

A double-tusked dicynodont and its biostratigraphic significance

Zubair Ali Jinnah^a and Bruce Rubidge^{b,*}

A new specimen of *Eodicynodon oosthuizeni*, discovered near Prince Albert Road in the Western Cape province of South Africa, has a double distinction. Of stratigraphic importance is the fact that it is the only specimen of *Eodicynodon* known from above the first maroon mudrocks of the Beaufort Group, a feature which has important implications for understanding the development of the earliest terrestrial environments of Gondwana during the middle Permian. Of anatomical significance is the presence of two canines on the left maxilla. This rare condition, known in only three dicynodonts, is here considered to be pathological and not the result of tooth replacement.

The rocks of the Karoo Supergroup of South Africa are internationally renowned for their rich record of fossil tetrapods, particularly therapsids, documenting a largely unbroken record of continental tetrapod biodiversity from the Permian to the Jurassic.^{1,2} Because the rocks of the Beaufort Group were deposited in a fluvial environment,²⁻⁵ laterally extensive lithological markers are scarce with the result that stratigraphic subdivision of these rocks for basin analysis purposes relies greatly on the eightfold biostratigraphic subdivision based on the fossil tetrapod record.⁶ Fossil tetrapod biodiversity in the Beaufort Group is dominated by anomodonts, including the most basal members of this clade, suggesting that this group originated in Gondwana.^{7,8} The fact that the tetrapod biomass comprises mostly anomodonts as the primary herbivores means that most of the biozones bear the names of anomodont genera.

The lowermost, and also the most recently recognized biozone, is the *Eodicynodon* Assemblage Zone. This zone occurs

only in the southwestern part of the Karoo Basin⁹ and contains several basal therapsid taxa as well as all known specimens of *Eodicynodon*, the most basal known dicynodont.^{10,11} The presence of this fossil assemblage, the oldest terrestrial tetrapod fauna from Gondwana,² heralds the onset of terrestrial conditions in the southern Karoo as the rocks comprising this biozone were deposited in a subaqueous delta plain environment.^{12,13} Recognition of this biozone at the base of the Beaufort Group coupled with the fact that it is restricted to the southwestern part of the Karoo Basin has led to new basin development models.^{13,14}

Currently, the *Eodicynodon* Assemblage Zone is recognized only between the towns of Rietbron in the east and Laingsburg in the west (Fig. 1), and all recorded specimens of *Eodicynodon* have been found below the lowermost, laterally continuous maroon mudrock bed of the Beaufort Group.^{12,13} Currently, the upper boundary of the *Eodicynodon* Assemblage Zone is defined on the first occurrence of *Tapinocephalus* and *Bradysaurus* and the absence of *Eodicynodon* and *Tapinocaninus*¹⁵ but the nature of the contact between the lower *Eodicynodon* and overlying *Tapinocephalus* assemblage zones is still uncertain. In 2002, Charlton Dube, a preparator at the Bernard Price Institute for Palaeontology, found a small dicynodont skull and isolated postcranial elements (specimen BP/1/6230) in rocks of the Abrahamskraal Formation on the farm Bloukrans (33°03.682'S, 21°33.240'E) in the Prince Albert district. Preparation revealed a complete skull, articulated mandible, and humerus. The presence of laterally flared pterygoid processes, postcanine teeth positioned lateral to the lower jaw when occluded, and a laterally located post-temporal fossa enable us to identify it with certainty as *Eodicynodon oosthuizeni*.^{10,11} This discovery is of significance as it is the first time *Eodicynodon* has been reported from above the lowermost maroon mudrocks of the Beaufort Group. The specimen was found 1062 m above the lowest continuous maroon mudrock bed of the Beaufort Group (Fig. 2). Reporting this discovery is important as tetrapod fossils are scarce in the lowermost Beaufort, with a field collecting average of only one specimen per week.

The contact between the Beaufort and underlying Ecce Group has previously been defined in several ways,¹³ including the first stratigraphic occurrence of laterally continuous maroon mudrocks. Extensive research in recent years has led to the acceptance that the contact should be placed at the top of the arenaceous Waterford Formation, which is considered to reflect a transition from a subaqueous to subaerial delta plain environment^{2,13} at the position of the palaeo-shoreline of the Ecce Sea.^{6,9}

^aSchool of Geosciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa.

^bBernard Price Institute (Palaeontology), School of Geosciences, University of the Witwatersrand.

*Author for correspondence. E-mail: bruce.rubidge@wits.ac.za

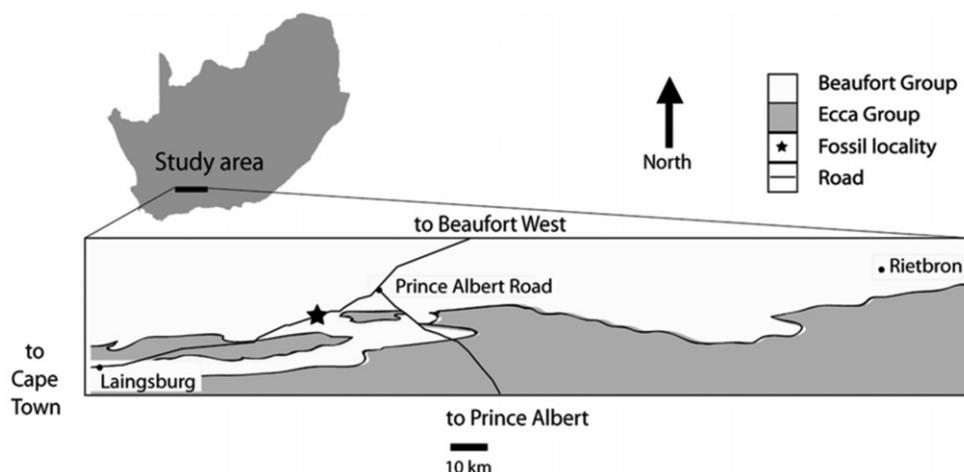


Fig. 1. Map of the study area, showing the location of BP/1/6230 in relation to the Ecce-Beaufort contact.

This means that the contact occurs between 331 and 663 m below the first laterally continuous maroon mudrocks of the Beaufort Group, depending on the locality.¹⁶ The stratigraphic position of the first maroon mudrocks does vary from place to place¹⁶ but is always within 700 m of the contact between the Abrahamskraal and Waterford formations (Fig. 2), and is considered to reflect a change from a more waterlogged delta plain to a drier fluvial environment.¹²

The fact that all specimens of *Eodicynodon* and the associated fauna from the *Eodicynodon* Assemblage Zone that have been collected to date are from below the first maroon mudrocks, has led to the idea that these animals inhabited a subaerial delta plain environment.^{12,13} In this environment, waterlogged conditions prevented extensive oxidation of sediments, as indicated by the green colour¹⁷ of the mudstones.¹⁸ This specimen extends the range of *Eodicynodon* into a drier fluvial environment, in which subaerial exposure allowed for oxidation of sediments, which then acquired their red colour.¹⁸ The discovery is important for future palaeoenvironmental interpretation and Karoo Basin modelling.

In addition to its stratigraphic importance, the specimen is also of significance as it is one of only three dicynodont specimens, of the thousands which have been collected from around the world, to preserve two canines on one side of the upper jaw (Fig. 3). The other specimens displaying this feature are single representatives of the younger and more derived genera *Emydops* (which has two canines on either side)¹⁹ and *Kannemeyeria* (which has a double tusk only on the left).²⁰

Double canines have been reported in gorgonopsians,^{21,22} therocephalians²³ and cynodonts²⁴ and have been considered to represent replacement canines as the roots of the canine teeth in theriodonts are closed (J.A. van den Heever, pers. comm.).²⁵ By contrast, our observations on the dicynodont specimens NMQR 2903 (*Eodicynodon*) and BP/1/4675 (*Kannemeyeria*) indicate that the roots of the canines of dicynodonts are open-ended (Fig. 4).^{*} Fortunately, the smallest specimen of *Eodicynodon* (NMQR 2903) has the lateral surface of the right maxilla weathered away and reveals a fully formed canine which has not yet erupted. This suggests that the presence of an erupted canine occurs only in older specimens of *Eodicynodon*. The skull lengths of eleven specimens of *Eodicynodon* from the collections of the National Museum in Bloemfontein and the Bernard Price Institute were measured, revealing a skull length ranging from 48 to 89 mm, which indicates that our specimen (skull length of 52 mm) is of intermediate size.

It is tempting to think that the double canine preserved in specimen BP/1/6230 is a replacement canine in an adolescent individual, but the fact that the *Eodicynodon* canine, like that of other dicynodonts, has an open-ended root supports Camp's²⁰ conclusion that the tusks were continuously growing in adult dicynodonts, and therefore needed no replacement. This contrasts with post-canine replacement, which

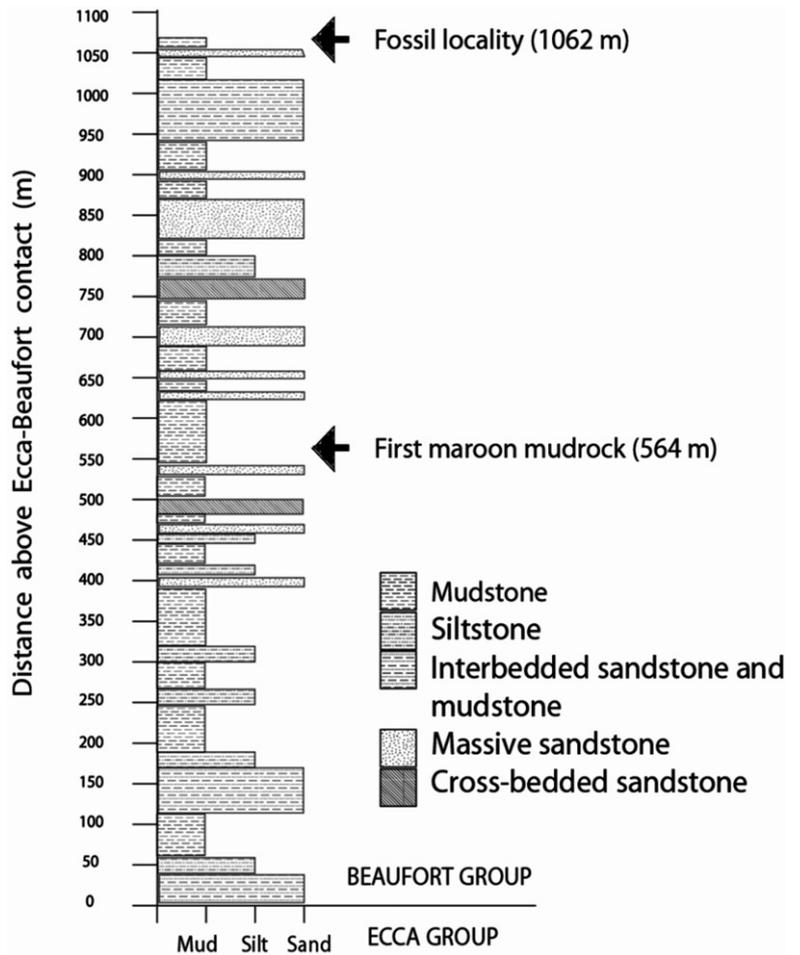


Fig. 2. Stratigraphic section of the Abrahamskraal Formation on the farm Bloukrans, showing the relative stratigraphic positions of the lowest maroon mudrocks at 564 m and that of *Eodicynodon* specimen BP/1/6230 at 1062 m (after F. Vitali, unpubl. data).

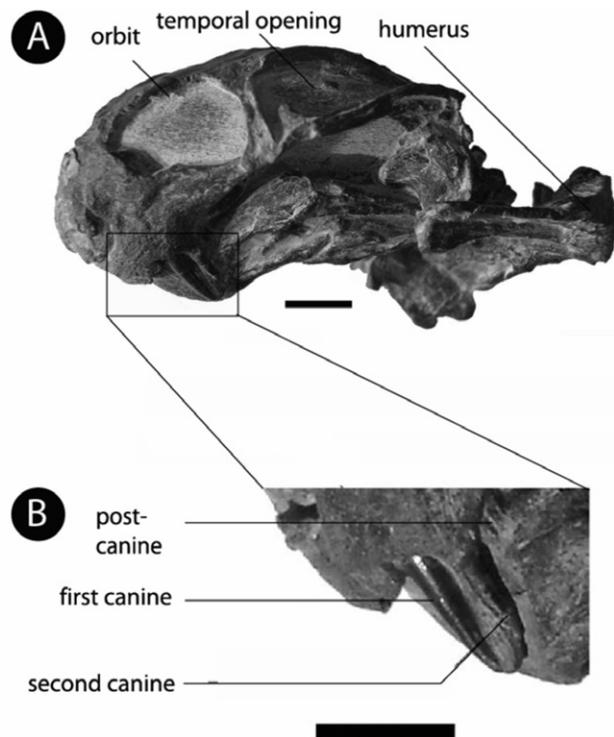


Fig. 3. A, Left lateral view of the skull of *Eodicynodon* (BP/1/6230). B, Close view of two tusks on left maxilla. Scale bars represent 1 cm.

*Abbreviations:

BP: Bernard Price Institute for Palaeontology, Johannesburg, South Africa. NMQR: National Museum, Bloemfontein, South Africa.

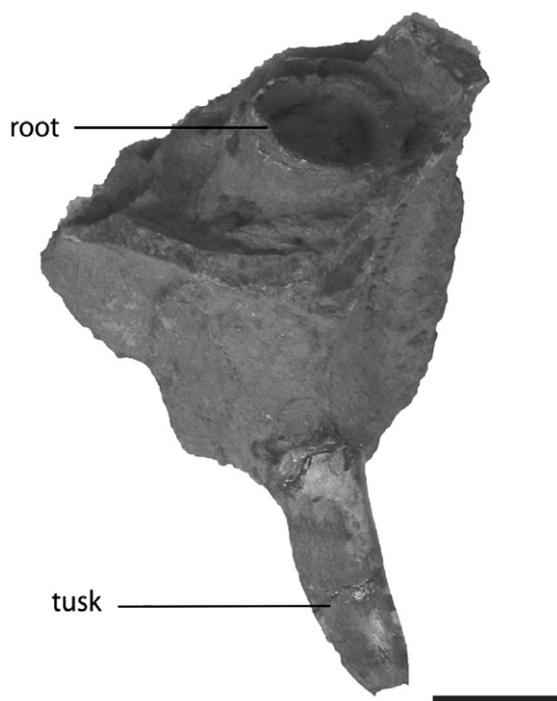


Fig. 4. Maxilla of *Kannemeyeria* (BP/1/4675) showing the open root of the canine. Scale bar represents 3 cm.

has been shown to have occurred in adult dicynodonts.²⁵ The fact that the canines of many mature dicynodont specimens (including *Eodicynodon*) are worn on the medial side endorses the view that they were possibly worn out by abrasion against the keratinous beak of the lower jaw.^{26,27} We thus consider the state of the double canine situation present in the *Eodicynodon* specimen (BP/1/6230) to be abnormal and possibly pathological. As theriodont therapsids are believed to have undergone repeated tooth replacement,^{22–24,25,28,29} continuously growing permanent canines were a unique specialization of dicynodonts.

The discovery of *Eodicynodon* specimen BP/1/6230 has dual significance. First, it increases the stratigraphic thickness of the lowermost biozone of the Beaufort Group by some 500 m, but as yet the nature of the contact with the overlying *Tapinocephalus* Assemblage Zone remains unclear; second, it reports the rare occurrence of a double canine in a dicynodont, which is here shown to be pathological.

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