A theropod tooth from the Late Triassic of southern Africa

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An isolated, large recurved and finely serrated tooth found associated with the prosauropod *Euskelosaurus* from the Late Triassic part of the Elliot Formation is described here. It is compared to the Triassic thecodonts and carnivorous dinosaurs and its possible affinity is discussed. The tooth possibly belongs to a basal theropod and shows some features similar to the allosauroids. This tooth is of significance, as dinosaur remains except for some footprints and trackways, are poorly known in the Late Triassic horizons of southern Africa.

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1. Introduction

The Mesozoic sediments of the Elliot Formation, Karoo Supergroup, serve as rich repositories of vertebrate fauna, dominated by dinosaurs, turtles, fishes, therapsids, reptilian footprints and trackways. Fossil wood and conchostrachan crustaceans are also common. Based on the fossil content, the formation has been divided into two biozones. The lower *Euskelosaurus* range zone corresponds to the lower Elliot Formation while the upper *Massospondylus* range zone encompasses the middle and upper Elliot Formation. The two biozones have been assigned as Late Triassic (Carnian-Norian) and the Early Jurassic age respectively (Kitching and Raath 1984). The lower Elliot Formation mainly yields amphibians, the prosauropod *Euskelosaurus*, rauisuchians, cynodonts and theropod footprints and tracks (Olsen and Galton 1984; Gow and Latimer 1999). The upper Elliot Formation, on the other hand, exhibits a highly diverse faunal content and includes the prosauropod *Massospondylus*, ceratosaurian *Syntarsus*, fabrosaurid ornithischian, cynodonts, early mammals, protosuchian crocodilians and chelonians.

Previous work on the faunal assemblage of the lower Elliot Formation has shown an interesting and frequent association of the prosauropod remains with large, recurved and finely serrated teeth (Huene 1932; Charig *et al* 1965; Cooper 1980). These teeth were variously attributed to the carnosaurs (*Basutodon ferox* Huene 1932), prosauropods (Charig *et al* 1965; Cooper 1980), rauisuchians (Hopson 1984; Olsen and Galton 1984) and basal theropods (Galton and Heerden 1998). A serrated partial tooth collected near the Telle river in Lesotho, from the *Euskelosaurus* range zone of the Elliot Formation and found along with a partial scapula of *Euskelosaurus* is described here. The labial side of the isolated tooth is assumed to be of relatively greater convexity than the lingual, as commonly prevalent in the archosaurs (Sander 1997; Zinke 1998; Hungerbühler 2000). We compare the tooth with that of the thecodonts (rauisuchians, phytosaurs and ornithosuchians) and carnivorous dinosaurs in order to assess its possible affinity.

2. Description

SAM-PK-K10013 is a large, recurved and finely serrated tooth. The tip of the crown and the root are broken (figure 1A). The cross-section at the proximal end is

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Abbreviations used: BW, Basal width; FABL, fore-aft basal length; SD, serration density.

nearly rectangular with rounded edges (figure 1B). Towards the tip of the crown, the cross-section is leaf-like with a rounded mesial edge and a laterally compressed distal edge. It is markedly asymmetrical, with the labial side being more convex than the lingual side (figure 1C). The mesial and distal carinae bear distinct serrations with closely spaced denticles (figures 1D–E, 2) perpendicular to the tooth edge. The size of the mesial denticles gradually decreases towards the base and end at about 14 mm from the base. In contrast, the longer distal denticles are present right up to the base. The mesial-distal or the fore-aft basal length (FABL) measured near the basal end of the distal tooth keel perpendicular to the longitudinal axis of the tooth (Farlow *et al* 1991) is 18·6 mm and the tooth basal width (BW) measured perpendicular to FABL and at the same level as FABL is about 11 mm. The FABL/BW is thus about 2 : 1, which gives the tooth a very broad appearance in the mesial-distal direction. The denticles are square in outline (figure 1D–E) and asymmetric with the lingual side higher and more oblique than the labial side. Serration density (SD) as defined by Farlow *et al* (1991) of the anterior or mesial keel and the posterior or distal keel is 12 and 13 per 5 mm respectively.

3. Discussion

Isolated teeth collected from the Late Triassic-Early Jurassic period should be treated with caution and as suggested by Galton (1985), they could belong to any of the large carnivores present at that time. These include the thecodonts (rauisuchians, phytosaurs, ornithosuchians and parasuchids) and the theropods (herrerasaurids and ceratosaurs). In contrast to SAM-PK-K10013, the rauisuchian and phytosaur teeth are generally D-shaped or oval in cross-section (Benton 1986; Abler 1997), especially in the apical region (Hungerbühler 2000). Moreover, Hungerbühler (2000) considered the labio-lingually compressed carinae, which are morphologically separate from the body of the tooth crown as a unique feature in the phytosaurs.

The FABL of SAM-PK-K10013 is smaller than that calculated for *Terratosaurus* (figure 3A; c. 23 mm), a probable Late Triassic rauisuchian (Benton 1986). Another specimen SAM-PK-K1497 (figure 3B) is labio-lingually compressed, with an elliptical cross-section and with the FABL measuring about 10 mm. It is probably a rauisuchian tooth. Chatterjee (1978) considered the parasuchid teeth as elongate, symmetrically labio-lingually compressed

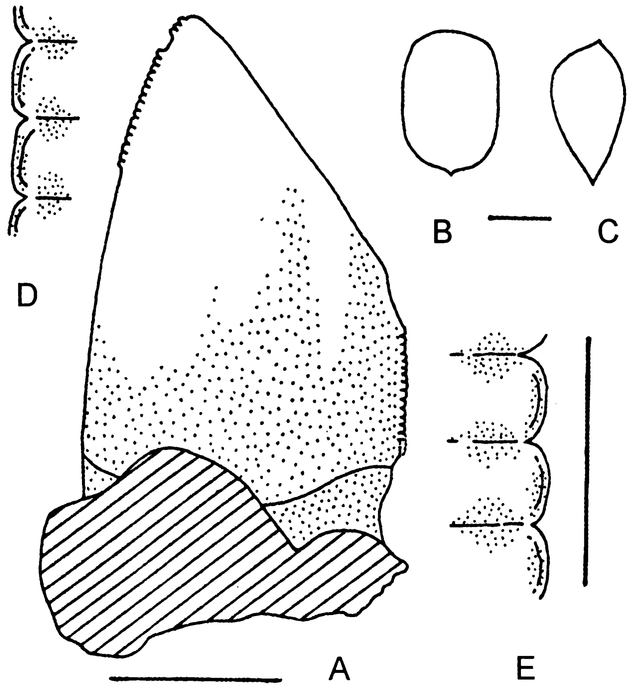

Figure 1. SAM-PK-K10013. (**A**), Partial theropod tooth in labial view; cross-sections, (**B**), at the base; (**C**), towards the tip of the crown; denticles at higher magnification at (**D**), mesial and (**E**), distal edge. Hatched lines indicate matrix covering. Scale bars equal to 10 mm for **A–C** and 1 mm for **D–E**.

Figure 2. Denticles in labial view. The dark distal edges indicate asymmetric presence of enamel on the labial and lingual sides. (× 57).

with finely serrated carinae. In contrast SAM-PK-K10013 shows a marked asymmetry, with the lingual side flattened relative to the labial side (figure 1C). Compared to SAM-PK-K10013, the teeth of the ornithosuchian *Euparkeria* (SAM-PK-K5867), known from the Early Triassic of South Africa are small (FABL about 3 mm), conical with oval cross section. The distal and mesial edges are feebly serrated. Although, not much detail is known about the teeth of the lagosuchians, which are distantly related to the dinosaurs (Abler 1997), it is generally accepted that they are small animals, having skull sizes between 33 to 140 mm (Paul 1988). Thus, it appears that the partial tooth described here belongs neither to a thecodont nor to a lagosuchian, and the question arises as to whether it could be from a carnivorous dinosaur.

Although "serrated teeth" is a plesiomorphic condition in theropods and caution should be exercised in assigning isolated tooth to a particular taxon, Fiorillo and Currie (1994) recognize that teeth have a certain degree of taxonomic utility. Recent studies have shown that theropod teeth can be differentiated based on their size, degree of curvature, and serration density in relation to overall tooth size (Farlow *et al* 1991; Abler 1992, 1997; Sander 1997; Zinke 1998). The calculated FABL of the largest maxillary teeth of the basal theropod *Herrerasaurus* (Sereno and Novas 1993) is smaller, more flattened and curved than SAM-PK-K10013. A partial maxilla containing serrated teeth and found associated with *Euskelosaurus* remains was recently considered as lacking the diagnostic dental characters of rauisuchians or *Herrerasaurus* (Galton and Heerden 1998), and was assigned to *Aliwalia rex*, a Late Triassic carnivorous dinosaur. The individual denticles in the tooth of *Aliwalia rex* are separated by diaphyses or gaps (figure 3C). FABL of the maxillary tooth of *Aliwalia rex* is calculated to be about 24 mm, which is again greater than that of SAM-PK-K10013. It is apparent from the above discussion that the latter tooth is quite different from that of the basal theropods (*Herrerasaurus* and *Aliwalia*).

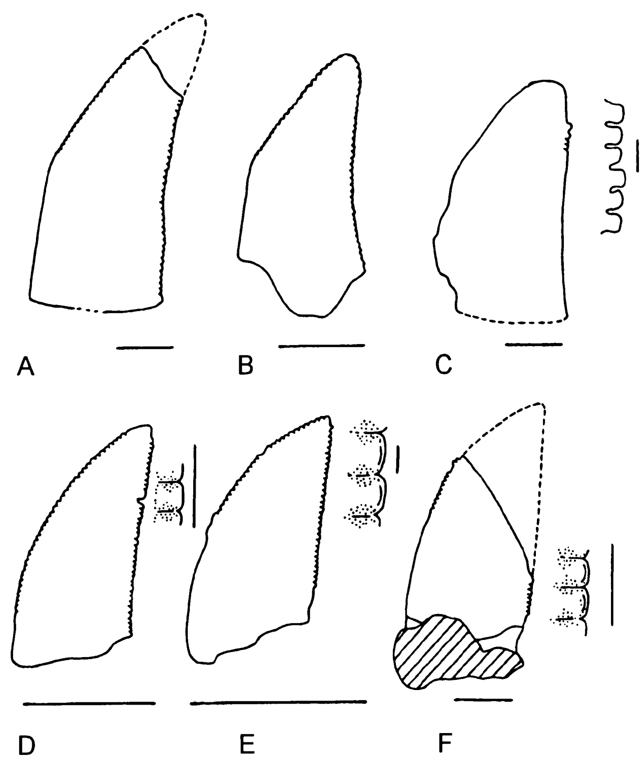

Figure 3. Comparison of serrated teeth of (**A**), a probable rauisuchian (after Benton 1986); (**B**), SAM-PK-K1497, a rauisuchian; (**C**), *Aliwalia rex* (after Galton and Heerden 1998); (**D**), 'Theropoda A' (after Fiorillo and Currie 1994); (**E**), probable allosaurid (after Zinke 1998) and (**F**), SAM-PK-K10013. For comparative purpose, all the teeth have been similarly oriented. Scale bars equal to 10 mm (for the tooth) and 1 mm (for the denticles) except for (**E**), where it is equal to 200 μm (for the denticles).

The maxillary teeth of *Syntarsus*, the only ceratosaurian dinosaur from the upper Elliot Formation of South Africa, are 'long, laterally compressed with strong backward recurvature' (Munyikwa and Raath 1999). The teeth are serrated along the entire distal edge while on the mesial edge only the apical regions have serrations. The FABL calculated for the largest maxillary tooth of *Syntarsus* (BP/I/5278, Raath 1980; Rowe 1989) is smaller and appear to be much more flattened and recurved than SAM-PK-K10013. Moreover, the distal serrations are larger and more widely spaced than the mesial serrations in *Syntarsus* (Munyikwa and Raath 1999). Abler (1997) pointed out that the teeth of coelurosaurs are elongated, laterally flattened and elliptical in cross-section.

Comparison of SAM-PK-K10013 with theropod teeth indicates a strong similarity with 'Theropod A', a large basal theropod (figure 3D; Fiorillo and Currie 1994) and the probable allosaurid tooth of Zinke (1998) (figure 3E). Similarity lies in the differential cross-section of the tooth at the base (rectangular with FABL/BW ratio of 2 : 1) and near the apex (lenticular and asymmetric), in the degree of curvature of the distal and mesial edges and in the asymmetric denticles. FABL, BW and SD of SAM-PK-K10013 (figure 3F) when compared with that of the different theropod and archosaur teeth (Farlow *et al* 1991) show that it falls within the allosauroid range. However SAM-PK-K10013 does not exhibit a well-developed median ridge on the lingual side and the blood grooves, which are characteristic of the allosaurid teeth (Zinke 1998). We realize that tooth morphology shows convergent developments in theropod evolution and specific assignment to a particular taxon based on a single tooth is injudicious and speculative. However, it is possible that SAM-PK-K10013 (figure 3F) is a tooth of a large basal theropod and shows certain features similar to the allosauroids.

Except for the ceratosaurian *Syntarsus* from the upper Elliot Formation and abundance of the ichnotaxa *Grallator* sp. (Olsen and Galton 1984), which were interpreted as the footprints of various small and large theropods (Ellenberger 1970; Olsen and Galton 1984; Galton and Heerden 1998), southern African fossil localities are generally poor in the skeletal remains of carnivorous dinosaurs. Moreover, tridactyl dinosaur tracks have been reported from the largely coeval Molteno Formation (Raath *et al* 1990) and from the basal part of the Elliot Formation (Gow and Latimer 1999). These have been attributed to unknown theropods, as the skeletal remains are yet to be recovered. Hence, instead of considering all isolated serrated teeth from these horizons as thecodont, the recovery of the teeth of *Aliwalia rex* (Galton and Heerden 1998) and our current finding show that in the Late Triassic localities where dinosaur remains are poorly known, isolated teeth deserve more attention.

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