

**A REVIEW OF THE EARLY LATE TRIASSIC  
KRASIEJÓW BIOTA FROM SILESIA, POLAND**

(Przegląd późnotriasowej fauny i flory z Krasiejowa na Śląsku Opolskim)

by

JERZY DZIK and TOMASZ SULEJ

(WITH 20 TEXT-FIGURES)

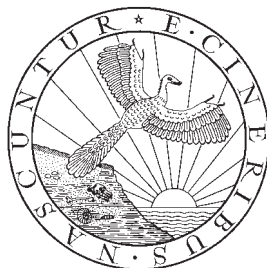
**OSTEOLOGY, VARIABILITY AND EVOLUTION  
OF *METOPOSAURUS*, A TEMNOSPONDYL FROM  
THE LATE TRIASSIC OF POLAND**

(Osteologia, zmienność i ewolucja labiryntodonta *Metoposaurus* z późnego triasu Polski)

by

TOMASZ SULEJ

(WITH 75 TEXT-FIGURES)



WARSZAWA 2007

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INSTYTUT PALEOBIOLOGII PAN im. ROMANA KOZŁOWSKIEGO

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# A REVIEW OF THE EARLY LATE TRIASSIC KRASIEJÓW BIOTA FROM SILESIA, POLAND

JERZY DZIK and TOMASZ SULEJ

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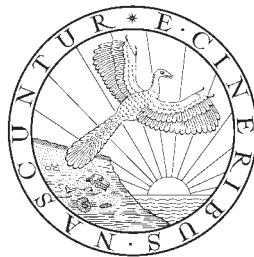
Mass accumulations of vertebrate fossils in the tetrapod “graveyard” at Krasiejów near Opole, SW Poland, occur in a vast lacustrine marly claystone horizon and claystone lenses of various extent within fluvialite cross-laminated mudstone. These fossil assemblages do not differ from each other in taxonomic composition, but the proportions of aquatic to land animals are dramatically different. We attempted to separate these two components of the assemblages to restore the original composition of the biota. The lacustrine biocoenosis component of Krasiejów includes characean algae, various molluscs and arthropods, ganoid and dipnoan fishes, the phytosaur *Paleorhinus*, and the temnospondyl amphibian *Metoposaurus* as the most common vertebrate. The capitosaurid labyrinthodont *Cyclotosaurus* probably occupied the lake shore. The inland vertebrate community was dominated by the herbivorous aetosaur *Stagonolepis* and the small herbivorous dinosaur *Silesaurus*, which probably were the prey for the rauisuchian *Teratosaurus*. The geological age of the Krasiejów strata can be determined, although with a rather low resolution, based on position of various members of its fauna in their evolutionary lineages. Biostratigraphic and sequence stratigraphy evidence may improve the precision of this dating. The strata seem to correspond with the upper part of the Weser Formation in Germany, believed to be of Late Carnian age.

Key words: Germanic Basin, Keuper, Carnian, flora, archosaurs, dinosaurs, stratigraphy.

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## INTRODUCTION

The Krasiejów claypit near Opole was the first discovered palaeontological locality in Poland with mass occurrence of articulated skeletons of Mesozoic amphibians and reptiles. It is somewhat surprising that despite centuries of geological investigations in Silesia, first monographed by Roemer (1870), the locality has remained undiscovered for so long. Most likely, previously accessible exposures were located outside the bone-bearing horizon. This situation changed after 1974, when the cement plant Strzelce Opolskie extended previously existing brickpits to a large quarry exploiting the Keuper mudstone and claystone. The quarried rock was being mixed with water and the suspended mud was pumped 17 km away to the cement mill. After a few years, the quarrying reached the fossiliferous bed, which dips northward at a low angle. Amateur collectors encountered pieces of fossil bones not long after excavations reached the bed's outcrop. The first specimens were brought to the attention of Magdalena Borsuk-Białynicka from the Institute of Paleobiology of the Polish Academy of Sciences in the early 1980's but precise locality information was unknown. Scientific excavations and research started at Krasiejów in 1993 with discovery of an almost complete phytosaur skull by the senior author. Preliminary results were published four years later (Dzik 1997: figs. 2.153, 154, 160, and 162) and a description of the locality and its fossil assemblage soon thereafter (Dzik *et al.* 2000; Dzik 2001).

Subsequently, extensive excavations were performed in 2000–2002, supervised by both authors and financially supported by the owner of the claypit, the Góraźdze cement plant. This fieldwork assembled a large collection of skulls, partially articulated skeletons, and isolated elements. An area with an accumulation of bone material, where skulls formed a kind of “pavement”, was left in place to arrange a museum exhibition *in situ*. The museum building has been already constructed by local authorities and the specimens on exhibition are being prepared. Excavations in the most fossiliferous bed continue during summer season, and are open to the public as a tourist attraction. Results of the ongoing research have been partially published in a series of papers initiated by Sulej (2002) and Dzik (2003a). The Krasiejów flora and fauna has been reviewed in popular booklets (Dzik 2003b; Sulej 2003) and a book in Polish (Dzik and Sulej 2004). The present paper summarizes the present state of knowledge of the Krasiejów palaeontology with suggestions regarding directions of future work.

In following chapters, the fossil taxa identified from Krasiejów are commented on, and illustrated with specimen photographs and preliminary restorations of the skeletons. The Krasiejów site is geographically and stratigraphically isolated, so there are difficulties with determining its position within the framework of geological and biotic evolution of the Germanic Basin during the Late Triassic Period. Most critical to this discussion is the exact geological age of the strata exposed at Krasiejów. Our review presents all the available biostratigraphic and evolutionary geochronological evidence.

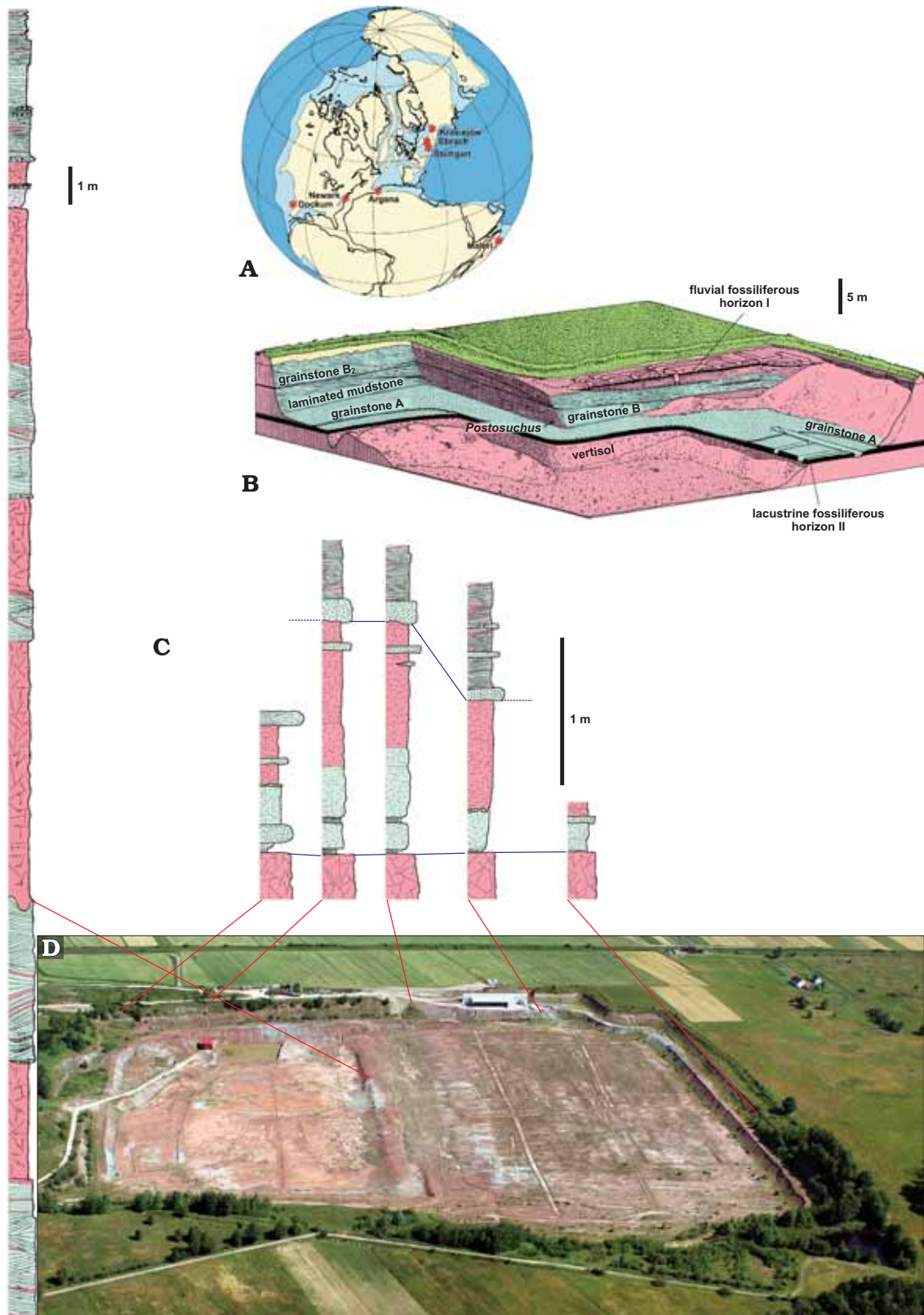


Fig. 1. Claypit at Krasiejów near Opole, Silesia. **A.** Late Triassic palaeogeography and position of Krasiejów in respect to roughly coeval vertebrate localities in the world. **B.** Diagrammatic presentation of the relationship between the lower lacustrine horizon and upper bone-bearing horizon forming a lens within fluvial sediments in the NE corner of the clay-pit (modified after Dzik 2003a). **C.** Composite stratigraphic column from the center of the quarry, with red palaeosols alternating with cross-laminated fluvial mudstone, and measured sections of the lacustrine bone-bearing horizons with intercalations of calcareous grainstone and its relationship to the vertisol below and fluvial variegated mudstone above. **D.** Aerial view of the quarry from south.

**Acknowledgments.** — We are thankful to the Vice-Mayor of Ozimek, Marek Korniak, for permission to use the aerial photograph of the Krasiejów claypit. We deeply appreciate comments by Jerzy Trammer (Warsaw University) and an anonymous reviewer, who offered many helpful suggestions (although we prefer evolutionary, instead of cladistic, approach to our data) and improved English grammar and style.

## SEDIMENTATION AND TAPHONOMY

The strata exposed at the Krasiejów claypit represent mostly marly mudstone and siltstone with calcareous grainstone lenses that are up to 10 m wide and 20 cm thick. The mudstone displays large-scale cross lamination indicating fluvial transport from varying directions, mostly from S or SE. The accumulated sediment was periodically exposed and eroded. Channel deposits indicate that the river meandered, with channel depths reaching at least 2 m, which is most apparent on the southern wall of the quarry. Periodically, the originally laminated mudstone was homogenised *via* pedogenic processes. The red soil horizons developed in conditions of prominent dry-wet seasonality (Szulc 2005).

The youngest palaeosol unit exposed in the Krasiejów claypit (vertisol; W. Bardziński, personal communication) shows a virtually flat erosional surface, with palaeotopography that does not exceed half a metre within the exposed outcrop. In places, a yellow, few centimetres thick intercalation of calcium-free clay separates it from the overlying rock unit. This ~1.0–1.5 m thick fossiliferous layer, unlike other mudstone or grainstone bodies in the exposure, maintains a similar thickness along the entire northern wall of the brickpit and extends to the middle of the eastern wall, southward to where the stratum was removed by Quaternary erosion. The bed thickness seems to increase westward. The lower and upper boundaries of the unit are easily recognizable (Fig. 1). All trenches dug throughout the exposed extent of the outcrop (over 1 km) encountered fossil bones and teeth. The fossiliferous rock consists of about 45% of clay minerals, about 40% of quartz and up to 10% of calcite (Zatoń *et al.* 2005).

Usually, the basal few centimetres of the bone-bearing bed are enriched in plant detritus or winnowed calcareous grains. Patches of plant detritus may include conifer twigs and leaves up to 30 cm long. Conchostracan shells, sometimes with closed valves, are very common in this layer. Almost all specimens of the crab-like giant cycloid crustaceans come from it as well as a few elytra of beetles. The lower half of the unit is gray, the upper variegated, tending to be dark reddish near the top. Near the boundary between the gray and reddish parts of the unit, calcareous concretions and lenses of grainstone with skulls and partially articulated skeletons occur in abundance. Reptile and amphibian skeletons have been collected also at the base of the unit (usually from patches of grainstone) and near the top of the unit. The top is usually delimited by an up to 20 cm thick grainstone layer. Above it, cross-stratified variegated mudstone, of the same kind as that exposed at the bottom of the claypit, is exposed.

Grainstone intercalations apparently originated *via* winnowing of the mudstone, which contains calcareous grains developed at various stages of diagenesis, mostly resulting from pedogenic processes (Szulc 2005). Presence of several such strictly horizontal intercalations at various levels within the approximately one metre thick fossiliferous unit contradicts the claim of Szulc (2005) that “the bone-bearing bed is a typical high-viscosity debris flow deposit, encompassing a relatively narrow sheet of replaced bone-bearing mudstones.” This interpretation is also in conflict with the common occurrence of thin horizontal concretionary layers with unionid bivalves having their valves closed, apparently killed after deposition of the sediment containing them. Moreover, the mass occurrence of charophyte gyrogonites (Zatoń and Piechota 2003; Zatoń *et al.* 2005), bivalves, ostracodes, and articulated ganoid fish skeletons strongly suggest lacustrine sedimentary conditions during formation of the unit (Dzik *et al.* 2000).

The Muschelkalk strata, now exposed in the elevated area 15 km to the south, had probably already eroded away at the time of sedimentation of the Krasiejów mud, and was apparently the main source of its calcium contents. The alkaline environment of the sediment had much bearing on the fossilization processes at Krasiejów. It protected the phosphatic bones against dissolution by humic acids (see Berna *et al.* 2004) but, at the same time, prevented preservation of organic matter. Plant remains are represented only as impressions of leaves in the rock with an iron oxide stain or as a calcitic crust of almost completely decomposed wood

fragments. Virtually no coalified plant material has been encountered and palynological sampling failed to provide taxonomically identifiable material.

The proposed lacustrine layer is in places very rich in vertebrae, skulls, and pectoral girdle bones of the labyrinthodont *Metoposaurus*. Skulls and bones of the phytosaur *Paleorhinus* are less common. Both are apparently the members of the local lacustrine community. Specimens of the capitosaurid temnospondyl *Cyclotosaurus* are third in number among large, easily recognizable tetrapods. It was probably a predatory amphibious animal living near the lake shore. However, typical terrestrial tetrapod remains are also represented in the lacustrine horizon. Usually these are isolated bones, but accumulations of disarticulated bones suggestive of decaying cadavers transported to the lake, deposited at its bottom and decomposed there, are common. Partially articulated skeletons have been also found. Articulated caudal armor plates of the aetosaur *Stagonolepis* and almost complete skeleton of the dinosaur *Silesaurus* are among them.

The degree of diagenetic compaction of the sediment is not great and mostly does not exceed one third of its original volume, as indicated by the degree of deformation of bivalve shells. This suggests that the mud was relatively firm and its dehydration proceeded rather quickly after deposition. We have not encountered any direct evidence of sinking of bones in a hydrated mud but in some cases their orientation (especially informative in case of strongly convex clavicles of *Metoposaurus*) suggests vertical deposition from suspension. Possibly, these were results of storm episodes. Bones preserved in grainstone were probably winnowed by episodic currents or waves.

Dark coloration of the sediment in the lower half of the lacustrine bed and dispersed pyrite grains (usually oxidised) indicate anoxic conditions in the sediment. Perhaps these conditions, unfavorable to scavengers and infaunal life, protected the bone material against bioerosion, while the alkaline conditions prevented their dissolution.

Bones and articulated skeletons can also be found outside the lacustrine horizon, in beds of fluvial origin exposed both below and above it. However, they probably did not survive pedogenesis in the red-colored palaeosols. A fragmentary small phytosaur skeleton of *Paleorhinus* was found near the bottom of the claypit, about 8 m below the lacustrine horizon. A few metres above the phytosaur, a disarticulated specimen of the aetosaur *Stagonolepis* was discovered (by K. Książkiewicz). 0.8 m above the lacustrine horizon, an associated incomplete skeleton of the rauisuchian *Teratosaurus* and bones of the dinosaur *Silesaurus* were deposited. The most prolific deposit is within a 1 m thick and 15 m wide lens of red clay within fluvial cross-laminated deposits in the NE corner of the quarry (Fig. 1B). About twenty skeletons of *Silesaurus* were found near the top of the lens (Dzik 2003a), mostly in its western part. Many disarticulated *Stagonolepis* specimens occurred somewhere deeper in the central part of the lens, whereas *Cyclotosaurus* and fragmentary bones of *Paleorhinus* and *Metoposaurus* were found at its base. Bivalves with shells replaced with calcite are characteristic for the unit but characean oogonia are absent.

Fossil bones from Krasiejów can be easily extracted from the soft clayish rock but they weather and fragment easily unless covered with a protective coating. During excavations, large specimens were protected with plaster and then cut off the rock, whereas isolated bones were impregnated *in situ* with cyanoacrylic glue. In laboratory, the soft clay can be easily removed with hot water. If the rock matrix is cemented with calcite, it is usually enough to brush the fossil with diluted formic acid. Concretionary limestone cover has to be removed with chisels, and the exposed bone can be cleaned with acid.

## THE KRASIEJÓW LAKE COMMUNITY

The two main bone-bearing horizons at Krasiejów differ dramatically in abundance of particular taxa but their fossil assemblages include the same two ecological components: a local *Metoposaurus–Paleorhinus* biota with a suite of fish and invertebrate fauna and algal flora, and an apparently allochthonous terrestrial *Aetosaurus–Silesaurus* biota with rare insects and vascular plant debris. With the exception of the probably semiaquatic *Cyclotosaurus*, most of the Krasiejów organisms can be assigned to one of those communities. The lacustrine community is represented by a larger number of specimens and its tetrapods are one of the most spectacular aspects of the Krasiejów graveyard.

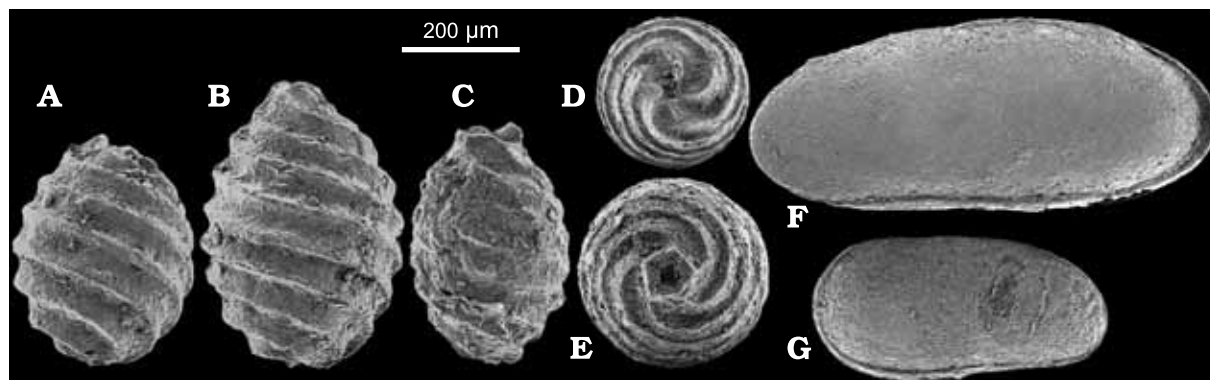


Fig. 2. A–E. Variation in shape of characean gyrogonites from the lacustrine horizon at Krasiejów. F. Associated ostracod *Darwinula* sp. G. Ostracod *Suchonella* sp.

## FLORA

The most abundant sedimentary facies at Krasiejów are not suitable for preservation of organic matter and especially of delicate aquatic plants. The only evidence of their existence are their physiologically calcified organs and diagenetic carbonate external casts of their thalli. Presumably, a significant part of the calcareous grains within the mudstone and the grainstone intercalations are originally derived from these casts. The characean gyrogonites prove that at least some of them formed around these algae.

**Charophytes.** — Charophyte gyrogonites are abundant in the bone-bearing lacustrine horizon at Krasiejów, with frequencies exceeding three thousand per kilogram of rock, but rare in fluvial deposits above and below it (Zatoń *et al.* 2005). In places, they are concentrated by winnowing into patches of “gyrogonite sand”, where they are the dominant identifiable skeletal component of the rock (Fig. 2A–E).

Based on the presence of specimens with an apical neck and separation of spirals at the summit that form denticles and specimens whose profile of the apex remains rounded, with a pentagonal opening, Zatoń *et al.* (2005) distinguished four species, namely *Stellatochara germanica* Kozur *et* Rheinhardt, 1969, *Stomochara starozhilovae* (Kisielevsky, 1969), *Stenochara kisielevskiyi* Bilan, 1988, and *Porochara triassica* (Saidakovsky, 1985). Each species is highly variable in shape and there is no possibility to identify any discrete characters in quantitative measurements of the gyrogonites from Krasiejów (Zatoń and Piechota 2003; Zatoń *et al.* 2005). In fact, characters used to recognize these four “species” have not been demonstrated to be heritable in modern taxa. They could be ecophenotypic traits. This is indirectly suggested by the lack of change of relative abundance of the four morphologies across the bone bed (Zatoń *et al.* 2005: fig. 2).

## INVERTEBRATES

**Unionid bivalves.** — Bivalves are the most common macroscopic fossils in the lacustrine bone-bearing horizon at Krasiejów (Fig. 3). The original aragonite has not survived diagenesis. The shells are preserved mostly as imprints in the claystone, more or less deformed *via* compaction, though the shell interior is sometimes filled with a calcareous concretionary matrix preserving the original shape. Such concretions, formed inside the shell and sometimes encompassing several specimens with closed valves, probably in life position, occur in continuous horizons near the top of the lacustrine bed, extending for a dozen metres. In grainstone intercalations, the shell matrix may be replaced with calcite and such preservation is common in the upper fluvial bone-bearing horizon. Great accumulations of open valves may underlie concretionary lenses with bones of large tetrapods, probably as a result of winnowing of the sediments.

Most of the fossilised specimens are subadult, but various ontogenetic stages are represented. The claystone preserves fine details of the shell surface and it is clear that the juvenile ornamentation (Fig. 3C), so characteristic for at least some Mesozoic unionid bivalves, is represented only by concentric rugae disappearing in the posterior area. The phylogenetic significance of this feature of the Krasiejów species remains to be clarified. Either these are not unionids, representing an early continental offshoot of an underived marine lineage, or the zigzag pattern of juvenile ribs originated in the unionids independently of their trigoniid relatives.



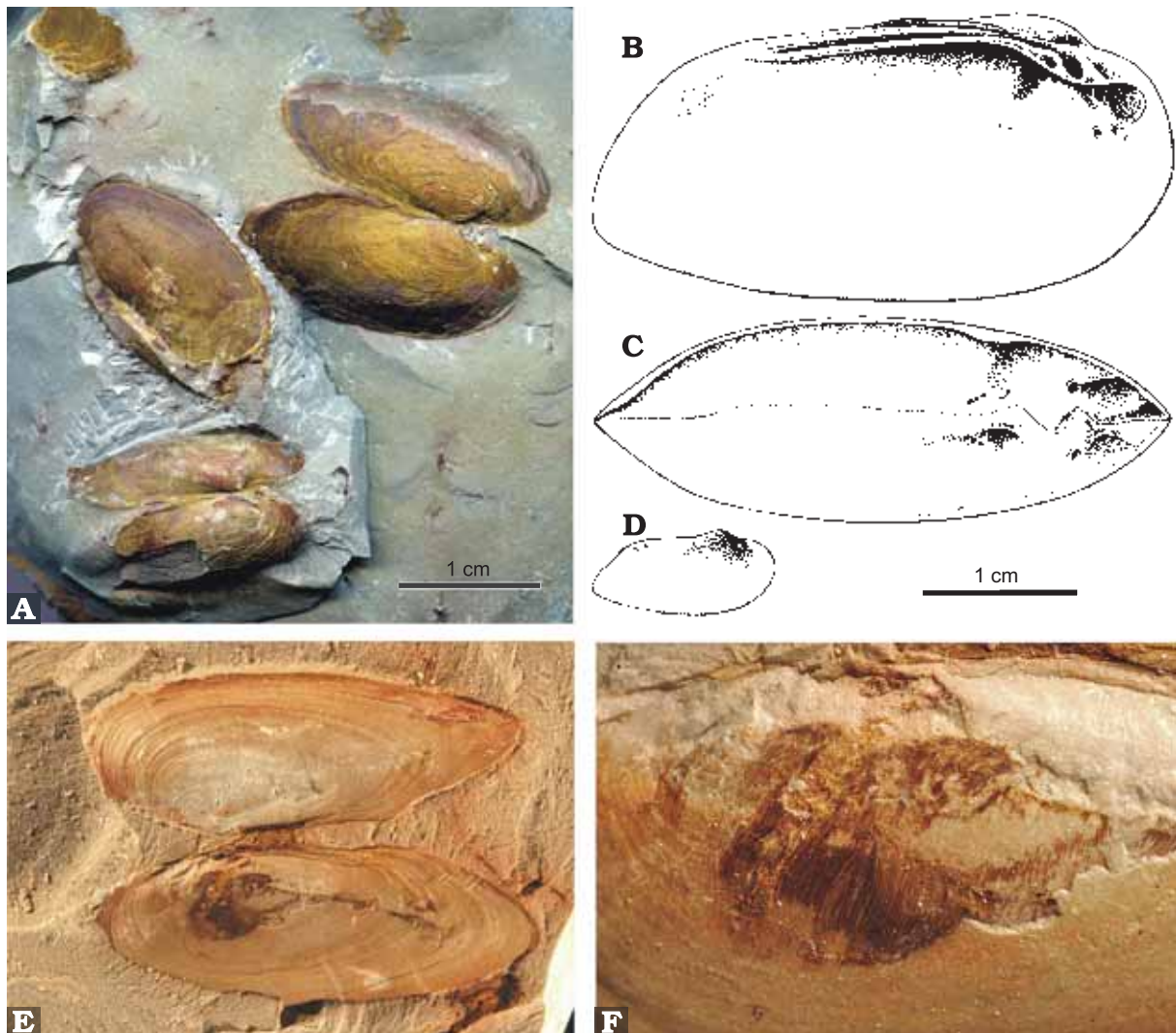


Fig. 3. Unionid bivalves from the lacustrine bed at Krasiejów. **A**. Accumulation of opened shells. **B**, **C**. Restoration of the left valve and interior of closed valves showing disposition of muscle attachment scars. **D**. Ornamentation of juvenile shell. **E**, **F**. Three-dimensionally preserved gills in a specimen with opened valves.

A probable clue to identifying true affinities of the Krasiejow bivalve species is their muscular system, represented by well preserved muscle attachment scars. Their trigoniid affinities seem to be supported by the rather common preservation of gills. These are preserved as dark stained filaments with visible three-dimensional organization of the particular filaments and lamellae (Fig. 3D, E). Presumably, mineralization of the gill soft tissue was possible owing to calcium phosphate deposits, which occur in gills of extant unionid bivalves (Whyte 1992). Mineralised bivalve gills are known in the fossil record elsewhere, but they are invariably associated with trigoniid bivalves (Klug *et al.* 2005). The valves of the specimens from Krasiejów with preserved gills are widely open. Their preservation was thus probably enhanced by the marly clay surrounding the soft tissue, but not necessarily the concretionary calcium carbonate, which probably formed somewhat later in diagenesis.

**Gastropods.** — Only one gastropod specimen has been recovered from Krasiejów. It resembles high-spired valvatids or small viviparids in general shape but is too poorly preserved to be taxonomically determinable.

**Conchostracans.** — Olempska (2004) identified an abundant conchostracan fauna dominated by *Laxitextella laxitexta* (Jones, 1890) in the main fossiliferous horizon of Krasiejów. Their shells, closed or open, form local accumulations (Fig. 4) or are dispersed across the bed. Whether they were living permanently in the lake or were transported occasionally from marginal pools has not been determined. Olempska (2004) used differences in ornamentation of the shell to distinguish five taxa representing at least two genera within

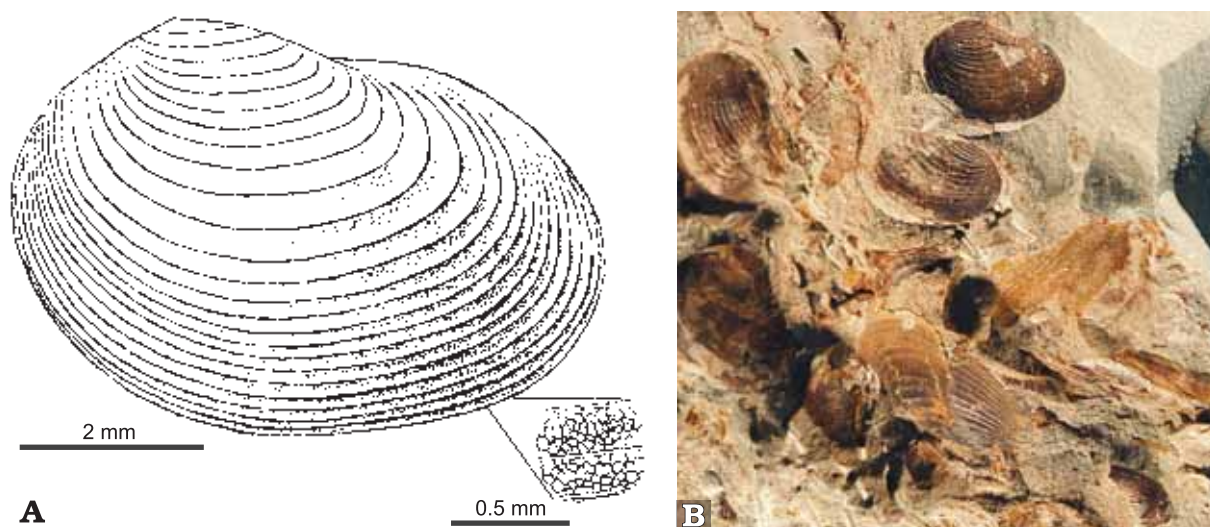


Fig. 4. Conchostracans (spinicaudatans) *Laxitextella* from the lacustrine horizon at Krasiejów. **A.** Restoration of the right valve of the carapace. **B.** Mass occurrence of mostly articulated valves.

a small sample taken from the basal part of the lacustrine bed. This is a rather unusual occurrence for these ecologically opportunistic organisms, because they tend to form monospecific mass occurrences. It has to be kept in mind; however, that the extent of intraspecific variability of diagnostic characters has not been determined. Comparative study of these features in extant species of conchostracans is needed to test the validity of the palaeontological taxonomy.

**Ostracods.** — The most common ostracod species in the Krasiejów lacustrine bed belongs to *Darwinula*, and like its extant relatives, it was probably a non-swimming infaunal organism living on a muddy bottom in fresh to slightly brackish waters (Olempska 2001, 2004). These ostracods also occur with a similar frequency in fluvial strata above the bone-bearing horizon, where the abundance of characean oogonia is strongly diminished (Zatoń *et al.* 2005). Rare specimens of *Suchonella* co-occur with *Darwinula* in the lacustrine bed (Fig. 2F, G; Olempska 2004).

**Cycloids.** — Probably the most unusual member of the Krasiejów invertebrate fauna is a crab-like crustacean with an oval carapace that has a diameter up to 5 cm. The dorsal surface of the carapace is ornamented with sub-radial striations and rather prominent tubercles (Fig. 5). These are clearly relatives of the cycloid lineage of *Halicyne*, known to range from the Late Carboniferous to Late Triassic (Schram *et al.* 1997).

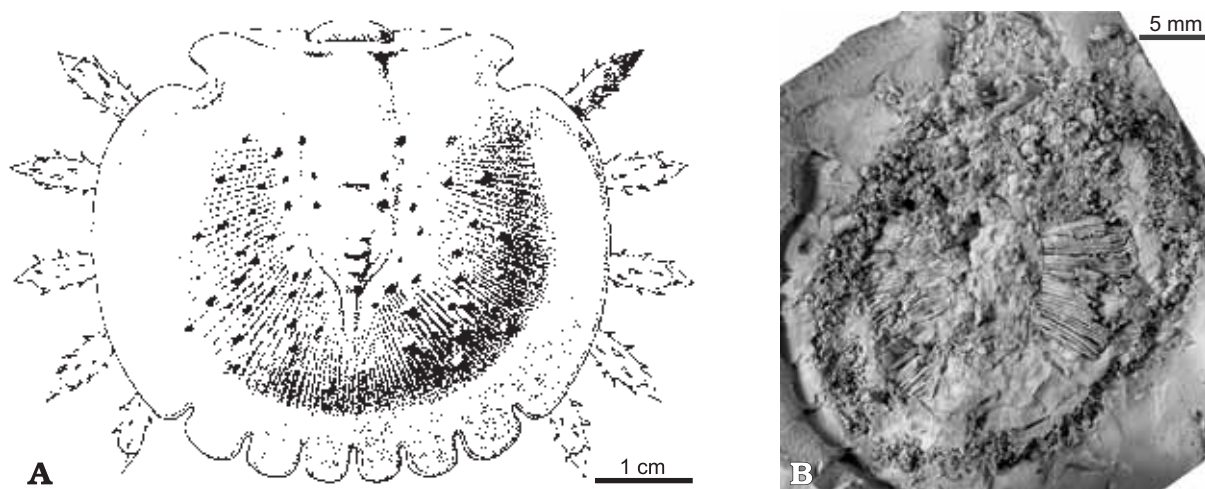


Fig. 5. The cycloid crab-like crustacean from the lacustrine bed at Krasiejów. **A.** Restoration of the animal in dorsal view. **B.** Specimen with well preserved gills.

The Krasiejów form is different from all other cycloids in having a series of incisions in the posterior margin that separate rounded lobes. Fragmentarily preserved limb appendages were strong and spinose. Similar to other *Halicynne*-like cycloids, under the carapace, on both sides of the body, large gill-like structures are present. They are rather heavily calcified (at least dorsally), and are composed of numerous segments with a U-shaped cross section that open ventrally. Interpretation of this structure, proposed to represent gills similar to the book-lungs of chelicerates (Gall and Grauvogel 1967), is a rather troublesome issue. Cycloids represent a branch of early copepods (Schram *et al.* 1997) but there is no structure in the anatomy of extant copepods that can be homologised with gills of such organization. The only possibility at present is that these are serial enfoldings of the ventral cuticle, corresponding in distribution to the respiratory fields of the Branchiura, which are living relatives of the copepods. This may strengthen early suggestions of a relationship between cycloids and branchiurans. Whether the crab-like adaptations of the Triassic cycloids developed from parasitic or free benthic mode of life of their ancestors, remains to be clarified.

## FISH

Taphonomic conditions in the Krasiejów site were generally not favorable to preservation of taxonomically identifiable fossils of fishes. The assembled material definitely underestimates their ecological importance and contribution to biological productivity of the local lacustrine ecosystem. Most specimens are isolated scales and crushed bones. Yet, they allow an initial estimate of minimum fish diversity of the assemblage.

**Ganoids.** — Ganoid fish scales and teeth occur with high frequency in the lacustrine fossil-bearing horizon at Krasiejów, but articulated specimens are rare and difficult to extract from the rock. The most informative specimens are preserved within small limestone concretions. In two of them, details of the skull bones are recognizable and the relative position of pectoral, pelvic and anal fins can be seen (Fig. 6). Two other ar-

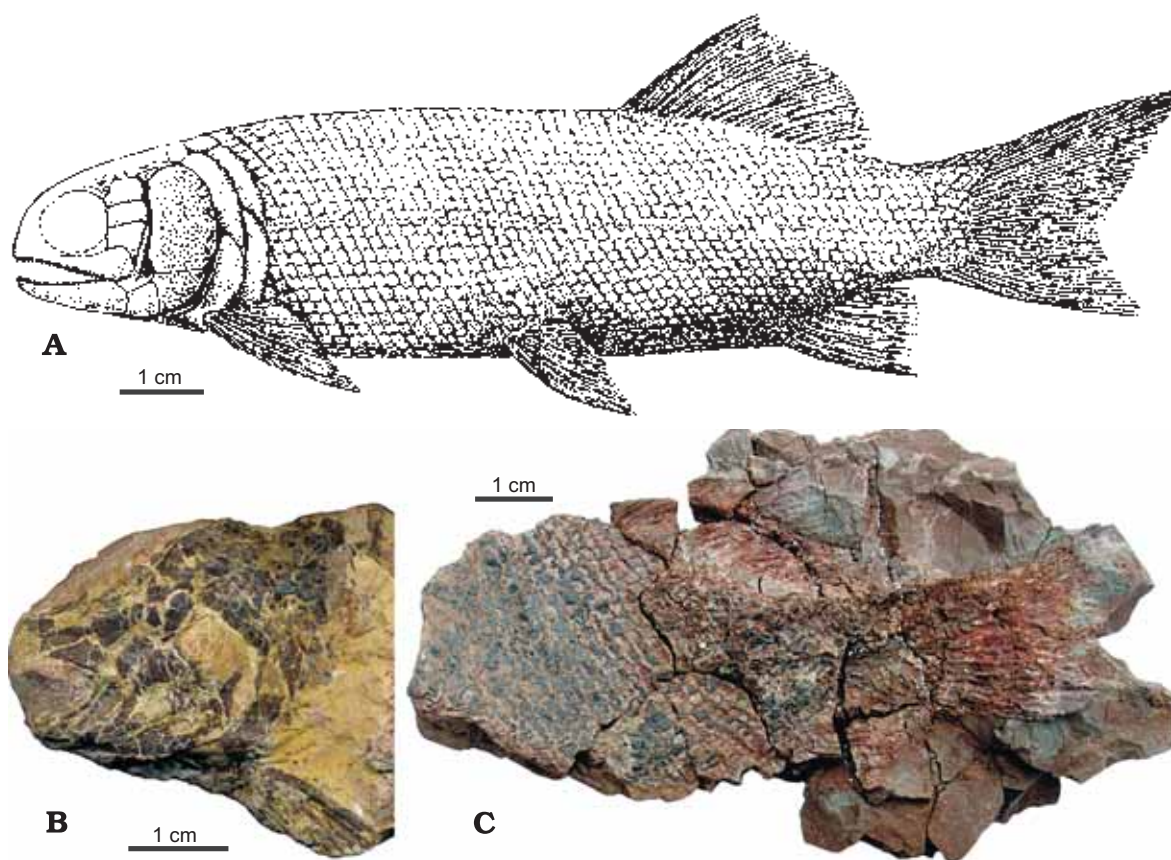


Fig. 6. A ganoid fish from the lacustrine bed at Krasiejów, possibly "*Dictyopyge*" *socialis* (Berger, 1843). A. Preliminary restoration of the body. B. Anterior part of the body with head and pectoral fins preserved in calcareous concretion. C. Posterior part of the body preserved in clay (specimen collected by K. Książkiewicz).

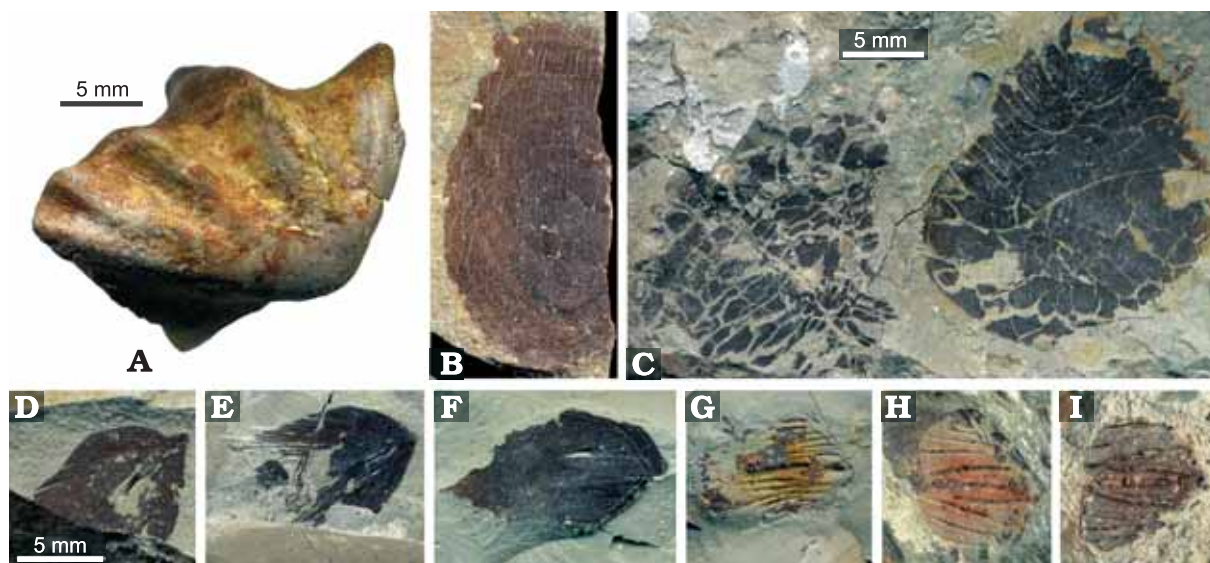


Fig. 7. The dipnoan and problematic fish from the lacustrine bed at Krasiejów. A. Tooth plate of *Ceratodus silesiacus* Roemer, 1870. B, C. Scales possibly belonging to the same species. D–I. Fish scales with feather-like organization and longitudinal ribs.

ticulated specimens in clay matrix show dorsal, pelvic, anal, and caudal fins. Whether all represent the same species is not certain, but their scales are indistinguishable and in two well preserved skulls the shape of operculum is virtually the same. The most characteristic skull feature is the presence of a series of postopercular bones with smooth surface and serrate posterior margins, like in the row of small scales following them posteriorly. Other scales are smooth and rhombic in outline, with weakly developed riblets at the posterior margin. At this time, we are unable to determine the taxonomic assignment of the Krasiejów fish. These specimens could be “*Dictyopyge*” *socialis* (Berger, 1843), known from mass occurrences in the Ladinian *Semionotus* Sandstone at Haarth near Coburg (Hauschke and Wilde 1999), but the published data available to us do not describe enough diagnostic characters for comparison with the Krasiejów material. Its relationship to the type species of the genus, *D. macrura* (Redfield, 1841) from the Late Triassic of the Newark Group remains to be clarified, but they are unlikely to be congeneric (Schaeffer and McDonald 1978), and the Krasiejów species definitely does not represent this genus. Instead, closely similar, although also inadequately described, is *Guizhoueugnathus analilepidus* (Liu, 2003) from the *Keichousaurus* horizon of the Late Triassic of Guizhou, China (Liu *et al.* 2003; Liu 2004).

**Dipnoans.** — Several isolated tooth plates have been found in the lacustrine horizon at Krasiejów (Fig. 7A). They may represent *Ceratodus silesiacus* Roemer, 1870, the type stratum and locality of which is the “Lissauer Breccie” at Lisów near Lubliniec (Roemer 1870). This is in the same area as Krasiejów but of somewhat younger, although still not precisely determined, Late Triassic age (Szulc *et al.* 2006). A few large thin bones with concentric increments may also belong to this dipnoans (Fig. 7B). More enigmatic is the taxonomic assignment of feather-like scales known from numerous specimens (Fig. 7C).

Among the most bizarre Krasiejów fossils with possible fish affinities is an isolated jaw bone (maxilla?) with a row of transversely oriented bean-like crushing teeth with smooth and flat surfaces (Fig. 9B). At least superficially, it resembles pycnodont and colobodont jaws (Poyato-Ariza and Wenz 2002) but we have not encountered anything truly similar in the available literature and tetrapod affinities of the fossils cannot be excluded.

## AMPHIBIANS

Fishes were likely a major part of the diet of lacustrine tetrapods inhabiting the Krasiejów lake, particularly for the large labyrinthodont *Metoposaurus*. There is little doubt that the even larger carnivorous capitosaur *Cyclotosaurus* also entered the lacustrine environment, but it probably preyed mostly on terrestrial animals, which is commented on in the next section.

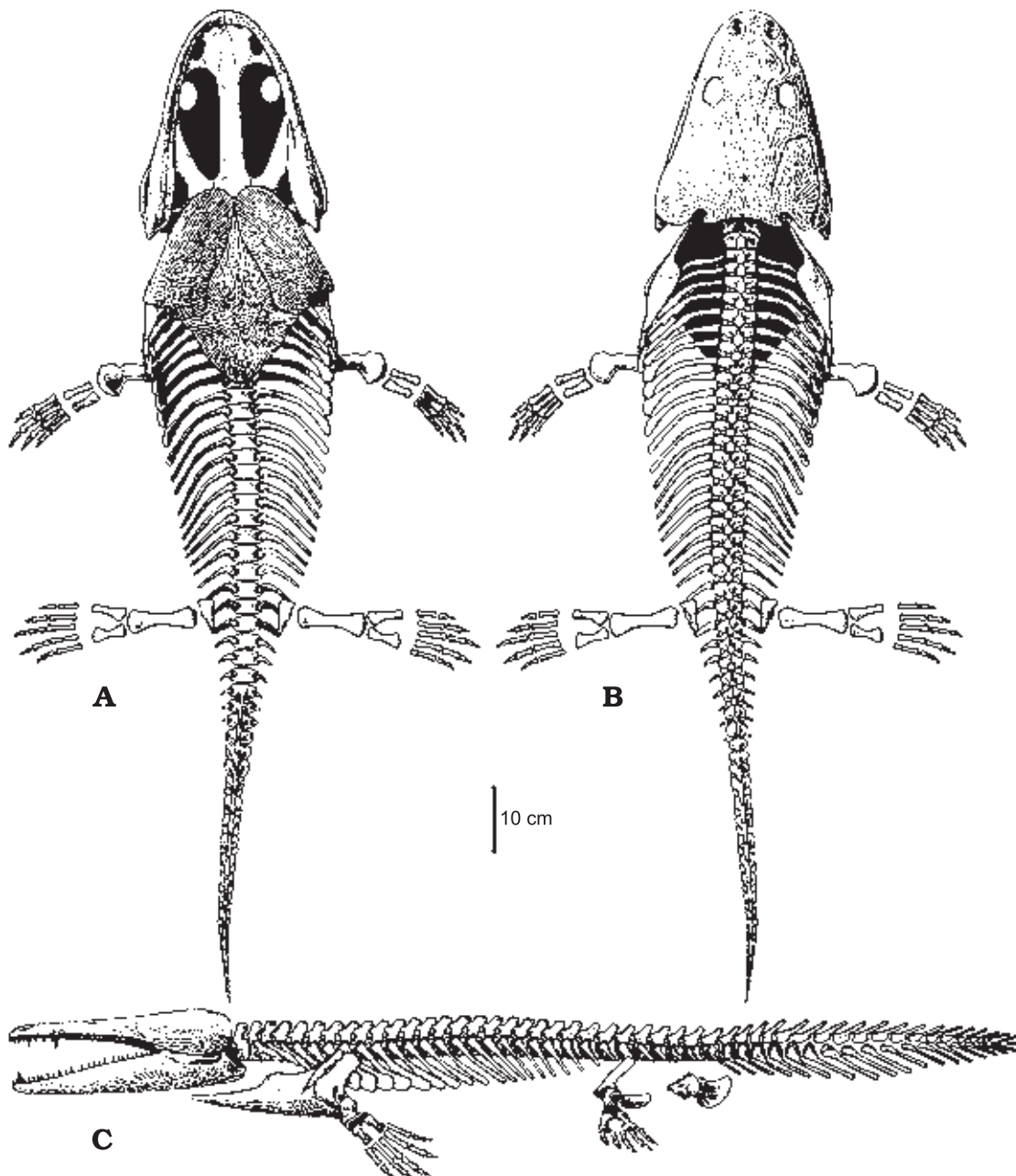


Fig. 8. Restoration of the skeleton of *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 in ventral (A), dorsal (B), and left lateral (C) views (modified from Sulej this volume).

Among Krasiejów problematics there is a small jaw bone (maxilla) with a smooth external surface suggestive of reptilian affinities, armed with sharp conical thecodont teeth (Fig. 15B). Their most characteristic aspect are four longitudinal furrows, remotely resembling dentine folds in labyrinthodonts. Until more complete specimens are found, the affinity of this fossil is unclear.

**Metoposaurs.** — Metoposaur bones are the most common remains of large tetrapods at Krasiejów. They represent a single species. The variability of its skeleton is now well known because of the abundant material that enables restoration of the whole skeleton (Sulej 2002 and this volume; Konietzko-Meier and Wawro 2007; Barycka 2007). The metoposaurs were large, with the largest complete skull specimen measuring 47.5 cm long. A recently modified restoration of the animal (Fig. 8; Sulej this volume) shows a flat skull roof, heavily armored pectoral girdle, and a strong flat tail. The animal was evidently well adapted to aquatic life and may not have been able to enter land.

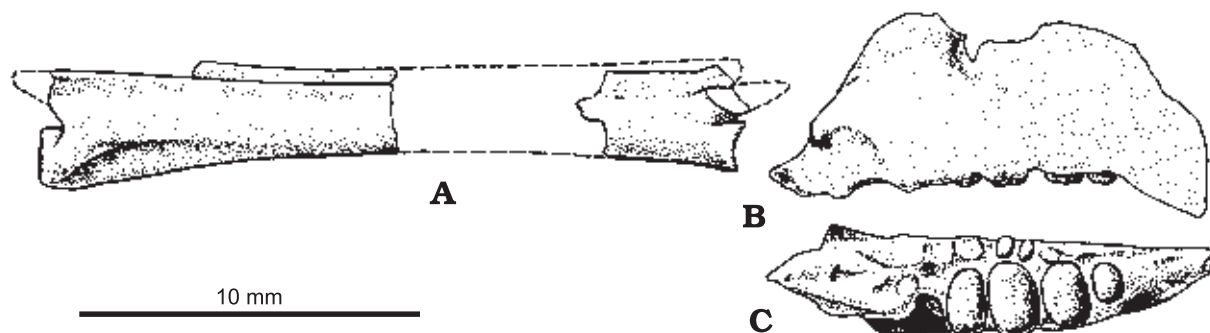


Fig. 9. Problematic isolated vertebrate bones from the lacustrine horizon at Krasiejów. **A.** Caudal vertebra of a pterosaur or cervical vertebra of *Tanytropheus*. **B, C.** Jaw bone of a pycnodont fish or an unidentified tetrapod in labial and occlusal views, respectively.

The Krasiejów metoposaurus is very similar to those of the type population of *Metoposaurus diagnosticus* (Meyer, 1842) from the Schilfsandstein (Stuttgart Formation) of Baden-Württemberg but shows a statistically significant difference in proportions and location of several skull roof bones. Standard deviations from the means of at least one character do not overlap, therefore the Polish and German populations have been distinguished as separate subspecies (Sulej 2002; Milner and Schoch 2004). The name *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 was introduced for the former. It remains unclear; however, whether these are biological subspecies (geographic races) or chronosubspecies (segments of the same lineage), as discussed in the Geologic Age section of this paper.

## REPTILES

At least some Krasiejów reptiles were piscivorous. The most spectacular is the archosaur *Paleorhinus*, but these may also include numerous smaller indeterminate forms.

**Phytosaurs.** — Phytosaurs are the second most abundant specimens among tetrapods in the Krasiejów fossil material. These may not be the first phytosaurs found in Silesia. The isolated tooth described and illustrated by Roemer (1870) as *Megalosaurus cloacinus* from Lubsza near Woźniki, about 30 km from Krasiejów, may have belonged to a phytosaur. The species name was originally based on taxonomically indeterminate Triassic teeth from the Knochen Breccia at Bebenhausen near Tübingen, Germany. The generic one refers to a Jurassic dinosaur.

*Paleorhinus* material from Krasiejów includes several skulls (Fig. 10), partial articulated postcranial skeletons, and numerous isolated bones. Individuals of various ontogenetic stages are represented, forming an ontogenetic series (Fig. 11). This may help in evaluating the diagnostic importance of those skull structures which grew allometrically. The most complete skeleton is a juvenile (skull length about 40 cm) with still unfused centra and neural arches of the trunk vertebrae (see Irmis 2007). Its antorbital fenestra and orbits are larger than in adult specimens. The best preserved skull is 64 cm long, some incomplete specimens are much larger. The palate is completely preserved in at least two skulls from Krasiejów (Dzik 2001) and is not significantly different from the palate structure of *Paleorhinus bransonii* from Texas (Lees, 1907) or German “*Ebrachosuchus*” *broili* (see Kuhn, 1936), but different in having much narrower choanae from that restored for the Indian Maleri Formation species classified as *Parasuchus hislopi* by Chatterjee (1978; International Commission of Zoological Nomenclature 2003). Another apparent difference with *Parasuchus* is that the shape of the external mandibular fenestra is narrower and extends further anteriorly in the Krasiejów specimens. This character may be ancestral (plesiomorphic) in the lineage, as it is present also in the Ladinian proterochampsid *Chanaresuchus bonapartei* Romer, 1971 (Romer 1971) and in “*Zanclodon*” *arenaceus* E. Fraas, 1896 from the Schilfsandstein at Feuerbacher Heide in Stuttgart, Germany (Hungerbühler 2001).

“*Zanclodon*” *arenaceus* is known from a 23 cm long fragmentary mandible preserving the symphyseal with teeth and the rami crushed and pressed to each other. For a long time, the specimen was considered to be the mandible of a phytosaur, but Hungerbühler (2001) redescribed the original specimen and rejected any relationship to the phytosaurs. However, in all identifiable aspects, the specimen does not differ significantly from corresponding parts of the juvenile Krasiejów *Paleorhinus*, which is clearly a phytosaur. Admittedly,

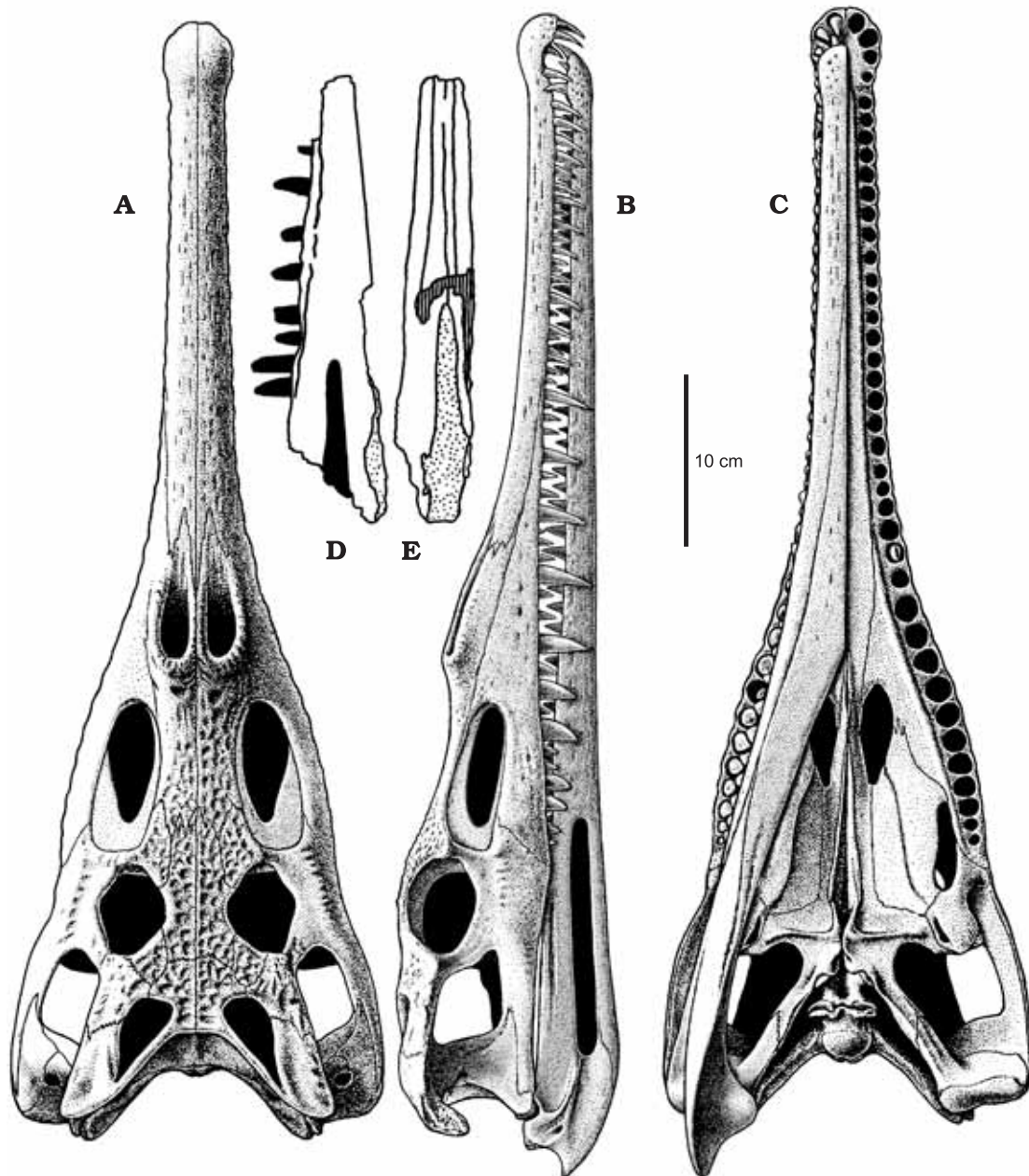


Fig. 10. Restoration of the skull of *Paleorhinus* cf. *arenaceus* (E. Fraas, 1896) (A–C) compared with the holotype of the species (D, E; after Hungerbühler 2001).

its incompleteness and poor state of preservation make it unclear if the type of “Z.” *arenaceus* represents the same species as the Krasiejów *Paleorhinus*. Because the Feuerbacher Heide Schilfsandstein and Krasiejów share species of *Metoposaurus*, it might be possible that they also share the same species of phytosaur. Until more data on the Schilfsandstein phytosaurs is available, we suggest that the name *Paleorhinus* cf. *arenaceus* (E. Fraas, 1896) is used for the Krasiejów material.

## LAND ORGANISMS OF KRASIEJÓW

The far-reaching adaptations to pelagic life of the two dominant inhabitants of the Krasiejów lake (unlike present-day river dolphins they were not ecological invaders from marine environments) make sense only if

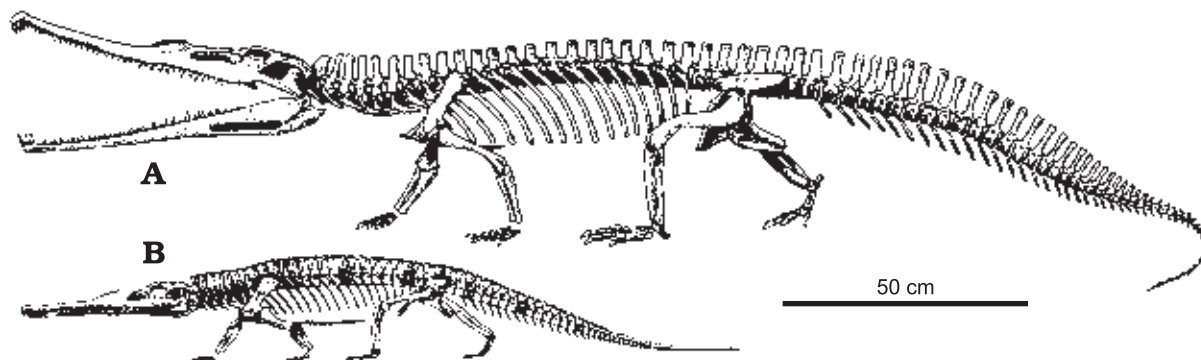


Fig. 11. Restoration of the skeleton of *Paleorhinus* cf. *arenaceus* (E. Fraas, 1896). A. Mature specimen (modified drawing of M. Lubka). B. Juvenile (after Dzik *et al.* 2000).

its waters extended far to the central parts of the Germanic Basin. How large the lake basin was has to be determined by revision of the subsurface data. In the quarry, the abundance of vertebrate fossils seems to increase northward and possibly the shore of the lake was not far to the south of the quarry. The fossil material transported to the lake by floods, streams, and rivers provides some hints regarding the composition of terrestrial biota near the slopes of the Variscan mountains of the Sudetes. The most numerous fossils of land tetrapods have been obtained from the upper fluvial horizon, but virtually all data on coeval flora and invertebrate fauna comes from the basal layer of the lacustrine bed.

## FLORA

Plant detritus is very common in patches of the gray clay near the base of the lacustrine bone-bearing horizon. Most of it is unidentifiable and these specimens are mostly rusty traces of decomposed lignite. However, some plant remains show relief and can be given a taxonomic assignment.

**Vascular plants.** — The most common identifiable plant remains at Krasiejów are seeds and cone scales of conifers (Fig. 12). They are invariably preserved as impressions stained with iron minerals. Rarely, small remnants of coalified wood can be found as compressed trunks under a calcite crust. The cones represent at least two distinct species but they are hard to match with associated leaves.

The most common cone scales are composed of five distal lobes and two wider lateral structures, sometimes showing a bulge on the adaxial surface (Fig. 12A). The plant is characterised by very peculiar female cones that are traditionally classified as *Glyptolepis keuperiana* Schimper, 1872 (Mägdefrau 1963), but the holotype of that species shows different scales, with eight uniform lobes and an obtuse apex on each scale (Axsmith and Taylor 1997). The cone scales with paired lateral structures are typical of the type species of *Pseudohirmerella* Arndt, 2002, *P. platysperma* (Mägdefrau, 1953) from the Stuttgart Formation (Schilfsandstein), but they are of much more robust appearance and are distinct at least at the species level. The bulges were first described as seeds, later were reinterpreted as arils by Arndt (2002). Axsmith *et al.* (2004) proposed that these are actually casts of empty, seed-bearing depressions.

Scales of *Pseudohirmerella* that are very similar to those from Krasiejów have already been reported from the Schilfsandstein of Baden-Württemberg (Mägdefrau 1963: pl. 4: 8; Kelber and Hansch 1995: fig. 221), *Semionotus* Sandstone of Franconia (Mägdefrau 1953: pl. 4: 4; this unit corresponds to the Stubensandstein) in Germany, and the Upper Stockton Formation of Pennsylvania (Axsmith and Taylor 1997). No species-rank name is available for the bearer of these scales and the Krasiejów *Pseudohirmerella* plant taxon awaits description.

Seeds similar in size to the depressions on the lateral bulges are abundant in the Krasiejów material. One could expect that the most common cone scales should match the most common co-occurring leaf-bearing twigs. If so, this conifer species had relatively long and narrow sharply pointed leaves. The shapes and sizes of the leaves display significant variation, which may represent growth series and/or intraspecific variability.



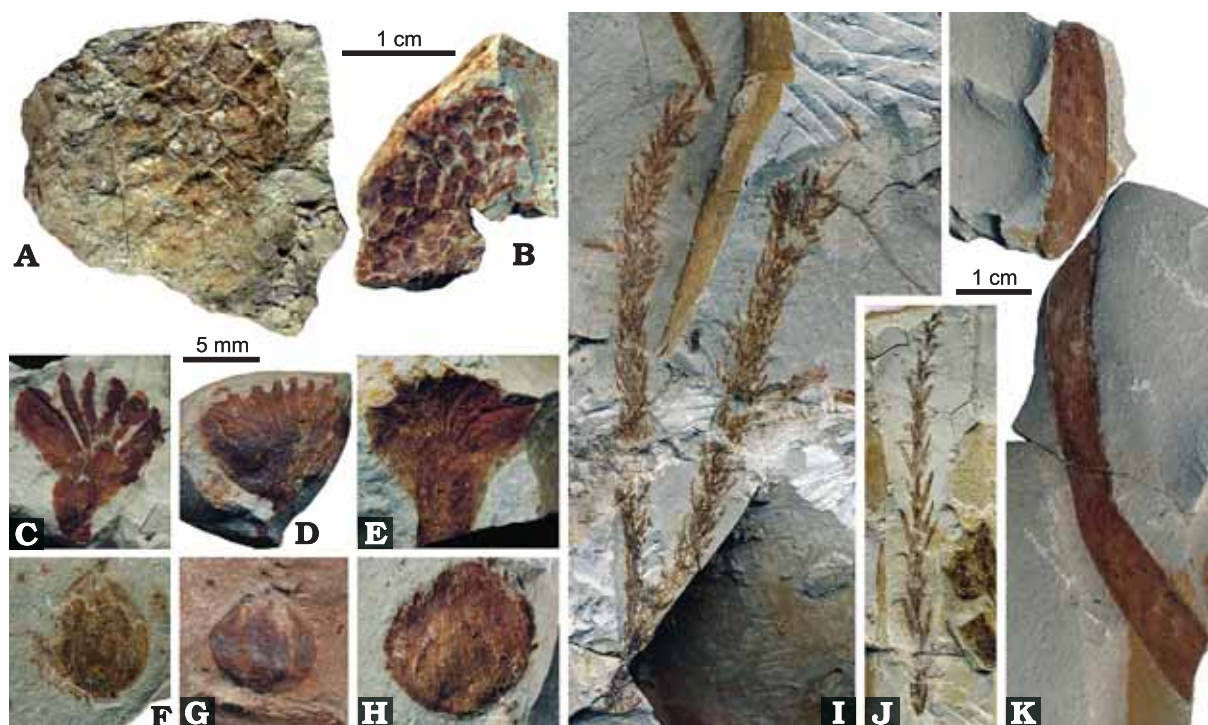


Fig. 12. Conifers from the basal layer of lacustrine horizon at Krasiejów. **A.** Seed cone of “*Pachylepis*” *quinquies* (Linck, 1951). **B.** Undetermined male? cone. **C–E.** Cone scales of *Pseudohirmerella* sp. n.; note imprint of a seed on D. **F–H.** Isolated large seeds. **I, J.** Old and early twigs probably belonging to *Pseudohirmerella* sp. n. **K.** “*Desmiophyllum*” leaf.

There seems to be no problem with the species name for the second conifer occurring in Krasiejów, which is known from articulated, although incomplete female cones with seeds. Scales of the cone are tightly disposed, and of rhombic shape. Each scale bears five seeds (Fig. 12C). This is the characteristic feature of “*Pachylepis*” *quinquies* (Linck, 1951), previously known from the Upper Gipskeuper and Schilfsandstein of Baden (Kräusel 1952). Unfortunately, the generic name is problematic. The name *Pachylepis* Kräusel, 1952 is preoccupied by *Pachylepis* Lessing, 1832 (subjective synonym of *Hieracium* Linné, 1753; Asteraceae) and *Pachylepis* Brongniart, 1833 (replaced with *Widdringtonia* Endlicher, 1842; Cupressaceae) so another name must be introduced for this genus of a Triassic conifer. An incomplete cone bearing smaller rhombic scales found in proximity may represent a male reproductive organ of this or other species. No leaves can be matched with these cones. There were only tape-like leaves lacking main nerve („*Desmiophyllum*” of Kelber and Hansch 1995) in the same place where the cones were found (Fig. 12E).

A small piece of a *Pterophyllum*-like cycad leaf has been found at Krasiejów (D. Zdebska, personal communication 2003).

## INVERTEBRATES

**Insects.** — Coleopteran elytra are rare in the plant detritus. Among a few specimens one is especially informative, showing prominent ornamentation with series of punctae along the wing. It is probably a cupedid, but only remotely similar forms have been described from the Late Triassic, and this specimen represents probably a new species (Fig. 13).

## AMPHIBIANS

Only one species of the Krasiejów amphibians was probably able to walk over the land (with some difficulty) and hunt terrestrial animals.

**Capitosaurs.** — Several complete or nearly complete skulls and numerous bones of *Cyclotosaurus* have been found in both the lacustrine and fluvial bone-bearing horizons at Krasiejów. The species they represent,

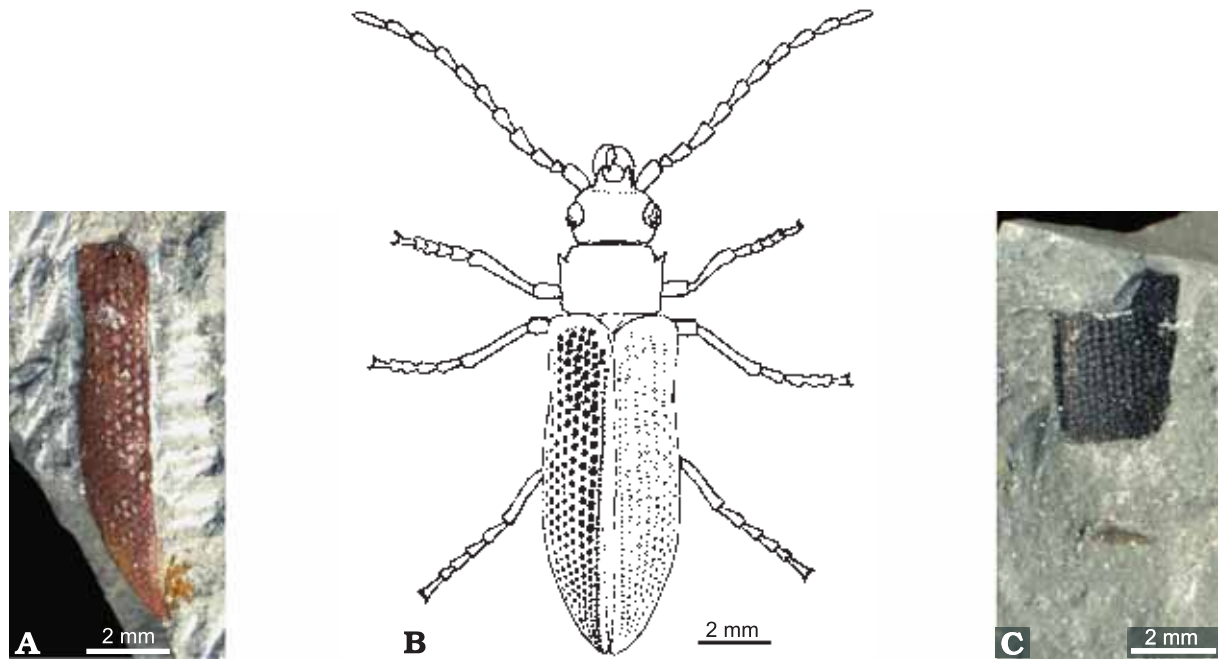


Fig. 13. Coleopterans from Krasiejów. **A, B.** A cupedid elytron, photograph and restoration fit in a contour of the insect. **C.** A finely pitted elytron.

*C. intermedius* Sulej *et* Majer, 2005 (Fig. 14), received its name because its skull proportions are intermediate between the older Schilfsandstein *C. robustus* Meyer *et* Plieninger, 1844 and geologically younger *C. mordax* Fraas, 1913 from the Stubensandstein of Baden-Württemberg (Sulej and Majer 2005).

The weak development of the lateral line furrows on the skull suggests that *Cyclotosaurus* lived partly on land. Its large teeth and overall body size, with a skull more than 0.5 m long, make it the largest predator of the Krasiejów fauna. It may have been an ecological analogue of present-day crocodiles.

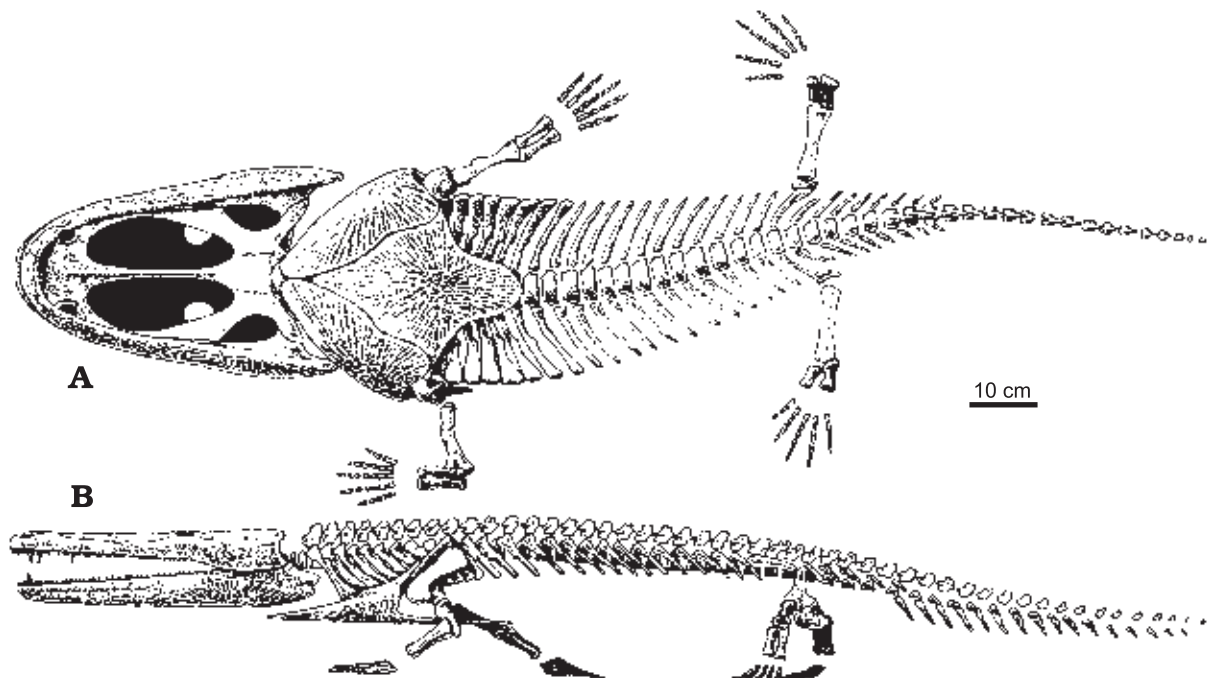


Fig. 14. Restoration of the skeleton of *Cyclotosaurus intermedius* Sulej *et* Majer, 2005 in ventral (**A**) and left lateral (**B**) views.

## REPTILES

Only a fraction of the diversity of terrestrial reptiles inhabiting the local Triassic landscape is probably documented with fossils at Krasiejów. Furthermore, not all of the existing fossils have been identified taxonomically. The Krasiejów community of terrestrial tetrapods is dominated by archosaurs but there is unpublished evidence that another community, with dicynodonts as its largest in size animals, lived in the same time in other places in the region.

**Sphenodonts.** — An almost complete dentary with teeth completely fused with the bone demonstrates presence of herbivorous squamates in Krasiejów (Fig. 15). The specimen awaits taxonomic study.

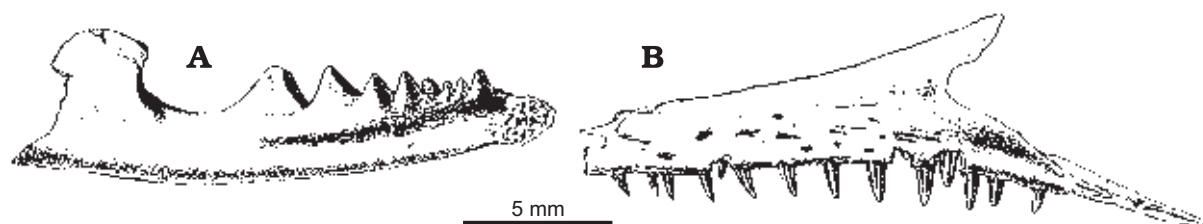


Fig. 15. Isolated jaw bones of small tetrapods from the lacustrine bone-bearing horizon at Krasiejów. **A.** A sphenodontian dentary. **B.** Maxilla of unidentified vertebrate.

**Pterosaurs(?).** — A single vertebra with extreme elongation similar to caudal vertebrae of pterosaurs (Dalla Vecchia 2001) or cervical vertebrae of *Tanystropheus* has been found (Fig. 9A). If it is *Tanystropheus*, the Krasiejów specimen represents the youngest occurrence of the lineage, elsewhere only known from marine strata.

**Aetosaurs.** — Virtually all regions of the skeleton are represented by several mostly disarticulated aetosaur skeletons from Krasiejów, with articulated regions in some specimens. Osteoderms are very similar in outline and ornamentation to those of *Stagonolepis robertsoni* Walker, 1961 from the Lossiemouth Sandstone, Scotland (Walker 1961). There are several differences in the skull; however, substantiating opinion of the junior author that they represent separate species (Fig. 16). The skull of the Krasiejów species is much larger than in *S. robertsoni*, with a smaller number of teeth and a different profile.

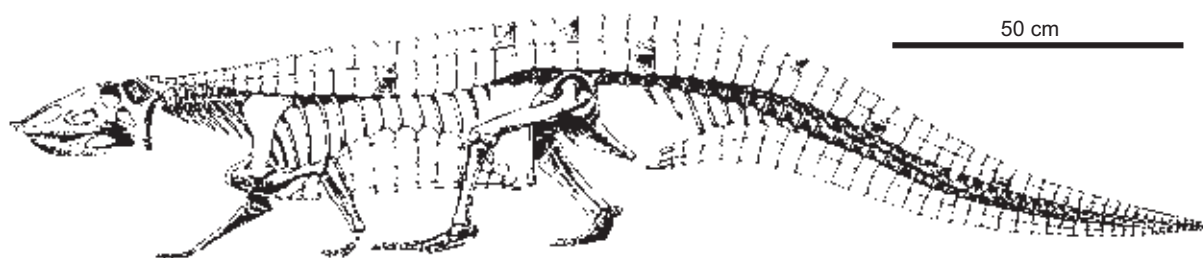


Fig. 16. Restoration of the skeleton of *Stagonolepis* sp. n. from Krasiejów in left lateral view.

The typical aetosaur adaptations believed to indicate herbivory are fully developed in this species but the teeth do not show any signs of occlusal wear. They are serrated, laterally compressed sidewise, and show constriction at the base of the crown. Apparently, the food of this early aetosaur was rather soft.

**Rauisuchians.** — Massive, serrated teeth of the Krasiejów rauisuchian are rarely recovered from either bone-bearing horizon but the most complete material comes from an isolated occurrence between them. Disarticulated bones of most of the skull, neck and part of the tail of the same specimen enabled partial restoration of the animal (Sulej 2005). It is quite similar to the slightly younger *Teratosaurus suevicus* von Meyer,

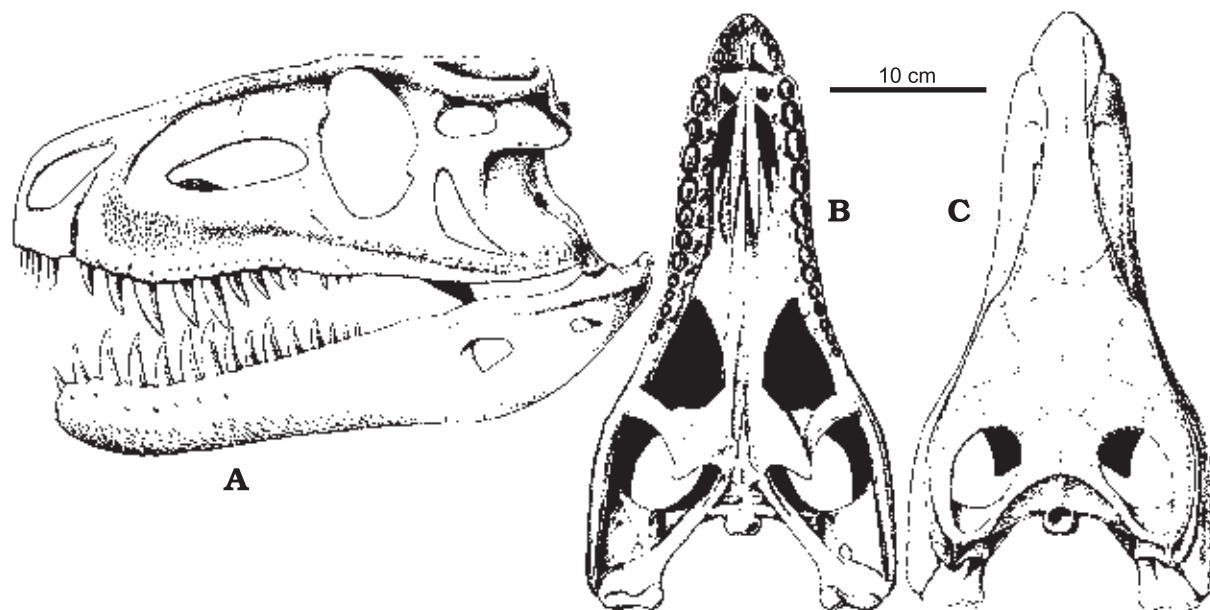


Fig. 17. Restoration of the skull of *Teratosaurus silesiacus* Sulej, 2005 from Krasiejów in left lateral (A), ventral (B), and dorsal (C) views (modified after Sulej 2005).

1861 from the Stubensandstein at Heslach, Württemberg, which is known from an isolated maxilla. The Krasiejów maxilla is different enough to substantiate separation at the species level as *Teratosaurus silesiacus* Sulej, 2005 (Fig. 17). The still younger *Postosuchus kirkpatricki* Chatterjee, 1985 from the Dockum Formation of Texas is more advanced in having massive skull with relatively narrow fenestra. The possible ancestor of the Krasiejów rauisuchian could have been geographically close *Batrachotomus kupperzellensis* Gower, 1999 from the Ladinian Lettenkohle of Baden-Württemberg. The whole Laurentian lineage evolved towards stronger construction of the skull roof; already in *Batrachotomus* the prefrontal is very large. At the same time, sides of the skull developed some mobility, being elastically connected with the robust skull roof. We speculate that this mobility is an adaptation to cutting flesh of armored aetosaurs, which enabled teeth to penetrate junctions between armor plates (Sulej 2003).

There is little doubt that additional archosaur species are represented by fossils from Krasiejów. Among them there is a long cervical vertebra of size comparable with that of *Teratosaurus* with the diapophyses and parapophyses located near the anterior end of the centrum and a few other vertebrae, all bearing a sharp medial rib along the ventral side of the centrum. This differentiates them from all other associated archosaurs.

**Dinosaurs.** — Probably the most characteristic member of the Krasiejów tetrapod fauna is its only member of the dinosaur lineage, *Silesaurus opolensis* Dzik, 2003. The phylogenetic position of this species is evidenced by the structure of its hind legs. The calcaneum and astragalus form a mesotarsal joint and are clear adaptation to fast bipedal running. Hind limbs of this kind are the first sign of being a member of the lineage leading to dinosaurs. The presence of a pyramidal ascending process of the astragalus makes *Silesaurus* more derived than the earliest known mesotarsal archosaurs from the Los Chañares assemblage (Ischichuca Formation) of Argentina (i.e., *Lagerpeton* and *Marasuchus*). *Silesaurus* was also advanced in the construction of its pelvis relative to other basal archosaurs. It has a relatively narrow pubis and vertically oriented ischia, the latter being an exclusive dinosaurian feature. Another feature of *Silesaurus*, placing it above the earliest mesotarsal archosaurs in the lineage leading to dinosaurs, is the buttressing of the diapophyses with vertebral laminae in its cervical vertebrae.

The lack of exclusively dinosaurian features did not convincingly placed *Silesaurus* within the Dinosauria when its preliminary description was prepared (Dzik 2003a). More material has since been collected (Fig. 18), and character evidence from the sacrum and skull is much more complete, enabling a more definite placement of the animal in the phylogenetic tree of dinosaurs. Additional preparation of one of the original

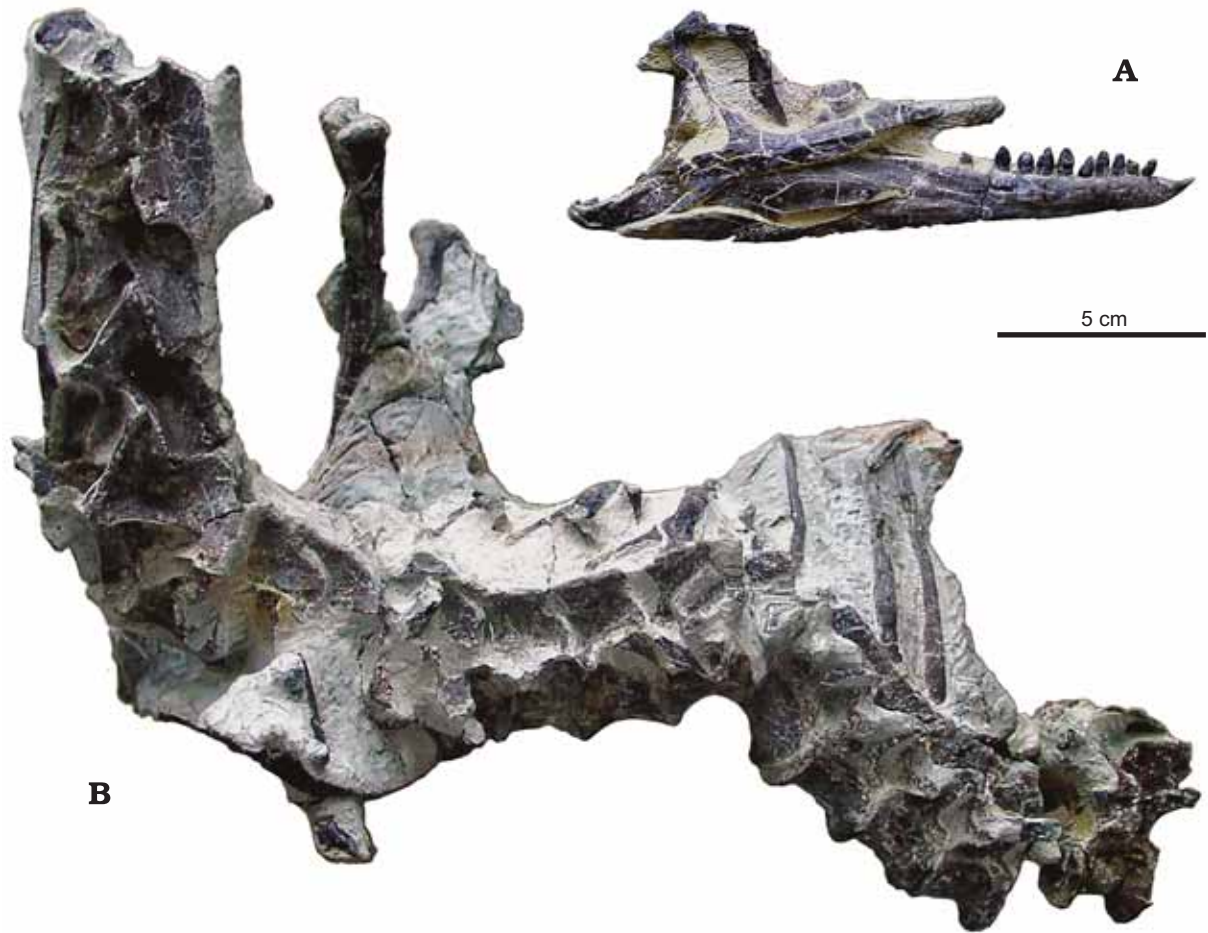


Fig. 18. Articulated partial skeleton of *Silesaurus opolensis* Dzik, 2003 from the lacustrine horizon at Krasiejów; skull (A) and neck with pectoral girdle (B).

articulated specimens revealed that the second sacral of *Silesaurus* has completely developed ribs. It appears thus to be on the dinosaurian level in the development of sacrum, with three sacrals firmly connected by their ribs with the ilium (Fig. 19). Although, sacrum composed of three vertebrae independently developed also in other archosaurs.

*Silesaurus* remains the only Carnian herbivorous mesotarsal archosaur with complete skeleton known. It is probable that it belongs to the ornithischian lineage, despite the plesiomorphic saurischian structure of its pelvis, preserved also in fragmentarily known and poorly preserved but definitely more advanced *Pisano-saurus* from the Ischigualasto Formation of Argentina (Irmis *et al.* 2007). The major ornithischian character of *Silesaurus* is a beak at the tip of mandible (Fig. 20). The symphysis does not show permanent junction of dentaries and they clearly had significant mobility, although their tip was apparently armed with horny cover. One might guess that in subsequent evolution a separate ossification (prementary) developed under the horny beak to stabilize its construction (Dzik 2003a; Ferigolo and Langer 2007). Obviously, until the gap in record between the Carnian *Silesaurus* and Jurassic *Lesothosaurus* is filled with data on reasonably complete skeletons of ornithischians, this interpretation must remain a hypothesis.

Because the Ischigualasto Formation is radiometrically dated at  $227.8 \pm 0.3$  Ma (Rodgers *et al.* 1993) and the Late Carnian strata in Italy biostratigraphically correlated with Krasiejów at  $230.91 \pm 0.33$  Ma (Furin *et al.* 2006), *Silesaurus* may appear to be the oldest known dinosaur in the world. Its relatives are also known from the Santa Maria Formation of Brazil (Ferigolo and Langer 2007), the Chinle Formation of New Mexico (Irmis *et al.* 2007), and possibly the Bull Canyon Formation of Texas (Nesbitt *et al.* 2007). This focuses more attention to the problem of the exact age of the Krasiejów material.

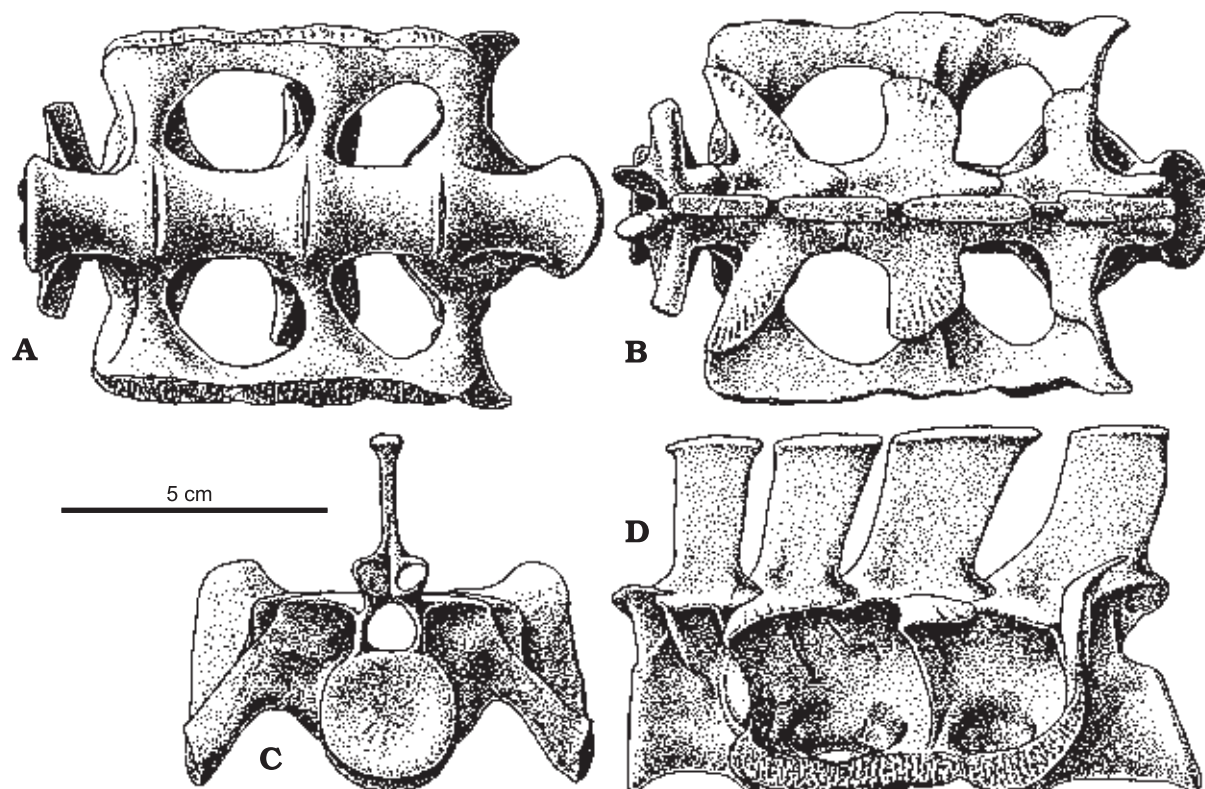


Fig. 19. Corrected restoration of the sacrum of *Silesaurus opolensis* Dzik, 2003 from Krasiejów in dorsal (A), ventral (B), anterior (C), and left lateral (D) views.

## GEOLOGICAL AGE OF THE KRASIEJÓW GRAVEYARD

The borehole Ozimek 1a, drilled 5 km west of Krasiejów and Lubliniec IG, and about 20 km northeast of it, enables to estimate the position of the fossiliferous strata with respect to the Schilfsandstein, the most characteristic lithologic unit of the lower Keuper in the area. In the Ozimek 1a core, the last gypsum inclusions in mudstone with numerous marly and calcareous intercalations continue to about 50 m above the 38 m thick Schilfsandstein unit (Kłapciński 1993). At Krasiejów, a shallow borehole shows that gypsum nodules and gypsum layers up to 3 cm occur about 20 m below the main bone-bearing horizon (Szulc 2005). Macroscopic crystals of celestite have been found at the bottom of the claypit, about 9 m below the fossiliferous horizon (Bzowska *et al.* 2004). One may thus conclude that there is evidence for playa (sabkha) conditions in proximity to the fossiliferous stratum.

The top of the gypsum-bearing unit was for a long time considered to be the lower boundary of the rather imprecisely defined “Rhaetian” (Bilan 1975) until Deczkowski *et al.* (1997), with some palynological support from borehole units well above the gypsum-bearing horizons, moved it to the beginning of Norian. This idea was supported recently by Szulc (2005), who identified the strata containing gypsum as the Weser Formation in eastern Germany, and those above as the Arnstadt Formation.

No palynological evidence is available for the Krasiejów section, and the subsurface rock units in western Poland probably corresponding to it are barren of pollen material (Orłowska-Zwolińska 1983). Only the available fossil evidence can thus be used to determine the age of the strata. The identity of the rock unit exposed at Krasiejów with the Arnstadt Formation can be immediately dismissed because of the conchostracan evidence. Olempska (2004) identified an abundant conchostracan fauna with *Laxitextella laxitexta* in the main fossiliferous horizon of Krasiejów. According to Bachmann and Kozur (2004: p. 49), this species occurs also in Germany in the Coburg Sandstone (Hassberge Formation), immediately above the Lehrberg

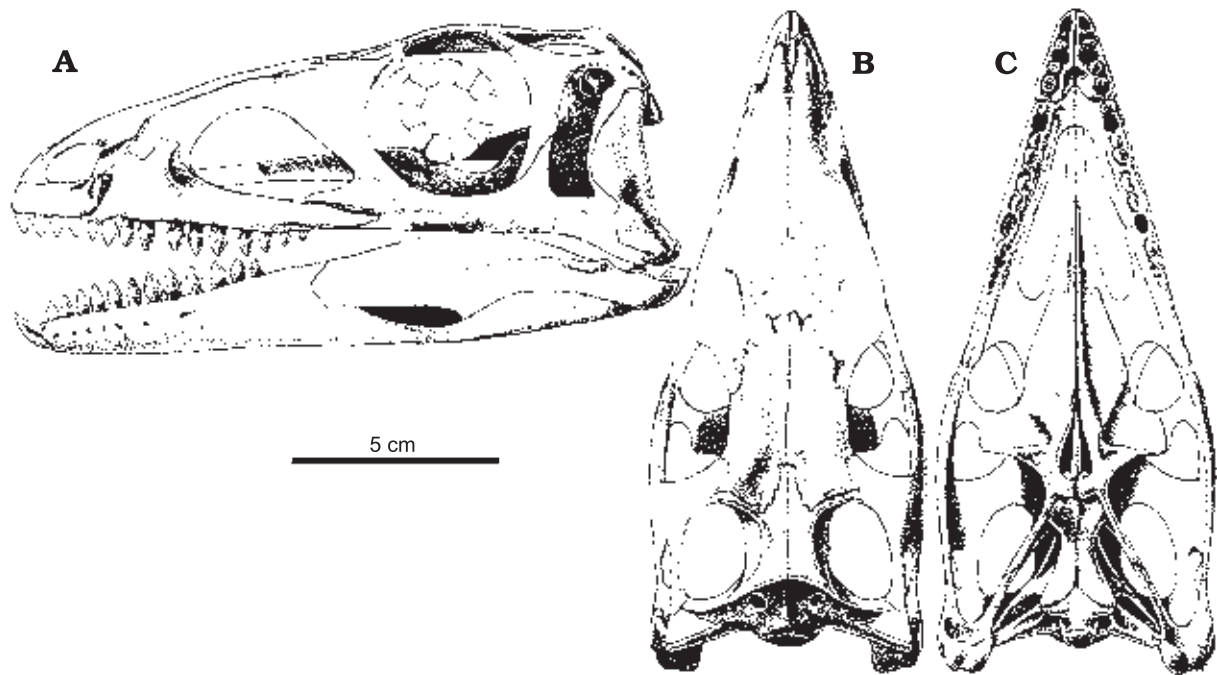


Fig. 20. Restoration of the skull of *Silesaurus opolensis* Dzik, 2003 from Krasiejów in dorsal (A) and left lateral (B) views.

Beds (Steigerwald Formation). The Coburg Sandstone is correlated with the middle part of the late Carnian (Tuvalian) Weser Formation (formerly Oberer Gipskeuper). According to Bachmann and Kozur (2004: p. 49), “there is a distinct change from the upper Carnian faunas with many strongly sculptured *Laxitextella* [...] to weakly sculptured lower Norian fauna of *Howellisaura* and *Eustheria*” (p. 29). In the Germanic Basin, these authors claim, there is a sedimentary hiatus between the Weser Formation and the Arnstadt Formation covering the whole early Norian.

The same age of the Krasiejów strata has been derived from the vertebrate evidence by Dzik *et al.* (2000; Dzik 2001). Hunt and Lucas (1991; Lucas 1998; Lucas *et al.* 2007) proposed that the co-occurrence of *Paleorhinus* with *Metoposaurus* was indicative of their *Paleorhinus* “biochron” (questioned by Lehman and Chatterjee 2005: p. 343). The oldest specifically identifiable German phytosaur, the long-snouted “*Ebrachosuchus*” *broili*, represented by several skulls (Kuhn 1933, 1936), comes from the Blasensandstein of Franconia. Notably, the Blasensandstein is correlated with the Coburg Sandstone by Bachmann and Kozur (2004).

It can thus be rather safely concluded that the Krasiejów fossiliferous strata are not younger than the Weser Formation, with the strongest affinity to the middle part of the unit, corresponding to the Coburg Sandstone and the Blasensandstein of Franconia.

This age determination is consistent with differences between the Krasiejów amphibians and those from apparently younger and older strata in Germany. Thus, *Cyclotosaurus intermedius* is clearly intermediate between its relatives from Schilfsandstein (Carnian Weser Formation) and Stubensandstein (Norian Arnstadt Formation). Some uncertainty remains regarding its relationship to *Cyclotosaurus ebrachensis* Kuhn, 1932 from the Blasensandstein of Franconia. This unit is similar to Krasiejów in the occurrence of *Paleorhinus* phytosaurs, but not metoposaurs. The *C. ebrachensis* specimen, suggested by Schoch and Milner (2000) to be conspecific with the Stubensandstein *C. mordax*, is much smaller in size than *C. intermedius* and the anatomical differences between them may be partially due to allometry (Sulej and Majer 2005).

Probably the most precisely known evolutionary lineage for dating the Krasiejów strata is offered by the metoposaurs. As interpreted by Milner and Schoch (2004), in Germany, *Metoposaurus diagnosticus diagnosticus* ranges from its type horizon Schilfsandstein to the upper part of the Lehrberg Beds. Its upper limit was determined on the basis of a single skull found immediately above the third Lehrbergbank.

*Metoposaurus diagnosticus krasiejowensis* ranges from the Kieselsandstein to the Middle Stubensandstein. If the Lehrbergbank specimen represents the modal value of morphologic variability of its population and the subspecies of *Metoposaurus* are temporal (chronosubspecies), the Krasiejów lacustrine horizon is not older than the Kieselsandstein. If it represents extreme morphology of its population or we are dealing with geographic races, the original dating of the Krasiejów fauna as coeval with the Lehrberg beds remains valid (Sulej this volume).

The only basis for correlation between continents and with marine strata is offered by phytosaurs from Krasiejów. They belong to a species of *Paleorhinus*, geologically the oldest and anatomically the least derived of phytosaurs, with nostrils located significantly in front to the orbits (Buffetaut 1993; Long and Murry 1995). *Paleorhinus* is known from the Colorado City Member of the Dockum Group and Camp Spring Member of the Tecovas Formation of Texas, Popo Agie Formation of Wyoming, Mesa Redondo Member of the Chinle Formation of Arizona, Pekin Formation (Newark Supergroup) of Pennsylvania, Irohalene Member of the Timesgadiouine Formation (Argana Group) of Morocco, the Blasensandstein in Germany, and the Maleri Formation of India (Lucas 1998). In many places, the more advanced phytosaur *Rutiodon* succeeded *Paleorhinus* in younger strata.

The most important record is the discovery of a species-indeterminate fragment of *Paleorhinus* skull in marine strata of Late Carnian age in the Alps (Huene 1939). In marine strata of Norian age, more derived phytosaurs occur (Renesto and Paganoni 1998; Renesto and Lombardo 1999; Gozzi and Renesto 2003). The snout in the Krasiejów species is relatively short, shorter than all known phytosaurs except for *Paleorhinus sawini* from Texas (Long and Murry 1995). The degree of the snout elongation in *Paleorhinus* is believed to express an evolutionary advancement of particular species (e.g., Gregory 1969; Gregory and Westphal 1969; Chatterjee 1978).

The idea that the very presence of *Paleorhinus* allows precise determination of the age of strata containing it has a fundamental weakness: neither the origin of the lineage nor its subsequent evolution is known. We do not know for how long the anatomical features of the genus existed and how they changed in the course of evolution. One might guess that the evolutionary roots of phytosaurs are in the Proterochampsidae, close to *Chanaresuchus* from the Ischichuca Formation of the province Rioja in Argentina. It shows signs of translocation of nostrils towards orbits. Its age is probably Ladinian, much earlier than the Krasiejów fauna. The co-occurrence of *Metoposaurus* or *Stagonolepis* does not help, because there are the same problems with the knowledge of their evolution. Actually, despite the claims of Hunt and Lucas (1991; Lucas 1998; Lucas *et al.* 2007) all three lineages differ in their stratigraphic ranges, and there is no reason to expect that they should have the same ranges.

The conclusion from the biostratigraphic and evolutionary evidence for the Krasiejów assemblage leaves thus no doubt that it is roughly coeval with the Weser Formation in Germany, and probably of Carnian age. Until more data is available on the evolution of tetrapods occurring at Krasiejów, the only possibility to improve dating precision is to identify possible short range environmental changes at Krasiejów of correlative value with the Germanic basin. We originally assumed (Dzik *et al.* 2001) that the lake sedimentation episode within the fluvial sequence exposed at Krasiejów is an expression of a more extensive, rising erosional base level event within the Germanic Basin. A similar event is recognizable within the Weser Formation as the Lehrberg Beds. They are interpreted as the termination of the cycle of rising sea level that began after the sedimentation of the Schilfsandstein (Aigner and Bachman 1998; Bachmann and Kozur 2004). The Schilfsandstein of the Germanic Basin is believed to be coeval to the Austrian Lunz Formation, both are an expression of a worldwide late Early Carnian (Julian) pluvial event (Hornung *et al.* 2007).

The only evidence, that may contradict this correlation and age, is the identification of *Metoposaurus diagnosticus diagnosticus* in the Lehrberg beds by Milner and Schoch (2004). If our explanation of this disparity with earlier proposed interpretation of the evolution of *Metoposaurus* lineage is not correct, the Krasiejów strata could be coeval to the topmost units of the Weser Formation (e.g., Coburg Sandstone). The Germanic Basin Late Carnian (Tuvalian) evaporates (Oberer Gipskeuper) are thought to result from a temperature rise and may correspond to the Austrian Opponitz Formation (Hornung *et al.* 2006), where the *Paleorhinus* skull was found. Recently obtained radiometric Pb<sup>206</sup>/U<sup>238</sup> dating of a Late Carnian volcanic ash from Italy date it at 230.91 ± 0.33 Ma (Furin *et al.* 2006). Thus, this is an approximate absolute age of the Krasiejów biota.



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