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A juvenile gomphodont cynodont specimen from the *Cynognathus* Assemblage Zone of South Africa: implications for the origin of gomphodont postcanine morphology

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The partial skull and lower jaws of a small gomphodont cynodont from the *Cynognathus* Assemblage Zone of South Africa has a well-preserved postcanine dentition distinctly different from that of contemporaneous adult *Diademodon* and *Trirachodon.* On the basis of its small size and great amount of tooth replacement it is interpreted to be a juvenile individual. The postcanines are compared with those of adults and juveniles of *Diademodon* and traversodontids and is seen to differ from them. Comparison with adults of *Trirachodon* shows some unique postcanine resemblances, such as well-developed anterior and posterior many-cusped cingula and three transverse cusps joined by a prominent ridge. Thus it is identified as a probable juvenile *Trirachodon* of uncertain species. Unlike in *Trirachodon* adults, tall central and internal cusps of the upper postcanines lie close together on the medial side of the crown, separated from the tall external cusp by a deep valley. In these features it shows a striking resemblance to the traversodontid *Scalenodon angustifrons,* but not to more primitive traversodontids. The lower postcanines superficially resemble those of traversodontids in that two cusps (central and internal) are very tall and the posterior basin is elongated, but, unlike in traversodontids, the external cusp is present, though relatively small. Evidence of tooth replacement occurs in the incisors, canines, and postcanines. At least two replacement waves of gomphodont teeth are indicated, as well as replacement of small, possibly sectorial teeth at the rear of the tooth row. Probable homology of (at least) the external and internal cusps in the three gomphodont families suggests that the common ancestor also possessed transversely-expanded crowns developed from an external sectorial position (homologous with the ancestral blade-like tooth) and a hypertrophied internal cingulum.

Keywords: Cynodontia, Gomphodontia, *Trirachodon,* Triassic, *Cynognathus* Assemblage Zone, tooth succession, tooth evolution.

INTRODUCTION

Gomphodonts are a clade of derived non-mammalian cynodonts characterized by the possession of transversely expanded postcanine teeth with crown-to-crown occlusion. These molar-like postcanines, characterized as 'gomphodont' teeth, are generally considered to be specialized for processing a predominantly herbivorous diet (Hopson 1971). If the contentious Tritylodontidae are omitted (see discussions in: Hopson & Kitching 2001; Abdala & Ribeiro 2003), three family-level groups of gomphodont cynodonts are recognized: Diademodontidae, Trirachodontidae and Traversodontidae. In all three families, the expanded postcanines show a progressive decrease in crown wear from the first expanded tooth to the last, indicating that the teeth decrease in age from front to back with no indication of replacement within the row. However, this simple replacement sequence may not be sufficient to explain gomphodont tooth succession, for most taxa show evidence of more complex replacement patterns involving teeth of other morphologies. Furthermore, replacement patterns have been studied in growth series of very few species (e.g. *Scalenodon angustifrons* (Crompton 1955); *Diademodon* sp. (Hopson 1971)), so large portions of the full ontogenetic series are unknown for most taxa.

Diademodontids appear to represent the most primitive condition of dental morphology and replacement pattern among gomphodont cynodonts (Fourie 1963; Hopson 1971; Osborn 1974). In *Diademodon,* the tooth rows end in a series of three or more teeth in which the crown morphology grades from the fully expanded type to a fully sectorial (bladelike) type. *Diademodon* also appears to be primitive among gomphodonts in having the anterior expanded teeth sequentially replaced by simpler, more pointed, non-occluding postcanines (Crompton 1963; Hopson 1971). In trirachodontids and traversodontids, the anterior series of simple teeth is not seen, but sectorial teeth often occur at the rear of the tooth row, though the intermediate morphologies of *Diademodon* do not occur; rather, sectorial crowns usually lie immediately behind fully expanded teeth (Crompton 1955). In more derived taxa of traversodontids, such as *Massetognathus* and *Exaeretodon,* posterior sectorial teeth are unknown and the entire postcanine series appears to consist only of fully expanded teeth.

Disagreement also persists with regard to the homologies of the main postcanine cusps among the three gomphodont families and also between gomphodonts and their carnivorous ancestors with more sectorial postcanines. As noted by Abdala & Ribeiro (2003, p. 534), it appears that the external, sectorial, border of the postcanines in *Diademodon* is homologous with the sectorial postcanines of non-gomphodont cynodonts, with the expanded medial portion of the tooth originating by hypertrophy of the lingual cingulum of the ancestor, as

was first proposed by Watson (1913). A similar origin of the postcanine crown pattern in traversodontids, through medial expansion of the lingual cingulum of an ancestral sectorial tooth, was advanced by Goñi & Goin (1987). *Trirachodon,* however, appears to complicate this picture because, as originally noted by Rowe (1986), and recently discussed by Abdala & Ribeiro (2003), the transversely widened lower postcanines seem to result from rotation of the longitudinally elongated posterior sectorial teeth, so that the main fore-aft cusps of the sectorial crown appear to be homologous with the three main transversely-aligned cusps of the more anterior teeth. Thus, two conflicting hypotheses of primary homology exist to account for the occluding postcanines of gomphodonts (Abdala & Ribeiro 2003).

The description of a small gomphodont skull from the collection of the South African Geological Survey (now the Council for Geoscience) in Pretoria provides the opportunity to address some of the problems of tooth succession and tooth homology described above. This specimen, JSM 100, is a partial skull with lower jaws in place of a small, undoubtedly immature, gomphodont from the *Cynognathus* Assemblage Zone of South Africa. Although information on the locality at which it was collected appears to be missing, I consider it to be sufficiently important to warrant description for it shows evidence of active tooth replacement at the time of death and possesses an unusual postcanine crown morphology. I will make the case that the specimen is a juvenile individual belonging to the genus *Trirachodon,* though to which species, *T. kannemeyeri* or *T. berryi,* cannot be determined. If correctly identified, this would be the first juvenile *Trirachodon* known.

MATERIALS AND METHODS

The skull, JSM 100, was borrowed in 1975 and prepared at the University of Chicago by Ms Claire Vanderslice using needles under a binocular microscope. The horizontal ramus of the left dentary was freed from the skull, which permitted the crowns of the left upper and lower postcanine dentition to be fully prepared and illustrated.

The colour of the enamel is noted in the description of the teeth because it is an indication of enamel thickness. The dentine is white, whereas the enamel has been diagenetically darkened, so that the thick enamel on the lateral and posterior surfaces of the larger postcanine cusps is a deep brown, effectively masking the underlying dentine, whereas the thin enamel on the canines and in the postcanine basins is orange to light yellow because it is less effective at concealing the white dentine.

I initially identified the specimen as a juvenile *Trirachodon,* but preparation of the postcanine teeth showed that they were unexpectedly distinct from those of the contemporaneous species, *T. kannemeyeri* and *T. berryi.* Rather, they show similarities to the postcanines of adult traversodontids. However, further study of the postcanines has indicated a number of similarities with the postcanines of adult specimens of *Trirachodon* and differences from those of both juveniles and adults of *Diademodon,* the only other genus of gomphodonts currently known from the *Cynognathus* Assemblage Zone of South Africa, and from juveniles and adults of traversodontids, at present unknown in Beaufort sediments, but known from contemporaneous sediments in Argentina (Bonaparte 1966).

In the descriptions of the dentition, the abbreviation PC (upper case) is used for upper postcanines and pc (lower case) for lower postcanines. In addition, the main cusps of the upper and lower postcanines are designated by upper and lower case abbreviations respectively.

DESCRIPTION

Skull and lower jaws

The outer surfaces of the skull and dentaries are poorly preserved and sutures are not visible. The bone of the palate and all but the outer surfaces of some of the postcanine teeth were still embedded in matrix and so were protected from weathering and erosion and are extremely well-preserved. Several loose teeth lying against the palate (Figs 1 & 2) testify to the fact that the skull was buried with minimum postmortem transport.

The skull is complete back to at least the middle of the temporal fossa. As preserved, it measures about 45 mm at the dorsal midline. The palate is complete to a level just in front of the pterygoid flanges and the postcanine tooth rows are fully preserved. The preorbital length is about 20 mm and orbital diameter about 10 mm (see Table 1). Assuming the midpoint in skull length lay near the centre of the orbit, as in small generalized cynodonts (Hopson 2001, fig. 5), total skull length may have been about 50 mm. This is about half the length of the holotype skull of *Trirachodon kannemeyeri* (Seeley 1895).

The snout is rather low and flat, sloping downward only slightly from the low sagittal crest to the tip of the snout. The last upper gomphodont tooth lies below the anterior half of the orbit. In dorsal view, the snout narrows smoothly to a rounded tip, without a lateral expansion at the level of the canines. Though the area is damaged, the zygomatic arches are parallel to the midline and the temporal fossa is narrow. In ventral view, the secondary palate extends back to the level of the contact between the third and fourth postcanines, indicating that it ends a short distance in front of the orbit. The postcanine tooth rows are set in from the nearly straight lateral margin of the maxilla and the two tooth rows diverge only slightly toward the rear. The contribution of the palatine to the secondary palate is relatively short. The rear of the vomer is exposed in the roof of the choana; its midventral keel is exposed behind the secondary palate. The palatines and anterior ends of the pterygoids are exposed in the primary palate.

The rather massive lower jaw has a smoothly convex lower border that increases in depth from the rounded symphysis to the blunt angular process. The fused symphysis extends back to the level of the upper canines. The outer side of the horizontal ramus is broadly rounded and the lower postcanine row is set in from its outer margin.

The skull shows no special features that ally it with a particular family of gomphodonts. It shows a few resem-

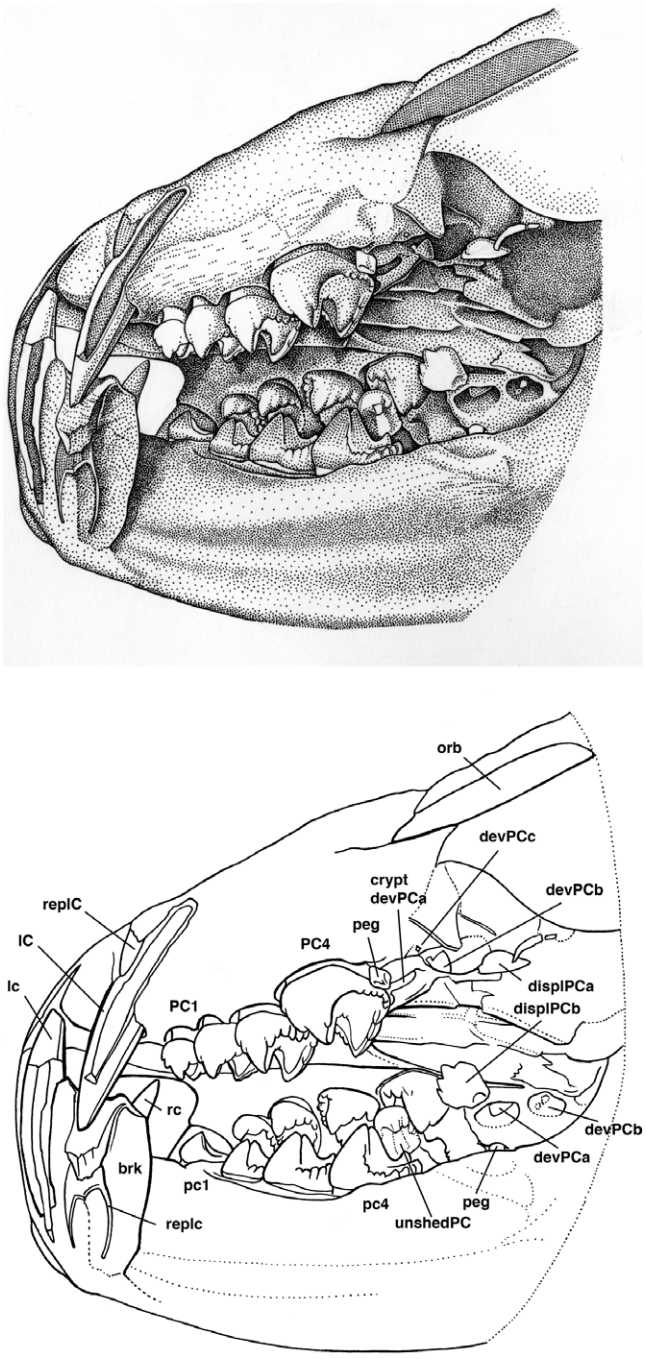

Figure 1. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Anterior portion of skull in oblique posteroventrolateral view, with left lower jaw removed to show the left upper postcanines and the lingual side of the right upper and lower postcanines. Features are identified in the line-drawing. Because of the oblique view, a scale bar is omitted, but the preorbital skull length is about 20 mm. Abbreviations are at the end of the text.

Table 1. Measurements of JSM 100, juvenile ?*Trirachodon*.

Skull			**mm**
Preorbital length:	Right:		18.8
	Left:		21.6
Interorbital width:			10.6
Dorsoventral diameter orbit:	Right:		9.0
	Left:		10.4
Length secondary palate (from anterior tip of snout):			19.4
Height of snout at level of anterior margin of orbit:			15.3
Width of snout at level of upper canines (estimated):			15.0
Lower jaw			
Length of lower jaw from anterior end to angle:			35.7
Depth of symphysis below upper canines:			7.5
Depth of mandible below pc1:			7.2
Depth of mandible below pc3:			8.7
Canines			
Upper			
A-P diameter at base:	Right:		2.6
	Left:		2.7
Height from alveolus (estimate; tip of tooth missing):		Right:	5.2
Lower			
A-P diameter at base:	Left:		2.3
Height from alveolus:	Left:		5.0
Diastemata behind canines			
Length upper diastema:	Right:		1.4
	Left:		1.7
Length lower diastema:	Left:		3.9
Postcanines			
Length upper (PC1–4) row (parallel to midline of palate):	Left:		12.6
Length lower (pc1–4) row (parallel to midline of palate):	Left:		11.4
(greatest length):	Left:		11.6

Individual upper left postcanines

	PC1	PC2	PC3	PC4
Length:	2.3	2.5	2.9	3.8
Width:	2.5	3.6*	4.9	6.6

Small tooth behind PC4:	Length: 0.8	Width: 1.5
Sectorial tooth at rear of left tooth row ('displPCa' in Figs 1 & 2):	Length: 1.7	Width: 1.0
Developing tooth crown in second alveolus:	Length: 1.9	
Displaced crown behind right PC4: ('displPCa' in Figs 1 & 2):	Length: 2.1	
Small unshed right postcanine ('unshedPC' in Fig. 1):	Length: 1.8	Width: ~2.0

Individual lower left postcanines:

	pc1	pc2	pc3	pc4	Erupting pc 5
Length:	2.3	2.9	3.3	4.3	5.4 (est.)
Width:	1.7	2.0 (est.)	2.6	3.5	3.9

Sectorial tooth behind pc5:	Length: 1.9	Width: 1.4

*External surface damaged

blances to *Trirachodon* (such as inset of the cheek teeth from the outer margin of the maxilla and dentary) that differ from what is seen in adults of *Diademodon*; however, when comparison is made with juvenile individuals of *Diademodon,* these distinctions are no longer present.

Dentition

Incisors

The incisor regions of the skull and lower jaws are damaged, with only the first and second incisors in the right dentary preserving crown morphology. No incisors are preserved in the left dentary and only incomplete teeth are preserved in the premaxillae.

In the left premaxilla are preserved a cross-section of the root of the first incisor, the exposed wall of the alveolus of the second incisor, and a probable partial section of the root of the third incisor. Evidence of the expected fourth incisor is lacking due to skull damage.

In the right premaxilla are preserved the cross-section of the root of the first incisor and a longitudinal section of the alveolus of the second incisor. Evidence of the third and fourth incisors is lacking due to damage combined with incomplete preparation.

On the lower right are two preserved incisors that are probably the first and second. The matrix-filled space between the second incisor and the lower canine probably held a third incisor, as it does in *Trirachodon* specimens, where the third incisor lies very close to the canine. The second incisor is fully erupted and the tip of the crown of the first incisor is just erupting. Both teeth are spatulate with a convex labial profile and a lingual profile that is convexly-rounded basally and concave more apically. The crown of the second incisor is damaged mesially, but the erupting crown of the first incisor is undamaged and has a mesial ridge separating the more transversely-convex labial surface from the very slightly convex lingual surface. The lingual enamel in this tooth is lighter, therefore thinner, than the labial enamel, which bears fine longitudinal crenulations.

Canines

All four canines are preserved (Figs 1–3). The lower canines lie anterior to the upper canines, their tips extending into palatal fossae that lie anteromedial to the upper canines. The upper canine lies anterolateral to the first postcanine, with a short diastema, about one-third the length of the first postcanine, separating the two teeth.

The lower canine is separated from the lower first postcanine by a long diastema, about twice the length of the first postcanine.

The upper left canine is damaged, with an exposed longitudinal section of root extending nearly to the dorsal margin of the maxilla. The partially damaged crown possesses a distal longitudinal ridge, which appears to lack serrations. An unerupted canine crown is exposed anterior and slightly medial to the functional canine root. Its enamel has fine longitudinal crenulations and is darker, therefore thicker, than that of the functional canine.

The complete right upper canine has a slightly convex anterior profile and a slightly concave posterior profile. It is relatively short with a slight anterior inclination. Its anterior surface is smoothly rounded transversely and the posterior surface forms a sharp ridge showing no evidence of serrations. When viewed from the lingual side, a very narrow ridge is seen to extend up the anterolingual surface, presumably from the unexposed apex of the crown. Toward the upper end of the crown the ridge widens into a broad, low raised area.

The root of the lower left canine is exposed in longitudinal section. The crown is damaged, but shows a posterior ridge and an anterointernal low, thin ridge behind the functional canine. The crown of a replacing canine lies within the jaw behind the functional canine. It extends below the root of the first postcanine (as seen on a transverse break). Its enamel has irregular longitudinal crenulations and is darker (thicker) than that of the functional canine.

The crown of the right lower canine is exposed only on its lingual side. Its enamel is very thin, as on the other functional canines. A thin ridge extends along the anterointernal face of the tooth from its apex to the base of the preserved enamel and the posterior margin of the crown bears a sharp ridge. The tip of the replacement

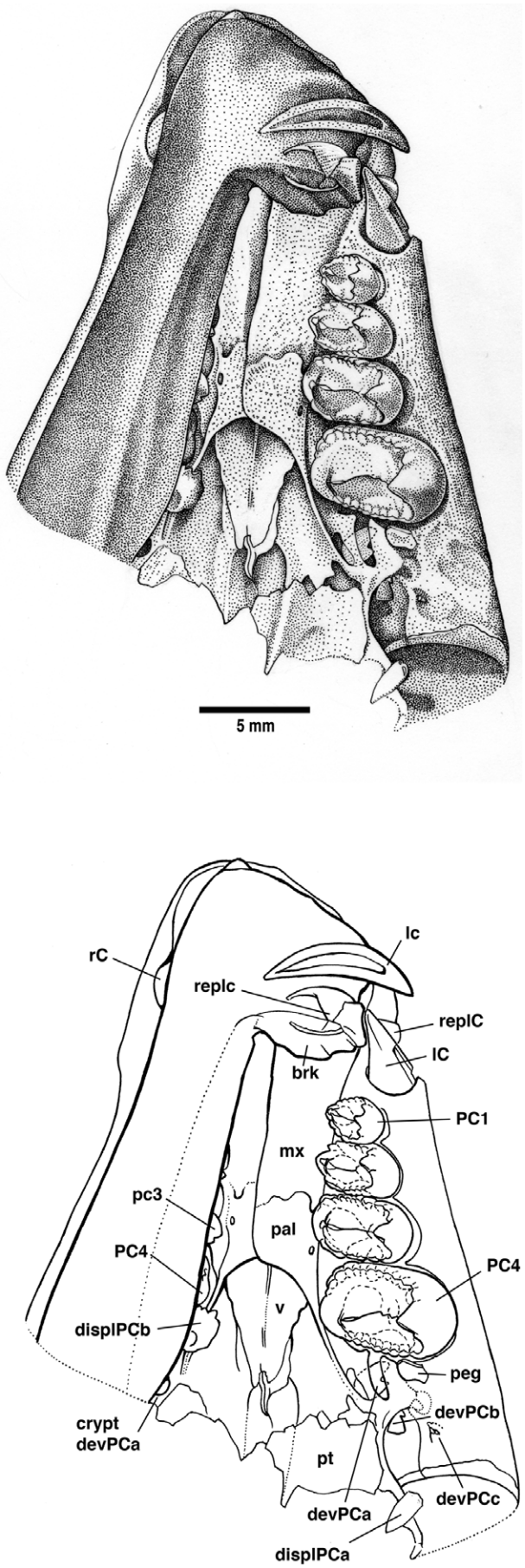

Figure 2. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100. Anterior portion of skull in ventral view, with left lower jaw removed to show the left upper postcanines. Features are identified in the line-drawing.

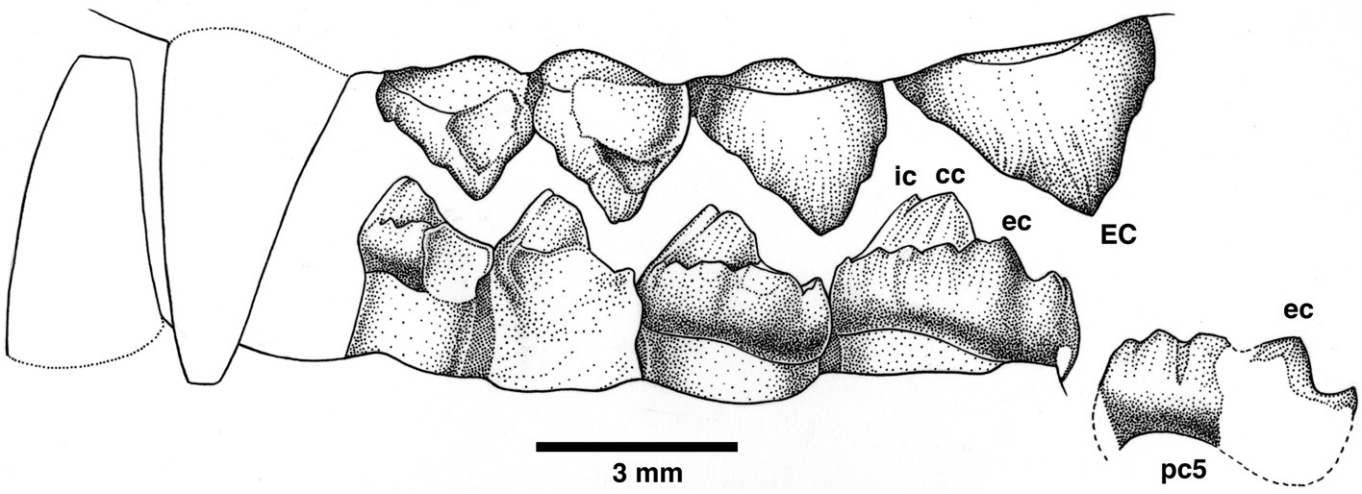

Figure 3. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left canines and postcanines in lateral view. Unerupted lower postcanine 5 was exposed through preparation into the jaw.

canine is exposed on the dorsal margin of the jaw behind the functional canine.

Postcanines – general observations

Each postcanine tooth row contains four transversely-expanded functional teeth, which increase in size toward the rear. Additional teeth of differing morphologies lie posterior to the four expanded postcanines, including erupting teeth and developing teeth in their crypts. In the maxilla, a small peg-like tooth (Figs 1 & 2, peg) lies behind the labial half of postcanine 4 on each side. Neither PC4 is fully erupted, that on the right being less erupted than that on the left. Between the partially-erupted right PC4 and the fully-erupted PC3 is a small tooth that partially overlaps the crowns of each (Fig. 1, unshedPC).

Lingual to the small peg-like tooth behind PC4, on both sides, is a crypt containing a developing crown (Fig. 2, devPCa). A second crypt immediately behind the first also contains a forming crown (devPCb). On both sides, posterior to the peg-like tooth and labial to the crypt of the second developing tooth, is a small pit that on the left side contains a tiny isolated cusp (devPCc) but on the right shows no trace of a developing tooth.

Two teeth lie in the matrix against the palate, one behind the second crypt on the left side (Figs 1 & 2, displPCa) and the other behind the inner margin of the erupting PC4 on the right (displPCb). Their original sites in the maxilla (or mandible) cannot be determined. They are described more fully below.

In the right lower jaw, behind the last functional postcanine (pc4), is a bulging area of bone with a possible foramen on its surface. On the left side, behind pc4, was a partially erupted crown, which was further exposed by preparation into the jaw. This large tooth has the same crown pattern as the preceding tooth. The principal external cusp and the posteroexternal accessory cusp behind it were separated from the crown postmortem and lie deeper within the jaw; they are restored in place on the main part of the crown in Figs 3, 7 and 8.

The left lower jaw was prepared free of the skull in order to expose the crowns of the postcanine teeth. The following description is based primarily on the left postcanine series, with some details added from the right series.

Upper postcanines

From PC1 to PC4, the individual teeth increase greatly in size and in transverse relative to longitudinal diameter (Figs 3–6). The crowns are oriented transversely in the skull and each lies more labially than its predecessor. All share the following features:

1) A single tall external cusp at midlength on the crown,

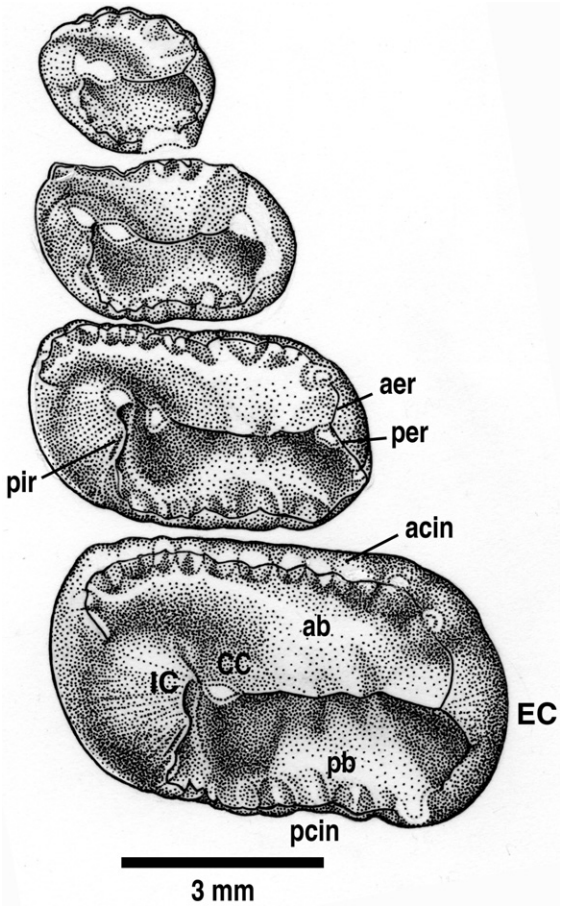

Figure 4. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left upper postcanines 1–4 in crown view.

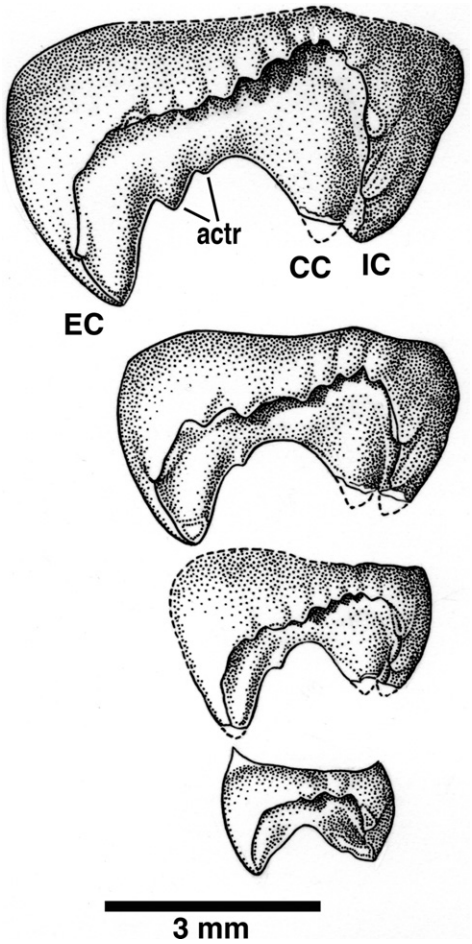

Figure 5. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left upper postcanines in posterior view, with PC4 at the top and PC1 at the bottom.

with a ridge sloping anteriorly from its apex that bears a prominent accessory cusp near its base and a posterior ridge bearing a smaller cusp near its base.

2) Two slightly lower cusps on the internal half of the crown, a slightly taller internal cusp and a lower central cusp, separated from one another by a shallow notch. The lingual cusp has a posterior ridge bearing one or two small cusps, but it lacks an anterior ridge.
3) A centrally-located transverse ridge links the apices of the three cusps. From the apex of the external cusp the ridge slopes steeply toward the base of the crown, then curves inward to a low point at about the transverse centre of the crown and slopes more gradually to the apex of the central cusp. A short ridge joins the apices of the central and internal cusps. In PCs 2–4, one or two small cuspules lie on the ridge lingual to the base of the external cusp.
4) A transverse row of cingulum cusps forms the anterior and posterior margins of the crown, enclosing shallow anterior and posterior basins. The cingula are continuous with the anterior and posterior ridges on the main external cusp and with the posterior ridge on the main internal cusp. The anterolingual cingulum ends at the base of the internal cusp, the anterior face of which is smoothly rounded, and the anterior basin extends lingually across the anterior face of the internal cusp. On PC4, the cingulum ridge extends about one-third of the way up the internal cusp and terminates in a small cusp. The cingulum ridge on the anterior face of the external cusp extends to the base of the crown directly anterior to the apex, whereas the ridge on the posterior face of the cusp curves laterally from the apex, then inward toward the base of the cusp, where it joins the cingulum ridge.
5) The anterior face of the twinned central and internal cusps ascends more steeply to the basin than does the posterior face. In crown view, the anterior face is aligned posteroexternally at a low angle to the transverse axis of the crown, whereas the posterior face is oriented anteroexternally at a greater angle to the transverse axis.
6) The anterointernal face of the external cusp, anterior to the transverse ridge, is oriented at an angle of 45 degrees or more to the transverse ridge. The posterointernal face of this cusp is oriented posteroexternally at greater than 45 degrees. This means that the anterior face of the external cusp is oriented more longitudinally than the posterior face.

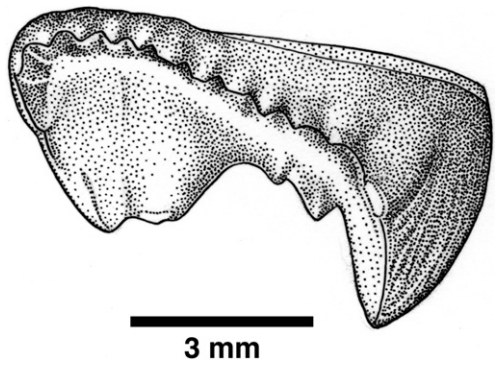

Figure 6. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left upper fourth postcanine in anterior view.

From PC1 to PC4, the enamel increases in rugosity on the three main cusps. The anterior and posterior basins are smoother and the enamel is much thinner than on the cusps, appearing a very light yellow, as opposed a rich amber or brown on the main cusps.

Postcanine 1: this small tooth is oval in crown view, being slightly wider than long. The anterior margin is slightly more rounded than the posterior, so the anterior basin is slightly wider than the posterior. Anterior and posterior marginal cingula extend lingually and basally from the ridges on main external cusp. The anterior cingulum has four small cusps (excluding the prominent cusp on the anterior ridge of the external cusp). The posterior cingulum has three or four larger posterior cingular cusps (damage prevents an accurate count) and two small cusps on the posterior ridge of the internal cusp. The central transverse ridge lacks cuspules on its basal portion. On both left and right sides, the posterior internal ridge bears a prominent wear facet on the enamel that extends along the entire ridge.

Postcanine 2: this tooth is about half again as wide as PC1, though only slightly longer anteroposteriorly. The anterior and posterior margins of the crown are nearly straight and parallel to one another. The enamel of the apical part of the posterointernal ridge shows a posteriorly-sloping

wear facet. The anterior cingulum has five cusps, the labial- and lingual-most being the largest. (The left PC2 is damaged but the right preserves the cuspules missing on the left.) The posterior cingulum has seven cusps, the second from the external side being the largest. At the base of the external cusp, the transverse ridge bears a single small accessory cusp.

The enamel of the apical part of the posterointernal ridge shows a posteriorly-sloping wear facet. The central portion of the ridge has a well-developed wear facet with longitudinal striations and a central exposure of dentine on the second cusp from the apex. The most lingual two posterior cingulum cusps are also truncated by wear facets. Behind the lateral slope of the central cusp, on the slope toward the posterior valley, is a shallow concavity that may reflect an occlusal area for a lower cusp.

Postcanine 3: this tooth is about one-third wider and longer than PC2. The anterior cingulum has ten cuspules, with the three outermost and two innermost being largest. The anteroexternal ridge bears a small cusp. From the innermost cingulum cusp, a short ridge bearing a small cuspule curves up on to the anterinternal face of the internal cusp. On the posterior cingulum are three large cusps on the labial half and two smaller cusps on the lingual half. On the posterointernal ridge is a small basal cusp, separated from the lingual-most cingulum cusp by a V-shaped notch, and two larger cusps closer to the apex of the internal cusp. On the base of the transverse ridge internal to the main outer cusp is a single small accessory cusp.

Postcanine 4: this tooth is about one-third wider than PC3 and about 40% longer. The anterior ridge on the external cusp has a well-developed accessory cusp (damaged on the left side), but a posterior accessory cusp is not present, although a basal swelling on the posterior ridge may represent this cusp. On the central transverse ridge at the base of the external cusp is a small accessory cusp, as in PCs 2 and 3, with a smaller cuspule lingual to it. The anterior cingulum bears 10 relatively small cusps. A deep V-shaped notch separates the innermost cusp from an anterointernal ridge on the basal half of the main internal cusp. This ridge has a small cusp basally and a larger cusp capping the ridge. On the right side, a definite anterointernal ridge is absent and the basal cusp (here a free-standing cusp) is larger than that on the left. The more apical cusp is separated by a small gap from the basal cusp and forms an elongate low bulge on the side of the internal cusp.

The posterior cingulum and posterior basin slope basally toward the internal side of the crown. A row of five distinctly-spaced cingulum cusps slopes toward the lowest part of the cingulum. At the basalmost part of the cingulum is a very small isolated cusp. More lingually, the posterointernal ridge, which bears two small basal cusps, extends to the apex of the main internal cusp. At about one-third of the distance from the basal cusps to the apex, the ridge bears a prominent cusp (damaged on the left but complete on the right). At about two-thirds of the distance from the basal cusps to the apex the ridge bears a second prominent cusp.

Small gomphodont postcanine: between the partially-erupted right PC4 and the fully-erupted PC3 is a small tooth (Fig. 1, unshedPC) that lies between the lingual halves of the two crowns, partially overlapping each. This small tooth is expanded transversely, but is less than half the width of PC3, being about as wide as PC1. It has a pattern of main cusps that appears similar to that of the upper postcanines, i.e. an external and internal cusp and a probable central cusp adjacent to the inner cusp (all worn or damaged), and an anterior and posterior cingulum of small cusps. Its enamel is very thin and, therefore, lighter than that of the larger crowns. A remnant of root remains on its posterolabial margin. This tooth is interpreted as the last remnant of a preceding functional tooth row that has been almost entirely shed and supplanted by a subsequent replacement wave of larger teeth. There is no evidence of a comparable tooth on the left side, where PC4 is more fully erupted.

Peglike tooth behind PC4: behind the labial half of the upper PC4 on both sides is a small transversely-ovate, peglike tooth (Figs 1 & 2, peg). On the better-preserved right side, the crown has at least two cusps, the labial of which is the larger. The outer side of this tooth is not exposed, so there may be a third, more labial, cusp.

Developing postcanines: lingual to the small peglike tooth, on both sides, is a crypt opening via a foramen that is oval on the right side but, because of damage, is narrower and more elongated on the left (Fig. 1, crypt devPCa). In the crypt on the left side is a developing crown with a large anterior cusp and a smaller cusp behind it (Fig. 2, devPCa). It is possible that the forming crown is a transversely-expanded tooth and that the cusps are the main internal cusp and the adjacent posterior accessory cusp. The inner side of the tooth inclines more ventrolaterally than that of the functional fourth PC, suggesting the more external portion of the forming crown lies deeper within the maxilla, above and partially behind the small peglike tooth. The enamel of the forming crown has longitudinal crenulations and is a slightly darker brown than that of the functional PC4, suggesting it is thicker. In the comparable oval pit on the right side, only the main cusp of the developing crown is visible in its crypt.

Immediately behind the crypt lying internal to the small oval tooth on each side is a second crypt containing a developing crown (Figs 1 & 2, devPCb). On the right side, the crypt is a circular depression in which lies a forming tooth with two small cusps. Along the anterointernal side of the depression is the section of a larger fragment of tooth with thin enamel. Whether it is part of the same crown as the two small cusps is uncertain. On the left, the depression is larger than on the right and has an irregular shape, probably due to damage. It contains a developing crown consisting of a large main cusp joined to a small more anterior cusp. The enamel of this crown is lighter than that of the more fully developed crown anterior to it and is only very slightly crenulated. As the functional upper postcanines lack an anterior accessory cusp, it is uncertain whether the forming crown is part of a transversely-expanded tooth or of a more narrow, sectorial-type, tooth.

On both sides, posterior to the small transversely-ovate functional tooth and external to the crypt of the second developing tooth, is a small pit that on the left side contains a tiny isolated cusp (Figs 1 & 2, devPCc) but on the right shows no trace of a developing tooth. From its position immediately behind the small ovate functional tooth, it appears that this developing crown may be part of the same replacement wave as that tooth and distinct from the wave producing the transversely-expanded (gomphodont) postcanines exposed more medially.

Teeth of unknown original position: two additional posterior teeth are preserved, the original locations of which are uncertain. One is in matrix behind the second unerupted crown on the left (Figs 1 & 2, displPCa). It is a sectorial type tooth with a small anterior cusp and a larger posterior cusp. The labial side of the crown is broadly rounded and the lingual side is more vertical. The root is stout and about twice the height of the crown. It does not seem to be implanted in an alveolus, so may have fallen from a possible alveolus between the ovate peg-like tooth and the small developing tooth behind it.

The second tooth of unknown location has been displaced from its original position and lies against the palate behind the internal margin of the right PC4 and medial to the first crypt containing a developing crown (Figs 1 & 2, displPCb). The tooth lies on its side so the full crown cannot be seen. It is uncertain whether it is an upper or lower tooth. The crown appears to be oval, with a large cusp and two much smaller accessory cusps that curve around the front (as preserved) of the crown, suggesting a basin on the side opposite the main cusp. The tooth lacks a root, which seems to have been eroded away, as matrix on the base of the tooth suggests the root was absent at the time of death.

At present, it is not possible to be sure of the original site of this tooth. If it is an upper, it may have fallen from the round second pit behind the right PC4. As noted above, this pit has a remnant of dentine and enamel along its wall, which may be a remaining part of this tooth. In this case, if the main cusp is labial, the two accessory cusps would be anterior. The upper postcanines have an accessory cusp on the anterior slope of the main cusp and a second accessory cusp anterointernal to the first. However, it is also possible that this tooth is a lower, in which case the main cusp would probably be on the labial side and the accessory cusps would be posterior. There is a possible alveolus on the inner side of the base of the coronoid process from which this tooth may have been shed immediately postmortem.

Lower postcanines

The following description is based mainly on the left postcanine row (Figs 3, 7–9) , which was separated from the upper dentition. As in the uppers, the lower postcanines increase greatly in size from first to fourth, and the unerupted pc5 is much larger than pc4. The crowns are longer than wide and roughly rectangular in outline. Their long axes are parallel to the long axis of the jaw. All share the following features:

1) The anterior two-thirds of the crown bears a large rounded internal cusp closely joined to a slightly lower, oval central cusp that lies posteroexternal to it. A ridge extends from the apex of the lingual cusp to that of the central cusp, the tips being separated by a shallow notch. From the base of the notch anterior and posterior grooves extend down the conjoined cusps and fade into the surface of their common base. The apical ridge crosses the oval central cusp and descends to a basal platform, where it passes posteroexternally and ascends the inner surface of a much lower, but nonetheless prominent, external cusp. The ridge joining the three main cusps is oriented at about 45 degrees to the long axis of the tooth.
2) External and anteroexternal to the conjoined central and labial cusps is a basal cingulum enclosing a narrow basin, which is bounded posteriorly by the main labial

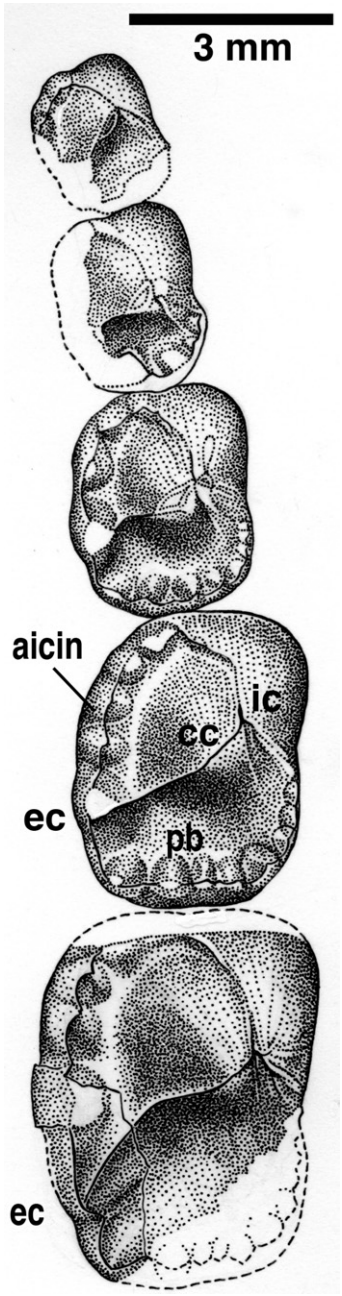

Figure 7. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left lower functional postcanines 1–4 and unerupted pc5 in crown view.

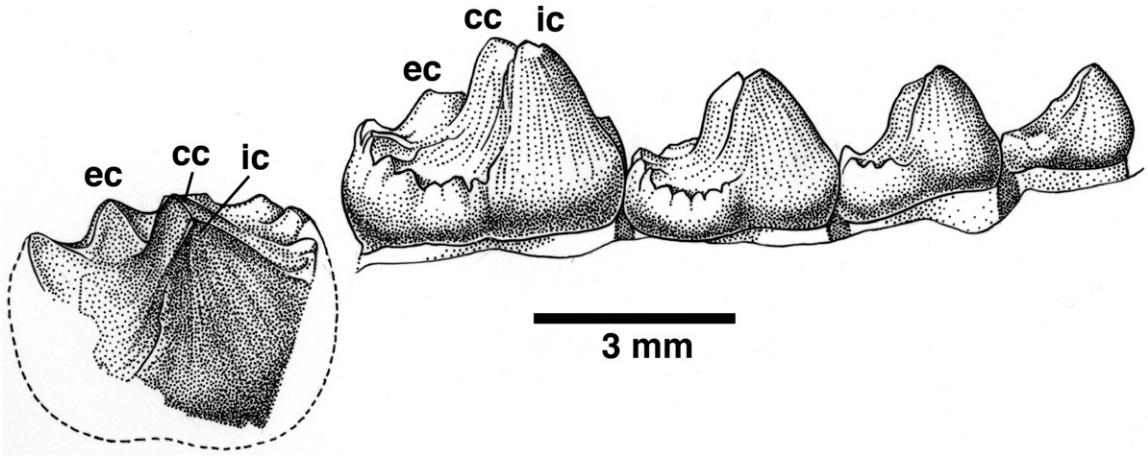

Figure 8. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left lower functional postcanines 1–4 and unerupted PC5 in medial view.

cusp (which is the largest cusp on the outer margin of the tooth) and the ridge extending from this cusp to the central cusp. At its narrow anterointernal end, the basin is bounded by a narrow ridge that extends upward a short distance from the inner-most cingulum cusp on to the anteroexternal face of the main internal cusp.

3) Posterior to the three main cusps is a shallow basin bounded posteriorly and posterointernally by a series of cingulum cusps. The basin is about one-third the length of the crown and is slightly concave antero-posteriorly and slightly convex transversely, with its inner side lower than its outer side.

Postcanine 1: on the left side, the posteroexternal part of this tooth is damaged, but, at the time the drawings were made, was otherwise complete (the main internal and central cusps were subsequently broken off). The right pc1 is more complete. The anteroexternal cingulum has two relatively large cusps anterior to the main labial cusp. All of the cusps on the posterior cingulum have been eroded away by tooth wear. The enamel in the central part of the posterior basin on both first postcanines has been worn away, leaving a planar facet on the dentine.

Postcanine 2: the outer side of the left pc2 is heavily damaged and that of the right pc2 is obscured by slight damage and some remaining matrix. Therefore, the number of cusps on the anteroexternal cingulum cannot be determined. On the posterior cingulum of the left pc2, two small internal and two larger, though damaged, posterior cusps are preserved. Probably one and at most two more posteroexternal cusps were present. The apex of the central cusp is truncated by a posteroventrally-sloping wear facet on the enamel; dentine is exposed by wear at the truncated tip of the cusp. The more pointed tip of the internal cusp is also truncated by a flat wear facet.

Postcanine 3: the anteroexternal cingulum has three cusps, a small anterior cusp adjacent to the base of the main internal cusp and two larger more external cusps. The tips of the internal and central cusps are truncated by wear, as in pc2.

Postcanine 4: the large pc4 has four cusps on the anteroexternal cingulum. Posterior to the main external cusp is a notch behind which is a relatively large posteroexternal cingulum cusp. Internal to this cusp are four additional posterior cingulum cusps. On the internal side of the posterior valley are three smaller cingulum cusps, and at the base of the main lingual cusp is a very small cusp. A short distance above this cusp is a low oval cusp with its long axis directed toward the apex of the main cusp.

Erupting postcanine 5: a partially erupted left pc5 was prepared out behind pc4. The apex of its main lingual cusp is at the level of the posterior cingulum of pc4. In order to remove the left lower jaw containing the postcanines from the skull, fine saw cuts were made immediately behind pc4 and across the lower part of the coronoid process. The cut across the horizontal ramus

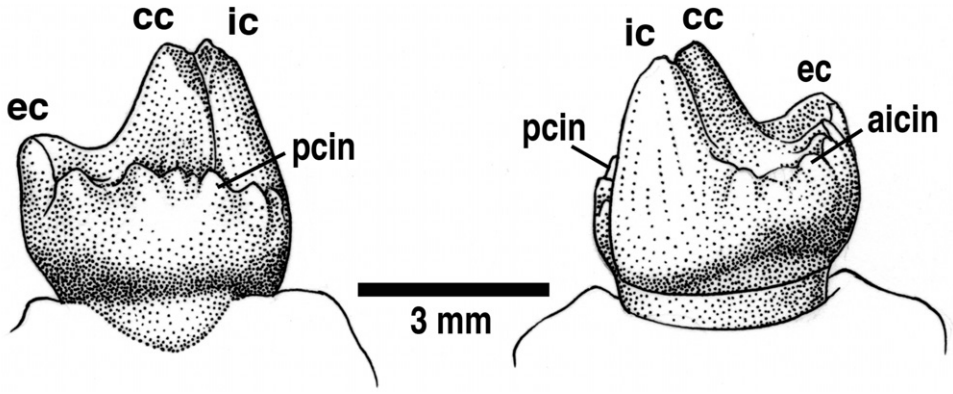

Figure 9. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left lower fourth postcanine in posterior (left) and anterior views. In the anterior view, the front of the tooth is rotated slightly to the right so a portion of the posterior cingulum is visible.

removed the anterior-most part of pc5, but most of the crown is intact. The lingual side of the posterior basin is not preserved, but the main labial cusp and the cingulum cusp behind it, though broken away from the crown, are nonetheless well-preserved and restored in place on the crown in the figures. The erupting pc5 is tilted lingually so that the main cusps are inclined inward at about 45 degrees. The crown morphology is of the same pattern as of the preceding teeth, although this tooth differs in having a distinct ascending ridge on the posterointernal side of the main internal cusp. This ridge ends at the posterior groove between the internal and central cusps where it terminates in an oval cuspule. Anterior to this ridge, the enamel of the convex internal surface is very dark and rugose, with dorsoventral crenulations. External to the ridge, the posterior surface of the internal cusp is transversely concave and the enamel is of a lighter colour and is more finely crenulated. The enamel on the transversely convex rear face of the central cusp is of the same character.

The anteroexternal cingulum preserves three external cusps, the remnant of a more anteroexternal cusp, and a small cusp at the base of the very shallow groove between the central and internal cusps. Only the posteroexternal cusp of the posterior cingulum is preserved behind the main external cusp.

Posterior sectorial tooth: behind the centre of the unerupted pc5, above its posteroexternal cingulum cusp, is the remnant of a small longitudinally elongate tooth, the crown of which is very damaged. Its partially exposed root indicates it was mature and in place. An alveolus on the right side, behind the crypt of the unerupted pc5, presumably represents the site for this sectorial tooth. An isolated tooth of comparable size and shape lies on the palate behind the tooth row (Figs 1 & 2, displPCa). This may be the tooth from the empty right alveolus.

Tooth replacement

Incisors and canines of this immature specimen were undergoing rapid replacement at the time of death. Of the two preserved incisors, that interpreted here as the first right incisor is erupting, with only its apex exposed above the alveolar margin, and the second right incisor is fully erupted.

Both upper canines appear to be incompletely erupted, as their alveoli are larger than their crowns and they only slightly overlap the dorsal margin of the dentary. A developing replacement crown lies within the maxilla anterior to the left erupting canine. The right lower canine appears to fill its alveolus more completely than do the upper canines. The tip of a replacement canine is erupting on the dorsolingual side of the jaw behind the functional canine. The left lower canine is damaged and its alveolus is not well exposed, so its degree of eruption relative to the right side is uncertain. A replacement crown is exposed on the left side within the jaw behind the lower canine. Because of difficulty of preparation, it could not be determined whether the tip of this replacing tooth is erupting.

In the postcanine series, the posterior decrease in the degree of wear and of eruption (as indicated by decrease in amount of exposure of roots) demonstrate that the first four teeth have erupted sequentially from front to back. At the rear of both upper and lower tooth rows are unerupted postcanines, the crown morphology of which is similar to that of the functional postcanines (known in the lower dentition and presumed to be the case in the uppers), thus demonstrating that the same sequence of eruption is continuing. In the upper jaw, a second incompletely formed crown lies posterior to the unerupted crown lying immediately behind the fourth postcanine, indicating the likelihood of additional teeth of comparable morphology. Such additional replacement teeth are not seen in the lower jaws, though one would presume they are present within the bone.

As in some other gomphodont cynodonts, small teeth occur at the rear of the functional tooth row, posterior to the main labial cusp. Here, these teeth have a transversely ovate outline rather than the longitudinally ovate outline usual in gomphodonts. Behind this tooth on the left side, lateral to the second developing crown described above, is a small pit containing the apex of a very small ovate cusp with a keeled margin. On the right side is a comparable pit, which lacks a visible crown.

To add to the complexity of the replacement series, a small gomphodont tooth, presumably representative of a previous wave of replacement lies between the right upper PC3 and the erupting PC4.

The crown of the rootless tooth lying in the matrix behind the right PC4 may have belonged to the series represented by the transversely ovate tooth behind PC4. If so it may have been shed from a position in which a replacing tooth is developing. Likewise, it may have been shed from a more medial position, where it would be replaced by a developing PC5. In this case, it may be part of the older series of gomphodont teeth represented by the small tooth lying between right PCs 3 and 4. Finally, it might be part of the older series in the lower jaw, being shed from behind lower pc4 and perhaps lateral to the erupting pc5.

To summarize the inferred pattern of postcanine tooth succession in this individual, the remnant of an earlier wave of gomphodont postcanine replacement is indicated by a small heavily worn upper gomphodont tooth that was about to be shed. The small peg-like tooth behind the outer half of PC4 may be part of this replacement wave, as may be the tiny developing tooth behind the peg-like tooth. A more recent replacement wave is represented by the four functional upper and lower gomphodont teeth and the unerupted fifth and perhaps sixth gomphodont crowns behind them.

DISCUSSION

Identification of JSM 100 as a probable juvenile *Trirachodon*

Specimen JSM 100 is determined to be a eucynodont on the basis of the fusion of its symphysis and a gomphodont cynognathian on the basis of its transversely expanded, occluding postcanines showing a pattern of sequential rather than 'alternate' replacement. It is determined to be

a juvenile individual on the basis of the great amount of tooth replacement that was occurring at the time of death and its small size relative to the much larger size of undoubted adult individuals of the gomphodonts *Diademodon* and *Trirachodon,* the only certainly valid genera currently recognized from the *Cynognathus* Assemblage Zone of South Africa (Hopson & Kitching 1972; Kitching 1995).

In its postcanine dentition, JSM 100 more closely resembles adult individuals of *Trirachodon* than of *Diademodon,* notably in the presence of three well-defined transversely-oriented cusps in both upper and lower teeth and in the presence of anterior and posterior cingula usually with a relatively large number of small cusps. In *Diademodon,* the central and internal cusps of the upper postcanines are low and poorly differentiated, the transverse ridge is less well-defined, and, more significantly, the lower postcanines possess only two rather than three principal cusps (Crompton 1972, fig. 3A; personal observation). Finally, immature specimens of *Diademodon* of about the same skull length (about 50 mm) have very different postcanine teeth from those described above, including a series of anterior pointed teeth that replace the gomphodont series and more posterior teeth with oval crowns that are about twice as long as wide and that appear to grade continuously into more posterior sectorial teeth (Hopson 1971).

Comparison of the postcanines of specimen JSM 100 with adult traversodontids, especially *Scalenodon angustifrons* (Crompton 1955, 1972), show some striking resemblances, discussed in detail below. However, when JSM 100 is compared with adult and juvenile individuals of the contemporaneous Argentine traversodontid *Andescynodon mendozensis* (Goñi & Goin 1988), the postcanines are distinctly different, with both the upper and lower crowns of *Andescynodon* possessing a distinctive multicusped sectorial external portion and a single anteriorly-located internal cusp joining the main external cusp by a transverse crest on the anterior margin of the crown.

My conclusion from these comparisons is that JSM 100 is most likely to be a juvenile individual belonging to a species of *Trirachodon.* It will be referred to as ?*Trirachodon* sp. in the subsequent discussion.

Comparison of postcanine crown patterns in gomphodont cynodonts

In Figs 10 and 11 are compared representative upper and lower postcanines of *Trirachodon kannemeyeri,* juvenile ?*Trirachodon* sp. (JSM 100), and *Scalenodon angustifrons,* all drawn from specimens. Only in JSM 100 are the upper and lower teeth known to be from the same individual. The upper row consists of crown views (with the posterior side in the uppers and anterior side in the lowers toward the top of the page) and the lower row of posterior views.

The upper postcanines of all three share the following features:

1) Three main cusps oriented transversely on a crown that is mediolaterally wider than long.
2) A prominent transverse ridge connects the apices of the three main cusps.
3) A well-developed anterior and posterior cingulum, usually joined at each end to the apices of the external and internal cusps and enclosing anterior and posterior basins.
4) The external cusp is the most robust, though not always the tallest.
5) Small accessory cusps on the transverse crest between the external and central cusps (and in adult *T. kannemeyeri* on the ridge between the central and internal cusps as well).

The lower postcanines of all three share the following features:

1) Transverse ridge joining apices of main cusps.
2) Posterior cingulum enclosing posterior basin.
3) Posteroexternal ridge from cingulum to apex of main external cusp (which may not be homologous in all three).

The juvenile ?*Trirachodon* sp. shares with adult *T. kannemeyeri* the following similarity in the upper postcanines:

1) Posterior and (usually in *T. kannemeyeri*) anterior cingulum composed of a continuous row of distinct cusps.

They share the following similarities in the lower postcanines:

1) Three cusps in a transverse row joined by a prominent ridge.
2) Well-developed basin bounded by a cuspidate cingulum extending anterior to the external cusp and its adjacent transverse ridge, though the basin is labially displaced in the juvenile.
3) Complete posterior cingulum formed by a continuous row of distinct cusps that extends between the external cusp and the base of the internal cusp, enclosing a broad posterior basin.

The juvenile ?*Trirachodon* sp. shares with *Scalenodon angustifrons* the following similarities in the upper postcanines:

1) Main cusps much taller than those of *T. kannemeyeri* adult.
2) Central and internal cusps conjoined on lingual side of the crown and separated from the external cusp by a deep valley.
3) Anterior basin anteroposteriorly longer than in *T. kannemeyeri* adult.
4) Small accessory cusps present on transverse ridge near base of notch between external and central cusps.

They share the following similarities in the lower postcanines:

1) Crown longer than wide, with elongation of the posterior basin.
2) Two rather than three enlarged main cusps (of which the homology of the more labial cusp is uncertain).

Major differences nevertheless exist between the juvenile ?*Trirachodon* sp. and *Scalenodon angustifrons*:

1) The external shear between the main lower labial cusp and the longitudinal inner face of the external cusp that characterizes traversodontids is absent in ?*Trirachodon* sp.
2) *S. angustifrons* lacks an external cusp and an anteroexternal cingulum and basin in the lower postcanine

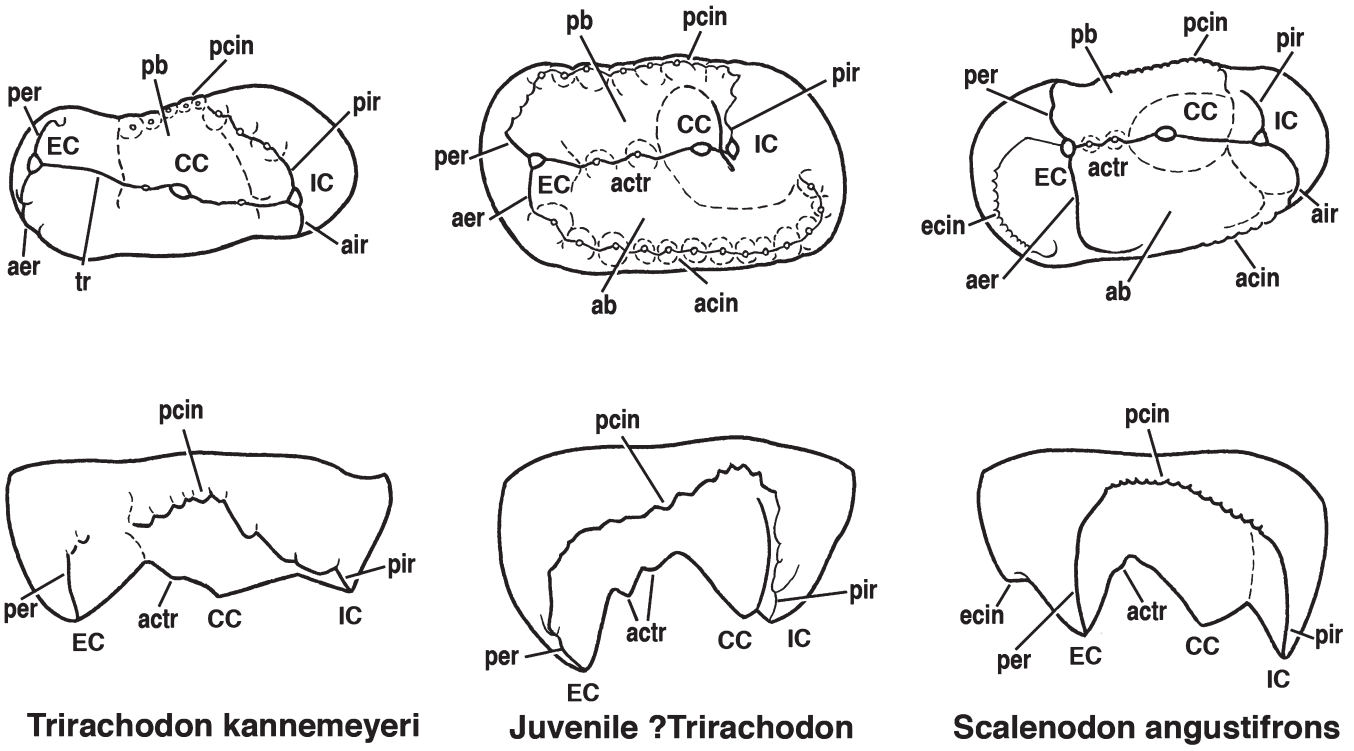

Figure 10. Comparison of upper postcanines in crown and posterior views of *Trirachodon kannemeyeri,* the juvenile specimen of ?*Trirachodon* sp., and *Scalenodon angustifrons.* A distinct anterior cingulum is usually present in *T. kannemeyeri* postcanines. Not to scale.

(although an anteroexternal cusp or narrow anterior cingulum is sometimes present in traversodontids)

Although the dental resemblances of the juvenile ?*Trirachodon* specimen to the traversodontid *S. angustifrons* are striking, their phylogenetic and evolutionary significance is uncertain. As noted above, *Pascualgnathus* and *Andescynodon* as the oldest and probably most basal traversodontids (Abdala & Ribeiro 2003) differ from later traversodontids in having only two main cusps in the upper postcanines and *Andescynodon* differs in having the transverse ridge of the upper teeth on the anterior half of the crown. Thus, it would appear that there is no direct phylogenetic connection between the dental pattern of the juvenile ?*Trirachodon* and the later *S. angustifrons.* Nonetheless, the resemblance in cusp patterns suggests that at least the external and internal upper cusps and the lower internal cusp of trirachodontids and traversodontids may be homologous. This further suggests that, as in *Diademodon* and traversodontids, the postcanine crown pattern of trirachodontids evolved from a primitive sectorial-type tooth by medial hypertrophy of an internal cingulum. Unlike the other two families, trirachodontids modified the external side of the tooth by losing the anterior and, especially, the posterior accessory cusps so that all longitudinal shear on the inner side of the main external cusp was lost.

Under the above interpretation of cusp homologies, only the external cusp of the *Trirachodon* postcanine shares any homology with the longitudinally sectorial crown of the carnivorous ancestor. Thus, the concept of the entire postcanine of *Trirachodon* originating from the entire sectorial tooth rotated 90 degrees (Rowe 1986; Abdala & Ribeiro 2003, fig. 4C) is untenable. The more likely interpretation of specimens in which the posterior two or three 'gomphodont' postcanines appear to be sectorial teeth progressively rotating into a transverse position is that the gomphodont teeth must develop in a longitudinal position at the rear of the narrow mandible; subsequently, as the mandible grows back and increases in diameter, the erupting teeth rotate into a fully functional transverse orientation. The last postcanine, which is oriented in line with the long axis of the dentary, probably is a sectorial tooth, as is commonly seen in both upper and lower jaws of *T. kannemeyeri.*

Under the interpretation of cusp homologies advanced here, the external and internal cusps of the upper postcanine are homologous in the three gomphodont families. A central cusp occurs in *Diademodon,* where it is low and poorly defined, so the three transversely-oriented cusps of the upper postcanines of diademodontids and trirachodontids are probably homologous as well. It is also likely that the two main cusps in the lower postcanines of diademodontids and traversodontids are homologous. This suggests that the central lower cusp of trirachodontids is a neomorph. Therefore, I conclude that the gomphodont postcanines of all three families are homologous as transversely expanded teeth that meet in crown-to-crown occlusion. This is contrary to the interpretation of Goñi and Goin (1987) on the origin of the traversodontid crown pattern directly from a sectorial-toothed Permian or Early Triassic ancestor.

Ontogeny of postcanine tooth function in *Trirachodon*

The transversely expanded postcanines of adult *Trirachodon* appears to be specialized for crushing and grinding, with no longitudinal and little transverse shearing involved. The juvenile specimen described here has taller cusps with steeper sides, suggesting the possibility

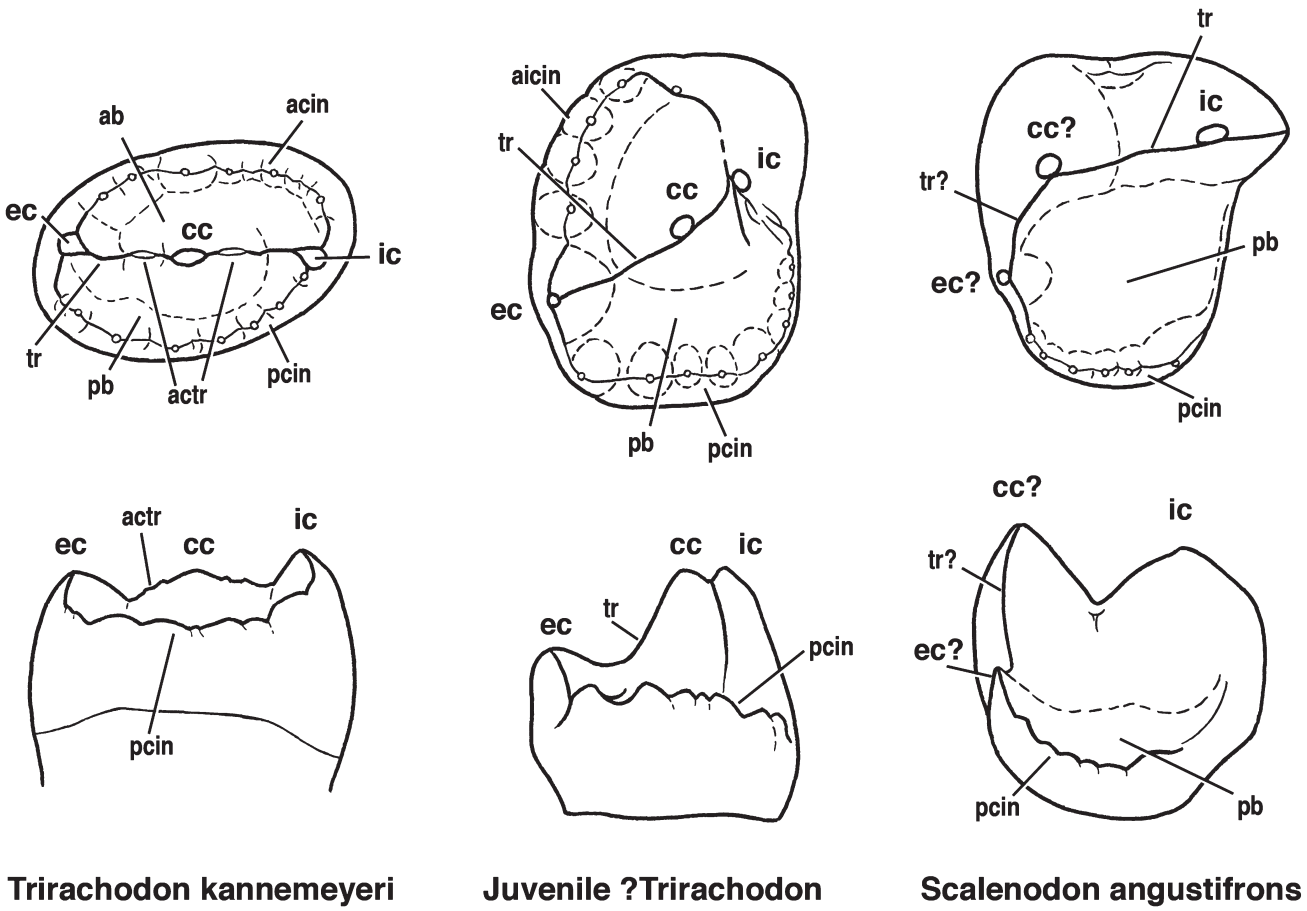

Figure 11. Comparison of lower postcanines in crown and posterior views of *Trirachodon kannemeyeri,* the juvenile specimen of ?*Trirachodon* sp. and *Scalenodon angustifrons.* Not to scale.

of some shear in addition to crushing. Posteriorly-sloping wear facets on the posterointernal ridges of both upper and lower anterior postcanines indicate that the internal cusp of each lower tooth contacted and slid up the rear of the next upper tooth forward, leaving wear surfaces on the posterointernal ridge of that upper tooth. The lower central and internal cusps then moved back across the posterior cingulum of the upper, wearing down its cingulum cusps. Each lower tooth then slid up and back against the anterior face of the next upper tooth back, leaving wear on the posterointernal ridge of the lower. The first part of the chewing stroke would have brought the transverse ridge of the lower to meet, or at least approach, the transverse ridge of the next upper forward, perhaps creating some cutting of the food. During the second, more retractive, portion of the chewing stroke, the main lower cusps (cc and ic) would have moved the food back into the anterior basin of the next upper tooth and then would have ground it against the anterior face of the main upper cusps (primarily CC and IC) by sliding back and down the inclined plane formed by those cusps (see Fig. 3), though probably only for a short distance.

As *Trirachodon* individuals matured, these taller and narrower (with respect to their length) postcanines would have been replaced by broader lower-cusped teeth, presumably with a more exclusively grinding function. Comparison of the posterior views of the postcanine of *T. kannemeyeri* and ?*Trirachodon* sp. (Figs 10 & 11) suggests that the main ontogenetic broadening of the tooth in successive replacements occurred on the medial half of the crown.

I thank Dr André Keyser for facilitating the loan of specimen JSM 100. I also wish to thank M. Claire Vanderslice for both the exceptionally fine preparation and the beautiful drawings of the specimen. My research was supported by National Science Foundation Research Grant BMS75-01159. Finally, I wish to acknowledge the importance to me of Dr James W. Kitching's friendship and support over the years. Wandering through the B.P.I. Karoo fossil collection with James, and listening to the story of each specimen he collected, was one of the great learning experiences of my life.

ABBREVIATIONS

ab	anterior basin
acin	anterior cingulum
actr	accessory cusps on transverse ridge
aicin	anteroexternal cingulum
aer	anteroexternal ridge
air	anterointernal ridge
brk	break
CC	upper central cusp
cc	lower central cusp
cc?	possible homologue of lower central cusp
crypt devPCa	crypt of developing upper postcanine (PC5?)
devPCa	developing upper postcanine (PC5?)
devPCb	developing upper postcanine (PC6?)
devPCc	developing upper lateral postcanine
displPCa	complete sectorial tooth loose in matrix
displPCb	rootless tooth loose in matrix
EC	upper external cusp
ec	lower external cusp
ec?	possible homologue of lower external cusp
ecin	external cingulum
IC	upper internal cusp
ic	lower internal cusp
lC	left upper canine
lc	left lower canine
mx	maxilla

orb	orbit
pal	palatine
pb	posterior basin
PC	upper postcanine
pc	lower postcanine
pcin	posterior cingulum
peg	peg-like upper tooth
per	posteroexternal ridge
pir	posterointernal ridge
pt	pterygoid
rC	right upper canine
rc	right lower canine
replC	replacement left upper canine
replc	replacement left lower canine
tr	transverse ridge
tr?	possible homologue of transverse ridge
unshedPC	unshed small worn gomphodont postcanine
v	vomer

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