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# ‘RAUISUCHIAN’ MATERIAL FROM THE LOWER ELLIOT FORMATION OF SOUTH AFRICA: IMPLICATIONS FOR LATE TRIASSIC BIOGEOGRAPHY AND BIOSTRATIGRAPHY

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**Abstract** - ‘Raurisuchians’ are non-crocodylomorph pseudosuchian archosaurs that played  
important roles in terrestrial Triassic ecosystems. Because they are generally considered to  
have gone extinct in the end-Triassic mass extinction, they are potentially useful for relative  
dating of terrestrial strata. Despite the abundance of fossils of this group in South America,  
East Africa and Laurasia, there is currently no published definitive raurisuchian fossil record  
from southern Africa. However, several fragmentary archosaurian remains representing  
potential members of this grade have been recovered from the latest Triassic lower Elliot  
Formation of South Africa. Here, we critically review this material and show that it

represents a modest diversity of raulisuchians. These records are the southernmost palaeolatitudes that these animals are known to have occurred and the first definitive remains from southern Africa.

**KEY WORDS – ‘Raulisuchia’ – Late Triassic – lower Elliot Formation- Archosauria**

## Introduction

The clade Pseudosuchia refers to living crocodylians and their stem lineage within the clade Archosauria (Gauthier & Padian 1985; Nesbitt 2011). Within Pseudosuchia, crocodylians (crown group) and their crocodylian-like relatives form the clade Crocodylomorpha. The closest relatives of crocodylomorphs are included with them within the clade Paracrocodylomorpha (Nesbitt 2011). Among Paracrocodylomorpha, ‘Raulisuchia’ is a grade of large, carnivorous, Triassic-aged non-crocodylomorph archosaurs (Gower 2000), referred to in this paper as raulisuchians (sensu Nesbitt et al. 2013). Whether or not raulisuchians form a clade and the relationships amongst raulisuchian taxa are matters of debate (e.g. Gower 2000; Brusatte et al. 2010; Nesbitt 2011; Nesbitt et al. 2013; Nesbitt & Desojo 2017).

In this study, we consider ‘Raulisuchia’ to minimally include non-crocodylomorph loricatans, Poposauroida, and *Ticinosuchus* (e.g., Butler et al. 2011; Nesbitt 2011; Nesbitt et al. 2013; Roberto-Da-Silva et al. 2018). Although Raulisuchia under our use is paraphyletic, research by Brusatte et al. (2010) recovered a monophyletic Raulisuchia including the clades Raulisuchoida and Poposauroida, but this has received little support in subsequent analyses. Nevertheless, even within a paraphyletic ‘Raulisuchia’ as in our use, there are a number of well-supported monophyletic lineages, such as Poposauroida and its monophyletic subclades (e.g. Ctenosauriscidae), and Raulisuchidae (Butler et al., 2011; Nesbitt 2011; Nesbitt et al. 2013; see Figure 1).

Most raulisuchians, such as *Prestosuchus*, *Stagonosuchus*, *Luperosuchus*, *Saurosuchus* and *Postosuchus*, were large-bodied carnivores (Nesbitt et al. 2013; Nesbitt & Desojo 2017). Other body plans, found within Poposauroida, included gracile bipeds, such as *Effigia* and *Poposaurus* (Nesbitt & Norell 2006; Gauthier et al. 2011), semi-aquatic forms, such as *Qianosuchus* (Li et al. 2006), sail-backed quadrupeds, such as *Arizonasaurus* and

*Ctenosauriscus* (Nesbitt 2005; Butler et al. 2011), and herbivores, such as *Shuvosaurus* and *Lotosaurus* (Nesbitt et al. 2013).

(INSERT TABLE ONE)

(INSERT FIGURE ONE)

(INSERT FIGURE 2)

Rauisuchians are present in the fossil record from the late Early Triassic through to the Late Triassic and have been found on all continents except Australia and Antarctica (Gower 2000; Nesbitt et al. 2013). The earliest branching member of the grade in some phylogenetic hypotheses (e.g. Nesbitt 2011), *Ticinosuchus ferox*, is from Switzerland, and other early-occurring specimens from the late Olenekian and early Anisian are found in Western Europe, Russia, China and North America (Butler et al. 2011), potentially suggesting a Laurasian origin for the group (Nesbitt et al. 2013). The stratigraphically youngest taxa, from the late Norian, include *Effigia*, *Vivaron* and, potentially, *Postosuchus* from the United States, *Teratosaurus suevicus* from Germany, and *Fasolasuchus* from Argentina (Nesbitt et al. 2013). There is currently no definitive record of rauisuchians from the Rhaetian. The only potential exception is *Effigia*, which of undetermined late Norian or Rhaetian age (Nesbitt et al. 2013).

In southern Africa the rauisuchian fossil record is poor, although a few previous papers have suggested their presence. The only possible rauisuchian taxon named based on body fossils is *Basutodon ferox* Huene, 1932, based on a single tooth from the lower Elliot Formation (Huene 1932; Kitching & Raath 1984; Gauffre 1993a; Galton & van Heerden 1998; Knoll 2004). *Basutodon* has since been considered a *nomen dubium* because its morphology is plesiomorphic for archosauriforms (van Heerden 1979; Knoll 2004), but the specimen may represent some form of rauisuchian because its morphology is consistent with that of other known members of the grade. Additionally, the ichnogenera *Pseudotetrasauropus* and

1 *Sauropodopus* are hypothesized to have been produced by rauisuchians (Galton & van  
2 Heerden 1998; Knoll 2004). A partial maxilla (SAM-PK-K383; reviewed and described in  
3 this work) of a carnivorous archosaur, from the Elliot Formation of Lesotho has been  
4 suggested by some authors to represent a rauisuchian (Kitching & Raath 1984; Galton & van  
5 Heerden 1998; Nesbitt et al. 2013). In Namibia, GSN F377 is an associated, but not  
6 articulated, partial skeleton of a large archosaur from the uppermost Omingonde Formation  
7 of supposedly Middle Triassic age. It was originally identified as the non-archosaurian  
8 archosauriform genus *Erythrosuchus* (Abdala & Smith 2009). However, Arcucci suggested it  
9 could be referred to *Rauisuchia* based on the presence of osteoderms and features of the  
10 cervical ribs (pers. comm. cited in Abdala & Smith 2009). Some of the authors of the current  
11 paper are working on this specimen and will present an analysis of it elsewhere.

12 Most of the specimens presented in this study are from the Late Triassic lower Elliot  
13 Formation (see ‘Geological Setting’ section below). The tetrapod fauna of the lower Elliot  
14 Formation consists of several herbivores of varying body sizes, including sauropodomorph  
15 dinosaurs (Knoll 2004), and cynodont (Knoll 2004) and dicynodont (Kammerer 2018)  
16 therapsids. The similarly-aged Chinle Formation in the United States has yielded  
17 dinosauromorphs, theropod dinosaurs, rauisuchians, other pseudosuchians, phytosaurs and  
18 numerous other tetrapods such as drepanosaurs and dicynodonts (Irmis et al. 2007). In the  
19 Norian Los Colorados Formation of Argentina, sauropodomorphs, theropods, and therapsids  
20 co-occur with rauisuchian, ornithosuchid and aetosaurian pseudosuchians (Arcucci et al.  
21 2004; Baczko & Desojo 2016; Desojo & Ezcurra 2016). A similar fauna is observed in  
22 Europe in the Löwenstein Formation of Germany, which includes sauropodomorph dinosaurs  
23 and pseudosuchian predators including the rauisuchian *Teratosaurus* (Brusatte et al. 2009;  
24 Meyer 1861; Nesbitt et al. 2013; Yates 2003a). The latest Triassic Lisowice Formation of  
25 Poland has yielded the archosaur *Smok wawelski* as a large-bodied predator (Niedzwiedzki &  
26 Budziszewska-Karwowska 2018) a large dicynodont, and small archosaur fragments,  
27 including pterosaur elements (Sulej & Niedzwiedzki 2018). The Lisowice Formation suffers  
28 from a lack of research into the taxonomic composition of its tetrapod fauna. As such, future  
29 research may enhance our understanding of the formation’s tetrapod population. These Late  
30 Triassic terrestrial ecosystems prominently feature large archosaurian carnivores and, as such,  
31 it is expected that the group would be present in South Africa.

1 Despite the limited mention in published works, major fossil collections in South African  
2 institutions contain specimens that have been catalogued as rautisuchians, but not previously  
3 described. The purpose of this paper is to review and identify this material. We subsequently  
4 provide a synthesis of the implications of these identifications in terms of biostratigraphy,  
5 palaeobiogeography and palaeoecology.

## 7 **Geological Setting**

8 The Karoo Supergroup is a large foreland basin that covers the majority of South Africa's  
9 land area (Catuneanu et al. 2005). The Karoo Supergroup is subdivided into the Dwyka  
10 Group, a late Carboniferous glacial deposit; the Ecca Group, an early Permian marine  
11 deposit; the Beaufort Group, a middle Permian through Early Triassic series of fluvio-  
12 lacustrine deposits; the informally named "Stormberg Group", a series of Late Triassic  
13 through Early Jurassic fluvio-lacustrine deposits; and the Drakensberg Group basalts  
14 (Catuneanu et al. 2005). The Stormberg is separated from the Beaufort by a stratigraphic  
15 hiatus (Turner 1983; Catuneanu et al. 2005). The Stormberg Group is divided into the  
16 Molteno, Elliot and Clarens formations (SACS 1980). These formations are Late Triassic  
17 (Carnian–Norian), Late Triassic through Early Jurassic, and Early Jurassic in age respectively  
18 (Olsen 1980; Olsen & Galton 1977, 1984; Anderson et al. 1998; Catuneanu et al. 2005;  
19 Kitching & Raath 1984; Knoll 2004, 2005). The specimens presented in this study are  
20 derived from the Elliot Formation.

21 The Elliot Formation comprises the Upper Triassic lower Elliot (Norian–Rhaetian) and the  
22 lower Jurassic upper Elliot Formation (Hettangian–Sinemurian) (Olsen & Galton 1984;  
23 Kitching & Raath 1984; Knoll 2004, 2005; Bordy et al. 2004b; McPhee et al. 2017). These  
24 divisions are based on lithostratigraphy, and are mostly coincident with the biozonation into  
25 the stratigraphically older '*Euskelosaurus*' (Huxley 1866) Range Zone (mostly coincident  
26 with the lower Elliot Formation) and the stratigraphically younger *Massospondylus* Range  
27 Zone (mostly coincident with the upper Elliot Formation; Kitching & Raath 1984). Recent  
28 work has questioned the taxonomic validity of '*Euskelosaurus*' (e.g. Yates 2003b, McPhee et  
29 al. 2017). The lower Elliot Formation is broadly contemporaneous with numerous Late  
30 Triassic deposits globally that contain rautisuchian fossil records, such as North America's  
31 Chinle Formation (Novak 2004; Nesbitt et al. 2013). The upper Elliot Formation has been

1 assigned a lower Jurassic age based on correlation to, for example, Canada's McCoy Brook  
2 Formation of the Newark Supergroup with which it shares the basal crocodylomorph  
3 *Protosuchus* (Olsen & Galton 1984; Sues et al. 1996; Lucas & Hancox 2001).

4 The lower Elliot generally characterised by red-purple mudstone and multi-storey cliff-  
5 forming sandstone units with well-developed lateral accretion surfaces and irregular, erosive  
6 basal bounding surfaces, all of which represent perennial fluvial deposits (Bordy et al. 2004a,  
7 Bordy et al. 2004b). The upper Elliot comprises pedogenically altered mudstones (mostly  
8 siltstones) and intraformational conglomerates comprising reworked pedogenic nodules and  
9 bone fragments (Bordy et al. 2004b). The uEF sandstones are tabular, sheet-like bodies and  
10 the whole sequence indicates ephemeral depositional settings (Bordy et al. 2004b).

11 Evidence from geochemistry (Sciscio & Bordy 2017) and analysis of fluvial style and  
12 palaeocurrents (Bordy et al. 2004b) suggests that the lower Elliot sediments were deposited  
13 as the climate changed from humid to semi-arid, and the upper Elliot records a change from  
14 semi-arid to arid. This is a trend hypothesized to characterize the Late Triassic and Early  
15 Jurassic as a whole (Simms & Ruffell 1989). The Triassic-Jurassic boundary is marked by a  
16 strong greenhouse effect (Holz 2015). There were, however, periods of higher humidity  
17 during the late Norian, and a cooler period for much of the Rhaetian (Holz 2015). There is  
18 also evidence of an Early Jurassic spike in global humidity (e.g. Ruckweid et al. 2008; Ryseth  
19 2014). This is not represented in the upper Elliot Formation which continues to show  
20 geochemical evidence of semi-arid to arid climatic conditions during the same time interval  
21 (Sciscio & Bordy 2016).

22  
23  
24 (INSERT TABLE 2)

25 (INSERT TABLE 3)

## 26 27 **Methods and Materials**

Numerous South African fossil specimens have been informally identified as *Rauisuchia* in collection catalogues (see Table 2). However, in our review of the fossil material, only five specimens contain enough information to confidently identify them as non-crocodylomorph paracrocodylomorphs and we report upon those here. The taxonomic affinities of the specimens were identified using apomorphies where possible and by comparative anatomy to globally contemporaneous taxa. The phylogenetic definitions used in this paper are from Nesbitt (2011), except for the grade *Rauisuchia*, which is taken from Nesbitt et al. (2013) (see Table 1). Each specimen was described using standard anatomical description techniques. Our comparative dataset for these specimens includes thirteen specimens from various institutions studied first-hand, and eight descriptions from the primary literature, together encompassing fourteen taxa (see Table 3).

(INSERT TABLE 4)

(INSERT FIGURE 4)

## SYSTEMATIC PALAEOLOGY

ARCHOSAURIA COPE, 1869

PARACROCODYLOMORPHA PARRISH, 1993

### *Referred material*

BP/1/5302, anterior right dentary fragment (Figure 3).

### *Type locality and horizon*



Damplaats 55, close to Ladybrand, Free State province, South Africa (see Figure 2); Karoo Basin, Stormberg Group, upper part of the lower Elliot Formation, (Kitching & Raath 1984), Norian-Rhaetian (Late Triassic; Olsen & Galton 1984; Lucas & Hancox 2001; Sciscio et al. 2017).

## DESCRIPTION

BP/1/5302 is the anterior end of a dentary with a maximum dorsoventral depth of 82 mm and a maximum labiolingual width of 44 mm. It preserves the complete alveoli of dentary teeth 1–3, and the anterior margin of the alveolus for dentary tooth 4. The alveoli are labiolingually compressed and elliptical in dorsal view, as is typical for rauisuchians (e.g., *Postosuchus* Weinbaum 2011; *Arganasuchus* Jalil & Peyer 2007; *Decuriasuchus* De Franca et al. 2013; *Arizonasaurus* Nesbitt 2005). The tooth crowns are broken away, but their roots are preserved in situ in some positions. The teeth are thecodont. These anterior dentary teeth are deep-rooted, with the root of the fourth tooth extending for nearly three quarters of the depth of the dentary. The preserved alveolar margin of the dentary is horizontal in lateral view.

The lateral surface of the anterior end of the dentary is smooth, with no marked sculpturing. There are several small foramina ventral to the tooth row, but these are obscured by crushing. The dorsal margin is smooth and gently rounded along the anteriormost surface. This is similar to *Postosuchus* (Weinbaum 2011) and differs from some other pseudosuchians where the anterolateral margin of the dentary tapers to a sharper point anterodorsally (e.g. *Decuriasuchus*, De Franca et al. 2013; *Revueltosaurus*, Holliday & Nesbitt 2013). The dorsal margin then trends parallel to the ventral margin for the remaining preserved length of the dentary, a condition similar to that of *Postosuchus* (Weinbaum 2011).

The medial surface of the dentary is relatively smooth. A low, bulging tumulus of bone is present at midheight at the posterior margin as preserved. This mound forms the dorsal border of a dorsoventrally low, anteriorly extensive Meckelian groove. The groove tapers anteriorly, ending a short distance posterior to the anterior margin; it participated in the dentary symphysis. This position is far anterior to that of the typical archosaurian condition, but it is also present in the rauisuchid *Polonosuchus* (ZPAL Ab III 563; Brusatte et al. 2009) as well as some crocodylomorphs such as *Alligator* and *Kayentasuchus* (Nesbitt 2011).

1 The dorsal margin of the medial surface, lingual to the alveoli, is shallowly crenulated, with  
2 lingual bulges at each tooth position. In dorsal view, a labiolingually narrow, deep, prominent  
3 groove extends anteroposteriorly along the boundary between the alveoli and this margin.  
4 This feature is also shared with *Polonosuchus* (ZPAL Ab III 563; Brusatte et al. 2009) and  
5 *Arganasuchus* (ALM 5; Jalil & Peyer 2007).

6 Whereas there is some morphological overlap between BP/1/5302 and the basal  
7 archosauriform clade Erythrosuchidae, there are several important differences. Firstly, the  
8 dorsal margin of the dentary is horizontal in lateral view. This contrasts with *Erythrosuchus*  
9 (e.g. BP/1/3893) which possesses a prominent dorso-ventral expansion at the level of the  
10 fourth alveolus with the anteriormost portion of the dentary being slightly ventrally deflected.  
11 Secondly, the Meckelian groove of *Erythrosuchus* terminates at the level of the fifth alveolus  
12 (Gower 2003), whereas the Meckelian groove in BP/1/5302 extends far anteriorly and  
13 participates in the dentary symphysis. Finally, the alveoli are labio-lingually compressed but  
14 not as strongly as in *Erythrosuchus* (BP/1/3893).

### 16 ***Taxonomic affinities***

17 There is some morphological overlap between BP/1/5302 and erythrosuchid archosauriforms.  
18 However, the presence of a far-anteriorly extending Meckelian groove and a lack of  
19 dorsoventrally expanded anterior dentary differentiate the specimen from *Erythrosuchus*.  
20 Furthermore, there is no known record of erythrosuchids younger than the Middle Triassic  
21 (Ezcurra 2016). Average pseudosuchian body size exceeded that of avemetatarsalians  
22 throughout the Late Triassic, a trend which rapidly reversed in the Early Jurassic (Turner &  
23 Nesbitt 2013). BP/1/5302 can be distinguished, by inference, from contemporaneous  
24 theropods (e.g. *Zupuysaurus* Arcucci & Coria 2003) due to its large size. Furthermore, it  
25 features a far anteriorly extending Meckelian groove, which is also present in the raiisuchid  
26 *Polonosuchus* (Nesbitt 2011). The specimen also compares closely to raiisuchians such as  
27 *Arganasuchus* and the raiisuchid *Postosuchus*. However, because none of the  
28 synapomorphies of Raiisuchidae are features of the dentary, it cannot be confidently referred  
29 to the clade (Nesbitt 2011).

(INSERT FIGURE 4)

(INSERT FIGURE 5)

### *Referred material*

BP/1/5163, fragmentary osteoderms, isolated teeth, fragments of caudal vertebral centra, rib fragments, other unidentifiable fragments. The specimen is associated but not articulated (Figures 3, 4).

### *Locality and horizon*

Roodebloom, close to Ladybrand, Free State province, South Africa; Karoo Basin, Stormberg Group, lower Elliot Formation, approximately 34 metres above the Elliot-Molteno contact, “*Euskelosaurus*” RZ (Kitching & Raath 1984), Norian–Rhaetian (Late Triassic; Olsen & Galton 1984; Lucas & Hancox 2001; Sciscio et al. 2017).

## **DESCRIPTION**

### **Dentition**

The specimen includes six relatively complete teeth and several other tooth fragments. The teeth are all labiolingually compressed. Three of them have markedly recurved anterior margins and more vertical posterior margins. The other three show strong curvature on both margins (see Figure 4). This distinction is also present in other loricatans, such as *Postosuchus*, where the anterior maxillary teeth are strongly recurved whereas the mid-maxillary teeth have a comparatively straight posterior margin (Weinbaum 2011). The teeth

of BP/1/5163 are serrated on both the anterior and posterior margins, with the anterior serrations ending midway along the apicobasal height of the tooth.

The serrations are relatively large when compared to other large archosaurian carnivores, such as most other archosaurs (e.g. phytosaurs, other paracrocodylomorphs) and theropod dinosaurs, which typically have a serration density of 3-7 serrations per millimetre (Nesbitt 2011). In BP/1/5163, there are only two serrations per millimetre in those teeth with less pronounced recurvature, and three serrations per millimetre in those teeth with more pronounced recurvature. This serration density is atypical of archosaurs in general but similar to a number of rauisuchians, including the undescribed Tanzanian archosaur '*Pallisteria*' (Paul Barrett pers. comm. 2019), *Postosuchus* (Weinbaum 2011, three serrations per millimetre), and *Vivaron* (Lessner et al. 2016, three serrations per millimetre). *Prestosuchus* teeth, by contrast, have a density four serrations per millimetre (Mastrantonio et al. 2019). The serrations are roughly rectangular in shape with slightly rounded corners in labial or lingual view. They are quite shallow and do not extend far past the carina.

## **Osteoderms**

The osteoderms are represented by three fragments of which only one is relatively complete (see Figure 5). They are elongate and sub-rectangular in shape. The external surfaces are sculptured and patterned with radiating grooves from the centre. The external surfaces also feature a high median groove with smooth, rounded dorsal margins as present in *Batrachotomus* (SMNS 91048; Gower & Schoch 2009). The relatively complete osteoderm is dorsoventrally deeper than the other osteoderm fragments. The internal surfaces of the osteoderms are smooth and flat with the ventral surface of the more complete osteoderm being slightly concave. They are roughly triangular in cross-section. The broad morphology is very similar to the paramedian osteoderms of *Fasolasuchus* (PVL 3850), *Batrachotomus* (SMNS 83252; Gower & Schoch 2009) and *Rauisuchus* (BSPG AS XXV 94; Lautenschlager & Rauhut 2015).

## **Caudal vertebrae**

1 There are two fragments of caudal vertebrae. The largest of these has a centrum width of  
2 60mm, larger than the 40mm width of the first caudal in *Postosuchus kirkpatricki* as recorded  
3 by Weinbaum (2013). The width is comparable to that of *Saurosuchus* (PVSJ 615; Trotteyn  
4 et al. 2011). Additionally, the preserved height of the centrum is 72mm, with the dorsal  
5 margin largely broken away. The centra of the caudal vertebrae of *Postosuchus kirkpatricki*  
6 tend to be only slightly higher than wide (Weinbaum 2013). The centrum width of the smaller  
7 vertebra is 30 mm, comparable to the 28 mm width of the eleventh caudal of *Postosuchus*  
8 *kirkpatricki* (Weinbaum 2013).

### 10 ***Taxonomic affinities***

11 For BP/1/5163, the presence of paramedian osteoderms as well as their morphology is  
12 suggestive of loricatan affinities. The external morphology of osteoderms in other  
13 archosauriform clades differs in key areas. For example, phytosaurs have osteoderms that are  
14 dorsoventrally flatter and spear-shaped in dorsal view (Stocker & Butler 2013), and aetosaurs  
15 have mediolaterally longer subrectangular osteoderms with extensive pitting on their dorsal  
16 surfaces and an anterior articular lamina (Desojo et al. 2013). Dorsal osteoderms are  
17 uncommon among dinosaurs and therapsids, and currently unknown among the other  
18 tetrapods found in the Elliot Formation. Whereas the latter observation may change with  
19 future research, there is a strong case for rauisuchian affinities of these osteoderms based on  
20 comparative anatomy. The external morphology of the osteoderms most closely resembles  
21 those of *Fasolasuchus* (PVL 3850), *Rauisuchus* (Lautenschlager & Rauhut 2015),  
22 *Prestosuchus* (Scheyer & Desojo 2011), and *Batrachotomus* (Gower & Schoch 2009). The  
23 low serration density on the teeth is potentially indicative of rauisuchid affinities. However,  
24 no unambiguous synapomorphies of any group within Rauisuchia are present. Rather, this  
25 specimen can tentatively be assigned to the latter based on comparative anatomy due to the  
26 combination of osteoderm morphology, tooth morphology and body size.

28 (INSERT FIGURE 6)

(INSERT FIGURE 7)

*Referred material*

BP/1/8120, dentary fragments (Figures 5, 6).

*Type locality and horizon*

Foutainie 331, close to Fouriesburg, Free State province, South Africa; Karoo Basin, Stormberg Group, lower Elliot Formation (Kitching & Raath 1984), Norian–Rhaetian (Late Triassic; Olsen & Galton 1984; Lucas & Hancox 2001; Sciscio et al. 2017).

**DESCRIPTION**

BP/1/8120 consists of four fragments of a large dentary. It preserves the complete alveoli of ten teeth and partial margins of three more, two of which are on the same block, suggesting a minimum of twelve teeth. A fragment of the anteriormost portion of the dentary (Figure 6) includes the alveoli of dentary teeth 1–3 and the distal tip of a replacement crown for the third tooth. Its dorsal margin is largely broken off anterior to the third alveolus. A larger fragment of the posterior portion of the dentary (Figure 7) contains four complete alveoli and the anterior margin of a fifth, with a length of 115 mm and a maximum depth of 54 mm, though an unknown amount of the dorsal margin is missing. The ventral side of its medial surface preserves a portion of the articulation surface for the splenial. Two more fragments are of unknown orientation. One of them contains two alveoli and another contains one complete alveolus and the partial margins of two more (Figure 6).

The teeth are thecodont and deep-rooted with alveoli extending into the far ventral portions of the dentary. The tooth crowns are large with maximum anteroposterior lengths of 25 mm, comparable in size to those of *Postosuchus kirkpatricki* (Weinbaum 2011), *Arganasuchus* (Jalil & Peyer 2007), and *Saurosuchus* (Alcober 2000). They are labiolingually compressed, as is typical of rauisuchians and other predatory archosaurs (Nesbitt 2011). The preserved

1 replacement tooth crown is serrated with a serration density of two per millimetre. These  
2 serrations are relatively large in comparison to other pseudosuchians (Nesbitt 2011) and  
3 similar to those of BP/1/5163 and to '*Pallisteria*' (Paul Barrett pers. comm. 2019).

4 The preserved anterior fragment is of similar size to BP/1/5302. The lateral surface of this  
5 fragment is smooth with four small nutrient foramina penetrating the cortical surface. These  
6 foramina are located quite far ventral to the dorsal margin of the dentary. These foramina are  
7 not present in, for example, *Postosuchus* (Weinbaum 2011), *Arizonasaurus* (Nesbitt 2005),  
8 *Prestosuchus* (Mastrantonio et al. 2019) and *Saurosuchus* (Alcober 2000). The ventral  
9 margin is gently rounded, and the medial surface is smooth. The dorsal surface features a  
10 broken, but prominent V-shaped groove running along the lingual margin, which is filled  
11 with matrix. This feature is seen in the rauisuchid *Polonosuchus* (Brusatte et al. 2009) and is  
12 very similar to the condition in BP/1/5302. This suggests that BP/1/8120 and BP/1/5302 may  
13 represent the same taxon, or at least a small clade sharing this synapomorphy.

14 The lateral surface of the fragment of the posterior portion of the dentary is smooth and bears  
15 four visible foramina arranged horizontally along the dorsoventral midline of the dentary.  
16 The dentary bulges laterally in the portion ventral to these foramina. The ventral portion of  
17 the medial surface is broken along the articular surface for the splenial. The splenial  
18 articulated far ventrally, similar to the condition in *Postosuchus kirkpatricki* (Weinbaum  
19 2011) and *Prestosuchus* (Mastrantonio et al. 2019) but different from the more medial  
20 articulation seen in other rauisuchians (e.g. *Arganasuchus* Jalil & Peyer 2007). Part of the  
21 Meckelian canal is exposed along the dorsal margin of this contact.

### 23 ***Taxonomic affinities***

24 The dentary preserved in BP/1/8120 is similar to that of BP/1/5302 in terms of size and the  
25 presence of a labial groove running anteroposteriorly along the tooth row in the anterior  
26 portion of the dentary. This may suggest that the two specimens are conspecific.  
27 Additionally, the presence of the labial groove and the far anteriorly ending Meckelian  
28 groove suggests phylogenetic affinity with *Polonosuchus* and, by extension, the clade  
29 Rauisuchidae. However, due to the lack of rauisuchid synapomorphies present in the  
30 preserved material, the assignment of these specimens to Rauisuchidae remains tentative.

(INSERT FIGURE 8)

#### *Referred material*

SAM-PK-K383. Partial right maxilla, including the portion of the bone posterior to the anterior margin of the antorbital fenestra, with four disarticulated but associated teeth and other associated fragments (Figure 8).

#### *Locality and horizon*

Likhoele, Mafeteng, Lesotho, tentatively lower Elliot Formation (Norian-Rhaetian), or potentially base of upper Elliot Formation (upper Elliot fauna have been collected from the same locality, Crompton 1964) of latest Triassic or Early Jurassic age (Olsen & Galton 1984; Lucas & Hancox 2001; Sciscio et al. 2017, McPhee et al. 2017).

### **DESCRIPTION**

The specimen consists of most of a large (maximum preserved length = 25 cm; maximum height of the posterior process = 11 cm) posterior portion of a right maxilla and associated teeth. The specimen was prepared in acid to illuminate fine detail. Unfortunately, during this process the teeth fell out of their respective alveoli. As such, the original position of each tooth within its respective alveolus is uncertain. Gaps in the surfaces of the bone were filled using an unknown epoxy compound.

The lateral surface of the maxilla bears a mixed pattern of smooth and rough texture. The ventral margin is anteroposteriorly straight. The dorsal margin of the maxilla indicates that an antorbital fenestra was present and a clear antorbital fossa is located on the entire dorsolateral portion of the posterior process of the maxilla. The combination of these two character states



1 is a synapomorphy of Archosauria (Nesbitt 2011). A slightly sloped surface delineates the  
2 antorbital fossa from the rest of the lateral surface of the maxilla. This is similar to  
3 *Saurosuchus* (PVL 32), *Batrachotomus* (SMNS 52970), *Arizonasaurus* (MSM 4590),  
4 *Fasolasuchus* (PVL 3850), and Triassic crocodylomorphs (e.g., *Dromicosuchus*, NCSM  
5 13733). In *Postosuchus kirkpatricki* (TTU-P 9000) and *Polonosuchus* (ZPAL Ab III 563), a  
6 thick ridge separates the antorbital fossa from the rest of the lateral surface. The antorbital  
7 fossa in SAM-PK-K383 deepens and bends dorsally anteriorly. The posterior process of the  
8 maxilla has a similar dorsoventral height at both anterior and posterior ends of the antorbital  
9 fenestra, a character-state present in *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus*  
10 (ZPAL Ab III 563), basal crocodylomorphs (e.g., *Dromicosuchus*, NCSM 13733),  
11 *Saurosuchus* (PVL 32), *Prestosuchus* (UFRGS 0156-T), and *Fasolasuchus* (PVL 3850). The  
12 posterodorsal portion of the posterior process is highly mediolaterally compressed relative to  
13 the mediolaterally thick ventral portion. The dorsal extent of the alveoli marks the transition  
14 between the thick ventral portion and the much thinner dorsal portion. A thin posterodorsal  
15 portion is also present in *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus* (ZPAL Ab  
16 III 563), *Saurosuchus* (PVL 32), *Prestosuchus* (UFRGS 0156-T, 0629-T), *Fasolasuchus*  
17 (PVL 3850), and *Arizonasaurus* (MSM 4590) and in early crocodylomorphs (e.g.,  
18 *Terrestriisuchus*, NHMUK PV R9579). The posteriormost portion of the posterior process  
19 tapers posteroventrally and would have been overlapped by the anterior portion of the jugal.  
20 A few small nutrient foramina are located just dorsal to the ventral border of the maxilla.  
21 The preserved portion of the maxilla preserves seven alveoli. The incomplete posteriormost  
22 alveolus is the smallest of the preserved alveoli whereas the other alveoli are nearly the same  
23 diameter. Alveoli one and seven preserve teeth in situ.

24  
25 The medial surface of the maxilla preserves a distinct step separating the alveolar margin  
26 from the rest of the medial side. Galton (1985) identified this feature in *Teratosaurus*  
27 *suevicus* and termed it the dental groove. This groove is present in a variety of  
28 archosauriforms and likely housed the soft tissue dental lamina (Brusatte & Sereno 2007). A  
29 slight groove is located just ventral to and parallel to the step. Posteriorly, the groove  
30 shallows. A few small foramina are within the groove. The interdental plates are largely  
31 fused, a character state present in a small number of suchians including *Postosuchus*  
32 *kirkpatricki* (TTUP 9000), *Fasolasuchus* (PVL 3850), *Polonosuchus* (ZPAL Ab III 563), and  
33 *Teratosaurus suevicus* (NHMUK OR38646) but not in early crocodylomorphs (Nesbitt  
34 2011). A slight ridge on the anteromedial portion marks the posterior extent of the palatal

process of the maxilla. The thickened portion of the medial side gradually tapers posteroventrally.

Two large foramina are located on the medial side of the maxilla. The first is located dorsal to the space between alveoli two and three. The large foramen is not visible in medial view because the thickened medioventral portion hides it. The foramen opens posteriorly into a trough between the thickened medioventral portion and the mediolaterally thin posterodorsal portion. This foramen may be homologous to a foramen located in a similar position in *Teratosaurus suevicus* (NHMUK OR38646), *Polonosuchus* (ZPAL Ab III/563), *Postosuchus kirkpatricki* (TTUP 9000), *Arizonasaurus* (UCMP 36232), *Batrachotomus* (Gower 1999), *Silesaurus* (Dzik 2003), and other archosaurs and has been interpreted by Witmer (1995, 1997) as transmitting the maxillary nerve and maxillary vessels. The larger second foramen is located dorsal to the space between the fifth and sixth alveolus. The large foramen opens posteriorly and is partially visible in lateral view. It is not clear with what the foramen communicates.

Four well-preserved teeth were found with the specimen. Impressions of two other teeth were found with the specimen and may belong to the anterior portion of the maxilla. The teeth have serrations on both the anterior and posterior edges as well as at the tip. The square-shaped serrations number an average of 1.6 per millimetre. As with BP/1/5163 and BP/1/8120, this serration density is low in comparison to most other archosaurs (Nesbitt 2011). The longest tooth crown measures 85 mm. The teeth are only slightly posteriorly recurved at the tips. The posterior margin of the posteriormost tooth in the maxilla is convex, similar to that of *Polonosuchus* (ZPAL Ab III/563), *Postosuchus kirkpatricki* (TTUP 9000), and early crocodylomorphs (e.g., *Dromicosuchus*, NCSM 13733; *Hesperosuchus* “*agilis*”, CM 29894).

### ***Taxonomic affinities***

Even though SAM-PK-K383 only consists of a partial maxilla, teeth and an undiagnostic fragment of the pterygoid, the specimen bears close similarities to that of *Fasolasuchus* (PVL 3850), *Polonosuchus* (ZPAL Ab III/563), *Postosuchus kirkpatricki* (TTUP 9000), and basal crocodylomorphs (e.g., *Dromicosuchus*, NCSM 13733; *Hesperosuchus* “*agilis*,” CM 29894).

Some discrete character states of SAM-PK-K383, such as a consistent maxilla depth, fused interdental plates, and a straight ventral margin of the antorbital fenestra are not found in erythrosuchids or early theropods, but are present in rauisuchians (Nesbitt 2011, Ezcurra 2016). The preserved character states do not definitely preclude this specimen from being a large, early diverging crocodylomorph, given that there is growing evidence that large crocodylomorphs were present in the Late Triassic (e.g., *Redondavenator*, Nesbitt et al. 2005; *Carnufex*, Zanno et al. 2015). The latter scenario is unlikely however, given key morphological differences (e.g. the maxilla of SAM-PK-K383 is dorsoventrally higher and maintains a consistent depth along the length of the antorbital fenestra, as opposed to the condition seen in *Carnufex*; Zanno et al. 2015). Additionally, SAM-PK-K383 is substantially larger than other southern African crocodylomorphs from the Elliot Formation (Dollman et al. 2019).

(INSERT FIGURE 9)

POPOSAUROIDEA NOPCSA, 1923 sensu NESBITT, 2011

#### *Referred material*

NMQR 3554, near complete right ilium missing most of the postacetabular process and part of the preacetabular process (Figure 9).

#### *Locality and horizon*

Elliot Formation, precise provenance unknown (pers. comm. Elize Butler); Norian–Sinemurian (Olsen & Galton 1984; Lucas & Hancox 2001; Sciscio et al. 2017).

#### **DESCRIPTION**

NMQR 3554 is a medium-sized right ilium, with maximum preserved length and height of 210 mm and 185 mm, respectively. Most of the acetabulum is preserved apart from the anterior-most extent. The ischiadic peduncle has largely broken off and the postacetabular process is broken beyond the posteriormost extent of the acetabulum. The supraacetabular rim has partially broken away as has the anterior part of the preacetabular process.

The acetabulum is anteroposteriorly longer and dorsoventrally lower than those of rauisuchids (e.g. *Postosuchus*, Weinbaum 2011), and is deep ventral to the supraacetabular rim, a condition present in poposauroids (Gauthier et al. 2011). The supraacetabular rim projects laterally and the margin forms a rounded shelf over the acetabulum. The ventral-most portion of the acetabulum is mediolaterally thin. The ventral margin of the ilium would, if the postacetabular process and ischiadic peduncle were complete, form a slightly concave margin as seen in poposauroids (Nesbitt 2011).

The supraacetabular buttress (ridge on the dorsal surface of the supraacetabular rim) is strongly pronounced and laterally expanded. Its anteroposterior thickness is less than that of *Postosuchus kirkpatricki* (Weinbaum 2013) and comparable to that of *Poposaurus gracilis* (Gauthier et al. 2011). The dorsal-most extent of the ridge bears an anteriorly projecting crest, which is a character state of poposauroids (Weinbaum & Hungerbühler 2007; Nesbitt 2011). The anterior surface of this crest is strongly concave in anterior view. The posterior portion of the lateral surface is gently convex, and the crest forms a lip dorsal to the posterior surface of the supraacetabular buttress. The dorsal surface of the crest is hook-shaped with a strongly concave anterior surface, and a moderately convex posterior surface. The dorsal surface of the crest is noticeably rugose. This crest, while prominent, is less pronounced than in *Poposaurus gracilis* (Gauthier et al. 2011) and bears a resemblance to the condition seen in *Arizonasaurus* (Nesbitt 2005; Butler et al. 2011).

The preacetabular process is anteriorly projected. Whereas this process is broken close to the supra-acetabular buttress, the preserved portion is already level with the anterior-most extent

1 of the acetabulum. It would likely extend far anteriorly, a condition that is diagnostic of  
2 Poposaurioidea (Weinbaum & Hungerbühler 2007; Nesbitt 2011) and some early  
3 crocodylomorphs (Nesbitt 2011). The posterior part of the dorsal margin of the ilium, as  
4 preserved, is inclined posterodorsally, resulting in an inflected region of the dorsal margin  
5 above the midpoint of the acetabulum. This is similar to the condition seen in both species of  
6 *Poposaurus* (Gauthier et al. 2011). The posterior process is dorsoventrally low and can be  
7 seen to be tapering posteriorly even at its anterior-most portion.

8  
9 The lateral surface of the ilium is smooth in texture except for the crest dorsal to the  
10 supraacetabular buttress. The medial surface is characterised by deep depressions separated  
11 by prominent ridges, which represent articular surfaces for the sacral vertebrae. Two main  
12 articulation areas for the transverse processes and sacral ribs are present. On the anterior half,  
13 an arch-shaped groove is present dorsal to the articulation scar for the first sacral rib and  
14 represents the articular surface for the transverse process of the first primordial sacral  
15 vertebra. This results in the articular scars of the dorsal rib and the transverse process forming  
16 a ‘C’ shape. The dorsal articular surface for the first sacral rib is dorsoventrally wide and  
17 extends posterior to the anterior process. There is a deep depression curving anteroposteriorly  
18 along the anterior process and a fossa ventral to the preacetabular process. A mediolaterally  
19 high, but anteroposteriorly narrow, ridge separates the first and extending sacral rib scars.  
20 The second sacral rib scar is divided into three anteroposteriorly trending grooves, the medial  
21 of which is small and subtriangular. The anteroventral portion of the lateral surface of the  
22 ilium features a facet above the ischiadic peduncle. This is similar to the condition observed  
23 in the poposaurioid ilium SMNS 91401 (Butler et al. 2011).

## 24 25 ***Taxonomic affinities***

26 NMQR 3554 has distinct synapomorphies of Poposaurioidea including the presence of a  
27 laterally projecting supra-acetabular rim, an anterodorsally inclined crest dorsal to the supra-  
28 acetabular rim and a pre-acetabular process that extends anterior to the acetabulum (Nesbitt  
29 2011). The latter two character states suggest the specimen may be more closely related to  
30 *Poposaurus* than to any other poposaurioid (Nesbitt 2011).

## Discussion

### Summary of taxonomic affinities

Due to the fragmentary nature of the putative rauisuchian material from the Elliot Formation, previous researchers have been cautious in their interpretations given convergent similarities between rauisuchians, erythrosuchids and theropods, particularly in tooth morphology (Knoll 2004). SAM-PK-K383 has been mentioned in the literature before (e.g. Kitching & Raath 1984; Nesbitt et al. 2013) but not described. However, we can now identify at least five distinct, likely non-crocodylomorph paracrocodylomorph specimens from the Elliot Formation. Whereas each specimen can be referred to this grade based on comparative observations, they cannot, apart from NMQR 3554, be confidently assigned to any rauisuchian subclade based on synapomorphies. Because poposauroids, such as NMQR 3554, lack osteoderms, the presence of osteoderms in BP/1/5163 suggests at least two taxa of rauisuchians are present in the lower Elliot Formation, as also commonly recorded in other continental Late Triassic formations (Nesbitt et al. 2013).

In addition to morphology, the size categories of these animals are substantially larger than those of contemporaneous theropods which were relatively diminutive during the Triassic (Benson et al. 2018). Examples of small-to-medium bodied Late Triassic theropods include *Zupaysaurus* from the upper Los Colorados Formation (Arcucci & Coria 2003) and *Coelophysis* from the Chinle Formation (Colbert 1989). The maximum skull length of *Zupaysaurus* is 380 mm (Arcucci & Coria 2003). For reference, the maximum preserved length of the incomplete maxilla (SAM-PK-K383) is 250 mm. Within the context of the Elliot Formation, *Dracovenator*'s known tooth crowns do not exceed 50 mm (Yates 2005), indicating the taxon to be substantially smaller than, for example, SAM-PK-K383 which had tooth crown heights exceeding 85 mm. With the other specimens being of similar size

category, they would have substantially outsized contemporaneous theropods such as *Zupaysaurus*.

#### **Palaeoecology**

Late Triassic terrestrial ecosystems worldwide prominently feature rauisuchian carnivores, e.g., the Los Colorados fauna of Argentina (Arcucci et al. 2004; Baczko & Desojo 2016; Desojo & Ezcurra 2016) and the Löwenstein fauna of Germany (Brusatte et al. 2009; Meyer 1861; Nesbitt et al. 2013; Yates 2003a). We therefore expect that the group would be present in South Africa. However, it has long been noted that the Elliot Formation has a low relative abundance of body fossils of archosaurian carnivores, with the only two valid taxa being the upper Elliot Jurassic theropods *Dracovenator* and *Megapnosaurus* (Knoll 2005; Yates 2005). Given that fossils have been collected from the upper Elliot since the 1840s (e.g., Owen 1854), this low relative abundance, in both the lower and upper Elliot Formation, is likely not attributable to poor sampling. This stands in marked contrast to the rich ichnofossil records of potential carnivores, which includes tracks identified as belonging to theropod dinosaurs, rauisuchians, and crocodylomorphs (Ellenberger 1970; Ellenberger 1972; Knoll 2004). The lower Elliot Formation specimens described in this paper, with the exception of NMQR 3554 (for which dietary strategy is uncertain due to the absence of dental remains), therefore provide the first body fossil record of definitive archosaurian carnivores from the Late Triassic strata of South Africa.

The modest taxonomic diversity of archosaurian carnivores in the lower Elliot evidenced by the specimens in this study (at least matching that of the upper Elliot) indicates that further sampling of the lower Elliot formation may yield more complete and taxonomically diverse carnivore specimens. These rauisuchian carnivores would have had an extensive fauna of herbivores upon which to prey, including dinosaurs and therapsids (Knoll 2004; see Table 5). Despite the low relative abundance of rauisuchians in the Elliot Fossil record, our research shows that they were present across many different strata. This suggests that with further excavations, we will likely find additional skeletal material to build a deeper understanding of the role rauisuchians played in the taxonomic composition of the carnivorous fauna in the Late Triassic.

1 The tetrapod fauna of the lower Elliot bears many similarities to that of other Late Triassic  
2 deposits globally. This includes the presence of a diversity of sauropodomorph dinosaurs  
3 dicynodont therapsids, and now rauisuchian carnivores (shared with, for example, the Chinle  
4 Formation, Irmis 2005; and the Los Colorados Formation, Arcucci et al. 2004). In the case of  
5 dicynodonts, the lower Elliot seems to have a lower abundance of the group compared to  
6 contemporaneous formations (Kammerer 2018).

7 Interestingly, these similarities do not extend to other Late Triassic archosauriform lineages,  
8 such as Aetosauria and Phytosauria, which we found no evidence for in our review of Elliot  
9 material (we agree with Knoll [2004] that the aetosaur material reported by Kitching & Raath  
10 [1984] is unconfirmable). Much like rauisuchians, both groups were abundant and diverse in  
11 the Middle and Late Triassic and were extinct by the Triassic-Jurassic boundary after  
12 declining in the late Norian and Rhaetian (Desojo et al. 2013; Stocker & Butler 2013).  
13 Phytosaur fossils are globally present but are far more abundant in Laurasian deposits,  
14 particularly in the Chinle Formation (Irmis 2005; Stocker & Butler 2013). Additionally,  
15 phytosaurs have not been recovered from Argentina's Los Colorados Formation (Stocker &  
16 Butler 2013). The Gondwanan record of aetosaurs is also limited, though they have been  
17 recovered from Los Colorados (Bonaparte 1971; Stocker & Butler 2013). Given the ubiquity  
18 and high relative abundance of those groups in other Late Triassic deposits, it seems likely  
19 that they were simply not present in Triassic Elliot ecosystems. One possible explanation for  
20 this pattern of phytosaur and aetosaur exclusion are climatic differences between the Elliot  
21 Formation and other key Late Triassic deposits. Another possibility is that those lineages,  
22 particularly phytosaurs (given the lack of Argentinian record) were somehow excluded from  
23 higher-latitude areas (see following section) based on features of their physiology not shared  
24 by later-branching pseudosuchians. Therefore, we predict that further excavation and research  
25 into the lower Elliot Formation may yield more rauisuchians but will not likely produce  
26 phytosaurs or aetosaurs.

## 27 **Biogeography and biostratigraphy**

28 (INSERT TABLE 5)

29  
30



Rauisuchians are globally distributed throughout the Triassic, but their record at high latitudes is sparse (Gower 2000; Nesbitt et al. 2013). It is unclear if this apparent latitudinal distribution bias is real or rather a product of inadequate sampling and/or insufficient Middle- to-Late Triassic rock record (e.g., Close et al. 2017). The South African specimens described here would have occurred at palaeolatitudes of approximately 50 degrees south (Hinsbergen et al. 2015). This represents the upper limit of latitudinal range for pseudosuchian archosaurs as reported by Mannion et al. (2015). The presence of rauisuchians in South Africa therefore indicates that the group occurred in these comparatively high latitudes at the end of the Triassic just prior to their extinction, and with at least a modest taxonomic diversity.

Stratigraphically, these specimens are important for two reasons. Firstly, they include some of the latest occurring rauisuchians worldwide. The specimens described here, such as SAM-PK-K383, extend the range of rauisuchians, to near the Triassic-Jurassic boundary (see Figure 2), and very tentatively in the case of SAM-PK-383, into the lowermost Jurassic (Nesbitt et al. 2013). Secondly, these represent the first definitive record of rauisuchians from South Africa. Their presence in the lower Elliot Formation is therefore among the latest-occurring and highest-latitude yet known.

## Conclusion

This paper has identified definitive rauisuchian records from South Africa, representing at least two taxa. This is the first definitive record from South Africa and among the youngest, and highest latitude, record of rauisuchians globally. This is the first definitive record of large carnivore body fossils from the lower Elliot Formation in over a century of sampling. This illustrates the importance of comprehensive review of fossil collections to fully uncover the taxonomic diversity of past ecosystems.

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## **FIGURE CAPTIONS**

**Figure 1:** Phylogenetic relationships of rauisuchians. 1: Archosauria, 2: Pseudosuchia, 3: Paracrocodylomorpha, 4: Poposauroida, 5: Ctenosauriscidae, 6: Loricata, 7: Rauisuchidae, 8: 'Rauisuchia'.

**Figure 2:** Geographic and stratigraphic provenance of the specimens in this study.

**Figure 3:** BP/1/5302. Dentary in dorsal (A), medial (B) and lateral (C) views. Abbreviations: Al.1, alveolus one; Mec, Meckelian groove; Grv, groove. Scale bar = 30 mm.

**Figure 4:** BP/1/5163, dentition. Teeth in lateral view (A). Close-up of tooth in occlusal view (B). Examples of serrations in lateral (C) and occlusal (D) views. Abbreviation: Dnt, denticle. Scale bars = 30 mm (A and B), increments of 0.5 mm (C and D).

**Figure 5:** BP/1/5163, skeletal fragments. Vertebrae in lateral (A) and dorsal (B) views. Relatively complete osteoderm in ventral (C), dorsal (D), and lateral (E) views. Broken osteoderm in dorsal view (F). Scale bar = 30 mm.

**Figure 6:** BP/1/8120. Anterior dentary fragment in dorsal (A), lateral (B), and medial (C) views, and loose fragments (D). Abbreviations: Al, alveolus; Grv, groove; For, foramen; RT, replacement tooth. Scale bar = 30 mm.

**Figure 7:** BP/1/8120. Posterior dentary fragment in dorsal (A), lateral (B), and medial (C) views. Abbreviations: Al, alveolus; Ar.Spl, articulation surface for the splenial; Mec.C, Meckelian canal. Scale bar = 30 mm.

**Figure 8:** SAM-PK-K383. Maxilla in lateral (A), medial (B), and ventral (C) views. Close-up of a tooth in lateral and occlusal views (D). Schematic line drawings of the maxilla in lateral (E), medial (F), and ventral (G) views. Abbreviations: afo, antorbital fossa; al: alveolus; for, foramen; id, interdental plates; t, tooth. Scale bars = 50 mm (A, B, C), 10 mm (D).

**Figure 9:** NMQR 3554. Ilium in lateral (A) and medial (B) views. Abbreviations: Ac, Acetabulum; AP, anterior process; Fac, facet; PoP, posterior process; SAB, supra-acetabular buttress; SAR, supra-acetabular rim; SAS 1, sacral rib articular scar 1; SAS 2, sacral rib articular scar 2. Scale bar = 30 mm.

TAXON	DEFINITION
Archosauria	Least inclusive clade including <i>Crocodylus niloticus</i> and <i>Passer domesticus</i>
Pseudosuchia	Most inclusive clade including <i>Crocodylus niloticus</i> but not <i>Passer domesticus</i>
Paracrocodylomorpha	Least inclusive clade including <i>Poposaurus gracilis</i> and <i>Crocodylus niloticus</i>
‘Rauisuchia’	Paraphyletic grade including non-crocodylomorph paracrocodylomorphs + <i>Ticinosuchus ferox</i>
Loricata	Most inclusive clade including <i>Crocodylus niloticus</i> , but not <i>Poposaurus gracilis</i> , <i>Ornithosuchus longidens</i> , or <i>Aetosaurus ferratus</i>
Poposauroidea	Most inclusive clade including <i>Poposaurus gracilis</i> , but not <i>Postosuchus kirkpatricki</i> , <i>Crocodylus niloticus</i> , <i>Ornithosuchus longidens</i> , or <i>Aetosaurus ferratus</i>
Rauisuchidae	Most inclusive clade including <i>Rauisuchus tiradentes</i> but not <i>Aetosaurus ferratus</i> , <i>Prestosuchus chiniquensis</i> , <i>Poposaurus gracilis</i> , or <i>Crocodylus niloticus</i>

TABLE 1: Summary of taxonomic terms used in this paper. All definitions are from Nesbitt (2011), except for ‘Rauisuchia’ which is from Nesbitt et al. (2013).

Table 2  
[Click here to download Table: Tolchardetal2019Table2.docx](#)

SPECIMEN NUMBER	PROVENANCE	ELEMENTS	IDENTIFICATION PER THIS PAPER
BP/1/5135	Lower Elliot	Isolated large tooth	Archosauria indet.
<b>BP/1/5163</b>	<b>Lower Elliot</b>	<b>Isolated teeth, maxillary fragments, vertebrae and osteoderms</b>	<b>‘Rauisuchia’</b>
<b>BP/1/5302</b>	<b>Lower Elliot</b>	<b>Anterior part of right dentary</b>	<b>‘Rauisuchia’</b>
BP/1/6016	Lower Elliot	Fragment of jaw showing tooth in section	Archosauria indet.
BP/1/6058	Upper Elliot	Vertebra and fragments	Archosauria indet.
BP/1/6062	Upper Elliot	Tooth, osteoderm and fragments	Archosauria indet., potentially ‘Rauisuchia’
BP/1/6118	Lower Elliot	Partial tooth	Archosauria indet.
BP/1/6182	Lower Elliot	Isolated tooth and vertebra	Archosauria indet., potentially ‘Rauisuchia’
<b>BP/1/8120</b>	<b>Lower Elliot</b>	<b>Dentary fragments</b>	<b>‘Rauisuchia’</b>
NMQR 3081	Lower Elliot	Isolated postcranial elements	Indet.
<b>NMQR 3554</b>	<b>Elliot</b>	<b>Ilium</b>	<b>Poposauroidae</b>
<b>SAM-PK-K383</b>	<b>Elliot</b>	<b>Fragmentary jaw with large teeth and other fragments</b>	<b>‘Rauisuchia’, potentially Rauisuchidae</b>

TABLE 2: List of specimens identified as ‘Rauisuchia’ in South African fossil collections with the specimens included in this study in bold.



TAXON	SPECIMEN(S)	SOURCE(S)
<i>Postosuchus</i>	TTU-P 9000	Weinbaum 2011, 2013
<i>Polonosuchus</i>	ZPAL Ab III/563	Brusatte et al. 2009
<i>Batrachotomus</i>	SMNS 52970/91048	Gower & Schoch 2009, Gower 1999
<i>Rauisuchus</i>	BSPG AS XXV 60–68, 71– 100, 105–119, 121.	Lautenschlager & Rauhut 2015
<i>Saurosuchus</i>	PVL 32, PVSJ 615	Alcober 2000, Trotteyn et al. 2011
<i>Arizonasaurus</i>	MSM 4590, UCMP 36232	Butler et al. 2011
<i>Fasolasuchus</i>	PVL 3850	Bonaparte 1981
<i>Dromicosuchus</i>	UNC 15574	
<i>Prestosuchus</i>	UFRGS 0156-T, 0629-T	Mastrantonio et al. 2019
<i>Terrestrisuchus</i>	NHMUK PV R9579	
<i>Teratosaurus</i>	NHMUK OR38646	Galton 1985
<i>Hesperosuchus</i>	CM 29894	
<i>Poposaurus</i>		Gauthier et al. 2011
Poposauroida indet.	SMNS 91401	
<i>Arganasuchus dutuiti</i>	ALM 5	Jalil & Payer 2007

TABLE 3: List of taxa used for comparative anatomy with specimens and/or literature used as source.

BP	Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa
CM	Carnegie Museum of Natural History, Pittsburgh, USA
NCSM	North Carolina Museum of Natural Sciences, Raleigh, USA
NMHUK	Natural History Museum, London, UK
NMQR	National Museum, Bloemfontein, South Africa
PVL	Istituto Miguel Lillo, Tucumán, Argentina
SAM	Iziko South African Museum, Cape Town, South Africa
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
MSM	Arizona Museum of Natural History, Mesa, USA
TTU-P	Texas Tech University Museum, Lubbock, USA
UCMP	University of California Museum of Paleontology, Berkeley, USA
UFRGS	Institute of Geosciences, Laboratório de Paleovertebrados of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil
UNC	University of North Carolina, Raleigh, USA
ZPAL	Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

TABLE 4: List of institutional abbreviations.

TAXON	SOURCE
<b>Temnospondyli</b>	
Chigutisauridae indet.	Warren & Damiani 1999
<b>Dicynodontia</b>	
<i>Pentasaurus goggai</i>	Kammerer 2018
<b>Cynodontia</b>	
<i>Scalenodontoides macrodontes</i>	Crompton & Ellenberger 1957
<b>Sauropodomorpha</b>	
<i>Blikanasaurus cromptoni</i>	Galton & van Heerden 1985, 1998
<i>Eucnemesaurus entaxonis</i>	McPhee et al. 2015
<i>Eucnemesaurus fortis</i>	Yates 2007a
<i>Melanorosaurus readi</i>	Gauffre 1993b
<i>Plateosauravus cullingsworthi</i>	Yates 2003b, 2007
<i>Sefapanosaurus zastronensis</i>	Otero et al. 2015

TABLE 5: List of valid tetrapod taxa with body fossils from the lower Elliot Formation.



Figure1  
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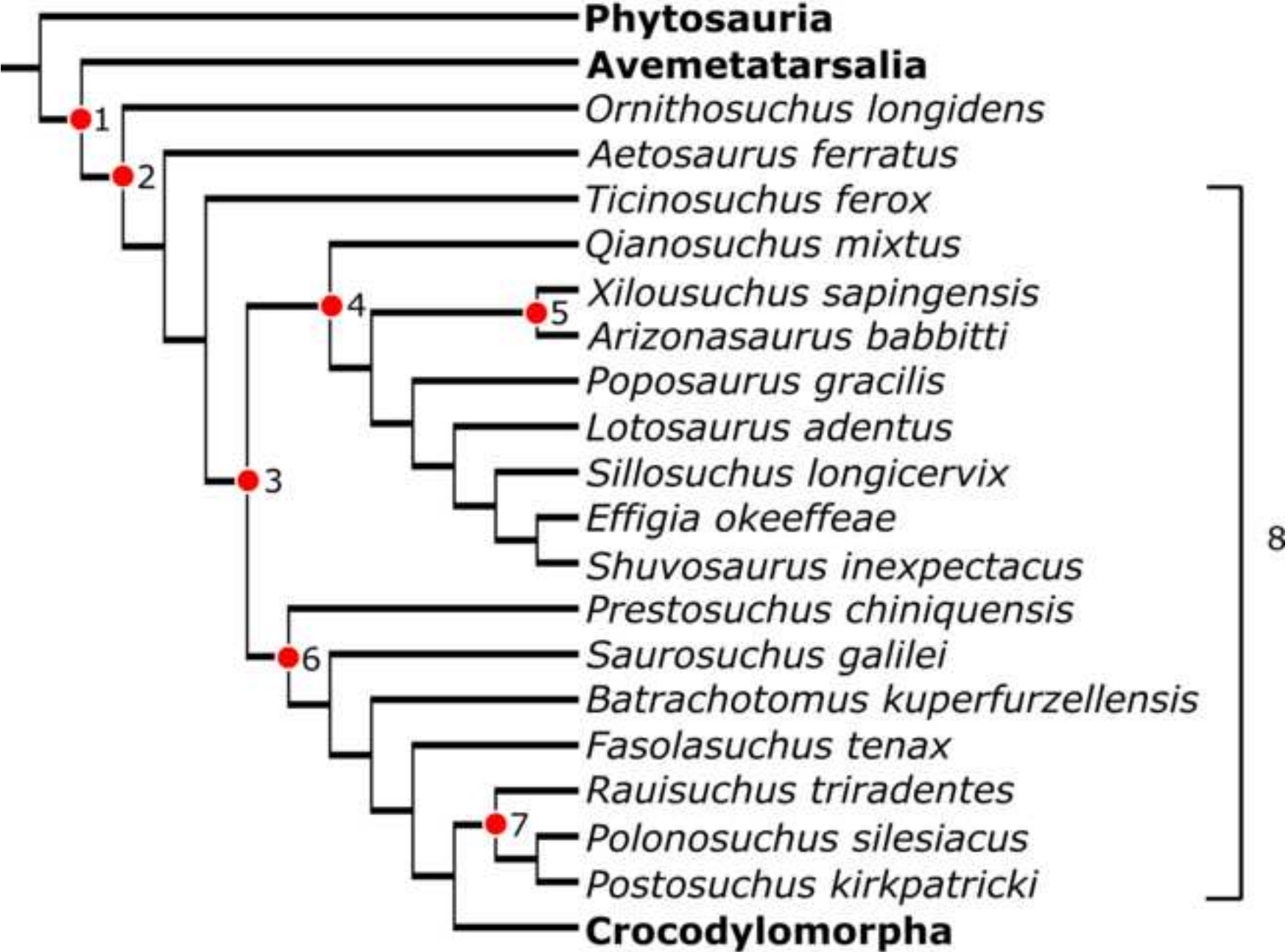


Figure2  
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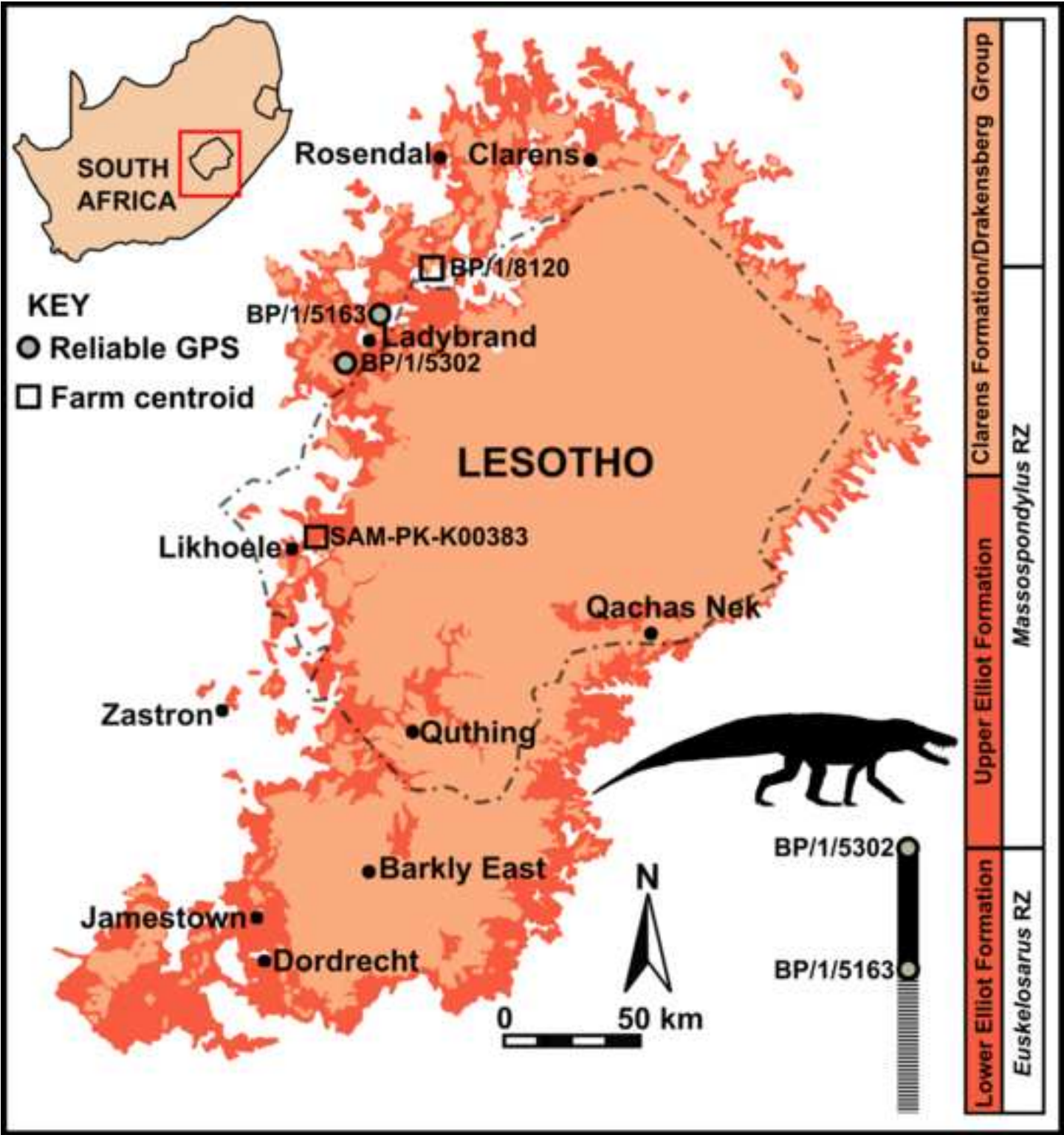
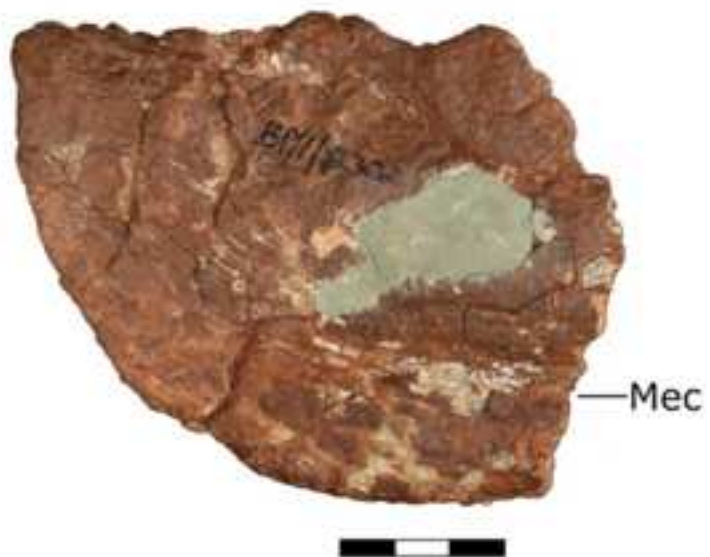


Figure3  
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A



B



C





Figure4  
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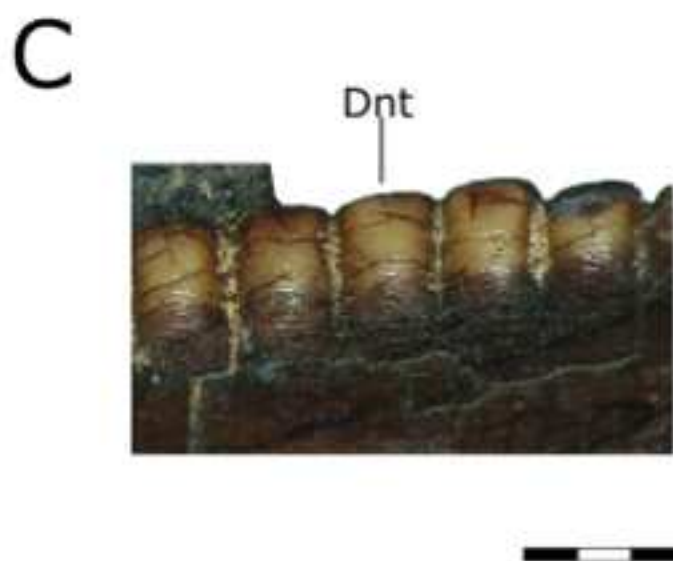


Figure5  
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A



B



C



D



E

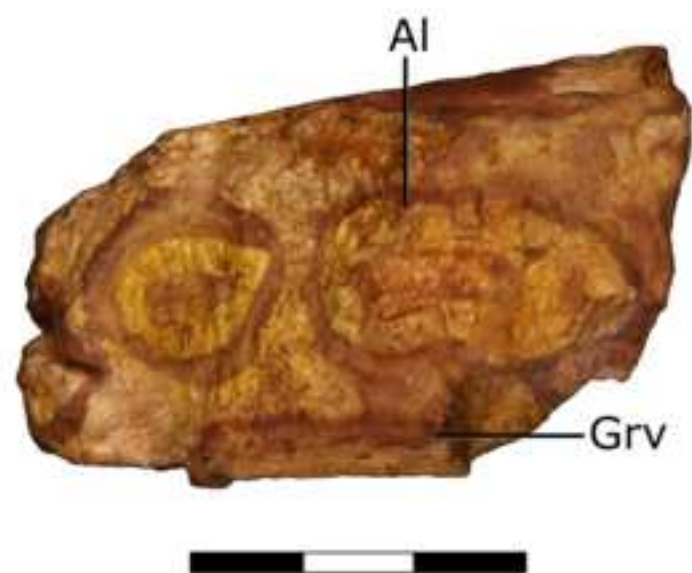


F



Figure6  
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A



B



C



D

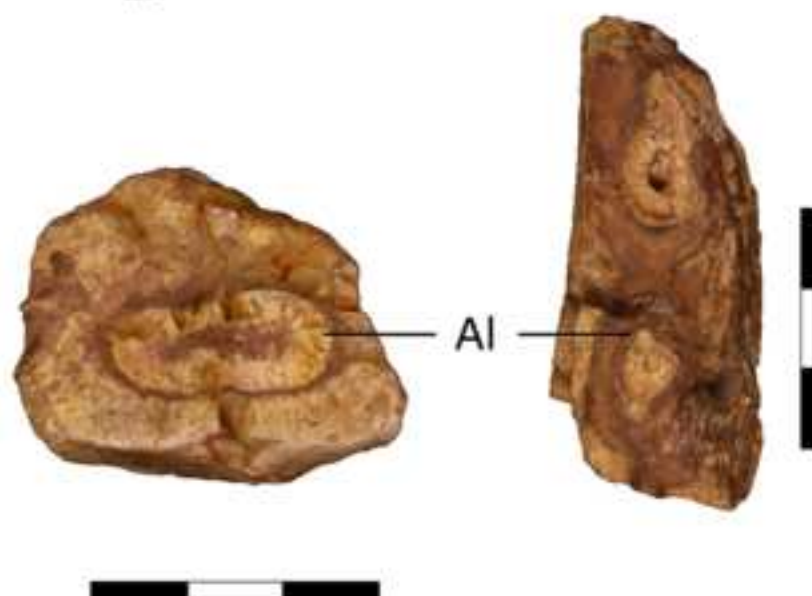




Figure7  
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A



B



C

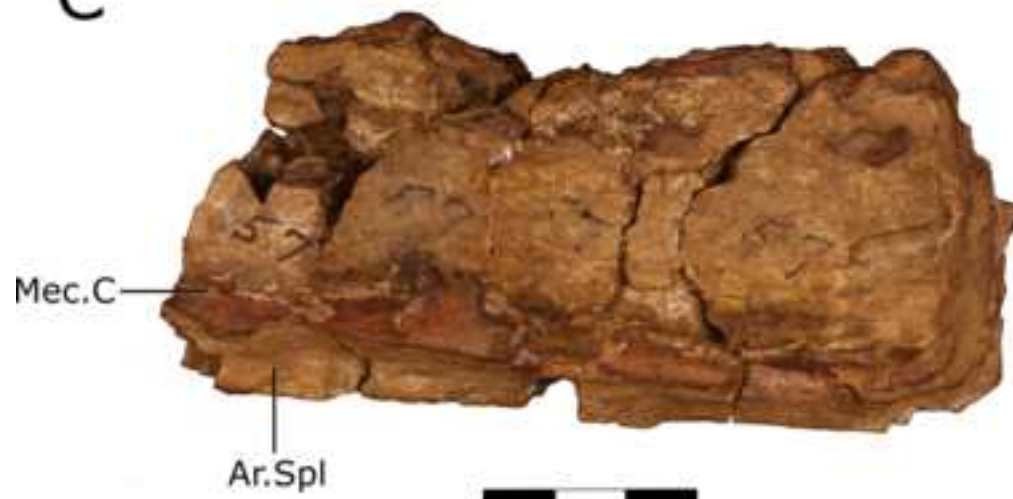


Figure8  
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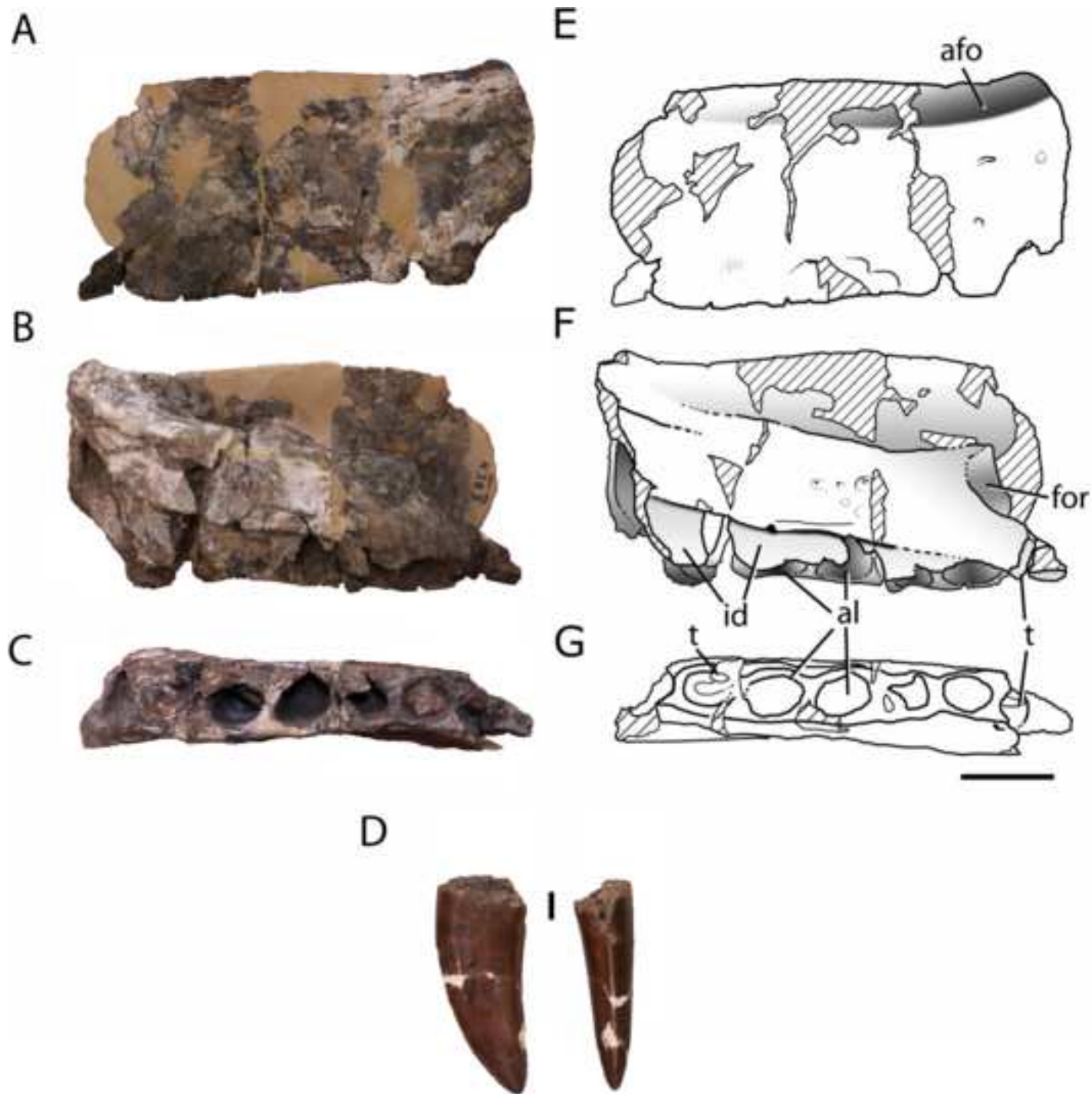
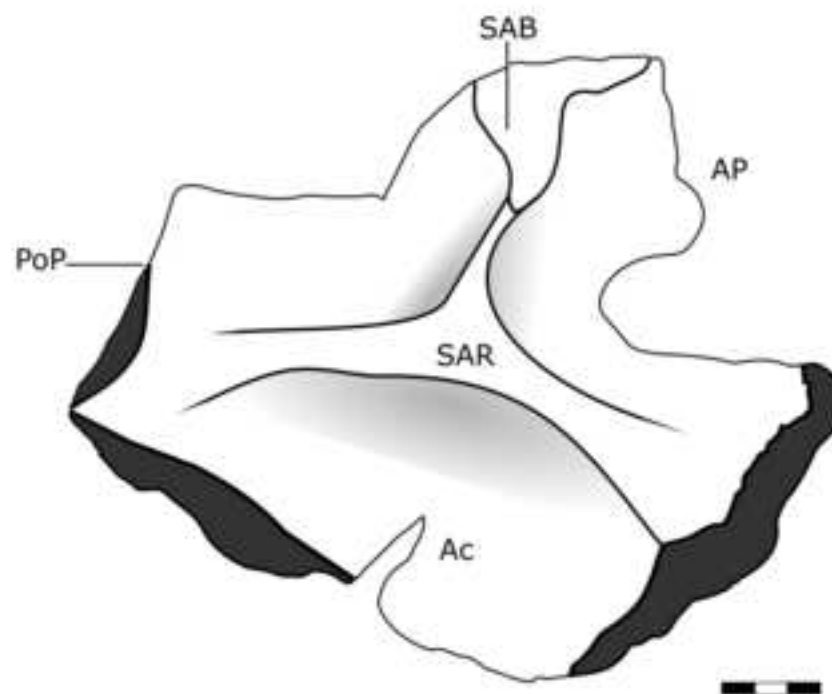


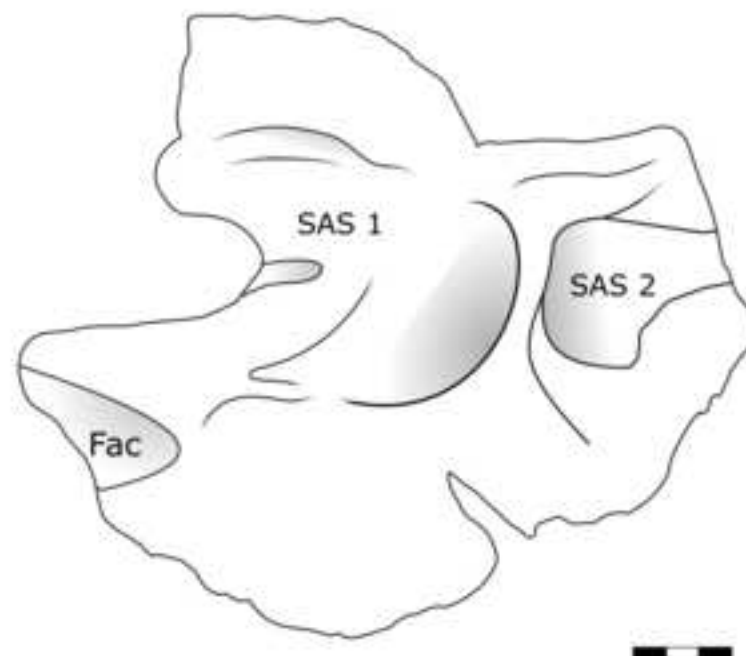


Figure9  
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A



B



# ‘RAUISUCHIAN’ MATERIAL FROM THE LOWER ELLIOT FORMATION OF SOUTH AFRICA: IMPLICATIONS FOR LATE TRIASSIC BIOGEOGRAPHY AND BIOSTRATIGRAPHY

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