THE FOSSIL CERCOPITHECOIDEA OF SOUTH AFRICA

by

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(Thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology of the University of Cape Town, South Africa.)

Published with the aid of a grant
from the Council for Scientific and
Industrial Research, South Africa.

PREFACE

This study of the fossil Cercopithecoidea of South Africa was made in the Department of Vertebrate Palaeontology and Physical Anthropology of the Transvaal Museum, Pretoria, South Africa. It is one of a series of research projects currently being undertaken there to investigate the Plio-Pleistocene mammalian fauna of South Africa. When correlated with the geological analyses of the various sites, these studies will reveal the ecological relationships and vertical succession of mammals associated with the South African prehominids - the Australopithecinae.

A considerable number of species of fossil baboon-like cercopithecoids have in the past been described by various authors from the fossiliferous limestone breccias of South Africa. The material to be described here includes a very considerable number of specimens of these species and, in addition, several hitherto unknown forms. Because of the additional material, and the lack of uniformity of the earlier descriptions of the known species, it was felt opportune to combine the description of the new material with a review of the previously described forms. For the sake of uniformity, the already described genera and species have been redescribed and defined.

This extensive amount of fossil cercopithecoid material has also been studied from the phylogenetic point of view. An attempt is made to trace cercopithecoid evolution - particularly in South Africa - in the light of this new material and also from what is known from other sources, both fossil and living.

As an aid to the differentiation of the fossil species, a description and statistical study of the skull and teeth of the living chacma baboon, *Papio ursinus*, was undertaken. For this reason, and because of its usefulness in relation to the taxonomy of the living forms, the results of this study are included here.

ACKNOWLEDGMENTS:

The new material to be described was excavated under the direction of the late Dr. R. Broom and Mr. J. T. Robinson of the Transvaal Museum, partly with the aid of a grant from the Nuffield Foundation. I am very grateful to them and also to the Director

and Board........

and Board of Trustees of the Museum for permission and facilities to describe it. The South African Council for Scientific and Industrial Research has financed both the study itself and the publication of the results and I am pleased to have this opportunity to acknowledge their support.

I gratefully acknowledge the assistance of Mr. J. T. Robinson, Professional Officer in charge, Department of Vertebrate Palaeontology and Physical Anthropology of the Transvaal Museum at whose suggestion and under whose supervision this work was carried out. For his continuous guidance and inspiration, this work, and I personally, owe him a great debt.

To my supervisors at the University of Cape Town, Professor J.H. Day and Dr. N.A.H. Millard, my thanks are due for valuable discussions and suggestions.

Mr. G. Abraham of the South African Bureau of Standards, Pretoria, helped greatly by discussions and advice in the statistical work.

Of the staff of the Transvaal Museum, I am particularily indebted to the following:

Mr. J.A.J. Meester of the Department of Mammalogy kindly assisted by taking the photographs for Part I.

Mr. C.K. Brain of the Department of Vertebrate Palaeontology and Physical Anthropology took the many excellent photographs used in Part II and was also kind enough to allow me to use certain of his unpublished geological data in Part III.

Mrs. N.F. Hemens and Mrs. T. Campbell produced the very clear illustrations in Part I from my rough sketches.

Mrs. N.F. Hemens was also most helpful by doing the typing of the preliminary drafts of this publication.

Cercopithecoid material was studied from the following collections in South Africa: The Anatomy Department of the University of the Witwatersrand, Johannesburg, the Bernard Price Institute for Palaeontological Research also of Johannesburg, the Kaffrarian Museum, Kingwilliamstown and the South African Museum, Cape Town. I should like to express my appreciation

to the controlling..........

to the controlling bodies and staffs of all these Institutions for their co-operation. Particularly, I should like to thank Professor R.A. Dart and Dr. P.V. Tobias of the University of the Witwatersrand, Dr. A.S. Brink and Mr. J.W. Kitching of the Bernard Price Institute and Dr. K.H. Barnard and Dr. L.D. Boonstra of the South African Museum.

Finally, it gives me much pleasure to acknowledge the assistance of my wife who typed the final draft of this work and gave me continuous encouragement throughout the two years which I have spent on this project.

SUMMARY.

This study of the fossil Cercopithecoidea of South Africa has been divided into three Parts.

In Part I, an illustrated description of the skull and teeth of Papio ursinus has been given which acts as a basis for the descriptions of the fossil cercopithecoids in Part II. The results of a cranial and dental statistical study, utilising one hundred measurements on each of forty-nine males and seven females of that same species, have also been included. These results were used in Part II for delimiting the fossil species and, in addition, yielded interesting information about the variability, also relationships and subspecies of P. ursinus which is given in Part I.

In Part II, a very large amount of new fossil cercopithecoid material has been described. The new material of the previously described species has enabled a much fuller description of these forms to be given. This has necessitated the sinking of one genus (Brachygnathopithecus) and four species (Simopithecus leakeyi, Gorgopithecus wellsi, Parapapio makapani and Brachygnathopithecus peppercorni). Also, Gorgopithecus darti had to be transferred to Simopithecus, Parapapio antiquus and Parapapio izodi to Papio and 'Parapapio' coronatus had to be described under "Species of Unknown Affinities" as the exact genus to which it belongs is now no longer certain. Other new material, mainly from Swartkrans, revealed the presence of three hitherto unknown species: Papio robinsoni, Cercopithecoides molletti and Simopithecus danieli.

Part III has been devoted to a review of the fossil Cercopithecoidea from the rest of the world and to a discussion of the probable inter-relationships and phylogeny of the South African cercopithecoid genera and species.

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PART I

CRANIOMETRY AND SKULL MORPHOLOGY OF *PAPIO URSINUS*.

CHAPTER 1.

INTRODUCTION.

In the study of the fossil Cercopithecoidea, usually only skull fragments and teeth are available for taxonomic purposes. It was therefore felt that the variability of these structures in a living species of the group should form a useful taxonomic standard of reference for the fossil forms. The object, then, of this preliminary study is to prepare a table of measurements of the skull and teeth of some living cercopithecoid and to analyse the variability of these characters statistically. The results of such a study should also be of interest for what light they cast on the present taxonomy of the Cercopithecoidea and for comparison with the statistics of the teeth of the chimpanzee, orang-utan and gorilla by Ashton and Zuckerman (1950) as amended by them (1951). The species chosen for this study is the South African chacma baboon, *Papio ursinus* (Kerr), which is the species of baboon today occupying the territory formerly inhabited by the fossil forms to be described later. An analysis of age and sex differences in this species has also been made and, as a basis for comparisons among the fossil forms, a short description of its skull and teeth has been included.

The status of many subspecies and even species of the living Cercopithecoidea - in particular the baboons - is at present a most contentious problem. The species chosen for this study is a case in point and a thorough re-study of the whole group is urgently required. Washburn (1950) states that "The attempt has been made repeatedly to divide the baboons into sharply defined groups. The chaos which has resulted is the result of expecting that plains forms, which have vast reaches of similar habitat open to them, will divide as the tree restricted monkeys do". This is the probable cause of the difficulties encountered in the lower taxonomic categories of this group and it seems likely that the different species are widely distributed and show no clear-cut differentiation into subspecies.

Partly because of this doubt as to their validity, no division has been made in this study into the subspecies given by Roberts (1951) which are based almost entirely on colour differences. This method of treatment was also necessitated by the fact that, for the available skulls, subspecific names were, in most cases, not recorded nor were the skins, which would have enabled these to be determined, kept. The localities given in the records would make it possible for a subspecific name to be assigned to each specimen but the small size of the available samples would not enable any conclusions to be drawn as to their validity. A local population from the Albany district, where Goldblatt's subspecies *Papio ursinus orientalis* occurs, and of which there are a reasonable number of specimens, has however been analysed separately for comparison with the statistics for the distribution of the species as a whole. This was a prerequisite of the study as the fossil forms to be dealt with represent what must undoubtedly have been evolving local populations. Besides clarifying the relationship between a local population and the species as a whole, this comparison may also give some clue as to the possibilities of a statistical, craniometric approach to the question of the validity of the present *Papio ursinus* subspecies.

A note on *Papio cynocephalus* (Linnaeus) and statistics for Haagner's '*Papio rhodesiae*' are included. Other than *P.ursinus*, these two forms are the only living species of *Papio* hitherto described from Southern Africa. These species were studied in an attempt to examine inter-specific differences within the genus statistically but, as will be explained later, this was found impracticable. The classification used throughout this work (see Appendix I) is a revision of that of Simpson (1945).

CHAPTER 2.

THE SKULL AND TEETH.

There appears to be no comprehensive text on the anatomy of *P. ursinus* comparable with, for example, that on the rhesus monkey edited by Hartman and Straus (1933). In a work on fossil forms, such a full treatment can, of course, not be contemplated but to simplify later comparative discussion of the fossil forms, a brief description of the skull and teeth of *P. ursinus* has been included in this introductory section. The description is supplemented by photographs and labelled drawings and it is hoped that, together, they will serve the limited purpose for which they are intended.

SKULL.

The species, *P. ursinus*, shows a high degree of sexual dimorphism - a feature well exemplified in the skull. The female skull is much smaller, lighter and less rugged than that of the male and the crests and ridges, so prominent on the male skull, are, in the female, either totally absent or much smaller because of the less well developed musculature. Compared to the female, the male muzzle is greatly elongated and the canines are exceptionally well developed. Also, the muzzle dorsum and the supra- and infra-orbital regions are very different in appearance. As the Cercopithecoidea in general show similar marked sexual dimorphism, this feature is a most important consideration in classifying their fossil forms. The various differences found between the sexes in this species will therefore be considered in more detail below.

Cranial capacities may give a useful index of sexual dimorphism within a species. Unfortunately, the only available figures for P. ursinus, those of Goldblatt (1926), do not include a sufficient number of females to be conclusive. Statistics calculated from his figures for the male (in cc.) are: $M = 191 \pm 3.1$; $\sigma = 13.9$; $N = 19$. The observed range for this sex is 165-210 cc. but as no estimate of the age of the various specimens is given, these figures (and the statistics above) may well include immature forms and be too low. The mean figure given by Goldblatt for the females is 158 cc. but it is based on a very small sample only - the exact figure not being given - and therefore can not be considered reliable.

For the anatomical description which follows, Sullivan's description of the skeleton of the rhesus monkey (1933) was found invaluable. The points on the skull used below are those in common use in human anatomy and physical anthropology. For convenience they are defined in Chapter 3.

(a) Norma dorsalis. (Figs. 1,2 and 3.)

The skull of P. ursinus is characterised, as in other baboons, by the great secondary elongation of the muzzle, particularly in the male. This feature is also found in certain other Cercopithecoidea but is otherwise unique among the Primates, although some Prosimii have retained the primitively elongated snout. This elongation is brought about by the lengthening of all the bones in the muzzle region but the maxillae in particular.

Anteriorly, the fused premaxillae are directed forward to a considerable degree, their anterior edge forming a semicircle when viewed from above. The incisor root sockets form marked eminences on these bones, the central pair being much larger than the lateral and having a distinct groove between them which leads back into the large, oval nasal aperture. The premaxilla forms the lateral margin of the nasal aperture and is continued above it, lateral to the nasal bone, by its nasal process. The vomer and the incisive foramina are visible through the nasal aperture on the internal surface of the palatine processes of the maxillae.

The posterior margin of the nasal aperture is formed by the fused nasal bones which then continue posteriorly, rising and

Fig. 1. *Papio ursinus* male (TM.11704). Skull - dorsal view. x ½

Fig. 2. *Papio ursinus* female (TM.727). Skull - dorsal view. x ½

narrowing to terminate just above the midpoints of the orbits at the naso-frontal suture. The upward slope of these bones (and the maxillae) in the infra- and inter-orbital regions becomes increasingly steep as it approaches the nasion and is finally almost vertical. In the male, the last steep rise is only over the last few millimeters whereas in the female, it starts even below the infra-orbital margin.

The maxilla is very large and forms the lateral, and with the nasal, the dorsal surface of the muzzle. Between the dorsal and lateral surfaces, a very strong and prominent ridge is developed in the male; in the female, this ridge is only weakly developed. The ridge can be traced, anteriorly from the line of the canine eminence along the muzzle dorsum, to the origin of the muzzle below the infra-orbital margin at the zygomatico-maxillary suture. This ridge is a strengthening structure transmitting the mechanical stresses set up in the muzzle due to its increased length; their greater development in the male results from its relatively much longer muzzle and its exceptionally large upper canine teeth. Although considerable in the male, the development of the ridges in *P. ursinus* is not nearly as great as in the drills and mandrills where they are also secondary sex characters and are rendered conspicuous by the brightly coloured overlying skin. From the ridges, the stresses set up probably pass either up through the inter-orbital constriction to the glabella region or via the zygomatic, round the lateral margin of the orbit to the lateral part of the well developed supra-orbital torus.

An analysis made for this study of the skull of *P.ursinus* by the split-line technique of Benninghoff (Seipel, 1948) and drawings of the anterior and lateral views of a "*Papio* sp." skull by Henckel (1931) giving the results of a similar study, show split lines to be present in these directions. Other split lines of interest on the *P. ursinus* skull shown up by this method are (i) lines passing from the incisors straight up the premaxillae and nasals to the glabella region between the supra-orbital tori

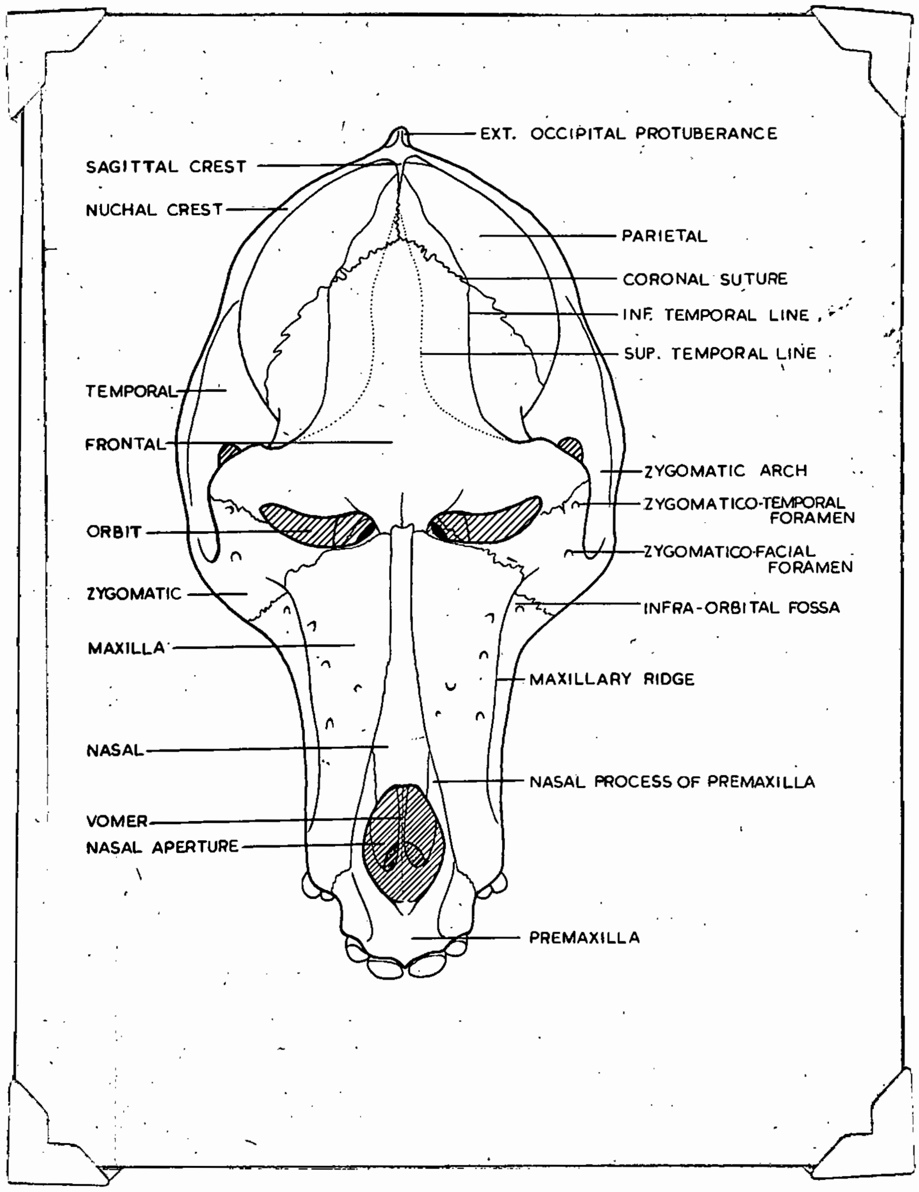

Fig. 3. Dorsal view of the skull of *Papio ursinus* (male).

and (ii) lines from the molar-premolar tooth row (and a small component from the canine) running along the lower lateral surface of the maxilla just above and parallel to the alveolar margin and then passing up the zygomatic bone and round the lateral margin of the orbit to the lateral end of the supra-orbital torus.

In cross-section, because of the great development of the ridges, the dorsum of the male muzzle is almost flat on its anterior half. Because of the weak development of the ridges in the female, and also the earlier upsweep of the nasals and maxillae in the infra-orbital region, the maxillae, in this sex, slope down quite sharply from the nasals to the maxillary ridges where the vertical, lateral surfaces of the muzzle begin. In both sexes, there are numerous foramina on the anterior two thirds of the dorsal surface of the maxillae for the branches of the facial nerve. The posterior part of the maxilla rises upwards to form the medial third of the infra-orbital margin and the lower half of the medial margin of the orbit. Laterally the maxilla meets the zygomatic.

The zygomatic is situated below the lateral half of the orbit and faces forward at an angle of about 120° to the alveolar margin. It is strengthened, particularly in the male, at the infra-orbital and lateral orbital margins as it must transmit the stresses from the maxillary ridge and molar-premolar tooth as described above. This bone forms the lateral two thirds of the infra-orbital margin and also the lower half of the lateral margin of the orbit. It gives rise at its ventro-lateral corner to a temporal process which forms, with the zygomatic process of the temporal, the strong zygomatic arch. In about the centre of the zygomatic, as viewed from the front, there is a zygomatico-facial foramen and where this bone meets the frontal, at about the mid-point of the lateral margin of the orbit, the zygomatico-temporal foramen is situated. This latter foramen may lie either on the zygomatic or the frontal bone.

The frontal forms the upper halves of the mesial and lateral margins and the whole of the dorsal margin of the orbit. The two frontals are completely fused except for a short portion of the metopic suture above the nasals and below the glabella region which remains visible throughout the baboon's life. The supra-orbital ridge is well developed in the male but only very slightly in the female; the supra-orbital notch and spine on the mesial part of the dorsal margin of the orbit is also much more marked in the male. Just behind the glabella region, there is a slight hollow on the frontal; laterally, just in front of the coronal suture and slightly above its sutures with the temporal and sphenoid, the frontal turns downwards and, as viewed from above, shows a considerable waisting. The frontal meets the parietal at the coronal suture.

The two parietal bones meet in the midline at the sagittal suture which, in the male, is elevated for a variable portion of its posterior part into the sagittal crest. There is no crest in the female. The parietals, together with the frontals and a small portion of the occipital posteriorly, form the dorsal wall of the calvarium; with the temporal, and parts of the sphenoid and frontal, they form the lateral wall. The inferior temporal line is well marked in the male, particularly in old specimens and runs from the posterior edge of the supra-orbital torus along the roof of the calvarium to join the sagittal crest a variable distance in front of the inion; the superior line is much less marked and also runs from the posterior edge of the torus to the sagittal crest but somewhat mesial to the inferior line. The inferior line is also prominent in the female but only as far as the coronal suture; the superior line is very weak and barely visible.

On the lateral side of the calvarium, below the parietal, is the temporal bone which, at its ventral edge, bends away from the calvarium and gives rise anteriorly to the zygomatic process already mentioned. On the posterior part of the calvarium, below the parietals, and articulating with them along the lambdoid suture, there is a small portion of the occipital. In the male, this bone is drawn out posteriorly into a well-developed nuchal crest which runs round to the mastoid region of the temporal. This crest is far less developed in the female. At the mid-point of the crest, the male has a very well developed external occipital protuberance (inion); in the female, this protuberance is much less developed. According to Washburn (1947), the nuchal crest develops to separate the large head-balancing muscles below the crest, from the large temporal muscles above on the calvarium. The sagittal crest is similarly developed by the forces set up in the functioning of the temporal muscle masses of each side. The larger crests in the male are thus accounted for by the greater degree of development of all these muscles.

(b) The orbit (Fig 4)

In the female, the orbit is almost round with some outward (i.e. mesial) expansion of the mesio-dorsal corner for the supra-orbital notch; in the male, due to the heavy supra-orbital torus and strengthening of the infra-orbital margin, the orbit is flattened and becomes oval in a mesio-lateral direction. The bones forming the margins of the orbit have already been described in (a) above and only the bones of the interior surfaces of the orbit will be dealt with here.

The interior is deep and cone-shaped with the outer margin forming the lip of the cone and the optic foramen the apex. The axis of the cone lies in an antero-lateral direction and faces slightly upwards. The dorsal wall of the interior of the orbit is made up by the frontal bone which also constitutes the lateral wall as far as the zygomatico-frontal suture and the mesial wall down to the lacrimal bone. The lower part of the lateral surface and also the ventral surface as far as the infra-orbital sulcus of the maxillary, is made up by the zygomatic. The remaining part of the mesial surface, and the ventral up to the sulcus, consists of the lacrimal. The lacrimal fossa, for the passage of the lacrimal duct, is situated in the latter bone.

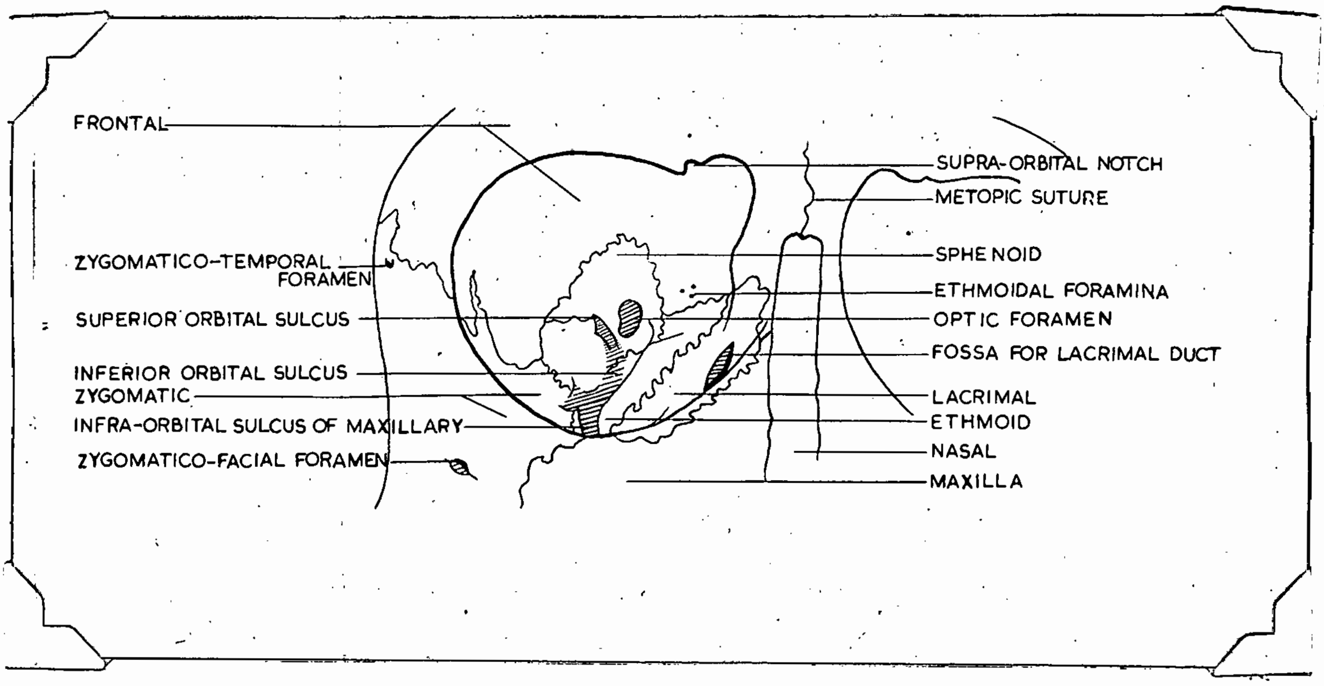

Fig. 4. Anterior view of the orbit of *Papio ursinus* (female)

The central part of the orbit is made up mainly by the sphenoid bone with the ethmoid situated on the mesial wall between the lacrimal (anteriorly), sphenoid (posteriorly), frontal (dorsally) and infra-orbital sulcus (ventrally). The optic foramen is in the sphenoid at the level of a line joining the zygomatico-frontal suture laterally, to the junction of the frontal and maxilla mesially and is on the mesial wall of the orbit. Ventro-lateral to the optic foramen is the very short superior orbital fissure which leads down into the longer inferior orbital fissure. The inferior fissure terminates just beyond the suture between the sphenoid and the zygomatic but just before it ends, it gives off a long mesial branch, the infra-orbital sulcus of the maxillary, which runs to the infra-orbital margin. In the infra-orbital sulcus is the orbital process of the maxilla. There are some foramina in the mesial wall of the orbit (but in the frontal bone) suggestive of the ethmoidal foramina. The orbital opening of the zygomatico-facial foramen is in the zygomatic in the ventro-lateral corner of the orbit: the opening of the zygomatico-temporal foramen is above the zygomatico-frontal suture in the lateral wall of the orbit.

(e) Norma lateralis (Figs. 5,6, and 7).

On the anterior end of the muzzle the forward projecting premaxillae can be seen. Prominent on the lateral surface of the muzzle, which is formed by the maxilla, there is a large depression, the maxillary excavation. It is bounded anteriorly by the canine eminence, dorsally by the maxillary ridge, posteriorly by the antero-dorsally facing zygomatic bone and ventrally by the alveolar margin. In the postero-dorsal angle of this excavation is the infra-orbital fossa with its multiple foramina. The profile view of the muzzle again reveals differences between the sexes. The almost vertical drop in the inter-orbital region of the female is relatively far greater and longer than in the male. The succeeding slope of the muzzle is also relatively steeper in the female.

Fig.5. *Papio ursinus* male (TM.11704). Skull and mandible - lateral view. x ½.

Fig.6. *Papio ursinus* female (TM.727). Skull and mandible - norma view. x ½.

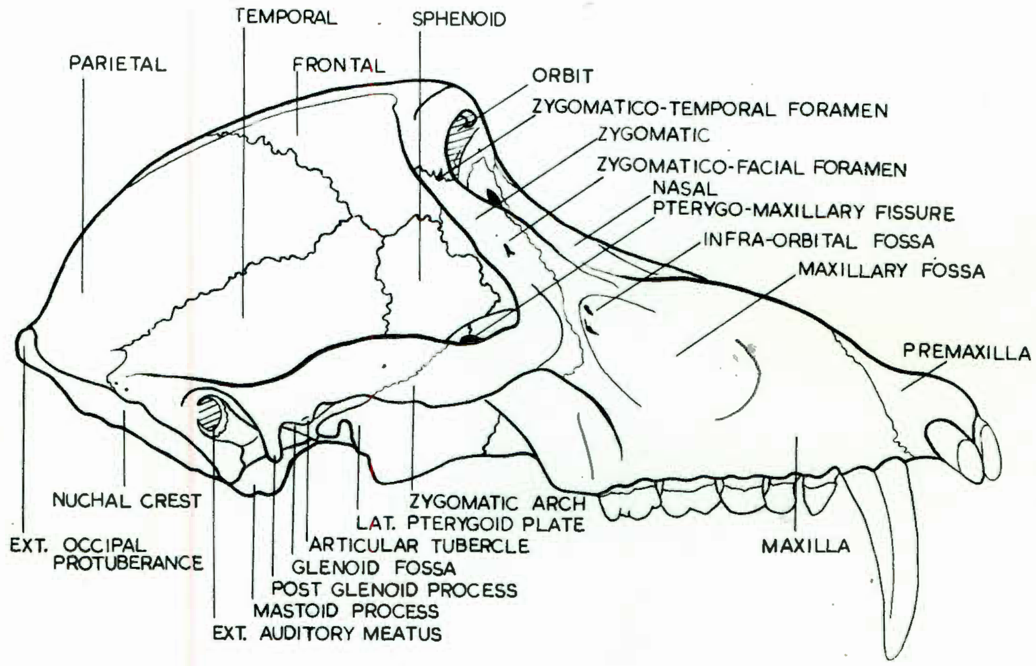

Fig. 7. Lateral view of the skull of *Papio ursinus* (male).

The lateral wall of the calvarium is formed by the frontal (antero-dorsally), the parietal (postero-dorsally), the sphenoid (antero-ventrally) and the temporal (postero-ventrally). The frontal and temporal meet for well over a centimeter on a common suture and there is no contact apparent externally between the sphenoid and parietal. The temporal fossa is situated in the area ventral to the temporal line, posterior to the zygomatic and maxilla and laterally bounded by the zygomatic arch. Its antero-ventral portion, the infra-temporal fossa, is very deep.

The pterygo-maxillary fissure is found in the infra-temporal fossa, between the anterior margin of the pterygoid process of the sphenoid and the posterior margin of the maxilla and at about the level of the zygomatic arch. The fissure is more or less divided into two parts by a process of either the sphenoid or the maxilla which may or may not make contact with the opposite bone. The upper portion is usually in the form of a fissure whereas the lower is more like a foramen. The pterygo-maxillary fissure leads into the pterygo-palatine fossa, the main connections of which are with the orbit through the infra- orbital fissure, the oral cavity through the posterior palatine foramen, the middle cranial fossa through the foramen rotundum, the petro-sphenoidal synchondrosis through the pterygoid canal and the nasal cavity through the very large spheno-palatine foramen.

At the ventral border of the infra-temporal fossa is the large ventrally directed lateral pterygoid plate of the sphenoid. On the temporal, just anterior to the external auditory meatus, is the large post glenoid (articular) process and anterior to it, the small articular tubercle. Behind the meatus, in the male, is a large ventrally directed process of the mastoid. The nuchal crest running round from the mastoid region to the large external occipital protuberance and the temporal lines and sagittal crest on the dorsal surface of the calvarium can also be seen.

(d) Norma basalis (Figs. 8,9 and 10).

The anterior portion of the palate is made up by the premaxillae which bear the four incisors. These bones are rough

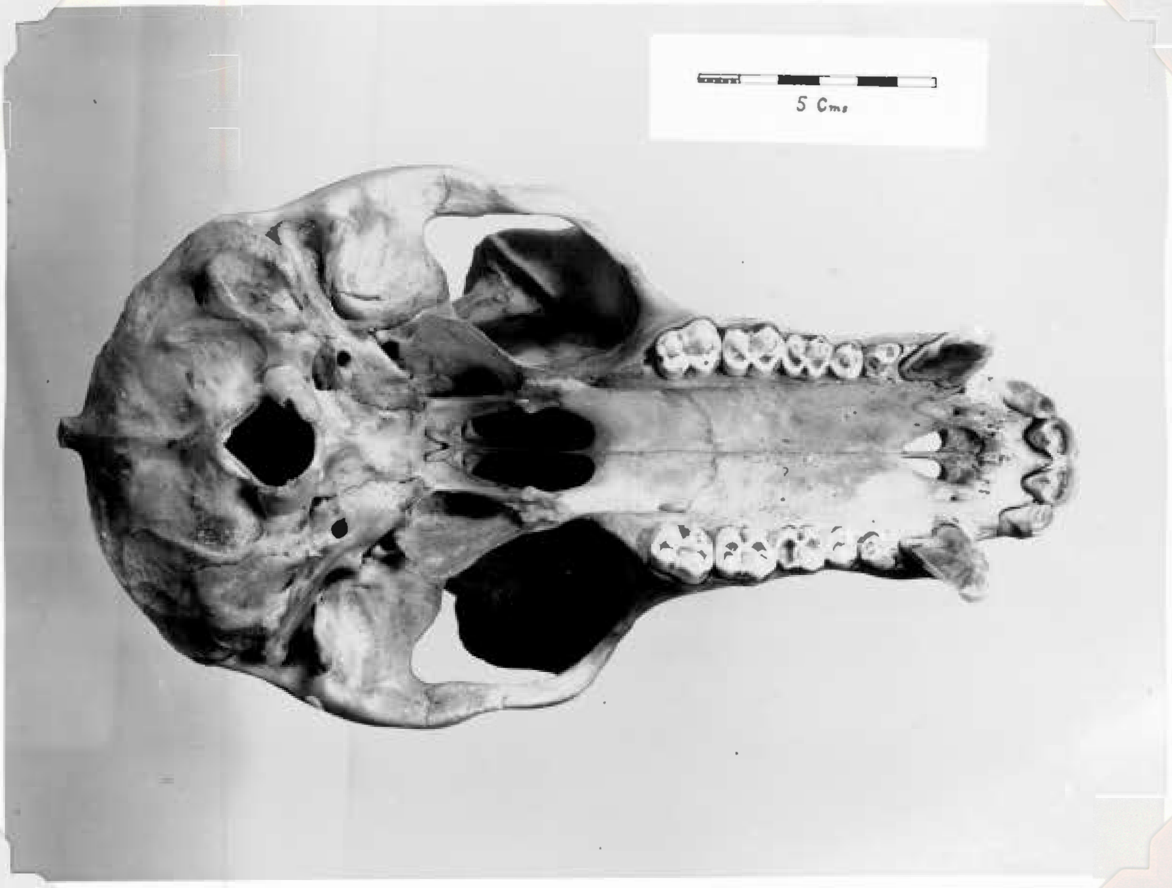

Fig.8. *Papio ursinus* male (TM. 11704). Skull - basal view. x ½.

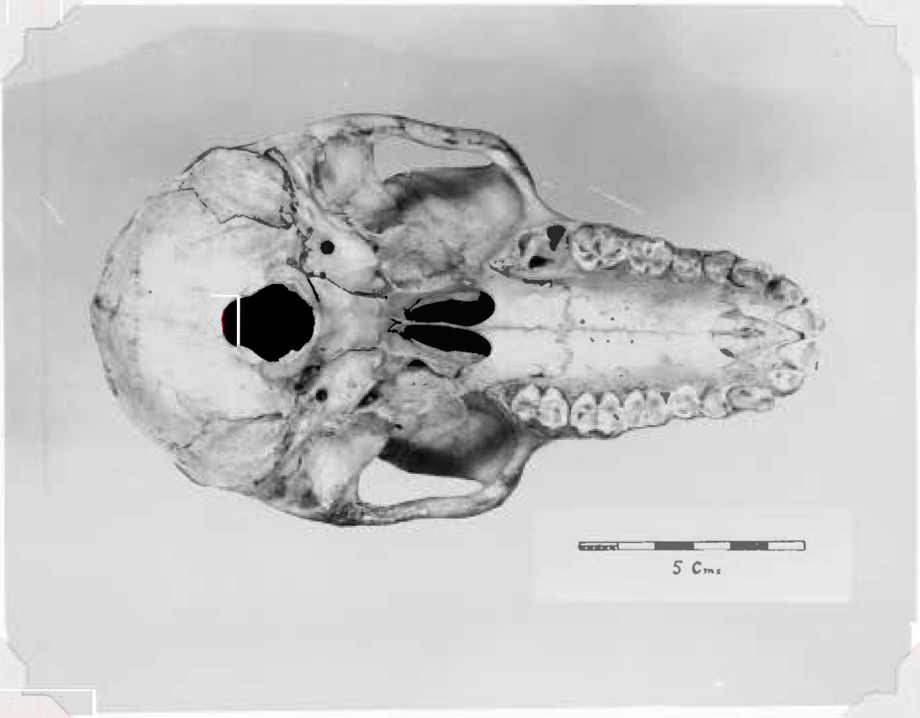

Fig. 9. *Papio ursinus* female (TM.727). Skull - basal view. x ½.

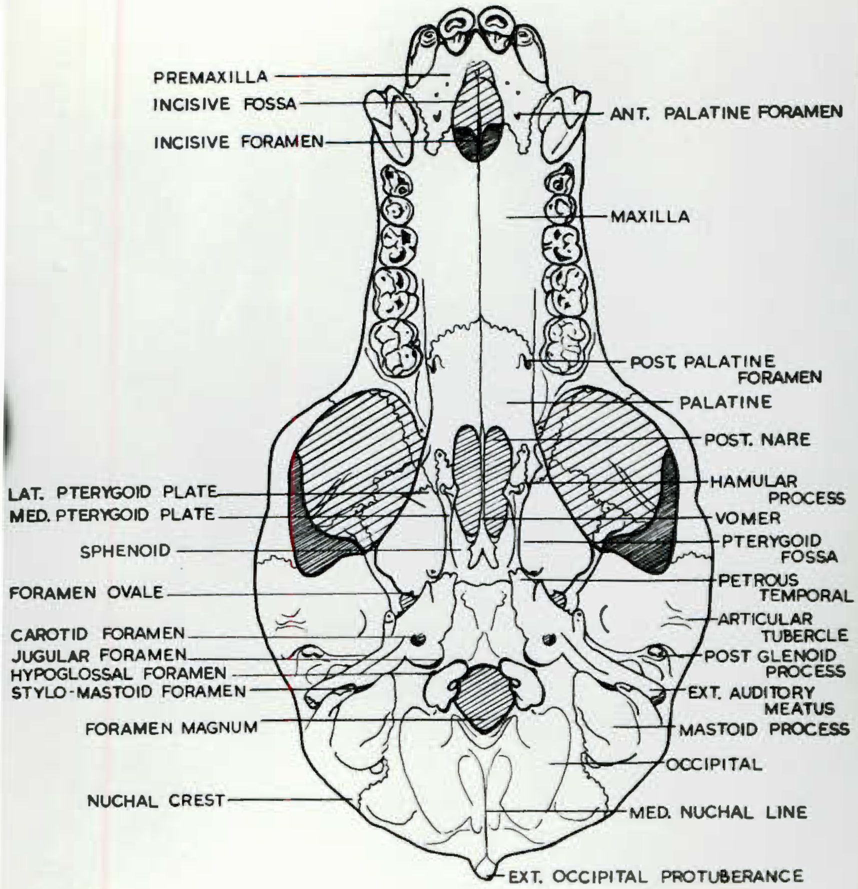

Fig. 10. Basal view of the skull of *Papio ursinus* (male).

and pitted and contain many small foramina. The two anterior palatine foramina and the anterior parts of the incisive fossa and foramina which lie between these are found in this bone; the posterior parts of the latter fossa and foramina are on the maxilla. The main, middle portion of the palate, which bears the canines, premolars and molars is formed by the maxillae. These bones also have numerous small foramina randomly distributed over their entire palatal surface. The posterior portion of the palate consists of the palatine bones and in them, just posterior to the palato-maxillary suture and mesial to the alveolar margins, are the two posterior palatine foramina which often each have a protecting bony shelf. Towards the posterior end of the palate in the midline is a palatine torus which terminates as the slightly projecting posterior nasal spine.

The palatine also forms the anterior margin of the posterior nare. The paired nares are separated by the vomer, which bifurcates where it joins the sphenoid which forms the posterior margin of these openings. The lateral wall of the posterior nare is formed anteriorly also by the palatine and posteriorly by the medial pterygoid plate of the sphenoid. On the anterior end of this medial plate is the hook-like hamular process. The lateral pterygoid plate is very much larger than the medial one and is directed downwards and outwards. Between these two plates the pterygoid fossa is found.

Situated on the temporal, posterior and somewhat mesial to the zygomatic process, is the glenoid fossa. Lateral to it is the articular tubercle and posterior to it is the post glenoid process. A short antero-posterior groove or fissure is often present mesial to the fossa. Between the anterior part of the petrous temporal and the posterior end of the lateral pterygoid plate of the sphenoid, the foramen ovale is found. It is linked to the infra-temporal fossa by a canal through the lateral pterygoid plate. Just ventral to foramen ovale, on the petrous temporal, is the pharyngeal opening of the eustachian tube. This tube runs postero-laterally into the tympanic cavity. The middle lacerate foramen, which should lie anterior to the foramen ovale, appears to be completely obliterated in *P. ursinus* by the petro-sphenoidal synchondrosis. On the petrous temporal, postero-lateral to foramen ovale, is the small ventrally directed styloid process. Mesial to it, and in about the centre of that bone, is the external carotid foramen. Posterior and slightly mesial to the carotid foramen, and lying between the temporal and the occipital, is the jugular foramen. The external auditory meatus lies posterior to the post glenoid process. It is directed postero-laterally.

On the occipital, mesial and posterior to the jugular foramen, is the large, centrally situated foramen magnum. On its antero-lateral margins there are two articular (occipital) condyles which are notched at the centre of their ventral borders. Dorsal to each condyle, and next to the jugular foramen, is the hypoglossal canal, which may be double. The small stylomastoid foramen is on the petrous temporal, in a line with, and midway between, the post glenoid process and the occipital condyle. The part of the occipital behind the foramen magnum is rough and ridged for the attachments of the many strong neck muscles. Posterior to the external auditory meatus in the male, the mastoid region is pulled out into a ventrally directed process. There is a well-marked median nuchal line (external occipital crest) leading to the external occipital protuberance but transverse nuchal lines below the nuchal crest are not readily discernable.

(e) Internal structure. (Fig. 11).

Because of the elongated muzzle, the nasal cavity and nasal aperture are exceptionally long, the latter being about one third of the total length of the muzzle. The nasal cavity is divided longitudinally into two equal halves - ventrally by the vomer and dorsally by the cartilagenous nasal septum, which fits into a groove on the dorsal surface of this latter bone, and by the ethmoid which divides a short postero-dorsal section. The vomer itself is only elevated a few millimeters above the floor of the

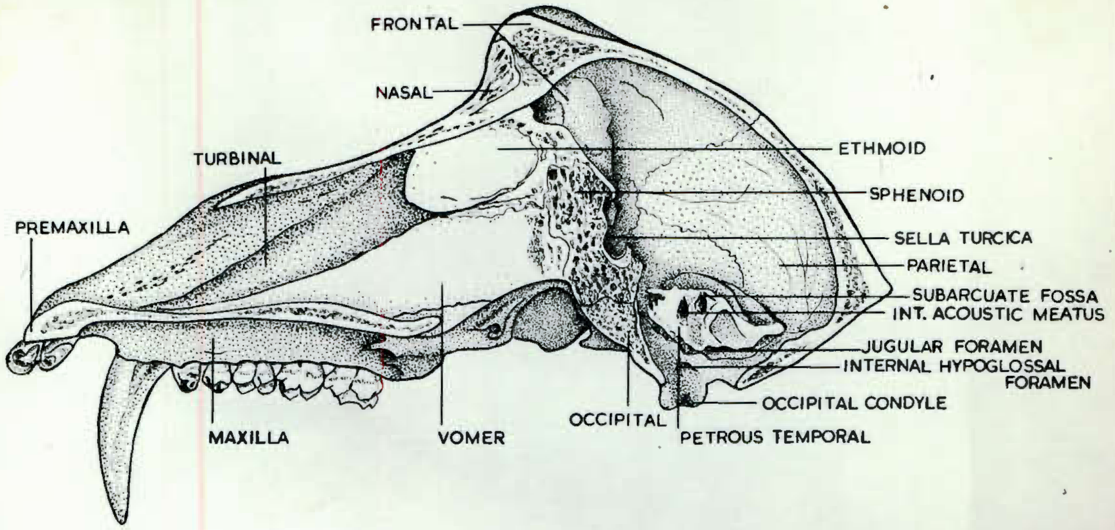

Fig. 11. Median sagittal view of the skull of *Papio ursinus* (male).

nasal cavity anteriorly but rises steadily posteriorly and by the time it has reached the posterior end of the cavity, it reaches about three quarters of the way up to the roof of the cavity. In each of the two nasal chambers, there are superior and inferior nasal conchae.

In the midline, the anterior wall of the calvarium, from above downwards, consists of the following bones: frontal, ethmoid, frontal, sphenoid and occipital. The dorsal wall of the calvarium consists principally of the frontal and parietal: the lateral wall of the parietal and small portions of the frontal, sphenoid and temporal: the ventral wall of occipital and temporal. The walls are grooved for the meningeal vessels and there are impressions for the cerebral gyri. The bone is thick in the male and the strengthening in the supra-orbital and nuchal regions is great. In the sagittal plane, where they are part of the anterior wall of the calvarium, the sphenoid and occipital are also thick but the bone, particularly of the latter, is cancellous and open. It is interesting that on the internal surface of the skull the parietal and the sphenoid make contact whereas they are always separated on the exterior of the skull by the frontal and temporal. This is due to the fact that the cranial bones often meet at a very acute angle and overlap: the sutures thus being different internally and externally. In this instance the temporal lies over the sphenoid, frontal and parietal externally.

In the anterior cranial fossa the only feature of interest is the small cribriform plate of the ethmoid through which foramina link this fossa to the nasal cavity. In the middle cranial fossa there are many important features. On the sphenoid is the hypophyseal fossa or sella turcica with a clinoid process at each corner. Just ventral to the anterior clinoid process is the opening to the supra-orbital fissure: just dorsal to this process is the optic foramen. Lateral to the middle of the sella turcica is the foramen rotundum leading to the pterygo-palatine fossa. Foramen ovale enters between the anterior part of the petrous temporal and the sphenoid. In the posterior cranial fossa the main feature is the large central foramen magnum, on the lateral walls of which are the hypoglossal canals. On about the centre of the petrous temporal is the subarcuate fossa and somewhat mesial and anterior to it is the internal acoustic meatus. The jugular foramen is found between the middle part of the petrous temporal and the occipital at the level of, and between, the hypoglossal canal and the internal acoustic meatus.

(f) The mandible (Figs. 5,6,and 12).

The mandible consists of two halves which are fused anteriorly at the mandibular symphysis. Each half is composed of a single bone, the dentary. In the male, the symphysis is very heavy and strong and its anterior surface is rough and pitted; in the female, it is far more delicate and does not have such a vertical anterior surface. In both sexes there are two prominent ridges running up the anterior surfaces of the symphysis. There is a sagittal canal running through the symphysis starting on the postetior surface and running dorsally and anteriorly to the anterior surface where it ends as the foramen symphyseosum. There are several foramina (the foramina mentalia) on the lower lateral surface of the symphysis and extending round on to the lower lateral edge of the corpus. The mental spine is situated on the ventral surface of the symphysis in the angle where the two corpora meet. It may be very small in the female.

There is a large, very deep fossa, the mandibular fossa, on the anterior part of the external surface of the corpus. By analogy with the rhesus monkey (Geist, 1933 and Huber, 1933), this fossa would seem to be opposite the opening into the cheek pouch and is probably related to it. The ventral edge of the corpus is rounded and thickened. On each side, the corpus decreases in height as it approaches the ramus. This is much more marked in the male because of its much heavier symphysis.

The ramus is very much thinner than the corpus but it is considerably broader. The angle between the corpus and the ramus is just over a right angle in the female but appears rather more obtuse in the male. This is again partly due to the heavier

Fig. 12. General view of the male mandible of Papio ursinus (TM.11704) approx. x 3/4.

male symphysis which lowers the anterior part of the base line used in measurements. The coronoid process is large, higher than the condyloid process and directed backwards. The sigmoid notch is moderately deep. There is a small triangular fossa on the external surface of the ramus below the coronoid process; on the internal surface of the ramus, there is the mandibular foramen with the mylohyoid line below it. At its posterior edge, the lower half of the internal surface of the ramus is roughened for muscular attachments (medial pterygoid muscle).

TEETH.

Dental characters are of great interest and importance in the study of fossil forms. Due to their hard enamel covering and unpalatability, teeth comprise the most common and best preserved fossil fragments. Because they give an indication of the diet, much information as to habits and, in some instances, even body form of the animal can be deduced from them. Teeth are usually characteristic for different species and most fossil mammal taxonomy is based primarily on comparative odontology.

P. ursinus has the deciduous and permanent dental formulae typical of the Cercopithecoidea and Hominoidea (Catarrhini) but shows the specialisations of its family, genus and species. At the higher taxonomic levels (from the odontological point of view) there are the bilophondont molars; at the lower levels there are differences in tooth shape and size. These will all be discussed in some detail below. Because of its functional importance, tooth wear has also been considered but it is obvious that all the wear facets described may not be found in the teeth of a single individual due to minor variations and malocclusion.

In the description of the teeth throughout this study, the following terminology applies: The surface of a tooth nearest the alveolar point in the upper jaw, or the point between the central incisors in the lower, is referred to as 'mesial' and the opposite surface as 'distal'. The inner surfaces of all the teeth, i.e. the surface nearest the tongue, will be considered as 'lingual' and the opposite or outer surface, as 'buccal'.

The tooth cusp terminology used in this study (Figs. 16 and 18) is adapted from Gregory (1920 b). For premolars the main cusps will be known merely as lingual and buccal; for the molars, the following will apply:

	mesio-lingual.	mesio-buccal.	disto-lingual.	disto-buccal.
upper:	protocone	paracone	hypocone	metacone
lower:	metaconid	protoconid	entoconid	hypoconid

The fifth cusp, found only on the distal end of the third lower molar, is the hypoconulid.

Individual teeth are numbered from the most mesial to the most distal and are abbreviated as follows:

(a) deciduous - incisors (di), canines (dc) and molars (dm).

(b) permanent - incisors (I), canines (C), premolars (P)
and molars (M).

Upper teeth are indicated by the number of the tooth being placed above the letter designating it e.g. M^1, and lower, by the number being placed below it e.g. M_1. If both upper and lower are being referred to, the number is put on the same line as the letter e.g. M1. In the case of the canine teeth, the upper tooth is shown with a horizontal line below it, $\underline{C}$, and the lower one with a similar line above it, $\overline{C}$; when both are referred to no line is used, C. In the Cercopithecoidea (and Hominoidea) the first two of the primitive four premolars have been lost; the two remaining ones are therefore designated P3 and P4.

(a) Deciduous Dentition. (Figs. 13,14 and 15).

Too few deciduous teeth are available for a statistical analysis of their characteristics to be made but they are briefly described below and the sizes of the teeth in the two available specimens are given in table 1. Unfortunately, the sexes of these two specimens were not recorded nor can they be determined easily in such young specimens.

Table 1. The Measurements of the Deciduous Teeth of *P. ursinus*. (in mm.)

Specimen No.	Upper teeth														
	di^1			di^2			$\underline{dc}$			dm^1			dm^2		
	h	b	l	h	b	l	h	b	l	b_m	b_d	l	b_m	b_d	l
TM.6618	7.7	5.0	7.7	7.3	5.0	7.0	9.0	5.7	7.3	6.8	6.3	8.6	-	-	-
TM.No.B1	6.8	5.0	6.7	6.2	4.7	6.9	8.4	5.0	7.3	6.6	6.6	8.3	7.5	6.9	9.6

Specimen No.	Lower teeth														
	di_1			di_2			$\overline{dc}$			dm_1			dm_2		
	h	b	l	h	b	l	h	b	l	b_m	b_d	l	b_m	bd	l
TM.6618	7.7	4.5	5.1	6.8	4.9	6.0	8.0	3.9	6.2	4.5	5.0	9.7	-	-	-
TM.No.B1	6.4	4.5	4.8	5.4	5.2	5.5	7.3	4.0	6.5	4.5	5.4	9.6	6.4	6.3	9.8

Fig. 13. Papio ursinus juvenile (TM.No.B1). Skull and mandible - lateral view. x 1.

Fig.14. Papio ursinus juvenile (TM.No. B1). Skull - basal view to show occlusal view of upper deciduous dentition x 1.

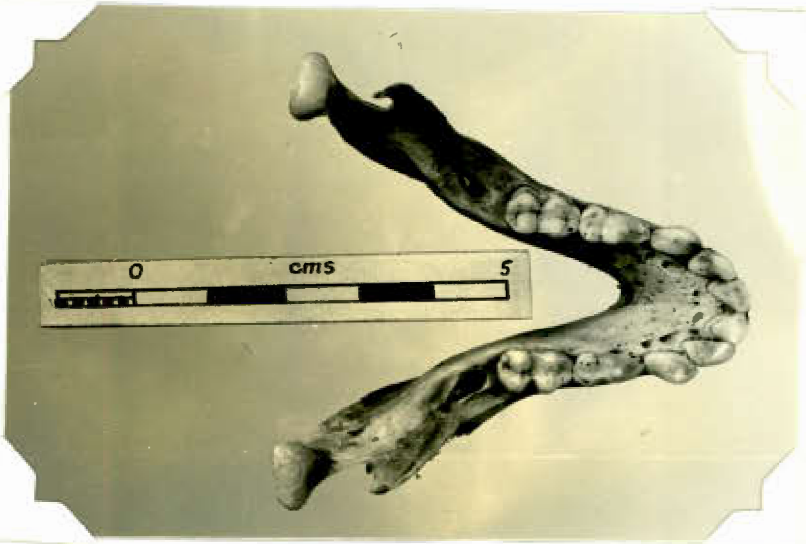

Fig. 15. Papio ursinus juvenile (TM.No.B1). Mandible - showing occlusal view of lower deciduous dentition x 1.

The deciduous dental formula of *P. ursinus* is: $di\frac{2}{2}$, $c\frac{1}{1}$, $dm\frac{2}{2}$. Essentially these teeth agree with their permanent successors in structure but with certain important differences. The incisors are rather short and squat but show no marked differences from their permanent equivalents. The canines, too, are short and squat teeth and in these two specimens appear to follow the adult female pattern to be described later. A diastema between dc and dm^1 is present in one skull only. The molars, dm1 and dm2, are bilophodont teeth with four cusps. Bilophodonty is a specialisation of the molars of the Cercopithecoidea which describes a condition in which there is a definite separation of the four cusps by a transverse groove into a mesial and distal pair. (This feature rules the group out of the main line of higher primate (hominoid) evolution).

The first upper deciduous molar (dm^1) is very much like the typical adult molar (to be described below) except for a fairly marked chamfering of the mesio-lingual corner, mainly on the lingual side. The second upper deciduous molar (dm^2) is very similar to the first, but it is considerably larger in size and the mesio-lingual corner shows less reduction.

The first lower deciduous molar shows a form intermediate between that of a typical adult lower molar and the modified P_3 of the adult to be described below. The crown of this tooth has become elongated forward anterior to the mesial pair of cusps, and on the occlusal surface of this portion, the anterior fovea is greatly increased in size. This mesial extension of the tooth is doubtless an adaptation, similar to the adult one P_3, to allow for the occlusion of the large upper canine. The crown of this tooth is more or less in the shape of a long, narrow isosceles triangle with the distal surface forming the base and the mesial surface being reduced more or less to an edge. The second lower deciduous molar is very similar to the adult lower molars (M_1 and M_2) but it appears to be somewhat elongated mesio-distally.

(b) Permanent Dentition. (Figs. 5,6,8,9,12,16,17 and 18).

The adult dental formula of *P. ursinus* is $I\frac{2}{2}$, $C\frac{1}{1}$, $P\frac{2}{2}$, $M\frac{3}{3}$. The sequence of eruption of the permanent dentition, according to Schultz (1935), is M1, I1, I2, M2, P3, P4, C, M3. The upper teeth follow directly after their lower equivalents but the eruption of P3 and P4 occurs close together and the order may be reversed in either jaw and even between the jaws. Although the C emerges before M^3, it is such a long tooth that it may only be fully erupted after this latter tooth. The ages at which the various teeth erupt is at present not known with certainty. The age groupings used in the tables and elsewhere are based on the above sequence and on the state of wear of M3. The actual groups used are defined in Chapter 3. The length of the alveolar margin behind M^3 and the position of the distal end of this tooth relative to the anterior root of the zygoma were used by Goldblatt (1926) for age determination. These criteria are applicable to mature adults only and, in any case, they were not found sufficiently accurate for use in this study.

(i) Incisors: The incisors are single-rooted teeth in which a sharp occlusal edge for biting is present. The teeth of the upper row, especially the central pair, are larger than their lower jaw opposites and overlap them anteriorly and laterally. All the incisors lean mesially but the lateral pairs more so than the central. The lower teeth bite into the occlusal surfaces of the upper teeth causing wear facets with the result that, in worn teeth, the occlusal surface of the upper row shows a bucco-lingual concavity. The occlusal surfaces of the lower teeth develop an acute downward slope from the buccal biting edge down the lingual surface, often almost as low as the alveolar margin. As it is impossible for normal occlusion to cause this wear of the lower teeth, the wear must be attributed to the biting of hard substances. There is also a wear facet on the upper part of the distal surface of I^2 where it meets the upper half of the mesial surface of $\bar{C}$. Besides being proportionally smaller, there are no sex differences in these teeth.

(ii) Canines. In the males, the canines are exceedingly well developed, more so in the upper jaw where, when the jaws are closed, they often project for half their length beyond the bottom of the lower tooth row. The crowns of both the upper and lower teeth have a robust base and then taper off to a sharp point. The four surfaces usually found on a tooth are not readily discernable in $\underline{C}$. The shape of this tooth in cross-section near the base of the crown is roughly triangular with the mesial surface as the base, the disto-lingual edge very acute and sharp and the distal and buccal surfaces forming virtually a single face (Fig. 16). In the $\overline{C}$ the four surfaces can be readily seen (Fig.17) but the crown shows an outward spiral twisting from the base up towards the tip. There is a well marked groove on the mesial surface of the $\underline{C}$ which is continued along the large single root of the tooth; on the $\overline{C}$ the groove is very shallow. The purpose of these grooves, particularly on the large upper 'stabbing teeth', is probably to facilitate rapid penetration and withdrawal of these teeth in fighting.

In addition to the wear facet on the $\overline{C}$ described under the incisors, the top third of the mesio-lingual edge of $\underline{C}$ wears on the top third of the distal surface of $\overline{C}$. This wear is caused by the $\underline{C}$ being distal to the lower because of the larger size of the upper incisors and the diastema between I^2 and $\underline{C}$. The lingual surface of the $\underline{C}$ wears on the mesio-buccal surface of P_3 with which it forms a type of 'carnacsial scissors'. This 'scissors' is probably used for biting hard foods and the disto-lingual edge of $\underline{C}$ is kept sharp by its wear on P_3. In old specimens wear causes a marked reduction in the size of the canines and the pulp cavity is often exposed.

In the male, the canines also serve several other important functions. Their main purpose is probably a defensive one against predatory carnivores, in particular the leopard, and they are used in a most unusual but most effective manner. The baboon grips the enemy, preferably on the underside of the throat, with its long upper and lower canines. It then grasps the animals body with its fore and hind limbs and pushes away violently. By this method it tears a huge wound and can very often kill an animal as large even as a leopard. The canines are also used offensively against males of the same species in fights over females or for leadership of the troop. Finally, they may also be used for predatory activities as baboons are reported to kill young lambs for the curdled milk in their stomachs (FitzSimons, 1911 and Marais, 1939) and even small buck and young antelope for their flesh (Stevenson-Hamilton, 1947).

In the female, the canines project only slightly beyond the occlusal plane and are altogether much smaller teeth than in the male. They show a similar structure to the male equivalents but the twisting and grooves described in these teeth are here virtually absent. Because of their much smaller size, the wear on the female canines is rather different to that on the male. Due to its occlusion with the mesial extension of P_3, the upper canine develops a facet sloping down across its occlusal surface from the buccal to the lingual faces. The occlusal surface of the $\overline{C}$ develops a similar facet also sloping down from the buccal to the lingual side but this facet is probably caused, similarily to the facet on the occlusal surface of the lower incisors, by the biting of hard foods and not by direct wear on another tooth. When wear is advanced, the $\underline{C}$ wears a deep facet across the lingual part of the occlusal surface of the $\overline{C}$ sloping downwards in a mesio-distal direction. It would also appear that the occlusal surface of I^2 wears down the buccal edge of the occlusal surface of $\overline{C}$. In old females the canines are worn down to the level of the incisors and appear to form part of that row. Their function in the female is probably mainly for the biting of food.

(iii) and (iv) Premolars and molars: The basic diet of the chacma baboon is very varied but they are, in nature, restricted to herbivorous and insectivorous habits. Normally they are not carnivorous and even the few isolated exceptions quoted above really require further corroboration. Their known dietary requirements include such diverse items as roots and bulbs, young shoots, berries and fruits, honey, beetles, scorpions and lizards. As the forelimbs are used for digging up roots or breaking off fruits, the main purpose of the teeth is to grind up the food after it has been bitten to a suitable size usually by the incisors but sometimes, particularly when rather hard, by the $\underline{C}$ and P_3 as already described. Because of the grit associated with the roots and tubers eaten, wear on the teeth is great.

The premolars and molars function as a single grinding unit and show many similarities. Due to the large canines, particularly in the male, the movements of the jaws are almost entirely restricted to up and down and forward and backward movements except in very old females where the canines have become sufficiently worn down to permit lateral movements. The restriction of lateral movement, and the displacement of the upper teeth in a buccal direction, results in the lower teeth being worn mainly on the buccal side of the occlusal surface and the upper teeth mainly on the lingual. An interesting adaptation in this connection, is the fact that the alveolar margin is lower, buccally on the mandible and lingually on the maxilla. In spite of the backward displacement of the maxillary canines and post-canine teeth relative to the lower ones, the two tooth rows terminate in the same vertical plane because M_3 is relatively long as a result of having a well developed hypoconulid. In the occlusion of the individual teeth of the premolar-molar series, the upper teeth thus lie slightly distal to their lower equivalents and, except M^3, occlude with two lower teeth. The root systems of the upper premolars and molars consist of two buccal and one lingual root on each tooth and, in the lower teeth, of one mesial and one distal root.

Premolars. The premolars are typically bicuspid teeth with approximately equal sized buccal and lingual cusps. Mesial and distal fovea are present, the latter being the larger of the two. P_3 is a most remarkably modified tooth. In the male, the mesial surface of the crown is greatly elongated and runs forward and downward at an angle, to well below the alveolar margin of the premolar-molar series; it occludes, as described above, with *C*. The foveae on the crown of this tooth are large and face somewhat lingually. In the female this elongation is of a similar nature but less well developed because of the smaller *C*. The mesial surface of the crown of P^3 also leans distally but at a very slight angle only. The slope is greater in the male than in the female. P^4 is a typical premolar and is considerably larger than P^3. P_4 is a longer, narrower tooth than P^4 and shows a certain degree of molarisation in its elongated distal portion on the end of which are two small cusps, one buccal and one lingual. In the male this tooth (P_4) leans very slightly distally.

Molars: The molars are all typically bilophodont and, although they differ in size, show the same structure in both sexes. The size relationships between the various molars are discussed in Chapter 5. The basic arrangement of cusps has already been described above but accessory cuspules are often also present. Thus, small cuspules are usually found in a mesio—buccal position in the lower jaw and in a mesio-lingual position in the upper. In addition, small distal cuspules can often be seen and there are sometimes traces of lingual or buccal accessory cusplets. A hypoconulid occurs typically on the distal end of M_3 only, but it was found to be absent in one specimen (TM.807).. In TM.791 a definite hypoconule (id) was found on all the upper and lower molars except M^1 and hypoconules were present on all the upper molars of TM. 756

No cases of congenital absence of teeth were noted in the specimens of *P. ursinus* examined but three specimens (5%) showed supernumerary molars. Upper supernumerary molars were present bilaterally in TM.11712 and TM.757; in TM.11709 M^4 was present on the left side only. In the lower jaw, TM.757 also showed a supernumerary molar on each side. The cusp arrangement and size of these teeth corresponded very closely in each case with that of the preceding tooth, i.e. the normal $M3$. (A female skull, TM.11713, not included in the statistical study, was found to have $M4$ present bilaterally in both the upper and lower jaws. In this specimen the upper pair, and in particular the left tooth, are much reduced in size and the number and arrangement of cusps bears no resemblance to that of the normal M^3. The lower supernumerary pair are not yet fully erupted but also seem to be at least slightly malformed). Schultz (1935) reports finding no $M4$ in 123 specimens but records that Shaw (1927) found 3.6% in "112 South African baboons" and that Bateson (1894) found supernumerary molars "in a baboon and a macaque among 419 Old World monkeys".

CHAPTER 3.

SYSTEM OF MEASUREMENTS.

Due to the specialisations of the various groups, the craniometric and dental measurements used in studies of the Primates vary greatly and no set of measurements is universally applicable. A system of measurements has therefore been specially devised for this study to meet its particular requirements. As the study is meant to act as a standard of reference for cercopithecoid fossil forms, which are mostly represented by small fragments only, this has entailed a large number of measurements being used. The angles in the skull, used by Goldblatt (1926), were however not included. These are interesting features but they are not practical measurements for use in taxonomy, as the skull must be sectioned in the median sagittal plane. In the arrangement of the measurements, an attempt has been made to divide them into functional groups, as no single measurement is an end in itself but must be viewed as part of a whole.

For measuring the various parts of the skull, an ordinary sliding caliper, accurate to the nearest millimeter, was found adequate but for certain awkward measurements, a pair of external calipers was preferred. For the teeth, and in certain instances where a greater degree of accuracy was required on the skull, a vernier sliding caliper, accurate to 0.1 mm., was used. Angles were measured with an engineer's bevel gauge. All measurements were taken before dividing specimens into their age groups in the P. ursinus study, or species in the fossil study, in order to remove any unconscious bias which would have been inevitable were the specimens prearranged.

Age groups have been based on tooth eruption and wear. As long as deciduous teeth are present, a specimen is considered juvenile; once M3 and C are fully erupted and in use, the specimen is taken to be mature. The immature adults are placed in a group between these two. Juveniles were further subdivided into two groups depending on whether any permanent teeth were present; mature adults were further subdivided into four groups depending on the amount of wear of M3 which is the last molar to erupt. The age groups used in this study are then as follows:-

Young juveniles	:	Only deciduous teeth present.
Juveniles	:	Deciduous and permanent teeth present.
Immature adults	:	M3 or C not yet fully erupted (i.e. not yet in use).
Young adults	:	All teeth fully erupted and in use. M3 only very slightly worn.
Adults	:	M3 worn appreciably.
Old adults	:	Considerable wear on M3.
Very old adults		Cusps on M3 worn flat.

(Skull suture closure was found to be of no help in delimiting the age groups used in this study. Goldblatt (1926) also found this age criterion of little value in P. ursinus).

Below follows a list, with definitions, of the terms and measurements used in this study. Measurement of length is in the antero-posterior direction; height is in the dorso-ventral plane and breadth is the dimension at right angles to both of these. When an oblique measurement is used, it is classed under the direction to which it most nearly approximates and as a measure of which it has been taken.

1. Principal points on the skull used for measurements (from Johnston and Whillis, 1946).

Alveolar point (prosthion)	:	The central point of the anterior margin of the upper alveolar arch.
Rhinion	:	The most prominent ('anterior' would be better for P. ursinus) point of the internasal suture.
Nasion	.	The central point of the frontonasal suture.
Inion	:	The most prominent point on the external occipital protuberance in the median plane.
Basion	:	The mid-point of the anterior margin of the foramen magnum.

Glabella : The point in the median plane at the level of the superciliary arches.

Bregma : The meeting point of the coronal and sagittal sutures.

Gonion : The outer margin of the angle of the mandible.

2. Measurements.

(a) Skull.

(i) General.

Greatest length - Alveolar point to inion.

Basal length - Alveolar point to basion.

Bi-zygomatic breadth - Maximum breadth between the lateral surfaces of the zygomatic arches.

(ii) Calvarium.

Height : Basion to bregma.

Basion to glabella.

Breadth : Minimum inter-frontal - Minimum breadth across the frontals posterior to the supra-orbital tori.

Greatest temporal - Greatest breadth above the zygomatic processes of the temporal.

Mastoid - Maximum inter-mastoid.

Length : Inion to glabella.

Inion to basion.

Foramen magnus : Breadth - Maximum internal.

Length - -ditto-

(iii) Muzzle.

Height : Posterior to M^3 - At right angles to the occlusal plane and from the alveolar margin.

Anterior to P^3 -ditto-

Breadth : Anterior to M^3 - Between the lateral surfaces of the maxillae.

Anterior to P^3 - -ditto-

	Dorsal to M^2	- Between the lateral surfaces of the two maxillary ridges.
Length :	Muzzle	- Nasion to alveolar point.
	Palate	- Alveolar point to posterior nasal spine.
	Nasal	- Nasion to rhinion.
Orbit :	Inter-orbital constriction	- At the level of the centres of the orbits.
	External orbital	- Between the lateral edges of the zygomatics and through the centres of the orbits.
	Height	- Through the centre of the orbit.
	Breadth	- -ditto-
Nasal aperture.	Breadth	- Maximum internal.
	Length	- -ditto-

(b) Mandible.

Height :	Gonion to condyle	- From the dorsal surface of the condyle.
	Gonion to coronoid	- From the top of the coronoid process.
	Posterior to M_3	- Up to the alveolar margin and at right angles to the occlusal plane.
	Anterior to P_4	- -ditto-
	Mental spine to most anterior point	- Most anterior point is taken as between the lower central incisors and at the level of thelowest point of the upper margin of their alveoli.
Breadth :	Bi-condylar	- Between the lateral surfaces of the condyles.
	Bi-gonial	- Between the lateral surfaces or the mandible.

Posterior to M_3 - Between the lateral surfaces of the corpus and at the alveolar margin.

Anterior to M_3 - -ditto-

Anterior to P_4 - -ditto-

Through mental spine - Across the base: between the lateral surfaces of the mandible.

At base of canines - Between the lateral parts of the canine eminences.

Length : Gonion to mental spine.

Across ramus at neck of condyle - At right angles to the mid-line of the ramus.

Condyle to most anterior point - Measured from the posterior surface of the condyle.

Angles : Ramus to corpus - The angle between the ramus midline kept parallel to the anterior margin, and the ventral edge of the corpus.

At symphysis - Between the main slope of the symphysis and the ventral edge of the corpus.

Between the corpora.

(c) Teeth. (Figs 16,17 and 18).

The measurements of the teeth require some preliminary remarks because of the innate difficulties involved in measuring irregular and closely applied surfaces. The 'length' of a tooth is its maximum mesio-distal dimension. It is measured by holding the caliper jaws at right angles to the line passing through the length of the tooth row. 'Breadth' is the maximum bucco-lingual measurement across a tooth and for this, the caliper jaws must be kept parallel to, and in a plane at right angles to, the vertical plane passing through the above line. These are the strict criteria of length and breadth. Deviations from these give diagonal and hence increased or decreased values. It should, however, be noted that the caliper itself may be held vertically, horizontally or at a position in between, depending on convenience and the types of surfaces involved, without affecting these conditions. In several instances it was found to be more accurate to partially dispense with these standards and to measure across definite points such as cusps, or at enamel line heights. These special cases are all defined below.

The measurements of the teeth have in no way been altered to allow for the effects of wear but as the specimens are divided into age groups, if the effects are great they should be apparent from the final tables. Measurements, as has been stated, are all maximal, hence where opposite surfaces of the crown of a tooth taper inwards from the occlusal surface to the base, with wear there will be a decrease in the dimension between these surfaces. This is the case with the lengths of the incisors, P^4 and all the molars which will thus show slight decreases with wear; the breadths of these teeth are all greatest at or near the base and hence will be unaffected. The canine breadth and length are taken at the base of the crown and neither will be affected by attrition. Because the length of P3 is measured from the cusp tip (see below) this dimension will be slightly reduced by wear but the breadth is greatest at the base and hence will be unaffected. In P_4 the buccal and lingual surfaces are almost parallel giving no change of breadth with wear. The distal surface of this tooth tapers inwards towards the base of the crown but the mesial may either taper inwards or broaden outwards - the latter being common in the male. From the resulting shape, there are usually minor decreases in length with wear but, in the latter case, a slight increase is also possible. Because of the small amounts involved, and the normal amount of error inevitable in tooth measurement, the effects of wear on all of the above dimensions are likely to be very small and of little or no significance.

Molar heights have, however, not been recorded in this study as wear is very rapid on these teeth and it would be very difficult to attempt to group specimens to study this character. Also, lingual and buccal heights differ considerably. Incisor and canine heights have been included but, although wear on these teeth is not quite as rapid as on the molars, these figures are taxonomically of doubtful value. Tooth row measurements may be greater or less than the sum of the individual teeth due either to looseness of teeth in old specimens, the presence of small natural diastemata, or the fact that the adjoining teeth usually have reciprocally curved mesial and distal surfaces. In all measurements, it is the maximum figure consistent with the definition of the particular measurement that is aimed at but where a series of measurements of the same dimension is taken, the mean value must, of course, be recorded.

(i) Incisors.

Height : On the buccal surface from enamel line to incisal edge.

Breadth : Bucco-lingual measurement at the lingual enamel line height.

Length : Mesio-distal length at incisal edge.

(ii) Canines.

Height : On buccal surface from enamel line to tip.

Breadth : Bucco-lingual measurement at the lingual enamel line height.

Length : Upper (a) L_1 - Distal surface to mesio-lingual border.

(b) L_2 - Mesial surface to disto-lingual border.

Lower - Mesio-distal length.

(The canine 'lengths' were all measured at the height of the mesial alveolar margin except in some fossil species where isolated canines were

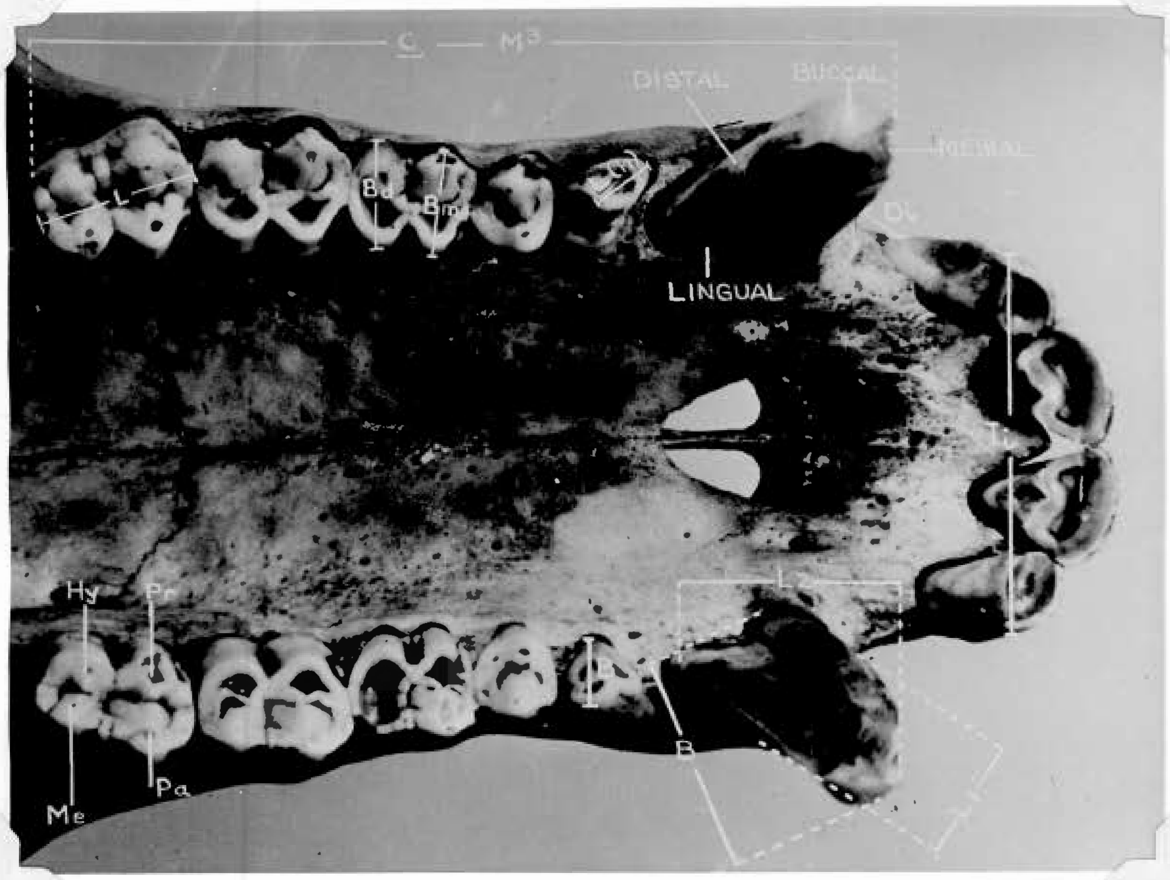

Fig.16. Occlusal view of male *Papio ursinus* upper teeth showing system of measurements and naming of cusps and surfaces. (For explanation, see Chapters 2 and 3).

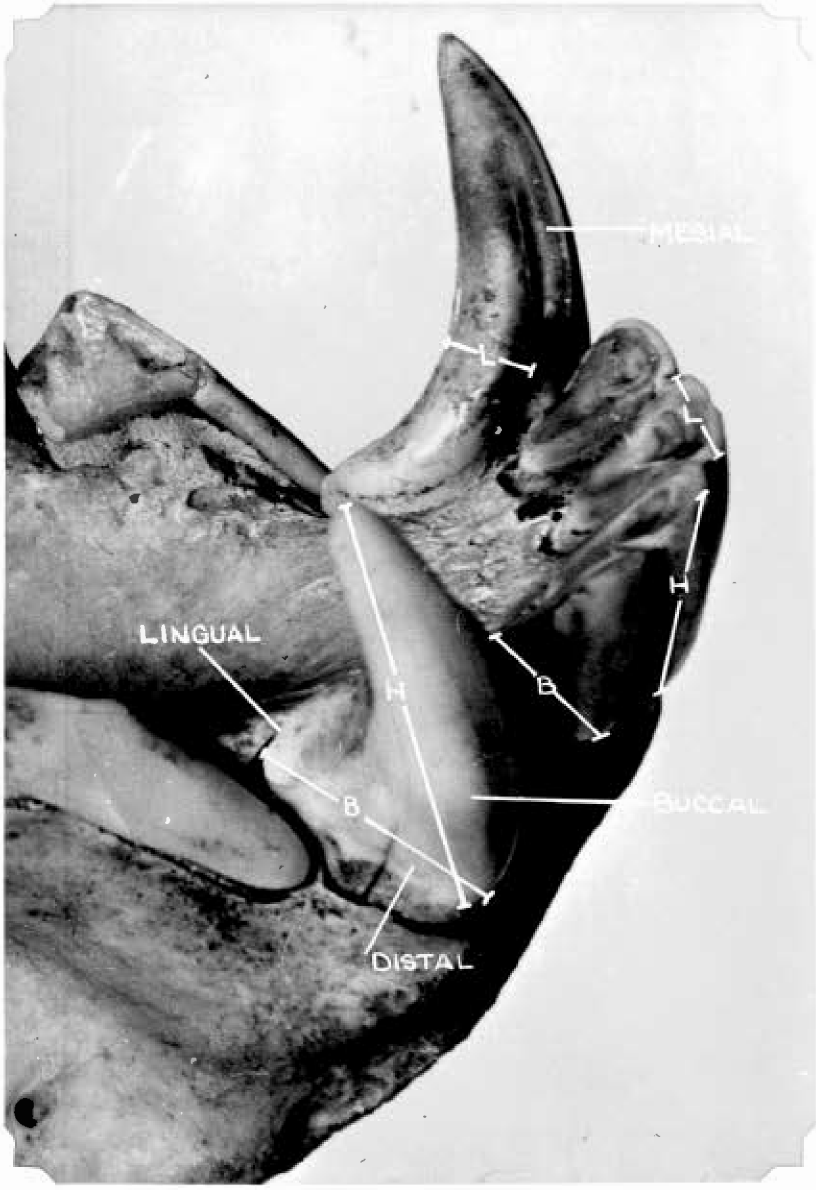

Fig.17. View of Papio ursinus male lower canines and incisors to show system of measurement and surfaces. (For explanation see Chapters 2 and 3).

measured at the mesial enamel line height. These two 'heights' are usually about coincident).

(iii) Premolar 3.

Breadth : Upper - Through buccal cusp.
Lower - Greatest bucco-lingual.

Length L(h) : Upper and lower - Diagonal measurement from most mesial point on enamel to tip of buccal cusp.

Angle : Lower (only) - Between the enamel line of the mesio-buccal surface and a line parallel to the occlusal plane meeting it at its most mesial point.

(iv) Premolar 4.

Breadth : Upper - Greatest bucco-lingual.
Lower - Through mesial cusps.

Length : Mesio-distal length.

(v) Molars.

Breadth : Through the following points:-

b_m Upper - Protocone and paracone.
Lower - Protoconid and metaconid.

b_d Upper - Hypocone and metacone.
Lower - Hypoconid and entoconid.

b_h Across hypoconulid. (This measurement is not one which can be taken accurately but it gives a useful indication of shape).

Length : Mesio-distal length. (In M3, this is up to distal surface; on other molars it is the effective occlusal surface).

(vi) Tooth rows.

P4 to M3 : Mesial surface of P4 to distal surface of M3.
C to M3 : Most anterior point of canine to distal surface of M3.

Incisor row : Between distal surfaces of lateral incisors (a) at incisal edge, (b) at enamel line.

(vii) Upper diastema.

From distal surface of I^2 to mesial of C at buccal enamel line heights.

CHAPTER 4.

STATISTICAL SUMMARY OF MEASUREMENTS.

In table 2 which follows, the means (M), the numbers of specimens involved (N), the standard deviations (σ) and the standard errors of the means (σ_M) of the various groups decided upon are given. In addition, for reasons which will be discussed later, the coefficient of variation was calculated for the total mature adult male group only. For the calculation of the standard deviation, (N -1) was used. The coefficient of variation (V) = $100\sigma/M$ (Simpson and Roe, 1939). In general, measurements of the skull are given to the nearest millimeter and of the teeth, to the nearest 0.1 mm. but there are several instances in the skull (the foramen magnum, orbit and nasal aperture) where an accuracy of 0.1 mm. has been recorded.

For the statistics calculated, the number of decimal places used has depended on the degree of accuracy of the primary measurements. Where the measurement was to the nearest millimeter, the mean was also taken to the nearest millimeter and the coefficient of variation to the nearest unit but the standard deviation and the standard error of the mean were taken to 0.1 mm. For measurements to 0.1 mm., the means were similarly taken to 0.1 mm. and the coefficient of variation to the nearest 0.1; the standard deviation and the standard error of the mean were taken to 0.01 mm. Where the digit after the number of decimal places stipulated above (in any category) is a five, it has been included; when the standard error of the mean is very small, it is given to two significant figures.

Mature adults, as applied to the tables, excludes both immature and very old forms. The latter have been excluded due to an unbalance between the numbers for Albany and the rest of South Africa. As the remaining age groups for these two areas are approximately equal, if these very old specimens are omitted, the composite statistics for both the Albany and the rest of South

Africa groups can be calculated and compared. The gaps in the primary tables are due to the specimens being very old (many date from 1895) and, in several cases, the teeth have been damaged or are missing and no measurement could be recorded. Where brackets are used, the measurement is doubtful due to minor damage. The sample used in this study includes forty-nine males and seven females.

Table 2. A statistical summary of certain cranial and dental measurements of *F. ursinus* (in mm.).

Group and total no. in group.	Statistic	Skull																
		General			Calvarium									Muzzle				
					Height		Breadth			Length		Foramen magnum		Height		Breadth		
		Greatest length	Basal length	Bizygomatic breadth	Basion-bregma	Basion-glabella	Min. inter-frontal	Greatest temporal	Mastoid	Inion-glabella	Inion-basion	Breadth	Length	Post. to M^3	Ant. to P^3	Ant. to M^3	Ant. to P^3	Dorsal to M^2
MALES																		
Immature adults. (6)	Mean	215	158.5	117	72	93	59	87	95	116	65.5	19.7	23.2	62	51	56	51	44
	Number	6	6	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	Std. dev.	12.4	11.3	4.5	1.5	4.8	2.6	2.9	4.0	4.1	2.0	0.77	1.66	5.4	4.1	3.4	2.8	1.3
	Std. error of mean.	5.1	4.6	2.0	0.60	2.0	1.0	1.2	1.6	1.7	0.81	0.32	0.68	2.2	1.7	1.4	1.1	0.53
Young adults. (13)	Mean	222	161	122	74	97	58	87	97	117	65	19.9	23.5	65	54	55	53	48
	Number	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
	Std. dev.	10.6	8.0	6.4	2.5	3.6	2.3	3.7	5.3	4.8	2.7	1.1	1.2	4.7	3.2	4.1	2.5	3.5
	Std. error of mean	2.9	2.2	1.8	0.69	1.0	0.65	1.0	1.5	1.3	0.75	0.30	0.32	1.3	0.88	1.1	0.69	0.98
Adults. (14)	Mean	229	167	127	74	99	59	87	97	117	66.5	19.8	23.1	64.5	54	57	54.5	49.5
	Number	14	14	12	10	14	14	14	14	14	14	14	14	14	14	14	14	14
	Std. dev.	9.9	8.6	6.2	1.95	4.4	3.6	3.3	5.4	4.9	2.6	1.05	1.39	4.1	2.3	2.8	2.6	3.4
	Std. error of mean.	2.6	2.3	1.8	0.62	1.2	0.96	0.88	1.4	1.3	0.71	0.28	0.37	1.1	0.62	0.76	0.70	0.92
Old Adults. (8)	Mean	229	166	127	72	97	59	87	100	118	67	19.6	22.5	65	54	58	54	48
	Number	8	8	7	7	8	8	8	8	8	8	7	7	8	8	8	8	8
	Std. dev.	10.8	8.8	3.5	2.2	3.7	2.3	2.2	3.4	3.8	3.0	0.82	1.61	5.1	3.8	2.1	1.2	2.1
	Std. error of mean.	3.8	3.1	1.3	0.83	1.3	0.81	0.79	1.3	1.4	1.1	0.31	0.61	1.8	1.4	0.76	0.44	0.73
Very old adults. (8)	Mean	229	166	125	72	97	58	86	96	120	67	20.0	23.6	65	54	57	56	51
	Number	8	8	7	3	8	8	8	8	8	8	6	6	8	8	8	8	8
	Std. dev.	6.3	6.4	4.6	1.5	1.6	1.0	2.2	4.6	4.2	2.8	0.50	1.72	2.8	2.3	2.5	2.5	3.2
	Std. error of mean	2.2	2.3	1.7	0.88	0.57	0.37	0.78	1.6	1.5	0.98	0.20	0.70	1.0	0.80	0.88	0.89	1.1
Mature adults: Albany. (18)	Mean	232	268	128	73	100	59	89	100	120	67	20.0	23.6	67	35	57	54	48.5
	Number	18	18	16	14	18	18	18	18	18	18	18	18	18	18	18	18	18
	Std. dev.	6.1	4.7	3.3	2.2	2.7	2.2	2.5	3.1	3.3	2.2	0.88	1.15	2.4	2.1	1.6	1.8	2.1
	Std. error of mean.	1.4	1.1	0.83	0.59	0.64	0.52	0.58	0.73	0.77	0.51	0.20	0.26	0.56	0.49	0.38	0.41	0.50
Mature adults: less Albany. (17)	Mean	221	161	121	73	95	59	65	95	115	65	19.6	22.5	62	33	56	53	49
	Number	17	17	16	16	17	17	17	17	17	17	16	16	17	17	17	17	17
	Std. dev.	11.6	10.3	6.6	2.4	6.7	3.3	2.7	4.9	4.4	2.6	1.10	1.37	4.9	3.5	4.4	2.8	4.1
	Std. error of mean.	2.8	2.5	1.7	0.61	1.6	0.83	0.65	1.2	1.1	0.63	0.28	0.34	1.2	0.84	1.1	0.67	1.0
Mature adults: total. (35)	Mean	226	164	125	73	98	59	87	98	117	66	19.8	23.0	65	54	56	54	49
	Number	35	35	32	30	35	35	35	35	35	35	34	34	35	35	35	35	35
	Std. dev.	10.5	8.7	6.2	2.2	5.5	2.9	3.2	5.0	4.5	2.7	1.00	1.35	4.5	2.9	3.3	2.5	3.2
	Std. error of mean.	1.8	1.5	1.1	0.41	0.93	0.49	0.53	0.84	0.76	0.45	0.17	0.23	0.76	0.48	0.55	0.43	0.54
	Coef. of var.	5	5	5	3	6	3	4	5	4	4	5.1	5.9	7	5.5	6	4	6.5
FEMALES																		
Mature adults: total. (7)	Mean	175	123	98	66	81	54	76	79	105	54	17.2	20.7	55	24	50	41	35
	Number	7	7	6	5	7	7	7	7	7	7	6	6	7	7	7	7	7
	Std. dev.	6.6	5.8	4.8	1.2	2.1	2.0	1.3	4.6	2.5	2.1	0.29	0.30	4.3	2.1	1.3	1.95	2.2
	Std. error of mean.	2.5	2.2	2.0	0.55	0.78	0.76	0.51	1.7	0.95	0.81	0.12	0.12	1.6	0.79	0.48	0.74	0.84
Type *F. rhodesiae.*	TM.4076	242	178	136	77	106	59	89	107	130	73	19.1	23.3	65	39	59	56	57

Skull cont.

Muzzle cont.

Mandible

		Length			Orbit				Nasal aperture		Height					Breadth					
		Muzzle	Palate	Nasal	Inter-orbital	Ext. orbital	Height	Breadth	Breadth	Length	Gonion-condyle	Gonion-coracoid	Post. to M_3	Ant. to P_4	Mental sp. to most ant. pt.	Bi-condylar	Bi-gonial	Post. to M_3	Ant. to M_3	Ant. to P_4	Through mental spine.
MALES																					
Im.	M	137	101	79	15.6	84.7	26.8	28.4	19.8	44.35	65	64.5	30.5	38.5	55.6	101	71	65	48	37	28
ad.	N	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	σ	9.5	7.2	8.1	2.44	3.46	1.47	0.75	1.51	2.13	7.0	5.4	3.3	2.6	4.7	2.1	3.0	1.9	1.8	2.9	1.7
	σ_M	3.9	3.0	3.3	1.10	1.56	0.60	0.31	0.62	0.87	2.9	2.2	1.4	1.1	1.9	0.86	1.2	0.78	0.73	1.2	0.69
Y.	M	143	107	84	14.3	88.9	26.6	28.8	22.1	46.7	63	66	31	38	56	108	74	61	48	37	29
ad.	N	15	15	15	15	15	15	15	15	15	15	15	13	13	13	12	12	12	12	12	12
	σ	9.7	6.1	5.1	1.22	5.17	1.71	0.92	1.91	4.47	4.0	3.25	2.3	2.6	3.45	4.6	5.7	3.7	3.2	1.5	3.8
	σ_M	2.7	1.7	1.4	0.34	1.43	0.47	0.26	0.53	1.24	1.1	0.90	0.64	0.78	1.0	1.3	1.7	1.1	0.92	0.43	1.1
Ad.	M	149	112	86	15.2	92.9	26.0	28.9	23.2	47.4	67	68	32.5	40	58	106	75	60	48	39	31
	N	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14
	σ	8.6	6.9	7.3	1.42	3.75	2.19	1.15	2.87	3.69	3.4	3.6	1.6	2.3	3.4	4.6	6.6	5.5	3.0	2.2	2.4
	σ_M	2.3	1.9	2.0	0.37	1.00	0.59	0.31	0.77	0.99	0.92	0.96	0.42	0.62	0.91	1.2	1.8	1.5	0.80	0.59	0.65
Old	M	149	113	86	15.0	94.1	25.8	28.9	23.7	48.2	66.5	68	32.	39.5	59.5	108	75	61	49	39	31
ad.	N	8	8	7	8	7	8	8	7	7	8	8	8	8	8	7	8	8	8	8	8
	σ	11.5	7.9	6.1	1.65	4.06	2.22	0.72	1.09	3.21	2.3	2.0	2.5	2.7	3.7	3.9	4.5	3.1	1.9	1.6	2.5
	σ_M	4.1	2.8	2.3	0.58	1.53	0.79	0.25	0.41	1.21	0.81	0.71	0.88	0.95	1.3	1.5	1.6	1.1	0.68	0.56	0.89
V.o.	M	146	114	84	14.4	93.1	25.7	29.3	25.9	47.0	68	71	33	39.5	57	102	73	61	49	38	31
ad.	N	8	8	8	8	8	8	8	8	8	8	8	8	8	6	7	7	8	8	7	7
	σ	5.3	1.3	5.4	1.20	4.66	1.87	0.75	2.57	2.01	3.4	3.8	1.3	3.5	3.0	3.7	5.0	3.8	1.58	1.7	2.0
	σ_M	1.9	0.45	1.9	0.42	1.65	0.66	0.27	0.91	0.71	1.2	1.3	0.46	1.25	1.2	1.4	1.9	1.3	0.55	0.61	0.77
Ma.	M	152	114	88	14.9	92.9	26.8	29.0	23.1	49.4	55	67.5	32	39.5	56	108	75	65	49	38	31
ad:	N	18	18	18	18	18	18	18	18	18	18	18	18	18	18	16	17	17	17	17	17
Alb.	σ	6.0	4.1	3.6	0.75	3.85	1.92	0.78	1.52	2.87	4.4	5.1	1.9	1.88	3.7	2.9	5.1	3.5	2.5	1.3	2.6
	σ_M	1.4	0.96	0.84	0.18	0.91	0.45	0.18	0.36	0.68	1.0	0.75	0.45	0.44	0.88	0.72	1.25	0.86	0.61	0.31	0.64
Ma.	M	141	107	81	14.7	90.2	25.5	28.7	22.7	44.9	65	67	31	39	57	102	73	59	48	36	30
ad:	N	17	17	16	17	16	17	17	16	16	17	17	17	17	17	17	17	17	17	17	17
less	σ	9.9	7.7	6.5	1.92	6.46	1.93	1.11	2.95	3.46	3.4	3.6	3.5	3.4	4.2	5.1	6.2	4.5	3.1	2.6	3.6
Alb.	σ_M	2.4	1.9	1.6	0.47	1.57	0.47	0.27	0.74	0.87	0.82	0.86	0.85	0.82	1.0	1.2	1.5	1.05	0.76	0.63	0.87
Ma.	M	147	110	85	14.8	91.6	26.2	28.8	22.9	47.3	65	67	32	39	57	105	74	61	48	38	30.5
ad:	N	35	35	34	35	34	35	35	34	34	35	35	35	35	35	33	34	34	34	34	34
tot.	σ	9.8	7.1	6.1	1.41	4.80	2.00	0.95	2.28	3.88	3.9	3.2	2.7	2.65	3.7	4.4	5.7	4.4	2.8	2.0	3.1
	σ_M	1.65	1.2	1.0	0.24	0.82	0.34	0.16	0.39	0.66	0.66	0.54	0.46	0.45	0.62	0.74	0.98	0.75	0.48	0.34	0.53
	V	7	6.5	7	9.5	5.2	7.6	3.3	10.0	8.1	6	5	8	7	6.5	4	8	7	6	5	10
FEMALES																					
Ma.	M	104	80	56	10.2	74.1	25.0	26.6	19.4	32.3	57	59	27	28	39	86	57	55	44	31	22
ad:	N	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
tot.	σ	4.5	4.75	3.95	0.88	2.51	1.48	0.75	1.48	2.75	5.8	5.9	2.2	3.4	5.3	2.7	3.2	1.8	1.3	1.4	1.6
	σ_M	1.7	1.8	1.5	0.33	0.69	0.56	0.28	0.56	1.04	2.2	2.2	0.83	1.3	2.0	1.0	1.2	0.68	0.49	0.53	0.60
P. rhod.		138	112	72	30.0	109.6	19.5	30.9	27.7	45.6	73	78	37	47	72	115	86	64	55	39	31

Mandible cont.

Teeth.

Upper

		Breadth cont.	Length			Angles			I^1			I^2			C				P3	
		At base of canines.	Gonion to mental sp.	Ramus at condyle neck.	Condyle to most ant. pt.	Of ramus to corpus.	At symphysis.	Between corpora.	h	b	l	h	b	l	h	b	l_1	l_2	b	l(h)
MALES																				
Im. ad.	M	31	81	48	156	132°	106°	43°	16.6	10.1	10.65	16.0	8.5	7.65	-	-	-	-	8.1	9.8
	N	6	6	6	6	6	6	6	6	6	4	6	6	6	1	1	1	1	5	4
	σ	3.4	3.8	3.7	2.7	3.9	2.3	2.5	1.63	0.61	1.02	1.18	0.13	0.57					0.40	0.88
	σ_m	1.4	1.6	1.5	1.1	1.6	0.95	1.0	0.66	0.25	0.51	0.48	0.053	0.23					0.18	0.44
Y. ad.	M	33	84	43	164	131°	107°	43°	15.2	9.7	10.6	14.2	8.5	7.8	47.5	10.7	10.5	13.3	7.9	9.9
	N	11	13	13	13	13	12	12	10	12	9	11	11	10	11	11	11	11	12	12
	σ	2.0	6.9	2.5	8.8	5.7	4.2	3.7	0.94	0.25	0.53	0.99	0.33	0.67	2.91	1.37	0.63	1.05	0.48	0.84
	σ_m	0.60	1.9	0.69	2.4	1.6	1.2	1.1	0.30	0.072	0.18	0.30	0.10	0.26	0.88	0.41	0.19	0.30	0.14	0.24
Ad.	M	34	87	45	169	133°	106°	41°	13.5	9.8	10.6	13.9	8.5	7.4	48.4	11.4	10.7	13.0	7.9	9.9
	N	14	14	14	14	14	14	14	11	11	8	10	11	8	13	13	13	13	11	17
	σ	1.8	6.6	2.7	8.2	2.5	7.7	4.4	1.01	0.45	0.71	1.38	0.45	0.41	5.39	0.63	0.67	1.00	0.36	1.23
	σ_m	0.48	1.8	0.72	2.2	0.67	2.1	1.2	0.30	0.14	0.25	0.44	0.14	0.14	1.49	0.17	0.19	0.28	0.11	0.34
Old ad.	M	34	87	44	169	132.5°	106°	41°	11.9	9.5	10.3	12.2	8.5	7.5	38.5	11.8	10.9	12.75	7.7	9.1
	N	8	8	8	8	8	8	8	8	8	8	7	7	7	8	8	8	8	6	7
	σ	2.9	6.0	2.7	9.1	4.6	3.2	4.8	1.82	0.28	0.57	0.87	0.22	0.82	5.85	1.24	0.99	1.19	0.32	0.88
	σ_m	1.0	2.1	0.96	3.2	1.6	1.1	1.7	0.64	0.10	0.20	0.33	0.08	0.31	1.60	0.44	0.35	0.42	0.13	0.33
V. o. ad.	M	32	87	43	169	130°	111°	40°	13.45	10.1	10.3	10.6	8.4	7.3	38.0	12.45	11.3	12.9	7.8	8.4
	N	6	8	8	6	8	7	8	4	6	5	6	8	7	5	8	8	8	7	7
	σ	2.3	4.6	1.1	3.7	4.2	14.1	3.4	4.21	0.79	0.66	4.01	0.58	0.76	6.95	1.44	1.06	1.86	0.73	1.56
	σ_m	0.96	1.6	0.40	1.5	1.5	5.3	1.2	2.11	0.32	0.27	1.64	0.21	0.29	3.11	0.51	0.37	0.66	0.28	0.59
Ma. ad. Alb.	M	34	89	45	171	132°	105°	41°	13.4	9.7	10.5	13.6	8.4	7.6	48.9	11.3	10.8	13.3	7.8	9.3
	N	17	10	18	18	18	17	17	16	17	14	16	17	13	18	18	18	18	14	17
	σ	1.8	5.0	1.9	5.08	3.1	4.05	3.65	1.88	0.75	0.53	1.48	0.36	0.61	6.57	1.27	0.74	0.99	0.45	0.83
	σ_m	0.44	1.2	0.44	1.2	0.74	0.98	0.88	0.47	0.18	0.14	0.37	0.087	0.16	1.55	0.30	0.17	0.23	0.12	0.20
Ma. Ad: less Alb.	M	35	85	44	162	133°	108°	42°	13.9	9.7	10.5	13.5	8.5	7.8	45.5	11.3	10.4	12.7	8.0	10.3
	N	16	17	17	17	17	17	17	13	14	11	12	12	10	14	14	14	14	15	15
	σ	2.8	6.8	3.3	9.5	5.2	6.6	4.9	1.75	0.46	0.71	2.01	0.39	1.29	4.84	1.005	0.70	1.06	0.37	1.08
	σ_m	0.62	1.6	0.80	2.3	1.3	1.6	1.2	0.49	0.12	0.21	0.58	0.11	0.41	1.29	0.27	0.19	0.28	0.095	0.27
Ma. ad. tot.	M	34	86	44	167	132°	106°	41°	13.6	9.7	10.5	13.5	8.4	7.5	45.2	11.25	10.6	13.0	7.9	9.7
	N	33	35	35	35	35	34	34	29	31	25	28	29	23	32	32	32	32	29	32
	σ	2.2	6.6	2.7	8.8	4.5	5.6	4.2	1.81	0.35	0.60	1.70	0.36	0.92	5.80	1.14	0.74	1.04	0.41	1.05
	σ_m	0.38	1.1	0.46	1.5	0.75	0.96	0.72	0.34	0.062	0.12	0.32	0.066	.18	1.02	0.20	0.13	0.18	0.076	0.19
	V	6.5	8	6	5	3	5	10	13.3	3.6	5.7	12.6	4.3	12.3	13.4	10.1	7.0	8.0	5.2	10.8
FEMALES																				
Ma. Ad. tot.	M	27	71	34	126	121°	127°	39°	10.1	8.6	9.4	9.3	7.35	6.5	12.4	7.5	6.4	6.6	6.9	7.3
	N	7	7	7	7	7	7	7	6	6	5	6	6	5	5	6	6	6	7	7
	σ	1.3	9.4	0.79	5.6	6.5	9.2	3.3	2.50	0.44	0.59	1.63	0.24	0.74	4.08	0.56	0.45	0.80	0.68	1.43
	σ_m	0.49	3.6	0.30	2.1	2.4	3.5	1.2	1.02	0.18	0.26	0.67	.097	0.33	1.82	0.23	0.18	0.33	0.26	0.54
P.rhod.		40	68	51	178	139°	104°	44°	-	-	-	16.7	8.6	-	31.0	11.9	11.4	13.3	8.0	8.9

Teeth cont.

Upper cont.

		P^4		M^1			M^2			M^3			Rows					Lower I_1		
		b	l	bm	bd	l	bm	bd	l	bm	bd	l	P^4-M^3	$\underline{C}$ - M^3	I. row (a)	I. row (b)	Diastema.	h	b	l
MALES																				
Im. ad.	M	9.0	8.7	10.0	9.5	12.0	11.9	11.4	14.65	12.4	11.2	15.1	49.0	71.9	30.35	33.9	7.5	15.5	9.4	8.1
	N	6	6	6	5	6	6	6	6	6	6	6	6	3	6	6	3	4	5	4
	σ	0.29	0.43	0.35	0.22	0.33	0.36	0.26	0.80	0.30	0.44	0.58	1.42	2.75	1.31	1.31	2.20	2.20	0.45	0.26
	σ_m	0.12	0.18	0.15	0.10	0.13	0.15	0.12	0.33	0.12	0.18	0.24	0.58	1.59	0.53	0.53	1.27	1.10	0.20	0.13
Y. ad.	M	9.1	8.5	10.4	9.8	11.9	12.3	11.4	14.4	12.9	11.2	14.8	48.9	75.7	32.0	35.9	9.9	14.2	9.2	8.2
	N	12	13	13	11	13	12	13	13	13	13	13	13	11	7	8	11	11	11	11
	σ	0.45	0.37	0.36	0.31	0.48	0.40	0.35	0.59	0.36	0.30	0.70	1.80	3.01	0.81	0.72	1.14	1.04	0.37	0.47
	σ_m	0.13	0.10	0.10	0.093	0.13	0.12	0.097	0.16	0.10	0.083	0.19	0.50	0.91	0.31	0.25	0.34	0.31	0.11	0.14
Ad.	M	9.0	8.2	10.8	9.7	11.55	12.8	11.4	14.2	12.6	11.3	14.7	48.1	75.8	32.5	36.0	10.7	12.2	9.4	7.9
	N	14	14	14	12	14	14	11	14	14	15	14	14	13	6	9	11	13	13	13
	σ	0.52	0.43	0.52	0.33	0.33	0.52	0.44	0.70	0.65	0.67	0.82	2.23	3.87	1.82	1.86	2.59	2.09	0.44	0.41
	σ_m	0.14	0.11	0.14	0.095	0.088	0.14	0.13	0.19	0.17	0.19	0.22	0.60	1.07	0.74	0.62	0.78	0.58	0.12	0.11
Old ad.	M	9.15	8.3	10.3	9.9	11.5	12.3	11.4	14.0	13.0	11.5	15.0	48.5	74.9	32.3	35.9	12.6	10.5	9.0	7.7
	N	8	8	8	5	8	8	5	8	8	8	8	8	8	5	5	7	7	7	7
	σ	0.35	0.54	0.40	0.31	0.25	0.48	0.23	0.80	0.62	0.63	0.59	1.91	3.08	0.99	0.94	1.39	1.79	0.28	0.35
	σ_m	0.12	0.19	0.14	0.14	0.088	0.17	0.10	0.28	0.22	0.22	0.21	0.68	1.09	0.44	0.42	0.53	0.68	0.105	0.13
V.o. ad.	M	9.1	8.4	10.3	9.8	11.3	12.8	11.9	14.2	13.2	11.6	14.7	47.3	75.6	30.2	34.8	10.2	7.2	8.9	7.1
	N	7	7	7	6	7	8	7	7	8	8	7	7	7	3	4	5	5	6	6
	σ	0.48	0.48	0.60	0.65	0.56	0.93	0.52	0.57	0.76	0.97	0.50	2.61	3.31	3.66	1.10	1.73	3.68	0.86	0.92
	σ_m	0.18	0.18	0.23	0.27	0.21	0.33	0.20	0.22	0.27	0.34	0.19	0.99	1.25	2.11	0.55	0.77	1.65	0.35	0.38
Ma. ad: Alb.	M	9.2	8.5	10.4	9.8	11.8	12.3	11.4	14.3	12.9	11.4	15.0	49.2	77.2	32.2	35.7	11.2	11.8	9.3	8.0
	N	17	18	18	13	18	16	16	18	18	18	18	18	18	11	13	17	18	18	18
	σ	0.36	0.40	0.30	0.27	0.49	0.37	0.35	0.59	0.47	0.58	0.54	1.30	1.82	0.90	1.20	1.98	2.42	0.37	0.40
	σ_m	0.087	0.094	0.071	0.075	0.12	0.087	0.088	0.14	0.11	0.14	0.13	0.30	0.43	0.27	0.33	0.48	0.57	0.087	0.094
Ma. ad: less Alb.	M	9.0	8.1	10.2	9.7	11.5	12.1	11.4	14.1	12.8	11.2	14.6	47.6	73.4	32.1	36.3	10.3	13.3	9.2	8.0
	N	17	17	17	15	17	16	13	17	17	16	17	17	14	7	9	12	13	13	13
	σ	0.52	0.45	0.52	0.35	0.44	0.51	0.39	0.78	0.64	0.49	0.82	2.33	3.60	1.67	1.39	2.31	1.66	0.46	0.54
	σ_m	0.13	0.17	0.13	0.090	0.11	0.058	0.11	0.19	0.16	0.12	0.20	0.57	0.96	0.63	0.46	0.66	0.46	0.13	0.15
Ma. ad: Tot.	M	9.1	8.3	10.3	9.75	11.6	12.25	11.4	14.2	12.8	11.3	14.8	48.5	75.5	32.2	35.9	10.8	12.5	9.2	8.0
	N	34	35	35	28	35	34	29	35	35	34	35	35	32	18	22	29	31	31	31
	σ	0.45	0.45	0.43	0.32	0.48	0.46	0.37	0.69	0.55	0.54	0.71	1.99	3.31	1.21	1.28	2.13	2.23	0.40	0.45
	σ_m	0.077	0.076	0.072	0.060	0.081	0.078	0.068	0.12	0.092	0.092	0.12	0.34	0.59	0.29	0.27	0.40	0.40	0.071	0.080
	V	4.9	5.4	4.2	3.3	4.1	3.8	3.2	4.9	4.3	4.8	4.8	4.1	4.4	3.7	3.6	19.7	17.8	4.3	5.6
FEMALES																				
Ma. Ad: tot.	M	8.2	7.5	9.6	8.9	10.5	11.1	10.3	12.7	11.6	9.6	13.0	42.1	69.7	27.4	29.6	5.6	9.4	8.3	6.7
	N	6	6	6	5	6	7	7	7	7	7	7	6	6	5	6	5	5	5	5
	σ	0.24	0.24	0.37	0.39	0.32	0.48	0.56	0.52	0.65	0.74	0.71	1.29	1.79	2.78	1.87	1.30	2.63	0.70	0.78
	σ_m	0.10	0.10	0.15	0.17	0.13	0.18	0.21	0.20	0.25	0.28	0.27	0.53	0.73	1.24	0.76	0.58	1.18	0.31	0.35
P. rhod.		9.2	8.1	10.2	9.6	11.5	12.8	12.0	13.5	13.8	11.9	14.6	45.6	72.3	-	-	21.0	13.7	10.0	7.8

Teeth cont.

Lower cont.

		I_2			$\overline{C}$			P_3			P_4		M_1			M_2			M_3			
		H	b	l	h	b	l	b	l(h)	angle	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
MALES																						
Im. ad.	M	14.9	8.45	7.4	31.7	14.3	7.5	6.4	26.7	43°	7.6	9.7	8.3	8.9	11.6	10.8	10.3	13.9	11.6	10.6	7.5	17.3
	N	4	4	4	6	6	6	6	6	6	4	4	3	4	5	6	6	6	6	6	4	5
	σ	0.99	0.17	0.57	1.03	0.93	0.39	0.70	1.66	9.7	0.22	0.35	0.30	0.22	0.35	0.24	0.24	0.62	0.25	0.21	0.77	0.65
	σ_m	0.50	0.085	0.285	0.42	0.38	0.16	0.29	0.68	4.0	0.11	0.17	0.18	0.11	0.15	0.10	0.10	0.25	0.10	0.086	0.39	0.29
Y. ad.	M	13.2	8.4	7.5	31.2	13.7	7.5	6.5	26.5	40°	7.6	9.7	8.7	8.9	11.5	11.0	10.4	13.9	11.7	10.5	7.1	17.2
	N	10	10	10	12	13	13	13	13	13	10	13	7	10	13	12	12	13	13	13	13	13
	σ	0.89	0.47	0.67	1.84	0.71	0.51	0.12	1.79	7.5	2.37	0.49	0.17	0.22	0.42	0.48	0.45	0.50	0.40	0.26	0.89	0.63
	σ_m	0.28	0.15	0.21	0.53	0.20	0.14	0.033	0.50	2.1	0.75	0.14	0.064	0.070	0.12	0.14	0.13	0.14	0.11	0.072	0.25	0.17
Ad.	M	12.2	8.4	7.05	29.8	14.1	7.6	6.6	26.4	39°	7.4	9.6	8.6	9.2	11.2	11.0	10.6	13.8	11.6	10.7	7.0	17.5
	N	13	14	14	14	14	14	14	14	14	12	14	8	5	14	10	13	14	14	14	14	14
	σ	1.58	0.42	0.45	2.67	0.85	0.52	0.45	2.55	6.6	0.36	0.71	0.44	0.30	0.52	0.62	0.47	0.77	0.54	0.59	0.75	0.96
	σ_m	0.44	0.11	0.12	0.71	0.23	0.14	0.12	0.68	1.8	0.10	0.19	0.16	0.13	0.14	0.20	0.13	0.21	0.14	0.16	0.20	0.26
Old ad.	M	10.3	8.3	6.6	29.0	14.1	7.6	6.3	25.6	35°	7.4	9.8	8.7	9.0	11.8	11.0	10.5	13.8	11.9	10.7	7.4	17.5
	N	7	7	7	8	8	8	8	8	8	8	8	7	7	8	7	5	8	7	8	8	8
	σ	1.15	0.44	0.48	4.80	0.79	0.26	0.59	1.60	9.4	0.19	0.65	0.28	0.41	0.36	0.45	0.24	0.82	0.51	0.44	0.59	0.64
	σ_m	0.43	0.17	0.18	1.70	0.28	0.091	0.21	0.56	3.3	0.067	0.23	0.11	0.15	0.13	0.17	0.11	0.29	0.19	0.16	0.21	0.23
V.o. Ad.	M	8.3	8.6	6.3	27.6	14.4	8.1	6.7	25.9	36°	7.6	9.9	8.8	9.1	10.9	11.75	10.8	14.1	12.5	10.9	7.8	18.0
	N	5	6	6	3	5	5	7	7	7	5	5	4	4	6	4	5	7	7	6	4	6
	σ	3.80	0.73	0.88	2.17	1.42	0.56	0.52	2.91	7.9	0.35	0.19	0.50	0.46	0.75	0.76	0.53	0.64	0.46	0.35	0.52	0.62
	σ_m	1.70	0.30	0.36	1.25	0.64	0.25	0.20	1.10	3.0	0.16	0.08	0.25	0.23	0.31	0.38	0.24	0.24	0.17	0.14	0.26	0.25
Ma. ad: Alb.	M	11.5	8.4	7.0	30.8	14.0	7.5	6.4	26.8	38°	7.5	10.0	8.7	9.0	11.6	11.1	10.8	14.0	11.8	10.7	7.1	17.5
	N	17	17	17	18	18	18	18	18	18	16	18	13	11	18	13	16	18	17	18	18	18
	σ	1.39	0.35	0.60	3.38	0.67	0.30	0.29	1.56	6.2	0.24	0.31	0.26	0.30	0.33	0.37	0.42	0.53	0.39	0.34	0.84	0.65
	σ_m	0.34	0.085	0.15	0.80	0.16	0.070	0.068	0.37	1.5	0.060	0.073	0.072	0.090	0.077	0.10	0.105	0.12	0.094	0.080	0.20	0.15
Ma. ad: less Alb.	M	12.8	8.4	7.0	29.3	13.9	7.6	6.6	25.9	42°	7.4	9.3	8.5	9.0	11.0	10.9	10.5	13.6	11.6	10.5	7.2	17.3
	N	13	14	14	16	17	17	17	17	17	14	17	9	11	17	16	14	17	17	17	17	17
	σ	1.76	0.52	0.57	2.65	0.92	0.58	0.42	2.47	7.3	0.32	0.60	0.36	0.35	0.43	0.57	0.47	0.77	0.55	0.56	0.70	0.91
	σ_m	0.49	0.14	0.15	0.66	0.22	0.14	0.10	0.60	1.8	0.85	0.15	0.12	0.11	0.10	0.14	0.13	0.19	0.13	0.14	0.16	0.22
Ma. ad: tot.	M	12.1	8.4	7.0	30.1	14.0	7.6	6.5	26.4	39°	7.5	9.7	8.7	9.0	11.5	11.0	10.5	13.8	11.7	10.6	7.1	17.3
	N	30	31	31	34	35	35	35	35	35	30	35	22	22	35	29	30	35	34	35	35	35
	σ	1.65	0.43	0.56	3.10	0.79	0.46	0.47	2.08	7.6	0.28	0.62	0.32	0.32	0.46	0.50	0.44	0.67	0.48	0.46	0.77	0.76
	σ_m	0.30	0.077	0.10	0.53	0.13	0.077	0.079	0.35	1.3	0.051	0.10	0.068	0.68	0.077	0.092	0.080	0.11	0.082	0.077	0.13	0.13
	V	13.6	5.1	8.3	10.3	5.6	6.1	7.2	7.9	19.5	3.7	6.4	3.7	3.6	4.1	4.5	4.2	4.9	4.1	4.3	10.8	4.4
FEMALES																						
Ma. ad. Tot.	M	8.3	7.6	5.5	11.2	8.5	5.0	4.8	10.8	41°	6.6	8.3	7.7	7.8	10.25	9.6	9.2	12.3	10.6	9.5	7.0	15.7
	N	5	5	5	6	6	6	7	7	7	4	5	4	3	6	6	7	7	7	7	7	7
	σ	2.18	0.46	1.06	2.89	0.66	0.26	0.22	2.13	7.0	0.40	0.33	0.64	0.61	0.22	0.45	0.60	0.42	0.61	0.95	0.68	0.70
	σ_m	0.97	0.20	0.47	1.18	0.27	0.10	0.083	0.80	2.6	0.20	0.15	0.32	0.35	0.089	0.18	0.23	0.16	0.23	0.36	0.26	0.26
<u>P.rhod.</u>		17.0	9.6	8.2	30.3	15.1	8.4	6.0	27.3	35°	7.0	8.6	8.5	8.7	11.0	10.8	10.9	15.1	12.8	11.0	8.0	18.4

Teeth cont.

Lower cont.

Rows

		$P_4 - M_3$	$\bar{C} - M_3$	I row (a)	I row (b)
MALES					
Im.	M	52.7	83.2	25.7	25.4
ad.	N	4	6	4	4
	σ	2.42	3.10	0.75	1.49
	σ_M	1.21	1.26	0.37	0.75
Y.	M	52.6	85.2	26.3	25.4
ad.	N	13	13	7	10
	σ	1.55	3.94	1.22	1.89
	σ_M	0.43	1.09	0.46	0.60
Ad.	M	52.2	85.9	26.2	25.6
	N	14	14	12	14
	σ	2.68	5.01	1.56	1.48
	σ_M	0.72	1.34	0.45	0.40
Old	M	52.6	86.8	25.3	25.9
ad.	N	8	8	7	7
	σ	1.93	3.24	0.30	0.91
	σ_M	0.68	1.14	0.11	0.34
V. o.	M	52.0	88.6	-	-
ad.	N	7	5	0	1
	σ	2.55	3.38	-	-
	σ_m	0.96	1.51	-	-
Ma.	M	53.2	88.3	25.9	26.0
ad:	N	18	18	15	17
Alb.	σ	1.46	2.09	0.96	1.37
	σ_m	0.34	0.49	0.25	0.33
Ma.	M	51.6	83.2	26.0	25.1
ad:	N	17	17	11	14
less	σ	2.41	4.32	1.81	1.55
Alb.	σ_m	0.58	1.05	0.55	0.41
Ma.	M	52.4	85.9	26.0	25.6
Ad:	N	35	35	26	31
tot	σ	2.10	4.19	1.35	1.49
	σ_M	0.35	0.71	0.26	0.27
	V	4.0	4.9	5.2	5.8
FEMALES					
Ma.	M	46.3	64.2	21.6	21.4
Ad:	N	6	6	5	5
tot.	σ	1.56	1.82	1.61	1.19
	σ_m	0.64	0.74	0.72	0.53
P. rhod.		52.6	84.5	26.5	29.4

CHAPTER 5.

CONCLUSIONS.

Several interesting points emerge from the statistics given in the previous chapter (table 2). The method of using and interpreting these figures also requires some discussion.

Bronowski and Long (1951) have suggested that, in work of this sort, multivariate analysis is necessary for the examination of quantitative differences. However, Yates and Healy (1951) have shown that affinities and differences do show up by comparing individual measurements. Further, they go on to point out that, when a specimen belongs to neither of two groups with which it is compared, the discriminant functions used may erroneously refer it to one or other of the groups. Never-the-less, these authors accept the value of discriminant functions in certain aspects of comparative anatomy but conclude that the large amount of calculation involved and the difficulties with incomplete data (particularly applicable to fossil studies) make it a technique which, at present, can not be generally applied. In this study, multivariate analysis has not been attempted but, where necessary, 'Student's' t test has been applied for comparing variance. Tooth row measurements have also been used which may show up cumulative differences but, alternatively, may have a negative effect by cancelling out reciprocal differences.

Growth changes in the skull of *P. ursinus* have been discussed by Zuckerman (1926) and consequently, this aspect has only been touched on here. Huxley (1932), working on Zuckerman's figures for juvenile, adult female and adult male skulls has derived a growth-coefficient of face-length on cranium length for *P.ursinus* of about 4.25. This is a very high value and the curve shows irregularities at both ends. However, figures for *P. ursinus* calculated from this study fall exactly on Huxley's curve and confirm both the high value and irregularities.

After the last teeth have fully erupted and come into use, an animal is generally taken to be fully adult. Gear (1926) noted that, in P. ursinus, there was subsequent growth of the muzzle. The statistics for males in this study confirms this and shows that it may be of sufficient magnitude to be of taxonomic importance. This late growth takes place only to a slight extent in the skull as a whole but is quite considerable in the muzzle region. It consists primarily of an elongation of the snout, mostly anterior to the nasal bones, but the breadth of the muzzle also shows increases. The male calvarium is very nearly at its maximum even before the teeth have fully erupted except that the nuchal crest, external occipital protuberance and mastoid regions become larger. The orbit and nasal aperture reflect the late growth of the muzzle as does the mandible; the foramen magnum confirms the early completion of growth in the calvarium. There are not a sufficient number of figures available for females to decide whether they show similar late growth.

The sexual dimorphism in the skull and teeth of this species can be assessed quantitatively from the statistics. The size differences between the sexes are seen to be so great, and to vary so much from one character to another, that it would be valueless to calculate composite figures of each character for the two sexes. Comparing the two sexes, and using mean values, the greatest length of the female skull was found to be 78% of that of the male but the lengths of the female muzzle and palate were found to be only about 71% of the equivalent lengths in the male. The orbits of both sexes are almost equal in size, the female dimensions being about 94% of those of the male. Numerous similar ratios between the various skull dimensions of the two sexes were also calculated from mean values. These were found to vary from 70% to 90%. Using the figures quoted above from Goldblatt (1926), it is interesting to note that the female brain volume appears to be about 83% of that of the male. In the mandible, a comparison of mean figures shows that the angles of the ramus to the corpus and at the symphysis are centered around different means in the two sexes, but the angle between the corpora is about the same in both sexes.

In the teeth, the sexual dimorphism is again strongly evident, the canines being a very obvious and extreme example. In the molars, there is a remarkably constant relationship between the sizes of the male and female teeth. Should such a constant relationship be a general rule in the group and hold for individuals, it may be of value in deciding whether a difference between two specimens or groups of specimens, is due to sex or their being different species. Using the mean measurements, the following were the percentages obtained in comparing the lengths and breadths of the individual female molars to their male equivalents in P. ursinus:

Molar length.

upper teeth :- 88-90.5
lower teeth :- 89-90.75
mean % :- 89.5

Molar breadth.

upper teeth :- 88-92.5
lower teeth :- 87.5-92
mean % :- 90

The relationship between the sexes, of the teeth anterior to the molars, can be deduced from a similar comparison of the figures for the tooth rows in males and females. The figures are again percentages of female over male lengths:

P4-M3 length.

upper row :- 86.8
lower row :- 88.4
mean % :- 87.6

C-M3 length.

upper row :- 79.0
lower row :- 74.7
mean % :- 76.8

These figures include the molars (for which the mean percentage was 89.5) and the slight reduction to 87.6% for P4 - M3 is probably mainly due to the error involved in the reciprocally curved mesial and distal adjoining tooth surfaces already mentioned. The reduction to 76.8% for C-M3 is however clearly significant and would appear to be due to the much smaller female canines. The ~~slightly~~ greater reduction of the figure for $\overline{C} - M_3$ is due to the relatively much smaller P_3 of the female which is only 41% of its length in the male. Also based on mean values, the length of the female incisor row was calculated to be about 83.5% of that of the male. It would thus appear that, because the female does not require large canines for fighting, these teeth have not become as greatly developed as in the male. The essential grinding and biting teeth - the premolars (except P_3 which functions with the $\underline{C}$), the molars and the incisors - are, however, well developed and, in fact, larger relative to the overall skull size than would be expected.

The tooth measurements in general merit still further consideration but from a different point of view. Working again off the mean figures, both in the upper and lower jaws of the males and females, the molars show a progressive increase in length from M1 to M3. Except for M_1, (where there is a reversal in both sexes) all the molars have a greater mesial than distal breadth. The mesial breadth itself, increases from M1 to M3 in each jaw: M2 and M3 vary slightly as to which is broader in distal breadth but both are broader than M1. In the premolar-molar series, in both sexes, the equivalent tooth breadths are all greater in the upper jaw: in length, P_3, P_4, and M_3 are greater than their upper equivalents but M^1 and M^2 are longer than their lower opposites. Both P4 - M3 and C - M3 are greater in the lower jaw. These relationships have been summarised in table 3. As stated, all these statements are based on mean values and, when applied to individual specimens, in many cases show exceptions. At most, they can only be taken to imply trends within the species as a whole. Because of the findings of Ashton and Zuckerman (1950) for a number of pongids, and a few random tests made in this study, variation between the two sides of the jaw of _P. ursinus_ has been taken to be negligible. This does not apply to dimensions greatly affected by wear, as it must be the exception, rather than the rule, for jaws to occlude quite perfectly.

As sexual dimorphism is too great for a composite figure for both sexes to be of any value, the coefficient of variation was calculated for the total mature adult, male group only, to give a measure of V in one sex of a living cercopithecoid. In the skull and mandible, the values all fall within the normal limits of four to ten (Simpson and Roe, 1939) but in the teeth there were a few exceptions. Of the only two very high values

Length:	P^3	>	P^4	M^1	<	M^2	<	M^3	P^4-M^3	C-M^3
	9.7		8.3	11.6		14.2		14.8	48.5	75.5
	(7.3)		(7.3)	(10.5)		(12.7)		(13.0)	(42.1)	(69.7)
	∧		∧	∨		∨		∧	∧	∧
	P_3	>	P_4	M_1	<	M_2	<	M_3	P_4-M_3	C-M_3
	26.4		9.7	11.3		13.8		17.3	52.4	85.9
	(10.0)		(8.3)	(10.25)		(12.3)		(15.7)	(46.3)	(64.2)

Breadth:	P^3	<	P^4	M^1	(bm	>	bd)	<	M^2	(bm	>	bd)	<	M^3	(bm	>	bd)
	7.9		9.1		10.3		9.75			12.25		11.4			12.8		11.3
	(6.9)		(8.2)		(9.6)		(8.9)			(11.1)		(10.3)			(11.6)		(9.6)
	∨		∨		∨		∨			∨		∨			∨		∨
	P_3	<	P_4	M_1	(bm	<	bd)	<	M_2	(bm	>	bd)	<	M_3	(bm	>	bd)
	6.5		7.5		8.7		9.0			11.0		10.5			11.7		10.6
	(4.8)		(6.6)		(7.7)		(7.8)			(9.6)		(9.2)			(10.6)		(9.5)

<u>Table</u>. 3. Size relationships in the upper and lower dentition of <u>P. ursinus</u> based on the mean figures (in mm.) of male and female (the latter in brackets).
<u>Note</u>: The female relationships between the lengths of P^3 and P^4, and the breadths (b_d) of M^2 and M^3, do not quite fit the male figures to which the signs primarily apply. These two minor discrepancies may well be due to the small size of the female samples.

found, the upper diastema and the angle of P_3, diastemata are notoriously variable and the angle of P_3 was a particularly difficult measurement to take accurately. The incisor and canine heights also gave high values but these do not reflect variability but the effects of wear. The high figures for the lengths of I2 (particularly I^2) result from the effects of wear, complicated by the mesial leaning of these teeth. A feature of these results is the constant low variability in the molar teeth (3.2 - 4.9), with the exception of the breadth of M_3 across the hypoconulid (b_h) which was not expected to give accurate figures. Because of their small range of variation (as measured by V) the measurements of the molars seem, potentially, to be useful taxonomic characters. It is interesting that there appears to be considerably less variation in the teeth of P. ursinus than was found by Ashton and Zuckerman (1950, 1951) for certain pongids.

With regard to inter- and intra-specific differences in the baboons, the results of this study have not been conclusive. A certain amount of preliminary ground has, however, been covered and there are indications of the lines which future research could follow.

The specimens from the Albany district represent only a local population of P.u. orientalis Goldblatt and are not a random sample of the whole of this subspecies which covers a far larger area. Comparing these figures to those for the rest of South Africa and to the total for the whole of South Africa (which of course includes these two groups), one can see what probable relationships are to be expected between a local population, the total remaining populations and the species as a whole.

Using the statistics of this study, one finds that the local population from the Albany district agrees very closely with the specimens from the rest of South Africa. In the teeth, the agreement is almost perfect but in the skull, mainly in measurements of length, there are several instances in which the means for the Albany group are slightly higher - although never more than even one standard deviation. Compared to the whole of South Africa, because the Albany and the 'rest' samples were purposely kept equal to facilitate their comparison, all differences found in the previous comparison are merely halved. As the two groups are not present in their natural proportions, this latter comparison is biased but agreement is so close in the first comparison that this must be of little consequence. That there are slight differences present between the groups is also of little significance because the differences found, and the samples on which they were based, are both small. Also, even the lowest taxonomic categories consist of a number of local populations in which statistical differences, due to selection or genetic drift, can be found.

Proof that subspecific differences are present depends on taxonomic considerations (mainly colour and size in the baboon) and an evaluation of these by the application of the 75% rule. This rule is variously interpreted (see Mayr, Linsley and Usinger, 1953) but in essence states that for a subspecies to be valid, 75% of its specimens must be clearly distinguishable from all those of the most similar subspecies. It does not seem unreasonable to suppose that when subspecies reach a stage where they fulfil these conditions, there should be some reflection of their segregation in the teeth and skull (Simpson, 1943). The possiblity, then, of there being well defined subspecies while there is such close agreement between the skull and tooth characters of a small local population and the rest of the species as a group, is very small. This agrees with the anticipated conclusion based on theoretical considerations (Chapter 1). A comparison of the measurements of the subspecific 'types' ~~in the tables~~ also shows no obvious taxonomic differences. It is, however, just conceivable, although extremely improbable, that subspecific differences, relative to the Albany group, may be cancelling one another out in the figures for the rest of South Africa and so making comparisons valueless. Before any final statement can be made as to the validity of the present subspecies of <u>P. ursinus</u>, measurements on random samples of the different subspecies will have to be compared statistically. These measurements, and any colour differences, should also be submitted to the 75% rule.

It was further intended to compare *P. ursinus* with *P. cynocephalus* to see whether specific differences occurred in the skull and teeth and if so, what their magnitude was. Roberts (1951) has based his description of *P.c. cynocephalus* on a group of specimens in the Transvaal Museum, from Salima, Nyasaland. These specimens differ markedly from specimens also labelled *P. cynocephalus* from N.E. Rhodesia, kindly lent to me by the Director of the Kaffrarian Museum, Kingwilliamstown.

In the Nyasaland group, the skull is rather smaller in size but otherwise very much like that of the equivalent sex of *P. ursinus*. In the Rhodesian group, on the other hand, the male skull is even smaller than that of the Nyasaland male and looks rather like that of a *P. ursinus* female. The skull is light and smooth and all the ridges and crests are very small. The temporal lines vary as to where they meet and may even join the nuchal crest separately several millimetors on either side of the inion. The female skulls of the two groups differ as much as those of the males.

As an example of the size variation, consider the greatest length of the mature male skull (in mm) :

Nyasaland : $M = 203 \pm 4.88$; $\sigma = 9.76$; $N = 4$.
Rhodesia : $M = 168 \pm 3.54$; $\sigma = 8.68$; $N = 6$.

Applying the 't' test (Simpson and Roe, 1939), a highly significant value is obtained:

$$t = 5.96^{**} \qquad \frac{P:\ 0.05}{2.306} \qquad \frac{P:\ 0.01}{3.355} \qquad \frac{D.F.}{8}$$

To obtain a 'highly significant value' when comparing an important character in two samples of what is supposed to be the same species, strongly suggests doubt either as to the randomness of the samples or the validity of the species.

On their face value, these two samples thus suggest either a marked subspecific difference or possibly even a specific one. However, it is quite possible that other African localities will supply intergrading forms. Unfortunately, only these twenty-seven specimens from two localities were obtained after requests to several Southern African museums. A large number of specimens from many localities in Africa will have to be studied to elucidate the status of this species and its subspecies.

In a separate paper (Freedman, 1955), the status of the species P.rhodesiae (Haagner) has been considered. It was shown that the single, captive animal on which the species was based is undoubtedly an abnormal P.ursinus. The only two other specimens ever referred to this species were shown by Roberts (1951) to be specimens of P.u.griseipes. It was therefore concluded that the species was invalid. Because of their length, it was not found possible to include all the measurements of the 'type' specimen and the comparative statistical tables of P.ursinus in that paper. The full P.rhodesiae figures are given in this study at the end of table 2 which includes the relevant comparative statistics of P.ursinus.

To summarise this study of P.ursinus, the following are the main results and conclusions:-

(1) An illustrated description of the skull and teeth has been given which will facilitate comparative discussion and eliminate unnecessary repetition in the fossil study which follows.

(2) A statistical analysis of the skulls and teeth of forty- nine males and seven females has been made. These results are to act as a guide to taxonomically reliable characters and the probable species limits of the fossil Cercopithecoidea.

(3) Huxley's growth coefficient of 4.25 for face length on cranium length has been confirmed.

(4) Growth, particularly in the muzzle, was shown to occur in the male after the last teeth have erupted and are in use. (There were too few specimens available to ascertain whether this also occurred in females).

(5) Sexual dimorphism was found to be great. Comparisons between characters of the skull in the two sexes, based on means, gave variable ratios. In the teeth, the ratio in the molars are remarkably constant.

(6) There are definite size trends between successive teeth in a tooth row and also between upper and lower tooth equivalents.

(7) The coefficient of variation for the large male sample only was calculated. The normal range of values was found, those for the molars being particularly low and constant. A broad comparison to certain published pongid data indicates less variation in this species than in the higher apes.

(8) No definite evidence of subspecies was found in the skull and tooth statistics calculated. Further, no important differences could be detected between samples representing a local population and the rest of the species. (As the validity of the present subspecies is in doubt, this does not necessarily imply that the methods used can not show up any subspecific differences which may occur in the fossil forms).

(9) Significant variation found between two samples of the species P.cynocephalus suggests that a re-study of this species is required.

(10) Figures confirming the invalidity of the species P.rhodesiae have been given.

PART II

THE FOSSIL CERCOPITHECOIDEA OF SOUTH AFRICA.

CHAPTER 6.

INTRODUCTION.

The limestone cave deposits of South Africa have yielded an abundance of Lower Pleistocene animal fossils, including the important fossil remains of the ape-men - the Australopithecinae. In the commercial exploitation of the lime deposits many thousands of specimens may have been destroyed in the kilns, but it was through the activities of these lime workers that the first Pleistocene fossil specimens were brought to the attention of South African scientists. It was at first almost solely in the search for man's progenitors that systematic, scientific excavations of the limestone breccias were undertaken. Not only has this work been successful in its primary purpose but, in addition, a large amount of associated faunal material has been found. Each group in the associated fauna, besides its obvious value in elucidating the past history of the animals concerned and their modern descendants, also helps in the building up of a comprehensive ecological picture of the South African Lower Pleistocene.

The deposits from which this fossil material comes were formed by the gradual accumulation of soil, bone and other debris in dolomite caverns. As this filling accumulated, it was slowly consolidated into a breccia by the deposition of calcite, a crystalline form of $CaCO_3$, dissolved out of the dolomite by percolating rain water. Besides the Australopithecinae, the faunal list from these deposits includes, among others, the fossilised remains of sabre-toothed cats, hyaenas, jackals, leopards, dogs, mongoose, horses, antelopes, buffalo, giraffes, pigs, hares, rodents, shrews, bats, golden moles, elephant shrews, monkeys, baboons, hyracoids, birds, lizards, and land snails. This monograph is concerned with the monkeys and baboons.

Limestone breccias may be exceedingly hard and in most of the worked South African deposits it has been found necessary to blast with dynamite in order to remove material for study. After blasting, the large blocks of breccia are broken up, sorted and examined, and all promising material is brought back to the laboratory. Here, pieces showing bone fragments are worked down to suitable size by hand (i.e. using hammer and chisel) before being completely developed in acid.

Although acid (HCl) was first used for preparing fossils over sixty years ago by Holm (1890), Toombs (1948) first used acetic acid for the development of bone fragments out of calcareous matrices. Since then, advances in the technique have been described in papers by Rixon (1949), Toombs and Rixon (1950) and Williams (1953). The technique is dependent on the fact that dilute acetic acid will react with and dissolve out the $CaCO_3$ cement of the breccia without appreciably affecting the embedded bone fragments. In the Division of Vertebrate Palaeontology and Physical Anthropology of the Transvaal Museum, Pretoria, South Africa, a 10% solution of acetic acid is used and exposed bone surfaces are given several coats of a weak solution of "Glyptal" in acetone (about 1 : 15) to impregnate, strengthen and protect the bone. (Glyptal cement is a cellulose ester produced by the Canadian General Electric Co. Ltd., Toronto, Canada. Used dilute, Glyptal has the advantage of being virtually transparent and drying rapidly).

After coating with dilute Glyptal, specimens are developed in glass or porcelain bowls with a fairly large amount of the dilute acid solution. The acid is completely changed approximately once every 48 hours. At least once per week - more often if the specimen shows signs of disintegrating - specimens are washed in several changes of ordinary tap water, for a total period of at least 24 hours, and then thoroughly dried. All freshly exposed bone surfaces are then treated with dilute Glyptal and, development is continued. When a large block of breccia containing only a small specimen has to be developed, it is often found advantageous to coat most of the fossil-free portion of the block with the Glyptal solution, only leaving a narrow border around the specimen. The specimen is thus developed out of the block much more rapidly.

When development is complete and the specimen washed and dried, excess Glyptal is removed with pure acetone or the special solvents provided by the makers and any weak places are strengthened with either Plaster of Paris or undiluted Glyptal. The final washing of the specimen must be particularly carefully done and should preferably continue for 48 hours. If all the acetate formed during development is not removed, it will crystallise out later and possibly damage the specimen. The final drying should also be very thoroughly done for, if even slight traces of moisture remain, any freshly applied Glyptal solution will turn 'milky'.

In all, there are now about 1,250 cercopithecoid specimens known from the South African limestone caves, and they are all referred to genera of the subfamily Cercopithecinae. These specimens, with the exception of *Papio spelaeus* and *Parapapio coronatus*, all date from the Lower Pleistocene. The probable time succession of the sites is discussed in Part III. The greatest single collection of these comes from Sterkfontein (over 550 specimens) but a very considerable number (over 300) comes from Swartkrans. Fair numbers of specimens (about 50-70 from each site) have also been found at Makapan, Kromdraai, Cooper's and Taungs and odd specimens are known from Skurweberg, Swartkrans II, Bolt's Farm, Minnaar's Cave, Graveyard and Gladysvale. (The locations of all these sites, and also most of the other sites referred to in Part II, are shown in figs. 19 and 20). About 85% of the above material was developed during the present study and has not previously been described.

Of this very large amount of material, it has only been possible to utilise about half in this study. This was due to a variety of reasons. Firstly, much of this material consists of very small or very badly damaged fragments which offer no clues at all as to their exact identity. Then, there is a considerable number of specimens, mainly from Sterkfontein, which was not used because they could not be sexed. (This point is further discussed in the introductory part of Chapter 7). Finally, there

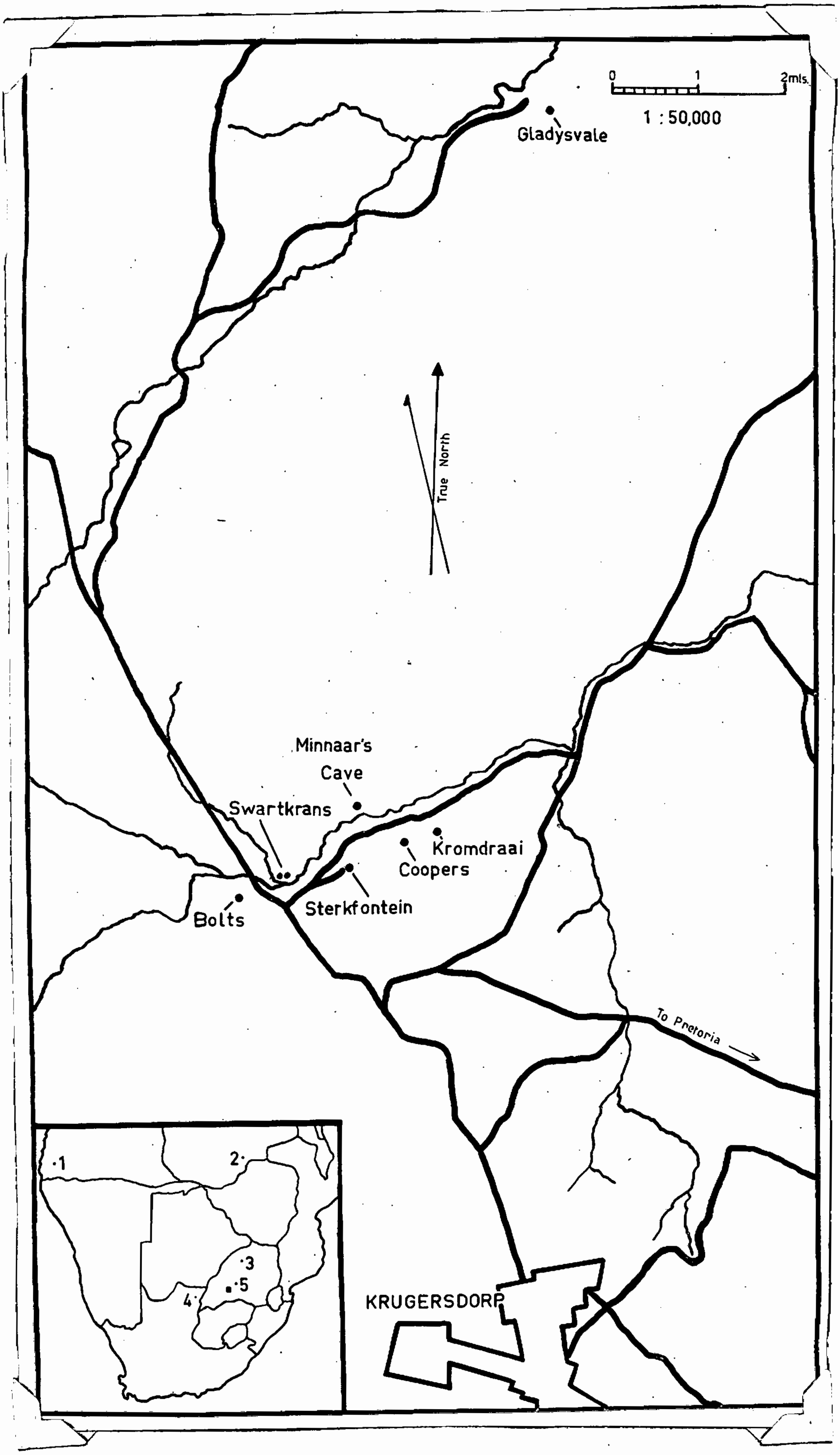

Fig.19. Map of the Sterkfontein area, near Krugersdorp, Transvaal, South Africa showing main sites. Inset map of Southern Africa gives the geographical position of the Sterkfontein area (small black square) and also several other important Southern African sites: 1) Humpata, Angola, 2) Twin Rivers, Northern Rhodesia, 3) Makapan, Transvaal, 4) Taungs, Cape Province and 5) Pretoria, Transvaal.
(Skurweberg lies between Pretoria and the Sterkfontein area).

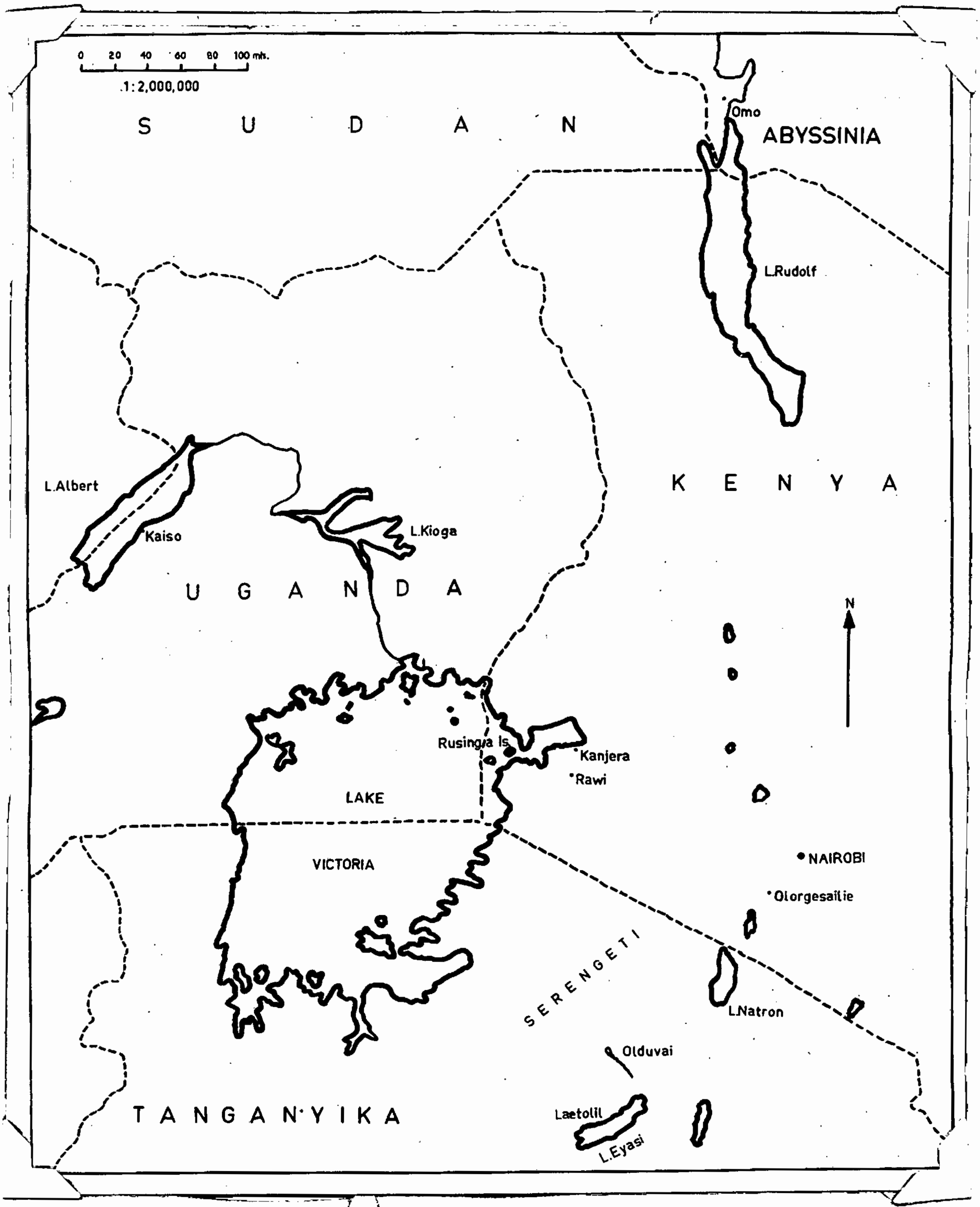

Fig.20. Map of East Afri showing the main sites in that area referred to in th study.

is a fairly large number of endocranial casts, a few post-cranial bones and some juvenile specimens without permanent teeth. These specimens were not used because, in sites where several similar-sized species occur, it may be impossible to decide to which species such specimens belong. As regards the endocranial casts, there are two further reasons why they have not been discussed in the present study. Most of the available casts are not parts of specimens in which teeth are preserved. Hence, overall size cannot be used for identification as neither the age nor the sex of the specimens can be determined. In addition, Le Gros Clark, Cooper and Zuckerman (1936) have shown that one cannot determine accurately either brain size or fissure pattern from endocranial casts.

The only previous review of the South African fossil Cercopithecoidea was by Broom (1940), although Dart (1949) gave a catalogue, with some short descriptions, of most of the South African cercopithecoid specimens known up to the time of his writing. Broom's descriptions of the various species were very brief and confined almost entirely to dental characters. Since then several new cercopithecoid species and genera have been described from various excavations in South Africa and it has been felt for sometime that a comprehensive, unified re-study of all these forms is required. In the course of the present study, besides material of undescribed species, a very considerable amount of hitherto undescribed material of known species has also been developed and this has been integrated into the review of the whole group. The new material has been found to include three new cercopithecoid species and, by increasing our knowledge of the range of variation of the known species, it has necessitated the sinking of one genus and four species and made several inter-generic changes necessary. For the sake of completeness, attention has also been given, either below or in Part III, to all other fossils of this group found in Africa, as well as to a number from other parts of the world. As the relevant material could not be personally examined, detailed descriptions of these species have, however, not been attempted.

To avoid needless repetition, the description of *Papio ursinus*, as given in Chapter 2 of this monograph, has been used as a basis for the descriptions of all the species which follow. It is mainly deviations from this description which are dealt with in detail. The definitions and terms used in the *P.ursinus* description (Chapter 3) are also all applicable below and all dimensions are in millimeters, unless another unit is specifically mentioned. Measurements are put in round brackets when they are not completely accurate due to damage or distortion. When measurements are put in square brackets, it means that they have not been taken personally and do not necessarily follow the definitions in Chapter 3. When any dimension is compared to its equivalent in *P.ursinus*, the comparison is always to the mean for that measurement in one or other of the sexes of that species.

In addition to the above, the following points on measurements are specifically applicable to the fossil forms:

1) When teeth are bilaterally present, the mean figures for the two teeth have been used.

2) Allowances have been made in most of these measurements for small matrix-filled cracks and very minor damage.

3) Lateral-ward curvature of the tooth row in many of the fossil species has resulted in differences between the measurements of a tooth row and the sum of the individual teeth comprising it.

4) Isolated teeth or small maxillary or mandibular fragments with teeth are very difficult to/~~xxxxxx~~ orientate so as to get a measurement to conform strictly to the criteria in Chapter 3.

The following abbreviations have been used in quoting the numbers of specimens from various institutions:

1) South African Museum, Cape Town, South Africa.
   CT. - All of these specimens come from Taungs, Cape Province, South Africa.

2) Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa.
   B.P.I. and/or L.W.P. - Makapan (limeworks), Transvaal, South Africa.

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

M. or AD. 1326/ - Makapan (limeworks), Transvaal, South Africa.
AD. 1238/ - Sterfontein, Transvaal, South Africa.

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

STS. - Sterkfontein,
SK. - Swartkrans,
KA. - Kromdraai (faunal site),
CO. - Cooper's,
BF. - Bolt's Farm,
Min. - Minaar's Cave,
SB. - Skurweberg,
Gl. - Gladysvale, this site has hitherto been known in the literature as Gladysvale and the name is retained here, although the correct name of the farm is Uitkomst,
SK.II. - Swartkrans II,
GY. - Sterkfontein underground or Graveyard,
M. - Makapan (limeworks). Only two numbers (M.10 and M.11),

) All sites in the Transvaal, South Africa.

T. - Taungs, Cape Province, South Africa.

Except where stated to the contrary, 'Makapan', in this monograph, refers to Makapan (limeworks) and 'Kromdraai' refers to the Kromdraai faunal site.

CHAPTER 7.

PARAPAPIO.

THE first known cercopithecoid fossils from South Africa were found in the limestone deposits near Taungs. At a meeting of the Royal Society of South Africa in 1920, Haughton demonstrated these specimens and suggested that they belonged to a single species for which he proposed the name *Papio antiquus*. His paper was published in the form of an abstract in the Minutes of the Proceedings for 1920 of the Transactions of the Royal Society of South Africa (1925).

These specimens were later re-examined by Gear (1926), together with some additional specimens from the collection of the Anatomy Department of the University of the Witwatersrand, Johannesburg, South Africa. Although he mentions receiving notes on the specimens from Haughton, Gear was apparently unaware of this author's prior naming and, on concluding that there were two species present, he named the one *Papio africanus* and the other *Papio izodi*. According to Gear's division, all the specimens examined and named by Haughton fall into the one species *Papio africanus* and two new specimens from the University of the Witwatersrand collection constitute the other species, *Papio izodi*. In view of Haughton's priority, the name *Papio africanus* falls away.

In their descriptions, neither Haughton nor Gear designated type specimens. There is no indication at all as to which (if any) specimen Haughton considered as the holotype of his species but Gear discusses one specimen of each of his two species in greater detail. These are undoubtedly the specimens which he considered to be the types. In 1937, Jones formally designated these latter two specimens as the lectotypes of the two species.

After the publication of Gear's paper, there followed a series of papers by Broom, and also one by Jones, in which the status and names of these two species are repeatedly discussed and changed. This confusion was mainly due to the fact that Broom did not at first realise that Haughton's name, *Papio antiquus*, was valid, despite his not having named a type specimen and also, that the two *Papio izodi* specimens were not among the material originally described by Haughton. In 1934, Broom concluded that the Taungs cercopithecoids represented only a single species, which he erroneously called *Papio africanus* Haughton. Jones (1937) accepted both of Gear's species but suggested that, while *Papio africanus* was clearly a *Papio*, *Papio izodi* belonged to "a different genus". It is interesting that in this same paper Jones created the genus *Parapapio* for some specimens from Sterkfontein (see below) but he apparently did not consider it to contain either of these two species. In 1940, however, Broom transferred both '*Papio africanus*' and *Papio izodi* to Jones' genus *Parapapio*, although he still doubted the validity of the latter species. In both this paper and in his 1946 monograph on the ape-men, Broom still considered Haughton's name (*P.antiquus*) to be a synonym of *P.africanus*. In 1948, Broom finally accepted both species as being valid and, in addition, Haughton's name for the first.

In this study it is proposed that whereas Haughton's species, *Parapapio antiquus*, is clearly a *Parapapio*, Gear's species, *Parapapio izodi*, because of the shape of its muzzle dorsum, is a *Papio*. The descriptions of these two species, together with more detailed reasons for their proposed taxonomic positions, are given below and under the genus *Papio*.

The genus *Parapapio* was actually created in 1937 by Jones for a group of fossil cercopithecoid specimens excavated at Sterkfontein. These specimens were said by him to represent a single species which he named *Parapapio broomi*. However, in an appendix to his paper, Jones added that another species (represented by 1238/24) similar to *Cercopithecus* and probably representing a new genus, was also present but that, before its relationships could be established with certainly, more material was required. Some years later, when more specimens had been excavated at Sterkfontein, Broom (1940), decided that there were actually three species included amongst the material examined by Jones and that they were all species of the genus Parapapio. He named the species slightly smaller than P.broomi, P.jonesi and the one slightly larger than P.broomi, P.whitei. (The specimen referred to by Jones above, 1238/24, was referred by Broom to P.jonesi but is actually a Cercopithecoides williamsi).

During the course of the present investigation, close on four hundred and fifty new Parapapio specimens were obtained from Sterkfontein breccia. There is therefore now a total of probably over five hundred and fifty fossil fragments of Parapapio known from Sterkfontein. Of these, over two hundred are small, badly damaged bone and tooth fragments and endocranial casts, all of little value in a taxonomic study of this sort. At least three hundred specimens, however, are either fair sized portions of the skull or mandible with teeth in place, or single, isolated teeth. Unfortunately, only eight or nine of these latter specimens are even fairly complete skulls and probably because of this, as will be explained below, instead of simplifying the taxonomy of the Sterkfontein Parapapio species, this large amount of new material has actually made classification more difficult.

It so happened that when Broom examined the Sterkfontein cercopithecoid material in 1940, the comparatively few specimens then available fell, on tooth size, fairly clearly into three groups. This division formed the basis of Broom's three species. When an attempt was made to sort out the large amount of new cercopithecoid material from this site into these three dental size groups, it was found that some of the specimens seemed to bridge the gaps between the species. Hence the paradox of the additional material apparently obscuring the true relationships of the Sterkfontein Parapapio species.

As there are far too few skulls available for the taxonomy of these specimens to be based on general skull morphology and dimensions, dental characters must primarily be relied on. Of these, dental morphology appears to be approximately uniform for the whole group and provides no basis for a division of the specimens.

In all of the other cercopithecoid genera to be described in this study, the various species - and in most cases the two sexes of each of those species as well - are clearly separable on tooth size. A large number of dental measurements were therefore tried for dividing the Sterkfontein Parapapio specimens into clear-cut species but none gave a completely satisfactory division. However, although most single dimensions show virtually all the Parapapio specimens of one sex to be linked, in most cases, there are three distinct modes in the distribution.

The most obvious conclusion would appear to be that the Parapapio specimens from Sterkfontein form a chronocline. However, the fact that the smallest of the three species, P.jonesi, is the only Parapapio species found at Swartkrans and Kromdraai, which are clearly more recent sites than Sterkfontein, makes this possibility most unlikely. The above conclusion is also contradicted by the fact that there was no apparent size increase (or decrease) in the Parapapio specimens between the bottom and the top of the Sterkfontein excavation (Robinson - personal communication). The possibility that the specimens represent three geographical subspecies which migrated successively or intermittently into the area was also considered, but the randomness with which the different size groups appeared throughout the deposit make this most improbable. Further, the range of variability of any one character for all these specimens seems unreasonably great for a single species. The coefficient of variation of the length of M_3 for example, is 10.4 for the whole group, whereas for the same dimension in P.ursinus it was found to be only 4.8.

The division finally adopted and given in tables 5,6,and 7 is based mainly on molar length, especially that of M3 and M2 in that order of importance. This has resulted in a reasonably clear separation into three species, each of which includes one of Broom's types. Table 4 shows the taxonomically most useful characters (the dimensions of M2 and M3) and also an extreme example of a dimension (P_3 l(h)) which shows complete overlap between the three species from this site. The position of an

Table 4. Observed ranges of the dimensions of certain teeth in the Sterkfontein *Parapapio* spp.

	M^2			M^3		
	bm	bd	l	bm	bd	l
P. jonesi ♂	10.4	9.6	9.5 - 10.8	10.8 - 10.9	8.0 - 8.9	10.1 - 10.4
♀	9.7 - 10.7	8.5 - 9.4	9.6 - 10.6	9.3 - 10.1	7.4 - 8.1	9.0 - 10.0
P. broomi ♂	10.6 - 12.1	10.5 -11.1	10.8 - 11.9	10.3 - 12.3	7.9 -10.3	10.4 - 12.1
♀	10.3 - 11.8	9.8 -10.8	9.8 - 11.8	10.2 - 10.8	8.2 - 9.0	10.4 - 12.0
P. whitei ♂	-	-	-	-	-	-
♀	12.1 - 13.6	10.9 -13.0	11.8 -13.3	12.8	11.0 -11.7	11.8 - 13.4

	M_2			M_3			P_3
	bm	bd	l	bm	bd	l	l(h)
P. jonesi ♂	9.1 - 10.0	9.0 - 10.0	10.3 - 11.1	9.2 - 10.0	8.3 - 9.3	13.0 - 13.8	12.8 - 17.2
♀	7.6 - 9.9	7.2 - 9.2	9.5 - 11.0	8.8 - 9.6	7.9 - 9.2	12.1 - 13.3	7.0 - 10.0
P. broomi ♂	10.0 - 10.2	9.5 - 10.6	10.9 - 11.7	10.0 - 10.5	8.5 - 9.7	14.7 - 15.3	12.5 - 17.0
♀	9.0 - 10.8	8.5 - 10.6	10.5 - 12.4	9.0 - 11.0	8.4 - 10.0	13.4 - 15.6	5.7 - 12.0
P. whitei ♂	10.4 - 10.9	10.6 - 10.8	12.2 - 12.3	11.1	9.6 - 10.7	15.5 - 16.5	16.4
♀	10.5 - 10.8	10.0 - 10.6	12.5 - 13.4	10.8 - 11.2	10.3 - 10.5	16.5 - 17.0	10.2 - 13.0

occasional specimen still remains doubtful and for the present, each such specimen has been included in the species with which it appears to have the most characters in common. In addition to the 'links' between 'adjacent' species, the dimensions of the teeth of the two sexes of any one species, with the exception of the C and P_3 also show overlap in almost every instance. This has necessitated using only specimens in which the sex can definitely be determined (using the C and P_3) and only about one hundred of the Sterkfontein specimens fall into this category.

Comparisons between *Parapapio antiquus*, from Taungs, and *P.broomi* (see below) show that the two species are remarkably similar in tooth size but differ very considerably in skull shape. Similarly, the tooth sizes of the two sexes of *P.broomi* overlap in most instances but the skull shapes and sizes are very different. This suggests that the *Parapapio* species at Sterkfontein probably differed more in skull characters than in dentition. The picture will only be clarified by the discovery of more relatively complete skull material. Broom's three species are thus retained for the present, as this appears to be the most logical interpretation of the available evidence. It must be emphasised, however, that tooth morphology and size do not appear to be especially helpful in classifying the *Parapapio* species - and most of the available material is dental. Hence, though it is moderately clear that three species are present at Sterkfontein, the specific identity of some individual dental specimens is uncertain and in this regard, strict accuracy is at present not possible.

In 1947, Mollet reported finding *P.broomi* at Makapan. The following year, Kitching, Wells and Westphal (1948) confirmed this report by recording further *P.broomi* specimens from that site and also reported finding a mandible of *P.jonesi* (60.M,M.215) there. Subsequently, Broom and Hughes (1949) decided that the Makapan *P.broomi* specimens had narrower molars and "numerous other difference" (which they do not specify) distinguishing them from the Sterkfontein *P.broomi* specimens. They concluded that these specimens represented a new species which they named *Parapapio makapani*. Broom and Hughes further suggested that the *P.jonesi* specimen was most likely a *Cercopithecoides williamsi*.

On the basis of the new material described in this study, it is clear that, in both cases, Broom and Hughes erred. Now that larger samples are available, it is seen that the Makapan *P.broomi* specimens match the specimens from the type site well. Also, the specimen referred by Broom and Hughes to *C.williamsi* could not possibly belong in the genus *Cercopithecoides* because its dental morphology is clearly of the *Parapapio* type. This latter specimen is rather small for a *P.jonesi* but quite difinite *P.jonesi* specimens have since been recovered from Makapan and it would seem best, at least for the present, to regard this specimen as also belonging to the species *P.jonesi*. Two specimens from Makapan (M.635 and M.632) described by Kitching (1952) as belonging to *Brachygnathopithecus peppercorni* (see Chapter 9 and also below) have been referred to *P.broomi* in this study.

Two further species, *Parapapio coronatus* Broom and Robinson, 1950 and *Parapapio angusticeps* Broom, 1940 have hitherto been included in this genus. Of these '*Parapapio*' *coronatus* has, in this study, been described under "Species of Unknown Affinities" (Chapter 13) because of certain difficulties with its classification. '*Parapapio*' *angusticeps* is without doubt a *Papio* and is described with the species of that genus in Chapter 8. The genus *Parapapio* thus now includes only four species, *P.broomi*, *P.jonesi*, *P.whitei* and *P.antiquus*, all fairly small, extinct baboons known only from South Africa.

Genus: *Parapapio* Jones, 1937.

Diagnosis:

The skull is characterised by the fact that, in the side view of both sexes, the frontal and nasal bones form a straight line, or smooth, only slightly concave curve, between the glabella and the posterior margin of the nasal aperture. The supra-orbital tori are very weakly developed and do not project forward in either sex. There are no deep maxillary fossae or strong maxillary ridges. Sexual dimorphism is usually quite marked in the skull but the difference is in size rather than morphology. Except for the canines and P_3, there is only a small statistical size difference between the teeth of the two sexes. Morphologically the teeth are indistinguishable from those of the genus *Papio*.

The type species is *P. broomi* and was established by Jones (1937).

Parapapio broomi Jones.

Parapapio broomi - Jones, 1937.
Parapapio broomi - Broom, 1940 and 1946.
Parapapio broomi - Mollett, 1947.
Parapapio broomi - Kitching, Wells and Westphal, 1948.
Parapapio makapani - Broom and Hughes, 1949.
Parapapio broomi - Dart, 1949.
Parapapio broomi - Cooke, 1952.
Brachygnathopithecus peppercorni - Kitching, 1952. (M.635 & M.632).
Parapapio broomi - Oakley, 1954 a and b.
Parapapio broomi)
Parapapio makapani) - Hopwood and Hollyfield, 1954.

Holotype:

A badly damaged male skull (STS.564) without teeth.

Repository of type:

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

Type site:

Sterkfontein, Transvaal, South Africa.

Referred material:

Forty-two specimens from Sterkfontein, ten from Makapan and one from Bolt's Farm. (For the numbers of these specimens see tables 5a, b, c, and d). Two skulls, M202, 1326/2 a male, and STS.254A, a female, are fairly complete and have been used as a basis of the description.

Description: (Figs. 21 - 30).

The skulls of both sexes of *P. broomi* are considerably smaller than those of the equivalent sexes of *P. ursinus*. Also, when the sizes of the male and female skulls of *P. broomi* are compared, it is seen that the male is not nearly as large, relative to the female, as is the chacma baboon. The ratio of female greatest length to male greatest length, as a percentage, is 77.4 in *P. ursinus* but 84.3 in *P. broomi*. The smaller relative size of the male of *P.broomi* is due to the muzzle lengths being more equal in the two sexes. Similar ratios to the above, calculated on muzzle length, gives 70.7% for *P.ursinus* and 76.7% for *P.broomi*. Thus, although sexual dimorphism is quite marked in the *P.broomi* skull, it is mainly an absolute size difference and not so much one of relative proportions as in *P.ursinus*. In addition, in neither sex, but particularly with regard to the male, is there the great secondary elongation of the muzzle found in the chacma.

One of the main morphological skull differences between this species and *P.ursinus* is in the profile shape of the muzzle dorsum. In all the specimens of both sexes in which the appropriate region is present, the frontal and nasal bones take the form of a shallow, smooth curve from the glabella to the posterior margin of the nasal aperture. In *P.ursinus*, there is a sharp drop in the inter-orbital region and then a more gentle slope down to the posterior margin of the nasal aperture. In both sexes of *P.broomi*, but particularly in the male, the muzzle dorsum is also not nearly as flat as in the equivalent sex of *P.ursinus*. In addition, there is virtually no developement of the maxillary ridges. The maxillary fossae appeared to be totally absent in the females (STS.254A) but in the males, there may either be no fossa at all (STS.534) or a very slight fossa (M.202, 1326/2). The zygomatic bones in both sexes face antero-laterally, in contradistinction to those of most other Cercopithecoidea, where they face more nearly directly forward.

A notable feature of the skull of both sexes, but particularly of the males, is the very weak development and lack of any forward projection of the supra-orbital tori. This feature appears to be characteristic of the genus *Parapapio*. The temporal lines of both the male and female are prominent when they leave the lateral end of the supra-orbital tori and cross the post-orbital constriction of the frontals. However, they then rapidly weaken and, even in the males, almost immediately disappear and can be traced no further. The zygomatic arches of both the male and female are slender. In the male, the post glenoid process is large (STS.534).

There is a marked protuberance of the frontals just posterior to the supra-orbital tori but the calvarium roof then falls away steadily posteriorly, down to the very slight nuchal crest. In norma basalis it is seen that the palate is rather broad and the line through the tooth row convex outwards. The posterior palatine foramen is large but is not protected by a lingula. Due to damage, very little can be seen on any of the specimens of the base of the calvarium but the external auditory meatus appears to be short and runs disto-laterally at much the same angle as in *P.ursinus*. In general, there appears to be considerably less morphological difference between the skulls of the two sexes than was found in *P.ursinus*.

It is only in the canines and P_3 that there is much difference between the male and female teeth. In morphology, the other teeth of the two sexes appear to be identical, but in size, there is a statistical difference which is very small and does not enable individual specimens without canines or P_3 teeth to be sexed with certainty on the dentition alone. Although very different in size, the teeth of this baboon are morphologically very similar to those of *P.ursinus*.

The only upper incisors known are in two female specimens (STS.368A and STS.393) and the teeth show no structural differences to the equivalents in the female chacma baboon. These, and also certain other specimens (e.g. STS260 - a male), show that there is a diastema present between the lateral incisor and the C. Quite a number of specimens of both sexes are known with C present in various stages of wear. The structure of these teeth is very similar to that in the equivalent sex of *P.ursinus*. but in the female, the tooth leans more buccalward and the mesial groove is more marked than in the female of *P.ursinus*. In the male of this species (STS.260 and STS.534), the C also appears to have the same proportions as in the male of *P.ursinus* but in the female, the measurement from the mesial surface to the disto-lingual edge of this tooth seems relatively greater than in the female chacma baboon.

Unlike the *P.ursinus* condition, P^3 lies very close up against the *C* and there is only a very slight extension of its enamel down towards the mesio-buccal root. Also, in the male, the mesial part of the tooth is not turned buccalward as much as in the same sex of *P.ursinus*. In both sexes, P^4 is a larger tooth than P^3 and has much the same structure as in the chacma baboon.

Very little can be said about the upper molars as they are so very similar to those of *P.ursinus*. However, the buccal surfaces of these teeth are perhaps slightly more vertical than those of *P.ursinus* and there seems to be slightly less development of the portion of the teeth in front of the mesial pair of cusps. The size relationships between and in the various upper molars appear to differ from those of *P.ursinus* only in that the teeth are smaller and M^3 shows signs of being slightly reduced. Mesio-lingual grooves are present on the lingual surfaces of almost all of the upper molars and accessory cusplets are seen on the lingual surface of M^2 on STS.251 and STS.274. On STS.378A, M^3 has a subsidiary cuspule on the cingulum at the distal end of the tooth. Table 5c shows the sizes of the upper teeth; B.F.21 fits well. Except that the two upper molars, M^2 and M^3 (M.635), are slighly large, the *Brachygnathopithecus peppercorni* specimens referred to this species (the above specimen and M.632) fit the type site specimens well. (On size, M.635 fits *P.whitei* better but as that species has not been described from Makapan, it would seem, *pro tem*, advisable to refer the two teeth to *P.broomi*.)

The teeth of the only fairly complete mandible known (STS.363), are very badly damaged but the specimen never-the-less seems clearly to belong to this species. The only other fairly good mandible (STS.562) is of the right half of the jaw only. The symphysis of this latter specimen is missing and the ramus is somewhat damaged but the teeth are well preserved. Broom (1940) made this specimen a 'neotype' but as the holotype of this species is still in existence, his usage of the term would appear to be incorrect. There are also a few specimens which are more fragmentary and these will also be used in the description below.

The mandibular symphysis is fairly long in the female (STS.363), reaching back to the middle of P_4; in the male (STS.323), it ends at about the level of the middle of P_3. The foramen symphyseosum and median sagittal canal are present in several specimens of both sexes (e.g. M.211 - a male, and STS.369B - a female). The anterior surface of the symphysis of the male is fairly steep in both STS.323 and M.211 and the latter specimen also shows two slight, converging lateral ridges on the upper part of this surface. The anterior surface of the symphysis of the female is not nearly as steep in specimens STS.363 and STS.369B as in the males, but in M.213 it is about the same. Female specimen STS.363 also shows the converging lateral ridges on this surface. There are no mandibular fossae in any of the specimens of either sex except M.211 where they are poorly developed. The mental foramen is large and single in both sexes (M.211 and STS.369B). Both STS.562 and STS.363, two female specimens, show that the ramus is bent inwards on its posterior edge, from the gonion up to a point about midway between the gonion and the condyle. No specimen shows the condyle and coronoid process in an undamaged state.

The lower incisors are present in specimens STS.323, a male and STS.369B a female. These teeth are much smaller than those in the equivalent sex of <u>P.ursinus</u> but they have identical structure and are worn in the same way as the teeth of that species. There are two fairly good specimens of the female $\overline{C}$ known, but the two specimens of the male equivalent available are very badly damaged and no description of them is possible. The unworn female $\overline{C}$ (STS.363) is mesio-distally broad but short in height when compared to the same tooth in the female of <u>P.ursinus</u>. In old females, $\overline{C}$ (STS.369B), like the equivalent in the female chacma baboon, is worn right down to the level of the incisors and seems to form part of that row.

There are numerous good examples of the lower premolars and molars of the female but fewer of the male. The main feature of P_3 in both sexes is the considerable amount of variation in the length l(h) and the angle at which the mesio-buccal extension lies. Compared to the <u>P.ursinus</u> female, the female mesio-buccal extension is short. P_4 also shows a fair amount

Table 5a. Measurements of the skull of *Parapapio broomi*.

	Males						Females	
	STS. 564	STS. 253	STS. 534	STS. 397	M. 202	1326/ 4A	STS. 254A	STS. 396A
GENERAL.								
Greatest length			158		(163)	(166)	(135)	
Basal length		(124)					94	
Bizygomatic breadth	(112)			100			(92)	94
CALVARIUM.								
Height:								
Basion-bregma	(66)							
Basion-glabella	(60)			72			(57)	
Breadth:								
Min. inter-frontal			(55)	51	54		(54)	
Greatest temporal	(80)			75			(72)	
Length:								
Inion-glabella	(100)		98		(100)	(99)		
Foramen magnum:								
Breadth				15.5			16	16.5
Length				15.0			19	16
MUZZLE.								
Height:								
Post. to M^3					53			
Ant. to P^3		25			27			
Breadth:								
Ant. to M^3				48	51			
Ant. to P^3		42			45		37	
Dors. to M^2		37			43			
Length:								
Muzzle			82		(88)	(89)	66	
Palate			65		(66)			
Nasal					43		34	
Orbit:								
Inter-orbital				11	10		9.0	
External orbital				72	81		(73)	
Height					24		24.7	
Breadth			24	24.4	29		26.5	
Nasal aperture:								
Breadth		18			18		14.2	
Length		37			34		24.8	

Table 5b. Measurements of the mandible of *Parapapio broomi*.

	Males.		Females.				
	STS. 323	M.211	STS. 562	STS. 363	STS. 335	STS. 369A	M.213
Height:							
Gonion-condyle			47				
Post. to M$_3$			25	26	26		29
Ant. to P$_4$	30	29					28
Mental sp. to most ant. pt.	(36)	(35)		32		29	
Breadth:							
Bigonial				44			
Ant. to M$_3$				41			
Ant. to P$_4$	34	29		26			
At base of canines.	24			20			
Length:							
Gonion to mental sp.				60			
Condyle to most ant. pt.				112			
Angles:							
At symphysis				150°			
Between corpora				36°			

Table 5c. Measurements of the upper teeth of *Parapapio broomi*.

	I^1			I^2			C				P^3		P^4		M^1			M^2			M^3			Rows	
	h	b	l	h	b	l	h	b	l_1	l_2	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	P^4-M^3	C - M^3
MALE:																									
STS.397																		10.6	(10.5)	11.8	10.3	8.8	11.3		
STS.379A											8.5	8.6	(9.1)	6.6	10.4		(10.3)					8.6			
STS.387											7.5	8.6	8.5	6.3	9.7	9.0	9.5	12.1	11.0	10.8	11.3	10.0	11.4	37.0	
STS.501											8.0	9.4	(9.2)	6.4	9.9	8.2	10.0								
STS.434								(9.8)			8.3	8.7	9.6	6.9											
STS.534							(36)	8.9	8.5	9.5			9.0						11.1	11.5	12.3	9.9	11.5	36.5	55.2
STS.555								(8)	(9)	(10)	8.7	7.6	8.8	6.8	10.3	9.9	10.8		10.8	11.2					
STS.360							29.5	9.2	9.0	10.1	8.0	7.1	8.6	6.7	9.6	9.0	9.8	12.0	(11.1)	11.9	12.3		12.1	39.4	56.8
STS.414B											7.6		8.7	6.7	9.5		9.9	11.2	10.7	11.7	10.5	7.9	10.4	37.4	
M.202 (1326/2)													8.5	6.5	9.4	8.4	10.0	11.1	10.1	11.2	10.4	9.0	10.8	37.7	
M.203 A & B											7.7	6.1	9.0	6.6	9.6		(9.0)	12.1	11.1	11.0	12.0	10.3	11.0	(37.1)	
M.632							(32	9.1	8.0	9.6															
FEMALE:																									
STS.393			5.6			4.1		6.7	5.8	5.5	7.2		9.6				8.4			9.8	10.8	8.2	10.8	(35.5)	(47.0)
STS.262											7.5	7.0			(10.1)	8.9	10.5	11.1	(10.1)	11.6					
STS.274												7.4		(6.3)	9.6	9.4	10.1	10.6	9.9	10.5					
STS.364								5.8	*(5.9)		7.5	5.5	7.1	6.5	(8.9)	8.5	(9.5)	10.6		11.2					
STS.366											7.1	7.6	7.9	7.0	9.1	8.5	9.5	10.5	9.8	11.0	10.3	(8.8)	10.9		
STS.322																					10.2	9.0	12.0	(39.3)	
STS.330			6.0	7.6		5.9											(9.3)			(11.4)			(10.4)	(35.7)	(48.7)
STS.339											7.6	5.1	8.4	6.1	9.9		9.6								
STS.346A	12.6	7.4	7.4	10.9	6.8	6.6	14.4	6.1	6.2	6.4	6.9	7.0	8.3	6.5	9.4										
STS.378A-D	9.4	6.4	8.0	7.3	5.5	6.4	10.0	5.6	*(5.5		7.8	7.7	(9.4)	6.6					10.5	11.0	10.6	8.6	11.4	37.3	50.0
STS.365A											7.0	5.4	8.3	6.2	9.8	8.7	9.6		10.1	10.8	10.8	9.0	11.4		
STS.544													7.7	6.1	9.0	8.5	9.5	10.5	9.9	10.8	10.5	9.0	10.7		
STS.397											7.8	7.2	8.1	6.5	9.6	9.4	10.1	11.6	10.6	11.8					
STS.251													8.4	6.7	9.8	8.5	9.8	11.5	9.6	10.9					
? SEX:																									
BF.81															9.6	8.7	8.5	(11.0)		10.9	10.3	8.6	10.6		
M.636																		12.5	11.0	12.5	12.1	10.6	12.6		

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* These figures are means for l_1 and l_2 which could not be taken separately because of damage.

Table 5d. Measurements of the lower teeth of *Parapapio broomi*.

	I_1			I_2			$\bar{C}$			P_3		P_4		M_1			M_2			M_3				Rows	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	P_4-M_3	$\bar{C}$-M_3
MALE:																									
STS.414A	10.4		6.0	9.5		5.7	(22.5)	(10.5)		5.7	15.0	6.9	7.2	7.6	7.8	9.7	10.1	9.5	11.7	10.0	8.5	5.8	14.7	42.0	(51.5)
STS.351																		9.7	11.4		9.7	6.3	15.0		
STS.380											18.5			6.5	8.3	9.4	10.2	10.4	10.9				(14.8)	41.5	
STS.383	10.6	7.4	6.0		7.4	5.9				5.7	16.0	7.4	8.3	7.8	8.0	10.5									
1838/13				11.3		5.7				6.6	17.0	6.9	7.4		8.5	9.5	10.0	9.8	11.0	10.1	9.1	5.8	15.3	42.3	
M.210 (1586/12)										5.4	16.3	6.9	7.5	7.8	7.7	9.6	10.2	9.6	11.4	10.5	9.6	5.6	15.3	43.0	
FEMALE:																									
STS.562										6.5	(9.1)	(7.5	7.1	8.9	8.8	9.8	10.6	10.2	11.7	10.7	10.0	7.5	15.6	45.8	54.2
STS.569A,B	5.0	6.5	4.4	5.8	5.0	4.5	7.6	6.6	4.5	5.5	7.1			8.6	8.5	6.8				10.2	9.2	6.4	14.9		
STS.571										(5.5)	9.0		(7.2)				10.4	9.8	12.4	10.2	9.2		14.6		
STS.563							11.6	7.7	5.5	5.8	8.6	7.3	7.3			(7.5)			(10.7)		9.6		(15.5)	40.9	54.6
STS.555										5.3	10.3	6.6	7.5				9.7	9.1	12.4	9.7	8.9		15.1	(44.5)	
STS.566													7.6	8.1	8.1	10.2	9.3	9.0	11.5						
STS.385										5.3	5.7	7.1	6.5	8.4	9.0	9.0	10.8	10.0	11.8	11.0	9.9		15.4	41.0	
STS.386										5.0	5.8	6.9	6.7			8.9	9.5				9.3		15.0	40.8	
STS.411A,B												6.5	7.2	7.6	7.3	9.4	9.0	8.5	11.5	9.0	8.4	6.4	(14.0)		
STS.565																			(10.5)				14.5		
M.215, SSM. B.P.I.										5.5	8.0	6.6	6.4	8.1	8.3	8.6	10.4	10.6	11.4	10.3	9.5	5.7	14.0	40.8	
Tvl. M10 (1886/13)										5.8	12.0	7.9	7.4	8.6	8.6	9.6	10.5	10.0	11.0	10.4	9.6	6.7	(14.0)	(41.5)	
M.216										5.6	12.0	7.3	7.5	8.6	8.3	9.4									

Fig.21. *Parapapio broomi* male (M.202). Skull - dorsal view. x 1.

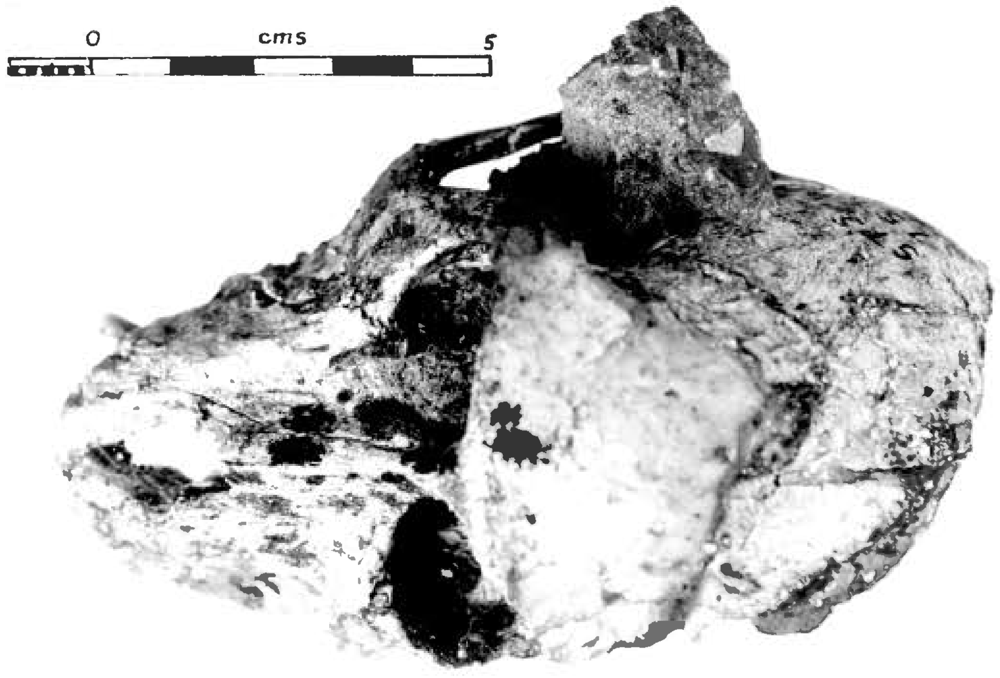

Fig.22. *Parapapio broomi* female (STS.254A). Skull - dorsal view. x 1.

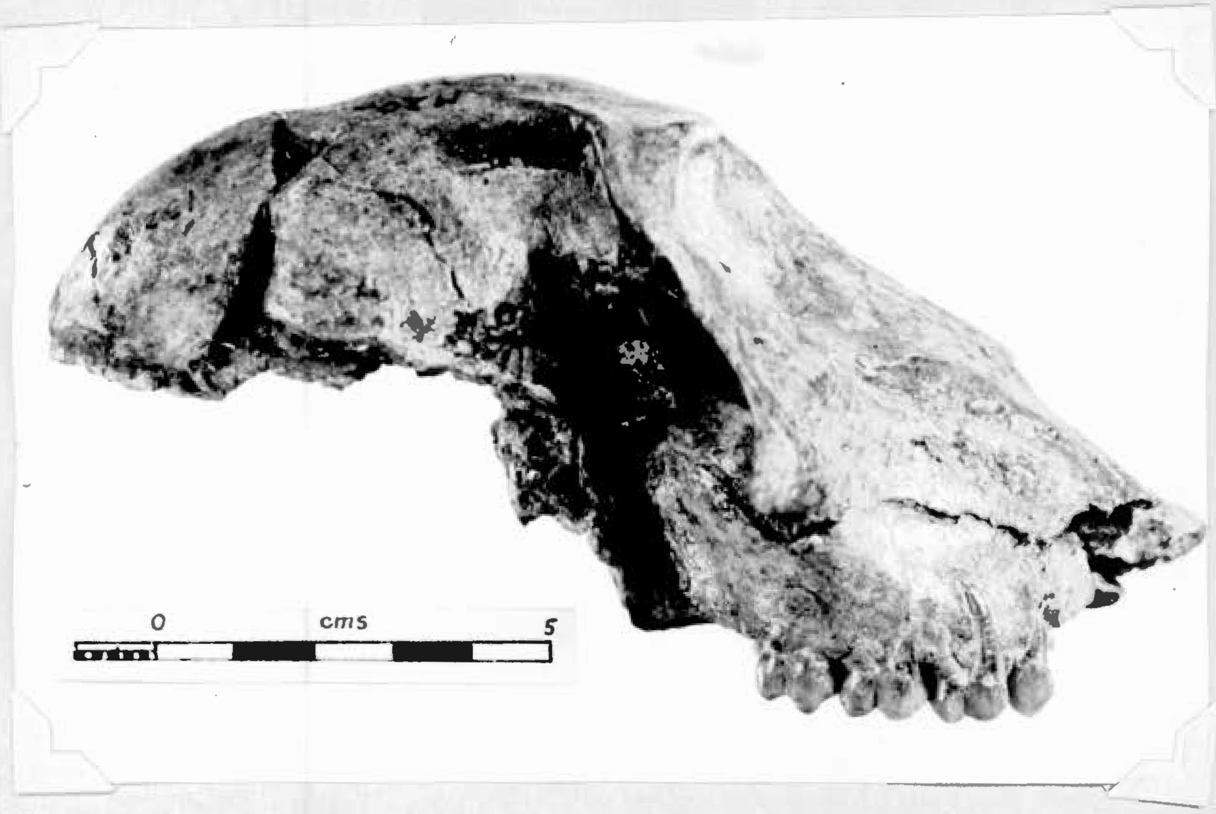

Fig.23. Parapapio broomi male (M.202). Skull - norma lateralis. x 1.

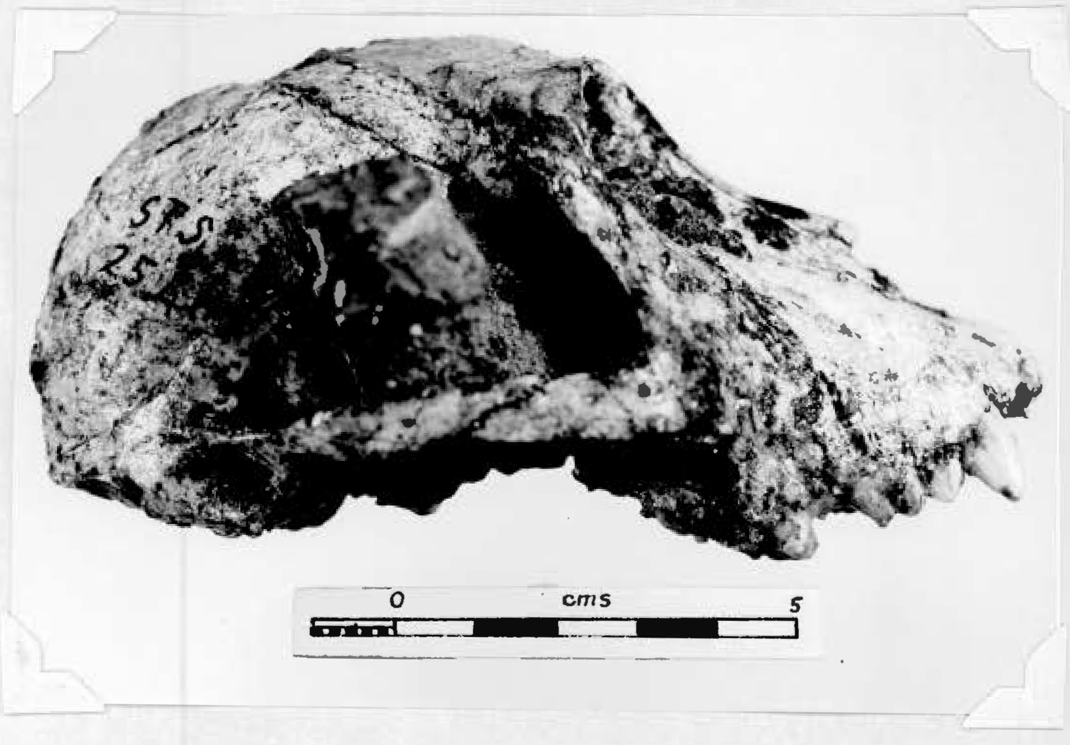

Fig.24. Parapapio broomi female (STS.254A). Skull- lateral view. x 1.

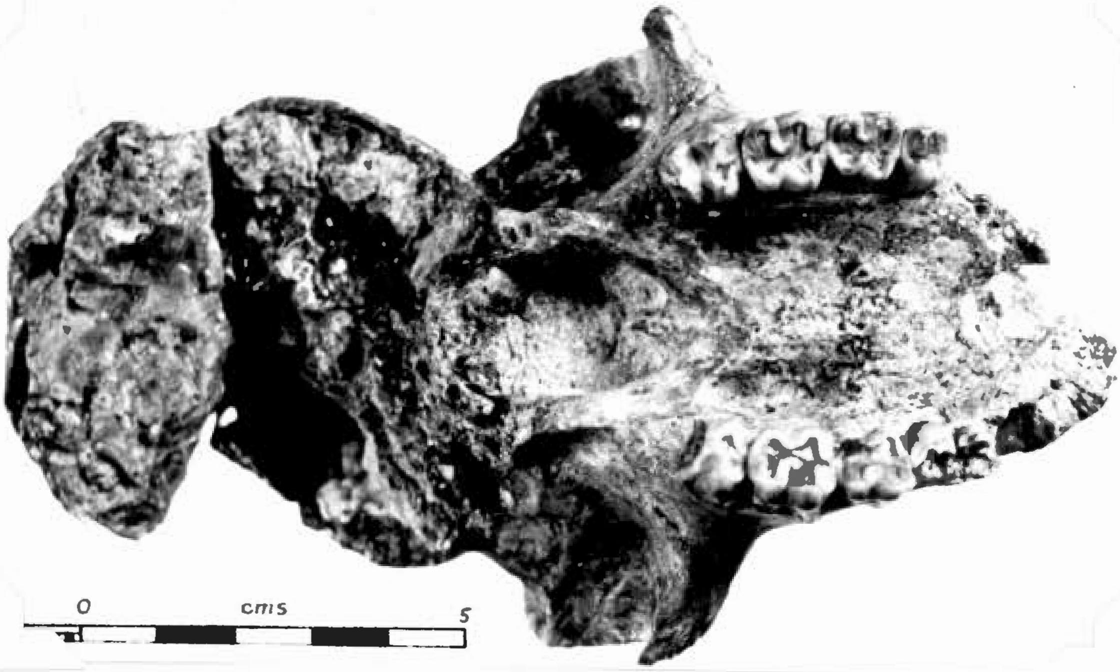

Fig.25. *Parapapio broomi* male (M.202). Skull - basal view. x 1.

Fig.26. *Parapapio broomi* female (STS.266). Occlusal view of upper teeth. x 1.

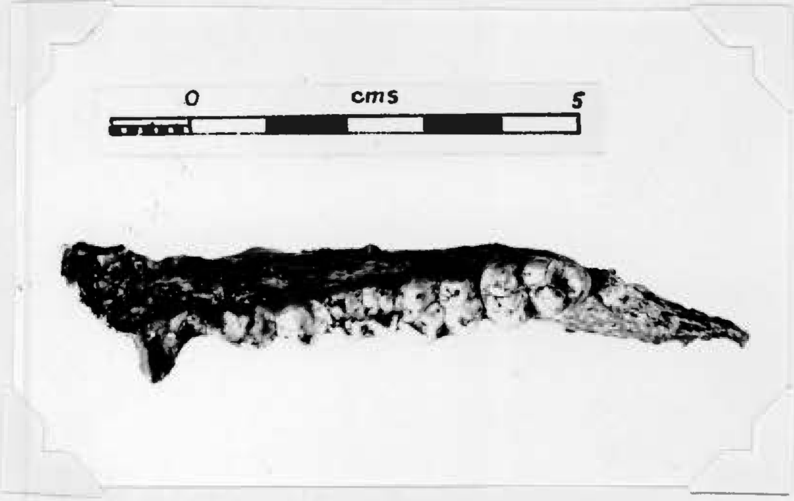

Fig.29. *Parapapio broomi* male (STS.414A). Occlusal view of lower teeth. x 1.

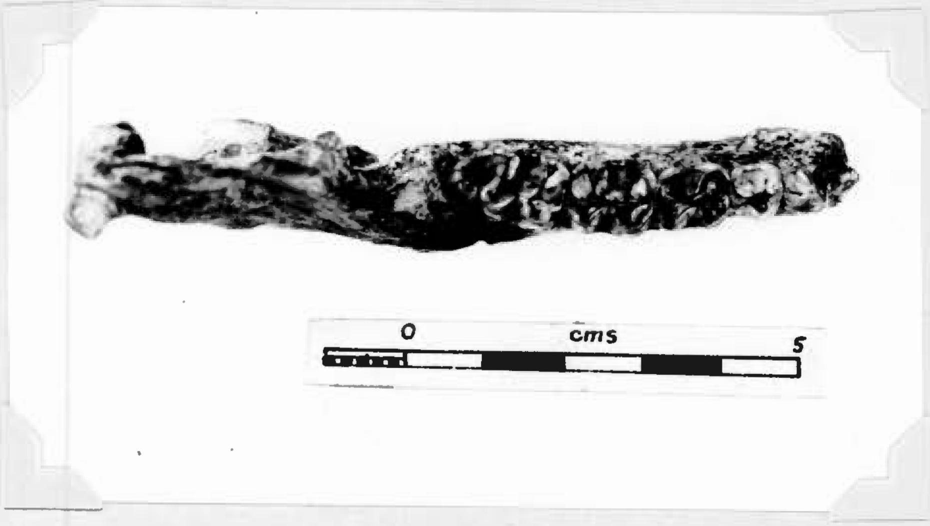

Fig.30. *Parapapio broomi* female (STS.562). Occlusal view of lower teeth. x 1.

of variation (see table 5d) but its structure is essentially the same as in the chacma baboon. As in the upper jaw, the lower molars are very similar in morphology and size relationships to the equivalent teeth of P.ursinus but, as has been stated, the male and female teeth cannot be separated. on size. The overall shape of the lower molars seems more variable generally than those of P.ursinus. A mesio-buccal groove, as in the chacma baboon, is commonly present on the buccal surface. A disto-buccal groove is also present on the buccal surface of M_2 of a few specimens (e.g. STS.411A, STS.353 and STS.268). Some specimens (e.g. M.213) show an exceptional amount of wear of the teeth and were presumably very old individuals.

Measurements:

See tables 5a, b, c and d.

Remarks:

In dental size, this species lies about midway between Parapapio jonesi and P.whitei. There is, however, insufficient skull material of these two species for comparison with P.broomi. In addition, P.broomi is very similar in skull and tooth size to Parapapio antiquus but differs from this species in the shape of the muzzle ~~dorsum~~ (see comparison under P.antiquus). In dental morphology, these four Parapapio species are all very similar except for the reduction of the distal part of M^3 in the female of P.antiquus.

Parapapio jonesi Broom.

Parapapio jonesi - Broom, 1940.
Parapapio jonesi - Broom, 1946.
Parapapio jonesi - Kitching, Wells and Westphal, 1948. (60M)
Cercopithecoides williamsi - Broom and Hughes, 1949 (60M, M.215)
Parapapio jonesi - Dart, 1949.
Parapapio jonesi - Hopwood and Hollyfield, 1954.

Holotype:

A damaged female skull, STS.565, with almost full dentition

Repository of type:

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

Type site:

Sterkfontein, Transvaal, South Africa.

Referred material:

Twenty-four specimens from Sterkfontein, three from Makapan, three from Swartkrans, two from Kromdraai and one from Taungs. (For the numbers of these specimens, see tables 6a, b, c and d).

Description: (Figs. 31 - 38).

Of the male skull, only two badly damaged muzzles are known (STS.250 and STS.367). In STS.250, which is the more complete specimen, the nasal bones slope downwards considerably more steeply than in the Parapapio broomi male. The muzzle must therefore have been relatively (as well as absolutely) shorter. In both the above specimen and STS.367, the two halves of the muzzle dorsum also slope down laterally rather steeply. On the more vertical lateral sides of the muzzle, there are shallow maxillary fossae present. The infra-orbital foramina are multiple in both of the above specimens. The type skull, STS. 565, is the only female skull known. It is extensively damaged and, although the muzzle is fairly complete, all that remains of the calvarium is a poor, damaged endocranial cast, with only small areas still covered by bone. This skull only appears to differ significantly from that of the female P.broomi in its smaller size.

Of the male upper dentition, there are only the very worn and damaged teeth of the two specimens mentioned above. Of the female, in addition to the teeth of the type skull, there are, among others, two very good specimens, STS.547 and STS.372A. Parts of the upper incisors can be seen on STS.547 and C is present in STS.372A but all the other specimens of both sexes have only premolars and molars present. However, the alveolus of STS.250 shows that the male C was large. None of the available upper teeth, as far as can be seen, show morphological differences from the teeth described for P.broomi except that the female C appears to be rather more similar to that of the female of P.ursinus.

This latter tooth does not lean as much buccalward, nor is the measurement from the mesial surface to the disto-lingual edge relatively as great, as in *P.broomi*. There are mesio-lingual grooves present on the lingual surfaces of most of the molars and on the right M^2 of STS.372A there is a lingual accessory cusplet. The table of the upper tooth sizes of this species (table 6c) shows that, in size, the specimens from Swartkrans, Taungs and Kromdraai fit this species well. As far as can be seen, they are also similar in structure.

The known mandibles of *P.jonesi* from Sterkfontein are very similar to those of *P.broomi*. No male specimen with an intact symphysis is known but the anterior surface of the female symphysis is not very steep (STS.355) and two converging ridges are present on this surface. The incisal shelf in the female may be long (STS.355), reaching back to the level of the distal end of P_3, or it may be shorter (STS.390A), ending at about the level of the middle of that tooth. The mental foramen is single in the female (STS.355). Neither of the above mentioned female specimens nor the male specimen, STS.542, has a mandibular fossa present. In the female specimen STS.390A, the posterior edge of the ramus is turned inwards as in the *P.broomi* female. From the cast of the ramus of STS.542, it is apparent that in the male the sigmoid nothh was very shallow.

The small female *P.jonesi* mandible from Makapan (M.215, 60M.) shows much the same structure as the above specimens but the two female specimens from Swartkrans (SK.414 and SK.573A) are rather different. In both of the two from Swartkrans, the symphysis has a narrow, constricted appearance when viewed from the front - probably mainly because of the fairly large and quite deep mandibular fossae on the lateral surfaces of the corpora. The anterior surface of SK.414 slopes very gradually as in the *P.broomi* female (STS.363); in SK.573A, the slope of this surface is considerably steeper. The incisal shelf on SK.573A is steeper than that of SK.414 but both are fairly long reaching back to the level of the distal part of P_3. SK.573A also shows the same inward turning of the posterior edge of the ramus as was described in the *P.broomi* and Sterkfontein *P.jonesi* specimens. The mental foramen is multiple in both specimens. More material is required before the importance of the differences in these latter two specimens can be evaluated.

As regards the lower dentition, there are a fair number of specimens of both sexes known but female specimens again predominate. Except for incisors, which are only present in one female specimen (STS.355), all the different types of tooth of both sexes are well represented. The female $\overline{C}$ is more similar to that of the *P.ursinus* female than is that of the female of *P.broomi*. It is, relatively, neither as short in height nor as broad mesio-distally as in the latter species. Mesio-buccal grooves on the buccal surfaces of the molars are only present on a few of the specimens. The apparent frequent absence of these mesio-buccal grooves may well be due to the great amount of wear on the known molars which makes it difficult to ascertain for certain whether these grooves were present or not. Other than on the above points, the lower teeth are morphologically indistinguishable from those of *P.broomi*; in size, they are smaller but with some overlapping of the *P.broomi* sizes. P_3 is as variable in both sexes of this species as it is in *P.broomi*. The lower teeth of the specimens from Makapan, Swartkrans and Kromdraai match those from Sterkfontein in morphology and also in size (table 6d). As in *P.broomi*, the sizes of the male and female (upper and lower) molars overlap.

Measurements:

See tables 6a,b,c, and d.

Remarks:

P.jonesi is the smallest of the *Parapapio* species and it is primarily based on the group of specimens from Sterkfontein. Only a very few specimens are known from Makapan, Swartkrans, Kromdraai and Taungs which appear to match those specimens, and these are mostly small fragments. Because of the difficulties in the taxonomy of the *Parapapio* species discussed earlier, it would seem possible that, when more complete material becomes

Table 6a. Measurements of the skull of *Parapapio jonesi*.

	Males		Females
	STS.250	STS.367	STS.565
GENERAL.			
Greatest length			(135)
Bizygomatic breadth			(85)
CALVARIUM.			
Breadth:			
Min. inter-frontal			(50)
Greatest temporal			68
Mastoid			70
Length:			
Inion-glabella			(88)
MUZZLE.			
Height:			
Ant. to P^3	45		22
Breadth:			
Ant. to M^3		48	46
Ant. to P^3	39		35
Dors. to M^2		42	30
Length:			
Muzzle			(65)
Palate			51
Orbit:			
Inter-orbital			10
Height			23
Breadth			26
Nasal aperture:			
Breadth		17	
Length		34	

Table 6b. Measurements of the mandible of *Parapapio jonesi.*

	Males			Females					
	STS. 542	STS. 255	STS. 348	STS. 390A	STS. 356	M.212	M.215, 60M.	SK. 414	SK. 573A
Height:									
Gonion-condyle	57			48					
Gonion-coronoid	58								
Post. to M_3	29	31		26				21	22
Ant. to P_4	26		26	25	27	26	21	20	25
Mental sp. to most ant. pt.				26	26	(24)	(21)	28	28
Breadth:									
Bigonial				43					
Post. to M_3								54	
Ant. to M_3				40				43	41
Ant. to P_4				29	29	(27)	27	24	27
Through mental sp.					21			21	18
At base of canines				21	23		20	21	21
Length:									
Gonion to mental sp.	65			56					55
Ramus at condyle neck	31			(28)					
Condyle to most ant. pt.				98					
Angles:									
Ramus to corpus				116°					
At symphysis								139°	
Between corpora				32°			40°	43°	

Table 8c. Measurements of the upper teeth of *Parapapio jonesi*.

	I^1			I^2			C				P^3		P^4		M^1			M^2			M^3			Rows	
	h	b	l	h	b	l	h	b	l_1	l_2	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	P^4-M^3	C - M^3
MALE:																									
STS.367																	(9.3)			10.8	10.8	8.0	10.1		
STS.250											7.5	(4.3)	7.7	(5.6)	9.0	8.6	7.5	10.4	9.6	9.5	10.9	8.9	10.4	(32.5)	
FEMALE:																									
STS.565											6.7	3.5	7.5	5.8	8.9	7.7	8.6			(9.6)	9.5	7.4	9.0	33.3	45.0
STS.547	11.0		6.9	8.5		4.9					7.3	6.8	7.7	6.4		8.4	9.5	10.7	9.2	10.5	10.0	8.1	9.9	34.2	
STS.576A							9.0	6.0	*(6.1)		7.3	6.5	7.8	6.3	8.7	7.4	8.9	10.2	8.5	10.5	10.1	8.1	10.0	33.3	
STS.456											6.9		7.6	5.5	8.7		8.7								
SK.543							7.1	(5.0)		(5.3)	7.6	(4.7)	7.9	6.0	9.0	(8.9)	8.2			(10.6)					
SK.576	8.3	6.7	6.5	5.5	6.1	4.9	7.5	6.6	*(6.0)		6.7	5.4		6.5	8.6	7.6	8.8								
? SEX:																									
KA.175																	8.7	9.6	8.9	9.9	9.4	7.9	9.7		
T.14													8.2	7.1	8.3	7.9	8.4	9.7	9.4	9.8					

* These figures are means for l_1 and l_2 which could not be taken separately because of damage.

Table 6d. Measurements of the lower teeth of *Parapapio jonesi*.

	I_1			I_2			$\overline{C}$			P_3		P_4		M_1			M_2			M_3				Rows	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	$P_4 - M_3$	$\overline{C}-M_3$
MALE:																									
STS.379B											15.5	7.6	(7.0)	(8.4)	(8.2)	10.8	10.0	10.0	10.8						
STS.343												7.3	7.5			8.4	9.3	9.0	11.1	9.5	8.3		15.3	39.9	
STS.348								6.9	6.0	5.0	11.8	6.3	6.4												
STS.370										6.0	17.2	6.4	7.0	7.8	8.0	9.4	9.1	9.0	11.0	9.3	8.4		(15.3)		
STS.396										5.7	15.8	7.3	6.8												
STS.337						5.8	17.5	(10.5)	(6.4)	5.2		7.3	7.5	8.0	7.9	8.2	(9.8)	9.8	10.7						
STS.358										5.3	15.7	6.6	7.0	8.1	8.2	9.5	10.0	9.9	10.5	10.0	9.3	4.6	15.0		
M.211,59M. B.P.I.										5.3	16.7	7.0	7.2	7.5		8.7									
FEMALE:																									
STS.409										4.7	7.2	6.3		7.4	7.5	7.8	9.3	9.1	9.6	9.1	8.3	4.6	12.8	36.1	
STS.366	7.1	6.3	4.9	6.0	6.2	4.3	8.3	7.1	4.1	4.7	8.5	6.3	6.5	7.3	7.2	8.9	9.1	9.2	10.4						
STS.374 A-B										5.0	8.7	6.3	6.4	7.5		8.8	9.1	9.0	10.2	9.3	8.3	4.8	12.4	37.3	
STS.381							10.3	7.7	3.4	4.5	9.3	7.3	6.4			(7.0)	9.8	8.7	10.5	9.6	8.6	5.5	12.8	36.0	50.2
STS.449												7.2			7.9	8.4	9.5	9.1	10.4		9.2		13.3	38.1	(50.5)
1238/12												6.0	6.8	6.9	7.4	8.5	8.7	8.5	10.6	8.8	7.9	5.0	13.2	39.1	
STS.317							8.6	7.6	(4.1)	5.5	10.0	6.8	6.8	7.4	7.2	9.0									
STS.380										5.0	9.6	6.4	6.2	7.4		8.2	9.1		10.7					(39.3)	
STS.313										(4.9)	(8.3)	6.3	7.0						10.3						
STS.390 A-B							13.9	7.3	4.8	5.4	9.7	7.0	6.3	7.6	7.4	9.0	9.9	9.4	11.0	9.4	7.9	5.3	13.0	39.2	
STS.399										5.3	8.8			7.6	7.7	8.8	9.3	9.2	10.4						
SK.414										4.5		6.3	7.1	7.3	7.6	7.9	9.0	9.1	10.1	9.2	8.3	5.5	13.2	38.4	
SK.378A	2.0	6.2	4.3	2.5	6.2	5.2	6.0	7.0	4.4	4.4	7.0	6.6	7.1	7.4	7.7	8.8	9.1	8.7	10.1	9.3	8.3		12.4	37.1	50.2
M.215,60M								6.7	5.9	5.0	7.7	5.7	6.0	6.7	6.7	8.7	7.6	7.3	9.5				11.0	34.8	48.2
M.213										5.0	9.6	5.9	6.7	7.3	7.3	9.0	(9.3)	8.4							
? SEX:																									
KA.176																	9.5	9.1	(10.5)	9.3	8.1	4.8	12.1		

Fig.31. Parapapio jonesi female (STS.565). Skull - dorsal view. x 1.

Fig.32. Parapapio jonesi female (STS.565). Skull - lateral view. x 1.

Fig.33. *Parapapio jonesi* male (STS.250). Occlusal view of upper teeth. x 1.

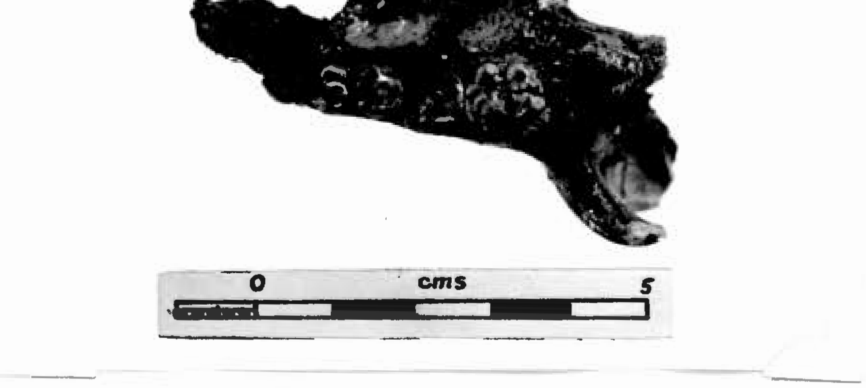

Fig.34. *Parapapio jonesi* female (STS.372A). Occlusal view of upper teeth. x 1.

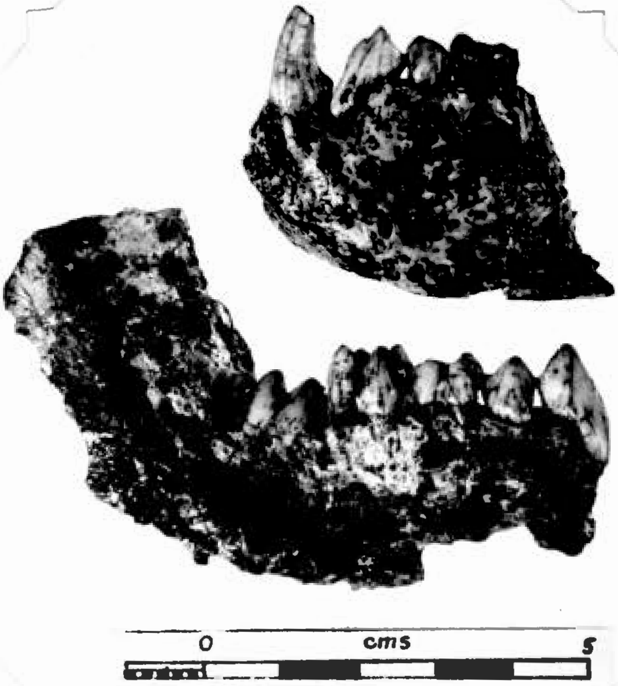

Fig.35. *Parapapio jonesi* male (STS.348, above and STS.270, below). Lateral view of mandibular fragments and lower teeth. x 1.

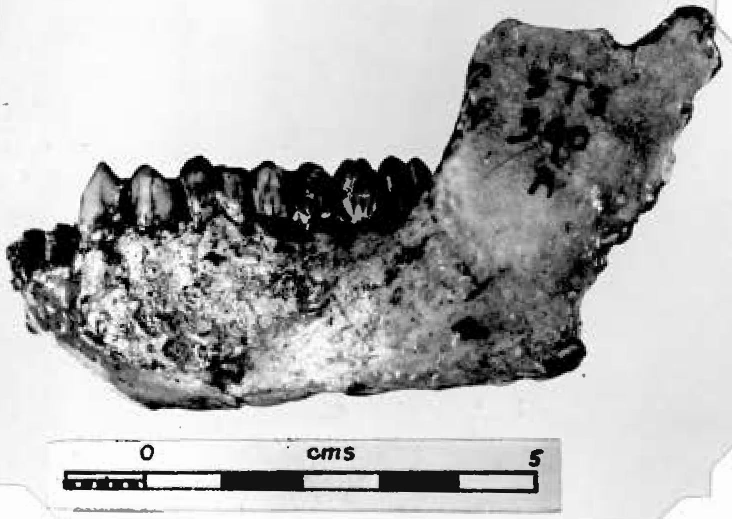

Fig. 36. *Parapapio jonesi* female (STS.390A). Mandible - lateral view. x 1.

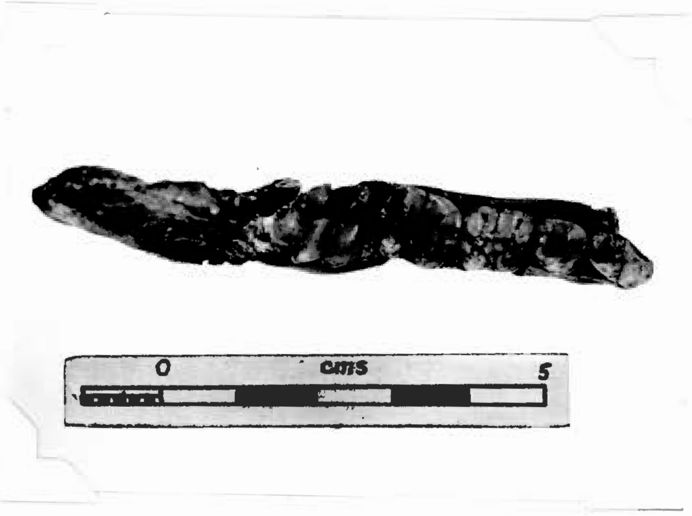

Fig.37. Parapapio jonesi male (STS.270). Occlusal view of lower teeth. x 1.

Fig. 38. Parapapio jonesi female (STS.390A). Occlusal view of lower teeth. x 1.

available, the specimens from one or other of these sites may well turn out to belong to a separate species or, more likely, subspecies of *P. jonesi*. The Swartkrans specimens, of which only two good lower jaws and a maxillary fragment are known, already suggest that they should have subspecific status. It would seem best for the present to consider the specimens, other than those from Sterfontein, as being provisionally referred to *P. jonesi*.

Parapapio whitei Broom.

Parapapio whitei - Broom, 1940.
Parapapio whitei - Broom, 1946.
Parapapio whitei - Broom, 1948.
Parapapio whitei - Dart, 1949.
Parapapio whitei - Broom, and Robinson, 1950.
Parapapio whitei - Hopwood and Hollyfield, 1954.

Holotype:

Right half and the anterior part of the left, of a female mandible, STS.563. $I_1 - M_3$ present on the right and $I_1 - P_4$ on the left.

Repository of type:

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

Type site:

Sterkfontein, Transvaal, South Africa.

Referred material:

Thirteen specimens from Sterkfontein. (For the numbers of these specimens see tables 7a, b and c). Female specimen STS.259 is the only known skull fragment of any size. It consists of the premaxilla, most of the maxilla and a small piece of the nasal, of the left side of the muzzle - all rather distorted.

Description: (Figs. 39 - 44).

The muzzle dorsum of the female, STS.259, slopes laterally downwards quite steeply from the side of the nasal. There is no trace of a maxillary ridge separating the dorsum from the more vertical lateral surface of the muzzle. The lateral surface of the muzzle slopes outwards slightly from the muzzle dorsum to the alveolar margin and there appears to be no maxillary fossa present. The zygomatic process of the maxilla is situated at about the level of the centre of M^3.

There are no upper incisors of either sex known and only two female specimens (STS.259 and STS.370B) have *C* tooth. The female *C* on STS.370B is by far the better preserved of the two specimens and it is very similar in shape to that of the female *P.broomi* i.e. it is relatively shorter in height but longer (mesial surface to disto-lingual edge) than the equivalent tooth of the *P.ursinus* female. The other specimen, STS.259, is very badly worn but also shows the increased length. From the alveolus on the male specimen (STS.389B) it is apparent that the male *P.whitei* *C* was about as large as that of the male chacma baboon. (The dimensions of this alveolus would make the approximate measurements of the male *C*: breadth, 11.5 mm; distal surface to mesio-lingual edge, 10.5 mm; mesial surface to disto-lingual edge, 11.5 mm).

Of the upper post-canine teeth, only one tooth - a very worn P^4 of STS.389B - is known of the male but there are several female specimens having upper premolars and molars. The female premolars are very similar to those of the *P.broomi* and *P.ursinus* females in morphology but in size, they are slightly larger than either. In the female molars of *P.whitei* (and to a lesser extent in those of *P.broomi* as well) the length and the mesial breadth are more nearly equal than in *P.ursinus*. The lengths of the *P.whitei* female molars are similar to those of the female of *P.ursinus* but the breadths are slightly larger even than those of the male of that species. The dental size differences between this species and *P.broomi* are clearer than those between that species and *P.jonesi*. This is particularly the case in the breadths of M^2 and M^3 where there is almost no overlap at all. Mesio-buccal grooves are present on most of the *P.whitei* female molars and there are buccal accessory cusplets on M^1 and M^2 of

STS.263 and STS.370B. (The latter two specimens are listed separately in table 7b but they both, almost certainly, belong to one and the same individual).

Both male and female mandibles are known. The symphyseal region of the male mandible, STS.389A, is particularly heavy but, although bigger than that of the *P.broomi* males, it is not nearly as large as that of the *P.ursinus* males. The incisal shelf of this specimen almost reaches the distal end of P_3 but it does not slope down steeply. The anterior surface is also not very steep and its lateral converging ridges are not very marked. The damaged symphysis of the type mandible (STS.563), gives some idea of this region in the female. It would appear to have been very similar in structure to that of the *P.broomi* female. A very shallow mandibular fossa is present in both of the above specimens but, in the male, the mental foramen is multiple and, in the female, it is single.

The ramus of the male mandible, STS.533, is fairly well preserved and that of the female, STS.563, is in particularly good condition except that the top of the coronoid process is missing. Both of these specimmns show that, as in *P.broomi*, the lower part of the posterior edge of the ramus is turned inwards and, particularly in the female type specimen, it is also thickened and ridged. In STS.533 the sigmoid notch is very shallow. In both of the above mentioned specimens, there is a thickened ridge (crista endocondyloidea) on the inner surface of the ramus, which runs antero-ventrally from the condyle and disappears near the mandibular foramen.

Examples of all of the lower teeth are known but there are few specimens in all and almost all those of the male are rather badly damaged. The only available lower incisors and canines are on STS.389A, a male specimen and STS.563, a female specimen. The incisors, as far as can be seen, are very similar in structure to those of *P.broomi* and *P.ursinus* but, especially those of the male, are small when compared to their equivalents in the latter species. Similarly, the $\overline{C}$ teeth of *P.whitei* are very

Table 7a. Measurements of the mandible of *Parapapio whitei*.

	Males			Female
	STS. 369A	STS. 359	STS. 555	STS. 563
Height:				
Gonion-condyle			53	53
Post. to M_3		31	26	
Ant. to P_4	33		(31)	27
Mental sp. to most ant. pt.	40			34
Breadth:				
Ant. to M_3		49		
Ant. to P_4		34		
Through mental sp.	28			
At base of canines.	28			
Length:				
Gonion to mental sp.				62
Ramus at condyle neck				33
Condyle to most ant. pt.				114
Angles:				
Ramus to corpus			114°	121°
At symphysis				125°
Between corpora	46°			

Table 7b. Measurements of the upper teeth of *Parapapio whitei*.

	I^1			I^2			$\underline{C}$				P^3		P^4		M^1			M^2			M^3			Rows	
	h	b	l	h	b	l	h	b	l_1	l_2	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	$P^4 - M^3$	$\underline{C} - M^3$
MALE:																									
STS.369B													8.6	6.7			(10.4)								
FEMALE:																									
STS.259											7.7	4.5	8.3	5.8	10.0	9.2	9.7	12.3	11.1	11.8	12.8	11.0	13.1	37.9	51.7
STS.263											7.6	9.1	9.1	7.8	10.8	10.4	10.8	13.0	12.2	13.3					
STS.256													9.2	6.5	10.6	10.0	10.6	12.1	11.7	13.0			(13.4)	(41.3)	
STS.545											(8.3)	6.9	8.6	7.0	10.9	10.3	11.0								
STS.370B							16.0	7.0	7.3	(8.8)		9.2	8.7	7.4			10.7	13.0	12.0	13.2					
? SEX:																									
STS.305																		(13.6)	13.0	12.0	12.8	11.7	11.8		
STS.462																10.1		13.0	10.9	13.0					

Table 7c. Measurements of the lower teeth of *Parapapio whitei*.

	I_1			I_2			$\bar{C}$			P_3		P_4		M_1			M_2			M_3				Rows	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	$P_4 - M_3$	$\bar{C} - M_3$
MALE:																									
STS.342																(9.5)			(11.9)	11.1	9.6		16.8	(45.0)	
STS.369A	6.3	7.3		7.2	7.2	5.7		10.8	6.5	5.4	16.4	7.0	8.1			(9.8)									
STS.358										5.7				8.4	8.5	9.1	10.9	10.8	12.2	11.1	10.4	6.8	15.8		
STS.359										5.5		7.1	7.5	8.2	8.8	9.4	10.4	10.6	12.3	11.1	10.7	6.2	16.5	45.7	
FEMALE:																									
STS.363	9.0	6.8	5.8	9.0	6.4	5.3	14.8	7.8	6.5	5.5	10.8	7.4	7.2	8.4	8.7	9.9	10.6	10.3	13.0	11.2	10.8		(16.5)	(46)	(63)
STS.382										6.0	10.2	7.7	7.6	9.2	9.1	10.3	10.8	10.0	12.5	10.8	10.5		16.5	(46.0)	
STS.370A				11.0		5.0	12.4	(8.0)	6.5	5.8	(13.0)	6.5	8.0	8.4	8.5	10.5	10.5	10.6	13.4				(17.0)		

Fig.39. *Parapapio* *whitei* female (STS.259). Lateral view of maxillary fragment and upper teeth. x 1.

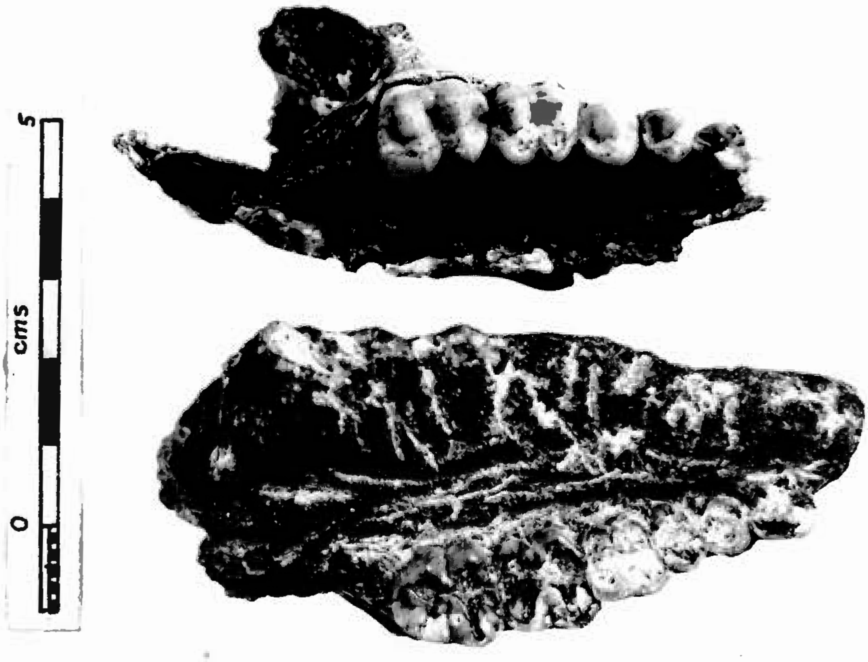

Fig.40. *Parapapio* *whitei* female (STS.263, above and STS.259, below). Occlusal view of upper teeth. x 1.

Fig.41. *Parapapio whitei* male (STS.389A). Lateral view of mandibular fragment. x 1.

Fig.42. *Parapapio whitei* female (STS.563). Mandible - norma lateralis. x 1.

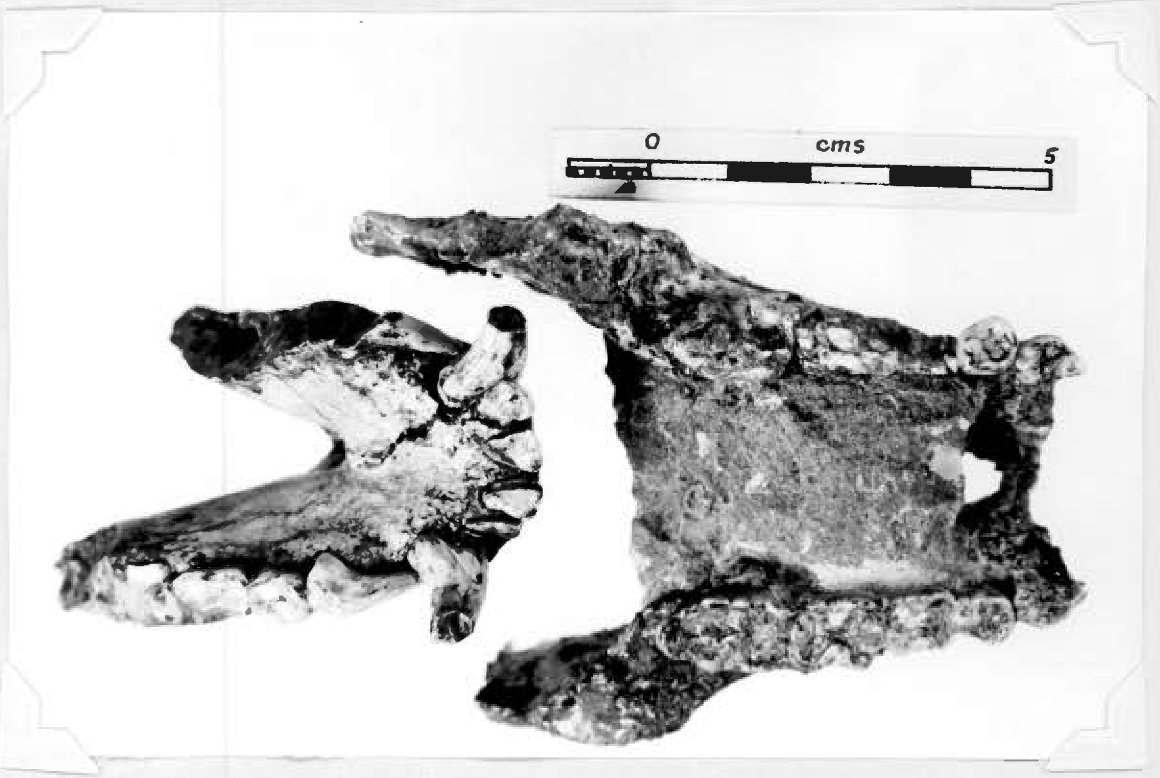

Fig.43. *Parapapio whitei* male (STS.389A, left and STS.359, right). Occlusal view of lower teeth. x 1.

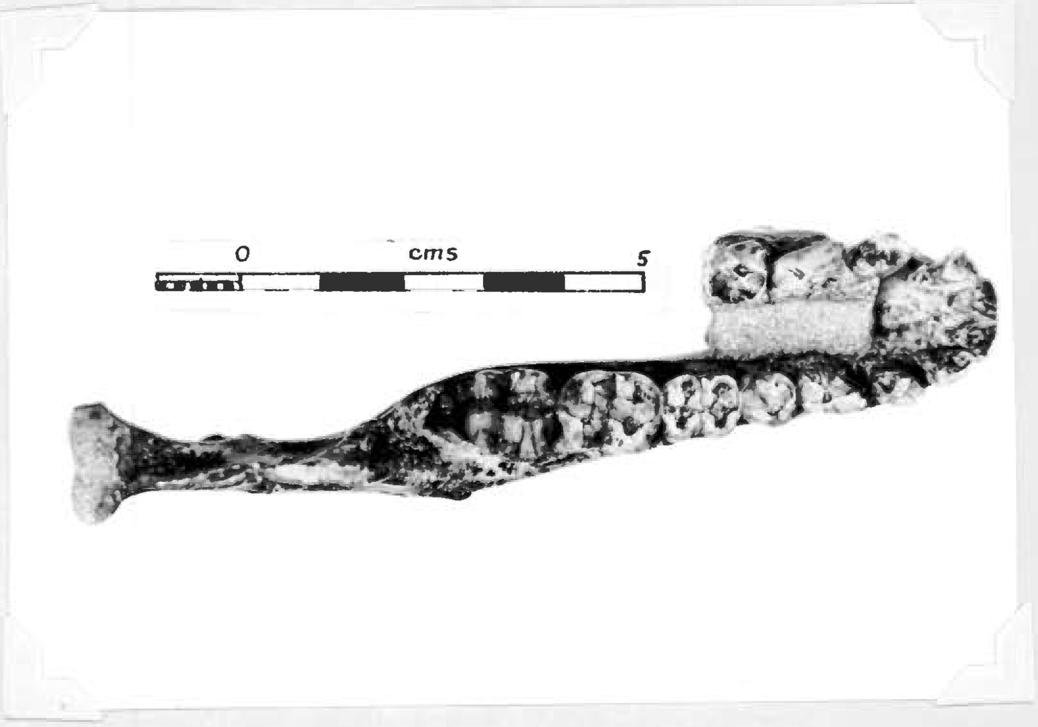

Fig.44. *Parapapio whitei* female (STS.565). Occlusal view of lower teeth. x 1.

similar in morphology to their counterparts in the above two species but, while the female tooth is about the same size as that in the female of P.ursinus, the male tooth is considerably smaller, particularly in breadth, than its equivalent in the male of that species.

The morphology of the lower premolars and molars of both sexes is again very similar to that of P.broomi and P.ursinus. The male teeth are too damaged and worn to show any detailed structure but in the females, there are mesio-buccal grooves on most of the molars and disto-buccal grooves on STS.563 and STS.370A. M_2 of STS.370A, and M_2 and M_3 of STS.563 and STS.352, have small lingual accessory cusplets. As in the upper teeth the dental size separation between this species and P.broomi is clear, particularly on M_2 and M_3. The lengths of the teeth of P.whitei are similar to those of the female of P.ursinus but the breadth dimensions are more similar to those of the males of that species.

Measurements:

See tables 7a, b and c.

Remarks

Morphologically the teeth of Papio and Parapapio are indistinguishable and, in this species, the shape of the muzzle dorsum in lateral view, one of the most important differences between these genera, cannot be determined. The main reasons for including this species in the genus Parapapio are (1) the absence of clear sexual dimorphism in the teeth, other than the C and P_3, and (2) the greater resemblance to Parapapio in minor details (e.g. the absence of a maxillary fossa and the lack of a maxillary ridge) of the single known (female) cranial fragment, STS.259.

Parapapio antiquus (Haughton).

Papio antiquus - Haughton, 1925.
Papio africanus - Gear, 1926.
Papio Africanus Haughton - Broom, 1934.

Papio africanus Gear	-Jones, 1937.
Parapapio africanus (Gear)	-Broom, 1940.
Parapapio africanus (Gear)	-Broom, 1946.
Parapapio antiquus (Haughton)	-Broom, 1948.
Parapapio africanus Gear	-Dart, 1949.
Parapapio africanus (Gear)	-Hopwood and Hollyfield, 1954.

Lectotype:

A skull (CT.5364) selected by Jones (1937), almost certainly of a male but lacking teeth and the posterior part of the calvarium.

Repository of type:

South African Museum, Cape Town, South Africa.

Type site:

Taungs, Cape Province, South Africa.

Referred material:

Eighteen specimens from Taungs. (For the numbers of these specimens see tables 8a,b,c and d). A number of calvaria and endocranial casts have, in addition, been referred to this species by Haughton (1925), Gear (1926) and Dart (1949). There are three fairly good specimens of the male skull: CT.5364, CT.5356 and T.10 (an immature adult), and two of the female: Tvl.639 and T.17 (muzzle only). which have been used for the description of the skull.

Description: (Figs. 45 - 54).

In the male, the skull is slightly larger generally than in the female and the muzzle is relatively slightly longer. The overall amount of sexual dimorphism in the skull does not, however, appear to be very great. In both sexes the nasal bones run almost straight from the glabella region to the posterior margin of the nasal aperture. Thus, when viewed in profile, the dorsal surface of the muzzle has only a very slight concavity. On the side of the nasal, the maxilla at first slopes down laterally at a slight angle only, then almost vertically from about the level of the centre of the infra-orbital margin to the alveolar margin. The resulting muzzle dorsum is considerably flatter than that in *P.broomi* and the lateral surfaces of the muzzle are also more vertical. A shallow maxillary fossa is present laterally on the side of the muzzle. Some twelve millimeters below the central part of the infra-orbital margin, there are four or five fairly widely separated infra-orbital foramina. The nasal aperture in both sexes is rather small but the orbits are fairly large and similar in shape to those of the female of *P.ursinus*. The zygomatic process of the maxilla is situated at about the level of the mesial half of M^3 and the zygomatic arch, in the male, is particularily robust.

The supra-orbital tori are weak in the female and only very slightly better developed in the male. The temporal lines can only be seen in two specimens (Tvl.639, a female and T.11, a specimen of doubtful sex). Both specimens have the lines well developed in the region from the tori, across the post-orbital constriction and onto the dorsal wall of the calvarium. Unfortunately, due to damage and weathering in both specimens, the lines cannot then be traced further clearly but it appears as if they then became very much weaker. In T.11, the only specimen in which the relevant region is undamaged, there is a transverse groove across the calvarium posterior to the supra-orbital tori. This groove is followed by a large eminence of the frontal but thereafter the parietals slope down quite rapidly to the inion. There is no evidence of a sagittal crest in either sex and even in the male the nuchal crest appears to have been very weak. Viewed from below, the dental arcade is horse-shoe shaped in both sexes but in the male, it is mesio-distally longer. There is no good specimen showing the base of the calvarium.

No upper incisors of either sex are available but from the alveoli in the male specimen CT.5364, it would seem that the male teeth were similar in size to those of the male of *P.broomi*. The size relationships and structure of the C of the two sexes (CT.5360 and T.22, two males and T.17, a female) are also similar to those seen in the type species of this genus. In the premolars too, these two species appear to be very similar but too few specimens are available, as in fact of all the anterior upper teeth, for an accurate comparison to be made.

The male upper molars are present in CT.5356, T.10 and T.22 but in the latter specimen they are too worn to be of value for description. T.10 has M^1 and M^2 present and almost unworn; CT.5356 has all three molars preserved but M^1 is badly damaged. These teeth all show the usual arrangement of the four main cusps and in both specimens there are small but well marked mesio-buccal cuspules. On both M^1 and M^2, T.10 has a mesio-lingual groove marking off what was probably a cuspule and there is also a fairly large lingual accessory cusplet on M^1 but only a minute one in the equivalent position on M^2. The upper molars of the female can be seen in Tvl.639, T.16, T.17, T.20 and T.25. (The latter two fragments probably come from the same individual). From table 8c it is not obvious how these teeth differ in size from those of the male but it would appear that they were probably, on an average, slightly smaller. An important dental morphological difference between the sexes is the considerable amount of reduction of M^3 in the female. This reduction is quite clear in all three of the female specimens in which this tooth is present. The tooth is considerably narrowed and reduced distally and both of the main distal cusps, but particularly the buccal one, are very small and low. T.20 and T.25 are comparatively well preserved specimens and show the mesio-buccal cuspules and mesio-lingual grooves described above in the male molars.

A comparison of the mandibles of the two sexes shows that the male mandible (T.12) is slightly longer than that of the female (T.18 and T.27). This male mandible also has a rather higher symphysis than that of the females and, in addition, shows traces of the anterior, converging ridges so often seen in this subfamily. In both sexes the foramen symphyseosum is present on the anterior surface of the symphysis and there is only an exceedingly shallow mandibular fossa on the corpus. Specimen AD.944 is the only one with an undamaged ramus but unfortunately the sex of the specimen is unknown. In this specimen the ramus is rather vertical and not very high but otherwise it shows no unusual features.

There are two poor specimens (T.12 and T.23) of the lower dentition of the male and three good specimens (T.18, T.21 and T.27) of the female. Specimens T.21 and T.27 show the female incisors well but there is only a small piece of one incisor present on a single male specimen (T.23). The female teeth are much the same size and structure as those of P.broomi and exhibit the same type of wear. No male $\bar{C}$ is available but female lower canines are present in T.21 and T.27. These teeth closely follow the pattern and size of the female P.broomi $\bar{C}$. In T.21 the $\bar{C}$ is very much worn down and, as described in the female of P.ursinus, the tooth in this stage of wear seems to form part of the incisor row. The male and female P_3 both show the typical structure and size relationships described throughout this genus. In P_4, both the male (T.23) and female (T.27) have the enamel extending a short distance down the buccal part of the mesial root; a condition similar to that in P^3 of Papio robinsoni. The few male and female molars that are not damaged conform closely in pattern and size to those of P.broomi. As in the upper teeth, there appears to be no definite size difference between the teeth of the two sexes. In size and structure, both the upper and the lower teeth, with the exception of the female M^3, are thus very similar to those of P.broomi.

Measurements:

See tables 8a,b,c and d.

Remarks:

The absence of any reduction of the male M^3 is rather unexpected as reduction is characteristic of all the known female M^3 teeth. This difference might seem to suggest that the specimens CT.5356 and T.10 which have hitherto been referred to this species as males, may actually be the males of another, or more probably the other, species found at Taungs, namely Papio izodi.

Table 8a. Measurements of the skull of _Parapapio antiquus_.

	Male		Female		? Sex
	CT. 5364	CT. 5356	Tvl. 639	T.17	T.11
GENERAL.					
Greatest length			(143)		
Bizygomatic breadth		(96)			
CALVARIUM					
Height:					
Basion-bregma			58		
Basion-glabella			70		
Breadth:					
Min. inter-frontal			(55)		53
Greatest temporal		78	69		
~~Mastoid~~					
Length:					
Inion-glabella			(90)		
Inion-basion			47		
MUZZLE.					
Height:					
Ant. to P^3	22			20	
Breadth:					
Ant. to M^3	48	51		46	
Ant. to P^3	36				
Dors. to M^2	37		35		
Length:					
Muzzle	85				(77)
Palate	66		63	(62)	
Nasal			34		37
Orbit:					
Inter-orbital	8.5		8		7
External orbital			74		70
Height	24.4		22.6		23
Breadth	25.2		26.6		25
Nasal aperture:					
Breadth	17.5		17		16
Length					27

Table 8b. Measurements of the mandible of <u>Parapapio antiquus</u>.

	Male	Female		? Sex
	T.12	T.18	T.27	AD.944
Height:				
Ant. to P_4		26	23	
Mental sp. to most ant. pt.	38	29	29	
Breadth:				
Post. to M_3	61			
Ant. to M_3	51	(42)	42	
Ant. to P_4	36	30	28	
Through mental sp.	39	24	23	
At base of canines	28	24	24	
Length:				
Gonion to mental sp.		(47)		
Ramus at condyle neck				31
Angles:				
Ramus to corpus				(101°)
At symphysis		138°		
Between corpora	37°	(27°)	25°	

Fig.45. *Parapapio antiquus* male (CT.5364). Skull - dorsal view. x 1.

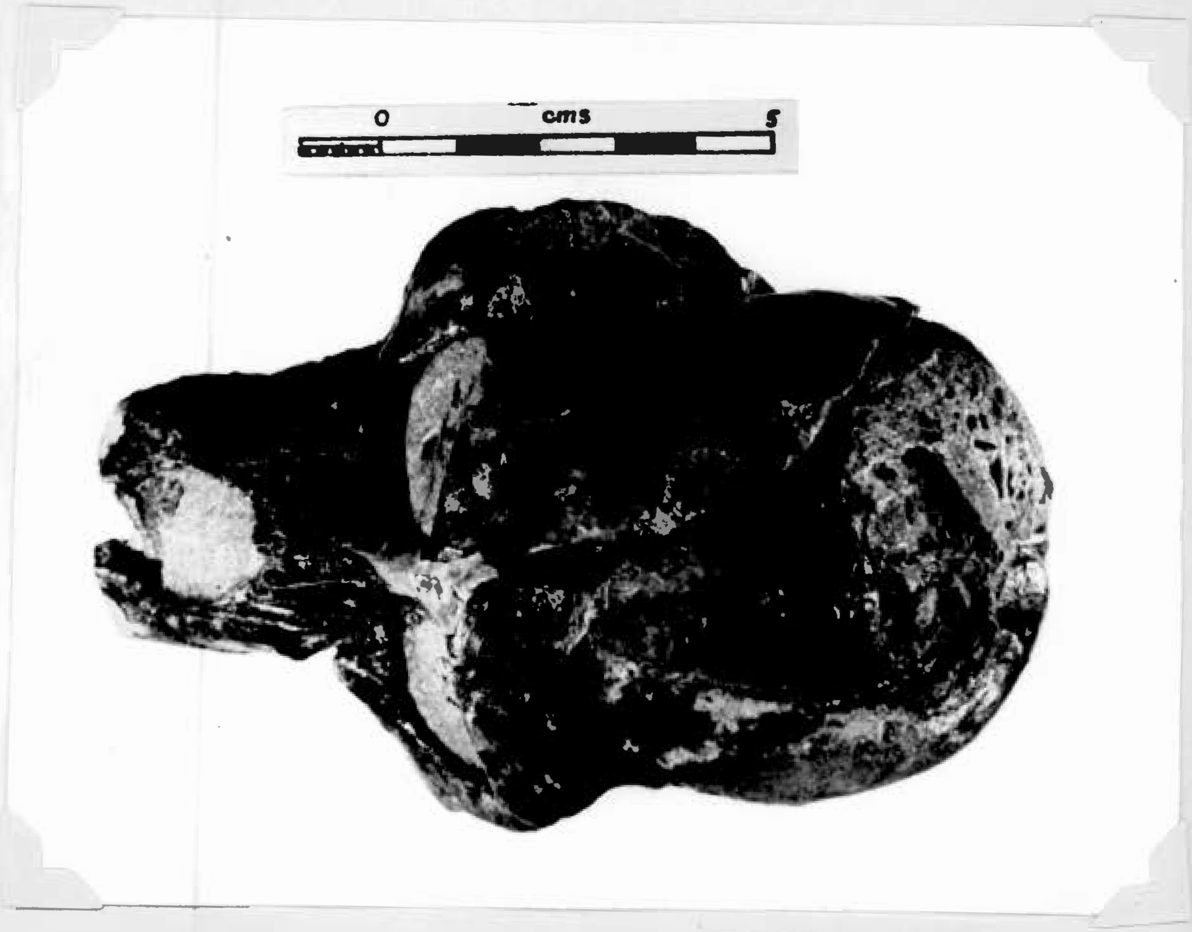

Fig.46. *Parapapio antiquus* female (Tvl.639). Skull - dorsal view. x 1.

Fig.47. *Parapapio antiquus* male (CT.5364). Lateral view of skull fragment. x 1.

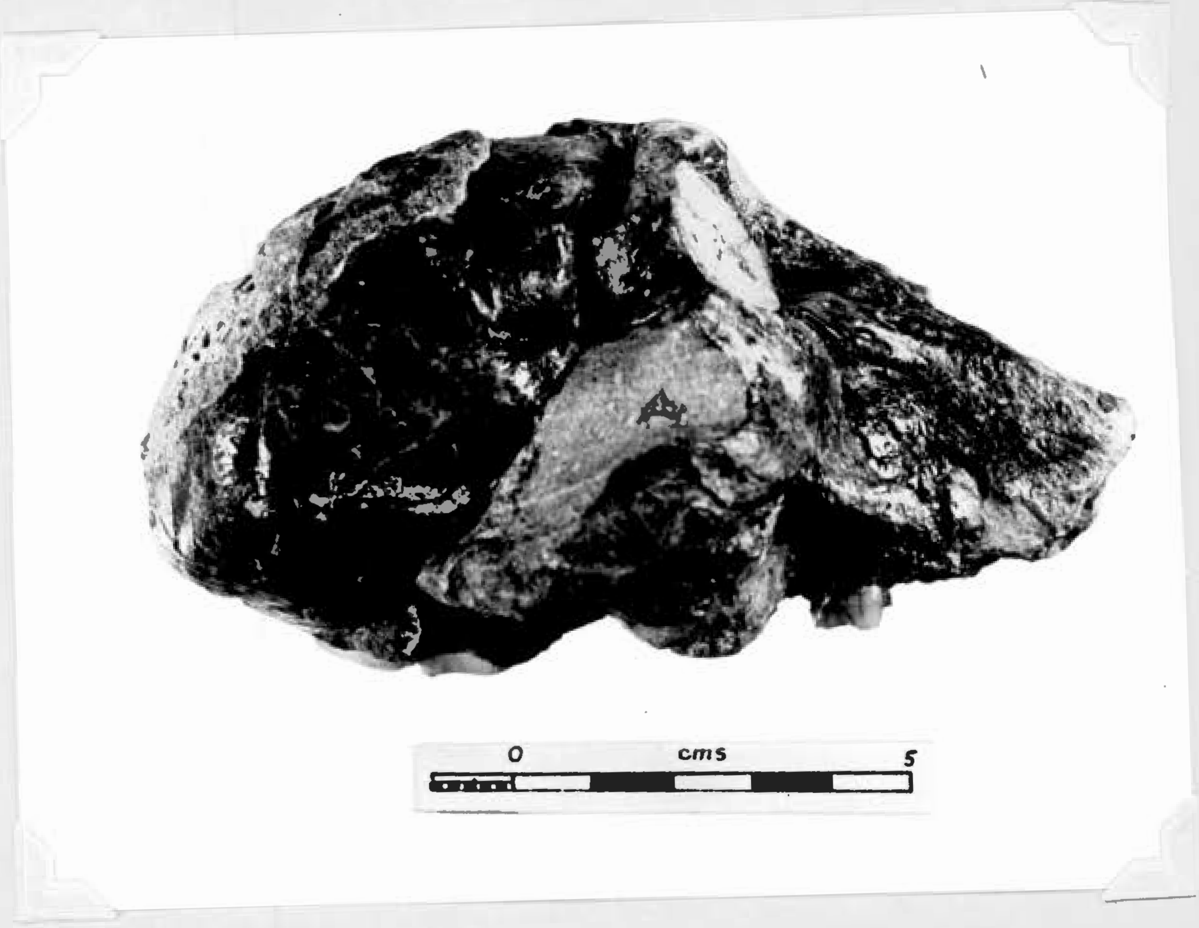

Fig.48. *Parapapio antiquus* female (Tvl.639). Skull - norma lateralis. x 1.

Fig.49. Parapapio antiquus male (CT.5356). Occlusal view of upper teeth. x 1.

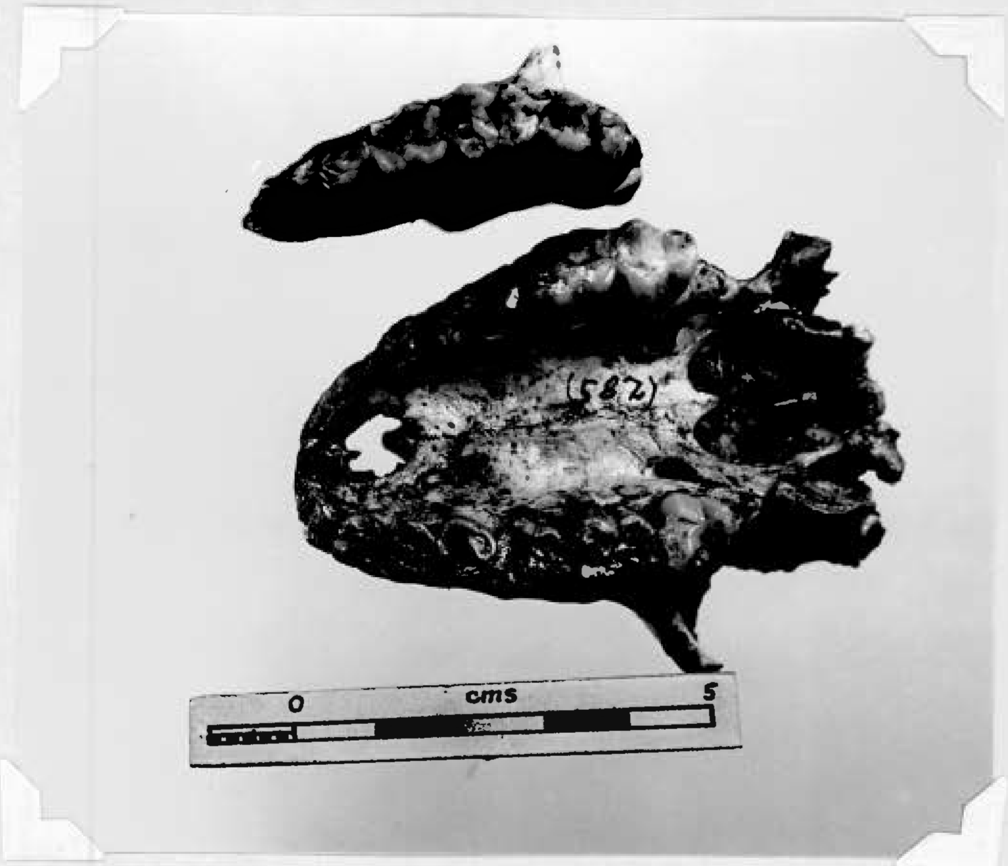

Fig.50. Parapapio antiquus female (T.25, above and T.17, below). Occlusal view of upper teeth. x 1.

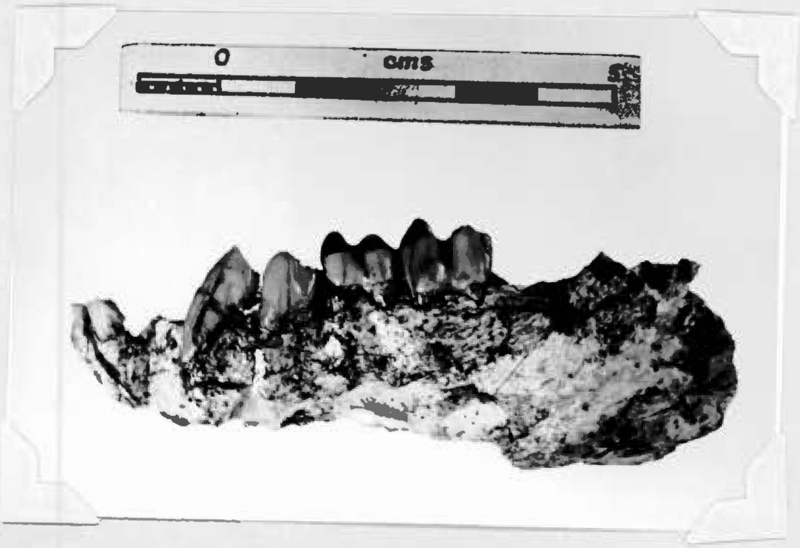

Fig.51. Parapapio antiquus male (T.23). Lateral view of mandibular fragment and lower teeth. x 1.

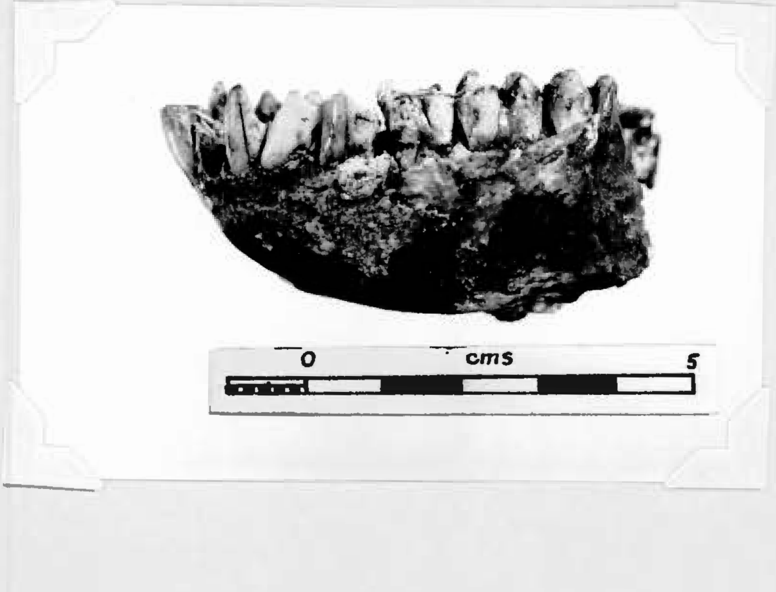

Fig.52. Parapapio antiquus female (T.27). Lateral view of mandibular fragment and lower teeth. x 1.

Fig.53. *Parapapio antiquus* male (T.23). Occlusal view of lower tooth fragments. x 1.

Fig.54. *Parapapio antiquus* female (T.27). Occlusal view of lower teeth. x 1.

(No males of *P. izodi* are known and the distal part of the female M^3 is only very slightly reduced).

Of the two specimens under discussion, CT.5356 is slightly damaged in the dorsal muzzle region but what remains quite clearly indicates that it could not possibly have had the sharp drop in the inter-orbital region associated with the latter species (see under *P. izodi*). Specimen T.10 does appear to have the sort of drop in this region which one would expect in a male *P. izodi* but the relevant region is considerably distorted. Further, the dentition of the specimen shows that it was still immature and immature specimens, due to the relatively large brain size, often have a short muzzle with a steep dorsal surface. The drop in the inter-orbital region could thus be due either to distortion or immaturity or to a certain amount of both. The teeth of this specimen match those of the previously described one (CT.5356) both in size and structure and it would seem therefore, on balance of evidence, that it too is a male of *P. antiquus.*

CHAPTER 8.

PAPIO.

This genus includes a number of living and fossil baboons of Africa and also certain fossil forms from the Lower Pleistocene of India. The first fossil cercopithecoid to be described from South Africa was assigned to the genus Papio and came from the lime deposits at Taungs in the Cape Province. This species was named Papio antiquus by Haughton (1925) but was subsequently transfered to the genus Parapapio by Broom (1940 and 1948) and is described with the species of that genus in Chapter 7. In the year following the publication of Haughton's species, Gear (1926) described another new fossil cercopithecoid from Taungs - Papio izodi. This form was also transferred by Broom (1940) to Parapapio but it would seem that its affinities are with Papio.

In 1936, Broom described the skull of a large fossil baboon which he found in the collection of the Transvaal Museum, Pretoria, as Papio spelaeus. Some years later (1946), together with Jensen, he described a fossil cercopithecoid mandible from the limeworks dumps at Makapan as another new species of this genus. As discussed elsewhere (Chapter 9) this species, Papio darti, was transferred to the genus Gorgopithecus by Kitching (1953). The type (and hitherto only known specimen) clearly shows the Simopithecus type of dentition and the species is therefore described in this study as Simopithecus darti.

It may be as well to mention here Remane's contention (1925), with which Dietrich apparently agrees (see below), that the differences between Simopithecus and Papio are insufficient to warrant separate generic status for the former. Remane's doubts as to the validity of the genus Simopithecus are due to insufficient skull material being available at the time he wrote and also to his failure to consider dental morphology in the genus. The description of the typical premolar and molar structure in Simopithecus (Chapter9) and also the descriptions of the skull of this genus in that same chapter and in Leakey (1943) make it abundantly clear that the genus is valid and differs considerably from Papio.

A new species of Parapapio (P.angusticeps) was established by Broom (1940) for some fossil cercopithecoid remains from Kromdraai, Transvaal. On the material then available, the species seemed to show a strong relationship to the Parapapio group but recent additional material, recovered from both the type site and Cooper's, which is only a short distance away, makes it quite obvious that this is a form of Papio. The species is therefore transfered to this genus. More new material, in this case from the nearby Swartkrans excavations, is clearly of a different, much larger species of Papio which is very similar to, but not identical with, the living chacma baboon. The name Papio robinsoni is proposed for this new species in honour of Mr. J.T.Robinson of the Transvaal Museum who has contributed greatly to our knowledge of both the fossil Cercopithecoidea and, more particularly, the Australopithecinae of South Africa.

In addition to these species, Wells (1943) has recorded a partial cranium of an old male Papio comatus (Papio ursinus) from Wonderwerk Cave, Kuruman, Cape Province, but the dating of this specimen is uncertain, although not older than Middle Pleistocene. Also, Peabody (1954) has listed "Papio (and related baboon genera)" from the Australopithecus Cave dry phase (lower level) and wet phase (upper level), Black Earth Cave (lower and upper levels), Witkrans Cave lower level (M.S.A.) and upper level (L.S.A.) and also Iscor - all sites on the Kaap Escarpment. It would appear that the material on which this list is based is at present being studied in America and no descriptions have so far been published.

From the more northern parts of Africa, Dietrich (1942) described a fossil cercopithecoid from Kenya which he named Papio (Simopithecus) serengetensis. (Dietrich thus apparently feels that 'Simopithecus' only merits subgeneric status). A good female mandible and a number of isolated teeth are known of this species from the grey tufa of various gorges in the South Serengeti - but no skull material has so far been found. Dietrich compares his material with the fossil species, *Simopithecus oswaldi* Andrews and the still living species, *Papio neumanni* (Matschie). (In 1939, Dietrich described some single teeth from the Lake Eyasi region (Laetolil), Tanganyika, as *Papio* sp. cf. *neumanni*).

As far as can be seen from Dietrich's drawings and photographs (and these are not very clear), the teeth of his species do not appear to show the typical *Simopithecus* molar pattern (see Chapter 9) and in size (see Appendix II) they are rather smaller than those of *S.oswaldi*. In both morphology and size, the teeth seem more like those of the small fossil forms of *Papio* and *Parapapio*, but without skull remains, it would seem unwise to attempt to classify this species generically.

Dietrich also mentions a fossil cercopithecoid from Olduvai IV described by Remane, according to Dietrich, as a "*Papio* (*S*) sp." - but he does not compare or describe that material. He is probably referring to the juvenile skull actually described by Remane (1925) as a "*Papio* sp." In this specimen only one permanent tooth, M^1, is fully erupted but M^2 is visible in its crypt. From Remane's photographs the teeth appear similar in structure to those of *Papio* (and *Parapapio*) spp. The dimensions of M^1 are: length - 10.9mm. and breadth - 8.5mm., which are smaller than the equivalents in *S.oswaldi* and *P.*(*S.*)*serengetensis*. (The dimensions (l x b) for *S.oswaldi* in millimeters are 12 - 13.5 x 10- 11 and for *P.*(*S.*) *serengetensis*, 11.5 x 10.5). Even though juvenile, the skull shape is clearly that of a *Papio* rather than a *Parapapio*.

Oakley (1954b) has recorded "teeth and two limb bones of a fossil baboon, probably a large species of *Papio*" from Twin Rivers, Northern Rhodesia, but as yet there has been no detailed description of these specimens. Recently Dr. H.B.S. Cooke kindly showed me a single isolated tooth which is one of the specimens referred to by Oakley. It is a male left upper canine of either a *Parapapio* or, more probably a small *Papio* such as *P.angusticeps*. The mesial groove is rather broad and there is a well developed wear facet on the disto-lingual edge. The top portion of the crown of the tooth is missing and the resulting surface is smooth but has two deep grooves running from the distal to the lingual surfaces. Although possibly caused by exceptional wear, damage or malocclusion, the shape of, and the grooves on, this surface also suggest the possibility that this tooth may have been artificially worked after death.

There are thus now five species of the genus *Papio* known from South Africa - four fossil (*P.izodi*, *P.robinsoni*, *P.angusticeps* and *P.spelaeus*) and one living (*P.ursinus*). They are all clearly separable on skull and tooth size and, in most cases, in skull morphology as well. Dental structure in the various species is very similar but there are certain comparatively minor differences.

Genus: *Papio* Erxleben, 1777.

Diagnosis: (as based on the South African fossil and living species only).

The genus is characterised, particularly in the males, by a long, secondarily elongated dog-like snout. In profile, the dorsal surface of the muzzle shows a sharp, distinct drop in the inter-orbital region and then a much more gradual slope down to the alveolar point. Particularly in the males, the muzzle dorsum is greatly flattened and the maxillary ridges are well developed. A maxillary fossa is usually present. The cusps on the molars are more or less sub-equal, although the mesial pair is almost invariably slightly larger than the distal. There is comparatively little development in these teeth mesial or distal to the four main cusps. Morphologically, the teeth are indistinguishable from those of *Parapapio*. Sexual dimorphism is marked in all the species of this genus.

The type species is *Papio papio* (Desmarest), 1820.

Papio izodi Gear.

Papio izodi - Gear, 1926.
Papio africanus - Broom, 1934. (Probably AD.946)
Papio izodi - Jones, 1937.
Papio izodi - Broom, 1940.

Papio izodi - Broom, 1948.
Papio izodi - Dart, 1949.
Papio izodi - Hopwood and Hollyfield, 1954.

Lectotype:

A badly damaged skull (AD.992), almost certainly of a female, selected by Jones (1937). Only fragments of three teeth are present.

Repository of type:

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

Type site:

Taungs, Cape Province, South Africa.

Referred material:

Three specimens all of which come from Taungs. AD.946 is a female muzzle with its badly damaged mandible still attached; T.13, a muzzle with teeth, by comparison with AD.946, is virtually certainly also a female specimen although it lacks canines: CT.5357 is an endocranial cast and damaged mandible of an individual of unknown sex but from its overall size, probably also a female. No male specimens of this species are thus known. (Specimen AD.993, which was included in this species by Gear (1926), has not been discussed as it consists of a calvarium only and its affinities would seem to be uncertain).

Description: (Figs. 55 - 58).

The muzzle of AD.992 is slightly crushed and distorted, and a small portion of the inter-orbital region of AD.946 is missing. Never-the-less, from both of these specimens it is clear that in the female of this species, there is a sharp drop in the inter-orbital region followed by a more gradual slope down to the posterior margin of the nasal aperture. The concavity in this region, as seen in profile view, is almost as great as that in *Theropithecus gelada*. Although most of the calvarium is missing in the specimen with the complete muzzle (AD.946), and the anterior part of the muzzle is lost from the specimen with the complete calvarium (AD.992), it is still obvious that the female muzzle was relatively long and snout-like

In AD.946 it can be seen that the zygomatic process of the maxilla is situated at about the level of the mesial half of M^3 and there appear to be three infra-orbital foramina on the maxilla below the orbit. In neither of the two female specimens described above is there any trace of a maxillary fossa on the lateral surface of the muzzle. A notable difference between the female of this species and that of _Parapapio antiquus_ is shown in the coronal sections through the posterior part of the rostrum of the muzzles of the two species (Gear 1926). The outline of such a section takes the form of a smooth curve in _P.izodi_ whereas in _P.antiquus_ it is very rectangular and forms roughly three sides of a square.

From the small portion preserved, it would seem that the supra-orbital tori were moderately developed in AD.946 but rather less well developed in AD.992; in both of these female specimens there is a shallow transverse groove running across the calvarium behind the tori. In AD.992, the only specimen known with certainty which has the calvarium fairly well preserved, there is a slight eminence of the frontals in the midline behind this groove. On the right frontal bone of this specimen, a small section of the temporal line can be seen and it is fairly well developed. A portion of the dorsal wall of the calvarium is then missing but the line can again be traced on the posterior part of the parietal. Here it is very weak and runs almost parallel to, and about 20 mm. from, the sagittal suture. (There is of course no sagittal crest present). At about the level of the lambda, the line swings laterally to join a ridge in this region which is described below.

Just below the lambdoid suture a prominent ridge is formed around the back of the skull. There is a broad, fairly deep groove above it and a shallower one below. Laterally,/the ridge becomes weaker and eventually, after being joined by the temporal line (as described above) it appears to join the very weak nuchal crest below it. (One cannot be quite certain of this as the bone in the mastoid region is badly damaged). In the midline, the crest of the ridge is about 12 mm. above the nuchal crest and probably forms the most posterior part of the calvarium. The inion region has unfortunately been lost and the base of the skull is too badly damaged to show any detailed structure.

The upper dentition of AD.946 is mostly still embedded in matrix and all that remains of the teeth of AD.992 are three broken molars. Fortunately, specimen T.13 has all three molars present and well preserved. From the buccal surfaces of the upper teeth of AD.946, the only parts of these teeth visible, it can be seen that the central incisor is larger than the lateral and that the latter tooth does not lean strongly mesially as in most other _Papio_ species. One can also see that the _C_ is of the small female type and the two premolars both appear to lean distally. The molars on T.13 show no unusual features and in size are similar but possibly slightly larger than those of _P.antiquus_. Unlike the latter species, there is only very slight reduction of the distal part of M^3. There appear to be small subsidiary mesio-lingual cuspules present on all the molars.

The sex of the best available mandible (CT.5357), cannot be determined with certainty but, as stated above, is probably that of a female. The upper anterior part of the symphysis and both rami have unfortunately been lost from this specimen. The only feature worthy of comment on the damaged corpora is the absence of mandibular fossae. The only other known mandible, AD.946 is from its small canines clearly that of a female. It is however, too damaged and eroded to be of any value at all for description. Most of the buccal surfaces of P_3 and P_4 of AD.946, and the buccal and occlusal surfaces of M_2 and M_3 of both this specimen and CT.5357 can be seen. From this restricted view of the lower dentition all that can be ~~stated~~ concluded is that these teeth appear to show no variations from the _Papio-Parapapio_ pattern. On both M_2 and M_3 there are mesio-buccal

Table 9a. Measurements of the skull of *Papio izodi*.

	Females.		
	AD.992	AD.946	T.13
GENERAL.			
Greatest length	(138)		(130)
CALVARIUM.			
Height:			
Basion-bregma	60		
Basion-glabella	72		
Breadth:			
Min. inter-frontal	51		
Greatest temporal	72		
Length:			
Inion-glabella	(90)		
Inion-basion	53		
MUZZLE.			
Height:			
Post. to M^3	45	42	
Ant. to P^3		17	
Breadth:			
Ant. to M^3	42	47	45
Length:			
Muzzle		88	
Nasal		42	

Table 9b. Measurements of the mandible of *Papio izodi*.

	? Sex.
	CT.5357
Breadth:	
Bigonial	49
Post. to M_3	50
Ant. to M_3	44
Through mental sp.	25
Length:	
Gonion to mental sp.	60
Angle:	
Between corpore	36°

Table 9c. Measurements of the upper teeth of *Papio izodi*.

	M^1			M^2			M^3			Rows.	
	bm	bd	l	bm	bd	l	bm	bd	l	$P^4 - M^3$	$\underline{C} - M^3$
FEMALE:											
AD.946			(10.5)			(12.0)				(41)	(54.5)
AD.992						(12.0)					
T.13	9.5	9.1	9.7	11.2	10.2	11.6	11.4	9.4	11.2	(37.5)	

Table 9d. Measurements of the lower teeth of *Papio izodi*.

	M_2			M_3			
	bm	bd	l	bm	bd	bh	l
FEMALE:							
AD.946		10.1	12.2	10.5	9.1	6.6	16.3
? SEX:							
CT.5357			13.5				16.5

Fig. 55. *Papio izodi* female (AD.946). Skull and part of mandible - lateral view. x 1.

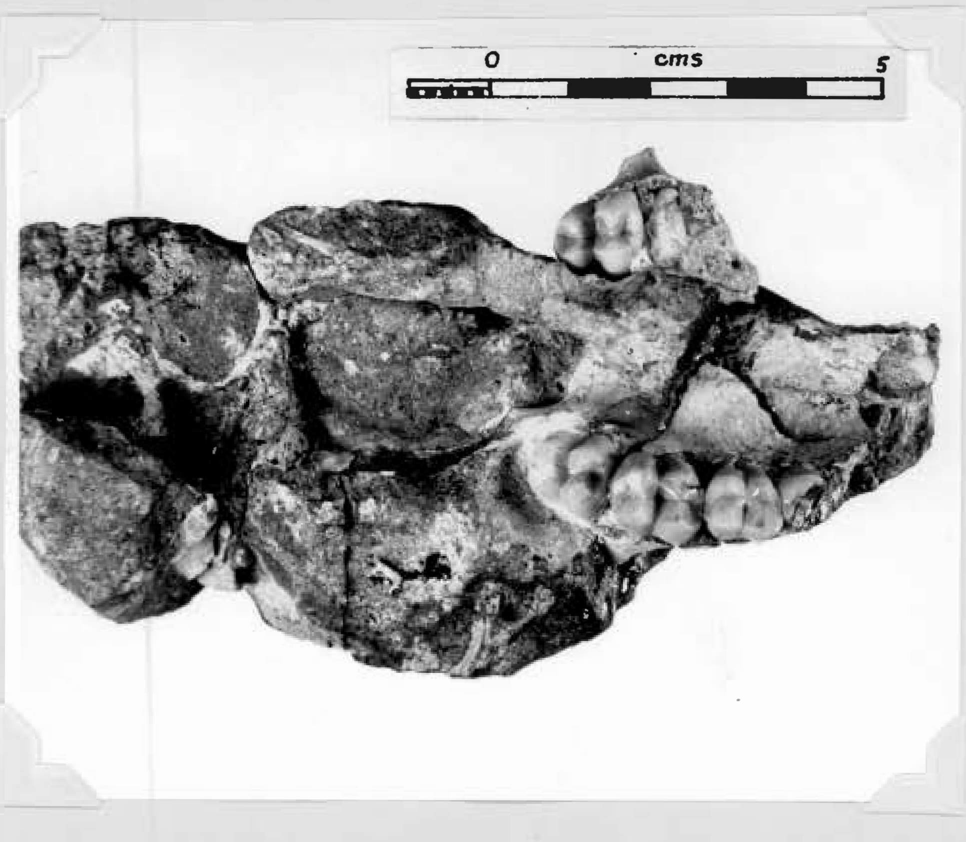

Fig. 56. *Papio izodi* female (T.13). Occlusal view of upper teeth. x 1.

Fig. 57. Papio izodi ?sex (CT.5357). Lateral view of mandibular fragment and teeth. x1.

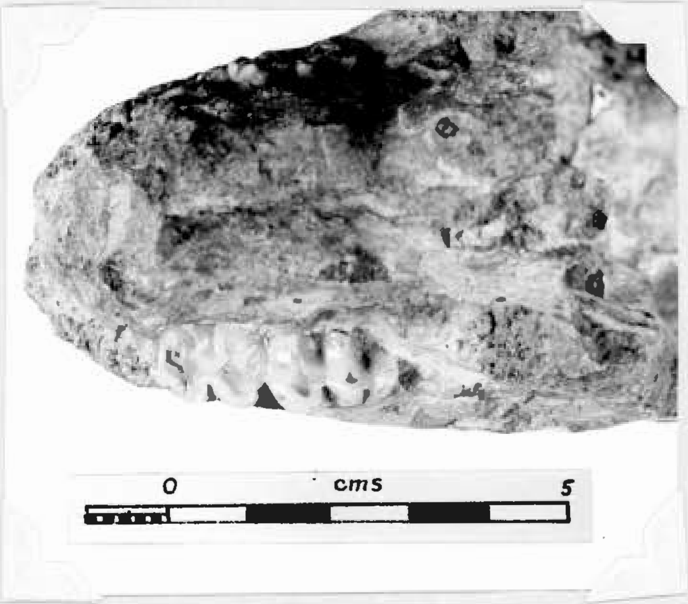

Fig. 58. Papio izodi ?sex (CT.5357). Occlusal view of lower teeth. x 1.

grooves present in front of the protoconid. In size these teeth, like those of the upper jaw, appear to be slightly larger than those of *P. antiquus*.

Measurements:

See tables 9a, b, c and d.

Remarks:

The shape of the female muzzle (AD.992 and AD.946) clearly shows the reason for referring these specimens to the genus *Papio* rather than *Parapapio* as proposed by Broom (1940 and 1948). Whereas in *Parapapio* (as described in Chapter 7) the dorsal surface of the muzzle, as viewed from the side, only shows a slight concavity from the glabella region to the posterior margin of the nasal aperture, in these two specimens there is the distinct sharp drop in the inter-orbital region, followed by the more gradual slope down to the posterior margin of the nasal aperture typical of *Papio* species.

By analogy with the other cercopithecoid species, and those of the genus *Papio* in particular, it would seem virtually certain that the male muzzle in *P. izodi* was very similar to that of the female and had a similar drop in the inter-orbital region. In all probability, the muzzle in this sex was also relatively (and absolutely) longer than in the female and showed at least some development of the maxillary ridges. Maxillary fossae were probably also present. The muzzles of the two male specimens (T.10 and CT.5356) discussed under *P. antiquus*, do not appear to fit this description.

Papio robinsoni sp. nov.

Dinopithecus ingens - Broom, 1940. (SB.2).
Parapapio sp. - Robinson, 1952.
Papio sp. - Oakley, 1954 a and b.

Holotype:

A good male muzzle, SK.555, with almost complete dentition.

Repository of type:

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

Type site:

Swartkrans, Transvaal, South Africa.

Referred material:

There are ninety-two specimens from Swartkrans, six from Cooper's, three from Swartkrans II, and one each from Kromdraai, Gladysvale, Skurweberg and Bolt's Farm. (For the numbers of these specimens see tables 10a - d).

The material from Swartkrans includes:

A second good male muzzle (SK.560). (No material of the male calvarium is known).

A very good female skull (SK.558) in which the muzzle is somewhat distorted and the calvarium lacks the basal region.

Another female specimen (SK.557) showing the muzzle, left zygomatic arch and left lateral and basal portions of the calvarium.

A very good female muzzle and palate (SK.562).

A female mandible (SK.407) complete except for the rami.

From Skurweberg, there is the posterior part of the muzzle and the antero-dorsal part of the calvarium of a male (SB.2).

Among the specimens from Cooper's there is a particularly good female mandible (CO.134A) which only lacks most of the rami, and also specimen CO.134B which is the almost complete mandible of a juvenile male.

From Swartkrans II there is included an almost complete skull of a female (SKII.25).

Description: (Figs. 59 - 68).

The muzzle dorsum of the male is very flat, more so even than in <u>P.ursinus</u>. Also, the nasals lie slightly below the level of the maxillary ridges instead of rising progressively higher above them towards the posterior part of the muzzle as they do in the chacma baboon. Another interesting feature of the male muzzle dorsum is the fact that the two maxillae meet in the midline and cover the nasal bones from about the level of the infra-orbital foramina to about 1cm. below the nasion (SK.560). Of all the specimens of P.ursinus in the collection of the Transvaal Museum (about eighty in all) a similar feature was found to occur in only a single female specimen (TM.11713) - and even here, the maxillae only joined for about a centimeter at the level of the infra-orbital foramina and then separated again. The maxillary ridges of the male of P.robinsoni are broader but less rugged than those of the same sex of P.ursinus and the nasal aperture in the former species is also rather larger. In length the male muzzle is shorter than that of P.ursinus (121 mm. as compared to 147 mm.) but in breadth, it is about equal. The male palate of the two species is very similar but there is no lingula over the posterior palatine foramen in P.robinsoni. The zygomatic arch of the male (SK.602) is less robust than that of the chacma.

The muzzle dorsum of the Skurweberg male specimen (SB.2) is unfortunately damaged in the midline and it cannot be seen whether the maxillae overlap the nasals. The general shape of the muzzle is, however, very similar to that described above for the Swartkrans specimens. The shape of the orbits and the degree of development of the supra-orbital tori are very similar to those of the male of P.ursinus.

The female muzzle of P.robinsoni is shorter but of about the same breadth, both on the dorsum and at the alveolar margin, as that of the female chacma baboon. Also, the maxillary ridges are not as well developed nor are the maxillary fossae quite as large (SK.562). It does not seem as if the maxillae overlapped the nasals in this sex (SK.558) but at the point where specimen SK.562 is broken (about one centimeter below the infra-orbital margin) the nasal bones are only about 3.5 mm. wide whereas at the equivalent point in the female of P.ursinus they are 5.5 - 6mm. wide. The orbits, zygomatic arch and calvarium are very similar in shape to those of the chacma baboon but slightly smaller in all of their dimensions (SK.558). The degree of development of the temporal lines and the nuchal crest is much the same in both species. The palate is of equal breadth but shorter and more horseshoe-shaped than that of the female of P.ursinus. There appear to be no structural differences in the morphology of the base of the skull of the two species (SK.557). The greatest length of the female skull of P.robinsoni is rather considerably less than that of P.ursinus (mean length in P.robinsoni = 159mm.; in P.ursinus = 175mm.).

The female skull from Swartkrans II (SKII.25) is very similar to those of the females from the type site described above. However, the considerable amount of damage and distortion in all of those specimens, and also in this one, makes an exact comparison difficult. In would seem that the muzzle in SKII.25 may have been narrower and the line through the tooth row more convex outwards. Also, there are possibly differences in the muzzle dorsum, but this latter region is particularly badly crushed in the Swartkrans II specimen and it is difficult to be certain. Similarly, the orbits seem rather smaller and the calvarium rather flatter but again damage and distortion may well be the cause of the apparent differences.

The teeth of the two sexes of P.robinsoni show marked sexual dimorphism and also several important differences from their equivalents in P.ursinus. Except for the incisors, of which there are none known of the male and only one very worn set from a female (SK.571B), good examples of all the teeth of the upper dentition of this species have been found. The female upper incisors and the C of both sexes appear virtually indistinguishable from those of the chacma baboon both in size and shape but the upper premolars of the two species differ very considerably.

The upper premolars of both sexes of this species, of which there are several specimens (e.g. SK.602 and SK.555 - males and SK.598 and SK.557 - females) are considerably larger than those in the corresponding sexes of P.ursinus. The mean values for the Swartkrans P.robinsoni premolars (with the equivalent figures for P.ursinus in brackets) are:- b x l or l(h), in mm.

male : P^3- 9.6 x 11.3 (7.9 x 9.7); P^4- 10.2 x 8.7 (9.1 x 8.3)

female : P^3- 8.4 x 8.6 (6.9 x 7.3); P^4- 9.4 x 7.5 (8.2 x 7.3).

On P^3, the extension of the enamel down onto the mesio-buccal root in both sexes is greater than that seen in the equivalent sex of the chacma baboon. In the male, this extension of enamel is very great and similar in appearance to that in the equivalent tooth of the male of Papio angusticeps which is described below. In both sexes, P^3 also lies very close up against the C tooth (SK.602 - a male and SK.571B - a female) and the small post-canine diastema of P.ursinus is here absent. P^4 is an extremely large tooth but its size in due to a general increase in its dimensions and not to a greater degree of molarisation.

The upper molars are very similar to those of P.ursinus but the buccal surfaces are slightly more vertical and, because of the rather large contact facets, the teeth appear to be slightly cramped. Mesio-lingually there is a vertical groove on the lingual surface and mesio-buccally there appears to be a small cuspule on the buccal surface of almost all the known molars. On the distal cingulum of most examples of M^3 there are small subsidiary cuspules and M^1 of SK.456 and SK.458 have small buccal accessory cusplets. The wear and root arrangement are similar to those described for P.ursinus and in size, they have almost exactly the same proportions and overall dimensions.

The two male upper teeth from Kromdraai (KA.160) and the teeth on the two male maxillae from Cooper's (CO.134D and CO.106B and C) are slightly small in most of their dimensions when compared to the male specimens from the type site. However, the extension of the enamel down the mesio-buccal root is the same as that described above and in general morphology they also match the Swartkrans specimens well. There are subsidiary mesio-buccal and mesio-lingual cuspules on M^1 and M^2 of all three specimens. The teeth of SKII.25 and the skull fragment from Gladysvale (G1.1) are both of female specimens and they are virtually identical to the Swartkrans female teeth in morphology. In size, most of their dimensions are slightly smaller than those of the Swartkrans females but a few are larger (see table 10c).

The available mandibles are mostly rather fragmentary and in none are the rami present. There are several specimens of the male lower jaw and in these the symphysis is fairly long, stretching back as far as the level of the distal part of P_3 (SK.572). The incisal shelf in this sex slopes down and back at much the same angle as in *P.ursinus* but the anterior surface of the symphysis is not quite as steep as in that species (SK.572 and SK.568). The maxillary fossa is of variable size and depth (SK.408 and SK.572). In the female mandible the symphysis is broader and the corpora are further apart than in the corresponding sex of *P.ursinus* (SK.407). The maxillary fossa is very shallow (SK.409, SK.407 and SK.421). The foramen symphyseosum and the median sagittal canal through the symphysis can be seen in specimens of both sexes.

The mandibles of the specimens from Cooper's, Swartkrans II and Bolt's Farm conform fairly closely to the above description with the possible exception of the depth and shape of the maxillary fossa. Of the male mandibles, the fossa of CO.134B (an immature specimen) is perhaps slightly deeper than that in the Swartkrans specimens and that of SKII.26 is rather a lot deeper. In the female lower jaws, the maxillary fossa of BF.20 is similar to that of the type site females but the fossa of CO.134A is considerably deeper.

With the exception of male incisors, quite a number of each of the different types of lower teeth of both sexes are known. The female lower incisors (SK.410 and SK.427) are rather worn but seem in no way distinguishable from those of the female of *P.ursinus*. There is only a single isolated male $\overline{C}$ of this species known, (SK.530) and it seems very similar to the equivalent tooth of the *P.ursinus* male but it shows an exceptional amount of wear. There are three specimens (SK.410, SK.421 and SK.407) with well preserved female $\overline{C}$ teeth present and these are also very similar to their equivalents in the *P.ursinus* female. Wear on the female $\overline{C}$ of specimen SK.421 is great and it is mainly on the lingual surface as in the female of *P.ursinus*.

The male P_3 is shorter and broader in *P.robinsoni* than in

P.ursinus and the anterior fovea (SK.408) is also considerably larger. Wear is also different on this tooth and specimens SK.406 and SK.423 show that the facet on the mesial extension is spiral, starting almost horizontal at the distal part of the tooth and twisting over buccally to become parallel to the lateral surface of the corpus at the mesial end. The female P_3 is broader and longer than in the female chacma baboon and the anterior fovea is again slightly larger (SK.410). In both sexes, P_3 lies very close to $\overline{C}$ and in fact overlaps it buccally. Both the male and female P_4 are broader but of about equal length to the equivalent teeth in P.ursinus and the structure of the teeth in the corresponding sexes of the two species is very similar.

The lower molars of both sexes are very similar in size to those of P.ursinus but M_2 is slightly broader and M_3 slightly longer; in morphology, the main differences are that in P. robinsoni the buccal surfaces are more vertical and the buccal intercusp clefts narrower. As in the upper teeth, there is evidence of cramping in the lower molars. Subsidiary cusp formation is quite common and occurs, for example, mesio-buccally on M_1 and M_2 (SK.419 and SK.445 - males) and on the cingulum between the two main distal cusps and the hypoconulid on M_3 (SK.407 - a female). There are also lingual accessory cusplets on M_1 and M_2 (SK.445 - a male).

The dentition of the Swartkrans II male mandible (SKII.26) shows the same cramping of the molars and overlapping of the $\overline{C}$ by P_3 described above. The teeth are very similar in shape to those of the Swartkrans males but in size they are mostly smaller, particularly in the lengths of M_1 and M_2 (see table 108). The teeth of the female mandible from Bolt's Farm (BF.20) again show similar cramping and overlapping: in size they vary from slightly larger to slightly smaller than those of the female specimens from the type site.

In the mature male mandible from Cooper's (CO.134B), excavation of the unerupted P_3 shows that this tooth is exceptionally long - l(h) is about 30mm. whereas in the three known

Swartkrans males it is only 23.5 - 24.5mm. Also, P_4 leans backwards rather more than in the Swartkrans males and there is a groove, running up the buccal side of the mesial surface, not seen in those specimens. The molars are very similar to those from the type site. On M_2 there is a lingual accessory cusplet, and also two subsidiary cuspules on the mesial surface, one buccal and one lingual. The teeth of the female specimens from this same site (CO.134A and CO.118) are badly worn but do not seem to differ from those of the typical females from Swartkrans described above. In size, the teeth of these two specimens are also very similar to those of the specimens from Swartkrans.

Finally mention must be made of a juvenile skull from Swartkrans II (SKII.27) which is, without doubt, the most perfectly preserved cercopithecoid specimen known from the Sterkfontein area excavations (Figs. 69 - 72). Except for small portions of the internal walls of the orbits and a small piece of the posterior part of the palate, the complete skull and mandible with full deciduous dentition is perfectly preserved without the slightest trace of distortion. Acid development has removed all the matrix and the fine skull and dental detail can be clearly seen.

A comparison of this specimen with the two P.ursinus juveniles of unknown sex described in Part I, and which are in a comparable state of tooth eruption, shows that it is morphologically very similar. However, in skull and dental size it is quite considerably smaller and, in addition, its muzzle is relatively shorter. P.robinsoni is known to occur at Swartkrans II and in size and general morphology the adult of this species closely resembles the adult of P.ursinus. The juvenile specimen described above is also from Swartkrans II and similarly closely resembles the juvenile of P.ursinus in morphology. It differs, however, in absolute and relative size in such a way as to suggest the possibility of its being of opposite sex. It would therefore seem probable that the two P.ursinus juvenile specimens of unknown sex are males, and specimen SKII.27 is a juvenile female of P.robinsoni.

This probability is strengthened by the fact that the deciduous molars of SKII.27 are smaller than those of CO.106B and C which is definitely an immature male of *P.robinsoni*. The latter are in turn of a similar size to the two juvenile *P.ursinus* specimens. (Although the *dc* of CO.106B and C is smaller than that of the *P.ursinus* specimens, it is broader and mesio-distally longer than that of the Swartkrans II juvenile).

Measurements:

See tables 10a, b, c and d.

Remarks:

This new species was created for a large fossil form of *Papio* which is the predominant cercopithecoid found in the Swartkrans deposit. It is considerably larger than *Papio angusticeps* and in addition differs from that species in other ways as described above. Although almost as large as, and very similar in general shape to, *Papio ursinus*, there are several important differences in the teeth and muzzle (see above) which quite clearly merit their specific separation. Previously, Broom (1940) had referred a specimen from Skurweberg (SB.2) to *Dinopithecus ingens*, probably as that species was the only large fossil baboon known at the time and had been described from that site. The specimen has no teeth, but the muzzle shape, as far as can be seen, agrees with that described for this new species. In addition, Robinson (1952) referred to a *Parapapio* from Swartkrans and Oakley (1954 a and b) to a *Papio*. Both were undoubtedly specimens of this new species.

This species probably also occurs at Cooper's, Kromdraai, Swartkrans II, Gladysvale and Bolt's Farm. Unfortunately, there are, in most cases, only single fragmentary specimens known from these sites (and Skurweberg) and these do not match those from the type site, or each other, quite exactly. Because of their morphological similarity, it would seem probable that the slight size differences between them are only minor intra-specific variations due to small time differences between the sites of to local population effects at the same horizon. When

Table 10c. Measurements of the skull of *Papio robinsoni*.

	Males			Females					
	SK. 555	SK. 560	SB.2	SK. 557	SK. 558	SK. 562	SK. 565	SK. 592	SKII. 25.
GENERAL.									
Greatest length				160	158				158
Basal length				112					120
Bizygomatic breadth									(96)
CALVARIUM.									
Height:									
Basion - bregma									57
Basion - glabella									82
Breadth:									
Min. interfrontal					51				50
Greatest temporal					68				(65)
Mastoid					73				
Length:									
Inion - glabella					92				111
Inion - basion				51					(41)
MUZZLE.									
Height:									
Post to M^3	48	44			(48)	43			
Ant. to P^3	31	27				22	17		25
Breadth:									
Ant. to M^3	59	57				52			45
Ant. to P^3	56	57				41	44	59	39
Dors. to M^2	48	55	50			36			34
Length:									
Muzzle	125	(117)			(85)				71
Palate	(107)			73	(76)	76		(61)	
Nasal	(72)		66		47				40
Orbit:									
Inter-orbital	(13)		10.5		7				
Ext.-orbital			112		(68)				
Height			20		22.5				(21)
Breadth	28.5		24.5		25.5				(23)
Nasal aperture:									
Breadth	26	24				15			
Length	(42)	48				36			

	SK.408	SK.572	SK.423	SK.417	SK.430	SK.368	SKII.26	SK.407	SK.409	SK.410
Height:										
Post. to M_3					31			28		
Ant. to P_4	30	34	36	38			33	27	29	
Mental sp. to most ant. point		55				51	45	(27)		32
Breadth:										
Post. to M_3								62		
Ant. to M_3							43	51		
Ant. to P_4	34						34	34		
Through mental sp.	25						20	22	25	23
At base of canine		33				29	26	25		24
Angles:										
At symphysis	131°							137°		
Between corpora	30°						40°	30°		

Table 10c. Measurements of the upper teeth of *Papio robinsoni*.

	I^1			I^2			C				P^3		P^4		M^1			M^2			M^3			Eqns.	
	h	b	l	h	b	l	h	b	l_1	l_2	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	$P^4 - M^3$	C - M^3
MALE:																									
SK.555							(46.0)	12.5	12.6	16.1	9.3	11.5	9.6	6.6				12.8		14.0	13.2	11.6	14.6	47.7	
SK.608							(49.5)	(11.5)	(11.0)	(14.5)	10.1	13.2	10.5	8.6	11.1	10.5	11.9	12.5	11.1	14.2	12.6	10.5	13.7	46.5	70.0
SK.560																	9.8	13.2	12.0	13.4					
SK.558															10.7	9.7	10.5								
SK.629													10.5	8.0											
SK.579								(11.7)	10.4	13.6															
SK.551							(50.0)	10.8	11.0	13.9															
SK.554													9.9	9.1	10.7	10.0	12.6	12.0	11.0	14.7	12.5	10.6	14.8		
SK.574A-B													10.9	7.9	12.1		(12.9)	13.7	12.6	14.6	13.5	10.9	14.9	(51.0)	
SK.455																		12.6	11.0	14.4					
SK.444																		12.2	11.5	14.9					
SK.484																		11.9	10.9	13.0					
SK.465															10.7	9.5	12.4	12.1	10.9	14.0					
SK.459																					12.4	11.4	14.0		
SK.456															10.6	9.4	12.1	12.8	10.9	14.2					
SK.449											9.4	(10.5)	9.6	9.2											
SK.497																		12.0	11.4	13.5					
SK.509																					12.4	10.5	13.5		
SK.499																		13.1	(12.1)	13.2					
SK.498												(10.0)	10.0	9.0											
SK.519													10.1	8.9											
SK.614																		(14.0)	12.3	15.0	12.9	10.0	14.0		
SK.605															13.0		11.9								
SK.565											9.4														
SK.625																						10.2	13.6		
SK.615															10.9	9.6	11.9								
SK.544															10.6	10.0	11.1	12.5	12.0	13.7					
SK.500																					12.6	10.5	14.4		
SK.503																		12.9	12.5	14.0					
SK.590																		11.9	10.9	14.2			(13.5)		
CO.134D											8.4	11.9	8.9	7.5	10.9	10.2	11.9	12.2	11.5	14.1					
CO.106B-C *	9.0	dm^1 6.8	6.2	8.5	dm^2 7.6	9.5	6.1	dc 6.4	5.1						10.2	9.1	12.0	11.5		14.4					
KA.160																		11.6	11.1	13.6	11.2	10.6	13.9		
SK.547							(59)					12.0					(11.0)			(14.5)					

Table 10c cont.

	I^1			I^2			$\underline{C}$				P^3		P^4		M^1			M^2			M^3			Rows	
	h	b	l	h	b	l	h	b	l_1	l_2	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	P^4-M^3	$\underline{C}$ - M^3
FEMALE:																									
SK.558											7.8	7.5	8.6	7.5	9.8	9.0	10.5		10.6	12.9	11.1	9.2	11.6	41.5	
SK.557											8.7	8.6	9.3	7.9	9.8	9.1	10.4	11.5	10.5	13.0	11.7	10.1	12.8	42.4	
SK.571B	4.7	6.6	7.4	7.7	6.9	6.5	12.0	7.7	6.8	7.2	8.3	9.7	(10.5)	7.6	10.6	9.6	9.4	12.5	11.3	12.8	12.2	10.0	12.7	41.4	55.9
SK.[illegible]											8.5	8.0	8.9	7.0	9.1	8.4	10.5	11.7	10.1	13.0	11.6	9.6	12.2	39.7	
SK.[illegible]															9.9	9.4	8.7	11.7	10.5	12.2			12.4		
SK.[illegible]											8.5	9.4	9.6	8.2	10.0	9.0	11.0	11.4		13.5					
SK.[illegible]														7.0				11.4							
SK.[illegible]																	(10.0)	11.6	10.0	12.5	11.6	8.6	11.6	(39.5)	
SK.476																		11.2	10.0	12.3	11.3	9.1	12.0		
SK.475																					11.4	9.0	12.9		
SK.[illegible]																		11.8	10.5	13.0					
SK.[illegible]																					11.2	8.8	12.2		
SK.446											8.6	8.2	9.6	(7.5)											
SK.[illegible]																					11.2	9.4	12.2		
SK.[illegible]																					10.6	9.0	12.6		
SK.[illegible]																					11.5	8.9	11.9		
SK.[illegible]																					11.3	9.8	12.0		
SKII.[illegible]				9.2	5.2		(9.4)	(6.6)	(6.1)	(6.4)	7.2	8.1	8.0	6.9	9.0	8.5	9.9	10.8	10.4	12.4	11.3	10.4	13.3	(40.4)	
01.1							4.4	8.0	6.5	6.6	8.1	4.9	8.1	7.6	9.5	10.3	9.5	11.8							
JUVENILE:																									
SKII.27 *	6.8	dm^1 5.7	7.8	7.4	dm^2 6.2	8.0	7.0	$\underline{dc}$ 6.0	4.0						8.8	di^1 5.7	6.5	8.0	di^2 8.9	5.2					

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* The measurements of the deciduous incisors and canines are: h, b and l; of the deciduous molars: bm, bd and l.

Table 10d. Measurements of the lower teeth of *Papio robinsoni*.

	I_1			I_2			$\overline{C}$			P_3		P_4		M_1			M_2			M_3				Rows	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	P_4-M_3	$\overline{C}$ - M_3
MALE:																									
SK.408										7.0	24.3	7.8	8.9	8.0	8.0	11.8	10.5	9.7	15.8	10.6	9.9	7.2	17.8	51.5	
SK.406										7.6	24.5	8.2	10.1	9.9	9.1	10.3			(15.3)						
SK.435										7.5	25.5	8.6	9.4	9.4	9.5	10.2	13.1	12.2	14.8	13.0	11.5	7.8	19.8	(52.7)	
SK.417												7.8	9.3	8.6		10.8	12.0		13.5				17.7	51.4	
SK.550										7.3		7.9	9.5	8.0	8.5	10.5	10.9								
SK.530							26.3	12.0	7.6																
SK.445														9.3	9.1	12.6	11.3	10.9	15.8						
SK.436														8.5	8.8	10.5		10.0	13.4						
SK.464															8.4	(11.0)	10.7	10.6	13.9						
SK.419														9.5	9.6	12.2	11.8	10.8	14.3						
SK.439																	10.0	9.8	13.1	11.2	9.9	6.8	(17.8)		
SK.451																				11.7	10.2	6.8	17.5		
SK.449												7.7	9.9												
SK.478												7.8	10.0												
SK.520												7.8	(9.9)												
SK.521												8.4	9.6												
SK.611												8.4	10.4												
SK.596																				11.7	9.4	7.1	18.4		
SK.616												7.9	9.0												
SK.599														7.9	8.0	12.0	10.1	9.6	13.3						
SK.615														8.2	8.2	11.6									
SK.522										7.7															
SK.462															9.2	11.9									
SK.430																	11.7	10.8	13.8	12.4	10.8	7.8	17.8		
CO.134B											(30)	6.8	9.1	9.1	9.3	11.0	11.0	10.4	13.4				19.1		
CO.115												7.0	8.7	9.0	9.5	(10.8)									
SKII.26				4.0	7.8	4.4	(22.0)	12.0	7.5	5.9	30.0	7.8	9.3	8.8	8.9	9.1	11.3	(10.4)	12.8	11.9	10.4	7.8	17.8	48.0	
SK.454										(7.2)	19.6	9.0	10.0												
SK.547							(27)				(20)		9.8			(11)			(14)						

Table 10d cont.

	I_1			I_2			$\overline{C}$			P_3		P_4		M_1			M_2			M_3				Rows	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	$P_4 - M_3$	$\overline{C} - M_3$
FEMALE:																									
SK.407				11.0	6.9	6.0	14.0	8.9	5.2	5.1	11.4	6.5	7.6	7.5	8.0	9.5	9.7	9.4	12.1	10.5	9.3	6.8	16.3	45.3	63.4
SK.371A	4.3	6.0	5.6	5.7	7.4	5.4	10.8	8.6	5.5	5.8	11.7	7.4	8.9	8.3	8.6	8.9	9.8	9.6	11.5	10.4	8.7	6.2	17.3	46.4	64.4
SK.421							13.2	9.7	5.5	5.7	12.4	7.7	8.8		8.7	8.7	(11.0)	10.0	13.6	10.6	9.6	6.8	15.6	44.4	62.5
SK.410	11.5	6.0	7.5	11.3	6.9	6.2	14.8	8.6	5.5	5.4	14.4	6.8	8.2												
SK.417	14.0	7.8	7.0	12.5	6.9	6.8	14.5	8.4	4.9	5.5	12.0														
SK.384							14.0	10.0	6.0																
SK.609										5.8	14.5														
SK.409												7.5	8.2	8.0	8.0	10.0	9.7		11.9	10.2	9.0	6.0	15.3	45.7	
SK.416																	10.2	10.0	11.4	10.7	9.4	6.7	16.4		
SK.457															8.5		10.2	9.5	13.5	10.8	9.0	6.7	16.7		
SK.459																		10.9	12.2	10.5	9.0	6.5	16.8		
SK.540																	8.9	8.6	12.4	9.2	8.8	6.2	16.0		
SK.488																	10.0	9.5	12.5						
CO.154A		5.8	(6.0)	4.6	7.6	4.2		7.3	4.5	5.2	12.9	6.4	8.5	8.3	9.1	9.1	10.5	10.5	11.8	11.5	10.2	7.1	16.7	44.9	(62.9)
CO.116														9.3	8.3	8.6	10.5	10.4	11.6						
EV.80							7.5	5.3	4.1	5.0	8.9	7.5	8.7	8.2	9.3	9.3	10.4	10.7	11.9	11.1	10.1	6.2	16.7	44.6	60.1
SK.464										6.4	15.2	8.9	10.7												
SK.480										7.1	15.0														
SK.619										7.8	15.4														
SK.617												8.9	9.1												
JUVENILE:																									
		di_1			di_2			$\overline{dc}$							dm_1			dm_2							
SKII.87*	3.7	3.5	4.2	3.6	3.2	4.1	6.2	6.0	8.5					4.0	4.4	7.8	8.6	5.5	8.1						

* The measurements of the deciduous incisors and canines are : h, b and l; and of the deciduous molars : bm, bd and l.

REPRINTED FROM THE ANNALS OF THE TRANSVAAL MUSEUM, VOL. XXII, NO. 3
24 JANUARY 1955
PRINTED IN GREAT BRITAIN

THE STATUS OF *PAPIO RHODESIAE* (HAAGNER) 1918

BY L. FREEDMAN
Transvaal Museum, Pretoria

(With 1 Plate)

THE status of the so-called Rhodesian baboon has long been a contentious problem among taxonomists of the Southern African Cercopithecoidea. First described by Haagner (1918) as *Choiropithecus rhodesiae*, Allen (1939) reduced it to a subspecies of *Papio cynocephalus* while, recently, Roberts (1951) re-instated it as a full species, *P. rhodesiae*.

Haagner's original description was based on a single, live, male specimen from the National Zoological Gardens, Pretoria. The baboon had been received in 1913, together with two other similar specimens, from 'Central Rhodesia' and, 'noticing well-marked differences from young Chacmas', Haagner kept this specimen to see whether these differences would persist. The fate of the other two specimens was not recorded. Some five years later, when he considered it adult, he described the animal. His criteria for creating the new species were that it was larger than any Chacma or Yellow baboon he had ever seen and that, though its build was like the Chacma, its coloration was similar to the Yellow baboon. The baboon died in 1924 and its skull and skin (T.M. 4078) are now in the collection of the Transvaal Museum.

Haagner later (1919) extended his description of the species by describing a skull and skin from Marandellas, Southern Rhodesia. Roberts (1951), who considered the 'type' valid, referred this new specimen to *P. ursinus griseipes* to which subspecies he considered it more closely related. In the Transvaal Museum there is a large skull collection of *P. ursinus* and a smaller one of *P. cynocephalus*; the skin collections are, however, rather small. An examination of all these, together with another group of *P. cynocephalus* skulls from the Kaffrarian Museum, Kingwilliamstown, leaves little doubt that the Marandellas specimen (T.M. 757) does indeed belong to the '*ursinus*' group. From the literature and inquiries to other museums in Southern Africa, it would appear that no single other specimen has ever been definitely assigned to this group and the status of the species thus hinges entirely on the single type specimen.

Much of the discussion which follows depends on the contention that the characters in which *P. rhodesiae* differs from *P. ursinus* are primarily due to the single known individual of the former having spent the bulk of its life in a 'zoo'. That animals in zoological gardens often develop skeletal abnormalities is a well-known fact—an instance of osteomalacia in a captive baboon, *P. hamadryas* (Ashley-Montagu, 1935), being a case in point. Several other baboon specimens in the Transvaal Museum collection support this viewpoint. Because of the pure and often synthetic nature of 'zoo' diet, vitamin and trace element deficiencies doubtless underlie many of the skull abnormalities found. In Haagner's type, the whole skull is rough and pitted in a most unusual fashion as may be seen from Pl. XXII, fig. 1. A *P. cynocephalus* skull (T.M. 11708) exhibits a similar roughness and, as it is also a 'zoo' specimen, confirms the ossification irregularities of captive existence. This latter specimen also agrees with the Rhodesian specimen by showing an abnormal mesial leaning of I^2. It might be thought that in the case of the Rhodesian baboon the left I^2 leans so greatly because of the absence and resorption of the socket of the left I^1, but the socket of the right I^2 confirms the exceptional angle. Of interest in this connexion is the fact that the incisors do not meet when the jaws are closed, and that the right I_1 has developed a cavity on its occlusal surface. Another skull peculiarity is that the muzzle is set at a slight angle to the calvarium, being deflected to the left.

In the mandible, another *P. cynocephalus* zoo specimen (T.M. 3191) has abnormalities in common with *P. rhodesiae*. In both these baboons the angle of the jaw at the gonion takes the form of a gentle curve rather than the meeting point of two lines, and the coronoid process makes an accentuated backward sweep which is most unusual. Pl. XXII, fig. 2, illustrates these features in *P. rhodesiae*.

Around the tips of the canines, P_3 and I^2 are deep grooves, while the cusp tips of M_3 are marked off in a similar way. The nutritional upset, coinciding with capture and change of diet, is no doubt responsible, and the markings must therefore also give an indication of the age at capture. The change in diet also affects the teeth in another way. In wild specimens, even before M^3 is fully erupted, the wear on the other teeth of the molar-premolar series is greater than in this specimen. The dentition is fully erupted in *P. rhodesiae* and there is evidence, to be presented later, that the specimen is of advanced age yet, despite this, there is little wear on the molars. This apparent paradox is resolved when one realizes that their captive diet lacks the grit and sand usually mixed with their food. The upper canines, which wear directly by their occlusion against the lower third premolars, show the greater degree of wear one would expect in an aged specimen.

No definite information seems to be available on the age at which teeth erupt in *Papio*, although their sequence is well known. From the markings on the teeth described above it would seem that, when the type of *P. rhodesiae* was captured, the permanent dentition had only just started erupting. By analogy with the figures given by Schultz (1935) for the macaque and chimpanzee, it would seem that this baboon was then at least 3–4 years old. Therefore, when it died 11 years later, it must have been at least 14 or 15 years of age but more probably even older. Under 'zoo' conditions, where animals do not have to face the elements and natural enemies, one would expect greater age to be attained than in the wild state.

It is interesting to compare the measurements of *P. rhodesiae* with a table incorporating 100 measurements on each of sixty *P. ursinus* skulls. The table itself occupies a considerable amount of space and will be published elsewhere in connexion with the study for which those measurements were primarily made, but the conclusions with regard to *P. rhodesiae* are summarized here. In the dimensions of the teeth the measurements for '*rhodesiae*' fall within the observed range for *P. ursinus*, with the exception of the incisors in which abnormality has already been indicated. In the skull, with the few exceptions to be discussed below, all the measurements fall within three standard deviations of the means for *P. ursinus*, but the grossness of the Rhodesian baboon is evident. Most of the measurements can actually be matched from the equivalent '*ursinus*' group, but this specimen shows by far the largest number of maximal measurements.

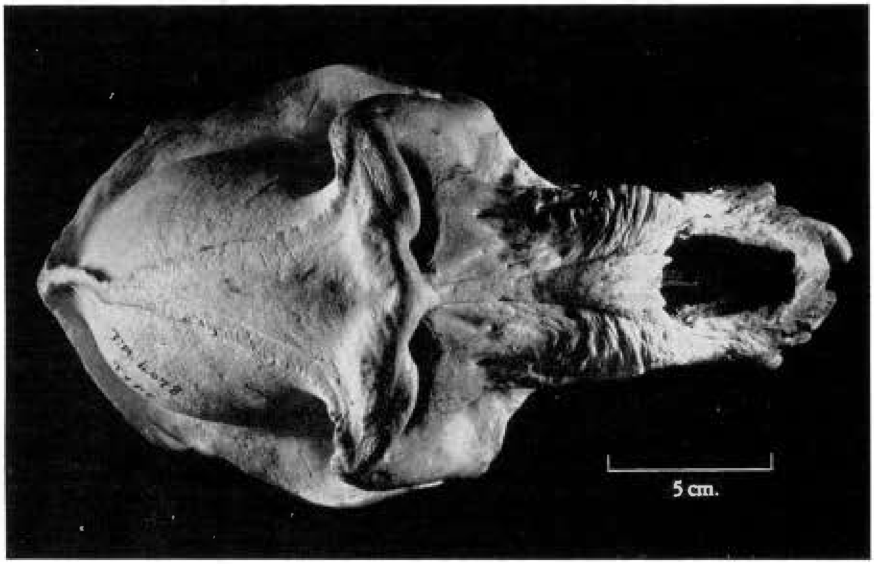

Fig. 1.

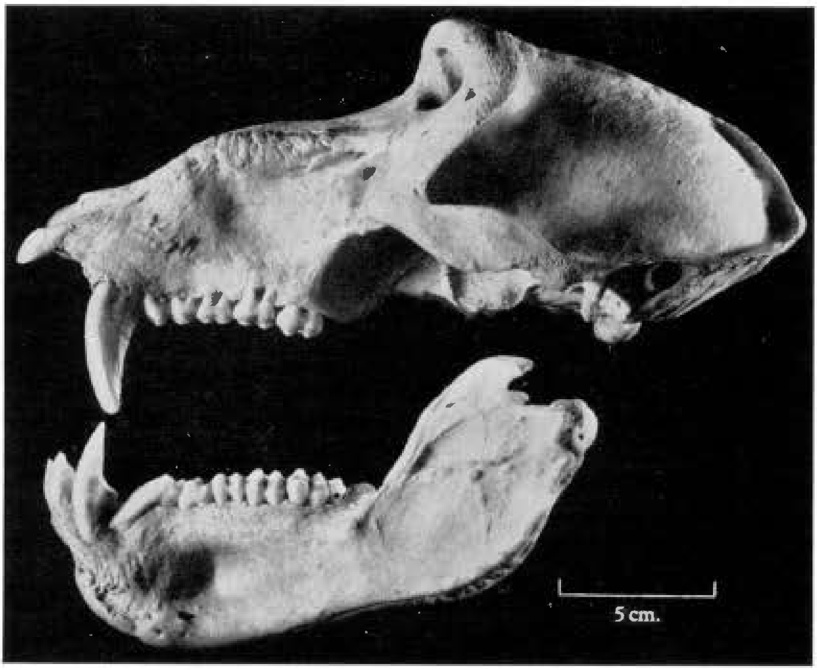

Fig. 2

Fig. 1. Dorsal view of male *P. rhodesiae* skull (T.M. 4078).
Fig. 2. Lateral view of male *P. rhodesiae* skull and mandible (T.M. 4078).

Probably, because of its age and abnormal diet, the tendinous origins and insertions of the cranial muscles of this baboon have become greatly ossified. The slightly greater general size, when compared to *P. ursinus*, can well be explained by this increased ossification, particularly of the sagittal and nuchal crests. The *P. cynocephalus* skull (T.M. 3191) previously referred to also shows these large crests. This greater ossification also extends generally over the skull, and particularly to the nasal ridges and supraorbital tori and, of the five measurements which fall outside three standard deviations, three are connected with the orbit. The fourth is a measure of the length of the symphysis whose whole anterior surface is greatly over-ossified and ridged, and the fifth is related to the aberrant coronoid process of the ascending ramus.

Roberts (1951) points out that the muzzle is relatively short and the calvarium rather flattened. To this can be added the unusual shape of the nasal aperture and the very large mandibular condyles. As all these occur in this single specimen only, and because of the obvious abnormality already indicated, it is felt that none of them can be taken to prove specific difference and are unique to this specimen. Roberts's criteria for subspecific differentiation in the baboons are based primarily on colour and, where measurements are used, there is great overlapping. Until a suitable study is made utilizing cranial and dental characters as well as the above, it seems that these subspecies will continue to be unsatisfactory and the precise subspecific classification of this (and other) specimens must remain confused and doubtful.

Much has been written by Haagner (1918, 1919) and Roberts (1951) on the colour resemblance of this specimen to *P. cynocephalus*. There are not a sufficiently large number of skins available at present to discard this difference to the Chacma with absolute certainty, but the available evidence is at least very strong. There is great colour variation among the *P. ursinus* skins, ranging from an almost black in the Cape (T.M. 7051) to much lighter shades, with some yellow, in specimens from Northern Bechuanaland (T.M. 6615). In fact, Roberts (1951) himself remarks that this latter specimen, which is his *P. u. chobiensis* type, is very similar though not quite as yellow as the *P. rhodesiae* type. On the other hand, a *P. c. cynocephalus* skin (T.M. 3191) is a much brighter yellow than the Rhodesian skin. After examining these and all the other available skins, it seems to the writer that the resemblance is by far closest to the *P. u. chobiensis* colour.

The creation of this new species on the basis of the slender differences of a single, living, captive animal would seem to have been most unsatisfactory. In addition, after over 30 years no other specimen has been assigned to the group, although specimens of two closely allied species have been described from the same locality. The conclusion is here advanced that the type of *P. rhodesiae* is an abnormal specimen but, despite this, can be fitted into the species *P. ursinus*. As the species rests entirely on this one specimen, it is submitted that the species *P. rhodesiae* is invalid.

ACKNOWLEDGEMENTS

This paper was written as part of a research programme sponsored by the South African Council for Scientific and Industrial Research. My thanks are due to the Director and Board of Trustees of the Transvaal Museum, Pretoria, for facilities and access to material, and also to the Kaffrarian Museum, Kingwilliamstown, for the loan of *P. cynocephalus* skulls. During the course of this work Mr J. A. J. Meester was most helpful and Mr J. T. Robinson greatly assisted by discussions and suggestions.

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