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

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Abstract - ‘Rauisuchians’ 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 rauisuchian 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 rauisuchians. These records are the southernmost palaeolatitudes that these animals are known to have occurred and the first definitive remains from southern Africa.

KEY WORDS – ‘Rauisuchia’ – 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, ‘Rauisuchia’ is a grade of large, carnivorous, Triassic-aged non-crocodylomorph archosaurs (Gower 2000), referred to in this paper as rauisuchians (sensu Nesbitt et al. 2013). Whether or not rauisuchians form a clade and the relationships amongst rauisuchian taxa are matters of debate (e.g. Gower 2000; Brusatte et al. 2010; Nesbitt 2011; Nesbitt et al. 2013; Nesbitt & Desejo 2017).

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

Most rauisuchians, such as Prestosuchus, Stagonosuchus, Luperosuchus, Saurosuchus and Postosuchus, were large-bodied carnivores (Nesbitt et al. 2013; Nesbitt & Desejo 2017). Other body plans, found within Poposauroidea, 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).

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

Most of the specimens presented in this study are from the Late Triassic lower Elliot Formation (see ‘Geological Setting’ section below). The tetrapod fauna of the lower Elliot Formation consists of several herbivores of varying body sizes, including sauropodomorph dinosaurs (Knoll 2004), and cynodont (Knoll 2004) and dicynodont (Kammerer 2018) therapsids. The similarly-aged Chinle Formation in the United States has yielded dinoauromorphs, theropod dinosaurs, rauisuchians, other pseudosuchians, phytosaurs and numerous other tetrapods such as drepanosaurs and dicynodonts (Irmis et al. 2007). In the Norian Los Colorados Formation of Argentina, sauropodomorphs, theropods, and therapsids co-occur with rauisuchian, ornithosuchid and aetosaurian pseudosuchians (Arcucci et al. 2004; Baczko & Desojo 2016; Desojo & Ezcurra 2016). A similar fauna is observed in Europe in the Löwenstein Formation of Germany, which includes sauropodomorph dinosaurs and pseudosuchian predators including the rauisuchian Teratosaurus (Brusatte et al. 2009; Meyer 1861; Nesbitt et al. 2013; Yates 2003a). The latest Triassic Lisowice Formation of Poland has yielded the archosaur Smok wawelski as a large-bodied predator (Niedzwiedzki & Budziszewska-Karwowska 2018) a large dicynodont, and small archosaur fragments, including pterosaur elements (Sulej & Niedzwiedzki 2018). The Lisowice Formation suffers from a lack of research into the taxonomic composition of its tetrapod fauna. As such, future research may enhance our understanding of the formation’s tetrapod population. These Late Triassic terrestrial ecosystems prominently feature large archosaurian carnivores and, as such, it is expected that the group would be present in South Africa.
Despite the limited mention in published works, major fossil collections in South African institutions contain specimens that have been catalogued as rauisuchians, but not previously described. The purpose of this paper is to review and identify this material. We subsequently provide a synthesis of the implications of these identifications in terms of biostratigraphy, palaeobiogeography and palaeoecology.

Geological Setting

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

The Elliot Formation comprises the Upper Triassic lower Elliot (Norian–Rhaetian) and the lower Jurassic upper Elliot Formation (Hettangian–Sinemurian) (Olsen & Galton 1984; Kitching & Raath 1984; Knoll 2004, 2005; Bordy et al. 2004b; McPhee et al. 2017). These divisions are based on lithostratigraphy, and are mostly coincident with the biozonation into the stratigraphically older ‘Euskelosaurus’ (Huxley 1866) Range Zone (mostly coincident with the lower Elliot Formation) and the stratigraphically younger Massospondylus Range Zone (mostly coincident with the upper Elliot Formation; Kitching & Raath 1984). Recent work has questioned the taxonomic validity of ‘Euskelosaurus’ (e.g. Yates 2003b, McPhee et al. 2017). The lower Elliot Formation is broadly contemporaneous with numerous Late Triassic deposits globally that contain rauisuchian fossil records, such as North America’s Chinle Formation (Novak 2004; Nesbitt et al. 2013). The upper Elliot Formation has been
assigned a lower Jurassic age based on correlation to, for example, Canada’s McCoy Brook Formation of the Newark Supergroup with which it shares the basal crocodylomorph *Protosuchus* (Olsen & Galton 1984; Sues et al. 1996; Lucas & Hancox 2001).

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

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

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).

(Systematic Palaeontology)

Archosauria Cope, 1869

Paracrocodylomorpha Parrish, 1993

_Referred material_

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

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

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

**Taxonomic affinities**

There is some morphological overlap between BP/1/5302 and erythrosuchid archosauriforms. However, the presence of a far-anteriorly extending Meckelian groove and a lack of dorsoventrally expanded anterior dentary differentiate the specimen from *Erythrosuchus*. Furthermore, there is no known record of erythrosuchids younger than the Middle Triassic (Ezcurra 2016). Average pseudosuchian body size exceeded that of avemetatarsalians throughout the Late Triassic, a trend which rapidly reversed in the Early Jurassic (Turner & Nesbitt 2013). BP/1/5302 can be distinguished, by inference, from contemporaneous theropods (e.g. *Zupaysaurus* Arcucci & Coria 2003) due to its large size. Furthermore, it features a far anteriorly extending Meckelian groove, which is also present in the rauisuchid *Polonosuchus* (Nesbitt 2011). The specimen also compares closely to rauisuchians such as *Arganasuchus* and the rauisuchid *Postosuchus*. However, because none of the synapomorphies of Rauisuchidae are features of the dentary, it cannot be confidently referred to the clade (Nesbitt 2011).
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**
There are two fragments of caudal vertebrae. The largest of these has a centrum width of 60 mm, larger than the 40 mm width of the first caudal in *Postosuchus kirkpatricki* as recorded by Weinbaum (2013). The width is comparable to that of *Saurosuchus* (PVSJ 615; Trotteyn et al. 2011). Additionally, the preserved height of the centrum is 72 mm, with the dorsal margin largely broken away. The centra of the caudal vertebrae of *Postosuchus kirkpatricki* tend to be only slightly higher than wide (Weinbaum 2013). The centrum width of the smaller vertebra is 30 mm, comparable to the 28 mm width of the eleventh caudal of *Postosuchus kirkpatricki* (Weinbaum 2013).

**Taxonomic affinities**

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

(INSERT FIGURE 6)
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
replacement tooth crown is serrated with a serration density of two per millimetre. These
serrations are relatively large in comparison to other pseudosuchians (Nesbitt 2011) and
similar to those of BP/1/5163 and to ‘Pallisteria’ (Paul Barrett pers. comm. 2019).

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

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

Taxonomic affinities

The dentary preserved in BP/1/8120 is similar to that of BP/1/5302 in terms of size and the
presence of a labial groove running anteroposteriorly along the tooth row in the anterior
portion of the dentary. This may suggest that the two specimens are conspecific.
Additionally, the presence of the labial groove and the far anteriorly ending Meckelian
groove suggests phylogenetic affinity with Polonosuchus and, by extension, the clade
Rauisuchidae. However, due to the lack of rauisuchid synapomorphies present in the
preserved material, the assignment of these specimens to Rauisuchidae remains tentative.
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
is a synapomorphy of Archosauria (Nesbitt 2011). A slightly sloped surface delineates the antorbital fossa from the rest of the lateral surface of the maxilla. This is similar to *Saurosuchus* (PVL 32), *Batrachotomus* (SMNS 52970), *Arizonasaurus* (MSM 4590), *Fasolasuchus* (PVL 3850), and Triassic crocodylomorphs (e.g., *Dromicosuchus*, NCSM 13733). In *Postosuchus kirkpatricki* (TTU-P 9000) and *Polonosuchus* (ZPAL Ab III 563), a thick ridge separates the antorbital fossa from the rest of the lateral surface. The antorbital fossa in SAM-PK-K383 deepens and bends dorsally anteriorly. The posterior process of the maxilla has a similar dorsoventral height at both anterior and posterior ends of the antorbital fenestra, a character-state present in *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus* (ZPAL Ab III 563), basal crocodylomorphs (e.g., *Dromicosuchus*, NCSM 13733), *Saurosuchus* (PVL 32), *Prestosuchus* (UFRGS 0156-T), and *Fasolasuchus* (PVL 3850). The posterodorsal portion of the posterior process is highly mediolaterally compressed relative to the mediolaterally thick ventral portion. The dorsal extent of the alveoli marks the transition between the thick ventral portion and the much thinner dorsal portion. A thin posterodorsal portion is also present in *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus* (ZPAL Ab III 563), *Saurosuchus* (PVL 32), *Prestosuchus* (UFRGS 0156-T, 0629-T), *Fasolasuchus* (PVL 3850), and *Arizonasaurus* (MSM 4590) and in early crocodylomorphs (e.g., *Terrestrisuchus*, NHMUK PV R9579). The posteriormost portion of the posterior process tapers posterodorsally and would have been overlapped by the anterior portion of the jugal. A few small nutrient foramina are located just dorsal to the ventral border of the maxilla. The preserved portion of the maxilla preserves seven alveoli. The incomplete posteriormost alveolus is the smallest of the preserved alveoli whereas the other alveoli are nearly the same diameter. Alveoli one and seven preserve teeth in situ.

The medial surface of the maxilla preserves a distinct step separating the alveolar margin from the rest of the medial side. Galton (1985) identified this feature in *Teratosaurus suevicus* and termed it the dental groove. This groove is present in a variety of archosauriforms and likely housed the soft tissue dental lamina (Brusatte & Sereno 2007). A slight groove is located just ventral to and parallel to the step. Posteriorly, the groove shallows. A few small foramina are within the groove. The interdental plates are largely fused, a character state present in a small number of suchians including *Postosuchus kirkpatricki* (TTUP 9000), *Fasolasuchus* (PVL 3850), *Polonosuchus* (ZPAL Ab III 563), and *Teratosaurus suevicus* (NHMUK OR38646) but not in early crocodylomorphs (Nesbitt 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
of the acetabulum. It would likely extend far anteriorly, a condition that is diagnostic of
Poposauroidea (Weinbaum & Hungerbühler 2007; Nesbitt 2011) and some early
crocodylomorphs (Nesbitt 2011). The posterior part of the dorsal margin of the ilium, as
preserved, is inclined posterodorsally, resulting in an inflected region of the dorsal margin
above the midpoint of the acetabulum. This is similar to the condition seen in both species of
Poposaurus (Gauthier et al. 2011). The posterior process is dorsoventrally low and can be
seen to be tapering posteriorly even at its anterior-most portion.

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

Taxonomic affinities

NMQR 3554 has distinct synapomorphies of Poposauroidea including the presence of a
laterally projecting supra-acetabular rim, an anterodorsally inclined crest dorsal to the supra-
acetabular rim and a pre-acetabular process that extends anterior to the acetabulum (Nesbitt
2011). The latter two character states suggest the specimen may be more closely related to
Poposaurus than to any other poposauroid (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 poposauroroids, 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.
The tetrapod fauna of the lower Elliot bears many similarities to that of other Late Triassic deposits globally. This includes the presence of a diversity of sauropodomorph dinosaurs, dicynodont therapsids, and now rauisuchian carnivores (shared with, for example, the Chinle Formation, Irmis 2005; and the Los Colorados Formation, Arcucci et al. 2004). In the case of dicynodonts, the lower Elliot seems to have a lower abundance of the group compared to contemporaneous formations (Kammerer 2018).

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

**Biogeography and biostratigraphy**

(INsert Table 5)
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.

REFERENCES


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**Declarations of interest: none.**
**FIGURE CAPTIONS**

**Figure 1:** Phylogenetic relationships of rauisuchians. 1: Archosauria, 2: Pseudosuchia, 3: Paracrocodylomorpha, 4: Poposauroidea, 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 *Crocodylus niloticus* and *Passer domesticus*
Pseudosuchia | Most inclusive clade including *Crocodylus niloticus* but not *Passer domesticus*
Paracrocodylomorpha | Least inclusive clade including *Poposaurus gracilis* and *Crocodylus niloticus*
‘Rauisuchia’ | Paraphyletic grade including non-crocodylomorph paracrocodylomorphs + *Ticinosuchus ferox*
Loricata | Most inclusive clade including *Crocodylus niloticus*, but not *Poposaurus gracilis*, *Ornithosuchus longidens*, or *Aetosaurus ferratus*
Poposauroidea | Most inclusive clade including *Poposaurus gracilis*, but not *Postosuchus kirkpatricki*, *Crocodylus niloticus*, *Ornithosuchus longidens*, or *Aetosaurus ferratus*
Rauisuchidae | Most inclusive clade including *Rauisuchus tiradentes* but not *Aetosaurus ferratus*, *Prestosuchus chiniquensis*, *Poposaurus gracilis*, or *Crocodylus niloticus*

**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).
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<th>IDENTIFICATION PER THIS PAPER</th>
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**TABLE 2:** List of specimens identified as ‘Rauisuchia’ in South African fossil collections with the specimens included in this study in bold.
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TABLE 3: List of taxa used for comparative anatomy with specimens and/or literature used as source.
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<tr>
<td>NMQR</td>
<td>National Museum, Bloemfontein, South Africa</td>
</tr>
<tr>
<td>PVL</td>
<td>Istituto Miguel Lillo, Tucumán, Argentina</td>
</tr>
<tr>
<td>SAM</td>
<td>Iziko South African Museum, Cape Town, South Africa</td>
</tr>
<tr>
<td>SMNS</td>
<td>Staatliches Museum für Naturkunde, Stuttgart, Germany</td>
</tr>
<tr>
<td>MSM</td>
<td>Arizona Museum of Natural History, Mesa, USA</td>
</tr>
<tr>
<td>TTU-P</td>
<td>Texas Tech University Museum, Lubbock, USA</td>
</tr>
<tr>
<td>UCMP</td>
<td>University of California Museum of Paleontology, Berkeley, USA</td>
</tr>
<tr>
<td>UFRGS</td>
<td>Institute of Geosciences, Laboratório de Paleovertebrados of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil</td>
</tr>
<tr>
<td>UNC</td>
<td>University of North Carolina, Raleigh, USA</td>
</tr>
<tr>
<td>ZPAL</td>
<td>Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland</td>
</tr>
</tbody>
</table>

**TABLE 4:** List of institutional abbreviations.
<table>
<thead>
<tr>
<th>TAXON</th>
<th>SOURCE</th>
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<tbody>
<tr>
<td>Temnospondyli</td>
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<tr>
<td>Chigutisauridae indet.</td>
<td>Warren &amp; Damiani 1999</td>
</tr>
<tr>
<td>Dicynodontia</td>
<td></td>
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<tr>
<td>Pentasaurus goggai</td>
<td>Kammerer 2018</td>
</tr>
<tr>
<td>Cynodontia</td>
<td></td>
</tr>
<tr>
<td>Scalenodontoides macrodentes</td>
<td>Crompton &amp; Ellenberger 1957</td>
</tr>
<tr>
<td>Sauropodomorpha</td>
<td></td>
</tr>
<tr>
<td>Blikanasaurus cromptoni</td>
<td>Galton &amp; van Heerden 1985, 1998</td>
</tr>
<tr>
<td>Eucnemesaurus entaxonis</td>
<td>McPhee et al. 2015</td>
</tr>
<tr>
<td>Eucnemesaurus fortis</td>
<td>Yates 2007a</td>
</tr>
<tr>
<td>Melanorosaurus readi</td>
<td>Gauffre 1993b</td>
</tr>
<tr>
<td>Plateosauravus cullingsworthi</td>
<td>Yates 2003b, 2007</td>
</tr>
<tr>
<td>Sefapanosaurus zastronensis</td>
<td>Otero et al. 2015</td>
</tr>
</tbody>
</table>

TABLE 5: List of valid tetrapod taxa with body fossils from the lower Elliot Formation.
‘RAUISUCHIAN’ MATERIAL FROM THE LOWER ELLIOT FORMATION OF SOUTH AFRICA:
IMPLICATIONS FOR LATE TRIASSIC BIOGEOGRAPHY AND BIOSTRATIGRAPHY

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