## by

# **D.M.** Avery

South African Museum, P.O. Box 61, Cape Town, 8000 South Africa.

#### ABSTRACT

The micromammalian fauna from Sterkfontein Members 4, 5E and 6 comprises 34 species. These include six insectivores, three bats, three elephant shrews and 22 rodents. Most of these taxa, or their equivalents, have been previously recorded. Four or five new additions were recovered from deposits probably belonging to Late Pleistocene Member 6, which have previously received little or no attention. Some previously recorded taxa were not found, but this was probably due to differences in identification rather than to the absence of these forms from the sample.

KEYWORDS: micromammals, Pleistocene, Sterkfontein, systematics

# INTRODUCTION

Sterkfontein (26°01'S; 27°44'E) is one of the best known South African palaeoanthropological sites, having produced a wealth of hominid remains ascribed to at least three genera (Clarke 1994). The site has been excavated and described almost continuously since the first hominid specimen was published by Broom (1939). Initially, Member 5 collections were treated as contemporary, but Clarke (1994) and Kuman (1994, 1996) have shown that Member 5E includes earlier deposits containing Oldowan artefacts underlying deposits with Early Acheulean material. Their detailed work has further revealed that solution of the breccia in Member 5E led to mixing of material in the upper parts, particularly above 15 ft (4.6 m) but to a lesser extent down to 22 ft (6.7 m) (Kuman 1996). The site continues to be excavated in imperial measurements because the grid system was laid out in feet. In the present report the original measurements are given with metric equivalents in brackets. Current age estimates are: 2.8 to 2.6 my for Member 4; 2.0 to 1.7 my for the Oldowan deposits; about 1.5 my for the Early Acheulean sample; and >0.10 my for Member 6 (Clarke 1994, Clarke & Tobias 1995, Kuman pers. comm.) (Table 1).

Previous micromammalian samples, belonging to A.R. Hughes's pre-1969 collections from the Sterkfontein Type Site (STS), Dumps 1 & 2, Dump 8 and STW/H2, have been described by Pocock (1969, 1987). These were all considered to have come from Member 5, which is the second youngest of six members identified by Partridge (1978). Other material from the Type Site, which was described by De Graaff (1960), may have come from Member 4 (Brain 1981). Denys (1990) listed taxa found in a sample from the Sterkfontein Extension Site (SE), which lies within Member 5 West. The material reported here was collected by R.J. Clarke and K. Kuman since 1991 in Member 5 and comes mainly from Member 5 East. There are small samples from the adjacent Member 4 and from the Middle Stone Age (MSA), which is designated Member 6 (Tobias *et al.* 1993) and is a later infill that divides Member 5 East from Member 5 West. A final, possibly contaminated, sample derives from Member 5 West in the area previously excavated by Robinson (1962).

There is generally little difference in the micromammals from Sterkfontein and Swartkrans even though the former includes material that is both older and younger than that from Swartkrans, which has been discussed recently (Avery 1998). This paper is therefore confined to providing information on species not present at Swartkrans, and other supplementary remarks where appropriate. A separate study of the environmental implications of the Sterkfontein micromammalian fauna is in progress (Avery in prep.).

#### **MATERIAL AND METHODS**

Basic excavation units were 3 ft (0.9 m) square and generally 1 ft (0.3 m) deep. In the following discussion the material has been lumped into seven larger groups of units. Table 1 provides a general description of the grouped units and details of the assignments of individual units are available on request. Species represented are given in Table 2, together with the units in which they occur. Mandibles and maxillae were employed for identifications and computation of minimum numbers of individuals. Length and breadth of the lower first molar in Steatomys were measured (Figure 1) and unpaired ttests were performed to determine whether more than one species was represented (Table 3). Percentage length of M, to M, in Sterkfontein Mus sp. was used as a basis for unpaired t-tests to compare the fossil material with modern M. minutoides and M. musculus (Table 4).

TAB	
Excavation units at Sterkfontein that	yielded micromammalian material

Member	Code*	Culture	Distribution*	Depth <sup>§</sup>	Comments	my B.P
6	M6	MSA	N59-60, Q58	18-28 ft (5.5-8.5 m)	Infill into M5	± 0.10
5	M5	ESA/MSA ?mixed	M63, N63-64,O64	12-16ft (3.7-4.9 m)	?decalcified deposit	
6/5	M6/5	ESA/MAS ?mixed	O59-61,O64/64, p59-61	13-13 ft (4.0-7.0 M)	possible mixing with M5	
5 East	M5E-A	Early Acheulean, ?mixed with MSA	O58, P53-54, P57-58, Q51-57, R50, R52-57, S52-57, T53-56	16-22 ft (4.9-6.7 m)	above 22 ft	± 1.5
5East	M5E-O	Oldowan	P53-54,P57-58, Q52-57, R52-57, S52-56, T55-56	22-34 ft (6.7-10.4 m)	Oldowan Infill below 22 ft	± 2.0-1.7
5East/4	M5E/4		Q49-52, R49, S51, T52-54	14-29 ft (4.3-8.8 m)	boundary between members	mai - 8 - 6 - 10 - 10 - 10
4	M4		N46/O45/P45L, Q48-50, R49-51, S50	13-30 ft (4.0-9.1 m)		± 2.8-2.6

Code: abbreviation used in other tables and figures

Distribution: horizontal distribution of samples

§ Depth: vertical distribution of samples

# SYSTEMATICS Insectivora

Chrysochloridae

Amblysomus Pomel, 1848 (golden mole)

For the present all smaller specimens are assigned to Amblysomus, as they were at Swartkrans (Avery 1998). It is possible that two taxa are represented but Bronner (1996) has demonstrated that there can be considerable intra-populational variation within Amblysomus. In the Sterkfontein material, all specimens show an alveolus for M, although not all alveoli are the same size. The number of teeth is variable in modern chrysochlorids (Ellerman et al. 1953, Bronner 1996). This could be part of an evolutionary trend or it could be due to the unusual sequence of tooth replacement, as suggested by Bronner (1996). There is also variation in the extent to which talonids occur in the fossil material. However, the situation is not as clear as it is at Swartkrans, where there is generally a talonid on  $P_4$  but not on  $M_1$  (Avery 1998). Of the four examples of  $P_4$ , one each from M5E-A and M5 have talonids while another from M5E-A and one from M6 do not. One M<sub>1</sub>, from M5E-A, has a slight talonid whereas the other, from M5E/M6, has none. It could be inferred that the earlier specimens represent a population in which this feature was in the process of disappearing and that by about



Length and breadth of Steatomys lower M1



120 000 years ago the process had been completed. Many more specimens will, of course, be required to determine the correctness of this proposition. It will also be necessary to compare the fossil specimens with Bronner's (1996) detailed database.

# Chlorotalpa sclateri (Broom, 1907) (Sclater's golden mole)

One mandible that may be referable to *Chlorotalpa* sclateri was recovered from M5E-O. The genus was listed by Pocock (1987) and the extinct form *C. spelea* was recorded by De Graaff (1960). The fossil and modern forms are separated solely on cranial proportions (Broom 1941) and there is no *a priori* reason to propose that the present mandible belongs to an extinct species. The absence of *Chlorotalpa* sclateri from later samples and from the area today indicates that this taxon has not inhabited the region for a considerable period.

#### Soricidae

Crocidura silacea Thomas, 1895 (lesser grey-brown musk shrew)

Broom (1948) mentioned the occurrence of *Crocidura* sp. at Sterkfontein but subsequent workers failed to confirm the presence of this genus. As a result

it has been accepted that Crocidura did not occur in the Sterkfontein Valley (Meester 1955; Pocock 1987; Avery 1998). It would appear, however, that the reason previous workers did not find it was that they were examining Early Pleistocene material. The present sample includes two mandibles from M6 and a palate from M6/M5, which suggests that it was a late arrival in the valley. The palate includes alveoli for only three teeth between I<sup>1</sup> and P<sup>4</sup>, thereby clearly identifying the specimen as Crocidura rather than either Myosorex or Suncus, and the left P4 belongs to Crocidura and not Myosorex. The body of a right mandible includes a P that lacks both the protostylid and the metaconid typical of Myosorex (Butler & Greenwood 1979). The buccal cingulum of the molars is anteriorly broad, and the M, has an entoconid, which is a feature of Crocidura silacea (Meester 1963). The mandible is comparable in size with the Myosorex material, which suggests that it belongs with C. silacea rather than the considerably smaller Suncus material. The posterior half of a left mandible exhibits various features indicative of Crocidura rather than Myosorex. These include the shape of the condyle, the location of the muscle attachment on the condyle, and M<sub>1</sub> with the posterolingual rib and buccal cingulum as in Crocidura.

#### TABLE 2

Species of micromammals represented in Sterkfontein samples with total minimum number of individuals. † indicates extinct species. Modern species listed according to Wilson & Reeder (1993). See Table 1 for details of excavation units.

Family	Species	Common Name	M6	M5	M6/ M5E	M5E -A	M5E -O	M5E /M4	M4
1.2.1.2.1.2.1.2.1						-	-		
Chrysochloridae	Amblysomus sp.	golden mole	х	х	х	х	х	х	
	Chlorotalpa cf. sclateri	Sclater's golden mole					х		
	Chrysospalax villosus	rough-haired golden mole			х	х		х	х
Soricidae	Crocidura cf. silacea	grey musk shrew	х		х				
	Myosorex tenuis	forest shrew	х		х	х	х	х	х
	Suncus varilla	lesser dwarf shrew	х		х	х	х	х	
Rhinolophidae	Rhinolophus cf. capensis	Cape horseshoe bat	х		х		ж		
	Rhinolophus cf. clivosus	Geoffroy's horseshoe bat	х	х	х	х	х		
Vespertilionidae	Myotis tricolor	Temminck's hairy bat	х		х	х	х		
Muridae	Saccostomus campestris	pouched mouse			х				
	Dendromus melanotis	grey climbing mouse	x	х	х	х	х	х	х
	Malacothrix typica	large-eared mouse	х	х	х		х		
	Steatomys parvus	tiny fat mouse	х	х					
	Steatomys pratensis	fat mouse	х	х	х	х	х		
	Tatera cf. leucogaster	bushveld rat	х	x	х	х	х		
	Acomys cf. spinosissimus	common spiny mouse					х		
	Aethomys chrysophilus	red veld rat	х	х	х		х		
	†?Dasymys sp.	swamp rat	х	х	х	х	х	х	х
	Mastomys natalensis s.1.	multimammate mouse	х		x	x	х		
	Mus sp.	pygmy mouse	х		x	x	x		
	Rhabdomys pumilio	striped mouse	х	х	x	x	x		x
	Thallomys cf. paedulcus	tree rat	x						
	Zelotomys cf. woosnami	Woosman's desert rat	x	х	х	х	х		
	Mystromys albicaudatus	white-tailed rat	x	х	х	x	х	х	х
	*Proodontomys cookei				х	x	x	x	x
	Otomys irroratus	vlei rat	x	х	х	х	х		
	Otomys saundersiae	Saunders's vlei rat	x	x	х	х	х	х	х
	Otomys sloggetti	Sloggett's rat		х	х	x	х		х
Mvoxidae	Graphiurus sp.	dormouse	х		х	х	х		
Bathvergidae	Cryptomys hottentotus	common molerat	x	x	x	x	х	x	х
	Georychus capensis	Cape molerat		x			x		
Macroscelididae	Elephantulus intufi	bushveld elephant-shrew	x	x	x	x	x	x	х
maeroseemanaae	Elephantulus fuscus	Peters's short-snouted				x		x	
		elephant-shrew							
	Macroscelides proboscideus	round-eared elephant	x						
		shrew							
a farm plants	Minimum number of individuals re	epresented	308	138	430	371	866	42	36

Myosorex tenuis Thomas and Schwann, 1905 (dark-footed forest shrew)

Most of the soricid material is referable to Myosorex and there is no reason to suggest that a different species is represented at Sterkfontein from that occurring at Swartkrans. Material has previously been assigned to the extinct M. robinsoni (De Graaff 1960), which was at one time said to be an ancestral form of M. varius (Brain 1981, based on an implied relationship in Meester [1958] but not an explicit relationship in the original diagnosis [Meester 1955]). Butler & Greenwood (1979), on the other hand, consider M. robinsoni to be a close relative of modern M. cafer tenuls, as understood by Heim de Balsac & Meester (1977) and Meester et al. (1986), or M. tenuis, as recognized by Hutterer (1993) and accepted here. The disposition of the anterior palatal foramina has been discussed previously (Avery 1998). It therefore needs only to be pointed out here that the pattern in the two Sterkfontein specimens (one each from M5E-A and M6) where it is visible is closer to M. varius than M. cafer, as shown by Meester (1958). It conforms, however, to the pattern in M. cafer tenuis shown by Butler & Greenwood (1979) so that it would appear that the Sterkfontein material should be assigned to M. tenuis sensu Hutterer (1993).

# **CHIROPTERA**

Rhinolophidae Rhinolophus Lacepede, 1799 (horseshoe bat)

Present evidence agrees with Pocock's (1987) findings that two species of *Rhinolophus* are represented and tends to support his assignment of the larger specimens to *R. clivosus*. This identification is based on the fact that, in the four specimens where it is preserved, the  $P_3$  alveolus is located outside the toothrow as it is in *R. clivosus*. It is not possible to determine whether the smaller specimens should be assigned to *R. darlingi*, as suggested by Pocock (1987), or to *R. capensis*, as proposed for Swartkrans (Avery 1998).

## RODENTIA

#### Muridae

# Saccostomus campestris Peters, 1846 (pouched mouse)

Saccostomus campestris, as presently understood (Musser & Carleton 1993), may well comprise more than one species in southern Africa (Gordon 1986; Gordon & Rautenbach 1980). However, until additional species are formally recognized and their morphological characteristics are established, it is necessary to refer material to S. campestris sensu lato, as was previously discussed for Gladysvale (Avery 1995). Four mandibles referable to S. campestris have been recovered from adjacent squares O59 and O60 at depths from 17 ft (5.2 m) to 19 ft (5.8 m). These constitute the first S. campestris specimens recorded from the Sterkfontein Valley australopithecine sites. It is significant that the deposits that yielded this material are Upper Pleistocene (K. Kuman, pers. comm.). Moreover, the apparent absence of *S. campestris* from earlier deposits supports Denys's (1990) hypothesis that the taxon migrated south some time after about 1.6 my.

Three lower first molars from Sterkfontein measure 2.2 x 1.3 mm, 2.1 x 1.3 mm and 2.1 x 1.4 mm. These measurements lie within the range of S. campestris as given by Denys (1990) whereas two molars from the Cave of Hearths fall within the size range of East African S. mearnsi (Denys 1990). What is more important, the Sterkfontein specimens should be referred to S. campestris rather than to S. mearnsi using the various features in M, listed by Denys (1988) to distinguish the two species. Only an indication of a link between the anterior two cusps (a-lab, a-ling) (cusp terminology after Musser 1981) and the central two cusps (pd, md) was found in the more worn specimen while no link existed in the less worn specimens. Conversely, in the two less worn individuals the cusps pd, md and hd, ed (the central and posterior rows respectively) are already joined, thereby indicating that the two pairs of cusps are not deeply separated.

Saccostomus campestris occurs in some units at Gladysvale (Avery 1995). It could be argued that its presence suggests that these units are younger than those that have not yielded the taxon. The presence of S. campestris with one possible Proodontomys cookei in the Pink Breccia appeared to nullify this hypothesis. However, re-examination of the specimens concerned (both right mandibles without cheek teeth) has led to the conclusion that they should be assigned to Mastomys sp. rather than S. campestris. Measurements of two S. campestris lower first molars (2.2 x 1.4 mm and 2.1 x 1.4 mm), from units S18.E6 and S19.E6, fall within the range of S. campestris, as given by Denys (1990). These specimens also accord with Denys's (1988) description of S. campestris rather than that of S. mearnsi.

## Steatomys parvus Rhoads, 1896 (tiny fat mouse)

Previously, only one species of *Steatomys* has been recorded from the Sterkfontein Valley (Pocock 1987, Denys 1990, Avery 1998). The present study revealed three mandibles (one from M6 and two from M5) that belong to a second, smaller species than the rest of the specimens. Length and breadth of M1 in these mandibles are lower than they are in all other samples (Figure 1). Unpaired *t*-tests of length and breadth of lower M1 show that there is a significant difference between the small individuals and both the earlier M5E-O material and, more significantly, the apparently contemporary sample from M6 (Table 3).

All three mandibles contain  $M_{1-2}$  but the teeth in one mandible are little worn while the others are in a more advanced state of wear. The unworn first molar of the small species has a maximum length of 1.7 mm whereas four specimens of the larger species from the same sample have an average length of 2.0 mm. The teeth in the Sterkfontein mandibles are more closely comparable with *S. krebsii* than with *S. pratensis*. The unworn first molar shows no trace of a cingular conule and is

Maximum Length			Maximum Breadth			
Samples	df	t	Samples	df	t	
M5E-O, M6	9	-3.65**	M5E-O, M6	9	-3.41**	
M5E-O, M6/5	20	-2.61*	M5E-O, M6/5	20	-3.05**	
M5E-O, Spar	5	2.46	M5E-O, Spar	5	4.79**	
M6, M6/5	23	-0.39***	M6, M6/5	23	-0.33	
			M6, Spar	8	4.49**	
M6/5, Spar	19	3.98***	M6/5, Spar	19	4.05***	

Results of unpaired t-tests to determine whether samples of *Steatomys* sp. belong to different species, based on maximum length and breadth of lower M1. Spar is modern *S. parvus. t*-values are significant at the at the 1% (\*\*) or 0.1% (\*\*\*) level.

relatively narrow, although this is difficult to quantify. Examples of modern *S. parvus* were not available for study. However, Thomas & Wroughton (1905) remark that the closest relative of *S. minutus* (now included in *S. parvus* [Musser & Carleton 1993]) appears to be *S. pentonyx* (now *S. krebsii* [Musser & Carleton 1993]). This view seems to be implicitly supported by Roberts (1931) in his descriptions of *S. chiversi* (now *S. krebsii* [Musser & Carleton 1993]) and *S. c. tongensis* (now *S. parvus* [Musser & Carleton 1993]). It seems probable therefore that the small Sterkfontein specimens should be referred to *S. parvus*.

Steatomys parvus does not currently occur closer than northern KwaZulu-Natal, which is some 500 km to the east of Sterkfontein. On geographical grounds it could therefore be considered more reasonable to assign the material to S. krebsii, which does occur in the region today. Moreover, in some areas (e.g. the Western Cape) some mandibles of S. krebsii are close in size to some of S. parvus. However, modern specimens from nearer Sterkfontein are larger and very similar in size to the nearest S. pratensis (Roberts 1951). Besides, Steatomys krebsii and S. pratensis are not found together in northeastern South Africa today (Rautenbach 1982) although they do occur together elsewhere (Skinner & Smithers 1990). On balance it seems most likely that the species represented is S. parvus but the matter requires further investigation.

## Dasymys Peters, 1875 (water rat)

The status of *Dasymys* has been discussed at some length elsewhere (Avery 1998) where it was concluded that two species are probably represented at Swartkrans. The sample from Sterkfontein is much smaller but supports the previous contention (Avery 1998) that this genus requires attention. At Swartkrans the two putative species are represented approximately equally. The two taxa were separated initially on the presence or absence of a crest between the anterolingual cusp and metaconid on the lower first molar. In the Sterkfontein sample there is a crest in 15 out of 16 specimens where the feature is visible; the exception may not show the feature because it belonged to a young individual. This age difference could, however, be significant because there is some evidence at Swartkrans that age, or degree of tooth wear, may have caused an artificial distinction between the two forms. If the difference is real, it is of interest that the young specimen was recovered from Member 4 whereas the other specimens came from later members, including M6. This would indicate that two putative species apparently co-existed for a considerable period. It would further suggest that modern Dasymys *incomtus* (represented by the species without the crest) was already present more than two million years ago whereas the second species, if it is extinct, became so within the last 120 000 years. Denys (1990) and Misonne (1969) both considered that the Pleistocene Dasymys (presumably the crested form) possessed some features that are more advanced than those found in D. incomtus and the Sterkfontein specimen may support their contention. Crawford-Cabral (1983) found D. incomtus and D. nudipes to be sympatric in one region of Angola, which provides a modern analogue for the co-occurrence of two species in the Sterkfontein Valley. However, the molars of D. nudipes are very similar to those of D. incomtus and do not exhibit the crest found in the fossil material (Crawford-Cabral & Pacheco 1989; pers. obs.).

TABLE4

Results of unpaired *t*-tests to determine whether samples of *Mus* spp. are separable based on percentage length of lower M1 to lower M2. *t*-values are significant at the 5% (\*) or 0.1% (\*\*\*) level.

Samples	df	t	
M. minutoides, M. musculus	28	5.45***	
M. minutoides, Mus sp.	18	4.01***	
M. musculus, Mus sp.	14	1.33*	

# TABLE 5 Micromammalian taxa recorded from Sterkfontein by various workers, with the units examined. † indicates extinct species. STS is the Type Site, STW the West Pit, and SE the Extension.

			This paper	Denys 1990	Pocc 1987	ock 1969	De Graaff 1961	1960
				SE	STS & STW	Dump 8*	?STS	STS**
Insectivora	Chrysochloridae	Amblysomus sp	x			1.00		
	omysoomoriaav	Chlorotalpa sclateri	x					
		†Chlorotalpa spelea						х
		Chlorotalpa sp.			х			
		Chrysospalax villosus	х					
		Chrysospalax sp.			х			
	Soricidae	Gen. nov.			х			
	Solicidae	t Myosorer rohinsoni	x					
		Myosorex tenuis	x					^
		Myosorex sp.			x	x		
		Suncus infinitesimus			cf.	х		
		Suncus varilla	х		cf	x		1000
<b>O</b> 11	D11 1 111	Suncus sp.						х
Chiroptera	Rhinolophidae	Rhinolophus capensis	ct.			c		
		Rhinolophus ciivosus Rhinolophus darlingi	C1.		CI.	CL		
	Vespertilionidae	Myotis tricolor	x		cf	CL		
	· · · · · · · · · · · · · · · · · · ·	Miniopterus schreibersi			cf.			111063
Rodentia	Muridae	Saccostomus campestris	x					
		Dendromus melanotis	x			cf		
		Dendromus mesomelas		1.1			х	c£
		Dendromus sp.		х	х			
		Malacothrix typica	x	-				
		Malacolnrix sp.		x	х	x		1000
		Steatomys parvus	x					0.00
		Steatomys sp.	~	x	x	x		the second
		Tatera brantsii		**	*	A	cf.	cf.
		Tatera leucogaster	cf.		cf.			100
		Tatera sp.		х		х		
		Acomys spinosissimus	c£.					
		Acomys sp.		x	x			
		Aethomys chrysophilus	х		х	cf	c	
		Aethomys namaquensis		v			CL.	ct.
		Arvicanthis sn		~			2	2
		Dasymys incomtus					x	cf.
		?†Dasymys sp.	x	x	x	х		
		Grammomys sp.		x				10 30
		Lemniscomys sp.		х				100.000
		Mastomys coucha					x	
		Mastomys natalensis	s.l.			c£		c£
		Masiomys sp. Mus minutoidas		x	X	х		-6
		Mus musculus				cf		CL.
		Mus sp.	x	x	x	CL.		
		Pelomys fallax					cf.	cf.?
		†Rhabdomys 'minor'				x		
		Rhabdomys pumilio	x				cf.	cf.
		Rhabdomys sp.		х	х			
		Inallomys paedulcus	cf.					
		Zelotomys woosnami Zelotomys co	CL					0.000
		Mustromus albicaudatus	Y	x	X			1.5
		† Mystromys hausleitneri	~	x	x	v	v	v
		†Proodontomys cookei	x	~	x	~	~	^
		<i>†Otomys gracilis</i>		x	x	cf	x	х
		Otomys irroratus	х				LaT-	200
		Otomys saundersiae	х					1000
	Manufid	Otomys sloggetti	х					
	Myoxidae	Graphiurus sp.	x		x	X		
	Datnyergidae	Cryptomys notientoius	х		X	CI.		
		Georychus capensis	¥		X		х	X
Macroscelidea	Macroscelididae	†Elephantulus antiquus	•		x			
		Elephantulus brachyrhynchus			cf.			
		Elephantulus fuscus	х					
		Elephantulus intufi	х					
		†Elephantulus langi (= broomi)			c			х
		Macroscelides proboscideus	x		ct			0
		Intylogale spiersi					Contraction in contract	2
		No. of taxa recognized	34	15+	30	19	11	17
		<u> </u>						17

\* M5 (Brain 1981)

\*\* probably M4 (Brain 1981)

+ Muridae only

#### Mus Linnaeus, 1758 (mouse)

There are seven mandibles referable to Mus from Sterkfontein, two each from M6, M5E/M6 and M5E-O, and one from M5E-A. All specimens possess the first molar while three also have the second molar. Neither of the M6 lower first molars has an anterocentral cusp, which is present in the others. All have a posterior cingulum but only two have posterolingual cusplets. This variation is similar to that found at Swartkrans and is not useful in determining the species involved. The amount of reduction in three preserved third-molar alveoli suggests M. minutoides but the percentage length of M, to that of M, indicates a significant difference from modern M. minutoides and M. triton (Figure 2). In this feature both the Sterkfontein and the Swartkrans material is closest to Mus musculus, which probably implies the presence of the same or closely allied species at both sites.



Figure 2. Mean, maximum and minimum percentage length of M to M<sub>2</sub> in modern *M.triton* (TMMtri) from the Transvaal Museum, and *M.minutoides* (ZM Mmin) and *M.musculus* (ZM Mmus) in the South African Museum compared with fossil *Mus.* sp. from Sterkfontein (SAFT) and Swartkrans (SKX1, 2 and 3). Sample size: TM Mtri - 9; ZM Mmin - 16; ZM Mmus - 10: SFT - 3; SKX1 - 16; SKX2 - 9; SKX3 - 2

#### **DISCUSSION**

The list of species from Sterkfontein appears to be long (Table 5) when the work of De Graaff (1960, 1961), Pocock (1969, 1987) and Denys (1990) is combined with the results of the present study. However, there are many cases of alternative specific identifications and the maximum number of taxa identified in one sample is 34. A further 11 were either not found or not accepted. Reasons for differences in specific identifications vary. In some instances one of two closely related modern

species may be represented. Examples are Rhinolophus capensis and R. darlingi, Dendromus melanotis and D. mesomelas, and Aethomys chrysophilus and A. namaquensis. There are also several possible chronospecies and it is perhaps a matter of opinion whether the extant form or a fossil antecedent is represented at Sterkfontein. These include Myosorex robinsoni- tenuis and Elephantulus broomi - intufi (see Corbet & Hanks 1978). Finally, genera such as Arvicanthis, Pelomys and Mylogale were at one time considered to be represented (De Graaff 1960) but have not been reported more recently. Conversely, genera such as Chrysospalax, Grammomys, Lemniscomys and Zelotomys were later added to the list (Pocock 1987, Denys 1990) and still other additions are proposed in this report. It is therefore clear that there is a critical need for a re-examination of all available material based on current taxonomy. Such a consistent examination should eliminate duplications and inaccuracies, and can be expected to reduce the list still further.

Some of the new additions listed in this report almost certainly result from the inclusion of Late Pleistocene samples for the first time rather than from differences of taxonomic opinion. This is suggested by the exclusive occurrence of four genera and one species in the later samples (Table 2), where only Macroscelides proboscideus was previously listed (Table 5). It will thus be important in future work to distinguish between samples of such different ages when compiling faunal lists. By providing intermediate examples, later material from Sterkfontein will also be important for evaluating the likelihood that species found in the Early Pleistocene levels are distinct from modern taxa. Early Pleistocene forms seem previously to have been considered extinct solely because of their age but there is no intrinsic reason why a species may not exist for two million years. It is also worth emphasizing that size alone is not a good criterion for distinguishing non-contemporary taxa. Thus, the two species of Steatomys in M6 can be distinguished on size because they are contemporary. Conversely, asynchronous samples cannot be separated on this basis even if they have a significantly different mean size (Table 3) because extraneous factors such as climate may influence size (Klein 1991).

The present samples confirm the richness of the Sterkfontein micromammalian fauna shown by Pocock (1987). At the same time, they highlight the amount of work that still needs to be done before the fauna is properly understood.

#### **ACKNOWLEDGEMENTS**

Dr K. Kuman of the University of the Witwatersrand made the material available for study and answered many questions about the stratigraphy of the site. This work comprises part of a larger project that is supported by the Foundation for Research and the South African Museum. An anonymous referee provided useful constructive criticism. AVERY, D.M. 1995. A preliminary assessment of the micromammalian remains from Gladysvale Cave, South Africa. Palaeontol. afr. 32, 1-10.

- AVERY, D.M. 1998. An assessment of the lower Pleistocene micromammalian fauna from Swartkrans Members 1-3, Gauteng, South Africa. *Geobios* **31**, 393-414.
- BRAIN, C.K. 1981. The hunters or the hunted? Chicago & London, University of Chicago Press.

BRONNER, G.N. 1996. Non-geographic variation in morphological characteristics of the Hottentot golden mole, *Amblysomus hottentotus* (Insectivora: Chrysochloridae). *Mammalia* **60**, 707-727.

BROOM, R. 1939. On the affinities of the South African Pleistocene anthropoids. S. Afr. J. Sci. 36, 408-411.

BROOM, R. 1941. On two Pleistocene golden moles. Ann. Transvaal Mus. 20, 215-216.

BROOM, R. 1948. Some South African Pliocene and Pleistocene mammals. Ann. Transvaal Mus. 21, 1-38.

BUTLER, P.M. & GREENWOOD, M. 1979. Soricidae (Mammalia) from the early Pleistocene of Olduvai Gorge, Tanzania. Zool. J. Linn. Soc. 67, 329-379.

CLARKE, R.J. 1994. On some new interpretations of Sterkfontein stratigraphy. S. Afr. J. Sci. 90, 211-214.

CLARKE, R.J. & TOBIAS, P.V. 1995. Sterkfontein Member 2 foot bones of the oldest South African hominid. Science 269, 521-524.

- CORBET, G.B. & HANKS, J. 1978. A revision of the elephant-shrews, family Macroscelididae. Bull. Brit. Mus. (Nat. Hist.) Zool. 16(2), 5-111.
- CRAWFORD-CABRAL, J. 1983. Patterns of allopatric speciation in some Angolan Muridae. In: Van der Straeten, E., Verheyen, W.N. & De Vree, F., Eds, Third International Colloquium on the ecology and taxonomy of African small mammals. Ann. Mus. R. Afr. Cent. Sci. zool. 237, 153-157.
- CRAWFORD-CABRAL, J. & PACHECO, A. 1989. A craniometrical study on some water rats of the genus *Dasymys* (Mammalia, Rodentia, Muridae). *Garcia de Orta Ser. Zool.* 15, 1-10.
- DE GRAAFF, G. 1960. A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal System. Palaeontol. afr. 7, 59-118.

DE GRAAFF, G. 1961. A short survey of investigations of fossil rodents in African deposits. S. Afr. J. Sci. 57, 191-196.

- DENYS, C. 1988. Apports de l'analyse morphologique à la determination des espèces actuelles et fossiles du genre Saccostomus (Cricetomyinae, Rodentia). Mammalia 52, 497-532.
- DENYS, C. 1990. Implications paléoécologiques et paléobiogéographiques de l'étude de rongeurs Plio-Pleistocene d'Afrique orientale et australe. Unpubl. thèse de Doctorat d'état, Université Pierre et Marie Curie (Paris 6), Paris.
- ELLERMAN, J.R., MORRISON-SCOTT, T.C.S. & HAYMAN, R.W. 1953. Southern African mammals 1975 to 1951. London, British Museum (Natural History).
- GORDON, D.H. & RAUTENBACH, I.L. 1980. Species complexes in medically important rodents: chromosome studies of Aethomys, Tatera and Saccostomus (Rodentia: Muridae, Cricetidae). S. Afr. J. Sci. 76, 559-561.
- GORDON, D.H. 1986. Extensive chromosomal variation in the pouched mouse *Saccostomus campestris* (Rodentia, Cricetidae) from southern Africa: a preliminary investigation of evolutionary status. In: Coetzee, C.G., Schlitter, D.A. & Rust, H., Eds, Fourth International Colloquium on the ecology and taxonomy of African small mammals. *Cimbebasia* Ser A 8, 37-47.
- HEIM DE BALZAC, H. & MEESTER, J. 1977. Part 1. Order Insectivora, main text. In: Meester J. & Setzer H.W., Eds, The mammals of Africa: an identification manual. Washington DC, Smithsonian Institution Press.
- HUTTERER, R. 1993. Family Chrysochloridae. In: Wilson, D.E. & Reeder, D.M., Eds. Mammal species of the world. 2nd Ed. Washington & London, Smithsonian Institution Press.
- KLEIN, R.G. 1991. Size variation in the Cape dune molerat (*Bathyergus suillus*) and Late Quaternary climatic change in the southwestern Cape Province, South Africa. *Quat. Res.* 36, 243-256.

KUMAN, K. 1994. The archaeology of Sterkfontein - past and present. J. Human Evol. 27, 471-495.

KUMAN, K. 1996. Recent findings on the archaeology of Sterkfontein. In: Magori, C.C., Saanane, C.B. & Schrenck, F., Eds, Four million years of hominid evolution in Africa: papers in honour of Dr Mary Douglas Leakey's outstanding contribution in palaeoanthropology. *Kaupia* 6, 31-36.

MEESTER, J. 1955. Fossil shrews of South Africa. Ann. Transvaal Mus. 22, 271-278.

MEESTER, J. 1958. Variation in the shrew genus Myosorex in southern Africa. J. Mammal. 39, 325-339.

MEESTER, J. 1963. A systematic revision of the shrew genus Crocidura in southern Africa. Transvaal Mus. Mem. 13, 1-127.

MEESTER, J., RAUTENBACH, I.L., DIPPENAAR, N.J. & BAKER, C.M. 1986. Classification of southern African mammals. *Transvaal Mus. Mem.* 5, 1-359.

MISONNE, X. 1969. African and Indo-Australian Muridae: evolutionary trends. Ann. Mus. R. Afr. cent. (In-8°) Sci. zool. 172, 1-219.

MUSSER, G.G. 1981. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. Bull. Amer. Mus. nat. Hist. 168(3), 229-334.

MUSSER, G.G. & CARLETON, M.D. 1993. Family Muridae Subfamily Dendromurinae. In: Wilson, D.E. & Reeder, D.M., Eds, Mammal species of the world. 2nd Ed., 541-546. Washington & London, Smithsonian Institution Press.

PARTRIDGE, T.C. 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. Nature 275, 282-287.

- POCOCK, T.N. 1969. Appendix I. Micro-fauna provisionally identified from sieved material recovered thus far from Dump 8 at Sterkfontein, 1967-1969. In: Tobias, P.V. & Hughes, A.R. The new Witwatersrand University excavation at Sterkfontein. S. Afr. archaeol. Bull. 24, 168-169.
- POCOCK T.N. 1987. Plio-Pleistocene mammalian microfauna in southern Africa a preliminary report including description of two new fossil muroid genera (Mammalia: Rodentia). Palaeontol. afr. 26, 69-91.

RAUTENBACH, I.L. 1982. The mammals of the Transvaal. Pretoria, Ecoplan.

ROBERTS, A. 1931. New forms of South African mammals. Ann. Transvaal Mus. 14, 221-236.

ROBERTS, A. 1951. The mammals of South Africa. Johannesburg, The Trustees of the Mammals of South Africa Book Fund.

ROBINSON, J.T. 1962. Australopithecines and artefacts at Sterkfontein. Part I. Sterkfontein stratigraphy and the significance of the Extension Site. S. Afr. archaeol. Bull. 17, 87-107.

SKINNER, J.H. & SMITHERS, R.H.N. 1990. The mammals of the Southern African Subregion. 2nd Ed. Pretoria, University of Pretoria. THOMAS, O. & WROUGHTON, R.C. 1905. On a second collection of mammals obtained by Dr W.J. Ansorge in Angola. Ann. Mag. nat. Hist. (7)16, 169-178.

TOBIAS, P.V., CLARKE, R.J. & WHITE, H. 1993. 27th Annual Report of the Palaeo-Anthropology Research Unit, pp. 18-19. Johannesburg, University of the Witwatersrand.

WILSON, D.E. & REEDER, D.M. 1993. Mammal species of the world. 2nd Ed. Washington & London, Smithsonian Institution Press.

90