THE FOSSIL CERCOPITHECOIDEA OF SOUTH AFRICA

by

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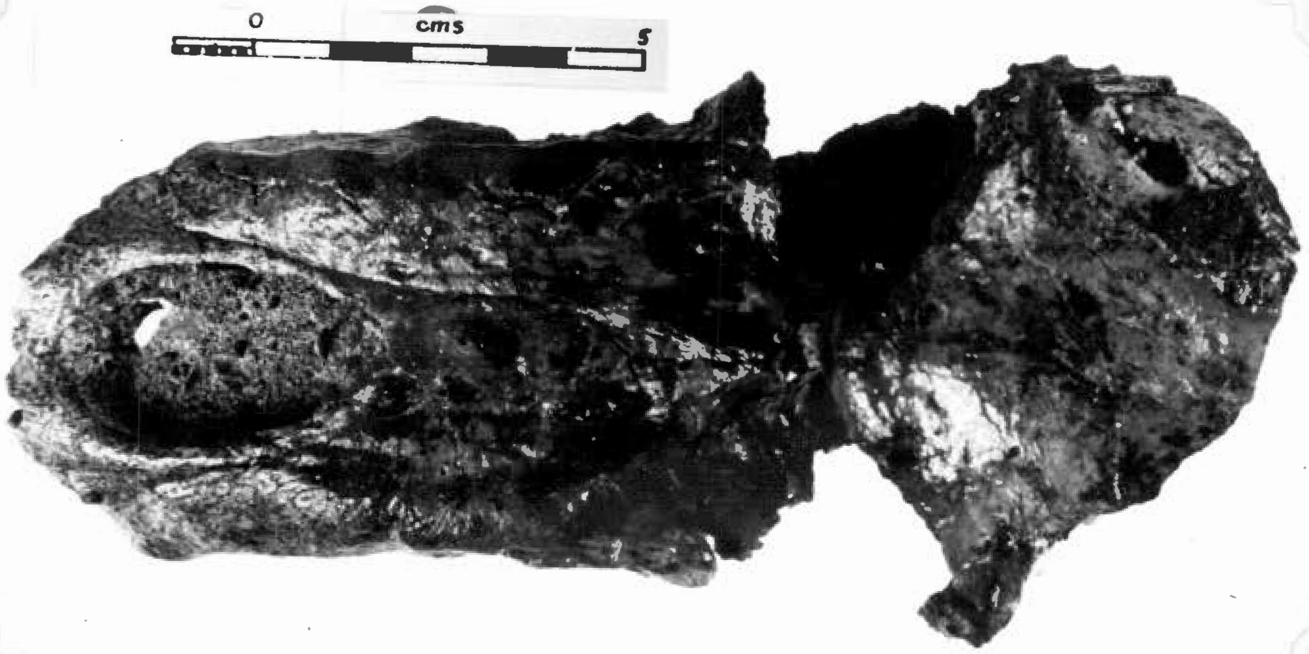

Fig. 59. Papio robinsoni male (SK.560). Muzzle - dorsal view. x 1.

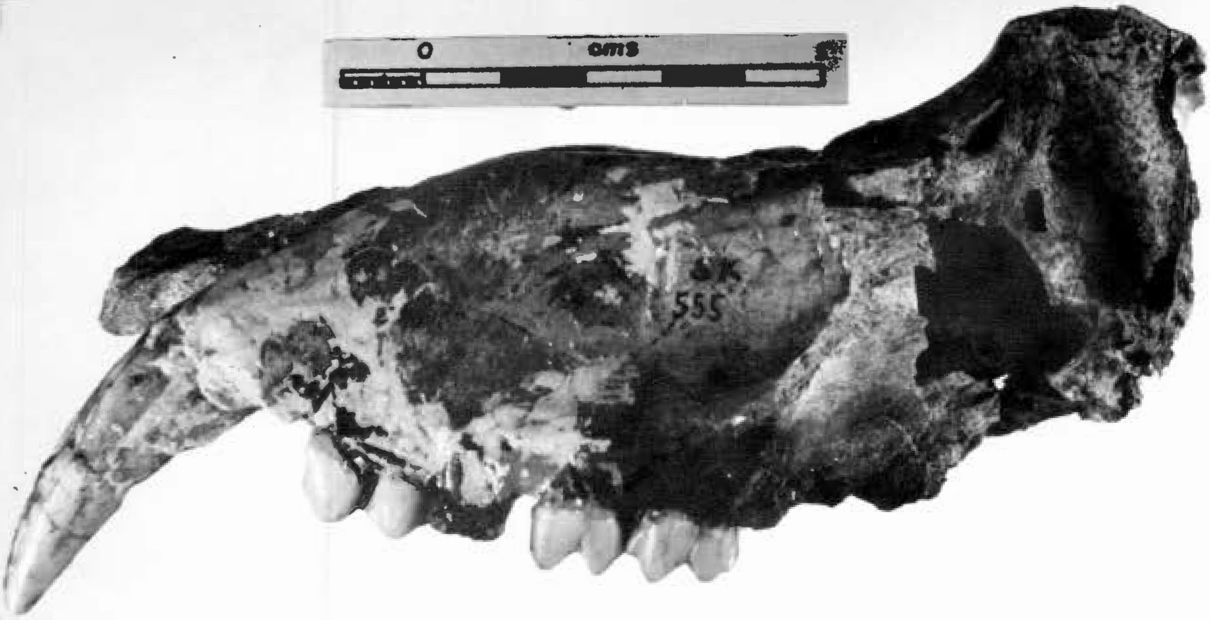

Fig. 60. Papio robinsoni male (SK.555). Muzzle - lateral view. x 1.

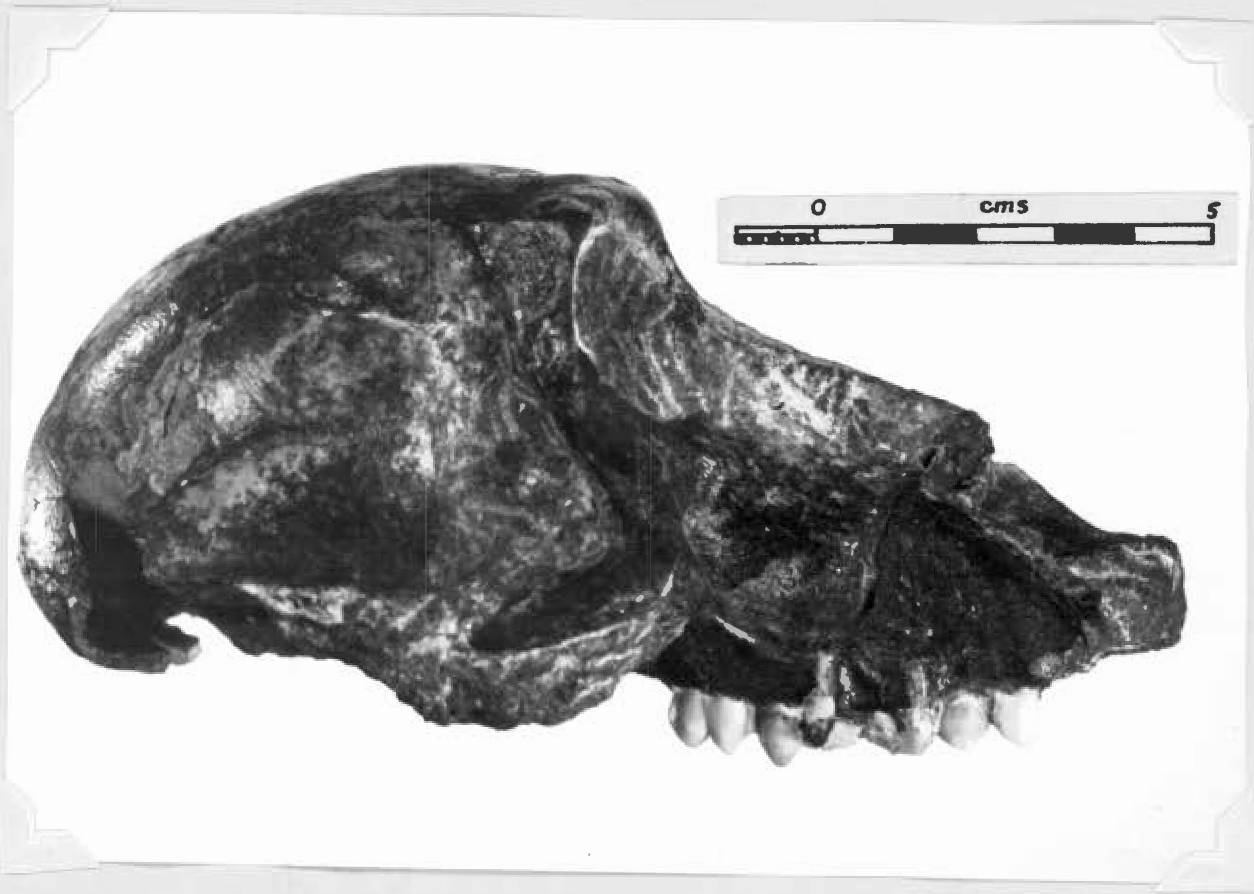

Fig. 61. Papio robinsoni female (SK.588). Skull - lateral view. x 1.

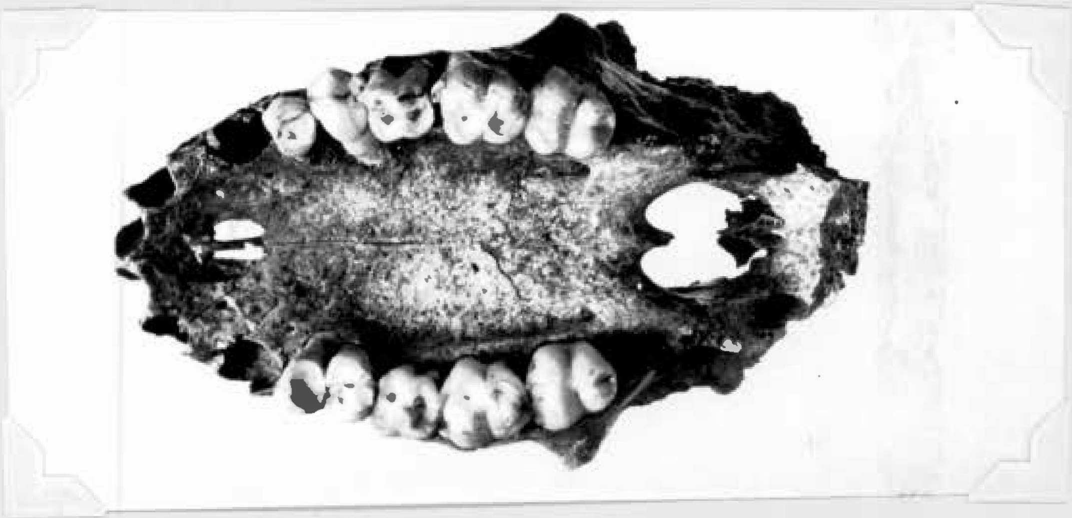

Fig. 62. Papio robinsoni female (SK.562). Palate showing abnormal left P^4. x 1.

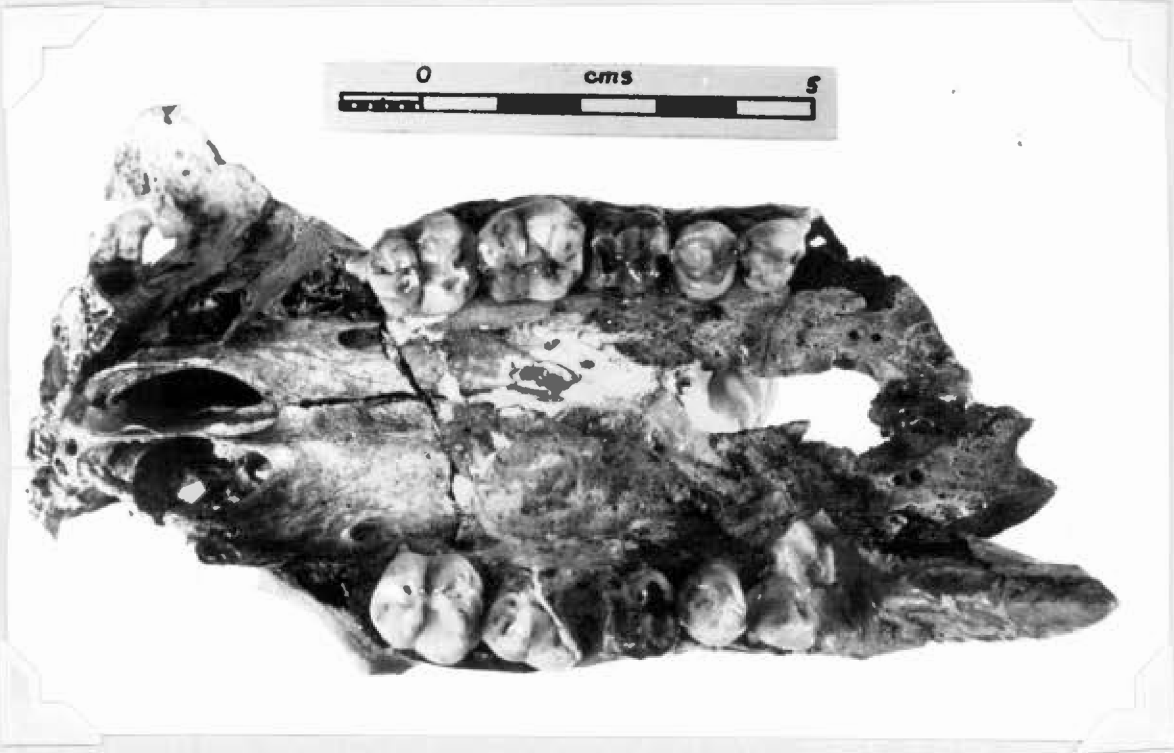

Fig. 63. Papio robinsoni male (SK.555). Occlusal view of upper teeth. x 1.

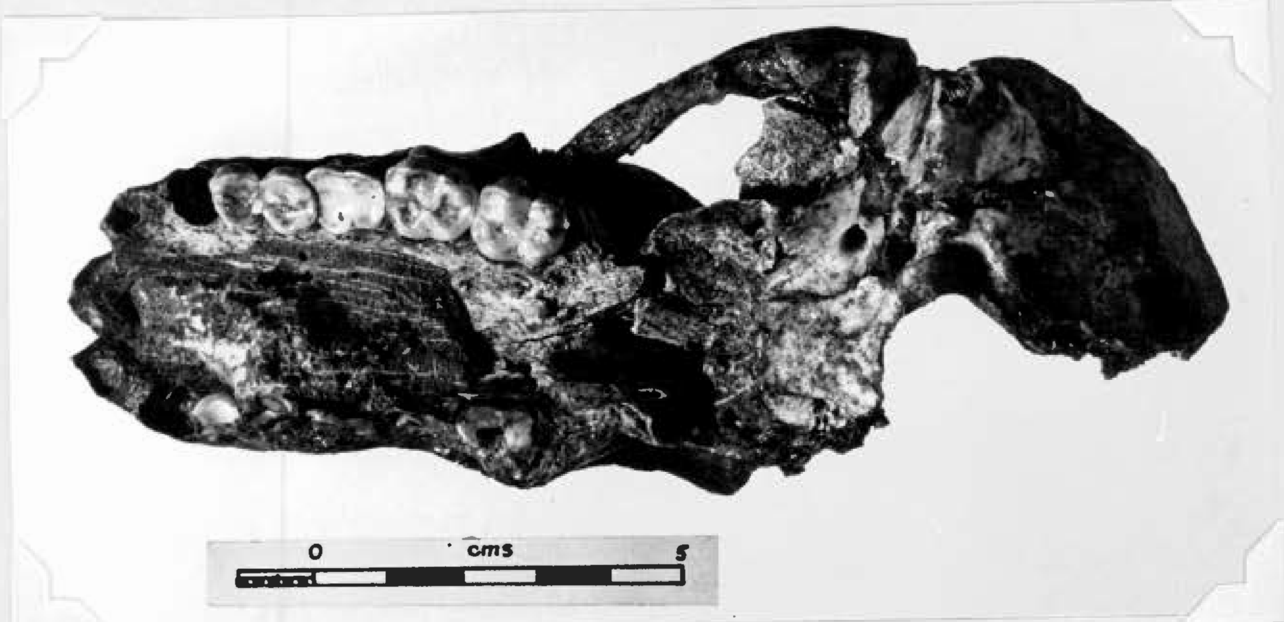

Fig. 64. Papio robinsoni female (SK.557). Occlusal view of upper teeth. x 1.

Fig. 65. Papio robinsoni male (SK.408). Lateral view of mandibular fragment and lower teeth. x 1.

Fig. 66. Papio robinsoni female (SK.407). Lateral view of mandibular fragment and lower teeth. x 1.

Fig. 67. *Papio robinsoni* male (SK.408). Occlusal view of lower teeth. x 1.

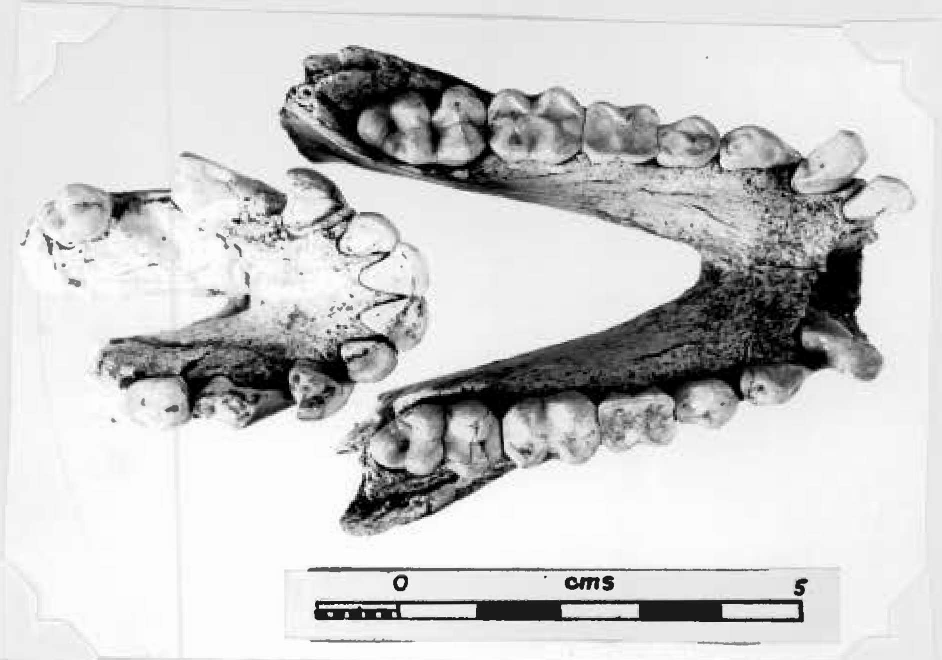

Fig. 68. *Papio robinsoni* female (SK.407, right and SK.410, left). Occlusal view of lower teeth. x 1.

Fig. 71. Papio robinsoni(?) juvenile (SKII.27). Skull - basal view. x 1.

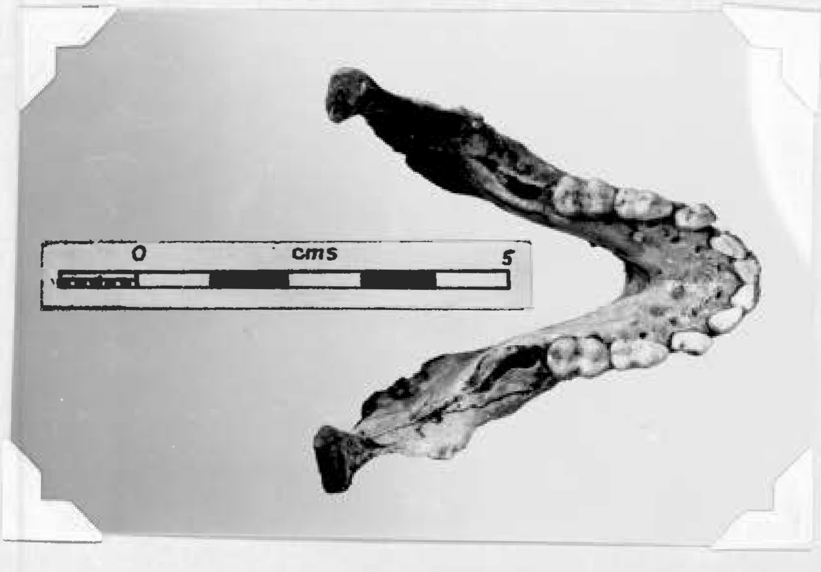

Fig. 72. Papio robinsoni(?) juvenile (SKII.27). Occlusal view of lower teeth. x 1.

Fig. 69. Papio robinsoni(?) juvenile (SKII.27). Skull - dorsal [redacted] . x 1.

Fig. 70. Papio robinsoni(?) juvenile (SKII.27). Skull and mandible - [redacted]. x 1.

more material becomes available, it is possible that some of these forms may be found to merit subspecific status. There is also a small group of seven specimens from Swartkrans itself which are listed separately at the end of each sex in tables 10c and d. The dimensions of these few specimens also do not quite match those of the rest of the specimens described from Swartkrans as _P.robinsoni_, although morphologically they appear to be indistinguishable. These specimens may possibly come from an isolated pocket or slightly different level than the others.

In examining the dentition of _P.robinsoni_ two abnormal teeth were found. M^3 of SK.436, a male specimen, is badly malformed and the whole tooth pattern is abnormal. The alveolus of the left P^4 of SK.562, a female, is situated some 5mm. lingual to the rest of the tooth row and the tooth leans buccalward across the palate at an angle of about 45° (Fig.62).

Papio angusticeps (Broom).

Parapapio angusticeps - Broom, 1940.
Parapapio angusticeps - Broom, 1946.
Parapapio angusticeps - Hopwood and Hollyfield, 1954.

Holotype:

A very good female skull, KA.194, with almost complete dentition.

Repository of type:

Division of Vertebrate Palaeontology and Physical Anthropology, Transvaal Museum, Pretoria, South Africa.

Type site:

Kromdraai, Transvaal, South Africa.

Referred material:

Thirteen specimens from Kromdraai, sixteen from Cooper's and one from Minaar's Cave. (For the numbers of these specimens see tables 11a - d).

There are two rather good skulls from Cooper's, a male specimen (CO.100) lacking the right and posterior walls of the calvarium and an almost mature female specimen (CO.101) in which the dorsal and most of the lateral walls of the calvarium are missing.

Description: (Figs. 73 - 81)

The muzzles of the two sexes of this species, apart from size, fit the respective descriptions of the male and female of P.ursinus almost exactly, except that the maxillary ridges in both sexes are weaker and the maxillary fossa of the male extends posteriorly under the infra-orbital margin. A similar excavation under the orbit also occurs in the female of both species but it is deeper in P.angusticeps. In the female (KA.194 and CO.101), the nasal aperture also seems relatively shorter and broader and there appears to be greater narrowing of the nasal bones towards, and in, the inter-orbital region. In this sex too, the nasal processes of the premaxillae are exceptionally long (KA.194 and CO.101). There are multiple infra-orbital foramina in both sexes and the zygomatic process of the maxilla is situated at about the level of the mesial part of M^3. In the male the zygomatic bone lies rather more vertically than in the chacma baboon and the orbit appears less dorso-ventrally flattened. The inter-orbital region seems somewhat narrow in both sexes. Because of the secondary elongation of the muzzle and the presence of a large C, the male palate is rather rectangular with some posterior narrowing whereas that of the female is more horseshoe-shaped and wider posteriorly.

The supra-orbital tori of both the male and female of P.angusticeps are about as well developed as those in the same sex of P.ursinus but the frontals sweep upwards to the tori so that a fairly deep depression is present posterior to them. On the anterior part of the calvarium, the temporal lines are fairly well marked in the male (CO.100) and can be traced clearly to a point some twenty millimeters posterior to the bregma. Unfortunately, the posterior portion and base of the calvarium is missing, in this the only male skull known, but it would seem from the degree of convergence of the lines that they probably met anterior to the inion. From a small portion of the left mastoid region still present on this specimen, it is apparent that a fairly large and shelf-like nuchal crest was present in this sex. In the female specimen (KA.194), the temporal lines can be traced on the posterior part of the calvarium all the way down to the nuchal crest and they meet the crest separately some ten millimeters on either side of the inion. In this sex the inion is prominent but the nuchal crest very weak. In both the male and female the zygomatic arch is moderately robust and the external auditory meatus lies at much the same angle as in the chacma baboon.

Except for the male incisors, there are examples of all the teeth of the upper dentition. The female upper incisors show the same structure and wear described for the equivalent teeth of that sex of *P.ursinus* and, as in that species, both the central and lateral pairs lean mesially. There are five good specimens (see table 11c) showing the male $\underline{C}$ and it is relatively lower than that of the chacma. This tooth does not show the faint vertical grooves often seen running up the lingual and distal surfaces of its equivalent in *P.ursinus* but the deep mesial groove always present in the latter is also found in *P.angusticeps*. The female $\underline{C}$ (CO.101) is very similar to that seen in the female of *P.ursinus* both in morphology and relative size. In the female, KA.194, the $\underline{C}$ is worn down to below the level of the molar-premolar row.

In structure, the male P^3 resembles the equivalent tooth of *P.robinsoni* more than it does the one in *P.ursinus*. The tooth shows a considerable forward, and some downward, extension of its mesial (mainly mesio-buccal) portion (particularly in CO.117). As a result, it comes close to resembling a female P_3 except that in this case the extension is much less and the anterior fovea has become almost as large as the posterior one. The female P^3 and P^4 of both sexes are very similar to the equivalent teeth in *P.ursinus* but they do not seem proportionally quite as broad. Both premolars of CO.101, a female specimen, and P^4 of KA.174, a male, show faint vertical grooves on the lingual surface on either side of the main lingual cusp. Compared to the size of the molars, the premolars of P.angusticeps show a more similar relationship to P.ursinus than to P.robinsoni i.e. the premolars are not as large, relative to the molars, as those in P.robinsoni.

The upper molars of this species appear more slender than those of either P.ursinus or P.robinsoni and there is a greater amount of reduction in the distal breadth measurement of M^3. Compared to these two species, the buccal surface is also more vertical, the lingual inter-cusp clefts are larger, the cusps seem relatively slightly higher and the foveae slightly deeper. On the mesio-lingual corner of the lingual surface, there are invariably grooves or pits present and on the female specimen, CO.101, there are, in addition, large lingual accessory cusplets and, near the disto-lingual corner of the lingual surface, vertical grooves and small cingular cuspules. In size, M^2 is larger in all its dimensions than M^1 but its relationship with M^3 varies from slightly larger to slightly smaller. In their various dimentions, the upper teeth are similar in size to those of Parapapio broomi but there is a clear size difference between the teeth of the two sexes in this species (see table 11c). Deciduous molars are present on KA.155 and they are morphologically similar to those described for P.ursinus.

Unfortunately, very few specimens of the mandible of this species have so far been recovered, although a fair number of lower teeth are known. There are, however, four mandibular fragments of fair size (KA.166A, CO.115, CO.112 and CO.103) but these are all of male specimens. These show that, in this sex, the mandibular fossa was shallow, the mandibular foramen multiple and the incisal shelf rather steep. The only lower incisors known are those of a female (KA.168C) and these are too worn to show any detailed structure. The only female $\bar{C}$ teeth hitherto found are on this same specimen. Although very worn, it can never-the-less still be seen that this tooth was morphologically very similar to that of the female of P. ursinus and that it develops similar wear facets. Only two broken fragments of male $\bar{C}$ teeth are known (CO.136 A and C) and little can be concluded as to their shape and size.

The male P_3 (KA.166A, CO.136A and CO.115) is very much larger than that of the female (KA.168) but otherwise seems to present no unusual morphological features. However, P_3 of specimen CO.136A shows a most unusual degree and type of wear. The wear facet is on the mesial extension of the tooth and takes the form of a large v-shaped depression with its deepest part on the mesial side of the mesio-distal mid-point. The facet is so deep that it all but cuts the tooth in two. A single worn male P_4 is known from specimen KA.166A and two worn P_4 teeth are known from Female specimens (KA.168B and CO.135A); none of these teeth appear in any way structurally different to the equivalents in the chacma baboon.

There are quite a number of lower molars available for study but these are mainly from male specimens; the few female teeth known are too worn to show any structure. The male molars are very similar to those of that sex in P. ursinus but the buccal surface is rather more vertical and the buccal inter-cusp cleft is smaller. Mesio-buccally on all the molars, and on the cingulum of M_3 between the metaconid, entoconid and hypoconulid, there are small cuspules on almost all of the specimens. Specimen KA.166A is interesting in that it has an erupting fourth lower molar which is identical in structure to that of a normal M_3. There are a few damaged lower teeth from Minaar's Cave (Min.1A and B) which probably belong to a male of this species. The measurements of these teeth are given at the end of table 11d. More material is required before a certain diagnosis of these specimens can be made.

Measurements:

See tables 11a,b,c and d.

Table 11a. Measurements of the skull of *Papio angusticeps*.

	Male	Female
	CO.100	KA.194
GENERAL.		
Greatest length		139
Basal length	120	99
Bizygomatic breadth	108	91
CALVARIUM.		
Height:		
Basion-bregma	65	(64)
Basion-glabella	80	
Breadth:		
Min. inter-frontal	49	(49)
Greatest temporal	(76)	67
Mastoid	(84)	72
Length:		
Inion-basion		48
MUZZLE.		
Height:		
Post. to M^3	54	
Ant. to P^3	30	21
Breadth:		
Ant. to M^3	47	45
Ant. to P^3	44	36
Dors. to M^2	36	31
Length:		
Muzzle	91	78
Palate	72	
Nasal	51	
Orbit:		
Inter-orbital	10.6	
External orbital	(75)	
Height	22.2	
Breadth	26.2	
Nasal aperture:		
Breadth	18.5	15.4
Length	(35)	20.6

Table 11b. Measurements of the mandible of *Papio angusticeps*.

	Male	
	KA.166A	CO.115
Height:		
Ant. to P_4	32	
Breadth:		
Ant. to P_4		32

Table 11c. Measurements of the upper teeth of *Papio angusticeps*.

	I^1			I^2			$\underline{C}$				P^3		P^4		M^1			M^2			M^3			Rows	
	h	b	l	h	b	l	h	b	l_1	l_2	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	$P^4 - M^3$	$\underline{C} - M^3$
MALE:																									
KA.156							(27)	(8.5)	(7.8)	(8.8)	7.7	8.5	7.9	6.0			(10.5)	11.8	10.5	11.6	11.7	9.1	11.1	37.5	
KA.161													8.5	7.3	10.5	9.3	10.8	11.5	10.5	11.7					
KA.174													7.9	7.4	8.8	8.4	10.6								
CO.100							(30)	9.5	9.1	10.7	7.5	8.0	8.1	6.9				10.8	9.9	12.2	10.9	8.8	12.4	39.5	58.8
CO.117											8.2	10.5	8.4	7.2	9.2	8.4	9.5	11.0	9.7	12.4					
CO.137								9.3	(9.4)	(11.5)															
CO.102																				12.0	11.7	8.4	12.4		
CO.105A-B																		12.4	10.5	12.7	12.1	9.3	12.8		
FEMALE:																									
KA.194							[illegible]	6.0	5.9	5.3	7.0	4.7	7.7	6.1	8.9	8.2	9.0	10.4	9.7	11.2	10.5	8.3	10.6	35.7	46.7
KA.157											7.4	8.6	8.7	7.0	9.0		(9.6)	10.8	9.4	12.6					
KA.155 *		dm^1 5.6	8.0	7.5	dm^2 6.5	8.7									8.7	7.5	10.3								
KA.167											7.0	3.8	7.8	6.7	9.6	8.3	10.2								
CO.101	10.4	7.7	8.5	10.7	6.5	5.8	14.0	6.2	6.1	7.0	7.4	10.0	7.6	7.6	8.7	8.0	10.3	10.9	9.6	12.6	10.9	9.0	12.0		
CO.135													8.3	6.4	9.9	8.7	10.3	11.6	11.0	12.4	12.0	8.9	11.3	38.5	
CO.127																					10.3	8.6	11.6		
CO.128																					10.4	9.0	11.0		
CO.109A																		10.9	9.6	11.0	11.7	8.0	10.6		

Table 11d. Measurements of the lower teeth of *Papio angusticeps*.

	I_1			I_2			$\overline{C}$			P_3		P_4		M_1			M_2			M_3				Rows	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	$P_4 - M_3$	$\overline{C}-M_3$
MALE:																									
KA.166 A-B							21.9	12.2	6.7	6.2	19.1	6.4	8.3			10.0			12.3	10.7	10.0		14.6		
KA.165															8.0	10.1	9.3	9.4	12.4	9.9	9.0	6.2	14.3		
KA.179																				10.4	8.9	6.8	15.6		
KA.151 *	(13)		6.4		dm$_1$ 5.2	8.3	6.8	dm$_2$	9.2					7.8	7.8	10.9									
KA.163														8.1	7.9	10.2			11.7						
CO.136A-C								11.0	6.7	5.9	15.4	7.2	8.1				9.7	9.5	11.6						
CO.115										5.6	19.1			7.8	8.4	10.4	10.0	9.9	12.1	10.5	8.8	5.2	14.6		
CO.103																	10.1	9.8	11.9	10.4	8.6	4.7	14.2		
CO.108A																				10.6	9.1	6.1	15.0		
CO.112																	9.5	8.9	12.6	9.9	9.6	7.1	14.9		
Min.1A-B	17.0	8.0	6.7	14.7	8.0	7.6	(27.0)	(12.0)	(7.0)	5.5	(21+)	7.0	8.1												
FEMALE:																									
KA.168	3.0	6.7	4.9	4.5	6.7	3.9	10.0	9.1	5.7	5.4	7.3	7.4	7.7	8.7	8.4	9.4			(11.5)						
CO.135B												6.5	7.9	8.7	8.5	9.4									

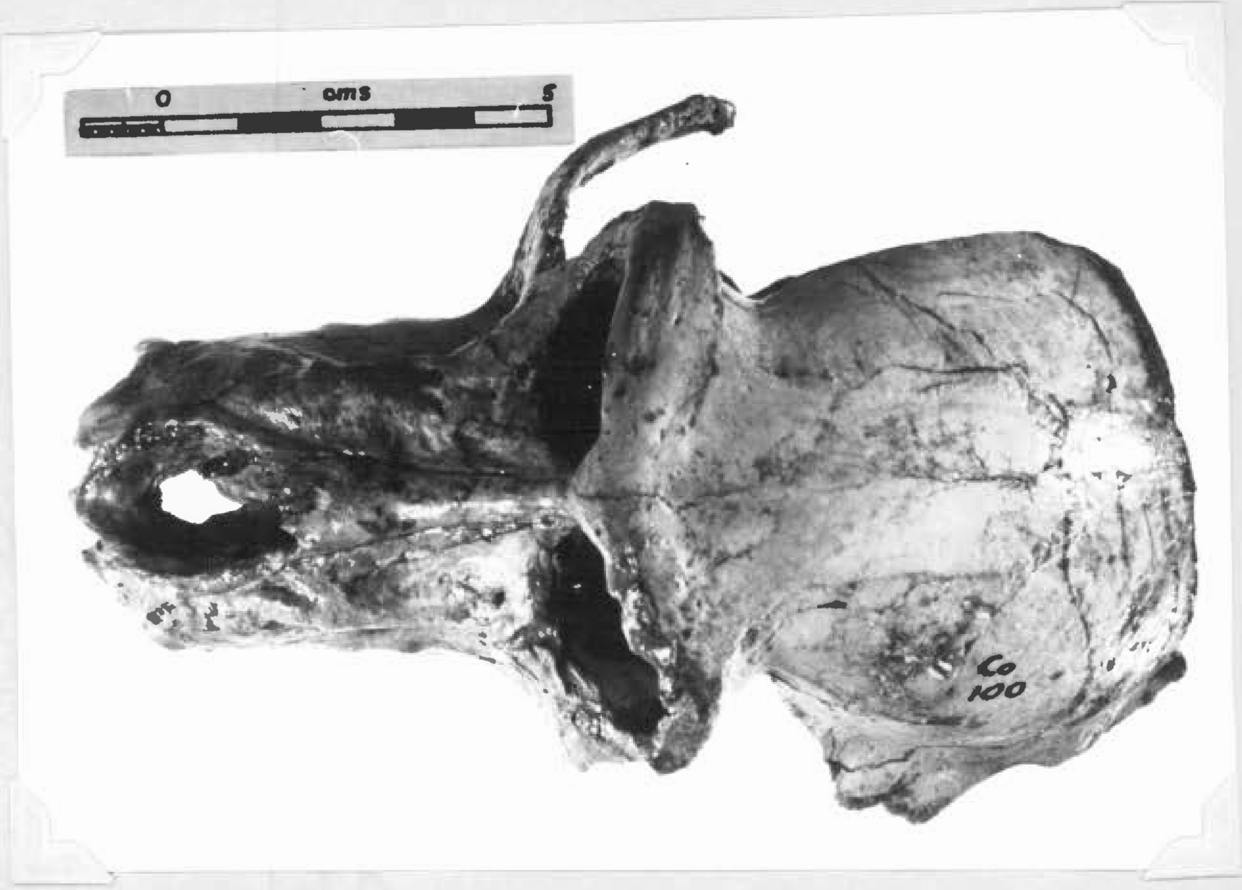

Fig. 73 Papio angusticeps male (CO.100). Skull - lateral view. x 1.

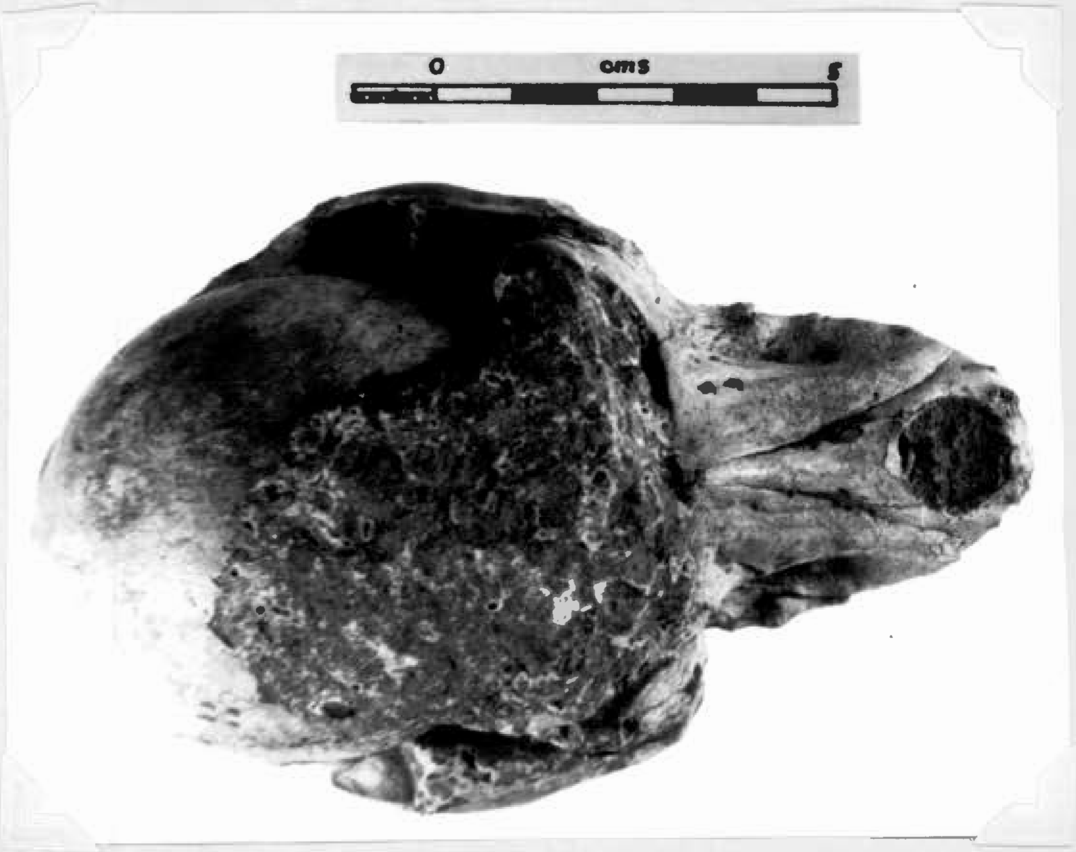

Fig.74 Papio angusticeps female (KA.194). Skull - dorsal view. x 1.

Fig.75 Papio angusticeps male (CO.100). Skull - lateral view. x 1.

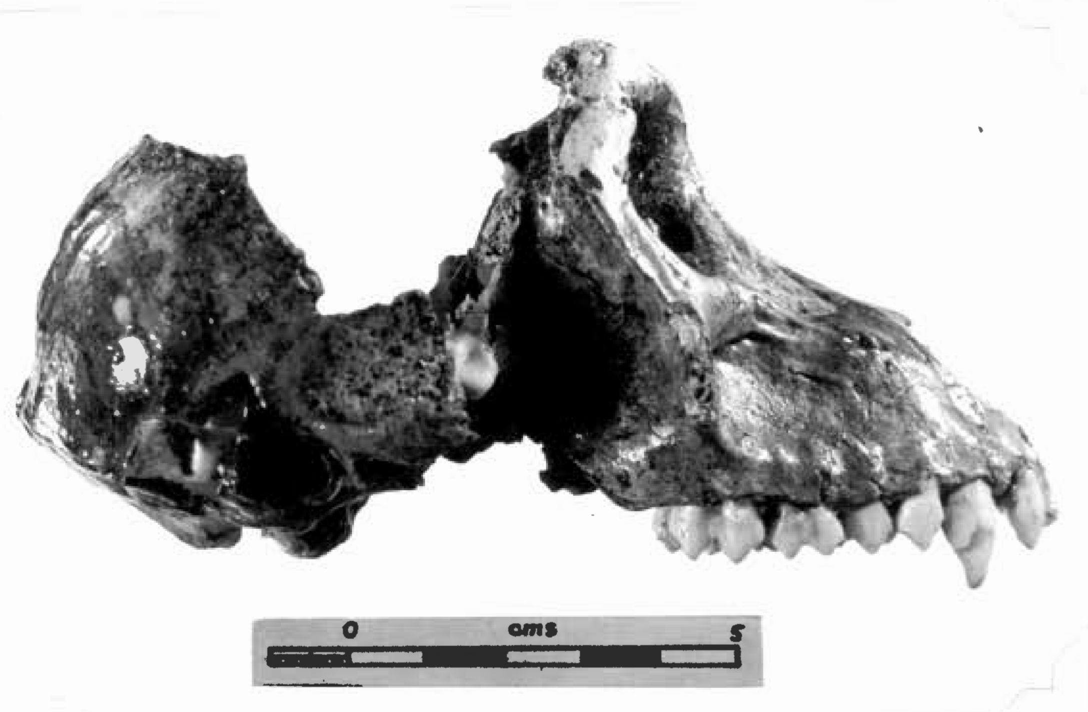

Fig.76 Papio angusticeps female (CO.101). Skull - lateral view.
x 1.

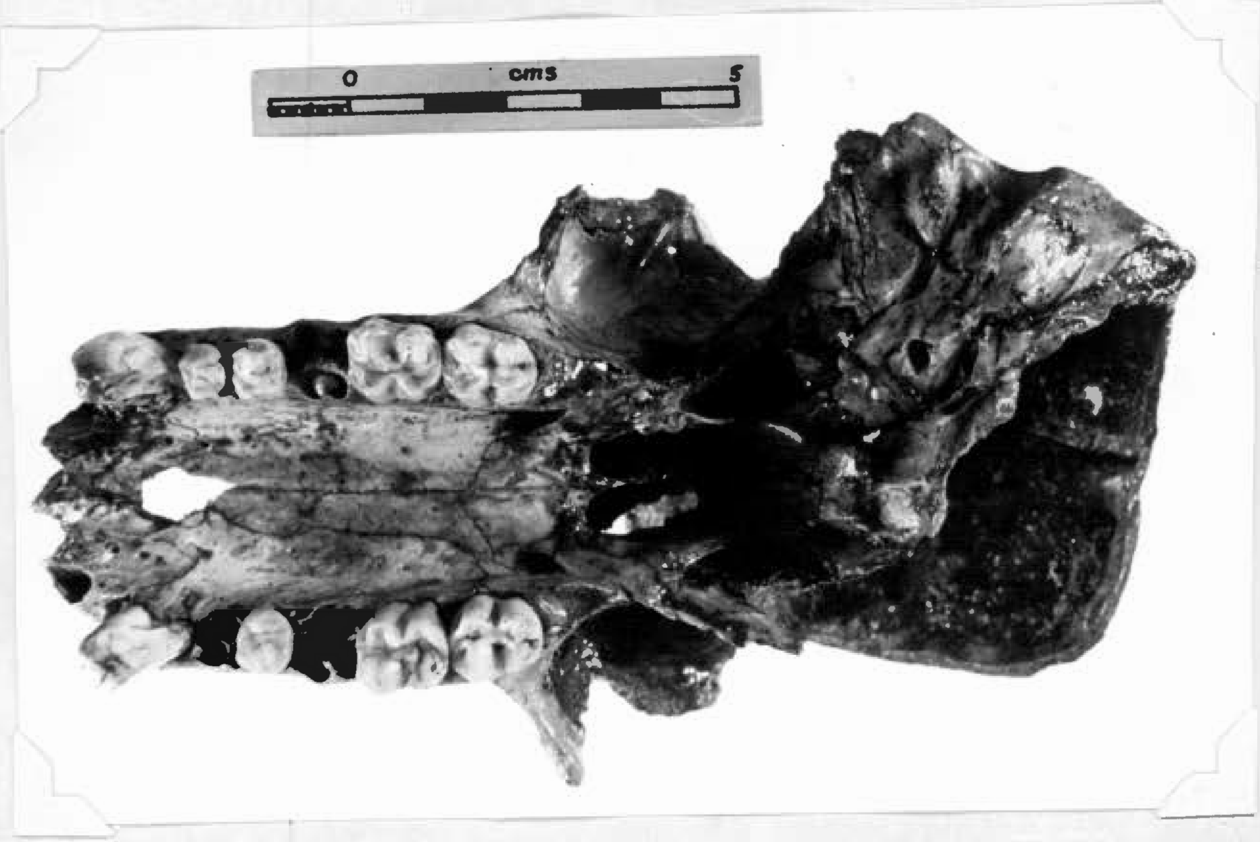

Fig.77 Papio angusticeps male (CO.100). Skull - basal view. x 1.

Fig. 78 Papio angusticeps female (CO.101). Skull - basal view. x 1.

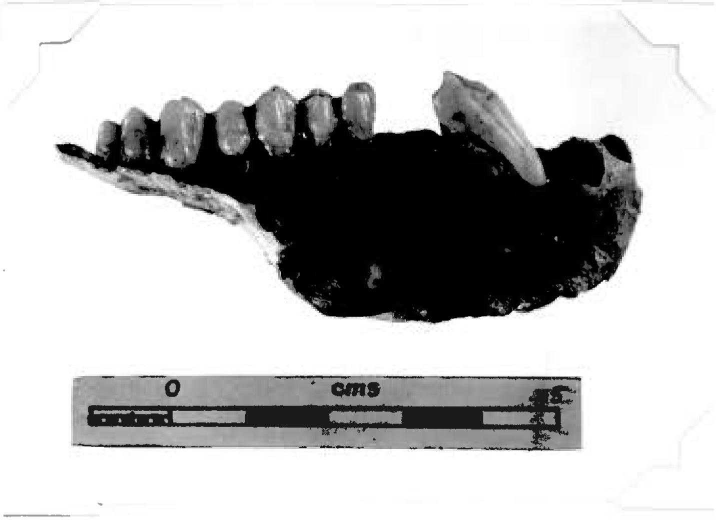

Fig.79 <u>Papio</u> <u>angusticeps</u> male (CO.115). Lateral view of mandibular fragment and lower teeth. x 1.

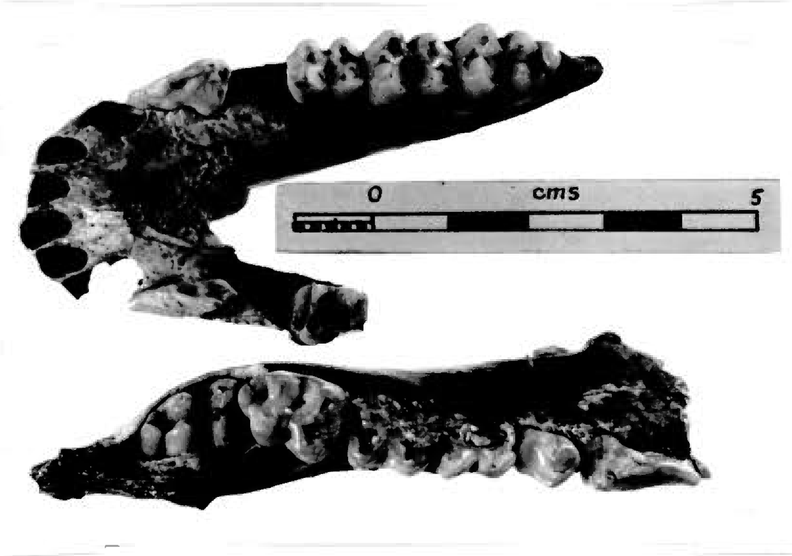

Fig.80 <u>Papio</u> <u>angusticeps</u> male (CO.115, above and KA.166A, below). Occlusal view of lower teeth. Note M_4 in KA.166A. x 1.

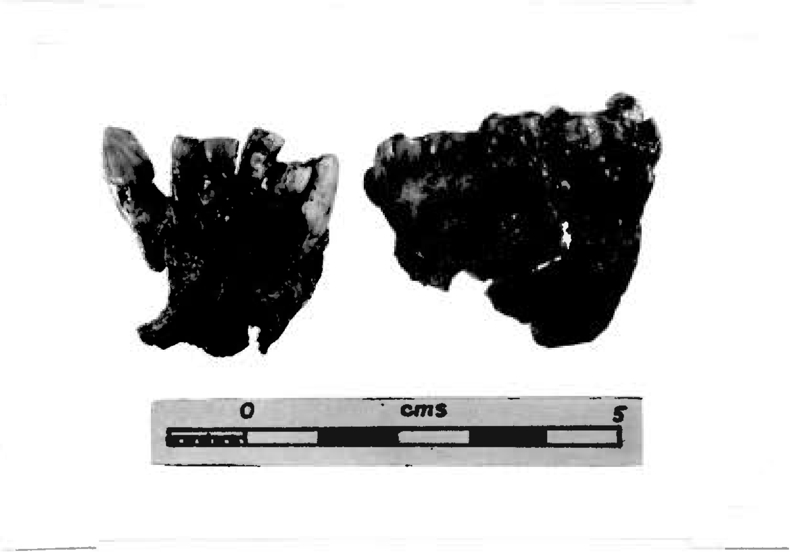

Fig.81 <u>Papio</u> <u>angusticeps</u> female (CO.135B, right and KA.168C, left). Buccal view of lower teeth. x 1.

Remarks:

The type skull of this species (KA.194) lacks most of the inter- and supra-orbital regions and at the time when Broom first described this species (1940) no other more complete skull was known. (This is, in fact, the only specimen Broom describes, although he mentions the existence of two others). Broom doubtless assumed that, in shape, the missing region was similar to that characteristic of the known species of <u>Parapapio</u> (see Chapter 7), which this species otherwise resembles quite closely. He therefore referred the species to that genus.

A considerable amount of new material has since been recovered from both the type site and the nearby site, Cooper's. No good skulls were found in the material excavated from Kromdraai but from Cooper's there are two fairly complete skulls CO.100, a male and CO.101, a female, which from their dentition and general skull morphology, clearly belong with the specimen described by Broom from Kromdraai as <u>Parapapio angusticeps</u>. Both of these specimens (Figs.75 and 76) show the typical dog-like muzzle of a <u>Papio</u> with the steep drop in the inter-orbital region. A re-examination of the type specimen clearly shows that it too must have had a similar <u>Papio</u>-like muzzle and not the slightly concave dorsal muzzle contour of a <u>Parapapio</u>. Further, the new material has also shown that there is marked sexual dimorphism in the skull and teeth of this species. This feature is characteristic of <u>Papio</u> but not <u>Parapapio</u>. It is therefore proposed that the species hitherto known as <u>Parapapio angusticeps</u> be transfered to the genus <u>Papio</u>.

<u>Papio spelaeus</u> Broom.

<u>Papio spelaeus</u> - Broom, 1936.
<u>Papio spelaeus</u> - Broom, 1940.
<u>Papio spelaeus</u> - Broom and Jensen, 1946.
<u>Papio spelaeus</u> - Hopwood and Hollyfield, 1954.

Holotype:

The calcite-encrusted muzzle of a male, Tvl.211, with a number of badly damaged teeth still present.

Repository of type:

Division of Vertebrate Palaeontology and Physical Anthropology, Transvaal Museum, Pretoria, South Africa.

Type site:

'Pretoria', South Africa. (see Remarks).

Referred material:

Nil.

(Broom (1940) mentioned a few isolated teeth from Kromdraai "which probably belong to this species". There is no clue at all as to which teeth he was referring to but they were probably teeth of Gorgopithecus major or Papio robinsoni, two large species which have been described from Kromdraai subsequent to his paper).

Description: (Figs.82 - 84).

This specimen is totally encrusted by a thin layer of almost pure calcite except for the teeth of the left side which have been cleaned up to facilitate measurement. A number of small aquatic mollusc shells are adherent to the surface and, in a few small areas, there are also some sand grains. In several places, including the teeth, there are small calcite-filled cracks which, together with the general crust, probably exaggerates slightly the already large size and heavy appearance of the fossil.

The specimen is considerably damaged but, as the calcite crust is continuous and unbroken, the damage must have occured before fossilisation commenced. The muzzle and palate are almost intact, but the zygomatic arches, the zygomatic bones and the whole of the calvarium, with the exception of the right mastoid region, is missing. Of the teeth, C to M^3 are present on the left but they are all badly damaged; on the right, only P^3 to M^1 remain but as they are still heavily encrusted with calcite, no structure can be seen of measurements taken.

Morphologically, this specimen is very similar to the male of P.ursinus except that the muzzle is more rugged looking, the maxillary ridges better developed and the maxillary fossae relatively larger and deeper. Broom (1936) compared the glenoid regions of several species of living baboons with that of P.spelaeus and he gives comparative diagrams of the lateral views of this region. Because the bone is still covered with calcite, one cannot be certain that the observed differences are real and not due to differences in the thickness of the calcite layer or damage which the calcite layer obscures. Thus, the apparent small size of the mastoid and post glenoid processes mentioned by Broom may not be valid differences at all, but due to damage. It would, however, appear that, as viewed in norma basalis, there was a particularly broad groove present between the external auditory meatus and the glenoid fossa region. Except for the muzzle breadth measurements, which are slightly larger, the rest of the available skull dimensions fall within the statistical limits of those of the male chacma baboon. It should be noted, however, that, when taking measurements, it is very difficult to allow accurately for the thickness of the calcite coating.

In the dentition, the resemblance to P.ursinus is again very strong. No unusual features can be seen on the broken upper premolars, and the small basal portion of the C which is present is only sufficient to indicate that this tooth was clearly of the large male type. Little can also be seen of the structure of the upper molars because of the extensive damage but the central fossae seem rather large and the lingual and buccal inter-cusp clefts relatively deep. In the size of these latter teeth, however, the basis of the specific distinction between this species and P.ursinus is clear. The length dimensions of M^2 and M^3 just fit at the extreme top of the statistical probability range of the chacma baboon but the breadth measurements fall clearly above even that limit. As in P.ursinus, the mesial molar breadths are greater than the distal, and M^2 is shorter than M^3.

Measurements:

See tables 12a and b.

Table 12a. Measurements of the skull of <u>Papio spelaeus</u>.

	Male
	Tvl.211
CALVARIUM.	
Breadth:	
Greatest temporal	(90)
Mastoid	(110)
MUZZLE.	
Height:	
Post. to M^3	67
Ant. to P^3	39
Breadth:	
Ant. to P^3	66
Dors. to M^2	57
Length:	
Muzzle	(141)
Palate	115
Nasal	81
Nasal aperture:	
Breadth	26
Length	49

Table 12b. Measurements of the upper teeth of <u>Papio spelaeus</u>.

	M^2			M^3			Rows	
	bm	bd	l	bm	bd	l	P^4 - M^3	$\underline{C}$ - M^3
MALE.								
Tvl.211	13.8	13.2	15.9	14.6	14.0	16.9	54.5	82.0

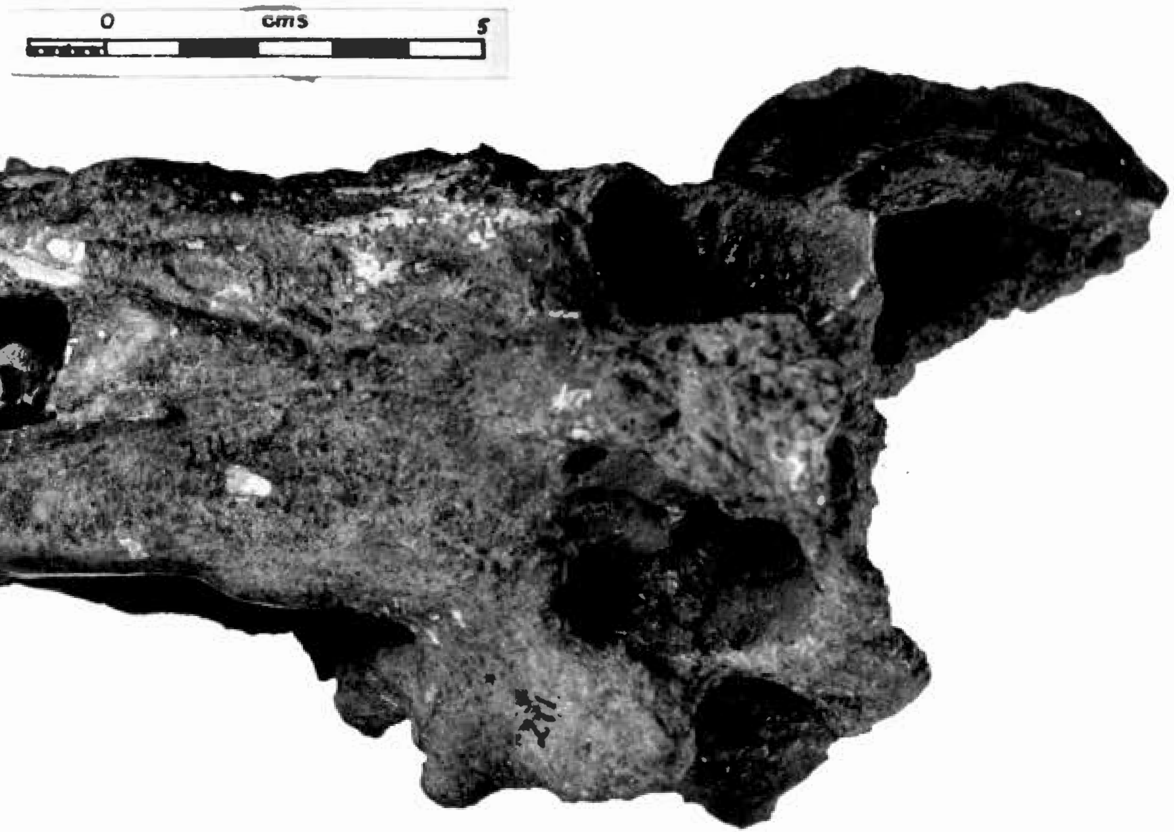

Fig.82 Papio spelaeus male (Tvl.211). Muzzle - **dorsal view.** x 1.

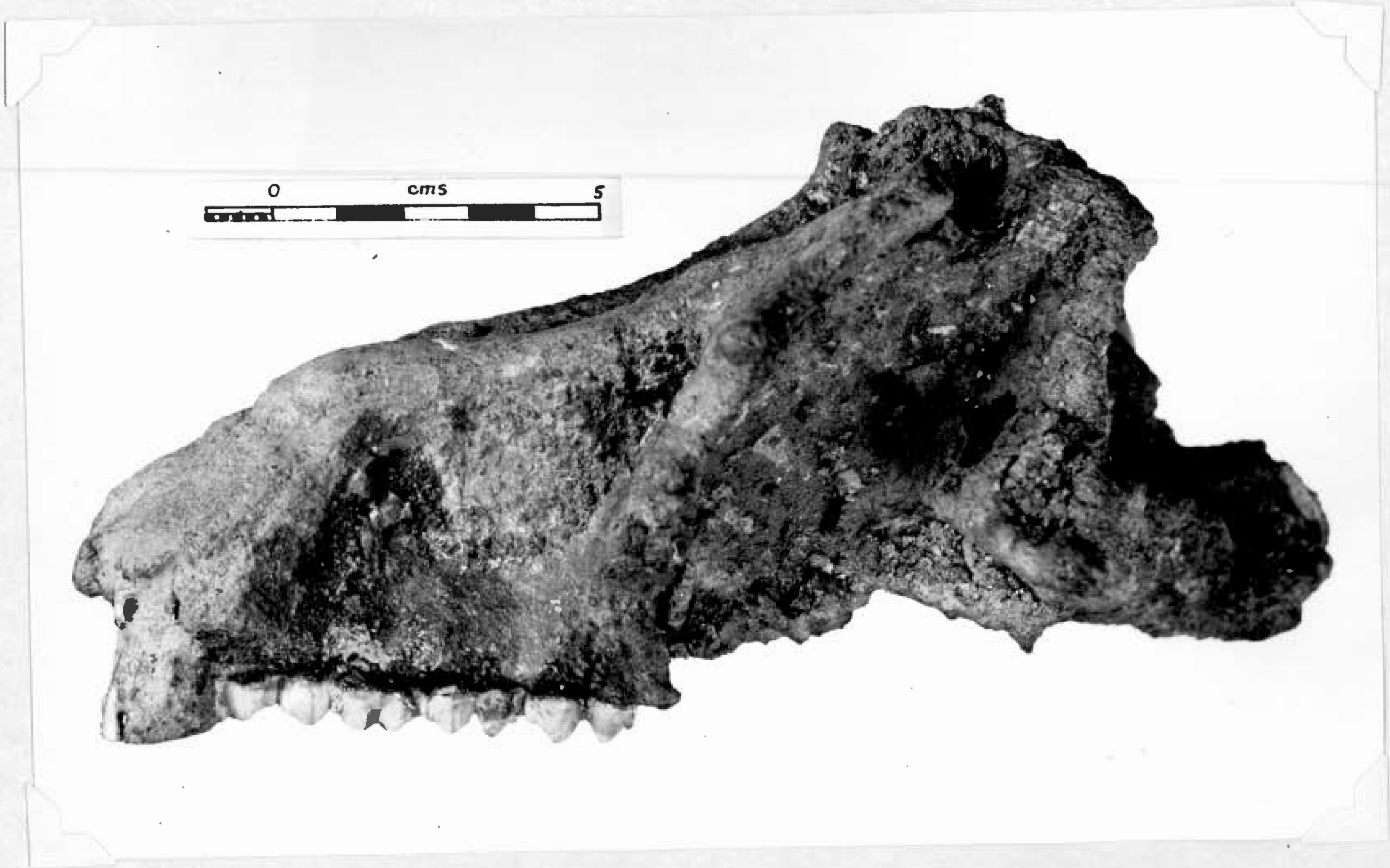

Fig. 83 Papio spelaeus male (Tvl.211). Muzzle - norma lateralis. x 1.

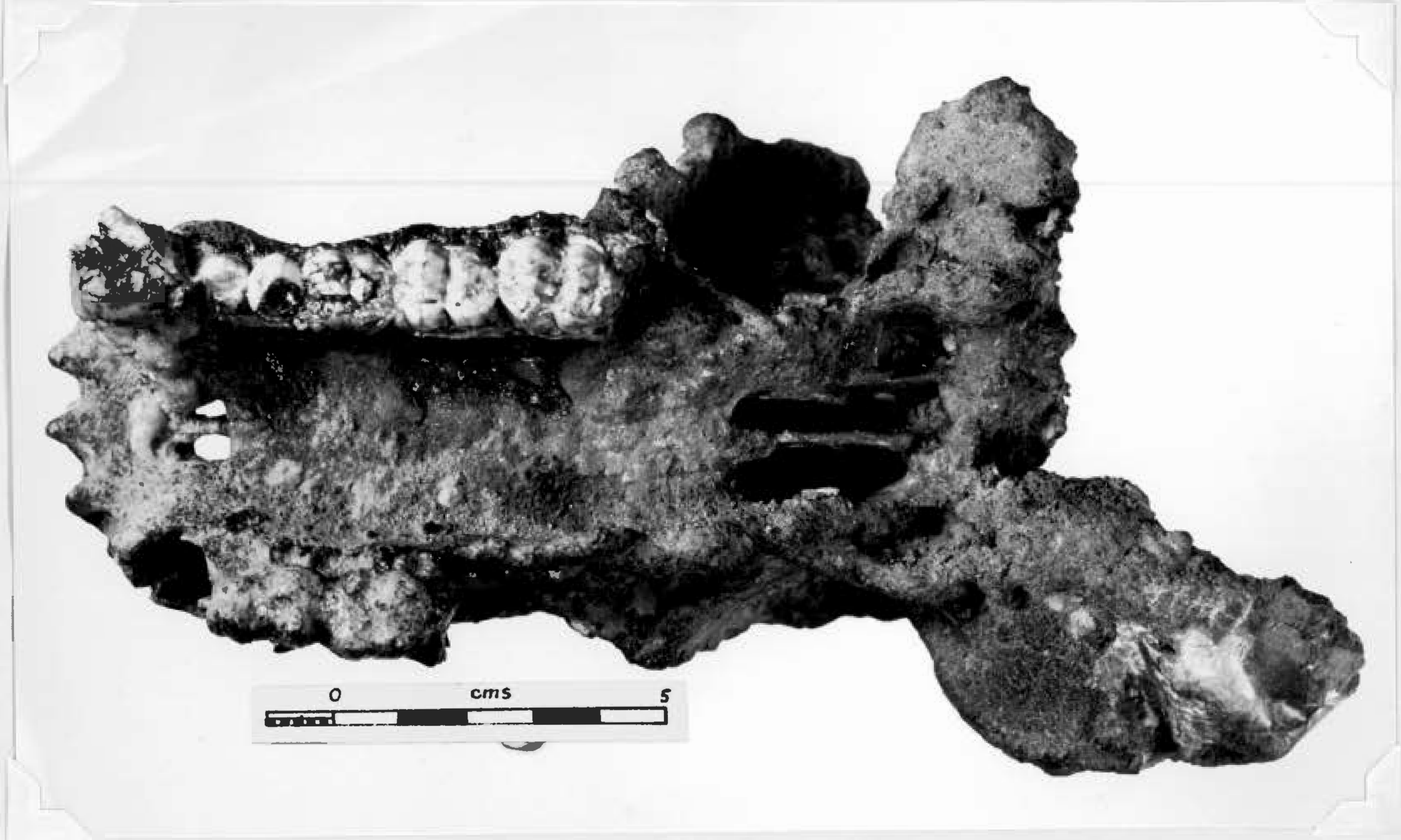

Fig.84 *Papio spelaeus* male (Tvl.211). Muzzle - basal view. x 1.

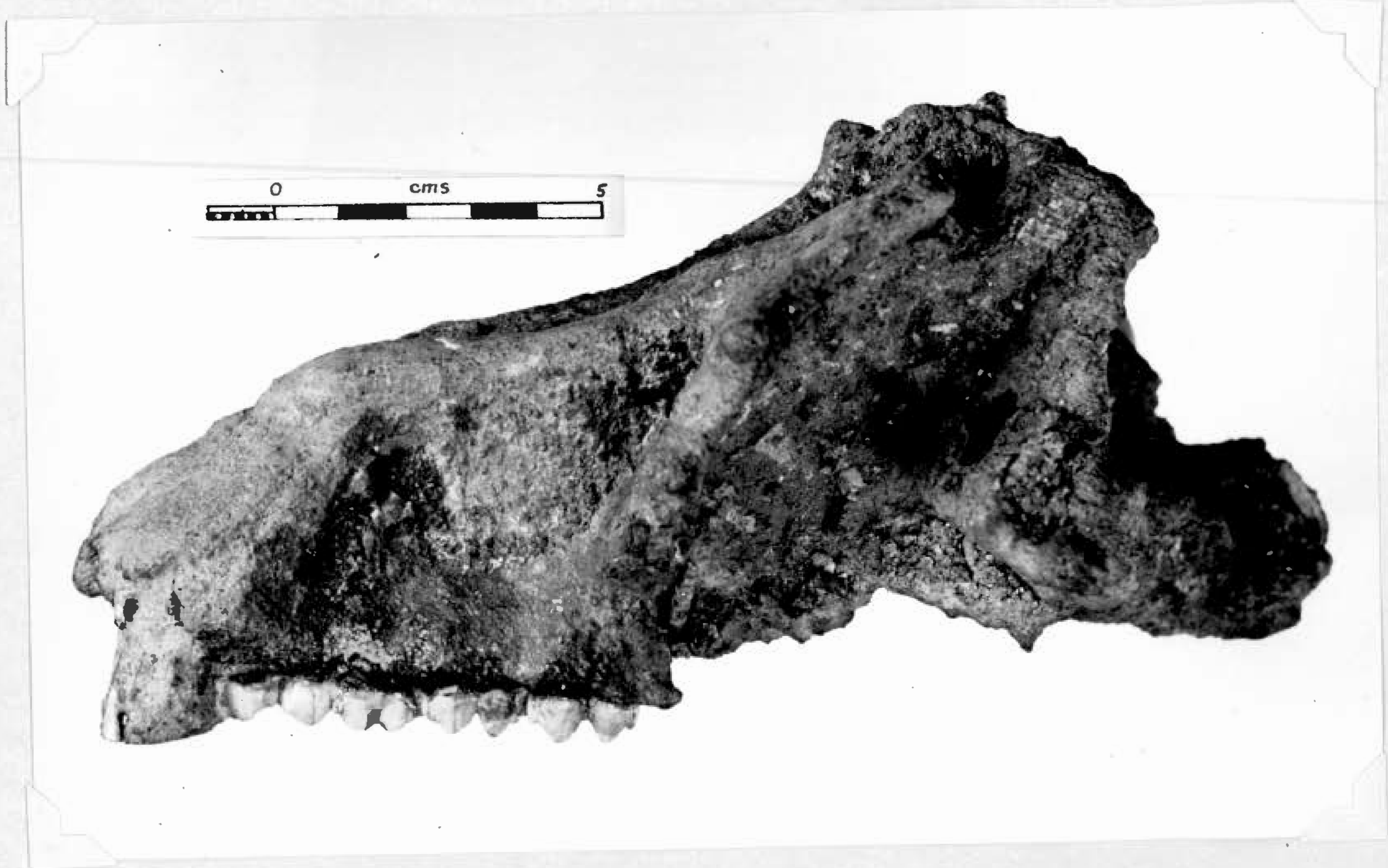

Fig. 83 *Papio spelaeus* male (Tvl.211). Muzzle - norma lateralis. x 1.

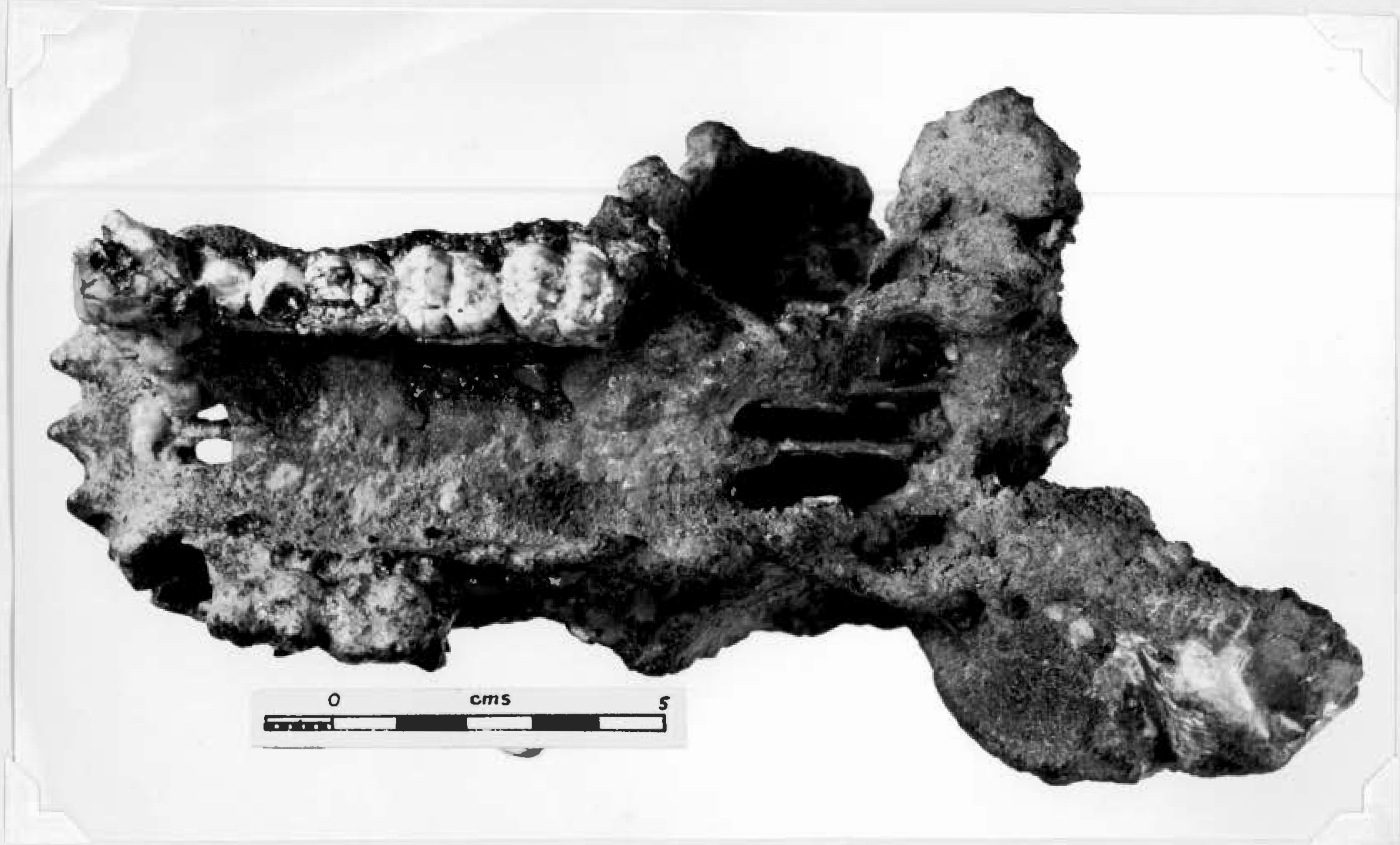

Fig.84 Papio spelaeus male (Tvl.211). Muzzle - basal view. x 1.

Remarks:

It might well be suggested that P.spelaeus is only a subspecies of P.ursinus. This would be a most acceptable suggestion were it not for the fact that in Part I of this study no clear cranial or dental size differences appeared to exist between the currently accepted subspecies of the chacma baboon. It would therefore seem that the large muzzle breadth dimensions and the large size of M^2 and M^3, particularly in breadth, are differences of specific magnitude. (The possibility of this species being a large Pleistocene form of P.ursinus is discussed in Chapter 14).

This species also shows similarities to Papio robinsoni but the morphological differences described between the latter and P.ursinus apply more or less equally to P.spelaeus. In tooth size the molars of P.spelaeus are clearly larger than those of P.robinsoni. There is no point in attempting a comparison with 'Papio rhodesiae', as Broom did, as that species has since been shown to agree almost perfectly with P.ursinus and not to be a valid species (Freedman, 1955). The teeth of P.spelaeus are considerably smaller than those of Dinopithecus ingens.

Broom came across the specimen on which this species is based in the collection of the Transvaal Museum and the only record of its acquisition is the entry: "Pretoria - Presented by the German Consul 7/1921. Picked up on the surface". Its method of preservation was clearly different to that of all the other specimens described in this study and it is of importance in connection with the dating to consider what that method was. In 1940, Broom stated that the specimen "has clearly been taken out of some cave" but he does not amplify that statement. It is quite probable that the specimen did come out of a cave but it had almost certainly not been weathered or blasted out of a breccia deposit. The thin layer of calcite encrusting the specimen may have been formed as a result of water dripping onto the surface after percolating through dolomite. However, because of the smooth even encrustation over the whole of the specimen, it is more probable that the fossil lay in a pool or spring, the water of which contained calcium carbonate in solution.. Alternate exposure and submersion during the wet and dry seasons respectively would then have caused the formation of such a calcite layer. The adherent molluscs make it apparant that this water was either in the open or, more likely, just inside the entrance to a cave where, on exposure, the specimen would get some protection. Preservation such as that described above would almost certainly limit the age of the fossil to the Holocene.

CHAPTER 9.

SIMOPITHECUS.

The first species of this genus was described by Andrews (1916) from material brought back by Dr. F. Oswald from near the Homa Mountain in Kenya. Because of its unique features Andrews created a new genus and called the species *Simopithecus oswaldi*. In 1934, Hopwood described a second species of this genus, *S.leakeyi*, from material collected by Dr. L.S.B. Leakey at Olduvai, Tanganyika. Later, Hopwood (1936), described additional material of these two species from their respective type sites and in 1943, Leakey described some good specimens of *S.oswaldi* from Homa, or Kanjera as it is better known. As will be discussed below, there does not appear to be valid grounds for the specific differentiation of *S.leakeyi* and it is proposed that this species be sunk in the synonymy of *S.oswaldi*.

As discussed in Chapter 8, Dietrich (1942) has described a species from East Africa as *Papio* (*Simopithecus*) *serengetensis* (i.e. using '*Simopithecus*' as a subgeneric name) and Remane(1925) considers *Simopithecus* a synonym of *Papio*. It has, however, been pointed out in that chapter that Dietrich's species is probably either a *Papio* or *Parapapio* and that, because of its unique premolars and molars (see below), the genus *Simopithecus* is undoubtedly valid. In addition, the material described under *Dinopithecus brumpti* from Omo, Abyssinia by Arambourg (1947), most probably contains at least some material which should be referred to this genus and quite possibly *S.oswaldi*. The point is discussed further in Chapter 10. Leakey (1951), in his East African faunal tables, has mentioned that *Simopithecus* spp. also occur at Olorgesailie, Kaiso and Rawi.

In 1946, Broom and Jensen described a lower jaw from Makapan which they called *Papio darti*. Kitching (1953) transferred this species to the genus *Gorgopithecus* but it is quite obvious from the tooth structure that it should be referred to the genus

Simopithecus. In this same paper, Kitching describes another lower jaw, also from Makapan, as a new species which he called *Gorgopithecus wellsi.* This specimen undoubtedly also belongs to the genus *Simopithecus* and is, in fact, almost certainly another individual of the species described by Broom and Jensen as *Papio darti*. It is thus proposed to group these two specimens (and also some odd upper molars and some female fragments described below) into the single species, *Simopithecus darti.*

In 1952, Kitching described a new genus and species *Brachygnathopithecus peppercorni* on the basis of six fragments from Makapan. Of this type material, the two lower jaw fragments (M.633 and M.634) would seem to belong to a female *S.darti*, "the unworn isolated left lower third molar" (M.636) is an M_3 probably of a female of this same species, the "M^1 and M^2" (M.635) are M^2 and M^3 of *Parapapio broomi*, "the lower left canine" (M.632), is a male left $\underline{C}$, also of *Parapapio broomi* and the left $\underline{C}$ (M.631) most probably comes from a male *Cercopithecoides williamsi*. These specimens are each described under their respective species.

A considerable number of specimens of the genus *Simopithecus* have recently been recovered from the Swartkrans excavations. These specimens represent a new species and the name *Simopithecus danieli* is proposed in honour of Daniel Maseko, who has worked in the Transvaal Museum for more than twenty years and been associated with much of the fossil collecting and preparation work.

Of the three species of *Simopithecus* hitherto described, *S.darti* has considerably smaller teeth than either of the other two species but *S.danieli* and *S.oswaldi* differ only in that M^2 and M^3 (at least in the female) are slightly longer in the former (see tables 13a and b). On the available skull material, which is very meagre (see below), the only important difference between the species which one can be certain of is the considerably greater height of the female muzzle in *S.danieli* as compared to *S.oswaldi*.

Table 13a. Observed range in P^4 and the upper molars of *Simopithecus* spp.

	P^4		M^1			M^2			M^3		
	b	l	bm	bd	l	bm	bd	l	bm	bd	l
S.oswaldi ♂	9.5	9.5	12.5		14	13.5-14.6		16.7-20.6	14		18.8-19
♀	9 - 10	7 - 7.5	10 - 11		12 -13.5	12-13		15 -15.5	12 - 13		15.5-16.5
S.darti ♂						13.3-14.9	12.8-13.6	16.8-17.9		12.2	19.1
♀	8.6-8.8	7.5- 7.8	9.9	9.4-9.5	12.0	12.1-.2.2			12.7	10.2	16.9
S.danieli ♂ ♀	9.0-10.7	7.3-9.5	10.9-12.2	9.9-10.9	11.7-15.1	13.6-14.9	12.3-13.3	15.9-18.1	14.0-14.5	12.2-12.3	16.6-17.6

Table 13b. Observed range in P_4 and the lower molars of *Simopithecus* spp.

	P_4		M_1			M_2			M_3		
	b	l	bm	bd	l	bm	bd	l	bm	bd	l
S.oswaldi ♂			12		16.4	16		21.5			
♀	7-8	9	9.5		11 - 13	11.5		14 - 16	11		17.5-26
S.dafti ♂	8.1- 9	9.0-10.4	9.6-10		11 - 11.8	12 - 12.3		15.9-16	12.5 - 13.2		21.0
♀	7.1	8.2		9.0	9.6	11.2	11.2	13.1	12.1	10.8	18.9
S.danieli ♂	8.5-10.0	10.6-12.0	9.6-11.8	10.4-12.3	13.1-15.8	12.2-14.1	12.0-13.8	17.1-20.3	13.2-16.5	13.3-15.2	25.5-26.5
♀	7.8- 8.4	9.4- 9.5	9.8-10.5	10.0-11.4	11.3-12.5	12.2-12.8	11.7-12.5	14.8-15.6	13.1-13.8	12.0-12.9	20.1-22.7

Genus: *Simopithecus* Andrews, 1916.

Diagnosis:

This genus is characterised by a typical form of premolar and molar. The cusps are high, and the foveae, fossae and clefts between them deep. A high ridge of enamel joins the buccal cusps in the lower molars and the lingual cusps in the upper. The unworn and worn appearance of these teeth is unique in the Cercopithecoidea and clearly defines the group. Too little material is at present available for the generic features of the skull to be accurately described but it is clear that they represent a large baboon in which there is marked sexual dimorphism in the skull as well as in the teeth. In *S.oswaldi*, the only species in which good skulls are available, the skull is robustly constructed and relatively short and broad. The palate is wide and the zygomatic arch heavy. In the male, there is a large sagittal crest. There are only a few mandibles of all three species known and the only common feature apparent would seem to be the fact that the ramus is almost at right angles to the corpus and relatively high.

The type species is *S.oswaldi* and was described by Andrews (1916).

Simopithecus oswaldi Andrews.

Simopithecus oswaldi - Andrews, 1916.
Simopithecus leakeyi - Hopwood, 1934.
Simopithecus oswaldi) - Hopwood, 1936.
Simopithecus leakeyi)
Simopithecus oswaldi - Leakey, 1943.
Simopithecus oswaldi)
Simopithecus leakeyi) - Hopwood and Hollyfield, 1954.

Holotype:

The facial portion of a female skull and an almost complete female mandible probably of the same individual.

Repository of type:

British Museum (Natural History), London.

Type site:

Homa fossil beds, Kanjera, Kenya.

Referred material:

By Andrews (1916): A number of specimens from Kanjera, which probably "indicate the presence of at least four individuals" - one of which is listed above as the type.

By Hopwood (1934): M.14680 from Olduvai IV (formerly the type specimen of *S.leakeyi*) and M.14681, site unknown (formerly a paratype of that same species).

By Hopwood (1936): One specimen (M.14936) and "numerous fragmentary remains of other individuals" from Kanjera. As *S.leakeyi* three specimens from Olduvai (M.14939 - Bed II, M.14938 - Bed I and a specimen for which no number is given, from Bed II).

By Leakey (1943): Three good specimens from Kanjera (a male skull, a fragmentary female skull and a juvenile mandible).

Description:

The material of this species was not available to me but detailed, illustrated descriptions are already in the literature by Andrews (1916) and Leakey (1943). Consequently only a brief summary of this species will be given here. The female skull is almost as large as that of the female of *P.ursinus* but that of the male is rather smaller than its equivalent in that species. The skull of both sexes is broad, fairly short and heavily constructed and the dental arcade is almost rectangular in shape. There are no maxillary fossae present. In the male, there are particularly well developed sagittal and nuchal crests. The tooth row is situated rather further back relative to the zygomatic process of the maxilla than in the chacma and the individual teeth are large. The premolars and molars have a particular type of structure, characteristic of the genus, which will be described below under *S.darti* and *S.danieli*. The mandible has no mandibular fossae and the rami are rather high and almost at right angles to the corpus.

Measurements:

See tables 14a, b, c and d.

Table 14a. Measurements of the skull of *Simopithecus oswaldi*.

	Leakey (1943)		Hopwood (1936)	Andrews (1916)
	Male	Female	Female (M.14936)	Female
GENERAL.				
Greatest length	207	166.5?	172	
Bizygomatic breadth	133	109	115?	110
CALVARIUM.				
Breadth:				
Min. inter-frontal	47.5	39	51	
Max. frontal breadth		73.5		
Greatest squamosal (?)	98.5			
Length:				
Inion - glabella	125	114		
MUZZLE.				
Height:				
Depth of face (orbit to alveolar border).				45
Breadth:				
Above canines (muzzle)	50			
Above M^3 (muzzle)	62.5			
At midpoint of M^2 (palate)	31		38?	
Between M^1 (palate)				28
At P^3 (palate)	28			
Facial (between points where malar-maxillary suture crosses inf. margin of jugal).	77.5	84?		
Min. malar-maxillary	37	31		
Condyle-basal			133	
Length:				
Muzzle	107.5	76?		
Nasal	58			
Orbit:				
External orbital	86			
INTERNAL BRAIN CASE.				
Breadth	67			
Length	93			

Table 14b. Measurements of the mandible of *Simopithecus oswaldi*.

	Andrews (1916)
	Female
Height:	
At M^3	31
At M^1	33
Length:	
Condyle to most ant. point	130
Of symphysis	46

Table 14c. Measurements of the upper teeth of Simopithecus oswaldi.

	C				P^3		P^4		M^1		M^2		M^3		Rows.	
	h	b	l_1	l_2	b	l	b	l	b	l	b	l	b	l	Molar row	P^3- M^3
MALE:																
- (Leakey, 1943)					9.5	8	9.5	9.5	12.5	14	13.5	18	14	19	49.5	65.5
M.14681 * (Hopwood, 1934)											13.5	16.7	14	18.2		
M.14939 * (Hopwood, 1936)											14.6	20.6				
FEMALE:																
- (Andrews, 1916)		7	8		8	7	10	7	11	12	13	15	13	15.5	43	
- (Leakey, 1943)					8.5	7.5	9	7.5	10	13.5	12	15.5	12	16.5	44	51.5
M.14936 (Hopwood, 1936)																53

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* Formerly S.leakeyi.

Table 14d. Measurements of the lower teeth of <u>Simopithecus oswaldi</u>.

	$\bar{C}$			P_3		P_4		M_1		M_2		M_3		Rows	dm_4	
	h	b	l	b	l	b	l	b	l	b	l	b	l	$P_3 - M_3$	b	l
MALE:																
M.14680 * (Hopwood, 1934)								12	16.4	16	21.5				9	12.5
FEMALE:																
- (Andrews, 1916)				7	10	8	9		11		14	11	20			
- (Leakey, 1943)	9.5	5.5	9	6	8	7	9	9.5	13	11.5	16	11	17.5			
M.14938 * (Hopwood, 1936)													21.9	72		
- * (Hopwood, 1936)													26	±72		

* Formerly <u>S.leakeyi</u>.

Remarks:

Hopwood (1934) gave as his reason for making *S.leakeyi* a separate species the fact that "the length of the second lower molar is approximately 40% greater than that of *S.oswaldi* Andrews". The only mandible of *S.leakeyi* which Hopwood mentions in that description is his type specimen (M.14680) which is a male - and no male lower teeth had been then (or in fact are even now) described in the literature on *S.oswaldi* As female M_2 teeth were known at that time, it seems that his 40% difference was due to sexual dimorphism and not specific difference. In table 14a - d all the available measurements of *S.oswaldi* are given and those of *S.leakeyi* have been included and marked with an asterisk. The only difference of any magnitude which can be found between the teeth of the two species is in the length of the female M_3. It is well known that this tooth is very variable but even so, the length of the smaller M_3 of the female *S.leakeyi* is only 1.9mm. longer than that of the female *S.oswaldi* - a difference of about 10% only. With only two comparable specimens of each species known, this 'difference' would seem to be very slender grounds for upholding the specific difference between the two populations - especially when all the other dimensions aggee so very closely. Further, although the five fragments of *S.leakeyi* all come from Olduvai I - IV, whereas the *S.oswaldi* material all comes from Kanjera, these two excavations are only about 200 miles apart and Leakey (1951) has shown that Kanjera and Olduvai IV are of about the same age. It is therefore pwoposed that the species *S.leakeyi* be sunk.

Simopithecus darti (Broom and Jensen).

Papio darti - Broom and Jensen, 1946.
Papio darti - Mollett, 1947.
Papio darti - Kitching, Wells and Westphal 1948. (B.P.I.16M. and 32M.)
Dinopithecus sp. - Broom and Hughes, 1949. (B.P.I.16M. and 32M.)
Papio darti - Broom and Robinson, 1949.
Papio darti - Dart, 1949.
Brachygnathopithecus peppercorni - Kitching, 1952. (M.633, M.634 and M.636).
Gorgopithecus wellsi - Kitching, 1953. (B.P.I.M626, 16M. and 32M.).
Gorgopithecus darti - Kitching, 1953.
Papio darti - Hopwood and Hollyfield, 1954.

Holotype:

A damaged male mandible with some badly damaged teeth (M.201,1326/1).

Repository of type:

Anatomy Department, University of the Witwatersrand, Johannesburg, South Africa.

Type site:

Dumps of the old lime-kilns at Makapan, Transvaal, South Africa.

Referred material:

Eleven specimens from Makapan:-

Three male right M^2 teeth (B.P.I. Nos. 16M., 32M. and M.233?) and one damaged male M^3 (M.675) - all rather worn. 16M. and 32 M. are referred from *Gorgopithecus wellsi*.

Two female maxillary fragments, M.669 and M.672, (possibly of the same individual) which together show P^3 to M^1 and part of M^2. There is also a beautifully preserved unworn female M^3 (M.636) which was previously listed as *Brachygnathopithecus peppercorni*.

(No skull fragments of descriptive value are known of either sex. The two imperfect skulls mentioned by Broom and Jensen (1946) in connection with this species (probably AD.1326/4A and AD.1326/6) have no teeth but would seem more probably to be skulls of *Parapapio broomi* males).

A male lower jaw, B.P.I. No. M.626, (hitherto the type of *Gorgopithecus wellsi*) which has lost both rami, the left corpus behind P_4 and the anterior part of the symphysis but what remains is in a good state of preservation. The teeth present are P_3 and P_4 on the left and P_3 - M_3 on the right. They are perfectly preserved and quite undamaged. An isolated left P_4 of a male (M.674) is also known.

A female mandibular fragment (M.633) which consists of a small portion of the symphysis and most of the anterior part of the right corpus with P_4 - M_3 present but very considerably worn.

There is also a very small female mandibular fragment (M.634) from the left side with a worn P_4. Both of these specimens were previously included in <u>B.peppercorni</u>.

Description: (Figs. 85 - 90).

The male and female upper teeth which have been referred to this species all conform closely to the <u>Simopithecus</u> upper premolar and molar patterns as seen in the type species, [illegible] and also in <u>S.danieli</u> to be described below. In size, the female teeth are quite considerably smaller than those of the male (table 15b).

The teeth in the female maxillary fragments (M.672 and M.669) are all considerably worn. P^3 and P^4 of both specimens show faint grooves on the buccal surface, one mesial and one distal, to the main buccal cusp. The anterior foveae of these teeth would also appear to have been rather large. M^1 is very worn and M^2 rather damaged but both conform closely to the description of the isolated female M^3 (M.636) to be described below.

The male M^2 (16M., 32M and M.233?) shows the same four main cusps as were seen in <u>P.ursinus</u> but the teeth are much larger and the buccal surface is more vertical. The teeth are characterised by the great development of the region of the teeth mesial to the paracone where a large cuspule and deep fovea are formed. The development of this area is so great in 32M. that the mesio-buccal corner of the tooth is considerably in front of the mesio-lingual. There is a smaller cuspule situated mesio-lingually which is marked off by a deep groove; disto-lingually, there is a similar but much shallower groove present. (These latter features can be best seen on 16M. which is rather a lot less worn than 32M. - M.233? has lost its distal portion). Disto-buccally, a large cuspule and fovea are found which, although not quite as marked as those seen mesio-lingually, are never-the-less strongly developed. Buccally, the cingular ridge between the outer cusps is high and a large fossa is formed between it and the buccal enamel infolding. The worn appearance of these molars is very characteristic and the infoldings of enamel from the buccal and lingual sides almost meet mesial and distal to the mesial pair of cusps. On the distal part of the molar, behind the four main cusps, the enamel infoldings from either side come close together near the midline of the tooth and then swing together towards the buccal surface where they meet. The male M^3 (M.675) is rather badly damaged but shows essentially the same structure as the M^2 just described.

The isolated female M^3 (M.636) is quite unworn and clearly shows the pattern of a third upper molar of this genus. (This tooth could not be a M_3 as suggested by Kitching (1953) primarily because it has the root pattern typical of an upper molar i.e. one lingual and two buccal roots). The tooth is almost the same breadth as that of the equivalent tooth of the male <u>P.ursinus</u> but it is considerably longer. There is a large deep central fossa which is marked off from almost equally large anterior and posterior foveae by the transverse ridges which join the mesial and distal pairs of cusps respectively. On the mesial end of the tooth, there is a small lingual and a large buccal cuspule - the former being marked off by a very deep groove and the latter by a shallow one. On the cingulum at the distal end of the tooth there are three well marked cuspules - a small one buccally and larger ones lingually and distally. There are two grooves on the buccal surface marking off the buccal and distal of these subsidiary cuspules. It was probably these subsidiary distal cuspules which created the impression that this tooth was a M_3. The height of all four main cusps of this tooth, and in particular that of the mesial pair, is great and the cleft between the two main lingual cusps is very deep.

There are two specimens available for the description of the male mandible. The type specimen, M.201, which lacks most of the left, and the whole of the right ramus and also the right corpus behind M_2, and specimen M.626, which is the former type specimen of <u>Gorgopithecus wellsi</u>. The anterior surface of the symphysis of M.201 is almost vertical and has two strong converging ridges. Most of this surface is missing in M.626 but, from a small dorsal portion which is still present, it would appear to have been very similar. The incisal shelf, which is formed by the dorsal portion of the symphysis on the lingual side of the anterior part of the dental arcade, appears to differ quite considerably in the two specimens. In M.626 it is slightly shorter, narrower and more slender generally than in M.201 and slopes down more steeply. This difference is actually of no great magnitude, but at first glance appears to be so, because in M.626 the alveolar part of the symphysis is broken off and the mandibular fossae are considerably deeper.

What appears to be an important difference between M.201 and M.626 is found when comparing the mandibular fossae. In M.626 the fossae are very large and deep while in M.201, they are almost totally absent. Variation in the size of this fossa was found to be very great in examining P.ursinus for Part I of this study and the amount of difference found between these two specimens in this feature (and also in those mentioned above), certainly does not merit their specific separation as proposed by Kitching (1953). Other than on the above points, the two mandibles agree very closely. Both show a considerable decrease in the height of the corpus as it nears the ramus and also a very similar lateral shelf buccalward of the distal part of M_3 where the anterior margin of the ramus joins the corpus.

Little information about the female mandible can be gleaned from the only two known fragments, M.633 and M.634. It would, however, appear that the mandible was rather heavily constructed but with a comparatively small symphysis.

The lower dentition will be described mainly from the two male mandibles (M.201 and M.626) and the two female lower jaw fragments (M.633 and M.634). The teeth of all these specimens show the typical Simopithecus lower premolar and molar pattern and size relationships (see Remarks). (Most of the teeth present on the type specimen are very badly damaged. Never-the-less, sufficient molar structure remains for the Simopithecus pattern to be clearly seen). From the alveoli and broken teeth in the male specimens, all that can be concluded about the incisors is that they appear to have been very small teeth for such a large animal - there is no evidence at all as to the shape and size of these teeth in the female. From similar evidence, it seems probable that in the male the $\overline{C}$ was a large tooth, about the same size as that of the male P.ursinus. An idea of the female $\overline{C}$ can be gained from the alveolus on M.633. At first glance it would appear that this was a fairly large tooth but when it is remembered that P_3 is missing and that its extended mesial portion and root still has to be fitted in between this alveolus and what remains of P_4, it must be concluded that the tooth was small and probably about the same size as that in the female P.ursinus.

The male P_3 is very similar in shape and size to that of the male chacma baboon but P_4 is considerably broader and rather more similar to its equivalent in the male of Gorgopithecus major. In both male mandibles it can be seen that on this latter tooth there is a small anterior and a large posterior fovea and that on its buccal surface, as in G.major, there are vertical grooves converging upwards on either side of the main buccal cusp. Typical of the genus is the fact that on P_4 the buccal and lingual enamel infoldings meet behind the main cusps and run together up to the distal surface; mesial to the cusps, the infoldings also run together for a short distance from the mesial surface of the tooth to the main buccal cusp. These features are seen on both the type mandible (M.201) and M.674, which both also show that this tooth is considerably molarised. Of the female premolars there is no example of P_3, and P_4 is too worn, even on M.634, to show much structure but what little can be seen conforms with that described for the male and fits the genus Simopithecus.

The lower molars of all the known male and female mandibles are very worn and only show the outline of the typical Simopithecus lower molar pattern. However, this is quite sufficient to conclusively refer these specimens to that genus. M_1 and M_2 have the usual four cusps and M_3 has, in addition, a large well developed posterior portion behind the distal cusps with a well marked hypoconulid.

In the male lower molars, the cleft between the two buccal cusps is large and deep and similar to that on the lingual side of the upper molars. The central fossa between the mesial and distal pairs of cusps is very large. There must have been large well developed mesio-lingual cuspules (and probably foveae as well) at least on M_2 and M_3, and smaller mesio-buccal cuspules on all three molars. M_1 and M_2 also have fairly large disto-lingual cuspules. On M_2 and M_3 the close proximity of the buccal and lingual enamel infoldings, mesial and distal to the mesial pair of cusps, can be seen; M_1 is too greatly worn to show this feature well. The part of M_3 behind the distal pair of cusps has these infoldings coming close together for a third time in both of the known male specimens. The close proximity of these infoldings from opposite sides results in the molars appearing to be strongly pinched together between the mesial and distal pairs of cusps and, on M_3 (and to some extent on M_2) again behind the distal pair. This appearance is typical of the genus <u>Simopithecus</u>.

Despite the great wear of the teeth of the female specimens, the typical pinched appearance described above is still apparent between the pairs of cusps on M_2 and M_3 and also behind the distal pair of cusps on M_3. The large central fossa and traces of some of the subsidiary cuspules (the mesio-buccal on M_2 and M_3 and the disto-lingual on M_2) can still be seen. The arrangement of one mesial and one distal root can be seen on specimen M.633.

Measurements:

See tables 15a, b and c.

Remarks:

As discussed above, although the teeth of the type specimen (M.201) are very badly damaged, sufficient molar structure remains, in particular on the left M_3 and the right M_2, for the specimen to be quite confidently referred to the genus <u>Simopithecus</u>.

Table 15a. Measurements of the mandible of <u>Simopithecus darti</u>.

	Male	
	M.201	M.626
Height:		
Post. to M^3	33	(31)
Ant. to P^4	34	43
Breadth:		
Ant. to P^4	45	37
Ant. to M^3	54	
Through mental sp.	38	
At base of $\bar{C}$		27
Length:		
Gonion - most ant. point	115	
Mental sp. to most ant. pt.	60	61
Angles:		
Ramus to corpus	95°	
Between corpora	40°	

Table 15b. Measurements of the upper teeth of Simopithecus darti.

	P^3		P^4		M^1			M^2			M^3		
	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
MALE:													
M.227,M.32 B.P.I.								14.9	13.6	17.9			
M.226,M.16 B.P.I.								13.3	12.8	16.8			
M.233 (?)								13.4					
M.675												12.2	19.1
FEMALE:													
M.636											12.7	10.2	16.9
M.672)	7.7	5.7	8.6	7.8	9.9	9.4	12.0	12.2					
M.669)*			8.8	7.5		9.5	12.0	12.1					

*Probably from the same individual.

Table 15c. Measurements of the lower teeth of Simopithecus darti.

	P_3		P_4		M_1			M_2			M_3				Rows.	
	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bH	l	P_4-M_3	$\overline{C}$-M_3

Fig. 85. Simopithecus darti male (32M., right; 16M., left). Occlusal view of right M^2. x 1.

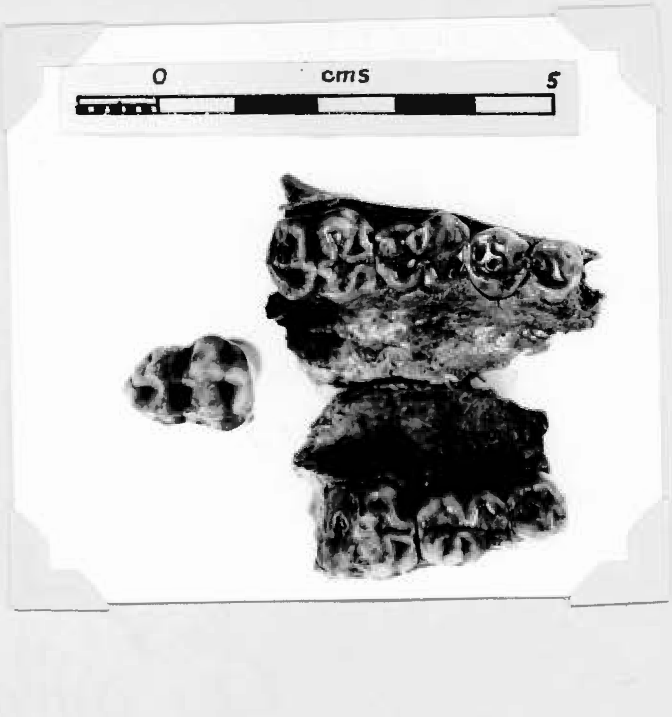

Fig. 86. Simopithecus darti female (M.636, left; M.672, upper right; M.669, lower right). Occlusal view of upper teeth. x 1.

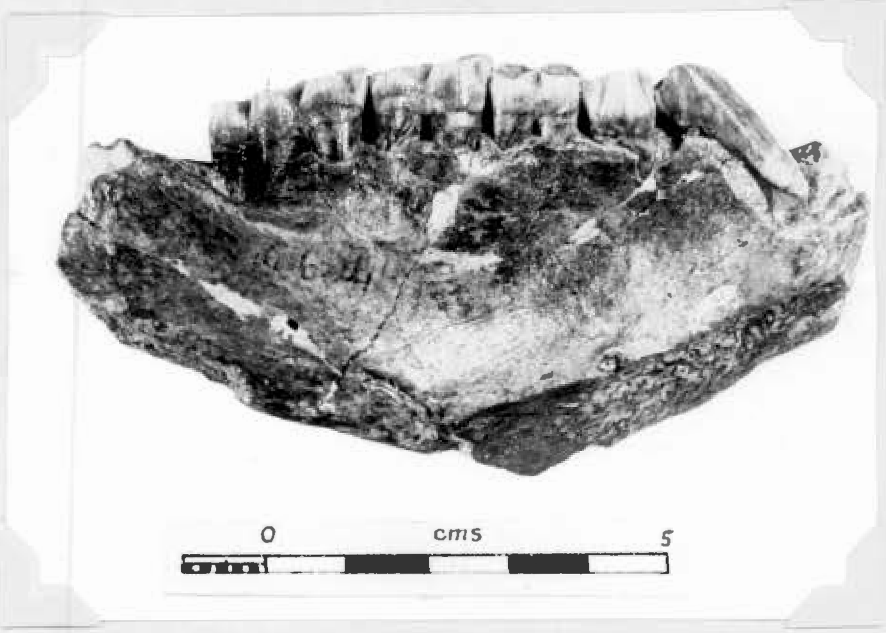

Fig. 87. Simopithecus darti male (M.626). Lateral view of mandibular fragment and lower teeth. x 1.

Fig. 88. Simopithecus darti female (M.633). Lateral view of mandibular fragment and lower teeth. x 1.

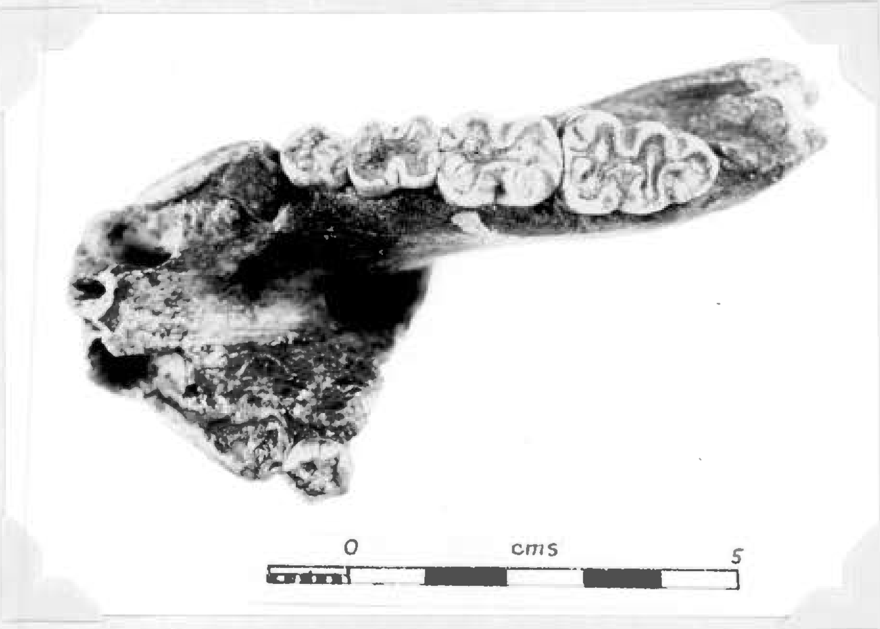

Fig. 89. Simopithecus darti male (M.626). Occlusal view of lower teeth. x 1.

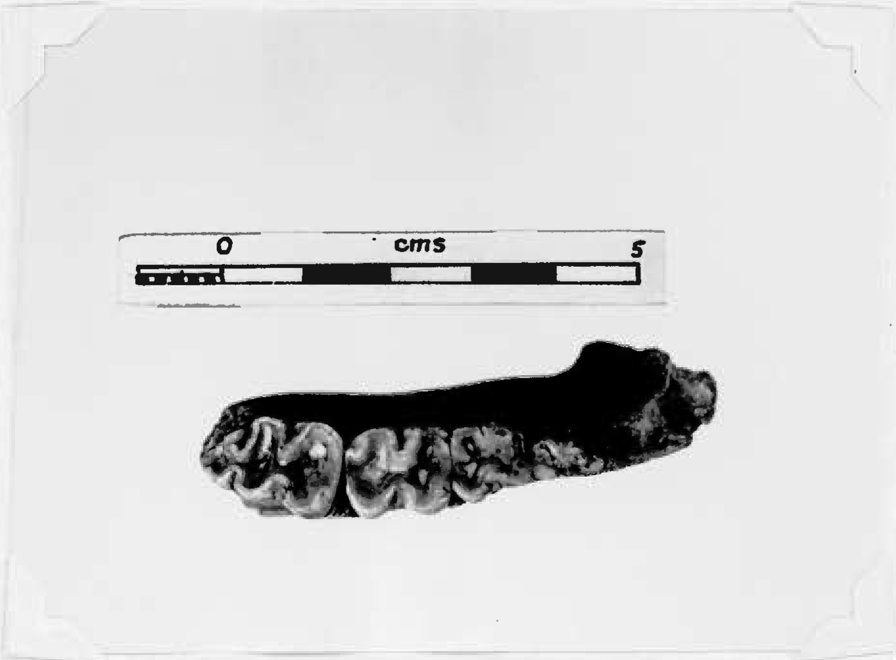

Fig. 90. Simopithecus darti female (M.633). Occlusal view of lower teeth. x 1.

Furthermore, the teeth of the Gorgopithecus wellsi type (M.626) even more clearly conform to the Simopithecus lower molar pattern and, in addition, match those of the above specimen almost perfectly in both size (table 15c) and morphology. With the exception of P_4, none of the teeth of either of these specimens bear any close resemblance to those of Gorgopithecus major. The few large upper molars, hitherto referred to G.wellsi are equally clearly of the Simopithecus type and, in size, fit well with both of the above mandibles. It would seem most unwise to uphold the existence of two species at the same site, and what was almost certainly about the same time (Cooke, 1952), on the slender basis of two mandibles in which the dentition is virtually identical and of which the mandibles themselves only show differences of minor morphological details, well within the range of variation of a single species. It is therefore proposed that the species hitherto known as Gorgopithecus wellsi be sunk and the specimens referred to it transferred to this species.

The teeth of the three specimens (M.633, M.634 and M.636) formerly referred to Brachygnathopithecus peppercorni also show the Simopithecus tooth pattern quite distinctly. When compared to those of the male specimens of S.darti (tables 15b and c), the teeth show the size relationship which, by analogy with the other species of this genus, one would expect between the two sexes of a species of Simopithecus. It would therefore seem reasonable to presume that these specimens are S.darti females. As all the other specimens previously considered type material of B.peppercorni fit quite clearly into other known genera and species (see above), the genus Brachygnathopithecus and its one species B.peppercorni must be sunk.

Simopithecus danieli sp. nov.

Simopithecus sp. - Robinson, 1952.
Simopithecus sp. - Oakley, 1954a.

Holotype:

A slightly crushed female muzzle (SK.563) and two fairly complete halves of a mandible (SK.402 and SK.405) almost certainly all from the same individual. Most of the teeth are present.

Repository of type:

Division of Vertebrate Palaeontology and Physical Anthropology, Transvaal Museum, Pretoria, South Africa.

Type site:

Swartkrans, Transvaal, South Africa.

Referred material:

Seventeen specimens from Swartkrans. (For the numbers of these specimens, see tables 16a, b, c and d).

There is an almost complete but very badly crushed skull (SK.561) and nine small maxillary fragments with teeth, all of females - but not a single skull fragment or upper tooth of a male. There are, however, a number of mandibles and lower teeth of both sexes.

Description: (Figs. 91 - 97).

The female skull is that of a large baboon, about intermediate in size between a male and female of P.ursinus. The skull was probably somewhat nearer that of the former in size but it had a relatively shorter muzzle. In size and general appearance, it must have been very similar to that of the S.oswaldi female but with a considerably higher muzzle.

On the side of the nasals a very slightly flattened dorsum is formed by the maxilla which then slopes down very steeply to the alveolar margin. On the side of the muzzle, where the maxillary fossa is usually found, there is only a slight excavation in SK.563 and none at all in SK.561. The infra-orbital foramen is large and single and situated on the maxillary side of the zygomatico-maxillary suture, some 13mm. below the infra-orbital margin. The zygomatic process of the maxilla is above the mesial half of M^3 and the zygomatic arch itself is very robust.

The supra-orbital tori of SK.561 are considerably thickened and the temporal lines are strongly marked until they reach a little over midway between the tori and the bregma. The whole of the rest of the calvarium is particularly badly crushed and distorted in this specimen but at the posterior end it can be seen that there is a large nuchal crest. The mastoid region is not very greatly developed. The external occipital protuberance is small, but the median nuchal line leading up to it is fairly prominent and there may also have been a slight sagittal crest on the calvarium above it. The wall of the external auditory meatus is thick and the meatus itself lies obliquely across the base of the skull. The foramen magnum and basi-occipital can also be seen but present no unusual features.

The clear sex size differences in the lower teeth (see table 16d) make it quite obvious that all of the upper teeth available of this species must be female as their sizes are all too near those of the three known female specimens - SK.561, SK.563 and SK.564 (table 16c). The only incisors present are those on SK.561 and they are very worn and rather damaged. All that can be seen with certainty is that they are particularly small teeth and that the lateral pair lean mesially as in <u>P.ursinus</u>. This same specimen also has the <u>C</u> present bilaterally but rather worn. Fortunately there is also another specimen (SK.564) in which this tooth is present and here, although slightly damaged, it is almost completely unworn. This tooth is shorter and considerably broader than that in the female <u>P.ursinus</u> but it is otherwise very similar in structure. The <u>C</u> teeth in SK.561 are worn down almost to the heights of the incisors and premolars; each has a large wear facet which is slightly concave and slopes down quite steeply from the buccal to the lingual surface.

The upper premolars and molars are very large teeth indeed and they are actually considerably larger than the equivalent teeth of the male chacma baboon. Each premolar has a pair of high cusps, of which the buccal one is very large and the lingual one slightly smaller; it also has two deep foveae of which the posterior one is considerably larger than the anterior. P^4 is larger than P^3, the mesial surface of which does not slope backwards as in P.ursinus. There are fairly deep grooves running up the lingual surface on either side of the main inner cusp of P^4 (SK.561, SK.564 and SK.567) which are similar to those described on the buccal surface of P_4 of S.darti. On SK.561 and SK.567, a similar groove is also found on P^3, distal to the main lingual cusp only. There is a suggestion of a small mesio-buccal cuspule on P^4 on specimens SK.561 and SK.567 and on almost all the other premolars there seems to be some extra development in this region.

The upper molars all show the typical Simopithecus structure as described in detail for S.darti. The enamel infoldings, the subsidiary mesial and distal cuspules and, in addition, buccal accessory cusplets are all found on these teeth. Examples of all three molars are present in this species and it can be seen from table 16c that M^2 is much larger than M^1 but only slightly bigger than M^3.

For the description of the mandible, there are only a few badly damaged fragments of both sexes. The male mandible must have been quite considerably larger than that of the female and, as in the lower dentition, this size difference gives some idea of the amount of sexual dimorphism in the species. This comparison suggests that the size difference between the sexes of this species was somewhere between that described for the two sexes in P.ursinus and S.oswaldi.

The only mandible in which the symphysis is present is that of a female (SK.411). In this specimen the symphysis reaches back dorsally to about the level of the midline of P_4 and the incisal shelf formed is almost horizontal. Anteriorly, the symphysis is similar but slightly larger than that of the female of P.ursinus and the foramen symphyseosum and traces of the vertical ridges seen in that species, are also present here. In both the male and the female mandibles the corpus is very thick but rather low and has only a very shallow mandibular fossa present on the anterior part of its lateral surface. A broad lateral shelf is formed buccalward of the distal part of M_3. The rami of a female (SK.402 and SK.405) and an immature male (SK.403) have a large coronoid process and deep sigmoid notch. The ramus appears to have been more nearly at right angles to the corpus in both sexes of this species than in even the female of *P.ursinus*. The height of the ramus is also relatively greater than in either sex of the chacma baboon.

Of the lower incisors, only female examples have been preserved and these only in a single specimen (SK.411). Unfortunately the teeth of even this specimen are very worn but it can still be seen that, as in the upper jaw, the incisors are very small teeth. The one female $\overline{C}$ (SK.405) which is present is also very worn but appears to have been more or less the same size as that in the female *P.ursinus*; the single male $\overline{C}$ available is still erupting but appears to be much the same in size and structure as that of the male *P.ursinus*.

The male P_3 is a considerably broader tooth than that of the male of *P.ursinus* but it has the same structure, and the length (l(h)) is, if anything, slightly shorter than that in the chacma. In SK.411, the female P_3 is much shorter and broader than in the female *P.ursinus* but in SK.405 it is almost identical to its equivalent in that species. The male P_4 is a very larger tooth indeed and besides the two main cusps, at least two fairly large subsidiary cuspules can be seen, one lingual and one buccal, on the cingulum of the molarised distal part of the tooth. This tooth is considerably larger and broader than in *P.ursinus* and shows the same two vertical buccal grooves described on the equivalent tooth of *S.darti* and *Gorgopithecus major*. In SK.569, P_4 is truly enormous and in fact would seem, on size criteria, different enough to merit specific separation. The molars of this latter specimen are also huge but all attempts, on the limited amount of material at present available, to find two clearcut species of *Simopithecus* at Swartkrans have proved futile. The female P_4 is slightly larger than that of the male P.ursinus. It has the same two buccal grooves described above on the male tooth.

The lower molars of the two sexes have the typical Simopithecus pattern as described for S.darti and only differ, both between the sexes and from S.darti, in size. From the available material, the unworn structure of M_2 and M_3 can be seen. The unworn M_2 on both SK.426 and SK.403 (two males) has four large high cusps, the mesial and distal pairs of which are separated by a very large central fossa which is open lingually. On the buccal surface opposite this fossa, and separated from it by a ridge of enamel which joins the two main buccal cusps, there is a deep cleft. There is a small anterior fovea in front of, and a large posterior fovea behind the four main cusps. These latter two foveae are both situated on the lingual half of the tooth. Mesio-buccally and disto-buccally there are deep vertical grooves running up the tooth which mark off small cuspules.

The unworn M_3 can best be described from the male specimen (SK.569). This tooth is virtually identical, except in size, to that of the female SK.405 but in another female (SK.411) there is relatively less elongation of the part of this tooth behind the main pair of distal cusps. The structure of the main part of this tooth ie. mesial to and including the distal pair of cusps, is identical to that of M_2 except that there are two small lingual accessory cusplets. The lingual cusp of both the mesial and distal pairs is slightly in front of the buccal. (To a slighter degree, this is also the case in the other molars). The part of this tooth behind the distal pair of cusps has a very large fovea on the lingual side and a fairly deep cleft on the buccal, separated by a ridge which runs back from the hypoconid to the hypoconulid and is the continuation of that described above between the two main buccal cusps. On the distal part of the lingual cingulum, between the entoconid and hypoconulid, there are two small subsidiary cuspules.

Table 16a. Measurements of the skull of *Simopithecus danieli*.

	SK.561	SK.563
	Female	Female
CALVARIUM.		
Breadth:		
Min. interfrontal	47	
MUZZLE.		
Height:		
Ant. to P^3		46
Length:		
Muzzle	(90)	
Orbit:		
Inter-orbital	12	
External orbital	(80)	

Table 16b. Measurements of the mandible of *Simopithecus danieli*.

	SK.402
	Female
Height:	
Gonion-condyle	76
Gonion-coracoid	79
Post. to M^3	29
Ant. to P^4	29
Length:	
Ramus at condyle neck	39
Condyle to most ant. pt.	144?

Table 16c. Measurements of the upper teeth of *Simopithecus danieli*.

	I^1			I^2			$\underline{C}$				P^3		P^4		M^1			M^2			M^3			Rows.	
	h	b	l	h	b	l	h	b	l_1	l_2	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	$P^4 - M^3$	$\underline{C} - M^3$
MALE: nil																									
FEMALE;																									
SK.561	6.8	6.6	(5.2)	8.7	(5.9)	(5.7)	11.5	8.5	8.2	7.5	9.1	8.4	9.0	7.9	10.9	9.9	12.4	15.8	12.3	17.2	14.2	12.2	17.6	52.9	67.2
SK.563 *											8.9	6.0	10.0	7.3	10.9	10.7	(12.0)	15.6	12.5	16.6	14.5			(49.5)	
SK.564							(14.0)	8.5		(9.0)	10.0	9.6	10.6	9.2	12.0	10.6	15.1	14.5	13.2	18.1					
SK.575B-C														8.2	11.3	10.7	11.7	(14.2)	13.3	15.9					
SK.567											9.8	9.9	10.2	9.2											
SK.479																					14.0	12.5	16.6		
SK.507															12.0	10.8	15.0								
SK.597															12.2	10.8	14.9								
SK.461																10.9		14.9	13.3	17.1					
SK.495													10.6	9.5											
SK.448											9.7	(11.3)	10.7	(9.5)											

Table 16d. Measurements of the lower teeth of *Simopithecus danieli*.

	I_1			I_2			$\overline{C}$			P_3		P_4		M_1			M_2			M_3				Rows	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	$P_4 - M_3$	$\overline{C} - M_3$
MALE:																									
SK.426										6.6	25.1	8.5	10.8		10.4	13.2	12.3	12.0	17.1						
SK.569										7.8		10.0	12.0	11.8	12.5	13.8	14.1	13.8	20.3	14.7	13.3		26.5	72.2	
SK.405														9.6		13.1	12.2	12.0	17.3	13.2					
SK.581												8.9	10.6												
SK.491																				16.5	15.2		(25.5)		
FEMALE:																									
SK.405) SK.402)*							10.3	8.7	5.4	5.6	11.3	7.8	9.4	(10.5)	11.4	12.2	12.8	12.4	15.6	13.8	12.9	11.1	22.7	54.9	74.3
SK.411										6.0	10.8	8.4	9.5	10.1	10.2	(11.3)	12.7	12.5	15.4	13.4	12.0	10.3	20.1	(54.5)	
SK.575A														9.8	10.0	12.5	12.2	11.7	14.8	13.1	12.6	8.5	21.8		

* Almost certainly from the same individual.

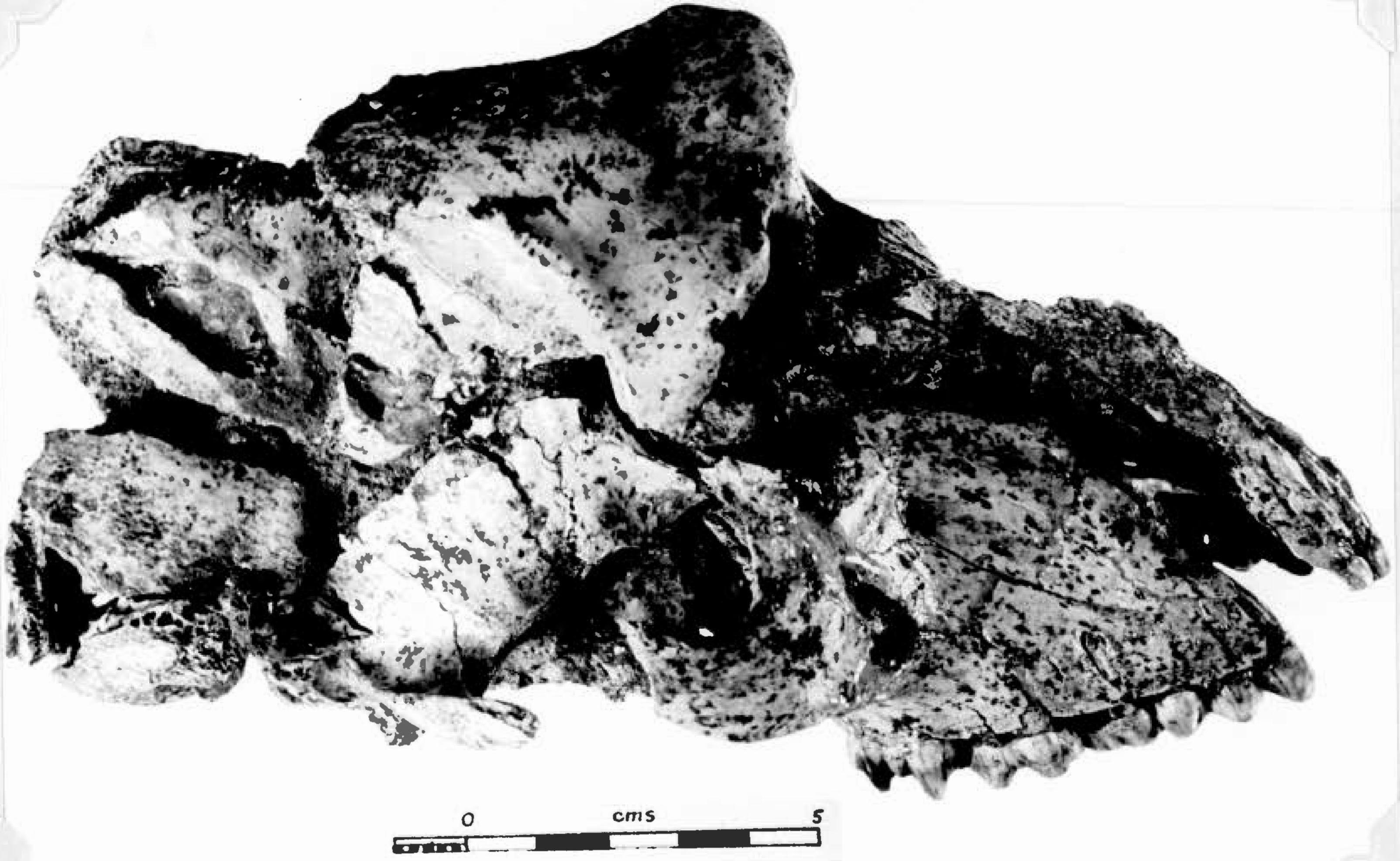

Fig. 91. *Simopithecus danieli* female (SK.561). Lateral view of crushed skull. x 1.

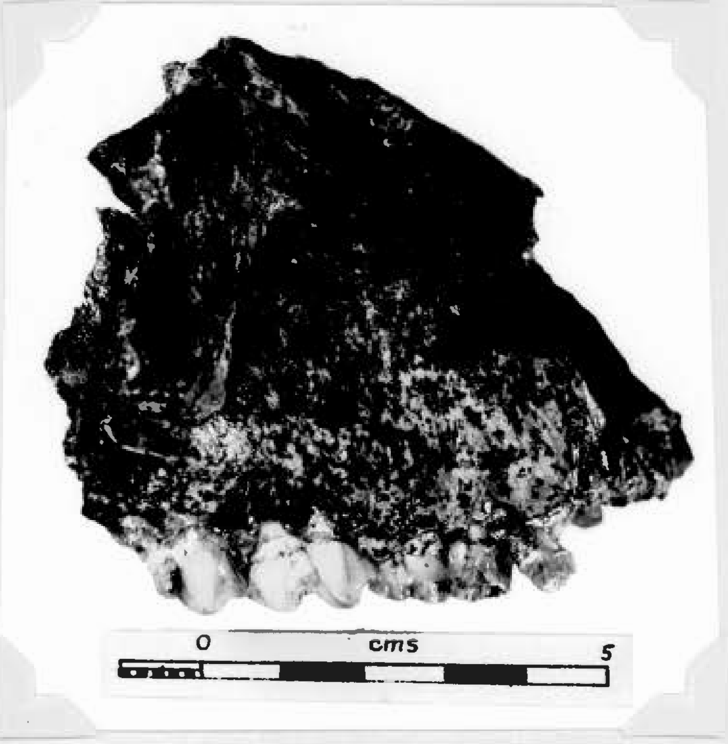

Fig. 92. *Simopithecus danieli* female (SK.563). Muzzle - lateral view. x 1.

Fig. 93. *Simopithecus danieli* female (SK.564). Occlusal view of upper teeth.
x 1.

Fig. 94. Simopithecus danieli male (SK.569). Lateral view of mandibular fragment and lower teeth. x 1.

Fig. 95. Simopithecus danieli female (SK.405). Lateral view of mandibular fragment and lower teeth. x 1.

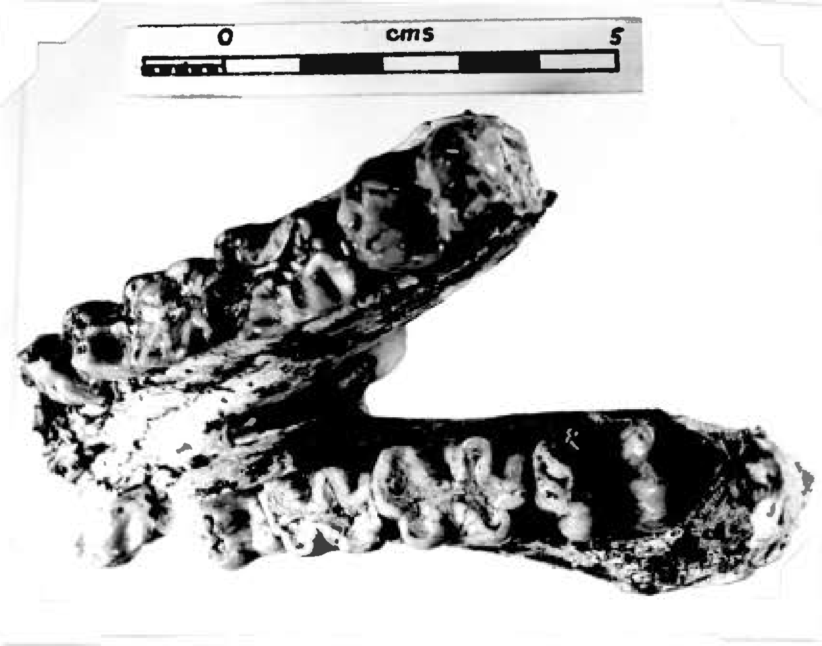

Fig. 96. Simopithecus danieli male (SK.569). Occlusal view of lower teeth. x 1.

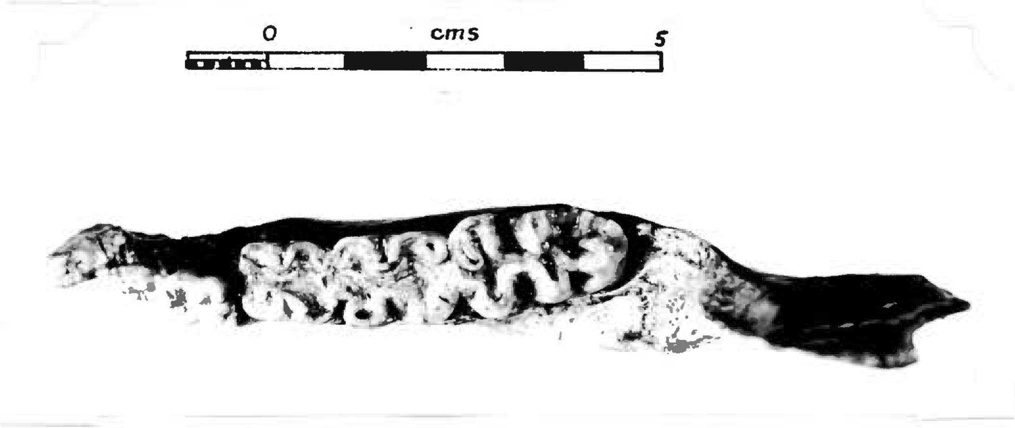

Fig. 97. Simopithecus danieli female (SK.405). Occlusal view of lower teeth. x 1.

Measurements:

See tables 16a, b, c and d.

Remarks:

From the structure of the unworn M_2 and M_3 described above, one can deduce how the characteristic appearance of the typical worn Simopithecus lower (and hence upper) molar develops. The ridge separating the lingually situated foveae and central fossa from the deep mesial and distal vertical grooves and the large intercusp cleft, wears down. This reveals the two separate walls which form this ridge, thus producing the characteristic appearance of the close buccal and lingual enamel infoldings. As one proceeds distally from M_1 to M_3, the structure of the individual teeth more closely approximate that of the unworn condition.due to the differential amount of wear caused by the successional eruption. In these teeth the closeness of the enamel infoldings from opposite sides becomes less and less as wear becomes greater. After a certain point has been reached, it becomes difficult to see the typical generic structure.

The unpredictable nature of the sample which is found of a fossil species (or indeed a fossil fauna) is well illustrated by the material so far known of this species. There are eleven specimens of the female skull and upper teeth but not a single skull fragment or upper tooth of a male. Of the mandibles on the other hand, there are three female and five male specimens.

(There is a pelvis mentioned under Dinopithecus ingens (in Remarks) which, on size, could fit equally well in this species).

CHAPTER 10.

DINOPITHECUS.

This genus was established by Broom (1937) for two specimens of a new species of large baboon, Dinopithecus ingens, from Schurweberg, Transvaal, South Africa. Later, Broom (1940) included another specimen (probably SB.2) from the same site. In 1949, Broom and Hughes mentioned that "a new form of large baboon occurs at Swartkrans, which may be a Dinopithecus" but they did not describe any material. During the course of the present study, a large number of specimens were found in breccia from that site which clearly belong not only in the genus Dinopithecus but in the species D.ingens. The new material considerably extends our knowledge of this species.

(Dart (1950) and Mouta (1950) mention material of baboons of large size, perhaps identical with D.ingens, from the limestone caves of Leba near Humpata, Angola, but neither author describes the material).

In 1947 Arambourg described a number of new cercopithecoid fossil specimens from the Omo Valley, Abyssinia and came to the conclusion that their dentition referred them to the genus Dinopithecus. He further decided that the form was specifically distinct from the only previously known species of that genus, D.ingens, and he proposed the name Dinopithecus brumpti for the new species. Interesting features described by Arambourg on both the upper and lower teeth of his specimens, are the vertical wrinkles on the enamel with some horizontal marking. (The horizontal markings may be the perikymata found on all primate teeth). The dental measurements of this species, as given by Arambourg, are as follows (1 x b in mm.):- M^2 - 17.7 x 14: M^3 - 20 x 12; M_1 - 14.5 x 12; M_2 - 17 x 12.3; M_3 - 23 x 14.

In deciding the taxonomic position of his specimens, Arambourg compares the sizes of the available teeth with those of both living and fossil species. He gives the sexes of the three living species he uses for comparison as male but he does not record the sexes of the two fossil species on which his conclusions are primarily based. Actually, the *D.ingens* teeth which he uses are also those of a male (all the teeth hitherto described are of male specimens) but those of *S.oswaldi* are of a female as he states that he is using the type specimen of that species. Furthermore, only molar teeth have so far been found of *D.brumpti* and the sex or sexes of the teeth of that species used in his comparisons cannot therefore be determined. Conclusions based on a comparison of specimens of opposite sex of species which show considerable sexual dimorphism cannot be considered significant when no allowance is made for this fact.

Arambourg's photographs of the dentition of this baboon show that the available teeth are rather worn and damaged but two teeth at least, M_3 (plate XXX, fig.2) and M_2 (plate XXVII, fig.7) seem clearly to show the typical *Simopithecus* molar pattern. Thus at least some of Arambourg's specimens will have to be referred to *Simopithecus* and a re-examination of all the material for possible affinities to that genus would seem to be necessary. On tooth size too, the *D.brumpti* specimens appear to match the larger species (mostly the males - see tables 13a and b) of *Simopithecus*. However, because of the scanty, unbalanced sample available of this genus, the determination of the exact taxonomic position of Arambourg's specimens will probably have to await further material of all the species

Genus: *Dinopithecus* Broom, 1937.

Diagnosis:

Dinopithecus is a genus of very large, extinct baboons which exhibit considerable sexual dimorphism. The skull is large and rugged and with, at least in the female, a fairly long muzzle. There are only faint traces of maxillary fossae in the female but the temporal lines are strong and there is a large nuchal crest in both sexes. The male has a well developed sagittal crest. The genus is characterised by large, broad teeth and a P_3 which, in the male, is comparatively short and has a particularly large anterior fovea. There is a tendency for the posterior foveae of the premolars to be divided into two by an enamel ridge and the molars often show many subsidiary cuspules which may be quite large.

The type species is D. ingens and was described by Broom (1937).

Dinopithecus ingens Broom.

Dinopithecus ingens - Broom, 1937.
Dinopithecus ingens - Broom, 1940.
Dinopithecus ingens - Broom and Jensen, 1946.
Dinopithecus ingens - Broom, 1946.
Dinopithecus ingens - Broom and Robinson, 1949.
Dinopithecus ingens - Broom and Hughes, 1949.
Dinopithecus ingens - Oakley, 1954b.
Dinopithecus ingens - Hopwood and Hollyfield, 1954.

Holotype:

Most of the left, and part of the right corpus, both with some damaged teeth, of a male mandible, SB.7.

Repository of type:

Division of Vertebrate Palaeontology and Physical Anthropology, Transvaal Museum, Pretoria, South Africa.

Type site:

Schurweberg, Transvaal, South Africa.

Referred material:

One specimen from Schurweberg and thirty-seven specimens from Swartkrans. (For the numbers of these specimens see tables 17a, b, c and d).

Three very good female skulls with teeth (SK.553, SK.600 and SK.603) are known but there is only one very fragmentary specimen of a male skull (SK.599). This latter specimen only shows the supra-orbital and mastoid regions and parts of the basi-occipital and zygomatic arch. The two male upper molars (M^2 and M^3) of SB.3 described by Broom (1937) from Schurweberg are badly crushed and expanded and their dimensions (see tables 17c) may well be too large. There are thirteen specimens of the male lower teeth and mandible (SK.401 is particularly good) but not a single lower tooth or mandibular fragment of a female.

Description: (Figs. 98 - 104).

The female of this species has a particularly large skull - possibly slightly larger even than that of the female of _Simopithecus danieli_. As far as can be judged, that of the male was considerably larger and more rugged than that of the female and the amount of sexual dimorphism was probably quite considerable. The female muzzle is long and dog-like as in the modern chacma baboon and in two of the specimens (SK.553 and SK.603) there are extremely shallow maxillary fossae. Although most of the muzzle rostrum and the inter-orbital region are broken in the three known female specimens, it would appear that there was only some slight flattening of the dorsal part of the muzzle. From about the level of a parasagittal plane through the centre of the infra-orbital margin, the lateral surface of the muzzle slopes down to the alveolar margin fairly steeply, but not vertically as in _Papio ursinus_. In SK.553 one can see indications of a weak maxillary ridge. There are multiple infra-orbital foramina and in SK.553, five in all can be counted. A portion of the left zygomatic bone can be seen in the male specimen (SK.599). It is particularly large and broad and probably faced forward at much the same angle as that of the male of _P.ursinus_. The zygomatic arch in this specimen is very robust. The zygomatic process of the maxilla is situated at the level of the anterior part of M^3 in the female.

The female supra-orbital tori are moderately well developed; those of the male are quite exceptionally strong and heavy and the inter-orbital region is also notably broad. In both the male and the female, but particularly in the former sex, the temporal lines are well marked and they would appear to have met at about the bregma. In the male, a definite sagittal crest is formed in this region (SK.599) but it cannot be traced far as most of the parietals and all of the occipital are missing in the single available specimen. It is very doubtful if a sagittal crest was present in the female. Specimens SK.604B and SK.553 show that a prominent nuchal crest was formed in the female and from the mastoid region of the male specimen (SK.599) it is apparent that in this sex, too, there was a similar but probably even more shelf-like nuchal crest. The general shape of the female calvarium is similar to that in the female of *P.ursinus*.

In both sexes, the occipital condyles are large and the basi-occipital bone wide. Also, the external auditory meatus is short and broad and lies at about the same angle as in *P.ursinus*. In the male, the mastoid region is particularly well developed and both the glenoid fossa and the post glenoid process are very large.

Among the Swartkrans specimens, there is an interesting juvenile skull (SK.554). This specimen has I^1 and M^1 already in place and slightly worn, and on size, these teeth would appear to make this specimen a female. The base of the calvarium is pushed in but the skull is otherwise almost perfectly preserved. The muzzle is relatively long and shows a considerable drop in the inter-orbital region; the calvarium is rather long and would seem to have been somewhat flattened. The supra-orbital tori are weak but the temporal lines are already fairly prominent. The deciduous teeth are considerably worn but it can be seen that they are of similar type to, though of course much smaller than, the permanent upper dentition of this species to be described below. On dm^1 there is some slight mesial elongation in front of the mesial pair of cusps and also slight chamfering of the mesio-lingual corner - both similar to that seen in the deciduous dentition of the young chacma baboon.

For the description of the upper dentition of this species there are numerous female teeth but only a few of the male. Never-the-less, it is quite clear that the teeth show considerable sexual dimorphism (see table 17c). The female upper dental arcade is horseshoe-shaped with some posterior narrowing and from SB.3 it would seem that the shape was similar in the male but probably with less posterior narrowing. In morphology, the teeth of *D.ingens* resemble those of *Gorgopithecus major* very closely but the teeth of the latter/show no sexual dimorphism and are considerably smaller in all their dimensions than those of even the female of *D.ingens*.

No upper incisors are present on any of the known male specimens but they are present in two female skulls (SK.604A and SK.574). In addition, there are a number of isolated incisors and the two central incisors on the juvenile specimen (SK.554). It is probable, on size criteria, that these teeth also belong to female specimens. All these incisors are very large but otherwise show no unusual features. The single available female *C* (SK.574) is badly damaged but it is clearly small and similar in shape to (but larger than) that of the female of *P.ursinus*. There are two very fine examples of the male *C* (SK.546 and SK.578B). It can be seen that they, too, show a similar structure to the equivalent tooth of the male of *P.ursinus* but, they are shorter in height, considerably broader and mesio- distally longer than in that species.

The upper premolars are even larger than those of *Simopithecus danieli* but, in structure, they are almost identical to those of *Gorgopithecus major*. Those of the male specimen , (SK.546) are extremely large and the posterior fovea of P^3 is unusual in that it is divided into two by a thin, low ridge of enamel running disto-lingually from the buccal cusp. There is a similar division of the posterior fovea of P^4 on a female specimen (SK.443). The enamel on P^3 extends a short distance down towards the mesio-buccal root in both the male and the female (e.g. SK.578A - a male and SK.440 - a female).

Almost all the upper molars except M^1 of the juvenile specimen (SK.554), are considerably worn but the strong resemblance of these teeth to the equivalents of *G.major* is yet again apparent. In size, the female molars are about as broad as, but rather shorter than, those of the *S.danieli* females and larger generally than those of *G.major*. The male molars, are, of course, far larger than those of *G.major* (there being no clearcut sexual dimorphism in the teeth of that species) and there are no male *S.danieli* upper molars for comparison. In both sexes, M^2 is the largest of the upper molars in all its dimensions; it is usually only slightly larger than M^3 but always considerably bigger than M^1. The portion of the tooth in front of the mesial pair of cusps shows considerable development in all of the upper molars and both buccally and ligually there are indications of cuspules in most of the specimens. Mesio-lingually there is usually a groove or pit on the lingual surface and mesio-buccally there is a small fovea on the occlusal surface in fromt of the paracone. On the almost unworn M^1 of SK.554 one can see that the central fossa is large and deep and the enamel ridge joining the two lingual cusps is much thicker than that joining the buccal two. The posterior fovea is slightly larger than the anterior one. The lingual surfaces of all the molars slope down relatively slowly from the occlusal surface to the alveolar margin and the inter-cusp cleft on this surface is very deep; on the buccal surface, the cleft between the main outer cusps is rather shallow but, especially on M^2 and M^3, there may be a small cuspule present in this cleft (SK.603).

From the size of the teeth (see discussion below) it would seem that all the known mandibular fragments are from male specimens. The best of these is specimen SK.401 which is damaged on the ventral surface of the symphysis and has lost both rami but still clearly shows that the male mandible is robust and heavy. The anterior surface of the symphysis of this specimen is almost vertical and has two converging bony ridges running up on either side of the foramen symphyseosum. The incisal shelf slopes down quite steeply and is fairly long, reaching to about the posterior part of P_3. In this same specimen, and also in SB.7 and SK.424, there is only a slight mandibular fossa on the lateral surface of the corpus. The ramus lies at about the same angle to the corpus as in P.ursinus (SK.404 and SK.422) and the lower part of the anterior edge of the ramus forms a short, broad shelf on the corpus, lateral to M_3 (SK.401).

Of the lower dentition, there are three known male specimens (SB.7, SK.424 and SK.401) but none of certain females. An examination of table 17d, which gives the dimensions of the lower teeth, shows that the amount of variation of the dental dimension of the specimens of unknown sex from those of the known males is very small. From the upper teeth (table 17c) it has, however, been seen that there is considerable sexual dimorphism in the dentition. It would therefore seem virtually certain that, with the possible, but doubtful, exception of SK.428 and SK.470, all these teeth must come from males.

No lower incisors or canines are available but from the alveoli on SK.401 it would seem that, in the male, the former were rather small teeth but the latter tooth was probably considerably larger than its equivalent in *P.ursinus*. P_3 is a very broad, robust tooth but does not show relatively or absolutely as much mesio-distal elongation as in the males of *P.ursinus* or *Simopithecus danieli*. As in the upper dentition, the overall shape of this tooth resembles that of its equivalent in *Gorgopithecus major* but it differs considerably even from the tooth in that species. On the disto-lingual portion of the mesial extension of this tooth, just anterior to the main buccal cusp, there is a large fovea which is far longer and deeper than that seen in any other cercopithecoid described in this study. Behind the main (buccal) cusp in SB.7 the large posterior fovea is divided into two by a ridge of enamel. P_4 is a large tooth with a well developed pair of cusps, one buccal and one lingual; in SK.510, there appears to be a third cusp on the disto-lingual corner of the cingulum. When viewed from the occlusal surface, the posterior fovea is seen to be considerably larger than the anterior. The mesial surface of this tooth leans back quite considerably and there are indications on the buccal surface of vertical grooves on either side of the main outer cusp (SK.510).

The male lower molars are large teeth and show quite considerable variation in size and, to a lesser extent also in minor morphological details. The teeth are about as broad but rather shorter than the equivalents in the male of *S.danieli* and they are only slightly larger generally than those of *G.major*. In shape, the lower molars, like the upper, closely resemble those of *G.major* but the anterior and posterior foveae and the central fossa are larger than in that species. These two species also share the tendency to have multiple subsidiary cuspules but the trait is more common in this species. In *D.ingens*, these subsidiary cuspules are often found on the cingulum between the two main lingual cusps and also between the entoconid and hypoconulid. In addition, they occur between the two main buccal cusps in several of the specimens where they are particularly large in specimens SB.7 and SK.455. (In the latter specimen, the cuspule is quite exceptionally well developed and is probably abnormal). On M_2 and M_3 there are marked mesio-buccal grooves or pits but all the M_1 teeth present are too worn and damaged to show whether this feature was present on them too. The worn molars of this species show some slight resemblance to *Simopithecus* in the close buccal and lingual enamel infoldings between the main cusp pairs.

Measurements:

See tables 17a,b,c and d.

Remarks:

Broom (1946) stated that "An imperfect pelvis with sacrum and three lumbar vertebrae are known, which may belong to the giant baboon *Dinopithecus ingens*. The specimens came from Sterkfontein, and possibly from the Plesianthropus Cave, but this is uncertain". These specimens have also been referred to by Broom (1940) and Oakley (1954b), and Broom and Robinson (1949) have mentioned a femur which they suggest probably belongs to *D.ingens*, but they give no locality for the specimen. None of the above fragments were found in association with cranial or dental material and, on size, they could equally well belong to the newly described *Simopithecus danieli*. In addition, amongst the material labelled 'Sterkfontein' and developed during this study, there is a maxillary fragment (STS.265) and a mandibular fragment (STS.365) both of which have well preserved teeth which agree perfectly with those of *D.ingens*. Further, from material said to come from Kromdraai, there are two specimens (KA.169 and

Table 17a. Measurements of the skull of *Dinopithecus ingens*.

	Female	
	SK.553	SK.600
GENERAL.		
Greatest length	(193)	
Basal length	138	
Bizygomatic breadth	(124)	
CALVARIUM.		
Height:		
Basion-bregma	(76)	
Breadth:		
Min. inter-frontal	(68)	
Greatest temporal	(87)	
Mastoid	94	
Length:		
Inion-glabella	(125)	
Inion-basion	(58)	
Foramen magnum:		
Breadth	19	
Length	20	
MUZZLE.		
Height:		
Post. to M^3	(60)	
Ant. to P^3	23	
Breadth:		
Ant. to M^3		53
Ant. to P^3	(50)	46
Length:		
Muzzle		(120)
Palate	(88)	
Orbit:		
External-orbital	(104)	

Table 17b. Measurements of the mandible of *Dinopithecus ingens*.

	Male	
	SK.401	SB.7
Height:		
Post to M_3	37	37
Ant. to P_4	36	38
Breadth:		
Bigonial	(87)	
Post. to M_3	82	
Ant. to M_3	64	
Ant. to P_4	50	53
Through mental spine	(42)	40
At base of canines	34	
Length:		
Gonion-mental spine	(95)	
Angles:		
At symphysis	102°	
Between corpora	40°	

Table 17d. Measurements of the lower teeth of *Dinopithecus ingens*.

	P_3		P_4		M_1			M_2			M_3				Rows	
	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	$P_4 - M_3$	$\overline{C} - M_3$
MALE.																
SB.7	8.6		9.3	10.8		10.7	(13.5)	13.0	12.6	(16.3)	14.0	12.6	7.5	21.4		
SK.424			9.2	(12.0)		(10.0)	(12.0)									
SK.401	7.9	21.0	9.3	10.4	10.9	10.8	11.9	13.1	12.8	16.2	13.7	10.9		(21.5)	(59.5)	
SK.455								13.0	13.3	16.2	13.7	11.7	8.9	22.7		
SK.510			9.9	11.7												
SK.404							12.5	(13.3)	12.8	17.0	13.6	10.8		21.5		
SK.422											12.8	12.5	11.6	22.3		
SK.474											13.8	10.8	7.7	(21.4)		
SK.492											14.5	12.8	10.4	21.5		
SK.628A-B						10.3	13.0	13.0	(12.6)	16.2						
SK.432								12.7		16.2						
SK.428											13.0	10.9		20.0		
SK.470											12.6	10.0		20.0		
FEMALE.																
Nil																

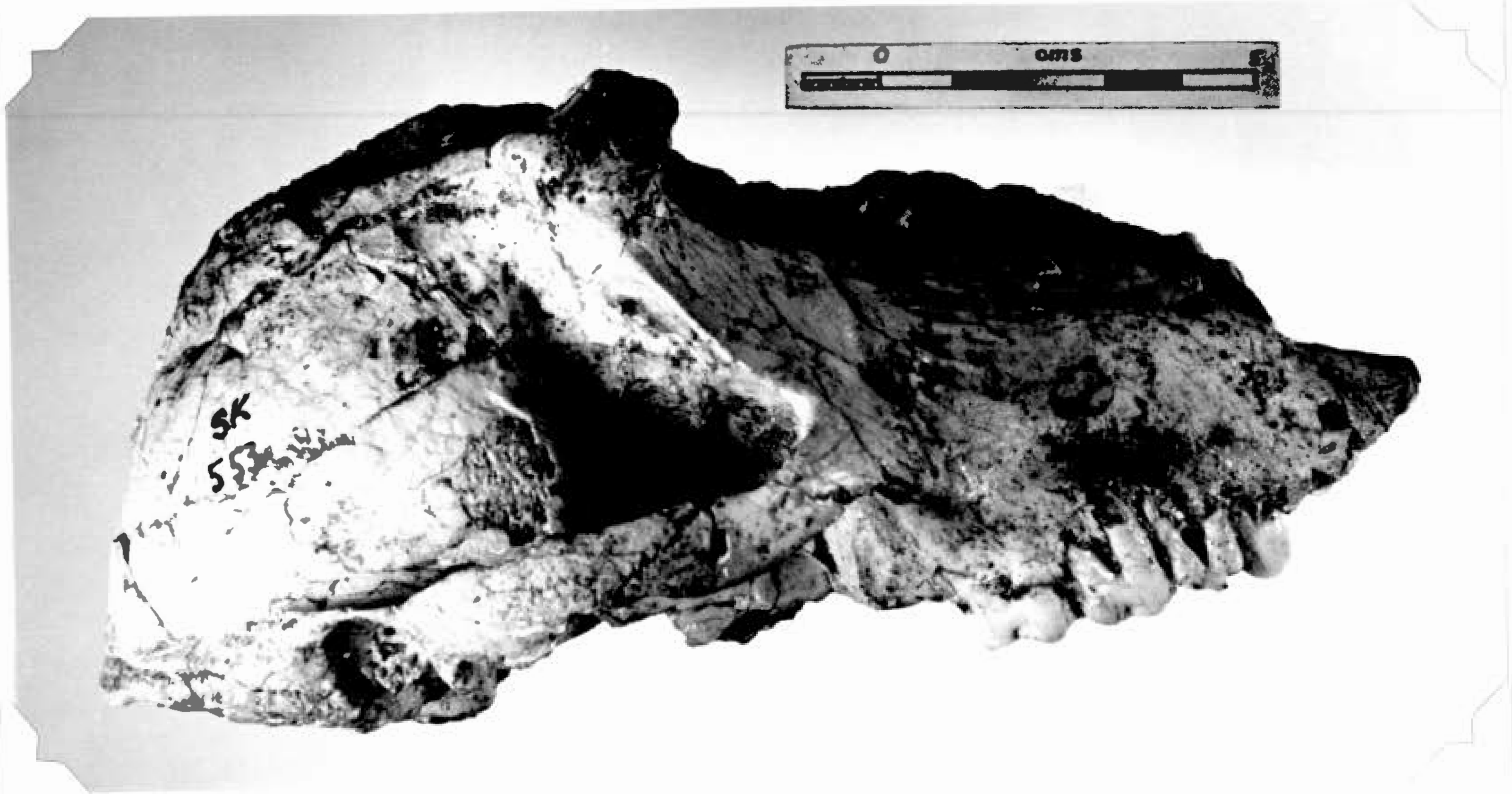

Fig. 98. *Dinopithecus ingens* female (SK.553). Skull - norma lateralis. x 1.

Fig.99. *Dinopithecus ingens* male (SK.546). Lateral view of maxillary fragment and upper teeth. x 1.

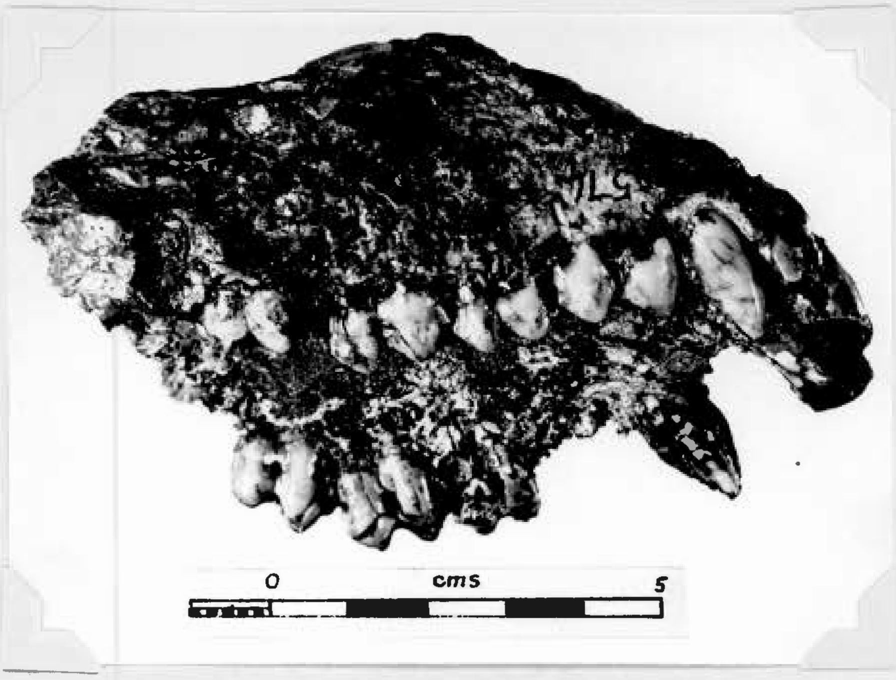

Fig.100. *Dinopithecus ingens* female (SK.574). Buccal and lingual views of the upper teeth. x 1.

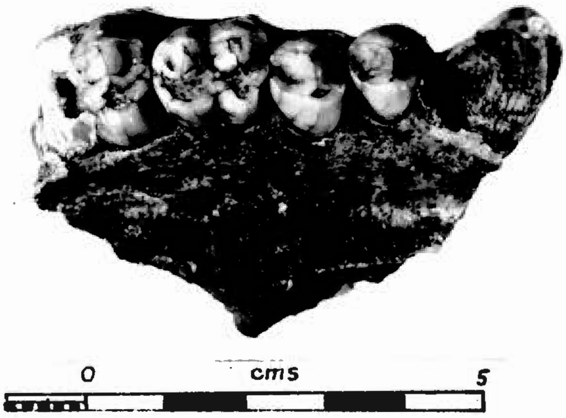

Fig.101. *Dinopithecus ingens* male (SK.546). Occlusal view of the upper teeth. x 1.

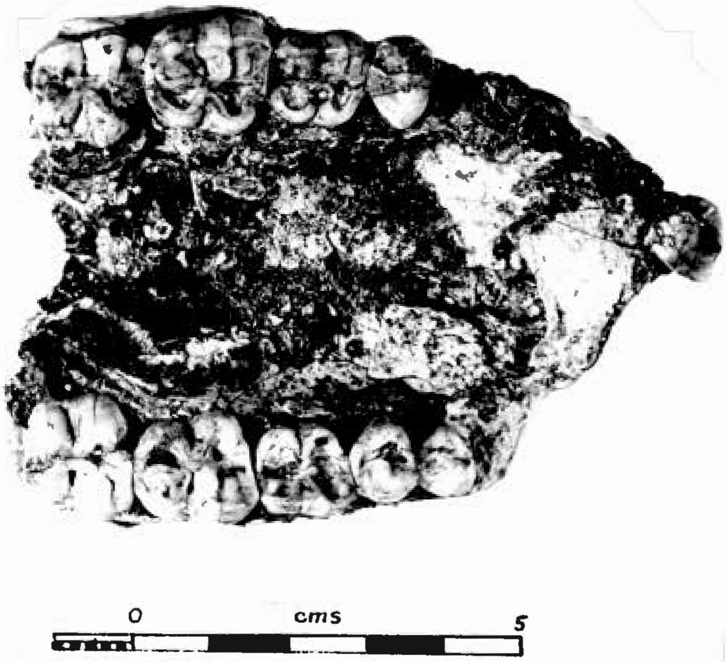

Fig.102. *Dinopithecus ingens* female (SK.604A). Occlusal view of the upper teeth. x 1.

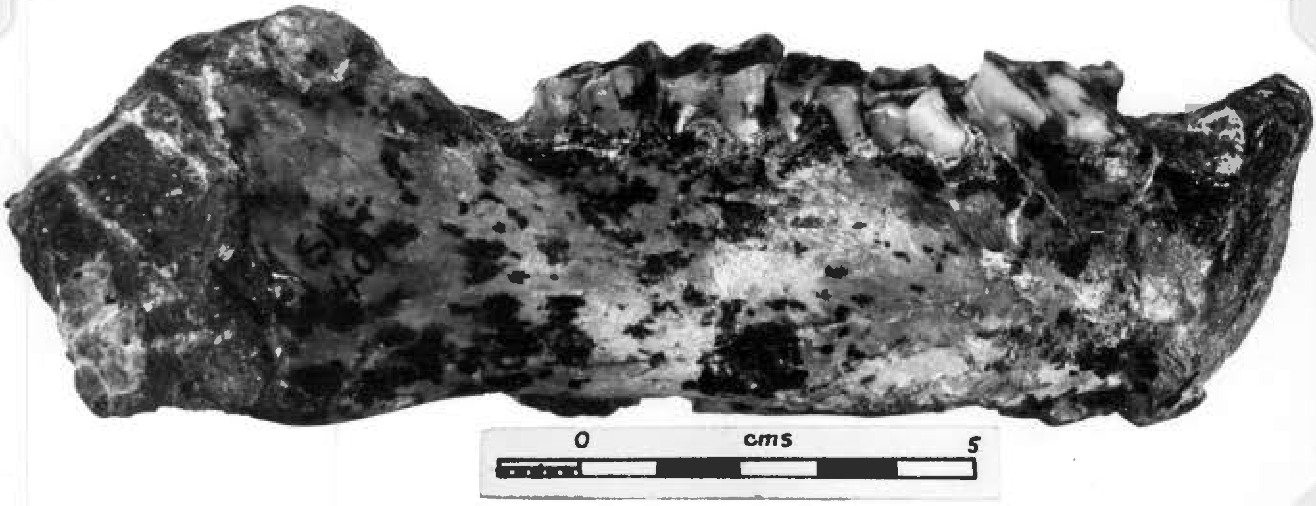

Fig.103. Dinopithecus ingens male (SK.401). Mandible - lateral view. x 1.

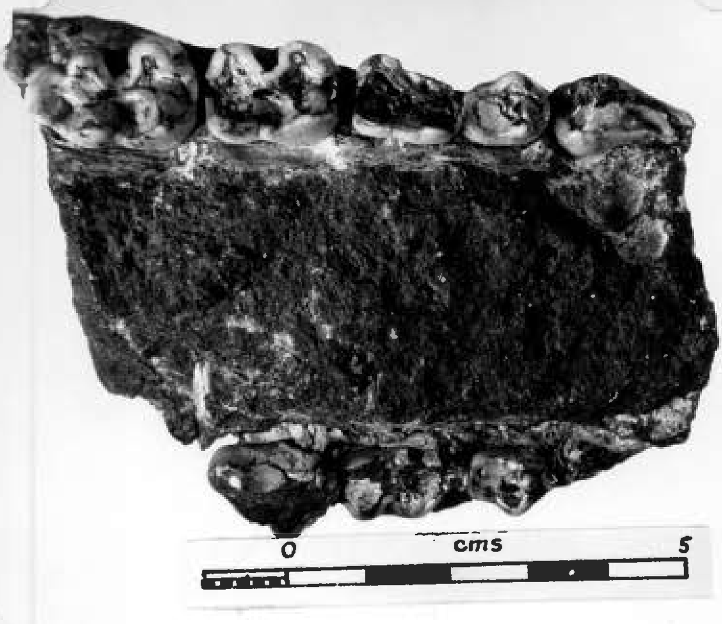

Fig. 104. Dinopithecus ingens male (SB.7). Occlusal view of lower teeth. x 1.

KA.183) which on dental size also fit well into the species *D.ingens*. Unfortunately, there is some doubt about the localities of all of the above specimens and, for the present, it would seem wiser to await further material before accepting the presence of *D.ingens* (and/also possibly *S.danieli*, in the case of Sterkfontein) at either of these sites.

(SB.2, which was referred to this species by Broom (1940), would seem more probably to be the skull of a male *Papio robinsoni*).

CHAPTER 11.

GORGOPITHECUS.

In 1940, primarily on the basis of two very worn teeth, M^2 and M^3, Broom described a new species of Parapapio which he called P.major. (He mentions that "a few teeth have been found" of this species but he only discusses the above two). Broom states that "In size these teeth agree pretty closely with those of the living South African baboon Papio comatus, [Papio ursinus] but the 3rd. differs in having no trace of the 5th cusp which is invariably present in all the skulls I have been able to study. It thus agrees in structure with the 3rd. molars of the species of Parapapio, and it seems safer to place the new form in this genus". It is very difficult to understand how this statement came to be made as the relevant tooth has no fifth cusp - and neither do those of either Papio or Parapapio! Nowhere in his short description is there any clue as to what Broom had in mind. (As no lower teeth were known at the time, he could not have been thinking of M_3, which in any case, has a fifth cusp in Papio, Parapapio and this species). The only other reasons for creating this species given by Broom are the facts that, compared to P.ursinus, "The pit in front of the antero-internal cusp is very much larger in the new species; while the division between the internal cusps is a narrow groove in P.comatus [P.ursinus] and a wide groove in the new form". Despite the slender and partially invalid grounds for establishing this new species, when describing with Robinson (1949), new material from Kromdraai which matched the two type teeth of P.major, a new genus, Gorgopithecus, had to be created for the species because of several unique features of the skull.

In 1952, Robinson suggested that the species Gorgopithecus major might have to be transferred to the genus Simopithecus and, presumably following him, Oakley (1954a) referred to Simopithecus from Kromdraai and Hopwood and Hollyfield (1954) list this species as Simopithecus major. The new material now available of G.major and of the genus Simopithecus make it quite clear that Gorgopithecus is a valid genus.

Recently, Kitching (1953) described a lower jaw of a new species, Gorgopithecus wellsi, from Makapan and at the same time transferred the species Papio darti to Gorgopithecus. As discussed in Chapter 9, the specimens which have been referred to those two species all clearly belong in the genus Simopithecus and 'G.wellsi' is a synonym of Simopithecus darti.

Genus: Gorgopithecus Broom and Robinson, 1949.

Diagnosis:

This is a large form of baboon in which there is apparently only slight sexual dimorphism in the skull. The male muzzle is relatively short (compared to that of the P.ursinus male) but that of both sexes is unusually high and very narrow. The maxillary excavations are very deep and affect the maxilla below the orbit. In the male, the orbits are laterally elongated and the inter-orbital area is broad: the frontals sweep up to the supra-orbital tori. The teeth are similar in shape to, and almost as large as, those of the female of Dinopithecus ingens. The upper molars have at least slight extra development of the mesio-buccal corner. Except for the canines and P3, the known teeth do not appear to show sexual dimorphism.

The type species is G.major and was described by Broom (1940).

Gorgopithecus major (Broom).

Parapapio major	- Broom, 1940.
Parapapio major	- Broom, 1946.
Gorgopithecus major	- Broom and Robinson, 1949.
Gorgopithecus major	- Robinson, 1952.
Simopithecus	- Oakley, 1954a.
Simopithecus major	- Hopwood and Hollyfield, 1954.

Holotype:

Two linked teeth, M^2 and M^3, (KA.193) considerably worn and of unknown sex.

Repository of type:

Division of Vertebrate Palaeontology and Physical Anthropology, Transvaal Museum, Pretoria, South Africa.

Type site:

Faunal site, Kromdraai, Transvaal, South Africa.

Referred material:

Eleven specimens from Kromdraai. (For the numbers of these specimens, see tables 18a, b and c).

There is an almost complete male skull (KA.192) which, although rather badly crushed and distorted, provides an excellent basis for the description of the male cranial characters. The base of the skull is unfortunately still embedded in a large block of matrix which it is at present not possible to develop. Except for I^2 and M^3, all the teeth are present on the right side but they are considerably worn; I^1, P^3, P^4 and the damaged $\underline{C}$ and M^1 are present on the left. For the description of the female skull, there is only a muzzle with part of the zygomatic arch (KA.153). $\underline{C}$ to M^3 are present on the right side and $\underline{C}$ to P^4 on the left.

For the description of the mandible, there are only two badly damaged specimens (KA.150 - a male, and KA.152 - an immature adult of unknown sex). In KA.150, P_3 - M_3 are present bilaterally and a broken $\overline{C}$ and I_2 are also present on the right; in KA.152, P_4 - M_3 are present on the right and only M_3 on the left.

Description: (Figs. 105 - 111).

The overall size of the male skull is almost as large as that of the male of *P.ursinus* but the muzzle is relatively shorter and the calvarium relatively longer. Part at least of the reason for this difference in proportions is the fact that, although the zygomatic process of the maxilla of the male is at about the same level relative to the teeth (M^3) in both species, in *P.ursinus* the anterior-facing surface of the zygomatic bone slopes back at an angle of about 135° whereas in *G.major* it is almost vertical.

The muzzle thus starts more or less directly under the orbit in G.major but considerably in front of it in P.ursinus.

The shortness of the muzzle in G.major is accentuated by its exceptional height and narrowness. Instead of having a large, flat or rounded dorsum made up of the nasals and maxillae as in the males, and to a lesser extent the females, of so many of the other Cercopithecoides, in this species the maxilla drops down steeply from close to the side of the nasal bones and nasal aperture to the alveolar margin. This feature can be seen in both the male skull and the female muzzle. From the nasion, also in both sexes, the short nasal bones run almost horizontally to the posterior edge of the nasal aperture. There is then a steep drop from this point to the anterior margin of the aperture on the premaxillae. In the male skull, the premaxillae are crushed down and splayed out but in the female muzzle it can be seen that these bones lie rather more vertically than in P.ursinus. The nasal processes are very long and reach up to the posterior margin of the very long nasal aperture. On the side of the muzzle in both sexes, there is a large, deep maxillary fossa which actually continues posteriorly past the level of the infra-orbital margin excavating into the maxilla. The zygomatic arch of both the male and the female is heavily built.

For the rest of the description of the skull one must rely entirely on the crushed male specimen (KA.192) but from a comparison of the muzzles of the two sexes, it would seem that there was little difference, in size at any rate, between the male and female skulls. In the skull of this male specimen, the orbits, as preserved, appear laterally elongated and oval in shape. This is probably only partly due to the effects of the crushing. The inter-orbital area is very broad and the supra-orbital tori are raised up a considerable amount from the calvarium roof. Both of these latter features resemble the condition in 'Parapapio' coronatus and in the female specimen of Cercopithecoides williamsi from Sterkfontein.

On the calvarium roof, the temporal lines are weak and converge rapidly towards a point approximately corresponding to the bregma. They then diverge slightly again and rum almost parrallel before finally converging again slowly to a point just anterior to the inion where they fuse. There is a well developed nuchal crest round the posterior end of the calvarium with a large inion where this crest meets the fused temporal lines. The shape of the calvarium is difficult to reconstruct because of the appreciable amount of crushing and the base of the skull is still embedded in matrix. A description of these two areas will have to await further specimens or until this one can be completely developed.

Broom and Robinson (1949) noted the resemblance of the teeth of this species to those of the chacma baboon (and most of the comparisons below are made with that species) but it seems that, although considerably smaller, they probably resemble those of Dinopitheous ingens even more closely. In comparing the male and female teeth of this species, with the exception of the canines and P3, there is no indication of the male teeth being larger and, in point of fact, from the few teeth available for comparison (tables 18b and c), it is often the female tooth which is bigger.

For the description of the upper dentition, there are the male and female specimens described above (and under Referred material), the two type molars (KA.193), a good maxillary fragment of unknown sex with $P^3 - M^3$ present (KA.194) and four separate isolated teeth. Viewed from the occlusal surface, the dental arcades of both the male and female appear to be very similar in shape and size to that of the male of P.ursinus, except that the female tooth row is slightly shorter due to the smaller C.

The only upper incisors known of this species are the two male I^1 teeth of KA.192. These teeth are considerably worn but it can be seen that they are slightly smaller in size than those of the P.ursinus male and that their occlusal surface is almost square with a concave bucco-lingual facet. The male C (KA.192) appears to be very similar to that of the male chacma baboon but the teeth are unfortunately rather damaged and considerably worn in this specimen. The female C (KA.153) is also very worn and damaged but appears to have been rather broader and mesio-distally longer than in the female of P.ursinus.

The premolars of this species also seem similar in structure to those of the chacma but they are too badly worn to show whether there were any differences in the details of the cusp and fovea arrangement. The mesial surface of P^3 does, however, not lean back as greatly as it does in P.ursinus. Instead, there is only a very slight backward lean in the G.major male P^3 (KA.192) and almost none at all in that of the female (KA.153). The lingual surface of P^4 (and to a slight extent that of P^3 as well) is much less vertical in this species than in the chacma baboon. The base of the crown is very much broader than the occlusal surface and the breadth measurement of these teeth, and particularly P^4, is much greater in G.major than in the male of P.ursinus. The single available female P^4, (KA.153) is considerably larger than the one known male equivalent. (KA.192).

The upper molars all have large contact facets and the root system is that common to all the Cercopithecoidea described in this study. Superficially, these teeth resemble those of Dinopithecus ingens more than those of any other genus. In size, except for M^3, the upper molars are all broader and longer than those of the P.ursinus male but most of the measurements (including M^3) fall below those of the female of D.ingens. The molars are all broader mesially than distally and in length, M^2 is considerably longer than M^1 and also slightly longer than M^3. The lingual surfaces of the upper molars are similar to those of D.ingens in that they are much more vertical than in P.ursinus - this results in less narrowing of the crown of the molar towards the occlusal surface. There are rather well developed subsidiary mesio-buccal cuspules on almost all of the upper molars known and even those which do not have actual cuspules, show some extra development in this region. There are also mesio-lingual cuspules on all the specimens with M^3 present, and on the type M^2 and M^3 there is, in addition a small fovea present in this region. Between the buccal cusps of M^2 of KA.192 and M^2 and M^3 of KA.154, there are small accessory cusplets.

For the description of the mandible, there are only two very badly damaged specimens, KA.150 and KA.152. The former is a male fragment which shows a small part of the symphysis and the anterior and upper posterior parts of the right corpus; the latter is an immature adult of unknown sex and has most of the posterior part of the right corpus and the lower portion of the ramus preserved. All that can be deduced from these two specimens is that it would seem that there was a shallow mandibular fossa present and that a lateral, converging ridge, similar to that found in many baboons, ran up the anterior surface of the symphysis.

Of the lower dentition, besides the teeth of KA.150 and KA.152 (see under Referred material), there are only two isolated specimens of M_3 and a single isolated M_2 known of this species. Thus, the only lower incisors (I_2) and canines are in the male specimen, KA.150. As far as can be seen, I_2 is very similar to that in the male of *P.ursinus* but $\overline{C}$ is narrower in breadth and slightly longer in mesio-distal length than its equivalent in that species.

The only P_3 teeth known are also found in the male mandible, KA.150. The tooth has the typical extension of the mesial surface found in this family, but is shorter than in the *P.ursinus* male and the wear facet for $\underline{C}$ is rather more horizontal. This wear facet has resulted in a small apparent cusp being formed some 7 mm. anterior to the main cusp but on the lingual side of the tooth. P_4 is a very large tooth in both KA.150 and KA.152, and is moderately molarised. On KA.152, it is far less worn than on the male specimen and it is seen to have a pair of well developed [illegible] cusps, one buccal and one lingual, situated between a small anterior and a large posterior fovea. On the buccal surface of P_4 of both specimens, there are two vertical grooves, one just mesial and the other just distal to the outer cusp. The mesial of these two grooves is small but the distal

Table 18a. Measurements of the skull of <u>Gorgopithecus major</u>.

	Male		Female
	KA.192*		KA.153
CRANIUM.			
Greatest length	212	(200)	
Bizygomatic breath	152	(130)	
CALVARIUM.			
Breadth:			
Min. inter-frontal	69	(65)	
Greatest temporal	95	(85)	
Length:			
Inion-glabella	123	(116)	
MUZZLE.			
Height:			
Ant. to P^3	29		28
Breadth:			
Ant. to M^3	62	(54)	
Ant. to P^3	58	(50)	45
Length:			
Muzzle	93	(86)	83
Nasal	36		33
Orbit:			
Inter-orbital	17		
External orbital	93		
Height	23		
Breadth	34		
Nasal aperture:			
Breadth	20		18
Length	36		34

* The figures in brackets are estimated, corrected figures to allow for distortion and crushing.

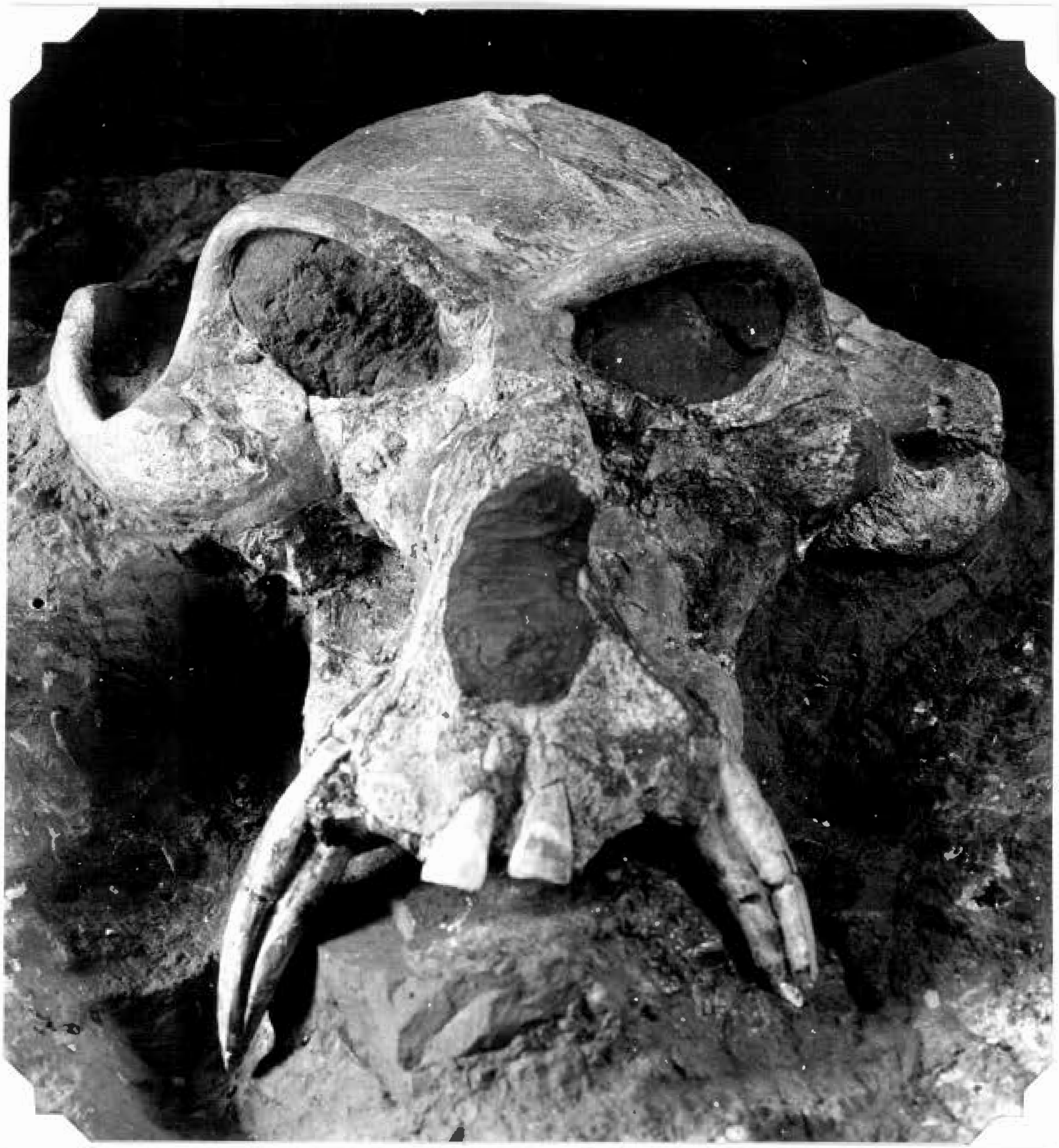

Fig.105. *Gorgopithecus major* male (KA.192). Skull - anterior view. x 1. (Photo: J.T. Robinson).

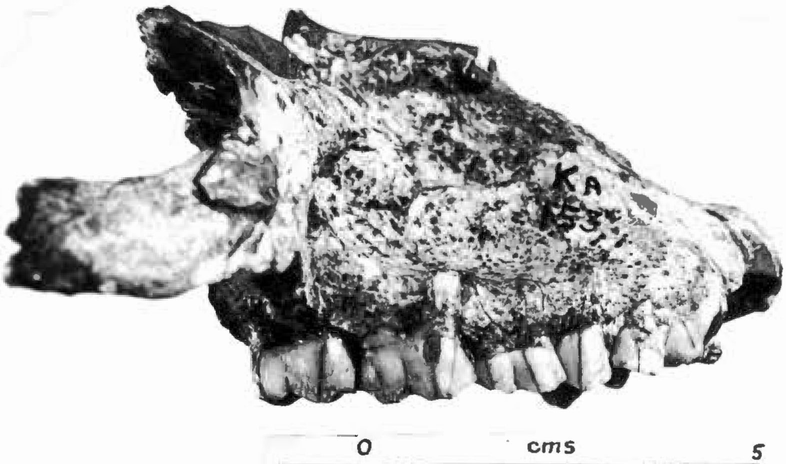

Fig. 106. *Gorgopithecus major* female (KA.153). Lateral view of maxillary fragment and upper teeth. x 1.

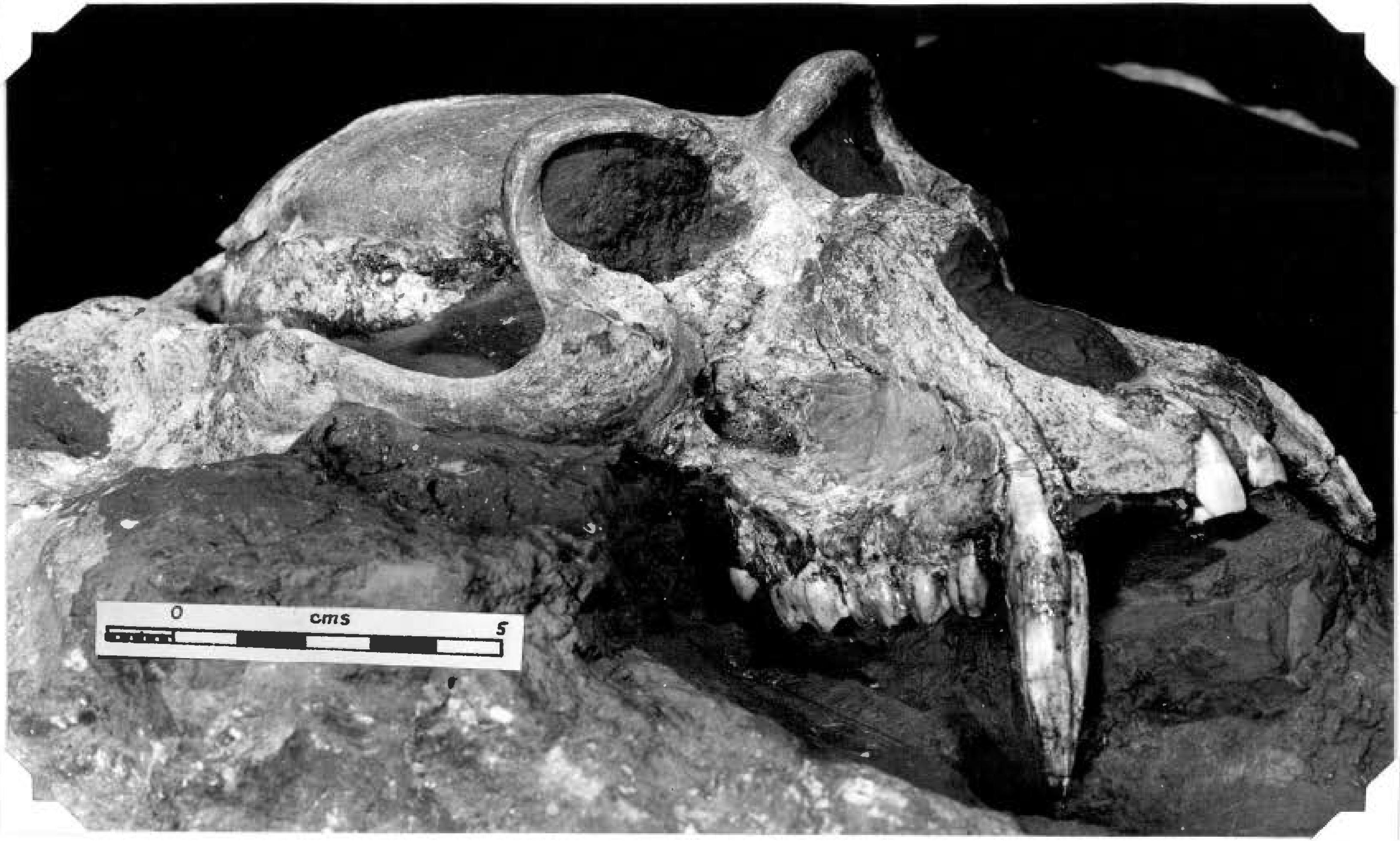

Fig.107. *Gorgopithecus major* male (KA.192). Skull - antero-lateral view. x 1. (Photo: J.T. Robinson).

Fig.108. *Gorgopithecus major* male (KA.192). Occlusal view of upper teeth. x 1.

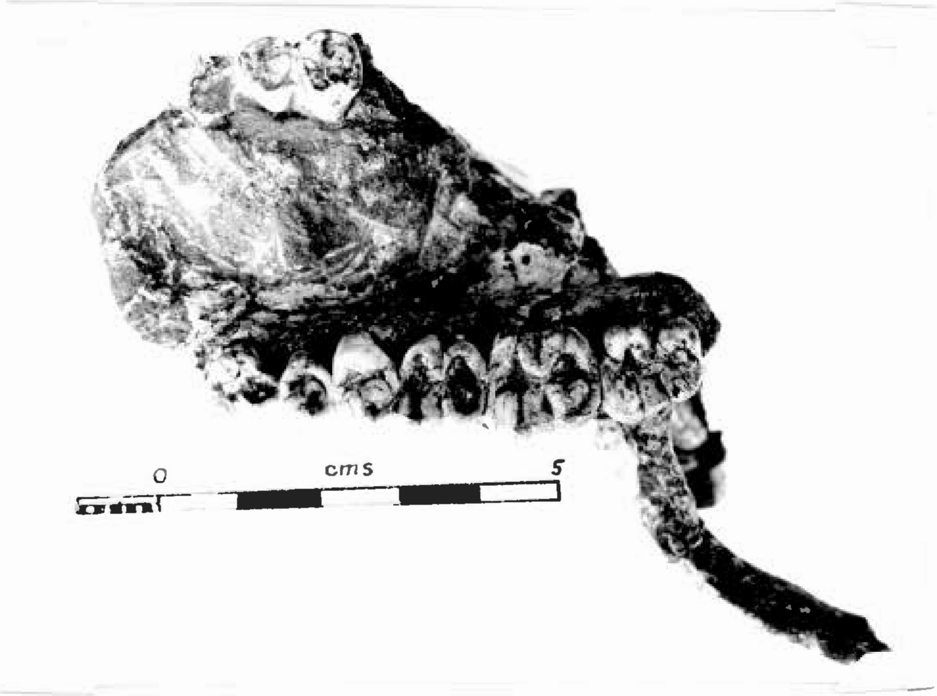

Fig.109. *Gorgopithecus major* female (KA.153). Occlusal view of upper teeth. x 1.

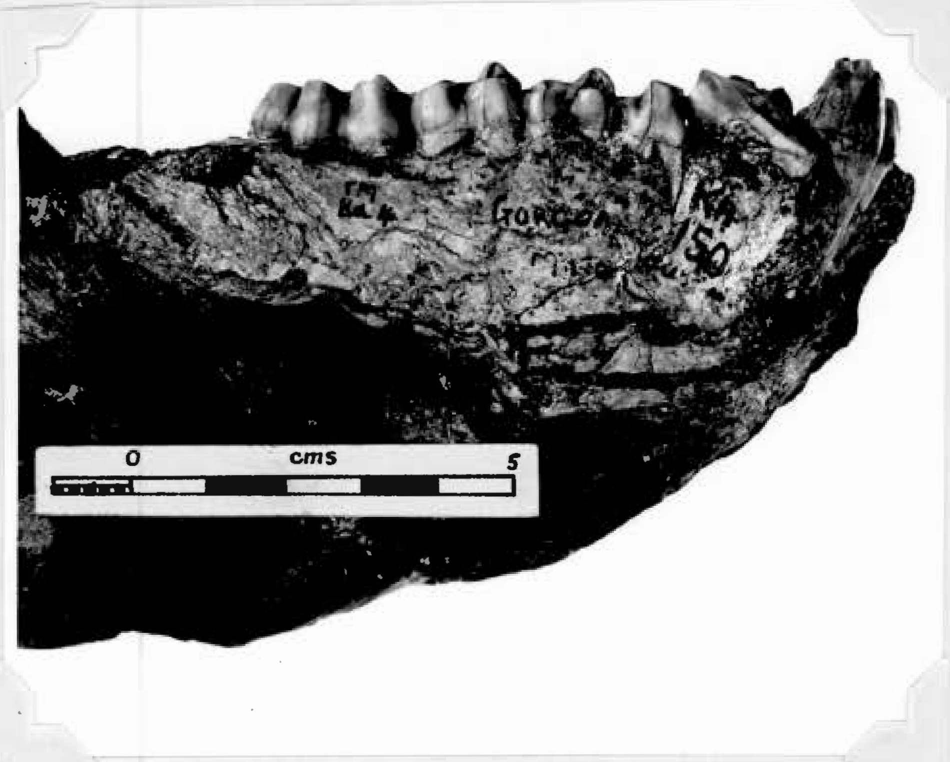

Fig.110. Gorgopithecus major male (KA.150). Lateral view of mandibular fragment and lower teeth. x 1.

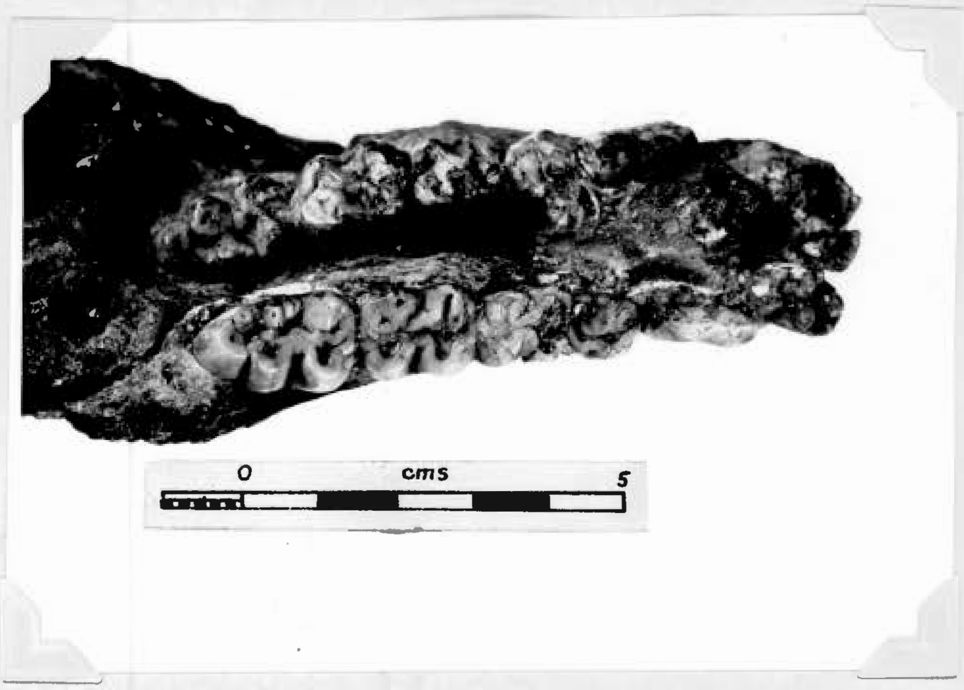

Fig.111. Gorgopithecus major male (KA.150). Occlusal view of lower teeth. x 1.

one is large and appears to mark off the well developed posterior part of the tooth.

The lower molars are very large teeth and show the same cusp and cleft arrangement as in P.ursinus. The buccal inter-cusp clefts are large and deep and M_3 has a well developed hypoconulid. Most of the molars of KA.150 and KA.152 have fairly deep mesio-buccal grooves on the buccal surface and several of these teeth also have lingual accessory cusplets. On M_3 of both these specimens there are also several small cuspules on the lingual cingulum between the entoconid and the hypoconulid. As in D.ingens, the buccal surfaces of the lower molars slope less than in P.ursinus. Like in the upper molars, these teeth are considerably larger than those of the P.ursinus male but there are no D.ingens female lower molars for comparison.

Measurements:

See tables 18a, b and c.

Remarks:

The advisability of replacing the 'type specimen' concept, particularly in palaeozoology where only fragments are usually available, by a type series (eg. the hypodigm of Simpson, 1940), is very well illustrated by this species. The two type teeth (KA.193) are considerably worn and hence very little of their structure can be seen. Further, as there appears to be no sexual dimorphism in the molars of this species, the teeth cannot even be sexed. Fortunately, however, there is no known species which is very similar in skull morphology or dental size to G.major, and it appears virtually certain, from size and general appearance, that the type teeth belong in the same species as the skull fragments KA.192 and KA.153 from which the main diagnostic features of the species and genus have been described.

CHAPTER 12.

CERCOPITHECOIDES.

This genus includes all the fossil monkey remains so far found in South Africa. Only one other fossil monkey has been described up to the present from the rest of Africa and that is mesopith *Cercocebus ado* Hopwood, 1936 from the Middle Pleistocene of the Vogel River (Laetolil) Beds of Tanganyika. Unfortunately, the only available description of this species is a very brief note without either drawings or photographs and no useful comparisons between this species and *Cercopithecoides* can be made. A summary of this description is given in Appendix III.

Hitherto, the genus *Cercopithecoides* was represented by only one species, *C.williamsi* Mollett, 1947. For the description of this species, Mollett had available only a single damaged male skull and mandible from Makapan. Since then, two further lower jaws were discovered at the same site which Broom and Hughes (1949) "were inclined to refer" to this species - but they gave no description of them. Of these, the one specimen (LW.7/48) clearly belongs in this species but the other (60M.) is a *Parapapio jonesi*.

During the course of this study, in addition to further specimens from Makapan, a considerable number of specimens belonging to this genus, and almost certainly to this species, were found in breccia excavated from Sterkfontein. Single specimens were also found in material from Cooper's and Taungs. Unfortunately, the type skull from Makapan is that of a male and in the new material, the only fairly complete skull is that of a female from Sterkfontein. However, as discussed below, it would seem that the differences found between these two skulls can all reasonably be ascribed to sexual dimorphism. In the teeth, the specimens found at Makapan, Sterkfontein, Cooper's and Taungs agree closely and, at least until further material is available, they are all best grouped together in the species *C.williamsi*.

In addition to the above new material, specimens of this genus were also recovered from Swartkrans, Graveyard and Swartkrans II. These specimens are very fragmentary and only dental comparisons can be made. From these it is quite clear that this form belongs to the genus *Cercopithecoides* but is specifically distinct from *C.williamsi* in that its teeth are larger (see table 19) and show minor morphological differences. The name *C.molletti* is proposed for this new species in honour of Dr. O. D. van der Spuy Mollett who first described this genus.

Hopwood and Hollyfield (1954) have suggested that *Cercopithecoides* may be a synonym of *Macaca*. In the light of the new material described in this study, it seems quite clear that this genus merits separate generic status.

Genus: *Cercopithecoides* Mollett, 1947.

Diagnosis:

This is a genus of fairly large, extinct monkeys which have a very short muzzle and comparatively large brain. The orbits are large and there are shallow maxillary fossae present. In both sexes, but particularly in the female, there is a transverse groove running across the skull posterior to the supra-orbital tori. In the female, the supra-orbital tori are raised above the calvarium roof. The zygomatic process of the maxilla of both sexes is situated at about the level of M^2. The mandible has a typical, very flat, anterior surface and a well marked lateral ridge (prominentia lateralis) on the posterior part of the corpus. The teeth are small and cramped, P^3, M^3 and M_3 being particularly small but the latter tooth never-the-less still having a small extension with a hypoconulid behind the distal pair of cusps. The molars have a quite typical structure. The central fossae are particularly large and deep and the cusps are very high. There are deep v-shaped inter-cusp clefts, lingually on the upper and buccally on the lower molars. The mesial surfaces of the cusps (at least in the worn lower molars) slope at a more acute angle than the distal. Although there is sexual dimorphism in the skull, except for the canines and P_3, there appears to be none in the teeth.

The type species is *C.williamsi* and was described by Mollett (1947).

Table 19. Observed ranges of the upper and lower molar dimensions of *Cercopithecoides* spp. (in mm.).

	M^1			M^2			M^3		
	bm	bd	l	bm	bd	l	bm	bd	l
C.williamsi ♂ and ♀	-	-	7.8 - 8.9	9.0 - 10.2	8.8 - 9.1	9.0 - 9.9	9.1 - 9.5	7.3 - 8.2	8.7 - 9.5
C.molletti ♂ and ♀	8.4 - 9.6	7.8 - 9.0	8.9 - 9.7	9.9 - 11.6	8.6 - 10.0	9.6 - 11.4	10.1 - 11.0	8.2 - 9.0	10.8 - 11.0

	M_1			M_2			M_3		
	bm	bd	l	bm	bd	l	bm	bd	l
C.williamsi ♂ and ♀	6.2 - 7.4	6.4 - 7.3	7.7 - 8.7	6.8 - 8.3	6.8 - 8.6	8.5 - 9.6	7.7 - 8.3	7.1 - 8.8	10.9 - 12.4
C.molletti ♂ and ♀	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	-

Cercopithecoides williamsi Mollett.

? monkey - Jones, 1937.(STS.350 = 1238/24).
Parapapio jonesi - Broom, 1940.(STS.350 and STS.366).
Cercopithecoides williamsi - Mollett, 1947.
Cercopithecoides williamsi - Broom and Hughes, 1949. (LW.7/48).
Cercopithecoides williamsi - Dart, 1949.
Brachygnathopithecus peppercorni - Kitching, 1952. (M.631).
Cercopithecoides williamsi - Hopwood and Hollyfield, 1954.

Holotype:

A damaged skull (AD.1326/3) and mandible (M.2038) of an old male. Most of the dentition is present but considerably worn and badly damaged.

Repository of type:

Anatomy Department, University of the Witwatersrand, Johannesburg, South Africa.

Type site:

Abandoned dumps of limeworks at the entrance to Makapan Valley, Transvaal, South Africa.

Referred material:

Five specimens from Makapan, seventeen from Sterkfontein, and one each from Taungs and Cooper's. (For the numbers of these specimens, see tables 20a, b, c and d).

Of these, only one skull is sufficiently complete for a determination of it's sex to be made. ~~The one is the male type specimen from Makapan and the other~~ It is a fairly complete female specimen (STS.394) from Sterkfontein. (Sex determination is mainly based on the canines and P_3 - there dows not appear to be clear sexual dimorphism in the other teeth of this species). There are a number of good specimens of the mandibles of both sexes.

Description: (Figs.112 - 120).

The most notable feature of the skull of both sexes is the extremely short muzzle which, in the male, appears to be even shorter, relative to the overall length of the skull, than in the female. The premaxilla is short and, in the male, because of the large canine eminences, its anterior margin is almost straight and only projects forward slightly. Although the relevant area is damaged in the available specimens of both sexes, the nasal bones also appear to have been relatively rather shorter in the male than in the female and this is the partial reason for there being a much larger nasal aperture in the former sex. On the side of the nasals and nasal aperture, the maxilla slopes down very steeply to the alveolar margin.

The orbits in this species are as large as, and similar in shape and size to, those of the female of P.ursinus but they are separated by an extremely broad inter-orbital area. The female orbit is slightly larger than that of the male - a not unusual situation in the Cercopithecoidea. In the regions below and lateral to the orbit, the zygomatic bone faces almost directly forward. The zygomatico-facial foramen is present at the infra-lateral corner of the orbit, the zygomatico-temporal foramen is on the zygomatico-frontal suture and there are three infra-orbital foramina present a short distance below the centre of the infra-orbital margin. There is a shallow maxillary fossa present below and lateral to the infra-orbital foramina. The zygomatic process of the maxilla, as in most monkeys, is situated rather far forward relative to the teeth - in this species at about the level of M^2.

The supra-orbital tori are badly eroded in the male but appear to have been only slightly thickened. There is a transverse groove running across the skull just posterior to them. In the female, the tori are large and raised above the calvarium roof. Behind them there is a groove similar to that in the male but much larger and deeper. The supra-orbital region was thus considerably different in these two specimens, but the differences are almost certainly due to sexual dimorphism.

Due to the bones of the roof of the calvarium having been lost in the male skull, one cannot be sure whether the temporal lines were marked and if so, whether they joined posteriorly to form a sagittal crest. However, from the endocranial cast which remains, it can be seen that the calvarium was rather flatter dorsally than in *Papio* or *Cercopithecus*. In the female specimen the anterior part of the temporal line is undamaged and forms a prominent thick ridge running from the supra-orbital torus, across the post-orbital constriction of the frontal onto the roof of the calvarium. The line is then damaged and finally can be traced no longer as the posterior portion of the skull is missing. From the angle at which the line runs it would, however, seem probable that the lines from opposite sides met on the posterior part of the calvarium.

The whole base of the male skull is badly damaged but that of the female, anterior to the foramen magnum, is fairly well preserved. Also, there are two ~~other~~ specimens of unknown sex (STS.252 and STS.361) in which this region is preserved. The foramen magnum is large in STS.394A but noticeably smaller in STS.252; the articular condyles appear to be fairly large in both of the above two specimens. The angle at which the basi-occipital and basi-sphenoid lie, can be seen in several specimens and is shallow, as in *Cercopithecus* - not steep as in *Papio*. The external auditory meatus, part of a region considered of taxonomic importance by Broom (1936), can be seen in STS.252 and STS.394A. It runs almost transversely across the base of the skull. STS.252, the only skull in which the relevant area is preserved, does not show a prominent inion - perhaps as it is most likely a female skull. A nuchal crest is present in both the male type skull and the female STS.394A.

The upper dental arcade of the female, STS.394A, is horseshoe-shaped, whereas that in the male type specimen is more nearly rectangular; viewed from the side, the occlusal plane of the male is slightly convex. The teeth in both of these specimens appear to be small when compared to the overall size of the skull but, never-the-less, they give the impression of being crowded. From the few measurements that are available of the upper and lower teeth (tables 20c and d), it seems clear that, except for the canines and P_3, there is no sexual dimorphism in the teeth of this species.

Of the upper incisors, there are only a few fragments present in the male type specimen, but there is also evidence of their size from the empty alveoli in the female STS.394A. From these all that can be concluded is that the teeth appear to have been very small. There are, on the other hand, a number of good specimens of the *C* of both sexes. Of the male, there is M.631, which was previously referred by Kitching (1952) to *Brachygnathopithecus peppercorni*, the broken *C* teeth of the type specimen and the tooth in STS.350, a specimen which was formerly referred to *Parapapio jonesi* by Broom (1940). The *C* in all of these specimens is relatively about as large as that in the male of *P.ursinus*. In both STS.250 and M.631, there is a deep mesial groove present and, in the latter specimen, the tooth is convexly curved buccalward. Of the female *C* there are two specimens, STS.394A and M.666. (The latter specimen is one of a group from Makapan recently found and developed by Mr.J.W. Kitching of the Bernard Price Institute for Palaeontological Research, Johannesburg, and kindly lent to me for description). In both of the above specimens, the tooth is very short in height but the breadth and mesiodistal length are proportionally quite great. The size relationship between the *C* of the male and female, is thus similar to that found between the sexes in *P.ursinus*.

There are several examples of P^3 (not all of which are measurable), and it appears characteristic of this species that this tooth is very small. P^4 is considerably broader than P^3 (STS.350, a male and STS.394A, a female) but neither of these teeth show any unusual morphological features. There are quite a number of specimens of the upper molars (see table 20c) but all are rather worn. In occlusal view, they appear rather square but with a greater mesial than distal breadth; all have large contact facets. M^3 is smaller than M^2 but not as much so as in *Cercopithecus*. From M.665 and M.666, although the breadth of M^1 cannot be measured accurately, it would appear that M^2 was considerably larger than M^1. (The specimens M.665 and M.666 may well come from the same/female individual). Mainly from the less worn

M^3 on STS.252 (a specimen of unknown sex), M.665 and M.666, it appears that the molar cusps were high and the central fossae large and deep. There are large v-shaped inter-cusp clefts on the lingual side, between the protocone and hypocone, of all the molars of STS.392 (a specimen of unknown sex) and STS.394A (a female). In STS.392, there are cingular ridges across the lingual inter-cusp clefts and in STS.394A there is a small lingual accessory cusplet on M^3. The molar roots can be seen on the right side of the type skull and they conform to the pattern described for P.ursinus. The teeth of the female specimen from Taungs (T.15), conform to the above description and match, in size, their equivalents from Makapan and Sterkfontein (table 20c).

Only a few rather damaged specimens of the male and female mandible are known but from these it appears that, except in size, there was very little difference between those of the two sexes. As far as can be judged, it also seems that the mandibles from Makapan, Sterkfontein and Cooper's agreed well in size and morphology.

The symphysis in this species is rather short, ending posteriorly at about the middle of P_3 (LW.7/48, a male). Its anterior surface is typically flattened in all of the specimens in which the region is preserved. On LW.7/48, the sagittal canal running through the symphysis, from the fossa on the posterior surface to the foramen symphseosum on the anterior surface, can be seen. There is no mandibular fossa on the lateral surface of the anterior part of the corpus in either the male, LW.7/48 or the females, STS.394A and CO.116.

The ramus, as seen on the male type specimen and STS.344 (a specimen of unknown sex), is short but broad. It has a large coronoid process which is higher than the condyle and separated from it by a long deep sigmoid notch. The angle between the ramus and the corpus in STS.344 is about 120° i.e. about the same as that in the female of P.ursinus. An interesting feature, and one apparently characteristic of the mandible of this species, is the way in which the anterior margin of the ramus joins the corpus and is continued forward. This meeting takes place well buccalward of M_3 and a shelf (prominentia lateralis) is formed on the upper postero-lateral part of the corpus which continues forward and downward fusing with and broadening the corpus on its lower portion as far as M_2.

The lower dental arcade (eg. LW.7/48 - a male and STS.394B - a female), like the upper shows evidence of crowding. There are large contact facets between adjacent teeth and P_4 lies obliquely across the tooth row as if to save mesio-distal space. The two sides of the tooth row converge only very slightly.

The only lower incisors known are in the female specimen M.665B and are very small teeth. The lower canine of the male, as judged by its damaged remains in the type mandible and the alveoli in LW.7/48 and STS.366 would seem to have been a large tooth. Its size in the female can be seen in STS.394B and M.665B and is small. The $\overline{C}$ thus confirms the size relationship of the canine of the two sexes seen in the upper jaw.

The occlusal surface of the male P_3 in LW.7/48 has a fairly deep anterior fovea, followed by an exceptionally large posterior fovea. This latter fovea is incompletely divided by a well developed ridge of enamel which runs disto-lingually from the very high buccal cusp to meet a weaker ridge incompletely marking off the disto-lingual corner of this tooth. Another male specimen, STS.366, also shows the large size of the posterior fovea and a trace of the weak ridge across the disto-lingual corner. The female examples of this tooth are rather worn and damaged but STS.394B shows traces of a similar arrangement to that in the males. As in the other Cercopithecoidea in this study, the mesial portion of P_3 is considerably elongated in the male but rather less so in the female (see table 20d). In both sexes this extension has a wear facet for the upper canine. On P_4 there is a small deep anterior fovea in both the male and the female but the posterior fovea cannot be made out clearly in any of the specimens as there is a deep transverse wear facet (caused by P^4) across the distal part of all of the available specimens. The tooth leans distally in both sexes.

There are quite a number of specimens from which to describe the lower molars of this species (see table 20d). The usual four cusps are present on M_1 and M_2, and M_3 has in addition, a small but definite hypoconulid behind the distal pair of cusps. The cusps on all three of the molars are very high and, at least when worn, the mesial surface slopes rather more acutely than the distal. The central fossae are large and deep, and there are particularly big v-shaped buccal inter-cusp clefts. The lower molars thus show a similar structure to that found in the upper but the cusp heights, central fossa depths and inter-cusp cleft sizes all appear to be greater. This structure has resulted in a very characteristic appearance of worn lower molars. The lingual cusps stand up very high (the buccal ones having been worn down), and the deep fossae and clefts between the mesial and distal pairs of cusps seem to divide each tooth particularly sharply into two parts. When viewed from the side, the molar cusps appear to lean forward because of the mesial surfaces being steeper than the distal.

Measurements:

See tables 20a, b,c and d.

Remarks:

The upper and lower teeth of the type specimen are very considerably worn and damaged and it is impossible to measure these teeth accurately or to see any details of their structure. Fortunately however, the crowding and shortness of both the upper and lower tooth rows can be seen, and also the small size of P^3 and the characteristic lateral ridge on the posterior part of the corpus of the mandible. These features clearly link the new material with the type specimen.

When grouped under their sites, there would appear to be certain small size differences between the lower teeth of the specimens from Makapan and Sterkfontein e.g. the length of M_1 and the distal breadth of M_3. There is at present too little material to check statistically whether these slight differences are taxonomically significant but they would appear to be only

Table 20a. Measurements of the skull of *Cercopithecoides williamsi*.

	Male	Female	? Sex
	AD.1326-3	STS.394A	STS.252
GENERAL.			
Greatest length	154		
Basal length	101	87	
Bizygomatic breadth	108		
CALVARIUM.			
Height:			
Basion-bregma	61		
Basion-glabella	78	71	
Breadth:			
Min. inter-frontal	53	(50)	
Greatest temporal	75		72
Length:			
Inion-glabella	111		
Inion-basion	54		42
Foramen magnum:			
Breadth		17.5	16.2
Length		20	19.2
MUZZLE.			
Height:			
Post. to M^3	68		
Ant. to P^3	26	16	
Breadth:			
Ant. to M^3	43	41	
Ant. to P^3	37	32	
Length:			
Muzzle	69	53	
Palate	56		
Nasal	21		
Orbit:			
Inter-orbital	15	15	
External orbital	82	(80)	
Height	24	26.7	
Breadth	27	26.4	
Nasal aperture:			
Breadth	20		
Length	39		

Table 20b. Measurements of the mandible of *Cercopithecoides williamsi.*

	Male	Female	? Sex
	LW.7/48	STS.394B	SBS.344
Height:			
Gonion-condyle			46
Gonion-coracoid			54
Post. to M_3		23	30
Ant. to P_4	24	20	
Mental sp. to most ant. point.	28	(25)	
Breadth:			
Ant. to M_3	42	(45)	
Ant. to P_4	29	30	
At base of canines	23	22	
Length:			
Gonion to mental sp.		47	
Ramus at condyle neck			31
Angles:			
Ramus to corpus		126°	123°
At symphysis	(105°)		
Between corpora	45°		

Table 20c. Measurements of the upper teeth of *Cercopithecoides williamsi*.

	$\underline{C}$				P^3		P^4		M^1			M^2			M^3			Rows.	
	h	b	l_1	l_2	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	$P^4 - M^3$	$\underline{C} - M^3$
MALE:																			
AD.1326/3																		(31)	(45)
STS.350	26.3	7.2	9.0	11.0	6.4		8.2	5.8			(8.2)								
STS.347															9.5		9.1	(31.7)	
M.631	(32)	8.0	7.8	12.3															
FEMALE:																			
STS.394A	(12.0)	7.8		(5.8)	6.0	5.7	7.6	5.2			(7.8)			9.4			(9.3)	(32)	(45)
M.666 *											8.5			9.4			9.0	31.5	
M.665A *											8.5			9.9			9.0	31.6	
T.15											8.1	(9.0)		9.0		7.7	8.9	(30.8)	
? SEX:																			
STS.392											8.9	10.0	9.1	9.8	9.1	8.2	9.5		
STS.252												10.2	8.8	9.5	9.1	7.3	8.7		
STS.341													9.0				9.1		

* Possibly from the same individual.

Table 20d. Measurements of the lower teeth of *Cercopithecoides williamsi*.

	$\bar{C}$			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	$P_4 - M_3$	$\bar{C} - M_3$
MALE:																			
M.2058																		(37)	
LW.7/48				5.7	15.2	5.6	7.0	6.5	7.5	8.7	7.9	8.5	9.5	8.1	8.8	5.5	11.7	35.7	
STS.366				5.2	15.5	5.4	6.6	6.6	7.0	7.7	(7.6)	(7.8)	8.5	7.7	7.8	5.8	11.5	34.5	
STS.300								6.2	6.4	8.1	6.8	6.8	8.7						
FEMALE:																			
STS.394B		(6.5)	(4.6)	5.1	10.4	5.2	6.5	7.4	7.3	8.0	8.3	8.6	9.1	8.5	8.2	5.5	12.4	36.0	49.1
STS.552				4.1	9.8										7.6	3.6	10.9	34.5	
CO.116		6.5	4.0	5.3	7.9	5.5	7.0						(9.0)				(12.0)	35.5	49.5
? SEX:																			
M.622						5.5	6.9	6.6	7.2	8.4	7.9	8.3	9.5	8.1	8.6	5.0	12.0	35.8	
STS.518											8.0	7.8	9.5						
STS.344											8.2	8.4	9.6	8.3	8.2	5.0	11.7		
STS.288													8.8	8.0	7.1	4.5	11.6		
STS.279											7.9	8.0	9.0	7.9	7.8	5.0	11.2		
STS.516															7.6		12.0		
STS.525											7.4	7.5	9.0						
STS.290 *								6.4	6.5	8.1	5.9	dm_2 5.7	7.7						

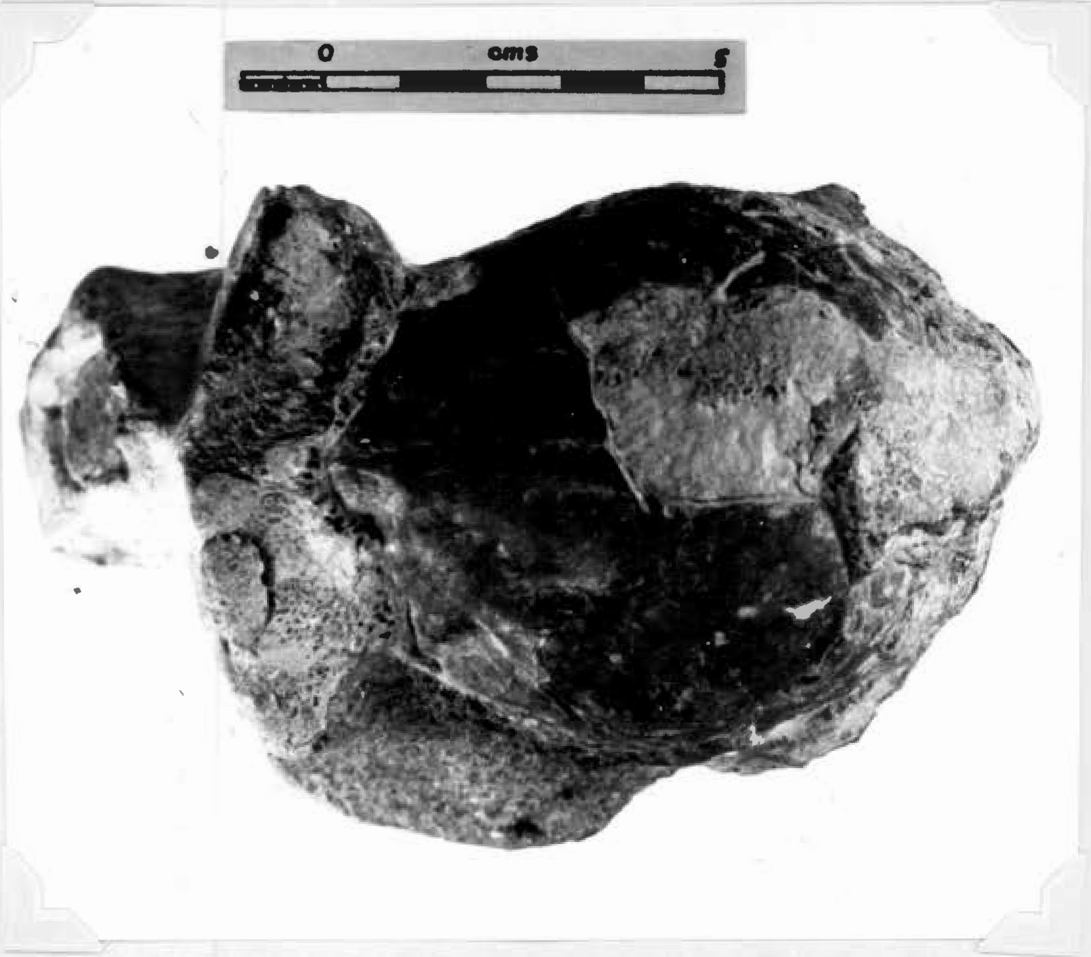

Fig.112. Cercopithecoides williamsi male (AD.1238/3). Skull- dorsal view, x 1.

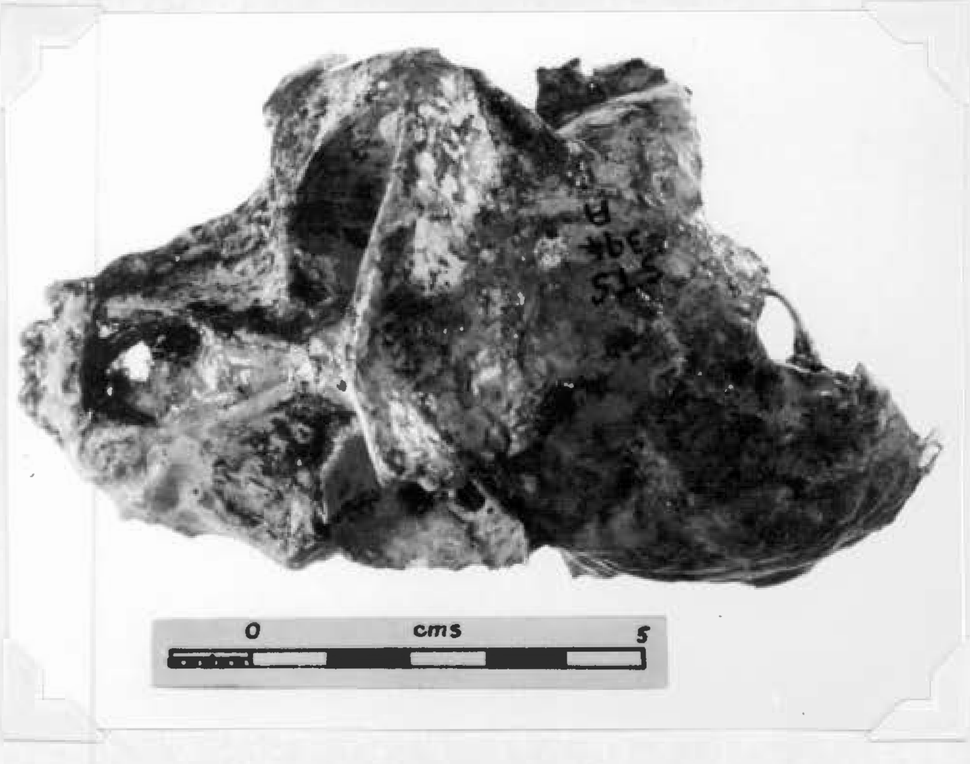

Fig.113. Cercopithecoides williamsi female (STS.394A). Skull- dorsal view. x 1.

Fig.114. *Cercopithecoides williamsi* male (AD.1238/3). Lateral view of the skull and mandibular ramus. x 1.

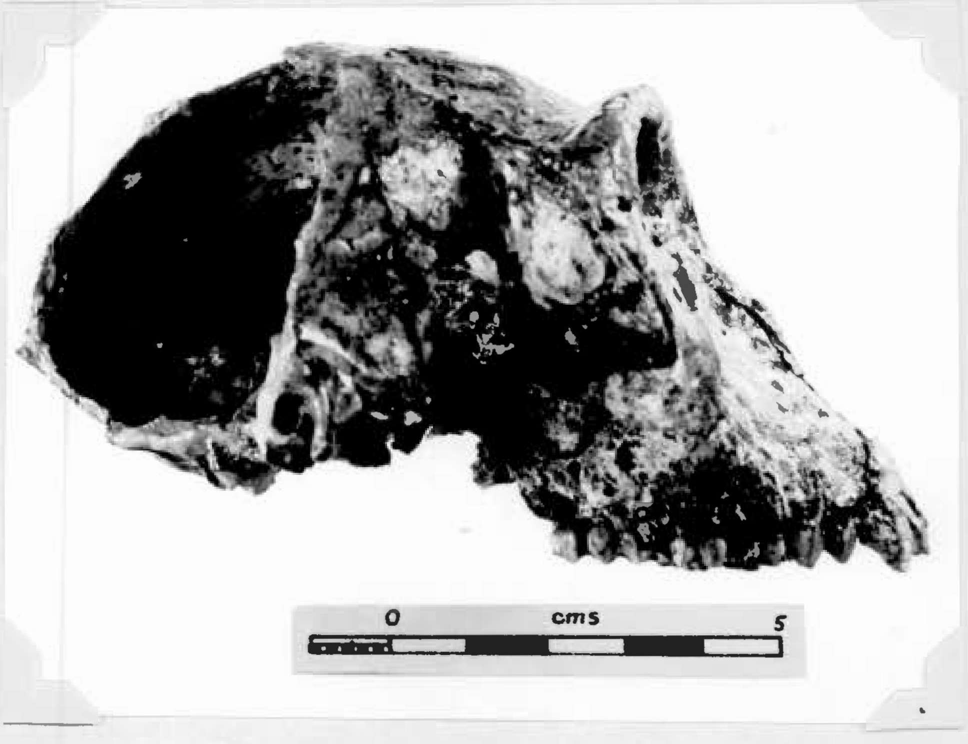

Fig.115. *Cercopithecoides williamsi* female (STS394A). Skull - lateral view x 1.

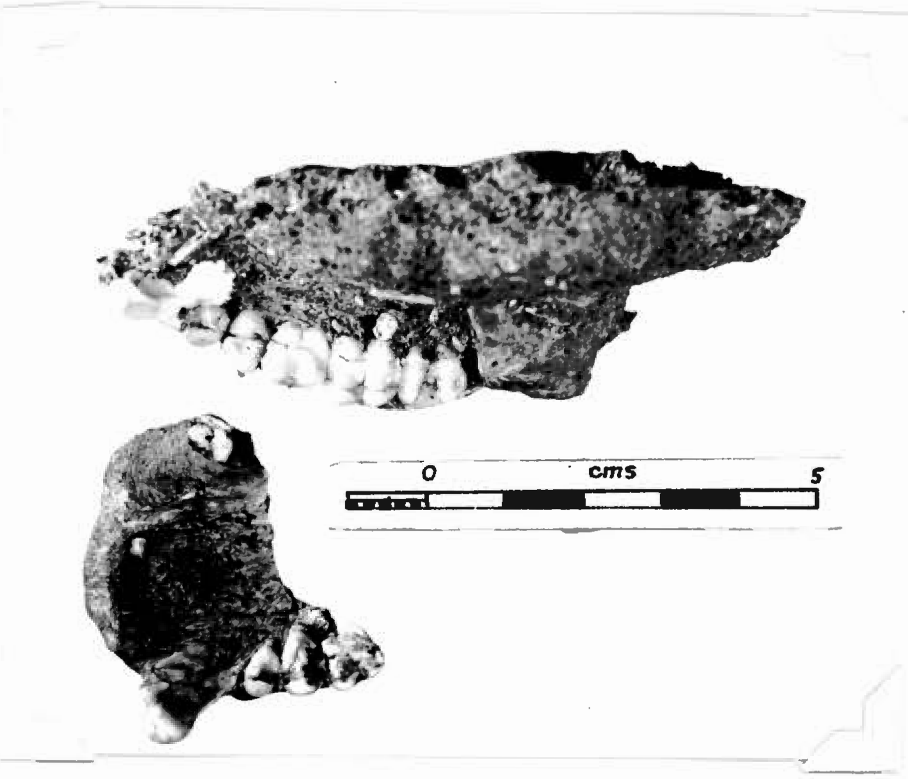

Fig.116. *Cercopithecoides williamsi* male (STS.350) below, and female (M.666) above. Occlusal view of upper teeth. x 1.

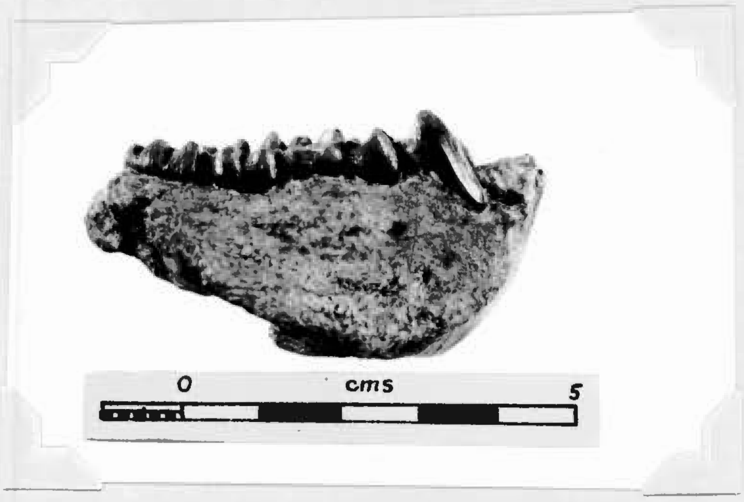

Fig.117. *Cercopithecoides williamsi* male (LW.7/48). Lateral view of mandibular fragment and lower teeth. x 1.

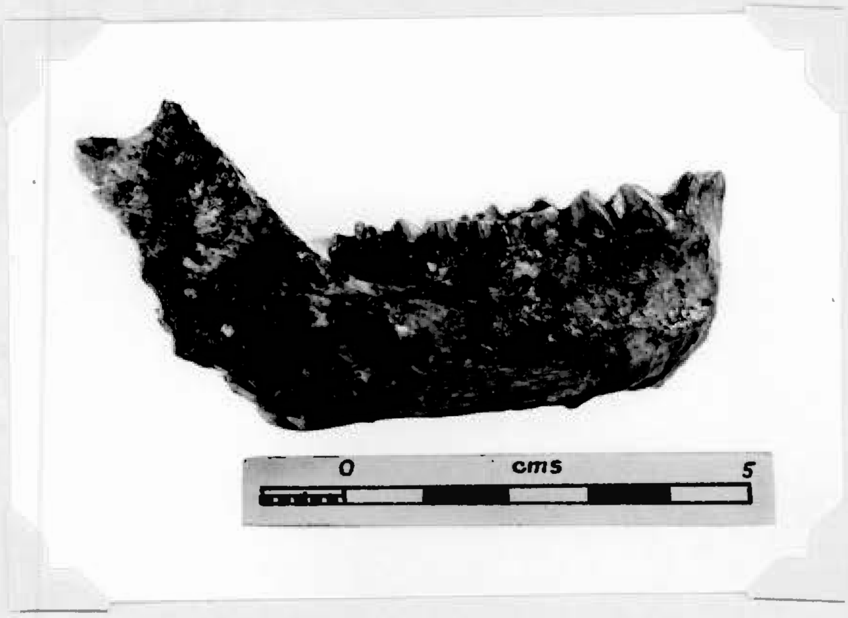

Fig.118. *Cercopithecoides williamsi* female (STS.394B). Lateral view of mandible and lower teeth. x 1.

Fig.119. *Cercopithecoides williamsi* male (LX.7/48). Occlusal view of lower teeth. x 1.

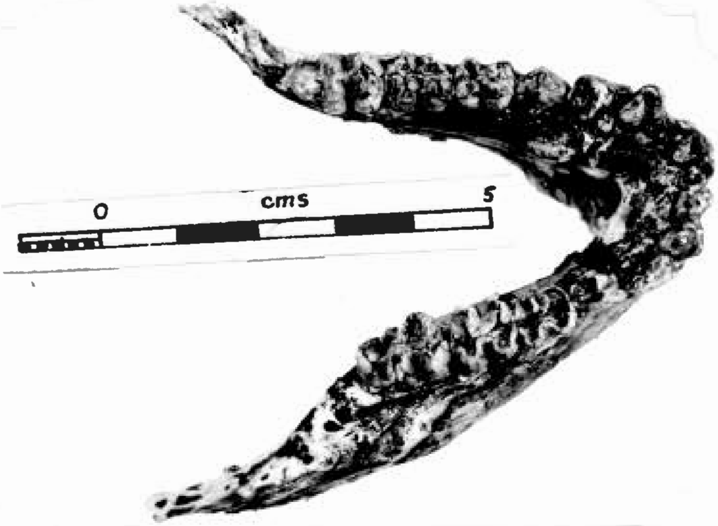

Fig.120. *Cercopithecoides williamsi* female (STS.394B). Occlusal view of lower teeth. x 1.

minor intra-specific population variations due to slight geological and time separation.

The one specimen from Cooper's (a mandible, CO.116) appears to be identical to those from Makapan and Sterkfontein but the teeth show a quite exceptional amount of wear. For example, the whole crown of M_1 has been worn away bilaterally and only the tops of the roots remain. This excessive wear obscures any possibly minor differences in tooth pattern or size which may have existed between it and the specimens from Sterkfontein and Makapan.

Partially embedded in the matrix on the inner surface of the right ramus of the type skull, is a first cervical vertebra (atlas). It is badly damaged but would seem, on size, to belong to this species - and probably to the type skull itself. It shows no unusual features. The first, and part of the second cervical vertebrae were also found with the skull STS.394A. These are also rather damaged but similarly appear to be in no way unusual.

<u>Cercopithecoides</u> <u>molletti</u> sp. nov.

Semnopithecine monkey - Robinson, 1952.
Semnopithecine monkey - Oakley, 1954a.
<u>Semnopithecus</u> - Oakley, 1954b.

Holotype:

A palate with teeth of an adult male (SK.551).

Repository of type:

Division of Vertebrate Palaeontology and Physical Anthropology, Transvaal Museum, Pretoria, South Africa.

Type site:

Swartkrans, Transvaal, South Africa.

Referred material:

Four specimens from Swartkrans, two from Swartkrans II and one from Graveyard.

SK.552 is a left maxillary fragment of a specimen of unknown sex with all the left molars present but considerably worn. Other than the type, this is the only known skull fragment.

Of the mandible there are six specimens, one male (GY.1), two female (SK.412 and SK.624) and three of unknown sex (SK.579, SKII.28B and SKII.29). In only SK.412 can much of the structure of the mandible be seen.

Description: (Figs. 121 - 124).

From the male type specimen SK.551 and the specimen of unknown sex, SK.552, the position of the zygomatic process of the maxilla can be seen. It lies between the distal part of M^1 and the distal part of M^2 i.e. in about the same position as in C.williamsi. From the very small piece of the premaxilla present on the type specimen, it would seem that this bone was also rather flat anteriorly as in the male of C.williamsi. These are the only skull characters which can be described from the available material and the rest of the evidence for placing these specimens in this genus and separating them specifically from C.williamsi is derived from the examination of the upper and lower dentition and mandible.

The teeth of the male upper dental arcade (SK.551) exhibit the same cramping and squarish shape described in the previous species. This specimen also shows a feature not mentioned previously but which occurs in a slightly less marked degree in C.williamsi as well. In looking at the dental arcade from the occlusal view, the buccal surfaces of M^1, M^2 and M^3 form a more or less smooth curve (somewhat more convex outwards in this species than in C.williamsi). There is then a definite step inward to P^4 which forms a fairly smooth and almost straight line with P^3 and C. Sufficient suitable material is at present not known of either the upper or lower dentition but it would appear (tables 21c and d) that, like in C.williamsi, except in the canines and P_3, there was no sexual dimorphism in the teeth of this species.

The male C and upper premolars do not appear to differ in morphology or size from those of C.williamsi. P^3 is again a particularly small tooth and the large male C has a large lingual facet resulting from contact with P_3. On the upper molars, in both SK.551 and SK.552, the wide v-shaped inter-cusp clefts on the lingual suffaces are very large and the small cingular ridges across the lower margins of these clefts rather prominent. On M^3 this ridge projects upwards as two small cusplets in both specimens. In SK.551 the right M^3 has a small subsidiary cuspule on its distal portion behind the hypocone and metacone. An important difference from *C.williamsi* is the fact that in all the upper molars of this species there are fairly prominent inter-cusp clefts on the buccal surfaces with small cingular ridges across their lower margins. Other than on these points, the upper molars agree very closely with those of *C.williamsi* except for the larger size of M^3 in SK.551 and all the molars in SK.552 (see table 21c).

The only fairly complete mandible known is that of specimen SK.412 which, by its P_3 and $\bar{C}$ alveolus, is clearly that of a female. The rami are missing and the teeth are badly damaged but the two corpora and the symphysis are well preserved and agree closely with those of *C.williamsi*. The lateral ridge on the posterior part of the corpus (prominentia lateralis) and the flat anterior surface of the symphysis are the same as those described in *C.williamsi*. The foramen symphyseosum is present on the anterior surface of the symphysis and is linked to the foramen in the fossa on the posterior surface. The symphysis itself reaches to the middle of P_3 and there is very slight hollowing on the lateral surface of the corpus in the position of the mandibular fossa. The male specimen from Graveyard (GY.1) also shows the typical flat anterior surface of the symphysis and, in addition, two foramina in the position of the foramen symphyseosum. The symphysis of this specimen (probably because it is a male) seems to be rather broader than that in the female SK.412. Specimen SK.579 (of unknown sex) has a portion of the prominentia lateralis present. The few mandible (and skull) measurements available are all about the same as those of *C.williamsi* (tables 20a and b).

The lower teeth of this species, although mostly worn and damaged, appear to agree well with the basic structure described for their equivalents in *C.williamsi*. From the incisor alveoli in GY.1 (a male) and SK.412 (a female), the small size of these teeth is apparant. The female $\overline{C}$ in SK.624 is too badly damaged to show any structure but it is clearly a very small tooth; the alveolus of the male $\overline{C}$ in GY.1 is that of a large tooth. What little can be seen of the lower premolars (SK.412, SK.624 and GY.1) appears to be the same as that described for C.williamsi. (The P_3 specimens are too worn to show whether the occlusal surface had the same arrangement as was seen in that species). Morphologically, the lower molars are also very similar to those of C.williamsi but, as do the upper, they show the characteristic features of the genus (high cusps, large central fossae and wide, buccal inter-cusp clefts) in an accentuated form. The steeper slope of the mesial surfacesof the worn cusps, as compared to the distal, can be clearly seen. In size, M_2 of SK.412, SKII.29 and SK.579, are larger, particularly in length, than their equivalents in C.williamsi (compare tables 20d and 21d). The molars of the two specimens from Swartkrans II (SKII.28B and SKII.29), as far as can be seen, seem to fit into this species both in size (table 21d) and morphology.

Measurements:

See tables 21a, b, c and d.

Remarks:

This species has in common with C.williamsi the main features of the dental morphology which constitute the diagnostic characters of the genus Cercopithecoides. However, there are certain details of dental structure in which they differ e.g. the presence of buccal inter-cusp clefts with cingular ridges on the upper molars of C.molletti only and the more accentuated form of various dental characters in both the upper and lower molars of this same species. Furthermore, there are significant size differences in the dimensions of the upper and lower molars of the two species. For example: The mean length of M^3 of C.williamsi is 9.1 mm. with a standard deviation of 0.25 (based on eight specimens). The two equivalent lengths of C.molletti known are 10.8 mm. and 11.0 mm. Mayr, Linsley and Usinger (1953) state that "M ± 3S.D. includes

Table 21a. Measurements of the skull of *Cercopithecoides molletti*.

	Male
	SK.551
MUZZLE.	
Breadth:	
Ant. to M^3	41
Ant. to P^3	(35)

Table 21b. Measurements of the mandible of *Cercopithecoides molletti*.

	Female
	SK.412
Height:	
Ant. to P_4	21
Mental sp. to most ant. point	24
Breadth:	
Ant. to M_3	46
Ant. to P_4	30
Through mental sp.	22
At base of canines	20
Angles:	
At symphysis	117°
Between corpora	39°

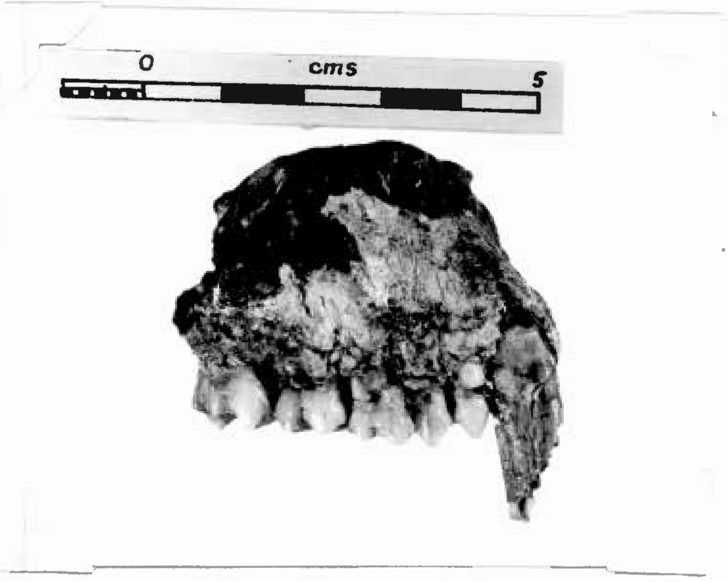

Fig.121. *Cercopithecoides molletti* male (SK.551). Lateral view of maxillary fragment and upper teeth. x1.

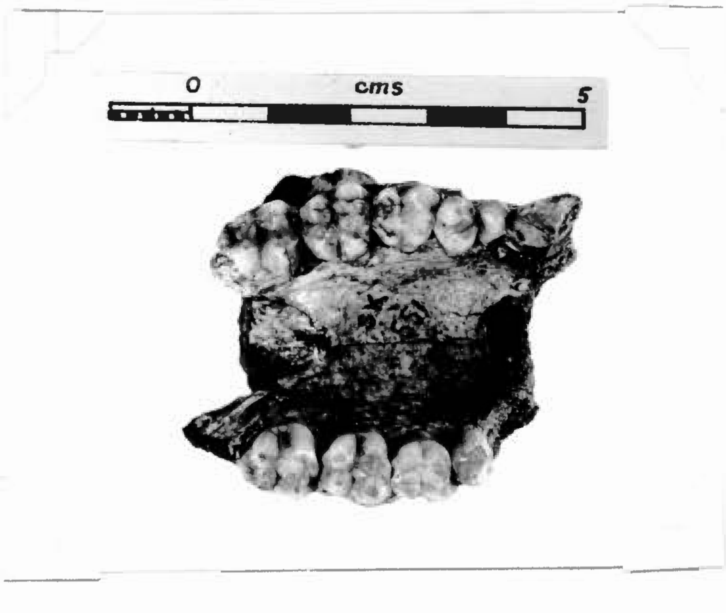

Fig.122. *Cercopithecoides molletti* male (SK.551). Occlusal view of upper teeth. x1.

Fig.123. *Cercopithecoides mollotti* female (SK.412) above, and ?sex (SK.579) below. Lateral view of mandibular fragments and lower teeth. x1.

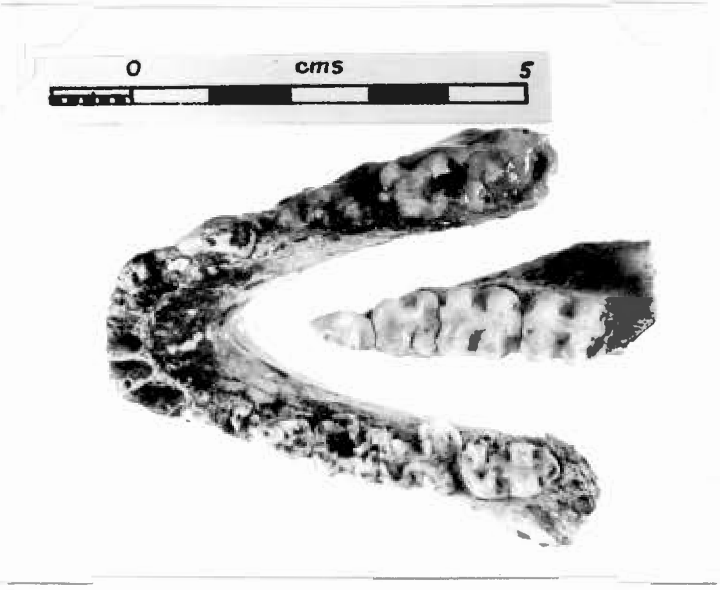

Fig.124. *Cercopithecoides molletti* female (SK.412). Occlusal view of mandible. In centre, specimen of unknown sex (SK.579). Occlusal view of lower teeth. Both x1.

99.73 per cent of the population". Both specimens of *C.molletti* are over seven times the standard deviation greater than the mean for *C.williamsi*. Because of the small number of measurements available of *C.molletti*, Student's t test could not be applied but instead, d/σ (Simpson and Roe, 1939) has been used. According to these authors, when comparing one specimen with a population, any value of d/σ greater than 2.5 is "usually significant" and any value greater than 3 is "almost always significant" in indicating that the specimen does not come from the given population. The value of d/σ obtained when comparing the two *C.molletti* M^3 lengths with those of the statistically estimated population of *C.williamsi* is 7.347.

No differences in size or morphology were found between the teeth of the various subspecies of *P.ursinus* (Chapter 5) nor were any significant differences found in these characters between specimens from different sites in any of the fossil species described in this study. It would therefore seem quite clear that the differences between *C.williamsi* and *C.molletti* merit their specific separation. (The few measurements available of the skull and mandible are about the same in both species but the known specimens of *C.molletti* are too few and fragmentary for one to draw any definite conclusions).

Robinson (1952) suggested semnopithecine affinities for the Swartkrans monkey. Subsequently, Oakley (1954b) referred to *Semnopithecus* from that site. From the material now available, this species clearly belongs in the genus *Cercopithecoides* but the exact affinities of that genus are at present not quite clear.

CHAPTER 13.

SPECIES OF UNKNOWN AFFINITIES.

'*Parapapio*' *coronatus* Broom and Robinson.

Parapapio coronatus - Broom and Robinson, 1950.
Parapapio coronatus - Hopwood and Hollyfield, 1954.

Holotype:

A well preserved calvarium, with the face and upper dental arcade missing (KA.195).

Repository of type:

Division of Vertebrate Palaeontology and Physical Anthropology, Transvaal Museum, Pretoria, South Africa.

Type site:

Kromdraai, Transvaal, South Africa. In a surface pocket in the breccia deposit from which the specimens of the ape-man, *Paranthropus robustus robustus* were recovered. This pocket was mainly composed of completely unconsolidated wind-blown dust and humus and is probably of much more recent origin than the breccia deposit below it. The specimens are clearly only subfossil and Broom and Robinson suggest that they date from the Upper Pleistocene.

Referred material:

Two mandible fragments, KA.196 and KA.197, from the same pocket as the type.

Description: (Figs 125 - 129).

The type specimen (KA.195) consists of an almost perfect calvarium only; the whole of the anterior part of the skull in front of a plane running through the nasion dorsally and two points just anterior to the articular tubercles on the zygomatic arches ventro-laterally, is missing. In size this specimen is about intermediate between the male and female of *P.ursinus* but in morphology it differs from that species very considerably. In their original description of this species (1950), Broom and Robinson suggest that the type calvarium is that of a male but, in the absence of the muzzle and teeth, the evidence for this suggestion is conflicting and it would seem preferable to leave the question of sex in obeyance until more material becomes available. The open sutures suggest that the calvarium is that of a young individual but this criterion of age was not found completely reliable in the P.ursinus study.

One of the most interesting features of this calvarium is the unusual shape of the supra-orbital tori. They are not particularly heavily built but when viewed from above, it can be seen that they project forward very far in the midline, and even towards the lateral ends the forward development is far greater than in the chacma baboon. The frontals sweep up to the supra-orbital tori and a broad, distinct trough is formed transversely across the calvarium which marks off the tori from the rest of the roof of the calvarium. This shape of supra-orbital torus is similar to that seen in Cercopithecoides williamsi Gorgopithecus major and Theropithecus gelada but in none of these species is the development as great, particularly in the midline, as in this baboon. The inter-orbital constriction is extremely wide and the orbit itself very broad; these features are probably both related to the great forward development of the supra-orbital tori.

The temporal lines start on either end of the supra-orbital tori. As they cross the post-orbital constriction of the frontal and until they reach the sagittal suture, they converge and take the form of well marked, prominent, bony ridges. From this suture backwards, the lines are very weak and they run posteriorly over the parietals more or less parallel to one another but converging slightly until just before they reach the lambdoid suture. Here they start diverging slightly and the two lines finally join the nuchal crest separately, each some 14 mm. lateral to the inion.

Because of the great development of the tori, the frontal bone is relatively longer than in the chacma baboon. The central portion of this bone takes the form of a large, rounded dome bounded by the trough behind the supra-orbital tori anteriorly, the temporal lines laterally and a slight transverse depression just anterior to the sagittal suture posteriorly. At the posterior end of the calvarium, there is a quite large nuchal crest. It runs from the fairly well developed mastoid regions on either side to what must have been a rather large inion in the centre. (The inion has been slightly damaged during fossilisation). More of the occipital bone lies above the nuchal crest than in <u>P.ursinus</u>.

On the lateral sides of the calvarium, the parietal makes contact with the sphenoid for about 2 mm. on the right side and for about 4 mm. on the left. Direct external contact between these two bones was never found in any of the <u>P.ursinus</u> specimens examined. Viewed from the side it is also seen that the external auditory meatus is ovoid in cross section and that its axis leans forward at an angle of about 45° to the vertical. The post glenoid process is large and lies close up against the external auditory meatus.

On the base of the calvarium the whole planum nuchalae is rough and ridged and the median nuchal line is prominent. The foramen magnum is slightly oval transversely, in contradistiction to that of <u>P.ursinus</u> in which the antero-posterior axis is always longer. The lateral part of the articular tubercle on the zygomatic arch is fairly large and the glenoid fossa well defined. The external auditory meatus runs almost transversely across the base of the skull. Broom (1936) and Broom and Robinson (1950) have dealt at length with the shape and relationship of the external auditory meatus and surrounding structures in several cercopithecoid species and they consider this region taxonomically important. The arrangement of this area, and indeed that of the whole calvarium of this species, is clearly different to that of any cercopithecoid dealt with in this work.

Of the two mandibular fragments found in the same pocket as the type calvarium, KA.197 consists of a small portion of the ramus and corpus from the right side with M_2 and M_3 in place and KA.196 is part of a left corpus with P_3 - M_2 still in position. The teeth of KA.196 are rather badly worn but those of KA.197 are much less worn and rather better preserved. The P_3 of KA.196 is of the female type and as the M_2 on this specimen is slightly larger than that of KA.197 (see table 22b), it would seem that this specimen may also be of a female - but this is by no means certain. Because of the different degree of wear, it seems clear that these two mandibular fragments are not from the same individual.

Very little can be seen of the structure of the mandible from the above two fragments . From KA.197 the region where the anterior margin of the ramus meets the corpus can be described. It is very similar to that in the female of P.ursinus but it appears as if the ramus may have been slightly more vertical. There is a rather broad shelf lateral to M_3 and behind this tooth there is about 1 cm. of free alveolar margin. In KA.196, there does not appear to have been a maxillary fossa.

On KA.196, P_3 is seen to be a broad tooth with a rather short mesio-buccal extention and fairly large anterior fovea; P_4 is a large tooth in both length and breadth. The molars on both this specimen and KA.197 have a typical Papio - Parapapio molar morphology and M_3 of KA.197 has a large subsidiary cuspule between the entoconid and the hypoconulid. In size, these teeth could belong in either the genus Parapapio or Papio but they do not actually match any species in either quite exactly. As the specimens are probably only subfossil and of comparatively recent origin, a relationship with Papio would seem more likely.

Measurements:

See tables 22a and b.

Remarks:

Broom and Robinson (1950) at the end of their description

Table 22a. Measurements of the skull of '*Parapapio*' *coronatus*.

	? Sex
	KA.195
CALVARIUM.	
Height:	
Basion-bregma	66
Basion-glabella	88
Breadth:	
Min. inter-frontal	56
Greatest temporal	80
Mastoid	84
Length:	
Inion-glabella	112
Inion-basion	50
Foramen magnum:	
Breadth	18.4
Length	17.3
Orbit:	
Inter-orbital	17.6
External orbital	83
Breadth	28.5

Table 22b. Measurements of the lower teeth of '*Parapapio*' *coronatus*.

	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
MALE:														
Nil														
FEMALE:														
KA.196	5.5	10.2	7.6	8.1	8.4	8.2	9.9	10.5	9.4	12.0				
? SEX:														
KA.197								9.7	9.4	11.4	10.0	8.7	6.5	15.6

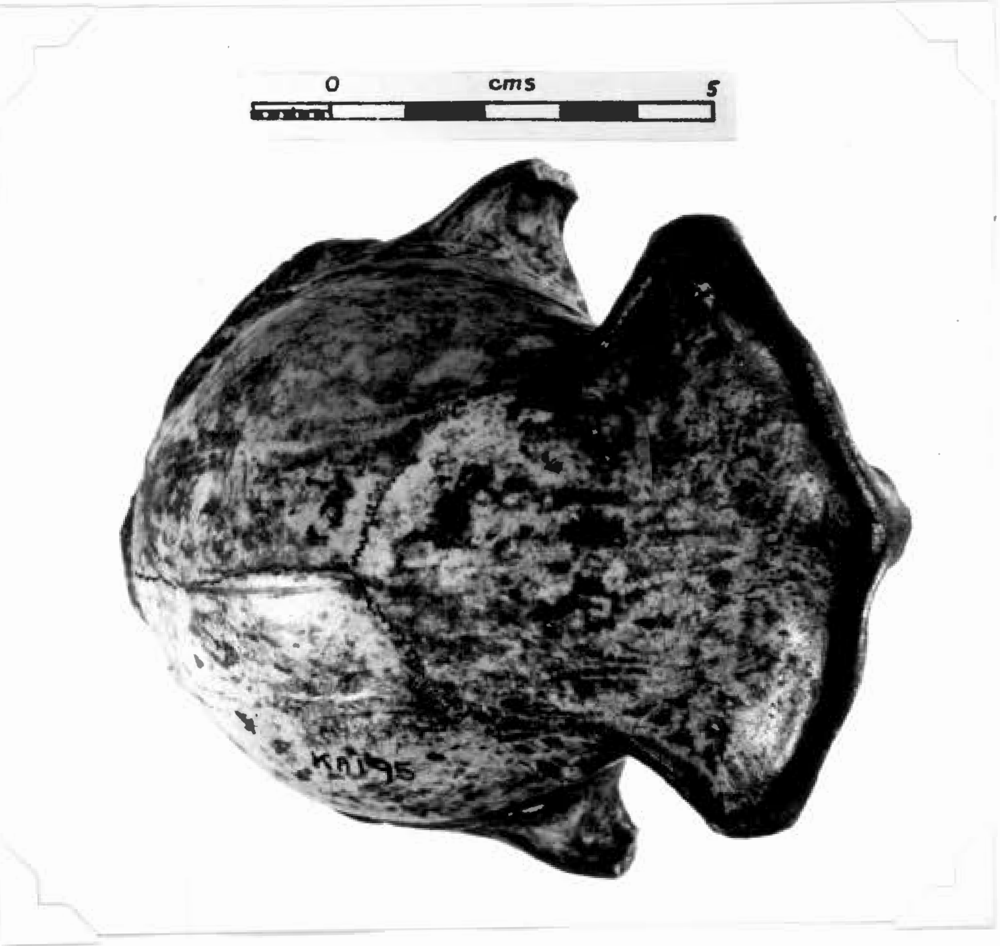

Fig.125. '*Parapapio*' *coronatus* ? sex (KA.195). Calvarium - dorsal view. x 1.

Fig.126. '*Parapapio*' *coronatus* ? sex (KA.195). Calvarium - norma later[redacted] . x 1.

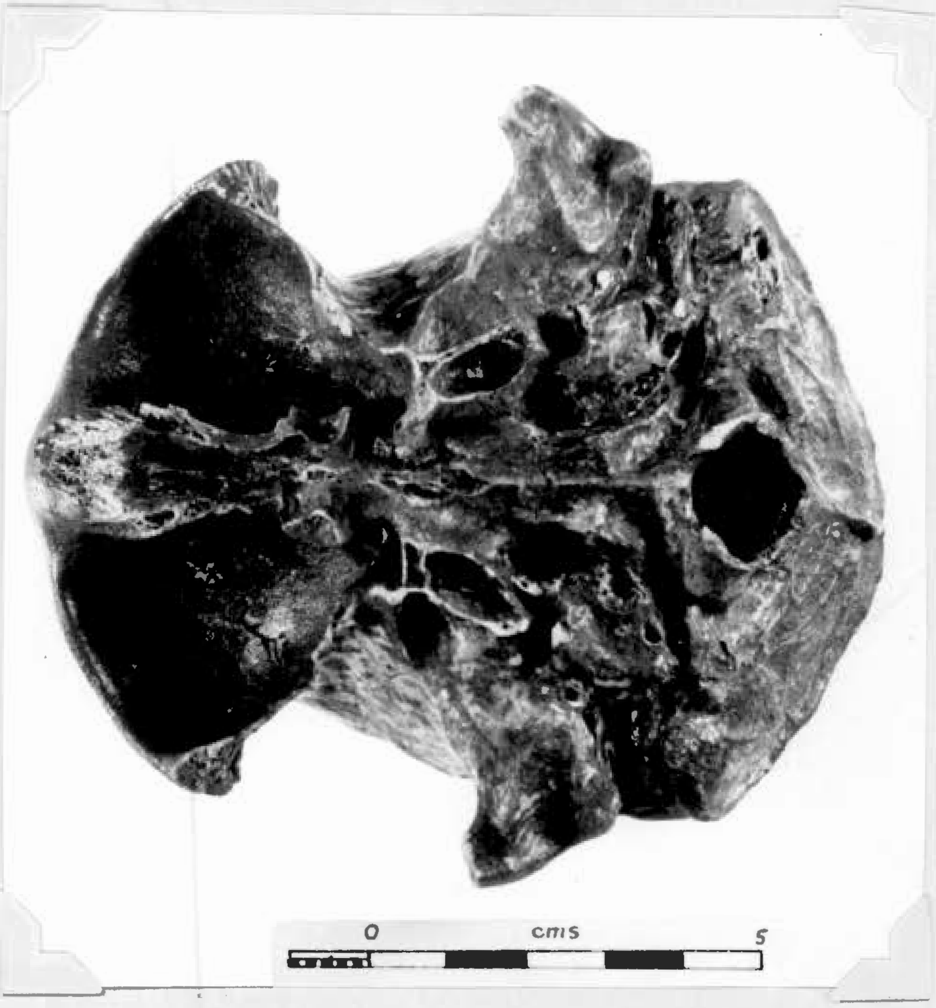

Fig. 127. 'Parapapio' coronatus ? sex (KA.195). Calvarium - basal view. x 1.

Fig.128. '*Parapapio*' *coronatus* female (KA.196) above and ? sex (KA.197) below. Lateral view of mandibular fragments and lower teeth. x 1.

Fig.129. '*Parapapio*' *coronatus* female (KA.196) above and ? sex (KA.197) below. Occlusal view of lower teeth. x 1.

suggest that when a complete skull is found, this species will have to be referred to a new genus. Unfortunately, no new material has been found in the interim, but the wealth of new material of the other South African fossil Cercopithecoidea, has made it possible to describe those forms in greater detail. It is now clear that the type calvarium of this species is quite different to that of any other cercopithecoid hitherto described from South Africa, although it does show some resemblance to species of the genera *Cercopithecoides*, *Gorgopithecus* and *Theropithecus*.

At the time of their original description, the mandibular fragments found with this calvarium seemed quite clearly to belong in *Parapapio*. It now seems more probable that they belong in *Papio* but they could also belong in a third quite different genus. Except that they were found in the same pocket as the type calvarium, there is no evidence which positively links them with that specimen.

There is thus doubt as to which genus the mandibular fragments belong and also uncertainty as to whether or not they belong in the same species as the calvarium, which itself suggests either a new genus or one of three known genera (see above). The wisest course would appear to be to consider these specimens as of uncertain affinities until further material becomes available.

PART III.

SOUTH AFRICAN QUATERNARY CERCOPITHECOID PHYLOGENY.

CHAPTER 14.

DISCUSSION.

The consensus of opinion today is that the three superfamilies of the suborder Anthropoidea (see Appendix I) - the Ceboidea, the Cercopithecoidea and the Hominoidea - each took separate origin from an early (probably Eocene) prosimian (Simpson, 1949a). While the Ceboidea originated and developed separately in South America, the other two superfamilies evolved together in the Old World. The Ceboidea have a different dental formula and also differ considerably in a number of other ways from the Old World forms and they need not be considered further in this study.

There is little direct evidence on the origin and early development of the Cercopithecoidea and Hominoidea and it was at first thought that they had a common origin from a prosimian ancestor. A small fossil form, *Parapithecus fraasi* Schlosser, 1911, of which a single mandible is known from the Lower Oligocene of the Fayum, Egypt, was considered to have been on this common stem (Gregory, 1920b). Current opinion (e.g. Le Gros Clark, 1954) now regards this species as a primitive pongid and the separate origin of the two groups is, at present, the accepted theory.

There is no direct fossil evidence which links the Prosimii and the Cercopithecoidea although Le Gros Clark (1949) considers that the prosimian genus *Amphipithecus* may represent a stage "leading to the establishment of the catarrhine dental formula". Bilophodont molars are one of the most characteristic features of the Cercopithecoidea and it is therefore of interest that some of the Archaeolemuridae, an extinct family of Madagascar lemurs, developed bilophodont upper molars (Gregory, 1920a). The same genus also developed a short face and expanded brain case, but, as Gregory notes, "their true status as lemurs is revealed by their retention of many highly significant lemuroid features in the skull and skeleton". The cercopithecoid-like features of these lemurs were almost certainly only parallel developments and the precise prosimian group from which the Cercopithecoidea arose is at present not known.

The superfamily Cercopithecoidea has only one family, the Cercopithecidae, with two subfamilies, the Cercopithecinae and the Colobinae. Three of the earliest forms which show reasonably definite cercopithecoid features are Apidium phiomensis Osborn, 1908, Moeripithecus markgrafi Schlosser, 1911, and Oreopithecus bambolii Gervais, 1892. Apidium is known from a lower jaw fragment from the Lower Oligocene of the Fayum, Egypt, Moeripithecus also from a lower jaw fragment from the Lower Oligocene of the Fayum, Egypt and Oreopithecus from specimens from the Lower Pliocene of Italy and Bessarabia. Two recent studies, one by Remane (1951) on Apidium and Oreopithecus and the other by Le Gros Clark (1949) in which he deals with Apidium and Moeripithecus, have shown that the above three species clearly show incipient stages in the evolution of the true cercopithecoid bilophodont molar. These three genera are all listed by Simpson (1945) as belonging in the family Cercopithecidae but as being of uncertain subfamily. Besides these forms, the only other reference to fossil material of the early stages in the evolution of the Cercopithecoidea, is the following statement by Gregory (1920b): "That the ancestors or relatives of the later Cercopithecidae were present in the Lower Oligocene of Egypt is also extremely probable from the fact that the American Museum expedition in 1907 discovered there a frontal portion of a skull which resembles closely the corresponding part of some of the smaller Cercopithecinae".

Fossils of true Colobinae have been found from several parts of the Old World. There are two genera of which all the species hitherto described are now extinct, Dolichopithecus Depéret, 1889, from the Pliocene of France and Mesopithecus Wagner, 1839, from the Lower Pliocene of Greece, South Russia, Czechoslovakia and Persia (Simpson, 1945). MacInnes (1943) has described some fossil cercopithecoid specimens from Rusinga and Kiboko Island, Kenya (Lower Miocene) which he lists as "Mesopithecus Wagner sp.?".

The structure of the teeth is, according to MacInnes, "almost exactly similar to that of *Mesopithecus pentelici* Wagner, but the lower molars are somewhat smaller than those of the latter species, and they are also relatively narrower". MacInnes feels that there is at present insufficient material for a close comparative study but refers them to this group until more material is found. Besides these two genera, species of *Presbytis* Eschecholtz, 1821 (= *Semnopithecus* Cuvier, 1825) are known from the Lower Pleistocene of India (the Karnul Caves - Lydekker, 1886a and the Siwaliks - Lydekker, 1886b). None of these fossil Colobinae appear to show any particularly close relationship to the South African fossil Cercopithecoidea which all belong to the other subfamily - the Cercopithecinae - and we can therefore pass on to discuss that group.

An early fossil form referred to the Cercopithecinae is *Libypithecus markgrafi* Stromer, 1913 from the Middle Pliocene of Wadi Natron, Egypt. This species is represented by two damaged skulls (Stromer, 1913 and Edinger, 1938) which from their unusual shape are quite clearly different to the South African fossil Cercopithecinae. Another early member of this subfamily is a species which was described as *Procynocephalus wimani* Schlosser, 1924. The species is known from Hsin-An-Hsien (Schlosser, 1924) and Choukoutien (de Chardin and Pei, 1934) both sites in China. This species is described by Schlosser (1924) as resembling *Macaca* in the relative length and shape of its muzzle but as being very similar to *Papio* (= *Cynocephalus*) in its teeth and in particular its molars. In 1938, de Chardin suggested sinking this genus and transferring its one species to *Papio* because of its greater resemblance to species of that genus. He also suggested that the ages of the sites from which these specimens came was Villafranchian (i.e. Lower Pleistocene). In this paper, de Chardin also described new material of this species, including post-cranial fragments.

Of *Macaca* and *Papio*, which also have numerous living species, there have been fossil finds from most parts of the Old World. Quaternary macaque fossils have been found in India (Lydekker, 1886b), North Africa (e.g. Romer, 1928 and Arambourg, Boule, Vallois and Verneau, 1934), China (Schlosser, 1924 and de Chardin and Young 1929) and Europe (e.g. Bernsen, 1930). Species of the genus Papio are known as fossils from the Lower Pleistocene of India (P. subhimalayanus (von Meyer), 1848 and P. falconeri (Lydekker), 1886), North Africa (P. atlanticus (Thomas), 1884) and South Africa (described above in Part II). Of the genus Cercopithecus, fossil material is mentioned by Simpson (1945) from the Middle Pliocene of India; Cooke (1950) and Peabody (1954) also record Cercopithecus sp. from Africa (Holocene).

In addition to the above material, various parts of Africa (mainly South Africa) have also yielded numerous fossil specimens of the genera Parapapio, Simopithecus, Dinopithecus, Gorgopithecus Cercocebus and Cercopithecoides. These have all been described in Part II of this study and are listed together in Appendix IV which shows the distribution of all the cercopithecoid fossils known from Africa.

Of the living Cercopithecoidea, with the exception of the whole of the genus Cynopithecus and some species of Macaca and Comopithecus which are found in Asia (Macaca is also known from Gibraltar), the whole subfamily Cercopithecinae is restricted to Africa; of the subfamily Colobinae, the whole of the genus Colobus is found in Africa but all of the other genera in Asia only (Simpson, 1945). In South Africa today there is only a single species of the genus Papio (P. ursinus) and two species of the genus Cercopithecus (C. mitis and C. aethiops), each with several subspecies (Roberts, 1951 and Ellerman, Morrison-Scott and Hayman, 1953).

From the above brief review of what is known of the origin and evolution of the Cercopithecoidea, it is obvious that our knowledge of the history of the group is very fragmentary indeed. Thus, the numerous specimens of the fifteen species representing six genera which are known from South Africa, and are described in the earlier part of this monograph, should be of great value in elucidating the phylogeny of the group. Unfortunately, for reasons explained below, the value of the South African material in this connection is not as great as might be expected.

When the South African limestone caves were first studied, Broom (1946), on faunal grounds, postulated different ages for the various sites but Haughton (1948) and King (1951), on geological grounds, suggested that all the sites were about contemporary. Recent work on the geology of the sites correlated with the faunal descriptions, notably by Robinson (1952), Oakley (1954a and b), Peabody (1954) and Brain (1955 and unpublished data) has clearly shown that the sites are of different ages. Further, these authors were able to deduce convincingly both the relative and absolute dating of the sites. From these it is now clear that the deposits all date from the Lower Pleistocene and the total period covered by them is about 250,000 years. Work on the relative dating of the sites is at present still in progress but the sequence of the main excavations (from the oldest to the most recent) appears to be: Sterkfontein - Makapan - Swartkrans - Kromdraai, with Taungs probably roughly the same age as Sterkfontein, and Cooper's most likely following Kromdraai. Makapan may overlap both Sterkfontein and Swartkrans. The Sterkfontein type site covers the longest single period (possibly as much as 100,000 years); the other sites probably vary from about half to, in most cases, considerably less than half of this period.

In discussing the dating of the South African sites, use has often been made of the presence or absence of certain cercopithecoid genera to support conclusions reached. In the light of the results of the present study, several of these references no longer hold. Thus Robinson (1952), in discussing the genus *Parapapio*, mentions three species from Sterkfontein, one from Kromdraai and two from Swartkrans. Of these, the three species from Sterkfontein are still valid, but the Kromdraai form he referred to has been transferred to *Papio* (*P. angusticeps*) and there appears to be only one *Parapapio* at Swartkrans (*P. jonesi*). However, in the present study a *Parapapio* (*P. jonesi*) was found at Kromdraai and a new species of *Papio* (*P. robinsoni*) was described from Swartkrans. This author also mentions a new species of

Simopithecus and a Semnopithecine monkey from Swartkrans. These two species have now both been described, the first as *Simopithecus danieli* and the second as *Cercopithecoides molletti*. The monkey is very similar to *C.williamsi* and clearly belongs in the same genus but (as discussed below) the affinities of that genus are, at present, not clear. Finally, Robinson mentions *Gorgopithecus major* from Kromdraai which he suggests is "somewhat similar" to the Swartkrans *Simopithecus* and which therefore "may also have to be referred to this genus". In the light of the new material it is clear that the genus *Gorgopithecus* is valid and quite distinct from *Simopithecus*, in spite of some similarity.

In two of his papers dealing with the dating of the South African sites, Oakley (1954a and b) also includes references to fossil cercopithecoids. When discussing Taungs, this author (1954a) writes of "the presence of *Parapapio* closely approaching the modern *Papio*". As a result of a transfer made in the present study, a *Papio* (*P.izodi*) as well as two species of *Parapapio* (*P.jonesi* and *P.antiquus*)is now known to occur at Taungs. From Swartkrans, Oakley mentions *Papio*, *Simopithecus* and a semnopithecine monkey in 1954a, and *Papio* and *Semnopithecus* in 1954b. Prior to Oakley's statement, there would not appear to be mention of a *Papio* from Swartkrans but, as stated above, in the present study, a *Papio* (*P.robinsoni*) has been described from that site. The *Simopithecus* and the monkey which he lists from Swartkrans have been dealt with above, but it should be noted that Oakley goes further than Robinson in that he actually places the monkey in the genus *Semnopithecus*. The probable presence of *Parapapio broomi* at Makapan (Oakley, 1954a) has been confirmed in the present study. Writing of Sterkfontein, this author (1954b) states that the fauna does not include "(...*Papio* unless the so-called *Dinopithecus* found here is really a giant *Papio*)". Oakley is here presumably referring to the pelvis and vertebrae mentioned by Broom (1940 and 1946). These bones are too large for any known *Papio* but could belong to either *Dinopithecus ingens* or *Simopithecus danieli*. Unfortunately, as has been explained in Chapter 10 (Remarks), there is some doubt as to the exact provenance of these specimens. It might be added, that during the present study, no remains of *Papio* were found at Sterkfontein and, on the available material, *Dinopithecus* appears to be a valid genus. Oakley (1954a) lists both *Papio* and *Simopithecus* from Kromdraai and in 1954b, he writes of the presence of "*Papio* and the absence of *Parapapio*"at this site. Previous to Oakley, there appears to have been no reference to *Papio* at Kromdraai, although *Parapapio angusticeps* had been described at that site by Broom (1940). However, as stated above, it was decided in the present study to refer this latter species to the genus *Papio* and, in addition, a *Parapapio* (*P.jonesi*) was found at this site. Oakley's reference to *Simopithecus* at Kromdraai is probably a step further based on Robinson's (1952) paper and refers to *G.major*.

Appendix IV(A) shows the distribution of the South African fossil Cercopithecoidea, and it can be seen that, in most cases, the successive sites show significant cercopithecoid faunal changes with new species and genera appearing, disappearing and reappearing. The South African sites are all found within a radius of about 150 miles and, with the exception of Taungs, which is considerably drier, the climatic conditions are (and probably - but not necessarily - were at any particular time) very similar. Thus it does not seem likely that the faunal differences could be due to geographical factors. Zeuner (1950) states that "There appears to be a fastest rate of evolution of species of the animal kingdom under natural conditions, namely about 500,000 years per species-step". Therefore, from the geologically short period of time allocated to the series of South African sites, it seems quite obvious that the faunal changes between the sites could not be due to *in situ* evolution. The vagaries of sampling are doubtless important in determining which specimens and species are preserved but it is extremely unlikely that these would be sufficient to account for the great faunal differences found. From work by Brain at present in progress in this Department, it is now clear that the climate during the period covered by the sites varied considerably. It would therefore seem that the most obvious and probable cause of the faunal replacements was sucessive migrations into and out of the area as a result of local and / or distant environmental changes. Further, it appears from Appendix IV(A) and the discussion below, that there is some conflict between the currently accepted time sequence of the sites and the apparent morphological series within the cercopithecoid material. The geology and all the other faunal material hitherto described, supports the time sequence given above and it must therefore be assumed that the disagreements of the cercopithecoid material are similarly accounted for by the unpredictable nature of fossil sampling and migrations from areas in which apparently antecedent forms survived.

Before taking up the discussion of the various South African fossil cercopithecoids, there is one further point worth elaborating. As has been stated elsewhere (introdution to Part II) the vast majority of the faunal material so far excavated from the South African limestone deposits consists of skull or mandible fragments and teeth. It is well known that, because of their hard enamel coating, teeth are the least destructable parts of the animal body - but the reason for the differential survival of skull and mandible fragments over post-cranial bones is not quite so obvious. The most likely predators responsible for killing the animals whose remains have been preserved in the cave breccias, are the lions, leopards and sabre-toothed cats described by Ewer (1955c and d), and the Australopithecinae. Dart (e.g. 1949) considers that the ape-men were the predators mainly on the evidence of the types of fracture of the fossil baboon skulls found in the deposits, which he considers resulted from blows by implements of some sort. Whether, after being killed, the prey was then dragged into the caves by the predators, or whether carrion-feeders such as the hyaenas described from the South African sites by Ewer (1954, 1955a and 1955b) later brought the carcasses in, is debatable. In connection with the latter possibility, Hughes (1954) examined two lairs of living hyaenas but could find no bones. This would seem to suggest that the fossil fragments found in the deposits are not the remains of Lower

Pleistocene hyaena lairs. There are, however, two species of hyaena known from South Africa today, the spotted hyaena (*Crocuta crocuta*) and the brown hyaena (*Hyaena brunnae*) and Hughes does not state with which species he is dealing. These two species (and the fossil forms) may well differ in habits and Hughes' evidence cannot therefore be considered conclusive. The relatively large amount of skull material found in the deposits must at present be attributed to the fact that this portion of the body (with the exception of the brain which may well have been eaten) is less palatable than the rest of the animal and, at least for a carnivore, is probably also comparatively difficult to handle. The post-cranial bones were probably mostly crushed for their marrow content - a delicacy still sought after today by both man and the carnivores.

Of the fossil cercopithecoid species hitherto described from South Africa, those from Taungs appear to be, morphologically, the most primitive. The most recent dating, as given above, also suggests that this site and Sterkfontein are the oldest of the South African deposits. In all, there are three baboon-like species, *Parapapio antiquus*, *Parapapio jonesi* and *Papio izodi* and one monkey-like species, *Cercopithecoides williamsi*, known from Taungs and they are all small forms. Of these, *Parapapio antiquus* is very similar in size and dental morphology to *Papio izodi* and these two species may represent a morphological stage not far from the point at which the genera *Parapapio* and *Papio* started diverging from a common stem.

As has been stated in Chapters 7 and 8, the dental morphology in *Papio* and *Parapapio* is very similar. The diagnostic differences between them are mainly in the profile shape of the muzzle dorsum, and the absence in *Parapapio* of clear sexual dimorphism in the molars and well developed supra-orbital tori and maxillary ridges.

There are possibly also differences in the relative length of the muzzle when compared to the length of the calvarium but at present insufficient skulls are available for this point to be statistically assessed. The validity of the present diagnostic features of *Parapapio* with regard to other African

Cercopithecidae and the inter-relationships between all the genera of this family will have to await detailed cranial and dental studies of the living species.

The only other species of *Parapapio* at present known from Taungs, *P.jonesi*, is a rather smaller form than *P.antiquus*. As described in Chapter 7, this species seems to form a morphological series with *Parapapio broomi* from Sterkfontein and Makapan, and *Parapapio whitei* from Sterkfontein. Because of the short time span involved, and the conflicting sequence of the sites, these three species do not however form a true phylogenetic series. *P.jonesi* would seem, comparatively, to have been a rather successful species in South Africa as it is found in almost all the major excavations (see Appendix IV(A)) and thus covers virtually the whole period from which South African fossil cercopithecoid remains have been recovered.

The monkey-like form from Taungs, *Cercopithecoides williamsi*, bears a fairly strong resemblance to a number of genera including *Macaca* in its dental morphology. However, it has an extremely short face - shorter even than that found in genera such as *Cercocebus* - and there is a deep transverse groove posterior to its supra-orbital tori, reminiscent of *Theropithecus* and *Gorgopithecus* and '*Parapapio*' *coronatus*. The exact affinities of this species to the living and other fossil cercopithecoids are not at present clear. Like *Parapapio jonesi*, this species too would seem to have had a comparatively long time range (see Appendix IV(A)).

From Sterkfontein, three species of *Parapapio* (*P.jonesi*, *P.broomi* and *P.whitei*) and the monkey *Cercopithecoides williamsi*, are known. Of the new forms, *P.broomi* and *P.whitei* show a progressive increase in size over *P.jonesi* but, from the little cranial material at present available, no major change in morphology is apparent.

At Makapan, which follows Sterkfontein, *C.williamsi*, *P.jonesi* and *P.broomi* are still present but a new species and genus, *Simopithecus darti*, has now made its appearance. The genus *Simopithecus* is characterised by its unique dental morphology and does not show any obvious close relationship to any other of the known fossil Cercopithecoidea, although there is perhaps some very slight dental resemblance to Gorgopithecus and Dinopithecus. Among the living cercopithecoids, Simopithecus shows some similarity, also in dental morphology, to Theropithecus. There are only two other species of this genus known, S.oswaldi from East Africa and S.danieli to be listed below from Swartkrans. Rather few specimens of the three species are known and these do not enable comparisons to be made easily. However, all three were large baboons with S.darti the smallest and the other two probably of about equal size.

At Swartkrans we still find Parapapio jonesi but otherwise there is a complete change of cercopithecoids. S.darti is replaced by the larger S.danieli; C.williamsi is replaced by a larger monkey, C.molletti; a new large species of Papio, P.robinsoni, is now present as well as a still larger baboon of a new genus, Dinopithecus ingens. This invasion of the area by a number of large forms is very interesting but its cause is at present not apparent. The new species of Papio is very much larger than, and morphologically different to, the form found at Taungs, P.izodi. It appears to be only slightly smaller than the living species, Papio ursinus, and, except for the male muzzle dorsum and certain dental details, is also morphologically very similar to that baboon. C.molletti is mainly known from its dentition and all that can be said with certainty is that it belongs to the genus Cercopithecoides and has slightly larger teeth than C.williamsi. The giant baboon D.ingens does not appear to have any close affinities with other known cercopithecoids, except perhaps for the species described as D.brumpti from Angola (see Chapter 10). There is, however, some dental similarity to Gorgopithecus and, as stated above, perhaps also to Simopithecus. In skull shape it differs considerably from Gorgopithecus but has some resemblance to Simopithecus and Papio.

Parapapio jonesi and Papio robinsoni are still present at Kromdraai which follows Swartkrans in the currently accepted time series, but another species of Papio, P.angusticeps, and a species of a new genus, *Gorgopithecus major*, are also found. *Papio angusticeps* is very similar to *Papio robinsoni* in dental morphology but, in the shape and structure of the muzzle dorsum, it is more similar to *P.ursinus*. In size, *P.angusticeps* is considerably smaller than either *P.ursinus* or *P.robinsoni*. It would thus appear, that *P.angusticeps* was of the morphological type (and size) which could have been antecedent to both *P.robinsoni* and *P.ursinus* but, being a contemporary of *P.robinsoni*, it is most improbable that it was itself that ancestor. *G.major*, as has been stated above, has slight dental resemblances to *Dinopithecus* and possible also to *Simopithecus* but in its skull shape, and the absence of sexual dimorphism in the molars, it differs clearly from both of these genera.

At Cooper's, the site which is probably the most recent of the larger excavations, *P.robinsoni* and *P.angusticeps* are still found but *G.major* and *Parapapio jonesi* are no longer present. In addition, *C.williamsi* makes a reappearance. The presence of this latter species at Cooper's is surprising as it had apparently previously been replaced by *C.molletti* at Swartkrans.

No dating has as yet been attempted for the other sites listed in Appendix IV(A). Very little cercopithecoid material is at present known from them, and it would seem unwise to attempt their relative dating on the basis of these few specimens. However, when the geology and other fauna of these minor sites have been worked out, it will be interesting to see if the relative dating suggested by the cercopithecoid material agrees.

If the proportionate number of specimens of a species in a deposit reflects the relative abundance of that species at the time when the specimens were being incorporated into the deposit, the following would appear to be true:

1) The most common cercopithecoid species at Taungs was *Parapapio antiquus*.

2). There was probably a proportional increase in numbers of *Cercopithecoides williamsi* between Sterkfontein and Makapan but a decrease in the *Parapapio broomi* figures over the same period.

3) Papio robinsoni, from being the most common form at Swartkrans decreased considerably in proportion by Kromdraai and Cooper's, and at both of these latter sites, Papio angusticeps was the most common baboon. (At Kromdraai, the proportion of P.robinsoni is actually less than at Cooper's).

4) At Kromdraai, Gorgopithecus major was almost as common as P.angusticeps.

It must be stressed here, that the postulate stated above depends on many variables and consequently, the statements based on it must be treated with the greatest caution. Predators, parasites, disease, the availability of food, ecological cycles, periodic fluctuations, climatic change, evolutionary trends, pure chance and numerous other factors, all affect the composition of the sample of a faunal population found in a deposit. Thus, appropriate variation in any of these factors could affect the validity of the postulate itself or any of the statements based on it.

An interesting point emerges from the review of the Lower Pleistocene cercopithecoids of South Africa. As we work upwards from the oldest to the most recent of the deposits, there is at first a steady progressive increase in size of the largest cercopithecoid species known at each site. Thus, Papio izodi and Parapapio antiquus of Taungs are followed by the larger Parapapio whitei of Sterkfontein. At Makapan, there is then the considerably larger Simopithecus darti and finally, at Swartkrans, the largest known cercopithecoids, Dinopithecus ingens and Simopithecus danieli. After Swartkrans, there is a decrease in size to Gorgopithecus major at Kromdraai and then possibly another, but lesser decrease to Papio robinsoni at Cooper's. This size cycle probably reflects some long term environmental or evolutionary trend.

Little is known about cercopithecoid phylogeny in South Africa after the Lower Pleistocene period from which the sites described above date. A pocket on top of the Kromdraai ape-man site yielded the three specimens of the species known as 'Parapapio' coronatus. The dating of these specimens is uncertain but probably considerably more recent than Lower Pleistocene and Broom and Robinson (1950) suggest Upper Pleistocene. The lower dentition which is present in two of the specimens, appears to be that of a Parapapio or Papio (more probably the latter) but the supra-orbital tori of the associated calvarium are greatly developed and show some resemblance to those of Gorgopithecus, Cercopithecoides and Theropithecus. The association of the mandibular fragments and calvarium in a single species may not necessarily be correct.

The species Papio spelaeus, of which the exact locality is unknown, appears to date from comparatively recent times - possibly even Holocene - and is phylogenetically interesting. Simpson (1949b) writes that "The existence of a robust Pleistocene subspecies or temporal race of a Recent species is a common phenomenon". P.spelaeus resembles P.ursinus very closely but is significantly larger and has therefore been given separate specific status (see Chapter 8). These two species may also be an example of the principle that a size decrease has taken place in some phyletic lines during the Quaternary.

Of the genus Cercopithecus, which today has two species in South Africa, there appears to be no fossil evidence at all except for mention by Peabody (1954) of a possible specimen from the upper level of the Black Earth Cave, on the Karp Escarpment, which is almost certainly Holocene. Perhaps the fauna of the Cave of Hearths (Makapan) or the Vaal River gravels will yield some information about this genus.

The known South African fossil Cercopithecoidea thus almost all fall into a geologically short period just following the Plio-Pleistocene boundary and are only known from a rather small, climatically very nearly homogeneous area. They come from a period very considerably after the origin and primary radiation of the group and a large number of genera and species were then already spread throughout the Old World.

From the discussion of the South African Lower Pleistocene deposits, it is apparent that the successive cercopithecoid species found there are forms which migrated into the area from other parts and that no important in situ evolution apparently took place at the sites. Information about the actual evolution of these forms will probably come from more northern parts of Africa when (and if) further pre-Pleistocene cercopithecoid fossil discoveries are made there.

Through the portion of the Quaternary following the period from which the bulk of the South African fossil cercopithecoid specimens are known, the six genera and fifteen species hitherto described (and there were certainly species and probably genera also, of which we have no fossil record), were reduced to two genera (Papio and Cercopithecus) and three species (P.ursinus, C.mitis and C.aethiops). It would therefore seem that the peak of radiation of the group was already well passed and that the number of species and genera was in process of reduction. This view is further evidenced by the drastic changes in cercopithecoid fauna between the various sites.

As has been stated above, there is no evidence at all as to the origin and affinities of the genus Cercopithecus and one can not therefore speculate on the probable lineage of the two present day species. There are however, several fossil species of Papio known from the various deposits and it may be profitable to speculate on the probable course of the Pleistocene line leading to P.ursinus (and possibly P.cynocephalus as well).

P.angusticeps is of the general morphological form and, possibly too, of the size which one would expect in an early ancestor of the chacma baboon. However, a number of factors seem to mitigate against this species being in the direct line leading to P.ursinus. There appears to be a fair amount of evidence from other mammals (e.g.Hooijer, 1950) for a decrease in size over the latter portion of the Quaternary and, as mentioned above, P.spelaeus may well be evidence of this in the lineage of P.ursinus. It would seem unlikely that there was sufficient time during the remaining portion of the Pleistocene for the descendants of P.angusticeps to have evolved to about the size of P.spelaeus and then still to reduce again to the size of

P.ursinus.

Contemporary with *P.angusticeps*, the species *P.robinsoni* is found which is almost as large as and also very similar in morphology to *P.ursinus*. The meeting of the nasal bones on the male muzzle dorsum, a character in which *P.robinsoni* is virtually unique, was found in a slightly different form, in a single female specimen of *P.ursinus* (Chapter 8). Thus, this species is also a possible ancestor to the chacma baboon. However, both *P.robinsoni* and *P.angusticeps* have certain minor dental differences in common (see Chapter 8) which may be specialisations ruling them both out of the direct ancestory of *P.ursinus*.

On balance of evidence, it would seem that the Lower Pleistocene ancestor of *P.ursinus* was a species, at present unknown, about the size of *P.robinsoni*, but possibly more similar to *P.angusticeps* in general skull shape. In dental morphology it probably differed slightly from both of these species. During the latter portion of the Pleistocene, the descendants of this species probably evolved into a form very similar or identical to *P.spelaeus*. Finally, towards the end of the Pleistocene and during the Holocene, this large species became reduced in size and evolved into the species *P.ursinus*.

The taxonomy of the living Cercopithecoidea has in the past been based almost exclusively on external characters (Elliot, 1913 and Pocock, 1926) whereas the taxonomy of fossil forms must of necessity almost always depend entirely on dental and osteological characters. Hence it has not been possible to discuss the full phylogenetic relationships between the fossil and living species. A text is in preparation by Hill (Hill, 1953) which may enable this to be done in the near future.

APPENDIX I.

CLASSIFICATION OF THE SUPERFAMILY CERCOPITHECOIDEA.

(modified after Simpson, 1945).

(a) Classification (to Superfamilies) of the Order Primates Linnaeus, 1758.

- Suborder 1: Prosimii Illiger, 1811.
  - Infraorder 1: Lemuriformes Gregory, 1915.
    - Superfamily 1: Tupaioidea Dobson, 1882.
    - 2: Lemuroidea Mivart, 1864.
    - 3: Daubentonioidea Gill, 1872.
  - Infraorder 2: Lorisiformes Gregory, 1915.
  - 3: Tarsiiformes Gregory, 1915.
- Suborder 2: Anthropoidea Mivart, 1864.
  - Superfamily 1: Ceboidea Simpson, 1931.
  - 2: Cercopithecoidea Simpson, 1931.
  - 3: Hominoidea Simpson, 1931.

(b) Detailed Classification of the Superfamily Cercopithecoidea Simpson, 1931.

- Family: Cercopithecidae Gray, 1821.
  - Subfamily 1: Cercopithecinae Blanford, 1888.
    - Genera : *Macaca* Lacépède, 1799.
      - †*Lybipithecus* Stromer, 1913.
      - †*Simopithecus* Andrews, 1916.
      - *Cynopithecus* Geoffroy, 1835.
      - *Cercocebus* Geoffroy, 1812.
      - †*Parapapio* Jones, 1937.
      - †*Dinopithecus* Broom, 1936.
      - †*Gorgopithecus* Broom and Robinson, 1949.
      - *Papio* Erxleben, 1777.
      - *Comopithecus* Allen, 1925.

Mandrillus Ritgen, 1824.

Theropithecus Geoffroy, 1843.

Cercopithecus Brünnich, 1772.

Allenopithecus Lang, 1923.

Erythrocebus Trouessart, 1897.

Subfamily 2: Colobinae Elliot, 1913.

Genera : † Mesopithecus Wagner, 1839.

† Dolichopithecus Depéret, 1889.

Presbytis Eschscholtz, 1821.

Pygathrix Geoffroy, 1812.

Rhinopithecus Milne Edwards, 1872.

Simias Miller, 1903.

Nasalis Geoffroy, 1812.

Colobus Illiger, 1811.

Subfamily uncertain.

Genera: † Moeripithecus Schlosser, 1911.

† Apidium Osborn, 1918.

† Oreopithecus Gervais, 1872.

† Cercopithecoides Mollett, 1947.

†=extinct.

APPENDIX II.

DENTAL MEASUREMENTS OF *PAPIO* (*SIMOPITHECUS*) *SERENGETENSIS* (MM.).

(From Dietrich, 1942).

a) Upper teeth	(l x b)	
P^3	7.5 x 9	Single loose teeth.
P^4	8 x 9.5	
M^1	11.5 x 10.5	
M^2	12 x 11	
M^3	11.8 x 10.8	
P^3 - M^3	48.5	Combined OK rows.

b) Lower teeth	(l x b)	
P_3	7.5 x 4 +	UK Gar. Ur. female.
P_4	8 x 5 +	
M_1	9 x 7	
M_2	11 x 8	
M_3	14 x 9	
P_3 - M_3	51	
$\bar{C}$ - M_3	58.5	
P_3 - M_3	54	UK Vo 9/10. 38 male.
M_3	16.3 x 11	Single loose teeth.
	15.4 x 9.5	
	15 x 9	
	14 x 9	
	13 x 8	

APPENDIX III.

Cercocebus ado Hopwood.

Cercocebus ado - Hopwood, 1936.
Cercocebus ado - Dietrich, 1939.
Cercocebus ado - Hopwood and Hollyfield, 1954.

Holotype:

A weathered left mandibular ramus of a female (M.14940).

Repository of type:

British Museum (Natural History), London.

Type site:

Vogel River (Laetolil) Beds, Tanganyika. (Approximate long. 35° 10' E., lat. 3° 10' S.).

Referred material:

Nil.

Diagnosis:

"A *Cercocebus* in which the female has the premolar-molar series nearly 45 per cent. longer than that of a female *C.galeritus* and approximately equal to that of a very large *C.torquatus torquatus*. Cusps of the lower cheek-teeth higher and more slender than in either of the Recent species; talonid of lower M3 stronger". (Hopwood, 1936).

Measurements: (from Hopwood, 1936).

Length of premolar-molar series - 46.2 mm.
Length of M3 - 12.5 mm.
Breadth of M3 - 10 mm.
Length breadth index of M3 - 80

Remarks:

Dating - Middle Pleistocene. (Kent, 1941). A fuller description and illustrations are required before this species can be properly assessed.

(Hopwood defines *Cercocebus* as being "Distinguished from *Colobus* by the shape of the corpus mandibulae, the structure of the third molar, and the pronounced basal swelling of the labial cusps of the lower cheek-teeth").

APPENDIX IV.

THE DISTRIBUTION OF THE AFRICAN QUATERNARY FOSSIL CERCOPITHECOIDEA.

A. SOUTH AFRICA (based on Part II of this study).

	Taungs	Sterkfontein	Makapan (limeworks)	Swartkrans	Kromdraai (faunal site)	Cooper's	Swartkrans II	Graveyard	Gladysvale	Minaar's Cave	Bolt's Farm	Skurweberg	'Pretoria'	Kromdraai (above ape-man breccia)
Parapapio antiquus	x													
" jonesi	x	x	x	x	x									
" broomi		x	x								x			
" whitei		x												
'Parapapio' coronatus														x
Papio izodi	x													
" robinsoni				x	x	x	x		x		x	x		
" angusticeps					x	x				x				
" spelaeus													x	
Simopithecus darti			x											
" danieli				x										
Dinopithecus ingens				x								x		
Gorgopithecus major					x									
Cercopithecoides williamsi	x	x	x			x								
" molletti				x			x	x						

NOTE: Besides the species listed in the above table, Wells (1943) mentions P.ursinus from the Wonderwerk Cave, Kuruman and Peabody (1954) lists "Papio (and related baboon genera)" from the Australopithecus Cave (lower and upper levels), Black Earth Cave (lower and upper levels), Witkrans Cave (lower and upper levels) and Iscor - all sites on the Kaap Escarpment. The latter author also lists "?Cercopithecus (monkey)" from the upper level of the Black Earth Cave. In addition, Robinson (1952) mentions "a baboon (Papio) indistinguishable from the modern chacma baboon" from Graveyard. Robinson's specimens were not available to me but in view of the new species P.robinsoni being so similar to the chacma baboon it would seem probable that his specimens were of thés new species.

B. EAST AFRICA (modified after Leakey, 1951).

	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Olorgesailie	Omo	Laetolil (Vogel River and Serengeti Plains)	Kanjera	Kaiso	Rawi
Simopithecus oswaldi	x	x	x	x				x		
Simopithecus sp.					x				x	x
Dinopithecus brumpti						x				
Papio (*Simopithecus*) *serengetensis*							x			
Papio (*Simopithecus*) sp.				x						
Cercocebus ado							x			

*In addition, *Papio* sp. cf. *neumanni* is mentioned by Dietrich (1939) from the Lake Eyasi region (Laetolil), Tanganyika and *Papio neumanni* is listed by Hopwood (1931) from the Makalian deposits Elmenteita, and probably also MacInnes Site, Kenya. *

	Ain Jourdel Algeria	Algeria (various sites)	Wadi Natron Egypt
Papio atlanticus	x		
Macaca spp.		x	x

D. OTHER PARTS OF AFRICA.

	Humpata, Angola	Twin Rivers, N. Rhodesia	Mumbwa Cave (upper levels -Bantu) N. Rhodesia
Dinopithecus sp. cf. *ingens* (Mouta, 1950)	x		
Papio or *Parapapio* sp. (this study)		x	
Cercopithecus sp. (Cooke, 1950)			x

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