

https://dspace.org/

Palaeontologia africana Volume 26 Number 7

1987
Bernard Price Institute for Palaeontological Research
http://hdl.handle.net/10539/17131

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

PALAEONTOLOGIA AFRICANA

Series of miscellaneous papers
published by
BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH

Volume 26 Number 7 ISSN 0078-8554 11 November 1987

PLIO-PLEISTOCENE FOSSIL MAMMALIAN MICROFAUNA OF SOUTHERN AFRICA — A PRELIMINARY REPORT INCLUDING DESCRIPTION OF TWO NEW FOSSIL MUROID GENERA (MAMMALIA : RODENTIA).

by

T.N. Pocock

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.

ABSTRACT

Analyses are presented of the mammalian component of rich microfaunal fossil breccia collections mainly of owl pellet origin from the Transvaal Plio-Pleistocene australopithecine sites Kromdraai, Sterkfontein and Makapansgat Limeworks, with briefer references to Swartkrans, Langebaanweg and the Makapansgat Cave of Hearths.

Identification of rodent incisors has proved useful in showing *Cryptomys robertsi* to be a distinct extinct species occurring with *C. hottentotus*, and in indicating, through the common possession of doubly ridged incisors, a relationship between *Mystromys*, the Cricetomyidae and certain fossil Cricetodontidae.

The fossil assemblages are generally similar to modern ones but elephant shrews (several species) and dormice are relatively commoner, and the once dominant cricetid *Mystromys* has declined in favour of the murid *Mastomys*. Two genera, *Crocidura* and *Saccostomus* are absent from the older fossil sites, appearing only in the more recent Cave of Hearths, while on the other hand there are certain lineages now extinct. Of these *Mystromys darti* Lavocat has been rediscovered in abundance in *in situ* Rodent Corner breccia at Makapansgat, yet it is totally absent from other parts of the Limeworks deposit, suggesting a more complex stratigraphy than previously realised. It is referred to a new genus, *Stenodontomys*, with a second species from Langebaanweg. Another extinct cricetid previously known under a manuscript name as *"Mystromys cookei"*, common to Makapansgat, Taung and the Krugersdorp district sites, is formally described for the first time also under a new generic name, *Proodontomys*.

On microfaunal evidence Makapansgat is definitely older than the Krugersdorp sites, of which Kromdraai is perhaps the oldest and Swartkrans the youngest. Certain extinct fossils link Makapansgat to Langebaanweg (*Stenodontomys*), Kromdraai (*Macroscelides proboscideus vagans*) and Taung (*Gypsorhychus*). Suggestions that Taung is significantly younger than other australopithecine sites are not supported.

CONTENTS

	Page
Introduction	70
Studies on Rodent Incisors	70
Status of *Cryptomys robertsi* Broom	70
Relationships of the genus *Mystromys*	70
Kromdraai, Sterkfontein and Swartkrans	72
Composition of the faunas	72
Possible implications for dating of the sites	75
Langebaanweg	75
Cave of Hearths	76
Makapansgat Limeworks	76
Exit Quarry Basal Red Mud (EXQRM) Collection	76
Makapansgat Rodent Corner *In Situ* (MRCIS) Pink Breccia Collection	76
Makapansgat Limeworks Dump (MLWD) Collection	76
Taxonomic section	82
Proodontomys n. gen.	82
Stenodontomys n. gen.	86
Acknowledgements	90
References	90

MS Accepted 9 April 1987

Palaeont. afr., **26** (7): 69—91 (1987)

©
Bernard Price Institute
for Palaeontological Research
University of the Witwatersrand, Johannesburg
PO Wits
2050
1987

INTRODUCTION

The present paper is in the nature of a preliminary report on continuing work begun about twenty years ago on a part-time basis in the field of fossil vertebrate microfauna mostly of owl pellet origin (Davis, 1959) from Plio-Pleistocene sites in Southern Africa. My introduction to the field in collaboration with the late Dr. D.H.S. Davis was initially as an ornithologist with an interest in owl pellet analysis mainly with a view to the identification of fossil bird remains in a large collection made from an approximately 5 metre (18 ft) layer of decomposed breccia at Kromdraai B (KB) by Dr. C.K. Brain in 1956.

STUDIES ON RODENT INCISORS.

Status of *Cryptomys robertsi* Broom.

Besides the identification of avian fossils (Pocock, 1971), my own principal contribution to the sorting and analysis of the KB collection lay in the classification of the large numbers of isolated rodent incisors present. This bore fruit in two significant respects.

Firstly, it was shown that the fossil mole-rat remains previously assigned to *Cryptomys robertsi* Broom (1937) were a mixture of two species. One is *Cryptomys robertsi* distinguished by larger molars but narrower incisors, mesiodistal breadth about 60% of buccolingual depth. The other with smaller molars but broader incisors (breadth 80-90% of depth) is virtually indistinguishable from the modern large species found in the southern Transvaal, O.F.S. and Eastern Cape today, now regarded as forms or subspecies of *C. hottentotus* (De Graaff, 1975). Since the typical form of this species is a relatively small one, weakish in both incisors and molars, from the Western Cape, it is necessary to refer to the fossil by a subspecific name as *C.* cf. *h. natalensis* (the form occurring in the southern Transvaal today). Previous workers including Broom himself have confused the two, since while the type of *C. robertsi* is a mandible, two supposed "co-type" skulls are *C.* cf. *h. natalensis* . Material classified by De Graaff (1960) from various sites also contains elements of more than one species, but his figure 31c is "good" *C. robertsi* , agreeing well with the type.

Relationships of the genus *Mystromys* .

Secondly, as a finding of possible significance in the classification of living as well as fossil muroid rodents, it was found that the incisors of *Mystromys* could be distinguished from those of the accompanying murines, gerbilles, etc. by the presence of a pair of characteristic ridges or striations defining a slightly raised band running lengthways along the middle of the anterior enamel face of both the upper and lower incisors (fig. 1). For many years the character was used merely to identify fossils as *Mystromys* and it was not until 1980 that it was noticed that precisely the same character occurs in at least the lower incisors of all three genera of the small African cricetid sub-family or family (Chaline *et al.* , 1977), Cricetomyinae, viz. *Beamys*, *Cricetomys* and *Saccostomus* (fig.2). The occurrence of *Mystromys* as a



Figure. 1 Left mandible of *Mystromys* cf. *hausleitneri*, inferior aspect showing ridges and band on enamel of lower incisor. Makapansgat EXQRM fossil x 10.



Figure. 2 Similar ridges and bands on the lower incisors of *Cricetomys gambianus*, Transvaal Museum (TM) specimen x 5.

geographically very isolated cricetine in Southern Africa has long been the subject of comment (Ellerman, 1941; Broom, 1948a; Lavocat, 1956), and this hitherto apparently overlooked incisor character constitutes *prima facie* evidence for answering the question posed by Lavocat (1978) in a review: — "With which of the Muroidea is the genus *Mystromys* related?" *Mystromys* also resembles the three cricetomyine genera in several of the respects in which Hershkovitz (1962) found it to differ from *Phyllotis*, a South American genus to which relationship had been suggested (Ellerman, 1941; Broom, 1948a),e.g. the very long coronoid process of the mandible (figs. 3,4), and the inflated sac-like pre-orbital foramina. These apparent links between *Mystromys* and the Cricetomyinae reinforce the arguments of Petter (1964, 1966) that the molars of the latter are essentially cricetid and not murid in character and are also geographically satisfying in making *Mystromys* look much less isolated than before in Southern Africa. (As another possible indication of closer relationship than hitherto realized it may be noted that *Mystromys* and *Cricetomys* are two of only four rodents according to Maddock and Perrin (1983) known to possess gastric papillae).



Figure. 3 *Mystromys* right mandible (lower left) external aspect compared with two of *Saccostomus campestris*. Note similarly large coronoid processes. *Mystromys* is a beautifully preserved Makapansgat MRCIS fossil *c.* 3 m.y. old, *Saccostomus* from recent owl pellet debris, Chinoyi Cave, Zimbabwe. x 3,33.

Apart from the above four genera, ridged incisors appear to be very rare in modern muroid rodents. With only one exception, a wide variety examined to date all possess smoothly convex lower incisors (or grooved in some otomyines). Forms seen include most African and some Asian Muridae (Murinae and Hydromyinae), gerbilles, dendromurines and some 32 genera of Palaearctic and N and S American Cricetinae and Arvicolinae. The exception is *Nyctomys* (fig. 5) of Central America, found to possess a single weak ridge on the lower incisors. More or less similar structures — ridges, striations, "raised lines" or flat bands — are however reported for various fossil cricetine or cricetodont genera such as *Eucricetodon* (Lindsay, 1978), *Cricetodon*, *Fahlbuschia*, *Democricetodon*, *Eumyarion* (Mein and Freudenthal, 1971) and many of the North American Miocene cricetids (Martin, 1980; Martin and Corner, 1980). Judging from unillustrated descriptions, *Democricetodon* may be the fossil genus closest in its incisor characters to *Mystromys*; this genus with *Fahlbuschia* also shares with *Mystromys* the character of possession of the entepicondylar foramen of the humerus (Mein, 1968), and is also of significance as a suggested ancestor of the living European hamster *Cricetus*, type genus of the Cricetidae (Mein and Freudenthal, 1971). Modern *Cricetus* and its closest relatives *Mesocricetus* and *Cricetulus* do not, however, possess such features on the incisors. Either the ridges have been lost in the course of evolution, or one should look elsewhere for the antecedent of the hamsters.



Figure. 4 Internal aspect of right mandibles of *Mystromys* (lower lt.), *Beamys major* (upper rt.). *Saccostomus campestris* (lower rt.) and *Phyllotis darwinii* (upper lt.). Note the differences in posterior processes of S. American *Phyllotis* as compared with the three African forms. *Beamys* and *Phyllotis* are TM specimens, *Mystromys* and *Saccostomus* as in fig. 3. x 3,33.



Figure. 5 Two right mandibles of *Mystromys* (centre and right) compared with pair of mandibles of Central American *Nyctomys sumichras* found to possess singly ridged lower incisors. Note huge difference in coronoid processes eliminating any possibility of close relationship. *Mystromys* are MRCIS fossils, *Nyctomys* an AMNH specimen. x 3,33.

This apparent link via the incisor character to some (not all) of the Cricetodontidae tends to support the suggestion of Lavocat (1961) that *Mystromys* may be a living member of this ancient group of otherwise extinct Oligocene to Miocene rodents. Further work is however necessary before the significance of the above findings can be fully assessed.

KROMDRAAI, STERKFONTEIN AND SWARTKRANS: Composition of the faunas.

Composition of the mammalian component of the microfauna of some of the australopithecine sites in the Blaaubank River Valley of the Krugersdorp district is given in Table 1. It includes the following collections:

(a) The Kromdraai B (KB) collection already referred to, collected by Brain from decalcified breccia and studied by Davis (1959) and myself (Pocock, 1971).

(b) Combined Sterkfontein collections (also from decomposed breccia) labelled STS/Dumps 1 & 2, STS/Dump 8 and STW/H2, collected prior to 1969 by A.R. Hughes and studied by myself. Apart from not as yet including loose incisors, analysis is on the same basis as for KB, with only cranial material being used for identification except to a small extent for golden moles and bats.

(c) A collection from Kromdraai A (KA), the "faunal" or non-australopithecine site close to KB, also collected by Brain in 1956 but mainly prepared from breccia and partly sorted by L.A. Brain. It is obviously incomplete, lacking besides post-cranial bones and isolated incisors, the maxillae of the dominant rodents *Mystromys* and *Otomys* , so that its quantitative significance is somewhat suspect.

Quantitative data from the third australopithecine site in the valley, Swartkrans, are not at the moment available, although material collected by J.T. Robinson in 1951 from decalcified breccia and studied by Davis has been seen. Also not included are certain more recent collections from both Kromdraai and Sterkfontein for which sorting and cataloguing is incomplete. These include the Kromdraai B East (KBE) collection, collected and prepared by the acetic acid technique from breccia blocks by Vrba (1981) and Vrba and Panagos (1982), and more recent collections by Hughes from the Sterkfontein Extension (SE) systematic excavation grid. Both show certain differences from the earlier collections, e.g. while generally similar to KB, the KBE collection lacks the characteristic small parrot *Agapornis* (Pocock, 1971), and *Cryptomys* is less common and apparently all *C. robertsi*. A remarkable result from the SE grid is that the hitherto extremely rare "*Mystromys cookei*" (one specimen identified out of *c.* 100 000 in Table 1) is much commoner in at least part of the grid, one square having yielded four specimens (different individuals) out of only 199.

As can be seen from Table 1, *Mystromys hausleitneri*, whose modern descendant *M. albicaudatus* is regarded as an indicator of Savannah Grassland (Davis, 1962),is by far the most abundant small mammal, with a remarkably similar percentage of about 52% in all three collections, so that it is amongst the less common forms that differences between the sites must be sought. Since the sites are only 2-3 km apart in the same valley, such differences can be due only to temporal ecological changes. Thus the greater abundance of forms like *Tatera*, *Zelotomys*, *Malacothrix* and *Macroscelides*, with *Otomys* and *Dasymys* reduced, suggest a somewhat drier climate at Sterkfontein than during the KB era. KA also seems somewhat drier than KB with conditions particularly suitable for the climbing grass mouse *Dendromus*. The *Praomys-Mastomys* group, of which *M. natalensis* is so prominent in the modern microfauna, is absent altogether at KB, although *Praomys* is present in low abundance at Sterkfontein and KA. This and other differences confirm that KB and KA, only *c.* 50 m apart, cannot be contemporaneous, a conclusion already reached on the basis of differences in the megafauna (Freedman and Brain, 1972; Hendey, 1973).

Although the very high abundance of *Mystromys hausleitneri* causes the Cricetinae with two species to exceed the Murinae (and indeed all the other micromammals put together) in numbers of individuals, the latter are represented by many more genera and species. This is worth emphasizing since a statement by Davis (1959) that Cricetinae exceed Murinae seems to have been misinterpreted to imply the latter to have been rare in Plio-Pleistocene times in Southern Africa. This supposed rarity led to the conclusion that the Murinae had only recently arrived by immigration during the early Pleistocene, and hence to the further erroneous suggestion that *Otomys*, usually the next most abundant rodent in the assemblages after *Mystromys*, was not a murid at all but some sort of cricetid or nesomyid (Chaline *et al.*, 1977; Lavocat, 1973, 1978; Misonne, 1969, 1971). (The Nesomyidae are a Malagasy muroid family with a few E. African fossil representatives.) These ideas have since been refuted on fossil evidence from Langebaanweg showing the Murinae to have been well-established and diversified in S. Africa as long ago as the time of the Mio-Pliocene boundary — five million years before the Present (myBP) — with several species including a form transitional between the murines and the otomyines (Pocock, 1976). Hence, far from being non-murids, the Otomyinae represent a highly successful locally modified offshoot of the Murinae.

Most of the species are representatives of modern genera. Some are in fact more or less indistinguishable from the extant species — these include *Tatera* cf. *leucogaster*, *Dendromus* cf. *melanotis*, *Steatomys* cf. *krebsii*, and *Cryptomys* cf. *h. natalensis*, as well as most of the bats. Others, while differing and often clearly more primitive, are apparently ancestral to the modern forms (Davis, 1962). These include besides the representatives of *Nasilio* , *Mus* , *Malacothrix* , *Rhabdomys*, *Acomys*, *Aethomys* and *Dasymys*, the two dominant species *Mystromys hausleitneri* and *Otomys gracilis* both

TABLE I

KROMDRAAI AND STERKFONTEIN MAMMALIAN MICROFAUNA

			Kromdraai B Min. No. Individuals	%	Sterkfontein Min. No. Individuals	%	Kromdraai A Min. No. Individuals	%
Rodentia:	Bathyergidae:	*Cryptomys* cf. *h. natalensis*	40	2,96	147	4,14	1	0,27
		C. robertsi Broom	38	2,81	5	0,14	1	0,27
	Pedetidae:	*Pedetes* sp.	—	—	2	0,06	—	—
	Gliridae:	*Graphiurus (Claviglis)* sp.	30	2,22	31	0,88	1	0.27
Muroidea:	Cricetidae:	*Mystromys hausleitneri* Broom	710	52,59	1881	52,97	189	51,36
		"M. cookei" Davis *ms.*	50	3,70	1	0,03	5	1,36
	Dendromurinae:	*Dendromus* sp.	12	0,89	136	3,83	59	16,03
		Steatomys sp.	6	0,44	50	1,44	5	1,36
		Malacothrix sp.	8	0,59	98	2,76	11	2,99
	Gerbillidae:	*Tatera* cf. *leucogaster*	21	1,56	150	4,22	3	0,82
		Desmodillus sp.	2	0,15	—	—	—	—
	Muridae							
	(Otomyinae):	*Otomys gracilis* Broom	178	13,19	341	9,60	24	6,52
	(Murinae):	*Dasymys* sp.	34	2,52	15	0,42	2	0,54
		Rhabdomys sp.	4	0,30	38	1,07	7	1,90
		Lemniscomys sp.	11	0,81	—	—	—	—
		Aethomys cf. *namaquensis*	9	0,67	—	—	2	0,54
		A. cf. *chrysophilus*	15	1,11	11	0,31	—	—
		Acomys sp.	11	0,81	1	0,03	—	—
		Zelotomys sp.	1	0,075	159	4,48	25	6,79
		Praomys sp.	—	—	52	1,46	3	0,82
		Mus. sp.	5	0,37	9	0,25	18	4,89
		Gen. Indet. (cf. *Praomys*)	2	0,15	—	—	—	—
Lagomorpha:	Leporidae:	*Pronolagus* sp.	—	—	5	0,14	—	—
Insectivora:	Macroscelididae:	*Elephantulus antiquus* Broom	127	9,41	192	5,41	9	2,45
		E. (Nasilio) cf. *brachyrhynchus*	13	0,96	2	0,06	—	—
		Macroscelides cf. *proboscideus*	—	—	42	1,18	—	—
		M. proboscideus vagans	3	0,22	—	—	1	0,27
	Soricidae:	*Myosorex* sp.	8	0,59	76	2,14	—	—
		Suncus cf. *varilla*	1	0,075	16	0,45	—	—
		S. cf. *infinitessimus*	—	—	25	0,70	—	—
	Chrysochloridae:	*Chlorotalpa* sp.	5	0,37	16	0,45	2	0,54
		Chrysospalax sp.	2	0,15	6	0,17	—	—
		Gen. nov.	—	—	2	0,06	—	—
Chiroptera:	Rhinolophidae:	*Rhinolophus* cf. *capensis*	1	0,075	—	—	—	—
		Rh. cf. *clivosus*	—	—	21	0,59	—	—
		Rh. cf. *darlingi*	—	—	14	0,39	—	—
	Emballonuridae:	*Taphozous* sp.	—	—	3	0,08	—	—
	Vespertilionidae:	*Myotis* cf. *tricolor*	1	0,075	1	0,03	—	—
		M. cf. *welwitschii*	1	0,075	—	—	—	—
		Eptesicus cf. *hottentotus*	1	0,075	—	—	—	—
		Miniopterus cf. *schreibersii*	—	—	2	0,06	—	—
Hyracoidea:	Procaviidae:	*Procavia* sp.	—	—	1	0,03	—	—
		TOTAL	1350	100,01	3551	100,00	371	99,99

named by Broom in 1937 from Schurveberg, a non-australopithecine site near Pretoria (Broom, 1937). Both are smaller than the modern forms in the Transvaal today, respectively *M. albicaudatus* and the sibling species, *O. irroratus* and *O. angoniensis*, although a smaller species *O. saundersiae* is very similar to *O. gracilis* and still occurs further south in the Cape Province and southern O.F.S. It differs in having distinctly narrower incisors, otherwise there might be a case for merging the fossil with the earlier named living species (Roberts, 1929). Apart from size, *O. saundersiae* also resembles *O. gracilis* in sometimes having as few as five laminae in its third upper molar, although it may also have as many as seven (Roberts, 1951); *O. gracilis* generally has 5-6 with seven seen in a few specimens from only one locality, Swartkrans. *O. irroratus* and *O. angoniensis* always have 6-7, never five.

Shrews are represented by *Myosorex* and the smaller forms of *Suncus* with no sign of the prominent modern genus *Crocidura*. Of the elephant shrews, *Elephantulus antiquus* Broom (1948a) is commonest at all sites with smaller numbers of a representative of the subgenus *Nasilio*, very close but not identical to mod-

ern *E. (N). brachyrhynchus*. It may or may not be the species *Elephantomys* (later *Elephantulus*) *langi* Broom (1937, 1948a). This name is in any case invalid by pre-occupation and must be replaced by *E. broomi* Corbet and Hanks (1968). Proper identification of this species has been bedevilled by the fact that the "numerous mandibles" accompanying the type maxilla of "*E. langi*" appear to be lost and are hence unavailable for examination. Butler and Greenwood (1976) have tentatively identified *E. broomi* (=*langi*) with certain "*Nasilio*"-like mandibles, although they lack the third molar which normally characterizes *Nasilio*. In doing so they have neglected the very real possibility that the mandibles which Broom did not figure and barely described (1937) were not conspecific with the maxilla, and actually represent the common *E. antiquus*, a species which he did not describe until 11 years later (1948a), again with a maxilla as type. The question cannot be satisfactorily settled without finding the missing mandibles or reinvestigating the type locality, Schurveberg near Pretoria.

A further complication is the occurrence at both Kromdraai and Swartkrans of a few mandibles otherwise indistinguishable from *E. antiquus* and certainly not "*Nasilio*" (cf. *brachyrhynchus*) which nevertheless possess the third lower molar — precisely the main character which is supposed to distinguish *Nasilio* from *Elephantulus* (Thomas and Schwann, 1906). It is quite possible that these mandibles represent a different species, but in the absence of any other character distinguishing them it seems safer to regard them as variants of *E. antiquus*.

Certainly to name these variants as a new species would create more problems than it would solve; for instance, who is to say whether the type maxilla of *E. antiquus* belonged to an individual with or without the third lower molar in its mandibles? In any case, the finding strengthens the case for not recognising *Nasilio* as anything more than a subgenus of *Elephantulus*.

Kromdraai B is further distinguished by yet another species of elephant shrew, a dwarf form originally believed on the basis of three fragmentary mandibles with well worn teeth to be a new dwarf fossil species of *Elephantulus*. But a much better specimen with five good unworn teeth has been found in the more recent KBE collection. An intact mandible with worn teeth has also turned up in material from Kromdraai A (KA). These show it to be almost certainly conspecific with the form described by Butler and Greenwood (1976) as *Macroscelides proboscideus vagans* from Makapansgat. At Sterkfontein this is replaced by a form of *Macroscelides* 25% larger, very close to modern *M. proboscideus*. Besides smaller size, the Kromdraai form differs also in lacking a distinct metaconid in its P_3 (a character which could not be checked in the only known Makapansgat P_3 owing to heavy wear). Hence it seems preferable to regard *vagans* as a full species and not a subspecies of *M. proboscideus*. The latter is confined to arid environments in adaptation to which it possesses greatly enlarged bullae. Whether or to what extent *M. (p.) vagans* possessed such enlarged bullae is not known, and since Kromdraai B apparently had a somewhat wetter environment than the present (Vrba, 1981), it must be regarded as very doubtful if *M. vagans* should be regarded as in any way an indicator of aridity ("drier than at the present time") as Butler and Greenwood (1974) did in reporting it from Makapansgat.



Figure. 6 Three left mandibles of *"Mystromys cookei"* Davis (MS) from Kromdraai B showing occlusal aspect of molar toothrows and typical appearance of these KB fossils — a few white, mostly black, often encrusted. x 4.

Like the elephant shrews (Davis, 1959) dormice are relatively commoner in the fossil collections than they are in equivalent modern owl pellet assemblages. The single fossil species is a relatively large form comparable with *Graphiurus (Claviglis) monardi* of tropical Africa rather than with the small *G. (C). murinus* and *G. (C). platyops* of southern Africa — an opposite trend to that seen in the muroid rodents *Mystromys* and *Otomys*, whose modern representatives are larger than their fossil antecedents.

While most of the species either certainly or probably represent the antecedents of extant forms, a few are extinct lineages without modern descendants. Of these *Cryptomys robertsi* has already been mentioned. Another, occurring at all the sites, is a cricetine first discovered by Davis over a quarter of a century ago and given by him the manuscript name "*Mystromys cookei*". It has never formally been described, although included in a list by Cooke (1978) as "*Mystromys* sp. n. (Davis)". Curiously, it was represented at Kromdraai B by numerous mandibles (fig. 6) but no maxillae, but Davis had a few maxillae from elsewhere including Swartkrans and in the "Camp Collection" Gladysvale and Taung (Camp 1948; Peabody, 1954), the latter being his projected type locality. It was suspected from the procumbency of the lower incisors that the uppers might be prodont and on this basis a single rather peculiar upper incisor was tentatively assigned to it, an assignment that was not to be confirmed until a decade later (see below).

Possible implications for dating of the sites.

Precise absolute dating of the sites remains elusive, but they are generally believed to be *c.* 1,5-3 million years old (Tobias and Hughes 1969; Tobias, 1978; Brain, 1981). Originally usually referred to vaguely as "early Pleistocene", this tends to shift them well into the Pliocene, since the Plio-Pleistocene boundary has now been fixed at 1,6 myBP (Haq *et al.*, 1977).

Apparent evolutionary trends can be seen in a few of the lineages which may have significance in relative dating of the sites. Thus, in addition to the case of *Macroscelides* already referred to, Sterkfontein *Malacothrix* is closer in the size of its teeth to modern *M. typicus* than that of Kromdraai, and only at Swartkrans does *Otomys* occasionally attain a 7-laminate M^3 similar to the modern forms. These trends suggest that Kromdraai is the oldest and Swartkrans the youngest of the sites with Sterkfontein intermediate.

This is contrary to previous opinion, e.g. Ewer and Cooke (1964),and the evidence cannot be regarded as conclusive. More work is necessary especially at Swartkrans where the equivalence of Robinson's material from decalcified breccia to Member 1 breccia has not yet been established. Moreover, the microfauna may not be representative of the site as a whole, since there is evidence at all of them of material of different ages being involved. At Sterkfontein, all the microfauna is believed to derive from Member 5 (A.R. Hughes, pers. comm), while Broom's australopithecine skull came from the possibly much older Member 4. Brain (1978) reports intermingling of older and younger breccias at Swartkrans, and the complexity of Kromdraai is attested by the differences between the KB, KBE and KA collections. The KA collection is intermediate between KB and Sterkfontein, resembling the former in the presence of *M. p. vagans* and the latter in the substantial presence of *Praomys* and *Zelotomys* (absent and very rare especially at KB).

Given the uncertainties, the following order from oldest to youngest is tentatively suggested:

1. Kromdraai B
2. Kromdraai A
3. Sterkfontein (Member 5)
4. Swartkrans (Robinson collection)

It may be noted here that Grine (1982) has recently, on the basis of a study of the teeth of robust australopithecines, also tentatively suggested Kromdraai B to be older than Swartkrans.

LANGEBAANWEG

This is the oldest site dealt with, dating from the "latest Miocene — early Pliocene" between 3,5 and 7 myBP (Hendey, 1978), but most probably from the time of the Mio-Pliocene boundary about 5 myBP (Hendey, 1981). It is also very different ecologically in being in a sandy coastal environment so that it is not surprising that the dominant micromammals are forms like *Bathyergus*, much smaller than modern, and *Chrysochloris*. *Mystromys* is present but not abundant. A fossil genus *Euryotomys*, important in demonstrating *Otomys* to be a modified murid and not a cricetid or nesomyid, has already been published (Pocock, 1976). The accompanying checklist of other forms can be corrected in that the "*Mus* sp.(larger)" should be re-assigned to the genus *Acomys*. The retention of a distinct cusp t3 (labial anterocone) but not t1 (anterostyle) in the third upper molar is distinctive for this genus — the reverse is more common in many other murine genera (fig. 7). Most of the species are obviously more primitive than their modern equivalents but it is interesting to note that the smaller of the two *Aethomys* spp. is barely different from living *A. namaquensis* , which is therefore a particularly long established species.

This site is mentioned here mainly to draw attention to the presence of a dwarf cricetine which was called *"Mystromys* cf. *darti"* at a time when *M. darti* of Makapansgat was known to me only by Lavocat's (1956) description. Reacting to a copy of my paper (Pocock, 1976), Dr. F. Petter kindly sent me drawings of the type material of *M. darti* pointing out its closeness to *Petromyscus*, a relict genus of uncertain affinities (Ellerman, 1941) confined to very arid terrain in Namibia. Lavocat (1956) compared *M. darti*



Figure. 7 Left maxilla of *Acomys* sp. from Langebaanweg showing occlusal aspect of toothrow. Note presence of district t3 but not t1 in the third molar. This appears to be a characteristic of this genus, since in addition to the S. African forms *A. spinosissimus and A. subspinosus*, it has also been observed in BM(NH) specimens of *A. caharinus* (E. Africa), *A. russatus* (N. Africa) and *A. dimidiatus* (Persian Gulf). SEM photograph x 20.

in detail with *Petromyscus*, regarding it as a link between *Mystromys* and *Petromyscus*, itself in turn possibly connectant to the Dendromurinae (Lavocat, 1959). The problem of the relationships of these dwarf cricetids from Makapansgat and Langebaanweg will be returned to later.

CAVE OF HEARTHS

This site, although only about 1,5 km distant from the Makapansgat Limeworks, differs vastly in time, being much younger. Precise dating is again uncertain, but while beyond the 50 000 year range of carbon-14 dating (Mason and Turton, 1971), on evidence of human cultural activities it appears to cover all of the Middle and part of the Early Stone Age up to perhaps 500 000 years BP. Hence the microfaunal collections from this site may be any age between these limits. As such it is the only known microfaunal site in the Transvaal intermediate between the Pliocene or very early Pleistocene and the Holocene.

Besides material reported on by de Graaff (1960), a box of unsorted material collected by Dr. J.W. Kitching in 1957 was made available to me at the Bernard Price Institute for Palaeontological Research (BPI). This material is interesting in that while *Mus* has attained its modern guise of *M. minutoides* with its highly characteristic 2.3.1. lower alveolar formula (Davis, 1965) (2.2.2. in older fossils), both *Mystromys* and *Otomys* have not, and must still be assigned to Broom's (1937) fossil species rather than to their modern equivalents. Also the genera *Saccostomus* and *Crocidura*, unknown in older material, have made their appearance (De Graaff, 1960), while "*Mystromys cookei*" is absent, presumably extinct.

(The significance of molar roots in distinguishing species in the Muridae is sometimes questioned. The three-rooted M_2 of *Mus minutoides* and its close allies (*indutus, bufo*, etc), with one anterior and two divergent posterior roots, is apparently a unique and highly characteristic feature in the murines and has evidently evolved in conjunction with and as compensation for the great reduction of M_3 in these species. It does not occur in the other species found in South Africa — the slightly larger *M. triton*, the proodont *M. neavei* (Petter and Matthey, 1975; Pocock, 1974) and the introduced *M. musculus*, nor in Asian species such as *M. booduga* and *M. cervicolor*, all of which have a more normal 2.2.2. or 2.2.1. lower alveolar formula).

MAKAPANSGAT LIMEWORKS

In contrast to all the preceding sites, material mainly collected and prepared by myself is dealt with here, the exception being BPI material previously studied by de Graaff (1960) and made available for comparison and re-evalution. Several distinct collections have been made, and while much of the material is still in various stages of processing and cataloguing, many findings of significance are already available. It may be noted that while the first collection took place in 1973 it involved only one part of the deposit, others not being sampled until late 1980, so that one of the more remarkable findings with possible implications for dating and stratigraphy did not become available until 1981.

Major collections include the following:

A. Exit Quarry Basal Red Mud (EXQRM) Collection

Large blocks of richly microfossiliferous dry red mud collected in 1973 from the back of the Exit or North-East Quarry (Maguire, 1980) were supplemented by further collections in 1980-3 to give the EXQRM collection in which the dominant micromammals of the genera *Otomys* , *Mystromys* and *Myosorex* are now represented by *c.* 400-500 minimum number of individuals each (Table 2, first two columns). Much of this material is particularly easy to prepare, simply by the action of water in disintegrating dried mud, although there are also hard consolidated layers and a good deal of tedious sorting is necessary to separate all specimens from quantities of nodules and clods, some of which may also contain specimens. Many specimens show chemical alteration rendering especially the teeth a translucent yellow, orange or orange-brown colour — an exquisitely beautiful cutglass-like effect. The chemistry involved and its possible relevance to the stratigraphy, sedimentology and taphonomy of the Limeworks is under investigation and will be reported elsewhere.

B. Makapansgat Rodent Corner *in Situ* (MRCIS) Pink Breccia Collection

The collection was prepared by the action of dilute acetic (or formic) acid on a 17,9 kg block of richly fossiliferous pink breccia plus a further *c.* 5 kg of associated fragments collected *in situ* from a spot northwest of the archway on the path leading to the back of the Exit Quarry and above the small "Rodent Cave" at the Rodent Corner — see the map of Maguire (1980). Unlike those of the EXQRM, or from the decomposed breccia of the Krugersdorp sites, fossils prepared from this breccia by the acid technique tend to be very fragile and often fragmentary, but with care and the liberal use of "Glyptal" cement, some beautiful specimens, mostly white (usually with dendritic black markings), rarely blackened, can be recovered. Also there are numerous isolated molars including the valuable unworn ones of juveniles, never found in the other collections. This can result only from *in situ* fossilization of owl pellets without transport effects in which loose teeth will tend to get lost or, in the case of juveniles, destroyed. For analysis, see Table 2, middle columns.

C. Makapansgat Limeworks Dumps (MLWD) Collection

This refers to blocks of microfossil-rich breccia of uncertain provenance sorted (by size and appearance) and stacked near the shed at the entrance to the Limeworks. Some pieces are pink breccia identical in appearance to that of the Rodent Corner

TABLE 2

MAKAPANSGAT MAMMALIAN MICROFAUNAL COLLECTIONS

			EXQRM Min. No. individuals	%	MRCIS Min. No. individuals	%	MLWD/III Min. No. individuals	%
Rodentia:	Bathyergidae:	*Cryptomys* cf. *hottentotus*	10	0,37	26	1,80	4	1,37
	Gliridae:	*Graphiurus (Claviglis)* cf. *monardi*	45	1,66	16	1,10	4	1,37
	Cricetidae:	Cricetinae: *Mystromys* cf. *hausleitneri*	398	14,70	151	10,43	34	11,68
		M. sp.n. (dwarf)	—	—	3	0,21	1	0,34
		Proodontomys cookei	82	3,03	53	3,66	20	6,87
	Dendromurinae:	*Dendromus* sp.	125	4,62	32	2,21	16	5,50
		Steatomys sp.	48	1,77	99	6,84	4	1,37
		Malacothrix sp.	2	0,074	7	0,48	—	—
	Petromyscinae:	*Stenodontomys darti*	—	—	246	16,99	—	—
	Gerbillinae:	*Taterillus* sp.	1	0,037	4	0,28	—	—
	Muridae:	Otomyinae: *Otomys* cf. *gracilis*	494	18,24	272	18,78	39	13,40
		O. *(Myotomys)* cf. *sloggetti*	12	0,44	10	0,69	2	0,69
		Murinae: *Dasymys* sp.	76	2,81	11	0,76	11	3,78
		Rhabdomys sp.	114	4,21	46	3,18	13	4,47
		Aethomys cf. *namaquensis*	155	5,72	39	2,69	19	6,53
		A. cf. *chrysophilus*	5	0,18	4	0,28	—	—
		Praomys sp.	22	0,81	35	2,42	3	1,03
		Acomys sp.	162	5,98	112	7,73	21	7,22
		Mus sp.	145	5,35	24	1,66	29	9,97
Lagomorpha:	Leporidae:	*Pronolagus* sp.	9	0,33	3	0,21	—	—
Insectivora:	Macroscelididae:	*Elephantulus antiquus*	156	5,75	56	3,87	10	3,44
		E. (Nasilio) cf. *brachyrhynchus*	4	0,15	1	0,07	—	—
	Soricidae:	*Myosorex* cf. *varius*	515	19,02	148	10,22	47	16,15
		Suncus cf. *varilla*	50	1,85	33	2,88	11	3,78
		S. cf. *infinitessimus*	1	0,037	—	—	—	—
		Diplomesodon fossorius	3	0,11	2	0,14	—	—
	Chrysochloridae:	*Calcochloris hamiltoni*	12	0,44	1	0,77	2	0,69
Chiroptera:	Rhinolophidae:	*Rhinolophus* cf. *darlingi*	40	1,48	6	0,41	1	0,34
		R. cf. *clivosus*	2	0,074	3	0,21	—	—
	Vespertilionidae:	*Eptesicus* cf. *hottentotus*	10	0,37	2	0,14	—	—
		E. cf. *bottae*	3	0,11	1	0,77	—	—
		Miniopterus sp.	4	0,15	1	0,07	—	—
	Nycteridae:	*Nycteris* sp.	1	0,037	—	—	—	—
	Megadermatidae:	Gen. nov	1	0,037	1	0,07	—	—
Carnivora:	Viverridae:	*Helogale* sp.	1	0,037	—	—	—	—
		TOTAL:	2708	99,99	1448	100,02	291	99,98

(which is Bed A of Member 4 of Partridge, 1979); in others the fossils are embedded in a red matrix (Member 2) and in still others are associated with almost sediment-free travertine (Member 1). Analysis of the largest of three pieces developed to date (MLWD/III) appears in the last columns of Table 2. It was a 3 kg travertine block.

Significant results from these collections are:—

(a) *Mystromys*, while still common, is less dominant than at the Krugersdorp district sites, being rivalled by *Otomys* and *Myosorex*. This doubtless reflects an ecological difference similar to that still existing today with more bush and scrub and less grassveld at Makapansgat.

(b) Both the dominant rodents, *Mystromys* and *Otomys*, show indications of being more primitive than at the Krugersdorp sites, confirming the greater antiquity of Makapansgat, for which suggested (if disputed) dates of 3,7 (cave-opening) (Partridge, 1973), approximately 3,0 (Member 3 — palaeomagnetic evidence) (Mc Fadden *et al.*, 1979) and 2,6 myBP (Member 3 — palaeontological) (White *et al.*, 1981) are available. Makapansgat *Mystromys* differs from *M. hausleitneri* Broom from Sterkfontein in that the anterocone of M^1 and anteroconid of M_1 are on average shorter and either simple or only weakly divided. Also there is much less tendency to development of an extra intermediate rootlet between the main roots of these teeth. Distinct rootlets are generally present in the first molars of modern *M. albicaudatus*, with *M. hausleitneri* intermediate in having usually a bump or nubbin and only occasionally a distinct rootlet in these positions.

(c) Even more significantly, Makapansgat *Otomys*

cf. *gracilis* is notable in that unworn juvenile molar teeth show signs of murine cusps demonstrating descent from Langebaanweg *Euryotomys* which has the enlarged M^3 of the Otomyinae but otherwise typically murine molars (Pocock, 1976). In M^1 all nine murine cusps t1 to t9, including the thickening representing t7, can be recognised, and even the prestyle or mesial conule of *Euryotomys* may exceptionally be present. Also the maxillary foramen in front of M^1, normally very small in other muroids but enlarged in *Otomys* and *Parotomys* is quite small, diameter usually 0,2 to 0,4 mm. A few specimens, however, do show it enlarged to 0,6 mm, the usual size in *O. gracilis* from Kromdraai and Sterkfontein. In modern otomyines it is typically an elongate foramen 0,8 to over 1 mm long (see relevant illustrations of Roberts (1951) and de Graaff (1981). The significance of this enlargement in the otomyines from the pinprick size in other muroid rodents does not appear to be known).



Figure. 8 Right upper incisors demonstrating existence of two forms of *Otomys* at Makapansgat. Above:— *O.* cf. *gracilis* . Below:- *Otomys (Myotomys)* cf. *sloggetti.* Both EXQRM specimens x 12,5.

(d) Besides the common *O.* cf. *gracilis*, there is a second rare otomyine species distinguished by narrower and more weakly grooved incisors (fig. 8) and only 4-5 instead of 5-6 laminae in its third upper molars. This is apparently the ancestor of the extant *O. (Myotomys) sloggetti*, but it also shows affinity with *Prototomys campbelli* Broom (1948a), described on a single mandible from Taung, in possessing a cusp at the anterolabial corner of the second lower molar. This is the cusp designated "Sv" in the terminology of Misonne (1969) or "labial anteroconid" in that of Jacobs (1978) for the cusps of murid teeth. It is also very rarely present (2 specimens) in some of the *O.* cf. *gracilis* specimens. It is perhaps worth noting that this cusp is retained in at least some specimens of the M_2 of *Nesokia*, an Asian murine reaching North Africa which has evolved laminate molars rather similar to those of *Otomys* but without the expanded M^3. Evidently this cusp is the last to disappear when murid evolution proceeds in the direction of entirely laminate molars.

(e) The Bathyergidae are represented only by *C.* cf. *hottentotus*, smaller than the *C.* cf. *natalensis* of the Krugersdorp area, with no sign of *C. robertsi* nor of the Giant Rodent Mole *Gypsorhychus makapani* Broom (1948b). The absence of the latter from the microfaunal collections may however merely be due to its being too large to figure in the diet of a Barn Owl-sized predator, and several specimens (a skull, two mandibles and several incisors) have subsequently been identified from the meso- and megafaunal collections derived from both the "Grey Breccia" (Member 3) (Partridge, 1979) and the overlying "Pink *Cercopithecoides* Breccia" (Member 4). This extinct genus is known only from Makapansgat and Taung whence originally described by Broom (1934, 1939), a fact which suggests that these two sites, which share also many other extinct forms including *Australopithecus africanus*, cannot be too far apart in time. Suggestions (e.g. Partridge, 1973) that Taung, the type locality of *A. africanus* (Dart, 1925), is much younger than not only Makapansgat but also all the other S. and E. African australopithecine sites should be treated with considerable caution.

As Broom (1939) noted, *Gypsorhychus* with its flattened ever-growing rootless teeth is ostensibly a specialized or "advanced" form and it is curious that it is extinct while more primitive forms — especially *Georychus* — survive. Incidentally, there seems to be no justification for assigning Makapansgat fossils to *Heterocephalus*, the genus of the Naked Mole Rat of the East African desert areas, rather than to *Cryptomys* as is done in some lists (Lavocat, 1978; Cooke, 1978).

(f) Of the shrews, *Myosorex* is very common with the dwarf genus *Suncus* subordinate and again no sign of *Crocidura*; the extinct giant shrew *Diplomesodon fossorius* Repenning (1965) is present but rare. It is another instance of a specialized form, advanced in the loss of one of the upper antemolar teeth as compared with most of the other soricid genera, now extinct at least in Africa (the genus survives in central Asia). It is known only from the Makapansgat Limeworks, having been described from a piece of breccia sent on exchange to the University of Colorado. It was evidently relatively more common in this "Colorado Block" with 22 specimens recovered in addition to the type mandible.

(g) Elephant shrews are represented mainly by *E. antiquus* with some *E. (Nasilio)* cf. *brachyrhynchus*. *Macroscelides proboscideus vagans* (Butler and Greenwood, 1976), also described from the Colorado Block, has not been found although as

noted above it has been identified in the Kromdraai collections. The apparent M_3-bearing variant of *E. antiquus* occurring at Kromdraai and Swartkrans has not been found at Makapansgat.

(h) Gerbilles are remarkably rare in the three collections detailed in Table 2. Most of the extant Southern African genera and species are confined to arid terrain so that their absence is not unexpected, but the genus *Tatera* is prominent in modern owl pellets from many parts of South Africa including Makapansgat, and is known as a fossil from the Krugersdorp and Taung sites (Davis, 1959; De Graaff, 1960). However, gerbilles have not been found at all in any of the MLWD material developed to date by either de Graaff (1960) or myself. Curiously, the single gerbilline mandible and the several molar teeth found respectively in the EXQRM and MRCIS collections appear closer to the extant East African genus *Taterillus* rather than to any of the S. African genera including *Tatera*.

Yet despite its absence from all three collections listed in Table 2, *Tatera* does occur in some Limeworks breccia, since it was found by de Graaff in his "Rodent Cave" material, and by myself in a small piece of brown breccia casually picked up in the Exit Quarry pathway and used experimentally in trying formic acid instead of acetic acid for development. Significantly this little piece also yielded the rare extinct shrew *Diplomesodon fossorius*, which appears to rule out the possibility of its being a piece of much more recent material.

It has been established that neither the Colorado Block nor de Graaff's "Rodent Cave" material (pers. comm. from J. W. Kitching and A.S. Brink) were collected *in situ* but from so-called "fallen blocks" stacked along the pathway north of the archway. Since significant differences are indicated between material collected *in situ* (MRCIS) and from these fallen blocks, it is necessary to distinguish the latter by a new appellation, viz. the Makapansgat Rodent Corner Dump (MRCD) material.

(i) Lavocat (1956) described a new dwarf fossil cricetine, *Mystromys darti*, on the basis of a mandible and maxilla from a small breccia fragment picked up in the Limeworks. It was sought unsuccessfully by me in the initial 1973 EXQRM collection and its total absence therein has been confirmed by further collecting. Nor is it present in any of the MLWD breccia developed to date either by de Graaff (1960) or by myself. But early in 1981 the first small breccia fragment picked up under the Rodent Corner face and developed experimentally yielded two tiny maxillary fragments and a M^1 tooth which, with the help of Petter's drawings, were identified without any doubt whatever as the hitherto rare and missing *M. darti*. Subsequent development of the main MRCIS block yielded nearly 2000 further specimens — mandibles, maxillae, premaxillae, molars and incisors, representing a minimum of 246 individuals. As such it is one of the two most abundant species in the assemblage, being rivalled only by *Otomys* which exceeds it only on a count of upper incisors — on other elements *M. darti* would marginally prevail.

With this new wealth of material it is possible to describe it more fully and re-evaluate its relationships. It differs in many significant respects from typical *Mystromys*, in which it was originally included obviously because of sympatry (Lavocat, 1956), and it clearly deserves separation on at least the generic and perhaps also the sub-familial level. Consequently a new genus is erected for it. (Formal description of new taxa follows in a separate section). Besides dwarf size (fig. 9), comparable to other dwarf muroid genera such as *Mus*, *Micromys*, *Dendromus*, and the American cricetines *Baiomys* and *Reithrodontomys*, *"Mystromys" darti*, differs from *Mystromys* in the following respects which in combination are certainly of generic import:— absence of ridges on the incisors; coronoid process of the mandible small, not reaching back almost as far as the condyle; lower third molars less reduced, about 2/3 size of the second molars (about 1/2 in *Mystromys*) and in the presence of styles and lophs in the molars which are not normally present in *Mystromys*. The presence of an enterostyle linked by an enteroloph to the protocone in M^{1-2} is particularly significant in separating *"M." darti* not only from *Mystromys* but also from most other Cricetidae.



Figure. 9 Illustrating the dwarf size of *"Mystromys"* (now *Stenodontomys) darti* (lt. max and rt. mand., MRCIS) as compared with two rt. mandibles of *Mystromys* cf. *hausleitneri* (MLWD/III specimens) and one of *"Mystromys"* (now *Proodontomys) cookei* (EXQRM, bottom rt.). x 3.

Re-evaluation of the Langebaanweg *"Mystromys* cf. *darti"* in the light of the above confirms it as being very close to *M. darti*, differing only in a few minor details, so that it can be described as a second species of the new genus.



Figure. 10 Left maxilla of *"Mystromys"* (now *Stenodontomys*) *darti* showing typical cricetine pattern of upper molar toothrow. SEM photograph x 20.

The closest living relative of *"M." darti* is perhaps not so much *Petromyscus*, with which Lavocat (1956) compared it in some detail, as *Delanymys* Hayman, which was not described until 1962 (Hayman, 1962), several years after the fossil *"M." darti*. (In the description of *Delanymys brooksi*, an East African dwarf mouse with a very long tail, the possibility of the two being conspecific was considered and rejected). *"M." darti* resembles *Delanymys* in the possession of the mesoloph in the upper molars, absent in *Petromyscus*, but differs from both in that the enterostyle has not developed into the proportions of a major cusp and it also lacks the shortened rostrum and projecting capsular process of *Delanymys*. Nevertheless it quite likely represents the basic stock from which both are derived, linking them to the Cricetidae or Cricetodontidae and perhaps also the Dendromurinae, as Lavocat (1964) has suggested. Consequently *"M." darti* can be assigned to the subfamily Petromyscinae Roberts (1951) (see also Petter, 1967) which Chaline, Mein and Petter (1977) have recently united with the Dendromurinae in a new family Dendromuridae. While, however, there is much to be said for the view that groups such as the Gerbillinae, Dendromurinae and Cricetomyinae have as much right to family rank separate from the Muridae as has the Cricetidae, *"M." darti* seems much too close to the Cricetidae to separate it from them. But for the presence of the enterostyle in its otherwise typically cricetine molars (fig. 10) and the wide geographic separation, one could refer it to a genus such as *Baiomys* of North America. Hence it seems preferable to retain at least the Petromyscinae as a subfamily of the Cricetidae.

Regarding the curious distribution of *"M." darti* in the Limeworks, it has been established by further collecting that it occurs not only throughout the *in situ* pink breccia (part of Partridge's (1979) Member 4) on the north face above the archway, but also extends into the underlying red muds (Member 2) described in detail by Turner (1980), having been found in material collected *in situ* from the southern "lintel" of the archway itself (Archway South Lintel *in situ* — ASLIS collection). Hence *"Mystromys" darti* characterises the entire Rodent Corner-Archway formation, yet it does not appear to occur anywhere else in the Limeworks since, in addition to its complete absence from all the EXQRM and MLWD material developed to date, it does not occur even in any of the MRCD "fallen block" breccia developed to date either. De Graaff (1960) did in fact claim a single M_1 tooth in his "Rodent Cave" (=MRCD) collection, but this is incorrect since re-examination of the specimen (Mf 74) shows it to belong to *Dendromus*.

What are the implications of this striking difference between the abundance of *"M." darti* in the MRCIS and its total absence in the other collections? Obviously *"M." darti*-rich breccia cannot be contemporaneous with material lacking it, and quite the simplest explanation is that the Rodent Corner formation is older than those lacking it, with the animal having somehow become extinct in the interval. It is rather unfortunate that, of the *"M." darti*-deficient breccias, only the EXQRM is still stratigraphically in context. Being both horizontally and vertically furthest into the hillside, the EXQRM is ostensibly the oldest fossiliferous material in the whole Limeworks, but owing to the possibility of filling of underground cavities through solution channel effects (common in dolomitic structures) this is by no means certain. Of course there are other possibilities, but besides requiring more complex scenarios, there is some supporting evidence for greater antiquity of the *"M." darti*-bearing MRCIS in that the new genus is known elsewhere only from the indisputably older Langebaanweg site. In any case, the finding that different parts of the Limeworks are palaeontologically non-equivalent holds obvious implications for the stratigraphy of the site; these implications have been considered more fully elsewhere by Maguire (1985).

There are few clues as to the reasons for the decline of *"M." darti* from relative abundance —

16% (mammalian component only) of our collecting owls' diet during the Rodent Corner era — to zero at (presumably) later dates, since the rest of the assemblage seems little affected. There are however some shifts in proportions — for instance *Steatomys*, generally an inhabitant of sandy terrain near streams and swamps (De Graaff, 1981), has declined from about 7% to less than 2%. *Cryptomys*, *Malacothrix* and *Praomys* are others showing a probably significant decline. On the other hand *Mus* and *Dendromus* have apparently benefitted from the disappearance of their fellow-dwarf mouse, increasing from a combined total of only 4% to 11% and 15% in the EXQRM and MLWD respectively. Others showing appreciable increase are *Myosorex* and *Dasymys*. Somewhat wetter conditions with a decline in open ground in favour of dense vegetation is suggested.

Perhaps a clue to the disappearance of *"M." darti* lies in its relationship to *Delanymys*, described as "quite common (where it occurs) but of very restricted biotope" (Misonne, 1971) — the borders of peaty sedge swamps in bamboo forest (Hayman, 1962). If *"M." darti* was also such an animal with a very specialized ecological or vegetational requirement, it might have been vulnerable to an environmental change having only a relatively slight effect on the rest of the assemblage. Nevertheless it remains a complete mystery why a genus which had survived and even thriven from the time of the Langebaanweg Varswater Formation to that of the Makapansgat Rodent Corner, a period believed to be approximately 2 million years, should have disappeared apparently quite suddenly — since there is no evidence (e.g. changes in other lineages) to suggest that the interval between the MRCIS and the EXQRM-MLWD eras was a particularly long one.



Figure. 11 Seven MRCIS specimens of pre-maxillae with incisor of *"Mystromys"* (now *Proodontomys) cookei* demonstrating highly pro-odont upper incisors. All internal aspect except for one in lower rt. corner. The relatively thick enamel (25% of depth) is evident in several of the specimens. x 3.



Figure. 12 Upper and lower incisors of *"Mystromys"* (now *Proodontomys) cookei* (right), radius of curvature of upper 70% that of lower, compared with the 50% of those of *Beamys* (left) as an example of an orthodont muroid. x 2,75.

(j) Since *"M." darti* was originally described as a new dwarf species of *Mystromys*, it is curious that there appears to be a genuine dwarf species of the genus present amongst the Makapansgat fossils. It is represented in the MRCIS collection by three mandibles differing little from *M.* cf. *hausleitneri* except for being 30% smaller. A single M_1 tooth in MLWD/III may represent the same form. It has not been found in the EXQRM but, because of its obvious rarity, less significance can be attached to this absence than in the case of *"M." darti*.

(k) By the finding in the EXQRM of maxillary specimens with premaxilla and incisor attached it was possible to confirm the suspicion (see above) that *"Mystromys cookei"* Davis (MS) was indeed highly pro-odont, and it is now possible to describe it more fully than would have been possible on the material previously available from Kromdraai and elsewhere. (A further good associated specimen is now known also from the KBE collection.)

Its strong pro-odonty (fig. 11) is reflected in the radius of curvature of the upper incisors, being 70% that of the lowers as against about 50% in a normally orthodont muroid (fig. 12). In addition it shows a



Figure. 13 Left mandible of *"Mystromys"* (now *Proodontomys) cookei*, internal aspect showing characteristic dendritic black markings of MRCIS specimens, hypsodont molar crowns with weak cusps and plain occlusal surface, bilobate single alveolus for the fused roots of M_3 and thick enamel of incisor. x 5.



Figure. 14 Right mandible of *"Mystromys"* (now *Proodontomys*) *cookei* (above), internal aspect, compared with one of the *M.* cf. *hausleitneri* (below), both MRCIS specimens. Note in former more hypsodont molar crowns with weaker cusps, procumbent incisor (tip well below occlusal plane of molars), very strong coronoid process, hooked angular process and capsular process extending well into, and protruding from the condylar process x 3,33.

number of characters associated with pro-odont "siezer-digger" type incisors (Hershkovitz, 1962), such as thicker than normal incisor enamel with a roughened surface, molars hypsodont with weak cusps quickly wearing down to a plane occlusal surface (fig. 13), and procumbent lower incisors whose capsular processes extend into and project outwards from the condyles (fig.14) — as in other pro-odont muroids such as *Uranomys* (African Muridae) and *Galenomys* (S. American Cricetidae). In this assemblage of characters it shows parallelism with, for instance, the unrelated molerats Bathyergidae — more especially the subfamily Georychinae — as well as with the less distant burrowing vole *Ellobius* extant in Asia and known from N. Africa as a fossil (Lavocat, 1978). Possible close relationship to *Ellobius* is perhaps worthy of further study, but at the moment it seems more probable that *"M. cookei"* evolved separately and the similarities are due to convergence. In comparison with *Ellobius* the angular process is less strongly modified, the molars are less prismatic and vole-like, and the incisors equally pro-odont but less protuberant. Also the upper molars are 3-rooted (2 in *Ellobius*). The post-cranial skeleton has not been recognised even tentatively and there is at the moment no evidence that the animal was definitely a burrower — like *Ellobius* and the georychines.

It resembles *Mystromys* in the simplified cusp pattern of the molars lacking embellishments such as the mesoloph(id) and various styles and stylids, in the very large coronoid processes of the mandible (figs. 9,14), and in the quite unbeaded frontals, but besides the characters associated with pro-odonty enumerated above, it also differs in lacking the ridges on the incisors typical of *Mystromys*. Also the infraorbital foramen is wide, not ventrally constricted as in most modern muroids including *Mystromys*. Although quite probably related to *Mystromys*, it clearly differs at the generic level, and a new genus is therefore erected for it. Davis' manuscript specific epithet *"cookei"* (in honour of Professor H.B.S. Cooke) is retained for the type species of the new genus. The new genus may not be monotypic since there appears to be a second species at Langebaanweg, distinguished by cusps of molars more alternate and posteroloph(id) less reduced; however, as only a broken mandible is available at the moment, it would be inappropriate to describe it yet.

To summarise the salient findings, it seems clear on the evidence of the microfauna that Makapansgat is, as suspected on other grounds, the oldest of the Transvaal australopithecine sites, showing suggestive links in two of its four extinct genera to Langebaanweg and Taung. Several different microfaunal assemblages distinguished by the appearance or disappearance of certain forms can be recognised. Some of them are unfortunately now stratigraphically out of context, but it is clear on the evidence of the two which are still *in situ* that the stratigraphy is rather more complex than previously realised. This aspect has been discussed further elsewhere by Maguire (1985).

TAXONOMIC SECTION

It remains to describe formally the new taxa mentioned in the preceding text. The nomenclatural system of Reig (1977) is used to describe the molar teeth of cricetid rodents; note that one new term, enteroflexus, must be introduced into this system in order fully to describe the upper molars of *"M." darti* (fig. 15).

Class	MAMMALIA
Order	RODENTIA
Sub-order	MYOMORPHA
Superfamily	MUROIDEA
Family	CRICETIDAE
Subfamily	CRICETINAE

***Proodontomys* n. gen.**

Diagnosis:

Cricetine rodents of moderate size characterised by strongly pro-odont siezer-digger upper incisors and procumbent lower incisors; enamel of incisors thickened and in uppers with a roughened surface; capsular processes of the mandible extending into and projecting prominently from the condylar processes; angular processes also well developed, the tips somewhat hooked; molars hypsodont but rooted, pattern simplified without subsidiary lophs and styles, cusps weak, distinguishable only in unworn juvenile teeth, rapidly wearing to a plane occlusal surface; interorbital region of frontals rounded, not beaded, pinched or square. Infraorbital foramina wide, not ventrally constricted.

Type Species:— *P. cookei*, n. sp.

Included Species:— *P. cookei*

Holotype:— MRCIS/23A. rt. mandible, intact except for loss of M_3 (fig. 16).

Type Locality:— Makapansgat Limeworks



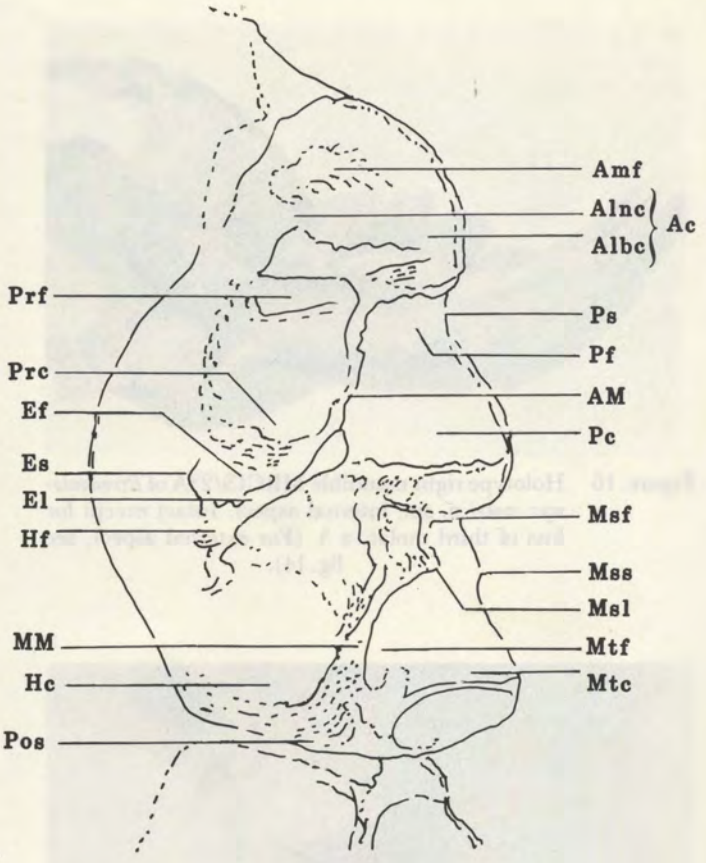


Figure. 15 Left upper first molar of *"Mystromys"* (now *Stenodontomys*) *cookei*, SEM photograph x 60, illustrating the nomenclatural system of Reig (1977). One new term, enteroflexus, is included.

Abbreviations:

Ac	Anterocone
Albc	Anterolabial Conule
Alnc	Anterolingual Conule
Amf	Anteromedian Flexus
AM	Anterior Mure
Ef	Enteroflexus
El	Enteroloph
Es	Enterostyle
Hc	Hypocone
Hf	Hypoflexus
MM	Median Mure
Msf	Mesoflexus
Msl	Mesoloph
Mss	Mesostyle
Mtc	Metacone
Mtf	Metaflexus
Pc	Paracone
Prc	Protocone
Prf	Protoflexus
Pf	Paraflexus
Ps	Parastyle
Pos	Posteroloph

Stratigraphic Zone:— *In situ* pink breccia at the Rodent Corner, part of the Member 4 of Partridge (1979), age uncertain but probably middle Pliocene, 2,5 to 3,5 myBP

Distribution:— Known from Makapansgat Limeworks, Kromdraai A & B, Sterkfontein (Member 5), Swartkrans, Gladysvale and Taung.

Paratypes:-(Makapansgat Limeworks):

MRCIS/	23B	1 rt.	mandible, intact, all teeth but heavily worn.
	23C	1 rt.	maxilla, all teeth.
	23D	1 lt.	maxilla, all teeth (fig. 17).
	24	16 rt.	mandibles (8 — no incisor).
	25	17 lt.	mandibles (5 — no incisor).
	26	13 lt.,	10 rt. maxillae.
	27	6 lt.,	2 rt. premaxillae with incisor; 1 rt. premaxilla fragment without incisor.
	28	45 lt.	upper incisors.
	29	33 rt.	upper incisors.
	30	24 rt.	lower incisors.
	31	23 lt.	lower incisors.
	32	24 lt.	M_1 molars.
	33	26 rt.	M_1 molars.
	34	15 lt.	M_2 molars.
	35	18 rt.	M_2 molars.
	36	10 lt.,	6 rt. M^1 molars.
	37	6 lt.,	4 rt. M^2 molars.
	38	5 lt.,	3 rt. M_3, 1 lt., 1 rt. M^3 molars.
EXQRM/46		60 rt.	mandibles (30 without incisor).
	47	82 lt.	mandibles (36 without incisor).
	48	36 rt.	maxillae.
	49	26 lt.	maxillae.
	50	A. rt.	maxilla with premaxilla and incisor.



Figure. 16 Holotype right mandible MRCIS/23A of *Proodontomys cookei* n. sp., internal aspect. Intact except for loss of third molar. x 5. (For external aspect, see fig. 14).

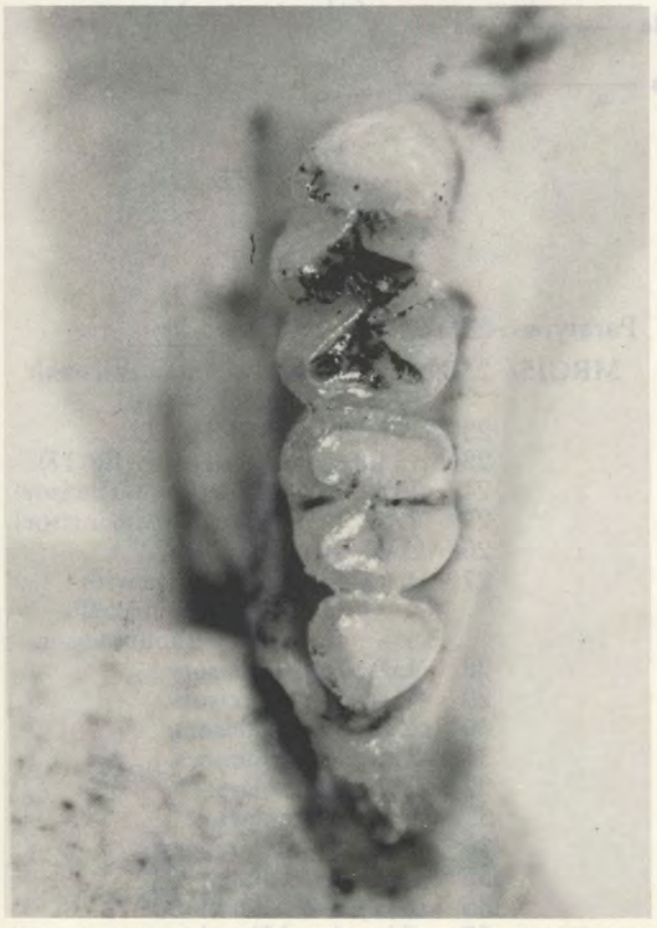


Figure. 17 *Proodontomys cookei* n. sp. Left maxilla MRCIS/23D showing occlusal aspect of toothrow. x 14,5.

B. pair of premaxillae with incisors.
C. rt. maxilla with premaxilla and incisor (intact infra-orbital foramen).
51 19 rt. lower incisors.
52 20 lt. lower incisors.
53 30 lt. upper incisors.
54 28 rt. upper incisors.
55 13 lt. 8 rt. premaxillae with incisor.
56 9 lt. 5 rt. premaxillae without incisor.
57 Associated specimens: A. rt. max. + pre-max.; B. lt. max + palate.
58 A & B. 2 Pairs frontals, one with part of rt. pre-maxilla. C-N. 12 Molars : 2 lt., 3 rt. M_1; 4 rt., 1 lt. M^1; 1 rt., 1 lt. M^2.

RCIS/X-81/3	A-E	2 lt. lower incisors; 2 lt., 1 rt. upper incisors.
MLWD/I/3E		1 lt. lower incisor.
MLWD/11/6		1 lt. upper incisor; 2 rt. M^1; 1 rt. M^3.
MLWD/III/	19	5 lt., 4 rt. mandibles (without incisor except 1 rt.)
	20	3 lt., 3 rt. maxillae; 2 lt., 1 rt. premaxillae (without incisor)
	21	18 rt., 6 lt. lower incisors.
	22	15 rt., 7 lt. upper incisors.
	23	25 lt. lower molars : 6 M_1, 10 M_2, 9 M_3.
	24	23 rt. lower molars : 9 M_1, 10 M_2, 9 M_3.
	25	20 lt. upper molars : 10 M^1, 6 M^2, 2 M^3.
	26	17 rt. upper molars : 6 M^1, 8 M^2, 3 M^3.
MRCF/1/F		1 lt. M_3 molar.
ASLIS/XI-81/3		1 rt. mandible; 1 rt., 1 lt. maxillae (different individuals); 1 rt. M^2 molar.

Referred Material (from other sites):—

Kromdraai A & B (material collected in 1956):

KA/	20	3 rt., 5 lt. mandibles; 1 rt. maxilla; 2 lt. upper incisors; 1 rt. M1 molar.
KB/0-6/	69	17 lt. mandibles (2 without incisors).
	70	9 rt. mandibles (2 without incisors).
	71	12 lt., 8 rt. lower incisors; 1 lt. M_1 molar.
KB/12-18/	196	17 lt. mandibles (2 without incisors).
	197	9 rt. mandibles (3 without incisors).
	198	Incisors : 4 lt., 4 rt. lower; 1 rt. upper.

Kromdraai BE collection (material not yet fully catalogued, B numbers referring to blocks of breccia):

KBE/B73	5 rt., 3 lt. mandibles; 2 rt., 1 lt. upper, 2 rt., 1 lt. lower incisors.
KBE/B84	2 lt., 1 rt. mandibles; 1 lt., 2 rt. lower, 2 lt., 1 rt. upper incisors.
KBE/B80	2 lt., 1 rt. mandibles; 1 rt. lower incisor.
KBE/B76	1 rt. mandible; 2 lt. lower incisors.
KBE/B75	1 rt. mandible (no incisor). 1 rt. maxilla; 3 lt., 2 rt. lower incisors.
KBE/B63	3 lt. mandibles; 1 rt. maxilla; 2 lt., 1 rt. lower, 2 lt., 5 rt., upper incisors.
KBE/B23	1 lt. lower incisor.
KBE/B83	1 rt. maxilla with premaxilla and incisor; 3 lt. mandibles; 1 lt. maxilla; 2 lt.lower, 1 lt. upper incisors.
KBE/B30	1 lt. lower, 1 rt., 1 lt. upper incisors.
KBE/B61	3 lt. mandibles (2 without incisors); 4 rt. mandibles (3 without incisors); 1 lt. maxilla. Incisors:– 6 lt., 4 rt. lower, 7 lt., 5 rt. upper.
KBE/B77	1 rt. mandible; 2 rt., 1 lt. upper incisors.
KBE/B130	1 lt. upper incisor.
KBE/B101	2 rt. mandibles; 1 lt. maxilla; 2 rt., 1 lt., upper incisors.
KBE/B102	1 lt., 1 rt. mandibles; 1 lt. maxilla; 1 rt. premax + incisors; 2 lt., 2 rt. upper incisors.
KBE/B104	1 lt., 1 rt. mandibles; 1 lt., 1 rt. lower, 1 lt. upper incisor.
KBE/B49	1 lt. upper incisor.
KBE/B42	2 rt., 1 lt. upper, 1 lt. lower incisors.

Swartkrans (a few small breccia fragments only):

ZWKB/3	2 lt. mandibles.

Sterkfontein:
Dumps: STS/D1+2/73: 1 rt. mandible.
Grid: SEG/W59/10′5″-11′5″/1: 2 rt., 1 lt. mandible; 1 rt. lower incisor.

Taung and Gladysvale:
Specimens seen from these localities in the Camp Collection are no longer available and their current whereabouts are unknown to me. I have a note that the Kromdraai B mandibles agreed well in all respects with those from Taung, the originally intended type locality.

Diagnosis:

Size slightly smaller than *Mystromys hausleitneri* adult mandible with incisor 18-20 mm, molar toothrows *c.* 4,8 mm long. Upper incisors pro-odont, their radius of curvature *c.* 70% that of the lower; enamel of incisors thick, between 20% and 33% the depth of the tooth on the lingual face. Especially in the lower incisors, the dentine bulges out and the enamel falls away at the interface to give a somewhat grooved effect. Enamel surface of especially the upper incisors roughened by fine vermiculate to pinnate markings, but without the characteristic ridges of *Mystromys*. Anterocone(-id) of first molars simple, not bifid. Cusps of molars opposite, not alternate, with reduced posteroloph(-id) in first and second molars. In unworn teeth posteroloph of upper M^{1-2} not distinguishable from hypocone, but posterolophid more distinct in lower M_{1-2}. Metacone and hypocone distinct in unworn M^{1-2} but united in early wear by disappearance of posteroflexus separating them to give a simple trilophodont pattern to the first and a bilophodont to sigmoid pattern to the second molar; similarly for the entoconid, hypoconid and posterolophid of the lower M^{1-2}. Unworn first lower molars possess a pit or fossetid near the middle of the posterior border of the anteroconid and another between the hypoconid, entoconid and posterolophid. Third upper molars less than half the size of second, similar to *Mystromys* in unworn cusp pattern, but soon becoming bilophodont and eventually cylindrical with wear. Upper molars usually 3-rooted (2nd rarely 4-rooted), but roots of third molars above and below fused in a single alveolus. Cusp rows united by mures centrally situated except for labial junction of anteroconid with protoconid in first lower molars.

Incisive foramina long, penetrating to between the middle of the first molars. Palate narrow, its width equal to or less than the length of first upper molars, and long, extending 1,5 to 2 times the length of the third molars behind those molars. Masseter burr on the maxilla not at all raised, i.e. no masseter "knob". In the mandible, inferior and superior masseter ridges weak, meeting in a V somewhat lower down and further back below the front of M_1 as compared with *Mystromys*. Coronoid process of mandible very large, extending back about as far as condyle. Lower incisors procumbent, their capsular projections extending into and projecting outwards from the condylar processes.

Measurements:

Holotype mandible (adult, moderately worn teeth, M_1 relatively large):-

Length mandible plus incisor 18,0mm

Greatest depth (coronoid to angular process) 9,6mm

Length M_1	:	2,05mm
Width M_1	:	1,23mm
Length M_2	:	1,36mm
Width M_2	:	1,29mm

Alveolar length tooth row 4,7mm
Alveolar length M_{1-2} 3,3mm
Measurements of a few other selected individual specimens:

Mandible MRCIS/23B: old individual with heavily worn teeth, length of mandible plus incisor 20,3mm.

Maxillae: Two MRCIS specimens, one left (MRCIS/23C), one right (MRCIS/23D), have all teeth. The left has a relatively larger M^1 but smaller M^3, and teeth in a lesser degree of wear (which also slightly affects the measurements) (Table 3).

Right maxilla with premaxilla EXQRM/57A has M^1 2,05mm long and incisive foramen 6,0mm beginning 2,4mm behind the incisor, and penetrating 1,1mm between the first molars. The accompanying lt. maxilla 57B possibly from the same individual

TABLE 3

UPPER TOOTH ROW MEASUREMENTS OF *PROODONTOMYS COOKEI* (2 SPECIMENS)

	MRCIS/23C Lt. maxilla	MRCIS/23D Rt. Maxilla
Length M^{1-3}	4,49	4,33
Length M^1	2,25	2,05
Length M^2	1,37	1,37
Length M^3	0,82	0,94
Breadth M^1	1,37	1,48
Breadth M^2	1,33	1,48
Breadth M^3	0,94	0,97

(M^1 2,04 mm) has the palate attached. The palate is 2,3mm broad across the first molars and it extends 1,3mm behind the 3rd molar.

For the purpose of statistical toothrow measurements, mandibles and maxillae possessing undamaged (although often excessively worn) teeth from the MRCIS and EXQRM collections have been combined to provide an adequate sample.

Statistical Measurements (Table 4):

TABLE 4

TOOTHROW MEASUREMENTS OF *PROODONTOMYS COOKEI* (MRCIS AND EXQRM SPECIMENS)

	Max	Mean	Min	No. of Specimens
Lower toothrow (mm)				
Length M_{1-3}	4,58	4,30	4,14	7
M_{1-2}	3,46	3,29	2,98	30
M_{2-3}	—	2,50	—	1
M_1 only	2,07	1,90	1,69	6
M_2 only	1,48	1,41	1,32	6
Upper toothrow (mm)				
Length M^{1-3}	4,49	4,25	4,03	7
M^{1-2}	3,63	3,33	3,19	16
M^{2-3}	—	2,33	—	1
M^1 only	2,05	1,92	1,80	7
M^2 only	1,51	1,37	1,22	14

Incisors: Owing to the fragility of MRCIS specimens, the EXQRM/51-53 specimens have been preferred for measurement of a representative selection (excluding damaged and obviously juvenile specimens) (Table 5).

Subfamily PETROMYSCINAE

***Stenodontomys* n. gen.**

Diagnosis:

Muroid rodents of dwarf size, mandible and incisor *c.* 11-12 mm long, molar toothrows *c.* 3 mm, comparable in size to extant dwarf genera such as *Mus*, *Micromys*, *Dendromus*, *Baiomys*, and *Reithrodontomys*, and apparently linking the typical cricetines with the dendromurines via the Petromyscinae. Molars brachybunodont, of typical cricetine pattern with mesoloph(-id) present in first and second molars but differing in the constant presence of an enterostyle in M^{1-2} linked to the protocone by an enteroloph creating a new flexus, the enteroflexus, quite distinct from the hypoflexus. Small conical styles such as a mesostyle (M^{1-2}), parastyle (M^1) and mesostylid (M_{1-2}) frequently but variably present in the first and second molars.

Third molars not greatly reduced, lower about two-thirds and upper about half the size of corresponding second. Axis of third lower molar markedly offset lingually from that of second. Lower molars 2-rooted, upper 3-rooted but with roots of third sometimes reduced to two. Roots and their alveoli roundish, little flattened in cross-section. Enamel surface of incisors smoothly rounded without grooves or ridges; occlusal surfaces relatively long, not notched as in *Mus*. Exposed portions of incisors lemon-yellow.

Incisive foramina broad, penetrating to between anterior roots of first molars. Palate broad and long (as defined by Hershkovitz, 1962).

A roundish to oval slightly raised masseter knob present in the maxilla. Inferior masseteric ridge of mandible ends anteriorly under the front edge of first molar, not displaced backwards as in the dendromurines and often in *Mus*; superior masseteric ridge faint only, sometimes indiscernible, meeting the inferior ridge under the posterior root of M_1. Coronoid process of mandible small, not reaching back towards condyle as in *Mystromys* and *Proodontomys*.

Type Species: *Mystromys darti* Lavocat

Included Species: *S. darti* (Lavocat); *S. saldanhae* n. sp.

TABLE 5

INCISOR MEASUREMENTS OF *P. COOKEI* (EXQRM SPECIMENS).

	Depth (mm) Min-Av-Max	Width (mm) Min-Av-Max	Enamel Thickn. % of Depth	No. of specimens measured
Upper	1,07-1,36-1,50	0,82-1,02-1,12	20,3-25,8-32,6	43 (21 rt., 22 lt.)
Lower	1,22-1,38-1,59	0,70-0,93-1,10	21,4-25,7-32,1	31 (15 rt., 16 lt.)

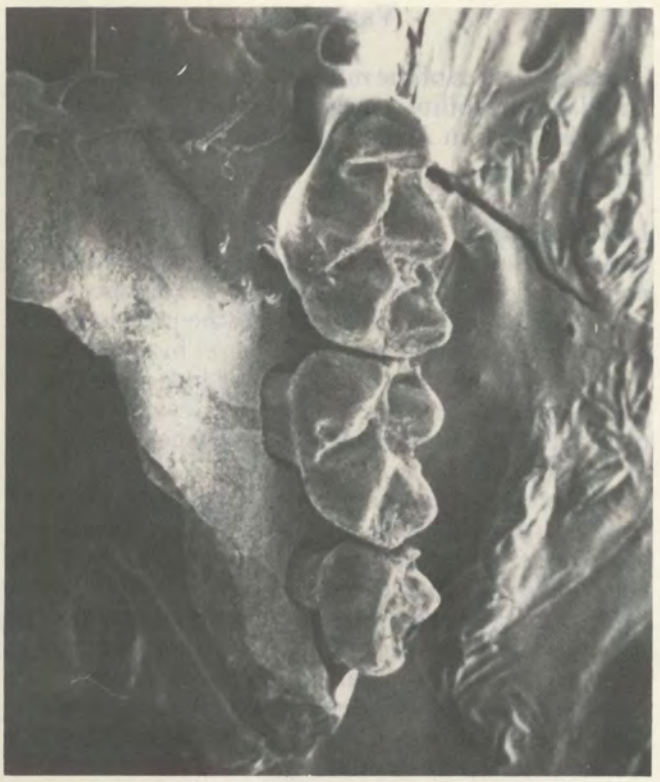


Figure. 18 *Stenodontomys darti*. Left maxilla, SEM photograph x 20. Same specimen as in fig. 10, but tilted to show mesostyles in M^{1-2}.



Figure. 19 *Stenodontomys darti*. Left lower toothrow, SEM photograph x 20. Third molar about 2/3 size of 2nd, not as reduced as in *Mystromys, Mus* and especially the Dendromuridae; axis of M_3 markedly offset from that of M_2 as in many cricetines but not *Mystromys*.

***Stenodontomys darti* (Lavocat).**

Revised diagnosis:

Characters of the genus plus:— molars relatively narrow, width of 2nd upper molar *c.* 75-80% of its length; 3rd upper molar 2-rooted; angular process of mandible not markedly hooked. (figs 10, 18-21).

Referred Material:—

MRCIS/1: 91 rt. mandibles with incisor
2: 92 rt. mandibles without incisor
3: 105 lt. mandibles with incisor
4: 78 lt. mandibles without incisor
5: 93 rt. maxillae
6: 116 lt. maxillae
7: 8 rt., 7 lt. premaxillae with incisor
8: 217 rt. upper incisors
9: 224 lt. upper incisors
10: 155 rt. lower incisors
11: 117 lt. lower incisors
12: 113 lt. M^1
13: 99 rt. M^1
14: 58 lt M^2
15: 64 rt. M^2
16: 22 lt. M^3
17: 14 rt. M^3
18: 131 lt. M_1
19: 140 rt. M_1
20: 116 lt. M_2
21: 106 rt. M_2
22: 90 lt. M_3
23: 82 rt. M_3

RCIS/X-81/2: 1 rt., 1 lt., mandibles; 1 rt. maxilla

MRCF/I/A: rt. max with M^1;
B: rt. max with M^2;
C: rt. M^1

ASLIS/XI-81/5: 1 lt., 1 rt. mandibles; 1 rt., 1 lt. upper incisors.

Measurements:

Eleven intact mandibles with incisor measure 11,35 to 12,25 mm (mean 11,9 mm). The incisive foramina commence 1,1 to 1,4 mm behind the upper incisors, and penetrate about 0,2 mm between the anterior roots of the first molars; their width is about 0,6 mm. The palate is 1,0 to 1,25 mm wide from the midline to the lingual root of the first molar, and extends 0,1 to 0,2 mm behind the third molar.



Figure. 20 *Stenodontomys darti*. Right mandible, intact except for loss of M_3. x 8



Figure. 21 *Stenodontomys darti*. Right mandible, edentulous, showing roundish molar alveoli. x 12,5.

For the dimensions of the lower molars, the 50 specimens of MRCIS/3 which possess at least one molar have been taken as a representative selection; similarly, 87 specimens of MRCIS/6 provided dimensions for the upper molars (Table 6).

An apparent discrepancy with the measurements of the type as given by Lavocat (1956) is readily resolved by inspection of his photographed figures when it is apparent that the length of M_3 should be 0,81 mm and not 0,51 as given. The toothrow measurement M_{1-3} should apparently also be corrected by the same amount from 2,80 to 3,10 mm.

TABLE 6

DENTAL DIMENSIONS OF *STENODONTOMYS DARTI*.

	Min. -Mean -Max.	No of Specimens
Length M_{1-3}	2,85-2,94-3,11mm	6
Length M_{1-2}	2,08-2,18-2,38	17
Length M_{2-3}	1,77-1,81-1,88	4
Length M_1	1,07-1,16-1,30	41
Length M_2	0,94-1,01-1,08	30
Length M_3	0,76-0,80-0,85	11
Breadth M_1	0,73-0,76-0,80	41
Breadth M_2	0,75-0,79-0,84	30
Breadth M_3	0,68-0,70-0,71	11
Length M^{1-3}	2,80-2,89-3,03	13
Length M^{1-2}	2,22-2,31-2,41	25
Length M^{2-3}	1,56-1,58-1,60	4
Length M^1	1,20-1,33-1,42	71
Length M^2	0,94-0,98-1,02	53
Length M^3	0,53-0,585-0,63	17
Breadth M^1	0,70-0,77-0,83	71
Breadth M^2	0,70-0,76-0,80	53
Breadth M^3	0,60-0,65-0,70	17
Upper incisor		
Depth	0,83-1,01-1,22	130
Breadth	0,46-0,54-0,60	58
Occl. length	1,00-1,03-1,05	126
Lower incisor		
Depth	0,74-0,84-0,92	53
Breadth	0,41-0,47-0,53	53
Occl. length	1,60-1,95-2,25	41

Variation:

Certain features of the molars are extremely variable (similar variability in the presence or absence of styles is found in *Mus* and *Acomys* in the same collection).

Lower molars:
Nineteen out of 40 specimens of M_1 possess a definite mesostylid; in the remaining 21 it is indistinct to absent. It is usually separated from the mesolophid (a spur jutting from the posterior mure) by a valley, but in two instances the two structures link up so that in these cases the mesolophid in effect reaches the lingual edge of the tooth instead of petering out halfway as it usually does.

An ectostylid is a constant feature of M_1, M_2 and usually also M_3. In seven out of 41 first molars it is joined to the posterior mure by a distinct crest, the ectolophid, of which there is no sign in the remaining 34. Structures such as the mesostylid and ectolophid present in M_1 are not necessarily repeated in M_2; they are generally weaker and often absent altogether even when well developed in M_1. The mesolophid, nearly always distinct in M_1, also tends weaker, often indistinct in M_2.

Upper molars:
A distinct parastyle is present in at least 45 out of 72 first upper molars - the others include specimens in which it may have been removed by damage or heavy wear, as well as being possibly present but indistinct; however, it is definitely absent in most of them.

When present, it varies from a relatively large rounded bump to a small but pointed conical peak. It is usually symmetrically situated in the mouth or angle of the paraflexus but may be somewhat displaced anteriorly towards the anterocone or posteriorly towards the paracone. It is not usually present in the second molar, but in one case where it occupies a posterior position up the side of the paracone of M^1 it is present in a similar situation in M^2. It may also be double — as in one instance in which the mesostyle is also double.

A mesostyle is distinctly present in 48 out of the 72 specimens — absent, faint or possibly removed by wear in the remaining 24. It varies in position from angularly situated in the mouth of the mesoflexus (19 instances) to more posteriorly on the edge of the metacone (23 instances), and in 6 cases it is double, i.e. there are two mesostyles, one in each position. When present in the posterior position it is often joined by the mesoloph which in these cases penetrates to the buccal edge of the tooth instead of petering out halfway as is more usual. There are 13 instances of this, including one of the cases where the mesostyle is doubled.

A small protostyle is rarely present in the entrance of the protoflexus, and a small style may rarely be present in the entrance of the hypoflexus behind the enterostyle; these observations have not yet been quantified.

Regarding the second upper molar, it is present in 53 of the 87 specimens chosen for detailed examination, including 15 in which M^1 is lost. A mesostyle is present in 32 and absent in 21 of the 54. Its presence is not necessarily correlated with that in M^1, since it is present in three instances when absent in M^1, and vice versa in seven other cases. Moreover, it is generally always angularly situated, never posteriorly as is often true of M^1. It is single in cases where double in M^1; however it is double in one of the specimens which lack M^1. The posterior half of M^2 is slightly narrower than that of M^1 and the mesoloph is generally weaker, frequently indistinct; it never reaches the edge of the tooth as it may do in M^1.

Stenodontomys saldanhae, n. sp.

Diagnosis:

Very similar to *S. darti* (including size), but distinguished by second upper molar broader, breadth about 85 % of its length, third upper molar 3- and not 2-rooted, and tip of angular process of mandible markedly hooked.
Holotype: L20566 B/S-1. Left maxilla with M^{1-3} (fig. 22)



Figure. 22 *Stenodontomys saldanhae* n. sp. Holotype left maxilla, S.A.M. specimen L 20566/S-1. SEM photograph x 20.

Type Locality: Langebaanweg "E" Quarry, Varswater Formation, probably early Pliocene, *c.* 5 myBP (Hendey, 1981).
Paratypes: L20746/S-1 rt. mandible with M_1, M_3 and incisor (tip broken off) (fig. 23).
L20746/S-2 rt. mandible with M_1 and incisor, posteriorly broken.
L20746/S-3 lt. mandible, anteriorly broken, no teeth, alveoli of M_{2-3}, posterior processes intact.



Figure. 23 *Stenodontomys saldanhae* n. sp. Right mandible with M_1 and M_3, S.A.M. specimen L 20746/S-1. S.E.M. photograph x 20.

Measurements and notes:
Mandible L20746/S-1: M_1 1,16 mm long, 0,65 mm broad.
M_3 0,80 mm long, 0,62 mm broad.
Toothrow M_{1-3} 2,93 mm long.
Mandible L20746/S-2: M_1 1,15 mm long, 0,71 mm broad.
The incisor has depth 0,73 mm, width 0,45 mm and occlusal length 1,8 mm.
Mandible L20746/S-3: Lacks teeth, but is useful in confirming the markedly hooked angular process seen also in S-1 to be a constant character (fig. 24).



Figure. 24 Comparison of *Stenodontomys saldanhae* (upper three mandibles, 1 lt., 2 rt.) with *S. darti* (lower three mandibles, all rt.) Note more hooked angular process in *S. saldanhae*. x 3,25.

Neither M_1 appears to possess a mesolophid or mesostylid; an ectostylid is present in both, joined to the mure by an ectolophid in the second specimen. Holotype maxilla L20566B/S-1: M^1 1,37 x 0,78 mm; M^2 0,97 x 0,82 mm; M^3 0,53 x 0,62 mm

Note that the breadth of M^2, 85% of its length, falls outside the limits for *S. darti*, for which it is usually about 76%, and does not exceed 80% in any measured specimen. In contrast, the lower molars M_1 and M_3 are narrower than those of *S. darti*.

M^1 possesses a weak parastyle, and a distinct mesostyle posteriorly situated and joined to the mesoloph. In M^2, the mesostyle is larger than in M^1, angularly situated, and also clearly linked to the mesoloph, a condition not encountered in any *S. darti* specimens. Examination of more specimens is desirable to gauge variability and how constant or otherwise are the apparent differences from *S. darti*.

The species is named after the Saldanha Bay area in which Langebaanweg lies, and hence indirectly after Antonio de Saldanha, an Iberian admiral of the early sixteenth century.

An abstract of the paper has been published (Pocock, 1985) in consequence of an early version having been read at a meeting of the Palaeontological Society of Southern Africa in Pretoria in July, 1982.

ACKNOWLEDGEMENTS

I am indebted to the following:

For my introduction to the field via the KB collection:— the late Dr. D.H.S. Davis.

For the loan of fossil specimens or permission to collect:—Drs. C.K. Brain and E.S Vrba, Transvaal Museum (Kromdraai and Swartkrans), Prof. P.V. Tobias and Mr. A.R. Hughes (Sterkfontein), Dr. Q.B. Hendey (Langebaanweg) and Prof. M.A. Raath and Prof. J.W. Kitching (Makapansgat).

For the loan of recent specimens:— Transvaal Museum and British and American Museums of Natural History.

For help in collecting at Makapansgat at various times:— Dr. R.J. Clarke, Mr. A.R. Hughes, the late Mr. B. Maguire and Dr. J.M. Maguire.

For the loan of equipment and other photographic assistance:— Mr. A.R. Hughes, Mr. P. Faugust and Dr. J.M. Maguire. Scanning Electron Microscope photographs were taken by Dr. M.J. Witcomb and the line drawing was done by Mrs. Joan van Gogh and Ms D. Pearce. Mrs. C. Kennedy and Mrs. D. Smith typed various drafts of the paper.

REFERENCES

Brain, C.K. 1978. Some aspects of the South African australopithecine sites and their bone accumulations. *In:* Jolly, C. (ed.) *Early Hominids of Africa*. 131-161. Duckworth: London.

————. 1981. *The hunters or the Hunted? An introduction to African cave taphonomy*. Univ. of Chicago Press: Chicago & London. 365 pp.

Broom, R. 1934. On the fossil remains associated with *Australopithecus africanus*. *S. Afr. J. Sci.*, **31**, 471-480.

————. 1937. On some new Pleistocene mammals from the limestone caves of the Transvaal *S. Afr. J. Sci.*, **33**, 750-768.

————. 1939. The fossil rodents of the limestone cave at Taung. *Ann. Transv. Mus.*, **19(3)**, 315-317.

————. 1948a. Some South African Pliocene and Pleistocene mammals. *Ann. Transv. Mus.*, **21**, 1-38.

————. 1948b. The giant rodent mole *Gypsorhychus*. *Ann. Trans. Mus.*, **21**, 47-49.

Butler, P.M. and Greenwood, M. 1976. Elephant shrews (Macroscelididae) from Olduvai and Makapansgat. *Fossil Vertebrates of Africa*, **4**, 1-56, Academic Press: London.

Camp, C.L. 1948. University of California African Expedition — Southern Section. *Science*, **108**, 550-552.

Chaline, J., Mein, P. and Petter, F., 1977. Les grandes lignes d'une classification évolutive des Muroidea. *Mammalia*, **41**, 245-252.

Cooke, H.B.S. 1978. Faunal evidence for the biotic setting of early African hominids. *In:* Jolly, C, (ed.), *Early hominids of Africa*. 267-281. Duckworth: London.

Corbet, G.B. and Hanks, J. 1968. A revision of the elephant shrews, family Macroscelididae. *Bull. Br. Mus. nat. Hist. (Zool.)*, **16**, 47-111.

Dart, R.A. 1925. *Australopithecus africanus*, the man-ape of South Africa. *Nature (London)*, **115** (2884), 195-199.

Davis, D.H.S. 1959. The Barn Owl's contribution to ecology and palaeoecology. *Proc. First Pan-Afr. Ornithol. Congr. 1957, Ostrich Supp.* **3**, 144-153.

————. 1962. Distribution patterns of southern African Muridae with notes on their fossil antecedents. *Ann. Cape. prov. Mus.*, **2**, 56-76.

————. 1965. Classification problems of African Muridae. *Zool. afr.*, **1** (1), 121-145.

De Graaff, G. 1960. A preliminary investigation into the mammalian microfauna in Pleistocene deposits of caves in the Transvaal System. *Palaeont. afr.*, **7**, 79-118.

————. 1975. Part 6.9 Family Bathyergidae. *In:* Meester J. and Setzer, H.W. (eds). *The Mammals of Africa: An Identification Manual*. Washington DC: Smithsonian Institution Press.

————. 1981. *The rodents of Southern Africa*. Butterworths: Pretoria.

Ellerman, J.R. 1941 *The families and genera of living rodents*. Vol. 2 London: British Museum (Natural History).

Ewer, R.F. and Cooke, H.B.S. 1964. The Pleistocene mammals of Southern Africa. *In:* Davis, D.H.S. (ed.) *Ecological Studies in Southern Africa*. 35-48. Den Haag: Dr W. J. Junk.

Freedman, L. and Brain, C.K. 1972. Fossil cercopithecoid remains from the Kromdraai australopithecine Site (Mammalia; Primates). *Ann. Trans. Mus.*, **28**, 1-16.

Grine, F.E. 1982. A new juvenile hominid (Mammalia: Primates) from Member 3, Kromdraai Formation, Transvaal, South Africa. *Ann. Trans. Mus.*, **33**, 165-239.

Haq, B.U., Berggren, W.A. and Van Couvering, J.A. 1977. Corrected age of the Pliocene/Pleistocene boundary. *Nature (London)*, **269**, 483-488.

Hayman, R.W. 1962. A new genus and species of African rodent. *Rev. Zool. Bot. Afr.*, **65**, 129-138.

Hendey, Q.B. 1973. Carnivore remains from the Kromdraai australopithecine site (Mammalia:— Carnivora). *Ann. Trans. Mus.*, **28**, 99-112.

————. 1978. Late Tertiary Hyaenidae from Langebaanweg, S.A. and their relevance to the phylogeny of the family. *Ann. S. Afr. Mus.*, **76**, 265-297.

————. 1981. Palaeoecology of the late Tertiary fossil occurrences in "E" Quarry, Langebaanweg, South Africa, and reinterpretation of their geological context. *Ann. S. Afr. Mus.*, **84** (1), 1-104.

Hershkovitz, P. 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. *Fieldiana: Zool.*, **46**, 1-524.

Jacobs, L.L. 1978. Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. *Mus. N. Arizona Press Bull. Ser.*, **52**, 1-103.

Lavocat, R. 1956. La Faune de ronguers des grottes a Australopitheques. *Palaeont. afr.*, **4**, 69-75.

————. 1959. Origine et affinités des Ronguers de la sous-

famille des Dendromurinés. *Cr. Acad. Sci. Hebd. Paris,* **248**, 1375-1377.

————. 1961. Le gisement de vertebres fossiles de Beni Mellal. *Notes Mem. Serv. Geol. Maroc.,* **155**, 1-144.

————. 1964. On the systematic affinities of the genus *Delanymys* Hayman. Proc. Linn. Soc. Lond., **175**, 183-185.

————. 1973. Le Ronguers du Miocene d'Afrique Orientale. 1. Miocene inférieur. *Mem. Trav. E.P.H.E. Institut de Montpellier* **1**, 1-284.

————. 1978. Rodentia and Lagomorpha. *In:* Maglio, V.J. and Cooke, H.B.S. (eds) *Evolution of African Mammals*: 69-89. Harvard University Press.

Lindsay, E.H.(1978) *Eucricetodon asiaticus* (Matthew and Granger) an Oligocene rodent (Cricetidae) from Mongolia. *J. Paleontol.*, **52**, 590-595.

Maddock, A.H. and Perrin, M.R.1983. Development of the gastric morphology and fornical bacterial/epithelial association in the white-tailed rat *Mystromys albicaudatus* (Smith 1834) *S. Afr. J. Zool.*, **18**, 115-127.

Maguire, B. 1980. Further observations on the nature and provenance of the lithic artefacts from the Makapansgat Limeworks. *Palaeontol. afr.,* **23**, 127-151.

Maguire, J.M. 1985. Recent geological, stratigraphic and palaeontological studies at the Makapansgat Limeworks. *In:* Tobias, P.V. (ed). *Hominid Evolution: Past, Present and Future*: 151-164. New York: Alan R. Liss, Inc.

Mason, R.J. and Turton, J. 1971. Multivariate analysis of Cave of Hearths Middle Stone Age artefact assemblage. *Occ. Pap. Univ. of Witwatersrand Dept. of Archaeology.,* **7**, 1-38.

Martin, L.D. 1980. The early evolution of the Cricetidae in North America. *Univ. Kansas paleontol. Contrib.,* **102**, 1-42.

———— and Corner, R.G. 1980. A new genus of cricetid rodent from the Hemingfordian (Miocene) of Nebraska *Univ. Kans. paleontol. Contrib.* **103**, 1-5.

McFadden, P.L., Brock, A. and Partridge, T.C. 1979. Palaeomagnetism and the age of the Makapansgat hominid site. *Earth and Planet. Sci. Lett.,* **44**, 373-382.

Mein, P. 1968. Détermination de l'humérus de quelques Cricetidae fossiles. *Colloques Internat. C.N.R.S.,* **163**, 515-521.

Mein, P. and Freudenthal, M. 1971. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) de Tertaire de l'Europe. *Scripta geol.,* **2**, 1-37.

Misonne, X. 1969. African and Indo-Australian Muridae, evolutionary trends. *Ann. Mus. r. Afr. cent., Ser. 8vo., Zool.,* **172**, 1-219.

————. 1971. Rodentia (main text) Part 6.0, pp 1-39. *In:* Meester J. and Setzer, H.W. (eds). *The Mammals of Africa: An Identification Manual.* Washington DC: Smithsonian Institution Press.

Partridge, T.C. 1973. Geomorphological dating of cave opening at Makapansgat, Sterkfontein, and Taung. *Nature (Lond.),* **246**, 75-79.

————. 1979. Re-appraisal of lithostratigraphy of Makapansgat Limeworks hominid site. *Nature (Lond.),* **279**, 484-488.

Peabody, F.E. 1954. Travertines and cave deposits of the Kaap Escarpment of South Africa, and the type locality of *Australopithecus africanus* Dart. *Bull. geol. Soc. Amer.,* **65**, 651-706.

Petter, F. 1964. Affinités du genre *Cricetomys*. Une nouvelle sous-famille de Ronguers (Cricetidae), les Cricetomyinae. *C. R. Acad. Sci. Paris,* **258**, 6516-6518.

————. 1966. Affinités des genres *Beamys*, *Saccostomus* et *Cricetomys*. (Ronguers, Cricetomyinae). *Ann. Mus r. Afr. cent., Tervuren, Ser. 8vo, Zool.* **144**, 13-25.

————. 1967. Particularités dentaires des Petromyscinae Roberts 1951. (Ronguers, Cricetidés). *Mammalia,* **3**, 217-224.

————. and Matthey, R. 1975. Genus *Mus*. Part 6.7 pp 1-4. *In:* Meester J. and Setzer, H.W. (eds.). *The Mammals of Africa: An Identification Manual.* Washington, DC: Smithsonian Institution Press.

Pocock, T.N. 1971. Pleistocene bird fossils from Kromdraai and Sterkfontein. *Proc. 3rd Pan-Afr. Ornithol. Congr. 1969. Ostrich Supp.* **8**, 1-6.

————. 1974. New mammal record for genus *Mus* for southern Africa. *S. Afr. J. Sci.,* **70** (10), 315.

————. 1976. Pliocene mammalian microfauna from Langebaanweg: a new fossil genus linking the Otomyinae with the Murinae. *S. Afr. J. Sci.,* **72**, 58-60.

————. 1985. Plio-Pleistocene mammalian microfauna in Southern Africa. *Ann. geol. Surv. S. Afr.,* **19**, 65-67.

Reig, O.A. 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). *J. Zool., Lond.,* **181**, 227-241.

Repenning, C.A. 1965. An extinct shrew from the early Pleistocene of South Africa. *J. Mamm.,* **46**, 189-196.

Roberts, A. 1929. New forms of African mammals. *Ann. Transv. Mus.,* **13**, 82-121.

————. 1951. *The Mammals of South Africa.* Cape Town: Central News Agency.

Thomas, O., and Schwann, H. 1906. The Rudd exploration of South Africa — V. List of mammals obtained by Mr. Grant in North East Transvaal. *Proc. zool. Soc. Lond.,* **1906**, 575-591.

Tobias, P.V. 1978. The South African australopithecines in time and hominid phylogeny with special reference to the dating and affinities of the Taung skull. *In:* Jolly, C. (ed.), *Early Hominids of Africa.* 45-84. London: Duckworth.

————. and Hughes, A.R. 1969. The new Witwatersrand University excavation at Sterkfontein. Progress report, some problems and first results. Proceedings of Conference "The Quaternary in S. Africa", University of Cape Town, 1969. *S. Afr. Archaeol. Bull.,* **24**, 158-169.

Turner, B.R. 1980. Sedimentological characteristics of the "Red Muds" at Makapansgat Limeworks. *Palaeontol. afr.,* **23**, 51-58.

Vrba, E.S. 1981. The Kromdraai australopithecine site revisited in 1980: recent investigations and results. *Ann. Transv. Mus.,* **33**, 17-60.

———— and Panagos, D.C. 1982. New perspectives on taphonomy, palaeoecology and chronology of the Kromdraai apeman. *Palaeocology of Africa,* **15**, 13.

White, T.D., Johanson, D.C. and Kimbel, W.H. 1981. *Australopithecus africanus*: its phyletic position reconsidered. *S. Afr. J. Sci.,* **77**, 445-470.