

CT scanning, rapid prototyping and re-examination of a partial skull of a basal crocodylomorph from the Late Triassic of Germany

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Abstract An incomplete skull (SMNS 12352) from the Norian (Late Triassic), found at the same locality (Pfaffenhofen, Germany) as *Procompsognathus triassicus*, has previously been attributed to either a theropod or a crocodylomorph. The specimen is partially embedded in matrix and, therefore, was CT scanned so that the concealed portion could be visualized and a 3D model could be printed by means of rapid prototyping. Mainly based on the separation between the nasal and the antorbital fossa, the skull likely pertains to an indeterminate basal crocodylomorph (non-Crocodyliformes), which is, however, distinct from *Saltoposuchus connectens*.

Keywords Archosauria · *Procompsognathus* · *Saltoposuchus* · Stubensandstein · 3D printing

Abbreviation

SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany

1 Introduction

Huene (1921) noted the existence of a second specimen of *Procompsognathus triassicus* found in 1908 in the same strata and at the same locality (Pfaffenhofen, Baden-Württemberg, Germany) as the incomplete dinosaur skeleton (SMNS 12591, two pieces) that forms the type of the taxon (Fraas 1913). This second specimen consists of half a skull (SMNS 12352; Fig. 1) and a manus (SMNS 12352a), which were found purportedly in close association. Huene (1921) was unable to find significant distinctive morphological characters differentiating the specimens SMNS 12591a (a skull originally attributed to *P. triassicus*) and SMNS 12352. He noted slight differences, but considered that they were probably age- or sex-related. Huene (1921) concluded that a shared generic identity was undeniable and assigned SMNS 12352 to *P. cf. triassicus*. Huene (1921) noted, especially in the skull, resemblances between *Procompsognathus* and “pseudosuchians” (this taxon name was then used for a polyphyletic grouping of Archosauriformes; see Huene 1920). Furthermore, in his monumental monograph on the Saurischia, Huene (1932, p. 343) underlined the similarity in both the skull and part of the postcranial skeleton between *Procompsognathus* and “pseudosuchians” such as *Saltoposuchus*. In the same way, Boule and Piveteau (1935, p. 471) judged that the skull of *Procompsognathus* resembles both that of some pseudosuchians (*Aetosaurus*) and that of primitive birds.

Ostrom (1978) compared *Compsognathus longipes* with *P. triassicus* as part of his monograph on the former taxon. He noted that the referral of SMNS 12352 to *P. triassicus* should be viewed with scepticism. Ostrom (1981) expanded upon his opinion regarding the identity of this specimen, considering it not referable to *Procompsognathus*, but not offering details as to its real affinities. Welles

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Fig. 1 SMNS 12352, incomplete skull and mandibles, “sphenosuchian” crocodylomorph. *Scale bar* = 5 cm

(1984), in his anatomical study of *Dilophosaurus wetherilli*, suggested that SMNS 12352 has characteristics of *Pseudosuchia* and might well be referred to *Saltoposuchus connectens*. Sereno and Wild (1992) offered a well-argued interpretation of the nature of the main specimens classified as *Procompsognathus*. These authors concluded that SMNS 12352 can be referred to the crocodylomorph *S. connectens*.

The aim of this paper is to revise the systematic position of SMNS 12352. Information provided by further preparation that has revealed partially the left lateral surface of the skull and, above all, high-resolution X-ray CT data (Fig. 2) and full preparation of another key specimen (SMNS 12591a) will be used for this purpose. This paper builds upon previous work carried out by Knoll (2008).

2 Materials and methods

The specimen was scanned on a Phoenix vltomelx s (General Electric) CT scanner with a voltage of 200 kV and a current of 200 μ A. The pixel matrix was 512 \times 512 and the slice thickness was 0.096 mm. The next step was to virtually isolate the skull in Rapidform2006 (Inus Technology) by eliminating all the voxels that did not represent bony or dental material, but represented instead sandstone matrix or plaster. This was done by taking as criteria the spatial position and the absorption values of the voxels (removing voxels that were outside the skull area and those with absorption below the threshold value of 7,500). The resulting data was corrected for plastic deformation undergone by the skull during diagenesis using iterations and a best-fit

method. Then, the virtual model was enlarged with scale factor 5. The 3D printing was carried out using a Z406 (Z Corporation). The resulting model (Fig. 3) in plaster-based material was finally coated with polyurethane for fixing.

Even though the use of CT-scan is today common in palaeontology, this is not the case for rapid prototyping technologies (see Bristow et al. (2004) for one of the few published examples in the field of fossil archosaurs). However, rapid prototyping allows the replications of specimens whose complex morphology, fragility or state of physical preparation would make any traditional molding difficult if not impossible.

3 Systematic palaeontology

Archosauriformes Gauthier et al. 1988 sensu Nesbitt 2011
 Archosauria Cope 1869 sensu Sereno 2005
 Pseudosuchia Zittel 1890 sensu Senter 2005
 Suchia Krebs 1974 sensu Nesbitt 2011
 Paracrocodylomorpha Parrish 1993 sensu Sereno 2005
 Loricata MERREM 1820 sensu Nesbitt 2011
 Crocodylomorpha Hay 1930 sensu Nesbitt 2011

Description SMNS 12352 (Figs. 1–3) was described to a certain extent by Huene (1921), Ostrom (1981), and Sereno and Wild (1992) and this will not be repeated here. The CT scanning coupled with rapid prototyping revealed characters that were, until then, concealed. For instance, the long tooth roots could be visualized. More interestingly, data on the anatomy of the palate could be obtained. The preserved portion of the skull in SMNS 12352 revealed the choanae completely. They are shaped like long ellipsoids (as in *Pseudhesperosuchus jachaleri* (Bonaparte 1972, Fig. 24)), between which a ventral septum extends longitudinally along most of the palate. The latter is presumably formed by the vomers rostrally and the pterygoids caudally. This septum subsides toward the rostral portion of the palate, which is formed by the premaxillae and maxillae. Caudally, the palate bears a median dorsal process probably constituted by the palatines.

Discussion Ostrom (1981, p. 189) assumed that SMNS 12352 does not belong to *Procompsognathus* essentially on the basis of the following differences: (1) it was probably much deeper dorso-ventrally than SMNS 12591a; (2) it has the caudal boundary of the antorbital fossa sloping rostrally instead of caudally as in SMNS 12591a; and (3) it has the antorbital fenestra situated more caudally than in SMNS 12591a. He added that SMNS 12352 has also a longer maxillary tooth row and more strongly developed variation in tooth size.

Sereno and Wild (1992, p. 444) noted that the difference in skull profile is suspect because of the differing type of

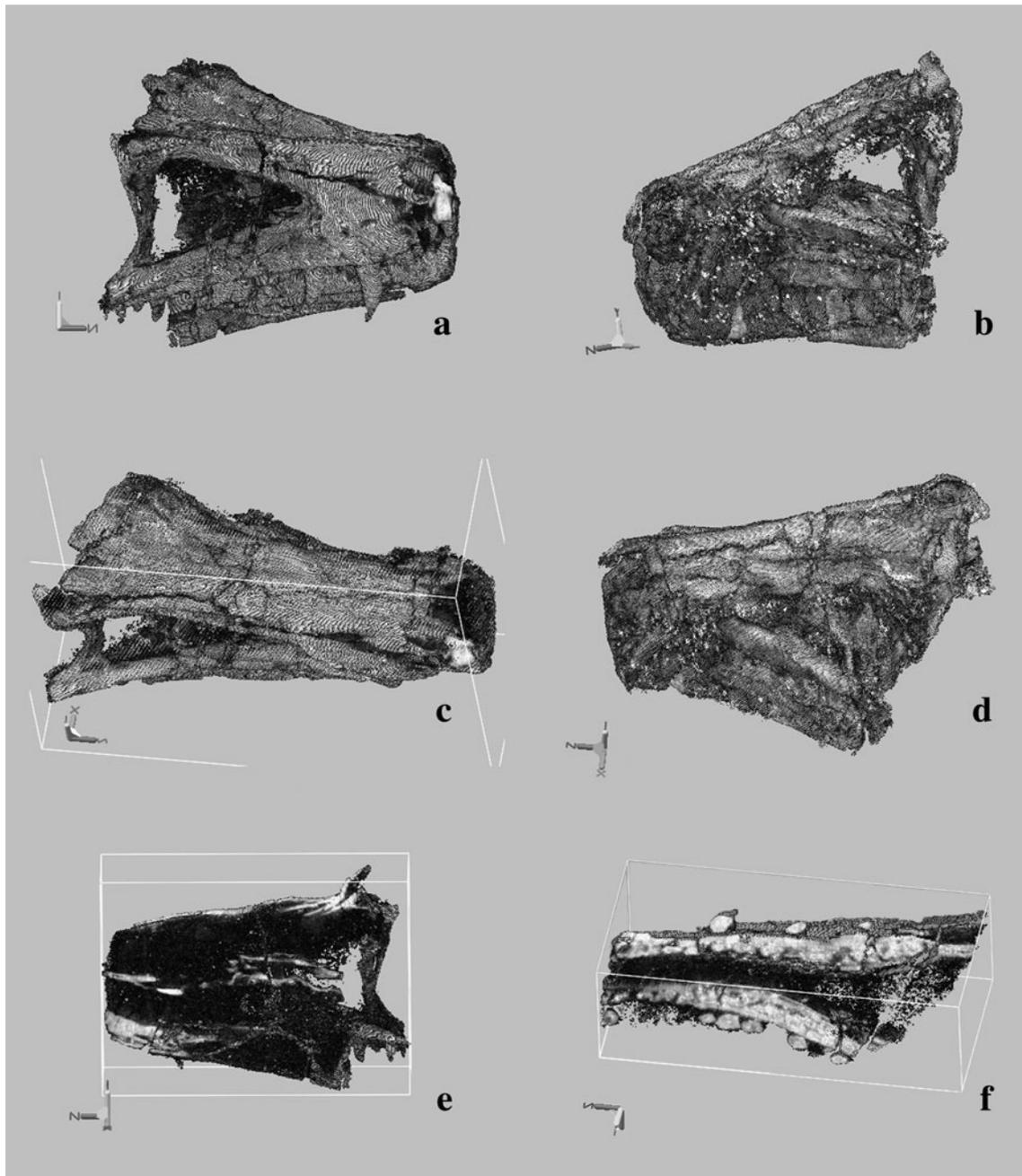


Fig. 2 SMNS 12352, incomplete skull and mandibles, “sphenosuchian” crocodylomorph. CT scans: **a** right lateral view; **b** left lateral view; **c** oblique right dorsal view; **d** oblique left dorsal view; **e** sagittal cut; **f** transverse cut. Z is directed rostrally, I dorsally, and X sinistrally

deformation experienced by each specimen. They added that the distinctions in the shape and position of the antorbital fossa and fenestra are due to misidentification of the palatine as part of the lacrimal in SMNS 12591a.

Whereas difference (1) is indeed problematic following the deformation of both specimens, we believe that distinctions (2) and (3) put forward by Ostrom (1981) are correct. The rostradorsal inclination of the caudal margin of the antorbital fossa of SMNS 12352 is conspicuous and

has no equivalent in SMNS 12591a, in which the fossa appears quite open caudally (Fig. 4a, b). Furthermore, we interpret the antorbital fenestrae of the two specimens as completely distinct in position and, above all, shape. Whereas the antorbital fenestra of SMNS 12591a is round and placed in the caudodorsal corner of the fossa (Fig. 4a, b), that of SMNS 12352 is longitudinally elongated and positioned in the caudoventral corner (as in *Litargosuchus leptorhynchus* (Clark and Sues 2002, Fig. 2)). In addition,

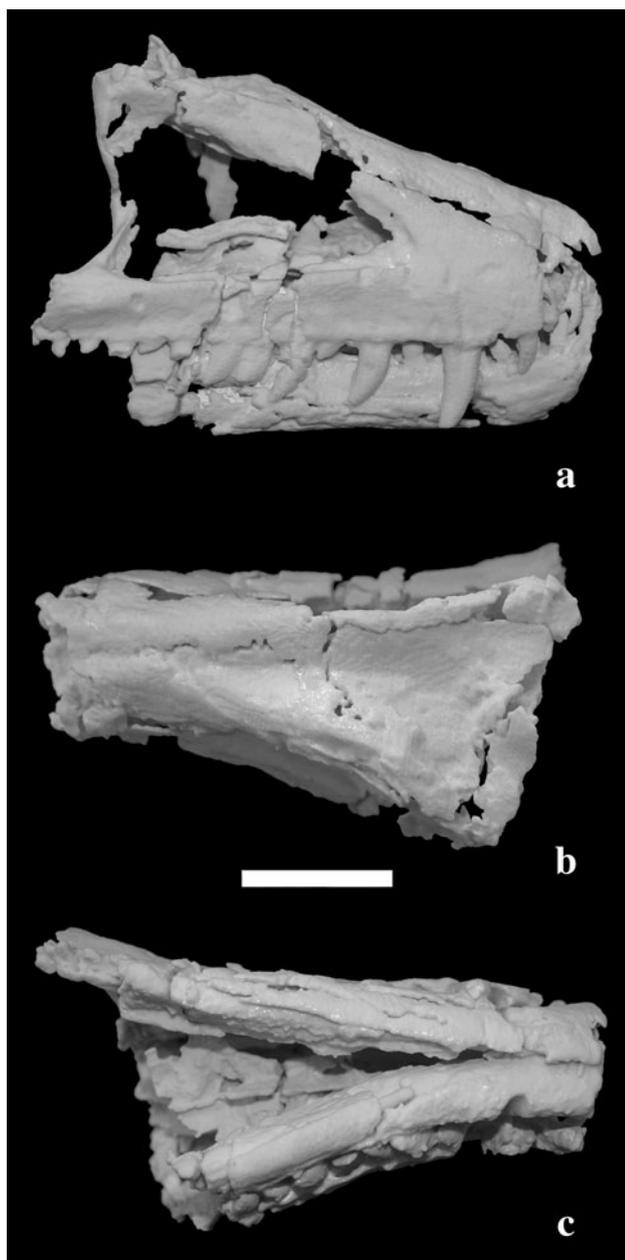


Fig. 3 SMNS 12352, incomplete skull and mandibles, “sphenosuchian” crocodylomorph. Rapid prototyping model: **a** right lateral view; **b** dorsal view; **c** ventral view. Scale bar = 5 cm

there are significant dental differences between the two specimens. Previous authors did not note that the teeth of SMNS 12352 show similar denticles on both carinae, whereas those of SMNS 12591a are more derived in having stronger denticles on the distal edge. The apices of the crowns are also directed distinctly more caudally in SMNS 12591a than in SMNS 12352. Finally, SMNS 12352 has curved mandibles (labially concave, as in e.g., *Dibothrosuchus elaphros* (Wu and Chatterjee 1993, Fig. 4c)), whereas SMNS 12591a has straight mandibular rami

(Fig. 4d). We, therefore, concur with Ostrom (1981) in rejecting the hypothesis that SMNS 12591a and SMNS 12352 belong to the same species.

Sereno and Wild (1992) assigned SMNS 12352 to *S. connectens*. Yet there are some differences between SMNS 12352 and SMNS 12596 (the type material of *S. connectens*) that cast doubt on a shared specific identity. In SMNS 12352, the rostral tip of the antorbital fenestra diverges from the ventral margin of the antorbital fossa, whereas in SMNS 12596 (Fig. 5) the entire ventral border of the antorbital fenestra along its tip is parallel to the ventral margin of the fossa. In addition, the tip of the antorbital fenestra forms a sharper angle in SMNS 12596 than in SMNS 12352 and, at the level of the rostral part of the antorbital fenestra, the depth of the lateral surface of the maxilla is clearly greater than the depth of the antorbital fenestra in SMNS 12596 but not in SMNS 12352.

In light of these differences, we consider that SMNS 12352 is certainly not referable to *S. connectens*. However, whether or not this specimen belongs to another basal crocodylomorph, or to a different terrestrial carnivorous archosaur, is not easy to resolve because of its incompleteness.

Welles (1984, p. 171) remarked that SMNS 12352 is similar to the Chinese Early Jurassic taxon *Lukousaurus yini* (Young 1948; Fig. 1, pl. 1). Young (1948, p. 78) previously noted similarities between *Procompsognathus* and *Lukousaurus*, and he provisionally considered the latter as a coelurosaur. Welles (1984, p. 171) considered *Lukousaurus* as seemingly a pseudosuchian rather than a theropod, but nonetheless listed it as “Theropoda, incertae sedis” (Welles 1984, p. 177). Norman (1990, p. 296) considered the partial type skull of *Lukousaurus* as “theropod-like”, but Irmis (2004, p. 14) suggested that this material is most likely from a crocodylomorph. *Lukousaurus* is an enigmatic taxon of carnivorous archosaur based essentially on the rostral portion of a small skull (with a triangular antorbital fenestra). It awaits re-description, but the published evidence (Young 1948, Fig. 1, pl. 1) shows no affinity with tetanuran (absence of maxillary fenestra, etc.) or coelophysoid (absence of subnarial diastema, etc.) theropods. In contrast, it looks pseudosuchian-like and especially “sphenosuchian”-like (shape and size of the antorbital fossa, etc.) so that we consider *Lukousaurus* a possible “sphenosuchian” and certainly not a theropod.

Welles (1984, p. 173) also underlined the striking differences between SMNS 12352 and the corresponding part of *Dilophosaurus*. He concluded that SMNS 12352 is “quite unrelated to *D. wetherilli*”. He also concurred with Ostrom (1981) in considering SMNS 12352 not referable to *Procompsognathus*. He judged it very much like *S. connectens* so that it might well be placed in this species.



Fig. 4 SMNS 12591a, nearly complete skull and mandibles, indeterminate theropod. **a** Left lateral view, **b** right lateral view, **c** dorsal view, and **d** ventral view. *Scale bar* = 5 cm

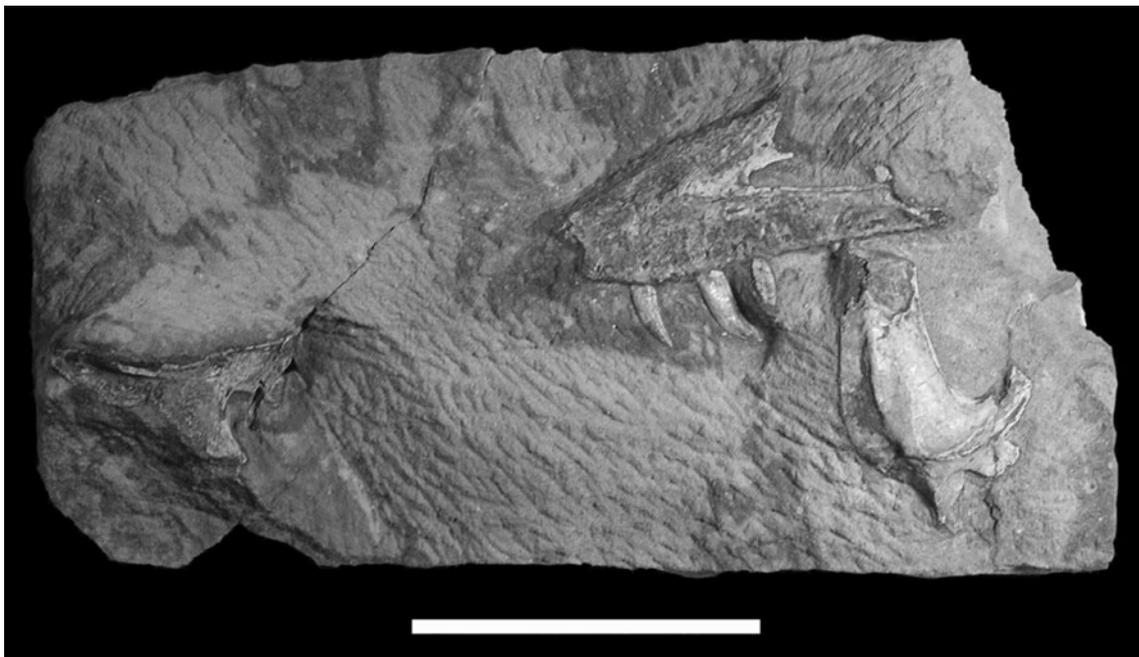


Fig. 5 SMNS 12596, left maxilla, left squamosal, and left quadrate, *S. connectens*. *Scale bar* = 5 cm

Paul (1988, p. 247) proposed that SMNS 12352 resembles the snout of a herrerasaurid dinosaur and also suggested the presence of a herrerasaurid in the Middle Stubensandstein of Pfaffenhofen on the basis of the

proximal end of a femur (Galton 1985, pl. 4; Figs. 5–8). However, the latter specimen (SMNS 51958) is too deformed to warrant a positive taxonomic assignment. We suggest that it should be regarded as *Saurischia* indet. (see

also Langer 2004, table 2.1). Be that as it may, SMNS 12352 differs from *Herrerasaurus ischigualastensis* (Langer 2004) in many respects, such as the proportionally much smaller size of the antorbital fenestra within the antorbital fossa, the less rounded outline of the antorbital fenestra, and the non-participation of the jugal in the antorbital fenestra. SMNS 12352 is, therefore, probably not a herrerasaurid theropod. Likewise, it is definitely not a tetanuran theropod because of the lack of any synapomorphies of this clade (such as a maxillary fenestra). The situation is similar with respect to ceratosaurians, although SMNS 12352 presents at least one coelophysoid synapomorphy (Tykoski and Rowe 2004, p. 67), i.e., the sharp dorsal curvature of the maxilla alveolar border at its rostral end.

Unfortunately, the temporal region, in which the cranial specialisations of crocodylomorphs are above all situated, is not preserved in SMNS 12352. From the five crocodylomorph cranial synapomorphies listed by Sereno and Wild (1992, pp. 445–447), two cannot be assessed because of incompleteness (synapomorphies 4 and 5 of Sereno and Wild (1992)), one is also consistent with dinosaurian affinity (synapomorphy 2 of Sereno and Wild (1992); character 44, state 1 in Nesbitt (2011)), and two are actually observable in SMNS 12352. These are the nasal separated from the antorbital fossa (synapomorphy 1 of Sereno and Wild (1992); character 37, state 0 in Nesbitt (2011)) and the jugal excluded from the antorbital fenestra and fossa (synapomorphy 3 of Sereno and Wild (1992); character 69, state 1 in Nesbitt (2011)). The rostral extension of the jugal may have been fairly similar in the crocodylomorph *Dromicosuchus grillator* (Sues et al. 2003, Fig. 2) and the theropod “*Syntarsus*” *kayentakatae* (Paul 1993, Fig. 2d) and the exclusion of the jugal from the antorbital fenestra was not recovered as a crocodylomorph synapomorphy in the analysis of Nesbitt (2011). Clark et al. (2001, p. 698) discussed the separation of the nasal from the antorbital fossa, and this constellation was confirmed as a crocodylomorph synapomorphy by Nesbitt (2011). On this basis, we agree with Sereno and Wild (1992) in attributing SMNS 12352 to a crocodylomorph, but we consider that it represent a species distinct from *S. connectens*, and not necessarily of the same genus. The basal position of SMNS 12352 within the Crocodylomorpha, namely its “sphenosuchian” nature, is indicated most notably on the basis of the smooth external surface of the skull and the mandible, a sculptured surface having been considered as a crocodyliform synapomorphy (Clark 1994). SMNS 12352 does not possess the character state “maxilla terminating in front of orbit in lateral view”, which was previously considered as a “sphenosuchian” synapomorphy (Wu and Chatterjee 1993).

4 Conclusions

We conclude that SMNS 12352 (as possibly also is the case for SMNS 12352a (Knoll 2008)) is from an indeterminate basal crocodylomorph that is, however, distinct from *S. connectens*. The “sphenosuchian” synapomorphies proposed by Wu and Chatterjee (1993) do not fully match the character states of SMNS 12352 and, in any case, the most recent results on “sphenosuchian” phylogeny strongly suggest that this is a paraphyletic group along the crocodylian stem (Clark et al. 2004; Nesbitt 2011).

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