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NEW FOSSIL CERCOPITHECOIDEA FROM THE LOWER PLEISTOCENE CAVE DEPOSITS OF THE MAKAPANSGAT LIMEWORKS, SOUTH AFRICA

by

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CONTENTS

Introduction 70
Acknowledgements 70
Stratigraphy and locality of the new specimens 70
Description and discussion of the new specimens 71
A. Colobidae 71
(1) *Cercopithecoides williamsi* (M.3055)
B. Cercopithecidae 74
(2) *Parapapio jonesi* (M.3057, M.3058, M.3059, M.3060, M.3061, M.3051)
(3) *Parapapio broomi* (M.3056, M.3063, M.3065, M.3067, M.3070, M.3075, M.3082)
(4) *Parapapio whitei* (M.3062, M.3072)
(5) *Simopithecus darti* (M.3071, M.3073, M.3074, M.3083)
References 86

ABSTRACT

So far about 70 specimens of five species of Cercopithecoids have been recorded from the Makapansgat Limeworks. The present paper adds the descriptions of another 20, some of them being the most complete skulls known of these species:

Cercopithecoides williamsi is represented by a nearly complete male skull; its large upper teeth confirm the invalidity of the former species *C. molletti.*

Parapapio jonesi is represented by parts of a young female and two adult males. The male material is the most comprehensive known of this species and made it possible to give a reconstruction of the male skull. Specimen M.2961, described by Freedman (1960) as *Parapapio broomi,* is referred to *P. jonesi.*

Of *Parapapio broomi* 7 new specimens are recorded and described. A fragmentary male skull (M.3065) and a very large mandible (M.3067) most probably belong together, giving a good idea of the male skull of this species.

Of *Parapapio whitei* the first fairly complete male skull could be prepared and described. In the light of the new specimen, some of the male specimens, formerly referred to this species (Freedman 1960; 1965) should be removed.

Simopithecus darti is represented by a nearly complete and undistorted skull of a subadult female, with the mandible being in situ. In addition, a nearly complete mandible of a young male and a fragmentary maxilla of an old male could be described. Some of the teeth of these specimens nearly equal those of *Simopithecus danieli* from Swartkrans.

ZUSAMMENFASSUNG

Von den unterpleistozänen Höhlenbreccien von Makapansgat, Südafrika, die u.a. zahlreiche Australopithecinen geliefert haben, sind bisher auch etwa 70 Cercopithecoidea bekannt geworden. Die gegenwärtige Untersuchung fügt weitere 20 Exemplare hinzu, darunter mehrere nahezu vollständige Schädel, die die Morphologie sämtlicher fünf Arten beträchtlich erweitern.

Cercopithecoides williamsi, ein Colobide, ist durch einen nahezu kompletten männlichen Schädel vertreten. Der Unterkiefer fehlt, aber die oberen Zähne liegen im Grössenbereich der mittlerweile unterdrückten Art *C. molletti.*

Parapapio jonesi ist durch Teile eines jungen Weibchens und zweier erwachsener Männchen repräsentiert. Das männliche Material ist recht vollständig und vermittelt erstmals einen Eindruck von der Schädelmorphologie dieser Art. Exemplar M.2961, das von Freedman (1960) zu *Parapapio broomi* gestellt wurde, gehört wahrscheinlich ebenfalls zu *P. jonesi.*

Von *Parapapio broomi* werden 7 neue Exemplare beschrieben. Ein sehr grosser, aber fragmentarischer männlicher Schädel (M.3065) und eine grosse Mandibel (M.3067), die wahrscheinlich zusammengehören, bilden eine gute Grundlage für eine erste Rekonstruktion des gesamten Schädels.

Von *Parapapio whitei* konnte erstmals ein annähernd kompletter männlicher Schädel gefunden werden. Einige der Exemplare, die von Freedman (1960; 1965) zu dieser Art gestellt wurden, sollten besser wieder daraus entfernt werden.

Simopithecus darti, wahrscheinlich ein naher Verwandter des rezenten *Theropithecus gelada,* ist durch einen nahezu vollständigen Schädel, mit Mandibel in situ, eines subadulten Weibchens vertreten. Es ist das bisher vollständigste Exemplar dieser Fossil-Gattung. Weiterhin wird ein nahezu kompletter Unterkiefer eines jungen Männchens und der obere Zahnbogen eines alten Männchens beschrieben.

Die vorliegenden Funde werden jeweils beschrieben und diskutiert, die metrischen Angaben sind in Tabellen zusammengestellt.

INTRODUCTION

Fossil Cercopithecoids from the Pleistocene cave breccias of South Africa were first mentioned by Haughton (1925). Since that time a large number of additional specimens have been recovered and described by various authors. All material, known before 1957, was examined and restudied by Freedman (1957); at that time about 1 250 specimens were available, about 550 originating from Sterkfontein, 300 from Swartkrans and about 50 to 70 each from Makapansgat, Kromdraai and Cooper's. Odd specimens were known from some other places, listed in Appendix IV A of Freedman (op.cit.). In addition, Freedman (1961; 1965) has described further Cercopithecoids from Makapansgat, Taungs, Bolt's Farm and Witkrans.

From Makapansgat Limeworks so far about 70 specimens of Cercopithecoidea are recorded; the present study adds another odd 20, some of them being the most complete skulls so far known from this site. This material was prepared by the author between March and September 1970 at the Bernard Price Institute for Palaeontological Research, Johannesburg, where these specimens are also housed.

The classification of the living Cercopithecoidea is mainly based on external characteristics and on soft parts (skin and fur colours, morphology of the genitals and intestines), the skull, teeth and other skeletal parts either being considered too uniform or too variable under changing functional conditions (Pocock 1925). This seems to render nearly impossible satisfactory systematics of fossil Cercopithecoidea, consisting, as they do, only of hard parts. Indeed, the classification of these fossil forms is still very problematical. Most of the known material is very fragmentary, mainly consisting of teeth. Therefore, at the present moment, the system of the fossil South African Cercopithecoidea is almost entirely based on tooth characters, or, because of their uniform structure, only on different tooth sizes. Broom (1940), for example, based the classification of the genus *Parapapio* mainly on three categories of molar size, which seemed to emerge from the scant material available to him. But the same author was not able to give a workable differential diagnosis for both the taxa *Parapapio* and *Papio.* At the moment we still lack species definitions for the Pleistocene Cercopithecoidea of South Africa, but Freedman (1957) at least succeeded in establishing fairly satisfying definitions of the 6 genera, known from these deposits. The species, however, are still a kind of working model, reflecting the morphological diversity of the fossil material, but possibly being far from representing natural units.

A comprehensive biological analysis of extant species shows also that small adaptive modifications can form typical patterns which are liable to taxonomic interpretations on the species and genus level (Davis 1964; Maier 1970). A detailed functional analysis of fossil skeletons, combined with palaeoecological considerations, could help to ascertain and to evaluate even small differences between the various forms of fossil Cercopithecoids. In the skull this would apply mainly to the adaptative modifications of the masticatory apparatus, and in the postcranial skeleton to the limb proportions. It becomes evident then that the knowledge of as complete material as possible is of especial importance in such an uniform taxon as the Cercopithecoidea.

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THE STRATIGRAPHY AND LOCALITY OF THE NEW SPECIMENS

As yet little attention has been spent on an exact localization of the fossils found in the South African cave deposits. Most of the material was gained by the activities of the limeworkers and then recovered from the mining dumps. The texture and colour of the matrix sometimes allowed the original locality level to be assessed more or less accurately, but normally only a rough assignment was possible. Fortunately, most of the new Cercopithecoids from Makapansgat to be described below can be exactly localized. In 1963 (according to information by Mr. J. W. Kitching

and Mr. B. Maguire) a large block of 'pink breccia' (Upper Phase I) fell down from the right wall of the limeworker's quarry main entrance, which proved to be particularly rich in Cercopithecoid remains. Probably also, most of the material of the former 'Cercopithecoid dump' was derived from this part of the 'pink breccia'. This area, having yielded Australopithecines as well, therefore seems to be worth a careful and systematic excavation.

Being the main source of the present material, it may be useful to make a few remarks on the sedimentological and palaeontological characteristics of the "Upper Phase I'-breccia of the Makapansgat Limeworks. According to Brain (1958) the Phase I-material is characterized by the mixture of residual cave earth and of surface-derived materials. In the upper parts of the 'Upper Phase I' there is an increasing percentage of surface material to be observed: "The conclusion is that the cave entrance was being progressively enlarged, and admitted larger and larger quantities of surface-derived debris" (Brain 1958; p. 112). Because of the mixed origin of the included sand grains, their morphology and frequency distribution do not allow conclusions as to the climatic conditions.

Therefore we are still bound to make inferences on the nature of the past environment from the fossil fauna. At once, there becomes evident a striking difference in the frequency spectrum of the faunal elements within the different sediment layers: whereas in the lower parts of the Makapansgat deposit ('basal red' and 'Grey breccia') the Bovidae comprise about 90% of the fossil remains, in the 'pink breccia' the Primates dominate with about 80%. There is, however, not much change in the members of the fauna themselves. For example, all of the six forms of Primates (*Cercopithecoides williamsi, Parapapio jonesi, Parapapio broomi, Parapapio whitei, Simopithecus darti* and *Australopithecus africanus*) occur in both the lower and the upper layers. Doubtful is the occurrence of *Parapapio jonesi* in the 'pink breccia' and of the large *Parapapio whitei* in the 'grey breccia'.

Mr. J. W. Kitching was kind enough to compile for this publication a list of the mammals other than Primates, which were so far recorded from the 'pink breccia' of the Makapansgat Limeworks:

Notochoerus sp.
Potamochoeroides sp.
Hippopotamus sp.
Metaschizotherium sp.
Gigantohyrax maguirei
Procavia cf. antiqua
Elephas cf. recki
Oreotragus major
Makapania broomi
Syncerus caffer
Hyaena cf. makapani
Lepus or *Pronolagus*
Hystrix sp.

A more detailed examination most probably would produce some more forms, especially Bovidae, but even now, this variety of mammals seems to indicate a highly diversified surrounding of the ancient cave, reaching from dense forest to savannah-like conditions. Probably the Makapansgat valley had a more or less perennial water course which was accompanied by a gallery forest whereas on the higher levels bush and open grassland persisted. The examination of the microfauna of the Makapansgat deposit, at least some of which came from the 'pink breccia', was indicative of very varied ecological conditions as well (De Graaf 1961).

DESCRIPTION AND DISCUSSION OF THE NEW SPECIMENS

A. Colobidae

(1) *Cercopithecoides williamsi* MOLLETT 1947

This is the only kind of Colobid monkey known from the Pleistocene cave deposits of South Africa. It is referred to the monotypic genus *Cercopithecoides,* which is not yet known from East Africa. In South Africa, however, it is quite common, having been recovered from all of the more important lower and middle Pleistocene sites. There seems to exist a size increase, the forms from the older deposits being slightly smaller than those of the later ones. This led Freedman (1957) to create a new species *C. molletti* for the larger forms from Swartkrans and Graveyard, but subsequent finds closed the size gap, indicating a continuous chronocline (Freedman 1960). At Makapansgat, this species is known from both the 'grey breccia' and the 'pink breccia', the type specimen (M.2038) originating from the latter.

Specimen M.3055 (Figs. 1–4; Tables II–III)

This specimen is a nearly complete and undistorted skull without mandible. Although there is some minor damage, it is the most perfect male skull known so far. It was the only specimen of *Cercopithecoides* found during this recent examination of the Makapansgat breccia. Only a few undetermined Rodent remains were found in the close vicinity of the present skull.

Before fossilization, the incisors and canines, the rostral parts of the nasal bones, the lateral plate of the right pterygoid and the right auditory capsule had been lost or damaged. Some parts of the parietal and occipital, the left temporal, the left jugal arch and the left sphenoid are missing due to post-fossilizational damage. On the left side, an excellently preserved endocranial cast is exposed. The premolars and molars are in very good condition; the last molars being hardly worn and the alveolae of the canines being very large, we can conclude to have the skull of a young adult male.

Cercopithecoides williamsi is a comparatively large Colobid, all living forms from Africa being distinctly smaller. According to Verheyen (1962) the average maximum length of the large *Colobus abyssinicus* is 119 mm, compared with 146 mm in the present specimen. Only some of the Colobids from the Pleistocene of East Africa are still larger (Leakey 1969).

In the present skull, the muzzle length amounts only to about 63% of the length of the braincase; in the type skull this relation is 60%. With the skull orientated on the occlusal plane the muzzle dorsum shows a fairly steep and straight outline, the nasals being comparatively short and elevated. The glabellar region appears to be well developed when seen from the norma lateralis, and it is separated from the vault of the calvaria by a well excavated transverse groove. The calvaria itself shows a well rounded contour, reaching its maximum height at the bregma; this point, however, is scarcely elevated above the supraorbital tori. The nuchal crests are very pronounced, resulting in a dorsally protruding inion, situated at about the level of the meatus acusticus externus. As a consequence, the nuchal plane and the foramen magnum lie at the same level as the alveolar margin, and the condyles being at the same level as the teeth. Many of the extant colobids in comparison exhibit an elevated braincase and a more vertical nuchal plane, as was true for the large and advanced *Paracolobus* from East Africa. The skull proportions of *Cercopithecoides* are very aberrant from the normal colobid-type.

The type skull, when seen from its right side, seems to possess a very flat and elongated braincase, which hardly rises above the eyebrows. This feature was stressed by Mollett (1947) and Freedman (1957), but a close examination reveals that especially this right half of the calvaria was subjected to considerable distortion, the left half showing more normal proportions. In the measurements of the braincase, the new skull resembles the type very closely, the slight differences probably being due to different age and to distortion. The skull M.2999 from the 'grey breccia', in comparison, has a distinctly shorter, higher and broader braincase.

The temporal crests are fairly well marked on the frontals, only to become very faint lines on the parietal bones. The temporal lines do not meet one another medially (minimum distance 16 mm) nor do they reach the nuchal crests; thus the insertion area of the temporalis muscle is very restricted. Unfortunately the inion region shows too much damage to reveal the exact morphology of the nuchal and temporal crests; both are separated, however, by a shallow groove of about 10 mm breadth. Laterally the inferior temporal lines are confluent with the posterior root of the jugal arch, separated from the supramastoid crest by the same groove.

The nuchal plane has a nearly horizontal orientation, not being as steeply sloping as in most of the other Colobidae. Due to some damage, not much of its morphological details can be seen any more. Medially there is a well marked external occipital crest, the condylar fossae are considerably excavated, and they are separated from the anterior condylar canals by transverse bony ridges. These ridges again are separated from the prominent and pointed mastoid processes by very deep and distinct mastoid notches, indicating strong digastric muscles. The occipital condyles form an angle of about 100° with each other. The basilar part of the occipital bone shows a typical median crest between the insertion areas of the prevertebral neck muscles; the spheno-occipital junction is still visible.

The external auditory meatus is separated from the articular fossa and the small postglenoid process by a groove, and it abuts against the mastoid, with which it is fused medially up to the jugular foramen. The carotid foramen lies about 20 mm medial to the lateral margin of the auditory meatus. Just in front of this foramen a very pronounced spine arises, forming the medial wall of the foramen ovale. This spine is compressed more than in the cercopithecids, and it does not include parts of the sphenoid bone. The apex of the petrous temporal ends at the posterior margin of the medial pterygoid plate. The overall length of the tympanic and petrosal bone is about 37 mm; its lateral parts have a transverse orientation, the medial parts lie nearly antero-posteriorly, forming an angle at about the jugular foramen.

The frontal bone possesses a metopic suture right from the nasion to the bregma. The deepness of the ophryonic groove behind the supraorbital tori is about 3 mm medially and about 6 mm laterally in the present specimen; only in some of the female skulls this groove seems to be more pronounced. The supraorbital tori themselves are quite slender, being about 5 mm thick on average, compared with about 10 mm in skull M.2999. The anterior margins of the tori supraorbitales form an obtuse angle of about 137°; this probably is a consequence of an incomplete forward orientation of the orbits, which is also reflected by the broad interorbital region of the Colobidae. At the pterion the frontal bone seems to be excluded from contact with the temporal bone, but the sutures are not clearly visible. The orbits are comparatively large and nearly rounded; in older specimens there seems to occur a certain increase in breadth and a reduction in height, the latter due to the thickening of the supraorbital arcs (Ehara & Seiler 1970).

In *Cercopithecoides* the lacrimo-maxillary suture runs right across the fossa lacrimalis; this arrangement is very typical for the Colobidae (Vogel 1966), whereas in the Cercopithecidae this fossa is entirely framed by the lacrimal bone. The interorbital region is very broad in *Cercopithecoides,* but in both the present specimen and in the type skull the orbitae are not cleaned sufficiently to take accurate measurements. Most probably in all skulls of *Cercopithecoides williamsi* the interorbital breadth is larger than 20 mm. According to Verheyen (1962) the index

$$\frac{\text{Interorbital Breadth} \times 100}{\text{Muzzle length}}$$

is the most valuable characteristic for distinguishing Cercopithecidae and Colobidae. By this criterion *Cercopithecoides* is very distinctly a colobid (s. Verheyen, op.cit.; Graph 22).

The zygomatic bone is comparatively small and gives rise to a slender jugal arch, which does not show a marked lateral expansion, and which lies only slightly below the level of the infraorbital margin. Due to an increased height of the face, in most of the cercopithecids the jugal arch is more lowered in its position. The zygomatic process of the maxilla in the present skull is situated dorsally to the distal half of the second molar. In female skulls and in M.2999 it lies even more rostral, reflecting the shortness of the muzzle. The posterior root of the jugal arch is quite broad and strong, anteriorly forming a high and sharp infratemporal crest. The articular eminence is considerably thickened and slightly oblique, the medial part being more posterior; there is not much transverse concavity.

The lengths of the muzzle and the palate are identical in the present skull and in the type. Probably due to age differences, resulting in an increased growth of the alveolar processes, the height of the face is distinctly larger in the latter. Specimens M.2999 and M.3000 have a somewhat shorter muzzle, but the face height in the former is the same as in the type skull. The infraorbital area in all known skulls is characterized by a small but marked excavation; just below the orbits, the maxilla is pierced by three infraorbital foramina on each side. Otherwise, the maxillae do not show much relief; there is only a faint thickening above the roots of the canines, but no distinct maxillary crests and canine fossae are developed. The nasal bones are damaged distally, but they show an internasal suture and a broad outline, which features are also very typical for both *Cercopithecoides* and most of the Colobidae. Because of the shortness of the nasal bones, the nasal aperture is comparatively long.

A very significant feature of *Cercopithecoides williamsi* is the shortness of its premaxilla, which is wedged between the maxillae and hardly protrudes rostrally. The square outline of the muzzle in dorsal view is mainly due to this transversely cut anterior margin of the premaxilla, and this appearance is stressed by the large canines, causing a wide anterior breadth of the muzzle. The lateral wings of the premaxilla frame the nasal aperture right up to the short nasal bones.

The posterior margin of the hard palate is just at the same level as the distal ends of the last molars. This margin does not have a crest as in M.2999, nor are the posterior palatine foramina as slit-like as in this specimen. The incisive fossa is situated just behind the alveolae of the incisors. The breadth of the hard palate increases from 18 mm at the last molars to 26 mm at the first premolars. The tooth rows are also very close at M^3 (37 mm, measured between the lateral surfaces), then they diverge to a maximum breadth across the mesial half of M^2 (45 mm) and converge to about 41 mm across P^3 and C.

The angle between the palate and the pharyngeal base of the braincase is 126° in the present skull; in the type skull it is 124° and in M.2999 about 122°. This means that the declination of the palate in *Cercopithecoides williamsi* is distinctly larger than in both *Papio* (130°–170°; Frick 1960) and *Parapapio* (see below).

The alveolae of the incisors are very small and rounded, as is to be expected from the small teeth, known from other specimens. The lateral alveolae are slightly larger than the medial ones, which is in accordance with the tooth measurements in M.3000. The morphology of the premaxilla and the incisors is a strong argument for aligning *Cercopithecoides* with the Colobidae. The alveolae of the canines are large and show a triangular outline. The mesial margins have a small bony process, which must have fitted into the mesial groove of the male canines.

The premolars and molars are distinctly smaller than in the similar-sized *Parapapio antiquus* and *P. broomi,* but they resemble those of the smaller species, *Parapapio jonesi.* The molars are square, resulting in Breadth/Length-Indices of about 100. All molars have a reduced breadth across the distal pair of cusps. Tooth P^4 is distinctly larger than the very small P^3; M^1 is the smallest of the molars, whereas M^2 is both the longest and the broadest; but the reduction of the third molar is quite inconspicuous.

The molars exhibit many morphological features, which are typical for the Colobidae: lingually the mesial and the distal cusps are separated by broad V-shaped incisions, as already noticed by Freedman (1957). In the unworn teeth of the present specimen, the lingual cusps (protocone and hypocone)are higher than the buccal ones (paracone and metacone), which is just reverse in the Cercopithecidae. The lingual cusps, however, are worn down faster, resulting in the usual, medially inclined tooth surface of the cercopithecoids. The transverse crests are very high and sharp; in comparison with the Cercopithecidae, these crests in the colobids are conserved over a long span of the lifetime (Welsch, 1967). The mesial and distal foveae are not quite as developed in *Cercopithecoides* and other colobids as they are in many cercopithecids. The occlusal plane possesses a slight antero-posterior convexity in *Cercopithecoides,* a feature which is also more typical for colobids than for cercopithecids.

Conclusions: The new skull of *Cercopithecoides williamsi* most closely resembles the type specimen, which came from the same site. The differences in the shape of the braincase and in the height of the face are due to some distortion and to the greater age at death of the type specimen. The male skull M.2999 from the 'grey breccia' of Makapansgat is altogether more stout and robust, but it does not seem to be opportune at the moment to draw any taxonomic conclusions from these differences.

The present skull, being the most complete male specimen of its taxon, yields much new morphological information, especially on the brain-

case, including its base. The most conspicuous features are the deep mastoid notch, the pronounced klinorrhynchy of the base of the skull and the limited insertion area of the temporal muscle.

Unfortunately, there are not many male upper teeth available for comparison, but the teeth of the present specimen are distinctly larger than all known so far of *Cercopithecoides williamsi,* and, apart from the M^3, even exceed slightly those of the type skull of *C. molletti* (SK551) from Swartkrans. Freedman (1961) therefore was right when again dropping this latter species. The new skull from the Makapansgat Limeworks even renders doubtful the existence of a chronocline (beginning with the Sterkfontein specimens and ending with those from Swartkrans, the specimens from Makapansgat being intermediate), which was established by Freedman (1961) on lower tooth material alone.

Numerous morphological characteristics, of which the most important ones have been mentioned in the descriptive part, make it highly probable that *Cercopithecoides* was a member of the cercopithecoid family Colobidae. This was not always seen clearly in the past: Mollett (1947) discussed similarities of *Cercopithecoides* with *Theropithecus, Simopithecus* and also with *Cercopithecus* and *Macaca.* Robinson (1952) seems to have been the first to recognize the 'semnopithecine' affinities of this form, but Hopwood & Hollyfield (1954) still considered *Cercopithecoides* to be a synonym of *Macaca,* and Freedman (1957; p.246) concluded: "The exact affinities of this species to the living and other living cercopithecoids are not at present clear". In 1961 (p.32) he again stated: "Detailed comparisons with other living and fossil African forms (and possibly Asian types as well) will have to be made in an effort to elucidate the affinities of this genus". As a result of his detailed craniological studies on the smaller African Cercopithecoidea, Verheyen (1962) came to the conclusion, "que *Mesopithecus* et *Cercopithecoides* sont très probablement des représentants des Colobinae" (p.176). Especially valuable criteria for an understanding of the basic differences in the facial skeleton between Cercopithecidae and Colobidae were summarized by Vogel (1966). Although he did not consider *Cercopithecoides* directly, it becomes clear from his paper that this genus shares most of the significant features with the Colobidae. The classification of *Cercopithecoides* within the Colobidae, however, is far from being clear and needs further investigation.

The extant Colobidae are highly specialized arboreal leaf-eaters with complicated stomach adaptations (Kuhn 1964). Most of them have entirely reduced thumbs in adaptation to a semibrachiating locomotion. Therefore, there is a high probability that the fossil *Cercopithecoides williamsi* belonged to the same adaptation type as well, and that this genus consequently would be indicative of densely forested areas in the vicinity of the australopithecine caves. Possibly there existed a kind of tropical fringe forest along the rivers of the nearby valleys, which provided *Cercopithecoides* (and perhaps some of the smaller Cercopithecids like *Parapapio jonesi*) with its habitat.

B. Cercopithecidae

As among the living Cercopithecoidea of Africa, in the Pleistocene deposits of that continent the Cercopithecidae are more numerous and varied than the Colobidae. But whereas today only two genera with three species of Cercopithecidae exist in South Africa, there are so far known five fossil genera and thirteen species of this family. This striking difference in the composition of the Primate fauna, which is also to be observed in several other mammalian orders, probably indicates much more favourable ecological conditions during Pleistocene times. At Makapansgat there have been recovered so far three species of *Parapapio* and *Simopithecus darti,* all of which are represented in the following account. As in Sterkfontein, no true baboons of the genus *Papio* were found at Makapansgat.

(2) *Parapapio jonesi* BROOM, 1940

By tooth dimensions, this species is the smallest of the fossil Cercopithecidae of South Africa. Unfortunately so far only one fairly complete female skull (Sts 565; type) and a few very fragmentary remains of the male muzzle are known of this important species. Important, because it seems to have existed for a comparatively long period and to have been spread also in East Africa (Patterson 1968). It occurs in most of the more important Pleistocene deposits of South Africa, both in the older and in the younger ones.

Specimens M.3057, M.3058, M.3059 (Fig. 5; Tables III–IV)

The following three specimens most certainly belonged to the same animal, and are therefore discussed together. In connection with various postcranial elements (scapula, humerus, radius, etc.) they were found close together in the 'basal red' breccia. M.3057 consists of a small, nearly complete braincase, but the muzzle is broken off just underneath the orbits; no upper teeth are available therefore. M.3058 consists of both corpora of a small mandible, of which all teeth are preserved in very good condition. M_3 is not yet erupted and the second deciduous molars are still present. Judged by the morphology of the canines and the first premolars, which must have been just erupted, the present animal was a young female of about 4 to 5 years (Schultz 1933). M.3059 is a complete set of upper incisors, which lay together just between the braincase and the mandible; stuck into a premaxilla model of plasticene, they fit exactly on the front teeth of the mandible M.3058 (Fig. 5).

As mentioned above, there is only the female type skull known so far, where the braincase shows much damage. The present braincase exhibits much

morphological detail, but is is only a subadult animal with many features not yet fully developed.

The overall length of the present skull was roughly determined by fitting mandible and braincase together; the skull probably was slightly smaller than the type skull, which would be in accordance with the age difference of both specimens. For the same reason the bizygomatic breadth may be smaller in the new female skull. The length of the braincase exceeds that of the type skull, but in the latter the bone cover of the endocranial cast is missing in the occipital region. By the same method as mentioned above, the muzzle length could be roughly estimated at about 58 mm, which is expectedly shorter than in the adult type skull. Indeed, the preserved parts of the facial skeleton, i.e. the upper half of the orbital frame, look still very undeveloped and juvenile. There is, however, a distinct transverse groove behind the weak supraorbital tori and the well pronounced glabella. These features closely resemble those of the type specimen, but are quite unlike, for example, those of *Parapapio antiquus*. The vault of the calvaria rises distinctly above the orbital roof, and it is equally rounded both towards the occipital and towards the lateral sides. The frontal bone shows no sign of a metopic suture. The parietal bones are very extended, whereas the squamae of the temporal bones are rather small, but are in contact with the frontals in the pterion region. The supraoccipital squama reaches far up dorsally, forming a crest-like lambdoid suture with the parietals. The external occipital protuberance (identical with the inion) is well marked and lies about 15 mm below lambda. Both the external occipital crest and the two nuchal lines are only weakly developed. The temporal crests are very small and the temporal lines cannot be seen any more. The insertion area of the temporal muscle obviously was very restricted, however, and it probably did not reach farther backward than to the mastoids, which do not form any prominent processes. The zygomatic processes of the temporal bones are weak and give rise to low supramastoid and infratemporal crests.

Although the temporal fossae are shallow, the minimum interfrontal breadth is narrow in both known skulls. The maximum temporal and the bimastoid breadths are very similar in both specimens. The lateral walls of the calvaria being nearly vertical in female *Parapapio jonesi*, the temporal breadth even may exceed the mastoid breadth, as it does in the present skull. As the squama occipitalis is fairly steep, the occipital part of the braincase is not as lowered as in *Parapapio antiquus*. The external auditory meatus is rather short and it is separated from both the mastoid and the articular fossa by only shallow grooves. At the jugular and the carotid foramina the tympanic plate bends into an antero-posterior direction. The total length between meatus externus and petrous apex is 34 mm. The stout petrosal process is situated medial to the lateral plate of the pterygoid, whereas in *Cercopithecoides* it was just behind. The mandibular nerve pierces this lateral plate by two small foramina.

The foramen magnum and the occipital condyles are rather small in the new specimen, the condylar fossae are well excavated. The postglenoid process is 9 mm wide and 6 mm high, the articular fossa lies just at the same level as the external ear opening and the articular eminence is narrow and concave in transverse direction. Unlike extant baboons, in *Parapapio* this eminence is not very thickened and normally lies at a more dorsal level than the ear capsule.

The mandible, M.3058, is very slender and has an undeveloped sloping symphysial region. There is a mental foramen on each side of the chin, the symphysis itself is pierced by a symphyseal foramen, opening about 5 mm below the incisors. The incisal shelf is short and sloping, reaching backward to about the midst of the first premolars. On the right side the anterior part of the ascending ramus is preserved, showing that it must have been nearly vertical.

The medial incisors are considerably stronger than the lateral ones; both have longish foveae on their lingual aspects. The canines are hardly higher than the unworn incisors. The first premolars possess a comparatively long anterior enamel facet, indicating that the upper canines of female *Parapapio jonesi* are of considerable length, which is confirmed by the data of Freedman (1957). These first premolars show very conspicuous posterior foveae. The second deciduous molars are not yet replaced by the second premolars, but they are very worn. The first permanent molars show considerable wear as well, but the second molars seem to have been erupted not long before the death of this animal.

By the size of its molars, this specimen undoubtedly fits in the species *Parapapio jonesi*, the second molars, together with specimen M.215 from Makapansgat, so far being the smallest of this taxon. The incisors of the present mandible are comparatively large, the canines and first premolars matching the range of *P. jonesi*.

The medial pair of the upper incisors, M.3059, is remarkable for its large size and shovel-like form, whereas the lateral ones are less specialized. If they belong to the present female skull and mandible, which seems very likely, these incisors would indicate a considerable specialization of the frontal dentition in an otherwise quite small and primitive cercopithecid. This enlargement of the medial incisors, which is very significant for the African Papionini, thus would have to be dated back right to the Plio-Pleistocene boundary.

Specimens M.3060 and M.3061 (Figs. 6, 7 & 9; Tables II–IV)

These two specimens most probably also belong together. Both parts lay 5 cm apart from each other in a fine grained brownish breccia, with no other fossils nearby. Next to the mandible

M.3060 an isolated neck vertebra of a cercopithecid was found, (M. 3061 a), which most probably belonged to the same animal as well.

M.3060 is the lower and posterior part of a cercopithecid braincase and the most posterior piece of the right maxilla with M^3 preserved completely. The whole upper half of the braincase and nearly the whole facial skeleton are eroded or blasted away. The fossilized bone of this specimen has a much harder consistency than those found in the ordinary 'pink breccia' and, according to Mr. J. W. Kitching, this specimen could come from the lowest part of the 'Upper Phase I'. Due to their hardness, specimens M.3060 and M.3061 exhibit many morphological details.

M.3061 is a nearly complete and undistorted male mandible, with all teeth well preserved, except the incisors, the right canine and P_3. Both the skull fragment and the mandible seem to fit together exactly, and the last molars of the right side interlock very well. Therefore there are good reasons for assuming that both pieces belonged to the same large male skull of about 170 mm maximum length. The upper last molar of M.3060 lies at the lower border of the observed range of *Parapapio broomi* and slightly above that of *P. jonesi*; however, there are only two male M^3 known of the latter species, both coming from Sterkfontein. The lower teeth of the mandible M.3061 match, however, the range of *Parapapio jonesi*, M_2 and M_3 being shorter than any *P. broomi*. Considering the skull morphology of this and of the specimen M.3051, to be described below, as well, there are good arguments in favour of the present fossil being a big male of *Parapapio jonesi*.

The most interesting feature of the fragmentary braincase M.3060 is its steep and rounded occipital region and the horizontally orientated nuchal plane. Although this region is not known of males of *Parapapio broomi*, it can be gathered from the dorsally expanded calvaria of M.202, M.2961 and M.3065 that this taxon most probably possessed rather a high and pointed inion. The temporal lines of the present specimen meet about 25 mm above the inion under an angle of about 60°. The adjacent temporal crest remains very low, and both lines diverge again 10 mm above the inion, forming a small triangular inion-area, which is bounded occipitally by the low nuchal crest. This marked but low nuchal crest extends laterally into the supramastoid crest and into the posterior root of the zygomatic process of the temporal bone. The preserved zygomatic process of the right side is very strong in this specimen, and it forms a high and sharp infratemporal crest anteriorly. The jugal arch is of considerable strength and it has a height of 13 mm at its anterior end. The zygomatic process of the maxilla starts just behind the last molar, thus indicating a considerable protrusion of the muzzle and the tooth rows, which are also reflected by a 10 mm long alveolar process behind the teeth. The articular eminence is very broad (22 mm) and long, but it is not much elevated; the articular fossa is bound by a strikingly large postglenoid process (breadth 12 mm, height 9 mm) posteriorly.

On the nuchal plane, nearly all of the insertion marks of the neck muscles are clearly visible. Conspicuously deepened are the areas of the musculus rectus capitis posterior just in front of the inferior nuchal lines; consequently these lines and the external occipital crest are to be seen very clearly. The mastoids are not very prominent, but the mastoid notches are quite distinct and the mastoid processes are pointed. The axes of the two occipital condyles meet each other at an angle of about 100°; the whole condylar part is well elevated above the nuchal plane, the basioccipital and the condyles being at about the same level as the tooth rows. In front of the condyles the insertion areas of the longus capitis muscle form deep impressions. The spheno-occipital suture on the steeply ascending pharyngeal face of the base of the braincase is closed; the small part of the hard palate being preserved in the present specimen forms an angle of about 140° with the base of the braincase. The choanal region is laterally bounded by well developed pterygoid plates, the lateral of which is pierced by the mandibular nerve. The auditory capsule (overall length 40 mm) lies more oblique than in the female and is less bent in its middle part.

The completely preserved M^3 of the right side is very broad and conical in its mesial breadth, but shows considerable reduction across the distal cusps. This distal reduction is not as pronounced in the preserved distal half of M^2. Both teeth are considerably worn and exhibit a typical papionine pattern of the enamel loops and of the wear.

The ascending rami of the mandible M.3061 show a backward inclination of about 30°, and they are not very high. The chin region does not show much relief and rises only at an angle of about 50° against the lower border of the corpora. In their outline the corpora of the present specimen are very similiar to those of the mandible 122–66K, described from Kanapoi by Patterson (1968).

The symphysis is not very strong and thickened, with the incisal shelf being comparatively short (24 mm length, reaching backward towards the midst of P_3) and sloping. At the sides of the symphysis and the anterior part of the corpora there are no signs of any mandibular fossae. The oblique lines are very thick and show two well marked tubercles on the lower part of their anterior margin, probably indicating the main insertions of the tendons of the temporalis muscle. Consequently, there exist two very broad grooves behind the last lower molars.

The ascending rami show conspicuous triangular depressions below the coronoid processes, indicating strongly developed deep parts of the masseter muscle. The angle of the mandible is not very pronounced, but is slightly thickened and has

several tubercles at its medial aspect. The condyles are about 18 mm broad and 6 mm long; they are slightly notched at their posterior margin. Although the coronoid processes are slightly higher than the condyles, they are not very well developed and not directed backward; the mandibular notches are very shallow as a result.

All teeth of this specimen are considerably worn, showing that it was a middle-aged male. The dimensions of the first lower premolar fit into *Parapapio jonesi* rather than into *P. broomi.* The length of P_4 is intermediate between the means of these two species, but it does not show the broadening, which is very often to be observed in *Parapapio broomi.* M_1 again is intermediate in length, but in breadth falls nearly below the range of *P. broomi.* M_2 is below the observed length range of male *P. broomi* and matches the length and breadth dimensions of *P. jonesi* fairly well. The length of the systematically important M_3 lies distinctly (with one exception) below that of *P. broomi,* although this being the longest M_3 so far reported for *P. jonesi*; the same is true for the breadth measurements of this tooth.

To conclude, it seems highly probable that the present mandible M.3061 belonged to a comparatively large male of *Parapapio jonesi* rather than to *P. broomi,* but this question would seem to need further statistical testing. Consequently, also the skull fragment M.3060, most probably belonging to this mandible, would have to be referred to *P. jonesi,* and hence would be the first known male braincase of this species.

*Specimen M.3051** (Fig. 8; Tables II–IV)

This specimen consists of a nearly complete, but bilaterally crushed and distorted male skull, embedded in the 'basal red' breccia of the Makapansgat Limeworks. Although most of the upper parts of the skull are missing or dislocated, it provides a fairly good idea of the overall morphology.

The orbital and nasal skeleton is displaced about 40 mm from the maxilla, but the taxonomically important glabellar region is fairly well preserved on the right side. The roof of the calvaria is broken into pieces, most of which are missing; the occipital region, however, is available. The lower part of the muzzle, the jugal arch, the temporal fossae, the outer ear region and the mastoid of the left side, as well as the complete mandible are in situ. Also the occipital condyles and a few upper neck vertebrae are visible. The fossilization of whole corpses seems to be not uncommon in the 'basal red' breccia, and systematic excavations of these layers could provide the very necessary information on the postcranial skeletons of the South African Pleistocene cercopithecoids.

The present specimen, fortunately enough, has complete tooth sets with the exception of the upper incisors. Most of the teeth are, however, not in a position to allow accurate measurements of their breadth. Nevertheless, the size and morphology of the teeth suggest that the present specimen belongs to *Parapapio jonesi* as well, thus being by far the most complete male skull of this species.

The preserved parts of the supraorbital region show clearly that the present specimen is a typical *Parapapio* because the torus supraorbitalis and the glabella are hardly protruding, although they are of some strength. The nasal bone is not sloping steeply between the orbits and there is only a very shallow transverse groove behind the glabella.

The overall length of this specimen is strikingly large when compared with the small teeth, and it coincides fairly well with the estimated length of the specimen M.3060/3061. Although the muzzle must have been quite strong and elongated, it is still distinctly shorter than the braincase; but this is even true for the very elongated *Parapapio whitei* (see below).

The braincase is poorly preserved, mainly its occipital and basal parts being available. The parietals seem to have been of the short and rounded type as in specimen M.3060. They are sloping fairly steeply towards the inion, without forming a conspicuous sagittal crest. The nuchal crests, however, are quite strong, and both these and the temporal lines form a flat and triangular inion region, which lies at a comparatively low level. The nuchal plane is mostly crushed but it most probably had a more broad and rounded outline rather than an elongated and pointed one as in *Parapapio whitei.* Whereas the mastoid of the left side is quite flat, but again shows a distinct notch and process, the condylar part of the occipital bone probably was elevated, the left condyle being situated at the same level as the upper tooth rows. The articular fossa is separated from the auditory meatus by a very high and strong post-glenoid process (10 mm broad, 11 mm high). The anterior part of the jugal arch is of considerable breadth (11 mm) and its anterior root lies above the last molar. In most of these features the present skull exhibits many similarities to M.3060.

The zygomatic bone is strong, and its lateral margin rises at a steep angle, which is very different from that in the male *P. broomi* (M.202). The temporal crest of the frontal is deeply incised behind the orbits, this feature being similiar in the latter species. Together with the well rounded braincase and the comparatively high face, these characteristics would indicate a comparatively strong and steep postorbital part of the temporal muscle.

The left side of the maxilla shows a deep and large canine fossa, dorsally bounded by a sharp maxillary crest. On the right side parts of the muzzle dorsum are exposed, showing a flat area wrinkled with several grooves of the infraorbital nerves and bounded laterally again by a pronoun-

* Prof. P. V. Tobias kindly allowed me to describe this specimen, which is housed in the collection of the Anatomy Department of the Medical School, Johannesburg.

ced maxillary crest. The canine fossa results in exposed anterolateral roots of the first two molars. The premaxilla is partly preserved on the left side; it is much protruded and possesses large alveolae.

The mandible in this specimen is nearly exactly as long as in M.3061, but it has a comparatively higher and steeper ascending ramus. This being a younger male, however, the growing alveolae could have resulted in similar conditions as in the older M.3061. Again, the corpus is quite slender without showing canine fossae or crest formations at the chin region. The strength and shape of the symphysis seems to coincide with that of the mandible M.3061 and with that of Kanapoi. The channel behind the last molars is broad, excavated and laterally bounded by a strong oblique line. The coronoid processes are distinctly higher than the condyles of the mandible; both processes are separated by a shallow mandibular notch. The angle of the mandible is very pronounced in this specimen.

Unfortunately there does not exist much upper tooth material of *Parapapio jonesi* for comparative purposes. The upper canines are very high and slender in the present specimen and in this respect exceed all known canines of *Parapapio broomi*. The dimensions of the two upper premolars are all considerably below the mean values of both male and female *Parapapio broomi* and match very closely those of female *P. jonesi*; in three of these measurements, the values even fall outside the observed range of the males of *Parapapio broomi*. Although the molars of the present specimen are larger than most of the known teeth of *P. jonesi*, they are again distinctly below the mean values of *P. broomi* and below the observed range of the males of this species. The lower teeth of the specimen M.3051 compare very well with those in M.3061, which have been shown to be close to *Parapapio jonesi*.

Specimen M.2961 (see Freedman, 1961)

In 1961 Freedman described and depicted a fairly complete male skull from the 'grey breccia' of Makapansgat, which he referred to *Parapapio broomi*, although he observed numerous morphological differences with the other known skulls of this species. Examination of the new material of *Parapapio jonesi* led to the assumption that this specimen M.2961 could also belong to this species. Unfortunately there are only the last two molars of the right side preserved in this specimen, but in length they fall distinctly below the range of *Parapapio broomi* and are fairly close to the mean values of *P. jonesi*. In the breadths, however, there are more similarities with *P. broomi*. (see Table I)

Due to the lack of the front teeth, there cannot be taken any measurements of the tooth rows; however, the distance between the distal margin of the canine alveolus and the distal margin of M^3 is about 40 mm in M.2961 against 41.5 mm in M.3051, showing that not only the molars but also the premolars must have been very short in specimen M.2961.

TABLE I

		M.2961	$\bar{X}$ *P jonesi* males only	$\bar{X}$ *P broomi* males only
M^2	l	10,4	10,2	11,1
	mb	(12,5)	10,4	11,5
	db	(11,1)	9,6	10,8
M^3	l	(10,3)	10,3	11,2
	mb	11,5	10,9	11,4
	db	9,5	8,5	9,3

In the skull of M.2961 the contours of the braincase are rather different from those in *Parapapio broomi*: it does neither show the elevation just behind the glabella nor the depression thereafter, but it is well rounded all over. The temporal lines meet behind the bregma, but they do not seem to form any conspicuous sagittal crest. As Freedman pointed out already, the glabellar region is quite advanced in the present specimen, the interorbital width is greater and the nasals drop more steeply than in *P. broomi*. There is an internasal suture on the postero-superior 30 mm of the nasal bone. The maxillary crests are well developed, more than in the known specimens of both *Parapapio broomi* and *P. whitei*; they are short, however, and converge anteriorly. The infraorbital margin and the zygomatic bone are shifted forward, similar to the conditions in *P. broomi* (M.202). The canine fossae are shallow in their posterior part; this is different in M.3051, but there is some distortion in this area of the skull. In specimen M.2961, being older than both M.3051 and M.3060, some of the morphological differences may be attributed to age differences. To conclude, it seems probable that this specimen M.2961 is to be referred to *Parapapio jonesi* as well. Together, the three specimens, described here, could give for the first time a fairly complete picture of the male skull of this species; in Fig. 9 a combination of the known features is tried.

Conclusion: For the first time, more or less complete male skulls of *Parapapio jonesi* could be described. Although their teeth belong to the same size category as that of the female type, the size of the skulls is considerably larger, indicating a high degree of sexual dimorphism. The skull of this species does not exhibit, however, the elongated appearance of the males of *Parapapio broomi* and *P. whitei* (see below), but it is more stout and high; the braincase is more rounded and does not show exaggerated crests. The muzzle is comparatively short, but nevertheless possesses more pronounced maxillary crests and canine fossae than those two species.

Even the small female specimen M.3057/3059 has very large and specialized medial incisors; this character is very typical for the papionine Cercopithecidae of Africa, but it is not met with in the closely related Macacini of the Eurasiatic

region or in the African Theropithecini, living sympatric with the Papionini. Apparently, this distinct character evolved very early.

All of the presently described specimens of *Parapapio jonesi* were recovered from either the 'basal red' or the 'grey breccia' of the Makapansgat Limeworks. In the upper parts of this deposit, this species seems to be rare, at least. Nevertheless, this species of the genus *Parapapio* seems to have the widest distribution, both in space and time. As the Colobid *Cercopithecoides williamsi* it occurs in most of the South African deposits, perhaps suggesting a similar habitat for both forms.

(3) *Parapapio broomi* JONES 1937

This type species of the genus *Parapapio* is the best known of this taxon, both in tooth and in skull morphology. It is recorded from Sterkfontein, Makapansgat and Bolt's Farm. In the first two sites, this species seems to be the most abundant Cercopithecoid, and also of the present new material, most of the specimens are to be referred to *Parapapio broomi*. This species is found in the 'grey breccia' and in the 'Upper Phase I' (pink breccia) of Makapansgat Limeworks. In tooth size it is about intermediate between *Parapapio jonesi* and *P. whitei*. All of the new specimens, described here, come from the 'pink Cercopithecoid breccia'.

Specimen M.3056 (Tables II–III) is a fairly complete and undistorted skull, most probably of a female. Before fossilization, the whole occipital bone was broken off exactly along its sutures, both mastoids and auditory capsules being left. Possibly also the missing left jugal arch was lost before fossilization. The premaxilla and the most anterior parts of the maxillae, together with all of the front teeth were lost afterwards. This skull was split during preparation just underneath the orbits, resulting in a battered condition of the upper facial skeleton. The premolars are badly damaged on both sides, and of the molars only the right M^3 is complete. The shortness of the face and the considerable amount of wear of all of the teeth indicate that this was an old female.

Specimen M.3070 (Figs. 10 & 11; Tables II–III) consists of a nearly complete facial skeleton of a very old female. In addition, there are preserved parts of the base of the skull with the outlines of the foramen magnum. Even the premaxilla is fairly complete, but it must have lost its teeth before fossilization. There is a crack along the left maxilla, resulting in a slight distortion of that part of the muzzle and in the loss of the external frame of the left orbit. The whole calvaria is missing from 20 mm behind the glabella. The teeth of the left side are fairly complete, but the canine and the last molar are partly damaged; the last molar is the only complete tooth of the right side.

Specimen M.3082 (Table III) consists of the left half of a female muzzle, comprising premaxilla, maxilla and zygomatic bone. The incisors and the canine are lost, but the alveolar sockets are preserved; that of the canine is so small that it must have belonged to a female. The premolars and molars are complete and without much damage and wear. The remains of this young female *Parapapio broomi* were found a few inches apart from the skull M.3073 of *Simopithecus darti*.

Specimen M.3065 (Fig. 12; Table II) is a very large skull of a male cercopithecoid. It consists of the right half of the facial skeleton (without nasal and premaxillary bones) and of the upper parts of the braincase. Most of the left and basal parts are missing due to prefossilizational damage. The big right canine is partly preserved, but most teeth of the premolar and molar series are very fragmentary, with mostly only the roots left. M^1 exposes a small area of the occlusal surface which is very worn and indicates that this was a very old male. In overall size the present skull even seems to exceed slightly the new skull of a male *Parapapio whitei* (M.3072; see below), but the teeth seem to have been distinctly shorter than in this species. Further, it seems possible that this skull belonged to the very large mandible M.3067, found next to it, which clearly can be aligned with *P. broomi*. Therefore this specimen is tentatively referred to *Parapapio broomi* as well.

Specimen M.3067 (Fig. 13; Table IV) is an extremely long and strong male mandible, of which the right half is nearly complete, whereas on the left side there are preserved only the parts anterior to the first molar. There is some distortion in the symphysial region and, as a consequence, the incisors are missing. The corpus of this mandible is long and high, but it does not have any mandibular fossa; at its rostral end, the chin region slopes backward rising at an angle of about 45° against the lower margin of the corpus. There is only a slight crest formed below the canines, where the mental foramina open. The ascending ramus is inclined backward at about 40° from the vertical axis and it is very broad. The right condyle could be restored in its proper position, and it becomes evident that it does not lie much above the occlusal plane. The coronoid process is lost, and the anterior border of the ascending ramus is more rounded than in *Parapapio jonesi*. Its oblique line is separated by a channel of 10 mm breadth from the posterior alveolar process. Compared with the extraordinary maximum length of the mandible the tooth row appears to be rather small. The molars are very worn and have lost some length due to considerable wear between adjacent teeth. In most tooth measurements the teeth of this specimen are even below the mean values of *Parapapio broomi*, and in all cases fall outside the observed range of *P. whitei*. This striking disproportion coincides with those of the above skull, and a reconstruction (Fig. 14) shows convincingly that this male with the tooth size of a typical *P.*

broomi possessed an extremely elongated muzzle, exceeding even that of *P. whitei.*

Specimen M.3063 (Fig. 13; Table IV) consists mainly of the right half of a female mandible, which is fairly complete, with only the symphysial region and the tip of the coronoid process missing. The left corpus is present as well, but it is badly damaged and without teeth. The ascending ramus is moderately steep and high. The right tooth row is complete from C to M_3, the latter tooth just having been erupted. Some of the anterior teeth show minor damage.

Specimen M.3075 (Table IV) is also a half mandible of a young female, which is broken just at the symphysis, with the left half preserved. The corpus is fairly long and slender, the ascending ramus rising steeply with about 10° backward inclination. The coronoid process is lacking again. The first premolar and the first molar are badly damaged.

Morphological Discussion: The two new female specimens of *Parapapio broomi,* M.3056 and M.3070, together yield a fairly comprehensive picture of the whole skull, which is so far only known from Sterkfontein. The supraorbital arcs and the supraglabellar fossa are scarcely developed in both female skulls. The calvaria rises almost immediately behind the glabella, and it forms a well-rounded vault, dropping rather steeply towards the inion. The postorbital constriction is fairly narrow, but the temporal breadth in the female M.3056 nearly equals that of the male *Parapapio whitei.* The temporal lines probably do not meet medially in the females of this species. As far as can be seen, the nuchal planes lie rather horizontally and the mastoids are moderately developed in both specimens. Due to the considerable breadth of the braincase, the auditory meatus is quite long (in contradiction to Freedman's statement) and oblique. The postglenoid process is quite short in M.3056, and the articular fossa is very much deepened, its floor lying at the same level as the dorsal margin of the outer ear opening. The jugal arch appears to be short and of medium strength in both specimens; its anterior root, starting above the distal half of M^2, is situated much lower than the infraorbital margin.

The facial skeleton is especially well preserved in M.3070, where the muzzle appears to be quite slender and converging anteriorly. Whereas in this specimen the muzzle is more low and elongated, in M.3056 the face is more stout and high, although the missing parts render a comparison difficult. In this latter specimen there are, however, very faint maxillary crests and very shallow canine fossae, but there is still no flattening of the muzzle dorsum. In M.3070, there are only a few furrows of the infraorbital nerves, but otherwise the lateral surfaces of the muzzle slope down in virtually straight lines from the nasal to the alveoles, resulting in a triangular shape of the transverse section. Lateral to the 3 or 4 separate infraorbital foramina there are shallow infraorbital fossae. In both skulls the nasals have a distinct concave contour, especially evident in M.3070, where it is undamaged; here it also shows an internasal suture, but this could also be due to unnatural cracking. In this specimen the nasal aperture is short and ovoid in outline; it is framed by the lateral wings of the premaxillary bones which reach up to the antero-lateral margins of the nasal. The premaxilla is protruding and of rounded outline at its anterior margin. The orbits are comparatively large in both specimens.

The tooth rows are slightly convex laterally, the palate is narrower and deeper in M.3056 than in M.3070. Both specimens also differ considerably in their degree of declination of the palate, which is 43° in M.3056, but only 32° in M.3070. This angle is known, however, to vary very much in extant baboons (Frick, 1960). Although there are considerable age differences between these two specimens, their teeth compare fairly well; both show a reduction of breadth across the distal cusps of M^3. In both, P^4 and M^1 are short, compared with the average of the species, whereas M^3 is comparatively long, but does not fall outside the observed range. The lengths of the tooth rows of M.3070 closely match the averages for *Parapapio broomi.*

Specimen M.3065: There is one fairly complete male skull of *Parapapio broomi* from the 'grey breccia' of Makapansgat (M.202) for comparison. In the shape of the braincase, the glabellar region and the muzzle, there are numerous similarities with M.202, although the new skull seems distinctly more elongated and the whole tooth rows shifted more anteriorly. Altogether, the skull M.202 seems to be about 15 to 20 mm shorter than M.3065, and possibly the time difference between the deposition of the 'grey breccia' and the 'pink breccia' could be responsible for the increased size of the latter. The supraorbital region is hardly developed in this skull, nor is there a transverse groove behind the flattened glabella. Behind the glabella a well marked protuberance of the frontals is present, which was also noticed by Freedman (1957) in his specimens; it reaches its highest point about 35 mm posterior to the glabella. At the bregma the contour line is slightly depressed, then it rises again to form a sagittal crest. Both temporal lines meet 15 mm behind bregma and the starting bony crest seems to indicate that there existed a pronounced sagittal crest and a prominent inion, similar to those seen in M.3072 (see below). This elongated and bulb-like shape of the braincase seems to be very typical for both *Parapapio broomi* and *P. whitei,* but is not met with in the other two species of *Parapapio.*

The muzzle is very elongated in this specimen, but at the same time it is less high than in the equally sized *P. whitei.* The zygomatic bone is very broad and strong; together with the zygomatic

process of the maxilla, the infraorbital wall is shifted forward considerably. The tooth rows lie even more rostrally, so that the zygomatic process starts behind the last molar. Very different from *P. jonesi* and from *P. antiquus* is the absence of any true maxillary crest; as in *P. whitei* there is just a faint and rounded elevation at the exit of the infraorbital foramina, but no crest and canine fossa whatsoever. In this old male, the forward-growth of the alveolar processes (Scott, 1967) was very advanced, as is indicated by the great length of the postmolar alveolus.

Unfortunately there is much damage of the teeth, but their overall length can be determined fairly accurately. The length of the molars seems to fit well that of the males of the few so far described males of *P. whitei,* but as will be shown below, these specimens should mostly be referred to *P. broomi.* The large new male of *P. whitei* (M.3072), found in the same breccia, possesses considerably larger teeth. In addition, Fig. 14 shows that this skull fits well on to the mandible M.3067, which also shows more similarities with *P. broomi* than with *P. whitei.*

There can be no doubt, however, that both *P. broomi* and *P. whitei* are very closely related morphologically, and mainly differ in tooth size. At the moment, there is still a gap between the two size categories, which might well be closed, however, when additional material becomes known.

The mandibles of this species do not need any further discussion. Fig. 13 shows both a male (M.3067) and a female (M.3063) for comparison, with the female even possessing the larger teeth. The immense degree of sexual dimorphism, indicated by the skull material, becomes evident in the mandibles as well. Although hardly pronounced in tooth size, the females are only about 76% of the male skull in length. This observation is in contrast to Freedman's statement that it was less (84 .3%) in *Parapapio broomi* than in *Papio ursinus* (77.4%).

Conclusions: The majority of the specimens from the 'pink breccia' of the Makapansgat Limeworks is to be referred to *Parapapio broomi.* It seems to have been sympatric with *Cercopithecoides, Simopithecus* and *Parapapio whitei.* The presence of *P. jonesi* in this upper layer is doubtful, the best specimens of this taxon all coming from either the 'basal red' or the 'grey breccia'.

The female skulls, though fragmentary, yield a fairly complete picture of the skull morphology of this species, so far best known from Sterkfontein. Both specimens indicate that there was a considerable amount of variation in the shape of the muzzle. The first male skull of *Parapapio broomi* from the 'pink breccia' appears to be of very great length, even exceeding that of *P. whitei.* The orbital region is very unspecialized in this male and the muzzle shows an extreme elongation. As in *P. whitei* there are no distinct maxillary crests and canine fossae.

If this skull is rightly assigned to *P. broomi,* then there existed a considerable sexual dimorphism, the female skulls being only about three quarters as long as those of the males. Apart from the tooth size, *P. broomi* seems to be very similar to *P. whitei,* both being sympatric. However, it is more reasonable at the moment to assume that they were closely related species, which somehow fitted into different ecological niches. Additional material may well fill the gap between the two forms and reveal the existence of one highly variable species.

(4) Parapapio whitei BROOM 1940.

Up till 1957 *Parapapio whitei* was only known from Sterkfontein. In 1961, Freedman referred 6 specimens from Makapansgat to this species, and in 1965 the same author recorded this species from Bolt's Farm and from Taung. As is discussed below, a revision of this species seems to be very necessary, in the light of the new material.

Specimen M.3072. (Fig. 15; Tables II–IV)

This specimen consists of a large male skull with parts of the right mandible in situ. It came from the 'pink breccia' of the Makapansgat Limeworks. There is some damage, both pre- and post-fossilizational. The anterior part of the left jugal arch and the lower parts of the left maxilla and premaxilla together with the left teeth are missing; on the right side the entire jugal arch is broken off, but still indicate a steep and high parietal are removed as well; both supraorbital tori are damaged to some degree. But in general, the remaining parts are fairly complete and undistorted; the whole braincase, including its base, and the right side of the muzzle with all teeth of the right side are present. Of the mandible, the right ascending ramus is completely preserved, whereas the lower and anterior parts of the horizontal ramus are missing; all premolars and molars are complete (except P_3) and in excellent condition. After casting, the lower jaw was separated from the skull.

Specimen M.3062: This is a male mandible, the teeth of which are very large and fit the size of *Parapapio whitei* very well. The incisors and canines were lost before fossilization; the right P_3 most probably was lost afterwards, but it is present on the left side. Apart from the first molars, and the left premolars, the teeth are preserved in good condition; the moderate wear of the last molar indicates a middle-aged male. The posterior margin and the upper half of the ascending ramus are broken off, but still indicate a steep and high ramus, closely comparable with that of M.3072.

Morphological discussion: In 1957, Freedman had practically no male skull and upper teeth material of *Parapapio whitei* available, but there existed about 4 fairly complete mandibles. The molars of the females of this species were

distinguished by their enormous length which lay markedly above the size-range of both sexes of *Parapapio broomi*. In 1961, Freedman described a robust male muzzle from the grey breccia of Makapansgat (M.2962) and in 1965 a complete skull from Bolt's Farm (56785). Although both of these specimens had distinctly shorter teeth, this author referred them to *P. whitei*. Apart from some isolated teeth, only the new skull, however, matches the tooth dimensions of those females mentioned above. It seems improbable that the males had much smaller teeth than the females.

The present skull M.3072 is very much elongated; it resembles the skull M.3065, here referred to *P. broomi*, in many respects, but the face is higher in this specimen. Again, the supraorbital arcs and the glabella are very undeveloped and flat; there is no ophryonic groove whatsoever. Instead there is the same dorsal protuberance of the frontals and the adjacent depression at the bregma as described for *Parapapio broomi*. There is a low and small sagittal crest just behind the bregma. It is probable that the upper temporal lines, which cannot be identified, meet there. The real sagittal crest only starts 20–25 mm behind the bregma; it gradually rises to its maximum height of about 8 mm, which is reached at the external occipital protuberance. Together with the moderately developed nuchal crests there is formed a very pointed and prominent inion. The interfrontal constriction being narrow and the maximum temporal breadth being rather large, the braincase forms an elongated bulb, when seen in norma dorsalis. The length of the braincase nearly equals that of male *Papio ursinus*, the latter possessing only a thicker glabella. The morphology of the braincase of specimen 56785 (see Freedman, 1965; fig. 7) is entirely different from that of both the skulls of *P. broomi* and of *P. whitei*.

Although the muzzle is elongated considerably, it is only about 83% of the braincase length. The interorbital and nasal slope gently between the orbits and form a slightly concave contour. The nasion lies right up at the glabella; the nasal bones form a keel-like crest with a longitudinal suture running down to their rostral margin. Proximally it seems to be a true internasal suture, distally it looks more like a split due to transversal pressure. The orbits themselves are comparatively small, as is the whole upper facial skeleton; this is a very conspicuous difference with both the male skulls, described by Freedman, but it is very similar to the conditions in the males of *Parapapio broomi*. The infraorbital face wall and the strong zygomatic bone again slope anteriorly and laterally, and there is no indication of any canine or infraorbital fossae. The zygomatic process of the maxilla lies dorsally to the mesial half of M^3. The two faint maxillary ridges start at the openings of the 2 or 3 infraorbital foramina and end above the roots of the canines. These ridges cause shallow depressions lateral to the nasal bones.

In dorsal view, the posterior root of the jugal arch seems to be quite narrow, but the broad (22 mm) articular fossa reaches far medially at the underside of the skull; on the right side, a break-section exposes many air cells in the temporal bone lying above the articular area. The postglenoid process is smaller than in the males of *Parapapio jonesi*. The nuchal plane shows a distinct triangular outline, due to the prominent inion. The inion is at a distinctly higher level than in *P. jonesi*; thus the nuchal plane slopes more steeply in *P. whitei*. The foramen magnum is at about the same level as the alveolar border, and it is distinctly elevated above the nuchal plane. The mastoids are still separated by a suture from the occipital bone. They are not very prominent, but show marked processes and notches. As is to be expected in such an elongated skull type, the external auditory meati are long and run obliquely.

The sphenoccipital suture is still visible in this specimen, lying between the posterior margins of the pterygoid fossae. These are quite large and deep; the lateral plates of the pterygoids are of considerable size and height. The palate forms an angle of about 131° against the pharyngeal face of the base of the braincase, showing a considerable declination of 49°. The left alveolar processes are missing, but on the right side they are very steep and high (10 mm).

Of the incisors, the right mesial one is just split in half, but the lateral incisor is fairly complete. Both do not seem to have been very large. The upper canines are slender and not excessively long. The upper two premolars are of considerable size, and they fit the size of some specimens previously referred to *P. whitei*; they do not differ too much from *P. broomi*, but this species is remarkable for the size of its premolars. The length of the first molar by far exceeds those of *P. broomi*, and also for *P. whitei* it is the largest M^1 so far known. Its breadths are within the range of the larger females of this species.

Also the last two molars are only comparable in size with the largest females of *P. whitei*, *Parapapio broomi* and most of the other known skull material having much lower values.

The first premolar of the lower jaw is slightly longer than in males of *P. broomi*; also the second premolar is longer and broader, but matches the size of the previously known specimens of *P. whitei*. The first two lower molars again are enormously elongated and they are distinctly beyond the averages of the known *P. whitei*, not to mention *P. broomi*. The last molar of M.3062, however, is comparatively short for *P. whitei*, although being within the range of this species and being outside that of *P. broomi*. Against that, the M^3 of M.3062 is the largest molar so far recorded for the genus *Parapapio*, and is close to the means of *Papio ursinus*.

Although the mandibles of these two male *Parapapio whitei* are distinctly shorter and less robust than the male M.3067, above referred to *P.*

broomi, their tooth rows are much longer than in this specimen. This would support the view that *P. whitei* is not just a large sized *P. broomi,* but that it was actually a slightly smaller animal, possessing a higher degree of molar enlargement.

Conclusions: The present specimen M.3072 is especially valuable for its completeness and for the fact that both the upper and the lower dentitions are present. It is actually the first male specimen which fits the female type specimen (STS 563). It is slightly larger than this specimen, but that is to be expected of a large male. The skull morphology suggests close relationships with *Parapapio broomi,* which is quite distinct in tooth size, however.

All larger skull remains, referred to this species by Freedman, probably should better be replaced in the light of the new evidence. The large muzzle M.2962 compares fairly well with the large males of *Parapapio broomi,* both in structure and in tooth size. Specimen 56785 from Bolt's Farm is very aberrant in the whole shape of the braincase and of the facial skeleton; the robust build of the circumorbital region even shows some resemblance with the genus *Papio,* as does the outline of the calvaria. In tooth size, however, it matches *P. broomi.* As with the other faunal elements of Bolt's Farm it seems to be quite different from those of both Sterkfontein and Makapansgat.

(5). Simopithecus darti (BROOM & JENSEN) 1946.

This is the largest form of the Cercopithecoidea of Makapansgat, and it was described in 1946 by Broom & Jensen as *Papio darti.* It was only Freedman (1957) who recognised that this species should be aligned with the genus *Simopithecus,* at that time only known from East Africa. At Swartkrans, another, larger *Simopithecus* was found which was put in a new species, *Simopithecus danieli,* by Freedman (1957).

The type specimen (M.201) came from the 'pink breccia' of Makapansgat, but there is also material recorded from the 'grey breccia' of that site. All of the new specimens were found in the 'pink breccia' of the Upper Phase I.

So far only mandible and maxillary fragments, as well as isolated teeth, were known; the new material adds considerably to our knowledge of *Simopithecus darti.* The genus *Simopithecus* has been studied repeatedly within the last decade (Leakey & Whitworth, 1958; Jolly, 1964) and it became highly probable that this form is very similar to the extant *Theropithecus gelada,* and that both are very distinct from the true baboons. This led Jolly (1966) to establish a separate tribe Theropithecini for these two genera. The sister tribe would then be the Papionini, comprising the Mangabeys, Drills and Baboons. These classificatory problems have been discussed at some length by the present author (Maier, 1970).

Specimen M.3073 (Figs. 17–20; Tables II–IV) is the nearly complete skull of a young female, with the third molars not yet erupted. The mandible is in situ, but it is slightly distorted. There is some prefossilizational damage: parts of the right temporal squama with the zygomatic process are missing; the right zygomatic bone is somewhat displaced; the anterior tips of the premaxilla and the chin are damaged and the angle of the left mandible side is broken off. The skull itself is virtually undistorted and shows many new morphological details.

The present skull was associated with numerous postcranial bones which, judged by their size, probably belonged to the same specimen. Just beside the skull a right mandible of *Oreotragus major* and several skull fragments of *Parapapio broomi* (M.3082) were found. The significance of this first complete skull of *Simopithecus darti* is also discussed in a separate paper (Maier, in prep.).

Specimen M.3071 (Fig. 20; Table IV) is a nearly complete mandible of an immature male *Simopithecus.* The incisors are either damaged (right side) or missing (left side) and the canines are not fully erupted; the last molars are still in their crypts, but could be seen by X-ray. The chin shows some damage and the upper parts of the right ascending ramus were damaged before fossilization, whereas the ramus of the left side is complete.

Specimen M.3074 (Table IV) consists of a very fragmentary mandible of an old male of *Simopithecus.* Only parts of the symphysial region and the horizontal corpus of the right side are preserved. Most of the teeth have only their sockets and roots left, but nevertheless give a rough idea of the overall dimensions in an adult male for comparison with the young male M.3071.

Specimen M.3083 (Table III) consists of a fragmentary palate and maxilla with both tooth rows in situ. Only parts of the premaxilla are preserved, and that of the left side is displaced medially. All teeth are very worn and mostly damaged; the canines are large and tusk-like, indicating that the present specimen belonged to a very old male of *Simopithecus darti.* It is the first male palate which is known so far of this species.

Morphological discussion: The most striking difference between the skull of M.3073 and the skulls of *Parapapio* and *Papio* is their different proportioning. Whereas the latter show a marked elongation of the muzzles and braincases, the present specimen is distinguished by its increased height of the skull. The braincase is comparatively rounded, and it is much elevated above the lower facial skeleton and the tooth rows. The proportioning is well reflected by the steep and high ramus ascendens, both in the female and in the male mandible.

Both in tooth and in skull size *Simopithecus darti* is the largest Cercopithecoid from the Makapansgat Limeworks. Most probably, the body size of this species was close to that of the extant *Papio ursinus*; the same is true for the degree of sexual dimorphism.

The supraorbital torus is not very pronounced in this young female skull, but it is still more protruding than in the genus *Parapapio*. The transverse groove behind the torus is comparatively well developed, especially in its lateral parts. 10 mm behind the glabella, the vault of the calvaria rises quite steeply, but is more flattened in the area of the bregma. The parietal part of the calvaria is not sloping steeply, because the inion is situated at a high level. The supraoccipital bone and the lambda are reaching on to the dorsal aspect of the calvaria, the latter lying about 15 mm above the protuberantia externa.

The temporal crests are well pronounced on the anterior part of the frontal, but then become faint lines, which do not meet medially; their minimum distance amounts to about 15 mm. The nuchal crests are only pronounced above the mastoids. The posterior root of the jugal arch is broad and strong, as is the jugal arch itself. The nuchal plane is distinguished by its extreme shortness, which is also responsible for the rounded appearance of the whole braincase. The mastoids are comparatively well pronounced, showing a well-marked notch and process on the left side of the skull. The condylar part of the occipital bone is not as elevated as in some of the skulls of *Parapapio*; the foramen magnum is more or less rounded and of comparatively large size. The choanal and the palatal region is not prepared in the present skull in order to support the brittle bone of which it is made. The postglenoid process is about 9 mm high and the articular fossa and eminence are at the same level as the long auditory meatus. The articular eminence is broad (23 mm) and concave.

Whereas the braincase is not too different from that in many skulls of *Parapapio* (apart from the short occipital region), the muzzle shows more peculiarities. The weakly pronounced glabellar and nasal region drops very steeply between the orbits to give the muzzle dorsum a nearly vertical and concave outline. The nasal itself is long and narrow, without any trace of an internasal suture. The orbits are nearly round and, due to the comparatively weak circumorbital frame, the upper face appears to be quite narrow. This narrowness is underlined by the very high and broad zygomatic bones which give rise to the strong jugal arches. This infraorbital face-wall is nearly vertical, the zygomatic process of the maxilla lying dorsally to M^2. In adult females most probably these features would have been more clearly expressed because the posterior alveolar processes obviously are not yet fully developed in this immature specimen.

There are two faint maxillary ridges, originating at the largest of the infraorbital foramina (about 10 mm below the infraorbital margins), and converging towards the nasal aperture. These maxillary ridges also slope downward, and they are not of the *Papio* or *Parapapio*-type; they resemble much more the maxillary crests of the extant *Theropithecus gelada*. Below these ridges shallow, but well marked, canine fossae are developed. The premaxilla does not protrude much, but its lateral wings, framing the small nasal aperture, reach the lateral sides of the nasal bone. The muzzle breadth across the molars corresponds roughly to that of *Papio* and *Parapapio*, but across the canines and the premolars it is very narrow. The mandible of specimen M.3073 is distinguished by its high and narrow ramus ascendens. The corpus is comparatively narrow and slender; its height decreases anteriorly, and there seems to have existed only a small chin. The lateral surface of the corpus shows some depressions, which are not comparable with true mandibular fossae, however. Behind the second molars, the corpus is thickened due to the large third molar being in its crypt; the same feature is to be observed in the mandible M.3071. The ramus rises at nearly right angles, and it possesses triangular fossae of considerable size and depth. The coronoid process is higher than the condyle, and both are separated by a deeply incised sigmoid notch; the same is true for the male mandible M.3071. The condyle, which is only preserved on the left side, is quite massive, and it is more strongly developed at its medial side; its posterior aspect does not exhibit a deepening, which was observed by Leakey & Whitworth (1958) in several specimens of *Simopithecus oswaldi*. Both the male and the female mandible coincide in the shape of the mandibular condyles.

The teeth are not prepared properly in the skull M.3073, the tooth rows still being in occlusion. On the right side the surface of the molars could be cleaned and they exhibit a surface structure which is typical for the genus *Simopithecus*. The upper incisors are eroded on the left side as are the lower ones on the right; nevertheless the remaining incisors show that the upper medial one is broadened to some degree whereas the lateral incisor and both of the lower ones are quite small and unspecialized. In no case do they protrude as in the Papionini. The upper canines are quite well developed and they exceed the premolars by about 5 mm in height. The lower canines are less conspicuous; the mesial facet of the lower P_3 is of considerable length. The upper premolars are very small whereas the upper molars have a very large size, only encountered in *Simopithecus*, even exceeding that of *Papio ursinus*. The first molar is considerably worn, but the second one is only slightly abraded at its mesio-lingual cusp.

The second lower premolar is about the same size as that of the female *Papio ursinus*. The lower molars are again very elongated in M.3073 exceeding clearly even the males of the extant baboons.

The present specimen yields the first information about the female front teeth (incisors and canines). The upper premolars fit well the female teeth recorded by Freedman, but the first molar is larger than in his specimens. There exists no comparative female material of M^2; in M.3073 it is slightly smaller than in the known males, and it slightly exceeds M.2967 of unknown sex (Freedman, 1961). Inferrring from this specimen, we could expect the unerupted M^3 to be about 17,5 mm long.

In the P^4 there is very conspicuous sexual dimorphism; in the males it obviously is more than 9 mm long, whereas in the females it is only slightly above 8 mm. The specimens M.3027 and M.3035 (Freedman, 1961; Table 20) consequently should be referred to males. Both newly recorded specimens of *Simopithecus darti* show distinctly longer first lower molars than in the specimens recorded by Freedman. The female M.3073 possesses a very large M^2, being longer than any recorded specimen of *S. darti* both male and female. In both the lengths of M_1 and M_2 it is very close to the values recorded for *Simopithecus danieli* from Swartkrans which, however, shows a distinctly larger P_4. The same disproportion between upper premolars and molars seem to be distinctive for *Simopithecus darti* and *S. danieli* as well.

The two male mandibles M.3071 (immature) and M.3074 display interesting age differences. Whereas in the young specimen the chin region is very undeveloped (some parts are missing), the old male shows pronounced crests at the side of the very strong symphysis as is met with in the type mandible (Broom & Jensen, 1946). In the subadult animal, the anterior margin of the corpora is very sloping, whereas old males tend to develop vertical or even protruding chin formations. There is a kind of mandibular fossa in both M.3074, M.201 and M.621, but this is not yet developed in the young specimen.

The height of the ramus ascendens of specimen M.3071 is not as large as in the described female specimen, but the present male must have been distinctly younger. The high vertical ramus of the mandible seems to be very characteristic for the genus *Simopithecus,* although not many complete specimens are known so far. In the giant form *Simopithecus jonathani* from Olduvai Bed IV, this feature attained extreme dimensions (Leakey & Whitworth, 1958).

The incisors of the present mandible (M.3071) are heavily damaged, but they seem to have been high and narrow (the same was observed in the yet undescribed specimen M.3081 of the collection of the Anatomy Department in the University of the Witwatersrand). The just erupting canines and first premolars are very crowded, indicating that there must still take place considerable growth of the symphysial region of the mandible; the same conclusion is suggested by the undeveloped incisal shelf, and by the very large length difference of C–M_3 between M.3071 and M.3074, the latter comparing well with the type specimen.

Although being heavily damaged, specimen M.3083 yields valuable new information on the upper tooth row of the male *Simopithecus darti.* Whereas in the female M.3073 the upper tooth rows seem to converge anteriorly, the new male specimen shows a very square outline of the tooth arch. Both tooth rows run parallel, the breadth between the canines being very large. Although the premaxillae are damaged and distorted, it appears that they were not much protruded; on the left side, the premaxilla still shows the roots of the incisors, which seem to have been small and widely separated. This would underline the broad and square contours of the tooth arch, and make it very well comparable with the male specimens of *Simopithecus oswaldi,* published by Leakey (1943).

The teeth of this specimen being mostly damaged to some degree, they nevertheless provide some measurements of the upper tooth row of male *Simopithecus darti,* about which nothing was known so far. The length dimensions compare fairly well with those in large males of *Papio ursinus,* but the breadth of the tooth arch of *Simopithecus darti* is distinctly larger than in the chacma baboon.

Conclusions: The newly presented material of *Simopithecus darti* comprises the first complete skull of a female, the first fairly complete mandible of a young male and the first, though fragmentary, palate of an adult male. These specimens add considerably to our knowledge of the South African representatives of the genus *Simopithecus.*

Leakey & Whitworth (1958) pointed out that an elevated braincase and a lowered and short face are very typical for the East African forms of *Simopithecus.* The new skull from Makapansgat, although belonging to a subadult female, already shows this increase in the height of the face and the lowering of the tooth rows. This proportioning is reflected by the very high and steep ramus ascendens of the mandible, encountered both in the male and the female.

The functional meaning of the lowering, instead of the protruding, of the tooth rows most probably is the development of a so-called "high linkage" of the mandible. This "high linkage" is very typical for extremely herbivorous and graminivorous mammals; analogous adaptations, for example, are found in the robust form of the australopithecines. Possibly these adaptations of the masticatory apparatus and the peculiar structure of the molars are suggestive of grass-eating, and *Simopithecus* possibly was a dweller of open grassland (Jolly, 1970).

Already Andrews (1916), when he described the first *Simopithecus* from Kanjera, East Africa, saw the close structural connections between this fossil form and the extant *Theropithecus gelada.* This large cercopithecoid is restricted to the higher

levels of the North Ethiopian plateaux, and it is a highly terrestrial and graminivorous animal as well (Starck & Frick, 1958; Crook & Aldrich-Blake, 1968). The close relationship between *Simopithecus* and *Theropithecus* has been confirmed by various authors in recent years, the latter form being considered as the sole remnant of a widespread Pleistocene group of terrestrial cercopithecids.

The South African species of *Simopithecus* seems to be smaller and more primitive than most of the East African ones, belonging to the Lower and Middle Pleistocene. The very primitive structure of the supraorbital region would coincide with an old age for the Makapansgat form, the species of Swartkrans, *S. danieli,* being only slightly advanced. The specializations of the masticatory and tooth apparatus, however, are already highly developed in both *Simopithecus darti* and *S. danieli.* The muzzle shape of the new female skull shows more similarities with *Theropithecus gelada* than with the Middle Pleistocene *S. oswaldi.*

The new material exhibits very large sized molars, more or less fitting the range of the Swartkrans material. Possibly additional finds would close the gap between *Simopithecus darti* and *S. danieli.*

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TABLE II

SKULL MEASUREMENTS OF THE NEWLY DESCRIBED SPECIMENS FROM MAKAPANSGAT

	Cercopithecoides williamsi	*Parapapio jonesi*	*Parapapio jonesi*	*Parapapio jonesi*	*Parapapio broomi*	*Parapapio broomi*	*Parapapio broomi*	*Parapapio whitei*	*Simopithecus darti*
	male M.3055	female M.3057	male M.3060	male M.3051	female M.3056	female M.3070	male M.3065	male M.3072	female M.3073
Max. Length	146	(130)	(165)	(170)	(145)	(143)	(190)	185	161
Basal length	103	–	–	123	–	102	–	132	113
Bizygom. Br.	(98)	(80)	(110)	–	(95)	98	–	110	(105)
Basion-Bregma	62	63	–	–	–	–	–	66	67
Basion-Glabella	78	69	–	–	–	74	–	86	80
Min. Interfront	52	49	–	–	51	(50)	(52)	53	52
Max. Temporal Br.	73	70	74	–	76	–	(76)	77	80
Bimastoid Br.:	81	69	79	–	(77)	–	–	79	–
Inion-Glabella	104	93	–	–	96	–	(115)	115	107
Inion-Basion	49	44	52	55	–	–	–	58	49
For. magnum. Br.	17	14	18	–	–	18	–	17	20
Length	18	17	18	(18)	–	19	–	20	20
Muzzle height pM^3	–	–	–	–	54	–	(49)	61	–
anterior P^3	25	–	–	–	–	15	(27)	24	28
Muzzle Br. ant. M^3	44	–	–	–	51	52	–	–	50
ant. P^3	44	–	–	–	(37)	37	–	–	36
dorsal M^2	47	–	–	–	(38)	(37)	–	44	30
Nasion-Prosthion	66	(58)	–	–	(75)	72	(95)	95	87
Staphylion-Prosth.	57	–	–	68	(60)	61	(65)	78	–
Nasion-Rhinion	–	–	–	–	–	34	–	53	53
Interorbit. Br.	(19)	7	–	–	9	9	(10)	12	12
External Orbit. Br.	80	60	–	–	69	68	(72)	(75)	76
Orbit Height	26	22	–	–	24	23	25	23	26
Orbit Breadth	26	23	–	–	25	25	28	25	26
Nasal Apert Br.	17	–	–	–	–	16	–	20	17
Nasal Apert. L	(30)	–	–	–	–	25	–	36	(27)
Height alveole-Tori	63	–	–	–	64	57	69	71	78
Height alv.- infra orbital margin	34	–	–	(45)	38	33	43	47	50

TABLE III

MEASUREMENTS OF THE UPPER TEETH OF THE NEWLY DESCRIBED SPECIMENS.

				Cercopithecoides	*Parapapio jonesi*			*Parapapio broomi*			*Parapapio whitei*	*Simopithecus darti*	
	Upper teeth			M.3055 right	M.3055 left	female M.3059	male M.3051	M.3056	female M.3070	M.3082	male M.3065	male M.3072	female M.3073	male M.3083
I	1		l	4.7*	4,0*	7,5	–	–	–	–	–	–	8,7	–
			b	5,2*	4,6*	6,5	–	–	–	–	–	–	–	–
			h.	–	–	12,0	–	–	–	–	–	–	(10,5)	–
I	2		l	4,9*	5,0*	5,1*	–	–	–	–	–	–	6,0	–
			b	4,7*	4,5*	5,6	–	–	–	–	–	–	–	–
			h.	–	–	10.0	–	–	–	–	–	–	9,5	–
C			l	13,1*	13,2*		(10,2)	–	(6,5)	–	(12)	(12,0)	8,0	(14)
			b	10,2*	10,7*		(8,2)	–	(6,0)		(8,5)	–	–	12,0
			h	–	–		33,0	–	–		–	–	13,5	–
P	3		1(h)	6,2	(6,2)		7,3	–	–	7,8	–	8,0	(7,8)	–
			l	5,0	(5,2)		6,5	–	(5,5)	6,1	(7,0)	7,5	6,7	(7,0)
			b	6,7	(5,8)		7,1	–	(8,0)	7,9	–	8,4	–	(7,0)
P	4		l	5,7	5,8		6,2	6,0	5,8	6,7	(6,5)	7,0	(7,7)	(7,0)
			b	7,8	(7,1)		7,8	–	8,7	8,7	–	8,9	–	(9,5)
M	1		l	8,9	(9,3)		9,2	8,6	8,9	10,5	(9,5)	11,8	13,2	(10,0)
			mb	8,7	(9,1)	male	(9,2)	(8,5)	9,8	9,9	–	10,7	–	←
			db	8,5	8,5	M.3060	–	–	9,1	9,1	–	9,4	–	–
M	2		l	10,4	10,4	–	10,6	11,1	11,3	11,5	(11,5)	13,3	16,5	(15,0)
			mb	10,1	10,1	–	(11,5)	(11,1)	12,1	12,2	–	12,7	–	(14,0)
			db	8,5	8,5	10,9	–	–	10,5	10,5	–	11,1	–	
M	3		l	10,2	10,2	10,8	10,6	12,5	11,9	11,3	(12,0)	13,8	–	19,0
			mb	9,8	9,8	11,7	(10,5)	11,0	12,2	11,8	–	13,0	–	(14,0)
			db	8,3	8,1	9,2	8,5	8,9	9,2	9,4	–	10,3	–	(12,0)
P	4	–	M3	34,2	34,0		35,9	37,0	(37,0)	38,7	(39,5)	44,3	–	(55)
M	1	–	M3	28,9	29,2		30,3	31,5	(32,0)	33,0	(34,0)	38,0	–	(46,5)
C		–	M3	(50,9)	(50,9)		53,6	–	(49,0)	50,7	(57,0)	62,8	–	(76)

* Alveole measurements

() Values inaccurate due to damage or inaccessibility.

TABLE IV

MEASUREMENTS OF THE LOWER TEETH IN THE NEWLY RECORDED SPECIMENS

Lower Teeth			*Parapapio jonesi* female M.3057	male M.3061	male M.3051	*Parapapio broomi* male M.3067	female M.3063	M.3075	*Parapapio whitei* male M.3062	M.3072	*Simopithecus darti* male M.3071	M.3074	M.3081	female M.3073
I	1	l	5,6	–	5,0	–	–	–	–	–	(7,4)	–	6,9	5,5
		b	5,7	–	–	–	–	–	–	–	(7,0)	–	–	–
		h	10,0	–	8,5	–	–	–	–	–	(12,5)	–	6,0	8,0
I	2	l	(4,7)	–	5,1	–	–	–	–	–	(5,7)	–	6,4	5,0
		b	5,8	–	–	–	–	–	–	–	(7,0)	–	–	–
		h	8,5	–	9,5	–	–	–	–	-	(11,0)	–	5,5	7,5
C		l	4,7	6,7	(5,0)	6,9	(6,5)	–	–	–	(7,5)	(7,5)	(7)	(6,1)
		b	6,7	11,0	(9,5)	10,7	–	–	–	–	(11,0)	(12,5)	13,1	–
		h	(10,0)	17,5	22,0	22,0	12,0	–	–	–	(22,5)	–	(25)	10,5
P	3	1(h)	10,2	14,0	13,9	14,3	10,5	–	18,0	–	17,5	–	24	10,0
		b	4,3	4,6	–	(5,0)	5,9	–	–	6,0	7,3	–	(7,2)	–
P	4	l	7,5*	7,0	6,6	6,8	7,9	7,2	7,4	7,8	9,5	–	8,4	8,2
		mb	5,3											
		b db	5,5	6,3	(6,7)**	7,3	8,2	(8,5)	7,5	7,8	8,4	–	7,7	–
M	1		8,5	8,9	9,2	8,8	10,6	(9,8)	(10,0)	11,4	12,6	–	11,7	12,4
		mb	6,4	6,9	7,4	8,0	8,6	–	–	9,0	9,9	–	(10,5)	–
		db	6,5	7,4	(7,5)**	7,9	8,0	–	–	8,7	10,4	–	(9,8)	–
M	2		9,5	10,7	10,5	10,9	11,8	12,0	12,4	13,2	15,7	–	(13,9)	16,1
		mb	8,3	9,2	9,2	9,8	9,8	10,3	10,6	10,8	12,5	–	–	–
		db	7,9	9,4	9,2	9,3	9,0	–	9,9	10,4	11,6	–	–	–
M	3	1	–	13,7	13,7	15,4	14,4	14,9	17,5	16,1	(22,0)+	(23,5)	(19,8)	–
		mb	–	9,7	9,4	10,6	(9,6)	10,0	11,6	11,0	(13,3)+	–	–	–
		db	–	8,5	(8,0)**	8,8	8,1	8,5	10,0	9,4	(11,5)+	–	–	–
P	4–M3		–	39,9	(41,0)	41,7	44,2	44,0	47,0	48,5	(58,0)+	(60)	(54,6)	–
M	1–M3		–	33,0	(33,8)	35,3	36,5	(36,0)	40,0	40,7	(47,5)+	(51)	–	–
C –	M3		–	62,4	(64,3)	66,5	60,0	–	(68,0)	70,5	(77,5)+	(85)	(87)	–

* deciduous molar
** breadths could not be measured quite exactly
\+ measured from X-ray

TABLE V

Upper Teeth		UPPER TEETH: *Cercopithecoides williamsi* m. & f. n	x̄	*Parapapio jonesi* m n	x̄	*Parapapio jonesi* f n	x̄	*Parapapio broomi* m n	x̄	*Parapapio broomi* f n	x̄	*Parapio whitei* m n	x̄	*Parapio whitei* f n	x̄	LOWER TEETH: *P. jonesi* m. & f. n	x̄	*P. broomi* m. & f. n	x̄	*P. whitei* m. & f. n	x̄
P 3	1 (h)	3	6,0	1	4,3	5	5,4	7	8,0	10	6,6	2	7,7	4	7,4	–	–	–	–	–	–
	b	5	6,2	1	7,5	6	7,1	8	8,0	10	7,4	2	8,3	3	7,9	–	–	–	–	–	–
P 4	l	5	5,6	1	5,6	6	6,0	10	6,6	14	6,4	2	7,0	6	6,9	20	6,8	15	7,2	5	7,7
	b	5	8,0	1	7,7	5	7,7	11	8,9	12	8,4	2	9,2	6	8,7	22	6,7	13	7,1	5	7,1
M 1	l	10	8,5	2	8,3	6	8,7	9	9,9	14	9,6	2	10,0	6	10,7	20	8,6	15	9,3	7	9,7
	mb	4	9,2	1	9,0	5	8,8	9	9,8	12	9,5	2	10,1	5	10,5	17	7,5	12	8,2	5	8,5
	db	3	8,5	1	8,6	5	8,0	6	9,0	10	8,8	–	–	5	9,8	15	7,6	13	8,2	5	8,8
M 2	l	10	9,7	2	10,2	4	10,3	10	11,1	17	11,1	3	12,0	6	12,7	19	10,4	15	11,4	6	12,6
	mb	7	9,9	1	10,4	2	10,5	7	11,5	12	11,1	2	12,3	6	12,4	19	9,3	13	10,1	5	10,6
	db	6	9,1	1	9,6	2	8,9	9	10,8	13	10,1	2	11,0	6	11,4	18	9,0	13	9,7	5	10,5
M 3	l	11	9.6	2	10.3	3	9,6	8	11,2	12	11,0	2	11,7	2	13,3	13	12,7	16	14,7	6	16,4
	mb	7	9,7	2	10,9	3	9,8	8	11,4	11	10,7	3	11,9	1	12,8	11	9,3	11	10,2	5	11,1
	db	5	8,1	2	8,5	3	7,9	7	9,3	10	8,8	2	9,4	1	11,0	12	8,4	14	9,3	5	10,3
P 4 –	M 3	9	31,8	1	32,5	3	33,3	7	37,7	7	36,3	2	39,2	2	39,6	11	37,8	11	41,9	4	45,7
C –	M 3					1	43,1	2	56,0	3	48,6			1	51,7						

Mean values of the known upper and lower teeth of South African Ceropithecoids, mainly according to Freedman. These figures serve for comparison of the newly presented material.



Fig. 1 *Cercopithecoides williamsi* M.3055 seen from the right side. Scale in cm.

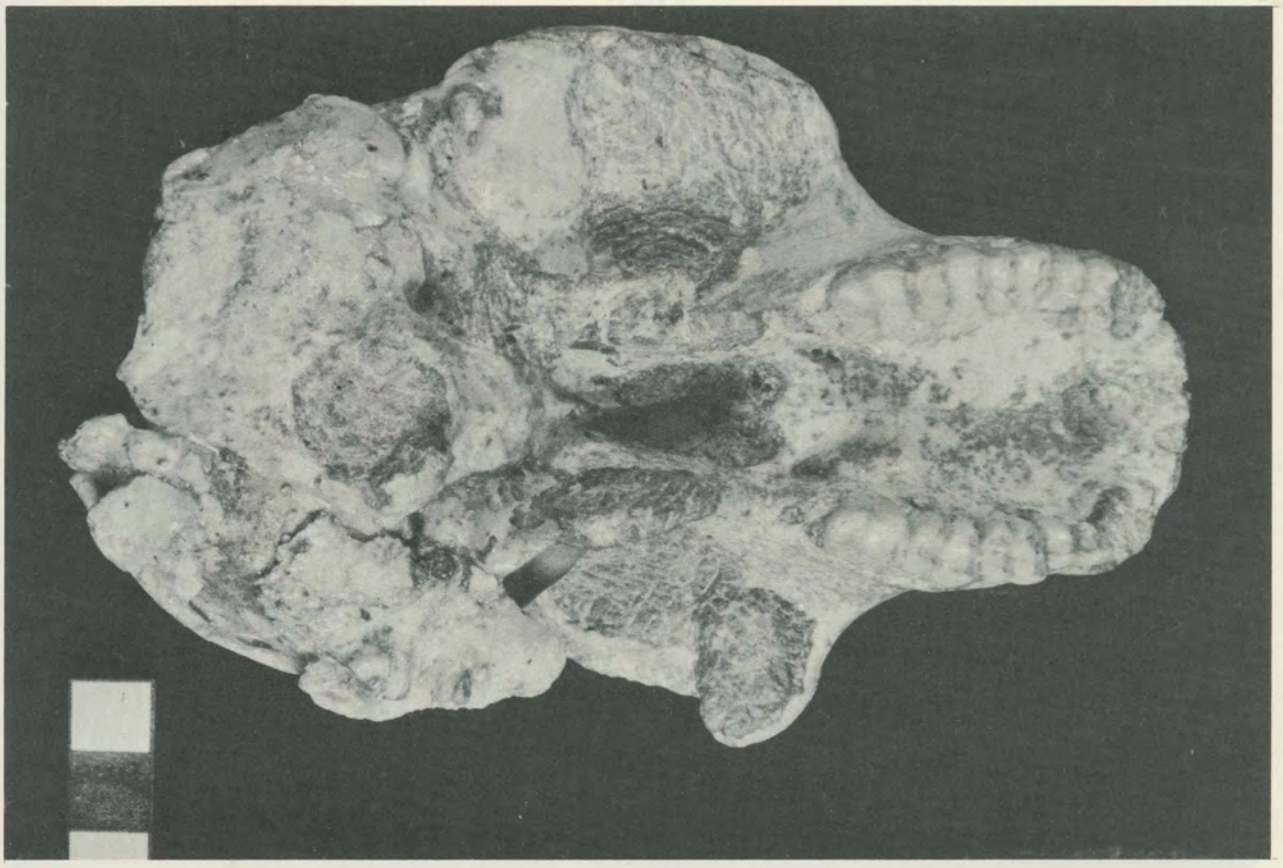


Fig. 2 Basal view of *Cercopithecoides williamsi* M.3055. Note the divergent tooth rows. Scale in cm.



Fig. 3



Fig. 4

Fig. 3 *Cercopithecoides williamsi* M.3055 seen in norma dorsalis. The skull is orientated on the occlusal plane. Scale in cm.

Fig. 4 *Cercopithecoides williamsi* M.3055 seen in norma frontalis. Scale in cm.

Fig. 5 Lower jaw (M.3058) and upper incisors (M.3059) of a young female of *Parapapio jonesi*. Their position is reconstructed. Note the specialized medial incisors. Scale in cm.

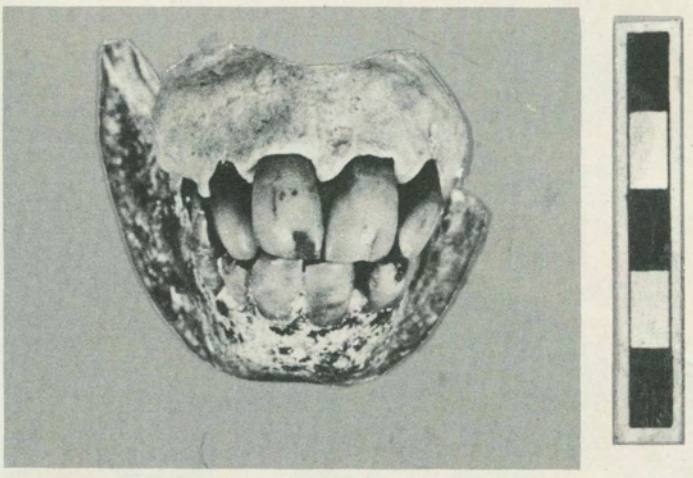


Fig. 5

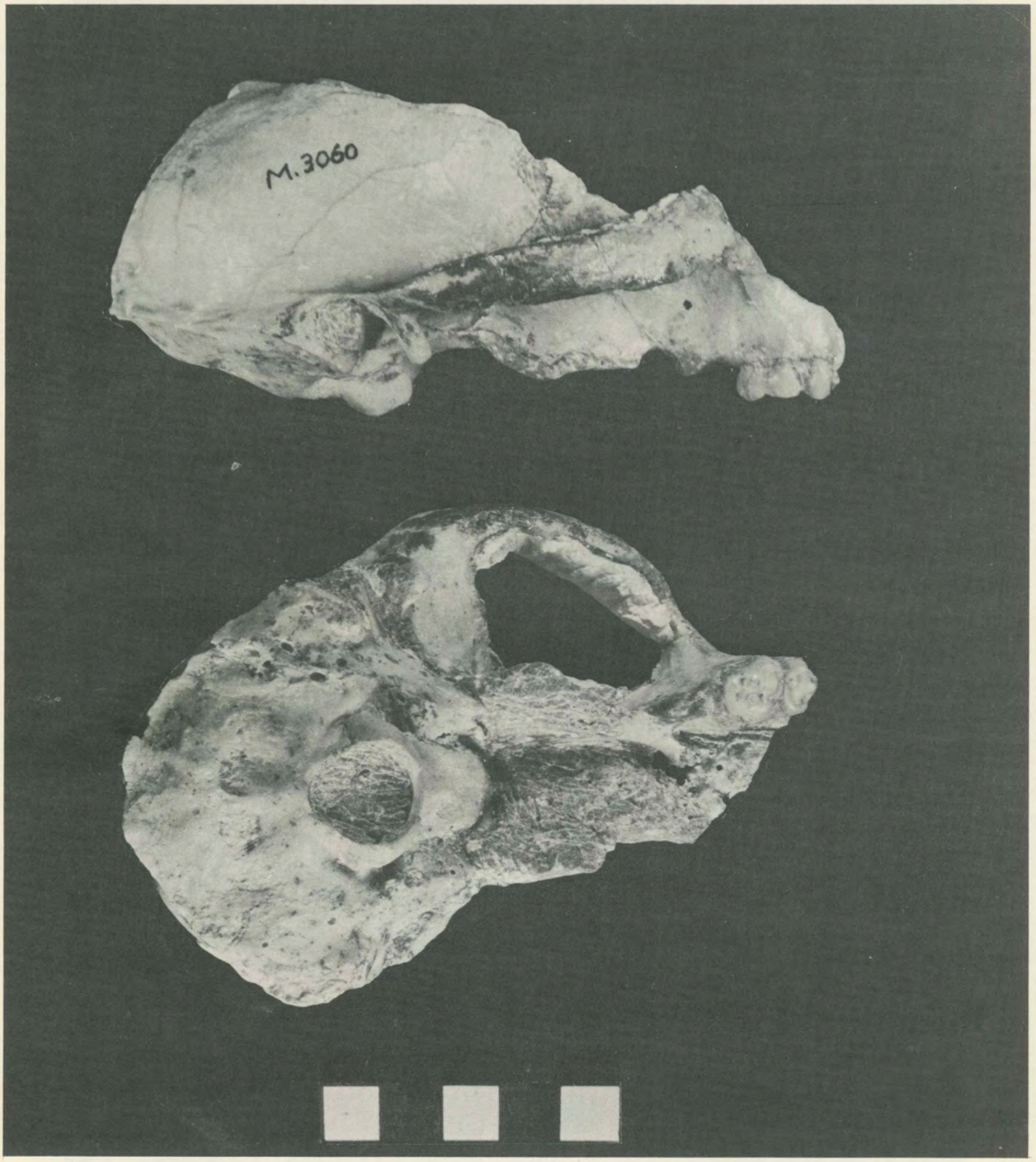


Fig. 6 Specimen M.3060 seen from below and from the right side. Scale in cm.

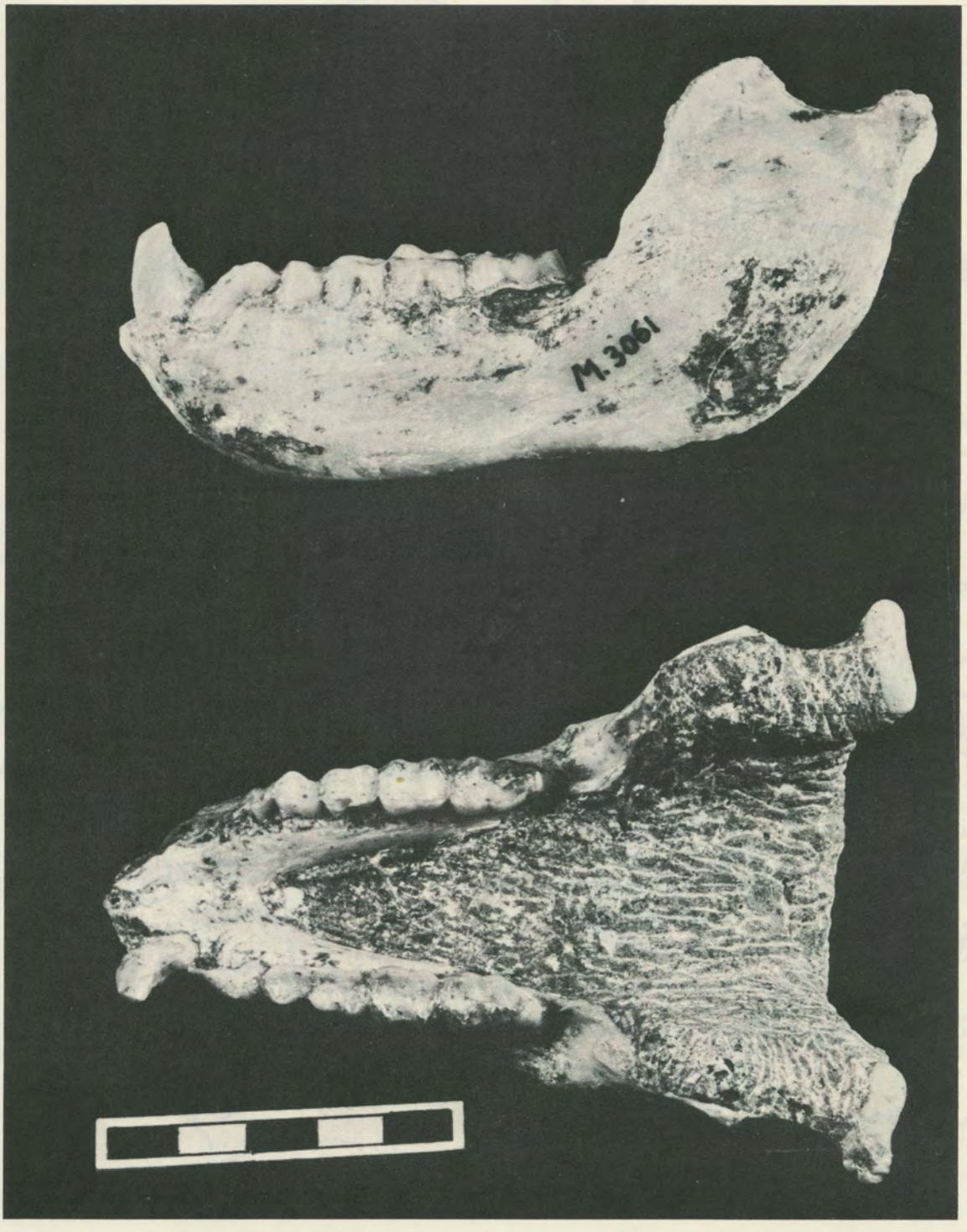


Fig. 7 Specimen M.3061 (*Parapapio jonesi*) from the left side and in occlusal view. Scale in cm.

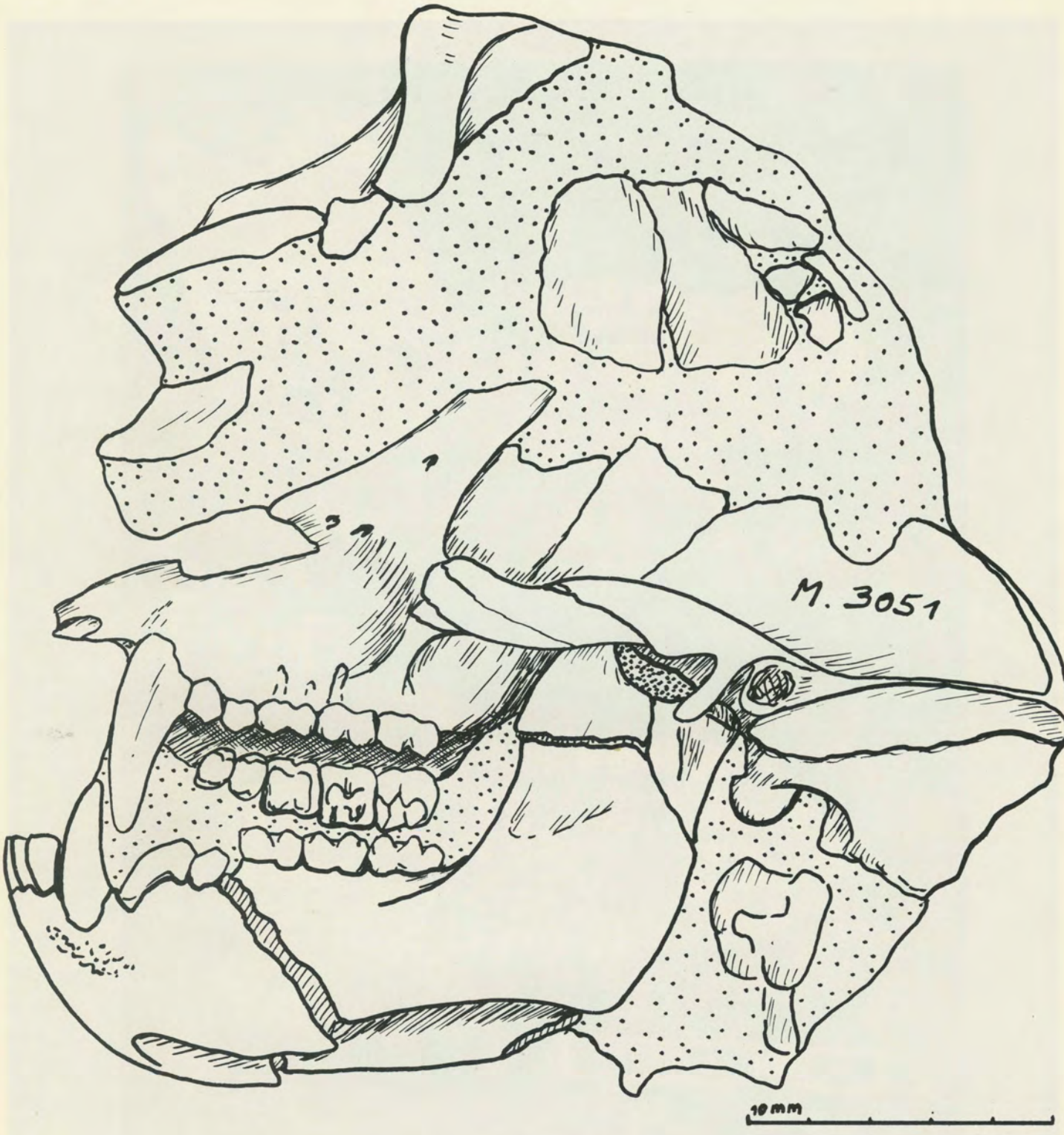


Fig. 8 Male skull of *Parapapio jonesi* (M.3051) from the 'basal red' of the Makapansgat Limeworks. The skull is bilaterally crushed and the upper parts of the skull are displaced.

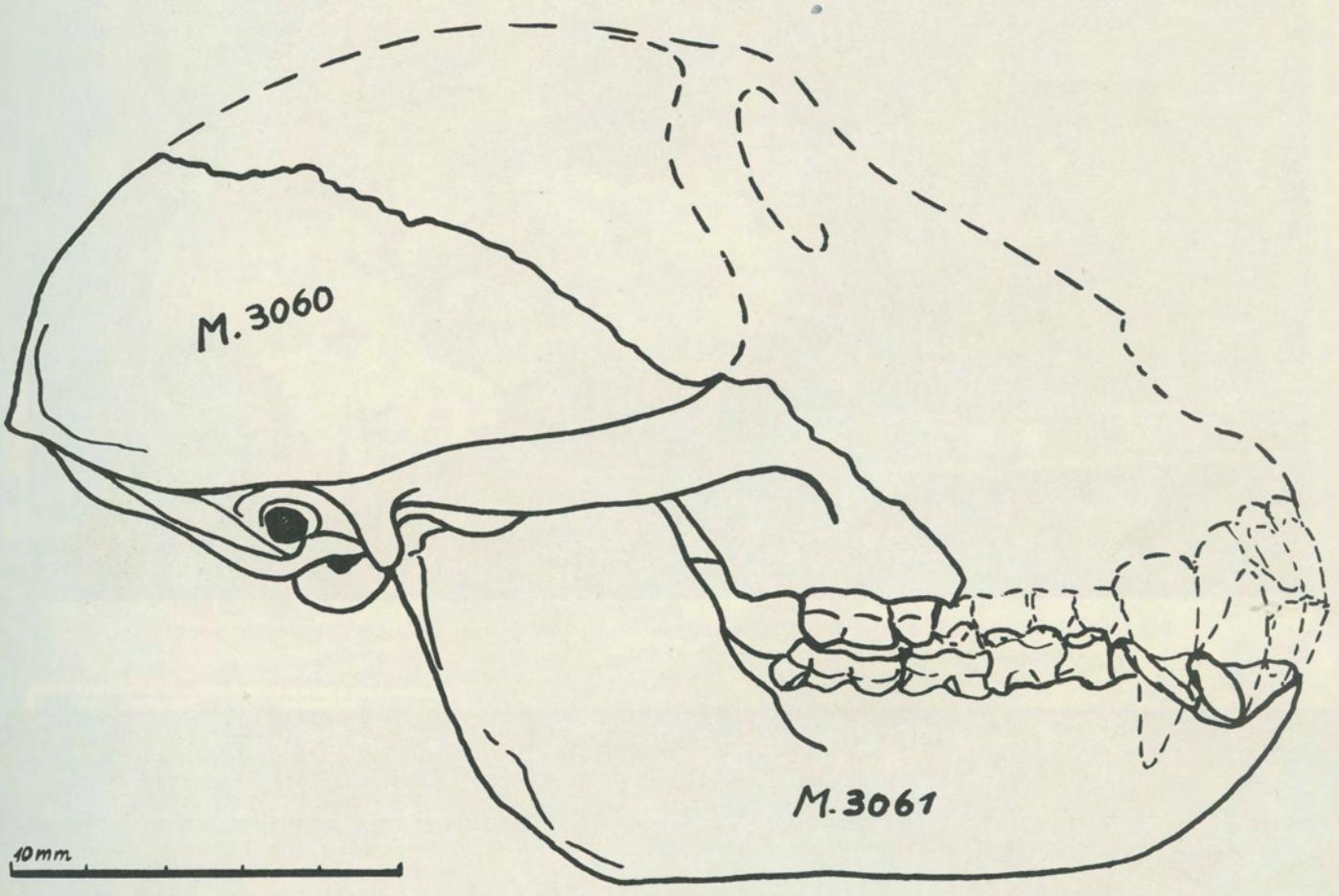


Fig. 9 Reconstruction of the male skull of *Parapapio jonesi* based on the knowledge of several fragmentary specimens. The solid line shows the specimens M.3060 and M.3061, which most probably belong together; the dashed lines are based on the specimens M.2961 and M.3051.



Fig. 10 Frontal view of the female *Parapapio broomi* M.3070. The left zygomatic bone is retouched in dashed lines. Scale in cm.

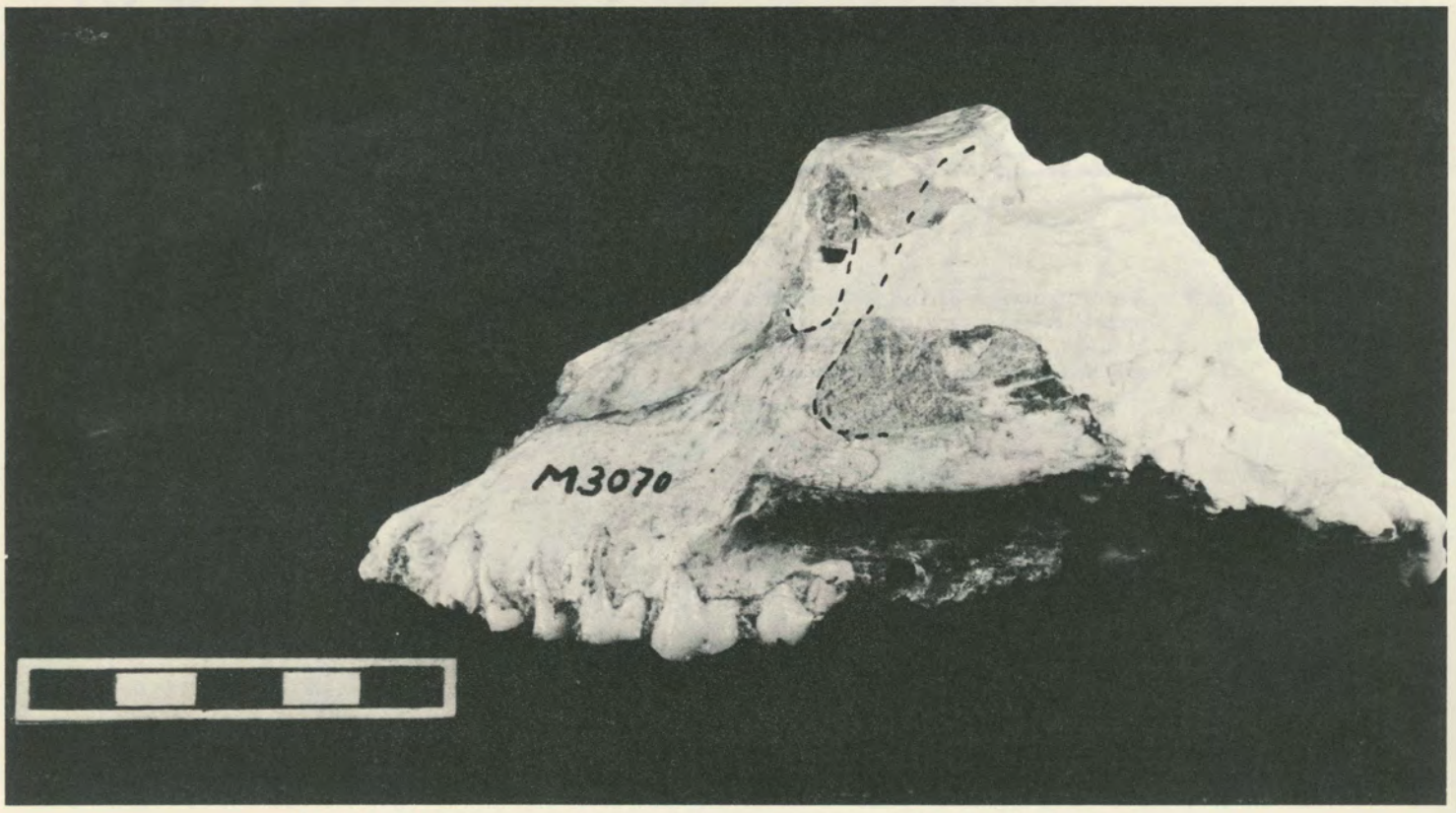


Fig. 11 Lateral view of the female *Parapapio broomi* M.3070. Scale in cm.

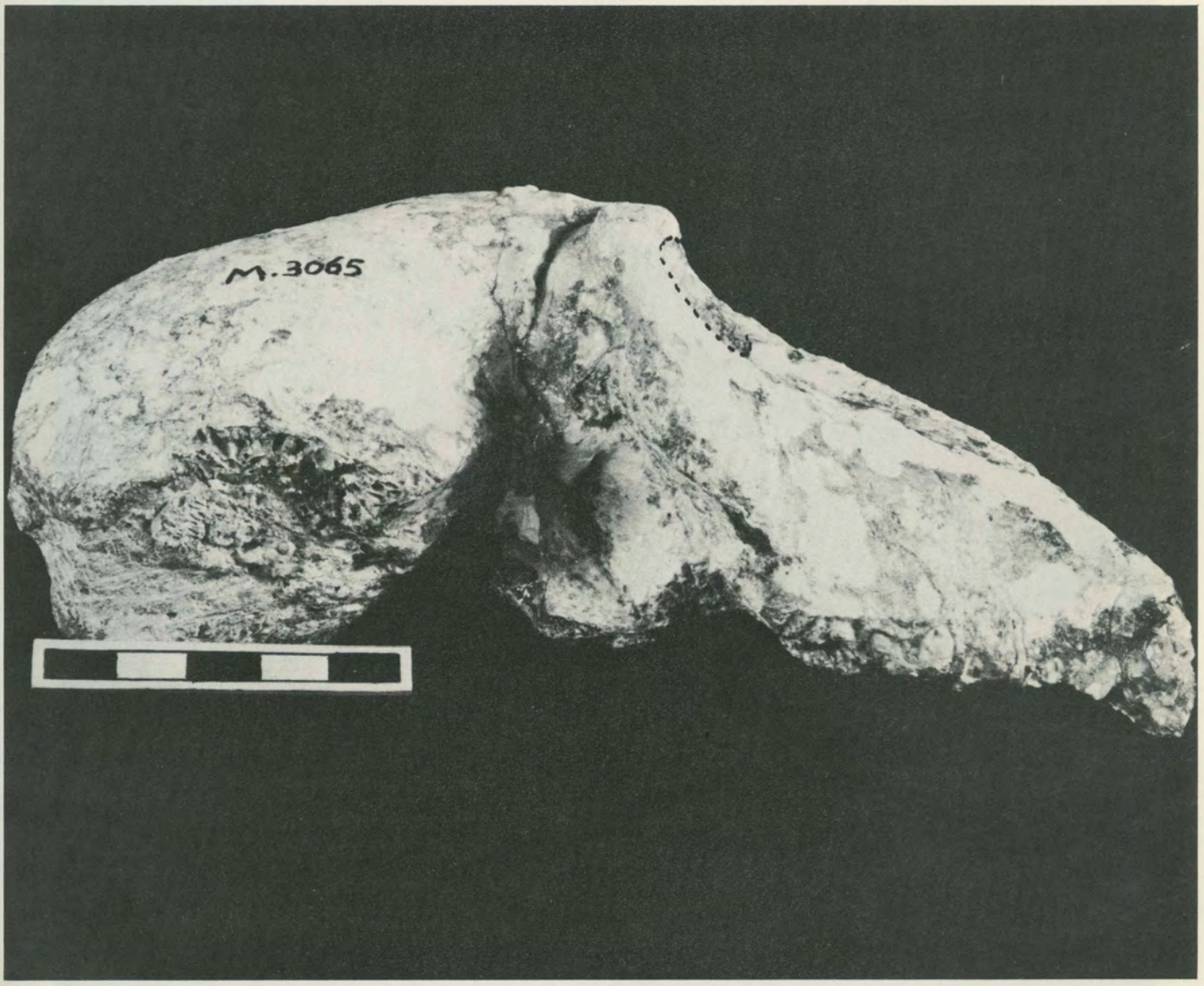


Fig. 12 Lateral view of the incomplete male skull of *Parapapio broomi* M.3065. The posterior and lower parts of the braincase are missing. Scale in cm.

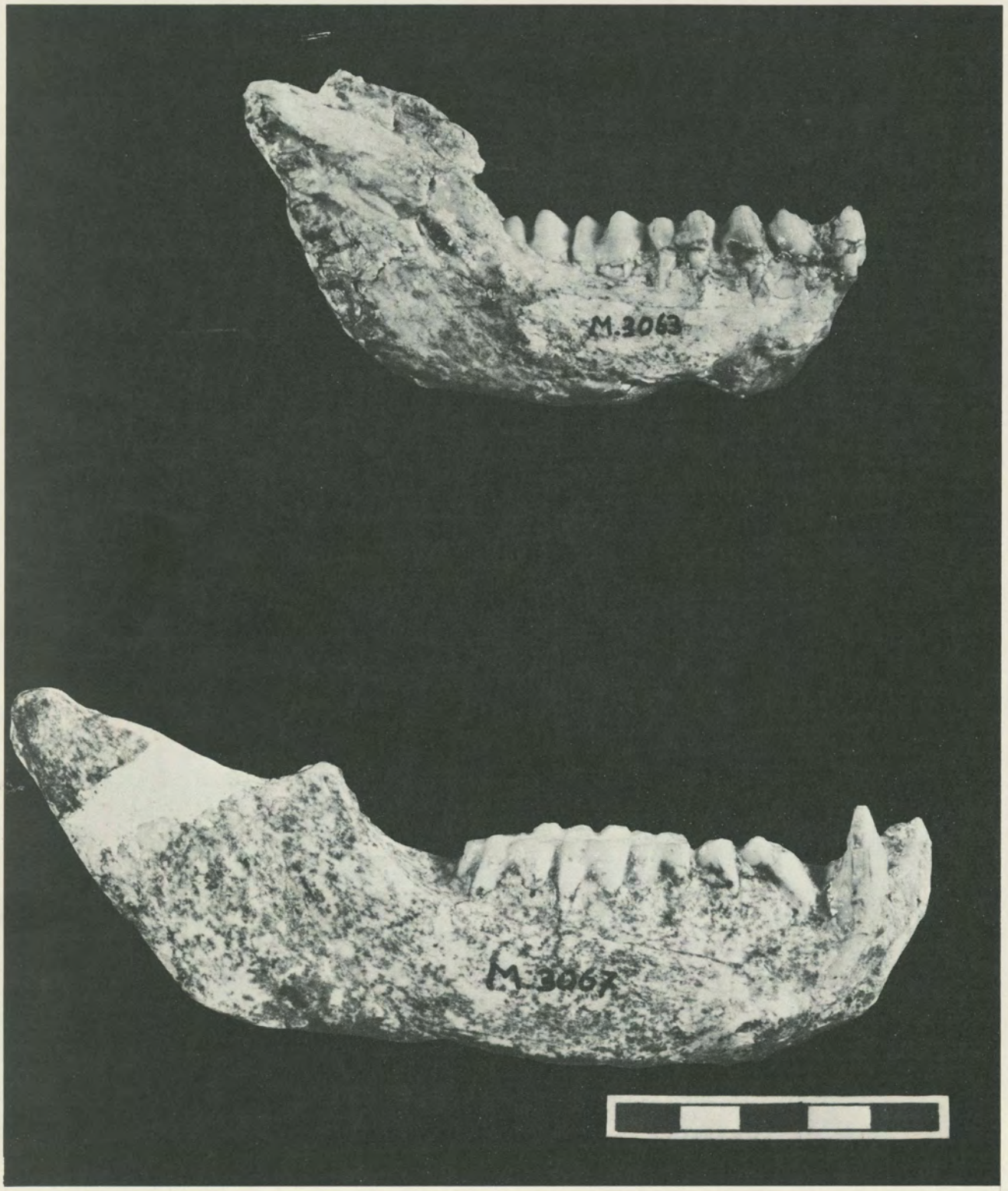


Fig. 13 Male (M.3067) and female (M.3063) mandibles of *Parapapio broomi*. The teeth of the female are even slightly larger than in the male. For both the scale is in cm.

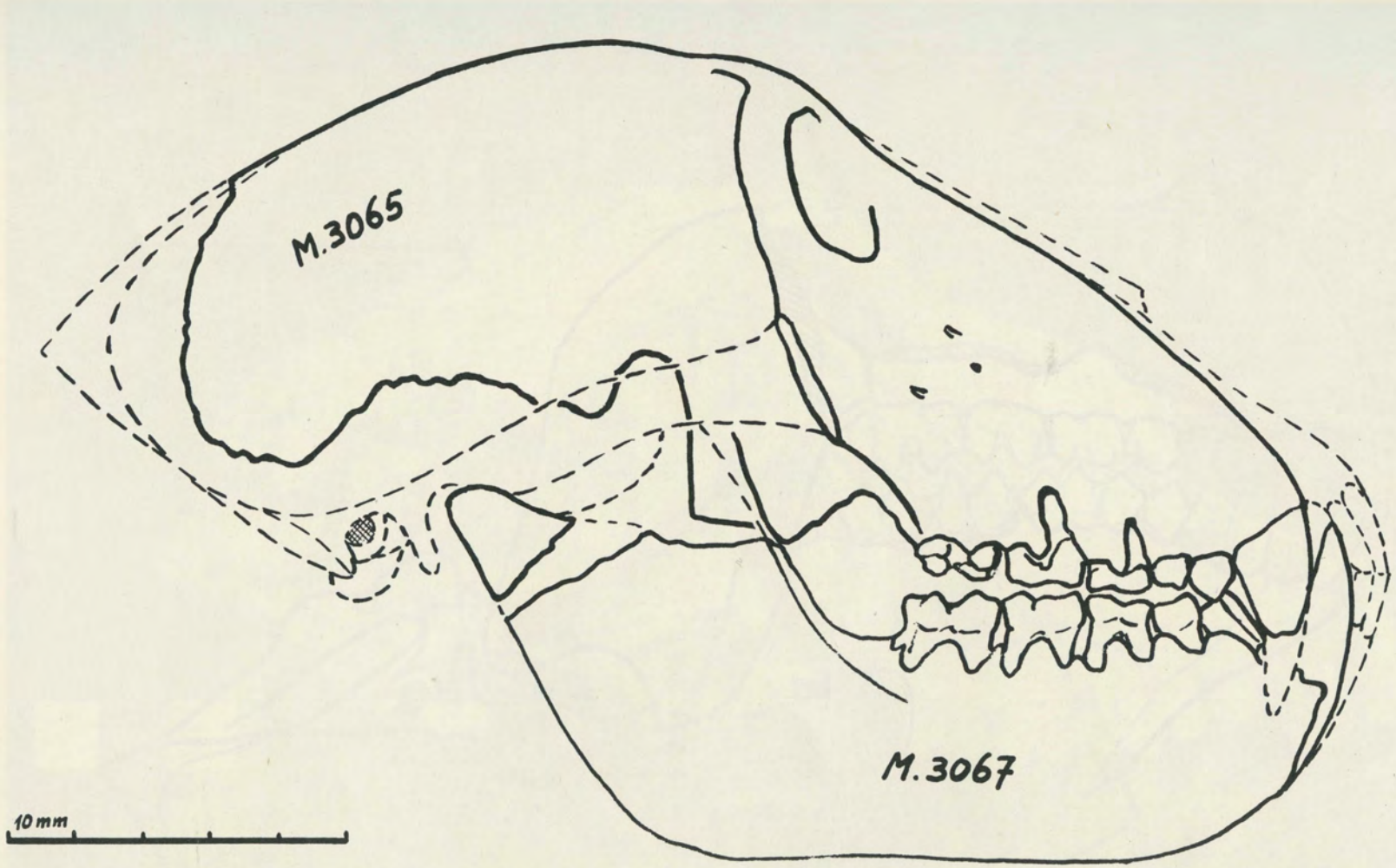


Fig. 14 Reconstruction of the male skull of *Parapapio broomi*. The figure is based on the two specimens M.3065 and M.3067, which most probably belonged to the same animal. The reconstructed parts (dashed lines) are based upon specimen M.3072.

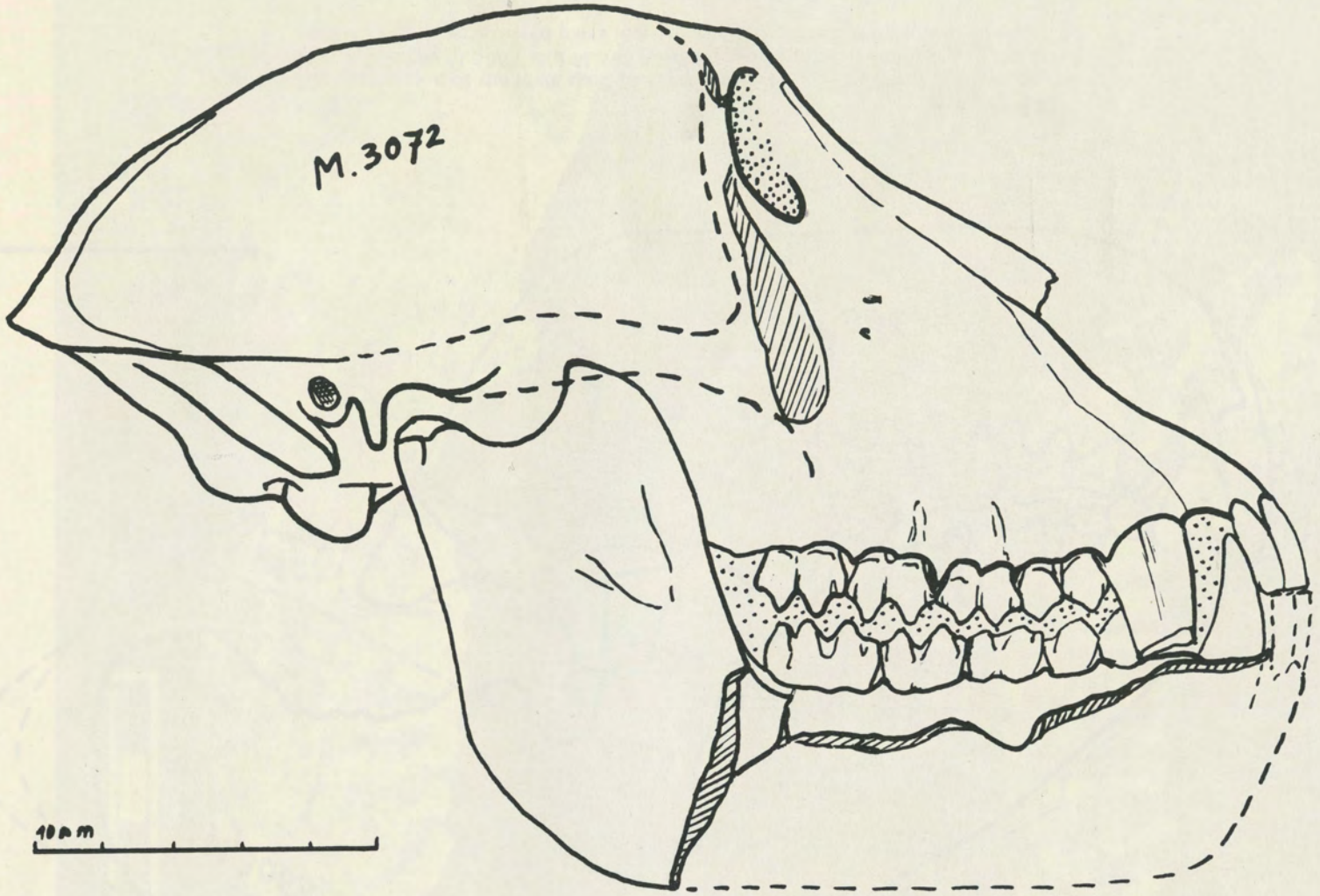


Fig. 15 Male skull of *Parapapio whitei* (M.3072). The solid line shows the preserved parts with the mandible in its original position; the dashed lines are reconstructed. As all of the line drawings, this one is based on a pantograph.

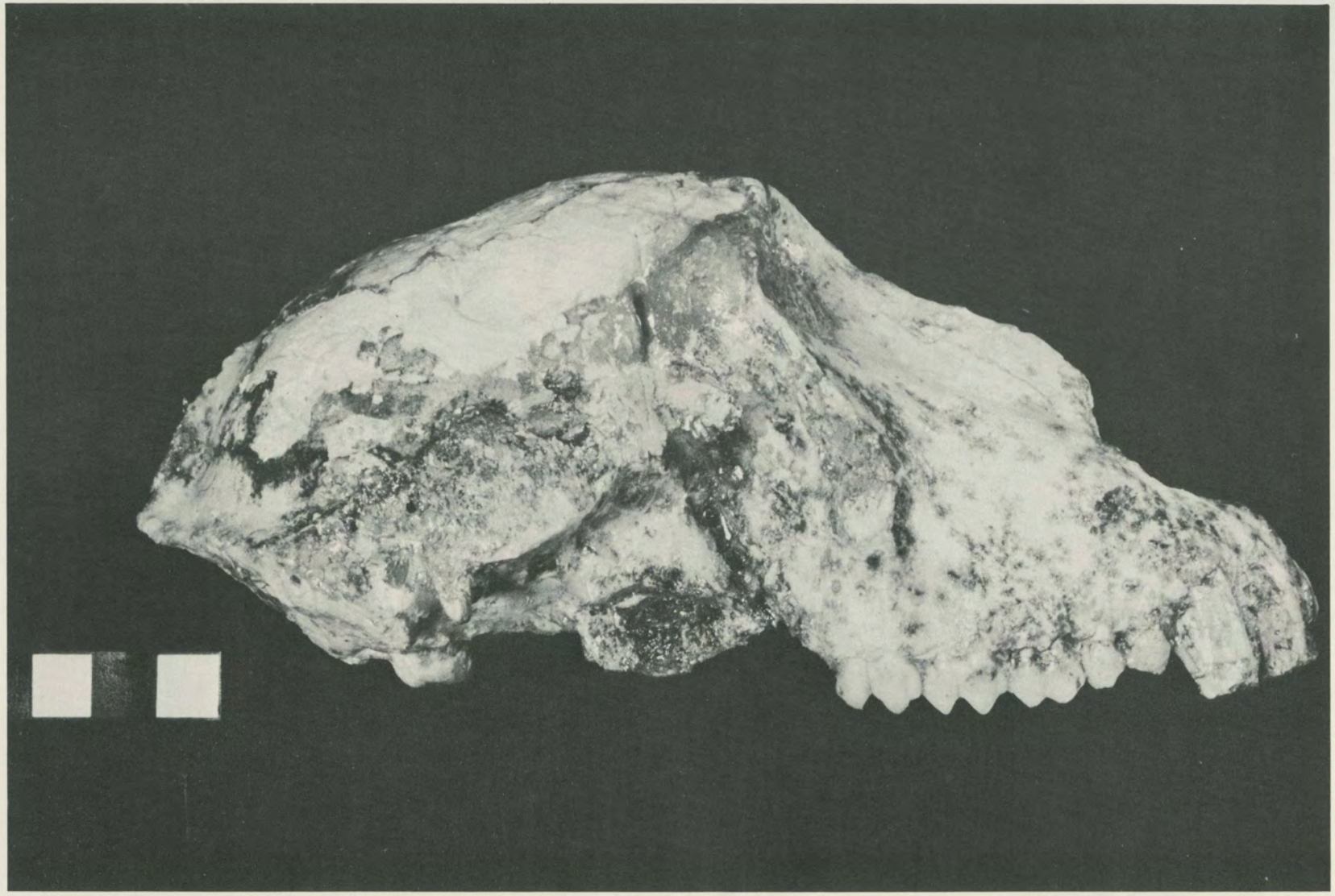


Fig. 16 Male skull M.3072 of *Parapapio whitei* after removal of the mandible. Scale in cm.



Fig. 17 Lateral view of the female skull M.3073 of *Simopithecus darti*. Scale in cm.

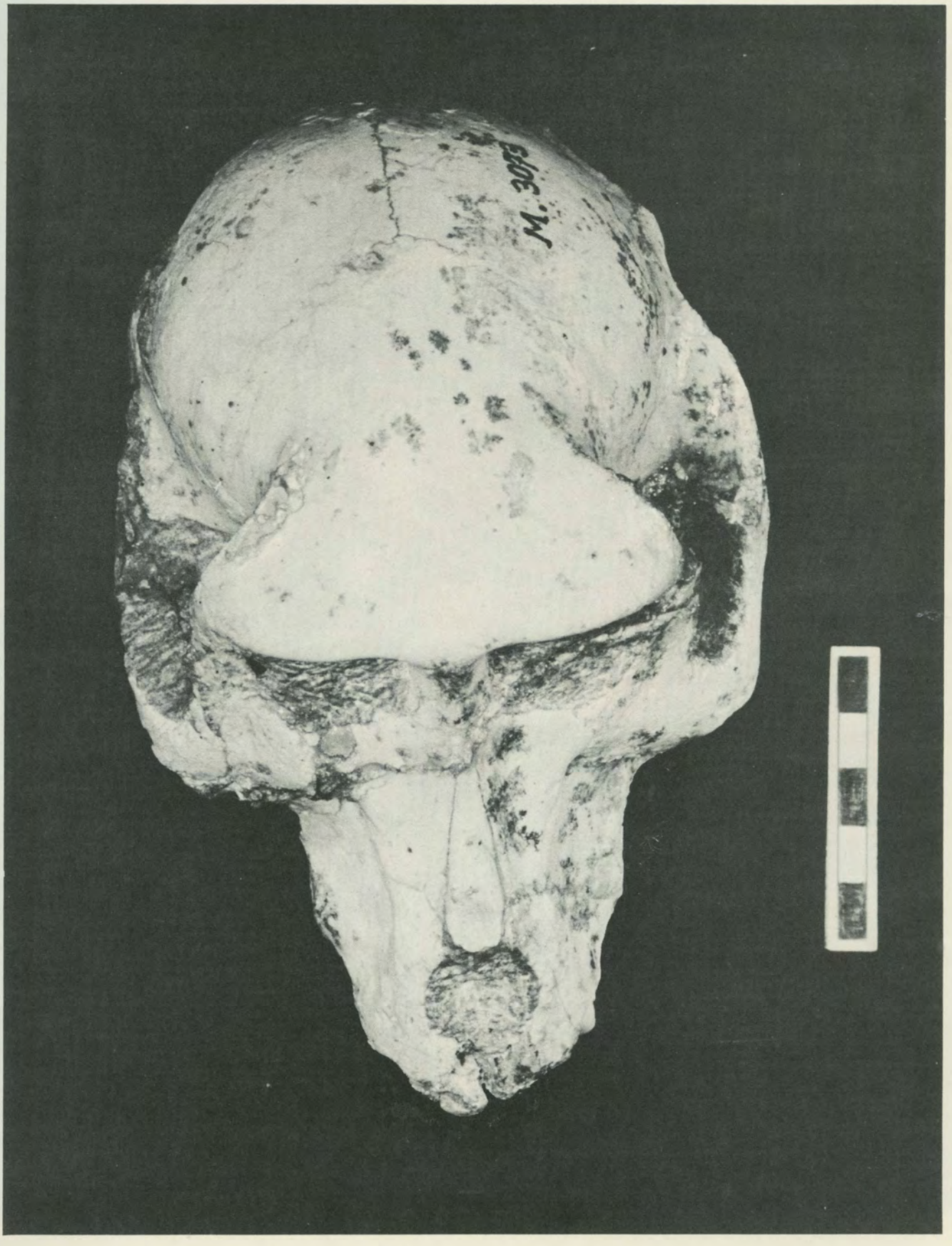


Fig. 18 Antero-dorsal view of the female skull M.3073 of *Simopithecus darti*. Scale in cm.



Fig. 19 Frontal view of the female skull M.3073 of *Simopithecus darti*. Note the slight distortion of the mandible and the comparatively broad medial incisors. Scale in cm.

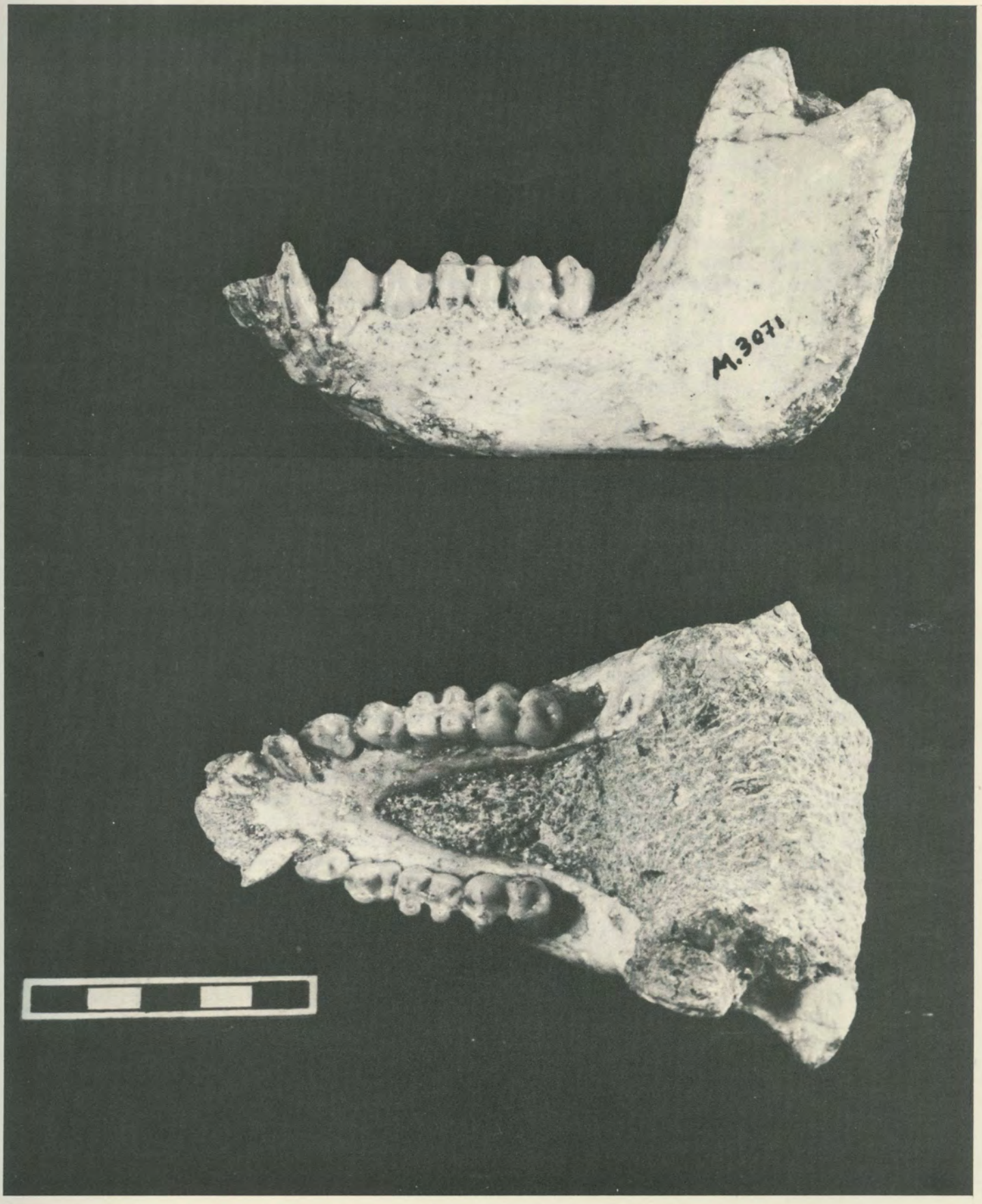


Fig. 20 Lateral and occlusal view of the male mandible M.3071 of *Simopithecus darti*. Note the height of the ascending ramus and the morphology of the molars. Scale in cm.