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

BY

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ABSTRACT

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

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

I. INTRODUCTION

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

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

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

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

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

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

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

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

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

II. Material and Method

1. *Origin*

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

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

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

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

2. *Preparation*

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

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

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

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

3. *Method*

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

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

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

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

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

Table I

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

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

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

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

III. A Note on the Geology and Geography of the Deposits

1. *The geology of the deposits*

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

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

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

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

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

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

It therefore appears that:

(a) The occurrence of sands of Kalahari type in these cave deposits does not necessarily indicate absolute chronology.

(b) Chronology based on particular faunal associations should be accepted with some degree of reserve.

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

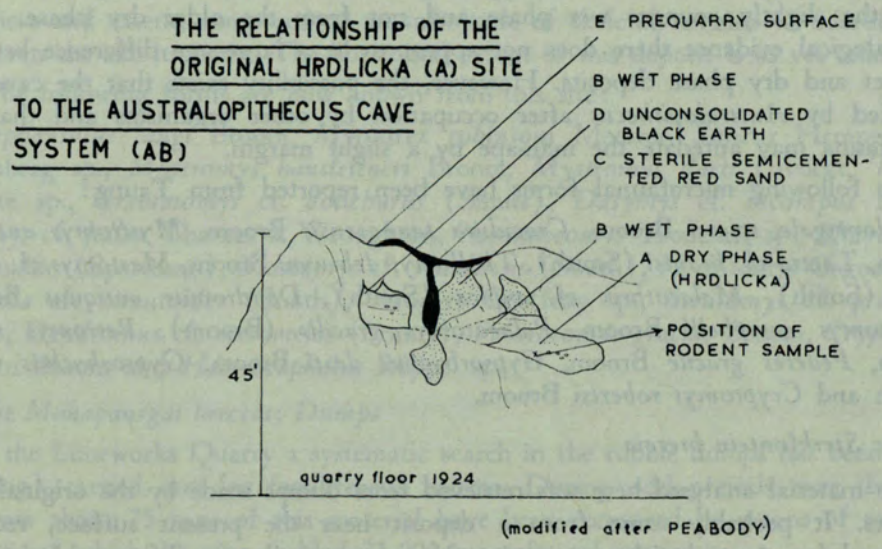

Figure 27

3. *The Taung breccia*

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

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

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

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

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

The following microfaunal forms have been reported from Taung:

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

4. *The Sterkfontein breccia*

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

The following microfaunal forms have been reported from Sterkfontein:

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

5. *The Makapansgat breccia: Rodent Cave*

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

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

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

(After Brain, 1958)

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

The following forms are now known from this site:

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

6. *The Makapansgat breccia: Dumps*

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

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

The dumps have now yielded the following forms:

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

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

7. *Makapansgat: Cave of Hearths*

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

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

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

The following microfaunal elements are now known from this site:

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

IV. Systematic Analysis

ORDER INSECTIVORA

Family Macroscelididae

Elephantulus langi (Broom) 1937
Elephantomys langi Broom 1937
Elephantulus langi Broom (1948)

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

Type site: Schurveberg, near Pretoria.

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

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

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

Sterkfontein

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

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

Rodent Cave

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

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

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

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

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

Limeworks Dumps

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

Remarks: The Pm_{2-4} in Mf.169 have been compared with *E. intufi* and with the description of *E. langi* by Broom. They agree very well with both. The sockets of the I_{1-3}, C, Pm_1 and M_{1-4} are present, but the posterior sockets of the M_2 have been damaged. The Pm_1 appears to have been a double rooted tooth. The dental series in the type has a length of 14.5 mm., compared with 14.7 mm. in the present specimen.

Cave of Hearths

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

Remarks: Specimen Mf.167 is well preserved and compares favourably with the type material. The anterior portion of the snout has been broken off at the level of the posterior root of the Pm^1. The Pm^2 is definitely molariform, with two outer cusps, the posterior one being the smaller. There is a third, still smaller cusp on

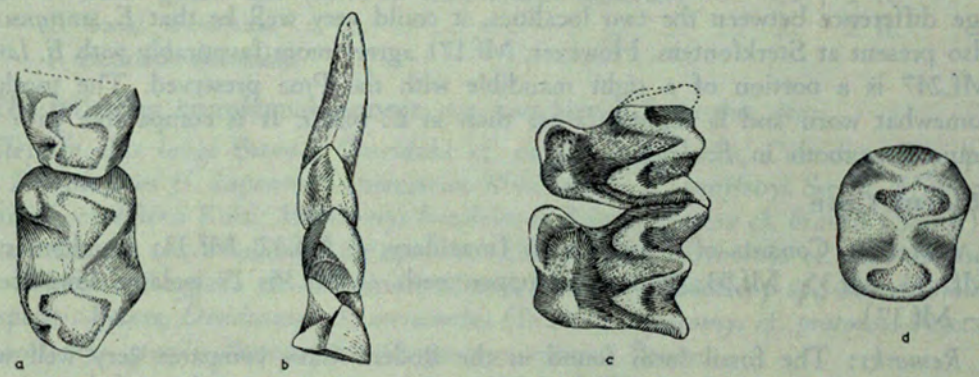

Fig. 28a — Mf.35. *Elephantulus langi*: occlusal view of PM_4 and damaged Pm_3. × 10.
b — Mf.37a. *Myosorex robinsoni*: occlusal view of anterior mandibular teeth. × 10.
c — Mf.61. *Rhinolophus* cf. *capensis*: occlusal view of M^{1-2}. × 10.
d — Mf.3. *Mystromys antiquus*: occlusal surface of M^2. × 10.

the outside, while on the inside there are two minute cusps close together. The Pm^3 has been damaged on its buccal side. The Pm^4 and M^1 agree closely with those in *E. intufi*.

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

M. spiersi Broom 1948.

M. spiersi Broom et al. (1946.)

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

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

Diagnosis: Mandible with three incisors, combined length about 3.5 mm.; canine not much larger than incisors; two small single rooted premolars; Pm_3 long anterior cusp with shorter posterior cusp; latter transverse, with a groove on the inside only; Pm_4 large, hypsodont, four inner and two outer enamel folds; M_1 slightly larger than M_2 and essentially similar to Pm_4, being only shorter and broader; three inner and two outer enamel ridges with a vertical groove on the anterior side; M_2 essentially the same, somewhat smaller.

Sterkfontein

Material: Only one specimen (Mf.216), a left isolated Pm_4 with roots broken away.

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

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

FAMILY SORICIDAE

Crocidura taungsensis Broom 1948

Crocidura taungsensis Meester (1955)

Type: Imperfect specimen, maxilla with the incisor, Pm^4 and M^{1-3} well preserved. Transvaal Museum, no number supplied.

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

Diagnosis: Very small form, upper dental series measuring about 7 mm.; anterior cusp on the Pm^4 small, the M^3 being relatively small.

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Taung

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

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

Cave of Hearths

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

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

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

Crocidura Wagler sp.

Cave of Hearths

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

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

Myosorex robinsoni Meester 1955

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

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

Type Site: Swartkrans, near Sterkfontein.

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

Sterkfontein

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

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

Rodent Cave

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

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

Specimen Mf.37a (figure 28B) shows a very small canine wedged between the I_2 and Pm_4. In general morphology it does not differ appreciably from the cotype. Specimen Mf.36 shows the alveoli of the I_2, C and Pm_4 clearly and indicates a very small root of the canine. The Pm_4 structure corresponds closely with the Swartkrans specimen.

Limeworks Dumps

Material: Consists of 5 specimens (Mf.219, Mf.220, Mf.221 are mandibular fragments; Mf.223 refers to two M_2 teeth).

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

Suncus Hemprich & Ehrenberg sp. — Meester 1955

Sterkfontein

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

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

Rodent Cave

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

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

Limeworks Dumps

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

Remarks: In Mf.217 all the teeth are missing, exposing the sockets of the left side, but only to the level of the Pm^4 on the right side. The premaxillary region and the posterior part of the skull have been broken away. The skull is not very large, although it is rather wide across the maxillae. Specimen Mf.218 has three beautifully-preserved teeth (Pm^4M^{1-2}) very similar to those of the modern *Suncus*.

ORDER CHIROPTERA

Suborder Microchiroptera

Family Rhinolophidae

Rhinolophus cf. *capensis* Lichtenstein

Rodent Cave

Material: Consists of 7 specimens (Mf.57—60, mandibular elements; Mf.61, maxillary fragment; Mf.62, left upper canine; Mf.63, isolated M_2).

Remarks: Very much like *Rhinolophus capensis,* though distinctly smaller. The Pm_4 in Mf.57 has a distinct cingulum but not as pronounced as in the modern form. In the former the height of the tooth above the cingulum is 1.7 mm., compared with 2.0 mm. in the latter. The height of the jaw immediately behind the Pm_4 is 1.5 mm. and 1.7 mm. respectively. In Mf.58 the Pm_4 has a slightly broader posterior cingulum ledge. The corresponding height of the lower jaw in this specimen is 1.8 mm. In general the teeth appear to be smaller than in the previous specimen, which is also the case in Mf.59. In the latter the curvature between the coronoid process and the mandibular condyle is flatter than in the modern form.

In Mf.61 (see figure 28c), one of the few cranial fragments of this bat recovered from the investigated material, the M^3 seems to have been smaller than in the modern form, judging from the size of the alveoli. The M^{1-2}, although they closely resemble those of the recent bat, are definitely smaller and not so broad. The isolated canine (Mf.62) is large and strong, gradually curved, and has the same dimensions as in modern specimens. The cingulum is well developed and the root is strong.

Rhinolophus cf. *geoffroyi* Smith

Cave of Hearths

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

Remarks: Specimen Mf.257 appears to be slightly larger than the modern species. The teeth, too, are more robust. Part of the jugal arch is present anteriorly. The specimen includes the posterior alveolus of the Pm^4 and those of the M^1. In Mf.259 the alveoli of both incisors are clear, while the symphysial region as a whole is in good condition. The alveoli of the Pm_2 and Pm_4 are vacant, but the three molars well preserved.

Compared with the modern bat, the fossil is slightly smaller. The jaw (Mf.259) is also more curved. Molar patterns are comparable, but the incisor is smaller and the mental foramen is situated more posteriorly, below the Pm_2.

Miniopterus cf. *schreibersii* Kuhl

Cave of Hearths

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

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

ascending ramus and angular process have been broken away, but the symphysial region is undamaged. The alveoli of the I_{1-2} and canine are present, the I_2 apparently having been smaller than the I_1, while the canine must have been a well developed tooth. The Pm_4 and M_{1-3} form a well-preserved tooth row. It appears as if more that two premolars were present in this individual. In Mf.262 the M_3 is also larger than in the modern form. It has a well-developed cingulum.

ORDER RODENTIA

Suborder: Myomorpha

Family Cricetidae

Subfamily Cricetinae

Mystromys antiquus Broom 1948

Mystromys antiquus Broom et al. (1946)

Mystromys antiquus Lavocat (1956)

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

Type site: Taung.

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

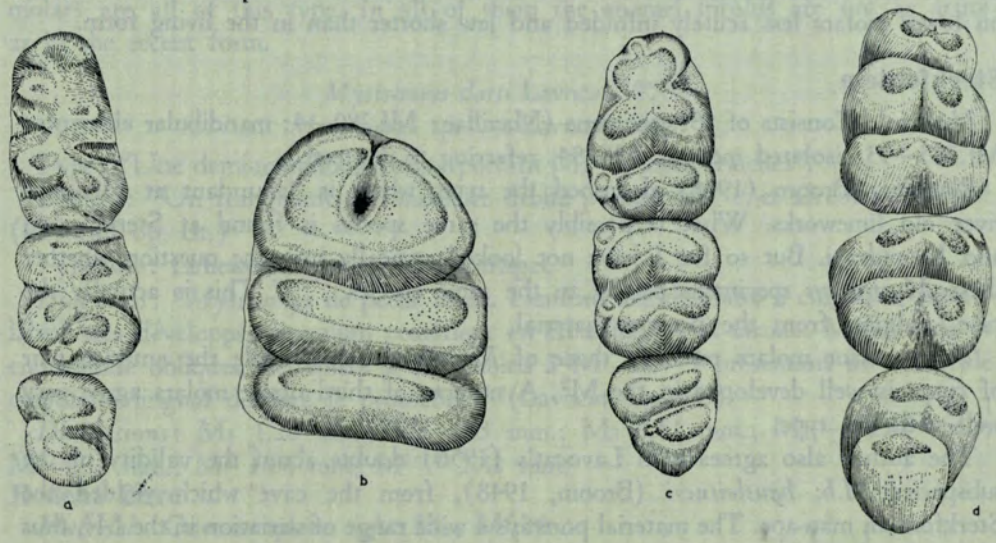

Fig. 29a — Mf.72. *Mystromys hausleitneri:* occlusal surface of M_{1-3}. × 10.
b — Mf.5. *Tatera* cf. *brantsi:* occlusal surface of M_1. × 10.
c — Mf.341. *Grammomys* cf. *dolichurus:* occlusal surface of M_{1-3}. × 10.
d — Mf.117. *Pelomys* cf. *fallax:* occlusal surface of M_{1-3}. × 10.

Taung

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

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

Mystromys hausleitneri (Broom) 1948.
Mystromys hauslichtneri Broom 1937
Mystromys hausleitneri Lavocat (1956)
Mystromys hausleitneri Lavocat (1957)

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

Type site: Probably Schurveberg, near Pretoria.

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

Sterkfontein

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

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

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

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

Rodent Cave

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

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

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

Limeworks Dumps

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

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

Cave of Hearths

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

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

Mystromys darti Lavocat 1956
Mystromys sp. — Lavocat (1957)

Type: "Une demi-mandibule droite portant $M_{1—3}$ assez fraiches".

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

Type site: Limeworks quarry, Makapansgat.

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

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

Rodent Cave

Material: One complete right M_1, Mf.74.

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

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

Subfamily Gerbillinae

Tatera cf. *brantsi* (Smith)
Tatera sp. — Lavocat (1957)

Taung

Material: Consists of 16 specimens (Mf.5, a mandibular ramus; Mf.6—7, two M_1 teeth; Mf.8a—c, three groups of 13 molars).

Remarks: The M_1 crown structure is typical, with three transversely elongated enamel sections surrounding dentine centres. It is the largest tooth in the series. The anterior oval section is almost square and its characteristic infold medially is very pronounced. The jaw itself (Mf.5) does not differ much from modern material. The ventral mandibular crest in the symphysial region is less pronounced in the fossil. The incisor root is exposed to the level of the M_3 and it exhibits the fine grooves, visible to the naked eye, which are characteristic of this species.

The M_1 (see fig. 29B) appears to be slightly more rounded and robust than in a modern specimen used for comparison; it is nearly as long, but the anterior oval section is not quite rounded.

The average value for the greatest occlusal length of the M_1 in 10 *Tatera* specimens was found to be 3.52 mm., the variation ranging between 3.1 and 3.8, with $\sigma = 0.23$. The value for the greatest tooth breadth was found to be 2.49 mm., the variation ranging between 2.2 and 2.8, with $\sigma = 0.18$. The values of the measurements obtained for the fossil specimens were compared with these figures and subjected to the t-test for significance. It was found that $t = 1$ with $N = N\text{-}1$, that is, 9. The value of t from Fischer's t-tables for small samples was 0.4 and 0.2, that is, between 20% and 40% for the greatest occlusal length and breadth respectively. Consequently the difference in value obtained for the fossil and recent material is not very significant. The fossils are, therefore, referred to the existing genus.

Sterkfontein

Material: Consists of 2 specimens (Mf.309, Mf.310, both left isolated M_1 teeth).

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

Cave of Hearths

Material: One specimen (Mf.313, a damaged mandible with damaged M_1 and complete M_2).

Remarks: The M_1 has been damaged anteriorly. There is a small connection lingually between the first and second transverse sections of the M_2. In spite of the damage and wear, it obviously resembles *T. brantsi*.

Tatera Lataste sp.

Rodent Cave

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

Remarks: The best example indicating the presence of this gerbil is the well preserved right M_1 (Mf.92). Compared with fresh material it has a somewhat smaller anterior lamina, presenting an enamel outline which is virtually heart-shaped. The inflection on the anterior lamina is in the middle of the tooth, unlike the more frequent condition where it is directed towards the buccal side. Apart from this difference the tooth agrees closely with modern specimens. The 11 isolated molars (Mf.93) do not exhibit any irregular features.

Family Muridae

Subfamily Murinae

Thallomys cf. *paedulcus* (Sundevall)

Cave of Hearths

Material: Consists of three specimens (Mf.336, maxillary fragment; Mf.370, mandibular fragment; Mf.371, isolated M_1).

Remarks: In Mf.366 the M^1 is five-rooted with its anterior section and T.1 not deflected back. There are eight cusps on this tooth. The teeth are moderately worn. The M^2 has an isolated anterior lingual cusp buccally (T.3) on the anterior edge. The M^3 is very much like the M^2 but on a much smaller scale. The tooth row is not very broad or robust. In Mf.370 the M_1 is worn, but on the prominent cingulum edge a small cusp adjacent to the buccal posterior cusp can be seen. The anterior and middle pairs of cusps form the characteristic murid pattern. The tooth is not large compared with modern material. In Mf.371 the M_1 has a prominent ridge on the buccal edge with a small cusp adjacent to the posterior buccal cusp.

Grammomys cf. *dolichurus* (Smuts)

Rodent Cave

Material: Consists of 5 specimens (Mf.105, Mf.111, Mf.113—5, all isolated M_1 teeth).

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

Lundholm (1955) has investigated the lower molars of a number of murid genera. *Thallomys* and *Grammomys* both have a tendency to develop external ridges on the molars, especially on the M_1 and M_2. *Grammomys* is a genus close to *Thallomys*, but the latter has two frontal cusps in the M_1, while the former has three. The specimens listed here would then all appear to be *Grammomys*. This genus has hitherto not been known as a fossil in Southern Africa.

Limeworks Dumps

Material: Consists of three specimens (Mf. 338, isolated M_1; Mf.341, mandible with incisor and M_{1-3}; Mf.342, isolated M_1).

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

Dasymys cf. *incomtus* (Sundevall)
Dasymys sp. — Lavocat (1957)

Sterkfontein

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

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

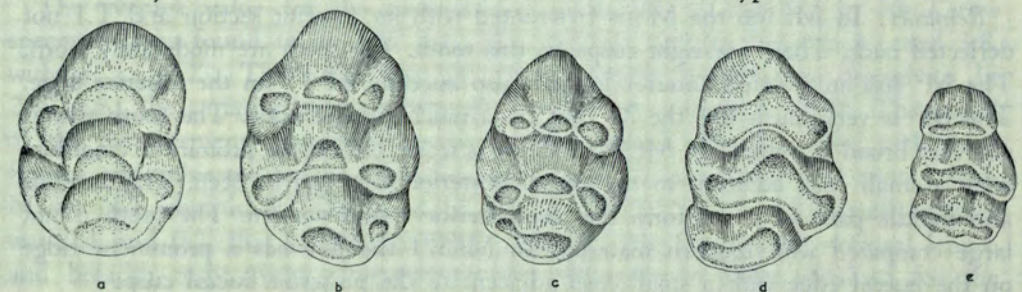

Fig. 30a. — Mf.320. *Dasymys* cf. *incomtus:* occlusal view of M^1. × 10.
b — Mf.335. *Rhabdomys* cf. *pumilio:* occlusal view of M_1. × 10.
c — Mf.336. *Aethomys* cf. *namaquensis*: occlusal view of M^1. × 10.
d — Mf.98. *Acomys* sp: occlusal view of M^1. × 10.
e — Mf.381. *Saccostomus campestris:* occlusal view of M^1. × 10.

Pelomys cf. *fallax* Thomas & Wroughton
?Pelomys sp. — Lavocat (1957)

Sterkfontein

Material: Mf.317, a damaged right lower jaw with M_{1-2}.

Remarks: The specimen is a well preserved jaw of a swamp rat. There is a good ungrooved incisor. The molars are as large as in the modern type, the M_{1-2} length being 4.8 mm. compared with 4.9 mm. in the fossil. Identification from this locality tentative.

Rodent Cave

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

Remarks: The molars in Mf.117 (see figure 29D) are in perfect condition and do not differ appreciably from those of the modern form. The M_{1-3} length is 6.3 mm., compared with 6.4 in a recent mandible.

Limeworks Dumps

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

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

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

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

Rhabdomys cf. *pumilio* (Sparrman)

Sterkfontein

Material: Mf.319, an M^1.

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

Rodent Cave

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

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

Limeworks dumps

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

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

Aethomys cf. *namaquensis* (Smith)

Sterkfontein

Material: Mf.321, an isolated left M_1.

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

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

Limeworks dumps

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

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

Aethomys cf. *chrysophilus* (de Winton)

Cave of Hearths

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

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

Mastomys cf. *natalensis* (Smith)

Taung

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

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

Sterkfontein

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

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

Rodent Cave

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

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

Limeworks dumps

Material: Mf.340, an isolated left M_1.

Remarks: Identification tentative.

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

Sterkfontein

Material: Mf.322, an isolated right M_1.

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

Rodent Cave

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

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

Limeworks dumps

Material: Mf.343, an M^1.

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

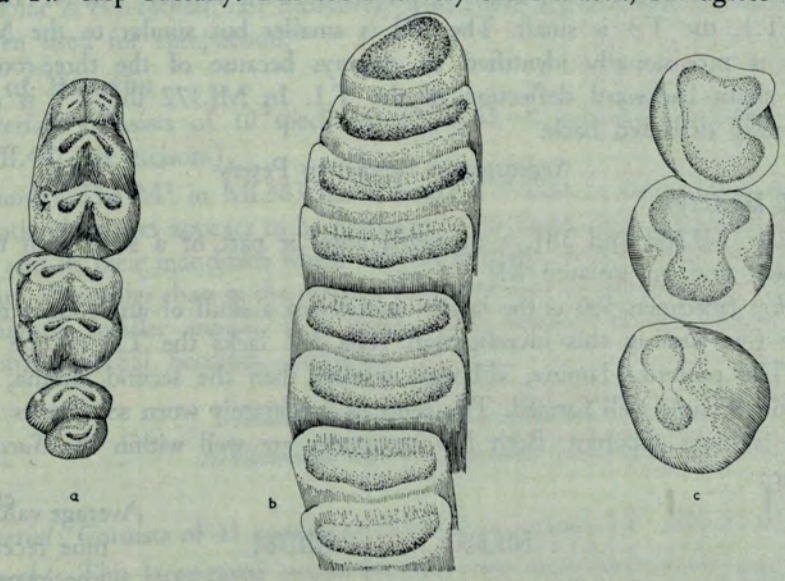

Fig. 31a — Mf.9. *Mastomys* cf. *natalensis:* occlusal view of M_{1-3}. × 10.
b — Mf.14. *Palaeotomys gracilis:* occlusal view of M_{1-3}. × 10.
c — Mf.423. *Cryptomys robertsi:* occlusal view of M_{1-3}. × 10.

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

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

Cave of Hearths

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

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

Acomys Geoffroy sp.

Rodent Cave

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

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

Cave of Hearths

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

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

Saccostomus campestris Peters

Cave of Hearths

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

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

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

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

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

Subfamily Dendromurinae

Dendromus cf. *mesomelas* (Brants)
Dendromus sp. — Lavocat (1957)

Sterkfontein

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

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

Rodent Cave

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

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

Limeworks dumps

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

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

Cave of Hearths

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

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

Malacothrix cf. *typica* (Smith)
Malacothrix sp. — Lavocat (1957)

Taung

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

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

?Malacothrix makapani sp. nov.

Limeworks dumps

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

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

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

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

Steatomys cf. *pratensis* Peters

Rodent Cave

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

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

Cave of Hearths

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

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

Subfamily Otomyinae

Palaeotomys gracilis Broom 1937

Palaeotomys gracilis — Lavocat (1957)

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

Type site: Probably Schurveberg, near Pretoria.

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

Taung

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

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

Sterkfontein

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

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

Rodent Cave

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

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

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Limeworks dumps

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

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

Cave of Hearths

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

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

Suborder Hystricomorpha

Family Bathyergidae *inc. sedis.*

Cryptomys robertsi Broom 1937

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

Type site: Probably Schurveberg, near Pretoria.

Diagnosis: Moderately large species with one mandible measuring "from the front of the incisor to the back part of the angular portion of the jaw 40 mm." The shape of the back part of the jaw is different from any species Broom was able to compare it with and a distinct ridge passes forward on the outer side of the jaw from the condyle, not entirely attributable to the roots of the lower incisors. The teeth are relatively small; crown low "and each tooth has the enamel of the upper half folded in on both the outer and inner sides" (Broom, op. cit.). In one specimen the fourth Pm, M_1 and M_2 together measure 5.2 mm.

Taung

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

Remarks: Specimen Mf.17 is very similar to the M_1 described by Broom (1937). It is about the same size but the enamel folds on the occlusal surface are not as deep. Due to damage, Mf.18 is tentatively identified. This form has not previously been recorded from Taung.

Sterkfontein

Material: Consists of five specimens (Mf.423, jaw with Pm_4, M_{1-2}; Mf.424, four isolated molars).

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

Rodent Cave

Material: Consists of 7 specimens (Mf.164, a right mandibular fragment with Pm_4; Mf.165, six isolated teeth).

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

Limeworks dumps

Material: Mf.364, a palate with left and right alveoli; Mf.365, damaged jaw with M_1.

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

Cave of Hearths

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

Remarks: The two M^3 specimens are very similar. They are the first upper teeth of this animal found in fossil form and while the accompanying mandible is toothless, the present material is not strictly comparable with that from the other sites. It compares favourably with the modern *Cryptomys,* but its specific identification must be regarded as tentative.

Unidentifiable cranial remains

Taung

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

Sterkfontein

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

Rodent Cave

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

Limeworks dumps

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

Cave of Hearths

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

Post-cranial remains

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

Table II

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

Non-microfaunal elements

Taung

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

Sterkfontein

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

Limeworks dumps

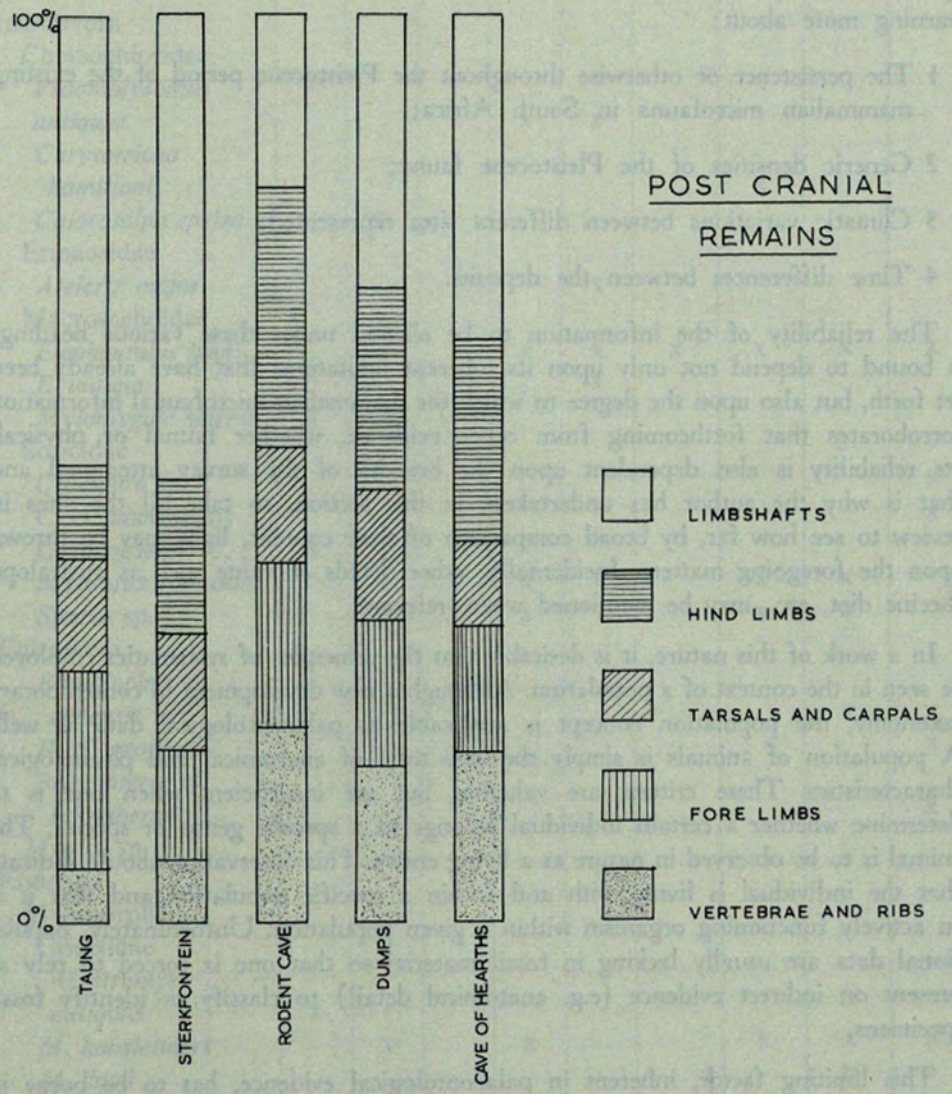
The microfaunal breccia from this locality is highly contaminated with the remains of "foreign" animals. These include: An assortment of lacertilian cranial and post-cranial elements (Mf.302, Mf.247); ten bird skeletal elements (Mf.275); an isolated primate Pm^1 (Mf.303); nineteen cranial and fifteen post-cranial Lagomorph elements (Mf.304, Mf.278); one cranial and eleven post-cranial bovid specimens (Mf.306, Mf.276); six felid specimens (Mf.307, Mf.279); eight hyracoid elements (Mf.277); 471 bone fragments (Mf.270, Mf.271); 300 similar fragments, but possibly of avian origin (Mf.273).

Rodent Cave

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

Cave of Hearths

The non-microfaunal contamination at this site is also quite low. The specimens recovered include: A lagomorph molar root (Mf.300); ten bird elements (Mf.299, Mf.311); 38 small fragments of bone (Mf.298).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TAUNG
STERKFONTEIN
RODENT CAVE
DUMPS
CAVE OF HEARTHS
POST CRANIAL REMAINS
LIMBSHAFTS
HIND LIMBS
TARSALS AND CARPALS
FORE LIMBS
VERTEBRAE AND RIBS

Figure 32

V. Discussion

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

1 The persistence or otherwise throughout the Pleistocene period of the existing mammalian microfauna in South Africa;

2 Generic densities of the Pleistocene fauna;

3 Climatic variations between different sites represented;

4 Time differences between the deposits.

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

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

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

Table III

The Fossil Microfauna in South Africa subsequent to this Survey

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

	Ta	St	Sw	Kr	BF	Sch	MpD	MpR	MpC
T. cf. *paedulcus*									
Grammomys cf. *dolichurus*							x	x	x
Dasymys bolti					x				
D. cf. *incomtus*		x						x	
? Arvicanthis sp.		x							
Pelomys cf. *fallax*		?x					x	x	
?Lemniscomys sp.								x	
Rhabdomys cf. *pumilo*		x					x	x	
Aethomys cf. *namaquensis*		x					x		
A. cf. *chrysophilus*									x
Mastomys natalensis	x	x					x	x	
?Zelotomys sp.								x	
Leggada minutoides		x					x	x	x
L. major					x				
Acomys sp.								x	x
Saccostomus campestris									x
Dendromurinae									
Dendromus antiquus	x								
D. cf. *mesomelas*		x					x	x	x
Malacothrix typica	x								
?Malacothrix makapani							x		
Steatomys cf. *pratensis*								x	x
Otomyinae									
Palaeotomys gracilis	x	x		x			x	x	x
Prototomys campbelli	x								
Hystricomorpha									
Hystric cf. *africae-australis*							x		
H. major							x		
H. cristata		x							
Xenohystrix crassidens							x		

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

* Locality abbreviations:

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

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

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

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

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

A. *INSECTIVORA*

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

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

ii. The Erinaceidae with *Atelerix major* Broom (1937) as the fossil hedgehog has hitherto only been found at Bolt's Farm and only one individual is known. It has not been encountered in the other deposits analysed here. This is not surprising as this animal does not constitute part of the usual diet of owls.

iii. The Macroscelididae or elephant shrews have been shown to occur at all the sites investigated, in addition to the Bolt's Farm and Schurveberg localities where they were first identified; but this fossil, *Elephantulus langi* Broom, has not been recorded from Taung. This little animal may of course be recovered from the latter locality during some future analysis. Nevertheless, we know now that it has existed over a very considerable span of time, for the Sterkfontein and Makapansgat localities go back to the early Pleistocene while the more recent Stone Age Cave of Hearths breccias from which it comes are dated by the Earlier Fauresmith Culture. In other words, this long-lived form has apparently ceased to exist within the last ±50,000 years.

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

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

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

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

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

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

The genera *Myosorex* (*robinsoni* Meester) and *Suncus* Hemprich and Ehrenberg (sp.) have been found at Sterkfontein and at the Rodent Cave and Dumps at Makapansgat. The *Suncus* material seems to be too close to the recent material to erect a new species rank on such slight differences. This has already been commented upon by Meester (1955). The validity of the species *Myosorex robinsoni* may be seriously questioned, especially in Mf.37 from the Sterkfontein breccia. In this specimen, a small cusplet supposed to be absent in the fossil material is definitely present on the posterior aspect of the I_2. However, a more extensive investigation is required before this species is finally sunk. The matter should be reviewed on a statistical basis.

B. *CHIROPTERA*

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

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

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

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

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

C. *RODENTIA*

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

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

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

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

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

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

(b) The Gerbillinae were encountered in the majority of the localities. On the whole, the gerbils, based on the structure of the M_1, seem to be on the same evolutionary level as the recent material. The fossil teeth lie within the recent size range and the M_1 is very much like the modern material. The genus *Tatera* has been reported from all the localities except the Limeworks Dumps. The Taung material is very similar to the recent morphology. The genus is furthermore archaic but persistent. The Sterkfontein specimens are not more than subspecifically distinct (if at all) from the recent *Tatera brantsi*. In the gerbil material from the Rodent Cave there is a queer M_1 with a virtually heartshaped anterior lamina. This specimen is kept apart provisionally until further gerbil comparative material becomes available from this locality. This feature has not been found in recent comparative material.

(c) The Murinae, like the Gerbillinae, had already attained the same evolutionary level as the recent comparative material. The inherent difficulty of separating the various genera (not to mention species) on isolated skeletal fragments has aptly been summarized by Lavocat (1957). "Hormis trois portions de crânes de *Palaeotomys* et une de *Mystromys*, ces formes ne sont représentées que par des mandibules ou des dents isolées, ce qui explique que l'indication de certains genres soit accompagnée de points d'interrogation. En effet, on sait que en général les dentures mandibulaires sont peu caractéristiques. D'autre part, en ce qui concerne les Murinés seuls, ceux-ci sont représentés actuellement dans les régions interessées par des genres vivants, comprenant 37 espèces divisées en multiples sous espèces; à quoi il faut adjoindre les autres formes pouvant exister dans des territoires voisins. Or, on sait que les caractères des dents sont extrêmement peu étudiés par les zoologistes; il est donc impossible de trouver dans la Bibliographie des descriptions vraiment précises, encore moins des figurations des diverses formes actuelles . . . Si ces caractères sont généralement très typiques avec des dentures complètes, il faut reconnaitre qu'il

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

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

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

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

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

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

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

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

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

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

The genus *Aethomys* recorded from Sterkfontein, the Dumps and the Cave of Hearths is also somewhat problematical. Lundholm's (op. cit.) reasons for separating the genera *Thallomys* and *Grammomys* have been mentioned above. He also points out that the genus *Grammomys* can hardly be distinguished from *A. namaquensis* on the structure of the M_1. The identifications of these specimens is thus tentative.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

2. *Specific densities of the Pleistocene microfauna*

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

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

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

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

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

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

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

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

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

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

Table IV

Species density in Percentage per Locality

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

[k] Locality abbreviations as per table III.

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

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

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

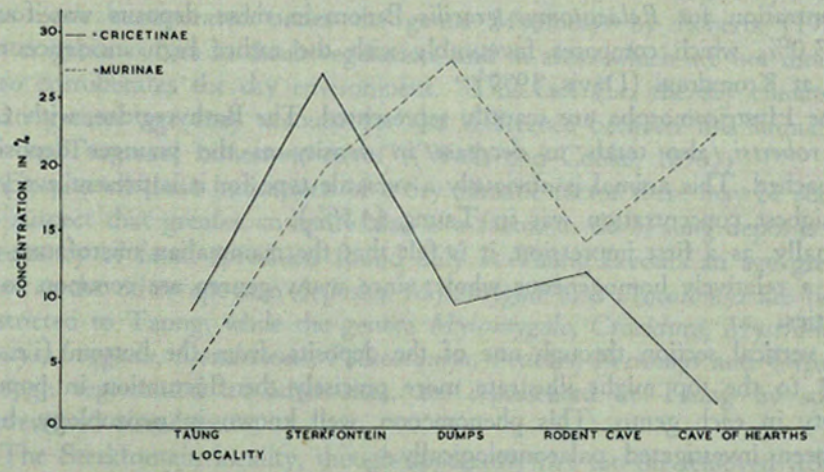
Graph I shows the relative frequencies (in percentages) of this cricetine form and the murids found in the deposits. It has been found that the Cricetinae are dominant at Taung (9.0%) and at Sterkfontein (26.7%) and this subscribes what Davis (op. cit.) has concluded at Kromdraai. However, there is a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

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

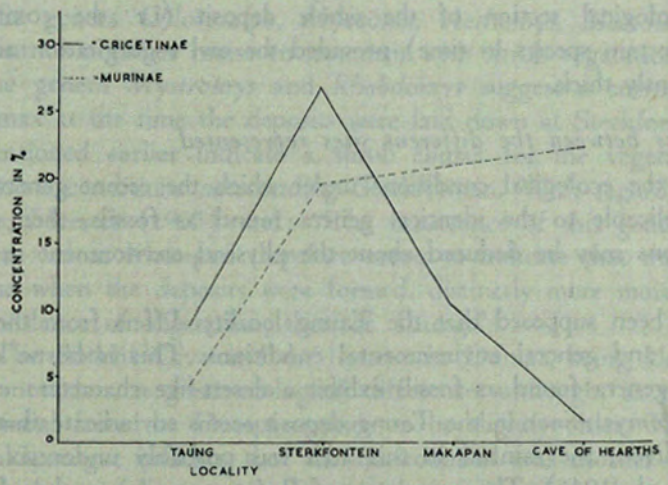
The Gerbillinae also reveal a gradual decrease in numbers like the white-tailed rats, mentioned above.

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

GRAPH I



GRAPH II



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

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

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

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

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

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

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

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

3. *Climatic variations between the different sites represented*

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

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

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

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

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

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

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

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

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

4. *Time differences between the deposits*

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

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

Table V

Extant and Extinct Genera and Species in the Deposits

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

* For locality abbreviations see Table III.

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

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

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

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

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

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

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

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

Table VI

Genera Common to the Different Localities

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

* Locality abbreviations as per Table III.

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

Table VII

Species Common to the Different Localities

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

* Locality abbreviations as per Table III.

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

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

Summary

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

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

(iii) There is evidence of an ecological non-equivalence between Sterkfontein and the Makapansgat localities.

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

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