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A NEW RAUISUCHIAN REPTILE (DIAPSIDA: ARCHOSAURIA) FROM THE LATE TRIASSIC OF POLAND

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ABSTRACT—A crushed rauisuchian skull and several vertebrae belonging to a single individual have been found in the Upper Triassic strata at Krasiejów, Poland, probably corresponding in age to the Lehrberg Beds (late Carnian) of Baden-Württemberg, Germany. A maxilla of *Teratosaurus suevicus* from the early Norian (Stubensandstein at Heslach) is similar to that of the Krasiejów specimen. The dorsal process of the maxilla is more oblique than in *T. suevicus*, the medial anterior foramen is set on the medial side, contrary to being exposed anteriorly in *T. suevicus*, and foramina for replacement teeth are not connected by a dental groove and are set in straight line. A new species of *Teratosaurus* is proposed to accommodate the Polish material, and a more complete diagnosis of the genus is presented.

INTRODUCTION

Rauisuchians were the largest terrestrial carnivores during the Middle and Late Triassic, recorded so far from Africa, Asia, Europe, and North and South America (e.g., Gower, 2000). Some early forms possibly occur in the Early Triassic of Russia (Sennikov, 1995; Gower and Sennikow, 2000). Despite their importance, rauisuchians are poorly understood and much work remains to be done on their morphology and systematics (Gower, 2000). The only Late Triassic European rauisuchian known well enough to substantiate its taxonomic distribution is *Teratosaurus suevicus* Meyer, 1861, from the Stubensandstein of northern Württemberg (Long and Murry, 1995). The species and genus were originally based on a right maxilla. Galton (1985) referred an ilium from the same stratum, earlier described as belonging to *Phytosaurus kapffi* Meyer, 1861, to *Teratosaurus suevicus*. In 2000, during excavations organized by the Institute of Paleobiology, Polish Academy of Sciences, at the Krasiejów locality in the Opole Silesia (Dzik et al., 2000), two students, Michal Ploch and Magdalena Knap, found a small accumulation of rauisuchian bones that are the focus of this paper.

In Krasiejów, fossils occur mainly in two horizons that have yielded fossil assemblages virtually identical in species composition but basically different in their relative proportions of specimen numbers. In the lower lacustrine horizon, bones of the metoposaurid amphibian *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002a, and the phytosaur *Paleorhinus* cf. *arenaceus* Fraas, 1896 (Dzik et al., 2000), predominate. A new species of the aetosaur *Stagonolepis* (Dzik, 2001) and a new species of *Cyclotosaurus* (Sulej and Majer, 2005) are the second most abundant forms. In the upper deltaic horizon, the fossil assemblage is dominated by the aetosaur *Stagonolepis* and a dinosauromorph (Dzik, 2003). The accumulation of rauisuchian bones was found between the two main horizons, although a single tooth was found also in the upper horizon. Bones of the dinosauromorph also occur among the accumulation of the rauisuchian bones. The purpose of this paper is to describe the morphology and present a restoration of the skull of the new taxon from Krasiejów, and to interpret its systematic affiliation.

Institutional Abbreviations—BMNH, Natural History Museum, London; **TTUP**, Texas Tech University, Lubbock; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw; **ISI**, Indian Statistical Institute, Calcutta.

Anatomical Abbreviations—apmx, articulation for premaxilla; **aec**, articulation for ectopterygoid; **aj**, articulation for jugal; **aq**, articulation for quadrate; **dg**, dental grove; **dp**, descending process of nasal; **f**, medial anterior foramen; **fct**, foramen for chorda tymmpani; **fo**, lateral anterior foramen; **hs**, horizontal shelf; **htf**, additional lower temporal fenestra; **j**, jugal; **l**, lacrimal; **m**, maxilla; **msf**, median symphyseal facet; **n**, nasal; **q**, quadrate; **qf**, quadrate foramen, **qj**, quadratojugal; **p**, palatal process; **pl**, palatine; **pm**, premaxilla; **pp**, posterodorsal process of premaxilla; **prf**, prefrontal; **pt**, pterygoid; **s**, foramina for replacement teeth; **san**, angular; **sq**, squamosal; **vew**, vertical wall.

SYSTEMATIC PALEONTOLOGY

As discussed below, the maxilla of the Krasiejów specimen differs only slightly from the holotype of *Teratosaurus suevicus*. Although the available evidence on the German species is very limited, it is likely that both findings, close to each other both in time and geographic space, belong to the same local lineage. Therefore, they are classified in the same genus and the new data from Krasiejów it is used to amend its diagnosis. The suprageneric taxonomy of rauisuchians is confused (Gower, 2000) and their overall monophyly is in doubt (e.g., Parrish, 1993). For the purposes of this paper, three families are recognized—Rauisuchidae, Poposauridae, and Chatterjeeidae. Some authors (e.g., Parrish. 1993) further separate rauisuchids in this concept into Rauisuchidae and Prestosuchidae. It is beyond the scope of this paper to reassess the phylogeny of rauisuchians, and the features understood to diagnose these families are necessarily a mix of probable plesiomorphies and synapomorphies.

ARCHOSAURIA Cope, 1869
RAUISUCHIA Huene, 1942
Family RAUISUCHIDAE Huene, 1942

The following characters indicate that *Teratosaurus* belongs to the Rauisuchia (Chatterjee and Majumdar, 1987): skull large, tall, with antorbital and accessory subnarial fenestrae; antorbital fossa strongly recessed; teeth robust, recurved, laterally compressed with serrated edges; lack of palatal dentition; ilium with supra-acetabular rugose ridge(s).

Teratosaurus is placed in the family Rauisuchidae on the basis of the following characters: cervical centra short and high, similar to *Postosuchus* Chatterjee, 1985, *Tikisuchus*, Chatterjee and Majumdar, 1987, and *Fasolasuchus* Bonaparte, 1981, and in contrast to the relatively longer cervicals of the poposaurid *Poposaurus* Mehl, 1915, and the chatterjeeid *Chatterjeea* Long and Murry, 1995. Further differences from poposaurids and chatterjeeids include a supra-acetabular rugosity that lacks associated accessory ridges and an ilium with a small, narrow anterior blade which does not extend beyond the pubic process.

Genus *TERATOSAURUS* Meyer, 1861

Diagnosis—A rauisuchian with subdivided lower temporal fenestra, and a small and dorsally angulated premaxilla. The long descending process of the nasal is inserted between the posterior process of the premaxilla and the dorsal process of the maxilla, which does not contribute to the naris. In lateral view, the nasal is arched anteriorly and straight posteriorly. The naris is a little smaller than the anteriorly tapered antorbital fenestra. The maxilla has 13 maxillary alveoli. Its palatal process is large. The suture between the maxilla and lacrimal is V-shaped. The prefrontals form a "brow," without a notch in the edge of the skull roof. Two paramedial rows of caudal scutes are present.

Remarks—*Teratosaurus* shares with *Postosuchus* and *Tikisuchus* (pers. obs.) a uniquely derived additional lower temporal foramen (relatively the largest in *Teratosaurus*) situated below the upper temporal fenestra, and a corresponding pattern of the temporal region. It differs from *Postosuchus* in the relatively smaller and dorsally angulated premaxilla. The descending process of the nasal is longer than in *Postosuchus* because it is inserted between the posterior process of the premaxilla and the dorsal process of the maxilla. In lateral view, the nasal is arched anteriorly and straight posteriorly, contrary to the posteromedially depressed form in *Batrachotomus*. The naris is a little smaller than the anteriorly tapered antorbital fenestra; it is relatively smaller than in *Batrachotomus* and larger than in *Postosuchus*. The maxilla has a large palatal process, unlike *Postosuchus*, and the dorsal process does not contribute to the naris, in contrast to *Batrachotomus*. The suture between the maxilla and lacrimal is V-shaped unlike the condition in other rauisuchids. The prefrontals and squamosals form a lateral rugose ridge on each side of dermatocranium. The prefrontals form a "brow" above the orbits as in *Postosuchus*, with both genera lacking any notch in the edge of the skull roof above the orbits. *Teratosaurus* and *Postosuchus* have 13 maxillary alveoli, more than the 11 alveoli in *Tikisuchus*. Two paramedial rows of caudal scutes are present as in other rauisuchians (where known) except *Saurosuchus* and *Fasolasuchus*, which have a single row of caudal scutes.

TERATOSAURUS SILESIACUS *sp. nov.*

Type Locality—Krasiejów, Opole Silesia, Poland.

Type Horizon—Late Carnian, probably Drawno Beds coeval to the Lehrberg Beds of Germany.

Etymology—Name refers to the region Opole Silesia, from which it comes.

Holotype—ZPAL Ab III 563: right and left maxilla, premaxillae, nasals, prefrontals, palatines, quadrates, and fragments of dentary; left jugal; right lacrimal, quadratojugal, squamosum, pterygoid, surangular and articular; fragment of atlas articulated with axis and third cervical vertebra, twelve articulated caudal vertebrae, five caudal scutes, and pieces of cervical ribs (Figs. 1–4). The specimen is held in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Diagnosis—A *Teratosaurus* with the 'medial anterior foramen' of the maxilla located on its medial surface. The dorsal process of the maxilla is strongly oblique. The foramina for replacement teeth are not connected together by a dental groove, and are set in straight line.

Remarks—The maxilla of *Teratosaurus silesiacus* differs from that of *Teratosaurus suevicus*, in that the medial anterior foramen located under the palatal process is visible only in medioventral view, whereas it is exposed anteriorly in *T. suevicus*. The dorsal process is more oblique than in *T. suevicus*. The foramina for replacement teeth are not connected together by a dental groove as in *T. suevicus*. These foramina are set in a straight line, whereas in *T. suevicus* this line is curved anteriorly.

DESCRIPTION

Skull

The disarticulated bones of the skull fit each other in size and it is assumed they belonged to the same individual. The skull reconstructions presented in Figure 3 have been assembled from the available bones.

Maxilla—Both maxillae are preserved. The left maxilla is more complete, although the posterior part is broken (Fig. 1 A, D). The main body is tall, laterally compressed and the ventral margin, as seen in lateral view, is convex. The maxilla forms most of the border to the antorbital fenestra, and holds a large proportion of the surrounding antorbital fossa.

The maxilla has a complete palatal process (anteromedial process of Galton, 1985), which is directed anteroventrally and protrudes only slightly in front of the anterior edge of maxilla. It is dorsoventrally compressed, short, and tapers anteriorly. Its medial facet has a groove in its anterior part and a ridge in its posterior part; the ventral facet has a shallow depression.

The left maxilla has an almost complete dorsal process. Although the edge of the surface that articulates with the lacrimal is damaged, it seems that the suture was a posteriorly open V-shape.

The medial anterior foramen as defined in *Teratosaurus suevicus* by Galton (1985:fig 1E, marked as f; Fig. 4A, B, D herein) opens under the palatal process and is directed ventromedially. The smaller lateral anterior foramen of Galton (1985:fig 1E, marked as fo; Fig. 4A, B, C herein) is on the anterior surface of maxilla in the Krasiejów specimen. Ventral to this foramen, the anterior surface of the maxilla is concave, obliquely inclined and slightly overlaps the adjacent surface of the premaxilla to form a small subnarial fenestra.

On the medial side of the maxilla, a facet for articulation with the palatine is preserved as a ridge and an associated slight depression that is in front of and below the ridge. The ridge extends to above alveoli 6, 7, 8, and the depression above alveolus 5.

Infraorbital foramina (Galton, 1985) are visible above alveoli 5 and 6, close to the border of the antorbital foramen. Two foramina are located above alveoli 8 and 9.

Ten complete alveoli and a partial eleventh alveolus are preserved in the left maxilla. Eleven alveoli are preserved in the right maxilla. Since the posterior borders of both maxillae are broken, it seems that the maxilla had more than 11 alveoli. Small replacement teeth are visible through the foramina above the alveoli. These foramina are not connected by a groove. In the left maxilla, small replacement teeth are visible in the foramina above alveoli 1–3, 5–7, and 9.

Premaxilla—The median symphyseal facet of the premaxilla is triangular and smooth; it is very similar to that in *Postosuchus kirkpatricki* (Chatterjee, 1985). The ventral edge of the symphysis rises posteriorly. The posterodorsal process of the premaxilla is incomplete in both specimens. However, the facet for articulation with this process is visible on the descending process of the nasal (Fig. 1E), and the posterodorsal process of the premaxilla probably extended up to the most posterior edge of the naris (Fig. 1H). The posterolateral articulation of the premaxilla with the maxilla is loose. The palatal processes are incompletely preserved in both specimens. The medial facet of the palatal process of the left maxilla has a groove that probably articulated with the palatal process of the premaxilla. The left premaxilla has four alveoli. Four unquestionable alveoli are clearly observed in the right premaxilla and a small cavity at its posterior edge may represent a fifth alveolus.

Nasal—The left nasal has a dorsoventrally compressed descending process (Fig. 1E) that inserted between the maxilla and

FIGURE 1. *Teratosaurus silesiacus* sp. nov. ZPAL Ab III 563. Left maxilla in lateral (**A**) and medial (**D**) views. Right lacrimal in medial (**B**) and lateral (**C**) views. Left nasal in lateral (**E**) and medial (**J**) views. Right nasal in dorsal view (**G**). Premaxilla in medial view (**F**) and lateral (**H**) views. Caudal vertebrae in lateral view (**K**).

the posterodorsal process of the premaxilla. Anteriorly, the nasal possesses a long process, triangular in cross-section that is oriented almost vertically at the anterior end. The facet for articulation with the anterodorsal process of the premaxilla is well preserved (Fig. 1J). The right nasal has its posterior part preserved; the surface for articulation with the lacrimal is partially visible.

Lacrimal—The right lacrimal is almost complete. Dorsolaterally, there is a thickened, rugose ridge that extends back from that on the nasal (Fig. 1B, C). The area for articulation with the nasal is wide and concave. The flat lateral surface of the lamellar part of the lacrimal forms the posterodorsal part of the antorbital fossa. The anterior edge of this area is slightly convex in lateral view. It formed a probably slightly overlapping articulation with the dorsal process of the maxilla.

The posterior border of the antorbital fossa is formed by a ridge that extends along the length of the descending ramus of the lacrimal. This ridge bears distinct striae aligned with its long axis. The lower part of the ridge forms a conspicuous surface, probably for articulation with the jugal.

Prefrontal—The right and left prefrontals are preserved. The prefrontal (Fig. 4E, F) is a large triangular plate forming a ledge overhanging the orbit. Its lateral edge is rugose. Each example has traces of the surfaces for articulation with the lacrimal (anteromedially), frontal (medially) probably postfrontal (posteriorly), and postorbital (posteriorly). All surfaces with articulation with the bones of skull roof are similar. They are slightly oblique and rather narrow.

Squamosal—The right squamosal is a complex bone with five projections (Fig. 4G). Two projections on the dorsal surface bordered the upper temporal fenestra and articulated with the parietal and the postorbital. The lateral margin of the upper temporal fenestra formed a rugose ridge, which probably continued back from that on the prefrontal. Under the dorsal projections, there is a hook-like ventral projection, which has a cotyle for the reception of the quadrate head. The ventrolateral projection is

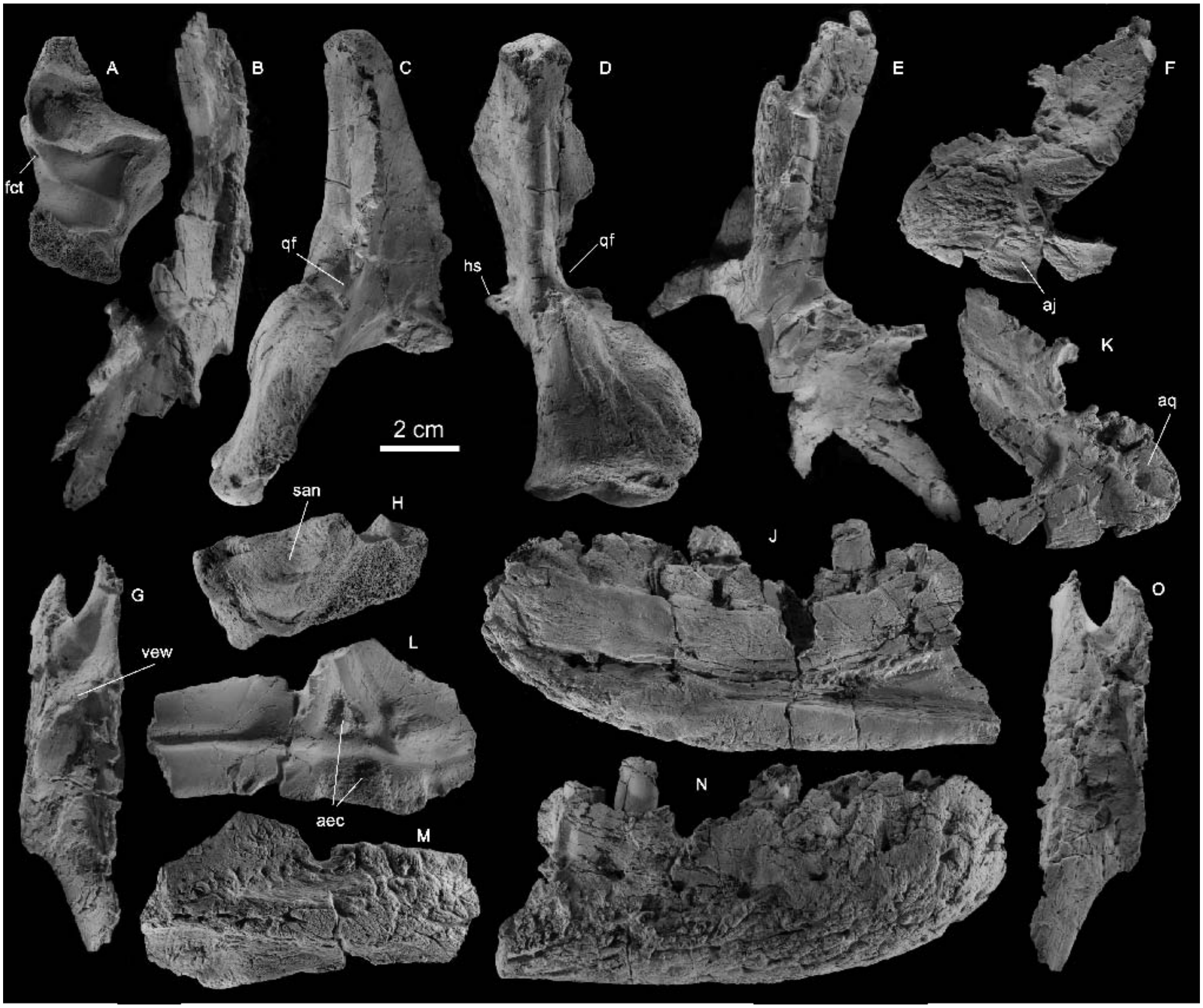

FIGURE 2. *Teratosaurus silesiacus* sp. nov. ZPAL Ab III 563. Right articular articulated with fragmnt of surangular in dorsal (**A**) and lateral (**H**) views. Right pterygoid in ventral (**B**) and dorsolateral (**E**) views. Right quadrate in lateral (**C**) and posterior (**D**) views. Right quadratojugal in lateral (**F**) and medial (**K**) views. Left palatine in dorsal (**G**) and ventral (**O**) views. Right dentary in medial (**J**) and lateral (**N**) views. Left jugal in ventral (**L**) and lateral (**M**) views.

broken. Above it, a strong lateral projection forms an almost vertical wall, which probably overhangs the quadratojugal. The posterodorsal, posterior, and ventral edge of the additional lower temporal fenestra is clearly visible. Overall, the squamosal is like that of *Postosuchus kirkpatricki* (Chatterjee, 1985) and *Tikisuchus romeri* (pers. obs. of ISI R 305).

Jugal—The main body of the left jugal is preserved. The posterior process has fairly straight dorsal and ventral margins (Fig. 2L, M). In transverse section, the posterior process is medially concave and laterally convex. Although it is incomplete, knowledge of its extent comes from the lateral surface of the quadratojugal, by which it was overlapped laterally.

The anterior and ascending processes are broken. In transverse section, the ascending process is triangular at its base. Its medial surface bears a distinctive ridge, at the end of which there is a surface for articulation with the ectopterygoid. A fragment of the anterior process of the jugal is preserved in contact with the left maxilla.

Quadratojugal—A fragment of the right quadratojugal is preserved (Fig. 2F, K). The lower part of the ascending ramus has a broken dorsal edge. The ventral edge forms the posterodorsal corner of the lower temporal fenestra. The fossa for articulation with the quadrate is visible on the medial face of the element. The articular surface for the jugal is long and strongly indented.

Palatine—The palatine of *Teratosaurus silesiacus* is known from almost complete left and fragmentry right bone. The anterior of the element is more robust than the posterior (Fig. 2G, O). The region between the choana and suborbital fenestra is long relative to the length of the palatine. The lateral edge forms an expanded facet for articulation with a low ridge on the medial surface of the maxilla. The posteromedial border of the choana is thickened. The dorsal surface of the palatine bears an oblique and vertical wall, which separates the nasal and muscular fossa (Witmer 1997). The ventral surface bears two ridges, which cross each other and they run diagonally. The medial edge forms a fold

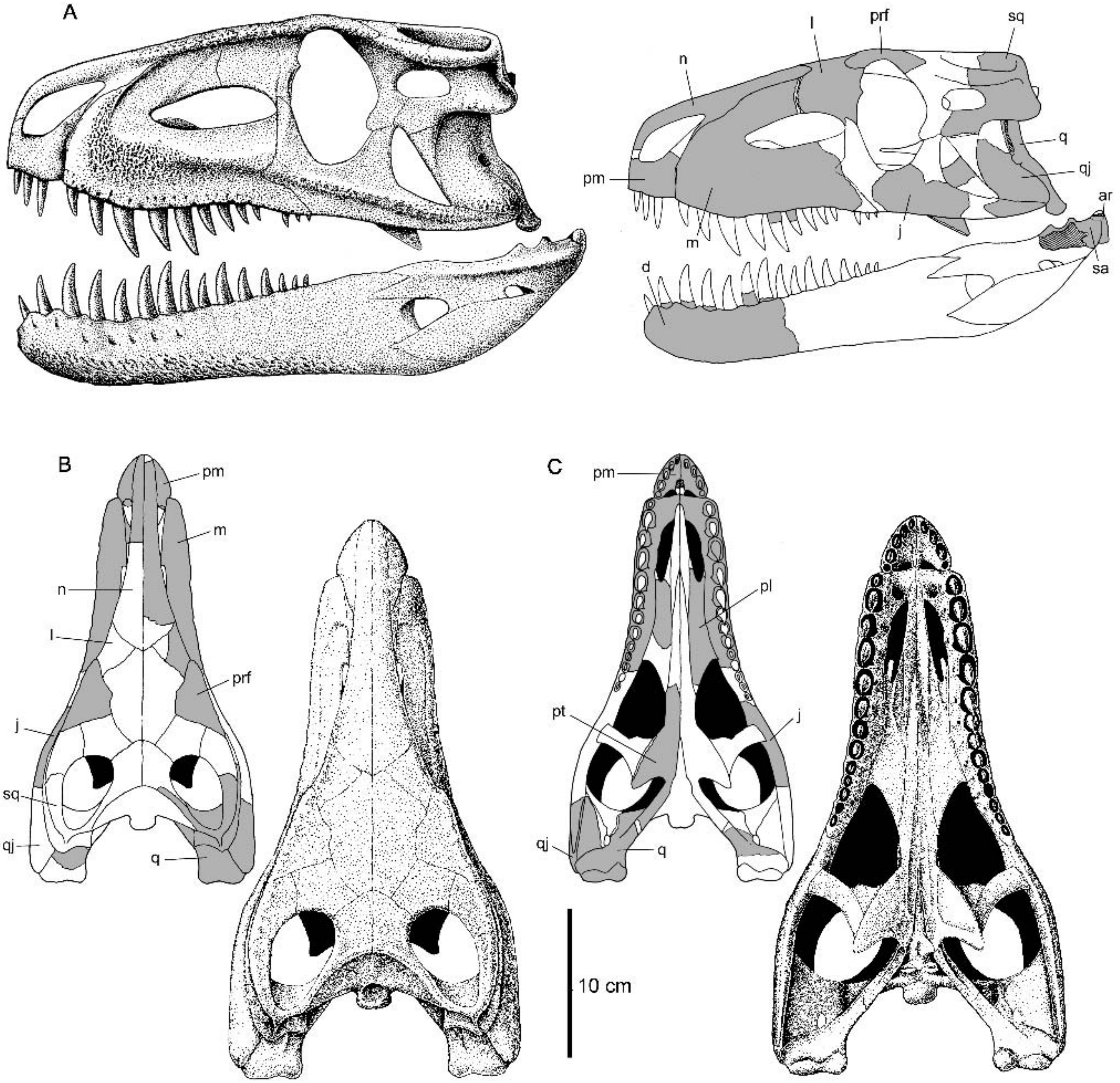

FIGURE 3. *Teratosaurus silesiacus* sp. nov. Reconstruction of the skull and mandible in lateral (**A**), dorsal (**B**) and ventral (**C**) views. Preserved bones are gray on the smaller drawings.

that probably forms part of the articulation with the pterygoid and vomer.

Pterygoid—The right pterygoid is preserved, though the anterior ramus is broken (Fig. 2B, E). The lateral edge of the posteroventral ramus of the pterygoid is mostly damaged, although its central part is preserved and exhibits a cleft for the ectopterygoid. The posterior edge of this ramus is strongly thickened. The quadrate ramus is strongly expanded. Its ventral edge is curved posteriorly and forms a narrow shelf.

The articulation with the basipterygoid process of the basisphenoid is similar to that of many Triassic archosaurs. It consists of a simple facet on the medial wall of the base of the quadrate ramus, and an opposing medial projection that hooks around onto the medial surface of the basipterygoid process.

Quadrate—The morphology of the quadrate is known from the essentially complete right and fragmentary left elements. A rounded dorsal head fits into a cotyle on the squamosal. A strong posterior ridge extends along the main axis of the quadrate (Fig. 2C, D). Lateral to this lies a thin, narrow wing that contacts the posterior edge of the descending ramus of the squamosal. Anteromedial to the posterior ridge lies the high, wide and thin pterygoid ramus. Its ventral edge bears a narrow, medially directed shelf. Below the lateral wing, the edge of a large quadrate foramen is visible. Above the condyle for the mandible, the posterolateral edge of the quadrate bears a well-defined facet for articulation with the medial edge of the quadratojugal. The condyle is divided into two parts. A shallow but well-defined groove is seen on the posterior surface of the distal end of the quadrate,

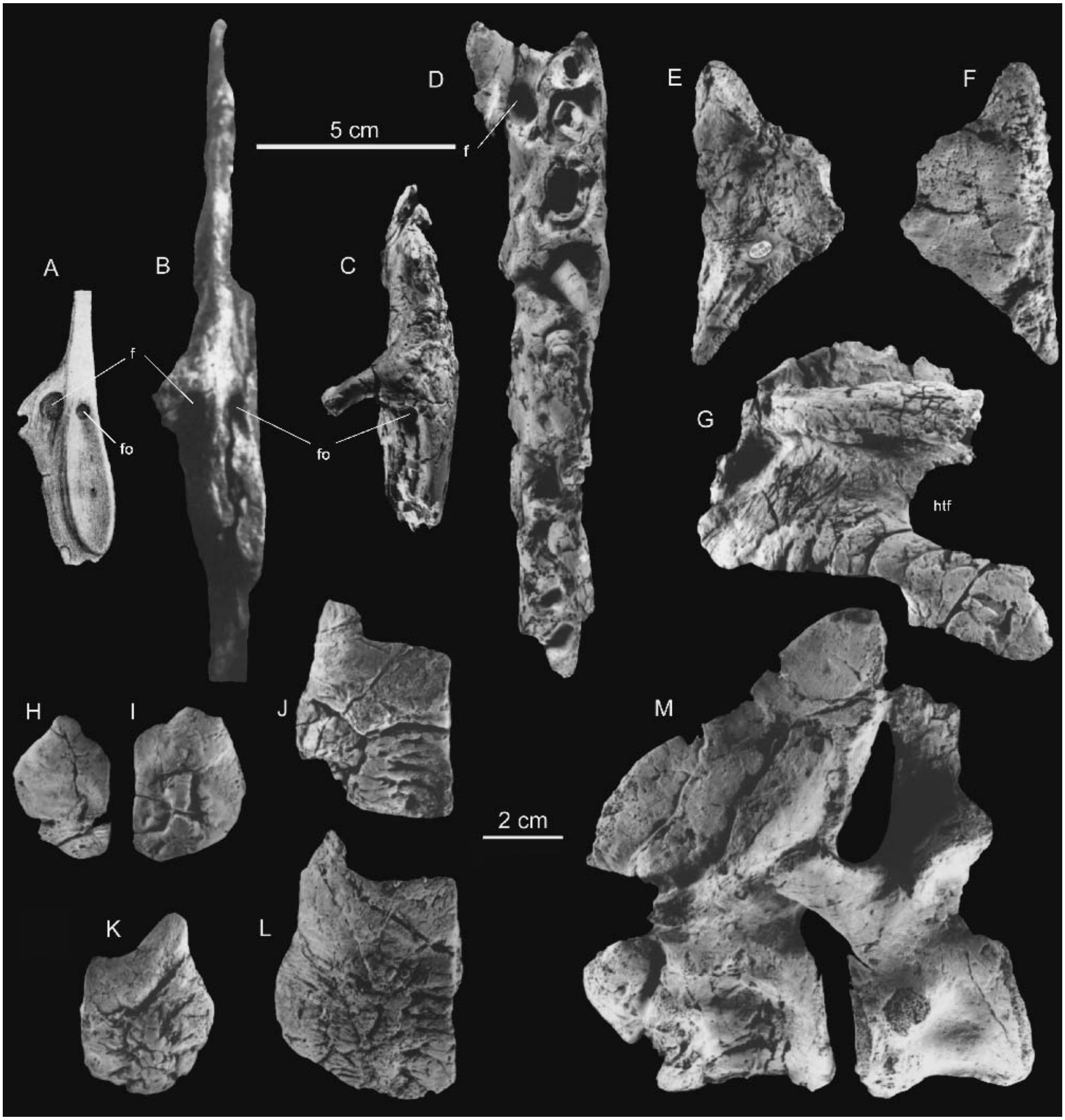

FIGURE 4. Comparison of maxilla of *Teratosaurus silesiacus* sp. nov. and *Teratosaurus suevicus* in anterior view (**A–C**). Maxilla of *Teratosaurus suevicus* reproduced from Meyer (flipped horizontally to aid comparison), 1861:pl. VII 3 (**A**); reproduced from Galton (flipped horizontally), 1985:fig. 1E (**B**). Maxilla of *Teratosaurus silesiacus* sp. nov. ZPAL Ab III 563 in anterior (**C**) and ventral (**D**) views. Left prefrontal in ventral (**E**) and dorsal (**F**) views. The right squamosal in lateral view (**G**). Caudal scutes in dorsal views (**H-L**). Three articulated cervical vertebrae in lateral view (**M**). Upper scale for A–G. Lower scale for H–M.

extending from the medial border of the quadrate foramen. On the anterior surface of the quadrate, a well-defined ridge extends from the posteroventral end of the pterygoid ramus to just above the lateral half of the condyle.

Dentary—The anterior parts of left and right dentary are preserved (Fig. 2J, N). The right is more complete, including a portion that held the first to the eighth tooth. The lateral face is almost planar, and bears a series of vascular foramina. The ventral edge is strongly rugose. On the medial side, near the ventral margin, the dentary bears a groove that was probably covered by the splenial. The interdental plates are firmly attached to the main body of the dentary.

Articular—A fragment of the right articular is preserved (Fig. 2A, H). The medial tongue-like and ascending processes of the retroarticular region (Gower 1999) are broken. However, the preserved part of the medial tongue-like process preserves the foramen for the chorda tympani branch of the facial nerve. A transverse, trough-like depression lies between the posterior border of the cotyle and a hooked ascending process.

Surangular—The fragmentary right surangular is preserved in articulation with the articular. Only a part of the retroarticular region is preserved. It extends posteriorly almost to the end of the articular (Fig. 2H).

Vertebrae

Three articulated cervical vertebrae were found: a fragment of atlas, the axis and the third cervical vertebra. The centrum of the atlas is preserved as a crescentic structure, with a rounded anterior surface (Fig. 4M). The centra of the axis and third cervical vertebra are a little longer then tall. The neural spine of the axis is triangular in lateral view. The prezygapophyses of the axis are rather small relative to the stout postzygapophyses. The latter are supported on the arch by a posterodorsal ridge. The small diapophyses lie slightly beneath the prezygapophyses, and they are directed ventrally. The parapophyses and two parallel hypapophyses are damaged.

The neural spine of the third cervical is incomplete. Its prezygapophyses and postzygapophyses are of equal size. The prezygapophyses extend beyond the anterior of the centrum. Both the diapophyses and parapophyses are clear and circular. The hypapophysis anteriorly forms a single ridge that is posteriorly divided into two ridges.

Nine articulated caudal vertebrae are preserved. Their facets for the haemal arches are pronounced (Fig. 1K). The preserved caudal neural spines are moderately tall, plate-like and angled posterodorsally. The prezygapophyses are directed anterodorsally, and the postzygapophyses posterodorsally. Both sets of processes extend beyond the faces of the centrum. The ventral surface of the centrum is smooth and convex. Thin, plate-like transverse processes are present in the first seven caudal vertebrae. The haemal arches are longer than the neural spines. The haemal canal is low and narrow. It seems that the preserved caudal vertebrae come from the anterior part of the tail.

Dermal Armor

Five dermal scutes were found. The two larger plates are rectangular (Fig. 4H-L), with an anteriorly directed process at their lateral margin. The proceeding plate articulated with this process. The smaller plates are leaf-shaped. Their anterior processes are set in the middle of the anterior margin. Surfaces for articulation in all the preserved scutes are suggestive of two paramedial rows being present. The size of the armor plates and their occurrence with the preserved vertebrae suggests that these were caudal scutes.

DISCUSSION

The stratigraphically and geographically closest occurrence of a rauisuchian complete enough to allow comparison is that of the congeneric *Teratosaurus suevicus.*

Specific Identity of the New Polish Specimen

The maxilla from Krasiejów is similar to the holotype (BMNH 38646) of *Teratosaurus suevicus* in general morphology. However, the dorsal process is more oblique than in *T. suevicus* (Fig. 5). Galton (1985) proposed that the V-shaped suture with the process of the lacrimal is diagnostic for the species. Although the edge of the left maxilla from Krasiejów, which forms this suture, is slightly damaged, it seems that the suture was also V-shaped. Colbert (1962) figured the maxillary fenestra in the base of the dorsal process in the maxilla of *T. suevicus*. The maxilla of the rauisuchid from Krasiejów does not have this fe-

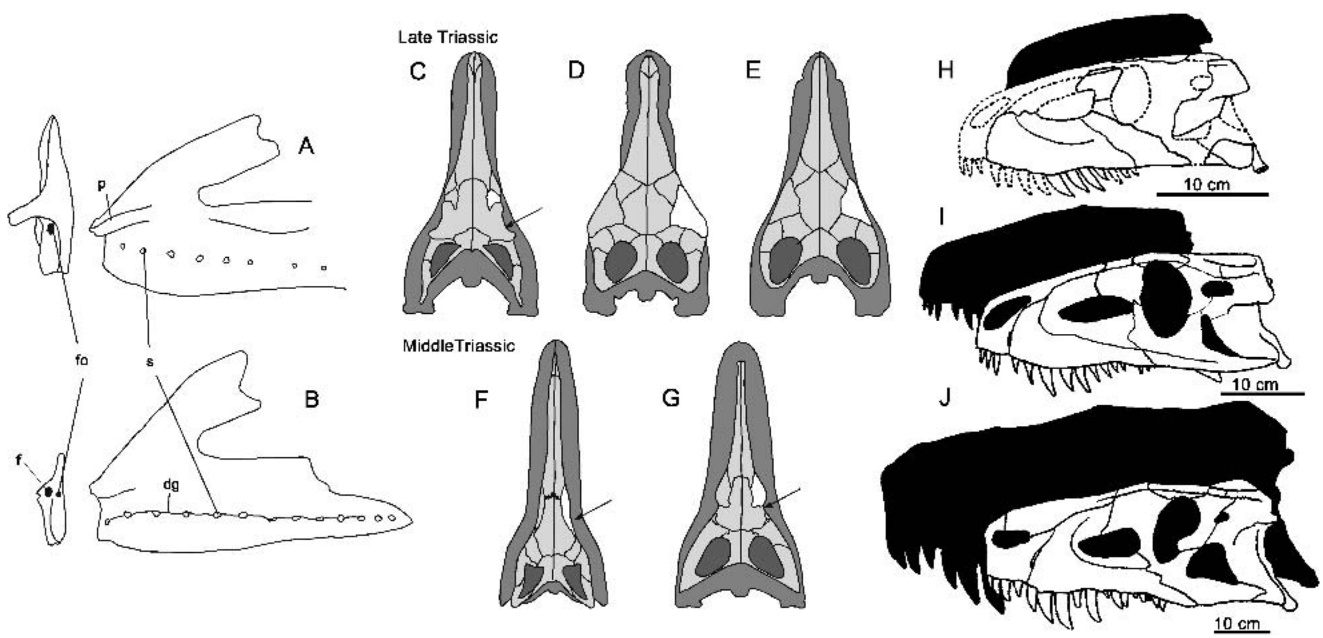

FIGURE 5. Comparison of the maxilla of *Teratosaurus suevicus* and *Teratosaurus silesiacus sp. nov.* in medial and anterior view (**A**–**B**). **A**. – based on ZPAL Ab III 563, left maxilla, **B**.– based on Galton, 1985:fig. 3A. Comparison of the skulls of rauisuchians in dorsal view; prefrontal is white, arrow marks the notch in the edge of skull roof (without scale): *Saurosuchus galilei* (**C**), *Postosuchus kirkpatricki* (**D**), *Teratosaurus silesiacus sp. nov* (**E**)*, Luperosuchus fractus* (**F**), *Batrachotomus kupferzelensis* (**G**). Comparison of the skulls of rauisuchians with derived lower temporal fenestra: *Tikisuchus romeri* (**H**), *Teratosaurus silesiacus sp. nov.* (**I**), and *Postosuchus kirkpatricki* (**J**) in lateral view. The shadows behind show skulls in the same scale as *T. silesiacus*. *Saurosuchus galilei* is based on Alcober, 2000:fig. 11 C, *Postosuchus* is based on reconstruction of Long and Murry, 1995:fig. 123, *Luperosuchus fractus* Romer 1972:fig 1., *Batrachotomus kupferzelensis* Gower, 1999:fig. 2B. Reconstruction of *Tikisuchus* is based on personal observations.

nestra as Meyer (1861) and Galton (1985) demonstrated is also the case for *T. suevicus*.

In the holotype of *Teratosaurus suevicus*, the palatal process of the maxilla is not preserved (Galton, 1985: fig. 3a; pl. 1, figs. 1, 5). The palatal process of *T. silesiacus* is less prominent in front of the anterior edge of the maxilla than Meyer (1861:pl. 45, figs. 1, 2) showed in his reconstruction of *T. suevicus*. It is hypothesised that, similar to *Batrachotomus kupferzellensis* Gower, 1999, the opposite maxillary palatal processes met along the midline in their anterior part, where the medial facet of the palatal process has a groove. The palatal process of the premaxilla probably fits into this groove. The vomers probably laid on the ventral surface of the palatal processes of the maxilla.

According to Galton (1985), the medial anterior foramen visible in BMNH 38646 in anterior view is for the maxillary artery and the inferior orbital nerves (branch of trigeminal nerve V). Benton (1986) probably incorrectly described it as a deep socket for reception of the premaxilla. In specimens from Krasiejów this foramen is visible in medioventral view. The setting of this foramen on the medial side of the maxilla seems to be connected with the structure of an articulation between the maxilla and premaxilla. In the rauisuchian from Krasiejów, the area of the articulation is smooth and rounded. The anterior border of the maxilla reaches over the premaxilla in dorsal view, and forms a loose, potentially movable joint. The presence of the medial anterior foramen on the area of contact between the maxilla and premaxilla possibly indicates that in *T. suevicus* the connection was potentially less movable than in *T. silesiacus*.

The infraorbital foramen (Galton, 1985), visible on the medial side of the maxilla, above alveoli 5 and 6 and close to the border of the antorbital foramen, was possibly for the passage of a branch of the superior alveolar nerve and/or maxillary vein (Galton, 1985). The foramen is located above alveoli 6 and 7 in *Teratosaurus suevicus*. The two foramina above the eighth and ninth alveoli were possibly also for blood vessels and nerves.

The maxillae from Krasiejów probably had more than 11 alveoli. It is possible that there were 13 alveoli as in *T. suevicus*. The foramina for replacement teeth are not connected together by a dental groove, in contrast to the situation in *T. suevicus* (Galton, 1985). The foramina are set in a line, which is less curved (Fig. 5A, B) than in *T. suevicus*.

Resemblance between the maxillae from Heslach and Krasiejów is close enough to tentatively classify them in the same genus *Teratosaurus*. The new material from Krasiejów allows a more complete diagnosis of this genus. The differences between the maxillae (the only element that can be compared in detail in the two taxa) of *T. suevicus* and *T. silesiacus*, taken together with the great distance in time of about 4 million years between these animals, suggest that they probably belong to different species.

Comparisons With Other Genera

One of the best known rauisuchians is *Postosuchus*, represented by the single species *P. kirkpatricki* (Chatterjee, 1985). Its type horizon is the Cooper Canyon Formation of the Dockum Group; early Norian (Long and Murry, 1995). *Postosuchus* is also reported from the late Carnian (*Paleorhinus* Biochron) at Otis Chalk (Long and Murry, 1995).

The skull of *Teratosaurus silesiacus* is very similar to that of *Postosuchus kirkpatricki* (Fig. 5I, J). Both have a derived lower temporal fenestrae and a similar structure of the following bones: the quadratojugal strongly protrudes anterodorsally; the premaxilla has a triangular symphyseal facet, the nasal, lacrimal, prefrontal, squamosal, and probably the postorbital have a continuous rugose longitudinal ridge. The squamosal bears a deep, wide sulcus ventral to the longitudinal ridge. The triangular prefrontal is greatly enlarged and rugose (Fig. 5I, J). In both *Teratosaurus* and *Postosuchus* the centrum of the axis is as long as it is tall. The tail is laterally compressed. The new species was probably similar to *P. kirkpatricki* in general view. *P. kirkpatricki* was a medium-sized (3 m long) heavily built rauisuchid, a large-skulled and short-necked, non-cursorial quadruped (Long and Murry, 1995).

Despite many similarities between *Postosuchus* and *Teratosaurus,* they show significant differences that substantiate their generic distinction. *Postosuchus* has a lower sub-fenestral part of the maxilla and a smaller naris (Fig. 5I, J). It also has a smaller and dorsally angulated premaxilla. In *Postosuchus*, the additional lower temporal fenestra is smaller than in *Teratosaurus* from Krasiejów. The nasal of *Postosuchus* does not have any substantial ventral process (Chatterjee, 1985; Long and Murry, 1995) and the snout of *Postosuchus* is narrower in dorsal view, with a broader anterior part (Fig. 5I, J). The premaxillae of *Postosuchus* do not have palatal processes or they are incompletely preserved in the known material. The region between the choana and suborbital fenestra is long relative to the length of the palatine in *Teratosaurus*, and short in *Postosuchus*.

The skull of *Teratosaurus* from Krasiejów has very large prefrontals, similar to those of *Postosuchus*. Both are different from other rauisuchian skulls (Fig. 5). Only *Batrachotomus* has a similarly large prefrontal with a convex lateral margin, but it has a notch in the lateral edge of the skull roof (Fig. 5C-G) similar to that of the non-rauisuchian archosaur *Sphenosuchus* (Walker, 1990) and *Chanaresuchus* Romer, 1971. In *Saurosuchus* Reig, 1959 and *Luperosuchus* Romer, 1971, the skull roof has a very slight notch, but its lateral edge extends sharply lateral. In *Luperosuchus*, the postfrontal is very narrow and long.

The remaining rauisuchians are very different from *Teratosaurus*. *Poposaurus* has an ilium with a more anterodorsally-inclined supra-acetabular 'buttress' and a longer anterodorsal process (Long and Murry, 1995), and the same features are present in *Bromsgroveia* Galton, 1985, and *Lythrosuchus* Long and Murry, 1995. In *Stagonosuchus* Huene, 1938, and *Prestosuchus* Huene, 1942, the ilia do not have a supra-acetabular rugosity (Gower, 2000). *Prestosuchus* has two or three armor plates per vertebral segments (Parrish, 1993). The size of the armor plates found with a fragment of the caudal part of a neural spine suggests that *Teratosaurus* had one pair of plates per each vertebral segment, as in most crocodylotarsans (Sereno, 1991).

Batrachotomus has a maxilla with a proportionately longer anterior part of the bone compared to *Teratosaurus*. The premaxilla of *Batrachotomus* has a relatively shorter posterodorsal process and the maxilla contributes to the margin of the naris, whereas the maxilla of *Teratosaurus* is excluded from it. The nasals of *Teratosaurus* are arched anteriorly and straight posteriorly; in *Batrachotomus* they form a 'Roman nose' and are depressed posteromedially.

In *Saurosuchus* and *Teratosaurus*, the dorsal surface of the palatine bears an oblique and vertical ridge, which separates the nasal and muscular fossae (Witmer 1997). In *Saurosuchus*, *Fasolasuchus*, and *Luperosuchus*, the posterodorsal process of the premaxilla is significantly longer, and the subnarial fenestra is more elongate than in *Teratosaurus*. *Saurosuchus* and *Fasolasuchus* have a single row of scutes on the tail. *Tikisuchus* also has an additional lower temporal fenestra (Fig. 5H, I) and its maxilla has a palatal process and medial anterior foramen similar to *Teratosaurus* (personal observation). However *Tikisuchus* has only 11 maxillary alveoli. The rugose ridge on the squamosal is much less extended laterally and the jugal is more massive in *Tikisuchus* than in *Teratosaurus*. The fossa antorbitalis maxillaris (Witmer, 1997) at *Tikisuchus* is more delicate than in *Teratosaurus*.

Chatterjeea and *Sillosuchus* Alcober and Parrish, 1997, have relatively more expanded iliac blades, more overhanging dorsal acetabular borders, and more elongate vertebral cervical centra than *Teratosaurus*. *Heptasuchus* Dawley et al., 1979, has only three premaxillary teeth and the opening between the premaxilla and maxilla is perhaps larger than in *Teratosaurus*.

In summary, *Teratosaurus* would seem to most closely resemble genera that are considered to be rauisuchid rauisuchians. Among these genera, it most closely resembles *Postosuchus* and *Tikisuchus*, especially in the derived form of the subdivided lower temporal fenestra. Gower (2002) identified a possible braincase synapomorphy for *Tikisuchus* and *Postosuchus*, but braincase of *Teratosaurus* is unknown. More morphological work and detailed phylogenetic analyses are required to further investigate the possibility that *Teratosaurus*, *Postosuchus*, and *Tikisuchus* form a natural group within Rauisuchidae (Sulej, 2002b).

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LITERATURE CITED

Alcober, O. 2000. Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rauisuchidae). Journal of Vertebrate Paleontology 20: 302–316.

Alcober, O., and Parrish J. M. 1997. A new poposaurid from the Upper Triassic of Argentina. Journal of Vertebrate Paleontology 17:548–556.

Benton, M. J. 1986. The Late Triassic reptile *Teratosaurus*–a rauisuchian, not a dinosaur. Palaeontology 29:293–301.

Bonaparte, J. F. 1981. Description de “*Fasolasuchus tenax*” y su significado en la sistemarica y evolucion de los thecodontia. Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” 3:55–101.

Chatterjee, S. 1985. *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. Philosophical Transactions of the Royal Society of London, B 309:395–460.

Chatterjee, S., and Majumdar, P. K. 1987. *Tikisuchus romeri*, a new rauisuchid reptile from the Late Triassic of India. Journal of Paleontology 61:787–793.

Colbert, E. H. 1962. Dinosaurs. Their Discovery and Their World. Hutchinson and Co, London, 288 pp.

Cope, E. D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Transactions of the America Philosophical Society 14:1–252.

Dawley, R. M., J. M. Zawiskie, and J. W. Cosgriff. 1979. A rauisuchid thecodont from the Upper Triassic Popo Agie Formation of Wyoming. Journal of Paleontology 53:1428–1431.

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

Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. Journal of Vertebrate Paleontology 23:556–574.

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

Galton, P. M. 1985. The poposaurid thecodontian *Teratosaurus suevicus* Meyer, plus referred specimens mostly based on prosauropod dinosaurs, from the middle Stubensandstein (Upper Triassic) of Nordwürttemberg. Stuttgarter Beiträge zur Naturkunde (B) 116:1–29.

Gower, D. J. 1999. The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. Stuttgarter Beiträge zur Naturkunde (B) 280:1–49.

Gower, D. J. 2000. Rauisuchian archosaurs (Reptilia, Diapsida): an overview. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 218:447–488.

Gower, D. J. 2002. Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. Zoological Journal of the Linnean Society 136:49–76.

Gower, D. J., and Sennikov, A. G. 2000. Early archosaurs from Russia; pp. 140–159 in M. J. Benton, E. N. Kurochkin, M. A. Shishkin, D. M. Unwin (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge

Huene, F. 1938. Ein großer Stagonolepidae aus der jüngeren Trias Ostafrikas. Neues Jahrbuch für Geologie und Paläontologie (B) 80: 264–278.

Huene, F. 1942. Die fossilien Reptilien des Südamerikanishen Gondwanalandes. Ergebnisse der Sauriergrabungen in Südbrasilien, 1928/1929. C. H. Beck'she, München, 332 pp.

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

Mehl, M. G. 1915. *Poposaurus gracilis*, a new reptile from the Triassic of Wyoming. Journal of Geology 23:516–522.

Meyer, H. 1861. Reptilien aus dem Stubensandstein des oberen Keupers. Palaeontographica A 6:253–346.

Parrish, J. M. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. Journal of Vertebrate Paleontology 13:287–308.

Reig, O. A. 1959. Primeros datos descriptivos sobre nuevos reptiles arcosaurios del Triassico de Ischigualasto (San Juan, Argentina). Revista de la Asociación Geológica Argentina 3:257–270.

Romer, A. S. 1971a. The Chañares (Argentina) Triassic reptile fauna. VIII. A fragmentary skull of large thecodont, *Luperosuchus fractus*. Breviora 373:1–8.

Romer, A. S. 1971b. The Chañares (Argentina) Triassic reptile fauna. XI. Two long-snouted thecodonts, *Chanaresuchus* and *Gualosuchus*. Breviora 379:1–22.

Sereno, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. Society of Vertebrate Paleontology Memoir 2:1–53.

Sennikov, A. G. 1995. Ranniye Tekodont Vostochnoy Yevropy. Trudy Palaeontologicheskogo Instituta RAN 263:1–141.

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

Sulej, T. 2002b. New materials of the only known Late Triassic rauisuchian archosaur from Europe. 8th International Symposium on Mesozoic Terrestrial Ecosystems, Conference Abstract Book, Appendix, Cape Town, 19.

Sulej, T., and Majer, D. 2005. The temnospondyl amphibian *Cyclotosaurus* from the Late Triassic of Poland. Palaeontology 48:157–170.

Walker, A. D. 1990. A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (Late Triassic or Early Jurassic) of South Africa. Philosophical Transactions of the Royal Society of London, B 330:1–120.

Witmer, L. M. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstructions in the fossil record with an analysis of the function of pneumaticity. Society of Vertebrate Paleontology Memoir 3:1–65.

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