NOTES ON SOME CHALICOTHERE REMAINS FROM MAKAPANSGAT

By G. L. Webb

Abstract

This paper deals with the South African chalicothere remains from Makapansgat, Potgietersrus, with mention of those from Serengeti described by Dietrich. From Makapansgat there are 12 post-cranial remains comprising 2 terminal phalanges, 1 intermediate phalanx, 1 co-ossified phalanx, 1 carpal or tarsal bone, 2 metacarpals, 2 tibiae, 2 innominates and 1 scapula: and 74 cranial remains. This latter figure is made up of 45 isolated teeth, of which 36 are upper teeth and 9 are lower teeth, 7 maxillary fragments and 22 mandibular fragments.

The South African form, classified as *Metaschizotherium transvaalensis* is compared with the American forms *Moropus elatus* and *Moropus petersoni* and is found to resemble more closely in size *M. elatus*.

The reasons for retaining the classification of *M. transvaalensis* are given and discussed.

Finally the relationship of the Makapansgat specimens to the osteodontokeratic culture is discussed.

Introduction

The chalicotheres are unique in possessing a combination of grazing teeth and short feet with phalanges terminating in claws and not in hooves.

African chalicotherine remains are scarce; a phalangeal bone in the Kaiso Beds of Uganda was the first indication that this type of animal had lived in Africa. This bone was described in very general terms by Andrews (1923) without generic identification. No further paper appeard on this subject until Dietrich (1942) described some chalicotherine remains from South Serengeti, Tanganyika. They consisted chiefly of a metacarpal, a phalanx and a tooth which Dietrich identified as belonging to Von Koenigswald's genus *Metaschizotherium*. In spite of the fact that this genus belongs to the Upper Miocene fauna of Europe, Dietrich referred his Pleistocene specimens to the same genus since they retained the low-crowned molar form of the European type.

In 1949 three isolated teeth and a terminal phalanx, recovered from the Limeworks Quarry of the Makapansgat Valley in the Potgietersrus District, Transvaal, were described by George (1950) who placed them in the same genus *Metaschizotherium* but as a new species *M. transvaalensis*.

The metacarpal and phalanx from Serengeti belong to the second digit of the left manus but unfortunately both are fragmentary and no comparative measurements were given by Dietrich. The tooth on which Dietrich based his classification was a right upper second molar which had been heavily worn. The tooth is almost complete and the following table gives the comparative measurements of the genotype *M. fraasi* from Steinheim, *M. hennigi* from Serengeti and *M. transvaalensis* from Makapansgat. The measurements of *M. transvaalensis* and *M. hennigi* are almost identical except for the breadth/length index

where *M. transvaalensis* agrees more closely with *M. fraasi*. Without any knowledge of the range of variation of this index in any of the species it is uncertain what weight is to be attached to these varying proportions.

	M. fraasi	*M. hennigi*	*M. transvaalensis*
Anterior-posterior diameter ..	46mm.	55mm.	53mm.
Transverse diameter	36mm.	40mm.	42mm.
Height at paracone	30mm.	33mm.	33mm.
Height at protocone	—	12mm.	12mm.
Breadth/length index	78·26	72·72	79·24

There is an unfortunate error in Hopwood and Hollyfield 'An Annotated Bibliography of the Fossil Mammals of Africa'. They state on p. 151 that *M. transvaalensis* (George, 1950) comes from Tanganyika, it should of course read Transvaal, South Africa.

Thus very little is known about the African chalicotheres. Their remains, although present in Pleistocene deposits, are exceptionally rare so it is extremely important to place them on record when found, however fragmentary they may happen to be.

Chalicothere remains from Makapansgat

The collection of chalicotherine remains in the Bernard Price Institute for Palaeontological Research is still small but has increased substantially as compared with the four fragments available in 1949 when the first remains were recovered. Of the more than 50,000 fragments recovered from Makapansgat Limeworks breccia the vast majority belong to the Artiodactyla. Only 86 belong to the Chalicotheroidea, i.e. a ratio of approximately 1 in 568. Of these 86 fragments 74 or 84·0% are cranial, the remaining 12 are post-cranial and comprise two terminal phalanges, 1 intermediate phalanx, 1 co-ossified phalanx, 1 carpal or tarsal bone, 2 metacarpals, 2 tibiae, 2 innominates and 1 scapula.

Of the 76 cranial remains 45 or nearly 60% are isolated teeth (36 upper and 9 lower), the remaining fragments being 7 maxillary, and 22 mandibular fragments.

All these specimens, the majority isolated from the basal grey breccia, have been cleaned, numbered and catalogued and are in the collection at the Bernard Price Institute for Palaeontological Research.

The chalicothere remains all come from the basal grey breccia at Makapansgat with the exception of three specimens that came from the immediately overlying part of the pink breccia. No specimens have been recovered from the higher or "cercopithecoides" portion of the Phase 1 breccia.

General description of the chalicothere skeleton

As the skeleton altered considerably during the evolution of the group the following brief description is only general but will serve as an introduction to the discussion of the remains.

Early skulls were long and relatively low but later forms show a marked shortening of the preorbital region. The preorbital and post-orbital portions are approximately subequal in length. In later forms, e.g. *Macrotherium*, the maxilla drops vertically and the nasals are retracted and seldom project beyond the second premolar. A very definite feature is the orbit being completely open behind; in early forms the orbit was above the second molar whereas later it lay just above the last molar.

The brain case is small and restricted giving rise to high sharp sagittal and lamboidal crests for the attachment of the masticatory muscles.

The post glenoid process is heavy.

The basioccipital and basisphenoid usually have a sharp median keel becoming confluent with the vomer in the nasal passage.

The palate is usually wide in the region of the cheek teeth but the premaxillaries become very narrow and short.

The basicranial foramina are characteristic for all chalicotheres. The optic foramen is situated slightly behind the postorbital boundary and a long furrow runs back from this to the foramen lacerum anterius which is found directly above the foramen rotundum. An alisphenoid canal is present and the foramen ovale opens just behind this canal but in front of the bulla. Behind the ovale is the foramen lacerum medius and at the back of the bulla found close together are the foramen lacerum posterius and the condylar foramen. A large stylomastoid foramen is present.

The mandible is usually long with a slender horizontal ramus. The ascending ramus is wide but the lower angle projects below the border of the horizontal ramus. The coronoid process usually extends avove the condyle.

There is considerable diversity in the number of teeth in both the upper and lower jaws. There are usually three brachyodont upper molars, quadrate in shape with well developed mesostyles. The three lower molars are double crescents with typical separated metastylids. Incisors and canines are present in the earlier forms but have been lost in the later forms particularly from the upper jaw. The first deciduous molars and premolars are lost in both upper and lower jaws. The dental formula is most probably ?, 0, 3, 3/3—0, 1—0, 3, 3.

The post-cranial skeleton is perissodactyl-like with a few distinct features that are typical of the chalicotheres.

The neck and pelvis are elongated.

The forelimbs are longer than the hind limbs. Early forms had tetradactyl fore feet, the later ones tridactyl. The hind feet are tridactyl. The chalicothere metapodials have a characteristic 'ball and ridge' articulation with the phalanges.

165M. Left Scapula fragment.

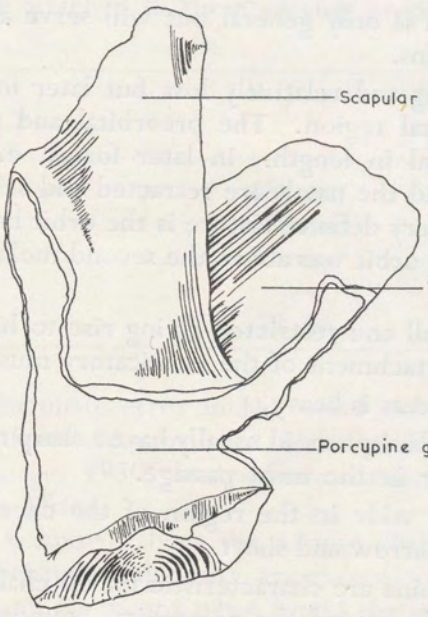
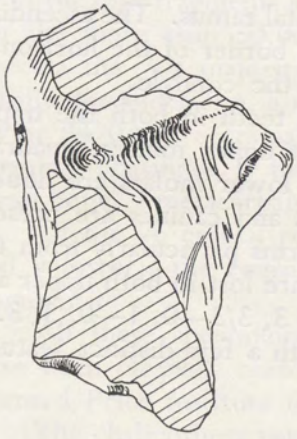


FIGURE 16

14112M. Proximal end of left Metacarpal II.



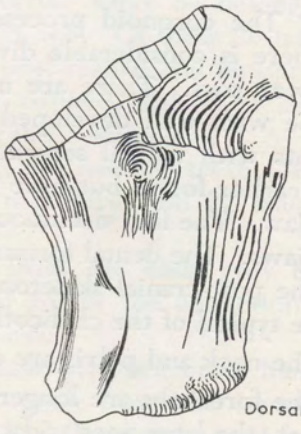


FIGURE 17

In all but the most primitive form *Eomoropus* the terminal phalanges are laterally compressed, pointed and deeply bifid.

Caudal vertebrae have been found in the various deposits and therefore they are regarded as having been tailed creatures.

The Makapansgat remains show that *Metaschizotherium transvaalensis* was a fairly massive creature. The drawings that have been made to illustrate them were made with the aid of a dioptograph, for the use of which I am obligated to the kindness of Professor P. V. Tobias and the staff of the Department of Anatomy in the Medical School of the University of the Witwatersrand.

Post-cranial remains from Makapansgat

Of the 12 post-cranial fragments none is complete. This is not due only to the damage they sustained before fossilisation but also to damage during the mining. This latter damage has been represented in the drawings by cross-hatching.

Their fragmentary condition would have rendered them undecipherable without having access (through the generosity of the Director of the Natal Museum in Pietermaritzburg, who kindly loaned me a copy) to 'The Osteology of the Chalicotheroidea' (Holland and Peterson, 1914) that enabled us to identify the fragments.

A. *The forelimb*

165M. Left scapula. (Figure 16, $\times \frac{1}{2}$.) This specimen is part of the distal end of a left scapula. The area between the glenoid cavity and the scapular blade and spine has been extensively gnawed by a porcupine. Only the medial and central parts of the articular surface of the glenoid cavity are present. The bone has also sustained damage of the articular surface and the blade through mining, but in addition it is obvious that the scapular spine had been broken by some accident other than porcupine gnawing before fossilisation. As the bone is so incomplete it is impossible to give any further valuable information or measurements concerning it.

14112M. Left metacarpal II. (Figure 17, $\times \frac{1}{2}$.) This specimen, damaged mainly during mining, is the proximal end only of a left metacarpal II; part of the head and shaft are missing. The lower end of the shaft shows signs of use as though by pounding before fossilisation. The specimen is markedly expanded in the proximal region and is therefore a metacarpal II and not metacarpal III or IV, both of which lack this characteristic.

13636M. Right metacarpal IV. (Figure 18, $\times \frac{1}{2}$.) The distal portion of a right metacarpal IV had a small part of the shaft broken across during mining. The larger protuberance on the dorsal surface is on the radial side and serves to distinguish it from metacarpal III where it is on the ulnar side. Metacarpal IV is also the only one in which the antero-posterior diameter of the distal end is greater

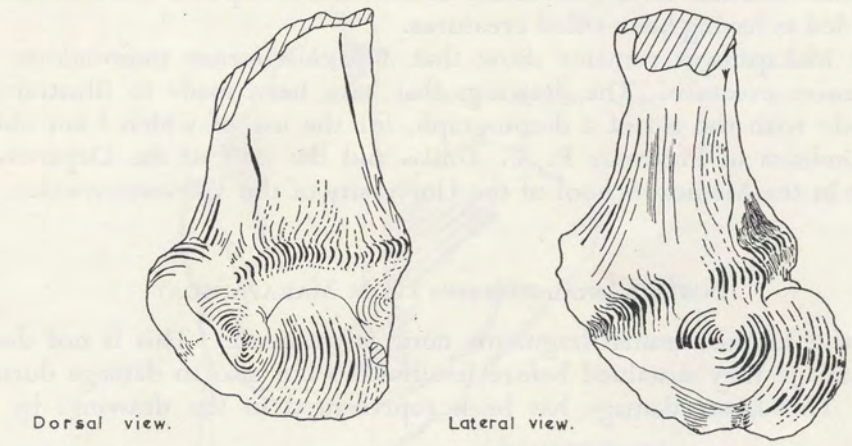


FIGURE 18

than the transverse diameter. The shaft becomes more circular in cross section proximally.

14111M. Intermediate phalanx. (Figure 19, $\times \frac{1}{2}$.) This fragment of an intermediate phalanx of the right manus has been recognised from the grooved nature of its anterior articulatory surface; otherwise the specimen has been extensively damaged during mining.

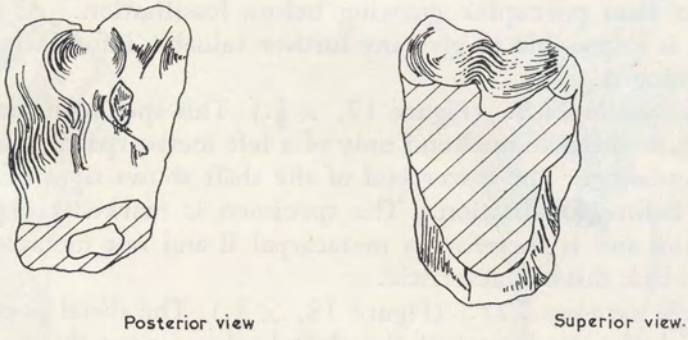


FIGURE 19

B. *The hindlimb*

5362M. Right innominate. (Figure 20, $\times \frac{1}{2}$.) This small fragment of a right pelvic innominate includes part of the acetabulum and ilium. The specimen was so badly damaged during mining that no comparative measurements that seemed useful could be taken.

12486M. Right innominate. (Figure 21, $\times \frac{1}{2}$.) This specimen comprises most of the acetabular region of a right pelvic innominate bone. Within the acetabulum there is a deep concave depression for the attachment of the ligamentum teres such as is characteristic of chalicotheres, no other animal having quite so marked a depression. The ilium, ischium and pubis are all missing—mainly as a result of mining—giving the specimen a triangular shape.

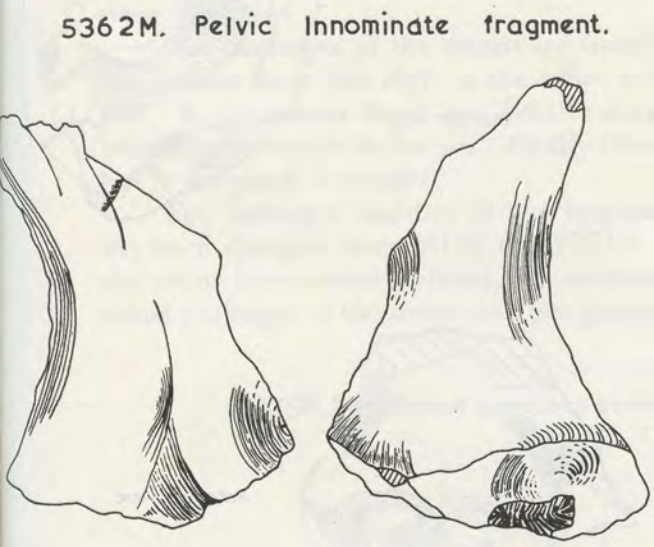


FIGURE 20

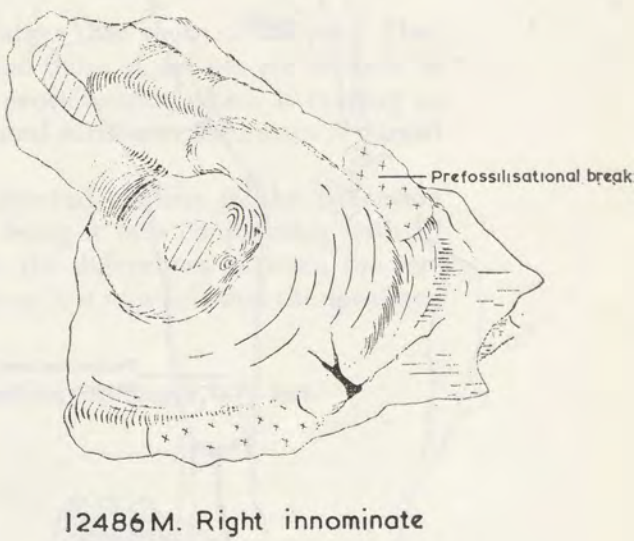


FIGURE 21

Despite the fact that most of the fractured surface is recent and due to mining there is sufficient trace of old fracturing and wear to show that the bone had acquired its present form before fossilisation, except for its ischial portion which has been broken away recently. It is also obvious that the margin of the acetabular cavity has been so broken and worn by use that its original shape has been considerably modified. The cavity itself is also irregular and roughened. The prefossilisational marks near the depression may have been caused during the extraction of the femoral head from the cavity. Towards the edge of the cavity some fine chisel marks are apparent, due to the preparation of the specimen and these must not be confused with the prefossilisation ones. This bone could have served as a receptacle in which food was pounded or crushed.

2043M. Right tibia, proximal end. (Figure 22, $\times \frac{1}{2}$.) Although recognisable as a proximal part of a tibia this specimen was badly broken during mining and no useful comparative measurements can be recorded. The ridges for the attachment of the muscles on the posterior surface are clearly visible. The subtriangular outline of the shaft is a characteristic feature of the chalicothere tibia. On the lateral surface there is a portion of the surface bone which has been lost before fossilisation.

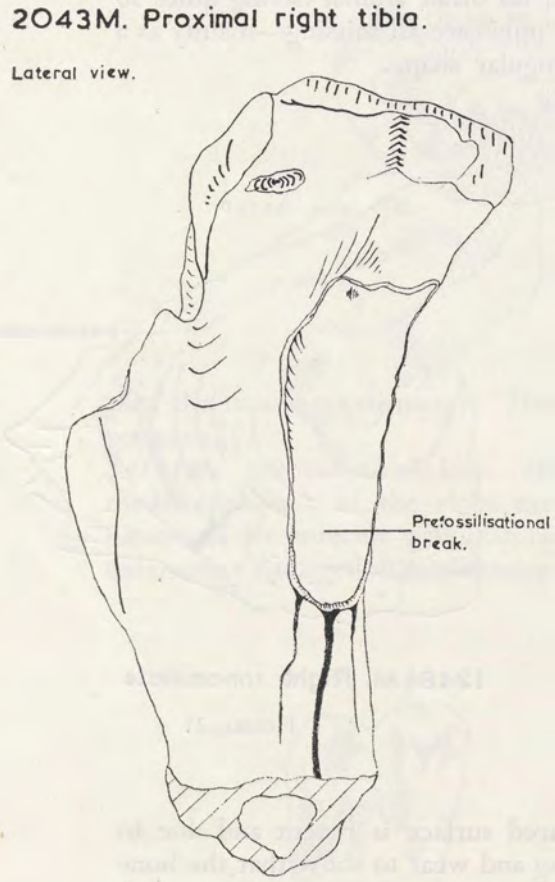


FIGURE 22

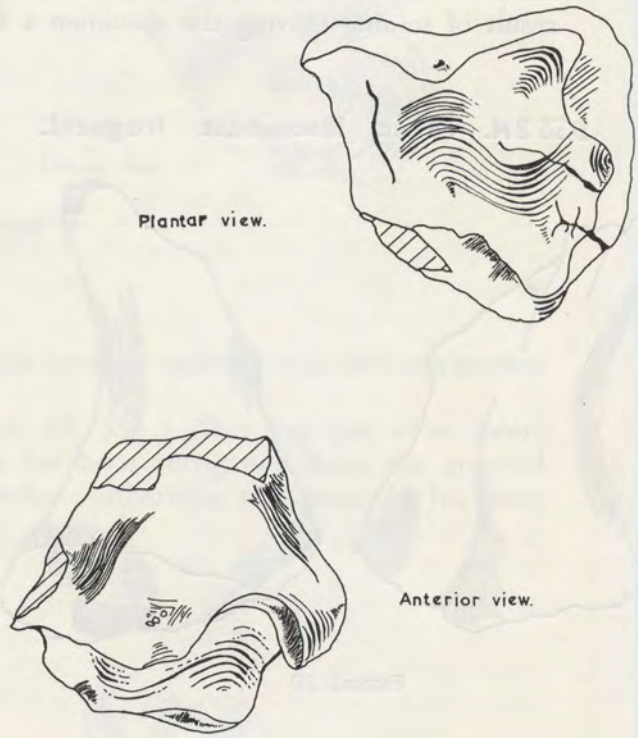


FIGURE 23

5974M. Right tibia, distal end. (Figure 23, $\times \frac{1}{2}$.) This damaged fragment of a right tibia is characterised by the broad lip-like posterior malleolus. It has no connection with the specimen described above and must have come from a second creature.

13635M. Left co-ossified phalanx. (Figure 24, $\times \frac{1}{2}$.) This specimen is a left duplex bone of the pes, most probably from digit II. A duplex bone arises from

the fusion of the proximal and intermediate phalanges. There is very little of the proximal articulatory surface present owing to the battered condition before fossilisation of the region surrounding and involving it. The distal surface externally on the dorsal side seems also to have been pounded away.

13633M. Phalanx. This specimen is also very fragmentary and it is difficult to determine whether it belonged to the manus or to the pes. Probably it is part of a duplex bone.

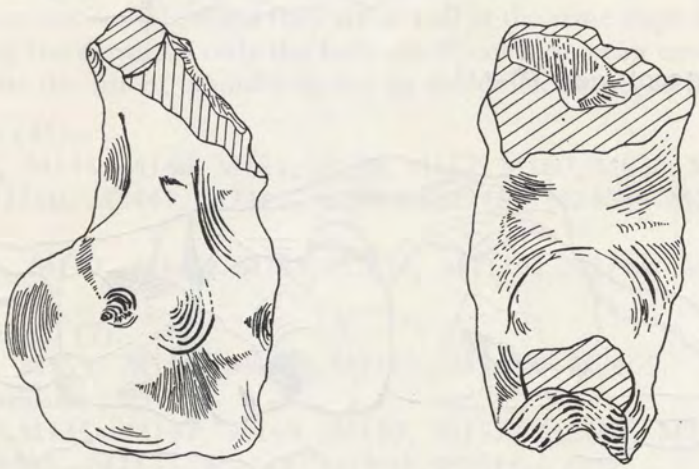
C. *Terminal phalanges*

It is difficult to determine whether a terminal phalanx comes from the manus or the pes unless a complete hand or foot is recovered. However, with the help of Holland and Peterson's text and diagrams two terminal phalanges were identified.

The phalanges of the manus are usually larger than those of the pes. They vary in size from one digit to the other whereas those of the pes are uniform in size. In the manus there is a definite dorsal protuberance which is missing or only slightly visible in the pes. Finally the ventral surface in the manus is curved but in the pes it is straight.

The catalogue number of the original terminal phalanx in the collection has been changed from M159 to 12773M to bring it into conjunction with all the other post-cranial remains. According to the differences between the terminal phalanges of the manus and pes given above it is now felt that the specimen

13635M. Coössified proximal & intermediate phalanges, left pes.

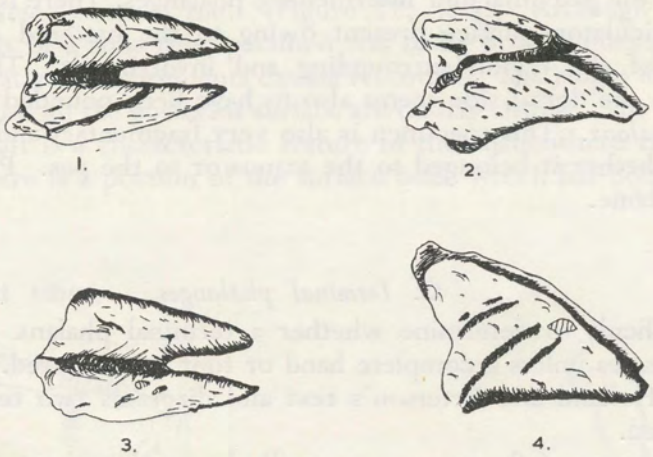


Tibial view

Dorsal view.

FIGURE 24

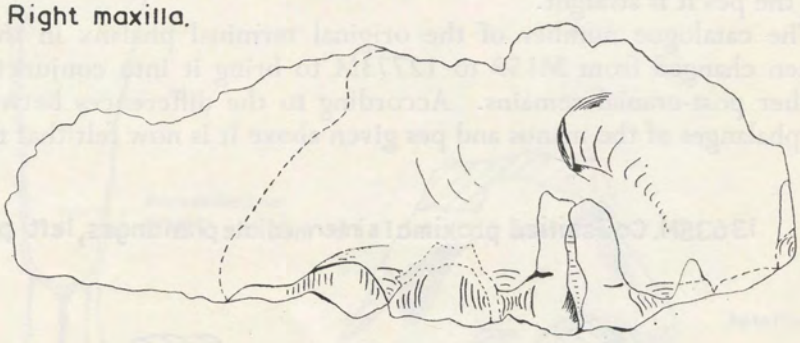
12773M and 13814M Ungual phalanges.



M12773. 1. Anterior view, 2. Lateral view.
M13814. 3. Anterior view, 4. Lateral view.

FIGURE 25

M153 Right maxilla.



Lateral view. P^4- M^3

Occlusal view. P^4- M^3.

FIGURE 26

12773M belongs to digit II or III of the pes rather than to digit III or IV of the manus as originally described.

12773M. Terminal phalanx. (Figure 25, $\times \frac{1}{2}$.) This is one of the original specimens recovered and has been described by George in 1950 in *S. Afr. J. Sci.* but for the reasons given above is now taken to come from digit II or III of the pes.

13814M. Terminal phalanx. (Figure 25, $\times \frac{1}{2}$.) This specimen is also from the pes and most likely also came from digit II or IIII.

Both of these terminal phalanges were broken off before fossilisation just anteriorly to their articulatory surfaces. The tips of the claws in 13814M have been broken recently. These two specimens had apparently been used before fossilisation both having been broken near their articulatory surfaces and the claws in 12773M being worn down.

The measurements below show the similarity in size of both the specimens and emphasizes the reasons for identifying them as being part of the pes.

	12773M.	*13814M.*
Greatest length of broken specimen	57mm.	55mm.
Greatest transverse diameter at plantar surface ..	34mm.	32mm.
Length of cleft along dorsal surface	57mm.	51mm.
Length of cleft along plantar surface	30mm.	22mm.
Greatest height	35mm.	38mm.

Cranial remains from Makapansgat

It was stated earlier that 84% of the chalicothere remains are cranial and consist predominantly of isolated teeth. There are 45 isolated teeth, 7 fragments of maxilla and 22 mandibular fragments. It has thus been possible to obtain an almost complete set of the upper and lower dentitions although some of the specimens are not complete and they are not all at the same stage of development. In describing the dentition only the best specimens have been used and described in detail, but the list of cranial remains in the collection is as follows:

Isolated teeth (45).

Uppers, M145, M146, M151, M155, M157, M160, M638, M2144, M2145, M2147—M2150, M2441, M2442, M2444—M2451, M2453—M2462, M2468—M2470.

Lowers, M140, M141, M148, M154, M1116, M2143, M2463, M2464, M2467.

Maxillary remains (7).

M144, M153, M156, M158, M2142, M2438, M2465.

Mandibular remains (22).

M131, M135—M137, M149, M150, M152, M2141, M2151, M2427—M2433, M2435—M2437, M2439, M2440, M2466.

A. *Superior dentition.* The presence or absence of incisors or canines cannot as yet be determined as no premaxillary remains or isolated upper incisors or canines

have been recovered. Unfortunately too there are no premolars in the collection but the three molars are represented although in a rather fragmentary form.

The most prominent feature of the upper permanent molars is the W-shaped ectoloph. In addition there are two unequally large internal conical cusps. On

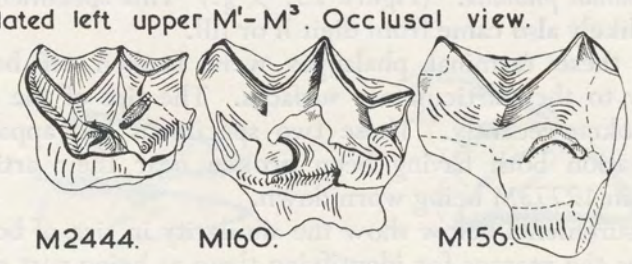
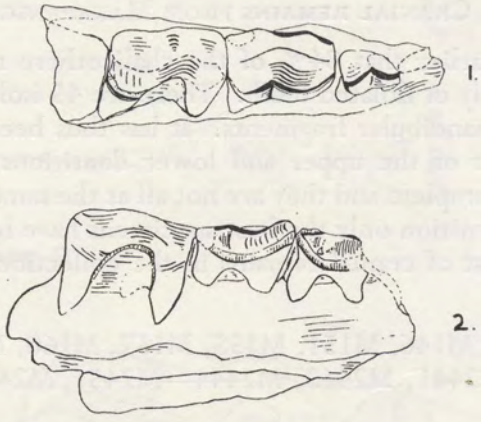


FIGURE 27

the internal face of the teeth there is a prominent but smoothly rounded cingulum. There is little or no difference in the configuration of the crowns of the three molars except that the features become more marked in each successive molar (see Fig. 27). In transverse diameter all three molars are fairly similar but there



M 131. Right mandible P_3 - M_1.

1. Occlusal view 2. Lateral view.

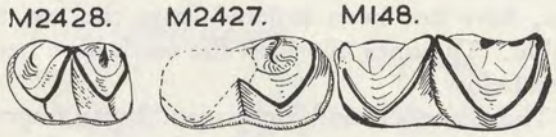
FIGURE 28

is a large increase in antero-posterior diameter between M^1 and M^2 but only a slight, if any, increase between M^2 and M^3.

Unfortunately the superior dentition is the lesser well represented, there

being no premolars and mostly fragmentary molars, those present being three right and one left M^1, two right and three left M^2, one right and one left M^3.

M153 is a maxillary fragment of an aged specimen bearing P^4—M^3, highly worn by natural abrasion but the teeth were also greatly damaged by mining. All the other specimens are isolated teeth except M156, which is a maxillary fragment with part of M^2 and a fragmentary M^3.



Lower left P_4, M_2, M_3. Superior view

FIGURE 29

B. *Inferior dentition*. In the remains from Makapansgat Limeworks there is an isolated lower incisor but whether there were 1, 2 or 3 incisors and one or more canines can only be known when an anterior portion of the lower jaw has been recovered.

Generally in chalicotheres P_1 is absent and P_2 a simple tooth of small size. We have not found any examples of a P_2 at Makapansgat but P_3 has developed the typical molariform pattern although it is still a fairly small tooth (see Fig. 28).

P_4 shows a marked increase in size, especially in the antero-posterior direc-

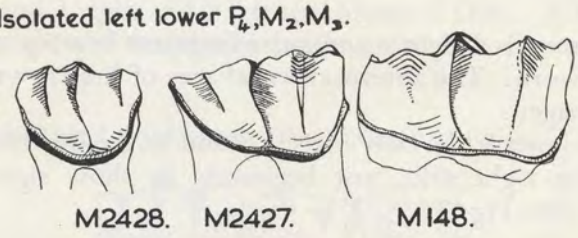


FIGURE 30

tion, and also has the characteristic W-shaped outline externally. The postero-internal area of the tooth is also particularly well developed. In both P_3 and P_4 on the external surface there is a cingulum while internally the tooth is almost smooth.

In the molar series the only two specimens of M_1 are both fragmentary as a result of mining and exhibit little structural detail. The crown pattern of M_1 is similar to that of P_4 but more definitely developed while the cingulum is less prominent. There is an increase in both antero-posterior and transverse

diameters between M_1 and M_2; thus M_2 although a much larger tooth still has the same general characteristics as the preceding tooth with the exception of the cingulum which in M_2 is well developed postero-externally. M_3 is a still longer tooth but lacks the third lobe which is found in the European and Asiatic species. Externally and posteriorly the cingulum is prominent but the tooth is smooth internally.

The majority of the lower teeth from Makapansgat, other than the very fragmentary pieces, have not been isolated from the jaw but include adjacent parts of the mandible. The ones in which the teeth have been used for measurements are described below.

M131 and M135. These are left and right mandibular fragments from the same jaw. Both bear PM_3—M_1, although M135 is far more fragmentary than M131. However, in both jaws the teeth are so extremely worn that the details of their structure are undecipherable. (See Fig. 28, $\times \frac{1}{2}$.)

M140. This is an isolated left P_4 which is well worn. One root has been recently broken.

M2428. This is a left mandibular fragment bearing a slightly worn P_4 which is the best in the collection. (See Figs. 29 & 30, $\times \frac{1}{2}$.)

M150. This is a left mandibular fragment bearing a DM_4 and an erupting M_1, the tooth still being below the superior surface of the jaw.

M2427. This is a left mandibular fragment with an almost complete M_2 (Figs. 29, 30). Unfortunately a portion of the superior surface of the tooth has been broken recently. The cingulum is well developed in this tooth.

M148. This is an isolated left M_3 complete except for the roots. This specimen although worn is the most complete lower tooth in the collection. (See Figures 29 & 30, $\times \frac{1}{2}$.)

M152. This specimen is a right mandibular fragment bearing an almost complete M_3 which is well worn. The antero-external area of the crown has unfortunately been recently damaged.

M1116. This specimen is the only incisor found in the deposit. It is a complete specimen from the right side, just beginning to show signs of wear on the anterior surface. (See Fig. 31, $\times \frac{1}{2}$.)

Measurements of M1116.

Complete length of specimen	65mm.
Length of tooth only	37mm.
Width at anterior surface	22mm.
Transverse (greatest) diameter	17mm.

C. *Deciduous dentition.* The upper deciduous dentition is made up of three molars all of which are represented in the collection as isolated teeth as follows: 2 right and 5 left specimens of DM^2, 7 right and no left specimens of DM^3, and 5 right and 2 left specimens of DM^4.

DM^2 is much longer antero-posteriorly than transversely especially in

comparison with the permanent series. This greater length is due to the presence of a prominent protostyle which unites with the protocone to give a long ectoloph (see Fig. 32, $\times \frac{1}{2}$). Internally the tooth is surrounded by a heavy cingulum becoming lighter externally. DM^3 and DM^4 increase progressively in size and show the typical molariform pattern even better than the permanent teeth. Internally the cingulum is heavy, becoming almost smooth externally.

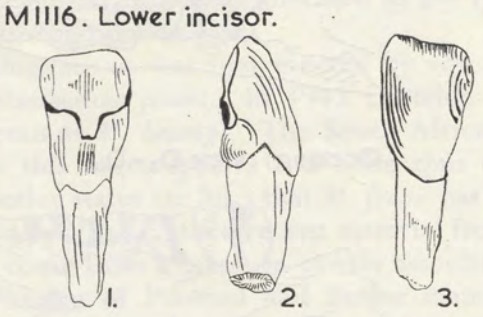


FIGURE 31

It is not known if inferior milk incisors or canines were present; probably they were. The three deciduous molars of the lower dentition are represented in the collection as follows: 3 right specimens of DM_2, 2 right and one left specimens of DM_3, and 2 right and 2 left specimens of DM_4. All these specimens are contained in mandibular fragments and are not isolated. (Compare figures 33 & 34, $\times \frac{1}{2}$.)

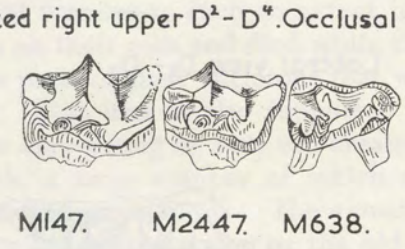


FIGURE 32

In this series DM_2 is a simple tooth with a long narrow crown, DM_3 is almost twice as long as the preceding tooth and is molariform in every respect. DM_4 is only slightly longer than DM_3 but has a greater transverse diameter, otherwise there is practically no difference between them. In all these inferior deciduous molars the cingulum is but slightly developed.

D. *Comparison with the American forms.* Wherever possible comparative measurements between the South African form and the two American species *Moropus elatus* and *Moropus petersoni* have been taken. From these measurements it is clear that the South African form and *M. elatus* compare closely in size whereas

M 2151. Right mandible

Occlusal view. $D_2 - D_4$

Lateral view. $D_2 - D_4$

FIGURE 33

M637. Right mandible.

Lateral view. $D_2 - D_3$

Occlusal view. $D_2 - D_3$.

FIGURE 34

M. petersoni appears to have been much smaller. The measurements were taken on some of the post-cranial remains and on a series of the upper and lower molars. With regard to the measurements of the teeth, the transverse diameters

were more often than not identical but the antero-posterior diameters were slightly higher (1—2 mm.) in the American form.

Discussion

As the collection contains only two complete adult teeth (M148 & M160) all the others being either broken or fragmentary, identification and description have both been difficult. However, it is obvious that only one genus and species is present and that the remains can all be allocated to the type named by George (1950) as *Metaschizotherium transvaalensis*.

The genus *Metaschizotherium* was first erected by von Koenigswald in 1932 with the type *Metaschizotherium fraasi*. In 1942 Dietrich placed the Serengeti specimens into this genus as *M. hennigi*. The South African specimens are very closely comparable to this latter species and were thus classified as *M. transvaalensis*. However, Butler states (*in litt.*) that *M. fraasi* has now been transferred to the genus *Phyllotillon* by Viret. More recent material from Olduvai, collected by Leakey, appears to come from a creature closely associated with *Ancylotherium pentelicum* from the Pontian of Pikermi and Butler maintains that *M. hennigi* and consequently *M. transvaalensis* should both be transferred to this genus. This view is in agreement with the work of Schaub, 1943 and Thenius, 1953. If this suggested transfer were to take place then it is obvious that the genus *Metaschizotherium* would disappear. However, until remains which are more complete are recovered, that will enable direct comparison to be made between the South African form and those from Olduvai and Pikermi, the classification of the Makapansgat specimens will remain as *Metaschizotherium transvaalensis*.

Taking into consideration the maxillary and mandibular remains, only two of the mandibles are known to be a pair and none of the maxilla are thought to accompany the mandibles and therefore the minimum number of chalicotheres represented in the deposit is thought to be 17.

The fact that so many creatures were accessible and yet the cranial remains outnumber the post-cranial remains to such an extent indicates that the animals did not come to the caves on their own and died while they were there but were killed first and only those parts of their skeletons that were going to be utilised were taken to the caves. This idea is also supported by the fact that all the remains come from either very young or very old creatures. This is particularly noticeable from the teeth, a large number of which are deciduous while the remaining ones show heavy signs of wear. The remains show that the chalicotheres were large beasts and so the young or the old would more easily be a prey to the hunter.

Relationship of the chalicothere remains to the osteodontokeratic culture

It has been stated already that the chalicothere remains account for only 86 of the 50,000 and more fragments recovered from about 10 tons of the Phase 1 breccia, i.e. ·072% of the total remains.

Secondly it was noted that 74 or 84% of the fragments were cranial (or more precisely dental, i.e. isolated teeth and fragments of upper and lower jaws containing one or more teeth).

The 12 post-cranial fragments (apart from the damaged left scapula, the damaged upper and lower fragments of a right tibia and the two innominate fragments) came from a right manus and a left pes.

Yet it has been established that at least 17 chalicotheres had been at the disposal of the creatures responsible for the deposition of the bones within the cave.

The deposit at Makapansgat was originally attributed by Professor Dart (1925) to primitive mankind and was subsequently suspected and finally proven by numerous discoveries since 1947 to be australopithecine-bearing in the upper and lower strata of the Phase I and also in the Phase II breccia.

It is unnecessary for me to recapitulate here the reasons he has advanced (Dart 1957) for believing that the bone deposit was made by these earliest representatives of mankind in the Transvaal, but it is desirable to point out to what extent his contentions are supported, or not, by these fragments under the detailed scrutiny which I have been able to give them.

In the first place it is characteristic of primitive human deposits to find the remains of very old and very young animals, those most easily captured.

In the second place it is obvious that, even if the flesh of the 17 chalicotheres was consumed by the australopithecines, they did not transport into the cave any of the very restricted skeletal parts of these creatures other than those of which they hoped to make some use.

In the third place the only reason advanced hitherto for a creature selecting jaws and pieces of jaws is either to sharpen their teeth upon them, as porcupines do, or to use them as ripping tools, saws and scrapers as human beings did.

I have pointed out that porcupine marks are present on the scapula; they are not found on any other of the fragments nor are they found elsewhere on these bones or with any degree of frequency on the other fragments of the deposit.

None of these chalicothere teeth could serve as ripping tools or saws, but as scrapers of flesh they would be virtually everlasting. (Vide plates I & II.)

Judging from the number of mandibles in the deposit these were the parts most sought after, the size of their teeth and accompanying fragment of mandible being very convenient (see figs. 28 & 33) especially in comparison with the maxillae which were very large. The lower teeth, which are much smaller and not as strong as the upper teeth, were apparently useful, if still in the jaw, but not when isolated.

In order to make scraping tools of these large teeth it was necessary to shatter the jaws, breaking them across, after removing the ascending ramus in the case of the lower jaws and breaking off the maxillae or even extracting the individual teeth in the case of the upper jaws. Specimens M2435 and M2428 are

excellent examples of mandibular fragments showing the prefossilisational blows that shattered them.

However useful the mandibular teeth were, even when furnished with a natural handle, there are actually more isolated maxillary teeth present than mandibular fragments; the only justification for this was their presumably greater effectiveness as scrapers owing to their wider and rougher cutting surfaces.

The clue to australopithecine interest in the manus and pes probably lay, as Professor Dart (1957) suggested, in the scratching or digging ability of the clawed terminal digits.

The only other fragments to be accounted for are the damaged scapula which had probably served as an axe, the tibia which was doubtless a club and the two innominates. These provided the most capacious and strongest type of natural mortar that was available for the australopithecines—other than those of rhinoceros—in which to pound any food they desired to crush with the aid of inferior metacarpal extremities such as are often found in an abraded and rounded condition in the breccia. The chalicothere metacarpal bones may have served as such pestles as the ends of many other abraded metacarpals both artiodactyl and perissodactyl appear to have done.

Acknowledgments

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In conclusion I welcome this opportunity of expressing my thankfulness to the South African Council for Scientific and Industrial Research, whose provision of a technical assistant to Professor Dart has enabled me to carry out this investigation during my tenure of that post.

Bibliography

Andrews, C. W., 1923. 'An African Chalicothere'. *Nature, Lond.*, No. 2819, 112: 696.

Brain, C. K., 1958. 'Transvaal Ape-man Bearing Cave Deposits.' Tvl. Mus., Pretoria.

Colbert, E. H., 1934. 'Chalicotheres from Mongolia and China in the American Museum.' *Bull. Amer. Mus. nat. Hist.*, 67, Art. 8: 353-387.

Colbert, E. H., 1935. 'Studies on Indian Fossil Mammals III.' *Amer. Mus. Nov.*, No. 798: 1.

Cooke, H. B. S. and Wells, L. H., 1956. 'Fossil Bovidae from the Limeworks Quarry, Makapansgat, Potgietersrust.' *Paleont. Afr.* IV; 5.

Dart, R. A., 1925. 'Australopithecus Africanus: the Man-ape of South Africa.' *Nature, Lond.*, 115: 195-199.

Dart, R. A., 1957. 'The Osteodontokeratic Culture of Australopithecus prometheus.' Tvl. Mus. Pretoria.

Dietrich, W. O., 1942. 'Altestquartäre Säugetiere aus der Südlichen Serengeti, Deutsch-ostafrika.' *Palaeontographica*, Bd. XCIV. Abt. A: 105.

George, M., 1950. 'A Chalicothere from the Limeworks Quarry of the Makapan Valley, Potgietersrust District.' *S. Afr. J. Sci.*, 46, No. 8.

Gregory, W. K., 'Evolution Emerging.' Vols. 1 and 2.

Holland, W. J. and Peterson, O. A., 1914. 'The Osteology of the Chalicotheroidea. *Mem. Carnegie Mus.*, 111, No. 2.

Hopwood, A. T. and Hollyfield, J. P., 1954. 'An Annotated Bibliography of the Fossil Mammals of Africa, (1742—1950)', p. 151.

Romer, A. S., 'Vertebrate Palaeontology.' Various pages.

Romer, A. S. 'Man and the Vertebrates.' Various pages.

Schaub, M., 1943. *Schweitz. Palaeont. Abh.* 64 (2): 1-36.

Stirton, R. A. 'Time, Life and Man: the Fossil Record.' Various pages.

Thenius, E., 1953. *Ann. Geol. Pays Hellenique.* 5: 97-106.

Zittel, K. A. 'Textbook of Palaeontology.' 111: 165.

Plate I.

Maxillary remains from Makapansgat to show their broken nature and the chiefly isolated state in which the teeth were found. All the teeth come from the right side except the extreme left specimens in the first and third rows from the top and the third specimen from the left in the third row from the top. Unless otherwise stated all the occlusal surfaces are worn by natural abrasion. In the specimens where only partial or no roots appear these have all been recently broken. All recent breaks are due to the processes of mining and preparation.

Represented in the Plate are five examples of DM^3, five examples of DM^4, three examples of M^1, three examples of M^2, and three maxillary fragments bearing more than one tooth. Despite the fact that there are numerous examples of the same tooth they are not all at the same stages of growth—some being newly erupted while others have occlusal surfaces which are heavily worn. In the paper as complete a set of each dentition as was available has been described but not each individual fragment recovered. (Refer to Text Sections 8A and 8C and Figs. 13, 14, and 19.)

Top Row: 1. Left M^1 (lower left edge damaged recently otherwise complete); 2. Right DM^3 (complete except for roots); 3. Right DM^4 (occlusal surface heavily worn); 4. Right DM^3 (lower left edge shows prefossilisational breaks, lower right edge is recently broken, occlusal surface heavily worn); 5. Right DM^3 (numerous recent breaks on outer surface of tooth, part of broken maxilla still attached); 6. Right DM^4 (complete, newly erupted tooth).

2nd Row: Right M^1 (numerous recent breaks on all surfaces); 2. Right DM^4 (complete except for recent break on outer wall); 3. Right DM^3 (occlusal surface heavily worn, part of maxilla still attached with broken margins worn smooth, compare with Top Row specimen 5 whose margins are rough and unused); 4. Right DM^3 (outer wall recently broken, edges of the attached maxilla are worn smooth by manual use); 5. Right DM^4 (complete except for small recent break on lower right edge); 6. Right DM^4 (left side of tooth recently damaged, portion of maxilla still present).

3rd Row: 1. Left M^2 (anterior half of tooth recently broken off, occlusal surface well worn); 2. Right M^1 (outer surface recently broken, occlusal surface heavily worn); 3. Left maxillary fragment bearing M^2 and M^3 (note prefossilisational exposure of root of M^2 and area around base of M^3, broken maxillary margins are worn smooth by manual use, see Fig. 14); 4. Right M^2 (complete well worn tooth, part of maxilla still present shows signs of manual use); 5. Right M^2 (original and most complete specimen in the collection, see Text Sections 3 and 4 and Fig. 14).

4th Row: 1. Right maxillary fragment bearing P^4—M^3 (worn virtually to the roots by natural abrasion, numerous recent breaks are visible all over the specimen, this is one of the specimens from the pink breccia, see Text Section 5 and Fig. 13); 2. Right maxillary fragment bearing P^4—M^2 (worn virtually to the roots by natural abrasion, this whole specimen was badly broken during mining).

PLATE I

Plate II.

Mandibular remains from Makapansgat to show the fractured state in which pieces of the jaw and teeth were found, noting especially the fact that there are no isolated teeth as there were amongst the maxillary remains. There are eight right and eight left mandibular fragments and one right incisor; the right mandibular fragments are the 3rd and 4th specimens in the top row, 2nd and 4th specimens in the 2nd row and the complete 3rd row. Unless otherwise stated all the occlusal surfaces have been worn by natural abrasion. All recent breaks are due to the processes of mining and preparation.

Represented in the Plate are all the examples which make up a complete lower dentition except for a P_2. There are nine fragments bearing one tooth only and seven bearing more than one tooth as well as the isolated right incisor. In the paper as complete a set of each dentition as was available has been described and in addition some individual descriptions of the specimens which have been used for measurements and comparisons are given. (Refer to Text Sections 8B and 8C and Figs. 15, 16, 17, 18, 20 and 21).

Top Row: 1. Left DM_3 (complete, mandible recently broken posteriorly but anteriorly all breaks are prefossilisational). 2. Left DM_4 (tooth and jaw show extensive recent damage). 3. Lower right incisor (early stages of normal wear evident, the only isolated lower tooth recovered, see Text section 8B and Fig. 18). 4. Right mandibular fragment bearing DM_2 and DM_3 (teeth complete and newly erupted, all breaks prefossilisational, an excellent scraper, see Text section 10 and Fig. 21). 5. Right DM_4 (both tooth and jaw show recent damage).

2nd Row: 1. Left DM_4 with a M_1 just erupting (large number of recent breaks present which obscure the prefossilisational breaks). 2. Right mandibular fragment (teeth recently broken at roots, mandible itself also shows recent breaks). 3. Left mandible bearing P_3—M_1 (two outer teeth fragmentary, occlusal surface of P_4 heavily worn, lower portion of jaw worn away by use and molar roots on externo-lateral surface exposed). 4. Right mandibular fragment bearing P_3—M_1 (occlusal surface of teeth heavily worn, deep crack along lower surface is prefossilisational, below crack jaw is worn away by use). These latter two specimens belong to the same animal and are two of the specimens which come from the pink breccia. (See Text section 8B and Fig. 15.)

3rd Row: 1. Right M_3 (tooth complete except for small recent break on the right, all other breaks prefossilisational and margins all worn smooth by manual use, note exposure of root where mandible was originally broken, an excellent scraper, see Text section 10). 2. Deciduous molar (both tooth and jaw very fragmentary hence no clearer identification). 3. Right mandibular fragment (probable M_1 present worn virtually to roots, empty sockets of probable M_2 visible, no recent breaks, specimen has been well gnawed by porcupine). 4. Right mandibular fragment bearing DM_2—DM_4 (occlusal surface of teeth worn by natural abrasion, mandible recently broken anteriorly. See Fig. 20).

4th Row: 1. Left lower molar (probable M_1 occlusal surface recently broken off, tooth still attached to part of jaw on one side free on the other, no breaks apparent on free surface, margins of mandible all worn smooth by manual use). 2. Left mandibular fragment (M_2 and M_3 recently broken off flush with the mandible, note the deep prefossilisational cracks, reverse side is indented (opposite crack on right side) probably due to blows given during breaking of the jaw, lower portion of left side of jaw has been scooped out). 3. Left P_4 (tooth complete, mandible shows blow mark on extreme lower right edge, other breaks are recent, see Figures 16 and 17). 4. Left M_2 (occlusal surface recently broken, jaw also recently broken both anteriorly and posteriorly, see Figures 16 and 17).

PLATE II