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A non-mammaliaform cynodont from the Upper Triassic of South Africa: a therapsid Lazarus taxon?

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The tetrapod record of the 'Stormberg Group', including the Lower Elliot Formation, in the South African Karoo is widely dominated by archosaurian reptiles, contrasting with the therapsid dominion of the subjacent Beaufort Group. The only therapsids represented by skeletal remains in the Upper Triassic Lower Elliot Formation are the large traversodontid cynodont *Scalenodontoides macrodontes* and the recently described tritheledontid cynodont *Elliotherium kersteni*. Here we present a fragmentary lower jaw that provides evidence of a third type of cynodont for the Upper Triassic of South Africa. The fossil is tentatively assigned to the Diademodontidae. The latter representative of this family is known from the Late Anisian, and its tentative record in the Norian Lower Elliot Formation, if confirmed, will represent a case of Lazarus taxon. Thus, Diademodontidae apparently disappeared from the fossil record by the end of the Anisian and then reappeared in the Norian of South Africa, a stratigraphic interval of some 21 million years. This new cynodont record, together with the recently described Tritheledontidae, show that cynodonts are now the second most diverse tetrapod group in the Lower Elliot fauna.

Keywords: Lower Elliot Formation, Karoo Basin, Lazarus taxon, Diademodontidae.

INTRODUCTION

The South African Karoo Basin preserves the most comprehensive record of non-mammaliaform therapsids in the world. The oldest representatives of this group and their subsequent diversification are recorded in the Permian and Triassic rocks of this basin over a time span of approximately 32 million years (Hancox & Rubidge 2001; Rubidge & Sidor 2001). Among the groups that evolved during this time are the cynodonts, which first appeared near the end of the Permian, approximately 252 millions years ago, and include Mammalia as their living descendants.

Cynodonts were an important component of the vertebrate faunas of the Early Triassic *Lystrosaurus* Assemblage Zone (AZ) and the overlying Early to Middle Triassic *Cynognathus* AZ of the Beaufort Group (Rubidge 1995; Hancox & Rubidge 2001). The *Cynognathus* AZ, the uppermost faunal assemblage of the Beaufort Group, encompasses the strata of the Burgersdorp Formation (Hancox & Rubidge 2001) and is informally subdivided into three faunas (Hancox *et al.* 1995; Damiani & Hancox 2003), namely subzone A (late Olenekian), subzone B (early Anisian), and subzone C (late Anisian). Seven cynodont taxa are known from the *Cynognathus* AZ, with the large-bodied herbivorous/omnivorous *Diademodon tetragonus* Seeley, 1894, the only known representative of the Diademodontidae, being one of the most common. *Diademodon* is the most abundant cynodont of the subzone B fauna, but in subzone C it has a scanty record (Abdala *et al.* 2005), and apparently became extinct by the end of Beaufort Group sedimentation in the early Middle Triassic.

The South African tetrapod record resumes in the Upper Triassic (Norian) Lower Elliot Formation of the 'Stormberg Group', and is highlighted by a marked faunal turnover when compared to that of the Beaufort Group. The Lower Elliot Formation is dominated by archosaurian reptiles (especially dinosaurs) whereas the only named therapsids are the traversodontid cynodont *Scalenodontoides macrodontes* Crompton & Ellenberger, 1957, and the new tritheledontid cynodont *Elliotherium kersteni* Sidor & Hancox, 2006. Here we describe a partial lower jaw from the Lower Elliot Formation that provides evidence of a third cynodont from the Upper Triassic of South Africa. The mandible is tentatively assigned to the Diademodontidae and represents by far the youngest record of that group.

GEOLOGICAL SETTING

The Elliot Formation is a fluvial redbed sequence, with some aeolian input towards the top (Visser & Botha 1980; Smith & Kitching 1997; Bordy *et al.* 2004a). It is dominated by red floodplain siltstones with minor channel and splay sandstones. Kitching & Raath (1984) were the first to recognize different subunits in the Elliot Formation, establishing two biozones and a tripartite lithostratigraphic subdivision. Bordy *et al.* (2004a,b,c) replaced this tripartite system with a two-fold lithostratigraphic subdivision that corresponds to the biostratigraphic subdivision. Argillaceous rocks of the two intervals differ little, although pedogenic horizons are more prevalent in the Upper Elliot Formation (Smith & Kitching 1997; Bordy *et al.* 2004a).

The lower jaw fragment, BP/1/5724, comes from the farm Edelweiss 698 (29°06'37.3014"S, 27°19'16.5"W) in the Ladybrand District, eastern Free State Province, South Africa (Fig. 1). The sauropod *Antetonitrus ingenipes* Yates & Kitching, 2003, some remains of other dinosaurs, most likely *Melanorosaurus*, and fragmentary temnospondyl

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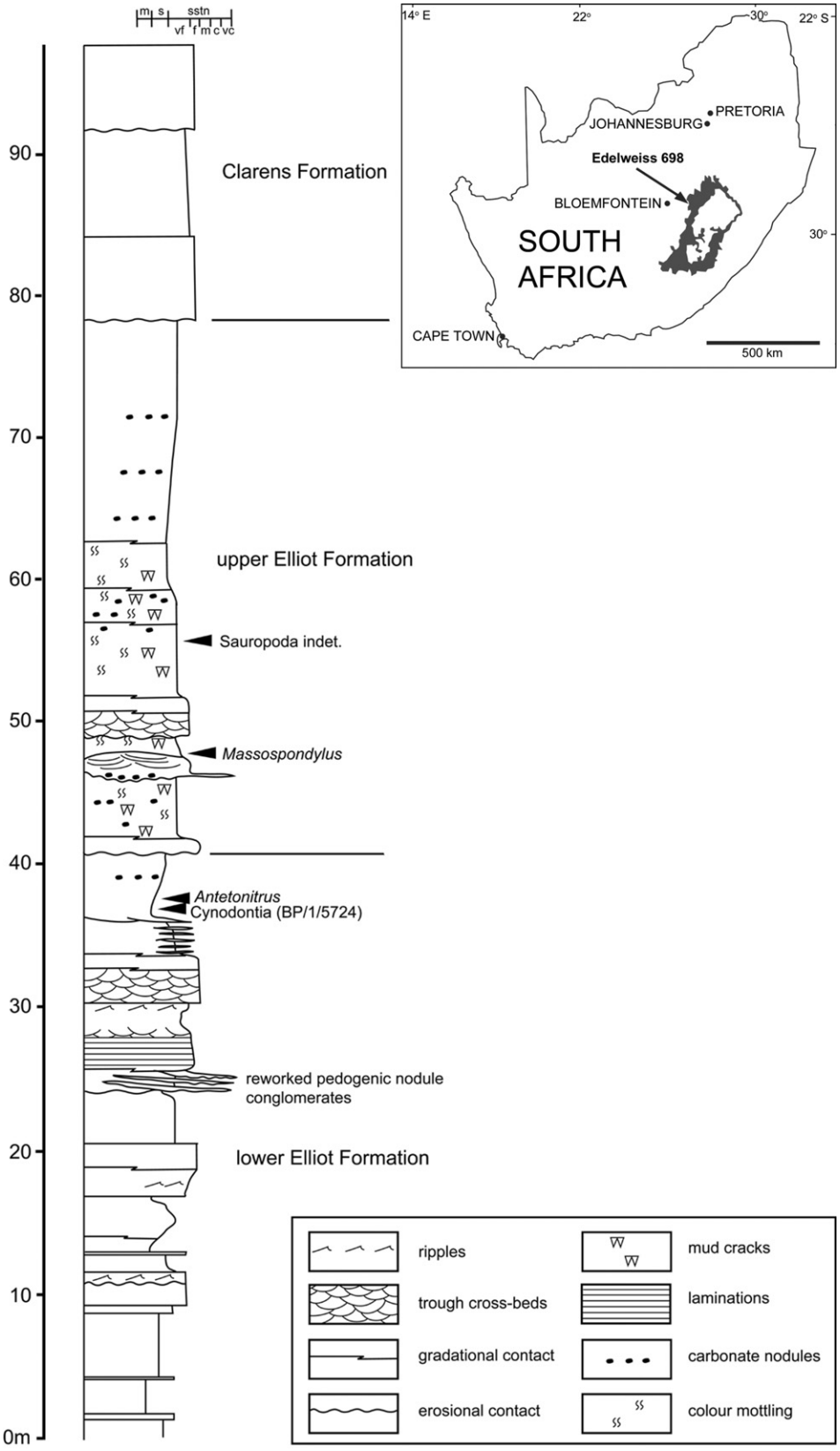


Figure 1. Stratigraphic section through the Elliot Formation at Edelweiss 698, Ladybrand District, Free State Province, South Africa, with fossil occurrences indicated. Note that the base of the Elliot Formation is not exposed at the locality. Inset, map of South Africa shows location of Edelweiss 698 and aerial extent of the 'Stormberg' Group.

remains are also known from this locality. Vegetation covering on hill slopes at Edelweiss largely confines the exposures of the Elliot Formation to a saddle between two low hills. Red siltstones predominate the lithology, with greenish and reddish-grey channel sandstones (2–10 m thick) more prevalent in the lower half of the section (Fig. 1). Argillaceous rocks in this part of the sequence consist of massive mudstone and siltstone packages, with rare and poorly developed calcareous pedogenic horizons with occasional greenish-grey mottling. In the upper half

of the section channel sandstones are comparatively scarce, but there is a marked increase in grain size of the argillaceous rocks towards the top of the Formation. Well-developed pedogenic horizons, characterized by calcareous nodules, rhizocretions, desiccation cracks, and purple to reddish-grey mottling, occur extensively. We interpret the tripartite paleosol between 52–63 m to be the local expression of the *Tritylodon* Acme Zone (Kitching & Raath 1984; Smith & Kitching 1997).

BP/1/5724 was collected immediately above the thick channel deposit between 25–36 m in the lower half of the section (Fig. 1). The lenticular shape and lateral accretion surfaces at the base of this channel sandstone is consistent with the narrow, fixed, and meandering channels interpreted for the Lower Elliot Formation (Bordy *et al.* 2004c), as opposed to the lateral sandsheets and ephemeral fluvial deposition of the Upper Elliot Formation (Bordy *et al.* 2004a,b). Overall, the nature of the channel sandstones, the paucity of well-developed pedogenic horizons, and the stratigraphic position of the *Tritylodon* Acme Zone in relation to BP/1/5724, suggests that the latter is placed in the Lower Elliot Formation. This is fully consistent with biostratigraphic data: remains of *Melanorosaurus* were recovered from the same level as BP/1/5724, which indicates that the horizon pertains to the '*Euskelosaurus*' Range Zone (*Melanorosaurus* Range Zone of Yates 2004) of the Lower Elliot Formation. A review of the vertebrate and ichnological evidence suggests a Norian age for the Lower Elliot Formation (Lucas & Hancox 2001; Knoll 2004). Lucas & Hancox (2001) cautioned that the biostratigraphic correlations of this unit were not strong, but the suggested age is reinforced by the close relationship between *Elliotherium kersteni* and *Chaliminia musteloides* from the Norian Los Colorados Formation of Argentina (Sidor & Hancox 2006).

DESCRIPTION

BP/1/5724 consists of a portion of a right lower jaw that preserves the posterior portion of the horizontal ramus of the dentary, including several teeth, and the beginning of the coronoid process (Fig. 2). The jaw fragment corresponds to a medium-sized animal with a skull length of approximately 200 mm. The ramus is dorsoventrally deep but narrow from side to side and somewhat broader in its dorsal region than ventrally. The dorsal margin of the jaw is distinctly convex laterally in cross-section.

The labial surface (Fig. 2a) of the jaw is rather flat throughout except dorsally, where it forms a gently curving shelf that accommodates the dental arcade. There is no evidence of the lateral crest of the dentary. Two distinct bone fibre orientations are visible on this surface: a dorsal region in which the fibres are oriented parallel to the direction of the coronoid process, and a less extensive, ventral region at the base of the jaw in which the fibres are oriented posteroventrally, towards the angle of the dentary.

The lingual surface (Fig. 2b) is slightly convex and there is a well-developed trough for the postdentary bones separating the dorsal and ventrally directed fibres of the dentary. The postdentary elements are not preserved with the exception of a small splint of bone anteriorly that is probably part of the splenial. Close to the dorsal margin of the dentary, where the coronoid process begins to rise, is a scar which we interpret as the facet for articulation of the coronoid bone.

The tooth arcade is displaced slightly toward the lingual side of the jaw. Ten tooth alveoli are preserved, four of which retain broken teeth with the remaining alveoli being filled with matrix (Fig. 2c). The postcanines display thecodont implantation and have a single root, as is evident in the section at the anterior end of the jaw and from dissection of the lingual surface of the tooth-bearing fourth alveolus (Fig. 2b). The four broken teeth retain no vestiges of the original crown morphology. Remnants of the external enamel of the crown are observed in the mesial and distal margins of the fourth postcanine. The preserved bases of the postcanine crowns are slightly ovoid to circular in cross-section. The most striking aspect of the dental arcade is the position of the alveoli of the last four postcanines, which are located on the ascending margin of the coronoid process and appear slightly enlarged anteroposteriorly.

DISCUSSION

Taxonomic affinities of BP/1/5724

Specimen BP/1/5724 represents a new therapsid record for the Lower Elliot Formation, clearly distinct from *Scalenodontoides macrodontes* or *Elliotherium kersteni.* The overall configuration of the dentary, the thecodont implantation of the postcanines, and the presence of a postdentary trough are together indicative of therapsid affinities, while the marked depth of the postdentary trough and the prominent coronoid process provide compelling evidence that the specimen is a cynodont. The comparatively small size of the teeth and the circular crown bases of the preserved teeth indicate that they are plainly different from those of *Scalenodontoides* (Hopson 1984, fig. 1C). In addition, the latter feature precludes placement of BP/1/5724 in either Traversodontidae, which have quadrangular lower postcanines, or Trirachodontidae with ovoid/ellipsoid lower postcanines (Crompton 1955, fig. 5), although not the probainognathian *Aleodon.* Both the circular bases of the teeth and their single roots exclude the Tritylodontidae (Ginsburg 1962: fig. 3; Cui & Sun 1987) a group of cynodonts that are particularly well represented in the Upper Elliot Formation (Smith & Kitching 1997). By contrast, both of these characters are shared with the Diademodontidae.

The most intriguing feature of BP/1/5724 is the presence of alveoli on the ascending margin of the coronoid process. In some cynodonts such as *Probainognathus* and *Chiniquodon* (Romer 1969, 1970), the postcanine series ends in front of the coronoid process. Observations of other cynodonts show that the last lower postcanines continue behind the coronoid process and are often partially (e.g. *Thrinaxodon,* BMNH R511, R511a; *Cynognathus,* Broili & Schröder 1934) or totally (e.g. *Exaeretodon,* Bonaparte 1962; *Aleodon,* UMCZ T906) concealed when viewed laterally. In *Diademodon* the condition is somewhat

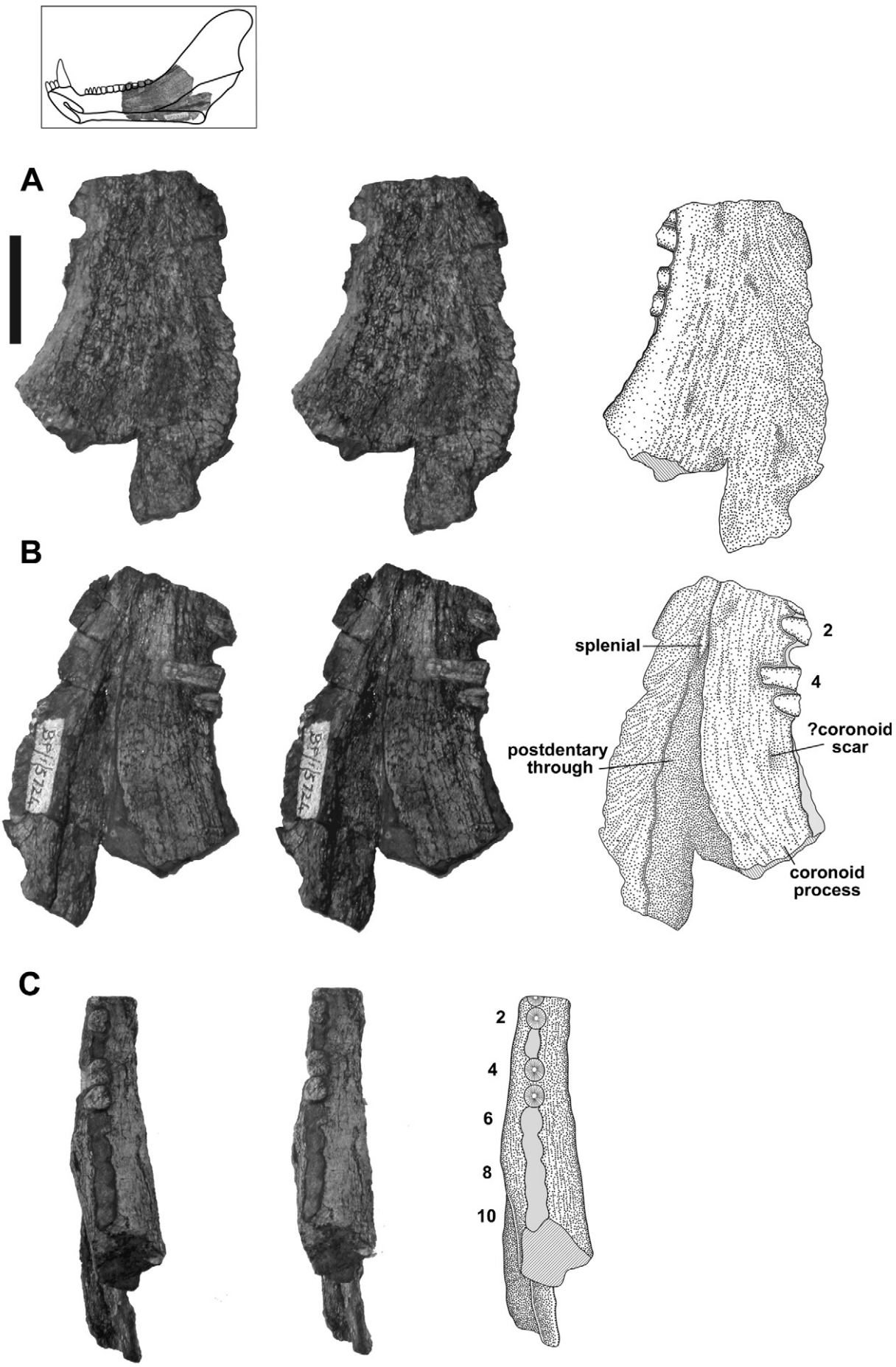


Figure 2. Stereophotographs and interpretive drawings of BP/1/5724 in (**A**) labial, (**B**) lingual, and (**C**) occlusal views. Numbers refer to tooth positions, as discussed in the text. Inset, BP/1/5724 superimposed on the mandible of *Diademodon,* viewed lingually (after Brink 1963). Scale bar = 3 cm.

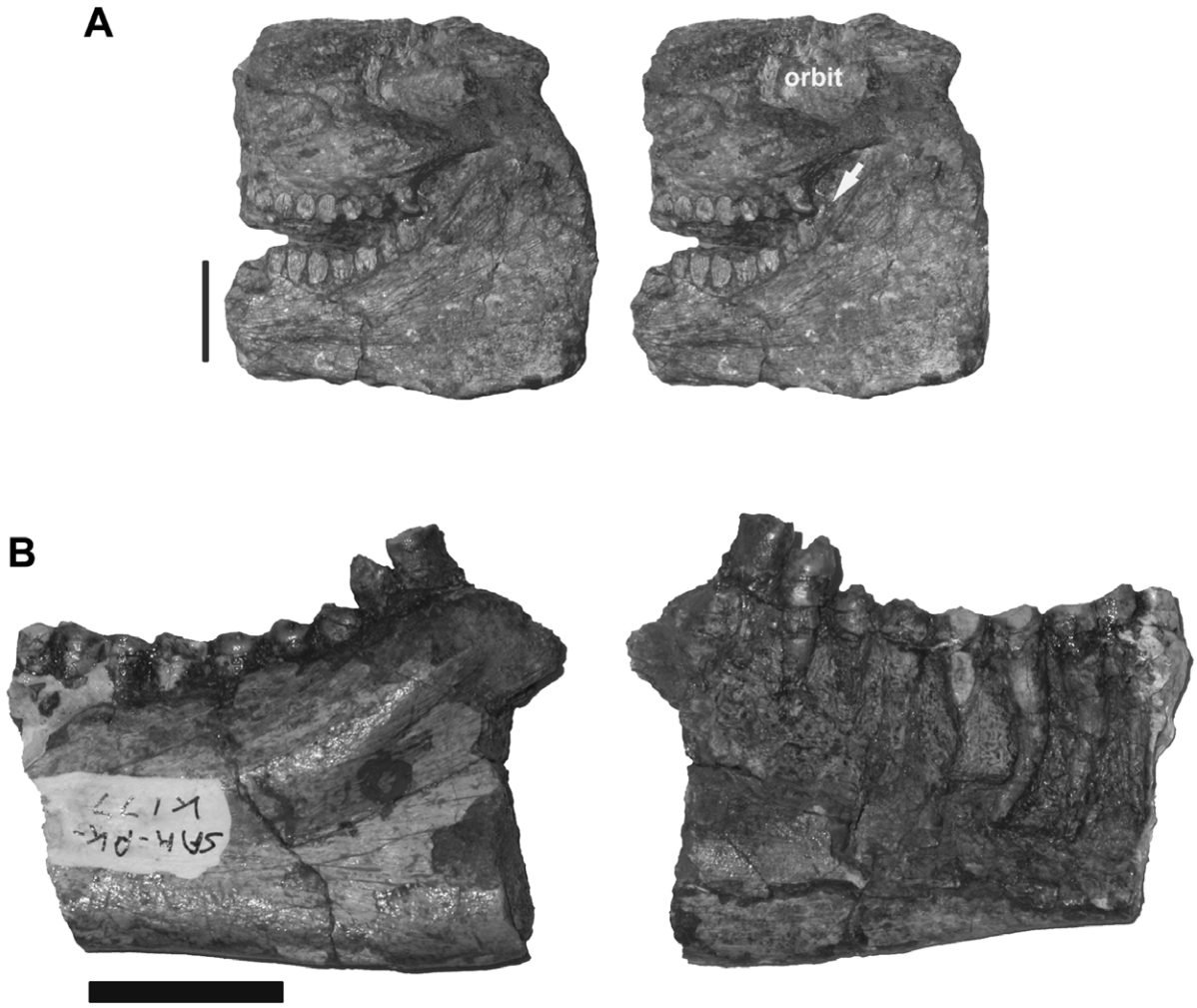


Figure 3. **A**, Stereophotograph of a partial skull and lower jaw of *Diademodon* in lateral view (BP/1/1169). Arrow indicates the location of the last lower postcanine. Note the different orientation of the fibres in the lower jaw. Scale bar 3 cm. **B**, Labial and lingual view of the partial left lower jaw of *Diademodon* (part of specimen SAM-PK-K177). Note the extension of roots in the lingual view. Scale bar = 2 cm.

variable: (1) the dental series may finish just anterior to the coronoid process (e.g. SAM-PK-4002); (2) the last postcanine may be concealed in lateral view by the rising margin of the process (e.g. SAM-PK-K5877); (3) the last postcanines may be implanted well along the ascending margin of the coronoid process (e.g. BP/1/1169, SAM-PK-K177, MB R1004) (Fig. 3). To our knowledge, the third arrangement is recorded only in *Diademodon* and in a small lower jaw (NM QR3251) of the trirachodontid *Langbergia modisei* from subzone A of the *Cynognathus* AZ (Abdala *et al.* 2006). Based on the combination of postcanine bases that are circular in outline, and tooth alveoli that are located on the ascending margin of the coronoid process, we consider the most plausible identity for BP/1/5724 to be diademodontid.

The Post-Anisian gomphodont cynodont record

Gomphodont cynodonts [*sensu* Abdala & Ribeiro (2003) and Abdala *et al.* (2006), i.e. including Diademodontidae, Trirachodontidae and Traversodontidae, but not Tritylodontidae] appear in the late Olenekian and by the Anisian had already diversified into the three main groups: Trirachodontidae, Diademodontidae and Traversodontidae. The Trirachodontidae and Diademodontidae are thought to have become extinct by the end of the Anisian, although Lucas *et al.* (1999) assigned three isolated teeth from the Redonda Formation of New Mexico, originally attributed to the archosauromorph taxon Trilophosauridae (see Lucas *et al.* 1999, 332), to Trirachodontidae, which, if correct, would extend the temporal range of that group into the Rhaetian. However, Abdala *et al.* (2005, 2006) regarded this record as tenuous because the teeth differ from trirachodontid gomphodont postcanines (i.e. two of them lack cingular cusps on one of the bucco-lingually expanded margins). In addition, the strongest evidence presented by Lucas *et al.* (1999) to demonstrate the cynodont affinity of these teeth is the presence of columnar enamel. The enamel microstructure is not clear in the illustration provided by Lucas *et al.* (1999, fig. 4), probably because the tooth was not sectioned and polished. Therefore, the interpretation of the tubules as columnar units (or synapsid columnar units) that they provide does not seem guaranteed. In addition, columnar enamel is also widely distributed among reptiles, in some cases with columnar units having a similar diameter to that of synapsids (Sander 1999). More recently, the teeth from the Redonda Formation were considered to represent an indeterminate cynodont by Heckert (2004). At this stage, we are not able to confirm a cynodont identity for these teeth.

Traversodontids, by contrast, have a rich post-Anisian record, the youngest being in the latest Norian to Rhaetian faunas of Saint-Nicolas-de-Port, France, and Habay-la-Vieille, Belgium (Godefroit & Battail 1997, but see Hopson & Sues 2006). In Gondwana, the youngest traversodontid record is that of *Scalenodontoides* from the Norian Lower Elliot Formation. Abundant traversodontids in the rich Ladinian and Carnian faunas of South America (Rogers *et al.* 1993, 2001; Abdala & Ribeiro 2003) support the notion that traversodontids were the only gomphodont cynodonts to survive beyond the Anisian. However, the specimen described herein suggests the survival of Diademodontidae beyond the Anisian, as a residual component of Ladinian to Norian faunas, at least in southern Gondwana. Diademodontidae then would be a Lazarus taxon (Erwin 1996), apparently disappearing from the fossil record by the end of the Anisian (Crompton 1955; Brink 1963; Hammer 1995; Smith & Swart 2002; Abdala *et al.* 2005) then reappearing in the Norian of South Africa, a stratigraphic interval of some 21 million years.

Fauna of the Lower Elliot Formation

The tetrapod fauna of the Lower Elliot Formation (reviewed in Anderson *et al.* 1998; Galton & Van Heerden 1998, and Knoll 2004) is characterized by an abundance of dinosaur body fossils, particularly sauropodomorphs (Yates, pers. obs.). This includes five sauropodomorphs (Galton & Van Heerden 1998; Yates 2003; Yates & Kitching 2003), an unnamed ornithischian (Butler 2005), and one dinosaur *incertae sedis* (*Aliwalia rex*). This dominance is also expressed in the footprint record (Ellenberger 1970; Olson & Galton 1984), with three of the four types of ichnofamilies interpreted as produced by Archosauriformes-like animals and two of them, *Brachychirotherium* and *Grallator,* being the more abundant types in the formation (Olson & Galton 1984). *Grallator* tracks are thought to pertain to a theropod (Olson & Galton 1984).

The Lower Elliot fauna also includes teeth with crenulated margins, maxillary and lower jaw fragments, and large postcranial bones associated with osteoderms attributed to rauisuchids (Hopson 1984; Galton & Van Heerden 1998), while cranial and mandibular remains of large chigutisaurid temnospondyls also occur (Warren & Damiani 1999). In stark contrast to the therapsid-dominated Beaufort Group fauna, the only therapsids represented by body fossils in the Lower Elliot fauna are the traversodontid *Scalenodontoides macrodontes,* currently known from at least seven specimens (Crompton & Ellenberger 1957; Hopson 1984; Gow & Hancox 1993; Knoll 2004; Battail 2005; Abdala, pers. obs.), the tritheledontid *Elliotherium kersteni* represented by its holotype skull (Sidor & Hancox 2006), and the diademodontid BP/1/5724. In addition, the ichnofossil *Pentasauropus* is attributed to dicynodonts (Olson & Galton 1984). Nevertheless, cynodonts now comprise the second most diverse tetrapod group in the Lower Elliot fauna. Three groups of cynodonts, Tritheledontidae, Tritylodontidae and Mammaliaformes, are also represented in the Lower Jurassic Upper Elliot Formation, but only tritheledontids are common to both the Lower and Upper Elliot faunas.

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INSTITUTIONAL ABBREVIATIONS

BMNH	Natural History Museum, London
BP	Bernard Price Institute for Palaeontological Research, Johannesburg
MB	Humboldt Museum für Naturkunde, Berlin
NM	National Museum, Bloemfontein
SAM	South African Museum, Cape Town
UMZC	University Museum of Zoology, Cambridge.

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