

https://dspace.org/

Fossil and subfossil primates from the limestone deposits At Taung, Bolt's farm and Witkrans, South Africa

Freedman, Leonard

1965-12
Bernard Price Institute for Palaeontological Research
http://hdl.handle.net/10539/16058
None

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

FOSSIL AND SUBFOSSIL PRIMATES FROM THE LIMESTONE DEPOSITS AT TAUNG, BOLT'S FARM AND WITKRANS, SOUTH AFRICA

By Leonard Freedman

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

ABSTRACT

(1) New fossil and subfossil cercopithecoid specimens are described from the limestone deposits at Taung, Bolt's Farm and Witkrans, South Africa.

(2) The following first reports are made:
   (*a*) *Parapapio whitei* from Bolt's Farm.
   (*b*) *Parapapio whitei* from Taung.
   (*c*) *Papio ursinus* from Witkrans.
   (*d*) *Cercopithecoides williamsi* from Bolt's Farm.

(3) The following first descriptions are given:
   (*a*) *Parapapio whitei* male cranium.
   (*b*) *Parapapio whitei* female cranium.
   (*c*) *Parapapio antiquus* male cranium.

(4) The morphological and size differences in the male crania of the *Parapapio* spp. are described.

(5) The affinities of the genus *Cercopithecoides* to the Colobinae are discussed.

INTRODUCTION

A very considerable number of Primate specimens was excavated by the University of California African Expedition from the various deposits at Bolt's farm, Taung and Witkrans, South Africa. These specimens are all now housed in the Museum of Paleontology at the University of California, Berkeley, where they were examined by Dr. H. B. S. Cooke in 1957-1958 and then sent to the writer for description. The remaining fauna and the geology of the sites are discussed in an unpublished paper by Cooke. The most important of the new primate specimens are described and classified below. The measurements used are from Freedman (1957); the photographs are oriented on the occlusal plane.

The new specimens all belong in the superfamily Cercopithecoidea and a number represent the first report of certain species from these sites. The material includes specimens which show anatomical regions not previously described and the material in general increases our knowledge of the range of variation within the various species. The species found in the new material are: *Parapapio antiquus*, *Parapapio broomi*, *Parapapio whitei*, *Papio ursinus*, *Papio wellsi*, *Papio robinsoni*, and *Cercopithecoides williamsi*.

**Now:* Department of Anatomy, University of Sydney, Sydney, N.S.W., Australia.

Besides the material described below, there are a large number of post-cranial bones, juvenile specimens and skull fragments which are clearly cercopithecoid. Due to the incompleteness of our knowledge of the fossil forms of this superfamily, the specimens cannot at present be classified further with any degree of certainty. It was therefore felt that it was better to omit description of this material for the present.

PARAPAPIO Jones, 1937

The new material includes specimens of the species *Parapapio broomi* and *Parapapio whitei* from Bolt's Farm. The latter species has not previously been reported from this site and only a single maxillary fragment with teeth (B.F. 21) of *P. broomi* (Freedman, 1957) was previously recorded from this site.

From Taung, the new material includes specimens of *Parapapio antiquus* and *Parapapio whitei*. *P. whitei* has not previously been reorded from this site.

No specimens of the genus *Parapapio* were found in the new material from Witkrans.

Parapapio broomi Jones, 1937

Referred material. Four new specimens from Bolt's Farm, all from pit 23.

(1) Specimen 56786 is a badly damaged cranium with most of the base and muzzle missing. In the small remaining left posterior part of the maxilla, only M^2 and M^3 (the latter still in its crypt) are present. The specimen was probably from a female.

(2) Specimen 56792 is a small anterior portion of the muzzle of a female with P^3—M^2 on the left and P^3, M^1 and M^2 on the right.

(3) Specimen 56796 is the symphyseal region and right corpus of a female mandible. I_1—P_3 are present on the left and I_1—M_3 on the right, almost all in a good state of preservation.

(4) Specimen 56787 is the badly damaged left corpus and ramus of a mandible of unknown sex. Only M_3 is present and undamaged.

Description. The identification of specimen 56786 is not easy as most of the muzzle is missing and the specimen is from an immature individual. However, from the small portions of the nasal bones and maxillae present, it does seem as if the muzzle shape was similar to that seen in *P. broomi* females. There is a slight concavity in the profile contour, but that shape is sometimes found in females of this species—particularly when immature.

The muzzle dorsum in the same specimen, 56786, is separated from the sides of the muzzle by a very weak maxillary ridge. The maxillary fossae were either very shallow or absent. The slope of the orbits and the parts of the maxillae lying below the infero-lateral part of the orbits is shallow and not almost vertical, as in *Papio robinsoni* and most of the *Papio* spp. The supra-orbital tori are weak and separated from the calvaria roof by a very shallow

ophryonic groove. The calvaria shape is similar to that previously described for *P. broomi* (Freedman, 1957).

Specimen 56792 is only a small fragment and shows no morphological features of interest. The upper teeth of both this specimen and 56786 are of the *Papio-Parapapio* type; on size (Table 3), some dimensions (e.g. P^3) are slightly larger than those previously found in this species.

The female mandible, 56796, has virtually no mandibular fossa; the symphyseal region is too damaged to show detailed structure. Mandible 56787 is broken and distorted but there is some suggestion that the ramus was displaced slightly lateral to the corpus. On size and morphology, the lower teeth fit those previously described for *P. broomi*.

Measurements. See Tables 2—4.

Remarks. The new material confirms the presence of *P. broomi* at Bolt's Farm, where only a single specimen was previously known.

Parapapio whitei Broom, 1940

Referred material. Two specimens from Bolt's Farm and three from Taung.

(1) Specimen 56785, from pit 23 at Bolt's Farm, is an almost complete male cranium. The zygomatic arches are missing and so is part of the calotte, but there is an endocranial cast present where the bone is missing in the latter region. P^4—M^3 are present bilaterally and, except for both P^4 teeth and the right M^1, they are in a fair state of preservation.

(2) Specimen 56794 is a single broken male left *C*, also from pit 23 at Bolt's Farm.

(3) Specimen 56614 is a very badly crushed right half of the muzzle of a male from pit 5a at Taung. The right *C* to P^4 are present, but the *C* has lost its distal third. Small parts of the three right molars are also present.

(4) Specimen 56652 is a part of a female cranium from pit 5 at Taung. Most of the muzzle is present but, of the calvaria, only the left anterior portion remains. The left M^1—M^3 are present, but very badly damaged.

(5) Specimen 56613, from pit 5 at Taung, is the badly crushed anterior part of the maxilla and palate of an immature female. The right P^3—M^1 and the left P^4—M^2 are present and well preserved; the right M^3 can be seen in its crypt.

Description. A single male muzzle was recently referred to *Parapapio whitei* from Makapan (Freedman, 1961b), but no other good cranial material is known of the male of this species. The new material described below includes a very fine cranium (56785) and a crushed muzzle (56614).

Specimen 56785 is the cranium of a large robust male. In norma lateralis, the profile shape (Fig. 1) dips fairly steeply between the orbits and then becomes more horizontal over the muzzle dorsum. The area in which the angle changes is slightly damaged, thus accentuating the concavity. However, the profile shape is clearly of the *Parapapio* type. The muzzle dorsum is large and slightly

TABLE 1
Cranial Measurements (in mm.)

SPECIES SEX & NUMBER	GENERAL			CALVARIA								
				Height		Breadth			Length		Foramen Magnum	
	Greatest Length	Basal Length	Bizygomatic Breadth	Basion-Bregma	Basion-Glabella	Min. interfrontal	Greatest temporal	Mastoid	Inion-Glabella	Inion-Basion	Breadth	Length
P. whitei *Male* 56785	167	117	(111)		81	54	(92)		110	54		
P. antiquus *Male* 56604 *Female* 56694 56608	(144)		95			57 52	74		95			
P. wellsi *Female* 56606	142	101	(92)	55	71	52	72	75	98	42	15·6	14·0
P. robinsoni *Male* 56765 *Female* 56767 56797	(153) (158)	(106)	(96) (94)	64	77	52 52	 74	78	100 100	52	17·2	19·0
C. williamsi *Female* 56784 56778		(90)	(96)		77	52	72					

TABLE 1 (*Continued*)

SPECIES SEX & NUMBER	MUZZLE													
	Height		Breadth			Length			Orbit				Nasal Aperture	
	Post. to M^3	Ant. to P^3	Ant. to M^3	Ant. to P^3	Dors. to M^2	Muzzle	Palate	Nasal	Inter-orbital	Ext. orbital	Height	Breadth	Breadth	Length
P. whitei														
Male														
56785	60	27	53	43	46	88	71		13·7	85·6	26·7	(28·3)	19·1	29·3
P. antiquus														
Male														
56604		21				84								
Female														
56694		15	46	35		68			9·0	(69·5)	21·5	24·2	18·5	
56608			50	35										
P. wellsi														
Female														
56606		26	49	35	40	68	59	(34)	10·8	75·3	22·6	25·6	16·9	(24·5)
P. robinsoni														
Male														
56765			(53)	48			(89)							
Female														
56767		26	(48)	(38)		68	67		7·4		(22·3)	23·3		
56797		20	49	39	41	76		35	(11·0)	(80·5)	25·1	27·5	(21·7)	31·0
C. williamsi														
Female														
56784		22	42	38		54	51	24	19·1	79·4			14·1	27·0
56778		24	43	35									17·9	28·0

TABLE 2
Mandibular Measurements (in mm.)

SPECIES SEX & NUMBER	Height			Breadth					Length		
	Post. to M_3	Ant. to P_4	Mental sp. to most anterior pt.	Post. to M_3	Ant. to M_3	Ant. to P_4	Through mental sp.	At base of canines	Gonion to mental spine	Ramus at condyle neck	Condyle to most anterior pt.
P. broomi *Female* 56796		24	30				24	20			
P. robinsoni *Male* 56766	30										
56768		37	41		(44)	37	22	28			
Female 56770	26	22	27	49	40	24	18	16	68		
? sex 56769	25										
56772	31										
56773	31										
C. williamsi *Female* 56784	24	21	26			29	27	21		32	(95)

TABLE 3
Measurements of the upper teeth (in mm.)

SPECIES SEX & NUMBER	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	C-M^3
P. broomi																			
Female																			
56786												11·7	10·9	11·2	10·5	9·3	10·9		
56792					8·1	8·0		6·4			(10·4)			(11·5)					
P. whitei																			
Male																			
56785									9·9		9·9	11·7	10·9	11·7	10·8	9·0	11·7	37·7	
56794		9·0	8·4	9·0															
56614					8·4	7·3	9·1	7·8											
Female																			
56652												12·5	11·0	11·7					
56613							8·3	6·9	10·2	9·0	11·1	11·4	10·2	(13·0)		(9·4)			
P. antiquus																			
Male																			
56604	(22)										(9·8)							(38·5)	(54·0)
Female																			
56694								6·7		8·7	(8·9)	11·3	9·6	10·9	10·9	7·7	9·8	35·8	
56608					7·3	7·4	8·2	6·8	9·1	7·7	9·2	10·5	9·1	11·0	10·4	7·2	9·6	35·9	
P. wellsi																			
Female																			
56606										9·4								(38·5)	
P. robinsoni																			
Male																			
56765						10·6	10·2	8·7	10·9	9·6	(10·3)	12·4	11·6	15·3	13·4	10·5	16·0		
56766					7·8	9·6	8·7	7·8	9·8	(9·1)	(11·4)	11·5	10·2	13·6	11·7	9·2	14·6	(45·5)	
Female																			
56767									(10·0)	9·5	(10·3)	11·4	10·5	11·8	11·4	9·9	13·0		
56797								7·2			(10·6)			(12·8)					
P. ursinus																			
Male																			
56701					8·7	8·3	9·2	9·0	11·0	11·1	12·5	13·0	12·2	15·8					
56701a	(47)	(10·8)	(11·5)	(13·6)															
V4743FEP																			
43/122 x		12·6	11·6	12·7															
56697e	(47)	(10·8)	(10·1)	(11·9)															
56697f	(49)	(10·9)	(10·8)	(13·3)															
Female																			
56700										9·0			10·5	11·8	11·5		13·5		
? Sex																			
56699a															(12·0)		13·2		
56697a																10·2	13·5		
56698a															12·8	10·5	14·9		
56696b															12·3	10·0	13·9		
56702c															13·0	10·3	14·1		
C. williamsi																			
Female																			
56784																8·2	10·7		45·8
56778					6·8	6·4	8·7	6·0	9·2	8·9	8·5	10·9	10·3	9·3					
Taung																			
Female																			
56610					7·3	5·6	7·6	6·7	9·5	8·8	10·0	11·6	10·0	12·2					

TABLE 4
Measurements of the lower teeth (in mm.)

SPECIES SEX & NUMBER	$\overline{C}$			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	C-M_3
P. broomi																			
Female																			
56796**	(10·9)	(5·1)	(6·9)	(5·7)		6·9	6·6	7·7	7·9	9·1	9·5	9·3	11·0	9·9	9·1	6·0	13·5	40·1	(52·6)
? Sex																			
56787														9·3	7·5	5·9	14·2		
P. robinsoni																			
Male																			
56766				5·6	21·0	7·4	8·5	8·3	8·7	10·4	10·2	9·6	12·9	11·0	10·3	8·2	16·8	49·1	
56768				6·8	19·1	7·5	9·2	8·9	9·0	9·8	10·9	10·7	13·2	10·9					
Female								7·4	8·5		9·7	9·4	12·4	10·7	9·2	6·7	16·1		
56770																			
56771				5·2		7·3	8·3	8·5	9·0	10·5	10·3	10·0	13·0	11·2	10·3	6·5	17·0		
? Sex																			
56769						6·7	8·3	8·0	9·0	9·3	10·0	9·9	12·0	10·0	8·9	6·8	15·0	44·5	
56772*..														11·0	9·8	6·7	16·8		
56773*..											10·5	10·4	13·4	10·9	10·0	7·2	17·0		
56774									8·9		10·0	10·3	13·0						
56706											9·8	9·5	11·6	10·0	9·7	7·6	16·0		
P. ursinus																			
Male																			
56773				6·7	20·4	(7·6)	8·9	(9·0)	9·5	10·5	10·9	10·9	12·8	11·7	9·8	7·3	17·7		
56699b										(10·4)									
56702a					25·9														
Female																			
56703						(7·5)							(12·1)						(45·7)
? Sex																			
56697b														11·0	9·6		18·5		
56697c														13·0	11·1	7·6	19·8		
56698b														12·4	11·2	7·8	18·8		
56696a														10·1	10·2	6·9	16·9		
56697d							(9·6)												
C. williamsi																			
Female																			
56784				4·9		5·5	6·9							8·8	(9·4)	6·4	13·7	37·9	
Taung																			
Male																			
56660					17·2		8·0			(10·7)			(11·8)	9·1	8·5		12·4	(42·5)	
56618						7·2	8·2												
56693						8·1	7·9	8·5	9·3	10·5	(10·5)	(10·7)	12·7	(11·2)	10·4		14·7	45·5	
Female																			
56691	11·0	7·9	4·6									10·2		(10·5)	10·3		15·6		
56623				5·4			7·8												
56626				5·0	8·3		7·3	7·7	7·9	9·4									
? Sex																			
56655						(7·0)		7·5	7·8	(9·5)			(11·3)	9·4	8·8			-	

	I_1			I_2			ROWS	
	h	b	l	h	b	l	I (*a*)	I (*b*)
**56796	6·1	6·4	5·0	5·8	6·5	4·6	17·0	15·8

* ? one individual

concave on each side from nasal bone to maxillary ridge. The maxillary ridges are not well developed in this specimen. The sides of the muzzle are almost vertical and only slightly excavated by maxillary fossae. The maxilla is very robust below the lateral half of the orbit and the roots of the zygomatic arches are very strong. Specimen 56614 is very badly crushed, but, as far as can be seen, it appears to have had a muzzle similar to that described above.

In specimen 56785, the anterior portions of the temporal lines are robust and curve inwards rapidly. On the small posterior part of the calvaria present there is a slight sagittal crest which might have extended forwards for as much as one third of the distance between inion and glabella. From the mastoid region, a well-developed shelf-like occipital crest extends around to the inion.

A most unusual feature is present on either side of the new male calvaria (56785), just above the zygomatic process of the temporal bone. Usually in this region the sidewalls of the calvaria curve down smoothly to deviate laterally into the medial root of the zygomatic process, forming a broad ledge at the inferior margin of the squamous temporal. In specimen 56785 this region displays a large outward bulging of bone which reduces the medial zygomatic root to a very narrow ledge. The feature is present bilaterally but on the left side the posterior portion of the region has been lost. The outer table of bone is missing here and it can be seen that the underlying space is occupied by air cells, similar to those seen in the mastoid region postero-inferior to it. (A similar external appearance, the mons temporo-sphenoidalis, which was described by Dart (1924) in Bushmen, is not formed by pneumatization, but is an outward curve of the bones of the calvaria sidewall to accommodate the expanded temporal lobe of the brain.)

Viewed from below (Fig. 2), the great depth of the palate bounded by almost vertical alveolar processes can be seen. The foramen magnum is very small.

The female specimen, 56652, is considerably damaged and distorted. The left side of the muzzle is rough and uneven, but the right side is completely smooth. The orbits appear very large, particularly supero-inferiorly, the profile shape rather *Papio*-like in the deepness of the concavity, the nasal aperture large and the muzzle extremely high (Fig. 3). How much of all this is due to distortion is difficult to assess.

There is no bony prominence in the region above the zygomatic process of the temporal of this female specimen. The zygomatic arch is short and not very robust. The temporal lines are reasonably well developed anteriorly but, after a sharp initial inward curve, they appear to run directly posteriorly and finally to curve slightly laterally. In size, this specimen is considerably smaller and less robust than the male of this species as described above.

The new male and female upper teeth (Table 3) fit their equivalents as described previously (Freedman, 1957 and 1961b) in both size and morphology.

Measurements. See Tables 1 and 3.

Remarks. The description of the male cranium of this species is a significant

addition to our knowledge of the fossil Cercopithecoidea and, particularly, to that of the *Parapapio* species. The taxonomy of this genus is still not wholly satisfactory, but the description of the crania of the male *P. whitei* and the male *Parapapio antiquus* (see below) in this paper show that, although on dental size and morphology (except for P_3 and the canines) the sexes within each species cannot be separated, there are considerable differences in size and morphology in the crania of the two sexes of *Parapapio* species. Further, the great difference in size and morphology between the crania of the males of the species *P. antiquus* and *P. whitei* (which can now also be compared with the known males of *P. broomi*) indicate that, although there is overlap in size between the *Parapapio* species on almost all dental dimensions, as more crania are recovered, so more differences in morphology appear which more clearly separate the various species.

Of the female cranium of *P. whitei*, only one piece of any size has hitherto been recovered and that is only a left maxilla with teeth (STS. 239). When compared with females of the species known from Taung, the new female, 56652, appears to fit best in *P. whitei*. However, an accurate description of the female calvaria of this species will only be possible when a less distorted specimen is found.

Parapapio antiquus (Haughton), 1925

Referred material. Three new specimens from Taung.

(1) Specimen 56604, from pit 5a, is an almost complete well preserved male cranium. Its base and the left part of the palate are still embedded in matrix. On the right, C—M^3 are present, but the occlusal surfaces of these teeth are still embedded in the block.

(2) Specimen 56694 is from pit 5b and consists of a damaged female cranium lacking the base and posterior part of the calvaria. P^4—M^3 are present on the right and P^3—M^3 on the left, but only the left molars are undamaged.

(2) Specimen 56608, from pit 5a, is the damaged palate of a female. The left P^3—M^3 are well preserved and not very greatly worn. A number of other teeth, including the right and left I^1 and right P^4, M^2 and M^3 are present, but, except for the M^2, they are all badly damaged.

Description. Specimen 56604 (Fig. 4) is the first good male cranium with teeth of this species to be recovered. Morphologically, the specimen closely resembles the fairly complete female cranium (Tvl. 639) previously described (Freedman, 1957) and also the female specimen (56694) to be described below. On size, the muzzle of this new male specimen is longer than that of the females and similar to that of the male (C.T. 5364) previously referred to this species by Freedman (1957). (Some doubt about this latter specimen belonging in *P. antiquus* was expressed by Freedman (1961a)).

The muzzle of 56604 has a large flattened dorsum in which the maxillae only slope down gently on either side of the nasals. The sides of the muzzle are



FIG. 1—Lateral view of the male cranium of *Parapapio whitei* (56785)

almost vertical and the maxillary fossae are large, but not deeply excavated. The supra-orbital tori are weak and the calvaria roof rises for some distance posterior to them. The zygomatic arch is moderately robust and the anterior parts of the temporal lines prominent. The calvaria is considerably eroded, but it appears as if a slight occipital crest was present, at least laterally.

Specimen 56694, the female calvaria, shows the typical profile shape of a *Parapapio*. The muzzle dorsum is fairly flat and the sides of the muzzle are almost vertical with large but shallow maxillary fossae. The general shape is thus similar to that of the previously described female of this species (Tvl. 639). The supra-orbital tori of the new specimen are, however, very weak and the calvaria roof rises steeply for a short distance behind them.

Only the lateral surfaces of the upper teeth can be seen in the male 56604. The *C* is large and might not have been fully erupted. P^3 shows an extension of the enamel on to the mesio-buccal root. The distal portion of M^3 shows some

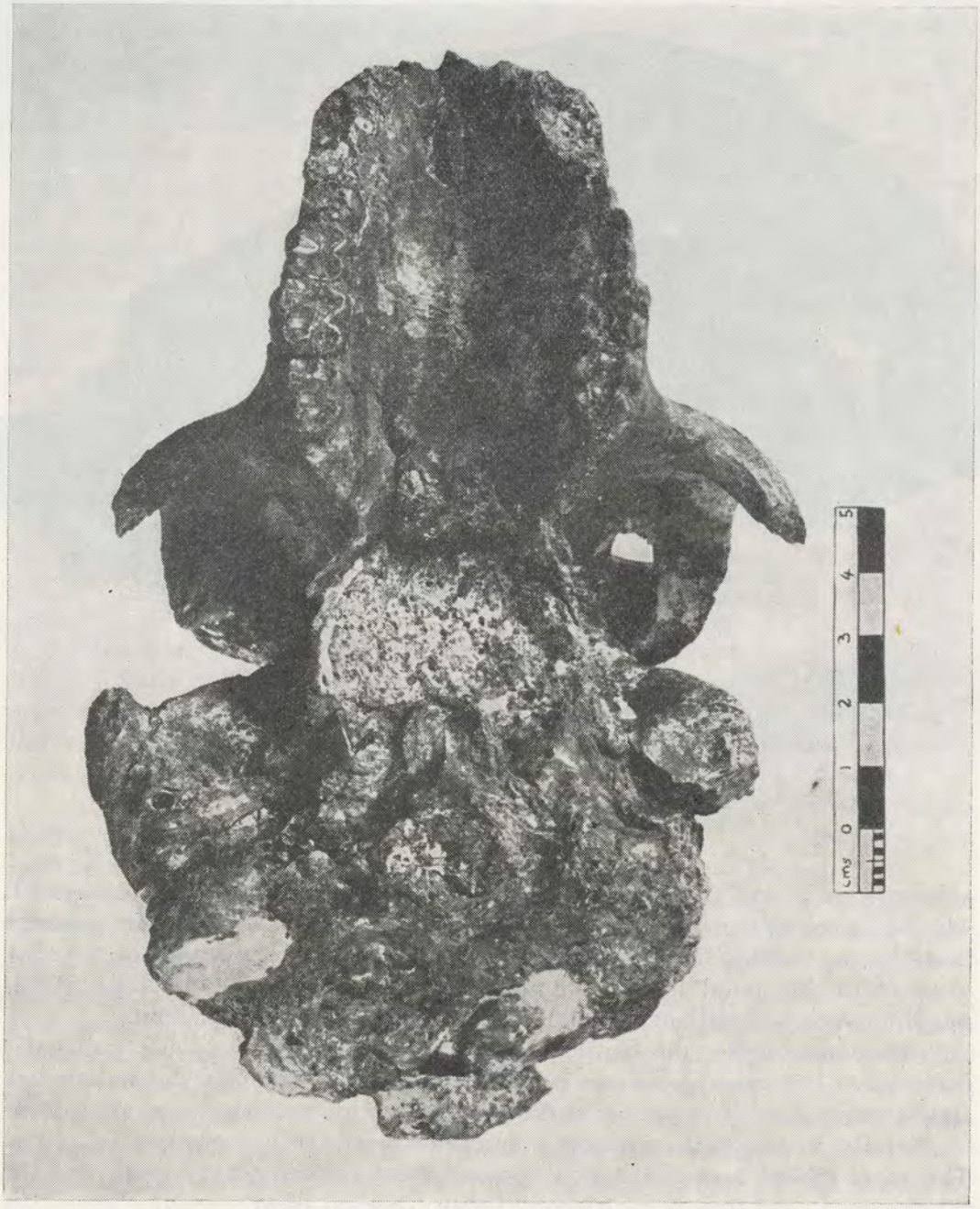


FIG. 2—Basal view of the male cranium of *P. whitei* (56785)



FIG. 3—Lateral view of the female cranium of *P. whitei* (56652)

reduction, but exactly how much cannot be seen as it is still partially embedded in matrix.

The upper teeth in the females 56694 and 56608 (Fig. 5) fit the sizes and morphology of these teeth as previously described in this species (Freedman, 1957 and 1961a). Of particular interest is the great reduction of M^3, especially distally, which these specimens share with those specimens previously described with this tooth present (Tvl. 639, T. 17, T. 20 and T. 25).

Measurements. See Tables 1 and 3.

Remarks. The new material described above is valuable because of two points which it illustrates. The first is the characteristic reduction of M^3 in at least the females of this species and the second is the sexual dimorphism in the size and morphology of the cranium. This latter point is also illustrated by the new material of *Parapapio whitei* and has been discussed above under that species.

PAPIO Erxleben, 1777

The new material includes a number of specimens belonging in the genus *Papio*.

From Taung there are two good *Papio* crania which are referred below to *Papio wellsi*. In addition, in a large block of breccia from that same site, of which only a cast was available to me, there are at least two more crania which can be assigned to this same species.

A number of new specimens of *Papio robinsoni* are described below from Bolt's Farm. Previously, only a single female mandible of that species (B.F. 20) was known from Bolt's Farm (Freedman, 1957).

The new material from Witkrans Cave described below is very fragmentary, but almost certainly all belongs in the species *Papio ursinus*. Previously, Peabody (1954) had listed "*Papio* (and related baboon genera)" from that site.

Papio wellsi Freedman, 1961

Referred material. From Taung, two new skulls (1 and 2 below) are hereby referred to *P. wellsi* and two other skulls (3 below) must almost certainly also be included in this species.

(1) Specimen 56606 from pit 5a is a female cranium lacking only the left zygomatic arch. The specimen is in an excellent state of preservation except for the teeth which are either broken or absent.

(2) Specimen 56605, also from pit 5a, is another well preserved female cranium. The base is still embedded in breccia but, as far as can be seen, no teeth are present.

(3) In a block, 56831, from site 5b, there are at least two good crania, probably female and of this species.

Description. Specimen 56606 is a slightly larger cranium than those of this species previously described (S.A.M. 11728 and T .13—Freedman, 1961a), particularly



FIG. 4—Left: Supero-lateral view of the male cranium of *Parapapio antiquus* (56604). Right: Lateral view of the female cranium of *Papio wellsi* (56605)



FIG. 5—Basal view of female palate of *P. antiquus* (56608)

in the breadths of the muzzle and calvaria. In profile view (Fig. 6), the drop in the inter-orbital region is steep, the drop being further accentuated by the fairly robust supra-orbital tori (Fig. 7). The maxillary fossae are only slightly excavated in the new specimen and the nasal aperture is rather small (Fig. 8). The portion of the maxilla below the orbit is large and gives rise to a robust zygomatic process. There is a large well-marked notch on the inferior part of the maxilla, just before it gives rise to its zygomatic process. The palate (Fig. 9) is horseshoe-shaped and deep and heavy bars of bone limit the posterior palatine foramina posteriorly. The specimen is generally very well preserved and many details of structure—including even the turbinals—can be seen.

Specimen 56605 (Fig. 4) has its base still embedded in a block of matrix,



FIG. 6—Lateral view of the female cranium of *Papio wellsi* (56606)

but its morphology is very similar to that of the new female specimen described above. However, the supra-orbital tori are slightly less robust and the maxillary fossae are more deeply excavated. From the cast of the large block, 56831, the two specimens in that block, which appear to be females of this species, appear to fit well the above and previous description of *P. wellsi* females (Fig. 10).

Measurements. See Tables 1 and 3.

Remarks. The new material agrees well with the previous description of this species (Freedman, 1961a) and adds knowledge of a number of features and of the variability within the species. The new descriptions of the maxilla and zygomatic arch are of particular interest. Unfortunately no new useful dental material is available for study. Because of the similar sizes of the cercopithecoid species found at Taung, a number of new mandibles cannot be assigned with any degree of certainty and are dealt with in a separate section below.

Papio robinsoni Freedman, 1957

Referred material. From Bolt's Farm six new specimens are referred to this species (1—6 below) and seven (7, 8 and 9 below) are referred doubtfully. Except specimens 56797 and 56795, which come from pit 23, all the material comes from pit 6.

(1) Specimen 56795 is a damaged male muzzle, with *C*—M^3 present on the left and the *C* and parts of P^3—M^3 on the right.

(2) Specimen 56766 consists of a bilaterally crushed male muzzle. P^3—M^3 are present on the right and P^3—M^1 on the left. Almost all of these teeth are well preserved and not very worn. An associated right mandibular corpus, almost certainly from the same individual, has P_3—M_3 present, very well preserved and only slightly worn.

(3) Specimen 56767 is a fairly well preserved and almost complete female cranium, lacking only a small left lateral part of the muzzle and calvaria. M^1—M^3 are present on the right and are fairly well preserved.

(4) Specimen 56797 is another almost complete female cranium in which the calvaria is crushed and the teeth are all badly broken.

(5) Specimen 56768 consists of the symphyseal region and most of both corpora of a male mandible. Left P_3—M_2 and right I_2 and P_3—M_3 are present and fairly well preserved.

(6) Specimen 56795 is a small anterior portion of a male mandible with left I_1 and I_2, and the *C* still erupting.

(7) Specimen 56770 is a badly damaged female mandible lacking completely the superior parts of both rami. M_1—M_3 are present on the left and M_2 and M_3 on the right.

(8) Specimen 56771 is the complete lower dentition of a female.

(9) Five specimens (56769, 56772, 56773, 56774 and 56706) each consist of a small posterior part of a mandible with teeth. The sexes of these specimens are not known.



FIG. 7—Dorsal view of the female cranium of *P. wellsi* (56606)

Description. The new material of the male cranium is restricted to two damaged muzzles, 56765 and 56766. The first of these specimens appears to be considerably more robust than the second. The main features of 56765 are a fairly steeply sloping anterior end to the muzzle and only slightly excavated maxillary fossae. Specimen 56766 is characterised by extremely large, deeply excavated maxillary fossae. Unfortunately, the interesting muzzle dorsum region, in which the two maxillae meet over the nasals in the male of this species, has been lost from both specimens.



FIG. 8—Anterior view of the female cranium of *P. wellsi* (56606)

The new female cranial material includes two fairly complete specimens, 56797 and 56767. In general, both specimens fit the description of the female of this species given previously (Freedman, 1957). Of the two specimens, 56797 has a considerably larger muzzle with rather less excavated maxillary fossae and a larger flatter muzzle dorsum. The temporal lines are well developed in 56767. In neither specimen do the maxillae meet over the nasals in the midline.

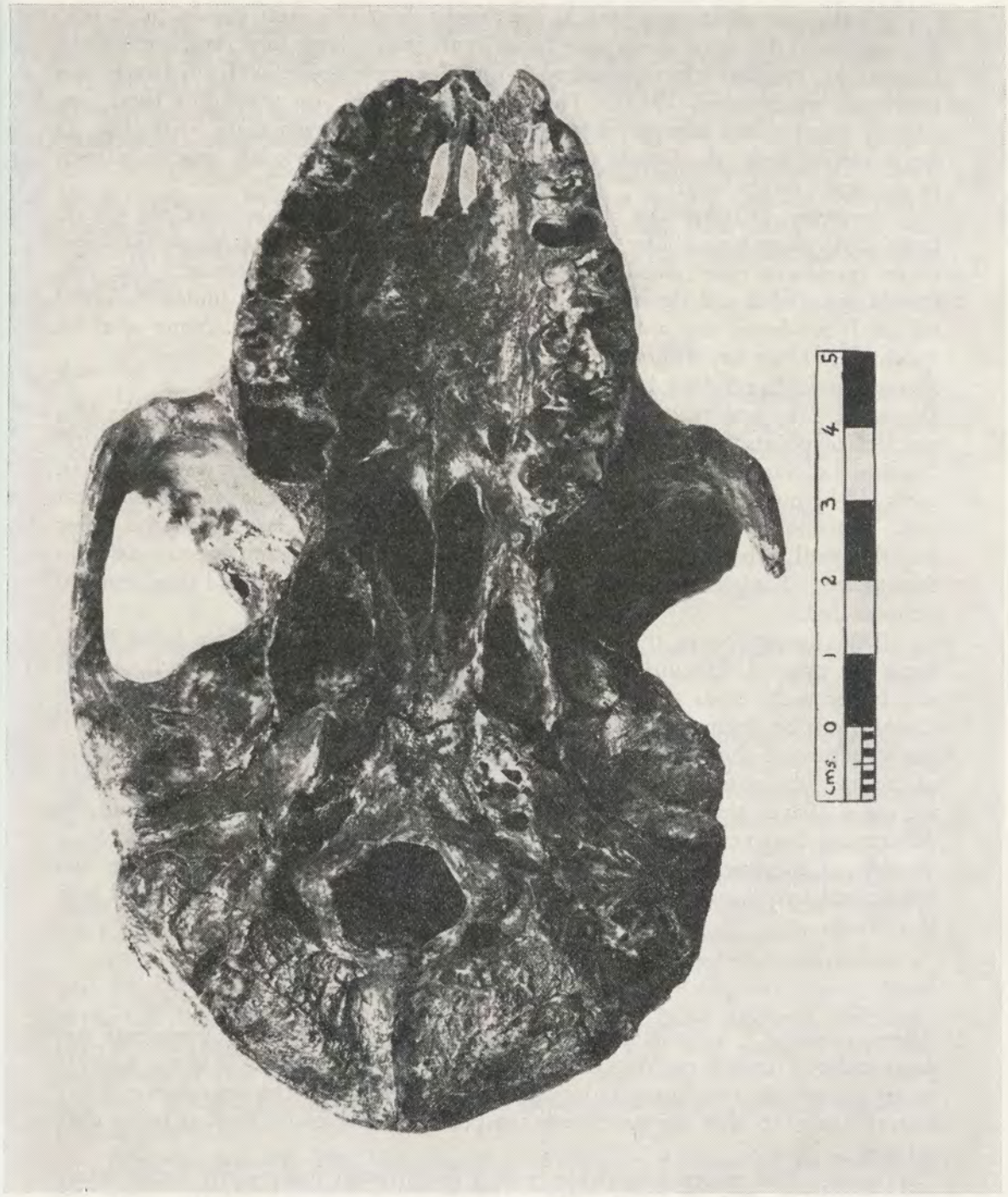


FIG. 9—Basal view of the female cranium of *P. wellsi* (56606)

Of the new male upper teeth, the large robust *C* is well shown in 56765. The molars of this same specimen (Table 2) are rather large in certain dimensions (M^2 and M^3 lengths) when compared to the specimens described from Swartkrans previously (Freedman, 1957). The molars of 56766, on the other hand, are slightly small when compared to those of the Swartkrans male material. As far as can be seen, the female upper molars fit those previously described both in size and morphology.

Specimen 56768 is the robust anterior portion of a male mandible with a large fairly deep mandibular fossa; 56795 is an even smaller anterior fragment of an immature male mandible and shows no features of interest. The two female mandibles and those of unknown sex (described above under Referred material) on dental size and morphology could fit this species. None of these specimens shows any diagnostic details of mandibular structure.

Measurements. See Tables 1—4.

Discussion. The two new male muzzles and the two new female crania vary in a number of points of both size and morphology, but these probably fall within the limits of variability which were indicated by the previously known material. It should be noted, however, that the two female specimens come from different pits. The one new male upper dentition appears slightly large, and the other slightly small, when compared to that of the male *P. robinsoni* specimens from Swartkrans. A slight extension of the range for the species would thus seem to be indicated.

The description in this paper of good *Parapapio whitei* crania from Bolt's Farm has created difficulties in the taxonomy of certain mandibular fragments and lower teeth from this site. Fairly complete mandibles of *P. robinsoni* and *P. whitei* can be distinguished by a study of the size of the canines (mainly male), the structure of the anterior surface of the mandible and the presence and size of the mandibular fossa. Small non-diagnostic regions of the mandible and teeth are too similar in the two species to be separated. Until more is known about the differences between the mandibles and lower teeth of these two species, a number of specimens will have to remain uncertain taxonomically. The two female and five mandibular fragments of unknown sex described above fall into this category.

Papio ursinus (Kerr), 1792

Referred material. A number of small maxillary and mandibular fragments and some isolated teeth from Witkrans are referred to this species. It is not possible to say for certain how many individuals are represented. The appearance of the material suggests that the specimens are probably best considered as being only subfossil.

Description. The material available is very fragmentary and mostly rather badly damaged. A male left maxillary fragment with some teeth (56701), parts of a male mandible with teeth (56773) and a left mandibular corpus with teeth

(56703) of a female are the only specimens whih include parts of the cranium or mandible. These are all only small fragments and show little morphological detail. Of the dentition, there are, in addition, eight isolated incisors, four male *C* teeth and over two dozen isolated premolars and molars. The best preserved of these specimens have been measured.

Measurements. See Tables 3 and 4.

Remarks. On size, morphology and probable dating, there is nothing to exclude these fragments from being assigned to the species *Papio ursinus*. However, it should be pointed out that the dimensions of these teeth (like those of *P. ursinus*) differ very little from the middle Pleistocene species *Papio robinsoni* known from Swartkrans, Cooper's, Kromdraai, Bolt's Farm, etc.

CERCOPITHECOIDES Mollett, 1947

The new material from Bolt's Farm includes three specimens which are referred to *Cercopithecoides williamsi*, the single species now recognised in the genus *Cercopithecoides* (Freedman, 1961b). This is the first record of this genus from Bolt's Farm.

No specimens of this genus were found in the material from Taung or Witkrans.

Cercopithecoides williamsi Mollett, 1947

Referred material. Three new female specimens recovered from Bolt's Farm. Specimens 56784 and 56782 come from pit 23 and specimen 56778 comes from pit 6.

(1) Specimen 56784 is the complete cranium and mandible of an old female. The cranium lacks only the right zygomatic arch and the posterior part of the calvaria; the mandible lacks the left gonial region, the right corpus posterior to M_2 and the right ramus. Of the teeth, only the right I^1 and the right M_3 are missing, but the teeth which are present are all very worn and badly damaged.

(2) Specimen 56782 is another female cranium and mandible, but it is very badly bilaterally crushed. Only general features of the cranium and mandible can be discerned; the teeth are very badly damaged and fragmented.

(3) Specimen 56778 is the anterior portion of the muzzle of a third female, with P^3—M^2 bilaterally present and in a fairly good state of preservation. Parts of the left I^2 and the right M^3 are also present, but in a badly damaged condition.

Description. The three new female specimens agree well with material of female individuals of this species previously described from the Taung, Sterkfontein, Makapan and Swartkrans limestone cave deposits in South Africa (Freedman, 1957 and 1961b).

In norma lateralis (Fig. 11), specimen 56784 is very similar to the only good previously described female skull of this species (STS. 394A). However, the supra-orbital tori are more robust and the initial angle of the nasals below the



FIG. 10—Block of breccia from Taung containing a large number of skull and post-cranial cercopithecoid specimens (56831)

tori is rather steeper. Posterior to the tori, the ophryonic groove is even deepe in the new specimen than in the Sterkfontein specimen and the rise of the calvaria roof behind the groove is steeper. In the new specimen, the temporal lines, particularly anteriorly, are very well-marked and may have met anterior to the inion; the zygomatic arch of this specimen is robust. As far as can be seen, female 56782, the badly crushed specimen, conforms to the description of the female skull as given here and previously. The specimen is interesting in that it shows a very long post-glenoid process (about 12 mm.). This process is also long in STS. 394A, but shorter in 56784.

Viewed from the front (Fig. 12), the new female cranium, 56784, shows its very wide inter-orbital measurement and a marked downward curve of the supra-orbital tori medially towards the glabella. The nasal bones in this specimen are most peculiar in that they are flat and lie on a lower plane than the long nasal processes of the maxilla, which project forwards as ridges on either side of them. The canine eminence in all three new specimens is well marked. On the left canine eminence of 56784 there is a fairly large opening with raised edges which may have been caused by the root of the *C* emerging or by an apical abscess.

The palate of 56784 (Fig. 13) shows similar features to those described in the male M. 2999 (Freedman, 1961b), namely, the long slit-like posterior palatine foramina, bars of bone bounding the palate posteriorly and the raised posterior part of the inter-palatine suture.

Of the upper female dentition, the incisors are again seen to be very small and the *C* large, in both 56784, where these teeth are present, and in 56778, where the sockets of the teeth give a good indication of the tooth size. The pre-molars and molars of 56784 are very badly damaged, but those of 56778 are fairly well preserved and fit the previously described pattern for the species. In the latter specimen (56778), large cuspules are present buccally and lingually between the main cusps on M^2 and buccally only on M^1.

The new female mandible, 56784, conforms to the description of the mandible of this species as previously given (Freedman, 1957). The symphyseal region is flattened and fairly steep and a single foramen symphyseosum is present. On the antero-inferior part of the corpus there is a single mental foramen (Fig. 11). The ramus, in the fashion described previously for this genus, is antero-posteriorly long, and displaced buccal to M_3, forming a broad ledge next to this tooth (Fig. 14). The coronoid process is very large and much higher than the condyle, which shows virtually no neck. The crushed mandible of 56782 is similar to the one just described.

The lower teeth of 56784 (Fig. 14) are very worn and badly damaged, but follow the patterns and sizes of the equivalent teeth as previously described.

Measurements. See Tables 1—4.

Remarks. The existence of *C. williamsi* at Bolt's Farm is proved by this new material. There is no obvious difference between the material from the two pits. The new material, although not very extensive, confirms and extends the



FIG. 11—Lateral view of the female cranium and mandible of *Cercopithecoides williamsi* (56784)

description of a number of features previously described from single specimens of this species. Too few dental dimensions are available for a statistical comparison with specimens of the species from other sites, but even the few known show that the Bolt's Farm material is probably most closely linked to those from Swartkrans. From what is known of the relative dating of the South



FIG. 12—Anterior view of the female cranium of *C. williamsi* (56784)

African limestone cave deposits, this would fit in with the previously proposed chronocline in the *C. williamsi* material (Freedman, 1961b).

With regard to the affinities of the genus, which are at present still obscure, a few relevant remarks can now be made. The bilophodont molars seem clearly to indicate that the genus should be placed in the Cercopithecidae. The prominent tempora lines and the very large coronoid process both suggest a par-

ticularly large temporalis muscle. The zygomatic arch is robust, suggesting that masseter was also a relatively large muscle. The small molars with high cusps and rather deep infoldings of enamel between the cusps, plus the relatively large masticatory muscles described above, might well be indicative of a chopping—possibly leaf-eating—function. The general skull shape, with short muzzle and relatively large female canines, is of the type associated with the monkey-like Cercopithecidae. It therefore seems that *C. williamsi* was probably a leaf-eating cercopithecoid with monkey-like characters in the skull. As this pattern of features is that seen in the modern Colobinae, it is proposed that the genus Cercopithecoides, of which *C. williamsi* is the only known species, be included in the Colobinae, as suggested previously by Robinson (1952).

Discussion

The following are the cercopithecoid species now known to occur at the sites discussed in this paper:—

1. Witkrans: *Papio ursinus*.
2. Bolt's Farm: *Parapapio broomi* (pit 23), *Parapapio whitei* (pit 23), *Papio robinsoni* (pits 6 and 23) and *Cercopithecoides williamsi* (pits 6 and 23).
3. Taung: *Parapapio jonesi*, *Parapapio whitei* (pits 5 and 5a), *Parapapio antiquus* (pits 5a and 5b), *Papio wellsi* (pits 5a and 5b), *Papio izodi* and *Cercopithecoides williamsi*.

Except for *Parapapio jonesi*, *Papio izodi* and *Cercopithecoides williamsi* from Taung, specimens of all of these species were found in the new material described in this paper.

A number of specimens from Taung which have not been described above require comment. As discussed in a previous paper (Freedman, 1961a), the cercopithecoid species known from Taung (with the exception of *C. williamsi*) are of rather similar dental size and morphology. As a result, unless diagnostic regions are present, it is very difficult to assign certain specimens. Of a number of specimens which fall into this category, two new cranial specimens might be mentioned. Specimen 56610, an immature crushed female muzzle from pit 5a, shows a superficial resemblance to *Parapapio antiquus*. However, the crown of an unerupted M^3 can be seen which appears to be large when compared with those of the described equivalents of that species and the specimen is thus best left in abeyance. The measurements of the upper teeth of this specimen are included in Table 3 under Taung. Also, specimen 56653, a very fragmentary muzzle and mandible with teeth of a female from pit 5, probably belongs in *Parapapio whitei*. No measurements are possible on the specimen and, because of the similarity in size of the Taung species, it too is best left in abeyance.

The new material from Taung does not include good associated crania and mandibles and hence, as was found in the study quoted above, the mandibles recovered from this site cannot be classified with any degree of certainty. For



FIG. 13—Basal view of the female cranium of *C. williamsi* (56784)

the sake of completeness, the best of the new mandibles recovered from Taung are listed and briefly described below and their measurements included at the end of Table 4.

Mandibles from Taung.

(1) Specimen 56660 from pit 5b, is the well preserved mandible of an

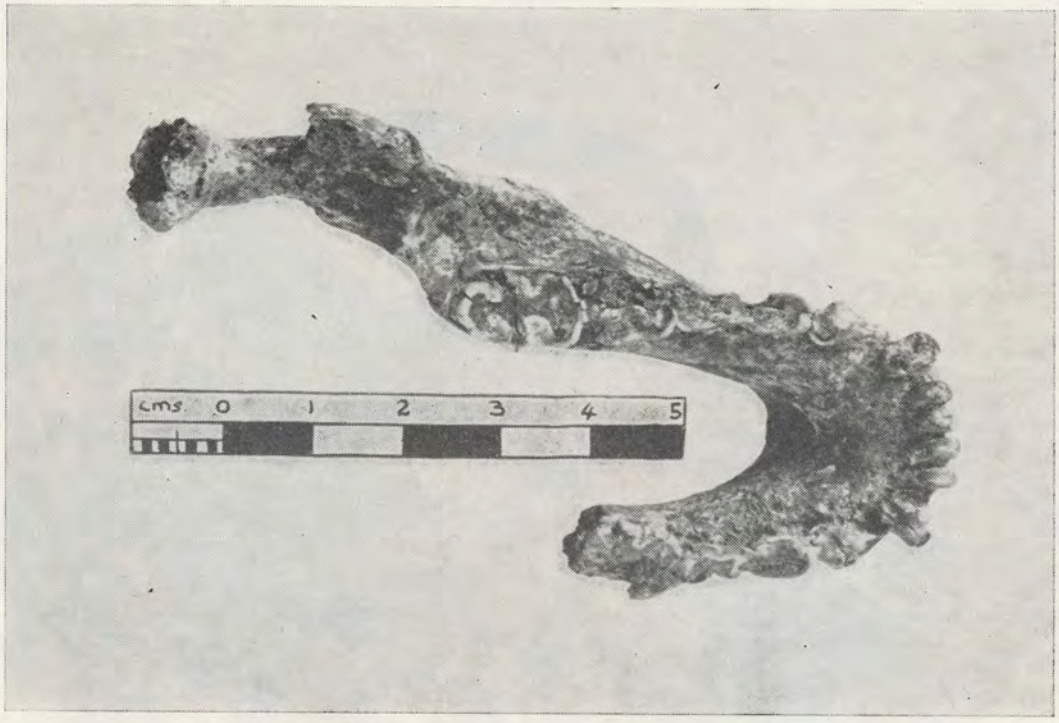


FIG. 14—Occlusal view of the female mandible of *C. williamsi* (56784)

almost mature male (Fig. 15). Only the left ramus is completely missing. Of the teeth, the right *C*—M_3 and the left M_1—M_3 are present and most are fairly well preserved.

(2) Specimen 56618, from pit 5, is the symphyseal region and left corpus of a male. On the right the damaged *C* is present; on the left the *C*—P_4 are present and some fragments of the molars.

(3) Specimen 56693, from pit 5b, consists of the almost complete left corpus with P_3—M_3, and part of the right corpus with M_1, M_2 and the anterior half of M_3. The left teeth are very worn, but only slightly damaged; the right teeth are badly damaged. The specimen comes from a male individual.

(4) Specimen 56691, from pit 5b, is a badly damaged, but almost complete mandible of a female, lacking only the rami. The left *C* and right M_3 are the only relatively undamaged teeth.

(5) Specimen 56623, from pit 5, is a female symphyseal region and the anterior parts of the right and left corpora. The left I_1—P_4 and the right I_1—M_2 are present, but posterior to P_3 on the right and P_4 on the left all are badly damaged.

(6) Specimen 56626, from pit 5, is part of the right corpus of a female mandible with P_3—M_1.

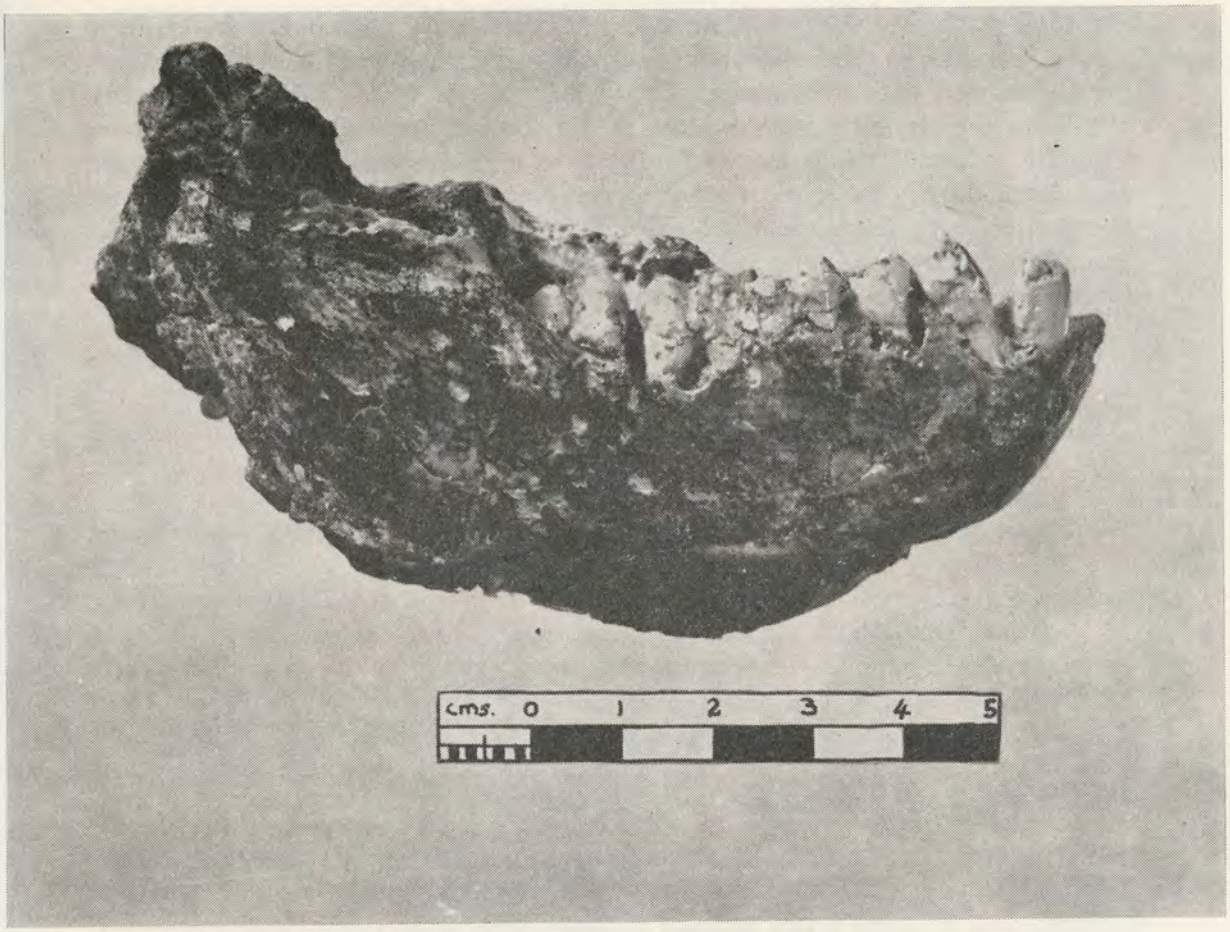


FIG. 15—Lateral view of a male mandible from Taung (56660)

(7) Specimen 56655, from pit 5, is part of the left corpus of a mandible of a specimen of unknown sex. P_4—M_3 are present, mostly badly damaged.

(8) Specimen 56831, from pit 5b, is a large block (Fig. 10) with a number of cercopithecoid specimens partially embedded in matrix. Among these there are four good mandibles. The best specimen is an almost complete male mandible with most of the teeth still present and the next best is the left half of a mandible with P_4—M_3. There is also a small posterior portion of a mandible and a juvenile mandible.

ACKNOWLEDGMENTS

My thanks are due to Professor R. A. Stirton and the University of California for allowing me to borrow and describe the above material. The University of the Witwatersrand kindly made me a grant to transport the material from

and back to the Museum of Paleontology, University of California. Dr H. B. S. Cooke, formerly of the Department of Geology, University of the Witwatersrand, greatly assisted with information about the localities of the various specimens. Whilst in the United States of America, Dr Cooke prepared most of the above material and made preliminary identifications. The Wenner-Gren Foundation, New York, kindly made me a grant to study *Colobus* monkeys in East Africa for comparison with *Cercopithecoides*. The photograph used for Fig. 10 was kindly loaned to me by Dr Cooke. Miss A. Scot Skirving, Department of Anatomy, University of Sydney, kindly typed the final draft of this paper.

References

Dart, R. A., 1924. The Rooiberg cranium. *S. Afr. J. Sci.*, 21: 556-568.

Freedman, L., 1957. The fossil Cercopithecoidea of South Africa. *Ann. Transv. Mus.*, 23: 121-262.

Freedman, L., 1961a. New cercopithecoid fossils, including a new species, from Taung, Cape Province, South Africa. *Ann. S. Afr. Mus.*, 46: 1-14.

Freedman, L., 1961b. Some new fossil cercopithecoid specimens from Makapansgat, South Africa. *Palaeont. Afric.*, 7: 7-45.

Peabody, F. E., 1954. Travertines and cave deposits of the Kaap Escarpment of South Africa, and the type locality of *Australopithecus africanus* Dart. *Bull. geol. Soc. Amer.*, 65: 671-705.

Robinson, J. T., 1952. The Australopithecine-bearing deposits of the Sterkfontein area. *Ann. Transv. Mus.*, 22: 1-19.