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THE *PARAPAPIO* SPECIES OF STERKFONTEIN, TRANSVAAL, SOUTH AFRICA

by

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ABSTRACT

The premolar and molar dimensions of the *Parapapio* specimens hitherto described from the South African lower Pleistocene deposits at Sterkfontein have been re-examined. The relatively minor sexual dimorphism in these teeth (except P3 length) was confirmed. 103 new cercopithecoid specimens from Sterkfontein were tentatively assigned to the 3 previously described *Parapapio* spp. from that site. The new and old samples of each species were compared and then pooled. Analysis of this new enlarged sample, and also the newly available distribution data of *Parapapio* from other South African deposits, both tend to support the validity of *3 Parapapio* spp., *P. jonesi, P. broomi* and *P. whitei*, at Sterkfontein.

INTRODUCTION

The South African lower Pleistocene limestone deposits have yielded, over the years, a very considerable number of fossil cercopithecoid specimens. In the most recent review of the material recovered (Freedman, 1957), about 1 250 specimens were examined and, since then, several additional significant groups of specimens have been reported (Freedman, 1960, 1961 & 1965). From this material a total of 6 genera, including 14 species, have been described.

Of this large and varied cercopithecoid assemblage, about 600 specimens come from Sterkfontein and almost all of the material has been referred to 3 species of the genus *Parapapio*. (A few specimens of *Cercopithecoides williamsi* are present). The genus *Parapapio* was first described by Jones (1937) for a batch of specimens from Sterkfontein, all of which he included in the type species *P. broomi*. Subsequently, Broom (1940) decided that the Sterkfontein material included not one but 3 species of *Parapapio* and he named a slightly larger species *P. whitei*, and a smaller one, *P. jonesi*. Material of these 3 species has now also been described from various other South African limestone deposits, namely Swartkrans, Makapan, Taung, Bolt's Farm and Kromdraai (Freedman, 1970). In addition, Broom (1940) re-studied some *Papio* material from Taung and transferred it to *Parapapio* (= *P. antiquus*). Although the various *Parapapio* species were originally differentiated primarily on the basis of dental size variations, subsequent studies utilising more and better material have since revealed a number of morphological cranial and dental differences between the 4 described species. The present study will, however, only be concerned with dental metrical features.

Recent work at Sterkfontein (Tobias and Hughes, 1969) has brought to light a further good sample of cercopithecoid specimens. The present paper is concerned with re-examining statistically the specific validity of the 3 *Parapapio* species at Sterkfontein in terms of the premolar and molar teeth, assessing the newly recovered material and putting on record the premolar and molar size statistics for the total samples now available of each of the 3 *Parapapio* species from this site.

MATERIALS AND METHODS

The Sterkfontein material of *Parapapio* previously described by Freedman (1957) was used for the initial analyses of this study. The new material available from Sterkfontein included a total of 565 specimens of which 103 (Appendix 1–3) were used in the later dental metrical analyses. The area from which the new material came is listed as STW, D13, 1969–1970 (Tobias & Hughes, 1969). This area is a rubble dump near the East Pit and consisted of "large masses of blasted-out breccia" resulting from the early lime working. The material is rich in bone; a considerable variety of mammals and other vertebrates are represented (Tobias & Hughes, 1969).

The system of measurements used in this study follows Freedman (1957). Breadth measurements are mesial (bm) and distal (bd); length is maximum (l). Measurements in brackets (Appenddix) are approximate due to damage. Measurements were taken to the nearest 0,1 mm but mean values are given to 2 decimal places. Where only one decimal place is given in the tables for a 'mean value' only a single observation was available.

ANALYSIS

A large amount of *Parapapio* material from Sterkfontein is now available. However, only a small proportion of those specimens can be assigned with certainty to a specific sex and species. Further, because of the fragmentary nature of the specimens, insufficient numbers are available in such groups for multivariate analyses of, say,

P3–M3 or even M1–M3 of either the upper or the lower jaw. Even when analyses of particular single teeth for such comparisons are attempted, most sample sizes are still statistically small.

(a) Sexual Dimorphism.

Fortunately, one of the features of the genus *Parapapio* is the very small statistical size difference between the sexes in the premolars (except P3 length) and the molars. To examine the possibility of pooling the sexes in the comparisons contemplated, it was therefore decided to compare the dimensions of these teeth in the two sexes by "t" tests. Where only a single specimen of one sex was available for a particular comparison, a modified "t" test (Simpson, Roe & Lewontin, 1960, p. 183) was used. For this initial study only the previously described and sexed material (Freedman, 1957) was utilised.

Tables 1A and 1B show the results of this analysis. Of the 71 "t" tests performed, in the upper dentition only 5 tests were significant at or above the 5% level and in the lower teeth 9 tests revealed this level of significance. Inadequate male samples of *P. whitei* severely limited the number of upper dentition tests possible but the lower teeth comparisons in this taxon confirm the very low degree of dental sexual dimorphism in the genus. It will be noted that, possibly because of the small sample sizes, in 6/14 *P. broomi* lower dimensions, 4/13 *P. jonesi* upper dimensions and 11/16 *P. whitei* measurements, the female mean figure is actually larger than that of the male. This finding is surprising in view of the larger overall size of the male cranium as compared with that of the female in all of the comparisons hitherto possible (Freedman, 1957 and 1965).

From the results of the analysis of metrical sexual dimorphism in the premolar–molar dentition of the 3 *Parapapio* spp., it would seem that pooling of data from the 2 sexes for inter-specific comparisons can be validated except, as expected, for P3 l(h).

(b) Comparison of the 3 *Parapapio* spp. at Sterkfontein.

Still using the previously described material only, a comparison was next made of the premolar and molar dimensions of the 3 *Parapapio* spp. from Sterkfontein, using pooled male and female data. The results are shown in Tables 2A and 2B and "t" tests are again used to assess the comparisons. Of the 39 tests on upper tooth dimensions, 31 are significant at the 5% level or higher; using only the molars, 26/27 tests were significant. In the lower tooth comparisons, of the 42 "t" tests performed, 31 were significant at the 5% level or better; in the molars, 27/30 tests were significant. The *P. whitei–P. broomi* comparisons of the lower teeth include the fewest number of significant "t" test results, but even here, 7/10 molar dimensions differ at the 5% level or higher. For each dimension in both the upper and lower teeth the pattern is consistently: *P. whitei* >*P. broomi* >*P. jonesi*.

(c) Comparison of the new and old samples of each of the 3 *Parapapio* spp. from Sterkfontein.

The 103 newly excavated *Parapapio* specimens from Sterkfontein used in this study include only a very few fairly complete cranial and mandibular specimens (Plates 1 and 2); most of the specimens are only single teeth or small groups of teeth. All of these specimens were tentatively classified on the assumption of 3 progressively larger species being present. (In the Appendix they are listed under individual tooth types as *P. jonesi, P. broomi* and *P. whitei*). Assignment was essentially subjective and based on overall size and apparent size discontinuities. The 3 groups resulting (= sample I) were then compared by "t" tests with the earlier sample (Freedman, 1957) from the same site (= sample II). Of the 31 upper tooth comparisons made (Table 3A), only 3 tests (2 of these in *P. whitei*) were significant at the 5% level or higher; in the 32 lower tooth comparisons (Table 3B), again only 3 significant differences (all in *P. jonesi*) were found. Because of the paucity of material of *P. whitei,* only P^3, P^4, M^1 and M_3 could be compared. Of the 11 tests on these *P. whitei* teeth, 2 were significant, 1 at the 0,01% level and the other at 0,001% level. Comparing the various mean values for samples I and II for all 3 species, in the upper teeth the new sample mean values were greater than those of the old sample in all but 7 of the 31 instances; in the lower teeth, the new sample mean was greater than the old in only 11 out of the 32 comparisons made.

(d) Statistical summary of the dimensions of the upper and lower premolar and molar dimensions of the *Parapapio* spp. from Sterkfontein.

Tables 4A and B are derived from the combined old and new samples. The numbers of specimens of *P. whitei* are mostly still small but the *P. broomi* and *P. jonesi* samples are now mostly over 10 and half of the samples include over 20 individual measurements. An oddity is the fact that the numbers of *P. broomi* specimens in the various categories are about double those of *P. jonesi* in the upper teeth, whilst in the lower teeth the *P. jonesi* numbers are mostly greater. It is not at present clear whether these differences could be due to chance effects or to misassignments. The coefficients of variation (C.V.) and the standard deviations (S.D.) are, for the most part, reasonable, except for P3 l(h). These dimensions (and those of the canines) exhibit sexual dimorphism and hence high standard deviations and coefficients of variation are to be expected when the 2 sexes are lumped. The other high values for these statistics are for certain upper tooth dimensions (e.g. P^3 b, P^4 l and M^1 l) of *P. whitei.* Sample sizes are small here and the high values result from single rather large specimens.

(e) Size-frequency distribution of M_3 of *Parapapio* spp. from Sterkfontein.

To investigate further the *Parapapio* specimens from Sterkfontein, it was decided to re-examine one of the major diagnostic criteria hitherto used for classifying this material. For this purpose the M_3 tooth was selected. This tooth was chosen as the hypoconulid makes identification certain, whereas with the other molars there is often some uncertainty as to the position of the tooth in the toothrow, and damaged roots may even make an upper-lower tooth distinction difficult. Further, for this tooth a good sample of over 50 specimens was available. This sample includes the previously described material (Freedman, 1957), which had only been utilized if the sex could be determined, and the new batch of specimens (Appendix) in which every available specimen was measured.

Figure 1 is a histogram of M_3 l for 48 specimens of these 2 batches of *Parapapio* specimens from Sterkfontein. With no selection or subdivision the distribution is obviously bimodal and possibly trimodal. When 2 dimensions of M_3 (mesial breadth, bm, and maximum length, l) are plotted for the 41 available specimens (Fig. 2), there is an apparent cluster below about 10,5 mm breadth and 13,5 mm length, and another less clear group above about 11,0 mm breadth and 16,0 mm length. For making the second subdivision, a cut off at about 16,0 mm appears clear; for the breadth, 11,0 mm seems the logical point on the basis of overall tooth size, as a lower cut off would include teeth very much shorter and hence unreasonably much smaller in overall size. Subdivisions at these two length-breadth positions result in 3 groups which correspond with the 3 species postulated for this material.

The separation of the 3 species using the breadth and length of M_3 becomes more obvious if the 2 dimensions are combined into indices (Table 5). Two indices have been used; the robustness value, bm x l, and the crown module, $(bm + l)/_2$ (Goose, 1963). For the robustness values there is only overlap between *P. jonesi* and *P. broomi*. This overlap is due to a single large tooth, a male *P. jonesi* (STS. 258); the next largest tooth in *P. jonesi* has a robustness value of only 123,69. For the crown module ranges there is no actual overlap but the same single large male *P. jonesi* tooth just equals the lowest *P. broomi* figure.

DISCUSSION

It has been previously noted (Freedman, 1957) that the overall ranges for each dimension (by sex) of the pooled *Parapapio* material from Sterkfontein (i.e. of all 3 species together) appear to be too great for a single species, when a modern cercopithecoid species (*Papio ursinus*) is used as a standard. The possibility was also considered that the whole of the *Parapapio* material might represent a simple, temporal size increase, as the Sterkfontein material is generally believed to have accumulated over a considerable time. However, during excavation of the site there was no apparent evidence of such a size increase up through the deposit (Robinson—personal communication).

Analysis of the distribution of the *Parapapio* material from the other South African limestone deposits where this genus has been found also tends to discount the possibility that the Sterkfontein *Parapapio* material represents a chronocline. Thus, examination of Table 6 shows that only at Sterkfontein and Makapan are all three *Parapapio* species present. These are, however, the only 2 sites from which reasonable numbers are available and it is also interesting to note that the 3 species are present at these sites in very similar proportions. (The value of *chi square* obtained on comparing these two distributions is 1 803 with 2 degrees of freedom, which is well below the 5% level of significance). Although numbers are small at the other sites, it is noteworthy that at Taung only *P. jonesi* and *P. whitei* have been recovered, whilst from Bolt's Farm only *P. broomi* and *P. whitei*. Of special interest is the fact that only *P. jonesi* has been found at both Swartkrans and Kromdraai, which are both of more recent age than Sterkfontein and Makapan (Brain, 1958). These latter findings all take on added significance when one recalls that *P. broomi* is by far the most common form at both Sterkfontein and Makapan, whilst *P. whitei* is the least common.

Maier (1970) has recently described twenty important new specimens from Makapan which he refers to the 5 previously described species from that site. Of this very good material, he refers 6 specimens to *P. jonesi*, 7 to *P. broomi* and 2 to *P. whitei*. He also suggests that, on the basis of this new material, several previously described *Parapapio* specimens from Makapan require reclassification. Maier gives very full anatomical descriptions of the new specimens and is able to extend considerably our morphological knowledge of the populations of these 3 species at that site. However, although detailed measurements of the various specimens are included, he has not attempted any detailed metrical comparisons. It would seem that a full statistical re-assessment of the 69 *Parapapio* specimens now known from Makapan (similar to that made here for Sterkfontein) would be extremely valuable. The two populations could then be compared both morphologically and metrically and, hopefully, would resolve a number of the presently contentious aspects.

The analyses made earlier, and also the above considerations, all seem to support the probability that the Sterkfontein *Parapapio* material represents 3 species and the scanty cranial evidence available also tends to support this same hypothesis (Freedman, 1957 and 1965). A recent study by Swindler, McCoy and Hornbeck (1966) is also of interest in this connection, as these authors have shown that, on dental metrical data alone, two extant cercopithecoid species, *Papio ursinus* and *Papio anubis*,

show very considerable overlap for all dental dimensions studied.

From the foregoing analysis and review, it would then seem that 3 species of increasing size, *P. jonesi, P. broomi* and *P. whitei*, still best account for the *Parapapio* material hitherto described from Sterkfontein.

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TABLE 1 A

STATISTICAL COMPARISON OF THE MALE AND FEMALE UPPER PREMOLAR AND MOLAR TEETH IN EACH OF THE 3 *PARAPAPIO* SPP. FROM STERKFONTEIN (in mm)

Species	Statistics	P^3		P^4		M^1			M^2			M^3		
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
P. broomi	Male	8,15	8,33	8,94	6,63	9,90	9,03	9,95	11,47	10,87	11,38	11,34	9,04	11,34
	Female	7,33	6,49	8,32	6,47	9,52	8,77	9,63	10,86	10,11	10,98	10,53	8,77	11,09
	"t"	** 4,02	* 2,54	* 2,16	1,19	1,86	0,76	1,35	1,62	*** 4,41	1,58	2,01	0,70	0,76
	d.f.	12	13	16	15	14	10	15	9	12	15	9	9	10
P. jonesi	Male	7,5	4,3	7,7	5,6	9,00	8,60	8,30	10,40	9,60	10,15	10,85	8,45	10,25
	Female	7,05	5,38	7,70	6,03	8,77	7,83	8,87	10,45	8,85	10,13	9,80	7,87	9,63
	"t"	1,15	0,73	0,00	2,71	1,75	1,29	0,88	0,12	1,24	0,03	3,21*	1,29	1,45
	d.f.	3#	2#	2#	3#	2	2	4	1	1	3	3	3	3
P. whitei	Male	–	–	8,6	6,7	–	–	10,4	–	–	–	–	–	–
	Female	7,87	7,42	8,78	6,90	10,57	10,00	10,56	12,83	11,82	12,72	12,80	11,35	12,77
	"t"	–	–	0,44	0,23	–	–	0,29	–	–	–	–	–	–
	d.f.	–	–	4#	4#	–	–	4#	–	–	–	–	–	–

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001
modified "t" test (Simpson, Roe & Lewontin, 1960, p. 183)

TABLE 1 B

STATISTICAL COMPARISON OF THE MALE AND FEMALE LOWER PREMOLAR AND MOLAR TEETH IN EACH OF THE 3 *PARAPAPIO* SPP. FROM STERKFONTEIN (in mm)

Species	Statistics	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
P. broomi	Male	6,00	14,5	7,15	7,75	7,97	8,03	9,80	10,15	9,93	11,33	10,05	9,10	5,95	14,83
	Female	5,50	8,37	6,98	7,14	8,27	8,34	9,09	9,93	9,43	11,56	10,13	9,30	6,77	14,71
	"t"	1,60	*** 5,60	0,53	1,74	0,79	0,74	1,32	0,41	1,10	0,53	0,17	0,44	1,51	0,29
	d.f.	8	8	6	8	6	6	8	7	7	9	5	8	3	10
P. jonesi	Male	5,45	14,95	7,01	7,05	8,08	8,08	9,10	9,64	9,54	10,78	9,50	8,67	4,60	13,2
	Female	4,90	8,69	6,50	6,66	7,36	7,47	8,42	9,31	9,02	10,39	9,20	8,35	5,04	12,82
	"t"	** 3,13	*** 9,00	2,10	* 2,32	*** 5,07	** 4,25	1,78	1,51	* 2,38	2,04	1,03	0,88	1,10	1,41
	d.f.	12	12	15	13	10	9	13	12	11	13	6	7	4	7
P. whitei	Male	5,53	16,4	7,05	7,80	8,30	8,65	9,38	10,65	10,70	12,13	11,10	10,23	6,5	16,17
	Female	5,77	11,33	7,20	7,60	8,67	8,87	10,17	10,63	10,30	12,97	11,00	10,40	–	16,67
	"t"	1,12	2,40	0,26	0,41	1,04	1,13	** 5,01	0,08	1,70	* 2,91	0,67	0,39	–	1,34
	d.f.	4	2 #	3	3	3	3	5	3	3	4	3	3	–	4

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001
modified "t" test (Simpson, Roe & Lewontin, 1960, p. 183)

TABLE 2 A

STATISTICAL COMPARISON OF THE UPPER PREMOLAR AND MOLAR TEETH (in mm) OF *PARAPAPIO* SPP. FROM STERKFONTEIN (DATA FROM FREEDMAN, 1957)

Species		P^3		P^4		M^1			M^2			M^3		
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
P. broomi: Mean		7,64	7,23	8,59	6,54	9,64	8,81	9,65	11,23	10,49	11,12	10,90	8,89	11,19
P. jonesi: Mean		7,10	5,28	7,66	5,90	8,74	8,07	8,62	10,16	9,12	10,14	10,22	8,10	9,88
P. whitei: Mean		7,87	7,42	8,75	6,87	10,57	10,00	10,53	12,83	11,82	12,72	12,80	11,35	12,77
P. broomi vs *P. jonesi*	"t"	2,06	2,08	** 2,98	*** 3,92	*** 5,58	** 3,08	*** 4,78	** 3,26	*** 5,53	*** 3,60	1,62	* 2,28	*** 4,20
	d.f.	19	17	21	20	24	19	28	18	20	20	14	14	15
P. jonesi vs *P. whitei*	"t"	* 2,70	1,35	*** 6,21	* 2,48	*** 9,43	*** 6,21	*** 5,40	*** 8,96	*** 6,95	*** 6,91	** 4,71	*** 7,52	** 5,13
	d.f.	6	6	9	9	9	10	10	9	9	9	5	5	6
P. whitei vs *P. broomi*	"t"	0,65	0,19	0,52	1,55	*** 4,28	*** 4,60	** 3,55	*** 5,12	*** 4,87	*** 5,76	** 3,26	*** 4,83	** 3,61
	d.f.	17	17	22	21	21	17	24	19	21	21	11	11	13

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001

TABLE 2 B

STATISTICAL COMPARISON OF THE LOWER PREMOLAR AND MOLAR TEETH (in mm) OF *PARAPAPIO* SPP. FROM STERKFONTEIN (DATA FROM FREEDMAN, 1957)

Species		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
P. broomi: Mean		5,63	11,16	7,06	7,23	8,20	8,24	9,31	10,07	9,72	11,42	10,19	9,30	6,22	14,72
P. jonesi: Mean		5,07	10,78	6,77	6,82	7,51	7,59	8,61	9,29	9,02	10,42	9,30	8,40	4,95	12,71
P. whitei: Mean		5,65	12,60	7,14	7,68	8,52	8,78	9,71	10,64	10,46	12,55	11,06	10,30	6,50	16,42
P. broomi vs *P. jonesi*	"t"	***3,77	0,32	1,68	**2,85	***4,22	***3,88	**3,01	***3,92	**3,10	***5,97	***4,73	***4,95	***4,96	***8,31
	d.f.	31	31	31	33	27	26	33	30	29	32	20	24	15	27
P. jonesi vs *P. whitei*	"t"	**3,20	1,02	1,44	***4,44	***4,91	***6,07	***3,98	***5,31	***4,88	***9,92	***11,00	***8,17	***5,06	***12,01
	d.f.	23	20	23	23	20	18	25	22	21	23	14	15	8	17
P. whitei vs *P. broomi*	"t"	0,12	0,74	0,36	1,99	1,33	*2,46	1,39	*2,20	*2,56	***4,25	**3,56	***4,14	0,58	***5,96
	d.f.	18	17	16	18	15	16	20	16	16	19	14	17	9	20

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001

TABLE 3 A

COMPARISON OF THE UPPER PREMOLAR AND MOLAR TEETH (in mm) OF TWO SAMPLES OF 3 SPECIES OF *PARAPAPIO* FROM STERKFONTEIN (I = NEW SAMPLE; II = 1957 SAMPLE)

Species	Statistics	P^3		P^4		M^1			M^2			M^3		
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
P. jonesi	M (I)	–	–	7,87	5,95	8,55	8,10	8,93	10,44	9,26	10,50	9,85	8,86	10,00
	M(II)	7,10	5,28	7,77	6,11	8,74	8,07	8,62	10,16	9,12	10,13	10,08	8,07	9,85
	"t"	–	–	0,67	0,42	0,64	0,06	0,73	1,05	0,62	1,61	0,71	2,99 *	0,70
	d.f.	–	–	8	8	7	7	11	8	8	12	10	9	11
P. broomi	M(I)	7,70	7,80	8,45	6,75	9,82	8,92	9,95	11,43	10,50	11,21	10,60	8,92	10,87
	M(II)	7,65	7,16	8,60	6,54	9,64	8,81	9,65	11,23	10,49	11,18	10,98	9,09	11,21
	"t"	0,21	0,85	0,55	1,19	1,00	0,47	1,19	0,62	0,05	0,15	0,98	0,45	1,16
	d.f.	20	19	24	23	23	18	24	19	22	26	19	18	20
P. whitei	M(I)	9,5	8,4	9,93	7,90	11,1	10,7	13,2	–	–	–	–	–	–
	M(II)	7,87	7,42	8,75	6,87	10,57	10,08	10,53	12,83	11,82	12,72	12,80	11,35	12,72
	"t"	3,74	0,39	5,44 ***	1,67	1,16	1,07	5,43 **	–	–	–	–	–	–
	d.f.	2	3	7	6	3	4	5	–	–	–	–	–	–

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001

TABLE 3 B

COMPARISON OF THE LOWER PREMOLAR AND MOLAR TEETH (in mm) OF TWO SAMPLES OF 3 SPECIES OF *PARAPAPIO* FROM STERKFONTEIN (I = NEW SAMPLE; II = 1957 SAMPLE)

Species	Statistics	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
P. jonesi	M(I)	5,15	14,55	6,17	6,97	7,23	7,40	9,18	8,70	8,28	10,44	8,99	7,92	5,00	12,75
	M(II)	5,07	10,78	6,69	6,82	7,51	7,59	8,61	9,29	9,02	10,42	9,30	8,40	4,95	12,71
	"t"	0,25	1,58	1,76	0,76	1,09	0,73	1,62	2,72 *	3,31 **	0,11	1,91	2,35 *	0,26	0,17
	d.f.	19	18	24	22	18	16	23	26	25	27	16	18	13	19
P. broomi	M(I)	4,8	15,0	7,0	7,1	7,97	8,03	9,87	9,20	9,00	11,40	9,82	8,96	6,22	14,52
	M(II)	5,63	11,16	7,06	7,23	8,20	8,24	9,31	10,00	9,72	11,42	10,19	9,30	6,22	14,72
	"t"	1,92	1,04	0,15	0,27	0,78	0,72	1,28	2,09	1,63	0,05	1,67	1,75	0,02	0,92
	d.f.	13	14	12	14	13	14	16	13	13	15	21	24	18	26
P. whitei	M(I)	–	–	–	–	–	–	–	–	–	–	11,4	10,4	6,1	15,3
	M(II)	5,65	12,60	7,14	7,68	8,52	8,78	9,71	10,64	10,46	12,55	11,06	10,30	6,50	16,42
	"t"	–	–	–	–	–	–	–	–	–	–	2,05	0,22	0,77	2,10
	d.f.	–	–	–	–	–	–	–	–	–	–	4	4	1	5

"t" test significance levels: * = 0,05; ** = 0,01, *** = 0,001

TABLE 4 A

STATISTICAL SUMMARY OF THE DIMENSIONS OF THE UPPER PREMOLAR AND MOLAR TEETH (in mm) OF *PARAPAPIO* SPP. FROM STERKFONTEIN

Species	Statis-tics	P^3		P^4		M^1			M^2			M^3		
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
P. jonesi	M	7,10	5,28	7,80	6,08	8,70	8,08	8,69	10,30	9,19	10,29	9,97	8,43	9,93
	N	5	4	10	10	9	9	13	10	10	14	12	11	13
	S.D.	0,31	1,63	0,20	0,46	0,36	0,55	0,64	0,42	0,34	0,46	0,55	0,58	0,38
	C.V.	4,4	30,9	2,6	7,6	4,1	6,8	7,3	4,1	3,8	4,4	5,5	6,9	3,8
P. broomi	M	7,66	7,31	8,57	6,59	9,68	8,84	9,72	11,29	10,49	11,19	10,87	9,05	11,12
	N	22	21	26	25	25	20	26	21	24	28	21	20	22
	S.D.	0,48	1,46	0,58	0,38	0,37	0,43	0,54	0,68	0,51	0,56	0,80	0,70	0,61
	C.V.	6,2	20,0	6,7	5,8	3,9	4,9	5,5	6,0	4,8	5,0	7,4	7,7	5,5
P. whitei	M	8,28	7,62	9,14	7,13	10,68	10,18	10,91	12,83	11,82	12,72	12,80	11,35	12,77
	N	4	5	9	8	5	6	7	6	6	6	2	2	3
	S.D.	0,87	1,97	0,66	0,85	0,42	0,54	1,09	0,55	0,77	0,65	–	–	– –
	C.V.	10,5	25,9	7,2	11,9	4,0	5,2	10,0	4,3	6,5	5,1	–	–	– –

TABLE 4 B

STATISTICAL SUMMARY OF THE DIMENSIONS OF THE LOWER PREMOLAR AND MOLAR TEETH (in mm) OF *PARAPAPIO* SPP. FROM STERKFONTEIN

Species	Statistics	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
P. jonesi	M	5,08	11,16	6,61	6,85	7,47	7,56	8,72	9,10	8,77	10,43	9,18	8,21	4,97	12,73
	N	21	20	26	24	20	18	25	28	27	29	18	20	15	21
	S.D.	0,40	3,33	0,56	0,38	0,40	0,41	0,73	0,60	0,65	0,42	0,36	0,49	0,35	0,54
	C.V.	7,8	29,8	8,5	5,6	5,4	5,4	8,3	6,5	7,4	4,1	4,0	6,0	7,1	4,3
P. broomi	M	5,57	11,40	7,06	7,22	8,15	8,20	9,40	9,95	9,62	11,42	10,00	9,14	6,22	14,63
	N	15	16	14	16	15	16	18	15	15	17	23	26	20	28
	S.D.	0,46	3,59	0,39	0,44	0,46	0,44	0,70	0,60	0,62	0,52	0,55	0,51	0,53	0,57
	C.V.	8,2	31,5	5,5	6,2	5,6	5,4	7,4	6,1	6,4	4,6	5,5	5,6	8,5	3,9
P. whitei	M	5,65	12,60	7,14	7,68	8,52	8,78	9,71	10,64	10,46	12,55	11,12	10,32	6,37	16,26
	N	6	4	5	5	5	5	7	5	5	6	6	6	3	7
	S.D.	0,23	2,80	0,45	0,37	0,39	0,22	0,46	0,21	0,31	0,55	0,19	0,38	0,38	0,62
	C.V.	4,1	22,2	6,3	4,8	4,6	2,5	4,7	2,0	3,0	4,4	1,7	3,6	5,9	3,8

TABLE 5
OBSERVED RANGES FOR TWO INDICES (ROBUSTNESS VALUE & CROWN MODULE) FOR 41 M_3 TEETH OF THE 3 *PARAPAPIO* SPP. FROM STERKFONTEIN

Index	*P. jonesi* (N = 15)	*P. broomi* (N = 20)	*P. whitei* (N = 6)
Robustness value	103,32 – 130,00	126,00 – 166,92	172,05 – 184,80
Crown module	10,35 – 11,50	11,50 – 13,15	13,30 – 13,85

TABLE 6
NUMBER OF SPECIMENS OF *PARAPAPIO* DESCRIBED FROM VARIOUS SOUTH AFRICAN LIMESTONE DEPOSITS

Species	Taung	Sterkfontein	Makapan* (limeworks)	Swartkrans	Kromdraai (faunal site)	Bolt's Farm
P. jonesi	1	25	15	3	2	0
P. broomi	0	43	34	0	0	5
P. whitei	3	14	5	0	0	2

* Excluding Maier (1970)

APPENDIX 1

MEASUREMENTS (in mm) OF NEW *PARAPAPIO* MATERIAL FROM STERKFONTEIN
1. SPECIMENS TENTATIVELY ASSIGNED TO *P. JONESI*

(a) Upper teeth

Spec. No.	P^3 b	P^3 l(h)
STW 18	8,1	7,5

Spec. No.	P^4 b	P^4 l(h)
STW 18	–	7,0
23	7,8	–
27	8,0	6,1
77	7,8	5,8

Spec. No.	M^1 bm	M^1 bd	M^1 l
STW 18	–	–	9,3
23	9,1	8,6	9,6
53	8,0	7,6	7,9

Spec. No.	M^2 bm	M^2 bd	M^2 l
STW 18	11,1	9,6	11,0
20	10,2	9,4	10,7
23	10,3	9,0	10,6
24	–	–	10,2
27	10,6	9,3	10,4
34	10,0	9,0	10,1

Spec. No.	M^3 bm	M^3 bd	M^3 l
STW 18	10,5	–	10,4
20	9,7	8,2	10,0
24	–	–	9,8
27	9,9	8,2	10,1
49	10,0	9,0	10,3
50	10,1	9,0	9,8
72	9,4	9,0	9,6
81	9,4	9,1	10,1

(b) Lower teeth

Spec. No.	P_3 b	P_3 l(h)
STW 3	5,2	15,4
57	5,1	13,7

Spec. No.	P^4 b	P^4 l(h)
STW 3	6,2	7,2
9	6,2	6,5
46	6,3	7,1
78	6,0	7,1

Spec. No.	M_1 bm	M_1 bd	M_1 l
STW 3	(7,6)	(7,9)	10,0
9	–	–	8,4
22	(7,0)	(7,2)	8,3
46	–	–	9,2
82	7,1	7,1	10,0

Spec. No.	M_2 bm	M_2 bd	M_2 l
STW 3	8,8	8,3	11,2
9	8,9	7,9	10,1
11	(9,3)	8,8	10,4
15	8,8	8,6	11,0
22	8,6	8,0	10,1
33	9,1	–	10,3
46	–	8,5	9,8
51	7,8	8,0	10,2
64	9,0	8,4	10,8
65	8,0	8,0	10,5

Spec. No.	M_3 bm	M_3 bd	M_3 bh	M_3 l
STW 3	8,8	7,5	4,8	13,0
9	8,9	7,6	4,6	12,5
11	–	8,4	5,0	12,8
22	9,0	8,1	–	12,6
33	9,1	7,7	4,6	13,0
43	9,2	8,1	5,4	13,0
53	9,5	8,6	5,2	12,6
56	8,4	7,4	5,4	12,3

APPENDIX 2

MEASUREMENTS (in mm) OF NEW *PARAPAPIO* MATERIAL FROM STERKFONTEIN (continued)
2. SPECIMENS TENTATIVELY ASSIGNED TO *P. BROOMI*

(a) Upper teeth

Spec. No.	P^3 b	P^3 l(h)
STW 10	7,2	7,4
14	7,7	5,9
58	7,6	9,0
84	8,2	8,6

Spec. No.	P^4 b	P^4 l(h)
STW 10	8,5	7,2
12	8,7	5,9
14	8,6	7,5
58	8,5	6,6
84	7,9	6,1
2	8,5	7,2

Spec. No.	M^1 bm	M^1 bd	M^1 l
STW 2	10,1	9,1	10,3
6	9,6	8,5	10,3
10	9,7	9,1	10,5
58	9,5	9,0	9,5
67	10,0	8,8	9,5
74	10,1	9,0	9,6

Spec. No.	M^2 bm	M^2 bd	M^2 l
STW 2	11,9	11,2	12,1
10	11,4	10,3	11,4
12	11,0	10,1	10,5
14	11,2	9,9	11,1
25	–	10,4	11,2
58	12,1	11,2	11,7
63	10,5	10,2	10,5
67	12,4	11,4	12,1

Spec. No.	M^3 bm	M^3 bd	M^3 l
STW 12	(11,5)	9,0	10,7
58	10,8	9,0	11,2
30	9,3	–	11,7
73	11,0	9,4	10,7
87	11,1	9,0	10,8

APPENDIX 3

MEASUREMENTS (in mm) OF NEW *PARAPAPIO* MATERIAL FROM STERKFONTEIN (continued)

2. SPECIMENS TENTATIVELY ASSIGNED TO *P. BROOMI* (continued)

(b) Lower teeth

Spec. No.	P_3 b	P_3 l(h)
STW 70	4,8	15,0

Spec. No.	P_4 b	P_4 l(h)
STW 1	7,0	7,1

Spec. No.	M_1 bm	M_1 bd	M_1 l
STW 61	8,3	8,3	10,4
83	7,5	7,7	9,2
1	(8,1)	(8,1)	10,0

Spec. No.	M_2 bm	M_2 bd	M_2 l
STW 1	9,5	9,0	11,0
69	8,9	8,9	11,7
83	9,5	9,1	11,1

Spec. No.	M_3 bm	M_3 bd	M_3 bh	M_3 l
STW 1	9,8	8,7	5,8	14,1
8	9,6	8,6	5,9	14,8
13	11,0	9,4	–	14,7
17	9,5	8,2	6,5	13,8
32	10,4	8,8	6,0	14,2
37	10,1	9,7	6,0	14,5
38	10,2	9,8	7,0	14,6
40	9,3	8,3	6,0	14,7

Spec. No.	M_3 (contd.) bm	M_3 (contd.) bd	M_3 (contd.) bh	M_3 (contd.) l
STW 41	9,4	9,0	5,9	14,6
42	9,9	9,4	6,8	15,6
47	9,5	8,7	6,8	14,8
83	9,2	8,9	5,7	13,8

3. SPECIMENS TENTATIVELY ASSIGNED TO *P. WHITEI*

(a) Upper teeth

Spec. No.	P^3 b	P^3 l(h)
STW 21	9,5	8,4

Spec. No.	P^4 b	P^4 l(h)
STW 31	10,1	–
35	10,0	8,6
21	9,7	7,2

Spec. No.	M^1 bm	M^1 bd	M^1 l
STW 21	(11,1)	(10,7)	13,2

M^2 Nil

M^3 Nil

(b) Lower teeth

P_3	M_1
Nil	Nil
P_4	M_2
Nil	Nil

Spec. No.	M_3 bm	M_3 bd	M_3 bh	M_3 l
STW 36	11,4	10,4	6,1	15,3

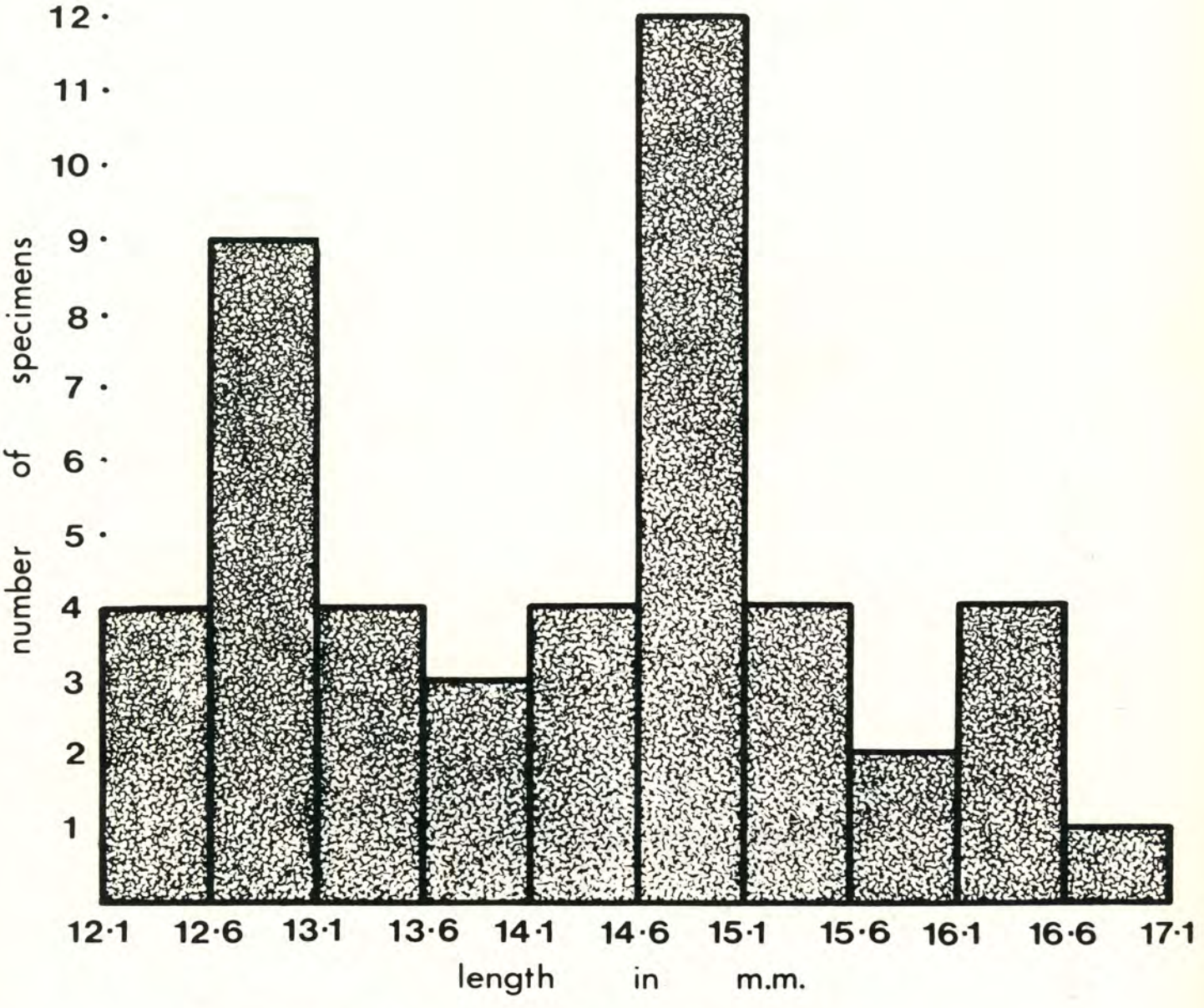


Fig. 1. Histogram of the length (l) of 48 specimens of M_3 of *Parapapio* spp. from Sterkfontein.

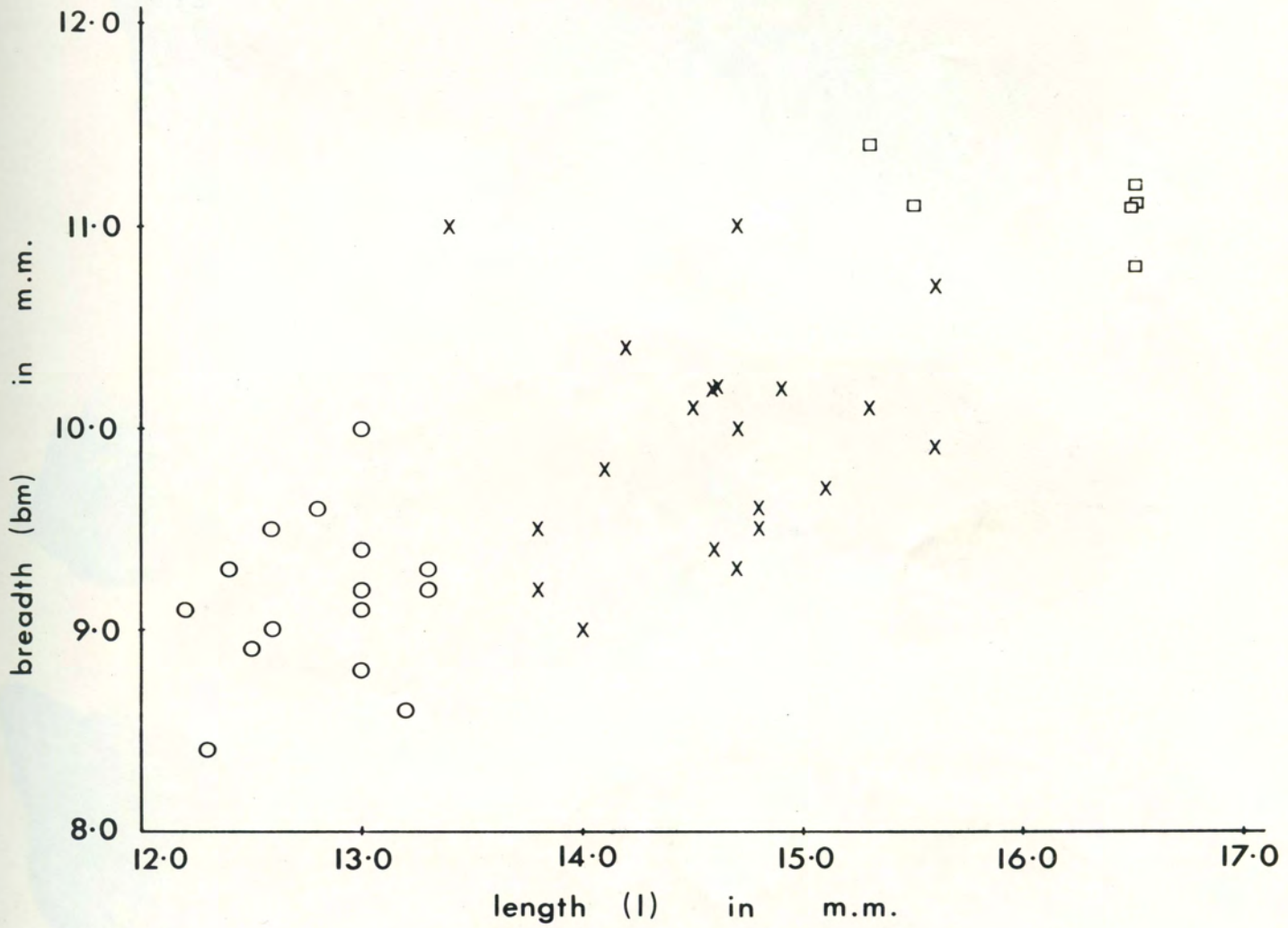


Fig. 2. Scattergram of the length (l) and mesial breadth (bm) of 41 specimens of M_3 of *Parapapio* spp. from Sterkfontein. ○—*P. jonesi*; ×—*P. broomi*; □—*P. whitei*.



Plate 1 From above downwards, dorsal, lateral and ventral views of *P. broomi* female cranium (STW 12).

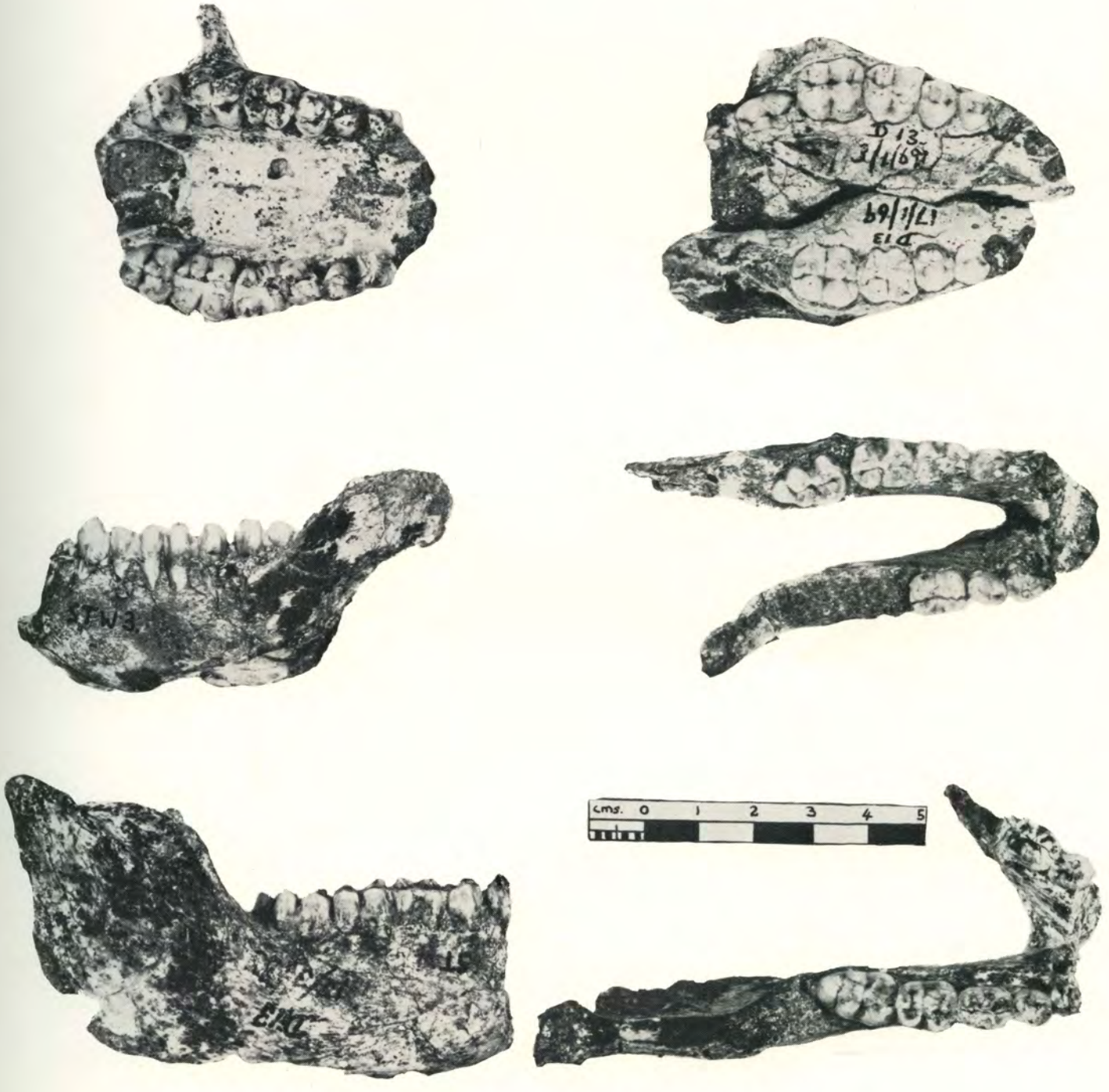


Plate 2 Top: Palates of *P. broomi* females (left, STW 58; right, STW 10)
Centre: Lateral and occlusal views of *P. jonesi* male mandible (STW 3).
Bottom: Lateral and occlusal views of *P. broomi* ? female mandible (STW 1).