

The taxonomic status of *Parathrinaxodon proops* (Therapsida: Cynodontia), with comments on the morphology of the palate in basal cynodonts

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The holotype and only specimen of *Parathrinaxodon proops*, a cynodont from the Upper Permian Kawinga Formation, Tanzania, is redescribed. Upper postcanines from the middle of the tooth row are ovoid in outline, presenting a large main cusp and tiny anterior and posterior accessory cusps on the sectorial margin. Anterior and posterior lingual cusps on the crown indicate the presence of a lingual cingulum. The overall postcanine morphology is remarkably similar to that of *Procynosuchus delaharpeae*, a Late Permian cynodont particularly common in the lower Beaufort Group of South Africa. The presence of a complete osseous palate and a medial palatal opening between the maxillae (=vomerine fossa) in *Parathrinaxodon proops* remain the main differences previously reported between this species and *Procynosuchus delaharpeae*. Restudy of the palate of *Parathrinaxodon proops* indicates that there exists some degree of deformation, particularly notable in the broken and distorted vomer. The supposed presence of the complete secondary palate and of the medial palatal opening in *Parathrinaxodon proops* are interpreted as resulting from a slight horizontal displacement of the long, and originally free, palatal processes of the maxilla and palatine. It is concluded that *Parathrinaxodon proops* is synonymous with *Procynosuchus delaharpeae*. This synonymy is problematic because *Parathrinaxodon proops* Parrington 1936 would have priority over *Procynosuchus delaharpeae* Broom 1937, but the latter is the best known Late Permian cynodont. Consequently, we propose to conserve *Procynosuchus delaharpeae* as the valid name for this cynodont based on article 23, section 9 (Reversal of precedence) of the International Code of Zoological Nomenclature. An analysis of the Kawinga fauna, using genus as the taxonomic unit for comparison, indicates strong similarity (67%) with faunas from the *Tropidostoma*, *Cistecephalus* and *Dicynodon* assemblage zones from the South African Karoo.

Keywords: *Parathrinaxodon*, *Procynosuchus*, Late Permian, Tanzania, cynodonts.

INTRODUCTION

Late Permian cynodonts, besides representing the earliest record of the group, are the phylogenetically most basal members of the Cynodontia, the monophyletic group that includes extant mammals. Ten species of Late Permian cynodonts have been recognized since 1972, the year in which Hopson & Kitching (1972) published their revision of cynodonts, and Mendrez (1972a,b) redescribed and discussed the identity of two South African Late Permian cynodonts. At least six of the 10 Late Permian cynodonts have a disputed taxonomic status (Table 1). Cynodonts of this age are recorded in South Africa (Broom 1938, 1948), Russia (Sushkin 1927; Tatarinov 1968a,b), East Africa (Kemp 1979; Parrington 1936), and, most recently, Germany (Sues & Boy 1988).

In East Africa, basal cynodonts of Late Permian age are known from the Madumabisa Mudstones from the Luangwa Valley in Zambia (Kemp 1979) and the Kawinga Formation (=Usili Formation; Wopfner 2002) of the Ruhuhu Valley, Tanzania (Parrington 1936). The only specimen known from the former rock unit is an almost complete skeleton assigned to *Procynosuchus delaharpeae* Broom by Kemp (1979), and which represents a juvenile individual (Abdala, pers. obs.). Specimens from the Ruhuhu Valley include an incomplete skull described by Parrington (1936) as *Parathrinaxodon proops*, and an incomplete and poorly preserved skull attributed by von Huene

(1950) to *Procynosuchus delaharpeae*.

Since its description, the affinities of *Parathrinaxodon*

Table 1. Taxonomy and distribution of Late Permian cynodonts.

Taxon	Country
<i>Cynosaurus suppostus</i> (Owen 1876)	SA
<i>Dvinia prima</i> Amalitzky 1922	R
<i>Cyrbasiodon boycei</i> Broom 1931 ^a	SA
<i>Parathrinaxodon proops</i> Parrington 1936	T
<i>Nanictosaurus kitchingi</i> Broom 1936 ^b	SA
<i>Procynosuchus delaharpeae</i> Broom 1937	SA, T, Z, G ^f
<i>Protocynodon pricei</i> Broom 1949 ^c	SA
<i>Nanocynodon seductus</i> Tatarinov 1968 ^d	R
<i>Uralocynodon tverdokhlebovae</i> Tatarinov 1987	R
<i>Cyrbasiodon vladimiriensis</i> Tatarinov 2004 ^e	R

^aConsidered a synonym of *Procynosuchus delaharpeae* by Hopson & Kitching (1972), and Battail (1991). Taking into account the poor preservation of the type and only specimen of *Cyrbasiodon boycei*, Hopson & Kitching (1972) retained *P. delaharpeae* as the valid name for the species. Mendrez (1972b) considered *C. boycei* as a valid taxon.

^bConsidered a synonym of *Cynosaurus suppostus* by Hopson & Kitching (1972) and Sidor & Smith (2004), it was regarded as a valid species by Van Heerden & Rubidge (1990). *Nanictosaurus rubidgei* Broom 1940 (regarded as a valid species by Van Heerden 1976) and *Nanictosaurus robustus* Broom 1940 were considered as junior synonyms of *N. kitchingi* by Van Heerden & Rubidge (1990).

^cConsidered a synonym of *Procynosuchus delaharpeae* by Hopson & Kitching (1972) and Battail (1991), it was regarded as a valid species by Mendrez (1972a).

^dConsidered as Galesauridae (at that time including *Thrinaxodon*) by Tatarinov (1968b) and most recently as *Thrinaxodontidae* by Battail & Surkov (2000). Hopson & Kitching (1972) included it in *Procynosuchidae*.

^e*Cyrbasiodon* was considered a synonym of *Procynosuchus* by Hopson & Kitching (1972) and Battail (1991). See 'a' above.

^fThe specimen from Germany was identified as *Procynosuchus* sp. by Sues & Boy (1988).

Abbreviations: G: Germany; R: Russia; SA: South Africa; T: Tanzania; Z: Zambia.

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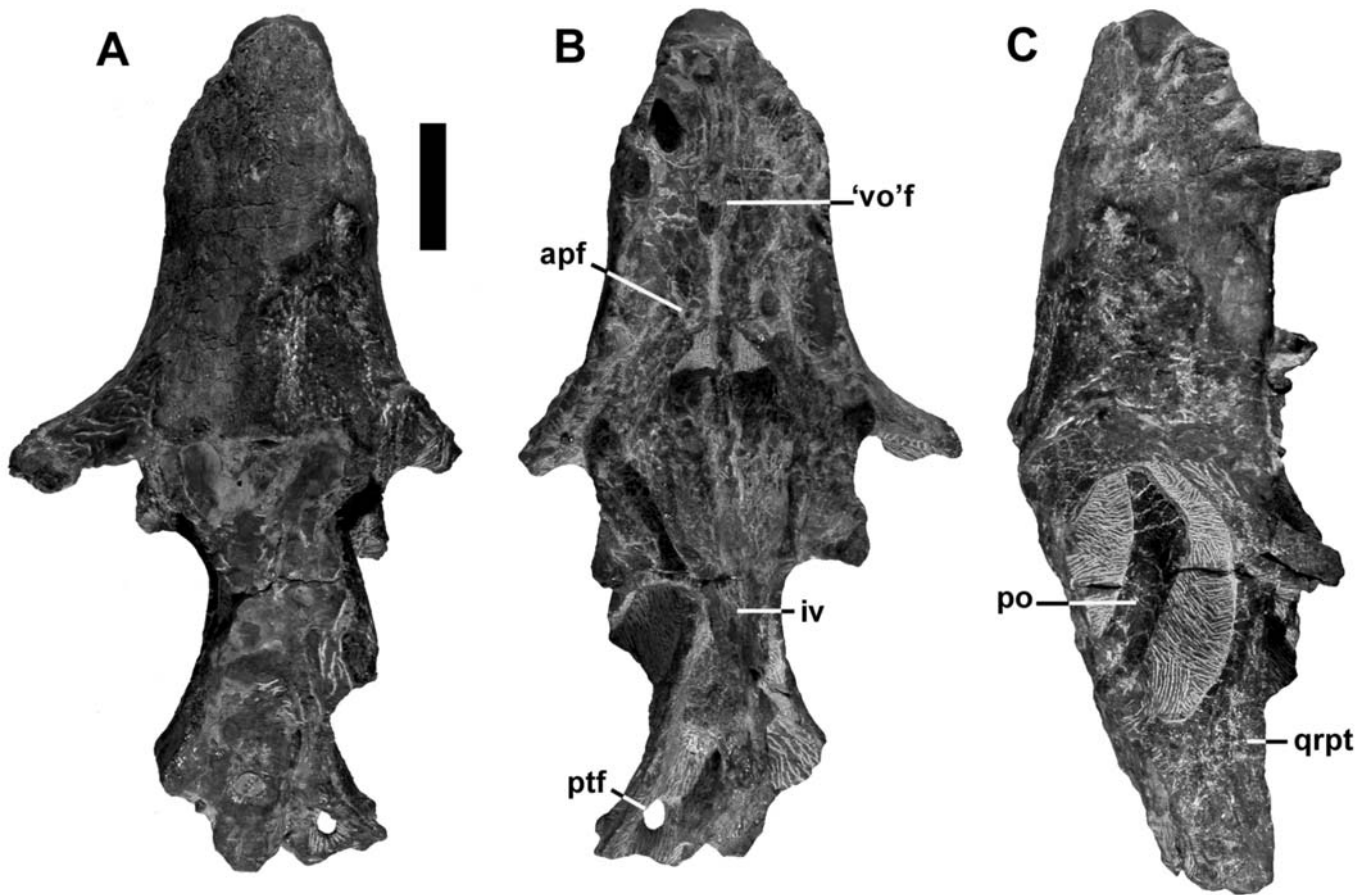


Figure 1. A, dorsal, B, ventral, and C, right lateral views of *Parathrinaxodon proops* holotype, UMZC T.810. Abbreviations: apf, anterior palatal foramen; iv, interpterygoid vacuity; po, displaced portion of the postorbital bar; ptf, pterygoparoccipital foramen; qrpt, quadrate ramus of the pterygoid; 'vo'f: vomeric fossa. Scale bar = 2 cm.

proops have been subject to differing interpretations. Parrington (1936) believed it to be most similar to *Dvinia prima* from the Russian Upper Permian and to *Thrinaxodon liorhinus* from the Lower Triassic of South Africa. Parrington (1936) also suggested that *Cyrbasiodon boycei* was probably related to *Parathrinaxodon proops*. Hopson & Kitching (1972) and Mendrez (1972a,b) included the species in the family Procynosuchidae, whereas Van Heerden (1976) suggested it is a member of the Galesauridae. Battail (1982, 1991) also implied a more derived position for *Parathrinaxodon* than for *Procynosuchus* and *Dvinia*, whereas Hopson (1991; see also Sidor & Smith 2004) considered it indistinguishable from *Procynosuchus*.

Here we present a descriptive update of the holotype and only known specimen of *Parathrinaxodon proops* and discuss its taxonomic identity. We have avoided a complete redescription of the specimen and instead refer the reader to Parrington (1936) for more details. In addition, we propose an explanation for the presence of the 'vomeric fossa' in the palate of Late Permian cynodonts. We also compare the Kawinga fauna with Late Permian faunas from the South African Karoo.

Institutional abbreviations: BMNH, The Natural History Museum, London; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; OUMNH, Oxford University Museum of Natural History; RC, Rubidge collection, Wellwood, Graaff-Reinet; SAM, Iziko Museums (South African

Museum), Cape Town; UMZC, University Museum of Zoology, Cambridge.

MATERIAL

The holotype of *Parathrinaxodon proops* (UMZC T.810) is represented by a partial skull lacking both zygomatic arches, part of the brain case and the lower jaw (Figs 1 & 2). The following comparative materials of *Procynosuchus delaharpeae* were also consulted: BP/1/226, 591, 1545, 1559, 2600, 3758, 5832; OUMNH TSK34; RC 5, 12, 72, 92, 132; SAM-PK-K-338, K8511. Sources of information on the Russian cynodont *Dvinia prima* included Tatarinov (1968b) and casts of the holotype (UMZC T.1016) represented by a snout, and of the complete skull originally assigned to *Permocynodon sushkini* (UMZC T.299; see Tatarinov 1968b).

DESCRIPTION

The basicranial length of UMZC T.810 is estimated to be 130 mm, with a snout length of 53 mm and the palate reaching approximately 45 mm (Table 2). The dorsal bones of the skull are preserved only as far posteriorly as the anterior orbital margin, whereas the skull is almost complete ventrally, lacking only the posterior portion of the basicranium (Figs 1 & 2). Zygomatic arches from both sides are missing. The tips of the dorsal processes of both premaxillae are preserved between the anterior portions of the nasals (Fig. 2A). Additional preparation of the material revealed a displaced portion of the right postorbital bar in

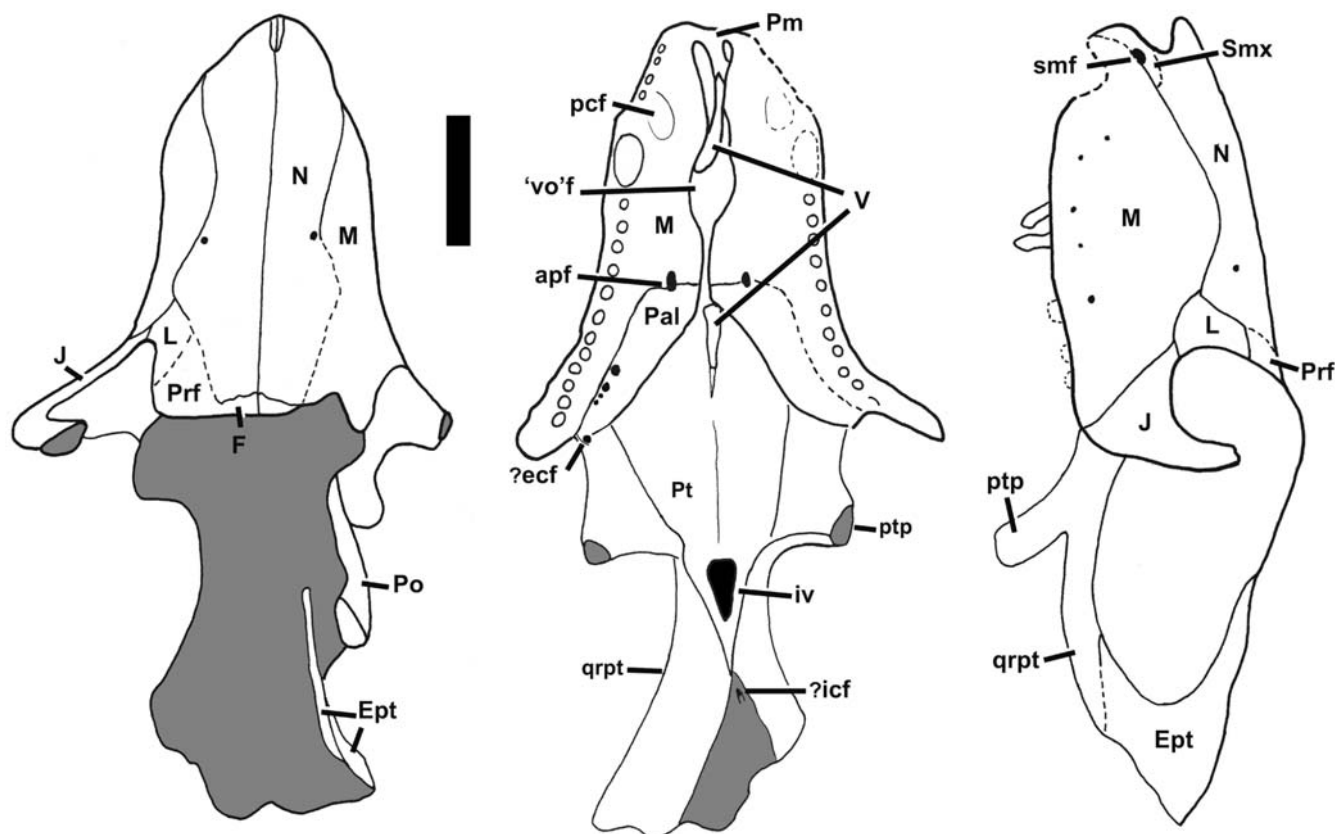


Figure 2. Interpretative drawings of *Parathrinaxodon proops*. **A**, dorsal, **B**, ventral, and **C**, left lateral views. Abbreviations: apf, anterior palatal foramen; ?ecf, ectopterygoid foramen; Ept, epipterygoid; F, frontal; ?icf, internal carotid foramen; iv, interpterygoid vacuity; L, lacrimal; M, maxilla; N, nasal; Pal, palatine, pcf, paracanine fossa; Pm, premaxilla; Po, displaced portion of the postorbital bar; Pt, pterygoid; ptf, pterygoparoccipital foramen; ptp, pterygoid process; qrpt, quadrate ramus of the pterygoid; smf, septomaxillary foramen; Smx, septomaxilla; V, vomer; 'vo'f, vomerine fossa. Shading indicates broken bone surface; dashed lines indicate broken bone and interpreted sutures. Scale 2 cm.

the middle of the interorbital region (Figs 1C & 2A).

In the anterior portion of the palate, the vomer is broken and somewhat displaced (Figs 2B & 3A). It is not possible to recognize sutures between the premaxilla and the maxilla. A median fossa between the maxillae is observed from the level of the anterior border of the canine, which extends to the level of the third postcanine and appears limited posteriorly by the palatal processes of the maxillae (Figs 2B & 3A). The palatal processes of the maxillae and palatines are very close to, but not in contact with, their counterparts. Well developed anterior palatal foramina indicate the location of the suture between the maxilla and the palatine. The latter bone has very short palatal projections, whose anterior portions lie close to each other, whereas the posterior portions are widely separated,

forming part of the ventral margin of the choana (Figs 1B, 2B & 3A). There is a series of foramina in the palatal process of the palatine, close to the suture with the maxilla (Fig. 2B). Similar foramina are also seen in *Procynosuchus* (Kemp 1979: fig. 2; RC 5). A foramen at the base of the transverse process of the pterygoid is interpreted as an ectopterygoid foramen, but sutural margins of the ectopterygoid are not discernible.

The basicranial girder is wide and an interpterygoid vacuity exists anteriorly between the well-developed ridges of the pterygoid (Figs 1B & 2B). The suture between the quadrate ramus of the pterygoid and epipterygoid is visible on the right side of the skull, and the quadrate ramus of the pterygoid is considerably extended posteriorly.

There are four right incisor-like teeth, and considering the incomplete preservation of the anterior portion of the snout, one or two more teeth could have been present as suggested by Parrington (1936). The anterior extension of the maxilla, as far as the level of the septomaxillary foramen in lateral view (Fig. 2C), indicates that two of these teeth are possibly implanted in the maxilla. It is not possible, however, to identify the premaxilla-maxilla suture in the palate in order to determine if these elements are indeed maxillary precanines. The second incisor-like tooth is the best preserved and is simple and conical. There is no clear evidence, except perhaps the better state of preservation, that this tooth could be in an emergent state as suggested by Parrington (1936). There are 10 left

Table 2. Skull and snout lengths (in mm), percentage of the snout in relation to the basal skull length and number of upper postcanines in the larger specimens of *Procynosuchus delaharpeae* and in *Parathrinaxodon proops* (in bold).

Specimen	Basal skull length	Snout length	Snout/basal skull length	Postcanine number
RC 5	129	54	41%	10
UMCZ T810	130*	53	41%	10/11
RC 130	132	56	42%	10/11
BP/1/3748	142	66	46%	10
RC 92	144	64	44%	9?10

/: different number of postcanines in left and right sides of the skull;

?: uncertainty in the number of teeth;

*: estimated measurement.

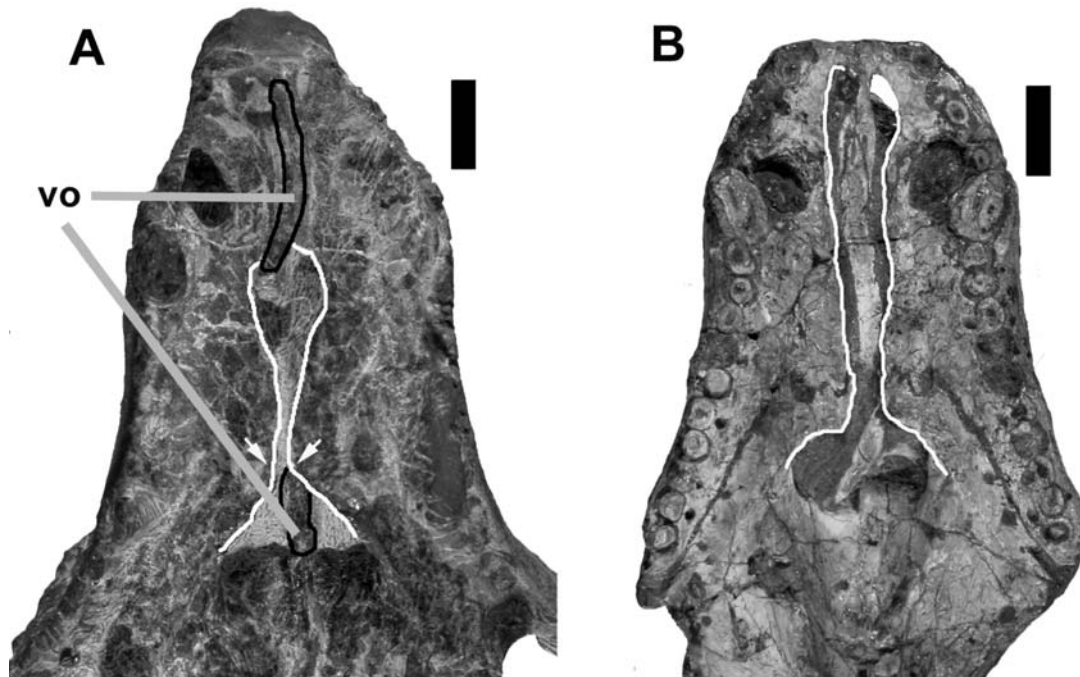


Figure 3. Palate of **A**, *Parathrinaxodon proops* (UMZC T810), and **B**, *Procynosuchus delaharpeae* (RC 5). The medial borders of the palatal processes are highlighted in white. The arrows in **A** indicate the region where deformation has brought together the palatal processes of the maxillae and the palatines to produce the vomerine fossa (see text for details). Abbreviations: vo, broken and distorted vomer in *Parathrinaxodon proops*. Scale bars = 1 cm.

and 11 right postcanines, the anteriormost of which (first and third) are simple, possessing a main cusp with small anterior and posterior accessory cusps. A crenulated ridge is observed on the posterior border of the tooth crown. An isolated postcanine crown corresponding to the sixth left postcanine is slightly expanded bucco-lingually and ovoid in crown view (Fig. 4A). The tooth has a broken main cusp, with tiny anterior and posterior accessory cusps at the same level on the crown, both of which are similarly developed. A partially preserved lingual cingulum with one posterior and two anterior cusps is also recognized. Part of the anterior portion of the cingulum is broken, whereas the posterior portion seems to have been affected by wear (Figs 4A & 4B).

DISCUSSION

Parrington (1936) regarded *Parathrinaxodon proops* as being most similar to *Dvinia prima* from the Late Permian of Russia. The similarities included the relatively small snout, the anteriorly oriented orbits, the dental formula, and, in particular, the nature of the postcanine crowns. In addition, he found these two taxa to be similar to the Early Triassic *Thrinaxodon* because of the postcanine tooth morphology (i.e. a large main cusp and small accessory anterior and posterior cusps; lingual cingular cusps), and suggested a close relationship between them. Finally, Parrington (1936) also suggested that *Cyrbasiodon boycei* was related to *Parathrinaxodon*, *Dvinia* and *Thrinaxodon*. At that time, *C. boycei* was considered a therocephalian; it is currently included with procynosuchid cynodonts, though there is disagreement on its taxonomic identity (see Table 1). After the description of *P. proops*, Broom (1937, 1938, 1948) described several new cynodonts from the Late Permian of South Africa, all of which are now regarded as synonymous with *Procynosuchus delaharpeae*

(Hopson & Kitching 1972; Battail 1991). Mendrez (1972a,b) considered *P. proops* to be a procynosuchid and regarded the contact of the posterior portions of the palatal processes of the maxillae, the presence of a narrow median slit in the

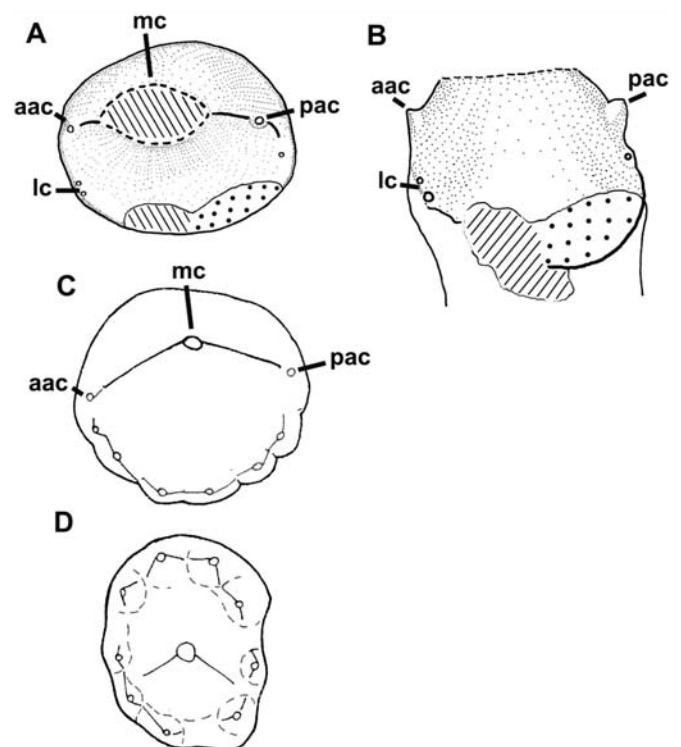


Figure 4. **A**, crown, and **B**, lingual views of the left upper sixth postcanine of *Parathrinaxodon*; **C**, crown view of the left upper second postcanine of *Procynosuchus*; **D**, crown view of left upper twelve postcanine of *Dvinia*. Abbreviations: aac, anterior accessory cusp; lc, lingual cingulum; mc, main cusp; pac, posterior accessory cusp. Hachure indicates broken tooth surface; heavy stipples indicate possible wear facet. In **A**, **C** and **D** anterior is to the left and lingual to the bottom. Figures 3C and 3D after Crompton (1972).

Table 3. Differences previously proposed between *Parathrinaxodon proops* and *Procynosuchus delaharpeae* (Mendrez 1972a,b; Battail 1991) and condition of those characters in *P. proops* after this study (in bold).

	<i>P. proops</i>	<i>P. delaharpeae</i>
Osseous secondary palate	Complete/ incomplete	Incomplete
Median slit in the anterior portion of the palate (=vomerine fossa)	Present/ absent	Absent
Precanine teeth	Absent/?	Present

anterior part of the palate and the absence of precanine teeth as the principal differences from *Leavachia duvenhagei* (= *P. delaharpeae*; see Table 3). Van Heerden (1976) included *P. proops* within the Galesauridae, which at that time also included *Thrinaxodon*. Features in *P. proops* supporting this assignment were the lack of an interpterygoid vacuity, the absence of precanine teeth, the lack of a prominent lingual cingulum on the postcanines and the presence of a complete secondary palate. Battail (1982, 1991) regarded the postcanine morphology of *P. proops* to be very similar to that of *P. delaharpeae*, but he considered the presence of the secondary palate and the absence of maxillary precanines in *P. proops*, as major differences between these species (Table 3).

Parathrinaxodon proops and *Procynosuchus delaharpeae* show ovoid to circular postcanines in crown view, with labial margins lacking cingula and large main cusps and smaller anterior and posterior accessory cusps (see Figs 4A & 4C). The lingual margin of the sixth left postcanine of *P. proops*, the only tooth in which it is possible to observe the lingual face of the crown, is not well preserved, but cusps forming a lingual cingulum are present. These dental features in *P. delaharpeae* and *P. proops* are remarkably distinct from those found in *Dvinia prima* (compare Figs 4A & 4C with Fig. 4D). In addition, the ovoid outline of the postcanine crown and the tiny size of the accessory cusps on the sectorial margin contrast with the antero-posteriorly enlarged postcanines of *Thrinaxodon liorhinus*, in which the accessory cusps are relatively larger (Crompton 1963). The postcanine morphology of *P. proops* thus represents the strongest evidence for conspecificity with *P. delaharpeae*. Other features of UMZC T.810 shared with *P. delaharpeae* are the number of postcanines and the

proportion of the snout in relation to overall skull length (see Table 2).

The most intriguing feature remaining in *P. proops* is the presence of an opening in the palate between the maxillae (Parrington 1936: fig. 8), a feature also described in the Russian cynodont *Dvinia prima*, where it was termed the vomerine fossa (Tatarinov 1968b: fig. 2). Careful study of UMZC T.810 shows that although at first sight the snout looks undistorted, the anterior portion of the palate shows that the vomer is broken and displaced from its original position, indicating some degree of deformation of the palate (Fig. 3A). Considering the position of the vomerine fossa in UMZC T.810, we suggest that this 'fossa' is the result of the medial dislocation of the palatal processes of the maxilla. A slight horizontal displacement of the long, and originally free, palatal processes of the maxilla and palatine in specimens of *Procynosuchus delaharpeae* (Fig. 3B) would result in the contact (or quasi contact) of these processes, producing an artefact similar to the vomerine fossa. Examination of a cast of the holotype of *Dvinia prima* (UMZC T.1016) seems to confirm Hopson's (1991) observation that the palatal processes of the maxilla and the palatine do not come into contact in this species (contra Tatarinov 1968b). The sum of evidence suggests that an open secondary palate was the condition present in the Late Permian cynodonts *Procynosuchus*, *Dvinia*, and *Cynosaurus*, and persisted in the Early Triassic *Galesaurus* and *Progalesaurus* (see Sidor & Smith 2004). On the other hand, *Nanictosaurus* is the only Late Permian cynodont evincing a closed secondary palate, in that there is a contact between the palatal processes of the maxillae and the palatines (van Heerden & Rubidge 1990). The Early Triassic *Thrinaxodon* also exhibits a closed secondary palate (Kemp 1982; Hopson & Kitching 2001; Sidor & Smith 2004), but it should be noted that some well-preserved specimens of this taxon (e.g. BMNH R 511, R 511a, R 3731; BP/1/5208; Fig. 5) show the palatal processes of the maxillae and the palatines adjacent to, but not actually in contact with, their counterparts. Comments about the lack of contact of the halves of the osseous secondary palate in *Thrinaxodon* were also made by Van Heerden (1972). In addition, this condition is also figured in the detailed description of the skull of *Thrinaxodon* (Fourie 1974: figs 1, 8B & 9), although Fourie (1974: 357)

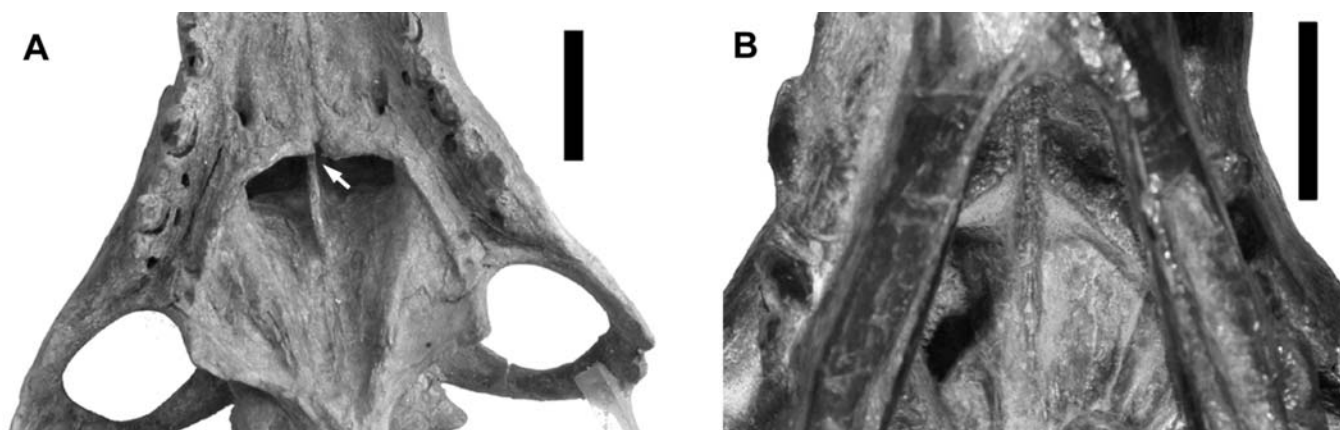


Figure 5. Palate of *Thrinaxodon liorhinus*. **A**, BMNH R.511, **B**, BP/1/5208. Arrow in **A** indicates palatal processes of the palatines close but not in contact. Note the vomer interposed between the palatal processes of the palatines in **B**. Scale bars = 1 cm.

Table 4. Tetrapod list and faunal analysis of the Kawinga Formation.

Kawinga taxa	Endemic	Shared with South Africa	Shared with Scotland	Total
Amphibia	1			1
Pareiasauria		2		2
Dicynodontia	2	3	1	6
Gorgonopsia	2	7		9
Terocephalia	1	1		2
Cynodontia		1		1
Total	6 (29%)	14 (67%)	1 (5%)	21

*: endemic taxa.

Abbreviations: C, *Cistecephalus* Assemblage Zone; CZ, *Cistecephalus* Zone; D, *Dicynodon* Assemblage Zone; T, *Tropidostoma* Assemblage Zone. The gorgonopsia *Tetraodontonius* is not included because of uncertainty in its taxonomic assignment. Data from King (1988), Sigogneau-Russell (1989), Gay & Cruickshank (1999), Maisch (2002), Maisch & Gebauer (2005) and Angielczyk (pers. comm., 2004). South African faunal assemblages after Rubidge *et al.* (1995), except for *Cistecephalus* Zone after Kitching (1977).

states 'the two halves of the palate meet each other in a sutura harmonia', that is to say, by means of a simple apposition of contiguous rough surfaces (Gray 1988). The unusual condition of the palate found in these specimens of *Thrinaxodon* can be interpreted as an individual variation not related to ontogeny, since the basal skull length of specimens showing this 'quasi closed' palate, ranges between 71 to 84 mm, close to the largest skull size for the species (96 mm). In addition, the palate seems to be completely closed in tiny juvenile specimens described by Estes (1961).

Taxonomic status of *Parathrinaxodon proops*

Recognizing that *Parathrinaxodon proops* Parrington and *Procynosuchus delaharpeae* Broom are conspecific raises some concerns about nomenclatural priority. Following article 23, section 1 of the International Code of Zoological Nomenclature (ICZN 1999), *Parathrinaxodon proops* Parrington 1936 has publication priority over *Procynosuchus delaharpeae* Broom 1937. However, considering the extensive use of the latter name by most recent therapsid workers (e.g. Kemp 1982, 1988; Hopson & Barghusen 1986; Rowe 1993; Hopson 1994; Sidor & Hopson 1998; Hopson & Kitching 2001; Rubidge & Sidor 2001; Sidor 2001, 2003; Sidor & Smith 2004), and because that taxon represents the best known Late Permian cynodont, we propose to conserve *Procynosuchus delaharpeae* as the valid name for this cynodont based on article 23, section 9 (Reversal of precedence) of the Code.

Comments on the Kawinga fauna

Parathrinaxodon proops comes from outcrops of the Kawinga Formation, at Stockley's site B.19 (Stockley 1932) in the Ruhuhu Valley near Mount Kingori. The recorded

fauna from the site B.19 also includes the dicynodont genera *Kingoria*, *Rhachiocephalus*, *Kawingasaurus* and *Pristerodon*; the gorgonopsian genera *Arctognathus* and *Scylacops*; the therocephalian genus *Theriognathus* and the dubious *Silphioictoides*; and indeterminate pareiasaurs (Kemp 1969; Gay 1987; Gay & Cruickshank 1999). Tanzanian material of *Pristerodon* (= *Cryptocynodon parringtoni* Huene 1942) was recently reassessed as *Diictodon parringtoni* by Maisch (1995), although Angielczyk (pers. comm., 2004) considers the species '*Cryptocynodon*' *parringtoni* as a new endemic taxon, different from both *Diictodon* and *Cryptocynodon*.

An analysis of the Kawinga fauna at a generic level indicates six endemic tetrapod taxa and 14 that are also known from localities of the *Tropidostoma*, *Cistecephalus* and *Dicynodon* assemblage zones from the nearby South African Karoo (Table 4). The percentage of endemism at this level (29%) is clearly lower than the percentage of taxa shared with the Karoo faunas (67%). The analysis of endemism in the Kawinga fauna changes radically if we consider taxa at the specific level. Maisch (2002) reports 18 of 26 species (69%) of the Kawinga Formation as being endemic. It is common practice, at least for Permo-Triassic vertebrate faunas, to use the genus (e.g. Lucas, 1998a,b) or even the family (e.g. Shubin & Sues 1991) as index taxa for assessing faunal similarity. Genera, therefore, seem more appropriate than species for analysis of faunal endemism, in which case, species of the Kawinga fauna, which are closely related (i.e. included in the same genus) to taxa from the Karoo and/or other basins, should not be considered as evidence of endemism. Regarding cynodonts, the only taxon represented in east African faunas, *Procynosuchus*, is also the first cynodont, and the only one of Late Permian age, with a global distribution. This taxon is the

commonest cynodont in the *Dicynodon* Assemblage Zone of the South African Karoo, and is also recorded in Germany (Sues & Boy 1988) and Russia (Tatarinov 2004), if we accept Hopson and Kitching's (1972) synonymy of *Cyrbasiodon* with *Procynosuchus*. Other taxa from the Kawinga fauna with widespread distribution are the dicynodonts *Dicynodon* and *Geikia*. The first genus is also known from Zambia, Scotland, China, Laos and Russia (King 1988), although a recent phylogenetic analysis suggest that at least one South African and two Russian species are not closely related (i.e. the genus *Dicynodon* is not monophyletic; Angielczyk & Kurkin 2003). *Geikia* is also represented in the Cuttie's Hillock Sandstone, near Elgin, Scotland, which is considered equivalent with the *Dicynodon* AZ (King 1988; Maisch & Gebauer 2005).

It is a pleasure to dedicate this contribution to the memory of the late J. W. Kitching, indeed the most influential palaeontologist in increasing our understanding of the Karoo vertebrate faunas. For access to the collections, we thank M. Raath and B. Rubidge (Bernard Price Institute for Palaeontological Research, University of the Witwatersrand), S. Kaal and R. Smith (South African Museum, Cape Town), R. Rubidge (Rubidge collection, Wellwood), J. Clack and R. Symonds (University Museum of Zoology, Cambridge), T. Kemp (Oxford University Museum of Natural History) and S. Chapman (The Natural History Museum, London). P. Mukanela at the Bernard Price Institute undertook further preparation of UMCZ T810, generously permitted by J. Clack. A first version of this work benefited from suggestions by R. Damiani and M. Raath. Comments and suggestions on the last version of this manuscript by B. Battail, J. Clack, J. Hopson, T. Kemp and C. Sidor, and update of the dicynodonts from the Kawinga Formation and comments about the Kawinga fauna by K. Angielczyk are acknowledged. Financial support was provided by the University of the Witwatersrand through a Postdoctoral Research Fellowship awarded to FA. The Royal Society of London and PAST (Palaeontology Scientific Trust, Johannesburg) provided FA grants that enabled a research visit to the United Kingdom.

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