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A new cynodont record from the *Tropidostoma* Assemblage Zone of the Beaufort Group: implications for the early evolution of cynodonts in South Africa

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A new specimen of cynodont has been recovered from the lower Upper Permian levels of the *Tropidostoma* Assemblage Zone of the South African Karoo Basin. A series of characters, including the presence of an interpterygoid opening, triconodont postcanine teeth, which are circular in crown view, a probable lingual cingulum, and most significantly, the presence of a masseteric fossa high on the coronoid process, allows this specimen to be assigned to the Procynosuchidae. However, unlike most procynosuchids, precanine teeth are absent and the incisors are represented by four left and five right upper and probably, three lower teeth. Considering the small size of the new specimen from the *Tropidostoma* Assemblage Zone we identify it as a juvenile *Procynosuchus delaharpeae*, the only species currently recognized in the genus. The low number of incisors and absence of precanines in this specimen are interpreted as ontogenetic variation (i.e. juvenile characters). This discovery extends the biostratigraphic range of *Procynosuchus*, as it is now recorded in three assemblage zones, indicating that this taxon is the longest-lived cynodont in the Karoo Basin. The new specimen of *Procynosuchus* and the recently described *Charassognathus gracilis*, are the oldest global records of cynodonts, and indicate an earlier initial radiation of this lineage than was previously thought.

Keywords: *Procynosuchus*, Cynodontia, South Africa, biostratigraphy, Late Permian.

INTRODUCTION

The importance of non-mammaliaform cynodonts in understanding the origin and evolution of mammals is well established. They display several features that illustrate the gradual acquisition of mammalian characteristics and are closely related to Mammaliaformes (=mammals of many authors including for example Hopson & Barghusen 1986 and Kielan-Jaworowska *et al.* 2005). Until recently, the earliest representatives of this group were known from the latest Late Permian (Wuchiapingian-Changhsingian, Catuneanu *et al.* 2005) of South Africa, Zambia, Tanzania, Germany and Russia (Kemp 1979; Tatarinov 1968, 1987, 2004; Sues & Boy 1988; Van Heerden & Rubidge 1990; Rubidge 1995; Battail & Surkov 2000; Abdala & Allinson 2005). A maximum of five non-mammaliaform cynodont taxa (although two are dubious; see Abdala & Allinson 2005: Table 1) are found in the *Dicynodon* Assemblage Zone (AZ) of the Karoo Basin, representing one of the most diverse Late Permian fauna. However, a new cynodont, *Charassognathus gracilis* from levels of the older *Tropidostoma* AZ (Teekloof Pass near Fraserburg) of the Karoo Basin was recently described (Botha *et al.* 2007). In addition, the record of *Procynosuchus*, previously restricted to the *Dicynodon* AZ (Rubidge & Sidor 2001; Sidor & Smith 2004), has recently been extended to the uppermost *Cistecephalus* AZ (Botha *et al.* 2007).

Here we present a new cynodont record consisting of a skull and articulated mandible recovered from Leeu Kloof 43, Beaufort West District, Western Cape Province, South Africa by J.W. Potgieter in 2002. The new material was collected from the *Tropidostoma* AZ and has features that allow it to be identified as a procynosuchid. The new record indicates an early phase of cynodont diversification in the *Tropidostoma* AZ, suggesting a more ancient origin of this group in South Africa than was previously thought.

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MATERIALS AND METHODS

The new specimen (SAM-PK-K10138) consists of a complete skull of a small individual. It is dorso-ventrally compressed and cracked. Both upper dental series are visible, but the left teeth are better preserved.

Material of the following taxa was examined for comparison:

Charassognathus gracilis: SAM-PK-K10369; *Cynosaurus suppostus*: AM 4947; BMHN R1718; SAM-PK-4333; BP/1/3926, 4469; *Dvinia prima*: casts of the holotypic snout (UMZC T.1016) and of the complete skull of the holotype of *Permocynodon sushkini* (UMZC T.299); *Nanictosaurus kitchingi*: TM 279; RC 47 and *Procynosuchus delaharpeae*: BP/1/226, 591, 650, 1545, 1559, 2600, 3758, 5832; OUMNH TSK34; RC 5, 12, 72, 92, 132; SAM-PK-K-338, K8511, K10395; UMCZ T.810.

Table 1. Cranial measurements of SAM-PK-K10138 (in mm).

Basal skull length	56.1
Snout length	27
Orbital length	11.4
Temporal region length	18.6
Interorbital distance	17
Transverse process width	17.7
Maxillary bicanine width	21.7
Upper postcanine row length	12.2
Mandibular length	51

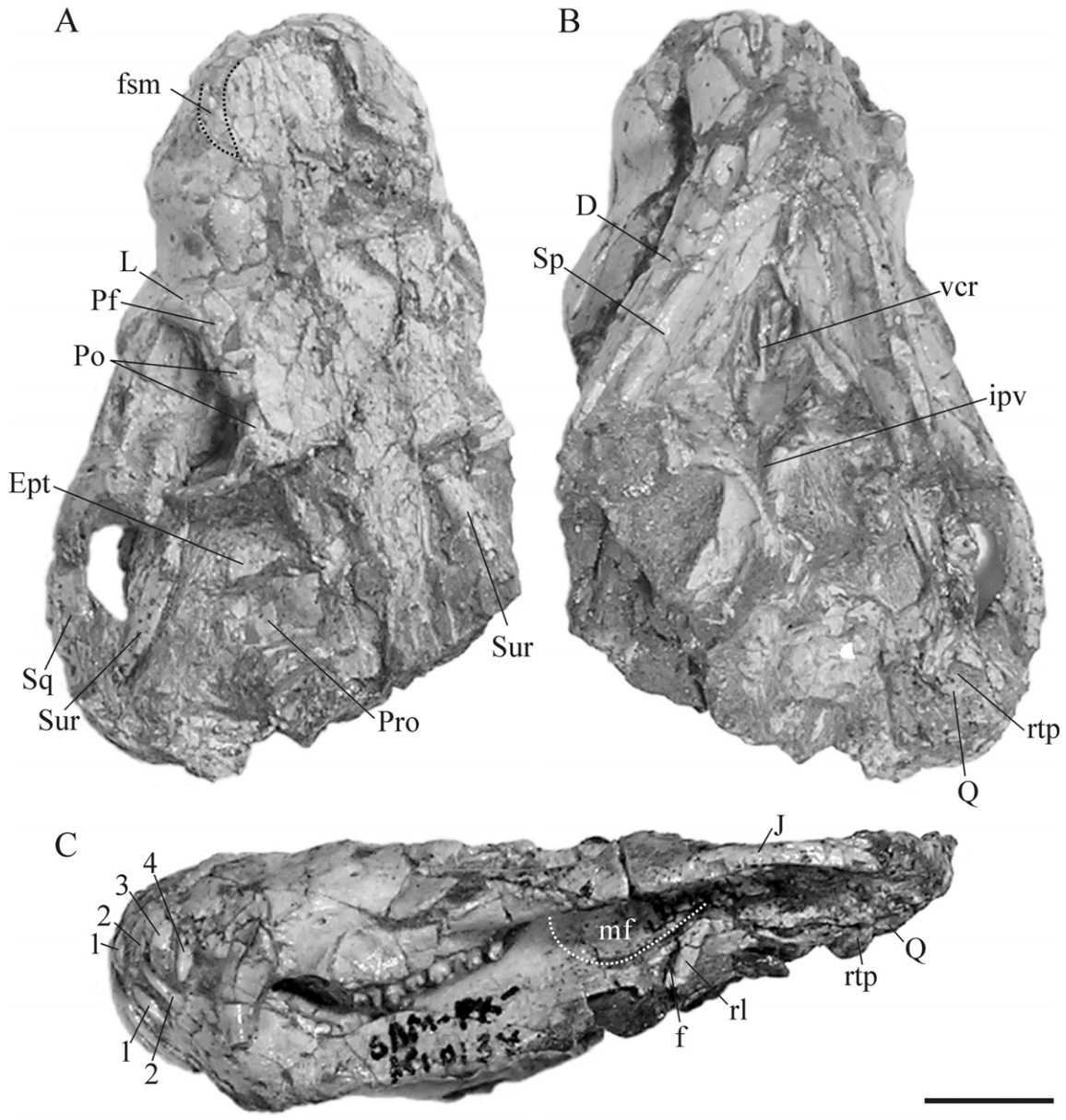


Figure 1. SAM-PK-K10138. **A**, dorsal, **B**, ventral, and **C**, left lateral views. Abbreviations: D, dentary; f, foramen between the dentary and the angular; fsm; facial process of the septomaxilla; ipv, interpterygoid vacuity; L, lacrimal; mf, masseteric fossa; Pf, prefrontal; Po, postorbital; rl, reflected lamina of the angular; Sp, splenial; Sq, squamosal; Sur, surangular; vcr, vertical crest of the vomer. Arabic numbers indicate left upper and lower incisors. Scale bar = 10 mm.

DESCRIPTION

The small (56.1 mm long) skull has a triangular overall morphology, with the snout somewhat longer than the temporal region (see Table 1) and the maximum width located in the middle of the temporal region (Fig. 1A). The skull is dorso-ventrally crushed with most of the bones showing fractures (see Fig. 1), although some sutures can be observed. The lower jaw is tightly occluded to the skull, but some preparation was possible around the upper postcanine series that allowed an almost complete view of the crowns.

In anterior view, the internasal process of the premaxilla is extended between the nasals, and a well-developed facial process of the septomaxilla can be observed on the left side of the skull (Fig. 1A). There are a series of nutritive foramina on the maxilla in the region adjacent to the canines and one large foramen placed posteriorly to these. The lacrimal is particularly short and the inter-orbital region is wide (Fig. 1A). The parietal foramen is not visible, probably due to crushing. A slender left zygomatic arch is preserved, lacking a suborbital angulation or descendent process (Fig. 1C). Only a small fragment of the left epipterygoid is preserved as a laminar bone. The prootic is visible on the left side and consists of a flat bone situated below the parietal.

In palatal view (Fig. 1B), a wide posterior portion of the vomer is visible and the median crest is directed ventrally. The palatal processes of the palatines do not meet in the midline, indicating that a complete secondary osseous palate was absent. A triangular interpterygoid vacuity is present, followed by a wide basicranial girder. The craniomandibular articulation on the left side is poorly preserved, but a remarkably large quadrate/quadratojugal complex is observed.

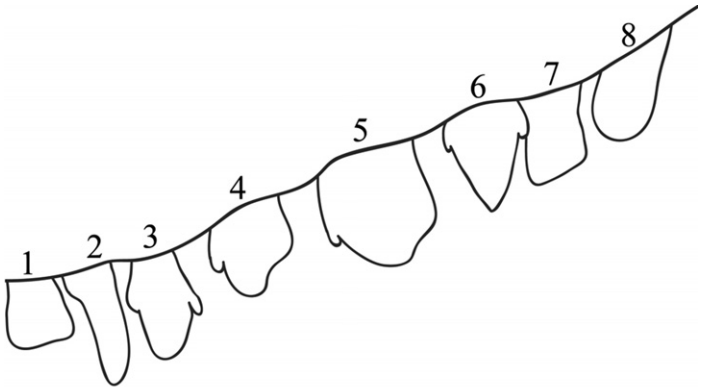


Figure 2. Left upper postcanine series of SAM-PK-K10138. Scale bar = 2 mm.

The anterior lower jaw has an unfused symphysis and many nutritive foramina. The coronoid process of the dentary is low and the masseteric fossa, which lies high on the coronoid process, can be observed on both sides of the lower jaw (Fig. 1C). The posterior margin of the dentary extends to approximately the middle of the temporal fossa. The surangular is a narrow strip of bone dorsal to the angular, extending back to the level of the craniomandibular joint (Fig. 1C). The anterodorsal portion of the left reflected lamina of the angular is preserved, showing a well-developed upward and posteriorly directed crest. A small fossa between the dentary and the angular is present. The posterior portion of the reflected lamina is not preserved and the lateral face of the angular can be seen below the surangular. The left postdentary bar is complete, showing a rounded and well-developed retroarticular process of the articular in ventral view (Fig. 1B, C). On the ventral margin of the horizontal rami, sutures separate the dentary laterally from a large splenial medially.

Four conical upper incisors are observed on the left side of the premaxilla (Fig. 1C), whereas on the right side there is a space with an erupting first incisor, followed by three incisors, and a small tip of an erupting fifth tooth. Two leaf-shaped lower incisors are preserved on both sides, but there is additional space for a third. The fourth upper incisor is smaller than the previous three and there is a small diastema between this tooth and the upper canine (Fig. 1C). Serrations are absent from both the incisors and canines. There is no evidence of precanines. A diastema is also visible between the upper canine and the postcanine dentition. Eight left (Fig. 2) and six right tricuspidate upper postcanines are preserved. The first, seventh, and eighth left postcanines are poorly preserved and do not provide any useful information. The second postcanine is cone-shaped and appears to have only an anterior accessory cusp. Anterior and posterior accessory cusps are present on the third, fourth and fifth postcanines. The sixth postcanine is in eruption and has a high, upwardly directed main cusp, with anterior and posterior accessory cusps placed at the same height on the crown (Fig. 2). On the right maxilla, most of the postcanine crowns are only partially preserved, but it is possible to observe that they are expanded lingually (i.e. circular in occlusal view), suggesting the presence of a lingual cingulum.

DISCUSSION

The record of a second cynodont from the *Tropidostoma* AZ represents an important increase in our knowledge of early cynodont evolution. The triconodont pattern of the postcanines seen in labial view, i.e. a dominant main cusp, with anterior and posterior accessory cusps (also present in *Charassognathus gracilis*), is the oldest postcanine morphology in cynodonts.

Late Permian cynodonts from South Africa and Russia are diverse, with at least four species in each region (Abdala & Allinson 2005). South Africa contains *Procynosuchus delaharpeae, Cynosaurus suppostus, Nanictosaurus kitchingi* and, the recently described, *Charassognathus gracilis* (Botha *et al.* 2007). Russia includes *Cyrbasiodon vladimiriensis, Uralocynodon tverdokhlebovae, Dvinia prima* and *Nanocynodon seductus,* although due to their dental similiarities, the first two species may in fact represent a single taxon.

Procynosuchids (including *Procynosuchus delaharpeae, Cyrbasiodon vladimiriensis* and *Uralocynodon tverdokhlebovae,* see Tatarinov 1987, 2004; Battail & Surkov 2000) have bucco-lingually expanded postcanines that are circular in occlusal view, whereas those of *Dvinia prima* are transversely ovate. In *Nanictosaurus kitchingi* and *Nanocynodon seductus,* the ellipsoid postcanines are clearly more laterally compressed than in procynosuchids and *D. prima,* but they also display cingular cusps on the lingual margin (Van Heerden & Rubidge 1990; Battail & Surkov 2000). In *Cynosaurus suppostus,* the postcanines are simple, ovoid in shape and lack a cingulum. In *Charassognathus gracilis,* the occlusal morphology of the upper postcanines cannot be determined because the upper teeth are preserved in tight occlusion with the lower postcanines.

Most of these early cynodonts show triconodont postcanines when observed labially. *Charassognathus gracilis, Nanictosaurus kitchingi* and *Nanocynodon seductus* have high main cusps with smaller anterior and posterior accessory cusps low on the crown (Van Heerden 1976; Van Heerden & Rubidge 1990; Battail & Surkov 2000; Botha *et al.* 2007). However, some variation does exist in the height of the main cusp and the development of the accessory cusps on the crown. In *C. gracilis,* the accessory cusps are exceptionally tiny and the anterior accessory cusp is placed slightly higher than the posterior accessory cusp (Botha *et al.* 2007). In *Nanictosaurus kitchingi* and *Nano-*

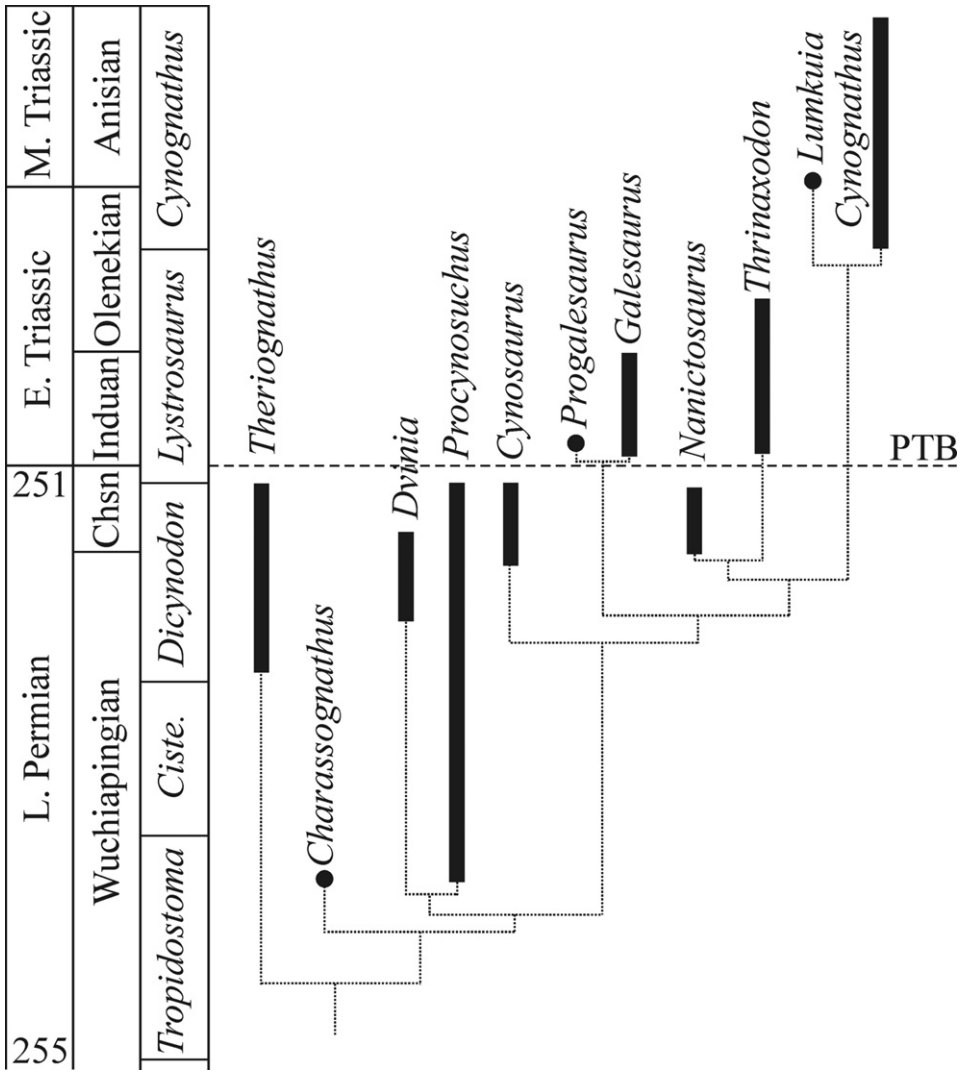


Figure 3. Extended biostratigraphic range and phylogenetic position of *Procynosuchus* plotted against the South African Permo-Triassic biostratigraphy. Vertical bars and solid circles indicate taxon ranges and single specimen occurrences, respectively. Abbreviations: Chsn, Changhsingian; *Ciste., Cistecephalus* Assemblage Zone; PTB, Permo-Triassic boundary. Numbers indicate million years ago. Stratigraphic chart follows Catuneanu *et al.* 2005. (Modified from Botha *et al.* 2007.)

cynodon seductus the accessory cusps are more distinctive and are placed at the same level on the crown (Van Heerden & Rubidge 1990; Battail & Surkov 2000). In contrast, the postcanines of *Cynosaurus suppostus* have a posterior accessory cusp, and even a second posterior accessory cusp in the posterior-most teeth, whereas the anterior accessory cusp is barely visible (see Van Heerden, 1976: figs 14–19). Procynosuchids also have three cusps visible in labial view, but the main cusp is not very high compared to the accessory cusps.

Some variations in features of the anterior dentition of basal cynodonts are well known. *Procynosuchus delaharpeae* and *Dvinia prima* have five or more upper and four or more lower incisors, whereas the majority of cynodonts have four upper and three lower incisors (Hopson & Barghusen 1986; Hopson & Kitching 2001). This is also the case in *Charassognathus gracilis, Nanictosaurus kitchingi, Cynosaurus suppostus* and *Nanocynodon seductus*; the latter species are known only from a mandible with three incisor alveoli (Tatarinov 1987; Van Heerden & Rubidge 1990; Botha *et al.* 2007). In addition, *P. delaharpeae* and *D. prima* are the only cynodonts in which the presence of upper precanine teeth on the maxilla in front of the canine was reported (Tatarinov 1968; Hopson & Kitching 1972; Hopson & Barghusen 1986; Kemp 1979).

The triconodont morphology can be clearly observed in the third and erupting sixth postcanines of SAM-PK-K10138. They exhibit a high main cusp, and anterior and posterior accessory cusps placed at the same height on the crown (Fig. 2). The right postcanine crowns are broken, and careful preparation revealed that the teeth were expanded lingually, suggesting the presence of a lingual cingulum. This morphology closely resembles that observed in postcanines of *Procynosuchus* (Kemp 1979). The presence of the postcanine pattern described above, combined with primitive cynodont features such as the interpterygoid vacuity, a masseteric fossa high on the coronoid process and incomplete secondary palate indicate that SAM-PK-K10138 is a specimen of *Procynosuchus delaharpeae*. However, notable differences exist between the anterior dentition of the new individual and *P. delaharpeae.* SAM-PK-K10138 has five right and four left upper incisors, most likely three lower incisors, and no precanines. Hopson and Kitching (1972) synonymized

several species of basal cynodonts proposed mostly by Broom, as members of *Procynosuchus delaharpeae.* This lumping exercise resulted in a neater taxonomy because many species erected by Broom were based on poorly preserved fossils with no proper diagnostic features or size related characters that may have been related to ontogeny. Hopson & Kitching's (1972) proposal presented a general diagnosis for cynodont families and a list of valid species with synonymy, but individual variations in valid taxa were not thoroughly discussed. Five or more upper and four lower incisors, as well as the presence of precanines were considered as diagnostic features of procynosuchids by Hopson & Kitching (1972) and are widely accepted as typical characters of this group (e.g.; Hopson & Barghusen 1986; Sidor & Hopson 1998; Sidor & Smith 2004). BP/1/650 is a small specimen (approximately 5 mm in basal skull length) originally described as *Protocynodon pricei* by Broom (1949; see also Mendrez 1972), and was included in the synonymy of *P. delaharpeae* by Hopson & Kitching (1972). This specimen was described originally as having six incisors and no precanines (Broom 1949), whereas Mendrez (1972) redescribed the specimen indicating the presence of five or six incisors and one or two precanines. First hand examination of BP/1/650 demonstrates the presence of five upper incisors and no precanines on the right side (the anterior dentition is not preserved on the left side). However, examination of other juvenile and adult specimens assigned to *Procynosuchus delaharpeae* (Rubidge Collection and the Bernard Price Institute Collection) indicates that precanines are usually present and can vary from one to three teeth. SAM-PK-K10138 and BP/1/650 are about the same size (approximately 60 mm), well below the 140 mm skull length of the largest specimens of *P. delaharpeae.* Considering these skull size differences, we interpret the unexpected features in the anterior dentition of SAM-PK-K10138 and BP/1/650 as individual variation, probably related to ontogeny.

IMPLICATIONS FOR EARLY CYNODONT DIVERSITY

Procynosuchus, the most abundant cynodont amongst the Late Permian *Dicynodon* AZ fauna of South Africa, was also recently reported from the uppermost *Cistecephalus* AZ (Botha *et al.* 2007). The discovery reported here results in *Procynosuchus* being the first and only cynodont to have crossed two assemblage zone boundaries in the Karoo Basin. In addition, it is also the only cynodont to have had a global distribution at the end of the Permian, when this group was represented by at least six different taxa in a clear diversification phase (Abdala & Allinson 2005). The discovery of this taxon in the older *Tropidostoma* AZ represents an important biostratigraphic extension of its range, and confirms that it is the longest-lived cynodont from the Karoo Basin. This finding also has important implications for early cynodont diversity, when results of recent phylogenies proposing sister group relationships between *Procynosuchus* and the Russian *Dvinia* (Abdala 2007; Botha *et al.* 2007; Fig. 3) are considered. The record of *Procynosuchus* in the *Tropidostoma* AZ suggests a ghost extension of the Russian taxon to the same age, indicating that cynodonts had already begun a process of incipient diversification and dispersion, by the early Late Permian, far earlier than previously thought.

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INSTITUTIONAL ABBREVIATIONS

AM	Albany Museum, Grahamstown.
BMNH	Natural History Museum, London.
BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.
OUMNH	Oxford University Museum of Natural History, Oxford.
RC	Rubidge Collection, Wellwood, Graaff-Reinet.
SAM-PK	Iziko South African Museum, Cape Town.
TM	Transvaal Museum, Northern Flagship Institution, Pretoria.
UMZC	University Museum of Zoology, Cambridge.

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