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# A large predatory archosaur from the Late Triassic of Poland

GRZEGORZ NIEDŹWIEDZKI, TOMASZ SULEJ, and JERZY DZIK

Niedźwiedzki, G., Sulej, T., and Dzik, J. 2012. A large predatory archosaur from the Late Triassic of Poland. *Acta Palaeontologica Polonica* 57 (2): 267–276.

We describe a new large predatory archosaur, *Smok wawelski* gen. et sp. nov., from the latest Triassic (latest Norian–early Rhaetian; approximately 205–200 Ma) of Lisowice (Lipie Śląskie clay-pit) in southern Poland. The length of the reconstructed skeleton is 5–6 m and that of the skull 50–60 cm, making *S. wawelski* larger than any other known predatory archosaur from the Late Triassic and Early Jurassic of central Europe (including theropod dinosaurs and "rauisuchian" crurotarsans). The holotype braincase is associated with skull, pelvic and isolated limb-bones found in close proximity (within 30 m), and we regard them as belonging to the same individual. Large, apparently tridactyl tracks that occur in the same rock unit may have been left by animals of the same species. The highly autapomorphic braincase shows large attachment areas for hypertrophied protractor pterygoideus muscles on the lateral surface and a wide, funnel-like region between the basal tubera and basipterygoid processes on the ventral surface. The skeleton (cranial and postcranial) possesses some features similar to those in theropod dinosaurs and others to those in large crocodile-line archosaurs ("rauisuchians"), rendering phylogenetic placement of *S. wawelski* difficult at this time.

Key words: Archosauria, "Rauisuchia", Dinosauria, Norian–Rhaetian, Late Triassic, Poland.

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## Introduction

A new vertebrate-bearing locality of Late Triassic (latest Norian–early Rhaetian) age was recently reported from near Lisowice village (Lipie Śląskie clay-pit) in southern Poland (Dzik et al. 2008a, b). Since then, numerous vertebrate fossils have been collected from the clay-pit, including remains of a dicynodont and bones of archosauromorphs. Among the fossils, probably the most intriguing are the remains of a large predatory archosaur, which was tentatively identified by Dzik et al. (2008a) as a theropod dinosaur from features of the braincase and frontal. More material of the archosaur, including additional postcranial bones, was collected from this site in 2009 and 2010. Bones were found as three accumulations in a 2 m thick rock body, one accumulation including the skull bones and the others accumulations of postcranial elements. Because the bones match each other in size and preservation, and because there are no overlapping elements, these three accumulations seem to represent the disarticulated skeleton of a single individual (Fig. 1). We present here a short description of the new predatory archosaur, in which we compare it with other carnivorous Triassic archosaurs and provide evidence that it is a new species. The primary purpose of this paper is to name and diagnose this new taxon, which is clearly distinct from all known Triassic archosaurs. As this is an initial report, we do not extensively discuss the phylogenetic position of this taxon here (this task will be the subject of the first author's Ph.D. thesis), and for the time being we refrain from assigning it to one of the major predatory archosaur groups common in the Late Triassic (Ornithosuchidae, "Rauisuchia" or perhaps Theropoda; see Gower and Wilkinson 1996; Langer and Benton 2006; Brusatte et al. 2010a, b; Langer et al. 2010; Nesbitt 2011).

*Institutional abbreviation*.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

## Systematic palaeontology

Diapsida Osborn, 1903
Archosauromorpha von Huene, 1946
Archosauria Cope, 1869



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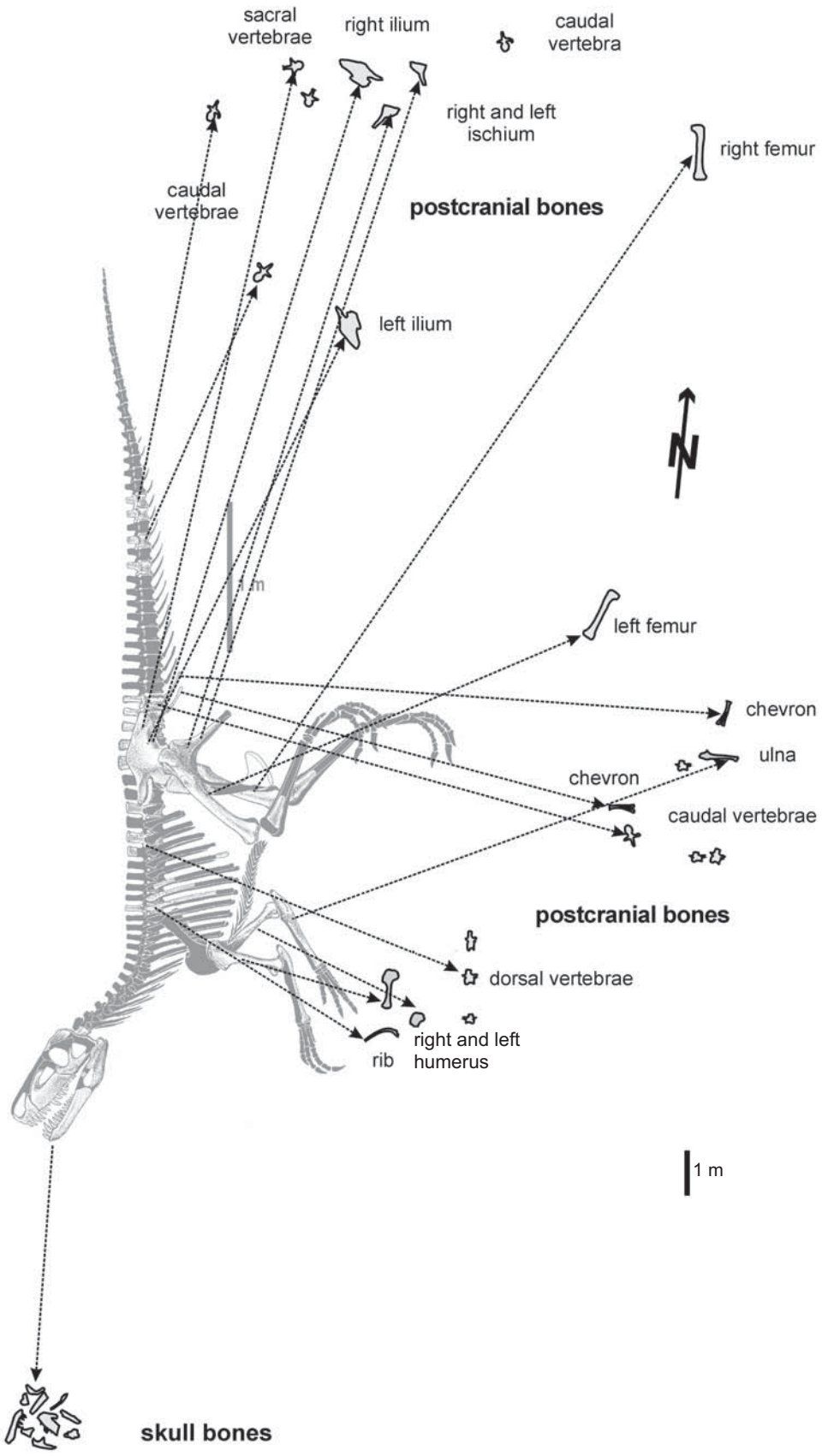



Fig. 1. Field sketch showing distribution of *Smok wawelski* gen. et sp. nov. bones within the dark fine-grained mudstone lens at Lipie Śląskie clay-pit at Lisowice and their inferred routes of dislocation from the cadaver, presumably by scavengers or by water currents. Particular bone outlines are enlarged to show their orientation. Large tridactyl footprints were found somewhat above this level and outside the mapped area.

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## Genus *Smok* nov.

*Type species*: *Smok wawelski* sp. nov.; see below.

*Etymology*: From Polish *smok*, a dragon.

*Diagnosis*.—As for the type and only species.

## *Smok wawelski* sp. nov.

Figs. 2–6, 7A.

*Etymology*: In reference to Wawel Hill in Kraków. *Smok wawelski* was a legendary dragon living in the cave at the Wawel Hill in Kraków in the region of southern Poland near the excavation site.

*Holotype*: ZPAL V.33/15, ventral part of the braincase with basioccipital and basisphenoid and a separate articulating piece of the right exoccipital-opisthotic, including approximately half of the paroccipital process (Figs. 2D, 3). This specimen is associated with a partially preserved skeleton; probably representing a single individual (see below; Fig. 1).

*Type locality*: Lisowice (Lipie Śląskie clay-pit) about 2 km west of Lubliniec, Silesia, southwestern Poland (Dzik et al. 2008a).

*Type horizon*: The strata exposed in the Lipie Śląskie clay-pit are correlatable with the upper part of the subsurface Zbąszynek Beds and lower part of the Wielichowo Beds (Late Triassic: latest Norian–early Rhaetian). These formations apparently continue into the Exter Formation of the Upper Keuper in the east German part of the Germanic Basin (see Franz et al. 2007a, b). Well-preserved vertebrate bones occur in a lenticular body of clayish, grey mudstone in the northern part of the Lipie Śląskie clay-pit. They are mostly covered with a calcareous and pyritic crust or embedded in limestone concretions. The fossil assemblage includes a large dicynodont, a small dinosauromorph, small archosaurs (pterosaur, poposauroid), a large capitosaur, a small plagiosaurid amphibian, dipnoan fish, a hybodont shark, and palaeonisciform fish (Dzik et al. 2008a, b).

*Referred material*.—Specimens ZPAL V.33/16–56, 97–102, 220, 238, 239, 295–298, 300, 302–304, 306–309, 311–314, 461, 507. All specimens were found in a 1.5 m thick horizon of claystone and mudstone (from the same horizon as the holotype specimen). The site extends for about 35 m roughly in a north-south direction and 20 m in an east-west direction, covering an area of some 700 $m^2$. Within this area, the bones form three accumulations (Fig. 1). Within the accumulation of skull bones, some were still in close association. Skull bones include: right premaxilla (Fig. 4A), left maxilla (Fig. 4B), both jugals (Fig. 4C), both frontals (Fig. 4D), parietal (Fig. 4E), left quadrate, left exoccipital, complete left dentary (Fig. 2B), three fragments of right dentary, left surangular, left angular, both splenials, and 17 isolated teeth (Fig. 6) of different sizes (with two teeth of very large size that do not belong to the same individual).

Whereas the skull bones occurred in close proximity to each other, the postcranial elements were rather widely dispersed (Fig. 1). Some 10 m north of the skull was found the right humerus, the proximal part of right ulna, a dorsal rib, the left femur, dorsal and caudal vertebrae, and two chevrons. Ten metres further north, we found the right femur, pelvic bones, and caudal and sacral vertebrae. The almost complete pelvis (Fig. 5) comprises partially preserved pubes, complete and partially preserved ilia, and partially preserved ischia fitting precisely to each other; this is strong evidence that they belong to the same individual. Both complete femora (Fig. 2C) were found in association with the pelvic elements. Despite being scattered over a rather wide area, the dispersal of the bones approximately reflects their original spatial relationships in the skeleton. The skull, forelimbs, hind limbs, and pelvic bones are arranged along an arch that corresponds to their original position in the body lying on its right side (Fig. 1). This suggests that the entire set of bones in this area, which correspond in size and do not show any duplication of elements, belongs to a single individual.

A right premaxilla (ZPAL V.33/461) and a partially preserved left pubis (ZPAL V.33/49) that may be referable to this taxon (that match the general size and morphology of the referred material of *Smok*) were collected in the same clay-pit, but at a different location and stratigraphic level. We therefore consider them as additional referred material. No other large archosaur bones have been found at Lisowice.

*Ichnological material*.—Six large and robust tridactyl tracks (ZPAL V.33/219, 508–510, and two uncollected specimens), preserved as natural casts and moulds (about 35–50 cm long), were also found at this site in sandstone layers about 1 m above the bone-bearing horizon (see Dzik et al. 2008b). These tracks are similar in shape to those made by Jurassic theropods, especially to tracks thought to be made by tetanurans or other mid-to-large bodied theropods (Gierliński et al. 2001, 2004). Because the crus and pes of *Smok* are unknown, it is not possible to conclusively demonstrate that it was the trackmaker.

*Diagnosis*.—Autapomorphies among archosaurs are designated with an asterisk (*) and the remaining features provide a diagnosis differentiating *Smok wawelski* from other carnivorous archosaurs (including currently known theropod dinosaurs, "rauisuchians", crocodylomorphs, ornithosuchids, and phytosaurs). Braincase with funnel-like expansion between the basal tubera and basipterygoid on the ventral surface, which is rounded in outline, much wider than the remainder of the ventral braincase, and indented by a deep pit at its caudal corner*. Nearly entire lateral surface of basisphenoid excavated by a deep fossa for the pterygoideus musculature, such that the midline region between the left and right fossae is extremely thin (< 2 mm)*. Short, sheet-like crista tuberalis (= metotic strut of many authors). Base of the paroccipital process higher than dorsal rim of occipital condyle. Premaxillary body longer than tall, massive, with four large teeth, poorly developed narial fossa, lacking subnarial gap and subnarial foramen between premaxilla and maxilla. Maxilla elongated, with a high body that retains a constant dorsoventral depth as it continues caudally, and with 11 or 12 teeth. Antorbital fenestra low and triangular in outline. Antorbital fossa small, developed only around anterior part of antorbital fenestra. Maxillary and dentary tooth crowns recurved distally, with serrations along both edges and with marginal enamel wrinkles. Postorbital process of jugal curved strongly posteriorly, such that its anterior margin is markedly convex*. Humerus with distinct longitudinal torsion of shaft. Deltopectoral crest less than 30% of length of

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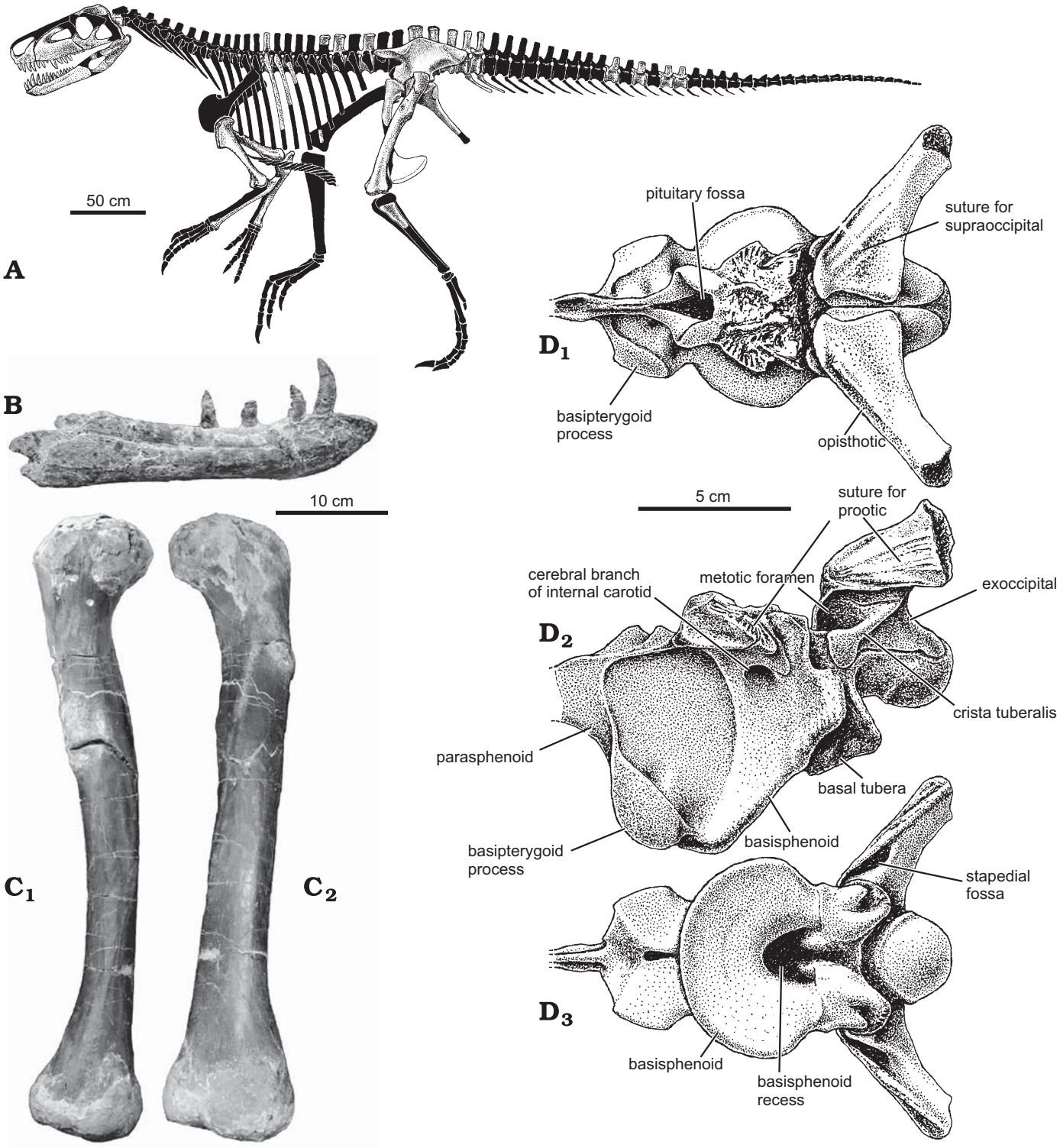



Fig. 2. A predatory archosaur *Smok wawelski* gen. et sp. nov., Lisowice (Lipie Śląskie clay-pit), Late Triassic (lates Norian–early Rhaetian). **A**. Skeletal restoration. **B**. Right dentary, ZPAL V.33/25, in lateral view. **C**. Left femur ZPAL V.33/45 in lateral ($C_1$) and cranial views ($C_2$). **D**. Reconstruction of partially preserved braincase ZPAL V.33/15,16, in dorsal ($D_1$), left lateral ($D_2$), and ventral ($D_3$) views.

humeral shaft. Ilium tall (less than 3.5 times longer craniocaudally than tall above acetabulum), robust with a dorsally extending buttress above the acetabulum, a triangular rugosity on posterior iliac blade, and an antitrochanter, but without a brevis fossa (sensu Novas 1996). Anterior process of ilium elongated such that it reaches past the cranial level of the pubic peduncle. Large, ovoid antitrochanter-like structure on the medial acetabular wall of the ilium, immediately

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caudal to pubic peduncle*. Sacrum composed of three vertebrae, two are broadly attached to ilia through sacral ribs. The transition from the femoral shaft to the femoral head is interrupted by a notch and shallow depression. Femur with a mound-like lesser trochanter (= anterior trochanter) that is not elevated, a ridge-like fourth trochanter, and no trochanteric shelf.

*Description*.—The skull reconstruction is based on specimens ZPAL V.33/15, 16, and 19–27. The skull length of *Smok wawelski* is estimated to be 48 to 57 cm based on the premaxilla, maxilla and jugal bones (Fig. 4).

The premaxilla and maxilla (Fig. 4A, B) are closely and tightly articulated, so that there is no space for a subnarial gap along the tooth row (such as that present in some basal theropod dinosaurs and ornithosuchid crurotarsans: Rauhut 2003; Langer and Benton 2006; Brusatte et al. 2010a), a subnarial foramen on the lateral surface between the bones, or a laterally facing slit-like opening between the bones that has often been described in "rauisuchian" archosaurs (Benton and Clark 1988, but see Nesbitt 2011). On the premaxilla (Fig. 4A), the narial fossa is shallow and only slightly expanded into the cranioventral corner of the external naris. This feature is clearly visible on both known premaxillae (ZPAL V.33/19 and V.33/461). On the medial surface, the palatal process is a large, extensive flange that projects far medially to articulate with the opposing premaxilla on the midline.

The maxilla is a large and robust bone (Fig. 4B), which comprises an ascending process dorsally and a main body caudally. There is no discrete rostral ramus, set off from the ascending process by a concave step; rather, the rostral surface of the main body and ascending ramus describe a smooth, convex arc. The main body maintains a relatively constant depth as it continues caudally. The antorbital fenestra is an elongate, triangular opening that tapers to a point rostrally; it is bordered by an antorbital fossa that is deeply inset rostroventral to the fenestra, but is not expressed ventral to the fenestra on the lateral surface of the maxilla. Because the fossa is not present underneath the fenestra, this surface of the maxilla is smooth, without any rugose rim separating the fossa from the subcutaneous lateral surface of the bone. On the medial surface, the rostromedial process (= palatal process) is an extensive flange that projects far medially to articulate with the opposing maxilla and form a broad palate, which also includes the palatal process of the premaxillae (see above).

The jugals are both incomplete, but clearly there was a pronounced convex ridge on the lateral surface of the bone underneath the antorbital fenestra and orbit. The ascending process for the postorbital is strongly curved caudally (Fig. 4C). On the medial surface, there are two distinct articular depressions for the ectopterygoid, which are separated by a deep, non-articular furrow.

The frontal and postfrontal are co-ossified (Fig. 4D), but their suture is clearly visible, on both sides of the skull. The frontal did not contribute to the orbital rim, as there is a continuous series of articular surfaces for the lacrimal, prefrontal, and possibly palpebral on the lateral surfaces of the frontal and postfrontal. The supratemporal fossa continues rostrally onto the frontal and postfrontal and is demarcated rostrally by a pronounced rim (Fig. 4D). The posterior wall of the parietal forms a relatively straight caudal surface of the skull in dorsal view. Only the left parietal is known, but it is clearly unfused to the unpreserved right bone. There is a small sagittal crest along the midline (Fig. 4E).

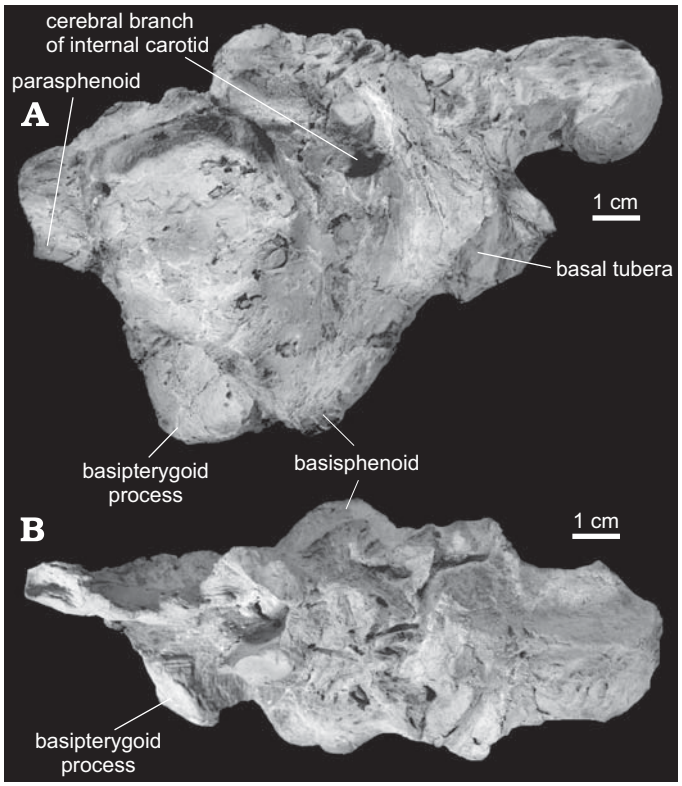



Fig. 3. A predatory archosaur *Smok wawelski* gen. et sp. nov., Lisowice (Lipie Śląskie clay-pit), Late Triassic (lates Norian–early Rhaetian). Partially preserved braincase, ZPAL V.33/15, in left lateral (**A**) and dorsal views (**B**). Note that the right exoccipital-opisthotic, which is preserved as a separate piece, is not shown in the photo but is depicted in the reconstruction drawing in Fig. 2D.

In the highly derived braincase, two remarkable autapomorphies are apparent. First, on the ventral surface of the basisphenoid, between the basal tubera and basipterygoid processes, is a wide, funnel-like structure (Figs. 2D, 3). This region is circular in outline and projects laterally relative to the remainder of the ventral surface, unlike the condition in most archosaurian braincases in which the region between the tubera and basipterygoid processes is constricted (e.g., Gower 2002; Rauhut 2004; Brusatte et al. 2010c; Nesbitt 2011). At its caudal corner, immediately rostral to the basal tubera, is a deep, inset pit that appears to end blindly and not connect to any internal pneumatic recesses. Second, on the lateral surface of the braincase, nearly the entire basisphenoid is excavated by a broad fossa, demarcated rostrally by a sharp ridge and caudally by the region of the bone that includes the fenestra ovalis and various foramina for the inter-

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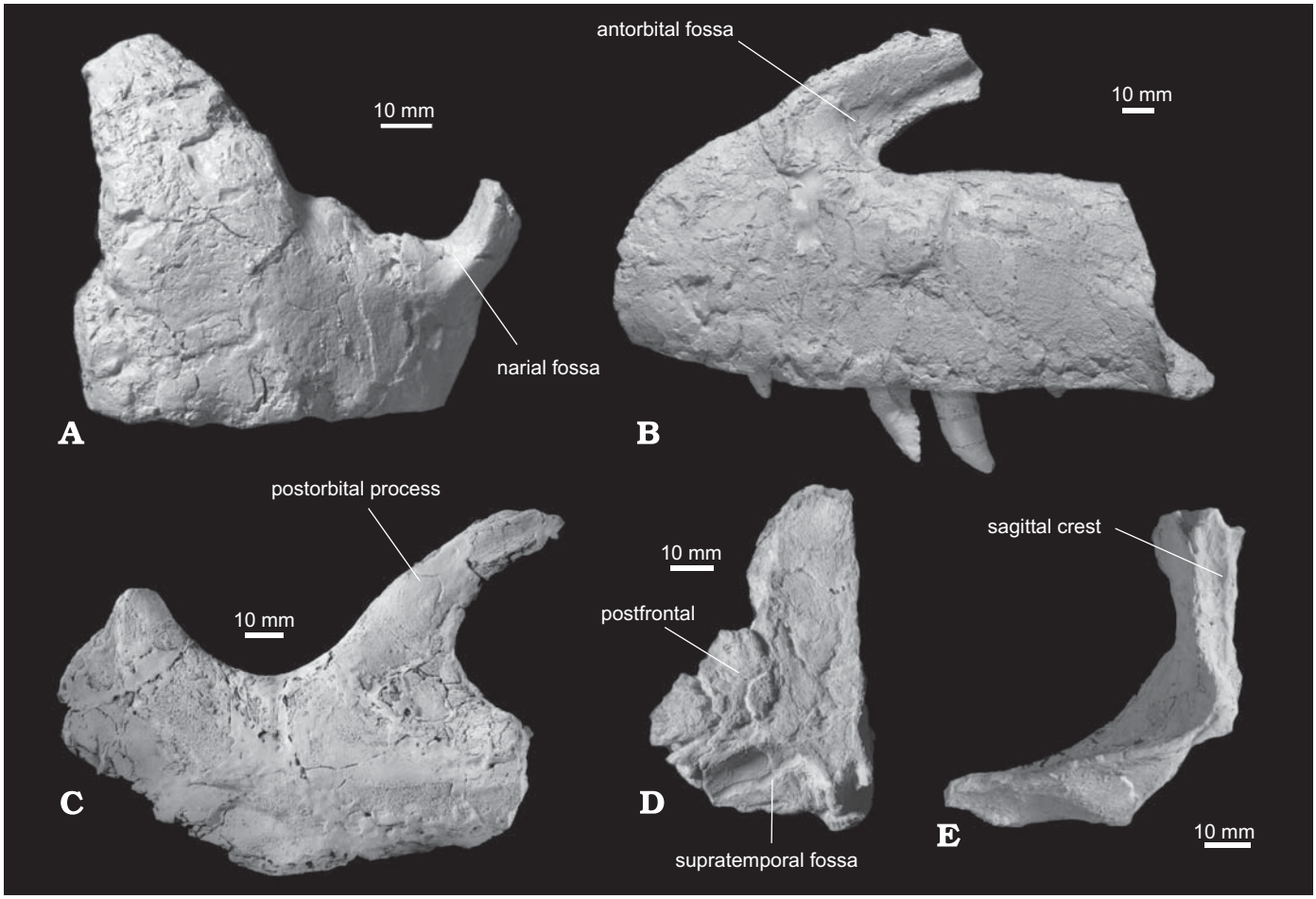



Fig. 4. A predatory archosaur *Smok wawelski* gen. et sp. nov., Lisowice (Lipie Śląskie clay-pit), Late Triassic (lates Norian–early Rhaetian). **A**. Right premaxilla, ZPAL V.33/19, in lateral view. **B**. Left maxilla, ZPAL V.33/20, in lateral view. **C**. Left jugal, ZPAL V.33/97, in lateral view. **D**. Left frontal, ZPALV.33/21, in dorsal view. **E**. Left parietal, ZPAL V.33/98, in dorsal view.

nal carotid and cranial nerves. The left and ridge fossae are so inset that merely a few millimetres of bone are present between them; clearly, this region is so thin that it does not include any internal pneumatic recesses like those common in theropod dinosaurs (Rauhut 2004). It is likely that this fossa is an increased attachment area for large pterygoideus musculature, which connected to this region of the braincase (Holliday and Witmer 2007, 2008). There does not appear to be a rugose and pronounced preotic pendant on the basisphenoid, which commonly anchors enlarged pterygoideus muscles in large theropods (Chure and Madsen 1998; Holliday and Witmer 2008).

On the posterior surface of the braincase, a sheet-like crista tuberalis (= metotic strut) is visible, separating the caudal and lateral surfaces of the braincase (Fig. 2D). There is no clear exit foramen for the hypoglossal (XII) nerve on the posterior surface of the basioccipital medial to the crista. The base of the paroccipital process is situated higher than the dorsal rim of the occipital condyle and the condyle is nearly spherical in shape, comprised primarily of the basioccipital but also the short lateral pedicels of the exoccipital-opisthotics.

Maxillary and dentary tooth crowns are distally curved with serrations along both edges and enamel wrinkles (Brusatte et al. 2007), which sweep down and away from the serrations on the distal margins of the labial and lingual surfaces (Fig. 6). The maxilla and dentary both have a low number of teeth (maxilla: 11 or 12; dentary: 14), whereas the premaxilla has four large alveoli that are more circular than those of the maxilla and dentary.

The dentary bears a marked lateral groove, which demarcates an emargination that corresponds to half the transverse width of the bone. The rostral dentary is not expanded relative to the caudal portion of the bone, and the groove for the dental lamina is widely visible in dorsal view (from the robust mediolateral thickness of the bone here). The surangular is marked by a pronounced shelf on its lateral surface, and the surangular foramen was either small or absent.

The proximal region of the humerus preserves a deltopectoral crest that is approximately 30% of the length of the bone and continuous with the proximal surface, not offset from it by a discrete notch. The medial margin of the proximal humerus is strongly arched (Sereno 1991). The head is a bulbous, ovoid structure that is convex proximally and overhangs the caudal, but not the cranial, surface of the proximal humerus. The distal end of the humerus bears two confluent but distinct, rounded condyles for articulation with the radius

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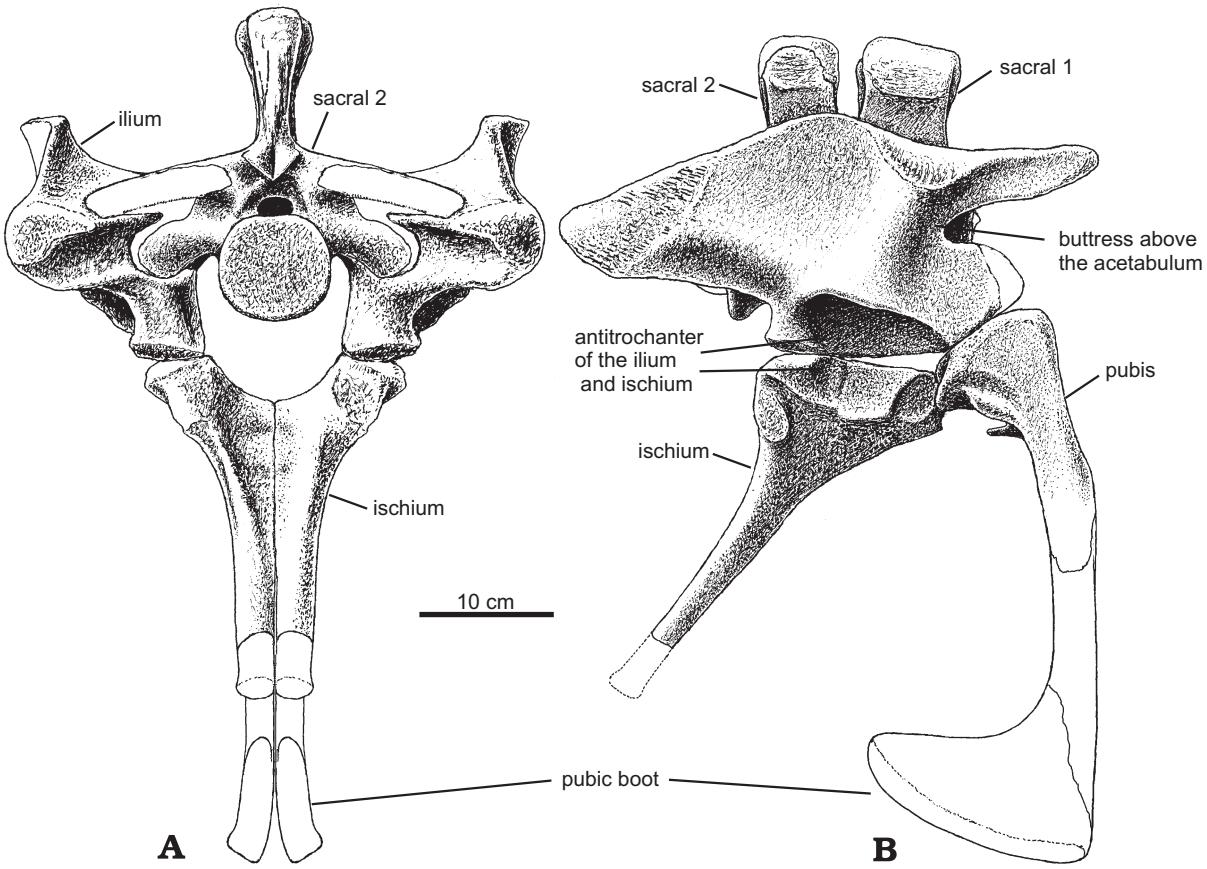



Fig. 5. A predatory archosaur *Smok wawelski* gen. et sp. nov., Lisowice (Lipie Śląskie clay-pit), Late Triassic (lates Norian–early Rhaetian). Pelvic girdle with sacrals (based on specimens ZPAL V.33/298, 300, 302–304), in posterior (**A**) and lateral (**B**) views.

and ulna, as in most archosaurs. The longitudinal torsion of the humeral shaft is easily visible, as the axis of the distal condyles is rotated more than 45° from the long axis of the proximal surface.

In the almost complete set of pelvic bones represented in the collection (Fig. 5), the sacral ribs fit well in depressions on the ilia, although their distal ends are not preserved. Two main sacral vertebrae were present (and are preserved), and the attachment sites on the medial ilium suggest that a dorsosacral also made contact with the tip of the preacetabular process. The ilium is a large, robust bone whose dorsal blade is tall (the craniocaudal length of the blade is less than 3.5 times the height above the acetabulum). The preacetabular process is smaller and more gracile than the postacetabular process, and no brevis fossa (sensu Novas 1996 and Langer and Benton 2006) is present. The acetabulum is closed, as the ventral margin of the ilium is convex. There is a distinct antitrochanter on the ischial peduncle, continuous with the antitrochanter on the ischium. Cranially, the acetabular wall of the ilium is marked by a unique structure: a nearly flat, ovoid surface, offset from the antitrochanter and smooth surface of the remainder of the acetabulum. Its function is unknown, but it may have acted somewhat like the iliac+ischial antitrochanter to limit the range of motion of the femur cranially. There is a pronounced buttress on the lateral surface of the ilium, continuing dorsally from the supraacetabular crest and expanding in craniocaudal width dorsally (Gower 2000).

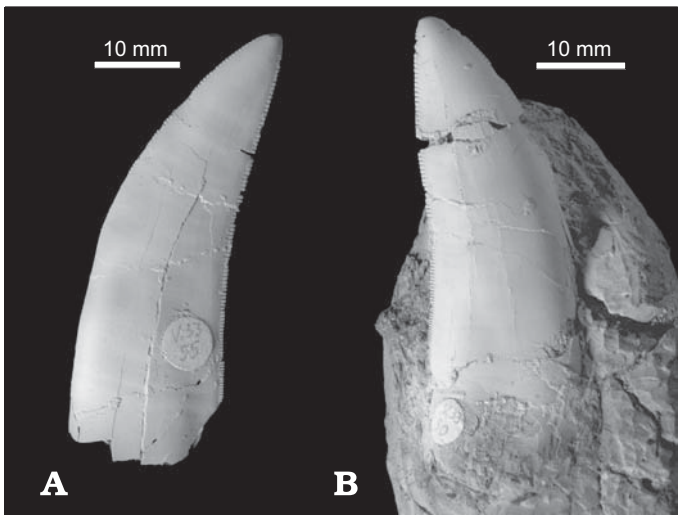



Fig. 6. A predatory archosaur *Smok wawelski* gen. et sp. nov., Lisowice (Lipie Śląskie clay-pit), Late Triassic (lates Norian–early Rhaetian). Isolated teeth in lateral view. **A**. ZPAL V.33/55. **B**. ZPAL V.33/50.

Two incomplete pubes suggest this bone was elongated and distally terminated in a large pubic "boot" (Fig. 5B). Although incompletely preserved, the pubes ZPAL.V.33/49

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Fig. 7. Comparison of the morphology and sizes of femur bones of the Late Triassic archosaurs (all in anterior views). **A**. Femur of *Smok wawelski* gen. et sp. nov., ZPAL V.33/45, Lisowice (Lipie Śląskie clay-pit), Late Triassic (lates Norian–early Rhaetian). **B**. Femur of *Liliensternus liliensterni* (Huene, 1934), MB.R.2175.7.1, Grossen Gleichberg, Germany, Late Triassic (early Rhaetian). **C**. Femur of *Postosuchus kirckparicki* Chatterjee, 1985, TTU-P9002, Miller's Ranch Quarry, Texas, USA (Norian).

and ZPAL.V.33/99 indicate that the obturator foramen was closed ventrally and that the obturator plate was strongly reduced (Hutchinson 2001a). The ischium has a large antitrochanter, which is separated from the pubic peduncle by a narrow, but deeply inset, non-articular notch. The caudal edge of the proximal region bears a rugose, depressed muscle scar, which is separated from an elongate groove on the posterior surface distally. These structures are probably homologous with the ischial tubercle (Hutchinson 2001a).

The femur (Figs. 2C, 7A) is bowed cranially and has a head whose long axis projects craniomedially in proximal view, approximately 45° relative to the long axis of the distal condyles. The head is continuous distally with the shaft; the two are smoothly confluent and not offset by a discrete notch or emargination (Nesbitt 2011). The head is ovoid in proximal view and expands in width medially; it has two tubera on its cranial surface and one on its caudal surface, as is plesiomorphic for archosaurs (Nesbitt 2011). There is no distinct antitrochanteric fossa on the caudolateral corner of the proximal end (Novas 1996). The cranial surface of the proximal femur, immediately below the head, bears a mound-like muscle attachment, which is in the position of the anterior (= lesser) trochanter of many archosaurs and likely homologous (Hutchinson 2001b). There is no trochanteric shelf linking this structure with the greater trochanter, however. The greater trochanter, visible on the lateral surface of the proximal end, is convex dorsally. There is also an elongate, rugose, but low fourth trochanter on the caudal surface. Distally, there is a groove on the lateral surface between the fibular condyle and lateral condyle.

*Remarks*.—As this paper is a preliminary report naming *Smok wawelski* as a new taxon and noting its most salient features, we provide only a general discussion on its potential phylogenetic position. A more complete description of the osteology of *S. wawelski*, along with a more comprehensive treatment of its phylogenetic position, will be the subject of the first author's Ph.D. thesis, which is currently in progress. Determining the phylogenetic position of *Smok* is difficult, as it possesses many features that are common in disparate groups of basal archosaurs. This is a general problem that plagues current studies of Triassic archosaurs: homoplasy, convergent evolution, and reversals were common during the evolution of these animals, which makes cladistic analyses potentially prone to serious errors (e.g., Brusatte et al. 2010a; Nesbitt 2011). It is now known that some dinosaurs and Triassic crocodile-line archosaurs were highly convergent on each other (e.g., Benton and Clark 1988; Parker et al. 2005; Nesbitt and Norell 2006; Nesbitt 2007; Brusatte et al. 2008), and nearly every character that was once considered a confident diagnostic feature of dinosaurs (e.g., Bakker and Galton 1974) is now known in at least some crocodile-line taxa (Brusatte et al. 2010b; Nesbitt 2011). Therefore, instead of providing a new cladistic analysis or making a firm statement about the phylogenetic position of *Smok*, we review characters that: (i) confirm its status as an archosaur and (ii) may be shared with some archosaurs, and thus may place it within archosaur ingroups.

*Smok* is clearly an archosauromorph, as it possesses many features recently reviewed by Nesbitt (2011) that are present in members of this group. These include the absence of a parietal foramen, the presence of a jugal-quadratojugal contact, an antorbital fenestra, and teeth with serrations. *Smok* is also a member of Archosauria (which Nesbitt 2011 used to refer to the group comprising the most recent common ancestor of crocodiles and birds and their descendants), as it possesses palatal processes of the maxilla that meet on the midline and a rostromedial tuber on the proximal femur.

Placing *Smok* within Archosauria is more challenging. It possesses some features that are common in dinosaurs, and have long been regarded as characters unique to dinosaurs (and, in some cases, their closest dinosauromorph relatives). These include a supratemporal fossa that extends onto the frontal, three sacral vertebrae, an antitrochanter extending onto the ilium, and an anterior trochanter on the femur (Bakker and Galton 1974; Gauthier 1986; Sereno 1991, 1999; Langer and Benton 2006; Brusatte et al. 2010a, b; Nesbitt 2011). Some features, especially of the braincase, seem reminiscent of larger and more derived theropods, including an increased attachment area for the pterygoideus musculature on the lateral surface of the braincase (Holliday and Witmer 2008). However, other features are shared with

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some crocodile-line archosaurs, especially "rauisuchians" such as *Postosuchus* and *Polonosuchus* (Chatterjee 1985; Long and Murry 1995; Sulej 2005; Brusatte et al. 2009; Weinbaum 2011). These include a triangular antorbital fenestra, flange-like palatal processes on the premaxilla and maxilla, a bifurcated articular surface for the ectopterygoid on the jugal, and a buttress on the lateral surface of the ilium above the acetabulum (Gower 2000; Brusatte et al. 2010a; Nesbitt 2011). Finally, *Smok* also possesses several primitive archosaur or archosauromorph features, which may be unexpected in a derived "rauisuchian" or theropod, including a seemingly non-pneumatic braincase (which clearly lacks the subsellar and lateral basipterygoid recesses: Rauhut 2004), paroccipital processes that are located dorsal to the occipital condyle, a postfrontal, spine tables on the dorsal vertebrae, and a closed acetabulum.

*Geographic and stratigraphic range*.—Type locality and horizon only.

# Conclusion

Clearly, *Smok wawelski* possesses a mosaic of primitive archosaur, crocodile-line archosaur, and dinosaur characters. Its discovery shows that large predators were represented in the Late Triassic of Central Europe, contributing to a rich community that included a large dicynodont, a small poposauroid, and a small dinosauromorph. Previously known remains of large predators from this region include theropods such as *Liliensternus* and "rauisuchians" like *Polonosuchus* and *Teratosaurus*, but these were much smaller than *Smok* (Fig. 7). *Smok* was a huge animal for the Late Triassic, and is probably among the largest archosaurs from anywhere in the world (compared to *Postosuchus*, *Fasolasuchus*, *Liliensternus*, and *Gojirasaurus*, as well as *Zupaysaurus*; see Gower and Wilkinson 1996; Brusatte et al. 2010a, b; Langer et al. 2010). The fine preservation of the holotype and referred material of *Smok*, along with the large percentage of bones preserved from across the skeleton, also present a remarkable opportunity for understanding the anatomy of large European Late Triassic carnivores in unprecedented detail. Additional description of the material, as well as a more comprehensive analysis of its phylogenetic position, will follow.

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