

Lower Triassic postcanine teeth with allotherian-like crowns

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The Allotheria are fossil mammals with upper and lower postcanines usually showing two longitudinal rows of cusps separated by a central valley. The group comprises the poorly known haramiyids, mostly represented by isolated teeth, and the notably diverse and long-lived multituberculates; its monophyly is uncertain. The oldest records of this particular group are the Late Triassic (Norian–Rhaetian) haramiyids. We present here postcanines with haramiyid-like crowns that were recovered from the Lower Triassic of South Africa. A distinguishing feature of the new teeth is that they are single-rooted. This is the oldest record of mammal-like teeth with crowns having parallel rows of cusps, representing a temporal extension of some 43 million years from similar crown patterns of haramiyids and tritylodontids. This finding reinforces evidence of the remarkable faunal turnover of therapsids in the Early/Middle Triassic, at which time an explosive origin followed by a rapid early diversification of herbivorous/omnivorous forms with occluding expanded postcanines took place.

Introduction

The Beaufort Group of the South African Karoo shows an abundance and diversity of non-mammalian synapsids, which have allowed for biostratigraphic subdivisions ranging from Middle Permian to Middle Triassic.¹ The youngest of these biozones, the *Cynognathus* Assemblage Zone (AZ), comprises the full extent of the Burgersdorp Formation of the Tarkastad Subgroup (J. Hancox, pers. obs.), and is further subdivided into three informal subzones.² The oldest, Subzone A, is characterized by the presence of fishes, temnospondyl amphibians, primitive archosaurs, cynodonts and bauriid theroccephalians.^{2–5} This subzone is currently considered to be Upper Olenekian in age, corresponding approximately to 247–245 Myr ago.⁶

Therapsids with postcanines showing longitudinal rows of cusps separated by a basin are first known from the end of the Triassic in both tritylodontids and haramiyids.^{7,8} The detailed crown morphology of these animals is remarkably different, however. Tritylodontids have two or three rows of crescentic cusps separated by grooves, which are directed posteriorly in upper postcanines and anteriorly in lowers.^{9,10} Haramiyids also exhibit two or three rows of cusps, usually separated by a basin. The cusps are rounded, directed straight upwards/downwards and generally of unequal height.^{7,8,11,12} Formerly, tritylodontids, haramiyids and multituberculates were grouped together,^{13,14} but nowadays it is agreed that tritylodontids are late non-mammaliaform cynodonts with debated cladistic relationships.^{15–18} Although many authors consider haramiyids and multituberculates as closely related, forming the allotherians,^{7,8,19–21} the phylogenetic placement of Haramiyida is not clear. An alternative hypothesis of close relationships between this group and tritylodontids in a pre-mammalian clade was

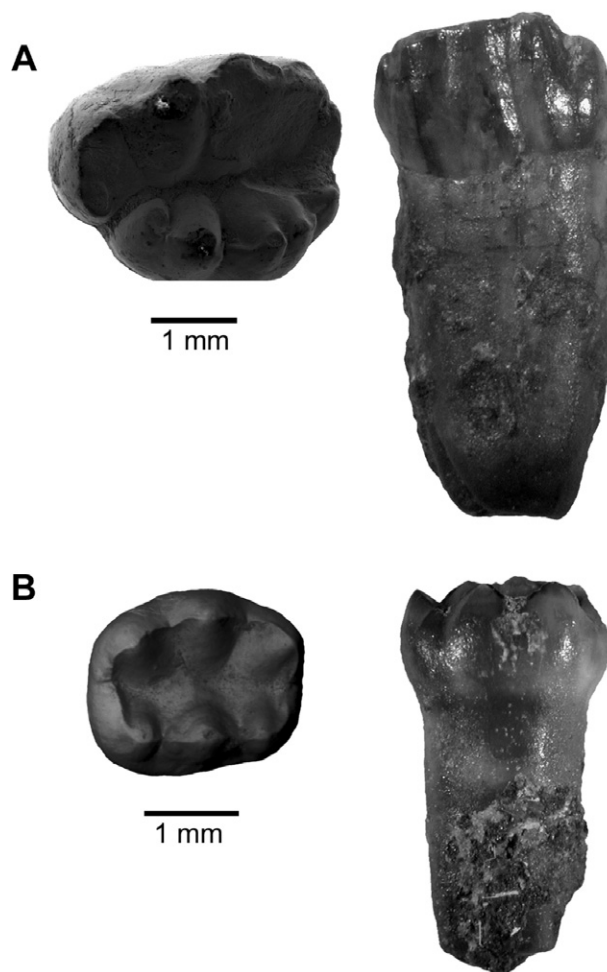


Fig. 1. Allotherian-like teeth. **A**, Occlusal and lateral views of BP/1/6515 (Pattern 1); **B**, occlusal and lateral views of BP/1/6516 (Pattern 2).

found to be most parsimonious from an unconstrained search, whereas relationships between haramiyids and multituberculates (i.e. allotherian hypothesis) were found in trees seven steps longer.^{8,22}

We present here a new record of four therapsid postcanines discovered from lag deposits on the farm Driefontein 11 in the Bethlehem District, northeastern Free State province, close to the town of Paul Roux. From the same lag deposits were also recovered chondrichthyan fin spines, a large number of lungfish tooth plates, two saurichthyid-like jaw fragments, numerous actinopterygian scales, micro-ichthyofaunal remains including teeth attributable to the hybodontid freshwater shark *Lissodus*, and postcanine teeth of bauriid theroccephalians (ref. 5 and F. Abdala, pers. obs.). The levels of this lag deposit represent the lower horizons of the Burgersdorp Formation of the Karoo Supergroup, corresponding to the *Cynognathus* AZ (Subzone A). The new teeth reported here show two longitudinal rows of cusps separated by a basin (Fig. 1). (The first notice of these remarkable teeth was recently released in an addendum of a paper²³ and disclosed without our knowledge.) This is the oldest evidence for this kind of postcanine pattern in therapsids and extends the record of this crown morphology by some 43 million years. This record also highlights the notable increase in diversity of therapsids showing postcanines with expanded and occluding crowns. Two trirachodontids (*Langbergia* and *Trirachodon*⁴), bauriid theroccephalians¹⁸ and the new form presented here are therapsids with expanded crowns discovered in Subzone A (Fig. 2). In addition, the phylogenetic placement of

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Diademodon^{4,17,18} suggests that this gomphodont cynodont should also have been present in Subzone A.

Description

Considering the overall morphology of the crown of the new form, two basic patterns are recognized. Pattern 1 is represented by the largest tooth of the sample (BP/1/6515, collection of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand) and has an ovoid-shaped crown with two rows with five cusps each separated by a wide basin (Fig. 1A). The second pattern (BP/1/6514, 6516 and 6517) shows crowns of rectangular shape with variation in the number of cusps. BP/1/6516 is the most symmetrical in overall crown morphology, with three cusps in each longitudinal row (Fig. 1B), whereas BP/1/6517, which is the smallest postcanine, has three cusps on either side of the basin and a single cusp on one margin connecting both rows of cusps. BP/1/6514 shows a curved row with four cusps and a straight row with three cusps. Three teeth show apparent wear facets (see occlusal view in Fig. 1A). However, most of the possible wear facets could not be confirmed with a scanning electron microscope, because of the lack of striations. The only established wear facets are on postcanine BP/1/6517, where the striations on two wear facets are bucco-lingually orientated, indicating a transverse (ecte-ental) movement of the lower jaw. As in Haramiyavia,²⁴ the anteroposterior (palinal) movement, expected in animals with these kinds of crowns,^{7,12} cannot be confirmed.

Discussion

The presence of an undivided root with a crown showing rows of cusps separated by a basin produces a noteworthy combination of features in the new postcanines. Divided roots are frequently considered as a synapomorphy of mammaliaforms,^{25–28} but in tritylodontids upper postcanines show several roots (up to six²⁹), whereas in the lower postcanines the number varies between one and two,^{29,30} the latter being the most common condition in the group. Accordingly, some authors consider the division of the postcanine root as a synapomorphy at the level of Mammaliaforma, therefore including tritylodontids.¹⁵ In addition, a hypothesis of multiple independent origins of multi-rooted postcanines in cynodonts was recently advanced.³¹ Whatever the case, the presence of a single root and the morphology of the root in the new teeth from the *Cynognathus* AZ represent a clear difference with tritylodontids and haramiyids. Even though the tritylodontid *Bienotheroides* shows one root in the lower postcanines, they are extremely long and recurved posteriorly.³⁰ This represents a remarkable difference in morphology from the single, downwardly directed root typical of most non-mammaliaform cynodonts, and present in the new teeth. The single root also suggests the placement of the new taxon outside Mammaliaformes, a group in which all basal members show divided roots.

The crown morphology of the teeth links this Lower Triassic form with haramiyids. If the allotherian hypothesis is considered, a long ghost range of around 90 Myr separates the oldest records of multituberculates and haramiyids. This great temporal gap may cast additional doubt on the phylogenetic relationships between allotherians and can be considered as providing indirect support (in the way of a far less extended ghost range of 43 Myr) to the hypothesis of close relationships between haramiyids and tritylodontids, as proposed by recent cladistic analyses.^{8,22,32} We should explore another alternative, however: the independent development of similar crown morphology in therapsid postcanines. The recent proposal of the dual

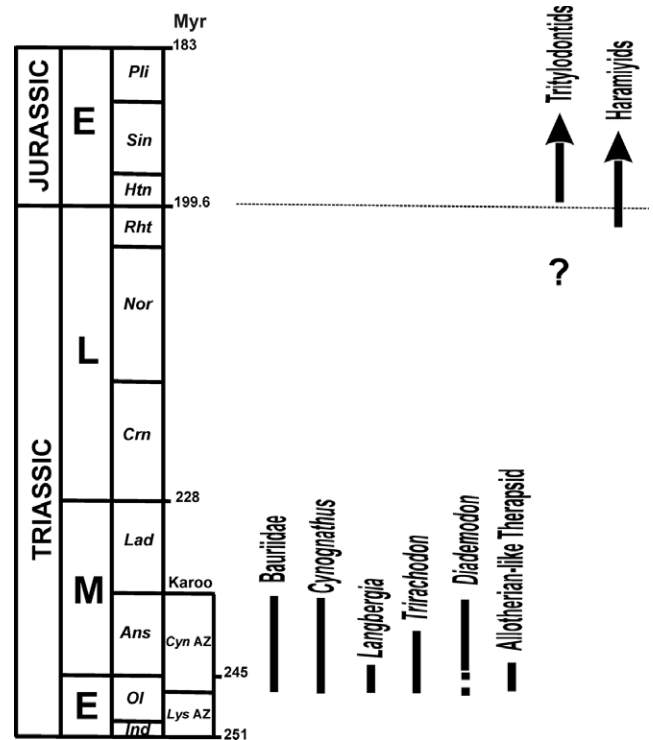


Fig. 2. Record of therapsids from the base of the *Cynognathus* Assemblage Zone (Lower Triassic) of the Karoo, South Africa. Tritylodontids and haramiyids were previously known as the oldest therapsids with parallel rows of cusps on the postcanines. The dashed line for *Diademodon* indicates that the taxon is not recorded in the base of the *Cynognathus* Assemblage Zone but its presence is suggested by phylogenetic analyses.^{4,17,18} The question mark refers to the postcranial elements from the Norian of Argentina (Los Colorados Formation), considered here as a tentative record of tritylodontids. Abbreviations: Ans, Anisian; Crn, Carnian; Cyn AZ, *Cynognathus* Assemblage Zone; E, Early; Htn, Hettangian; Ind, Induan; L, Late; Lad, Ladinian; Lys AZ, *Lystrosaurus* Assemblage Zone; M, Middle; Nor, Norian; Ol, Olenekian; Pli, Pliensbachian; Rht, Rhaetian; Sin, Sinemurian. Time scale follows ref. 6.

origin of tribosphenic molars³³ is perhaps one of the most famous examples. This landmark morphology of mammal molars was recently reinterpreted as occurring independently in lineages arising in the Middle Jurassic of Gondwana (Australosphenida) and the Early Cretaceous of Laurasia (Boreosphenida). Another clear example of this situation involving nonmammaliaform cynodonts, is the case of the Early Triassic *Thrinaxodon*, with some of its lower postcanines remarkably similar to *Morganucodon* lower molars.^{34, 35} In addition, *Thrinaxodon* shows single-rooted postcanines, whereas morganucodontids, which are first known from the Late Triassic,⁸ have divided roots. A further complication of this scenario is that the crown morphology of *Thrinaxodon*/*Morganucodon* lower postcanines is also acquired by convergence in *Prozostrodon*, a non-mammaliaform cynodont from the Upper Triassic of Brazil, which shows single-rooted postcanines with a furrow interpreted as an incipient division of the root.^{36,37}

The new taxon from Subzone A of the *Cynognathus* AZ improves our knowledge of the early diversification of therapsids with bucco-lingually expanded postcanines, which first appeared, already quite diverse, at the end of the Early Triassic (Fig. 2). The new taxon also documents that the first record of therapsids with postcanines showing parallel rows of cusps separated by a basin occurred approximately 43 Myr earlier than previously thought. Features of the crown indicate closest similarity with haramiyids, but it is also clear that the independent acquisition of similar crown morphology in unrelated lineages of cynodonts remains a strong possibility. We therefore

consider this new form from the *Cynognathus* AZ as a non-mammaliaform cynodont, but defer its assignment to any particular group (contra ref. 23). More material of this intriguing taxon is necessary to provide additional clues regarding its precise taxonomic/phylogenetic placement.

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