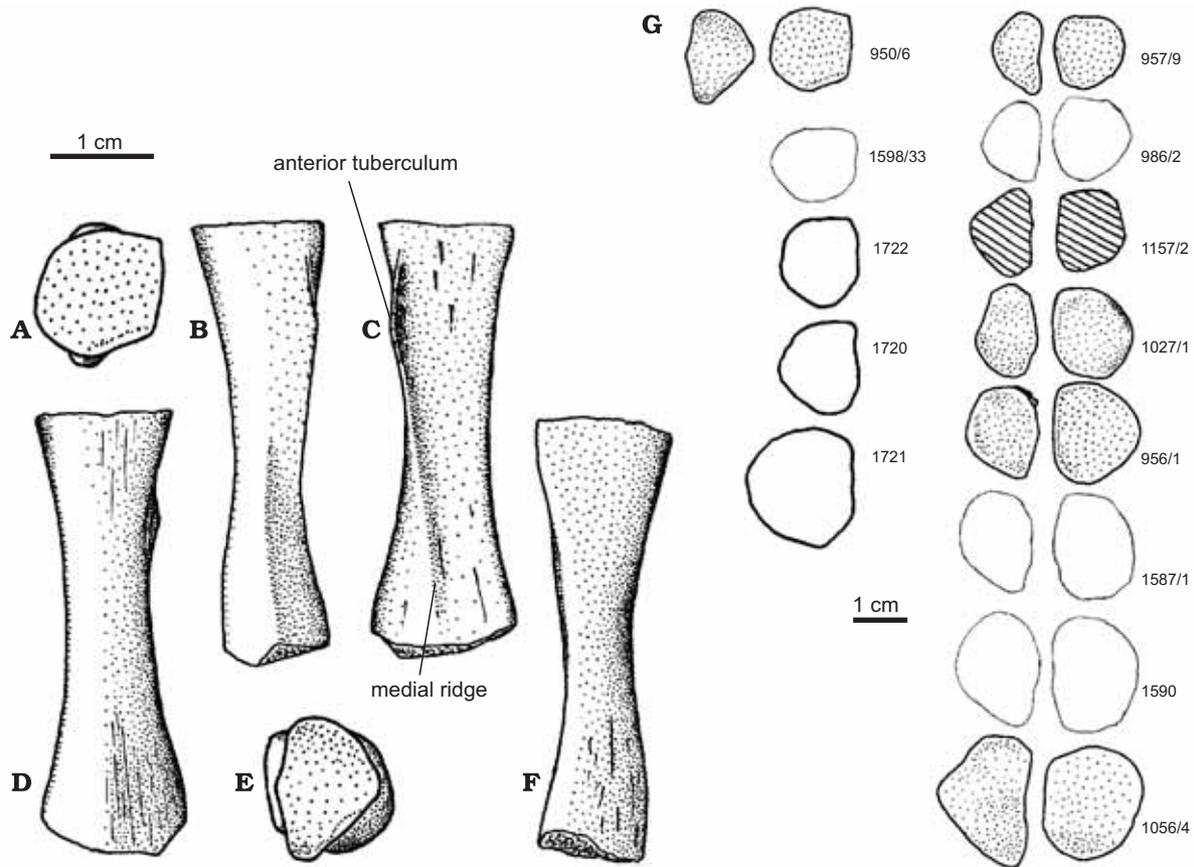


Fig. 55. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of radius based on ZPAL Ab/III/950/6 and variability of radius heads, in proximal (A), anterior (B), medial (C), lateral (D), distal (E), and posterior (F) views. G. Heads in pairs: distal on the left, proximal on the right; numbers of specimens ZPAL AB/III are shown beside the drawings.

radius is convex but it does not bear a medial ridge, which is present in *Eryosuchus* (Ochev 1972) and *Mastodonsaurus* (Schoch 1999).

Ulna. — In contrast to the rather symmetrical radius, the ulna is more distinctly curved and rotated (Figs 56, 57). The olecranon process is rather low and its base (posterior edge of the ulna) is straight and narrow. The “*incisura radialis*” (Ochev 1972) is slightly marked on the anterodorsal surface of the proximal head. The medial side of the proximal head is much more pointed than the lateral side. The distal head is retorted and the anterior edge is directed anteromedially. It is oval in ventral view and very convex in anterolateral view. Its posteromedial surface is flat and the anterolateral surface is convex and bears “*crista m. extensoris carpi ulnaris*” (Ochev 1972). The base of the olecranon process is serrated. The anterior side of the shaft bears a few pits.

The ulna is very similar to that element of *Eryosuchus* (“*Parotosuchus*”) (Howie 1970) especially in the lateral view with the widened distal part (although it is more rotated in *Metoposaurus diagnosticus krasiejowensis*). Also the olecranon process is much narrower than in *Eryosuchus*. The ulna is represented only by the four specimens so its variability is difficult to determine.

Manus. — As in all other metoposaurids the carpalia are unpreserved. Almost all metacarpals and digits of *Metoposaurus diagnosticus krasiejowensis* are represented in the collection (Figs 61, 62). In the articulated specimen ZPAL Ab/III/1717, the elements are slightly moved from their natural position. Two digits are preserved. The completeness of the digits was determined according to the articulated specimens of *Dutuitosaurus* (Dutuit 1976). It seems that *Metoposaurus diagnosticus krasiejowensis* has phalanges formula 2 3 3 2. The metacarpals and digits are flat ventrally and convex dorsally. The last digits are narrower than in *Dutuitosaurus* and their dorsal edge bears minute nodes. The whole last digit is hooked. This suggests that they had keratinous claws, like Recent *Xenopus*. The metacarpals and digits have the same proportions as in *Dutuitosaurus*.

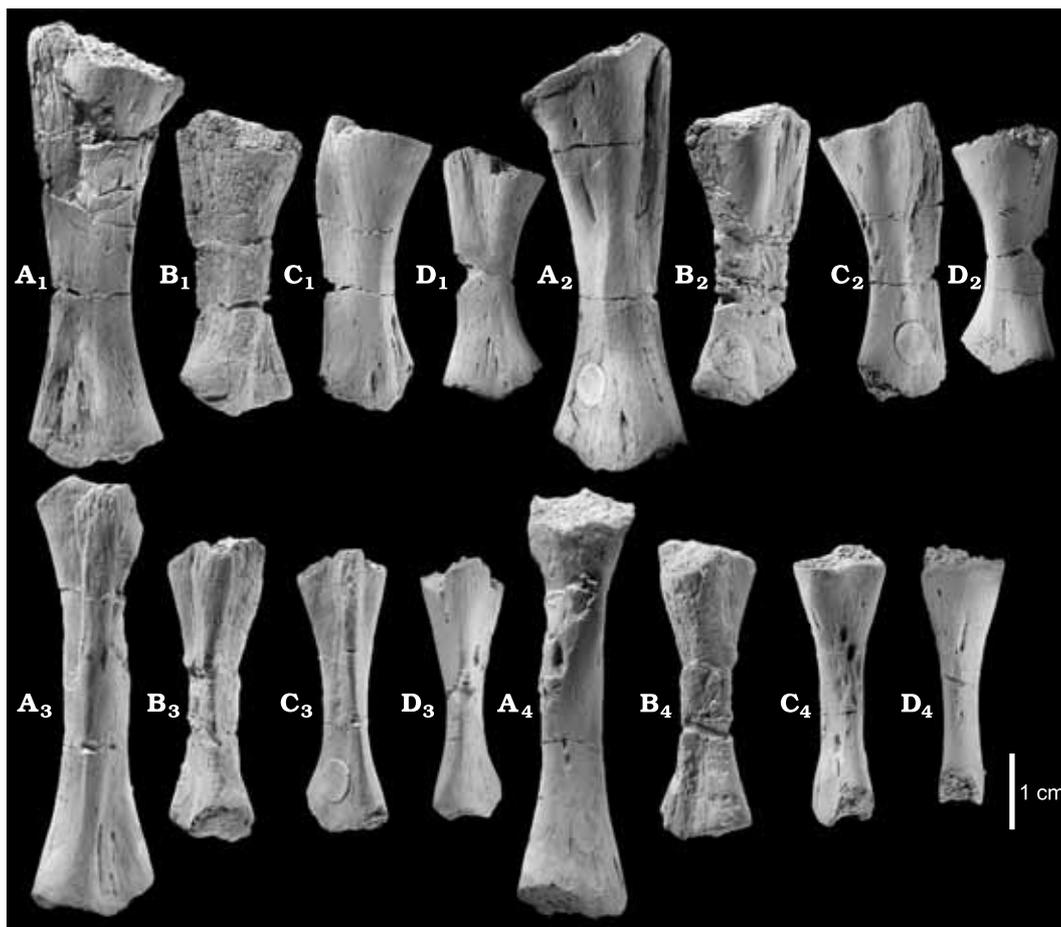


Fig. 56. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of ulnae. Specimens ZPAL AbIII/1559 (A), ZPAL AbIII/1 (B), ZPAL AbIII/1568 (C), and ZPAL AbIII/1831 (D), respectively in lateral (A₁, B₁, C₁, D₁), medial (A₂, B₂, C₂, D₂), posterior (A₃, B₃, C₃, D₃), and anterior (A₄, B₄, C₄, D₄) views.

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Ilium. — It consists of the narrow dorsal shaft and a posteriorly much widened base, as in all temnospondyls (Schoch 1999). However, in the largest specimens of *Benthosuchus*, the dorsal end of the shaft bifurcates, which according to Schoch (1999) is a plesiomorphic condition. There is still a question of whether the single and narrow posterodorsal shaft of the metoposaurids is a paedomorphic (compared with *Benthosuchus*) or advanced condition.

The shaft cross-section shape is oval to nearly rounded near the base of the shaft. Farther dorsally, it flattens and gradually broadens both anteriorly and posteriorly to the long axis. Generally, the shaft is straight, although in a few cases it is sinusoidal (Figs 58, 59). Although there is a great variability in the shape of the shaft, it seems that some ontogenetic changes can be determined. The inclination of the long axis of the shaft (in lateral view) becomes smaller, the dorsal end becomes wider, but its thickness does not increase. The dorsal end is compressed and the dorsal area, at which the sacral rib contacts is oblique, as visible in anterior view. In lateral view, it may be straight or convex. In a few cases, there are additional prominences. It is markedly less variable than the shaft of *Benthosuchus sushkini* (Bystrow and Efremov 1940: fig. 82). In a few cases, the medial part of the dorsal termination bears small pits and ridges. In the middle part, the shaft bears the “linea obliqua” (Bystrow and Efremov 1940), and “crête oblique externe” (Dutuit 1976) on the lateral surface. It is continued on the medial surface as “crête oblique interne” (Dutuit 1976).

The base of the ilium in the ventral view has the shape of a right triangle with the lateral edge as a hypotenuse. The entire ventral surface is roughened and contacts the cartilage. In the small specimens, the ventral facet is almost horizontal (in anterior view) and forms a distinct edge at the acetabulum. In the largest speci-

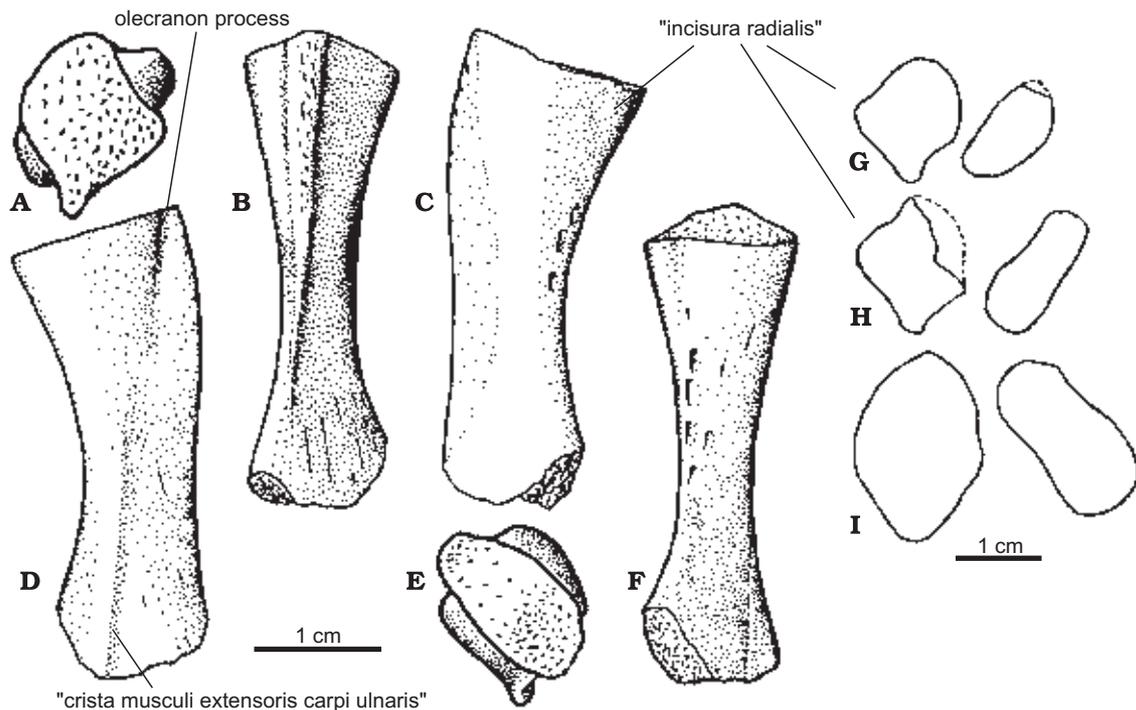


Fig. 57. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of ulna based on ZPAL AbIII/1 and ZPAL AbIII/1568, and variation of heads of ulna, in proximal (A), posterior (B), medial (C), lateral (D), distal (E), and anterior (F) views. Heads of ZPAL AbIII/1568 (G), ZPAL AbIII/1 (H), and ZPAL AbIII/1559 (I).

mens, the ventral facet is more oblique and the acetabulum margin is less distinct. The anterior and medial surfaces of the base are slightly concave in ventral view. The acetabulum is rounded in small specimens and becomes rectangular in the largest. In many cases, the acetabulum has additional roughened surface on its anterodorsal edge. It looks like uvula of the acetabulum surface (ZPAL AbIII/1587/3, AbIII/1028/1, and AbIII/901/2 on Fig. 58). The maximum width of the base is relatively larger in large specimens than in small ones. The ilia of *Metoposaurus* and *Dutuitosaurus* do not differ. In the width of the ilium base, they are similar to *Buettneria howardensis*. In *Mastodonsaurus*, the entire ilium is much slimmer than that of *Metoposaurus* (Schoch 1999). *Mastodonsaurus* has a rounded acetabulum with the centre above the ventral edge of the ilium. In *Eryosuchus*, the centre is even higher. In *Metoposaurus diagnosticus krasiejowensis*, it is always under the edge of the ilium. However, the importance of these differences is weakened by the great variability of this character in the population of *Benthosuchus sushkini* (Bystrow and Efremov 1940: fig. 82).

Ischium. — The ischium is like in other metoposaurids. Its dorsal edge is concave and smooth, widened anteriorly (Figs 60, 61). Its medial part is sharpened and the posterior part bears an area with small ridges that looks like an insertion of a muscle, but there is variability in these aspects. The other edges were continued as cartilage and are roughened. The anterior edge is wide and convex in dorsolateral view. In anterior view, its medialodorsal edge is straight and the lateroventral edge is very convex. The lateroventral surface of the ischium is smooth and it bears posterior and anterior depressions. The mediodorsal surface bears a slight fossa externa – “gouttière diamétrale externe” (Dutuit 1976) and insertion to interischial ligament (Dutuit 1976), which is visible only in large specimens. In all specimens the ventral part of the mediodorsal surface bears many elongated vascular foramina. Despite the variability of the dorsal edge the morphology of ischium is rather stable.

Femur. — The femur is well known in the capitosaurids (Watson 1958; Howie 1970; Ochev 1972) and the femur of the metoposaurids is similar. The main difference concerns the rotation of the proximal and distal heads in metoposaurids. Their main axes are rotated in 90° similarly to *Eryosuchus* and *Bulgosuchus gargantua* Damiani, 1999, whereas in *Benthosuchus*, *Mastodonsaurus*, and the Carboniferous colosteid *Greererpeton* they are in the same plane. The proximal head forms a distinctive, wide convexity of the acetabular torus on its anterior surface, which is rectangular in dorsal view (Figs 63, 64). Its shape is formed



Fig. 58. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of ilia. Specimens: ZPAL AbIII/1668/1 (A), ZPAL AbIII/135 (B), ZPAL AbIII/1587/3 (C), ZPAL AbIII/1028/1 (D), ZPAL AbIII/1585 (E), ZPAL AbIII/506 (F), ZPAL AbIII/1562 (G), ZPAL AbIII/985 (H), ZPAL AbIII/901/2 (I), ZPAL AbIII/1069/2 (J), ZPAL AbIII/1105/1 (K), and ZPAL AbIII/632 (L), respectively in lateral (A₁, B₁, C₁, D₁, E₁, F₂, G₁, H₁, I₁, J₁, K₁, L₁), medial (E₂, F₂, G₂, I₂, K₂, L₂), posterior (K₃, L₃), and anterior (K₄, L₄) views.

by the iliac depression that occurs in the anterodorsal surface of the proximal head. It is similar to *Eryosuchus* (“*Parotosuchus*”) (Howie 1970). It suggests that this part of the head contacted the acetabulum of the ilium, which has a similar rectangular shape. Both are more rounded in smaller specimens. Although the acetabular torus in many large specimens is rectangular in proximal view, it may have various shapes. In a few specimens, it is difficult to recognise because of deformations. The wide ridge that forms the trochanter is smooth on its proximal part. The trochanter is rectangular in cross section. Its anterior edge widens distally and form a drop-like muscle insertion at its distal end. Distally, the edge becomes thinner and is called adductor crest

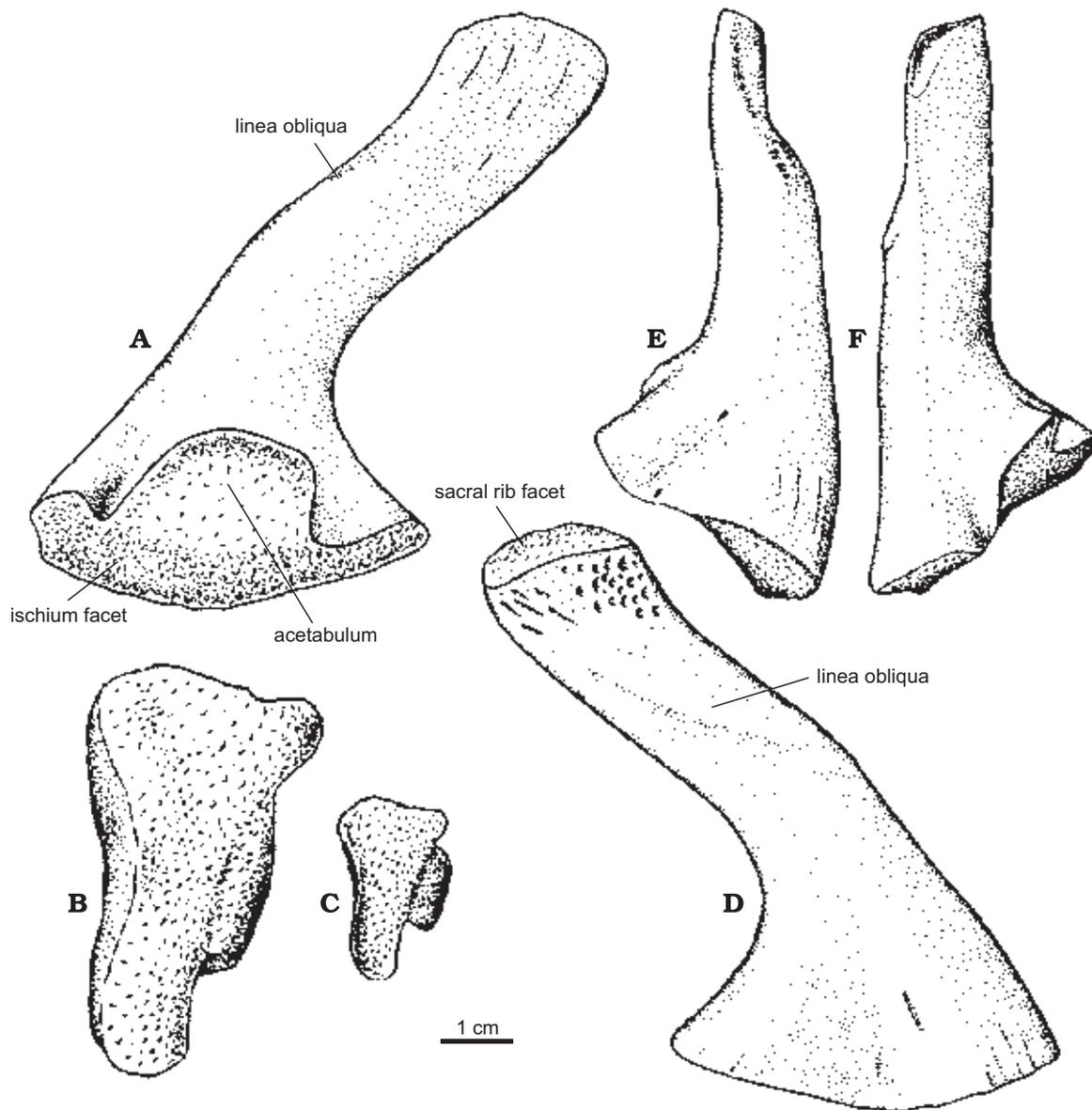


Fig. 59. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of ilium based on ZPAL Ab/III/632 and ZPAL Ab/III/135, in lateral view (A), ventral view of the large head (B), ventral view of small head (C), medial view (D), anterior view (E), and posterior view (F).

(Howie 1970; Schoch 1999), “crista aspera femoris” (Ochev 1972) or “trochanter tetricus” (Bystrow and Efremov 1940). The adductor crest passes into the ridge on the part of distal head articulated with the fibula. It is twice as thin as the articulation area for tibia. The condyles of distal head are separated by “fossa tendinalis” dorsally (Bystrow and Efremov 1940) and “fossa poplitea” ventrally (Bystrow and Efremov 1940). The shape of the condyles in distal view is various but some tendencies are recognizable. The articulation area for the tibia is rounded ventrally and pointed dorsally. The articulation area for the fibula may be flat or pointed dorsally and rectangular ventrally. The “fossa tendinalis” has a various depth but generally becomes deeper with an increasing size.

Some femora bear the muscle insertion (probably muscle adductor) on the anterior side of the proximal head on the level of the trochanter. Among 14 right heads of the femur, five exhibit this insertion (ZPAL Ab/III/507, Ab/III/189, Ab/III/979/1, Ab/III/16340, and Ab/III/1125/2). Among 25 left heads of the femora, 11 exhibit this insertion (ZPAL Ab/III/1592, Ab/III/123, Ab/III/995, Ab/III/1645, Ab/III/1139/2, Ab/III/876, Ab/III/1639, Ab/III/1601/3, Ab/III/1638, Ab/III/1637, and Ab/III/1616).

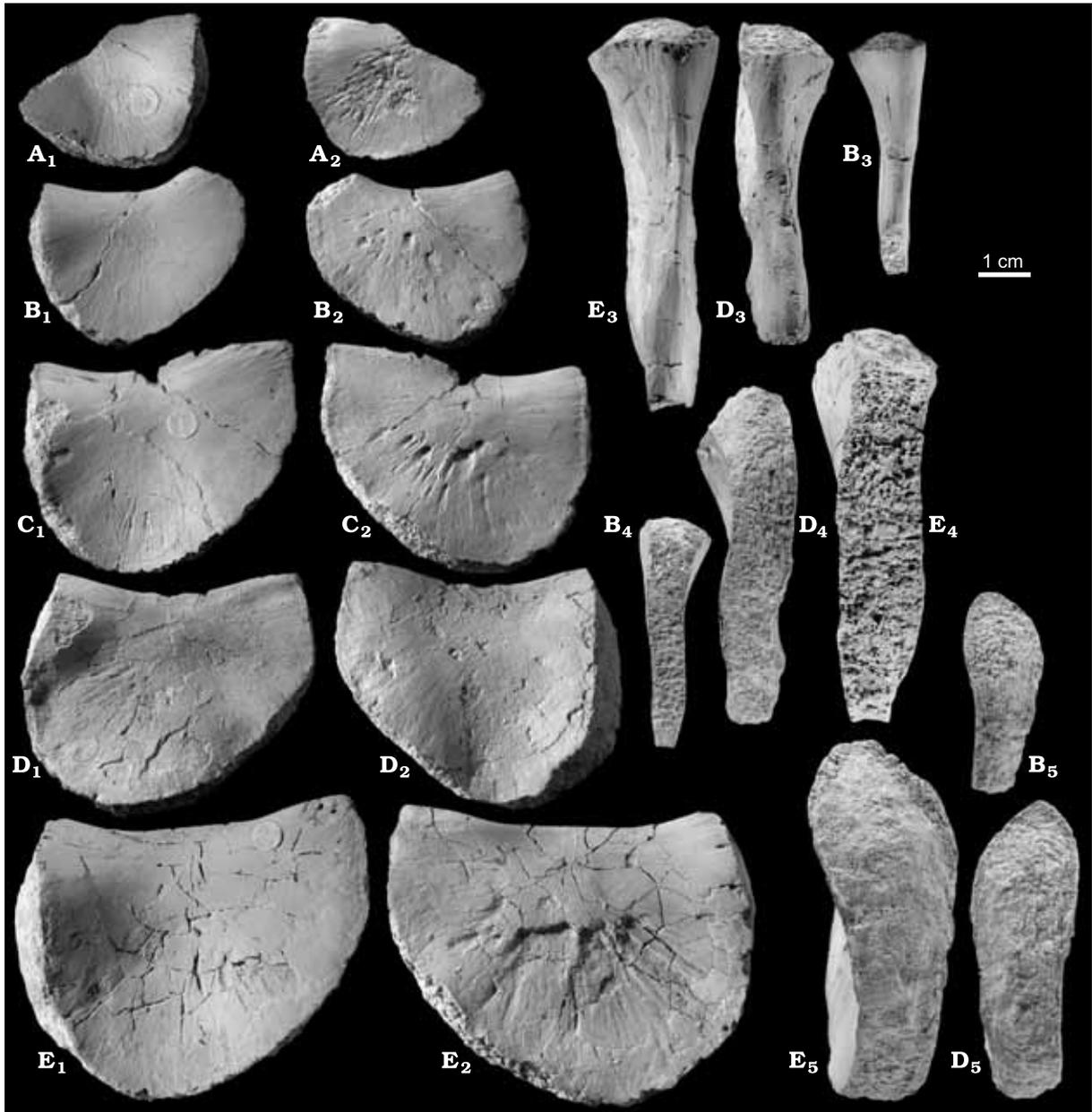


Fig. 60. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of ischia. Specimens ZPAL AbIII/305 (A), ZPAL AbIII/1718 (B), ZPAL AbIII/1599 (C), ZPAL AbIII/140 (D), and ZPAL AbIII/651 (E), respectively in lateroventral (A₁, B₁, C₁, D₁, E₁), medialodorsal (A₂, B₂, C₂, D₂, E₂), lateralodorsal (B₃, D₃, E₃), medialoventral (B₄, D₄, E₄), and anterior (B₅, D₅, E₅) views.

Although the Mesozoic temnospondyls have the femur less ossified than Palaeozoic forms, they always bear a Y shaped system of adductor crest and trochanters according to Warren and Snell (1991). It seems that this character is not stable. The Y shaped system is present in *Mastodonsaurus* (Schoch 1999) and *B. howardensis* (Sawin 1945), where the “fossa intertrochanterica” (Ochev 1972) forms an additional triangular surface with marked posterior edge. It is similar in this respect to the femur of the Permian *Desmospondylus*. In the femur of *Metoposaurus diagnosticus krasiejowensis*, *M. maleriensis*, and *Dutuitosaurus*, the “fossa intertrochanterica” is concave and forms a trough that passes distally at the trochanter similarly to the Triassic *Eryosuchus* (“*Parotosuchus*”) (Howie 1970), *Benthosuchus*, and the Permian *Cacops* (Williston 1910). It is difficult to point a link between the presence and lack of the type Y system and the phylogeny or way of life.

The femur of *Metoposaurus diagnosticus krasiejowensis* has a relatively thicker distal head than that of the *Dutuitosaurus*. The “fossae tendinalis and poplitea” are much deeper in *Metoposaurus diagnosticus*

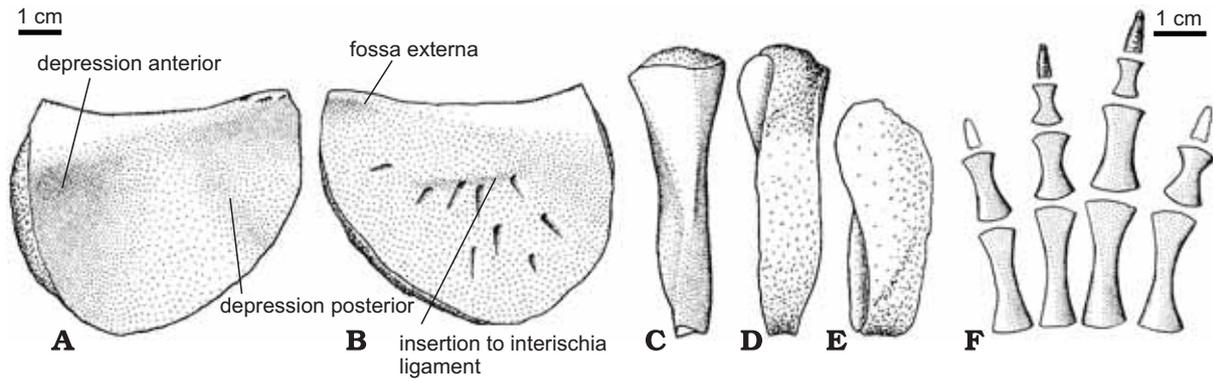


Fig. 61. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of ischium based on ZPAL AbIII/651, ZPAL AbIII/1599 and manus based on ZPAL AbIII/1717, in lateroventral (A), medialodorsal (B), laterodorsal (C), medialoventral (D), and anterior (E) views. F. Manus in dorsal view.

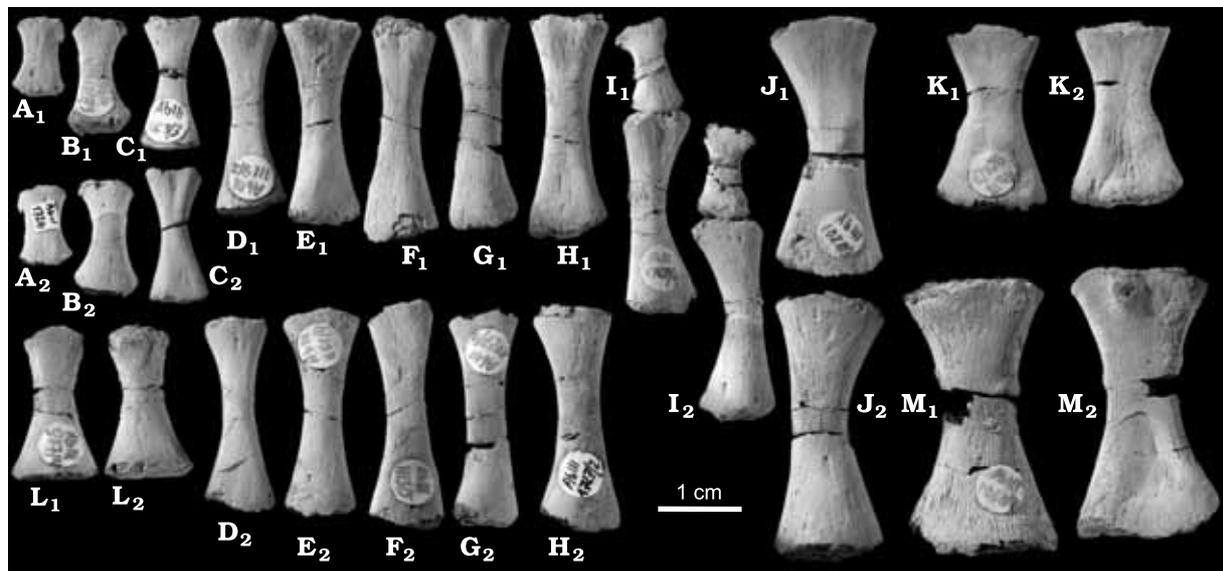


Fig. 62. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of phalanges. Probably of manus (A–I), probably of pes (J–L). Specimens ZPAL Ab/III/1726 (A), ZPAL Ab/III/1727/3 (B), ZPAL Ab/III/1163/3 (C), ZPAL Ab/III/1119/2 (D), ZPAL Ab/III/1161/4 (E), ZPAL Ab/III/1113/5 (F), ZPAL Ab/III/1727/1 (G), ZPAL Ab/III/1727/2 (H), ZPAL Ab/III/1727/4 (I), ZPAL Ab/III/1028/3 (J), ZPAL Ab/III/901/3 (K), ZPAL Ab/III/937/4 (L), and ZPAL Ab/III/1068/4 (M), respectively in ventral (A₁, B₁, C₁, D₁, E₁, F₁, G₁, H₁, I₁, J₁, K₁, L₁, M₁) and dorsal (A₂, B₂, C₂, D₂, E₂, F₂, G₂, H₂, I₂, J₂, K₂, L₂, M₂) views.

krasiejowensis. The proximal head of the femur of *Dutuitosaurus* does not have the distinctive rectangular torus. Its interior trochanter is much wider and is rectangular in dorsal view in *Metoposaurus diagnosticus krasiejowensis*.

The femur of metoposaurids is similar to that of the *Eryosuchus* (“*Parotosuchus*”) *pronus* (Howie 1970), although the distal roughened surface of the interior trochanter is smaller, less oblique, and shorter. The femur of *Mastodonsaurus* (Schoch 1999) is flatter than in the metoposaurids. The interior trochanter is weakly distinctive in this species.

Tibia. — It is similar in most regards to that of other stereospondyls but more slender than in *Mastodonsaurus* (Schoch 1999), *Benthosuchus* (Bystrow and Efremov 1940), the Permian anthracosaurid amphibian *Archeria* (Romer 1957), and the colosteid *Greererpeton* (Godfrey 1989). The bone is most similar to that of *Eryosuchus* (“*Parotosuchus*”) (Howie 1970). The head is two times wider than the body shaft, whereas the distal end is a little wider than the body as in *Mastodonsaurus* (Schoch 1999) and *Eryosuchus* (“*Parotosuchus*”) *pronus*. In ZPAL AbIII/1560, the distal end is two times wider than the shaft but it reflects probably a pathological state.



Fig. 63. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of femora. Specimens ZPAL AbIII/302 (A), ZPAL AbIII/1579 (B), ZPAL AbIII/995 (C), ZPAL AbIII/979/1 (D), ZPAL AbIII/1020/3 (E), ZPAL AbIII/507 (F), and ZPAL AbIII/956/1 (G), respectively in ventral (A₁, B₁, C₁, D₁, E₁, F₁, G₁), dorsal (A₂, B₂, C₂, D₂, E₂, F₂, G₂), anterior (A₃, B₃, C₃, D₃, E₃, F₃, G₃), and posterior (A₄, B₄, C₄, D₄, E₄, F₄, G₄) views.

The cnemial crest forms a longitudinal ridge occupying the medial portion of the proximal medial surface (Figs 65, 66). A shallow fissure (“planum popliteum” of Bystrow and Efremov 1940) occurs medially to the cnemial crest. In *Metoposaurus diagnosticus krasiejowensis*, in majority of specimens, the fissure continues

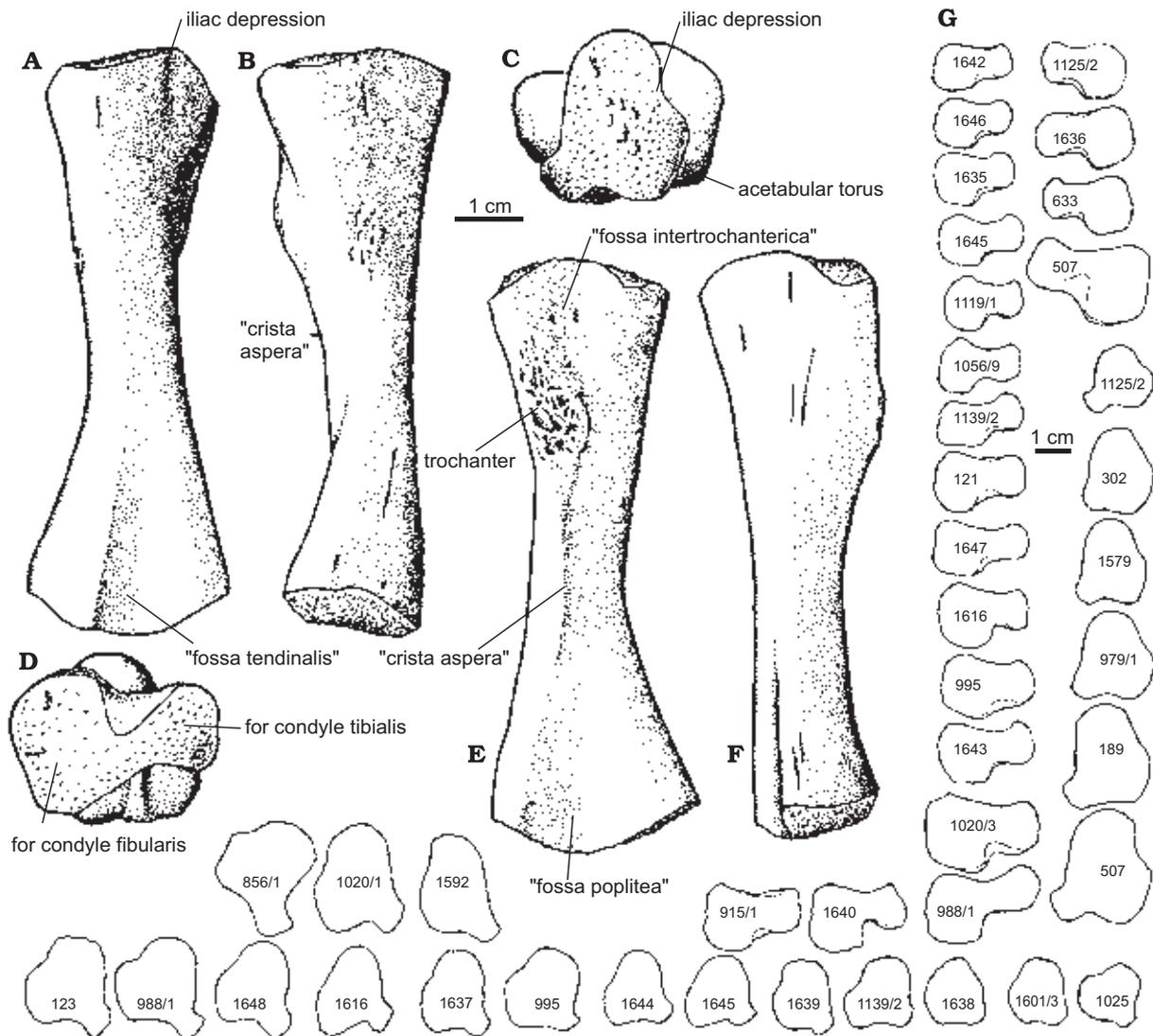


Fig. 64. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of right femur based on ZPAL AbIII/979/1 and variability of heads of femur, in dorsal (A), posterior (B), proximal (C), distal (D), ventral (E), and anterior (F) views. G. Pairs of heads, at left proximal head, at right distal head; numbers of specimens ZPAL AB/III are shown on the drawings.

proximally behind the cnemial crest, similarly to *Eryosuchus*. But in ZPAL AbIII/1584, AbIII/1560, AbIII/934/2, and AbIII/1583, the cnemial crest extends proximally more than the fissure beside it. The cnemial crest is very prominent in ZPAL AbIII/1113/1 and AbIII/1560, like in *Benthosuchus*, or only weakly marked as in ZPAL AbIII/1558. It is never as wide as in *Mastodonsaurus* and various morphologies of the cnemial crest are not connected with the size of the bone. The cnemial crest extended lingually up to 2/5 of its length. It is shorter than in *Benthosuchus*.

In *Archeria* and *Greererpeton*, the cnemial crest marks the point of insertion of the triceps (quadriceps) femoris muscle (Romer 1957). But in *Metoposaurus diagnosticus krasiejowensis*, the crest is smooth and the lateral edge of the bone beside the crest is rugate. It is possible that the triceps (quadriceps) femoris muscle was inserted to the lateral edge of the head. It is not confluent with a crest for insertion of the puboischitibialis muscle as in *Greererpeton*, in which it sweeps medialolaterally on the medial side of distal part of the tibia. In *M. diagnosticus krasiejowensis*, the insertion, that probably corresponds to puboischitibialis muscle, occupies the medial portion of the distal end. It is visible in ZPAL AbIII/1113/1 and AbIII/634 as numerous small crests.

The upper part of lateral side of the tibia in ZPAL AbIII/634 is marked with a robust crest (tibial tuberositas of Bystrow and Efremov 1940), parallel to the lateral outline. In the largest specimen ZPAL



Fig. 65. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of tibia. Specimens ZPAL AbIII/1113/1 (A), ZPAL AbIII/1028/4 (B), ZPAL AbIII/1558 (C), ZPAL AbIII/1587/2 (D), ZPAL AbIII/586 (E), ZPAL AbIII/634 (F), and ZPAL AbIII/1584 (G), respectively in medial (A₁, B₁, C₁, D₁, E₁, F₁, G₁), lateral (A₂, B₂, C₂, D₂, E₂, F₂, G₂), posterior (B₃, D₃, F₃, G₃), and anterior (B₄, D₄, F₄, G₄) views.

AbIII/1113/1, the rugosities are very pronounced. They presumably formed the major area of attachment for the flexor musculature of the thigh (Romer 1957). In ZPAL AbIII/634, proximal to this crest, the edge of the articulation with femur is turned inside out. In *Greererpeton* (Godfrey 1989) and in *Archeria* (Romer 1957), this part of the tibia is covered by longitudinal striations, which could accommodate the ligament and face of the knee (Romer 1957). Such striations are not seen in *Metoposaurus*, *Benthosuchus*, and *Parotosuchus*. A low anterior tibial crest (Bystrow and Efromov 1940), that is very pronounced in *Benthosuchus*, is distally to the rugose ridge. In *Metoposaurus diagnosticus krasiejowensis*, it is confluent with the insertion of unknown muscle that continues up to the articulation with tibial. It is well visible in ZPAL AbIII/1558.

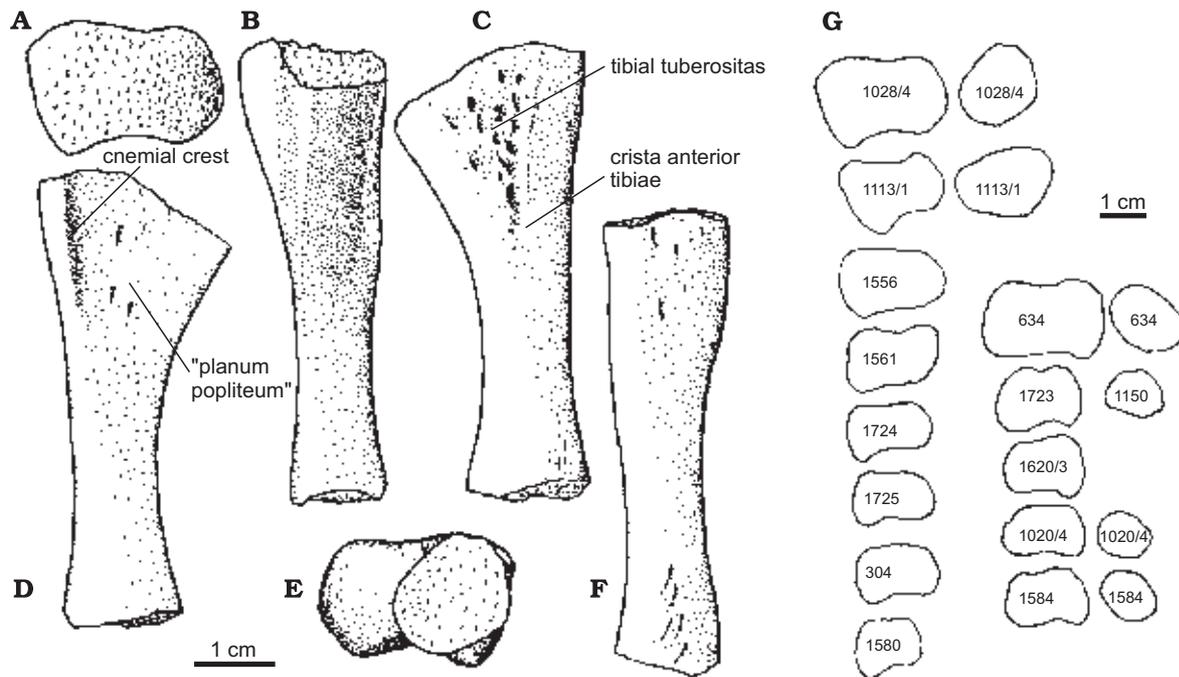


Fig. 66. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of right tibia based on ZPAL AbIII/634 and variability of heads, in dorsal (A), posterior (B), lateral (C), medial (D), anterior (E), and lateral (F) views. G. Pairs of heads, at left proximal head, at right distal head; numbers of specimens ZPAL AB/III are shown on the drawings.

Dutuit (1976) wrote that the corpus of the tibia was triangular in cross section and in larger specimens have three faces, but in small specimen of *Dutuitosaurus* the body of the tibia is oval in cross sections. In *Metoposaurus diagnosticus krasiejowensis* all specimens are triangular in cross section, although the shape of drop better corresponds to their outline. There is a sharp crest on the mesial side of the corpus which presumably separates areas covered by extensor and flexor muscle group (Romer 1957). The distal articulating face of the tibia is ovoid in ZPAL AbIII/634, AbIII/301, and AbIII/1584, but in specimens ZPAL AbIII/934/2, AbIII/1150, and AbIII/1113/1 it is roughly triangular, with flat flexor surfaces. The articulation with tibial is straight in anterior view, in contrast to rounded in *Greererpeton* (Godfrey 1989) and *Archeria* (Romer 1957) and oblique in *Benthosuchus*. In ZPAL AbIII/1597 and AbIII/1028/4 the articulation with the tibial is tilted ventrally, like in *Mastodonsaurus* (although not so strong) but in other specimens it is straight. The distal end of the bone is „twisted” on the shaft, so that the plane of the extensor surface at the distal end is turned 30° medially in respect to the proximal end of the shaft.

In the large tibia of *Dutuitosaurus*, on the anterior edge, there are some ridges (Dutuit 1976: fig. 69), which are absent in *Metoposaurus diagnosticus krasiejowensis*. In this species, the cnemial crest is not so far extended anteriorly like in *Dutuitosaurus* (Dutuit 1976: fig. 9D). In *Metoposaurus maleriensis*, the distal end is very wide.

Fibula. — The fibula of *Metoposaurus diagnosticus krasiejowensis* has the characteristic shape seen in many stereospondyls; laterally flattened, distally anteroposteriorly expanded and anterior edge broadly concave in medial view (Figs 67, 68). The most characteristic feature of the fibulae of most stereospondyls represented in the metoposaurids, *Benthosuchus* (Bystrow and Efremov 1940) and *Eryosuchus* (“*Parotosuchus*”) (Howie 1970) is the tuberosity of the distal anteromedial corner of the bone forming a groove (“the sulca fibularis” of Bystrow and Efremov 1940) at the border with the shaft (Fig. 68E). The fibula at mid-length is proportionately stout and convex on both sides.

The proximal head is similar to that in other stereospondyls, in that the articular surface for the femur is a crescentic oval, somewhat convex in outline along its lateral margin, and concave on the opposite edge (Fig. 68C, D). The posterior area bears a lateral ridge, which in some specimens is absent, forming flat posterior area (ZPAL AbIII/1570 and AbIII/1573).

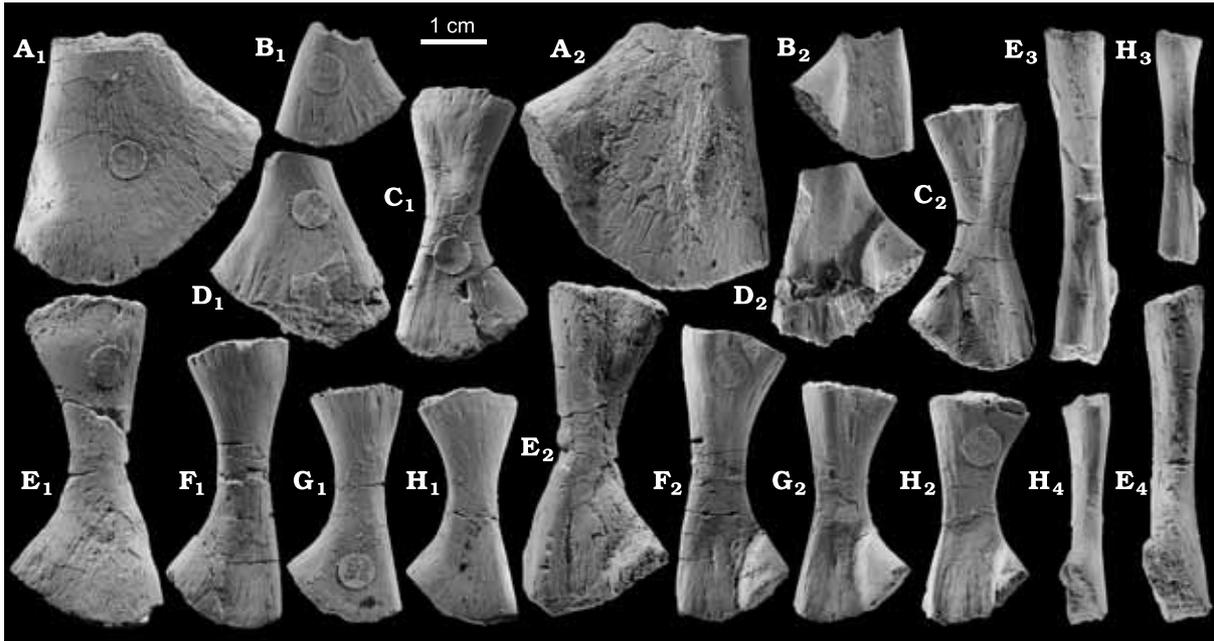


Fig. 67. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Ontogenetic series of fibulae. Specimens ZPAL AbIII/298 (A), ZPAL AbIII/1575 (B), ZPAL AbIII/300 (C), ZPAL AbIII/299 (D), ZPAL AbIII/1571 (E), ZPAL AbIII/1033/4 (F), ZPAL AbIII/1539 (G), and ZPAL AbIII/1573 (H), respectively in lateral (A₁, B₁, C₁, D₁, E₁, F₁, G₁, H₁), medial (A₂, B₂, C₂, D₂, E₂, F₂, G₂, H₂), posterior (E₃, H₃), and anterior (E₄, H₄) views.

The proximal head is similar to that of *Dutuitosaurus*, but it is less slanted medially (Fig. 69P). In *Buettneria howardensis* (Sawin 1945), *Dutuitosaurus*, and *Metoposaurus maleriensis* the head is very wide. The only specimen of *B. howardensis*, shown by Sawin (1945), has proximal head much narrower than in other metoposaurids.

Articular face of the distal head is gently curved, as in *Benthosuchus* and *Eryosuchus* (“*Parotosuchus*”). On the anterior surface of the distal head, there is a weak rugosity, in contrast with *Eryops*, in which the rugosity is pronounced (Romer 1947). It was presumably destined for the joint ligaments and perhaps for an accessory quadriceps insertion (Romer 1947). On the posterior margin, below the head the bone has a rugose area (Fig. 68B). According to Romer (1947), such rugosity in *Archeria* is presumably associated with attachment of the iliofibularis muscle. Early reptiles (e.g., *Limnoscelis*) have the proximal head circular in cross-section.

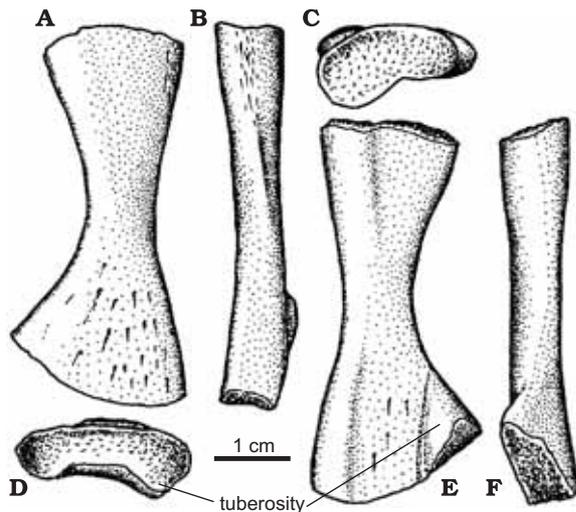


Fig. 68. *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów. Reconstruction of the fibula based on the ZPAL AbIII/1571, in lateral (A), posterior (B), proximal (C), distal (D), medial (E), and anterior (F) views.

attached of the iliofibularis muscle. Early reptiles

(e.g., *Limnoscelis*) have the proximal head circular in cross-section. The fibula of *M. diagnosticus krasiejowensis* is broad and greatly flattened distally. On the medial face of the distal part, there are two prominences: a longitudinal ridge on the posterior edge and a distinct tuberosity on the anterior edge (Fig. 68). The lateral ridge (“*crête postéro-interne*” of Dutuit 1976) continues as a prominent structure down for most of the length of the distal expansion, giving the posterior surfaces a somewhat concave section. The ridge may be prominent as in ZPAL AbIII/1571, very weak as in ZPAL AbIII/1033/3, or absent as in ZPAL AbIII/1033/4. Such a ridge is present in *Archeria* but it was not described in *Benthosuchus*, *Eryosuchus* (“*Parotosuchus*”), and *Mastodonsaurus*.

In *M. diagnosticus krasiejowensis* the tuberosity of the distal head is of various sizes (Fig. 67), and is not correlated with the size of the whole bone. In largest

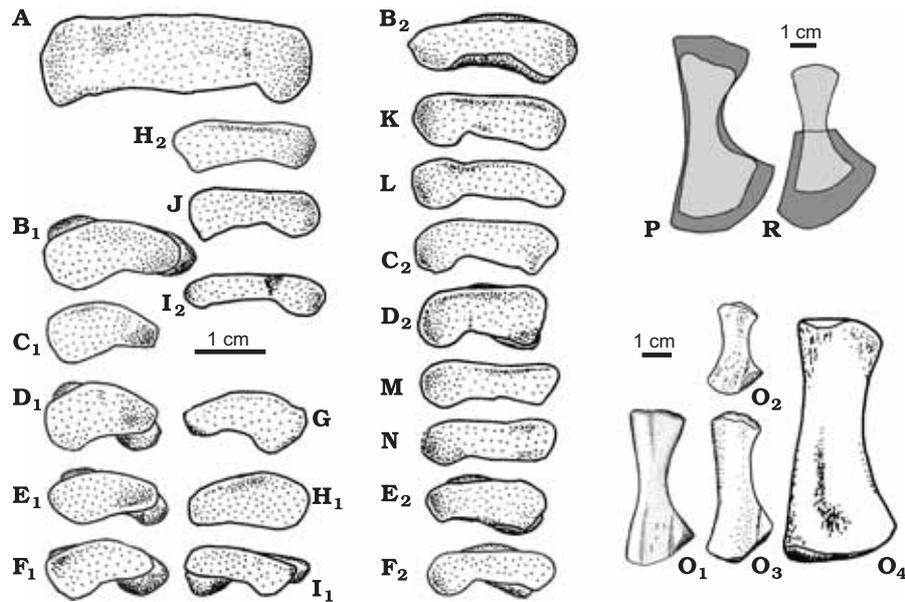


Fig. 69. Fibulae of stereospondyls and *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 from Krasiejów (A–N, P, R₁). A. ZPAL AbIII/298. B. ZPAL AbIII/1571. C. ZPAL AbIII/1033/3. D. ZPAL AbIII/1033/4. E. ZPAL AbIII/1573. F. ZPAL AbIII/1539. G. ZPAL AbIII/1729. H. ZPAL AbIII/1570. I. ZPAL AbIII/300. J. ZPAL AbIII/1575. K. ZPAL AbIII/1574. L. ZPAL AbIII/1572. M. ZPAL AbIII/970/3. N. ZPAL AbIII/1576. O. Comparison of temnospondyls with known fibula, *M. d. krasiejowensis* (O₁), *Eryosuchus* (“*Parotosuchus*”) *pronus* (from Howie 1970) (O₂), *Benthosuchus sushkini* (from Bystrow and Efremov 1940) (O₃), and *Mastodonsaurus giganteus* (from Schoch 1999) (O₄). P. Outline of *Dutuitosaurus ouazzoui*. R. Outline of *M. d. krasiejowensis*. Drawings in proximal (B₁, C₁, D₁, E₁, F₁, G, H₁, I₁), distal (A, B₂, C₂, D₂, E₂, F₂, I₂, J), medial (O₁, O₂, O₃, O₄), and lateral (P, R) views respectively.

specimens of *Dutuitosaurus* (Dutuit 1976) and *B. howardensis* (Sawin 1945), the tuberosity is rugose. According to Dutuit (1976), the size of the eminence suggests that a strong recurrent muscle was inserted, which was used mainly during retropulsion, when the limb acted as a paddle in water or while walking on the land.

In *Eryops*, the distal end is relatively narrow and thick (Romer 1947). According to Godfrey (1989), in *Greererpeton* (articulated specimen), the distal articular surface has two parts. The extended anterior part (tuberosity of metoposaurids) articulates with the intermedium and the lateral part articulates with the fibular. In *Benthosuchus*, the tuberosity is only the anterior part of the facet for fibular. In *Mastodonsaurus* the tuberosity is absent (Fig. 69O₄).

According to Romer (1947), the broad distal head in *Archeria* is presumably correlated with expansion of the fibular and proximal end of the astragalus, as in reptiles. In this group, in contrast to the temnospondyls, the fibula articulates with the fibular and astragalus by a broad hinge joint. The tuberosity possibly served for articulation of the fibula with the intermedium, which is rather wide in *Archeria*. It remains unknown why the tuberosity has so characteristic lateral edge with distinct groove in the stereospondyls.

According to Dutuit (1976), the fibula of *Dutuitosaurus* does not show any ontogenetic changes, but he also wrote that torsion of the distal and proximal ends is more apparent in larger specimens. In a large specimen of *Dutuitosaurus*, the torsion is about 20° (Dutuit 1976). In *M. diagnosticus krasiejowensis*, the average torsion is 14° without any ontogenetic trend, but the fibulae of *Dutuitosaurus* are much larger than those of *M. diagnosticus krasiejowensis*. In *Greererpeton* the angle has 45–50° (Godfrey 1989), in *Archeria* 35° (Romer 1947), and in *Benthosuchus* 37° (Bystrow and Efremov 1940).

Although there are great differences in size of the fibulae between *M. diagnosticus krasiejowensis* and *Dutuitosaurus* it seems that they differ in the growth rate of the distal head (Fig. 70). In *Dutuitosaurus*, the width of the distal head increases faster than in *M. diagnosticus krasiejowensis*. It may be a result of exponential growth of the distal head in metoposaurids. Even so, there are differences with the growth rate of the proximal head. The rate is the same in the three species of metoposaurids *Dutuitosaurus*, *M. diagnosticus krasiejowensis*, and *Buettneria howardensis* (Fig. 70). The faster growth of the distal head can be connected with a continuous increase of the angle between the facets of fibular and intermedium. This angle is smaller in *Dutuitosaurus* than in *M. diagnosticus krasiejowensis* even in specimens of similar size.

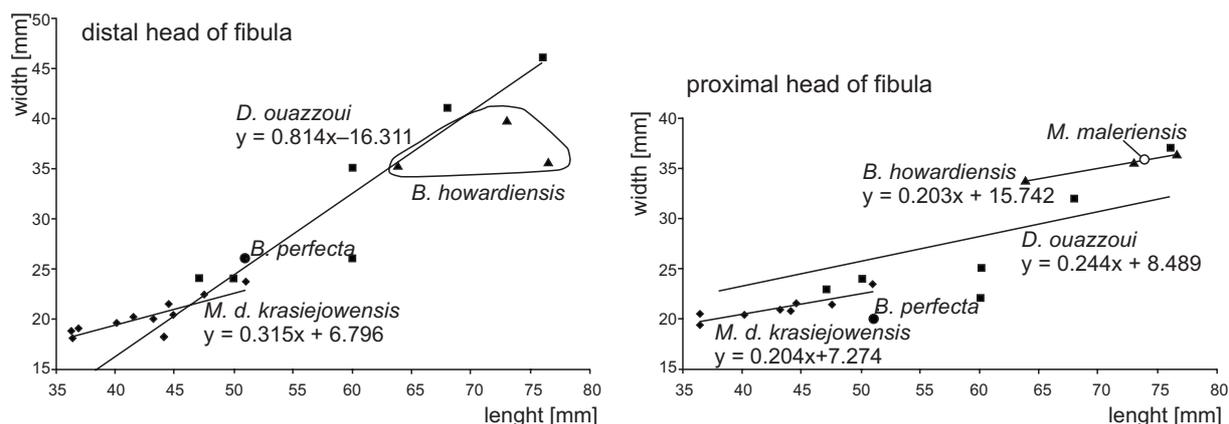


Fig. 70. Scatter-plots showing differences of growth rate of fibula of *Metoposaurus diagnosticus krasiejowensis*, *M. maleriensis*, *Dutuitosaurus ouazzoui*, *Buettneria howardensis* (from Sawin 1945), and *B. perfecta* (from Case 1932).

The fibula of *Metoposaurus diagnosticus krasiejowensis* is more similar to that of *Benthosuchus* (Bystrow and Efremov 1940) than to that of *Eryosuchus* (“*Parotosuchus*”) (Howie 1970). *Eryosuchus* has a very wide shaft, and the anterior edge is concave, like the posterior edge. In anterior view, the fibula of *M. diagnosticus krasiejowensis* has a narrower shaft and less convex proximal head than in *Benthosuchus*. In these characters, it is similar to the fibula of *Archeria*. It is interesting that *Mastodonsaurus* has a much different fibula. It is much thicker, the posterior border is poorly concave, and the articular surfaces are almost straight in posterior view. The *Eryosuchus* fibula is more similar to *M. diagnosticus krasiejowensis* than *Mastodonsaurus* (Schoch 1999).

Pes. — Little can be said about the anatomy and size of the foot of *Metoposaurus diagnosticus krasiejowensis*, for the elements interpreted as metatarsals are disarticulated. They are more massive than the metacarpals, like in the articulated specimens of *Dutuitosaurus ouazzoui* (Fig. 62J–L).

VARIABILITY OF METOPOSAURS

Majority of species of Palaeozoic and Mesozoic temnospondyl amphibians are known from single specimens. Complete skeletons are very rare. The unusually numerous metoposaurid material from Krasiejów allows to determine the range of intraspecific variation. The recognition of phenotypic plasticity may help in a better understanding the taxonomic value of some osteological features.

Notably, the first paper on the variability of temnospondyl amphibians dealt with the metoposaurids. Case (1932) measured 23 humeri of the metoposaurid *Buettneria perfecta* but he did not comment on the results. Later in the first taxonomic revision of the Metoposauridae, Colbert and Imbrie (1956) presented a statistical analysis of skulls of the North American metoposaurids. They used four measurements of the skull and distinguished only three species instead of nine described earlier. Their interpretation has been questioned by other authors (Chowdhury 1965; Hunt 1989; Hunt 1993; Long and Murry 1995; Sulej 2002). In the last revision of the family, Hunt (1993) defined nineteen morphological features in the whole family Metoposauridae and performed a cladistic analysis based on them. Their variability in populations was not discussed.

Papers concerning temnospondyl amphibians tend to deal exclusively with the taxonomy or phylogeny. The ontogeny is rarely discussed. In the first description of the ontogeny of *Benthosuchus sushkini*, Bystrow and Efremov (1940) distinguished two stages in its ontogeny after metamorphosis. Changes in ontogeny of the capitosaurid skull, based on data from different species, were presented by Warren and Hutchinson (1988) and Damiani and Warren (1997). Similar method was used by Shishkin *et al.* (1996) for the ontogeny of skull of the rhinesuchids and lydekkerinids. This method was criticised by Steyer (2003) as “inadequate because it was reconstructed from different species (...) the ontogeny of a genus or of family does not exist.” He described the ontogeny of *Watsonisuchus madagascariensis* Steyer, 2003. In yet another study, the vari-

ability of the pelvic girdle of the temnospondyl *Sclerocephalus haeuseri* Goldfuss, 1847 was described by Meckert (1993). A thorough descriptions of the ontogeny of *Archegosaurus decheni* Goldfuss, 1847 and *Acanthostomatops vorax* Credner, 1883 were recently presented by Witzmann (2006) and Witzmann and Schoch (2006a), respectively. Schoch (2006) showed the ontogeny of almost all skeletal elements of trematosaurid *Trematolestes*. Changes in proportions of the skull and possible mechanism of this process have not been discussed in these works apart from the paper of Shishkin *et al.* (1996). There are other publications about early stages of the ontogeny in temnospondyls (*e.g.*, Schoch 2003, 2004; Werneburg 2001; Schoch and Fröbisch 2006) but these are of little relevance regarding *Metoposaurus* because only late stages of its ontogeny can be studied.

The variability of eight parameters of the skull of *Thoosuchus yakovlevi* Ryabinin, 1927 (15 skulls) and *Benthosuchus* (7 skulls) was the subject of study by Getmanow (1981). He showed differences in the rate of growth of various regions of the skull. For instance, the snout of *Thoosuchus* elongated only in large individuals. He argued that the area of rapid growth, that was identified by differences in bone sculpture, on the dermal bones of skull roof, does not indicate that bones in this region grew really fast. In his subsequent papers, Getmanow (1986, 1989) figured individual differences in the anterior palate of the benthosuchids. He showed that this taxon represented an evolutionary transition from the capitosaurids to trematosaurids, the two groups of the Triassic stereospondyls. Getmanow showed that the individual variability of *Thoosuchus* and *Benthosuchus* initiated the later diversification of trematosaurids. Although Getmanow (1981, 1986, 1989) presented ontogenetic changes and proposed developmental mechanisms, he did not study differences in the range of individual variability. Samples of 8 and 15 skulls were probably too small for such a study. Numerous specimens from Krasiejów give an opportunity to study phenotype plasticity in more detail.

In Krasiejów, small individuals, having the skulls about 22 cm in length, are very rare. The most numerous are skulls 27–30 cm in length. The number of larger skulls gradually decreases. The largest skull is 47.5 cm long. It seems that only adult and old individuals are represented; probably the younger stages lived in different environment, like Recent crocodiles do (Gans and Tinkle 1977). Juvenile specimens of metoposaurids are known only in *Apachesaurus gregorii* Hunt, 1993. A skull smaller than metoposaurid ones from Krasiejów is known from the Lehrberg Beds of Germany, but its similarity in proportions to adults suggest that it was an adult too.

The nonparametric variability of particular bones was presented in the descriptive part of this paper and in few cases it will be discussed in context of the evolution of the metoposaurids. The variability of shape of the proximal and distal head of limb bones is presented mainly on figures in the descriptive part of the paper.

It is assumed that the intraspecific variability of *Metoposaurus* is a sum of genetic variability, developmental constraints and environmental influences, as it was already shown for the morphological variations of the turtle shell (Claude *et al.* 2003). Identification of separate causes of variability in a fossil assemblage is not impossible. However, it seems that allometry expresses mainly the genetic regulation of growth. Moreover, variability ranges of some characters may disclose differences in selective pressure acting on particular elements.

ALLOMETRY OF CRANIAL BONES

Allometric growth of the skulls of *Metoposaurus* from Krasiejów is expressed in different rates of growth of various regions of the skull. The skull regions bearing sensitive organs have a very low rate of growth. The length of both the orbits and nares increased very slowly in ontogeny (Fig. 19) and the standard deviation of both parameters is rather small. Comparing the rate of growth of the interorbital distance, the width of the orbits, and their distance from the margin of the skull, it is clear that the interorbital area grew faster than the orbits and the margin of the skull (Fig. 18). But in the case of nares, such correlation does not occur. The internasal area grew slightly faster than the width of the nares (Fig. 17).

It seems that orbit size increased very slowly, as already known in other temnospondyls (Shishkin *et al.* 1996; Colbert and Imbrie 1956). They slightly elongated in ontogeny. The width of the otic notch increased very slowly, especially in comparison to the width of the tabular horn (Fig. 18). This confirms the idea that the otic notch enclosed the tympanic membrane and that its size was stable in ontogeny. Although the metoposaurids grew almost for their whole life, their sense organs achieved a final size much earlier. It is

generally known that the orbits are very large in juvenile vertebrates; however, this is not the case of nares, as their size and shape are variable in the Krasiejów material.

The whole skull of the temnospondyls expanded during growth especially in some regions, characterised by long ridges forming the sculpture of dermal bones (Moodie 1908; Sulej 2002). There are two main regions of fast growth in the skull: the anterior one between nares and orbits and the posterior between orbits and pineal foramen. Getmanow (1981) claimed that the bone did not grow faster in these characteristic regions, but in the Krasiejów material the posterior region of fast growth is evident. The measurements of the parietal show that in the region with long ridges the bone really expanded faster than the part with isometric pits (Fig. 19).

In the European lineage of *Cyclotosaurus*, Sulej and Majer (2005) showed a decrease of concavity of the posterior margin of the skull roof. It was measured also in the Krasiejów material of *Metoposaurus diagnosticus krasiejowensis*, but in this population the posterior, concave margin of the skull roof became shallower in ontogeny.

The allometry was observed also in the structure of palate. The length of the interpterygoid vacuities had a high rate of growth ($\beta = 0.5$), almost twice as large as the length of the subtemporal window ($\beta = 0.3$; Fig. 19). The interpterygoid vacuities make the skull lighter. During the growth, the mass bone increases with the cubic (equals change of the volume) and the skull strongly increases the mass. The fast extension of the interpterygoid vacuities makes the skull relatively lighter, without a substantial reduction of rigidity.

Probably the reason for the faster growth of the width of the palatal ramus of pterygoid was the same as in the case of the width of the cultriform process (Fig. 19). The cultriform process is a beam lying in the long axis of the skull. Its mechanical role is to join the anterior palate region with its posterior part. It prevents breaking the skull roof during its upward movement. The main force acted on the cultriform process along its long axis. Mechanical pressure acting on the palatine ramus of the pterygoid was more complicated. The palatine ramus of the pterygoid joined the lateral part of the upper jaw with the posterior part of the palate. The forces acted on this element in various directions therefore it had to be more stronger. This strengthening must have to be achieved by building its cross section area, larger than in the cultriform process. The measurements show that the width of its ramus increased faster than the width of the cultriform process.

DIFFERENCES IN THE STABILITY OF CRANIAL BONES

The phenotypic variability is a result of genetic variation, developmental constraints, and natural selection. According to Wagner *et al.* (1997), “the suppression of phenotypic variation is called a canalisation. Depending on the causes of phenotypic variation one speaks either of genetic or environmental canalisation. Genetic canalisation describes insensitivity of a character to mutations, and the insensitivity to environmental factors is called environmental canalisation”. According to Stearns *et al.* (1995), “canalization describes the process by which phenotypic variation due to genetic or environmental disturbances is reduced by developmental mechanisms” and he reported measurements of environmental canalisation for various fitness components for *Drosophila melanogaster*. Beldade *et al.* (2003) showed the dominant role of natural selection, rather than internal constraints, in shaping the existing variation of diversity of butterfly wing patterns. It seems that the environmental canalisation can be observed also in population of *Metoposaurus* from Krasiejów.

The minimal width of the palatine ramus of the pterygoid was measured and it is only slightly variable. Its standard deviation from the mean is two times smaller than the deviation of the width of the cultriform process (Fig. 19). It is probably a result of the natural selection, controlling the elements essential for mechanical stability of the skull. The cultriform process took only the sagittal forces and its width was not as important as the width of the palatine ramus of the pterygoid. It takes sagittal, transverse and resultant force of both previous. It is possible that the narrow range of variability of the width of the palatine ramus of the pterygoid is an example of an environmental canalisation.

The length and width of the orbits have also a very low range of variability (Figs 18, 19). The interorbital width is less stable. It is connected with the essential role of the orbits as the place of probably the most important sense of the metoposaurids. Similarly, the internasal width is less stable than the length and width of the nares (Fig. 17). However, the internasal width is more variable than the interorbital width and the width of the nares increase in the same rate as the internasal width, contrary to the case of the orbits.

The measurements of the parietal showed that the length of that bone has a wider range of variability than the length of the posterior end of the bone measured from the centre of pineal foramen (Fig. 19). It is related to the region of faster growth in the anterior part of the parietal, but probably the growth of the postpineal part was controlled more precisely in connection with the brain structure covered by this part of the bone. In contrast to this fact, the width of the lacrimal is much more variable (Fig. 17).

DIFFERENCES IN MORPHOLOGICAL VARIABILITY OF TEMNOSPONDYL SPECIES

The increase of competition makes the range of variability decreasing. It seems that a similar situation characterised various populations of the metoposaurids. In the three analysed parameters of humerus (Fig. 52), the population of *Dutuitosaurus* from Argana Formation has a larger range of variability (standard deviation) than the populations of *Metoposaurus* from Krasiejów and *M. maleriensis* from the Maleri Formation. The difference is especially striking in comparison between *Dutuitosaurus* and *Metoposaurus*, because both populations were found as large accumulations of skeletons or bones. Their taphonomy suggests that they were accumulated over a quite short time. In spite of these similarities, the variability ranges are very different. There is a possibility that it is related to an ecological background of these localities. It seems that in the population of Krasiejów metoposaurids lived in an ecosystem in which the competition was more intense. It is difficult to identify the subject of this competition. The first guess is that it was food. In both localities, the large fish-eaters phytosaurs occur together with the metoposaurids. In Krasiejów, the large capitosauroid *Cyclotosaurus* was also found. There is a possibility that they competed for food or other environmental factors, and that this competition caused the range of variability to be smaller than in Argana. Another explanation of this difference may be various time-span of accumulation of these materials or other taphonomic factors.

The problem of the differences in the variability between species and its stability concerns also the taxonomy and rules of erection of a new taxons. It is especially important in the case of specimens from different localities. Some differences may be always discerned but the question is if they are “important” enough. It seems that knowledge of variability of each group of organism may help to resolve such problems. Assuming that the range of variance is rather stable in the group, the population variability may help to judge if two specimens belong to two different or just one species. In this paper, some elements of such a standard are presented.

The variability in position of the lacrimal towards the orbits margin is widely considered as diagnostic among temnospondyls and especially for metoposaurids. The usefulness of this character; however, depends on a sample size, because of its considerable variability. Sengupta (2002) used the width of the lacrimal to diagnose *Metoposaurus maleriensis*, but this parameter is very variable in the skulls of *M. diagnosticus krasiejowensis* (Fig. 17) and appears to be taxonomically useless. According to Damiani (2001), the crista muscularis extending laterally on the pterygoid is unique for *Cherninia megarhina*. In the Krasiejów material, a large variability is seen in its shape. It seems thus, that the position of the crista muscularis should not be used as diagnostic character for *Cherninia*.

The dorsal surface of the postglenoid area has a deep groove aligned to the long axis of the mandible – fossa postglenoidalis (Schoch 1999). It varies considerably in width and depth, but is always straight. Similarly to *Mastodonsaurus*, variation in most morphological traits of the postglenoid area of *Metoposaurus* is broad; hence a species identification based on only a mandible fragment must remain problematic.

RECONSTRUCTION OF THE SKELETON AND LIFE STYLE

Despite disarticulation of most bone materials from Krasiejów, some specimens contribute significantly to the knowledge of the anatomy of *Metoposaurus*. Their articulated caudal fin is the best preserved among all known metoposaurids. Specimens with 5–6 dorsal intercentra articulated with neural arches and some specimens of articulated skulls, mandibles, clavicles and interclavicles are also helpful in reconstructing the entire skeleton. While preparing the reconstruction, articulated specimens known from the literature (Fraas

1889; Dutuit 1976) were also used. The body length and limbs proportions were based on the articulated specimens of *Dutuitosaurus ouazzoui* from the Argana Formation of Morocco. The proportions of the dorsal vertebrae to ribs and the pectoral girdle were based on the best-preserved specimen SMNS 5143 of *Metoposaurus diagnosticus diagnosticus* from the Schilfsandstein of Württemberg. The position of ribs was determined on the basis of articulated specimens of *M. diagnosticus* (SMNS 5143) and *Dutuitosaurus*.

VERTEBRAL COLUMN

The numerous and well-preserved intercentra and neural arches allow to distinguish eleven types of vertebrae presumably representing different regions of the column. The number of vertebrae in each type was determined from the articulated specimens of *Dutuitosaurus ouazzoui* from the Argana Formation of Morocco and *Metoposaurus diagnosticus diagnosticus* from Schilfsandstein of Württemberg. The articulated fragments of vertebral column from Krasiejów were essential in reconstructing the axial skeleton.

In basal temnospondyls, a vertebra consists of a large intercentrum, small pleurocentrum, and neural arch. In Krasiejów, no pleurocentrum was found. Actually, pleurocentra are unknown in most other metoposaurid species with the exception of single specimen of *Dutuitosaurus*, in which two articulated mid-dorsal vertebrae bear them. This isolated occurrence suggests that they were developed as cartilaginous disks that under normal conditions did not fossilise. Their ossification was probably pathological, but is useful for identifying their position. They are articulated with the intercentrum laying behind it, which is rare among temnospondyls. Shishkin (1987, 1989) showed that such relation “intra-segmental integration” of intercentrum and pleurocentrum is present also in the dvinosaurs and is connected with amphiseptal type of segments, in which case the intercentrum forms a functional element with the pleurocentra and the neural arch, that are set behind it. He found this condition primary in both phylogeny and ontogeny of the temnospondyls, in the rhipidistian *Osteolepis* and in various parts of the vertebral column of the temnospondyls *Dendrerpeton*, *Acropolis*, *Zatrachys*, *Platyops*, *Dvinosaurus*, and *Dutuitosaurus*. The most advanced temnospondyls, like the trematosaurids and capitosaurids (e.g., *Mastodonsaurus*), have a resegmented functional element consisting of intercentrum, which formed a functional element with pleurocentrum, and the neural arch set in front of it. Assuming that in all metoposaurids the middorsal vertebrae represent the amphiseptal type, it seems that they early terminated their development. This may support the idea of neotenus nature of the metoposaurids, proposed by Shishkin (personal communication).

In the ancestral amphiseptal condition, the rib was articulated with the two following functional elements (Shishkin 1987, 1989). In the later stages of ontogeny and evolution of temnospondyls, the rib was articulated only with the anterior one, like in the cervical and postcervical vertebrae of metoposaurids. In most stereospondyls, the parapophysis occurs on the single intercentrum, as in the entire vertebral column of *Mastodonsaurus* (Huene 1922; Schoch 1999). A similar situation is known in *Eryosuchus*. In all metoposaurids, the parapophysis occurs on two neighbouring intercentra in the presacral and sacral region of vertebral column, like in the plagiosaurids (Shishkin 1987, 1989). In the reconstruction presented here, their sequence is based on the articulated specimens of *Dutuitosaurus ouazzoui* and *Metoposaurus diagnosticus diagnosticus* (Figs 31, 32). Such an arrangement was also described by Hellrung (2003) for the plagiosaur *Gerrothorax pustuloglomeratus*. She showed that the situation in *Gerrothorax* and metoposaurids is similar to the Recent turtle *Chelus fimbriatus* and is due to stiffening of the vertebral column. In both groups, it was probably related to the way of swimming, in which the lateral bending of the body was limited. The very wide- and flat-bodied plagiosaur probably did not bent in lateral plane at all. The parapophyses, present on the two neighbouring vertebrae, occur also in the Recent horse, which is related with stiffening of the dorsal part of the vertebral column, that bends slightly only in dorsoventral plane (Faber *et al.* 2001 and personal observations). In metoposaurids, a position of the parapophysis (between the intercentra) in presacral region of the vertebral column is characteristic for the amphiseptal condition. It seems that it is an additional confirmation of the primitive condition of at least a part of the metoposaurid vertebral column. The morphology of atlas, axis, third and fourth vertebrae of *Metoposaurus* suggests that the neck was relatively flexible. Their neural arches are fused with the intercentrum and prezygapophyses are flat. The intercentra have convex anterior-surfaces well fit to the concave posterior surfaces. In the following intercentra, this feature is not apparent.

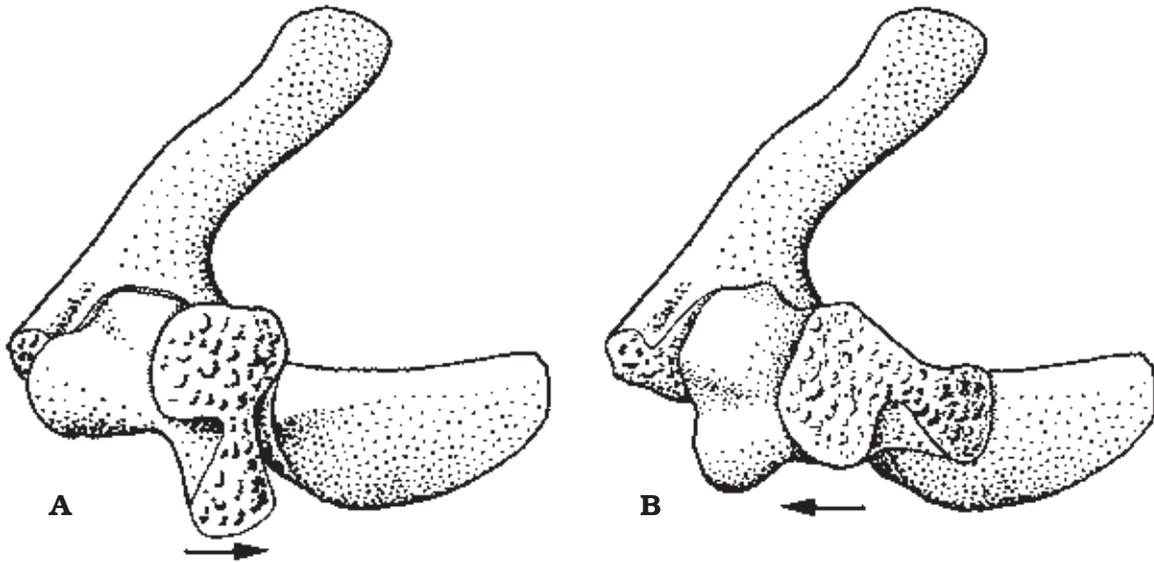


Fig. 71. *Metoposaurus diagnosticus krasiejowensis* from Krasiejów. Reconstruction of pelvic girdle and rotated femur in lateral view. **A.** Distal head of femur set vertically during power stroke. **B.** Distal head of femur set horizontally during recovery stroke.

The intercentra of the region where the vertebral column contacts the shoulder girdle are flat anteriorly and posteriorly. The neural arches have almost vertically set prezygapophyses (vide postcervical vertebrae). This suggests that in this region the lateral bending of the vertebral column was very limited. It was probably connected with articulation of the vertebral column with the shoulder girdle. A stiffening of the vertebral column, in the region of contacting limbs, was apparently essential for the swimming.

The mid-dorsal vertebrae have slightly oblique prezygapophyses, and small parapophyses occur on one intercentrum. This region was probably slightly flexible. The caudal vertebrae have very long spine processes and the chevrons. They form the caudal fin, which was flexible mostly in lateral direction.

The intercentra of dorsal and sacral vertebrae are fully ossified and form quite short disks, not connected with the neural arches. In the dorsal and sacral region, they have anterior and posterior surfaces concave or the posterior surface is almost flat. This condition resembles that in the trunk of plesiosaurs and, to some degree, the ichtiosaurs, confirming the aquatic mode of life.

MODE OF SWIMMING

In the articulated specimens of *Dutuitosaurus lyazidi* from the Argana Formation, the manus and pes have unusually large size in comparison to other temnospondyls. Since all metoposaurids are similar in many aspects, it seems that this character is common for the group, perhaps with the exception of the *Apachesaurus gregorii*, otherwise different from other metoposaurids (Hunt 1993). Comparison of *D. lyazidi* with the reconstructions of *Mastodonsaurus* and *Paracyclotosaurus* shows that metoposaurids had manus and pes almost twice as large as the other two forms. If they were aquatic animals, as argued by Steyer *et al.* (2004) based on the bone structure, and Barycka (2007) based on the morphology of the humerus, their limbs with a large autopodium must have been used as flippers, similarly as in the sea turtles such as *Chelonia mydas* and seals *Arctocephalus pusillus*. These animals swim by symmetrical and synchronous movements of the limbs (*e.g.*, Aleev 1976). This mode of swimming demands specific modifications of limb bones.

The femur of *Mastodonsaurus*, *Benthosuchus*, and *Greererpeton* has both heads flat dorsomedially (Huene 1922; Schoch 1999; Bystrow and Efremov 1940; Godfrey 1989). It seems that this was connected with the use of limbs. The movement of the femur was mainly dorsoventral and strongly limited in the anteroposterior direction. The lateral movement of the body rather than anteroposterior movements of the femur makes the main propulsion similar to that preserved in the articulated Permian terrestrial amphibian *Limnoscelis* (personal observation). In the metoposaurids the main axes of the proximal and distal heads are set at 90° to each other (Fig. 64). Differences between underived temnospondyls and metoposaurids are probably related to their way of locomotion.

The position of the femur in respect to the ilium may be reconstructed owing to the similarity of the shape of acetabulum of the ilium and the shape of the posterior prominence of the proximal head of the femur. They seem to fit to each other very well during the movement, which generated thrust to the swimming animal. During this movement the axis of distal head was set vertically in lateral view and the axes of zeugopodium (tibia and fibula) and autopodium were also set vertically (Fig. 71). The trochanter was set posteriorly to optimise work of the muscle (probably puboischiofemorales externum), which pulled the leg posteroventrally. This muscle was attached to the ischium, which was ossified, unlike the cartilaginous pubis. This movement might serve only to repulsion of water while the leg acted as a flipper. This construction is much different from that in *Mastodonsaurus*, which has the femur flattened dorsoventrally, and the pubis and ischium ossified. It is very similar to the situation in *Archeria*, which probably could walk on the land.

While the femur was in the horizontal position and the long axis of the distal head was set vertical during the rowing motion, the trochanter was in posterior position, optimal for pulling the femur posteriorly. In the case of humerus the situation is not so clear, various modes of movement are possible, but it is almost sure that forelimbs worked like hind limbs, similarly to the tortoise *Chelonia mydas*. The general shape of the humerus with two flat ends is similar in the metoposaurids and in seals (Post 1999). The distal head is much wider than in the capitosaurids. It may be related to the large manus and the use of the whole forelimb as a flipper.

The glenoid of the scapula directed posterolaterally and slightly ventrally suggests that the humerus had a quite limited range of movement in horizontal plane. In the maximum anterior position, it was probably at right angle to the long axis of the body like in modern frogs (Nauwelaerts *et al.* 2004). In the end of propulsion, it was probably almost parallel to the long axis of the body.

During swimming in water, a coordination of movements of particular part of the body is important. Symmetrical and synchronous actions of the limbs is essential. The lateral bending of the trunk would disturb the swimming. It is probably the reason why parts of the vertebral column connected with the shoulder and pelvic girdle were rigid in the metoposaurs, as discussed in the previous chapter. The stiff axial skeleton additionally assured that the limbs worked simultaneously (Fig. 72). However, the tail was flexible, probably being used as a rudder.

Also the plesiosaurs swam by symmetrical and simultaneous movements of the limbs and their trunk was rather rigid (Sanders *et al.* 2004). The metoposaurids have disk-shaped dorsal intercentra not fused with the neural arches, similarly to the vertebrae of plesiosaurs. In case of plesiosaurs and ichthyosaurs, the disk-shaped centra originated from longer and fused vertebrae of their terrestrial ancestors. The similar disk-shaped vertebrae of the Cretaceous sharks Lamnidae (*e.g.*, *Lamna obliqua*) originated from chondral vertebrae. In various groups of animals, with their adaptation to fully aquatic mode of life, their vertebrae became disk-shaped independently from their previous shape. The question why the disk-shaped vertebrae are essential for pelagic large animal is still open, but the metoposaurids probably are a one more example of this rule. It seems that this similarity to plesiosaurs suggest that the metoposaurids used their limbs in the way similar to plesiosaurs.

Another problem is the way of walking of the metoposaurids on the land. They had almost cosmopolitan distribution. If they were not able to swim in the sea (like most amphibians) they had to walk on land to invade distant areas. Their limb bones were probably too delicate to lift the body above the ground and perhaps they moved on the belly like seals (*e.g.*, Aleev 1976) pushing back from the ground by limbs.

PHYLOGENY OF THE METOPOSAURIDS

The origin of the metoposaurids remains contentious and the presentation of this issue is not the aim of this paper. However, some observations on the Krasiejów material may be helpful in future studies on the metoposaurid phylogeny.

According to Romer (1947), Dutuit (1976), Hunt (1993), and Carroll (2001), the metoposaurids originated from the Triassic Brachyopidae. Säve-Söderbergh (1936) and Shishkin (1973) joined metoposaurids with the Permian *Trimerorhachis*. Warren and Black (1985) grouped the metoposaurids with the capito-

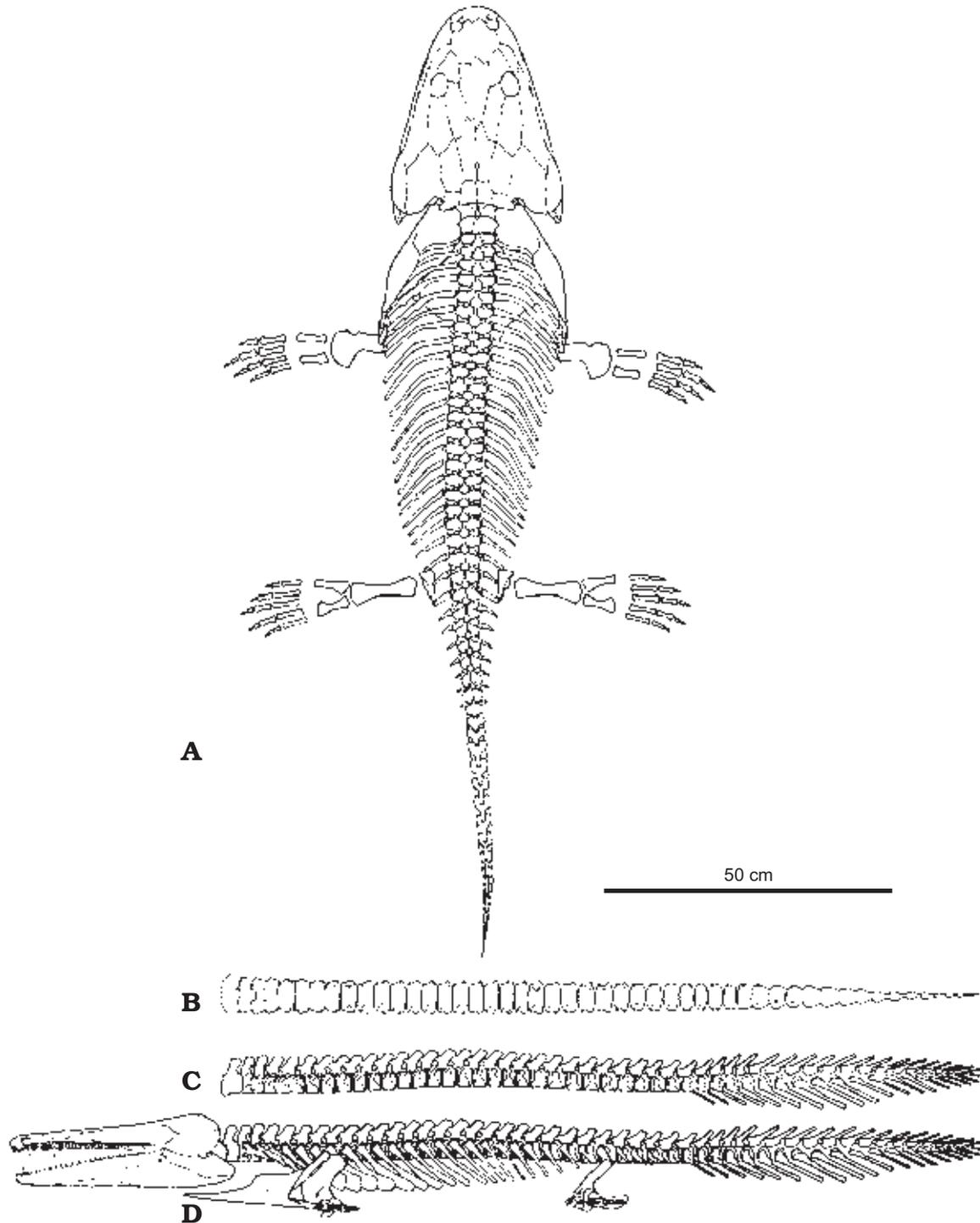


Fig. 72. *Metoposaurus diagnosticus krasiejowensis* from Krasiejów. Reconstruction of the skeleton. **A.** Dorsal view. **B.** Vertebral column in dorsal view, neural arches not fused remain. **C.** Vertebral column in lateral view. **D.** Entire skeleton in lateral view, with the limbs during recovery stroke.

saurids into the “capitosaurian group”. Similarly, Steyer (2002) stated that the Metoposauridae has a common ancestor with the Capitosauridae. According to Milner (1990), Schoch and Milner (2000), Damiani and Yates (2003), Witzmann and Schoch (2006b), and Schoch *et al.* (2007), the metoposaurids originated from the trematosaurids. Similarly, Yates and Warren (2000) set the Trematosauroidea, Metoposauroidea, and Brachyopoidea in the clade Trematosauria.

Among these interpretations, the hypothesis of the relationship of the metoposaurids with the trematosaurids, proposed by Säve-Söderbergh (1935), seems the most doubtful, although there are some similarities between these two groups. Both have the anteriorly situated and laterally displaced orbits, close to margin of skull (Damiani and Yates 2003). In both groups, the postglenoid area is formed mainly by the prearticular and surangular (Nilsson 1943), distinct tabular horns, and elongated bones of postorbital skull roof region (Damiani and Yates 2003). The premaxilla of metoposaurs and some trematosauroid: *Trematosuchus sobeyi* (Shishkin and Welman 1994), *Tirraturhinus smisseni* Nield, Damiani *et* Warren, 2006 bears fossa subrostralis media on the palatine side. Most of characters used by Damiani and Yates (2003) as common for Metoposaurids and *Tremosaurus* are common also in *Trimerorhachis* or some Brachyopids. However, there are characters, which make the metoposaurids different from trematosaurids and contradict this interpretation. Let us consider the structure of the skull, mandible, clavicle, and centra of vertebra.

In the skull of the metoposaurids, the exoccipital forms a suture with the pterygoid perpendicular to the long axis of the skull and visible in ventral view, whereas the suture with parasphenoid is oblique to the long axis of the skull. In most of the trematosaurids, the suture of the exoccipital with the pterygoid is parallel to the long axis of the skull and in ventral view covered by the parasphenoid (Romer 1947; Damiani and Yates 2003), although in *Trematolestes* (Schoch 2006) it is similar to metoposaurids, but in this form the suture of the exoccipital with the parasphenoid is perpendicular to the long axis of the skull.

The infraorbital canal on the lacrimal of the metoposaurids possesses the Z-shaped lacrimal flexure, whereas the Trematosauroidae lack the distinct lacrimal flexure (Shishkin 1980). In metoposaurs, the temporal canal terminates on the supratemporal, whereas in trematosaurid *Trematolestes* it runs to the end of the tabular horn (Schoch 2006). The metoposaurid quadrate condyle is subtriangular in ventral view, whereas the trematosaurids have a rectangular quadrate condyle (Säve-Söderbergh 1936; Schoch 2006; Damiani and Yates 2003). The chigutisaurid *Keratobrachyops australis* Warren, 1981 and some brachiopids have the quadrate most similar in ventral view to that of the metoposaurids. In the metoposaurids, the cultriform process is very wide, but narrow in the trematosaurids (Romer 1947). It has a long exposure of the anterior end, contrary to the lack of this structure in trematosaurids (Romer 1947; Steyer 2002; Damiani and Yates 2003; Schoch 2006). The metoposaurids possess a large paraquadrate foramen and small paraquadrate accessory foramen, whereas the trematosaurids have only small paraquadrate foramen (Romer 1945; Steyer 2002; Damiani and Yates 2003; Schoch 2006). The metoposaurids lack the sphenethmoid; the crista orbito-temporalis and lamina orbito-nasalis surround the parietal foramen on its ventral side similarly to the brachiopid *Bathignathus poikilops* (Damiani and Jeannot 2002). *Tremosaurus* has the sphenethmoid (Säve-Söderbergh 1936) and a T-shaped ridge on the ventral side of the parietal foramen (Werneburg 1993).

In the skull of some brachiopids and metoposaurids, there is no anterior wall in the rounded foramen for X nerve in the exoccipital (Shishkin 1967, 1991), whereas in all capitosaurids and trematosaurids the X nerve left the skull through large vagus foramen. In 25% of investigated skulls of *Metoposaurus diagnosticus diagnosticus*, the postorbital contacts the parietal, like in *Dvinosaurus* and other genera of the Brachyopoidea *sensu lato*. This condition is unknown in typical “stereospondyls” (Shishkin personal communication).

The mandibles of the brachiopids, plagiosaurids and metoposaurids have a posterior tongue of the articular extending posteriorly between the surangular and the prearticular along the dorsal surface of the retroarticular process (Warren 1981; Hellrung 2003). This makes them different from other Triassic temnospondyls, except *Cyclotosaurus* Sulej *et* Majer, 2005. The metoposaurids have the prearticular anteriorly short in the mandible. In the trematosaurids, it extends anteriorly behind the anterior end of the Meckelian foramen (Schoch and Milner 2000: fig. 71), whereas in the metoposaurids it does not.

The metoposaurid clavicles have an indentation in the medial clavicular blade. It is characteristic also only for the Brachyopidae (Warren and Marsicano 2000). The metoposaurid intercentrum is fully ossified and the pleurocentrum was cartilaginous. The atlas of the metoposaurids and brachiopids has an oval area for condyles with their long axes horizontally oriented (Shishkin 2000). The trematosaurids have intercentra neorachitinous.

In contrast to so many basic distinctions in respect to the trematosaurids, the similarity between metoposaurids and *Trimerorhachis* was noticed by Säve-Söderbergh (1935). Romer (1947) mentioned the following similarities of both genera: the orbits anteriorly located, “the skull greatly flattened, endochondral ossification greatly reduced, the interpterygoid vacuities much enlarged, rows of palatal teeth developed.” According to

Romer (1947), the similarity of the metoposaurids and *Trimerorhachis* is a parallelism, but the presence of the large paraquadrate foramen in both forms, which is unknown in other temnospondyls, is difficult to explain in this way. Assuming that, as proposed by Shishkin (1973) the metoposaurids have common roots with the Brachyopidae, and *Trimerorhachis* is close to their ancestor. The following characters are *a posteriori* important in phylogeny of metoposaurs: lack of the vagus foramen, the contact of the postorbital and parietal, the subtriangular quadrate, the large paraquadrate foramen, long anterior exposure of the cultriform process, articular extending posteriorly into the dorsal area of the retroarticular process, clavicles with an indentation in the medial edge, and atlas with horizontal long axes of condyles. The functional meaning of this characters is still very difficult to recognise.

The deep and rounded recess, described by Dutuit (1976) for *Dutuitosaurus ouazzoui* as “sinus pterygoidei”, is below the oblique crest on the posterior side of the ascending ramus of the pterygoid. This character diverges the metoposaurids from the majority of other stereospondyls. The biological significance of these features remains to be recognised.

EVOLUTION OF THE METOPOSAURIDS

Metoposaurids are known from a short period of time, the oldest findings being reported from the early Late Carnian and the youngest from the Middle Norian (Hunt 1993; Langer 2005). They were found in many localities of continental strata in the North America and from single localities on other continents. Generally, the age correlation is well-founded only between geographically close localities. Despite all the limitations, it seems possible to propose a scenario of their evolution. The first attempt was done by Hunt (1989, 1993), but he did not refer to the stratigraphic succession, although some stratigraphic data helpful in determining relationship among the American species were mentioned. According to this author, the type horizon of *Buettneria bakeri* is the Camp Springs Member of the Dockum Formation, dated as early Late Carnian. The type horizon of *Buettneria perfecta* is Tecovas Member of the Dockum Formation dated as late Late Carnian. *Apachesaurus gregorii* comes from the Upper Redonda Formation of the ?Mid Norian. Long and Murry (1995) were more cautions in determining the age distribution of the American species. According to them, *B. bakeri* is known only from ?Mid Carnian sediments, *B. perfecta* from ?Mid and Late Carnian (possibly also Early Norian), and *Apachesaurus gregorii* from the Late Carnian and Early Norian sediments. *B. bakeri* and paratypes of *B. howardensis* are known from the “Pre-Tecovas” horizon, which is considered as the oldest in the Dockum Group, which is based on the faunal content rather than lithostratigraphy. Localities, from which *B. perfecta* is known, belong also to this horizon (Long and Murry 1995), but the species never occur in the same locality. To conclude, in the North American localities *B. bakeri* is surely in the group of the oldest species and *A. gregorii* is surely younger. The position of *B. perfecta* and *B. howardensis* is ambiguous.

In Europe, *Metoposaurus diagnosticus diagnosticus* is older than *M. diagnosticus krasiejowensis* as proposed by Sulej (2002) and confirmed by Milner and Schoch (2004). In Morocco, *Arganasaurus lyazidi* was found in earlier horizons of the same formation than *Dutuitosaurus ouazzoui* (Dutuit 1976; Jalil 1996). Hunt (1993) dated them as the late Late Carnian and early Late Carnian.

The main character that differentiates the metoposaurid species is the relation of the lacrimal to the orbit (Colbert and Imbrie 1956; Hunt 1989, 1993; Milner 1994; Schoch and Milner 2000; Sulej 2002). Although Chowdhury (1965) claimed that the variability in the position of the lacrimal in the American specimens is very wide, the more abundant Krasiejów material shows that the variability is rather small and this character may be useful in the analysis of metoposaurids phylogeny, although with some caution. The value of this character may be confirmed by its connection with the shift of the prefrontal in relation to the lacrimal. In the metoposaurids, there are two groups of species from different strata and localities, which differ in position of the lacrimal in respect to the orbit margin.

The group with the lacrimal external to the orbit includes *Buettneria bakeri*, *Dutuitosaurus ouazzoui*, *Arganasaurus lyazidi*, and *Apachesaurus gregorii*. They show a tendency towards decreasing depth of the otic notch (Hunt 1993; Gregory 1980) and decreasing body size (Fig. 73). This tendency is well visible in both genera from the Argana Formation, *Arganasaurus lyazidi* and *D. ouazzoui*. The younger *A. lyazidi* is distinctively smaller, and has a shallower otic notch (Dutuit 1976; Hunt 1993). *Apachesaurus gregorii* (the youngest species from the North America) is also very small and has the otic notch even shallower than *A.*

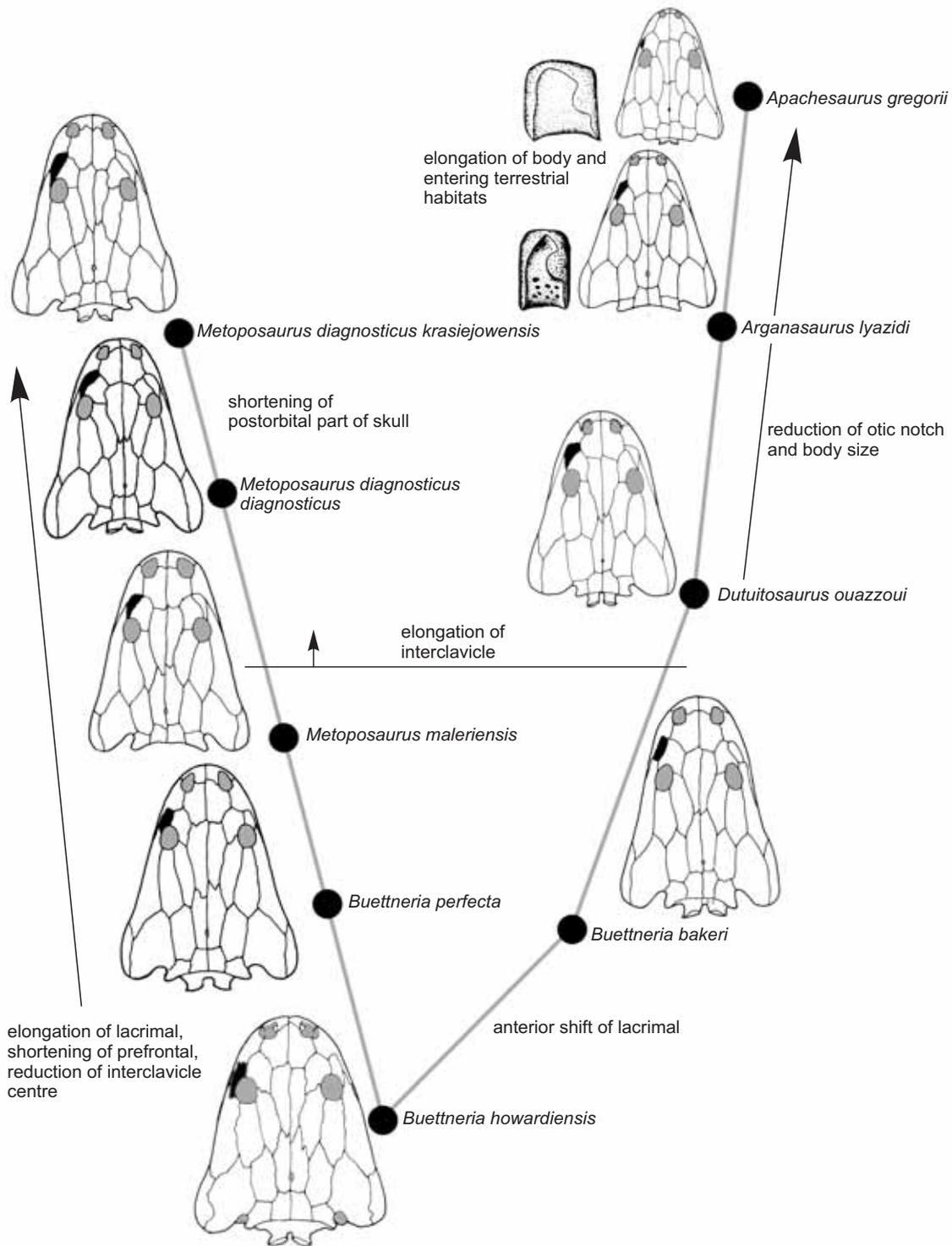


Fig. 73. The phylogeny of metoposaurid species. See also Fig. 74.

lyazidi (Hunt 1993). It seems that *A. gregorii* is the youngest in this group. It was probably a more terrestrial species because of small size, weakly defined lateral line system, well-developed acetabulum, and the intercentra longer than in other metoposaurids (Hunt 1993). According to Hunt (1993), *Buettneria bakeri* is the oldest known metoposaurid. It is probably a descendent of this lineage.

The group of species with the lacrimal forming the orbit's margin includes *Buettneria howardensis*, *B. perfecta*, *Metoposaurus maleriensis*, *M. diagnosticus diagnosticus*, and *M. diagnosticus krasiejowensis*

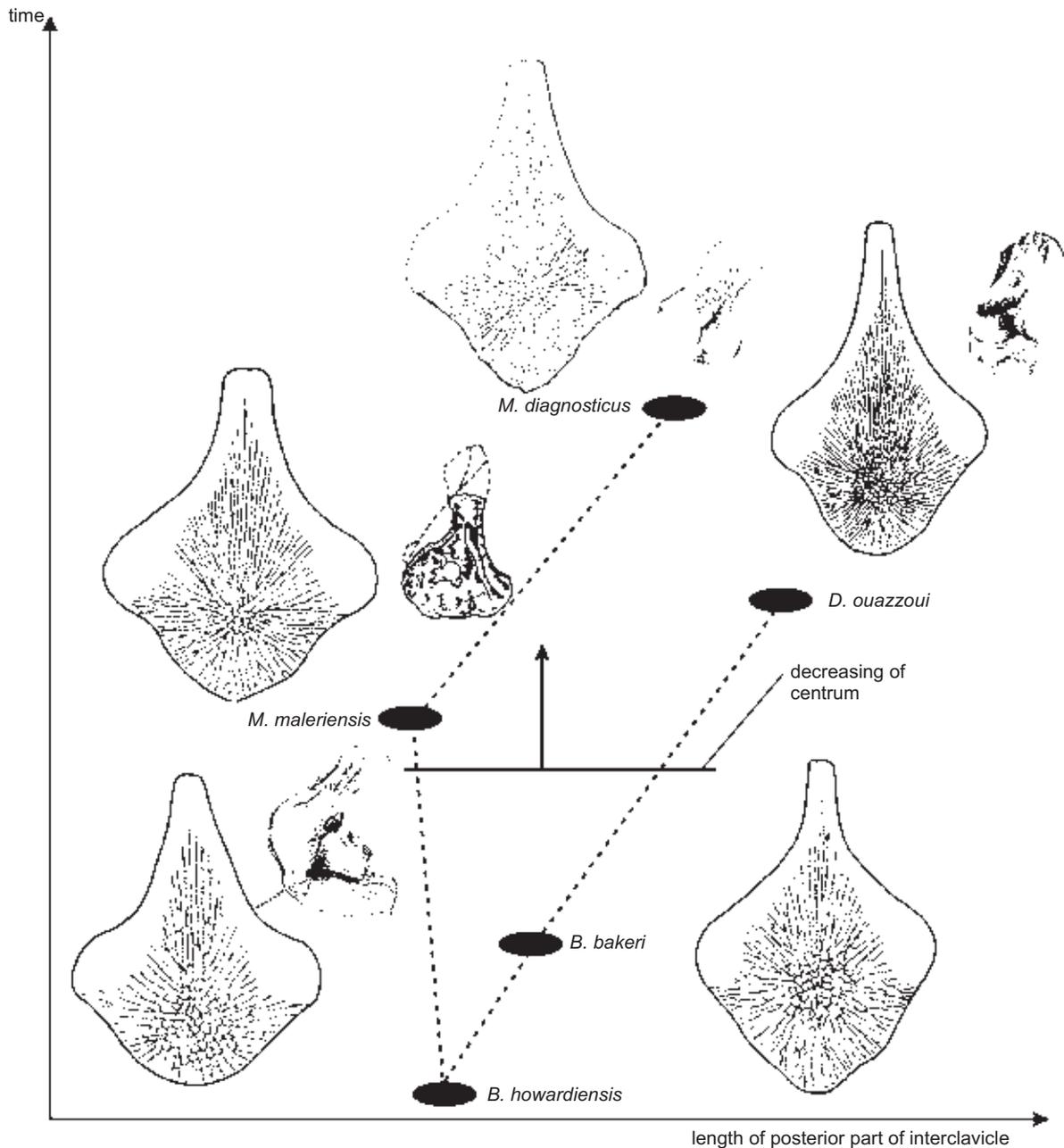


Fig. 74. Evolution of interclavicles and scapula of metoposaurids in two lineages. For changes in interclavicles see scatter-plot on Fig. 42; compare also with Fig. 73.

(Fig. 72). In this group, the general tendency towards elongation of the posterior part of the interclavicle (Figs 42, 73) is apparent. Decrease in size of the central area with polygonal pits on the interclavicle can be observed (Fig. 74), although to quantify these differences is difficult. *Buettneria* species have a very short posterior part of the interclavicle with a large “centre”. A similar tendency to elongation of the interclavicle seems to characterise the group of metoposaurids with the lacrimal out of the orbit. *Dutuitosaurus* has the longest interclavicle with a large “centre”. The interclavicles of *Arganasaurus* and *Apachesaurus* have not been studied from this point of view.

Within the group with the lacrimal out of the orbit, *B. bakeri* has a similar sculpture of the centrum of interclavicle to *B. perfecta*, which has the lacrimal that forms the margin of the orbit. In these species the large area of the centrum bears the polygonal pits. This character is common for all species of *Buettneria*, from North America, and it distinguishes them from the European and Indian species of the genus *Metoposaurus*.

There is a possibility to show the tendency to anterior elongation of the lacrimal and anterior shortening of the prefrontal (Fig. 73). It is related to the tendency to approach of the nasal to the lacrimal. They are separated in *Buettneria howardensis* and *B. perfecta* and bordering in *Metoposaurus*. In most skulls from Krasiejów the anterior end of the lacrimal is closer to the nares than the top of the prefrontal (see chapter about the nasal). However, the variability in this skull character is so great that there are even specimens showing the character typical for other species. The top of the prefrontal much longer anteriorly than the lacrimal is visible in one pictured skull of *B. howardensis* (Savin 1945: fig. 3) and in one of *B. perfecta* (Case 1922: fig. 1). In another pictured skull of *B. perfecta* (Hunt 1993: fig. 8), the character is typical for *Metoposaurus diagnosticus krasiejowensis*. This character is also variable in *B. bakeri* (Case 1932). In *Metoposaurus maleriensis*, both margins of the bones are at the same level. Another character concerning skull roof bones, which demands more studies, is the length of the suture of the postfrontal and supratemporal. The tendency to its shortening is visible on Fig. 73. It is variable in *M. diagnosticus krasiejowensis* and probably in the other species as well.

The evolutionary tendency to elongation of the interclavicle and reduction of the pitted central area may be related to the origin of the metoposaurids. This is a normal feature of the ontogeny of the skull and interclavicle and was described for *Sclerocephalus* by Boy (1988) and Schoch (2003), as well as for the skull of the capitosaurid by Warren and Hutchinson (1988) and Steyer (2003). If the metoposaurids were neotenuous forms, information on mature characters was apparently silenced in their genome. In their ancestor, the skull, including the lacrimal, and the interclavicle elongated in the ontogeny. In both lineages of the metoposaurids, successive species extended the ontogeny as a case of evolutionary reversal to the original state. This required a change in regulation of the development of the anatomy of the skull. The process of the ontogenetic shift of the orbits posteriorward, by elongation of preorbital bones *e.g.* the lacrimal, was stopped at the early ontogeny in an unknown archaic metoposaurids but later in the evolution the position and length of the lacrimal may have been regulated separately.

It seems that a similar mechanism regulated the evolution of the interclavicle (Figs 42, 74). Both *B. howardensis* and *M. maleriensis*, with a very short interclavicle, represent very early ontogenetic state of its development. The elongated interclavicle of *Metoposaurus* and *Dutuitosaurus* probably corresponds to a more mature ontogenetic state of the ancestor of metoposaurids. Considering both subspecies of *M. diagnosticus*, it may be suggested that the process of elongation was stopped or even reversed, as the older form from Krasiejów has a shorter interclavicle and the parietal (Sulej 2002; Milner and Schoch 2004).

In the juvenile forms of temnospondyls, the area of dermal bones is covered by isometric ornamentation. Later in the ontogeny, at the bone borders, grooves and ridges appear and they gradually became longer. It suggests that the interclavicles with large central area with polygonal pits represent younger stages of the ontogeny. The decrease in size of the central area with polygonal pits during the evolution of metoposaurids on the interclavicle can be interpreted as a reversal of the neoteny.

The two groups of metoposaurids represent separate lineages (Fig. 73). It seems that in the mid Late Carnian the *Buettneria bakeri* initiated a new lineage, which had the lacrimal out of the orbit margin. The tendency to decreasing size and depth of the otic notch, and elongation of the interclavicle was already apparent.

In the lineage *Buettneria howardensis* → *Metoposaurus diagnosticus krasiejowensis*, there was a tendency to decrease ossification of various elements. *Buettneria* has a more ossified braincase than *Metoposaurus*. The prootic was still preserved in *B. perfecta* (Wilson 1941) and in *B. howardensis* (Savin 1945). In the humerus, scapula, and fibula a similar tendency towards decreased ossification and gracilization is observed. The *Buettneria howardensis* humerus and scapulocoracoid are more ossified than in its successors. This tendency is well visible in the scapulocoracoid and scapula of *B. howardensis*, *Metoposaurus maleriensis*, and *M. diagnosticus krasiejowensis* (Fig. 74). It seems that in this series the direction of the glenoid of scapula evolved from the lateroventral direction in *B. howardensis* to posterolateral in *Metoposaurus diagnosticus krasiejowensis*. This means the more posteriorly directed limbs, which are useful only in water as a paddle. Additionally, the tendency to gracilization of various elements of postcranial skeleton may be connected with an adaptation to the aquatic environment.

Another character, that confirms that *B. howardensis* and *B. bakeri* are the most primitive metoposaurids, is the sculpture on the pterygoids and parasphenoid. In other metoposaurids species, such sculpture does not

exist. A similarly vanishing sculpture was observed in various lineages of the temnospondyls (Schoch and Milner 2000).

GEOCHRONOLOGICAL IMPLICATIONS

The stratigraphic occurrences of the metoposaurids suggest the following scenario: *Buettneria howardensis* and later *B. perfecta* originated and lived in North America already before the Schilfsandstein sedimentation in Europe, when *Metoposaurus diagnosticus diagnosticus* appeared. The Maleri Formation in India seems to be older than the Schilfsandstein in Europe. The lineages with the lacrimal out of the orbits should be considered independently. The Argana Formation seems younger than the earliest locality with *B. bakeri* and older than the first occurrence of *Apachesaurus gregorii*.

Assuming that the succession of *Paleorhinus*, *Rutiodon*, and *Pseudopalatus* (Long and Murry 1995; Lucas 1998) is at least partially correct, a correlation of the above evolutionary scenario with the succession of phytosaurs can be attempted. Species *Buettneria howardensis*, *B. perfecta*, *Metoposaurus maleriensis*, *B. bakeri*, and *D. ouazzoui* may be set in the “biochron” *Paleorhinus* (Long and Murry 1995, Lucas 1998), whereas *A. lyazidi* and *A. gregorii* in the later “biochron” *Rutiodon* or *Pseudopalatus*.

The geological age of the Krasiejów bone bearing horizons is still discussed. The proposal by Dzik *et al.* (2000) that it is an equivalent of the Lehrberg Beds was recently challenged by Milner and Schoch (2004) on the basis of stratigraphic reassignment of the metoposaur specimen SMNS 56633. This skull is from the Rote Wand (Sulej 2002), as specified on the label attached to the specimen, and it was identified as *Metoposaurus diagnosticus diagnosticus*. The new data from Krasiejów does not contradict this assignment. Milner and Schoch (2004) confirmed this identification, but they showed that the specimen actually originated from the horizon lying immediately above the third Lehrbergbank (upper part of the Lehrberg Beds), which is younger than the Rote Wand. Additionally, they showed that in the Keuper of Germany, *M. diagnosticus krasiejowensis* ranges from the Kieselsandstein to the Middle Stubensandstein. They thus suggested that the Krasiejów material is younger than the Lehrberg Beds.

Milner and Schoch (2004) concluded that the Krasiejów beds are equivalent to Kieselsandstein. However, there is some evidence that they are coeval to the Lehrberg Beds. Biostratigraphic relationship of the Krasiejów horizon to the Lehrberg Beds and Kieselsandstein is problematic. The phytosaur *Paleorhinus* (Kuhn 1932, 1936; Hunt and Lucas 1991), probably the same species that in Krasiejów and the Württembergian Schilfsandstein (Dzik and Sulej this volume), occur up to the Kieselsandstein, which does not allow using it in testing the correlation hypothesis. According to Olempska (2004) “based on the evidence from spinicaudatan *Laxitextella laxitexta* and *Laxitextella* sp. A, it can be concluded that the age of the Krasiejów spinicaudatan assemblage probably lies within the middle-late Carnian time span”. She suggested that they are older than Kieselsandstein; however, it is not a strong statement because no spinicaudatan (Conchostracans) is known from the Kieselsandstein and Blasensandstein.

The basis for correlation of the Krasiejów strata with the Lehrberg Beds is that the main fossiliferous horizon in Krasiejów (the lower one) is probably of a lacustrine origin, being inserted in fluvial strata. The occurrence of the horizontal lacustrine deposits over a large area suggests elevation of the erosional base. They are thus likely to be accumulated during a transgressive episode, probably the first one after the Schilfsandstein sedimentation time. In fact, in the German Keuper, the Lehrberg Beds are remains of the first transgression after the Schilfsandstein (Aigner and Bachmann 1992). The Kieselsandstein, suggested by Milner and Schoch (2004) as coeval with Krasiejów, was accumulated during a regression (Aigner and Bachmann 1992). Seegis (1997: pl. 2, fig. 8) illustrated the red claystone underlying the carbonatic Middle Lehrberg Bank in the Lehrberg Beds sequence at Hohenhaslach. It is identical to the paleosols (vertisols) identified by Szulc (2005) in Krasiejów. The occurrence of vertisols may be helpful in correlating the Silesian and German successions of the Keuper.

The two different subspecies could live at the time of the Lehrberg Beds sedimentation in different regions of the Germanic Basin. In such interpretation, *M. diagnosticus diagnosticus* lived in the western Germanic Basin, from at least the Schilfsandstein to the Lehrberg Beds sedimentation. The subspecies *M. diagnosticus krasiejowensis* lived in the area of the Lehrberg Beds deposition in the eastern part of the Basin. *M. diagnosticus diagnosticus* is generally older than *M. diagnosticus krasiejowensis* and possibly at the beginning of the Schilfsandstein this form lived in both regions. The Schilfsandstein is a period of lower sea

level and there is a possibility that it is the reason that the population of *M. diagnosticus* was divided into eastern and western, with restricted gene flow between them. The land was an efficient barrier separating the populations, which evolved in different way. The new subspecies originated from the eastern population. The transgression took place during the Lehrberg Beds sedimentation and an opportunity of migration appeared. Later in the Kieselsandstein time of regression up to the Middle Stubensandstein, *M. diagnosticus krasiejowensis* occurred in the western part of the basin. If this interpretation is true the two subspecies of *M. diagnosticus* are not chronosubspecies. They are rather geographic races.

These discrepancies in the within-basin correlation are of minor importance from evolutionary point of view. It is generally believed that both the Schilfsandstein and Kieselsandstein belong to the same sedimentary cycle within the Late Carnian (Bachman and Kozur 2004; Beutler 2005).

TAXONOMIC NOMENCLATURE

Class **AMPHIBIA** Linnaeus, 1758

Order **TEMNOSPONDYLI** Zittel, 1888

Family **Metoposauridae** Watson, 1919

Emended diagnosis. — Large oval widely separated orbits situated in the anterior half of the skull; nares large; a suture of the exoccipital with pterygoid perpendicular to long axis of the skull and visible in ventral view; very wide the cultriform process with a long exposure of the anterior end; the quadrate condyle subtriangular in ventral view; deep and rounded sinus pterygoidei below the oblique crest on the posterior side of the ascending ramus of the pterygoid; a posterior tongue of the articular extends posteriorly between the surangular and the prearticular along the dorsal surface of the retroarticular process; the prearticular short anteriorly; the parapophysis on two neighbouring intercentra of the presacral and sacral region; the clavicles with an indentation in the clavicular blade; the manus and pes unusually large; the femur with the main axes of the proximal and distal heads set to each other at 90°.

Genus *Metoposaurus* Lydekker, 1980

Type species: *Metoposaurus dignosticus* Meyer, 1842.

Emended diagnosis. — The interclavicle with relatively long posterior part and small “centre” of sculpture consisting of isometric pits; the glenoid of scapula directed posterolaterally; the braincase weakly ossified; the humerus, scapula, and fibula relatively slender.

Metoposaurus diagnosticus von Meyer, 1842

Type horizon and locality: Schilfsandstein, Germany; Feuerbacher Heide, near Stuttgart, Württemberg, Germany.

Emended diagnosis. — In majority of skulls, the anterior top of the lacrimal closer to nares than the top of the prefrontal; the interclavicle with posterior part longer than in *Metoposaurus maleriensis* and the “centre” of sculpture consisted of isometric pits smaller; the glenoid of scapula directed more posteriorly than in *M. maleriensis*.

Metoposaurus diagnosticus krasiejowensis Sulej, 2002

Type horizon and locality: Probably Drawno Beds coeval to the Lehrberg Beds of Germany; Krasiejów, Opole Silesia, Poland.

Diagnosis.—Very short prepineal part of the parietal with the high 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); ontogenetically, the length of the parietal follows the regression formula $y = 0.29x - 5.74$ (y , length of prepineal part of parietal; x , skull width). After Sulej (2002).

Remarks. — Some of Krasiejów skulls possess a large quadrate foramen and small paraquadrate foramen, but they are variable and this character remains unknown in other subspecies and species.

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APPENDIX 1

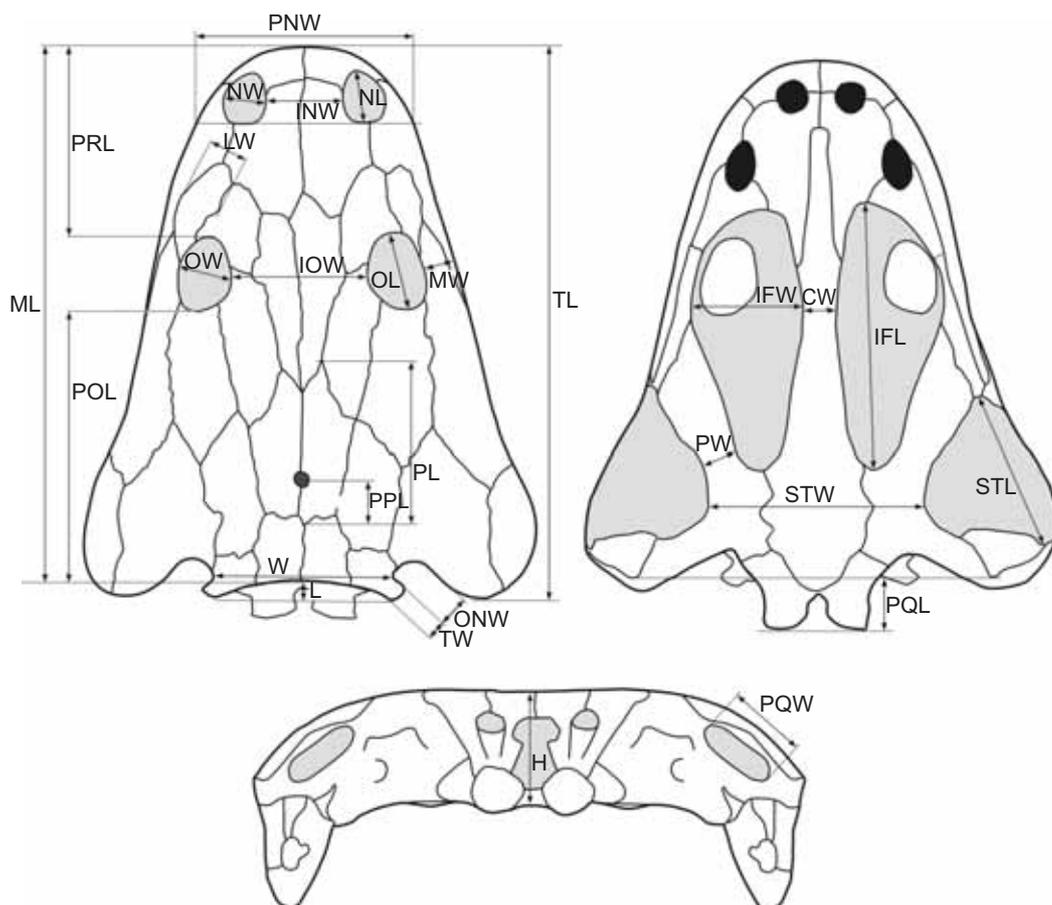


Fig. 75. Explanations of skull measurements and abbreviations: CW, minimal cultriform process width; H, height of occipital part of skull; IFL, interpterygoid foramen length; IFW, interpterygoid foramen width; INW, intranarial width; IOW, intraorbital width; L, depth of posterior skull roof margin; LW, lacrimal width; ML, length of skull roof in midline; MW, width of margin at orbit; NL, narial length; NW, narial width; OL, orbital length; ONW, otic notch width; OW, orbital width; PL, parietal length; PNW, postnarial skull width; POL, postorbital length; PPL, length of postpineal part of parietal; PQL, post-quadrate length of exoccipitals; PQW, paraquadrate foramen width; PRL, preorbital length; PW, minimal palatine ramus of pterygoid width; STL, subtemporal foramen length; STW, minimal width between subtemporal foramina; TL, total length of skull roof; TW, tabular horn width; W, intra-notch width.

Cranial measurements (in millimetres) of *Metoposaurus diagnosticus krasiejowensis* from Krasiejów. Underlined are estimates obtained by doubling a preserved half. For abbreviations see Fig. 75.

ZPAL AbIII	ML	IOW	TL	PNW	PRL	POL	W	IFL	IFW	H	STW	STL	OL	OW	PQL	PL	LW	NL	INW	PPL	TW	PQW	CW	PW	MW	NW	L	ONW	
684	272	70	287		93	142	92	155	58	32	105	83	39	26	24	85	22	26		19	11	25	17	20	14			12	
892	274	70	298		96	138	94	150	58	46	104	84	39	30	18			29	35		11	30	21	18	14	19		14	
1683	276			100	98	140	85	146	52	54	102	82	40	27		84	19	28	35				19	17	18				
682	278	72	294	108	99	143	91			43			38	30	21	88	16	27		21	10				13	16	10	18	
1660	278		292	111	95	143		149		56	120	82	40	28		83	24	29	40	20		27	21	15	17			16	
1166	284	77	303	112	99	146	98	155	59	58	112	88	39	28	17			28	39		12		28	22	15	21	12	14	
1679	286	74			99	149		151				100	38	32															
1165	287	72	305	111	105	143	86	150	60	47	106	85	39	27		86	16		38	23		30	24	19	16	21			
995	288	72		113	DP	144		150	62	49	115	88	39	31		89	17	30	40	23		28	20	18	20				
923	289	74			99	147		151	58	44	109	85	41	29	20						12			20	15			12	
1682	290		315	114	104	143	89	156	64	45	110	87	40	29	15	88	19	31	40				23	18	19				
894	291	74	313	114	106	144	92	155	58	52	114	86	42	29	16	89	19	33	42	22		31	22	15	22				
870	295	76		109	DP	152				48			39	30		88	18	29	32	22					16	19			
883	295	77			103	152	95	164	57	43	116	93	39	31	20	92	18	31		24			21	15	20				
893	295	78		119	104	151		164	58	45	115	93	41	30	19	92	17		38	25		34	21	15	20				
4	295	80	310	116	109	148	93	152	60	51	109	82?	39	31	18	87	21	31	41	22	11	26	27	22	20	20		14	
914	296	80		115	103	151	106	153	61	48		90	39	32				32	41		12		25	19		21	15	15	
854	298	76		110	105	156		151	56	50	111	90	39	27	15			30	41			28	19	12	19				
5	300			105	95	155				60	110					16	30	42					21		20				
872	300		307	106	106	151	96	150	60	57			42	29								27	22	17					
871	303	81		119	106	154		156	60	51	98	87	43	32			20	34	42				29	18	15	20			
1673	305	80		120	110	155	102	164	65				40	30		96	23	32		24	11		26	18	22	15		15	
816	305	82			109	154		160				88	40	30				33	42										
868	307	79		113	DP	155	106	165	69	52	123	90		33	19	97	17	30	39	23		24	21	26	16	21		17	
1675	307	80	330	113	110	160	95		61			90	40	26		89	15	31		23	10		25	19	14	21	15	18	
318	308	81	319	120	109	155	98					41	31			93	24	30	47	21	10					21	14	21	
1199	311	82	332	118	111	158	97	164	65	54	120	90	40	30	24	95		33	45	23	11	38	28	22	17	19		18	
1191	318	82			117	162		160				95	42	30				35.5	37										
688	320	85	322	120	114	163	103	166	65	54	123	95	44	31	16	91	22	32	44	23			27	20	16	19		19	
1674	320	87	335		110			178	71.5	63	129.5	96	44	33	23		16	34	43				23	24	17	21		16	
1681	322	80						162	64	57		101	45	34			18	32	41				30	22	17	21			
681	322	86		119	113	170		169		64	124	100	40	32		99	15	31	41	24				24	16	21			

ZPAL AbIII	ML	IOW	TL	PNW	PRL	POL	W	IFL	IFW	H	STW	STL	OL	OW	PQL	PL	LW	NL	INW	PPL	TW	PQW	CW	PW	MW	NW	L	ONW	
358	323	84	339	130	114	158	106	166	72	73	127	92	49	34	24	94	18	33	35	27	12	44	19	23	18	26	11	17	
992	332	90			120	170		173	69	52	126		43	30	19	100	23	32	46	24			30	23	18	19		16	
882	339	93			122								44	32				36	45										
890	352	98	370		127	173	111	183	72	70	140		48	33	19								33	25	19				
873	355		368	117	125	186	108	180	67	59	125	96	44	32	23	117	20	35	43	29			28	24	13	21		18	
1685	362				127			192	63	58	134		52		18								30	26					
881	365	89	382	138	129	186	122	179	74	63	142	112	46	37				36	46		17	40	29	28	19	26		17	
3	375	109	389	142	132	194	116	190	92	63		105?	51	32		117	14	36	50	27			28	30	19	24			
1192	470	124	498	166	164	243	146	260	93	67	170	142	60	41	27	151	34	46	59	31	26	48	31	31	26	30		20	
10	475	132			174	248	154	242	98	77	180	148	59	40		143	24	42	65	33	33		34	36	26	32	20	21	
1684					124			178	73			107	49	34									23	22					
1680							102			63	114	90										11	34					14	
1007						116	72				96	68			12	68				19		25		16				10	
7																													
8						144																							
1116		67				140	91	140	56	56		80	39	28		92			37	25	11		25	18	13		11	15	
408		69						154				81	41	30					33										
40							86			55																			16
880		72	300		94			150	56	41	105	79	38	25									25	23					
683		74				150	93	156	59	46	125	91	38	29	20						22	13	28	24	18	16		18	
1665		75		108		154	100	156	59	43	108	81	36	28	25	91	19			23			21	19	13				
916		73				152						39	25			93	17			26					18				
886								164			114												24	21				17	
6		78				140																							
1194		78				145							39	30				32											
1						148						88	40	30															
996		77		110		141	96	146	59	44	110	86	44	27		80	19		40	18	10		24	21	16	18	15	17	
161																													
994		83				163	109	169	66	60	127	95	43	33	19	95	19		48	22	13		25	21	16			19	
11		84				154	102	164		62	122	93	45	32	17	98	18			26		38	26	24	19			13	
869						166		175	68	56	124	104	44	33	13	103	23			26			30	24	21				
2					115													32											
1016		95					113	187	70	59	130	DA	50	33	19	106	23			26				26	14			21	
993						176	109		68	54	136	99			28	103				25	14		26	22				22	

APPENDIX 2

THE ONTOGENETIC VARIABILITY OF *METOPOSAURUS* FROM KRASIEJÓW

SKULL

1. The processus supraoccipitalis of postparietal in cross-section has the shape of curved drop in small and average-size skulls and it is oval in large skulls.
2. In smaller skulls, the suture of the postparietal with tabular is placed laterally from the processus supraoccipitalis. In the largest skulls, the processus supraoccipitalis bears this suture anteroventrally.
3. In the posterior part of the postparietal, medially to processus supraoccipitalis, a distinctive prominence is developed, which is massive in the largest skulls.
4. The ventral side of the tabular bears the processus paroticus, which is generally blade-like in cross-section, but in the largest skull it is oval.
5. The supraoccipital fenestra is variable in shape. Usually, it is oval. In small skulls, the oval is set horizontally and vertically in large ones.
6. The tabular horn markedly widened in ontogeny, whereas the width of the otic notch increased only slightly.
7. Between the ventral edge of the pars supraquadrata (quadratojugal) and the quadratum is deep groove that was probably filled by cartilage. In the largest skulls, it is smaller because of the quadrate more ossified.
8. The variability of the width of distance between the nares is much larger than the variability of the length and the width of the orbits.
9. The length of both the orbits and nares increased very slowly in ontogeny.

MANDIBLE

1. In small specimens, the articular is not preserved. In the most numerous, medium size specimens it is partly preserved but only the posterior part of this element is ossified. It forms the posterior part of the articulation jaw surface that forms a tubercle, referred to as the postglenoid ridge.
2. In the largest specimens, the top of the hamate process is roughened.
3. In the small and medium-size specimens, the prearticular sharply terminates dorsally at the contact with the articular, but in large specimens it forms a horizontal shelf, which is a small part of the glenoid area.
4. The posterior dorsal surface of the coronoid forms a large roughened prominence at the suture with the surangular invisible in labial view. It is a part of the coronoid process and is especially well developed in the largest specimens.
5. In the largest specimens, the large roughened prominence of the coronoid, at the suture with the surangular, is especially well developed.
6. In the largest specimens, the predominantly roughened medial surface and smooth anterior and posterior ridges of the symphysis are very distinctive.

VERTEBRAL COLUMN

1. In thoracic vertebrae, the chordal incisure is overgrown and decreased in size in ontogeny.
2. In the smallest specimens of the axis, third, and fourth vertebrae, the neural arch is not fused with the intercentrum.
3. The parapophysis of the axis decreased in size in ontogeny.

SHOULDER GIRDLE

1. The supraglenoid foramen of the scapula is open ventrally in small specimens. Later in ontogeny, it closed.

2. In the smallest scapula, the ventral blade is much shorter than the shaft with glenoid facet. Later in ontogeny, it was much longer.
3. The glenoid facet of the scapula in small specimens is flat and convex in large ones.

PELVIC GIRDLE

1. In ontogeny, the inclination of the long axis of the ilium shaft (in lateral view) decreased in size, whereas the dorsal end widened.
2. In small specimens of the ilium, the ischium facet is almost horizontal and forms a distinct edge at the contact with the acetabulum. In the largest specimens, the ischium facet is more oblique and the margin of the acetabulum is less abrupt.
3. The acetabulum is round in small specimens and tends to be rectangular in the largest.
4. The dorsomedial surface of the ischium bears an indistinct fossa externa and insertion to interischial ligament, which is visible only in large specimens

LIMB BONES

1. In the femur, torus acetabularis has generally a rounded shape in smaller specimens, and later it developed a rectangular shape.
2. In the femur, the shape of the condyles in distal view is variable. The articulation area for the fibula may be flat or pointed dorsally and rectangular ventrally.
3. In the femur, the fossa tendinalis has a various depth but generally deepens in ontogeny.

THE NON-ONTOGENETIC VARIABILITY OF *METOPOSAURUS* FROM KRASIEJÓW

SKULL

1. The inter-rostral fenestra (on the suture between premaxillae) usually is distinct but weakly defined in some skulls.
2. The outline of the naris is variable. Its shape varies from longitudinally oval to triangular or trapezoid.
3. The width of the lacrimal is very variable.
4. The anterolateral sculptured region of the nasal with small polygonal pits is of variable size.
5. The posterior margin of the postparietal is sculptured up to its edge or there is a smooth slope that widens medially.
6. Occipital area of the postparietal bears a marked pit near the sagittal suture. The shape of this pit is variable, usually it is shallow but in some skulls very deep and then the sagittal suture near the pit is distinct.
7. The margin of the choana formed by the maxillary is variable, in most skulls it is weakly defined and rounded, but in a few cases is solid and sharply outlined.
8. In most cases, there is a single vomerine tusk in the socket, but in a few cases there are two and sometimes even three tusks.
9. The ventral surface of the basal plate of the parasphenoid may be smooth or with weak transverse and oblique ridges.
10. The crista muscularis on the parasphenoid may be very distinct or weakly developed, in some specimens even barely visible. Usually, it is present only on the parasphenoid but in a few cases it extends over the pterygoid.
11. The minimum width of the cultriform process, which forms the margin of the interpterygoid vacuities is very variable. The width of the anterior part of the cultriform process is also very variable.
12. The columna verticalis of the exoccipitals in some specimens bears an additional small process directed anteriodorsally
13. The length of the suture of the right nasal and left frontal is very variable, in 3% of the skulls there is no such suture.
14. The suture of the nasal with the lacrimal is not developed in all skulls. In 11% of the studied skulls, at least one nasal does not form this suture. This depends on the relationship between the anterior top of the

lacrima and the prefrontal. In most skulls from Krasiejów, the anterior top of the lacrima is closer to nares than the top of the prefrontal; however, in 4% the top of the prefrontal is closer, and in 11% (n = 72, left and right bones were counted separately) both bones top at the same level.

15. Medially, the lacrima forms a part of the orbital rim (53 studied skulls), although in one skull both lacrimals and in two skulls are separated from the orbit margin.
16. The suture of the postfrontal with the supraorbital is not developed in some specimens. In 27% of 41 studied skulls, at least right or left postfrontal/supraorbital suture is lacking.
17. The paraquadrate foramen is well visible in five specimens. The medial wall that forms the medial margin of the paraquadrate foramen may be situated more medially or more laterally. But in four other studied specimens, there is no trace of the medial wall.

MANDIBLE

1. The shape of the torus arcuatus of the surangular is very variable, its lingual edge may be flat or may form a vertical wall.
2. The fossa postglenoidalis varies considerably in width and depth.
3. In most cases, the surangular is divided from the prearticular by a more or less ossified articular, but in one specimen the articular is covered by surangular and the prearticular.
4. In a few cases, entire articular is preserved. The articular extends anteriorly up to the termination of the hamate process and forms a posterior spine that builds the dorsal margin of the postglenoid area. The posterior tongue of the articular extends posteriorly between the surangular and the prearticular along the dorsal surface of the retroarticular process.
5. The shape of the chorda tympani foramen is much variable. It may be vertical or horizontal.
6. The dentary bears a short teeth row. In a few cases, there is no such tooth arcade laterally to symphysis.
7. The length of the Meckelian foramen is variable. It has usually three-fourths of the length of the adductor window but in one specimen it is shorter than half of that length.

VERTEBRAL COLUMN

1. In the atlas, the lateral vertical ridges on the anterior surface of the neural arch are variable, they are prominent or low.
2. The diapophyses and parapophyses of the axis are generally short, but in one specimen they are quite prominent.
3. The parapophysis of the post-cervical and anterodorsal intercentra may be slightly longer than the half length of the intercentrum or almost as long as the latera in its ventral length. Its shape may be circular or more subtriangular.
4. In the perisacral intercentra, the shape and height of both parapophyses is variable. It may be semicircular or triangular, also the distance between them is variable. They may be very close or rather distant from each other.
5. The caudal vertebrae are very variable, in some specimens their left and right sides are much different.
6. The anterior and posterior parapophyses of postsacral vertebrae are of similar size and occur very close to each other. In some cases, they are united.
7. In anterocaudal intercentra, the base of chevrons generally is developed on the anterior part of ventral surface of the intercentrum, but in a few cases at the posterior edge.
8. In rib type C, the proximal head is flat or bent. Only a few ribs have faces with a slight furrow between shafts of the tuberculum and capitulum.
9. In rib type C, distal end in lateral view can be straight or curved.
10. In rib type C and D, the length of the processus uncinatus is very variable.

SHOULDER GIRDLE

1. The posteriolateral edges of the interclavicle show a great variety of shapes. They are convex or straight, but more usually they are more or less concave.
2. Some interclavicles have a strong inclination for the clavicle, but some have the connection almost straight. There is a gradation between these extremes.

3. In a few interclavicles, a large triangular trace of an insertion of muscles occurs on their dorsal side.
4. In the clavicles, the indentation of the plate is well developed but in a few cases it is hard to recognise.
5. The ridge on the ascending crest of the clavicle is variable. Generally, it is distinct but in a few cases only slightly marked.
6. The torus anterior of the clavicular plate may be pointed or round. The trough may run to the anterior termination of the ascending crest or it may terminate earlier and in that case the ascending crest smoothly goes into torus anterior.
7. In the clavicle, the ridges of sculpture run until the anterior edge of the plate, but in a few cases they terminate earlier, and the smooth area marginalis occur.
8. The shape of that margin of the clavicle, which contact the counterpart clavicle, is straight or curved or its edge is serrated. The clavicles probably did not contact.
9. The glenoid of the scapula is generally rectangular but there is a great variety of its shape. The sulcus glenoidalis may be well developed or not. The anterior surface of the glenoid shaft may be flat.
10. In the cleithrum, the shape of the head and the anterior margin of the area clavicularis are very variable. The anterior margin of the area clavicularis may form an extended shelf or the shelf may form an additional shaft directed ventrally. The lamina suprascapularis may form a large process or various additional prominences.

PELVIC GIRDLE

1. Generally, the ilium shaft is straight, although in a few cases it is strongly sinusoidal.
2. The medial part of the ischium is sharpened and the posterior part bears an area with small ridges that looks like an insertion of a muscle, but there is variability in these aspects.

LIMB BONES

1. The length of the anterior margin of the humerus is variable.
 2. In the humerus at the middle of the long trace of cartilage, there is a prominence, which has a variable size and shape. It may be only slightly developed, with a narrow base or its base may be very wide and markedly high. In the largest specimen, it forms a large surface on the anteroventral side of the head.
 3. In the humerus, the posterior edge of the proximal head and the posterior edge of the distal head forms an angle in ventral view, which may be almost right or much obtuse.
 4. The roughened connection of the supinator process and ectepicondyle has a variable width or may vanish. The supinator process is divided from the ectepicondyle by the smooth bone area.
 5. The "gouttière longitudinale interne" of the radius is generally present but in some specimens is not developed.
 6. In the tibia, a shallow fissure of "planum popliteum" continues proximally behind the cnemial crest, but in some specimens, the cnemial crest extends proximally more than the planum popliteum beside it.
 7. In the tibia, the cnemial crest is very prominent, or only weakly marked.
 8. In the tibia, the distal articulating face is ovoid or roughly triangular.
 9. In the tibia, the articulation with the tibiale is tilted ventrally, or it is straight.
 10. In the fibula, the lateral ridge (crête postéro-interne) can be prominent, very weak, or absent.
 11. In the fibula, the tuberosity is of various size.
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