A SYSTEMATIC REVISION OF THE BATHYERGIDAE (RODENTIA) OF SOUTHERN AFRICA

by

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Submitted in partial fulfillment of the
requirements for the degree of

DOCTOR OF SCIENCE

in the

FACULTY OF SCIENCE,
Pretoria University,
PRETORIA.

November 1964

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CHAPTER 1

INTRODUCTION

During the past decade it has become clear that taxonomic research on the mammals of Southern Africa has become a necessity. Our knowledge pertaining to many orders and families is often haphazard and scattered and this has led to a virtually chaotic taxonomic position for many groups. It is unlikely that new animals will be discovered in this area and therefore the time may be ripe for revision and synthesis of the information of the fauna hitherto gained.

As far as past research is concerned, the attention has largely been directed to the larger mammalian species which occur in Southern Africa while the smaller mammals were neglected to a certain extent. However, there has been a revival of interest in the smaller mammals during the past 15 to 20 years and the possibility of interesting, rewarding and important research has become evident. A good example of this approach is afforded by the vast amount of work done by the Medical Ecology Unit of the South African Institute for Medical Research in Johannesburg, in order to determine the rodents which act as vectors in the distribution and transmission of plague. At the same time valuable taxonomic information is gained. On a more theoretical basis, the revision done by Meester (1963) on the Southern African forms of <u>Crocidura</u> (shrews), stands out as a prime example of the new research attitude towards the smaller mammals. Similar types of revision will eventually lead to a

workable/...

workable, practical taxonomy, a necessity which is still lacking for Southern African mammals up to date. It may furthermore be noted that taxonomic revisions can not be undertaken for all mammalian groups as yet, due to the absence of available study material, lack of relevant information and other similar gaps in our knowledge.

Apart from attempts to consolidate the taxonomy and matters relating thereto, the concept of the ecosystem should be stressed. This useful concept has been neglected in the past, but it is of prime importance in order to understand the intricate mechanism and balance of nature. To date, very little is known about the role played by the smaller mammals in the ecosystem and therefore all facets of information are vitally important for a better understanding of the interrelationships between soil, plants and animals.

This dearth in our knowledge, particularly as far as the rodents are concerned, is probably due to the fact that the taxonomy of this interesting mammalian order is still in a fluid state. In addition, information concerning aspects of ecology, ethology and paleontology is meagre. Absence of this kind of data is especially noticeable in the case of fossorial rodents such as the bathyergids or mole-rats.

The mole-rats (Order Rodentia, family Bathyergidae) are typically Ethiopian animals. Due to their fossorial way of life certain specializations have been developed which are also found in other unrelated fossorial rodent families including the Spalacidae and Geomyidae. These animals all show suppressed development of the eyes, immensely enlarged incisors and/or claws adapted for digging (Ellerman, 1940, 3). As far as the bathyergids are concerned, it is stated that they have relatively unknown affinities and it appears that they have become fossorial secondarily which has led to a special set of adaptive features.

Beddard (1902, 480) lists a number of features which characterize the several genera contained within the Bathyergidae and which may briefly be paraphrased as follows: eyes small; pinnae of ears reduced to a fringe of skin surrounding external auditory meatus; legs and tail short; a tendency for reduction in the hair-covering of the body which reaches its culmination in the nearly naked sand-puppy _Heterocephalus_, presently occurring only in Somaliland and Kenya; all the genera are fossorial (i.e. _Bathyergus_, _Heliophobius_, _Heterocephalus_, _Georychus_ and _Cryptomys_); and incisors standing out in front of the closed lips.

Sclater (1901) lists a number of bathyergids occurring in Southern Africa and this was followed in 1939 by Allen in his wellknown checklist for African mammals. Roberts (1951) in his already classical work, 'The Mammals of South Africa' described the various genera, species and subspecies which he thought occurred in Southern Africa, while this was followed by yet another revision of Southern African mammals by Ellerman, Morrison-Scott and Hayman in 1953. All these works attempted to summarize and interpret the then existing knowledge of Southern African mole-rats, more or less from a taxonomic point of view. This has led to a diversity of interpretations, especially as far as the validity and status of the different species and subspecies are concerned.

In the course of this work, special reference will be made to Roberts (1951) and Ellerman et.al. (1953). In the latter, many clearly different forms of bathyergids are lumped together while the former has possibly oversplit the bathyergid species and subspecies to too great an extent. In the present work an attempt is made to find evidence which may merge the two widely diverging interpretations as far as the specific and subspecific taxa of the bathyergids are concerned.

The aim of this work is therefore a revision of the taxonomy of the mole-rats which occur to the south of the Cunene river on the western part of the African continent and the Sambezi river on the eastern half. However desirable, a Pan-African revision of the Bathyergidae is not possible at present and would take a considerable time to complete. Consequently, the extra-limital genera (i.e. north of the Cunene and Sambezi rivers) Heterocephalus (Fornaria) and Heliophobius (Myoscalops) are not considered in this work and the attention is focussed on the three Southern African genera viz. Bathyergus, Georychus and Cryptomys.

For the purposes of the present work, these three genera and their respective species are subjected mainly to a morphological and statistical comparison. It is evident that this approach will contribute a greater amount of evidence than comparing the animals either ecologically or ethologically. Very little is known about the latter aspect although Eloff (1951, 1952, 1958) has investigated behavioural aspects con-

cerning/...

cerning Bathyergus and Cryptomys (mainly under laboratory conditions). Furthermore, very little is known about the embryology, cytogenetics and physiology of the mole-rats. However, any relevant information concerning the ecology, ethology, embryology and physiology has been incorporated in the present work. It is doubtful, however, whether aspects of embryology and physiology could contribute substantially to unravelling problems concerning specific or subspecific status.

The main body of enquiry of this revision will be directed at the specific and subspecific levels of bathyergid taxonomy. The subspecies concept has been severely critisized recently, while being upheld by other authorities and for an excellent review of the diverging interpretations, the reader is referred to Meester (1963). According to Meester, some workers (e.g. Davis, 1949) confine their attention in taxonomic work to the species as the smallest taxon while Ellerman et.al. (1953) is openly sceptical about the validity of the trinonem. Wilson and Brown (1953), Gosline (1954) and Burt (1954) propose doing away with the subspecies concept entirely or"... at least not giving it formal nomenclatural recognition" (Meester, 1963, 3). On the other hand, Mayr (1954) and Smith and White (1956), while being aware of the shortcomings of this category have produced arguments for its retention. Edwards (1954) and Pimentel (1959) have attempted to standardize the subspecies concept by using statistical inferences, retaining it for geographically isolated populations showing a specified degree of difference (84% joint non-overlap)(Meester, 1963, 3).

The objective reality of this category as a biological unit is proposed by Edwards (1954) and Pimentel (1959) who attempt to solve this problem by referring only those populations to it, which are morphologically divergent and geographically isolated. However, as Meester quite rightly points out: "... from the museum taxonomist's point of view, the biological reality of the subspecies seems to be a secondary consideration. It seems more practical to regard it, with Mayr (1954, 87), as 'a purely subjective category,... a strictly utilitarian classificatory device for the pigeonholing of population samples'. This does not imply that the subspecies can have no objective reality, merely that it need not express any one particular reality". (Meester, 1963, 3).

Still paraphrasing Meester, it is evident that such an interpretation of the subspecies concept allows this concept to be a flexible unit, provided that it is clearly recognisable. This advantage should be used with discretion, otherwise the conventional species is divided into numerous ill-defined and ".... often unrecognisable units". To my mind, this has often been done in the past (e.g. Roberts, 1951) as far as the Southern African mole-rats are concerned, and the subspecies concept lost whatever taxonomic usefulness it may have had.

MATERIAL

The taxonomic revision which forms the greater portion of this work has been done on the genera and species listed below.

Genus Bathyergus: Bathyergus suillus suillus, B.s. intermedius, B.janetta janetta, B.j.inselbergensis/...

B.j.inselbergensis and *B.j.plowesi*.

Genus *Georychus*: *Georychus capensis capensis*, *G.c.canescens* and *G.c.yatesi*.

Genus *Cryptomys*: *Cryptomys hottentotus hottentotus*, *C.h.cradockensis*, *C.h.bigalkei*, *C.h.transvaalensis*, *C.vandami*, *C.caecutiens*, *C.damarensis*, *C.ovamboensis*, *C.holosericeus holosericeus*, *C.h.orangiae*, *C.h.vetensis*, *C.h.valschensis*, *C.h.vryburgensis*, *C.bocagei*, *C.nimrodi*, *C.darlingi*, *C.beirae*, *C.zimbitiensis*, *C.natalensis natalensis*, *C.n.langi*, *C.n.aberrans*, *C.n.junodi*, *C.n.streeteri*, *C.n.jamesoni*, *C.n.arenarius*, *C.n.mahali*, *C.anomalus*, *C.montanus*, *C.komatiensis komatiensis*, *C.k.stellatus*, *C.k.melanoticus*, *C.k.zuluensis*, *C.rufulus* and *C.jorisseni*.

The following museums and institutions have contributed to the completion of this investigation by loaning specimens or by permitting me to examine their collections. The capital letters preceding the names listed below indicate abbreviations used throughout this work for the various collections:

TM Transvaal Museum, Pretoria.
ME Medical Ecology Centre, Johannesburg.
KP Kruger Park Museum, Skukuza.
NM Natal Museum, Pietermaritzburg.
KM Kaffrarian Museum, King William's Town.
AM Albany Museum, Grahamstown.
PE Port Elizabeth Museum and Oceanarium.
DM Durban Museum.

SA South African Museum, Cape Town.
RM National Museum, Bulawayo.
MM McGregor Memorial Museum, Kimberley.
EM East London Museum.

This revision of Southern African bathergids is based on the examination of 1,423 skins and 1,338 skulls allocated as follows:

	Skins	Skulls
Bathyergus suillus	163	157
B. janetta	130	125
Georychus capensis	115	102
Cryptomys hottentotus	411	374
C. damarensis	38	36
C. holosericeus	80	77
C. darlingi	66	58
C. nimrodi	–	–
C. bocagei	9	8
C. beirae	5	5
C. natalensis	336	327
C. komatiensis	70	69

The following type specimens, housed in the Transvaal Museum were studied:

Bathyergus suillus intermedius Roberts 1926, TM. 2171, ♂, collected 1/10/1917, Klaver, Cape Province.
Bathyergus janetta plowesi Roberts 1946, TM. 9795, ♀, collected 12/6/1942, Oranjemund, South West Africa.
Georychus capensis yatesi Roberts 1913, TM. 1243, ♂, collected 26/10/1912, Belfast, Transvaal.
Cryptomys transvaalensis Roberts 1924, TM. 2463, ♀, collected 19/12/1919, border of bushveld, Zoutpan road, Transvaal.

Cryptomys/...

Cryptomys vandami Roberts, 1917, TM. 1487, ♂, collected 12/1/1915, Griffin mine, Leydsdorp district, Transvaal.

Cryptomys cradockensis Roberts 1924, TM. 2389, ♀, collected 5/10/1918, Cradock, Cape Province.

Cryptomys ovamboensis Roberts 1946, TM. 8229, ♂, collected 2/6/1937, Ondongwa, South West Africa.

Cryptomys bigalkei Roberts 1924, TM. 2806, ♀, collected 14/7/1921, Glen, Orange Free State (and co-type, TM. 2949, ♂, collected 16/9/1921, Glen, Orange Free State).

Cryptomys natalensis Roberts 1913, TM. 1245, ♀, collected 10/12/1912, Wakkerstroom, Transvaal.

Cryptomys jamesoni (Roberts). 1913, TM. 581, ♀, collected 4/6/1907, Houghton, Johannesburg, Transvaal.

Cryptomys anomalus (Roberts) 1913, TM. 1252, ♀, collected 23/2/1913, Skinner's Court Valley, Pretoria, Transvaal.

Cryptomys arenarius (Roberts) 1913, TM. 1265, ♀, collected 3/3/1913, Rietondale (East), Pretoria, Transvaal.

Cryptomys mahali (Roberts) 1913, TM. 1272, ♀, collected 9/5/1913, Rosslyn, Pretoria, Transvaal.

Cryptomys langi Roberts 1929, TM. 4928, ♂, collected 6/1927, Karkloof, Natal.

Cryptomys aberrans (Roberts) 1913, TM. 587, ♂, collected 10/10/1911, Port St. Johns district, Cape Province.

Cryptomys vetensis Roberts 1926, TM. 3512, ♀, collected 18/7/1922, Taaiboschspruit, Vet River, Orange Free State.

Cryptomys orangiae Roberts 1926, TM. 2810, ♀, collected 4/8/1921, Glen, Orange Free State.

Cryptomys/...

Cryptomys holosericeus valschensis Roberts 1946, TM. 2518, ♂, collected 18/6/1920, Bothaville, Orange Free State.

Cryptomys zimbitiensis Roberts 1946, TM. 559, sex unknown, collected 31/1/1908, Zimbiti, Mocambique.

Cryptomys pretoriae (Roberts) 1913, TM. 1244, ♂, collected 19/1/1913, Skinner's Court Valley, Pretoria, Transvaal.

Cryptomys natalensis pallidus Roberts 1917, TM. 2044, sex unknown, collected 12/7/1916, Nwanetzi river, Transvaal.

Cryptomys montanus Roberts 1926, TM. 2838, ♀, collected 17/11/1921, Groenkloof, Pretoria, Transvaal (and co-type TM. 2837a, ♂, collected 16/11/1921, Groenkloof, Pretoria, Transvaal).

Cryptomys palki (Roberts) 1917, TM. 2085, ♂, collected 24/3/1917, Venterskroon, Transvaal.

Cryptomys junodi Roberts 1926, TM. 4175, ♂, collected 20/8/1924, Masiyeni, Mocambique.

Cryptomys komatiensis (Roberts) 1917, TM. 1765, ♀, collected 9/9/1915, Arnhemburg, Carolina, Transvaal.

Cryptomys rufulus (Roberts) 1917, TM. 606, ♀, collected 26/9/1907, Tzaneen Estate, Transvaal.

Cryptomys stellatus (Roberts) 1917, TM. 1950, ♂, collected 22/6/1915, Inkomati river, Transvaal.

Cryptomys melanoticus Roberts 1926, TM. 2123, ♀, collected 7/7/1917, Balloon Farm, Makoetsi river, Transvaal.

Cryptomys natalensis streeteri Roberts 1946, TM. 4334, ♀, collected 20/8/1924, Hektorspruit, Transvaal.

Cryptomys komatiensis zuluensis Roberts 1926, TM. 5002, ♀, collected 10/11/1927, St. Lucia Bay, Natal.

Live/...

Live specimens of *Bathyergus suillus* (2 individuals) and *Cryptomys natalensis* (10) were observed in the laboratory for varying lengths of time.

METHOD

The following abbreviations are used for measurements and statistical terms:

H.B.	Head and body length
T.	Tail length
H.F.	Hind-foot length
C.B.	Condylo-basal length
B.C.	Braincase width
I.W.	Interorbital width
Z.W.	Zygomatic width
M.W.	Muzzle width
U.T.R.	Length of upper tooth row
L.J.	Length of lower jaw
L.T.R.	Length of lower tooth row
M.	Arithmetic mean of sample
N.	Number of observations
S.D.	Standard deviation
C.V.	Coëfficient of variation
$S.E._m$	Standard error of the mean
C.D.	Coëfficient of difference
% J.N.O.	Percentage joint non-overlap
t	A value distributed in a definite way, used to estimate probabilities in comparisons of several parameters estimated from small samples
P.	Probability that a difference can be ascribed to chance.

The nature of this investigation necessitated a statistical approach in order to unravel the

various/...

various problems which presented themselves, especially on the subspecific level. The different statistical approaches and procedures described by Simpson and Roe (1939), Mayr, Linsley and Usinger (1953) and Cazier and Bacon (1949) were consulted and largely followed. Whenever skulls were available, the following eight measurements were taken on each skull (provided that the relevant portions of the skulls were undamaged): condylo-basal length, width across the brain-case at the level of the squamosal constriction, interorbital width, zygomatic width, muzzle width, length of upper tooth row, length of lower jaw and length of lower tooth row. Definitions of the various lengths and breadths are given below. Comparisons with figures and values obtained by other workers have been avoided as far as possible. In some cases t-values were calculated in order to test statistically the differences between populations.

The following information, as available from the specimen tags was recorded: sex, locality, head-body length, tail length and hind-foot length. This implies that the various 'field measurements' have not been remeasured on the specimens available for study. Study skins tend to stretch to a certain extent when prepared and different preparators have different methods in preparing specimens so that the final result is hardly ever an exact copy of the original dimensions of the animal. Study skins are therefore often larger than the values obtained for the original field measurements. These figures are thus accepted for the purposes of this work at their face value. Furthermore, it is well known that

different/...

different people who measure these animals when they are collected, use different techniques and approaches. This leads to an additional possible source of error, and consequently these figures and values derived from museum labels are to be accepted with a certain degree of reservation.

Definitions of the standard measurements, taken where possible on all the specimens studied, are as follows:

Field measurements:

Head and body length - From the anterior tip of the nose to the base of the tail, taken by bending the tail up at right angles to the body.

Tail length - From the base of the tail - found as above - to the tip of the caudal vertebra, excluding the hair.

Hind-foot length - From the most proximal point of the heel to the tip of the longest toe, excluding the claw (s.u.).

Skull measurements:

Condylo-basal length - From the anterior portion of the premaxillaries (gnathion) in front of the upper incisors to the most caudad portion of the left condyle (condylion).

Braincase width - The width across the braincase where the squamosal makes a definite medially directed constriction, i.e. just anterior to the external auditory meatus.

Interorbital width - The narrowest point across the frontals, nearly on the suture between the frontals and squamosals.

Zygomatic width - The greatest width across the two zygomatic arches on the level of the jugal bones.

Muzzle width - The width across the muzzle on the suture between the premaxillaries and the maxillary portions of the zygomatic arches.

Upper/...

Upper toothrow length - The distance from the occlusal level of the third premolar (anterior edge) to the posterior edge of the occlusal surface of the last molar.

Lower jaw length - The distance between the edge of the alveolar rim of the lower incisor (where the outer edge of the lower incisor enters the alveolus) to the dorsal surface of the condyle articulating with the glenoid fossa of the skull.

Lower toothrow length - The distance between the most anterior point of the occlusal surface of the anterior molar to the most posterior rim of the occlusal surface of the hindmost molar.

Except where otherwise stated, all measurements used in this work are in the metric system. Millimeters are used exclusively in the systematic descriptions.

All the skull measurements were taken with the same sliding vernier calipers, reading to 0.1 mm. Field measurements were taken with a steel rule.

Statistical analyses have been made wherever available samples were of sufficient size to permit evaluation. In the tables, the measurements for males, females and unsexed animals are listed separately, for certain measurements show significant sexual dimorphism. When less than five animals from any of these categories were available from one locality, all the available individual measurements are listed. However, when five or more than five specimens were available, the mean, observed range, standard deviation and number of observations are listed instead.

The illustrations which are incorporated in this work are all accompanied by their appropriate comments. Graphs showing variation in condylo-basal length are included for the majority of species.

The age of each specimen was determined according to the following scheme: 'adult' with complete permanent dentition, all teeth showing some degree of wear; 'young adult' with complete permanent dentition, but of recent acquisition; 'juvenile' (immature) with permanent dentition incomplete. These categories are arbitrary since no individuals of exactly known age were available for study.

Whenever mention has been made of vegetation and veld types, the classification followed is that by Acocks (1947). For information concerning vegetation and related matters of Mocambique, Southern Rhodesia and South West Africa, Keay (1959) has been consulted. The rainfall data has been obtained from the 'Normal Annual Rainfall' map of South Africa, printed by the Government Printer and issued in 1957.

In the distribution maps, use has been made of the locus mapping system as used by Davis (1949) and others. The distribution patterns thus obtained do not necessarily indicate the absolute limits and ranges of the species, for in many cases, the distributional data is scanty.

Virtually all the localities in Southern Africa where examples of bathyergids have been collected or recorded are listed in a gazetteer at the end of this work together with their map coordinates and loci. Since the bathyergids are a wide-ranging and abundant family, persons working with Southern African collections may save much time by

referring/...

referring to the gazetteer of the localities recorded on museum labels.

ACKNOWLEDGEMENTS

During the course of this study I have received helpful and friendly assistance from many persons. First and foremost I am particularly indebted to Prof. F.C. Eloff, Head of the Department of Zoology, University of Pretoria, under whose direction this revision was done. Throughout the course of my studies, Prof. Eloff's enthusiasm and sound critisism was a constant source of encouragement and inspiration. Furthermore, I would like to thank him for the cordial and pleasant atmosphere in his department, facilitating the completion of this work.

To Dr. J.A.J. Meester, Director of the Kaffrarian Museum, King William's Town, my sincere thanks are due for his constructive criticism during the initial stages of this work. I am especially grateful to him for his suggestion of this problem and his invaluable advice and assistance in working out a plan of attack upon it.

To the directors and custodians of the various museums and institutions who generously loaned specimens to me or permitted me to examine the collections of mole-rats under their care, I extend my heartiest thanks. I am indebted to the Transvaal Museum, Pretoria; Natal Museum, Pietermaritzburg; Kaffrarian Museum, King William's Town; Albany Museum, Grahamstown; Port Elizabeth Museum and Oceanarium; Durban Museum; South African Museum, Cape Town; National Museum of Southern Rhodesia, Bulawayo; McGregor Memorial Museum, Kimberley and the

East London Museum. This appreciation is also due to Dr. D.H.S. Davis, Government Ecologist of the Medical Ecology Unit in Johannesburg and Mr. R. Knobel, Director of the National Parks Board. A special word of thanks is extended to the latter organization, especially to Mr. R.J. Labuschagne, assistant-director, and the chief wardens of the Kruger National Park (Mr. A. Brynard) and Kalahari Gemsbok National Park (Mr. J. le Riche) at Skukuza and Twee Rivieren respectively. Many fruitful discussions pertaining to the bathyergids were held with Dr. U. de V. Pienaar, chief biologist of the Kruger National Park. These gentlemen did everything in their power to facilitate various aspects of field work undertaken concerning the bathyergids occurring in areas allocated to their care.

Members of the staff of the Transvaal Museum deserve a special word of thanks: Mr. O.P.M. Prozesky, ornithologist, collected bathyergid specimens for me during his various field trips; Mr. C. Coetzee, mammalogist, always willingly allowed access to the specimens under his care; and finally, Mrs. T. Campbell, chief librarian, (assisted by Mrs. M. Thomas) always offered their services in finding the required literature.

Appreciation is also expressed to the Council for Scientific and Industrial Research for financial support during two years of this research.

Many others have contributed suggestions and critisisms for which I am grateful. I wish to ack-acknowledge my indebtness to my colleague, Mr. J.A.J. Nel for his assistance in all matters pertaining to the termination of this research. I would like to

thank/...

thank Prof. B.I. Balinsky, Head of the Department of Zoology, University of the Witwatersrand most sincerely for placing at my disposal the magnificant darkroom facilities, required for the preparation of the illustrations of this work. A special word of thanks is due to my father-in-law, Mr. M.J. de Kock, who helped me in innumerable ways (especially as far as the preparation of the illustrations are concerned) to the completion of this work. His effort is sincerely appreciated. Mrs. T.M. Zimmermann did more than her fair share in proof-reading the manuscript and her help is recorded with sincere thanks.

It is a pleasure to compliment Mrs. M.Petzer on the efficient way she typed the final copy of this work and her unfailing willingness to meet and solve emergent problems associated with preparatory phases of this work at all hours of the day. Miss H. Pisart, who prepared a number of illustrations for this work, is also thanked most heartily.

Finally, a special note of praise must go to my wife, deserving more than the usual acknowledgement. During the preparation of this work, she was a constant source of encouragement and her able assistance with the manuscript and illustrations is greatly appreciated.

CHAPTER 2

THE ORIGIN OF THE BATHYERGIDAE AND THE PALEONTOLOGICAL RECORD

The origin of the Bathyergidae, and problems relating thereto, is shrouded in a mist of many uncertainties. To a large extent this is due to the absence of sufficient paleontological data. A number of fossil forms (to be discussed briefly below) are known from Asian deposits (especially in Mongolia) and from various African localities, but it has to be emphasized that the possible bathyergid nature of the Mongolian finds is still open to debate. Consequently, phylogenetic relationships are still largely unknown both from an overall phylogenetic point of view and as far as the interrelationships of the different genera are concerned.

Simpson (1945, 213) correctly maintains that any decisive indications of their ancestry ".... are overlain and obscured by specializations for a highly specific and peculiar mode of life, and a definitive arrangement cannot be expected until less specialized ancestral forms are found. Supposed ancient allies, like Tsaganomys (now believed to be sciuromorph), have been claimed, but it now seems improbable that any are true bathyergoids." Simpson accordingly treats the Mongolian forms Tsaganomys and Cyclomylus as sciuromorphs in his well known classification of mammals. (See below).

It is probable that the bathyergids have a pronounced affinity with the hystricomorphs (see below), but a number of other authorities do not accept the mole-rats as hystricomorphs. Schaub (1953, 399) finds that the bathyergids are so highly specialized that closer affinities are entirely unknown. Romer (1958, 501) regards them as an early specialized offshoot of primitive sciuromorph stock, not closely related to any other group. Wood (1955, 185) states that the best guess is perhaps that these animals separated from the Paramyidae (i.e. Sciuromorpha) in the early or middle Eocene. On the other hand, one has the opinion of Burke (1936, 137, 138) who concluded that the Mongolian _Tsaganomys_ was related to _Ardynomys_, an early Oligocene semi-fossorial cylindrodontid (i.e. sciuromorph). This interpretation was also accepted by Wilson (1949, 93), who called them specialized cylindrodontines.

Tullberg (1899) was the first to place the bathyergids with the hystricomorphs (Landry, 1957, 66), concluding that these forms must have split off at the very base of the hystricomorph line and hence deserved equal rank with the three classical suborders (see below). Landry also accepts the late Oligocene Mongolian forms (_Tsaganomys_ and _Cyclomylus_) to be true bathyergids. Furthermore, he maintains that these Mongolian specimens were as highly specialized as the living forms, and that consequently the family must have split off from the hystricomorph-types during the early part of the Tertiary. This conclusion fits in with the fact (as mentioned by Tullberg) that in the bathyergids the scaphoid (radiale) and lunar bones of the wrist are unfused, a primitive rodent characteristic.

Furthermore, Landry (p. 74) states that a decision as to which of the living Old World hystricomorphs are related to the bathyergids is not easy, for the former are all highly specialized. The hystrids as such are far too specialized although some are known as fossils from the late Miocene. The hystricids are really the adaptive antithesis of bathyergids in that the trend among hystricids is toward larger and larger nasal cavities, well illustrated in extreme forms such as *Hystrix africae-australis* and *Hystrix cristata*, where the nasal cavity is as large as the brain case. However, the most primitive porcupine, *Trichys*, does not show this nasal expansion, and it is possible that such an unspecialized hystricid could have given rise to the bathyergids. However, there is no evidence at all that it did so.

Landry (1957, 74) also discussed certain points of similarities between the cane rat *Thryonomys* and *Bathyergus*. Both forms possess grooved upper incisors, recurved lower incisors and a short diastema in the lower tooth row. He then continues to give reasons for believing that the rostrum of *Bathyergus* is not primitive among the bathyergids and this reduces the similarities to the presence of grooved incisors - which in itself is hardly impressive evidence for classifying the bathyergids with the Thryonomyidae. The grooved incisors may have developed by means of

evolutionary/...

evolutionary parallelism.

An interesting line of thought as to the possible origin of the bathyergids is given by Landry, when he discusses a very generalized Old World hystricomorph, Petromys. This form is known as the African rock "rat". Landry (p. 74) states that it is to such a form as this that we would expect a primitive hystricomorph to be related. Paraphrasing Landry rather lengthily, his line of thought runs more or less as follows: Among the Old World hystricomorphs the otic region of Petromys resembles that of the bathyergids rather closely. In these forms, as in many other rodents, the mastoid part of the bulla bulges backward between the lateral process of the supra-occipital and the paroccipital processes of the exoccipitals so that there is a wide expanse of mastoid surface at a deeper level than at the occipital fingers which surround it. In Thryonomys and the hystricids the paroccipital process is much closer to the lateral process of the supra-occipital so that only a little of the mastoid shows between the processes. This seating of the mastoid in a notch of occipital bone is apparently a primitive rodent character for it is found in many rodents. A long lateral process of the supra-occipital is not limited to the hystricomorphs, nor is it even found most frequently among them. The specialization of the otic region (i.e. the paroccipital process being closer to the lateral process) in all other Old World hystricomorphs besides Petromys leaves it the closest relative of the bathyergids by default.

Landry (p. 75) furthermore postulates

then/...

then that some primitive rat-like hystricomorph, more or less similar in general appearance to the living Petromys gave rise to the Bathyergidae. Such a form however, was still more primitive than Petromys in that the scaphoid and lunar elements were not fused and that it certainly possessed less specialized cheekteeth.

Although Burke (1936, 137, 138) has concluded that the Mongolian fossils are cylindrodontid in nature, (i.e. sciuromorph) Landry (1957, 73) can not accept the possibility that the highly specialized hystricognath jaw could possibly be derived from the jaw of cylindrodonts. Yet one does find a typical hystricomorphine jaw structure in the bathyergids. Landry maintains that in fossorial rodents which have come from sciurognath stock (e.g. Spalax occurring in the Mediterranean region, Ellobius which is found in Eastern Europe and Asia and Rhizomys, another Asiatic form) and whose crania have become modified as that of Tsaganomys for fossorial life, the typical sciurognath lower jaw is retained. According to him, an exaggerated hystricognath jaw is, therefore, not part of the adaptation to a fossorial mode of life.

As has been indicated above, the meagre paleontological data available concerning the bathyergids come from Asian and African deposits. The Asian finds are much older geologically speaking and will be discussed briefly below.

Matthews and Granger (1923) described Tsaganomys altaicus and Cyclomylus lohensis as bathyergids from Hsanda Gol (Late Oligocene) in Mongolia/...

Mongolia. According to Landry (1957, 72) the greater part of a skull and jaws are figured, but from these drawings it cannot be ascertained whether the jaws were hystricognath. On the other hand, Teilhard de Chardin (1926) also described *T.altaicus* from Upper Oligocene deposits in western Kansu (Mongolia) and figures an almost complete lower jaw, which in ventral view is decidedly hystricognath (Landry, p. 72), with the angular portion curving up at the posterior end exactly as in the bathyergids. From these illustrations it is clear that the infraorbital foramen is small while the roots of the upper incisors apparently do not reach back beyond the first premolar. Landry (p. 72) states however, that it can not be ascertained from Teilhard de Chardin's figures whether the pterygoid fossae are broken through to the orbits, a point which would be crucial in deciding its hystricomorph or bathyergid character.

In 1937, Bohlin also reported *Tsaganomys altaicus* from Upper Oligocene deposits in Western Kansu, and these finds are beautifully illustrated in his paper. In these specimens the enamel does not surround the tooth prism entirely as Matthews and Granger have stated to be the case in their specimens. In the m $\overline{3}$ only the posterior outer half of the tooth possesses enamel while in the other molars the anterior portions are all devoid of encircling enamel. The upper molars are partially encircled by enamel and this corresponds to the Hsanda Gol specimens. From Bohlin's figures, the lower jaws look decidedly hystricognath.

In addition to the above mentioned finds, Young and Chow (1956, 456) described some Oligocene mammals from Lingwu, Northern Kansu (Mongolia) which included some broken incisors and a fragment of a lower jaw which they referred to as Cyclomylus lohensis. They state that these fossils resemble Tsaganomys but that they are smaller and that the roots of the cheekteeth are constricted and tend to be closed at the lower ends. The crowns are comparatively low while there is a trace of an external fold on the antero-external side of the fourth lower premolar. The incisors are relatively large, with flat enamel surfaces and ornamented with "barely visible fine striae". These authors state that Teilhard de Chardin's smaller forms correspond more or less in size to theirs. (Teilhard de Chardin divided his fossil specimens into two groups, based on size: i.e. larger and smaller forms). C.lohensis has also been reported from Tatal-Gol, Mongolia by Vinogradov and Gambarian (1952).

The differing interpretations as to the possible phylogenetic and taxonomic position of these Mongolian finds has briefly been commented upon above, e.g. the opinions held by Burke (1936), Wood (1955) and Wilson (1949). These authors all interpret these finds as semifossorial specialized cylindrodontid sciuromorphs. On the other hand, some of Landry's (1957) arguments have also been listed above where he argues for the hystricomorph, and consequently bathyergid nature of these fossils. As has been related above, he cannot see how the hystricognath jaw could have developed from the sciuromorph lower jaw and he furthermore maintains, quite rightly, that the following information is necessary before the correct nature of these fossils can finally be settled:

(i) the tympanic bullae of Tsaganomys and Cyclomylus should be opened, in order to ascertain whether the malleus and incus are fused (as they are in the bathyergids) and

(ii) that sections of the incisors should be made and the patterns of the enamel prisms checked (for they have a definitive arrangement in the hystricomorphs) and finally

(iii) to find out whether the pterygoid fossa communicates with the orbit.

In his work, Landry did not investigate these aspects (probably due to the fact that the specimens were not available) and he concludes that Matthews and Granger were probably right in accepting the genera Tsaganomys and Cyclomylus as bathyergids and in his own work Landry treats and accepts these fossils accordingly.

If this interpretation is accepted (and in the present work a number of facts are briefly discussed pointing to the hystricomorph nature of the bathyergids - see Chapter 5 - one can agree with Landry in stating that the earliest possible records of hystricomorphs in the Old World has been yielded by Oligocene deposits of Mongolia when the ctenodactylids and bathyergids first appear.

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It is interesting to note that the late Dr. Robert Broom also accepted these Mongolian fossils as bathyergids. Broom (1934, 476) states that although these forms are not at all closely related to the South African Pleistocene giant rodent mole Gypsorhychus (see below) "... they are interesting in showing that the giant rodent moles occur as far back as Oligocene.... times and (that they were) widely distributed over the Old World."

I have not seen these controversial fossils personally and it may seem wise to refrain from any further comments about their interpretation and the possible validity of such an interpretation. If an opinion may be voiced, it may be well to point out, that apart from the clearly hystricomorph jaw, the essential morphological criteria as far as the cranium is concerned, are still missing, as listed by Landry. Furthermore, the fact that Ardynomys (a definite cylindrodont) has also been found in Late Oligocene Asian deposits (and bearing Burke's (1936) opinion in mind) it may well be that these animals are not bathyergids, as assumed by Matthews and Granger, as well as by Landry. The facts pertaining to these fossils were discussed rather lengthily in the above paragraphs, as to allow the reader to draw his own conclusions about the possible taxonomic position of these scantily represented fossils.

When the attention is focussed on Africa for paleontological data, the fossils seem to offer firmer ground. The different fossil finds will be discussed briefly below, in a sequence corresponding to the geological strata and age of the deposits.

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The earliest African bathyergid is known from the Oligocene-Miocene boundary from South West Africa and has been named Bathyergoides neotertianius. Stromer (1924) reported this fossil from deposits south of Luderitz Bay. This preliminary notification was followed in 1926 by a fuller description (Stromer, 1926). (Hopwood and Hollyfield, 1954, 132).

Bathyergoides neotertianius is only known from a few fragmentary jaws and Broom (1934, 475) states that judging from Stromer's figures, these fossils are considerably nearer to Georychus than to Bathyergus, and that the molars are short rooted teeth with folded enamel, quite different to the type of tooth structure found in Gypsorhychus. He thus concludes that these South West African fossils are not closely allied to the Pleistocene form, Gypsorphychus, nor to the Mongolian genera as already related above.

Apart from this lower Miocene genus (which apparently is unquestionably bathyergid in its nature) there is a pronounced gap in African paleontological data as far as the bathyergids are concerned, for all the other bathyergid fossils have been found in Pleistocene deposits. Incidentally, this paucity of material from deposits ranging from Miocene to Upper Pliocene formations applies to other rodents as well.

Starting with the extralimital fossil bathyergids (i.e. north of the Cunene and Sambezi rivers), Heterocephalus quenstedti is to be mentioned. This fossil species of the extant 'sand puppy' from Somaliland was discovered by the Kohl-Laren'schen expedition to Central and Eastern Africa in 1937-1939 and was described in a preliminary note by Dietrich (1941). This find from Lower Pleistocene deposits in Tanganyika was described more fully in a subsequent paper by Dietrich (1942, 66) together with illustrations. It evidently points to the presence of these bathyergids in the early Quaternary of East Africa. The overall resemblance to the extant Heterocephalus glaber of Abyssinia and Somaliland is great.

It is interesting to note that this genus has had a far greater geograhical distribution in the past. Lavocat (1957, 133) reported this genus from the Makapansgat breccias of the Central Transvaal. Furthermore, the presence of another form, also from this locality, Heterocephaloides darti, has also been recorded by Lavocat (personal communication). The elements representing this genus are a few isolated teeth and portions of lower jaws. As far as I am aware, no description of these fossils has yet been published.

From Pleistocene deposits in South Africa, an interesting form of a giant rodent mole has been recorded, viz. Gypsorhychus. According to Broom, three species, darti, minor and makapani are represented in Southern African breccias.

In 1930, Broom announced the discovery of the first specimen in breccias associated with the ape-man Australopithecus africanus found at Taung in 1925. This type was named Gypsorhychus darti, after Prof. R.A. Dart, who first described the australopithecine Taung "child". The specimens were sufficiently preserved to be identified and it appeared

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that they are rather larger than skulls possessed by Bathyergus. The remains consisted of the following:

(i) the anterior half of one skull with both upper and lower jaws preserved in part (type specimen);
(ii) much of a second snout with most of the frontal region present as well as an imperfect palate.

The present author was unable to trace the type specimen needed for closer, more detailed inspection.

Broom (1934, 474) described these fossils in greater detail and provided illustrations of the dorsal and lateral views as well as the occlusal surfaces of the upper molars. In the same paper he postulated that Gypsorhychus is allied to Georychus for the following reasons:

(i) The upper incisors project forward as in Georychus;
(ii) there are no grooves on the upper incisors;
(iii) in Bathyergus the anterior portions of the nasals widen out in front near the nostrils, while in Georychus this widening does not occur and the latter condition is also found in Gypsorhychus;
(iv) the arrangement of the sutures in the posterior nasal region of the skull, as well as the structure of the lateral walls of the frontals and maxillae, correspond in Georychus and Gypsorhychus.

There are a number of morphological aspects in which the fossil Gypsorhychus differs from

Georychus and which may be tabulated as follows:

(i) there is no incisor bulge or ridge below the optic foramen in the fossil form as is the case in *Georychus*;

(ii) the frontal region in *Bathyergus* and *Georychus* is narrower than in *Gypsorhychus*;

(iii) the snout of *Gypsorhychus* is about twice as long compared to the extant *Georychus*.

The teeth of *Gypsorhychus* are interesting: they are not like those found in *Bathyergus* or *Georychus*. The maxillary teeth consist of four molariform molars, the first three broad and flat with unfolded enamel, while the fourth molar is triangular with (probably) folded enamel. Broom thought it possible that the molars were permanently growing and the flattened nature and persistant growth also applied to the teeth of the mandible (Broom, 1934, 475). Although only the front half of the lower jaw has been preserved, the lower jaw probably had a similar structure to that of *Georychus*.

These specimens were also illustrated (norma dorsalis) by Broom (1948, 48). Additional information about dimensions were also supplied: "basal length" of skull probably 70 mm., while the length of the nasals in the type was 26.5 mm.

Another *Gypsorhychus* specimen was discovered in 1937 in Hrdlicka's Cave, Buxton near Taung and was first described and referred to by Broom (1939, 315) as *G.darti*, (later renamed *G.minor* - see below). This find consisted of a practically complete skull without a mandible and illustrations of the dorsal and

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ventral aspects accompanied the description. The right incisor was missing, as well as the premolar and three molars of the left side in addition to the premolar of the right maxilla. All the tooth sockets were well preserved. The incisors were not grooved as in Bathyergus and as in the case of G.darti the maxillary teeth differed from all the living species, in being flattened, permanently growing, consisting of flattened dental plates. The dimensions of the first molar on its worn surface was 5.2 mm. x 1.2 mm., with the second molar having similar dimensions. The third molar was folded on its inner surface and the teeth "..... differ very greatly from those not only of other known Bathyergids, but apparently from all other rodents" (Broom, 1939, 316).

As is the case in G.darti, this specimen could also not be traced.

On page 316 Broom states that the general shape and structure of the skull agrees well with that of Cryptomys and other living allied genera, with the size of the skull comparable to that of Bathyergus and Cryptomys ansorgei. The length of the skull from the gnathion to the top of the occipital crest was 54 mm. while the width across the zygoma was 40 mm. The nasals are as long as in C.ansorgei and the facial portion of the maxilla resembles Bathyergus to a greater extent due to its small infra-orbital foramen as well as the flat palateal portion in front of the premolars. On the other hand, "the little hard palate formed by the palatines resemble that of Cryptomys more than of Bathyergus". This Gypsorychus specimen had large air sinusses in its

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frontal region but in other respects the "agreement with the giant Cryptomys is close." Furthermore, "the parietal and squamosal regions are also similar to those in Cryptomys and this also applies to the posterior part of the base of the skull" (Broom, 1939, 316). The premaxillaries are similar to those of the three extant living genera in South Africa. In the fossil the upper incisors project a little more than in Cryptomys but not much more than in Georychus. An important point of resemblance is that the posterior growing root of the incisor is situated a little behind and above the last molar, as is found in Cryptomys. According to Broom, "... it thus differs from Cryptomys, Georychus and Heliophobius, but of course it resembles these genera in this character more than it does Bathyergus".

This specimen, described in 1939, was also figured in Broom and Schepers (1946, 26-27) as G.darti but in 1948 Broom changed the name of the specimen to G.minor. The reason for doing this was that he found this specimen to be considerably smaller than the type specimen of G.darti, on which this species was originally founded. The basal length of G.minor is about 54 mm. (in G.darti about 70 mm.), while the length of the nasals in G.minor equals about 19 mm., (compared to 26.5 mm. in G. darti). Apart from size, the two specimens agreed fairly closely, but Broom finds that the difference in size is too great to accept these fossils as representing one species. Furthermore, he supplies the following points of difference:

G.minor	*G.darti*
(i) snout relatively narrower	(i) snout wider
(ii) a deeper groove on the premaxilla above the incisors	(ii) groove shallower
(iii) temporal muscles smaller, for the muscular impressions are further backwards	(iii) temporal muscles larger, for impressions are further forward (Broom, 1948, 49)
(iv) infraorbital canal smaller	(iv) infraorbital canal larger
(v) teeth smaller	(v) teeth larger judged by the sockets of the third upper molar
(vi) the toothrows of the molars more divergent.	(vi) toothrows of molars more convergent.

Broom concludes (1939, 316) that this giant rodent mole (i.e. *Gypsorhychus*) is a specialized and not primitive type, closely related to *Cryptomys*.

During 1946 the anterior part of a lower jaw of another *Gypsorychus* specimen was found at Makapansgat, in the Central Transvaal. It consisted of a perfect incisor "with the three molars in nearly perfect condition and the socket of the 4th premolar" (Broom, 1948, 48).

Although the mandible is imperfect Broom attached a new specific name to this find, i.e. *G. makapani*. According to him, the shape of the anterior part of the mandible differs considerably from *G.darti*, especially the symphysis which is

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deeper while the jaw seems to be more powerfully built.

The type specimen is housed in the Division of Physical Anthropology and Paleontology of the Transvaal Museum, Pretoria.

The lower incisor is large, its undamaged and exposed portion measuring 32 mm., whilst near the base its width is 5 mm., "with the thickness slightly more" (Broom, loc. cit.). As is evident from the brief description of the Taung material given in the preceding paragraphs, the lower molars of Gypsorhychus are not satisfactorily known. The first upper molar of G.darti measures 5.8 x 1.8 mm. and 5.2 x 1.3 (1.2) mm. in G. minor. Broom states that it is unlikely that the first upper and lower molars would differ much in size. The socket of the fourth lower premolar of G. makapani is a broad oval, measuring 5.2 x 2.4 mm. The first lower molar in this specimen, being well preserved, measures, according to Broom, 7.0 x 1.9 mm., the second molar 6.8 x 2.0 mm. and the third lower molar 6.8 x 1.5 mm. I have remeasured the first lower molar of G. makapani and found it to be 6.4 x 1.7 mm. (compared to 7.0 x 1.9 mm. which Broom obtained). From these figures it may be deduced that the molars of G. makapani are considerably larger than the molars found in the other two species.

During 1959 a virtually complete skull (although badly damaged in some sections) was extracted from the Makapansgat breccias and the authorities of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, kindly allowed me to investigate and describe this skull. (Fig. 1.1, 1.2). This description has not yet been completed but a number of morphological aspects may be enumerated. The two rows of molars are present, with the occlusal surfaces of the left side damaged. The m $\underline{1}$ measures 5.9 x 1.6 mm. and the m $\underline{2}$ 5.5 x 1.4 mm. The molars are also platelike, molariform, without folded enamel while the third molar is triangular, also without a folded posterior-medial portion. There is a pronounced incisor ridge present below the optic foramen. The distance between the anterior points of the nasals and the posterior rim of the occiput is approximately 55 mm. - this figure could not be determined accurately, for the nasal elements are missing. Similarly, the jugals are missing, and the estimated width across the zygomatic arches is about 44 mm. The rightsided tympanic bulla is present.

The correct identification of this specimen is considerably hampered by the absence of the Taung specimens which are not available for detailed comparison. The only other alternative is to compare this specimen with the natural size drawings which accompanied the different descriptions by Broom. Furthermore, many structural elements which Broom uses for comparative puposes, are missing in this specimen, e.g. the nasals.

This specimen has a number of features common to both G.darti and G.minor as well as a few which do not correspond to either. The skull shows a general overall agreement in structure to Georychus, as Broom has remarked for G.darti, but in both cases the fossils are much larger than the extant genus.

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As in G.darti, the frontals are wide and the snout is reasonably long. The first upper molar of this specimen measures 5.9 x 1.6 mm. which corresponds very well with the similar tooth in G.darti (i.e. 5.8 x 1.8 mm.). However, here the resemblance to G.darti ends. According to Broom, G.darti probably had folded enamel on the third molar: this feature is defintely lacking in this specimen. Furthermore, G.darti had no incisor bulge below the optic foramen while in this specimen there is a very clear ridge visible. Broom did not define his 'basal length' measurement, obtained for G.darti, which he gave as "about 70 mm." On looking at the natural size illustration (Broom, 1948, 48) this length probably represents the distance between the anterior points of the nasals to the dorsal posterior rim of the occipital region. (It may be pointed out that the posterior part of the drawing illustrating the skull of G.darti was "reconstructed" after the structure of the occiput in G.minor). The equivalent distance in the specimen under consideration is estimated to be 55 mm. (due to the absence of the nasal elements as related above), which corresponds reasonably well with the value Broom obtained (apparently based on the same points of measurement) for G.minor i.e. 54 mm.

Comparing the natural size drawing of G. minor (Broom 1939, 315) with this specimen, the overall size is more or less comparable. As far as the incisor bulge below the optic foramen is concerned, there is no information available for G.minor and this also applies to the width of the frontals and length of the snout. Morphologically, there are

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no obvious differences in the structure of the molars between the Makapan specimen and *G.minor* (i.e. molariform, platelike, etc.) but one point of difference relating to the posterior third upper molar is evident however: Broom stated that this tooth had an enamel fold on its postero-medial rim, which is absent in this specimen. Although there is a very marked resemblance in size between the Makapansgat fossil and *G.minor*, it is also evident that the individual molar teeth of the maxillae are far larger in the newer find than in *G.minor* which is evident from the following comparison:

	G.minor	*Makapansgat specimen*
right m $\underline{1}$:	5.2 x 1.2 (1.3) mm.	5.9 x 1.6 mm.
right m $\underline{2}$:	5.2 x 1.2 mm.	5.5 x 1.4 mm.

In recent genera (especially in *Bathyergus*) it is a fairly general rule that the length of the lower toothrow (as well as the individual teeth) is longer than the upper toothrow. In the lower jaw found in 1946, it seems that the dimensions of the m $\overline{1}$ (6.4 x 1.7 mm.) could possibly form a reasonably acceptable counterpart for the Makapansgat skull and the impression is gained that the erection of the species *makapani* may have been premature, when based on overall size alone. On the other hand, the difference in size between the molars of the Makapan skull and *G.minor* are very pronounced indeed, which may justify the acceptance of *G.makapani* as a valid species.

As far as the evidence goes (related briefly above), I am prepared to accept the Makapansgat skull tentatively as an example of *G.makapani*

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(hitherto unknown), but this assumption has to allow for the following facts:

(i) that the original specimens of G.darti and G.minor were not available for direct comparison;

(ii) that the skull has a strong size resemblance to G.minor (apart from the size of the molar teeth); and

(iii) that actual points of comparison, which could be gleaned from the published accounts, could often not be used, due to the damaged nature of the Makapansgat specimen.

The foregoing paragraphs have related somewhat lengthily, various aspects of the giant fossil rodent moles or mole-rats which occur in the South African Pleistocene deposits. This has been done purposely because these finds are examples of bathyergids which are known as fossils from Southern Africa, and it serves to illustrate how little material is available for possible conclusions. Secondly, it is also clear that the interpretations which may be held at present are bound to be changed in future when (possibly) more material becomes available. Thirdly, this information has been given to illustrate and possibly justify Broom's remarks concerning G.darti and G.minor respectively: "It will be seen that we have in this fossil form a new genus of Bathyergid mole allied to Georychus but.... (which) cannot be ancestral to Georychus, nor is it likely to have evolved from Georychus as we have it today. But very probably Georychus and the giant fossil mole have had a common ancestor" (Broom, 1934, 475), and that *G.minor* is a specialized and not primitive type, "closely related to *Cryptomys*" (Broom, 1939, 316).

Apart from the fossil genus *Gypsorhychus* which occurs in australopithecine deposits (where they may have served as additional titbits for the *Australopithecus* diet (Broom and Schepers, 1946, 31), the extant genus *Cryptomys* also occurs in Pleistocene breccias (de Graaff, 1960, 88).

Cryptomys robertsi (Broom, 1937, 1) is a fossil species based on a type housed in the Transvaal Museum, Pretoria. According to Broom, the type site is probably Schurveberg, near Pretoria. It is a 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 hind portion of the jaw is different to any species Broom was able to compare it with (de Graaff, *op.cit.*), having a distinct ridge passing forward on the outer side of the jaw from the condyle, a peculiarity which is not entirely attributable to the roots of the lower incisors. The teeth are relatively small. In one specimen the pm, m $\overline{1}$ and m $\overline{2}$ together measured 5.2 mm., with the tooth crowns low "and each tooth has the enamel of the upper half folded in on both the outer and inner sides" (Broom, *op.cit.*).

The distribution of this fossil is interesting: it has been identified in all the Pleistocene fossiliferous localities hitherto analysed (de Graaff, 1960, 104). The material is scantily represented however: the frequency of these fossils

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tend to decrease in abundance as the younger Pleistocene deposits (e.g. Makapansgat compared to the older Taung) are approached. The versatility of this species is illustrated by its presence in all Pleistocene breccias hitherto investigated (de Graaff, 1960, 110).

When the later Pleistocene fossiliferous breccias are considered, one finds that there are quite a number of localities (e.g. along the Vaal river, Transvaal, Vlakkraal in the Orange Free State, etc.) but that their mammalian microfaunal element is not satisfactorily known. Some information on the Hopefield area (where the neanderthaloid Saldanah man was found) is available however. Amongst the microfaunal mammalian fossils found in this vicinity, a number of mole-rat fossils have come to light. This material is housed in the South African Museum, Cape Town. According to Prof. R. Singer (personal communication), the extant genera <u>Bathyergus</u> sp. (cf. <u>suillus</u>) and <u>Georychus</u> sp. (cf. <u>capensis</u>) have tentatively been diagnosed from Elandsfontein, a few miles to the west of Hopefield. Today both these species occur mainly in the south-western Cape and from this data it may be deduced firstly, that they are already resident in that area for a considerable span of time; secondly, that the fossils are not more (if anything) than subspecifically distinct from the living forms. This is the only evidence hitherto where the extant <u>Bathyergus</u> and <u>Georychus</u> are known to be represented in the fossil or sub-fossil state.

From what has been briefly discussed above regarding the paleontological data of the bathyergids in Africa, the only definite fact emerging is that they are all definitely bathyergid (compared to the uncertain status of the Mongolian finds). Some interesting historical zoogeographical facts have also emerged (e.g. the Pleistocene distribution of Heterocephalus and Cryptomys) but it is clear that, based on fossil evidence alone, very little information has come to light about the possible phylogenetic relationships between the extant and fossil forms. I have none the less attempted a possible provisional phylogenetic scheme (based on very little information) and it is offered here for what it may be worth, bearing in mind its very tentative nature (Fig. 2.3).

CHAPTER 3

A SHORT HISTORY OF THE TAXONOMY OF THE BATHYERGIDAE

Although it is not the intention of this work to attempt solving phylogenetic problems and other aspects on supergeneric rank of the bathyergids, it should serve a useful purpose to give the reader a short review of the history of classification of the bathyergids.

Wood (1955, 165) states that the current classification of the rodents is inadequate and that there are two general philosophies underlying the current classification:

(i) A theoretical ideal, in which the classification should reflect interrelationships of the animals involved and this implies the use of various criteria which are not agreed upon by all authorities on the animals concerned. Consequently, forms of uncertain relationship are either grouped together and assigned to a position in a classification in a more or less arbitrary manner, or they are indicated as *incertae sedis*. The latter point of view has been advocated by Simpson (1945).

(ii) The other alternative is a classification involving the use of key characters resulting in a system based on different criteria into which all the different forms can fit. This approach has been used extensively by Ellerman (1940). According

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to Wood (op.cit.) this solves the problem as to where to place all the various families of rodents, but leaves many of them in positions that do not seem to be correct from a phylogenetic point of view.

An obvious deficiency concerning the evolution of rodents in general is the dearth of paleontological data, especially with a sharp break in rodent history at the Eocene-Oligocene boundary. Wood maintains (quite rightly) that this situation still holds, particularly for African rodents where the fossil history of rodents is poorly known (see de Graaff, 1961, 191). As a result of his detailed paleontological work, Wood stresses the fact that parallelism in rodents extends to the structure of the infraorbital region as well as to the teeth and these results indicate that the whole basis of rodent classification must be derived and that no classification based on key characters "is likely to agree with one based on the phylogeny of the order" (p.166). It is his opinion that one is not to rely on morphological criteria alone until it has been demonstrated by phylogenetic studies to be valid. In Wood's proposed classification he stresses the occurrence and development of similar physical features independently in diverse and geographically isolated groups of rodents. In a later paper (1958), Wood even poses the question "are there rodent sub-orders?" and this question has also been discussed by various other authorities, e.g. Kretzoi (1943). The latter author divides the rodents in but two suborders while at the other extreme the order is divided into seven suborders (Wood, 1955) which could

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perhaps be increased to as many as eleven, according to a suggestion by Lavocat (1956, 52-53).

If this is the current overall position of the supergeneric ranks of the rodents (for further details the reader is referred to some of the papers quoted above), it is clear that the correct systematic position of the bathyergids is also still far from finalized.

A brief discussion on the history of classification concerning the bathyergids can be found in Landry (1957, 65). These aspects are elaborated upon to a certain extent in the present work.

The mole-rats were listed as a subfamily under the Muridae (Myomorpha) in 1838 by Waterhouse (Landry, op.cit.) while in 1855 Brandt first proposed the subdivision of the simplicidentate rodents into the three classical suborders ("waste-paper baskets", Ellerman, 1940, 8). This subdivision into Sciuromorpha, Myomorpha and Hystricomorpha was based on the structure of the masseter muscle. This system has also been called the "classical" arrangement by Simpson (1945). Brandt names the bathyergids Spalaces subhystriciformes (Landry, 1957, 66) and as Waterhouse has done in 1838, Brandt also placed them under the myomorphs.

Alston (1876) largely followed this classification of Brandt but merged the bathyergids with the spalacids in a single family, also under the Myomorpha.

In 1887 (and also 1924) Winge placed the mole-rats as a subfamily (tribe) Bathyergini under the Hystricidae (Hystricomorpha) (Landry, 1957, 66).

Ellerman/...

Ellerman (1940, 21) feels that Winge's classification of the Hystricidae is unnatural "... with the inclusion of the Bathyergidae". As a basis for his classification, Winge used the structure of the paroccipital process, which to Ellerman seems to be a very variable character "even within a genus". Winge also appreciated the virtual impossibility of dividing the rodents into three or four groups "with any likelyhood of the arrangement being correct" (Wood, 1955, 168), and so split them into nine groups (Ellerman, op.cit.) attempting to avoid the difficulties of the classical approach (Wood, op.cit.).

Thomas (1896) again placed the bathyergids under the myomorphs (as Waterhouse, Brandt and Alston have done previously) "but divorced them from the spalacids" (Landry, 1957, 66), where they were provisionally placed by Alston. Landry also states that although Waterhouse, Brandt and Alston recognised the hystricognathid jaws of the bathyergids, they were more impressed "by habitus resemblances of these forms to other burrowing rodents and also by the fact that the tibia and fibula of the bathyergids are fused distally as in the myomorphs" (p. 66). These facts presumably also prompted Thomas to place them under the myomorphs. According to Ellerman (1940, 7), "this classification is admittedly nothing more than a rearrangement of an earlier classification of Alston".

Landry (1957, 66) states that Tullberg (1899) was the first to amass considerable evidence in favour of placing the bathyergids with the hystricomorphs. Apart from Winge's interpretation (1887) it is clear that this is definitely the case.

Tullberg/...

Tullberg also felt that the classical threefold arrangement of the rodent order was not correct and he classified the rodents on a different basis to that of Alston or Thomas. He split the rodents into two major groups, the Sciurognathi and Hystricognathi based on the inflection or lack of inflection of the angle of the lower jaw and these subdivisions were again divided into the Sciuromorphi and Myomorphi on the one hand and the Hystricomorphi and Bathyergomorphi on the other. According to Wood (1955, 167), this division of Tullberg was based on the structure of the infraorbital foramen and the masseter muscle.

The Bathyergomorphi thus formed a subtribe of the tribe Hystricognathi. It is Ellerman's (1940) opinion that this is perhaps the best classification of the order that has hitherto been done. Landry, (op.cit. p. 66) mentions the fact that Tullberg was the first person to provide sound evidence for placing the bathyergids with the hystricomorphs, for it "was he who pointed out that these forms possess in common such important features as the fused malleus and incus, the sacculus urethralis, the extention of the internal pterygoid muscles through the pterygoid fossa into the orbit, as well as the hystricognath jaw."

The next classification to be taken into consideration was the one proposed by Weber (1904 and also 1928). In this case, the bathyergids are listed as a separate group, the "tribus" Bathyergoidea. Ellerman (1940, 13) finds that as far as the superfamily grouping is concerned, this classification is quite acceptable. However, Weber indicates no

closer/...

closer affinities or possible relationships of the bathyergids with any other rodents.

Weber's classification was followed by the scheme proposed by Miller and Gidley (1918) who again abandoned the classical triple subdivision and divided the rodent order into five superfamilies, based on the zygo-masseteric structure. The mole-rats are credited with superfamily rank, the Bathyergoidae, equal in rank to the other four superfamilies (i.e. Sciuroidae, Muroidae, Dipodoidae and Hystricoidae). Ellerman (p. 17) states that this classification attends much more to detail characters than either those of Winge or Weber. As was the case in Weber's classification, these authors also refrained from indicating possible affinities for the bathyergids.

In his well known Checklist of African mammals, Allen (1939) treated the bathyergids as a separate family.

Ellerman (1940) attempted to combine as far as possible various morphological criteria which appeared (to him) to be correct in the classifications of Thomas, Tullberg, Weber, Miller and Gidley and finally Winge, although he followed Tullberg in his major groupings. In this way, the bathyergids are interpreted as a major subdivision (Bathyergomorph series) of the Hystricognathi coordinate with the Hystricomorph series (p. 23).

Simpson (1945) again classified the rodents according to the Brandtian three-fold scheme and he placed the bathyergids _incertae sedis_ within the hystricomorphs (p. 99). This authority states that although these animals are fairly abundant and quite

well/...

well known, there are few more doubtful points of classification than the affinities of the bathyergids. However, he also says (p. 213) the following: "Everyone agrees that they are extraordinarily isolated among rodents, and those who commit themselves further agree that if they have any special, though distant, affinity it is with the hystricomorphs". (For further remarks on the supposed 'isolation' of these animals, see Chapter 5 in the present work).

Romer (1933, second edition 1945, Seventh Impression 1958, 501) is one of the few authors who place the bathyergids under the Sciuromorpha, and this is evidently based on the possible cylindrodontid nature of the Oligocene Mongolian fossils, <u>Tsaganomys</u> and <u>Cyclomylus</u>. (See Chapter 2 in the present work). (It is interesting to note that in the work done by Landry (1957, 66) he states, that as far as he was aware, no one has grouped the bathyergids with the sciuromorphs.) Romer included them under the sciurids "for want of any better place to put them" (Romer, 1958, 501), but that they "are sometimes associated, rather dubiously, with the hystricomorphs because they show an out-turned angular region of the lower jaw seen in characteristic members of that suborder". Romer states however that there are no other features suggesting such relationships and ".... the diagnostic masseteric structures are of the primitive type seen only in the early sciuromorphs." This statement is however not borne out by the work done on these forms by both Tullberg (1899) and Landry (1957). Romer furthermore mentions the fact that these bathyergids are not closely related to any other group and they are placed as a superfamily Bathyergoidea within the suborder Sciuromorpha (Romer, 1958, 625).

Lavocat (1951) reverts back to the dual classification proposed by Tullberg and in his classification he especially emphasises the structure of the mandible. Although ".... he presents only a partial classification of the order, it is definitely an advance in separating the "Hystricognathes" into "Orthohystricognathes: Rongeurs sud-américains" and "Parahystricognathes: Formes palaearctiques et africains" (Wood, 1955, 168). The bathyergids are consequently placed under the latter group.

Roberts (1951) suggests separate suborder rank for the bathyergids, the Bathyergomorpha, equivalent to the Hystricomorpha, Sciuromorpha, Dipidomorpha and Myomorpha in rank. (According to Wood (1955, 194) Roberts gives no indication whether this term may have been used previously by some one else.)

Schaub (1953) also discussed the classification of rodents with special emphasis on the hystricomorphs. He does not agree with the other authorities using such characters as the infraorbital foramen and masseter muscle as the basic criteria for classification. It may be concluded that he feels that dental characters may also be used (without danger of aspects due to dental parallelisms) which may indicate relationships, although according to Wood (1955, 169) Schaub may not accept parallelisms in other structures.

Schaub proposed the erection of a new suborder, the Pentalophodonta to include all forms with teeth having a five-crested ancestry. This suborder is divided into two infra-orders, the Palaeotrogomorpha and Nototrogomorpha. The latter infra-order contains the South American hystricomorphs (= suborder Caviomorpha (suggested by Simpson in 1950) and erected by Wood and Patterson (1959) in a review of the South American rodents.) The former infra-suborder, Palaeotrogomorpha contains the superfamilies Theridomyoidea, Hystricoidea and Castoroidea, together with a series of families, _incertae sedis_, including among others, the Bathyergidae, Spalacidae and Rhizomyidae (Wood, 1955, 169).

One of the more recent classifications of rodents has been attempted by Wood (1955). In this case, Wood retains the classical suborders of Brandt, i.e. the Sciuromorpha, Myomorpha and Hystricomorpha and adds the Theridomyomorpha and Caviomorpha as new suborders. The bathyergids are retained as a separate suborder, the Bathyergomorpha, as was suggested (possibly for the first time) by Roberts (1951).

Landry (1957) has provided some of the latest data concerning the possible classification of the bathyergids. He clearly treats them as hystricomorph rodents and he also accepts the splitting of the rodents into sciurognath and hystricognath lineages as was proposed by Tullberg (1899). Summarizing the Old World Hystricomorpha, he credits the mole-rats with superfamily rank (Bathyergoidea) containing a single family (Bathyergidae) and two subfamilies, the Bathyerginae (including _Bathyergus_, _Cyclomylus_ and _Tsaganomys_ as genera) and the Heterocephalinae (with _Cryptomys_, *Georychus*, *Heliophobius* and *Heterocephalus* as genera). The other superfamilies which he considers and which are equal in rank to the Bathyergoidea, are the Ctenodactyloidea, Petromyoidea, Thryonomyoidea and Hystricoidea (Landry, 1957, 80, 97).

In connection with the facts given above concerning the classification of the mole-rats it is clear that three main tendencies emerged since 1838, i.e. to isolate them and to treat them as an isolated group, or, alternatively to place them either with the myomorphs, or with the hystricomorphs or, in one isolated instance, with the sciuromorphs. These facts may be summarised as follows:-

CONSIDERING THE BATHYERGIDS AS			
(a) An isolated group	(b) Sciuro-morpha	(c) Myo-morpha	(d) Hystrico-morpha
		Waterhouse (1838)	
		Brandt (1855)	
		Alston (1876)	
			Winge (1887)
		Thomas (1896)	
			Tullberg (1899)
Weber (1904)			
Miller and Gidley (1918)			
			Winge (1924)
Weber (1928)			
Allen (1939)			
			Ellerman (1940)
			Simpson (1945) *inc. sedis.*
	Romer (1945, 1958)		
			Lavocat (1951)
Roberts (1951)			
			Ellerman *et. al.* (1953)
			Schaub (1953) *inc. sedis.*
Wood (1955)			
			Landry (1957)

It/...

It is clear that with few exceptions the earliest taxonomists regarded them as myomorphs. During the 20th century (especially since 1940 onwards) the weight of evidence tends to place the bathyergids with the hystricomorphs. On the other hand, during the course of the 20th century, a number of authorities accepted them provisionally as an isolated group. Furthermore, it is clear that even in the more recent literature there is still no general overall agreement where the mole-rats are to be placed taxonomically. It is not unreasonable to assume their stronger hystricomorph affinities and for the purposes of the present work, they are considered as such (see below for a brief discussion of anatomical features pointing to their hystricomorph relationship). However, Simpson (1945) expressed the following warning which should also be borne in mind: "While awaiting better evidence, it is considered inadvisable to base a major division of rodents on these few aberrant genera".

CHAPTER 4

DESCRIPTION OF THE SKULL OF BATHYERGUS, CRYPTOMYS AND GEORYCHUS

In order to facilitate comparisons of the features of skulls referred to in this work it may serve a useful purpose to describe the skull of *Bathyergus* to a greater extent. Apart from brief descriptions of some salient features, there is no virtually complete account of a bathyergid skull available in the existing literature. The terminology used in this chapter corresponds to the accepted nomenclature without implying rigid homologies between the different elements of the skull compared with similar elements in skulls of other animals. This aspect can only be put in proper perspective by a detailed study of these elements during ontogenetic development and this embryological information is not available to date.

The description which follows is based on a skull of *Bathyergus suillus* (Schreber) and the reasons for choosing this species are two-fold:

(i) in this species, the largest bathyergid skull is encountered, facilitating easier identification of the various units of the skull. *B. janetta*, the only other species within the genus is a far smaller animal;

(ii) *B. suillus* has a fairly wide geographical distribution in the south-western Cape Province and is therefore the most likely to be encountered.

The description of the skull of Bathyergus which follows below, will then be supplemented by short notes about the skulls of Georychus and Cryptomys, especially emphasizing those aspects of their crania which differ from Bathyergus. Where no further comments are offered, it is inferred that what has been said for Bathyergus, is also applicable to both Georychus and Cryptomys.

General Appearance:

The skull of Bathyergus is rather elongate, (Fig. 4.1), the average length from gnathion to the posterior dorsal rim of the occipital region being approximately 50.0 mm. Seen from the lateral aspect, it is more or less flattened dorsally, tapering with a small angle downwards towards the muzzle. The skull is robust and strongly built as would be expected in fossorial animals. The greatest width is across the zygomatic arches.

In contract to Bathyergus, the skulls of Georychus and Cryptomys are much smaller: the average length as defined above being approximately 42.0 mm. and 32.0 mm. for Georychus and Cryptomys respectively. Seen from the lateral aspect, both these skuls have a definite convex curvature dorsally, compared with the flat dorsal aspect of the skull in Bathyergus. Furthermore, the skulls of Georychus and Cryptomys are not as robust and sturdily constructed as is the case in Bathyergus. (Fig. 4.2, 4.3).

Naso-maxillary region:

In Bathyergus the nasals to a certain extent protrude dorsally above the underlying premaxillaries, tapering to a point posteriorly on reaching the frontals, while anteriorly they terminate bluntly after widening slightly before the anterior rim is reached. There seems to be no special structure for the attachment of the nose pad, as is found in many chrysochlorids. The lateral edges of the nasal elements are limited

by/...

by the well developed premaxillaries except for the most posterior portion where they are bound and fused to the frontals. Anteriorly, the nasals form the dorsal edge of the aperture of the external nares.

The foramen of the external nares (seen from the front of the skull), is almost square in appearance being wider dorsally than ventrally and narrower transversely than its height. The ventral rim, formed by the premaxillaries (which incidentally also forms the lateral walls) is narrower than the dorsal rim made up by the anterior portions of the nasal elements.

The **premaxillaries** are strong and well developed bulging out laterally to house the strong upper incisors. On the dorsal surface of the premaxillaries are small openings (irregularly spaced), probably for exit of small branches of the olfactory nerve innervating the sensitive nose and snout. The premaxillaries taper down laterally and medially and fuse in the midventral line to form the strong diastemic region of the snout. Anteriorly, they are also in contact with each other just above the upper incisors (forming the lower rim of the external nares) and each premaxilla sends down a wedgelike protrusion between the two incisors extending to about half-way down the length of the exposed incisors. Where the two premaxillaries meet medially dorsal to the incisors there is a small elevation which may present a clear gnathion. Posteriorly, the premaxillary elements make contact with the frontals by means of a wedgelike structure, while laterally and ventrally they fuse with the

maxillaries/...

maxillaries by means of a clearly defined suture. On this suture, in the midventral line of the skull are two small, elongate (but nevertheless well developed) anterior palatine foramina.

The muzzle protrudes and is relatively narrow in comparison to the rest of the skull.

As far as the naso-maxillary region of Georychus and Cryptomys is concerned, the following may be pointed out: in Georychus the contact made by the anterior rim of the frontals with the posterior rim of the nasals are not as sharply pointed as in Bathyergus. In Cryptomys the posterior portions of the nasals terminate a short distance before reaching the main body of the frontal elements and the latter send out a rostrally directed process, meeting the posterior rim of the nasals. Although there is a certain degree of variation in this character, this aspect may be used as a criterium to distinguish between skulls of Georychus and Cryptomys.

Furthermore, in Georychus and Bathyergus the nasal elements tend to bulge out laterally to a certain extent (more or less in the middle portion of these elements) while this is not the case in Cryptomys. In this instance, the outer edges of the nasals form a more or less straight line from the front to the back.

Looking at the skulls of Georychus and Cryptomys from the norma anterior it will be seen that the shape of the exterior nasal foramen looks something like an inverted triangle, compared to the more "squared" condition in Bathyergus. This also seems to be a feature in which individual variation will be encountered.

Finally, in Cryptomys the large incisors housed in the premaxillaries underlying the nasals do not seem to bulge out laterally to such an extent as is the case in both Bathyergus and Georychus. Comparatively speaking, the muzzle in Cryptomys is far less robust compared to the other two genera, which may seem to be surprising, in view of the fact that the muzzle is an important portion of the skull during burrowing activities.

The orbital region and zygomatic arches:

In Bathyergus the frontals are strongly developed, fusing with the posterior tapered points of the nasals and the wedgelike protrusions of the posterior premaxillaries antero-dorsally. Antero-dorsolaterally and dorso-laterally they fuse with the ascending

portion/...

portion of the maxilla and lachrymals as well as the orbitosphenoid respectively. Near its point of contact with the lachrymals (which are very small elements), the frontals widen out laterally to a certain extent. Postero-laterally, they are limited by the squamosal process of the zygomatic arch while medio-posteriorly they make contact with the parietal elements. The two frontal elements are separated by a small medial ridge, which is a forward extension of the sagittal crest between the parietals. This ridge forks into two near the broadening of the frontal elements as described above. There is a marked interorbital constriction across the frontals slightly anterior to the suture of the squamosal process of the zygoma. There is no indication whatsoever of a postorbital process on the frontals. Consequently, the orbits are in open contact with the temporal region.

Within the orbit there is a lachrymal element present in addition to a large, orbitally situated lachrymal foramen. This foramen is situated dorso-laterally more or less on the suture between the anterior part of the lachrymals and the perpendicularly ascending portion of the maxilla (through which passes the infraorbital foramen). In juvenile or adult specimens, the sutures limiting the lachrymal elements can not be distinguished easily due to a very strong ankylosis with the surrounding elements. Ventrally and postero-ventrally the lachrymal is connected to the maxilla and orbitosphenoid respectively.

The orbitosphenoid element has the usual mammalian position and also has a number of distinct

foramina/...

foramina. The functions of these various foramina have not yet been determined, and the following nomenclature is therefore tentative. On its anterior border, there is a spheno-palatine foramen. Posteriorly, the orbitosphenoid is depressed medially resulting in a groove which is limited dorsally by the frontals, posteriorly by the pterygoid fossa breaking through into the orbit (see below) and ventrally mainly by the maxillaries. Within this groove is a small optic foramen followed by an equally small more posteriorly situated anterior lacerum foramen.

Seen from the dorsal aspect the zygomatic arches are rather wide, consisting of the usual elements, i.e. a maxillary complement anteriorly, a separate jugal element in the middle and a squamosal portion posteriorly. The jugal element extends ventrally slightly beyond the squamosal contribution so that seen from the norma dorsalis it can be seen as a small piece of bone jutting posteriorly from below the squamosal contribution to the zygoma. The maxilla is joined to the jugale anteriorly by means of a dove-tail joint while posteriorly the jugal is overlain by the squamosal contribution.

The jugal arches are solidly constructed; the maxilla forms a more or less perpendicular transverse plate through which a small, nearly circular infraorbital foramen passes. This maxillary portion of the zygoma does not form an antero-posteriorly directed perpendicular plate in front of the orbits as is found in many murids. Just ventral to each infraorbital foramen near the suture

between/...

between this element and the jugal, the maxilla shows a flattened, horizontal surface which may serve as an insertion point for the muscles closing the diastema (zygomatic plate).

The squamosal portion of the zygoma forms the elongated anteriorly-posteriorly directed glenoid fossa for articulation with the condyle of the mandible. Its lateral edge is supplied by the jugal element itself, and on the whole, the fossa is wide allowing a certain laterally-directed movement of the lower jaw in addition to the usual front- and backward movements.

As is the case in both Bathyergus and Cryptomys, the frontal elements in Georychus are limited postero-laterally by the squamosal process of the zygoma and postero-medially by the parietals. However, the distance between these two squamosal processes on either side is greater in Georychus than in Bathyergus or Cryptomys.

In view of the fact that the roots of the upper incisors are situated in the pterygoidal region in both Cryptomys and Georychus, a number of differences are bound to be present in the orbital region compared to Bathyergus. In the former two genera the lachrymal foramen is situated at a slightly higher (more dorsal) level in order to allow the incisor to pass below it. As is the case in Bathyergus, the infraorbital foramen within the orbit is small and Landry (1957, 66) ascribed this condition (i.e. the reduction) of the infraorbital foramen as secondary.

As in the case of Bathyergus, the precise role played by the different foramina in the orbital region of Cryptomys and Georychus is tentatively named and presented below. However, due to the large incisors, there is no sphenolateral foramen in either Georychus or Cryptomys and the optic foramen shares a common aperture with the anterior lacerum foramen, in the shape of a well developed groove (above the incisor sheath) through which one can see more or less into the braincase.

The jugal element in Georychus and Bathyergus meets the maxillary component anteriorly by means of a dove-tail joint. In Cryptomys, however, the jugal bone fits into a long groove on the maxillary component. This feature has been used by Roberts (1951, 382) to distinguish between members of the subfamily Georychinae (i.e. containing the genera Georychus and Cryptomys).

The thickened, horizontal surface below the infraorbital foramen on the maxillary portion of the zygoma as described for Bathyergus is present in both Georychus and Cryptomys but is the least developed in the latter genus. In some skulls of this genus, it may virtually be said to be absent altogether.

The glenoid fossa in Georychus and Cryptomys is comparatively speaking shallower and broader than in Bathyergus. This may be correlated with the fact that the former two animals utilize their incisors during tunneling and this would imply a greater degree of moveability and motility of the mandibles in relation to the cranium, than is needed in Bathyergus.

The braincase:

The parietals, forming the dorso-medial section of the braincase are bound anteriorly and dorso-laterally as well as laterally by the posterior frontals and squamosal elements respectively. A conspicuous feature is the presence of a well developed sagittal crest, the posterior portion of which is formed by the supra-occipitals and not by the parietals. This ridge also extends rostrally between the frontals (although not as high and pronounced as between the parietals) as related above. Posteriorly the parietals are limited by the supra-occipitals, i.e. they do not reach the posterior rim of the skull.

In Georychus and Cryptomys the posterior rim of the parietals are more or less on the edge of the nuchal crest, compared to the condition in Bathyergus where the supra-occipitals contribute to the dorsal surface of the skull to a certain extent. In other words, in Georychus and Cryptomys the posterior edge of the parietals extend caudally to a greater extent than in Bathyergus.

The squamosal units, forming the dorso-lateral complement of the braincase are rather elongate structures extending backwards from about the posterior third of the frontals to the nuchal crest of the supra-occipitals. Near the posterior portion of the squamosal process of the jugal arch, is a small foramen apparently leading directly into the braincase, via the squamosal. Immediately anterior to the external auditory meatus the squamosals have a marked medially directed constriction, more or less mid-way between the squamosal portion of the zygoma and the posterior portion of the squamosals butting against the lateral extensions of the supraoccipitals. Seen from the dorsal side, the impression is created that the braincase is hereby constricted - this however, is not the case.

The constriction of the squamosals in Georychus corresponds to a greater degree to that found in Bathyergus, while in Cryptomys the hind (caudal) portion of this lateral notch is not so long as in either Bathyergus or Georychus. The length of the braincase in Cryptomys accordingly seems to be shorter.

The squamosals are limited anterolaterally by the descending frontals, and ventrally by the alisphenoid and tympanic bullae while posteriorly they are limited by the supraoccipitals. Anterior to the external auditory meatus, just below the constriction made by the squamosals (see above) and just posterior to the squamosal portion of the zygomatic arch, there is a large foramen of which the antero-ventral and dorsal walls are furnished by the squamosals while the posterior edge is supplied by the auditory bullae. This foramen leads directly into the dorso-lateral portion of the braincase but it could not be established what its possible function is. A similar situation is encountered in many murids which correspond to the postglenoid foramen. It may therefore be assumed that this is the equivalent foramen in the bathyergids.

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The antero-latero-ventral section of the braincase is constructed to a great extent by the alisphenoid. In bathyergids the alisphenoid elements are largely ventral to the squamosals. Dorsally, the alisphenoid meets the squamosal, antero-dorsally the frontals while it makes contact with the palatine and maxillary elements antero-ventrally. Postero-ventrally, it tapers to a point, meeting the basisphenoid close to the mid-line of the skull.

In Bathyergus the alisphenoid makes contact with the palatine and maxillary elements by means of a thin sheet of bone which forms a lateral wall to a canal which in actual fact is the pterygoid fossa which has broken through from its original posterior position anteriorly into the orbit.

In both Georychus and Cryptomys the pterygoid fossa has not broken through into the orbit (i.e. below the alisphenoid as described above) due to the presence of the roots of the incisors in the pterygoid region.

Posteriorly, the alisphenoid is separated from the tympanic bulla by a large foramen lacerum medius. The medial edge of the alisphenoid forms part of the pterygoid fossa.

In neither Georychus or Cryptomys is the foramen lacerum medius so well developed as in Bathyergus and it is the least developed in Cryptomys.

On looking into the pterygoid fossa from its posterior opening, it will be seen that there is a small bony canal on the outer wall of the pterygoid fossa. This canal is very flimsy, and may be complete or present in part, or in some cases, absent altogether. If present, this small canal leads into the orbit in Bathyergus and into the braincase in Georychus and Cryptomys.

On the alisphenoid, lateral to the pterygoid fossa and anterior to the foramen lacerum medius, is a well developed foramen ovale. Anterior to this foramen are three smaller apertures, all leading into the braincase and which may or may not all be present simultaneously or even symmetrically on both sides. The anterior two lie more or less dorso-ventrally to one another (the dorsal one being larger) and both occur more or less in line with the anterior rim of the glenoid fossa. In the absence of ontogenetical data, it can not be stated specifically what their possible functions are.

In Georychus and Cryptomys a well developed foramen ovale is also present. The distance between the hindrim of this foramen and the anterior part of the bulla is very small in Cryptomys in comparison to Bathyergus. In Georychus, the apertures referred to above in Bathyergus are also variable and this also applies to Cryptomys, where the largest dorsally situated foramen (more or less on the anterior rim of the glenoid fossa) is often the only one present.

The ventral portion of the braincase is made up by the following elements: a strong, well developed basioccipital which is separated from the bulla by a slitlike foramen lacerum posterius. Immediately anterior to the exoccipital condyles, within the exoccipital, is a well developed foramen condylare. Anteriorly, the basioccipital meets the basisphenoid (near the pointed antero-medial portion of the bullae) which in turn is bound laterally by the palatines and makes contact anteriorly with the presphenoid. The sutures between the basisphenoid and palatine elements are not clear, while the vomer can be seen within the nares interni. Dorsal to the medially-directed anterior point of

the/...

the tapering bulla, on the basisphenoid (near the point of fusion of this element with the posteriorly pointed alisphenoid), is a small but distinct foramen, the Eustachian aperture.

In *Cryptomys* the basioccipital is a relatively narrow element in comparison to *Georychus* or *Bathyergus*, while the distance between the bullae and exoccipitals is also very slight so that the foramen lacerum posterius as well as the condylar foramen is not easily seen in *Cryptomys*. In this respect *Georychus* corresponds reasonably well to the condition found in *Bathyergus*.

Posteriorly, the walls of the braincase are constructed by the supraoccipitals dorsally and the exoccipitals ventrally. The suture between these elements can not be detected with ease in adult specimens. Postero-dorsally, the supraoccipitals form a strong nuchal crest which folds over dorsally and posteriorly on the vertical surface of the occipital region. The supraoccipitals encroach a small distance on to the dorsal surface of the skull, contributing to the structure of the posterior part of the sagittal crest, as related above. Furthermore, they consequently fuse with the posterior edges of the parietals and squamosals. The nuchal crest of the supraoccipitals send out laterally directed flanges strengthening the auditory bulla postero-dorsally. This flange bends ventrally, just posterior to the external auditory meatus. On the occipital surface of the supraoccipitals one finds a varying number of small foramina. The median portion of the dorsal rim of the foramen magnum is also supplied by the supraoccipital element.

In both *Georychus* and *Cryptomys* the nuchal crest does not fold over dorsally and posteriorly on the surface of the occipital region as in *Bathyergus*. In these genera, the nuchal crest is not as well developed.

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The dorso-lateral, lateral and ventral portions of the foramen magnum are supplied by the exoccipitals. The midventral portion however, is made up by the posterior part of the basioccipital. The foramen magnum has a more or less squarish appearance with the ventral rim semi-circular.

Ventro-lateral to the foramen magnum the exoccipitals supply two strong, well developed condyles for articulation with the atlas. Laterally, the exoccipital elements also strengthen the posterior-lateral parts of the bullae by means of two strongly developed paroccipital processes. These paroccipital processes do not reach beyond the level of the dorsal portions of the exoccipital condyles and terminate rather bluntly, with a similar type of thickened bony surface as was found on the maxillary portion of the zygoma, as related above. These may serve as areas for attachment of the neck muscles.

The paroccipital processes in Georychus and Cryptomys are not as big as in Bathyergus. In Bathyergus they are broad and blade-like while in the former two genera they are much narrower. In Cryptomys the distal ends of these processes end in a thickened notch, to a far greater degree than is found in Georychus.

The surface of the occipital region is more or less scalloped, i.e. not smooth. The occipital region does not slope forwards and this feature is assumed to be primitive in Bathyergus (Landry, 1957, 71). Seen from the norma posterior the skull of Bathyergus is relatively flat and wide.

On the other hand, the occipital regions of Georychus do slope or slant rostrally to a certain degree and seen from the posterior aspect, the skull of Georychus is not as flat and wide as in Bathyergus. In the case of Cryptomys, the skull seems to have been "flattened" on the lateral sides giving this skull a more "rounded" appearance.

The anterior inner wall of the braincase is constructed by a strongly developed cribriform plate (more or less on the inner (medial) side of the orbitosphenoid) and possesses the usual number of small apertures for exit of branches of the olfactory nerve .

The palatal region:

The presence of a pair of anterior palatine foramina has already been mentioned (see above). Behind this point (if seen from the ventral aspect of the skull), the strong and well developed maxillary elements are raised to a certain extent to house the two rows of molar teeth (Fig. 4.4).
On the anterior surface of this 'elevation' the ridges made by the roots of the first cheekteeth can be seen clearly. From this point laterally, the maxillae give rise to the maxillary complement of the zygoma (where the flattened bony surface on the ventral anterior portion of the zygoma is to be seen) and also to the transversely directed horizontal plate through which the infraorbital canal passes from the outer side of the snout to the orbit. Immediately in front of this plate, the maxilla fuses with the premaxillaries, dorsally with the frontals and posteriorly with the lachrymals.

The maxilla, dorsal to the toothrows, fuses with the orbitosphenoid. Behind the last molar, it fuses with the palatine elements. Medially, between the two toothrows, the two maxillae are separated by a small elevated ridge.

The distance between the toothrows is very narrow indeed, not wider than the width of a single toothrow.

In Georychus (Fig. 4.5) and Cryptomys (Fig. 4.6) there is a small bulge or elevation immediately behind the last molar element and lateral to the palatal elements, housing the pulp cavities of the caudally developed incisors. This point also corresponds to the most anteriorly situated portion of the pterygoids. In Bathyergus, the palate is flat, with a small medial ridge while a pronounced medial ridge is present in Georychus, and also to a certain extent in Cryptomys. The palatal region of Cryptomys is more rounded than in either of the two other genera. The toothrows in Georychus and Cryptomys are much more convergent posteriorly than in Bathyergus, where they are more or less parallel.

The palatines, (merging anteriorly with the posterior maxillary-palatal elements) are not very broad and provide the ventral rim of the internal choanae. Laterally, they fuse with the alisphenoid (which then forms the pterygoid fossa) while dorsally they meet the basisphenoid and vomer elements to form the 'roof' of the internal nasal passage, which is relatively large.

The internal choanae are relatively smaller in Georychus and Cryptomys compared to Bathyergus. Consequently the distance between the vertical parts of the pterygoids is much narrower in Georychus and Cryptomys. In Georychus, these vertical pterygoid plates tend to diverge to a certain extent, while they are parallel in Bathyergus and Cryptomys.

The perpendicular portion of the palatines (which meets the alisphenoid to form the pterygoid fossa) are accentuated and extended posteriorly by fusion with the pterygoids. The pterygoidal elements thus fuse with the palatines anteriorly and the basisphenoid dorsally, while the posterior perpendicular margin of the pterygoids make contact with the antero-medial portions of the auditory bullae.

The auditory region:

The auditory bullae in Bathyergus are strong and well developed. Landry (1957, 71) even calls them large and thus finds another primitive feature/...

feature in the skull of Bathyergus. The bullae taper to a point antero-medially, meeting the posterior portion of the basisphenoid and the posteriorly directed perpendicular portions of the pterygoids (already described above). The ventro-medial edge of the bulla is limited by the basioccipital (between which the slit-like foramen lacerum posterius is found) while the posterior end of the bulla is strengthened by the exoccipital paroccipital process (see above). Postero-laterally, the bulla extends between the paroccipital process ventrally and the supraoccipital flange dorsally and this portion consists of the mastoid element of the skull. In other words, the mastoid unit also takes part in the formation of the tympanic bulla. The supraoccipital portion lying dorsal to the mastoid complement extends ventrally to about the same level as the more posterior paroccipital process. Anterior to this flange, below the level of the ventral rim of the external auditory meatus, is a small stylomastoid foramen.

The external auditory meatus is more or less oval in shape, while the length of the ear passage is about 6 mm.

Dorsally and antero-laterally, the bulla is connected to the squamosal while the ventral portion is separated from the alisphenoid by means of the large foramen lacerum medium. The dorsal portion of the bulla provides the posterior part of the rim of the postglenoid foramen.

In Georychus and Cryptomys, the bullae are also, relatively speaking, large. In these genera, the posterior lacerum foramen is not as clear as in Bathyergus and in Cryptomys, the paroccipital processes are not so enlarged.

The external auditory meatus is also oval shaped in Georychus and is virtually circular in Cryptomys. As would be expected, the length of the outer ear canal is far shorter in these genera. Similarly, the foramen lacerum medium is not as clear as is the case in Bathyergus.

The middle ear region, containing the ear ossicles, has received a considerable amount of attention in the past. One thinks immediately of the classic work on ear bones by Doran (1876) in which the ear bones of Bathyergus are also discussed. The following brief account of the ear ossicles in Bathyergus has been paraphrased from Doran's paper. The genus Bathyergus exhibits in its ossicles a feature which distinctly allies it to the cavies and porcupines. The head of the malleus is much elongated anteriorly (though not as much as in the hystrids): the neck is thin and constricted with a distinct laminar expansion below it. The manubrium is rather short and relatively wide near the base, getting very narrow towards the tip with a distinct processus brevis present. A small stout tubercle occurs on its inner border representing the processus muscularis, as in squirrels. The head of the body is completely fused to that of the incus by their articular surfaces, the contour of which is deeply marked all round the seat of ankyloses. This bony union involves the neck and a part of the inner border of the manubrium, from the root to close above the tubercle of the tendon of the tensor tympani. The manubrium is fused to the processus longus of the incus, nearly down to the point where it turns inwards to the head of the stapes. According to Doran, this ankyloses was observed by Hyrtle. "Whilst the malleus differs from the hystricine

malleus/...

malleus in the head being less produced forwards, the incus is distinguished from that of the porcupines in having the very shallow body and proportionally large crura seen in the rest of these fossorial animals. The posterior crus is particularly long. The processus brevis is as well developed as in Spalax or Ellobius, and hence different from the same in Rhizomys".

The stapes is a large bone, though not proportionally as great as in Spalax. In both these animals the crura are straight, not very long and widely divergent, the base being very broad and extremely convex towards the vestibule. The crura are inserted some distance from both extremities. "There does not appear to be any bony canal between the crura; at least such does not exist in the skulls of Bathyergus in the college collection " (Doran, 1876, 413).

The description of the ear ossicles in Bathyergus has been given at some length above, for very often in the existing literature it is only stated that in all bathyergids the malleus and incus within the middle ear are fused, without any indication as to how these elements are fused.

Cockerell, Miller and Printz (1914, 440) state that in Tachoryctes (an extra-limital bathyergid-like rodent as far as this work is concerned), the arrangement is essentially similar to that of Bathyergus as described and figured by Doran. In the former genus however, the malleus and incus are not completely fused.

The lower jaw:

The lower jaw is solidly and stockily built (Fig. 4.1). There is an obvious correspondence in structure to the typical hystricognath type of jaw.

In Bathyergus the symphysis between the two hemi-jaws ankylose at an early age (Roberts, quoted in Shortridge, 1934, 318) but this fusion is evidently not very strong.

As is well known, this symphysis is not fused in Georychus and Cryptomys, allowing a certain degree of freedom of movement between the two lower incisors (see later) which is effected by the transverse muscle.

Seen from the ventral aspect, each hemi-jaw has a conspicuous alveolar sheath for its incisor and this sheath leads virtually into the condyle where the open roots of the lower incisors are situated.

The ascending ramus of the jaw is relatively low resulting in an anteriorly situated coronoid process and a well developed rounded condyle. The coronoid process is a small, sharp, dorso-posteriorly pointing element.

In Georychus (Fig. 4.2) the ascending ramus ascends at a slightly larger angle and this portion of the lower jaw is slightly higher than in Bathyergus. This impression is further strengthened in the case of Cryptomys. Comparitively speaking, the coronoid process in Cryptomys is much higher than in Georychus and Bathyergus so that the "valley" between the coronoid process and the condyle of the mandible is much deeper in Cryptomys. The longer coronoid process in Cryptomys curves caudally to a greater extent than in either Georychus or Bathyergus, the latter having a very short coronoid process (Fig. 4.3).

It is especially the angular portion of the jaw which creates the strong hystricognath impression. The angular portion springs from the outer side of the bony alveolar incisor sheath, so that, when seen from the ventral aspect, there is a deep linear groove

(immediately/...

(immediately lateral to the incisor) between the angular and dental portions. Seen from the lateral aspect, the angular portion reaches far beyond the condyle. The inner edge of the angular is scalloped and more or less flattened on its lower border.

Seen from the ventral aspect, the groove between the angular portion of the jaw and the incisor alveolus is not as deep in Cryptomys or Georychus as is the case in Bathyergus. Furthermore, seen from the lateral aspect, the angular portion does not extend caudally beyond the condyle of the jaw to such an extent in Georychus and Cryptomys as is the case in Bathyergus. Still seen from the lateral aspect, the angle the angular portion of the jaw makes with the main axis of the jaw is far more pronounced in Georychus and Bathyergus in comparison to Cryptomys where this point of departure from the main body of the jaw is far more gradual.

There is a small but definite mental foramen on the anterior outer side of the lower jaw (below the posterior portion of the first molar) more or less on the same level where the angular portion leaves the main body of the lower jaws. A small mandibular foramen (on the inner posterior part of the ascending ramus) is also present, more or less behind the level of the fourth molar element, some distance dorsally on the ascending ramus (inner surface).

The dentition:

As far as the teeth are concerned, the incisors will first be discussed briefly which will be followed by a short discussion of the molar complement.

The upper incisors are very long, and as Beddard (1902, 480) has mentioned, stand out in front of the closed lips in all the bathyergids. Sclater (1901, 72) also relates the fact that the incisors are so long that they are always visible, the lips not being large enough to cover them. The upper incisors are more heavily curved than the lower incisors, and the former pair lie anterior to the lower incisors when the mouth is in the normal closed position.

In Bathyergus these teeth (in contrast to the lower incisors) are heavily grooved and these grooves run down the middle of the teeth. Their colour is usually white and they arch posteriorly with a gentle curvature to "a point situated above the anterior grinding teeth..." (Roberts, quoted in Shortridge, 1934, 319). Owen (1868, 296) already remarked that the incisors are broader than the occlusal surfaces of the molars.

Comparing the upper incisors of Bathyergus to the other bathyergids, Landry (1957, 70) has pointed out that they are short and broad, not reaching farther back than the infraorbital foramen itself. This foramen is reduced in size and does not (or scarcely) transmit a slip of the masseter (see below). In spite of this the rostrum is greatly enlarged (described below) and Landry interprets this enlargement as secondarily correlated with the enlargement of the incisors, for the nasal cavity is still much reduced in comparison to that of other rodents. As a comment on Landry's remarks, it may be added that a widened nasal passage would probably be a greater hinderance to fossorial animals. Landry furthermore states that this widening of the upper incisors has further encroached on the size of the infraorbital foramen and completed the exclusion of the masseter muscle from the muzzle (p. 70).

The/...

The upper incisors in Bathyergus have been termed scalpriform. They grow from persistent pulps (as do all incisors in the Rodentia) while the anteriorly situated enamel of the tooth does not extend to its posterior surface.

In contrast to the upper incisors of Bathyergus, these teeth are not grooved, in Georychus and Cryptomys. Although the infraorbital foramen is small in these forms, it is relatively larger than encountered in Bathyergus and this may be due to the fact that the pulp cavities of these teeth are situated in the pterygoidal region, as related above. It is likely that a small slip of the masseter passes through this aperture in Georychus and Cryptomys. The upper incisors are comparitively speaking not as wide as in Bathyergus (although still broader than the molars) and consequently these incisors have not encroached on the size of the infraorbital foramen as is the case in Bathyergus, thus not effecting the exclusion of the masseter muscle from the muzzle.

Sclater (1901, 72) has remarked that the incisors in the case of Bathyergus may sometimes be over 3" (76.2 mm.) in length of which half protrudes beyond the alveolus. These two teeth are separated in the lower jaw by a small hiatus.

The incisors of Georychus measures up to 2" (50.8 mm.) in length, while those of Cryptomys can attain 1½" (38.1 mm.)

The lower incisors are also big structures but are not grooved on their anterior surface. They are rather long, also growing from persistent pulps which are situated ventrally to the condyle of the jaw. These large incisors are thus partially responsible for the deep fissure which is present between the edge of the incisor sheath and the angular process (see above).

The incisors are separated from the molars by a well developed diastema, which is shorter than the premaxillary-maxillary diastema of the skull.

The/...

The molar teeth of Bathyergus are rooted, and, according to Landry (1957, 71) deeply hypsodont, if not actually evergrowing. There are four teeth in each maxilla, as well as in each hemi-jaw, and in all cases they decrease in size from the front to the back.

The molars are simple structures with re-entering folds in juveniles only (Sclater 1901, 72) while Weber (1928, 269) describes them as having had outer and inner enamel folds originally. The molars are somewhat oval in section surrounded by a ring of well developed enamel, gradually disappearing with age. (Sclater, op. cit.). The central portions of the teeth are built up by dentine.

The first upper grinding tooth has a protocone, which fuses with a hypocone posteriorly. Buccally, the anterior paracone is separated from the posteriorly situated metacone by an enamel groove. The second tooth is essentially the same except that the lingual anterior protocone is separated from the hypocone by an enamel fold. This arrangement is also found in the third molar element and in this case the outer (buccal) and inner (lingual) enamel folds are much clearer. The posterior tooth of the maxillary grinding teeth, is the smallest element of the tooth row and in this case the metacone is present while the hypocone is absent.

The lower molar elements also decrease in size from the front to the back and the first tooth has an enamel fold on the buccal side, separating the anteriorly situated protoconid from the posterior

hypoconid/...

hypoconid. The second tooth has enamel folds on both inner and outer surfaces (i.e. lingual and buccal) which is better developed on the buccal side separating the protoconid from the hypoconid. In the first tooth the metaconid and endoconid tend to fuse and this applies to the second molar element as well. The third tooth has a strong buccal enamel fold separating the protoconid from the hypoconid while the last element is provided with a protoconid, hypoconid and metaconid, the endoconid being absent or under-developed.

The upper toothrow is usually shorter in its total length than the lower toothrow.

The homology of these grinding teeth is at present in a state of confusion. Sclater (1899, 225, 1901, 71) and Weber (1928, 269) suggest the following dental formula:

$$i\ \frac{1}{1}\ :\ c\ \frac{0}{0}\ :\ pm\ \frac{1}{1}\ :\ m\ \frac{3}{3}\ =\ 20.$$

On the other hand, Thomas (1909, 111) and Roberts (1951, 379) propose the following scheme:

$$i\ \frac{1}{1}\ :\ c\ \frac{0}{0}\ :\ pm\ \frac{2}{2}\ :\ m\ \frac{2}{2}\ =\ 20.$$

The two premolars in this scheme would correspond (according to Thomas) to the third and fourth premolars, while the molars would be the first and second molars of the original mammalian dental formula.

Landry (1957, 14) mentions the fact that Tullberg (1899) stated that the motion of the jaw in hystricomorphs is propalinal and that in other groups (e.g. the sciurognaths) this movement is prevented by the cusps of the teeth. This propalinal

grinding/...

grinding is also possible in bathyergids, and consequently in Bathyergus, due to the occlusal surfaces of the molars being plane (Landry, 1957, 12). Landry (*op. cit*. p. 9) states that *Petromys* is the only hystricomorph that he has examined whose teeth are not flat-crowned.

CHAPTER 5

ON THE HYSTRICOMORPH AFFINITIES OF THE BATHYERGIDAE AND THEIR TAXONOMIC 'ISOLATION'

Various authors (e.g. Romer, 1958, 501, and Simpson 1945, 212, amongst others) have commented on the taxonomic 'isolation' of the bathyergids. The former included them within the sciuromorphs ".... for want of any better place to put them", while the latter states that there ".... are few more doubtful points in classification, concerning animals that are fairly abundant and quite well known, than the affinities of the bathyergoids...." and that everyone "... agrees that they are extraordinarily isolated among rodents". However, both these authorities state that they are sometimes associated with the hystricomorphs, and Simpson, in his well known work on the classification of mammals has included the mole-rats _incertae sedis_ within the hystricomorphs.

In the more recent literature, Landry (1957) mentions a number of reasons (based on his own observations, and those of Tullberg (1899), Parsons (1894, 1896), and Dathe (1937) amongst others), why the bathyergids should be accepted as hystricomorphs. Landry furthermore states that the socalled isolation of the bathyergids may have been over-emphasized hitherto. This author also blames Thomas (1909) to a certain extent for this concept of isolation, especially when Thomas's article on tooth homologies of the bathyergids is taken into consideration./...

consideration.

It may therefore serve a useful purpose to consider briefly the various arguments, for and against the placing of the bathyergids with the hystricomorphs and why they are accepted as hystricomorphs in the present work. As far as some of these arguments are concerned, a number of them have been mentioned earlier on in this work but for the sake of clarity some recapitulation on a number of these aspects will be necessary in this chapter.

A. Hystricomorph affinities in the skull

In the preceding pages, a fairly detailed description of a skull of Bathyergus has been given, together with comments on the skull of Georychus and Cryptomys. However, as far as certain structural features are concerned, (e.g. the infraorbital foramen, the pterygoid fossa as well as aspects of tooth morphology), these structures justify a fuller discussion, not only in terms of Bathyergus, but also as far as the family Bathyergidae is concerned.

1. Teeth

Regarding the teeth of bathyergids, Landry (1957, 67) offers a number of interesting speculations which may be dealt with briefly at this point. Thomas (1909) speculated on the homologies of the cheekteeth of the bathyergids, especially the East African form Heliophobius. This genus, posesses at one time or another "..... six cheekteeth, the highest number known in any rodent or lagomorph" (p.67). However, these teeth are not all present simultaneously and as the anterior tooth gets worn away another one forms at the posterior end of the toothrow.

Consequently, there are seldom more than four cheek-teeth present simultaneously and in addition, the last tooth may never become functional. Thomas assumed that these teeth of Heliophobius represented premolars 2, 3 and 4 and molars 1, 2 and 3. The m 3 is not always developed, and therefore Thomas felt that this tooth is the first one of the set to be depressed due to its position in proximity to the roots of the incisors (e.g. in Cryptomys and Georychus). This led to a reduction of freedom, development and use. Thomas argued, that the next tooth i.e. the m 2 may be the next to have disappeared, but he prefers to consider, ".... without real proof", that the pm 2 is the next to be suppressed, for in young specimens with unworn teeth it is smaller than the one next to it (i.e. the pm 3). However, in equally young Georychus specimens ".... the two anterior teeth are practically equal in size" (Thomas, 1909, 111). "From this, therefore, cutting off a tooth at each end of the series, it would follow that in the 4-toothed members of the family, Georychus and Bathyergus, the formula is P 3-4, M 1-2". (Thomas, op. cit. p.111). This would therefore also apply to Cryptomys.

Landry (1957, 67) then states, quite rightly, that if Thomas' assumptions are really true, then, ".... of course, the bathyergids must be far removed from the rest of the rodents ", leading to the concept of 'isolation' of the bathyergids among the rodents. "If Heliophobius really retains the primitive second upper premolar and the lower second and third premolars, it must have separated off from the rest of the rodent stock at least in the

Paleocene/...

Paleocene, and probably in the Cretaceous. Indeed, if lagomorphs and rodents are descended from a common stock as implied by Simpson in grouping them together as "Cohort Glires", bathyergids must have come off the protogliroid stock before the rabbits did".

It seems far more probable to Landry that the extra teeth in Heliophobius represent new dental elements which have been added on to the posterior end of the usual mammalian molar series, such as has happened in the South African carnivore Otocyon. This seems plausible in view of the fact that the posterior teeth in Heliophobius ".... push in from behind as the more anterior teeth are worn away" (p. 68). This could be brought about by a persistant dental lamina budding off two extra tooth germs.

Furthermore, Landry also doubts Thomas' homologies of the cheekteeth. In order to follow the replacement of the teeth, he examined a series of Heliophobius skulls. Although he did not see absolutely unworn first cheekteeth, the youngest specimen he had available had only the first two teeth with very little difference in size between the two. All the teeth were shaped roughly like an inverted cone "..... with a broad top and narrow base". As the teeth wear down, they decrease in size until, ".... when the first tooth is almost gone, it is represented by a tiny peg. The disparity in size between the first and second tooth increases as the teeth are worn." Landry therefore doubts Thomas' notion that ".... the tooth row of Georychus represents the tooth row of Heliophobius with one tooth lopped off from each end. Rather, the tooth row of Heliophobius represents the tooth row of Georychus with two neomorphic teeth added to the back end" (Landry, 1957, 69). In the case of Bathyergus, Georychus and Cryptomys, Landry thus interprets the four molar elements to represent P4, M1, 2 and 3, based on the annotations of a figure of the cheekteeth of Heliophobius which Landry supplies on p. 68.

Once the additional teeth of Heliophobius is seen as a specialization of that particular genus, "... the taxonomic remoteness of the Bathyergidae considerably decreases" (Landry, 1957, 69).

According to Landry (1957, 71), the cheekteeth of Bathyergus, in contrast to the other bathyergids, are deeply hypsodont. It is therefore possible that the bathyergids were derived from a hypsodont hystricomorph. The majority of the bathyergids are slightly hypsodont and this would imply that a hypsodont tooth evolved into a brachyodont one, ".... a decidedly unusual occurence among mammals". However, Landry goes on to state that the teeth of the bathyergids do however show a degenerate appearance suggesting that they are reduced hypsodont teeth. The posteriorly-directed extension of the incisors, combined with a narrowing of the anterior region of the snout may have necessitated a shortening of the length of the cheek teeth in order to allow the incisor to pass above them, as is the case in Georychus and Cryptomys. This lack of space in the skull could not accommodate both the deep alveolar part of the hypsodont molars as well as the long upper incisors. "If selection pressure for long incisors was strong enough, there would automatically/...

automatically be strong selection pressure for a reduction in length of the molars, especially if the diet of the animal were changed to softer food". Landry (1957, 71).

As was mentioned earlier on in this work, Tullberg (1899) stated that the motion of the lower jaw is propalinal in hystricomorphs, while this movement is prevented by cusps on the occlusal surfaces of the teeth in other groups e.g. the sciurognaths. The fact that bathyergids also show propalinal grinding may thus point to a hystricomorph affinity. It should however the pointed out that flat-crowned teeth are not limited to the hystricomorphs and for further information on this matter, the reader is referred to Landry (1957, 9-16).

An interesting bit of evidence pointing to the hystricomorphine nature of the bathyergids is found in the histology of the enamel of the incisor. Landry (p. 25) gives an excellent account of this aspect which will be paraphrased briefly at this point. Tomes (1850) investigated the possibility of obtaining useful taxonomic characters from the microscopic structure of the teeth of rodents and he found that the arrangement of prisms of enamel in the incisors was characteristic for each of the three classical suborders.

These enamel prisms run from the dentine to the surface of the tooth, arranged in lamellae next to the dentine, but towards the outside of the tooth these lamellae are broken up and the enamel prisms proceed uniformly to the surface, parallel to each other. According to Landry, in alternate lamellae the prisms are parallel. The differences between the different suborders are found in these lamellae. "In both the sciuromorphs and the myomorphs the lamellae are composed of transverse layers of single prisms running at right angles, or nearly so, to prisms in the subadjacent layer, so that a thin cross section of the incisor shows a diamond-shaped pattern in the region of the enamel where the prisms criss cross each other. In longitudinal section one can see the principal distinguishing characteristics of the suborders. The myomorphs are distinguished by their rugose lamellae, the projections from the prisms in one layer fitting into corresponding depressions in the next layer." (Landry, 1957, 25).

The histological structure of the hystricomorph enamel is different however. In this case the lamellae are not just one prism deep but correspond to thick layers of prisms giving the enamel in longitudinal section a distinctive appearance. "The prisms are thrown into transverse waves, and the prisms of adjacent layers are 180° out of phase; that is, at the position along a prism at which it swings farthest to the left, the prisms immediately below it and above it will be farthest to the right." Furthermore, in the outer part of the enamel, as usual, the "... prisms are straight and not arranged in lamellae and there is usually a sharp change in the angle of the direction of the prisms at a point where the lamellae cease". According to Landry, the histology of the incisor enamel of the bathyergids is typically histricomorph.

2. The pterygoid fossa

Returning once again to some aspects of features in the bathyergid skull, the question of the pterygoid fossa has to be raised.

The breaking down of the anterior wall of the pterygoid fossa so that it communicates with the orbit (see above) is an important hystricomorph character. The internal pterygoid muscle of the typical hystricomorph passes through the tunnel formed by the connection of the pterygoid fossa with the orbit (Landry, 1957, 9). In Bathyergus this muscle passes to the orbit in the normal hystricomorph manner (Landry, op.cit. p. 70). This is made possible by the fact that the incisors are short and their persistant pulp cavities are situated slightly in front of and dorsal to the first cheek teeth elements.

Landry (op.cit.) states that in most of the bathyergids however, the pterygoid fossa opens into the braincase (p. 9). This is also related to the great development of the incisor, especially in Georychus and Cryptomys. In these cases, the incisors have pushed posteriorly into the pterygoid bone, shutting off the pterygoid fossa from the orbit and "... forcing the internal pterygoid muscle up into the brain case. The internal pterygoid **thus** takes origin from the posterior side of the incisor sheath" (p. 9). In Bathyergus the incisors are short and the pterygoid fossa opens into the orbit as in other hystricomorphs.

The most important character correlated with the fact that the pterygoid fossa breaks through into the orbit (as in Bathyergus), is, (according to Landry, p. 9), the propalinal chewing, a basic functional adaptation of the hystricomorphs. This in turn leads to the flat occlusal surfaces of the grinding teeth found in the bathyergids (i.e. absence of cusps). The lengthening of the internal pterygoid muscle which has occurred in the bathyergids gives a stronger pull to the jaw in an antero-posterior direction. "If the forward extension of the masseter is of prime importance in producing a strong bite at the incisors, the pterygoid muscles are of prime importance in closing the cheek teeth against one another and rubbing anteroposteriorly". This movement, in fact, then leads to propalinal grinding. Tullberg (1899) states that in hystricognaths ".... the movement of the jaw in chewing is always more definitely in a direction paralleling the zygomatic arch..." and Landry (p. 9) agrees with Tullberg that this propalinal chewing is the basic functional adaptation of hystricomorphs.

These facts clearly point to the hystricomorph affinity of the bathyergids. In Bathyergus (which does not tunnel with the aid of its incisors and where the incisors are thus smaller) the usual hystricomorph condition is found; in Georychus and Cryptomys, who utilize their incisors during tunneling operations, these incisors have become enlarged causing an alteration in structure from the basic hystricomorph pattern.

3. The structure of the mastoid portion of the bulla

The possibility of an ancestral Petromys-like animal giving rise to the bathyergids as postulated by Landry (p. 75) has been mentioned above (see Chapter 2 of the present work). It will be

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recalled that Landry finds Petromys probably the most generalized of all Old World hystricomorphs and considers it as a type that could have been related to the bathyergid line. In this form (as in the bathyergids) the mastoid covers a wider expanse at a deeper level between the lateral processes of the supraoccipital and the paroccipital processes of the exoccipitals. In the hystricids, the mastoid shows only a small surface between these processes. However, a long lateral process of the supraoccipital is not limited to the hystricomorphs, and, as has been stated above, due to the otic specialization which has occurred in the Old World hystricomorphs, Petromys (an undoubted hystricomorph) is left as "....the closest relative of the bathyergids by default" (Landry p. 75).

4. Structure of the infraorbital foramen

Landry (1957, 66, 67, 70) has mentioned a number of features as far as the small infraorbital foramen in the bathyergids is concerned and some of his arguments are to be paraphrased rather lengthily in this connection.

It is known that bathyergids posess all the characteristic hystricomorph features, with the exception of the enlarged infraorbital foramen. Winge (1887, 1924) postulated that this reduction could be secondary because he believed that this foramen was enlarged in primitive rodents and that a reduced infraorbital foramen was secondarily in all rodents in which it is reduced. Tullberg (1899) and Parsons (1894) admitted that a slip of the anterior deep part of the masseter muscle (i.e. the musculus masseter medialis) does pass through

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this foramen, at least in Cryptomys. Ellerman (1940, 44) states that in some bathyergids, especially in certain species of Cryptomys the infraorbital foramen is "starting to transmit muscle" through this foramen. In some cases, as in C. mellandi, this foramen may be as much enlarged as in the much reduced type of foramen found in the Rhizomyidae. Furthermore, Ellerman states that the size of the infraorbital foramen is evidently a variable character, for in Cryptomys the foramen may be larger on the one side of the skull than on the other in individual cases. Ellerman goes on to state (p. 44) that it appears to him "singularly unlikely that, having taken such a large step forward in evolution as the enlargement of this canal for muscle transmission (as it seems an unusual character among Mammalia to say the least), these families (e.g. Geomyidae, Sciuridae, Castoridae, Bathyergidae and Heteromyidae) should go even further in evolution and, so to speak, develop covering over this canal so that it does not transmit again".

Landry (p. 67) states that if Ellerman is following Tullberg, he follows blindly and not logically for in the same sentence in which he states that Cryptomys is beginning to transmit the muscle through the foramen, Ellerman also gives an example of a rodent which has reduced the foramen to the same size of that of Cryptomys (i.e. in some Rhizomyidae). Landry thus concludes that if we accept the fact that reduction has occurred in the rhizomyids, it can no longer be insisted that it could not have occurred in Cryptomys (and therefore

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in the bathyergids). On page 66 Landry then poses the question: why has no one made the obvious assumption that the bathyergids are hystricomorphs in which the infraorbital foramen has become reduced secondarily?

As far as Bathyergus is concerned, Landry (p.70) states that the small infraorbital foramen does not transmit a slip of the masseter. Yet in spite of the small foramen and absence of the masseter from the rostrum, the rostrum of Bathyergus is enlarged. According to Landry, this enlargement is secondary and may be correlated with the broadening of the incisors which has occurred during the evolution of this genus, for the nasal cavity is very much reduced (see above) compared to other rodents. This widening of the incisors has further encroached on the size of the infraorbital foramen and "... completed the exclusion of the masseter from the rostrum".

Landry (1957, 71) gives further evidence and reasons for believing that the reduction of the infraorbital foramen is secondary and correlated with adaptation in the bathyergids for fossorial life by demonstrating a similar occurrence in the microtines, especially the genus Ellobius.

5. The fusion of the malleus and incus

One of the most important morphological characters of the hystricomorphs mentioned by Tullberg (1899) is the fusion of the two outer ear ossicles, the malleus and incus. This condition is also found in the Bathyergidae and again indicates their affinity with the hystricomorphs. What the significance of this fusion could be, is not easy to determine.

6. Structure of the lower jaw

The hystricomorphs all possess a peculiar type of angular process of the lower jaw, and Tullberg considered it to be the most important common feature of the Hystricognathi. Viewed from the ventral aspect, the 'origin' of the angular process is lateral to the incisor alveolus, while in the sciurognath type of jaw the angular portion arises from the ventral portion of the incisor alveolus. The essential idea here is that in the ".... sciurognaths the inside of the angular process of the sciurognath jaw is at the inside of the alveolar sheath, whereas in the hystricognath jaw the inside of the angular process is lateral to the outside of the incisor alveolar sheath". (Landry, 1957, 6). This hystricomorphlike arrangement is encountered in the bathyergids and thus points once again to the hystricomorph nature of the mole-rats.

The facts briefly discussed above, indicate a definite hystricomorph affinity of the bathyergids, based on structural features of the skull. However, the postcranial skeleton also indicates a number of features, which are to be discussed briefly below.

B. Hystricomorph affinities in the postcranial skeleton

1. The limbs

According to Landry (1957, 67) the only indication that the bathyergids are extraordinarily isolated amongst the rodents is the fact that the scaphoid and lunar elements of the manus are separate and that the tibia and fibula are fused at

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their distal ends. The former is apparently a genuinely primitive character (i.e. implying that they may have split off from the basal rodent stock before these elements fused in the majority of rodents) while the latter is probably a habitus character related to digging and Landry does not doubt that it could have arisen among the hystricomorphs at any time. These aspects would be clarified considerably if the appropriate fossil forms could be found. In the mean-time, by means of this explanation, the taxonomic remoteness of the mole-rats is considerably decreased, although by themselves, these arguments do not place the bathyergids within the hystricomorphs.

Focussing our attention on the humerus however, the following may be mentioned: a character which all the hystricomorphs share (including the bathyergids) is the absence of the entepicondylar foramen on the distal humerus. This foramen usually forms a funnel through which the median nerve passes on its way to the zeugopodium. This characteristic however, is not restricted to the hystricomorphs alone: the earliest rodents (aplodontoids of Simpson, 1945) all posessed this foramen, as do most placental mammals. The sciuromorphs tend to retain this foramen, the hystricomorphs to lose it, while it occurs irregularly in the myomorphs.
The fact that this foramen is almost never found in the hystricomorphs indicates that it was lost in the early history of the group (Landry, p. 20). Again, this argument does not place the bathyergids definitely within the hystricomorphs, but taken on its face

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value, tends to strengthen the notion that they are to be placed within the hystricomorphs. Correlated with certain features of the skull described above (and with other features to be described below) the absence of this foramen in the bathyergids also points to their hystricomorph affinity.

C. Hystricomorph affinities in the reproductive organs and musculature

According to Landry (p. 17), Tullberg (1899) quoted another useful character which occurs in the hystricomorphs i.e. the sacculus urethralis. This feature was also studied extensively by Cole (1897), Pocock (1922) and Dathe (1937).

In the glans penis, just below (and communicating with) the urethral orifice, is an invagination. During erection of the penis this little sac everts, protruding a balloon-like extension which projects beyond the tip of the penis. In many hystricomorphs, there are two little horns at the bottom of this sac, which during copulation, are on the tip of the balloon and it may serve some titilatory effect during copulation. Dathe points out that there are many small spicules all over the penis except for a medial lane on the ventral surface which is free of them. This arrangement holds for all hystricomorphs. According to Landry, this arrangement is present only in the hystricomorphs and bathyergids and affords excellent evidence for placing the bathyergids with the hystricomorphs.

I have not seen an erect penis in any of the genera considered during the progress of this work, but on the flaccid penis the spicules on the surface of the penis in Bathyergus are clearly visible

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with the aid of a steroscopic dissection microscope. As far as the myology of the bathyergids is concerned, the reader is referred to the classical papers by Parsons (1894, 1896), who worked on the comparative aspects of rodent myology. Landry (1957, 30) states, that all hystricomorphs (including the bathyergids) have a muscle called the scapuloclavicularis which "... runs from the clavicle, where it may be continuous with the subclavius, to the spine and vertebral border of the scapula, forming a sheet of muscle over the supraspinatus. This muscle is not found in any other rodent, but surprisingly enough it is well developed in lagomorphs. According to Parsons, this muscle is innervated by the same branch of the brachial plexus which in man innervates the subclavius".

Furthermore, Landry states that Bensley (1926) described the scapuloclavicularis in the rabbit under the name of pectoralis tertius, being a subdivision of the pectoral musculature. If, according to Landry, this is to be accepted this muscle is not homologous to the scapuloclavicularis of rodents, but Bensley does not mention the innervation of this pectoralis tertius, nor "... does Parsons state whether or not he investigated the innervation of the scapuloclavicularis in rabbits. There is a possibility, therefore, that the two muscles are not homologous." (p. 30).

Landry could not find a homologue of this muscle in other mammals, and while it is apparently only found in rodents and lagomorphs, this tends to confirm the notion that these two orders are related. He states, that if they are, this hystricomorph character must be a primitive rodent feature.

The possible presence of this muscle in the bathyergids thus also places the mole-rats within the hystricomorphs and may also confirm the view that the Bathyergidae is an ancient offshoot from the basal hystricomorph stock.

Another myological character listed by Parsons for the hystricomorphs is the structure of the digastric muscle "... whose two bellies are continuous or at best separated only by a slight constriction. In myomorphs and sciuromorphs, on the other hand, there is a well marked tendon between the two bellies, as in man. Moreover, in myomorphs and sciuromorphs the anterior two bellies are joined across the midline by a tendinous arcade which is absent in hystricomorphs in which the anterior two bellies are widely separated " (Landry p. 30). However, this distinction is not absolute, for amongst the sciurognaths Cricetus, Microtus, Myodes and Hydromys (according to Parsons) show no tendon between the two bellies but the anterior two bellies are still in close contact. Even in hystricomorphs, there is a constriction of the muscle between the two bellies "... and there is a flat tendinous reinforcement at this point so that a lack of a tendinous part in hystricomorphs is not immediately obvious. It seems to me that there could be, and probably are, all sorts of intermediate conditions between a completely tendinous interruption and a completely muscular one. The important difference between the two is whether or not the anterior belly of the digastric is attached to its fellow across the midline" (Landry, 1957, 31).

The hystricomorphine structure has the two anterior bellies diverging from each other as they are traced backwards. In the bathyergids (Bathyergus and Georychus) the digastric is as in murids i.e. the anterior two bellies lie close besides each other but there is no tendinous cross connection between them i.e. corresponding to the hystricomorphs. This, according to Landry (p. 31) could be pointed to as another primitive hystricomorph feature of the bathyergids.

Another feature mentioned by Parsons as being characteristic of the hystricomorpha is the absence of the transverse mandibular muscle in the lower jaw. This muscle is peculiar to rodents and runs across the anterior ends of the two halves of the jaw. It is usually superficial to the mylohyoid in the Muridae, where it may be better developed than in other groups. It consists of a bundle of fibres running across the two hemi-jaws close to the symphysis and serves to diverge the tips of the lower incisors since the symphysis of the jaw is unfused in the majority of rodents. Amongst the hystricomorphs this symphysis is more tightly fused than usual (probably correlated with the propalinal grinding motion) and consequently this transverse muscle is unimportant. However, Landry (p. 31) points out that the bathyergids have the most freely moveable jaws of any rodent and in these animals the muscle is consequently well developed. This may again point to the fact that the mole-rats have come off from the early hystricomorph stock before the rest of the hystricomorphs began to lose this muscle.

The muscle has undoubtedly been retained in terms of survival value and even Tullberg (1899, 349) remarked that the spreading of the incisors is important in the handling of small round objects and the handling of these during gnawing. This is especially true if it be kept in mind that the main diet of the bathyergids consists of bulbs and other subterranean roundish objects.

Another myological feature common to all hystricomorphs (Parsons) is the uniting of the tendons of the flexor hallucis longis (flexor fibularis) with the flexor digitorum longis of the sole of the pes. An exception to this arrangement amongst the hystricomorphs are the bathyergids where the flexor digitorum longis is better developed than in other rodents, with its tendon inserting onto a sesamoid bone at the base of the first metatarsal and therefore it does not fuse with the flexor hallucis longis. This may again point to the early breakaway of the bathyergids from hystricomorph stock and I am inclined to interpret this as another habitus character: the hindfeet of the animals are used extensively to clear the passages and tunnels from excavated soil and a separation of these two muscles would allow greater flexibility of the pes and therefor greater manipulative effect.

Landry (1957, 32) states that in all hystricomorphs which he has dissected the panniculus carnosus muscle takes origin, not from the inner side of the humerus next to the insertion of the latissimus dorsi as in most mammals, but from the outside of the scapula at the ventral end of the spine, the acromion process and the greater tuberosity

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and deltoid crest of the humerus. To him it seems likely that the attachment of the panniculus on the outside of the arm is a hystricomorph character. I have found that this condition also exists in Bathyergus and therefore, again points to their hystricomorph affinity.

Summarizing the data discussed on the previous pages, it is clear that it may be grouped into four categories:

a. Facts pointing to the apparent taxonomic isolation of the bathyergids;
b. Facts pointing to their hystricomorph affinities;
c. Facts which may point to their hystricomorph nature;
d. Facts pointing to non-hystricomorph affinities.

a. As far as the first category is concerned, mention may be made of the homology of the teeth which is most likely based on a past misinterpretation of the facts. The size of the infraorbital foramen is satisfactorily explained by correlating it with the development of the incisors while the separate scaphoid and lunar elements in the manus may be due to the very ancient nature of the bathyergids. Seen from this point of view, the bathyergids may not be so isolated taxonomically as was thought at first.

b. The undoubted hystricomorph affinities are borne out by the following facts: the histological structure of the enamel of the upper incisors; the structure of the pterygoid fossa; features of the mastoid portion of the bulla; the fusion of the malleus and incus in the middle ear; the anatomical

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features of the lower jaw; the presence of the scapuloclavicularis muscle and the insertion of the musculus panniculus carnosus; and finally, the morphology of the male copulatory organ.

These are all relatively clearcut examples pointing to their hystricomorph nature.

c. On the other hand, a number of features may point to their hystricomorph affinity, but bearing in mind the fact that many of these aspects could be encountered in the sciurognaths (sciuromorphs and myomorphs) as well. It seems that these features, although present or absent in the hystricomorphs, have undergone certain modifications in the bathyergids, which can be correlated to their fossorial mode of life and may thus have survival value. Examples of these aspects are: the presence of the well developed transverse mandibular muscle; the structure of the digastric muscle; the insertion of the flexor digitorum longis; the absence of the entepicondylar foramen in the distal humerus and the propalinal grinding of the molars.

d. Finally there are some aspects pointing to non-hystricomorphine affinities, e.g. the presence of a well developed clavicle and the distally fused tibia and fibula. The former aspect has not been discussed in the previous pages but it may be mentioned that this element is widespread and well developed in the sciuromorphs and myomorphs. In the hystricomorphs, this element is usually small, or virtually absent. It may be pointed out that a strong, well developed clavicle (as found in the bathyergids) is a common feature in all animals who need greater motility and manipulative ability of the forearm. Bathyergus, especially uses its forearms during tunneling, and this genus, as well as Georychus and Cryptomys, use their hands during feeding, in a similar fashion as mice and squirrels utilize it.

The distally fused tibia and fibula is also to be found in the majority of rodents and may also be interpreted as a habitus character, as has been mentioned above.

Based on the information presented above, I am virtually convinced about the hystricomorph affinities of the Bathyergidae. In the past they may have been associated rather dubiously with the hystricomorphs (with one noticeable exception i.e. the paper by Landry) but for the purposes of the present work they are accepted as highly specialized hystricomorphs.

CHAPTER 6

ASPECTS OF THE BIOLOGY OF THE BATHYERGIDAE

It should be stressed that very little information about the biology of the Bathyergidae is available at present. This may be partially due to the fossorial nature of the animals and the fact that relatively little fieldwork has been undertaken in the past. In this respect one thinks immediately of modern techniques which can be applied to fossorial or semi-fossorial animals e.g. the use of radio-active isotopes which can be applied to determine activity patterns etc., as well as other interesting aspects of behaviour. An excellent example of this approach is the work by Godfrey and Crowcroft (1960). In this case the European mole Talpa was subjected to investigations with the aid of radio-active cobalt and a Geiger counter. It is evident that the possibilities for interesting research as far as the behavioural aspects of the mole-rats are concerned has hardly been begun to be exploited.

The data presented below (scanty as it may be), is based on the existing literature and partially on my own field observations. Much of the evidence given in this chapter may seem to be irrelevant but it may serve a useful purpose in pointing to future research possibilities on the biology of this interesting group of rodents.

On analysing the information available at present, it was found that many facets of the biology of the three genera were identical and this information (for the purposes of this chapter) has been compounded for Bathyergus, Georychus and Cryptomys. It will become evident that very little biological information is available on Georychus, while a greater amount of detail concerning behavioural and other biological aspects of Bathyergus and Cryptomys is to be found in the literature, mainly in the papers by Eloff (1951, 1952, 1958).

General behaviour

As far as the bathyergids are concerned, the overall impression gained is that the animals are rather short tempered. This is especially noticeable when they are captured in the field, or when housed in cages in laboratories. There is no information available about their behaviour when they occur normally within their tunnels. According to Eloff (1951, 142) this aggressiveness has been noted by other observers as a marked characteristic of all blind moles.

When on the surface of the soil, there is random movement but no real fleeing (Eloff, 1951, 142). They are extremely sensitive to air currents (this also applies when they are within their tunnels) and a violent reaction is evoked when one blows into the face of a captured specimen. It reacts with snapping movements with its enormous incisors, accompanied by a snorting type of grunt while the whole animal retreats backwards rapidly for a distance of four-to-six inches keeping its head and snout directed at the source of irritation.

When these animals are captured alive they are usually unsettled and agitated but after a while they soon calm down under captive conditions. This has been described very aptly by Moseley (1879) in the case of <u>Bathyergus</u>, when after capture, the animal assumed a "sulking attitude". Furthermore, these animals are apparently not socially inclined and appear to be willing to fight instantly whenever the opportunity arizes, especially if two (captured) individuals (even if they are of different sexes) do not come from the same tunnel system.

<u>Habitat</u>

In view of the fact that these animals are predominantly fossorial it stands to reason that burrowing is an important activity. Not much is known about this aspect although Eloff (1951, 1952) has managed to keep a number of individuals alive under laboratory conditions so that some idea concerning their burrowing activities could be gained. <u>Bathyergus</u> is well adapted to burrowing, not by means of its large incisors but using the well developed claws of the front foot. The amount of time spent burrowing during the day is unknown. Personally, I timed a captured specimen which was released on soft riverine soil after soaking rains. The animal could submerge its head and front limbs in approximately 90 seconds, the major portion of the digging being executed by the claws. Sporadically it bit the ground frantically and savagely with its incisors but this activity may have been induced by the relatively unnatural conditions which prevailed

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(e.g. capture, etc.). It is quite possible however that the incisors are used to a certain extent during normal burrowing operations.

In contrast to Bathyergus however, both Georychus and Cryptomys employ their incisors to a much greater extent during digging while the forefeet are used mainly to clear the passages from loosened soil.

The tunnels or burrows are permanent constructions i.e.they are used over and over again. The main incentive for the extention of these burrows appears to be the acquisition of new feeding grounds where new and untapped food resources are available. The direction of tunneling is therefore possibly determined by the geographical distribution of the food supply, as well as by the prevailing conditions of the soil (texture, humidity, etc.)

On the average, the diameter of the tunnels of Bathyergus vary between 5-8" and are at least 7-8" below the surface of the soil. They are usually constructed in loose, soft soils. In the south-western Cape there are many areas consisting of loose, unconsolidated, sandy soil types (often in the shape of coastal sand dunes) and in these soils there is usually a high degree of drainage, especially in the higher lying parts. During the rainy season in the Western Province parts of the tunnel systems are often flooded and submerged and especially on the Cape Flats it is evident that the tunnels are constructed in higher lying land, less easily subjected to flooding. In many cases, these burrows appear on the sides of the relatively stationary dunes.

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As would be expected, the diameter of the tunnel in Cryptomys is far smaller, averaging 2-3". One also finds the tendency in this genus for construction of tunnel systems in higher lying ground. Compared to Bathyergus, the genus Cryptomys occurs in a much wider spectrum of soil-types - varying from loose sandy soils (e.g. vicinity of Pretoriuskop, Kruger National Park) to hard, stony soils (e.g. near Fountains, immediately south of Pretoria). No information is at present available concerning the diameter of the tunnels in the case of Georychus. It is expected to be more or less intermediate in size between those of Bathyergus on the one hand and Cryptomys on the other.

In a Bathyergus tunnel system there are not as many side tunnels (which may be called cul-de-sac's) as one finds in the tunnel system of Cryptomys. The scarcity of these side tunnels is a striking feature in the tunnel system of a dune mole-rat.

The excavated earth from the tunnels are heaped up on the surface (i.e. mole-hills) and they lie more or less parallel with the direction of the tunnel. However, it is not always easy to follow the direction of the tunnels in this way due to the fact that they often turn sharply to the left or to the right and the mole-hills then often tend to present a confusing picture. However, it is obvious that these mole-hills present a more or less straight line which may have certain curvatures. On closer inspection, it can be seen that these heaps are pushed up more or less in two parallel rows with the actual main tunnel lying approximately between them. The distances between these hills are not

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constant and are thus irregularly spaced, either to the left or to the right of the main tunnel (see Fig. 6.1).

The main tunnel has side branches leading to the surface of the soil (through which the excavated soil is pushed out) and which make an angle of approximately 45° with the surface of the soil. The excavated soil within the side tunnel immediately below the mole-hill is usually tightly packed, making the tunnel system air tight at that point. (This may not always be the case however). The mole-hills are large (depending on the size of the tunneler), and in Bathyergus are approximately 23" in diameter and about 12-15" high. The hills are far smaller in Cryptomys measuring approximately 12" in diameter and usually they are not higher than 8" in the case of Cryptomys hottentotus. In wet or damp soil, the soil is pushed out from the side tunnel in the shape of bundles, reminding one somewhat of toothpaste being squeezed out of a tube. The (more or less) solid bundles are clearly visible on top of the mole-hill where they usually dry out in the sun and in their shape they correspond to the size of the tunneler and consequently to the diameter of the tunnel. According to Eloff (1952, 211) the main incentive for tunneling (and consequently throwing up the mole-hills) - constituting the removal of excess soil from the tunnels - is to obtain food.

The way these side tunnels are constructed is excellently described by Eloff (1951, 142), and the following information has been paraphrased from that account.

The first contact the animal makes with the air on the surface of the ground is with its snout when boring the side tunnel until it ruptures the surface. After this, its hindquarters come into contact with the air on the surface of the soil frequently especially when the mole-hill is still in its initial stage, as the excavated soil is pushed outwards.

It is not known whether the juveniles are as efficient at tunneling or digging as the adult specimens. Occasionally (usually on higher lying territory) there are smaller mole-hills interspersed with the larger ones and which may represent the excavatory activities of the young.

Although it may be assumed that digging or tunneling is an instinctive adaptation in the bathyergids it is of interest to note that this activity does not commence before the animals attain a certain minimum age. Eloff (1952, 210) has found that juvenile specimens (which were taken from a nest) only developed an inclination for boring into the surface of the soil after approximately six weeks. This activity pattern was not observed before the animals attained this age. This implies that even in the absence of parents who could thus not condition their offspring as far as digging is concerned, they did so instinctively at a certain age.

The rate of burrowing is not known. This will obviously also be determined by soil conditions. However, based on my own experience, one locality was encountered (a <u>Bathyergus</u> tunnel system near Malmesbury) where three new heaps were thrown up during the night, extending the range of

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the tunnel by approximately seven feet. The volume of sand displaced by means of this activity was approximately 2 cubic feet (see Fig. 6.2).

The length of the tunnel system is determined by the geographical position of the nest, the distance between the nest and feeding grounds and probably also by the physical nature of the soil. A tunnel system of <u>Cryptomys</u>, which was opened by me (the H.B. length of the animal being approximately 120 mm.) attained a length of 60 feet, not taking into consideration the various side tunnels or parallel tunnels. The length of tunnels constructed by <u>Bathyergus</u> are very often much longer: I have followed and opened up such a tunnel system in the Citrusdal district for more than 250 feet without reaching any terminus.

The orientation of these animals below the surface of the soil has been investigated by Eloff (1951, 1952), and it appears that the main orientation mechanism occurs by means of echo localization. (See under orientation and sense organs, below).

Occasionally one finds a hole which leads directly to (into) the main tunnel: this aperture may be used by the animal when leaving the tunnel system to come out on top of the soil and which is not sealed off during its visit to the outside world. Why the animal leaves the tunnel system, is not known: an individual may be pushed out by others, or it may seek new foraging grounds. The latter alternative could evidently be done just as efficiently without leaving the tunnel.

The mole-rat's action when the tunnel system has been disturbed has also been described very aptly by Eloff (1952, 214). Assuming that the soil of the mole-hill is removed and that the side tunnel has been opened up, it will be seen that within a relatively short time the mole-rat (Cryptomys) will stick out its head so as to spy on its environment. It then goes back (reversing down the side tunnel) to fetch fresh soil in order to plug up the hole. In one specific instance Eloff and his co-workers opened up 12 side tunnels, which were all plugged between 9 a.m. and 2 p.m.

Eloff also investigated the manner in which the mole-rat detects damage to its tunnel system. These experiments were conducted in glass cages, filled with soil. On opening a portion of the tunnel system, e.g. a side tunnel, it will be seen that the mole-rat comes along in the intact portion of the tunnel in the direction of the opening. Occasionally a pumping action is executed by the entire body: the abdomen is flattened, as if the animal inspires: then the spinal column is curved, bent ventrally, and this action is repeated a half-a-dozen times or so. The animal then comes nearer to the opening and repeats these movements. Eventually, on coming below the opening the head is inserted into the opening of the side tunnel from the main tunnel and the animal moves up into the side tunnel. If a sudden disturbance is detected, the animal slips back down the side tunnel. This process is then repeated. Precise observations have shown that the animal reacts to a change in the pressure of the air within the tunnel system. The pumping actions apparently displaces a volume of air in the tunnel which goes up via the side tunnel. The inflow and outflow of air via the leakage is then followed up and the opening or leakage is thus detected. After having localized the damage, the animal then proceeds to fetch soil in order to plug the opening. The soil is then pushed out by means of the hindfeet, a few strong convulsions of the body is excecuted, and the soil fastened in position with the vibrations of the hindfeet which last approximately 1 second and which are excecuted at the rate of approximately 25 vibrations per second with a declining amplitude. In this way, the damaged portion of the tunnel system is repaired. Occasionally, the mole-rat also uses its head to stamp the plug into its final position. Sometimes, more than one mole-rat helps with the reparation of the leakage. In the field one finds that the repaired portion is plugged up to the extent of approximately 4 ft. This, according to Eloff (1952, 215) is evidently a defensive behaviour, for it complicates matters for the predator in localizing the tunnel.

While carting the soil to and fro (i.e. extending its run, or repairing a leakage in the tunnel system), it has been noted by Eloff (1952, 213) that Cryptomys cleans its fur between these trips by means of vibrations of the skin with a vibration rate of 20 tot 25 vibrations per second. In this way, soilparticles etc. are removed from the skin and pelage.

It has not yet been observed whether two individuals can pass each other within the tunnel. Mechanically, this should however be possible with mutual co-operation.

The/...

The soil in which the tunnels are constructed is often very damp and consequently it may be assumed to be damp in the tunnel as well. However, there is no information available about the relative humidity within the burrows. This would obviously vary with the local rainfall and other climatic conditions. Similarly, no data is available about the temperatures occurring within the tunnels. In view of the fact that the tunnel system is an isolated structure, it is not unreasonable to assume that a relatively constant humidity and temperature is maintained within the system.

No definite information is available as to whether the tunnel systems are communal runs i.e. whether both males and females occurring within one system, use the same tunnels. It does seem likely that this occurs.

Whether there is a difference in digging behaviour between the two sexes, and which sex is responsible for the actual construction of the tunnels, is also unknown.

A fact which is often overlooked, is that the farthest point of any tunnel system is usually approximately 12" or more beyond the last mole-hill i.e. the tunnel does not terminate immediately below the last hill.

The depth of the tunnels below the surface of the soil also depends to a certain extent on the physical condition of the soil and the availability of food. In one system of Bathyergus which I followed for a considerable length, the depth below the surface varied between 6" tot approximately 3'5". The actual mechanism of the digging movements of

Cryptomys has been observed by Eloff (1952, 211), under laboratory conditions. These mole-rats were kept in glass cages filled with damp soil and in view of the fact that they often tunneled close to the inner surface of the glass their mode of digging could be observed.

It was observed that the animal bores with its lower incisors, which have a certain degree of mobility because the two hemi-jaws are not ankylosed at the symphysis. The frontfeet are used to push away the loosened soil, using the frontfeet alternatively, up to 25 movements per second, until a small heap of soil is formed below the animal. The hindfeet continue this action until the soil is behind the animal. Assuming that the mole-rat has completed the construction of a side-tunnel leading to the surface, the mole-rat maintains its forwardly directed digging as explained above. After the soil has been concentrated behind the animal, the animal reverses, pushing the soil out via the side tunnel with its hindquarters emerging a short distance on top of the surface of the soil. While walking backwards, the lower incisors are pushed into the soil of the bottom of the tunnel, especially when pushing the soil up the incline of the side tunnel. After a number of similar trips it is then seen that a number of shorter movements are executed by the hindquarters, followed by a vibratory movement of the hindfeet against the lower surface of the excavated soil. These vibratory movements last approximately one second with a speed of 25 to 30 vibrations per second. These vibratory movements have a specific physical meaning, i.e. securing each particle of soil which has been excavated and which closes up the side tunnel. The mole-hill covering the aperture of the side tunnel is thereby prevented from caving back into the side tunnel (especially when the soil is dried out by the sun) and similarly, it makes the tunnel system airtight at that point.

Nests

Very often, nests occur more or less at the one end of a tunnel system and all other tunnels leading from such a nest usually converge at the feeding grounds. In one case however, (in the vicinity of Citrusdal) I opened up a tunnel system of Bathyergus and it appeared that the nest was situated more or less in the middle of the home range, with feeding grounds to the left and right of the tunnels (Fig. 6.3). Consequently, these nests are not always terminally situated in a specific system. No firm generalizations can be made therefore concerning the geographical position of the nest. According to Roberts (1951) the nests often occur in higher lying ground but this is not always the case. A Bathyergus nest recovered from the banks of the Olifants River in the Citrusdal area, was actually located within a trough and would easily be flooded, if the drainage of the surrounding soil was not sufficient. The nest of Bathyergus, constructed from roots, leaves, etc. (i.e. vegetable matter from the immediate surroundings) is built in a nest chamber, approximately 15" in diameter, and usually at least 24" below the surface of the soil. There are various tunnels leading to and from the nest and in one specific case, the nest was not very much deeper than the tunnels leading to the nest.

Two/...

Two nests of Bathyergus, which I have managed to acquire, were not appreciably deeper down than the tunnels. Nor did the tunnels approach the nest with an irregular spiral, as is the case in Cryptomys (de Graaff, 1962, 158) where the nests are situated at a deeper level than the tunnels of the tunnel system.

The nests are constructed entirely from vegetable matter as indicated above and all these roots, leaves, bracts, etc. are intertwined so that a round structure is obtained, which fits more or less snugly in the surrounding nest chamber.

It is not certain how Bathyergus uses this nest within the nest chamber. We do not know whether it (or they) get on top of this structure or whether it gets into this mass of vegetation and whether the circular shape of the nest is retained by the size of the surrounding nest chamber. A nest removed from a tunnel system was put into a plastic bag: a captured Bathyergus eventually bit its way through the plastic bag and went to lie inside this mass of vegetation. It is however not known whether they do so under normal circumstances.

It may further be emphasised, that these nests are not easy to obtain, due to the great amount of physical work involved in excavating this structure.

Activity

It has been observed that Bathyergus is far more active during the rainy season in the Cape (i.e. winter rainfall area) compared to the dryer, less humid periods of the summer months and a general impression is gained that these animals, i.e. the bathyergids, are more active after rainfall. This

seems/...

seems obvious, for after downpours the soil is softer and easier to dig through. In addition (at least in the western Cape), these tunnels are often damaged by flooding or by sagging in of the roofs of the tunnels etc., which may induce the animals to greater activity. Good soaking rains will often damage the tunnels leading to the feeding grounds while the nests (often, not always) lying on or in ground with a higher level, are not damaged. In the drier periods (i.e. the summer months) this is generally not the case, and therefore less activity may be expected.

As has been indicated above, the daily activity rhythmn is not known and consequently it cannot be stated how much time is spent burrowing, sleeping, etc. Instances are known where the animal walks around on the surface of the soil in broad daylight. I have obtained one such a specimen of Bathyergus in the Citrusdal district at 13.00 hours on a clear sunny day. The reason why the animal leaves its tunnel system is not known: whether they are ejected by other individuals after fights, or whether foraging for new food reserves, or collecting nesting materials. However, certain indications point to a greater amount of activity (i.e. burrowing etc.) occurring at dawn or at sunset. This may imply that they are lying still during the warmer periods of the day. It should be borne in mind though, that the differences in temperature, humidity, etc., occurring within the tunnel system is of a low order.

Locomotion

The individual movements executed by each limb during locomotion have not yet been analysed.

On/...

On the surface of the soil, the animals create a so-called 'club foot' impression i.e. the front feet (hands) are turned inwards to a certain extent, with the major portion of the weight resting on the outer edge of the hand or pulse. When walking on the surface, they walk stuntily, with a 'wobbly' motion. Based on my own experience, it appears that they do not walk long distances uninterrupted: i.e. they stop often (after perhaps two or three feet) to investigate their surroundings. This frequent stopping may also be correlated with the fact that for orientation (in any case within the tunnels and probably when on the surface of the soil as well) the animals use echo-localization, (ref. Eloff, 1951, 1952) in view of the fact that their sense of sight and possibly of smell seem to be rather poorly developed. Sclater (1901, 73) states that on the surface of the ground the powers of locomotion in <u>Bathyergus</u> are somewhat limited.

On the other hand, these animals are apparently exceedingly agile when fossorial conditions are prevalent (i.e. when occurring within the tunnel). The whole tunnel system reminds one somewhat (in a modern sense) of an underground railway system. The actual speed which can be attained below the surface of the soil is not known. However, on opening up a portion of the tunnel system, and awaiting the animal's reaction, it becomes clear that they can turn around with lightning speed to retrace their steps.

At present, there is no information available whether these animals are good swimmers or not. However, it seems fairly safe to assume that they

would/...

would be able to cope with emergencies, for all animals have an innate capacity for swimming whenever the need arises. The ability to swim would undoubtedly be an asset especially during certain months of the year when the tunnels tend to be flooded to a certain extent in the western Cape Province. On the other hand, the possibility exists that they may sense the danger signs instinctively, and without prior warning will move to higher lying ground.

The orientation of the mole-rat below the surface of the soil is intimately bound up with its habitat and surroundings. Therefore, the next aspect to which attention is briefly directed is the question of orientation.

Orientation

More information is available concerning this ethological aspect of the bathyergids, than of other facets of their behaviour. This is largely due to the very interesting work done by Eloff (1951, 1952) on the behavioural aspects of Bathyergus and Cryptomys. Although it appears that Eloff concentrated more on Cryptomys as far as ethology is concerned, the same general and overall results seems to be applicable to Bathyergus as well, with certain minor deviations. Damage to the tunnel system may be caused by several factors "..... the most important of which are large and small Ungulates, rain, dogs and man". "In this manner, tunnel damage may be a daily occurence where cattle and horses are grazing. A tunnel may be damaged to such an extent that, for fairly long distances, it cannot be used.

However,/...

However, where such damage occurs in connection with mole systems, a proper connection between even widely separate undisturbed tunnel systems is effected in a remarkably short time and correct manner, while at the same time, the mole displays highly developed powers of orientation. No matter how severely damaged these tunnel systems may be, either cutting off the moles in the veldt from the nest or _vice versa_, these animals reach their goal unfailingly without trial or error." (Eloff, 1951 a, 1001).
Eloff (_loc.cit._) may be quoted as far as the actual description of the experiments are concerned: "Briefly, the experiments were conducted as follows: (a) In one set of experiments a tunnel was opened up for a certain distance, for example, fifty feet from its terminal portion in the veldt; (b) in another set of experiments the tunnel was opened up between nest and veldt terminus; (c) in still another set of experiments the tunnels radiating from the nest were opened up all around the nest for some distance veldtwards."

Although these circumstances described above, are applicable mainly to _Cryptomys_, Eloff states that this orientation capability also applies to _Bathyergus suillus_ e.g. in experiment (b) above, the mole-rat, after "plugging one opening, bored another tunnel parallel to the portion opened up, connecting up correctly with the remaining intact portion, the opening of which was then also plugged" (p. 1001). "This process of boring parallel to destroyed tunnels has been observed to be repeated as many as twelve times."

The ability of these animals to orientate themselves without the sense of sight is therefore remarkable. Eloff (1951) has shown that these animals can overcome obstacles such as extensive damage to their tunnel systems in a characteristic manner "... and will do so even after some months of hard labour and continual hindrance" (p. 136). It is interesting that it was found that individual mole-rats react differently to these hindrances: e.g. some individuals (when recent tunnels have been opened up) will keep as close as possible to the original route, "... resorting more and more to burrowing under tunnels previously opened up. Others do not bore quite so near to the recent tunnel and therefor do not need to burrow under existing tunnels. Also some plug the tunnel-ends nearest to the nest more often than others do and for longer distances. Some deviate to the right only, some to the left only and others to either side." (p. 136-137).

Based on this type of experiment mentioned above, "... no matter whether the tunnel was disturbed at the far end, at the nest end, or in between veldt and nest, the mole always showed a remarkable urge and ability to orientate itself. If disturbed in the veldt the mole ran back, but then there was such a strong urge to tunnel in the original forward direction that disturbing its work a dozen times during two months and involving roughly 200 ft. of repeated tunneling would not prevent it persuing that direction. Eventually, after two months it reached its original veldt-locality! Several other investigations of this type corroborated this observation.

It is clear that the mole's urge to reach its nest for protection should be strong. Especially when it is disturbed it seeks protection **nestward** or in its nest. Similarly the **drive** veldtwards in search of food is strong. The problem of orientation is, however forced on one's attention. An explanation must be found on existing sense organs and on instinctive adapatation **to** the environment." (Eloff, 1951, 140).

Such an explanation seems to indicate the animals's sensitivity to air currents and its sense of hearing. As the present author has noticed, and as is well known from the existing literature, there is no external stimulus to which the mole-rat is so sensitive as to a current of air. Other types of stimuli hardly ever evoke a more violent reaction, and it is quite feasible that this **reaction** plays an important part in the life and habitat of the animal. The animals usually plug openings in their tunnel systems very rapidly. I have seen this time and again in the field, both in the case of Cryptomys and **Bathyergus**. For instance, when a tunnel was opened in a system of Bathyergus in the Citrusdal district, the animal came to investigate after only two minutes had elapsed.

As Eloff (1951, 142) states quite correctly, the wind directions at any given time of the year at a certain locality are fairly constant. On the other hand, certain minor local differences may **arize** e.g. where a certain type of shrub grows year after year, where there are trees, and other factors, e.g. stones and rocks of varying size, causing changes in airpressure and movement. Keeping in mind the animals sensitivity to air currents it is possible that the animal uses the side tunnels leading to the surface of the soil, or the mole-hills as gauges of the surface air condition "... and especially of the permanent conditions. These may provide his cues for orientation from moment to moment....". In addition, the mole-rat may use all his other available senses (p. 143), especially "... the kinaesthetic, smell and hearing". Furthermore, its orientation in space is probably enhanced by repetition, for these tunnel systems are permanent structures, being used over and over again, and therefore it becomes familiar with its run "... with almost mechanical precision". It is also known that these animals live in a certain locality for many generations so that it is possible that fixed sources of sound or noise may provide cues. Eloff then concludes (and which is an acceptable conclusion) that an explanation of the orientation behaviour must be looked for in a combination of senses and factors such as sensitivity to air currents and the use of its auditory apparatus.

Sense organs

From the facts given on the preceeding pages, relating to the orientation of the mole-rats below the surface of the soil, it is evident that these animals must have a well developed sense of hearing. The other sense organs need to be discussed briefly as well.

The opinion is generally held that the mole-rats are able to see for short distances and that they are able to distinguish between light and darkness (Shortridge, 1934, 322). This opinion is also held by Sclater (1901, 73) who states that Bathyergus can make use of its eyes to a certain extent.

Shortridge/...

Shortridge (1934, 323) states that the eyes in Cryptomys, although minute, are ".... wide open, prominent, and apparently not altogether functionless; if one moves a finger or a stick gently in front of a captured specimen, it follows the movement with its head, although it may merely sense some slight air disturbance: on the other hand it twists its head as if to peer around in a short-sighted manner, the presumption being that it can see indistinctly for a few inches". (Shortridge, 1934, 323). In addition, many farmers also believe that the animal is not quite blind, for if a stick be pointed near its snout region, it reacts (Eloff, 1958, 293).

It is doubtful whether the sense of sight is of any importance, in view of the fact that the animals live in pitch dark tunnels. Eloff (1952, 218) could not demonstrate any sensitivity to light in the eyes of the mole-rats which were kept under laboratory conditions. Furthermore, specimens of Cryptomys do not shun the sides of the glass cages with light passing freely into their tunnel systems (Eloff, 1958, 295). He also subjected Cryptomys and Bathyergus to bright flashes of light thrown on their eyes when these animals were kept in darkness, yet this evoked no reaction at all. Blinking of the eyes is evoked by brief and slight currents of air blown on to the surface of the eye. Eloff also mentions the interesting fact that occasionally Cryptomys specimens with healthy but fused eye-lids are obtained in the veld. These mole-rats are apparently normal in all respects, e.g. weight, health and behaviour, which shows that the absence of sensitivity to light had no adverse affect on them.

Furthermore/...

Furthermore, experiments trying to condition the animals to light, failed after several hundred combined presentations of conditioned and unconditioned stimuli (light and a jet of air respectively) whereas"... in control experiments they became conditioned to heat even after 25 combined presentations of heat and a jet of air" (Eloff, 1958, 295).

On the surface of the soil both <u>Cryptomys</u> and <u>Bathyergus</u> may walk about with closed eyes and only tend to open them when they become excited. Eloff found that young mole-rats used for maturation studies also showed no sensitivity to light, while their general behaviour gave no indication of even the feeblest type of light sensitivity.

It is clear that the high sensitivity of the snout region and the cornea of the eye to air currents, sufficiently explains ".... how this blind animal so correctly detects perforations of its burrows or nests" (Eloff, 1958, 294).

Based on the laboratory investigations by Eloff, it is possible to state that the sense of smell in the mole-rats is poorly developed. The animal can not locate food, or members of its colony with the aid of smell (Eloff, 1952, 218). It is stated (Eloff 1951, 140) that its sense of smell is apparently not much higher developed than its sense of sight. While working out loosened soil in the veldt it does not react to the presence of a person coming very close to its body. "Also behaviour during courtship shows that smell is of minor importance."

On the other hand, it is now known that the mole-rat's sense of hearing is well developed al-

though/...

though there seems to be a total disregard of distant noises, no matter how intense. However, it reacts to nearby auditory stimuli "... which signifies probably a sensitivity only to stimuli of direct biological meaning to the mole" (Eloff, 1951, 141). These noises include teeth-grinding noises, squeaky noises and vibrations (e.g. those caused by walking). The importance of the sense of hearing in the mole-rats has already been commented upon above.

The sense of touch is apparently delicately adapted to its mode of eating, and it is possible that the sense of touch, together with the kinaesthetic sense play an important part in connection with the animals easy movements within the tunnel system. As an example, it may be quoted that the "... bend from the main to the side-tunnel is followed backward with great precision, sometimes with no visible touching of the walls" (Eloff, 1951, 141).

Facilitating the sense of touch, mention must be made here about the well developed vibrissae which all the genera possess, together with the stiffened, bristle-like hairs which are to be found on the outer lateral surfaces of the front- and hind-feet. Added to this, one also finds longer hairs in the dorsal pelage in all three genera and which may also serve a tactile function, so that it seems as if the tactile sense is well developed. The vibrissae, in conjunction with the incisors (which bite into the bulbs) are employed during the localization of bulbs for feeding (Eloff, 1952, 213). Similarly, it is stated that its mate is also recognised by the sense of touch (p. 219). Tactile stimuli which are applied to the body of the mole-rat in a careful and calm way, evokes no reaction (p. 223).

Voice

When these animals are captured, they usually give ".... vent to a series of grunts" (Sclater, 1901, II, 73) accompanied by a savage and threatening attitude. This applies to Bathyergus, Georychus and Cryptomys. On being irritated by a current of air ejected on to its body, it "very often utters a low grunt" (Eloff, 1951, 142). This has been found in the case of Cryptomys. Grunts, however, are not the only sounds these animals can make: I have kept a number of Cryptomys specimens in captivity and during their sojourn in captivity they often 'communicated' with each other by means of a series of high-pitched squeaks.

In the case of Bathyergus, Moseley (1879) also described the angry, half-snarling and half-grunting noises these animals emit on being captured.

Food and Feeding

There are possibly two main factors determining the geographical distribution of the mole-rats: firstly, the physical condition of the soil and secondly, the availability of the food supplies. Both these factors may prove to be interdependent.

Food is evidently located by searching within the soil by means of tunneling (and thereby extending their ranges), or by foraging on the surface of the soil, especially at night. The former alternative may however be the more correct interpretation. The localization of food by means of extentions of the tunnel systems is probably facilitated by the sense of touch. Eloff (1952, 213) maintains that the food is detected by tooth pressure, in addition to its tactile sense, which is apparently well developed in the snout and submental vibrissae region (Eloff, 1958, 295). In one experiment, dummy bulbs were made of plaster of Paris and surrounded by dry husks of Homeria bulbs which were readily taken and pealed, but not nibbled. "A fresh bulb may be in full view, but if it is not touched with the snout or the submental vibrissae it is not taken" (p.295). I have found exactly the same type of behaviour in a Cryptomys specimen which was fed with carrots. The animal would stumble along on the surface of the soil in its cage, and in view of the fact that the ventral border of the mandibles are usually kept close to the surface of the soil, would react only if the food were touched by its submental vibrissae. It would jerk back its head and body and then reinvestigate the object, before commencing to eat.

In the field, the tunnels leading from the nests all apparently radiate in the direction of the food reserves.

As would be expected, these mole-rats are entirely vegetarian in their feeding habits.

As far as I am aware, these animals have not yet been observed in the wild during the process of eating and the information which is available has been unravelled by Eloff (1952, 213). The depth of the tunnels usually correspond to the depth of the bulbs in the soil (at least at the feeding grounds). Under laboratory conditions, Eloff has made the following observations on the feeding method of Cryptomys:

On/...

On encountering a <u>Homeria</u> bulb (which is localized by smell (possibly) and tactile sense (tooth pressure, as was mentioned above)), all interest in burrowing activity is lost and the connection of the stem of the plant with the bulb is severed by a snip of the incisors. By means of the incisors, the husks are then removed. This procedure is done at a rapid pace, but exact observations have shown that this activity is also accompanied by rapid vibrations of the hands. Firstly, these vibrations follow each other rapidly and secondly, during these vibratory movements of the hands the bulb is held by means of the incisors. As soon as the husks are removed, to the satisfaction of the eater, these vibrations only occur in exceptional cases. These vibrations are important in loosening the husks from the bulb and are often executed at more than 30 vibrations per second. The vibrations of the hands occur alternately, while the vibrations executed by the hind-feet in ramming new soil after reparation to a perforation in a tunnel system (as described above) occur simultaneously. Having removed the husks from the bulb, the animal commences nibbling with its incisors and chewing with its molars, at a speed of approximately 10 movements per second, occasionally accompanied by a vibration of one or the other front leg. According to Eloff, the mole-rat's reaction to eat is so strong, that if captured and presented immediately thereafter with a bulb, the animal viciously grabs the bulb and commences to eat the bulb.

I have also kept a number of specimens (<u>Cryptomys</u> and <u>Bathyergus</u>) alive in captivity, and observed the same type of feeding behaviour as described by Eloff. However, no vibratory movement of the hands were seen in the case of Bathyergus. Based on my own experience, the following information may be added in connection with the feeding behaviour of Cryptomys under laboratory conditions:

The animal (a male) was fed regularly every day with at least one carrot, and on this carrot diet it lived for a number of months. Before presenting it to the animal, the carrot was usually sliced into discs approximately 1½" to 2" thick. At feeding time (usually at 8.30 a.m.) the specimen was usually restless and agitated but after the sliced carrot was supplied and the initial excitement had decreased, the first contact was usually made with the submental vibrissae. It would then grab a slice with its incisors and commence with the vibrations of the front paws. It would nibble round the circumference of the carrot slice, as if pealing off the outer thin layer of skin. (This action is possibly similar to the movements seen in the case of Cryptomys removing the husks from the bulbs). As soon as the slice was picked up, the neck would arch backwards for a second or so, suspending the food in the air for a short while. It would then walk around with the food in its mouth and settle down on the surface taking the food between its fore-feet. It assumed a sitting or squatting position, hind-feet wide apart, the stumpy tail used as a small stilt. It could well be that these vibratory movements are intended to shake off any additional particles of grit or sand clinging on to the food or on to the soles or between the fingers of the hand. This may well be so, for Shortridge (1934, 322) states that he has never found sand in the mouth of Cryptomys and "nor are the teeth worn in the manner that might be expected if the teeth were habitually used for biting through grit". Finally, the description of Grant (quoted in Shortridge 1934, 324) may be mentioned: "In captivity (i.e. the mole-rats) when feeding they often sit up on their haunches and hold the food in the fore-paws like ordinary rats and mice".

Eloff (1952, 216) states that food is hoarded especially during the winter months. The bulbs are apparently carried between the incisors (the lower ones being free to move apart), ensuring a better grip (Roberts, quoted in Shortridge 1934, 325).

The question of storing food in special chambers has been mentioned by various authors. Dreyer (1910, 4) states that all the genera have the habit of storing their surplus food in specially constructed "storage chambers". He states that the stored tubers and bulbs are prevented from growing by previously having their "eyes" (buds) eaten out. Fitzsimons (1919-1920, 149) states that the bulbs have the tops carefully bitten off to prevent them from sprouting. "When potatoes are available, all other forms of diet are neglected, and entering the potato fields, these destructible rodents carry off the tubers to their subterranian retreats and store them up. The crafty little fellows are well aware that in the moist earth the potatoes would soon begin te sprout, so, to prevent this, the buds or eyes of the tubers are carefully nipped out."

Bishop/...

Bishop (1948, 3) states: "Die kos word in spesiale kamertjies weg van die hooftonne (1), gewoonlik twee voet of meer onder die grond, opgeberg. Op hierdie wyse bou die mol 'n goeie voorraad op vir tye wanneer gewasse skaars is".

In the case of Georychus, Roberts (1951, 382) states that the bulbs are usually carried to a storage chamber in some high ground close by. Similarly, for Cryptomys Roberts (p. 384) maintains that they all have the same habit in common of forming a large chamber for the storage of bulbs as a reserve for consumption, "when the feeding grounds are waterlogged or when the soil is too hard for facile burrowing; but one species is known to make a practice of feeding upon certain large tubers (presumably not storing bulbs in that case), nibbling off each day as much as it requires, and another species is known to make large mounds for the storage of bulbs above the flood level of the karroo plains. From the storage chambers, which are normally situated in higher ground that is not likely to be flooded tunnels are made in any and all directions for the purpose of finding bulbs; .....".

On the other hand, Shortridge (1934, 319) poses the question whether Bathyergus does store up food. He concludes from the freedom of movement of the lower jaws of Georychus and Cryptomys that this enables these genera to obtain a better grip on the bulbs which are carried along the tunnels to the storage chambers. In Bathyergus, the lower jaws are ankylosed and "possibly, therefore, Bathyergus does not store up food?". It thus seems that this question of storing food is not yet entirely settled,

and/...

and for that matter it may be said that I, although having opened up and dug out many a Cryptomys from its system (in addition to nests), have not yet come across these so called "storage chambers".

The food eaten, is apparently not chewed very thoroughly. According to Tullberg (quoted in Landry 1951, 71) the bathyergids (Georychus and Bathyergus) do not chew their food very much for large pieces of roots (up to 10 mm. in length) have been found in the stomach.. This has also been seen by me in specimens of Cryptomys captured in the Kruger National Park where portions of roots, bulbs and succulent rhizomes measuring 7-8 mm. in length, were found in stomachs.

Concerning the actual plants which are eaten, some specific data is available. Eloff (1952, 211, 1958, 294) states that Cryptomys specimens especially select Homeria and Moraea (both of the family Iridceae), and in the absence of these, Cyperus-bulbs (family Cyperaceae). As far as Georychus is concerned, Sparaxis grandiflora bulbs (family Iridaceae) and Zantedeschia (Richardia) (family Araceae) tubers are readily eaten (Dreyer 1910, 6, Sclater, 1901, II, 76). Furthermore, they are apparently especially fond of potatoes.

The plants eaten by Bathyergus are less precisely known, and in the existing litereature it is stated that they feed "on roots and bulbs" (Dreyer, 1910, 5, Sclater, 1901, 73).

Shortridge (1934, 325) states that the food of Cryptomys consists mainly of bulbs, tubers, and other roots, especially bulbous grass-roots. Roberts has also found fragments of Aloe leaves in Cryptomys

burrows/...

burrows. "Only certain kinds of bulbs are eaten; others appear to be occasionally attacked (as, in gardens, agapanthus, onions, dahlias). In Kaffraria, a small species of blue iris (Moraea), known as 'tulp', which is extremely poisonous to cattle, seems to be preferred above almost anything else by C. hottentotus. In consequence, this iris and many other indigenous bulbs are difficult to propagate in local gardens."

Roberts (quoted in Shortridge 1934, 325) states that the diet in Cryptomys consists exclusively of vegetable matter like grass roots and bulbs and that they are troublesome in consequence where potatoes and other tuberous crops are cultivated, especially where the animals are plentiful. It may also be that in South West Africa Cryptomys feeds on Pseudogaltonia (family Liliaceae) (Shortridge, 1934, 321).

Finally, Bishop (1948, 2-3) gives an interesting account of the plants eaten by Georychus and Cryptomys: "Hierdie knaagdiere vreet 'n groot verskeidenheid van wortels en knolle, en is besonder lief vir tuingewasse, soos aartappels, patats, geelwortels, witwortels, uie, die wortels van pieterselie, blaarslaai, angeliere en baie ander blombolle".

Before leaving the subject of food, the following interesting observations are worth mentioning. Normally these animals are herbivorous, but Fox (quoted in Shortridge 1934, 325) found that Cryptomys species occurring in Northern Nigeria will eat earthworms greedily, although they show no partiality to insects. On the other hand, Barret-Hamilton has found white ants in the stomach of

C.hottentotus/...

C.hottentotus while Shortridge found the hard heads of cockchafer larvae in the stomachs of C.hottentotus on one or two occasions (Shortridge, 1934, 325).

An important aspect of feeding is the animal's water requirements. In captivity they do not seem to show any interest in water even if it is presented to them. Fitzsimons (1919-1920, 155) states that the mole-rats even occur in the centre of the Kalahari desert, "where their mounds may be found at least a hundred miles from water". A feasible explanation is that these animals obtain their necessary water from ingested food (bulbs, etc.) as well as in the form of metabolic water.

The possible influence of the nature of the diet on the animals has been mentioned by Roberts (1951, 385). In Southern Africa, some species e.g. C. hottentotus and C. damarensis have a wide distribution with little local variation in phenotype. "The habits of the species are such as to confine them to small areas where food is plentiful and when this food differs, new forms have evolved, where as when the food remains much the same over great tracts, such as the Karoo or the Kalahari Desert, little change takes place".

Social life

As far as Cryptomys is concerned, it has been stated by Eloff (1951, 142) that there is no actual group life, for the tunnels do not allow a number of mole-rats to be together boring for food. On the other hand, in the later publication, Eloff (1952, 215) states: "Daar word gewoonlik gemeen dat die mol 'n alleenloper is. Dit is egter foutief.

Die mol leef in klein kolonies van ongeveer ses of meer in 'n gemeenskaplike nes". The latter statement seems to be the correct interpretation.

It is well known that one specific tunnel system can ramify into a large number of tunnels, but hitherto, it is accepted that each tunnel system has only one nest. These tunnel systems are also sometimes called colonies and I have in my possesion a collection of Cryptomys specimens from the Witbank district consisting of six female specimens and one male specimen, all from the same colony. Furthermore, six specimens obtained from the Kloof district, Natal, all come from the same burrow. It is therefore evident that these animals are not solitary beings and do lead a certain degree of social life, within a tunnel system.

It is interesting to note that animals coming from different tunnel systems act very aggresively towards each other and are instantly ready to fight, whether they are of the same or opposite sexes. On the other hand, on capturing specimens from the same tunnel system, these specimens get on together very well indeed. Similarly, in the case of Bathyergus, they do occur in tunnel systems which contain more than one specimen. This evidence can be deduced from information on museum labels.

When two specimens of Bathyergus were captured in the Citrusdal area, coming from two different colonies, I put them together in a container, at approximately 15.30 hours and immediately they started fighting. They were both males and the one specimen got hold of the other's nose and

inflicted/...

inflicted a relatively minor injury. Yet, immediately after this brief fight, the hurt animal behaved in a different way, and before nightfall the injured specimen died, probably as a result of its injuries. It is known that the naso-oral region is of the utmost importance to the bathyergid individual and it thus appears that even the slightest (or apparently so) injury may develop into a lethal injury.

Similarly, in the case of Georychus, when placed together in captivity, they instantly fight. A short account of this aspect is to be found in Fitzsimons (1919-1920, 150). They invariably damage each other so severely that both (often) succumb to the wounds inflicted by the enormous incisors. "Often the victor devours portion of the victim".

Roberts (1951, 385) has raised a number of interesting points about the social organization of Cryptomys. "Firstly, that the younger animals are usually first to be trapped, but when the traps are left in the same places for several days thereafter, the older animals are then caught; this suggests that the older animals drive out the younger ones to forage and bring back food to the storage chamber, so that they can subsist without the labour of burrowing. Secondly, on a number of occasions, only males have been trapped in single colonies, which seems to point to segregation of the sexes of the males at certain times." On studying the information on the museum labels in a large series of specimens, sufficient data is still lacking to confirm these statements positively.

Symbionts/...

Symbionts and Commensalisms

An interesting case of symbiosis which has come to light during the researches by Eloff (1952, 223, 1958, 293) is the fact that Cryptomys shares its tunnel system (and possibly its nest) with the frog Cassina senegalensis. Before these facts came to light, it was not known where these frogs retreated when the pans dried up during winter. On opening the nests and tunnel systems, it was found that these frogs inhabit the tunnels. Within the nest there are insects, grubs, etc. which may provide food for the amphibian. In addition, in the tunnels, there is a certain humidity and warmth, for if the frog is deprived from humidity, it shrivels up and dies. On one occasion, Eloff found no less than 15 frogs in one nest. The mole-rat, which normally bites and snaps violently whenever an object touches its body, does no bodily harm to the frog. This is probably due to the fact that the movements executed by the frogs are slow and gradual and therefore evokes no reaction on the part of the mole-rat. Incidentally, the frogs evidently reach the nests via the tunnels, which are constructed in the direction of the edges of the pans where Homeria bulbs are abundant.

Another interesting observation is made by Shortridge: in the case of Cryptomys he often found white ants inhabiting old Cryptomys mounds and ".... which may on such occasions form the nuclei of ordinary ant-hills" (1934, 322).

In the nest of Cryptomys, I have come across the larva of Gonopus (Coleoptera, Tenebrionidae) in the Kruger National Park, while in the Kalahari

Gemsbok/...

Gemsbok Park, lizards (Mabuia sp.) and scorpions (e.g. Opisthopthalmus pictus, O. wahlbergi, O. carinatus and Parabuthus granulatus) were encountered in or near the tunnel systems of Cryptomys damarensis.

Reproduction

Detailed aspects of courtship behaviour under natural conditions are not known, and the act of mating has not yet been observed. Furthermore, it is not known whether the males are monogamous or polygamous. The latter seems to be the most likely alternative.

Some indication of courtship behaviour in Cryptomys has been described by Eloff (1951, 140-141), under laboratory conditions. "The animals often run against each other, whereupon the fierce female immediately charges, the male producing squeaky 'pleading' noises which cause the female to behave quite differently, e.g. walking in front of the male lifting up one hindleg. However, the mole's nose is then kept near the female's external sex organ in the characteristic male animal fashion. Much more intensive work must be done in this connection". Personally, I observed exactly the same pattern of behaviour in captured specimens obtained in the Shingwedzi district in the Kruger National Park.

It has already been mentioned that the respective pairs apparently recognize each other by means of their tactile sense and possibly by means of smell, although the latter sense does not seem to play a very important role in mate recognition.

In the genus Georychus the males are usually equal in size to the females, while the

females/...

females are usually smaller than the males in other genera. However, in Cryptomys there are many instances where the sexes are of the same size. In the case of Bathyergus however, the males are usually definitely larger than the females.

The oestrus cycle of the female has not been determined for any of the three genera. It is probable that they are monoestric annually and that mating occurs towards the end of winter in the case of Bathyergus. In this genus the greatest number of foetuses found in pregnant females were three: these specimens are housed in the South African Institute for Medical Research, Plague Division. In two females there was one foetus in the right uterine horn and two in the left. The weight of one foetus equalled 5 grams and the maternal specimens were trapped on the 18th and 20th of August 1954 respectively. Mating therefore must have occurred some weeks earlier, i.e. towards the end of July.

In another Bathyergus female remnisces of placentae which were retained could be demonstrated. In this case the distribution of young was 3/1 i.e. three foetuses in the left, and one foetus in the right uterine horn. This animal was not pregnant when trapped i.e. the placental scars were relicts of the previous breeding cycle.

As far as Cryptomys is concerned, Shortridge (1934, 325) collected two females, each containing five foetuses from the Grootfontein district, South West Africa on April 26th. He also suspects that the mole-rats have a fixed breeding season.

Actual embryological data about the bathyergids is not yet available e.g. there is no indication of the length of the gestation period.

Smears made from the testes of Bathyergus specimens indicated ripe sperms on the 10th of July 1954 and the 10th of August 1954. This then also points to the possibility of sexual activity towards the end of winter in the south western Cape.

Theoretically, it would be possible for a Bathyergus female to have a litter of six, for the number of mammae usually consist of two pairs pectoral and one pair inguinal (=6), but cases occur where there are two pairs inguinal (Roberts 1951, 382). As far as Cryptomys is concerned, litters of six are known to occur (Eloff, 1952, 210).

Nothing is known about the post-natal development and aspects of parental care as far as the three genera are concerned.

According to Eloff (1952, 211) the genus Cryptomys will propagate quite readily under laboratory conditions as long as a sufficient supply of Homeria bulbs are available.

According to Thomas (quoted in Shortridge 1934, 326) the mammary formula of Cryptomys appears to be always six as indicated from spirit specimens from all localities in the British Museum. On the other hand, Roberts states that in the plateau area of the Transvaal he has never found any of the forms of Cryptomys with inguinal mammae, the two pectoral pairs only being present. According to Shortridge (1934, 326) the pectoral mammae are nearly always longer in C. damarensis than the inguinal mammae for they are apparently used more often. The inguinal mammae are often under-developed in immature breeding females ".... although doubtless coming into use with age when full litters are produced. It is suggested that the inguinal mammae may be absolescent in species of Cryptomys." Roberts (quoted in Shortridge) recorded a specimen of Cryptomys with eight mammae (2 pectoral, 4 lateral, 2 inguinal) but suggested that the additional lateral pair may be abnormal.

It is no easy matter to distinguish the sexes externally in many forms of adult Cryptomys specimens. The testes of the male may descend during the breeding season, as in rats. The females (indicated by large mammae), often start breeding before reaching maturity (Shortridge, 1934, 327). It is not exactly known how long the young remain in the nests, although Eloff has stated that only after six weeks or so, do they show any inclination for digging. Eloff (1951, 141) speculates on a number of reasons why the young mole-rat starts boring away from the nest. In the first instance, it may be to search for food, for after weaning, this would be a necessary requirement. Secondly, it may thereby be starting a new system, leading eventually to the animal having its own nest.

Physiological

An important physiological activity in any animal's life is the act of sleeping. The bathyergids tend to sleep in an upright position (as observed under laboratory conditions) with the head tucked between the front legs, close to the chest. This sleeping attitude has been observed by me in

both/...

both Bathyergus and Cryptomys. It is however not known how much of each day is spent sleeping, either in Bathyergus, Georychus or Cryptomys, under natural conditions. An answer to this question can not be given until modern techniques (such as radio-active tagging) are applied.

The bathyergids are very sensitive to fluctuations in temperature. Eloff (1952, 218, 1958, 295) has also discussed this aspect. By means of a specially constructed activity wheel, experiments were conducted to test the possible negative or positive behaviour towards such contrasting stimuli as (i) cold on the one side and heat on the other side of the experiment and (ii) a current of air on the one side and absence of a current of air on the other. In this way it was found that in the case of Cryptomys, a temperature difference of 2°C was discriminated, preference being given to 21°C as compared to 19°C.

Similarly, I have kept captive specimens alive under laboratory conditions. A heater had been burning round the clock under the table on which the glass cage containing a specimen of Cryptomys stood. In this way, the soil was warmed to some extent. For two consecutive days the heater had not been switched on. The date of the experiment was May 8th, i.e. towards the approach of mid-winter, when the drop in temperature can be rather severe, with very cold nights. Consequently the animal got chilled, especially at night, in addition to the fact that the laboratory is south facing. As the laboratory was entered on the third day, the animal seemed sick: its movements were heavy and clumsy and when it walked about (which it did with great effort) it often rolled over on to its side. The physical condition of the animal was so poor that it was tentatively decided to destroy the animal. It was given a carrot which it nibbled with great effort. Here again, it seems that the urge to eat is a deeprooted instinctive action, no matter under what circumstances or in what physical condition the animal may be. Its aggressive nature was subdued: chewing movements were slowed down and this was apparently done without interest. During the day the animal was transferred to the north side of the building where it got a fair amount of sun. The patho-physiological effects wore down and towards 16.00 hours it had resumed its usual nature again: being aggressive and ready to fight at the slightest pretext. All traces of the clumsy gait had disappeared and the animal moved deftly through its cage.

It is possible that the metabolism of the animal may have slowed down to such an extent that it exhibited a kind of cold-stupor. They are evidently very susceptible to cooling down, and this may be expected, for they are accustomed to more or less constant temperature conditions within their tunnel systems.

The question whether these animals hibernate has also not yet been settled, although Shortridge (1934, 324) states quite definitely that the mole-rats in Southern Africa become partly dormant during the colder months "... until about September (the Southern Spring)."

Coupled/...

Coupled to physiological aspects of the animals, is the question of longevity. No direct information is available at present as far as natural conditions are concerned. Eloff (1958, 300) once removed six young mole-rats approximately one week old from their nest and was able to keep and rear them for three years for maturation studies. Apart from this, very little is known about the gerontology of the bathyergids.

In order to study them physiologically, it is necessary to keep these animals in captivity. A photograph of cages in which they thrive in captivity is to be found in Eloff (1952). Furthermore, Fitzsimons (1919-1920, 149-150) states that in captivity these animals live and thrive when fed on bulbs, roots, tubers and fruits. The cage must be warm, "and earth provided for the creature to amuse and excercise itself in, by burrowing". In addition, Fitzsimons adds that these animals make interesting pets and in the course of time become tame. However, it is inadvisable to attempt to handle them for, without prior warning, they often become excited and bite fiercely. When keeping several specimens in the same cage (especially if the newcomer does not hail from the same tunnel system or colony), it is necessary to isolate the newcomer behind a wiremesh partition until the others become familiar with it. Only then, if the partition is withdrawn, will they not fight.

Parasites

Information concerning the parasites associated with the bathyergids is meagre. Shortridge (1934, 325) states that no external parasites

were/...

were observed on any South West African Cryptomys specimens, although he collected extensively in that area. Roberts (quoted in Shortridge, 1934, 325) states that they are not infested with fleas, although a certain type of lice is to be found on them. This may refer to the sucking lice recorded as parasites on bathyergids by Bedford (1932, 401). De Meillon, Davis and Hardy (1961, 266) have reported the occurrence of at least five flea genera associated with Bathyergus and Cryptomys.

Although I have frequently trapped and collected Cryptomys, I have not come across any evidence of the presence of fleas or sucking lice. In collaboration with the Biological Section of the National Parks Board at Skukuza in the Kruger National Park, a number of mites which occur on Cryptomys have been recorded. Nematodes and cestodes are also known as parasites from Bathyergus, Georychus and Cryptomys. The available information is summarized in the accompanying table. For a more detailed discussion of parasitological aspects pertaining to the bathyergids, see de Graaff (1964, 113).

Table 6.1: Parasites of Bathyergidae in Southern Africa

Genus and species	Parasites	Locality	Source
Bathyergus suillus	PLATYHELMINTHES		
	Gen.et.sp.indet.	Houtbay	Ortlepp (personal communication).
	NEMATHELMINTHES		
	Trichuris sp.	Strandfontein	" " "
	Heterakis macrospiculum	" "	Ortlepp (1939, 98)

Libyostrongylus/...

	Libyostrongylus bathyergi	Strandfontein	Ortlepp (1939, 78)
	Longistriata bathyergi	" "	Ortlepp (1939, 87)
	ARTHROPODA		
	Ixodes alluaudi	South Africa	Theiler (1962, 226)
	Haemaphysalis leachii mühsami	" "	" " "
	Proenderleinellus lawrensis	-	Bedford (1932, 401)
	Cryptoctenopsyllus ingens	Cape Province	de Meillon et. al. (1961, 258)
Georychus capensis	PROTOZOA		
	Meistoma georychi	South Africa	Sandon (1941, 128)
	PLATYHELMINTHES		
	Echinococcus sp.	Wynberg	Ortlepp (personal communication)
	NEMATHELMINTHES		
	Trichuris sp.	" "	" " "
	ARTHROPODA		
	Ixodes alluaudi	South Africa	Theiler (1962, 227)
	Cryptoctenopsyllus ingens	Cape Flats	Bedford (1932, 458)
Cryptomys hottentotus	ARTHROPODA		
	Haemolaelaps capensis	Cape Province	Bedford (1932, 274)
	H. natalensis	King William's Town	Bateman (1960, 227)
	Ixodes alluaudi	South Africa	Theiler (1962, 227)
	Myonyssoides capensis	Grahamstown	Bedford (1932, 272)
	Cryptopsylla ingrami	Calvinia, Clanwilliam, Tulbagh, Port Elizabeth	de Meillon et.al. (1961, 187)
	Xenopsylla pirei	-	" " ",132
	Procaviopsylla creusae	-	" " ", 74
C.natalensis *	ARTHROPODA		
	Proenderleinellus hilli	Pietermaritzburg	Bedford (1932, 401)

C/...

C.komatiensis**	ARTHROPODA Androlaelaps marshalli	Faai experimental plots, Kruger National Park	de Graaff and National Parks Board Records
C. hottentotus vandami***	PLATHYHELMINTHES Inermicapsifer madagascariensis	Shingwedzi, Kruger National Park	" " "
	ARTHROPODA Haemolaelaps sp.	Pumbe sandveld, Kruger National Park	" " "
Cryptomys sp. ****	ARTHROPODA Dinopsyllus zuluensis?	Eshowe	de Meillon et.al. (1961,251-252).

Footnote. * : C. hottentotus in Bedford (1932)
** : C. hottentotus in de Graaff (1964)
*** : Cryptomys species in de Graaff (1964)
**** : Probably C.natalensis.

Predators

This aspect has also not received the attention it deserved in the past. Remains of skulls of Cryptomys occur frequently in owl pellets of the barn owl Tyto alba, and therefore points to the fact that the animals move around on the surface of the soil at night. Dogs undoubtedly occasionally come to grips with these mole-rats, but as would be expected of creatures with such enormous incisors (and their aggressive nature) they are not easy customers to deal with. It is known that cats often capture these animals (especially Cryptomys). A. Findlay Esq. (personal communication) states that his cat often kills and eats all mole-rats caught, in contrast to catching alive and often releasing any golden moles which it happens to catch.

Other predators which

seem to be of importance are snakes. In the Philadelphia area (between Malmesbury and Cape Town) it has been observed that mole snakes (<u>Pseudaspis cana</u>) prey on <u>Bathyergus</u>. Similarly, I have trapped a shield snake (<u>Aspidelaps scutatus</u>) in a mole-trap which was set in a tunnel of <u>Cryptomys</u>, near Shingwedzi, Kruger National Park. Subsequent investigation showed the presence of the hind quarters of <u>Cryptomys</u> in the stomach of the snake (Fig. 6.4).

<u>Genetical aspects</u>

In view of the fact that these animals occur in different isolated colonies or tunnel systems, and that there is virtually no tendency for interbreeding between individuals which come from different systems, it would seem reasonable to assume that there is a fair degree of inbreeding within such colonies. Consequently, it would not be unreasonable to expect a high degree of homozygosity within the genotypes of individuals and possibly within colonies. However, hitherto no actual genetical experimental work has been done in this direction.

The apparent isolation which exists between colonies has been aptly commented upon by Roberts (quoted in Shortridge, 1934, 325). "They are very local in my experience, seldom going far from certain spots, doubtless where certain bulbs or roots are always to be found, but not necessarily, as one would expect, where the soil is loose or sandy, very often remaining in the stoniest and hardest ground. I have known these animals to remain 18 years in certain places on rocky kopjes near Pretoria, while not far off, where the ground would seem to be far more suited to them, they never occur. But sandy conditions of soil are nevertheless better suited to them. They have doubtless originated there. They are the most conservative animals I know, and as they seldom leave their burrows, specific isolation is to be expected."

Dispersal

A note on the dispersal of these animals may be of interest. Basically, no information is available, apart from what is to be found in Shortridge (1934, 324). This author quotes Thomas who has stated the following: "One of the causes of wide distribution of similar forms of Cryptomys is no doubt the habit of these animals of frequenting in the dry season the empty beds of rivers, and then when the water comes down in flood, such as survive are carried along to make further colonies lower down, by which process the Cryptomys of rivers hundreds of miles in length are preserved from local isolation". As Shortridge has correctly pointed out however, this theory has not yet been supported by field observations.

Shortridge (p. 322) correctly states, that even where very abundant, the Cryptomys colonies are local. In favoured tracts large aggregations of mounds may be observed close together. Then, suddenly, for miles perhaps, there are none, after which they again appear. This type of distribution is often seen in the Orange Free State.

Economic implications and Eradication

These aspects can be approached as follows: the good that these animals do, and/or the damage they cause. The latter alternative leading to a brief discussion of possible methods of eradication.

Eloff (1954, 1,2) states that there is no doubt that the mole-hills alone, without the exposure of the lateral tunnels to the wind, have a most beneficial effect on the soil "for not only is the soil turned up, but the resultant increased porocity ensures the admission of water and air." As is known, when these tunnels are disturbed, (e.g. trampling down by livestock) the mole-rats burrow new parallel tunnels connecting the intact portions. "When large herds of game still roamed the open plains of the Free State, this factor certainly contributed in no small way to the burrowing of tunnels and consequently to the increase of porocity of the soil". During the dry seasons, through wind and water action, the lateral tunnels would certainly open up the main tunnels (after removal of the mole-hills) forming effective inlets for rain water into the soil below the hard surface layer of the ground.

Furthermore, Eloff is convinced that the preference Cryptomys shows for Homeria bulbs as well as for the nut grass Cyperus esculentus (the former being poisonous to cattle, the latter being a weed) keeps these undesirable plants in check. Areas (e.g. in the Free State) where mole-rats were numerous because of the presence of Homeria, Moraea and Cyperus were abandoned by them after three years when all these plants had disappeared. Homeria's usually grow in hollows where water collects and the presence of these plants in turn attract the mole-rats. They loosen the soil, so that these areas eventually become overgrown with red grass (Themeda), which is an important food source for cattle. Another aspect deserving attention is that Themeda seeds may lodge in, and spread further along a mole-rat tunnel where it germinates in the moist, cool mole-hill. These passages may then promote the spread of this grass. Eloff (1954, 2) also mentions another activity of the mole-rat which can be considered beneficial.

"These result from the instinct of the mole to burrow along the banks of a sluit or furrow which has more or less vertical walls. In this case, the lateral passages through which the mole pushes out loosened soil and which are formed on the side of the sluit, open, not on the surface but on the sides of the bank. The mole continues to burrow all along the steep bank until it finds a place less steep where it then burrows to the bottom level of the sluit. The mole can however burrow through very steep banks. This method of tunneling causes the banks to crumble and tends to level off the banks of such a sluit.

If sloping banks are less conductive to soil erosion than vertical banks, then we may well accept that this method of tunneling characterises the mole as a useful animal".

The possible usefulness of the pelt and the meat may be mentioned here. As far as Bathyergus is concerned, Roberts (1951, 380) maintains that the skin has not much value for it is rather thin and the fur is short. In contrast however, people living in the vicinity of Port Nolloth (Eloff, 1954, 3) regard the meat of the dune mole-rat as a delicacy when baked in an anthill and eaten with salt and pepper. This is probably understandable for the mole-rat is a clean animal without smell living exclusively on vegetable matter. Eloff has proved, that it can be reared and fattened in captivity on practically any kind of vegetable matter. People living in regions along the west coast of the Cape trap dune mole-rats for consumption during severe shortages of meat.

I have also seen dune mole-rats (Bathyergus) being trapped for food by coloured people in the Citrusdal district, even in times when there was no shortage of meat supply. These people use Bathyergus as the protein ingredient in stews and trap up to four or five mole-rats per household per week. It is said that often this forms their sole source of proteins, apart from fish which is occasionally purchased.

This is probably as much as can be said concerning the "credit balance" of the mole-rats. In terms of man and his agricultural and economic important ventures, the mole-rat, like the majority of indigenous mammals (in any geographical area) comes in direct conflict with mankind.

Seen in terms of economical implications, the following may be enumerated. During the days of the early colonists in the Cape, one of the important ways of transport was by means of horseback. Schreber (1792) already commented on the fact that due to the tunnels of Bathyergus, horse riding was a dangerous affair, for the horses damaging the tunnel systems fell into the holes up to their knees. Moseley (1879) provided the following interesting description: ".... in galloping over the sand one is very apt to be thrown head-long by one of their galleries giving way under the horse's feet. I had two such falls in one day. A clever horse, brought up in the country, learns however, whilst turned out on the run, to lift his foot out of a hole without stumbling."

Roberts (1951, 380) comments that in some places, where the ground is riddled with tunnels, it is dangerous to gallop on horseback "owing to the risk of the horses putting their feet through the surface into the tunnels and becoming a cropper" (Dreyer, 1910, 5) has commented in a similar vein.

It is generally known that these animals do a lot of damage in vegetable gardens. Roberts (1951, 380) however states, concerning Bathyergus, that they apparently do not enter gardens and therefore do not cause such extensive damage as Georychus and Cryptomys. This however, may be "due to their shyness and the pertinacity of residents, in the districts where they occur, in trapping them for food and the furry skins". As far as Georychus is concerned, it does a lot of damage to tuberous crops (Roberts, 1951, 382). Dreyer (1910, 5) has stated that this genus is the most directly injurous of the mole-rats. They are fond of potatoes and other vegetables and rob the farmer of a good percentage of his crop. Their destructivity in potato fields has also been mentioned by Fitzsimons (1919-1920, 154). As is the case in Cryptomys they spoil more than they can actually devour by their habit of gnawing a small portion of the substance and discarding the rest, which usually rapidly rots. Concerning Cryptomys, Eloff (1954, 2) says that when this genus directs its attention to cultivated lands, especially on small holdings, it usually

is /...

is a serious matter. They cause serious shortage and absorption of water through their tunnels and the possibility also exists that damwalls and furrows along river banks may be undermined, thereby hindering irrigation procedures. I have observed on a number of occasions, that <u>Cryptomys</u> is particularly fond of burrowing in soils which constitute the walls of ground dams and reservoirs.

Similarly, I have heard of a small-holding owner south east of Pretoria (on the Delmas road) who cannot cultivate any tuberous crop due to a heavy infection of <u>Cryptomys</u> on his property. A similar complaint was received from farmers in the Zoutpansberg district (on the road to Witvlag) where virtually nothing can be grown which is of direct economic importance, due to the presence of a large number of <u>Cryptomys</u> colonies.

Another important agricultural activity in the southern parts of South Africa, is the production of wheat. When the fields are ploughed, the <u>Bathyergus</u> specimens usually reside in their tunnel systems and nests. These structures are not destroyed by the ploughs, in view of the fact that they are too deep below the surface of the soil. When the wheat is sewn, the animals usually throw up their large mounds in these wheat fields. They do very little damage (relatively speaking) when the wheat germinates and when it has not yet grown to its full height. During the reaping season, the wheat is hoed by means of expensive agricultural machines which have large revolving blades, reminding one somewhat of an oversized lawnmower. Due to the height of the wheat the large mole-hills are usually not visible and these blades then cut through these sand

heaps,/...

heaps, for which they are naturally not constructed. It has been said that these mole-hills, pushed up by Bathyergus, shortens the life of these blades by a factor of approximately one half of its otherwise expected length of life. The farmers in those areas consequently regard these animals as absolute pests and try all kinds of means and methods to get rid of these large mole-rats.

Agricultural aspects aside, another interesting statement is to be found in Roberts (1951, 380). "It has also been stated that gangers on the railways are instructed to watch that these animals do not tunnel underneath the lines, as a few of these tunnels close together cause the lines to sag."

Furthermore, it is well known that Cryptomys especially, can do (and does) a lot of harm and damage to golf links, bowling greens and even tennis courts.

It is therefore not surprising that some research, as to how to eradicate and combat these animals has been undertaken in the past.

According to Eloff (1954, 2), the control of Cryptomys is a relatively easy matter once a knowledge of its habits are known and kept in mind. He states that the danger exists that the mole-rat may even be exterminated by injudicious methods of control, ".... whereby the balance of Nature will undoubtedly be disturbed, and tulips may become the first pest with which the cattle farmer in the Orange Free State will have to contend". The natural food of Cryptomys consists of the wild tulips (Homeria and Moraea) as well as the nut grass Cyperus which are all three undesirable plants. The mole-rat burrows solely with the object of locating these plants. Furthermore, they do not tolerate any opening caused by man or any other agency admitting an influx of air into the main passage. To control the mole-rats therefore, some tulip bulbs, with tops intact are dug up and each bulb is treated with strychnine - "about half the amount that will go on to the point of a knife is rubbed into incisions made round each bulb" (Eloff, 1954, 2). Two poisoned bulbs are pushed into the tunnel, the one pointing in one direction, the other in the other direction, the tops being allowed to project via the lateral passage. These lateral passages should not be closed and very soon the influx of air will induce the mole-rat to close up the opening. However, "... nothing is as important to the mole as the tulip bulb which he first of all pulls into the hole for food". Eloff states that a greater measure of success can be achieved when the passages leading from the nest are all baited in this way. This method described above, is probably an effective measure of control.

Dreyer (1910, 5) states that an effective control measure in the case of <u>Georychus</u>, is to lead water into their burrows and so to drown them. However it is doubtful whether this method of control is effective in view of the fact that the tunnel system can absorb an enormous amount of water. He also advocates the possibility of poisoned bait with strychnine. Carbon bisulphide is also used against the "blesmol": this often necessitates large quantities of the poison to be used, due to the extent of the passages and therefore the treatment is expensive. Furthermore, this chemical is also

liable/...

liable to damage the vegetables which it is purposed to protect. This method is also mentioned by Fitzsimons (1919-20, 156): the chemical evaporates, and the gas being heavy, will travel along the tunnels suffocating the inhabitants. This method is also effective against <u>Cryptomys</u>. Bishop (1948, 4) on the other hand, proposed the use of cyanide powders such as "Cyanogas" or "Calcid". In this case a specially constructed pump is needed (like those being used for the eradication of rodents). The humidity of the ground combines with the powder, and hydrogen-cyanide results which is injected into the tunnel and which is lethal when it is inhaled by <u>Cryptomys</u>. "Cyanogas" can however also be applied without the aid of a pump. In this case, the lethal fumes circulate through the tunnels very slowly, and it is possible that the mole-rat, on detecting a foreign smell, will plug off that part of the system.

Another way in which these animals may be eradicated is by means of the use of carbonmonoxide, the waste product of the ordinary internal combustion engine. These gases are led into the tunnels by means of a rubber hose (Bishop, 1948, 4). Others maintain that the use of gascartridges are effective: others however found no permanent positive reaction to this method.

Apart from these chemical methods of eradication, one may use traps. There are various types of traps produced commercially, all effective to a certain degree, often depending on the eradicator and his manipulative ability of the trap. <u>Bathyergus</u> is easily trapped by a kind of "rabbit gin", in which case

the/...

the animal is caught alive, usually by the hind-foot. Cryptomys can effectively be caught by means of a "snap-trap", which usually kills the animal outright. Another type is used extensively to trap Georychus in the south-western Cape, the so-called trapdoor trap. Cryptomys can be trapped by means of socalled tube traps. In this case, the animals are trapped alive and thus is especially useful for scientific purposes because the specimen is not damaged in any way at all. They can then be killed in a humane fashion with chloroform or ether.

Another method of eradicating these animals (e.g. Cryptomys) is to dig these animals out. Remove the soil above the main tunnel to about two to three inches above the tunnel: open the tunnel at the furthest end, and stand perfectly still above the opening: after a while (depending on the nature of the individual animal), it will come to investigate and the moment ground is being pushed out in order to plug the perforation, the spade can be inserted in front of the mole-rat and the animal scooped out.

Still another method employed to combat these animals, is to shoot them. A tunnel is opened up, (preferably near a new mole-hill) and if everything is quiet, the animal may appear within a few minutes. It can then easily be shot with a firearm. It is best to have the firearm ready for action because the slightest amount of movement will prompt the animal to retract. A good way is to lie flat on the ground with the mouth of the gun (pistol) directed at the opening of the tunnel. When the mole-rat appears, no additional/...

tional movements are required apart from pulling the trigger. It is often of no use firing into the earth which is brought along to plug the opening, for often the force of the bullet is stopped by the column of earth and the animal gets away. Once it has been frightened in this way, it does not return in due course to plug the opening. I have acquired a number of specimens of *Bathyergus* and *Cryptomys* in this way.

CHAPTER 7

A KEY TO SOUTHERN AFRICAN BATHYERGIDAE

In this chapter an attempt is made to provide a key to the South African Bathyergidae. The H.B. measurements used in this key represent minimum and maximum sizes recorded on museum labels. These figures may therefore be open to a certain amount of critisism. In contrast however, the C.B. length of the skulls were all taken by me (in the majority of cases) and these values may therefore offer a truer comparative yard-stick.

It is unfortunate that some species are poorly represented in the study collections in the various South African museums. This is especially true of Cryptomys bocagei, C.beirae and C.nimrodi. The identification of these species with the aid of this key may lead to difficulties and it may eventually be shown that these three species are in fact synonyms of C. darlingi.

It must also be pointed out that C. holosericeus has tentatively been retained as a separate species. There are indications (discussed elsewhere) that it may be possible to synonymise holosericeus with hottentotus, but this step has not been taken in the present work.

Family Bathyergidae

Burrowing forms. Infraorbital (anteorbital) foramen secondarily reduced, not or scarcely transmitting muscle. Zygomatic plate below infraorbital foramen.

Mandible/...

Mandible hystricognath (cf. sciurognath), the musculus masseter lateralis superficialis being the chief agent in distorting the angular process outwards, thus modifying form of mandible. Scaphoid and lunar elements in carpus not fused. Fibula reduced, often fully fused with tibia (trivial characteristic). Cheekteeth $\frac{4}{4}$, rooted, relatively simple. Eyes, ears and tail reduced. Five hind toes.

Upper incisors grooved, not extending beyond infraorbital foramen ....
.... subfamily Bathyerginae I.

Upper incisors not grooved, extending beyond infraorbital foramen into pterygoid region ....
.... subfamily Georychinae II.

I. Subfamily Bathyerginae

Upper incisors (heavily grooved on anterior surface), not extending into pterygoid region (reaching only to infraorbital foramen). Lower incisors ungrooved (cf. Georychinae). Angular process of mandible much drawn backwards. Size large, H.B. 170-330 mm. Claws of forefeet long, adapted to digging ....
.... <u>Bathyergus</u>.

II. Subfamily Georychinae

Upper incisors not grooved on anterior surface, extending into pterygoid region. Lower incisors ungrooved (cf. Bathyerginae). Angular process of mandible drawn backwards to a lesser degree. Size smaller, H.B. 102-200 mm. Claws of forefeet not long (i.e. not adapted to digging).

Cheekteeth/...

Cheekteeth with one fold each side in upper molar series (showing this enamel pattern even when well worn); hindmost molar cut late in life; face prettily coloured, black cap on head, white ring around ear, cheeks black, nose white; jugal bone fitting dove-tail fashion into zygomata. General colouration dark to greyish orange cinnamon .... Georychus.

Cheekteeth more or less simple, ringshaped in adults (showing enamel folds only in young specimens in exceptional cases); hindmost molar out earlier; colouration of face not as described above; jugal bone fitting into a long groove on the zygomata. General colouration uniform (usually) varying from black to cinnamon to brownish .... Cryptomys.

Genus Bathyergus.

1. Darker, with distinct dark dorsal band; size smaller on the whole.

	Males:	Females:
H.B.	170-235 mm., M = 205 mm.	170-206 mm., M = 183 mm.
C.B.	41.1-54.8 mm., M = 51.6mm.	40.4-50.7mm., M= 43.9mm.

.... B.janetta

Bathyergus janetta Thomas & Schwann 1904. Namaqua dune mole-rat.

Synonyms: B.j.janetta, B.j.inselbergensis, B.j.plowesi.
Range: Port Nolloth and adjacent areas (including Kamiesberg), and just across the mouth of the Orange river (Oranjemund).
Note: Ellerman et.al. (1953) regard janetta as only subspecifically distinct from suillus, but like Roberts (1951) recognize two subspecies viz. inselbergensis and plowesi.

2. Paler, with dorsal band indistinct (usually), or not visible; size larger on the whole.

Males/...

	Males:	Females:
H.B.	235-330 mm., M = 281 mm.	204-300 mm., M = 251 mm.
C.B.	53.5-74.4mm., M= 62.9mm.	45.5-66.9mm., M= 55.6 mm.

.... B.suillus

Bathyergus suillus (Schreber) 1782. Cape dune mole-rat.

Synonyms: Mus suillus, M. maritimus, Marmota africana, Bathyergus suillus suillus, B.s. intermedius.
Range: Southern and south-western Cape Province, from Knysna to Klaver.
Note: B.s.intermedius from Klaver is tentatively rejected.

Genus Georychus.

Size:	Males:	Females:
H.B.	177-200 mm., M = 189 mm.	155-204 mm., M = 182 mm.
C.B.	44.1-53.3mm., M=48.3 mm.	41.0-51.2mm., M=45.1 mm.

.... Georychus capensis

Georychus capensis (Pallas) 1778. Cape mole-rat, 'blesmol'.

Synonyms: G.c.capensis, G.c.canescens, G.c.yatesi.
Range: South-western and southern Cape coastal region, ranging to Nottingham Road, Natal, and Belfast, eastern Transvaal.
Note: It is tentatively suggested that the species is monotypic and not polytypic as believed.

Genus Cryptomys.

1. With outer wall of infraorbital foramen thickened.

a) Size large.

	Males:	Females:
H.B.	150-185 mm., M = 164 mm.	141-164 mm., M = 151 mm.
C.B.	32.2-44.1mm., M=36.2 mm.	31.6-38.2mm., M=35.3 mm.

Colour: Three colour phases:- reddish-brown, seal grey and slaty-grey ("black"). White frontal (occipital) patch present (varying in size and extent) which may extend as a white line sagittally on dorsal and ventral surfaces .... damarensis

Cryptomys damarensis (Ogilby) 1838. Damara mole-rat.

Synonyms: Bathyergus (=C.) damarensis, Georychus (=C.) lugardi, G.(=C.)micklemi, Cryptomys ovamboensis.

Range/...

Range: From Southern Rhodesia (Matetsi) and Bechuanaland, westwards to South West Africa, and also into Northern Rhodesia.

Note: This species has a wide geographical distribution. The validity of C.ovamboensis as a separate species is open to question.

b) Size large, but on the average slightly less than damarensis.

b') Size:

	Males:	Females:
H.B.	144-165 mm., M = 151 mm.	152-165 mm., M = 155 mm.
C.B.	29.9-34.4mm., M=31.9 mm.	32.5-35.0 mm., M=33.5 mm.

Colour: Pale ".... grey-drab, almost silver grey" (de Winton, 1897). Occurrence of white frontal (occipital) patch variable. Individuals tend to show a rich-brown sheen on the fur .... bocagei

Cryptomys bocagei (de Winton) 1896. Bocage's mole-rat.

Synonyms: Possibly C.kubangensis.

Range: Western Angola, southwards into the northern Kaokoveld in South West Africa.

Note: The measurements given above are based on extra-limital specimens from Mombola, Angola. The sample was small and therefore the position of bocagei in this key should be accepted with a certain degree of reservation.

b'') Size:

	Males:	Females:
H.B.	155 mm. (type specimen)	No data available.
C.B.	33.6-38.9 mm., M=35.8 mm. (Note: measurements from unsexed study skins and skulls).	

Colour: Varying between 'ecru-drab' and 'drab-grey' (Thomas & Wroughton). White frontal (occipital) patch usually present, not produced backwards onto the dorsal thoracic and lumbar surfaces (cf. damarensis) .... beirae

Cryptomys beirae (Thomas & Wroughton) 1907. Beira mole-rat.

Synonyms/...

Synonyms: *C. zimbitiensis*.
Range: Beira (Moçambique) and vicinity (e.g. Zimbiti) as well as at Gorongoza.
Note: The validity of *C.zimbitiensis* as a separate species is open to question. Study skins representing *C. beirae* are few in number and are of unknown sex. Size values given above are therefore open to question.

c) Size smaller (cf. *damarensis*, *bocagei* and *beirae*).

c') Size:

	Males:	Females:
H.B.	125-165 mm., M = 145 mm.	135-150 mm., M = 141 mm.
C.B.	30.6-37.9mm., M=33.3 mm.	31.0-36.5mm., M=32.6 mm.

Colour: Generally a uniform 'drab' (nearest to 'drab-grey' of Ridgeway), modified by the slaty-grey bases of the hairs showing through. White frontal (occipital) patch usually prominent, not extending beyond nape of neck (cf. *damarensis*, *bocagei* and *beirae*).... .... *darlingi*.

Cryptomys darlingi (Thomas) 1895. Mashona mole-rat.

Synonyms: None.
Range: Mashonaland, south-eastwards to Mt. Selinda, and south-westwards to Bulawayo and vicinity. Possibly Moçambique as well.
Note: It is possible that *beirae* and *darlingi* will eventually prove to be synonyms.

c'') Size:

	Males:	Females:
H.B.	146 mm. (type specimen).	No data available.
C.B.	No data available.	No data available.

Colour: Drably coloured (cf. *darlingi*). Frontal (occipital) patch absent. Ascending process of premaxillaries not extending backwards beyond nasals "... so that the suture between these bones and the frontals forms a simple, slightly bowed line, distinct from the complicated dove-tail pattern found in most of the *Georychi*" (de Winton) ..... *nimrodi*

Cryptomys/...

Cryptomys nimrodi (de Winton) 1896. Nimrod's mole-rat.

Synonyms: None.
Range: Only known from the type locality, i.e. Essex Vale, Southern Rhodesia.
Note: This species may prove to be a synonym of darlingi.

2. With outer wall of infraorbital foramen not thickened.

(a) Size large.

(a') Mammae: 2 pairs pectoral, 1 pair inguinal = 6.

	Males:	Females:
H.B.	125-160 mm., M = 141 mm.	125-145 mm., M = 138 mm.
C.B.	31.7-38.3mm., M=35.3mm.	30.4-34.2mm., M=32.7 mm.

Colour: 'cinnamon-buff' to 'clay-colour', with a decided yellower tinge (cf. natalensis), when a number of specimens are seen simultaneously. Colour geographically variable (cf. specimens from Vryburg). Frontal (occipital) patch usually absent .... holosericeus.

Cryptomys holosericeus (Wagner) 1843. Greater grey mole-rat.

Synonyms: Georychus (=C.) holosericeus, G.(=C.) vryburgensis, G.(=C.) orangiae, Cryptomys vetensis, C.bigalkei, and C.h. valschensis.
Range: North-western Cape Province (Kimberley, Vryburg), north-western Orange Free State, as well as at Glen, north of Bloemfontein. In the south-western Transvaal at Bloemhof and Wolmaransstad.
Note: C.bigalkei (originally described as a representative of the hottentotus group) has tentatively been included under holosericeus above. The possibility also exists however, that holosericeus should be synonymised with hottentotus. This seems to be strongly suggested by the evidence.

(a'') Mammae: 2 pairs pectoral = 4.

	Males:	Females:
H.B.	125-177 mm., M = 143 mm.	125-174 mm., M = 141 mm.
C.B.	30.4-38.1mm., M=34.8mm.	30.1-39.0mm., M=33.6mm.

Colour: On the average darker (more drab and dirtily coloured/...

coloured) than holosericeus, especially evident when a number of specimens are seen simultaneously. Colour geographically variable (cf. specimens from Swaziland). Frontal (occipital) patch usually absent .... natalensis.

Cryptomys natalensis (Roberts) 1913. Natal mole-rat.

Synonyms: Georychus (=C.) natalensis, G.(=C.) jamesoni, G.(=C.) arenarius, G.(=C.) anomalus, G.(=C.) aberrans, G.(=C.) mahali, Cryptomys montanus, C.junodi, C.langi and C.komatiensis zuluensis.

Range: Western Transvaal (e.g. Potchefstroom, Rustenburg), ranging eastwards to Johannesburg and Pretoria (northwards as far as Nylstroom). Also occurs in the eastern Transvaal (e.g. Wakkerstroom) extending eastwards to Pietermaritzburg and Durban, including north and south coast areas. Its southernmost coastal point of distribution seems to be Port St.Johns, while the northernmost point may be Masiyeni, north of the mouth of the Limpopo river.

Note: This species has been grossly oversplit.

(b) Size small.

(b') Mammae: 2 pairs pectoral, 1 pair inguinal, = 6.

	Males:	Females:
H.B.	105-150 mm., M = 120 mm.	100-160 mm., M = 119 mm.
C.B.	29.0-38.6mm., M=32.0mm.	27.2-36.4mm., M=31.2 mm.

Colour: More-or-less 'cinnamon-buff' to 'clay-colour', uniform. Colour geographically variable (cf. specimens from Knysna). Frontal (occipital) patch usually absent .... hottentotus.

Cryptomys hottentotus (Lesson) 1826. Hottentot mole-rat.

Synonyms: Bathyergus(=C.)hottentotus, B.(=C.) caecutiens, B.(=C.)ludwigii, Georychus (=C.) exenticus, G.(=C.)jorisseni, G.(=C.)albus, Cryptomys vandami, C.cradockensis, C. transvaalensis and C.hottentottus(sic) talpoides.

Range: South-western Cape, northwards to Namaqualand and eastwards along the coast to Port Alfred. Extends over a large portion over the eastern half of the Karoo, to the area south of Bloemfontein.

Occurs in the drier north-western Transvaal and ranges along the Marico and Limpopo rivers eastwards to north-eastern Transvaal (e.g. Leydsdorp).

Note: It is possible that *hottentotus* will eventually also have *holosericeus* as synonym, if aspects of geographic distribution, size, number of mammae and colouration are taken into consideration.

(b'') *Mammae*: 2 pairs pectoral = 4.

	Males:	*Females:*
H.B.	102-137 mm., M = 120 mm.	90-135 mm., M = 118 mm.
C.B.	26.5-34.6mm., M = 31.2mm.	28.6-32.6mm., M=30.6 mm.

Colour: A darker coloured species (cf. *hottentotus*), colour geographically variable (e.g. specimens from Tzaneen). Frontal (occipital) patch usually absent .... *komatiensis.*

Cryptomys komatiensis (Roberts) 1917. Komati mole-rat.

Synonyms: *Georychus(=C.)komatiensis*, *G.(=C.) rufulus*, *G.(=C.) stellatus*, *Cryptomys melanoticus* and *C.natalensis streeteri*.

Range: From Carolina, Barberton and Komatipoort in the eastern Transvaal ranging northwards and north-westwards to Acornhoek, Mariepskop and Balloon Farm on the Makoetsi river, Leydsdorp to the vicinity of Woodbush and Tzaneen.

Note: *C.natalensis streeteri* is here interpreted as a form of *komatiensis*.

CHAPTER 8

BATHYERGUS SUILLUS (SCHREBER) 1782

The first description of the Cape dune mole-rat (i.e. Bathyergus) was supplied by Schreber (1782), naming the animal Mus suillus. However, this was not the first bathyergid to be described from Southern Africa, for Pallas had already described the Cape mole-rat or "blesmol" (i.e. Georychus) in 1778.

Six years after Schreber's publication, Gmelin (1788) coined the name Mus maritimus for the identical animal while in the same year Thunberg also referred to this species as Marmota africana. Illiger (1811) erected the genus Bathyergus, for it was evident that the mole-rats could not be fitted into the same genus as the murids. In addition, Cuvier referred to the dune mole-rat as Orycterus in 1829. Consequently, in terms of priority rules concerning zoological nomenclature, it is evident that the generic name Bathyergus has priority over Orycterus and similarly the specific name suillus over maritimus.

The earliest mention of the dune mole-rat (according to Sclater, 1901, xi) was made by Abbé de la Caille who visited the Cape in 1750 to make certain astronomical observations. His journal (published in 1763) contains descriptions of a number of animals he encountered during his stay. According to Desmarest (1820, 323) this bathyergid was called the Taupe du Cap by de la Caille.

This early record of Bathyergus was followed by an account written by Masson in 1776 who also pointed out the existence of this animal. Masson, a gardener from the Royal Botanical Gardens at Kew, travelled extensively in South Africa between 1772 and 1776 in order to collect new plants for the improvement of the gardens (Sclater, 1901, xii).

Bathyergus was thus known to the early travellers, but the first satisfactory description of the species was transmitted to Professor Allamand of Leyden, Holland, by Col. Gordon who eventually commanded the Dutch forces at the Cape before the first occupation of the Cape by the English in 1795 (Sclater, 1901, II, 73). This description apparently appeared in the Dutch edition of de Buffon's work and was reprinted by de Buffon in his Histoire Naturelle (1774-1789). It has to be noted that no scientific name was attached to this early description of Bathyergus. Allamand called this bathyergid the Taupe de dunes, while de Buffon referred to it as Grande taupe du Cap (Desmarest 1820, 323).

In 1785 Sparrman also noted the occurrence of this bathyergid in the Cape Province and according to Sclater (1901, II, 71) ".... identified these animals with the African rat of Pennant". Furthermore, Thunberg in 1795 described this rodent as the "witte mol" from the vicinity of Cape Town; he also gave an account of certain behavioural aspects exhibited by these animals. The original edition of this account appeared in Swedish in 1788 which was translated into English in 1795. Many incidental accounts of the larger animals are given, which were afterwards separately published in the Memoirs of the St. Petersburg Academy for 1811 (Sclater, 1901, xiii).

Desmarest/...

Desmarest (1820, 323) refers to these animals as Bathyergue des Dunes and he gives the vernacular name used by the colonists as "Land-Moll." The same vernacular name was also reported by Smuts (1832). Furthermore, Allamand recorded that the Hottentot word for Bathyergus was "kauwhowba", meaning, "the hippopotamus mole" (Sclater, 1901, II, 71).

The ship H.M.S. "Challenger" undertook a voyage round the world between the years 1872-1876 and Moseley (1879, 145), the naturalist on board, wrote an interesting account of the habitat and habits of Bathyergus, i.e. the "sand mole" as it was named vernacularly by him. He had the opportunity to study this animal in the vicinity of Cape Town during the "Challenger"'s sojourn in Simonstown.

Sclater (1901, 71), Shortridge (1934, 318) and Allen (1939, 425) all refer to Bathyergus as the sand mole while Shortridge also lists the vernacular name "duinmol." Roberts (1951, 380) refers to it as Cape dune mole-rat and "Kaapse duinmol" while Ellerman et.al. (1953, 228) speak of the Cape sand mole, mole-rat and "duinmol."

The type localities given by Schreber (1782) and Gmelin (1788) are defined rather vaguely in both cases as the Cape of Good Hope. Schreber however states that Bathyergus lives "... am Vorgebirge der guten Hoffnung in den Dünen oder Sandhügeln der Kuste...." (p. 715).

As here understood Bathyergus suillus is a monotypic species confined mainly to the south-western Cape Province where it occurs endemically in the soft soils of coastal sand dunes and alluvial soils of river and stream banks.

The following synonyms are often included under Bathyergus suillus: Mus suillus Schreber, Mus maritimus Gmelin, Marmota africana Thunberg and Georychus maritimus A. Smith. Furthermore, during the course of this work, it has become evident that the subspecies Bathyergus suillus intermedius Roberts, does not appear to warrant the subspecies rank accorded to it by Roberts (1926, 261) and has therefore been regarded as a synonym of the typical B. suillus (Schreber).

Bathyergus suillus (Schreber)

Mus suillus Schreber,	Die Säugethiere, IV: 715, pl. 204B, 1782. Type locality: Cape of Good Hope.
Mus maritimus Gmelin,	Linn. Syst. Nat.ed. 13, I, 140, 1788. Type locality: Cape of Good Hope.
Marmota africana Thunberg,	Resa uti Europa, Africa, Asia, etc. I: 293, 318. pl.I, 1788. Type locality: Cape of Good Hope.
Bathyergus suillus intermedius Roberts,	Ann. Transv.Mus., 11 : 261, 1926. Type locality: Klaver, Cape Province.
Type specimen:	?
Type locality:	Defined vaguely as the Cape of Good Hope (Schreber, 1782, 715).

Distribution: (Fig. 8.1).

Occurs where-ever loose, unconsolidated coastal sand dunes are present in the south-western Cape

Province/...

Province. Recorded in the vicinity of Klaver (the northern-most known locality at present). Travellers Rest (the farthest inland locality known: approximately 50 miles from the coast), Kompanjiesdrift and Lambert's Bay. From thence southwards via Citrusdal, Het Kruis, Eendekuil, Malmesbury and Kersfontein to Cape Town where it occurs abundantly on the Cape Flats and adjacent areas. Similarly, they are found along the coast between Cape Town and Knysna including localities such as Bredasdorp, Stilbaai and Belvedere.

Diagnostic characters:

A very large species, in fact the largest bathyergid occurring in Southern Africa, H.B.: M = 281 mm. C.B.: M = 62.9 mm. (♂♂). Claws of front feet adapted to digging. Upper incisors grooved, not extending backwards into pterygoid region. Angular process of mandible drawn backwards. Colour cinnamon to drab-grey with an ill-defined brown band mid-dorsally, flanks and ventral surfaces drab-grey.

Colour:

General colour cinnamon above, some specimens portraying a better defined brown mid-dorsal band. The lateral and ventral pelages are paler and the overall colour has been described as a drab-grey (Thomas and Schwann, 1904, 180) while Sclater (1901, II, 71) described it as a slaty-grey. In the original type-description by Schreber (1782) the colour was described as whitish above, ".... mit Gelblichem überlaufen ....." and ".... an den Seiten und unten weissgrau". There is no trace of sheen on the fur.

The fur is soft, thick, woolly. The individual hairs are slaty-grey for the greater part of

their/...

their lengths, the tips being a light yellow or light brown. The base of the hair is a very dark grey, almost black. Because of wear the hair on the ventral surface is usually short, resulting in a grey ventral surface due to the basal grey portions of the hair showing through (Roberts, 1951, 380).

There is a buffy to white spot round each eye and the area around the muzzle and throat is also usually white. According to Roberts (op.cit.) these areas are usually albinistic in character.

Another feature pertaining to the colouration of these animals, is the fact that piebald varieties occur. Sclater (1901, II, 73) states that white varieties are not uncommon, but in the available study material used in the present work, I have come across one specimen only which could possibly be called white in a series of 163 skins.

The species is rather uniformly coloured. However, when ♂ and ♀ study skins from the different localities are compared it is found that the individuals (both sexes) from the more northernly situated localities (e.g. Klaver, Lambert's Bay, Kompanjiesdrift and Travellers Rest) are definitely paler in colour or of lighter hue. This pale colouration gradually darkens (i.e. the colour becomes "richer") as is illustrated by specimens from Cape Town and the Cape Peninsula. This tendency towards darker colouration is continued eastwards from Cape Town and very clearly seen in specimens from Zoetendalsvlei and Stilbaai which have a rich, lightbrown colour, while those from the farthest eastern locality i.e. Knysna, are fairly drab-grey i.e. dark. These differences in the colour of the dorsal pelage are only clear and illustrative when a number of specimens are compared simultaneously and collectively. When, for example, an individual study skin from Travellers Rest or Kompanjiesdrift is taken and placed between specimens from Cape Town, it is hardly possible to point out the single northern specimen. The same applies if a specimen from Kynsna is placed among specimens from Cape Town, Het Kruis or Travellers Rest; again, it is virtually impossible to discern the single eastern specimen.

No difference could be detected in the available study skins between winter and summer pelages. This uniformity is possibly explained by the fact that the environment within the tunnels remains more or less constant during the entire year. As has been commented upon earlier in this work, no clear-cut evidence of post-mortem discolouration could be detected in the study specimens.

It has already been stated that the specimens obtained in the north-west (Travellers Rest and vicinity) are of a paler hue compared to specimens from Cape Town, which in turn are more lightly coloured than the rich-brown colour exhibited by specimens from Stilbaai. The reason for this gradual and scarcely perceptable colour change may be correlated with rainfall: it is possible that the darker individuals (e.g. from Knysna, which falls within a high rainfall zone, 32-40" per annum) reacts phenotypically to the greater degree of moisture being present, by becoming darker. Similarly, the specimens from the drier northwest (e.g. Lambert's Bay, Kompanjiesdrift, etc., rainfall 8-12" per annum) are of lighter colour.

Finally/...

Finally, it may be mentioned that the individual hairs of the dorsal pelage in <u>B. suillus</u> portrays the typical agouti type of hair which shows a certain distribution of yellow and black pigments. Genetically, this is controlled by a multiple allelomorph series, the base of the hair being black, with a subdistal yellow band with a black or brown tip. The yellow and brown portions may merge. This type of hair occurs in many wild types of animals of most species (especially in rodents) and may serve a function of protective colouration (Hovanitz, 1953, 172).

<u>Size</u>: <u>Adult ♂♂</u>:

H.B. 235-330 mm., M = 281 mm.

T. 18-70 mm., M = 49 mm., (17.4% of H.B.)

H.F. 41-55 mm., M = 51 mm., (18.1% of H.B.)

C.B. 53.5-74.4 mm., M = 62.9 mm.

B.C. 18.7-25.2 mm., M = 21.3 mm., (13.8% of C.B.)

I.W. 9.2-11.5 mm., M = 10.2 mm., (16.2% of C.B.)

Z.W. 34.0-50.3 mm., M = 40.5 mm., (64.3% of C.B.)

M.W. 10.6-15.1 mm., M = 13.3 mm., (21.1% of C.B.)

U.T.R. 9.3-11.1 mm., M = 10.3 mm., (16.3% of C.B.)

L.J. 30.9-45.7 mm., M = 37.8 mm., (60.0% of C.B.)

L.T.R. 10.4-12.8 mm., M = 10.9 mm., (17.3% of C.B.)

<u>Adult ♀♀</u>:

H.B. 204-300 mm., M = 251 mm.

T. 27-61 mm., M = 45 mm., (17.9 % of H.B.)

H.F. 30-52 mm., M = 46 mm., (18.3% of H.B.)

C.B. 45.5-66.9 mm., M = 55.6 mm.

B.C. 19.7-22.3 mm., M = 20.3 mm., (36.5% of C.B.)

I.W. 9.3-11.8 mm., M = 10.1 mm., (18.1% of C.B.)

Z.W. 22.2-45.5 mm., M = 36.5 mm., (65.6% of C.B.)

M.W./...

M.W. 10.6-14.4 mm., M = 12.0 mm., (21.5% of C.B.)
U.T.R. 8.1-10.2 mm., M = 9.7 mm., (17.4% of C.B.)
L.J. 27.8-40.8 mm., M = 33.7 mm., (60.6% of C.B.)
L.T.R. 9.9-12.6 mm., M = 11.0 mm., (19.7% of C.B.)

These tables (above) are based on adult ♂♂ and ♀♀ collected over the entire distributional range of B. suillus.

A glance at the figures given above, will immediately convey the fact that those given of H.B., T. and H.F. for both sexes are rather unreliable. These were taken at their face value from the different labels attached to the available study skins. The observed minimum-maximum size range is often exceedingly large (e.g. the size variation in the tail lengths) - an individual with tail length of 18 mm. was classified as an adult specimen as was the individual with a tail length of 70 mm. The skull measurements (taken by myself) do not show this enormous amount of variation. The differences shown in external measurements are well explained by the following quotation from Doutt (1961, 293) who states that differences in external measurements ".... are the result of different measuring techniques on the part of collectors. It is apparent that external measurements should be handled with extreme caution. In fact, the external measurements made by one collector, using a slightly different technique, provided differences which were statistically highly significant and if we had not been aware of the reason for this difference we would have had what anyone would call a good subspecies from this locality. The skull measurements, if they all were made by one person should be strictly comparable, but if they were made by two or more individuals they may also be open to question, especially in statistical studies, which do draw very fine lines."

In the available study material, sexual dimorphism is apparent. When 13 ♂♂ and 13 ♀♀ from Travellers Rest are compared in respect of condylo-basal length, ♂♂ (M = 67.3 ± 4.845 mm.) are very significantly larger than the ♀♀ (M = 55.1 ± 2.905 mm.) at the 0.10% level (t = 7.5, 24 degrees of freedom, $P = \ll 0.001$).

Similarly, the condylo-basal length of 14 ♂♂ and 9 ♀♀ were taken at random, i.e. localities were not taken into consideration. In this case, the ♂♂ (M = 62.8 ± 4.360 mm.) are again significantly larger than the ♀♀ (M = 57.1 ± 3.415 mm.) at the 1.0% level (t= 4.73, 21 degrees of freedom, $P = \ll 0.01\%$)

All localities which have yielded sufficient material for study, show that the ♂♂ are constantly larger than the ♀♀.

With the kind permission of the authorities concerned, the following information concerning weight attained by these animals was derived from labels attached to study skins housed in the Plauge Research laboratories of the South African Institute for Medical Research, Johannesburg. A mature ♂ and ♀ from Tulbaghkloof weighed 495 and 386 gms. respectively when these animals were trapped. Another ♀ from the same locality weighed 425 gms., while still another ♀ from a nearby locality (Drostdy, Tulbagh) has a recorded weight of 512 gms.

Skull/...

Skull and dentition

For a full description of the skull of Bathyergus, see Chapter 4. Diagnostically the skull of B. suillus is rugged and robust with well developed sagittal and nuchal crests, especially in old ♂♂. Upper incisors grooved, not extending beyond the first upper cheek teeth. Skull rather flat and broad, conspicuously larger than skulls of B. janetta. The angular process of the mandible is drawn backwards to a considerable extent.

Discussion

As far as the synonymy is concerned, the following aspects may briefly be dealt with. As has been stated above, Bathyergus suillus (Schreber) was first described as Mus suillus in 1782. Some synonymy lists give this date as 1792. This has led to a certain amount of confusion in the past resulting in B. suillus still being referred to as B. maritimus as recently as 1958 (e.g. Eloff, 1958). It appears that the specific section of Schreber's work in which the dune mole-rat was described, appeared in 1782, while the actual volume (i.e. volume IV) was only completed in 1792. In 1788 Gmelin described the same animal as Mus maritimus and consequently some misunderstanding of the correct name had arisen. Sclater (1901) therefore refers to B. maritimus and lists Gmelin (1788) and Schreber (1792), in that order, in his synonymy list. For a full explanation on the dates of publication of Schreber's work, the reader is referred to Sherborn (1891, 587).

Thunberg also described this animal as Marmota africana in 1788. This narrative, a description of his travels in Europe, Africa and Asia between 1770

and/...

and 1779, was translated into English in 1795. The genus and species was changed by Lamarck (1796, 384) in a publication describing Thunberg's voyage to Japan, etc. The new designation was *Arctomis* (*sic*) *africana* and in the publications of the St. Petersburg Academy (1811) the spelling adhered to by Thunberg was *Arctomys africana*.

Ellerman *et.al.* (1953, 228) have tentatively regarded all forms of *Bathyergus* as conspecific. This procedure does not seem to be justified for *Bathyergus suillus* is decidedly a different species compared to the much smaller *B. janetta*. In fact, 13 years earlier, Ellerman (1940, 84), commented as follows: "Two well marked species are known, the "giant" *suillus*, and the moderate-sized *janetta*, which appears to have a less heavily ridged skull."

Apart from size and certain features of the skull there seems to be an absolute separation between *suillus* and *janetta* in all the material seen. This applies especially to colour. Roberts (1951, 380) has retained both species: *suillus* with two subspecies, (*B.s. suillus*, *B.s. intermedius*) and *B. janetta* with three subspecies: *B.j.janetta*, *B.j.inselbergensis* and ***B.j.plowesi***). As far as *suillus* is concerned, I am inclined to agree with Ellerman *et.al*. (1953, 228) in treating *B.s.suillus* and *B.s.intermedius* as synonyms while disagreeing with them in their interpretation of *suillus* and *janetta* as conspecific forms.

It is thus clear that Roberts adhered to a polytypic interpretation of *B.suillus*. According to Roberts, the reason for separating *suillus suillus* from *s. intermedius* rests largely on two aspects:

a)/...

a) The smaller overall size of B.s. intermedius

b) The fact that all six specimens of s. intermedius which are known to science at the present portray a conspicuous white spot on the forehead where as ".... those from the South usually have only a small spot in half the specimens." (Roberts, 1951, 381).

This latter statement has prompted me to investigate the occurrence of white spots on the foreheads in populations of B.s. suillus.

A total of 157 study skins were available for comparison, ranging from Knysna to Lambert's Bay, consisting of 62 ♂♂ and 63 ♀♀ as well as 32 unsexed specimens. The question whether a white frontal spot is to be classified as large (conspicuous), medium-sized or small is relative and will eventually depend on the interpretation of the investigator. For the purposes of this work, the white spots were divided into three categories: large, medium-sized and small.

In the study skins, the ♂♂ and ♀♀ occurred more or less in a 1:1 ratio. In the case of the ♂♂, 48.4%, (30 individuals) and in the case of the ♀♀ 47.6% (30 individuals) showed no sign of spotting at all. Interpreting Robert's remark rather broadly i.e. that the forms from the south only have a small spot in half the specimens, this conclusion then points to confirmation of the statement. It may well be that Roberts interpreted all the spots seen in the southern forms as small, while in actual fact many specimens have white patches covering a considerable area on their foreheads which can hardly be classified as small. Theoretically and in practice, it could be possible to obtain six study skins consecutively

from/...

from a certain locality, which would all show large frontal spots. Such localities could possibly include Eendekuil, Citrusdal and Het Kruis, which have yielded study skins with large and conspicuous patches.

Therefore, I am inclined to disagree with Roberts in using the absence or presence of the frontal spots as a criterium for subspecific distinction whenever it crops up a number of times in all members of a sample (e.g. at Klaver).

The first criterium, i.e. its smaller size, is a far more convincing one for separating <u>B. suillus suillus</u> from <u>B.s.intermedius.</u> This, however, is not statistically justified, as will be shown in the discussion below.

Although the type locality for <u>B. suillus</u> is defined rather vaguely as the Cape of Good Hope, and that it lives ".... am Vorgebirge ...." in the coastal dunes and soft sand hills, it is probable that Cape Town or a locality within its immediate surroundings was implied in the description of the type locality.

The skins available for study from Cape Town, the Cape Peninsula and adjacent Cape Flats could not be separated on the basis of colour. For macroscopic pelage colour comparisons, the males, females and unsexed specimens were compared simultaneously whenever they were collected at the same locality. In view of the fact that these specimens from in and near Cape Town showed no appreciable difference in colour the adult male and female specimens from Maitland, Cape Town and Strandfontein were treated together and the following statistical parameters for C.B. length and L.J. length were obtained, as shown in Table 8.1.

Table 8.1. C.B. length and L.J. length in B. suillus from Maitland, Cape Town and Strandfontein.

	C.B.	L.J.
♂♂	53.5-71.4 mm. M= 64.8 ± 6.480 mm. N= 6, C.V.= 10.5%	30.9-41.4 mm. M= 37.8 ± 4.083 mm, N= 5, C.V. = 10.8%
♀♀	52.9-66.9 mm. M= 59.5 ± 4.993 mm. N= 6, C.V. 8.3%	32.9-40.8 mm. M= 36.0 ± 3.323 mm. N= 5, C.V. = 9.2%

In both ♂♂ samples the C.V. values are slightly above the usually accepted 10% in the case of mammals. This may be due to the fact that these samples are not entirely homogeneous as far as ages of the different individuals are concerned. The values obtained in the case of the ♀♀ however, indicate that this procedure of lumping together was justified and that these specimens form a homogeneous sample.

Apart from Cape Town and vicinity, Bathyergus suillus extends eastwards to Knysna. Sclater (1901, II, 73) states that their distribution may extend as far east as Bathurst in the eastern Cape Province. However, the farthest eastern locality from which study skins are available is Knysna although Roberts (1951, xxvii), states Bathyergus to occur as far east as Plettenberg Bay along the coastal sand dunes. The nearest locality to Cape Town and Pensinsula from whence study skins are available is Zoetendalsvlei. Again on the basis of colour, these specimens are virtually indistinguishable from the Cape individuals, although of richer colour hue. The measurements of the skulls fall well within the variation range exhibited by the Cape Town specimens.

Similarly/...

Similarly, specimens collected at Bredasdorp and Stilbaai compare very well with those from Zoetendalsvlei on the basis of colour.

Nine study skins were available for study from Knysna and it has already been mentioned that the pelage of these specimens are a shade darker than other specimens from any other locality. The sample for the ♀♀ was too small for statistical manipulation, but this could be done in the case of the C.B. length and L.J. length in the ♂♂. The former value varied between 56.2-71.2 mm., M=63.3 ± 6.768 mm., N = 5, while the latter parameter varied between 34.0-43.5 mm., M = 38.2 ± 3.852 mm., N = 5 (Fig. 8.2). The direct graphical comparison with specimens from Cape Town makes it clear that there is no ground whatsoever for not treating the eastern forms conspecifically with specimens obtained in close proximity of the implied type locality.

The distribution of Bathyergus suillus extends not only to the east of Cape Town but to the north as well. Roberts (1951, 380) states that the specimens of the south (i.e. Cape Town and vicinity), are slightly larger compared to specimens occurring north of the Berg River and south of the Olifants River which are slightly smaller but still with the upper and lower tooth row measurements of "... the typical subspecies, (i.e. suillus) namely 10.5 - 11.7mm." Furthermore, they tend towards the "smaller subspecies" which occurs to the north of the Olifants River (i.e. Roberts' B.s.intermedius).

Table 8.2. The slightly smaller size of B.suilles from the area north of the Berg River and south of the Olifants River.

	U.T.R.		L.T.R.	
	♂♂	♀♀	♂♂	♀♀
Area south of Berg River: Cape Town, Cape Peninsula, Malmesbury, Kersfontein)	M=10.2 mm. (N=8)	M= 9.8 mm. (N=8)	M= 11.5 mm. (N=6)	M=11.4mm. (N=6)
Area north of Berg River and south of Olifants River: (Het Kruis, Eendekuil, Kompanjiesdrift, Lambert's Bay)	M=10.1 mm. (N=9)	M= 9.6 mm. (N=7)	M= 11.0 mm. (N=8)	M=10.5mm. (N=9)

In the statement by Roberts quoted above, he did not indicate whether he considered ♂♂ and ♀♀ together or whether the values he gave for the southern forms were based on separate sexes or unsexed animals. The important point is however, that he was correct in emphasizing the slightly smaller size of the animals occurring to the north of Cape Town, between the Berg and Olifants Rivers, as can be seen in Table 8.2.

In the case of 12 ♂♂ collected at Eendekuil, Het Kruis, Kompanjiesdrift and Lambert's Bay the average C.B. length was 62.2 mm., compared to 64.8 mm. in the Cape forms.

Obviously, there is not much difference between samples of the different populations which occur at the different localities. It seems to be a

safe/...

safe procedure therefore, to treat all these forms (occurring to the north of Cape Town) as conspecific as Roberts and others have done. On lumping the specimens together, 12 ♂♂ and 11 ♀♀ were available for comparison. That this step was justified is shown by the C.V. values of 7.2% and 7.6% for the C.B. length and L.J. length respectively in the ♂♂. Similar data for the ♀♀ gave a C.V. value of 5.3% and 6.5% respectively. It is furthermore evident that there is a considerable overlap of this material with that collected at Knysna and vicinity.

The area east of the Olifants River is also represented by a number of study skins, especially from Tulbagh and vicinity, Citrusdal and Travellers Rest near Clanwilliam. Once again, the colour of the pelage is exceedingly uniform although there is a possibility that the Travellers Rest specimens are a shade lighter than those trapped at Kompanjiesdrift. The lengths of the L.J. and C.B. for specimens from Travellers Rest, are shown in Table 8.3.

<u>Table 8.3</u>. C.B. length and L.J. length in <u>B. suillus</u> from Travellers Rest.

C.B.	L.J.
♂♂ M = 63.7 ± 4.485 mm. N = 12, C.V. = 7.0%	♂♂ M = 38.5 ± 3.661 mm. N = 17, C.V. = 9.5%
♀♀ M = 55.1 ± 2.905 mm. N = 13, C.V. = 5.2%	♀♀ M = 34.1 ± 1.910 mm. N = 14, C.V. = 5.6%

It is clear that there is a considerable degree of overlap between the specimens from Travellers Rest and those lumped together from Eendekuil, Kompanjiesdrift and Lambert's Bay.

Up to this point, the results obtained in the study of this species agrees well with the conclusions reached by Roberts (1951). In addition, a number of statistical parameters have been added. However, the inclusion of Bathyergus suillus intermedius Roberts from Klaver in the typical B.suillus requires some explanation (Fig. 8.3).

This supposed subspecies was described by Roberts (1926, 261) as very ".... similar to B. suillus of Cape Town, but with the white mark on the forehead much larger and more persistant, and the dimensions smaller, intermediate between the typical form and B. janetta Thomas and Schwann from Port Nolloth". In colour, these specimens are similar to the typical southern form (Roberts 1951, 381) excepting that ".... all of the six specimens from Klaver have a conspicuous white spot, whereas those from the south usually have only a small spot in half the specimens." Furthermore, Roberts has stated that they are smaller in size compared to the southern suillus suillus.

The length of the head and body in the type specimen (T.M. 2171, type locality, Klaver, ♂) was given as 258 mm. while a ♀ specimen measured 230 mm. The corresponding values for 40 ♂♂ and 50 ♀♀ collected at localities south of Klaver were M = 280.7 mm. and M = 250.8 mm. respectively.

As far as the white frontal spots are concerned, this has already been commented upon above. It is possible that the fact that all six specimens show this tendency could be ascribed to coincidence and that on more intensive trapping in the

area/...

area, specimens from this locality could be obtained which portray no frontal spots. The sample (N = 6) is too small to attach much value to the importance of this characteristic.

These animals were all collected between 22/9/17 and 2/10/17 by Roberts and Adendorff on the sandy flats at Klaver north of the Olifants River.

The sample consists of six specimens, an adult ♂, five ♀♀ (one old, three adult and one immature). No reliable statistical parameters could be obtained from the four adult female specimens due to the sample being too small. As is the case in specimens from other localities, sexual dimorphism is also evident here so that the ♂ and ♀ specimens could not be considered simultaneously. In this instance, a value for the standard deviation has been inferred from the mean of standard deviations in samples where calculation of this parameter is possible. For the C.B. length and L.J. measurements, the mean S.D. in two samples (from Kompanjiesdrift and Travellers Rest) are given in Table 8.4.

Table 8.4. Measurements of C.B. length and L.J. length in *B. suillus* from Kompanjiesdrift and Travellers Rest.

	C.B.	L.J.
Kompanjiesdrift	♀♀ M=54.8 ± 3.112mm. (N=8)	♀♀ M=32.8 ± 2.383 mm. (N=7)
Travellers Rest	♀♀ M=55.1 ± 2.905mm. (N = 13)	♀♀ M=34.1 ± 1.910 mm. (N = 14)
	Mean S.D. = 3.008 mm.	Mean S.D. = 2.147 mm.

These/...

These samples were chosen, for they are localities from which a fair amount of material is available for study and due to the fact that these two localities are the closest geographically speaking to the Klaver locality. It is further necessary to assume that sample means for the area represented by these small samples are representative of the populations from which they are drawn.

In comparing the C.B. length and L.J. measurements of the ♀♀ from Klaver and those from Travellers Rest/Kompanjiesdrift, the ♀♀ from the latter localities have M = 54.9 ± 3.008 mm. (N = 21) for C.B. length compared to M = 52.4 ± 3.008 mm. (N = 4) for the same measurement in the ♀♀ from Klaver. A C.D. value of 0.415 was obtained from these figures, indicating a J.N.O. of far less than 75%, a figure not significant for subspecific recognition.

Similarly, the differences between the L.J. measurements (four ♀♀ from Klaver, M = 30.5 ± 2.147 mm., 21 ♀♀ from Travellers Rest/Kompanjiesdrift, M = 33.6 ± 2.147 mm.) gave a C.D. value of 0.721 which again is far below the value of 1.28 (i.e. 90% J.N.O.), the conventional level for subspecific recognition. In this case, the J.N.O. value is approximately 77%.

In a similar fashion, the four ♀♀ from Klaver were compared independantly with the ♀♀ from Travellers Rest and the ♀♀ from Kompanjiesdrift. In the former comparison, a C.D. value of 0.45 (i.e. far below 75% J.N.O) and in the latter comparison a C.D. value of 0.39 (i.e. even less than the former value) was attained.

It/...

It is clear that there is a great degree of overlap in all cases. Based on these figures, it is therefore proposed in the present work that the subspecific rank of intermedius is not valid and that the species suillus be interpreted as monotypic.

Finally, it is evident that the possibility of a size cline exists in the available study material. It has been attempted above to prove that there seems to be no valid reason to credit the Klaver specimens with subspecific rank. If they are thus accepted as members of the nominate race the following observations become evident when C.B. length and L.J. length (♀♀) is considered: the smallest individuals occur at Klaver and the size increases gradually in a southernly direction via Kompanjiesdrift, until Cape Town and vicinity is reached where the largest specimens are encountered (See Table 8.5). This size gradually decreases when the Knysna locality is approached. The specimens from Travellers Rest however, (south east of Klaver) show a slight increase in size.

Table 8.5. Size variation in C.B. length in B. suillus.

	C.B.	L.J.
Klaver M =	52.4 mm. (N=4)	M = 30.5 mm. (N=4)
Kompanjiesdrift	54.8 mm. (N=8)	32.8 mm. (N=7)
Cape Town and vicinity	59.5 mm. (N=6)	36.0 mm. (N=5)
Knysna and vicinity	55.8 mm. (N=3)	33.7 mm. (N=3)
Travellers Rest	55.1 mm. (N=13)	34.1 mm. (N=14)

Biological:

All the known localities at which B. suillus have been collected are below 1,000' above sea-level. This is understandable in view of the fact that these animals are virtually confined to the soft sands and sand dunes adjoining the coast. This species is apparently not encountered on mountains and/or mountain slopes, where rocky substrata prevail.

Botanically speaking, the animals range through the following types of vegetation: Karroo succulent steppe, Cape macchia and temperate and subtropical evergreen forests (Keay, 1959). It is doubtful whether this geographical distribution points to any correlation, for it is unlikely that the animals live on the dominant plants on which the different vegetation maps are based. Virtually nothing is known about the food and feeding habits of Bathyergus suillus.

Furthermore, there seems to be no correlation with rainfall in the range where these animals occur. It seems that they do not occur at places with a rainfall less than 100 mm. (0-4") but do occur at various rainfall intensities up to 801-900 mm. (32-40") per annum, e.g. in the vicinity of Knysna and Belvedere.

It appears that the animals disperse via soft alluvial soils along the river beds. An interesting example of this kind of dispersal is seen in the case of the Travellers Rest specimens. These animals must have migrated beyond Klaver in a southernly direction along the Olifants river and then turned eastwards along the Doring river, (a tributary of the Olifants river) which flows between the Gifberge and Nardouw mountains. This river forms a wide flat sandy valley between the Bokkeveld mountains to the north and the Pakhuisberge to the south. Again, a tributary of the Doring River is the Brandewyn river which flows past Travellers Rest. At Travellers Rest the elevation rises slightly above 1,000'. Similarly, the animals may have migrated down the Olifants river to Citrudal but not further south down that river, for southwards the valley narrows down, squashed between the Kouebokkeveld mountains and the Olifantsriver mountains, both mountains giving rise to the north flowing Olifants River.

In a similar fashion, they may have spread from Lambert's Bay and Kompanjiesdrift via the Verlorenvlei river and Kruis River to Eendekuil and vicinity. Furthermore, they may have penetrated southwards via the Berg river up to Franschhoek, where Roberts has reported them (Roberts, 1951, 380). No specimens from this locality is available in the present study collection. The Cape and Cape Peninsula seems to be a natural cul-de-sac for these animals, and their eastward distribution could have occured via the Klein Berg river, past Wolseley, and down the Breede River, extending its range as far eastwards as Knysna and, according to Roberts (1951, xxvii), Plettenberg Bay.

Additional biological information pertaining to B. suillus has been given in Chapter 6 and will not be repeated here. Attention may however be drawn to the known parasites of this species, which include the following:

Plathyhelminthes: gen.et sp. indet.

Nemathelminthes: Trichuris sp., Heterakis macrospiculum, Libyostrongylus bathyergi, Longistriata bathyergi. Arthropoda: Ixodes alluaudi, Haemaphysalis leachii mühsami, Proenderleinellus lawrensis and Cryptoctenopsyllus ingens (de Graaff, 1964, 122).

Phylogenetic:

According to Roberts (1951, 343) the Bathyergidae contain a large number of species "seemingly indicating a modern origin, with the exception perhaps of Bathyergus." The animals may have invaded their present geographical localities from the north-west and have migrated, via the soft soils of the water courses down to the Cape and eastwards to Knysna via the Breede River. Probably an evolved species, seen in terms of its large size.

List of localities:

Belville, 4 (TM), Belvedere, Knysna, 5 (TM), Bredasdorp, 1 (TM), Cape Flats, 1 (SA), Cape Town, 2 (SA), Citrusdal, 4 (KM, TM), De Hoop, 1 (MM), Drostdy, Tulbagh, 1 (ME), Eendekuil, 3 (TM), Elsies River, 1 (SA), Goodwood, 1 (SA), Greenpoint, 1 (KM), Kersfontein, 1 (KM), Koeberg, 2 (SA), Hazendal, 1 (SA), Het Kruis, 10 (KM), Kalk Bay, 1 (SA), Klaver, 6 (TM), Knysna, 10 (SA, TM), Kompanjiesdrift, 48 (KM, NM, EM, PE, MM), Lambert's Bay, 5 (TM, MM), Maitland, 4 (TM), Malmesbury, 1 (TM), Mowbray, 1 (SA), Rondebosch, 1 (SA), Stilbaai, 3 (TM), Strandfontein, 2 (SA), Travellers Rest, 38 (NM, PE, KM, AM, EM), Tulbaghkloof, 1 (ME), Vogelsvlei, Gouda, 3 (ME), Wynberg, 1 (SA), Zoetendalsvlei, 2 (TM).

CHAPTER 9

BATHYERGUS JANETTA THOMAS & SCHWANN 1904

During 1903, Mr. C.H.B. Grant continued collecting natural history specimens in the Cape Colony for the British Museum. As far as that institution was concerned at that time, Namaqualand had been almost entirely neglected by collectors, with the exception of a few specimens obtained there by Dr. Andrew Smith about 1830, ".... and the little set collected by Dr. R. Broom at Port Nolloth in 1897 ..., being the only mammals that the Museum has ever received from that country" (Thomas & Schwann, 1904, 172). Among the specimens collected by Grant was a bathyergid which Thomas and Schwann thought to be worthy of specific distinction, and this animal they proposed to call Bathyergus janetta.

This find was also of interest as ".... being the second species of so peculiar and long known a genus as Bathyergus, otherwise confined to the Cape" (Thomas & Schwann, op.cit.). It is clearly darker in colour and smaller in size than the Cape representatives of the genus.

As here understood, Bathyergus janetta is a monotypic species, confined to the vicinity of Port Nolloth. This is in contrast to Roberts (1951, 381) who interprets this species as polytypic (i.e. recognizing B. janetta janetta, B.j. inselbergensis and B.j.plowesi as subspecies), and Ellerman et.al. (1953, 228) who consider this species to be conspecific with Bathyergus suillus.

Bathyergus/...

Bathyergus janetta Thomas & Schwann

Bathyergus janetta Thomas & Schwann, Proc. zool. Soc. No. 1: 180, 1904. Type locality: Port Nolloth, Cape Province.

B. j. inselbergensis Shortridge & Carter, Ann. S.Afr. Mus., 32: 290, 1939. Type locality: Ezelfontein, Kamiesberg, Cape Province.

B.j. plowesi Roberts, Ann. Transv. Mus. 20: 4, 315, 1946. Type locality: Oranjemund, South West Africa.

Type specimen: British Museum (Nat.Hist.), ♀, no.545, collected on August 3rd, 1903. Collector: C.H.B. Grant.

Type locality: Port Nolloth, Cape Province.

Distribution: (Fig. 9.1).

According to Thomas and Schwann it is common on the white sands of Port Nolloth. They also occur on the Kamiesberge, approximately 120 miles south-east of Port Nolloth. Furthermore, they are known to occur at Oranjemund (i.e. just to the north of the northern bank of the mouth of the Orange river).

Diagnostic characters:

In size much smaller than B. suillus, H.B. M = 205 mm., C.B. M = 516 mm. (♂♂). Dorsal area, for a breadth of about 2 inches, seal-brown, contrasting markedly with the drab-grey of the shoulders and sides. Ventral surface dark. Head usually blackish. Skull pronouncedly smaller than B. suillus, less heavily ridged. Incisors grooved, not extending beyond molars.

Colour

The most conspicuous feature in B. janetta is the medium dark band which runs along the back.

Thomas and Schwann have described the colour as seal-brown, covering virtually the entire dorsal area, with an average width of approximately two inches, which contrasts markedly with the drab-grey of the shoulders and sides. This drab-grey colouration does not differ materially from that seen in the Cape specimens (i.e. B.suillus). Ventrally, the fur is 'blackish-slaty' and on the whole, of a darker hue than in B.suillus. The chin area often has a sharply defined white patch. Furthermore, in contrast to B. suillus the majority of individuals show no frontal (occipital) spotting on the generally darkish coloured head: any tendency towards spotting is often represented only by a thin white stripe (line) along the top of the nose. As in B. suillus, the area round the ear is white and the brighter colour of the flanks commence just posterior to the ear. Proximally, the limbs are a dark slaty-grey while the hands and feet are usually off-white.

The fringing hairs of the tail are a dull whitish colour with the central part of the tail a pale brown.

Specimens from Kamiesberg differ from the coastal specimens in that the general colour above is silvery-grey instead of drab-grey and thus the seal-brown dorsal and occipital area tends to contrast more sharply with the flanks having an almost frosty appearance. Piebald varieties occur sporadically.

Size/...

Size:

Adult ♂♂:

H.B. 170-235 mm., M = 205 mm.
T. 41-52 mm., M = 48 mm., (23.4% of H.B.)
HF. 38-43 mm., M = 41.0 mm., (20.0% of H.B.)
C.B. 41.1-54.8 mm., M = 51.6 mm.
B.C. 16.7-19.5 mm., M = 18.4 mm., (35.6% of C.B.)
I.C. 8.9-10.2 mm., M = 9.4 mm., (18.2% of C.B.)
Z.W. 26.5-37.2 mm., M = 31.2 mm., (60.4% of C.B.)
M.W. 8.9-12.5 mm., M = 10.3 mm., (19.9% of C.B.)
U.T.R. 7.5-9.1 mm., M = 8.2 mm., (15.8% of C.B.)
L.J. 24.8-34.6 mm., M = 30.3 mm., (58.7% of C.B.)
L.T.R. 8.2-9.7 mm., M = 8.8 mm., (17.0% of C.B.)

Adult ♀♀:

H.B. 170-206 mm., M = 183 mm.
T. 40-50 mm., M = 44 mm., (24.0% of H.B.)
H.F. 34.40 mm., M = 37.6 mm., (20.5% of H.B.)
C.B. 40.4-50.7 mm., M = 43.9 mm.
B.C. 17.2-18.8 mm., M = 17.9 mm., (40.7% of C.B.)
I.C. 8.8-9.6 mm., M = 9.2 mm., (20.9% of C.B.)
Z.W. 26.5-33.8 mm., M = 28.4 mm., (64.6% of C.B.)
M.W. 8.6-10.8 mm., M = 9.2 mm., (20.9% of C.B.)
U.T.R. 7.0-8.2 mm., 7.6 mm., (17.3% of C.B.)
L.J. 25.4-31.6 mm., 26.8 mm., (61.0% of C.B.)
L.T.R. 7.6-9.2 mm., M = 8.3 mm., (18.9% of C.B.)

A comparison between B.suillus and B. janetta shows clearly that the former is much larger than the latter species from Port Nolloth: the mean H.B. length equals 281 mm. (♂♂) in the Cape specimens in contrast to 205 mm. (♂♂) in the specimens from Port Nolloth.

As/...

As was the case in B. suillus, sexual dimorphism is also evident in B. janetta. The ♂♂ are significantly larger than the ♀♀. When five ♂♂ and 12 ♀♀ from Port Nolloth are compared in respect of C.B. length, ♂♂(M= 51.6 mm. ± 9.65 mm.) are significantly larger than the ♀♀ (M = 43.9 mm. ± 2.549 mm.) at the 2-1% level (t = 2.9, 15 degrees of freedom, P = 0.20-0.10).

Skull and Dentition:

The skull of B. janetta appears to be less heavily ridged compared to B. suillus (Ellerman, 1940, 84). However, no further diagnostic characteristics are to be observed in the skull and dentition, apart from the fact that the M.W. compared to the B.C. width is proportionally greater in B. janetta than in B. suillus.

Discussion:

The two widely diverging points of view held by Ellerman et.al. (1953, 228) on the one hand, and Roberts (1951, 380, 381) on the other concerning the specific status of Bathyergus janetta is illustrated by the fact that the former regard all the forms of Bathyergus tentatively as conspecific whereas Roberts distinguishes between the species suillus and janetta. In the earlier work by Ellerman (1940, 84) the opinion was expressed that the genus contained two well-marked species, the "giant" suillus and the moderate-sized janetta.

It is therefore important to emphasize certain differences existing between suillus and janetta. Comparing B. suillus from the south with B. janetta from Port Nolloth and vicinity, it becomes

evident/...

evident that there is a definite difference in colouration: the former being drab-grey in comparison to the darker individuals with a seal-brown band on their backs in the case of the latter. Apart from differences in colour between the species they also differ greatly as far as size is concerned. The mean H.B. size of *suillus* (♂♂) has been found to be 281 mm. compared to 205 mm. in *janetta* (♂♂) from Port Nolloth. As has been stated elsewhere in the present work, linear measurements (especially as far as H.B. length, T. length and H.F. length are concerned) are often unreliable. However, the difference in size between *suillus* and *janetta* is also reflected in the mean C.B. length of the skull equalling 62.9 mm. in *B. suillus* and 51.6 mm. in *B. janetta*.

In order to provide further evidence illustrating differences which exist between *B. suillus* and *B. janetta* as far as their skulls are concerned, use was made of ratios rather than linear measurements according to the method described in Mayr, Storer and Usinger (1953, 136). Ratios are more useful as taxonomic characters than direct measurements because the variable factor of size is minimized (Mayr *et.al.*, *op.cit.*).

The ratio R is calculated and expressed in the formula $R = \frac{s\ (100)}{l}$, where s = the *s*maller of the two values and l = the *l*arger, thus expressing the size of the smaller value as a percentage of the larger. The ratios can be demonstrated visually in the form of scatter diagrams in which one value is plotted on the abscissa, the other on the ordinate. Using different symbols for the different species the

presence/...

presence or absence of overlaps between populations can be detected quickly.

The two scatter diagrams which have been prepared for the present work, are based on skulls of ♀♀ only in view of the fact that a bigger sample of ♀ janetta individuals was available for study.

As will be seen in fig. 9.2, the ratio $R = \frac{U.T.R.(100)}{C.B.}$ has been plotted graphically, thus expressing the length of the U.T.R. as a percentage of the C.B length. It is clear that there is a definite difference between the two species. In B.suillus the average length of the U.T.R. = 9.6 mm., i.e. approximately 17.2% of the C.B. length, while in B. janetta the corresponding values were 7.6 mm. and 17.3% respectively.

Similarly, the ratios $R = \frac{L.J.(100)}{C.B.}$ were determined and plotted in fig. 9.3, expressing the L.J. length as a percentage of the C.B. length. Again the differences between the two species become evident: in B. suillus the average length of the L.J. = 33.6 mm., i.e. approximately 60.2% of the C.B. length, while in B. janetta the corresponding values are 26.9 mm. and 61.4% respectively.

Statistical analysis of these scatter diagrams show that the group averages differ significantly in the two species.

Based on the results given above, I am inclined to conclude that we have here two separate species: differing in certain ratios in the skull, in overall body size and in colour. Therefore, I do not agree with Ellerman et.al. (1953) who interpret the forms suillus and janetta as conspecific.

For/...

For the purposes of this work, the two other 'accepted' subspecies, B.janetta inselbergensis and B.j.plowesi are provisionally treated as synonyms of B. janetta. Unfortunately, there is a paucity of material as far as these forms are concerned. In the case of B.janetta inselbergensis, only four specimens are known to science, while the subspecies B.j.plowesi has been defined on two specimens only.

The inselbergensis specimens were described by Shortridge and Carter (1939, 290) with type-locality Ezelfontein, near Kamiesberg in Namaqualand. The type specimen is housed in the Kaffrarian Museum, being an adult ♀, original number 977, collected on December 4th 1936 at an altitude of approximately 4,400'. Compared to the coastal individuals occurring at Port Nolloth, the general colour along the dorsal seal-brown area is a silvery-buff instead of a drab-grey in the coastal specimens. Consequently, the seal-brown dorsal and occipital areas contrast much more sharply with the flanks. According to Shortridge and Carter, this greater contrast is also seen in the dark forearms and thighs so that the flanks appear to have a frosty appearance. Other differences described by the authors, are that the dorsal tail hairs are slaty black basally instead of pale brown, with a buff-white colour terminally. The hairs on the forefeet "are whiter, less soiled looking, than in the typical janetta."

In order to evaluate the validity of the differences which exist between the inselbergensis material and the material from Port Nolloth, one is once again handicapped by the small sample in the former case. Statistically speaking, whenever a

difference/...

difference exists of ± 9 S.D., it is virtually one-hundred percent sure that one is dealing with two different species. Similarly, a value of 4.5 S.D. applies to subspecific differences. The available material from Kamiesberg was compared with material from Port Nolloth for the different measurements used in the present work: in all but two measurements (i.e. U.T.R. and L.T.R.) the values for B. janetta inselbergensis fall well within the 3 S.D. ranges exhibited by B. janetta specimens from Port Nolloth (See fig. 9.4).

Eventually, some information may become available which may serve as a basis for subspecific separation of B.j.inselbergensis from B.janetta janetta. However, this will only become evident when more material from Kamiesberg is obtained. It should also be remembered that the inselbergensis material was originally described as a mountain race of B.janetta and that the find was unexpectedly interesting, the ".... previously known forms being only known to occur in low-lying coastal sandplains". Consequently, they differ in their habitat which they occupy (4,000-5,000' compared to less than 1,000' above sea level) which may have induced the silvery-buff frosty colouration on the flanks. On the other hand, feet looking less soiled, is hardly a criterium for subspecific separation. The present author, on comparing the specimens from Kamiesberg to those obtained from Port Nolloth, found that phenotypically speaking, one could point to specimens from Port Nolloth which also showed a tendency for their flanks to be silvery buff. In other words, within the material from Port Nolloth, one can encounter specimens

which/...

which are phenotypically virtually identical to the specimens from Kamiesberg. This observation is in direct contrast to what Roberts (1951, 381) has stated: ".... the colour markings of the animal seem to indicate specific isolation of B. suillus and B. janetta." As far as size is concerned, Roberts stated that the mountain form is considerably larger than the coastal form and almost as large as B. suillus intermedius from Klaver. This larger size is apparent in all the different characteristics which were compared but these differences are not statistically acceptable. According to Roberts (1951, 381) these animals are only known from the type locality hitherto: but, he states, that they could probably be found elsewhere in the hills, e.g. between Springbok and Kamaggas, where he had seen mounds on strips of sandy ground.

Roberts (1946, 315) described Bathyergus janetta plowesi as another subspecies. The type locality was designated as Oranjemund, South West Africa (north of mouth of Orange River), the type being an immature ♀ $\underline{M3}$ erupted but not worn), T.M. no. 9795. In addition to the type specimen, another juvenile specimen (♂) was also collected at the same place. According to Roberts, the nature and distribution of the markings of the animals are much the same as in B. j. janetta from Port Nolloth, but, instead of being seal-brown dorsally, the area from the nose to the root of the tail is dark brown, almost black. This black colouration is also seen in ".... the cheeks, limbs and underparts from chin to vent, while the sides from the ears, side of neck and shoulders to upper part of thighs and side of rump

are/...

are almost white, with the barest trace of, instead of being conspicuously, buffy." According to Roberts (1951, 381) if one were to allow for the difference in age (the type of plowesi being immature), it would seem to be of the same size as the typical janetta from Port Nolloth. As has been stated for B. j. inselbergensis, I feel that too little material is available for the erection of a new subspecies. Many specimens from Port Nolloth are also darker than seal-brown dorsally, i.e. which could also be called black.

For the purposes of the present work, the two subspecies inselbergensis and plowesi are both considered to be conspecific and adult individuals should be obtained which may show these forms to be well within the variation range of B. janetta. However, it is proposed not to formally sink these two subspecies, but to retain them tentatively under janetta and to call them forms in the taxonomical sense of the word as defined by Mayr, Storer and Usinger (1953, 35). Until more evidence is forthcoming, I do not think that the subspecific rank credited to inselbergensis and plowesi is justified: this is also coupled to the fact that we do not as yet know exactly what the geographical range of B. janetta is.

It is known that B. janetta occurs in the white sands in the vicinity of Port Nolloth and extends inland up to 15 or 17 miles. There after however, information peters out. Similarly, Roberts (1951, 381) only assumed that the mounds seen between Kamaggas and Springbok could have been thrown up by B. janetta occurring on the mountains at Kamiesberg. Specimens (2 only) from Oranjemund have not yielded much regarding the geographical distribution of the supposed subspecies.

Shortridge (1934, 318) states that the distribution of B. janetta could possibly include the coastal sand dunes of Little (and Great?) Namaqualand. Similarly, he quotes Berseba hottentots informing him of the existence of a large "duin mol" along the coastal sand dunes between Luderitz and the mouth of the Orange river. According to Shortridge, this information was subsequently supported by several Europeans from Luderitz. Furthermore, the occurrence of the animals is said to be scarce. From this it can also be inferred how little is known about the animals and how tentative their subspecific ranks should be regarded. It could well be that with sufficient collecting, these forms would fall within the variation range exhibited by B. janetta from Port Nolloth (as specimens from Kamiesberg and Oranjemund have done).

Biological:

In contrast to Bathyergus suillus, where some information is available about the biology of the animals, virtually nothing is known about B. janetta. However, differences are to be expected, since B. janetta occupies more diverse habitats (e.g. mountainous regions) compared to B. suillus which appears to be limited to the soft soils of river tributaries and coastal sand dunes, below 1,000' above sea level.

Phylogenetic:

It is of interest to note that the M.W., compared to the B.C. width is proportionally greater in B. janetta than it is in B. suillus. In juvenile

skulls/...

skulls of bathyergids, the muzzle width is also proportionally greater than in adult specimens, where the width of the muzzle compared to the braincase width diminishes somewhat. This may be interpreted as a paedomorphic character which is still shown in _B. janetta_. It may be reasonable to assume from this that of the two species, _B. janetta_ is probably the oldest phylogenetically speaking, which has given rise in the course of time to the larger and possibly more advanced _B. suillus_. Advanced characteristics in this instance could be coupled to the larger size attained by _suillus_ and its greater geographical distribution.

List of localities :

Port Nolloth, 126 (KM, SA, NM, PE, TM, EM, MM),
Ezelfontein, near Leliefontein, Kamiesberg, 4 (KM),
Oranjemund, 2 (TM).

CHAPTER 10

GEORYCHUS CAPENSIS (PALLAS) 1778

The so called 'blesmol' was first referred to as Mus capensis by Pallas in 1778, the type locality being given as the Cape of Good Hope. According to Sclater (1901, II, 75), Masson (1776, 305) made the first allusion to the species as the "blesmol", while Buffon (1776, 193, 1782, 251) supplied the earliest description of this animal. Furthermore, Sparrman (1785, 211) supplied notes on the habits and occurrence of the animal, followed by Thunberg in 1795 (p. 262), describing and naming the animal as Marmota capensis.

In 1811, Illiger proposed the erection of a new genus for this species, viz. Georychus (p. 87). He used Mus capensis Pallas as the genotype for the suggested separate generic rank. Cuvier again referred to the identical animal as Mus buffoni in 1834 while Lichtenstein, editing Forster's Descriptiones Animalum (1844, 364) referred to this species as Fossor leucops. It was also referred to as Bathyergus capensis by a number of early authors (e.g. Smuts (1832, 49), Waterhouse (1842, 81)), while A. Smith (1826, 29) apparently first referred to this animal as Georychus capensis. Although the generic rank of these animals was already proposed in 1811, this misnaming of the specimens can only be ascribed to the possible non-availability of Illiger's proposal. Subsequent to Smith's 1826 description of the animal however, it has been constantly referred to as Georychus capensis by various authors (e.g. Grill

(1858,/...

(1858, 19), Layard (1862, 55) and Moseley (1892, 125)), to mention only a few examples from the 19th century.

For the purposes of the present work, the species is regarded as monotypic, occurring mainly in sandy or loose soils in the Western Province, extending eastwards to the eastern Cape Province and Natal (e.g. at Nottingham Road), while it has also been collected at Belfast and Ermelo in the Transvaal highveld.

Roberts (1951, 382) divided the species into three subspecies, based mainly on colour variations encountered in specimens from Knysna and Belfast. Ellerman _et.al_. (1953, 229) however, only accept the one species i.e. _Georychus capensis_ and list Roberts' proposed subspecies _Georychus capensis capensis_, _G.c. canescens_ and _G.c. yatesi_ as possible races. The interpretation adhered to by the present author corresponds to a great degree to that offered by Ellerman _et.al_. The possibility of the species being polytypic, as proposed by Roberts, is rejected.

Georychus capensis (Pallas)

Mus capensis Pallas, Nov. Spec. Quad. Glir. Ord., 76, 172, 1778. Type locality: Cape of Good Hope.

Mus buffoni Cuvier, _Ann. Sci. Nat. Zool_. (2) _1_: 196, 1834. Type locality: Cape of Good Hope.

Fossor leucops Lichtenstein, in Forster's _Descript. Anim_. (edited by Lichtenstein), 364, 1844. Type locality: Cape of Good Hope.

Georychus capensis canescens Thomas & Schwann, _Proc. zool. Soc_. 165, 1906. Type locality: Knysna, Cape Province.

Georychus capensis yatesi Roberts, _Ann. Transv. Mus_., 4: 92, 1913. Type locality: Belfast, Transvaal.

Type specimen:

Not in existance, according to Shortridge (1934, 328).

Type locality:

Vaguely described as the Cape of Good Hope by Pallas, while Shortridge (1934, 328) states that the type specimen was obtained from the Cape Flats near Cape Town.

Distribution: (Fig. 10.1).

Confined to the Republic of South Africa. In the Cape Province it occurs mainly near the coast. It is frequently encountered in the Cape Peninsula, and according to Roberts (1951, 382), extends into the mountains in the vicinity of Tulbagh and Worcester. Ellerman et.al. (1953, 229) state that specimens are known from Citrusdal and Nieuwhoudtville, the latter **locality** possibly being its most northern point of distribution in the western Cape area. From the Western Province, its range of distribution extends eastwards along the coast to the vicinity of Port Elizabeth, while Shortridge (1934, 328) also quotes specimens from the Bathurst district to the east of Port Elizabeth. Shortridge also states that specimens have been taken at Nottingham Road in Natal (approximately 65 miles inland from the Natal coast), while this species has also been collected at Belfast and Ermelo in the Transvaal highveld. It is of interest to note that no specimens have hitherto been collected between Belfast and Nottingham Road, nor between the latter locality and the Bathurst district apart from an isolated study skin taken in "Pondoland".

This/...

This species thus occurs sympatrically with the larger *Bathyergus suillus* and the smaller *Cryptomys hottentotus* in the Western Province and southern coastal belt to the Eastern Province.

Diagnostic characters:

The colouration of this species seems to be its most characteristic feature. The face is prettily coloured in black and white with the general overall colouration more or less buffy to buff-orange. The hindmost molars show infolding of the enamel pattern, even when well worn, and are cut late in life. The jugal bone fits into the zygoma in a dove-tail fashion. It is usually much larger than *Cryptomys* and far smaller compared to *Bathyergus*. The pelage is thick and woolly. Size smaller than *B. suillus*: H.B. M = 189 mm., C.B. M = 48.3 mm. (♂♂).

Colour:

The most characteristic feature of this species is the fact that the face is prettily marked (Roberts, 1951, 382), while the general colouration is more or less buff to buffy-orange "... with a variable tipping of brown to the hairs." The following parts of the face are usually white: muzzle, the areas round eyes and ears and a frontal patch. These white areas are usually projected against a background of black about the face. The facial markings vary in the amount of white and black present.

Dorsally, the colour of the pelage varies considerably ".... even in the same colonies from a dark greyish to an orange cinnamon...." (Roberts, 1951, 382) while the back has also been described as a uniform isabella-brown ("obsolete rufescens", Pallas). The hands, feet and tail are also white.

Complete or partial albinism is encountered, ranging from pure white individuals to light grey to creamy orange.

Geographical variation in colouration is evident. Specimens from the vicinity of Knysna are more drab-coloured, while specimens east of Port Elizabeth tend to be more brightly coloured, compared even with specimens from the Western Province.

Juvenile specimens are decidedly darker in colouration, portraying a slaty grey colour dorsally.

Size: Adult ♂♂:

H.B. 177-200 mm., M = 189 mm.
T. 25-40 mm., M = 31 mm., (16% of H.B.)
H.F. 30-35 mm., M = 32 mm., (16% of H.B.)
C.B. 44.1-53.3 mm., M = 48.3 mm.
B.C. 17.0-18.8 mm., M = 17.8 mm., (36.8% of C.B.)
I.W. 9.0-10.5 mm., M = 9.5 mm., (19.6% of C.B.)
Z.W. 35.1-39.9 mm.., M = 37.9 mm., (78.4% of C.B.)
M.W. 9.3-11.8 mm., M = 10.9 mm., (22.5% of C.B.)
U.T.R. 7.6-9.4 mm., M = 8.0 mm., (16.5% of C.B.)
L.J. 32.7-38.0 mm., M = 34.6 mm., (71.6% of C.B.)
L.T.R. 7.5-8.6 mm., M = 8.0 mm., (16.5% of C.B.)

Adult ♀♀:

H.B. 155-204 mm., M = 182 mm.
T. 20-33 mm., M = 26 mm., (14% of H.B.)
H.F. 27-35 mm., M = 29 mm., (15% of H.B.)
C.B. 41.0 - 51.2 mm., M = 45.1 mm.
B.C. 15.8-20.3 mm., M = 17.3 mm., (38.3% of C.B.)
I.W. 8.6-10.3 mm., M = 9.4 mm., (20.8% of C.B.)
Z.W. 30.1-40.4 mm., M = 32.8 mm., (72.7% of C.B.)
M.W. 8.4-11.7 mm., M = 9.4 mm., (20.8% of C.B.)
U.T.R. 6.8-8.5 mm., M = 7.8 mm., (17.2% of C.B.)
L.J. 28.4-37.8 mm., M = 31.6 mm., (70.0% of C.B.)
L.T.R. 6.6-9.6 mm., M = 7.8 mm., (17.2% of C.B.)

The/...

The size is geographically variable: specimens from the vicinity of Worcester tend to be larger than those of the Cape Peninsula. When nine ♀♀ from de Wet near Worcester are compared with five ♀♀ from Port Elizabeth, in respect of the zygomatic width, it was found that the former (M = 35.0 ± 2.526 mm.) are significantly larger than the latter (M = 30.3 ± 4.738 mm.) at the 1.0% level (t = 3.04, 12 degrees of freedom, P = 0.01).

Skull and dentition:

The skull is usually larger than in *Cryptomys*, while the jugal bone fits in a dove-tail fashion into the zygoma. Furtheremore, as was indicated earlier on in the present work (see Chapter 4 describing the bathyergid skull), the nasals do not project very far beyond the ascending processes of the premaxillaries on meeting the frontals as is the case in *Cryptomys*. The infraorbital foramen is small and rounded, the palate being narrow, not wider than the molar teeth (Sclater, 1901, 69). Generally speaking, the skull is robustly built, while sagittal crests are often present in old individuals. The mandibles are not ankylosed (as in the other genera of this family), permitting movement of the tips of the incisors for (possibly) the better gripping of bulbs for conveyance to storage chambers. The muzzle does not protrude in the living animal as in *Bathyergus* (Roberts, 1951, 382).

The upper cheek teeth have one narrow inner and outer fold each; these infoldings of enamel tend to remain present until the molars are well worn, whereas these infoldings are to be seen only in the young specimens of *Bathyergus* and *Cryptomys*. *Georychus*

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is thus the only member of the family without simplified rounded (ovate) cheek teeth in the adult. The lower cheek teeth have one outer fold persistant, and one inner fold, tending to become weak or obsolete (Ellerman, 1940, 86).

The posterior cheek teeth are cut late in life.

The upper incisors are not grooved (cf. Bathyergus), while their roots are situated in the pterygoidal region behind the molars, thereby possibly checking the development of the posterior molars in this genus as well as in Cryptomys. As was pointed out above, the lower ungrooved incisors have a limited degree of movement, due to the non-ankylozation of the two hemijaws at the symphysis.

Roberts (1951, 382) states that the normal number of teeth (i.e. molars) consists of two premolars and two molars above and below while in some abnormal cases a third molar is present above and/or below. This condition has however not been encountered in the study material available to the present author.

Discussion:

In the present work, Georychus capensis is regarded as a monotypic species (in contrast to the polytypic species interpretation adhered to by Roberts) and therefore this view requires some degree of explanation. Before discussing these aspects however, additional information should be given pertaining to aspects of size in this species.

Roberts (1951, 382) states that the ♂♂ are normally smaller than the ♀♀ in this genus whereas the reverse is usually the case in the other genera. As

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far as <u>Bathyergus</u> and <u>Cryptomys</u> are concerned, Roberts' observation seems to be correct, but in the present work I have come to the tentative conclusion that in <u>Georychus</u> the ♂♂ are also slightly larger than the ♀♀. In fact, the mean H.B. size for ♂♂ and ♀♀ was found to be 189 mm. and 182 mm. respectively, while the C.B. lengths were found to be 48.3 mm. and 45.1 mm. respectively. The greatest discrepancy in size was found in the width of the zygomatic arches, where the ♂♂ were far larger than the ♀♀.

Roberts (1951, 382-384) proposed a polytypic interpretation for <u>Georychus capensis</u> whereas in the present work this species is interpreted as monotypic. One of the main reasons why I am not inclined to acknowledge the different subspecies, is the great degree of variation in shade of colour, as well as in the facial markings, encountered within the species. Roberts (1951, 383) also commented on the occurrence of this individual variation and indicated that only average differences could be taken as a criterion ".... of the prevailing geographical types". It is of importance to note that in a series of 30 skins of all ages, collected at the same locality (de Wet near Worcester) not more than 100 yards square, no two specimens were exactly alike in colour. An element of doubt was raised by Roberts when he questioned the number of subspecies worthy of recognition in view of individual variation already noticed in respect of specimens collected at de Wet, Worcester and Tulbagh. Roberts (1951, 383) states that the typical form may be considered to extend over the western districts of the Cape Province, being replaced by the black-faced form, <u>Georychus capensis canescens</u> in the Knysna area.

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It must be pointed out however, that black-faced individuals are also encountered in specimens from the western Cape. The subspecies <u>canescens</u> was first described by Thomas and Schwann in 1906 on a male specimen, collected at Knysna in 1905, the type specimen being housed in the British Museum. It was described as a paler form, with a more "..... strongly contrasted black head" (p. 165). The general colouration of the body was described as being decidedly greyer than that found in the true <u>capensis</u>, the tone nearly matching "smoke-grey" on the fore-back, darkening to drab-grey on the hind-back. These authors also stated that the nose patch, eye patch and ear patch are each rather smaller than in <u>capensis</u>, while the background face colouration is really black instead of slaty blackish as in <u>capensis</u>. The crown patch seemed to be larger, more strongly contrasted, while the area below the ear patch is a greyish-white, continuous with the greyish white of the sides, throat and belly, thereby again differing from <u>capensis</u> in which the area below the ear is more or less tinged with buffy (referred to as the <u>area parotica ferruginea</u> by Pallas).

To my mind however, these differences are rather relative, especially if the fact is taken into consideration that similarly coloured specimens also occur in colonies from the typical <u>capensis</u> group. Therefore, based on colour alone, it is suggested that this subspecies is not recognized.

It is true, that when a number of Knysna specimens are seen simultaneously, the dorsal colouration has a "smoke-grey" merging into drab-grey colouring. We seem to have a parallel situation

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here with the genera Cryptomys and Bathyergus: in these genera, specimens from Knysna and vicinity are decidedly darker in colouration compared to the true C.hottentotus and B. suillus from the Western Province. This tendency towards a darker or drabber colour can possibly be correlated in all three genera with the greater degree of moisture and humidity present in the top soil, which could have a darkening phenotypic effect on the individuals. Similarly, Georychus specimens to the east of Knysna tend to be near "ochraceous-tawny" and of lighter colouration. This is also seen in Cryptomys hottentotus, where the lighter coloured specimens from Port Alfred are virtually identical to those from the western Cape, differing vividly from the Knysna specimens.

Furthermore, morphologically speaking, I could find no reasons for separating canescens as a separate subspecies from capensis. As an example, the zygomatic width may be quoted: when nine ♀♀ from de Wet, Worcester, are compared to five ♀♀ from Port Elizabeth in respect of the Z.W., a calculated C.D. = 0.64 was obtained, which is below 75% J.N.C. i.e. below the level of subspecific distinctness of separation. This result has also prompted me to synonymize canescens with capensis, based on the available study material (See fig. 10.2).

Finally, in 1913 Roberts described Georychus yatesi as a separate species from Belfast in the Transvaal Highveld (Roberts 1913, 92) and demoted the specimens from specific to subspecific rank in 1951. The overall description of yatesi compares favourably with the description of the typical capensis, but whereas the basal portions of the individual hairs are described as slaty grey in capensis, they are referred to as dark brown in the case of yatesi. The upper surface of the body was described as rich buff-orange merging with clear buff-orange flanks. It remains to be pointed out that a similar colouration can also be demonstrated in specimens from the western Cape (i.e. capensis) and that based on colouration, I feel that the highveld specimens do not deserve separate subspecific rank.

A number of differences in the skull was also described by Roberts (1913, 92). These included a larger braincase, and a more conspicuous outward projection of the frontals in the anterior angle of the orbital region. In the type specimen the coronoid process of the mandible is broad and rounded, not pointed as in specimens from the Cape (Roberts, 1951, 384). It is evident however, that these supposed differences can also be demonstrated to be present in the typical capensis species and that they do not seem to be of any diagnostic value.

As far as the dentition is concerned, the cheek teeth were described as being much larger in the first two molar elements in yatesi than in capensis, while the hindmost tooth in the upper jaw is smaller and of different pattern, not showing the lateral infoldings. As was the case in its colouration and skull, conditions supposedly indicative of the subspecific status of yatesi (referring to the molars) can also be seen in capensis specimens from the Western Province, as well as in specimens from Knysna.

It may thus be interpreted that yatesi does not deserve subspecific status when colouration and morphological aspects are compared. Unfortunately,

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the number of specimens from the Transvaal highveld are few, in fact only three specimens are hitherto available in study collections. It was therefore not possible to attain any statistical parameters of the eastern Transvaal specimens. The H.B. length, T. length and H.F. length given for the type are 180 mm., 25 mm., and 32 mm. respectively. This compares favourably with specimens collected in the western Cape Province.

When the facts given above are considered, it seems advisable that the subspecific rank of yatesi is not acknowledged, until a larger sample of these specimens become available for a more detailed statistical analysis.

Biological:

Very little is known about biological aspects of these animals.

As is the case in the other genera, they feed on bulbs and roots found by burrowing tunnels under the ground. They are inclined to burrow rather superficially under the soil and the mounds are smaller than would be expected if the size of Georychus capensis is compared to Cryptomys hottentotus (Roberts, quoted in Shortridge, 1934, 329). The mounds are however far smaller compared to those thrown up by Bathyergus. Blind tunnels in the tunnel system are often prevalent, while the main burrow ends in a somewhat rounded chamber with smooth walls where food is stored. It is stated that to prevent sprouting, eyes or buds are removed from tubers or bulbs by the incisors (Shortridge, 1934, 328). Landry (1957, 71) quotes Tullberg who pointed out that Georychus does not chew its food much, for large pieces of roots (up to 10 mm. in length)

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are found in the stomachs.

The claws are less obviously adapted to digging compared to Bathyergus, in the sense that the forefinger claws are shorter. This may imply that the upper and lower incisors are used more frequently when tunneling through harder soil. As far as this aspect of behaviour is concerned, there is thus a greater correspondence with Cryptomys.

They occur in cultivated (where they do much damage to tuberous crops) and uncultivated sandy soils.

The mammae usually consist of two pairs of pectoral and one pair of inguinal. In some (possibly abnormal ?) cases, two pairs of inguinals may be present.

Parasites include the following: Protozoa: Meistoma georychi. Plathyhelminthes: Echinococcus sp. Nemathelminthes: Trichuris sp. Arthropoda: Ixodes alluaudi and Cryptoctenopsyllus ingens (de Graaff, 1964, 123).

Nothing is known about breeding biology or predators.

Finally Beddard (1902, 481) may be quoted giving some interesting measurements concerning the alimentary canal of Georychus capensis: small intestine, 25" long (625 mm.,), caecum, 4" long (101.6 mm.), large intestine, 15" in length (381.0 mm.).

Phylogenetic:

Not much can be said concerning this aspect of Georychus capensis. It could well be that this genus is perhaps the oldest in the family, for the back teeth retain, until well worn, the infoldings of enamel that are to be seen in the young of other genera. It may therefore be an illustration of the Principle of Recapitulation. Furthermore, the genus is more closely related to Cryptomys than to Bathyergus, especially if the overall shape of the skull is taken into consideration, as well as the structure and configuration of the dental elements.

List of localities:

Alexandria, 6 (TM, AM), Bathurst district (Shortridge, 1934, 328), Belfast, 2 (TM), Bellville, 1 (TM), Bredasdorp, 1 (SA), Camps Bay, 2 (TM), Cape Aghulas (Ellerman et.al., 1953, 229), Cape Flats, 1 (SA), Cape Town, 6 (SA), Cederberg (Ellerman et.al., 1953, 229), Charlesford, Knysna, 2 (ME), Citrusdal 1, (TM), Constantia, 1 (SA), De Doorns, 2 (SA), De Wet, Worcester, 25 (TM), Diep Rivier, 1 (SA), Drostdy, Tulbagh, 4 (ME), East London, 1 (EM), Ermelo, 1 (TM), George, 2 (AM), Goodwood, 2 (SA), Grey's Pass, 1 (TM), Hout Bay (Ellerman et.al., 1953, 229), Kenilworth, Cape Town, 1 (MM), Knysna, 3 (SA, AM), Kuils River, 1 (SA), Maitland, 4 (TM), Nottingham Road, 1 (NM), Newlands, 2 (AM), Nieuwhoudtville (Ellerman et.al., 1953, 229), Paarl, 7 (TM, AM), "Pondoland", 1 (AM), Port Alfred, 1 (AM), Port Elizabeth, 18 (TM, AM, PM), Rondebosch (Ellerman et.al., 1953, 229), Stellenbosch, 1 (TM), Simonstown (Moseley, 1892, 125), Three Anchor Bay, 1 (TM), Tokai (Ellerman et.al., 1953, 229), Tulbagh, 2 (TM, SA), Wolseley, 3 (TM), Worcester, 1 (SA), Wynberg, 3 (SA, TM), Zoetendalsvlei, 3 (TM).

CHAPTER 11

CRYPTOMYS HOTTENTOTUS (LESSON) 1826

This bathyergid, known as the common mole-rat or Hottentot mole-rat was first described by Lesson in 1826 as Bathyergus hottentotus from the vicinity of Paarl, Cape Province. The locality was recorded as follows: "Vingt lieues de la ville du Cap, près le village de la Pearl, non loin montagnes de Drackenstein" (Ellerman et.al., 1953, 231). Lesson acted as apothecary on board the French ship Coquille during its voyage around the world, and he thus had the opportunity to encounter this mole-rat during the vessel's sojourn at the Cape.

The following year, in 1827, the same animal was described as B. caecutiens by Brants (1827, 37). The type locality was given vaguely as the eastern part of the colony of the Cape of Good Hope. This was followed in 1829 by yet another description of the identical animal by A. Smith (1829, 439) (vide Sclater, 1901, 78) who named it B. ludwigii and described it as inhabiting ".... various parts of South Africa". In the case of B. caecutiens, Roberts (1951, 397) nominated Knysna as the type locality, while the same author proposed Cape Town as the type locality for B. ludwigii (p. 391).

In 1779 Pallas described the 'blesmol' (i.e. Georychus capensis) from the Cape of Good Hope as Mus capensis (for date of publication see Sherborn, 1891a, 236). As was indicated earlier on in this work, the dune mole-rat Bathyergus was described subsequently/...

sequently in 1782 by Schreber as *Mus suillus*. In 1811, Illiger proposed the erection of the genus *Georychus* for *Mus capensis* and *Bathyergus* for *Mus suillus* for it was evident that these bathyergids differed radically from mice. It is therefore understandable that many subsequent descriptions of mole-rats used the generic ranks of *Georychus* and *Bathyergus* irrespective of the fact whether the different authors were describing *Bathyergus*, *Georychus* or *Cryptomys* as we understand the definition of the different genera today. This explains the fact that the early descriptions of *C.hottentotus* referred to this animal as *Bathyergus hottentotus*, *B. caecutiens* and *B. ludwigii*.

In later years, specimens of *Cryptomys* were referred to the genus *Georychus*, and this procedure was followed until the early years of the 20th century. This seems strange, for already in 1864 Gray proposed the name *Cryptomys* as a subgenus of *Georychus*, genotype *Georychus holosericeus* Wagner. It was only during the present century that the subgenus *Cryptomys* was gradually interpreted as a valid genus. Therefore, many of the species described for *Cryptomys* were first referred to as *Georychus*.

As here understood, *Cryptomys hottentotus* is a geographically variable monotypic species. It ranges from Namaqualand and the south-western Cape eastwards to the Eastern Province, northwards over large stretches of the eastern Karoo and into the southern Orange Free State. Furthermore, it also occurs in the north-eastern Transvaal low country extending westwards in the lower lying country along the Limpopo river, to the vicinity of Pilansberg in

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the central western Transvaal. It thus exhibits an extensive distribution pattern in the Republic of South Africa.

Cryptomys hottentotus (Lesson)

Bathyergus hottentotus Lesson, Voyage autour du monde sur la Coquille, Zool. 1: 166, 1826. Type locality: Vicinity of Paarl, Cape Province.

B. caecutiens Brants, Het Geslacht der Muizen, p. 37, 1827. Type locality: Cape of Good Hope. (Knysna, vide Roberts, 1951, 397).

B. ludwigii A. Smith, Zool. J. 4: 439, 1829. Type locality: Cape Town, vide Roberts, 1951, 391). (Sic ludovigii Sclater, 1899, 229).

Georychus exenticus Trouessart, Cat. Mamm. Viv. Foss. 1899. Error for caecutiens.

G. jorisseni Jameson, Ann. Mag. nat. Hist. 4: 466, 1909. Type locality: Waynek, Waterberg District, Transvaal.

G. albus Roberts, Ann. Transv. Mus., 4: 100, 1913. Type locality: Unknown.

G. vandami Roberts, Ann. Transv. Mus., 5: 273, 1917. Type locality: Griffin Mine, Leydsdorp District, Transvaal.

Cryptomys cradockensis Roberts, Ann. Transv. Mus., 10: 73, 1924. Type locality: Cradock, Cape Province.

C. transvaalensis Roberts, Ann. Transv. Mus., 10: 73, 1924. Type locality: Boekenhoutfontein, on border of bushveld, Pretoria district, Transvaal.

C.hottentottus/...

C. hottentottus (sic) talpoides Thomas & Schwann, *Proc. zool. Soc. Lond.*, p. 166, 1906. Type locality: Knysna, Cape Province.

Type specimen: ?

Type locality: Vicinity of Paarl, Cape Province.

Distribution: (Fig. 11.1)

Occurs in the south-western Cape (as far north as Ezelfontein, near Leliefontein, Namaqualand) and ranges eastwards along the coast to the vicinity of Port Alfred. From the Eastern Province it extends over the eastern half of the Karoo to the area south of Bloemfontein. In the Transvaal, it occurs in the drier western and north-western parts along the Marico and Limpopo rivers extending eastwards to the north-eastern Transvaal lowveld (e.g. Leydsdorp).

Diagnostic characters:

A small to medium sized species, H.B. M = 120 mm., C.B. M = 32.0 mm. (♂♂). Overall colour more or less 'cinnamon-buff' to 'clay colour' dorsally, with a slightly lighter hue on the ventral aspect. White occipital patch usually absent. Mammae: 2 pairs pectoral, 1 inguinal pair = 6.

Colour :

The overall colouration exhibited by this species is uniform whether the colour is 'cinnamon-buff', or 'clay colour' or even varying from 'reddish grey' to 'bluish grey' as the colour has been described for some specimens. The colouration tends to be lighter on the ventral surface than the dorsal surface. The individual hairs have dark-slaty grey bases while the tips show a fawn colouration.

The feet portray a pinkish colour in fresh specimens, darkening to light brown in museum specimens,

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while the tail shows the same dorsal and ventral colouration as the rest of the body.

The colour of the juvenile pelage is decidedly darker than that found in adult specimens.

In the available study specimens, there is no indication of any difference between summer and winter pelages, as far as colour is concerned.

The colouration in specimens representing C. hottentotus which I have seen, shows it to be geographically variable. Those from the south-western Cape tend to possess a richer buff colour, while those from Knysna and surrounding areas are decidedly darker, nearly matching Ridgeway's slate colour, or even darker. Specimens from Port Alfred again compare favourably with those from the western Cape. At the other end of the scale one finds the pale grey colour of specimens from the north-eastern and north-western Transvaal. This variation in colour may be correlated with climatic conditions, especially as far as the moisture content of the soil is concerned.

White patches on the heads are usually absent in this species, and although they do occur infrequently, these are exceptions to the rule.

Size: Adult ♂♂:

H.B.	105-150 mm., M = 120 mm.
T.	17-27 mm., M = 22 mm., (18.2% of H.B.)
H.F.	18-25 mm., M = 21 mm., (17.4% of H.B.)
C.B.	29.0-38.6 mm., M = 31.9 mm.
B.C.	13.0-15.7 mm., M = 13.9 mm., (43.4% of C.B.)
I.W.	6.2-7.7 mm., M = 6.7 mm., (20.9% of C.B.)
Z.W.	19.1-28.0 mm., M = 22.8 mm., (71.2% of C.B.)
M.W.	4.8-7.6 mm., M = 6.3 mm., (19.6% of C.B.)
U.T.R.	4.5-6.1 mm., M = 5.1 mm., (15.9% of C.B.)

L.J. 17.2-25.3 mm., M = 20.6 mm., (64.3% of C.B.)
L.T.R. 4.2-6.1 mm., M = 5.2 mm., (16.2% of C.B.)

Adult ♀♀:

H.B. 100-160 mm., M = 119 mm.
T. 17-26 mm., M = 21 mm., (17.6% of H.B.)
H.F. 17-25 mm., M = 20.8 mm., (17.4% of H.B.)
C.B. 27.2-36.4 mm., M = 31.2 mm.
B.C. 12.3-15.3 mm., M = 13.8 mm., (44.2% of C.B.)
I.W. 6.0-7.5 mm., M = 6.6 mm., (21.1% of C.B.)
Z.W. 18.4-25.3 mm., M = 22.0 mm., (70.5% of C.B.)
M.W. 4.9-6.9 mm., M = 5.9 mm., (18.9% of C.B.)
U.T.R. 4.6-5.9 mm., M = 5.1 mm., (16.3% of C.B.)
L.J. 16.9-24.1 mm., M = 20.2 mm., (64.7% of C.B.)
L.T.R. 4.3-6.0 mm., M = 5.1 mm., (16.3% of C.B.)

As can be seen from the tables above, the ♂♂ are slightly larger than the ♀♀, but these differences are statistically insignificant. Consequently, there seems to be no evident sexual dimorphism.

Some geographic variation in size occurs in C. hottentotus. Specimens tend to be smaller in the south-western Cape region while those occurring in the Eastern Province and north-eastern Transvaal tend to be larger.

Skull and dentition

The skull can be described as medium sized, and in mature ♂♂ the sagittal and lambdoid crests are but faintly developed. Braincase reasonably broad, interorbital constriction narrow. Nasals and muzzle region of skull slender. Infraorbital foramen more or less elliptical, variable in shape, without a thickened outer wall. Incisors strong, with molars well developed, decreasing in size from front to back.

Discussion/...

Discussion:

According to Ellerman et.al.(1953, 230) the Cryptomys hottentotus group has been much oversplit by Roberts in Southern Africa. It is stated by these authors, that the possibility exists that there may be only one very variable species in the Republic of South Africa. In order to appreciate these remarks it is necessary to review briefly the scheme followed by Ellerman et.al.

Ellerman et.al. define C. hottentotus as a smaller species (on the average), if compared with C. mechowi (an extra-limital species as far as the present work is concerned). In the latter (i.e. the "bigger" species) the H.B. dimensions attain 175 mm. and more, with skull-and-incisor length in adults varying between 45-66 mm. The "smaller" species has a H.B. length of less than 175 mm., while the greatest length of skull-and-incisors rarely reaches 45 mm.

This smaller species is again subdivided on the basis of size: in one group, the greatest length of the ♂ skull (including the incisors) rarely reaches 40 mm., (with certain exceptions), while ♀ skulls rarely reach 38 mm. for this measurement. A second group, is on the average a larger species (though not exceeding 175 mm. in H.B. length) while the greatest length of the ♂ skull is usually above 40 mm., and ♀♀ are rarely below 38 mm. This latter larger form, Ellerman et.al. treat as Cryptomys holosericeus while the former smaller form is referred to as C. hottentotus. It is this latter species which has been ".... much oversplit by Roberts in South Africa" (Ellerman et.al. 1953, 230), and I am inclined to agree with this statement.

Consequently/...

Consequently, Ellerman *et.al*. have tentatively defined *holosericeus* as above, and referred other named forms (all of which in the British Museum material have skull lengths less than 40 mm.) to the earliest named *hottentotus* as races. This includes specimens referred to as *C. damarensis*, *C. darlingi*, *C. nimrodi*, etc. They (i.e. Ellerman *et.al.*) state that they take no responsibility for the validity of races of Roberts which they have not placed in synonymy. Where Roberts had several forms occurring close together they have assumed that he was dealing with one individually variable form, and they have consequently placed certain names in synonymy.

This implies, that whereas Roberts may have oversplit the group, Ellerman *et.al*. may have overlumped. I can see no reason for a well marked species (e.g. *C. damarensis*, *C. darlingi*, etc.) to be demoted to subspecific rank (i.e. *C. hottentotus damarensis*, *C.h.darlingi*, etc.) and have retained *C.damarensis* and *C. darlingi* as clearly recognisable species in the present work. In such cases, I have thus followed Roberts, always bearing in mind that the lumping proposed by Ellerman *et.al*. was just and called for in some instances.

As was indicated in the list of synonyms of *C. hottentotus* in the present work, *C. hottentotus* and *C. caecutiens* are regarded as conspecific. Roberts (1951, 397) has retained *caecutiens* as a separate species while Ellerman *et.al*. (1953, 231) have interpreted *caecutiens* as a subspecies of *hottentotus*. As far back as 1895, Thomas remarked on the fact that he could not distinguish between '*Georychus caecutiens*' and '*Georychus hottentotus*'. I am inclined to agree with this statement, implying that there are no grounds for specific or subspecific separation. It has been mentioned above that size seems to be geographically variable in *C. hottentotus* and that specimens from the vicinity of Knysna are somewhat larger than those from other localities. Comparing material (♂♂) from the south-western Cape with that of Knysna, it was found that the average C.B. length for the former was 31.9 mm. and 33.7 mm. for the latter group. At a glance this difference in size may seem to be statistically significant. However, a C.D. value of 0.537 is attained which corresponds to a J.N.O. of less than 75%, i.e. below the level of subspecific distinctness. (A value of 1.28 corresponds to a 90% J.N.O. which is the accepted value for subspecific separation). Separation of *C.caecutiens* from Knysna from *C. hottentotus* (either as a species or subspecies), based on the C.B. length, does therefore not seem to be justified (See fig. 11.2).

Comparison of C.D. values of specimens from Port Elizabeth and Grahamstown with the C.D. value of Knysna specimens also gave numerical results which fall far below the level of subspecific distinctness.

The possibility exists that the overall darker grey colouration of the Knysna specimens could indicate grounds for subspecific separation. However, it is felt that this aspect is only an adaptation of these animals to the moister ecological conditions which prevail at Knysna and vicinity. It is a well known fact that animals occurring in the moister eastern districts of Southern Africa are darker than those occurring in drier western areas where animals usually show a pallid colouration.

Brants (1827, 38) described the Knysna forms as ".... eenvormig donkergraauw, de onderzijde iets lichter, alleen de borstelrige haaren der staart en de voeten morsig wit". The type specimen was described as 4 inches, 4 lines (i.e. 110 mm.) for the H.B. length, T. length 4 lines (= 8.4 mm.), with the H.F. 6¾ lines (=14.2 mm.). These figures are misquoted in Roberts (1951, 397): the head-body length is given as 4 ft. 4 inches (instead of 4 inches, 4 lines), tail as 4 inches (cf. 4 lines) and the hindfoot as 6¾ inches instead of 6¾ lines. As is evident from the figures given in the present work, the specimen(s) on which Brants based his description falls well within the range of observed variation of *C. hottentotus*, the exceptions being the tail and hind-foot which fall outside the minimum range.

Further comparison of values given for *caecutiens* by Roberts (1951, 603), based on three young adult to old ♂ specimens (i.e. Z.W., M = 21.2 mm., B.C., M = 13.4 mm., I.W., M = 6.7 mm., M.W., M = 6.0 mm., U.T.R., M = 5.5 mm., and L.T.R., M = 5.4 mm.), all fall within the range of variation given in the present work, implying no justification for taxonomic separation between *C.hottentotus* and *C.caecutiens.*

Some confusion exists about the person who named the species from Knysna. It is accepted, however, that Brants (1827, 37) gave the first official description of the animal and was thus known as *Georychus caecutiens* Brants. On the other hand, Brants (*loc.cit.*) credits the name to Lichtenstein and other 19th century papers relating to this species

(e.g./...

(e.g. Gray, 1864, 125) refer to it as Georychus caecutiens Lichtenstein.

Trouessart (1899, 588) apparently considered the description of coecutiens (sic) to have been published prior to that of hottentotus by Lesson and he thus listed hottentotus as a synonym of 'coecutiens'. This mistake was noted however, and rectified in the appendix (p. 1338) and he then referred to this species as exenticus.

The inclusion of the species Cryptomys vandami under C. hottentotus in the present work, requires some explanation. This species was based on a series of six skins and five skulls collected by van Dam and Bryer at Griffin Mine in the Leydsdorp district and was described by Roberts (1917, 273). The specimens were described as grey, "... paler than any other South African species...", with the nasals somewhat widened at the tip and the alisphenoid canal having the posterior opening exposed.

The reasons for synonymizing vandami with hottentotus are to be found in aspects relating to the mammae, colour, size and skull, and will briefly be discussed below.

As far as the mammae are concerned, the vandami specimens show the same arrangement as hottentotus, i.e. two pairs pectoral and one pair inguinal. This probably prompted Roberts (1951, 393) to state that this species (occurring in the north-eastern Transvaal low country, extending westwards to the Magalakwin river in north-western Transvaal) is a "... member of the C. hottentotus group,...." thus distinguishing it from C.komatiensis and C. natalensis which both occur to the south of the present/...

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As indicated above, the type and associated series of specimens of *vandami* was described as a pale grey. This is decidedly so, when a number of specimens are seen simultaneously. On the other hand, if specimens are compared individually and placed among *hottentotus* material, it is barely possible to identify the specimen under consideration. This light grey hue may again be an adaptation of the animal to the drier conditions existing in the north-eastern and north-western Transvaal which usually results in a decrease of colour intensity. Similarly, one finds an increase in colour intensity in wetter and more humid areas (e.g. the darker forms of *C. hottentotus* found at Knysna). It can furthermore be demonstrated that the identical colouration found in *vandami* is also present in specimens representing *hottentotus*. Similarly, the usual absence of the white patch on the head of *hottentotus* is also reflected in the absence of this character in *vandami*. These factors all point to the probability of *vandami* being conspecific to *hottentotus*.

Although Roberts (1951, 393) has stated that *vandami* is larger in size, this aspect is not demonstrated statistically convincingly in the material available for study to the present author. Table 11.1 will serve to illustrate this point.

Table 11.1. Overall resemblance in size of various skull measurements in C. hottentotus and C. vandami.

	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
C.hottentotus:								
various localities, M =	32.0 mm.	13.9 mm.	6.7 mm.	22.8 mm.	6.3 mm.	5.1 mm.	20.6 mm.	5.2 mm.
C.vandami:								
Njelele river, M =	31.9 mm.	14.1 mm.	6.7 mm.	22.5 mm.	6.1 mm.	5.1 mm.	21.6 mm.	5.3 mm.
Zwarthoek, M =	32.5 mm.	14.1 mm.	7.0 mm.	23.5 mm.	6.2 mm.	5.4 mm.	22.6 mm.	5.3 mm.
Montrose, M =	32.4 mm.	13.6 mm.	7.2 mm.	23.5 mm.	6.6 mm.	5.4 mm.	22.3 mm.	5.3 mm.

Furthermore, Roberts (1917, 273) has indicated that the lengths of the H.B., T. and H.F. of the type specimen of vandami (an old ♂) is equal to 133 mm., 17 mm. and 23 mm. respectively. It is evident, that these values fall within the range of variation found in C. hottentotus. (Compare values given for C. hottentotus under diagnostic characters above).

Finally, aspects of the cranial morphology of vandami may briefly be considered. Roberts (1917, 273) has stated that the posterior opening of the alisphenoid canal is exposed, as is the case in specimens which have been collected at Knysna and vicinity (i.e. hottentotus). Roberts points out that in this respect the skull of vandami is markedly different from C. natalensis and C. aberrans in which the posterior opening is hidden. On the other hand, he immediately continues to say that this character is variable in some other species as well and cannot therefore be relied upon. This implies that this character is not of diagnostic value for vandami and can be ignored. This strengthens the argument that vandami should be interpreted as a synonym of C.hottentotus.

In the same paper, describing C. vandami as a new species, Roberts (1917, 278) also commented on specimens collected by van Dam at Manetsi river, near Malala, Zoutpansberg district. The material consisted of two young adult ♂♂, as well as a young adult ♀ and a juvenile ♀. They were described as a more uniform grey than vandami, and according to Roberts, decidedly larger. However, they seemed to show nasal and other cranial characters of natalensis differing therefrom in being greyer and smaller, although not so small as komatiensis. This form Roberts named Georychus natalensis pallidus subsp. nov., characterized as above.

Allen (1939, 429) proposed a new name for this subspecies i.e. Cryptomys natalensis nemo in view of the fact that pallidus was preoccupied. (This does not refer to Georychus pallidus Gray, 1864, which in actual fact is a Heliophobius).

Eventually, Roberts (1951, 393) synonymized this subspecies with Cryptomys vandami. This fact again supports my contention that very little diagnostic features can be found in Cryptomys skulls due to the great amount of morphological variation encountered in the skulls. Although Roberts first placed the Malala specimens under Cryptomys natalensis, based on cranial characteristics, he evidently concluded at a later date (1951) that cranial differences between vandami and natalensis

were/...

were not so clear cut. If, furtheremore, they were accepted as members of the natalensis species, they would not fit geographically speaking in the known range of distribution of natalensis.

It must further be noted that Ellerman et.al. (1953, 233) placed vandami as a possible synonym under Cryptomys hottentotus komatiensis, as well as C. natalensis pallidus and C.n.nemo. This procedure does not seem to be correct for the known komatiensis forms do not possess any inguinal mammae (i.e. only two pairs of pectoral mammae are present), whereas vandami and synonyms do possess the inguinal mammae, thereby emphasizing the fact that they should rather be treated as members of the hottentotus species, which also has the inguinal mammae present.

In 1924 a new species was described by Roberts and named Cryptomys cradockensis. It was stated that this was a member of the C.hottentotus group but differing from hottentotus in being greyer in colour and larger in size. According to Roberts (1924, 73) the buffy colouring of the hair is present as in the typical C.hottentotus, but paler ".... and not so heavily laid on". The shape of the nasals and the skull was described as being generally the same as in hottentotus but on a larger scale.

The type specimen (an adult female, TM 2389) was trapped by van Dam at Cradock in the Karoo, on October 5th 1918. Roberts stated that this form also seems to occur at Grahamstown and he named it as a species as it is possible that it occurs in the same ground as the typical C.hottentotus and ".... it certainly intervenes between the ranges of hottentotus and rufulus which are not so readily recognised, and the differences between the species are not always defined clearly enough to enable one to judge of their exact status" (Roberts, 1924, 73). Furthermore, Roberts stated that cradockensis is perhaps the starting point of a divergence from C. hottentotus towards C.vandami of the north-eastern Transvaal, which again overlaps the range of C.rufulus (see later), the latter representing C.hottentotus on the foothills of the Drakensberg.

Figures enabling a comparison between specimens of C.hottentotus and C.cradockensis are given by Roberts (1924, 74). On closer inspection, one can see no reason why the cradockensis specimens are to be separated from hottentotus. Unfortunately, the material from Cradock is sparsely represented in the available study material and therefore a statistical comparison has not been possible. I am convinced of the fact, that if more specimens were available, the range of variation to be expected in cradockensis would become more clearly defined which would diminish the descrepancy in size between hottentotus and cradockensis which Roberts saw in the specimens from Cradock.

Returning for a moment to the figures supplied by Roberts (1924, 74) the following comparisons may be quoted and are presented in Table 11.2.

Table 11.2. Measurements given by Roberts (1924, 74) to illustrate differences in size between C. hottentotus and C. cradockensis.

	5 specimens, C.hottentotus	2 specimens, C.cradockensis
H.B.	115-125 mm.	115-124 mm.
Z.W.	22.5-23.5 mm.	23.0-24.3 mm.
I.W.	6.4-7.0 mm.	6.5-7.2 mm.
U.T.R.	5.0-6.0 mm.	5.3-5.8 mm.
L.T.R.	4.3-5.3 mm.	5.2-5.5 mm.

These are but a few examples of measurements given by Roberts, illustrating the fact that there is very little difference between hottentotus and cradockensis. Further comparison of figures pertaining to C.hottentotus given in the present work show that the cradockensis specimens fall well within the observed minimum-maximum ranges.

Furthermore, it is not clear why a new species (i.e. cradockensis) should be present in an area surrounded by hottentotus, especially if climatological and vegetational conditions surrounding Cradock (and prevailing at Cradock) is the habitat in which C. hottentotus is encountered.

In 1951 Roberts (1951, 391) demoted this species as a subspecies of hottentotus, for apart from the fact that they are slightly greyer and larger compared to the typical hottentotus, they do not otherwise offer any marked differences. In Roberts' work, the distribution of the species was given as the eastern districts of the Cape Province, about Cradock to Grahamstown ".... and also occurring at Plettenberg Bay and Knysna, and perhaps in the intervening districts." If subspecific rank for cradockensis, hottentotus and

caecutiens/...

caecutiens is accepted, it would imply that C.h.cradockensis and C.h.caecutiens occur sympatrically at Knysna, presenting a most confusing picture and a taxonomical absurdity.

Finally, Ellerman et.al. (1953, 231) have tentatively placed C.cradockensis as a synonym under C.h.caecutiens. By accepting that C.hottentotus, C.caecutiens and C.cradockensis are conspecific (as has been done in the present work), a more acceptable picture of the distribution of C.hottentotus in the Cape Province emerges.

Similarly, Cryptomys transvaalensis has been described by Roberts (1924, 73) as a new species. According to Roberts, it is hardly different in size from C.hottentotus but it can be distinguished from hottentotus by the shape of the nasals, the broader interorbital constriction and the greater length of the skull from the front of the molars to the condyles. Furthermore, Roberts has stated that in colour it is hardly separable from hottentotus, but the hair is shorter (not longer than six mm., as against seven mm., or more in hottentotus), while the hair on the ventral surface is very scanty, not serving to hide the skin.

Roberts (1924, 74) furthermore remarked, that all specimens trapped by him showed a peculiar expansion between the orbits of the skull, which ultimately, in the oldest ♂, forms a shell-like hood, projecting outwards.

In addition to the overall hottentotus-like affinities, Roberts furthermore pointed out that transvaalensis seems to be allied to C.vandami taking the latter's place in the western Transvaal bushveld districts. The possible differences between vandami and transvaalensis also refers to size and cranial morphology. The latter species is smaller, but with the interorbital constriction broader while the nasals are broad for the posterior two-thirds, the anterior third narrower, not posteriorly pointed, usually squared off to some extent with the apex of the nasals not markedly expanding.

On closer examination of these facts, it appears that these differences are not of vital importance. The type skull (an adult female, TM. 2463, trapped in gravelly soil on the farm Boekenhoutsfontein, on the border of the bushveld, Pretoria district, on December 19th, 1919) was compared with a skull of C.hottentotus from Lormarin, Paarl, and the exact replica of the nasal shape described for transvaalensis could be seen on skull No. TM 2205 from the south-western Cape. As far as the width of the interorbital constriction is concerned, I found that it is broader in juvenile Cryptomys specimens while it decreases in width as the animal grows older. It was found furthermore, that the skull of transvaalensis is in fact shorter than skulls from Paarl (i.e. hottentotus) in a similar age group.

It thus appears, that craniologically speaking there seem to be no real valid reasons for separation of transvaalensis from hottentotus. Furthermore, both these species possess inguinal mammae which again points to a similar genotype. It has already been stressed in the present work that vandami and hottentotus should be treated as synonyms and the mere fact that Roberts (1924, 73) has hinted that transvaalensis appears to be allied to vandami also points to the possible equivalence of transvaalensis with hottentotus.

Roberts (1924, 74) has pointed out that within the genus Cryptomys there seems to be a considerable amount of variation perceptable in series from various localities and that he was not at all sure that all specimens he placed tentatively with species would necessarily be correctly identified.

The distribution of transvaalensis, apart from the type locality, includes Jericho and other places to the west (e.g. Pilansberg and Buffelsdraai (near the junction of the Marico and Crocodile rivers)) whence it ranges in the north-western Transvaal bushveld regions, (along the Limpopo river), eventually being replaced by 'vandami' near the Magalakwin river.

Roberts (1951, 391) consequently demoted the transvaalensis specimens from specific to subspecific rank, which then already seemed to be a truer representation of the facts. In the present work however, I feel that even a subspecific rank is not justified for these animals and that C.transvaalensis should also consequently be treated as a synonym of C.hottentotus, as was the case in C. vandami.

It may also be pointed out, that Ellerman et.al. (1953, 233) have placed C. transvaalensis tentatively as a synonym of Cryptomys hottentotus jorriseni (see below).

As was indicated above, the distribution of C. transvaalensis (here treated as C.hottentotus), includes its type locality, i.e. Boekenhoutsfontein as well as Jericho, Pilansberg and Buffelsdraai, i.e.

more/...

more or less in the drier central western Transvaal. In 1909, H. Lyster Jameson described another new species of Cryptomys, from Waynek, in the Waterberg district of the Transvaal, to the west of Warmbad. This species was named Georychus jorisseni (1909, 466) and was described as being much smaller than C. hottentotus, with a rather warmer colouring. Compared to C. hottentotus, the skull was smaller and lighter, the zygomatic arches being depressed, giving the orbits a narrower outline when seen from above.

Unfortunately, I have not been able to study the type specimen personally (housed in the British Museum, ♀ , No. 402, B.M. No. 9.7.2.23). In the Transvaal Museum however, there is a very small sample of study skins collected at Waynek which was available for closer inspection.

In the paper describing the type specimen and associated series of skins, the geographical distribution is given as probably extending right across the bushveld in the northern Transvaal, as ".... a form which I can not, from available material, distinguish from it occurs in the Zoutpansberg, alongside of C. hottentotus....." (Jameson, 1909, 466). Roberts (1951, 397) describes the possible distribution of jorisseni as the western bushveld areas of the Transvaal in the Waterberg and Rustenburg areas, while Ellerman et.al. (1953, 233) state that the range includes the Rustenburg district, western Transvaal.

On comparing the available study skins from the type locality, with C. hottentotus specimens from the western Cape, it becomes evident that the overall resemblance is striking. When the skulls of jorisseni are compared to those of hottentotus, the differences described for the type specimen skull of jorisseni can not be demonstrated to be present in the skulls available in the Transvaal Museum.

In the original description of the type specimen, no indication is given concerning the number of mammae present in jorisseni. Roberts (1951, 397) has retained jorisseni as a valid species, and states that the inguinal mammae are lacking, and that jorisseni overlaps the distribution of transvaalensis, which has the inguinal mammae.

In contrast to Roberts, Ellerman et.al. (1953, 233) have interpreted jorisseni as a subspecies of C.hottentotus, and have tentatively placed transvaalensis as a synonym of C.h.jorisseni.

The fact that Roberts states that the inguinal mammae are absent, should to my mind, be accepted with some reservation. The study sample available in South Africa, is very small indeed and it is possible, that if a larger series becomes available, it may show that the females have in fact six mammae instead of four.

In the present work, the species jorisseni is thus tentatively interpreted as a synonym of C. hottentotus. This interpretation is partially based on the fact that the phenotypic resemblance to hottentotus and transvaalensis is pronounced and that I fail to see valid differences in the cranial morphology of jorisseni compared to hottentotus or transvaalensis. Furthermore, the species transvaalensis (i.e. C.hottentotus as here understood) occurs in close geographical proximity to the range of *jorisseni* - in fact Roberts has stated that these two species overlap. If thus interpreted, the specimens from Waynek fall naturally in the geographical distribution pattern of *C. hottentotus* in the Transvaal.

It may be pointed out that Roberts spells the species as jo*rr*iseni, compared to the original spelling of jori*ss*eni, also followed by Ellerman *et.al*.

Finally, the subspecies *Cryptomys hottentottus (sic) talpoides* has been described by Thomas and Schwann (1906, 166), from Knysna. They state that the material in the British Museum portrays similarities in essential characters to the true *hottentottus* (*sic*) but that the overall colour is much darker. The general colour of the upper surface has been described as a dark slaty grey (including the sides), while the hairs themselves are slaty grey, tipped with brown, nearly matching Ridgeway's 'slate colour'. The crown and a large area on the centre of the back are even darker still, the tips of the hairs being quite black. This dark area extends to the root of the tail. The belly has a dull slaty colour, the tips of the hairs being dull buffy. Furthermore, they state that this subspecies may be the Knysna representative of *C.hottentotus*, being darker than its allies elsewhere, as is usually the case with animals from forest regions.

Roberts (1951, 397) referred to this subspecies as a synonym of *Cryptomys caecutiens* while Ellerman *et.al*. (1953, 231) have done the same under *C.h.caecutiens*. The latter authors state that at Knysna, *C.h.caecutiens* would appear to occur in two colour phases. In view of the fact that *C.caecutiens* is not accepted as a separate species or subspecies

from/...

from C. hottentotus, it leads to the conclusion that it is also a synonym of C. hottentotus. If these facts were not interpreted as such, it is evident that a third subspecies (i.e. C.h. talpoides) would occur sympatrically at Knysna together with C.h.caecutiens and C.h. cradockensis - a totally untenable position.

Before leaving the discussion of taxonomic aspects of Cryptomys hottentotus, a few words must still be said on the species Cryptomys albus. This species was described by Roberts (1913, 100), as being pure white throughout with the skull smaller than in C.hottentotus (Roberts, 1951, 398). This species was described on the strength of two specimens without labels and another in spirits bearing a torn label with the words "--nberg, K.K., Jan., 1899". Roberts (1913, 100) states that it seems likely therefore that the three specimens all came from the same place, most likely Wynberg in the Cape Province. On the other hand, Roberts (1951, 398) later pointed out that the type locality for this species was not known, but that the material has been collected "... perhaps from Knysna, whence specimens are made up in the same way as the type and another specimen".

Apart from the pure white specimens, buffy-yellowish specimens are known from Tulbagh. According to Roberts (1951, 398) Thomas has stated this species to be an albino. The present author is inclined to agree fully with Thomas' verdict, that this socalled species is an example of albinism occurring in C.hottentotus, and that the buffy-yellowish species are examples of partial albinism, or a decrease in the intensity of the grey and dark pigments usually found in the pelage of C.hottentotus. Roberts has

indicated/...

indicated that the distribution of albus is probably restricted to the southern Cape Province only, which is quite in the middle of the normal distribution range of C. hottentotus. To my mind, there is no doubt that C.albus should ever have been described as a species and it is therefore placed in synonomy with C. hottentotus. Ellerman et.al. (1953, 234) have placed C.albus incertae sedis under their C.hottentotus group. They also refer to the spirit specimen as an albino.

On comparison of the available measurements, it is evident that skull measurements fall well within the observed range of variation in C. hottentotus.

Biological

Aspects of the biology of the hottentot mole-rat has been discussed in Chapter 6 of the present work. However, a number of factors remain to be discussed briefly.

From the foregoing discussion, it may have become evident that this species has a wide geographical distribution in South Africa, and it therefore occurs in diverse ecological habitats. It is adapted to the drier and more arid north-western Cape Province and north-western Transvaal and also to conditions of high rainfall and humidity in the vicinity of Knysna. No correlation of its geographical distribution with rainfall is evident.

Similarly, they occur in Karoo and Karroid veldtypes, coastal rhenosterbosveld and macchia, coastal forest and thornveld, false Karoo veldtypes, Mopaniveld, tropical bush and savannah veldtypes, as well as in Knysna forest conditions. As is the case with rainfall, no correlation is evident between the geographical distribution of this species and the vegetation. Unfortunately, the distribution of bulbous plants (on which these animals mainly subsist) is known rather poorly and I am inclined to think that such information (when available) would possibly show a certain degree of correlation.

As far as topography is concerned, it is evident that they occur predominantly in sandy soils, which are devoid to a large extent of stones and rocks. On closer inspection of a topographical map, it becomes evident that they often disperse in sandy soils, usually found near rivers or streams. As an example, specimens from the south-western Cape may be quoted. Specimens have been taken at Paarl and vicinity (e.g. the Cape Flats and Stellenbosch) which are all below 1,000' above sea level. In contrast, specimens have been collected at De Doorns and Matjiesfontein (approximately 2,000' above sea level) and where it seems that they have spread via the Hex river and Groot river respectively.

According to Roberts (1951, 391) they also excavate chambers in which bulbs are stored (as is possible in the case of <u>C.damarensis</u>) from which tunnels are made to certain places where bulbs are to be found. Roberts has stated that this chamber is usually on slightly higher ground than the feeding areas, but that on flat plains of the upper Karoo, where the ground in certain instances becomes completely submerged by floods, large mounds are "..... thrown up in which the storage chambers are made above the flood-level".

As is the case in other species of this genus, C.hottentotus feeds mainly on bulbs, tubers, fleshy rootstocks and, according to Shortridge (1934, 325), especially bulbous grassroots. They show preference for certain kinds of bulbs: in the vicinity of King William's Town, a small species of blue iris (Moraea sp.) occurs, which is poisonous to cattle, but seems to be preferred above almost anything else by C. hottentotus. Consequently, it is often difficult to propagate this iris and other indigenous bulbaceous plants in gardens. Shortridge states further that other garden plants are occasionally attacked including onions, agapanthus and dahlias. Roberts states (in Shortridge, 1934, 325) that potatoes and other tuberous crops are often ruined where these animals are plentiful.

Virtually nothing is known about the activity pattern of C. hottentotus. Normally, they do not occur above the ground, but they do come onto the surface at night as is evidenced by the fact that they occur in pellets of the barn own Tyto alba. They seem to burrow more vigorously after rainfall when many fresh mounds are thrown up during the night. Fitzsimons (1919-20, 157) has stated that they are active burrowers on moonlight nights but it is clear that activity of movement can be observed at all hours.

Apart from the barn owl Tyto alba referred to above, other known predators on C. hottentotus include snakes and herons. I have found the remains of a mole-rat in the stomach of the shield snake Aspidelaps scutatus collected in the vicinity of Shingwedzi in the Kruger National Park. The snake was

caught/...

caught in the mole-trap which points to the fact that it frequented the tunnels of Cryptomys in search of its prey. The mole snake Pseudaspis cana lives for the most part in abandoned animal holes or burrows and as its name implies lives almost exclusively on moles, rats, gerbilles and other small ground-living mammals. Their favourite item of diet are moles and mole-rats, in search of which they push their forepart of the body down through a mole-hill into the runway below and patiently wait in this position for their prey (Fitzsimons 1962, 165). Shortridge (1934, 323) has also commented on the fact that snakes are presumably among their chief enemies.

As far as the avian predators are concerned, there are well documented records of C. hottentotus being preyed upon by the barn owl (Davis, 1959, 147). It is also of interest to note that skulls of this species have been found in pellets of the grey heron (Sneyd Taylor, 1948, 209).

Mammals preying on C. hottentotus include the black-backed jackal Canis mesomelas and the silver jackal, Vulpes chama, for remains of C.hottentotus have been found during analysis of the stomach contents of these two canids (Bothma, personal communication).

Very little data is available concerning the breeding biology of the hottentot mole-rat. A ♀ specimen was taken at Stellenbosch in December containing five large embryos, while a specimen from Jericho in the western Transvaal was said to be gravid on March 21st. In ♂♂, the testes are usually abdominal.

Parasite./...

Parasite records include the following (de Graaff, 1964, 123):

Plathyhelminthes: Inermicapsifer madagascariensis.

Arthropoda: Haemolaelaps capensis, H.natalensis, Haemolaelaps sp. Myonyssoides capensis, Ixodes alluaudi, Cryptopsylla ingrami, Xenopsylla pirei and Procaviopsylla creusae.

Phylogenetic:

The closest relative of C.hottentotus appears to be C. holosericeus, which it resembles in colour and the possession of inguinal mammae. Furthermore, both species do not normally possess white frontal patches. In view of its pronounced smaller size, it could well be that C. hottentotus is the more primitive of the two species. It occurs in a greater variety of habitats which may point to a greater degree of genotypic plasticity when compared to the larger and more geographically localized holosericeus. It would seem that due to the possible greater genetic adaptibility, C. hottentotus succeeded in establishing itself successfully in divergent ecological niches.

List of localities:

Bathurst, 1 (AM), Bellville, 6 (TM), Bredasdorp, 3 (TM), Buffelsdraai, 10 (TM), Burgersdorp, 1 (TM), Centlivres, Uitenhage, 1 (TM), Clanwilliam, 1 (AM), Coega river, 3 (TM), Coldspring, 1 (AM), Cossack Post, Rosmead, 1 (TM), Cradock, 4 (TM), De Aar, 1 (AM), De Brug, 2 (TM), De Doorns, 2 (SA), De Wetsdorp, 1 (AM), Dortrecht, 4 (AM), East London, 17 (EL, SA), Eendekuil, 2 (TM), Ezelfontein, 9 (PE, AM, EL), Fauresmith, 1 (TM), Fort Beaufort,

2/...

2 (AM), Garcia forest, Riversdal, 5 (TM), Garies, 2 (TM), George, 2 (AM), Glennifer, Kei Road, 2 (AM), Gorge, 1 (KP), Graaff Reinet, 1 (AM), Grahamstown, 66 (AM, TM), Grootvadersbosch, 1 (TM), Hlati Road, 1 (KP), Howison's Poort, 1 (AM), Jericho, 3 (TM), Jonkersberg, 1 (TM), Kamiesberg, 3 (AM), Klaver, 8 (TM), King William's Town, 8 (PE, TM), Knysna, 17 (TM, AM, SA), Kompanjiesdrift, Lambert's Bay, 1 (NM), Letaba, 1 (KP), Lindanda, 2 (KP), Lormarin's, Paarl, 8 (TM), Mahewane, 1 (KP), Mahungumule, 1 (KP), Mashakadzi, 1 (KP), Matjiesfontein, 1 (TM), Middledrift, 1 (AM), Mlondozi, 5 (KP), Montrose, 6 (TM), Ngirivane, 1 (KP), Nieuwhoudtville, 1 (NM), Njelele river, 6 (TM), Nwanetzi-west, 1 (KP), Nwamayiwani, 1 (KP), Olifantsriver, van Rhynsdorp, 2 (TM), Queenstown, 1 (AM), Peddie, 1 (AM), Perseverance, 1 (PE), Phillipolis, 4 (TM), Philipstown, 4 (TM), Plettenberg Bay, 5 (TM), Port Alfred, 10 (AM), Port Elizabeth, 44 (PE, TM, AM), Pumbe, 4 (KP), Shibangwanene, 1 (KP), Shingomene, 1 (KP), Richmond, 1 (TM), Riebeeck Kasteel, 1 (SA), Satara, 1 (KP), Satara plots, 1 (KP), Seweweekspoort, 3 (TM), Shingwedzi, 2 (KP), Stellenbosch, 4 (TM), Sterkstroom, 1 (TM), Swellendam, 1 (AM), Tulbagh, 3 (TM), Wolseley, 6 (TM), Worcester, 6 (TM), Zoutpan, 3 (TM), Zoutpansberg, 12 (TM, SA), Zwarthoek, Zoutpansberg, 23 (TM).

CHAPTER 12

CRYPTOMYS DAMARENSIS (OGILBY) 1838

This species was first collected by Capt. Alexander during a journey into Damaraland on the South West African coast (probably in 1837), and was first exhibited to the Zoological Society in London on the 23rd of January 1838. At that meeting, Sir Richard Owen was in the chair and Mr. Ogilby directed the attention of the Society to the rare and new specimens contained in the collection made by Alexander, including this mole-rat (Ogilby, 1838, 5). The type specimen was subsequently purchased by the British Museum at the sale of Alexander's collection on the 8th of March 1838.

As here treated, C. damarensis is a monotypic species with a very wide geographical distribution, especially in the drier, western areas of Southern Africa.

The synonyms commonly included under C. damarensis are: C. lugardi (de Winton) and C. micklemi (Chubb). At first micklemi was regarded as a synonym of lugardi while Shortridge (1934, 320) provisionally listed lugardi and micklemi as geographical races of damarensis. Furthermore, C. ovamboensis Roberts does not appear to warrant the species rank accorded to it by Roberts (1946, 315), and is therefore also included as a synonym. Finally, Ellerman et.al. (1953, 232) treat damarensis as a race of hottentotus, i.e. C.h.damarensis. As far as the present author is concerned, this interpretation is not

accepted,/...

accepted, for *C. hottentotus* is morphologically and phenotypically clearly distinct from *C. damarensis*.

Cryptomys damarensis (Ogilby)

Bathyergus damarensis Ogilby, *Proc. zool. Soc.* London, p. 5, 1838. Type locality: "Damaraland", South West Africa.

Georychus lugardi de Winton, *Ann. Mag. nat. Hist.*, *1*: 253, 1898. Type locality: Kalahari desert, between Palapye and Lake Ngami, north-eastern Bechuanaland.

Georychus micklemi Chubb, *Ann. Mag. nat. Hist.*, *3*: 35, 1909. Type locality: Kataba river, upper Zambezi, western Northern Rhodesia.

Cryptomys ovamboensis Roberts, *Ann.Transv.Mus.*, *20*: 315, 1946. Type locality: Ondongwa, Ovamboland, South West Africa.

Type specimen:

In the British Museum (Natural History), London.

Type locality:

Not clearly defined. Usakos, South West Africa may here be nominated as type locality.

Distribution: (Fig. 12.1).

Occurs in the Kalahari Gemsbok Park, ranging northwards and westwards to South West Africa as far north as Ovamboland. Also extends eastwards through Ngamiland and the greater portion of the Kalahari desert in Bechuanaland into Southern Rhodesia (Matetsi, Roberts, 1951, 388).

Diagnostic characters:

A large species, H.B. M = 164 mm., C.B. M = 36.2 mm. (♂♂). Usually a dark slaty grey on both

dorsal/...

dorsal and ventral sides with the presence of a clear white frontal (occipital) patch. Mammae: 2 pectoral and 1 inguinal pair = 6.

Colour:

The majority of specimens are uniformly dark slaty grey in colour. Some specimens are virtually black. On the other hand, reddish-brown (Ogilby) specimens may be encountered and occasionally both the dark and brown colour phases occur simultaneously in a single burrow.

A definite white occipital patch is present in all individuals, varying in size and shape. It may be limited to the occipital region of the head, or may extend in the shape of a white stripe along the mid-dorsal and mid-ventral line.

The juvenile pelage is not markedly darker compared to adult specimens. This however, is the case in many other species.

Size: Adult ♂♂:

H.B. 150-185 mm., M = 164 mm.

T. 23-30 mm., M = 25 mm., (15.2% of H.B.)

H.F. 26-30 mm., M = 27 mm., (16.4% of H.B.)

C.B. 32.2-44.1 mm., M = 36.2 mm.

B.C. 13.9-16.9 mm., M = 15.2 mm., (41.9% of C.B.)

I.W. 7.2-8.4 mm., M = 7.3 mm., (20.1% of C.B.)

Z.W. 23.3-33.0 mm., M = 25.0 mm., (69.0% of C.B.)

M.W. 6.9-11.1 mm., M = 7.9 mm., (21.8% of C.B.)

U.T.R. 5.2-6.7 mm., M = 5.8 mm., (16.0% of C.B.)

L.J. 20.4-28.9 mm., M = 25.4 mm., (70.1% of C.B.)

L.T.R. 5.4-6.9 mm., M = 5.9 mm., (16.2% of C.B.)

Adult/...

Adult ♀♀:

H.B. 141-164 mm., M = 151 mm.
T. 25-32 mm., M = 28 mm., (18.5% of H.B.)
H.F. 26.28 mm., M = 27 mm., (17.8% of H.B.)
C.B. 31.6-38.2 mm., M = 35.3 mm.
B.C. 14.7-15.3 mm., M = 15.0 mm., (42.4% of C.B.)
I.W. 7.6-8.5 mm., M = 8.0 mm., (22.6% of C.B.)
Z.W. 25.1-30.3 mm., M = 27.1 mm., (76.7% of C.B.)
M.W. 6.8-10.0 mm., M = 8.1 mm., (22.9% of C.B.)
U.T.R. 5.5-6.4 mm., M = 6.0 mm., (16.9% of C.B.)
L.J. 21.2-27.0 mm., M = 24.1 mm., (68.2% of C.B.)
L.T.R. 5.3-6.2 mm., M = 5.8 mm., (16.4% of C.B.)

It is clear that the ♂♂ are slightly larger than the ♀♀. When the entire range of distribution of this species is taken into consideration, no geographical variation in size becomes apparent.

Skull and dentition:

Outer edge of the infraorbital foramen thickened, reducing the size of this foramen. Facial portion broad, while the auditory bullae are rather fuller than in most other species (de Winton, 1898, 251). The coronoid process of the mandible is shorter and further from the condyle, and according to de Winton (*op.cit.*) the intermediate space is level (i.e. more or less horizontal).

The molars in this species was described as "large in proportion" by de Winton (*op.cit.*). Apart from this observation they offer no other clear diagnostic features.

Discussion:

As far as the type area and distribution of this species is concerned, the following aspects may briefly be dealt with.

As/...

As was indicated above, the type specimen was collected somewhere in Damaraland, and no specific type locality has been given for damarensis. According to Roberts (1951, 388) Alexander did not penetrate north of Damaraland proper during his explorations, and therefore the vicinity of Usakos may here be nominated as a possible type locality for this species.

Eastwards, it has been collected at Gobabis and Sandfontein, while de Winton (1898, 253) designated the area between Palapye and Lake Ngami as the type locality for lugardi. Southwards in Bechuanaland, damarensis is known to occur at Lehutitung and on the Mababe flats (Dollman, 1910, 400) as well as west of Morokwen near the Molopo river.

According to Thomas (1927, 390) it extends westwards from the Gobabis district to within 20 to 25 miles from Windhoek while its southern distribution in the vicinity of Windhoek has as yet not been determined. Thomas however states that it does not range further south than Rehoboth. On the other hand, specimens have been collected in the Republic of South Africa in the Kalahari Gemsbok Park (at Union's End, Mata Mata and Twee Rivieren) which are all localities situated further south although much deeper inland.

To the north of Usakos, mole-hills of this species have been recorded at Kalkfield, Otjivarongo and in the vicinity of the Otavi junction, the latter locality already being in the Omaheke district, outside Damaraland proper.

From these localities, it extends westwards to the Kaokoveld, being plentiful in the south and

east/...

east, particularly where the sand-plains merge into Ovamboland. It extends as far west as Zesfontein, becoming scarcer in the northern Kaokoveld (Shortridge, 1934, 321).

Thomas (1927, 390) states that they are plentiful in Ovamboland, occurring anywhere between the Cunene river and the northern edge of the Etosha pan, while they are scarce in the wooded country between Namutoni and Tsumeb (Shortridge, op.cit.).

They also range northwards from Otavi through the Grootfontein district to as far north as the banks of the Okavango river and eastwards to the Caprivi strip and Ngamiland in Bechuanaland, eventually reaching the vicinity of Matetsi (north of Wankie) in Southern Rhodesia. This seems to be their easternmost distribution limit, while specimens have also been collected in Barotseland in Northern Rhodesia.

It may thus be concluded that geographically speaking, this species has the widest distribution of all Cryptomys forms in Southern Africa.

As far as the colouration of C.damarensis is concerned, a little more should be said on the subject for it presents a rather confusing picture.

In the type specimen of C.damarensis, Ogilby (1838, 5) described the colour as a uniform reddish-brown, both above and below, with a large irregularly shaped square white patch on the occipital region. White patches are also present on each side of the neck, just below the ears, meeting on the throat which was thus covered with a dirty dunnish-white. The tail is covered with coarse reddish-brown bristles while the paws are similarly coloured.

Gray (1864, 125) stated the type to be a uniform grey-brown, while Sclater (1899, 228) again followed Ogilby's description. This has led to an element of doubt as to what the colour is precisely. de Winton (1898, 253) on the other hand, described the colour of the synonym lugardi as seal brown, while Thomas (1927, 389) commented that all the specimens from Sandfontein and Gobabis were a uniform dark slaty colour. Chubb (1909, 33) again described **the** synonymic micklemi specimens collected by Micklem from the Kataba river, Upper Zambezi, as a bluish-black, including the limbs and tail.

St.Leger (1932, 963) reported on specimens collected in north-western Damaraland by Shortridge's Sixth Percy Sladen and Kaffrarian Museum expedition. At the different localities where C.damarensis was collected the specimens were all black or darkbrown in colour. Similarly, skins from Ondongwa, (central Ovamboland) (collected by Shortridge on one of his former expeditions) were pale brown in colour while others were dark brown. St.Leger (1932, 964) thus suggested that three colour phases can be expected in C. damarensis - dark (reddish) brown, pale (seal) brown and black. Confirmation of this is afforded by a series of skins from the Molopo river which in addition to black and dark brown skins contains a skin which intergrades so perfectly between brown and pale brown specimens that it is difficult to decide to which colour phase it belongs. St.Leger furthermore commented that C. damarensis is a reddish brown species, slightly more red in colour than the paler colour

phase/...

phase of lugardi while the skin of the type of micklemi is in the black colour phase.

Personally, I also had the opportunity to trap both black and pale (seal) brown specimens in a single tunnel system at Mata Mata on the western border of the Kalahari Gemsbok Park. This tends to confirm the fact that both the blacker 'micklemi' and paler 'lugardi' should be treated as synonyms, while the brown specimens also occur in a lighter or darker hue. The name damarensis was originally attached to the darker (reddish) brown specimens and in terms of priority, damarensis should thus be used.

As far as colour is concerned, it is evident that the black specimens of damarensis present a curious anomaly. Animals occurring in the dry west of Southern Africa usually present a pallid colouration while the colour usually darkens in the moister eastern areas. What specific adaptive significance can be attached to this phenotype (i.e. black specimens under desert conditions) is not clear.

Concerning the morphology of the skull, there is no character by which lugardi and micklemi differ, nor do these animals offer any points of anatomical difference compared to damarensis. Furthermore is it clear that the skulls differ greatly morphologically amongst themselves in size and detailed characters, as pointed out by St.Leger (1932, 963).

The inclusion of Cryptomys ovamboensis Roberts, as a synonym of C.damarensis in the present work needs some elucidation.

Specimens collected at Ondongwa, Ovamboland were referred to damarensis by Thomas (1926, 306), and those from elsewhere in the Kalahari to lugardi. Roberts (1951, 388) considered that the former collection represented an undescribed species "as they are by no means 'red-brown', or for that matter 'grey-brown'", as described for damarensis and lugardi respectively.

Roberts (1946, 315) described the colour of the type and five other specimens collected by himself at Ondongwa as between 'cinnamon-buff' and 'clay-colour'. The hair is short, the base light slaty grey with the tips buffy while the ventral pelage colour is slightly paler. Large white patches are present on the crowns as in C. damarensis, and it also shows the same variation in size and extent. Roberts maintains that Thomas recognised this difference in colour in the Ondongwa specimens as being distinct from specimens from the Cunene river and the Kaokoveld as well as the Kalahari desert, but still placed them as C. damarensis. Hitherto, ovamboensis is only known from the type locality.

I had access to the type specimen and the five other specimens of ovamboensis referred to above and can see no justification whatsoever, based on colour interpretation, for the specific separation of ovamboensis from damarensis. If placed among material representing the paler or darker brown colour phases of damarensis, it is barely possible to identify the Ondongwa specimens. A damarensis specimen in the pale brown colour phase, was collected by me at Mata Mata and there is no distinguishable difference (based on colour) between it and individuals from Ondongwa. The Ondongwa specimens are

in/...

in the light brown colour phase (cf. lugardi) and the mere fact that all six specimens from this locality shows this colouration may be ascribed to chance in the statistical sense of the word. Other localities are also known, where only the brown colour phase occurs.

As far as a comparison of size is concerned the following measurements of the type of C. ovamboensis (a fairly old ♂) and of a younger adult ♂ were compared with parameters obtained for damarensis ♂♂ in the present work. This is shown in Table 12.1.

Table 12.1: Comparison between C. ovamboensis and C. damarensis as far as H.B., T. and H.F. lengths are concerned. (♂♂).

	Type specimen (C.ovamboensis)	Young male (C.ovamboensis)	C. damarensis
H.B.	160 mm.	150 mm.	M = 164 mm.
T.	27 mm.	23 mm.	M = 25 mm.
H.F.	27 mm.	27 mm.	M = 27 mm.

From the above comparisons, it is evident that the size of ovamboensis falls well within the range of variation seen in damarensis.

Concerning the ovamboensis skull, Roberts (1951, 389) states that it appears to be the same as in C. damarensis. There seems to be no justification therefore for specific separation. Before leaving the skull, Roberts (1946, 315) also listed the width of the braincase at the posterior constriction (of the type specimen) as 7.8 mm. This value can not possibly be correct as the equivalent average value in C. damarensis specimens is 15.2 mm. (See fig. 12.2).

Finally, in view of the fact that

C.damarensis shows very little geographical variation (apart from the different colour phases and the shape and extent of the occipital patch) and seems to be a rather stable genotype ranging over an enormous portion of south-western Africa, it is not clear why, suddenly at a certain locality within its distribution range a new species should be present. According to Roberts (1951, xxix), Ovamboland has a number of recognized mammalian subspecies, but few definite species have been recorded, one of the exceptions being the presence of Cryptomys ovamboensis. As far as this mole-rat is concerned, the present author is thus not inclined to agree.

Biological:

In South West Africa, the southern limit of the red Kalahari sand, west of the railway is about the latitude of Rehoboth station which is also the southern limit of the range of C.damarensis in the Rehoboth district. This also applies to the distribution of many large bulbous plants (e.g. Pseudogaltonia) and the possibility of a correlation of distribution patterns of both animals and plants exists. Shortridge (1934, 321) states that the area south of Rehoboth (Great Namaqualand), is a 'hard-veld' region ".... sparsely clothed with a karroo type of vegetation, largely consisting of succulent-leaved plants".

In the Kalahari Gemsbok Park, it is known to subsist largely on the deeply rooted tubers of the gemsbok cucumber Citrullus naudinianus, constructing its tunnels past these tubers and gnawing off enough to satisfy its hunger at each visit. Roberts (1951,

388) mentions that they doubtless lay up stores of bulbs in some places, although actual proof of this is still lacking.

Much is still to be learnt about the breeding habits of this species. The only information hitherto available refers to two females collected in the Grootfontein district during the end of April, each containing five foetuses. Shortridge (1934, 325) suspects that these mole-rats have a fixed breeding season, although definite evidence is lacking.

There are six mammae present in C.damarensis while the pectoral mammae are nearly always longer (apparently more in use) than the inguinal mammae. The latter are usually undeveloped in immature breeding females and come into use with age when full litters are produced.

As far as other biological aspects are concerned, they apparently do not differ markedly compared to the other Cryptomys species. However, they are found mostly in fairly open sand plains, but do not avoid bush or thin forest as long as the soil is sandy and soft. They do not frequent rocky or stony regions, and in mountainous parts they extend along flat, sandy valleys. The distribution of local populations is thus often interrupted and disconnected (Shortridge, 1934, 321).

No further biological information, pertaining specifically to C.damarensis, is available.

Phylogenetic:

The black colour encountered in C.damarensis, a typical desert-like animal, has been referred to above as a curious anomaly, for most desert

animals/...

animals are generally pallid in colouration. Roberts (1935, 192) postulated that one could only conclude that in this case the blackness of colour specific to so many animals of the Congo region has been retained in this mole-rat as a specific character, even after the animals radiated into or was overtaken by desert conditions of the present time. This retention of the black colouration would also be aided by the fossorial habits of the animal, so that its colour would not be effected by the dry conditions as in other forms. This blackness is prevalent in West African animals, including birds, mammals and lower vertebrates (Roberts 1951, xxiii). Furthermore, Roberts (1935, 192) reported that on the border of the Ngamiland swamps the multimammate mice Rattus (Mastomys) coucha are darker than in the arid parts immediately to the south, and are undoubtedly more akin to those of Angola to the north-west. It is possible therefore that C.damarensis also originated in Angola, thence radiating southwards, despite the fact that a blackish species is not yet known from Angola.

In view of its large size, C.damarensis may be considered as an evolved species. It is likely that it has certain phylogenetic affinities with C.bocagei from Angola and C.darlingi from Rhodesia when phenotypic appearance is compared.

List of localities:

Damara Pan, 2 (TM), Erongo siding (Shortridge 1934, 320), Gemsbok Park, 1 (TM), Gobabis, 5 (TM), Grootkolk, 1 (TM), Kalkfield (Shortridge, 1934, 320), Kampspanne road, 4 (TM), Kano Vley (St.Leger, 1932, 963), Karakuwissa (St.Leger, 1932,

963/...

963), Kaotwe, 1 (TM), Kuke, 1 (TM), Kovares, 1 (TM), Lehutitung (Dollman, 1910, 400), Linyanti, 1 (RM), Mababe flats (Roberts, 1935, 236), Mashi river (Shortridge, 1932, 320), Mata Mata, 3 (TM), Matetsi, 5 (RM, AM, TM), 77 miles east of Maun, 1 (TM), Molopo river (Mafeking), 2 (SA), Morokwen (Shortridge, 1934, 320), Ngami lake (de Winton, 1898, 253), Numkaub (St.Leger, 1932, 963), Oas (Thomas, 1927, 390), Ondongwa, 5 (TM), Okahandja (Shortridge, 1934, 320), Otavi, 1 (TM), Otjivarongo (Shortridge, 1934, 320), "Ovamboland", 1 (TM), Palapye (de Winton, 1898, 253), Quickborn, 3 (TM), Sandfontein, 5 (NM, AM), Sebungwe, 3 (RM), Shorobe, 1 (TM), Ssanukanu village (St.Leger, 1934, 963), Twee Rivieren, 2 (TM), Wankie Game reserve, 2 (TM), Zesfontein (Shortridge, 1934, 320).

Extra-limital

Barotseland, 1 (RM), Balovale area, 2 (TM), Kataba river (Chubb, 1909, 35), Limalunga, 3 (PE), Mongu, 1 (PE), Nangweshi, 3 (RM, TM), Shangombo, 1 (TM).

CHAPTER 13

CRYPTOMYS HOLOSERICEUS (WAGNER) 1843

This species was first described by Wagner (1843, 373), based on three specimens which were made available to him in the (?) Leipzig Museum in Germany. Prior to the naming of this species the specimens under discussion were referred to as representatives of the hottentot mole-rat, C. hottentotus. Wagner however, noticed that certain aspects mentioned in the original description of the type of C. hottentotus, did not fit these three specimens entirely and he was therefore prompted to distinguish between C. hottentotus and C. holosericeus mainly on the larger size and different colouration of the latter.

According to Wagner, the type specimen was obtained by a donation of a collection of skins belonging to Herrn Feldmesser Leeb, from Graaff-Reinet. The second specimen was purchased at the "Krebsch'en Auktion", while the third was obtained from the botanist Drege.

Thomas (1895, 238) emphasized the fact that C. holosericeus was described on three specimens which were collected at different localities, and that therefore, the specimens may eventually prove to be of different species. In view of the fact that Graaff-Reinet is the first mentioned locality, the specimen from there should be taken as the type.

Thomas and Schwann (1906, 166) pointed to the fact that mole-rats "... referred of recent years

to/...

to *G. hottentotus* prove on closer examination to be referable to two species, a larger and a smaller, of which the former is more northern and eastern, the latter more southern and western in distribution; but whether and how far they overlap we are not at present able to say with any certainty". Thomas had seen Wagner's three specimens and he found that the two "adult" specimens were referable to the larger species while the "young" specimen could be placed with the smaller species (i.e. *C. hottentotus*). It is to be noted, however, that Wagner, in his original description of the *holosericeus* species, stated that the one specimen had only attained about two-thirds of its "possible" length (i.e. presumably the smaller specimen). The measurements given by Wagner appear to have been taken from one of the larger specimens, fixing the name of *holosericeus* on the latter.

As here understood, *Cryptomys holosericeus* is a monotypic species, occurring in the north-western Cape Province as well as in the north-western Orange Free State and south-western Transvaal.

Cryptomys holosericeus (Wagner)

Georychus holosericeus Wagner, in Schreber, Säugth. Suppl. *3*: 373, 1843. Type locality: Graaff-Reinet district, Cape Province.

Georychus vryburgensis Roberts, *Ann. Transv. Mus.*, *5*: 274, 1917. Type locality: Vryburg, northern Cape Province.

Cryptomys bigalkei Roberts, *Ann. Transv. Mus.*, *10*: 73, 1924. Type locality: Glen, north of Bloemfontein, Orange Free State.

Cryptomys/...

Cryptomys orangiae Roberts, Ann. Transv. Mus., 11: 259, 1926. Type locality: Glen, north of Bloemfontein, Orange Free State.

Cryptomys vetensis Roberts, Ann. Transv. Mus., 11: 259, 1926. Type locality: Taaiboschspruit, Vet river, Orange Free State.

Cryptomys holosericeus valschensis Roberts, Ann. Transv. Mus., 20: 316, 1946. Type locality: Bothaville, northern Orange Free State.

Type specimen: (?) Leipzig Museum, Germany.

Type locality:

Graaff-Reinet, Cape Province.

Distribution: (Fig. 13.1).

In comparison with C. damarensis or C. hottentotus, C. holosericeus does not display such a wide geographical distribution. It occurs in the north-western Cape, in the vicinity of Kimberley, ranging northwards to the vicinity of Vryburg. It also occurs in the north-western Orange Free State (e.g. in the vicinity of Bothaville) as well as at Glen north of Bloemfontein. Across the Vaal river, this species is encountered at Bloemhof and Wolmaransstad in the south-western Transvaal.

Diagnostic characters:

In most respects in colour and structure like C. hottentotus, but the species tends to be yellower in colouration and considerably larger in size H.B. M=141 mm., C.B. M=35.3 mm. (♂♂). The mammae consist of two pairs of pectoral, and one inguinal pair, as is the case in C. hottentotus.

Colour:

The overall colouration of this species is

a/...

a yellow-buff, uniformly distributed over the dorsal surface, while tending to be slightly lighter coloured below. The bristles on the tail show the same colouration, while the feet show a pinkish colouration in the living specimens, tending to turn brown in study skins. The absence of any white patches or marks on or in the vicinity of the head, is a constant feature in this species.

The colouration tends to show some geographical variation. This is well illustrated in specimens from the Vryburg district which are decidedly browner than specimens from the Bothaville district. However, in each population, all the various colour gradations can be expected and these colour differences are only clear when a number of study skins from the same locality are studied simultaneously.

Size: Adult ♂♂:

H.B. 125-160 mm., M = 141 mm.
T. 19-30 mm., M = 24 mm., (17.0% of H.B.)
H.F. 19-27 mm., M = 24 mm., (17.0% of H.B.)
C.B. 31.7-38.3 mm., M = 35.3 mm.
B.C. 13.3-15.9 mm., M = 14.9 mm., (42.2% of C.B.)
I.W. 6.8-7.9 mm., M = 7.2 mm., (20.3% of C.B.)
Z.W. 21.1-28.6 mm., M = 25.4 mm., (71.9% of C.B.)
M.W. 5.8-7.9 mm., M = 7.0 mm., (19.8% of C.B.)
U.T.R. 5.3-6.8 mm., M = 5.9 mm., (16.7% of C.B.)
L.J. 21.1-25.9 mm., M = 23.8 mm., (67.4% of C.B.)
L.T.R. 5.3-7.1 mm., M = 6.2 mm., (17.5% of C.B.)

Adult/...

Adult ♀♀:

H.B. 125-145 mm., M = 138 mm.

T. 18-28 mm., M = 23 mm., (16.6% of H.B.)

H.F. 18-28 mm., M = 22 mm., (16.5% of H.B.)

C.B. 30.4-34.2 mm., M = 32.7 mm.

B.C. 14.1-15.3 mm., M = 14.7 mm., (44.8% of C.B.)

I.W. 7.1-7.9 mm., M = 7.2 mm., (22.0% of C.B.)

Z.W. 21.4-24.7 mm., M = 23.4 mm., (71.5% of C.B.)

M.W. 5.6-6.6 mm., M = 6.3 mm., (19.2% of C.B.)

U.T.R. 5.2-6.1 mm., M = 5.8 mm., (17.7% of C.B.)

L.J. 19.8-22.7 mm., M = 21.4 mm., (65.4% of C.B.)

L.T.R. 5.6-6.7 mm., M = 5.9 mm., (18.0% of C.B.)

Sexual dimorphism in size is apparent: when 22 ♂♂ and 21 ♀♀ of C. holosericeus are compared in respect of C.B. length, ♂♂ (M=35.3 mm. ± 1.881 mm.) are significantly larger than the ♀♀ (M=32.7 ± 1.091 mm.) at the 1% level (t = 2.7, 41 degrees of freedom, P = 0.01).

Skull and dentition:

Roberts (1951, 393) has stated that the nasals in C. holosericeus are broad near the back but narrowing more or less to a point at the back. He furthermore states that the condyles do not project behind the paroccipital processes. As far as the present author is concerned, it is felt that too much variation can be expected in these characteristics to make them of diagnostic value.

The skull of holosericeus is ruggedly built, on the average larger than the skull of C. hottentotus, while it corresponds more or less in size to that attained by damarensis, but differing therefrom in the absence of the thickening of the outer wall of the infraorbital foramen. Ellerman et.al. (1953, 231) state that the greatest length of the ♂ skull (including incisors) is usually not below 40 mm., while the corresponding length in ♀ skulls is rarely below 38 mm.

There are no diagnostic features in the dentition of *C. holosericeus* on which this species could possibly be separated from other *Cryptomys* species.

Discussion:

A few remarks on the type locality of *C. holosericeus* are pertinent here. It has been indicated above that the specimens representing *C. holosericeus* in Wagner's material have probably been collected at different localities. In fact, only the skin which served as the type specimen has been described as coming from Graaff-Reinet, while the localities of the other two specimens have not been indicated. If Graaff-Reinet is accepted as the type locality for this species, it is evident that it is located in the middle of the geographical distribution exhibited by *C. hottentotus* in the eastern Karoo. This raises the question why another species should suddenly occur under identical ecological conditions under which *C. hottentotus* seems to thrive and to which it is adapted.

Furthermore, if Graaff-Reinet is accepted as the real type locality, this would imply an extended southern distribution pattern for *C. holosericeus* which does not fit the logical distribution pattern of *C. holosericeus* in the north-western Cape and Orange Free State. When the known localities for *C. holosericeus* specimens are plotted on a distribution map, it becomes evident that the supposed type locality (i.e. Graaff-Reinet) falls entirely outside the present known range of distribution of holosericeus.

It would be of interest to know where the other two specimens, referred to by Wagner, were collected. It could well be that they were collected in the present known areas of distribution of holosericeus. It is also not clear from Wagner's description whether Herrn Feldmesser Leeb was resident at Graaff-Reinet, or whether he received the specimen from someone else who gave Graaff-Reinet as the locality where the specimen was collected.

In considering these few remarks mentioned above, I am inclined to raise the possibility that the accepted type locality as proposed for C. holosericeus should be accepted with some reservation and doubt.

The validity of C. holosericeus as a separate species has also been queried on a number of occasions. As an example, Thomas (1895, 238) has mentioned the fact that he could not distinguish 'G. hottentotus', 'G. ludwigii' and 'G. holosericeus' from 'G. caecutiens'. As has been indicated in the present work elsewhere, the former two and latter species are synonyms under the species Cryptomys hottentotus. It is thus interesting to note an element of uncertainty on the validity of C. holosericeus held by Thomas.

On the other hand, Thomas and Schwann (1906, 166) stated that specimens referred to 'G. hottentotus' in the past, could on closer examination be referred to a larger and smaller species.

To what extent and how far these two species overlapped, they could not state with certainty. The difference in size is chiefly in general bulk, so that it is not easy to give any single dimension which would distinguish the two at all stages. They suggested that the alveolar length of the tooth row (above 6.5 mm. in the larger and below in the smaller) would be as convenient as any. Comparing old skulls only, the larger species (i.e. C. holosericeus) may attain 36 mm. and over in basal length, while the smaller (i.e. hottentotus) rarely reaches 33 mm. The latter figures given by Thomas and Schwann correspond reasonably well with the C.B. lengths found for holosericeus and hottentotus respectively in the present work. The present author is therefore inclined to tentatively retain the species rank of C. holosericeus instead of merging it under hottentotus, as has been suggested in some circles. This retention is based mainly on differences in overall bulk of the two species, whereas aspects of colouration, cranial morphology and number of mammae could point to reasons for synonymizing C. holosericeus under C. hottentotus, the latter name having priority by approximately 17 years.

The way Ellerman et.al. (1953, 230, 231) have proceeded to interpret the genus Cryptomys in Southern Africa has been reviewed briefly in the chapter discussing aspects of C. hottentotus in the present work. Because of the fact that the species C. holosericeus is involved in that discussion, facts pertaining to C. holosericeus may briefly be recapitulated here.

Ellerman/...

Ellerman _et.al_. have divided the genus _Cryptomys_ into a larger (_C. mechowi_ - extralimital as far as the present work is concerned) and smaller species. The former reaches a H.B. length of 175 mm. and more (skull with incisors in adults 45-66 mm.) while the latter reaches a H.B. length of 180 mm. in only two specimens (both _C. damarensis_) in a very long series of skins. The greatest length of the skull (with incisors) rarely reaches 45 mm.

This smaller species is again subdivided into a smaller and larger species. The former has the greatest length of the ♂ skull (including incisors) only reaching 41 mm. once and rarely 40 mm., while in the Republic of South Africa the ♀ skulls rarely reach 38 mm. in length. These forms are thus taken in under _C. hottentotus_.

On the other hand, in the so-called larger species, the greatest length of the ♂ skull (with incisors) is above 40 mm., while the ♀ skull length is rarely below 38 mm. (i.e. _holosericeus_).

Ellerman _et.al._ (1953, 234), based on the definition of _C. holosericeus_ given above, thus accept _holosericeus_ as the only other species in Southern Africa (apart from _C. hottentotus_), and therefore placed _'G.' vryburgensis_, _C. orangiae_, and _C. vetensis_ as subspecies (races) under _C. holosericeus_, including the subspecies originally proposed by Roberts (1946, 316) named _C. holosericeus valschensis_.

Taxonomically speaking, this procedure points to a considerable degree of simplification of aspects relating to C. holosericeus in South Africa. It will be evident that I have largely followed this classification and is therefore in full accord of the proposals postulated by Ellerman et.al.

It could be, however, that Ellerman et.al. have largely followed Roberts (1951, 393) in these concepts. In his now classical work, 'The Mammals of South Africa' (1951), Roberts had already demoted all specimens originally credited with specific rank to subspecific level under the nominate species C. holosericeus, viz. Cryptomys holosericeus holosericeus (=Georychus holosericeus), C.h. vryburgensis (= Georychus vryburgensis), C.h.orangiae (= C.orangiae) and C.h. vetensis (= C. vetensis) while retaining the subspecific status of C.h. valschensis as originally proposed by Roberts in 1946.

The present author is inclined to simplify the picture even further by not acknowledging any subspecies, but to interpret C. holosericeus as a variable monotypic species.

Unfortunately, virtually no material of C. holosericeus collected at or near the supposed type locality is available for study in the present analysis. Only one skin, collected at Graaff-Reinet is available in the Albany Museum collection and in this study specimen the skull is inside the skin, while there are no measurements concerning the H.B., T. and H.F. lengths. The colour and size of the animal fall within the range of variation encountered in Cryptomys hottentotus, and must therefore be regarded as belonging to this species.

Therefore, a statistical comparison between specimens from the supposed type locality of

<u>holosericeus</u> and other localities could not be undertaken. It was however possible, in some instances to compare parameters of the different subspecies.

Table 13.1: Comparison of certain skull measurements in Vryburg and Bothaville samples of *Cryptomys holosericeus* (♀♀):

Measurement	Vryburg M_1	SD_1	Bothaville M_2	SD_2	C.D.	% J.N.O.
C.B.	33.8 mm.	2.691	32.2 mm.	2.841	0.28	<< 75%
L.J.	22.3 mm.	2.080	21.2 mm.	1.954	0.27	<< 75%
Z.W.	24.7 mm.	2.519	22.7 mm.	1.825	0.46	<< 75%

On closer inspection of Table 13.1 above, it is clear that <u>C.h. vryburgensis</u> and <u>C.h. valschensis</u> from Vryburg and Bothaville respectively, are decidedly not subspecifically distinct when some skull measurements in adult ♀♀ are compared. In these (and other measurements), a J.N.O. of far less than 75% is obtained, i.e. very much below the level of conventional subspecific separation (See also fig. 13.2).

Unfortunately, no further similar comparisons could be made in view of the fact that samples from other localities were either not homogeneous (i.e. juveniles and adults) or the samples of such populations were too small for statistical manipulation.

However, a comparison of the mean values for H.B. length, C.B. length and L.J. length in adult males from Taaiboschspruit, Bothaville and Vryburg was made as is shown in Table 13.2.

Table 13.2: Comparison of mean values for H.B., C.B. and L.J. lengths in *C. holosericeus*.

Measurement	Taaiboschspruit	Bothaville	Vryburg
H.B.	M=136 mm. (n=4)	M=135 mm. (n=9)	M=135mm.(n=2)
C.B.	M=34.0mm. (n=4)	M=35.5mm. (n=9)	M=33.1mm.(n=3)
L.J.	M=22.3mm. (n=4)	M=24.0mm. (n=9)	M=22.1mm.(n=3)

As will be seen, these figures compare remarkably well, again pointing to the possible equivalence of *C.h. vetensis*, *C.h. valschensis* and *C.h. vryburgensis*. It is a pity that the comparable samples of Vryburg and Taaiboschspruit are so small, and I am convinced of the fact that if more material becomes available for study, the existing differences will be further diminished.

It may have been noticed that nothing as yet has been said about the inclusion of *Cryptomys hottentotus bigalkei* and *Cryptomys orangiae* (i.e. *C. holosericeus orangiae*) as synonyms under *C. holosericeus*, and this procedure therefore requires some explanation.

Roberts (1924, 73) described a new species, *Cryptomys bigalkei* (type locality Glen, north of Bloemfontein) on four mole-rats collected by R. Bigalke at Glen on July 14th 1921. According to the original description, these specimens were seemingly allied to *C. 'cradockensis'* (i.e. *C. hottentotus* as far as the present work is concerned) but there is a dark obscure dorsal line along the back. The face is dark with pale buffy white spots over the ears and eyes, and the cheeks are yellowish buffy showing up

clearly/...

clearly against the general dark colouration of the face (Roberts, 1924, 73).

The H.B. lengths in both an adult ♂ and ♀ specimen (the latter being the type specimen) were given as 125 mm. and 116 mm. respectively, while the zygomatic width measurements were given as 28.3 mm. and 24.0 mm. respectively.

Roberts (1951, 391), however, demoted the species rank credited to this animal to subspecific rank in 1951 (interpreting bigalkei as a subspecies of hottentotus), while Ellerman et.al. (1953, 233) followed the same procedure. In 1951 Roberts described bigalkei as similar in colour to the typical form (i.e. hottentotus hottentotus), ".... but larger in size and the grinding teeth larger, the hindfoot longer".

Roberts (1926, 259) described a second new species from the same locality (i.e. Glen) which he named Cryptomys orangiae. The colour in this species was described as uniform buffy in both sexes (in this respect like other members of the C. holosericeus group) but differing from C. holosericeus in having the nasals straight, not pointed, nor bulging out at the sides. The dimensions of a pair fully adult, old specimens were given as follows:

	♂	♀
H.B.	150 mm.	140 mm.
H.F.	26 mm.	24 mm.

Other measurements were also given, which could not be used for comparison, due to the fact that they are not considered for the purposes of the present work.

Subsequently/...

Subsequently, in 1951, Roberts (1951, 393) also demoted the species *orangiae* to subspecific rank under *C. holosericeus holosericeus*, while Ellerman *et.al*. (1953, 235) followed the same procedure.

Both the type specimens of *C. bigalkei* and *C. orangiae* are housed in the Transvaal Museum and I had the opportunity to see and compare the specimens. After comparison, I have come to the tentative conclusion that there seems to be no justification for specific or subspecific separation between *bigalkei* and *orangiae* on the one hand or to separate the specimens from Glen specifically or subspecifically from *holosericeus*. This tentative conclusion is based on aspects to be presented in tabular form below.

Table 13.3: A comparison of measurements of *C.hottentotus*, *C. bigalkei*, *C. orangiae* and *C. holosericeus* indicating a closer relationship of *orangiae* and *bigalkei* to *holosericeus* than to *hottentotus*.

♂♂:(Adult):

Measurement	*C.hottentotus*	*C.bigalkei*	*C.orangiae*	*C.holosericeus*
H.B.	105-150 mm. (M= 120 mm.)	125 mm.	150 mm.	125-160 mm. (M= 141 mm.)
T.	17-27 mm. (M= 22 mm.)	25 mm.	19 mm .	19-30 mm. (M= 24 mm.)
H.F.	18-25 mm. (M= 21 mm.)	22 mm.	26 mm.	19-27 mm. (M= 24 mm.)
I.W.	6.2-7.7 mm. (M= 6.7 mm.)	7.5 mm.	-	6.8-7.9 mm. (M= 7.2 mm.)
Z.W.	19.1-28.0 mm. (M= 22.8 mm.)	28.3 mm.	-	21.1-28.3 mm. (M=25.4 mm.)
U.T.R.	4.5-6.1 mm. (M= 5.1 mm.)	6.0 mm.	-	5.3-6.8 mm. (M= 5.9 mm.)

Continued/...

L.J.	17.2-25.3 mm. (M= 20.6 mm.)	24.7 mm.	-	21.1-25.9 mm. (M= 23.8 mm.)
L.T.R.	4.2-6.1 mm. (M= 5.2 mm.)	5.8 mm.	-	5.3-7.1 mm. (M = 6.2 mm.)
♀♀: (Adult):				
H.B.	100-160 mm. (M= 119 mm.)	116 mm.	140 mm.	125-145 mm. (M= 138 mm.)
T.	17-26 mm. (M = 21 mm.)	-	19 mm.	18-28 mm. (M= 23 mm.)
H.F.	17-25 mm. (M= 21 mm.)	20.5 mm.	24.0 mm.	18-28 mm. (M= 22 mm.)
I.W.	6.0-7.5 mm. (M= 6.6 mm.)	7.3 mm.	7.5 mm.	7.1-7.9 mm. (M= 7.2 mm.)
Z.W.	18.4-25.3 mm. (M= 22.0 mm.)	24.0 mm.	25.6 mm.	21.4-24.7 mm. (M= 23.4 mm.)
U.T.R.	4.6-5.9 mm. (M= 5.1 mm.)	6.3 mm.	6.0 mm.	5.2-6.1 mm. (M= 5.8 mm.)
L.J.	16.9-24.1 mm. (M= 20.2 mm.)	21.6 mm.	23.6 mm.	19.8-22.7 mm. (M= 21.4 mm.)
L.T.R.	4.3-6.0 mm. (M= 5.1 mm.)	6.2 mm.	6.1 mm.	5.6-6.7 mm. (M= 5.9 mm.)

Unfortunately this data could not be manipulated statistically in view of the fact that comparable samples of populations under discussion were too small.

When the measurements given in the table above are considered, it becomes evident that both species, bigalkei and orangiae, show a greater degree of correspondence with C. holosericeus than to C. hottentotus, especially as far as the measurements of I.W., Z.W., U.T.R., L.J. and L.T.R. (♂♂) are concerned, while there is a great correspondence in the ♀♀ concerning the I.W., Z.W., U.T.R., L.J. and L.T.R. between bigalkei and orangiae. This latter fact

points/...

points to the possible equivalence of the two species.

Although Roberts (1926, 259) has stated that orangiae differs from C. holosericeus in the structure of the nasals, I am not inclined to accept this difference as being of diagnostic value in view of the great amount of individual variation found in the structure of the nasals, even within the holosericeus group. Similarly, the colour of orangiae was described as being slightly lighter yellowish than the typical form (i.e. holosericeus) (Roberts, 1951, 393), the skull of about the same size (although the condyles projected further backwards), while the hind-foot is supposed to be slightly longer.

C. bigalkei was described (Roberts, 1924, 73) as having an obscure dark dorsal line: this feature is, however, found constantly in specimens representing C. holosericeus, while it is also seen occasionally in C. hottentotus. This characteristic is therefore not of diagnostic value either.

If it is accepted that C. orangiae is a synonym of C. bigalkei, which in turn is a synonym of C. holosericeus, the emerging pattern of distribution of these species involved becomes clear and logical. This eliminates the necessity of regarding the possibility of two species existing side by side in the Glen area north of Bloemfontein (Ellerman et.al. 1953, 230), while the range of C. holosericeus is extended logically to the south. Roberts had already indicated (1926, 259) that the species orangiae extended westwards from Glen in the sandveld a little to the south of Bothaville (the type locality of

C./...

C. holosericeus valschensis), whereas he also stated that specimens obtained near Bothaville, differing but slightly from the Bothaville specimens (as well as those collected in the Parys district), could probably be referred to C. bigalkei.

To my mind, C. holosericeus has been grossly oversplit by Roberts. By synonymizing these forms, a clearer picture emerges concerning the species holosericeus, and it also removes the difficulty of explaining the occurrence of two species (i.e. bigalkei and orangiae) under identical ecological conditions (e.g. at Glen), while it is also not clear what factors could possibly be effective for the development of at least five subspecies (i.e. holosericeus, orangiae, vetensis, valschensis and vryburgensis) in the north-western Orange Free State and adjacent areas.

Further considerations of the various original descriptions given for the supposed different species all point to the fact that they are not in reality different. For example, Cryptomys vetensis was described as the ♂♂ being slightly, the ♀♀ much darker than orangiae (Roberts, 1926, 259) with body and skull proportions as in orangiae, but the molars being decidedly larger. These differences are however average rather than absolute and difficult to define when all forms are taken into account. Similarly, the specimens from Vryburg were described as grey-brown, but if the specimens are considered individually, and placed amongst specimens from other localities, it is no easy matter to identify the odd specimen.

Reviewing the discussion in the above paragraphs, the indications seem to point to the fact that C. holosericeus is in fact not a good and valid species. If all the factors are taken into account, the possibility exists that C. holosericeus may eventually be synonymized with C. hottentotus. This possibility may rest largely on the following arguments:

(a) Within different populations (colonies) of C. hottentotus, one often encounters large specimens, which are well beyond the limits of size variation for this species. They tend to fall within the range of size variation exhibited by C. holosericeus. Such individuals are encountered in localities including Wolseley, Grootvadersbosch, Knysna and possibly Graaff-Reinet, all within the geographical range of C. hottentotus. This applies to both postcranial and cranial measurements. It may therefore point to a possible equivalence between the two species as far as size measurements are concerned.

(b) The overall correspondence in colouration of the pelage in C. hottentotus and C. holosericeus is striking. The exact colour tint exhibited in the former species can be shown to exist in the latter. Although holosericeus tends to be yellower than hottentotus when a number of specimens are seen simultaneously, this difference in colour seems to be average rather than absolute. This feature may thus also point to the conspecific nature of the two species.

(c) There is a certain amount of uncertainty concerning the limits of geographical distribution of hottentotus and holosericeus. As interpreted

in/...

in the present work C. hottentotus occurs in an area to the south of Bloemfontein, while C. holosericeus occurs at Glen, to the north of Bloemfontein. At present, it is not possible to draw a line indicating the limits of each species. Therefore it is not possible to determine the degree of overlap existing between hottentotus and holosericeus.

On the other hand, if holosericeus is interpreted as a synonym of hottentotus, the range of distribution of hottentotus would logically be extended to the north, eliminating the break in distribution which presently exists in the geographical range of hottentotus (See fig. 11.1.).

(d) Finally, if hottentotus and holosericeus were interpreted as the same species, it would eliminate the necessity of explaining the occurrence of two species and subspecies at a certain locality (eg. Glen), occurring under identical environmental conditions, i.e. C. hottentotus bigalkei and C. holosericeus orangiae.

The step of synonymizing holosericeus with hottentotus has however not been taken in the present work, but it may be incipient. This reservation is largely based on the following considerations:

(i) The species holosericeus dates back to 1843 and is therefore a well "established" species. It could well be that study skins and skulls are available which would justify its retention as a separate species.

(ii) I have not seen the type specimen (if in existence) personally, and

(iii) I find it advisable to withold the synonymizing of holosericeus with hottentotus until further details (based on future research) will become

available/...

available which would probably finalize the question.

Biological:

Very little is known about the biology of C. holosericeus and Roberts (1951, 393) states that their habits are like those of C. hottentotus. It may just be pointed out that the work done by Eloff (1951, 1952, etc.) on behavioural aspects of C. bigalkei would imply that in fact C. holosericeus was considered if the taxonomic interpretation presented in the present work is accepted.

Phylogenetic:

C. holosericeus is probably a comparatively evolved species, which is reflected in its large size. Its closest relative appears to be C. hottentotus resembling it in colour and number of mammae. It is, however, much larger than C. hottentotus and shows a smaller range of geographical distribution. This may point to a specialized genotype, highly adapted to certain (possibly specialized) environmental conditions. This possibility may explain the relatively limited distribution pattern exhibited by C. holosericeus.

List of localities:

Angra Pequina, Bothaville, 22 (TM), Barkley West, 6 (MM, SA, AM), Bloemhof, 6 (TM), Braklaagte, Parys, 2 (TM), Coalbrook, 2 (TM), Fourteen Streams, 1 (TM), Glen, 8 (TM), Junction, Vet-Sand rivers, 1 (NM), 'Kuruman division', 1 (SA), Maquassie, 2 (TM), Modder river, 3 (SA), Odendaalsrust, 5 (TM), Rietpan, Kimberley, 1 (MM), Sand river, 1 (NM), Taaiboschspruit, Vet river, 5 (TM), Vryburg, 17 (TM, AM).

CHAPTER 14

CRYPTOMYS DARLINGI (THOMAS) 1895

This bathyergid species was first described by Thomas (1895, 239) from specimens collected at Mazoe and Salisbury in Mashonaland, Southern Rhodesia. Mr. J. Ffolliot Darling obtained the mole-rats at the former locality, while Mr. G.A.K. Marshall collected the Salisbury material. This species was named by Thomas after Mr. Darling, taking one of Mr. Marshall's Salisbury specimens as the actual type.

As here understood, C. darlingi is a monotypic species, occurring predominantly on the Mashonaland plateau.

Cryptomys darlingi (Thomas)

Georychus darlingi Thomas, Ann. Mag.nat.Hist., Ser. 6, 16: 239, 1895. Type locality: Salisbury, Southern Rhodesia.

Type Specimen:

British Museum (Natural History), No. 95.7.16.4. Collected May 14th 1895 by G.A.K. Marshall.

Type locality:

Salisbury, Southern Rhodesia.

Distribution: (Fig. 14.1).

Mashonaland, southwards to Mount Selinda and the lower lying area of Matibi in eastern Southern Rhodesia. From the type locality, it also ranges south-westwards to Selukwe and the vicinity of Bulawayo.

Diagnostic/...

Diagnostic characters:

A medium to large sized species, H.B. M = 145 mm., C.B. M = 33.3 mm. (♂♂). More or less intermediate in size between the larger *C. damarensis* and smaller *C. hottentotus*. Dorsally and ventrally, the pelage is a drab-grey, while an occipital white patch (variable in extent and occurrence) is usually present. Mammae: 2 pectoral pairs, 1 inguinal pair = 6.

Colour:

Thomas (1895, 239) has described the colour of *C. darlingi* as being a uniform drab (nearest to the drab-grey of Ridgeway). This basic colouration is modified by the slaty-grey bases of the hairs showing through. The ventral pelage is more or less identical to that of the dorsal aspect but slightly more slaty. Apart from the slaty-grey base of the individual hairs, their tips are fawn coloured. The pelage has been described as short, close and velvety (Thomas, 1895, 239), while the hairs barely reach a length of five millimeters on the back.

The feet and tail have a pinkish colour in the fresh or living condition while the bristles on the limbs and tail have the same colour as the body pelage. Thomas (*loc.cit.*) is of the opinion that the tail may be narrower than in '*C. caecutiens*' (i.e. *C. hottentotus*). The dorsal and ventral colouration thus intergrades without a pronounced line of demarcation.

As is the case in the majority of *Cryptomys* species, the juvenile pelage is decidedly darker compared to the colour portrayed by the adult.

Colouration/...

Colouration in adult specimens shows a certain degree of geographical variation. This is evident, when comparing not only different populations or colonies, but even within specimens from the same tunnel system. Examples from the eastern Melsetter district are decidedly darker compared to those collected at Salisbury, which tend to be yellower in colour, while specimens from Bulawayo show a definite light-grey hue.

The occurrence of the white occipital patch is also variable. In specimens seen by me, it varied from its complete absence to large and well developed patches, although never attaining the size found in <u>C.damarensis</u>. Thomas (1895, 239) described his specimens as having large and prominent triangular patches averaging 14 mm. long x 8 mm. wide. He furthermore remarked on the similarity in size and shape of the occipital patch in his specimens. I can also confirm Thomas' observation that whenever these occipital patches are present, irrespective of size, they do not extend beyond the nape of the neck.

The corners of the mouth may often be stained brown in specimens which is undoubtedly the result of staining by plant juices from plants eaten by the animals.

<u>Size</u>:	<u>Adult ♂♂</u>:
H.B.	125-165 mm., M = 145 mm.
T.	8-13 mm., M = 10 mm., (6.8% of H.B.)
H.F.	21-30 mm., M = 23 mm., (15.8% of H.B.)
C.B.	30.6-37.9 mm., M = 33.3 mm.
B.C.	13.0-15.9 mm., M = 14.7 mm., (44.1% of C.B.)
I.W.	6.3-7.7 mm., M = 7.2 mm., (21.6% of C.B.)

Z.W./...

Z.W. 20.8-28.2 mm., M = 24.4 mm., (73.2% of C.B.)

M.W. 6.0-8.2 mm., M = 7.2 mm., (21.6% of C.B.)

U.T.R. 4.7-5.6 mm., M = 5.3 mm., (15.9% of C.B.)

L.J. 19.0-25.4 mm., M = 21.7 mm., (65.1% of C.B.)

L.T.R. 4.9-5.9 mm., M = 5.5 mm., (16.5% of C.B.)

<u>Adult ♀♀</u>:

H.B. 135-150 mm., M = 141 mm.

T. 10-10 mm., M = 10 mm., (7.0% of H.B.)

H.F. 20-24 mm., M = 22 mm., (15.6% of H.B.)

C.B. 31.0-36.5 mm., M = 32.6 mm.

B.C. 13.9-15.1 mm., M = 14.4 mm., (44.1% of C.B.)

I.W. 6.8-7.4 mm., M = 7.0 mm., (21.4% of C.B.)

Z.W. 21.3-27.2 mm., M = 23.3 mm., (71.4% of C.B.)

M.W. 6.5-7.6 mm., M = 6.9 mm., (21.1% of C.B.)

U.T.R. 4.7-5.5 mm., M = 5.1 mm., (15.6% of C.B.)

L.J. 20.0-25.0 mm., M = 21.2 mm., (65.3% of C.B.)

L.T.R. 5.1-5.8 mm., M = 5.3 mm., (16.2% of C.B.)

As can be seen from the tables above, the ♂♂ are usually slightly larger than the ♀♀, but this difference is not statistically significant and does not point to any degree of sexual dimorphism. When 13 ♂♂ (M= 33.3 ± 2.557 mm.) and five ♀♀ (32.6 ± 1.951 mm.) from Shawerombi, Melsetter district, Southern Rhodesia, are compared in respect of C.B. length it appears that the difference is not significant at the 90-80% level (t= 0.23, 16 degrees of freedom, P= 0.90-0.80).

Very little geographical variation in size is evident.

<u>Skull and dentition</u>:

Aspects pertaining to the skull have been described by Thomas. The skulls are rather broad and

heavy/...

heavy, the braincase large and rounded, while the nasals have been described as short, more or less evenly expanded on each side, not constricting anteriorly. The ascending processes of the premaxillaries surpass the nasals posteriorly by about two millimeters, closing in towards the midline behind the nasals. In the material seen by me, the structure and configuration of the nasals seem to be a variable characteristic. As is the case in C. damarensis, (and C. nimrodi for that matter), the infraorbital foramina are higher than broad, the bases forming their outer boundaries being nearly as thick as that forming their floors. As in other species, the size of this foramen is variable, even within one individual. The teeth are well developed and strong, the last molar element being the smallest. As in other species, this conforms to the usual molar pattern encountered in other Cryptomys species (See Fig. 14.2).

Discussion:

Ellerman et.al. (1953, 232) have placed C. darlingi as a race (subspecies) of C. hottentotus. This does not seem to be justified, for C. hottentotus is a far smaller type of animal while a definite difference in the colour of the pelage also exists. Furthermore, these two species are well separated geographically.

Roberts (1951, 390), on the other hand, has maintained the specific rank of C. darlingi as proposed by Thomas, but gives no additional information about the species apart from what Thomas has already given in 1895. It would thus seem that Roberts' interpretation of the status of the species is more

correct/...

correct.

Apart from these taxonomical observations it would appear that C. darlingi creates no intricate complications as far as synonymy etc. is concerned and that it is a reasonably clearcut and recognisable species.

A certain degree of phenotypic geographical variation (especially as far as colouration is concerned) is however encountered. As was indicated above, specimens from the eastern parts of Southern Rhodesia (e.g. from Melsetter district) are decidedly darker in colour compared to specimens from the western localities of its range (e.g. Bulawayo). This may be correlated with environmental factors such as moisture. On the other hand, there seems to be very little difference in overall size between specimens derived from different localities.

It is of interest to note that the H.B. size given for the type by Thomas is 128 mm., which is far below the mean value attained from specimens considered in the present study (i.e. M = 145 mm.) although it still falls within the observed minimum-maximum range of 125-165 mm. Similarly, a collection of specimens made by Darling in the Mazoe district showed a collector's measurement (taken in the flesh) of H.B. = 125 mm., which is also on the small side (de Winton, 1896, 808). This would imply that the species as such (based on values obtained in the present work) is in actual fact larger than originally suspected by Thomas, who referred to this species as a ".... little species.....".

Biological/...

Biological:

Unfortunately very little biological information is available pertaining to this species. Since C. darlingi was first collected in Mashonaland towards the end of the last century, very little additional biological information has been gathered. It is reported to have been very common in those years and Thomas already expressed the hope that collectors would send many more specimens so that something could be learnt about the seasonal, age and sexual variations of this species. These requirements have as yet not been fulfilled (although a fair-sized sample is available in the form of study skins), and the ecological and biological observations of these animals have been grossly neglected.

This mole-rat occurs in woodland areas where several species of Brachystegia and Julbernardia are dominant over extensive areas. Other dominant plant genera include Terminalia, Combretum and Acacia between which open valley grasslands occur (Keay, 1959). These conditions are especially prevalent in areas near Salisbury and Selukwe. Specimens from the Melsetter area and Mount Selinda live in more montaine communities including evergreen forest, grassland and woodland communities. According to Thomas (1895, 240) the collector of the type series stated it to be very common on the open veld.

This species is mainly confined to the higher lying Mashonaland plateau, on the average about 4,000' above sea level. On the other hand, specimens have been collected in the Melsetter district (at Shawerombi) and also in the Matibi district which lie at 5,900' and 2,000' above sea level respectively.

The species has two pairs of pectoral and one pair of inguinal mammae. Information concerning breeding is very meagre: a ♀ was collected at Selukwe on July 25th 1955 which contained three foetuses nearly on full term.

Phylogenetic:

Thomas (1895, 239, 240) regards C. darlingi as more closely allied to C. damarensis than to 'G. caecutiens' (i.e. C. hottentotus). It is separated from the latter by the occurrence (usually) of the white crown patch, its shorter fur and the thick outer wall of the infraorbital foramen. It can be distinguished from C. damarensis by its conspicuously smaller size and less extended crown patch as well as shorter nasal elements.

The present author is inclined to agree with these observations, for the overall phenotypic impression gained from C. darlingi is that it represents a smaller and somewhat "watered-off" form of C. damarensis.

List of localities:

Bulawayo, 10 (RM, NM), Chisawassah, 4 (SA), Chipinga, 1 (RM), Enterprise district, near Salisbury, 2 (RM, TM), Inyanga, 4 (RM, TM), Khami dam, near Bulawayo, 4 (RM), Mt. Selinda, 9 (TM), Macheke, 2 (RM), Munenga river, 2 (RM), Mazoe near Salisbury, (Thomas, 1895, 238), Salisbury, 6 (RM), Shawerombi, Melsetter district, 39 (RM), Selukwe, 4 (RM), Stimela's Drift, Matibi district, 1 (TM), Umtali, 1 (RM), Vumba, 7 (NM, RM, TM).

CHAPTER 15

CRYPTOMYS NIMRODI (DE WINTON) 1896

This Cryptomys species was first collected by C.F. Selous in Matabeleland near Essex Vale in the vicinity of Bulawayo between August and October 1895. The specimens on which the species is founded were, however, all taken in November 1895. de Winton (1896,806) named this species in honour of the "mighty hunter" and based his description on four skins (one adult, three juveniles) and five skulls (two adults and three juveniles) (de Winton, op.cit., 808).

Although I have had access to a considerable number of Cryptomys study skins from Southern African localities, I could not convincingly refer any specimens to the species under discussion. Therefore, all further information pertaining to this species, to follow below, has been culled from the available literature.

As here understood, C. nimrodi is regarded as a monotypic species occurring mainly in the vicinity of Essex Vale and perhaps in the immediate surrounding districts. Hitherto, it is only known from the type locality (Roberts, 1951, 389).

Cryptomys nimrodi (de Winton)

Georychus nimrodi de Winton, Proc. zool. Soc. Lond., p. 808, 1896. Type locality: Essex Farm, Matabeleland.

Type specimen:

Housed in the British Museum, (Natural History)/...

History). de Winton selected as a type, a specimen marked as follows by the collector: "No. 46, Mole, ♂, caught 18 Nov., 1895".

Type locality:

Essex Vale, Southern Rhodesia.

Distribution: (Fig. 15.1).

Hitherto, known only from the type locality.

Diagnostic characters:

According to the original description the size of C. nimrodi is much as in C. hottentotus and C. darlingi, while it differs from the latter in the absence of the triangular white patch on the nape.

Colour:

A drab coloured species (no further information available) without the occipital patch found in C. damarensis and C. darlingi.

Size:

No comparative data is available for discussion in the present work. For the type specimen, H.B. and H.F. measurements were given as 147 mm. and 24.5 mm. respectively while the skull has a basilar length of 31 mm. and a greatest width of 27 mm. In a sample of adult males of C. darlingi the mean H.B. length was determined as 145 mm. in the present work, which indicates that the size of the type of C. nimrodi falls well within the range of size variation found in C. darlingi.

Skull and dentition:

de Winton (1896, 808) stated that the skull of C. nimrodi can at once be distinguished from its allies by ".... the ascending processes of the premaxillaries not extending backward beyond the nasals, so that the suture between these bones and

the/...

the frontals forms a simple slightly bowed line, very distinct from the complicated dove-tail pattern found in most of the Georychi." Furthermore, the sagittal crest is faintly developed, the interparietal bone rounded, the zygomata not so bowed out anteriorly as in C. hottentotus, while the outer walls of the infraorbital foramina are thick. The size of these foramina vary, while the skull recedes to the narrowest point between the orbits rather abruptly from the lachrymal projections. The frontals show no posterior lateral inflation in the interorbital region. Still paraphrasing de Winton, it is stated that the postnarial aperture (internal nares) is rather wide while the back of the palate is slightly cut away on either side ".... leaving a projecting point in the middle line: .....". Finally, de Winton described the posterior opening of the alisphenoid canal as being larger than is found in C. hottentotus.

No information is available on the dentition of C. nimrodi and it may tentatively be assumed that it shows no marked differences compared to other Cryptomys species.

Discussion:

As was pointed out above, this species is hitherto only known from the type locality, which was described as Essex Farm, Matabeleland. In this case de Winton has quoted Selous' (collectors) label attached to the type specimen. On page 806 de Winton (1896) stated that a collection of nearly 50 specimens were made at Essex Vale near Bulawayo, Matabeleland. Essex Farm must however be in Essex Vale since Selous' collection was made there (Ellerman et.al. 1953, 232).

Ellerman et.al. (loc. cit.) have regarded C. nimrodi as a race (subspecies) of C. hottentotus, while Roberts (1951, 389) has retained its specific rank. Not having seen the type specimen or associated series of specimens, the present author is not in a position to judge.

It is evident that de Winton based this species mainly on craniological aspects. Specimens that have been collected in the vicinity of the type locality (e.g. on the Essex Vale road, Bulawayo) did not show the "simple slightly bowed line" of the suture between the premaxillaries, nasals and frontals and have been regarded as specimens of C. darlingi in the present work. In the sample available for study to me, only one specimen (RM 4777) showed this configuration described for C. nimrodi, but this specimen was collected at Khami dam to the west of Bulawayo falling within the distribution range of C. darlingi. In other specimens near the latter locality the normal 'dove-tail' arrangement is clearly present. This points to the possibility that this character, as described by de Winton for C. nimrodi may also be encountered in other species and can not as such be interpreted as a diagnostic character for nimrodi.

As was the case in C. damarensis (where C. ovamboensis was described from Ondongwa which is geographically situated in the middle of the distribution range of C. damarensis) it is not clear why C. nimrodi suddenly occurs in the typical geographical distribution range of C. darlingi. If Bulawayo is accepted as the furthest (hitherto known) western point of distribution for C. darlingi, and Matibi in south-eastern Rhodesia (from whence C. darlingi is known) are connected by a line, the locality for C. nimrodi falls within the distribution range of C. darlingi. This could point to the possibility that C. nimrodi will eventually prove to be a synonym of C. darlingi, while for the purposes of the present work it is provisionally retained as a separate species. This possibility is also strengthened by the fact that de Winton stated that the zygomata resembled those found in darlingi while it also resembled darlingi in the thicker outer walls of the infraorbital foramen. The drab colouration (so characteristic for darlingi) is also described for nimrodi.

Finally, when one takes into consideration the amount of variation found in the shape, size and occurrence of the white occipital patch in both C. damarensis and C. darlingi it is clear that the absence of this patch in C. nimrodi need not necessarily be a diagnostic feature.

Biological:

Very little is known about biological aspects of this species. They appear on the surface of the soil after the onset of the rainy season (de Winton, 1896, 808).

Phylogenetic:

In view of the scarcity of information on this species, very little can be said about possible phylogenetic aspects. According to de Winton (1896, 808), the species is unquestionably related to C. darlingi as far as colour and craniological aspects are concerned.

List of localities:

Essex Vale (de Winton, 1896, 808).

CHAPTER 16

CRYPTOMYS BOCAGEI (DE WINTON) 1896

This species, vernacularly known as Bocage's mole-rat, was first described by de Winton (1897, 323) naming it Georychus Bocagei, in honour of the distinguished Portugese naturalist, Prof. Barboza du Bocage of the Lisbon Museum. Bocage has done much to advance knowledge of the fauna of Angola and de Winton was entrusted with describing a number of rodents from Angola, which ultimately would have been presented to the British Museum in London.

As far as distribution of this species is concerned, it seems to be fairly widely spread in the western parts of Angola, ranging southwards across the Cunene river into the northernmost portion of South West Africa. It is for this reason that this species is considered in greater detail, although its main area of distribution lies extralimitally as far as the present work is concerned. Unfortunately this species is poorly represented in Southern African collections.

Cryptomys bocagei (de Winton)

Georychus Bocagei de Winton, Ann. Mag. nat. Hist., 20: 6: 323, 1897. Type locality: Hanha, Angola.

Type specimen:

Old, aged ♂, in alcohol, B.M. no. 97.8.6.22, British Museum, London.

Type locality:

Hanha, Angola.

Distribution/...

Distribution: (Fig. 16.1).

This species seems to be widely spread in western Angola, spreading southwards across the Cunene river to a number of localities in South West Africa. To what extent its range extends eastwards in Angola, is not known.

Diagnostic characters:

A large species, H.B. M = 151 mm., C.B. M = 31.9 mm., (♂♂) more or less intermediate in size between *C. damarensis* and *C. darlingi*.

Colour:

The colour has been described as a pale drab-grey, almost silver grey (de Winton, 1897, 323). I am not inclined to agree with the description of the colour as silver grey - at least not when the specimens available for study are considered. The Transvaal Museum specimens all create a drab-grey, dirtyish impression with an overall brownish tinge. The occurrence of a white frontal spot is variable.

Size: Adult ♂♂:

H.B.	141-165 mm., M = 151 mm.
T.	7-12 mm., M = 10 mm., (6% of H.B.)
H.F.	19-22 mm., M = 20 mm., (13% of H.B.)
C.B.	29.9-34.4 mm., M = 31.9 mm.
B.C.	13.6-14.7 mm., M = 14.3 mm., (44.8% of C.B.)
I.W.	7.5-7.9 mm., M = 7.7 mm., (24.1% of C.B.)
Z.W.	21.0-24.6 mm., M = 22.5 mm., (70.5% of C.B.)
M.W.	6.0-6.9 mm., M = 6.4 mm., (20.0% of C.B.)
U.T.R.	5.0-5.7 mm., M = 5.3 mm., (16.4 % of C.B.)
L.J.	19.8-23.0 mm., M = 20.9 mm., (65.5% of C.B.)
L.T.R.	5.5 mm., M = 5.5 mm., (17.2% of C.B.)

Adult/...

Adult ♀♀:

H.B. 150-165 mm., M = 155 mm.

T. 6-15 mm., M = 11 mm., (7% of H.B.)

H.F. 20-24 mm., M = 24 mm., (13% of H.B.)

C.B. 32.5-35.0 mm., M = 33.5 mm.

B.C. 13.7-15.6 mm., M = 14.5 mm., (43.2% of C.B.)

I.W. 7.3-8.4 mm., M = 7.7 mm., (22.9% of C.B.)

Z.W. 23.3-24.4 mm., M = 23.6 mm., (70.4% of C.B.)

M.W. 6.2-6.9 mm., M = 6.6 mm., (19.7% of C.B.)

U.T.R. 4.8-5.3 mm., M = 5.1 mm., (15.2% of C.B.)

L.J. 21.2-22.9 mm., M = 21.8 mm., (65.0% of C.B.)

L.T.R. 4.9-5.6 mm., M = 5.3 mm., (15.8% of C.B.)

Skull and dentition:

The skull is broader and stronger than that encountered in C. hottentotus but the zygomata are not bowed outwardly in their anterior portion so much as in that species or in C. damarensis. The infraorbital foramen is long and narrow, broadest in its lower portions, the outer walls being thin or moderately thick. On the other hand, Roberts (1951, 385) has stated that the outer wall of the infraorbital foramen is thickened.

The dentition seems to offer no diagnostic features.

Discussion:

The taxonomic position of C. bocagei is not clear, partly due to the fact that very little material is available for study. I feel that this is probably not a good species, and its relationship to C. darlingi (resembling it phenotypically and morphologically rather closely) is obscure. It may eventually be shown to be a synonym of C. darlingi.

It/...

It is however very different from C. damarensis, occurring to the south of its range. Until such time when a more complete series of study skins and skulls is obtained, the possibility of the presence of subspecies can not be demonstrated. Such series of adult specimens from the different localities are still wanting, and de Winton did not find it possible to distinguish between the different forms from different localities. It may thus tentatively be interpreted as a monotypic species.

It must be pointed out that a similar species was described as Georhychus (sic) kubangensis by Monard in 1932 (see Roberts, 1951, 389) from Kuvango in Angola. This species is smaller than C. bocagei and Roberts has suggested that this difference in size may be due to difference in age. It must be stressed that the type specimen was never designated and according to Hill and Carter (1941) (in Ellerman et.al. 1953, 232) the specimen probably came from Rio Mbalé in Southern Angola.

Biological:

Virtually nothing is known about biological aspects relating to this species. It can only tentatively be assumed that its overall life cycle corresponds to that found in other Cryptomys.

Phylogenetic:

In view of the uncertain taxonomic status of this species, facts pertaining to the phylogeny of these animals are obscure. In material that I have seen, a relationship to C. darlingi is suggested when aspects of cranial morphology, size, colouration and overall appearance are taken into consideration.

List/...

List of localities:

Hanha (de Winton, 1897), Mombola, Angola, 10 (TM), Ondjeva, South West Africa, 1 (TM), Ongha, South West Africa, 1 (SA), and between Ondongera and Ukuambi, Ovamboland (Shortridge, 1934, 327).

CHAPTER 17

CRYPTOMYS BEIRAE (THOMAS & WROUGHTON) 1907

This species was first collected by Mr. C.H.B. Grant during one of his many exploratory trips in Southern Africa, in the vicinity of Beira, Mocambique and was described by Thomas and Wroughton (1907, 780). The authors pointed out the fact that although Beira and vicinity has been known as a paradise for sportsmen, no scientific collection of mammals appeared ever to have been made until Grant first collected this mole-rat species there.

The validity of the specific rank accredited to this form is open to question but I have retained it as a valid species in the present work. Unfortunately, this species is poorly represented in study collections in South African museums. Future research may demote this species to subspecific rank, or it may even be usurped entirely in the species darlingi as a synonym.

As here understood, C. beirae is a monotypic species, occurring mainly in the vicinity of Beira. Further particulars about its geographical distribution is at present unknown although it has been recorded in the Gorongoza district in Portuguese East Africa (Roberts, 1951, 390). The species C. zimbitiensis, described by Roberts (1946, 315) is treated as a synonym of beirae in the present work.

Cryptomys beirae (Thomas & Wroughton)

Georychus beirae Thomas & Wroughton, Proc.zool.Soc., Lond., p.780/...

p. 780, 1907. Type locality: Beira, Moçambique.

Cryptomys zimbitiensis Roberts, Ann. Transv. Mus., 20: 315, 1946. Type locality: Zimbiti, about 20 miles inland from Beira, Mocambique.

Type specimen:

British Museum, No. 7.6.2.98. Collected by C.H.B. Grant, Nov. 28th, 1906. Adult male.

Type locality:

Beira, Portuguese East Africa.

Distribution: (Fig. 17.1).

Although the type locality was given as Beira, Portuguese East Africa, Ellerman et.al. (1953, 232) state that it occurs south of the Zambezi river i.e. north of Beira. Apart from being recorded in the Gorongoza district, no further information about its geographical distribution is available at present.

Diagnostic characters:

Specimens belonging to this species are slightly larger than C. darlingi, C.B. M = 35.8 mm., (unsexed specimens) but smaller than C. damarensis. The dorsal surface is described as 'ecru-drab' to 'drab-grey'. Ventral colour the same as above (Thomas & Wroughton, 1907, 781).

Colour:

The general colour above is stated to be between 'ecru-drab' and 'drab-grey'. The individual hairs are slate-grey at their bases and have fawn-coloured tips. Thomas & Wroughton (loc. cit.) described the ventral colouration as being the same as that on the dorsal side while the fawn tips of the hairs are less conspicuous.

A/...

A white occipital patch is usually present showing a great amount of variation in shape. Thomas & Wroughton state the size of the patches to be approximately half an inch in diameter in the specimens used for describing the species.

Size:

The sample available for study to me consisted of four unsexed specimens, showing the following mean values:

H.B.	No data.
T.	No data.
H.F.	No data.
C.B.	33.6-38.9 mm., M = 35.8 mm.
B.C.	14.8-15.4 mm., M = 15.0 mm., (41.8% of C.B.)
I.W.	8.1-8.4 mm., M = 8.2 mm., (22.9% of C.B.)
Z.W.	26.5-27.0 mm., M = 26.7 mm., (74.5% of C.B.)
M.W.	7.5-9.3 mm., M = 8.2 mm., (22.9% of C.B.)
U.T.R.	5.7-6.0 mm., M = 5.8 mm., (16.2% of C.B.)
L.J.	21.4-24.9 mm., M = 23.1 mm., (64.5% of C.B.)
L.T.R.	5.4-6.6 mm., M = 6.1 mm., (17.0% of C.B.)

Skull and dentition:

According to Thomas and Wroughton (1907, 781), the skull is but slightly smaller than that of 'G. lugardi' (i.e. C. damarensis), and slighter in construction in specimens of corresponding age. Nasals reasonably well developed, not pointed anteriorly. Ascending processes of premaxillaries not projecting beyond posterior nasals to a great extent (cf. C. nimrodi). The lambdoid crest makes a re-entering angle where it meets the sagittal crest. There appear to be no diagnostic features attached to the dentition.

Discussion/...

Discussion:

In view of the very small sample of this species, available for study purposes, comparison with other species is greatly hampered. Ellerman et.al. (1953, 232) have placed beirae as a subspecies of hottentotus while Roberts (1951, 390) has maintained it as a separate species.

Thomas & Wroughton (1907, 780) have commented upon the geographical distribution of this species, and their conclusion was that it appears to be more closely allied to 'G. lugardi' (i.e. pale colour phase of C. damarensis) found in the west than to C. darlingi of Mashonaland intermediate in geographical position. As far as I am concerned, this conclusion does not seem to be justified. Phenotypically speaking, there is very little difference between the colouration of C. darlingi and C. beirae and the overall lighter and yellower colouration of the latter species can only be demonstrated if a number of specimens are compared simultaneously. In fact, specimens from Salisbury (C. darlingi) also show a similar lighter colouration compared to other specimens of C. darlingi and it is virtually impossible to distinguish the two species on the basis of colour alone. Furthermore, 'G. lugardi' (i.e. C. damarensis) was first described by de Winton (1898, 253) as 'seal brown', while the Beira specimens are decidedly between 'ecru-drab' and 'drab-grey'. C. darlingi shows a similar colouration.

Furthermore, C. beirae is decidedly smaller than the larger C. damarensis while only slightly larger than C. darlingi. On comparing all the data obtained for the various skull measurements, it appears that all the values for C. beirae are slightly larger than those of C. darlingi but in all instances, they do not lie outside ± 1.5 S.D. above the values obtained for C. darlingi. The only exception is the length of the L.T.R. It is evident that there is a considerable amount of overlap between the skull parameters of both species, and that I have only retained C.beirae as a species due to lack of suitable comparative material. Its retention is therefore tentative.

The inclusion of C. zimbitiensis Roberts under C. beirae seems to be justifiable however, although, here again, there is a serious paucity of material. C. zimitiensis was described by Roberts in 1946 on a few specimens collected at Zimbiti, about 20 miles inland from Beira. He described the colour as being altogether yellower than C. beirae, which, on comparison with specimens of C. beirae, is not at all evident to the present author. The specimens from Zimbiti are described as having a large white mark on their throats which is also seen in C. beirae. The structure of the infraorbital foramen is very similar in both forms while Roberts states that the bullae in zimbitiensis are more swollen. On comparison of the bullae of C. beirae, it is evident that this is a very relative feature. The various measurements of the skulls (based on the type, an old specimen and on two others) correspond virtually entirely to the sizes obtained for C. beirae. If the series of C. beirae were large enough, it would undoubtedly overlap all the values of C. zimbitiensis.

Apart/...

Apart from size considerations, it is not clear why another species should suddenly crop up 20 miles inland from Beira where the climatic, vegetational, and other conditions are similar. I can therefore see no justification for the retention of C. zimbitiensis as a separate species and it is suggested that only one species, C. beirae (itself not easily distinguishable from C. darlingi) exists in the area between Beira and the Zambezi river, and the vicinity of Gorongoza.

Ellerman et.al. (1953, 234) have not placed C. zimbitiensis in synonymy with C. beirae probably due to the fact that they have not seen the specimens from Zimbiti.

A further interesting point is that Roberts has taken as the type of C. zimbitiensis, a specimen collected by Grant in the vicinity of Beira - i.e. C. beirae. In fact, Grant's number given to this specimen (7.6.2.97) is just one figure below that number which serves as the type of C. beirae (7.6.2.98) in the British Museum. If it is assumed that this specimen is an example of C. zimbitiensis it may be compared to specimens known as beirae: when such a comparison is made, it is clear that there is absolutely no difference between the supposed zimbitiensis and beirae forms.

Biological:

Very little is known about biological aspects of this species. Thomas and Wroughton (1907, 776) postulated that the scarcity of mammals (especially the smaller ones) could be explained by the fact that there is an annual flooding of the country resulting in large numbers being drowned during the rainy season. Any additional biological information regarding this species is non-existent however.

Phylogenetic:

No information available at present.

List of localities:

Beira, 4 (TM), Zimbiti, 5 (TM), Gorongoza, (Roberts, 1951, 390).

CHAPTER 18

CRYPTOMYS NATALENSIS (ROBERTS) 1913

The so-called Natal mole-rat *Cryptomys natalensis*, was first described as a species by Roberts (1913, 94) based on a series of 11 skins. The type specimen was collected at Wakkerstroom (near the Transvaal-Natal border) in December 1912.

On the average this species is slightly darker in colour than *C. holosericeus*, while there is little difference in average size. In contrast, however, it differs from *C. holosericeus* as far as the number of mammae are concerned: in *C. holosericeus* the inguinal mammae are present, while in *C. natalensis* the inguinal mammae are constantly absent.

C. natalensis occurs in the vicinity of the Rand and Pretoria (as far north as Nylstroom, and as far west as Rustenburg), ranging eastwards to Wakkerstroom (the type locality) and further south-eastwards into the uplands of Natal eventually reaching the coastal areas to the north and south of Durban.

Roberts (1951, 394) has split the species *natalensis* into eight subspecies, but the present author fails to see the necessity of this procedure, as will be indicated below. As far as the present work is concerned, this species is regarded as monotypic.

Apart from the nominate race, *C. natalensis natalensis*, the following described forms are treated as subspecies by Roberts: *C. n. langi*, *C.n. aberrans*, *C.n. junodi*, *C.n. streeteri*, *C.n. jamesoni*, *C.n. arenarius* and *C.n. mahali*. In addition to these

subspecies/...

subspecies which are regarded as synonyms in the present work, - with the exception of C.n. streeteri (which I interpret as a form of Cryptomys komatiensis)- it is proposed to include the species C. anomalus and C. montanus as well as the subspecies C. komatiensis zuluensis as synonyms under C.natalensis as well.

Cryptomys natalensis (Roberts)

Georychus natalensis Roberts, Ann. Transv. Mus., 4: 94, 1913. Type locality: Wakkerstroom, Transvaal.

Georychus jamesoni Roberts, Ann. Transv. Mus., 4: 95, 1913. Type locality: Houghton, Johannesburg, Transvaal.

Georychus arenarius Roberts, Ann. Transv. Mus., 4: 96, 1913. Type locality: Rietondale, Pretoria, Transvaal.

Georychus anomalus Roberts, Ann. Transv. Mus., 4: 96, 1913. Type locality: Skinner's Court Valley, Pretoria, Transvaal.

Georychus aberrans Roberts, Ann. Transv. Mus., 4: 97, 1913. Type locality: Port St. Johns, Cape Province.

Georychus mahali Roberts, Ann. Transv. Mus., 4: 108, 1913. Type locality: Rosslyn, Pretoria, Transvaal.

Cryptomys montanus Roberts, Ann. Transv. Mus., 11: 260, 1926. Type locality: Klapperkop, Pretoria, Transvaal.

Cryptomys junodi Roberts, Ann. Transv. Mus., 11: 260 1926. Type locality: Masiyeni, north of the mouth of the Limpopo river, Mocambique.

Cryptomys/...

Cryptomys langi Roberts, Ann. Transv. Mus., 13: 119, 1929. Type locality: Karkloof, Howick district, Natal.

Cryptomys komatiensis zuluensis Roberts, in 'The Mammals of South Africa', p. 396, 1951. Type locality: Lake St. Lucia, Natal.

Type specimen:

Housed in the Transvaal Museum, Pretoria, old ♀, collected 10.12.1912 at Wakkerstroom, Transvaal.

Type locality:

Wakkerstroom, Transvaal.

Distribution: (Fig. 18.1).

C. natalensis is found in western Transvaal (e.g. at Potchefstroom, Koster and Rustenburg), ranging eastwards to Johannesburg and northwards to Pretoria. To the north of Pretoria it occurs at Nylstroom, while eastwards from Pretoria it occurs at Bronkhorstspruit, Witbank and intervening districts eventually reaching the escarpment at Wakkerstroom. From here it spreads northwards to a point south of Carolina and eastwards to Swaziland as well as southwards into Natal including the north and south coast areas. Its southernmost point of distribution along the coast of the Indian ocean is Port St. Johns in the Cape Province, while its known northernmost limit along the coast seems to be in the vicinity of Masiyeni, a little to the north of the mouth of the Limpopo river.

Diagnostic characters:

A large species, H.B. M = 143 mm., C.B. M = 34.8 mm., (♂♂) i.e. about the size of C. holosericeus, but differing in colour (i.e. being darker and not as buffy as C. holosericeus). Furthermore, it differs from/...

from <u>holosericeus</u> in the absence of the inguinal mammae.

<u>Colour</u>:

The colour can be described as a dirtyish dark slaty grey which tends to be richer in colour on the dorsal aspect compared to the ventral surface. The colour in the two sexes appear to be alike, although Roberts (1951, 394) found the ♀♀ to be darker than the ♂♂ in <u>C. natalensis aberrans</u> (Port St. Johns) and <u>C.n. langi</u> (Karkloof, Howick district).

As in all other species of <u>Cryptomys</u>, the young specimens are darker than the adults.

On the whole, the colour is relatively uniform in all specimens of this species. With certain exceptions, there is little evidence of a marked degree of geographical variation in colour. As an example, specimens collected at different localities in the Swaziland areas are decidedly darker than specimens from Wakkerstroom, while specimens from Masiyeni have a definite warmer and lighter colour.

As a rule, a white frontal or occipital patch is absent in all individuals of this species.

<u>Size</u>: <u>Adult ♂♂</u>:

H.B.	125-177 mm., M = 143 mm.
T.	17-29 mm., M = 21 mm., (14.6% of H.B.)
H.F.	20-32 mm., M = 25 mm., (17% of H.B.)
C.B.	30.4-38.1 mm., M = 34.8 mm.
B.C.	13.2-17.0 mm., M = 15.0 mm., (43.1% of C.B.)
I.W.	6.8-8.1 mm., M = 7.4 mm., (21.2% of C.B.)
Z.W.	21.5-28.5 mm., M = 24.7 mm., (70.9% of C.B.)
M.W.	6.1-8.3 mm., M = 6.9 mm., (19.8% of C.B.)
U.T.R.	5.1-7.0 mm., M = 5.7 mm., (16.3% of C.B.)
L.J.	20.4-26.1 mm., M = 23.1 mm., (66.3% of C.B.)
L.T.R.	5.0-7.1 mm., M = 5.9 mm., (16.9% of C.B.)

<u>Adult</u> /...

Adults ♀♀:

H.B. 125-174 mm., M = 141 mm.
T. 17-29 mm., M = 21 mm., (14.8% of H.B.)
H.F. 20-30 mm., M = 24 mm., (17.0% of H.B.)
C.B. 30.1-39.0 mm., M = 33.6 mm.
B.C. 13.2-18.8 mm., M = 15.0 mm., (44.6% of C.B.)
I.W. 6.4-8.0 mm., M = 7.3 mm., (21.7% of C.B.)
Z.W. 21.5-28.6 mm., M = 24.0 mm., (71.4% of C.B.)
M.W. 5.9-8.5 mm., M = 6.4 mm., (19.0% of C.B.)
U.T.R. 5.1-7.1 mm., M = 5.6 mm., (16.6% of C.B.)
L.J. 20.3-26.3 mm., M = 22.2 mm., (66.0% of C.B.)
L.T.R. 5.0-7.1 mm., M = 5.8 mm., (17.2% of C.B.)

Although not phenotypically evident directly, sexual dimorphism is apparent when subjecting the figures given above to statistical manipulation. As an example, the C.B. lengths may be quoted: when the ♂♂ (M= 34.8 ± 1.700 mm.) are compared to the ♀♀ (M = 33.6 ± 1.526 mm.), the ♂♂ are very significantly larger than the ♀♀ at the 0.1% level (t = 8.5, 219 degrees of freedom, P= 0.001).

Skull and dentition:

The skull is large and robust, while the incisors tend to curve more sharply downwards than in C. holosericeus or C. hottentotus. In some cases, the zygomata tend to bow downwards to a level below the level of the palatines, anterior to the molars. As far as the structure of the nasals are concerned, a great deal of morphological variation is seen, indicating that the nasals can not be used as a diagnostic criterium.

Apart/...

Apart from the incisors which tend to bow downwards more sharply, very little diagnostic features are offered by the structure and arrangement of the teeth.

Discussion:

The systematics of C. natalensis presents an extremely confusing picture when the available literature is consulted. As was indicated in the synonymy list, the following forms were all originally described as species by Roberts: 'Georychus' natalensis, 'Georychus' aberrans, 'Georychus' jamesoni, 'Georychus' arenarius, 'Georychus' mahali, 'Georychus' anomalus, Cryptomys montanus, C. junodi and C. langi, while a subspecies of C. natalensis was described as C.n.streeteri. In 1951, Roberts (pp. 394, 395) demoted the specific status of langi, aberrans, junodi, jamesoni, arenarius and mahali to subspecific rank under the nominate race of C. natalensis. This resulted in the C. natalensis group being regarded as polytypic with eight subspecies (i.e. C.n.natalensis, C.n.langi, C.n.aberrans, C.n.junodi, C.n.streeteri, C.n.jamesoni, C.n. arenarius and C.n.mahali with Wakkerstroom, Karkloof, Port St. Johns, Masiyeni, Hektorspruit, Houghton Estate, Rietondale and Rosslyn as the respective type localities).

The specimens were originally described as separate species, based mainly on difference in the colour of the pelage as well as craniological differences (e.g. the structure of the nasals, mandible and the curvature of the incisors.)

On the other hand, one has the opinion of Ellerman et.al. (1953, 234, 235) concerning C. natalensis to consider as well. These authors

placed/...

placed the originally described species (i.e. natalensis, aberrans, anomalus, mahali, junodi and langi) as subspecies of Cryptomys holosericeus, while the originally described species of jamesoni, arenarius and montanus were placed as synonyms under Cryptomys hottentotus jamesoni of their Cryptomys hottentotus group. It must be pointed out however, that montanus was placed in synonymy tentatively (Ellerman et.al. 1953, 233).

Roberts' procedure, in demoting the specimens from specific rank (as originally interpreted by him) to subspecific rank, was significant indicating that Roberts eventually (in 1951) doubted the validity of the specific status originally accorded to the specimens.

When Roberts' 1951 treatment of the C. natalensis species is compared to that proposed by Ellerman et.al. in 1953, it becomes evident that Roberts may be nearer to the correct interpretation of the facts. This statement rests on the following considerations:

1. To my mind, the genus Cryptomys has been grossly overlumped by Ellerman et.al., resulting in too simple a picture of the genus in Southern Africa. I fail to see why only two species (i.e. C. hottentotus and C. holosericeus) are worthy of specific recognition, especially if such well marked species as C. damarensis and C. darlingi occur. These, and other species, are all placed as races under either hottentotus or holosericeus by Ellerman et.al. Roberts has accepted the occurrence of a greater number of species, which seems to be a truer representation

of the facts.

2. C. natalensis, C. aberrans, C. anomalus, C. mahali, C. junodi and C. langi constantly possess two pairs of mammae (i.e. 2 pairs of pectoral), while C. holosericeus constantly shows 3 pairs of mammae (2 pairs pectoral, 1 pair inguinal). If these forms are now placed as races under C. holosericeus (as was proposed by Ellerman et.al.) one encounters the situation that some races have four mammae while others have six. The constant absence of inguinal mammae in natalensis (in contrast to the constant presence of inguinal mammae in holosericeus) has prompted me to retain C. natalensis as a separate species of holosericeus. In this case, Robert's treatment of C. natalensis (i.e. retaining it as a species) seems preferable and I have followed this interpretation.

3. Similarly, the species C. jamesoni, arenarius and montanus do not have the inguinal mammae. If they are placed as synonyms under C. hottentotus (as has been proposed by Ellerman et.al.), then once again one has the situation that the species hottentotus constantly shows the inguinal mammae, but that suddenly, within its range of distribution, certain populations from certain localities possess no inguinal mammae. In view of the fact that the inguinal mammae are absent in jamesoni, arenarius and montanus, it is more acceptable to group them under natalensis where this pair of mammae is also constantly absent. This has been done by Roberts (1951, 395) and I am inclined to adhere to this interpretation.

In the present work, it is proposed to go one step further in the direction indicated by Roberts

(1951, 394, 395) with regard to the subspecific status. As far as I am concerned, it is felt that there seems to be little reason for accepting Roberts' subspecific rankings, that they are not to be accepted as valid, and that C. natalensis should be interpreted as a variable, monotypic species (See fig. 18.2). Furthermore, the species known as C. anomalus from Skinner's Court Valley, Pretoria, and C. montanus from Klapperkop, Pretoria, are also considered as representatives of C. natalensis in the present work. The way Ellerman et.al. have interpreted the latter two species has already been indicated above, while Roberts (1951, 395, 397) has retained them as separate species. In order to justify the proposed procedure followed in the present work, a more detailed discussion of the facts will be given below.

Cryptomys natalensis was described as a separate species by Roberts (1913, 94) from material collected at Wakkerstroom in December 1912. It differed from C. holosericeus mainly in its slightly darker colouration, in the absence of inguinal mammae as well as having the incisors more sharply curved downwards (Roberts, 1951, 394). In the original description, the nasals were described as "... pointed at the back, widest at about two-thirds of the length from the front and with the foremost third produced straight forward to the tip or with a very slight broadening at the tip."

It must be emphasised however, that even in the series from which the type specimen was selected, a degree of variation in the structure of the nasals can be demonstrated - the nasals being either straight forward at the tip, or they can also show a slight broadening at the tip. This again demonstrates my contention that little diagnostic value can be attached to the nasals in view of the great amount of individual variation which is encountered.

Following the description of 'Georychus' natalensis, Roberts (1913, 95) described 'Georychus' jamesoni on three specimens taken at Houghton Estate, Johannesburg in July 1907. It was described as being very similar to natalensis, although being somewhat smaller in size while the mammae also consisted of two pectoral pairs only. Roberts pointed to some differences pertaining to the nasals however, and described them as being ".... intermediate in shape between natalensis and arenarius". In the latter, the nasals were described as narrow, being only slightly broadened at about the middle of their length ".... and posteriorly squared or at any rate not pointed ...." (Roberts, 1913, 96).

Since 1907, no other specimens from this type locality have been collected and the grand total still stands at the three original specimens. When these specimens are compared with specimens from Wakkerstroom, it becomes evident that one finds the identical nasal configuration, described for jamesoni, in specimens of natalensis from Wakkerstroom. In view of the fact that natalensis and jamesoni are virtually identical in colour and size (see Table 18.1, below), the present author has seen fit to synonymize the latter with the former. It is unfortunate that the samples available for comparison are too small for further statistical investigation.

The/...

The distribution of jamesoni was given as the highveld about Johannesburg and northwards to the hills above Pretoria (Roberts, 1951, 395) and all known specimens from Johannesburg were considered as representatives of jamesoni for comparative purposes in the Table below.

TABLE 18.1: A comparison of certain skull measurements in C.natalensis and C.n.jamesoni

	♂♂					♀♀				
	C.B.	I.W.	Z.W.	U.T.R.	L.J.	C.B.	I.W.	Z.W.	U.T.R.	L.J.
Wakkerstroom (C.natalensis)	M=36.4 mm. N = 4 (35.2 – 37.4 mm.)	M=7.8 mm. N = 4 (7.7 – 8.0 mm.)	M=26.2 mm. N = 4 (25.6 – 26.6 mm.)	M=5.7 mm. N = 2 (5.4 – 6.0 mm.)	M=24.1 mm. N = 4 (22.9 – 25.1 mm.)	M=36.3 mm. N = 2 (36.2 – 36.5 mm.)	M=7.7 mm. N = 3 (7.3 – 8.1 mm.)	M=25.9 mm. N = 3 (23.0 – 28.3 mm.)	M=5.7 mm. N = 3 (5.5 – 6.0 mm.)	M=23.0 mm. N = 3 (20.6 – 24.7 mm.)
Johannesburg (C.n.jamesoni)	M=34.9 mm. N = 4 (32.0 – 38.0 mm.)	M=7.8 mm. N = 5 (7.2 – 817 mm.) S.D. = 0.5523	M=24.2 mm. N = 4 (21.6 – 28.5 mm.)	M=6.2 mm. N = 3 (6.2)	M=23.2 mm. N = 5 (20.5 – 25.8 mm.) S.D. = 2.004	M=32.3 mm. N = 2 (29.9 – 34.8 mm.)	M=7.6 mm. N = 2 (7.1 – 8.1 mm.)	M=23.7 mm. N = 2 (20.5 – 26.9 mm.)	M=5.2 mm. N = 2 (5.0 – 6.0 mm.)	M=22.2 mm. N = 2 (20.1 – 24.4 mm.)

On comparing the mean values given above, it becomes clear that there is little difference in size between C. natalensis and C. jamesoni and I am convinced of the fact that the differences which exist (or come to the surface in Table 18.1) will be further diminished if more specimens become available for study. It is therefore felt that there is no justification for the retention of jamesoni, either as a species of subspecies.

In the same year, Roberts (1913, 96) also described a new species of mole-rat from Rietondale (East), Pretoria, which was named 'Georychus' arenarius. It was described as differing from 'G'. jamesoni in having narrow nasals, which were only slightly broadened at the middle of their length while "..... posteriorly they are squared or at any rate not pointed". The premaxilla is ".... produced straight back considerably beyond the back of the nasals in all specimens examined".

The type specimen was an old ♀, taken in March 1913, having a H.B. length of 145 mm., T = 20 mm. and H.F. = 25 mm., while it also showed the absence of the inguinal mammae. The corresponding measurements for the type of C. jamesoni were 135 mm., 15 mm. and 24 mm. respectively.

Some specimens of the type series were taken in white sandy soil and were rather lighter coloured than is the rule. Other specimens taken in red soil not far off, had the fur stained by the soil. To what extent the soil has staining capabilities on the fur of mole-rats is however not clear. One would rather be inclined to think that this was not so much

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a question of the fur being stained by the soil, rather than interpreting it as an example of adaptation of the animals to their environment.

In 1951, Roberts (p. 395) referred to '*G.' arenarius* as the subspecies *Cryptomys natalensis arenarius* (Roberts) and described the specimens as typically rather paler in shade of colour than *C.n.jamesoni*. The nasals are straight-sided and that *arenarius* was on the average larger in size. It was stated furthermore, that *arenarius* was almost indistinguishable from *jamesoni*, ".... so that this name may have to be dropped". The present author is in full agreement with this verdict, and has therefore synonymized *arenarius* with *jamesoni* which in turn does not warrant either specific or subspecific separation from *Cryptomys natalensis*.

In the same paper in which '*G.' natalensis*, '*G'. jamesoni* and '*G'.arenarius* were described as new species, yet another new species named '*G'.aberrans* was described by Roberts, based on specimens collected at Port St. Johns, Pondoland. This form was described as being quite different from all the preceding species, in having the nasals pointed at the back "..... swelling out broadly forwards, then tapering down to a very narrow neck, and finally swelling out again at the tip: the nasals measure 4.2 at the broadest part, 1.4 at the neck, and 2.6 at the tip." (Roberts, 1913, 97, 98). According to Roberts, this peculiarity is very pronounced and is quite distinct in a young adult and even in a very young specimen with only three visible molars.

The type specimen is a very old ♂, *ex* the collection of H.H. Swinny, and the type was taken in

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October, 1911. The H.B., T. and H.F. measurements are given as 159, 14 and 22 mm., respectively.

I am not entirely convinced that the pitcher-shaped nasals are to be found only in C.natalensis aberrans from Port St. Johns. On closer inspection, a similar nasal structure (to a greater or lesser extent, in any case), can be shown to be present in specimens from Arnhemburg, Carolina district (C. komatiensis), Wakkerstroom (type locality of C.natalensis), and Vryburg (C.holosericeus). It is thus felt that the pitcher-shaped nasals is not of important diagnostic value and certainly not of enough importance for the erection of a new species.

As far as colour is concerned, it is stated that C.n.aberrans corresponds in colour to C.n.langi (see below), which in turn is very similar in general appearance to C.n.natalensis (Roberts, 1951, 394). When the Port St. Johns specimens are compared with those collected at Wakkerstroom, it becomes evident that there is a great degree of phenotypic correspondence. At both localities, white frontal or occipital patches are usually absent, while all specimens from these two localities have no inguinal mammae. Furthermore, in both natalensis from Wakkerstroom and aberrans from Port St. Johns, the zygomata bow downwards more, so that they lie below the level of the palate in front of the molars. A further cranial factor pointing to the actual similarity between natalensis and aberrans is found in the projection of the upper incisors, the index angle of which is not more than 105 in both natalensis and aberrans (Roberts, 1951, 394). Finally, it may be

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pointed out that Roberts found the ♂♂ of aberrans (as in C.n.langi) to be lighter coloured compared to the darker coloured ♀♀.

As is so often the case, the number of available specimens from a certain locality is too small for statistical analysis. This also concerns the number of specimens from Port St. Johns. Although I can thus offer no statistical parameters to strengthen my arguments, it seems fairly certain that C.natalensis aberrans (Roberts) is not specifically or even subspecifically distinct from C.natalensis (Roberts) when external features (e.g. size, colour) and craniological characters (e.g. size, shape of nasals, structure of zygomata etc.) are taken into consideration.

The species, 'G'. mahali was also first named and described by Roberts in 1913 (1913 a, 108), from Rosslyn, some five miles north-west of Pretoria North. According to Roberts (op.cit.) the species was first discovered at Bleskop, a small native village seven miles east of Rustenburg. Four specimens were taken, of which two were kept alive but escaped one week later. Roberts stated this species to be very locally distributed, and that it was only observed at one other place along the railway line, namely at Rosslyn. At Rosslyn it was found to be very abundant, where five specimens were taken (two very young ones were kept alive, but also escaped subsequently.) The type specimen is an adult ♀ selected from the remaining three Rosslyn specimens.

This species was described as being similar to ".... the small reddish coloured species...." found to the east of the Drakensberg, but differed therefrom

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in being larger in size (Roberts, 1913, 108). The nasals were described as being so distinctly different from those of another larger species found at Rosslyn, that there was no doubt, according to Roberts, of their being a different species. This other large species referred to above, is evidently Cryptomys anomalus (to be discussed below).

The species taken at Rosslyn, appear to be referable to C. anomalus in all respects, but for the greater breadth of the nasals in one old ♀ (Roberts, 1913 a, 108).

As has been done so often in the present work, it must be emphasized again that there is a great degree of morphological variability present in the extent and size of craniological features found in different individuals, even coming from the same tunnel system. Roberts states that in C. anomalus the premaxilla does not extend beyond the back of the nasals in some cases: in the case of the old ♀, serving as an example of 'G'. mahali, the back of the nasals are squared and the premaxilla does not extend backwards either. In the two younger specimens, this is not the case i.e. the premaxillae extend slightly beyond the back of the nasals, and whether later development would have produced a similar configuration to that found in the old ♀, is, according to Roberts, open to question.

To the mind of the present author, it is clear that there seems to be no valid reason for accepting 'G'. mahali as a separate species or subspecies based on the broader nasals found in one single specimen only. The inguinal mammae are also

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in being larger in size (Roberts, 1913, 108). The nasals were described as being so distinctly different from those of another larger species found at Rosslyn, that there was no doubt, according to Roberts, of their being a different species. This other large species referred to above, is evidently Cryptomys anomalus (to be discussed below).

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To the mind of the present author, it is clear that there seems to be no valid reason for accepting 'G'. mahali as a separate species or subspecies based on the broader nasals found in one single specimen only. The inguinal mammae are also

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lacking, as in all forms of *natalensis* and the subspecies *C. natalensis mahali* (as interpreted by Roberts, 1951, 395) is synonymized with the species *Cryptomys natalensis* in this work.

With the description of *Cryptomys anomalus* by Roberts (1913, 96) greater confusion concerning the taxonomy of *Cryptomys* in the vicinity of Pretoria was created. This form, originally described as a new subspecies (Roberts, 1913, 96), was described as a large form, with long and narrow nasals, about the same breadth throughout their length.

In 1951, Roberts (p. 395) described the colouration and size of *anomalus* as being "..... much as in the forms of *C.natalensis*, though tending to be greyer in adults, but much larger in size than *jamesoni* and *arenarius* occurring in the same neighbourhood, and larger also than *mahali*; the inguinal mammae absent; the nasals long and straight-sided as in *arenarius*". It is interesting to note that in the original description of the type specimen (a fairly old ♀, collected at Skinner's Court Valley, Pretoria on 23rd of February 1913) three pairs of mammae were noted - 1 in front, 2 at side = 6. The presence of a second lateral pair is probably abnormal. The measurements pertaining to the type were given as 140 mm., 21 mm. and 26 mm. for the H.B., T. and H.F. respectively.

In the same paper, Roberts (1913, 99) also described *'G'. pretoriae* as a separate species, based on one single specimen, an adult (not old ♂) also collected at Skinner's Court Valley, Pretoria on the 19th of January, 1913. The H.B., T. and H.F.

dimensions were given as 140 mm., 20 mm. and 24 mm. respectively. On comparison of these measurements with those given for anomalus (see above), it becomes evident that there is absolutely no valid reasons for accepting the species status of pretoriae. Roberts (1913, 99) stated that pretoriae was very similar to 'G'. talpoides (originally described as a subspecies of C. hottentotus by Thomas and Schwann from Knysna) but that it was much larger in size, with a stronger suffusion of sandy buff on the under surface, sides and cheeks. The fact that a talpoides-like form was found side-by-side with a grey coloured species would seem to show that it is distinct and not only a subspecies of C. hottentotus.

Roberts continues (1913, 99) to state that the fact that the darker coloured pretoriae species occurs in the open veld at Pretoria "... explodes the fallacy that the dark colouration is due to residence of the species in forested regions".

Although the original description of pretoriae referred to an adult, but not old ♂, this specimen was called an immature ♂ by Roberts in 1951 (p. 395). I have seen the type specimen and am satisfied that the specimen is in fact immature, which would possibly explain the darker colouration (which reminded Roberts of talpoides). In 1951, Roberts demoted the specific rank of pretoriae as a synonym under C. anomalus. This procedure is understandable and acceptable, for it is not clear why two species should occur in the identical habitat at Skinner's Court Valley in Pretoria.

In 1917, Roberts (1917, 5) described yet another species, 'G'. palki, based on a type specimen

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and a series of five younger specimens. The type was an old ♂, taken at Viljoenskroon on the banks of the Vaal river in the Potchefstroom district on March 24th, 1917, with H.B., T. and H.F. lengths of 150 mm., 22 mm. and 29 mm. respectively. Roberts described this species as being most closely allied to 'G'. anomalus in having long and narrow nasals with the same buffyish colouration. It differed from this species and other members of the group in having a distinct semi-circular notch in the upper anterior angle of the ocular area of the skull, which affected a thinning of the arch of the maxilla above the infraorbital foramen and opposite the infraorbital process. Furthermore, in two adult specimens the hindmost molar is very large, equal in dimension to the foremost tooth. In the type series, the only ♀ trapped was immature and the number of mammae could not be ascertained.

Roberts continues to state that besides these specimens two other animals were captured in another colony (probably in close vicinity where the type series was collected) which consisted of an adult ♀ and a young adult ♂, showing all the characteristics of 'G'. natalensis mihi (Roberts, 1917, 5) including the number of mammae (i.e. 2 pectoral pairs, without the inguinal pair). On closer inspection, it is clear, that we are dealing here with C. natalensis and in 1951 Roberts (395) synonymized 'G'. palki with C. anomalus.

It thus becomes evident that even on the specific level, C. anomalus was grossly oversplit in the past. In the present work, it is suggested that

C. anomalus should in turn be synonymized with C. natalensis.

When five ♂♂ from Skinner's Court Valley (anomalus) are compared to five ♂♂ from Rosslyn (mahali) in respect of C.B. length, no significant difference can be found (t = 1.17, P = 0.3-0.2, 8 degrees of freedom) at the 30-20% level (M = 33.6 ± 4.055 mm. and M = 35.3 mm. ± 2.229 mm. for anomalus and mahali respectively). Similar comparisons pertaining to other skull measurements do not indicate any significant differences statistically speaking. This has led to the conclusion that C. anomalus is morphologically identical to C. mahali and C.arenarius and in view of the fact that the latter can not be distinguished from jamesoni which is virtually identical to C. natalensis, it follows that C. anomalus is to be regarded as a synonym of C. natalensis.

In all instances, a C.D. value far below 1.28 is attained, indicating not even a subspecific difference, let alone specific differences.

In 1926, Roberts (1926, 260) described yet another species from the vicinity of Pretoria. This was named Cryptomys montanus, the type specimen, an adult ♀, having been collected at Klapperkop, Pretoria. It was described as a small species, similar to C. transvaalensis (interpreted as a synonym of C. hottentotus in the present work) in colour and size, but differing therefrom in having no inguinal mammae "....in which respect it approaches C. arenarius ...., from which it differs again in its smaller dimensions." (Roberts, 1926, 260). It was stated to occur in the same ground as C. anomalus on the hills, amongst stones

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on the hillsides, or in the valleys, but does apparently not so frequently find its way amongst the yellow shale in which C. anomalus is reported to have been plentiful, while C. arenarius occurs more in a sand-belt running east and west between the Magaliesberg and Daspoort ranges.

On closer inspection, however, there seems to be little evidence pointing to the retention of C. montanus as a separate species. In 1951, Roberts (p. 397) described it as a dull coloured species, resembling C. natalensis jamesoni, which also occurs in the neighbourhood, while the mammae also lack the inguinal pair. Again it was stated to be consistently smaller in size. In the latter publication, the distribution was given as occurring in ".... stony ground, in the Fountains Valley, Pretoria", which incidentally is adjacent to the type locality viz. Klapperkop.

As far as size is concerned, eight ♂♂ from Fountains Valley have shown a mean C.B. length of 35.7 mm. (S.D. = 2.083 mm., min. - max. variation 33.6 - 39.2 mm.) which compares very favourably with 35.3 mm. (M) of five ♂♂ from Rosslyn (S.D. = 2.299 mm., min.-max. variation 32.7-37.5 mm.) In the material available to me for study, the ♂♂ therefore do not show a consistently smaller size. In a sample of five ♀♀ from Groenkloof (immediately below Klapperkop), the mean C.B. length obtained was 30.8 mm. (S.D. = 1.031 mm., min.-max. variation 29.7-32.5 mm.) and this compares favourably with a mean value of 33.2 mm. obtained from eight ♀♀ from Rietondale (S.D. = 1.224 mm., min.-max. variation 31.9-35.0 mm.).

These/...

These figures, give a C.D. value of 1.06 which lies between 85-86% J.N.O. i.e. below the conventional level of 90% for subspecific difference. In view of these facts, I have seen fit to synonymize C. montanus under C. natalensis, especially when factors other than size, (e.g. general overall colouration and the number of mammae) are also taken into consideration.

In the same paper in which C. montanus was described, the species Cryptomys junodi was also described by Roberts (1926, 260). The type specimen was collected at Masiyeni, a little to the north of the mouth of the Limpopo river in Portuguese East Africa. It was described as a buffy coloured species, in that respect not distinguishable from C. aberrans of Pondoland, but being distinguishable in aspects relating to the skull. Compared to the Port St. Johns form, the nasals are less or not so pinched-in markedly near the apex while the overall impression created by the skull is that it is broader and more massive, the muzzle being longer as well. The nasals are broadest near the back, opposite the infraorbital foramina, narrowing thence forward to the tip (sometimes narrower subapically), while the back portion narrows rapidly to a blunt point. The posterior processes of the maxilla project about a millimetre behind the nasals but they do not converge and meet. The incisor teeth are larger and form a wider arch than in either aberrans or natalensis and the bullae are larger so that the mastoid width is greater.

The type specimen, an adult ♂, was trapped by van Dam on August 20th, 1924, with a series of about a dozen specimens showing uniformity.

In/...

In 1951, Roberts (p. 395) described the distribution of the species as follows: "The coastal tract, from just north of the Limpopo River southwards, at least to Maputa, just south of the border of Portuguese South-East Africa".

If the type specimen is compared to specimens representing C. natalensis, it becomes obvious that there is no justification for the retention of junodi as either a separate species or even as a subspecies under C. natalensis. This becomes evident even when looking at the measurements given by Roberts comparing the type of aberrans with the type of junodi, as the following size measurements will indicate: H.B. aberrans, 150 mm., junodi 157 mm., Z.W. 28.0 mm., 30.2 mm., B.C. 14.7 mm., 14.5 mm., I.W. 7.6 mm., 6.9 mm., M.W. 8.7 mm., 8.7 mm., length of palate, 22.5 mm., 23.0 mm., U.T.R. 5.5 mm., 5.8 mm.

Cryptomys langi was described by Roberts from Karkloof, Howick district, Natal in 1929. This species was described as being very similar in general appearance to C. natalensis from Wakkerstroom, with the nasals having the same shape but differing from C. natalensis in having the upper incisors more forwardly projecting while the ♂♂ were lighter in colour and darker in the ♀♀. The overall colour for the ♂♂ was described as a general greyish-buffy, the underfur being pale slate grey with buffy tips, the head, top of feet and tail more buffy, while the underparts are more whitish. The ♀♀ are darker, the underfur slate grey with very little external buffy colouring, the top of the nose whitish, but the face

much/...

much the same as the underparts of the body. The feet and tail were paler than in the ♂.

The young specimens are said to be darker than the adults while the young ♂♂ are lighter than adult ♀♀.

The skull resembles C. junodi to a great extent especially in respect of the projection of the incisors, the angle index of which is about 115-120 as against not more than 105 in natalensis and aberrans. The skull however is less massive in construction, the nasals more pointed posteriorly, the infraorbital foramina more perpendicular while the posterior border of the mandibular angle is more rounded than squared. In langi, as well as junodi the zygomata do not bow downwards to such a degree as in natalensis and aberrans i.e. they lie above the level of the palate in front of the molars. In junodi the palatine foramina lie further forward, their anterior ends in advance of a line drawn across the front of the zygomata, whereas in natalensis and langi they lie behind that line.

The distribution of langi was given as the middle districts of Natal about the Karkloof and Dargle areas.

When the C.B. length of a number of ♀♀ is considered (including specimens from the type locality, as well as surrounding districts, e.g. Dargle, Estcourt), M = 33.6 mm. which is exactly the value attained for the corresponding mean value in the case of C. anomalus from Skinner's Court, Pretoria. Similarly, ♂♂ from Pietermaritzburg give a mean value of 33.4 mm. which is exactly the mean

derived/...

derived for C. arenarius from Rietondale. These factors all therefore seem to point to the equivalence of C. langi with C. natalensis, and langi is therefore synonymised with natalensis in the present work.

Finally, the status of Cryptomys komatiensis zuluensis remains to be considered. It may have been Roberts' intention to publish a description of this subspecies before the publication of 'The Mammals of South Africa' in 1951. This was never done and the description as given in Roberts (1951) stands as being the original one (Editor's Footnote, Roberts, 1951, 396).

This mole-rat was interpreted as a subspecies of C. komatiensis, in colour like the typical form from the Carolina district, ".... but the muzzle and incisors are much broader and the molar teeth slightly larger, the nasal longer and broader" (Roberts, 1951, 396). The type is an adult ♀ from Lake St. Lucia with two pairs of pectoral and no inguinal mammae. Another specimen had been collected in the Mkuzi Game Reserve.

I feel however, that this mole-rat should rather be interpreted as a representative of C. natalensis. The various measurements given by Roberts (1951, 612) all point to the larger nature of the Zululand specimens, which indicate closer affinity to natalensis than to the smaller komatiensis (See Chapter 19). Furthermore, if these specimens are interpreted as being representatives of C. natalensis, they fit logically into the geographical distribution pattern of natalensis. Their resemblance to C. junodi (i.e. C. natalensis,

occurring/...

occurring in the coastal tract from the Limpopo river southwards to Maputa, just south of the border of Mocambique) is great. As I see the picture, C. komatiensis does not occur to the east of the Lebombo mountain range. It is therefore tentatively proposed in this work, that C.k.zuluensis should be synonymised with C. natalensis.

Biological:

Aspects relating to the biology of C. natalensis are few and meagre. However, a number of tentative interpretations can be put forward.

The species occurs in widely diverging vegetational veldtypes. This is illustrated by the fact that they occur in a pure grassveld type near the escarpment at Wakkerstroom as well as in temperate and transitional forest and scrub types found in the uplands of Natal. The veld types in Swaziland, where C. natalensis has been collected can be described as a mountain sourveld while at Port St. Johns and Maputa they occur in coastal tropical forest types (= coastal forest thornveld). The highveld area, which includes false grassveld types also supports populations of this species, while north of the Magalies mountains (e.g. at Nylstroom) they are encountered in tropical bush and savannah veld types, often referred to as sour bushveld. In the western portions of Transvaal (e.g. at Potchefstroom), they occur in pure grassveld types (Cymbopogon-Themeda veld).

It is clear that there seems to be no definite correlation between the distribution of this species and the vegetation.

As far as soil types are concerned, there is a greater degree of correlation evident. It seems as if they occur predominantly in undifferentiated fersialitic soils. Topographically, they range from sea level to areas 7,000' above sea level (e.g. near Wakkerstroom).

This species probably avoids drier and more arid areas. They occur plentifully in the Johannesburg-Pretoria district with an average rainfall figure of 24-32" per annum while Swaziland and Natal varies between 40-50" of rain per annum. The area near Port St. Johns receives as much as 60-70" per year, and yet this species is encountered. In a number of instances, additional information as to where specimens were trapped, can be derived from the labels attached to the specimens and often it is stated that they were collected near marshes or vlei's.

Information in connection with reproduction is also scattered. A gravid ♀ has been trapped in Pretoria during November, while pregnant ♀♀ were also trapped near Brooklyn (Pretoria) and Muckleneuk Hill (Pretoria) during February and April respectively, each containing one embryo only. Similarly a gravid ♀ was collected at Uitkomst near Krugersdorp during February. It would thus seem that pregnant ♀♀ are to be expected more frequently during the summer months indicating a certain periodicity during the year in terms of reproduction.

An adult ♀, trapped in Pretoria, weighed 121 gms.

Virtually nothing is known about the predators or parasites, or food preferences.

Phylogenetic/...

Phylogenetic:

Relationships of *C. natalensis* are not clear. Genetically speaking it may be reasonable to assume a greater affinity with *C. komatiensis* which also has two pairs of pectoral mammae only. This is in contrast to *C. hottentotus* or *C. holosericeus* where the inguinal mammae are also present. Its wide geographical distribution may also point to a certain degree of plasticity in its genotype, enhancing adaptive abilities for a greater spectrum of divergent ecological conditions.

List of localities:

Balgowan, 1 (NM), Benoni, 1 (TM), Bleskop, Rustenburg, 2 (TM), Blokspruit, Pretoria, 1 (TM), Boksburg, 4 (TM), Breyten, 1 (TM), Bronkhorstspruit, 7 (TM), Brooklyn, Pretoria, 31 (TM), Bulwer, 1 (NM), Dargle, 4 (TM), Dullstroom, 1 (TM), Durban, 2 (DM, NM), Elandsfontein, Pretoria, 2 (TM), Empangeni, 4 (NM), Esparanza, South Coast, 1 (NM), Estcourt, 2 (SA, NM), Fairfield, Rustenburg, 2 (TM), Forbes Reef, 7 (TM), Fountains, Pretoria, 6 (TM), Garstfontein, Pretoria, 2 (TM), Geelhoutkop, Nylstroom, 5 (TM), Groenkloof, Pretoria, 8 (TM), Hillcrest, 2 (AM), Hilton Road, 1 (TM), Hogsback, 3 (TM), Howick, 1 (SA), Ingwavuma, 4 (TM), Irene, 5 (TM), Johannesburg, 8 (SA, TM), Karkloof, 2 (TM), Kendal, 1 (SA), Knoppieslaagte, 1 (TM), Koedoespoort, Pretoria, 3 (TM), Koster, 3 (TM), Krugersdorp, 2 (TM), Malvern, 2 (TM), Manderston, 1 (NM), Maputa, 2 (TM), Masiyeni, 5 (TM), Mooivlei, Rustenburg, 4 (TM), Mountain View, Pretoria, 1 (TM), Mseleni, 3 (NM), Mungazi, 2 (TM, NM), Ngoya forest, 1 (TM), Nylstroom, 22 (TM), Pietermaritzburg, 40

(NM), Port St. Johns, 2 (TM), Potchefstroom, 1 (TM), Randfontein, 2 (TM), Rietondale, Pretoria, 14 (TM), Rietspruit, Nylstroom, 1 (TM), Roodeplaat, Pretoria, 1 (TM), Rooi Krans, Rustenburg, 4 (TM), Rosslyn, Pretoria, 19 (TM), Skinner's Court, Pretoria, 15 (TM), Steynsdorp, 7 (TM), Ubombo, 1 (TM), Uitkomst, 1 (TM), Umhlati River, 2 (TM), Venterskroon, 7 (TM), Waterkloof, Pretoria, 5 (TM), Wakkerstroom, 7 (TM), Welgegund, Rustenburg, 1 (TM), Zwartkops, Pretoria, 9 (TM).

CHAPTER 19

CRYPTOMYS KOMATIENSIS (ROBERTS) 1917

This species was first collected in the vicinity of the farm called Arnhemburg, in the Carolina district, Transvaal, and was first named and described by Roberts (1917, 272). Although the species resembles *C. natalensis*, it was recognized as being different due to its smaller size and the fact that the incisors project forward in a wider arch compared to *C. natalensis*. On the other hand, the inguinal mammae are always absent, as is the case in *C. natalensis*.

This species has also been oversplit by Roberts (1951, 396, 397) and it is therefore proposed to synonymize a number of species and subspecies in the present work. As here understood, *C. komatiensis* is regarded as a monotypic species.

The species is confined predominantly to the eastern Transvaal, ranging from the area east of Carolina, northwards to Barberton and Komatipoort, through the southern section of the Kruger National Park to Mariepskop and Acornhoek, eventually reaching Tzaneen and Woodbush on the eastern escarpment of the Drakensberg in the north. It thus seems to be adapted to hilly and mountainous areas.

Cryptomys komatiensis (Roberts)

Georychus komatiensis Roberts, *Ann. Transv. Mus.*, *5*: 272, 1917. Type locality: Arnhemburg Farm, Carolina district, Transvaal.

Georychus/...

Georychus rufulus Roberts, *Ann. Transv. Mus.*, *5*: 272, 1917. Type locality: Tzaneen, Transvaal.

Georychus stellatus Roberts, *Ann. Transv. Mus.*, *5*: 272, 1917. Type locality: Komatipoort, Transvaal.

Cryptomys melanoticus Roberts, *Ann. Transv. Mus.*, *11*: 4, 260, 1926. Type locality: Baloon Farm, Makoetsi River, Leydsdorp district, Transvaal.

Cryptomys natalensis streeteri Roberts, *Ann. Transv. Mus.*, *20*: 4, 316, 1946. Type locality: Hektorspruit, Transvaal.

Type specimen:

An adult ♀, TM. No. 1765, collected on September 9th, 1915.

Type locality:

Arnhemburg, Carolina district, Transvaal.

Distribution: (Fig. 19.1).

Occurs in alluvial soils below the escarpment in the Carolina district, possibly ranging to the north and south of this locality. In a southernly direction it is replaced by *C. natalensis*. North-easternly, it is found in the vicinity of Barberton and Komatipoort. From this point westwards and north-westwards through the southern half of the Kruger National Park, Acornhoek, Mariepskop and Baloon Farm on the eastern side of the Drakensberg escarpment at or near the Makoetsi River in the Leydsdorp district. Thence northwards it ranges to the vicinity of Woodbush and Tzaneen.

Diagnostic characters:

A small-sized species, H.B. M= 120 mm., C.B. M = 31.2 mm. (♂♂), reminding one somewhat of

C./...

C. hottentotus, but differing from that species in the absence of inguinal mammae. Colour more variable than in *C. natalensis*. ♂♂ slightly larger than the ♀♀. Frontal (occipital) patch usually absent.

Colour:

The overall colouration of this species is reminiscent of the colouration found in *C. natalensis*, although it seems to be far more homogeneous. No description of the colouration of the type specimen has been given. Specimens from Tzaneen have been described as sandy-buffish (nearest to the so-called pinkish-cinnamon of Ridgeway). On the other hand, specimens from Komatipoort are even more brightly coloured. It can thus be inferred that colour seems to be individually and geographically variable. This is also borne out by the fact that specimens from the eastern escarpment of the Drakensberg are usually slightly darker than the forms of Arnhemburg, especially as far as the ♂♂ are concerned.

Size: Adult ♂♂:

H.B.	102-137 mm., M = 120 mm.
T.	11-29 mm., M = 16 mm., (13.3% of H.B.)
H.F.	15-25 mm., M = 20 mm., (16.6% of H.B.)
C.B.	26.5-34.6 mm., M = 31.2 mm.
B.C.	12.9-14.8 mm., M = 13.9 mm., (44.5% of C.B.)
I.W.	6.5-7.9 mm., M = 7.0 mm., (22.4% of C.B.)
Z.W.	18.1-24.9 mm., M = 22.0 mm., (70.5% of C.B.)
M.W.	5.3-7.4 mm., M = 6.4 mm., (20.5% of C.B.)
U.T.R.	4.4-7.5 mm., M = 5.2 mm., (16.6% of C.B.)
L.J.	18.4-22.4 mm., M = 20.4 mm., (65.3% of C.B.)
L.T.R.	4.4-6.8 mm., M = 5.2 mm., (16.6% of C.B.)

Adult/...

Adult ♀♀:

H.B. 90-135 mm., M = 118 mm.

T. 12-23 mm., M = 17 mm., (14.4% of H.B.)

H.F. 18-23 mm., M = 20 mm., (16.9% of H.B.)

C.B. 28.6-32.6 mm., M = 30.6 mm.

B.C. 12.8-14.5 mm., M = 13.7 mm., (44.7% of C.B.)

I.W. 6.1-7.3 mm., M = 6.7 mm., (21.8% of C.B.)

Z.W. 19.5-23.2 mm., M = 21.1 mm., (68.9% of C.B.)

M.W. 5.5-6.7 mm., M = 5.9 mm., (19.2% of C.B.)

U.T.R. 4.3-6.0 mm., M = 5.0 mm., (16.3% of C.B.)

L.J. 17.7-21.2 mm., M = 19.6 mm., (64.0 of C.B.)

L.T.R. 4.4-6.2 mm., M = 5.0 mm., (16.3% of C.B.)

Some degree of sexual dimorphism is present, although not phenotypically obvious. When the ♂♂ are compared to ♀♀ in respect of the C.B. lengths, sexual dimorphism becomes apparent at the 5% level of probability (i.e. t = 2.05, 44 degrees of freedom, P = 0.05).

Size in this species seems to be geographically stable. Samples from Hektorspruit (C.B. length M = 31.4 mm., (♂♂)) do not differ substantially from similar samples derived from Mariepskop (M = 31.7 mm.) while specimens from Woodbush (virtually its northernmost point of distribution) shows a value of 31.6 mm. for the same measurement.

Skull and dentition:

The skull is of smaller dimensions than C. natalensis and not as ruggedly and strongly constructed. Again, there seems to be a great degree of variation in the size and extent of the cranial elements (i.e. the patterns exhibited by the sutures), so that virtually nothing of diagnostic value can be derived from them.

As far as the molare are concerned, no diagnostic information can be gained from these structures. It has been stated that the incisors project forward in a wider arch, but this seems to be a relative, rather than an absolute characteristic.

Discussion:

As was the case in C. natalensis, it appears that the species komatiensis has also been oversplit. Originally the following species were described by Roberts: 'G'. komatiensis, (Arnhemburg, Carolina district, 1917), 'G.' rufulus (Tzaneen, 1917), 'G'. stellatus (Komatipoort, 1917) as well as Cryptomys melanoticus (Baloon Farm, Makoetsi river, Leydsdorp district, Transvaal, 1926).

In 1951 Roberts (p. 396) placed the latter two species as subspecies of Cryptomys komatiensis (i.e. C.k. stellatus and C.k. melanoticus), while he retained the species rank for C. rufulus.

Ellerman et.al. (1953, 233) have, on the other hand, placed C. komatiensis as a race under their C. hottentotus group (i.e. C.h. komatiensis) and have tentatively placed C. rufulus and C. melanoticus as synonyms of C.h. komatiensis. It is interesting to note, however, that 'G'. stellatus (i.e. C.h. stellatus of Ellerman et.al.) has not been placed in synonymy with C.h. komatiensis, in this respect differing from Roberts, who, in 1951 demoted stellatus from specific to subspecific rank under C.k. komatiensis.

Furthermore, it is of interest to note that Ellerman et.al. have also tentatively placed C. vandami as a synonym under the subspecies

C./...

C.h. komatiensis, while *'G'. natalensis pallidus* (accepted as a synonym under *C. vandami* by Roberts in 1951) and *C. natalensis nemo* (to replace the name *pallidus* Roberts, preoccupied), are also treated accordingly. If this procedure is correct, it would imply that in some populations of *komatiensis* the inguinal mammae are absent, while being present in others.

On the other hand, if these various species and subspecies (excluding the *vandami* individuals) are synonymized, as is being proposed in the present work, the pattern of distribution exhibited by *C. komatiensis* becomes more logical and understandable. This eliminates the necessity of finding an explanation for the occurrence of at least two species (the one with at least three subspecies) in the eastern and north-eastern Transvaal.

'G'. komatiensis was originally described as being allied to *C. natalensis*, in having the same general characters but being much smaller in size. These remarks are borne out by measurements obtained in the present work. The mean H.B. length for ♂♂ was found to be 120 mm., in contrast to 143 mm. in *C. natalensis*. Similarly, the C.B. lengths in *komatiensis* and *natalensis* were found to be 31.2 mm. and 34.8 mm. (♂♂) and 30.6 mm. and 33.6 mm. (♀♀) respectively. Apart from size, it appears that the incisors project forwards in a slightly wider arch than is the case in *C. natalensis*.

As was indicated above, this species was demoted to subspecific rank (as the nominate subspecies) by Roberts in 1951. In the synonyms given under *C. k. komatiensis*, a typological error has

occurred/...

occurred: the date of description of the species 'G'. komatiensis is given as 1913, (Roberts, 1951, 396) which should in fact read 1917.

Similarly, 'G'. stellatus was described in 1917 (p. 272) as a separate species from Komatipoort, and the description was based on a single (and hitherto only known) specimen. Referring this specimen to a new species, may have been due to the fact that a white frontal spot is present, which may have prompted Roberts to recognize the specimen as different. Its colouration was described as more brightly coloured than 'G'. rufulus (which was described as a pinkish-cinnamon). On the other hand, Roberts (1951, 396) demoted this species to subspecific rank, while he pointed out that the white frontal spot may be abnormal as it occurs sporadically in other forms as well. The skull of stellatus was described as being readily distinguishable by the narrow interorbital constriction, a character which is usually constant in all species of Cryptomys. On closer inspection, however, it becomes clear that this feature may not be so diagnostic as was orginally thought, for a certain amount of variation in this characteristic is encountered.

Although Roberts (1917, 272) took Arnhemburg in the Carolina district as the type locality for the species described as komatiensis, he states that another specimen, trapped at Arnhemburg, may be referable to this species (i.e. stellatus). The occurrence of two closely related forms at the same locality does not seem to be taxonomixally palatable, and this fact has also induced the present author to synonymize stellatus with komatiensis. When the type

specimen/...

specimen of stellatus is compared to specimens representing komatiensis, I fail to see any phenotypic differences between the two so-called subspecies. Unfortunately, the sample-size of stellatus does not allow any statistical comparison.

In 1917, Roberts (p. 272) also described 'Georychus' rufulus as a new species from Tzaneen. Its colour was described as being a sandy-buffyish (close to pinkish-cinnamon), while the specimens were of small size. In this respect, it corresponds rather well with C. hottentotus but differs therefrom in the absence of inguinal mammae. Roberts (1951, 397) has described its distribution as follows: from the type locality (i.e. Tzaneen) northwards to the Zoutpansberg (i.e. cutting across the distribution range of C. vandami), southwards to Barberton district (i.e. cutting across the distribution pattern of C. melanoticus, C. jamesoni), and again near Durban (cutting across the pattern of C. natalensis) and possibly also near Pirie, near Kingwilliamstown! (which is in the geographical range occupied by C. hottentotus). It is evident that this supposed pattern of distribution for C. rufulus is ridiculous and can not be accepted. It is more logical to assume this animal to be a synonym of komatiensis, which occurs at Arnhemburg, Komatipoort, Hektorspruit, Acornhoek, Baloon Farm, further northwards along the eastern face of the Drakensberg escarpment, until the area and vicinity of Tzaneen is approached. Roberts stated that this species overlaps the distribution pattern of the slightly larger komatiensis (p. 397), often occurring close to it at the same localities.

The/...

The close correspondence in overall size between *rufulus* and *komatiensis* is reflected in Table 19.1.

Table 19.1: Overall correspondence in size between *C. rufulus* and *C. komatiensis*.

	♂♂:		♀♀:	
	Tzaneen	Arnhemburg	Tzaneen	Arnhemburg
H.B.	M= 123 mm.	M= 123 mm.	M= 122 mm.	M= 119 mm.
C.B.	M= 31.4 mm.	M= 31.7 mm.	M= 30.4 mm.	M= 31.9 mm.
L.J.	M= 20.6 mm.	M= 21.0 mm.	M= 19.3 mm.	M= 20.2 mm.

These few measurements show very clearly that *C. komatiensis* from Arnhemburg is slightly, though not significantly, larger than *C. rufulus* from Tzaneen and surrounding areas, and that apart from size considerations, there seems to be no justification for the separation of *rufulus* from *komatiensis*. They do not differ significantly in size, colouration, phenotype or morphology.

Similarly, *Cryptomys melanoticus* was described as a new species by Roberts (1926, 260) from Baloon Farm, near the Makoetsi river, Leydsdorp district. This species was originally described as being closely allied to *C. komatiensis*, but differing therefrom in that the female is normally darker than the male, ".... almost black in some cases", while the males are usually coloured like *komatiensis*, "... perhaps darker on the average only". Compared to *C. rufulus*, it is slightly larger in size (which occurs in the same ground!) and beyond these average dimensions there are no outstanding differences in the skulls.

As far as *melanoticus* is concerned, Roberts

(1951,/...

(1951, 396) states that this form is apparently very variable in colour (to a greater extent than is usual) and that specimens in different localities also vary, being more uniform in colour in some places than in others. He states furthermore, that the distribution of melanoticus overlaps the distribution of rufulus from which it is by no means always easy to separate except on size. As far as size is concerned, the present author finds it virtually impossible to discriminate between these species (or as they were later interpreted, subspecies) on size only.

Therefore, it was felt that the logical step in the present work would be to treat these two described forms as conspecific and to place stellatus, melanoticus and rufulus under C. komatiensis.

Finally, the inclusion of Cryptomys natalensis streeteri as a synonym under C. komatiensis in the present work, requires some explanation. This animal was originally described as a new subspecies (Roberts, 1946, 316), with the type locality Hektorspruit. It was described as a smaller and browner form (near cinnamon brown) compared to C. natalensis with corresponding changes in the skull (i.e. being lighter and narrower compared to C. natalensis from Karkloof and Masiyeni in Portuguese East Africa, although the incisors are arched to the same degree).

On studying the type specimen, I have come to the conclusion that the specimen is a representative of komatiensis rather than natalensis. This is seen in the size of the specimen as well as its colouration. Furthermore, if the geographical distribution of *komatiensis* is considered, it can be taken to occur from Arnhemburg, east of Carolina, ranging through to Barberton and further northwards to Komatipoort and other localities to the south of the Kruger National Park. The present author fails to see the feasibility of *natalensis* suddenly appearing in the range occupied by *komatiensis*.

Table 19.2: Comparison of certain measurements of *C. komatiensis*, *C. natalensis streeteri* and *C. natalensis*.

	(Arnhemburg) *Cryptomys komatiensis*	(Hektorspruit) *Cryptomys natalensis streeteri*	*Cryptomys natalensis*
♂♂:			
H.B.	M = 123 mm.	M = 120 mm.	M = 143 mm.
C.B.	M = 31.7 mm.	M = 31.4 mm.	M = 34.8 mm.
L.J.	M = 21.0 mm.	M = 20.9 mm.	M = 23.1 mm.
♀♀:			
H.B.	M = 119 mm.	M = 118 mm.	M = 141 mm.
C.B.	M = 31.9 mm.	M = 30.3 mm.	M = 33.6 mm.
L.J.	M = 20.2 mm.	M = 19.9 mm.	M = 22.2 mm.

It is clear that these figures speak for themselves, indicating that *C. natalensis streeteri* is in fact much closer to *C. komatiensis* than to *C. natalensis*. The differences between *komatiensis* and *natalensis streeteri* are so small (e.g. C.B. length and L.J. length in ♂♂) as to be statistically insignificant. It is therefore proposed, to place the subspecies *C. natalensis streeteri* as a synonym under the species *C. komatiensis*.

Biological/...

Biological:

It seems that this species prefers higher lying areas, although it is not restricted thereto and seems to occur in diverse and different soil types. In the Carolina district, it occurs in alluvial soils in the valleys below the Drakensberg escarpment while it prefers the hilly country about the eastern escarpment at its foothills from Acornhoek, Mariepskop and northwards to Woodbush. As a rule it may be said to occur in stony ground.

Further biological information about this species is virtually non-existant.

Phylogenetic:

The closest relative of *C. komatiensis* appears to be *C. natalensis*, although the two species differ considerably in size. In both species the inguinal mammae are absent, possibly indicating a similar basic genotype.

List of localities:

Arnhemburg, Carolina district, 10 (TM), Acornhoek, 3 (TM), Barberton, 2 (TM), Dzueni, 1 (KP), Faai-Stungwane Fire Break, 7 (KP), Hektorspruit, 8 (TM), Krantzview, Carolina district, 1 (TM), Legogote, 1 (SA), Mariepskop, 25 (TM), Tzaneen, 5 (TM), Warmbad, Carolina district, 4 (TM), Woodbush, 8 (TM).

CHAPTER 20

SUMMARY AND CONCLUSIONS

The data on which the interpretations and conclusions of this study rest are derived from three sources: pertinent records from the literature, unpublished field notes of others and my own field observations.

The origin of the family Bathyergidae is obscure. This is partially explained by the absence of paleontological information. The possible taxonomic position of the Mongolian fossils Tsaganomys altaicus and Cyclomylus lohensis (accepted as bathyergids by some authors) is discussed. In addition, the known bathyergid fossils from African deposits (Heterocephalus quenstedti, Heterocephaloides darti, Bathyergoides neotertiarius, Gypsorhychus darti, G. minor, G.makapani, Cryptomys robertsi, Bathyergus cf. suillus and Georychus cf. capensis) are briefly reviewed. It appears that the genus Bathyergus shows little relationship with the fossils listed above, while there seems to be a closer relationship between the extinct genus Gypsorhychus and the extant genera Cryptomys and Georychus. Further collecting of fossil forms will no doubt uncover additional information concerning the origin and phylogenetic diversity of the Bathyergidae.

Past attempts at taxonomically grouping the genera and species of bathyergids are presented and discussed. They were either treated as an isolated group, or placed among the myomorphs and hystricomorphs and in one isolated instance among the sciuromorphs. For the purposes of the present work, the mole-rats are interpreted as specialized hystricomorphs.

A detailed discussion of the cranial morphology of Bathyergus is presented, supplemented by notes indicating those points of difference where Cryptomys and Georychus differ from Bathyergus. During the preparation of the present work it has become evident that there is a great degree of individual variation encountered in the different cranial elements (in extent, size and structure). This implies that cranial elements (e.g. the nasals), used as diagnostic characters, should be treated with a certain degree of reservation, especially as far as specific and subspecific levels are concerned.

Aspects relating to the so-called taxonomic 'isolation' of the bathyergids are also presented. It is tentatively concluded that this 'isolation' has been over-emphasized in the past. Data pertaining to the skull, post-cranial skeleton, myology and reproductive system all point to the hystricomorph affinity of the bathyergids.

Data concerning the biology of the bathyergids are discussed at length. It is clear that there is a broad, overall resemblance as far as biological aspects are concerned between Bathyergus, Cryptomys and Georychus. The existing differences are relative rather than absolute. It must be stressed that very little is known concerning the biology of Georychus. In fact, as far as all three genera are concerned, many biological facets await future investigation and research. The possibility of the application of modern techniques (e.g. radio-active tagging) to

unravel/...

unravel biological questions concerning the mole-rats is stressed. Nothing is known about home range, daily activity rhythmn, food preferences and reproduction. It is therefore not clear what role these animals play in the ecosystem of nature.

In the present work, a new key for the identification of the various Southern African bathyergids is proposed, based on all the accumulated evidence. Unfortunately some species are poorly represented as study skins and skulls in Southern Africa, and the application of this key may lead to certain difficulties in identification in the case of Cryptomys bocagei, C. beirae and C. nimrodi.

All the bathyergid species encountered in Southern Africa are interpreted as monotypic in this work. The present arrangement recognizes 12 species i.e. Bathyergus suillus, B. janetta, Georychus capensis, Cryptomys hottentotus, C.damarensis, C.holosericeus, C.darlingi, C.nimrodi, C.beirae, C.bocagei, C.natalensis and C. komatiensis. This interpretation therefore differs greatly from that offered by Roberts (1951) who regarded Bathyergus suillus, B. janetta, Georychus capensis, Cryptomys hottentotus, C.holosericeus, C. natalensis and C. komatiensis as polytypic species. Similarly, the taxonomic position of the bathyergids as I see it at present, also differs radically from the interpretation adhered to by Ellerman et.al. (1953). These authors regard B.suillus and B.janetta as conspecific, while in the present work they are interpreted as two separate species. As far as Cryptomys is concerned, Ellerman et.al. only accept C.hottentotus and C.holosericeus to occur as species in Southern Africa, while all the

other/...

other described species are treated as races or are placed in synonymy under either hottentotus or holosericeus. I am not inclined to accept this interpretation for it is felt that the taxonomy of the bathyergids in Southern Africa is thereby simplified to too great an extent. I fail to see why well-marked species such as C.damarensis and C.natalensis do not deserve specific recognition. To this must be added that there exists an element of doubt concerning the validity of C.holosericeus as a separate species.

As here understood, Bathyergus suillus is a monotypic species, while B.s.intermedius is treated as a synonym. Ellerman et.al. (1953) have regarded B.suillus and B.janetta as conspecific, but this possibility is rejected in the present work. With the aid of ratios it is shown that suillus and janetta are different species and that these differences are statistically valid. B.suillus is the largest bathyergid found in South Africa, limited to coastal regions between Lambert's Bay and the vicinity of Knysna. Colour geographically variable.

Similarly, Bathyergus janetta is accepted as a monotypic species in the present work. The proposed synonyms include B.j.inselbergensis and B.j.plowesi. It is found that too little material is available for proper definition of the supposed subspecies. The geographical distribution of this species is rather localized i.e. occurring mainly in the vicinity of Port Nolloth and adjacent areas. B.janetta is far smaller than B.suillus, showing little geographical variation in colour.

In contrast to Roberts (1951), Georychus capensis is also accepted as a monotypic species as has

been/...

been done by Ellerman *et.al*. (1953). *G.c.canescens* and *G.c.yatesi* are treated as synonyms. This procedure has been adhered to in the present work in view of the fact that diagnostic characters listed for *canescens* and *yatesi* can also be demonstrated to be present in *capensis*. The pattern of distribution of this species is interesting: ranging along the coast from Cape Town to Knysna and also occurring at Nottingham Road, Natal and at Belfast in the Transvaal. Geographical variation in colour is found. Phylogenetically, the genus *Georychus* shows a greater degree of relationship to *Cryptomys* than to *Bathyergus*.

The small to medium-sized *Cryptomys hottentotus* is interpreted as a monotypic species in the present work. The synonyms include *C.caecutiens*, *C.vandami*, *C.jorisseni*, *C.albus*, *C.hottentotus cradockensis* and *C.h.transvaalensis*. The species is geographically variable as far as size and colouration is concerned. It exhibits an extensive distribution pattern in South Africa, ranging along the coast from Klaver to the Eastern Province, northwards over large stretches of the Karoo into the southern Orange Free State. It is also encountered in the north-western and north-eastern Transvaal. It therefore occurs in diverse ecological habitats.

The monotypic Damara mole-rat *Cryptomys damarensis* has *C.lugardi*, *C.micklemi* and *C.ovamboensis* as synonyms. It has a very wide geographical distribution, confined to the drier, western half of Southern Africa. This is the only species where polymorphism in colouration is encountered i.e. specimens occur in three colour phases. Furthermore, it is the largest *Cryptomys* species found in Southern Africa. It is

likely/...

likely that it has certain phylogenetic affinities with C. bocagei from Angola and C. darlingi from Rhodesia when phenotypic appearance and aspects of cranial morphology are considered.

The validity of Cryptomys holosericeus is open to question. A number of aspects seem to suggest the possibility of synonymizing holosericeus with hottentotus, but this step has not been taken in the present work. As here understood, C.holosericeus is a monotypic species occurring in the north-western Cape Province and north-western Orange Free State. The following described forms are treated as synonyms: C.holosericeus orangiae, C.h.vetensis, C.h.valschensis, C.h.vryburgensis and C.hottentotus bigalkei. The colouration shows geographical variation. The possibility of Graaff-Reinet (hitherto accepted as the type locality of C.holosericeus) being the type locality for this species is questioned.

The fact that C.holosericeus may eventually by synonymized with C.hottentotus is based on the following aspects:

(i) Variation in size encountered in C.hottentotus and C.holosericeus. Adult individuals of the former species may attain the large size of the latter species, while adult specimens of the latter species may fall well within the range of variation of the former species.

(ii) There is a pronounced resemblance between hottentotus and holosericeus as far as phenotypic and morphological aspects are concerned.

(iii) The limits of geographical distribution of hottentotus and holosericeus are not clear. If holosericeus is interpreted as a synonym of hottentotus,

the/...

the break in geographical distribution which presently exists in the case of hottentotus will be eliminated.

Ellerman et.al. (1953) have placed Cryptomys darlingi as a race of C.hottentotus while Roberts (1951) has retained it as a separate species. The latter interpretation is followed in the present work. This species occurs predominantly on the Mashonaland plateau in Rhodesia and no synonyms are known. Future research could well result in the fact that C. bocagei, C.nimrodi and C.beirae will be interpreted as synonyms of C.darlingi. A certain amount of geographical variation in colour is evident in this species. Phylogenetically it seems to be related more closely to C.damarensis than to C.hottentotus.

As far as Cryptomys nimrodi is concerned no specimens available for study can convincingly be referred to this species. Therefore, all the information given in the present work has been extracted from the existing literature pertaining to this species. It is known only from the type locality viz. Essex Vale in Matabeleland, Southern Rhodesia. Geographically, it falls within the range of distribution of C.darlingi and its possible relationship to C.darlingi is suggested as far as colour and craniological aspects are concerned. The validity of C.nimrodi as a separate species is open to question.

Cryptomys bocagei from Angola also occurs in the northernmost parts of South West Africa and is therefore included and discussed in greater detail in the present work. The taxonomic position of this species is not clear. As is the case in C. beirae, study specimens are few in number. It is felt that this is probably not a good species and its possible relationship to C.darlingi (resembling it phenotypically and morphologically rather closely) is obscure.

The validity of the species rank of Cryptomys beirae from Beira and vicinity is also open to question but it has tentatively been retained as a separate species. This species may eventually be synonymized with C.darlingi. As here understood, C.beirae is a monotypic species with C.zimbitiensis as a synonym.

Cryptomys natalensis is like-wise interpreted in the present work as a monotypic species. Its synonyms include: Cryptomys natalensis langi, C.n.aberrans, C.n.junodi, C.n.jamesoni, C.n.arenarius, C.n.mahali, C.anomalus, C.montanus and C.komatiensis zuluensis. This species has also been grossly oversplit in the past. Colour is geographically variable and it exhibits an extensive range of distribution occurring in the Transvaal, Natal and southern portion of Mocambique. It is a large species and phylogenetically it has certain affinities with C.komatiensis.

Finally Cryptomys komatiensis remains to be considered. This species is confined mainly to the eastern Transvaal. It is a small species, and the following described forms are interpreted as synonyms: C.komatiensis stellatus, C.k.melanoticus, C.rufulus and C.natalensis streeteri. The colour is geographically variable. As is the case in C.natalensis, the inguinal mammae are constantly absent in C.komatiensis possibly indicating some phylogenetic

relationship./...

relationship.

It is to be emphasized that the ideas and proposals embodied in this work are not to be interpreted as the last word on the subject. The taxonomic position of the mole-rats in Southern Africa is still very fluid (especially as far as the genus *Cryptomys* is concerned), subject to future research and interpretation. It is felt, however, that the major overall result which has emerged from the present work is the considerable simplification of taxonomical data concerning the Bathyergidae in Southern Africa.

* * * * *

GAZETTEER

In the gazetteer which follows localities are listed which have been referred to in the present work. Both the Latitude - Longitude coördinates and the locus are given for each locality.

The application of this locus system has been very aptly described by Meester (1963, 106) and the following description has been paraphrased from that work. The locus system is used to facilitate the mapping of locality records and is applied as follows: each degree square is divided into four equal-sized (half-degree) squares, A, B, C and D. Each of these is again divided into quarter-degree squares, a, b, c and d. The locus of a certain locality corresponds to one of these quarter-degree squares. When reference is made to the locality, the degree Latitude and Longitude are combined to form a single value, followed by the code letter of the first half-degree and then the code letter of the quarter-degree square in which the locality is situated. For the conversion of Latitude-Longitude coördinates to locus, the following conversion table is used:

Minutes latitude	Minutes longitude	Code
0-14	0-14	Aa
	15-29	Ab
	30-44	Ba
	45-59	Bb
15-29	0-14	Ac
	15-29	Ad
	30-44	Bc
	45-59	Bd

30/...

30-44	0-14	Ca
	15-29	Cb
	30-44	Da
	45-59	Db
45-59	0-14	Cc
	15-29	Cd
	30-44	Dc
	45-59	Dd

Following this system the locus for Citrusdal, for example, with Latitude-Longitude coordinates 32°35' S., 19°01' E. becomes 3219 Ca. In plotting it, the locus is located in the degree square 32° South Latitude, 19° East Longitude, within the quarter-degree square a of the half-degree square C.

In the case of the Kruger National Park localities, the code (as defined above) is also given but not the exact Latitude and Longitude coordinates. The biologists of the Park have subdivided the game reserve into three sections: northern, central and southern. Each section has been divided into equal-sized numbered squares, facilitating pin-pointing of localities. These annotations are given in the present work. Following this system, Satara, for example, is referred to as C 71, 2431 Bd, Hlati Road as N 151, 2331 Ad, Faai-Stungwane fire break as S 49, 2531 Ab, etc.

This gazetteer lists 334 localities. The correct coördinates for 28 localities (slightly more than 8%) could not be determined accurately. They have, however, been listed in view of the fact that they are referred to in the text.

Locality/...

Locality	Lat.	Long.	Locus
Acornhoek, Transvaal	24°35' S.,	31°04' E.	2431 Ca
Alexandria, Cape Province	33°39' S.,	26°24' E.	3326 Cb
Angra Pequina 8, Bothaville, Orange Free State	27°29' S.,	26°32' E.	2726 Bc
A(a)rnhemburg 151, Carolina, Transvaal	26°03' S.,	30°50' E.	2630 Bb
Balgowan, Natal	29°22' S.,	30°03' E.	2930 Ac
Balloon Farm, Makoetsi river, Leydsdorp	Exact locality uncertain		
Barberton, Transvaal	25°47' S.,	31°03' E.	2531 Cc
Barkley West, Cape Province	28°31' S.,	24°31' E.	2824 Da
Bathurst, Cape Province	33°31' S.,	26°49' E.	3326 Db
Beira, Mocambique	19°50' S.,	34°52' E.	1934 Dd
Benoni, Transvaal	26°10' S.,	28°19' E.	2628 Ab
Belfast, Transvaal	25°42' S.,	30°02' E.	2530 Ca
Bellville, Cape Town, Cape Province	33°54' S.,	18°39' E.	3318 Dc
Belvedere, Knysna, Cape Province	34°03' S.,	22°59' E.	3422 Bb
Bleskop, Rustenburg, Transvaal	25°41' S.,	27°22' E.	2527 Cb
Bloemfontein, Orange Free State	29°07' S.,	26°11' E.	2926 Aa
Bloemhof, Transvaal	27°39' S.,	25°36' E.	2725 Da
Blokspruit, Pretoria	Exact locality uncertain		
Boekenhoutfontein, Transvaal	25°31' S.,	28°06' E.	2528 Ca
Boksburg, Transvaal	26°13' S.,	28°18' E.	2628 Ab
Bothaville, Orange Free State	27°24' S.,	26°37' E.	2726 Bc
Braklaagte, Parys, Orange Free State	26°57' S.,	27°37' E.	2627 Dc
Bredasdorp, Cape Province	34°32' S.,	20°03' E.	3420 Ca
Breyten, Transvaal	26°18' S.,	29°59' E.	2629 Bd

Bronkhorstspruit/...

Bronkhorstspruit, Transvaal	25°49' S.,	28°45' E.	2528 Dd
Brooklyn, Pretoria, Transvaal	25°45' S.,	28°13' E.	2528 Cc
Bubube fire break, Kruger National Park	N 106		2331 Ab
Buffelsdraai, Transvaal	25°08' S.,	27°42' E.	2527 Ba
Bulawayo, Southern Rhodesia	20°09' S.,	28°35' E.	2028 Ba
Bulwer, Natal	29°48' S.,	29°46' E.	2929 Dd
Burgersdorp, Cape Province	30°58' S.,	26°20' E.	3026 Cd
Camps Bay, Cape Town, Cape Province	33°57' S.,	18°23' E.	3318 Cd
Cape Aghulhas, Cape Province	34°49' S.,	20°01' E.	3420 Cc
Cape Flats, Cape Town, Cape Province	33°56' S.,	18°41' E.	3318 Dc
Cape Town, Cape Province	33°56' S.,	18°29' E.	3318 Cd
Carolina, Transvaal	26°04' S.,	30°08' E.	2630 Aa
Cedarberg, Cape Province	32°22' S.,	19°10' E.	3219 Ac
Centlivres, Uitenhage, Cape Province	33°39' S.,	25°28' E.	3325 Cb
Charlesford, Knysna, Cape Province	34°02' S.,	23°03' E.	3423 Aa
Chipinga, Melsetter, Southern Rhodesia	20°12' S.,	32°37' E.	2032 Ba
Chishawasha, Salisbury, Southern Rhodesia	17°47' S.,	31°14' E.	1731 Cc
Clanwilliam, Cape Province	32°11' S.,	18°54' E.	3218 Bb
Citrusdal, Cape Province	32°35' S.,	19°01' E.	3219 Ca
Coalbrook, Orange Free State	26°51' S.,	27°52' E.	2627 Dd
Coega River, Cape Province	33°46' S.,	25°39' E.	3325 Dc
Coldspring, Cape Province	Exact locality uncertain		
Constantia, Cape Town, Cape Province	33°59' S.,	18°26' E.	3318 Cd

Cossack/...

Cossack Post, Rosmead, Cape Province	±31°29' S., 25°07' E.	3125 Ac
Cradock, Cape Province	32°10' S., 25°37' E.	3225 Ba
Damara Pan, Central Kalahari, Bechuanaland Protectorate	22°05' S., 22°27' E.	2222 Ab
Dargle, Natal	29°28' S., 30°07' E.	2930 Aa
De Aar, Cape Province	30°39' S., 24°02' E.	3024 Ca
De Brug, Orange Free State	29°09' S., 25°48' E.	2925 Bb
De Doorns, Cape Province	33°28' S., 19°40' E.	3319 Bc
De Hoop, Cape Province	34°26' S., 20°22' E.	3420 Ad
De Wet, Worcester, Cape Province	33°36' S., 19°31' E.	3319 Da
De Wetsdorp, Orange Free State	29°34' S., 26°41' E.	2926 Da
Diep Rivier, Cape Town, Cape Province	34°02' S., 18°28' E.	3418 Ab
Dortrecht, Cape Province	31°22' S., 27°03' E.	3127 Ac
Drostdy, Tulbagh, Cape Province	33°14' S., 19°12' S.	3319 Aa
Dullstroom, Transvaal	25°25' S., 30°06' E.	2530 Ac
Durban, Natal	29°52' S., 30°59' E.	2930 Dd
Dzueni, Kruger National Park	S 99	2531 Bd
East London, Cape Province	33°02' S., 27°55' E.	3327 Bb
Eendekuil, Cape Province	32°42' S., 18°53' E.	3218 Db
Elandsfontein, Pretoria, Transvaal	Exact locality uncertain	
Elsies Rivier, Cape Town, Cape Province	33°55' S., 18°39' E.	3318 Dc
Empangeni, Natal	28°45' S., 31°53' E.	2831 Dd
Enterprise, Salisbury, Southern Rhodesia	Exact locality uncertain	
Ermelo, Transvaal	26°31'S., 29°59' E.	2629 Db
Erongo siding, South West Africa	21°42' S., 15°52' E.	2115 Db

Esparanza/...

Esparanza, South Coast, Natal	30°20' S., 30°38' E.	3030 Bc
Essex Vale, Matabeleland, Southern Rhodesia	20°17' S., 28°56' E.	2028 Bd
Estcourt, Natal	29°01' S., 29°52' E.	2929 Bb
Ezelfontein, Kamiesberg, Cape Province	30°23' S., 18°06' E.	3018 Ac
Faai-Stungwane fire break, Kruger National Park	S 49	2531 Ab
Fairfield, Rustenburg, Transvaal	24°35' S., 27°12' E.	2427 Ca
Fauresmith, Orange Free State	29°45' S., 25°19' E.	2925 Cd
Forbes Reef, Swaziland	26°10' S., 31°06' E.	2631 Aa
Fountains Valley, Pretoria, Transvaal	25°57' S., 28°12' E.	2528 Cc
Fourteen Streams, Cape Province	28°04' S., 24°53' E.	2824 Bb
Fort Beaufort, Cape Province	32°46' S., 26°37' E.	3226 Dc
Franshoek, Cape Province	33°55' S., 19°06' E.	3319 Cc
Gaberones, Bechuanaland Protectorate	24°39' S., 25°54' E.	2425 Db
Garies, Cape Province	30°34' S., 17°59' E.	3017 Db
Garcia Forest, Riversdal, Cape Province	33°57' S., 21°14'E.	3321 Cc
Garsfontein, Pretoria, Transvaal	25°48' S., 28°17' E.	2528 Cd
Geelhoutkop, Nylstroom, Transvaal	24°17' S., 28°24' E.	2428 Ad
Gemsbokpan, Kalahari, Bechuanaland Protectorate	21°43' S., 21°38' E.	2121 Da
George, Cape Province	33°58' S., 22°25' E.	3322 Cd
Glen, Orange Free State	28°57' S., 26°20' E.	2826 Cd
Glennifer, Kei Road, Cape Province	32°42' S., 27°33' E.,	3227 Da
Gobabis, South West Africa	22°28' S., 18°58' E.	2218 Bb

Goodwood/...

Goodwood, Cape Town, Cape Province	33°54' S., 18°34' E.	3318 Dc
Gorge, Kruger National Park	C 2	2331 Dc
Gorongoza, Mocambique	Exact locality uncertain	
Graaff-Reinet, Cape Province	32°15' S., 24°32' E.	3224 Bc
Gravelotte, Transvaal	23°57' S., 30°36' E.	2330 Dc
Grahamstown, Cape Province	33°18' S., 26°32' E.	3326 Bc
Greenpoint, Cape Town, Cape Province	33°54' S., 18°24' E.	3318 Cd
Grey's Pass, Citrusdal, Cape Province	32°37' S., 18° 58' E.	3218 Db
Griffin Mine, Leydsdorp, Transvaal	Exact locality uncertain	
Grootfontein, South West Africa	19°34' S., 18°06' E.	1918 Ca
Grootkolk, Kalahari Gemsbok National Park, Cape Province	24°54' S., 20°06' E.	2420 Cc
Grootvadersbosch, Swellendam, Cape Province	33°50' S., 20°53' E.	3320 Dd
Hanha, Angola	12°35' S., 13°44' E.	1213 Da
Hazendal, Cape Town, Cape Province	33°57' S., 18°31' E.	3318 Dc
Hektorspruit, Transvaal	25°26' S., 31°41'E.	2531 Bd
Het Kruis, Piketberg, Cape Province	32°35' S., 18°44' E.	3218 Da
Hillcrest, Natal	29°47' S., 30°46' E.	2930 Dd
Hillside, Bulawayo, Southern Rhodesia	20°12' S., 28°35' E.	2028 Ba
Hilton Road, Pietermaritzburg, Natal	29°33' S., 30°19' E.	2930 Cb
Hlati Road, Kruger National Park	N 151	2331 Ad
Hout Bay, Cape Peninsula, Cape Province	34°03' S., 18°21' E.	3418 Ab
Houghton, Johannesburg, Transvaal	26°09' S., 28°03' E.	2628 Aa

Howisonspoort/...

Howisonspoort, Grahamstown, Cape Province	33°24' S., 26°25' E.	3326 Ad
Hogsback, Swaziland	Exact locality uncertain	
Howick, Natal	29°29' S., 30°13' E.	2930 Ac
Ingwavuma (Ngwavuma), Natal	27°08' S., 32°01' E.	2732 Aa
Inyanga, Southern Rhodesia	18°13' S., 32°44' E.	1832 Ba
Irene, Transvaal	25°51' S., 28°13' E.	2528 Cc
Jericho, Transvaal	25°20' S., 27°48' E.	2527 Bd
Johannesburg (at Observatory), Transvaal	26°11' S., 28°04' E.	2628 Aa
Jonkersberg, Cape Province	33°55' S., 22°14' E.	3322 Cc
Kalk Bay, Cape Peninsula, Cape Province	34°07' S., 18°27' E.	3418 Ab
Kalkfield, South West Africa	Exact locality uncertain	
Kamaggas, Cape Province	29°48' S., 17°30' E.	2917 Dc
Kamiesberg, Cape Province	30°19' S., 18°04' E.	3018 Ac
Kampspanne Road, Kalahari Gemsbok National Park, Cape Province	± 26°20' S., 20°20' E.	2620 Ad
Kano Vley, South West Africa	19°12' S., 19°19' E.	1919 Ab
Kaotwe, Ghanzi, Bechuanaland Protectorate	22°34' S., 23°14' E.	2223 Ca
Karakuwissa (Karakuwisa), South West Africa	18°57' S., 19°43' E.	1819 Dc
Karkloof, Natal	29°25' S., 30°16' E.	2930 Ab
Kendal, Transvaal	26°04' S., 28°57' E.	2628 Bb
Kenilworth, Cape Town, Cape Province	33°59' S., 18°29' E.	3318 Cd
Kersfontein, Berg River, Cape Province	33°36' S., 18°51' E.	3318 Db
Kimberley, Cape Province	28°48' S., 24°46' E.	2824 Db
King William's Town, Cape Province	32°53' S., 27°24' E.	3227 Cd

Khami/...

Khami Dam, near Bulawayo, Southern Rhodesia	20°09' S., 28°26'E.	2028 Ab
Klapperkop, Pretoria, Transvaal	25°47' S., 28°13' E.	2528 Ca
Klaver, Cape Province	31°47' S., 18°37' E.	3118 Dc
Knoppieslaagte, Transvaal	Exact locality uncertain	
Knysna, Cape Province	34°02' S., 23°03' E.	3423 Aa
Koeberg, Cape Town, Cape Province	33°55' S., 18°27' E.	3318 Cd
Koedoespoort, Pretoria, Transvaal	25°44' S., 28°17' E.	2528 Cb
Komatipoort, Transvaal	25°26' S., 31°57' E.	2531 Bb
Kompanjiesdrift, Cape Province	32°07' S., 18°27' E.	3218 Ab
Koster, Transvaal	25°52' S., 26°54' E.	2526 Dd
Kovares, South West Africa	19°03' S., 14°20' E.	1914 Ab
Krantzview, Carolina, Transvaal	Exact locality uncertain	
Krugersdorp, Transvaal	26°06' S., 27°46' E.	2627 Bb
Kuilsrivier, Cape Town, Cape Province	33°18' S., 24°22' E.	2324 Ad
Kuke, Bechuanaland Protectorate	23°18' S., 24°22'E.	2324 Ad
Kuruman, Cape Province	27°26' S., 23°26' E.	2723 Ad
Lake Ngami (at Motlhatlogo), Ngamiland, Bechuanaland Protectorate	20°27' S., 22°52' E.	2022 Bd
Lambert's Bay, Cape Province	32°05' S., 18°18' E.	3218 Ab
Lehutitung, Bechuanaland Protectorate	23°58' S., 21°53' E.	2321 Dd
Legogote, Transvaal	25°14' S., 31°06' E.	2531 Aa
Leliefontein, Cape Province	Exact locality uncertain	
Letaba, Kruger National Park	N 246	2331 Dc
Leydsdorp, Transvaal	23°59'S., 30°31' E.	2330 Dc
Lindanda Plots, Kruger National Park	C 123	2431 Db

Linyanti/...

Linyanti, Eastern Caprivi, South West Africa	18°06' S., 24°02' E.	1824 Aa
Luderitz, South West Africa	26°38' S., 15°06' E.	2615 Ca
Mababe Flats, Bechuanaland Protectorate	19°03' S., 24°09' E.	1924 Aa
Macheke, Southern Rhodesia	Exact locality uncertain	
Mafa, South West Africa	± 17° 'S.,16° 'E.	1716 Ca
Mafeking, Cape Province	25°53'S., 25°38'E.	2525 Dc
Maitland, Cape Town, Cape Province	33°55'S., 18°18'E.	3318 Cd
Magalakwin River, Transvaal	24°05'S., 28°54'E.	2428 Bb
Mahewane, Kruger National Park	N 119-120	2331 Ba
Mahungumule, Kruger National Park	N 151	2331 Bc
Malala, Zoutpansberg, Transvaal	Exact locality uncertain	
Malvern, Durban, Natal	29°53'S., 30°56'E.	2930 Dd
Malmesbury, Cape Province	33°27'S., 18°44'E.	3318 Bc
Mamaranga, Groot Letaba, Transvaal	Exact locality uncertain	
Manderston, Natal	29°44'S., 30°26'E.	2930 Cb
Maputa, Ngwavuma, Natal	26°59'S., 32°45'E.	2632 Dd
Maquassie, Transvaal	27°18'S., 26°00'E.	2726 Ac
Maribashoek, Transvaal	24°31'S., 26°31'E.	2426 Da
Marico River, (at Marico's draai) Transvaal	24°31'S., 26°31'E.	2426 Da
Mariepskop, Pelgrimsrust, Transvaal	24°35'S., 30°50'E.	2430 Db
Matjiesfontein, Cape Province	33°14'S., 20°35'E.	3320 Ba
Mashakadzi, Kruger National Park	N 118	2331 Ab

Mashi/...

Mashi river, (at Kongola) E. Caprivi, South West Africa	17°47'S.,	23°20'E.	1723 Cd
Masiyeni, Mocambique	Exact locality uncertain		
Mata Mata, Kalahari Gemsbok Park, Cape Province	25°46'S.,	20°00'E.	2520 Cc
Matetsi, Southern Rhodesia	±18° 'S.,	26° 'E.	1826 Ba
Matoppos Road, Bulawayo, Southern Rhodesia	Exact locality uncertain		
Maun, Ngamiland, Bechuanaland Protectorate	19°59'S.,	23°25'E.	1923 Cd
Mazoe, Southern Rhodesia	17°31'S.,	30°58'E.	1730 Db
Melsetter, Southern Rhodesia	19°48'S.,	32°52'E.	1932 Dd
Middledrift, Cape Province	32°49'S.,	26°59'E.	3226 Dd
Mlondozi, Kruger National Park	C 165, C 170		2531 Bb
Modder River, Cape Province	29°02'S.,	24°38'E.	2924 Ba
Mombola, Angola	11°33'S.,	14°25'E.	1114 Db
Montrose Estates, Zoutpansberg, Transvaal	22°54'S.,	29°37'E.	2229 Dc
Mookeetsi, Transvaal	23°16'S.,	30°05'E.	2330 Ac
Mowbray, Cape Town, Cape Province	33°56'S.,	18°28'E.	3318 Cd
Mooivlei, Rustenburg, Transvaal	Exact locality uncertain		
Moorddrift, Transvaal	24°17'S.,	28°58'E.	2428 Bd
Morakwen, Transvaal	26°08'S.,	23°46'E.	2623 Bb
Mountain View, Pretoria, Transvaal	25°41'S.,	28°10'E.	2528 Ca
Mount Selinda, Chipinga, Southern Rhodesia	20°27'S.,	32°40'E.	2032 Bc
Mseleni, Natal	27°22'S.,	32°32'E.	2732 Bc
Muckleneuk, Pretoria, Transvaal	25°47'S.,	28°13'E.	2528 Cc

Nagwacht/...

Nagwacht, Bredasdorp, Cape Province	34°35'S.,	20°07'E.	3420 Cb
Namutoni, South West Africa	18°48'S.,	16°58'E.	1816 Dd
Newlands, Cape Town, Cape Province	33°58'S.,	18°28'E.	3318 Cd
Ngirivane, Kruger National Park	C 69		2431 Bc
Ngoya forest, Natal	28°47'S.,	31°37'E.	2831 Dc
	to		
	28°52'S.,	31°41'E.	2831 Dc
Njelele-Limpopo rivers confluence, Transvaal	22°21'S.,	30°22'E.	2230 Ad
Nkokodzi, Kruger National Park	N 138		2331 Ab
Nieuwhoudtville, Cape Province	31°23'S.,	19°06'E.	3119 Ac
Nottingham Road, Natal	29°22'S.,	29°59'E.	2929 Bd
Numkaub, South West Africa	18°37'S.,	19°42'E.	1819 Da
Nwamayimani, Kruger National Park	N 131		2331 Ab
Nwanetzi-Limpopo rivers confluence	22°20'S.,	30°37'E.	2230 Bc
Nwanetzi-West, windmill, Kruger National Park	C 81		2431 Bc
Nylstroom, Transvaal	24°42'S.,	28°24'E.	2428 Cb
Oas, South West Africa	22°42'S.,	19°25'E.	2219 Cb
Odendaalsrust, Orange Free State	27°52'S.,	26°41'E.	2726 Dc
Ofcolaco, Leydsdorp, Transvaal	24°06'S.,	30°22'E.	2430 Ab
Okahandja, South West Africa	21°58'S.,	16°55'E.	2116 Dd
Olifants River, Van Rhynsdorp, Cape Province	±31°40'S.,	18°30'E.	3118 Da
Omaheke, South West Africa	Exact locality uncertain		
Ondongera, South West Africa	Exact locality uncertain		
Ondongwa (Ondangua), South West Africa	17°57'S.,	16°01'E.	1716 Cc

Oranjemund/...

Oranjemund, South West Africa	28°33'S.,	16°24'E.	2816 Cb
Oshoek, Ermelo District, Transvaal	26°36'S.,	29°40'E.	2629 Da
Otavi, South West Africa	±19° 'S.,	17° 'E.	1917 Cb
Otjivarongo, South West Africa	20°27'S.,	16°40'E.	2016 Bc
Ongha, South West Africa	Exact locality uncertain		
Ondjeva, South West Africa	17°02'S.,	15°43'E.	1715 Ba
Paarl (Lormarin's), Cape Province	33°53'S.,	19°03'E.	3319 Cc
Palapye, Bechuanaland Protectorate	22°33'S.,	27°08'E.	2227 Ca
Peddie, Cape Province	33°11'S.,	27°07'E	3327 Aa
Perseverance, Cape Province	Exact locality uncertain		
Phillipolis, Orange Free State	30°15'S.,	25°16'E.	3025 Ad
Phillipstown, Cape Province	30°26'S.,	24°28'E.	3024 Ad
Pietermaritzburg, Natal	29°36'S.,	30°22'E.	2930 Ad
Pilansberg, Transvaal	25°15'S.,	27°07'E.	2527 Ac
Pirie Forest, Cape Province	32°46'S.,	27°12'E.	3227 Cc
Plettenberg Bay, Cape Province	34°03'S.,	23°22'E.	3425 Ab
Plumstead, Cape Town, Cape Province	34°01'S.,	18°29'E.	3418 Ab
Port Alfred, Cape Province	33°36'S.,	26°53'E.	3326 Db
Port Elizabeth, Cape Province	33°58'S.,	25°36'E.	2916 Bd
Port Nolloth, Cape Province	29°16'S.,	16°52'E.	2916 Bd
Port St.Johns, Cape Province	31°37'S.,	29°33'E.	3129 Da
Potchefstroom, Transvaal	26°44'S.,	27°04'E.	2627 Ca
Power Station, Pretoria, Transvaal	25°44'S.,	28°08'E.	2528 Ca

Pretoria/...

Pretoria (station), Transvaal	25°45'S.,	28°11'E.	2528 Cc
Pumbe, Kruger National Park	C 52		2431 Bd
Queenstown, Cape Province	31°53'S.,	26°52'E.	3126 Dd
Quickborn 205, Otjivarongo, South West Africa	21°09'S.,	17°07'E.	2117 Aa
Randfontein, Transvaal	26°11'S.,	27°42'E.	2627 Ba
Rehoboth, South West Africa	23°19'S.,	17°05'E.	2317 Ac
Richmond, Cape Province	31°25'S.,	23°57'E.	3123 Bd
Riebeeck Kasteel, Cape Province	33°23'S.,	18°54'E.	3318 Bd
Rietondale, Pretoria, Transvaal	25°44'S.,	28°13'E.	2528 Ca
Rietpan, Kimberley, Cape Province	Exact locality uncertain		
Rietspruit, Nylstroom, Transvaal	Exact locality uncertain		
Rondebosch, Cape Town, Cape Province	33°57'S.,	18°28'E.	3318 Cd
Rio Mbalé, Angola	Exact locality uncertain		
Roodeplaat, Pretoria, Transvaal	25°35'S.,	28°21'E.	2528 Cb
Rooikrans 760, Rustenburg, Transvaal	24°53'S.,	27°39'E.	2427 Dc
Rosslyn, Pretoria, Transvaal	25°38'S.,	28°06'E.	2528 Ca
Rustenburg, Transvaal	25°40'S.,	27°14'E.	2527 Ca
Salisbury, Southern Rhodesia	17°50'S.,	31°04'E.	1731 Cc
Sandfontein 468, Gobabis, South West Africa	22°19'S.,	19°59'E.	2219 Bd
Santa Cruz Mission, Caprivi	16°20'S.,	22°09'E.	1622 Bd
Satara, Kruger National Park	C 71		2431 Bd
Satara Plots, Kruger National Park	C 81		2431 Bd

Sebungwe/...

Sebungwe, Southern Rhodesia	Exact locality uncertain		
Selukwe, Southern Rhodesia	19°40'S.,	30°00'E.	1930 Ca
Senanga, Southern Rhodesia	16°07'S.,	23°15'E.	1623 Ab
Seweweekspoort, Cape Province	33°22'S.,	21°25'E.	3321 Ad
Shawerombi, Melsetter district, Southern Rhodesia	Exact locality uncertain		
Shangombo, Southern Rhodesia	16°20'S.,	22°08'E.	1622 Ac
Shibangwanene, Kruger National Park	C 2		2331 Dc
Shingomene, Kruger National Park	N 64		2231 Cd
Shingwedzi, Kruger National Park	23°13'S.,	31°34'E.	2331 Ba
Shorobe, Ngamiland, Bechuanaland Protectorate	19°43'S.,	23°44'E.	1923 Da
Silwane, Groot Letaba, Transvaal	Exact locality uncertain		
Simonstown, Cape Province	34°11'S.,	18°27'E.	3418 Ab
Skinner's Court valley, Pretoria, Transvaal	25°43'S.,	28°09'E.	2528 Ca
Springbok, Cape Province	29°40'S.,	17°52'E.	2917 Db
Ssanukanu village, Grootfontein, South West Africa	18°06'S.,	20°23'E.	1820 Ab
Stellenbosch, Cape Province	33°56'S.,	18°51'E.	3318 Dd
Sterkloop, Woodbush, Transvaal	±23°47'S.,	30°03'E.	2330 Cc
Sterkstroom, Cape Province	31°34'S.,	26°33'E.	3126 Da
Steynsdorp, Transvaal	26°07'S.,	30°39'E.	2630 Ba
Stilbaai, Cape Province	34°22'S.,	21°25'E.	3421 Ad
Strandfontein, Cape Town, Cape Province	34°05'S.,	18°34'E.	3418 Ba

Swellendam/...

Swellendam, Cape Province	34°01'S.,	20°27'E.	3420 Ab
Taaiboschspruit, Vet River, Orange Free State	28°29'S.,	26°41'E.	2826 Bc
Thamalakane River	19°59'S.,	23°25'E.	1923 Cd
Three Anchor Bay, Cape Town, Cape Province	33°54'S.,	18°24'E.	3318 Cd
Tokai, Cape Province	34°03'S.,	18°24'E.	3418 Ab
Travellers Rest, Cape Province	32°04'S.,	19°05'E.	3219 Aa
Tsumeb, South West Africa	19°14'S.,	17°43'E.	1917 Ba
Tulbagh, Cape Province	33°18'S.,	19°09'E.	3319 Ac
Twee Rivieren, Kalahari Gemsbok Park, Cape Province	26°26'S.,	20°38'E.	2620 Bc
Tzaneen, Transvaal	23°50'S.,	30°10'E.	2330 Cc
Ubombo, Natal	27°34'S.,	32°05'E.	2732 Ca
Uitkomst 75, Krugersdorp, Transvaal	25°54'S.,	27°46'E.	2527 Dd
Ukuambi, Ovamboland, South West Africa	17°52'S.,	15°40'E.	1715 Dc
Umtali (station), Southern Rhodesia	18°59'S.,	32°40'E.	1832 Dc
Union's End, C.P.	24°45'S.,	20°00'E.	2420 Cc
Usakos, South West Africa	21°59'S.,	15°35'E.	2115 Dc
Venterskroon, Transvaal	26°53'S.,	27°16'E.	2627 Cd
Vet- and Sand rivers confluence, Orange Free State	28°05'S.,	26°24'E.	2826 Ab
Viljoenskroon, Orange Free State	27°13'S.,	26°57'E.	2726 Bb
Vlakfontein 46, Carolina, Transvaal	26°12'S.,	30°29'E.	2630 Ab
Vogelsvlei, Gouda, Cape Province	33°19'S.,	19°03'E.	3319 Ac
Vryburg, Cape Province	26°47'S.,	24°45'E.	2624Dd
Vumba, Southern Rhodesia	19°07'S.,	32°46'E.	1932 Bb

Wakkerstroom/...

Wakkerstroom, Transvaal	27°21'S.,	30°09'E.	2730 Ac
Warmbad, Carolina district, Transvaal	Exact locality uncertain		
Waterkloof, Pretoria, Transvaal	25°47'S.,	28°15'E.	2528 Cd
Weynek, Warmbad, Transvaal	24° 27'S.,	27°42'E.	2427 Bc.
Welgegund, Rustenburg, Transvaal	Exact locality uncertain		
Windhoek, South West Africa.	22°24'S.,	17°06'E.	2217 Ca
Wilgekuil, Rustenburg, Transvaal	Exact locality uncertain		
Witbank, Transvaal	25°52'S.,	29°13'E.	2529 Cc
Wolmaransstad, Transvaal	27°12'S.,	25°58'E.	2725 Bb
Wolseley, Cape Province	33°25'S.,	19°12'E.	3319 Ac
Woodbush, Transvaal	23°49'S.,	29°54'E.	2329 Dd
Worcester, Cape Province	33°39'S.,	19°25'E.	3319 Cb
Wynberg, Cape Town, Cape Province	24°00'S.,	18°29'E.	2418 Ab
Zesfontein, South West Africa	±19° 'S.,	13° 'E.	1913 Ba
Zimbiti, Mocambique	±19° 'S.,	34° 'E.	1934 Db
Zoetendalsvlei, Cape Province	34°34'.,	19°58'E.	3419 Db
Zoutpan, Transvaal	25°24'S.,	28°06'E.	2528 Ac
Zoutpansberg, Transvaal	±23°00'S.,	30°15'E.	2330 Ab
Zwarthoek 320, Zoutpansberg, Transvaal	23°59'S.,	29°53'E.	2329 Dd
Zwartkops, Pretoria, Transvaal	25°50'S.,	28°10'E.	2528 Cc

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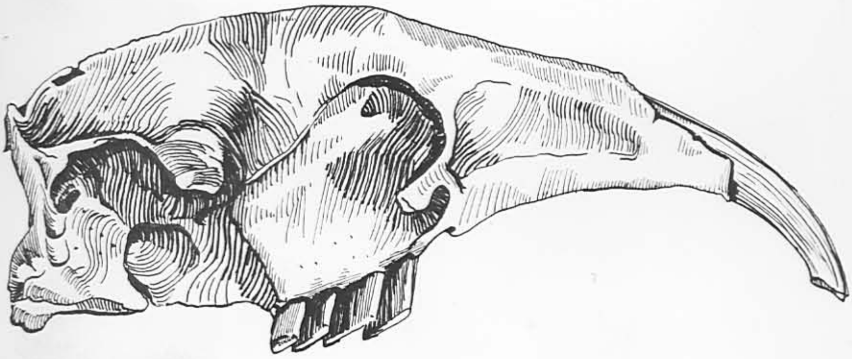

Fig.2.1: Skull of Gypsorhychus makapani, lateral view. x1$\frac{1}{2}$.

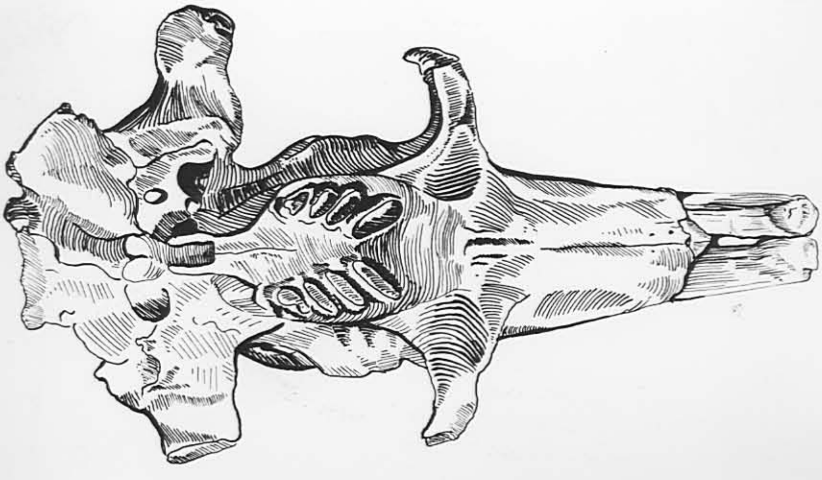

Fig.2.2: Skull of Gypsorhychus makapani, ventral view. x1$\frac{1}{2}$.

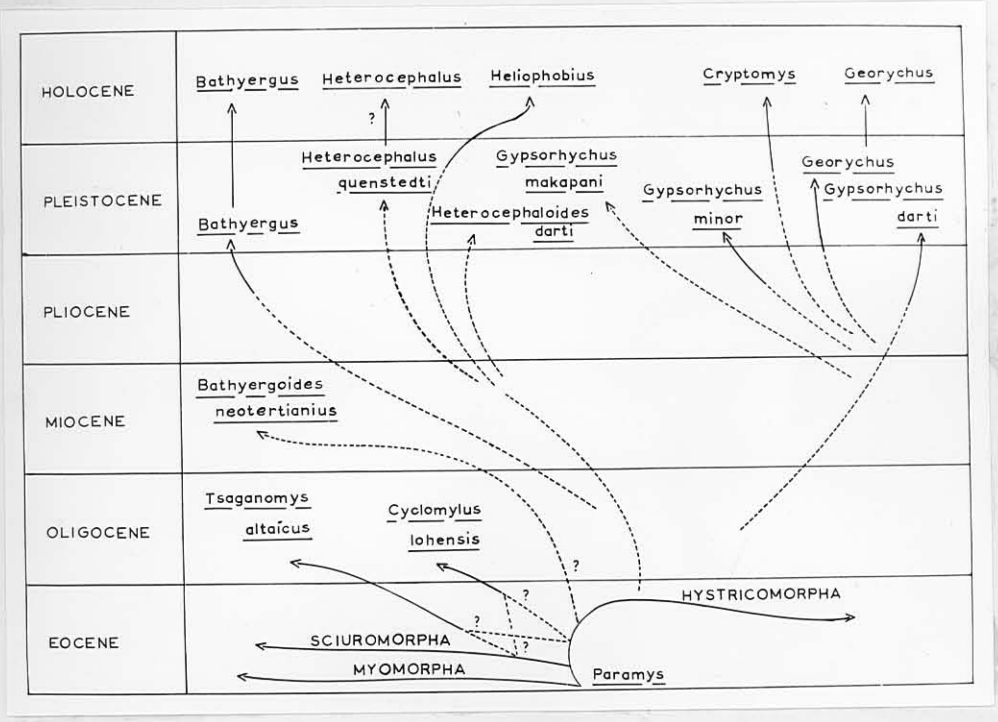

Fig.2.3: Tentative phylogenetic scheme indicating possible relationships between extinct and extant bathyergids.

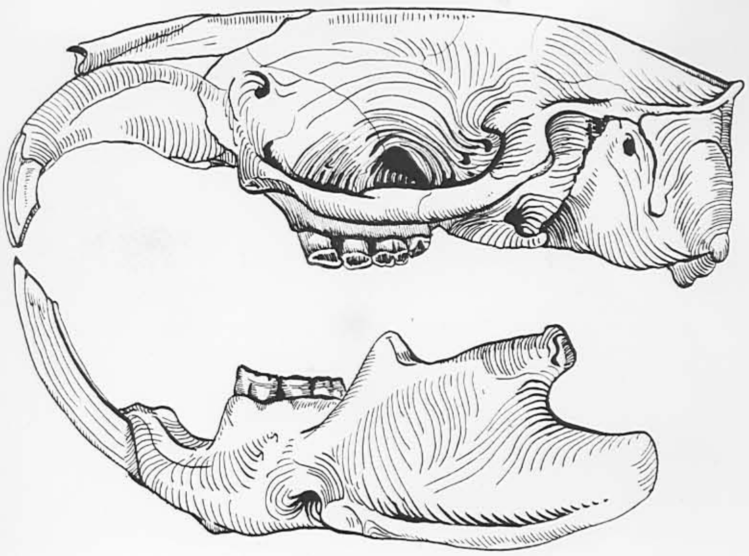

Fig.4.1: Skull of Bathyergus suillus, lateral view, x1½.

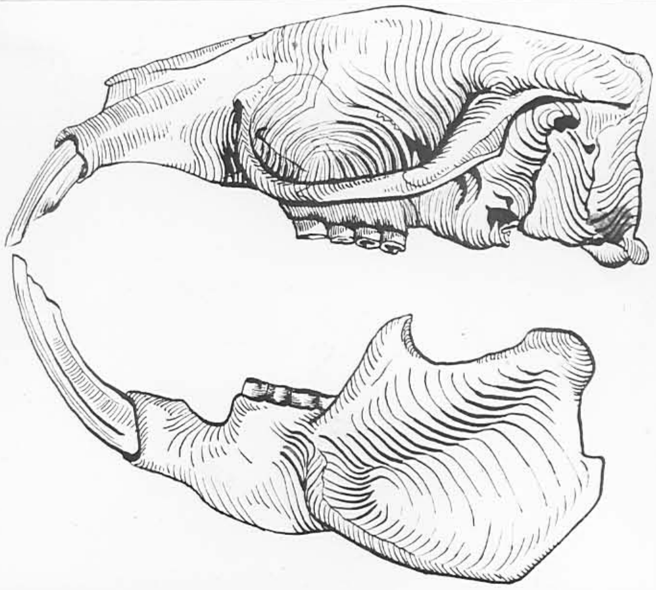

Fig.4.2: Skull of Georychus capensis, lateral view. x1½.

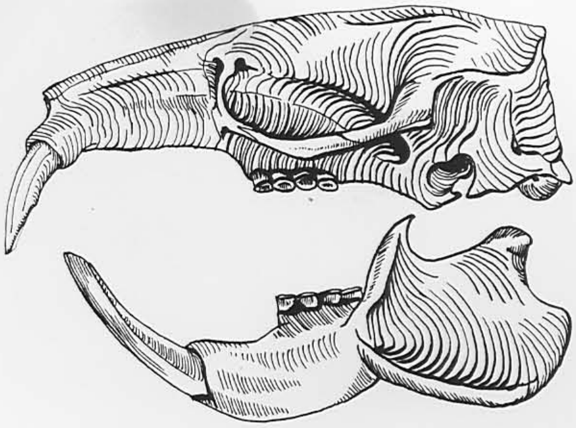

Fig.4.3: Skull of Cryptomys sp., lateral view. x1½.

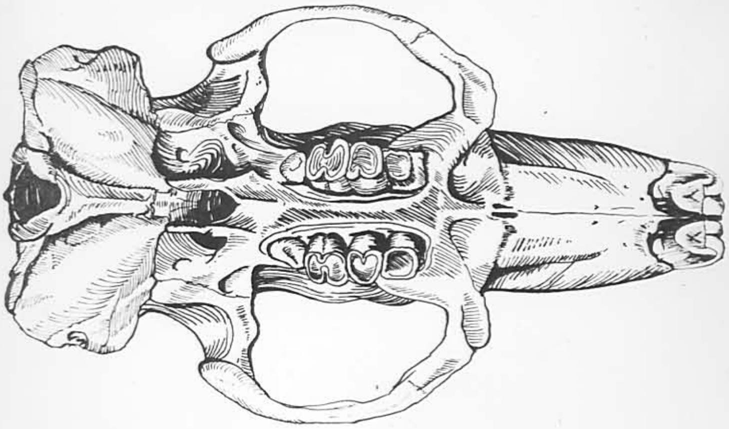

Fig.4.4: Skull of Bathyergus suillus, ventral view. x1½.

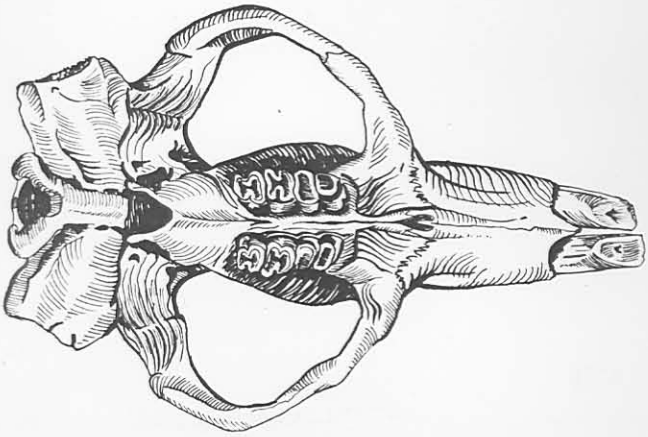

Fig. 4.5: Skull of Georychus capensis, ventral view. x1½.

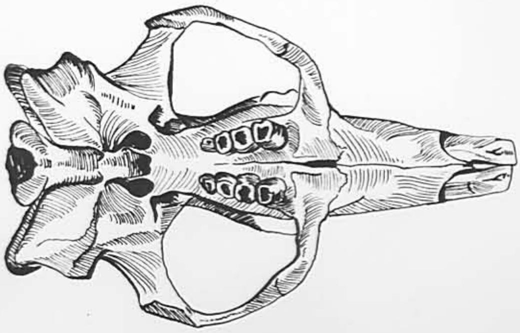

Fig.4.6: Skull of Cryptomys sp., ventral view, x1½.

Fig.6.1: Mole-hills of Cryptomys hottentotus, more or less indicating the direction of the main tunnel. Near Waterpoort, Zoutpansberg district, Transvaal.

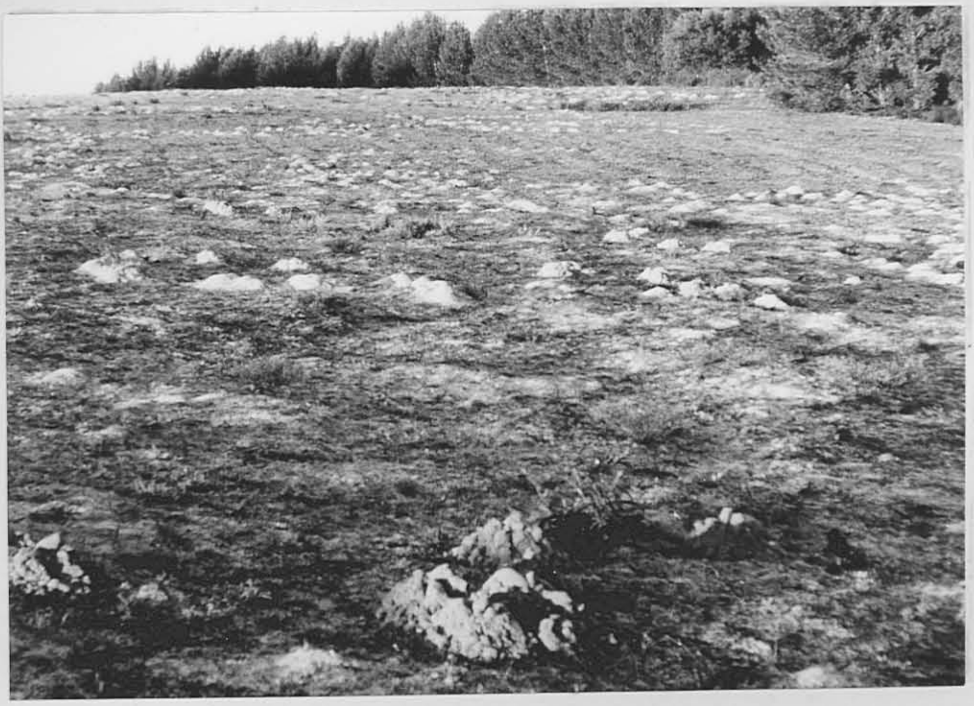

Fig.6.2: Mole-hills of Bathyergus suillus. Fresh heaps in foreground were pushed up during the early morning. Note the vast number of mole-hills on this field. Near Malmesbury, Cape Province.

Fig.6.3: A nest of _Bathyergus suillus_. Note size, shape, depth below surface of the soil and nest chamber. Near Citrusdal, Cape Province.

Fig.6.4: A shield snake, _Aspidelaps scutatus_ trapped in a _Cryptomys_ tunnel. Note remains of hindquarters of a _Cryptomys_ specimen which was regurgitated when the snake was drowned in alcohol after capture. Near Shingwedzi, Kruger National Park.

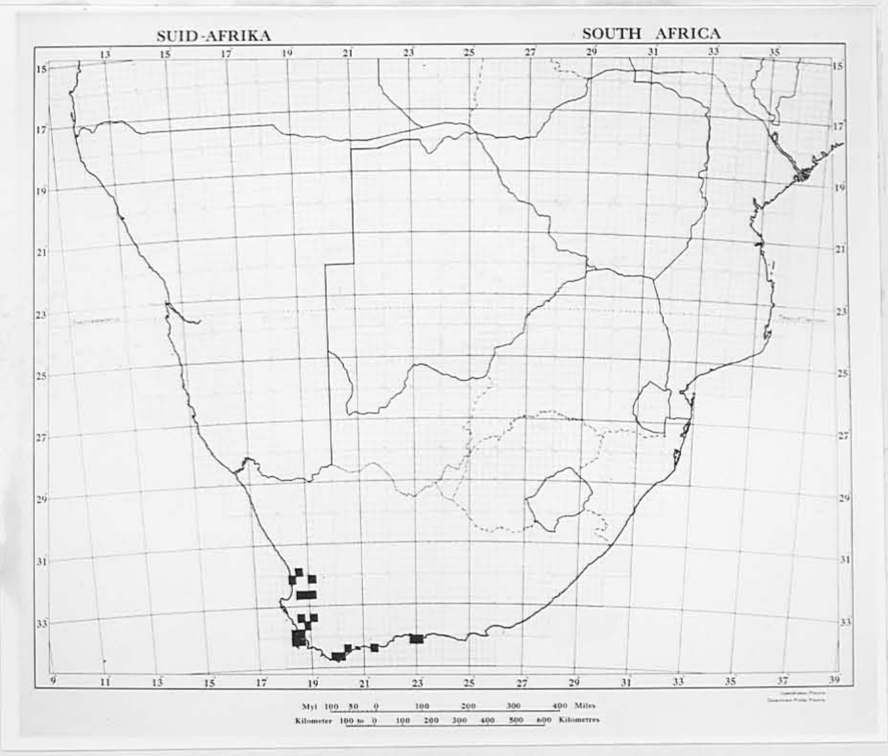

Fig.8.1: Distribution of Bathyergus suillus in Southern Africa.

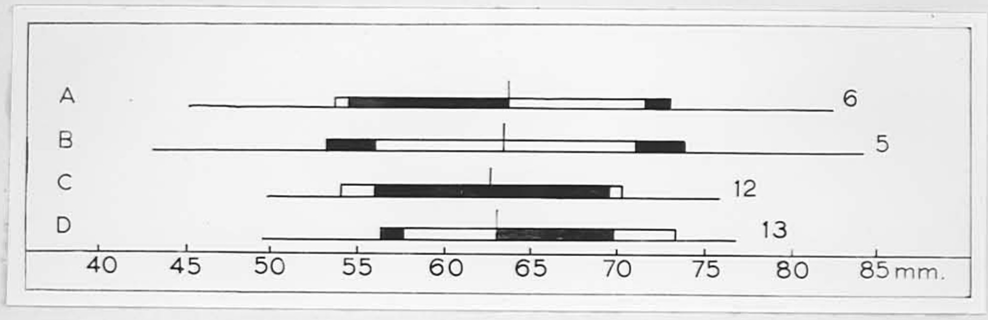

Fig.8.2: Variation in condylo-basal length in Bathyergus suillus from: Cape Town, Mowbray, Greenpoint, Elsies River, Maitland, Belville, Plumstead and Strandfontein (all Cape Peninsula), (A); Knysna (B); Eendekuil, Het Kruis, Kompanjiesdrift, Lambert's Bay (C); and Traveller's Rest (D). (♂♂). Vertical line = arithmetic mean; horizontal line = ± 3 x standard deviation; solid horizontal bar = mean ± 1.5 x standard deviation; open horizontal bar = observed range. Adjacent figures indicate number of observations.

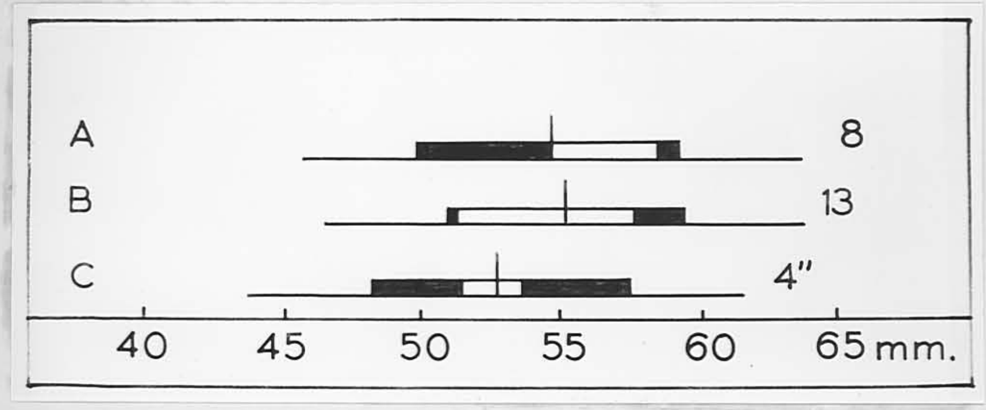

Fig.8.3: Variation in condylo-basal length in *Bathyergus suillus* from: Kompanjiesdrif (A); Traveller's Rest (B); and Klaver (C). S.D. value for Klaver (") inferred. (♀♀). Further explanations as in fig.8.2.

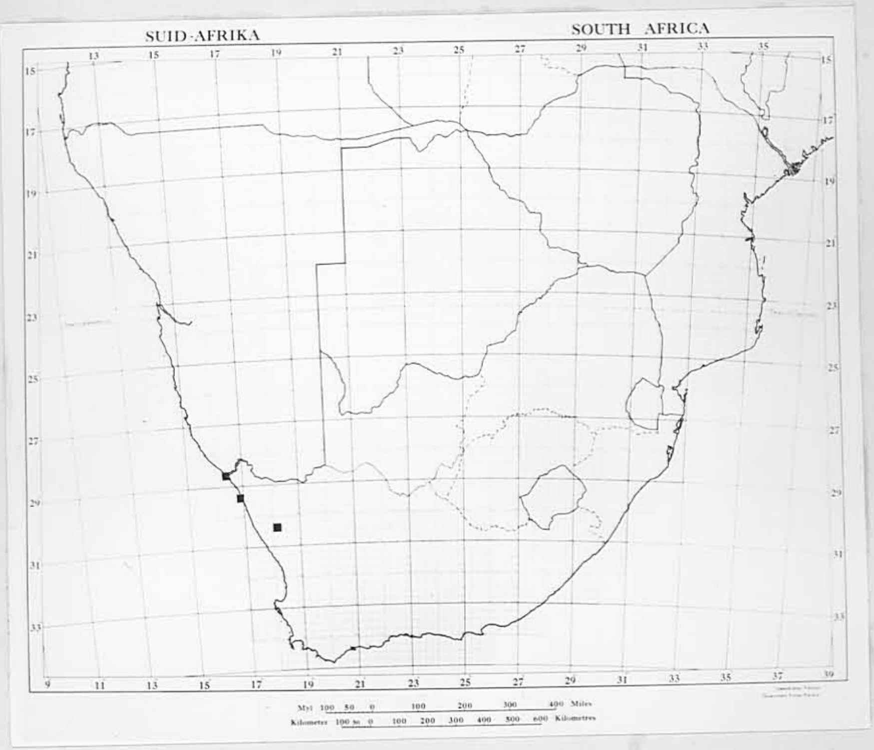

Fig.9.1: Distribution of Bathyergus janetta in Southern Africa.

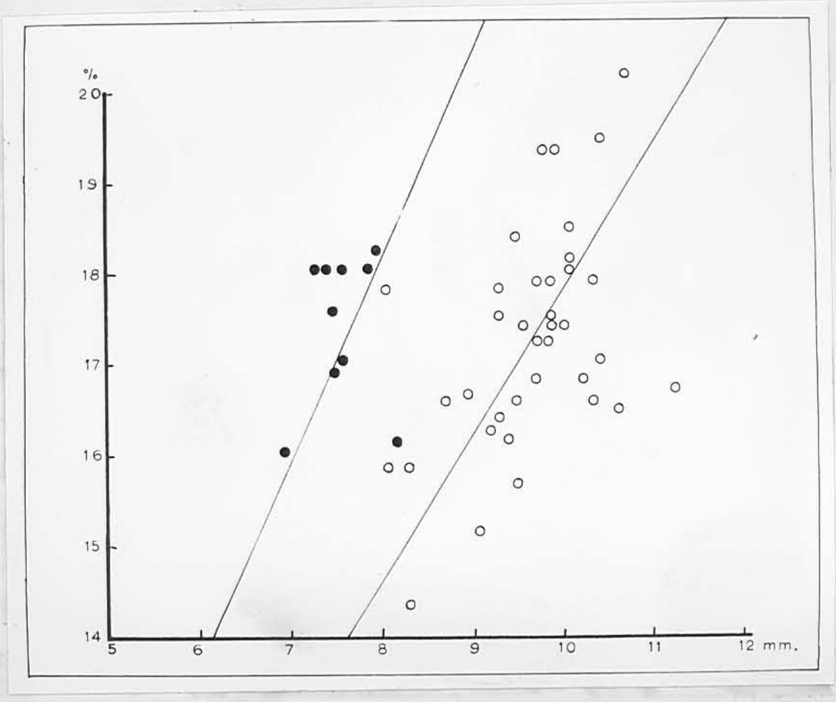

Fig. 9.2: Scatter diagram, showing ratio of upper tooth row (abscissa) plotted against percentage upper tooth row of condylo-basal length (ordinate) in *Bathyergus suillus* (open circles) and *Bathyergus janetta* (solid circles). See text for further explanation.

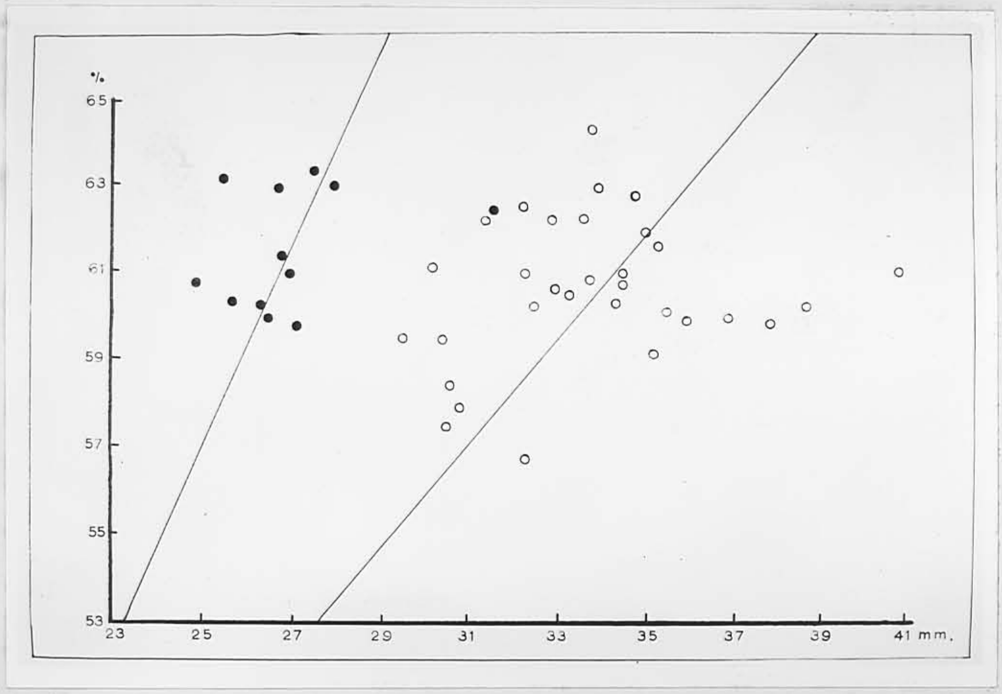

Fig. 9.3: Scatter diagram showing ratio of lower jaw (abscissa) plotted against percentage lower jaw of condylo-basal length (ordinate) in *Bathyergus suillus* (open circles) and *Bathyergus janetta* (solid circles). See text for further explanation.

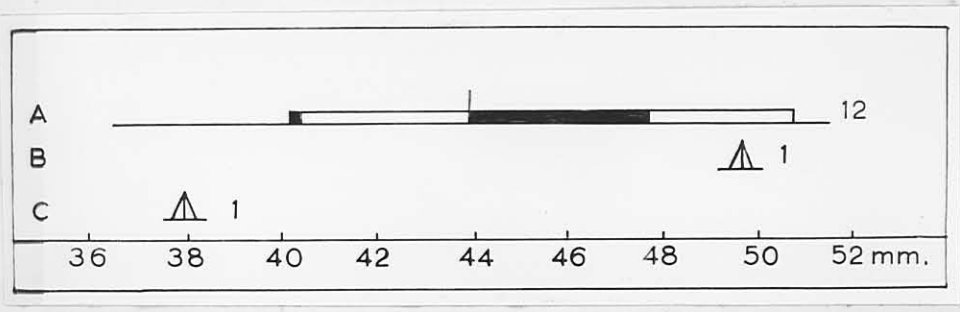

Fig.9.4: Variation in condylo-basal length in *Bathyergus janetta* from: Port Nolloth (*B.j. janetta*) (A); Kamiesberg (*B.j. inselbergensis*) (B); and Oranjemund (*B.j. plowesi*) (C). (♂♂). Further explanations as in fig. 8.2.

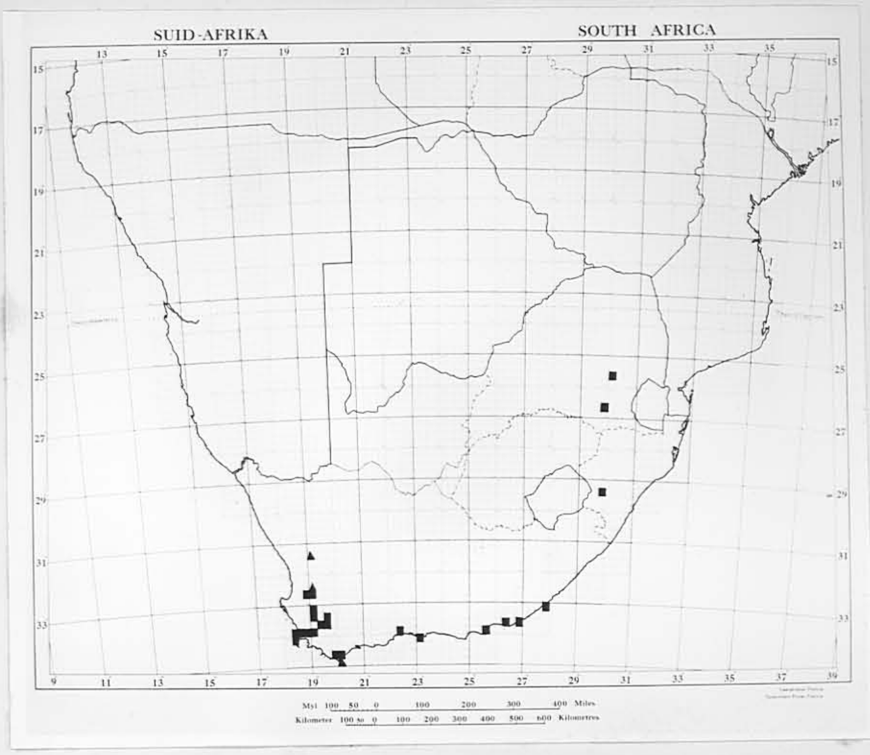

Fig.10.1: Distribution of *Georychus capensis* in Southern Africa. Solid squares : study skins and skulls. Solid triangles : literature records.

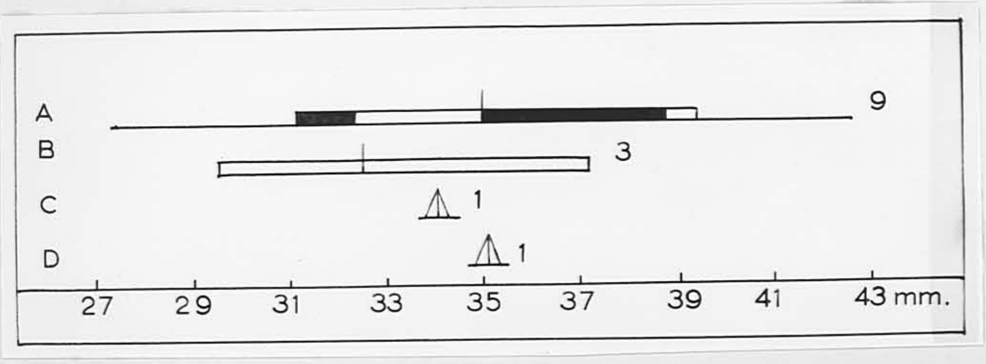

Fig. 10.2: Variation in zygomatic width in *Georychus capensis* from : de Wet, Worcester (A); Knysna (B); Ermelo (C); and Belfast (D). (♀♀). Further explanations as in fig. 8.2.

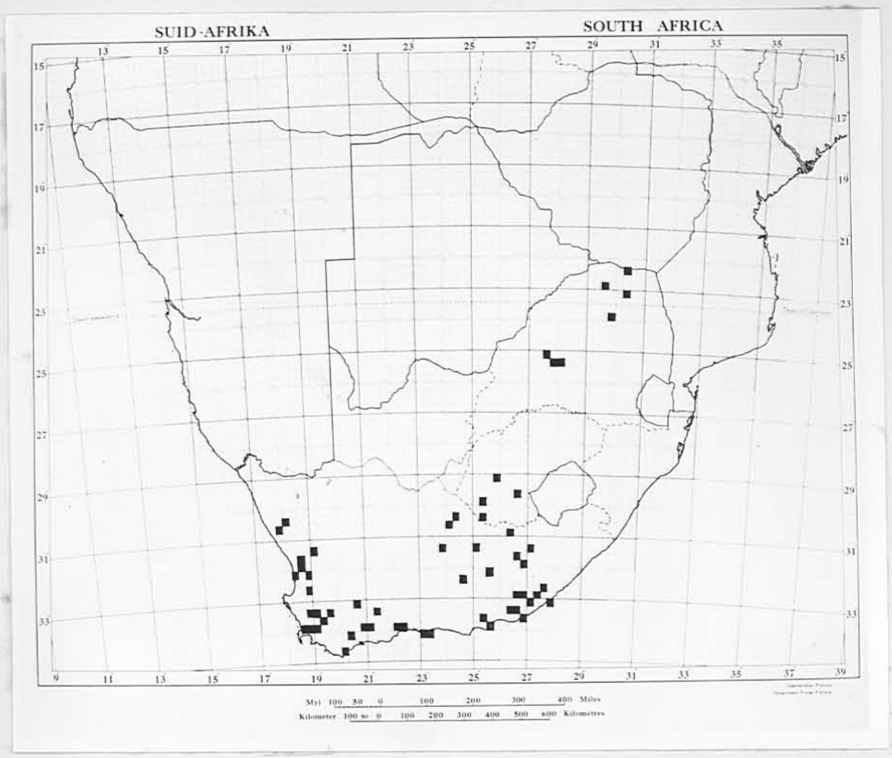

Fig. 11.1: Distribution of *Cryptomys hottentotus* in Southern Africa.

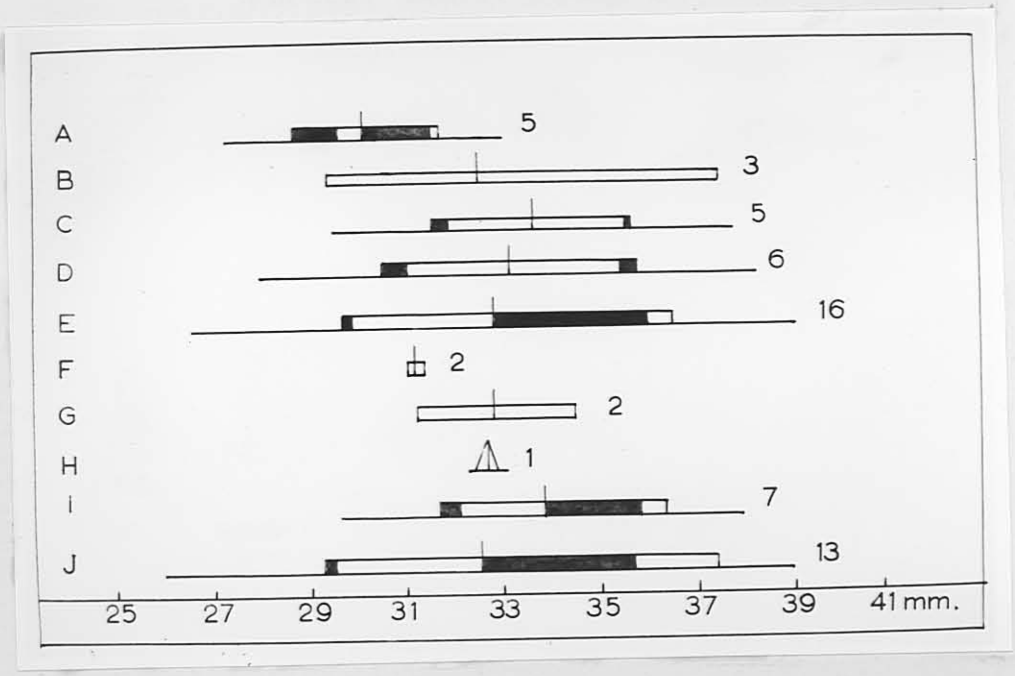

Fig.11.2: Variation in condylo-basal length in *Cryptomys hottentotus* from: Lormarin's, Paarl (A); Wolseley (B); Knysna (C); Port Elizabeth (D); Grahamstown (E); Jericho (F); Zoutpan (G); Fauresmith (H); Mookeetsi (I); and Zwarthoek, Zoutpansberg (J). (♂♂). Further explanations as in fig. 8.2.

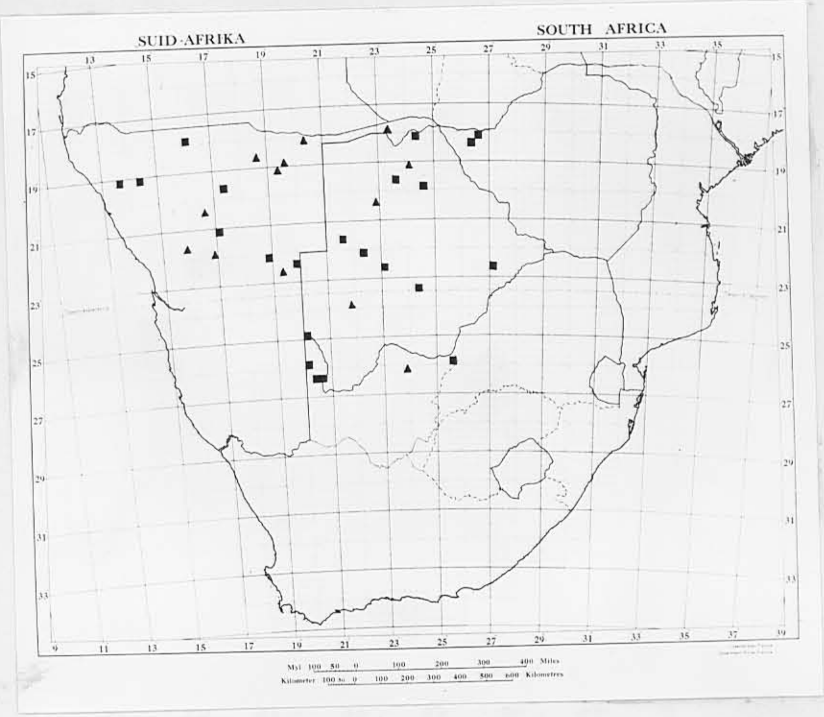

Fig.12.1: Distribution of *Cryptomys damarensis* in Southern Africa. Solid squares : study skins and skulls. Solid triangles : literature records.

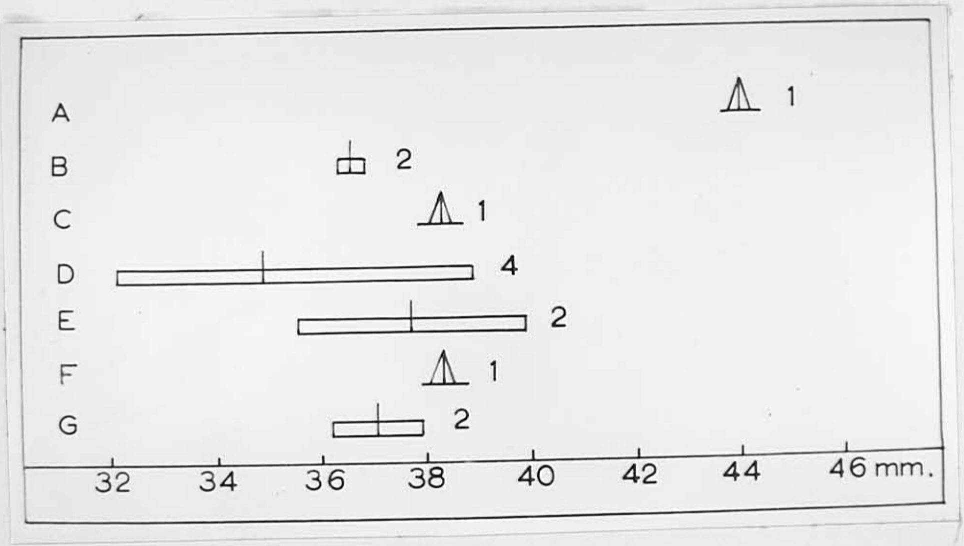

Fig.12.2: Variation in condylo-basal length in *Cryptomys damarensis* from: Kampspanne Road, Kalahari National Park (A); 77 miles east of Maun (B); Damarapan (C); Gobabis (D); Okahandja (E); Ondongwa (F); and Matetsi (G). (♂♂). Further explanations as in fig. 8.2.

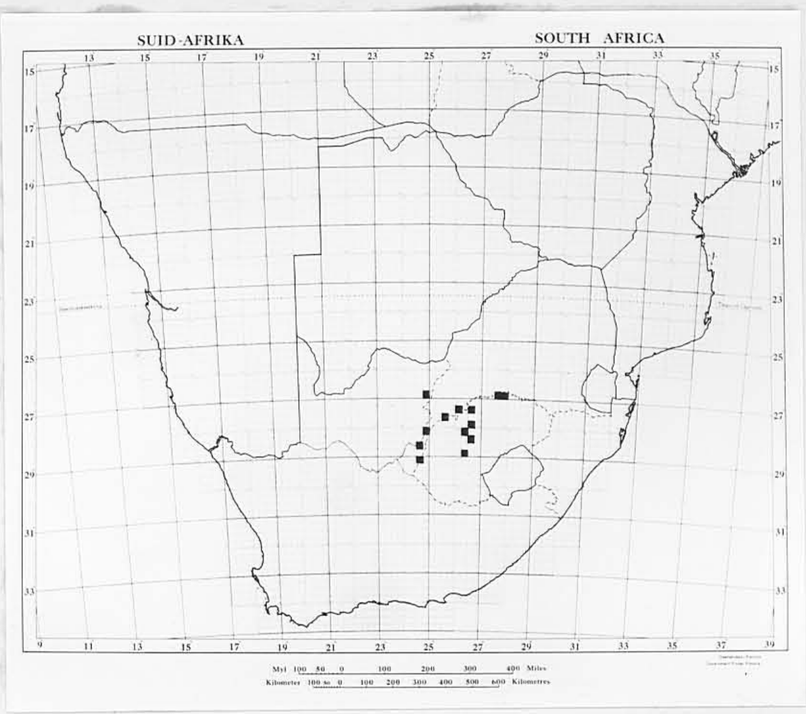

Fig.13.1: Distribution of *Cryptomys holosericeus* in Southern Africa.

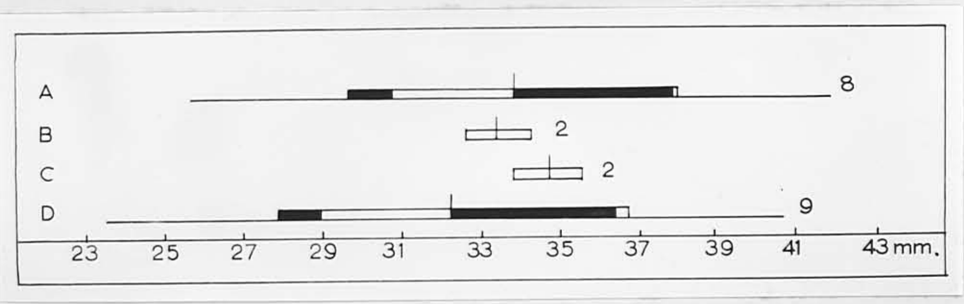

Fig.13.2: Variation in condylo-basal length in *Cryptomys holosericeus* from: Vryburg (A); Bloemhof (B); Glen (C); and Bothaville (D). (♀♀). Further explanations as in fig. 8.2.

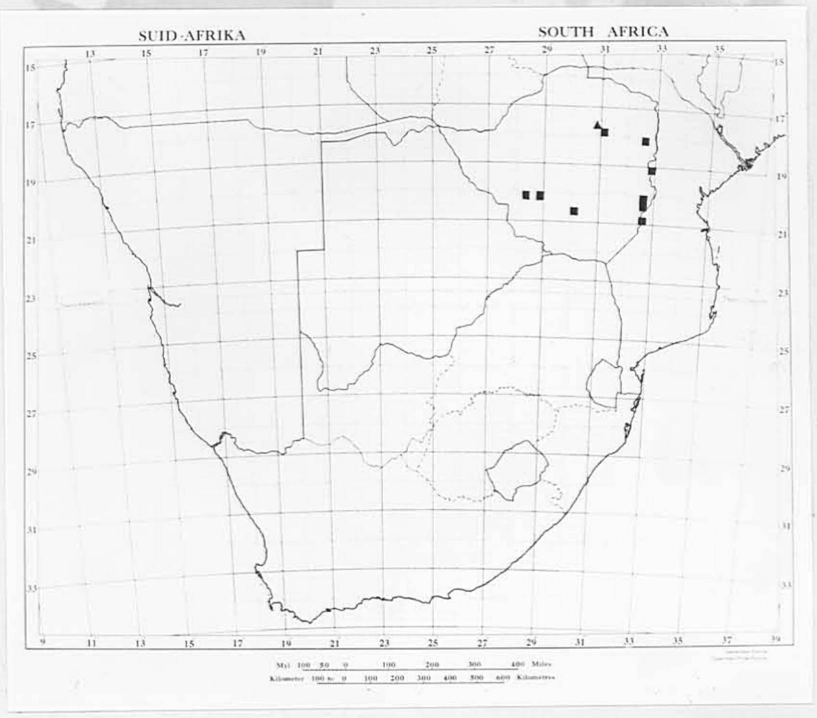

Fig.14.1: Distribution of Cryptomys darlingi in Southern Africa.

Fig.14.2: Variation in condylo-basal length in Cryptomys darlingi from: Mount Selinda (A); Inyanga (B); Matoppos Road (C); Bulawayo (D); Melsetter district (E); and Salisbury (F). (♂♂). Further explanations as in fig. 8.2.

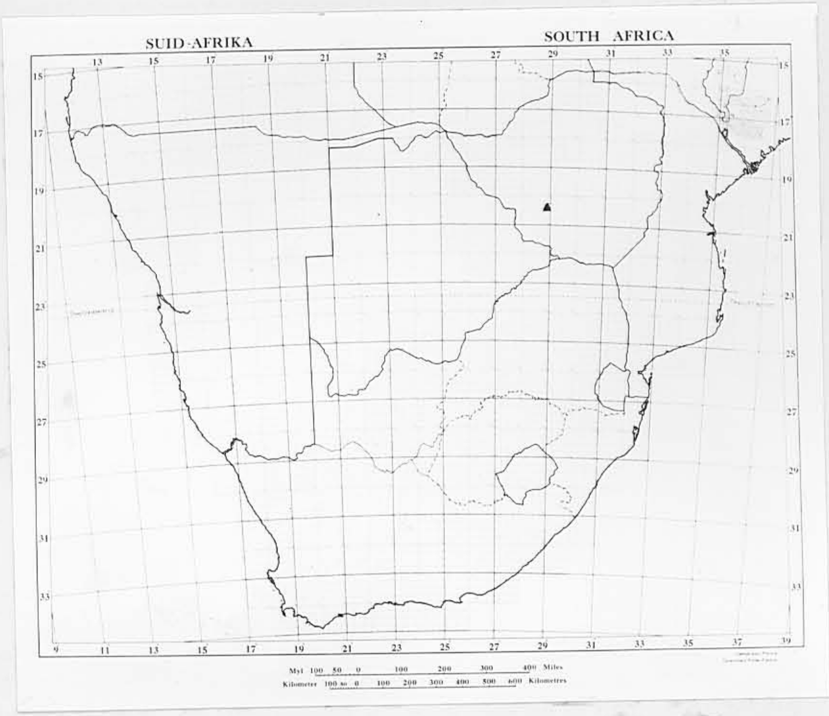

Fig.15.1: Distribution of Cryptomys nimrodi in Southern Africa. Solid triangle, literature record.

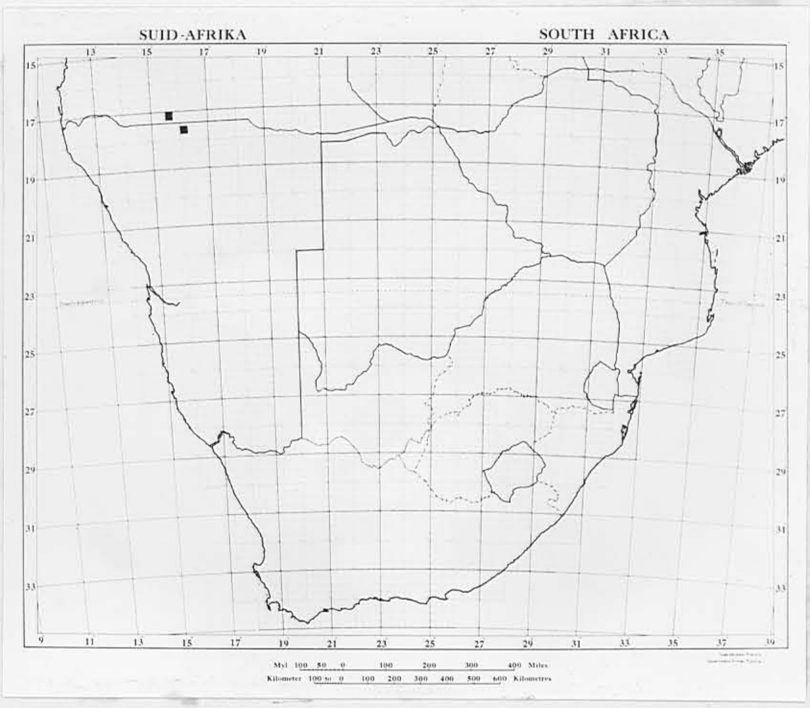

Fig.16.1: Distribution of Cryptomys bocagei in Southern Africa.

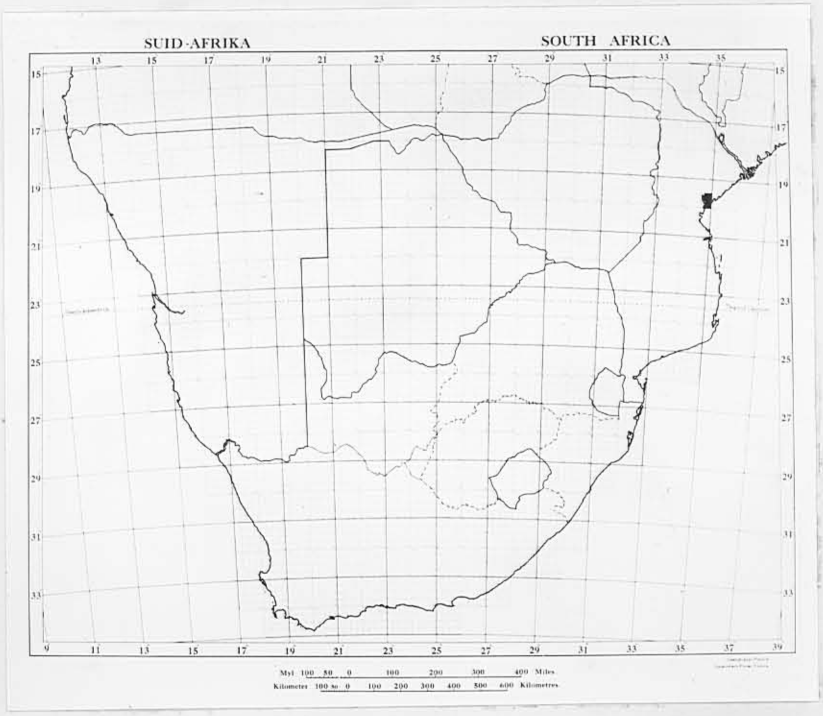

Fig.17.1: Distribution of *Cryptomys beirae* in Southern Africa.

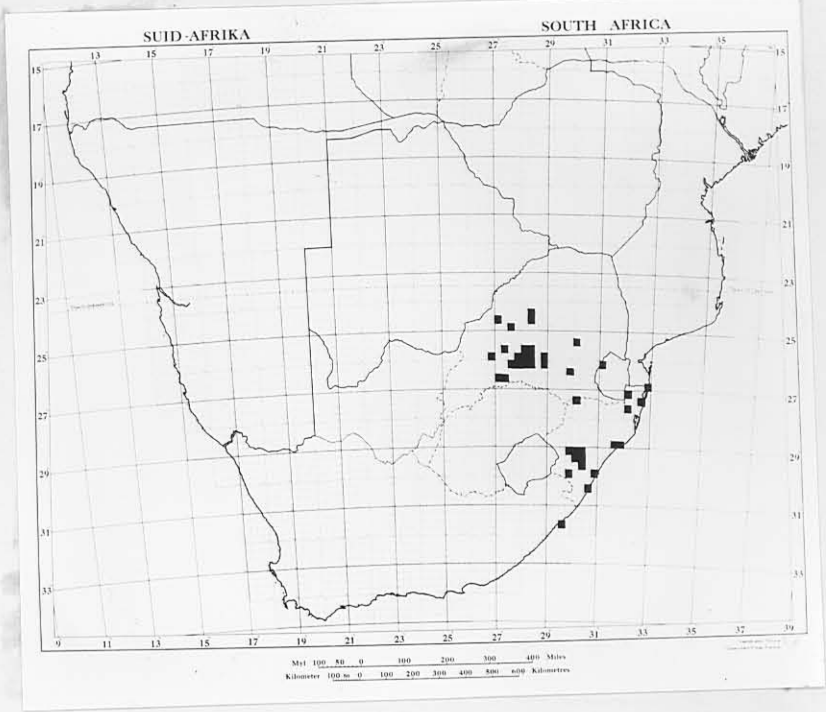

Fig.18.1: Distribution of <u>Cryptomys natalensis</u> in Southern Africa.

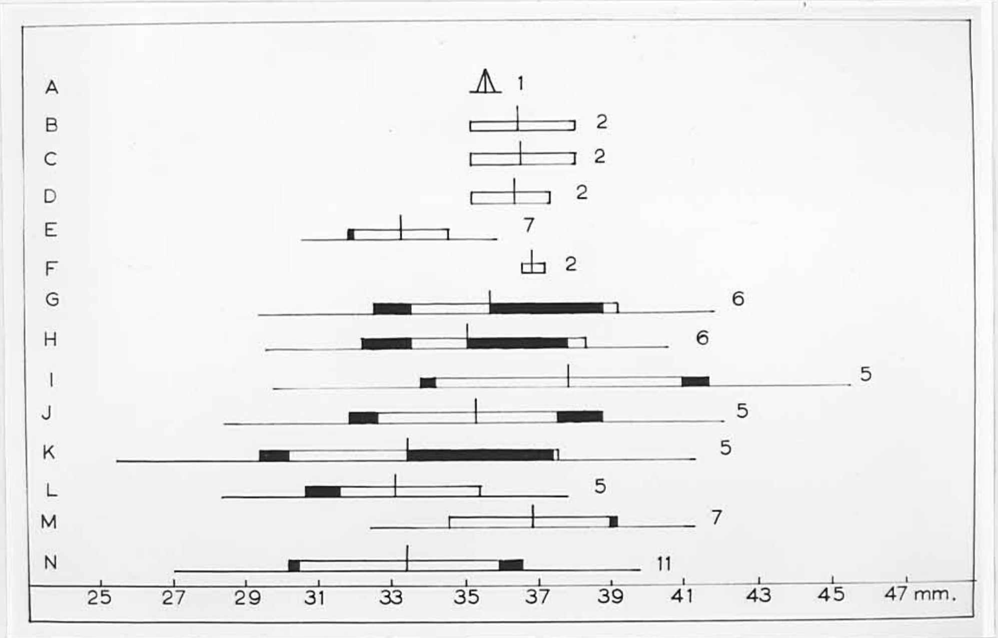

Fig.18.2: Variation in condylo-basal length in <u>Cryptomys natalensis</u> from: Koster (A); Venterskroon (B); Johannesburg (C); Wakkerstroom (D); Forbes Reef (E); Waterkloof (F); Fountains (G); Zwartkops (H); Brooklyn (I); Rosslyn (J); Rietondale (K); Wilgekuil (L); Nylstroom (M); and Pietermaritzburg (N). (♂♂). Further explanation as in fig. 8.2.

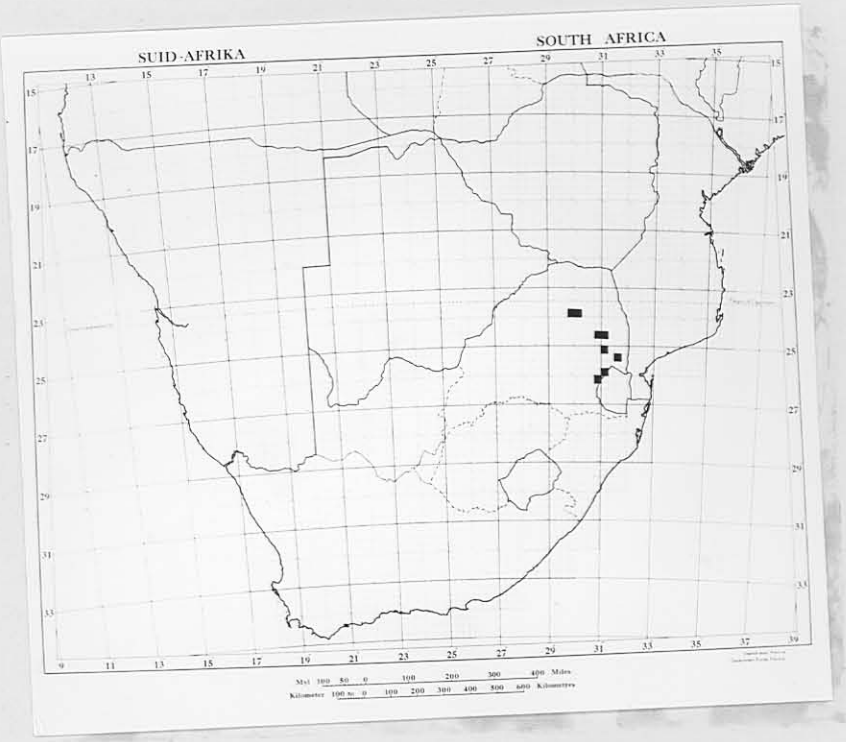

Fig.19.1: Distribution of *Cryptomys komatiensis* in Southern Africa.

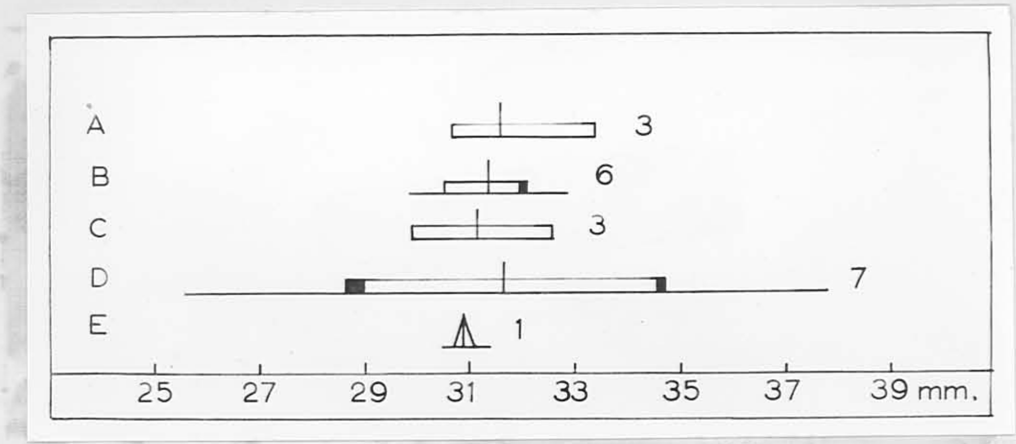

Fig.19.2: Variation in condylo-basal length in *Cryptomys komatiensis* from: Arnhemburg (A); Hektorspruit (B); Acornhoek (C); Mariepskop (D); and Tzaneen (E). (♂♂). Further explanations as in fig. 8.2.

Measurements of *Bathyergus suillus*. ♂ = Male. ♀ = Female. – = Unknown sex.

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Lambert's Bay	♂	273	70	52	63.5	20.7	10.3	40.3	12.5	10.7	36.9	–
	♂	275	67	52	62.4	20.4	10.1	40.7	12.2	9.4	37.4	10.6
	♂	245	48	47	59.8	21.2	10.5	–	12.1	10.3	35.0	–
	♀	223	38	47	54.3	19.7	9.5	35.0	11.0	9.1	32.5	10.9
	♀	204	45	42	49.3	20.0	10.5	33.0	11.1	–	30.1	10.5
Kompanjles-drift	♂	305	54	55	65.5	21.4	10.6	43.8	13.6	10.9	39.5	11.6
	♂	290	52	50	53.8	20.3	9.2	36.3	11.7	10.3	32.0	10.9
	♂	240	55	47	55.7	19.2	9.3	34.0	11.8	–	33.5	–
	♂	315	65	55	66.2	20.4	10.8	43.9	13.6	–	40.7	11.3
	♂	–	–	–	63.8	21.5	10.4	–	13.0	–	38.2	–
	♂ imm.	150	34	33	–	–	–	–	–	–	–	–
	♂ imm.	195	46	39	–	–	–	–	–	–	–	–
	♀♀	256(9) 235-280 S.D.=17.32	54(9) 47-61 S.D.=4.975	47(9) 45-50 S.D.=1.581	54.4(8) 49.6-58.2 S.D.=3.112	20.5(8) 19.5-21.5 S.D.=0.560	10.0(8) 9.7-10.3 S.D.=0.240	36.1(7) 32.8-38.5 S.D.=2.064	11.9(10) 11.0-12.9 S.D.=0.595	9.8(5) 9.4-10.1 S.D.=0.288	32.8(7) 30.3-35.5 S.D.=2.383	10.6(5) 10.1-11.2 S.D.=0.470
	♀ imm.	190	43	40	–	–	–	–	–	–	–	–
	♀ imm.	170	40	36	37.6	18.6	9.3	–	9.2	–	23.5	–
	– –	–	–	–	56.5(20) 46.5-68.1 S.D.=4.888	20.6(23) 19.0-22.3 S.D.=0.904	10.0(25) 9.5-10.8 S.D.=0.308	36.2(20) 29.4-42.6 S.D.=3.620	12.0(25) 9.5-13.7 S.D.=0.999	9.7(22) 9.2-10.5 S.D.=0.390	33.7(23) 26.9-39.1 S.D.=3.088	10.6(20) 9.6-11.7 S.D.=0.570
Traveller's Rest	♂♂	284(16) 225-315 S.D.=23.3	54(16) 25-65 S.D.=10.02	53(16) 46-57 S.D.=2.826	63.7(13) 57.3-72.9 S.D.=4.145	21.2(15) 19.3-23.2 S.D.=1.101	10.5(15) 10.1-11.5 S.D.=0.370	39.8(9) 36.5-46.9 S.D.=1.047	13.5(17) 12.1-14.8 S.D.=0.850	10.3(14) 9.3-11.1 S.D.=0.528	38.5(17) 32.7-45.7 S.D.=3.661	11.0(12) 10.4-11.9 S.D.=0.609
	♂ imm.	205	40	41	–	–	10.9	–	11.3	–	29.0	–
	♂ imm.	200	42	39	42.3	20.2	10.3	28.0	10.6	–	26.2	–
	♂ imm.	170	35	35	–	–	–	–	–	–	–	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	♀♀	261(18) 230-280 S.D.=14.350	49(18) 36-60 S.D.=6.964	48(18) 44-54 S.D.=2.092	55.1(13) 51.2-57.5 S.D.=2.905	20.7(13) 19.8-22.3 S.D.=0.930	10.3(14) 9.8-11.3 S.D.=0.483	35.9(13) 22.2-40.0 S.D.=4.505	12.3(16) 10.6-13.5 S.D.=0.857	9.6(10) 9.2-10.2 S.D.=0.290	34.1(14) 30.4-37.4 S.D.=1.910	10.6(13) 9.9-11.5 S.D.=0.383
	♀ imm.	130	30	30	-	-	-	-	-	-	-	-
	♀ imm.	146	31	34	-	-	-	-	-	-	-	-
Eendekuil	♂	285	35	-	63.6	22.8	11.0	42.0	13.2	10.0	39.4	10.8
	♂	280	40	-	61.1	22.8	10.1	41.7	13.4	9.5	37.3	10.2
	♀	245	35	-	52.2	20.0	9.6	33.6	11.3	9.3	32.9	9.9
Citrusdal	♂	-	-	-	74.4	21.9	10.2	50.3	15.2	-	44.4	-
	♀	246	57	45	57.1	21.0	10.9	35.4	12.1	-	34.5	-
	♀ imm.	164	25	34	-	19.5	10.2	-	10.1	-	24.7	-
	- imm.	142	25	29	-	-	-	-	-	-	-	-
Het Kruis	♂	278	50	-	70.3	22.4	10.2	46.2	14.1	10.8	41.8	11.8
	♂	290	50	53	61.1	20.0	10.7	37.4	12.5	9.3	37.2	10.7
	♂	295	50	50	-	-	-	-	-	-	-	-
	♀	265	50	52	-	-	-	-	-	-	-	-
	--	-	-	-	67.0(5) 59.1-73.9 S.D.=6.370	22.9(5) 20.9-25.2 S.D.=1.581	10.4(5) 10.2-11.0 S.D.=0.327	52.3(5) 37.4-47.3 S.D.=4.677	14.7(5) 13.4-16.3 S.D.=1.139	10.4(5) 10.0-11.1 S.D.=0.452	41.2(5) 36.8-45.0 S.D.=3.242	11.4(5) 10.7-12.2 S.D.=0.674
	- imm.	-	-	-	58.8	21.0	10.0	37.7	12.3	9.5	36.5	-
Tulbaghkloof	♂	236	32	42	53.8	20.8	10.4	35.5	13.4	-	32.3	-
	♂	276	34	52	-	-	-	-	-	-	-	-
	♀	205	30	40	49.6	19.0	10.1	33.0	11.5	-	29.5	-
	♀	213	27	40	53.1	19.9	10.5	35.0	11.1	10.7	32.3	11.2
	♀	275	35	55	61.8	19.9	10.4	40.1	13.4	10.3	36.9	12.0
	♀	230	30	47	54.5	19.6	10.3	36.4	12.1	10.1	33.0	11.2

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Drostdy, Tulbagh	♀	260	35	46	57.7	21.1	9.7	38.4	11.9	10.0	37.1	11.0
Vogelsvlei,	♂	246	34	35	54.9	20.5	10.3	36.0	12.4	10.1	32.6	11.2
Gouda	♂	289	35	54	–	–	–	–	–	–	–	–
	♀	278	27	45	60.3	19.5	9.6	38.6	12.6	9.6	36.0	10.8
Kersfontein	♀	245	35	43	–	–	11.8	35.8	11.8	9.2	31.5	10.9
Malmesbury	♂	–	–	–	65.3	23.2	9.5	40.8	14.3	9.8	38.2	10.6
Elsies Rivier	♀	–	–	–	52.9	–	9.8	–	11.0	10.3	32.9	11.4
Belville	♂	302	18	55	69.8	22.4	10.5	45.7	14.7	–	–	–
	♂	320	30	50	66.5	23.1	10.3	43.4	13.3	10.3	39.5	11.4
	♀	250	43	45	56.9	19.1	10.2	37.3	11.3	9.5	–	–
	♀	270	30	50	57.6	21.0	10.2	36.8	12.3	8.3	–	–
Maitland	♂	262	60	48	61.7	20.8	9.8	–	12.9	10.8	36.7	12.1
	♀	250	55	48	63.5	20.5	9.7	41.2	13.0	–	37.9	12.1
	♀ imm.	185	35	41	46.7	18.6	9.8	28.3	11.3	8.4	27.9	8.8
	♀ imm.	200	40	44	49.7	19.9	10.3	32.8	11.0	9.5	26.9	10.8
Hazendal	♂	–	–	–	71.4	20.9	10.4	47.0	15.1	10.0	41.4	11.2
Cape Town	♂	199	34	41	–	20.9	10.6	36.1	13.1	9.9	39.0	11.9
	♀	138	45	30	–	–	11.7	45.5	13.9	10.9	33.3	11.4
Greenpoint	♀	–	–	–	66.9	21.8	10.4	45.0	14.4	11.2	40.8	12.5
Mowbray	♀	–	–	–	59.6	20.2	–	37.4	11.9	9.1	35.2	10.2
Cape Flats	♂	–	–	–	–	22.6	9.3	45.5	13.3	10.4	–	–
Koeberg	♂	235	32	44	53.5	20.4	9.4	35.2	10.6	10.2	30.9	–
	♀	240	44	51	–	–	–	–	–	–	–	–
Plumstead	–	–	–	–	–	–	9.9	–	12.2	10.5	35.9	11.8

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Strandfontein	♂	–	–	–	65.9	21.4	10.4	–	13.9	10.8	39.6	12.0
	♀	–	–	–	55.3	20.0	9.4	36.5	10.5	9.9	33.6	–
Zoetendalsvlei	♂	330	63	56	72.6	21.1	11.2	46.9	14.3	11.0	42.3	12.3
	♀	300	40	52	61.1	20.6	10.5	38.1	13.5	10.4	35.8	11.8
Bredasdorp	♂	290	40	50	–	22.9	–	–	–	10.5	42.1	12.8
De Hoop	–	–	–	–	69.0	21.8	11.4	46.8	15.1	10.6	–	–
Stilbaai	♂	270	55	48	58.2	20.9	10.2	38.6	12.8	10.4	36.4	11.4
	♀	245	50	46	54.1	19.9	9.4	35.5	11.9	9.7	34.0	10.9
	♀	260	50	50	56.7	20.8	9.5	–	12.1	9.8	34.5	–
Knysna	♂	259	41	46	63.3(5)	20.4(5)	9.8(5)	41.4(5)	13.8 (5)	10.4	38.2(5)	11.4(5)
					56.2-71.2	19.5-21.3	9.6-10.1	35.9-45.8	12.9-16.1	10.9	34.0-43.5	11.0-11.8
	♂	–	–	–	S.D.=6.768	S.D.=0.707	S.D.=0.790	S.D.=4.255	S.D.=1.415	10.5	S.D.=3.852	S.D.=0.310
	♂	–	–	–								
	♂	–	–	–						10.1		
	♂	–	–	–						–		
	♀	207	31	30	45.5	19.6	10.0	29.8	11.5	8.1	27.8	–
	♀	267	40	–	57.9	20.3	9.9	39.0	12.7	10.4	34.6	11.4
	♀	–	–	–	64.2	21.5	10.1	–	14.0	10.6	38.6	12.6
	–	–	–	–	58.8	19.8	10.0	37.2	12.3	10.5	35.7	11.5
	–	–	–	–	56.9	19.9	10.1	37.2	13.0	10.6	34.3	11.2
Belvedere,	♂	–	–	–	57.1	19.5	10.0	37.1	13.1	–	35.2	12.2
Knysna.	♂	–	–	–	54.6	18.7	10.0	34.0	12.5	–	32.9	11.6
	♂	–	–	–	60.3	22.3	10.1	34.9	13.6	–	36.9	10.8
	♀ Imm.	–	–	–	46.1	19.9	10.0	–	11.0	–	27.7	–

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Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Klaver	♂	258	43	45	60.5	19.7	10.0	37.9	12.2	8.4	34.3	9.9
	♀	190	48	40	52.4	19.1	8.8	32.6	11.1	8.7	30.6	9.6
	♀	203	40	45	51.1	18.3	9.4	32.0	11.0	8.1	30.4	9.2
	♀	210	40	40	53.1	18.9	9.5	34.0	12.1	9.3	30.5	10.0
	♀	230	65	48	53.1	19.3	9.6	33.1	11.9	8.4	30.7	9.3
	♀ Imm.	180	48	40	44.0	13.5	9.8	29.3	10.2	-	26.9	10.0

Measurements of *Bathyergus janetta*

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Port Nolloth	♂♂	205(9)	47(9)	41(9)	51.9(5)	18.4(6)	9.4(9)	31.2(6)	10.3(9)	8.2(6)	30.3(9)	8.8(6)
		170-235	41-52	38-43	41.1-54.8	16.7-19.5	8.9-10.2	26.5-37.2	8.9-12.5	7.5-9.1	21.4-34.6	8.2-9.7
		S.D.=21.500	S.D.=2.958	S.D.=1.803	S.D.=9.650	S.D.=1.074	S.D.=1.279	S.D.=4.420	S.D.=3.280	S.D.=0.521	S.D.=3.701	S.D.=0.519
	♀♀	183(10)	44(10)	37(10)	43.9(12)	17.9(11)	9.2(13)	28.4(11)	9.2(15)	7.6(11)	26.8(13)	8.3(10)
		170-206	40-50	34-40	40.4-50.7	17.2-18.8	8.8-9.6	26.5-33.8	8.6-10.8	7.0-8.2	25.4-31.6	7.6-9.2
		S.D.=11.640	S.D.=2.539	S.D.=2.119	S.D.=2.549	S.D.=0.564	S.D.=0.070	S.D.=1.944	S.D.=0.574	S.D.=0.335	S.D.=1.679	S.D.=0.440
	♀	187	38	34	-	-	-	-	-	-	-	-
	--	-	-	-	44.0(67)	18.3(71)	9.2(79)	28.5(56)	8.4(84)	7.7(55)	26.7(78)	8.6(58)
					35.0-58.5	16.5-20.9	8.4-10.1	23.1-39.2	7.9-12.2	6.3-9.2	20.9-35.4	7.1-10.2
					S.D.=5.187	S.D.=0.755	S.D.=0.098	S.D.=7.777	S.D.=2.719	S.D.=0.667	S.D.=4.338	S.D.=0.686
Ezelfontein	♂	280	52	51	-	-	-	-	-	-	-	-
	♂	200	44	41	41.7	18.8	9.3	28.3	9.5	-	25.9	-
	♀	235	46	41	-	18.8	8.5	-	-	9.3	-	10.0
	♀	230	44	45	49.5	18.9	8.9	33.3	10.5	9.4	31.1	9.5
Oranjemund	♂ Imm.	-	-	-	35.9	17.9	8.8	23.0	8.1	6.0	22.4	7.3
	♀	-	-	-	37.9	18.5	8.8	-	8.5	7.0	24.1	7.7

Continued/...

Measurements of Georychus capensis

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Grey's Pass	♀	160	20	26	43.5	16.0	9.4	31.2	9.1	7.5	29.1	8.1
Tulbagh	♀	-	12	30	46.2	17.5	9.2	36.1	9.6	8.2	32.7	8.1
	-	-	18	32	47.9	17.6	9.0	34.9	9.7	7.8	32.7	8.6
Drostdy,	♀	187	18	27	48.0	17.0	9.4	35.7	9.5	8.0	33.4	7.7
Tulbagh	♀	145	20	20	45.0	17.9	9.4	36.4	9.6	7.8	-	8.6
de Wet, Worcester	♂♂	193(7)	29(10)	32(10)	48.3(7)	17.8(8)	9.6(10)	36.6(9)	10.6(10)	8.1(10)	33.7(10)	8.0(7)
		185-200	20-40	30-35	45.6-51.0	17.2-18.8	9.0-10.5	32.1-39.9	8.7-11.8	7.3-9.4	29.8-38.0	7.6-8.6
		S.D.=20.820	S.D.=19.520	S.D.= 5.426	S.D.=3.101	S.D.=0.557	S.D.=1.311	S.D.=2.850	S.D.=3.272	S.D.=1.814	S.D.=2.568	S.D.=1.193
	♀♀	192(10)	28(10)	31(10)	47.5(10)	17.6(10)	9.6(10)	35.0(9)	10.0(10)	8.4(6)	32.5(10)	
		180-200	33-38	30-35	44.6-51.2	16.1-19.1	9.0-10.3	32.2-39.3	9.0-11.7	6.8-8.5	30.4-36.1	-
		S.D.=24.58	S.D.=16.92	S.D.=5.207	S.D.=2.528	S.D.=3.013	S.D.=1.433	S.D.=2.526	S.D.=0.953	S.D.=1.666	S.D.=2.150	
Worcester	-	-	-	-	47.6	17.3	9.1	36.3	9.6	7.7	33.2	8.4
Wolseley	♂	-	-	-	44.1	17.0	9.3	32.6	8.9	8.0	30.9	8.5
	♀	170	20	30	42.2	17.0	9.2	30.3	8.4	7.7	28.5	7.5
	♀	-	-	30	43.4	17.1	9.5	30.1	8.8	7.8	30.4	8.2
Tulbagh	♀	204	20	29	-	19.6	9.9	36.9	10.2	8.2	37.0	8.8
de Doorns	♂	-	-	-	52.0	18.3	9.0	39.1	11.6	6.6	36.9	7.5
Stellenbosch	♂	-	-	-	53.3	18.2	9.5	39.5	11.1	7.6	36.5	-
Cape Flats	♀ imm.	60	10	29	38.4	16.3	8.6	26.9	7.4	6.3	26.1	-
Cape Town	♀	150	21	24	44.2	16.7	8.6	32.7	9.4	-	31.7	7.4
	♀ imm.	-	-	-	42.6	17.1	9.3	30.2	9.2	7.4	30.5	-
	♀ imm.	150	21	27	41.9	17.1	8.8	29.3	.8.5	6.6	27.6	6.2
Camps Bay	♀	170	30	28	38.9	16.2	8.6	26.8	7.3	-	25.7	-
	♀ imm.	135	25	26	38.1	15.4	8.5	-	7.5	-	25.9	-
	-	-	-	-	47.1	17.0	9.6	36.5	9.9	7.0	32.6	6.2

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Three Anchor Bay	♀	155	27	27	41.1	17.3	9.1	28.8	8.6	6.8	28.2	7.2
Belville	♂	153	23	26	40.5	16.2	9.1	28.2	7.8	–	26.8	7.2
Goodwood	♀	–	–	–	–	–	–	–	–	–	28.5	6.6
Maitland	♀	143	25	28	41.0	16.4	8.3	29.3	8.3	–	28.4	7.6
	♀	162	28	28	44.8	16.9	9.0	31.0	8.5	7.2	29.8	7.2
	♀ imm.	145	31	28	39.0	16.3	9.6	29.7	8.1	–	26.8	–
	♀ imm.	146	28	27	38.9	16.7	8.8	27.0	7.7	–	26.5	–
Constantia	♀	–	–	–	39.8	16.2	–	–	8.4	7.1	26.9	7.8
Newlands	–	158	–	–	38.2	–	9.2	–	7.9	7.7	26.4	7.3
	– imm.	–	–	–	46.4	17.0	–	34.5	9.6	–	31.2	–
Dieprivier	♀	–	–	–	52.7	20.3	10.0	40.4	11.5	–	37.8	7.9
Paarl	♂	–	–	–	48.2	18.4	9.1	36.0	10.1	7.9	33.6	8.4
	♀	150	33	27	43.1	16.2	9.3	29.3	8.2	7.5	28.6	7.3
	♀ imm.	142	23	27	–	15.5	8.5	26.6	7.6	–	27.0	–
	♀ imm.	133	24	25	36.6	15.8	8.6	26.0	7.6	–	24.7	–
	–	–	–	–	48.3	17.7	9.2	36.9	10.1	8.0	34.0	8.3
	– imm.	–	–	–	39.4	15.7	8.9	–	8.2	–	29.1	–
Zoetendalsvlei	♀	157	26	25	41.2	16.5	9.5	29.7	8.8	6.4	27.9	6.7
	♀	155	28	26	40.5	15.8	8.9	29.1	8.8	6.9	26.2	7.5
	– imm.	87	20	19	26.5	13.7	7.9	18.0	5.1	–	–	–
George	♀	170	25	31	44.3	16.7	9.4	–	9.2	6.7	29.9	7.0
	– imm.	152	25	30	41.6	17.7	9.2	31.8	8.4	–	28.2	–
Knysna	♀	177	15	27	43.0	17.2	9.7	31.1	9.2	8.1	28.6	8.3
	♀	172	18	27	39.0	16.2	9.0	29.5	8.4	7.7	26.2	8.7
	♀	–	13	28	47.3	19.0	10.0	37.2	10.8	7.5	33.9	8.0
	♀	199	25	29	–	–	–	–	–	–	–	–
	♀ imm.	109	12	21	–	–	–	–	–	–	–	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Port Elizabeth	♂	-	-	-	49.6	18.9	10.3	38.4	11.9	7.7	35.0	8.1
	♂	-	-	-	-	-	-	31.2	10.3	-	-	-
	♂	171	-	-	40.4	16.4	9.5	30.0	9.3	7.0	-	-
	♂ imm.	157	21	28	41.0	16.6	9.5	30.3	9.7	-	27.4	-
	♀♀	-	-	-	-	-	-	30.3(5)	9.3(6)	-	-	-
								27.9-31.7	8.9-10.0			
								S.D.=4.738	S.D.=1.367			
Alexandria	♂ imm.	75	13	20	-	-	-	-	-	-	-	-
	♀	155	20	32	43.3	17.0	9.3	32.7	10.2	7.2	-	8.1
	♀ imm.	-	-	-	42.1	16.6	9.5	31.7	9.6	-	-	-
	-	-	-	-	-	-	-	-	9.1	6.4	-	7.4
	- imm.	75	15	20	-	-	-	-	-	-	-	-
Ermelo	♀	180	23	31	45.3	18.5	10.2	34.6	10.1	7.9	32.6	8.9
Belfast	♂	170	-	-	-	-	-	-	8.7	7.2	29.5	8.1
	♂	180	25	32	46.1	19.3	9.4	35.1	9.8	8.2	32.2	-

Measurements of Cryptomys hottentotus

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Lormarin's,	♂	114(5)	21	21(5)	30.2(5)	13.5(5)	6.4(5)	20.8(5)	5.7(5)	5.5	19.6(5)	5.0(5)
Paarl	♂	105-125	25	21-22	29.7-31.7	13.2-13.9	6.3-6.7	20.0-23.3	5.4-6.4	4.7	18.8-21.2	4.7-5.7
	♂	S.D.28.210	-	S.D.=0.547	S.D.=0938	S.D.=0.246	S.D.=0.179	S.D.=1.392	S.D.=0.415	-	S.D.=0.960	S.D.=0.403
	♂		25							-		
	♂		22							5.3		
	♀	103	24	21	28.9	13.4	6.6	-	5.0	-	18.0	-
	♀	120	24	21	32.7	14.1	6.6	22.9	6.2	5.5	21.3	5.1
	♀	115	22	22	31.0	13.5	6.3	21.1	5.3	4.8	20.4	4.7

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Belville	♂	103	20	22	31.7	14.2	7.1	22.1	6.4	5.5	21.1	5.2
	♂	108	26	21	–	–	–	–	–	–	–	–
	♀	108	20	20	31.6	13.8	6.8	22.3	6.0	5.0	21.3	4.7
	♀	110	23	20	–	–	–	–	–	–	–	–
	♀	103	18	21	30.6	14.5	6.9	22.3	5.9	5.1	20.0	4.9
	♀ imm.	84	25	20	28.0	13.4	6.5	–	5.4	–	18.4	5.2
Stellenbosch	♂ imm.	80	15	18	25.6	13.0	7.0	–	4.7	–	16.0	–
	♂ imm.	85	15	20	24.9	12.5	6.2	16.5	4.5	–	16.9	–
	♀	101	15	20	29.7	13.7	6.7	21.4	5.7	–	19.3	5.6
	♀	100	15	20	30.4	14.2	6.5	22.0	5.7	5.1	19.6	5.0
Riebeeck Kasteel	♂	–	–	–	30.4	13.3	6.1	19.8	5.8	4.9	20.1	–
Tulbagh	♂	–	–	18	28.0	12.6	6.5	19.2	5.3	4.7	18.0	5.0
	♂	130	10	20	29.3	13.8	6.5	20.0	5.3	–	18.0	4.8
	–	130	15	20	33.8	14.0	7.0	24.3	6.2	5.1	22.6	4.9
De Doorns	♀	–	–	–	32.4	13.7	6.7	22.2	5.7	5.4	21.5	5.4
Wolseley	♂	145	14	20	31.1	13.9	6.7	21.9	6.6	4.9	19.7	4.9
	♂	150	15	22	37.5	14.0	6.7	25.6	7.2	5.5	24.0	5.5
	♂	110	15	20	29.4	14.0	6.5	21.8	5.7	–	19.4	5.2
	♂ imm.	82	10	15	21.1	11.1	6.4	14.2	4.1	–	12.9	–
	♀	155	15	22	36.4	13.9	6.5	25.3	6.7	–	24.1	4.6
	♀	110	20	22	29.2	14.6	6.6	20.6	5.2	–	19.0	5.4
Worcester	♂	112	20	21	34.3	14.4	6.9	24.4	6.4	5.3	22.8	5.2
	♂	120	20	20	31.5	13.7	6.4	21.9	5.9	5.2	19.8	5.4
	♂	105	22	21	31.2	13.9	6.8	21.8	6.3	4.8	19.7	4.9
	♂ imm.	90	22	18	26.4	12.9	6.8	–	5.3	4.5	16.8	4.4
	♀	100	20	19	30.9	14.0	6.7	21.9	5.5	5.0	20.3	–
	♀	111	20	19	30.9	14.0	6.9	21.6	6.5	5.2	19.6	4.9

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Kompanjiesdrift	♀	103	22	19	–	–	–	18.4	4.9	–	–	–
Eendekuil	♀	100	10	20	27.2	12.9	6.5	18.5	5.5	4.9	16.9	4.9
	♀	126	14	22	31.1	14.1	6.7	21.9	5.3	4.7	20.0	4.8
Clanwilliam	♀	117	22	21	29.4	–	–	–	5.0	–	–	–
Nieuwhoudtville	♀	118	21	21	–	–	–	20.3	5.4	–	–	–
Klaver	♂	113	24	22	31.9	14.0	7.1	23.4	6.5	5.3	21.6	5.3
	♂	121	25	23	30.8	13.3	6.5	22.9	6.3	5.4	20.6	5.0
	♂ imm.	93	22	19	27.0	12.7	6.1	18.3	5.0	5.0	17.0	5.1
	♀	105	21	22	–	–	–	–	–	–	–	–
	♀	114	28	20	31.1	13.0	6.3	20.7	5.3	4.9	19.0	4.7
	♀	103	24	20	28.0	13.6	6.6	19.5	5.3	–	18.0	4.3
	♀	111	24	22	30.3	12.3	6.2	–	5.0	4.7	19.3	4.7
	♀	113	22	21	31.0	13.6	6.0	21.0	5.6	5.1	19.1	5.0
Van Rhynsdorp	♂	123	14	23	33.1	13.7	6.6	23.2	6.3	–	21.2	5.1
	♂	112	10	21	29.0	13.6	7.1	20.2	5.6	4.8	18.0	4.8
Kamiesberg	♂	135	21	22	–	–	–	–	–	–	–	–
	♂	111	20	22	–	–	–	–	–	–	–	–
	♂	115	22	21	–	–	–	–	–	–	–	–
Ezelfontein	♂	130	22	22	–	–	–	–	6.7	–	–	–
	♂	120	23	21	–	–	–	–	–	–	–	–
	♂	122	23	22	–	–	–	–	6.4	–	–	–
	♂	116	23	22	34.5	–	7.4	24.0	6.5	–	–	–
	♂	127	24	22	–	–	–	23.6	6.5	–	–	–
	♂	128	21	23	–	–	–	–	–	–	–	–
	♀	104	19	21	–	–	–	19.2	5.0	–	–	–
	♀	98	18	21	–	–	–	–	4.9	–	–	–
	♀	112	16	17	–	–	–	19.7	5.2	–	–	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Garies	♂	101	15	20	-	-	-	-	-	-	-	-
	♂	100	15	20	-	-	-	-	-	-	-	-
Matjiesfontein	♂	120	20	23	32.0	13.9	6.5	23.0	6.4	-	21.4	4.2
Cradock	♂	109	13	19	27.9	14.3	7.4	21.2	5.8	-	18.9	-
	♂	118	15	20	31.7	14.5	6.5	23.9	6.0	4.5	20.5	4.5
	♂	-	-	-	38.6	15.7	7.2	28.0	7.6	6.1	25.3	6.1
	♀	-	-	-	29.9	14.7	6.4	21.5	5.8	5.3	19.3	5.8
De Aar	♂	107	15	19	29.0	13.5	6.5	20.4	4.8	5.1	18.2	4.9
Phillipstown	♂	120	13	-	31.1	13.4	6.5	21.4	5.8	5.1	19.8	5.2
	♂	120	13	-	30.2	13.4	6.5	21.1	5.8	5.3	18.8	5.1
	♀	127	12	-	31.1	14.7	6.8	21.8	5.8	5.1	19.3	5.1
	♀	131	17	22	31.9	15.3	6.9	22.9	5.9	5.3	20.7	5.6
Phillipolis	♂	102	20	22	30.4	14.4	6.6	21.6	5.7	-	19.4	-
	♂	118	27	22	30.0	14.7	6.9	21.6	5.9	-	19.6	-
	♂	106	23	24	31.7	14.7	7.0	22.5	6.0	5.5	19.5	6.1
	♀	100	17	20	29.3	14.3	6.9	21.3	5.3	5.2	19.2	5.2
Richmond	♀	102	19	20	29.6	13.6	6.7	20.1	5.2	5.3	18.9	5.4
Sterkstroom	♀	123	22	21	30.4	14.1	6.8	23.3	6.2	5.8	20.7	5.5
Burgersdorp	♀ imm.	105	19	20	27.7	13.8	6.7	20.0	5.7	-	18.8	-
Rosmead	-	-	-	-	29.5	14.1	6.5	22.3	5.9	-	20.2	5.4
Grootvadersbosch	♀	125	25	22	34.0	13.6	7.5	24.6	6.5	4.9	22.9	4.5
Nachtwacht, Bredasdorp	♂	140	25	23	-	-	-	-	-	-	-	-
	♂	-	-	-	35.1	14.3	6.9	25.6	7.2	5.5	23.8	4.9
	♀ imm.	91	14	20	25.9	12.7	6.6	17.6	4.6	-	16.6	-
Swellendam	-	-	-	-	30.3	14.3	6.6	20.7	5.3	-	20.3	-

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Garcia Forest,	♂	117	23	23	31.7	14.8	6.7	23.6	6.2	5.0	22.5	5.9
Riversdal	♂	110	20	21	30.2	14.0	6.6	21.3	5.5	5.0	20.0	5.7
	♀	120	20	21	34.2	14.2	6.7	24.0	6.1	5.5	21.6	5.2
	♀	105	24	21	–	13.6	7.0	20.6	5.3	5.3	19.4	6.0
	♀	100	18	20	31.5	13.6	6.5	21.1	5.6	4.8	19.0	4.8
Seweweekspoort	♂	100	20	21	29.7	–	6.5	21.0	5.6	4.8	19.0	4.8
	– Imm.	96	19	16	27.0	13.2	6.5	18.0	4.8	4.6	17.0	–
	– Imm.	90	19	15	26.0	12.6	6.6	–	4.8	4.6	16.5	4.8
Jonkersberg	♀	118	21	19	31.8	13.4	6.6	22.7	6.5	4.6	20.7	4.7
George	♂	106	–	–	30.6	14.1	6.7	23.2	6.6	4.8	20.7	5.6
	♀	110	15	–	30.1	13.4	6.3	21.2	6.1	4.7	19.6	4.9
Knysna	♂♂	196	6	25	33.7(5)	14.1(7)	6.8(7)	27.1	6.9(7)	5.2(7)	22.2(7)	5.0(7)
		190	–	–	31.9-35.6	13.4-14.8	6.5-7.2	22.0	6.2-8.0	4.8-5.8	21.1-23.4	4.6-5.9
		–	–	–	S.D.=1.378	S.D.=0.580	S.D.=0.222	–	S.D.=0.636	S.D.=0.377	S.D.=0.933	S.D.=0.609
		–	–	–				25.7				
		143	22	27				–				
		143	12	20				26.0				
		117	14	19				–				
	♂	165	–	–	27.6	12.6	6.4	18.7	5.6	–	18.6	–
	♂	139	–	–	28.1	13.1	6.5	18.9	5.1	–	17.8	–
	♂	127	12	19	–	–	–	–	–	–	–	–
	♂ Imm.	101	13	19	24.3	–	6.1	–	4.6	–	16.0	–
	♂ Imm.	114	–	–	–	–	–	–	–	–	–	–
	♂ Imm.	114	12	17	29.4	13.3	6.6	–	5.7	–	18.6	–
	♀	152	–	25	27.5	12.0	6.2	–	5.4	4.8	18.0	–
	♀	171	–	19	–	–	–	–	6.2	4.9	20.6	4.7
	–	–	–	–	30.8	13.2	6.4	–	6.0	5.2	20.2	5.6
	–	–	–	–	31.4	13.4	6.5	–	6.0	4.9	20.2	4.8

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Plettenberg	♂	152	–	13	29.8	–	–	–	6.4	–	–	–
Bay	♂	190	–	19	33.3	14.1	6.5	–	6.5	4.9	22.0	–
	♂	139	–	19	29.5	13.6	6.5	20.2	5.5	5.0	19.4	5.6
	♀	–	–	–	34.3	14.3	7.1	26.5	7.7	5.1	23.7	4.9
	–	177	–	–	–	–	–	–	–	–	–	–
Centlivres	♀	135	10	14	30.1	13.5	6.7	21.8	5.9	5.1	19.4	5.5
Port Elizabeth	♂♂	133	13	–	33.2(6)	14.2	6.9	24.9(8)	7.0(11)	–	21.6	–
		133	17	22	31.1-35.5	15.3	7.5	21.7-28.2	5.9-8.2	5.6	22.4	5.2
		131	8	22	S.D.=1.728	14.7	7.1	S.D.=1.950	S.D.=0.856	5.8	23.2	5.4
		139	–	–	–	–	–	–	–	–	–	–
		–	–	25	29.3	–	–	21.5	–	–	–	–
		146	–	–	–	–	7.7	–	–	–	–	–
		–	–	–	28.0	14.1	6.9	21.1	–	–	–	–
		–	–	–	27.9	–	7.0	–	5.5	–	–	–
		107	–	–	–	–	–	20.8	5.7	–	–	–
		114	–	–	–	–	–	20.2	5.5	–	–	–
		110	12	14	26.2	13.0	6.2	–	5.0	5.5	16.8	–
	♂ imm.	92	11	18	25.0	13.2	6.9	16.9	4.8	–	15.3	–
	♂ imm.	101	–	–	27.2	–	–	17.9	5.0	–	–	–
	♂ imm.	94	14	20	27.6	14.0	6.8	18.8	5.0	4.8	17.2	5.2
	♂ imm.	102	12	18	26.2	13.3	6.7	18.2	4.9	–	16.2	–
	♀♀	127	–	–	–	–	–	–	–	–	–	–
		114	–	–	–	14.3	7.4	–	–	–	–	–
		127	19	38	–	–	–	–	–	–	–	–
		146	–	–	–	–	–	–	–	–	–	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
					30.4(7) 28.8-33.4 S.D.=1.546			21.9(12) 20.1-27.2 S.D.=2.092	6.3(16) 5.5-8.0 S.D.=0.692			
	♀ imm.		-	-	-	-	-	17.8	5.0	-	-	-
	♀ imm.	103	12	19	26.6	12.4	6.7	17.2	4.9	-	16.2	-
	♀ imm.	-	-	-	24.6	-	-	-	4.6	-	-	-
	♀ imm.	-	-	-	-	-	-	-	5.0	-	-	-
	-	-	-	-	30.0	-	-	-	6.4	-	-	-
	-	118	12	21	-	-	-	-	-	-	-	-
Perseverance	♀	139	-	38	-	-	-	23.2	6.5	-	-	-
Coega River	♂	117	14	18	29.0	13.6	6.6	21.2	5.9	5.1	18.8	5.1
	♂	118	14	18	28.3	13.2	6.3	19.2	5.4	4.6	18.7	5.1
	♂	114	13	18	28.9	13.9	6.8	19.9	5.4	5.0	18.3	5.4
Redhouse	- imm.	-	-	-	26.3	12.8	6.6	18.5	5.0	-	16.9	-
Howieson's Poort	♂	130	20	-	-	-	-	24.8	7.2	-	-	-
Grahamstown	♂♂				32.9(16) 29.9-36.5 S.D.=2.091	14.0(16) 13.3-15.4 S.D.=0.656	6.9(18) 6.3-7.7 S.D.=0.332	23.6(14) 20.6-26.3 S.D.=1.832	6.6(18) 6.0-7.6 S.D.=0.556		21.6(16) 19.3-24.0 S.D.=1.644	5.4(7) 5.0-6.0 S.D.=0.374
	♂	-	-	-	-	-	-	-	-	5.3	-	-
	♂	-	-	-	-	-	-	-	-	5.3	-	-
	♂	118	12	20	-	-	-	-	-	4.6	-	-
	♂	-	-	-	-	-	-	-	-	5.5	-	-
	♂	130	15	23	-	-	-	-	-	-	-	-
	♂	140	12	-	-	-	-	-	-	-	-	-
	♂	120	11	-	-	-	-	-	-	5.2	-	-
	♂	129	21	-	-	-	-	-	-	5.3	-	-

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	♂	100	12	–	–	–	–	–	–	–	–	–
	♂	110	14	22	–	–	–	–	–	–	–	–
	♂	90	14	–	–	–	–	–	–	–	–	–
	♂	116	12	21	–	–	–	–	–	–	–	–
	♂	–	–	–	–	–	–	–	–	5.0	–	–
	♂	125	15	–	–	–	–	–	–	–	–	–
	♂	–	–	–	–	–	–	–	–	–	21.5	5.6
	♂ imm.	88	14	–	–	–	6.7	20.1	5.9	–	18.9	–
	♂ imm.	81	11	–	27.6	12.7	6.2	19.9	5.3	–	–	–
	♂ imm.	104	13	–	28.7	12.9	6.1	–	5.7	–	–	–
	♀♀				32.7(10)	14.0(12)	6.7(14)	23.5(13)	6.5(14)	5.0(6)	21.4(10)	5.2(7)
					29.6-36.2	12.8-14.8	6.1-7.4	20.4-27.0	5.7-7.5	4.7-5.6	20.3-23.3	4.8-5.9
					S.D.=2.202	S.D.=0.682	S.D.=0.400	S.D.=1.811	S.D.=0.503	S.D.=0.322	S.D.=1.039	S.D.=0.355
	♀	115	16	21	–	–	–	–	–	–	–	–
	♀	125	26	21	–	–	–	–	–	–	–	–
	♀	145	17	22	–	–	–	–	–	–	–	–
	♀	130	14	22	–	–	–	–	–	–	–	–
	♀	102	10	–	–	–	–	–	–	–	–	–
	♀	112	11	22	–	–	–	–	–	–	–	–
	♀	132	12	23	–	–	–	–	–	–	–	–
	♀	106	11	20	–	–	–	–	–	–	–	–
	♀	108	15	–	–	13.3	–	–	–	–	–	–
	♀	160	15	24	–	–	–	–	–	–	–	–
	♀	106	10	–	–	–	–	–	–	–	17.1	–
	♀ imm.	91	13	–	–	–	–	–	–	–	–	–
	♀ imm.	92	10	17	27.3	13.4	7.0	19.2	5.3	–	–	–
	♀ imm.	75	12	–	28.5	13.8	6.6	20.5	5.9	–	19.0	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	–	110	15	22	–	–	–	–	–	–	–	–
	–	–	–	–	29.4	14.1	6.8	22.4	4.9	5.4	20.6	5.7
	–	–	–	–	32.3	14.2	6.8	23.0	6.2	–	21.8	–
	–	150	18	26	–	–	–	–	–	–	–	–
	–	–	–	–	33.0	14.1	7.2	–	7.2	5.6	22.1	–
	–	–	–	–	28.4	13.9	6.8	20.0	5.3	–	18.6	–
	–	–	–	–	–	–	–	–	–	–	19.5	–
	–	142	12	24	–	–	6.9	–	7.6	5.2	21.5	5.5
	–	145	15	26	–	–	–	–	–	–	–	–
	–	110	15	22	25.1	13.4	7.3	18.6	5.6	–	17.3	–
	–	150	17	23	36.0	15.2	7.5	28.0	8.1	6.2	25.1	–
	–	–	–	–	34.6	14.8	7.0	27.7	8.1	5.5	25.0	5.5
	–	137	13	25	34.3	14.7	7.9	25.4	7.2	5.3	23.0	5.5
	–	130	15	22	–	13.5	7.5	20.1	6.2	–	18.0	–
	–	131	–	–	29.5	13.9	7.0	21.5	6.2	5.3	19.5	5.9
	–	158	18	25	–	–	–	–	–	–	–	–
	–	–	–	–	–	–	7.0	–	6.4	5.3	21.2	6.1
	–	–	–	–	28.9	13.8	6.8	21.1	6.0	–	19.5	–
	–	–	–	–	–	–	–	–	5.8	–	19.1	–
	–	114	15	22	–	–	–	–	–	–	–	–
	–	96	18	22	29.3	13.5	6.7	20.6	5.8	5.3	19.6	–
Penrock	♂ imm.	–	–	–	–	–	7.2	–	5.1	–	16.0	–
Queenstown	♂	–	–	–	28.9	13.2	6.4	21.1	5.7	–	19.0	–
Port Alfred	♂	–	–	–	–	–	6.8	–	6.8	–	20.6	–
							6.9(6)		6.6(6)		20.4(6)	
	--						6.7-7.2		6.0-7.6		18.7-21.9	
							S.D.=0.204		S.D.=0.700		S.D.=1.351	

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	–	130	22	14	32.3	14.0	–	23.6	–	5.2	–	5.5
	–	105	11	22	29.9	13.2	–	20.8	–	5.9	–	5.7
	–	125	13	–	31.0	14.4	–	–	–	–	–	–
	–	148	14	22	–	–	–	25.9	–	5.4	–	5.5
	–	127	13	22	–	–	–	–	–	–	18.8	–
	–	127	12	22	–	–	–	–	–	–	–	–
	–	130	14	22	32.5	13.9	–	–	–	5.4	–	5.4
Fish River	♀	115	22	–	31.4	13.4	6.3	21.5	5.9	5.9	20.2	5.7
Fort Beaufort	♂	–	–	–	–	–	–	–	7.1	5.5	24.3	5.1
	–	–	–	–	–	–	–	–	5.8	5.7	–	–
East London	♂	–	–	–	–	14.4(5)	7.3	24.6	6.5(5)	5.2	21.7	5.2
	♂	–	–	–	31.4	14.4–14.7	–	–	6.1–7.1	–	–	–
	♂	–	–	–	31.2	S.D.=0.164	7.7	25.9	S.D.=0.365	5.5	21.5	5.5
	♂	–	–	–	29.7		6.8	20.4		–	18.6	–
	♂	–	–	–	33.5		6.9	–		–	22.5	–
	♂ imm.	–	–	–	–	13.1	7.2	18.0	4.9	–	17.9	–
	♂ imm.	–	–	–	–	–	6.2	–	4.1	–	–	–
	♀	–	–	–	31.1	14.8	7.0	23.9	6.5	–	19.5	–
	♀	–	–	–	29.0	13.7	7.2	21.6	5.8	–	–	–
	♀	–	–	–	–	–	7.3	23.7	6.9	–	–	–
	♀	120	15	25	30.9	13.3	6.5	21.8	6.3	–	20.0	–
	♀	–	–	–	–	–	–	–	–	–	20.9	–
	–	–	–	–	–	–	–	24.2	6.6	–	–	–
	–	120	–	19	–	–	–	–	–	–	–	–
Peddie	♂	144	10	–	–	–	7.0	24.0	7.3	–	21.1	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R	L.J.	L.T.R
Dortrecht	–	–	–	–	33.4	14.9	6.8	24.3	6.6	5.7	22.5	5.5
	–	86	17	17	34.3	14.4	6.6	25.2	7.2	–	22.5	–
	♂	96	21	–	31.7	14.3	7.2	23.3	6.2	–	20.1	–
	♂	–	–	–	29.3	13.6	6.5	–	5.5	–	19.2	–
Middledrift	♂	–	–	–	27.5	13.1	6.3	19.6	5.3	–	18.2	5.5
King William's town	♂	112	15	23	–	–	–	21.0	5.5(5) 5.0-5.9	–	–	–
	♂	110	15	19	–	–	–	19.1	S.D.=0.342	–	–	–
	♂	116	16	21	–	–	–	20.4		–	–	–
	♂	113	12	20	–	–	–	–		–	–	–
	♂	113	15	21	–	–	–	–		–	–	–
	♀	125	12	19	–	12.8	6.2	21.0	5.9	5.2	19.1	5.6
	♀	125	15	15	–	–	6.7	–	5.9	4.8	18.2	5.8
	–	126	16	23	–	–	–	–	5.9	–	–	–
Buffelsdraai	♂	100	20	22	29.6	13.5	6.7	21.4	6.0	–	19.6	–
	♂	112	23	22	29.0	13.3	7.2	20.5	5.5	–	19.7	–
	♂	110	17	23	28.3	13.9	6.9	–	5.5	–	19.0	–
	♂ imm.	96	17	22	–	–	–	–	–	–	–	–
	♀	110	20	23	29.0	13.8	7.0	–	5.7	–	19.5	–
	♀	130	22	22	34.4	14.0	7.1	24.9	7.0	5.4	22.5	5.5
	♀ imm.	97	17	20	–	–	–	–	–	–	–	–
	♀ imm.	100	17	22	–	–	–	–	–	–	–	–
	♀ imm.	96	17	21	27.1	–	6.9	–	5.3	–	17.6	–
	♀ imm.	92	17	20	–	–	6.6	–	4.6	–	16.5	–
Jericho	♂	128	21	33	31.1	14.1	7.0	23.2	5.8	5.7	21.0	5.8
	♂	128	22	23	31.4	13.4	7.1	–	6.2	5.2	22.2	4.7
	♀	130	20	23	32.3	14.3	7.2	25.0	6.7	5.4	22.3	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Zoutpan	♂	112	22	22	31.2	13.7	7.1	21.4	5.2	5.9	21.1	5.1
	♂	130	24	23	34.5	13.9	7.0	25.4	6.8	–	23.7	5.1
	♀	107	22	22	29.9	13.1	6.9	20.2	4.9	–	19.5	5.7
Waynek	♀ imm.	107	16	18	–	–	–	–	4.9	4.0	17.0	4.0
Moorddrift	♂	115	14	21	31.7	13.3	6.8	21.9	5.3	4.8	20.5	4.4
	♀ imm.	94	23	17	27.3	12.1	6.2	18.6	5.5	4.4	18.0	4.7
Fauresmith	♂	110	18	22	32.6	15.7	6.9	23.8	6.2	5.9	21.4	6.4
de Brug	♂	120	24	21	32.3	15.0	6.8	23.8	5.2	5.1	20.4	5.3
	♀	112	20	21	32.6	14.7	6.8	22.9	6.2	–	20.4	5.4
Griffin Mine	♀	123	17	23	28.9	14.2	6.8	19.9	4.9	5.5	19.4	5.2
	–	123	17	21	30.5	13.8	6.6	21.6	5.6	5.5	20.6	5.4
	–	123	17	23	30.1	14.4	6.9	21.0	5.3	5.4	19.9	5.5
	–	–	–	–	30.9	14.4	6.8	20.8	5.2	5.1	20.1	5.3
	–	119	17	23	–	–	–	–	–	–	–	–
	–	134	18	25	–	–	–	–	–	–	–	–
Gravelotte	♂	145	20	26	35.4	14.8	7.1	25.8	6.7	5.3	25.0	5.5
	♀	129	20	24	32.3	14.6	6.9	22.6	5.8	5.0	21.7	5.2
	♀	124	18	25	30.2	14.2	6.7	21.1	5.1	5.5	20.8	5.1
	♀ imm.	90	13	20	24.5	13.2	6.7	17.0	4.8	–	16.5	–
Mookeetsi	♂	124	18	26	33.8(7)	14.9(7)	7.0(7)	25.1(7)	6.8(7)	–	22.5(7)	5.3(6)
					32.1–36.3	14.6–15.5	6.7–7.3	23.3–23.4	6.2–7.5	5.2	20.8–24.5	4.6–5.8
	♂	150	18	25	S.D.=1.373	S.D.=0.310	S.D.=0.245	S.D.=1.508	S.D.=0.423	5.2	S.D.=1.215	S.D.=0.402
	♂	138	22	22								
	♂	136	22	23						–		
	♂	145	22	23						5.5		
	♂	149	22	22						5.5		
	♂	131	22	22						–		

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Mlondozi, Kruger National Park (K.N.P.)	♂	126	19	22	31.6	15.1	7.0	23.0	6.6	–	20.6	–
	♀	136	22	23	33.3	15.0	7.0	23.9	7.0	5.2	21.6	5.3
	♀	135	15	25	–	–	–	–	–	–	–	–
	♂	146	18	25	34.7	14.4	6.8	25.3	6.8	5.3	24.1	5.6
	♂	149	17	22	37.1	13.6	6.3	26.6	7.4	–	25.7	–
	♀	138	16	23	31.9	14.3	6.7	22.5	5.7	5.8	21.6	5.8
	♀	135	19	23	32.2	14.1	6.8	23.3	5.8	5.4	21.8	5.1
	♀	120	17	22	32.0	13.4	6.5	22.7	5.8	5.4	21.3	5.1
Lindanda, K.N.P.	♂	155	21	23	–	–	–	–	5.6	–	–	–
	♀	141	19	21	31.7	14.1	6.5	22.9	5.9	–	21.5	5.4
Nwanetzi-West, Windmill, K.N.P.	♂	131	10	20	29.8	14.2	7.0	21.7	5.5	5.1	20.2	5.3
Ngirivane, K.N.P.	♀	141	17	24	32.1	14.0	7.4	23.7	6.4	–	22.1	5.2
Satara, K.N.P.	♀	138	17	24	33.4	13.7	6.4	23.0	5.9	–	22.5	–
Satara experimental Plots, K.N.P.	♀ juv.	107	18	19	28.1	14.1	7.1	–	5.2	–	18.4	–
Shibangwanene Spruit, K.N.P.	♀	136	16	23	32.8	14.5	7.2	23.1	6.0	5.3	22.2	5.4
Gorge, K.N.P.	♀	137	17	22	32.0	14.1	7.4	–	6.4	5.4	22.0	5.4
Letaba, K.N.P.	♀	140	16	25	34.0	14.1	7.2	24.3	6.1	5.4	23.6	5.2
Mabewane block, K.N.P.	♀	157	15	25	34.5	15.1	6.8	24.9	6.3	6.0	23.7	–
Mashakadzi, K.N.P.	♀	137	14	22	31.3	14.3	6.9	–	5.6	–	21.3	5.4
Shingwedzi, K.N.P.	♂	154	11	27	35.6	14.8	7.2	26.0	7.1	–	24.3	–
Shingwedzi Main Road, K.N.P.	♀ imm.	140	19	22	29.4	14.6	7.0	20.9	5.4	–	–	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R
Bubube fire break, K.N.P.	♂ imm.	130	12	17	29.9	14.1	7.1	–	5.6	–	19.8	–
Shingomene, K.N.P.	♀	138	10	24	–	–	–	–	–	–	–	–
Hlati Road, K.N.P.	♀	140	18	24	32.8	14.3	6.7	22.9	5.7	5.4	21.2	5.3
Pumbe, K.N.P.	♂	152	16	24	33.4	14.4	7.1	25.0	7.2	–	22.3	–
	♀	154	19	26	35.1	15.0	7.0	25.9	7.0	5.7	24.5	5.4
	♀	146	18	24	33.2	14.0	7.3	24.0	6.2	5.5	22.8	6.0
	♀	153	17	23	35.5	13.9	6.9	23.9	6.3	–	24.0	–
Mahungumule, K.N.P.	♀	131	9	25	32.3	14.9	7.3	–	5.8	5.7	22.3	5.7
Nwamayiwani, K.N.P.	♀	155	19	23	33.6	14.8	6.8	23.4	6.1	–	22.8	5.2
Nkokodzi, K.N.P.	♂	136	12	25	33.3	13.9	6.9	25.0	6.8	–	23.2	5.1
Zwarthoek	♂♂	136	14	24	32.5(13)	14.1(13)	7.0(13)	23.5(13)	6.2(13)	5.4(10)	22.6(13)	5.3(13)
		145	14	24	29.5-37.4	13.3-14.8	6.6-7.4	20.5-27.4	5.3-7.8	5.1-5.9	20.0-26.8	4.7-6.2
		135	14	23	S.D.=2.137	S.D.=0.589	S.D.=0.299	S.D.=2.164	S.D.=0.718	S.D.=0.283	S.D.=1.826	S.D.=0.349
		155	14	24								
		129	14	24								
		136	14	22								
		130	12	22								
		121	12	21.5								
		136	–	22								
		145	14	24								
		136	14	22								
		132	14	21								
		132	14	23								
	♂ imm.	102	10	20	25.2	12.7	6.7	17.9	5.0	–	17.4	–

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	♀♀	136	15	24	31.1(9)	13.8(9)	7.1(9)	22.2(8)	5.8(9)	5.4(8)	21.3(9)	5.3(9)
		107	10	26	29.4-33.8	12.9-14.3	6.3-7.4	20.5-23.8	5.3-6.3	5.2-5.6	19.6-23.1	5.0-5.7
		135	14	25	S.D.=1.467	S.D.=0.457	S.D.=0.377	S.D.=1.238	S.D.=0.310	S.D.= 0.141	S.D.=1.185	S.D.=0.276
		127	12	24								
		121	-	21								
		123	12	22								
		129	14	22								
		129	14	23								
		126	14	23								
Njelela River	♂	131	12	23	32.4	14.1	6.8	22.5	6.2	5.2	22.2	5.5
	—	123	14	24	31.9(5)	14.1(5)	6.7(5)	22.5(5)	6.1(5)	-	21.6(5)	-
		143	16	24	30.7-34.6	13.9-14.6	6.5-7.0	21.7-23.2	5.7-6.6	5.1	20.6-24.3	4.7
		124	16	24	S.D.=1.607	S.D.=0.261	S.D.=0.192	S.D.=0.607	S.D.=0.336	5.1	S.D.=1.558	5.5
		127	16	23						5.1		5.4
		125	14	24						5.2		5.6
Zoutpansberg	♂	130	-	20	30.8	14.3	6.9	23.5	6.4	5.3	20.3	5.5
	♂	125	-	20	31.6	13.3	6.6	22.9	7.1	4.6	21.1	4.5
	♂	123	-	21	31.4	14.1	6.7	21.4	6.2	4.8	20.3	4.9
	♂	108	14	-	-	-	-	-	-	-	-	-
	♀	122	-	20	29.9	13.5	6.9	21.0	5.8	-	19.0	4.9
	♀	120	-	21	31.4	13.6	6.7	21.6	5.9	5.1	19.9	5.3
	♀	115	-	20	30.6	12.6	6.4	21.2	5.8	5.0	19.5	5.2
	-	-	-	-	29.6	13.6	7.1	23.1	6.9	4.7	21.1	4.6
	-	-	-	-	27.3	13.3	6.7	18.1	4.9	4.8	17.2	4.7
	-	-	-	-	26.1	13.4	6.3	-	5.4	-	18.1	5.0

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	–	–	–	–	27.3	13.1	6.6	20.1	5.1	–	17.8	–
	–	–	–	–	28.1	13.1	6.5	19.1	5.3	–	17.9	–
Montrose	♂	140	–	24	32.8	13.3	7.2	24.0	7.0	5.4	23.4	5.6
	♂	140	–	22	32.2	14.1	6.9	23.1	5.9	5.5	22.5	5.3
	♂	155	–	23	35.5	13.9	7.7	26.6	7.8	5.3	24.1	5.1
	♂	139	–	22	29.4	13.2	7.2	20.5	5.8	–	19.4	–
	♂ imm.	–	–	–	29.1	13.3	7.2	20.5	5.5	–	19.1	–
	♀	154	–	23	34.5	14.3	7.4	24.3	7.0	5.8	23.1	5.9
Silwane	–	136	17	24	31.6	14.0	6.9	22.3	5.9	5.5	21.4	5.7
Mamarange	♂♂	146	21	24	32.7(6)	14.3(6)	6.6(6)	23.7(5)	5.9(6)	5.5(6)	22.1(6)	5.7(6)
		131	21	24	30.3–35.7	14.1–15.0	6.5–6.9	22.0–26.3	5.4–7.1	5.2–6.1	20.4–24.5	5.3–6.4
		130	18	23	S.D.=2.142	S.D.0.350	S.D.=0.150	S.D.=1.768	S.D.=0.641	S.D.=0.327	S.D.=1.568	S.D.=0.459
		122	17	22								
		119	16	21								
		118	15	17								
	♀	126	17	22	32.0	14.7	6.7	23.2	5.7	5.7	21.3	5.5
	imm.	103	15	20	26.3	13.5	6.9	18.4	4.8	–	18.0	–

Measurements of Cryptomys damarensis

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Molopo, Mafeking	♂	150	20	26	–	–	–	–	–	–	–	–
	♂	117	20	22	–	–	–	–	–	–	–	–
Grootkolk	♀	–	–	–	38.2	15.3	8.1	30.3	9.8	6.4	26.4	5.9
Gemsbokpan	♂	130	25	28	32.8	13.9	7.7	23.3	6.9	5.4	20.4	5.4
Kampspanne Rd.	♂	–	–	–	44.1	16.9	8.4	33.0	11.1	6.7	28.9	6.9
	♀	–	–	–	–	–	–	–	8.6	6.3	24.2	6.1
	♀	–	–	–	–	–	8.5	–	10.0	6.3	27.0	6.1
	♀	–	–	–	–	–	–	–	–	6.2	–	6.2
Kuke	♂	135	25	27	33.8	14.3	7.4	23.9	7.6	5.2	22.3	5.7
77 miles east	♂	–	–	–	36.9	15.3	7.2	28.0	9.8	6.4	25.5	6.2
of Maun.	♂	–	–	–	36.4	15.5	7.8	27.4	8.3	6.1	23.3	6.0
Damara Pan	♂	154	30	30	38.3	16.6	7.8	27.1	9.1	5.6	25.5	6.4
	♀	148	32	27	34.8	14.7	7.9	25.1	7.9	6.1	23.1	–
Sandfontein	♂	152	26	29	–	–	8.1	–	8.9	6.0	23.0	–
	♀	141	25	25	–	–	–	–	–	–	–	–
Gobabis, Farm	♂	164	13	26	33.2	–	7.7	23.2	7.2	5.8	22.0	5.7
397	♂	185	16	30	38.9	15.5	8.3	28.9	8.8	6.1	26.7	5.8
	♂	178	17	26	35.4	15.9	7.4	27.7	8.3	5.6	24.0	5.5
	♂	167	14	27	32.2	14.9	8.2	23.9	6.9	5.5	21.3	5.5
	♀	164	14	28	–	–	7.8	–	6.9	5.5	22.9	5.6
Quickborn,	♂	–	–	–	39.9	15.2	8.1	29.7	9.1	6.0	26.0	6.1
Okahandja	♂	–	–	–	35.6	16.0	7.7	26.6	8.1	5.8	23.6	5.9
	♀	–	–	–	36.9	15.3	8.1	26.1	8.4	5.6	24.1	5.5
Waterberg	♀	–	–	–	31.6	14.8	7.6	–	6.8	5.6	21.2	5.3
	–	–	–	–	38.2	15.8	8.5	28.8	8.8	6.1	25.4	5.9
Kovares	♂	150	15	13	–	–	–	–	8.7	–	–	–
Otavi	♂	138	23	26.5	33.9	14.3	7.9	24.3	7.2	5.5	22.2	5.7
"Ovamboland"	–	–	–	–	32.4	14.6	8.0	–	7.6	6.2	21.8	6.4

Continued/...

Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Ondongwa	♂	160	27	27	38.3	15.5	8.0	28.9	9.3	6.1	26.0	6.8
	♂	120	25	15	31.2	14.2	8.0	22.4	6.7	–	20.4	–
	♂	130	19	26	32.4	14.4	7.9	23.8	7.4	6.3	21.1	6.4
	♂	110	20	12	29.2	14.1	8.1	21.7	6.4	–	19.3	–
	♂	140	25	15	–	–	–	–	8.8	6.5	–	6.3
Santa Cruz	♂	155	17	25	–	–	8.3	–	6.8	–	19.3	–
	♂	155	17	25	38.5	15.9	8.3	28.4	9.2	5.3	24.8	6.1
	♀	156	17	22	32.5	–	8.6	–	7.1	–	20.9	6.3
Matetsi	♂	190	–	–	36.2	15.7	8.2	26.9	8.0	–	24.3	–
	♂	–	–	–	37.9	14.6	8.1	–	8.4	5.9	24.6	6.1

Measurements of *Cryptomys holosericeus*

Modder River	♂	–	–	–	–	15.9	–	24.8	–	5.7	22.2	5.8
	♀	–	–	–	–	17.0	8.0	29.2	7.9	6.5	25.4	6.4
Barkly West	♂	–	–	–	38.3	–	–	–	8.3	7.7	25.4	–
	♂	–	–	–	–	–	–	24.7	7.0	–	–	–
	♂	–	–	–	–	–	–	22.4	6.0	–	–	–
	–	–	–	–	–	–	7.2	–	8.5	–	–	–
	–	–	–	–	32.7	–	6.4	23.8	5.9	–	22.0	–
Vryburg	♂	135	18	26	36.8	15.1	7.1	27.1	7.4	5.7	23.9	6.0
	♂	–	–	–	31.3	13.7	6.9	21.1	5.8	–	21.2	5.3

Continued/....

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	♂	136	12	22	31.2	13.8	7.2	23.7	6.2	–	21.4	–
	♂	–	–	–	29.0	13.8	7.0	19.8	5.3	–	19.3	–
	♀	115	21	23	33.8(8)	15.1(8)	7.4(8)	24.7(8)	6.6(8)	5.8(7)	22.3(8)	6.1(6)
	♀	145	21	24	30.8–37.9	13.9–15.9	6.6–7.9	21.5–28.2	5.5–8.0	4.9–6.3	20.0–26.0	5.1–6.9
	♀	125	21	23	S.D.=2.691	S.D.=0.595	S.D.=0.424	S.D.=2.519	S.D.=0.865	S.D.=0.461	S.D.=2.080	S.D.=0.581
	♀	85	20	22								
	♀	105	20	28								
	♀	138	12	22								
	♀	155	15	25								
	♀	150	13	22								
	–	155	17	26	36.6	15.0	7.4	26.7	7.1	6.1	24.8	6.5
	–	140	18	23	34.4	15.4	7.7	–	7.5	–	23.4	–
	–	128	15	22	31.4	14.0	7.4	–	6.4	–	21.0	–
	–	235	17	24	–	–	–	–	9.0	6.4	29.4	6.7
	–	180	16	25	–	–	–	–	–	–	–	–
Kuruman	♀	117	16	21	30.6	14.7	7.4	20.9	5.8	–	19.9	5.0
Fourteen Streams	♂	–	–	–	37.4	15.5	7.1	27.8	7.8	5.3	24.5	5.3
Maquassie	♂	152	28	25	36.1	15.1	7.8	26.9	7.9	5.6	24.4	6.0
	♀	114	28	22	30.4	15.3	7.9	22.2	5.9	–	20.3	5.8
Bloemhof	♂	98	17	19	29.0	13.6	7.0	19.6	5.3	–	19.3	6.3
	♂	109	21	21	31.4	13.3	6.8	21.7	5.7	5.9	21.0	6.2
	♂	132	23	26	34.9	14.7	7.6	25.2	6.7	–	23.8	–
	♂	152	21	27	37.7	15.9	7.9	27.8	7.9	5.9	25.1	6.8
	♀	123	24	23	32.6	14.2	7.3	23.5	6.2	–	20.8	–
	♀	132	27	24	34.2	15.3	7.6	24.0	6.5	5.2	22.7	5.6

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Taaiboschspruit, Vet River	♂	160	–	26	38.6	15.3	7.3	27.5	7.4	6.8	25.3	7.1
	♂	130	–	25	33.5	14.5	7.3	24.2	6.8	6.0	22.4	6.1
	♂	130	–	23	32.6	14.4	6.8	22.0	6.2	6.4	21.1	6.9
	♂	125	–	25	31.7	14.7	6.8	22.5	6.2	5.9	20.6	6.1
	♂ imm.	110	–	20	28.3	14.0	6.8	20.0	5.5	–	18.3	–
Glen	♂	145	–	–	–	–	7.5	26.2	7.3	6.1	24.9	6.0
	♂	148	29	26	38.3	15.1	7.4	28.6	7.5	6.4	25.9	6.3
	♀	120	25	22.5	–	–	7.3	21.4	6.0	–	20.5	6.4
	♀	112	24	20	30.6	14.1	7.5	21.5	5.6	6.1	19.8	6.7
	♀	116	–	20.5	32.4	15.0	7.3	23.6	6.2	5.8	2.6	6.1
	♀	125	25	22	35.4	14.3	7.6	28.9	7.8	5.8	24.7	5.6
	♀	130	19	24.5	35.5	14.6	7.5	25.6	6.5	6.0	23.6	6.1
	♀	138	20	21	34.4	14.6	7.4	25.3	6.6	5.5	22.2	6.3
	♀	130	20	21	33.8	14.6	7.5	–	6.5	5.6	23.0	6.5
Junction Sand/ Vet River	♂	116	18	19	30.3	14.5	6.6	21.2	5.8	–	20.0	–
Odendaalsrust	♂	128	23	22	33.1	15.3	7.7	23.5	6.3	6.2	21.9	6.2
	♂	105	24	22	31.0	13.9	7.3	–	5.9	6.2	21.0	6.3
	♀	122	15	22	32.9	14.2	6.8	23.3	6.1	5.3	21.2	5.8
	♀	132	29	22	32.5	15.1	7.9	23.6	6.7	6.1	21.5	6.3
	– imm.	100	24	23	28.9	14.0	6.8	19.6	5.3	–	19.4	–
Bothaville	♂	130	27	24	35.5(9)	15.2(9)	7.2(9)	26.3(8)	7.1(9)	6.0(9)	24.0(9)	6.2(9)
	♂	146	25	26.5	31.8-39.4	14.0-16.1	6.8-7.7	22.9-29.3	6.4-8.3	5.6-6.3	21.2-27.1	5.7-6.7
	♂	155	30	25	S.D.=3.008	S.D.=0.734	S.D.=0.295	S.D.=2.089	S.D.=0.704	S.D.=0.255	S.D.=2.147	S.D.=0.350
	♂	144	29	27.5								
	♂	123	19	22								
	♂	136	24	22								

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R
	♂	115	21	22								
	♂	145	21	25.5								
	♂	123	25	23								
	♂ imm.	100	15	20.5	28.3	13.4	7.3	18.6	4.9	–	18.3	–
	♀	112	20	22	32.2(9)	14.6(10)	7.1(11)	22.7(9)	6.3(11)	–	21.2(11)	5.7(6)
	♀	115	19	23.5	29.0-36.7	13.8-16.4	6.5-7.9	20.0-25.7	5.6-7.4	–	19.2-25.0	5.4-6.2
	♀	112	19	22	S.D.=2.841	S.D.=1.005	S.D.=0.388	S.D.=1.825	S.D.=0.632	–	S.D.=1.954	S.D.=0.360
	♀	103	19	21								
	♀	127	28	23								
	♀	129	29	24								
	♀	142	26	25								
	♀	115	20	22								
	♀	107	18	23								
	♀	144	25	27.5								
	♀	115	18	21								
	–	133	23	25	36.3	15.3	7.5	25.1	7.0	6.3	24.0	6.5
Parys	♂	130	12	24	33.8	14.7	7.9	23.9	6.8	5.7	22.9	6.5
	♂	138	15	26	35.3	15.7	7.7	24.5	7.0	5.8	23.5	6.2

Measurements of Cryptomys darlingi

Vumba	♂	113	10	19	27.0	–	7.1	–	5.6	4.6	17.3	5.4
	♂	127	8	12	–	–	–	–	–	–	–	–
	♀	–	–	–	29.4	13.8	7.6	–	6.5	–	19.0	–
	♀	133	11	12	–	–	–	–	–	–	–	–
	–	127	9	12	–	–	–	–	–	–	–	–

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Inyanga	♂	137	20	22	35.8	15.3	7.0	26.1	7.8	5.7	23.0	5.4
	♂	120	21	21	33.5	14.5	6.9	–	6.8	5.5	21.3	5.5
	♂	108	14	19	28.3	13.6	6.6	19.4	5.7	–	18.1	–
	♂	125	15	21	31.8	15.1	7.1	23.3	7.1	5.2	20.4	5.0
Stimela	♂	130	18	23	31.0	13.9	6.6	22.8	6.4	4.8	21.2	5.1
Mt. Selinda	♂	120	15	20	30.3(7)	13.7(7)	7.1(7)	21.8(6)	6.5(7)	5.4(7)	19.3(7)	5.6(7)
	♂	120	10	19	28.2-31.8	12.6-14.5	6.6-7.4	19.7-24.2	6.0-7.1	5.0-5.8	18.0-21.3	5.2-6.1
	♂	127	12	23	S.D.=1.276	S.D.=0.627	S.D.=0.269	S.D.=1.875	S.D.=0.383	S.D.=0.335	S.D.=1.110	S.D.=0.325
	♂	120	13	23								
	♂	127	15	21								
	♂	125	11	21								
	♂	126	7	20								
	♂ imm.	119	12	18	26.8	12.6	6.9	18.6	5.9	–	17.1	–
	♀ imm.	120	12	20	25.5	13.5	7.8	19.1	7.8	–	16.6	–
Matoppos Road	♂	102	10	20	32.1	14.1	7.0	22.5	5.8	–	21.0	–
	♀	94	11	21	31.0	14.0	6.9	–	6.0	5.5	20.6	–
	♀	113	12	25	33.8	14.6	7.2	24.8	6.2	–	23.0	–
20 Miles on Essex Vale Road	♀	127	–	–	–	14.0	6.9	22.1	5.6	–	19.8	–
Hillside	♂ imm.	118	15	24	–	–	–	–	–	–	18.1	–
Khami Dam	♂	124	21	22	34.4	14.8	6.7	25.7	7.0	4.9	23.5	4.8
	♀	115	10	24	30.9	14.2	6.5	21.5	5.6	5.5	20.9	5.8
	♀ imm.	41	–	–	25.6	13.4	6.6	–	4.5	–	16.5	–
Riverside, Bulawayo	♂	141	12	23	32.1	13.8	7.0	24.0	6.6	–	21.5	–
Bulawayo	♂	127	20	25	–	–	–	–	–	–	–	–
	♂	130	22	24	33.1	–	7.4	–	6.8	–	22.1	–

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Shawerombi,	♂♂	145(14)	10(14)	23(14)	33.3(13)	14.7(14)	7.2(14)	24.4(12)	7.2(14)	5.3(10)	21.7(14)	5.5(13)
Melsetter		125-165	8-13	21-30	30.6-37.9	13.0-15.9	6.3-7.7	20.8-28.2	6.0-8.2	4.7-5.6	19.0-25.4	4.9-5.9
		S.D.=3.873	S.D.=0.997	S.D.=2.560	S.D.=2.557	S.D.=0.680	S.D.=0.339	S.D.=2.522	S.D.=0.655	S.D.=0.353	S.D.=1.968	S.D.=0.345
	♀♀	141(9)	10(9)	22(9)	32.6(8)	14.4(8)	7.0(9)	23.3(7)	6.9(9)	5.1(6)	21.3(9)	5.3(9)
		135-150	10-10	20-24	31.0-36.5	13.9-15.1	6.8-7.4	21.3-27.2	6.5-7.6	4.7-5.5	20.0-25.0	5.1-5.8
		S.D.=6.200	S.D.=0.00	S.D.=1.716	S.D.=1.951	S.D.=0.545	S.D.=0.218	S.D.=1.890	S.D.=0.377	S.D.=0.287	S.D.1.624	S.D.=0.194
Salisbury	♂♂	143(5)	10(5)	22(5)	33.0(5)	14.5(5)	7.2(5)	24.8(5)	7.3(5)	5.2(5)	21.5(5)	5.4(5)
		135-150	10.0-10.0	20-24	31.1-33.7	14.0-15.2	6.7-7.7	23.3-26.9	6.9-8.1	4.8-5.5	20.3-22.2	5.1-5.6
		S.D.=6.708	S.D.=0.00	S.D.=1.483	S.D.=1.548	S.D.=0.442	S.D.=0.374	S.D.=1.431	S.D.=0.503	S.D.=0.270	S.D.=0.952	S.D.=0.192
	♀	140	10	23	31.6	14.7	7.5	24.2	7.2	5.1	21.2	5.2
Enterprise	-	141	-	22	-	-	-	-	-	-	-	-
Macheke	♂	-	-	-	37.7	14.6	7.0	26.7	7.9	5.1	24.0	5.4
Selukwe	♂	-	-	-	33.1	14.3	6.6	-	7.1	-	-	-
	♀	-	-	-	35.1	13.6	7.3	25.6	7.8	5.2	22.3	5.1
Chipinga	♀	120	15	25	-	-	-	22.0	6.9	-	-	-

Measurements of Cryptomys beirae

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Beira	-	-	-	-	38.9	15.4	8.2	-	9.3	6.0	24.9	6.1
	-	-	-	-	33.6	14.8	8.1	-	7.5	5.7	21.4	6.3
	-	-	-	-	35.7	14.9	6.1	27.0	8.1	5.8	23.2	5.4
	-	-	-	-	35.0	14.9	8.4	26.5	7.9	5.7	22.9	6.6
Zimbiti	♂	-	-	-	34.4	15.2	7.2	26.5	8.1	5.7	22.5	5.4

Measurements of Cryptomys bocagei

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Mombola, Angola	♂	144	12	20	31.2	14.7	7.5	21.9	6.1	–	20.0	–
	♂	145	7	19	32.2	14.5	7.7	–	6.6	–	20.8	–
	♂	165	11	22	34.4	14.7	7.9	24.6	6.9	5.7	23.0	–
	♂	160	10	22	–	–	–	–	–	–	–	–
	♀	154	6	24	35.0	15.6	8.4	–	6.8	5.3	22.9	5.5
	♀	150	12	21	32.5	13.7	7.3	23.3	6.6	4.8	21.2	5.2
	♀	165	12	20	33.9	14.4	7.6	24.4	6.9	5.2	22.0	5.6
	♀	152	15	22	32.6	14.6	7.5	23.3	6.2	5.1	21.2	4.9

Measurements of Cryptomys natalensis

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Koster	♂	141	19	26	35.6	14.9	7.4	25.3	7.1	5.9	24.4	6.0
	♀	141	26	23	34.7	15.3	7.3	24.7	6.4	6.9	23.6	6.8
	♀	126	22	24	31.7	15.0	7.4	22.0	6.3	6.0	21.8	6.4
Venterskroon	♂	145	25	28	38.0	15.2	7.4	25.6	7.2	6.0	24.8	6.7
	♂	141	25	27	36.3	15.0	7.6	25.1	7.5	5.8	24.8	6.6
	♂	134	21	26	33.7	14.8	7.2	–	6.4	–	21.9	6.6
	♂	134	17	25	35.2	14.6	7.2	26.2	7.4	5.4	24.1	5.8
	♀	147	25	26	37.3	16.4	7.3	27.3	7.0	5.8	25.1	6.5
	♀	127	20	26	34.4	14.7	7.1	23.4	6.5	–	22.3	6.7
	♀	117	17	24	31.5	13.9	7.2	21.3	5.1	–	20.6	6.3
Potchefstroom	♂	129	20	22	34.5	16.1	8.1	25.5	6.7	–	22.4	–
Johannesburg	♂	146	–	25	34.4	15.1	7.6	22.7	6.3	6.2	22.3	6.5
	♂	130	17	25	35.2	15.3	7.7	24.0	7.0	6.2	23.3	6.1
	♂	117	18	23	32.0	14.7	7.8	21.6	6.2	–	20.5	–

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	♂	160	22	26	-	-	7.2	-	6.9	-	24.3	6.2
	♂	-	-	-	38.0	17.0	8.7	28.5	7.4	6.2	25.8	6.1
	♀	115	22	22	29.9	14.9	7.1	20.5	5.1	5.0	20.1	-
	♀	152	17	28	34.8	16.8	8.1	26.9	6.8	6.0	24.4	5.8
	-	146	19	-	-	-	-	-	-	-	-	-
	—	-	-	-	-	-	7.8(5) 7.2-8.7 S.D.=0.552	-	6.7(5) 6.2-7.4 S.D.=0.503	-	23.2(5) 20.5-25.8 S.D.=2.00	-
Randfontein	♂	140	22	25	33.0	15.9	7.7	21.8	5.7	-	21.1	-
	♀	143	22	25	34.8	15.3	7.3	24.4	6.7	5.9	22.8	6.2
Krugersdorp	♂	147	25	27	35.7	15.8	7.2	25.7	6.8	5.8	23.7	6.6
	♂	137	23	25	35.1	15.2	7.6	-	6.6	5.4	23.8	5.6
Uitkomst	♀	122	20	23	32.8	14.9	7.3	23.1	6.2	5.2	21.0	5.0
Boksburg	♀	124	19	25	34.0	16.0	7.6	23.8	6.4	5.8	22.2	6.2
	♀	125	19	25	35.7	16.1	7.9	25.5	6.7	5.9	23.8	5.7
	♀	120	19	24	33.8	15.8	7.7	23.8	6.3	5.7	22.3	5.7
	♀	124	19	24	36.2	15.8	7.6	25.7	6.9	6.0	24.4	5.8
Bronkhorstspruit	♂	145	-	25	35.7	15.3	7.7	26.1	7.5	6.0	23.9	6.0
	♂	125	-	23	32.0	14.6	7.5	23.0	6.2	5.5	21.0	5.8
	♂	125	-	23	32.0	14.4	7.3	22.8	6.2	5.4	21.2	5.7
	♂	147	-	24	35.0	15.0	7.7	26.7	7.6	-	23.3	5.9
	♀	102	-	21	29.6	13.9	7.2	21.5	5.5	5.6	19.3	6.1
	♀	125	-	23	30.7	14.3	7.6	22.1	5.6	5.5	20.5	5.9
	♀	120	-	22	30.1	15.2	7.7	-	5.8	5.7	20.3	5.6
Dullstroom	♂	150	15	20	35.8	14.5	6.9	25.8	8.3	4.5	23.0	5.0
Vlakfontein, Carolina	♀	140	21	24	36.0	14.7	6.9	26.5	7.6	6.1	23.6	6.4
	♀	130	20	25	35.4	14.2	6.7	24.0	7.1	6.2	22.7	6.2

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Warmbad, Carolina	♂	135	15	24	34.2	14.7	7.6	24.9	7.4	5.7	22.4	5.7
	♀	125	14	22	32.6	14.5	7.0	22.4	6.5	4.3	21.2	4.4
	♀	115	15	20	29.5	13.6	6.1	19.8	5.8	4.9	19.0	5.0
	♀	105	16	21	28.6	13.8	6.9	19.6	5.5	–	18.5	–
Oshoek	♀ imm.	82	15	19	23.8	13.1	6.8	17.1	5.0	–	15.3	–
Wakkerstroom	♂	177	20	25	37.0	15.7	7.7	26.4	8.0	5.4	25.1	5.1
	♂	–	–	–	35.2	14.7	7.7	25.6	7.4	–	22.9	5.5
	♂	155	21	25	36.2	15.8	8.0	26.2	7.6	6.0	24.0	6.2
	♂	165	23	25	37.4	25.0	7.8	26.6	8.2	–	24.4	5.4
	♀	–	–	–	36.5	15.0	8.1	28.3	8.5	5.7	24.7	5.9
	♀	150	19	24	36.2	14.8	7.7	26.4	8.1	6.0	23.9	6.2
	♀	120	23	21	–	14.5	7.3	23.0	6.5	5.5	20.6	–
Steynsdorp	♀	125	18	22	31.6	14.2	6.8	21.9	6.4	5.1	21.3	5.1
	♀	125	20	22	30.4	13.7	7.1	22.0	6.3	5.1	20.9	5.7
	♀	115	13	21	29.3	13.9	7.1	21.6	5.6	5.3	18.7	5.4
Forbes Reef	♂	140	20	25	33.3(7)	14.0(7)	7.0(7)	23.2(7)	6.7(7)	5.8(7)	22.0(7)	6.0(7)
	♂	135	15	25	32.0-34.6	13.6-14.6	6.8-7.3	21.7-24.8	6.4-7.6	5.5-6.3	21.5-22.8	5.6-6.4
	♂	140	20	24	S.D.=0.886	S.D.=0.389	S.D.=0.177	S.D.=1.128	S.D.=0.470	S.D.=0.298	S.D.=0.49	S.D.=0.298
	♂	135	16	24								
	♂	127	17	23								
	♂	140	18	24								
	♂	144	20	25								
Hogsback	♀	130	18	23	34.0	14.9	7.7	23.3	6.3	6.0	22.1	6.3
	–	122	18	23	30.8	15.1	7.6	21.7	5.6	5.5	20.4	6.3
	–	104	15	21	28.0	14.4	7.4	19.4	5.6	–	18.5	–

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Groenkloof	♂	130	20	25	36.2	16.4	7.8	25.8	7.1	5.6	23.0	6.1
	♂	127	26	23	34.2	15.2	7.7	23.6	6.7	6.1	21.9	–
	♂	120	24	23	30.4	15.0	7.6	21.2	5.8	–	19.9	–
	♀	120	24	22	30.8(5)	14.7(5)	7.2(5)	21.5(5)	5.7(5)	5.2	20.1(5)	5.6
	♀	120	27	23	29.7-32.5	14.5-15.0	7.0-7.3	20.4-22.5	5.5-6.0	–	19.0-21.4	–
	♀	115	24	23	S.D.=1.031	S.D.=0.217	S.D.=0.122	S.D.=0.757	S.D.=0.192	5.6	S.D.=0.858	5.9
	♀	114	20	22						5.2		5.7
	♀	117	25	23						5.3		5.7
Waterkloof	♂	160	–	25	36.6	15.8	7.8	–	7.5	6.0	24.1	5.7
	♂	158	–	28	37.2	15.5	7.9	27.1	7.8	6.0	25.6	6.0
	♀	130	–	24	33.8	16.1	7.9	25.3	6.1	5.6	22.4	5.7
	♀	–	–	–	33.7	14.9	7.5	26.2	8.1	6.0	22.6	6.4
	–	–	–	–	36.7	15.8	7.9	26.2	7.0	5.7	24.4	5.8
Fountains	♂	148	–	25	35.7(6)	15.9(6)	7.8(6)	25.9(5)	7.1(6)	6.1(6)	23.6(6)	6.5(5)
	♂	130	–	25	33.6-39.2	15.4-16.3	7.4-8.2	23.9-28.6	6.5-8.3	5.6-6.4	21.8-26.8	6.2-7.1
	♂	140	21	26.5	S.D.=2.083	S.D.=0.356	S.D.=0.308	S.D.=2.176	S.D.=0.766	S.D.=0.378	S.D.=1.799	S.D.=0.343
	♂	150	–	27								
	♂	152	19	27								
	♂	140	–	24								
	♀	145	–	25	34.0	15.9	7.8	24.3	6.2	5.6	22.1	–
	♀	142	–	24	34.6	15.4	7.8	25.6	6.8	–	23.5	5.0
	♀	112	–	23	29.4	14.4	7.1	20.8	5.5	–	19.9	5.4
	♀	143	–	25	34.7	15.2	7.8	25.1	6.5	5.5	22.3	6.1
Zwartkops	♂♂	128	22	24	35.1(6)	15.3(6)	7.5(6)	25.1(6)	7.0(8)	5.8(6)	23.8(8)	6.0(8)
		145	17	24	33.6-38.3	14.8-16.6	7.3-7.7	23.2-28.8	6.1-8.3	5.6-6.1	21.5-27.3	5.7-6.3
		130	15	24	S.D.=1.822	S.D.=0.641	S.D.=0.160	S.D.=2.034	S.D.=0.889	S.D.=0.217	S.D.=2.123	S.D.=0.278
		147	21	26								
		183	22	27								

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
		160	14	28								
		135	14	26								
		138	14	25								
	♂	132	21	23	-	13.9	-	-	6.8	-	20.4	-
	♀♀	130	15	23	34.3(8)	15.5(9)	7.5(9)	24.6(8)	6.6(11)	5.6(6)	22.3(12)	6.0(10)
		152	21	24	30.0-37.4	14.1-16.6	7.0-7.9	20.1-27.4	5.8-7.8	5.2-6.2	19.3-25.7	5.6-6.6
		164	21	28	S.D.=2.294	S.D.=0.709	S.D.=0.300	S.D.=2.466	S.D.=0.677	S.D.=0.361	S.D.=1.918	S.D.=0.297
		153	18	26								
		134	19	23								
		164	15	25								
		131	13	23								
		160	17	29								
		162	25	28								
		130	20	22								
		142	14	26								
		129	15	23								
		132	22	24								
	♀ imm.	115	13	21	27.6	14.2	7.8	19.0	5.3	-	17.5	-
Brooklyn	♂♂	147	25	28	37.7(5)	16.0(5)	7.8(5)	27.3(5)	7.7(5)	6.1(5)	25.2(5)	6.0(5)
		145	25	27	34.2-41.0	14.8-17.7	7.5-8.1	24.9-30.4	6.6-8.9	5.7-6.6	22.9-28.2	5.6-6.7
		148	29	28	S.D.=2.612	S.D.=1.073	S.D.=0.224	S.D.=2.142	S.D.=0.876	S.D.=0.370	S.D.=2.031	S.D.=0.409
		-	-	-								
		164	28	29								
	♀♀	122	28	23	33.3(12)	15.1(12)	7.6(12)	23.5(12)	6.3(12)	5.7(5)	21.7(12)	5.6(5)
		132	-	26	29.9-37.2	13.8-16.2	7.2-7.9	21.1-26.2	5.6-6.9	5.4-6.5	19.0-24.1	5.1-6.4
		117	25	23	S.D.=2.733	S.D.=0.691	S.D.=0.213	S.D.=1.712	S.D.=0.502	S.D.=0.439	S.D.=1.979	S.D.=0.472
		125	25	26								

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
		142	22	25								
		138	31	25								
		145	21	27								
		120	21	23								
		138	25	27								
		135	30	25								
		114	17	22								
		115	21	23								
Pretoria	♂	132	23	26	36.1	16.1	7.7	24.8	7.1	5.9	23.7	6.6
	♀	120	15	20	34.6	15.9	8.2	24.6	6.5	–	23.1	6.5
	♀	143	14	24	33.5	15.6	7.7	23.9	6.9	5.9	21.9	5.7
	♀	130	25	20	35.6	16.2	7.3	25.0	6.7	6.0	23.0	6.3
	♀	160	17	26	37.7	15.9	7.7	25.0	8.2	5.9	24.3	6.3
Irene	♂	–	–	–	38.1	16.6	7.5	27.2	7.7	6.1	26.1	5.7
	♂	134	15	26	35.5	16.7	8.1	25.1	7.1	5.9	23.0	6.3
	♂	–	–	–	35.5	16.4	8.1	25.9	7.0	5.7	23.4	6.2
	♂	–	–	–	34.9	15.9	7.7	26.2	7.4	5.6	23.6	5.7
	♀	–	–	–	35.5	16.4	8.0	26.3	6.8	5.9	23.8	5.5
Knoppieslaagte	♂	120	18	24	36.0	15.6	7.5	24.6	6.6	6.1	23.5	5.7
Garstfontein	♂	142	23	27	36.1	15.5	7.9	25.3	7.3	5.7	24.1	6.1
	♀	130	21	25	34.7	15.3	7.8	26.2	7.3	5.5	24.1	6.2
Koedoespoort	♂	122	21	24	32.8	14.7	7.5	22.8	6.6	5.2	21.4	5.9
	♀	117	25	24	33.2	15.8	7.1	22.8	5.7	5.7	21.8	6.2
	♀	130	25	23.5	33.4	14.7	7.3	22.9	6.2	5.8	21.7	5.7
Mountain view	♂	140	21	28	37.4	15.5	7.8	27.0	7.4	5.8	25.0	–
Blokspruit	♀	127	16	22	31.0	14.3	6.9	22.3	6.4	–	20.6	5.6
Elandsfontein	♂	145	19	23	33.4	13.2	7.2	23.3	6.8	5.9	22.6	5.6
	♀	150	18	25	33.1	13.8	7.1	23.8	6.3	5.8	22.2	5.9

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W	M.W.	U.T.R	L.J.	L.T.R.
Rosslyn	♂	130	25	25	35.3(5)	15.3(5)	7.3(5)	25.8(5)	6.8(5)	-	23.7(5)	-
	♂	142	24	26	32.7-37.5	14.8-15.9	7.1-7.9	22.1-28.6	5.5-7.8	5.5	21.2-25.3	4.9
	♂	146	21	28	S.D.=2.299	S.D.=0.406	S.D.=0.321	S.D.=3.187	S.D.=1.115	5.5	S.D.=1.981	5.6
	♂	130	24	24.5						5.3		5.7
	♂	156	24	27						5.8		5.7
	♀	140	26	25	34.4(12)	15.3(12)	7.3(12)	24.8(11)	6.6(12)	5.5(8)	22.7(12)	5.4(8)
	♀	130	23	24	31.1-37.2	14.2-16.3	6.2-7.9	22.1-28.3	5.7-7.8	5.0-5.9	20.0-25.3	4.9-5.8
	♀	147	25	27	S.D.=1.811	S.D.=0.605	S.D.=0.492	S.D.=1.720	S.D.=0.623	S.D.=0.297	S.D.=1.491	S.D.=0.333
	♀	145	25	27								
	♀	150	20	26								
	♀	145	19	26								
	♀	120	21	24								
	♀	135	17	25								
	♀	145	26	25								
	♀	140	25	26								
	♀	135	27	25								
	♀	152	29	26								
	♀ imm.	80	19	16	-	12.2	7.3	14.4	4.6	-	14.1	-
	♀ imm.	121	-	23.5	29.9	14.9	7.5	20.4	5.3	-	19.6	-
Skinner's Court	♂	125	-	23.5	33.6(5)	15.4(5)	7.6(5)	23.6(5)	6.6(5)	-	22.0(5)	6.0
	♂	125	25	24	31.0-40.5	14.8-16.4	7.3-8.4	20.5-29.3	5.9-8.2	5.9	19.2-28.0	6.4
	♂	117	25	23	S.D.=4.055	S.D.=0.756	S.D.=0.432	S.D.=3.692	S.D.=1.018	-	S.D.=3.529	-
	♂	130	20	26						5.9		6.1
	♂	160	20	32						7.0		7.1
	♀	145	19	25	33.6(7)	15.6(7)	7.2(7)	24.5(6)	6.4(7)	-	22.2(7)	6.2(7)
	♀	140	21	26.5	30.8-35.1	15.0-16.7	7.0-7.6	22.3-26.0	5.9-6.8	-	20.0-23.6	5.8-6.6
	♀	135	17	24	S.D.=1.506	S.D.=0.547	S.D.=0.214	S.D.=1.656	S.D.=0.364	5.5	S.D.=1.413	S.D.=0.293

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	♀	105	19	22						–		
	♀	145	15	26						6.2		
	♀	135	20	23						6.1		
	♀	125	25	25						–		
	♀	110	21	22	28.6	14.3	7.1	19.3	5.5	–	18.2	–
	–	–	–	–	32.2	15.3	7.2	23.8	5.9	5.6	21.2	6.1
	–	–	–	–	28.7	14.5	6.9	–	5.4	5.4	18.5	5.8
Rietondale	♂	111	15	20	33.4(5)	15.1(5)	7.4(5)	23.1(5)	6.3(5)	5.2	22.1(5)	5.9(5)
	♂	130	20	25	30.2-37.5	14.6-15.5	6.9-7.8	21.3-25.2	5.6-7.1	5.2	19.6-25.3	5.7-6.2
	♂	117	19	–	S.D.=2.660	S.D.=0.363	S.D.=0.339.	S.D.=1.636	S.D.=0.608	–	S.D.=2.082	S.D.=0.207
	♂	145	20	27						6.0		
	♂	140	20	26						5.6		
	♂	110	20	22	29.6	13.7	7.1	–	5.1	–	18.5	–
	♀	120	22	24	33.2(8)	14.9(7)	7.2(8)	23.3(6)	6.1(8)	5.5(8)	21.8(8)	5.9(8)
	♀	132	18	25	31.9-35.0	14.2-16.3	6.8-7.7	21.9-25.9	5.8-6.8	5.0-6.2	20.7-24.3	5.3-6.3
	♀	111	15	20	S.D.=1.224	S.D.=0.690	S.D.=0.315	S.D.=1.546	S.D.=0.338	S.D.=0.403	S.D.=1.256	S.D.=0.352
	♀	125	26	24								
	♀	136	21	20								
	♀	111	15	22								
	♀	130	20	25								
	♀	115	17	23								
Pretoria-Town lands	♂	142	–	26	35.3	15.1	7.0	23.9	7.0	5.3	22.9	5.7
Kilmerton	♂	145	25	25	36.1	15.1	7.2	25.7	7.4	–	24.5	6.3
	♀	140	–	24	33.1	15.4	7.3	23.1	6.0	5.7	22.4	5.3
Power Station	♀ imm.	113	15.5	24.5	31.0	15.0	7.2	21.1	5.8	–	19.8	–
Roodeplaat	–	143	17	23	35.6	15.5	7.4	27.8	7.3	5.5	24.5	5.0

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Rooikrans/Rustenburg	♂	124	14	24	29.0	12.9	6.0	20.2	5.3	5.2	18.0	5.1
	♂	–	–	–	34.0	14.2	7.3	26.0	6.8	5.7	23.1	5.9
	–	138	19	27	35.2	14.7	7.6	24.9	7.0	6.0	23.5	5.9
	–	131	20	26	34.5	14.5	7.6	25.1	7.2	5.8	23.3	5.7
Fairfield	♂ Imm.	125	16	21	26.5	12.5	6.6	17.5	4.9	–	17.4	–
	♀ Imm.	131	17	22	29.4	13.4	6.8	19.4	5.5	4.6	18.9	5.1
Welgegund	♀	–	–	–	35.1	16.2	7.7	27.3	7.2	5.7	24.0	6.1
Wilgekuil	♂	154	12	26	33.1(5)	13.5(5)	7.0(5)	22.9(5)	6.3(5)	5.5	22.1(5)	5.8
	♂	138	18	25	31.6-35.4	12.9-14.1	6.7-7.4	21.9-24.9	5.8-7.0	–	21.0-24.5	–
	♂	140	18	25	S.D.=1.588	S.D.=0.466	S.D.=0.261	S.D.=1.494	S.D.=0.607	5.4	S.D.=1.531	5.6
	♂	160	18	27						5.2		5.4
	♂	133	15	25						5.3		5.3
	♀	130	15	25	31.2	13.6	7.0	21.7	5.7	4.5	21.6	4.8
Mooivlei	♂ Imm.	111	14	22	28.8	13.1	6.7	19.8	5.2	4.7	19.4	4.6
	♂ Imm.	118	15	21	27.7	12.7	6.5	18.5	5.2	5.1	17.9	5.2
	♀ Imm.	117	16	23	26.9	13.4	6.6	–	5.0	–	18.9	–
	♀ Imm.	119	17	24	28.2	12.7	6.2	18.7	4.9	5.2	18.3	5.3
Bleskop	♂	140	17	23	32.6	14.3	7.3	23.4	6.1	5.8	21.2	6.5
	♀	135	20	25	33.0	13.6	7.0	23.4	6.3	5.9	21.2	6.2
Geelhoutkop	♂	134	22	24	34.6	14.0	6.8	–	6.9	5.9	22.6	6.4
	♀	143	22	26	37.1	15.4	7.6	26.4	7.2	5.9	24.2	6.4
	–	145	27	26	37.3	15.4	6.9	25.9	7.5	5.5	23.9	5.9
	–	134	21	26	34.7	14.4	7.1	24.1	6.8	5.5	23.2	5.7
	–	140	22	26	34.5	14.8	7.4	23.9	6.8	5.6	22.8	6.4
Rietspruit/Nylstroom	♀ Imm.	95	15	18	24.5	12.4	6.6	15.7	4.5	–	15.5	–

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Nylstroom	♂	118	22	23	36.8(7)	15.0(7)	17.8(8)	25.8(7)	7.1(8)	5.4(8)	24.4(8)	5.4(8)
	♂	150	20	24	34.6-39.1	13.9-15.9	7.2-8.3	23.6-27.7	6.4-7.6	4.5-5.7	22.9-26.8	4.9-5.8
	♂	145	18	25	S.D.=1.469	S.D.=0.702	S.D.=0.399	S.D.=1.416	S.D.=0.403	S.D.=0.374	S.D.=1.100	S.D.=0.327
	♂	138	14	24								
	♂	142	18	25								
	♂	142	18	25								
	♂	155	19	25								
	♂	145	18	25								
	♀	143	17	24	33.9(10)	14.5(10)	7.6(10)	23.6(9)	6.1(10)	5.5(9)	22.4(10)	5.5(10)
	♀	130	16	23	31.7-36.2	14.3-15.1	7.0-8.2	22.1-26.8	5.7-6.7	5.3-5.9	21.0-24.5	5.0-6.1
	♀	145	20	24	S.D.=1.523	S.D.=0.305	S.D.=0.307	S.D.=1.432	S.D.=0.368	S.D.=0.171	S.D.=1.129	S.D.=0.389
	♀	125	16	24								
	♀	131	19	24								
	♀	144	20	25								
	♀	147	15	25								
	♀	120	17	25								
	♀	121	17	25								
	♀	132	18	25								
	♀ Imm.	96	15	19	25.3	11.7	5.8	16.3	4.8	4.2	16.3	4.4
	–	141	16	25	37.6	15.5	7.3	27.1	7.5	5.3	25.7	5.2
	–	142	16	25	33.0	14.7	7.0	23.4	6.1	5.6	22.3	6.3
	– Imm.	112	13	19	24.0	12.4	6.3	16.1	4.3	–	15.7	–
Ubombo	♀	120	26	20	30.1	13.2	6.9	20.4	6.2	5.2	18.6	5.8
Karkloof	♀	–	–	–	34.5	14.7	6.8	–	7.0	5.3	23.6	5.5
	♀	149	16	25	31.8	14.0	7.5	21.9	6.7	–	21.0	–
Hilton Road	♀	115	20	27	30.9	14.6	7.4	22.3	6.3	5.8	20.4	–

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Dargle	♂	152	17	22	–	14.8	7.4	23.6	6.7	5.6	21.1	6.2
	♀	130	17	20	32.5	13.8	7.2	21.9	6.4	–	21.0	–
	♀	125	19	22	33.1	18.8	6.4	23.2	6.6	5.8	21.4	5.8
	♀	164	17	22	32.2	14.9	6.9	–	6.4	5.7	21.1	6.2
Malvern	♂	120	20	21	31.9	14.3	7.1	22.2	5.4	5.4	22.2	5.8
	♀	121	19	21	29.7	14.3	7.1	21.8	6.2	5.2	20.0	5.3
Balgowan	–	–	–	–	–	–	–	–	7.9	–	–	–
Manderston	–	–	–	–	–	–	–	24.8	6.6	–	–	–
Esparanza	♂	135	–	–	29.5	13.8	7.0	21.5	6.2	–	18.8	–
Bulwer	♂	155	–	–	35.5	15.2	7.9	25.9	7.4	–	–	–
Estcourt	♀	90	17	24	34.6	15.6	8.0	25.4	7.8	5.4	23.6	5.9
	♀	–	–	–	–	–	–	–	7.6	–	–	–
Howick	♂	142	13	23	33.5	15.3	7.5	24.3	6.5	5.2	21.2	5.5
Hillcrest	–	–	–	–	32.1	14.3	6.9	24.2	6.6	–	21.6	5.5
	– Imm.	–	–	–	27.7	13.4	7.0	19.0	5.3	–	16.9	–
Pietermaritzburg	♂	125	15	–	33.4(11)	14.3(11)	7.2(12)	24.6(9)	7.2(15)	5.7(5)	22.2(14)	5.8(11)
	♂	140	10	–	30.4-25.9	13.6-15.1	6.6-7.9	22.1-26.5	6.2-9.3	4.8-6.1	20.3-23.6	5.1-6.4
	♂	130	–	–	S.D.=2.097	S.D.=0.441	S.D.=0.354	S.D.=1.300	S.D.=0.867	S.D.=0.514	S.D.=0.899	S.D.=0.388
	♂	130	10	–								
	♂	130	20	–								
	♂	130	14	–								
	♂	140	17.5	25.5								
	♂	155	–	–								
	♂	140	–	–								
	♂	135	–	–								
	♂	155	–	–								

Continued/....

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	♂	150	10	–								
	♂	145	20	–								
	♂	150	18	–								
	♂	128	15.3	27								
	♂	145	10	–								
	♂	140	20	20								
	♂	135	–	–								
	♂	155	–	–								
	♀	144	–	–	32.4	14.0	7.3(6)	–	6.8(6)	–	21.1	–
	♀	140	17	25.5	–	–	7.1–7.7	24.2	6.3–8.2	–	–	–
	♀	–	–	–	32.8	14.5	S.D.=0.216	23.6	S.D.=0.695	–	–	–
	♀	140	15	–	34.0	14.9	–	25.0	–	5.5	22.5	5.0
	♀	133	14	–	30.5	13.8	–	–	–	–	19.5	–
	♀	140	17	–	–	–	–	–	–	–	23.1	–
	♀	140	–	–	–	–	–	–	–	–	–	–
	–	–	–	–	32.6(7)	14.4(8)	7.1(10)	–	6.4(11)	–	21.4(8)	5.6(5)
		–	–	–	30.4–35.0	13.3–15.6	6.6–7.6	–	6.0–7.7	5.2	20.0–23.0	5.3–6.2
		–	–	–	S.D.=1.955	S.D.=0.725	S.D.=0.318	–	S.D.=2.181	–	S.D.=1.194	S.D.=0.358
		–	–	–						5.5		
		–	–	–				24.1		–		–
		–	–	–	–	–		23.2		–	–	–
		–	–	–	–			–		5.9		–
		–	–	–				–		–	–	–
		–	–	–				25.5		–		
		–	–	–	–	–	–	25.4		–	–	–
		–	–	–	–	–		–		–		–
		147	17	23	–	–	–	–	–	–	–	–

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Durban	♀	146	20	23	–	–	–	21.2	6.0	–	–	–
Empangeni	♀	145	–	–	31.9	13.4	6.6	23.5	6.0	5.5	21.0	5.4
	–	135	20	–	31.5	13.9	7.3	24.0	7.6	5.7	21.3	5.7
	–	130	20	–	30.6	14.2	7.4	22.3	6.4	5.4	19.7	5.5
	–	125	16	–	28.3	13.4	7.4	20.1	6.0	–	18.3	–
Mseleni	♂	150	12	26	–	–	–	–	–	–	–	–
	♂	138	14	24	–	–	–	–	–	–	–	–
	♀	174	20	28	39.0	14.9	6.8	28.6	8.5	7.1	26.3	7.1
Maputa	♀	145	24	25	34.0	14.8	7.5	23.6	7.1	5.7	22.4	5.3
	♀ imm.	120	18	22	28.1	13.2	7.3	18.3	5.6	–	17.9	–
Munguzi	♂	134	19	23	33.3	14.4	7.2	23.4	7.1	–	22.1	5.6
Ingwavuma	♂	140	15	20	32.4	13.6	7.3	–	6.6	5.3	21.3	5.6
	♀	140	15	20	27.7	12.5	6.6	–	5.9	–	18.4	–
	♀	111	10	15	–	13.6	–	–	5.3	–	17.0	–
	♀	120	10	15	32.5	–	7.8	–	6.8	–	21.1	5.7
Port St. Johns	♂	137	14	21	34.3	–	7.7	24.3	7.1	5.1	22.4	5.2
	♂	146	19	25	33.7	14.4	7.6	24.3	7.4	5.4	23.0	5.7
	♀	133	19	22	–	–	–	–	–	–	–	–
	♀	–	–	–	–	–	–	–	7.2	–	–	–

Measurements of Cryptomys komatiensis

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Krantzview	♀	125	13	22	32.2	13.7	7.1	23.2	6.5	5.3	21.2	5.3
Arnhemburg	♂	120	14	21	30.7	14.2	7.4	21.2	6.5	5.4	20.2	5.5
	♂	130	18	23	33.4	14.4	7.3	24.0	6.9	5.6	22.0	5.9

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Locality	Sex	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
	♂	120	16	21	31.2	13.8	6.8	22.2	6.4	5.0	20.9	5.2
	♂ imm.	108	16	21	29.0	13.9	7.1	19.9	5.7	–	18.9	–
	♂ imm.	115	14	21	29.6	13.9	7.0	20.2	6.0	–	18.8	–
	♂ imm.	102	20	19	26.8	12.2	6.3	16.6	5.0	5.2	16.6	–
	♀	120	14	21	30.8	14.1	7.0	21.4	6.1	5.3	19.6	5.4
	♀	118	20	23	32.5	14.3	7.3	–	6.0	5.8	20.6	5.6
	♀	120	20	23	32.5	14.2	7.3	21.6	6.2	5.4	20.5	5.8
	–	120	18	21	29.3	13.8	7.0	20.6	6.3	5.0	19.0	5.2
Legogote	♂	109	11	19	–	–	–	–	–	–	–	–
Barberton	– imm.	117	18	20	29.0	13.9	6.6	21.0	6.0	5.1	18.4	4.8
	– imm.	107	18	19	28.7	13.3	6.9	19.5	5.8	4.7	17.7	4.8
Hektorspruit	♂♂	120	15	20	31.4(6)	13.9(6)	7.2(6)	22.0(6)	6.5(6)	4.9(6)	20.9(6)	4.9(6)
		120	15	20	30.6-32.0	13.0-14.2	6.9-7.9	21.5-22.9	6.1-7.4	4.4-5.3	20.3-21.5	4.4-5.4
		–	–	–	S.D.=0.512	S.D.=0.453	S.D.=0.367	S.D.=0.532	S.D.=0.453	S.D.=0.344	S.D.=0.458	S.D.=0.350
		–	–	–								
		105	15	20								
		115	18	25								
	♀	118	20	20	31.0	12.9	6.6	21.6	5.6	5.3	20.5	5.1
	♀	90	12	18	29.6	14.1	7.0	19.9	5.6	4.6	19.3	4.8
Acornhoek	♂	115	–	20	31.2	31.8	6.5	22.8	6.6	5.1	19.8	5.2
	♂	116	29	20	29.9	13.7	6.6	21.1	5.7	7.5	19.5	5.3
	♂	128	–	21	32.6	14.2	7.0	–	7.0	–	20.9	5.2
Ofcolaco	♂	121	14	21	29.6	13.9	6.7	20.3	6.5	4.9	19.2	5.4
	♂	133	15	20	30.5	14.4	6.5	22.5	6.8	4.8	20.5	5.1
	♀	130	15	20	30.4	13.7	7.0	21.4	6.3	5.5	20.3	5.4

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Mariepskop	♂♂	137	-	22	31.7(7)	14.0(7)	7.1(7)	22.4(7)	6.6(7)	5.0(7)	20.7(7)	5.1(7)
		122	-	20	29.0-34.6	13.4-14.8	6.8-7.4	20.1-24.3	5.9-7.2	4.6-5.6	18.7-22.3	4.8-5.4
		127	-	20	S.D.=2.037	S.D.=0.450	S.D.=0.247	S.D.=1.513	S.D.=0.577	S.D.=0.336	S.D.=1.498	S.D.=0.203
		120	-	22								
		115	13	19								
		127	-	20								
		117	-	19								
	♂	117	-	20	-	-	6.6	-	5.8	5.3	18.8	5.9
	♂	115	-	18	28.2	13.2	7.0	20.1	5.9	4.5	18.6	4.7
	♂	102	-	15	26.5	12.9	6.7	18.1	5.3	4.8	17.6	4.9
	♀♀	117	-	20	30.5(7)	13.5(7)	6.6(7)	21.2(7)	5.8(7)	4.9(7)	19.5(7)	4.9(7)
		123	-	20	29.7-31.1	12.8-14.3	6.1-7.3	20.3-22.0	5.5-6.1	4.8-5.3	18.7-20.3	4.6-5.4
		120	-	19	S.D.=0.571	S.D.=0.582	S.D.=0.389	S.D.=0.577	S.D.=0.308	S.D.=0.211	S.D.=0.515	S.D.=0.251
		122	-	18								
		117	-	20								
		122	-	20								
		127	-	20								
	♀	117	-	18	28.6	12.8	6.2	19.2	5.5	4.9	18.5	4.8
	♀	117	-	17	27.2	13.4	6.7	18.7	5.1	-	17.3	-
	♀	112	-	18	29.6	14.3	7.2	20.7	6.1	5.2	18.6	5.4
	♀	120	-	18	28.4	12.9	6.7	20.6	5.8	5.2	18.2	5.2
	♀	107	-	18	28.1	13.1	7.1	20.4	5.9	5.1	18.6	5.0
	♀	129	17	22	-	-	-	21.5	6.4	-	-	-
	♀	122	-	18	27.9	13.2	6.7	19.0	5.5	-	17.9	-
	♀	109	-	17	27.8	13.6	6.6	18.9	5.2	4.7	17.6	-
Makoetsi River	- Imm.	105	15	19	27.1	13.6	6.7	19.2	5.5	-	17.6	-

Continued/...

Locality	Sex.	H.B.	T.	H.F.	C.B.	B.C.	I.W.	Z.W.	M.W.	U.T.R.	L.J.	L.T.R.
Dzueni	♀	138	16	22	33.1	14.3	6.7	23.5	6.2	5.7	22.1	5.8
Faai Plots	♂	117	17	18	28.1	13.4	6.6	19.3	6.0	5.1	18.0	5.3
	♂	103	15	21	30.7	14.0	6.9	20.6	6.1	5.3	20.2	5.6
	♀	113	12	19	29.2	13.8	6.6	21.3	6.3	–	20.5	5.3
	–	112	18	20	–	13.0	6.7	–	5.1	–	18.0	–
Faai-Stungwane	♂	128	19	24	35.0	12.9	6.7	23.8	7.4	5.5	22.1	5.7
	♀	116	21	20	30.8	13.4	6.9	20.7	6.1	–	20.3	5.6
	♀	128	19	21	32.1	13.8	6.7	22.8	7.1	5.8	21.2	5.5
Woodbush	♂	130	16	22	33.6	14.7	7.1	23.9	7.0	5.9	22.2	6.8
	♂	115	20	21	29.7	14.3	7.4	21.4	5.9	6.0	19.4	–
	♂ Imm.	108	114	19	–	–	–	–	5.8	–	17.7	–
	♀	120	19	20	30.0	13.4	6.6	21.0	6.1	6.0	19.1	6.2
	♀	135	–	22	30.9	14.3	7.0	22.3	6.6	6.0	19.3	5.3
	♀ Imm.	105	17	19	26.8	13.0	6.4	18.9	5.1	–	17.1	–
Sterkloop	♀	115	17	20	30.4	13.3	6.7	20.5	6.1	4.7	19.3	4.8
	♀	120	23	19	–	–	7.0	–	6.7	4.6	19.8	4.6
Tzaneen Estate	♂	125	15	20	30.9	14.1	7.3	22.6	6.5	5.2	20.3	5.3
	♀ Imm.	65	7	13	–	–	–	–	–	–	–	–
	♀ Imm.	110	17	19	–	–	–	–	5.1	4.7	17.8	4.9
	♀ Imm.	108	12	18	–	–	–	–	4.6	–	14.8	–
	– Imm.	95	13	12	–	–	–	–	4.1	–	–	–