

PALAEONTOLOGIA AFRICANA

Annals of the

BERNARD PRICE INSTITUTE

for

PALAEONTOLOGICAL RESEARCH

UNIVERSITY OF THE WITWATERSRAND

JOHANNESBURG

C O N T E N T S

REPORT OF THE HONORARY SCIENTIFIC DIRECTOR FOR THE YEAR ENDING 31st MARCH, 1960	i
THE FIRST FIFTEEN YEARS OF THE BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH	1
SOME NEW CERCOPITHECOID SPECIMENS FROM MAKAPANGAT, SOUTH AFRICA by L. FREEDMAN	7
FURTHER REVISION OF THE FOSSIL ELEPHANTIDAE OF SOUTHERN AFRICA by H. B. S. COOKE	46
A PRELIMINARY INVESTIGATION OF THE MAMMA- LIAN MICROFAUNA IN PLEISTOCENE DEPOSITS OF CAVES IN THE TRANSVAAL SYSTEM by G. DE GRAAFF	59
A NEW TYPE OF PRIMITIVE CYNODONT by A. S. BRINK	119
ON SOME SMALL THEROCEPHALIANS by A. S. BRINK	155

VOLUME VII 1960

**BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL
RESEARCH**

BOARD OF CONTROL

H. B. S. COOKE (Chairman), B. I. BALINSKY, R. A. DART, T. W. GEVERS,
S. H. HAUGHTON, F. G. HILL, B. W. PRICE, W. G. SUTTON, I. GLYN THOMAS,
P. V. TOBIAS.

STAFF

Honorary Director and Editor:

S. H. HAUGHTON, B.A. (Cantab.), D.Sc. Hon. LL.D. (C.T.),
F.R.S., F.G.S., F.R.S.S.Afr.

Scientific Officer and Assistant Editor:

A. S. BRINK, M.Sc., Ph.D.(Lond.)

Technical and Field Officer:

J. W. KITCHING.

Honorary Curator for Human Palaeontology:

R. A. DART, M.Sc.(Q'l'd), M.D., Ch.M.(Syd.), F.R.S.S.Afr.

Honorary Curator for Mammalian Palaeontology:

H. B. S. COOKE, M.A.(Cantab.), D.Sc., F.G.S., F.R.Met.S., F.R.S.S.Afr.

Honorary Curator for Palaeobotany:

EDNA P. PLUMSTEAD, D.Sc.

Laboratory Assistant:

REGENT HUMA.

PALAEONTOLOGIA AFRICANA

Annals of the

BERNARD PRICE INSTITUTE

for

PALAEONTOLOGICAL RESEARCH

UNIVERSITY OF THE WITWATERSRAND

JOHANNESBURG

VOLUME VII 1960

Published 1st August, 1961

REPORT OF THE HONORARY SCIENTIFIC DIRECTOR
FOR THE YEAR ENDING 31st MARCH, 1960

CONTENTS

REPORT OF THE HONORARY SCIENTIFIC DIRECTOR FOR THE YEAR ENDING 31st MARCH, 1960	i
THE FIRST FIFTEEN YEARS OF THE BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH	1
SOME NEW CERCOPITHECOID SPECIMENS FROM MAKAPANSGAT, SOUTH AFRICA by L. FREEDMAN	7
FURTHER REVISION OF THE FOSSIL ELEPHANTIDAE OF SOUTHERN AFRICA by H. B. S. COOKE	46
A PRELIMINARY INVESTIGATION OF THE MAMMA- LIAN MICROFAUNA IN PLEISTOCENE DEPOSITS OF CAVES IN THE TRANSVAAL SYSTEM by G. DE GRAAFF	59
A NEW TYPE OF PRIMITIVE CYNODONT by A. S. BRINK	119
ON SOME SMALL THEROCEPHALIANS by A. S. BRINK	155

REPORT OF THE HONORARY SCIENTIFIC DIRECTOR FOR THE YEAR ENDING 31st MARCH, 1960

In my previous report reference was made to visits paid to the Institute by overseas specialists for study purposes. The presence of these specialists in the Institute is greatly appreciated by our own small staff for the stimulating effect which personal contact and discussion of mutual problems have on its own studies. That this effect is also felt by our visitors is shown by the following extract from a letter written by Professor R. C. Stebbins, Professor of Zoology in the University of California, which is included in this report with his consent. "I should like to say that I regard the work of the Bernard Price Institute for Palaeontological Research as of a high order of quality. This is evident from the intensity of effort to develop and interpret an outstanding collection and the meticulousness with which it is prepared and curated. The effort of Dr. Brink and Mr. Kitching to maintain a collection of living reptiles is highly commendable. It seems to me that this approach can greatly broaden the understanding of the palaeontologist and facilitate his interpretation of fossil forms. Indeed, this unique feature was one of the things that attracted me, a zoologist, to the Bernard Price Institute." Professor Stebbins also wrote "Dr. Brink's knowledge of the palaeontology of the fossil reptile fauna and his ideas on the evolution of homoiothermy greatly stimulated my thinking."

COLLECTIONS IN THE INSTITUTE

The re-arrangement and more complete cataloguing of the collections, referred to in last year's report, enabled a rough enumeration in classes to be made during the course of the year. The figures obtained give some indication of the importance of the Institute as a storehouse of palaeontological material and of the large amount of specialist study needed for the exact identification of each individual specimen.

Mammals

Exclusive of the enormous tonnage of fossiliferous breccia that awaits development, nearly 70,000 individual bones have been prepared and sorted, of which about 900 cranial specimens have been specifically identified.

Reptilia

From the Karroo beds we have about 3,200 specimens. Of these, about 1,100 have been prepared for study and a quarter of this number have been identified. In addition, approximately 1,000 specimens from a single bone bed remain unsorted.

Amphibia

There are some 200 specimens catalogued, but few have been prepared for study.

Pisces

About 250 specimens.

Invertebrates

The number of catalogued specimens is 1,842.

Since this rough estimate was made, there has been housed in the Institute a considerable number of Karroo reptilian remains from the Nyassa Province of Portuguese East Africa which were sent to me for identification and which consist mainly of endothiodonts and a few interesting bones of a slender-limbed Therapsid.

FIELD COLLECTING

Apart from a visit to Makapan, where he was fortunate enough after extensive search to find a block containing the remainder of the Australopithecine skull which was partially embedded in a block found in December, 1958, Mr. James Kitching undertook no collecting in the Union during the year under review.

RESEARCH WORK

Two major lines of research have occupied Dr. Brink through the year. One is a continuation of his investigations into the systematics and inter-relationships of the members of the Gorgonopsia; progress in this is dependent on the rate at which skulls can be cleaned and prepared for study. The other is the study of small Therapsid skulls, partly by the method of serial sectioning, figuring of the sections and reconstruction of the skulls in wax. In this latter field, attention is being devoted particularly to a study of the adaptations of the organs of Jacobson to the closing of the internal nares by the development of a secondary palate — a significant research project bearing upon the development of the means for detecting odours in the early mammal-like forms.

The method of serial grinding adopted has given rise to a nomenclatorial problem. One small skull, partly encased in matrix and considered on visual examination to be an already described Therocephalian, proved to have internal features that could not be matched in any known genus. Dr. Brink was therefore forced to consider it as a new form; but the original specimen has been completely destroyed by grinding and its features are preserved only in a series of accurate drawings and in a wax model prepared therefrom which is four times the size of the specimen. What constitutes the "type" of this new genus?

Work has begun on the serial grinding of two amphibian skulls.

Mr. Kitching prepared a short note on a fossil puparium from Makapansgat, which Professor Dart presented at the meeting of S₂A₃ in Pietermaritzburg. Thanks to a generous grant by the Wilkie Foundation, he was enabled to undertake an overseas study tour during the course of which he worked at the Manchester Museum for almost two months and paid visits of several days each to the British Museum of Natural History, the Geological Museum in South Kensington, University College (London), the Museum of Archaeology and the Museum of Zoology (Cambridge), the Geological Institute at Utrecht and the Museum of Natural History at Leiden, in Holland, the Museum of Natural History in Paris, the Museum of Natural Sciences in Brussels, and the Coryndon Museum in Nairobi. Dr. R. C. M. Eager, Keeper of Geology in the Manchester Museum, reported in most favourable and enthusiastic terms on the assistance given to him by Mr. Kitching in undertaking a statistical survey of over 11,500 animal remains from the very important Upper Palaeolithic section in Pin Hole Cave, Derbyshire, which were stored in the Museum, and in comparing the bone-flake culture evidenced from this site with the osteodontokeratic culture of Makapansgat. Certain specimens from Pin Hole have been sent to us; and Professor Dart is collaborating with Mr. Kitching in preparing for publication the studies made by the latter.

In addition to the studies by others referred to in my last report, Miss Webb is investigating, under the direction of Professor Dart, all the Chalicotherium material possessed by the Institute.

PUBLICATIONS

Volume VI of *Palaeontologia Africana*, containing 6 original contributions, was published on 1st July, 1959. Material for Volume VII is being assembled and will shortly be delivered to the printers.

LIBRARY

The library continued to grow rapidly through the medium of exchanges and donations. Especial mention should be made of a very generous donation of surplus literature from the library of the Geological Survey in Pretoria. This donation includes an important series of *Palaeontologia Indica* and other papers of palaeontological interest.

OTHER MATTERS

The day-to-day maintenance of the Institute's collections, books and card catalogues consumes a considerable portion of the time of our permanent staff. For some years, Mrs. Sutherland rendered notable and gratuitous help in this regard, and we owe her many thanks for this assistance which, fortunately, will still be available to us. During the past year, Miss Webb has found time to

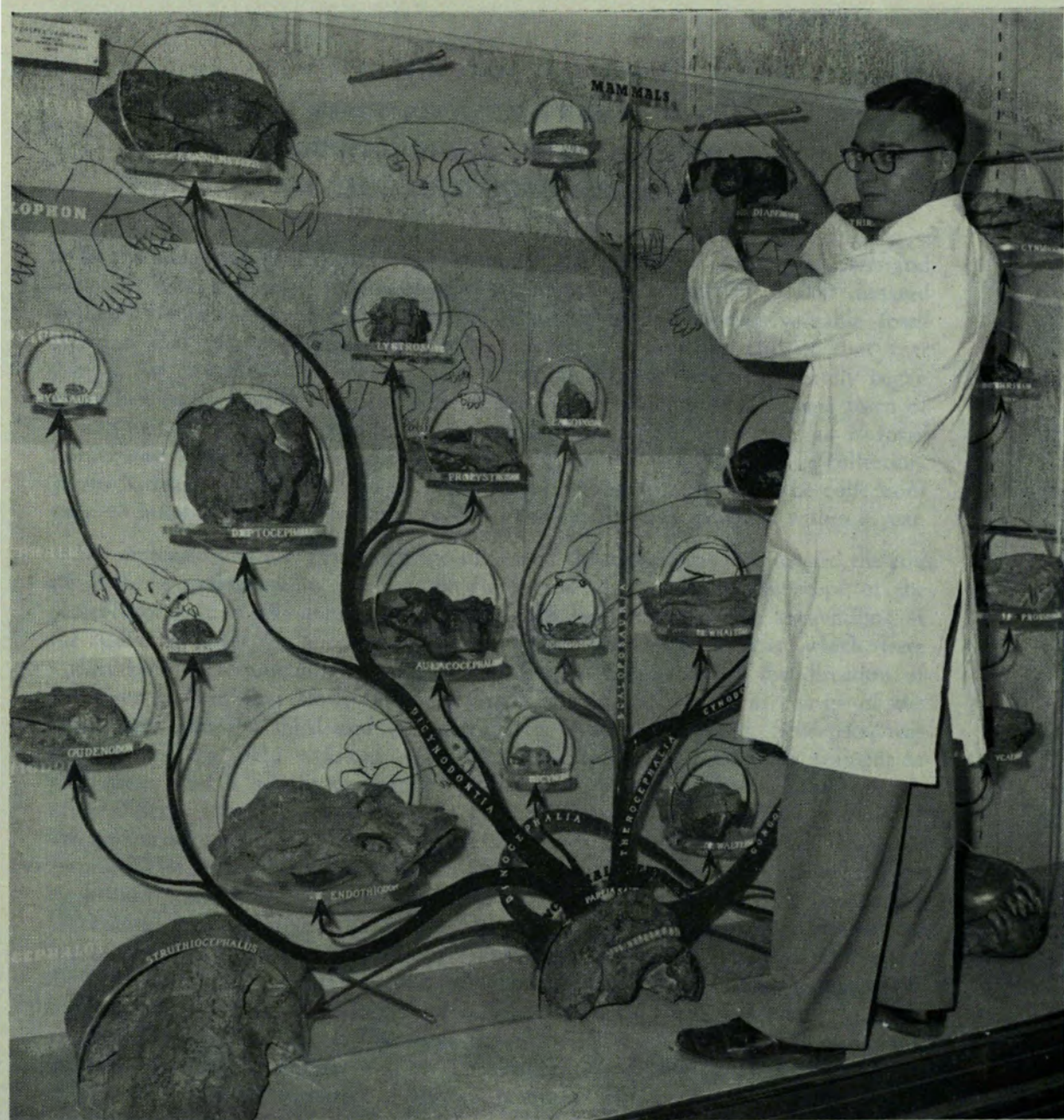
assist in the general administration thanks to Professor Dart by whom she is employed on a C.S.I.R. grant. It is hoped that, on her return from overseas in November, the Institute will again be granted her services in a part-time capacity.

At the request of Dr. Hoffman, the Institute agreed to partake, together with all the museums of the country, in an exhibition in the National Museum, Bloemfontein, on the occasion of the Union Festival. Our planned exhibit has been designed by Mrs. Edith Esson, an eminent art teacher of Johannesburg. The exhibit portrays a family tree illustrating the evolution of the mammal-like reptiles, in which the more important families will each be represented by at least one good skull drawn from our collections. Each skull will be supported by a perspex disc inserted in a circular hole in a large perspex sheet 8 ft. wide and 6 ft. high. The family tree is painted on the perspex, colours representing infra-orders, with carnivores and herbivores roughly separated. The perspex sheet is well removed from the back wall of the show-case, on which the succession of zones of the Beaufort series is depicted in colour. Each skull will stand at its appropriate level in the series and on the background will be a white outline sketch behind each skull depicting what is imagined to be the form of the living animal. For donating the sheets of perspex used in this interesting exhibit which will form a permanent feature of our future museum hall, the thanks of the Board are due to Messrs. Imperial Chemical Industries (S.A.) Ltd.

Thanks are due to Mrs. Esson not only for the interest and skill which she has displayed in the designing of this particular exhibit but also for the valuable assistance which she has rendered in the colouring of plaster casts of fossils which the Institute uses for exchange purposes. We look forward to more help from her in designing and executing the artistic requirements of our museum when the time is ripe.

Mr. Kitching's visit to Professor D. M. S. Watson in London resulted in the return to the Institute of most of the specimens which Watson borrowed on his visit to the Union in 1949. Three specimens were left in London in the hands of Dr. Robinson of the Zoological Department of University College, who will return them when she has completed certain comparative studies which she is undertaking.

12th April, 1960.



UNION FESTIVAL EXHIBIT

Photo Alan Peake, Friend Newspapers Ltd., Bloemfontein.

THE FIRST FIFTEEN YEARS OF THE BERNARD PRICE INSTITUTE FOR PALAEOLOGICAL RESEARCH

In the middle of 1945 there was established at the University of the Witwatersrand a small "Committee on Palaeontology" to administer a fund of £2,000 donated by Dr. Bernard Price for the purpose of salvaging and storing valuable fossil material that might otherwise be lost to science. Towards the end of that year Mr. J. W. Kitching was engaged as a technical assistant and immediately began to collect fossil reptiles from the Karroo beds in the vicinity of his home town of Graaff-Reinet, where he had already gained considerable experience as a fossil hunter and been largely responsible for building up the famous Rubidge collection. James Kitching was soon joined by his brother Ben and from nothing the collections grew to number some five hundred specimens of reptiles and amphibia within a year.

So impressed was Dr. Price with the success of the experiment that toward the end of 1946 he undertook to increase the funds and also to widen the scope of the project to include Pleistocene fossils. He thus helped to finance excavations at the Cave of Hearths in the Makapan Valley near Potgietersrus, which were undertaken in conjunction with the Archaeological Survey under the direction of Professor C. van Riet Lowe. Captain Guy Gardner was placed in charge of the excavations and the third and youngest of the Kitching brothers, Scheepers, was engaged as his field assistant. Two Africans were employed and trained as preparators and a steady stream of fossils began to emerge beneath their chisels to be described by Dr. Robert Broom of the Transvaal Museum. As a result of the enhanced status of the project the University Council agreed that it should become "The Bernard Price Foundation for Palaeontological Research", administered by a joint Committee of the Council and the Senate of the University under the Chairmanship of Professor C. J. van der Horst and with Dr. Price himself as one of the Members. The work of the Foundation was further extended to embrace the early Pleistocene cave breccias of the Makapansgat Limeworks in which Professor R. A. Dart was deeply interested, the funds and time available being divided more or less equally between the work in the Karroo and that at the two sites in the Makapan Valley. The collections grew apace and a number of descriptive papers appeared in various scientific journals.

Dr. Bernard Price took a keen personal interest in the work of the Foundation and his death in July 1948 was a severe loss. His generosity during his lifetime was continued through a bequest to the Foundation of a sum of £60,000 to

provide "a nucleus of housing accommodation" and a source of income "for a period of not less than ten years or more than twenty years". The Foundation was reconstituted in February 1949 as "The Bernard Price Institute for Palaeontological Research" under a Board of Control which replaced the former Committee and with one of the sons of Dr. Price (Mr. B. W. Price) in place of his late father. Death duties on the Estate served to reduce the bequest substantially and its ultimate value fell to £45,663 of which £15,000 was set aside for a Building Fund and the remainder invested to provide revenue. With a reasonable future thus assured, the Institute continued to expand its collections and improve the preparation of the material.

During 1947 and 1948 the Foundation was happily able to provide both help and advice to the southern phase of the University of California African Expedition and collaborated with Professor C. L. Camp and Dr. F. E. Peabody in their fossil studies. At the end of 1948 the distinguished British palaeontologist Professor D. M. S. Watson worked on the collections which the Foundation had assembled and submitted a comprehensive memorandum which evaluated the field of research in this region and helped materially to formulate the policy for the Institute. Professor Watson urged the appointment of a full-time palaeontologist and it was particularly fitting that in the latter half of 1949 the Board of the Institute selected Dr. A. S. Brink, a Stellenbosch graduate who had recently completed his Ph.D. in London under Professor Watson.

With Dr. Brink as Scientific Officer and Mr. Kitching as Field Officer and Laboratory Technician, the Institute has grown steadily in stature and they have remained the only full-time European members of the staff, aided from time to time by temporary Research Assistants supported by research grants. These research students have made full use of the facilities of the Institute in acquiring higher degrees and each of them now occupies a prominent post elsewhere. The Institute also enjoys the collaboration of a number of members of the staff of the University of the Witwatersrand who act as Honorary Curators. Professor C. J. van der Horst served both as Chairman of the Board of Control and as Honorary Director of the Institute but when he died suddenly at the end of 1951 he was succeeded by Professor T. W. Gevers as Chairman and Dr. S. H. Haughton — a member of the Board since 1947 — became the Honorary Scientific Director. In that year the Karroo collections topped the 2,000 mark and in 1952 the University made available near the Dental Hospital two "temporary" wooden hutments which the Institute still occupies!

Until 1953 the results of the research work carried out were printed in various scientific periodicals both in South Africa and overseas. In that year it was decided that publication of these results was an essential part of the contribution that the Institute should make to the advancement of palaeontological knowledge and the Board decided to issue its own series under the title "Palaeontologia Africana". This move justified itself immediately. The distribution of the publication is world

wide and has served to make the Institute very well known in palaeontological circles. Volume I was concerned entirely with papers on Karroo reptiles and Volume II was devoted to a bibliographical survey of Reptilia from the Karroo beds of Africa which has become a valuable reference work in this field of study. Volume III included accounts of mammalian fossils from the Makapansgat Limeworks and two short papers on invertebrates. The subsequent volumes have also been mixed in content, though the Karroo fossils still constitute the greater part of each issue. Quite apart from the extensive revisions carried out, the seven volumes published to date (including the present one) contain descriptions of no fewer than sixteen new genera and thirty-six new species of Karroo fossils, one new genus and eleven new species of fossil mammals and six new species of fossil invertebrates. More than one hundred papers dealing with material in the Institute's collections have also appeared in other publications.

The total collections of the Institute are now of considerable importance and the accumulation of this material in the short space of fifteen years is an achievement of no small magnitude. The latest figures approach 5,000 vertebrate specimens from the Karroo beds, including nearly 300 recovered in 1960 from the hitherto almost unknown deposits in the upper part of the Luangwa valley in Northern Rhodesia. The Karroo material must now rank as amongst the most important in the world and casts of some of the specimens have been prepared for exchange with other institutions. The collections of mammalian fossils from the australopithecine deposits at Makapansgat Limeworks now exceed 80,000 specimens, including 1,000 cranial fragments which have been identified specifically and many thousands of bone artefacts which are being classified by Professor R. A. Dart. In addition there are some thousands of mammalian teeth from stone age deposits, including the Cave of Hearths at Makapansgat. The invertebrate collections are still inadequate and no specialist has been available to study them but there are a few tons of Cretaceous limestone rich in fossils which await preparation and classification. Almost 2,000 invertebrate specimens are catalogued and the Institute possesses an exceptionally valuable and unique collection of microfossils from southern Africa which was assembled by a visiting scientist Dr. Y. H. Smutter. There are also substantial collections of fossil plants, which include the fruiting bodies of the Glossopteridae first recognised here by Dr. Edna P. Plumstead; to her has recently fallen the honour of being asked to describe the fossil plant material collected in Antarctica by the Fuchs and Hillary expeditions.

In recent years the Institute has received an ever-increasing stream of visiting scientists from many countries. Some have stayed only a few days examining particular specimens or groups but many have spent considerable periods working on the material. The australopithecine specimens have attracted many famous scientists and a few of them have worked also on the associated mammals. The Abbé Lavocat of Paris, for example, studied the microfauna and paved the way for further work by local scientists. The Karroo collections were first studied by such visitors as Professor Nils Holmgren of Stockholm, Professor Charles Camp of California

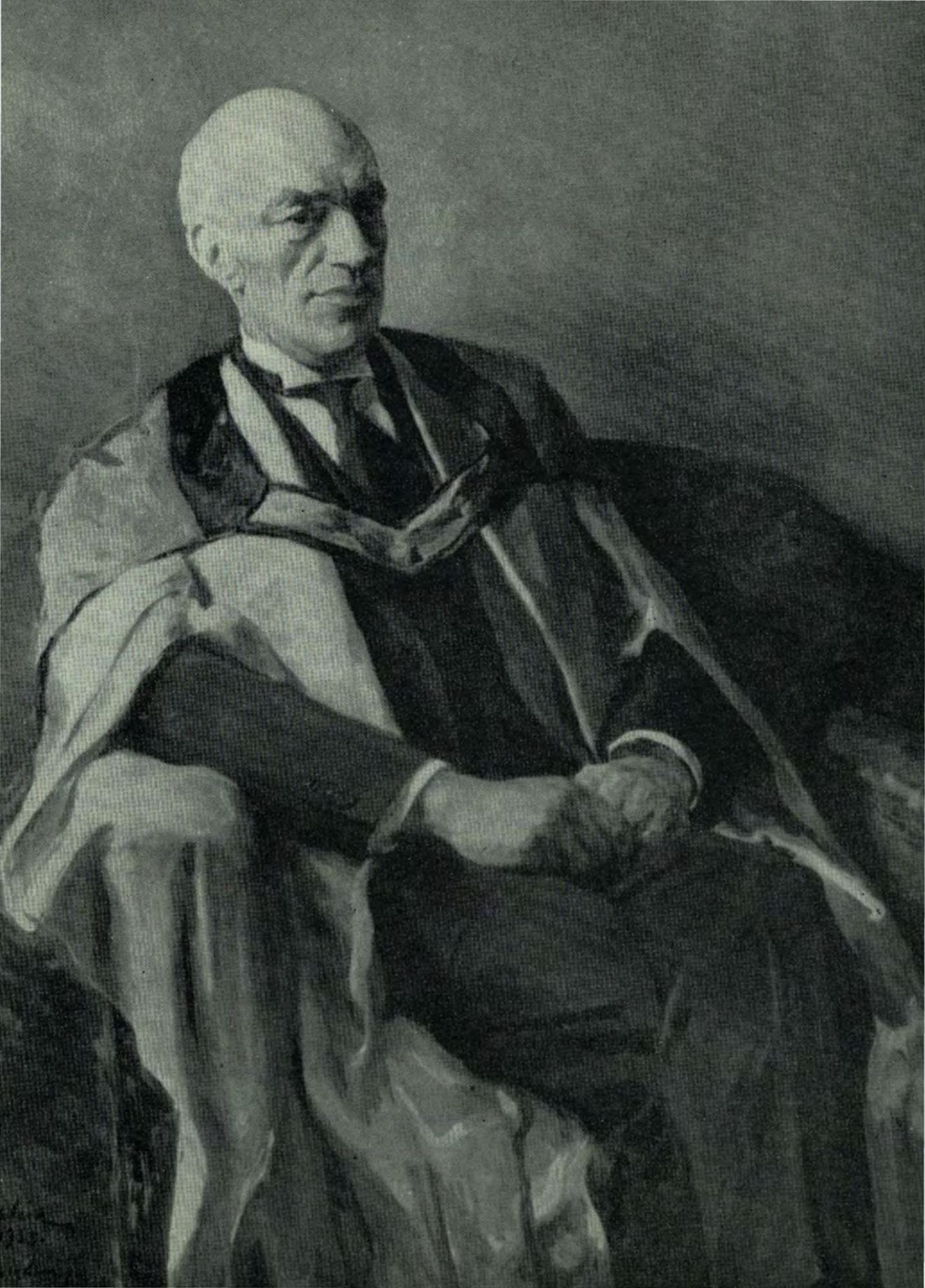
and Professor D. M. S. Watson of London; many others have followed in their footsteps. Recently an unusual project was undertaken by Professor R. C. Stebbins of the University of California who spent nearly a year examining median sections of Karroo reptile skulls to further his studies on the pineal eye. Facilities have also been provided for overseas students, such as Mr. A. A. Manten of Utrecht and Mlle Sigogneau of Paris, each of whom spent nearly a year in research and study at the Institute. Students from southern Africa and other palaeontologists working in this region are frequent and welcome visitors who have both gained from and contributed to the status of the collections. Material from the Institute has also been sent to specialists for study and description and several scientists have contributed to the value of the collections in this manner.

While the Institute has a proud record during its one and a half decades of life, its continued existence beyond the "not more than twenty years" specified by its benefactor will depend upon additional financial support. During the past ten years, although the number of full-time permanent scientific staff has remained at two, the essential annual expenditure has risen by a factor of three and increasing sums have had to be drawn from the capital of the endowment to meet current expenses. This process has, of course, reduced annually the revenue derived from interest on investment so that, with rising costs, the debit balance between expenditure and income is an ever-increasing sum. Although the University of the Witwatersrand is assisting in many ways, the financial position is fast becoming critical and unless further endowment is forthcoming to provide at least £70,000 in capital, the Institute will cease to function within the next ten years. Efforts to obtain such a sum within South Africa have so far met with scant success but it is hoped that somewhere there may be others with the generous and farsighted outlook of the late Dr. Bernard Price who will help to make possible the continued existence of the Institute. The dividend in scientific value during the past fifteen years has been very great and the resources of material for future study are almost unlimited. We hope that the proud record of the Institute may long continue.

H. B. S. COOKE
Chairman.

DR. BERNARD PRICE,
Founder of the Institute

*Photo: Leon Levson, from a life
painting by J. Epstein.*



SOME NEW FOSSIL CERCOPITHECOID SPECIMENS FROM MAKAPANGSAT, SOUTH AFRICA

By L. FREEDMAN

(Department of Anatomy, University of the Witwatersrand, Johannesburg)

ABSTRACT

Eighty-eight new fossil cercopithecoid specimens from Makapansgat, South Africa are considered. They are referred to the species *Parapapio broomi*, *P. jonesi*, *P. whitei*, *Cercopithecoides williamsi* and *Simopithecus darti*. With the exception of *P. whitei*, each of these species has previously been described from this site. The new material considerably extends our knowledge of all of the above species and the species *Cercopithecoides molletti*, previously described from Swartkrans, must now be sunk and the material referred to *C. williamsi*. Some remarks are made about the status of the South African species of the genus *Simopithecus*.

INTRODUCTION

Since the South African cercopithecoid material was last reviewed (Freedman, 1957), 134 new specimens have been recovered from the breccia in the limeworks dumps at Makapansgat near Potgietersrus in the Transvaal. Of this material, 88 specimens are either sizeable fragments showing interesting features, or include teeth which can be identified and measured. The new specimens were found to fit into 5 species, all previously described from the South African limestone caves and, except one (*Parapapio whitei*), all previously reported from Makapansgat. However, the material adds considerably to our knowledge of the morphology and variation of each of these forms and, in one case, necessitates certain taxonomic changes.

The system of measurements used below is the one described in Freedman (1957) and, unless stated to the contrary, all references to "the previous study" refer to that same review.

Parapapio Jones, 1937

There are 69 specimens of the genus *Parapapio* in the new material from Makapansgat. The material includes: 5 fairly large and 2 rather small portions of the skull, all with teeth, and 19 other specimens of upper teeth; 6 fairly large and 6 small parts of the mandible, all with teeth, and 19 other specimens of lower teeth; 8 specimens of various portions of the skull and 1 of the mandible with badly damaged or no teeth; 3 specimens each including both maxillary and mandibular fragments with teeth.

As discussed at length in the previous study, the present taxonomy within this genus is not wholly satisfactory but it appears to be the most suitable working arrangement until more complete skull material is found. The present sample

unfortunately helps only a little in filling this gap. The criteria proposed in the previous study for subdividing the Sterkfontein *Parapapio* material into the three species, *P. jonesi*, *P. broomi* and *P. whitei*, have thus again been used in this study. However, instead of only using the material of known sex, an attempt has been made to classify all the known *Parapapio* material from Makapansgat. For the reasons given above, and also because there might possibly be subspecific differences between the Sterkfontein and Makapansgat representatives of a species, (see later for this situation in *Cercopithecoides*), some specimens will undoubtedly have to be re-classified in due course.

Parapapio broomi Jones, 1937

Referred Material: 24 new specimens are referred to this species. These include: A fairly complete male skull (M.2961) and a male right maxilla (M.2963); a female skull (M.3037) which is fairly complete but rather badly crushed, a right female maxilla (M.3002) and the two halves of a female palate (M.2964 and M.2966) which almost certainly come from a single individual. There are 8 specimens of upper teeth of unknown sex (for their numbers, see Table 2). There are 3 specimens showing the symphysis and body of the male mandible (M.2978, M.2979 and M.2980) but there are no specimens of the female mandible. One female $\bar{C}$ and 6 specimens of lower teeth of unknown sex (some in small portions of the mandible) are also referred to this species (for their numbers see Table 4).

Description: (Figs. 1—3). The male skull (M.2961) lacks the anterior part of the muzzle, the zygomatic arches, lateral parts of the orbits and the base and posterior part of the calvaria. M^2 and M^3 are present on the right and M^2 on the left but they are all rather badly damaged. Although comparing well in size

Table 1
Measurements of the skull of *Parapapio broomi* (in mm.)

	Male	
	M.2961	M.2963
Calvaria		
Breadth		
Minimum interfrontal	53	
Muzzle		
Height		
Anterior to P^3		21
Breadth		
Anterior to M^3	53.5	54
Anterior to P^3		42
Dorsal to M^2	39	
Orbit		
Interorbital	13	
Height	24.5	

Table 2

Measurements of the upper teeth of *Parapapio broomi* (in mm.)

	I ²			$\frac{C}{-}$	P ³		P ⁴		M ¹			M ²			M ³			Rows
	h	b	l		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	P ⁴ -M ³
Male																		
M.2961														10.3	(11.5)			
M.2963							9.0	6.8	9.8	9.5	10.1	11.7	10.8	11.4	11.7	9.5	11.2	(38.8)
Female																		
M.2964)							8.5	6.4				11.8	10.2	11.1	11.5	9.0	10.6	(35.2)
M.2966)*							8.5	6.3				12.2	10.3	10.7	11.2	—	11.0	(36.3)
M.3037							—	6.2	9.0	8.8	9.6	11.0	9.9	11.4	10.8	8.8	10.8	36.5
M.3002												(10.9)	(9.4)	11.8	10.3	8.4	11.0	
?Sex																		
M.3011												11.0	10.2	10.8				
M.2977															11.6	9.4	10.6	
M.2969												10.5	9.6	11.0	—	8.8	10.6	
M.2975															11.8	9.8	11.2	
M.3008	9.9	6.3	6.0															
M.3015												11.8	11.6	11.5				
M.2970															11.2	9.7	10.2	
M.3016					8.0	(7.2)												

* Virtually certainly a single individual.

to the known specimens (Table 1 gives the measurements of the new specimens), when compared in detail with M.202 (1326-2), the specimen previously used in the description of the male skull of this species, a number of interesting differences are found.

Of considerable importance is the fact that when viewed in normal lateralis, there is a considerable drop in the profile of the muzzle in the interorbital region of M.2961 (Fig. 1). This drop is not as marked as in the male *Chacma* baboon, *Papio ursinus*, but is considerably more than in M.202 and very similar to that in the female of *P. ursinus*. The muzzle in M.2961 also has a larger maxillary fossa than that in M.202 and the muzzle dorsum is not flat but concave from side to side with the middle part (nasals) standing up considerably more prominently above the general level of the dorsum. In M.2963, the other new male specimen, the maxillary fossae are similar to those in M.202. In both M.2961 and M.2963, the maxillae have long nasal processes lateral to the nasals. The palate is deep in M.2961 but very much shallower in M.2963.

The orbits are more vertical and less laterally elongated in the new male specimen (M.2961) and its supraorbital notch is very well marked. The interorbital measurement is broader than in M.202 and a short metopic suture is present. There is a more marked depression followed by a less marked elevation behind the glabella in M.2961 than is seen in M.202.

On the calvaria, the inferior temporal lines are well developed and meet at a point considerably anterior to the inion (Fig. 2). (The portion of the calvaria behind which they meet is lost but from the general contour of the area it is clear that the meeting point was well in front of the inion.) The superior temporal lines can also be clearly seen and these lines meet about $3\frac{1}{2}$ cms. anterior to the meeting place of the inferior lines. They form a slightly elevated ridge which continues up to the meeting point of the inferior lines. On M.202, the inferior lines can be seen for only a short distance anteriorly and the superior lines can not be seen at all. The top of the calvaria appears to be somewhat higher above the occlusal plane than that of M.202.

The specimens of the skull included in the new female material of this species add little to our knowledge as they are too fragmentary or badly damaged.

The new specimens of the upper teeth (Fig. 3) do not show any morphological features in which they differ from the material previously described. The measurements of these specimens are listed in Table 2, and most of them fit the sizes

Table 3
Measurements of the mandible of *Parapapio broomi* (in mm.)

Height	Male		
	M.2978	M.2980	M.2979
Posterior to M ₃	29		
Anterior to P ₄	32	31	29

Table 4

Measurements of the lower teeth of *Parapapio broomi* (in mm.)

	$\bar{C}$			P_3		P_4		M_1			M_2			M_3				Rows
	h	b	l	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l	P_4-M_3
Male																		
M.2978				5.5	14.9	(7.5)	(7.0)	—	7.5	8.9	10.1	10.2	11.5	10.2	(9.1)	4.5	14.0	40.5
M.2980											—	9.8	11.5	9.8	9.0	5.7	14.5	
M.2979						7.3	6.8	7.8	7.5	9.2	10.4	—	11.3					
Female																		
M.2084	—	7.5	5.8															
?Sex																		
M.2982								—	8.1	(9.2)	10.0	8.7	10.5	10.2	8.9	5.7	14.8	
M.2968														10.8	9.5	4.0	13.3	
M.2993														—	9.2	3.5	15.5	
M.3024											10.0	—	11.8					
M.2994											9.6	8.9	11.8					
M.3018														9.6	9.4	6.6	15.7	





Fig. 2. *Parapapio broomi* male (M.2961). Dorsal view of skull.

previously given for the species quite well. Of the specimens of unknown sex included, M.3008, M.3015 and M.3016 could, however, possibly belong in *P. whitei* and M.2970 appears slightly small for *P. broomi*.

The 3 new male mandibles (Table 3) confirm most of the features previously described and, in addition, slightly extend our information about certain features. In M.2979 the slope of the anterior surface of the symphysis is rather gentle whereas in M.2980 it is slightly steeper. The mandibular fossa varies in the 3 specimens from shallow in M.2979 and M.2980 to almost absent in M.2978. The symphyseal region extends almost up to the distal end of P₃ in M.2979 but is shorter in M.2980. In M.2978 there is a large space between the distal end of



Fig. 3. *Parapapio broomi* male (M.2963). Occlusal view of upper teeth.

M₃ and the ascending ramus. The ramus in this specimen leans back at an angle of about 120° to the occlusal plane.

No female mandibles can definitely be referred to this species from the new Makapansgat material.

The new lower *Parapapio* teeth from Makapansgat have proved rather more difficult to classify than the upper — mainly because a number of single teeth

in the I₁ — M₁ group are involved and it is primarily on M₂ and M₃ that the classification of *P. broomi*, *P. jonesi* and *P. whitei* is based. Table 4 lists those specimens fairly clearly referable to *P. broomi*, while Table 10 lists lower teeth which could belong to *P. broomi* or *P. jonesi* and Table 11 lists specimens which could belong in *P. broomi* or *P. whitei*. Those listed in Table 4 appear to fit *P. broomi* clearly on size and morphology and do not show any new features.

Parapapio jonesi Broom, 1940

Referred Material: 12 new specimens are referred to *P. jonesi*. No new skull fragments are included in the new material but there are 5 isolated upper teeth

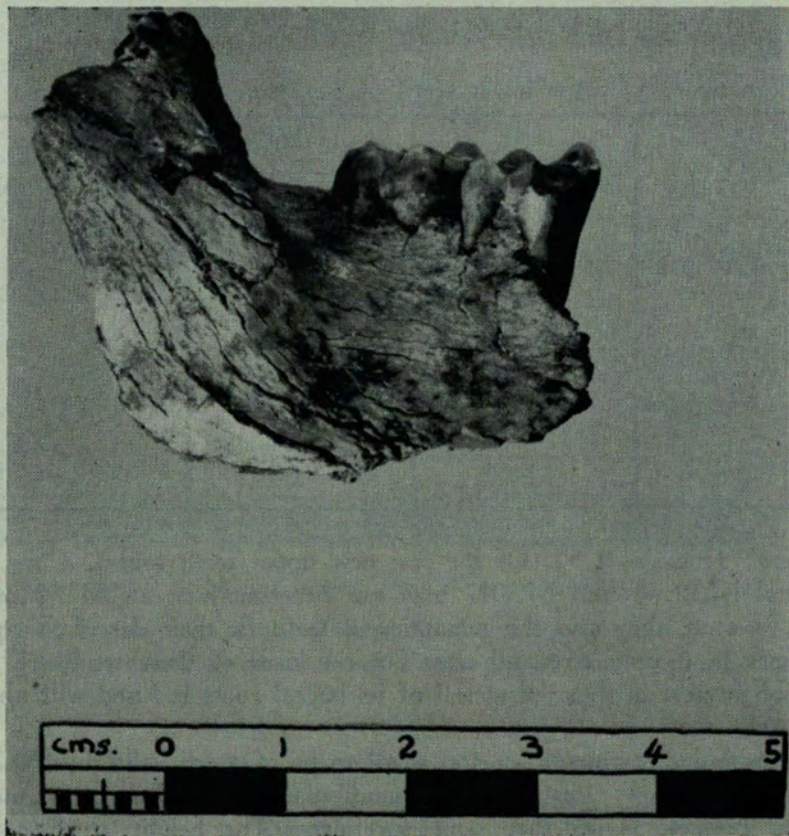


Fig. 4. *Parapapio jonesi* sex? (M.2984). Lateral view of mandibular fragment with M₂ and M₃.

of unknown sex, the numbers of which are given in Table 5. Of the mandible, there is one fragment with teeth from a female (M.2983) and another fragment also with teeth but of unknown sex (M.2984). There are also 5 isolated lower teeth of unknown sex, the numbers of which are listed in Table 6.

Table 5
Measurements of the upper teeth of *Parapapio jonesi* (in mm.)

	M ¹			M ²			M ³		
	bm	bd	l	bm	bd	l	bm	bd	l
?Sex									
M.2976	8.9	8.1	9.1						
M.3009							9.9	7.4	9.5
M.3013							9.6	8.2	10.0
M.3014							(10.2)	7.8	—
M.3017				10.2	8.6	9.5			

Table 6
Measurements of the lower teeth of *Parapapio jonesi* (in mm.)

	P ₄		M ₁			M ₂			M ₃			
	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
Female												
M.2983	6.3	7.5	7.2	6.9	9.0							
?Sex												
M.2984						—	8.8	10.0	9.2	8.0	—	11.1
M.3019									7.9	7.0	4.5	11.3
M.3021									8.3	8.2	4.9	13.2
M.2992						9.0	8.4	10.8				
M.3030									9.3	7.7	5.2	12.7
M.3032			7.0	7.1	8.8							

Description: (Figs. 4 & 5). Of the few new upper teeth found, 2 are damaged (M.3013 and M.3014) and M.3017 may not necessarily be an M². However, as far as can be seen, they and the remaining 2 teeth fit their described equivalents in this species in morphology and size. For the sizes of these teeth see Table 5. M.3014 is of interest in that the mesial of its buccal roots is fused with the lingual root.

The 2 mandibular fragments are too small to be of much value but M.2983, the female fragment, shows virtually no mandibular fossa. The only mandibular measurement possible is on that same specimen: The height anterior to P₄ is 24mm. The lower teeth (Figs. 4 & 5) are interesting in that they appear to be small, even for *P. jonesi*; in size, but not on morphology, one specimen (M.3019) is actually small enough for *Cercopithecoides williamsi*. The sizes of the new lower teeth are given in Table 6. The lower teeth in a specimen previously described (M.218, 60M) are also rather smaller than their equivalents in the Sterkfontein series of *P. jonesi*. (The number of this specimen was in error given as M.215, 60M in the previous study.)

Parapapio whitei Broom, 1940

Referred Material: 5 specimens are referred to this species from the new Makapansgat material and one, M.635, described in the previous study, is transferred to this species from *P. broomi*.

The new material includes 2 male muzzles with teeth (M.2962 and M.3003), and a right maxillary fragment of unknown sex, with $P^3 - M^1$ (M.2973). M.2962 has $P^3 - M^2$ on the right and $P^4 - M^3$ on the left all in good condition.

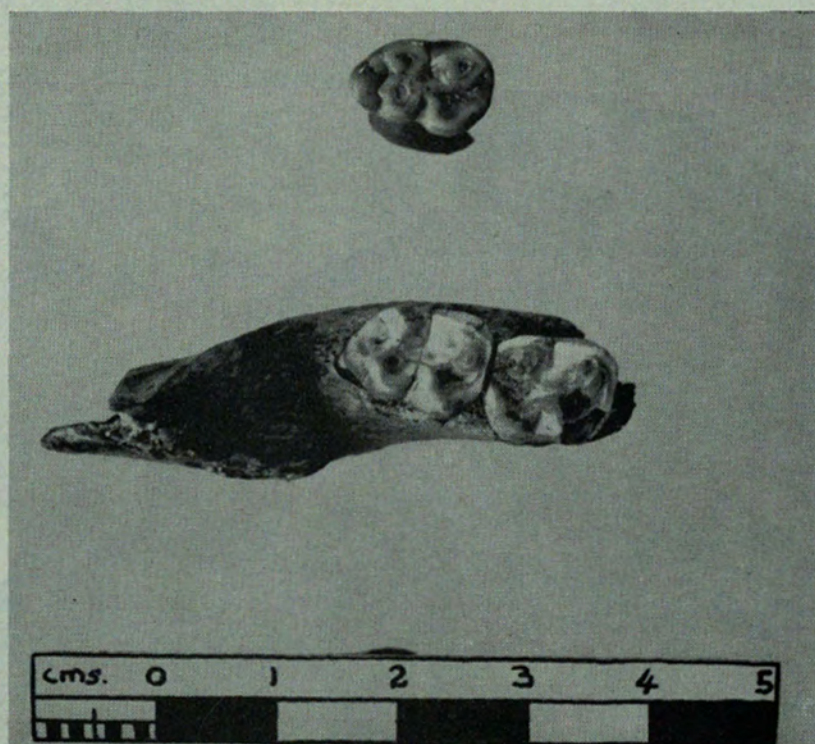


Fig. 5. *Parapapio jonesi* sex? (M.3091, above; M.2984, below). Occlusal view of lower teeth.

Table 7

Measurements of the skull of *Parapapio whitei* (in mm.)

	Male M.2962
Muzzle	
Height	
Anterior to P^3	(28)
Breadth	
Anterior to M^3	55
Anterior to P^3	46.5
Dorsal to M^2	41
Orbit	
Height	22
Breadth	(29)



Fig. 6. *Parapapio whitei* male (M.2962). Anterior view of skull.

M.3003 has P^4 — M^3 on the right but all are very worn and damaged. A small portion of a male mandibular symphysis with P_4 (M.2988) and part of a left mandibular corpus with P_4 and M_1 of an immature specimen of unknown sex (M.3007) are the only other 2 specimens of this species in the new material.



Fig. 7. *Parapapio whitei* male (M.2962). Lateral view of muzzle.

Description: (Figs. 6 — 8). The muzzle (M.2962) is the first male skull of any size to be referred to this species from either Sterkfontein or Makapansgat. On the right side, the specimen includes the orbit and supraorbital torus but on the left, most of the posterior part of the muzzle (and everything posterior to it)



Fig. 8. *Parapapio whitei* male (M.2962). Occlusal view of palate and upper teeth.

has been lost and the left anterior tip of the muzzle is also missing (Fig. 6). The other new muzzle (M.3003) shows the palate and anterior part of the muzzle but it is badly damaged and eroded.

Compared to the known male *P. broomi* specimens, M.2962 is considerably more

Table 8

Measurements of the upper teeth of *Parapapio whitei* (in mm.)

	P3		P4		M1			M2			M3			Rows
	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l	P4-M3
Male M.2962 M.3003	8.2	8.0	(9.2)	6.2	10.3	—	10.1	12.8	11.0	11.8 (12.5)	12.1 12.9	9.8	11.6	(40.6)
?Sex M.2973 M.635*			9.1	7.0	10.4	9.5	(10.0)	12.3	11.0	12.5	12.1	10.6	12.6	

* Described under *P. broomi* in previous study.

robust. (See Table 7 for the measurements of this specimen). The canine eminence is well developed and the supraorbital torus is prominent, two features not at all well marked in the known male *P. broomi* specimens. The new *P. whitei* male muzzle also has rather large maxillary fossae and the muzzle slopes up steeply and smoothly from the maxillary ridge to the midline (Fig. 7). The palate is extremely deep in both this specimen and M.3003.

In side view, the drop in the profile from the glabella down to the posterior edge of the nasal aperture appears to have been even steeper in M.2962 than in the male *P. broomi*, M.2961. (The area is damaged in M.2962 but was reconstructed to facilitate comparison.) The interorbital region in M.2962 was almost certainly very similar so that in M.2961. The small part of the inferior temporal line present in M.2962 is well marked.

The upper teeth (Fig. 8) in M.2962, M.3003, M.635 and M.2973 fit the morphological pattern for the genus well; in size, certain of their dimensions (see Table 8 for their sizes) are clearly larger than the equivalents in *P. broomi* and hence these specimens have been referred to *P. whitei*.

The new mandibular fragments are too small to be of any value for description of the mandible of this species. The new lower teeth fit the *Parapapio* morphological pattern well; in size (Table 9) they are interesting in that both new specimens are large when compared to the few known *P. whitei* teeth from Sterkfontein.

Table 9

Measurements of the lower teeth of *Parapapio whitei* (in mm.)

	P ₄		M ₁		
	b	l	bm	bd	l
Male M.2988	6.8	10.8			
?Sex M.3007	7.0	—	8.4	8.1	10.9

In the previous study it was suggested that M.635 fitted better with *P. whitei* than with *P. broomi* but that the specimen was *pro tem.* referred to *P. broomi* as very few specimens were available from Makapansgat and none other fitter *P. whitei*. A number of specimens are now being referred to *P. whitei* and this specimen can now also be referred to that species.

Parapapio sp.

Four batches of specimens are grouped under this heading: (1) 8 skull specimens, some fairly complete, some consisting of small portions only, but all either lacking

teeth or having very badly damaged teeth. Positive identification of these specimens is impossible but they all appear to belong in this genus. The specimens are:

M.3005 — a fairly complete skull of an immature adult (possibly female) of either *P. broomi* or *P. whitei*. The teeth are badly worn and damaged ($P^3 - M^2$) and no measurements are possible.

M.2997 — a small portion of a muzzle with very worn and badly damaged teeth belonging in either *P. broomi* or *P. whitei*.

M.3038 — Portion of a skull with no teeth, but showing the orbits, posterior part of the muzzle and a small portion of the frontals. In profile, there is rather more drop in the interorbital region than was assumed before the new material from Makapansgat was described.

M.3001 — a small portion of the frontals and the interorbital part of the nasals. The profile view of this specimen is similar to that of M.202, described in the previous study.

M.2996 — a small region of the posterior part of the muzzle. The interorbital drop in this specimen was probably steep.

M.3039 — a badly damaged specimen showing mainly a deep palate with very badly damaged teeth.

M.2998 — portion of a right maxilla with badly damaged teeth.

M.3043 — a good specimen of a calvaria including most of the base of the skull.

(2) This group consists of 12 specimens of the mandible and lower teeth which appear to be of *Parapapio* but can not be assigned to a species as most are of teeth anterior to M_2 .

M.3040 — consists of the symphysis and most of the left corpus of a female but the teeth have all either been lost or badly damaged.

Table 10

Measurements of the lower teeth of *Parapapio jonesi* or *P. broomi* (in mm.)

	P_3		P_4		M_1			M_2		
	b	l(h)	b	l	bm	bd	l	bm	bd	l
Male										
M.2995	5.3		13.4		—	8.0	(9.8)			
Female										
M.2985					—	—	9.1	9.5	—	—
?Sex										
M.3042					—	(7.6)	9.4	—	—	(11.0)
M.3020								9.5	9.2	10.7
M.3033			6.5	6.7						

Table 10 lists 5 specimens which could belong in either *P. jonesi* or *P. broomi* on dental size and morphology. Two of these specimens include portions of the mandible which can be measured: the height anterior to P₄ of M.2995 (a male) is 30mm. and the same measurement of M.2985 (a female) is 25mm.

Table 11

Measurements of the lower teeth of *Parapapio broomi* or *P. whitei* (in mm.)

	I ₁			I ₂			$\bar{C}$			P ₃		P ₄	
	h	b	l	h	b	l	h	b	l	b	l(h)	b	l
Male													
M.2986										5.9	—	7.3	8.1
M.3041	11.2	—	5.5	10.0	—	5.5					(16)		
?Sex													
M.3036	11.1	6.0	5.9	11.0	5.7	5.1							
M.3022												6.9	7.9
M.3028												6.5	7.5

Table 11 lists 5 specimens which on dental dimensions and morphology could belong in either *P. broomi* or *P. whitei*. M.3041, M.3036 and M.3028 could possibly even belong in *P. jonesi*.

M.3023 — is a male $\bar{C}$ which could belong in *P. jonesi*, *P. broomi* or *P. whitei*. Its dimensions (in mm.) are: h — 17.0; b — 10.0; l — 6.5.

(3) This group includes a juvenile skull and 4 deciduous teeth of unknown sex (3 upper and 1 lower) which appears to belong in the genus *Parapapio*.

The skull M.3004 (Fig. 9) has lost all its teeth anterior to M¹ but it is clearly that of a young juvenile cercopithecoid. The maxillae have been broken behind M¹, and M² can be seen lying well below the alveolar margin. The facial part of the skull is well preserved but most of the basal, left and posterior parts of the calvaria are damaged or missing. The skull shows the typical morphological features of the juvenile baboon — a relatively small, short face and a large calvaria. The teeth fit those of the genus *Parapapio*. The dimensions of the teeth (in mm.) are: M¹: bm — 9.6; bd — 8.8; l — 11.1. M²: bm — 11.5; l — (12.4). The breadth dimensions fit *P. broomi* whereas the length dimensions fit *P. whitei*. As M² had not yet erupted and M¹ did not have large adjacent teeth to wear it mesially and distally, the length measurements are probably large when compared with those of teeth in a tooth row and this specimen is probably a *P. broomi*.

(4) There are 3 specimens of this genus which include parts of the skull and mandible and both upper and lower teeth. Unfortunately they are rather damaged and difficult to develop.



Fig. 9. *Parapapio broomi?* juvenile (M.3004). Lateral view of skull.

Table 12

Measurements of dm^2 of *Parapapio* sp. (in mm.)

	bm	bd	l
?Sex			
M.3012	8.4	7.8	8.3
M.3010	7.9	6.8	7.8
M.2972	7.5	7.0	8.3

Table 12 gives the dimensions of 3 dm^2 of unknown sex.

Table 13

Measurements of the lower teeth of *Parapapio* sp. (in mm.)

	dm_2			M_1		
	bm	bd	l	bm	bd	
?Sex						
M.3006	6.4	6.7	8.7	8.0	8.3	10.0

Table 13 gives the measurements of one dm_2 of unknown sex.

They are:

M.3044 — The crushed right inferoposterior part of a calvaria and the right maxilla with M^2 ; also, the right ramus and posterior part of the body of a mandible with M_2 and M_3 .

M.3045 — left M_2 and M_3 in a mandibular fragment and parts of several upper and lower teeth.

M.3046 — right half of a female mandible with teeth and also some upper teeth, all badly damaged.

Discussion: The new *Parapapio* material from Makapansgat is of value from a number of different aspects.

Firstly, the number of specimens of each of the 3 *Parapapio* species at Makapansgat is interesting. Table 14 gives the numbers of specimens of *P. jonesi*, *P. broomi* and *P. whitei* at Sterkfontein and at Makapansgat and also these numbers expressed as a percentage of the total number of *Parapapio* specimens at the relevant site. The dental size distribution of the *Parapapio* specimens at the two sites is seen to be very similar, although there is some suggestion of a reduction at Makapansgat (the more recent site) in the number of the largest form, *P. whitei*.

Table 14

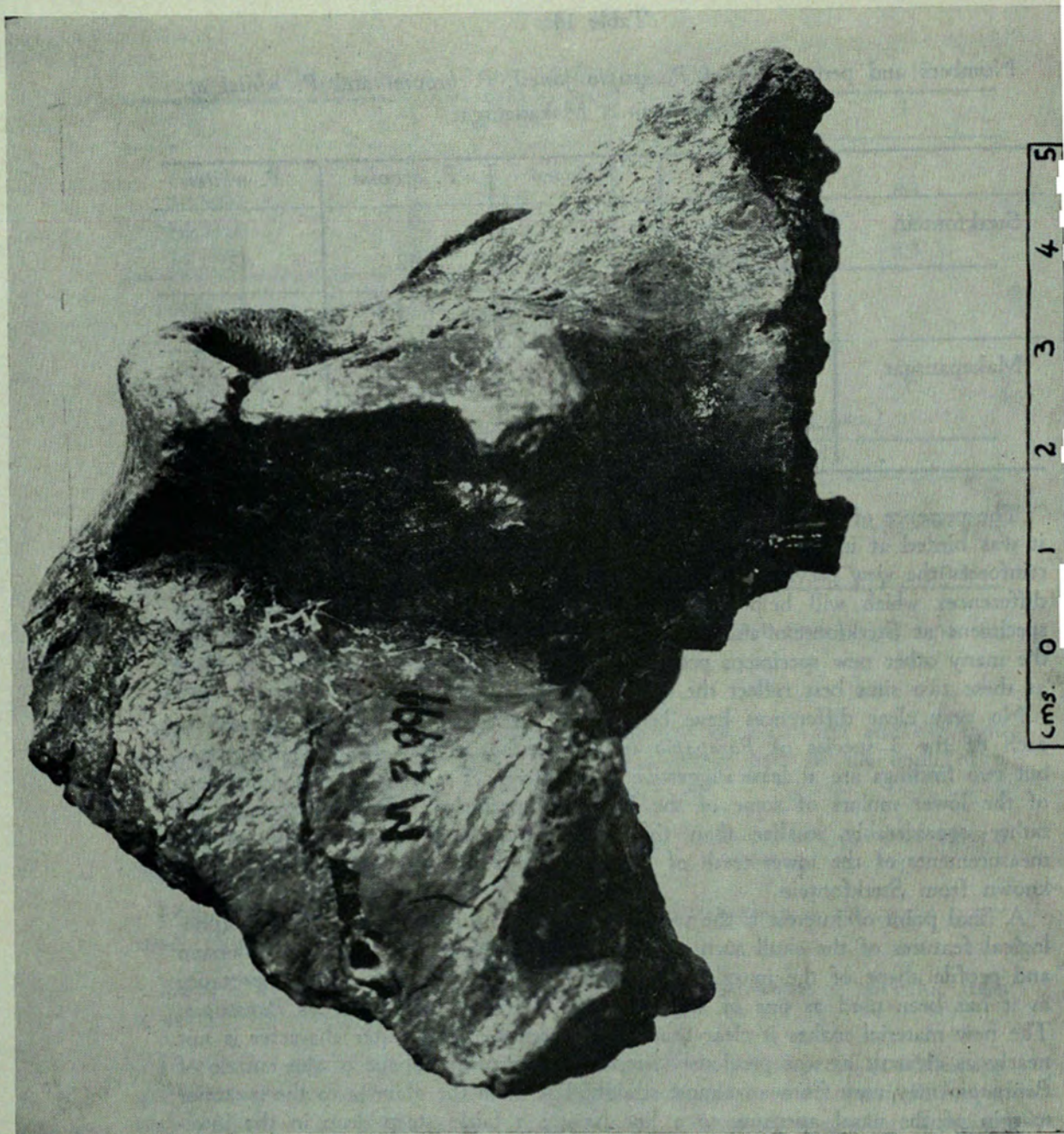
Numbers and percentages of *Parapapio jonesi*, *P. broomi* and *P. whitei* at Sterkfontein & Makapansgat

		<i>P. jonesi</i>	<i>P. broomi</i>	<i>P. whitei</i>
Sterkfontein	No. of specimens	24	42	13
	Percentage	30.5	53	16.5
Makapansgat	No. of specimens	15	34	4
	Percentage	28.5	64	7.5

The presence of *P. whitei* at Makapansgat is reported for the first time although it was hinted at in the previous study. The new muzzle of *P. whitei* (M.2962) reinforces the view previously expressed that there are probably morphological skull differences which will help clarify the taxonomic subdivision of the *Parapapio* specimens at Sterkfontein and Makapansgat. However, neither this specimen nor the many other new specimens prove conclusively whether the 3 species postulated at these two sites best reflect the true taxonomy.

No very clear differences have been found between the specimens referred to each of the 3 species of *Parapapio* from Sterkfontein and from Makapansgat, but two findings are at least suggestive that differences may exist. The dimensions of the lower molars of some of the *P. jonesi* specimens from Makapansgat are rather considerably smaller than those from Sterkfontein and certain of the measurements of the lower teeth of *P. whitei* are larger than any of this species known from Sterkfontein.

A final point of interest is the variability found in this genus of certain morphological features of the skull such as maxillary fossae, shape of the muzzle dorsum and profile shape of the muzzle. The latter feature is of considerable importance as it has been used as one of the diagnostic characters of the genus *Parapapio*. The new material makes it clear that the difference in this latter character is not nearly as clearcut as was previously supposed. The profile shape of the muzzle of *Parapapio* may vary from an almost straight line from the glabella to the posterior margin of the nasal aperture, to a line having a fairly steep drop in the inter-orbital region. The shape is thus more similar to that of *Papio* than was previously supposed but it is still considerably different. The absence of clear sexual dimorphism in the molars of *Parapapio* continues to be a significant feature separating this genus from *Papio*.



cm. 0 1 2 3 4 5

Cercopithecoides Mollett, 1947

A number of specimens belonging in this genus have been found in the new material from Makapansgat. The material includes specimens which necessitate a re-description of the male skull of *C. williamsi* and also a re-assessment of the taxonomy within the genus. The new material is all referred to the species *C. williamsi*.

Cercopithecoides williamsi Mollet, 1947

Referred Material: 10 specimens of this species were found in the newly recovered material from Makapansgat. These specimens include a very well preserved male skull (M.2999) which is described below, a good male muzzle with all 4 incisors (M.3000) and the interorbital portion and left maxilla with no teeth of a specimen of doubtful sex, but probably also a male (M.674). In addition, there is specimen M.2990 which has portions of the right and left corpora of a mandible with $P_3 - M_2$ on the right and M_2 and the mesial half of M_3 on the left, M.2989 and M.2987 which are mandibular fragments with single teeth and 4 isolated lower teeth (M.3025, M.3026, M.3029 and M.3031). Of these latter specimens, M.2990 and M.2989 are probably from males but the sexes of the other specimens are not apparent.

Description: (Figs. 10 — 14.) The new male skull (M.2999) has unfortunately lost all of its teeth with the exception of the left M^3 and that tooth is very worn and considerably damaged. The facial portion of the specimen is intact and very well preserved but the part of the skull posterior to an approximately vertical plane through the anterolateral corner of the left orbit and the posterior part of the right mastoid region is missing.

The type skull of *C. williamsi* (AD.1326-3) is the only male skull of this species hitherto described. It is a very complete specimen but the teeth, facial skeleton and calvarium are damaged in places and generally very eroded. Where bone is missing from the calvaria, an excellent natural endocranial cast has been exposed. Comparison of this specimen with the new skull (M.2999) immediately shows the very close resemblance between the two specimens in overall size, general shape and shortness of the face and shape and size of the dental arcade (Figs. 10 — 13). It appears clear that they both belong to the same species but that due to the damage and erosion of the type skull, a number of features of the male skull of *C. williamsi* require to be re-described.

The new specimens (M.2999 and M.3000) confirm the extreme shortness of the face and a concavity in profile between the nasion and posterior margin of the nasal aperture (Fig. 10). The nasal aperture itself is considerably shorter in the two new specimens (see Table 15) than in the type specimen and it is clear that, due to the damage, the dimension given for the type specimen was too great. The nasal aperture breadth shows considerable variation in the three specimens. On either side of the nasal aperture, the maxilla is flattened and

Table 15

Measurements of the skull of *Cercopithecoides williamsi* (in mm.)

		Male		?Sex
		M.2999	M.674	M.3000
Calvaria				
Breadth				
Minimum interfrontal	(58)			
Muzzle				
Height				
Anterior to P ³	30			
Breadth				
Anterior to M ³	46			
Anterior to P ³	43			
Length				
Muzzle	58.5			59
Palate	55			
Orbit				
Interorbital	22	19.5		19
External orbital	91			
Height	23			20
Breadth	29			
Nasal aperture				
Breadth	19			17.5
Length	(32.5)			32

faces anterosuperiorly (Fig. 11). The canine eminences are large and demarcate this flat antero-superior surface from the laterally facing sides of the muzzle. There are no maxillary fossae.

The nasal bones are extremely flattened and broad in M.2999 but in M.3000 they are rather more rounded. The high narrow appearance of these bones in the type specimen may be partly due to erosion in the region. A remarkable feature of M.2999 is the exceptionally broad interorbital measurement (Fig. 11). That great breadth is normal in this region of this species is confirmed by M.3000 and M.674 (see Table 15). The supraorbital tori are very robust in M.2999 and have a rough pitted appearance; there is a hollow between them in the midline. A marked transverse depression runs across the calvaria behind the tori and the short section of the inferior temporal line that can be seen on the right side of this specimen is very strongly developed (Fig. 12). The latter three features all indicate a remarkable robustness not formerly associated with, or anticipated in, this species.

Viewed from below (Fig. 13), the palate is rectangular in shape as in the type specimen. The incisive foramen is large and is flanked on each side by 2 — 3 anterior palatine foramina. The palate is somewhat uneven generally and pitted by numerous foramina. The posterior palatine foramina are large and slit-like in an anteroposterior direction and there is no lingula. The whole posterior part of the palate (the palatines) slopes superiorly on each side into the posterior palatine foramina.



Fig. 11. *Cercopithecoides williamsi* male (M.2999). Anterior view of skull.

The beautiful state of preservation of the new specimen (M.2999) allows numerous other anatomical features to be seen which are not often preserved in the usually damaged and fragmented cercopithecoid material from the South African limestone deposits. Thus, there are 4 large infraorbital foramina, a short patent metopic suture, and, although slightly damaged, the external acoustic meatus and mandibular fossa can be clearly seen. These latter structures show no unusual features.

As stated above, only the left M^3 is present in M.2999 and this is very worn and badly damaged (Fig. 13). The root sockets of all the other teeth, with the exception of the right I^1 and I^2 , can be clearly seen and the root pattern is as described for the other living and fossil Cercopithecoidea. A diastema is present between $\underline{C}$ and I^2 . On the right, I^1 and I^2 must have been lost some time before fossilization as their root sockets have been obliterated by alveolar bone. The only other information about the upper dentition from this new batch of specimens comes from M.3000 which has all 4 upper incisors present but very worn. Although small teeth, they are broad buccolingually. Broken fragments of the $\underline{C}$ are also present but they are sufficient to indicate only that the tooth was of large size.

The new lower jaw fragments are too small to give any new information about the mandible of this species and, morphologically, the new lower teeth fit the described pattern of *Cercopithecoides* well (Fig. 14). Certain of the teeth (e.g. M.3026 and M.3021) show some features, especially the large buccal intercuspal clefts, in a form similar to that previously described for *C. molletti*. In size, (see Table 16) the new specimens are larger in a number of dimensions than the specimens previously referred to *C. williamsi* and in certain of these dimensions they approach *C. molletti* closely. The implications of these differences from *C. williamsi* and resemblances to *C. molletti* are considered in the discussion below.

Discussion: The great interorbital breadth, the very robust supraorbital tori and the particularly well developed temporal lines of the new male skull material of *C. williamsi* do not assist in relating this genus to the known living or fossil South African Cercopithecoidea, although there is now some resemblance to the calvaria of '*Parapapio*' *coronatus*. With the relatively very large calvarium and extremely short face with small premolars and molars, it is difficult to interpret the new features, even allowing for the fact that the upper canines were rather large. Detailed comparisons with other living and fossil African forms (and possibly Asian types as well) will have to be made in an effort to elucidate the affinities of this genus.

In the previous study, the few Makapansgat *Cercopithecoides* specimens known were grouped with those of Sterkfontein in *C. williamsi*. Some of their dental dimensions appeared to be near or at the upper limits for that species but a clear separation of material from the two sites was not indicated. The dimensions of the lower teeth of M.2990, one of the new *Cercopithecoides* mandibular fragments from Makapansgat, would, if they were referred to *C. williamsi*, increase the ranges of 4 dimensions (M_1 bm, bd, l; M_2 bm) considerably.



Fig. 12. *Cercopithecoides williamsi* male (M.2999). Dorsal view of skull.

Table 16

Measurements of the lower teeth of *Cercopithecoides williamsi* (in mm.)

	P ₃		P ₄		M ₁			M ₂			M ₃			
	b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
?Sex														
M.2990	5.2	—	6.3	6.9	7.5	7.7	9.1	8.6	8.4	9.5	8.3			
M.2987											7.9	7.5	(3.5)	12.6
M.3029											8.3	7.5	—	11.3
M.3025					—	—	8.5							
M.2989			5.6	7.3										
M.3026								8.3	8.1	9.9				
M.3031					7.5	7.7	10.0							

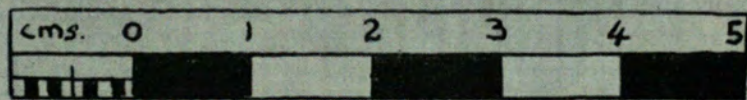
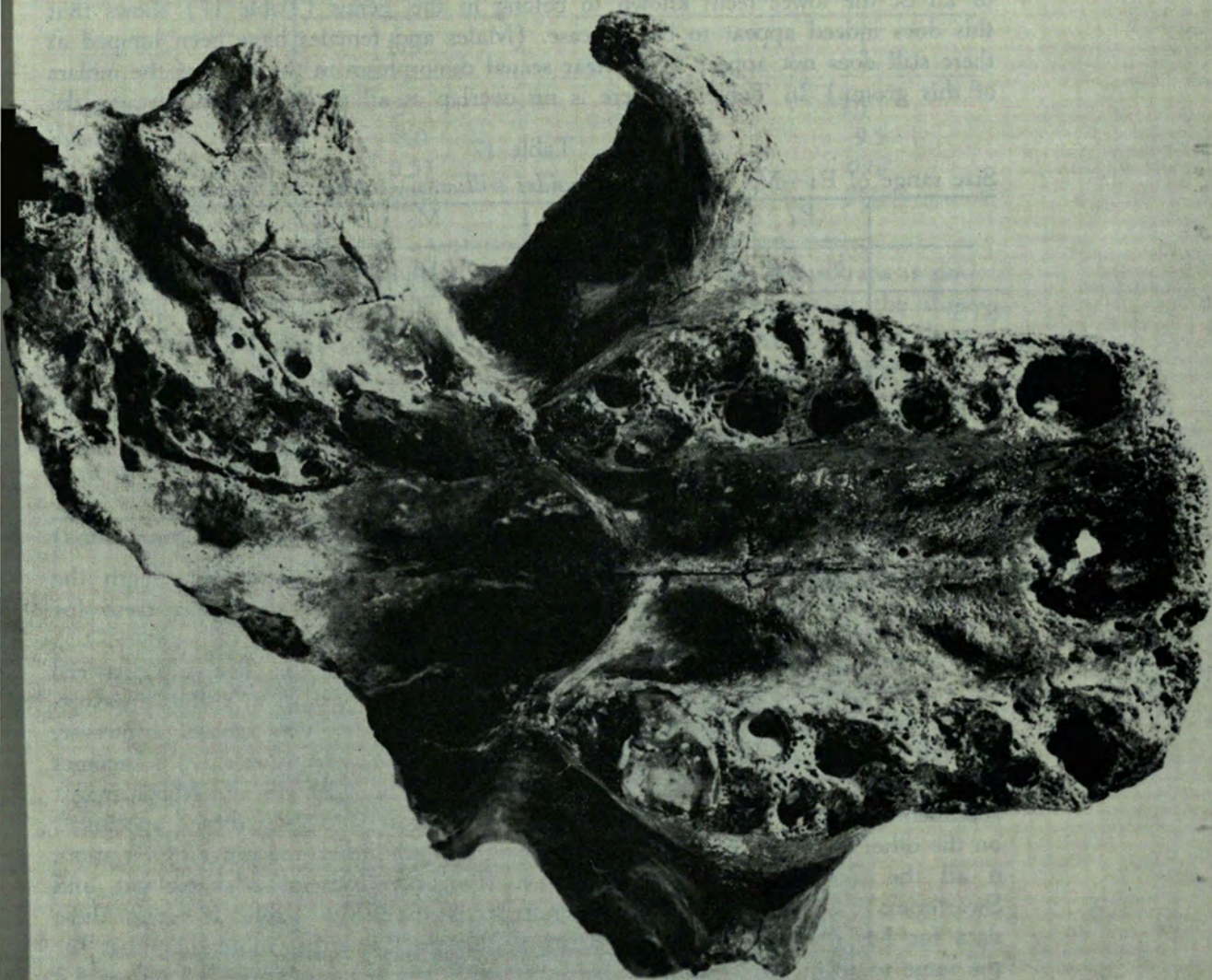


Fig. 13. *Cercopithecoides williamsi* male (M.2999). Basal view of skull.

Also, many of the other dimensions of the newly discovered fragments would fall near or above the maxima previously found for that species. This suggests that a dental size difference might be present between the *Cercopithecoides* specimen from Sterkfontein and those from Makapansgat. An analysis of the dimensions of all of the lower teeth known to belong in this genus (Table 17) shows that this does indeed appear to be the case. (Males and females have been lumped as there still does not appear to be clear sexual dimorphism in the sizes of the molars of this group.) In Table 17 there is no overlap at all in M₁ length between the

Table 17

Size range of P₄—M₃ of *Cercopithecoides williamsi*—males plus females—(in mm.)

	P ₄		M ₁			M ₂			M ₃			
	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
STS.	5.2	6.5	6.2	6.4	7.7	6.8	6.8	8.5	7.7	7.1	3.6	10.9
	5.4	6.6	7.4	7.3	8.1	8.3	8.6	9.6	8.3	8.2	5.8	12.4
MAK.	5.5	6.9	6.5	7.2	8.4	7.9	8.1	9.5	7.9	7.5	(3.5)	11.3
	6.3	7.0	7.5	7.7	10.0	8.6	8.5	9.9	8.3	8.8	5.3	12.6
SK.	6.3	6.2	7.2	7.5	8.2	8.2	9.0	10.4	8.8	8.9	—	—
	6.9	7.5	7.8	8.3	10.0	8.7	9.7	10.7				

(STS. — Sterkfontein; MAK. — Makapansgat, limeworks; SK. — Swartkrans)

Sterkfontein and Makapansgat specimens and in M₁ bd. and M₂ length the overlap is only very slight. There are insufficient data on the upper teeth for a similar analysis to be of value.

The new specimens have also considerably decreased the size gap between *C. williamsi* and *C. molletti*, although there is still no overlap in certain measurements, for example on M₂ bd and length, between the two species. However, with all the *Cercopithecoides* material arranged by sites, as in Table 17, it becomes apparent that the dental size differences between the Sterkfontein and Makapansgat specimens on the one hand, and the Makapansgat and Swartkrans specimens on the other hand, are of much the same magnitude. Further, the range of variation, if all the *Cercopithecoides* material (i.e. from Sterkfontein, Makapansgat and Swartkrans) is lumped together, is not really excessive. Table 18 gives these data for M₂. The coefficient of variation calculated is rather more than that for the same tooth in *Papio ursinus* where the values (in %) are bm — 4.5, bd — 4.2 and l — 4.9, but they are still within the limits for a species (4 — 10% according to Simpson and Roe, 1939). For the above reasons, it would seem that it would now be far wiser to lump all the known *Cercopithecoides* material into a single species, *C. williamsi* and to sink *C. moletti*. The small morphological differences which were described between the two species in the previous study have, as described above, been bridged in several instances and the others are very minor and are probably the result of small relative growth differences.

Table 18

Statistical variation of M₂ in *Cercopithecoides williamsi* — males plus females —
(in mm.)

	M ₂		
	bm	bd	l
Number	13	14	16
Mean	8.0	8.3	9.5
Standard deviation	0.51	0.74	0.67
Coefficient of variation	6%	9%	7%

The size increase from Sterkfontein, through Makapansgat to Swartkrans is now obvious and this sequence fits the currently accepted age sequence of the three sites from oldest through to most recent. The *Cercopithecoides* material must there-

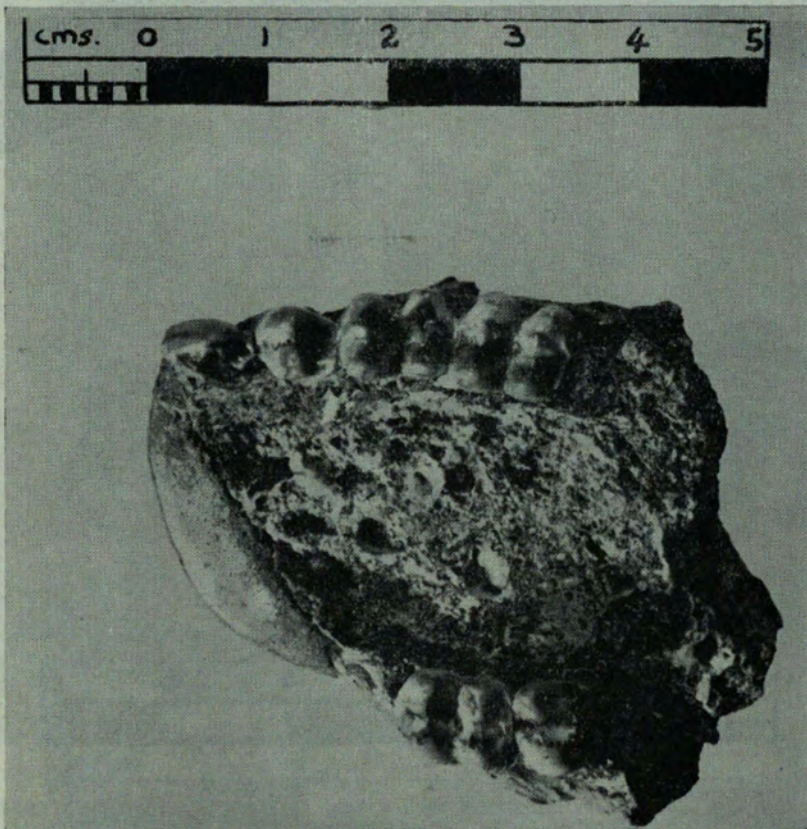


Fig. 14. *Cercopithecoides williamsi* sex? (M.2990). Occlusal view of mandibular fragment with teeth.

fore be regarded as forming a chronocline and it becomes necessary to decide whether the material from the three sites merits subspecific separation. Single *Cercopithecoides* specimens have previously also been described from Taungs, Graveyard and Cooper's and there are two specimens known from Swartkrans II. This material is at present too incomplete for classification in one of the three groups described above but, when more material from these sites is recovered, they may yet be found to bridge or extend the three size ranges postulated in Table 17. It would therefore seem that the most satisfactory arrangement at the



Fig. 15. *Simopithecus darti* (Above, M.2974; below left, M.2967; below right, M.2971). Views of upper teeth.

moment is to place all of the *Cercopithecoides* specimens into one species, *C. williamsi*, with the specimens from Sterkfontein, Makapansgat and Swartkrans forming a chronocline. More material from these, and the other sites mentioned above, may in the future require three subspecies to be created or may show a continuous gradation to exist in the material from all of the above sites.

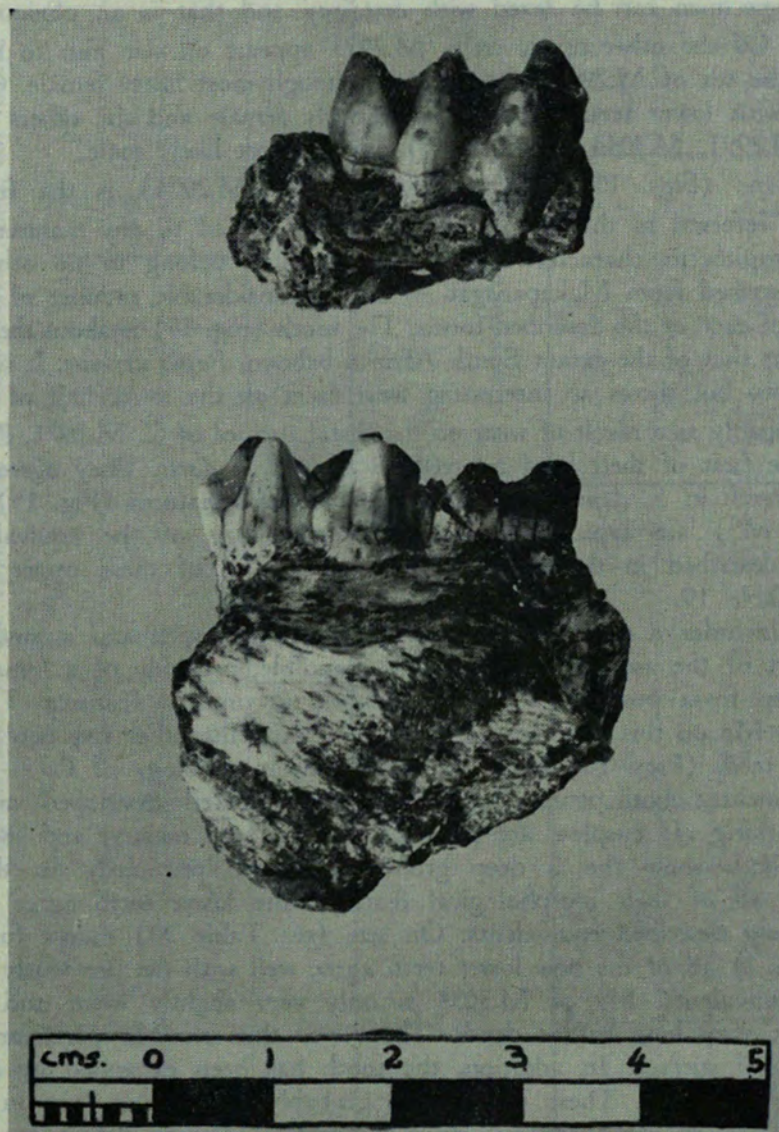


Fig. 16. *Simopithecus darti* sex? (Above, M.2991; below, M.3034). Lateral view of lower teeth.

Simopithecus Andrews, 1916.

There are nine specimens of this genus in the new material from Makapansgat and they can all clearly be referred to the species *S. darti*, which has previously been described from this site.

Simopithecus darti (Broom and Jensen), 1946.

Referred Material: The nine new specimens of this species are all either rather small maxillary or mandibular fragments with teeth, or isolated teeth. Only one specimen can be sexed with certainty and that is an obvious male $\underline{C}$ (M.2974). Of the other upper teeth, M.2971 appears on size also to be from a male, but the sex of M.2967 is uncertain, although most likely female. Of the six fragments with lower teeth, M.2981 is probably female and the others (M.3027, M.2965, M.2991, M.3034 and M.3035) are all most likely male.

Description: (Figs. 15 — 17.) The male $\underline{C}$ (M.2974) is the first of its kind to be referred to this species. Although not linked to any material showing typical *Simopithecus* characteristics, on size it could belong to no other species hitherto described from Makapansgat — and a considerable number of specimens are known of each of the described forms. The tooth (Fig. 15) is about the same size and shape as that of the extant South African baboon, *Papio ursinus*. It is comparatively unworn but shows an interesting wear facet on the lower half of its mesial surface, probably as a result of wear on the distal surface of $\bar{C}$. M.2971, P^3 and P^4 , are also the first of their kind referred to a male *S. darti*. They agree with the equivalent teeth in *S. danieli* and present no unusual features (Fig. 15). M.2967 (M^2 and M^3) are typical in size and morphology of the equivalent teeth previously described in this species. The sizes of all of these upper teeth are given in Table 19.

M.2981 includes a small posterior portion of the corpus and a small antero-inferior part of the ascending ramus of a mandible, probably of a female. Other than a deep fossa posterior to M_3 , it shows no unusual features. The height posterior to M_3 on this specimen is 36mm. This and the other five new specimens with lower teeth (Figs. 16 and 17) illustrate the morphology of P_4 — M_3 very well and include both worn and unworn teeth. Well developed mesiobuccal grooves marking off cusplets are present on all of the molars, and the two P_4 specimens both show the 2 deep grooves described previously on the buccal surface. In all of their morphological features, the lower teeth agree well with the previously described equivalents. On size (see Table 20) except for M.3034 (mainly M_2 1) all of the new lower teeth agree well with the previously described *S. darti* equivalents. M_2 of M.3034 is only very slightly worn and probably erupted not very long before death. There was thus no M_3 posterior to it to wear its distal surface. In addition, the tooth has been expanded by a number of matrix-filled cracks. These two factors probably account, at least in part, for the greater size of this tooth but more material is required before the specimen can be adequately assessed.

Measurements of the upper teeth of *Simopithecus darti* (in mm.)

	C				P ³		P ⁴		M ¹	M ²			M ³		
	h	b	l ₁	l ₂	b	l(h)	b	l		bm	bd	l	bm	bd	l
Male M.2974	(40)	11.5	11.2	13.6											
?Sex M.2971					8.0	(6.1)	10.0	8.6							
M.2967										13.3	12.0	15.8	13.3	11.6	17.4

Measurements of the lower teeth of *Simopithecus darti* (in mm.)[illegible]

Discussion: In a recent paper, Leakey and Whitworth (1958) report that much new fossil *Simopithecus* material has been discovered in East Africa in the last few years. Using this material, the authors give a considerably expanded description of the genus *Simopithecus* and propose that the East African species, *S. oswaldi*, be subdivided into 3 subspecies, *S. o. oswaldi* (from Kanjera), *S. o. olduvaiensis* (from Olduvai) and *S. o. mariae* (from Olorgesailie). The authors state that the size ranges of these three subspecies overlap but that there is "some indication that the *Simopithecus* at Olduvai was slightly larger than that found at Kanjera, and that the *Simopithecus* at Olorgesailie was still larger." A new giant form of *Simopithecus* from Olduvai, *S. jonathani*, is also described in their paper. This species is interesting in that the sizes of the teeth of the type specimen, a female, are almost exactly matched by the *S. danieli* males from Swartkrans.

Because of the considerable size range now attributed to *S. oswaldi*, more than double that of *Papio ursinus*, Leakey and Whitworth suggest that since "moderate size differences alone are insufficient grounds for specific differentiation in such

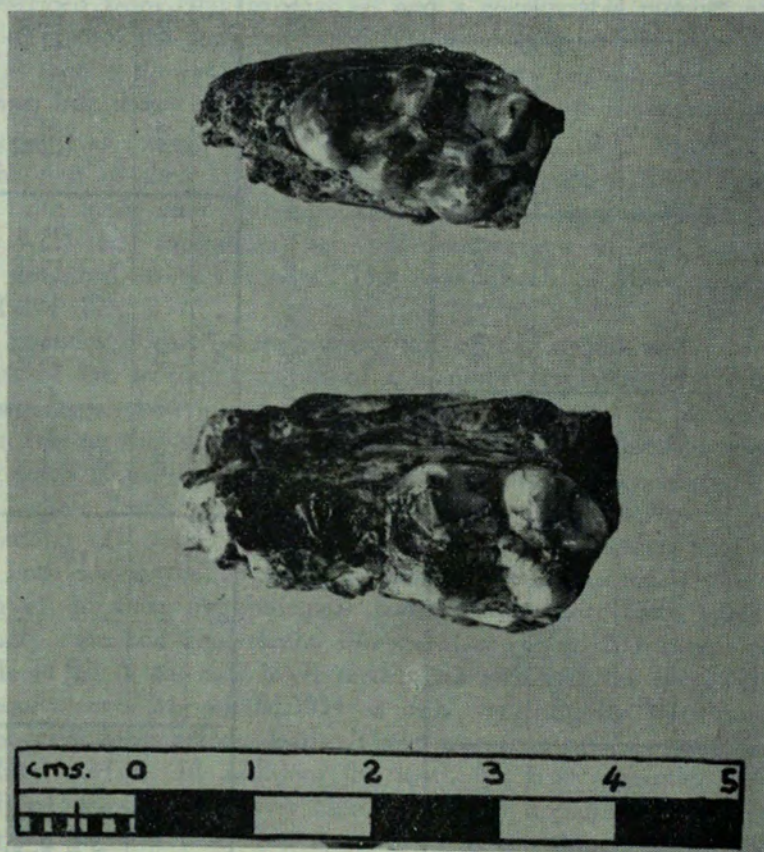


Fig. 17. *Simopithecus darti* sex? (Above, M.2991; below, M.3034). Occlusal view of lower teeth.

a group, it seems to us that the two South African species, *S. darti* and *S. danieli*, are better treated as geographical subspecies (or even a single subspecies) of *S. oswaldi*". However, they conclude by stating that, not having studied the material at first hand, they "do not wish to press this particular view unduly".

A single badly crushed female skull (SK.561) and a female muzzle (SK.563), both of *S. danieli*, are the only *Simopithecus* skull specimens of any size known from South Africa. A few fairly complete mandibular specimens of both *S. darti* and *S. danieli* are however known. In general, there is good agreement between the skulls and mandibles from South Africa and those from East Africa, but even on the meagre material available from South Africa, certain differences are apparent. The muzzle in SK.563 appears to be rather higher than in the *S. oswaldi* specimens illustrated and the maxillary fossa is deep in this South African specimen, although SK.561 is like the East African forms where there is no depression at all. The mandible M.621 (*S. darti*) has a very deep mandibular fossa and the symphyseal region slopes down very steeply between the premolars and behind the incisors. This latter specimen in particular thus shows characters which differ considerably from those of *S. oswaldi* but its teeth show the typical *Simopithecus* morphology.

In their paper, Leakey and Whitworth give only a single table of measurements. This table gives the ranges of the various dental dimensions of the premolars and molars, of the males and females together, for the whole of the species as now defined. In the two South African *Simopithecus* species, there are distinct size differences, in both species, between these teeth in the two sexes. Also, the specimens included in their table came from sites that are a considerable distance apart and are probably of rather different ages. Until the more detailed account which they are preparing for the *Fossil Mammals of Africa Series* appears, describing their material by sex and site, it is thus not possible to assess the taxonomic proposals which they make. For this reason, and because of the morphological differences discussed above, the name *S. darti* is retained in this paper for the *Simopithecus* specimens from Makapansgat. Similarly, *S. danieli* must continue, at least for the present, to be accepted as the valid name for the *Simopithecus* material from Swartkrans.

In this same paper, Leakey and Whitworth suggest that the specimen KA.150 from Kromdraai, which was previously referred to *Gorgopithecus major*, is a "*Simopithecus* (perhaps *S. oswaldi*)". That there are slight morphological similarities between the teeth of the genera *Gorgopithecus* and *Simopithecus* (and *Dinopithecus* as well) was mentioned in the previous study, but a re-examination of KA.150, and the relevant comparative material, reinforces the view expressed there, namely, that KA.150 does not show the typical dental morphological pattern of *Simopithecus* and definitely belongs in the species *G. major*. On a recent visit to South Africa, Dr. Leakey examined the relevant material and now agrees that this species is not a *Simopithecus*.

Finally, Leakey and Whitworth state in their paper that they consider that the material described by Dietrich (1942) as *Papio* (*Simopithecus*) *serengetensis* belongs in the genus *Simopithecus* and, in fact, they "see no reason to separate it from *S. oswaldi*". As stated previously, the illustrations of these specimens in Dietrich's paper are not very clear but the photograph of a mandible (Fig. 38) in particular does not show the very typical *Simopithecus* dental morphological pattern. In the drawings, the teeth depicted in Fig. 4 of Dietrich's paper for example do show some resemblance to the *Simopithecus* pattern but of the eleven molars for which lengths and breadths are given by Dietrich, only a single dimension of a single tooth (M^1 breadth) falls within the already very extensive ranges listed by Leakey and Whitworth for *S. oswaldi*. It would seem that Dietrich's specimens should be re-examined in the light of recent work, but, on the balance of evidence now available, they must be considered small fossil forms of *Papio* or *Parapapio*.

ACKNOWLEDGEMENTS

The collection and preparation of the material described in this paper was made possible mainly by grants to Emeritus Professor R. A. Dart, Department of Anatomy, University of the Witwatersrand, who has for many years organised research at Makapansgat. The grants were from the Wenner-Gren and Wilkie Foundations of the United States of America, the South African Council for Scientific and Industrial Research and the University of the Witwatersrand.

A number of workers have participated in the actual collecting, particularly Mr. J. W. Kitching, of the Bernard Price Institute for Palaeontological Research, Johannesburg, who also supervised the preparation of the specimens, and Mr. A. R. Hughes of the Department of Anatomy of the University of the Witwatersrand, to whom I am also indebted for the photographs which illustrate this paper. My thanks are due to the above individuals and also to the Institutions mentioned for their help and also for permission to describe the material.

I should also like to thank Professor P. V. Tobias of the Department of Anatomy of the University of the Witwatersrand, and Dr. J. T. Robinson of the Transvaal Museum, Pretoria, for discussions on the subject matter of this paper. Through the courtesy of the Director and Board of the Transvaal Museum, Dr. Robinson also arranged for me to study comparative fossil cercopithecoid material in the Museum's collection. Finally, I should like to thank my wife for typing the manuscript of this paper.

REFERENCES

- DIETRICH, W. O., 1942 Altestquartäre Säugetiere aus der südliche Serengeti, Deutsch Ost Afrika. *Palaeontographica*, 94, abt. A, 52-4.
FREEDMAN, L., 1957, The Fossil Cercopithecoidae of South Africa. *Ann. Transv. Mus.*, 23, 121-262.

LEAKEY, L. S. B. & WHITWORTH, T., 1958, Notes on the Genus *Simopithecus* with a Description of a New Species from Olduvai. *Occ. Pap. Coryndon Mus.*, no. 6, 1-14.

SIMPSON, G. G. & ROE, A., 1939, *Quantitative Zoology*. 1st. Ed. N.Y. and London: McGraw Hill Book Co. Inc.

ERRATUM

Subsequent to the printing of this volume the South African Council for Scientific and Industrial Research has made a substantial contribution towards the cost of publication of the paper by Dr. L. Freedman. This grant is greatly acknowledged.

FURTHER REVISION OF THE FOSSIL ELEPHANTIDAE OF SOUTHERN AFRICA

By H. B. S. COOKE

ABSTRACT

The South African fossil *Metarchidiskodon griqua* is regarded as indeterminable and hence as a *nomen vanum*; the generic name thus also falls away. A new method for representing graphically the main dimensional features of elephant molar teeth is applied to the fossil species from southern and East Africa. It is suggested that the genus *Palaeoloxodon* is not represented in these regions and that most of the extinct elephants must be placed in *Archidiskodon*. The species distinguished are *A. subplanifrons*, *A. broomi*, *A. exoptatus*, *A. recki* and *A. transvaalensis*, while *A. africanavus* and *A. archidiskodontoides* are of uncertain status. The North African "*Elephas*" *atlanticus* is placed in *Loxodonta* and the South African species *zulu* is regarded as a synonym. It is considered that the Pleistocene elephants of Africa have evolved within the continent itself.

INTRODUCTION

During the period from 1906 to 1939 there were described twenty-one supposedly extinct species of elephant from southern Africa. In 1947 the writer¹ attempted a revision of the material and reduced the number to eleven while, in the same year, Arambourg² rejected all the South African names. In 1955 Meiring³ added a new species *Archidiskodon scotti* and in 1958 Singer and Hooijer⁴ recorded, for the first time, a *Stegolophodon* which they wisely refrained from naming specifically. During 1956 the writer had the opportunity of examining large numbers of fossil proboscidean teeth at museums in Europe and in 1958 was able to study material in various institutions in the United States of America, the result of these studies being to invoke a far more critical attitude towards the multiplicity of species still recognised in southern Africa.

STATUS OF METARCHIDISKODON GRIQUA

One of the most serious problems is the status and position of "*Metarchidiskodon griqua*". Haughton⁵ described in 1922 a fragmentary lower molar which he named *Loxodonta griqua*. The generic reference was changed to *Archidiskodon* in 1928 by Osborn⁶ and in 1934⁷ he founded upon it the new genus *Metarchidiskodon*. In 1951 Dietrich⁸ discussed the phylogeny and taxonomy of some of the African fossil elephants and applied the generic name *Metarchidiskodon* to the majority of the fossil elephants from East and South Africa, including the abundant East African "*Elephas*" *recki*. The present writer stated in 1947 "It is unfortunate that it (the type specimen) is of so fragmentary a nature as this fact renders specific deductions very difficult . . . and the differences hardly seem to be even of

sub-generic rank . . . It would seem that the specific distinction of *Mammuthus griqua* must be accepted more because the nature of the material prevents its rejection than because it is a clearly identifiable form". There is even doubt as to whether it is a lower molar (Haughton⁵, Cooke¹) or an upper molar (Osborn⁶). The simple fact is that the specimen is not adequate for the proper definition and identification of specific characters and far too much has been built upon a very tenuous foundation. It is here proposed that the species be regarded as practically indeterminable (see Simpson⁹) and hence as a *nomen vanum* to which other material should not be referred. The genus *Metarchidiskodon* also falls away.

GRAPHICAL STUDY

Method

In his paper on *Archidiskodon scotti*, Meiring³ made a graphic comparison of the width and height of the teeth for the species named in South Africa and showed that a "width/height index $\frac{(\text{width} \times 100)}{\text{height}}$ " is more useful than the traditional length/breadth index, which cannot be employed on fossil teeth lacking some of their plates through damage. As far back as 1938, Arambourg¹⁰ used the converse ratio $\frac{\text{height}}{\text{breadth}}$ as a figure for "the hypsodonty". The present writer proposes that the ratio $\frac{\text{height} \times 100}{\text{breadth}}$ should be known as the "index of hypsodonty" and finds that it can be combined with the length/lamellae ratio to provide a useful method for representing graphically the main dimensional features of elephant molar teeth. In these diagrams the vertical axis represents the value of the index of hypsodonty (H/W) and the horizontal axis shows the value of the length-lamellae ratio (L/P). A single point thus serves to show for a particular molar the relationship between the maximum breadth of the widest lamella (W), the maximum height (H) of the tallest preserved plate (measured over the enamel) and the average thickness of a complete plate (which is also the complement of the lamellar frequency) derived from the length of the tooth (L) measured perpendicular to the plates, divided by the number of plates (P). Plots of this type for a number of specimens indicate the range of variation within a group. The index of hypsodonty is preferred to Meiring's index as high-crowned teeth are then shown in their most easily interpreted position towards the top of the diagram. Such plots are truly representative only when the real maximum height is known; in moderately worn teeth the height is usually measured on an unworn lamella (if one is present) and little error is introduced but it is clear that excessive wear will lead to displacement of the plotted position *down* the graph and an undue extension of the apparent range of variability.

Plots have been prepared for a number of species but the literature is somewhat defective and in some cases the writer has had to depend entirely on his own

measurements, with consequent reduction in the statistical quantity available. A few generalizations may be made. (a) Somewhat surprisingly, there is a considerable overlap between the plots for corresponding upper and lower molars, presumably because lower teeth are commonly a little narrower than uppers, thus tending to compensate to some extent for the higher crowns of upper molars; the difference between upper and lower teeth is most apparent in the very hypsodont species. (b) The lower teeth normally possess slightly thicker lamellae than the uppers and the limits for the lower teeth extend one or two units towards the right and those of upper teeth towards the left in the diagrams. (c) Second molars tend to have somewhat thinner lamellae than third molars and thus tend to lie a few units towards the left in the diagram; in the case of the most high crowned species they tend to lie below the mean values of the index of hypsodonty for the third molars.

Figures 18 and 19 represent data for 73 second molars and 30 third molars respectively of *Loxodonta africana* but only a proportion of the individual teeth are plotted so as to show the distribution without cluttering up the diagrams. Figure 20 is a plot for third molars of *Palaeoloxodon antiquus*, based on specimens from famous localities in Great Britain, Germany and Italy and covering the various "mutations". The differing averages for upper and lower teeth are well brought out. A few plots for *Archidiskodon meridionalis* from Italian localities are also shown in Figure 20 but, unfortunately, the writer possesses very limited numerical data on this species. Figure 21 shows plots for *Archidiskodon planifrons* and is based solely on material from the Upper Siwaliks in the collections of the British Museum (Natural History) and the American Museum of Natural History. Figure 22 represents Arambourg's data for "*Elephas*" *atlanticus* from North Africa¹⁰ and shows also the plot for his "*Elephas*" *africanavus* from Ichkeul, Tunisia¹¹.

These five diagrams furnish comparative data of value in a reconsideration of the described material both from East Africa and from southern Africa. While the method is useful for metrical comparisons it does not, of course, indicate other characteristics of the teeth such as the form of the plates or their number and these considerations must also be taken into account in assessing specimens.

The Material from South Africa

The named species from southern Africa, excluding the fragmental *Gomphotherium* sp. (Fraas¹²) and the recently described *Stegolophodon*⁴ are listed in Table I under their original names, together with some of the main measurements which are plotted in Figure 23. Inspection of the plots suggests the existence of four groups as indicated and these have been labelled A, B, C and D to facilitate discussion.

TABLE I

MAIN MEASUREMENTS OF MOLARS OF FOSSIL ELEPHANTIDAE FROM
SOUTHERN AFRICA

(Used in constructing the diagram of Figure 23)

	Pos	P	L	H	W	L/P	$\frac{H \times 100}{W}$
1 Archidiskodon subplanifrons Osborn 1928	RM ₃	$+5\frac{3}{8}$	153	64	101	27	63
2 A. cf subplanifrons Haughton 1932	RM ₃	+6	179	63	104	30	60
3 A. proplanifrons Osborn 1934	LM ₃	$8\frac{3}{4}$	253	62	103	29	60
4 A. andrewsi Dart 1929	LM ₃	$2\frac{1}{2} + 1\frac{1}{2}$	100+	60+	c80	25	75
5 Loxodonta griqua Haughton 1922 .	LM ₃ ?	+3+	97	81	86	32	94
6 Archidiskodon vanalpheni Dart 1924 .	RM ₃	$7\frac{1}{2} +$	235	131	112	31	117
7 A. milletti Dart 1929	LM ₃	$+7\frac{1}{2}$	222	118	108	28	109
8 A. loxodontoides Dart 1929	LM ₂	$+4\frac{3}{4}$	146	105	92	31	114
9 A. broomi Osborn 1928	LM ₃	6+	168	145	109	28	133
10 A. transvaalensis Dart 1927 . . .	RM ₃	$9\frac{1}{2}$	307	231	110	22	210
11 A. sheppardi Dart 1927	LM ₂	$10\frac{1}{2}$	246	188	100	21	180
12A Palaeoloxodon darti Cooke 1939 . .	LM ₃	$12\frac{1}{2} +$	234	219	94	19	233
12B " " LM ₃		$+8\frac{1}{2}$	212	160	95	25	169
12C " " RM ₃		+3+	60	209	93	20	224
13 Archidiskodon hankomi Dart 1929 .	RM ₃	16+	312	220	102	19	216
14A Elephas (Loxodon) zulu Scott 1907 .	LM ₃	12+	265	c95	85	22	112
14B " " RM ₃		12+	c260	c90	c85	22	106
15 Pilgrimia yorki Dart 1929	RM ₂	9	180	115	79	20	146
16 P. kuhni Dart 1929	LM ₂	$+4\frac{3}{4} +$	96	100	75	19	133
17 P. subantiqua Haughton 1932 .	RM ₂	$10\frac{3}{4} +$	243	105	84	22	125

18	<i>P. wilmani</i> Dart							
	1929	LM ²	7+	119	128	70	18	183
19A	<i>P. archidiskodontoides</i>							
	Haughton 1932 .	LM ₂	9+	148	145	94	16	154
19B	"	RM ²	7+	108	c120	94	15	128
20	<i>Archidiskodon scotti</i>							
	Meiring 1955 . . .	LM ₂	8½	196	67	91	23	74

Pos	= Position in dental series	P	= Number of plates preserved (+ indicates missing parts)
L	= Greatest length of molar perpendicular to plates	H	= Greatest height of enamel on tallest plate
W	= Greatest width of widest lamella (excluding cement)	$\frac{H \times 100}{P}$	Index of hypsodonty
L/P	= Length-Lamellae ratio		

Group A incorporates the low-crowned, wide, thick-plated species the writer had already¹ merged under the single species *Archidiskodon subplanifrons* Osborn 1928. Meiring's *A. scotti* is most probably a second molar as it shows signs of a posterior indentation and there is no valid reason to separate it from Osborn's species; it has associated with it a fine tusk of *Archidiskodont* character and an ulna, both of which make Meiring's account of particular interest and value. Most of the teeth are well worn and it has been suggested by Hooijer¹³ that Osborn's estimates of the heights are too low. This is probably true but it is still clear that the crown heights were never very great. In the type of "*proplanifrons*" the actual height of the almost intact fourth and fifth plates is 55 mm. (Haughton¹⁴, Osborn⁷) and it is restored to a maximum of 62 mm. (Cooke¹); it seems most unlikely that the anterior plates of this tooth could have been higher than 75 mm. In Meiring's *A. scotti* the eighth and ninth plates are barely worn and their height is 66 — 67 mm., with an estimated maximum height for the anterior plates of 80 mm. Arrows in Figure 23 indicate the adjusted positions for these teeth using estimated instead of measured heights. The South African specimens would then correspond fairly closely to those described by Hooijer from Bethlehem in Israel¹³, and the group would lie at the bottom fringe of the range for *A. planifrons* from the Siwaliks, shown in Figure 21. However, the plots of lower hypsodonty for *A. planifrons* are also based on worn teeth and if estimated heights were used the index of hypsodonty for this species would not fall below about 90 — 95. It is thus clear that the South African material still lies below the normal range for *A. planifrons* from the type area and there seems to be a reasonable case for regarding *A. subplanifrons* as a distinct African species. It is possible that Hooijer's material from Israel belonged to an emigrant colony.

Group B embraces a number of very thick-plated teeth of moderate crown height. In 1947 the writer¹ merged three of these (6, 7 and 8) as *A. vanalpheni* with

signs of a median expansion resembling the loxodont sinus but retained *A. broomi* (9) as probably separate as there was little sign of median expansion. The type of *A. broomi* is the anterior portion of an upper third molar (not a lower as Osborn stated⁶), the type of *A. loxodontoides* is an almost unworn anterior fragment of a second or even a first molar, and both the other specimens are posterior portions of second or third molars. Great variation in the form of the plates and development of a sinus has been observed by the writer in teeth of *A. meridionalis* in Italy, as well as marked simplification in pattern with advancing wear, so that there is no longer considered to be any good reason to separate these forms. The specific name *A. broomi*, dating from 1928, has priority. The fragment of "*Metarchidiskodon griqua*" might fall metrically within this group but its peculiar characters make it impossible to merge *A. broomi* with it and, as suggested above, *M. griqua* is best regarded as a *nomen vanum*.

Group C includes the type lower third molar of *Palaeoloxodon zulu* and also the three species "*Pilgrimia*" *yorki*, *P. kuhni* and *P. subantiqua* which the writer has already indicated¹ should be regarded as lower second molars and placed within the range of *P. zulu*. Arambourg^{2,10} suggested in 1938 that Scott's species fell within the range of the North African "*Elephas*" *atlanticus* and, having had the opportunity of examining material of this species in Paris as well as the South African specimens themselves, the present writer endorses the view that the two species cannot be distinguished one from the other.

Not at present assigned to this group are the rather peculiar upper molars of the type of *P. archidiskodontoides*¹⁴ (19A and 19B). The plates in these teeth are thick and in close contact with little intervening cement — a feature not reported in other material. There is a general resemblance in the form of the teeth to those of *P. recki* from East Africa, but in the latter the crowns are more hypsodont and the plates thinner than in *P. archidiskodontoides*. The fragments of skull and humerus differ markedly from *Loxodonta africana* and resemble *P. recki* of East Africa but are somewhat smaller, all features which are consistent with a related but possibly different species. More material is required before the problem can be settled.

Group D embraces the high crowned forms, of which *Palaeoloxodon transvaalensis* was the first to be described. *P. sheppardi* was merged with *P. transvaalensis* by Osborn⁷. The present writer¹ retained *P. hanekomii* as a distinct species on account of its apparently peculiar enamel islands but has since observed similar variations in paired teeth of *P. antiquus* from Italy and there is no longer any reason to separate *P. hanekomii* from *P. transvaalensis*. The writer's own species *P. darti* from the Victoria Falls¹⁵ must also be merged with *P. transvaalensis* but the material from Rhodesia is important in providing the only lower molar certainly belonging to this group. This lower tooth indicates a substantial gap between this species and the type of *P. zulu*. The specimen described under the name *P. wilmani*

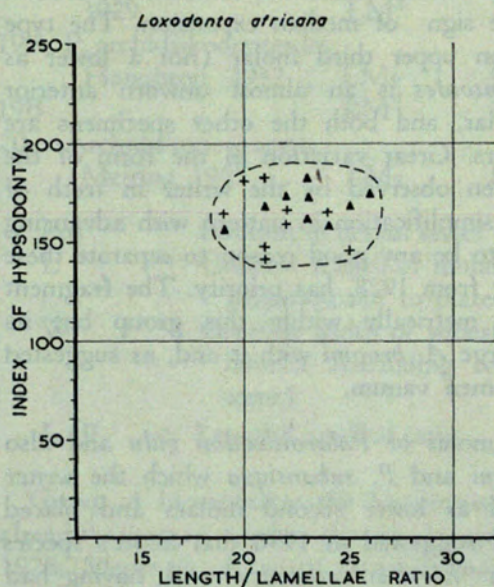


Figure 18

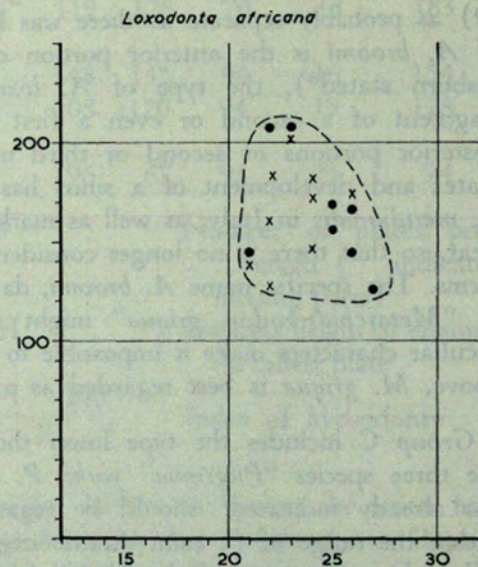


Figure 19

+ = M^2 x = M^3
 ▲ = M_2 ● = M_3

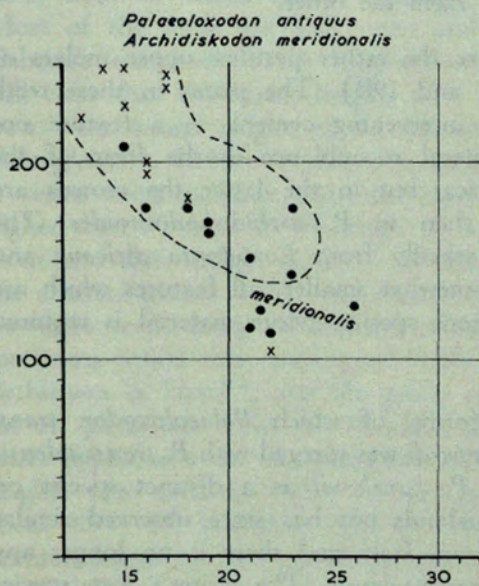


Figure 20

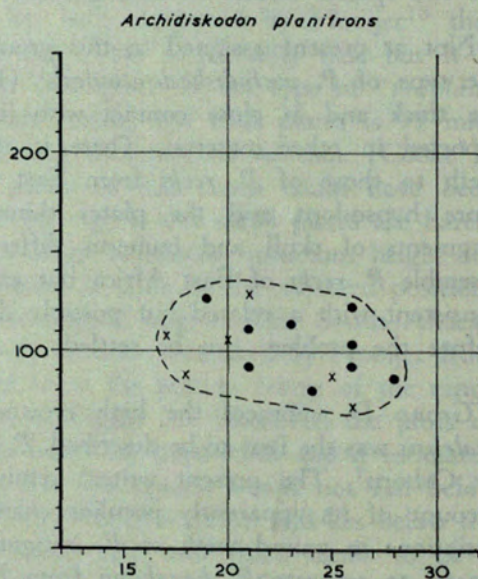


Figure 21

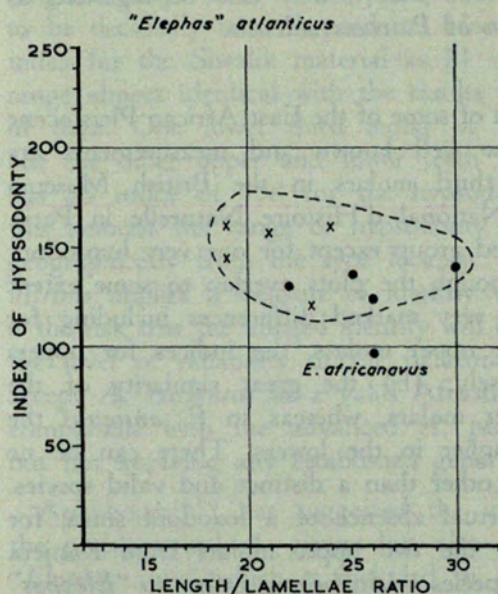


Figure 22

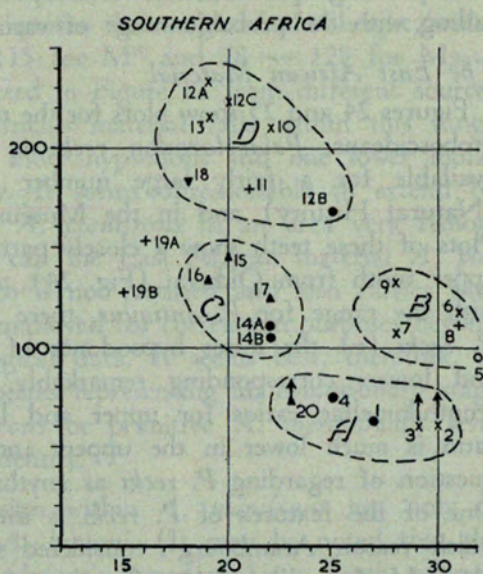


Figure 23

+ = M^2 x = M^3
 ▽ = M_1 ▲ = M_2 ● = M_3

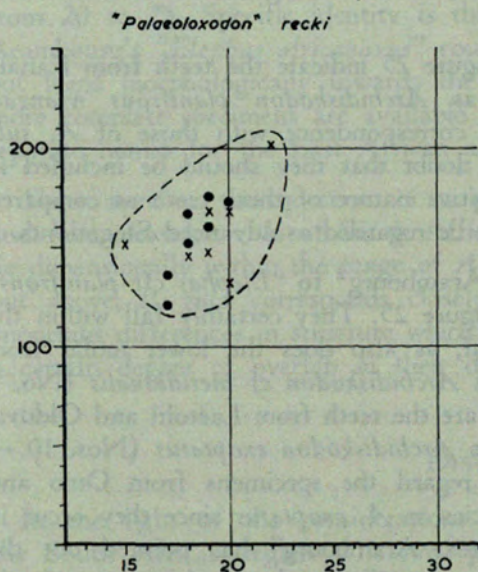


Figure 24

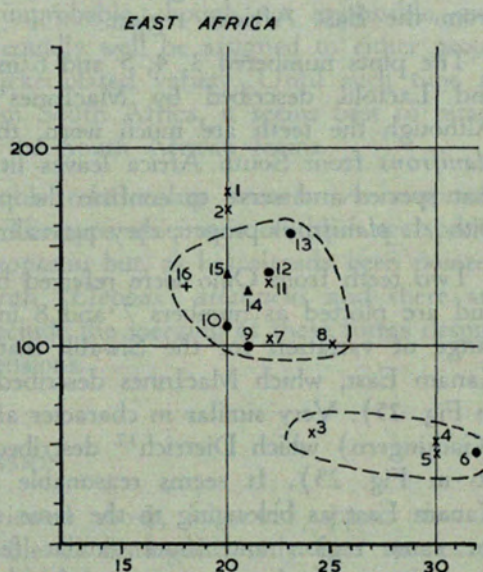


Figure 25

as a third lower molar is most probably a first molar and comparison with corresponding specimens of *P. antiquus* shows that it may also be regarded as falling with the probable range of variation of *P. transvaalensis*.

The East African Material

Figures 24 and 25 show plots for the teeth of some of the East African Pleistocene proboscideans. *Palaeoloxodon recki* is now well known and measurements are available for a fairly large number of third molars in the British Museum (Natural History) and in the Muséum National d'Histoire Naturelle in Paris. Plots of these teeth show a closely patterned group except for one very hypsodont upper tooth from Olduvai (Fig. 24). Although the plots overlap to some extent with the range for *P. antiquus*, there are very marked differences including for *P. recki* (a) the lesser hypsodonty of the upper molars, the indices for uppers and lowers corresponding remarkably closely; (b) the great similarity of the length-lamellae ratios for upper and lower molars, whereas in *P. antiquus* the ratio is much lower in the uppers and higher in the lowers. There can be no question of regarding *P. recki* as anything other than a distinct and valid species. One of the features of *P. recki* is the virtual absence of a loxodont sinus, for which reason Arambourg² considered that the two upper molars from Kanjera which MacInnes¹⁶ (p.94) referred to this species might belong rather to "*Elephas atlanticus*" and there is much to support this view despite the fact that the Kanjera specimens are slightly higher crowned than the Moroccan material. These two molars are plotted in Figure 25 as numbers 1 and 2 together with other teeth from the East African region.

The plots numbered 3, 4, 5 and 6 in Figure 25 indicate the teeth from Kanam and Laetolil described by MacInnes¹⁶ as *Archidiskodon planifrons nyanzae*. Although the teeth are much worn, their correspondence with those of *A. subplanifrons* from South Africa leaves little doubt that they should be included in that species and serve to confirm the primitive nature of these teeth as compared with *A. planifrons* proper; they may almost be regarded as advanced Stegodonts.

Two teeth from Omo were referred by Arambourg² to "*Elephas cfr planifrons*" and are plotted as numbers 7 and 8 in Figure 25. They certainly fall within the range of variation for the Siwalik material, as also does the lower molar from Kanam East, which MacInnes described as *Archidiskodon cf meridionalis* (No. 9 in Fig. 25). Very similar in character also are the teeth from Laetolil and Olduvai (Gadjingero) which Dietrich¹⁷ described as *Archidiskodon exoptatus* (Nos. 10 — 16 in Fig. 25). It seems reasonable to regard the specimens from Omo and Kanam East as belonging to the same species as *A. exoptatus* since they occur in the same region and share similar features. Arambourg² has pointed out the resemblance of *A. exoptatus* to *A. planifrons* and regards the former as simply a synonym. Hooijer¹⁸ similarly dismissed Arambourg's *Elephas africanavus*¹¹ as a synonym of *A. planifrons* because it falls within the range of variation of the latter species. However, when *A. exoptatus* and the other teeth here regarded

as belonging to the same group are considered as a whole, it is clear that the range overlaps that of *A. planifrons* but that the East African material tends to be decidedly more hypsodont. Hooijer quotes the range of the height/width index for the Siwalik material as 71 — 115 for M^3 and 78 — 125 for M_3 , a range almost identical with the results plotted in Figure 21 from different sources of data. One lower third molar of Dietrich's material falls within this range but the other upper and lower teeth are more hypsodont and one lower molar has an index of 158 for the hypsodonty. It seems unreasonable to extend by this amount the range of hypsodonty for *A. planifrons* in an area very remote geographically from the type locality. To call the East African material *A. planifrons* implies a measure of identity which is not justified and also carries with it the risk that the alleged identity will be employed for correlation purposes beyond the level of reliability of the palaeontological data. It seems best, therefore, to accept *A. exoptatus* as a valid African species representing an evolutionary stage comparable with the advanced *A. planifrons* or primitive *A. meridionalis* level but not implying any established genetic identity.

Arambourg^{2,10} has suggested the inclusion within *A. planifrons* not only of the problematical *A. griqua* but also of *A. broomi*. (It may be noted that the "*Elephas zulu*" which is included in Arambourg's synonymy is a tooth referred by Hopwood in 1926 and is not the type material of Scott's species of 1907.) The South African specimens of "Group B" in Figure 23 have length/lamellae ratios of 28 to 32 whereas *A. exoptatus* and its East African associates range from 20 to 25. Specific identity is thus improbable, though not impossible, and Arambourg's "*Elephas africanavus*" could equally well be assigned to either group but leans morphologically towards the thicker-plated variety. Until such time as more complete specimens are available from South Africa, it seems best to retain separate names for the East African and the South African forms.

There remains the question of a possible relationship between *A. exoptatus* and *Palaeoloxodon zulu* of South Africa. The type specimens of the latter species lie dimensionally within the range of *A. exoptatus* but, as has already been pointed out above, *P. zulu* corresponds closely with "*Elephas*" *atlanticus* and there are important differences in structure which preclude the merging of these forms despite a certain degree of overlap in their dimensions.

DISCUSSION

In the light of the considerations reviewed above, it would appear that in the South African region it is now possible to distinguish only four species of extinct true elephant in the Pleistocene, though a unique specimen at present not adequately known occupies an isolated position as a fifth species *P. archidiskodontoides*; in addition there are two primitive mastodonts, *Trilophodon* (*Gomphotherium*) and *Stegolophodon*. The living African elephant is also present in the

fossil and semi-fossil state, usually in superficial deposits of later Pleistocene age. In East Africa four extinct elephants are also recognisable, as well as the living species and the archaic *Anancus kenyensis* and *Stegodon kaisensis*. From North Africa a large number of forms have been described but their present status is somewhat uncertain and it is not the purpose of this account to discuss them. The position is summarized in Table II.

TABLE II

South Africa	East Africa	North Africa
<i>Loxodonta africana</i>	<i>L. africana</i>	<i>L. africana</i>
" <i>Elephas</i> " <i>atlanticus</i>	<i>E. atlanticus</i> (?)	<i>E. atlanticus</i>
<i>Palaeoloxodon</i> <i>transvaalensis</i>	<i>P. recki</i>	<i>E. aff. meridionalis</i>
<i>Archidiskodon broomi</i>	<i>A. exoptatus</i>	<i>E. africanavus</i>
<i>A. subplanifrons</i>	<i>A. subplanifrons</i>	<i>E. cf. planifrons</i>
<i>Stegolophodon</i> sp.	<i>Stegodon kaisensis</i>	<i>Stegolophodon</i> sp.
<i>Trilophodon</i> sp.	<i>Anancus kenyensis</i>	<i>Anancus osiris</i>
		<i>Mastodon</i> sp.
also <i>incertae sedis</i>		
<i>P. archidiskodontoides</i>		<i>E. jolensis</i>
		<i>E. pomeli</i>

The striking parallelism of the occurrences in each region makes it tempting to suggest that the number of species could be still further reduced. From Figures 23 and 24 it might well be supposed that *P. recki* and *P. transvaalensis* had a considerable overlap in range. While the *relative* dimensions give such an impression, it is largely due to the greater height of the southern forms being compensated in the index of hypsodonty by a greater breadth. The upper molars in the East African collections have a maximum crown height of 165 mm. and the more usual figure is 115 — 120 mm., while the width ranges from 75 to 93 mm. as compared with heights of over 200 mm. for *P. transvaalensis* and widths of 93 to 110 mm. The lower molars of *P. recki* are 73 to 92 mm. wide and the maximum crown height is 150 mm., compared with a width of 95 mm. and a height of 160 mm. for the only lower molar of *P. transvaalensis*; the length/lamellae ratio of the latter is 25 compared with a maximum of 20 for *P. recki*. It would thus seem unwise at present to merge the two species. Similar arguments apply to the separation of *A. exoptatus* (80 to 91 mm. wide and with a length/lamellae ratio of 20 to 23) and *A. broomi* (92 to 112 mm. wide and with length/lamellae ratios of 28 to 31), though *E. africanavus* does occupy an intermediate position.

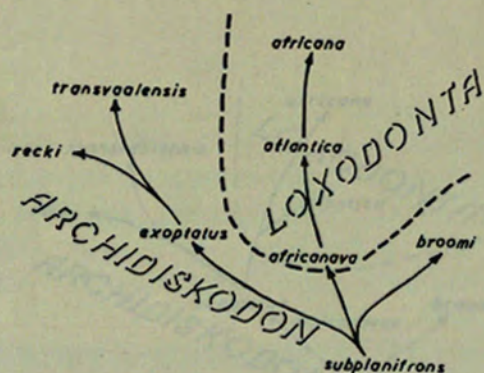


Figure 26

Arambourg has long employed the broad generic term "*Elephas*" for the African fossil elephants and this procedure has much to recommend it. The East African material was referred to *Palaeoloxodon* because of a supposed relationship of *P. antiquus* with *P. recki* which Arambourg has demonstrated² to be superficial and unreal. The resemblance of the skull structure to that of *Archidiskodon meridionalis* leaves little doubt as to its affinities. The South African "*P.*" *transvaalensis* parallels the American *Archidiskodon imperator* rather than the European *Palaeoloxodon antiquus* in dental structure. "*Elephas*" *atlanticus* shows many of the characteristics of the living African elephant and may well be placed in the same genus. There is thus no good reason to regard *Palaeoloxodon* as being represented in Africa at all except, perhaps, in parts of the North African littoral. Incipient loxodont features are present in the teeth of *A. subplanifrons* and *A. exoptatus* and a possible phylogeny may be suggested in Figure 26. This does not differ fundamentally from that proposed by Dietrich⁸, though it differs considerably in specific details. The presence of *Stegodon* and of *Stegolophodon* in the early Pleistocene indicates that the true elephants in Africa may well have evolved from a member of this stock quite independently of the Indian *Archidiskodon planifrons* and its descendants. It appears impossible, at this stage, to avoid using the generic name *Archidiskodon* for the African fossils but this should not be taken to imply too close an Asiatic connection. It seems very likely, as Arambourg¹¹ has suggested, that the Pleistocene elephants of Africa have evolved within the continent itself, paralleling the stages of progress observed elsewhere but not linked to Europe and Asia by periodic invasions as Osborn and others have suggested. The Oligocene and Miocene proboscidea suggest the existence of a basic stock in this continent from which "exports" to Europe and Asia may have been more significant than "imports".

REFERENCES

1. COOKE, H. B. S. (1947) Variation in the molars of the living African Elephant and a critical revision of the fossil Proboscidea of southern Africa. *Amer. J. Sci.* 245: 434—457; 492—517.
2. ARAMBOURG, C. (1947) Contribution a l'étude géologique et paléontologique du Bassin du Lac Rodolphe et de la basse vallée de l'Omo. Part II — Paléontologie. *Mission scientifique de l'Omo 1932 — 1933 I. fasc. 3.* Paris, Mus. Hist. nat. 1947.
3. MEIRING, A. J. D. (1955) Fossil proboscidean teeth and ulna from Virginia, O.F.S. *Researches Nas. Mus. Bloemfontein* 1(8): 187—202.
4. SINGER, R. and HOOIJER, D. A. (1958) A *Stegolophodon* from South Africa. *Nature, Lond.* 182: 101—102.
5. HAUGHTON, S. H. (1922) A note on some fossils from the Vaal River Gravels. *Trans. geol. Soc. S. Afr.* 24: 11—16.
6. OSBORN, H. F. (1928) Mammoths and Man in the Transvaal. *Nature, Lond.* 121: 627—673.
7. OSBORN, H. F. (1934) Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa. *Amer. Mus. Novitates* No. 741: 1—15.
8. DIETRICH, W. O. (1951) Daten zu den fossilen Elefanten Afrikas und Ursprung der Gattung *Loxodonta*. *N. Jb. Geol. Paläont. Abh.* 93(3): 325—378.
9. SIMPSON, G. G. (1945) The principles of classification and classification of the Mammals. *Bull. Amer. Mus. nat. Hist.* 85.
10. ARAMBOURG, C. (1938) Mammifères fossiles du Maroc. *Mem. Soc. Sci. nat. Maroc.* 46: 1—74.
11. ARAMBOURG, C. (1952) Note préliminaire sur quelques éléphants fossiles de Berbérie. *Bull. Mus. nat. Hist. nat. Paris* Ser. 2, 24: 407—418.
12. FRAAS, E. (1907) Pleistocene Fauna aus der Diamantseifen von Süd-Afrika. *Z. dtsh. geol. Ges.* 59: 232—243.
13. HOOIJER, D. A. (1958) An early Pleistocene mammalian fauna from Bethlehem. *Bull. Brit. Mus. (nat. Hist.) London*, 3(8): 267—292.
14. HAUGHTON, S. H. (1932) On some South African Proboscidea. *Trans. roy. Soc. S. Afr.* 21: 1—18.
15. COOKE, H. B. S. and CLARK, J. D. (1938) New fossil elephant remains from the Victoria Falls, Northern Rhodesia, and a preliminary note on the geology and archaeology of the deposit. *Trans. roy. Soc. S. Afr.* 27: 287—319.
16. MACINNES, D. G. (1942) Miocene and post-Miocene Proboscidea from East Africa. *Trans. Zool. Soc. Lond.*, 25: 33—106.
17. DIETRICH, W. O. (1942) Ältestquartäre Säugetiere aus der südlichen Serengeti, Deutsch-Ostafrikas. *Palaeontographica* 94(A): 43—133.
18. HOOIJER, D. A. (1955) *Archidiskodon planifrons* (Falconer et Cautley) from the Tatrot zone of the Upper Siwaliks. *Leidse geol. Med.* 20: 110—119.

A PRELIMINARY INVESTIGATION OF THE MAMMALIAN MICROFAUNA IN PLEISTOCENE DEPOSITS OF CAVES IN THE TRANSVAAL SYSTEM*

BY

G. DE GRAAFF

(Department of Zoology, University of Pretoria)

ABSTRACT

This investigation aims to extend our knowledge of the fossil mammalian microfauna found in the *Australopithecus*-bearing breccias of the Transvaal System at Taung, Sterkfontein and Makapansgat. The available data derived from other localities such as Kromdraai and Bolt's Farm have been incorporated. The origin of these fossils, the method of extraction from the breccias, and a brief review of the geological nature of the deposits under consideration are discussed.

Nearly 10,000 skeletal elements taken from five localities were studied, including 2,000 cranial fragments. The species represented are described systematically and a new species *Malacothrix makapani* is described. The contents of the breccia have been analysed statistically, on the dental complements of the various smaller mammals such as elephant shrews, bats and rodents. The information thus gained holds prospects for learning more about the persistence of the recent mammalian microfauna during the Pleistocene; the generic densities during the Pleistocene; and climatic and time differences between the different fossiliferous localities. Some forms such as *Elephantulus langi*, *Palaeotomys gracilis* and *Cryptomys robertsi* were stable genotypes ranging over a great span of time. In these breccias there is a preponderance of *Mystromys hausleitneri* and *Palaeotomys gracilis* while the true murids are numerically of lesser importance. The Taung deposit is ecologically different and the oldest, followed by Sterkfontein which slightly antedates Makapansgat.

I. INTRODUCTION

Our knowledge of the fossil mammalian microfauna from the cave deposits in the dolomitic limestones of the Transvaal System is scanty and it is the purpose of this study both to extend the data and to see how such knowledge may throw light on the microfaunal creatures themselves and on the deposits in which they occur.

* Abridged version of dissertation presented for the Degree of Master of Science in the University of the Witwatersrand.

Zoologists in South Africa have shown little interest in these small mammals. This neglect may be due, firstly, to the tedious work involved and, secondly, to the absence hitherto of a suitable series of recent comparative material. The comparative material is still far from being sufficient. In addition, as Simpson (1945) has rightly said: "This inherent difficulty of the subject, its demand for special knowledge and techniques, and its relatively unsensational and, to many palaeontologists, unattractive nature have discouraged and retarded research on fossil rodents."

In preparation for the examination of the fossil material the author undertook a study of the contents of owl pellets.

A knowledge of the contents of contemporary pellets is fundamental in identifying the fossil genera of small animals. Hitherto only Kolbe (1946) and Davis (1958, 1959) have investigated this aspect substantially. Davis (1959) was concerned with studies of the species of small animals forming the prey of the Barn Owl *Tyto alba affinis* and other species of owls, as part of a general ecological survey of the small mammals associated with maintenance of bubonic plague and other animal reservoir diseases in southern Africa. As a by-product contributions have been made to small mammal systematics, geographical distribution, population ecology and craniology. The knowledge so gained is also relevant to a comparative study of the fossil small mammals found in the rodent breccia associated with the ape-man cave deposits in the north-west Cape (Taung) and the Transvaal (Sterkfontein, Swartkrans, Kromdraai and Makapan).

Davis suggested "that when the small fossil mammals are better known it will be possible to find amongst the living species in different parts of southern Africa species-assemblages ecologically similar to the cave faunas. If the great majority of the fossil small mammals were deposited by owls, the analyses which have been done will provide the necessary comparative yardstick. Finally, any light that can be thrown on the evolutionary history of the small mammals during the Plio-Pleistocene period will be of much value. In the first place it will help to establish the taxonomic status of the existing small mammal fauna and secondly it will contribute to an understanding of the present-day distribution patterns of the species, which are known in considerable detail."

The studies by the present author are concerned with the three better known man-ape deposits in the dolomite caves of the Transvaal System, viz. Taung in the north-eastern Cape near Bechuanaland, Sterkfontein near Krugersdorp in the southern Transvaal, and Makapansgat Limeworks near Potgietersrust in the central Transvaal. The stone-age deposits of the Cave of Hearths near the latter locality are also discussed.

The material was prepared under the direct supervision of the writer and his colleagues in the Bernard Price Institute for Palaeontological Research.

The microfauna may hold a key position, more important than many other faunal groups for unraveling secrets of past climatic fluctuations and general environmental conditions at the time *Australopithecus* lived. If, therefore, this work assists in the more thorough investigation of the microfauna in these deposits, it will have achieved its prime purpose.

II. MATERIAL AND METHOD

1. Origin

The habits and ecology of the barn-owl *Tyto alba affinis* have already been investigated to some extent (Kolbe, 1946; Davis, 1958, 1959). The contents of regurgitated owl pellets reveal the composition of the mammalian microfauna in the area in which the owl operates. Chitty (1935) has shown that the short-eared owl (*Asio flammeus*) regurgitates pellets at regular intervals (usually twice in 24 hours) and this occurs normally at one of its regular roosts. A mass of furry round objects collects below the roost, each completely filled with the skeletal remains of its prey. After a lengthy period a considerable quantity of pellets accumulates.

The barn-owl reveals the same habits as the short-eared owl. If it is accepted that ecological conditions affecting the recent barn-owl were not appreciably different during Pleistocene times, then there is no reason to imagine that the habits of the Pleistocene "ancestor" differed greatly.

When an owl occupies a ledge in a cave to serve as a roost, the accumulation of pellets below will, after many years, form quite a large deposit. With the progress of time aeolian agents introduce sand and dust which intermingle with the pellets, while moisture turns it into a muddy mixture. In dolomite caves, binding then takes place by means of calcium carbonate. As the cave gradually fills up with debris and the roof thins by erosion, the ledge becomes inhospitable and the roost vanishes, leaving the pellet deposit submerged deeper underneath the incoming debris.

The material analysed here is derived from such owl regurgitations. The skeletal remains occur in a jumbled mass embedded in hard breccia, consisting mainly of soil particles and binding calcium carbonate.

2. Preparation

The breccia blocks containing microfauna remains were kindly placed at the author's disposal by the Bernard Price Institute. Additional material from the Makapansgat Limeworks was collected by the author in 1956 and 1957. All the material was prepared with the acetic acid technique, using a maximum concentration of 15% acid; higher concentrations were found to be too severe for these fragile bones.

Diluted glyptal cement was employed to protect exposed specimens against corrosion. Each block of breccia was subjected to an initial surface corrosion in 15% acid for 15 — 18 hours. Subsequent concentrations used ranged between 5%

and 10%, depending on the number of bones exposed and the solidity of the breccia. After the acid had lost its potency the blocks were rinsed in cold water and the excess mud was carefully brushed away. The soil that accumulated in the bottom of the container was allowed to dry and retained for any future analysis that might prove desirable. The blocks were then left in the sun to dry. Exposed bone fragments were carefully loosened with the aid of a sharp needle.

The cycle of glyptal painting, acid immersion, washing and drying was repeated until eventually all the specimens in the entire block had been extracted. A very fine meshed sieve facilitated the sorting. Owing to the fragility of these small elements damage could not be avoided. However, a very high proportion of intact material has been recovered. The treatment applied to blocks from all the sites has been uniform; within the limits of accuracy that such an investigation permits, the samples are therefore comparable.

3. Method

The contents of the breccia blocks from the deposits have been treated uniformly according to a standard pattern. The cranial remains, especially upper and lower jaws with good dental complements, identify best the families and genera. Where possible, these identifications were substantiated by isolated molars and incisors. The postcranial material has been analysed extensively in a gross manner to assess numerical frequencies. The occurrence of non-microfaunal elements is recorded for its potential value in assessing the mode of origin of the deposits.

The cranial remains were compared with fresh material borrowed from the Transvaal Museum, Pretoria. These were supplemented by occlusal photographs of teeth of all the recent rodent genera available in South Africa. Post-cranial elements were classified with the assistance of mounted skeletons borrowed from the Anatomy Department of this University. Additional comparative material was retrieved from recent owl pellets collected in the Makapansgat caves.

The material was investigated under a binocular dissection microscope. The difficulty in manipulating these very delicate specimens was solved by using a small rod of plasticine. Excess matrix still adhering to the specimens, usually bound by the glyptal used as protection against the acid, was cleaned away with thinner solution applied with a delicate camel hair brush.

Collections of mammalian material in the Bernard Price Institute are catalogued as separate entities according to their localities. To avoid confusion, the present material is catalogued with its own consecutive series of numbers prefixed Mf (Microfauna).

All measurements are given in millimeters. Miller's (1912) dental nomenclature is used for the Murinae and Ellerman's (1941) for the Dendromurinae and Otomyinae. The classification used is in accordance with that of Simpson (op. cit.). Statistical symbols conform with their definitions as given by Milton-Smith (1938).

Table I

Locality	Microfaunal contents of breccia				Non-microfaunal contents of breccia		Total number of specimens per site
	Cranial (Cr.)	Post-cranial (P.Cr.)	Cr.:P.Cr.	Subtotal			
	%	%				%	
Taung	231 (49)	240 (51)	1:1	471	—	—	471
Sterkfontein	447 (15.4)	2391 (82.8)	1:5	2838	51	(1.8)	2889
Makapansgat							
Rodent Cave	796 (43.6)	1028 (56.3)	1:1.5	1824	2	(0.1)	1826
Dumps	221 (7.8)	1782 (62.2)	1:8	2005	859	(30.0)	2864
Cave of Hearths	386 (21.3)	1381 (76.0)	1:3.5	1768	49	(2.7)	1817
TOTALS	2084 (21.1)	6822 (69.1)		8906	961	(9.8)	9867

The nature of the material necessitates a statistical approach. The deposits are too numerous and too extensive to permit a detailed description of each fragment of the material, so the study is based on samples.

Table I is an analysis of the material recovered from the breccias. Of the 9,867 skeletal elements taken from the five localities under review, 2,084 were of cranial origin while 6,822 were post-cranial remains. A total of 961 specimens of non-microfaunal origin were recorded. The post-cranial remains (69.1%) were not determined, but merely sorted in gross fashion. The cranial remains (21.1%) have been used as extensively as possible for taxonomic determination. All the identifiable material from the non-microfaunal contribution (9.8%) has also been listed.

It is evident that the breccias from Taung and the Makapansgat Rodent Cave were very homogeneous, that is, there is little or no contamination by bones derived from larger animals.

III. A NOTE ON THE GEOLOGY AND GEOGRAPHY OF THE DEPOSITS

1. *The geology of the deposits*

The geology of the cave deposits in the Transvaal System is now fairly well known. Reference should be made to the writings of Van Riet Lowe (1945), Haughton (1947), Peabody (1954), Barbour (1949), King (1951), Bosazza, Adie and Brenner (1946), Cooke (1938, 1952), Wells & Cooke (1956), Dart (1952) and Robinson (1952). The petrographical aspects of the deposits have been carefully studied by Brain (1958) through detailed analyses at all the australopithecine sites. This study has led to fundamental deductions about the climatic variations at each site and is of particular importance.

2. *The geography of the deposits and its possible significance*

The three australopithecine localities lie approximately in a straight line, extending NE-SW between parallels 24° and 28° S, and 24° and 30° E. To the north-west of this line climatic conditions become progressively more arid and desert-like and in the opposite direction increasingly humid and sub-tropical.

The line passing through these caves does not separate arid regions from humid regions perfectly. Such a line would run in a direction more nearly north-south. Taung in the south-west reaches the arid, while Makapansgat in the north-east approaches the humid region. While the climate ranges from arid to humid parallel to this line, there is also a similar gradation along the line from Taung to Makapansgat.

If the Pleistocene climatic changes inferred in this region are connected with the glacial and interglacial episodes of the northern hemisphere, this climatological dividing line would have shifted eastward and westward correspondingly. During wetter periods all the caves were presumably enjoying a humid, sub-tropical climate, while in drier periods they came to lie in an arid environment. With the onset of a wet period, Makapansgat would probably be the first to become

humid, then Sterkfontein and subsequently Taung. With the termination of the period, Taung would be the first to become arid, then Sterkfontein and finally Makapansgat.

It therefore appears that:

- (a) The occurrence of sands of Kalahari type in these cave deposits does not necessarily indicate absolute chronology.
- (b) Chronology based on particular faunal associations should be accepted with some degree of reserve.

As the mammalian microfauna is inclined to be slightly more susceptible to climatic change than most microfaunal groups it is likely that, when fully known, the types present in the cave breccias could afford corroborative evidence concerning such climatic changes. Their effect on the fauna of the neighbourhood, indirectly influencing *Australopithecus* to some extent, may lead to a better understanding of the anthropo-archaeological nature of the breccias.

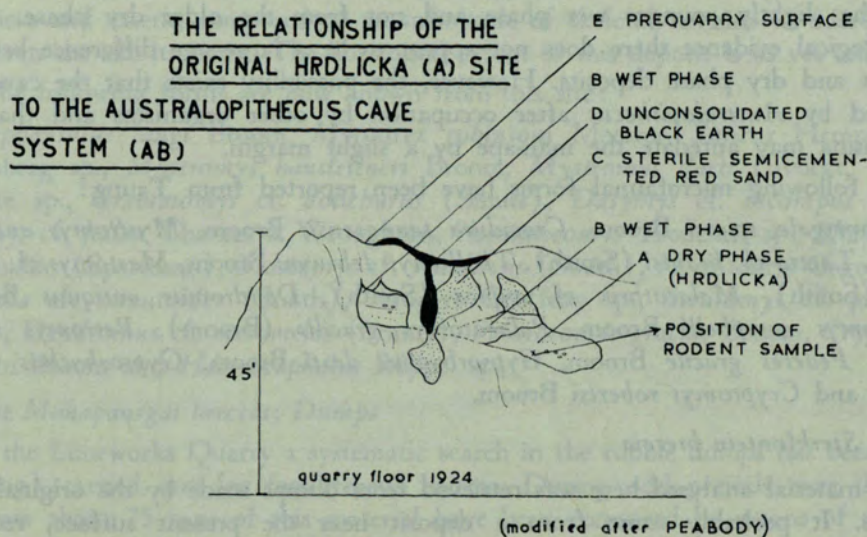


Figure 27

3. The Taung breccia

According to Peabody (1954) there are two types of australopithecine-bearing caves, those developing as solution cavities in bedrock dolomite and in travertine deposits on the dolomite. Sterkfontein and Makapansgat are of the former, while Taung was originally of the latter type.

The microfaunal deposit from Taung analysed here was in Hrdlicka's cave in the Thabaseek travertine. Unfortunately mining operations have destroyed the type site. However, Peabody has reconstructed its probable position and original features, from which the following vertical section is adapted (see figure 27):

5. Bedrock dolomite outcropping on the surface	11.0 ft.
4. Sterile coarse red sand, semi-cemented, devoid of fossils or artifacts	1.5 ft.
3. Pure sandy limestone with intercalated irregular lenses of red sandy limestone	1.5 ft.
2. Red sandy limestone	6.0 ft.
1. Bedrock Dolomite.	

Horizon 2 "seems to represent a dry phase and contains remains of turtle, baboon, small antelope, rodent, small carnivore, crab, and occasionally a surface showing what appears to be tracks of small mammals made originally in the soft dirt of the cave floor" (Peabody, op. cit.). Horizon 3 is of pure sandy limestone and appears to have been a wet phase. It contains only baboon remains and a few antelope. A sample of the rodent material referred to by Peabody has been utilised in this work.

Peabody has found evidence suggesting that *Australopithecus africanus* came from the slightly younger wet phase and not from the older dry phase. From mineralogical evidence there does not appear to be a large age difference between the wet and dry phase deposits. However, the possibility exists that the cave was occupied by *Australopithecus* after occupation by other organisms and that the microfauna may antedate the man-ape by a slight margin.

The following microfaunal forms have been reported from Taung:

Mylomygale spiersi Broom, *Crocidura taungensis* Broom, *Mystromys antiquus* Broom, *Tatera* cf. *brantsi* (Smith), *Thallomys debruyni* Broom, *Mastomys* cf. *natalensis* (Smith), *Malacothrix* cf. *typica* (Smith), *Dendromus antiquus* Broom, *Prototomys campbelli* Broom, *Palaeotomys gracilis* (Broom), *Petromys minor* Broom, *Pedetes gracile* Broom, *Gypsorhynchus darti* Broom, *Gypsorhynchus minor* Broom and *Cryptomys robertsi* Broom.

4. The Sterkfontein breccia

The material analysed here was retrieved from dumps made by the original lime workers. It probably came from a deposit near the present surface, recently excavated for *Australopithecus* remains. Numerous similar fossiliferous blocks from this site litter the area.

The following microfaunal forms have been reported from Sterkfontein:

Chlorotalpa spelea Broom, *Elephantulus langi* Broom, ?*Mylomygale spiersi* Broom, *Myosorex robinsoni* Meester, *Suncus Hemprich & Ehrenberg* sp., *Mystromys hausleitneri* Broom, *Tatera* cf. *brantsi* (Smith), *Dasymys* cf. *incomtus* (Sundevall), ?*Arvicanthis* Lesson sp., ?*Pelomys* cf. *fallax* Thomas & Wroughton, *Rhabdomys* cf. *pumilio* (Sparrman), *Aethomys* cf. *namaquensis* (Smith), ?*Mastomys* cf. *natalensis* (Smith), *Leggada* cf. *minutoides* (Smith), *Dendromus* cf. *mesomelas* (Brants), *Palaeotomys gracilis* Broom, ?*Hystrix cristata* Linnaeus and *Cryptomys robertsi* Broom.

5. *The Makapansgat breccia: Rodent Cave*

A particular site at the Makapansgat Limeworks is known as Rodent Cave. Owls do not penetrate deeply into caves to roost. Even today at Makapansgat they roost relatively near the entrance. Thus the location of the Rodent Cave supports the contention that the original cave entrance was along a south-west line, a portion of which is marked by this deposit.

A vertical geological section through the area from which the breccia was collected exhibits the following stratigraphy:

5. Hard pink breccia	20.0 ft.
4. Buff, bone-rich breccia	5.0 ft.
3. Red, calcified mud	10.0 ft.
2. Basal travertine	5.0 ft.
1. Bedrock dolomite.	

(After Brain, 1958)

The material was collected from the buff, bone-rich horizon (level 4) and its thickness and extent, composed of an infinitude of skeletal remains of microfauna, has given the site its name. The horizontal extent of this deposit is as yet unknown.

The following forms are now known from this site:

Elephantulus langi Broom, *Myosorex robinsoni* Meester, *Suncus* Hemprich & Ehrenberg sp., *Mystromys hausleitneri* Broom, *Mystromys darti* Lavocat, *Tatera* Lataste sp., *Grammomys* cf. *dolichurus* (Smuts), *Dasymys* cf. *incompus* Peters, *Pelomys* cf. *fallax* Thomas & Wroughton, ?*Lemniscomys* Trouesart sp., *Rhabdomys* cf. *pumilio* (Sparrman), *Mastomys* cf. *natalensis* (Smith), ?*Zelotomys* Osgood sp., *Leggada* cf. *minutoides* (Smith), *Acomys* Geoffroy sp., *Steatomys* cf. *pratensis* Peters, *Dendromus* cf. *mesomelas* (Brants), *Palaeotomys gracilis* Broom, *Cryptomys robertsi* Broom and *Heterocephalus* Rüppel sp.

6. *The Makapansgat breccia: Dumps*

At the Limeworks Quarry a systematic search in the rubble dumps has been (and is being) carried out for fossiliferous breccia. During odd periods over the last 11 years about 75 tons of this material have been recovered by means of manual sorting, of which 15 tons yielded 35,000 macrofaunal specimens.

Quite a number of breccia blocks are very rich in small skeletal elements. Some of this material was analysed. It was contaminated with material other than microfaunal, unlike the material from Rodent Cave. It must, therefore, have come from another locality in the cave, now either destroyed, or not yet located.

The dumps have now yielded the following forms:

Chrysotricha hamiltoni de Graaff, *Elephantulus langi* Broom, *Myosorex robinsoni* Meester, *Suncus* Hemprich & Ehrenberg sp., *Rhinolophus* cf. *capensis* Lichtenstein, *Mystromys hausleitneri* Broom, *Grammomys* cf. *dolichurus* (Smuts), *Pelomys* cf. *fallax* Thomas & Wroughton, *Rhabdomys* cf. *pumilio* (Sparrman), *Aethomys* cf. *namaquensis* (Smith), *Mastomys* cf. *natalensis* (Smith), *Leggada* cf. *minutoides*

(Smith), *Dendromus* cf. *mesomelas* (Brants), ?*Malacothrix makapani* sp. nov., *Palaeotomys gracilis* Broom, *Hystrix* cf. *africae-australis* Peters, *Hystrix major* Greenwood, *Xenohystrix crassidens* Greenwood, *Gypсорhynchus makapani* Broom and *Cryptomys robertsi* Broom.

7. Makapansgat: Cave of Hearths

This site, also situated in the Makapansgat valley, is celebrated for its archaeological importance. There is a well documented sequence of events which has been compiled in terms of stone cultures. At this site we have, therefore, for the first time in this investigation, material from datable breccias. The breccia came from an horizon known to represent the end of the Early Stone Age or the period of the earlier Fauresmith Culture, not less than 25,000 to 30,000 years ago.

Although the area from which the material came was removed during excavation, photographs and drawings are available from which a horizontal and vertical geological section could be constructed. Some of the material can still be seen in situ. The following is the sequence of strata in vertical section at the site:

5. Archaeological Beds 2—3, reddish-brown breccia	10 ft.
4. Archaeological Bed 1, reddish-brown breccia	2 ft.
3. Basal guano ash (level of microfaunal material)	2 ft.
2. Basal travertine	2 ft.
1. Bedrock dolomite.	

The following microfaunal elements are now known from this site:

Elephantulus langi Broom, *Crocidura* cf. *taungensis* Broom, *Crocidura* Wagler sp., *Rhinolophus* cf. *capensis* Lichtenstein, *Rhinolophus* cf. *geoffroyi* Smith, *Miniopiterus* cf. *schreibersi* Kuhl, *Mystromys hausleitneri* Broom, *Tatera* cf. *brantsi* (Smith), *Tatera* Lataste sp., *Thallomys* cf. *paedulus* (Sundevall), *Aethomys* cf. *chrysophilus* (de Winton), *Leggada* cf. *minutoides* (Smith), *Acomys* Geoffroy sp., *Saccostomus campestris* Peters, *Dendromus* cf. *mesomelas* (Brants), *Steatomys* cf. *pratensis* Peters, *Palaeotomys gracilis* Broom and *Cryptomys robertsi* Broom.

IV. SYSTEMATIC ANALYSIS

ORDER INSECTIVORA

Family Macroscelididae

Elephantulus langi (Broom) 1937

Elephantomys langi Broom 1937

Elephantulus langi Broom (1948)

Type: "Though no perfect skull has been obtained we have numerous mandibles, one good anterior portion of a skull with the maxillary teeth well preserved, some less satisfactory maxillae, and much of the anterior part of a skull" (Broom, 1937). Housed in the Transvaal Museum, Pretoria, no numbers.

Type site: Schurveberg, near Pretoria.

Diagnosis: "The fossil that occurs at Schurveberg will be seen to resemble considerably *Nasilio* and *Elephantulus*, but to differ from *Nasilio* in having only two lower molars and from *Elephantulus** in having the second upper premolar molariform . . ." (Broom, 1948).

Maxillary elements: Canine, Pm^{1-4} , M^{1-2} together measure 13.2 mm.; canine small; teeth compactly set; Pm^1 with large anterior, smaller second cusp and a trace of a third cusp; Pm^2 essentially similar, molariform; Pm^3 with two well developed outer cusps with the second somewhat smaller than the first and with two smaller but pronounced inner cusps; Pm^4 , M^1 and M^2 agree closely with the corresponding teeth in *Nasilio* and *Elephantulus*.

Mandibular elements: Dental series about 14.5 mm.; compares favourably with *Elephantulus*; M_3 absent; angular process horizontal.

Sterkfontein

Material: Consists of 2 specimens (Mf.171, Mf.247).

Remarks: Mf.171 agrees closely with the left Pm_4 in *E. intufi* and *E. langi*, the fossil type. At Bolt's Farm, close to the Sterkfontein site, Broom (1948) reported another fossil elephant shrew which he named *E. antiquus*. This form was determined on the maxillary teeth. The lower dentition is unknown. Though there is a slight age difference between the two localities, it could very well be that *E. antiquus* is also present at Sterkfontein. However, Mf.171 agrees more favourably with *E. langi*. Mf.247 is a portion of a right mandible with the Pm_3 preserved. The tooth is somewhat worn and is slightly larger than in *E. intufi*. It is comparable with the equivalent tooth in *E. langi*.

Rodent Cave

Material: Consists of 47 specimens (maxillary — Mf.32, Mf.33; mandibular — Mf. 34, Mf.35; Mf.53; 25 isolated upper teeth — Mf.36; 17 isolated lower teeth — Mf.37).

Remarks: The fossil form found in the Rodent Cave compares very well with the Schurveberg type. In the Pm^2 of Mf.32 the anterior cusp is large (when viewed from the buccal side) and is followed by a well-formed second cusp. As in Broom's specimen there is also a trace of a third cusp. The occlusal view shows two additional cusps of equal size. The greatest length and breadth of the tooth are respectively 1.8 mm. and 1.3 mm., compared with 1.9 mm. and 1.5 mm. in the type. Part of the maxilla had flaked away anteriorly exposing the right anterior root of the tooth. It is sturdy and reaches 2.4 mm. into the maxilla, measured from the weakly developed cingulum.

Specimen Mf.35 is a left mandibular fragment with the Pm_4 and Pm_3 in position (fig. 28a). The teeth are somewhat worn and the Pm_3 is damaged posteriorly.

* i.e. *E. rupestris* A. Smith in Ellerman et. al. (1953 p. 12).

Unfortunately no angular portion of any lower jaw was available for comparison. The condition of the 42 isolated teeth is excellent, especially the crowns of the molars, while quite a number have their roots intact.

Limeworks Dumps

Material: Consists of 6 specimens (Mf.169, Mf.170a—d).

Remarks: The Pm₂—4 in Mf.169 have been compared with *E. intufi* and with the description of *E. langi* by Broom. They agree very well with both. The sockets of the I₁—3, C, Pm₁ and M₁—4 are present, but the posterior sockets of the M₂ have been damaged. The Pm₁ appears to have been a double rooted tooth. The dental series in the type has a length of 14.5 mm., compared with 14.7 mm. in the present specimen.

Cave of Hearths

Material: Consists of 6 specimens (Mf.167, Mf.168, Mf.253—6). The first is a maxillary fragment, the rest portions of mandibles.

Remarks: Specimen Mf.167 is well preserved and compares favourably with the type material. The anterior portion of the snout has been broken off at the level of the posterior root of the Pm¹. The Pm² is definitely molariform, with two outer cusps, the posterior one being the smaller. There is a third, still smaller cusp on

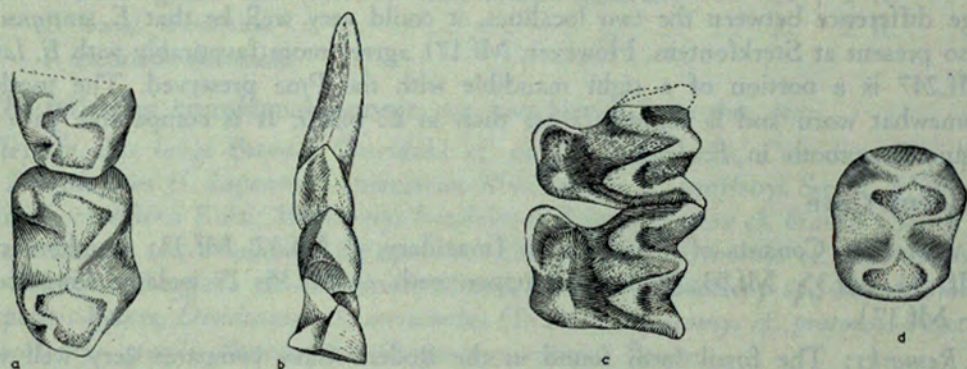


Fig. 28a — Mf.35. *Elephantulus langi*: occlusal view of PM₄ and damaged Pm₃. × 10.
 b — Mf.37a. *Myosorex robinsoni*: occlusal view of anterior mandibular teeth. × 10.
 c — Mf.61. *Rhinolophus* cf. *capensis*: occlusal view of M¹—2. × 10.
 d — Mf.3. *Mystromys antiquus*: occlusal surface of M². × 10.

the outside, while on the inside there are two minute cusps close together. The Pm³ has been damaged on its buccal side. The Pm⁴ and M¹ agree closely with those in *E. intufi*.

Specimen Mf.253 is useful because Broom remarks: "The lower jaw in one specimen which is complete, measures 24 mm., and the whole dental series is about 14.5 mm. The incisors are lost and their size unknown." In Mf.253 the lower incisor is present and it agrees clearly with the corresponding tooth in *E. intufi*, although it is more slender and not so squat as in the modern form.

M. spiersi Broom 1948.

M. spiersi Broom et al. (1946.)

Type: "The type specimen consists of a tooth-bearing portion of the left mandible, with three beautifully-preserved grinding teeth, the greater part of another grinding tooth and the sockets of the anterior teeth." (Broom, 1948.) It is housed in the Transvaal Museum, no number supplied.

Type site: The limeworks at Norlim, half a mile north of the cave which yielded the Taung man-ape.

Diagnosis: Mandible with three incisors, combined length about 3.5 mm.; canine not much larger than incisors; two small single rooted premolars; Pm₃ long anterior cusp with shorter posterior cusp; latter transverse, with a groove on the inside only; Pm₄ large, hypsodont, four inner and two outer enamel folds; M₁ slightly larger than M₂ and essentially similar to Pm₄, being only shorter and broader; three inner and two outer enamel ridges with a vertical groove on the anterior side; M₂ essentially the same, somewhat smaller.

Sterkfontein

Material: Only one specimen (Mf.216), a left isolated Pm₄ with roots broken away.

Remarks: This animal has so far only been described from the type site at Taung. It is regarded as "... a greatly specialized menotyphlan or elephant shrew of which the nearest living ally is *Petrodromus*. We may assume as probable that some early Pliocene elephant shrew allied to *Petrodromus* changed its habits and became vegetarian and developed rodent-like molars. This Menotyphlan is one of the most interesting fossil mammals discovered in recent years." (Broom, op. cit.)

Specimen Mf.216 is also definitely a hypsodont tooth and probably derived from a young individual. The anterior portion of the occlusal surface has been damaged; the posterior section shows three small cusps all quite unworn. There is a deep fold on the outside of the tooth, and one on the inside as well, tending to divide the tooth in two sections. Lingually the anterior section has a shallow inflection. Another small inflection occurs on the posterior portion of the tooth. This arrangement results in four distinct enamel folds on the lingual side and two strong folds buccally. The greatest antero-posterior length for this tooth is 2.4 mm. compared with 3.4 mm. in the type. The identification of the present specimen is, therefore, tentative. Unfortunately no further remains have been found at the other sites.

FAMILY SORICIDAE

Crocidura taungensis Broom 1948

Crocidura taungensis Meester (1955)

Type: Imperfect specimen, maxilla with the incisor, Pm⁴ and M¹⁻³ well preserved. Transvaal Museum, no number supplied.

Type site: Hrdlicka's cave in the Thabaseek travertine, Taung.

Diagnosis: Very small form, upper dental series measuring about 7 mm.; anterior cusp on the Pm⁴ small, the M³ being relatively small.

Taung

Material: Consists of 2 specimens (Mf.1a, Mf.2), both damaged mandibles.

Remarks: Broom's diagnosis of this fossil shrew was based on the anterior features of the snout. Unfortunately no lower dentitions or mandibles were then available. Meester (1955) has reinvestigated the fossil shrews in South African deposits and has concluded that *C. taungensis* is a valid species, even more decidedly so than Broom suspected. No fossil shrew, apart from *C. taungensis*, has been recorded from the Taung locality.

Cave of Hearths

Material: Consists of 26 specimens (Snout — Mf.224, Mf.225; mandibles — Mf.226—8, Mf.230—9, Mf.241—2; incisors — Mf.243—4; six molars — Mf.246).

Remarks: This large assemblage of fossil shrew remains is the most elaborate recovered from any of the localities. Many specimens are well preserved and have retained a high proportion of the identifiable features. All the specimens correspond closely with *C. taungensis* from Taung. They are all small and closely related to the modern *C. bicolor*.

In Mf.224 the Pm^3 is a small tooth compared with the Pm^4 . The dentition is almost completely missing from the second snout, Mf.225.

Crocidura Wagler sp.

Cave of Hearths

Material: Consists of 2 specimens (Mf.245, Mf.240, both mandibles).

Remarks: The material listed here is definitely a larger *Crocidura* species than *C. taungensis*. Its dimensions are so much larger that it probably represents a new species. At present it is enough to recognise the presence of a small and large *Crocidura*, the latter possibly new.

Myosorex robinsoni Meester 1955

Type: Skull (S.K.1001) with snout portion and good dentition.

Cotype: Mandible (S.K.1004) complete with entire tooth row. Both specimens are in the Transvaal Museum.

Type Site: Swartkrans, near Sterkfontein.

Diagnosis: General shape and size of skull as in the modern *Myosorex*; two foramina on dorsal aspect of skull; small Pm^1 ; no small additional cusplet behind the main cusp in I_1 ; C minute; Pm_4 with subsidiary cusplet on both lingual and buccal surfaces behind the main cusp.

Sterkfontein

Material: Consists of 2 specimens (Mf.251, Mf.252).

Remarks: This is the only *Myosorex* material recovered from Sterkfontein. The isolated molar Mf.251 (M_1) has the paraconid damaged.

Rodent Cave

Material: Consists of 15 specimens (Mf.36a, Mf.37a, Mf.39—44, Mf. 46—48, Mf.50, Mf.52, all mandibular fragments; Mf.54, Mf.56, first upper molars).

Remarks: Generally speaking, the specimens obtained in this analysis corroborate the conclusions about fossil shrews arrived at by Meester. While Meester had only one skull and one mandible for description, this analysis has yielded the extensive material listed above. However, the total absence of any reasonably complete skulls is regrettable.

Specimen Mf.37a (figure 28B) shows a very small canine wedged between the I₂ and Pm₄. In general morphology it does not differ appreciably from the cotype. Specimen Mf.36 shows the alveoli of the I₂, C and Pm₄ clearly and indicates a very small root of the canine. The Pm₄ structure corresponds closely with the Swartkrans specimen.

Limeworks Dumps

Material: Consists of 5 specimens (Mf.219, Mf.220, Mf.221 are mandibular fragments; Mf.223 refers to two M₂ teeth).

Remarks: This material is unfortunately badly preserved, salient identifying features having been destroyed. Nevertheless Mf.219 and Mf.220 could be identified as *M. robinsoni* on their slightly larger size compared with *Suncus*. Specimen Mf.221 is also slightly larger than a similar specimen, Mf.222, which is referred to the genus *Suncus*.

Suncus Hemprich & Ehrenberg sp. — Meester 1955

Sterkfontein

Material: Consists of 3 specimens (Mf.248—250, all left mandibles).

Remarks: Specimen Mf.248 is a beautifully-preserved specimen in which all the teeth are present, a condition rarely encountered. The length of the tooth row is 5.8 mm., compared with 6.05 mm. in the modern *Suncus*.

Rodent Cave

Material: Comprises 5 specimens (Mf.38, Mf.45, Mf.49, Mf.51, elements of lower jaws and Mf.55, an upper left incisor).

Remarks: Specimen Mf.38 is a mandibular fragment agreeing closely with the recent genus.

Limeworks Dumps

Material: Consists of 3 specimens (Mf.217, Mf.218, Mf.222, an anterior snout, maxillary fragment and a damaged mandible respectively).

Remarks: In Mf.217 all the teeth are missing, exposing the sockets of the left side, but only to the level of the Pm⁴ on the right side. The premaxillary region and the posterior part of the skull have been broken away. The skull is not very large, although it is rather wide across the maxillae. Specimen Mf.218 has three beautifully-preserved teeth (Pm⁴M¹⁻²) very similar to those of the modern *Suncus*.

ORDER CHIROPTERA

Suborder Microchiroptera

Family Rhinolophidae

Rhinolophus cf. capensis Lichtenstein

Rodent Cave

Material: Consists of 7 specimens (Mf.57—60, mandibular elements; Mf.61, maxillary fragment; Mf.62, left upper canine; Mf.63, isolated M₂).

Remarks: Very much like *Rhinolophus capensis*, though distinctly smaller. The Pm₄ in Mf.57 has a distinct cingulum but not as pronounced as in the modern form. In the former the height of the tooth above the cingulum is 1.7 mm., compared with 2.0 mm. in the latter. The height of the jaw immediately behind the Pm₄ is 1.5 mm. and 1.7 mm. respectively. In Mf.58 the Pm₄ has a slightly broader posterior cingulum ledge. The corresponding height of the lower jaw in this specimen is 1.8 mm. In general the teeth appear to be smaller than in the previous specimen, which is also the case in Mf.59. In the latter the curvature between the coronoid process and the mandibular condyle is flatter than in the modern form.

In Mf.61 (see figure 28c), one of the few cranial fragments of this bat recovered from the investigated material, the M³ seems to have been smaller than in the modern form, judging from the size of the alveoli. The M¹⁻², although they closely resemble those of the recent bat, are definitely smaller and not so broad. The isolated canine (Mf.62) is large and strong, gradually curved, and has the same dimensions as in modern specimens. The cingulum is well developed and the root is strong.

Rhinolophus cf. geoffroyi Smith

Cave of Hearths

Material: Consists of 4 specimens (Mf.257, Mf.259, Mf.261, Mf.263, the first a maxillary fragment, the latter three mandibular elements).

Remarks: Specimen Mf.257 appears to be slightly larger than the modern species. The teeth, too, are more robust. Part of the jugal arch is present anteriorly. The specimen includes the posterior alveolus of the Pm₄ and those of the M¹. In Mf.259 the alveoli of both incisors are clear, while the symphyseal region as a whole is in good condition. The alveoli of the Pm₂ and Pm₄ are vacant, but the three molars well preserved.

Compared with the modern bat, the fossil is slightly smaller. The jaw (Mf.259) is also more curved. Molar patterns are comparable, but the incisor is smaller and the mental foramen is situated more posteriorly, below the Pm₂.

Miniopterus cf. schreibersii Kuhl

Cave of Hearths

Material: Consists of three specimens (Mf.258, Mf.260, Mf.262, a maxillary fragment, a mandible and a mandibular fragment respectively).

Remarks: Specimen Mf.258 is larger than the modern form. In Mf.260 the

ascending ramus and angular process have been broken away, but the symphyseal region is undamaged. The alveoli of the I_1-2 and canine are present, the I_2 apparently having been smaller than the I_1 , while the canine must have been a well developed tooth. The Pm_4 and M_1-3 form a well-preserved tooth row. It appears as if more than two premolars were present in this individual. In Mf.262 the M_3 is also larger than in the modern form. It has a well-developed cingulum.

ORDER RODENTIA

Suborder: Myomorpha

Family Cricetidae

Subfamily Cricetinae

Mystromys antiquus Broom 1948

Mystromys antiquus Broom et al. (1946)

Mystromys antiquus Lavocat (1956)

Type: No description of the specimen is available, but the upper molar series has been figured. Transvaal Museum, No. 1557.

Type site: Taung.

Diagnosis: According to Broom it comes nearer to the living *M. albicaudatus* than to the fossil *M. hausleitneri*. The M^2 has only two transverse plates compared with three in *M. hausleitneri*. The M^1 teeth are rather similar, but the enamel infold in the M^3 is more pronounced.

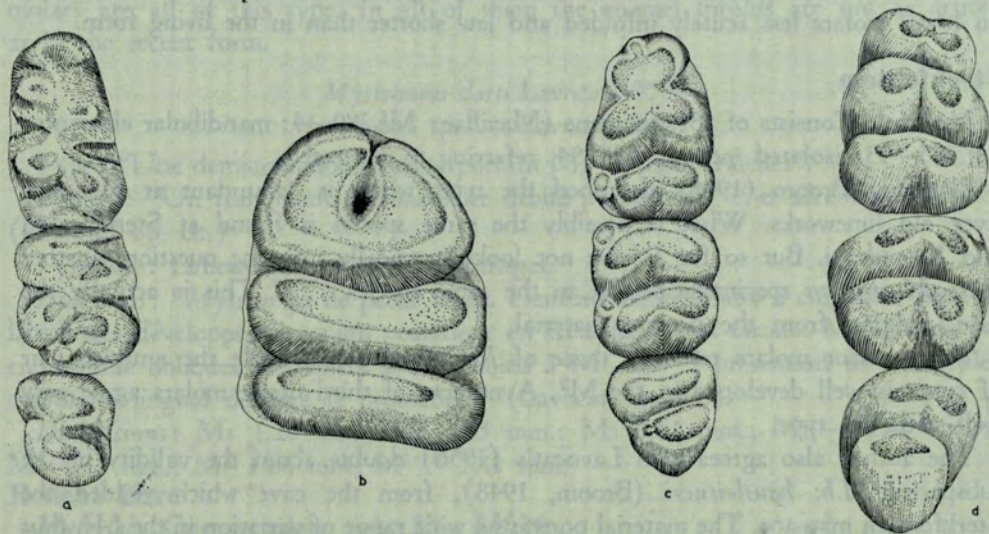


Fig. 29a — Mf.72. *Mystromys hausleitneri*: occlusal surface of M_1-3 . $\times 10$.
 b — Mf.5. *Tatera cf. brantsi*: occlusal surface of M_1 . $\times 10$.
 c — Mf.341. *Grammomys cf. dolichurus*: occlusal surface of M_1-3 . $\times 10$.
 d — Mf.117. *Pelomys cf. fallax*: occlusal surface of M_1-3 . $\times 10$.

Taung

Material: Consists of 21 specimens (Mf.3 is a portion of a maxilla while Mf.4 refers to 20 isolated molars).

Remarks: Specimen Mf.3 compares very favourably indeed with the type. Unfortunately no description was given by Broom, but he supplied a series of drawings which is quite useful. The M^2 in the present specimen has a greatest length of 1.9 mm. and a greatest breadth of 1.7 mm. In the type these measurements are 2.0 mm. and 1.8 mm. respectively (see figure 28D).

Mystromys hausleitneri (Broom) 1948.

Mystromys hausleitneri Broom 1937

Mystromys hausleitneri Lavocat (1956)

Mystromys hausleitneri Lavocat (1957)

Type: "... half a dozen good lower jaws and much of two skulls. Most of the mandibles show the molars in perfect condition and one of the skulls shows the upper molars in beautiful preservation" (Broom, 1937). Transvaal Museum, no numbers supplied.

Type site: Probably Schurveberg, near Pretoria.

Diagnosis: Agrees closely with *M. albicaudatus*. Skull shape slightly different, snout shorter with a wider palate. Length of front of incisor to back of M^3 is 16.3 mm., that is, shorter than in *M. albicaudatus*. Incisors more rounded; width across M^1 is 8 mm. compared with 7.5 in the living form. The anterior palatine foramen is shorter in the fossil. The M^2 has a pair of well developed anterior cusps, resulting in three transverse plates. The M^3 has three outer folds of enamel. Outer enamel on lower molars less acutely infolded and jaw shorter than in the living form.

Sterkfontein

Material: Consists of 93 specimens (Maxillae: Mf.280—4; mandibular elements: Mf.285—93; isolated molars: Mf.294, referring to 79 teeth).

Remarks: Broom (1948) described the type, which is "abundant at Hennops river old limeworks. What is possibly the same species is found at Sterkfontein and Kromdraai. But so far I have not looked critically into the question whether these *Mystromys* specimens belong to the same species . . ." This is actually the case, judging from the present material.

The anterior molars resemble those of *M. albicaudatus*, while the anterior pair of cusps is well developed in the M^2 . A number of third upper molars agree very well with the type.

The author also agrees with Lavocat's (1956) doubts about the validity of the subspecies *M.h. hausleitneri* (Broom, 1948), from the cave which yielded the Sterkfontein man-ape. The material portrays a wide range of variation in the M^2 , thus giving the impression of three enamel ridges on the outside, but with one on the inside. This variation is also found in recent material of *M. albicaudatus* and *M. fumosus*.

Rodent Cave

Material: Consists of 83 specimens (Mf.64 is a maxillary portion; Mf.65—8,

Mf.70—2 are mandibular elements; Mf.116 is an isolated M^3 while Mf.73 refers to 73 isolated molars.)

Remarks: As with Sterkfontein, the material from this site agrees very well with the type specimens. Mf.72 is the best preserved specimen (see figure 29A). This material also supports Lavocat's (1956) doubts on the validity of both the subspecies *M.h. hausleitneri* and *M.h. barlowi*.

Limeworks Dumps

Material: Consists of 28 specimens (three maxillary portions, Mf.266—8, and 25 isolated molars, Mf.269).

Remarks: All the specimens compare well with the type material.

Cave of Hearths

Material: Consists of 11 specimens (Mf.264 is a maxillary fragment while Mf.265 covers 10 isolated molars).

Remarks: The M^2 of Mf.264 is a good tooth, very much like that of *M. albicaudatus*, but with a small anterior transverse plate which is absent in the living form. It agrees otherwise with the type material, except that the enamel ridges on the edge of the tooth do not form such acute angles as are found in the recent form. The root system above the palate has been exposed; the anterior and posterior lingual roots have been fused to form one large blade-like root. On the dorsal aspect of the specimen part of the nasal passage has been exposed. The 10 isolated molars are all of this type. In all of them the enamel infolds are not as acute as in the recent form.

Mystromys darti Lavocat 1956

Mystromys sp. — Lavocat (1957)

Type: "Une demi-mandibule droite portant M_1 —3 assez fraîches".

Co-type: "Un fragment de maxillaire droite portant M^{1-2} et alvéoles de M^3 ." (Lavocat, op. cit.)

Type site: Limeworks quarry, Makapansgat.

Diagnosis: "*Mystromys* de petite taille. Denture mandibulaire à cingulum antéro-labial très développé, cingulum postérieur en crête longue et étroite. Métaconide et endoconide obliques, nettement à M^1 moins à M^2 . M^{1-2} présentant un tubercule cingulaire lingual derrière le protocône." (Lavocat, op. cit.)

Dimensions: M_1 1.25 mm.; M_2 1.03 mm.; M_3 0.51 mm.; M_1 —3 2.80 mm.; M^1 1.37 mm.; M^2 1.04 mm.; M^{1-2} 2.41 mm.

Rodent Cave

Material: One complete right M_1 , Mf.74.

Remarks: Only one tooth of this species was found, against 73 of *M. hausleitneri*, thus supporting Lavocat's view that it is a rare form. It is a very small form; its antero-posterior length is 1.3 mm. (compare 1.25 in the type). The obliqueness of the endoconid and metaconid to the tooth axis, as noted by Lavocat, is clearly confirmed.

It is not unlikely that Lavocat's material came from the Rodent Cave.

Subfamily Gerbillinae

Tatera cf. *brantsi* (Smith)

Tatera sp. — Lavocat (1957)

Taung

Material: Consists of 16 specimens (Mf.5, a mandibular ramus; Mf.6—7, two M₁ teeth; Mf.8a—c, three groups of 13 molars).

Remarks: The M₁ crown structure is typical, with three transversely elongated enamel sections surrounding dentine centres. It is the largest tooth in the series. The anterior oval section is almost square and its characteristic infold medially is very pronounced. The jaw itself (Mf.5) does not differ much from modern material. The ventral mandibular crest in the symphyseal region is less pronounced in the fossil. The incisor root is exposed to the level of the M₃ and it exhibits the fine grooves, visible to the naked eye, which are characteristic of this species.

The M₁ (see fig. 29B) appears to be slightly more rounded and robust than in a modern specimen used for comparison; it is nearly as long, but the anterior oval section is not quite rounded.

The average value for the greatest occlusal length of the M₁ in 10 *Tatera* specimens was found to be 3.52 mm., the variation ranging between 3.1 and 3.8, with $\sigma = 0.23$. The value for the greatest tooth breadth was found to be 2.49 mm., the variation ranging between 2.2 and 2.8, with $\sigma = 0.18$. The values of the measurements obtained for the fossil specimens were compared with these figures and subjected to the t-test for significance. It was found that $t = 1$ with $N = N-1$, that is, 9. The value of t from Fischer's t-tables for small samples was 0.4 and 0.2, that is, between 20% and 40% for the greatest occlusal length and breadth respectively. Consequently the difference in value obtained for the fossil and recent material is not very significant. The fossils are, therefore, referred to the existing genus.

Sterkfontein

Material: Consists of 2 specimens (Mf.309, Mf.310, both left isolated M₁ teeth).

Remarks: Both these specimens agree very well with the corresponding tooth in the modern *T. brantsi*.

Cave of Hearths

Material: One specimen (Mf.313, a damaged mandible with damaged M₁ and complete M₂).

Remarks: The M₁ has been damaged anteriorly. There is a small connection lingually between the first and second transverse sections of the M₂. In spite of the damage and wear, it obviously resembles *T. brantsi*.

Tatera latastei sp.

Rodent Cave

Material: Consists of 14 specimens (Mf.92, a good lower molar; Mf.93, refers to 11 loose molars; Mf.94, Mf.95, two fragmentary mandibles)

Remarks: The best example indicating the presence of this gerbil is the well preserved right M₁ (Mf.92). Compared with fresh material it has a somewhat smaller anterior lamina, presenting an enamel outline which is virtually heart-shaped. The inflection on the anterior lamina is in the middle of the tooth, unlike the more frequent condition where it is directed towards the buccal side. Apart from this difference the tooth agrees closely with modern specimens. The 11 isolated molars (Mf.93) do not exhibit any irregular features

Family Muridae

Subfamily Murinae

Thallomys cf. *paedulus* (Sundevall)

Cave of Hearths

Material: Consists of three specimens (Mf.336, maxillary fragment; Mf.370, mandibular fragment; Mf.371, isolated M₁).

Remarks: In Mf.366 the M¹ is five-rooted with its anterior section and T.1 not deflected back. There are eight cusps on this tooth. The teeth are moderately worn. The M² has an isolated anterior lingual cusp buccally (T.3) on the anterior edge. The M³ is very much like the M² but on a much smaller scale. The tooth row is not very broad or robust. In Mf.370 the M₁ is worn, but on the prominent cingulum edge a small cusp adjacent to the buccal posterior cusp can be seen. The anterior and middle pairs of cusps form the characteristic murid pattern. The tooth is not large compared with modern material. In Mf.371 the M₁ has a prominent ridge on the buccal edge with a small cusp adjacent to the posterior buccal cusp.

Grammomys cf. *dolichurus* (Smuts)

Rodent Cave

Material: Consists of 5 specimens (Mf.105, Mf.111, Mf.113—5, all isolated M₁ teeth).

Remarks: Specimen Mf.113 has a small anterior cusp between the two frontal cusps. There is a small ledge buccally on which a small cusp is present next to the posterior cusp. In Mf.114, 115 and 117 the small anterior cusp is also present. These specimens are not very robust and conform in size to the modern genus.

Lundholm (1955) has investigated the lower molars of a number of murid genera. *Thallomys* and *Grammomys* both have a tendency to develop external ridges on the molars, especially on the M₁ and M₂. *Grammomys* is a genus close to *Thallomys*, but the latter has two frontal cusps in the M₁, while the former has three. The specimens listed here would then all appear to be *Grammomys*. This genus has hitherto not been known as a fossil in Southern Africa.

Limeworks Dumps

Material: Consists of three specimens (Mf. 338, isolated M_1 ; Mf.341, mandible with incisor and M_1-3 ; Mf.342, isolated M_1).

Remarks: Specimen Mf.341 (see figure 29c) is a complete and well preserved jaw. The incisor is complete and ungrooved. The lower molars are all intact. The M_1 has a small anterior cusp medially between the two frontal cusps while a definite ledge has developed on the buccal edge of the tooth, with a small accessory cusp next to the posterior buccal cusp. The jaw itself has a well developed ventral mandibular ridge externally.

Dasymys cf. *incomtus* (Sundevall)

Dasymys sp. — Lavocat (1957)

Sterkfontein

Material: Consists of 2 specimens (Mf.318, Mf.320, a right and left M^1 respectively).

Remarks: The M^1 in Mf.318 is very worn; it is five-rooted and large, but not beyond the range of modern examples. The T.8 builds the whole of the posterior oval section. The T.1 is small while the T.7 is absent. In Mf.320 (see figure 30A) the anterior lamina with the T.1 is not deflected back to any extent. On the whole there is very little difference between the recent and fossil types.

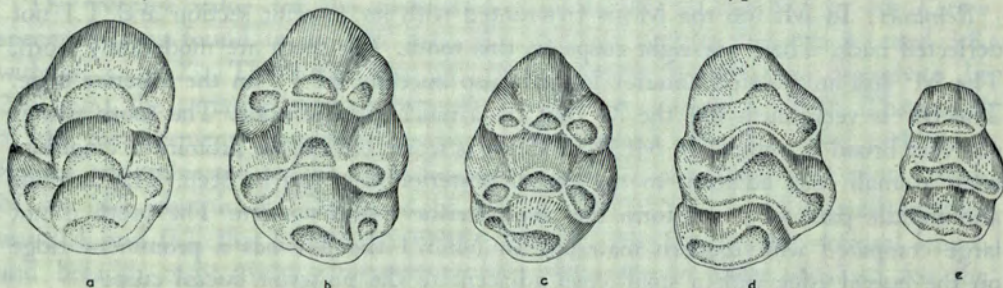


Fig. 30a. — Mf.320. *Dasymys* cf. *incomtus*: occlusal view of M_1 . $\times 10$.
b — Mf.335. *Rhabdomys* cf. *pumilio*: occlusal view of M_1 . $\times 10$.
c — Mf.336. *Aethomys* cf. *namaquensis*: occlusal view of M_1 . $\times 10$.
d — Mf.98. *Acomys* sp.: occlusal view of M_1 . $\times 10$.
e — Mf.381. *Saccostomus campestris*: occlusal view of M_1 . $\times 10$.

Pelomys cf. *fallax* Thomas & Wroughton

?*Pelomys* sp. — Lavocat (1957)

Sterkfontein

Material: Mf.317, a damaged right lower jaw with M_1-2 .

Remarks: The specimen is a well preserved jaw of a swamp rat. There is a good ungrooved incisor. The molars are as large as in the modern type, the M_1-2 length being 4.8 mm. compared with 4.9 mm. in the fossil. Identification from this locality tentative.

Rodent Cave

Material: Consists of 2 specimens (Mf.104, an isolated M^1 and Mf.117, a damaged mandible with intact tooth row).

Remarks: The molars in Mf.117 (see figure 29D) are in perfect condition and do not differ appreciably from those of the modern form. The M_1-3 length is 6.3 mm., compared with 6.4 in a recent mandible.

Limeworks Dumps

Material: Consists of 2 specimens (Mf.344—5, an isolated M^2 and M^1 respectively).

Remarks: The former is a four-rooted tooth, rather large and robust. It is hardly worn at all and there is a large isolated cusp (T.1) lingually on the anterior side. The T.2 is absent while there is a smaller underdeveloped cusp (T.3) buccally. The second lamina of the tooth has the characteristic three cusps (T.4, 5 and 6), while the posterior section has only one large oval cusp (T.8). There are no secondary cusps (T.7 and T.9) in the posterior section.

Specimen Mf.345 is also large and robust. The anterior section and lingual cusp (T.1) is not reflected back while all five roots are complete and intact. The posterior section is a large oval cusp (T.8) with no additional cusps.

This genus was also reported from Makapansgat by Lavocat (1957).

Rhabdomys cf. pumilio (Sparrman)

Sterkfontein

Material: Mf.319, an M^1 .

Remarks: It would be hazardous to separate the closely related genera like *Lemniscomys*, *Rhabdomys* etc., on a single tooth. This identification is therefore tentative. The first lamina with the lingual T.1 cusp is somewhat deflected backward while the posterior oval section (T.8) has a small cusp (T.9) buccally. The tooth is rather narrow and elongated, and not very robust. It compares favourably with recent material of this genus.

Rodent Cave

Material: Consists of 4 specimens (Mf.96, portion of a maxilla with M^{1-2} ; Mf.97, Mf.102, Mf.103, three M^1 teeth).

Remarks: In Mf.96 the first lamina of the M^1 is not as distorted as in some other genera. In the posterior section the T.7 is missing while the T.9 is very reduced. In the M^2 the arrangement is similar. Specimens Mf.102 and 103 have small buccal cusps (T.7).

Limeworks dumps

Material: Mf.335, a left M^1 .

Remarks: This tooth is in a beautiful state of preservation (see figure 30B). The anterior section and lingual cusp (T.1) are reflected posteriorly. There is a small buccal cusp (T.9) posteriorly.

Aethomys cf. namaquensis (Smith)

Sterkfontein

Material: Mf.321, an isolated left M_1 .

Remarks: The anterior root is strong and the posterior two are fused. There are two small roots in the middle, one buccally and the other lingually. There is an

extra cusp between the two frontal cusps, a small cusp between the buccal cusps of the anterior and middle sections, and still another on the buccal edge, level with the posterior buccal cusp. This is the first record of the genus *Aethomys* as a fossil in Southern Africa.

Limeworks dumps

Material: Consists of 3 specimens (Mf.336, 337, 339, three M^1 teeth).

Remarks: Specimen Mf.336 is the best preserved (see figure 30c). All three are five-rooted and have in their crown structure the T.7 missing and the T.9 reduced.

Aethomys cf. chrysophilus (de Winton)

Cave of Hearths

Material: Consists of three specimens (Mf.368, lower jaw with M_1-3 ; Mf.369 and 373, two isolated M^1 teeth).

Remarks: In the M^1 the anterior cusp (T.1) is slightly reflected lingually. The T.7 is absent and the T.9 is very small. The T.3 is smaller than the T.1. The centre row of cusps is large. In Mf.368 the molars are well preserved and display the typical murid structure.

Mastomys cf. natalensis (Smith)

Taung

Material: Consists of 2 specimens (Mf.9, a mandible with unworn molar series and Mf.10, mandibular portion with incisor and M_1).

Remarks: Specimen Mf.9 (see figure 31A) is provisionally referred to this species on account of (a) the slender, yellow, ungrooved incisor; (b) the molar morphology, especially the small extra cusps buccally on the M_1 and M_2 ; (c) the small size of the dental complement, measuring 4.9 mm. and comparing well with 5.0 in a modern specimen.

Sterkfontein

Material: Consists of two specimens (Mf.315—6, both isolated M_1 teeth).

Remarks: These specimens are also tentatively identified on size and general molar morphology.

Rodent Cave

Material: Consists of 8 specimens (Mf.99, 100, two M^1 teeth; Mf.106, 107, 108, 109, 110, 112, six M_1 teeth).

Remarks: This material compares well with modern *Mastomys* material but the specific identification should be regarded as tentative.

Limeworks dumps

Material: Mf.340, an isolated left M_1 .

Remarks: Identification tentative.

Leggada cf. *minutoides* (Smith)
Mus minutoides — Lavocat (1957)

Sterkfontein

Material: Mf.322, an isolated right M_1 .

Remarks: This is a very small tooth indeed, smaller than the equivalent tooth in the modern form, with which it agrees perfectly in structure. There is a well developed small ledge between the posterior lingual and buccal cusps. Its smaller size (length 1.7 mm. and breadth 1.1 mm. compared with 1.9 mm. and 1.4 mm. in the living type) may indicate a new species, but until more material is forthcoming, it is referred to the existing species.

Rodent Cave

Material: Consists of 2 specimens (Mf.118, a damaged M_1 and Mf.120, a mandible without teeth).

Remarks: The M_1 in Mf.118 is an even smaller tooth, but quite similar to that of the modern species. It is slightly on the slender side, measuring 1.6 mm. in length and 0.9 mm. in breadth.

Limeworks dumps

Material: Mf.343, an M^1 .

Remarks: The characteristic feature of this specimen is the very pronounced posteriorly deflected T.1 cusp on the anterior lamina. Posteriorly there is a small squashed T.9 cusp buccally. The tooth is very small indeed, but agrees very well

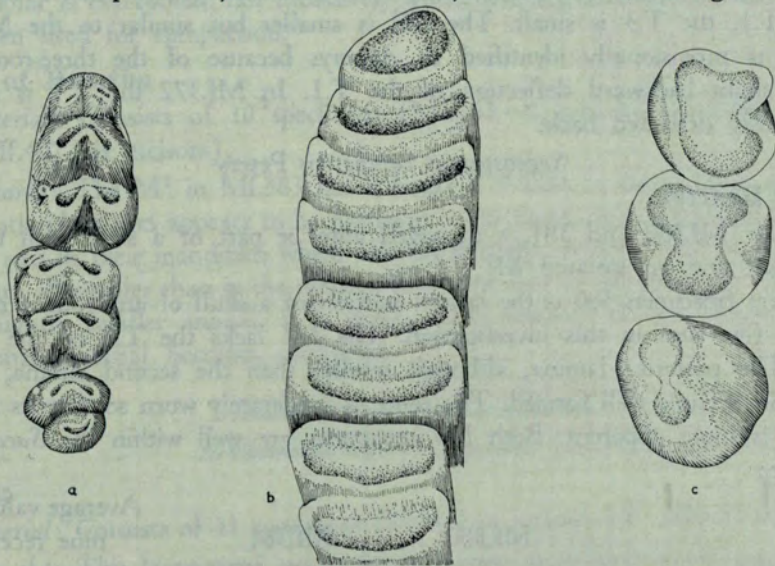


Fig. 31a — Mf.9. *Mastomys* cf. *natalensis*: occlusal view of M_1-3 . $\times 10$.
b — Mf.14. *Palaeotomys gracilis*: occlusal view of M_1-3 . $\times 10$.
c — Mf.423. *Cryptomys robertsi*: occlusal view of M_1-3 . $\times 10$.

with that of the living form. The length and breadth measurements are 2.0 mm. and 1.3 mm. respectively, compared with 2.2 mm. and 1.35 mm. as the average for ten

modern specimens. In the latter the range is 1.9 — 2.4 ($\sigma = 0.14$) for the length and 1.2 — 1.5 ($\sigma = 0.09$) for the breadth.

Cave of Hearths

Material: Consists of 15 specimens (Mf.119, Mf.374, Mf.375, mandibular portions with M_1-2 ; Mf.376, seven molars; Mf.377, mandibular fragment; Mf.378, Mf.379, two M^1 teeth; Mf.421, Mf.422, mandibles with M_1-2).

Remarks: All these specimens agree very well with the modern species

Acomys Geoffroy sp.

Rodent Cave

Material: Mf.98 and 101, a right and left M^1 respectively.

Remarks: In Mf.98 the anterior lamina is not reflected back as much as in *Mastomys* (see figure 30D). The anterior median cusp is not smaller than the corresponding cusps in the second and third laminae in *Ochromys*. The T.6 tends to bulge buccally. On the whole it compares well with the recent *Acomys*. This form has not been recorded previously as a fossil in South Africa.

Cave of Hearths

Material: Mf.367, a complete upper tooth row and Mf.372, an isolated M^1 .

Remarks: In Mf.367 all the roots on the buccal side are exposed. The M^1 has three roots, the M^2 four and the M^3 again three roots. The M^1 has its anterior lingual cusp (T.1) slightly deflected back; the T.8 has a small T.9 buccally, while the T.7 is absent and the T.6 tends to project outward slightly. The M^2 has a well isolated T.1, the T.3 is small. The M^3 is smaller but similar to the M^2 . The specimen is provisionally identified as *Acomys* because of the three-rooted M^1 and the slight backward deflection of the T.1. In Mf.372 the T.1 is also not conspicuously deflected back.

Saccostomus campestris Peters

Cave of Hearths

Material: Mf.380 and 381, a damaged anterior part of a skull with the right M^1 present and an isolated M^1 .

Remarks: Specimen 380 is the largest portion of a skull of any rodent recovered from the five sites in this investigation. The M^1 lacks the T.1 on the anterior lamina. The posterior lamina, although smaller than the second lamina, has the T.7, 8 and 9 cusps well formed. The tooth is moderately worn so that its laminate structure is more apparent. Both M^1 specimens are well within the *Saccostomus* size range:

	Mf.380	Mf.381	Average value for nine recent specimens
Length	2.5 mm.	2.4 mm.	2.43 mm.
Breadth	1.8 mm.	1.8 mm.	1.69 mm.
Interorbital constriction	4.8 mm.	—	4.7 mm.

The isolated M^1 (see figure 30E) is precisely like the tooth in Mf.380. It is distinctly four-rooted.

Statistically the two fossil specimens are inseparable from the modern *Saccostomus campestris*.

Subfamily Dendromurinae

Dendromus cf. *mesomelas* (Brants)

Dendromus sp. — Lavocat (1957)

Sterkfontein

Material: Consists of 12 specimens (Mf.332—4, mandibular fragments with M_1 teeth; Mf.420, nine incisors).

Remarks: There is no appreciable difference between these specimens and the modern *D. mesomelas*.

Rodent Cave

Material: Mf.145 and 146, isolated M^1 and M_1 respectively.

Remarks: These two specimens also compare favourably with the modern form. Lavocat (1957) has recorded this form from Makapansgat.

Limeworks dumps

Material: Mf.346, a damaged mandible with incisor and M_1 .

Remarks: In this specimen the incisor is complete, slightly worn and ungrooved. The molar is two-rooted, not excessively worn, and slightly smaller than in a recent specimen used for comparison.

Cave of Hearths

Material: Consists of 10 specimens (Mf.383—6, two M^1 and two M_1 teeth, and Mf.407, six incisors).

Remarks: The M^1 in Mf.383 has a larger T.9 than in the modern species. The zygomatic plate also appears to be narrower in the fossil. Specimens Mf.384 and 385 are in situ in their mandibles which also contain the incisors. The six incisors (Mf. 407) are all smaller than in the modern form and they are all grooved. Although this is a slightly smaller animal, it is provisionally referred to the extant form until additional material becomes available.

Malacothrix cf. *typica* (Smith)

Malacothrix sp. — Lavocat (1957)

Taung

Material: Consists of 11 specimens (Mf.12, an isolated M^1 ; Mf.13, ten incisors).

Remarks: This large-eared mouse has not been recorded from Taung previously, but Lavocat (1957) reported it from Makapansgat. The molar pattern agrees very well with *M. typica*, the most abundant recent species. This tooth is slightly larger than its recent counterpart. The recent specimen used for comparison measures 2.8 mm. in length, compared with 2.9 in the fossil.

Limeworks dumps

Type: An isolated left M^1 , the occlusal surface in perfect preservation, but with a somewhat damaged root system.

Diagnosis: A distinctly small type of *Malacothrix* with essentially the same morphological features of the M^1 as in recent species. The tooth is narrow and elongated, with a rather complex cusp pattern. There is a small extra cusp in front of the T.2. The T.3 is present, while the T.1 is slightly suppressed. The T.2 and T.3 are approximately of the same size. The T.4, T.5 and T.6 in the second lamina are normal. The posterior lamina has the T.8 and T.9, and a small extra posterior cusp leading out from the T.8 in the form of a small ledge. The T.8 is slightly larger than the T.9. All the cusps are rather distinct.

Remarks: The occlusal surface of the tooth is well preserved and moderately worn, indicating that the animal is mature. It is a four-rooted molar; the anterior large root is intact, as well as the small buccal root in the middle. The large sturdy posterior root has been slightly damaged and the small lingual root is missing.

The smaller size of this animal is evident in the light of the following measurements: Its length is 1.4 mm. and its breadth 1.0 mm. compared with 2.6 mm. and 1.43 mm. respectively as averages for 10 *M. typica* specimens. It would appear that a new form of *Malacothrix* is represented by this tooth. Lavocat (1957) has also reported a *Malacothrix* from this site, but unfortunately our specimens could not be compared. A new specific name is proposed but it is realized that much more material is required before it can be properly defined. In the meantime, there seem to be grounds for suggesting that the difference in size between the fossil and recent material is significant.

Steatomys cf. pratensis Peters

Rodent Cave

Material: Mf.143 and 144, isolated left and right M^1 teeth.

Remarks: This is the first occurrence of fossil fat mouse in Southern Africa. In size these two specimens are strictly comparable with the modern form. The length:breadth measurements are 2.3/1.5 mm. in the modern species, 2.2/1.4 mm. for Mf.143 and 2.3/1.3 mm. for Mf.144.

Cave of Hearths

Material: Mf.387, an isolated M^1 .

Remarks: There is a faint indication of a small cusp on the third section of the tooth, also noticed in the specimen used for comparison. There is a slight size difference between the fossil and the living form. The fossil tooth is slightly broader, but this may be due to excessive wear.

Subfamily Otomyinae

Palaeotomys gracilis Broom 1937

Palaeotomys gracilis — Lavocat (1957)

Type: The anterior two-thirds of a skull in a fairly satisfactory condition. Transvaal Museum, no number supplied.

Type site: Probably Schurveberg, near Pretoria.

Diagnosis: "It differs very clearly from any of the many species and subspecies at present alive in South Africa, with all of which I have compared it" (Broom, op. cit.). Nasals widely expanded in front; incisors deeply grooved; upper incisors exactly as in *Otomys*; upper molars relatively smaller with the posterior plates of the M^3 narrower than in *Otomys*. "The first and second laminae are subequal in width, but the third is considerably narrower, and the fourth is still narrower, while the fifth is only a little pillar" (Broom, op. cit.).

Taung

Material: Consists of 91 specimens (Mf.14, a mandibular ramus with intact teeth (see figure 31B); Mf.15a—f, 40 isolated molars; Mf.16a—b, 50 isolated incisors).

Remarks: The material from Taung can with little difficulty be identified as *Palaeotomys gracilis*. This animal, known from other sites, has not previously been recorded from Taung. In the Taung material the sixth lamina in the M^3 occurs more frequently than in the specimens described by Broom.

Sterkfontein

Material: Consists of 83 specimens (Mf.408—412, maxillary and mandibular portions with teeth; Mf.413a—b, 28 loose incisors, 14 upper and 14 lower; Mf.414a—g, 50 loose molars, 16 upper and 23 lower, with 11 uncertain).

Remarks: Specimen Mf.408 shows the M^3 with its characteristic five normal laminae and the sixth posterior pillar. This extensive amount of material shows that *Palaeotomys gracilis* was a frequent and widely spread species. All the molar and incisor elements are slender and small.

Rodent Cave

Material: Consists of 376 specimens (Mf.147—161, various maxillary and mandibular elements with teeth; M.162a—b, 129 isolated incisors, 58 upper and 71 lower; Mf.163a—g, 232 isolated molars, 75 upper, 145 lower and 12 unclassifiable).

Remarks: The abundance of the material representing this species in the Rodent Cave deposit is noteworthy. All the material agrees very well with the type material. This animal has also been recorded from Makapansgat by Lavocat (1957). The trifoliated condition of the M^3 referred to by Lavocat appears in a small number of specimens.

Limeworks dumps

Material: Consists of 85 specimens (Mf.348—359, various maxillary and mandibular elements with teeth; Mf.357a—f, 30 isolated molars, 13 upper, 16 lower, one uncertain; Mf.358a—b, 45 isolated incisors, 24 upper and 21 lower; Mf.359, a toothless mandible).

Remarks: Specimen Mf.348 is a good anterior snout of this fossil vlei-rat. All the material substantiate *P. gracilis* as a well founded fossil species.

Cave of Hearths

Material: Consists of 113 specimens (Mf.388—397, various maxillary and mandibular elements with teeth; Mf.398a—b, 58 isolated incisors; Mf.399a—f, 45 isolated molars).

Remarks: Although there are specimens approaching *Otomys irroratus* in size, the material in general represents a smaller form. It is indistinguishable from the earlier *Palaeotomys gracilis* material from the other sites.

Suborder Hystricomorpha

Family Bathyergidae inc. sedis.

Cryptomys robertsi Broom 1937

Type: "Numerous specimens of a fairly large rodent mole which must be placed in the genus *Cryptomys*" (Broom, 1937). Transvaal Museum, no numbers supplied.

Type site: Probably Schurveberg, near Pretoria.

Diagnosis: Moderately large species with one mandible measuring "from the front of the incisor to the back part of the angular portion of the jaw 40 mm." The shape of the back part of the jaw is different from any species Broom was able to compare it with and a distinct ridge passes forward on the outer side of the jaw from the condyle, not entirely attributable to the roots of the lower incisors. The teeth are relatively small; crown low "and each tooth has the enamel of the upper half folded in on both the outer and inner sides" (Broom, op. cit.). In one specimen the fourth Pm, M₁ and M₂ together measure 5.2 mm.

Taung

Material: Mf.17 and 18, two isolated molars.

Remarks: Specimen Mf.17 is very similar to the M₁ described by Broom (1937). It is about the same size but the enamel folds on the occlusal surface are not as deep. Due to damage, Mf.18 is tentatively identified. This form has not previously been recorded from Taung.

Sterkfontein

Material: Consists of five specimens (Mf.423, jaw with Pm₄, M₁—₂; Mf.424, four isolated molars).

Remarks: In Mf.423 the molar series is in a very good condition (see figure 31c). The three teeth together measure 5.3 mm. compared with 5.2 mm. in the type.

Rodent Cave

Material: Consists of 7 specimens (Mf.164, a right mandibular fragment with Pm₄; Mf.165, six isolated teeth).

Remarks: All these teeth are well worn and as a result they do not show any enamel infolding at all.

Limeworks dumps

Material: Mf.364, a palate with left and right alveoli; Mf.365, damaged jaw with M₁.

Remarks: It is unfortunate that all the teeth are missing from Mf.364. Upper teeth of this animal are singularly scarce in the material investigated. "I have no specimen showing the upper molars, but from the sockets I infer they agree with the lower molars" (Broom, 1937).

Cave of Hearths

Material: Consists of 3 specimens (Mf.400, maxillary portion with M³; Mf.401, a toothless damaged mandible; Mf.402, an isolated M³).

Remarks: The two M³ specimens are very similar. They are the first upper teeth of this animal found in fossil form and while the accompanying mandible is toothless, the present material is not strictly comparable with that from the other sites. It compares favourably with the modern *Cryptomys*, but its specific identification must be regarded as tentative.

Unidentifiable cranial remains

Taung

From this deposit a fragmentary murid molar (Mf.11), 81 incisors (Mf.19) and four toothless cranial fragments (Mf.20) could not be identified.

Sterkfontein

The unidentifiable specimens from this deposit are the following: Mf.231, Mf.314, murid maxillary fragments; Mf.323—330, murid mandibular elements; Mf.331, 6 murid molars; Mf.295, 220 loose incisors.

Rodent Cave

There are 21 mandibular elements (Mf.121—141), 54 isolated molars (Mf.142a—c) and 215 incisors (Mf.166) which could only be identified as murid.

Limeworks dumps

Among the material from this site 3 lower jaws (Mf.360—362), 7 isolated molars (Mf.363) and 62 loose incisors (Mf.297) are murid *incerti sedis*.

Cave of Hearths

Unidentifiable specimens are 20 molars (Mf.382), three mandibular elements (Mf.403—405) and 153 loose incisors (Mf.296).

Post-cranial remains

The results of a gross analysis of the post-cranial material are reflected in Table II and in figure 32.

Table II

	Taung	Sterkfontein	Rodent Cave	Limeworks dumps	Cave of Hearths
Vertebrae and ribs	15	135	172	234	154
Pectoral girdle and fore limbs	21	97	98	138	75
Tarsals and carpals	12	104	68	126	52
Pelvis and hind limbs	10	135	155	192	120
Limb bone shafts	48	412	102	266	200

Non-microfaunal elements

Taung

The total absence of skeletal elements derived from larger animals in this deposit is noteworthy.

Sterkfontein

Skeletal material not conforming with the microfauna analysed above includes: A jaw of a bird (Mf.416); a hyracoid distal femur (Mf.417); a felid distal humerus (Mf.418); a bovid proximal radius (Mf.419); 47 unidentifiable fragments (Mf.415).

Limeworks dumps

The microfaunal breccia from this locality is highly contaminated with the remains of "foreign" animals. These include: An assortment of lacertilian cranial and post-cranial elements (Mf.302, Mf.247); ten bird skeletal elements (Mf.275); an isolated primate Pm¹ (Mf.303); nineteen cranial and fifteen post-cranial Lagomorph elements (Mf.304, Mf.278); one cranial and eleven post-cranial bovid specimens (Mf.306, Mf.276); six felid specimens (Mf.307, Mf.279); eight hyracoid elements (Mf.277); 471 bone fragments (Mf.270, Mf.271); 300 similar fragments, but possibly of avian origin (Mf.273).

Rodent Cave

The only "foreign" elements contained in the breccia from this site are two fragments derived from limb bones of a bird (Mf.90—91).

Cave of Hearths

The non-microfaunal contamination at this site is also quite low. The specimens recovered include: A lagomorph molar root (Mf.300); ten bird elements (Mf.299, Mf.311); 38 small fragments of bone (Mf.298).

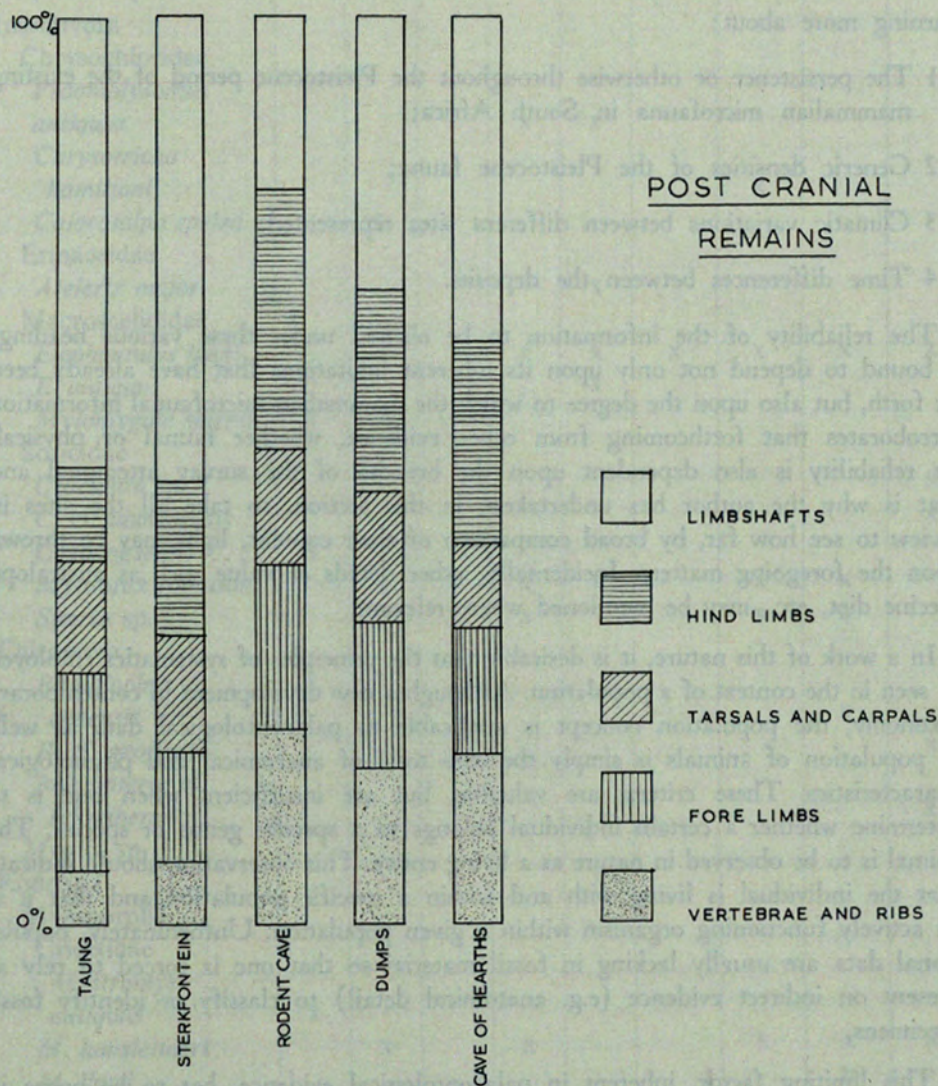


Figure 32

V. DISCUSSION

It was pointed out in the introduction that despite the limitations imposed upon an investigation of this sort, which is dependent, for the information it provides, upon the dietary selectivity of owls, the labour undertaken held the possibility of learning more about:

- 1 The persistence or otherwise throughout the Pleistocene period of the existing mammalian microfauna in South Africa;
- 2 Generic densities of the Pleistocene fauna;
- 3 Climatic variations between different sites represented;
- 4 Time differences between the deposits.

The reliability of the information to be elicited under these various headings is bound to depend not only upon its inherent limitations that have already been set forth, but also upon the degree to which the mammalian microfaunal information corroborates that forthcoming from other evidence, whether faunal or physical. Its reliability is also dependent upon the breadth of the survey attempted and that is why the author has undertaken, in this section, to take all the sites in review to see how far, by broad comparison of their content, light may be thrown upon the foregoing matters. Incidentally, other details of value such as australopithecine diet, etc., may be mentioned where relevant.

In a work of this nature, it is desirable that the principles of systematics employed be seen in the context of a population. Although a new development in contemporary taxonomy, the population concept is applicable to palaeontological data as well. A population of animals is simply the sum total of anatomical and physiological characteristics. These criteria are valuable, but are insufficient when one is to determine whether a certain individual belongs to a specific genus or species. The animal is to be observed in nature as a living entity. This observation should indicate that the individual is living with and within a specific population and that it is an actively functioning organism within a given population. Unfortunately, population data are usually lacking in fossil material so that one is forced to rely at present on indirect evidence (e.g. anatomical detail) to classify or identify fossil specimens.

This limiting factor, inherent in palaeontological evidence, has to be borne in mind in interpreting an assemblage of skeletal parts, a thanatocenose. Consequently, the author does not agree with the often proposed view that it is an easy matter to assign generic identifications to fossils. Many facts are taken into consideration before names are given and, valid or not, the species determined by previous investigators afford a synoptic idea of the mammalian microfaunal setting during the Pleistocene.

Table III

The Fossil Microfauna in South Africa subsequent to this Survey

Classification	Locality								
	Ta	St	Sw	Kr	BF	Sch	MpD	MpR	MpC
Insectivora									
Chrysochloridae									
<i>Proamblysomus antiquus</i>				x	x				
<i>Chrysotricha hamiltoni</i>							x		
<i>Chlorotalpa spelea</i>		x							
Erinaceidae									
<i>Atelerix major</i>					x				
Macroscelididae									
<i>Elephantulus langi</i>		x		x	x	x	x	x	x
<i>E. antiquus</i>					x				
<i>Myiomygale spiersi</i>	x	?x							
Soricidae									
<i>Crociodura</i> sp.									x
<i>C. cf. taungsensis</i>									x
<i>C. taungsensis</i>	x								
<i>Myosorex robinsoni</i>		x	x	x	x		x	x	
<i>Suncus</i> sp.		x	x	x			x	x	
Chiroptera									
<i>Rhinolophus</i> cf. <i>capensis</i>								x	
<i>R. cf. geoffroyi</i>									x
<i>Miniopterus</i> cf. <i>schreibersii</i>									x
<i>Myotis</i> sp.									
Rodentia					x				
Myomorpha									
Cricetidae									
<i>Mystromys antiquus</i>	x								
<i>M. hausleitneri</i>		x		x			x	x	x
<i>M. darti</i>								x	
<i>Tatera</i> sp.								x	
<i>T. cf. brantsi</i>	x	x		x					x
Muridae									
Murinae									
<i>Thallomys debruynei</i>	x								

	Ta	St	Sw	Kr	BF	Sch	MpD	MpR	MpC
<i>T. cf. paedulus</i>									
<i>Grammomys cf. dolichurus</i>							x	x	x
<i>Dasymys boliti</i>					x				
<i>D. cf. incomtus</i>		x						x	
<i>? Arvicanthis sp.</i>		x							
<i>Pelomys cf. fallax</i>		?x					x	x	
<i>?Lemniscomys sp.</i>								x	
<i>Rhabdomys cf. pumilo</i>		x					x	x	
<i>Aethomys cf. namaquensis</i>		x					x		
<i>A. cf. chrysophilus</i>									x
<i>Mastomys natalensis</i>	x	x					x	x	
<i>?Zelotomys sp.</i>								x	
<i>Leggada minutoides</i>		x					x	x	x
<i>L. major</i>					x				
<i>Acomys sp.</i>								x	x
<i>Saccostomus campestris</i>									x
<i>Dendromurinae</i>									
<i>Dendromus antiquus</i>	x								
<i>D. cf. mesomelas</i>		x					x	x	x
<i>Malacothrix typica</i>	x								
<i>?Malacothrix makapani</i>							x		
<i>Steatomys cf. pratensis</i>								x	x
<i>Otomyinae</i>									
<i>Palaeotomys gracilis</i>	x	x		x			x	x	x
<i>Prototomys campbelli</i>	x								
<i>Hystricomorpha</i>									
<i>Hystric cf. africanaustralis</i>							x		
<i>H. major</i>							x		
<i>H. cristata</i>		x							
<i>Xenohystric crassidens</i>							x		

	Ta	St	Sw	Kr	BF	Sch	MpD	MpR	MpC
<i>Pedetes gracile</i>	x								
<i>Petromys minor</i>	x								
<i>Hystricomorpha</i>									
<i>Incerte cedis</i>									
<i>Gypsorhynchus darti</i>	x								
<i>G. minor</i>	x								
<i>G. makapani</i>							x		
<i>Cryptomys robertsi</i>	x	x	x	x	x	x	x	x	x
<i>Heterocephalus</i> sp.								x	

* Locality abbreviations:

Ta	— Taung	MpD	— Makapansgat dumps
St	— Sterkfontein	MpR	— Makapansgat Rodent Cave
Sw	— Swartkrans	MpC	— Makapansgat Cave of Hearths
Kr	— Kromdraai		
BF	— Bolt's Farm		
Sch	— Schurberg		

Consequently, the material described in Part IV has been tabulated in Table III. This synoptic Table includes the specimens recovered in this analysis along with those fossils known from previous investigations. All the forms of smaller animals which could properly be classified under the inclusive term "mammalian microfauna" (such as the Insectivora, Chiroptera and Rodentia) have been incorporated therein.

The Hystricomorpha however are not microfauna, for they are rather beyond the usual size limit of normal owl prey. But they are rodents and in order to make Table III as complete as presently possible for rodents as well as the microfauna, the porcupines were also incorporated.

1. *The persistence or otherwise of the Orders hitherto recorded.*

The various orders of animals which have now been identified from the breccias (Table III) include the following:

A. INSECTIVORA

- The Chrysochloridae or Cape golden moles are known hitherto only from isolated finds belonging to three different genera of which one (*Proamblysomus antiquus* Broom 1948) is non-existent today. The remaining two genera are still extant (*Chrysotricha hamiltoni* de Graaff 1957, *Chlorotalpa spelea* Broom 1948) although the species were in both cases first recognised as fossils. The chrysochlorids are an intricate group taxonomically and far more fossil material will need to be collected to reveal the palaeontology of these queer mammals. Only four individuals have come from the different localities indicated in Table III. This low frequency is not surprising for they are fossorial animals and do not often (if at all)

fall prey to owls. These specimens were not found in the fossil owl pellet material of this analysis. The form from Makapansgat may even have been part of australopithecine diet (de Graaff, 1958); in that event, as Broom recognised, they must have been secured by digging.

- ii. The Erinaceidae with *Atelerix major* Broom (1937) as the fossil hedgehog has hitherto only been found at Bolt's Farm and only one individual is known. It has not been encountered in the other deposits analysed here. This is not surprising as this animal does not constitute part of the usual diet of owls.
- iii. The Macroscelididae or elephant shrews have been shown to occur at all the sites investigated, in addition to the Bolt's Farm and Schurveberg localities where they were first identified; but this fossil, *Elephantulus langi* Broom, has not been recorded from Taung. This little animal may of course be recovered from the latter locality during some future analysis. Nevertheless, we know now that it has existed over a very considerable span of time, for the Sterkfontein and Makapansgat localities go back to the early Pleistocene while the more recent Stone Age Cave of Hearths breccias from which it comes are dated by the Earlier Fauresmith Culture. In other words, this long-lived form has apparently ceased to exist within the last $\pm 50,000$ years.

The other fossil elephant shrew discovered at Bolt's Farm near Sterkfontein, *E. antiquus* Broom, has not been identified from the Cave of Hearths nor from any other deposit so far examined.

Mention must also be made of the queer aberrant type, *Myiomyale spiersi* Broom, first discovered in the breccia from Taung. This form, according to Broom et. al. (1946, 1948) represents a new Menotyphlan family. A specimen which is provisionally identified as an example of this animal has been isolated from the Sterkfontein breccia. It has not been found in any of the other localities, not even in the Taung breccia. The possible occurrence of this definitely archaic animal at Sterkfontein indicates correspondence in age between the two deposits. Instances are known where a genus persists over a very considerable span of time but, as will be seen later, this fact along with others supports the idea that Taung is rather older than Sterkfontein.

- iv. The Soricidae or shrews found as fossils are particularly important. From Taung (supposedly the oldest of all the deposits) the form *Crocidura taungensis* Broom has been identified. This was the only locality from which the genus *Crocidura* had been recorded previously as a fossil. It did not appear at Sterkfontein, nor in the Rodent Cave nor in the material derived from the Dumps at Makapansgat. However, the present study has revealed a form hardly distinguishable from *C. taungensis* in the Cave of Hearths. In Table III it is consequently indicated as

C. cf. taungensis. This little animal is somewhat larger than *Suncus* but smaller than the average *Myosorex*; thus it is of intermediate size, close to *C. bicolor*, as is also the type. There is no anatomical reason why this form could not be called *C. taungensis* Broom. However, until more material corroborates the author's determination, these specimens are not referred finally to the known fossil species.

In addition to this unexpected discovery, another species of the genus *Crocidura* has been recognised from the Cave of Hearths. This animal, apparently a much larger form than *C. cf. taungensis* may eventually prove to be an entirely new species.

It was quite unexpected that the genus *Crocidura* should be isolated from the Cave of Hearths and that this cave site should provide the first record of that genus as a fossil apart from Taung. The absence of *Myosorex robinsoni* Meester, which is found frequently as a fossil in Sterkfontein and the Limeworks Makapansgat, may indicate that *Myosorex* abandoned the Makapansgat valley as an ecological niche as long as $\pm 50,000$ years ago. However, these conclusions are tentative and it would be necessary to analyse further material from the Cave of Hearths from a higher (and consequently younger) horizon to arrive at greater certainty in the matter. *Crocidura* is the dominant genus found in the vicinity of the Cave of Hearths today and it may tentatively be suggested on the available evidence that this genus was gradually establishing itself, apparently at the expense of *Myosorex*. This serves as an example of the dynamic generic shift which possibly has occurred in this valley.

The genera *Myosorex* (*robinsoni* Meester) and *Suncus* Hemprich and Ehrenberg (sp.) have been found at Sterkfontein and at the Rodent Cave and Dumps at Makapansgat. The *Suncus* material seems to be too close to the recent material to erect a new species rank on such slight differences. This has already been commented upon by Meester (1955). The validity of the species *Myosorex robinsoni* may be seriously questioned, especially in Mf.37 from the Sterkfontein breccia. In this specimen, a small cusplet supposed to be absent in the fossil material is definitely present on the posterior aspect of the I₂. However, a more extensive investigation is required before this species is finally sunk. The matter should be reviewed on a statistical basis.

B. CHIROPTERA

From two localities, the Limeworks and Cave of Hearths in the Makapansgat valley, bat remains have been recovered. The specimens from the former locality have been compared to the recent *Rhinolophus capensis* Lichtenstein, to which they are very close morphologically. The taxonomy and systematics of the bats in Southern Africa is in urgent need of revision. The fossil

specimens are, as far as the author can determine, not much more than specifically distinct although the fossils tend to be slightly smaller. These specimens are thus provisionally referred to as *R. cf. capensis* in Table III. The specimens also agree fairly closely with *R. darlingi* Andersen.

The specimens from the Cave of Hearths are provisionally identified as *Rhinolophus cf. geoffroyi* and *Miniopterus cf. schreibersii*. It is felt that an investigation into these forms must be left to a specialist. The material, as far as it has been examined, is within the variation range of the two recent species with which it has been compared.

It is sufficient for the present to note that the genera *Rhinolophus* and *Miniopterus* were not recorded as fossils in the South African deposits prior to this investigation. It is also noteworthy that *R. capensis* does not occur at Makapansgat today.

The genus *Myotis* from Bolt's Farm (Broom, 1948), has not been recorded among this material.

C. RODENTIA

(i) *The Myomorpha*. The Myomorpha are very well represented in these deposits for they form the dominant owl prey.

(a) The Cricetinae "... is found mainly in the Northern Hemisphere, and is represented by only one genus (*Mystromys*) south of the Equator ..." (Roberts, 1951). This recent genus forms a considerable proportion of all the fossil specimens recovered in this work. The form *M. antiquus* Broom has been recorded from Taung. More material should be analysed to determine the validity of this species. From the small sample of specimens recovered here it may be accepted provisionally as valid but more specimens would clinch the matter especially as it has not been found in any other deposit.

M. darti Lavocat is the very small form reported from Makapansgat by Lavocat. This form has also been found during this search and appears to be a well defined species. It is evidently rare and has not been isolated from any other deposit.

M. hausleitneri Broom is apparently the species with the widest geographical distribution. It occurs at Sterkfontein and at all three Makapansgat sites. It is very near in morphology (especially the M^2) to the recent *M. albicaudatus* and in the material from the Cave of Hearths it is virtually impossible to differentiate the fossil from recent material except in size. The low density of this animal at the Cave of Hearths may imply that the fossil form was on its way out, using Makapansgat as an ecological niche. Like *Elephantulus*

langi, this species has persisted over a considerable span of time. The densities of *M. hausleitneri* in the Sterkfontein and Rodent Cave localities is by contrast high (see Table IV).

M. h. barlowi Broom, the Sterkfontein subspecies, has not been identified. Its validity has been queried by Lavocat (1956). The M^2 occlusal pattern of the modern forms like *M. albicaudatus* vary so widely that the supposed *M. h. barlowi* could not be differentiated from them. Hence only *M. hausleitneri*, *M. antiquus* and *M. darti* can be presently accepted as fossil species of this white-tailed rat.

- (b) The Gerbillinae were encountered in the majority of the localities. On the whole, the gerbils, based on the structure of the M_1 , seem to be on the same evolutionary level as the recent material. The fossil teeth lie within the recent size range and the M_1 is very much like the modern material. The genus *Tatera* has been reported from all the localities except the Limeworks Dumps. The Taung material is very similar to the recent morphology. The genus is furthermore archaic but persistent. The Sterkfontein specimens are not more than subspecifically distinct (if at all) from the recent *Tatera brantsi*. In the gerbil material from the Rodent Cave there is a queer M_1 with a virtually heartshaped anterior lamina. This specimen is kept apart provisionally until further gerbil comparative material becomes available from this locality. This feature has not been found in recent comparative material.
- (c) The Murinae, like the Gerbillinae, had already attained the same evolutionary level as the recent comparative material. The inherent difficulty of separating the various genera (not to mention species) on isolated skeletal fragments has aptly been summarized by Lavocat (1957). "Hormis trois portions de crânes de *Palaeotomys* et une de *Mystromys*, ces formes ne sont représentées que par des mandibules ou des dents isolées, ce qui explique que l'indication de certains genres soit accompagnée de points d'interrogation. En effet, on sait que en général les dentures mandibulaires sont peu caractéristiques. D'autre part, en ce qui concerne les Murinés seuls, ceux-ci sont représentés actuellement dans les régions intéressées par des genres vivants, comprenant 37 espèces divisées en multiples sous espèces; à quoi il faut adjoindre les autres formes pouvant exister dans des territoires voisins. Or, on sait que les caractères des dents sont extrêmement peu étudiés par les zoologistes; il est donc impossible de trouver dans la Bibliographie des descriptions vraiment précises, encore moins des figurations des diverses formes actuelles . . . Si ces caractères sont généralement très typiques avec des dentures complètes, il faut reconnaître qu'il

peut être difficile de décider entre certains genres voisins par des dents isolées, d'où les points d'interrogation dans la liste ci dessus."

Thirteen of the recent genera of this subfamily have thus far tentatively been identified as occurring also in the deposits.

Grammomys and *Thallomys* are two genera regarded as extremely closely related to one another. Ellerman (1941), however, says: "I doubt the validity of *Thallomys* from *Rattus* on the above mentioned characters of lower molars. The genus is retained mainly for convenience, though the molars are too angular for the genus *Rattus*." (page 74). However, even this is too slight a pretext for generic status.

Reference to Table III will show that *Thallomys debruyni* Broom (1948), from Taung, has been kept apart from the *Thallomys* material from the Cave of Hearths in Makapansgat. This has been done provisionally, for the following reasons: Broom described and founded the new species on a reasonably well preserved skull. In the present analysis, all the material of this genus consisted of isolated molars or sections of upper or lower molar series. In the type specimen, teeth are absent, so it was not possible to compare this material with the type through the absence of skeletal remains common to both. The teeth recovered agree fairly closely with the recent *T. paedulcus*.

Lundholm (1955) separates the genera *Thallomys* and *Grammomys* on the morphology of the M_1 and his scheme has also been used to classify these fossils. In the former, the M_1 has two frontal cusps, while in the latter the M_1 is provided with three frontal cusps. Both genera tend to develop an external buccal ridge on the M_1 and M_2 . Lundholm also agrees that *Thallomys* is closely related to *Grammomys*.

It is noteworthy that neither of these two genera has been recovered from Sterkfontein and that *Grammomys* is also absent from the Cave of Hearths.

The genus *Dasymys* has also been identified, but it was not located at the Limeworks Dumps or in the Cave of Hearths. Lavocat (1957) reported it from Sterkfontein. The fossil specimens are closely related to the recent forms and can hardly be differentiated. In the Transvaal Museum, a fossil species of this genus has been catalogued by Broom as *D. bolti* from Bolt's Farm. This form has not been described officially and, consequently, the material isolated in this work has been kept separate, for the former species still awaits investigation.

On the whole, *Dasymys* is rather closely related to *Arvicanthis* and identification from small skeletal fragments is difficult.

?*Arvicanthis* has been identified provisionally from the Sterkfontein breccia by Lavocat (1957). This genus ranges over Africa "from coast to coast" (Ellerman, 1941) but it does not occur in the Union of South Africa today. It has a very heavy dentition and is closely related to the genus *Rattus* by the genus *Aethomys* (Ellerman, op. cit.). ?*Lemniscomys*, also provisionally reported by Lavocat (op. cit.) from 'Makapan' is very much like *Arvicanthis*. The closely related genus *Rhabdomys* is also very much like *Arvicanthis* though its dentition is not as heavy. The former genus is also close to *Rattus*, but the molars are slightly more complex. The specimens identified as *Rhabdomys cf. pumilio* in this paper have been recorded as such because of their somewhat lighter dentition as compared with the other closely related forms. This group is extremely complex and much further taxonomic identification based on skeletal elements of living types in particular is needed. Consequently the identifications of these forms recorded from the localities in this work is purely tentative.

A frequent form is the rather well defined genus *Pelomys*. The material recovered is close in morphology to that of the recent *P. fallax*. These recent forms appear to be on the same evolutionary level as their fossil counterparts. Like *Dasymys*, it may occur at Sterkfontein and the Rodent Cave, but it has not been recorded from the Cave of Hearths. It has however been reported provisionally from the Limeworks Dumps (Lavocat 1957).

The genus *Aethomys* recorded from Sterkfontein, the Dumps and the Cave of Hearths is also somewhat problematical. Lundholm's (op. cit.) reasons for separating the genera *Thallomys* and *Grammomys* have been mentioned above. He also points out that the genus *Grammomys* can hardly be distinguished from *A. namaquensis* on the structure of the M₁. The identifications of these specimens is thus tentative.

Aethomys is also very close to the genera *Rattus* and *Arvicanthis*, i.e. it is a typical borderline genus. The latter two forms are, in turn, extremely complex groups.

The genus *Rattus* embraces a multitude of species, extremely difficult to separate. *Rattus* as such has not been identified from the breccias, and this is in line with the belief that it was introduced to this

part of the African continent recently. The genera *Myomys*, *Mastomys* and *Ochromys* are re-sorted under the genus *Rattus* as subgenera according to Ellerman (1941). In Roberts (1951), they each have generic status. The writer has found it impossible to separate these genera on their M^1 structure alone. They all have three-rooted first upper molars, they are all provided with a T.1 deflected (to a greater or lesser extent) in a posterior direction, and all three genera have eight cusps to the tooth. The T.7 is usually absent in all cases. Lundholm (1955) has, however, noted some slight differences in the lower tooth rows: e.g. *Ochromys* has no additional cusps on the M_1 or M_2 while the M_3 is rather reduced. For further details, the reader is referred to his article. It will be noticed that Lundholm accepts *Ochromys* as a definite, well-defined genus.

All the *Rattus*-like material recovered has provisionally been referred to the genus *Mastomys* cf. *natalensis*. There seems to be little difference in size between the recent and fossil material. The T.1 on the M^1 is displaced posteriorly next to the T.2 and T.3, while the M^1 is three-rooted. This little multimammate mouse has been recorded from Taung, Sterkfontein and the Limeworks site at Makapansgat. The genus also occurs in the Makapansgat vicinity today: therefore, its absence from the Cave of Hearths is unexpected. Subsequent analysis of material from the latter locality should certainly reveal this form.

The small mice, *Mus* and *Leggada* have characteristic occlusal molar surfaces and these forms are consequently easily identified. The genus *Leggada* is not accepted by Ellerman (op. cit.). However, in following Simpson's (1945) classification, all the specimens identified here have been referred to *Leggada* cf. *minutoides*. The fossil forms do not differ to a great extent from the recent material and the sudden increase of individuals at the Cave of Hearths (Table IV), is noteworthy. A new form, *L. major* Broom was named by Broom from Bolt's Farm, but has not yet been described. All the fossil specimens may be referred to this species on subsequent investigation, but for the time being, this material has been kept apart for the author has seen no features to justify the establishment of a new species.

Acomys has also been identified tentatively from the Rodent Cave and the Cave of Hearths. ?*Zelotomys*, a form provisionally reported from 'Makapan' by Lavocat (1957) has not been met during this analysis. Unfortunately, recent comparative material of this genus was not available for comparison.

The genus *Saccostomus* has been found in the Cave of Hearths breccia. This animal has not yet been recorded from any other fossiliferous breccia and this is the first note of its occurrence in the fossil state in South Africa. Morphologically speaking, there is not much difference in structure to be seen on the occlusal surface of the M^1 as compared with recent material. The fossil tooth, however, is slightly larger, as in the width of the interorbital constriction. The specimens recorded were seemingly adults, judging by the amount of tooth wear.

- (d) The Dendromurinae are also well represented in these deposits. They form a well defined group, but they have to be re-investigated taxonomically. A new species, *Dendromus antiquus* Broom, was identified by Broom from Taung. This new form was not described, but mentioned in one of Broom's publications (Broom & Schepers, 1946). The material recorded here has been found to be exceedingly close to the recent *D. mesomelas*. The material recorded here has been found in all the localities except Taung, strange to say. Meantime, the writer has retained Broom's new fossil species as genuine for Taung.

A *Malacothrix*, not very different from the recent *M. typica* has been recovered from the Taung breccia while a possible new form, ?*M. makapani* has been proposed in this work. The latter has only been found in the material from the Limeworks Dumps. The identification of this little animal, typical for South Africa, at Taung also demonstrates that it is a very old established genotype.

Finally, the genus *Steatomys* from the Rodent Cave and the Cave of Hearths could not be differentiated from the recent *S. pratensis*.

Hence, in broad outlines, the Dendromurinae also exhibit the same evolutionary stage as the recent members of this subfamily.

- (e) The subfamily Otomyinae or vlei rats are very well represented in the various localities. Together with *Mystromys hausleitneri* Broom, *Palaeotomys gracilis* Broom is the dominant species at all localities. This form is also the dominant genus at the Cave of Hearths, while the former species (*M. hausleitneri*) is apparently well on its way out at this locality.

Palaeotomys was apparently an extremely stable genotype ranging over a great span of time. It is probable that it became extinct within the Later Stone Age. A vertical grid system employed at the Cave of Hearths may show when this species actually terminated its existence. The recent *Otomys irroratus* is extremely abundant in the Makapansgat valley today and forms a considerable proportion of the prey of the recent barn owl.

In the breccias "... There appears to be only one species of fossil vlei-rat (*Palaeotomys*), which is a small form, whose nearest relative today in size seems to be *Otomys saundersiae* in the Cape coastal area; it also resembles, especially in its teeth, the Ice Rat of the Basutoland mountains, *Otomys sloggetti robertsi*" (Davis, 1959).

Prototomys campbelli Broom, the fossil form reported by Broom from Taung, has not been located during this work from the type locality nor from any other deposit.

- (ii) *The Hystricomorpha*. The Hystricomorpha are rather scantily represented in these deposits. These animals do not normally fall prey to owls for they are usually beyond the size with which an owl can cope. Reference to Table III shows clearly that the hystricomorphs are reasonably well known only from the Dumps, with isolated finds from Taung. The small form *Petromys minor* Broom (1939) and the springhare, *Pedetes gracile* Broom, both from the latter mentioned locality, have not been found. The latter forms may also have been part of the diet of *Australopithecus*.

No porcupine remains have been recovered from the Sterkfontein deposit during the course of this work although Broom et. al. (1946) isolated a number of teeth "... (differing) little from those of the living South African species, and probably belongs to *Hystrix cristata*".

Finally, members of the Bathyergidae occur in these deposits. The archaic form, *Gypsothyrus* and the three species (*darti*, *minor* and *makapani* — all named by Broom 1934, 1948a, the former two from Taung and the latter from Makapansgat), have not been recorded in the material used for this work.

Cryptomys robertsi Broom has an interesting distribution pattern. Unfortunately, not much of the upper dental complement is known, but a form comparing very well with *C. robertsi* has been isolated in all the deposits. However, the material is rather scantily represented.

It may be that some of the material listed under that name here represents the genus *Heterocephalus*. Unfortunately, no recent comparative material of this queer East African form was available during the preparation of this work. The latter genus is also reported (as a very rare form) by Lavocat from Makapansgat (1957).

2. Specific densities of the Pleistocene microfauna

The relative frequencies of the species recovered in the various localities, presented in Chapter IV, are significant.

The desirability of reporting palaeontological data not as static phenomena but as dynamic populations should need no emphasis, but this aspect is often neglected. Each fossil specimen is an end result of evolution at the time the organism died but, as fossils represent only a very small fraction of the once-living organisms, a relatively minor part of the totality of living organisms can be known as a result of objective palaeontological examination. Still, that small fraction must be gleaned.

The only opportunity we have of assessing populations of the various localities is by reckoning the minimum number of individuals recovered from each locality for each species. This has been calculated. Naturally, the values obtained for the various densities are tentative because of the relatively small sample recovered as compared with the material available, but at present still *in situ* at each spot. It is obvious that these figures are not absolute. However, they give an indication — if only from an owl's eyes' view — of the relative densities of the various species.

To calculate the minimal numbers of animals the left and right maxillary and mandibular elements were counted, and the minimum numbers of individuals present were assessed. The number of molars present in the jaws were counted and note was made of molars missing. The latter figure was subtracted from the isolated molars recovered. From the resulting difference of molars remaining or unaccounted for the minimum numbers of individuals represented by these molar teeth were added to the minimum value obtained from the maxillary and mandibular elements and their respective complements of teeth.

The incisors were not utilised for these calculations except in the case of the Otomyinae where isolated incisors were extremely abundant and could be subdivided roughly into upper and lower components.

The numerical values thus obtained were found not to be representative of the facts in a truly proportional way, because the various deposits under consideration were not all equally populous. Thus from Taung, a minimum total of only 22 individuals were recovered compared with 35 from Sterkfontein, 32 from the Limeworks Dumps, 77 from the Makapansgat Rodent Cave and 61 from the Cave of Hearths. Consequently, a grand total of 227 individuals is represented in this work. These figures were therefore expressed finally in percentages, which gives a better representation of the frequencies found.

The percentages obtained are given in Table IV. Only the species recorded in this work have been suitable for this purpose because, in most cases, little or no information of the number of individuals of the various genera and species reported by other palaeontologists is given.

If these percentages are reliable, the Insectivora as a whole form from 9.0 to 20.0% of owl diet, with an approximate average value of 14.5%. Except at Taung, the elephant shrews are fairly constant items accounting for roughly 3 — 5% of their sustenance, but the shrews fluctuate considerably. *C. cf. taungensis* (13.6%) was more popular than the larger *Crocidura* species (1.6%) found at the Cave of Hearths. The genus *Myosorex* has a very low incidence (2.8%) at Sterkfontein, but increases about threefold to 6.2% at the Dumps and 7.8% at the Rodent Cave, in Makapansgat valley. The opposite is seen in *Suncus*: a high frequency of 8.5% at Sterkfontein and a low one 3.1% and even 2.6% at the Makapansgat sites. The absence of both these genera from the Cave of Hearths was commented upon earlier.

The Chiroptera do not reveal any significant difference in frequency at the Cave of Hearths and the Rodent Cave, contributing about 5% to the owl diet. These animals are bound to be reported from the other places in the future, for they are fundamentally cave dwellers.

The Rodentia naturally form the greater proportion of all the specimens recovered. The Cricetinae (with the form *Mystromys hausleitneri* Broom) clearly indicates a steady decrease in the more recent deposits. Whether this is an example of extinction or of evolution into another type, cannot be stated: the other type being the recent *M. albicaudatus*. The occurrence of *M. antiquus* Broom has a 9.0% concentration at Taung. *M. darti* Lavocat, the small form from Makapansgat, has a very low frequency (1.3%).

Table IV
Species density in Percentage per Locality

Classification	Ta	St	MpD	MpR	MpC
Insectivora					
Macroscelididae					
<i>Elephantulus langi</i>		2.8	3.1	3.9	5.0
? <i>Mylomygale spiersi</i>		2.8			
Soricidae					
<i>Crocidura</i> sp.					1.6
<i>C. cf. taungensis</i>					13.6
<i>C. taungensis</i>	9.0				
<i>Myosorex robinsoni</i>		2.8	6.2	7.8	
<i>Suncus</i> sp.		8.5	3.1	2.6	
TOTAL	9.0	16.9	12.4	14.3	20.2

* Locality abbreviations as per table III.

Classification	Ta	St	MpD	MpR	MpC
Chroptera					
<i>Rhinolophus</i> cf. <i>capensis</i>				5.2	
<i>R.</i> cf. <i>geoffroyi</i>					3.2
<i>Miniopterus</i> cf. <i>schreibersii</i>					1.6
TOTAL				5.2	4.8
Rodentia					
Myomorpha					
Cricetidae					
Cricetinae					
<i>Mystromys</i> <i>hausleitneri</i>		26.7	9.3	10.4	1.7
<i>M. antiquus</i>	9.0				
<i>M. darti</i>				1.3	
TOTAL	9.0	26.7	9.3	11.7	1.7
Gerbilli ⁿ ae					
<i>Tatera</i> sp.				1.3	
<i>T.</i> cf. <i>brantsi</i>	9.0	5.6			1.6
TOTAL	9.0	5.6		1.3	1.6
Muridae					
Murinae					
<i>Thallomys</i> cf. <i>paedulus</i>					3.2
<i>Grammomys</i> cf. <i>dolichurus</i>			9.3	3.9	
<i>Dasymys</i> cf. <i>incomtus</i>		2.8			
<i>Pelomys</i> cf. <i>fallax</i>		2.8	3.1	1.3	
<i>Rhabdomys</i> cf. <i>pumilio</i>		2.8	3.1	2.6	
<i>Aethomys</i> cf. <i>namaquensis</i>		2.8	6.2		
<i>A.</i> cf. <i>chrysophilus</i>					3.2
<i>Mastomys</i> cf. <i>natalensis</i>	4.5	5.6	3.1	3.9	
<i>Leggada</i> cf. <i>minutoides</i>		2.8	3.1	1.3	9.6
<i>Acomys</i> sp.				1.3	3.2
<i>Saccostomus</i> <i>campestris</i>					3.2
TOTAL	4.5	19.6	27.9	14.3	22.4

Classification	Ta	St	MpD	MpR	MpC
Dendromurinae					
<i>Dendromus cf. mesomelas</i>		5.6	3.1	1.3	3.2
? <i>M. makapani</i>			3.1		
<i>Malacothrix typica</i>	4.5				
<i>Steatomys pratensis</i>				1.3	1.6
TOTAL	4.5	5.6	6.2	2.6	4.8
Otomyinae					
<i>Palaeotomys gracilis</i>	59.5	22.8	41.1	49.3	42.7
<i>Hystricomorpha inc. sed.</i>					
<i>Cryptomys robertsi</i>	4.5	2.8	3.1	1.3	1.6
TOTAL			100%		

The predominance of the fossil *Mystromys* in breccias from Kromdraai B (0—6) has been commented upon by Davis (1959): "The subfamily Cricetinae, now represented in southern Africa by one fairly widely distributed but rather uncommon species, *M. albicaudatus*, greatly outnumbers the subfamily Murinae, which are today the dominant group, with very many species."

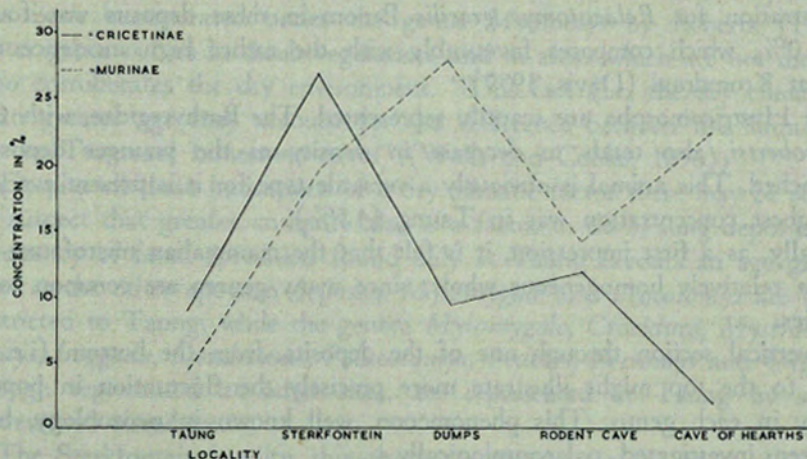
Graph I shows the relative frequencies (in percentages) of this cricetine form and the murids found in the deposits. It has been found that the Cricetinae are dominant at Taung (9.0%) and at Sterkfontein (26.7%) and this subscribes what Davis (op. cit.) has concluded at Kromdraai. However, there is a sudden drop in the concentration of cricetids at the Limeworks Localities in the Makapansgat valley with a minimum value attained (1.7%) in the Cave of Hearths. The murids, on the other hand, increase their numbers at the Dumps (27.9%) and although there is a decline in their occurrence at the Rodent Cave (14.3%), their density at the latter locality is still higher than the concentration of the cricetids (11.7%). It is also evident that an increase (22.4%) in the murids is manifest at the Cave of Hearths.

In Graph II the two Makapansgat Limeworks localities were treated as one, for they are geographically equivalent. The average concentrations for the two subfamilies in these two deposits were used. This graph clearly indicates a strong divergence in the importance of the murines and cricetines and tends to imply that the murids assumed the dominant role of rodents in Southern Africa, after the Sterkfontein breccias had been laid down, at the expense of the cricetids.

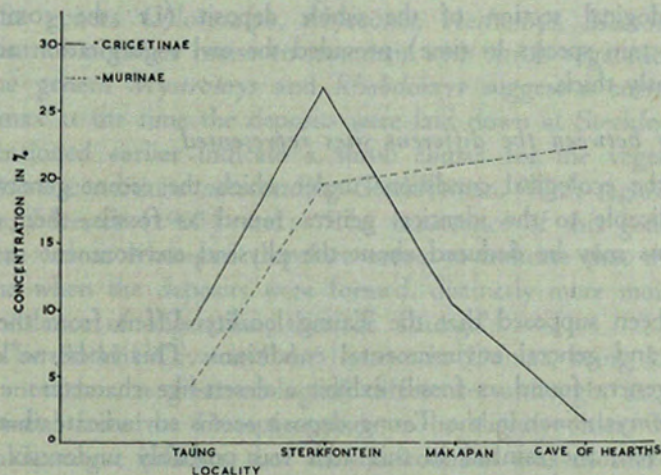
The Gerbillinae also reveal a gradual decrease in numbers like the white-tailed rats, mentioned above.

The Murinae are represented by a tolerably constant figure, usually below 5.0%, but the sudden increase of *Grammomys* cf. *dolichurus* (9.3%) at the Dumps and of *Leggada* cf. *minutoides* at the Cave of Hearths (9.6%) is unexplained. Of the 14 genera listed by Roberts (1951), occurring in South Africa, as subfamily Murinae, 9 have been recovered as fossils in this work,

GRAPH I



GRAPH II



while two more (*Mus* and ?*Lemniscomys*) are reported elsewhere (Lavocat, 1957).

As is the case in the Macroscelididae, the Dendromurinae occur constantly with the highest incidence of *Dendromys* cf. *mesomelas* recorded in Sterkfontein

(5.6%). The genus *Steatomys* is however not as frequent as the genera *Dendromus* and *Malacothrix*.

The vlei-rats (Otomyinae) apparently form the staple diet of the Pleistocene 'Barn'-owl and it may consequently be assumed that this form was one of the dominant genera alive during the deposition of the various deposits. The highest concentration has been found at Taung (nearly 60.0%) while the lowest density (22.8%) has been recorded from Sterkfontein. The average concentration for *Palaeotomys gracilis* Broom in these deposits was found to be 43.0%, which compares favourably with the rather high incidence of this form at Kromdraai (Davis, 1959).

The Hystricomorpha are scantily represented. The Bathyergidae, with *Cryptomys robertsi*, also tends to decrease in density as the younger deposits are approached. This animal is obviously a versatile type for it is present everywhere. Its highest concentration was in Taung (4.5%).

Finally, as a first impression, it is felt that the mammalian microfauna constitutes a relatively homogeneous whole, since many genera are common to many localities.

A vertical section through one of the deposits, from the bottom (i.e. oldest soils) to the top might illustrate more precisely the fluctuation in population density in each genus. This phenomenon, well known in neozoology, has not yet been investigated palaeontologically.

From the author's analysis, one can only deduce the relative density of a population of a given species, at the time the deposit was formed. The density of a genus or species in the whole deposit might be found by systematic analysis of a vertical geological section of the whole deposit (i.e. the community succession for a certain species in time) provided the owl regurgitation accumulation was sufficiently thick.

3. Climatic variations between the different sites represented

Assuming that the ecological conditions under which the recent genera seem to thrive are applicable to the identical genera found as fossils, then certain tentative conclusions may be deduced about the physical environment in which the fossils lived.

It has hitherto been supposed that the Taung locality differs from the other deposits in fauna and general environmental conditions. This is borne out by the fact that the genera found as fossils exhibit a desert-like character: e.g. the occurrence of *Petromys minor* in the Taung deposit seems to indicate that when *Australopithecus* lived, the rainfall in this area was probably under six inches a year (Broom et. al., 1946). The occurrence of *Pedetes gracile*, another dry-area type, also points to this possibility. Meester (1955) has commented on the fact that *Crocidura taungensis* is probably also a dry-area form, and that "... at the time the shrew-bearing deposits were formed (Taung) must have been an arid region". The occurrence of *Thallomys debuyini* also points to an arid biotope.

"*Thallomys* is what we may call a desert rat. In South Africa there are 16 species and subspecies, and of these, 10 are desert forms, and one species lives in the same conditions as *Petromys*" (Broom et al., op. cit.). *Malacothrix* cf. *typica* reported in this work also points to a dry environment and the same applies to the genus *Tatera* also reported here for the first time: these animals are mainly desert types. The most common genus found at Taung is the vlei-rat *Palaeotomys gracilis* (59.5% of the owl diet — see Table IV): this genus has been incorporated under the genus *Myotomys* by Roberts (1951). The latter genus occurs in shrub vegetation, and in areas which are not moist, so this also corroborates the dry environment. "This fact (i.e. the dry climate), rather than greater age may account for the difference between this fauna and that of the Transvaal Limestone caves" (Wells and Cooke, 1956).

Despite all these indications of a dry climatic factor there may be some reason to suspect that greater antiquity also is a factor in the Taung deposit. The high frequency of fossil specimens found only at Taung favours an age greater than that at the other ape-man deposits. *Mylomygale* and *Prototomys* are two genera restricted to Taung, while the genera *Mylomygale*, *Crociodura*, *Mystromys*, *Thallomys*, *Leggada*, *Dendromus*, *Palaeotomys*, *Pedetes*, *Petromys* and *Gypsorhynchus*, though represented at other sites, are represented at Taung by species not represented elsewhere.

The Sterkfontein locality, though apparently not too far removed from Taung in time, was more humid as can be seen from the mammalian microfauna. Some genera, like *Elephantulus* or *Tatera* do occur in arid regions, but it must be remembered that the latter genus occurs in savannah areas or even in forests. The genera *Chlorotalpa*, *Myosorex*, *Aethomys*, *Mastomys* and *Dasymys* all point to a rather moist environment with shrub vegetation and forested kloofs. The genera *Mystromys* and *Rhabdomys* suggest a surrounding grassveld subclimax at the time the deposits were laid down at Sterkfontein, while the genera mentioned earlier indicate a shrub climax for the vegetation — akin to the present conditions surrounding Sterkfontein. With regard to *Myosorex* at this site, Meester (1955) said: "The occurrence of this genus in the Sterkfontein area and at Makapan therefore seems to indicate that these areas were, at the time when the deposits were formed, distinctly more moist, and with a greater abundance of vegetation, than at Taung."

The Rodent Cave and the Limeworks Dumps, being identical geographically, do not show a great ecological difference, although, as will be seen later, the material from the Dumps appears to be slightly older. The small mammals of Makapansgat indicate that the environment was moister than that of Taung, and that a fair amount of vegetation was present then, as now. The genera present which are known to occur in, or to favour moist areas, especially with short vegetation and shrub are *Elephantulus*, *Myosorex*, *Mystromys*, *Grammomys*, *Palaeotomys*, *Dasymys*, *Dendromus* and possibly *Steatomys*. A few predominantly dry-area forms nevertheless occur at Makapansgat such as *Thallomys* and

Malacothrix. So it is possible that the ecological conditions between the Sterkfontein locality and the Makapansgat deposits were rather different: this possibility of ecological non-equivalence was commented upon by Ewer as a result of her study of the Carnivora (1956). The difference between these two sites may be illustrated by the presence at Makapansgat of the moisture-loving, littoral golden mole *Chrysotricha*, with a separate species of *Gypsorhynchus*, and the greater variety of porcupines at this site, all hitherto unrecorded from the Sterkfontein site. But the presence of *Malacothrix* shows that however moist the valley may have been, the surrounding territory must have been dry.

The general character of the faunas in Sterkfontein and Makapan are however not grossly different: they merely differ in detail.

The differences between the Cave of Hearths and the other older deposits offer no clear evidence of a change in climate during the Stone Ages, for these deposits are hardly equivalent. The genus *Crocidura* found here occurs in "any kind of habitat" and is consequently not indicative of any particular type of climate. The occurrence of *Mystromys* may indicate a more extensive development of grassveld as compared with today and may suggest that the area has reached its climax vegetation as at present. The increase in *Leggada* cf. *minutoides* may point to a warm sub-tropical environment; but far more work would need to be done upon numerous samples from various sites in the Makapansgat valley before it would be possible to draw valid conclusions about local changes of climate from microfaunal data.

4. Time differences between the deposits

An attempt has also been made to discover whether the interrelationships of these localities could be deduced from the mammalian microfauna. The percentages of extant and extinct genera and species have been calculated and compared in Table V. As in Table IV, the numerical values obtained were re-calculated as percentages for Table V, which gives perhaps a truer representation of the facts, because the grand totals of individuals and consequently genera and species varied considerably in the different deposits.

An attempt has been made to subject the Kromdraai and Bolt's Farm

Table V
Extant and Extinct Genera and Species in the Deposits

Locality*	Genera		Species	
	Extant %	Extinct %	Extant %	Extinct %
Ta.	71.4	28.6	20.0	80.0
St.	88.9	11.1	56.3	43.7
MpD.	84.2	15.8	47.3	52.7
MpR.	94.7	5.3	57.2	42.8
MpC.	93.4	6.6	64.3	35.7

* For locality abbreviations see Table III.

localities to similar treatment and to incorporate them in Table V. However, it was found that the percentages obtained were not significant at all, due to the relatively small number of forms known from these sites.

From Table V it would appear that the Taung deposit contains a higher ratio of extinct to living genera and a similar ratio in respect of extinct and living species. This is suggestive of a greater antiquity for the Taung deposit.

The difference in numbers of genera whether extant or extinct between Sterkfontein and the Limeworks Dumps (88.9% 11.1% and 84.2%, 15.8%) is not very appreciable, but it appears that the Rodent Cave (94.7%, 5.3%) is somewhat younger than the other two. This difference is also borne out by the figures in the species column. It is also clear that the Sterkfontein and Dumps localities are closer to Taung (71.4%, 28.6%) than the remaining two.

This comparison displays a considerable difference between the two deposits from the Limeworks: the Dumps and the Rodent Cave. This is shown in both the genus and species column. In both cases the Dumps material is obviously closer to Sterkfontein (extant genera 84.2% and 88.9% respectively) than to the Rodent Cave material (extant genera 94.7%). This fact lends support to the writer's contention mentioned earlier on in this work that the material from the Dumps (part of it in any case) came from another deposit inside the Limeworks, now totally destroyed or hitherto undiscovered. The Rodent Cave is thought to have been situated near the original entrance(s) of the cave. The Dumps material must have come from a deposit in the original cave which had been made uninhabitable for the roosting owl far earlier than the Rodent Cave roost. The extensive development of the Upper Phase I breccias on top of the material *in situ* at the Rodent Cave also indicates the relative recency of that deposit. Furthermore, the excessive contamination by skeletal remains not originally from small mammals in the Dumps material may be ascribed to the activities of the ape-men.

It is clear from Table V that the ratios of extinct to living genera and species is closely similar in the Rodent Cave and the Cave of Hearths. There is a marked difference between the ratios for these two sites and those for material from the Limeworks Dumps. It is inferred that the Rodent Cave approximated closely to the Cave of Hearths in time and that both are younger than the bulk of the material found at the dumps.

From a study of the mammalian microfauna certain tentative conclusions may be reached concerning the age relationships of the various deposits. Taung is in many respects isolated but is considered to be the oldest deposit. The Cave of Hearths is clearly the youngest and the Rodent Cave is close to it in age. Both are younger than the Dumps from the Makapan limeworks. The Sterkfontein deposit is more or less comparable in age to the Makapan Dumps.

At these five localities there occur a combined total of 36 genera. Table VI presents an analysis to show the number of genera present at one deposit and

the proportion of this number occurring at each of the other deposits. The left-hand column shows the deposit which is being compared and the number of genera it contains (out of a possible combined maximum of 36). The actual numbers of these genera present at each site is shown under the appropriate heading followed by the percentage (in brackets) e.g. of the 14 genera at Taung, seven occur at Sterkfontein and six at the Makapansgat Rodent Cave. The vertical columns cannot be read downward.

Table VI

Genera Common to the Different Localities

Locality*	Ta	St	MpD	MpR	MpC
Ta (14)	—	7 (50%)	7 (50%)	6 (45%)	7 (50%)
St (18)	7 (39%)	—	14 (78%)	11 (61%)	7 (39%)
MpD (19)	7 (37%)	14 (74%)	—	12 (63%)	6 (31%)
MpR (19)	6 (31%)	11 (52%)	12 (63%)	—	10 (53%)
MpC (15)	7 (47%)	7 (47%)	6 (40%)	10 (67%)	—

* Locality abbreviations as per Table III.

Table VIII presents an analysis of species on the same basis as that for genera in Table VI. The combined total of species for the sites is 41.

Table VII

Species Common to the Different Localities

Locality*	Ta	St	MpD	MpR	MpC
Ta (15)	—	5 (33%)	3 (20%)	3 (20%)	4 (27%)
St (16)	5 (31%)	—	11 (69%)	11 (69%)	7 (44%)
MpD (19)	3 (16%)	11 (57%)	—	11 (57%)	6 (32%)
MpR (14)	3 (21%)	11 (78%)	11 (78%)	—	7 (50%)
MpC (14)	4 (28%)	7 (50%)	6 (43%)	7 (50%)	—

* Locality abbreviations as per Table III.

From Tables VI and VII it is evident that the mammalian microfauna of Taung has relatively little in common with that of the other localities and this has been ascribed to a somewhat greater age and a more arid climate.

The Sterkfontein site shares nearly twice as many genera with the Dumps and the Rodent Cave as with the Cave of Hearths, which suggests a closer tie with the first two sites than with the last named. The Makapan Dumps show an affinity with Sterkfontein and the Rodent Cave and a more remote relationship to the Cave of Hearths. The Rodent Cave shares many genera with the Cave of Hearths but even more with the Dumps. This would seem to indicate that the Rodent Cave is closer in time to the Dumps than it is to the Cave of Hearths.

SUMMARY

1. This preliminary investigation deals with the fossil mammalian microfauna found in Pleistocene deposits in caves at Taung, Sterkfontein, and Makapansgat.

2. It needs to be stressed that this is a preliminary analysis and that the conclusions put forward are tentative and are not to be interpreted dogmatically.
3. This work represents a mere fraction of the colossal field which still awaits detailed research, both in the field and in the laboratory.
4. The overall taxonomy of, especially, the Rodentia is in a very fluid state and intensive research into the existing nomenclature, taxonomy and systematics is absolutely imperative in due course.
5. The faunal contents of the breccias derived from localities other than the deposits considered in this work are still virtually unknown. This gap in our knowledge seriously hampers the interpretation of the overall faunistic make-up of the fossil small mammals.
6. The Rodentia appear to have been exceptionally stable during the Pleistocene and many of the recent forms are not distinguishable from the fossil counterparts. This implies that a number of genera (such as *Tatera*) are extremely stable genotypes. It also denotes that the Rodentia are a stable and well adapted group (a high percentage of recent forms are not different from the fossils) compared with some other rapidly changing groups (like the Primates) where all the species, and a large number of genera, are extinct.
7. The fossil small mammals suggest a relatively homogeneous faunal assemblage. It was found that in many instances genera and species are common to a number of geographically widely separated sites.
8. It is also evident that some animals are found over a long range of time. In the Insectivora the species *Elephantulus langi* is an archaic form, while the Rodentia, *Mystromys hausleitneri*, *Palaeotomys gracilis* and *Cryptomys robertsi* are long-lived species.
9. In the five deposits analysed above, *Palaeotomys gracilis*, representing the Otomyinae, is the dominant animal found in these breccias (approximately an average of 42%), followed by the Murinae with 10 species (approximately 18%), then the Insectivora, with five genera (approximately 14%) and fourthly the Cricetinae with one genus, *Mystromys* (about an average of 10%). The other subfamilies, such as the Dendromurinae, Gerbillinae etc. are mostly below 5% and are of lesser importance.
10. It has also been demonstrated that the Cricetinae was the dominant subfamily, compared with the Murinae, at the time the Taung and Sterkfontein deposits were formed, and that the Murinae assumed their present dominant position after the deposition of the Sterkfontein breccias.
11. Concerning the faunistic composition and environmental conditions at the time the deposits were laid down, it is clear that:
 - (i) The Taung locality is definitely isolated faunistically and that it had a semi-arid environment. This corroborates conclusions derived from other sources.
 - (ii) The Sterkfontein deposit is not greatly different from Taung, but the area at that time appears to have been less arid.

- (iii) There is evidence of an ecological non-equivalence between Sterkfontein and the Makapansgat localities.
- 12. Excluding the Cave of Hearths, no conclusions can yet be postulated on the absolute age of the deposits based on this work, but a number of facts point to a possible interpretation of their relative ages.
 - (i) It appears that, apart from being ecologically different, Taung is also the oldest.
 - (ii) Sterkfontein follows closely after Taung, but it is not too widely separated in time from Makapansgat Limeworks either. Evidence points to the possibility that Sterkfontein is slightly older than Makapansgat.
 - (iii) It also appears that there was more than one breccia deposit bearing small mammals at Makapansgat Limeworks: one being the extant Rodent Cave, while others, antedating the Rodent Cave by a slight margin, has been excavated by limeworkers (Dumps).
 - (iv) The Cave of Hearths microfaunal horizon is considerably younger and is the only deposit properly dated as Earlier Fauresmith, or approximately 25 — 50,000 years.

ACKNOWLEDGEMENTS

I am indebted to the following persons:

Professor Raymond A. Dart, Emeritus Professor of Anatomy of the University of the Witwatersrand, for allowing me, while employed as his C.S.I.R. research assistant, to spend the time at the Bernard Price Institute for Palaeontological Research necessary to complete this work and also for his valuable advice and critical reading of the manuscript.

Dr. A. S. Brink, Scientific Officer at the Bernard Price Institute, for his valuable assistance in all the stages of preparation and keen interest he has taken in the progress of this work.

Mr. J. W. Kitching, Senior Technician at the Bernard Price Institute, for his help in preparing the specimens.

Dr. H. B. S. Cooke, Reader in Stratigraphic Geology, University of the Witwatersrand, who also read the manuscript and suggested many important improvements.

Professor B. I. Balinsky, Head of the Zoology Department, University of the Witwatersrand, who allowed this work to be concluded under the auspices of his department.

Dr. J. T. Robinson, Physical Anthropologist at the Transvaal Museum, Pretoria, for allowing me access to the fossil type material in his department.

Mr. D. H. S. Davis, Government Ecologist, Union Department of Health for his criticisms and useful help in identifying the closely related murid genera.

Finally, Dr. J. A. J. Meester, Mammalogist at the Transvaal Museum, Pretoria, for arranging the loan of fresh material under his care and also for his careful identifications of the shrews and assistance in identifying the bats.

REFERENCES

- BARBOUR, G. B. 1949. Makapansgat. *Scient. Monthly* 69, p. 141.
- BOSAZZA, V. L., ADIE, R. J. & BRENNER, S. 1946. Man and the Great Kalahari Desert, *J. Natal Univ. Coll. Scient. Soc.* 5:1—9.
- BRAIN, C. K. 1958. The Transvaal Ape-Man-Bearing Cave Deposits. *Tvl. Mus. Mem.* No. 11.
- BROOM, R. 1934. On the Fossil remains associated with *Australopithecus africanus*. *S. Afr. J. Sci.* 31:471.
- BROOM, R. 1937. On some new Pleistocene mammals from the Limestone caves of the Transvaal. *S. Afr. J. Sci.* 33:750.
- BROOM, R. 1937. Notices of a few more fossil mammals from the caves of the Transvaal. *Ann. Mag. nat. Hist.* London (10) 20:509.
- BROOM, R. 1939. The fossil rodents at the limestone caves at Taungs. *Ann. Tvl. Mus.* 19:315.
- BROOM, R. 1948. Some South African Pliocene and Pleistocene mammals. *Ann. Tvl. Mus.* 21:1.
- BROOM, R. 1948 a. The giant rodent mole *Gypsochrychus*. *Ann. Tvl. Mus.* 21:47.
- BROOM, R. & SCHEPERS, G. W. H. 1946. The South African Fossil Ape-Men. The Australopithecinae. *Tvl. Mus. Mem.* No. 2.
- CHITTY, D. 1935. A Laboratory Study of Pellet Formation in the Short-eared Owl (*Asio flammeus*). *Proc. zool. Soc.* 108A.
- COOKE, H. B. S. 1938. The Sterkfontein bone-breccia: a geological note. *S. Afr. J. Sci.* 35, p. 204.
- COOKE, H. B. S. 1952. Quaternary Events in South Africa. *Proc. First Pan-Afr. Congr. on Prehist.* 1947 Oxford: Blackwell: 96—106.
- DART, R. A. 1952. Faunal and climatic fluctuations in the Makapansgat valley: their relation to the geological age and promethean status of *Australopithecus*. *Proc. First Pan-Afr. Congr. on Prehist.* 1947. Oxford: Blackwell: 96—106.
- DAVIS, D. H. S. 1958. Notes on some small mammals in the Kalahari Gemsbok Park with special reference to those preyed upon by barn owls. Koedoe, *Tydskr. Wetensk. Nav. Nas. Parke.* No. 1.
- DAVIS, D. H. S. 1959. The Barn Owl's Contribution to ecology and palaeoecology. *Proc. First Pan-Afr. Ornith. Congr.* 1959 *The Ostrich, Supplement* Nr. 3.
- DE GRAAFF, G. 1957. A new Chrysochlorid from Makapansgat. *Palaeont. Afric.* 5, p. 21.
- ELLERMAN, J. R. 1941. The families and genera of living rodents. *British Mus. (Nat. Hist.)* London, Vols. 1 & 2.
- ELLERMAN, J. R., MORRISON-SCOTT, T. C. S., HAYMAN, R. W. 1953.

- Southern African Mammals. 1758—1951: A reclassification. British Museum Publication.
- EWER, R. F. 1956. The fossil carnivores of the Transvaal caves: two new Viverrids, together with some general considerations. *Proc. zool. Soc.* 126, p. 839.
- HAUGHTON, S. H. 1947. Notes on the Australopithecine-bearing rocks of the Union of South Africa. *Trans. geol. Soc. S. Afr.* 50, p. 55.
- KING, L. C. 1951. The geology of the Makapan and other caves. *Trans. roy. Soc. S. Afr.* 33, p. 121.
- KOLBE, F. F. 1946. A Case for the Barn Owl. *Afr. Wild Life*, Oct. 1946, Vol. I, No. 1, p. 6.
- LAVOCAT, R. 1956. La faune de rongeurs des grottes à australopithèques. *Palaeont. Afric.* 4, p. 69.
- LAVOCAT, R. 1957. Sur l'âge des faunes de rongeurs des grottes à australopithèques. In *Third Pan-Afr. Congr. on Prehist.* Livingstone, 1955.
- LUNDHOLM, B. G. 1955. Remarks on some South African Murinae. *Ann. Tvl. Mus.* 22, p. 321.
- MEESTER, J. 1955. Fossil shrews of South Africa. *Ann. Tvl. Mus.* 22, p. 271.
- MILLER, G. S. 1912. Catalogue of the mammals of western Europe in the British Museum, London. British Museum (Nat. Hist.) publication.
- MILTON-SMITH, G. 1938. A simplified guide to statistics. Rhinehart & Co. Inc. New York.
- PEABODY, F. E. 1954. Travertines and Cave deposits of the Kaap Escarpment of South Africa and the type locality of *Australopithecus africanus* Dart. *Bull. geol. Soc. Am.* 65, p. 671.
- ROBERTS, A. 1951. The Mammals of South Africa. C.N.A., Johannesburg.
- ROBINSON, J. T. 1952. The *Australopithecus*-bearing deposits of the Sterkfontein area. *Ann. Tvl. Mus.* 22, p. 1.
- SIMPSON, G. G. 1945. The Principles of Classification and a Classification of mammals. *Bull. Am. Mus. Nat. Hist.* Vol. 85.
- VAN RIET LOWE, C. 1945. A geo-archaeological note on Taung, Kromdraai and Sterkfontein. *Bull. S. Afr. Mus. Assoc.* 3, p. 309.
- WELLS, L. H. & COOKE, H. B. S. 1956. Fossil Bovidae from the Limeworks Quarry, Makapansgat, Potgietersrust. *Palaeont. Afric.* 4, p. 1.

ERRATUM

Subsequent to the printing of this volume the South African Council for Scientific and Industrial Research has made a substantial contribution towards the cost of publication of the paper by Mr. G. de Graaff. This grant is gratefully acknowledged.

A NEW TYPE OF PRIMITIVE CYNODONT

By A. S. BRINK

ABSTRACT

A very interesting ancestral type of Cynodont is described in reasonable detail from serial sections, graphical figures, and a complete wax model, four times natural size. The form is recognised as a new genus and species, for which the name *Scalopocynodon gracilis* is proposed. It is the earliest true Cynodont, from the base of the lower *Cistecephalus*-zone. Although its nearest allies are the somewhat later Silphedestids and Procynosuchids, it has unmistakably very close affinity with the base of the Ictidosuchid-Sceloposaurid branch of the Therocephalians. Thus new light is cast on the origin of the Cynodonts and their general relationship with the Therocephalia. The specimen was thought to be a *Scaloposaurus* before it was decided to subject it to serial grinding.

INTRODUCTION

When it was decided to subject the present specimen to serial grinding it had been identified, in its unclean state, as a Therocephalian assignable to a species of *Scaloposaurus*. The intention was to incorporate a description of this specimen's detailed structure into the following paper (page 155 of this issue of *Palaeontologia Africana*) dealing with some Scaloposaurids and related Therocephalians. However, soon after the process of grinding had commenced, on entering the anterior palatal region, it was discovered that the specimen represents a primitive Cynodont on account of its cleft secondary palate. More posteriorly the cheek teeth showed clearly that they are cusped.

At the level of the pterygoid processes sectioning was temporarily stopped, to reconsider the implications of this misinterpretation. It was clear that a description of this specimen would not fit in with the Therocephalians described in the following paper and that it should be dealt with in a separate publication. It was also considered that the specimen might prove to be the type of a new species of Procynosuchid and careful thought was given to the implications of destroying a type. At this stage it was decided to reconstruct in wax the anterior half of the skull, as far as it was then sectioned. The resultant model, although exhibiting some peculiar features, suggested that the specimen very likely represented a juvenile stage of an existing species of *Leavachia*, *Procynosuchus* or *Galecranium*, and it was decided to proceed with the sectioning.

Immediately on resuming the sectioning certain peculiarities presented themselves as renewed cause for alarm. A distinct Therocephalian-like interpterygoid fossa appeared in the sections. The postorbital bars appeared to have been incomplete. The dentaries terminated at the level where the postorbital bars should have been. Distinct Therocephalian-like reflected laminae of the angulars were encountered. It was then decided to reconstruct in wax, section by section as grinding proceeded, to ensure that wrong impressions would not ensue from misinterpretations of individual sections.

The final result was a rather successful wax model of a specimen which is unmistakably a Cynodont in its anterior half, but still quite Scaloposaurid-like in its posterior half. What the author feared actually happened: this wax model represents the type not of a new species but of a new genus of a Procynosuchid, or more likely a Silphedestid-like Cynodont.

TECHNIQUE

The technique employed in the preparation of the specimen for this paper is the same as that described for *Akidnognathus parvus* in the following paper (page 155 of this issue). Sectioning was at .5mm. intervals and reconstruction at 4 times natural size. It was discovered, unfortunately too late, that for a specimens of this size, .5mm. intervals were too great. Although results are perfectly satisfactory, it was considered that intervals of .25mm. would have produced better results, especially through the otic regions.

The only difference in the technical procedure followed was that colouring with Alizarine red proved to be unnecessary. Each section was left to dry in the sun for 15 minutes. The bone turned a clear white, while the matrix remained dark grey, giving as distinct a contrast as could be desired. This contrast was further exaggerated when a film of dilute glyptal was applied, to achieve a polish effect.

With this specimen a serious problem was solved. With previous specimens it was discovered that it is virtually impossible to section completely through the specimen up to the last trace of bone, especially when the most posteriorly situated bones (usually the occipital condyle bones) are exposed when the unclean specimen is embedded. Normally, well before the most posterior limit is reached, the specimen disintegrates, or becomes loosened from the embedding material. This difficulty was overcome as follows.

The specimen was made to stand with its long axis vertical, on its occipital condyles, on a pedestal of plasticene, about 1cm. high and of similar diameter, the latter standing centrally on the platform surface of the specimen holder of the grinding machine. A cylinder shaped from paper was placed tightly with an elastic band around the specimen holder and was made deep enough to cover the length of the specimen. Calistone was then poured into the container thus formed until it covered the tip of the snout of the specimen, the latter still standing free

from the cylinder sides on the plasticene pedestal. After the calistone had set, the paper cylinder was removed, the calistone "piston" loosened from the platform and the plasticene excavated. It was then left to dry properly.

The pit left by the plasticene was thoroughly cleaned with thinner solution and all traces of plasticene still adhering to the occipital region were removed. The pit was then filled with molten bees' wax at high temperature, allowing the wax to penetrate into the calistone and spread over the surface due to adhere to the specimen holder. After the wax in the pit had solidified the holder was heated and placed over this surface, allowing it to cool in its own time while pressure was applied to ensure that a firm fit was established.

A substantial column of bees' wax was thus extended from the specimen to the specimen holder and held the specimen in position until the last .50mm. of the condyle bone was sectioned.

It should be mentioned that the length of the plasticene pedestal was designed to allow for grinding to proceed to the ultimate limit (while using 1" ball bearings throughout) with still a positive reading on the micrometer screw at the last section. As it happened, the final section was reached with the micrometer reading at zero.

Another problem was, however, encountered where, on reaching the bee's wax in the section surface, the wax absorbed the carborundum paste very successfully and, being the softer medium, it formed effective "emery material" which was inclined to wear away the zinc plate instead of the latter wearing away the specimen. This difficulty was overcome by excavating the wax where exposed, with a dental scraper.

With the great success achieved in the wax model it is felt that the virtues of the particular brand of wax used should be emphasized. As mentioned in the previous paper, Dental Modelling Wax was used, a wax which is characterised by its extreme toughness and stability over wide temperature ranges.

This wax is purchased in plates of standard 1 mm. thickness. The plates are consistently and accurately 1mm. thick throughout, most unlike the "home-made" products achieved with the usual roller apparatus. In addition, it is sufficiently transparent to allow a tracing to be made directly on the wax with the wax plate placed over the section drawing.

The wax does not crumble or crack. It has a phenomenal elasticity. After cutting out the section information in the wax plate, the wax section can suffer considerable distortion and bending, but on superimposing it on the section drawing it can be returned to its proper shape.

Although it was necessary to use supports in the process of reconstruction, the final product is entirely free from such supports. Such supports that were used were lengths or plates cut from the wax. On completion of the model all supports could be removed and the product is so stable that it is virtually like handling a modern mammalian skull. The lower jaw could be made to articulate with the skull.

The procedure in building the wax model was as follows: Each section drawing obtained with the episcopo projector was traced directly on the wax, by placing the wax plate over the drawing and recording the information on the surface of the wax with a very sharp pencil. The pencil merely recorded delicate grooves which can clearly be seen, so that any sharp instrument can actually be used. A pencil was found to be more satisfactory, as it is inclined to pass more smoothly over the surface, without sinking into the wax, than a metal instrument is inclined to do.

The bone shapes were then cut out with a very finely pointed scalpel held vertically. The required wax elements representing the bones in the section were then made to adhere, correctly positioned, to the paper containing the section drawing. The wax is sufficiently sticky to adhere effectively to the paper while it is turned upside down and passed over the rods serving as a "base line" guide, until the new section comes to rest on the previous section already in position on the incomplete model. A glass plate was then pressed down over the paper to ensure that the newly introduced section will stick evenly and parallel and more effectively to the previous wax than to the paper, which it invariably did. The paper was then lifted away, the new wax section being in its correct position. To effect a more stable union, a hot probe was pressed through the uppermost two or three layers in as many places as possible, where surfaces were large enough.

With this method it was not necessary to cut whole sections as units. Each bone could be cut individually from small scrap pieces of wax and made to adhere to the paper in the correct positions. Thus a great measure of economy could be exercised with this rather expensive wax. However, expense should be no criterion when considering the time factor, the ease with which this method and material can be used, without continual re-melting and re-rolling of new wax plates.

Another advantage of this method is that it permits the representation of different bones in wax of various colours. The cutting of individual bones brings out sutural relations very clearly, even when using a single colour.

As in the case of *Akidnognathus parvus* no serious zig-zag problems were encountered. Bone surfaces were therefore smoothed over, both for added strength and to bring out sutural patterns more clearly.

At .5mm. intervals and projections at 4 times natural size, the wax thickness should theoretically have been 2mm., but in practice 1mm. plates were found to produce the best results. This is due to the fact that the wax increased in thickness around the margins as the required shapes were cut from it, and as each section was "welded" onto the model with the aid of a hot probe. At regular intervals check measurements were made with calipers to ascertain whether the thickness was increasing in the correct proportion. It was found that throughout the reconstruction every fifth section had to be represented by a double wax plate to ensure that the final total length of the model would also be, in proportion four times the natural length.

The specimen was purposely embedded at a slight angle to ensure that section planes would not be perfectly at right angles to the median plane. Thus information was encountered first on the one side and subsequently, some sections later, the same information was repeated on the opposite side. It often happens that a particular item of interest is missed due to bad preservation, the thickness of the interval, or because it was not expected to be showing at the particular level, and when grinding is continued the particular indistinct information is destroyed. When grinding perfectly at right angles to the median plane, the evidence is destroyed both sides simultaneously, but when grinding at an angle slightly off 90° , one can be on the alert to check on the opposite side for information missed. At the expected level grinding can be interrupted several times within the .5mm. interval to ascertain whether the required information might not present itself more clearly at an intermediate level.

Another useful method employed was to excavate consistently, before grinding each section, all the matrix well removed from the bone, with the aid of a dental emery wheel. The emery wheel was also passed lightly over the general surface to roughen it and to remove the film of glyptal. Grooves were also cut across the calistone surface radiating from the specimen outward to the circumference. These grooves, pits and general rough surfaces allowed for the better absorption and distribution of the carborundum paste. It reduced the actual surface and depth to be ground. It was found that, while the grooving and pitting took hardly a minute per section, a new level could be reached with a quarter the number of revolutions of the machine and consequently a quarter the time otherwise used. It also proved to be very economic as far as the consumption of carborundum powder is concerned. All restoration figures were obtained with the standard graphical method: the model was used only to assist in shading.

GENERAL DESCRIPTION AND DIAGNOSIS

The specimen is a complete skull with lower jaw in situ. In the model the lower jaw was made to articulate with the skull. Preservation on the whole is quite satisfactory. The dorsal surfaces of the nasals (posteriorly), the frontals and the parietals (anteriorly) were weathered, but outlines could be followed. However, in the prefrontal regions sutures could not be seen.

The posterior face of the skull was also badly weathered and damaged on the left side. The right side was complete, but sutural dispositions could not be ascertained clearly, especially between the supraoccipital, interparietal and tabular.

The left quadrate and stapes are lost.

The left alisphenoid is slightly displaced as a result of a force which also caused a fracture across the left pterygoid at the level where the quadrate ramus leaves the main body of the bone.

There are no postorbital arches, but it is difficult to say whether this condition is natural or artificial. There are postorbital bones lying close to the anterior ends of the parietals and some evidence was encountered of these bones having formed at least elementary projections marking the posterior borders of the orbits. On the left side the region of the postorbital bar was badly weathered and the bar could have been destroyed after fossilization, but on the right side the bar should have been encountered if it had not been destroyed prior to fossilization, because the region was well enclosed within the nodule.

Both temporal arches are incomplete from the levels at which the postorbital bars normally join, to the quadrate regions. Again, the left arch could have been damaged through weathering, but the right arch should have presented itself inside the nodule, had it not been damaged prior to fossilization. Enough of these arches is preserved to show that if they were complete they were extremely delicate, unlike the *Cynodont* condition and in line with the condition encountered in the *Scalosaurids*.

The author is, however, thoroughly convinced that both the postorbital bars and the temporal arches were incomplete in the natural condition. The skull as a whole shows very little signs of having experienced rough treatment before fossilization. Both juguls terminate at exactly the same level, slightly forward of where the postorbital bars should join, and in strikingly similar pointed fashion. Furthermore, the squamosals also form very similar shaped projections in the quadrate regions, terminating at exactly the same levels.

The only other damage is distortion, beyond recognition, of the orbitosphenoids and the inevitable missing internasal bridge.

Otherwise every single structural detail revealed itself surprisingly clearly in the wax model. The lower jaw especially is most satisfactory. The only bones among those present whose outlines are somewhat confusing are the pro-otics, supraoccipital, interparietal and tabulars. This is due to weathering, or otherwise to the section intervals having been too great.

The following list of measurements in mm. is useful for comparison with other related forms:

Total length of skull to occipital condyles	60
Length to edge of occipital plate	52
From premaxillaries to pineal foramen	45
From premaxillaries to anterior borders of orbits	25
From anterior borders of orbits to posterior borders of external nares	18
From premaxillaries to basioccipital	58
From premaxillaries to level of fenestra ovals	52
From premaxillaries to internal carotid foramina	43
From premaxillaries to level of pterygoid processes	35
From premaxillaries to anterior end of interpterygoid fossa	33
From premaxillaries to posterior end of vomer	29

From premaxillaries to posterior border of secondary palate	23
From premaxillaries to palatal foramina	20
Length of 7 upper incisors	9
Length of 4 lower incisors	5
Largest diameter of upper canine	3
Largest diameter of lower canine	2.5
Length of 8 upper cheek teeth	14
Length of 10 lower cheek teeth	18
Breadth of skull across jugals	34
Breadth of skull across squamosals	38
Minimum intertemporal breadth	7
Minimum interorbital breadth	12
Minimum breadth of snout behind canines	15
Breadth of canines	16
Minimum breadth of nasals	7.5
Maximum breadth of nasals	16
Length of dentaries	39
Length of surangulars	22
Breadth of symphysis across lower canines	10
Distance between outer surfaces of pterygoid processes	19
Distance between inner surfaces of upper canines	9
Distance between inner surfaces of lower canines	5
Distance between inner surfaces of last upper cheek teeth	18
Distance between inner surfaces of last lower cheek teeth	13
Total length of lower jaw ramus	53

There are some peculiar features about this skull which will be dealt with in more detail in the following pages; they are mentioned briefly here to indicate the basis on which the present diagnosis is formulated.

The dental formula is $i7\ c1\ pc8$ for the upper jaw and $i4\ c1\ pc10$ for the lower jaw. The upper canines are in the act of being replaced, the new teeth, situated anteriorly both sides, having reached about the same length as the predecessors. The two canines on either side are intimately lodged in the same socket and some degree of resorption of the root of the older tooth had taken place to make room for the new tooth. Almost every other tooth, both upper and lower, was accompanied by a successor in its socket, some still in a very elementary tooth-bud stage, others well advanced towards replacing their functioning fellows.

It is quite normal for the lower incisors to be fewer in number than the upper incisors, although in more advanced Cynodonts the difference is usually one tooth. Unfortunately this difference in number between the upper and lower incisors, is not known in the already described Procynosuchids and Silphedestids. The condition as a whole is at any rate different.

The 7 upper teeth are all unmistakably incisors; there are no small anterior canines. The Procynosuchids are all characterised by more than one canine and by only 5 incisors (perhaps 6 in *Galecranium*). The dental formula of the present specimen could in itself be regarded as a substantial criterion for recognising it as belonging to a different family, not unlikely the Silphedestidae.

On the right side there is slight evidence of a very vestigial small tooth in the maxillary in front of the large canine.

The larger number of lower cheek teeth appears also to be normal for such a primitive form. The anterior two lower cheek teeth actually oppose the upper canine.

The premaxillaries are strikingly shallow and highly placed, so that the incisors are generally carried at a level very high above that of the cheek teeth. The premaxillaries cannot accommodate large incisor roots, consequently the incisors are in general much smaller than the cheek teeth, while the anterior three teeth are considerably smaller than the four in front of the canines.

To compensate for a shallow, highly placed premaxillary region, the symphyseal region of the lower jaw is very deep indeed. The lower incisors are, however, equally small with the anterior two also much smaller than the posterior two.

The cheek teeth, both upper and lower, increase gradually in size backward, the posterior ones being more distinctly cusped in the typical Cynodont fashion.

The secondary palate is typically Procynosuchid. This type of cleft secondary palate is also found in members of the Galesauridae and it is quite likely also characteristic of the family Silphedestidae. If the Silphedestid palate is substantially different, the present specimen would then be more likely a Procynosuchid. However, on account of the dentition it would still have to be placed in a separate family. Provisionally it is left with a rather vaguely diagnosed Silphedestidae.

Both the absence of the temporal arches and the likely incompleteness of the postorbital bars suggest a close affinity with other Silphedestids, more than with the Procynosuchids. However, as these characteristics are not conclusive, it is inadvisable to be definite on its affinity with the Silphedestidae in this particular respect.

A more definite primitive characteristic is the shortness of the dentaries. The dentaries hardly reach to the level of the back of the orbit. The rest of the lower jaw bones therefore feature prominently through the temporal region. The reflected lamina of the angular is still Therocephalian-like or Procynosuchid-like.

The articular and quadrate bones are delicate and Therocephalian-like. Especially the quadrato-jugal suggests close affinity with a form like *Aneugomphius*. It is attached to the quadrate, but extends deeply as a wedge upward and inward into the squamosal, over the latter's posterior surface where it forms the external auditory meatus groove. The much larger quadrate wedge is loosely located in an excavation on the anterior face of this portion of the squamosal. These conditions are not known well enough in the Silphedestids and Procynosuchids so that it is unsafe to venture opinions on the exact proximity of this specimen to the Scaloposaurid Therocephalians. What can be said in general, and with some measure of confidence, is that this specimen indicates a closer affinity between the Procynosuchids and the Ictidosuchid-Scaloposaurid branch of the Therocephalians than had hitherto been appreciated.

The interpterygoid fossa and the nature of the bones surrounding it are also rather Therocephalian-like. Very odd indeed is the presence of at least one tooth either side on the pterygoid tuberosities. The alisphenoids are, on the contrary, very broad and Cynodont-like.

There are two occipital condyles of typical Cynodont structure. The basioccipital has not been withdrawn properly. The condyles can be described as having jointly a crescent shape, with the basioccipital forming the middle portion, at a level well forward of the lateral exoccipital portions.

Although the posterior face of the skull is not well preserved and somewhat unsuccessfully restored in the model, it is still clearly Therocephalian in form. The paroccipital processes are delicate and short. The post-temporal fossa is, however, rather small.

The interparietal region was not sharply crested. This region rather resembles that of *Ictidosuchops* or *Scaloposaurus*. The pineal foramen is situated far back as in these Therocephalians.

The specimen is undoubtedly pre-mature. Besides dental replacement many sutures are still inadequately closed. However, it does not appear to be very juvenile.

The specimen is introduced here as a new genus and species and is provisionally considered as a likely member of the family Silphedestidae, on condition that this family, when re-evaluated, will actually prove to be, as a whole or in part, ancestral to the Procynosuchids in general. While the present specimen, with at least some Silphedestids, is considered to be more primitive than the Procynosuchids it is acknowledged that in dental characteristics and the loss of the temporal arches and postorbital bars, they had evolved some distance away from the main line leading through the Procynosuchids to the higher Cynodonts.

SCALOPOCYNODON GRACILIS gen. et sp. nov.

(Figures 33 — 35)

Type: Complete skull with the lower jaw in situ, recorded as No. 346 in the collection of the Bernard Price Institute, from the base of the *Cistecephalus* zone on the farm Uitspanfontein in the Beaufort West district. The original specimen has been destroyed in the process of serial grinding. It is now represented by a complete and detailed wax model, four times natural size, and a full set of section drawings at .5mm. intervals.

Diagnosis: Primitive Cynodont; dental formula $i7, cl, pc8$ and $i4, cl, pc10$ for the upper and lower jaws respectively; very shallow premaxillary region; high symphyseal region; both upper and lower incisors very small anteriorly; cleft secondary palate; interpterygoid fossa large; pterygoid tuberosities carrying at least one tooth each; pterygoid processes long and slender; postorbital bars apparently incomplete; zygomatic arches evidently absent; quadrates delicate and streptostylic; parietals Scaloposaurid-like with pineal situated far back; paroccipital processes short and slender; post-temporal fossa small; occipital face primitive; two occipital condyles; dentaries short but with well formed coronoid processes; angulars and surangulars large; reflected lamina short, delicate, but still projecting freely behind the dentary.

STRUCTURE OF THE SKULL

The *basioccipital* is retracted from the occipital condyle to a greater extent than in the Procynosuchids. A similar condition is interpreted by Broom (1938b) for *Procynosuchus delaharpeae*, where the condyle has developed a crescent shape as a result of some degree of reduction on the part of the basioccipital, but the condition in the present specimen is distinctly more advanced. In *Leavachia* the arrangement appears to be more primitive, more like the typical Therocephalian trilobed single condyle as found in *Ictidosuchops* (Crompton 1955) or *Aneugomphius* (Brink 1956). The structure of the occipital condyle is not known in the other Procynosuchids or in any form considered at present as belonging to the Silphedestidae.

In other respects the basioccipital is of typical Therapsid build. It does not contribute to the margins of the jugular foramina. It forms, with the basisphenoid, insignificant tubera on the borders of the fenestrae ovals. These tubera are apparent only in the extent to which they reach sideways; they do not drag the lateral margins of the basioccipital downwards. On the ventral surface it has a small median ridge, with a foramen either side. On the side of the brain case it forms a smooth floor, concave in cross section and straight antero-posteriorly, sloping upwards to the front.

Posteriorly to the jugular foramen, on the side of the brain case, the basioccipital is smoothly joined to the exoccipital. In front of the jugular foramen it is, on the contrary, in rather loose contact with the opisthotic. Farther forward it presents a free margin ventrally to the vestibule.

The anterior margin of the basioccipital is fused, quite indistinguishably, with the basisphenoid. Nowhere in the sections could any trace of their suture be seen. This circumstance might indicate that the specimen is not quite as juvenile as other features tend to suggest. The region where this suture should be is covered ventrally by the parasphenoid.

The *exoccipitals* form the two major condyles for articulation with the vertebral column. The arrangement is no doubt typically Cynodont, where these condyles articulate with the separate left and right halves of the atlas, while the loose atlas intercentrum articulates with the basioccipital facet. This arrangement demands a trilobed odontoid process (atlas centrum) on the axis. The structure is, therefore, quite advanced.

The *exoccipitals* form the lateral borders of the foramen magnum. These margins are sharp and tend to constrict the foramen. They also contribute to the posteromedial margins of the jugular fossae. The sections did not reveal separate foramina for the twelfth nerve, penetrating the *exoccipitals*.

The portions forming the lateral margins of the foramen magnum have broad dorsolateral surfaces presenting substantial areas which find contact with the supraoccipital. In the specimen the impression is created that these contacts were not very firm.

The *exoccipitals* are not known properly in nearly related forms. They are comparable with those of *Aneugomphius*, although in the latter form they extend farther around the foramen magnum and jugular foramina.

The *supraoccipital* did not reveal itself satisfactorily in the sections, especially as regards the nature of its lateral margins. It is interpreted as a rather long bone reaching upward and forward from the dorsal margin of the foramen magnum and penetrating deeply between the parietals where the latter diverge to contribute to the occipital flanges.

At its most dorsal extremity it is well ossified, unlike the condition normally encountered in Cynodonts where this portion is often absent on account of it having been cartilaginous. This is added support for the view that this specimen is not very juvenile. At a lower level there are indications that it had been cartilaginous in a restricted section.

The *opisthotics* are not indistinguishably fused with the pro-otics to suggest a single periotic structure as Crompton (1955) found in *Ictidosuchops*. On the contrary, they appear to be in rather loose articulation with the pro-otics, but the exact nature of their relationship is rather confusing in the sections. This cannot be blamed entirely on the thickness of the sections. On the left side there is definitely some damage due to weathering. On the right side a crucial region across the fenestra ovalis, which is better preserved than on the left side, is obscured by a fragment of bone which might be the stapes; it might also be a foreign bone element. If it is the stapes, it lies with its medial end thrust into

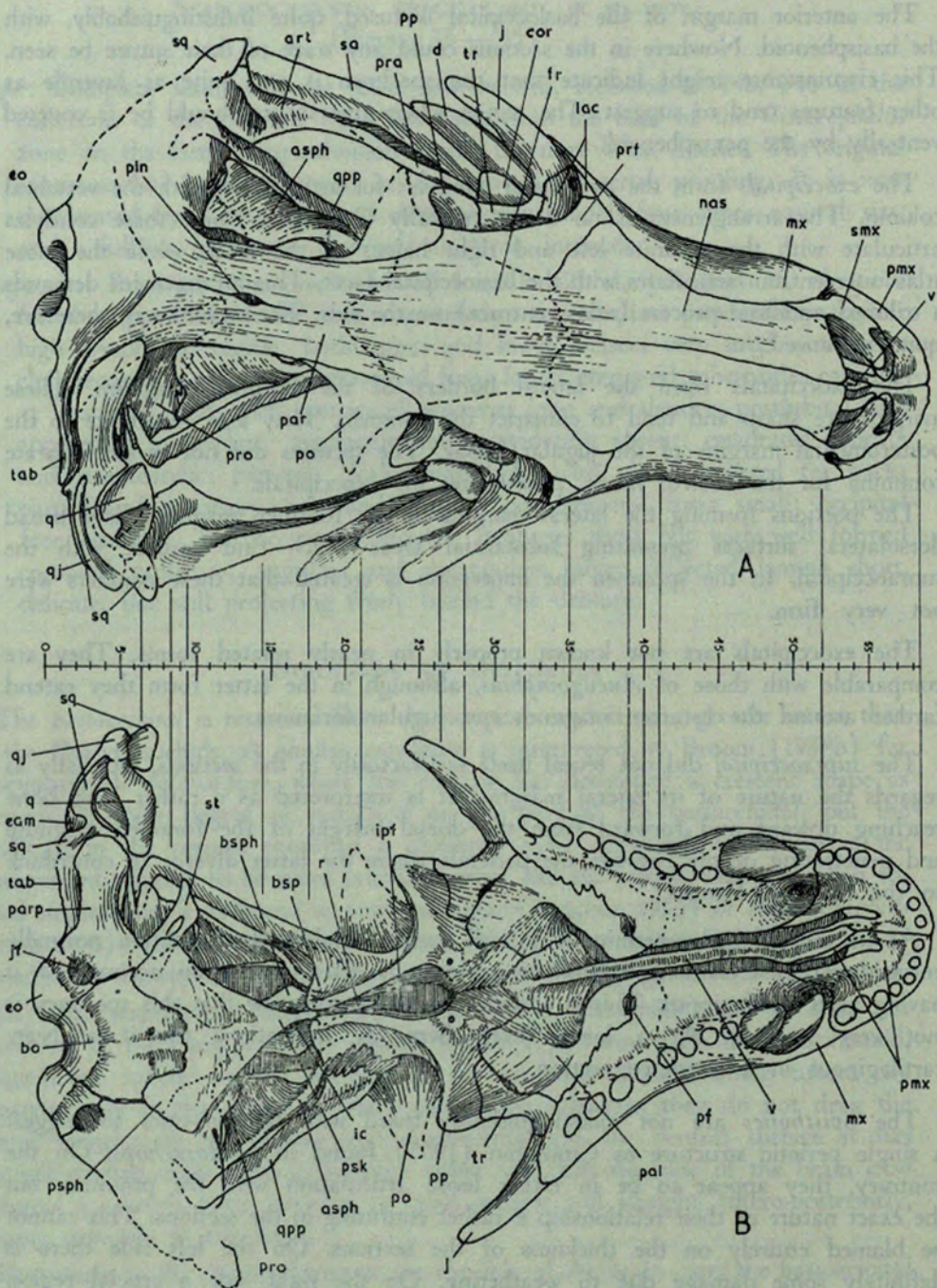


Figure 33

A, Dorsal and B, Ventral view of the skull of *Scalopocynodon gracilis*, graphically reconstructed from serial section. Twice natural size.

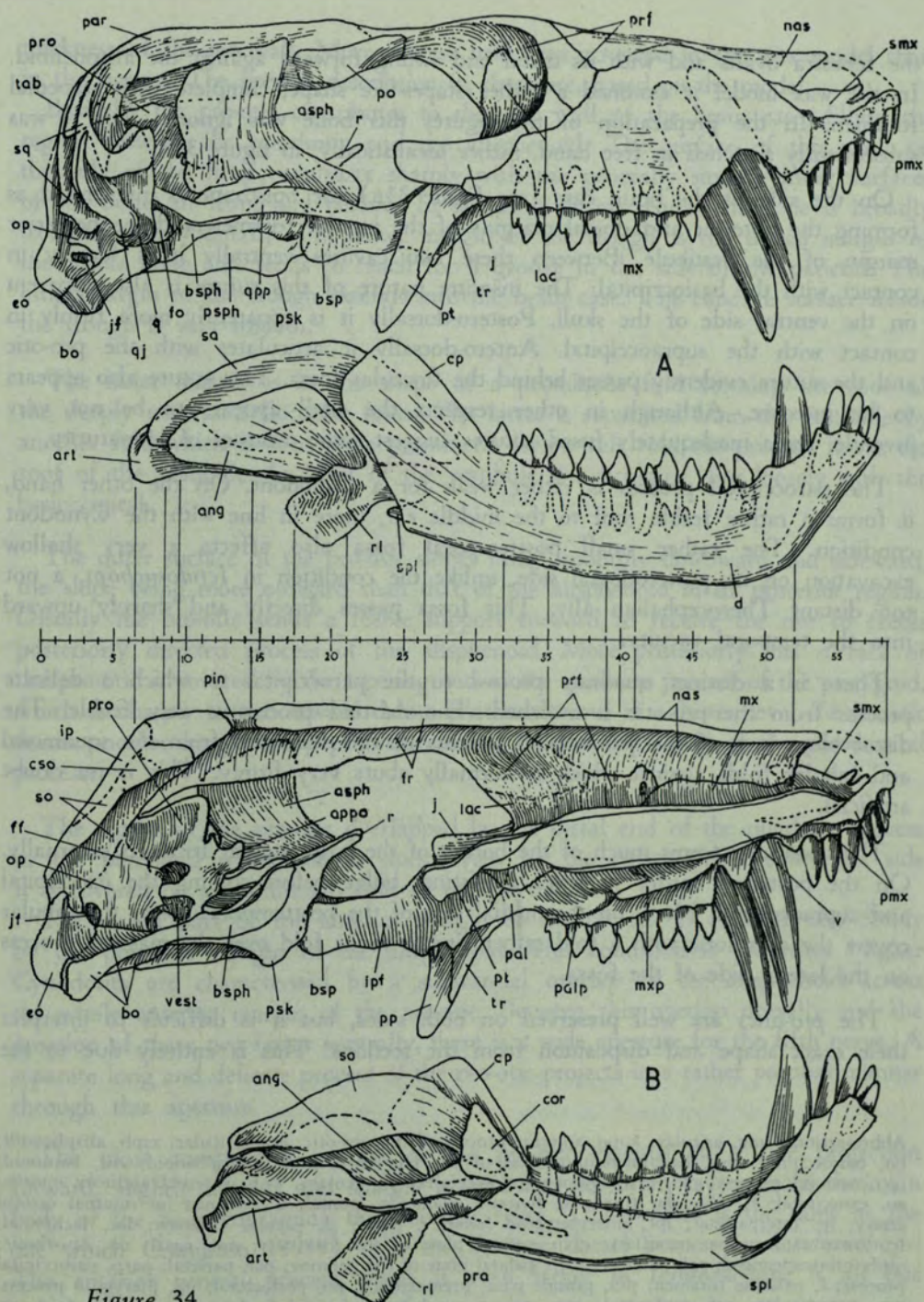


Figure 34

A, Lateral and B, Median view of the skull of *Scalopocynodon gracilis*, graphically reconstructed from serial sections. Twice natural size.
For abbreviations see page 132.

the fenestra ovalis and with its distal end swung forward against the alisphenoid. In the wax model it assumed a rather stapes-like shape, complete with stapedia foramen. In the preparation of the figures this bone was ignored, but it was subsequently sketched in free hand, rather idealistically, in figure 34B.

On the side of the brain case (see figure 33B) the opisthotic is interpreted as forming the anterior and dorsal margins of the jugular foramen and the posterior margin of the vestibule. Between these two cavities ventrally it is loosely in contact with the basioccipital. The insecure nature of this suture is also apparent on the ventral side of the skull. Postero-dorsally it is apparently more firmly in contact with the supraoccipital. Antero-dorsally it articulates with the pro-otic and the suture evidently passes behind the floccular fossa. This suture also appears to be insecure. Although in other respects the skull appears to be not very juvenile, these inadequately fused sutures suggest some measure of immaturity.

The paroccipital process is rather weak for a Cynodont. On the other hand, it forms a rather feeble roof to the middle ear, more in line with the Cynodont condition. The rather small posttemporal fossa also affects a very shallow excavation on its posterodorsal side, unlike the condition in *Ictidosuchops*, a not too distant Therocephalian ally. This fossa passes directly and sharply upward into the temporal vacuity.

There is a distinct quadrate process to the paroccipital to which a delicate process from the pro-otic is attached. The mastoid process is very feeble. The distal blunt end of the paroccipital process is well separated from the squamosal and tabular folds against which it normally abuts very firmly. This is no doubt artificial.

The opisthotic forms much of the border of the large jugular foramen externally. On the posterior border it forms a distinct bulge before joining the exoccipital and supraoccipital. Here, on the medial side of the posttemporal fossa, the tabular covers the opisthotic with a fold rather similar to its fold over the mastoid process on the lateral side of the fossa.

The *pro-otics* are well preserved on both sides, but it is difficult to interpret their exact shape and disposition from the sections. This is entirely due to the

Abbreviations: ang, angular; appo, anterior process of the pro-otic; art, articular; asph, alisphenoid; bo, basioccipital; bsp, basisphenoid process of the pterygoid; bsph, basisphenoid; cor, coronoid; cp, coronoid process; cso, cartilaginous supraoccipital; d, dentary; eam, external auditory meatus; eo, exoccipital; ff, floccular fossa; fo, fenestra ovalis; fr, frontal; ic, foramen for internal carotid artery; ip, interparietal; ipf, interpterygoid fossa; j, jugal; jf, jugular foramen; lac, lachrymal; lc, lower canine; mx, maxillary; mxp, palatal plate of the maxillary; nas, nasal; op, opisthotic; osph, orbitosphenoid; pal, palatine; palp, palatal plate of the palatine; par, parietal; parp, paroccipital process; f, palatine foramen; pin, pineal; pmx, premaxillary; po, postorbital; pp, pterygoid process; pra, prearticular; prf, prefrontal; pro, pro-otic; psk, parapsphenoid keel; psph, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; qpp, quadrate process of the pterygoid; r, rostrum; rl, reflected lamina; sa, surangular; smx, septomaxillary; so, supraoccipital; spl, splenial; sq, squamosal; st, stapes; tab, tabular; tr, transverse bone; uc, upper canine; v, vomer; vest, vestibule.

thickness of the intervals. More success had been achieved in the wax model than in the figures. The present description is, therefore, based on the model.

Basically the pro-otic contributes to the side wall of the brain case, filling the region between the opisthotic and the alisphenoid. The surface of this wall, on the side of the brain, contrasts sharply with the generally smooth inner surfaces of the bones in front and behind. In the most dorsal region the bone is broadly troughed longitudinally. The outer margin of the trough is the dorsal margin of the whole bone and tends to reach for a groove in the side of the parietal. The inner margin of the trough extends into the brain case. The concave surface inside the trough is very smooth.

The inner margin is in the shape of a prominent fold forming the roof of the deeply excavated floccular fossa. The latter is separated from the vestibule by another fold which is even more prominent. Below this fold the pro-otic forms the roof of the vestibule. In front of the vestibule it articulates very loosely with the basioccipital.

The outer surface of the pro-otic slopes fairly smoothly downward and sideward, the slope being more outward than that of the alisphenoid in its posterior region. Distally the pro-otic sends a feeble support forward to receive the not so feeble posteriorly directed process of the alisphenoid. More posteriorly this surface of the pro-otic is covered by the tapering end of the quadrate process of the pterygoid, which is sharply turned inward. More posteriorly and at a lower level the prootic forms another long slender process reaching for the distal end of the paroccipital process.

The region of the pro-otic overlapped by the distal end of the quadrate process of the pterygoid is exposed in dorsal view on the right side. On the left side it is covered by an additional fold of the pro-otic.

The dorsal part of the anterior margin of the pro-otic is covered very feebly by the posterior margin of the alisphenoid. This condition is primitive. Higher Cynodonts are characterised by a substantial overlap of the alisphenoid across the whole anterior margin of the pro-otic. Between this overlap dorsally and the junction of these two bones ventrally, there is a wide aperture for the fifth nerve. A separate long and delicate process of the pro-otic projects in a rather peculiar manner through this aperture.

The most conspicuous process of the pro-otic extends as a free projection forward, slightly upward and sharply inward into the brain cavity, from the main body of the bone containing the floccular fossa. This process is the same as the one which Crompton (1955) calls the anterior dorsal process in *Ictidosuchops*. The anterior ventral process which is even larger in *Ictidosuchops* is all but completely absent in the present form.

The *tabular* of the left side is entirely weathered away. It appears to be

complete on the right side, but its medial margin is obscure. The portion covering the posterior face of the parietal flange is quite thick. It lies very loosely against this flange. The space between the tabular and the squamosal below the parietal flange is rather considerable. This cavity appears to serve some significant purpose, as it is exaggerated by an excavation in the anterior face of the tabular which renders the bone extremely thin in the area above the posttemporal fossa. The portion of the bone forming the dorsal margin of this fossa is as thick as the portion above the excavation. The excavation is further enlarged by the general concavity of the posterior face of the portion of the squamosal lying in front.

This excavation is continuous with the general passage of the posttemporal fossa immediately below. It also communicates through a wide aperture below the tip of the parietal flange with the general region of the external auditory meatus. This is perhaps due to the fact that the inner margin of the meatus groove, which is usually a prominent fold of the squamosal, is very weakly developed. This fold would otherwise have closed the aperture. The excavation also communicates with the brain cavity directly inward, but this is evidently due, only incidentally, to the poor contact between the pro-otic and the supraoccipital.

Whatever the actual interpretation might be, should the present description be somewhat incorrect on account of the section intervals being too great, or whatever the purpose of the cavity is, the fact remains that the tabulars do not simply cover with firm contact the bones in front of them, as the impression is normally created.

The tabular extends farther downward on either side of the posttemporal fossa where it covers the paroccipital process in the usual manner.

The *interparietal* is evidently completely missing from the specimen. In the wax model an opening presented itself in the central part of the area normally covered by the interparietal. This opening, leading into the brain case, is in the position where the interparietal had contact with the cartilaginous portion of the supraoccipital. The interparietal evidently covered appreciable areas of the tabulars, as the tabular preserved in the specimen extends very close to the opening.

The *parietals* are very different indeed from those of the Procynosuchids. *Leavachia* (Broom 1948, Brink 1953) and *Procynosuchus* (Broom 1938b) are characterised by prominent median crests. In the present specimen the crest is not only absent but the general dorsal surface of the parietals, even behind the pineal opening, does not slope as much as in these otherwise primitive Cynodonts. Admittedly the weathering that affected especially the frontal region could have damaged the crest but the general outlines of the parietals could be traced quite clearly in the posterior region where the crest should have been most prominent. In addition a higher crest would have caused a more pronounced slope of the dorsal surfaces laterally, and it would have given the parietal flange preserved a higher dorsal margin on the border of the occiput. This margin is genuine and

undamaged in the sections and from its general nature it can safely be concluded that the crest was absent in the intertemporal region.

The parietal region is shaped more like that of the *Silphedestids*, where it is broad, moderately sloping outward posteriorly, and without a crest. The region differs, however, in that it does not become constricted behind the pineal. This constriction is also found in the *Procynosuchids*, as well as in the *Scaloposaurids* with which favourable comparisons can be made in other respects, such as the shorter and more delicate occipital flanges and the posteriorly situated pineal.

A peculiarity of the present specimen is that the parietals do not become narrower between the postorbitals. The distance to which the parietals extend forward of the pineal is also quite conspicuous. The fronto-parietal suture could not be located, but a sudden change in the slope of the roof surface evidently marks the position of this suture, at the level indicated in figure 34A. A comparable arrangement is found in *Aneugomphius*. A feature which is well revealed in the model is the deep groove laterally behind the alisphenoid, well above the ventral margin of the parietal, in which the dorsal margin of the pro-otic is loosely lodged.

The *postorbitals* have been severely damaged but their outlines as indicated in the figures are evidently correct. The left postorbital suffered considerable weathering but it is on this side that the shape of the bone could best be ascertained. On the right side the projection had broken off before fossilization, otherwise it should have been encountered inside the undamaged nodule.

The postorbital bars can quite readily be interpreted as having been complete, if the zygomatic arches were complete, but evidence is strongly in favour of considering the latter to have originally been exactly as figured (see *jugals* and *squamosals* below). The position where the postorbital bars should join the arches is well behind the level where the jugals terminate in the specimen. The postorbital bars must therefore have been incomplete in the natural state. Besides, the portions that are well preserved, flanking the frontals and parietals, show that these bones were very weakly developed. Especially the posterior projections flanking the parietals, which are very well developed in the *Procynosuchids*, are quite insignificant.

The shape of the projections tending to form postorbital bars is derived from the outlining of the area in which traces of bone were encountered on the left side.

In *Silphedestes* and *Silphedocynodon* the postorbitals are interpreted as having had no significant projections representing the postorbital bars (Brink 1951) while Broom (1949) interprets these bars, as well as the arches, to have been complete in *Silphedestes* and *Protocynodon*. Whether or not either bars or arches, or both, are actually incomplete in these forms, the fact remains that they are strikingly different from those of the *Procynosuchids* and that the condition in the present specimen is more comparable with the former than with the latter.

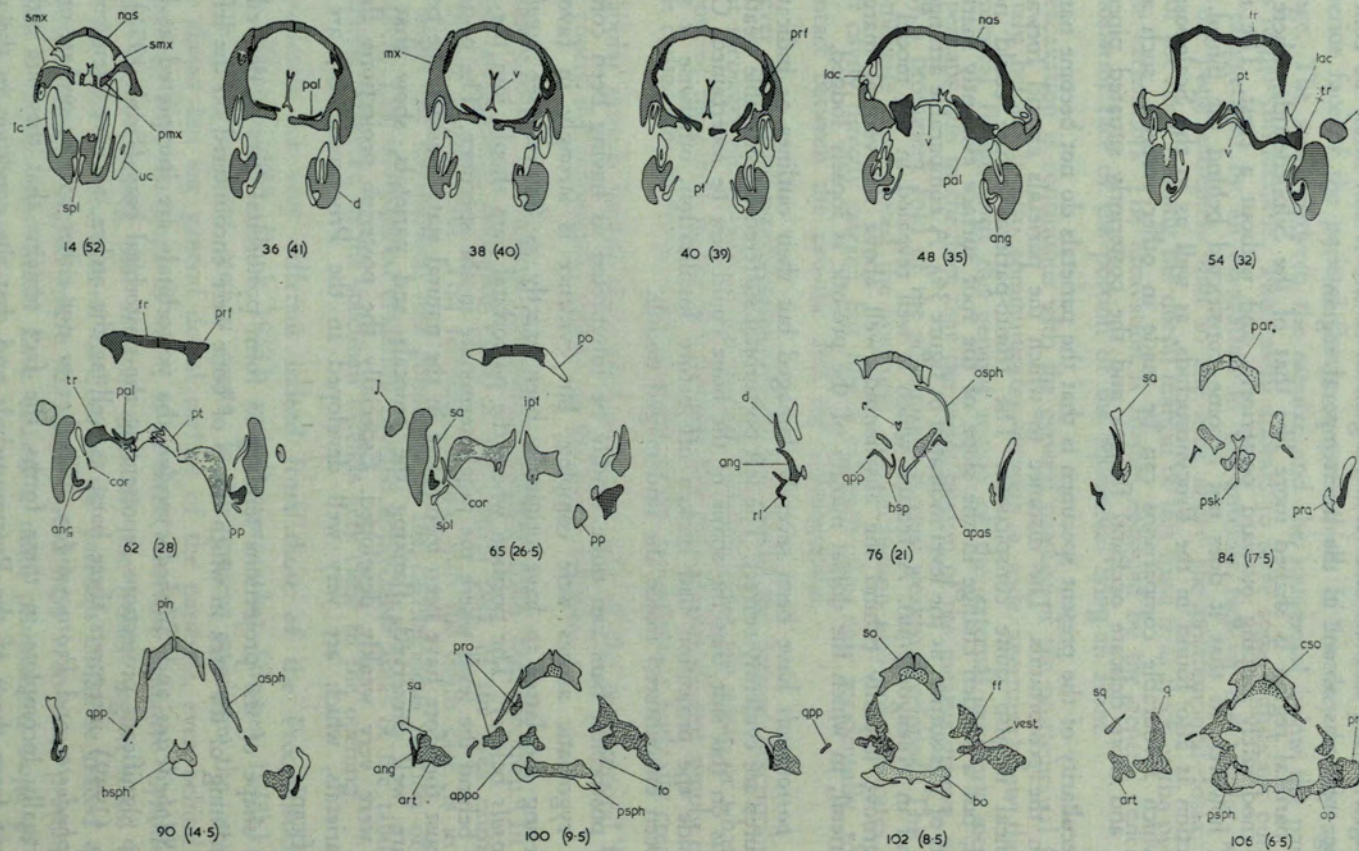


Figure 35

The *frontals*, together with the postorbitals, suffered very badly from weathering, although damage was not as severe as in the left occipital region. The frontal region could satisfactorily be restored in the model, but the sutures of the frontal bones could not be traced.

As mentioned above, the fronto-parietal suture is taken as extending at a level where there is a noticeable change in the slope of these bones on the dorsal surface. Anteriorly the fronto-nasal suture is taken as being level with the anterior borders of the orbits, as is the case with all related forms. The fronto-prefrontal sutures are interpreted as extending to the postorbitals, thus excluding the frontals from the dorsal borders of the orbits according to the Cynodont pattern. In view of the several other Therocephalian-like features in this skull it is, however, not unlikely that the frontals could actually have contributed to the dorsal borders of the orbits; the prefrontals are exceptionally long as interpreted in figure 34A, even excluding its considerable projection anteriorly on the side of the nasal cavity, as shown in figure 33B.

The ventral surface of the frontal region is generally flat and smooth, with no indication of fronto-nasal turbinal ridges. Laterally the frontals bend downward quite far to form the inside surfaces of the walls tending to separate the olfactory chamber from the orbits.

If this frontal region is correctly interpreted, it is quite obvious that it differs greatly from that of the Procynosuchids, where the frontals are very narrow. There appears to be a better correspondence in the structure of this region with the Silphedestids, in spite of the poor preservation in these forms.

The *prefrontals*, as mentioned above, apparently exclude the frontals from the dorsal borders of the orbits, but the contrary condition is still a fair possibility. They contribute more extensively to the walls separating the olfactory chamber from the orbits than the frontals. Anteriorly this wall extends low down and is covered laterally by an extensive dorsal fold of the lachrymal. This wall extends straight down only posteriorly where the frontal contributes to its inner surface. Anteriorly, where the lachrymal contributes to its outer surface, it does not extend straight downward, but at first sharply inward from the dorsal border of the orbit and subsequently downward. There is a deeply excavated cavity between this upper orbital wall and the portion above contributing to the roof of the skull in the anterior interorbital region.

The prefrontals separate the nasals from the lachrymals, a feature in which the present specimen differs profoundly from the Procynosuchids and one where

Figure 35

Section through the skull of *Scalopocynodon gracilis*. Figures below every section indicate the numbers of the sections, number 1 being the section where contact was first made at the premaxillaries, and the figures in brackets indicate the levels in millimeters according to the micrometer of the grinding apparatus. For convenience these levels are marked against a scale introduced in figures 33 and 34. All sections are natural size.

there appears to be a comparison with the Silphedestids. This condition is also found in *Aneugomphius* and *Ictidosuchops*.

In the Procynosuchids the prefrontals also fail to broaden in the region across the anterior orbital borders as is the case in the present specimen and the Scaloposaurids.

The *lachrymals* cover very small areas on the lateral face of the snout in front of the orbits, thus allowing the maxillaries to come within close reach of the orbital borders. They do not cover much of the dorsal surfaces of the jugals on the ventral margins of the orbits, unlike the condition in *Ictidosuchops* and somewhat comparable with that of *Aneugomphius*.

In the anterior orbital corner the foramen for the lachrymal duct is large and situated very close to the border. This canal extends forward through the lachrymal bone and is subsequently carried farther forward inside the anterior portion of the prefrontal. Both these bones are more extensive on the side of the nasal cavity than on the outside surface of the snout. The lachrymal canal opens inward at the very anterior extremity of the prefrontal. The arrangement is very similar to that described by the author for *Akidnognathus parvus* in the following paper (page 155 of this issue).

The lachrymal builds the whole anterior inner wall of the orbit, where it broadly overlaps the prefrontal. On the floor of the orbit it contacts the transverse bone.

The *nasals* are Cynodont-like in being very broad posteriorly, but Therocephalian-like in having lost contact with the lachrymals. Anteriorly the septomaxillaries do not penetrate as deeply along their lateral margins as in the Procynosuchids, another feature which is reminiscent of the condition in *Ictidosuchops* and other Scaloposaurids.

Although the anterior tips of the nasals are well preserved in the specimen, no sign of the premaxillaries having penetrated between them could be found.

The lateral margins of the nasals are bent down deeply on the side of the nasal cavity and are in normal fashion broadly overlapped by the maxillaries.

There is no trace of turbinal ridges on the ventral surfaces of the nasals.

The *septomaxillaries* exhibit the same general structure as that described by the author for *Akidnognathus parvus* in the following paper (page 155 of this issue). The only difference in the structure of the whole region which might affect the views expounded by the author in the previous paper on the significance of the septomaxillary structure is to be found in the nature of the floors of the external nares formed by the premaxillaries immediately behind these bones. The opening, situated in the position where the septomaxillary, premaxillary and maxillary meet on the side of the external naris, leads not only directly inwards into the nasal cavity, but also forward to open on the anterior face of the septomaxillary, where it is characteristically roofed by the prominent shelf-like projection of the ventral margin of the naris.

The general shape of this region is, however, rather peculiar on account of the premaxillaries being turned sharply upward. This condition may be slightly exaggerated by distortion, though it is surprising that distortion could influence so profoundly this very local region while the rest of the skull is reasonably unaffected. The height of the symphyseal region also suggests that the region as preserved is near to the natural condition. This up-turned nature of the premaxillary region has the effect of making the portions of the septomaxillaries, which normally contribute to the anterior surface of the snout, face almost directly upward, tending to form part of the floor of the external nares.

The portions of the septomaxillaries penetrating the nasals and maxillaries are not exposed on the side of the nasal cavity.

The premaxillaries are strikingly like those of *Procynosuchus* (Broom, 1937) in structure rather than shape and, on account of the secondary palate, very unlike those of *Akidnognathus*, *Ictidosuchops* or *Aneugomphius*. On the midline, immediately behind the anterior incisors, the two maxillaries form a conspicuous small boss, as is typical of even the latest Cynodonts like *Diademodon*. There are, no doubt, two small foramina situated anteriorly on either side of this boss, more directly behind the first incisors, as are found in *Akidnognathus*, *Moschorhinus*, and apparently all related Therapsids, but these were missed on account of the thickness of the section interval. The cleft in the incomplete secondary palate starts level with the posterior side of the boss. The cleft is very broad anteriorly in the premaxillary region where the ventral margin of the vomer drops to below the general level of the secondary palate. Initially the premaxillaries together form a substantial process supporting the anterior end of the vomer from below, but soon the left and right parts diverge to extend separately as long, slender tapering projections either side of the well-thickened ventral margin of the anterior end of the vomer.

The premaxillaries form the anterior halves of the excavations for the lower jaw canines and extend well backward on the margins of the palatine plates. These posteriorly directed processes, and those either side of the vomer, are exactly like those of *Procynosuchus* as illustrated by Broom in 1937 and 1938b.

The premaxillaries carry 7 incisors each, there being no doubt whatsoever that the 7th tooth either side is an incisor and not a canine. In contrast with the cheek teeth there are little signs of tooth replacement. In dental formula the present specimen stands well separated from both the *Procynosuchids* and the *Silphedestids*.

Due to the very insignificant depth of the premaxillaries anteriorly, the front incisors are very small. Those in front of the canines are appreciably larger.

There is no trace of an internarial bridge. The region between the septomaxillaries does not indicate the base of such a bridge and there is no sign of this process where it normally penetrates between the anterior ends of the nasals. However, there has no doubt been an internarial bridge which had suffered very effective destruction.

The *maxillaries* are very typically Procynosuchid as far as the secondary palate is concerned. This type of cleft secondary palate is, of course, also found in the Galesaurids, but it is quite evident that the present specimen is not a close ally of this family. It is unfortunate that the palate is not known in the Silphedestidae.

The feeling that the present specimen is closely allied with the Procynosuchids is enhanced by the fact that Broom (1937, 1938b) encountered a very similar degree of tooth replacement activity in *Procynosuchus delaharpeae*. Virtually every tooth, in the lower jaw more than in the upper, has a successor situated lingually. These successors are in various stages of development, from the most elementary tooth bud to almost fully erupted teeth still sharing a socket with the predecessor (in the lower jaw). In some cases it appears as though the new tooth is inclined to erupt from a separate socket well on the inside of the old tooth, these apparently being the most elementary buds.

It is unfortunately not possible to tell from the sections whether a particular tooth bud is very young or far advanced, because a tooth could show large in its full transverse section at a particular level, while at another level a more advanced tooth could be mistaken for a very early stage on account of the level having nearly missed it. For a successful study of the order of tooth replacement, section intervals should have been about .1mm.

From a dental point of view the present specimen is, however, not a typical Procynosuchid. It has only one canine in each maxillary which, on both sides, is in the act of being replaced, the new anterior tooth having reached about the same length as the posterior predecessor. The posterior is obviously the older, as its root had suffered some resorption to make room for the successor. This phenomenon rules out the possibility of considering the two teeth as separate canines.

On the right side there is vague evidence of a very rudimentary anterior canine which might bring the present specimen slightly closer to the Procynosuchids. A similar feeble tooth on the left side was not missed through the thickness of the interval; there is no room for a tooth on this side.

If the anterior canines are taken as a very significant diagnostic feature, which they should really be, the present specimen is even farther removed from the Silphedestids. However, the author feels that these anterior canines have apparently been quite readily discarded by various forms over rather short evolutionary ranges, as is also apparent in the Ictidosuchids and Scaloposaurids. While the number of canines may be taken as a good generic diagnostic feature, it is hardly reliable for a family diagnosis.

The presence of a rudimentary anterior canine obviously indicates that the specimen had very recently evolved from a stage characterised by more than one canine.

There is no maxillary antrum of any description.

The *transverse* bones are large and contribute substantially to the pterygoid processes, in a manner which appears to be rather Therocephalian-like. They also

extend deeply inward between the pterygoids and the palatines, quite unlike the condition normally encountered in the Therocephalia. A peculiar feature is the rather loose articulation of the transverse bone with the palatine, leaving a distinct gap halfway along this contact. This opening can rightly be called the suborbital fossa which is as much closed as in *Aneugomphius*. The position of the opening is, however, quite different. The Therocephalian suborbital fossa is always situated between the transverse bone, the palatine and the pterygoid, but in this specimen the pterygoid is well separated from its border. The condition in the present specimen can nevertheless readily be derived from the basic Therocephalian arrangement, with the foramen having nearly closed, apparently as recently as in *Aneugomphius*.

The *jugals* are firmly gripped anteriorly between the maxillaries, lacrymals and transverse bones. They form solid processes extending outward and backward to form in the normal way ventral borders to the orbits. However, in the present specimen, they do not reach back to meet the squamosals; neither do they contribute to postorbital bars. They taper gradually and terminate freely at a level forward of the position where the postorbital bars normally join the zygomatic arches.

The condition as found in the specimen might be interpreted as artificial, the left arch having weathered away if it had been preserved, while the right arch had broken away before fossilization. (The right side of the skull is otherwise undamaged except for the tip of the postorbital process, and was well enclosed in the nodule. The arch should have been encountered if it had not broken away before fossilization.)

The author is, however, thoroughly convinced that the condition as found is quite natural. These processes terminate at exactly the same level and in exactly the same shape. In the last two or three sections either side, in which they are revealed, it is quite clear that they taper to insignificant proportions, contrary to what is expected at this level where postorbital bars should join. The right should also have shown signs of ordinary damage at the tip of the process had the arch been broken before fossilization. Moreover, the squamosal projections which represent the zygomatic processes also terminate feebly at exactly the same level as one another and they are strikingly similar in shape. They appear in the first sections at their levels as minute crescents of bone, hardly what one would expect to find in a damaged zygomatic arch. Finally, a force which could have caused at least one arch to break off completely before fossilization should also have adversely affected the skull as a whole, but such adverse effects are certainly not apparent in the reconstruction. Prefossilization damage is limited to the internarial bridge, one postorbital process, the loss of one very streptostylic quadrate and the loss of apparently only one stapes.

The *squamosals*, as mentioned under *jugals* above, do not contribute towards the building of zygomatic arches, the condition being interpreted as natural and not artificial, for the several reasons given.

The feeble zygomatic projections have a shape which could only develop, as a product of degeneration, from a Therocephalian-like arrangement. This region could at no stage previously have had the characteristic Cynodont structure already elaborately developed in *Procynosuchus* and *Leavachia* where it has appreciable depth, a pronounced angle above the quadrate and where the dorsal margin leans outward to form a well defined external auditory meatus groove. With a great measure of degeneration the present condition could have developed from the arrangement found in *Aneugomphius* or *Ictidosuchops*, where the dorsal margin of the squamosal leans inward.

The zygomatic process extends freely outward and subsequently forward well above the quadratojugal wedge. The quadratojugal wedge rests on a fold of the squamosal which can be interpreted as an elaboration of the outer border of the elementary external auditory meatus groove. The inner border of this groove is apparent only ventrally where the paroccipital process abuts loosely against it. Dorsally this border is resorbed to an extent where it leaves an aperture leading to a conspicuous space between the tabular and the main body of the squamosal (see *tabulars* above). This main portion is concave posteriorly and convex anteriorly in sagittal section, and extends upward and inward to meet the parietal. The ventral half of this process reaches the pro-otic, but it is not comparable with the rather separate process found in the Scalopsaurids and Whaitsiids, extending below the posttemporal fossa to the pro-otic. In the specimen the posttemporal fossa reaches the temporal vacuity from below this process.

The quadrate wedge is loosely received in a cavity in the anterior face of the squamosal. This cavity is so large that the portion of the bone behind has been reduced to only the elementary auditory meatus groove, while the feeble zygomatic process and delicate quadratojugal support are the only portions extending laterally.

The *quadrate* and *quadratojugal* together form the condyle for the articulation of the lower jaw. Although the sections show them to be separable, they should be looked upon as a unit.

The quadrate forms a horizontal and transversely extending slender, cylinder-like condyle, articulating laterally with a small round condyle formed by the quadratojugal. The latter is perfectly in line with the former and is not indistinguishably fused. Above the transverse cylinder-like quadrate condyle the bone is constricted, but soon it expands again upward to form a rather large wedge lodged loosely in a cavity anteriorly in the squamosal. This wedge is nearly in the sagittal plane. It is shaped like a propellor blade, the lower part extending anteromedially-posterolaterally, while the upper tip is fully in the sagittal plane. The anterolateral surface is concave and the posteromedial surface convex. The anterior margin is straight, blunt and vertical; the posterior margin is sharp and broadly curved.

The groove into which this posterior margin of the quadrate wedge fits corresponds on the posterior face of the skull with the ridge forming the outer border of the external auditory meatus groove. The quadrate wedge penetrates so

deeply that the outer border of the meatus groove is virtually resorbed, leaving a rudimentary fold medially and a delicate process laterally. The quadrate wedge is visible in between in posterior view. The lateral process supports the quadratojugal wedge from below, while the zygomatic process of the squamosal anterodorsally apparently served as a check to the forward movement of this wedge. Although the slit into which the quadratojugal wedge fits appears to be rather narrow transversely, it still allows for a maximum swing of the quadrate in anteroposterior direction. The quadrate and quadratojugal are therefore jointly streptostylic.

The quadratojugal wedge is in the shape of a cutlass blade, with a moderately and convexly curved posterior blunt edge, while the anterior edge is sharp, convex in the lower half and concave in the upper half. It terminates dorsally in a very fine point. The blade itself is flat both sides and in cross section it lies truly in the sagittal plane, but in its length it extends parallel to the margin of the occipital crest immediately above (or at an angle of 45° to the horizontal plane). It also extends from the condyle somewhat backward so that the tip comes to lie directly behind (and some distance away from) the tip of the quadrate wedge.

The *stapes*, or a bone which can quite readily be mistaken for the stapes, is present on the right side. It is described under *opisthotics* above.

The *vomer* is typically Procynosuchid, and un-Therocephalian-like in that its ventral margin is not horizontally expanded. Anteriorly the ventral margin is thickened conspicuously enough to suggest reasonably close Therocephalian relationship.

On the whole, however, the vomer is a thin vertical plate with both upper and lower margins distinctly grooved. The groove in the upper margin obviously received the ventral margin of the cartilaginous mesethmoid. The grooved nature of the ventral margin evidently suggests that it found support in the soft tissues that linked the left and right palatal plates.

Anteriorly the vomer rests in a groove on the dorsal side of a median process formed by the premaxillaries. This process splits into separate elongated tapering projections which extend either side of the thickened ventral border of the vomer. From this level the median vertical plate extends freely, with no bony support, through the ventral part of the nasal cavity until it reaches the palatines dorsally to the internal nares and at the level of the posterior borders of the palatal plates. Here the palatines form an inverted V-shaped roof to the internal nares and the vomer firmly lodges itself in this groove. In this region the vomer is broadly expanded from its dorsal margin outward and downward, to overlap the palatines and the anterior ends of the pterygoids ventrally. The vertical plate below rapidly loses height and tapers out before reaching the posterior horizontal end of the vomer. The ventral margin of the vertical plate is already elevated well above

the palatal plates at a level far forward of the palatal foramina. From the level of the posterior borders of the palatal plates backward the median keel is not grooved along the ventral margin.

The *palatines* contribute much more substantially to the palatal plates than is apparent in ordinary ventral view. Their contributions to the palatal plates extend far forward and sideward above those of the maxillaries. Anteriorly they peter out into very thin films of bone.

It often appears, in a specimen not adequately cleaned, as though the palatal foramina are formed within the suture between the palatines and the maxillaries. In this specimen it is quite clear that these foramina penetrate through the centre of the palatal plates of the palatines, the maxillary plates merely reaching their anterior borders as a result of their broad overlap ventrally. In *Akidnognathus parvus* these openings are almost completely surrounded by the maxillaries, the palatines barely closing them off posteriorly. The whole structure is different, of course, on account of the nature of the elementary "secondary palate" ridges.

Forward of the posterior borders of the palatal plates the palatines contribute substantially to the side walls of the nasal cavity. Posteriorly these lateral vertical plates turn over inward to form roofs to the choanae. The anterior margins of these roofs are level with the posterior borders of the palatal plates. These margins are not sharp, but considerably thickened to form vertical walls extending transversely and upward, thus presenting with their posterior faces suitable areas for the insertion of the anterior oblique muscles of the eyes.

The posterior borders of the palatal plates are carried backward as two ridges either side, the outer ridge extending to the pterygoid process, while the inner ridge extends to the margin of the interpterygoid fossa. Between the two inner ridges the palatines extend upward and inward over the posterior end of the vomer and the anterior ends of the pterygoids, but they do not quite meet one another on the midline.

The *pterygoids* are strikingly similar to those of *Ictidosuchops*. They are Therocephalian-like, especially as they form between them a large interpterygoid fossa and as they bear at least one tooth each on a rather prominent tuberosity either side between the pterygoid processes. In the Procynosuchids the pterygoids are known to some extent only in *Procynosuchus delaharpeae*. In shape and general disposition there seems to be reasonable similarity, but apparently both the interpterygoid fossa and the tooth-bearing tuberosities are absent. The pterygoids are not known in already described Silphedestid-like forms. In the present specimen the pterygoids are Cynodont-like only in the appreciable length of the pterygoid processes.

The pterygoids meet one another firmly and with broad areas of contact, in front of the interpterygoid fossa, where they contribute to the forming of the dome-like

roof to the choanae. Their anterior tips extend forward over the vomer and their joint dorsal margin contains a groove continuous with the groove in the vomer anteriorly. This groove is carried back into the interpterygoid fossa.

At the level of the anterior border of the interpterygoid fossa the pterygoids form large Therocephalian-like tuberosities bearing at least one tooth each, a condition also reminiscent of that found in *Aneugomphius*. More laterally the pterygoids form conspicuously long processes guiding the lower jaw.

Either side of the interpterygoid fossa the pterygoids are continued backward as massive processes with deeply concave ventrolateral surfaces. The ventromedial edges contributing to the borders of the interpterygoid fossa are very thick, in contrast with the dorsolateral edges, bent downward sharply, which are very delicate indeed. At the level of the internal carotid foramina the margins of the former terminate abruptly and the pterygoids are continued backward only by the latter margins, forming the characteristic quadrate processes. These processes maintain their general breadth and thickness throughout; at no point do they lend any significant support to the alisphenoids. In this specimen, however, the quadrate processes do not make contact with the quadrates, but turn abruptly inward level with the latter to cover the pro-otics dorsolaterally. This arrangement has not yet been encountered in other Therapsids, but it may be due to inadequate preparation, preservation or investigation.

The projections tending to close the interpterygoid fossa posteriorly are in loose contact with the basisphenoid and the general articulation is strongly suggestive, as in the Scaloposaurids, of a recent loss of kinetism. This circumstance is supported by the grooves in the parietals into which the dorsal margins of the pro-otics fit very loosely, and the still inadequately ossified dorsal part of the supraoccipital.

The *alisphenoids* are Cynodont-like in being broadly expanded, but Therocephalian-like in their feeble overlap of the pro-otics. Their anteroventrally directed pterygoid processes are long and broad. They swing inward underneath the rostrum, barely touching the basisphenoid, and terminate loosely above the basisphenoid process of the pterygoids. Their terminal margins reach towards crests rising upward from the borders of the interpterygoid fossa, that is, from the medial margins dorsally of the basisphenoid processes of the pterygoids. The rest of the ventral margins of the alisphenoids conform very well with the dorsal margins of the quadrate processes of the pterygoids, but nowhere is there any real contact.

The anteroventral processes of the alisphenoids had evidently lifted away from the basisphenoid processes of the pterygoids. The natural condition must have been the same as that encountered by Broom (1938) in *Procynosuchus delaharpeae*.

The anterior margins of the alisphenoids are very thick. The alisphenoids broadly overlap the parietals dorsally, peculiarly enough, on the outside. How natural this

condition is can only be judged in terms of the distortion the skull had suffered, which is exceptionally negligible.

In spite of the difference in the extent of expansion, there is far greater similarity between the alisphenoids of this specimen and those of *Ictidosuchops*, than with those of *Procynosuchus delahapeae*.

The *orbitosphenoids* are very delicate thin plates of bone. They have been pushed out of their normal positions, both lying against the ventral surface of the left frontal and protruding from the brain case in front of the left alisphenoid. They might have suffered some additional damage and it is consequently inadvisable to evaluate them with any degree of confidence. If the two flakes actually do represent the complete bones, the arrangement is different from that encountered in higher Cynodonts like *Diademodon* (Brink, 1955). They could then not have formed a well enclosed chamber with the frontals above, to accommodate the olfactory lobes. Apparently they merely represented platelike ossifications of the sides of the otherwise normal trough-shaped cartilaginous orbitosphenoids, an indication of some degree of immaturity.

The *basisphenoid-parasphenoid* relationship is rather clear. The basisphenoid is a distinct continuation forward of the basioccipital, with which it appears to be already well fused as no suture was encountered. It grows narrower forward but expands again laterally across the internal carotid foramina, actually as two separate left and right swollen projections. These projections have delicate contacts above with the anteroventral processes of the alisphenoids and are very loosely touched ventrally by the basisphenoid processes of the pterygoids. Between them the parasphenoid passes upwards to form the rostrum. The internal carotid foramina are canals passing upward between the anterolateral lobes of the basisphenoid and the parasphenoid keel.

The parasphenoid covers the basisphenoid ventrally and laterally, the anterolateral lobes of the latter being the only parts visible in ventral view. Before passing upwards as the rostrum, the parasphenoid forms a short pointed keel very shortly behind the internal carotid foramina. The rostrum extends upward and forward well above the interpterygoid fossa, no doubt to support the orbitosphenoid structure and the brain behind the olfactory lobes.

The rostrum is V-shaped in cross-section, the V becoming larger and deeper backward. Shortly after the groove reaches the basisphenoid it suddenly becomes much deeper, much wider, more U-shaped, and drops to a lower level. This part is the sella tursica, but the dorsum sellae which is prominent in higher Cynodonts is conspicuously absent. There is a casual rise in the level of the floor, where the lateral border ridges also disappear, in the position of the dorsum sellae. Farther back the floor of the brain case is quite flat, where it widens to the level of the vestibules. The pro-otics have casual contact with the margins of this part of the basisphenoid.

STRUCTURE OF THE LOWER JAW

The *dentaries* are conspicuously short. They barely reach the level where the postorbital arches should be but, peculiarly enough, the coronoid processes are very well developed, better than in the *Procynosuchids*. They are bent upward more sharply and there is a more distinct angle posteroventrally, features in which this animal contrasts sharply with the *Silphedestids*. It is difficult to appreciate why these coronoid processes are so well formed, because they are too far forward for the effective attachment of the jaw muscles. This is especially surprising considering the absence of the jugal arches.

Apparently the temporal muscles operate the parietals and the surangulars, while the masseters, extending from the outer surfaces of the coronoid processes to the jugal processes evidently played a very minor role, perhaps largely effecting an antero-posterior movement of the jaw. There could not have been an effective remnant of the levator mandibulae. The degastricus muscles were inserted on the angulars, with the reflected laminae penetrating them in the direction of their pull.

Another conspicuous feature about the dentaries is the very high symphyseal region, with a distinctly angled, almost *Gorgonopsia*-like "chin". This feature suggests that the unusually large lower canines are an established characteristic of the animal.

The four incisors either side are nevertheless very small. They increase in size from the first to the fourth. None of the incisors showed signs of replacement, neither did the large canines except for one very small bud medially to the left tooth. The post-canines, on the contrary, are being replaced in a more prolific manner than the upper cheek teeth. Not only were tooth buds encountered with every tooth; in the case of the fourth tooth on the left side and the second, fifth and ninth teeth on the right side, the successors had erupted quite far, while the predecessors are still functional.

The *splenials* are not rod-like as in higher *Cynodonts*. They are flat strips of bone with their ventral margins slightly heavier than the dorsal margins. The former margins closely accompany the ventral margins of the dentaries, while the latter margins reach from halfway to the alveolar border anteriorly, to nearly within reach of it at the tenth tooth.

Anteriorly the splenials contribute substantially to the symphysis. From behind the symphysis they cover a well excavated groove on the medial side of each dentary, which run rather close to the ventral borders of these bones in comparison with the condition in higher *Cynodonts*. These grooves grow larger backward and in the posterior halves of their lengths they accommodate the anterior ends of the angulars. The splenials cover these anterior pointed ends of the angulars and extend backwards below them to just beyond the margin of the dentary. Above the angular tips they cover small corners of the coronoids.

The *coronoids* are small plates of bone lying immediately behind the last post-canine teeth on the inside of the coronoid processes. With the lower jaw closed, they slide against the outer faces of the pterygoid processes. They cover the anterior ends of the surangulars and prearticulars and are themselves covered very briefly over their anteroventral corners by the splenials.

The *surangulars* are flat plates of bone extending in arch-like fashion from the coronoid processes to the articulars. Each bone is properly boomerang-shaped, not only where the posterior half extends at an angle to the anterior half, but also where the two blades are not in the same plane. The anterior blade is nearly in the vertical plane while the posterior blade leans with its dorsal margin outward. The outer surface of the posterior blade is concave. Far back a ridge arises in the middle of the inner face, tending to cover the articular dorsally.

From behind the margin of the dentary the surangulars have rather strong dorsal margins. The ventral margins are very sharp.

The *angulars* are peculiar in that they fulfil three different functions. Consequently each bone consists of three contrastingly different parts. The most important part forms a stem which carries the dentary. It is projected forward as a long tapering process lodged firmly in the mental canal. Its dorsolateral surface is deeply troughed so that the mental canal is not properly filled by this process. The process is covered posteriorly by the prearticular and anteriorly by the splenial, but the mental foramen is left as a gap between these bones.

The second almost equally important part of the angular bone is a wide fan-like plate extending backward across the outer faces of the articular and the surangular. It serves to strengthen the rather delicate structure of this post-dentary region. It has a thick ventral margin accompanying the articular and a sharp dorsal margin where it broadly overlaps the surangular.

The third portion forms the characteristic reflected lamina with its peculiar Z-shape in cross section. The function of this lamina is obscure. It developed probably as a "reaction" to the substitution of the digastric muscles for the depressor mandibulae.

In this form the reflected lamina is smaller than in the *Procynosuchids*. They project more outward and downward, leaving substantial spaces between them and the fan-like posterior portions.

The *prearticulars* are elongated plates continuous with the anterior ends of the articulars. Their slightly expanded anterior ends penetrate below the coronoids, where they overlap the tips of the surangulars.

The *articulars* increase substantially in breadth backward, from where they join the prearticulars to where they form broad surfaces for articulation with the quadrates. These surfaces slope downward medially and extend convexly in approxi-

mately an anterior-posterior direction. The central parts of the articulation areas are slightly depressed to correspond with a slight swelling in the rod-like quadrate condyles.

There is a short process directed ventrally at the posterior end of each articular bone.

RELATIONSHIP

For a proper evaluation of the relationship of this interesting form it is best to summarise its characteristics and peculiarities while classifying them into various relevant categories. Firstly its Therocephalian-like features are balanced against its Cynodont-like features. Thereafter its proximity to the Procynosuchids or the Silphedestids is tested against lists of relevant characteristics. An endeavour is made to list the various items roughly in the order of their significance, but this order is somewhat prejudiced in favour of structural continuity.

A. *Therocephalian-like features.*

1. The interpterygoid fossa is perhaps the most striking Therocephalian feature. It is comparable in almost every detail with that of the Ictidosuchid-Scaloposaurid branch of the Therocephalia. It is absent in the Procynosuchids and all later Cynodonts but unfortunately the condition is not known in the Silphedestids.
2. The posorbital arches are evidently incomplete. This is a striking Scaloposaurid characteristic, but it is also found in the Silphedestids.
3. The zygomatic arches are interpreted as incomplete. If this interpretation is incorrect, the alternative is very delicate Scaloposaurid-like arches, most unlike the Cynodont type. However, incomplete arches are found in the Silphedestids. This condition could only develop from a Scaloposaurid-like arrangement.
4. The tooth-bearing tuberosities of the pterygoids are typically Scaloposaurid. This condition is not found in any Cynodont described so far. The region is, however, unknown in the Silphedestids.
5. Besides the interpterygoid fossa and the tooth-bearing tuberosities the general build of the pterygoids is more Therocephalian-like than Cynodont-like.
6. The transverse bones contribute rather substantially to the pterygoid processes. This is not very apparent, as the portions formed by the pterygoids are very elongated in the Cynodont manner.

7. The parasphenoid keel and rostrum is very similar to those of the Scaloposaurids and quite different from the condition in the Procynosuchids or later Cynodonts. This region is not known in the Silphedestids.
8. The sella tursica is not deeply excavated and the dorsum sellae is consequently weakly developed.
9. The posterior face of the skull is Therocephalian-like in general build, especially in the shallowness of the occiput and external auditory meatus areas. The occipital crests are low and not very sharp.
10. The paroccipital processes are short and slender. The Cynodont paroccipital is rather long and heavily built.
11. The squamosals have a feeble structure in the region of the quadrates.
12. The parietal region is not sharply crested. It is very like the Scaloposaurid condition, but a similar arrangement is found in the Silphedestids.
13. The pineal is situated far back.
14. There is a weak overlap between the alisphenoid and the pro-otics. While the alisphenoids are broad as in the Cynodonts they are in height more comparable with the Therocephalia.
15. There is no naso-lachrymal contact, a rather pronounced Therocephalian feature.
16. The prefrontals tend to broaden the antorbital region as in the Scaloposaurids.
17. It is not clear whether the frontals contribute to the orbital borders. If they do, which is just possible, this would be a significant Therocephalian feature.

B. *Cynodont-like features*

1. The cleft secondary palate is very typical of the type found in the Procynosuchids and Galesaurids. This type of palate is found nowhere in the Therocephalia. In spite of the long list of Therocephalian features given above, this characteristic alone is sufficient for reaching the conclusion that the specimen is a Cynodont. It is most unfortunate that the Silphedestid palate is not known.
2. The postcanine teeth are cusped in the typical Procynosuchid fashion.
3. The occipital condyle is Cynodont. It is more deeply crescent-shaped, presenting two more distinctly separate exoccipital condyles, than in the Procynosuchids.
4. The lower jaw symphysis is very advanced Cynodont-like.

5. In spite of their size the dentaries form good coronoid processes of rather advanced Cynodont shape.
6. The alisphenoids are very broad.
7. The pterygoid processes are very elongated.
8. The posttemporal fossae are small and they cause no serious excavation of the posterodorsal surfaces of the paroccipital processes. These processes also form feeble roofs to the middle ears.
9. The suborbital foramen had closed nearly completely.
10. If the frontals are actually excluded from the orbital borders, this circumstance can be taken as a good Cynodont feature.
11. The bone interpreted as quite likely a stapes has a stapedia foramen.

C. *Procynosuchid* and *un-Silphedestid-like* features

1. The secondary palate is similar in every respect to the type found in the *Procynosuchids*.
2. The vomer agrees perfectly with the *Procynosuchid* arrangement. It is not known in the *Silphedestids*.
3. The double exoccipital condyles appear to be even more advanced than in *Procynosuchus*.
4. The dentaries are short but with distinct coronoid processes.
5. The manner and extent of tooth replacement is similar to that found in the type of *Procynosuchus delaharpeae*.
6. The pterygoid processes are significantly elongated.
7. There is no significant suborbital fossa.

D. *Silphedestid* and *un-Procynosuchid-like* features

1. There are no zygomatic arches.
2. The postorbital bars are incomplete. The *Silphedestid* postorbitals are, however, apparently larger and do not form significant postorbital processes.
3. The interparietal crest is absent and the region is rather broad. The position of the pineal is not known in the *Silphedestids*.
4. The *Silphedestid* occiput appears to be comparable with that of the present specimen.
5. There is no naso-lachrymal contact.
6. The squamosals have a delicate build in the region of the quadrates.

Ē. *Features both un-Procynosuchid and un-Silphedestid*

1. The dental formula is different from both in that there are 7 incisors and one canine.
2. The highly placed and weakly developed premaxillaries are peculiar.
3. The depth of the symphysis is also unique for so early a Cynodont.
4. The anterior incisors are smaller than the posterior ones, an arrangement which is foreign to the Therocephalia and Cynodontia as a whole.
5. The canines are very large.
6. The parietal region is not constricted behind the pineal.
7. The height of the alisphenoid and the extent to which they overlap the parietals laterally is also rather peculiar.

The above analysis makes it unmistakably clear that the present specimen is a Cynodont, but one which has retained a remarkable number of Therocephalian characteristics. In fact, disregarding for a moment its few advanced characteristics like the loss of the anterior canines and the incomplete zygomatic arches and postorbital bars, this specimen can be taken as a form representing the stage where the Cynodont branch actually diverged from the Ictidosuchid-Scaloposaurid branch of the Therocephalia. The divergence must have taken place at the lower Ictidosuchid level, as both structure and age tend to suggest.

When the advanced features are taken into consideration it is clear that the present form had made some progress away from the level of origin, as the Scaloposaurids had progressed beyond the Ictidosuchid stage. It is interesting to note the similar changes occurred along both lines; the loss of anterior canines and the reduction of the postorbital and zygomatic arches.

It is also sufficiently clear from the above analysis that the present specimen is more at home with the inadequately known Silphedestids than with the Procynosuchids. However, the palate suggests that there is close affinity between these families, the Procynosuchids having specialized very early away from the Silphedestid line, as had the Bauriidae diverged from the Scaloposaurid line.

It is rather apparent that the "Silphedestids" actually represent more than one family. *Protocynodon* is a member of this branch, a form which appears to be structurally more primitive, but it is more recent in time than *Scalopocynodon*. *Silphedestes* and *Silphedocynodon* are also later forms and the branch apparently continued into the Cynognathus zone. No doubt, while the already described Silphedestids may represent more than one family, the present *Scalopocynodon* may represent yet another family.

The present investigation has made it eminently clear that the "Silphedestids" are not assignable to the Scaloposaurids as suggested by Watson and Romer (1956). In their classification they put the "Silphedestids" with the Scaloposaurids, thereby suggesting that although they are earlier in time, they are advanced forms, even if this is apparently based only on the extent of their degeneration. In all fairness it should, however, be noted that Watson and Romer did not know of a Silphedestid-like form with a Procynosuchid-like palate. Although the palate is unknown in the already described Silphedestids, their temporal regions are sufficiently comparable with that of *Scalopocynodon* to permit their transfer back to the Cynodontia, to conform with the classification suggested by Houghton and Brink (1954).

Watson and Romer (op. cit.) are also inclined to doubt whether the absence of the postorbital bars and zygomatic arches is natural. They suggest that the condition is due to damage. With these small specimens it is difficult to arrive at a definite conclusion either way; one can merely describe what the specimens tend to convey. However, for the several reasons mentioned above, the author is convinced that the absence of postorbital bars and zygomatic arches is the natural condition in *Scalopocynodon*. If it can be demonstrated that the already described "Silphedestids" actually had close affinity with *Scalopocynodon*, their missing arches might not be quite as artificial as Watson and Romer are inclined to believe.

LITERATURE CITED

- BRINK, A. S. (1951), Some small Cynodonts. *S. Afr. J. Sci.*, vol. 47, p. 338.
- BRINK, A. S., (1953), On *Leavachia duvenhagei* and some other Procynosuchids in the Rubidge Collection. *S. Afr. J. Sci.*, vol. 49, p. 313.
- BRINK, A. S., (1955). A study on the skeleton of *Diademodon*. *Palaeont. Afric.*, vol. iii, p. 3.
- BRINK, A. S., (1956), On *Aneugomphius ictidoceps* Broom and Robinson. *Palaeont. Afric.*, vol. iv, p. 97.
- BROOM, R., (1937), A further contribution to our knowledge of the fossil reptiles of the Karroo. *Proc. zool. Soc.*, p. 299.
- BROOM, R., (1938a), On the structure of the skull of the Cynodont *Thrinaxodon liorhinus* Seely. *Ann. Transv. Mus.*, vol. xix, p. 263.
- BROOM, R., (1938b), The origin of the Cynodonts. *Ann. Transv. Mus.*, vol. xix, p. 279.
- BROOM, R., (1948), A contribution to our knowledge of the vertebrates of the Karroo beds of South Africa. *Trans. roy. Soc. Edinb.*, vol. lxi, p. 577.

- BROOM, R., (1949), New fossil reptile genera from the Bernard Price Collection. *Ann. Transv. Mus.*, vol. xxi, p. 187.
- CROMPTON, A. W., (1955), A revision of the Scaloposaurids with special reference to kinesis in this family. *Res. Nas. Mus.*, vol. i, p. 149.
- HAUGHTON, S. H. & A. S. BRINK, (1954), A bibliographical list of Reptilia from the Karroo beds of Africa. *Palaeont. Afric.*, vol. ii, p. 1.
- WATSON, D. M. S. & A. S. ROMER, (1956), A classification of Therapsid reptiles. *Bull. Mus. Comp. Zool.*, Harvard, vol. 114, p. 37.

ON SOME SMALL THEROCEPHALIANS

By A. S. BRINK

ABSTRACT

The snout of a new specimen of *Akidnognathus parvus* is described in detail from serial sections at .5mm. intervals. Special reference is made to the structure of the septomaxillary and its possible morphological significance. It is suggested that its peculiar arrangement is relatable to a readaptation in the mode of smelling in mammal-like Reptiles. Additional descriptions deal with new specimens assignable to *Ictidostoma hemburyi*, *Ictidosuchops intermedius*, *Ictidosuchops bauroides* and *Ictidosuchoides longiceps*. All descriptions are accompanied by adequate figures. The new information adds little to existing views on the relationship of the families Ictidosuchidae and Scaloposauridae.

INTRODUCTION

An interest in the peculiar arrangement of the septomaxillary in Therapsids, especially with a view to its possible relationship to the organs of Jacobson and the change from the reptilian to the mammalian mode of smelling, has induced the author to grind serially the snout of a small Therocephalian in which these bones are well preserved. The intention was, and still is, to grind serially and graphically reconstruct in wax as many Therapsid specimens as possible, representing a cross-section of this fauna, with the object of creating a broad and clear comparative anatomical picture to which certain physiological considerations can be related.

It was in due course appreciated that there are not enough small duplicate specimens available, fit for serial grinding, with well preserved septomaxillaries, and at the same time also representing each major type of mammal-like reptile. Besides, at the very outset this task proved to be too ambitious for a single research project and the subject should better be dealt with in a series of phases. Each specimen, after serial grinding, presents itself as a subject for a substantial descriptive paper, more so when it draws attention to several other specimens which had previously suffered some neglect.

These are the circumstances which led to the presentation of this paper. The specimen serially sectioned is described first, with some emphasis on the septomaxillary and casual reference to some speculative views which the author holds about its peculiar nature. Thereafter descriptions follow of several other Therocephalians of similar size — not necessarily of close affinity.

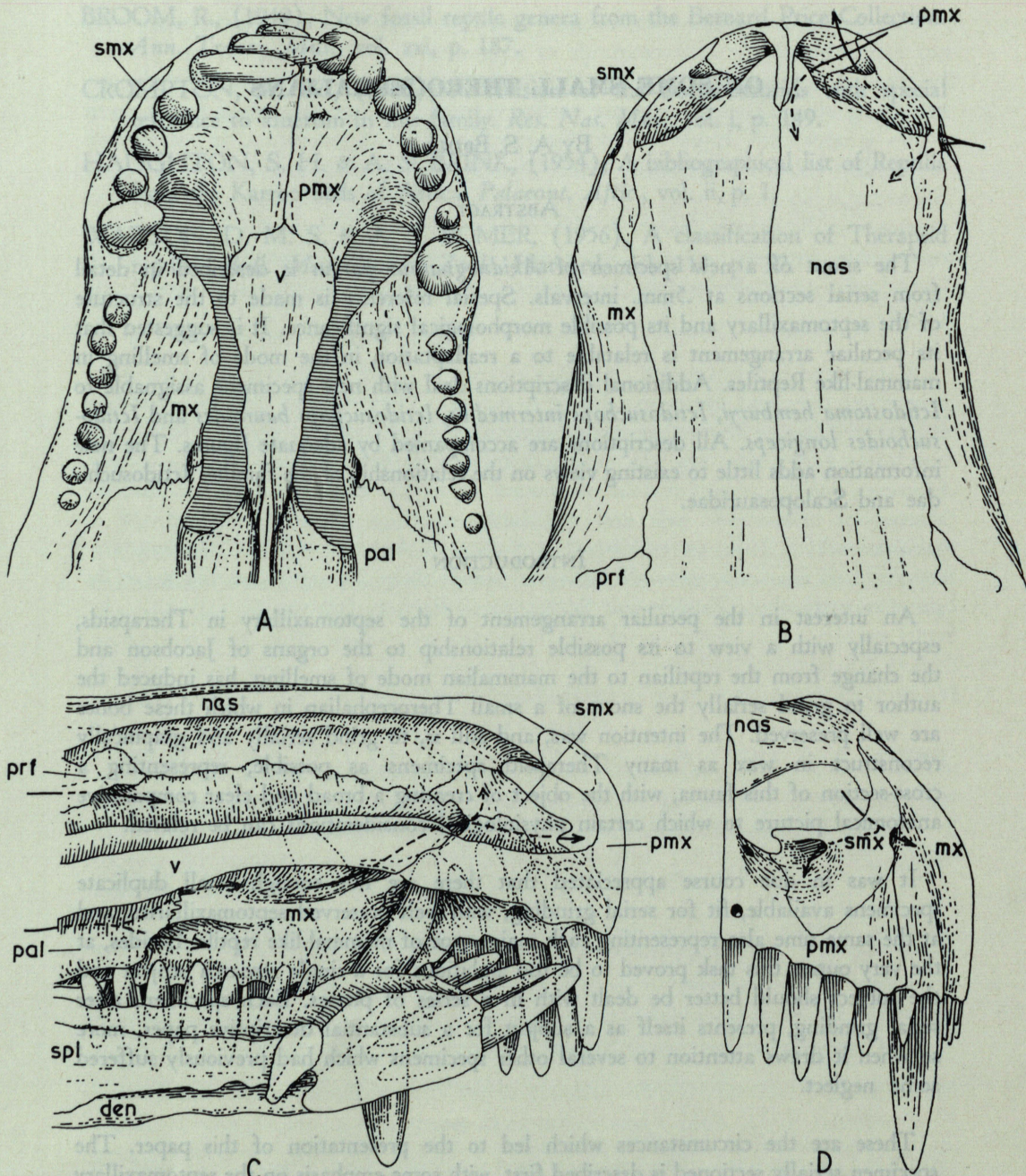


Figure 36

A, Palatal; B, Dorsal; C, Sagittal and D, Anterior views of the snout of *Akidnognathus parvus*, graphically reconstructed from a complete series of parallel sections at .5 mm. intervals. Twice natural size. For abbreviations see end of article.

Akidnognathus parvus Haughton
(Figures 36 and 37)

1918 HAUGHTON, S. H., *Ann. S. Afr. Mus.*, XII, p. 192, figs. 51, 52.

1932 BROOM, R., *Mammal-like Reptiles*, p. 64, figs. 20C, D.

Type: Skull in the South African Museum, Cape Town (No. 4021), from *Cistecephalus*-zone beds on the farm Zuurpoort in the Graaff-Reinet District.

Present specimen: Snout, serially sectioned, represented by a cast, a detailed wax model four times natural size and a complete series of section figures, in the Bernard Price Institute (No. 340) from the *Cistecephalus*-zone, near the *Endothiodon*-zone contact, on the Graaff-Reinet Commonage (Collector: Mr. B. J. Kitching).

The process of grinding was undertaken with the aid of the Croft Parallel Grinder. The specimen was embedded uncleaned in calistone and secured to the specimen holder with bee's wax. Section intervals are consistently .5mm., and every section was drawn with the aid of an Opague 1000 Delineascope (standard episcope of the American Optical Company). The episcope was secured to a stable horizontal bench surface at a distance from the "screen" calculated to project images at exactly 4 times natural size, with lens settings and focus fixed. The platform was made to drop lower than the design permits by securing the supports to left and right wooden strips of desired thickness and by removing the cross bar at the back on which the platform catches when it is desired to leave it in the open position.

A receptacle constructed of $\frac{1}{4}$ " masonite was bolted on to the platform. It was accurately constructed to receive the specimen holder, taken from the Croft Parallel Grinder, always in the same position. On raising the platform, the ground surface of the specimen was consistently from the first to the last section brought up against the glass pressure plate and it was thus ensured, with focus, lens setting and elevation fixed, that a standard 4 times natural size projection was obtained on a stable drawing board "screen", erected in the vertical plane. Moreover, successive projections proved to coincide exceptionally accurately as a result of the limitations of movement in the process to an absolute minimum. The only movement was bringing the specimen with holder from the Croft Grinder to the projector, but it fitted into the projector as accurately as in the grinder. The design of the platform elevating mechanism ensured the most accurate positioning against the glass pressure plate that could be desired. On the drawing board, standard sized paper with two standard holes were positioned over two fixed pegs, these holes having served as the base line for both graphical figuring and wax reconstruction. No base line indicator was associated with the specimen itself.

This procedure is exceptionally simple and easy to handle, without prejudicing accuracy. In fact, the procedure proved to be so accurate that hardly any ziz-zag difficulties were encountered in either figuring or reconstructing. The only disadvantage was tracing in the vertical plane. This could have been overcome by introducing a mirror, but it was considered that it would also introduce a certain measure of inaccuracy.

Grinding was performed with a standard No. 0 carborundum powder on a zinc plate. Each section was coloured with Alizarine Red and covered, when dry, with a thin coat of dilute glyptal cement, which had the effect of giving the surface a very glossy finish as though it had received the finest possible polish. This brought out all the details, especially colour contrasts, so clearly that detailed study under the binocular microscope proved to be hardly necessary. The projected image in total darkness (with the projector outside the dark room) was as clear as could be desired, even at only four times natural size.

The wax model was constructed with the aid of standard 1 mm. thick high stability "Modelling Wax" plates, an Amalgated Dental Product, "a specially toughened wax with wide temperature range particularly suitable for tropical climates".

Only the left half of the snout was reconstructed in wax (except for the vomer which is complete) to allow for a better study of the nasal cavity and to assist in preparing figure 36c.

When it was decided to subject the present specimen to serial grinding, the possibility was considered that it might turn out to be the type of a new form of Therocephalian, in spite of the fact that superficially it showed great likeness to another, much smaller specimen (which could subsequently be identified as an *Ictidosuchops baurioides*). As progress was made with the grinding, it became increasingly clear that it was quite a different form, but nothing could be done to avoid the possible situation where a type specimen would subsequently be represented by a wax model. Fortunately, however, after the specimen had been graphically figured and reconstructed in wax, it was discovered that it represents the form *Akidnognathus parvus*.

Identification is based on the following features:

- (1) The dental formula is $i5, c2, pc7$ as in the type.
- (2) The incisors are substantially larger than the post-canine teeth.
- (3) The fifth incisor is smaller than the other four, superficially quite near in size to the anterior canine, and there is a distinct diastema between these two teeth.
- (4) The seventh post-canine tooth either side is situated at a level forward of the posterior borders of the internal nares.
- (5) The palatal foramen on the palatine-maxillary suture is approximately at the level of the 5th post-canine tooth.

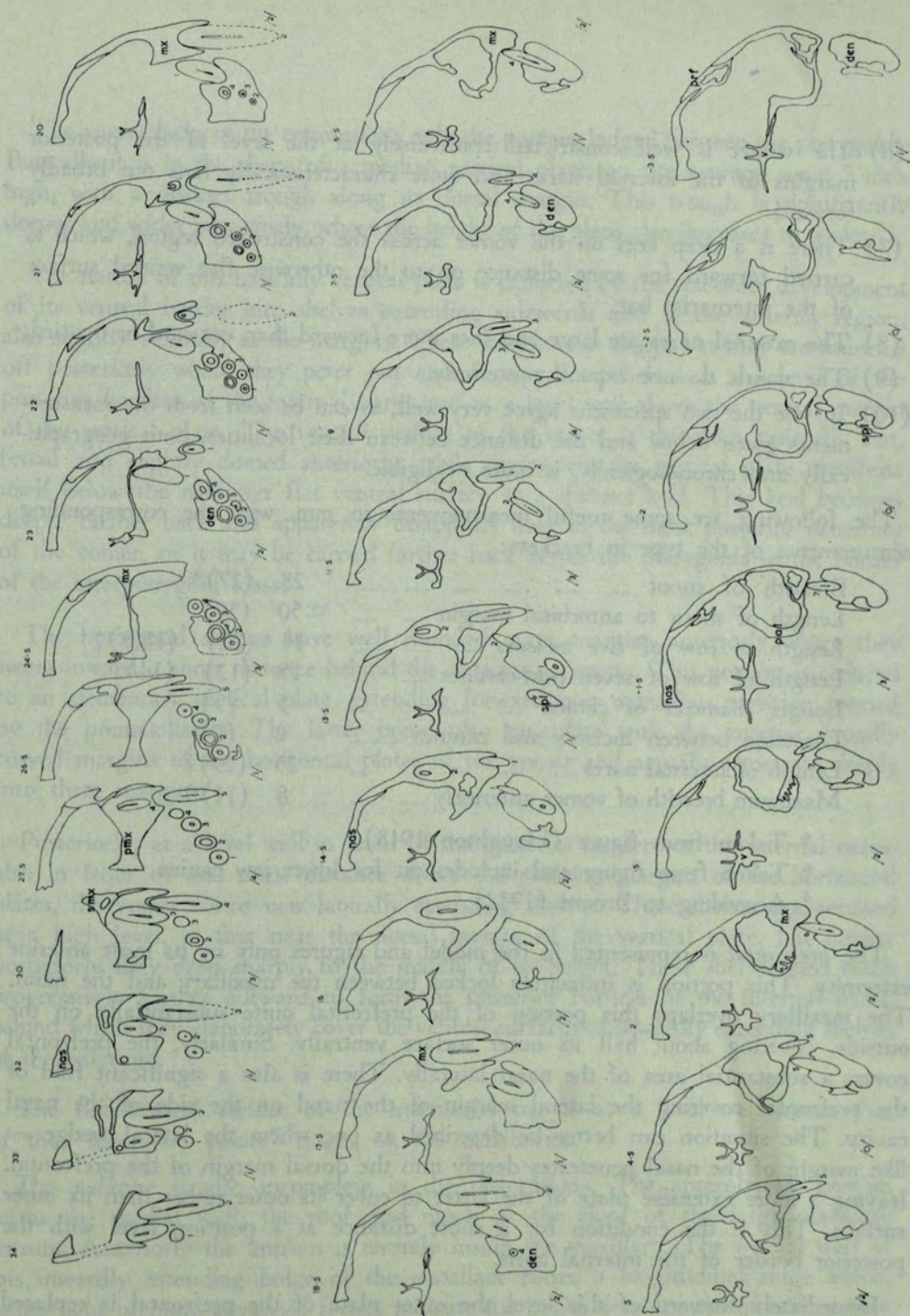


Figure 37

Series of sections following in order from left to right through the snout of *Akidnognathus parvus*.
Natural size.

Legend: Numbers above section figures are the levels in mm., 37 mm. being the level where first contact was made with the premaxillaries and grinding having been ceased at -3.5 mm. Numbers below and between section figures, between strokes, indicate, for easier interpretation, the number of sections at .5 mm. intervals that have been left out of the series in this illustration. Numbers accompanying teeth indicate their place in their respective incisor, canine and post-canine series.

For abbreviations see end of article.

- (6) The vomer is well constricted transversely at the level of the posterior margins of the internal nares and quite characteristically fans out broadly forward.
- (7) There is a deep keel on the vomer across the constricted region, which is carried forward for some distance on to the otherwise flat ventral surface of the internarial bar.
- (8) The external nares are large and face more forward than outward or upward.
- (9) The nasals do not expand posteriorly.
- (10) In size the two specimens agree very well, as can be seen from the measurements given below and the distance between their localities, both geographically and chronologically, is quite negligible.

The following are some useful measurements in mm. with the corresponding measurements of the type in brackets:

Breadth of snout	28	(27)*	
Length of snout to antorbital margin	±50	(50)	
Length of row of five incisors	14	(22)	(18.5)†
Length of row of seven post-canines	15	(12)	(14)‡
Longer diameter of canine	5	(5)	
Diastema between incisors and canines	2	(2)	
Length of internal nares	25	(29)†	
Maximum breadth of vomer anteriorly	8	(11)*	

* Taken from figure (Haughton 1918).

† Taken from figure and includes pit for lower jaw canine.

‡ According to Broom (1932).

The *prefrontal* is represented in the model and figures only by its most anterior extremity. This portion is intimately locked between the maxillary and the nasal. The maxillary overlaps this portion of the prefrontal quite substantially on the outside, covering about half its outer surface ventrally. Similarly, the prefrontal covers a substantial area of the nasal laterally. There is also a significant fold of the prefrontal covering the lateral margin of the nasal on the side of the nasal cavity. The situation can better be described as one where the lateral wedge — like margin of the nasal penetrates deeply into the dorsal margin of the prefrontal, leaving a more extensive plate of the latter to cover its outer rather than its inner surface. This is the condition for a short distance at a position level with the posterior border of the internal naris.

Immediately forward of this level the outer plate of the prefrontal is replaced by a similar fold of the maxillary, while on the side of the nasal cavity the inner plate becomes more extensive as it forms, in addition, the dorsal margin and roof of the foramen linking the nasal cavity with the vacuity accommodating the lachrymal duct. Shortly forward of this opening the prefrontal terminates.

The *vomer* lacks in the restorations only the portion lodged between the pterygoids. Basically it is in the shape of a median vertical plate, on the average some 5 mm. high, with a distinct trough along its dorsal margin. This trough is significantly deeper and wider posteriorly, where the height of the plate also increases to 6 mm.

The nature of this basically vertical plate is distorted by the elaborate development of its ventral border into shelves extending sideways and in the anterior region, also slightly ventrally at the margins. These margins are sharp, but they are rounded off posteriorly where they peter out and disappear as shelves at the level of the posterior borders of the internal nares and at a level well above the ventral margin of the vertical plate. The ventral surface of the vomer is therefore generally flat, broad and slightly domed anteriorly, while posteriorly the vertical plate manifests itself below the narrower flat ventral surface as a distinct keel. This keel becomes deeper farther back and apparently disappears only in the most posterior extremity of the vomer, or it may be carried farther back across the pterygoids to the border of the interpterygoid fossa.

The horizontal shelves have well rounded outer margins anteriorly where they swing inward a short distance behind the anterior extremity. This portion is reduced to an elementary vertical plate, extending forward over a median partition formed by the premaxillaries. The latter bones also articulate with the anterior broadly curved margins of the horizontal plates of the vomer and actually penetrate deeply into these margins.

Posteriorly, at a level well in front of the posterior borders of the internal nares, also in front of and some distance above the petering margins of the horizontal plates, the vomer forms new laterally extending shelves. These shelves are situated at a high level, at first near the dorsal margin of the vertical plate, but farther posteriorly they drop sharply to the middle of its height. These shelves also reach progressively farther outward to form the posterior borders of the internal nares, behind which they elaborately cover the ventral surfaces of inwardly extending shelves of the palatines.

The flat ventral surface of the internarial bar is at a level well above that of the "secondary palate" ridges on the maxillaries.

The *palatine* is also incomplete in the restorations. The anterolateral portion forms the medial wall, the roof and much of the floor of the large maxillary antrum. Anteriorly the antrum is entirely inside the maxillary. The medial wall of this inwardly extending bulge of the maxillary forms a longitudinal ridge which, in the light of more advanced forms, indicate the initial development of a secondary palate. This ridge is not carried back distinctly on to the palatine. Immediately below the ridge, still in the maxillary, is the palatine foramen, bordered posteriorly by the palatine. Haughton (1918) figures these foramina as situated more entirely inside the palatines, but the palatine-maxillary suture is so elaborately interdigitated

in this region that such a variation can quite likely occur within the same species. Otherwise, a slight under- or overdevelopment in the process of cleaning could also be responsible for presenting this difference.

Another foramen is situated directly above in the roof of the antrum, also in the maxillary and bordered posteriorly by the palatine. The palatine reaches farthest forward between these two foramina.

Dorsally on the roof of the antrum the palatine is met halfway by a shelf of the maxillary. This shelf is restored farther back to allow the palatine to form the whole of the roof. However, at the very level of the posterior border of the internal naris the palatine falls away from the maxillary, leaving a wide opening between the antrum and the nasal cavity. At this level it very abruptly sends a shelf inward to the vomer, the latter covering its ventral surface extensively. Exactly on the posterior border of the internal naris the palatine extension is not in the shape of an horizontal shelf; the margin is turned sharply upward to form a distinct vertical wall some 3 mm. high, extending transversely. The dorsal free margin of this wall is continuous with the border, formed by the palatine, of the wide opening between the antrum and the nasal cavity.

This vertical transverse wall served for the insertion of the anterior oblique muscles of the eye.

Along the floor of the maxillary antrum the palatine elaborately clasps the maxillary between extensive thin plates.

The *nasal* lacks its posterior extremity, but enough is preserved to show that, as in the type, it does not expand noticeably at the level of the anterior end of the prefrontal. This is a rather general Bauriamorph, or more particularly a Scaloposaurid characteristic.

The outer face of the downward inclined wedge-like lateral margin of the nasal is extensively covered by the prefrontal behind, the maxillary in the middle and the septomaxillary in front. Only the prefrontal endeavours to cover the nasal margin on the inside as well.

There is a distinct ridge running longitudinally some 5 mm. from the skull midline on the ventral surface of the nasal. This ridge evidently marks at least the initial development of a fronto-nasal ethmo-turbinal.

The *maxillary* is broadly depressed on the outside in the region above the roots of the cheek teeth and behind the slight bulge of the canine root. This depression does not affect the alveolar margin so that the snout is not constricted in dorsal view.

The maxillary carries a small canine in front on the border of the excavation for the lower jaw canine. The main canine is a large tooth and the sections show no indication, either left or right, of replacement — not even as far as elementary toothbuds are concerned. Behind the canine there are seven cheek teeth, subequal in size. On the right the fifth had been lost before fossilization, but quite likely after death, leaving an empty socket with no tooth bud. None of the cheek teeth show signs of recent or impending replacement.

All the cheek teeth are smaller than the incisors. The seventh cheek tooth is the smallest and equal in size to the anterior canine.

The elementary "secondary palate" ridge on the lingual aspect of the maxillary becomes progressively more crested forward of the palatal foramen and at the level of the canine, where the general inner face of the maxillary bulges markedly across the root, the crest becomes a distinct shelf, but turned upward to form a deep alcove. This deep hollow leads forward and upward to a foramen communicating with the outside surface of the snout. The crest of this upward inclined shelf also forms the anterior margin of the internal naris as it swings inward and backward to the vomer at a level immediately behind the tip of the lower jaw canine where the latter is in normal closed position. This portion of the border is formed by the premaxillary.

The *premaxillary* carries five teeth. The first four are quite large, but the fifth is reduced and the exposed crown is near in size to that of the first canine. When the roots are also compared, however, the fifth incisor is still substantially larger.

All the incisors (and the post-canine teeth) are directed straight down (excluding the last cheek tooth which leans with the crown backwards). The incisor roots curve slightly backwards in their sockets, the rather short root of the first tooth doing so somewhat more conspicuously. (Both canines either side project forward slightly.)

The premaxillary elaborately overlaps the maxillary on the side of the excavation for the lower jaw canine. Here, for some distance, it joins the maxillary in forming the upward turned crest, that is, the maxillary-premaxillary suture extends along the summit of the crest. Farther forward the premaxillary brings the crest inward to form the anterior border of the internal naris. More medially the premaxillary extends backward as a thin tapering projection cutting quite deeply into the border of the anterior rounded margin of the horizontal portion of the vomer. On the midline the premaxillary very suddenly attains substantial height as it builds, with its fellow of the opposite side, a median crest dorsally, continuous with the vertical plate of the vomer. The groove in the dorsal margin of the latter bone is not continued on to the premaxillary crest.

The premaxillary characteristically builds anteriorly, with its fellow of the opposite side, an internarial bridge which extends upward and subsequently backward, penetrating between the anterior ends of the nasals.

There is a peculiar canal penetrating the premaxillary. This canal extends well above and inside the root of the first incisor. Anteriorly it runs sharply downward to open on the surface immediately in front of the root of this tooth, shortly above the alveolar border. Dorsally it has a second opening intimately on the side of the base of the internasal bridge. The canal continues backward and has a third opening in the roof of the mouth immediately behind the first incisor.

The premaxillary builds a substantial floor either side in the anterior part of the nasal cavity. This floor is generally flat, somewhat depressed centrally. The floor rises very slightly towards the anterior margin of the internal naris. On the side of the mouth cavity the well excavated pit to receive the lower jaw canine is obtained more as a result of a reduction in the thickness of the bone laterally than of a general elevation of this massive plate-like shelf.

This floor in the anterior part of the nasal cavity is given a depressed appearance largely on account of the substantial upheaval anteriorly across the incisor roots, forming the ventral border of the external naris. Across this upheaval extends the septomaxillary. The otherwise fairly level floor extends straight forward to the anterior face of the snout through a narrow gap between the internasal bridge and a shelf-like crest of the septomaxillary. The floor also extends backward medially to the internal naris as a shallow groove above the horizontal shelf of the vomer, and laterally as a more distinct groove to the deep hollow between the upturned "secondary palate" crest and the bulge of the canine root.

The *septomaxillary* extends as a thin plate across the high and wide ventral margin of the external naris. It covers a considerably greater area on the anterior slope of this upheaval, formed by the roots of the incisors, than on the posterior slope. Medially it is entirely on the anterior slope and laterally it folds over to a slight extent on to the posterior slope, from where it continues backward and upward as a wedge lodged intimately between the nasal and the maxillary.

Along the crest of the upheaval forming the ventral border of the external naris, the septomaxillary grows quite thick and is traversed by a canal. This canal opens forward and inward into a conspicuously depressed area on the anterior face of the septomaxillary, this hollow being greatly exaggerated by the sharpness of the crest above, leaning forward as a roof over the foramen in particular and the depression in general.

The canal opens laterally into the foramen through which the trough in the nasal cavity above the "secondary palate" ridge leads to the outer face of the snout, immediately on the side of the external naris.

The sides of the depression on the anterior face of the septomaxillary do not slope towards the foramen, but towards the notch between the septomaxillary crest and the premaxillary internasal bridge, leading inward on the floor of the nasal cavity.

The general structure of this region is most peculiar, more so on account of the fact that it is typical of all carnivorous Therapsids, from the earliest Gorgonopsian, through all the Therocephalia and Cynodontia, to the most advanced Bauriarmorph. Quite conspicuous, too, is the fact that this peculiar arrangement is not characteristic of the herbivorous Dinocephalia and Anomodontia.

This arrangement has induced the author to consider to what extent it can be related to the organs of Jacobson and the function of smelling in animals where obviously a vast change must have occurred in this respect. These animals being transitional between reptiles and mammals must indicate how the change was effected from the reptilian way of smelling (basically by allowing the tongue to communicate directly with the organs of Jacobson) to the mammalian method of "sniffing". It is this interesting problem which induced the author to section the present specimen, but it was appreciated that a much broader picture is required before substantial conclusions can be formulated. The author intends, therefore, to section as many specimens as possible, representing the widest possible cross-section of Therapsids, to establish a detailed comparative anatomical picture on which more substantial views can be based. It was appreciated that this would be a lengthy and laborious task and that it would be advisable not to deal with the subject as a confined research project, but to report from time to time on results that are achieved. At this stage the author can only submit some speculative views, representing the line of thought on which this project is provisionally based.

At the outset it should be borne in mind that smelling is intimately associated with taste and that as far as the latter is concerned, the organs of Jacobson play a more definite and refined role than the taste papillae on the tongue. The tongue is also basically not intended to be a largely sensory taste organ, but a mechanical apparatus for assisting in the "manipulation" of food. It acquired a certain degree of taste sensitivity, but only to distinguish between major categories such as saltiness, sweetness, acidity and bitterness in their various degrees. The tongue must therefore decide immediately whether some particular food is consumable or not. The organs of Jacobson supplement by adding, through its ability to distinguish between the finer nuances in the field of odour, to an interpretation of the palatability of the food.

Smelling is therefore basically tasting and the organs of Jacobson are so conveniently situated in the roof of the mouth cavity or, otherwise, in the floor of the nasal cavity that they can detect odour either directly from the air inhaled or after it had become dissolved in the moisture of the mouth cavity.

In a reptile the detection of odour directly from the air inhaled is quite ineffective, firstly on account of the slow, irregular breathing and secondly on account of the dryness of the nasal passage. The organs of Jacobson are therefore directed toward the mouth cavity and in many forms the habit developed to allow the tongue to communicate directly with these organs. In many forms, too, the tongue is split and it is periodically projected from the mouth to allow odour to dissolve on its moist surface, after which it is retracted and passed through the internal nares to the organs of Jacobson.

In the mammal-like reptiles one major change contributed towards rendering this normal and basic way of tasting quite ineffective, that is, the development

of a secondary palate. As pointed out in a previous publication (Brink, 1956*) a secondary palate develops hand in hand with mastication, for three reasons:

- (1) To place the internal nares as far back as possible so as to allow the animal to breathe while masticating its food.
- (2) To prevent masticated food from passing into the nasal cavity.
- (3) To present a platform for the tongue to operate against in "handling" the masticated food.

It does not matter which one of these is taken as the principle function of the secondary palate. The major implication is that the communication between the tongue and the organs of Jacobson now becomes obstructed.

It would appear that the only alternative was for the organs of Jacobson to concentrate their attention directly to odours inhaled through the nasal cavity, thus changing their nature from taste to olfactory organs. This change could not be accomplished without involving a number of other significant adaptations.

The habit of mastication and the resultant development of a secondary palate cannot be regarded as having had a direct relatable effect upon the nature of the nasal cavity and breathing in general, other than that air now happens to pass for a longer distance through this cavity. To become effectively adapted for the function of smelling the nasal cavity had to undergo other changes, such as the extensive development of wet mucous tissues and additional elaborate ethmoturbinals to present the greatest possible surface for the inhaled air to pass over, so that the maximum amount of odour could be absorbed for detection. Mastication did, however, have a direct effect upon smelling in that it accelerated the general metabolism, which demanded an increased supply of oxygen, implying a faster rate of breathing, with or without reflections upon the significance of a diaphragm. This faster rate of breathing naturally facilitated the more effective absorption of odour in the nasal cavity and the diaphragm facilitated the phenomenon of deliberate "sniffing".

It should, however, be emphasised again that the major requirement for smelling is a wet nasal cavity with the greatest possible surface presented to the air passing through, and that this arrangement was not necessarily initiated as a direct consequence of the development of a secondary palate. The two developments cannot be interpreted as having occurred hand in hand, and it can virtually be taken for granted that some time passed between the stage when the organs of Jacobson had lost their communication with the mouth cavity and before they were amply re-adjusted to detect odour directly from the air "sniffed" through the elaborate nasal cavity. The peculiar nature of the septomaxillary must be indicative of an intermediate stage in this re-adaptation.

* *Palaeont. Afric.* iv, p. 77.

At the present stage of this investigation it appears that the characteristic depression on the anterior face of the septomaxillary lodged a gland which secreted a fluid used either for wetting the nostrils or for moistening the air to facilitate the absorption of odour. The shape of the depression suggests that here had been an effective communication directly between this gland and the organ of Jacobson while breathing might still have been at a slow tempo. The object was not to detect odour inside the nasal cavity, but on the outer surface of a wet nostril and upper lip. This would be the obvious arrangement for an animal that could not sniff, where it could detect odour in a breeze passing its nose. If the glands had an intimate relationship with the organs of Jacobson the latter may have been able to detect odour dissolved directly in the moisture of the nostrils and very effective "smelling" for the palatability of food could have been effected by bringing the nose in actual contact with it. Similarly, an occasional lick across the nostril while feeding may also have kept the organs of Jacobson effectively informed of the finer flavour of the food. The situation might even be interpreted as one where the organs of Jacobson, after losing their communication with the mouth, made a bold endeavour to re-establish communication along a different route, the only effective one being through the external nares, in the direction of the source of the odour and still within easy reach of the tongue.

The fairly large canal traversing the septomaxillary suggests a rich blood supply which provided the fluid secreted. In some Therapsid specimens a distinct groove leads from this depression back to the foramen on the side of the naris, which might indicate the effective venous drainage. The canal through the premaxillary with its opening into the depression, is evidently the approach of the nervous innervation, this nerve also sending a branch farther forward, apparently into the upper lip for greater general sensitivity.

Whatever the case might actually have been, at this stage it seems quite evident that in the Therapsids in general, the nasal cavity had not yet become adapted for smelling according to the mammalian arrangement. It is equally clear that some intermediate stage existed where the detection of odour was concentrated in a restricted locality, very far forward in the nasal cavity, perhaps more specifically in front of the nasal cavity in the external nostril. Subsequently all the other developments occurred which resulted in the adaptation of the entire nasal cavity to the function of detecting odour, as is the condition in mammals.

If this rather vague interpretation should eventually prove to be reasonably correct, answers will have to be found for a number of significant questions. First and foremost, the question will most definitely arise as to why this intermediate arrangement occurred only in the carnivorous Therapsids. Perhaps the herbivorous forms relied more on sight for the selection of their food. Perhaps their food had been so abundant that they were not required to search widely. Detection by smelling is quite definitely more important to a hunting carnivore than to a quietly grazing herbivore, although mammalian herbivores are quite dependent on odour for the

detection of approaching danger or in the selection of partners in the mating season. Nevertheless, herbivores might rely on hearing for the detection of approaching danger while odour in the mating season might be of less importance to a gregarious herbivore than to a lone marauding carnivore.

A second significant question that arises even at this stage is why all carnivorous Therapsids are characterized by this peculiar septomaxillary arrangement, from early forms which had typically reptilian palates and could taste in the typical reptilian manner, to advanced Cynodonts and Bauriamorphs with long established secondary palates and nasal cavities evidently quite near in structure to that of mammals. Perhaps soft secondary palates featured in early forms long before a bony secondary palate appeared on the scene. Even in the present specimen the "secondary palate" ridges on the maxillaries are so obviously directed towards the sharp edges of the horizontal palatal plate of the vomer, the latter in turn reaching towards the maxillary ridges, that the conclusion of a soft palate having effectively confined the internal nares to a level near or even behind the bony posterior borders seems quite unavoidable. In the present specimen as in the majority of Therocephalians and to a lesser extent perhaps the Gorgonopsians as well, such a soft partition separating the mouth cavity from the nasal cavity could already have induced these animals to devise a different method for the detection of odour. In the advanced forms the nasal cavities might have achieved the mammalian structure, but the nostril arrangement had apparently been found quite effective enough for its retention. Even modern mammals find wet nostrils advantageous for some particular reason. It is also likely that even after the mammalian nasal cavity arrangement had been well established, the septomaxillary gland could have been retained for the sole purpose of additionally moistening the inhaled air, in animals now breathing substantially fast in an arid environment. It is quite evident that the Cynodonts had supplemented the septomaxillary gland in this role with maxillary glands, so serious was the danger of losing too great an amount of water through evaporation directly from the blood in the lungs.

Another question to be clearly elucidated bears upon the circumstance that the septomaxillary arrangement is apparently very standard in structure throughout the carnivorous Therapsids, from the giant Gorgonopsians to the most delicate Scaloposaurid. This circumstance may serve to emphasize the significance to these animals of this peculiar arrangement, whatever it may in actual fact prove to be.

The *dentary* is very straight anteriorly, with virtually no curving upward of the symphyseal region. There are four very long incisors directed almost straight forward. They have all recently replaced their predecessors, remnants of which are still to be seen in the sockets. The canine is directed very markedly forward. There are seven post-canine teeth.

The *spenial* has suffered some damage both sides. Its structure as displayed in figure 36C may, therefore, be somewhat incorrect.

Ictidostoma hemburyi (Broom)
(Figure 38)

- 1912 BROOM, R., (*Ictidognathus hemburyi*) *Proc. zool. Soc.*, p. 865; pl. XCI, 10, 11.
 1914 BROOM, R., (*Ictidognathus hemburyi*) *Phil. Trans.*, B206, p. 47; pl. VI, 76.
 1915 BROOM, R., (*Ictidognathus hemburyi*) *Bull. Amer. Mus. nat. Hist.*, XXV, p. 117.
 1930 BROOM, R., (*Ictidognathus hemburyi*) *Phil. Trans.*, B 218, p. 371, pl. XXXIV, 39.
 1931 WATSON, D. M. S., (*Ictidognathus hemburyi*) *Proc. zool. Soc.*, p. 1186.
 1931 BROOM, R., *Rec. Albany Mus.*, IV, p. 161.
 1932 BROOM, R., *Mammal-like Reptiles*, p. 72, fig. 22c, d.
 1935 BOONSTRA, L. D., (*Ictidognathus hemburyi*) *Amer. Mus. Novit.*, 771, p. 11.

Type: Middle and snout portion of skull with mandibles in good preservation, from apparently high in the *Endothiodon* zone at Beaufort West, now No. 5520 in the American Museum of Natural History, New York.

Present specimen: Complete skull with right mandible in situ, left dislocated, posterior region not well preserved, from *Cistecephalus*-zone beds, about 2 miles northwest of Richmond in a river bed alongside the De Aar road. It is numbered 341 in the collection of the Bernard Price Institute.

The present specimen is referred here to the poorly described *Ictidostoma hemburyi* on two unsatisfactory features; size and dental arrangement. Although existing figures and descriptions portray very little in the line of structure it is still fairly evident that in size and shape the present specimen compares very favourably with the type. It is, in fact, of exactly the same size and the shape of the snout is strikingly similar, especially where it is sharply pointed, and the external nares are inclined to face more outward than forward. The nasals also do not expand posteriorly. For size comparison the following measurements in mm. are useful, those in brackets being the equivalents in the type:

From tip of snout to anterior borders of orbits	42	(42)
Antero-posterior diameter of orbit	20	(18)
Interorbital width	21	(19)
Breadth of snout across canines	28	(27)
Diameter of large canine	4	(3.5)
Row of 8 postcanine teeth	19	(17)
Row of six incisors	12	(10)
From tip of snout to pineal	71	
From tip of snout to occipital border	88	
Approximate total length of skull	100	
Intertemporal width	10	
Approximate total breadth of skull	67	

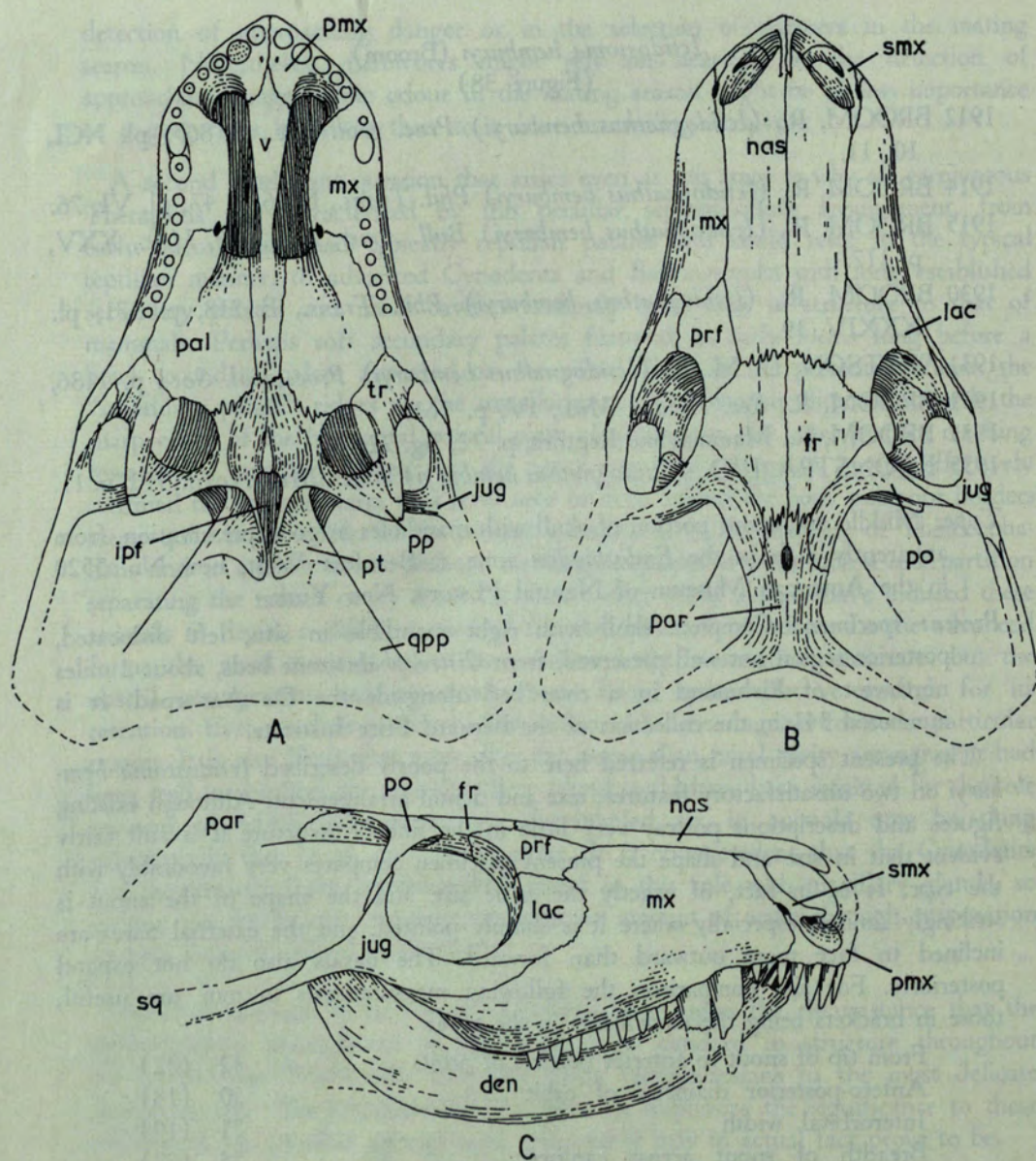


Figure 38

A, Palatal; B, Dorsal and C, Side views of the skull of *Ictidostoma bemburyi*. Natural Size.
For abbreviations see end of article.

As far as dental arrangement is concerned, not only does the present specimen agree in having six incisors, two canines and eight post-canines, but also in the more conspicuous features where the subequal incisors agree in general size range with the postcanine teeth. In both series the anterior teeth are appreciably larger than the posterior teeth.

The only difference between the new specimen and the type lies in the geological age. The type comes from *Endothiodon*-zone beds and, although this might be at a fairly high level, the Richmond site is well in the middle *Cistecephalus*-zone. This rather appreciable difference in age could justify the recognition of the new specimen as a form specifically distinct from *Ictidostoma hemburyi*, but it is inadvisable to do so while the separation of *I. hemburyi*, even specifically, let alone generically, from its nearest ally *Ictidognathus parvidens*, is anything but substantial.

Ictidostoma hemburyi does, however, appear to be different from *Ictidognathus parvidens*. In the latter the snout has a different shape, is much longer and more slender, features which could provisionally be regarded as more substantial than the number of post-canine teeth on which the generic distinction has thus far been based.

The present specimen is quite satisfactory. It lacks the left temporal and postorbital arches and although the outline of the posterior region of the skull is clear, substantial pre-fossilization damage has rendered it impossible to analyze it in detail. The left mandible is dislocated and associated with some other skeletal bones, principally of a front limb and some ribs, which have arranged themselves around the back and dorsal sides of the skull, the latter having become embedded on its side. The right angular is also dislocated.

The specimen seems to support views held earlier that this form is not a very close ally of the Scaloposaurids. It lacks the more delicate, slender build of the Scaloposaurids. The skull is deeper and the snout shorter and more robust. In having lost an anterior small canine it is an unlikely direct ancestral form. The postorbital bar is still complete. The dentary is more distinctly curved.

The palate is nevertheless rather Scaloposaurid-like, even though the secondary palate ridges are less distinct and still widely separated.

The nasals are Scaloposaurid-like in that they do not expand posteriorly.

There are definitely no postfrontals, unlike Broom's interpretation in his figure of 1932.

Ictidosuchops intermedius (Broom)

(Figures 39 & 40)

- 1938 BROOM, R., (*Ictidosuchoides intermedius*) *Ann. Transv. Mus.*, 19 p. 257, figs. 1—3.
1940 BROOM, R., (*Ictidosuchoides intermedius*) *Ann. Transv. Mus.*, 20 p. 161, figs. 1—5.
1941 BROOM, R., (*Ictidosuchoides intermedius*) *Ann. Transv. Mus.*, 20 p. 194, fig. 3.
1955 CROMPTON, A. W., *Res. Nas. Mus.*, 1, p. 149, figs. 1—7.

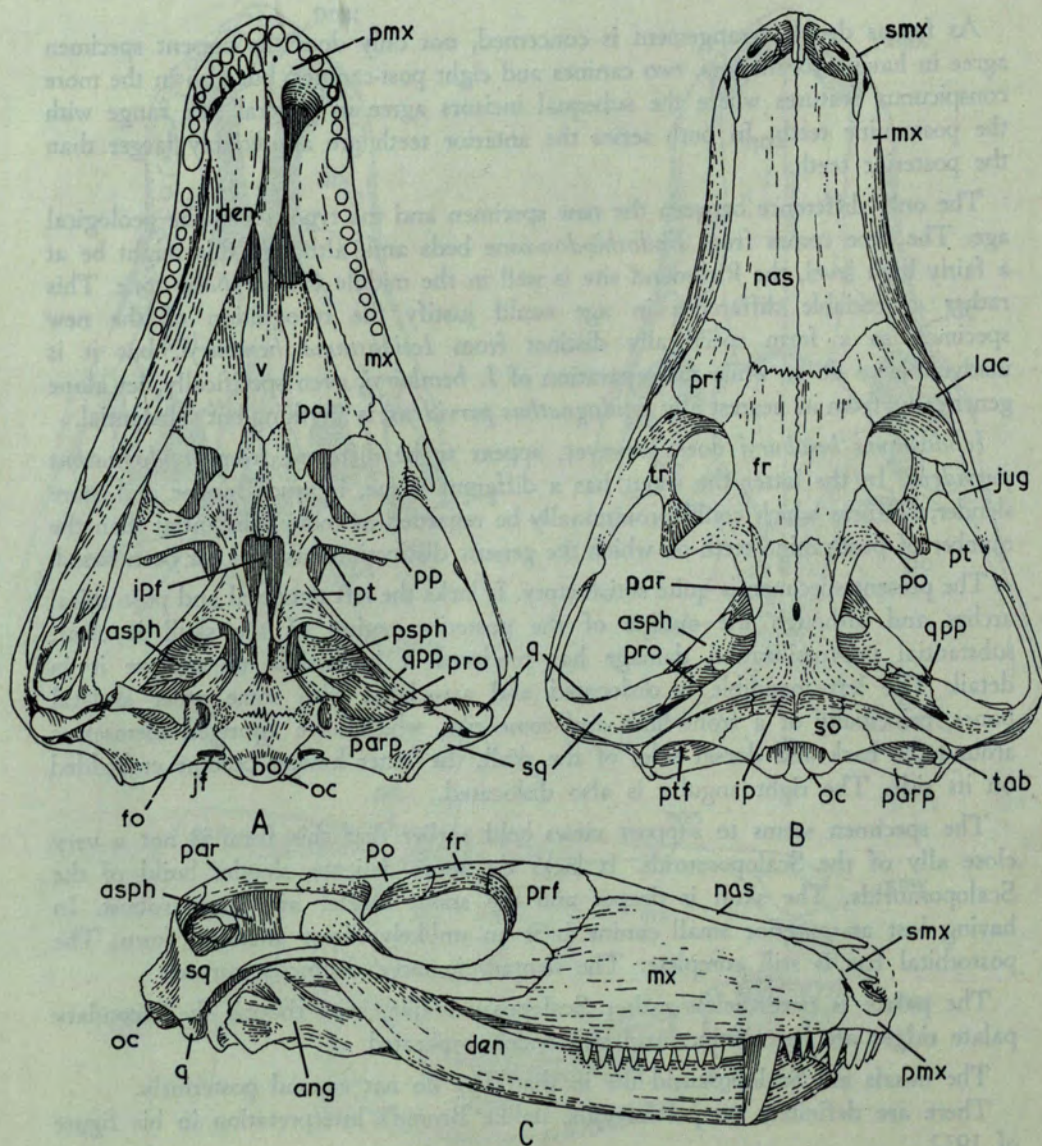


Figure 39

A, Palatal; B, Dorsal and C, Side views of the skull (No. 267) of *Ictidosuchops intermedius*. Natural size. For abbreviations see end of article.

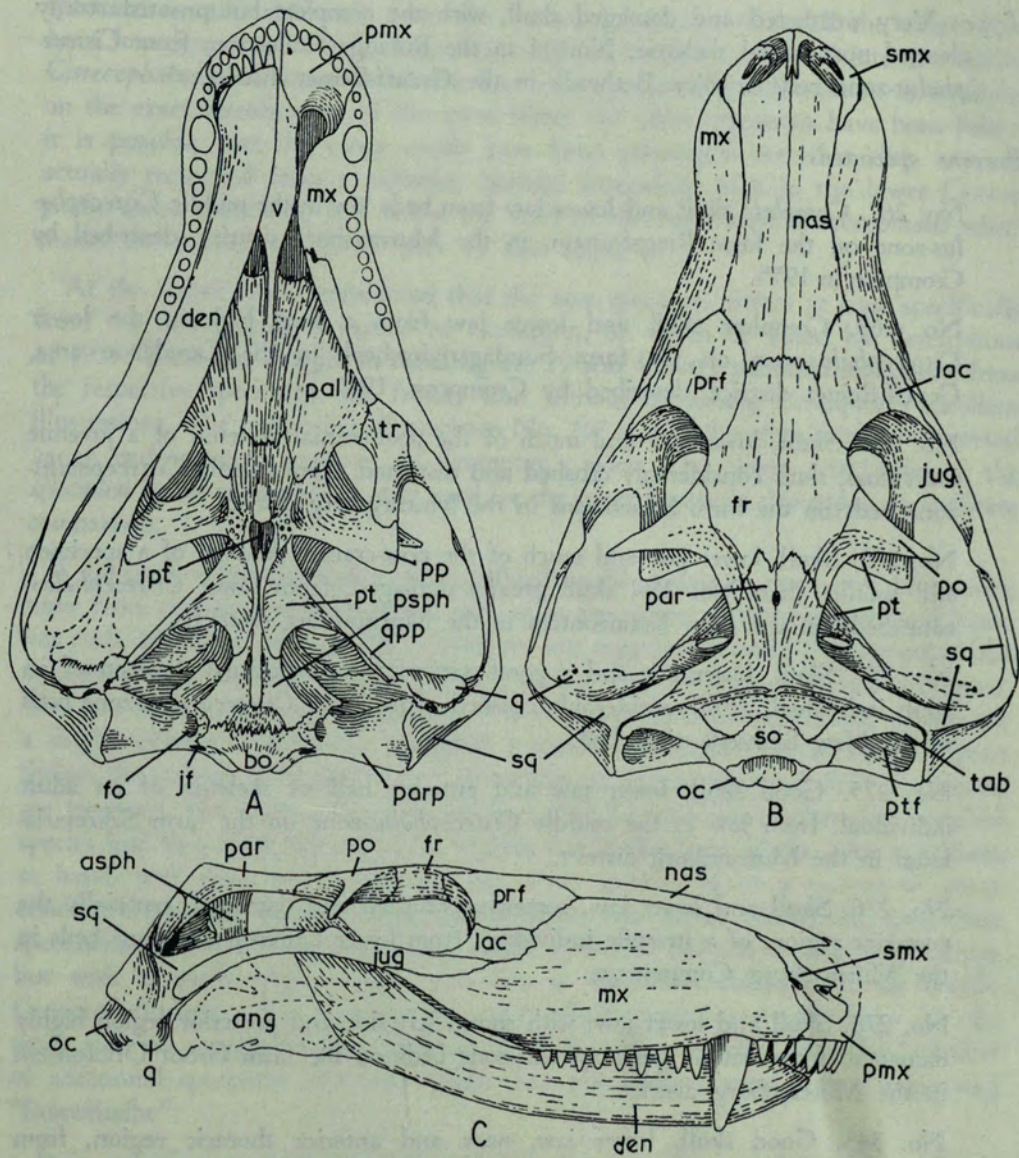


Figure 40

A, Palatal; B, Dorsal and C, Side views of the skull (No. 343) of *Ictidosuchops intermedius*. Natural size. For abbreviations see end of article.

Type: Very weathered and damaged skull, with the complete but unsatisfactorily cleaned post-cranial skeleton, No. 11 in the Rubidge Collection, from *Cistecephalus*-zone beds at New Bethesda in the Graaff-Reinet district.

Present specimens:

No. 267. Complete skull and lower jaw from beds low in the middle *Cistecephalus*-zone on the farm Ringsfontein, in the Murraysburg district, described by Crompton in 1955.

No. 268. Complete skull and lower jaw from a level high in the lower *Cistecephalus*-zone on the farm Sondagsriviershoek in the Camdeboo area, Graaff-Reinet district, described by Crompton, 1955.

No. 269. Skull, lower jaw and much of the post-cranial skeleton of a juvenile individual, skull considerably crushed and distorted, from middle *Cistecephalus*-zone beds on the farm Swaelkrans in the Murraysburg district.

No. 270. Skull, lower jaw and much of the post-cranial skeleton of a specimen still smaller than No. 269, skull greatly damaged, from lower *Cistecephalus*-zone beds on the farm Kraaifontein in the Murraysburg district.

No. 271. Skull, lower jaw and a good part of the post-cranial skeleton of an adult individual, skull considerably crushed, from lower *Cistecephalus*-zone beds in the New Bethesda river bed.

No. 275. Good skull, lower jaw and anterior half of skeleton of an adult individual, from low in the middle *Cistecephalus*-zone on the farm Sekretaris-kraal in the Murraysburg district.

No. 276. Skull and lower jaw, somewhat crushed and damaged, especially the posterior region, of a juvenile individual, from lower *Cistecephalus*-zone beds in the Murraysburg Commonage.

No. 278. Skull and lower jaw, with snout, left side and posterior region highly damaged, from middle *Cistecephalus*-zone beds on the farm Groot Driefontein in the Murraysburg district.

No. 343. Good skull, lower jaw, neck and anterior thoracic region, from *Endothiodon*-zone beds on the farm Driehoeksfontein in the Murraysburg district.

All the above specimens are in the collection of the Bernard Price Institute.

The discovery recently by Mr. J. W. Kitching of a specimen in the *Endothiodon*-zone (No. 343) which agrees very closely with *Ictidosuchops intermedius*, a typical *Cistecephalus*-zone form, has induced the author to investigate more closely several specimens in this collection, which had previously merely been identified. The new

specimen is quite definitely from the *Endothiodon*-zone, while all the others have been found in strata which range from high in the lower, to well into the middle *Cistecephalus*-zone. In view of the fact that no detailed information is available on the exact stratification of the areas where the other specimens have been found, it is possible that the range could have been misjudged and that they were all actually recovered from a narrower horizon somewhere high in the lower *Cistecephalus*-zone, apparently still below the level of the zone fossil *Cistecephalus* which marks the top of the lower part of this zone.

At the outset it was considered that the new specimen differs at least specifically from the two specimens loaned to Crompton, on which he based his descriptions of 1955. With this thought in mind figures 39 and 40 were prepared separately, from the respective specimens, the former also without consulting Crompton's excellent illustrations. The re-figuring of specimen No. 267 should therefore not be interpreted as an endeavour to improve on Crompton's work. The object was to figure the specimen in the same style as that used for the other figures in this paper, to facilitate comparison.

A comparison between figures 39 and 40 will readily indicate a number of differences, some more conspicuous than others, such as in the region of the interpterygoid fossa, but each difference, after careful evaluation, was regarded as possibly being either due to distortion, or incorrect interpretation in areas not well enough preserved or cleaned. The fact is that on structural grounds it is extremely difficult and unsafe to indicate a single substantial difference on which a specific distinction can be based. Nevertheless the striking difference in age is enough to suggest that two different species are involved. No doubt these two specimens would have been referred to separate species had they been the only ones known, but in the light of the other specimens at hand, and those described previously, there appears to be a variety of minor conditions ranging between and around these two forms. Evidently, too, these specimens do come from levels, not inside a narrow horizon as suggested above, but with a much wider range, from low in the lower to high in the middle *Cistecephalus*-zone, thus linking the upper *Endothiodon*-zone specimens to the series with no appreciable time interval. With the discovery of a substantial number of additional specimens this form might then eventually present a very interesting "formenreihe".

It is actually not specimens 343 and 267 that suggest a confusion here of two different species. Among the specimens listed above there are three (Nos. 269, 270, 271) that appear to differ more substantially but they are so highly distorted and crushed that it is here even more unsafe to rely on any particular feature in the different impressions they tend to create. Specimens 269 and 270, for example are smaller but their orbits are in proportions appreciably smaller than in the other specimens, while their skulls (including No. 271) appear to be narrower. The general impression is that No. 270 is not an *Ictidosuchops intermedius*, but a *Scaloposaurus constrictus*.

Table 1

	Type	Broom 1940	Broom 1941	No. 267	No. 268	No. 269	No. 270	No. 271	No. 275	No. 276	No. 278	No. 343
Total length of skull	92?	98	106	106	110	90	83	95	101	80	98?	100
Minimum breadth of skull	—	55	56	66	70	±45	±45	±50	61	±45	±60	64
Minimum breadth of snout	—	22	22	22	22	—	15?	—	20?	20?	25	22
Interorbital breadth	—	19	—	19	20	15?	14	14	20	18	18	18
From snout to pineal	—	72	—	78	83	66	±66	70?	77	64	75?	74
Length of snout to anterior borders of orbits	50	49	—	52	55	45?	43	43	50	40	±50	50
Minimum intertemporal width	—	12	—	12	14	11	—	10?	10	10?	10	10
Tip of snout to interpterygoid fossa	—	—	66	67	71	—	—	—	68	—	70?	67
Antero-posterior diameter of orbit	17?	21	—	23	21	14	15	20	21	17	±20	20
Length of row of post-canine teeth	15.5	18	19	20	24	16	±17	21	19	—	20	23
(Number of teeth in post-canine row)	(8)	(8)	(8)	(9)	(9)	(9)	(9?)	(9)	(9)	—	(9)	(9)

The idea was entertained at one stage in the initial investigation, that these three specimens are comparable with the types of *Ictidosuchops intermedius* and that the four specimens differ at least specifically from the rest of the specimens at hand and those described by Broom in 1940 and 1941. Should they actually prove to be generically different, the specimen described by Broom in 1940 will have to be taken as the type of *Ictidosuchops intermedius*, while the specimen described by Broom in 1938, with at least No. 271 in this collection, will have to remain as *Ictidosuchooides intermedius*, or be given a new generic name on account of the substantial difference between this form and *Ictidosuchooides longiceps*. The "*Ictidosuchooides intermedius*" specimens seem to be more closely related to *Ictidodracos longiceps* than to either *Ictidosuchooides longiceps* or *Ictidosuchops intermedius*. However, when difficulty is encountered in finding a substantial feature in which *Ictidodracos* differs from *Ictidosuchops*, it is realised that final conclusions about the intimate relationship of these forms had better wait until more undistorted specimens come to hand. Provisionally all specimens are here referred to *Ictidosuchops intermedius*.

Even in the light of the wider range of specimens at hand, it is not possible to elaborate, as far as structure is concerned, on Crompton's descriptions of 1955. It should, however, be mentioned here that the dental formula of this form is i6, c3, pc9. The maxillary-premaxillary suture suggests very obviously that it passes between the 5th and 6th teeth, but in depth, there is no doubt whatever that the 6th tooth is situated inside the premaxillary.

Table 1 gives a list of measurements in mm. for all the specimens provisionally recognised as *Ictidosuchops intermedius*.

Ictidosuchops baurioides Broom.
(Figure 41)

1940 BROOM, R., *Ann. Transv. Mus.*, XX, p. 162 fig. 6.

1941 BROOM, R., *Ann. Transv. Mus.*, XX, p. 212.

Type: Nearly complete, crushed skull, No. 30, in the Rubidge Collection from *Cistecephalus*-zone beds on the farm Zuurplaas in the Graaff-Reinet district.

Present specimen: Complete undistorted, slightly damaged skull, No. 342 in the collection of the Bernard Price Institute, from *Cistecephalus*-zone beds on the farm Bloupoort in the Murraysburg district.

The present specimen is quite definitely an *Ictidosuchops*, but it differs appreciably from *I. intermedius* as can clearly be seen when comparing figures 39 or 40 with 41. The other existing species are so poorly known that it is unsafe to introduce this specimen as a new species. There are some features about this new specimen which compares favourably with those of *I. baurioides*, hence its provisional reference to this species. The most conspicuous similarity is the rectangular (in cross section) blunt shape of the snout. The nasals reach far forward, with their anterior free margins so near to extending straight transversely that the external nares face

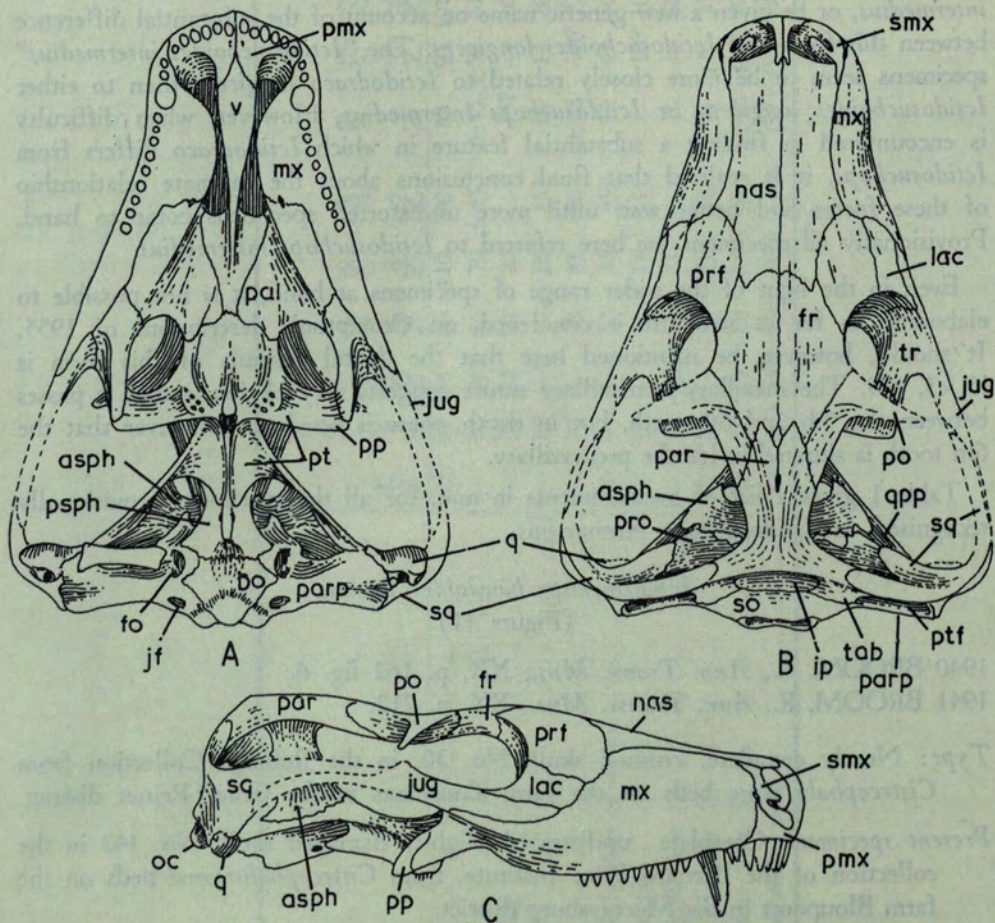


Figure 41

A, Palatal; B, Dorsal and C, side views of the skull of *Ictidosuchops baurioides*. Natural size.
 For abbreviations see end of article.

virtually straight forward. The septomaxillary wedges penetrating between the nasals and maxillaries are very feeble. This is apparently quite a characteristic *Ictidosuchops* feature and is distinctly different from the condition in *Ictidosuchoides*. Posteriorly the nasals are also similarly shaped in that they do not expand. The prefrontals are blunt anteriorly, also an *Ictidosuchops* feature differing from the *Ictidosuchoides* condition.

The major differences between the present specimen and the type are to be found in the posterior region of the skull, when comparing figures (fig. 41 with fig. 6A of Broom 1940). However, the type is a considerably crushed skull and it is obvious, not only in the light of the present specimen, but also of others described in this paper, that even in outline Broom's restoration is quite unreliable.

The present specimen is smaller and younger than the type. There are 6 incisors, 3 canines and 9 molars, the latter occupying 17 mm. With further growth in size the number of post-canines in this form could have increased.

Both temporal arches and both post-orbital bars are damaged. It is not possible, therefore, to establish whether the post-orbital bars were actually incomplete in the natural condition.

The parietals penetrate into the frontals each with its own wedge-like anterior end, in a manner comparable with that of *Ictidosuchops intermedius* and unlike the condition in *Ictidosuchoides* and *Ictidostoma*. There is a distinct, very small, preparietal, a feature which has proved in the past to have no diagnostic value whatsoever.

The interpterygoid fossa is well constricted but the tooth-bearing tuberosities either side are still well separated. These tuberosities are quite prolific in their tooth bearing, there being at least 6 long slender teeth on each.

The vomer expands broadly between the palatines. The maxillary secondary palate ridges approach the internarial bar quite closely, a distinct *Ictidosuchops* feature, and one on which a distinction from *Ictidosuchoides* can be based.

The following are some measurements in mm. with the corresponding measurements of the type in brackets.

Tip of snout to occipital condyle	79	(100?)
Tip of snout to occipital crest	71	(83?)
Tip of snout to pineal	60	(73)
Tip of snout to level of anterior borders of orbits	35	(43)
Breadth of snout across canines	22	(24)
Maximum breadth of skull	55	(63?)
Interorbital width	16	(3.5?)
Minimum intertemporal width	8	(11)

It is hoped that figure 41 successfully portrays the structural detail that can be gathered from the specimen and that any further detailed description will consequently be superfluous.

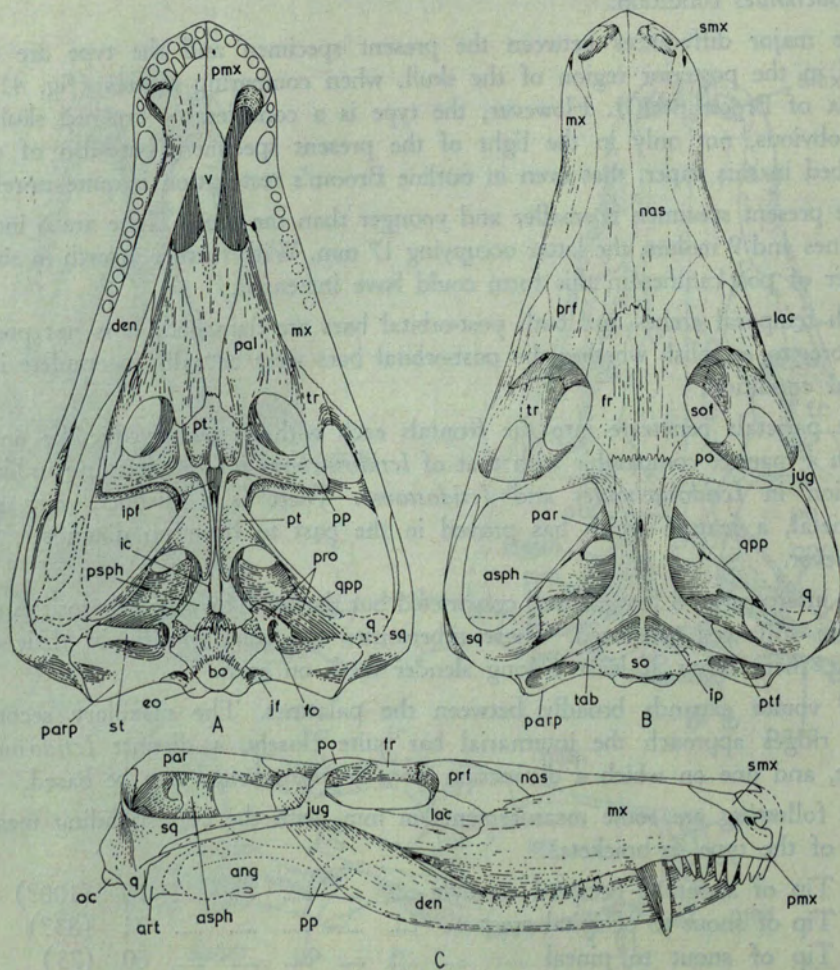


Figure 42

A, Palatal; B, Dorsal and C, Side views of the skull of *Ictidosuchoides longiceps*. Two-thirds natural size. For abbreviations see end of article.

Ictidosuchoides longiceps (Broom)
(Figure 42)

- 1920 BROOM, R., (*Ictidosuchops longiceps*) *Proc. zool. Soc.*, p. 343, figs. 1—3,
1930, BROOM, R., *Rec. Albany Mus.*, iv, p. 162.
1932, BROOM, R., Mammal-like Reptiles, p. 78, figs. 26B, c.
1934, BOONSTRA, L. D., *Ann. S. Afr. Mus.*, xxxi, p. 232, figs. 12—14.

Type: Skull in the British Museum of Natural History (No. R.5744) from beds which appear to be in the *Endothiodon*-zone or low in the *Cistecephalus*-zone, at Bruintjieshoogte, west of Somerset East, in the eastern Cape Province.

Present specimens:

No. 344. Good skull, snout damaged, better part of left mandible missing, from low in the middle *Cistecephalus*-zone on the farm Aasvoëlkrans in the Murraysburg district.

No. 345. Skull, snout good but posterior half badly crushed, no lower jaw, from low in the middle *Cistecephalus*-zone on the farm Sekretariskraal in the Murraysburg district.

Both specimens are in the collection of the Bernard Price Institute. Figure 42 is based entirely on No. 344.

The following table of measurements, based on Boonstra's list (1934), illustrates how well the two new specimens agree with the type. All measurements are given in millimeters:

Table II

	Type	No. 344	No. 345
Length of skull to occipital condyle	150?	138	131?
Length to basisphenoidal tubera	140?	125	114?
Length to pineal foramen	110?	104	—
From pineal to edge of occipital plate	18	18	—
From premaxillaries to front of orbits	75?	68	67
Width across squamosals	80?	79	—
Interorbital width	24	20	16?
Intertemporal width	10	10	—
Width of snout	27	28	27
Width across pterygoid flanges	40	42	41
Height of snout	22	22	22
Height of occiput	28?	28	—
Length of molar series	25	27	26
Diastema	5	4.5	4
Length covered by three canines	11	11	12
Space occupied by six incisors	—	17	17

The two new specimens are of exactly the same size when measurements in the anterior half of the skull are compared. Crushing of the posterior region in specimen No. 345 has caused an apparent shortening of the skull as a whole. These specimens are slightly smaller than the type and it is interesting to note that this difference in size is not reflected in measurements related to the dentition.

The new specimens add substantially to our knowledge of this genus and species. Although it is a close ally of *Ictidosuchus* and a typical member of the family Ictidosuchidae, it differs in having three canines, a narrower and flatter skull, and a more straight lower jaw. The number of post-canine teeth is not taken as a reliable characteristic.

The dental formula $i6, c3, pc9$ seems to be characteristic for the families Ictidosuchidae and Scaloposauridae. Apparently various members of both families changed this formula by merely losing some of the small insignificant teeth in front of the large canine. These could be the last incisor and/or the first or both small canines, thus presenting combinations ranging from $i6, c3$, to $i5, c1$. The number of post-canine teeth apparently varied with age. The dental formula, therefore, presents nothing on which a family diagnosis can be based.

In the specimens of both these families at present at the author's disposal, the palates as a whole also do not exhibit any feature which appears to be of family diagnostic value. The two families are indeed very closely related. The only differences between these two families which can be seriously considered are the complete postorbital bars, the posteriorly expanded nasals, the longer prefrontals and the larger septomaxillary wedges between the maxillaries and nasals, these features being to some extent characteristic of the Ictidosuchidae. Although combined they present a picture reasonably different from that found in the Scaloposauridae, it is to be appreciated that individually each feature carries little weight as far as family diagnosis is concerned.

The new information derived from all the specimens investigated does not present substantial material on which views about the more intimate relationship of these two families can safely be expanded.

ABBREVIATIONS

ang, angular; art, articular; asph, alisphenoid; bo, basi-occipital; bsph, basisphenoid; cor, coronoid; den, dentary; eo, exoccipital; fo, fenestra ovalis; fr, frontal; ic, foramen for internal carotid artery; ip, interparietal; ipf, interpterygoid fossa; jug, jugal; jf, jugular foramen; lac, lachrymal; mx, maxillary; nas, nasal; oc, occipital condyle; pal, palatine; par, parietal; parp, paroccipital process; pmx, premaxillary; po, postorbital; pp, pterygoid process; prf, prefrontal; pro, pro-otic; psph, parasphenoid; pt, pterygoid; ptf, posttemporal fossa; q, quadrate; qpp, quadrate process of the pterygoid; sa, surangular; smx, septomaxillary; so, supraoccipital; sof, suborbital fossa; spl, splenial; sq, squamosal; st, stapes; tab, tabular; tr, transverse bone; v, vomer.

Vol. I, 1953	(Published 1st February, 1954)		Price 15/6
Vol. II, 1954	(Published 1st February, 1955)		Price 20/0
Vol. III, 1955	(Published 1st May, 1956)		Price 15/6
Vol. IV, 1956	(Published 3rd April, 1957)		Price 15/6
Vol. V, 1957	(Published 1st June, 1958)		Price 12/6
Vol. VI, 1958	(Published 1st July, 1959)		Price 15/6
Vol. VII, 1960	(Published 1st August 1961)		Price 25/0