SOME NEW FOSSIL CERCOPITHECOID SPECIMENS FROM MAKAPANSGAT, SOUTH AFRICA

By L. Freedman
(Department of Anatomy, University of the Witwatersrand, Johannesburg)

Abstract

Eighty-eight new fossil cercopithecoid specimens from Makapansgat, South Africa are considered. They are referred to the species *Parapapio broomi, P. jonesi, P. whitei, Cercopithecoides williamsi* and *Simopithecus darti.* With the exception of *P. whitei,* each of these species has previously been described from this site. The new material considerably extends our knowledge of all of the above species and the species *Cercopithecoides molletti,* previously described from Swartkrans, must now be sunk and the material referred to *C. williamsi.* Some remarks are made about the status of the South African species of the genus *Simopithecus.*

Introduction

Since the South African cercopithecoid material was last reviewed (Freedman, 1957), 134 new specimens have been recovered from the breccia in the limeworks dumps at Makapansgat near Potgietersrus in the Transvaal. Of this material, 88 specimens are either sizeable fragments showing interesting features, or include teeth which can be identified and measured. The new specimens were found to fit into 5 species, all previously described from the South African limestone caves and, except one (*Parapapio whitei*), all previously reported from Makapansgat. However, the material adds considerably to our knowledge of the morphology and variation of each of these forms and, in one case, necessitates certain taxonomic changes.

The system of measurements used below is the one described in Freedman (1957) and, unless stated to the contrary, all references to "the previous study" refer to that same review.

Parapapio Jones, 1937

There are 69 specimens of the genus *Parapapio* in the new material from Makapansgat. The material includes: 5 fairly large and 2 rather small portions of the skull, all with teeth, and 19 other specimens of upper teeth; 6 fairly large and 6 small parts of the mandible, all with teeth, and 19 other specimens of lower teeth; 8 specimens of various portions of the skull and 1 of the mandible with badly damaged or no teeth; 3 specimens each including both maxillary and mandibular fragments with teeth.

As discussed at length in the previous study, the present taxonomy within this genus is not wholly satisfactory but it appears to be the most suitable working arrangement until more complete skull material is found. The present sample

unfortunately helps only a little in filling this gap. The criteria proposed in the previous study for subdividing the Sterkfontein *Parapapio* material into the three species, *P. jonesi, P. broomi* and *P. whitei,* have thus again been used in this study. However, instead of only using the material of known sex, an attempt has been made to classify all the known *Parapapio* material from Makapansgat. For the reasons given above, and also because there might possibly be subspecific differences between the Sterkfontein and Makapansgat representatives of a species, (see later for this situation in *Cercopithecoides*), some specimens will undoubtedly have to be re-classified in due course.

Parapapio broomi Jones, 1937

Referred Material: 24 new specimens are referred to this species. These include: A fairly complete male skull (M.2961) and a male right maxilla (M.2963); a female skull (M.3037) which is fairly complete but rather badly crushed, a right female maxilla (M.3002) and the two halves of a female palate (M.2964 and M.2966) which almost certainly come from a single individual. There are 8 specimens of upper teeth of unknown sex (for their numbers, see Table 2). There are 3 specimens showing the symphysis and body of the male mandible (M.2978, M.2979 and M.2980) but there are no specimens of the female mandible. One female $\overline{C}$ and 6 specimens of lower teeth of unknown sex (some in small portions of the mandible) are also referred to this species (for their numbers see Table 4).

Description: (Figs. 1—3). The male skull (M.2961) lacks the anterior part of the muzzle, the zygomatic arches, lateral parts of the orbits and the base and posterior part of the calvaria. M^2 and M^3 are present on the right and M^2 on the left but they are all rather badly damaged. Although comparing well in size

Table 1

Measurements of the skull of *Parapapio broomi* (in mm.)

	Male	
	M.2961	M.2963
Calvaria		
Breadth		
Minimum interfrontal	53	
Muzzle		
Height		
Anterior to P^3		21
Breadth		
Anterior to M^3	53.5	54
Anterior to P^3		42
Dorsal to M^2	39	
Orbit		
Interorbital	13	
Height	24.5	

Table 2

Measurements of the upper teeth of *Parapapio broomi* (in mm.)

	I^2			C	P^3		P^4		M^1			M^2			M^3			Rows
	h	b	l		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	P^4–M^3
Male																		
M.2961														10.3	(11.5)			
M.2963							9.0	6.8	9.8	9.5	10.1	11.7	10.8	11.4	11.7	9.5	11.2	(38.8)
Female																		
M.2964)							8.5	6.4				11.8	10.2	11.1	11.5	9.0	10.6	(35.2)
M.2966)*							8.5	6.3				12.2	10.3	10.7	11.2	——	11.0	(36.3)
M.3037							——	6.2	9.0	8.8	9.6	11.0	9.9	11.4	10.8	8.8	10.8	36.5
M.3002												(10.9)	(9.4)	11.8	10.3	8.4	11.0	
?Sex																		
M.3011												11.0	10.2	10.8				
M.2977															11.6	9.4	10.6	
M.2969												10.5	9.6	11.0	——	8.8	10.6	
M.2975															11.8	9.8	11.2	
M.3008	9.9	6.3	6.0															
M.3015												11.8	11.6	11.5				
M.2970															11.2	9.7	10.2	
M.3016					8.0	(7.2)												

* Virtually certainly a single individual.

to the known specimens (Table 1 gives the measurements of the new specimens), when compared in detail with M.202 (1326-2), the specimen previously used in the description of the male skull of this species, a number of interesting differences are found.

Of considerable importance is the fact that when viewed in normal laterality, there is a considerable drop in the profile of the muzzle in the interorbital region of M.2961 (Fig. 1). This drop is not as marked as in the male Chacma baboon, *Papio ursinus,* but is considerably more than in M.202 and very similar to that in the female of *P. ursinus.* The muzzle in M.2961 also has a larger maxillary fossa than that in M.202 and the muzzle dorsum is not flat but concave from side to side with the middle part (nasals) standing up considerably more prominently above the general level of the dorsum. In M.2963, the other new male specimen, the maxillary fossae are similar to those in M.202. In both M.2961 and M.2963, the maxillae have long nasal processes lateral to the nasals. The palate is deep in M.2961 but very much shallower in M.2963.

The orbits are more vertical and less laterally elongated in the new male specimen (M.2961) and its supraorbital notch is very well marked. The interorbital measurement is broader than in M.202 and a short metopic suture is present. There is a more marked depression followed by a less marked elevation behind the glabella in M.2961 than is seen in M.202.

On the calvaria, the inferior temporal lines are well developed and meet at a point considerably anterior to the inion (Fig. 2). (The portion of the calvaria behind which they meet is lost but from the general contour of the area it is clear that the meeting point was well in front of the inion.) The superior temporal lines can also be clearly seen and these lines meet about 3½ cms. anterior to the meeting place of the inferior lines. They form a slightly elevated ridge which continues up to the meeting point of the inferior lines. On M.202, the inferior lines can be seen for only a short distance anteriorly and the superior lines can not be seen at all. The top of the calvaria appears to be somewhat higher above the occlusal plane than that of M.202.

The specimens of the skull included in the new female material of this species add little to our knowledge as they are too fragmentary or badly damaged.

The new specimens of the upper teeth (Fig. 3) do not show any morphological features in which they differ from the material previously described. The measurements of these specimens are listed in Table 2, and most of them fit the sizes

Table 3

Measurements of the mandible of *Parapapio broomi* (in mm.)

		Male	
	M.2978	M.2980	M.2979
Height			
Posterior to M_3	29		
Anterior to P_4	32	31	29

Table 4

Measurements of the lower teeth of *Parapapio broomi* (in mm.)

	$\bar{C}$			P_3		P_4		M_1			M_2			M_3				Rows
	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	P_4–M_3
Male																		
M.2978				5.5	14.9	(7.5)	(7.0)	—	7.5	8.9	10.1	10.2	11.5	10.2	(9.1)	4.5	14.0	40.5
M.2980											—	9.8	11.5	9.8	9.0	5.7	14.5	
M.2979						7.3	6.8	7.8	7.5	9.2	10.4	—	11.3					
Female																		
M.2084	—	7.5	5.8															
?Sex																		
M.2982								—	8.1	(9.2)	10.0	8.7	10.5	10.2	8.9	5.7	14.8	
M.2968														10.8	9.5	4.0	13.3	
M.2993														—	9.2	3.5	15.5	
M.3024											10.0	—	11.8					
M.2994											9.6	8.9	11.8					
M.3018														9.6	9.4	6.6	15.7	

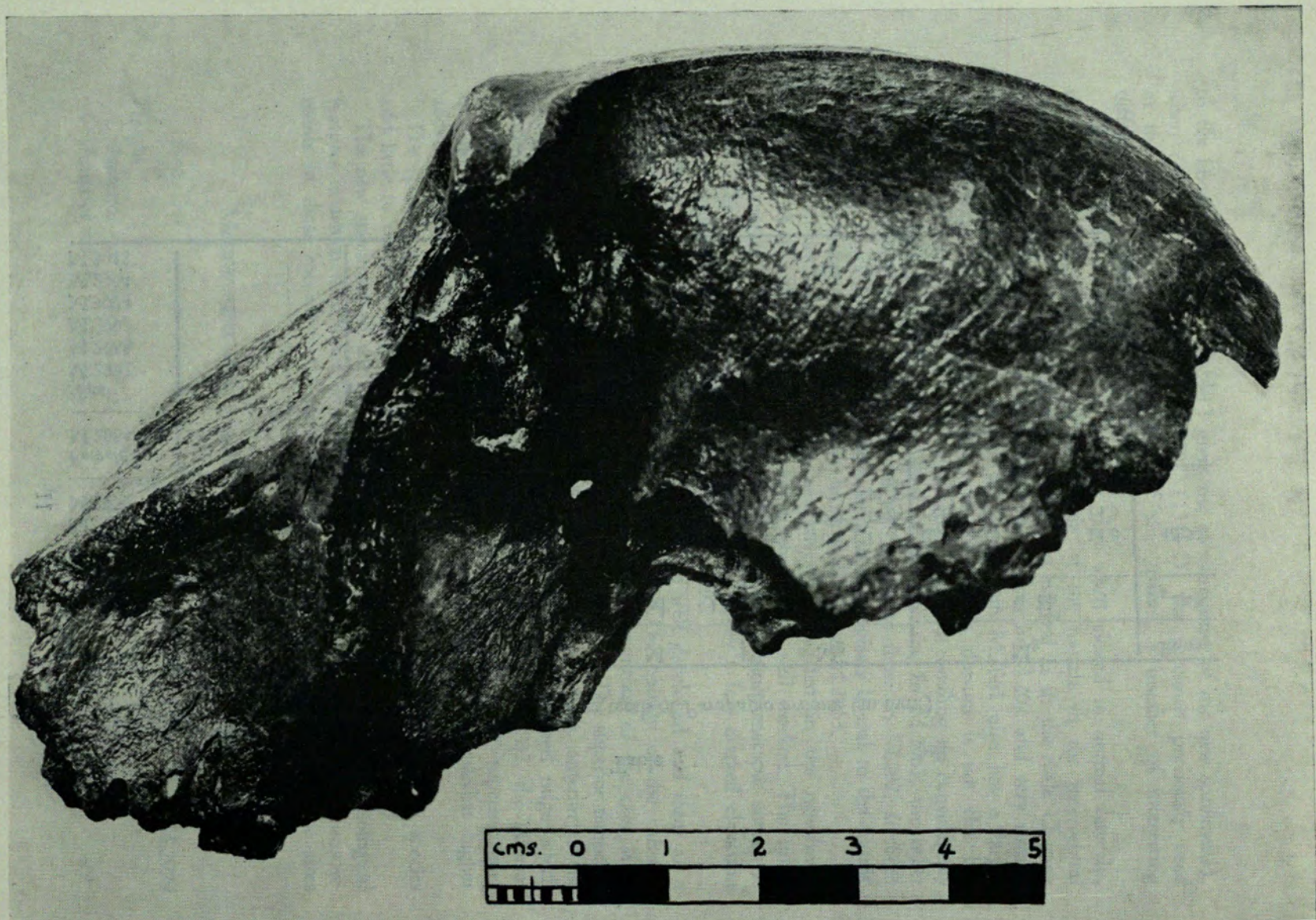

cms. 0 1 2 3 4 5

Fig. 2. *Parapapio broomi* male (M.2961). Dorsal view of skull.

previously given for the species quite well. Of the specimens of unknown sex included, M.3008, M.3015 and M.3016 could, however, possibly belong in *P. whitei* and M.2970 appears slightly small for *P. broomi*.

The 3 new male mandibles (Table 3) confirm most of the features previously described and, in addition, slightly extend our information about certain features. In M.2979 the slope of the anterior surface of the symphysis is rather gentle whereas in M.2980 it is slightly steeper. The mandibular fossa varies in the 3 specimens from shallow in M.2979 and M.2980 to almost absent in M.2978. The symphysial region extends almost up to the distal end of P_3 in M.2979 but is shorter in M.2980. In M.2978 there is a large space between the distal end of

Fig. 3. *Parapapio broomi* male (M.2963). Occlusal view of upper teeth.

M_3 and the ascending ramus. The ramus in this specimen leans back at an angle of about 120° to the occlusal plane.

No female mandibles can definitely be referred to this species from the new Makapansgat material.

The new lower *Parapapio* teeth from Makapansgat have proved rather more difficult to classify than the upper — mainly because a number of single teeth

in the I_1 — M_1 group are involved and it is primarily on M_2 and M_3 that the classification of *P. broomi, P. jonesi* and *P. whitei* is based. Table 4 lists those specimens fairly clearly referable to *P. broomi,* while Table 10 lists lower teeth which could belong to *P. broomi* or *P. jonesi* and Table 11 lists specimens which could belong in *P. broomi* or *P. whitei.* Those listed in Table 4 appear to fit *P. broomi* clearly on size and morphology and do not show any new features.

Parapapio jonesi Broom, 1940

Referred Material: 12 new specimens are referred to *P. jonesi.* No new skull fragments are included in the new material but there are 5 isolated upper teeth

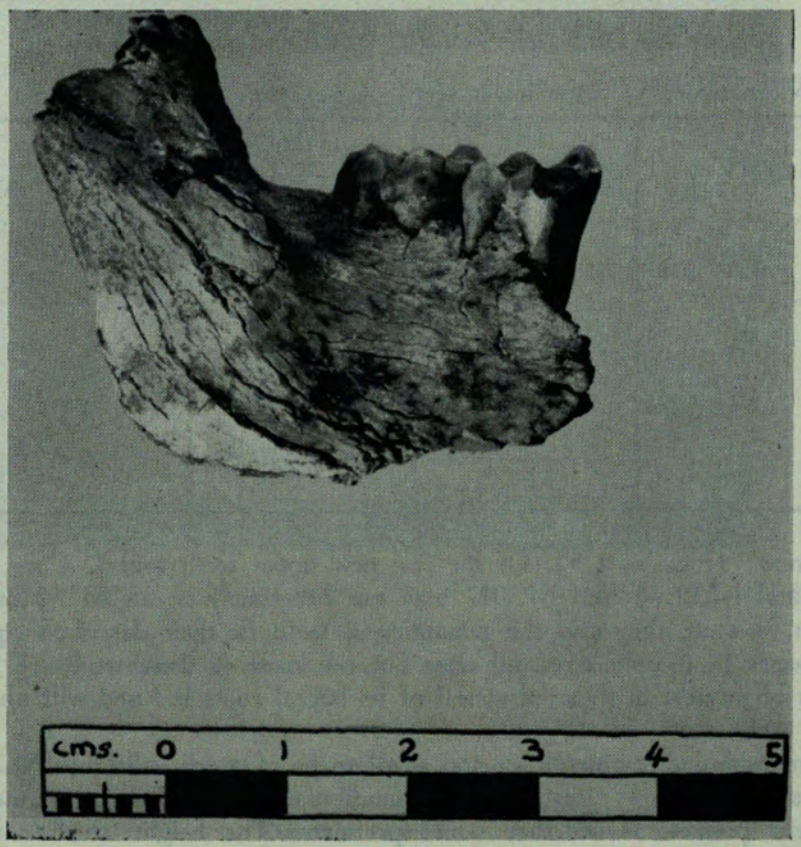


Fig. 4. *Parapapio jonesi sex?* (M.2984). Lateral view of mandibular fragment with M_2 and M_3.

of unknown sex, the numbers of which are given in Table 5. Of the mandible, there is one fragment with teeth from a female (M.2983) and another fragment also with teeth but of unknown sex (M.2984). There are also 5 isolated lower teeth of unknown sex, the numbers of which are listed in Table 6.

Table 5

Measurements of the upper teeth of *Parapapio jonesi* (in mm.)

	M^1			M^2			M^3		
	bm	bd	l	bm	bd	l	bm	bd	l
?Sex									
M.2976	8.9	8.1	9.1						
M.3009							9.9	7.4	9.5
M.3013							9.6	8.2	10.0
M.3014							(10.2)	7.8	——
M.3017				10.2	8.6	9.5			

Table 6

Measurements of the lower teeth of *Parapapio jonesi* (in mm.)

	P_4		M_1			M_2			M_3			
	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
Female												
M.2983	6.3	7.5	7.2	6.9	9.0							
?Sex												
M.2984						—	8.8	10.0	9.2	8.0	—	11.1
M.3019									7.9	7.0	4.5	11.3
M.3021									8.3	8.2	4.9	13.2
M.2992						9.0	8.4	10.8				
M.3030									9.3	7.7	5.2	12.7
M.3032			7.0	7.1	8.3							

Description: (Figs. 4 & 5). Of the few new upper teeth found, 2 are damaged (M.3013 and M.3014) and M.3017 may not necessarily be an M^2. However, as far as can be seen, they and the remaining 2 teeth fit their described equivalents in this species in morphology and size. For the sizes of these teeth see Table 5. M.3014 is of interest in that the mesial of its buccal roots is fused with the lingual root.

The 2 mandibular fragments are too small to be of much value but M.2983, the female fragment, shows virtually no mandibular fossa. The only mandibular measurement possible is on that same specimen: The height anterior to P_4 is 24mm. The lower teeth (Figs. 4 & 5) are interesting in that they appear to be small, even for *P. jonesi;* in size, but not on morphology, one specimen (M.3019) is actually small enough for *Cercopithecoides williamsi.* The sizes of the new lower teeth are given in Table 6. The lower teeth in a specimen previously described (M.218, 60M) are also rather smaller than their equivalents in the Sterkfontein series of *P. jonesi.* (The number of this specimen was in error given as M.215,60M in the previous study.)

Parapapio whitei Broom, 1940

Referred Material: 5 specimens are referred to this species from the new Makapansgat material and one, M.635, described in the previous study, is transferred to this species from *P. broomi.*

The new material includes 2 male muzzles with teeth (M.2962 and M.3003), and a right maxillary fragment of unknown sex, with P^3 — M^1 (M.2973). M.2962 has P^3 — M^2 on the right and P^4 — M^3 on the left all in good condition.

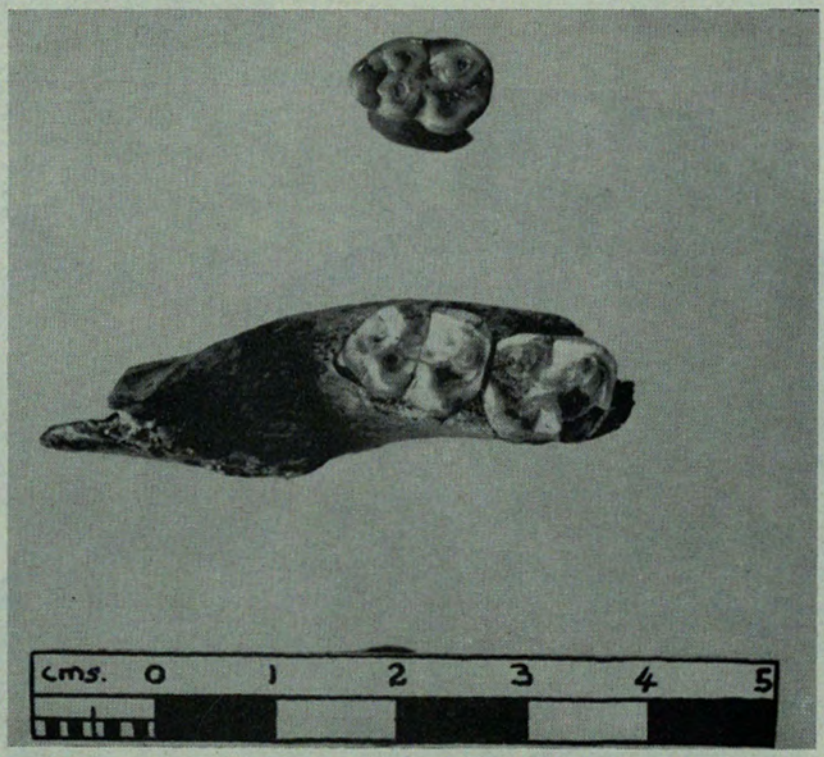


Fig. 5. *Parapapio jonesi* sex? (M.3091, above; M.2984, below). Occlusal view of lower teeth.

Table 7

Measurements of the skull of *Parapapio whitei* (in mm.)

	Male M.2962
Muzzle	
Height	
Anterior to P^3	(28)
Breadth	
Anterior to M^3	55
Anterior to P^3	46.5
Dorsal to M^2	41
Orbit	
Height	22
Breadth	(29)

Fig. 6. *Parapapio whitei* male (M.2962). Anterior view of skull.

M.3003 has P^4 — M^3 on the right but all are very worn and damaged. A small portion of a male mandibular symphysis with P_4 (M.2988) and part of a left mandibular corpus with P_4 and M_1 of an immature specimen of unknown sex (M.3007) are the only other 2 specimens of this species in the new material.

Fig. 7. *Parapapio whitei* male (M.2962). Lateral view of muzzle.

Description: (Figs. 6 — 8). The muzzle (M.2962) is the first male skull of any size to be referred to this species from either Sterkfontein or Makapansgat. On the right side, the specimen includes the orbit and supraorbital torus but on the left, most of the posterior part of the muzzle (and everything posterior to it)

Fig. 8. *Parapapio whitei* male (M.2962). Occlusal view of palate and upper teeth.

has been lost and the left anterior tip of the muzzle is also missing (Fig. 6). The other new muzzle (M.3003) shows the palate and anterior part of the muzzle but it is badly damaged and eroded.

Compared to the known male *P. broomi* specimens, M.2962 is considerably more

Table 8

Measurements of the upper teeth of *Parapapio whitei* (in mm.)

	P^3		P^4		M^1			M^2			M^3			Rows
	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	P^4–M^3
Male														
M.2962	8.2	8.0	(9.2)	6.2	10.3	——	10.1	12.8	11.0	11.8	12.1	9.8	11.6	(40.6)
M.3003								——	——	(12.5)	12.9	——	——	
?Sex														
M.2973			9.1	7.0	10.4	9.5	(10.0)							
M.635*								12.3	11.0	12.5	12.1	10.6	12.6	

* Described under *P. broomi* in previous study.

robust. (See Table 7 for the measurements of this specimen). The canine eminence is well developed and the supraorbital torus is prominent, two features not at all well marked in the known male *P. broomi* specimens. The new *P. whitei* male muzzle also has rather large maxillary fossae and the muzzle slopes up steeply and smoothly from the maxillary ridge to the midline (Fig. 7). The palate is extremely deep in both this specimen and M.3003.

In side view, the drop in the profile from the glabella down to the posterior edge of the nasal aperture appears to have been even steeper in M.2962 than in the male *P. broomi,* M.2961. (The area is damaged in M.2962 but was reconstructed to facilitate comparison.) The interorbital region in M.2962 was almost certainly very similar so that in M.2961. The small part of the inferior temporal line present in M.2962 is well marked.

The upper teeth (Fig. 8) in M.2962, M.3003, M.635 and M.2973 fit the morphological pattern for the genus well; in size, certain of their dimensions (see Table 8 for their sizes) are clearly larger than the equivalents in *P. broomi* and hence these specimens have been referred to *P. whitei.*

The new mandibular fragments are too small to be of any value for description of the mandible of this species. The new lower teeth fit the *Parapapio* morphological pattern well; in size (Table 9) they are interesting in that both new specimens are large when compared to the few known *P. whitei* teeth from Sterkfontein.

Table 9

Measurements of the lower teeth of *Parapapio whitei* (in mm.)

	P_4		M_1		
	b	l	bm	bd	l
Male M.2988	6.8	10.8			
?Sex M.3007	7.0	——	8.4	8.1	10.9

In the previous study it was suggested that M.635 fitted better with *P. whitei* than with *P. broomi* but that the specimen was *pro tem.* referred to *P. broomi* as very few specimens were available from Makapansgat and none other fitter *P. whitei.* A number of specimens are now being referred to *P. whitei* and this specimen can now also be referred to that species.

Parapapio sp.

Four batches of specimens are grouped under this heading: (1) 8 skull specimens, some fairly complete, some consisting of small portions only, but all either lacking

teeth or having very badly damaged teeth. Positive identification of these specimens is impossible but they all appear to belong in this genus. The specimens are:

M.3005 — a fairly complete skull of an immature adult (possibly female) of either *P. broomi* or *P. whitei*. The teeth are badly worn and damaged (P^3 — M^2) and no measurements are possible.

M.2997 — a small portion of a muzzle with very worn and badly damaged teeth belonging in either *P. broomi* or *P. whitei*.

M.3038 — Portion of a skull with no teeth, but showing the orbits, posterior part of the muzzle and a small portion of the frontals. In profile, there is rather more drop in the interorbital region than was assumed before the new material from Makapansgat was described.

M.3001 — a small portion of the frontals and the interorbital part of the nasals. The profile view of this specimen is similar to that of M.202, described in the previous study.

M.2996 — a small region of the posterior part of the muzzle. The interorbital drop in this specimen was probably steep.

M.3039 — a badly damaged specimen showing mainly a deep palate with very badly damaged teeth.

M.2998 — portion of a right maxilla with badly damaged teeth.

M.3043 — a good specimen of a calvaria including most of the base of the skull.

(2) This group consists of 12 specimens of the mandible and lower teeth which appear to be of *Parapapio* but can not be assigned to a species as most are of teeth anterior to M_2.

M.3040 — consists of the symphysis and most of the left corpus of a female but the teeth have all either been lost or badly damaged.

Table 10

Measurements of the lower teeth of *Parapapio jonesi* or *P. broomi* (in mm.)

	P_3		P_4		M_1			M_2		
	b	l(h)	b	l	bm	bd	l	bm	bd	l
Male M.2995	5.3		13.4		—	8.0	(9.8)			
Female M.2985					—	—	9.1	9.5	—	—
?Sex M.3042					—	(7.6)	9.4	—	—	(11.0)
M.3020								9.5	9.2	10.7
M.3033			6.5	6.7						

Table 10 lists 5 specimens which could belong in either *P. jonesi* or *P. broomi* on dental size and morphology. Two of these specimens include portions of the mandible which can be measured: the height anterior to P_4 of M.2995 (a male) is 30mm. and the same measurement of M.2985 (a female) is 25mm.

Table 11

Measurements of the lower teeth of *Parapapio broomi* or *P. whitei* (in mm.)

	I_1			I_2			$\overline{C}$			P_3		P_4	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l
Male													
M.2986										5.9	—	7.3	8.1
M.3041	11.2	—	5.5	10.0	—	5.5					(16)		
?Sex													
M.3036	11.1	6.0	5.9	11.0	5.7	5.1							
M.3022												6.9	7.9
M.3028												6.5	7.5

Table 11 lists 5 specimens which on dental dimensions and morphology could belong in either *P. broomi or P. whitei.* M.3041, M.3036 and M.3028 could possibly even belong in *P. jonesi.*

M.3023 — is a male $\overline{C}$ which could belong in *P. jonesi, P. broomi* or *P. whitei.* Its dimensions (in mm.) are: h — 17.0; b — 10.0; l — 6.5.

(3) This group includes a juvenile skull and 4 deciduous teeth of unknown sex (3 upper and 1 lower) which appears to belong in the genus *Parapapio.*

The skull M.3004 (Fig. 9) has lost all its teeth anterior to M^1 but it is clearly that of a young juvenile cercopithecoid. The maxillae have been broken behind M^1, and M^2 can be seen lying well below the alveolar margin. The facial part of the skull is well preserved but most of the basal, left and posterior parts of the calvaria are damaged or missing. The skull shows the typical morphological features of the juvenile baboon — a relatively small, short face and a large calvaria. The teeth fit those of the genus *Parapapio.* The dimensions of the teeth (in mm.) are: M^1: bm — 9.6; bd — 8.8; l — 11.1. M^2: bm — 11.5; l — (12.4). The breadth dimensions fit *P. broomi* whereas the length dimensions fit *P. whitei.* As M^2 had not yet erupted and M^1 did not have large adjacent teeth to wear it mesially and distally, the length measurements are probably large when compared with those of teeth in a tooth row and this specimen is probably a *P. broomi.*

(4) There are 3 specimens of this genus which include parts of the skull and mandible and both upper and lower teeth. Unfortunately they are rather damaged and difficult to develop.

Fig. 9. *Parapapio broomi?* juvenile (M.3004). Lateral view of skull.

Table 12

Measurements of dm^2 of *Parapapio sp.* (in mm.)

	bm	bd	l
?Sex			
M.3012	8.4	7.8	8.3
M.3010	7.9	6.8	7.8
M.2972	7.5	7.0	8.3

Table 12 gives the dimensions of 3 dm^2 of unknown sex.

Table 13

Measurements of the lower teeth of *Parapapio sp.* (in mm.)

	dm_2			M_1		
	bm	bd	l	bm	bd	
?Sex						
M.3006	6.4	6.7	8.7	8.0	8.3	10.0

Table 13 gives the measurements of one dm_2 of unknown sex.

They are:

M.3044 — The crushed right inferoposterior part of a calvaria and the right maxilla with M^2; also, the right ramus and posterior part of the body of a mandible with M_2 and M_3.

M.3045 — left M_2 and M_3 in a mandibular fragment and parts of several upper and lower teeth.

M.3046 — right half of a female mandible with teeth and also some upper teeth, all badly damaged.

Discussion: The new *Parapapio* material from Makapansgat is of value from a number of different aspects.

Firstly, the number of specimens of each of the 3 *Parapapio* species at Makapansgat is interesting. Table 14 gives the numbers of specimens of *P. jonesi, P. broomi* and *P. whitei* at Sterkfontein and at Makapansgat and also these numbers expressed as a percentage of the total number of *Parapapio* specimens at the relevant site. The dental size distribution of the *Parapapio* specimens at the two sites is seen to be very similar, although there is some suggestion of a reduction at Makapansgat (the more recent site) in the number of the largest form, *P. whitei.*

Table 14

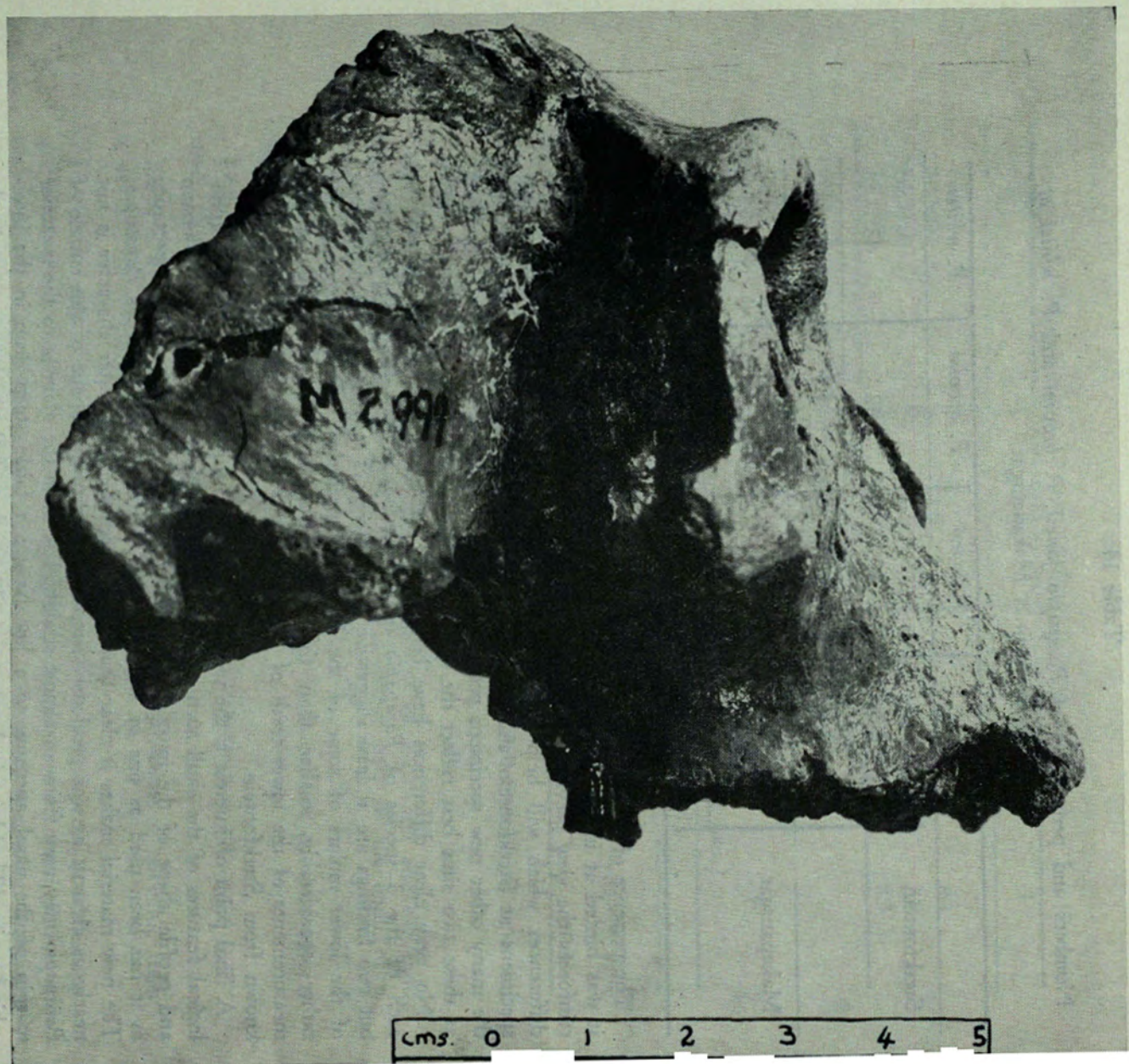
Numbers and percentages of *Parapapio jonesi, P. broomi* and *P. whitei at* Sterkfontein & Makapansgat

		P. jonesi	*P. broomi*	*P. whitei*
Sterkfontein	No. of specimens	24	42	13
	Percentage	30.5	53	16.5
Makapansgat	No. of specimens	15	34	4
	Percentage	28.5	64	7.5

The presence of *P. whitei* at Makapansgat is reported for the first time although it was hinted at in the previous study. The new muzzle of *P. whitei* (M.2962) reinforces the view previously expressed that there are probably morphological skull differences which will help clarify the taxonomic subdivision of the *Parapapio* specimens at Sterkfontein and Makapansgat. However, neither this specimen nor the many other new specimens prove conclusively whether the 3 species postulated at these two sites best reflect the true taxonomy.

No very clear differences have been found beween the specimens referred to each of the 3 species of *Parapapio* from Sterkfontein and from Makapansgat, but two findings are at least suggestive that differences may exist. The dimensions of the lower molars of some of the *P. jonesi* specimens from Makapansgat are rather considerably smaller than those from Sterkfontein and certain of the measurements of the lower teeth of *P. whitei* are larger than any of this species known from Sterkfontein.

A final point of interest is the variability found in this genus of certain morphological features of the skull such as maxillary fossae, shape of the muzzle dorsum and profile shape of the muzzle. The latter feature is of considerable importance as it has been used as one of the diagnostic characters of the genus *Parapapio*. The new material makes it clear that the difference in this latter character is not nearly as clearcut as was previously supposed. The profile shape of the muzzle of *Parapapio* may vary from an almost straight line from the glabella to the posterior margin of the nasal aperture, to a line having a fairly steep drop in the interorbital region. The shape is thus more similar to that of *Papio* than was previously supposed but it is still considerably different. The absence of clear sexual dimorphism in the molars of *Parapapio* continues to be a significant feature separating this genus from *Papio*.


M 2.991
cms. 0 1 2 3 4 5

Cercopithecoides Mollett, 1947

A number of specimens belonging in this genus have been found in the new material from Makapansgat. The material includes specimens which necessitate a re-description of the male skull of *C. williamsi* and also a re-assessment of the taxonomy within the genus. The new material is all referred to the species *C. williamsi.*

Cercopithecoides williamsi Mollet, 1947

Referred Material: 10 specimens of this species were found in the newly recovered material from Makapansgat. These specimens include a very well preserved male skull (M.2999) which is described below, a good male muzzle with all 4 incisors (M.3000) and the interorbital portion and left maxilla with no teeth of a specimen of doubtful sex, but probably also a male (M.674). In addition, there is specimen M.2990 which has portions of the right and left corpora of a mandible with P_3 — M_2 on the right and M_2 and the mesial half of M_3 on the left, M.2989 and M.2987 which are mandibular fragments with single teeth and 4 isolated lower teeth (M.3025, M.3026, M.3029 and M.3031). Of these latter specimens, M.2990 and M.2989 are probably from males but the sexes of the other specimens are not apparent.

Description: (Figs. 10 — 14.) The new male skull (M.2999) has unfortunately lost all of its teeth with the exception of the left M^3 and that tooth is very worn and considerably damaged. The facial portion of the specimen is intact and very well preserved but the part of the skull posterior to an approximately vertical plane through the anterolateral corner of the left orbit and the posterior part of the right mastoid region is missing.

The type skull of *C. williamsi* (AD.1326-3) is the only male skull of this species hitherto described. It is a very complete specimen but the teeth, facial skeleton and calvarium are damaged in places and generally very eroded. Where bone is missing from the calvaria, an excellent natural endocranial cast has been exposed. Comparison of this specimen with the new skull (M.2999) immediately shows the very close resemblance between the two specimens in overall size, general shape and shortness of the face and shape and size of the dental arcade (Figs. 10 — 13). It appears clear that they both belong to the same species but that due to the damage and erosion of the type skull, a number of features of the male skull of *C. williamsi* require to be re-described.

The new specimens (M.2999 and M.3000) confirm the extreme shortness of the face and a concavity in profile between the nasion and posterior margin of the nasal aperture (Fig. 10). The nasal aperture itself is considerably shorter in the two new specimens (see Table 15) than in the type specimen and it is clear that, due to the damage, the dimension given for the type specimen was too great. The nasal aperture breadth shows considerable variation in the three specimens. On either side of the nasal aperture, the maxilla is flattened and

Table 15

Measurements of the skull of *Cercopithecoides williamsi* (in mm.)

	Male		*?Sex*
	M.2999	M.674	M.3000
Calvaria			
Breadth			
Minimum interfrontal	(58)		
Muzzle			
Height			
Anterior to P^3	30		
Breadth			
Anterior to M^3	46		
Anterior to P^3	43		
Length			
Muzzle	58.5		59
Palate	55		
Orbit			
Interorbital	22	19.5	19
External orbital	91		
Height	23		20
Breadth	29		
Nasal aperture			
Breadth	19		17.5
Length	(32.5)		32

faces anterosuperiorly (Fig. 11). The canine eminences are large and demarcate this flat antero-superior surface from the laterally facing sides of the muzzle. There are no maxillary fossae.

The nasal bones are extremely flattened and broad in M.2999 but in M.3000 they are rather more rounded. The high narrow appearance of these bones in the type specimen may be partly due to erosion in the region. A remarkable feature of M.2999 is the exceptionally broad interorbital measurement (Fig. 11). That great breadth is normal in this region of this species is confirmed by M.3000 and M.674 (see Table 15). The supraorbital tori are very robust in M.2999 and have a rough pitted appearance; there is a hollow between them in the midline. A marked transverse depression runs across the calvaria behind the tori and the short section of the inferior temporal line that can be seen on the right side of this specimen is very strongly developed (Fig. 12). The latter three features all indicate a remarkable robustness not formerly associated with, or anticipated in, this species.

Viewed from below (Fig. 13), the palate is rectangular in shape as in the type specimen. The incisive foramen is large and is flanked on each side by 2 — 3 anterior palatine foramina. The palate is somewhat uneven generally and pitted by numerous foramina. The posterior palatine foramina are large and slit-like in an anteroposterior direction and there is no lingula. The whole posterior part of the palate (the palatines) slopes superiorly on each side into the posterior palatine foramina.

Fig. 11. *Cercopithecoides williamsi* male (M.2999). Anterior view of skull.

The beautiful state of preservation of the new specimen (M.2999) allows numerous other anatomical features to be seen which are not often preserved in the usually damaged and fragmented cercopithecoid material from the South African limestone deposits. Thus, there are 4 large infraorbital foramina, a short patent metopic suture, and, although slightly damaged, the external acoustic meatus and mandibular fossa can be clearly seen. These latter structures show no unusual features.

As stated above, only the left M^3 is present in M.2999 and this is very worn and badly damaged (Fig. 13). The root sockets of all the other teeth, with the exception of the right I^1 and I^2, can be clearly seen and the root pattern is as described for the other living and fossil Cercopithecoidea. A diastema is present between $\underline{C}$ and I^2. On the right, I^1 and I^2 must have been lost some time before fossilization as their root sockets have been obliterated by alveolar bone. The only other information about the upper dentition from this new batch of specimens comes from M.3000 which has all 4 upper incisors present but very worn. Although small teeth, they are broad buccolingually. Broken fragments of the $\underline{C}$ are also present but they are sufficient to indicate only that the tooth was of large size.

The new lower jaw fragments are too small to give any new information about the mandible of this species and, morphologically, the new lower teeth fit the described pattern of *Cercopithecoides* well (Fig. 14). Certain of the teeth (e.g. M.3026 and M.3021) show some features, especially the large buccal intercusp clefts, in a form similar to that previously described for *C. molletti.* In size, (see Table 16) the new specimens are larger in a number of dimensions than the specimens previously referred *to C. williamsi* and in certain of these dimensions they approach *C. molletti* closely. The implications of these differences from *C .williamsi* and resemblances to *C. molletti* are considered in the discussion below.

Discussion: The great interorbital breadth, the very robust supraorbital tori and the particularly well developed temporal lines of the new male skull material of *C. williamsi* do not assist in relating this genus to the known living or fossil South African Cercopithecoidea, although there is now some resemblance to the calvaria of *'Parapapio' coronatus.* With the relatively very large calvarium and extremely short face with small premolars and molars, it is difficult to interpret the new features, even allowing for the fact that the upper canines were rather large. Detailed comparisons with other living and fossil African forms (and possibly Asian types as well) will have to be made in an effort to elucidate the affinities of this genus.

In the previous study, the few Makapansgat *Cercopithecoides* specimens known were grouped with those of Sterkfontein in *C. williamsi.* Some of their dental dimensions appeared to be near or at the upper limits for that species but a clear separation of material from the two sites was not indicated. The dimensions of the lower teeth of M.2990, one of the new *Cercopithecoides* mandibular fragments from Makapansgat, would, if they were referred to *C. williamsi,* increase the ranges of 4 dimensions (M_1 bm, bd, l; M_2 bm) considerably.

Fig. 12. *Cercopithecoides williamsi* male (M.2999). Dorsal view of skull.

Table 16

Measurements of the lower teeth of *Cercopithecoides williamsi* (in mm.)

	P_3		P_4		M_1			M_2			M_3			
	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
?Sex														
M.2990	5.2	—	6.3	6.9	7.5	7.7	9.1	8.6	8.4	9.5	8.3			
M.2987											7.9	7.5	(3.5)	12.6
M.3029											8.3	7.5	—	11.3
M.3025					—	—	8.5							
M.2989			5.6	7.3										
M.3026								8.3	8.1	9.9				
M.3031					7.5	7.7	10.0							

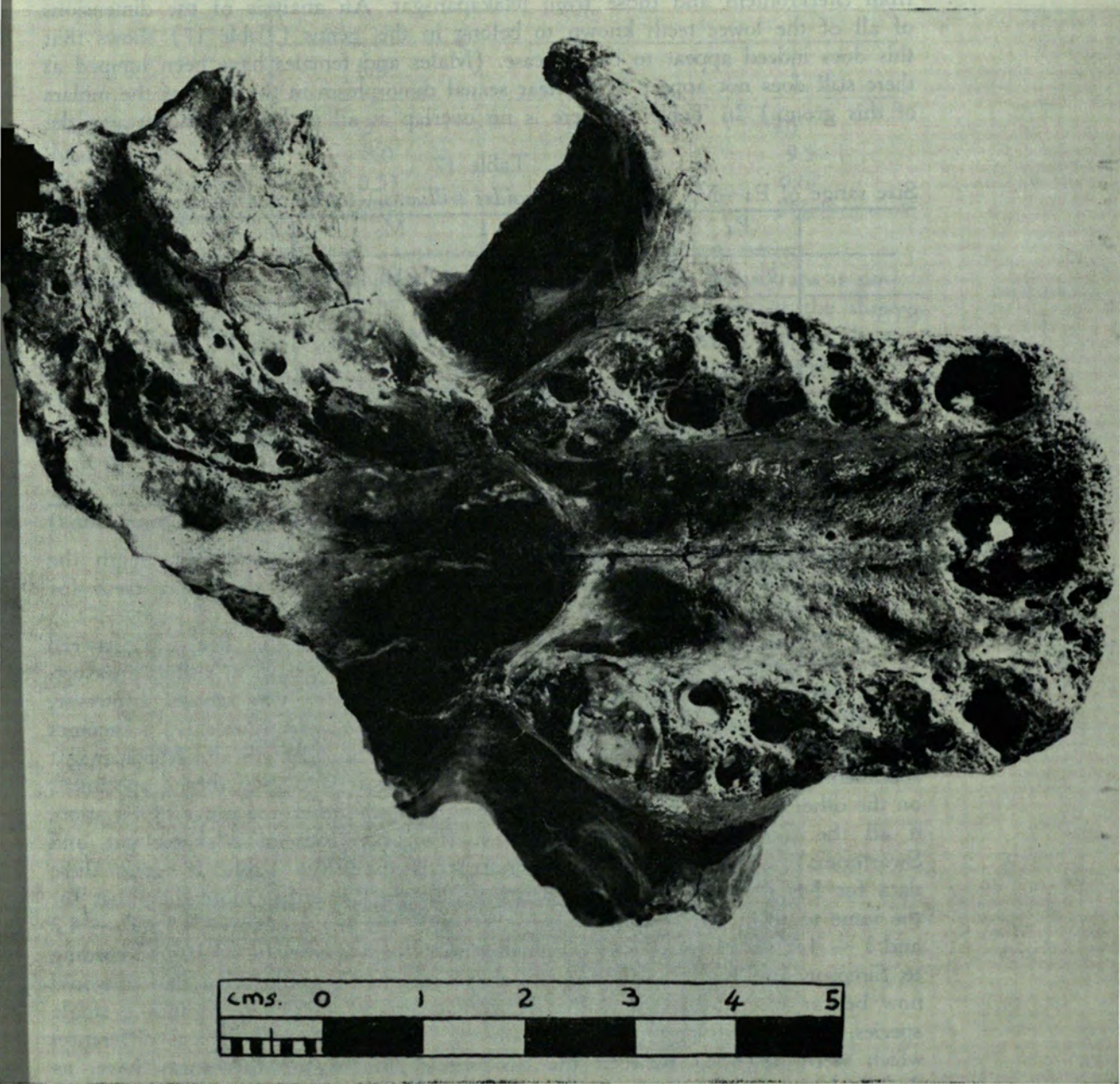


Fig. 13. *Cercopithecoides williamsi* male (M.2999). Basal view of skull.

Also, many of the other dimensions of the newly discovered fragments would fall near or above the maxima previously found for that species. This suggests that a dental size difference might be present between the *Cercopithecoides* specimen from Sterkfontein and those from Makapansgat. An analysis of the dimensions of all of the lower teeth known to belong in this genus (Table 17) shows that this does indeed appear to be the case. (Males and females have been lumped as there still does not appear to be clear sexual dimorphism in the sizes of the molars of this group.) In Table 17 there is no overlap at all in M_1 length between the

Table 17

Size range of P_4—M_3 of *Cercopithecoides williamsi*—males plus females—(in mm.)

	P_4		M_1			M_2			M_3			
	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
STS.	5.2 5.4	6.5 6.6	6.2 7.4	6.4 7.3	7.7 8.1	6.8 8.3	6.8 8.6	8.5 9.6	7.7 8.3	7.1 8.2	3.6 5.8	10.9 12.4
MAK.	5.5 6.3	6.9 7.0	6.5 7.5	7.2 7.7	8.4 10.0	7.9 8.6	8.1 8.5	9.5 9.9	7.9 8.3	7.5 8.8	(3.5) 5.3	11.3 12.6
SK.	6.3 6.9	6.2 7.5	7.2 7.8	7.5 8.3	8.2 10.0	8.2 8.7	9.0 9.7	10.4 10.7	8.8	8.9	—	—

(STS. — Sterkfontein; MAK. — Makapansgat, limeworks; SK. —Swartkrans)

Sterkfontein and Makapansgat specimens and in M_1 bd. and M_2 length the overlap is only very slight. There are insufficient data on the upper teeth for a similar analysis to be of value.

The new specimens have also considerably decreased the size gap between *C. williamsi* and *C. molletti,* although there is still no overlap in certain measurements, for example on M_2 bd and length, between the two species. However, with all the *Cercopithecoides* material arranged by sites, as in Table 17, it becomes apparent that the dental size differences between the Sterkfontein and Makapansgat specimens on the one hand, and the Makapansgat and Swartkrans specimens on the other hand, are of much the same magnitude. Further, the range of variation, if all the *Cercopithecoides* material (i.e. from Sterkfontein, Makapansgat and Swartkrans) is lumped together, is not really excessive. Table 18 gives these data for M_2. The coefficient of variation calculated is rather more than that for the same tooth in *Papio ursinus* where the values (in %) are bm — 4.5, bd — 4.2 and l — 4.9, but they are still within the limits for a species (4 — 10% according to Simpson and Roe, 1939). For the above reasons, it would seem that it would now be far wiser to lump all the known *Cercopithecoides* material into a single species, *C. williamsi* and to sink *C. moletti.* The small morphological differences which were described between the two species in the previous study have, as described above, been bridged in several instances and the others are very minor and are probably the result of small relative growth differences.

Table 18

Statistical variation of M_2 in *Cercopithecoides williamsi* — males plus females — (in mm.)

	M_2		
	bm	bd	l
Number	13	14	16
Mean	8.0	8.3	9.5
Standard deviation	0.51	0.74	0.67
Coefficient of variation	6%	9%	7%

The size increase from Sterkfontein, through Makapansgat to Swartkrans is now obvious and this sequence fits the currently accepted age sequence of the three sites from oldest through to most recent. The *Cercopithecoides* material must there-

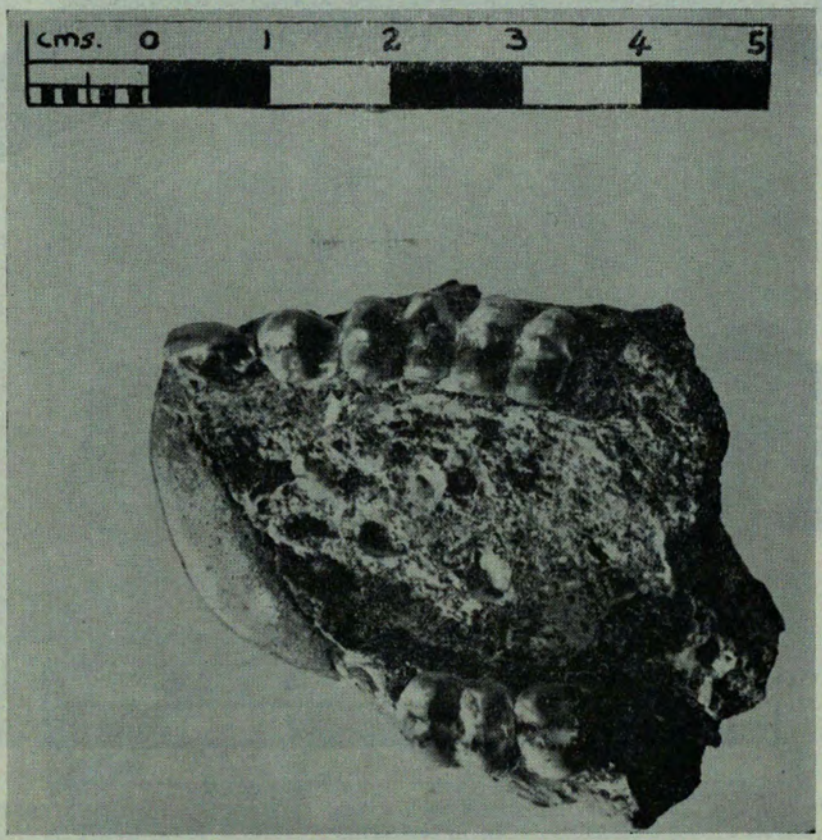


Fig. 14. *Cercopithecoides williamsi* sex? (M.2990). Occlusal view of mandibular fragment with teeth.

fore be regarded as forming a chronocline and it becomes necessary to decide whether the material from the three sites merits subspecific separation. Single *Cercopithecoides* specimens have previously also been described from Taungs, Graveyard and Cooper's and there are two specimens known from Swartkrans II. This material is at present too incomplete for classification in one of the three groups described above but, when more material from these sites is recovered, they may yet be found to bridge or extend the three size ranges postulated in Table 17. It would therefore seem that the most satisfacory arrangement at the

Fig. 15. *Simopithecus darti* (Above, M.2974; below left, M.2967; below right, M.2971). Views of upper teeth.

moment is to place all of the *Cercopithecoides* specimens into one species, *C. williamsi,* with the specimens from Sterkfontein, Makapansgat and Swartkrans forming a chronocline. More material from these, and the other sites mentioned above, may in the future require three subspecies to be created or may show a continuous gradation to exist in the material from all of the above sites.

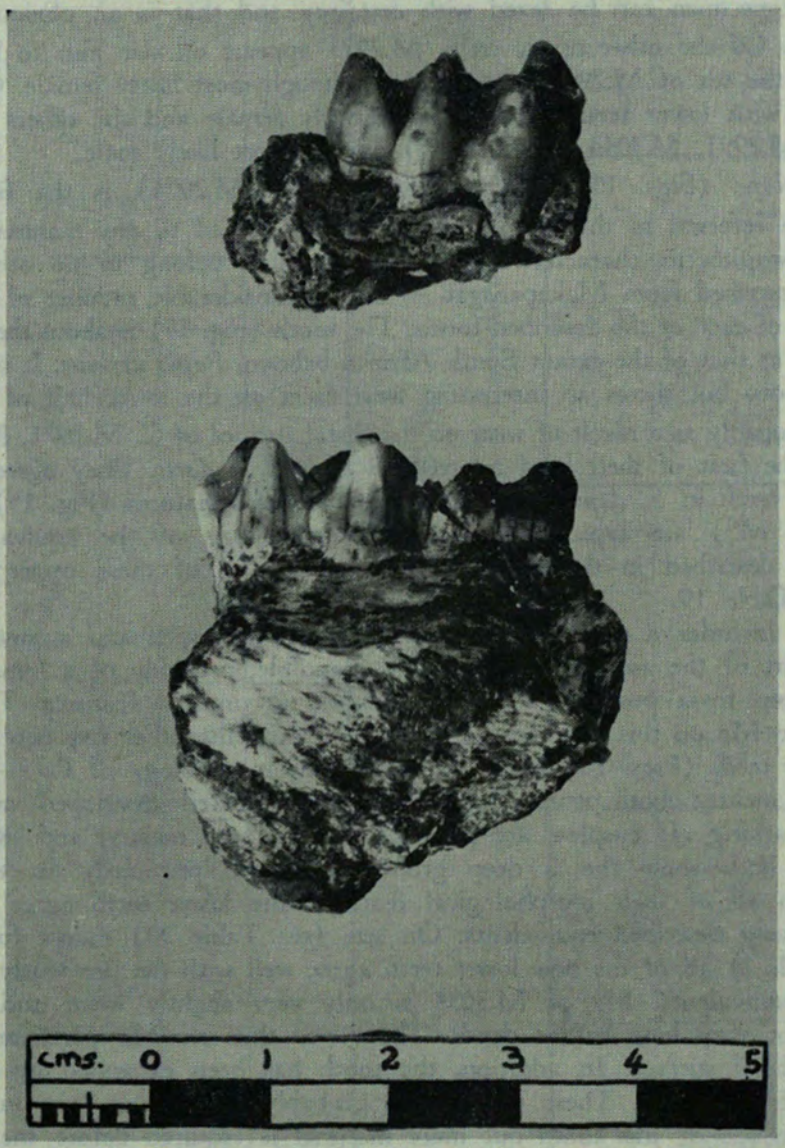


Fig. 16. *Simopithecus darti* sex? (Above, M.2991; below, M.3034). Lateral view of lower teeth.

Simopithecus Andrews, 1916.

There are nine specimens of this genus in the new material from Makapansgat and they can all clearly be referred to the species *S. darti*, which has previously been described from this site.

Simopithecus darti (Broom and Jensen), 1946.

Referred Material: The nine new specimens of this species are all either rather small maxillary or mandibular fragments with teeth, or isolated teeth. Only one specimen can be sexed with certainty and that is an obvious male $\underline{C}$ (M.2974). Of the other upper teeth, M.2971 appears on size also to be from a male, but the sex of M.2967 is uncertain, although most likely female. Of the six fragments with lower teeth, M.2981 is probably female and the others (M.3027, M.2965, M.2991, M.3034 and M.3035) are all most likely male.

Description: (Figs. 15 — 17.) The male $\underline{C}$ (M.2974) is the first of its kind to be referred to this species. Although not linked to any material showing typical *Simopithecus* characteristics, on size it could belong to no other species hitherto described from Makapansgat — and a considerable number of specimens are known of each of the described forms. The tooth (Fig. 15) is about the same size and shape as that of the extant South African baboon, *Papio ursinus*. It is comparatively unworn but shows an interesting wear facet on the lower half of its mesial surface, probably as a result of wear on the distal surface of $\overline{C}$. M.2971, P^3 and P^4, are also the first of their kind referred to a male *S. darti*. They agree with the equivalent teeth in *S. danieli* and present no unusual features (Fig. 15). M.2967 (M^2 and M^3) are typical in size and morphology of the equivalent teeth previously described in this species. The sizes of all of these upper teeth are given in Table 19.

M.2981 includes a small posterior portion of the corpus and a small antero-inferior part of the ascending ramus of a mandible, probably of a female. Other than a deep fossa posterior to M_3, it shows no unusual features. The height posterior to M_3 on this specimen is 36mm. This and the other five new specimens with lower teeth (Figs. 16 and 17) illustrate the morphology of P_4 — M_3 very well and include both worn and unworn teeth. Well developed mesiobuccal grooves marking off cusplets are present on all of the molars, and the two P_4 specimens both show the 2 deep grooves described previously on the buccal surface. In all of their morphological features, the lower teeth agree well with the previously described equivalents. On size (see Table 20) except for M.3034 (mainly M_2 l) all of the new lower teeth agree well with the previously described *S. darti* equivalents. M_2 of M.3034 is only very slightly worn and probably erupted not very long before death. There was thus no M_3 posterior to it to wear its distal surface. In addition, the tooth has been expanded by a number of matrix-filled cracks. These two factors probably account, at least in part, for the greater size of this tooth but more material is required before the specimen can be adequately assessed.

Table 19

Measurements of the upper teeth of *Simopithecus darti* (in mm.)

	C				P3		P4		M1	M2			M3		
	h	b	l_1	l_2	b	l(h)	b	l		bm	bd	l	bm	bd	l
Male															
M.2974	(40)	11.5	11.2	13.6											
?Sex															
M.2971					8.0	(6.1)	10.0	8.6							
M.2967										13.3	12.0	15.8	13.3	11.6	17.4

Table 20

Measurements of the lower teeth of *Simopithecus darti* (in mm.)

	P_4		M_1			M_2			M_3			
	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
?Sex												
M.3027	8.0	9.7										
M.2965			—	9.0	11.4	12.0	11.1	15.1	13.1			
M.2981						11.2	11.0	12.7	12.4	(11.7)	7.6	18.2
M.2991									13.4	11.4	7.3	20.5
M.3034						12.5	12.3	18.2				
M.3035	(8.6)	9.4										

Discussion: In a recent paper, Leakey and Whitworth (1958) report that much new fossil *Simopithecus* material has been discovered in East Africa in the last few years. Using this material, the authors give a considerably expanded description of the genus *Simopithecus* and propose that the East African species, *S. oswaldi,* be subdivided into 3 subspecies, *S. o. oswaldi* (from Kanjera), *S. o. olduvaiensis* (from Olduvai) and *S. o. mariae* (from Olorgesailie). The authors state that the size ranges of these three subspecies overlap but that there is "some indication that the *Simopithecus* at Olduvai was slightly larger than that found at Kanjera, and that the *Simopithecus* at Olorgesailie was still larger." A new giant form of *Simopithecus* from Olduvai, *S. jonathani,* is also described in their paper. This species is interesting in that the sizes of the teeth of the type specimen, a female, are almost exactly matched by the *S. danieli* males from Swartkrans.

Because of the considerable size range now attributed to *S. oswaldi,* more than double that of *Papio ursinus,* Leakey and Whitworth suggest that since "moderate size differences alone are insufficient grounds for specific differentiation in such

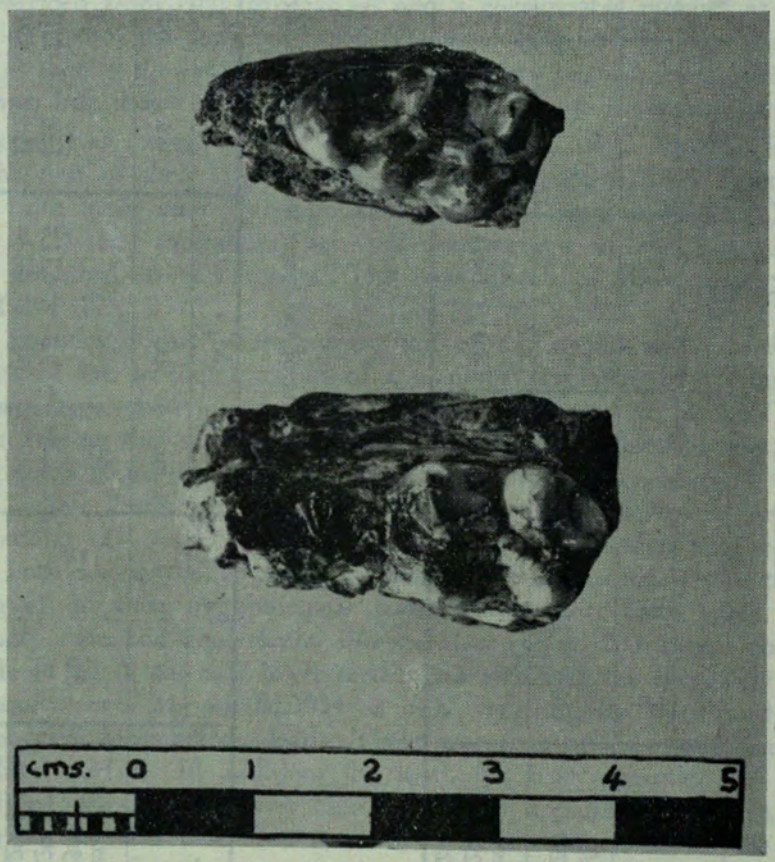


Fig. 17. *Simopithecus darti* sex? (Above, M.2991; below, M.3034). Occlusal view of lower teeth.

a group, it seems to us that the two South African species, *S. darti* and *S. danieli*, are better treated as geographical subspecies (or even a single subspecies) of *S. oswaldi*". However, they conclude by stating that, not having studied the material at first hand, they "do not wish to press this particular view unduly".

A single badly crushed female skull (SK.561) and a female muzzle (SK.563), both of *S. danieli*, are the only *Simopithecus* skull specimens of any size known from South Africa. A few fairly complete mandibular specimens of both *S. darti* and *S. danieli* are however known. In general, there is good agreement between the skulls and mandibles from South Africa and those from East Africa, but even on the meagre material available from South Africa, certain differences are apparent. The muzzle in SK.563 appears to be rather higher than in the *S. oswaldi* specimens illustrated and the maxillary fossa is deep in this South African specimen, although SK.561 is like the East African forms where there is no depression at all. The mandible M.621 (*S. darti*) has a very deep mandibular fossa and the symphysial region slopes down very steeply between the premolars and behind the incisors. This latter specimen in particular thus shows characters which differ considerably from those of *S. oswaldi* but its teeth show the typical *Simopithecus* morphology.

In their paper, Leakey and Whitworth give only a single table of measurements. This table gives the ranges of the various dental dimensions of the premolars and molars, of the males and females together, for the whole of the species as now defined. In the two South African *Simopithecus* species, there are distinct size differences, in both species, between these teeth in the two sexes. Also, the specimens included in their table came from sites that are a considerable distance apart and are probably of rather different ages. Until the more detailed account which they are preparing for the *Fossil Mammals of Africa Series* appears, describing their material by sex and site, it is thus not possible to assess the taxonomic proposals which they make. For this reason, and because of the morphological differences discussed above, the name *S. darti* is retained in this paper for the *Simopithecus* specimens from Makapansgat. Similarly, *S. danieli* must continue, at least for the present, to be accepted as the valid name for the *Simopithecus* material from Swartkrans.

In this same paper, Leakey and Whitworth suggest that the specimen KA.150 from Kromdraai, which was previously referred to *Gorgopithecus major*, is a "*Simopithecus* (perhaps *S. oswaldi*)". That there are slight morphological similarities between the teeth of the genera *Gorgopithecus* and *Simopithecus* (and *Dinopithecus* as well) was mentioned in the previous study, but a re-examination of KA.150, and the relavent comparative material, reinforces the view expressed there, namely, that KA.150 does not show the typical dental morphological pattern of *Simopithecus* and definitely belongs in the species *G. major*. On a recent visit to South Africa, Dr. Leakey examined the relevant material and now agrees that this species is not a *Simopithecus*.

Finally, Leakey and Whitworth state in their paper that they consider that the material described by Dietrich (1942) as *Papio* (*Simopithecus*) *serengetensis* belongs in the genus *Simopithecus* and, in fact, they "see no reason to separate it from *S. oswaldi*". As stated previously, the illustrations of these specimens in Dietrich's paper are not very clear but the photograph of a mandible (Fig. 38) in particular does not show the very typical *Simopithecus* dental morphological pattern. From the drawings, the teeth depicted in Fig. 4 of Dietrich's paper for example do show some resemblance to the *Simopithecus* pattern but of the eleven molars for which lengths and breadths are given by Dietrich, only a single dimension of a single tooth (M^1 breadth) falls within the already very extensive ranges listed by Leakey and Whitworth for *S. oswaldi*. It would seem that Dietrich's specimens should be re-examined in the light of recent work, but, on the balance of evidence now available, they must be considered small fossil forms of *Papio* or *Parapapio*.

Acknowledgements

The collection and preparation of the material described in this paper was made possible mainly by grants to Emeritus Professor R. A. Dart, Department of Anatomy, University of the Witwatersrand, who has for many years organised research at Makapansgat. The grants were from the Wenner-Gren and Wilkie Foundations of the United States of America, the South African Council for Scientific and Industrial Research and the University of the Witwatersrand.

A number of workers have participated in the actual collecting, particularly Mr. J. W. Kitching, of the Bernard Price Institute for Palaeontological Research, Johannesburg, who also supervised the preparation of the specimens, and Mr. A. R. Hughes of the Department of Anatomy of the University of the Witwatersrand, to whom I am also indebted for the photographs which illustrate this paper. My thanks are due to the above individuals and also to the Institutions mentioned for their help and also for permission to describe the material.

I should also like to thank Professor P. V. Tobias of the Department of Anatomy of the University of the Witwatersrand, and Dr. J. T. Robinson of the Transvaal Museum, Pretoria, for discussions on the subject matter of this paper. Through the courtesy of the Director and Board of the Transvaal Museum, Dr. Robinson also arranged for me to study comparative fossil cercopithecoid material in the Museum's collection. Finally, I should like to thank my wife for typing the manuscript of this paper.

References

DIETRICH, W. O., 1942 Altestquartäre Säugetiere aus der südliche Serengeti, Deutsch Ost Afrika. *Palaeontographica,* 94, abt. A, 52-4.

FREEDMAN, L., 1957, The Fossil Cercopithecoidae of South Africa. *Ann. Transv. Mus.*, 23, 121-262.

LEAKEY, L. S. B. & WHITWORTH, T., 1958, Notes on the Genus *Simopithecus* with a Description of a New Species from Olduvai. *Occ. Pap. Coryndon Mus.*, no. 6, 1-14.

SIMPSON, G. G. & ROE, A., 1939, *Quantitative Zoology*. 1st. Ed. N.Y. and London: McGraw Hill Book Co. Inc.

ERRATUM

Subsequent to the printing of this volume the South African Council for Scientific and Industrial Research has made a substantial contribution towards the cost of publication of the paper by Dr. L. Freedman. This grant is greatfully acknowledged.