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2023
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New 'rauisuchian' fossil material from the lower Elliot Formation of South Africa

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Received 15 February 2023. Accepted 16 October 2023

'Rauisuchians' are a grade of paracrocodylomorph archosaurs that evolved a diversity of body plans and played a key role in ecosystems worldwide throughout the Triassic. They are widely believed to have gone extinct during the end-Triassic mass extinction event, though the fossil record of rauisuchians in the latest Triassic is still poorly known. In this study, we describe new rauisuchian fossil remains from the lower Elliot Formation of South Africa. Based on comparative anatomical evidence, we assign these specimens to the pseudosuchian clade Rauisuchidae. The addition of this material to the existing southern African fossil record allows us, along with some new insights into the taxonomic affinities of previously published material, to identify the presence of at least three distinct taxa of rauisuchian in the Norian of southern Africa: two of the clade Rauisuchidae and one of the clade Poposauroidea. These likely filled the ecological role of apex predators in the Late Triassic of southern Africa. We also provide a revision of the stratigraphic record of 'rauisuchians' from the Elliot Formation and show that the existing record of rauisuchians in southern Africa, though among the youngest in the world, does not extend beyond the late Norian. Further exploration of the Elliot Formation and other terrestrial deposits at the Triassic–Jurassic boundary will be needed to assess whether rauisuchians survived until, or even beyond, the end-Triassic mass extinction event.

Keywords: Rauisuchidae, Late Triassic, Norian, palaeoecology, biostratigraphy, end-Triassic mass extinction.

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INTRODUCTION

Non-crocodylomorph paracrocodylomorphs, more commonly known as 'rauisuchians', were present throughout most of the Triassic, with recorded specimens from the Olenekian through to the end-Rhaetian, and specimens representing the grade have been recovered from all continents except Antarctica and Australia (Gower 2000; Nesbitt *et al*. 2013). Most were large-bodied carnivores such as *Prestosuchus*, *Saurosuchus*, *Batrachotomus*, and *Postosuchus* (e.g. Nesbitt *et al*. 2013; Nesbitt & Desojo 2017). Other forms included gracile, bipedal herbivores and carnivores (e.g. *Effigia* and *Poposaurus*, respectively; Nesbitt & Norell 2006; Gauthier *et al*. 2011), as well as sail-backed, quadrupedal carnivores and herbivores (e.g. *Arizonasaurus* and *Lotosaurus*, respectively; Nesbitt 2005, Zhang 1975). The group even features a potentially semi-aquatic form, *Qianosuchus* (Li *et al*. 2006). Most of the disparity in dietary strategy and body plan is found within a single lineage, the Poposauroidea, whereas most non-crocodylomorph loricatans were large-bodied carnivores (Nesbitt 2011; Nesbitt *et al*. 2013).

Until recently, the record of rauisuchians in southern Africa was poorly characterized. The first published record of a rauisuchian from the region is an isolated tooth from the lower Elliot Formation in Lesotho (Fig. 1) assigned to the taxon *Basutodon ferox* (Huene 1932), but this taxon lacks diagnostic features and is now considered a *nomen dubium* (Van Heerden 1979; Knoll 2004). Rauisuchian fossil material from the Elliot Formation of South Africa received scattered subsequent mentions (e.g. Kitching & Raath 1984; Hopson 1984), but no comprehensive review of southern African rauisuchian material was published during the 20th century (Knoll, 2004). More recent research is beginning to improve that knowledge – Tolchard *et al*. (2019) identified several fragmentary specimens from South African fossil collections as rauisuchian. These specimens were all either from the Upper Triassic lower Elliot Formation (*Scalenodontoides* Assemblage Zone, SAZ; Viglietti *et al*. 2020a) or of unknown provenance (see Discussion for further provenance information). Furthermore, Tolchard *et al*. (2021) described *Etjosuchus recurvidens*, an early branching loricatan from the Middle Triassic (Ladinian–Carnian) uppermost Omingonde Formation of Namibia known from a well-represented skeleton including a partial skull. This research points to an underappreciated diversity of rauisuchians in southern African Triassic strata.

The Elliot Formation is a series of fluvio-lacustrine red beds that preserve evidence of progressively aridifying continental ecosystems from the middle Norian to the Sinemurian (*c*. 220 to 195 Ma; Bordy *et al*. 2020). The

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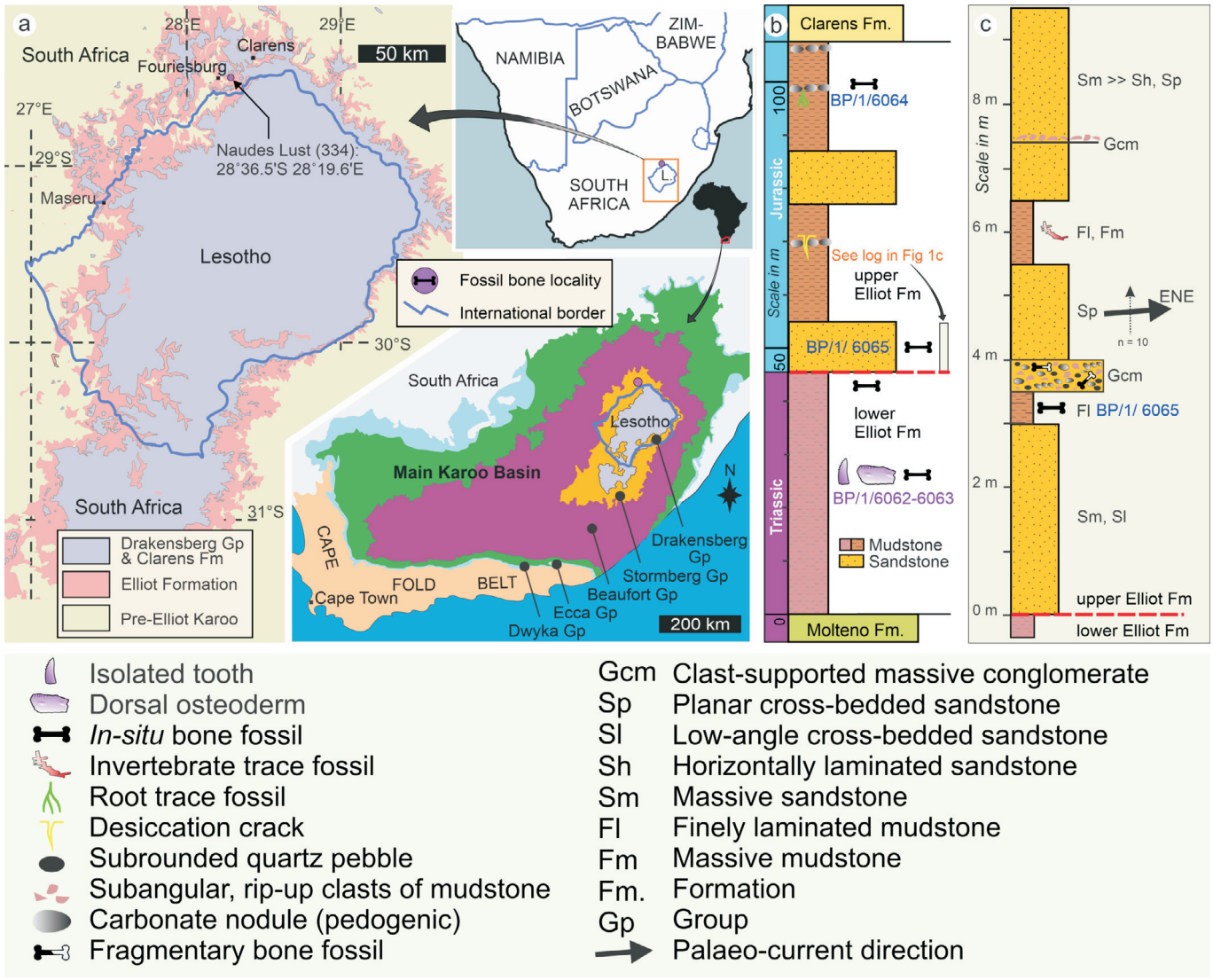


Figure 1. Geological and stratigraphical context of specimen BP/1/6062 in in South Africa. **a,** Location of the Naudes Lust 334 fossil locality within the main Karoo Basin. **b**, Stratigraphical context of the fossil specimens at Naudes Lust. **c**, Sedimentological log of the first sandstone unit (upper Elliot Formation) that overlies the mudstone layers that yielded specimen BP/1/6062 in the lower Elliot Formation. BP/1/6064 represents a long bone fragment of a sauropodomorph dinosaur, BP/1/6065 represents some unidentified bone fragments. All specimens were collected at Naudes Lust 334 in 2002.

known tetrapod fauna of the lower Elliot Formation constitutes the *Scalenodontoides* Assemblage Zone and includes sauropodomorph and theropod dinosaurs, chigutisaurid amphibians, an anomodont therapsid (*Pentasaurus goggai*; Kammerer 2018) and the eponymous gomphodont cynodont *Scalenodontoides macrodontes* (Kitching & Raath 1984; Knoll 2004; Battail 2005; Viglietti *et al*. 2020a). The lower Elliot Formation is widely regarded as Norian–Rhaetian (Olsen & Galton 1984; Knoll 2004; Sciscio *et al*. 2015; Bordy *et al*. 2020; Viglietti *et al*. 2020), biostratigraphically consistent with the presence of these fossil lineages, but in comparison with penecontemporaneous deposits elsewhere, it is markedly lacking in pseudosuchian representatives. The work of Tolchard *et al*. (2019) showed evidence for these taxa among historical records, but even so the lower part of the Elliot Formation remains drastically undersampled.

Another outstanding research question is where rauisuchians disappear from the fossil record. Current hypotheses hold that they were victims of the end-Triassic mass extinction (ETME), but most continental deposits do not bracket this extinction event and therefore lack the power to test this hypothesis. The Elliot Formation in southern Africa represents an ideal study area for understanding faunal shifts around the ETME, but the current sampling is too scarce to test hypotheses for the presumed extinction level at or near the boundary of the lower and upper Elliot Formation.

Here, we present a new record of Late Triassic rauisuchian fossil material, adding to the existing body of evidence in the southern African fossil record of late-occurring non-crocodylomorph archosaurs. In contrast to much of the previously published material, this specimen has high-resolution provenance data, providing a new definitive record of an African non-crocodylomorph paracrocodylomorph occurring at least as close to the Triassic-Jurassic boundary (TJB) as the late Norian or, possibly, Rhaetian.

MATERIAL AND METHODS

We describe fossil specimen BP/1/6062, which consists of an osteoderm and a large, isolated tooth. We describe

these fossils using standard anatomical comparative methods. Where possible, we apply the following adjectives to variation in anatomical directions: dorsoventral – 'high' and 'low'; mediolateral – 'wide' and 'narrow'; anteroposterior – 'long' and 'short'; exceptions to this standard are clearly marked. We use a diversity of comparative material including first-hand inspection of fossil material from southern Africa and assessment of published data from elsewhere in Pangea (Table 1). Comparative specimens sourced from the literature are appropriately referenced while those inspected first-hand are not. In line with most contemporary research, we use the term 'Rauisuchia' in this paper to refer to a paraphyletic grade of pseudosuchian archosaurs, consisting of non-crocodylomorph paracrocodylomorphs (including Poposauroidea and non-crocodylomorph loricatans) and a few closely related taxa (e.g. Butler *et al*. 2011; Nesbitt 2011; Nesbitt *et al*. 2013; Roberto-Da-Silva *et al*. 2018; Desojo *et al*. 2020; Nesbitt *et al*. 2020). While this term reflects the current consensus, Brusatte *et al*. (2010) recovered a monophyletic Rauisuchia whose relationships among non-crocodylomorph pseudosuchians are a matter of debate.

Geological background

The isolated tooth and dorsal osteoderm described herein were found in a mostly massive, red mudstone unit in the lower Elliot Formation at Naudes Lust (cadastral unit 334) in May 2002 by E.M.B. (Fig. 1b,c). At this locality, the Elliot Formation has a thickness of *c.* 107 m, and *c.* 80% of the strata are red, laminated to massive mudstone layers that show, up-stratigraphy, an increasing abundance of calcareous nodules, root trace fossils and desiccation cracks (Fig. 1b). Confined to the upper Elliot Formation, two medium-grained, mostly massive sandstone units of *c.* 10-m-thick each (Fig. 1b) are laterally discontinuous. The older sandstone was logged in detail (Fig. 1c), and shows typical characteristics of the upper Elliot Formation in the region (Bordy *et al*. 2016). It contains a *c.* 0.3 m thick layer of massive-to-weakly bedded, clast-supported conglomerate with rounded to subangular pebbles of calcareous nodule, mudstone and quartz as well as angular bone fragments. On average, the clasts are 1 cm in diameter with the subrounded quartz pebbles being the smallest (*c.* 0.5 cm). Overlying the conglomerate, a planar cross-bedded medium-grained sandstone yielded high-consistency measurements that show a high-to-moderate energy palaeo-flow towards ENE (Fig. 1c). Overlying the cross-bedded sandstone, massive-to-laminated light purple siltstone contains bone fragments and invertebrate trace fossils (simple tubes with a uniform diameter of *c.* 0.5 cm; Fig. 1c). These sedimentological and stratigraphical observations are consistent with the characteristics of the Elliot Formation in the northern part of the main Karoo Basin (Fig. 1a; Bordy *et al*. 2020), and with the documented regional palaeo-current trends in the upper Elliot Formation (Bordy *et al*. 2004a,b). Thus, the overall interpretation of a progressive aridification in a dryland setting from the Late Triassic into the Early Jurassic is herein upheld. Given

Table 1. List of comparative specimens used for this study. The 'Elements' column refers to the fossil material used for comparative purposes in this study and not necessarily to all elements assigned to a given specimen number. The refined lower Elliot Formation provenance of SAM-PK-K383 is presented in this study (see Discussion; Tolchard *et al.* 2019).

Specimen No.	Taxonomy	Provenance	Age	Elements	Source
BP/1/5163	'Rauisuchia'	Lower Elliot Formation, South Africa	Late Norian	Isolated teeth and osteoderms	Tolchard *et al.* 2019
BP/1/5302	'Rauisuchia'	Lower Elliot Formation, South Africa	Late Norian	Anterior part of right dentary	Tolchard *et al.* 2019
BP/1/8120	'Rauisuchia'	Lower Elliot Formation, South Africa	Late Norian	Dentary fragments	Tolchard *et al.* 2019
NMQR 3554	Poposauroidea	Elliot Formation, South Africa	Norian-Rhaetian	Ilium	Tolchard *et al.* 2019
SAM-PK-K383	'Rauisuchia'	Lower Elliot Formation, Lesotho	Late Norian	Fragmentary jaw with isolated teeth	Tolchard *et al.* 2019
BSPG AS XXV 94	*Rauisuchus tiradentes*	Santa Maria Formation, Brazil	Carnian	Osteoderms	Lautenschlager & Rauhut 2015
TTU-P 9000, 9002	*Postosuchus kirkpatricki*	Lower Cooper Canyon Formation (Dockum Group), United States	Norian	Teeth, osteoderms	Weinbaum 2011, 2013
NCSM 13731 (formerly UNC 15575)	*Postosuchus alisonae*	Deep River Basin, Newark Supergroup, United States	Late Carnian or early Norian	Osteoderms	Peyer *et al.* 2008
SMNS 90018	*Batrachotomus kupferzellensis*	Kupferzell, Crailsheim and Vellberg-Eschenau localities, Germany	Late Ladinian	Osteoderms	Gower & Schoch 2009
PVSJ 32	*Saurosuchus galilei*	Ischigualasto Formation, Argentina	Carnian	Osteoderms	Trotteyn *et al.* 2011
GSN F382	*Etjosuchus recurvidens*	Upper Omingonde Formation, Namibia	Ladinian	Osteoderms, teeth	Tolchard *et al.* 2021
ZPAL V.33/55	*Smok wawelski*	Lisowice locality, 'Woźniki Formation', Poland	Late Norian – early Rhaetian	Teeth	Niedźwiedzki *et al.* 2013

the limited exposure of the lower beds that yielded the described specimens, a more robust interpretation of the palaeoenvironment in the lower Elliot Formation is not possible.

SYSTEMATIC PALAEONTOLOGY

Archosauria Cope, 1869 (*sensu* Gauthier & Padian 1985)
Paracrocodylomorpha Parrish, 1993 (*sensu* Nesbitt 2011)
Loricata Merrem, 1820 (*sensu* Nesbitt 2011)

Referred material. BP/1/6062, isolated paramedian osteoderm, isolated tooth crown, some unidentifiable fragments.

Horizon and locality. Found in the lower Elliot Formation below the first sandstone exposed north of the Little Caledon River on farm Naudes Lust (334; SE of Clarens, E of Fouriesberg, 28°36.5′S, 28°19.6′E), Free State Province, South Africa (Fig. 1a). The locality yielded other specimens that are mainly of unidentified sauropodomorph dinosaurs (Fig. 1b,c).

Osteoderm

The single preserved osteoderm is missing the anteriormost projection and the posterior third of the body (Fig. 2). The preserved portion is longer than it is wide, and bears a conspicuous medially positioned keel on its dorsal surface. The osteoderm is bilaterally asymmetrical along the anteroposterior axis. Bilateral asymmetry is present in the presacral paramedian osteoderms of most rauisuchians, though not in the caudal osteoderms (Cerda *et al*. 2013). The overall morphology and size are similar to the posterior dorsal osteoderms of *Rauisuchus* (Fig. 3b [this paper]; BSPG AS XXV 94; Lautenschlager & Rahut [2015, fig. 16C]) and the dorsal osteoderms of *Postosuchus alisonae* (Fig. 3c [this paper]; NCSM 13731; Peyer *et al*. [2008, fig. 6B]). Based on these lines of evidence, we hypothesize that it represents a fragmentary dorsal member from the left side of the osteoderm series, based on the position of the anterior process extending from the anteromedial margin of the osteoderm.

The osteoderm in BP/1/6062 is long and subrectangular in dorsal view and tapers moderately in its mediolateral

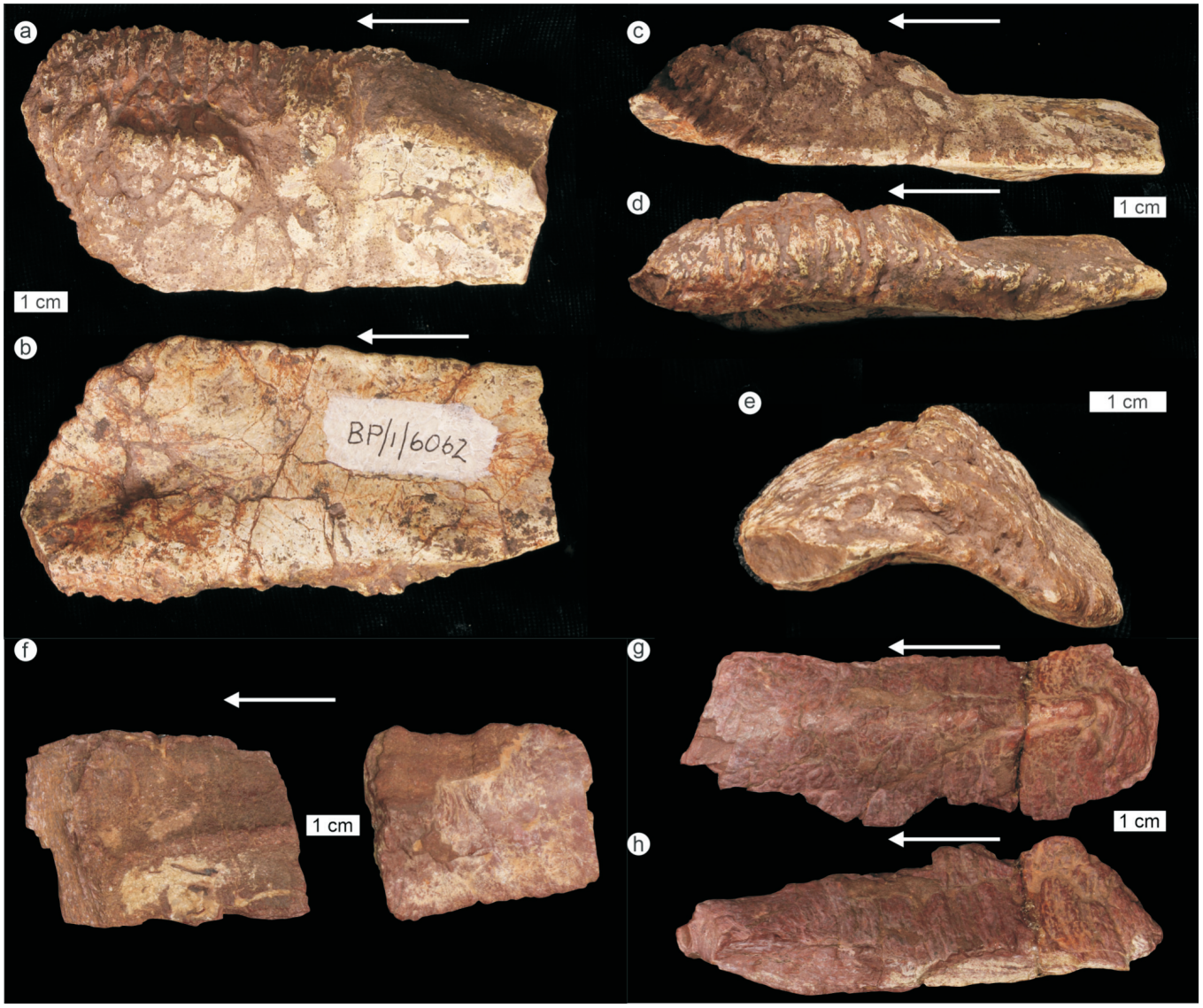


Figure 2. BP/1/6062. Dorsal osteoderm in dorsal (**a**), ventral (**b**), lateral (**c**), medial (**d**), and anterior (**e**) views. BP/1/5163. Dorsal osteoderm in dorsal view (**f**). Caudal osteoderm in dorsal (**g**), and medial (**h**) views. The medial view is mirrored from the better preserved lateral view for comparative purposes. Arrows indicate anterior direction.

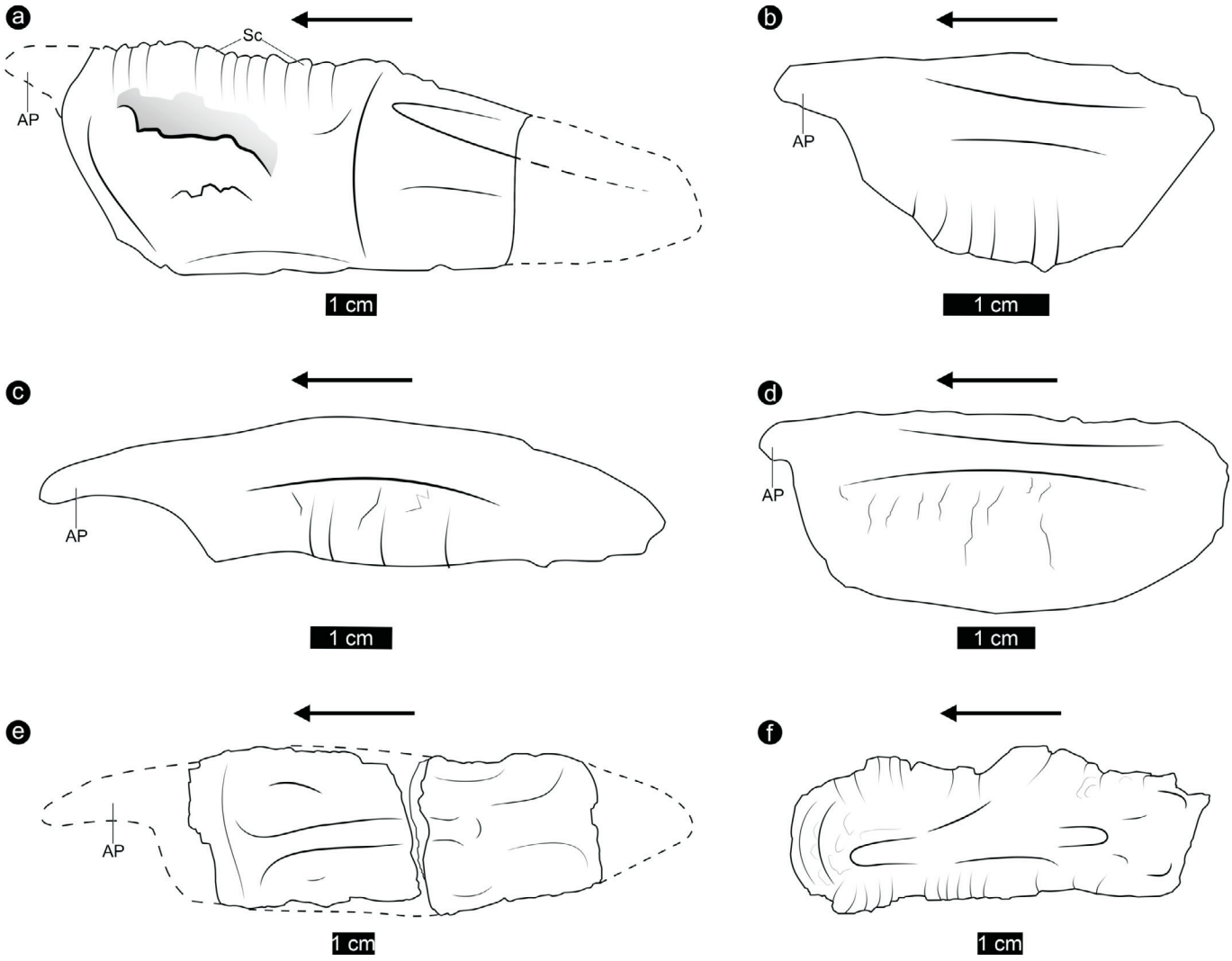


Figure 3. Interpretive line drawings of rauisuchian osteoderms in dorsal view. BP/1/6062 (**a**), posterior dorsal osteoderm of *Rauisuchus* BSPG AS XXV 94 (**b**; Lautenschlager & Rauhut [2015, fig. 16]), dorsal osteoderm of *Postosuchus alisonae* NCSM 13731 (**c**; Peyer *et al*. [2008, fig. 6]), dorsal osteoderm of *Batrachotomus* SMNS 90018 (**d**; Gower & Schoch 2009), BP/1/5163 (**e**, dorsal; and **f**, caudal osteoderms). Arrows indicate anterior direction. Dotted lines indicate reconstructed margins. Abbreviations: AP, anterior process; Sc, sculpturing.

dimension as it extends posteriorly. This shape is most similar to the posterior dorsal osteoderms in *Rauisuchus* (Fig. 3b [this paper]; BSPG AS XXV 94; Rahut [2015, fig. 16C]), and dorsal osteoderms of *P. alisonae* (Fig. 3c [this paper]; NCSM 13731; Peyer *et al*. 2008 [Fig. 6B]). It bears some resemblance to the dorsal osteoderms of *Batrachotomus* (Fig. 3d [this paper]; SMNS 90018; Gower & Schoch [2009, fig. 7M]), but in that taxon the osteoderms have rounder edges creating a more oval outline in dorsal view (Fig. 3d). There is also a resemblance in overall shape between the osteoderm in BP/1/6062 and those of *P. alisonae* (Fig. 3c [this paper]; NCSM 13731; Peyer *et al*. 2008, fig. 6B]), but the osteoderms of *P. alisonae* have a more pronounced bilateral asymmetry. The osteoderm in BP/1/6062 differs from the more squared dorsal osteoderms of earlier branching loricatans like *Saurosuchus* (PVSJ 32; Trotteyn *et al*. 2011, fig. 10]), *Fasolasuchus* (PVL 3850; Bonaparte [1981, fig. 20B]), and *Etjosuchus* (GSN F382).

The striated anterior margin of BP/1/6062 is inclined posteromedially at approximately a 45° angle relative to a mediolateral line. The lateral side of the anterior margin is missing, but comparison with the dorsal osteoderms of *Rauisuchus* (Fig. 3b [this paper]; BSPG AS XXV 94; Lautenschlager & Rahut [2015, fig. 16C]) and *Postosuchus alisonae* (Fig. 3c [this paper]; NCSM 13731; Peyer *et al*. [2008, fig. 6B]) strongly suggests that it bore a sharp, tapering, anteriorly projecting process (Fig. 3a). The medial margin is linear, extending strictly anteroposteriorly, and lacks striations or rugosities. The heavily striated lateral margin is gently laterally convex and is directed slightly medially as it extends posteriorly, resulting in bilateral asymmetry (Fig. 2a,b). The posterior margin is not preserved, but it is likely that it ended in a long, tapering triangular point, based on comparison to *Rauisuchus* (Fig. 3b; BSPG AS XXV 94; Lautenschlager & Rahut [2015, fig. 16C]) and *Postosuchus alisonae* (Fig. 3c [this paper]; NCSM 13731; Peyer *et al*. [2008, fig. 6B]). This contrasts with the presacral osteoderms of some earlier branching loricatans (e.g. *Etjosuchus*, GSN F382), and *Fasolasuchus* (PVL 3850; Bonaparte [1981, fig. 20B]) which tend to be more quadrangular in shape, and wider-than-long.

The osteoderm is dorsoventrally compressed and has a subtriangular transverse cross-section (Fig. 2e). The shape

of the cross-section is similar to the broken osteoderm in BP/1/5163 (Fig.2f). BP/1/5163 represents another rauisuchian specimen form the lower Elliot formation, including fragmentary osteoderms and isolated teeth, and was found *c.* 80 km SW from Naudes Lust (Tolchard *et al*. 2019). The broken osteoderm in BP/1/5163 (Figs 2f, 3e) is also bilaterally asymmetrical, and we assume it to be a presacral paramedian (likely dorsal) osteoderm for the same reasons as we assign the osteoderm in BP/1/6062 as such. The dorsal surface of the osteoderm in BP/1/6062 is convex and bears a prominent, anteroposteriorly extending ridge along its medial portion. This ridge is located slightly lateral to the transverse midline, and is more pronounced in the anterior portion of the osteoderm tapering gradually into the dorsal surface as it extends posteriorly. The osteoderm is proportionally lower relative to its length than dorsal osteoderms of, e.g. *Batrachotomus* (SMNS 90018; Gower & Schoch [2009, fig. 20B]). The proportionally low height of the osteoderm is similar to the dorsal osteoderm of *Postosuchus alisonae* (NCSM 13731; Peyer *et al*. [2008, fig. 6B]).

The anterior portion of the dorsal surface is highly sculptured, with numerous, closely spaced, mediolaterally oriented grooves on the lateral side of the mesial ridge, which become shallower and oriented more radially on the anterior margin (Fig. 2a). The sculpturing is less pronounced on the medial side of the ridge, but the surface is still rugose, with several anastomosing grooves and pits (Fig. 2a, Fig. 3a). Among loricatans, this morphology is most similar to *Rauisuchus* (Fig. 3b [this paper]; BSPG AS XXV 94; Lautenschlager & Rauhut [2015, fig. 16C]), and *P. alisonae* (Fig. 3c [this paper]; NCSM 13731; Peyer *et al*. [2008, fig. 6B]). There is an abrupt transition in the sculpturing of the dorsal surface, with the posterior half of the preserved portion being smooth with only very shallow and minute pits, differing from *Batrachotomus* (Fig. 3d [this paper]; SMNS 90018; Gower & Schoch [2009, fig. 7M]) and BP/1/5163 (Fig. 2f), and more similar to *Rauisuchus* (Fig. 3b [this paper]; BSPG AS XXV 94; Lautenschlager & Rauhut [2015, fig. 16C]), and *P. alisonae* (Fig. 3c [this paper]; NCSM 13731; Peyer *et al*. 2008, fig. 6B]). The osteoderms of the latter three taxa, however, present a far more gradual reduction in sculpturing between the anterior and posterior portions when compared to the osteoderm in BP/1/6062. This abrupt loss of sculpturing is, to our current knowledge, autapomorphic of the taxon represented by BP/1/6062. This feature also serves to differentiate the osteoderm in BP/1/6062 from those of BP/1/5163 (Figs 2a,d,f,g,h, 3a,e,f). The more complete of the two specimens associated with BP/1/5163 has more consistent and symmetrical sculpturing along the length of its dorsal surface (Figs 2g,h, 3f). We hypothesize that the latter osteoderm is from the caudal region based on bilateral symmetry and a prominent keel on the dorsal surface, similar to the caudal osteoderms of *Rauisuchus* (BSPG AS XXV 94; Lautenschlager & Rauhut [2015, fig. 16D]). This diagnosis considers the limited published information on serial variation available at the time of publication. Because of the poor condition of the second osteoderm morphotype in BP/1/5163, which we presume to be from the dorsal region as mentioned previously, it is hard to compare the sculpturing pattern. However, the fragment representing the anterior portion appears to be far less sculptured than the corresponding portion of the osteoderm in BP/1/6062.

The ventral surface is smooth and concave and features a conspicuous concavity at the anterior end of the osteoderm, likely representing an articular surface with the neural spine (Fig. 2b). This concavity is subtriangular, opening on the anterior margin of the osteoderm and then tapering to a point. A concavity with similar morphology is also present in the osteoderms of *Rauisuchus* (BSPG AS XXV 94; Lautenschlager & Rahut 2015). There is no similar concavity on the anterior portion of the ventral surface of the broken, asymmetrical osteoderm in BP/1/5163, providing an additional line of evidence to differentiate BP/1/6062 from that specimen.

Dentition

A single, isolated tooth crown is preserved (Fig. 4). It is broken at, or slightly below, the enamel-dentine transition at the root. The preserved apicobasal height of the crown is 61 mm.

The mesial margin of the tooth is strongly recurved, while the distal margin is only slightly recurved (Fig. 4a,b). This is similar to the morphological condition of the teeth of SAM-PK-K383, and some crowns preserved in BP/1/5163. It is labiolingually compressed and there is a shallow but distinct convexity along the apicobasal height of the (presumed) labial surface, mirrored with an equally subtle concavity on the (presumed) lingual surface. This asymmetry is also present in SAM-PK-K383 but not in BP/1/5163. The basal portion of the distal margin is moderately convex, similar to the isolated teeth of SAM-PK-K383, and the anterior maxillary teeth of *Postosuchus kirkpatricki* (TTU-P 9000; Weinbaum [2011, fig. 22B]).

The tooth is serrated partway down the mesial margin from the apex and along the entire distal margin (Fig. 4c). The serrations are rectangular in labial or lingual view and small, not extending far beyond the carina (Fig. 4a,b). Shallow enamel wrinkles (Brusatte *et al*. 2007) extend sub-perpendicularly, in the form of an arc, from the serrations along the posterior margin of the teeth (Fig. 4a). These wrinkles are subtly developed and similar to those of *Smok wawelski* (ZPAL V.33/55; Niedźwiedzki *et al*. 2013), and the carcharodontosaurid theropod dinosaur MNN GAD14 (Brusatte *et al*. 2007). The serration density of 1.6 serrations per millimetre is identical to that of SAM-PK-K383 and slightly lower than the density of two serrations per millimetre on the teeth of BP/1/5163. Like with other lower Elliot Formation paracrocodylomorphs previously described (Tolchard *et al*. 2019), this serration density is lower than in other rauisuchians (e.g. *Postosuchus kirkpatricki*, 3 serrations/mm; TTU-P 9000; Weinbaum 2011, *Etjosuchus*; 3.5 serrations/mm; GSN F382, *Smok wawelski*; 2.8–4 serrations/mm; Niedźwiedzki & Budziszewska-Karwowska 2018).

Overall, the morphology of this tooth is very similar to the teeth of the rauisuchian specimen SAM-PK-K383 from



Figure 4. BP/1/6062. Isolated tooth in labial (**a**), lingual (**b**), distal (**c**), mesial (**d**), and occlusal (**e**) views.

Likhoele in Lesotho (see Discussion, and Tolchard *et al*. 2019). Among loricatans, the BP/1/6062 tooth and the teeth of SAM-PK-K383 most strongly resemble those of the rauisuchid *Postosuchus kirkpatricki* (TTU-P 9000; Weinbaum 2011), and the archosaur *Smok wawelski* (ZPAL V.33/55; Niedźwiedzki *et al*. 2013). Along with the latter, these teeth bear a general superficial resemblance to those of Cretaceous carcharodontosaurid and tyrannosauroid theropod dinosaurs (Brusatte *et al*. 2007; Niedźwiedzki 2013; Niedźwiedzki & Budziszewska-Karwowska 2018), suggesting functional similarity in prey capture or consumption style.

DISCUSSION

While there is insufficient material to confidently assign BP/1/6062 phylogenetically beyond 'non-crocodylomorph loricatan', there are substantial anatomical similarities suggesting it is a member of the Rauisuchidae (*sensu* Nesbitt 2010). The osteoderm is subtriangular and bilaterally asymmetrical in a manner very similar to *Rauisuchus* (BSPG AS XXV 94; Lautenschlager & Rauhut[2015, fig. 3b]), and *P. alisonae* (NCSM 13731; Peyer *et al*. [2008, fig. 3c]), but differing from earlier branching loricatans, for example, *Batrachotomus* (SMNS 90018; Gower & Schoch [2009, fig. 3d]) and *Etjosuchus* (GSN F382). Osteoderm-based characters from the data matrix of Nesbitt (2010), and subsequent modifications thereof, provide further support for the placement of BP/1/6062 among rauisuchids. Shared with all non-crocodylomorph loricatans, the osteoderm in BP/1/6062 has a distinct anterior process (Character #403.1), and longer-than-wide presacral osteoderms (407.1). However, it features a distinct longitudinal bend near the lateral edge (404.1). This latter character state is present in all rauisuchids (*Rauisuchus*, *Polonosuchus*, and both species of *Postosuchus*) but absent in most early branching loricatans. It is, however, also present in *Batrachotomus*, preventing BP/1/6062 from being unequivocally referable to Rauisuchidae. Although the osteoderm is missing its anterior process and the posterior end, the preserved portion is highly similar to that of *Postosuchus alisonae* in terms of overall outline in dorsal view. As such, we tentatively reconstruct the specimen with a similarly sharp, curving anterior process and a tapering posterior end (Fig. 3a). The fragile nature of sharply projected processes make them more likely to break off during transportation, and given the abrupt, irregular fracture surfaces on the specimen, it is likely that they were worn away during attrition, likely in the erosional processes that exposed the osteoderm. Further to the shape, the sculpturing pattern on the dorsal surface bears meaningful resemblance to rauisuchids including *P. alisonae* (NCSM 13731; Peyer *et al*. 2008, Fig. 3c), and, especially, *Rauisuchus* (BSPG AS XXV 94; Lautenschlager & Rauhut 2015, fig. 3b).

The morphological features of the fossil specimens represented by BP/1/6062 suggests it represents a distinct species of non-crocodylomorph loricatan (possibly also represented by SAM-PK-K383) that is readily differentiable from the taxon represented by BP/1/5163 (possibly also represented by BP/1/5302, and BP/1/8120; see Tolchard *et al*. 2019). It is important to note that, as stated previously, it is difficult to compare the osteoderm in BP/1/6062 to those in BP/1/5163 because of the state of preservation of the latter. The preserved elements in BP/1/5163 provide sufficient detail to identify two distinct morphotypes of osteoderms, which likely reflect differences in the serial variation of osteoderm morphology.

The first osteoderm morphotype in BP/1/5163 (Fig. 2e,f) is broken and poorly preserved, but with an overall shape in dorsal view that appears similar to that of the osteoderm in BP/1/6062. We refer to the former osteoderm as a dorsal osteoderm based primarily on the presence of bilateral asymmetry, consistent with the condition typically seen in presacral osteoderms in rauisuchians (Cerda *et al*. 2013). The osteoderm in BP/1/6062 is larger and the dorsal surface is more extensively sculptured than the dorsal osteoderm in BP/1/5163 However, the overall morphological similarities between these two osteoderms, particularly in regards to overall shape in dorsal view and cross-section, is sufficient that it cannot be ruled out that the differences in their morphologies may represent serial variation in osteoderm morphology in a single taxon rather than two separate taxa. The lack of published data on serial variation in the morphology of rauisuchian osteoderms represents an important gap in the existing literature on the group that we recommend be addressed in future research.

The second, more complete, osteoderm in BP/1/5163 (Fig. 2g,h) is dorsoventrally higher and more bilaterally symmetrical along its anteroposterior axis compared to BP/1/6062. Based on bilateral symmetry around a prominent anteroposteriorly oriented dorsal keel we tentatively, refer to this morphotype as a caudal osteoderm. Given that the osteoderm in BP/1/5163 represents the only currently known specimen of this morphotype, it is not useful for direct comparison. However, the presumed caudal osteoderm in BP/1/5163 shares a similar size class with BP/1/6062. Assuming that both osteoderms in BP/1/5163 are from the same individual, it is, therefore, unlikely that the difference in size between the dorsal osteoderm in BP/1/6062 and BP/1/5163 is the result of ontogeny. Further material will be needed to effectively assess the morphological and, by extension, taxonomic diversity of rauisuchian osteoderms in the Elliot Formation of southern Africa.

While it is certainly plausible that the two osteoderms assigned to BP/1/5163 represent different parts of a series of osteoderms from the same individual (i.e. presacral dorsal, and caudal); there is a possibility that they represent different individuals or even different taxa given the fragmentary nature of the specimen. Further to the differences in osteoderm morphology, the tooth in BP/1/6062 differs from those in BP/1/5163 in that it is labiolingually asymmetrical and has a lower serration density than the teeth in BP/1/5163. The anatomical differences in the osteoderm are consilient with the evidence from the dentition, which supports that BP/1/6062 and BP/1/5163 most likely represent different taxa. The similarities in tooth morphology between BP/1/6062 and SAM-PK-K383 also possibly allow for referring SAM-PK-K383 to the same taxon as BP/1/6062, pending the discovery of further more diagnostic material.

Both morphotypes (i.e. the morphotype represented by BP/1/6062 and SAM-PK-K383; and the morphotype represented by BP/1/5163) bear a strong anatomical resemblance to taxa in the clade Rauisuchidae but many of these features are sufficiently homoplastic to prevent referral to this clade in lieu of richer data. Building on Tolchard *et al*. (2019), we are therefore able to confidently identify a minimum of three taxa of rauisuchian archosaur present in the uppermost Triassic Elliot Formation: one poposauroid (NMQR 3554), and two (inferred) non-crocodylomorph loricatans. BP/1/6062, along with BP/1/5163, BP/1/5302, and BP/1/8120 are from the older *Scalenodontoides* Assemblage Zone; NMQR 3554 is of unknown provenance. Tolchard *et al*. (2019) had tentatively assigned SAM-PK-K383 to the younger *Massospondylus* Assemblage Zone and, possibly, the upper Elliot Formation. However, given that the Likhoele locality (Mafeteng, Lesotho) from which SAM-PK-K383 is provenanced (Tolchard *et al*. 2019) has abundant, highly fossiliferous exposures of both the lower and upper Elliot Formation, we consider it far more plausible that specimen SAM-PK-K383 is from the lower Elliot Formation. Therefore, there is no current record of rauisuchian fossil material in southern Africa confidently collected from the Lower Jurassic. Nonetheless, these specimens represent some of the youngest rauisuchians yet discovered (e.g. Nesbitt *et al*. 2013).

BP/1/6062 was found in one of the more northerly exposures of the lower Elliot Formation of the main Karoo Basin (Fig. 1). The only currently published rauisuchian specimens with definitive stratigraphic provenance (BP/1/5163, and BP/1/5302) are from the southern parts of the lower Elliot Formation (Tolchard *et al*. 2019, Viglietti *et al*. 2020a). The Elliot Formation is characterized by a substantial thinning of exposed horizon south-to-north, requiring that at some level, the stratigraphy is diachronous along the extent of its geography (Bordy *et al*. 2020). Originating from approximately halfway through the exposed thickness of the lower Elliot Formation at Naudes Lust, it may be assumed that BP/1/6062 is late Norian in age, based on existing knowledge of age distributions across the Elliot Formation (Bordy *et al*. 2020). While the available evidence precludes determining precise stratigraphic relationships, we contend that BP/1/6062 is approximately contemporaneous with BP/1/5163 and BP/1/5302. While the addition of this new datapoint does not necessarily extend the stratigraphic range of rauisuchians, it does provide further evidence for a diversity of rauisuchian taxa in the latest Triassic of southern Africa, and shows that they were present in the northern extent of the main Karoo Basin area at this time.

The dentition in BP/1/6062 is ziphodont, serrated and

bears an enamel wrinkle pattern comparable to hypercarnivores like the carcharodontosaurid theropod dinosaur MNN GAD14 (Brusatte *et al*. 2007). In regards to the tetrapod ecosystem of the lower Elliot Formation, it is likely that rauisuchians filled the role of apex predator in southern Gondwana throughout the Late Triassic. This is consistent with the hypothesized trophic level of rauisuchians in other Norian deposits worldwide such as the Chinle Formation in North America (Drumheller *et al*. 2014) and the Lisowice locality in the informal Woźniki Formation of SW Poland (Qvarnström *et al*. 2019). Theropod dinosaurs only became more abundant and diverse in southern Gondwana in the Early Jurassic (Viglietti *et al*. 2020a,b; Abrahams *et al*. 2022), filling the role rauisuchians once filled. This transition seen in the Upper Triassic-Lower Jurassic Elliot Formation is consistent with a global pattern wherein paracrocodylomorphs became smaller and were replaced by theropod dinosaurs as the dominant terrestrial predators during the Late Triassic (e.g. Zanno *et al*. 2015; Hudgins *et al*. 2020). This turnover event is correlated with increasing atmospheric CO_2 content, rising temperatures and other major climatic changes that characterized the ETME (e.g. Hudgins *et al*. 2020). This change is reflected in the sedimentology and geochemistry of the Elliot Formation, which indicate an increasingly hot, dry climate (Bordy *et al*. 2004a,b; Sciscio & Bordy, 2016). The southern African rauisuchian specimens indicate that these late-occurring taxa reached large sizes as well as a modest taxonomic diversity even directly prior to the group's extinction.

CONCLUSION

BP/1/6062, collected in the lower Elliot Formation of South Africa, represents a new rauisuchian specimen from the Late Triassic of southern Gondwana. Globally, it provides further evidence for a continued taxonomic diversity of non-crocodylomorph paracrocodylomorphs in the later stages of the Triassic across Pangea. Locally, it extends the geographic range of rauisuchian fossil material recovered from the lower Elliot Formation and strengthens biostratigraphic correlation across the basin. Going forward, future research should aim to better understand the rauisuchian fossil record across the TJB, especially in the upper part of the *Scalenodontoides* AZ and within the lower *Massospondylus* AZ.

This project was supported by grant MND200718544868 (FBT) and AOP grants 118794 and 136526 (JNC). Opinions expressed and conclusions arrived at are those of the authors and are not necessarily to be attributed to COE PAL. We also gratefully acknowledge Richard J. Butler, and Julia B. Desojo as reviewers, and Kimberly E. J. Chapelle as editor for meaningfully contributing with their insightful comments to the overall quality of this study.

ABBREVIATIONS

Institutional

BP	Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa;
GSN	Geological Survey Museum, Windhoek, Namibia;
MNN	Musée National du Nïger, Niamey, Niger;
NCSM	North Carolina Museum of Natural Sciences, Raleigh, United States (includes the former UNC palaeontology collection);
NMQR	National Museum, Bloemfontein, South Africa;
PVSJ	División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina;
SAM	Iziko South African Museum, Cape Town, South Africa;
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany;
SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany;
TTU-P	Texas Tech University Museum, Lubbock, Texas, U.S.A.;
ZPAL	Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

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