BioOne COMPLETE

The Taxonomy and Anatomy of Rauisuchian Archosaurs from the Late Triassic of Germany and Poland

Authors: Brusatte, Stephen L., Butler, Richard J., Sulej, Tomasz, and Niedźwiedzki, Grzegorz

Source: Acta Palaeontologica Polonica, 54(2) : 221-230

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2008.0065

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The taxonomy and anatomy of rauisuchian archosaurs from the Late Triassic of Germany and Poland

STEPHEN L. BRUSATTE, RICHARD J. BUTLER, TOMASZ SULEJ, and GRZEGORZ NIEDŹWIEDZKI



Brusatte, S.L., Butler, R.J., Sulej, T., and Niedźwiedzki, G. 2009. The taxonomy and anatomy of rauisuchian archosaurs from the Late Triassic of Germany and Poland. *Acta Palaeontologica Polonica* 54 (2): 221–230. DOI: 10.4202/app.2008.0065

The German Late Triassic archosaur *Teratosaurus suevicus* is a historically important taxon, being the first described rauisuchian. Unfortunately the holotype is a single element, a maxilla, which is poorly preserved and incomplete. We redescribe this maxilla and identify a single potential autapomorphy. The fragmentary type specimen complicates attempts to refer additional material to this taxon, and other unassociated archosaur and rauisuchian specimens from the Mittlerer Stubensandstein of Germany cannot be referred to *T. suevicus* with any degree of confidence. The stratigraphically older *T. silesiacus*, from the upper Carnian of Poland, is represented by a much more complete and better preserved specimen. Comparison of the maxillae of *T. suevicus* and *T. silesiacus* reveals that the two are distinct taxa, contra recent suggestions, but also that they do not share any synapomorphies or a unique combination of characters relative to *Postosuchus kirkpatricki* and other rauisuchians. Thus, the Polish material must be transferred to a new genus, *Polonosuchus* gen. nov. Both *Polonosuchus* and *Teratosaurus* are very similar to *Postosuchus kirkpatricki*, and the three taxa are likely closely related.

Key words: Archosauria, Rauisuchia, taxonomy, Triassic, Germanic Basin.

Stephen L. Brusatte [sbrusatte@amnh.org], Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol, BS8 1RJ, UK; present address: Division of Paleontology, American Museum of Natural History, Central Park West at 79th St., New York, NY, 10024, USA and Department of Earth and Environmental Sciences, Columbia University, New York, NY, USA;
Richard J. Butler [butler.richard.j@gmail.com], Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK; present address: Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 München, Germany;
Tomasz Sulej [sulej@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818, Warszawa, Poland;
Grzegorz Niedźwiedzki [gniedzwiedzki@biol.uw.edu.pl], Instytut Zoologii, Uniwersytet Warszawski, ul. Stefana Banacha 2, PL-02-079 Warszawa, Poland.

Introduction

During the Middle–Late Triassic, prior to the origination and diversification of theropod dinosaurs, a group of crocodileline archosaurs called rauisuchians filled the large predator niche in many terrestrial ecosystems (Gower 2000). Over 20 rauisuchians have been named, beginning with *Teratosaurus suevicus*, described by Meyer (1861) on the basis of a single maxilla from the Norian of Germany (Figs. 1, 2). Long mistakenly believed to represent a theropod dinosaur, *Teratosaurus* is now regarded as a characteristic rauisuchian which was among the largest terrestrial predators in the Late Triassic of central Europe (Galton 1985; Benton 1986).

Since 1993, teams from the Institute of Paleobiology (Polish Academy of Sciences, Warsaw) led by Jerzy Dzik and TS have collected remains of Late Triassic vertebrates, invertebrates, and plants from the Krasiejów main claypit near Opole in southwest Poland. Fossils at this locality occur within an extensive lacustrine marly claystone horizon, and in claystone lenses within fluviatile cross-laminated mudstones (Dzik and Sulej 2007). Tetrapod remains are abundant, and include temnospondyls (Sulej 2002, 2007; Sulej and Majer 2004), phytosaurs (Dzik 2001; Dzik and Sulej 2007), aetosaurs (Sulej in press), the dinosauriform *Silesaurus* (Dzik 2003), and rare remains of rauisuchians (Sulej 2005). Reviews of the flora and fauna suggest a late Carnian age for this locality (Dzik and Sulej 2007).

Sulej (2005) described an associated specimen (ZPAL AbIII/563) comprising a partial skull (Fig. 3) and postcranium of a rauisuchian archosaur from the upper deltaic horizon at Krasiejów. Sulej (2005) noted strong similarities between the maxilla of this specimen (Fig. 3) and the holotype maxilla of *Teratosaurus suevicus* from the Norian of Germany (Figs. 1, 2; NHM 38646, formerly BMNH R38646). However, Sulej (2005) also recognised a number of characters that distinguish the two maxillae, and further noted an apparent temporal gap (of around 4 Ma, and maybe as long as 8 Ma) between the Polish and German specimens. As a re-

DOI: 10.4202/app.2008.0065

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

sult, Sulej (2005) described the Krasiejów specimen as a new species, *Teratosaurus silesiacus*. Later, in a review of tetrapods from Krasiejów, Lucas et al. (2007) dismissed the differences between the Polish and German specimens reported by Sulej (2005) and asserted that *T. silesiacus* is a junior synonym of *T. suevicus*.

We here provide an expanded description of NHM 38646 that supplements previous data (Galton 1985; Benton 1986) and allows for a more detailed comparison with the Polish material. We note several differences between the holotype of *T. suevicus* and the Polish specimens, which not only challenge the taxonomic assertions of Lucas et al. (2007), but indicate that there are no diagnostic characters—either unique synapomorphies or even a combination of characters—that unite the two supposed species of *Teratosaurus* to the exclusion of other rauisuchians. This necessitates removal of "*T.*" *silesiacus* from *Teratosaurus*, and requires the erection of a new generic name for the Polish material.

Institutional abbreviations.—NHM (formerly BMNH), Natural History Museum, London, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TTUP, Texas Technical University Museum, Lubbock, Texas, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Systematic palaeontology

Archosauria Cope, 1869

Crurotarsi Sereno and Arcucci, 1990

?Rauisuchia Huene, 1942

?Rauisuchidae Huene, 1942

Teratosaurus Meyer, 1861

Type species: *Teratosaurus suevicus* Meyer, 1861.

Diagnosis.—Same as for the only known species.

Teratosaurus suevicus Meyer, 1861

Holotype: NHM 38646, right maxilla.

Type horizon: Mittlerer Stubensandstein, Mittelkeuper (Late Triassic: ?middle Norian).

Type locality: Heslach, near Stuttgart, Germany, approximately 48.75° N 9.14° E (for further details, see Benton 1986).

Emended diagnosis.—Rauisuchian archosaur distinguished from all other rauisuchians by the possession of an autapomorphic prominent and sharp groove for the dental lamina on the medial surface of the maxilla, below which is a distinctive step separating the medial surface of the main body and the interdental plates. Differentiated from "*T.*" *silesiacus* by: a groove for the dental lamina (and associated tooth replacement foramina) deflected rostroventrally between alveoli 1 and 2; first maxillary alveolus smaller than subsequent alveoli; ventral margin of the maxilla convex anteriorly and straight posteriorly; the caudoventral groove on medial surface of the palatal process long and deep; absence of a prominent and sharply defined caudodorsally arched ridge extending from the base of the palatal process; absence of a deep fossa present dorsal to the palatal process.

Remarks.—Galton (1985) referred multiple teeth (NHM 38647, 38648; SMNS 5212, 9918, 53535, 53536) from the Mittlerer Stubensandstein of Germany to *Teratosaurus*, but we conservatively consider these Archosauria indet., as their fragmentary nature means that they do not possess clear diagnostic features of either the genus or species, and could conceivably belong to large theropod dinosaurs or any carnivorous archosauriform clade. Galton (1985: 9) suggested that a referred ilium, SMNS 52972, "may" have come from the same quarry at Heslach as the holotype, and could even represent the same individual. However, this cannot be confirmed from available locality data, and so we remove this specimen from the hypodigm of *T. suevicus*, pending the discovery of associated rauisuchian material from the Mittlerer Stubensandstein. We conservatively consider the ilium as Rauisuchia indet.: it possesses a dorsally-trending ridge above the acetabulum, as is characteristic of rauisuchians (Gower 2000; Brusatte et al. 2008, in press) and is extremely similar to the ilia of large rauisuchians in overall morphology (Huene 1942; Krebs 1965; Sill 1974; Chatterjee 1985; Sen 2005; Gower and Schoch 2009).

Several authors, beginning with Galton (1985), suggested that SMNS 52972 belongs to a "poposauroid" rauisuchian—a term that has long had a vague meaning due to lack of well-constrained phylogenies, a paucity of phylogenetic definitions for discrete clades, and the long-time chimaeric nature of *Postosuchus* (which was originally described based on the material of three taxa: one "rauisuchid" and two "poposauroids," clade terminology sensu Brusatte et al. 2008; Long and Murry 1995). Recent phylogenetic analyses have recovered a discrete clade centered on *Poposaurus*, which includes taxa such as *Arizonasaurus*, *Effigia*, *Lotosaurus*, and *Shuvosaurus* to the exclusion of the large, quadrupedal, predatory "rauisuchids" (e.g., *Batrachotomus*, *Postosuchus*, *Prestosuchus*, *Saurosuchus*, *Teratosaurus*) (Nesbitt 2007; Weinbaum and Hungerbühler 2007; Brusatte et al. 2008, in press). This clade has been defined as Poposauroidea (Weinbaum and Hungerbühler 2007). The ilium SMNS 52972 lacks three characters diagnostic of Poposauroidea or slightly less inclusive ingroup clades in the analysis of Brusatte et al. (2008, in press): a crest above the acetabulum that trends anterodorsally, a deep fossa anterior to the crest, and an articulation for the first sacral rib reaching the anterior margin of the preacetabular process medially. Thus, SMNS 52972 cannot be referred to Poposauroidea based on current concepts and definitions of this group, and instead is much more similar to the ilia of large "rauisuchids" such as *Postosuchus*.

A number of characters previously proposed as diagnostic of *Teratosaurus* (Galton 1985; Sulej 2005) can no longer be considered valid. Several of these characters refer to elements not preserved in the holotype of the genus (e.g., the premaxilla, nasals, prefrontals, ilium, osteoderms, etc.). Three characters of the maxilla have previously been proposed as di-

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

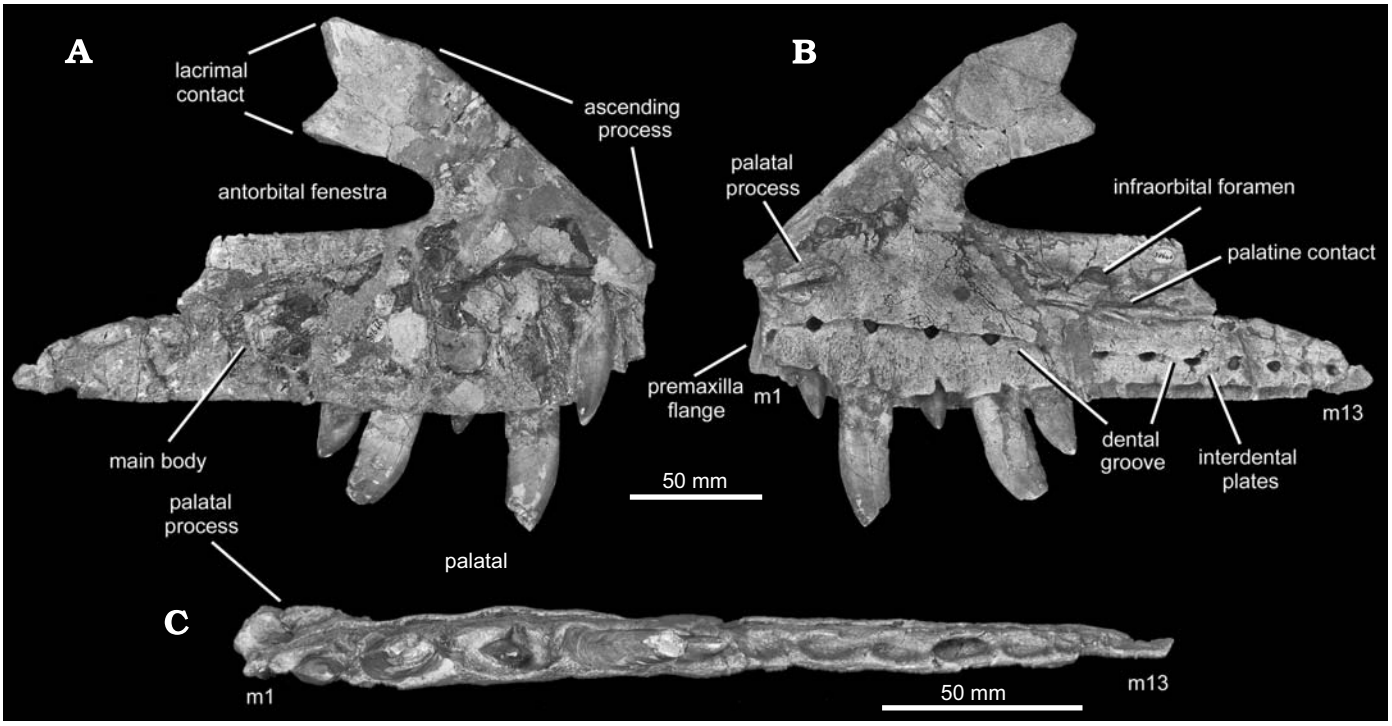


Fig. 1. Right maxilla of rauisuchian *Teratosaurus suevicus* Meyer, 1861 from Mittlerer Stubensandstein, Upper Triassic of Heslach, Germany, NHM 38646, holotype. Photographs in lateral (**A**), medial (**B**), and ventral (**C**) views. Designation "m" refers to maxillary tooth position.

agnostic: (1) 13 maxillary alveoli (Galton 1985; Sulej 2005); (2) palatal process is large (Sulej 2005); (3) suture between the maxilla and lacrimal is V-shaped (Galton 1985; Sulej 2005). Thirteen maxillary teeth and a large palatal process are both features also present in other rauisuchians, most notably *Postosuchus kirkpatricki* (Chatterjee 1985). The nature of the suture between the maxilla and the lacrimal cannot be assessed in the type specimen of *T. suevicus* (NHM 38646), because this area of the maxilla is broken and not fully prepared (see below). Similarly, in *T. silesiacus* this part of the maxilla is broken (Sulej 2005: fig. 1A, D), and the exact morphology of the suture cannot be determined.

Redescription.—First described and figured by Meyer (1861), the holotype maxilla of *Teratosaurus suevicus* was re-described briefly by Benton (1986) and Galton (1985). The best published photographs of the specimen were provided by Galton (1985: pl. 1) and an accurate line-drawing was provided by Benton (1986: fig. 1). Galton's (1985: fig. 3A) line-drawing is inaccurate in both its proportions and in the topographical relationships of several anatomical features; for example, his figure shows the 'infraorbital foramen' positioned ventral to the sutural surface for the palatine, when this foramen is actually positioned dorsal to the sutural surface.

The specimen is a right maxilla and is preserved in two pieces—most of the element is preserved as a single piece (and was figured as such by Benton 1986: fig. 1), whereas the rostrolateral corner of the maxilla is preserved separately (the two pieces were figured in articulation by Galton 1985: pl. 1: 1). Here we figure the maxilla both without the second smaller piece (Fig. 1A, C) and with that piece in place (Figs. 1B, 2). The maxilla is composed of a sub-rectangular main body which is broken at its caudal end, as well as an ascending process. The caudodorsal portion of the ascending process is partly unprepared, as noted by Benton (1986: caption to fig. 1), and consists of whitish-grey sandstone and glue (Fig. 1). Galton (1985) described this area as "well-preserved" and suggested that a V-shaped caudodorsal edge of the ascending process might be a diagnostic character for the species. Sulej (2005) also noted a supposed V-shaped notch in the maxilla of *T. silesiacus*, and suggested that it might be diagnostic for the genus (but see above). However, because this area is not fully prepared in the holotype, it cannot be determined if the observed V-shape is natural, or an artefact of taphonomic processes, breakage, or reconstruction. Much of the lateral surface of the maxilla is damaged, with the external bone surface missing (Fig. 1A). As noted by Benton (1986), the specimen is heavily cracked and has been repaired with glue and thickly coated with preservative in places.

The main body of the maxilla is deep and transversely compressed. The dorsal and ventral margins are approximately subparallel across their lengths, resulting in a rectangular-shaped main body that does not taper in depth posteriorly in the region underneath the antorbital fenestra. In lateral view, the ventral margin of the maxilla is nearly straight above alveoli 7–13, and gently convex above alveoli 1–6. Most of the lateral surface of the main body is damaged, and nutrient foramina can only be identified on the separate small rostrolateral fragment: three (possibly four) foramina are present in an irregularly spaced row above alveoli 1–3. Because of the dam-

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

age to the lateral surface of the maxilla, a distinct border to the antorbital fossa cannot be recognised. As in many rauisuchians, the antorbital fenestra is triangular in shape, and tapers in dorsoventral depth anteriorly (Fig. 1A, B). The anterior margin of the fenestra is smoothly rounded in *Teratosaurus*, similar to the condition in *Arganasuchus* (Jalil and Peyer 2007), *Batrachotomus* (Gower 1999), *Fasolasuchus* (Bonaparte 1981), and *Postosuchus kirkpatricki* (Chatterjee 1985). *Prestosuchus* (Barberena 1978) and *Saurosuchus* (Alcober 2000) exhibit a slightly different morphology, in which the fenestra tapers more sharply anteriorly, due to an ascending ramus oriented closer to horizontal than in the taxa listed above.

The ascending process projects caudodorsally at an angle of approximately 35° to the long axis of the main body. Few details of the morphology of this process can be determined due to its poor preservation and incomplete preparation (see above), although its rostral margin does appear to be slightly thickened. It is clear that the maxilla does not possess a separate rostral ramus, which in some rauisuchians is present as a discrete projection separated from the ascending ramus by a concave step; e.g., *Arganasuchus* (Jalil and Peyer 2007), *Arizonasaurus* (Nesbitt 2005), *Batrachotomus* (Gower 1999), *Effigia* (Nesbitt 2007), *Fasolasuchus* (Bonaparte 1981), *Ticinosuchus* (Krebs 1965), *Yarasuchus* (Sen 2005). Instead, *Teratosaurus* and other rauisuchians without a rostral ramus (e.g., *Postosuchus kirkpatricki*, *Saurosuchus*) exhibit a smoothly continuous and convex rostral margin of the ascending ramus.

At the rostral end of the main body, the maxilla possesses a bevelled, rostromedially facing surface (parts of which are present on both pieces of the maxilla) that would have laterally overlapped the premaxilla (Figs. 1, 2). This surface is concave both rostrocaudally and dorsoventrally. A similar articular surface has been described for *Batrachotomus* (Gower 1999: "a.pmx" on fig. 4) but in that taxon the surface is proportionally shorter dorsoventrally and forms a more distinct lobe-like process, restricted to the rostroventral corner of the main body. Immediately dorsal and lateral to this articular surface, a foramen is present that opens into a caudodorsally extending canal (Fig. 2B). As mentioned briefly by Galton (1985), the breakage of the lateral surface of the maxilla has exposed the route of this canal, which is represented by sediment infilling. The canal arches caudodorsally, reaching its maximum dorsal position above alveolus 3; it then arches caudoventrally and expands in dorsoventral depth, and is visible until a point level with the caudal margin of alveolus 4. This foramen and canal was identified by Galton (1985: "fo" on fig. 1E, "f", "c" on pl. 1: 1) as possibly housing a branch of the maxillary artery and the inferior orbital nerve; we use the term rostrolateral foramen for this opening (Fig. 2; Sulej 2005: fig. 4A–C).

Galton (1985) suggested that a subnarial fenestra was present between the premaxilla and maxilla in the holotype of *Teratosaurus*. This opening is common in rauisuchians, and is usually expressed as a dorsoventrally elongate slit that is at least three times as deep as long anteroposteriorly; e.g., *Postosuchus kirkpatricki* (Chatterjee 1985), *Saurosuchus* (Alcober 2000), *Yarasuchus* (Sen 2005). However, some taxa possess a smaller and more circular opening in this region, which is likely a homologous feature (see discussion in Gower 2000; e.g., *Batrachotomus*). Contra Galton (1985), the presence and morphology of this opening cannot be reliably assessed in the holotype of *Teratosaurus*, since the premaxilla is not preserved. Regardless, features of the maxilla suggest that this opening may have been small or entirely absent. Most importantly, the rostral surface of the maxilla is nearly vertical and lacks a distinct notch, which is often clearly visible in taxa that possess a distinctive subnarial opening (Chatterjee 1985: fig. 3; Alcober 2000: fig. 11).

On the medial surface of the maxilla, immediately caudodorsal to the premaxillary articular surface, there is a palatal process (anteromedial process of Galton 1985), which is directed rostroventrally, but is broken and incomplete at its rostral margin (Figs. 1, 2). The rostrolateral portion of this process is gently bevelled, probably for articulation with the posteriorly projecting maxillary process of the premaxilla. The preserved medial surface of the palatal process is generally convex along a rostrodorsal to caudoventral axis; however, at the caudoventral corner of the process this convexity is broken by two subparallel rostroventral-to-caudodorsally extending grooves. Of these two grooves, the more rostral in position is shallow and subtly developed, whereas the more caudal groove is deeply incised and at its posterior end merges smoothly with the medial surface of the maxilla. These grooves are likely for articulation with the opposing maxilla, and possibly the vomer. The palatal process overhangs a large and deep foramen that opens into a caudodorsally extending canal—this is the rostromedial foramen (Fig. 2; Sulej 2005) and is approximately twice the size of the rostrolateral foramen described above.

The medial surface of the maxilla is generally well-preserved (Fig. 1B). The most prominent feature of the medial surface is a deep and sharp groove, which separates the main body of the maxilla from the interdental plates. This groove, identified by Galton (1985) as the "dental groove", is present in archosaurs generally, and likely housed the soft tissue dental lamina (Edmund 1960; Brusatte and Sereno 2007). However, in *T. suevicus* the groove is especially prominent and sharp, and demarcates a distinct step between the main body and the interdental plates. The groove is not as sharp or distinct in *T. silesiacus* (ZPAL AbIII/563), *Postosuchus kirkpatricki* (TTUP 9000), and other rauisuchians in general, and its morphology is thus autapomorphic for *T. suevicus*. Ventral to the groove, the interdental plates are fused into a continuous lamina, and even the much smaller posterior plates are heavily fused. Fusion of the interdental plates is uncommon in crurotarsans, but is also present in *Postosuchus kirkpatricki* (TTUP 9000) and *Fasolasuchus* (Bonaparte 1981), and may be phylogenetically informative. The plates are unfused in *T. silesiacus* (ZPAL AbIII/563). Despite the fusion, it is apparent that individual plates of *T. suevicus* are large and nearly square shaped anteriorly, the largest being above alveoli 2–4, but taper in depth and become more trian-

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

gular posteriorly. Their medial surfaces are covered in a series of fine pits, which results in a roughened surface texture. Dorsally, the plates are separated by small replacement foramina, one for each tooth, which run along the sharp groove for the dental lamina. Ventrally, adjacent plates are separated by small triangular notches.

A prominent elliptical depression on the medial surface, above alveolus 7, was identified as the infraorbital foramen by Galton (1985). This feature is also present in *Arganasuchus* (Jalil and Peyer 2007), *Arizonasaurus* (Nesbitt 2005), *Batrachotomus* (Gower 1999), and *Postosuchus kirkpatricki* (Chatterjee 1985), and is probably a more general archosaur character. Other depressions on the medial surface may also represent foramina (e.g., Benton 1986: fig. 1), but are incompletely preserved and cannot be distinguished unambiguously from damage. Below the "infraorbital foramen" (not above it, as shown by Galton 1985: fig. 3A), and above alveoli 6–10, there are three rostrocaudally extending ridges that represent the sutural surface for the palatine. These ridges face almost entirely medially.

In total, parts of eight teeth can be identified, and there are 13 alveoli (Fig. 1). Alveolus 1 is considerably smaller in circumference than subsequent alveoli, and it contains an unerupted replacement tooth that is visible on the medial surface of the small rostrolateral fragment. This crown is considerably smaller than subsequent crowns, and is finely serrated on rostrolateral and caudomedial surfaces. Alveolus 2 contains a large and incompletely erupted crown; similarly incompletely erupted crowns are present in alveoli 4 and 6. Fully erupted crowns are present in alveoli 3 and 5. Galton (1985:7) also suggested that a fully erupted crown was present in alveolus 7, but has "most of [the] crown missing", whereas Benton (1986: 295) suggested that the tooth in alveolus 7 was "small". However, only fragments of this crown are visible, and only in lateral view where the lateral wall of the maxilla has broken away. In ventral view, the alveolus itself is infilled with matrix, such that it is not possible to determine the degree of eruption. Although Benton (1986) suggested that the posterior six sockets lack teeth, part of a crown is visible within alveolus 10, through the replacement foramina. The teeth are slightly recurved with oval cross-sections and finely serrated mesial and distal carinae. Erosion makes it difficult to confirm the presence of transverse enamel wrinkles, which are actually present on most rauisuchians (e.g., *Batrachotomus*: SMNS 52970) despite previously being considered a feature of derived theropod dinosaurs (Brusatte et al. 2007).

Comparison with rauisuchian material from Poland.— Sulej (2005) described a partial skull and postcranial skeleton of a rauisuchian from the Carnian of Poland (ZPAL AbIII/563) as a new species of *Teratosaurus*, *T. silesiacus*. The entire preserved skeleton of the holotype specimen of *Teratosaurus silesiacus*, including the maxilla (Fig. 3), was described in detail by Sulej (2005) and does not warrant redescription here. Overall, the maxilla of *T. silesiacus* is very similar to that of *T. suevicus*, but several differences are apparent.

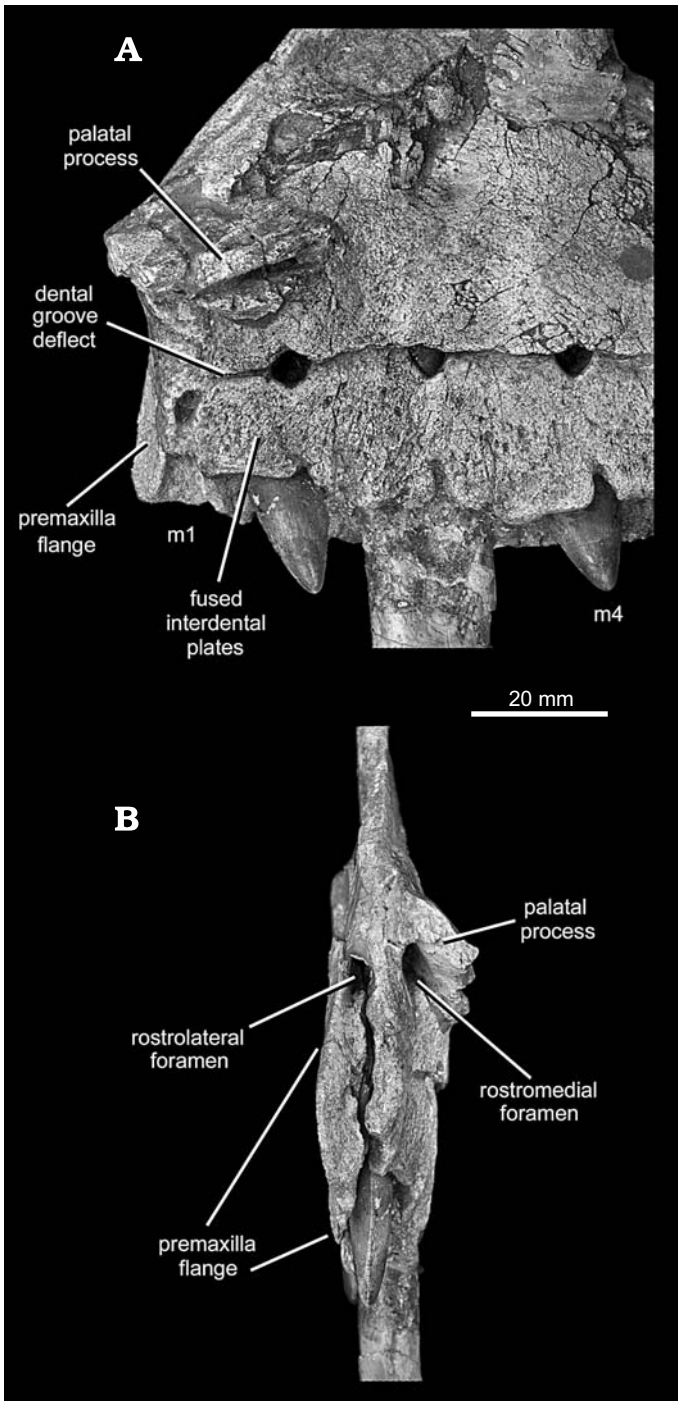


Fig. 2. Right maxilla of rauisuchian *Teratosaurus suevicus* Meyer, 1861 from Mittlerer Stubensandstein, Upper Triassic of Heslach, Germany, NHM 38646, holotype. Photographs in medial (**A**) and anterior (**B**) views. **A** is a close-up of the medial surface of the anterior end of the maxilla. Designation "m" refers to maxillary tooth position.

Sulej (2005) proposed a number of differences between the two species of *Teratosaurus*, most importantly several characters apparently present in *T. silesiacus* but not in *T. suevicus*: (1) rostromedial foramen of the maxilla on the medial surface; (2) ascending process of maxilla is strongly oblique; (3) foramina for replacement teeth are not con-

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

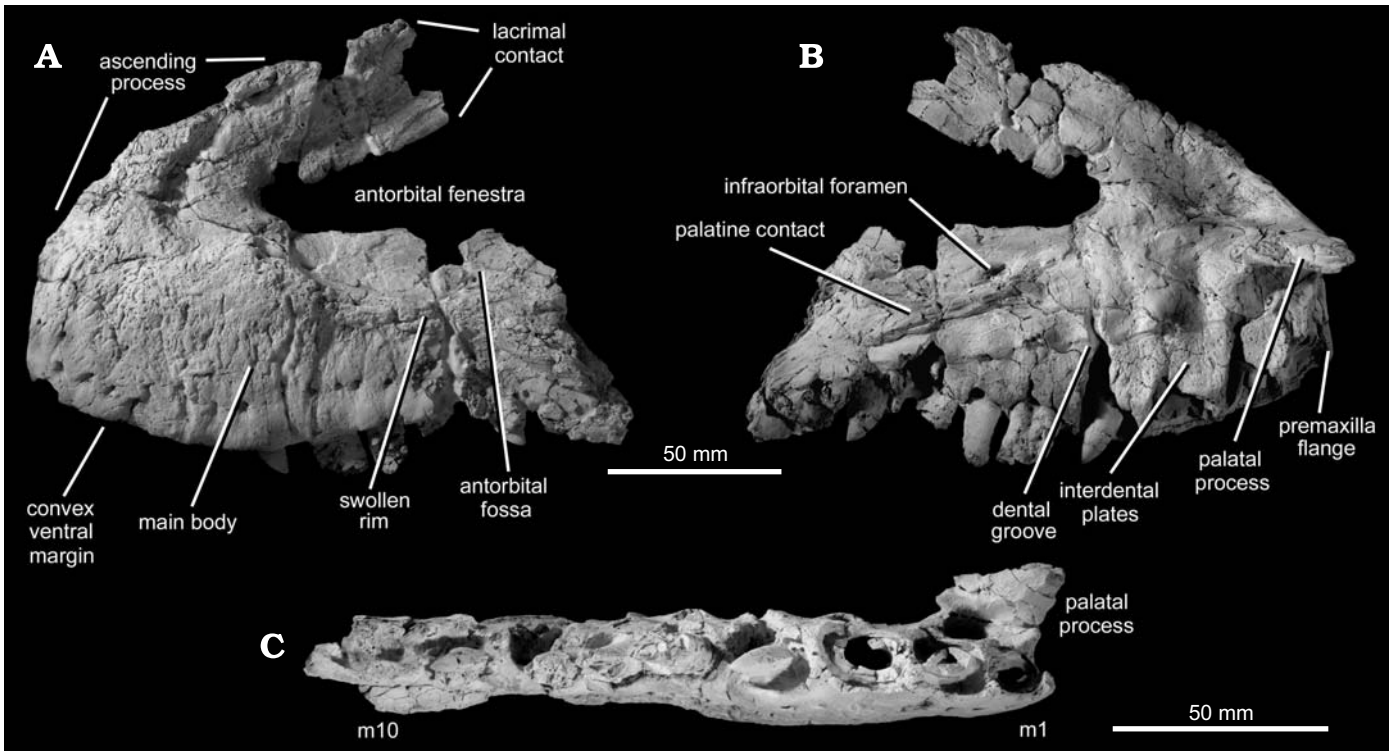


Fig. 3. Left maxilla of rauisuchian *Polonosuchus silesiacus* (Sulej, 2005) from Late Carnian, Upper Triassic of Krasiejów Claypit, Poland, ZPAL AbIII/563, part of holotype. Photographs in lateral (**A**), medial (**B**), and ventral (**C**) views. Designation "m" refers to maxillary tooth position.

nected together by a dental groove; (4) foramina for replacement teeth are set in a straight line. All of these characters were considered either inaccurate or of questionable significance by Lucas et al. (2007). In order to reassess the taxonomic status of *Teratosaurus silesiacus*, we begin by reassessing each of these proposed differences. Subsequently, we note a number of other differences based upon our re-examinations of both specimens.

(1) Rostromedial foramen orientation: Sulej (2005) suggested that the rostromedial foramen of *T. suevicus* opens rostroventrally and is visible in rostral view; by contrast, the equivalent foramen of *T. silesiacus* opens medioventrally and is not clearly visible in rostral view. Lucas et al. (2007) accepted this difference as genuine, but suggested that it could result from taphonomic processes. During our re-examination of the maxillae of both *T. suevicus* and *T. silesiacus* we have been unable to recognise a significant difference in the orientation of the opening of this foramen. Importantly, the foramen of *T. suevicus* is visible in rostral view largely as a result of the breakage of the rostral end of the palatal process. Therefore, we do not consider this feature to represent a genuine difference.

(2) Orientation of the ascending process: In order to assess the obliquity of the ascending process in both species, we measured the angle between a line drawn through the base of the palatal process and the midpoint of the caudodorsal margin of the ascending process, and a line drawn between the base of the palatal process and the midpoint of the caudal end of the main body. In both taxa this angle was approximately 35°. Therefore, there does not appear to be a significant difference in the obliquity of the ascending process in the two taxa.

(3) Dental groove on medial surface: Lucas et al. (2007) suggested that a distinct dental groove connecting replacement foramina on the medial surface of the maxilla, a distinctive feature of *T. suevicus*, is also present in *T. silesiacus*. As outlined above, we consider the distinct and sharp morphology of this groove to be an autapomorphy of *T. suevicus*. There is a corresponding groove present in *T. silesiacus* (Fig. 3B), as occurs in archosaurs generally. However, this groove is much subtler than that of *T. suevicus*, and in places even appears to be entirely absent (most clearly dorsal to the interdental plate overlying alveolus 3). Therefore, we consider this difference to be a valid distinction between *T. silesiacus* and *T. suevicus* (Sulej 2005; contra Lucas et al. 2007), and the sharp groove as the sole autapomorphy diagnosing *T. suevicus*.

(4) Orientation of tooth replacement foramina: Lucas et al. (2007) suggested that the alignment of the foramina for replacement teeth was no straighter in *T. silesiacus* than in *T. suevicus*, and dismissed this proposed difference. In fact, in *T. suevicus* the replacement foramina are positioned in a straight line along most of the tooth row (Fig 1B). However, at the rostral end the first two foramina are positioned more ventrally, with the first foramen being nearly adjacent to the alveolar margin (Fig. 2A). As a result, the dental groove connecting these replacement foramina curves ventrally at its rostral end. This is presumably due to the reduced size of the

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

first maxillary crown in *T. suevicus* (discussed in greater detail below). In contrast, in *T. silesiacus* the replacement foramina are set in a completely straight line, and do not arch ventrally towards the alveolar margin at the rostral end (Fig. 3B). Thus, we consider this difference to be a valid distinction between *T. silesiacus* and *T. suevicus* (Sulej 2005; contra Lucas et al. 2007).

A number of other differences between the maxillae of *T. silesiacus* and *T. suevicus* exist, which have not been previously noted or discussed. As noted above, the first (most rostrally positioned) alveolus in *T. suevicus* is substantially smaller than subsequent alveoli: its rostrocaudal length is less than a third of the length of alveolus 3 (Fig. 1C). The unerupted crown which occupied this alveolus is likewise much smaller than subsequent crowns. No such size difference between the most rostral alveolus and subsequent alveoli is observed in *T. silesiacus*: the first alveolus is only very slightly smaller in size than alveoli 2–4 (Fig. 3C). This difference cannot simply be a result of differences in the degree of eruption, because the first maxillary tooth is unerupted in the holotype specimens of both taxa (Sulej 2005). Furthermore, a very small first alveolus is seen in some (*Batrachotomus* [Gower 1999], *Postosuchus kirkpatricki* [TTUP 9000]) but not all (*Arizonasaurus* [Nesbitt 2005], *Prestosuchus* [Barberena 1978]; possibly *Tikisuchus* [Chatterjee and Majumdar 1987]) rauisuchians, and may be a character of phylogenetic significance for rauisuchian interrelationships.

The ventral margin of the maxilla in *T. suevicus* is straight along its caudal half (alveoli 7–13) and gently convex rostrally. By contrast, in *T. silesiacus* the ventral margin has a sinuous outline in lateral view: from the caudal end it arches upwards (reaching its highest point below alveolus 8) and then is strongly convex at the rostral end (maximum convexity is below alveolus 4) (Fig. 3A, B).

The morphology of the palatal process also differs between the two species. In both species a pair of rostroventrally-to-caudodorsally extending grooves is present on the caudoventral corner of the palatal process, for articulation with the opposing maxilla and possibly the vomer. In *T. silesiacus* the more caudal of these grooves is notably short in length and lacks a well-defined ventral margin; moreover, at its posterior end it is set above the level of the medial surface of the maxilla (Fig. 3B). In contrast, in *T. suevicus* this groove is proportionally much longer and merges smoothly with the medial surface of the maxilla (see above) (Fig. 1B). In addition, in *T. silesiacus* there is a prominent and sharply defined caudodorsally arched ridge that extends from the base of the palatal process and fades out above alveolus 3; no such ridge is present in *T. suevicus* despite the good preservation of this area. In *T. silesiacus* there is a prominent large fossa (possibly pneumatic and associated with the antorbital sinus of archosaurs: Witmer 1997) dorsal to the palatal process and the caudodorsally arched ridge. Although the equivalent area is poorly preserved and somewhat crushed in *T. suevicus*, an equivalent prominent fossa does not appear to have been present.

In addition to these anatomical differences, we also note significant differences in both size and stratigraphic position between *T. silesiacus* and *T. suevicus*. *T. suevicus* is significantly larger than *T. silesiacus* (maximum rostrocaudal length of the maxilla is 165 mm in *T. silesiacus* and 245 mm in *T. suevicus*). It is possible that *T. silesiacus* could represent an earlier ontogenetic stage of *T. suevicus*—the limited available material makes assessing the ontogenetic stage of either taxon difficult at present, particularly given the lack of data in general on ontogeny in basal archosaurs (Irmis 2007). However, the neurocentral sutures are fused in all preserved vertebrae in *T. silesiacus* (the axis, third cervical, caudals) which is consistent with a mature ontogenetic stage in archosaurs (Irmis 2007). The stratigraphic incongruity (with *T. silesiacus* known from the late Carnian, and *T. suevicus* from the middle Norian) cannot by itself be used to support specific level distinction; however, in combination with anatomical and size differences, it may be informative.

In summary, we consider two of the four differences between *T. silesiacus* and *T. suevicus* proposed by Sulej (2005) to be valid. We also recognise an additional four anatomical characters that differ between these taxa. Combined with differences in size and stratigraphic position, these anatomical differences provide strong evidence to support the distinctiveness of *T. silesiacus*. We therefore reject the proposal of Lucas et al. (2007) that *T. silesiacus* is a junior synonym of *T. suevicus*.

Taxonomy of the Polish rauisuchian material.—Clearly, the German and Polish rauisuchian specimens are distinct and belong to different taxa. With this established, it must now be determined whether these taxa can be united as sister taxa relative to other rauisuchians, the minimum requirement needed to retain the Polish material (ZPAL AbIII/563) in the genus *Teratosaurus*. If there is no such evidence, then the Polish taxon must be given a new generic name.

Ideally, in these cases it is best to use a phylogenetic analysis to test the validity of a genus, which in actuality is simply a monophyletic clade exclusive to all other taxa considered as genera in a given taxonomy. In this case, the fundamental question is whether the two species (*T. suevicus* and *T. silesiacus*) comprise a clade relative to *Postosuchus* and other rauisuchians. However, this is extremely problematic, as *T. suevicus* is only known from a small part of the skeleton (the maxilla) and including it in an analysis is likely to drastically increase the number of most parsimonious trees and may give a spurious result due to missing data alone. Furthermore, widespread missing data renders it likely that *T. suevicus* would be removed from the phylogeny altogether by certain consensus techniques that are useful for large analyses with extensive missing data and homoplasy (e.g., reduced consensus: Wilkinson 1994), a reality for higher-level archosaur analyses (Gower and Wilkinson 1996; Brusatte et al. 2008). Thus, we are hesitant to rely on phylogenetic analysis to test the validity of *Teratosaurus* based on data in hand, and instead focus our attention on diagnostic characters, both autapomorphies and unique combinations of characters.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

As the holotype of the type species of *Teratosaurus*, *T. suevicus* Meyer, 1861, is limited to a single maxilla (NHM 38646) and no other specimens can be definitely referred to this species (see above), any diagnostic features of the genus must be identified only on this element. The maxilla of *Teratosaurus* is extremely similar to that of *Postosuchus kirkpatricki*, and the two may be closely related as suggested by Sulej (2005). Our comparisons indicate that there are no unique synapomorphies shared by the German (NHM 38646) and Polish (ZPAL AbIII/563) maxillae that unambiguously differentiate them from *Postosuchus kirkpatricki* and other rauisuchians. In addition, we cannot even identify a unique combination of maxillary characters shared by the German and Polish material to the exclusion of *Postosuchus kirkpatricki*.

One possible feature that appears to be different in *Postosuchus kirkpatricki* and the German + Polish material is the size of the "subnarial" opening between the maxilla and premaxilla. This opening has been figured as large and slit-like in *Postosuchus kirkpatricki* (Chatterjee 1985; Long and Murry 1995) and as small or nonexistent in the German (Benton 1986) and Polish (Sulej 2005) material. However, the large size of the opening in *Postosuchus kirkpatricki* has been exaggerated in published figures, and the true size of this fenestra is similar to that in both the German and Polish material (Sterling Nesbitt, personal communication 2008).

Thus, as (1) the type species of *Teratosaurus*, *T. suevicus*, is valid; (2) *T. suevicus* and Polish material referred to *T. silesiacus* are distinct; and (3) there are no autapomorphies or a combination of characters that unite *T. suevicus* and the Polish material relative to *Postosuchus kirkpatricki* and other rauisuchians, a new generic name must be erected for the Polish material.

Genus *Polonosuchus* nov.

Etymology: From Latin *Polonia*, Poland, the country in which the holotype was found, and *souchos* or *suchus* (Greek term for the Egyptian crocodile god Sobek).

Type species: *Polonosuchus silesiacus* Sulej, 2005.

Diagnosis.—Same as for the only known species.

Polonosuchus silesiacus Sulej, 2005

Holotype: ZPAL AbIII/563, series of cranial and axial elements, including left and right maxillae, from a single associated individual.

Type horizon: Late Carnian (Late Triassic).

Type locality: Krasiejów, Opole Silesia, Poland (for further details, see Sulej 2005 and Dzik and Sulej 2007).

Emended diagnosis.—Rauisuchid rauisuchian archosaur with the following combination of characters: thick and swollen rim delimiting the antorbital fossa on the maxilla, which continues caudally onto the jugal; absence of rostral ramus of maxilla; rugose ridge on the lateral surface of the skull roof (nasals, lacrimal, palpebral, postorbital, squamosal); large triangular palpebral ossification dorsal to the orbit (previously identified by Sulej 2005 as an enlarged prefrontal, but clearly a separate ossification); deep pit on the caudodorsal corner of the lateral surface of the squamosal; subdivided lower temporal fenestra. Differentiated from *Teratosaurus* by: a medial groove for the dental lamina that is subtle and entirely absent in some places; groove for the dental lamina (and associated tooth replacement foramina) oriented in a straight line across its entire length; first maxillary alveolus approximately equal in size to subsequent alveoli; ventral margin of the maxilla sinuous and highly convex in outline; the caudoventral groove on medial surface of the palatal process short and poorly defined; a prominent and sharply defined caudodorsally arched ridge extending from the base of the palatal process; and a deep fossa present dorsal to the palatal process. Differentiated from *Postosuchus kirkpatricki* by: ventral margin of the maxilla sinuous and highly convex in outline; first maxillary alveolus approximately equal in size to subsequent alveoli; absence of fossa on the dorsal surface of the nasal; absence of dorsoventral expansion of the rostral end of the dentary.

Remarks.— The entire preserved skeleton of the holotype specimen of *Polonosuchus silesiacus*, including the maxilla, was described in detail by Sulej (2005) and does not warrant redescription here. Overall, the maxilla of *Polonosuchus* is very similar to that of *T. suevicus*, but several differences are apparent (see above). Although *Polonosuchus* has been separated from *Teratosaurus*, it is possible that further discoveries of *Teratosaurus* material may reveal characters shared by the two genera, thus supporting a sister taxon relationship. If this is the case, then *Polonosuchus* could be transferred back to *Teratosaurus*, although this is a subjective decision if the two are sister taxa. A detailed description of all previously described material of *Polonosuchus silesiacus*, as well as and new cranial and postrcranial bones, is in preparation by the authors.

Phylogenetic position of *Teratosaurus* and *Polonosuchus*

The higher-level phylogeny of basal archosaurs has been a consistent subject of disagreement for several decades (Gower and Wilkinson 1996) and rauisuchians have been a particular focus of debate. Although clearly members of the major clade Crurotarsi—the "crocodile line" of archosaur phylogeny—rauisuchians are poorly understood in a phylogenetic context. Not only are the interrelationships of rauisuchians poorly constrained, but there has been long-standing debate on whether a monophyletic "Rauisuchia" even exists (Gower 2000; Gower and Nesbitt 2006). Indeed, recent findings have revealed a range of size, dietary, and body plan diversity in rauisuchians (e.g., Alcober and Parrish 1997; Nesbitt 2003; Li et al. 2006; Nesbitt and Norell 2006), including several forms strikingly convergent with dinosaurs (Nesbitt 2007). This vast range of morphologies and widespread morphological convergence has made it difficult to offer a well-resolved and well-supported hypothesis of rauisuchian phylogeny.

Recently, Brusatte et al. (2008, in press) have provided a detailed phylogenetic analysis of higher-level archosaur

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

phylogeny, which considers the relationships of rauisuchians along with a range of additional archosaur groups. This analysis yields a well-resolved but poorly-supported phylogeny, which places all rauisuchians in a single, monophyletic group. One of the best supported nodes in the entire analysis is a sister taxon relationship between *Teratosaurus* (scored almost entirely on what we now call *Polonosuchus*) and *Postosuchus* (scored entirely on the species *P. kirkpatricki*). This clade is supported by several characters, including the unequivocal presence of a deep pit in the caudodorsal region of the lateral surface of the squamosal. Additionally, the two share several distinctive characters that are not optimised as unequivocal synapomorphies but are rare among crurotarsans: a rugose ridge on the lateral surface of the skull roof, an enlarged triangular palpebral dorsal to the orbit (previously identified by Chatterjee 1985 and Sulej 2005 as an enlarged prefrontal), and a subdivided lower temporal fenestra. Furthermore, as discussed in this paper, the two taxa possess maxillae that are incredibly similar in both overall morphology and possession of shared characters, and only a unique combination of characters can diagnose *Polonosuchus* relative to *Postosuchus*. As *Teratosaurus*—which here refers only to the type maxilla of *T. suevicus*—is extremely similar to *Polonosuchus* and *Postosuchus*, it is probable that it is also a member of this clade.

Brusatte et al. (2008, in press) place "*Teratosaurus*" and *Postosuchus* into a larger "rauisuchid" group that also includes *Rauisuchus* (Huene 1942) and *Tikisuchus* (Chatterjee and Majumdar 1987). *Rauisuchus* is the closest outgroup to the *Teratosaurus* + *Postosuchus* group, and the three taxa are united by several features, most importantly a rugose lateral ridge on the jugal that is a continuation of the heavily rugose rim delimiting the antorbital fossa on the maxilla. The "rauisuchid" clade is sister taxon to a "prestosuchid" clade that includes *Batrachotomus*, *Prestosuchus*, and *Saurosuchus*. Other rauisuchian taxa fall into two distinct clades: a basal grouping centered on *Ticinosuchus* (Krebs 1965) and a poposauroid clade including sail-backed forms such as *Arizonasaurus* and bipedal cursors heavily convergent on dinosaurs (e.g., *Effigia*, *Poposaurus*, *Shuvosaurus*).

Acknowledgements

The first two authors contributed equally to this project and are listed alphabetically. SLB and RJB thank Jerzy Dzik (ZPAL) and their coauthors for access to specimens and warm hospitality during their visit to Warsaw; Michael Benton (University of Bristol, Bristol, UK) and Sterling Nesbitt (American Museum of Natural History, New York, NY, USA) for their reviews; and Paul Barrett (NHM) for comments. SLB thanks Mike Benton, Julia Desojo (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina), and Max Langer (Universidade de São Paulo, Ribeirão Preto, Brazil) for collaborating on his in press archosaur phylogenetic analysis; and numerous curators and researchers for discussion and access to specimens in their care: Angela Milner and Sandra Chapman (NHM); Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany); Zhao Xijin and Xu Xing (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China); Rainer Schoch (SMNS); Tim Rowe and Lyndon Murray (Texas Memorial Museum, Austin, TX, USA); Sankar Chatterjee, Bill Mueller, and Jeremiah Kokes (TTUP); Ronan Allain (Muséum national d'Histoire naturelle, Paris, France). SLB was supported by a Marshall Scholarship for study in the United Kingdom, and his specimen visit to Warsaw was funded by a Paleontological Society MAPS Student Research Grant. Additional funding was provided by the Jurassic Foundation (to SLB and Roger Benson, University of Cambridge, UK) and the Bob Savage Memorial Fund at the University of Bristol (to SLB). RJB was supported during this work by a NERC Small Grant (NE/ F009933/1; awarded to Paul Barrett, David Gower and RJB, NHM). Photographs of *Teratosaurus suevicus* were taken by Phil Crabb of the NHM Photo Unit. Photographs of *Polonosuchus* were taken by Grażyna Dziewińska (ZPAL).

References

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.

Barberena, M.C. 1978. A huge thecodont skull from the Triassic of Brazil. *Pesquisias* 7: 111–129.

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

Bonaparte, J.F. 1981. Descripción de "*Fasolasuchus tenax*" y su significado en la sistemática y evolución de los Thecodontia. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 3: 55–101.

Brusatte, S.L. and Sereno, P.C. 2007. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology* 27: 902–916.

Brusatte, S.L., Benson, R.B.J., Carr, T.D., Williamson, T.E., and Sereno, P.C. 2007. The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology* 27: 1052–1056.

Brusatte, S.L., Benton, M.J., Desojo, J.B., and Langer, M.C. (in press). The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology*.

Brusatte, S., Benton, M., Ruta, M., and Lloyd, G. 2008. The evolutionary history and higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Vertebrate Paleontology* 28: 58A.

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.

Dzik, J. 2001. A new *Paleorhinus* fauna in the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 21: 624–627.

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. and Sulej, T. 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontologia Polonica* 64: 3–27.

Edmund, A.G. 1960. Tooth replacement phenomena in the lower vertebrates. *Royal Ontario Museum, Life Science Division, Contributions* 52: 1–190.

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

Gower, D.J. 1999. Cranial osteology of a new rauisuchian archosaur from

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

the Middle Triassic of southern Germany. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Palaeontologie)* 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. and Nesbitt, S.J. 2006. The braincase of *Arizonasaurus babbitti* —further evidence for the non-monophyly of rauisuchians. *Journal of Vertebrate Paleontology* 26: 79–87.

Gower, D.J. and Schoch, R.R. 2009. Postcranial anatomy of the rauisuchian archosaur Batrachotomus kupferzellensis. *Journal of Vertebrate Paleontology* 29: 103–122.

Gower, D.J. and Wilkinson, M. 1996. Is there any consensus on basal archosaur phylogeny? *Proceedings of the Royal Society of London Series B* 263: 1399–1406.

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

Irmis, R.B. 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology* 27: 350–361.

Jalil, N.-E. and Peyer, K. 2007. A new rauisuchian (Archosauria, Suchia) from the Upper Triassic of the Argana Basin, Morocco. *Palaeontology* 50: 417–430.

Krebs, B. 1965. Die Triasfauna der Tessiner Kalkalpen. XIX. *Ticinosuchus ferox* nov. gen. nov. sp. . *Schweizerische Paläontologische Abhandlungen* 81: 1–140.

Li, C., Wu, X.-C., Cheng, Y.-N., Sato, T., and Wang, L. 2006. An unusual archosaurian from the marine Triassic of China. *Naturwissenschaften* 93: 200–206.

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

Lucas, S.G., Spielmann, J.A., and Hunt, A.P. 2007. Biochronological significance of Late Triassic tetrapods from Krasiejów, Poland. *In*: S.G. Lucas and J.A. Spielmann (eds.), The Global Triassic. *New Mexico Museum of Natural History and Science Bulletin* 41: 248–258.

Meyer, H. von 1861. Reptilien aus dem Stubensandstein des oberen Keupers. *Palaeontographica* 7: 253–346.

Nesbitt, S.J. 2003. *Arizonasaurus* and its implications for archosaur divergence. *Proceedings of the Royal Society of London Series B* (Supplement to No. 270): S234–S237.

Nesbitt, S.J. 2005. Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. *Historical Biology* 17: 19–47.

Nesbitt, S.J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History* 302: 1–84.

Nesbitt, S.J. and Norell, M.A. 2006. Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proceedings of the Royal Society of London Series B* 273: 1045–1048.

Sen, K. 2005. A new rauisuchian archosaur from the Middle Triassic of India. *Palaeontology* 48: 185–196.

Sill, W.D. 1974. The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecodonts. *Bulletin of the Museum of Comparative Zoology* 146: 317–362.

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

Sulej, T. 2005. A new rauisuchian reptile (Diapsida: Archosauria) from the Late Triassic of Poland. *Journal of Vertebrate Paleontology* 25: 78–86.

Sulej, T. 2007. Osteology, variability and evolution of *Metoposaurus*, a temnospondyl from the Late Triassic of Poland. *Palaeontologia Polonica* 64: 29–139.

Sulej, T. (in press). The skull of an early Late Triassic aetosaur and the evolution of the stagonolepidid archosaurian reptiles. *Zoological Journal of the Linnean Society*.

Sulej, T. and Majer, D. 2004. The temnospondyl amphibian *Cyclotosaurus* from the Late Triassic of Poland. *Palaeontology* 48: 157–170.

Weinbaum, J.C. and Hungerbühler, A. 2007. A revision of *Poposaurus gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern U.S.A. *Palaeontologische Zeitschrift* 81: 131–145.

Wilkinson, M. 1994. Common cladistic information and its consensus representations: reduced Adams and reduced cladistic consensus trees and profiles. *Systematic Biology* 43: 343–368.

Witmer, L.M. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with analysis of the function of pneumaticity. *Society of Vertebrate Paleontology Memoir* 3: 1–73.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use