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COMPLEX MULTICUSPED POSTCANINE TEETH FROM THE LOWER TRIASSIC OF SOUTH AFRICA

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ABSTRACT—Two incisors and five postcanine teeth of complex crown morphology were found in the lower levels of the Burgersdorp Formation of the Beaufort Group, corresponding to the basal Subzone A of the *Cynognathus* Assemblage Zone (late Olenekian). All the teeth bear a single root and the postcanines show two rows of mesiodistally aligned cusps and a central basin or groove. Among the postcanines, two general patterns of crown morphology are recognized on the basis of relative length of the cusp rows, number of cusps per row, and width of the central area. Phylogenetic affinities of the described specimens remain unclear, and thus they are regarded as *Eucynodontia incertae sedis*. However, comparisons with non-mammalian cynodonts with labiolingually expanded postcanines show that they are most similar to those of *Aleodon*, *Candelariodon*, and some haramiyids. Many cynodont taxa such as *Aleodon*, *Candelariodon*, *Cromptodon*, haramiyids, and tritylodontids, which are probably not closely related to each other, have labiolingually expanded postcanines with cusps arranged mesiodistally in rows and a central basin; thus pointing to the homoplastic nature of dental morphologies in the cynodont lineage. The teeth presented here are the oldest record of therapsid teeth with crowns having parallel rows of cusps, representing a temporal extension of approximately 10 million years for this crown pattern.

INTRODUCTION

The Beaufort Group of the South African Karoo comprises a thick sedimentary sequence spanning the middle Permian to middle Triassic (Hancox and Rubidge, 2001). This succession is well known for its remarkable abundance and diversity of non-mammalian synapsids, which have allowed for its eightfold biostratigraphic subdivision (Rubidge, 1995). The youngest of these biozones, the *Cynognathus* Assemblage Zone (AZ), comprises the full extent of the Burgersdorp Formation of the Tarkastad Subgroup (P. Hancox, pers. observ.), and has been further subdivided into three informal subzones termed, from the base up, the A, B, and C subzones (Hancox et al., 1995; Shishkin et al., 1995). Subzone A is characterized by the presence of temnospondyl amphibians (e.g., *Kestrosaurus* and *Trematosuchus*), erythrosuchid archosaurs, bauriid thercephalians (Hancox et al., 1995; Hancox, 2000; Rubidge, 2005; Abdala et al., 2006), and cynodonts (e.g., *Cynognathus* and *Langbergia*). This basal subzone is currently considered to be late Olenekian in age, corresponding approximately to 247–245 Ma following the temporal scale of Gradstein and Ogg (2004).

Therapsids with postcanines showing longitudinal rows of cusps and a central basin are first known from the middle Triassic of Brazil (*Candelariodon barberenai*; Oliveira et al., 2011), Tanzania, and Namibia (*Aleodon brachyrhamphus*; Crompton, 1955; Abdala and Smith, 2009), followed by the records of tritylodontids and haramiyids at the end of the Triassic (Butler and MacIntyre, 1994; Butler, 2000; Kielan-Jaworowska et al., 2004).

Aleodon is considered by some scholars as a member of Chiniquodontidae (Battail, 1991; Hopson, 1991; see also Hopson and Kitching, 2001:figs. 7–8). On the other hand, Abdala and Giannini (2002) excluded this taxon from Chiniquodontidae because it lacks the diagnostic traits of this family and expressed that additional material is required for a confident taxonomic assignment.

Candelariodon is a recent addition to the knowledge of cynodonts, considered a eucynodont of uncertain affinities comparable to some postcanines of a specimen referred to *Aleodon* (NHMUK R10068) by Oliveira et al. (2011). These authors also found similarities between *Candelariodon* and some of the teeth presented here (preliminary descriptions published by Abdala et al., 2007; see below), disregarding possible affinities with haramiyids.

Initially, Marsh (1880) included tritylodontids, haramiyids, and multituberculates in Allotheria (see also Simpson, 1928); nowadays, it is agreed that tritylodontids represent late non-mammaliaform cynodonts, although their precise relationships are debated. Some authors consider them to be the sister group to mammaliaforms (Rowe, 1988; Wible, 1991; Liu and Olsen, 2010); in other cases they are considered to be closely related to traversodontid cynodonts (Hopson and Kitching, 2001). Most recently, they were found to be the sister clade to tritheledontids, closely related to mammaliaforms (Abdala, 2007).

Although many authors consider haramiyids and multituberculates to be closely related and members of Allotheria (e.g., Sigogneau-Russell, 1989; Miao, 1993; Kermack et al., 1998; Butler, 2000; Kielan-Jaworowska et al., 2004), the phylogenetic relationships of Haramiyida are by no means clear. An alternative hypothesis of a close relationship between haramiyids and

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tritylodontids in a pre-mammaliaform clade was found to be most parsimonious from an unconstrained search (Luo et al., 2002; see also Wood and Rougier, 2005), whereas relationships between haramiyids and multituberculates (i.e., the allotherian hypothesis) were found in trees seven steps longer (Luo et al., 2002). It should be noted, however, that the studies by Luo et al. (2002) and Wood and Rougier (2005) were not centered in non-mammalian cynodonts, but on Mesozoic mammaliaforms; therefore, the character sampling was not optimized to address this question.

A brief report of four postcanines with two longitudinal rows of cusps and a central basin or groove discovered in Subzone A of the *Cynognathus* AZ (Abdala et al., 2007) was presented in order to discuss a premature assignment of the specimens to Haramiyida (Hahn and Hahn, 2006; see also Hahn and Hahn, 2007). We present here a detailed description of this material, as well as an additional postcanine, and two incisor-like teeth. These teeth are the oldest evidence of postcanines with longitudinal rows of cusps and a central groove or basin in therapsids,

extending the record of this crown morphology by approximately 10 million years.

Institutional Abbreviations—BP/1/, Karoo fossil collection in the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; NHMUK, Natural History Museum, London, United Kingdom.

MATERIALS

The two incisor-like teeth (BP/1/6518–6519) and the five postcanine teeth (BP/1/6514–6517, 7161) were collected at the farm Driefontein 11 in the Bethlehem District, northeastern Free State Province, close to the town of Paul Roux (Fig. 1A).

Driefontein 11 is one of the most important of several lower Burgersdorp Formation sites in the northeastern Free State that contain *Cynognathus* AZ (Subzone A) fauna. The Burgersdorp Formation is unconformably overlain by the Upper Triassic Molteno Formation (of the Stormberg Group), which in the area comprises two medium- to coarse-grained sandstone units

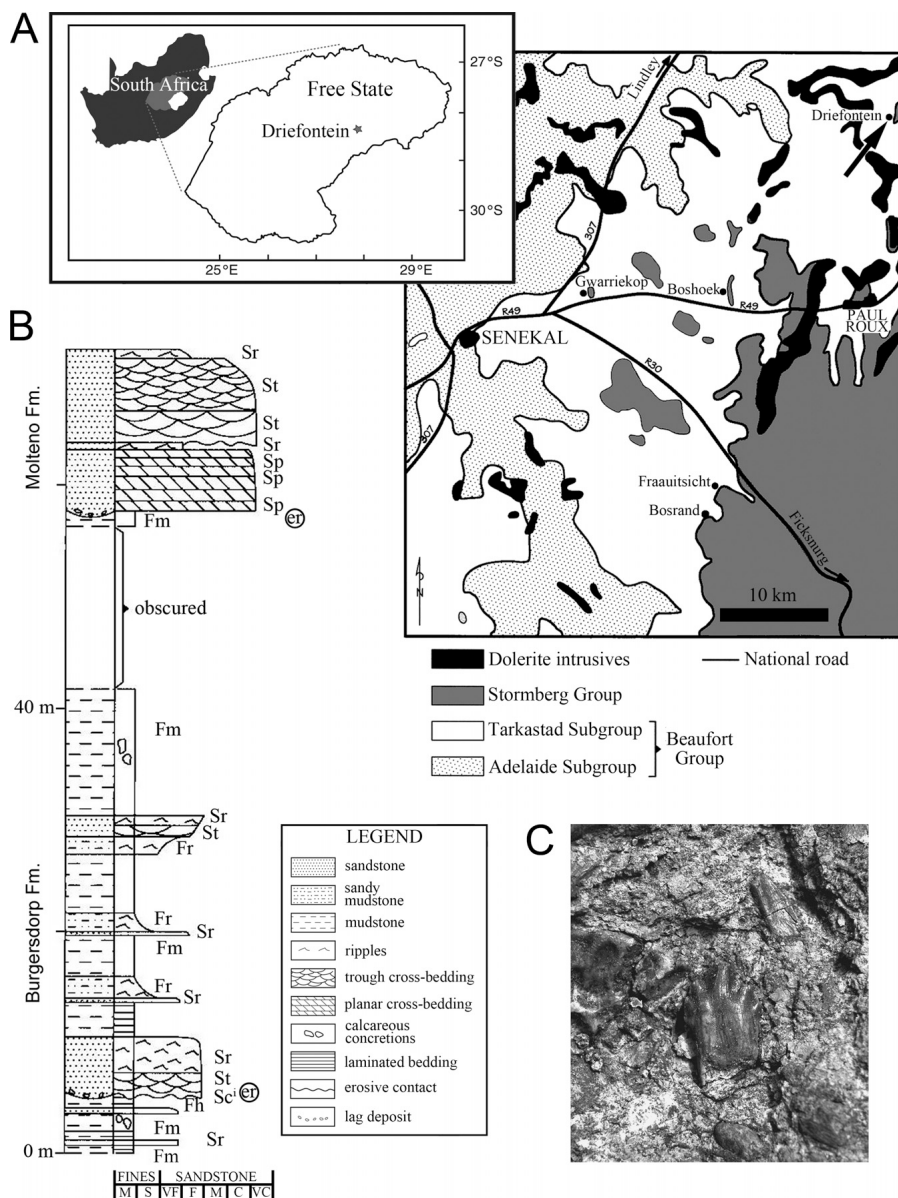


FIGURE 1. **A**, geological map showing the main stratigraphical units and the location of Driefontein 11 (star/arrow); **B**, sedimentological log of the Burgersdorp Formation at Driefontein 11; **C**, a detail of Burgersdorp Formation lag deposit depicting an isolated tooth and bone fragments. **Abbreviations:** er, erosive contact; Fh, horizontally laminated mudstone; Fm, massive mudstone; Fr, ripple cross-laminated mudstone; Seⁱ, intraclast-rich sandstone; Sp, planar cross-bedded sandstone; Sr, ripple cross-bedded sandstone; St, trough cross-bedded sandstone.

(Hancox, 1998, 2000). The contact with the underlying Katberg Formation is not exposed in the area. A stratigraphic section for Driefontein 11 is presented in Figure 1B. The Burgersdorp Formation in this area can be subdivided into a lower, horizontally laminated to massive, mudrock-dominated unit; a more sandstone-rich middle succession; and an upper, mudrock-dominated succession.

The lower unit at Driefontein 11 is ca. 5 m thick. The lowermost part is composed of dark reddish-brown (10R 3/4) laminated mudrocks followed by a coarsening upward succession of blue-gray siltstones and sandstones. The latter is weakly consolidated and may bear disarticulated, well-preserved fossils and lag concentrations. Overlying these lithologies, there may be either poorly laminated to massive dark reddish-brown (10R 3/4) mudrocks and siltstones, or intercalated laminated dark reddish-brown (10R 3/4) mudrocks and blue-gray siltstones.

The middle sandstone unit may be up to 3 m thick at Driefontein 11. The base of the unit may be evidence of erosional scour, being overlain by a lag accumulation of well-rounded clay pebbles, reworked burrow casts, bones, and coprolites. At Driefontein 11, the layer bearing the teeth described here occurs in this lag deposit (Fig. 1C), with the fossiliferous horizons situated on the slopes of a small hill centered around S28°17.391, E27°42.432. Above the lag accumulation, the depositional sequence is dominated by light gray (5Y 7/1), fine- to medium-grained, trough cross- to ripple cross-laminated sandstones, with rare intraformational lag deposits. The bases of these sandstone deposits may also preserve invertebrate trace fossils.

The upper part of the succession at Driefontein 11 is formed by a thick (up to 40 m) succession of dark reddish-brown (10R 3/4) mudrocks and intercalated thinner (>1 m) sandstone levels, which become more grayish-brown (5YR 3/2) towards the top of the succession. Evidence of limited desiccation and incipient pedogenesis (mudcracks, small calcareous nodules, rhizcretions, slickensides, and color mottling) occurs sporadically throughout the mudrock units. This part of the succession shows stacking of weakly developed calcic paleosols and the fossils have a thick hematitic covering.

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905
 CYNODONTIA Owen, 1861
 EUCYNODONTIA Kemp, 1982
 Gen. et sp. indet.
 (Figs. 1, 2, 4, 5)

Material—BP/1/6518–6519, two isolated incisors, and BP/1/6514–6517 and 7161, five isolated postcanine teeth.

Horizon—Lower horizons of the Burgersdorp Formation, Beaufort Group, Karoo Supergroup, South Africa. *Cynognathus* Assemblage Zone (Subzone A).

Age—Late Olenekian (Hancox et al., 1995; Hancox, 2000).

Associated Fauna—The fauna of the northern Burgersdorp Formation is dominated by temnospondyl amphibians, erythro-suchid archosaurs, and fishes, with rare occurrences of cynodonts, therocephalians, and procolophonids. The Driefontein 11 fauna is composed by the hybodontid freshwater shark *Lissodus*, the dipnoan *Ptychoceratodus* (see Bender and Hancox, 2003), the temnospondyls *Kestrosaurus dreyeri* and *Kestrosaurus kitchingi* (see Shishkin et al., 2004), *Parotosuchus dreyeri* (see Damiani, 2001), and *Bathignathus poikilops* (see Damiani and Jeannot, 2002), the procolophonid *Thelephon contritus* (see Gow, 1977; Modesto and Damiani, 2003), the diapsid *Palacrodon browni* (see Gow, 1999), an undescribed erythro-suchid, and the trirachodontid *Langbergia* (see Abdala et al., 2006). Additionally, from the same lag deposits that produced the teeth described here, the following fossils were recovered: chondrichthyan fin spines; a large number of lungfish tooth plates; five saurichthyid-like

jaw fragments; numerous actinopterygian scales; several micro-ichthyofaunal remains; fragments attributable to reptiles and archosaurs of uncertain affinities; and postcanine teeth of bauriid therocephalians (Bender and Hancox, 2003; F. Abdala, pers. observ.).

DESCRIPTION

Incisors

BP/1/6518 is a complete incisor with a single cusp that is highly convex mesially and concave distally (Fig. 2A–E). A blunt but well-defined enamel ridge surrounds the mesial concavity. There is a neck-like constriction separating the root from the crown. In cross-section the root is oval in shape, i.e., longer mesiodistally than labiolingually, with its diameter enlarging away from the crown. Wear is present on the tip of the crown (Fig. 2B–E). Three different wear planes or facets are recognized. Scanning electron microscopy (SEM) images of wear facet 1 show it to be a triangular plane with short, deep, and wide striations (Fig. 2C). The central facet (facet 2) is more rounded and has long, shallow, and narrow striations (Fig. 2D). The third facet (facet 3) is triangular in shape but interrupted by a central elevated ridge-like structure and has less developed striations (Fig. 2E).

BP/1/6519 is the distal tip of an incisor (Fig. 2F–I), which is similar in shape to the incisor described above in the degree of curvature, but lacks any wear facets. Several long and wide fissures with irregular margins are present on the distal surface of the tooth (Fig. 2H–I) but they appear to be artifactual.

Postcanines

Each postcanine tooth from Driefontein 11 has a simple, undivided root and two rows of aligned cusps. All of them show one of the rows curved and the other straight (or almost straight) in occlusal aspect. Comparisons with other forms (see below) suggest that the long axis of each tooth was oriented mesiodistally. Common features with certain taxa are recognized, making it possible to suggest a lower/upper and right/left position for the Driefontein 11 postcanines by direct comparison. However, these taxa are, in most cases, known by fragmentary specimens and the full dentition and/or each tooth position is as yet unknown. Thus, given the restricted comparisons and the ambiguous determination of the teeth placement, we prefer to use an arbitrary terminology to describe the postcanines from the Burgersdorp Formation. Consequently, the rows will be referred to as curved (C) or straight (S) and the cusps named as S or C, depending on their location on the straight or curved margin. We arbitrarily decided to orient the postcanines with the straight margin to the left. Thus, the cusps will be correlatively numbered from front (F margin) to back (B margin) without implying life orientation (Fig. 3).

Two general patterns of crown morphology have been recognized among the postcanine teeth. One of them is characterized by presenting numerous bulbous cusps, a narrow groove setting apart the S and C rows, and with one of the rows significantly longer than the other. The second morphological pattern displays fewer cusps bordering a central basin and cusp rows are subequal in length.

The first morphotype is represented by BP/1/6515, the largest tooth of the sample (Table 1). Its crown is oval in outline and bears five subequal cusps on each row separated by a narrow groove (Fig. 4A, C–D). The C row is shorter than the S row, and C cusps are comparatively smaller and closer to each other than S cusps. The F margin is wider than the B one (Fig. 4C). In both rows, cusps 2 and 3 are notably closer to each other than any of the other cusps. Cusps C1 and S1 are connected by an elevated ridge (Fig. 4A). In the B margin of the tooth (Fig. 4A, C–D), the central groove is open, although the S5 cusp partially closes it. S cusps are higher than those of the C row, and cusp S4 is the highest of the crown, but in an unworn state, the third cusp would

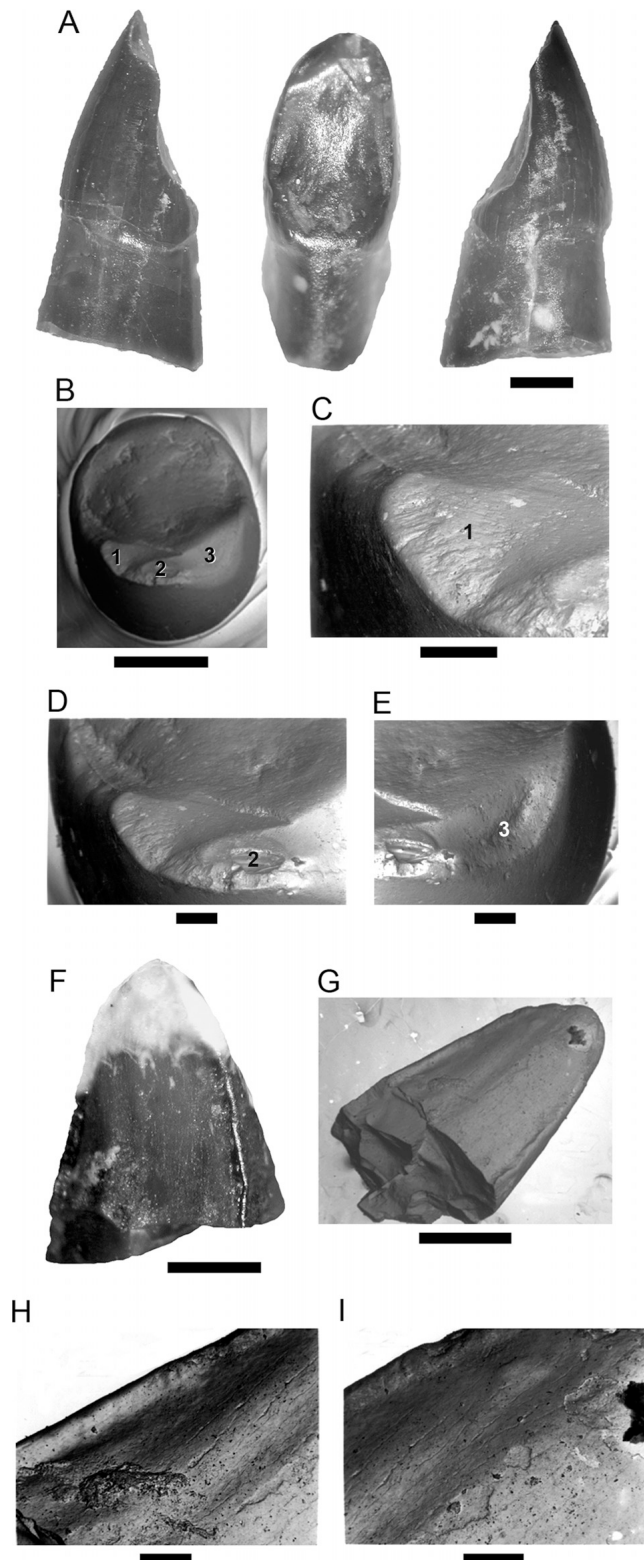


FIGURE 2. Optical and SEM images of **A–E**, BP/1/6518 and **F–I**, BP/1/6519. **A**, lateral and distal views of BP/1/6518; **B**, SEM image of the occlusal aspect of BP/1/6518; SEM close-ups of **C**, facet 1, **D**, facet 2, and **E**, facet 3 in BP/1/6518; **F**, optical and **G**, SEM images of BP/1/6519; **H–I**, SEM close-ups of the distal surface of BP/1/6519. **Key: 1, 2, 3**, wear facets. Scale bars equal 1 mm (**A–B, F–G**) and 200 μ m (**C–E, H–I**).

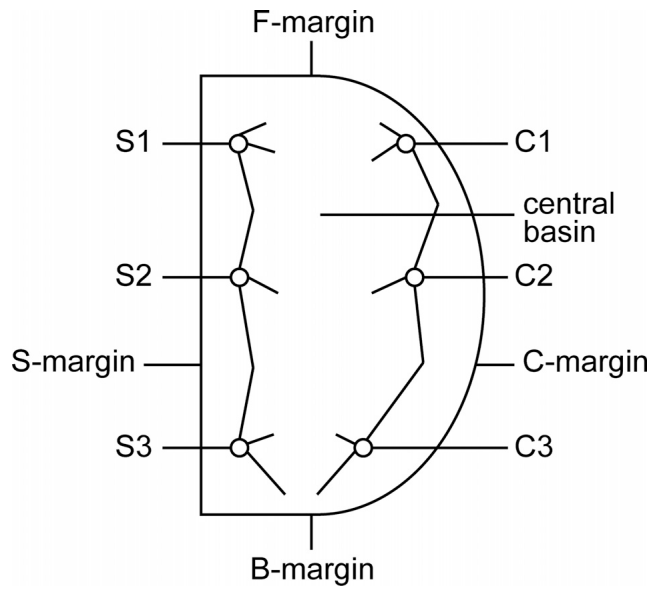


FIGURE 3. Schematic representation of a tooth with the nomenclature employed in this paper.

probably surpass the fourth one in height. There is a constriction of the tooth at the crown base (Fig. 4A). Two wear facets are observed on the S row. A large facet (facet 1; Fig. 4D, I) affects S2 and S3 internally, whereas a small facet (facet 2; Fig. 4D, J) is developed in the internal face of the S5. These areas were found to be devoid of striations when observed with an SEM, but a series of short (<100 μ m), deep, striations oriented in the S–C axis were observed on the margin of the ridge connecting S2 and S3 (Fig. 4D–E). BP/1/6514, 6516, 6517, and 7161 correspond to the second pattern. However, each one of these teeth has peculiar traits.

BP/1/6516 is the most equidimensional with a crown width/length ratio of 0.89 (Table 1). There are three cusps per longitudinal row, with cusps S2 and C2 being the highest (Fig. 4B). The basin is shallow and wide, and it is limited in both F and B extremes by low crests connecting the more external cusps of each row (Fig. 4B, F–G). A well-demarcated neck is present (Fig. 4B). No wear facets were identified, but striations parallel to the long axis of the tooth are visible under SEM on the external and internal surfaces of cusp S1 (Fig. 4G–H). Less prominent striations were observed on C1 (Fig. 4K). Moreover, faint longitudinal striations are present on the basin floor close to S1 (Fig. 4L).

The smallest postcanine, BP/1/6517 (Table 1), is oval in occlusal aspect, with three cusps per row and a well-defined neck (Fig. 5A, C, G). The cusps within each row are of similar height, but those on C row are taller than the ones in the S row (Fig. 5A). An accessory cusp, similar in height to the C cusps, is centered

TABLE 1. Crown measurements for Driefontein 11 teeth.

Specimen	Tooth	Width (mm)	Length (mm)	Height (mm)	Width/length
BP/1/6518	Incisor	2.09	—	3.37	—
BP/1/6514	Postcanine	2.19	2.72	—	0.81
BP/1/6515	Postcanine	2.68	3.62	—	0.74
BP/1/6516	Postcanine	2.04	2.29	—	0.89
BP/1/6517	Postcanine	1.40	1.87	—	0.75
BP/1/7161	Postcanine	1.50	2.08	—	0.72

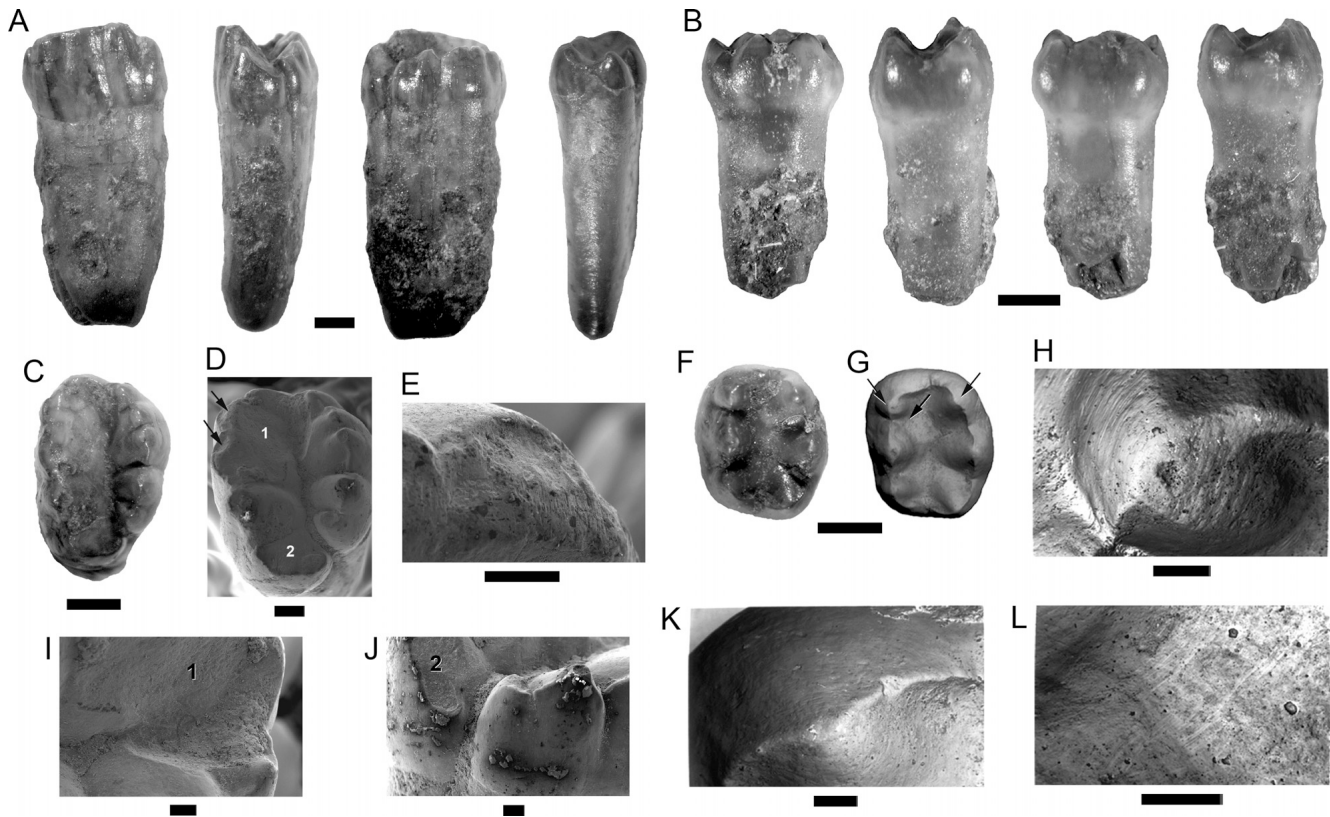


FIGURE 4. Optical and SEM images of **A, C–E, I–J**, BP/1/6515 and **B, F–H, K–L**, BP/1/6516. **A, B**, BP/1/6515 and **B**, BP/1/6516 in S, B, C, and F views; **C, F**, optical and **D, G**, SEM images of **C–D**, BP/1/6515 and **F–G**, BP/1/6516 in occlusal view; SEM close-ups of **E**, striations, **I**, facet 1, and **J**, facet 2 in BP/1/6515; SEM close-ups of striations on **H**, S1, **K**, C1, and **L**, basin in BP/1/6516. **Key:** 1, 2, wear facets; **arrows**, striations. Scale bars equal 1 mm (**A, C, F–G**), 500 μm (**D**), 200 μm (**E, I–J**), and 100 μm (**H, K–L**).

in the F margin of the tooth between the rows (Fig. 5C, G). The accessory cusp is connected by blunt low crests to the rows (Fig. 5A). The crest linking the accessory cusp to the C row is more developed than the crest connecting it to the lower S row (Fig. 5C, G). On the B margin, there is a low crest that is broken in its middle point but was evidently continuous, connecting the apices of S3 and C3 (Fig. 5A). Two wear facets, 1 and 2 (Fig. 5C–D, G–I), are recognized on the cusp C3. Both wear facets are slightly concave and situated on the inner side of the cusp but on opposite faces. Facet 2 (Fig. 5C–D, G–I) shows wider and deeper striations than those on facet 1 (Fig. 5C–D, G–H). The striations in both facets are transversely oriented with respect to the long axis of the tooth. In addition to the thin striations in facet 1, there are three deep and wide striations running at angles of ca. 30° – 40° with respect to the thinner striations (Fig. 5D). In the sector between wear facets 1 and 2, there is a deep depression that shows no sign of breakage and is tentatively interpreted as a wear facet. A similar structure, although smaller, is seen in the same sector of cusp C1. The cusps on the S margin show clear signs of apical wear. Moreover, there is an extensive wear surface on the whole external side of this row of cusps that removed the enamel covering. The enamel is a remarkably thin layer covering the cusps of the C row and most of the basin. The tips of the cusps on the C row were also affected by wear, but it is not so developed as in the S row.

BP/1/7161 (Fig. 5L–M) is very similar to BP/1/6517 so we will only describe the differences between them. These teeth probably represent right and left elements of the same taxon. BP/1/7161 has an accessory cusp that is connected to the adjacent cusps as in

BP/1/6517, but in BP/1/7161 the accessory cusp is placed on the B margin. Moreover, in BP/1/7161 the crests uniting the accessory cusp to the S and C rows are lower and taller, respectively, than in BP/1/6517. The central basin of BP/1/7161 is a narrow groove describing a zigzag trajectory, unlike the comparatively wider basin of BP/1/6517. Unlike the condition in BP/1/6517, cusp S2 in BP/1/7161 is higher than the adjacent ones. It is possible that this difference may represent different wear stages, although the wear on the external surface of the S row is comparable in both specimens. In BP/1/7161, the depression on the internal side of the C3 cusp is more developed than in BP/1/6517. Lateral to the S row, there is a clear concavity probably related to wear.

BP/1/6514 (Fig. 5B, E–F, J–K) is the second largest tooth (Table 1). Unlike the other postcanines described, a neck is lacking. In occlusal aspect (Fig. 5E–F), it is almost rectangular but the B margin is narrower than the F one. The central basin is narrow, with four remarkably bulbous C cusps and three S cusps. Cusp 3 is the taller of the C row (Fig. 5B). This cusp is set apart from the other three C cusps by a deep and narrow valley that continues as grooves that extend internally to the basin and externally to the base of the crown (Fig. 5B, E–F). The remaining three C cusps are poorly separated by valleys or grooves and all of them had their tips worn off (Fig. 5E–F). On the S row, the tips of the three cusps show evidence of wear (Fig. 5E–F). Cusp S3 is less worn, with the wear facet oriented internally. This cusp is separated from the others by a relatively wide valley. Cusps S1 and S2 show evidence of intensive wear, with the wear facets oriented externally. Due to the wear, the separation between these

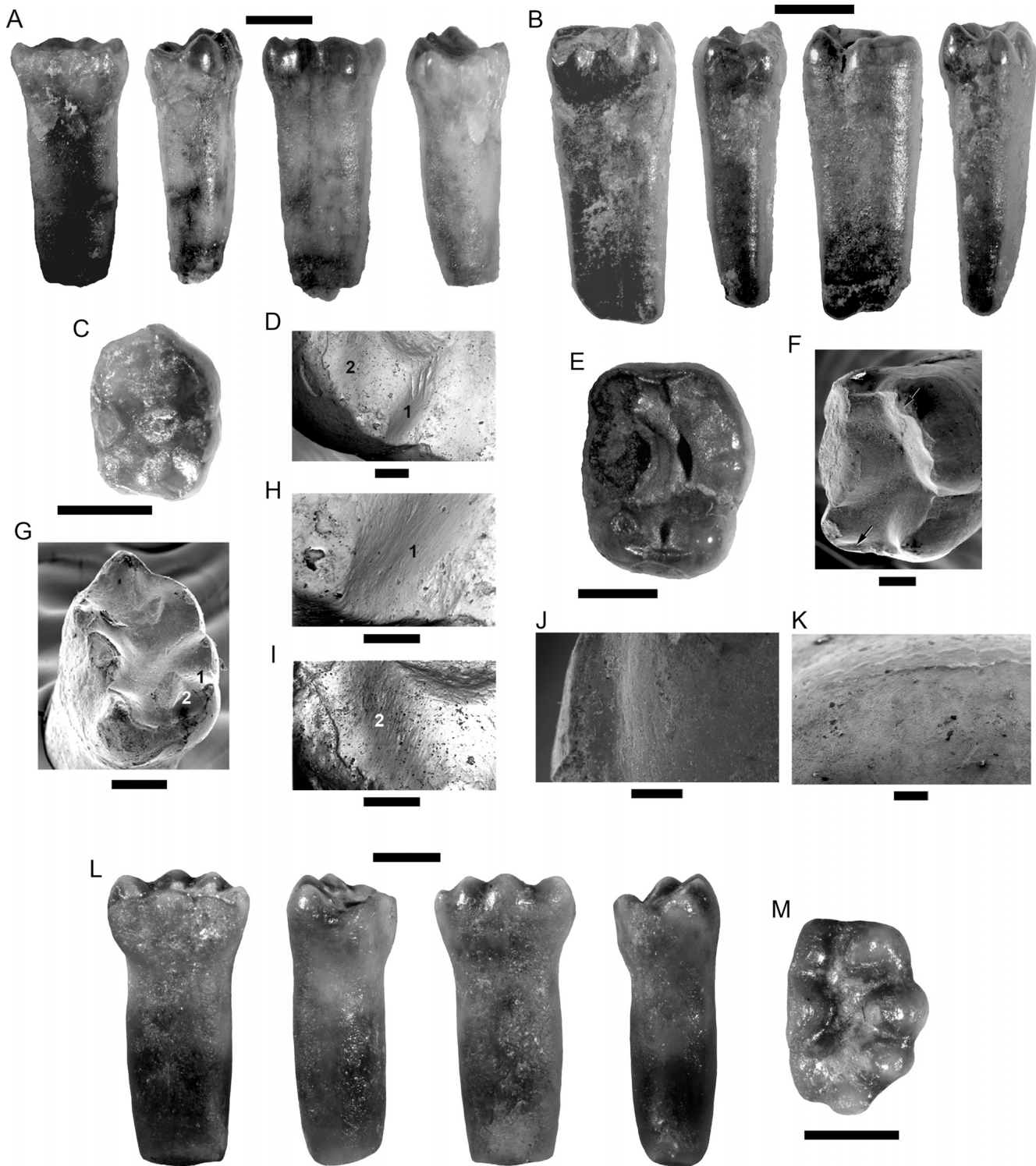


FIGURE 5. Optical and SEM images of **A, C–D, G–I**, BP/1/6517; **B, E–F, J–K**, BP/1/6514; and **L–M**, BP/1/6171. **A**, BP/1/6517 and **B**, BP/1/6514 in S, B, C, and F views; **C**, **E**, optical and **F–G**, SEM images of **C**, **G**, BP/1/6517 and **E–F**, BP/1/6514 in occlusal view; **D**, **H–I**, SEM close-ups of facets 1 and 2 in BP/1/6517; SEM close-ups of striations on **J**, S3 and **K**, C1 in BP/1/6514; **L**, BP/1/6171 in S, F, C, and B views; **M**, BP/1/6171 in occlusal view. **Key**: **1, 2**, wear facets; **arrows**, striations. Scale bars equal 1 mm (**A–C, E, L–M**), 500 μ m (**F–G**), and 100 μ m (**D, H–K**).

cusps is not preserved nor is their real height; however, it seems that cusp S2 was the largest and S3 the lowest. Cusps S3 and C3 are connected by a crest (Fig. 5B, E–F). On the B margin of the tooth, a crest behind the cusps S1 and C1 closes the central basin

(Fig. 5B, E–F). SEM images show the presence of transversely oriented striations on the internal surface of cusp S3 (Fig. 5F, J). Additionally, faint striations can be observed on cusps C1 to C3 (Fig. 5F, K).

DISCUSSION

The complete incisor BP/1/6518 (indistinguishable from the fragmentary incisor BP/1/6519) has some characters in common with the upper incisor H 14 described by Butler and MacIntyre (1994), such as the crown anteriorly overhanging the root and the presence of ridges on the mesial concave surface. In H 14 the ridge is described as being median, whereas in BP/1/6518 it is marginal. However, BP/1/6518 also has some features in common with the first two lower incisors of *Haramiyavia* (Jenkins et al., 1997), such as an upwardly inflected apex and the overall crown morphology. On the basis of the above comparison, it is not certain whether BP/1/6518 (and BP/1/6519) is an upper or lower incisor.

The morphology shown by the postcanine teeth described above (i.e., labiolingually expanded crowns, more than one row of mesiodistally aligned cusps, and a central basin or groove) is comparable to a few cynodont taxa: *Aleodon brachyrhamphus*, *Candelariodon barberenai*, *Cromptodon mamiferoides*, tritylodontids, and haramiyids.

Tritylodontid postcanine teeth display longitudinal rows of invariably crescent-shaped cusps (Sues, 1986; Maisch et al., 2004) and usually bear multiple roots. When a single root is present, it is curved posteriorly (Cui and Sun, 1987). The *Cynognathus* AZ postcanines described here do not exhibit these apomorphies. Thus, on the basis of the data available, they cannot be attributed to tritylodontids.

Aleodon brachyrhamphus and *Cromptodon mamiferoides*, two non-mammalian cynodonts of uncertain affinities (Abdala and Gianini, 2002), are represented by fragmentary material (Bonaparte, 1972; Crompton, 1955). Upper and lower postcanines are known for *Aleodon*, whereas only the lower postcanines of *Cromptodon* have been discovered. The lower postcanines of *Aleodon* and *Cromptodon* are similar in general traits. Although longer mesiodistally than labiolingually in occlusal aspect, these teeth are not sectorial but transversally expanded. They bear a labial row of mesiodistally aligned cusps with a main cusp and at least a mesial and a distal accessory cusp, and a wide platform-like cingulum lingually that may bear cuspsules and/or small cusps on its margin.

As described, the lower postcanines of *Aleodon* and *Cromptodon* are clearly different from those from Driefontein 11. However, a specimen assigned to *Aleodon* (NHMUK R10068, including imperfect upper and lower left jaws plus a skull fragment) bears two postcanines very much comparable to those described here. The NHMUK R10068 fragmentary left lower jaw preserves in place the five most anterior postcanines together with the left canine in process of being replaced, the root of the right canine, and several incisors. Whereas pc1 to pc3 of NHMUK R10068 are similar to the lower postcanines of the holotype, pc4 and pc5 bear subequal labial and lingual rows of mesiodistally aligned cusps and a shallow and wide central basin. The holotype of *Aleodon* and NHMUK R10068 may represent different ontogenetic stages, a fact that could explain the differences recognized between them. Nevertheless, it is also possible that these specimens are different taxa. A thorough analysis of the co-taxonomic nature of the holotype of *Aleodon* and NHMUK R10068 is needed.

The fourth lower postcanine of NHMUK R10068 is most similar to BP/1/6514. Given the similarities (see below), the latter might be interpreted as a left lower tooth, a proposal that is also supported by the wear facets recognized in this tooth. They both have a straighter labial row with fewer and smaller cusps than on the lingual more curved row and there is a better-developed valley setting apart the posterior-most cusp on the lingual row. However, pc4 of NHMUK R10068 is much more elongated mesiodistally with respect to its labiolingual extension than BP/1/6514; there are more, relatively larger, and better separated cusps in

the fourth postcanine of NHMUK R10068; and the basin is wider in BP/1/6514.

The fifth lower postcanine of NHMUK R10068 resembles BP/1/6515. Comparisons between these teeth point to a left lower position for BP/1/6515. These two teeth share the presence of a longer lingual row with more cusps than the labial one. However, the pc5 of NHMUK R10068 has fewer and larger cusps and a better-developed basin than BP/1/6515. In pc5 of NHMUK R10068, the lingual margin is more curved than the labial one and the mesial margin wider than the distal one, whereas, if correctly interpreted, the opposite situation occurs in BP/1/6515.

Upper postcanines of *Aleodon* (as preserved in NHMUK R10068) show different morphologies along the series, and sectorial as well as oval-shaped teeth in occlusal aspect are present. Among the non-sectorial morphologies, anterior-most teeth have a single labial cusp and a cingular platform lingually. More posterior complex morphologies present one or more tall labial cusps and at least three relatively large lingual cusps placed basally relative to the labial cusps. Hence, there is no close similarity to the postcanines from Driefontein 11.

Candelariodon barberenai, a recently described eucynodont from the Ladinian of Brazil (Oliveira et al., 2011) represented by a lower jaw bearing some teeth, also has labiolingually expanded single-rooted lower postcanines. Similar to *Cromptodon* and *Aleodon*, the crown expansion is attained in the more anterior postcanines by the development of lingual cusps. In these teeth, no distinct paired cusp rows separated by a basin are present, thus differing from the teeth from Driefontein 11. On the other hand, the last lower postcanine preserved (pc5) displays two low, parallel rows of mesiodistally aligned cusps separated by a basin that was described by Oliveira et al. (2011) as an occlusal depression, implicitly suggesting that it acted as a crushing area. Oliveira et al. (2011) noted that this tooth was clearly different from the postcanines of *Aleodon* (except for pc4 and pc5 of specimen NHMUK R10068) and *Cromptodon*, and resembled the general morphological traits of the specimens published by Abdala et al. (2007). When comparing the pc5 of *Candelariodon* with the Driefontein 11 postcanines, we find that there are close similarities, in particular with BP/1/6515, BP/1/6517, and BP/1/7161.

Comparison between the crown of pc5 of *Candelariodon* and BP/1/6515 suggests that the latter is a left lower tooth, a conclusion coincident with that drawn from the comparison of this element with *Aleodon* specimen NHMUK R10068. The fifth postcanine of *Candelariodon* shares with BP/1/6515 the presence of a lingual cusp row longer than the labial one. Additionally, the wear facets on the internal surface of BP/1/6515 cusps suggest that occlusion was similar to that of *Candelariodon*. On the other hand, pc5 of *Candelariodon* bears fewer cusps per row and has a wider basin. In addition, BP/1/6515 lacks a distal cusp such as cusp d' of *Candelariodon*.

BP/1/6517 and BP/1/7161 have a cusp comparable to d' of *Candelariodon*. On this basis and considering the worn surface present, these teeth are interpreted as right and left lower elements, respectively. BP/1/6517 and BP/1/7161 share with the pc5 of *Candelariodon* the presence of three cusps on the labial row, but unlike the Brazilian taxon, they lack a fourth lingual cusp. Moreover, the presence of a wide basin is also shared by these specimens and pc5 of *Candelariodon*. The depressions interpreted as being the result of wear in BP/1/6517 and BP/1/7161 suggest that the basin in these teeth acted as a crushing surface similar to what was interpreted for *Candelariodon*. However, the heavily worn external surface on the S row of BP/1/6517 and BP/1/7161 has no correlation in *Candelariodon*.

Allotherians, including multituberculates and haramiyids, show a great range of variation in their premolariforms and molariforms. Allotherian cheek teeth are double-rooted with characteristic crown patterns in which the rounded non-recumbent cusps are arranged into longitudinal rows separated by a deep

basin (Clemens, 1980; Butler, 2000; Kielan-Jaworowska et al., 2004). In particular, haramiyid lower postcanines (see Butler, 2000, for an outline of haramiyid tooth morphology) have one or two mesial main cusps. Distally, each main cusp is followed by a row of cusps decreasing in size. An accessory cusp mesial to the main cusp is usually present on the labial row of lower molariforms. In upper molariforms, the second cusp of the labial row is always the taller, whereas it is the distal cusp that is the taller one in the lingual row. The highest labial and lingual cusps may be connected by a crest forming a saddle-like structure in upper and lower molariforms. At the rear end of the lower postcanines and mesially in the upper ones, there is often a 'U'-shaped rim closing the central basin. Accessory cusps may be present, particularly in upper teeth, but do not alter the basic pattern described (e.g., Hahn, 1973; Sigogneau-Russell, 1989; Butler and McIntyre, 1994; Sigogneau-Russell and Hahn, 1995; Heinrich, 1999).

The Driefontein 11 postcanines and haramiyid molariforms share the presence of two rows of cusps and a central groove or basin. Moreover, a saddle-like and/or a 'U'-shaped structure are observed in some of the Driefontein 11 teeth. Some similarities in crown shape as seen in occlusal aspect, cusp number, and relative cusp number in each row are also recognized between certain teeth (see below). On the other hand, the postcanine teeth described here have only one root and exhibit different cusp relative proportions to those observed in haramiyids. Driefontein 11 postcanines also lack accessory labial or lingual cusps, thereby differing from most known upper molariforms of haramiyids (except for *Thomasia*). The absence of some of the distinct features characteristic of haramiyids precludes a confident assignment of the Driefontein 11 postcanines to the Haramiyida. However, given the close similarity, some of the Driefontein 11 postcanines deserve comparison with particular haramiyid taxa.

BP/1/6515 resembles the lower molariform of the haramiyid *Eleutherodon* in terms of overall crown morphology and in the presence of numerous cusps (more than four) in both rows (Kermack et al., 1998; Butler, 2000). However, BP/1/6515 is comparatively narrower and lacks any cusp in its proximal or distal margin closing the central basin. BP/1/6515 was interpreted as a left lower tooth by comparison with *Aleodon* and *Candelariodon*, but if *Eleutherodon* is used as a model, BP/1/6515 should be regarded as a right lower element. Given that we have not enough elements to decide if BP/1/6515 is more closely related to *Aleodon/Candelariodon* or to haramiyids, we regard the orientation of this tooth as uncertain.

BP/1/6514 was compared with *Aleodon* and identified as a left lower tooth; however, it also resembles the second upper molariform of *Thomasia* in the presence of one row of three large cusps, and an opposing row with a large cusp separated by a deep valley from a series of closely situated smaller cusps. If BP/1/6514 is interpreted on the basis of comparisons with *Thomasia*, the three-cusped S row should be regarded as lingual and the largest cusp on the opposite row as distal. Thus, BP/1/6514 would represent a right upper tooth, an inference not supported by the wear surface present. Additionally, the second upper molariform of *Thomasia* differs from BP/1/6514 in that it has five cusps (instead of four) in the row with the series of smaller cusps, a small cusp in the distal margin of the tooth, and an oblique distal margin (both mesial and distal margins are parallel in BP/1/6514). In view of the differences, it seems more likely that BP/1/6514 represents a taxon more closely related to *Aleodon* than to haramiyids, in particular *Thomasia*.

BP/1/6516 is more similar to the third upper molariform of *Thomasia*, which is rectangular in shape and exhibits three cusps in each row (Butler, 2000). By comparison with M3 of *Thomasia*, in which the distolingual corner is more projected distally than the distolabial one, BP/1/6516 is interpreted as an upper right tooth. Apart from the differences in cusp proportions, unlike the M3 of *Thomasia*, BP/1/6516 lacks a 'U'-shaped ridge mesially,

showing instead a more saddle-like structure (always of distal placement in the upper molariforms of haramiyids).

Postcanines in tritylodontid cynodonts are quite conservative in morphology, with differentiation restricted to only the comparison between upper and lower postcanines (Kühne, 1956; Sues, 1986). On the contrary, a noticeable variation in crown morphology is known to occur in other non-mammaliaform cynodonts (such as *Aleodon*, *Candelariodon*, and *Cromptodon*) as well as in haramiyids, with molariform teeth showing differences according to their location in the tooth row and their placement on upper or lower jaws (see, for example, Crompton, 1955; Jenkins et al., 1997; Butler, 2000; Abdala et al., 2002, 2007; Oliveira et al., 2011). Taking into account the different postcanine morphologies present in the teeth from the *Cynognathus* AZ, it seems that more than one taxon is represented in our sample. However, considering that large individual variation is a typical phenomenon, we approach the restricted evidence conservatively and, at this stage, we prefer to avoid performing any nomenclatural action and consider all these teeth as *Eucynodontia incertae sedis*.

Observation of the material with a stereomicroscope showed numerous wear facets on almost all teeth. However, most of the inferred wear facets could not be confirmed through SEM analysis because of the lack of striations. The only wear facets that showed striations were those on the postcanine BP/1/6517 and the incisor BP/1/6518. The striations observed on the two wear facets of BP/1/6517 are transversely oriented. The striations on the wear facet of BP/1/6518 are laterally oriented. Nevertheless, SEM analysis allowed the identification of faint striation-like marks on the surfaces of the cusps, on the ridges linking them, and on the basin floor. These wearing structures have transverse as well as longitudinal directions. Thus, the general absence of clearly diagnosable wear facets in the described material and the presence of striation-like structures oriented transversely and longitudinally make the interpretation of predominant masticatory movement a difficult issue. Considering the orientation of the striations in the facets of BP/1/6517, it may be assumed that transverse (ecto-ental) movement existed, whereas palinal movement, as expected in animals having these kinds of crowns (e.g., Simpson, 1926; Crompton, 1972; Butler and MacIntyre, 1994; Kermack et al., 1998), is suggested by the longitudinally oriented striations observed on BP/1/6516.

CONCLUSIONS

The teeth from the base of the *Cynognathus* AZ represent new cynodont taxa. The crown morphology of the postcanine teeth proves to be most similar to some of the teeth of *Aleodon*, *Candelariodon*, and certain haramiyids, due to the presence of aligned rows of cusps and a central basin or groove. However, the evidence at hand is insufficient to establish confidently the phylogenetic affinities of the postcanines from Driefontein 11.

SEM observations indicate a general lack of striations on tooth surfaces previously identified as probable wear facets using light microscopy. Therefore, evidence for interpreting jaw movement from wear facets is limited. The presence of wear facets with striations orientated transversely in BP/1/6517 suggests ecto-ental jaw movement and longitudinal striations on BP/1/6516 indicate palinal jaw movement.

The discovery of these South African postcanines shows that this complex morphological pattern was present 10 million years before than previously known in the therapsid lineage. These teeth provide additional evidence that the explosion in diversity that produced large and very specialized forms in the early Anisian (Abdala and Ribeiro, 2010) was well underway by the late Olenekian, which is also suggested by the presence of trirachodontids in the same deposits (Abdala et al., 2006). Finally, similarities found between complex teeth of various

distantly related taxa highlight the homoplastic nature of cynodont dentitions.

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