

https://dspace.org/

A new skull of Megazostrodon (Mammalia, Triconodonta) from the Elliot Formation (Lower Jurassic) of Southern Africa

Gow, Chris E

1986-06-30
BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH
http://hdl.handle.net/10539/16138

Downloaded from a DSpace repository. https://dspace.org/

PALAEONTOLOGIA AFRICANA

Series of miscellaneous papers
published by
BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH

Volume 26 Number 2 ISSN 0078-8554 30 June 1986

A NEW SKULL OF MEGAZOSTRODON (MAMMALIA, TRICONODONTA) FROM THE ELLIOT FORMATION (LOWER JURASSIC) OF SOUTHERN AFRICA

by

C.E. Gow

Bernard Price Institute for Palaeontological Research,
University of the Witwatersrand, Johannesburg

ABSTRACT

A skull of *Megazostrodon* with atlas and axis in articulation is described. The dental formula is I 4/4 C 1/1 Pm 5/5 M 5/5. Tooth wear is more advanced than in the type specimen and the lower molar series contains evidence of tooth replacement. The braincase differs remarkably from that of *Morganucodon*, the only contemporaneous triconodont in which the skull is adequately known. The lower jaw has an angular process similar to that of *Dinnetherium*. The earliest triconodonts appear to represent a modest radiation following the attainment of mammalian status.

CONTENTS

	Page
Introduction	14
Locality	14
Material	14
Methods	14
Identity of New Specimen	14
Description:	
The skull — lateral view	15
The skull — ventral view	15
The braincase and associated structures in lateral aspect	15
The braincase and associated structures in ventral aspect	16
The lower jaw	16
Dentition	17
The atlas axis complex	19
Discussion:	
Comparison with other early triconodonts	21
Relationships of earliest triconodont mammals	22
Acknowledgement	22
Abbreviations	22
References	23

MS accepted 15 November 1985

©
Bernard Price Institute
for Palaeontological Research
University of the Witwatersrand
1 Jan Smuts Avenue
Johannesburg 2001
1986

INTRODUCTION

The earliest fossil mammals of Lower Jurassic age have traditionally been placed in three groups. The Haramiyidae (Europe and North America) are known only from isolated teeth, they are implicated in the origin of the Jurassic–Cretaceous Order Multituberculata but remain enigmatic. *Kuehneotherium* from the Welsh fissure fillings is known only from lower jaws and isolated teeth and is regarded as ancestral to therian mammals. The Family Morganucodontidae are the earliest members of the Order Triconodonta and they are regarded as ancestral to prototherian mammals. *Morganucodon* itself occurs in Britain, China and North America, and the closely related genus *Erythrotherium* in southern Africa. Jenkins et al. (1983) strongly imply that they regard Kuehneotheriidae as a Family within the Order Triconodonta, and on the basis of the present study that is to be welcomed. *Sinoconodon* does not reside easily within the Morganucodontidae, but with new material now available (Jenkins et al. op. cit.) should soon become better known.

Of these forms *Morganucodon* has up to now been the only one in which the skull is known in detail (Kermack et al. 1981). When teeth were the only basis of comparison *Megazostrodon* was regarded as a morganucodontid (Crompton 1974). The recently described *Dinnetherium* (Jenkins et al. 1983) has not been placed in a family. The new skull of *Megazostrodon* described here shows that this genus is sufficiently different from *Morganucodon* to warrant a Family of its own. On the other hand the lower jaws of *Megazostrodon* and *Dinnetherium*, while different, share important features which could serve to unite them in a Family Megazostrodontidae. Crompton (1974) and Jenkins et al. (1983) have remarked on aspects of the dentition of megazostrodontids in which they are intermediate between morganucodontids and kuehneotheriids. In fact these three contemporaneous Families exhibit a mosaic of shared and derived characters which precludes ranking them in an ancestor-descendant sequence and obliges us to look further back in time for their common ancestor.

LOCALITY AND AGE

The specimen BP/1/4983 in the collections of the Bernard Price Institute for Palaeontological Research was collected on the farm Gertruida (farm number 38) near Clocolan in the Orange Free State by Prof. James Kitching. It is from the Elliot Formation (Redbeds) approximately three metres below the Clarens Formation (Cave Sandstone). Kitching (pers. comm.) estimates that the Elliot Formation is 80 metres thick at this locality. The age of the Upper Elliot Formation is considered to be Lower Jurassic (Olsen and Galton 1984).

MATERIAL

The specimen which consists of a nearly complete skull with atlas and axis in articulation is contained in a friable block of red siltstone. A few isolated vertebrae are scattered within the matrix. The skull suffered some lateral compression which resulted in considerable distortion. The left side of the skull was exposed to weathering which has resulted in the loss of the upper teeth on that side as well as the zygomatic arch and much of that side of the braincase. The specimen was also badly damaged in the articular region of the right squamosal; the tip of the coronoid process of the right dentary is missing.

METHODS

The block was impregnated in situ with diluted Glyptal Cement which achieved excellent penetration to consolidate the friable material. The dry block was backed with plaster of paris. Following initial preparation of the skull the block was reduced with a rock cutting saw. Waste was retained for future examination. The block containing the skull was given a resin and glass fibre jacket to facilitate handling and subsequent storage.

For the most part preparation was by means of extremely sharp fine needles held in a small pin vice. Near the teeth the matrix was haematitic, which necessitated careful repeated use of thioglycolic acid. The left lower jaw had a bad fossilisation crack running through the region of the third molar. This crack was opened and another break was generated behind the canine. The jaw and teeth could then be removed. Preparation of the right lower teeth was more difficult as the jaws were tightly clenched and the teeth held in a palatal fold accentuated by the lateral compression to which the skull had been subjected. Eventually it was possible to generate a crack through the necks of the right lower postcanine teeth and remove the jaw behind the canine. Individual teeth were then prepared out in sequence with needles and replaced on the jaw. A very thin cheesy white layer occured between matrix and fossil which helped as far as the teeth were concerned but which was difficult to distinguish from some of the more delicate bones.

Very dilute Glyptal was used as consolidant throughout. The drawings were prepared using a fine grid graticule in the microscope eyepiece and square ruled drawing paper. Coating material was removed from the teeth for drawing and they were subsequently recoated. Photographs were taken using a yellow filter to enhance contrast.

IDENTITY OF THE NEW SPECIMEN

Megazostrodon rudnerae (Crompton and Jenkins 1968) was defined on the presence of large external (buccal) cingula on the upper molar teeth. This feature distinguished it from all other "morganucodont" genera including the southern African *Erythrotherium* (Crompton 1964). Subsequently Crompton (1974) presented a detailed account of the dentition of *Megazostrodon* and compared it in detail to those of other early triconodonts.

The new specimen shows considerably more molar wear than the type and also has the first undoubted replacing molar recorded for a "morganucodont" mammal. It seems inadvisable to erect a

new species for this second skull on the basis of such slight differences as exist in the postcanine dentitions of the two specimens (detailed below).

Recently Jenkins et al. (1983) described a new triconodont mammal (*Dinnetherium*) from the Kayenta Formation of Arizona. The dentition and pattern of occlusion in this form are similar to *Megazostrodon*, including the large upper buccal cingula. Supposed unique features of the lower jaw of *Dinnetherium* are also possessed by the new specimen of *Megazostrodon*: they are not preserved in the type.

DESCRIPTION

The Skull — Lateral View (Figures 1 and 5)

The right side of the skull is badly eroded. The left side was completely enclosed in matrix but the matrix was deeply weathered and cracked. The cracks run through and within the superficial bones of the skull with the result that it is not possible to determine sutures in the preorbital region or within the orbit. The braincase is better preserved and is dealt with separately below. There is a distinct boss in the lacrimal region, possibly for the attachment of facial muscles. The fronto-parietal suture is distinct, the parietal-squamosal suture less so. The zygomatic arch (figs 1 and 6) is preserved attached to the lower jaw: the anterior contact with the skull is

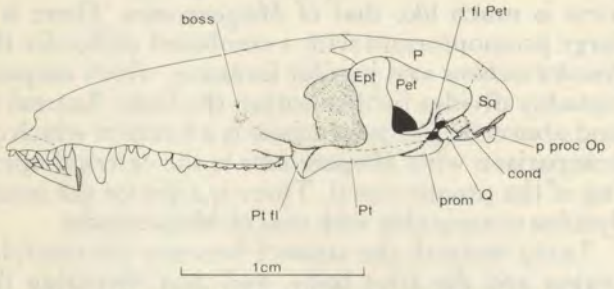


Figure 1. *Megazostrodon*. Left lateral view of skull with lower jaws removed posterior to lower canines.

sound but there is no posterior contact as a portion of the squamosal is missing. The arch lacks the strong dorsal arching depicted for *Morganucodon* (Kermack et al. 1981) and the skull lacks a sagittal crest. There is a robust pterygoid flange which is not separated from the rest of the pterygoid by a deep anterior incisure as is the case in *Morganucodon* (Kermack et al. 1981). Hopson (pers. comm.) states that there is no anterior incisure in *Morganucodon* .

The Skull — Ventral View (Figures 2 and 5)

The effects of distortion are apparent from the figures. Palatal sutures cannot be determined. The deep groove which held the left postcanine teeth is almost certainly an artifact of compression as it is entirely absent on the right side: the true condition of this region was probably very similar to that seen in *Morganucodon* (Kermack et al. 1981) which has pits for the lower post canine crowns. The ventral region between palate and braincase has suffered severe fossilisation damage and is indicated as matrix in Figure 2. The braincase is treated separately below.

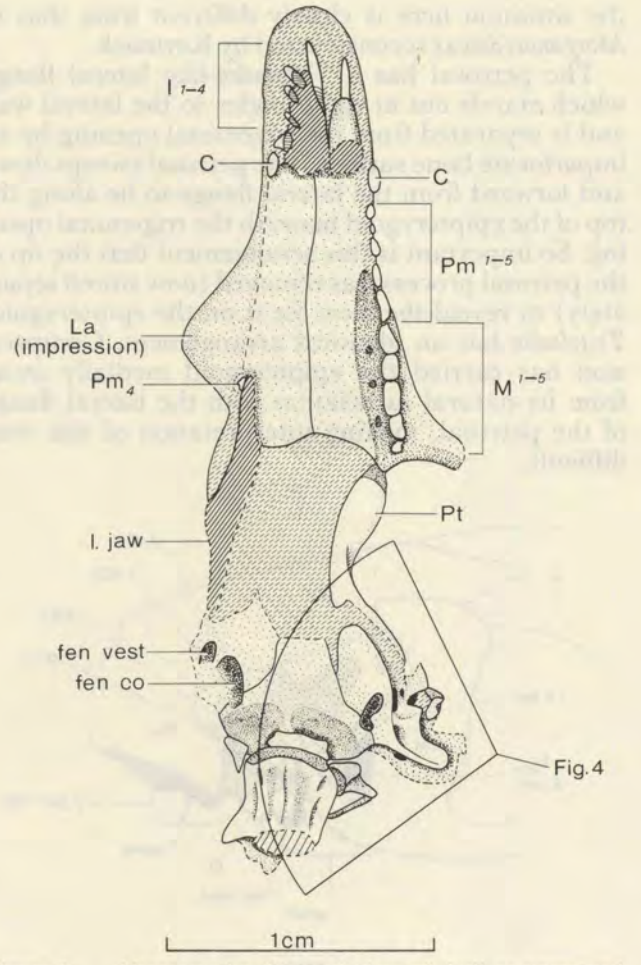


Figure 2. *Megazostrodon*. Ventral view of skull as preserved. Area between palate and braincase is badly damaged. Marked segment is shown in detail in Figure 4.

The Braincase and Associated Structures in Lateral Aspect (Figures 3 and 5)

As preserved the upper end of the epipterygoid lies against the lateral surface of the fronto-parietal contact. (The term epipterygoid is used advisedly to indicate strict homology with the equivalent element of cynodonts). It has a sinuous posterior border perhaps accentuated by crushing. The quadrate rami of epipterygoid and pterygoid cannot be differentiated, nor can their posterior limits be determined, and this region has been flattened against the promontorium of the petrosal. The median portion of the lateral surface of the petrosal is either incompletely ossified or incompletely preserved, perhaps as a result of post-mortem damage: this would require confirmation from additional material. The anterior lamina of the petrosal contacts epipterygoid and in all probability continues forward medial to the epipterygoid. I would reconstruct a similar relationship for *Morganucodon*, based on Kermack et al. (1981) Figure 1B. There can be no doubt about the single *Thrinaxodon*-like trigeminal opening: the borders are sound. (The exact conformation of this area may prove to be variable due to overgrowth of membrane bone as is the case in *Tritylodon* (Gow, in press). Be that as it may,

the situation here is clearly different from that in *Morganucodon* as reconstructed by Kermack.

The petrosal has a *Tritylodon*-like lateral flange which stands out at right angles to the lateral wall and is separated from the trigeminal opening by an imperforate bone surface. The petrosal sweeps down and forward from the lateral flange to lie along the top of the epipterygoid beneath the trigeminal opening. So important is this arrangement that the tip of the petrosal process was removed (now stored separately) to reveal the facet for it on the epipterygoid. *Tritylodon* has an identical arrangement. Compression has carried the epipterygoid medially away from its natural association with the lateral flange of the petrosal, making interpretation of this area difficult.

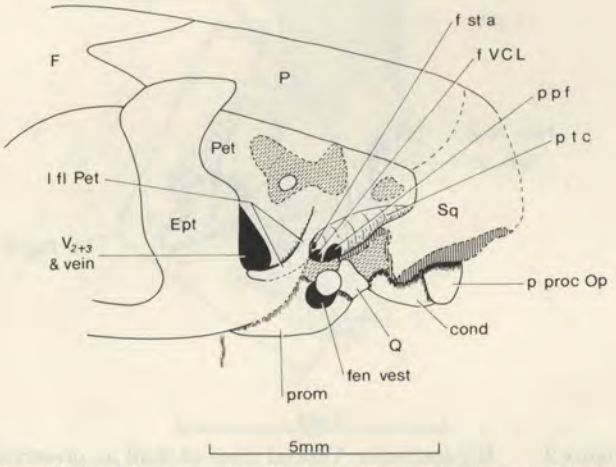


Figure 3. *Megazostrodon*. Lateral view of braincase. Dashed lines indicate matrix, vertical lines broken bone.

Just as in *Tritylodon* the lateral flange is pierced by a relatively large foramen for the *vena cerebralis lateralis* (this is the foramen which Kermack et al. (1981) call the exit for the VIIth cranial nerve) and a small, more dorsolaterally situated foramen probably for a branch of the stapedial artery (visible in fig. 5). Behind these is the pterygoparoccipital foramen. The post-temporal foramen is visible on the occiput (fig. 4).

Matrix retained between the lateral flange of the petrosal and the damaged squamosal contains a quadrate lateral to the *fenestra vestibulae*. The stapes was not preserved. It is not possible to develop the quadrate further without seriously weakening the specimen: in size and shape it is a normal "morganucodont" quadrate (Kermack et al. 1981, figs. 86, 87).

The Braincase and Associated Structures in Ventral Aspect (Figures 4 and 5)

The petrosal has two distinct parts to the paroccipital process; the more anterior process is derived at least in part from cynodont prootic. This is the component labelled paroccipital process by Kermack et al. (1981) for *Morganucodon*. *Megazostrodon* has an unexpectedly extensive posterior portion of the paroccipital process which is of opisthotic derivation. An

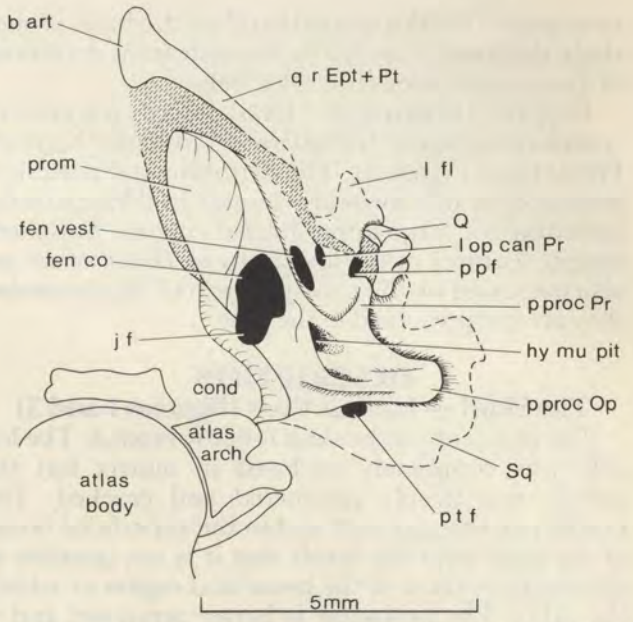


Figure 4. *Megazostrodon*. Ventral view of braincase. Dashed lines indicate matrix.

opisthotic portion of the paroccipital process of comparable extent is also seen in *Tritylodon*.

With the above exception, the petrosal in ventral view is much like that of *Morganucodon*. There is a large promontorium with a combined orifice for the *fenestra cochleae* and jugular foramen, which unquestionably divides further within the bone. Lateral to and above the *fenestra vestibulae* is a foramen which on comparison with *Morganucodon* is the external opening of the prootic canal. There is a pit for the *levator hyoideae* comparable with that of *Morganucodon*.

Lying beneath the contact between the condylar region and the atlas body, and thus obscuring the dens of the atlas, is a small transversely elongate bone, the atlas intercentrum.

The Lower Jaw (Figures 6, 7 and 8)

This description is based on the left lower jaw as much of the right jaw is missing. The jaws were separated from the skull behind the lower canines as the long slender symphysial region is tightly interlocked with the snout. A small wedge of dentary remains attached to the pterygoid flange. The zygomatic arch and supporting matrix have been left attached to the jaw. The top of the coronoid process of the dentary is missing.

The dentary has a coronoid boss to which the coronoid bone is applied. This boss forms a prominent dorsal swelling between the ramus and coronoid process of the dentary as seen in lateral and medial views. As is clear from Kermack et al. (1973, figure 7) the coronoid boss of *Morganucodon* does not interrupt the smooth contour between ramus and coronoid process. There is a thin but extensive angular process situated between a pseudangular process and the condyle of the dentary; this is supported by matrix laterally as the bone is badly shattered in this region. The angular process represents a ventral ex-



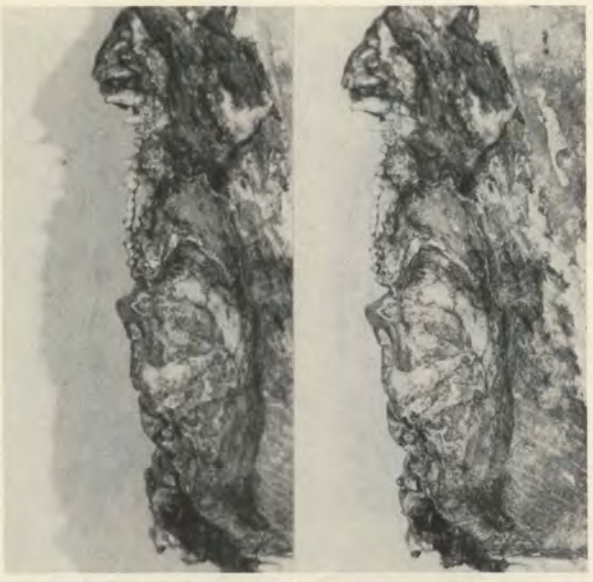


Figure 5. *Megazostrodon*. Stereophotographs of ventral aspect above and left lateral aspect below.

tension of the lateral ridge of the dentary seen in advanced cynodonts and *Morganucodon*, it is similar to the same process in *Dinnetherium* (Jenkins et al. 1983). The dentary condyle is robust but does not form a prominent projection as it is roughly confluent with the angular process below and the coronoid process above. The condylar region is very similar to that of the better preserved *Dinnetherium*.

There is a well developed groove for the postdentary bones which are slightly displaced. Articular and prearticular are preserved but the meeting of the two bones cannot be distinguished. The quadrate facet of the articular is nicely preserved orientated postero-medially. Above the articular–prearticular is a splint-like surangular and below it are fragmentary traces of angular.

Dentition

The dental formula is I 4/4 C 1/1 PM 5/5 M 5/5.

Incisors (Figures 1, 2, 6 and 7).

The incisor battery is very similar to that of *Morganucodon*. The right uppers are damaged by weathering but all four are well preserved on the left, they project forwards and the tips are well worn. Three lowers are present in the right dentary, four in the left. These teeth are angled progressively more anteriorly from back to front, and while they also have worn tips, they are appreciably longer than the uppers. Behind the upper incisors is a diastema bearing a depression which received the tip of the lower canine, as in *Morganucodon*.

Premolars (Figures 1, 2, 3, 5, 6, 7, 8, 15 and 16)

Premolars accord well with those of the type (Crompton 1974). Traces of five upper premolars are preserved on the weathered right side and all five are well preserved on the left. Five lowers are present in each dentary.

The first upper premolar is a caniniform tooth about half as long as the canine. The same is apparently true of the type though in the latter Pm^1 is damaged and displaced. This is quite unlike the condition in *Morganucodon* where the first premolar is the smallest.

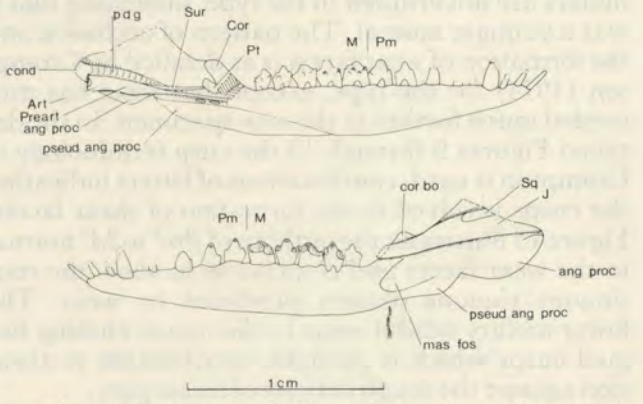


Figure 6. *Megazostrodon*. Left lower jaw and part of zygomatic arch.

Pm^2 is the smallest of the upper premolars, the crown has a pronounced distal swelling. The first two premolars are single rooted. Premolars three four and five increase progressively in crown height. All three have shear facets worn on the lingual surfaces of the "A" cusps. All three are mesiodistally expanded and double rooted and bear mesial and distal cusps. Pm^5 has distinct mesial and distal buccal cingulum cusps.

Lower premolars increase in height and mesiodistal length from front to back. As with the uppers the last three are double rooted. A slight distal swelling is present on all crowns while the last three have a small mesial cusplet as well. Pm_4 and Pm_5 had in addition what was clearly a tall distal cusp in line with the main cusp, though these are heavily worn. Mesial and distal cuspules of Pm_5 have strong cingulum ridges extending onto the buccal surface.

Molars (Figures 1, 2, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15 and 16)

There is a fully developed set of 5/5 molars. Fifth

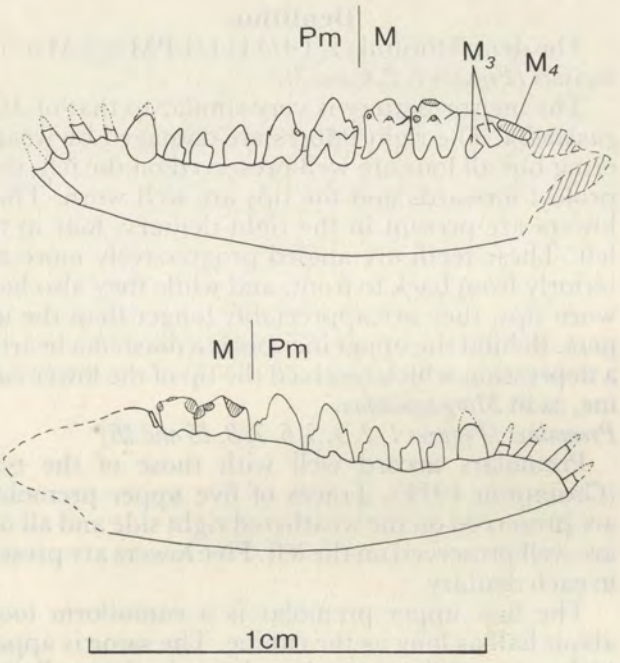


Figure 7. *Megazostrodon*. Right lower jaw. The crown of M_3 is missing: M_4 is attached to the skull.

molars are not erupted in the type, indicating that it was a younger animal. The pattern of occlusion and the formation of wear facets is as detailed by Crompton (1974) for the type, except that wear has proceeded much further in the new specimen. In the detailed Figures 9 through 13 the cusp terminology of Crompton is used, combinations of letters indicating the cusps involved in the formation of shear facets. Figure 13 illustrates the outlines of Pm^5 to M^5 normal to the wear facets and is included to show the continuous sinuous pattern produced by wear. The lower molars exhibit wear to the non-occluding lingual cusps which is probably attributable to abrasion against the tough cuticles of insect prey.

The molars differ from those of the type in one obvious respect only and that is the pattern of cusps on the buccal cingulum ridges of the uppers. These ridges are prominent in both specimens, swelling out well away from the mesiodistal crown axis. There are buccal cingulum ridges lateral to the anterior and posterior accessory cusps (cusps B, C), separated by the convexity of the main or "A" cusp. In the type each ridge bears several distinct cusps while in the new specimen each ridge is essentially single cusped (F and D cusps). These cusps are unworn. There is a very minor difference between the two specimens in the pattern of lingual cusplets on the lower molars. In Crompton's (1974) Figure 6B there is an undesignated cusp between cusps "e" and "g", incipient on M_1 and prominent on M_2 and M_3; in the new specimen this cusp is present on M_1 but absent from all the other molars. These slight differences in the non-occluding cusps are probably best regarded at this stage as due to individual variation and not subject to strong stabilising selection. There is also the problem of molar replacement which will be dealt with next.





Figure 8. *Megazostrodon*. Stereophotographs of lower jaws in buccal aspect above and lingual aspect below.

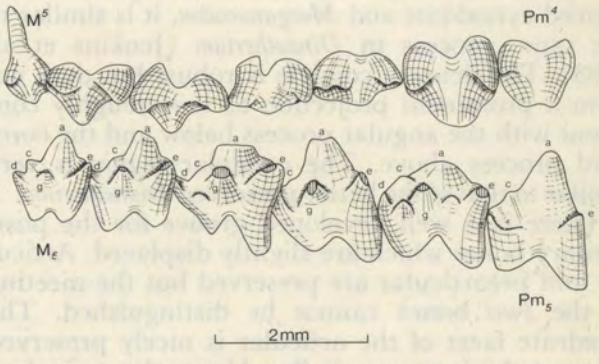


Figure 9. *Megazostrodon*. Left posterior postcanine teeth—non-occluding surfaces. Uppers in buccal and lowers in lingual view.

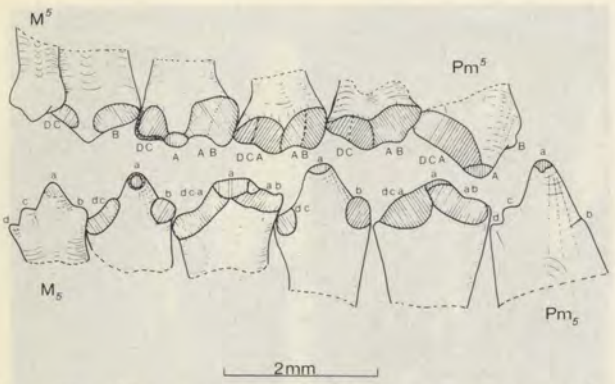


Figure 10. *Megazostrodon*. Left posterior postcanine teeth—occluding surfaces. Uppers in lingual and lowers in buccal view. Dashed lines on M^1 and M^2 indicate second phase wear produced by "b" and "dc" facets of M_2. Wear facets labelled according to cusps involved in their formation. Lettering follows Crompton 1974.

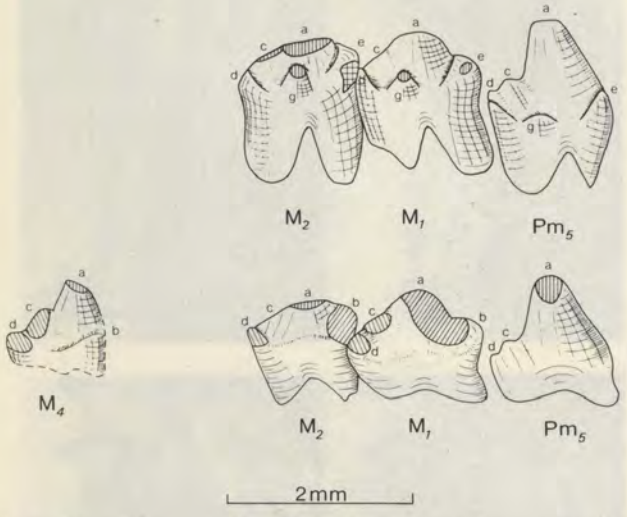


Figure 11. *Megazostrodon*. Right lower posterior postcanine teeth in lingual view above and buccal view below.

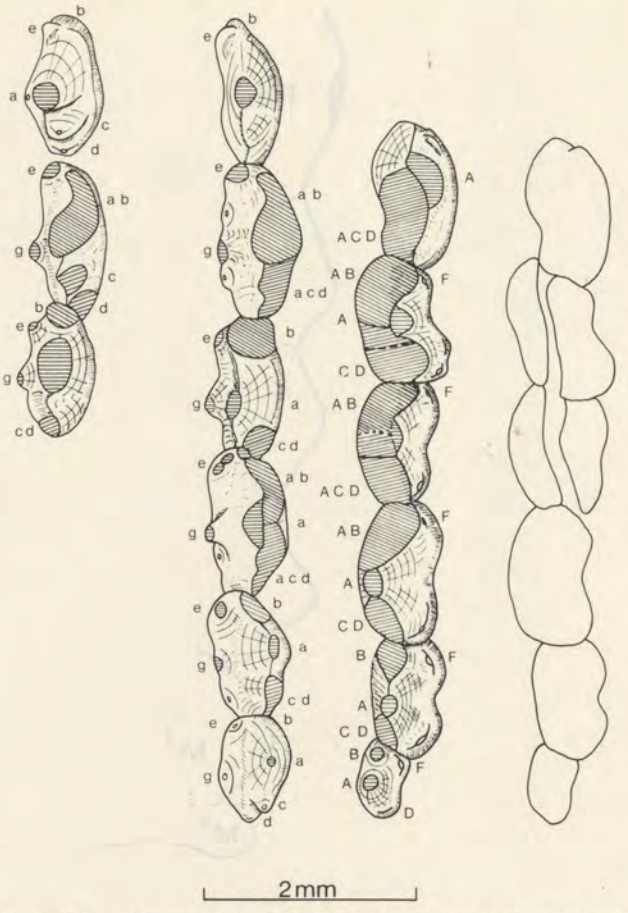


Figure 12. *Megazostrodon*. Approximate occlusal views of posterior postcanine teeth.
Left to right: right Pm_5 to M_2, left Pm_5 to M_5, left Pm^5 to M^5, outlines of left uppers showing the broad crack affecting M^1 and M^2 shown closed up in the detailed drawing.

In the new specimen the left M_2 is unquestionably a replacement — the first replacing molar known in a "morganucodont" mammal. This is deduced from several lines of evidence such as the mild state of wear relative to M_1 and M_3 and the fact that M^1, M^2 and M^3 exhibit roughly equivalent states of wear. Also, as is clear from Figures 10 and 12, M_2 could not have made the wear facets on M^1 and M^2, and most importantly, cusps "b"and "c" + "d" of M_2 have worn perceptibly deeper into the corresponding facets DCA of M^1 and AB of M^2 respectively, as indicated by dashed lines on the figures. Wear to the "a" cusp of the replacement M_2 could have been caused by contact with prey only as is the case with the lingual cusps on the lower molars.

It is also interesting to compare left and right M_1 and M_2. The right M_1 is very slightly less worn than the left. The right M_2 exhibits more "a" cusp wear and less "b" and "c+d" wear than the left. It therefore seems likely that "a" cusp wear is more rapid in a first generation molar, "a" cusp wear may remain minimal in second generation molars, at least until their worn counterparts are replaced, and hence constitute a useful means of recognition.

Molar replacement could well have been common in the Early Jurassic Triconodonta: it would be difficult to recognise without at least a complete molar series and preferably a full set of occluding molars.

The Atlas Axis Complex

The atlas and axis are robust elements in natural articulation with the skull. They have been exposed in ventral and lateral views only. Due to the presence of the atlas intercentrum no attempt could be made to prepare out the dens of the atlas. Regarding the atlas intercentrum Jenkins (pers. comm.) comments as follows:

"The facet-like appearance of its lateral ends probably represents ligamentous attachment to the ventral parts of the atlas arches, thus completing an osseoligamentous atlas ring (as in some cynodonts and other early mammals)". The various elements correspond well with what is known of these bones in related triconodonts (Jenkins and Parrington 1976) except that the atlas arches are not angled forwards as reconstructed by these authors. The separate at-



Figure 13. *Megazostrodon*. Left upper posterior postcanine teeth in outline, wear facets vertical to the plane of the paper.

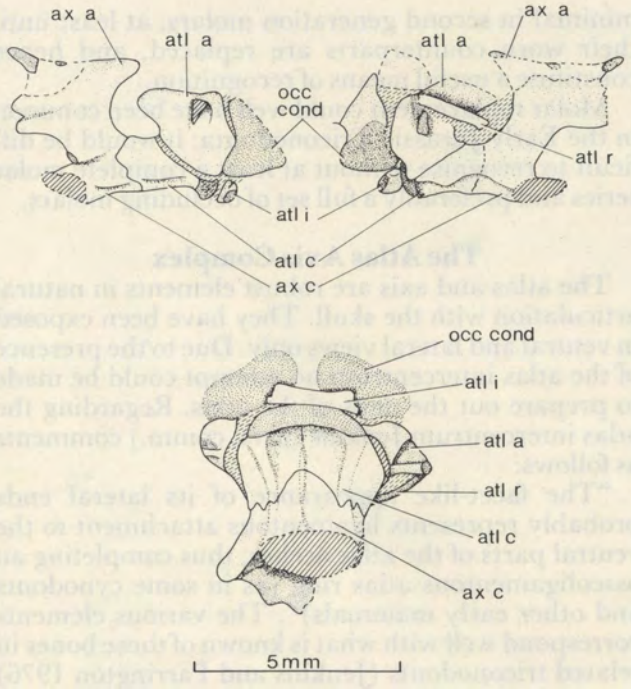


Figure 14. *Megazostrodon*. Atlas and axis. Lateral views above and ventral view below.

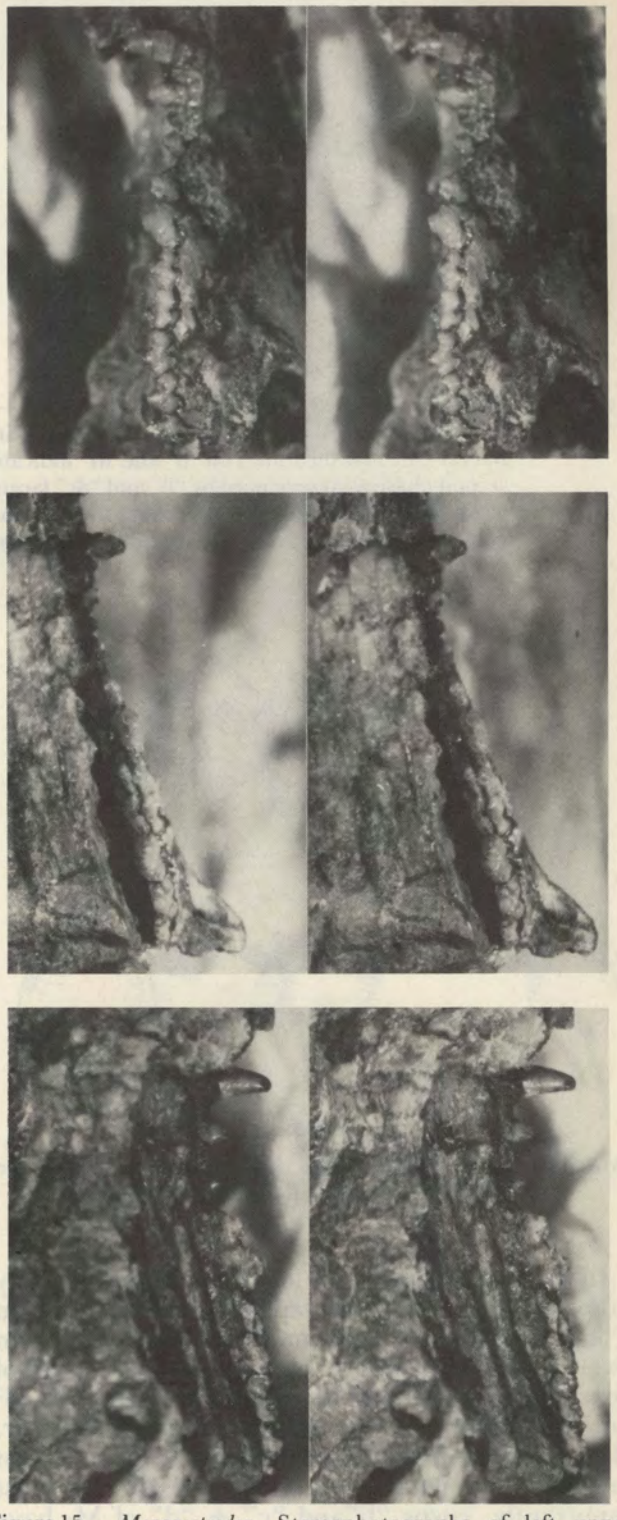


Figure 15. *Megazostrodon*. Stereophotographs of left upper dentition. From top to bottom: buccal, occlusal, lingual.

las arch elements have strong transverse processes which articulated with the first pair of cervical ribs (a rib is preserved in close association on the left side). Atlas and axis centra are fused and the suture is quite distinct. The axis arch is indistinguishably fused to its centrum; its anterior crest overhangs the atlas arches a little. The crest is drawn out posteriorly as well. A posterior zygapophysis is well preserved on the right side.



Figure 16. *Megazostrodon*. Stereophotographs of left lower dentition. From top to bottom: lingual, occlusal, buccal.

DISCUSSION

Megazostrodon compared with *Morganucodon* and *Dinnetherium*.

By analogy with *Thrinaxodon*, for which a good growth series is known, the absence of a sagittal crest in *Megazostrodon* is here interpreted as retention of the neotenic cynodont condition. The sagittal crest of *Morganucodon* is similar to that of mature cynodonts.

The single trigeminal opening of *Megazostrodon* may also be a neotenic cynodont character, though *Morganucodon* with separate openings for V2 and V3 is certainly different and seemingly more advanced in this respect, if correctly interpreted.

The lower canine in *Megazostrodon* lacks the constricted neck seen in the equivalent tooth of *Morganucodon*, and in this respect is more primitive.

These three characters together make *Megazostrodon* appear the more primitive animal but do not deny close relationship for the two genera.

It is in the structure of the petrosal that the most striking differences are seen. In *Megazostrodon* the lateral wall of the petrosal is short and imperforate between trigeminal foramen and lateral flange. In *Morganucodon* this region is more extensive; it is apparently separated by a gap from the epipterygoid and is pierced by large well defined foramina for V2 and V3. The post-temporal canal is more horizontal in *Megazostrodon*. The lateral flange of the petrosal and the foramina which penetrate it are exactly comparable in *Megazostrodon* and *Tritylodon*. In this area *Morganucodon* may be more similar than it appears due to incompleteness of the material and interpretive bias. The paroccipital process of *Megazostrodon* differs from that of *Morganucodon* in the same way that that of tritylodontids differs from the condition in carnivorous cynodonts in having a large component of opisthotic origin.

The angular and pseudangular processes of the dentary are derived characters shared by *Megazostrodon* and *Dinnetherium* and both genera have large buccal cingulum cusps on the upper molars. They are distinguished by the coronoid boss of the dentary being more prominent in lateral view in *Megazostrodon*, and minor differences in tooth crown morphology and occlusal pattern. A petrosal of *Dinnetherium* would be most valuable for comparison.

Tooth Replacement

Crompton (1974) and Parrington (1978) have been adamant that the early triconodonts exhibit true mammalian diphyodonty. Crompton noted that the posterior postcanine teeth of morganucodontids and keuhneotheriids have a tongue and groove relationship to align the teeth accurately to ensure precise occlusal relationships. He stated that alternate replacement would rule out precise occlusal relationships. The new specimen of *Megazostrodon* shows that molars may replace, the replacements moving into the tongue-and-groove arrangement and hence into a precise occlusal relationship. There may well be a constraint on replacement in the sense

that it happens at different times in upper and lower jaws, so ensuring an effective biting mechanism at all times.

Relationships of Earliest Mammals.

The earliest mammals are traditionally divided into two families, the Kuehneotheriidae containing only the poorly known *Kuehneotherium*, with teeth indicative of therian relationship, and the Morganucodontidae containing *Morganucodon*, *Erythrotherium*, *Megazostrodon* and possibly the poorly known *Sinocondon* (Crompton 1974). The Morganucodontidae are implicated in the ancestry of non-therian mammals (Kermack et al. 1981).

The "Morganucodontidae" share the dental formula I 4/4 C 1/1 Pm 5/5 M 5/5. Anything less than a fully developed dentition has doubtful taxonomic value. Fifth molars are uncommon but are known in the large sample of *Morganucodon* (Mills 1971). The closely allied *Erythrotherium* has M 4/4 but this was a young animal (Crompton 1974). Crompton (1974) noted similarities between the molars of *Megazostrodon* and *Kuehneotherium* regarding the triangular arrangement of the major cusps. Jenkins et al. (1983) remark that molar cusp height in *Dinnetherium* and *Kuehneotherium* is similar. They conclude:

"A simple dichotomy between morganucodontids (non therians) and keuhneotheriids (therians) no longer appears to be an accurate representation of the complex early evolution of mammals".

The petrosal of *Megazostrodon* is quite unlike that of *Morganucodon*. By analogy with cynodont taxonomy the differences are such that these genera must be placed in different families. Differences in dentition (presence of buccal cingulum cusps in *Megazostrodon*) are likely also significant at this level. Jenkins et al. (1983) refrained from placing *Dinnetherium* in a family. It now seems probable that it and *Megazostrodon* group together in a Family Megazostrodontidae on the basis of a shared dental character (buccal cingulum cusps on upper molars), and lower jaw structure (presence of angular and pseudangular processes).

It is apparent from their anatomy and distribution that the earliest mammals already represent a modest radiation following the attainment of mammalian status. It may indeed be possible to find still more primitive mammals in which small size and differentiated dentition with interlocking of adjacent molars is established, but with none of the specialisations of *Morganucodon* and *Megazostrodon*.

It is often the case that forms with quite remote common ancestry share evolutionary time grade characters. The close similarity of petrosal structure between *Megazostrodon* and tritylodontids exemplifies this phenomenon: it should not be regarded as indicative of sister group relationship.

ACKNOWLEDGEMENT

The discovery of a mammal skull from the Elliot Formation of southern Africa is an exceptional event and I would like to thank Prof. James Kitching for allowing me to work on this specimen. Profs. Farish Jenkins Jnr. and Jim Hopson are cordially thanked for their useful comments on the manuscript.

ABBREVIATIONS

ang. proc.	angular process
Art.	Articular
atl. a.	atlas arch
atl. c.	atlas centrum
atl. i.	atlas intercentrum
atl. r.	atlas rib
ax. a.	axis arch
ax. c.	axis centrum
b. art.	basal articulation
cond.	condyle
Cor.	Coronoid
Cor. bo.	Coronoid boss
Ept.	Epipterygoid
F	Frontal
fen. co.	fenestra cochleae
fen. vest.	fenestra vestibulae
f. st. a.	foramen for stapedial artery
f. VCL	foramen for vena cerebralis lateralis
hy. mu. pit	pit for levator hyoidei muscle
J	Jugal
jf	jugular foramen
La	Lacrimal
l. fl. Pet.	lateral flange of Petrosal
l. op. can. Pr.	lateral opening of prootic canal
mas. fos.	masseteric fossa
occ. cond.	occipital condyle
P	Parietal
p. proc. Op.	paroccipital process of Opisthotic
Pet.	Petrosal
p. d. g.	groove for post dentary bones
p. t. c.	post temporal canal
p. t. f.	post temporal fossa
prom.	promontorium
pseud. ang. proc.	pseudangular process
Pt	Pterygoid
Pt fl.	Pterygoid flange
p.p.f.	pterygoparoccipital foramen
Q	Quadrate
q.r. Ept. + Pt.	quadrate ramus of Epipterygoid and Pterygoid
Sq	Squamosal
Sur	Surangular

REFERENCES

Crompton, A.W. (1964). A preliminary description of a new mammal from the Upper Triassic of South Africa. *Proc. Zool. Soc. Lond.* **142**(3), 441–452.

————(1974). The dentitions and relationships of the southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae*. *Bull. Br. Mus. Nat. Hist. (Geol.)* **24**, 399–437.

Crompton, A.W. and Jenkins, F.A. Jr. (1968). Molar occlusion in Late Triassic mammals. *Biol. Rev.* **43**, 427–458.

Gow, C.E. (in press). The side wall of the braincase in cynodont therapsids,and a note on the homology of the mammalian promontorium. *S. Afr. J. Zool.*

Jenkins, F.A. Jr., Crompton, A.W. and Downs, W.R. (1983). Mesozoic mammals from Arizona: new evidence on mammalian evolution. *Science* **222**, 1233–1235.

Jenkins, F.A. Jr., and Parrington, F.R. (1976). The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. *Phil. Trans. R. Soc. Lond.* B. **273** (926), 387–431.

Kermack, K.A., Musset, F. and Rigney, H.W. (1973). The lower jaw of *Morganucodon*. *Zool. J. Linn. Soc.* **53**, 87–175.

Kermack, K.A., Mussett, F., and Rigney, H.W. (1981). The skull of *Morganucodon*. *Zool. J. Linn. Soc.* **71**, 1–158.

Mills, J.R.E. (1971). The dentition of *Morganucodon*. In Kermack, D.M. and K.A. Kermack eds. Early Mammals. Suppl. 1 *Zool. J. Linn. Soc. Lond.* **50**, 29–63.

Olsen, P.E. and Galton, P.M. (1984). A review of the reptile and amphibian assemblages from the Stormberg of Southern Africa with special emphasis on the footprints and the age of the Stormberg. *Palaeont. afr.* **25**, 87–110.

Parrington, F.R. (1978). A further account of the Triassic mammals. *Phil. Trans. R. Soc. Lond.* B **282**(989), 177–204.

Printed by The Natal Witness (Pty) Ltd