Systematics and biogeography of the genus *Mastomys* (Rodentia: Muridae) occurring in Namibia and adjacent countries.

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DEDICATION

This dissertation is dedicated to my father, Karl Eiseb, and my mentor, Cornelius Gerhardus “Neels” Coetzee, who both sadly passed away before the completion of the dissertation.

ZUSAMMENFASSUNG

Die Systematik der Gattung *Mastomys* im südlichen Afrika ist nicht gesichert und hat im Laufe der Jahre viele Veränderungen erlebt. Zudem sind die kleinen Säugetiere der Gattung *Mastomys* wichtige Nebenwirte für viele Krankheiten, die auch Menschen beinträchtigen können, und sie sind bedeutende landwirtschaftliche Schädlinge. Es ist jedoch nicht klar, ob die verschiedenen Arten den Menschen in einer ähnlichen Art und Weise beeinträchtigen. Daher ist das Wissen über den taxonomischen Status und das Verbreitungsgebiet der Mitglieder der Gattung *Mastomys* im südlichen Afrika von großer Bedeutung.

Das Ziel dieser Studie war, die Anzahl der *Mastomys*-Arten und ihrer geographischen Verbreitung in Namibia und Teilen von Botswana und Angola zu bestimmen. Im Ganzen wurden 352 Exemplare in diesen Ländern gefangen. Der methodische Ansatz umfasst sowohl traditionelle als auch geometrische Schädel-Morphometrie (396 Exemplare), Karyotypisierung mit einem Standard-Färbungsprotokoll (64 Exemplare) und Cytochrom-b-Gen-Sequenzierung (141 Exemplare).

Ergebnisse innerhalb der traditionellen Morphometrie-Studie lieferten keine klaren morphologischen Unterschiede zwischen den drei Arten, wohingegen die geometrische Morphometrie-Analyse erfolgreicher war. Hier zeigten die Ergebnisse bei drei Spezies deutliche dorsale und ventrale Unterschiede in der Schädelform.

Die Resultate der zytogenetischen und molekularen Methoden ergaben drei Formen von *Mastomys* mit unterschiedlichen Karyotypen und mtDNA in Namibia, Botswana und Angola. Diese wurden *M. coucha* (2n = 36, aFN = 60/60), *M. natalensis* (2n = 32, aFN = 57/58) und *M. shortridgei* (2n = 36, aFN = 51/52) zugeordnet. Die mtDNA Divergenz zwischen der Art *M. coucha* und *M. shortridgei* war relativ gering (1.3%), außerdem legte die „Moleküluhr“ (*molecular clock*) nahe, dass *M. shortridgei* ein aktueller Ableger von *M. coucha* (0.71 Mya) ist. Die chromosomalen Unterschiede zwischen *M. coucha* und *M. shortridgei* gehen auf perizentrische Inversionen zurück, die in den Chromosomen der früheren *M. shortridgei* Populationen aufgetreten sind. Perizentrische Inversionen verändern die

centromere Position des Chromosoms und beeinflussen direkt die Anzahl der Chromosomenarme im Karyotyp, nicht aber die diploide Anzahl.

Ein Modell der Entwässerungsentwicklung in Süd-Zentral-Afrika seit dem Mesozoikum erhellt die Ereignisse, die zu der späteren Divergenz des sumpfigen Lebensraum-Spezialisten *M. shortridgei* von dem semi-ariden Lebensraum-Generalisten *M. coucha* führten. Man nimmt an, dass der Paläo-Makgadikgadi See, im heutigen Botswana einen Großteil des östlichen Kalahari-Beckens bedeckte. Es könnte sein, dass Ausläufer früherer Populationen von *M. shortridgei* in Kontakt mit dem Paläo-Makgadikgadi See kammen und während des End-Pleistozäns bis zum frühen Holozän durch das Schrumpfen des Sees isoliert wurden. Im Laufe der Zeit haben sich die frühen Populationen von *M. shortridgei* an die lokalen sumpfigen Umweltbedingungen angepasst.

M. coucha und *M. natalensis* haben eine klar begrenzte geografischen Verteilung in Namibia, dies scheint durch Niederschlag beeinflusst zu sein: *M. coucha* tritt vor allem in den niederschlagsarmen Gebieten von Zentral-Namibia auf, *M. natalensis* dagegen in den niederschlagsreichen Gebieten im nördlich-zentralen und nordöstlichen Namibia und erstreckt sich bis nach Angola und in das nördliche Botswana hinein. Die *M. shortridgei*-Proben wurden nur in den Okavango-Sümpfen im Norden von Botswana und südöstlichen Angola gefunden.

Die Ergbnisse dieser Studie werden das gegenwärtige Verständnis der Systematik und Biogeographie der *Mastomys* im südlichen Afrika, auch als Voraussetzung für eine wirksame Schädlingsbekämpfung, verbessern.

SUMMARY

The systematics of the genus *Mastomys* in southern Africa is unstable and has experienced many changes over the years. Small mammals of the genus *Mastomys* are important reservoir hosts of many diseases affecting humans and they are significant agricultural pests. However, it is not clear if the different species affect humans in a similar way. Therefore, knowledge about taxonomic status and the distribution range of the members of the genus *Mastomys* in southern Africa is of great importance.

This study aims to summarise the patterns of morphological, cytogenetic and genetic variation of genus *Mastomys* across the south-west arid region of southern Africa, as well as clarifying the taxonomic status, identification keys and distribution limits in this region. A total of 352 specimens were trapped in these countries. The methodological approach included skull morphometrics- both traditional & geometric- (396 specimens), karyotyping using a standard staining protocol (64 specimens) and cytochrome-b gene sequencing (141 specimens).

Results obtained within the traditional morphometrics study did not yield clear morphological differences between the three species; however, geometric morphometrics analysis was more successful. Geometric morphmetrics results indicated clear differences, between the three species in the shape of the skulls based on landmarks from both the dorsal and ventral views.

Results obtained with cytogenetical and molecular methods revealed three forms of *Mastomys* with different karyotypes and mtDNA clades in Namibia, Botswana and Angola. These were assigned to *M. coucha* ($2n = 36$, $aFN = 60/60$), *M. natalensis* ($2n = 32$, $aFN = 57/58$) and *M. shortridgei* ($2n = 36$, $aFN = 51/52$). The mtDNA divergence between the species *M. coucha* and *M. shortridgei* was relatively low (1.3%), additionally the molecular clock estimated *M. shortridgei* to be a recent off-shoot of *M. coucha* (0.71 Mya). The chromosomal differences between *M. coucha* and *M. shortridgei* are due to pericentric inversions that occurred in chromosomes of ancestral *M. shortridgei* populations. Pericentric inversions alter centromere position

of the chromosome and directly influence the number of chromosome arms in the karyotype but not the diploid number.

A model of drainage evolution in south-central Africa since the Mesozoic may elucidate the events leading up to the eventual divergence of the swampy habitat specialist *M. shortridgei* from the semi-arid habitat generalist *M. coucha*. It is estimated that the lake Palaeo-Makgadikgadi, in present day Botswana, covered much of the eastern Kalahari basin. It could be that the peripheral ancestral population of *M. shortridgei* came in contact with the lake Palaeo-Makgadikgadi and was isolated with the shrinking lake Palaeo-Makgadikgadi during the End-Pleistocene to Early Holocene. Over time ancestral populations of *M. shortridgei* became adapted to the local swampy environmental conditions.

M. coucha and *M. natalensis* have a distinct geographical distribution in Namibia. This seems to be influenced by precipitation: *M. coucha* mainly occurs in the low rainfall areas of central Namibia, whereas *M. natalensis* occurs in higher rainfall areas of north-central and north-eastern Namibia, extending into Angola and northern Botswana. The *M. shortridgei* specimens were only trapped along the Okavango River swamps in northern Botswana and south-eastern Angola.

The results of this study will improve the current understanding of systematics and biogeography of *Mastomys* in southern Africa as the prerequisite of effective pest control.

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CHAPTER 1: INTRODUCTION

1.1. Rationale and scope of study

Rodentia is the largest order of living Mammalia, consisting of 2277 species; which is approximately 42% of the worldwide mammalian biodiversity (Wilson & Reeder, 2005). Hence, rodents are regarded as an extremely successful and well-defined assemblage of mammals, occurring throughout the world (De Graaff, 1981; Samuels, 2009). A consistent diagnostic character for all rodents is an upper and lower pair of arc-shaped, chisel edged incisors (Walker, 1968; Carleton, 1984); canines are absent and they are replaced by a comparatively long toothless gap, the diastema.

Rodents have adapted to most habitats and include terrestrial, fossorial, saltatorial, arboreal, gliding and semi-aquatic forms (Walker, 1968; Carleton, 1984). Most rodents are primarily omnivorous, feeding on bark, grass, seeds, other vegetation, insects and other animal matter. Some such as the grasshopper mice *Onychomys* feed on small vertebrates during certain months of the year (Jahoda, 1970). Rodents range in size from the smallest mice (e.g. *Micromys*, *Baiomys* and some *Mus*) which weigh only a few grams up to the largest living rodent, the Capybara, *Hydrochoerus hydrochaeris* that is pig sized and weighs up to 50 kg (Walker, 1968; Carleton, 1984).

Rodents are of great importance to mankind and knowledge of these creatures is of great value (De Graaff, 1981). Rodents often compete directly with man for natural resources. They thrive on plants and crops developed and domesticated by man, thereby competing directly with man for available food (Stenseth *et al.*, 2003). In many cases they are pests, feeding on and destroying agricultural crops and the damage they do to food stores is well known, where food is consumed or spoiled in silos, warehouses and individual homes (Stenseth *et al.*, 2003). They often carry parasites that transmit diseases to which man is susceptible, for example plague that ravaged Europe during the mid-14th century was transmitted by fleas from rats to humans (Meerburg *et al.*, 2009).

For the purpose of this study, rodents of the genus *Mastomys* Thomas, 1915 (Rodentia: Muridae) occurring in Namibia and neighbouring countries will be selected.

The African multimammate mouse genus *Mastomys* comprises of the following eight species that show little morphological separation, despite marked karyotypic differentiation (Britton-Davidian *et al.*, 1995; Musser & Carleton, 2005; Leirs, 2013; Monadjem *et al.*, 2015): *M. awashensis* Lavrenchenko, Likhnova & Baskevich, 1998; *M. coucha* (Smith, 1834); *M. erythroleucus* (Temminck, 1853); *M. huberti* (Wroughton, 1909); *M. kollmannspergeri* (Petter, 1957); *M. natalensis* (Smith, 1834); *M. pernanus* (Kershaw, 1921) and *M. shortridgei* (St. Leger, 1933).

1.2. Taxonomic history of genus *Mastomys*

The systematics of genus *Mastomys* has been very unstable, experiencing many changes according to different taxonomic treatments (e.g. Allen, 1939; Ellerman, 1941; Ellerman *et al.*, 1953; Missone, 1974; Meester *et al.*, 1986; Britton-Davidian *et al.*, 1995; Granjon *et al.*, 1997; Musser & Carleton, 2005).

At various times, different authors have either included the current genera as subgenera within *Praomys* Thomas, 1915, or have suggested linkages between them (Lecompte *et al.*, 2002). For example, *Hylomyscus* Thomas, 1926, *Mastomys* and *Myomys* Thomas, 1915 were considered as subgenera within *Rattus/Epimys* or *Praomys* (Ellerman *et al.*, 1953).

Thomas (1915) classified several genera under genus *Mus*, subgenus *Epimys*, based mainly on the mammary formula. The four subgenera were: *Aethomys*, *Praomys*, *Myomys* and *Mastomys*. However, these four subgenera were recognized as valid genera for the first time in 1939 by Allen. But Ellerman classified these four as subgenera of *Rattus* in 1941. Matthey (1958) subsequently, regarded *Rattus*, *Praomys* and *Mastomys* as distinct genera on the basis of chromosome studies. This was not supported by Davis (1965), who grouped *Mastomys*, *Myomys*, *Myomyscus* and *Hylomyscus* as subgenera of *Praomys*. However, Rosevear (1969), Meester *et al.* (1986) and Musser & Carleton (1993) proposed *Mastomys* as a separate genus on morphological grounds. The monophyly of *Mastomys* (Granjon *et al.*, 1997) was subsequently demonstrated via chromosomal analysis (Matthey, 1958; Lee & Martin, 1980; Britton-Davidian *et al.*, 1995), multivariate analysis of biometrical data (Van Der Straeten, 1979; Van Der Straeten & Robbins, 1997) and molecular results (Chevret *et al.*, 1994).

The genus *Mastomys* is represented in southern Africa by three species *Mastomys natalensis*, *Mastomys coucha* and *Mastomys shortridgei* (Meester *et al.*, 1986; Skinner & Chimimba, 2005). Coetzee (1975) and Green *et al.* (1980) stated that *M. natalensis* should be regarded as a species complex in southern Africa, since *M. natalensis* and *M. coucha* are sibling species. These two species were for many years considered to comprise a single species *M. natalensis* (Gordon, 1978; Meester *et al.*, 1986). In the late 1970s, cytogenetic evidence confirmed the existence of two sibling species *M. natalensis* and *M. coucha* (Gordon, 1978; Green *et al.*, 1978; Hallett, 1979).

Davis (1965) states that *M. shortridgei* closely resembles *M. natalensis* differing in having only five pairs of mammae which are arranged, as in *M. natalensis*, in a continuous row without clear separation into pectoral and inguinal sets, on the contrary Gordon (1985) described its mammary formula as being 8:8=16. According to Granjon *et al.* (1997), the karyotype of *M. shortridgei* is very similar to that of *M. coucha*, with 2n=36, aFN=50 with an almost complete G-band homology. However, *M. shortridgei* is poorly studied and its precise status still needs to be ascertained and will require other types of analysis other than morphology (cytogenetics, molecular phylogeny etc.) as its karyotype is closely related to that of *M. coucha* (Granjon *et al.,* 1997).

1.3. General species description

1.3.1. Morphology

1.3.1.1. The skull

The main skull characteristics distinguishing *Mastomys* species from other Murids are: the upper incisors are ungrooved; the greatest skull length in adults > 25 mm; and the mastoid process is narrow, forked and directed backwards, leaving an opening in the skull behind it (Fig. 1.1) (Lundholm, 1955; Meester *et al.*, 1986). The anterior palatal foramina reach from just between the molars up to the beginning of the middle root of M^1 and the palatine bone from the junction of M^1 and M^2 to the middle of M^2 (Robbins & Van der Straeten, 1989; Van der Straeten & Robbins, 1997; Van der Straeten, 1999).

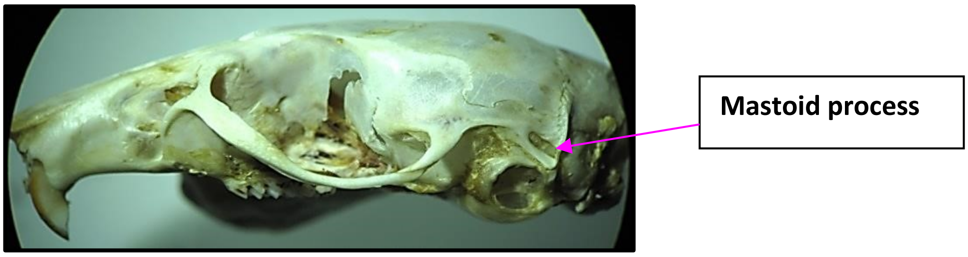


Figure 1.1. Mastoid process of *Mastomys*

1.3.1.2. Body morphology and colour

General body morphology for members of the genus *Mastomys* is that they are of small to moderate size, ±100-150 mm in body length with a tail of approximately the same size or shorter (Isaacson, 1975). The colour of the pelage varies considerably with the age of the animal and has also been noted to vary according to the terrain in which specimens are caught. The colour on the dorsal side may be grey to greyish-brown, brown or reddish buff, but it is lighter on the ventral side. The hairs of the belly are grey with white tips giving the belly its greyish aspect (Robbins & Van der Straeten, 1989; Van der Straeten, 1999). The unique feature is the large number of mammae in the female, which numbers from 8 to 12 pairs, which are continuously distributed from the pectoral to the inguinal region (Isaacson, 1975).

1.3.2. Distribution and habitat preference

According to Steppan *et al.* (2005), the murines originated in south-east Asia and expanded rapidly across all of the Old World. The fossil *Antemus chinjiensis* is considered to be the common ancestor of all murines, which was collected from 13.75 million-year-old Siwalik strata in north Pakistan (Jacobs & Downs, 1994; Freudenthal & Martin Suarez, 1999). Watts and Baverstock (1995) concluded that much of the murine radiation took place as a consequence of range expansion across the Old World followed by formation of geographic barriers to gene flow and any subsequent dispersal, leading to local radiations in each of the centres of diversity: Africa, Southeast Asia, Australia and New Guinea.

According to Ellerman *et al.* (1953) *Mastomys* distribution range extends from a southern limit in South Africa throughout Africa south of the Sahara up to a northern limit in Morocco on the far north-west. Because of its semi-commensal nature it has been suggested that this distribution is dependent on having followed early human population movements (Davis, 1953). The multimammate mice are thus extremely adaptable and one would expect to find variation in its basic ecology and behaviour. In northern Namibia it is commonly found in stacked thorn fences used for cattle enclosures and around cultivated fields (e.g. Millet and maize crops) (Coetzee, 1975; Massawe *et al.*, 2011). *Mastomys* can also be found in granaries and store rooms; and in thatch-roofed huts, which normally have walls built of clay-covered poles or sun-dried bricks (Coetzee, 1975; Monadjem *et al.*, 2011).

Mastomys natalensis is the most abundant and most widely distributed species in Africa (Fiedler, 1988; Musser & Carleton, 2005). It is recorded from 38 countries starting from South Africa through Mauritania and Morocco. The second most widely distributed species is *M. erythroleucus* which is recorded from 26 countries on the continent (Fiedler, 1988; Musser & Carleton, 2005). It is mainly found in central and west Africa and absent from northern and southern Africa. The third most widely distributed species is *M. huberti* and it is recorded from nine West African countries (Musser & Carleton, 2005).

The other species have limited distribution ranges. *Mastomys coucha* is found only in southern Africa. *Mastomys awashensis* is recorded only from Ethiopia where it prefers dry savanna and arable land; seemingly *M. shortridgei* has a restricted distribution along the Okavango River in Angola, Namibia and Botswana, where it was trapped amongst swamps and reed beds on the fringes of the river (Musser & Carleton, 2005).

Mastomys coucha is known to occur over a wide variety of habitats (Avenant, 1997). Rainfall is an important determinant of distributional patterns in the two species: *M. coucha* and *M. natalensis*, with *M. natalensis* generally occurring in areas receiving > 600 mm annual rainfall and *M. coucha* in drier areas with annual precipitation of < 700 mm (Gordon, 1984). The two species occur sympatrically within the 600-700 mm rainfall isohyets (Jackson & van Aarde, 2003). These data suggest that *M. natalensis* may not be able to tolerate the less mesic areas of the region. However, the absence of *M. coucha* from the wetter areas is unclear, although competitive exclusion could be involved (Jackson & van Aarde, 2003).

1.3.3. Behaviour

Mastomys is regarded as a semi-commensal rodent in most of Africa where it is found in close association with human habitation (Isaacson, 1975). The animal is nocturnal in habit and although omnivorous and having cannibalistic tendencies, it is mainly granivorous, living on seeds of wild grasses, corn, millet, maize and rice (Meester & Hallett, 1970).

In areas where true commensal rodent species such as *Rattus rattus* are present, *Mastomys* tends to give way (Shortridge, 1934; Davis, 1953; Monadjem *et al.*, 2011). This illustrates the peaceful nature of this rodent towards members of its own and other rodent species. Rarely does it fight, which probably indicates that its territorial instinct is very weak (Veenstra, 1958).

Mastomys is reluctant to make its own burrow, although it is capable of doing so in soft or cracked soil (Veenstra, 1958). By preference it will use burrows of other rodents, in southern Africa especially those of the gerbils *Gerbilliscus brantsii* and

Gerbilliscus leucogaster. The occupation of such burrows is usually for nesting purposes.

Shelter is taken in or under anything available, whether natural or man-made, e.g. outhouses, pole fences, plants, heaps of firewood, sheaves of grass, litter, refuse, sheets of corrugated iron, chicken runs, old tyres, or rubble. The multimammate mouse can climb and may be found in lofts. It is also a good swimmer and floater (Veenstra, 1958). These characteristics: its easy adaptability to the different environments provided by man and wild rodents respectively, are to a great extent responsible for its success as a genus.

The grouping pattern observed in multiple captures of numerous individuals suggests that social units are generally composed of one adult male, a number of adult females and juveniles. This grouping suggests a harem-like structure similar to the one described by Mihok (1979) for *Peromyscus maniculatus*, which can be classified as a polygynous mating system. In such a mating system, males rather than females are likely to compete intensely for mates, as variance in reproductive output is greater in males than in females (Dobson, 1982; Shields, 1987). This would explain the observed inter-male aggressiveness in dyadic encounters and avoidance in multiple captures.

1.3.4. Population Dynamics

In Senegal, the recent development of irrigated agriculture along the Senegal River has caused a significant extension of the distribution of *M. huberti* eastward, with an increase in population numbers and apparent individual survival (Duplantier, 1998). The relation between the quality (including duration, distribution, and total amount of rainfall) of the rainy season and variation in abundance has been studied in detail for *M. erythroleucus* from the Sahelian region of Senegal (Hubert & Adam, 1985). There, the reproductive period appeared to correlate quite closely with rainfall period, with pregnant females being recorded principally during the rainy months (Duplantier, 1998).

As a result, years with especially long rainy seasons are also years of extended reproductive periods, generally, for *Mastomys*, which may lead to outbreak situations, as observed in 1978-1979 (Granjon *et al.*, 2005). During such years, young born at the beginning of the reproductive period mature rapidly and breed during the same season (Granjon *et al.*, 2005).

In Tanzania, dynamics of populations of *M. natalensis* are similar, even though the rainy season is longer, with 2 distinct peaks of rainfall (Leirs *et al.,* 1993; 1996). In Tanzania, the onset of heavy rains (March-May) triggers reproductive activity, which more or less continues throughout the dry season. Then, if the first peak of the rainy season is high (December) maturation of the new generation is accelerated and these individuals may reproduce quicker, before the return of the main rainy season (Leirs *et al.,* 1996).

The situation is different in populations of *M. huberti* from the inner delta of the Niger River in Mali (Granjon *et al.,* 2005). Maximum abundance was observed in October 2002 immediately after the poorest rainy season of the study period, whereas rodent populations disappeared in October 2003 just after the end of the highest rainy season. The pattern of flooding interacts with local rainfall pattern in a complex way (Granjon *et al.,* 2005).

Although total rainfall and maximum flood height were highly correlated in this study, they may have contrasting effects on rodent abundance (Granjon *et al.*, 2005). By reducing areas available to rodents, floods probably reduce their numbers, occasionally to local extinction. Six months are sufficient for demographic recovery after a local population crash after an important flooding event (Granjon *et al.,* 2005).

The delay of the breeding period relative to the rainy season indicates somewhat different dynamics of populations of *M. huberti* in the inner delta of the Niger River compared to *M. erythroleucus* and *M. natalensis* in Senegal and Tanzania respectively (Granjon *et al.,* 2005).

This differs from the Kafue River floodplain in Zambia, where reproductions of small mammals (and especially *M. natalensis*) was concentrated at the height and end of the rainy season, and was at its minimum early in the dry season when populations were displaced by the flood (Sheppe, 1972). An important difference between the Zambian and Malian situation lies in the time lag between the rainfall and flood peaks, which is at least 4 months in Zambia compared to only 2 months in Mali. Another difference may be that rodents in the inner delta of the Niger River are less likely to escape flooding than on the more linear Zambian system; in the inner delta of the Niger, the near absence of topographic variation over a vast area makes the flooding affect a vast area uniformly (Granjon *et al.,* 2005), limiting refuges for rodents.

Germinating grasses are known to impact reproductive condition of the female *Mastomys* (Linn, 1991; Firquet *et al.,* 1996). In Tanzania, vegetation starts lush growth soon after the rains, and this is when the animals start breeding (Leirs *et al.,* 1994). Similarly in the Kafue flats of Zambia, rodents breed soon after the rains when vegetation growth is at its maximum; populations decline and reproduction stops when the area is flooded several months later (Sheppe, 1972).

1.3.5. Diet of *Mastomys natalensis*

Mastomys natalensis is known to feed on a variety of food materials, including seeds, insects, and grasses, whose consumption is subject to seasonal availability (Field, 1975; Leirs *et al.*, 1994; Oguge, 1995; Monadjem, 1998; Mulungu *et al.*, 2011a, 2011b).

In the dry season (June to October) of Swaziland, the diet of *M. natalensis* consisted entirely of foliage (Monadjem, 1998). Seeds were an important component of the diet in the wet months between November and May, while arthropods were part of the diet only in the middle of the wet season between January and April (Monadjem, 1998). Similar results were obtained of *Mastomys natalensis* diet in Tanzania by Leirs *et al.* (1994). Plant material was predominant in stomach contents, and also, grass and arthropod consumption corresponded broadly with rainfall and reproductive patterns (Leirs *et al.*, 1994).

1.3.6. Reproduction & Development

The average gestation period for *M. natalensis* has been determined as 23 days, with a 25 day interval between litters (Olif, 1953; Davis, 1963; Duplantier *et al.*, 1996). The age at first litter can be regarded as 54 days (Meester, 1960). This means that a female who has young at the onset of the breeding season might give birth to a fourth generation during the 9 to 10 months of the main breeding period (Coetzee, 1975).

Mean litter size of *M. natalensis* in Africa varies from approximately 10-13 in natural populations (Brambell & Davis, 1941; Chapman *et al.,* 1959; Coetzee, 1965; Hanney, 1965; Delaney & Neal, 1969; Chidumayo, 1984; Leirs & Verheyen, 1995; Monadjem, 1998; Makundi *et al.*, 2007) and approximately seven in laboratory colonies (Davis, 1963). Both Hanney (1965) and Coetzee (1967) found that the litter size is related to the body size of the females.

Coetzee (1967) recorded a 15.5% loss between the number of the ova formed and the number of healthy foetuses for *M. natalensis*. Meester (1960) showed a 17.3% death rate between birth and weaning age, and Hatt (1963) showed a 20.8% preweaning death rate. The mean age at death due to natural causes for the two laboratory stocks at the Medical Ecology Centre in Johannesburg is 395 and 487 days (Davis, 1963). De Wit (1972) calculated the estimated maximum life-span of free living *Mastomys* individuals as 339 days.

After a 21 day period, *M. erythroleucus* females gives birth to an average of 7.1 young, of which 80% survive to weaning (Duplantier *et al.,* 1996). The mean interval between two successive litters is 61 days (Duplantier *et al.,* 1996). *M. huberti* females: gives birth to young after 22 day gestation period. The mean litter size is 6.4 and 72% of newborn survive to weaning. Sixty eight days separate two successive litters (Duplantier *et al.,* 1996). *M. natalensis* females: gives birth to young after 21 day gestation period, produce 6.5 young every 53 days and only 50% of them survive to weaning (Duplantier *et al.,* 1996).

1.3.7. Public health and economic implications

Mastomys natalensis was shown to be highly resistant to experimental plague infection and *M. coucha* was shown to be highly susceptible to it (Isaacson, Taylor & Arntzen, 1983). *Mastomys coucha* has been implicated as the link between sylvatic (wild rodent) plague foci and the domestic environment in southern Africa.

Mastomys coucha is known to enter deserted gerbil burrows where it can become infected with plague and transfer it to rodents in the domestic environment, or to cats, dogs and man (Eckard, 1998). *Mastomys coucha* occurs in the plague enzootic (localized) areas of South Africa and in certain parts of the south-eastern Cape and former Transkei where both *M. coucha* and *M. natalensis* are found (Department of Health and Welfare, 1982).

Plague was first noticed in northern Namibia in 1931 (Groepe, 1993). This outbreak started in Northern Cape Province of South Africa and crossed into the central regions of Namibia from which it moved gradually to the northern areas where it became stabilized (Groepe, 1993; Shangula, 1998). It maintained foci in 2 districts, namely Engela and Onandjokwe in northern Namibia covering an area of 2000 km^2 (Shangula, 1998). Transmission is believed to be through flea bites or through the ingestion of infested animal tissue, by human beings. Mouse meat was considered a delicacy in this area (Shangula, 1998).

The number of plague cases recorded in Namibia between 1983 and 1997 are as follows: cases (3316), confirmed (645), deaths (128) with an average case-fatality rate of 3.86 (Shangula, 1998). Most laboratory confirmed cases occurred in the 9-10 year age group, followed by the 0-9 year age group (Shangula, 1998). Rodents found in the plague focal area were: *Rhabdomys pumilio*, *Tatera leucogaster* and *Mastomys* species (Groepe, 1993; Shangula, 1998).

1.4. Morphometric study of *Mastomys*

According to Zelditch *et al.* (2004), morphometrics is simply a quantitative way of addressing the shape comparisons that have always interested biologists.

Morphometrics seems closer to algebra or statistics than to morphology. Morphometrics is a branch of mathematical shape analysis. The way we extract information from morphometric data involve mathematical operations rather than concepts rooted in biological intuition or classical morphology. Morphometrics can be a branch of morphology as much as it is a branch of statistics.

Morphometric questions come from a variety of studies including: the nature and origin of polymorphism-sexual dimorphism, life stages, taxonomic-geographic variation in centroids, variation within and differences among taxa, assignment of individuals to taxa etc. (Marcus, 1990). There are two approaches to morphometrics practised today: Traditional Morphometrics and Geometric Morphometrics.

1.4.1. Traditional morphometrics

The word traditional refers to the body of statistical techniques available for morphometric analysis which have been applied in the past 20 or 30 years (Marcus, 1990). These include: Principal Component Analysis, Principal Coordinate Analysis, Factor Analysis, Discriminant Analysis, Canonical Variate Analysis and Multivariate Analysis of Variance (Marcus, 1990). The abovementioned statistical analysis techniques are largely applied to measurement or distance data (Marcus, 1990).

Traditionally, the variables used in morphometric analyses are usually lengths and widths of structures and distances between certain landmarks, and these are measured directly on the specimen (Rohlf, 1990). The results are expressed numerically and graphically in terms of linear combinations of the measured variable. It is not possible to recover the shape of the original form from the usual data matrices of distance measurements. The overall form of the organism is not used in the analysis (Rohlf & Marcus, 1993).

According to Zelditch *et al.* (2004), such a data set contains little information about shape, and some of that information is ambiguous. These kinds of data sets contain less information than they appear to hold because many measurements overlap or run in similar directions (Zelditch *et al.*, 2004). Several of the measurements radiate from a single point, so their values cannot be completely independent. Also missing from this type of measurement scheme is information about the spatial relationships among measurements. Finally, the measurements in this scheme may not sample homologous features of the organism (Zelditch *et al.*, 2004).

When all of the limitations of the traditional measurement scheme are considered, it is apparent that the number of measurements greatly overestimates the amount of shape information that is collected. The classical measurement scheme can be greatly improved by the box truss, a scheme developed by Strauss & Bookstein (1982) and Bookstein *et al*. (1985). This set of measurements samples more directions of the organism and the measurements are more evenly spaced.

The endpoints of all of the measurements are biologically homologous anatomical loci called- **landmarks**. These features make the truss an improvement over the classical measurement scheme, but it still produces a list of numbers (values of segment lengths).

One problem of the traditional morphometrics scheme is that it does not collect all of the information that could be collected. Many of the measurements are redundant and span large regions of the organism. We would need large number of samples before any mathematical manipulations or perform valid tests of hypothesis. The results would be, also, difficult to interpret because there would be overwhelming pieces of information for each specimen, for each trend or difference. We need to reduce the measurements to select that will be most likely informative.

It is clear that we need another method to get the same shape information but without the excessive redundancy. The first method (traditional morphometrics) also measures size rather than shape- each length is the magnitude of a dimension, a measure of size.

We should expect size to be the dominant explanation for the variance in traditional morphometrics because these measurements are measurements of size. We should be concerned about the possibility that the variance in shape is not fully explained by the variance in size, but is simply overwhelmed by it.

One other limitation of traditional morphometrics is that the measurements convey no information about their geometric structure.

1.4.2. Geometric morphometrics

Data are recorded to capture the geometry of the structure being studied (Corti *et al.*, 1996; Viscosi & Cardini, 2011). This is in the form of two-dimensional or three-dimensional coordinates of morphological landmark points (Fadda & Corti, 2000, 2001). The coordinates are more useful than traditional measurements, and the usual distance measurements can be computed from the coordinates (Rohlf, 1998, 2002). Emphasis is given to recording homologous landmarks; this allows a complete biological interpretation of the results. One can then report that certain structures have moved relative to others. The geometrical relationships among landmarks are not inherent in the raw coordinates themselves (Rohlf & Marcus, 1993).

Geometric morphometrics allows us to visualize differences among complex shapes with nearly the same facility as we can visualize differences among circles, kidneys and letters of the alphabet. Mathematics provides the models used to analyse data and the models underlying exploratory methods (such as principal component analysis). Mathematics provides a theory of measurement that we use to obtain data in the first place (Zelditch *et al.*, 2004; Viscosi & Cardini, 2011).

In geometric morphometrics shape is defined as "all the geometric information that remains when location, scale and rotational effects are filtered out from an object" (Kendall, 1977). Representing an organism solely by a configuration of landmarks leaves out some aspects of what we might normally mean by shape, such as curvature. Curvature is a feature of an object that remains after filtering out location, scale and rotational effects, but it is not captured effectively by the coordinates of a set of landmarks (Zelditch *et al.*, 2004; Webster & Sheets, 2010; Viscosi & Cardini, 2011).

Shape analysis plays an important role in many kinds of biological studies. A variety of biological processes produce differences in shape between individuals or their parts. Differences in shape may signal different functional roles played by the same parts, different responses to the same selective pressures as well as differences in processes of growth and morphogenesis (Zelditch *et al*., 2004; Webster & Sheets, 2010; Viscosi & Cardini, 2011).

According to Kendall's definition of shape, scale needs to be removed to extract differences in shape between two configurations (Kendall, 1977). This statement implies that scale provides a definition of size that is independent of the definition of shape (Kendall, 1977). Before computing geometric scale, we need to determine the location of the centre of the form (its "centroid") and calculate the distance between each landmark and the centroid. Centroid size quantity is obtained by computing geometric scale by calculating the square of each of those distances, summing all the squared distances, and then taking the square root of that sum. Centroid size is the one measure of size that is mathematically independent of shape. Centroid size may be correlated with shape because larger organisms are usually shaped differently than smaller ones (Zelditch *et al*., 2004; Webster & Sheets, 2010; Viscosi & Cardini, 2011).

The concept of homology plays a crucial role in landmark-based morphometrics. Homology has been stressed above all criteria for selecting landmarks in geometric morphometrics. The primary mathematical issue here is the interpretation of biological change as a deformation: a smooth mapping of one set of points to corresponding points in another form. The mapping only makes sense if the points are truly corresponding and that correspondence requires more than that landmarks have the same name (Zelditch *et al*., 2004; Webster & Sheets, 2010; Viscosi & Cardini, 2011).

Correspondence need not imply biological homology- we might think of homology in functional terms. We might view points as corresponding to each other because they are located at the end of an input lever arm in two different organisms. The landmark is not just serving a correspondence function; it must also be the same anatomical locus.

Biologists think about homology in terms of organismal parts or characters, whereas mathematicians think about homology in terms of individual loci (points) on those parts. Our objective, as biologists in selecting landmarks is to permit making inferences about the regions between them- we are not interested in the landmarks *per se*, but in shapes of the morphological structures on which those landmarks lie. The role of landmarks is to pin down those structures at discrete points that we can recognise as the same on all organisms. This means that the data *are* the landmarks, the individual loci. We need to recognise that structures are homologous as structures because they are discrete and recognisable in all specimens (Zelditch *et al.,* 2004; Webster & Sheets, 2010; Viscosi & Cardini, 2011).

We can also apply the same criteria to intersections of structures, or to their centres or to their tips. If discrete and recognisable structures are homologous as structures, then discrete and recognisable locations on them are, therefore, homologous as points. The mathematical framework for thinking of homology is the idea of a deformation; which extends the correspondence of sampled points to un-sampled points lying between. If we use a model of deformation, we can then draw a picture of change in shape that extends that change over the whole form. In that sense, the deformation *imputes* homology to intervening points (Zelditch *et al*., 2004).

Landmarks are: homologous anatomical loci; do not alter their topological position relative to other landmarks; provide adequate coverage of the morphology; can be found repeatedly and reliably; lie within the same plane (Zelditch *et al*., 2004). If we consider a sample of landmarks on the skull; when looking at the results, we can observe changes in the relative positions of landmarks that imply changes in the proportions of structures sampled by them. We can visualise the impact of those changes for the shape of the skull using the deformed grid that stretches where regions are enlarged and contracts where regions are reduced (Zelditch *et al*., 2004; Webster & Sheets, 2010; Viscosi & Cardini, 2011).

Bookstein (1991) classified landmarks into three categories: Type 1, Type 2 and Type 3. Type 1 landmarks are optimal, Type 2 is more problematic and Type 3 might not even be considered for landmarks. This classification is based on two interrelated considerations: one is that landmarks ought to be locally defined, and the degree to which they are locally defined determines their classification; the other is the type of epigenetic explanations in which they can enter.

Landmarks are locally defined when they are located by particular structures close to the point. For example, the intersection between three bony sutures is locally defined. For these Type 1 landmarks you do not need to mention any structures far away from that point (Bookstein, 1991). The Type 2 landmarks include such points as the tip of a tooth or end of a bony process, and they are defined as extremes of curvature or points furthest along some structure (Bookstein, 1991). The Type 3 landmarks are not defined by any structures surrounding or near any point; instead it is defined by being at an extreme distance from another point (Bookstein, 1991).

Type 1 landmarks allow you to identify directions of forces that impinge on a structure, or to recognise the effects of processes moving the landmarks (Bookstein, 1991). This is possible because Type 1 landmarks are surrounded in all directions. Type 2 landmarks are lacking information from surrounding tissues in at least one direction such that you cannot distinguish between several possible directions in which forces might be applied. For example, one possibility is that forces are applied laterally to a structure, along its boundary, but another possibility is that some combination of forces is applied perpendicular to the boundary, some outward and some inward (Bookstein, 1991).

1.4.3. Morphometrics study objectives

a) to assess error levels associated with morphometric characters in order to select characters and landmarks with low error levels for use in subsequent analysis
b) to investigate patterns of non-geographic (or intra population) size and shape variation at the level of sexual dimorphism and age variation; furthermore to decide whether to pool the specimens from different age classes and sexes for further geographic analysis
c) to define the nature and extent of geographic variation within and among populations of *M. coucha*, *M. natalensis* and *M. shortridgei*
d) to elucidate morphological and morphometric diagnostic characters to distinguish between the three species *M. coucha*, *M. natalensis* and *M. shortridgei*

e) to assess which method among traditional and geometric morphometrics is more effective to distinguish between the three species of *Mastomys*

1.5. Cytogenetical study of *Mastomys*

Cytogenetics is a branch of genetics that correlates the structure, number and behaviour of chromosomes with heredity and variation (White, 1973; Gupta, 1985). Scientist, Eduard Strasburger, discovered thread-like structures which appeared during cell division in the year 1875 (Stewart, 2008). These thread like structures were called chromosomes due to their affinity for basic dyes. The term chromosome is derived from two Greek words; chrom = colour, soma = body (Gupta, 1985). Chromosomes contributed to the division of cells and they are of prime importance as they carry the genes which are the hereditary material. Furthermore, chromosomes are of paramount interest for the understanding of evolutionary problems (Fredga, 1977).

Chromosome morphology changes during cell division and mitotic metaphase is the most suitable stage for studies on chromosome morphology. In mitotic metaphase chromosomes, the following structural features can be seen under the light microscope: chromatid and centromere. Each metaphase chromosome appears to be longitudinally divided into two identical parts each of which is called a chromatid. Both the chromatids of a chromosome appear to be joined together at a point known as the centromere. Therefore, centromere, is the region where two sister chromatids appear to be joined during mitotic metaphase (Stewart, 2008).

Depending on position of the centromeres, chromosomes can further be grouped as:
a) **Metacentric**: Centromere is located exactly at the centre of the chromosome, i.e. both arms are equal in size. Such chromosomes assume a ‘V’ shape at anaphase; b) **Submetacentric**: The centromere is located on one side of the centre point such that one arm is longer than the other. These chromosomes become ‘J’ or ‘L’ shaped at anaphase; c) **Acrocentric**: Centromere is located close to one end of the chromosome and thus giving a very short arm and a very long arm. These chromosomes acquire ‘J’ shape or rod shape during anaphase; and d) **Telocentric**:

Centromere is located at one end of the chromosome so that the chromosome has only one arm. These chromosomes are ‘I” shaped or rod shaped.

The general morphology (size and number of chromosomes, position of centromere, presence of secondary constriction and size of satellite bodies) of somatic chromosomal complement of an individual constitutes its karyotype. It can be defined as “the characteristic features by which a set of chromosomes of a species is identified”. Generally, karyotype is represented by arranging the chromosomes in descending order of size, keeping their centromeres in the same line. Thus the largest chromosome is placed on extreme left and the shortest on extreme right. The karyotype of a species can be represented diagrammatically showing all the morphological features of chromosomes. Such a diagram is known as an ideogram or an ideotype (Stewart, 2008).

Karyotype descriptions constitute the primary tool for rodent species identification, as it has been established and generally accepted that the reason behind the high diversity shown by this mammalian order is related to its high rate of chromosomal mutation (King, 1993; Corti, 2002).

In many taxa of rodents, the mechanisms of speciation often involve chromosomal rearrangements. Therefore karyotype analysis assumes a significant value and the chromosomes involved in such rearrangements can be identified by banding techniques (Filippucci & Kotsakis, 1995).

The most widely used banding methods are G-banding (Giemsa-banding), R-banding (Reverse-banding) and C-banding (Graphodatsky *et al.*, 2011). G-banding and R-banding produce a characteristic pattern of contrasting dark and light transverse bands on the chromosomes. Banding made it possible to identify homologous chromosomes and construct chromosomal nomenclatures for many species. With banding homologous chromosomes, chromosome segments and rearrangements could be identified.

One important source of karyotype variability in mammals is related to heterochromatin. Once the amount of heterochomatin is subtracted from total genome content all mammals have very similar genome sizes. Species of mammals differ considerably in the heterochromatin content and its location. Heterochromatin is most often detected using C-banding (Hsu & Arrighi, 1971) and early studies using C-banding showed that differences in the fundamental number (i.e., the number of chromosome arms) could be entirely due to the addition of heterochromatic chromosome arms. It is well documented that heterochromatin may consists of different types of repetitive DNA, not all seen with C-banding, and it can vary greatly between karyotypes of even closely related species.

In comparative cytogenetics, chromosome homology between species was proposed on the basis of similarities in banding patterns. According to Graphodatsky *et al* (2011), closely related species often have very similar banding patterns and karyotype divergence in most taxonomic groups follow their phylogenetic relationship although there are notable exceptions.

According to O'Connor (2008), cytogenetics entered the molecular era with the introduction of *in situ* hybridization, a procedure that allows researchers to locate the positions of specific DNA sequences on chromosomes. Most *in situ* hybridization procedures use fluorescent probes to detect DNA sequences, and the process is commonly referred to as FISH (fluorescence *in situ* hybridization) (Waters *et al.*, 1998; Trask, 2002; Speicher & Carter, 2005). FISH procedures are important in the determination of various chromosomal changes, including deletions, duplications and translocations (Waters *et al.*, 1998; Trask, 2002; Speicher & Carter, 2005).

FISH procedures were used successfully for chromosome studies in small mammals: bats of Madagascar (Richards *et al.*, 2010), African four-striped mouse *Rhabdomys pumilio* (Rambau & Robinson, 2003), African vlei rats *Otomys irroratus* (Engelbrecht *et al.*, 2011) and Neotropical rodents *Necromys lasiurus* and *Thaptomys nigrita* (Hass *et al.*, 2011). The use of FISH procedures was not feasible in this study because of lack of adequate equipment within Namibia.

1.5.1. Cytogenetical study objectives

- to determine the chromosome number (2n) and the autosomal fundamental number (aFN) of the studied *Mastomys* species.
- to describe chromosome morphology and characterize karyotypes of the studied *Mastomys* species.

1.6. Molecular study of *Mastomys*

The present study was mainly based on the analyses of mtDNA data which are valuable for understanding evolutionary relationships among species, populations and individuals (Irwin *et al.*, 1991; Russo, 2009). Animal mtDNA is a duplex, covalently closed circular molecule (Moritz *et al.*, 1987). Its gene content appears to be conserved: There are two ribosomal RNA (rRNA) genes, 22 transfer RNA (tRNA) genes and 13 protein genes which code for subunits of enzymes functioning in electron transport or ATP synthesis (Moritz & Brown, 1987; Moritz *et al.*, 1987; Russo, 2009). A "control" region is present, but lacks structural genes and contains sequences that initiate replication and transcription (Moritz & Brown, 1987).

Most research on animals has used single mitochondrial DNA genes to assess population or low-level taxonomic relationships (Rocha-Olivares *et al.*, 1999). Cytochrome b (cyt-b) has been considered one of the most useful genes for phylogenetic work, and is probably the best-known mitochondrial gene with respect to structure and function of its protein product (Esposti *et al.*, 1993). Cyt-b gene contains both slowly and rapidly evolving codon positions, as well as more conservative and more variable regions or domains overall (Farias *et al.*, 2001).

The cyt-b gene has been used for a diversity of systematic questions, from "deep" phylogeny (e.g. Irwin *et al.*, 1991; Cantatore *et al.*, 1994) to the population and recent divergence levels (Sturmbauer & Meyer, 1992). However, many problems have been encountered when using cyt-b, including base compositional biases, rate variation between lineages, saturation at third codon positions, and limited variation in first and second codon position, resulting in little phylogenetic information for "deep" evolutionary questions, or few informative sites for the third codon position at the population levels (Meyer, 1994).

Despite potential limitations of the cyt-b gene, it has proved useful in addressing questions about relationships among and within species for a range of taxa (Nicolas *et al.*, 2008a; Nicolas *et al.*, 2008b; Brouat *et al.*, 2009; Lamb *et al.*, 2014). The gene has also successfully been used to study systematic relationships in a number of murid rodents (Smith & Patton, 1993, 1999; Russo *et al.*, 2006; Nicolas *et al.*, 2010).

The analysis of the cytochrome b gene in this study was also augmented by a phylogeographic approach which represents an "mtDNA bridge between population genetics and systematics" (Avise *et al.*, 1987; Russo, 2009).

The field of phylogeography is a relatively recent discipline in which investigators seek to uncover the processes resulting in geographical patterns of genealogical lineages within species and among closely allied species (Avise, 2000). As a field of study integrating aspects of biogeography and phylogenetics, phylogeography involves combining historical hypotheses with spatial distributions of gene lineages. The discipline has developed over the last twenty years as the ability to assess genetic variation within populations through molecular techniques has improved (Albright, 2004). Since it involves within and, occasionally, among species variation, phylogeography is at the cusp of macroevolutionary phylogenetic studies and intraspecific microevolutionary processes (Avise, 2000). More recently, the cyt-b gene has been used successfully to study the phylogeographic structure of the species *Mastomys natalensis* across much of Africa (Colangelo *et al.*, 2013) and also other rodents (Moulin *et al.,* 2008; Brouat *et al.*, 2009; Bryja *et al.*, 2010).

In view of the existing confusion regarding the molecular diversity of *Mastomys*, the following PCR techniques will be used to examine genetic variations within and between populations of *Mastomys* throughout its distribution range in Namibia and adjacent countries (Botswana and Angola). This analysis shall also incorporate additional DNA sequences from other murid species that are closely related to *Mastomys* occurring in southern Africa and rest of the African continent. DNA sequences of *Mastomys* species from other parts of southern Africa as well as from additional taxa are already available from Genbank.

1.6.1. Molecular study objectives

- to determine the phylogenetic relationships of species comprising the African rodent genus *Mastomys* using sequence data from the mitochondrial cyt b gene

1.7. Main Study Objectives

- to clarify the taxonomic status and delimit species boundaries of *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia and adjacent countries using a wide range of morphometric, cytogenetic and molecular systematic techniques

- to determine the geographical distribution of *Mastomys* species occurring in Namibia and neighbouring countries in the southern African sub-region

- to determine the extent of morphological, cytogenetic and mitochondrial DNA variation within and between populations of *M. coucha*, *M. natalensis* and *M. shortridgei* from southern Africa

- to determine phylogenetic relationship of southern African *Mastomys* species to other *Mastomys* species occurring in Africa

CHAPTER 2: MATERIALS & METHODS

2.1. Morphometrics

2.1.1. Traditional morphometrics

Individuals were assigned to seven standard tooth wear classes based on previous studies done on rodents (Morris, 1972; Perrin, 1982; Dippenaar & Rautenbach, 1986), as is indicated in **Fig. 2.1.** and **Table. 2.1.** below. To reduce the effect of age variation, only adult classes IV-VI were considered, according to a study done on rodent genus *Aethomys* by Chimimba & Dippenaar (1994).

In total 384 skulls were utilized for traditional morphometrics data collection. Specimens housed in various museum collections were examined and recorded for geographic distribution and morphological variation analysis in addition to data from field studies. Specimens from following museums were utilized for this purpose: National Museum of Namibia, Windhoek, Namibia (NMNW); Museums of Botswana, Gaborone, Botswana (MB); Transvaal Museum, Pretoria, South Africa (TMSA); Amathole Museum, King Williams Town, South Africa (AMK); Durban Natural Science Museum, Durban, South Africa (DNSM); Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe (NMBZ); Museum für Naturkunde, Berlin, Germany (ZMHB); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Natural History Museum, London, United Kingdom (BMNH). These museums were selected to ensure getting a good representative sample for statistical purposes and geographical coverage.

An initial set of 61 linear cranial (35 skull, 9 mandible and 17 dental) measurements were recorded to the nearest 0.01 mm using a pair of Mitutoyo digital calipers (**Fig. 2.2 A-K**, described in **Table. 2.2.**). Characters were chosen on the principle of their representation in previous studies on *Mastomys* and other Muridae, and their ability to provide comprehensive characterization of rodent cranial morphology. To avoid the effects of bilateral asymmetry, bilateral characters were measured only on the right side.

The next step was to select the best characters that satisfy the following parameters: percentage measurement error (%ME), skewness (g_1), kurtosis (g_2) and normality (Shapiro-Wilk) (Sokal & Rohlf, 1981; Chimimba & Dippenaar, 1995; Hammer *et al*., 2001).

Following Cheverud (1982), character associations were investigated by cluster analysis of principal component (PCA) scores generated from standardized, statistically problem free characters. Selection of characters from within the cluster analysis generated sub clusters depended on three ancillary criteria in the following order of priority: (1) relative ease of measurement; (2) measuring points associated with frequently damaged areas of the skull; (3) previous use, particularly in original descriptions.

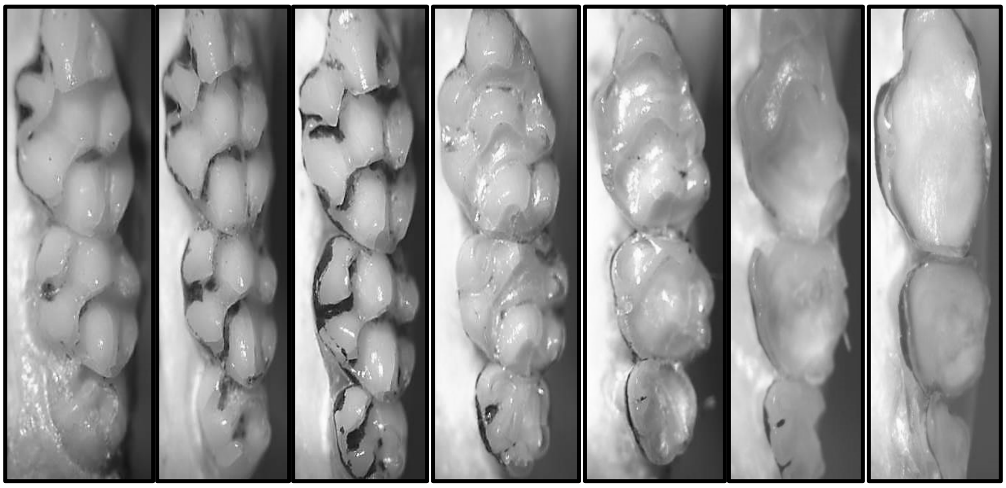


Figure. 2.1. Right maxillary tooth row of *Mastomys coucha* illustrating seven tooth wear classes arranged from Class I to Class VII

Table 2.1. Descriptions of tooth wear classes
(*Adapted from Chimimba & Dippenaar, 1995*)

Tooth Wear Class	**Description**
Class I	Cheek-teeth not fully erupted, M^3 conspicuously below eruption level of M^1 and M^2
Class II	Cheek-teeth fully erupted, M^3 somewhat smaller, cusps conspicuous but with no or very little wear
Class III	All cheek-teeth in apposition, minimal cusps wear
Class IV	Cusp wear obvious, but not extensive
Class V	Cusp wear extensive, but most cusps still distinguishable
Class VI	Cusp wear extensive, but traces of cusps not completely lost
Class VII	Tooth wear severe, occlusal surfaces worn smooth with no traces of cusps

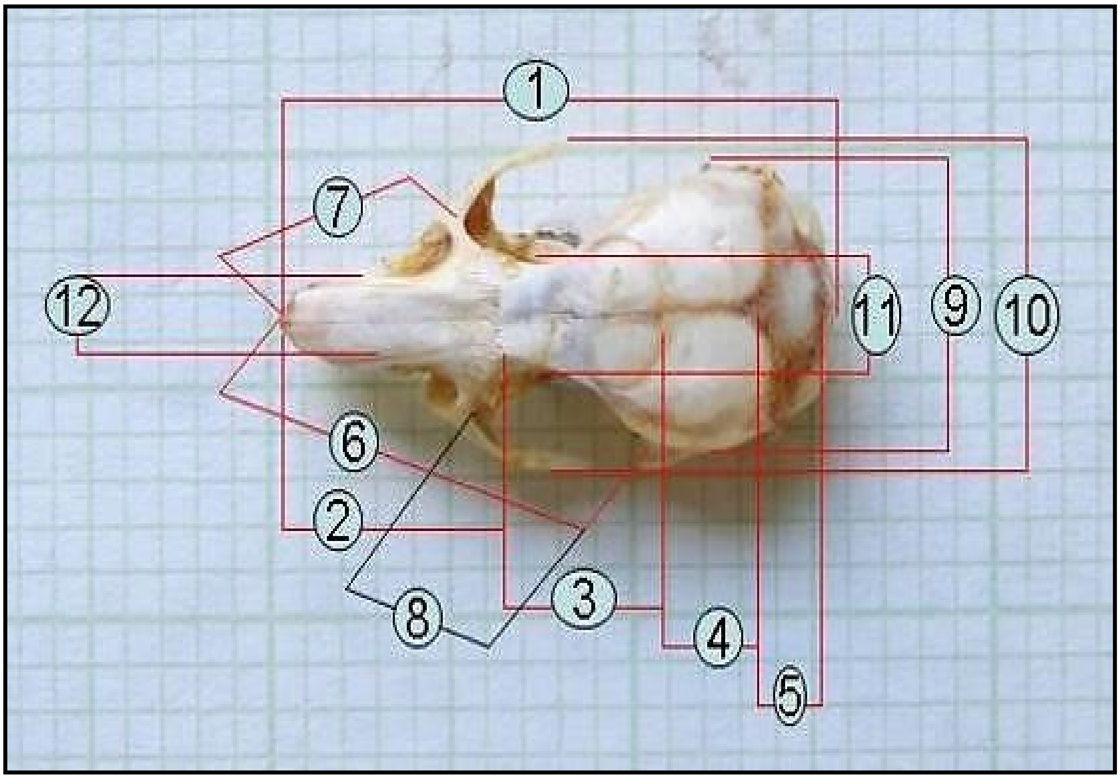


Figure 2.2. A) Skull dorsal view

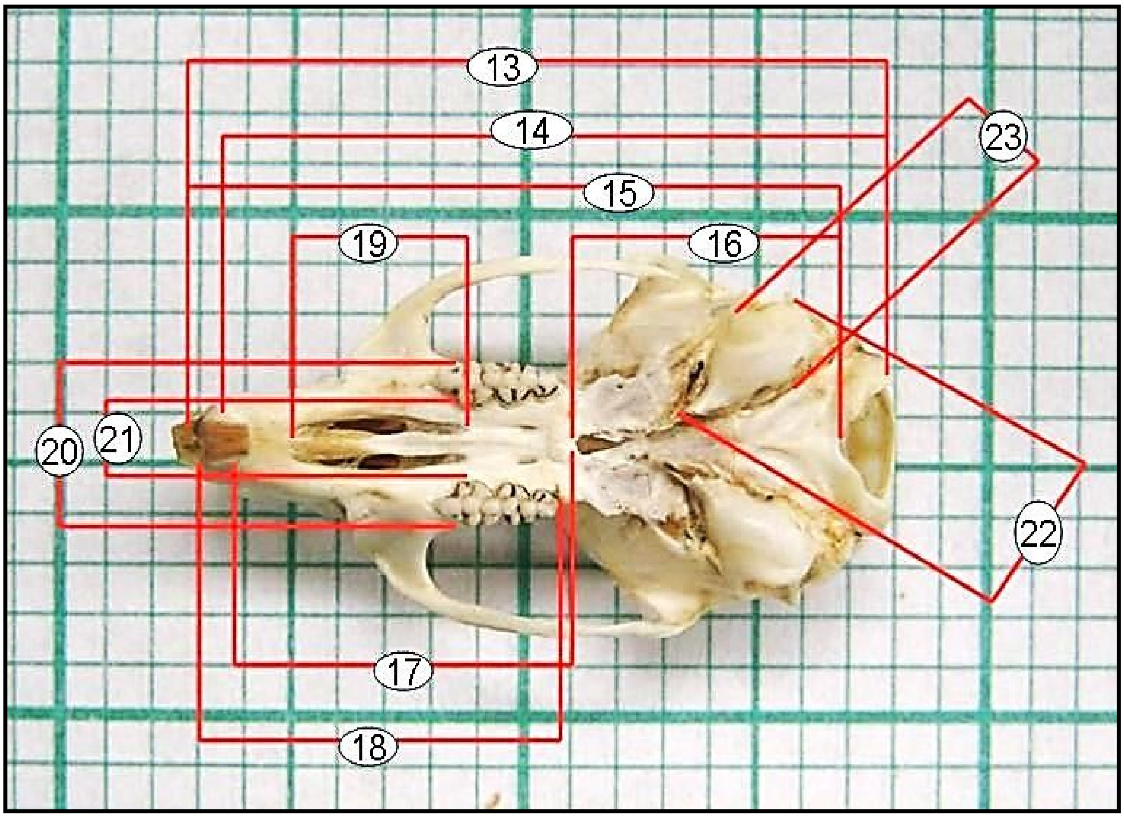


Figure 2.2. B) Skull ventral view

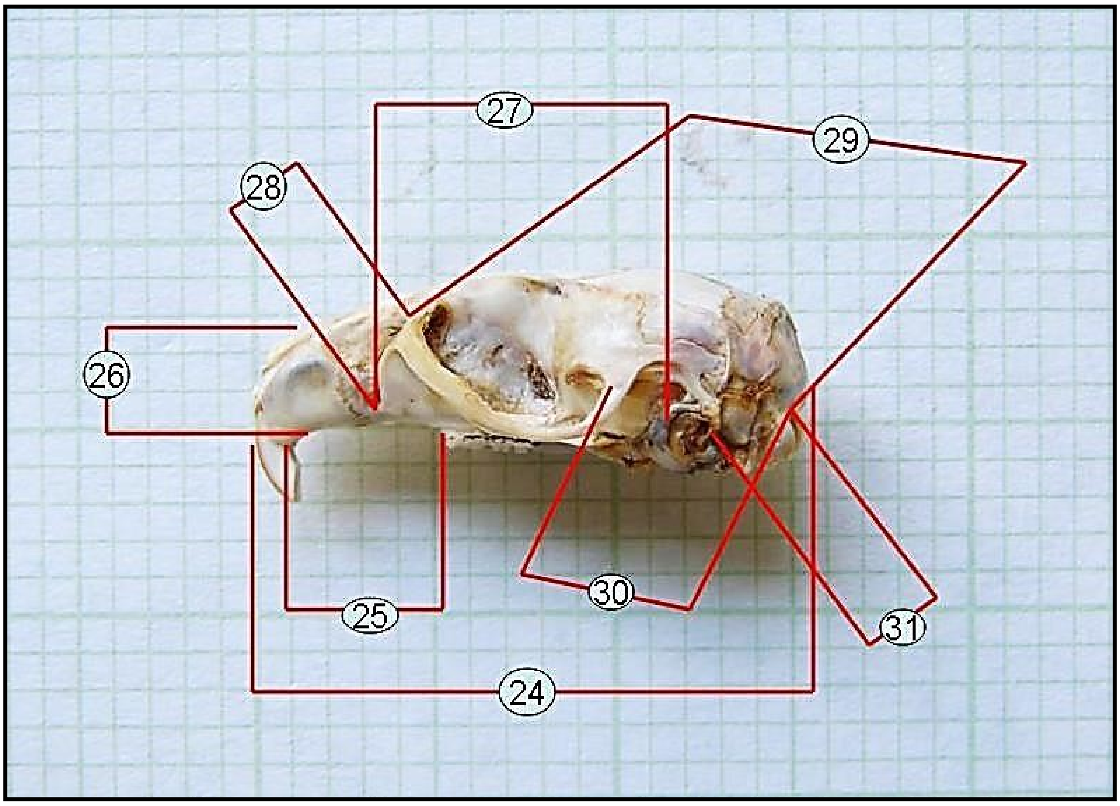


Figure 2.2. C) Skull lateral view

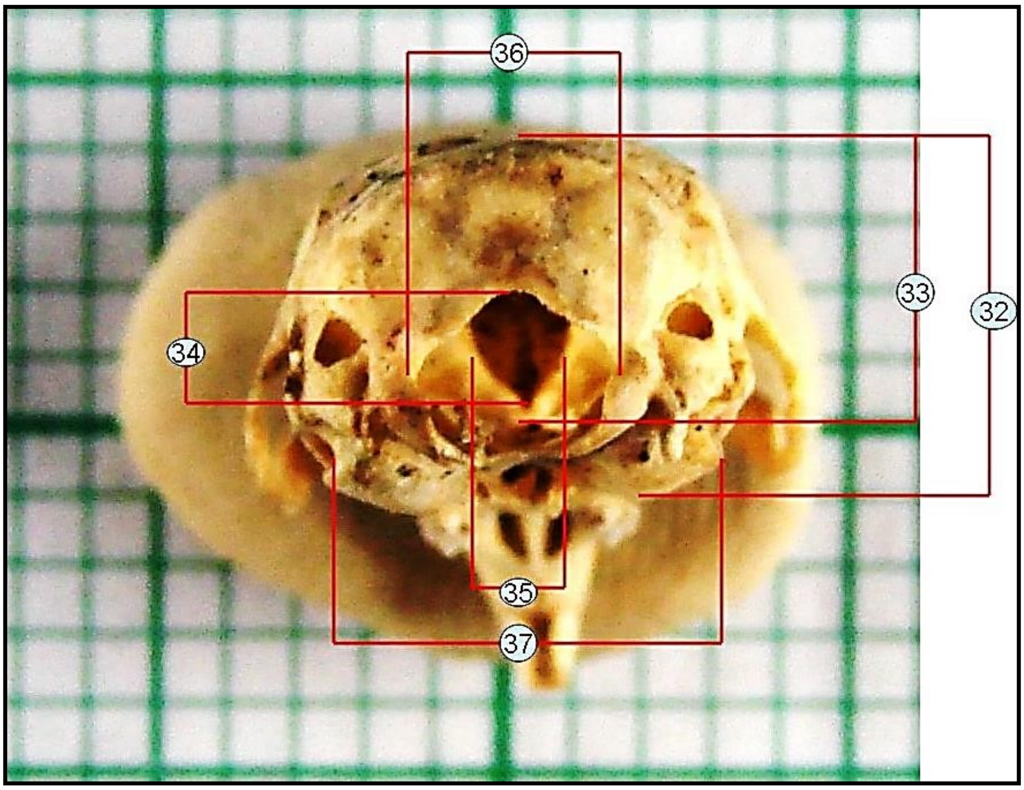


Figure 2.2. D) Skull posterior view

Figure 2.2. E) Skull anterior view

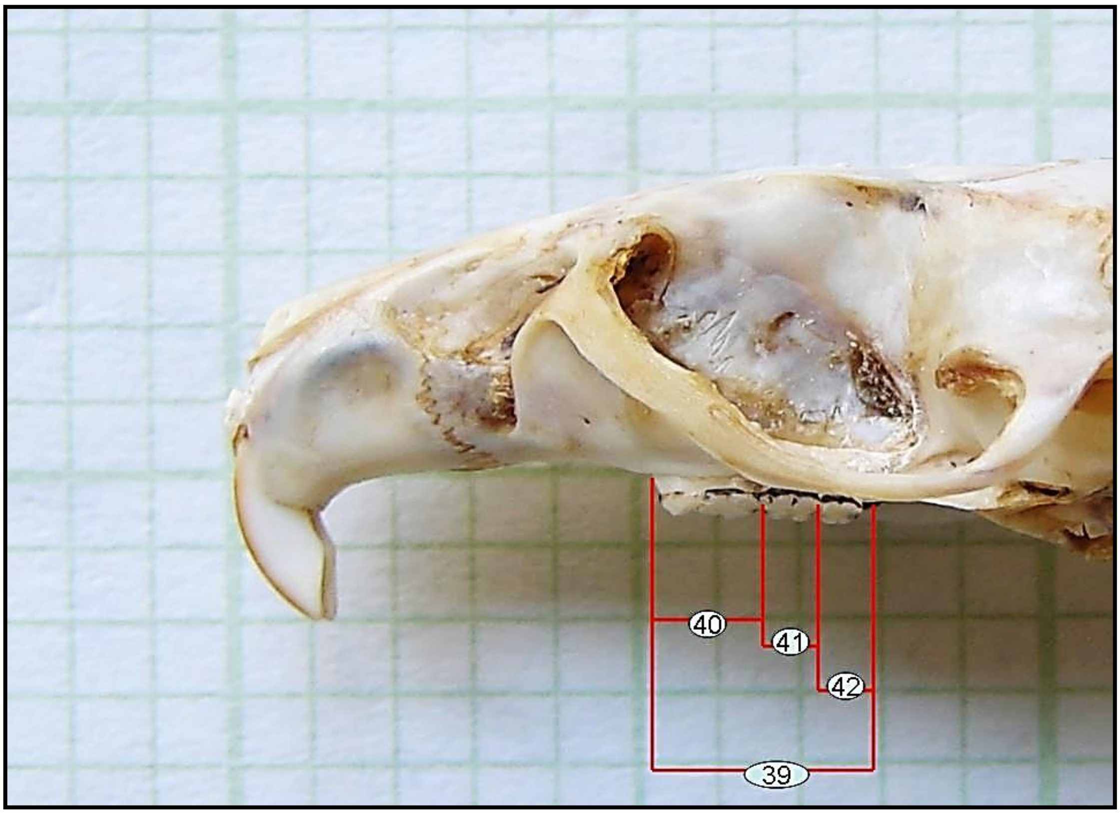


Figure 2.2. F) Skull lateral teeth view

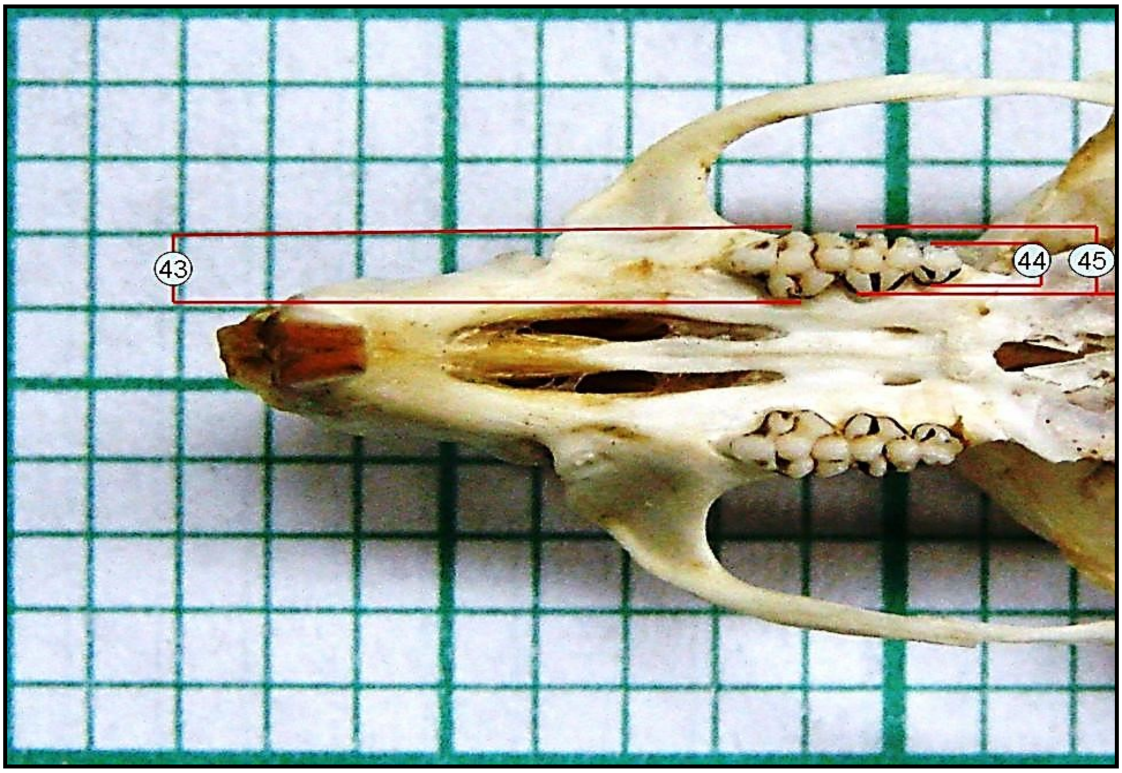


Figure 2.2. G) Skull ventral teeth view

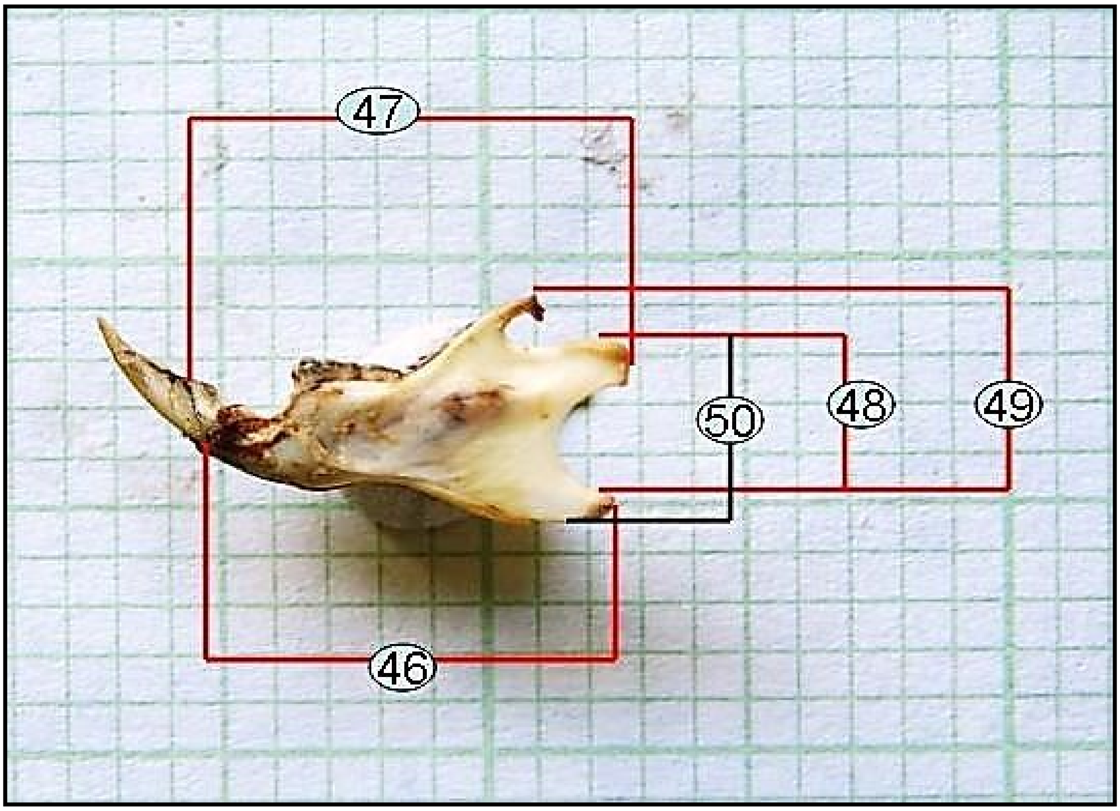


Figure 2.2. H) Mandible lateral A view

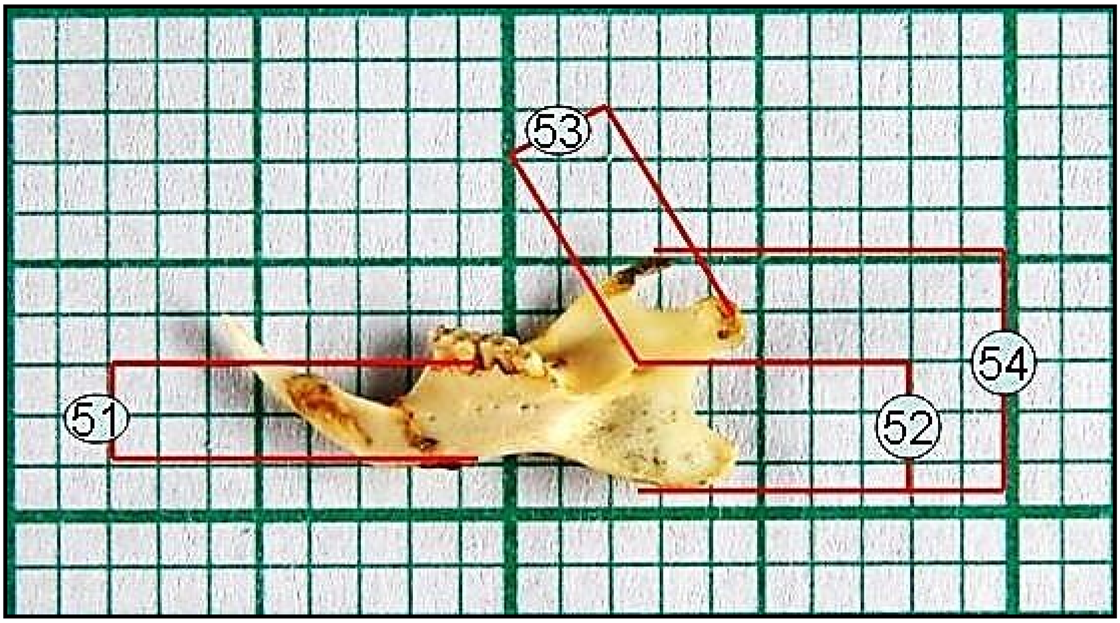


Figure 2.2. I) Mandible lateral B view

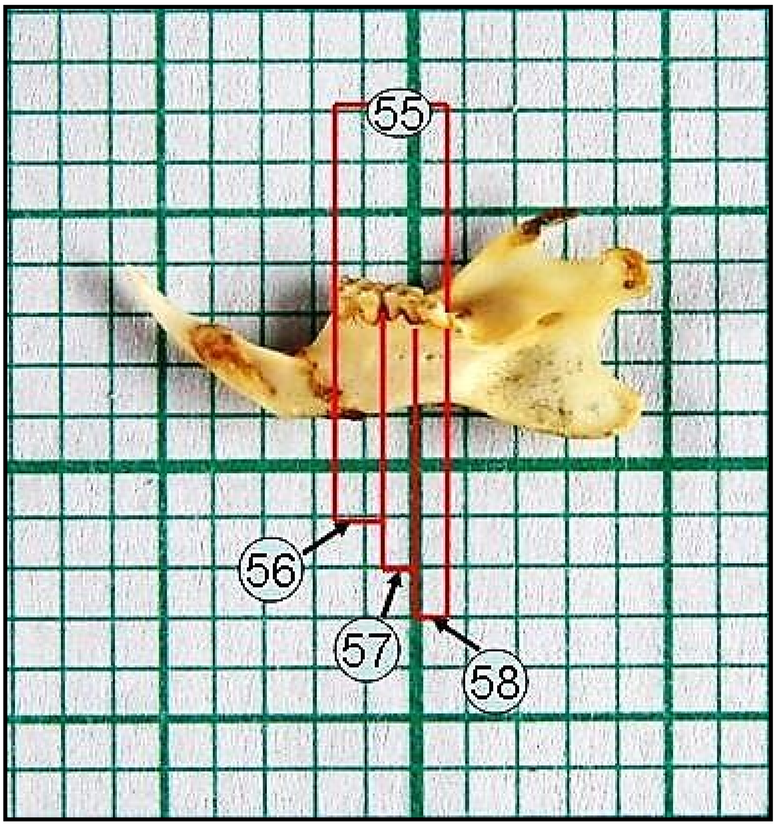


Figure 2.2. J) Mandible lateral C view

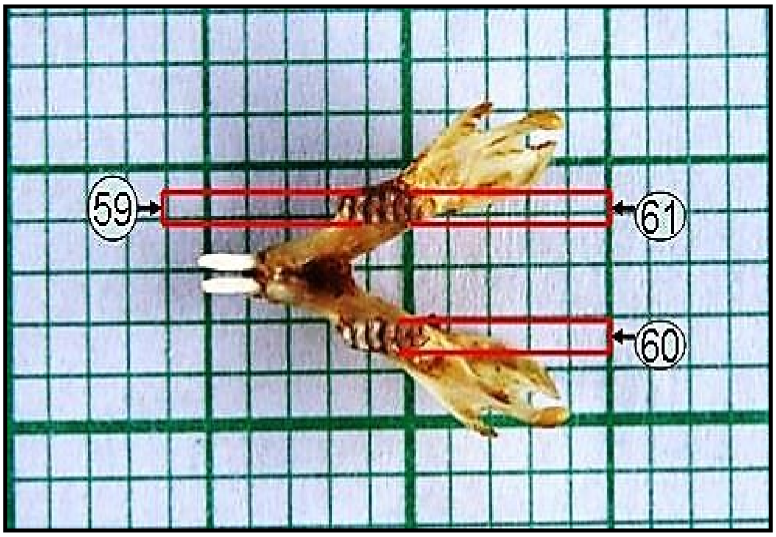


Figure 2.2. K) Mandible dorsal view

Table 2.2. Description of craniometrical characters collected from *Mastomys* skulls for Traditional Morphometrics (Figure 2.2.A-K)

Character	Character description
1-GLS-	Greatest length of skull, from anterior edge of nasals to posterior edge of occipital condyle, along longitudinal axis of skull
2-GLN-	Greatest length of nasals, from longest posterior projection of nasal wings to anterior most edge of nasal bones
3-FRO-	Greatest length of frontals
4-PAR-	Greatest length of parietals
5-INT-	Interparietal length, from intersection of sagittal suture and posterior end of parietal, perpendicular to posterior end of interparietal
6-NPP-	Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch
7-NPO-	Distance from anterior edge of nasals to posterior edge of postorbital bar
8-ZAL-	Zygomatic arch length, from posterior most part of anterior part of zygomatic arch to anterior most part of posterior part of zygomatic arch
9-BBC-	Breadth of braincase- width at dorsal root of squamosals
10-ZYW-	Greatest zygomatic width, between outer margins of zygomatic arches, perpendicular to longitudinal axis of skull
11-IOB-	Least breadth of interorbital constriction, least distance dorsally between orbits
12-NAS-	Nasal width, at anterior most point where nasals join premaxillae
13-CBL-	Condylobasal length of skull, from posterior most projection of occipital condyles to anterior edge of premaxillae
14-PIC-	Incisor to condyle length, from posterior surface of I^1 at alveolus to posterior most projection of occipital condyle
15-BSL-	Basal length of skull, from anterior most point of lower border of foramen magnum to anterior edge of premaxilla
16-PPL-	Post palatal length, from anterior most edge of hard palate to anterior most point on lower border of foramen magnum
17-PAL-	Palatilar length, from posterior edge of I^1 alveolus to posterior edge

	of hard palate
18-TRL-	Tooth row length, from anterior alveolus to posterior surface of M^3 alveolus
19-LPF-	Greatest length of longest palatal foramen
20-MAW-	Greatest maxillary width between labial crown edges of M^1
21-PWM-	Hard palate width at M^1 measured on lingual side of teeth at alveolus
22-BUL-	Greatest bulla length at 45° angle to skull axis
23-BUW-	Greatest bulla width at 45° angle to skull axis
24-ITC-	Incisor to condyle length, from anterior surface of I^1 at alveolus to posterior most projection of the occipital condyle
25-LOD-	Length of diastema, from posterior base of I^1 alveolus to anterior base of M^1 alveolus
26-HOR-	Height of rostrum, perpendicularly from a point directly behind incisors
27-IOE-	Distance from anterior base of zygomatic plate to anterior edge of ear opening
28-IZD-	Infraorbital-zygomatic plate distance, from dorsal edge of infraorbital foramen to anterior base of zygomatic plate
29-MPO-	Foramen magnum-postorbital bar length, from lateral edge of foramen magnum to anterior edge of postorbital bar
30-MPZ-	Foramen magnum-zygomatic arch length, from lateral edge of foramen magnum to anterior edge of posterior part of zygomatic arch
31-FME-	Foramen-magnum-external auditory meatus length, from lateral edge of foramen magnum to postero-dorsal edge of external auditory meatus
32-GHS-	Greatest height of skull perpendicular to horizontal plane through bullae
33-BCH-	Braincase height, from dorsal surface of sagittal crest to mid-ventral surface of basioccipital between anterior bullae
34-FMH-	Foramen magnum height- widest part of foramen in vertical plane
35-FMW-	Foramen magnum width- widest part of foramen magnum in a

	horizontal plane
36-CNW-	Greatest occipital condyle width perpendicular to skull axis
37-WAB-	Width at bullae on ear openings perpendicular to skull axis
38-FIB-	I^1 breadth- breadth of principal upper incisor at level of median edge of alveolus
39-UTR-	Crown length of maxillary tooth row, from anterior edge of M^1 at alveolus to posterior edge of M^3 at alveolus
40-LFM-	Length of M^1 along cingulum
41-LSM-	Length of M^2 along cingulum
42-LTM-	Length of M^3 along cingulum
43-WFM-	Greatest cross-sectional crown width of M^1
44-WSM-	Greatest cross-sectional crown width of M^2
45-WTM-	Greatest cross-sectional crown width of M^3
46-GML-	Greatest mandible length, in a straight line, from anterior edge of I_1 alveolus to posterior surface of angular process
47-MDL-	Greatest length of mandible (excluding teeth), from posterior surface of condylar process to anteroventral edge of incisor alveolus
48-AFA-	Angular process-mandibular condyle length, in straight line from ventral edge of angular process to mid-dorsal ridge of mandibular condyle
49-MRH-	Mandible-ramus height, from dorsal edge of coronoid process to ventral edge of angular process
50-MCA-	Mandibular condyle-angular process distance, in straight line from dorsal edge of mandibular condyle to ventral edge of angular process
51-LMH-	Least mandible height, perpendicularly from between posterior M_1 alveolus and anterior M_2 alveolus
52-MFA-	Mandibular foramen-angular process length, from anterior edge of mandibular foramen to posterior edge of angular process
53-MAF-	Mandibular foramen-articular facet length, from ventral edge of mandibular foramen to mid-postero-dorsal edge of articulating facet
54-CMH-	Coronoid mandible height, from dorsal edge of coronoid process to ventral edge of mandible in line with mandibular foramen

55-MTR-	Mandibular tooth row length, from anterior edge of M_1 alveolus to posterior edge of M_3 alveolus
56-LLM-	Length of M_1 along cingulum
57-LMS-	Length of M_2 along cingulum
58-LMT-	Length of M_3 along cingulum
59-WLM-	Greatest cross-sectional crown width of M_1
60-WMS-	Greatest cross-sectional crown width of M_2
61-WMT-	Greatest cross-sectional crown width of M_3

2.1.1.1. Error Measurement & Craniometric Character Selection

Morphometric data from measurement variables measured on a continuous scale are important in generating and testing evolutionary hypotheses and taxonomic hierarchies using various approaches (Bookstein, 1982; Reyment *et al.*, 1984). A concern common to all methods of analysing such data is measurement error, which may be defined as the variability of repeated measurements of a particular character taken on the same individual, relative to its variability among individuals in a particular group (Bailey & Byrnes, 1990).

As a test of measurement error, four skulls were measured three times for each character (Chimimba & Dippenaar, 1995; Richards, 2007; Rotherham, 2007). All these skulls are from adult (Tooth wear class V) *Mastomys natalensis* specimens collected at the same locality, Kapaku village (Kavango Region, Namibia).

Measurement error test was carried out by using three non-consecutive repeated measurements of 61 cranial characters per individual specimen. The order in which specimens were measured was chosen at random. Each individual was measured for all 61 characters before the next individual was measured. Specimens were randomized and measured again, until all individuals had been measured three times (Chimimba & Dippenaar, 1995; Richards, 2007; Rotherham, 2007). The 61 characters were always measured in the order they were defined (Refer to **Table. 2.2.**). These measurements were recorded to the nearest 0.01 mm using a pair of Mitutoyo digital calipers. All measurements were made without knowledge of previous measurement results (Bailey & Byrnes, 1990).

A two-way ANOVA was used to partition the total variance of each character into within- and among-individual components, i.e. the total sum of squared deviations from the grand mean (SS_{total}) was divided into among-individual (SS_{among}) and within-individual (SS_{within}) components (Bailey & Byrnes, 1990; Yezerinac *et al.*, 1992). Mean squared deviations (MS = SS/degrees of freedom) for each of these components was used to calculate variance components. Mean squared deviations of scores within individuals (MS_{within}) estimated the within-individual component of variance (s^2_{within}); the among-individual component (s^2_{among}) was calculated using the formula (Sokal & Rohlf, 1981): $s^2_{among} = MS_{among}\ MS_{within}/m$, where m is the number of repeated measurements.

Percentage measurement error was then calculated using the among- and within-individual variance components as $\%ME = s^2_{within}/s^2_{within} + s^2_{among}$ x 100 (Bailey & Byrnes, 1990; Yezerinac *et al.*, 1992). A total of 37 characters that scored a %ME of less than 10 were retained for further analysis.

The next step was to select the best characters that satisfied the following parameters: skewness (g_1), kurtosis (g_2) and normality (Shapiro-Wilk test) out of 37 characters that passed the %ME test (Sokal & Rohlf, 1981; Chimimba & Dippenaar, 1995; Hammer *et al.*, 2001). These were calculated from a homogenous sample of 34 specimens of *Mastomys natalensis* from the Hwange National Park, Zimbabwe (**Appendix One**). Out of these tests, 5 characters were discarded and 32 characters were retained.

Unweighted pair-group cluster analysis (UPGMA) was carried out on 32 characters that passed: %ME, skewness, kurtosis & test of normality.

The two-way ANOVA was calculated using the statistics software PAST version 2.17c (Hammer *et al.*, 2001). The software programme SPSS for Windows (version 21.0; IBM SPSS Statistics for Windows, 2012) was used to calculate the following: kurtosis, skewness, test of normality and the UPGMA.

2.1.1.2. Non-geographic Variation

Due to small sample sizes only individuals of *M. natalensis* (50 specimens, **Appendix Two**) from Hwange National Park (Zimbabwe) were tested for sexual size dimorphism and age class variation by one-way ANOVA and Principal Component Analysis (PCA). Individuals of tooth wear classes IV to VII were combined for further analyses.

The data set were screened for outliers using principal component analyses. Descriptive statistics (arithmetic mean, standard deviation and coefficient of variation) were computed for each of the 12 characters within each data set. Analyses were carried out with standardized data sets that were normally distributed, non-kurtotic and non-skewed (Richards, 2007; Rotherham, 2007).

The one-way ANOVA and PCA was calculated using the statistics software PAST version 2.17c (Hammer *et al*., 2001)

2.1.1.3. Geographic Variation

Museum specimens and specimens collected by the author (n = 377: 113 *M. coucha*, 206 *M. natalensis*, 46 *M. shortridgei* and 12 type specimens) were examined from Namibia, Botswana, Angola, Zimbabwe and South Africa (**Appendix Two**).

Data sets for each OTU were screened for outliers using principal component analyses. Descriptive statistics (arithmetic mean, standard deviation, and coefficient of variation) were computed for each of the 12 variables within each data set. Analyses were carried out with standardized data sets that were normally distributed, non-kurtotic and non-skewed (Richards, 2007; Rotherham, 2007).

Initially, a principal component analysis (PCA) was used to obtain principal axes that summarize the directions of greatest variation among each species separately. Due to small sample sizes only specimens of *M. natalensis* were tested for geographic variation by one-way ANOVA and Principal Component Analysis (PCA). The dataset of *M. natalensis* includes specimens from Hwange National Park (Zimbabwe, n = 37), Kavango Region (Namibia, n = 44) and KwaZulu-Natal (South Africa, n = 57).

Due to sample size constraints only *Mastomys* specimens from Namibia were used for the final analysis for discrimination between species. Canonical Variates Analysis (CVA) was used to order the populations of *M. coucha*, *M. natalensis* and *M. shortridgei* along the axes of maximum differentiation by maximizing between-population variation with respect to within population variation. Prior to the CVA analysis, a univariate one-way ANOVA test was carried out to determine the character(s) that shows best discrimination between *Mastomys* species in Namibia.

2.1.2. Geometric Morphometrics

Digital images of *Mastomys* skulls were captured using a Sony DSC-H5 cyber-shot camera mounted on a fixed stand with the lens downward facing. A length of 115 mm from the lens to the skull was maintained for the duration of the study. Following Mullin & Taylor (2002) and Taylor *et al*. (2004), the camera was positioned as far as possible from specimens, thus avoiding the effects of parallax. A spirit level was used to ensure the camera lens was always balanced and level. To ensure specimen placement was standardized and easily replicable, graph paper were used to place specimens on before image capture (Taylor *et al*., 2009). The camera was zoomed into the graph paper until 30 small squares were left on the graph paper (in the horizontal view) and this was then used for each and every specimen.

Thirteen dorsal and fourteen ventral landmarks were digitized and recorded from dorsal and ventral views of *Mastomys* crania using the software program TpsDig (version 2.17; Rohlf, 2013a). Following Bogdanowicz & Owen (1996), landmarks were only recorded from the right half of dorsal and left half of ventral views of *Mastomys* crania in order to avoid the effects of bilateral asymmetry. Positions of landmarks are described in **Figures 2.3. & 2.4.** and defined in **Tables 2.3. & 2.4.** Landmark data were saved in notepad files with a .tps extension for input into the thin-plate spline series of programs. TpsSmall (version 1.25; Rohlf, 2013b) was used to determine whether the amount of intra- or inter-population shape variation in a particular landmark data set was small enough to permit statistical analyses to be performed in the linear tangent space approximate to Kendall's shape space.

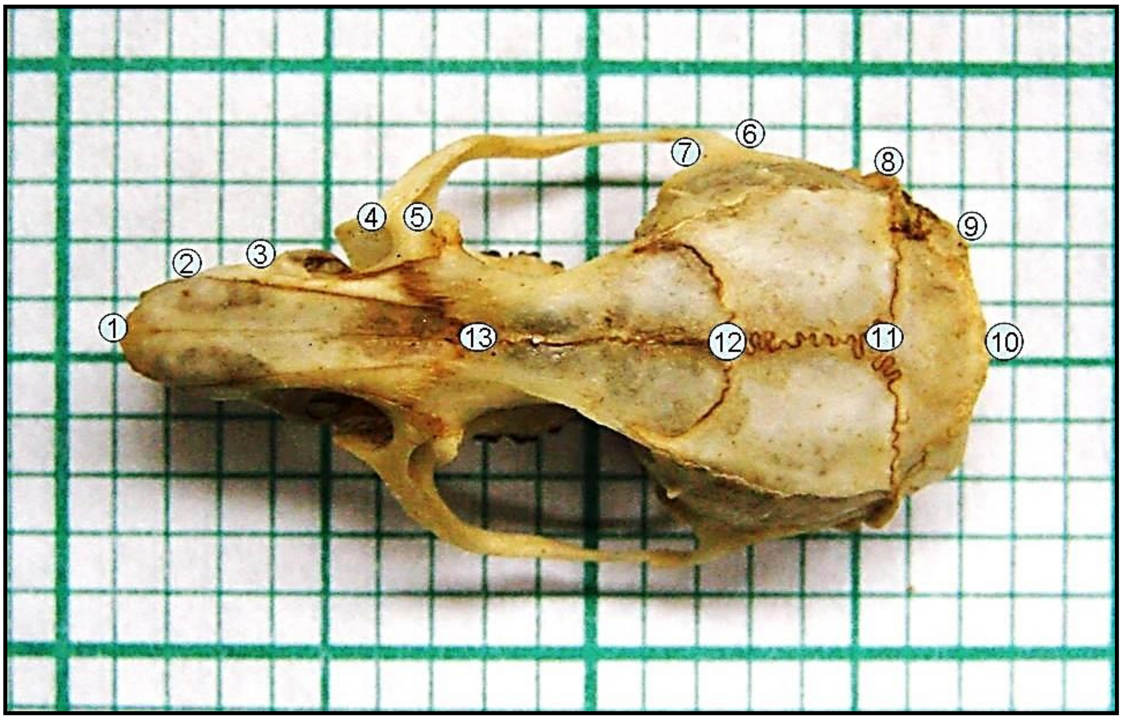


Figure 2.3. Landmarks collected on the dorsal view of the skull

Table 2.3. Descriptions of landmarks collected on dorsal view of the skull

Landmark	**Description**
1	Anterior tip of nasals
2	Anterior point at suture between nasals and premaxilla
3	Narrowest point of rostrum
4	Anterior point of upper maxillary process
5	Anterior point of interior orbit
6	Widest point of zygomatic arch
7	Posterior point of interior orbit
8	Exterior tip of auditory meatus
9	Edge of supraoccipital ridge
10	Posterior point of supraoccipital
11	Junction between interparietal, parietal, and midline
12	Junction between parietal, frontal and midline
13	Junction between frontal, nasals and midline

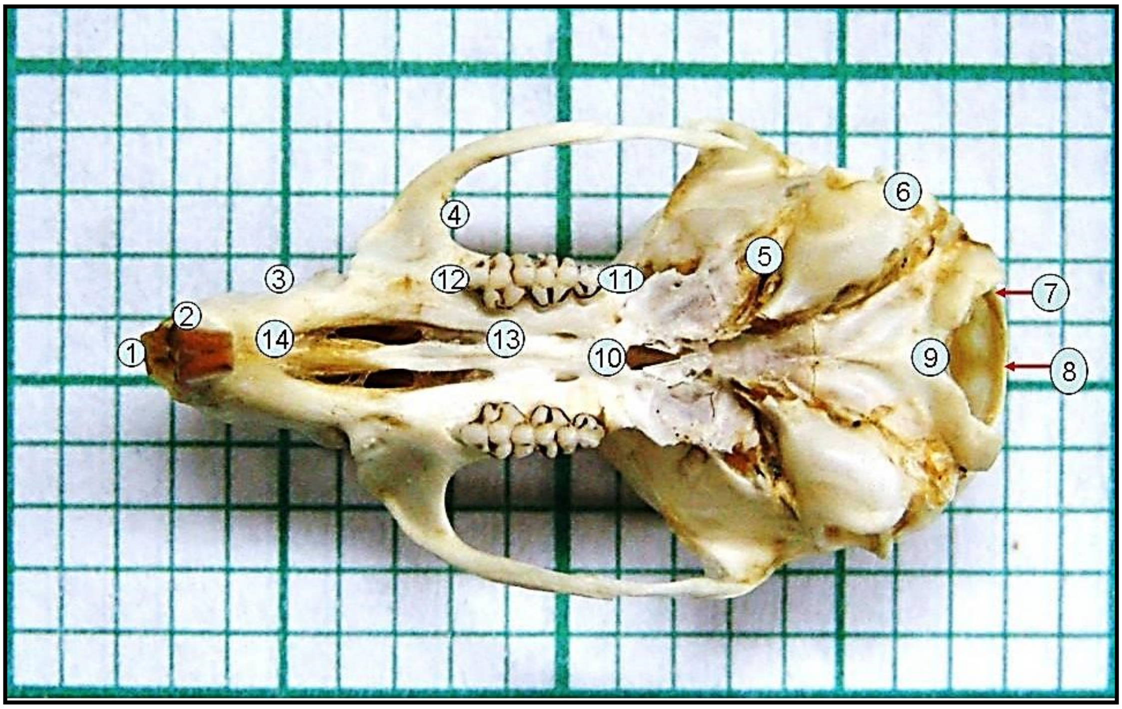


Figure 2.4. Landmarks collected on the ventral view of the skull

Table 2.4. Description of landmarks collected on ventral view of the skull

Landmark	**Description**
1	Anterior tip of nasals
2	Antero-lateral extremity of incisive alveolus
3	Widest point of rostrum
4	Anterior point of interior orbit
5	Maximum anterior curvature of tympanic bulla
6	Maximum external curvature of posterior tympanic bulla
7	Posterior intersection between foramen magnum and occipital condyle
8	Posterior extremity of foramen magnum
9	Anterior extremity of foramen magnum
10	Contact point between maxilla and palatine
11	Posterior edge of M^3
12	Anterior edge of M^1
13	Posterior tip of palatine foramen
14	Anterior tip of palatine foramen

2.1.2.1. Testing for digitization error

Two tests were conducted to investigate: (1) the level of precision of specimen placement under the camera and (2) the level of precision and accuracy of landmark placement on digitized images, following methods outlined in Fadda *et al*. (1997). Three undamaged specimens were randomly selected for use in the tests.

For the first test, the skulls of the three individuals were digitized once at one-week interval according to one view: dorsal skull. The second test used one randomly chosen image of each individual from dorsal view which was then duplicated ten times. Landmarks (**Figure 2.3**.) were successively collected three times at one-week intervals from: (1) each set of separate images for the view (test one specimen placement error) and (2) the duplicate sets of images for the view (test landmark placement error), using the programme TpsDig (version 2.17; Rohlf, 2013a).

Landmarks were collected from one-half of the skull to avoid the effects of bilateral symmetry following Bogdanowicz & Owen (1996). To test precision and accuracy levels, a relative warps analysis was conducted on landmark coordinate data, using the programme TpsRelw (version 1.49; Rohlf 2010). Following Fadda *et al*. (1997), precision levels were evaluated by examining the scatter of repetitions for each individual (test 1 and 2) and accuracy by the shape of the triangle connecting the three repetitions for the same individual (test 2).

2.1.2.2. Geographic Variation

A total of 404 individuals from four countries (Angola, Botswana, Namibia and South Africa, **Appendix Three**) were used to explore shape and size differences based on dorsal and ventral views as defined in **Tables 2.3 & 2.4**. Despite some age-related shape differences, individuals from tooth wear classes IV to VII were pooled for each OTU in order to increase sample sizes for further analyses.

The 2-D coordinates of each landmark were digitized using the tpsDig software version 2.17 (Rohlf, 2013a). The landmark configurations were superimposed (i.e. translated, rotated and scaled) with generalized least squares Procrustes procedure

(Rohlf & Slice, 1990). Shape variation was described through variables called partial warps. Algebraically, the partial warps are eigenvectors of the bending energy matrix, which describes how strong and localized is the deformation connected with the change of position of a landmark along each coordinate axis (Marcus *et al.*, 1996). The zeroth partial warps describes the uniform (affine) shape component, i.e. an infinite-scale shape change where parallel lines of the coordinate grid remain parallel, whereas non-affine components, described by all other partial warps, are more or less localized and visualized by deformation of the coordinate grid (Marcus *et al.*, 1996). The geometric size of the skull for each specimen was expressed as the centroid size, computed as the square root of the sum of squared distances from each landmark to the configuration centroid (Bookstein, 1991).

The program tpsRelw, version 1.49 (Rohlf, 2010) was used to compute a partial weight matrix (W) based on the consensus configuration of the data, as well as to compute a relative warps analyses (equivalent to a principal component analysis) of landmark data of OTUs for each of the two views for both males and females. Partial weight matrix (W) for dorsal and ventral views was subjected to a Canonical Variates Analysis (CVA) to test for difference between OTU's.

The software programme tpsRegr, version 1.38 (Rohlf, 2011) was used to obtain thin plate splines (deformation grids describing skull shape changes between species, magnified x 3) by regressing the original shape matrix onto the first (CV1) and second (CV2) projected canonical vectors. This technique was carried out for both the dorsal and ventral views of the skull.

2.2. Cytogenetics

2.2.1. General Field Sampling

Study sites were selected throughout Namibia, Angola and Botswana based on known habitat parameters for *Mastomys* species and with special proximity to the Okavango River, from its source in Huambo Province, Angola, to the Okavango River Delta in Botswana (**Fig. 3.29**). Animals were trapped over four nights per selected study site.

One hundred and forty (140) Sherman® live traps baited with a mixture of peanut butter, oats and bird seed were used to trap the animals, according to Hoffmann & Zeller (2005). Traps were baited and opened in late afternoon and checked the following morning. Trapped animals were sacrificed and the following measurements taken and recorded: head-body length, tail length, hind-foot length, ear length and body weight. The gender of the animal together with its age was recorded. Additionally, notes about the sexual activity of each animal specimen were taken and recorded. The animals were skinned and appropriate study skins were produced after which bone marrow, liver, heart, and/or muscle tissue samples were taken and preserved in 96% ethyl alcohol or frozen and stored for various taxonomic analyses later in laboratory which were morphometrics, cytogenetics and molecular systematics. Animal skulls were cleaned and stored together with the rest of the specimens for scientific analysis. Study skins and skulls together with all collected tissue samples were deposited at the National Museum of Namibia. Field sampling and processing was carried out with approval from the Ministry of Environment & Tourism, with granting of permits: 921/2005, 1049/2006 and 1541/2010.

2.2.2. Karyotyping

At least 2 males and 2 females were selected and kept alive in cages and were yeast stressed once 24hrs before karyotyping. Yeast solution was injected subcutaneously at a dosage rate of 0.1 ml per 25 g body mass. Animals were injected after 24hrs with 0.05% colchicine at a dosage rate of 0.1 ml per 10 g body mass, sacrificed one hour after injection with colchicine and femurs (and, when necessary, other long bones) were dissected out (Green *et al*., 1980; Baker & Qumsiyeh, 1988).

Bone marrow was flushed out of the bones into a centrifuge tube with 5 ml of 0,075M KCl prewarmed to 37 ºC (Green *et al*., 1980; Baker & Qumsiyeh, 1988). The bone marrow solution was incubated at 37 ºC for 17 minutes and was centrifuged at low rpm for 3 minutes. An ice-cold Carnoys fixative (3:1 methanol: acetic acid) was added to the solution in the tube (Green *et al*., 1980). The Carnoys fixative was changed at least 3 times until the supernatant was clear and the packed cell pellet was white (Green *et al*., 1980).

Finally, the solution was dropped from a height of 60 cm onto an ice-cold glass slide. Three to four drops per slide was carried out and at least six slides were produced for each individual animal. These slides were air-dried in a dust free place before staining.

2.2.3. Staining

The slides were stained with 10% Giemsa in phosphate buffer, pH 6.8, for five minutes (Baker & Qumsiyeh 1988). Field conditions in this study prevented doing banding techniques and the primary objective of this study was to identify species unambiguously and the observed differences in 2N and FN were sufficient for this without requiring banding.

2.2.4. Photographing and karyogram development

Preparations were scanned at about 200x and promising metaphases examined more closely at 400x on compound microscope Zeiss Axioplan 2. At least five metaphases per individual were examined and photographed with Zeiss AxioCam MRc5 photographic equipment.

The photographed metaphase spreads were screened to establish the diploid number (2n), gross morphology of the chromosomes and the fundamental number of the autosomal chromosome arms (aFN) (Green *et al.*, 1980; Baker & Qumsiyeh, 1988; Rautenbach *et al.*, 1993). Chromosomes were matched and presumptive homologous pairs arranged in large, medium and small sized metacentric and submetacentric groups while medium to small acrocentric group, with the sex chromosomes being grouped separately (Green *et al.*, 1980). Metacentric meaning that the two arms are approximately of equivalent length; submetacentric meaning the chromosome has a short and a long arm; and acrocentric meaning that only one arm is observed. The fundamental number that is referred to here is the autosomal fundamental number (aFN) and was determined by considering that both metacentrics and submetacentrics carry two arms whereas the acrocentrics have only one arm. The software package GIMP version 2.6 (2010) was used for manipulating the digital images for producing the final karyograms.

2.3. Molecular study

2.3.1. General field sampling

Study sites were selected throughout Namibia, Angola and Botswana based on known habitat parameters for *Mastomys* species and with special proximity to the Okavango River, from its source in the Huambo Province, Angola, to the Okavango River Delta in Botswana (**Fig. 3.29**). Animals were trapped over four nights per selected study site.

A total of 140 Sherman® live traps baited with a mixture of peanut butter, oats and bird seed were used to trap the animals, according to Hoffmann & Zeller (2005). Traps were baited and opened in late afternoon and checked the following morning. Trapped animals were sacrificed and the following measurements taken and recorded: head-body length, tail length, hind-foot length, ear length and body weight. The gender of the animal together with its age was recorded. Additionally, notes about the sexual activity of each animal specimen was taken and recorded.

The animals were skinned and appropriate study skins were produced after which bone marrow, liver, kidney, and/or muscle tissue samples were taken and preserved in 96% ethyl alcohol or frozen and stored for various taxonomic analyses later in laboratory which were morphometrics, cytogenetics and molecular systematics. Animal skulls were cleaned and stored together with the rest of the specimens for scientific analysis. Study skins and skulls together with all collected tissue samples were deposited at the National Museum of Namibia.

2.3.2. DNA extraction, amplification and sequencing

Mastomys DNA were extracted from liver/muscle tissues, which were preserved in 96% ethanol, by using a CTAB protocol (Winnepenninckx *et al*., 1993; Lecompte *et al*., 2002). A maximum of 25 mg of tissue was used, as overloading may result in decreased yield of DNA (Winnepenninckx *et al*., 1993; Lecompte *et al*., 2002).

The integrity of the extracted DNA was first assessed visually via agarose gel electrophoresis. Assessment was carried out to check that the DNA was of a high molecular weight which is necessary for the polymerase chain reaction (PCR). A 1% (w/v) agarose gel was made using 0.5x TBE, to which ethidium bromide (EtBr) (0.05 mg/ml) was added. Approximately 7 µl of each DNA sample was mixed with 1 µl of marker dye, bromophenol blue, before being loaded and run in 0.5x TBE buffer containing EtBr (0.05 mg/ml). Electrophoresis was conducted at 70 volts for 20 minutes. Ethidium bromide stained bands were visualised by trans-illumination with short wave UV light on a Uvitec transilluminator. The image was captured using an Uvitec camera and saved to disk using the Uvisave facility.

Due to the relatively long length of the cytochrome-b gene (1140 bp), it was PCR amplified as two overlapping fragments (Saiki *et al.*, 1988). These fragments were amplified by two primer pairs (Irwin *et al.*, 1991): L7 (5’-ACCAATGACATGAAAAATCATCGTT-3’) and H14896 (5’-TAGTTGTCGGGGTCTCCTA-3’) in the flanking region of the cytochrome-b gene (Lecompte *et al.,* 2002).

Amplifications were performed in 25 µl reactions containing 30-60 ng template DNA, 0.8 µl sterile water, 2.5 µl 10 X reaction buffer, 4 µl 25mM MgCl2, 0.5 µl 10mM deoxynucleoside-triphosphate mixture (dNTPs), 0.2 µl 5 U/ µl Taq polymerase and 4 µl of 6 µM primer dilution (forward and reverse) per reaction. The thermal cycling parameters used were as follows: 94 °C denaturation for 4 min; followed by 36 cycles of (94 °C for 40s, 50 °C for 45s and 72 °C for 40s); followed by 72 °C for 10 min extension (Lecompte *et al.*, 2002).

Mastomys material was sequenced directly from purified PCR products using the primers used for the initial amplifications. Approximately 100 pmol ml–1 of double-stranded PCR product was used in an automatic sequencer CEQ2000 (Beckman).

2.3.3. Construction of consensus sequences

Consensus sequences for each sample was constructed by checking forward and reverse chromatograms against each other for homology and, where discrepancies arose, making appropriate changes to this sequence. This process was carried out by using the Genome Assembly Program: Gap4 (version 4.10, 2006) (Bonfield *et al*., 1995).

Sequences were aligned with the software programme MEGA version 5.2 (Tamura *et al*, 2011) using the Clustal W option (Thompson *et al*., 1994). The alignment was also corrected by visual inspection. All cytochrome b sequences were trimmed to 755 nucleotides respectively due to the fact that sequences obtained in this study were of only 755 bp.

Out-groups used in alignments included: *Praomys degraaffi, Praomys jacksoni, Praomys tullbergi, Praomys misonnei, Praomys daltoni, Hylomyscus alleni, Hylomyscus parvus, Hylomyscus stella, Rattus norvegicus, Arvicanthis niloticus*, *Dasymys incomtus* and *Mus musculus* (Genbank accession numbers: AF518359, EU349778, EU349779, GU144783, HM443533, AF518328, AF518330, AF518331, AB033713, EF128080, AF141217, AB205301).

2.3.4. Data Statistics

Statistical analysis on the data set was carried out using MEGA version 5.2 (Tamura *et al*., 2011). These analysis included calculation of conserved, variable, parsimony informative and singleton sites. Nucleotide composition frequencies for individuals and nucleotide pair frequencies for groups were also calculated, as well as number of identical pairs, transitions and transversions among the sequences and the ratio of transitions to transversions.

2.3.5. Phylogenetic Analyses

Before analyses were carried out, jModelTest version 2.1.3 (Guindon & Gascuel, 2003; Dairiba *et al*., 2012) was used to determine which substitution model would work best for the cytochrome b data. It was found that the sequences best fit a HKY+G model (Hasegawa *et al.*, 1985) and analyses were subsequently performed using the assumptions of this model.

2.3.5.1. Genetic Distances

All genetic distances were calculated using the HKY+G model (Hasegawa *et al.*, 1985) in MEGA version 5.2 (Tamura *et al.*, 2011). Individual pairwise distances were calculated for the data set; groups within the data were defined according to OTU's (operational taxonomic units).

2.3.5.2. Neighbour Joining, Maximum Likelihood & Bayesian Analyses

Sequence data from cytochrome b were used to construct phylogenetic trees to represent relationships within and between various *Mastomys* samples and out-groups. Sequences used as out-group were obtained from Genbank and these included representatives samples of all *Mastomys* species recorded from the African continent and closely related mice species (Rodentia: Muridae). Neighbour-joining (NJ; Satou & Nei, 1987) and Maximum-Likelihood (ML; Felsenstein, 1981) methods were used to reconstruct phylogenetic relationships among haplotypes (Brouat *et al.*, 2009). NJ and ML analyses were conducted using MEGA version 5.2 (Tamura *et al.*, 2011). Reliability of nodes in generated trees was estimated using the bootstrap resampling analysis (1000 replications).

A Bayesian likelihood analysis was performed using MrBayes version 3.2.2 (Huelsenbeck & Ronquist, 2001) by using the cytochrome b sequence data. This analysis was performed under the HKY+G model (Hasegawa *et al.*, 1985) as determined by jModelTest. Four Markov chains (three heated and one cold) were run in all analyses and runs were initiated with random trees (Nicolas *et al.*, 2010). Two independent MCMC runs with 10 million generations per run each were conducted to ensure that the resulting tree was well-resolved. Trees and parameters were sampled every 1000 generations (Nicolas *et al.*, 2010; Colangelo *et al.*, 2013). Stationarity was assessed by examining the average standard deviation of split frequencies

(Huelsenbeck & Ronquist, 2001; Nicolas *et al.*, 2010). As the two runs converge onto the stationary distribution, it was expected that the average standard deviation of split frequencies to approach zero, reflecting the fact that the two tree samples become similar (Nicolas *et al.*, 2010; Ronquist *et al.*, 2011). The first 25% of sampled trees were discarded as burn-in, for each run (Bryja *et al.*, 2010; Nicolas *et al.*, 2010). From the remaining trees, a 50% majority rule consensus tree was constructed (Brouat *et al.*, 2009).

2.3.6. Phylogeographical Analyses

Nucleotide (π) and haplotype (*h*) diversities (Nei, 1987) were calculated using the programme DnaSP version 5.10.01 (Librado & Rozas, 2009). Phylogenetic relationships between haplotypes were also inferred by constructing a network using the Neighbour-net (NN) method (Lamb *et al.*, 2014) available in SplitsTree version 4.13.1 (Huson & Bryant, 2006). The NN computes splits graphs based on the distance matrix, producing a phylogenetic network that allows the visualization of conflict and ambiguous signals in the data set (Colangelo *et al.*, 2013).

2.3.7. Divergence Time Estimates

The aim of this method was to obtain tentative estimates for the timing of key events in the diversification of *Mastomys* lineages. Analyses were based on clades identified in the phylogenetic analysis (**Figs. 3.30 – 3.31**), and these were used to calculate the time to the most recent common ancestor (TMRCA), as indicated by Nicolas *et al.* (2008a). TMRCA estimates when genes last shared a common ancestor, and can be used as proxy for ancestral population age (Nicolas *et al.*, 2008a; Brouat *et al.*, 2009).

In order to estimate a rate of evolution and dates of divergence between the *Mastomys* lineages, a log-normal relaxed-clock analysis (Brouat *et al.*, 2009; Colangelo *et al.*, 2013) was performed as implemented in BEAST, version 1.7.5 (Drummond & Rambaut, 2007). A specific rate of change calibrated for murid rodents was determined since murid mtDNA has been shown to evolve at a faster rate than other rodents (Catzeflis *et al.*, 1992). Colangelo *et al.* (2013), stated that the fossil record of the genus *Mastomys* is scarce, and that the earliest record of *Mastomys cinereus*, which is closely related to *M. huberti*, *M. coucha* and *M. natalensis*, was dated to between 3.7 – 2.5 Mya (Denys, 1987).

As a calibration point, the interval 3.7-2.5 Mya was used for the split between all the *Mastomys* species (Colangelo *et al*., 2013). A lognormal distribution with an offset at 2.5 Mya, a median at 3.5 Mya and a 95% confidence interval ranging from 2.6 to 9.6 Mya was used (Colangelo *et al*., 2013). Secondly, the split between the genera *Praomys* and *Mastomys* was calibrated as 5.5-6.0 Mya, based on the earliest fossil of *Praomys* found in Lissasfa, Morocco (Geraads, 2002). An exponential prior for the split between the two genera, had a median date of 6.2 Mya, and a 95% confidence interval ranging from 5.5 to 9.2 Mya (Colangelo *et al*., 2013). Thirdly, the *Mus*/*Rattus* lineage split was employed, which is based on fossil records and estimated at 12 Mya (Jacobs & Downs, 1994). Since this date is an estimate, a normal distribution centred on 12 Mya with a standard deviation of 1 Myr was used, as stated in Nicolas *et al*., (2008) and Brouat *et al*., (2009).

A uniform prior, for the ucld.mean with minimum = 0.001 and maximum = 0.1 was set, based on calibrations by Colangelo *et al*. (2013) and literature (Faulkes *et al*., 2011; Horn *et al*., 2011).

Two independent runs of 10 million generations each, with burn-ins of one million, were performed; by using the same model as phylogenetic analyses (Brouat *et al*., 2009; Nicolas *et al*., 2010). These two runs were then combined in TRACER 1.5 (Rambaut & Drummond, 2007), which also provides options for examining effective sample size (ESS) values and frequency plots in order to check that the mixing of the MCMC chain was adequate (Brouat *et a*l., 2009; Nicolas *et al*., 2010).

CHAPTER 3. RESULTS

3.1. Morphometrics

3.1.1. Traditional Morphometrics

3.1.1.1. Error Measurement & Craniometric Character Selection

The **Table 3.1.** (**A** & **B**) provides some of the descriptive statistics for each craniometrical character. The percentage measurement error (%ME), arranged in increasing order of magnitude, ranged from 0.13 to 58.78%. Those characters with high %ME were often characters with high intra-individual measurement variability that were ill-defined or could not be accurately measured. In total 24 characters with %ME greater than 10% were considered to be unreliable and were discarded from the data set (Taylor *et al*., 1990). A number of 37 characters were retained for further analyses (Refer **Table 3.1.A**).

Descriptive statistics of 37 characters from 34 individuals sampled from HNP is indicated in **Table 3.2.** These are kurtosis (g_2), skewness (g_1) and test of normality (Shapiro-Wilk test). In total five characters (Breadth of braincase, Condylobasal length, Foramen magnum height, Mandibular foramen-angular process length and Cross-sectional crown width of M_1) were discarded which failed one of the tests and 32 characters were retained for further analyses.

Table 3.1. A) Cranial and dental characters arranged in increasing order of magnitude percentage measurement error (%ME)

Character	**Min Value**	**Max Value**	**Mean**	**%ME**
Length of M^3 along cingulum (**LTM**)	0.8	1.2	0.96	0.13
Greatest cross-sectional crown width of M^1 (**WFM**)	1.42	1.67	1.57	0.15
Greatest zygomatic width (**ZYW**)	14.05	15.59	14.82	0.25
Height of rostrum (**HOR**)	4.94	5.27	5.07	0.29
Greatest maxillary width between labial crown edges of M^1 (**MAW**)	5.8	6.6	6.2	0.67
Basal length (**BSL**)	26.16	27.75	26.87	0.7
Mandibular foramen-articular facet length (**MAF**)	3.79	5.09	4.24	0.7
Nasals to posterior edge of postorbital bar (**NPO**)	10.5	11.54	11.01	0.78
Mandibular foramen-angular process length (**MFA**)	3.66	5.21	4.61	0.91
Foramen magnum-postorbital bar length (**MPO**)	20.6	21.28	20.97	1.07
Greatest length of skull (**GLS**)	30.04	31.41	30.71	1.14
Greatest mandible length (**GML**)	14.21	14.89	14.7	1.18
Least breadth of interorbital constriction (**IOB**)	3.78	4.36	4.09	1.19
Greatest cross-sectional crown width of M_1 (**WLM**)	1.18	1.37	1.25	1.43
Incisor to condyle length, from posterior surface of I^1 at alveolus to posterior most projection of occipital condyle (**PIC**)	26.12	27.33	26.58	1.46
Palatilar length (**PAL**)	12.6	14.02	13.22	1.6
Condylobasal length of skull (**CBL**)	28.05	29.15	28.57	1.78
Breadth of braincase (**BBC**)	11.26	11.89	11.5	1.91
Length of M_3 along cingulum (**LMT**)	0.62	1.17	0.9	1.95

Zygomatic plate to ear opening (**IOE**)	15.78	16.55	16.11	2.4
Zygomatic arch length (**ZAL**)	10.28	11.66	11.2	2.45
Nasals to posterior part of zygomatic arch (**NPP**)	20.95	23.01	21.94	2.61
Greatest cross-sectional crown width of M^3 (**WTM**)	0.94	1.22	1.07	2.67
Mandible-ramus height (**MRH**)	7.84	8.79	8.42	2.82
Length of diastema (**LOD**)	7.87	8.9	8.38	3.58
Nasal width (**NAS**)	2.84	3.46	3.26	3.75
Braincase height (**BCH**)	8.63	9.15	8.9	3.86
Infraorbital-zygomatic plate distance (**IZD**)	4.95	6.04	5.36	4.96
Crown length of maxillary tooth row (**UTR**)	4.61	5.04	4.81	5.33
Greatest length of longest palatal foramen (**LPF**)	6.51	7.27	6.99	6.37
Foramen magnum height (**FMH**)	3.18	4.64	3.92	6.75
Greatest occipital condyle width (**CNW**)	6.61	6.91	6.7	7.04
Length of M^2 along cingulum (**LSM**)	1.16	1.36	1.25	7.11
Length of M_1 along cingulum (**LLM**)	1.84	2.07	1.97	7.33
Interparietal length (**INT**)	2.79	3.92	3.37	8.18
Width at bullae on ear openings (**WAB**)	9.62	10.32	10.07	8.29
Toothrow length, from anterior M^1 alveolus to posterior surface of M^3 alveolus (**TRL**)	14.36	15.33	14.93	9.36

Table 3.1. B) Cranial and dental characters arranged in increasing order of magnitude percentage measurement error (%ME)

Character	**Min Value**	**Max Value**	**Mean**	**%ME**
Greatest length of nasals (**GLN**)	11.8	12.78	12.27	10.18
Greatest cross-sectional crown width of M_2 (**WMS**)	1.11	1.33	1.25	10.96
Greatest length of parietals (**PAR**)	5.19	6.25	5.6	11.67
Hard palate width at M^1 measured on lingual side of teeth at alveolus (**PWM**)	2.52	3.25	2.85	14.94
Foramen magnum-zygomatic arch length (**MPZ**)	9.09	9.68	9.38	14.97
Greatest height of skull (**GHS**)	9.46	9.9	9.71	15.62
Incisor to condyle length, from anterior surface of I^1 at alveolus to posterior most projection of occipital condyle (**ITC**)	28.75	29.88	29.27	16.12
Foramen magnum-external auditory meatus length (**FME**)	4.68	5.38	4.97	16.15
Coronoid mandible height (**CMH**)	7.42	9.53	8.78	19.62
Greatest length of mandible (excluding teeth) (**MDL**)	15.81	17.08	16.38	21.53
Greatest cross-sectional crown width of M_3 (**WMT**)	0.89	1.06	1	26.15
I^1 breadth (**FIB**)	0.75	1.1	0.82	29.11
Least mandible height (**LMH**)	3.62	4.23	3.98	29.26
Foramen magnum width (**FMW**)	4.6	5.19	4.84	30.16
Mandibular condyle-angular process distance (**MCA**)	7.15	7.61	7.41	30.55
Greatest bulla width at 45° angle to skull axis (**BUW**)	4.45	4.87	4.69	32.52
Post palatal length (**PPL**)	10.95	11.77	11.52	33.67
Mandibular tooth row length (**MTR**)	3.96	4.46	4.31	34.26
Length of M_2 along cingulum (**LMS**)	1.09	1.42	1.21	36.18

Greatest length of frontals (**FRO**)	8.67	9.53	9.04	37.43
Greatest bulla length at 45° angle to skull axis (**BUL**)	6.24	8.06	7.24	40.54
Greatest cross-sectional crown width of M^2 (**WSM**)	1.32	1.54	1.44	48
Length of M^1 along cingulum (**LFM**)	1.81	3.03	2.16	56.77
Angular process-mandibular condyle length (**AFA**)	6.12	6.71	6.49	58.78

Table 3.2. Basic statistics (Arithmetic Mean, Standard Deviation [SD]) and results of the normality (Skewness [g_1], Kurtosis [g_2] & Shapiro-Wilk) tests.

Character	**Mean**	**SD**	**g_1**	**g_2**	**Normality**
Greatest length of skull (**GLS**)	28.95	1.048	-0.005	-1.011	.065
Interparietal length (**INT**)	3.31	0.337	-0.177	-0.162	.740
Nasals to posterior part of zygomatic arch (**NPP**)	20.57	1.077	0.044	-0.947	.613
Nasals to posterior edge of postorbital bar (**NPO**)	10.26	0.651	-0.507	-0.499	.241
Zygomatic arch length (**ZAL**)	10.65	0.473	-0.318	-1.073	.114
Breadth of braincase (**BBC**)	11.69	0.405	1.149	2.863	**.034**
Greatest zygomatic width (**ZYW**)	14.12	0.695	0.127	-0.814	.548
Interorbital breadth (**IOB**)	4.09	0.165	0.539	0.098	.192
Nasal width (**NAS**)	3	0.205	0.945	1.063	.052
Condylobasal length (**CBL**)	27.71	1.286	-0.102	-1.287	**.041**
Incisor to condyle length (**PIC**)	25.3	1.226	-0.261	-1.116	.103
Basal length (**BSL**)	25.82	1.344	-0.190	-1.150	.111
Palatilar length (**PAL**)	12.26	0.681	0.015	-0.641	.539
Tooth row length (**TRL**)	14.29	0.604	-0.102	-1.045	.247
Longest palatal foramen (**LPF**)	6.66	0.405	-0.573	-0.101	.217
Greatest maxillary width (**MAW**)	6.06	0.236	-0.073	-0.817	.213
Length of diastema (**LOD**)	7.72	0.518	-0.497	-0.792	.070
Height of rostrum (**HOR**)	4.73	0.298	-0.126	-1.269	.080
Zygomatic plate to ear opening (**IOE**)	15.1	0.697	-0.224	-1.091	.180
Infraorbital-zygomatic plate distance (**IZD**)	5.15	0.375	0.265	-0.572	.596
Foramen magnum-postorbital bar length (**MPO**)	19.96	0.800	0.033	-1.104	.231
Braincase height (**BCH**)	8.45	0.233	0.586	0.798	.480

Foramen magnum height (**FMH**)	4.14	0.227	-0.102	3.417	**.009**
Occipital condyle width (**CNW**)	6.63	0.221	0.113	-0.726	.458
Width at bullae on ear openings (**WAB**)	9.91	0.327	0.081	-0.747	.193
Length of maxillary tooth row (**UTR**)	5.06	0.205	-0.128	-1.112	.237
Length of M^2 (**LSM**)	1.25	0.129	0.280	0.302	.691
Length of M^3 (**LTM**)	0.95	0.115	-0.442	0.841	.527
Cross-sectional crown width of M^1 (**WFM**)	1.6	0.066	-0.046	0.406	.781
Cross-sectional crown width of M^3 (**WTM**)	1.1	0.075	0.244	-0.214	.572
Greatest mandible length (**GML**)	14.08	0.743	0.077	-1.099	.190
Mandible-ramus height (**MRH**)	7.75	0.492	-0.092	0.660	.535
Mandibular foramen-angular process length (**MFA**)	4.52	0.318	1.023	3.685	**.005**
Mandibular foramen-articular facet length (**MAF**)	3.92	0.319	0.309	0.777	.498
Length of M_1 (**LLM**)	1.95	0.130	-0.241	-0.316	.759
Length of M_3 (**LMT**)	0.94	0.101	-0.041	-0.410	.452
Cross-sectional crown width of M_1 (**WLM**)	1.27	0.074	-1.150	3.498	**.025**

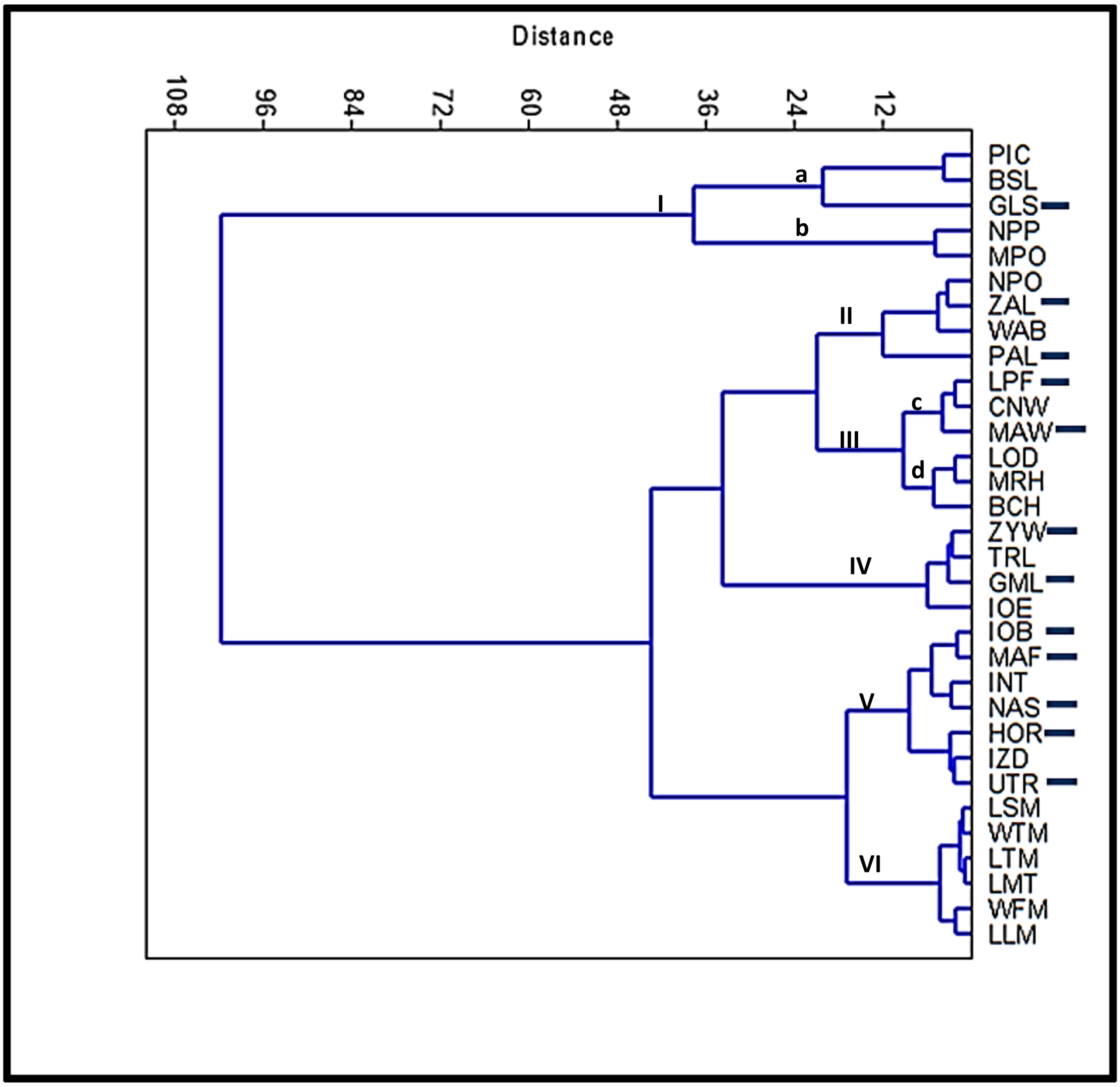


Figure. 3.1. Phenogram generated from a cluster analysis based on Euclidean distances between 32 craniometric characters of *Mastomys natalensis* from Hwange National Park, Zimbabwe (adults), using an unweighted pair-group mean analysis (UPGMA) clustering algorithm. Characters retained for further analyses are marked with a black bar. Cophenetic correlation coefficient = 0.85

The phenogram derived from UPGMA cluster analysis of the 32 craniometric characters is illustrated in **Fig. 3.1.** There are six major cluster of characters designated I-VI. Major cluster I consists mostly of "Mixed" Neurocranial/Orofacial functional set; characters here reflect size-related measurements that span the major functional units of the skull. Thus sub-cluster (**a**) comprising of 'Longitudinal distances' and sub-cluster (**b**) comprising of 'Oblique distances' (Chimimba & Dippenaar, 1995).

Major cluster II relates mainly to the Neurocranial functional set. This cluster includes measurements of the dorsal side of the cranium with the exception of PAL. Major cluster III relates mainly to the Orofacial functional set. The sub-clusters (**c**) and (**d**) within major cluster III comprising mainly of mandibular measurements (Chimimba & Dippenaar, 1995).

Major cluster IV relates mainly to the Neurocranial functional set. This cluster includes one measurement (ZYW) related to the configuration of the braincase, as well as upper toothrow length (TRL), which belongs to the dental phenotypic set in the Orofacial functional set, and distance from anterior base of zygomatic plate to anterior edge of ear opening (IOE) of "Mixed" Orofacial/neurocranial origin (Chimimba & Dippenaar, 1995).

Major clusters V & VI relates mainly to the Orofacial functional set. With major cluster V including measurements of the lateral region of the rostrum, the orbital and postpalatal regions and the toothrows and one mandibular measurement. Whereas major cluster VI including measurements are masticatory characters joining up at relatively low distances, suggestive of a tightly integrated dental submatrix (Chimimba & Dippenaar, 1995).

The final characters selected after the UPGMA analysis are: GLS, ZAL, ZYW, IOB, NAS, PAL, LPF, MAW, HOR, UTR, GML & MAF (Refer to **Table 2.2.** for description of characters). Selection of characters from within the cluster analysis generated sub clusters depended on three ancillary criteria in the following order of priority: (1) relative ease of measurement; (2) measuring points associated with frequently damaged areas of the skull; (3) previous use, particularly in original descriptions (Chimimba & Dippenaar, 1995; Richards, 2007; Rotherham, 2007).

3.1.1.2. Non-geographic Variation

Age variation

Results of a one-way analysis of variance indicated a statistically significant difference ($p < 0.05$) in means between juveniles (Age Classes I-III) and adults (Age Classes IV-VII) in 11 characters and no statistically significant differences ($p > 0.05$) only in one character (IOB) (Refer to **Table 3.3.**). Adults were found to be significantly larger than juveniles in 11 characters and no size differences were observed for the remaining character IOB (**Table 3.3.**). The one-way ANOVA results were congruent with the PCA results (**Fig. 3.2.**). Results of the principal component analysis (**Fig. 3.2.**) indicate that the first two PC axes accounted for about 92.77% of the total variation between juveniles and adults. A plot (**Fig. 3.2.**) of the individual principal component scores for each individual on the first two axes indicated that there was age variation in this population.

Table 3.3. Results of one-way ANOVA for age-class variation within *M. natalensis* (juvenile & adult)

	Juveniles Age Classes I-III				**Adults Age Classes IV-VII**					
Characters	**N**	**Mean**	**SD**	**CV%**	**N**	**Mean**	**SD**	**CV%**	***F*-value**	***P* value**
GLS	19	26.08	0.72	2.76	31	28.61	1.35	4.72	56.575	< 0.001
ZAL	19	9.42	0.40	4.25	31	10.49	0.54	5.15	56.715	< 0.001
ZYW	19	12.94	0.37	2.86	31	13.88	0.70	5.04	29.075	< 0.001
IOB	19	3.98	0.16	4.02	31	4.06	0.17	4.19	2.658	0.110
NAS	19	2.77	0.11	3.97	31	2.98	0.18	6.04	20.258	< 0.001
PAL	19	11.04	0.47	4.26	31	12.05	0.76	6.3	26.894	< 0.001
LPF	19	5.76	0.30	5.21	31	6.49	0.55	8.47	28.451	< 0.001
MAW	19	5.64	0.15	2.66	31	5.99	0.25	4.17	30.976	< 0.001
HOR	19	4.09	0.19	4.65	31	4.65	0.34	7.31	43.146	< 0.001
UTR	19	4.88	0.17	3.48	31	5.05	0.20	3.96	10.360	0.002
GML	19	12.48	0.47	3.77	31	13.96	0.84	6.02	49.798	< 0.001
MAF	19	3.41	0.25	7.33	31	3.84	0.36	9.38	21.619	< 0.001

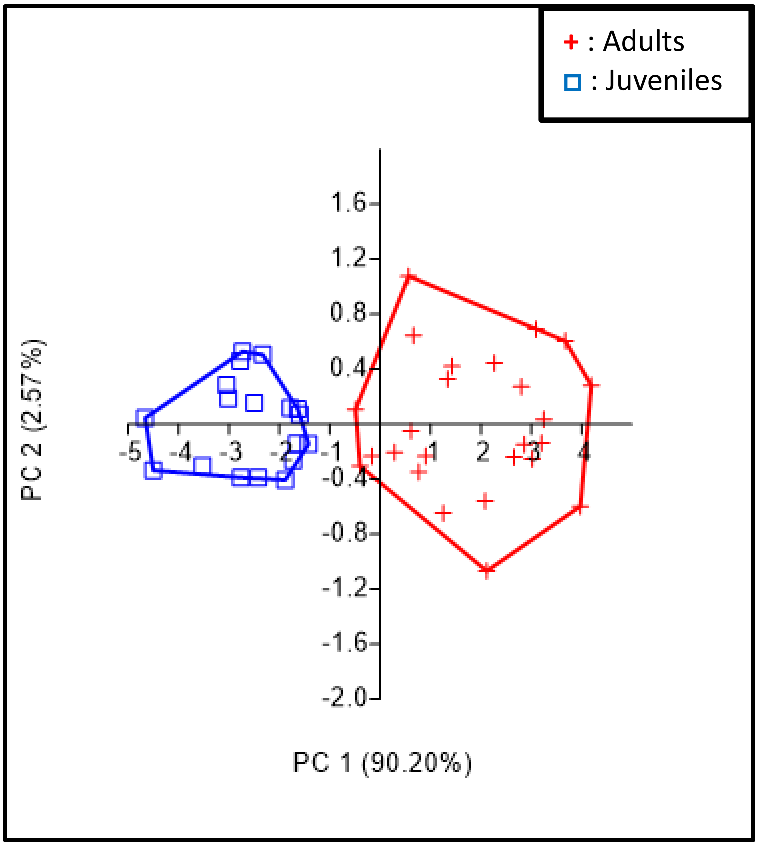


Figure 3.2. The first two axes from principal component analyses used to assess age class variation of *M. natalensis* from Hwange National Park (Zimbabwe)

Sexual dimorphism

Both univariate and multivariate analyses indicated that sexual dimorphism was not statistically significant in *M. natalensis*. **Table 3.4.** provides the F-values generated from the one-way ANOVA. The F-values were low and ranged from 0.04 (HOR) to 2.67 (GML). There were no statistically significant differences between males and females for all characters measured ($p > 0.05$) (**Table 3.4.**).

Figure 3.3. provides a scatterplot of the first and second PCA components (86.65%). Males and females were represented throughout the scatterplot, suggesting that age or each individual, rather than sex, was the major source of variation. All of these results (ANOVA and PCA) provided the basis for combining data for males and females into one group for the subsequent analysis of geographic variation (Mullin *et al*., 2001).

Table 3.4. Results of one-way ANOVA for sexual dimorphism from *M. natalensis* individuals

	Males				**Females**					
Characters	**N**	**Mean**	**SD**	**CV%**	**N**	**Mean**	**SD**	**CV%**	***F*-value**	**Sig.**
GLS	11	28.47	1.63	5.73	20	28.69	1.21	4.22	0.185	0.671
ZAL	11	10.46	0.64	6.12	20	10.51	0.49	4.66	0.051	0.822
ZYW	11	13.81	0.72	5.21	20	13.92	0.71	5.10	0.153	0.698
IOB	11	4.09	0.22	5.38	20	4.05	0.15	3.70	0.368	0.549
NAS	11	2.93	0.19	6.48	20	3.01	0.18	5.98	1.119	0.299
PAL	11	11.99	0.93	7.76	20	12.08	0.67	5.55	0.085	0.772
LPF	11	6.32	0.71	11.23	20	6.59	0.43	6.53	1.710	0.201
MAW	11	5.93	0.24	4.05	20	6.03	0.26	4.31	0.977	0.331
HOR	11	4.67	0.37	7.92	20	4.64	0.34	7.33	0.041	0.840
UTR	11	5.07	0.22	4.34	20	5.04	0.19	3.77	0.084	0.774
GML	11	13.64	1.00	7.33	20	14.14	0.70	4.95	2.672	0.113
MAF	11	3.76	0.47	12.50	20	3.88	0.29	7.47	0.741	0.397

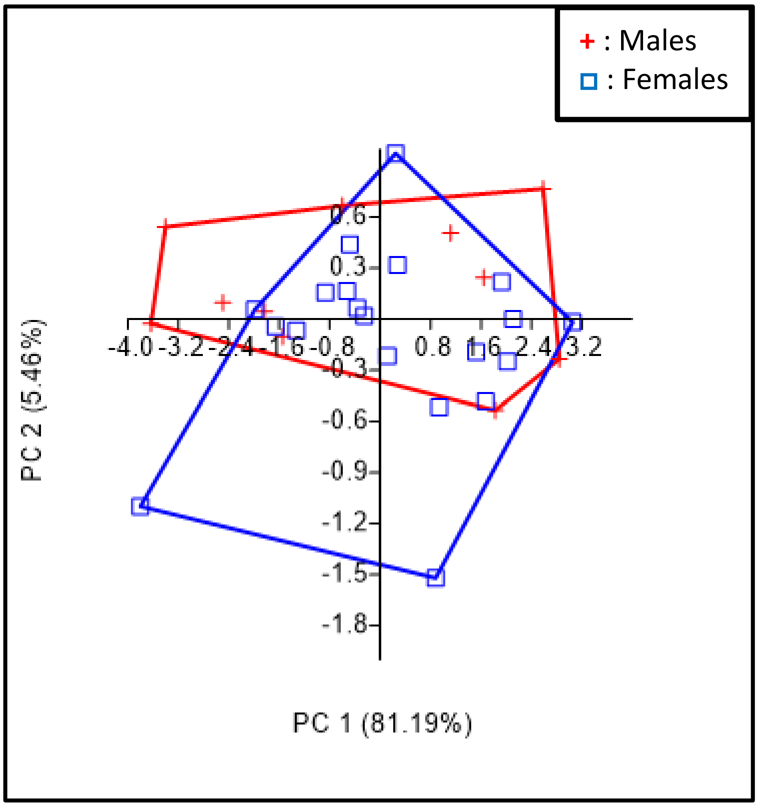


Figure 3.3. The first two axes from principal component analyses used to assess sexual dimorphism of *M. natalensis* from Hwange National Park (Zimbabwe)

3.1.1.3. Geographic Variation

M. coucha

The first principal component (PC1) accounted for 73.14% of the total variation within *M. coucha* samples from Namibia, Angola and Botswana (**Fig. 3.4.**; **Table 3.5.**). PC1 is interpreted here as a general size axis based on the positive sign and positive magnitudes of most character loadings. The second principal component (PC2), which accounted for 6.2% of the total variation, is interpreted as a general shape axis. Characters associated with the size of skull, such as length of skull (GLS) and greatest mandible length (GML) show high correlations with PC1, whereas palatilar length show positive and high loadings on PC 2 (**Table 3.5.**).

Along PC1, the most evident result is an increase in skull size, with the samples from Botswana larger than Namibian samples and Angolan samples larger than samples from Botswana (**Fig. 3.4.**; **Table 3.5.**). PC1 loadings indicate that samples from Botswana and Angola are composed of individuals with longer skull and mandible lengths (GLS & GML). Along PC2, the palatilar length (PAL) is larger in Namibia samples in comparison to samples from Botswana and Angola (**Fig. 3.4.**; **Table 3.5.)**.

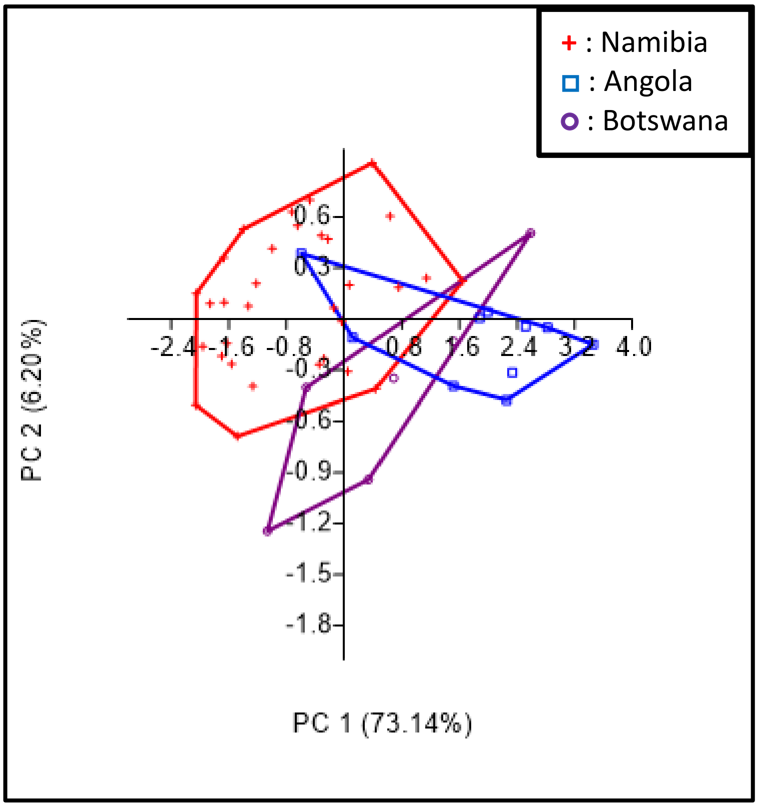


Figure 3.4. The first two axes from principal component analyses used to assess geographic variation within samples of *M. coucha*

Table 3.5. PCA loadings of first & second principal components, of *M. coucha* from Namibia, Botswana and Angola. Numbers in bold indicate vector correlations with magnitudes greater than 0.29.

Characters	**PCA loadings**	
	PC1	**PC2**
GLS	0.69	0.20
ZAL	0.20	0.27
ZYW	0.32	-0.30
IOB	0.08	0.00
NAS	0.03	0.04
PAL	0.26	0.59
LPF	0.20	0.25
MAW	0.12	-0.16
HOR	0.12	0.03
UTR	0.04	-0.13
GML	0.46	-0.58
MAF	0.14	-0.09

M. natalensis

Results of a one-way analysis of variance indicated statistically significant differences ($p < 0.05$) between specimens of *M. natalensis* from Namibia, Zimbabwe and South Africa, this for all the 12 characters measured. **Table 3.6.** provides the F-values generated from the one-way ANOVA. The F-values were very high and ranged from 5.63 (UTR) to 60.06 (PAL). The results obtained (**Table 3.6.**) also indicate that the *M. natalensis* specimens from South Africa were larger on average for all the 12 characters measured.

Table 3.6. Results of one-way ANOVA for differences between specimens of *M. natalensis* from Namibia, Zimbabwe and South Africa

	Namibia				**Zimbabwe**				**South Africa**					
Characters	**N**	**M**	**SD**	**CV %**	**N**	**M**	**SD**	**CV %**	**N**	**M**	**SD**	**CV %**	***F***	**Sig.**
GLS	40	28.24	1.84	6.53	43	28.05	1.31	4.65	53	30.25	1.21	4.02	34.14	0.000
ZAL	40	10.58	0.69	6.55	43	10.28	0.62	6.04	53	10.98	0.52	4.73	16.16	0.000
ZYW	40	13.63	0.97	7.12	43	13.72	0.67	4.90	53	15.01	0.75	4.97	45.62	0.000
IOB	40	4.00	0.17	4.29	43	4.05	0.17	4.31	53	4.29	0.17	4.01	38.57	0.000
NAS	40	2.96	0.25	8.53	43	2.92	0.21	7.16	53	3.14	0.26	8.27	11.25	0.000
PAL	40	12.46	0.81	6.47	43	11.84	0.68	5.76	53	13.44	0.69	5.14	60.06	0.000
LPF	40	6.60	0.54	8.17	43	6.31	0.50	8.00	53	7.19	0.45	6.28	40.08	0.000
MAW	40	5.91	0.29	4.84	43	5.93	0.26	4.44	53	6.36	0.25	3.88	44.92	0.000
HOR	40	4.59	0.41	8.86	43	4.53	0.33	7.29	53	4.96	0.35	7.15	20.49	0.000
UTR	40	4.88	0.19	3.94	43	5.01	0.19	3.88	53	5.02	0.23	4.49	5.63	0.005
GML	40	13.70	0.95	6.97	43	13.52	0.81	5.96	53	14.93	0.83	5.54	38.81	0.000
MAF	40	3.87	0.41	10.55	43	3.74	0.29	7.73	53	4.29	0.40	9.34	29.24	0.000

The first principal component (PC1) accounted for 86.86% of the total variation within *M. natalensis* samples from Namibia, South Africa and Zimbabwe (**Fig. 3.5.**; **Table 3.7.**). PC1 is interpreted here as a general size axis based on the positive sign and positive magnitudes of most character loadings. The second principal component (PC2), which accounted for 3.23% of the total variation, is interpreted as a general shape axis. Characters associated with the size of skull, such as length of skull (GLS) and greatest mandible length (GML) show high correlations with PC1, whereas those related to the width of braincase, such as greatest zygomatic width (ZYW) show positive and high loadings on PC2 (**Table 3.7.**).

Along PC1, the most evident result is an increase in skull size, with the samples from South Africa larger than samples from Namibia and Zimbabwe (**Fig. 3.5.**; **Table 3.7.**). PC1 loadings indicate that samples from South Africa are composed of individuals with longer skull and mandible lengths (GLS & GML). Along PC2, the greatest zygomatic width (ZYW) is also larger in South African samples in comparison to samples from Namibia and Zimbabwe (**Fig. 3.5.**; **Table 3.7.**).

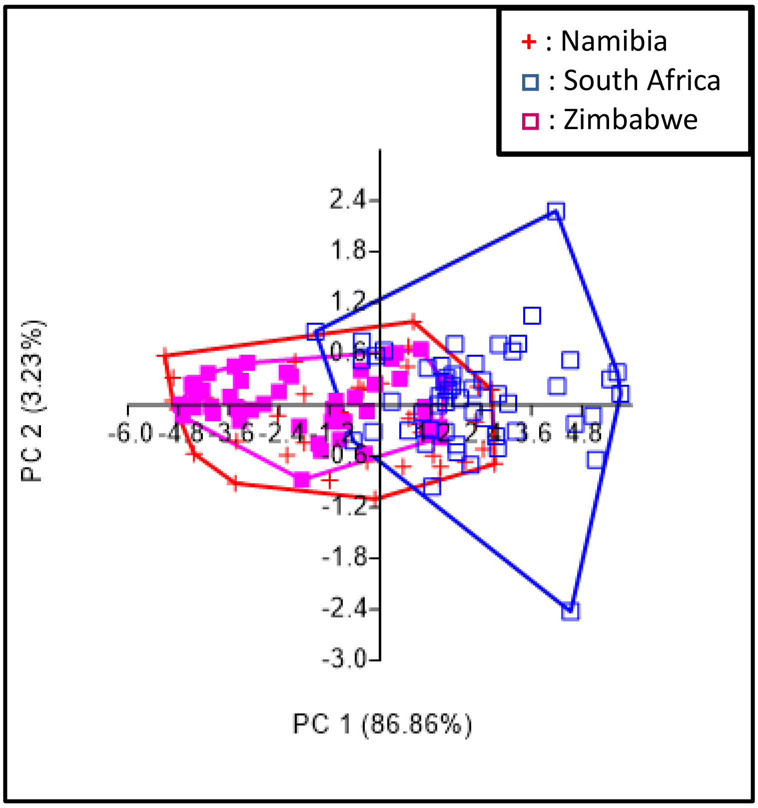


Figure 3.5. The first two axes from principal component analyses used to assess geographic variation within samples of *M. natalensis*

Table 3.7. PCA loadings of first & second principal components, of *M. natalensis* from Namibia, South Africa and Zimbabwe. Numbers in bold indicate vector correlations with magnitudes greater than 0.29.

Characters	**PCA loadings**	
	PC1	**PC2**
GLS	0.67	-0.52
ZAL	0.24	0.03
ZYW	0.35	0.61
IOB	0.05	0.02
NAS	0.06	-0.02
PAL	0.35	-0.20
LPF	0.20	-0.13
MAW	0.11	0.06
HOR	0.14	0.01
UTR	0.03	0.00
GML	0.38	0.54
MAF	0.14	0.06

All three species from Namibia

Results of a one-way analysis of variance indicated statistically significant differences ($p < 0.05$) between specimens of *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia. This was recorded for all the measured characters except: NAS ($p > 0.05$), HOR ($p > 0.05$) and MAF ($p > 0.05$). **Table 3.8.** provides the F-values generated from the one-way ANOVA. The character IOB {F (2,106) = 36.2} was the character with the highest F-value and it is the character that offers the best discrimination between the three species (Refer to **Table 3.8.** and **Fig. 3.6.**).

Table 3.8. Results of one-way ANOVA for differences between *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia

	M. coucha				***M. natalensis***				***M. shortridgei***					
Characters	**N**	**M**	**SD**	**CV %**	**N**	**M**	**SD**	**CV %**	**N**	**M**	**SD**	**CV %**	***F***	**Sig.**
GLS	34	27.55	0.87	3.17	40	28.24	1.84	6.53	35	28.40	1.32	4.65	3.464	0.034
ZAL	34	10.10	0.35	3.42	40	10.58	0.69	6.55	35	10.52	0.48	4.54	8.493	0.000
ZYW	34	13.44	0.48	3.53	40	13.63	0.97	7.12	35	14.11	0.73	5.14	6.976	0.001
IOB	34	3.82	0.18	4.83	40	4.00	0.17	4.30	35	4.22	0.23	5.48	36.2	0.000
NAS	34	2.91	0.22	7.45	40	2.96	0.25	8.53	35	2.89	0.21	7.31	0.767	0.467
PAL	34	12.22	0.49	4.02	40	12.46	0.81	6.47	35	12.73	0.49	3.81	5.748	0.004
LPF	34	6.41	0.37	5.81	40	6.60	0.54	8.17	35	6.94	0.39	5.64	12.87	0.000
MAW	34	5.75	0.25	4.32	40	5.91	0.29	4.84	35	6.11	0.19	3.05	18.38	0.000
HOR	34	4.44	0.24	5.32	40	4.59	0.41	8.86	35	4.58	0.32	7.05	2.086	0.129
UTR	34	4.77	0.21	4.36	40	4.89	0.19	3.94	35	4.88	0.20	4.18	4.055	0.020
GML	34	13.19	0.63	4.76	40	13.70	0.96	6.97	35	14.02	0.74	5.27	9.503	0.000
MAF	34	3.70	0.70	10.00	40	3.87	0.41	10.55	35	3.78	0.30	7.84	1.963	0.146

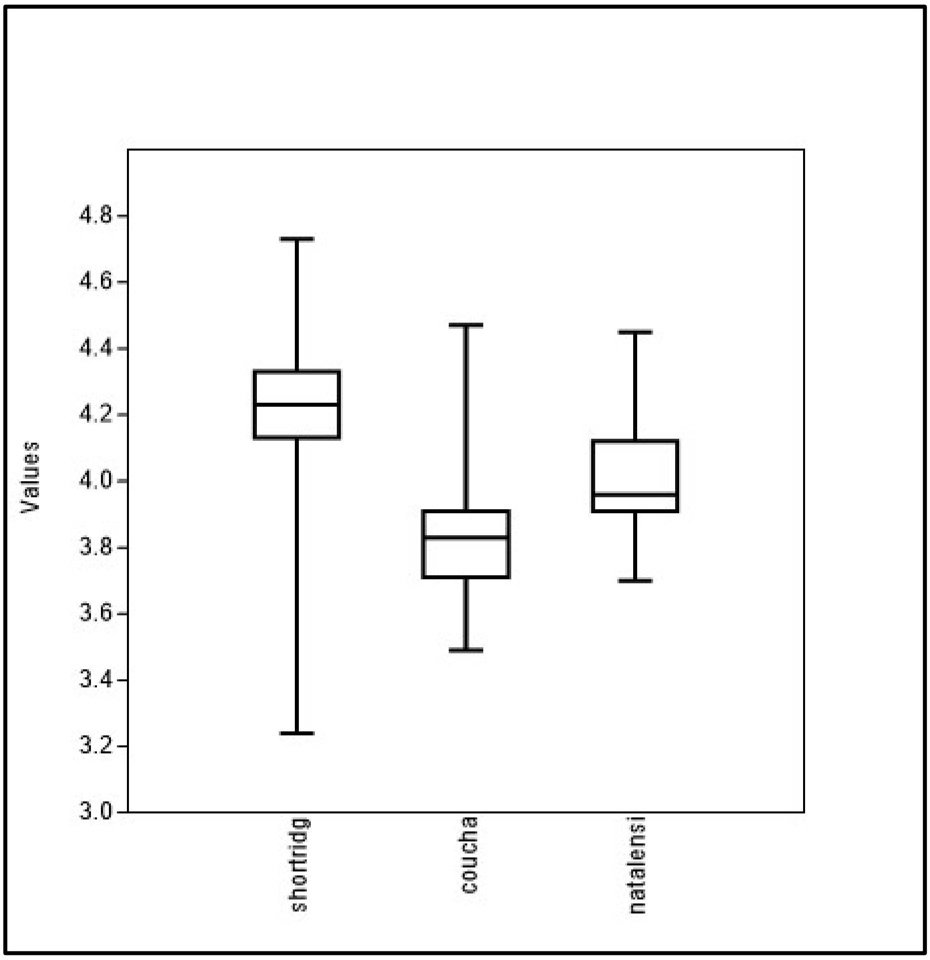


Fig. 3.6. Boxplot indicating mean differences in character IOB between the three species *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia– note non-overlap of 95% confidence limits

Principal component analyses of *Mastomys* individuals from Namibia are presented in **Figure 3.7.** There is no clear separation of individuals as indicated by the overlapping PCA scatter plot (**Fig. 3.7.**). The first 2 factors explained 85.54% of the total variation between the 12 cranial variables for the *Mastomys* specimens from Namibia, representing the three species: *M. coucha*, *M. natalensis* and *M. shortridgei*.

Character loadings for the first two principal components of individuals of the three species: *M. coucha*, *M. natalensis* and *M. shortridgei* are presented in **Table 3.9.** The main characters important in describing size differentiation and sample variation between the *Mastomys* species were: greatest length of skull (GLS, 72%), greatest zygomatic width (ZYW, 36%) and greatest mandible length (GML, 56%).

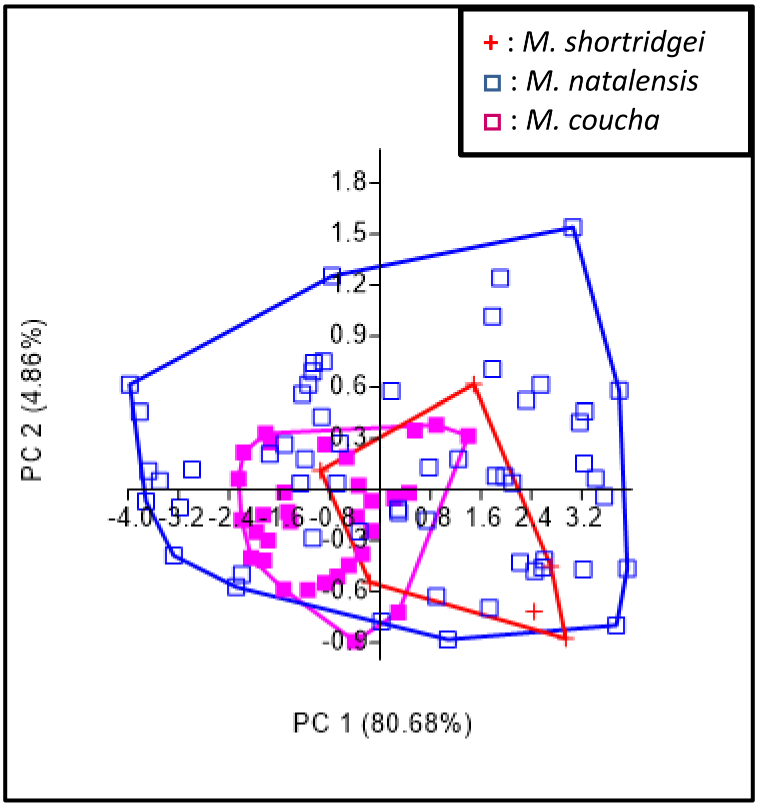


Figure 3.7. The first two axes from principal component analyses used to assess variation among samples of *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia

Table 3.9. PCA loadings of first & second principal components of *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia. Numbers in bold indicate vector correlations with magnitudes greater than 0.29.

Characters	**PCA loadings**	
	PC1	**PC2**
GLS	0.72	-0.64
ZAL	0.25	0.05
ZYW	0.36	0.38
IOB	0.05	0.13
NAS	0.05	-0.05
PAL	0.28	0.12
LPF	0.18	0.12
MAW	0.09	0.21
HOR	0.14	0.03
UTR	0.05	0.02
GML	0.37	0.56
MAF	0.13	0.17

Results from One-way MANOVA (Multivariate Analysis of Variance) of *Mastomys* specimens from Namibia revealed significant differences between group centroids of OTU's (Wilk's $\Lambda = 0.375$, F (24, 162) = 4.28, $p < 0.00001$). **Figure 3.8.** shows a plot of the first and second canonical variates axes. The first axis (CV1), explaining 69.61% of the variation, suggests generally that *M. shortridgei* specimens are distinct from *M. coucha* and *M. natalensis* specimens, although *M. shortridgei* overlap slightly with the other two groups due to a single individual grouping with *M. coucha* and *M. natalensis*.

The first canonical variates component (**Table 3.10**) was positively correlated with least breadth of interorbital constriction (IOB; 4.10), crown length of maxillary toothrow (UTR; 2.22) and zygomatic arch length (ZAL; 1.86). Two characters, nasal width (NAS; -1.56) and greatest zygomatic width (ZYW; -0.93) showed strong negative correlations on the first component.

The classification functions indicated that the probability of correct classification for specimens in the first (*M. coucha*) group was 88%, second (*M. natalensis*) group 84% and 83% for the third (*M. shortridgei*) group.

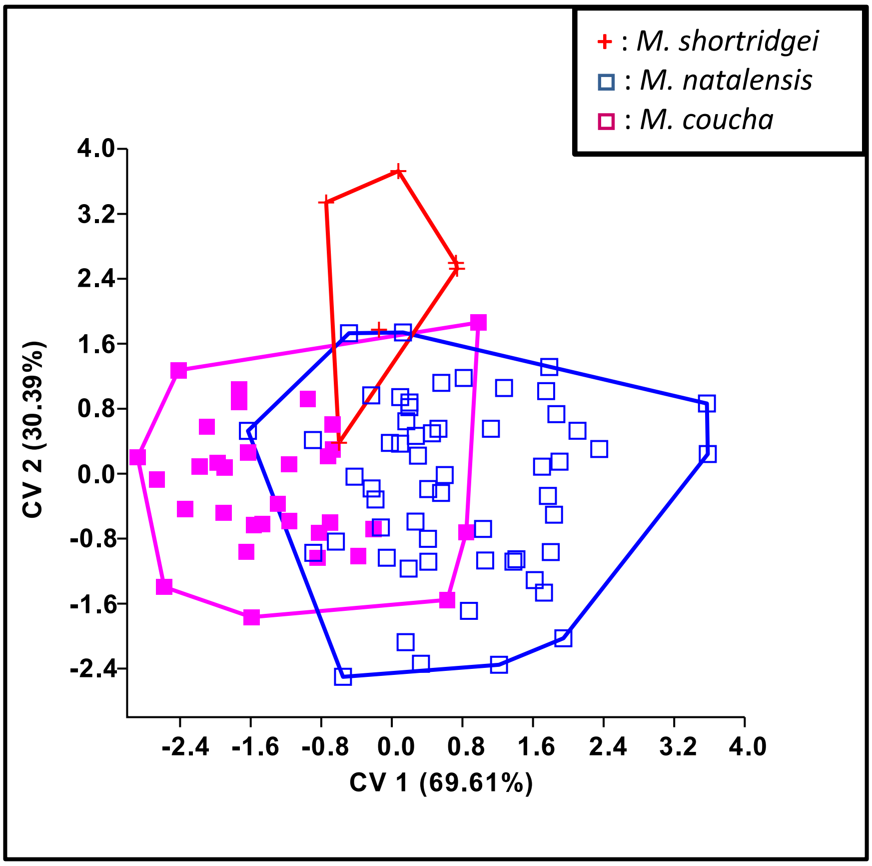


Fig. 3.8. Canonical variates analysis plot based on traditional linear skull measurements for *Mastomys* species from Namibia

Table 3.10. Loadings of variables on canonical variates components 1 and 2

Character	CVA loadings	
	CV1	CV2
GLS	-0.35252	0.90193
ZAL	1.864	-1.3641
ZYW	-0.92867	0.45484
IOB	4.1005	1.3969
NAS	-1.5584	2.9621
PAL	-0.56376	0.055726
LPF	0.001603	0.11228
MAW	0.10135	0.44681
HOR	0.50097	-2.7337
UTR	2.2242	-0.03827
GML	0.78857	-0.14316
MAF	-0.31479	-1.2248

3.1.2. Geometric Morphometrics

3.1.2.1. Testing for digitization error

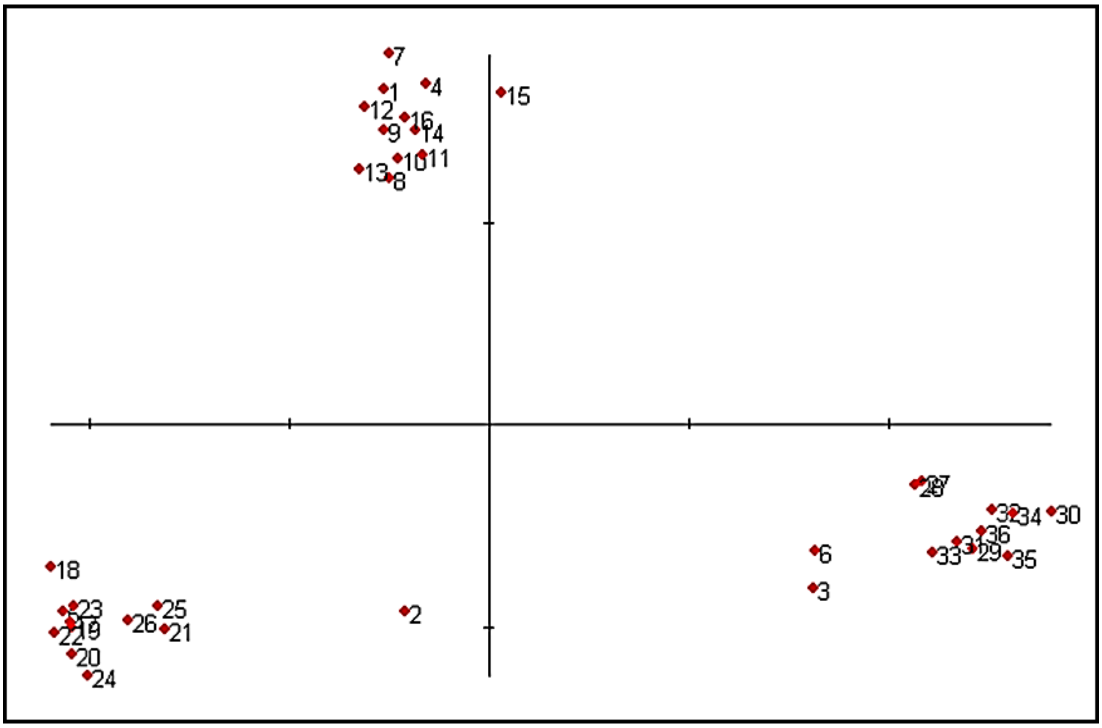


Figure 3.9. Relative warps plot for digitization error testing

High levels of differentiation were achieved between individuals for the dorsal view (**Fig. 3.9.**). Image data per individual sample overlapped and were grouped closely together indicating that placement of landmarks and specimens was precise (**Fig. 3.9.**). This result validates the effectiveness and accuracy of specimen placement and landmark digitization and implies that the method can be utilized for all the samples in the study.

3.1.2.2. Geographic Variation

3.1.2.2.1. Dorsal View

M. coucha- dorsal view

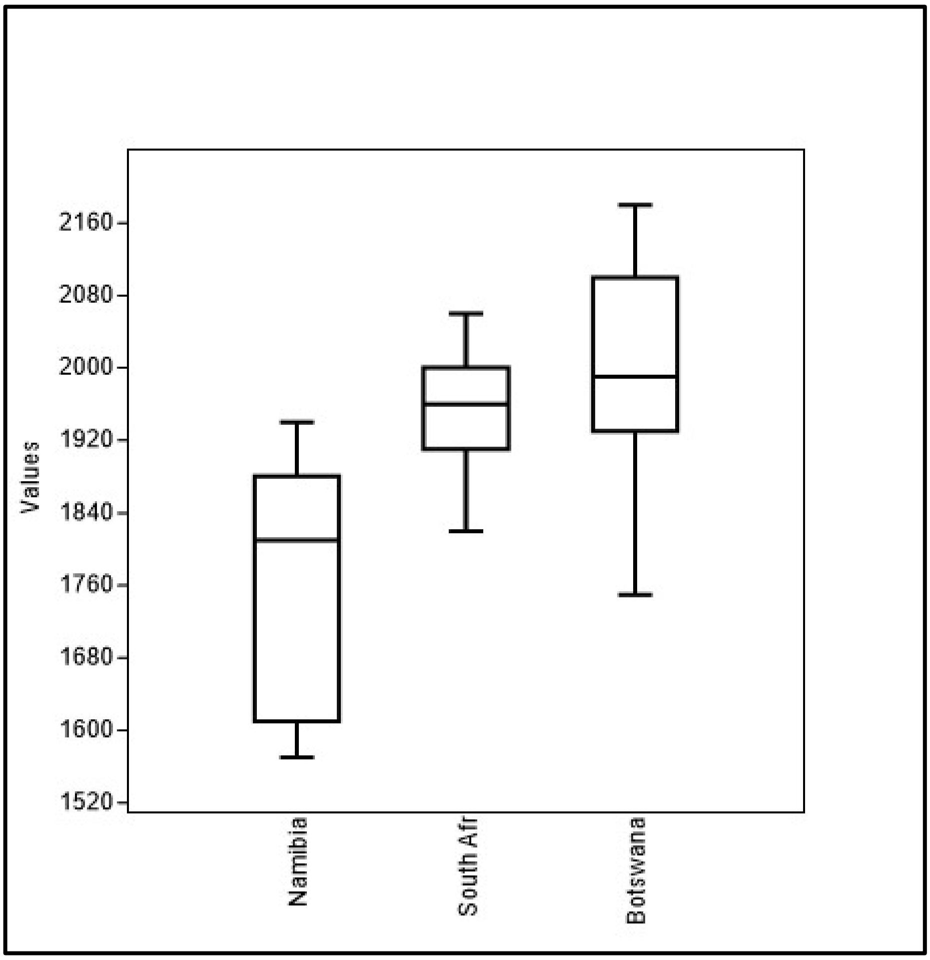


Fig 3.10. Centroid size differences between populations of *Mastomys coucha* from Namibia, South Africa & Botswana, for dorsal side of the skull.

A centroid size difference between population samples of *M. coucha* throughout the sub-region is reflected in **Fig 3.10**. Individuals from Botswana are larger on average than individuals from South Africa and Namibian individuals being the smallest on average (**Fig. 3.10**).

The two principal components (PC1 and PC2) due to dorsal skull shape (**Fig. 3.11.**) indicate that there is no clear separation between populations of *M. coucha* from Namibia, Botswana and South Africa. There is no clear division or clustering of individuals in groups and individuals from different localities (i.e. species) are all mixed together.

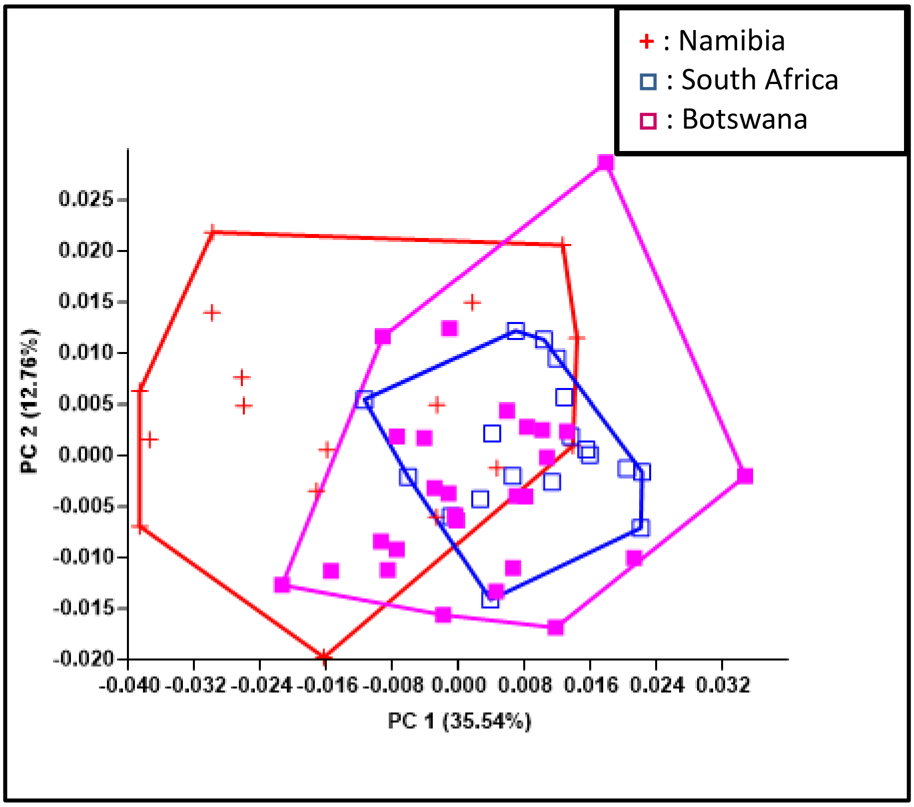


Figure 3.11. The first two axes from Relative warps analyses used to assess geographic variation within samples of *M. coucha*, from dorsal side of skull.

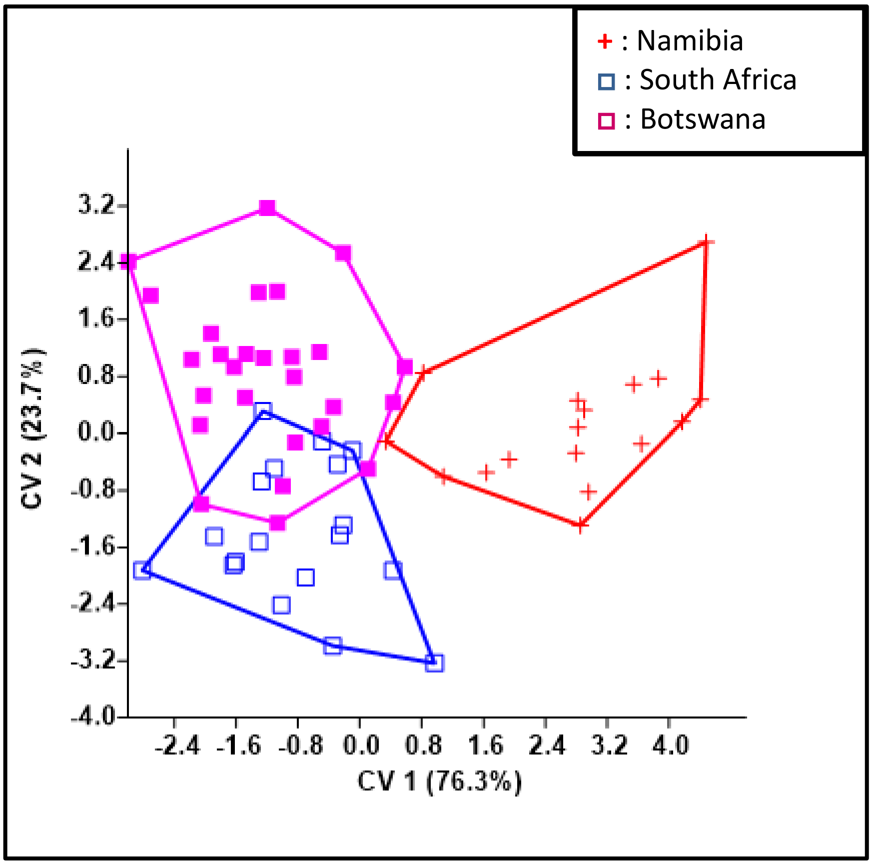


Figure 3.12. The first two axes from canonical variates analyses used to assess geographic variation within samples of *M. coucha*, from dorsal side of skull.

The CVA result separated *M. coucha* individuals from Namibia, whereas there is slight overlap between individuals from Botswana and South Africa (**Fig. 3.12**). The percentage variation represented by the first axis (CV1) is 76.3% (**Fig. 3.12.**).

M. natalensis- dorsal view

A centroid size difference between population samples of *M. natalensis* throughout the sub-region is reflected in **Fig 3.13.** Individuals from Namibia are larger on average than individuals from South Africa and Angola (**Fig. 3.13.**).

The two principal components (PC1 and PC2) due to dorsal skull shape (**Fig. 3.14.**) indicate that there is no clear separation between populations of *M. natalensis* from Namibia, South Africa and Angola. There is no clear division or clustering of individuals in groups and individuals from different localities (i.e. species) are all mixed together.

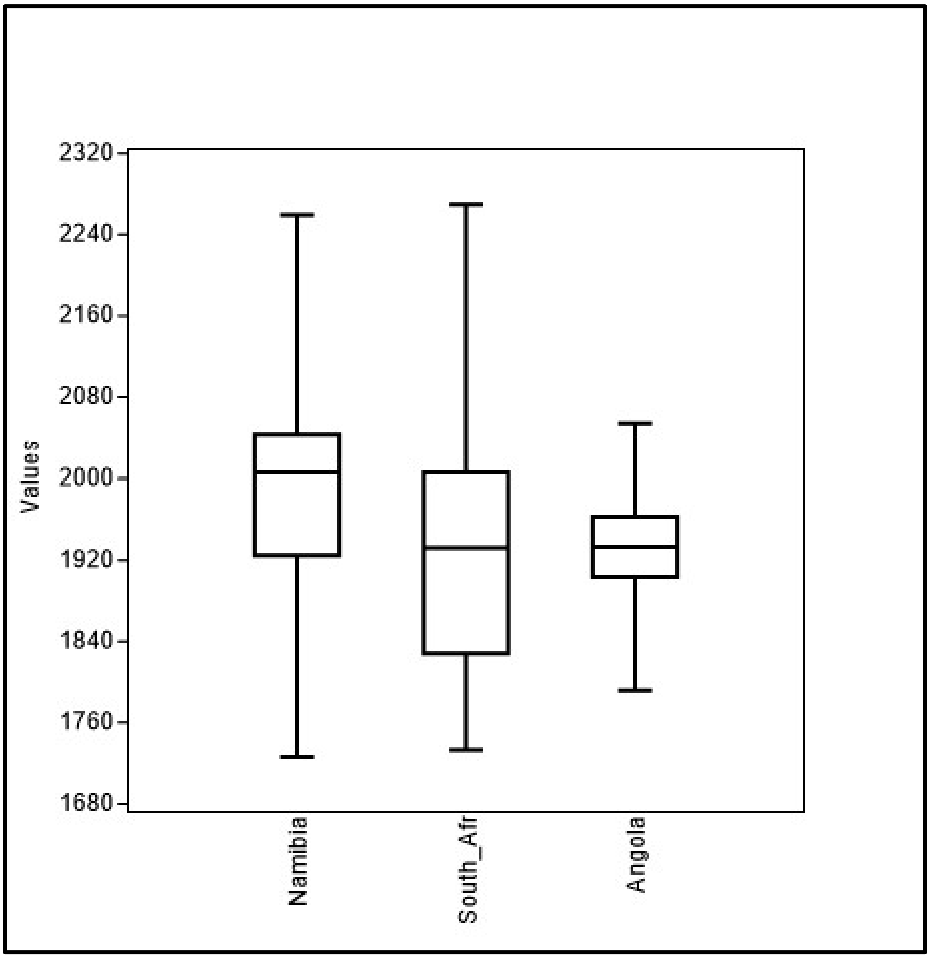


Figure 3.13. Centroid size differences between populations of *Mastomys natalensis* from Namibia, South Africa & Angola, for dorsal side of the skull.

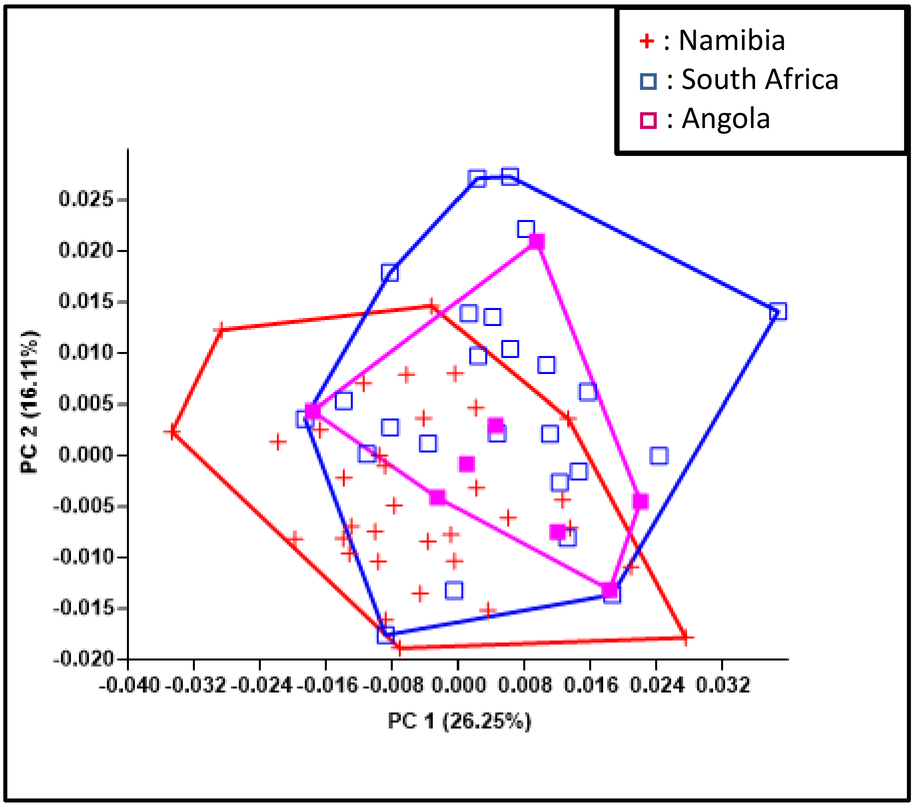


Figure 3.14. The first two axes from Relative warps analyses used to assess geographic variation within samples of *M. natalensis*, from dorsal side of skull

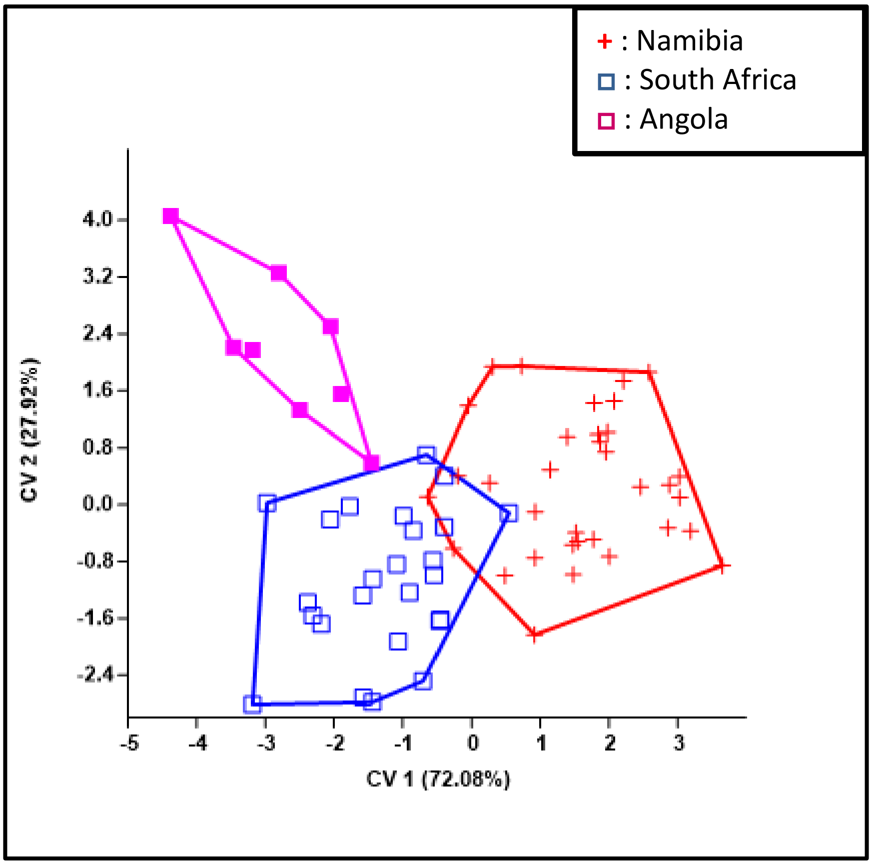


Figure 3.15. The first two axes from canonical variates analyses used to assess geographic variation within samples of *M. natalensis*, from dorsal side of skull

The CVA result separated *M. natalensis* Angolan individuals from that of Namibia and South Africa, whereas there is slight overlap between individuals from Namibia and South Africa (**Fig. 3.15.**). The percentage variation represented by the first axis (CV1) is 72.08% (**Fig. 3.15.**).

All species- dorsal view

Centroid size differences between the three species from Namibia are indicated in **Fig. 3.16.**, with minimal overlap in 95% confidence limits. Specimens of *M. shortridgei* are distinctly larger on average than those of *M. natalensis* which are distinctly larger than those of *M. coucha* (**Fig. 3.16.**).

The two principal components (PC1 and PC2) from PCA of dorsal skull shape (**Fig. 3.17.**) indicate that there are no clear shape differences between specimens of the three species *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia.

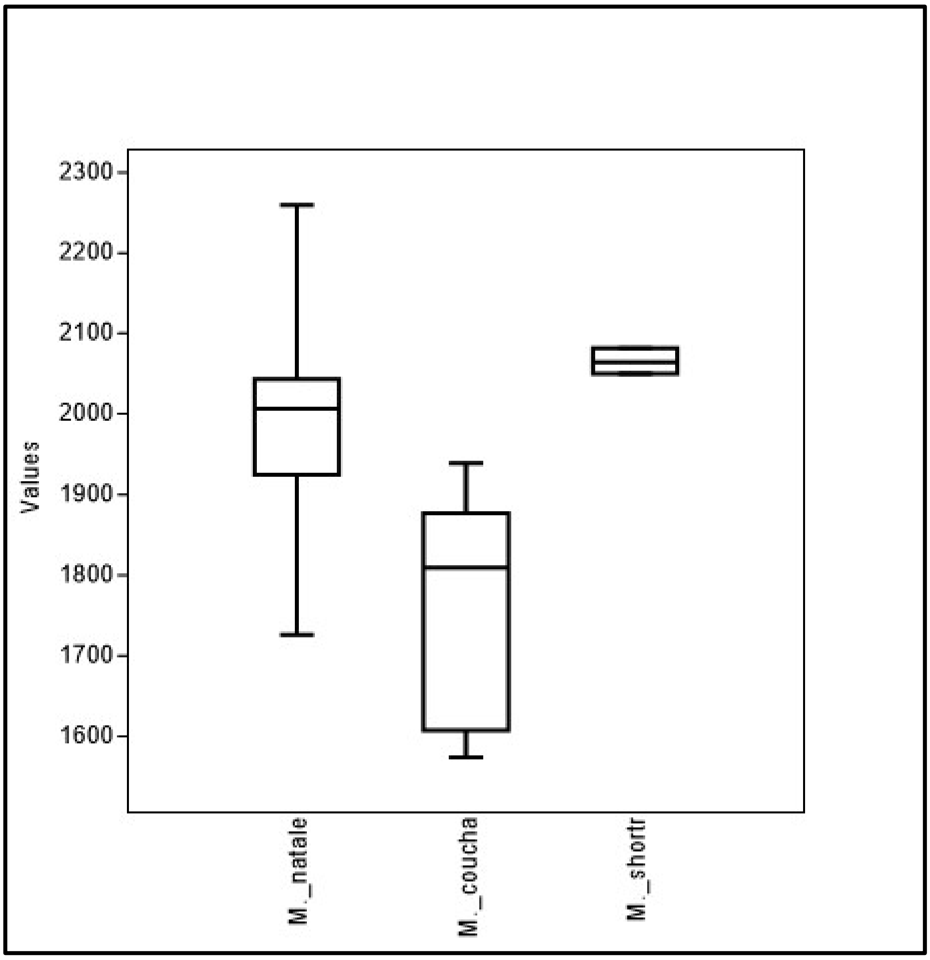


Figure 3.16. Centroid size differences between populations of *M. coucha*, *M. natalensis* & *M. shortridgei* from Namibia, for dorsal side of the skull

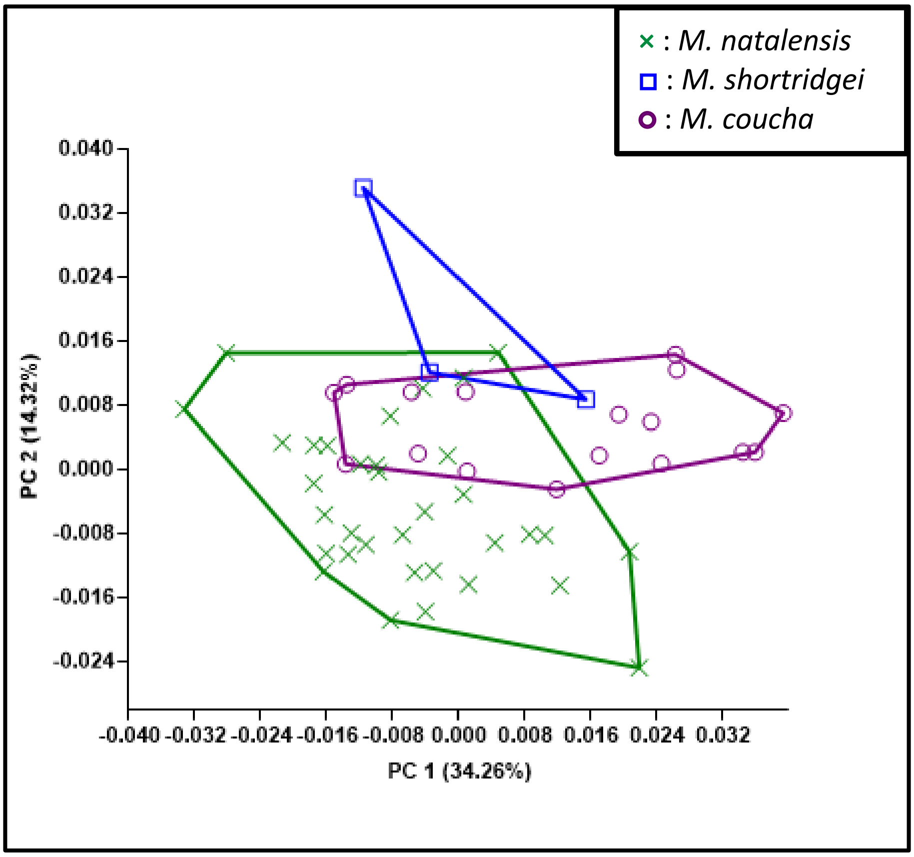


Figure 3.17. The first two axes from Relative warps analyses used to assess variation among samples of *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia, for dorsal side of skull

However, results from One-way MANOVA (Multivariate Analysis of Variance) of the three species *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia revealed statistically significant differences between group partial weight matrices of OTU's (Wilk's $\Lambda = 0.056$, F $(44, 60) = 4.38$, $p < 0.0005$). **Figure 3.18** shows a plot of the first and second canonical variates axes showing that all three species are completely discriminated on dorsal shape.

On the visualizations of dorsal view, on CV1 the cranial shape of *M. natalensis* appeared to be characterised by a disproportionately longer and more elongated nasal bone, and cranium generally than that of *M. coucha* and *M. shortridgei* (**Fig. 3.18**). On CV2, the distinctive skull shape difference exhibited by *M. shortridgei* is a much shorter and fatter nasal bone than that of *M. coucha* and *M. natalensis*.

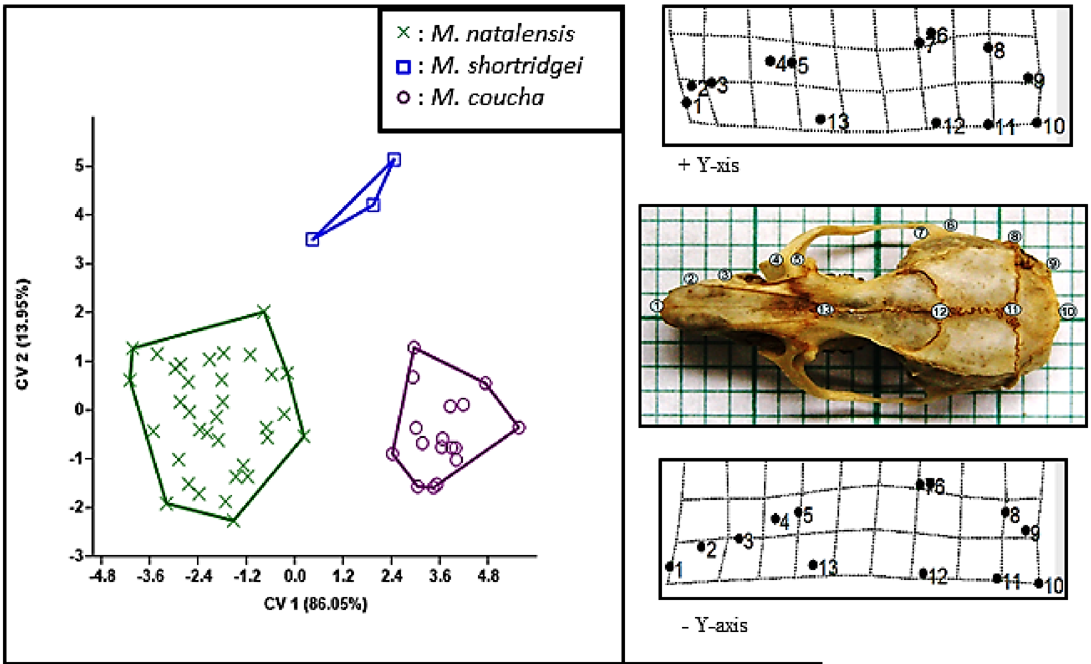
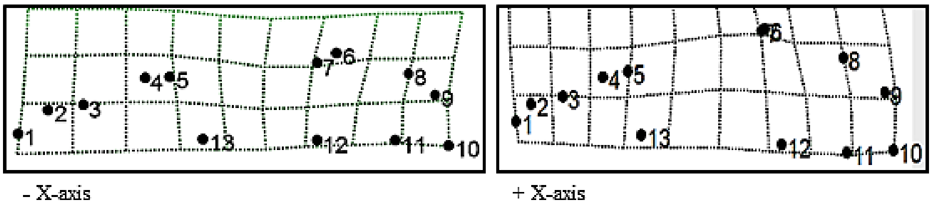


Figure 3.18. The first two axes from canonical variates analyses used to assess variation among samples of *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia, for dorsal side of skull. Thin plate splines depict deformations at the relevant landmarks (magnified 3x).



3.1.2.2.2. Ventral view

M. natalensis- ventral view

A centroid size difference between population samples of *M. natalensis* from Namibia and South Africa is reflected in **Fig 3.19**. There is no clear size differences indicated between specimens from Namibia and South Africa (**Fig 3.19**).

The two principal components (PC1 and PC2) due to ventral skull shape (**Fig. 3.20**) indicate that there is no clear separation between populations of *M. natalensis* from Namibia and South Africa. There is no clear division or clustering of individuals in groups and individuals from different localities (i.e. species) are all mixed together.

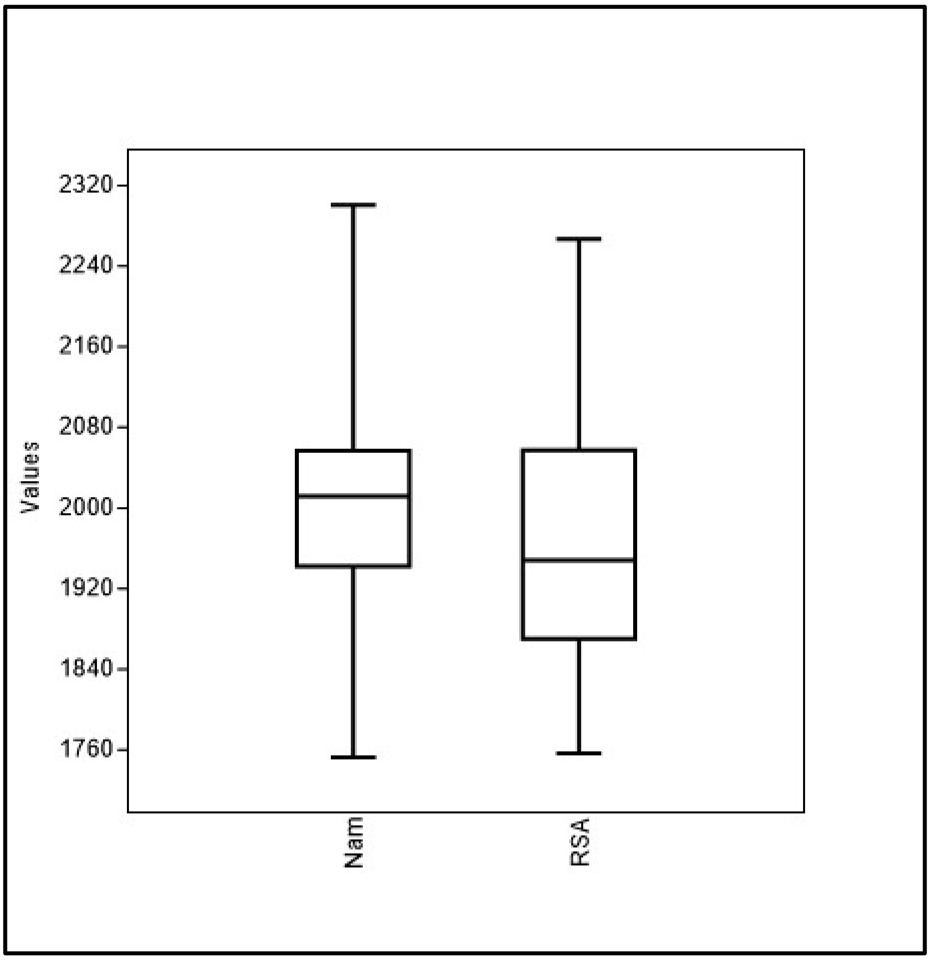


Figure 3.19. Centroid size differences between populations of *Mastomys natalensis* from Namibia and South Africa, for ventral side of the skull

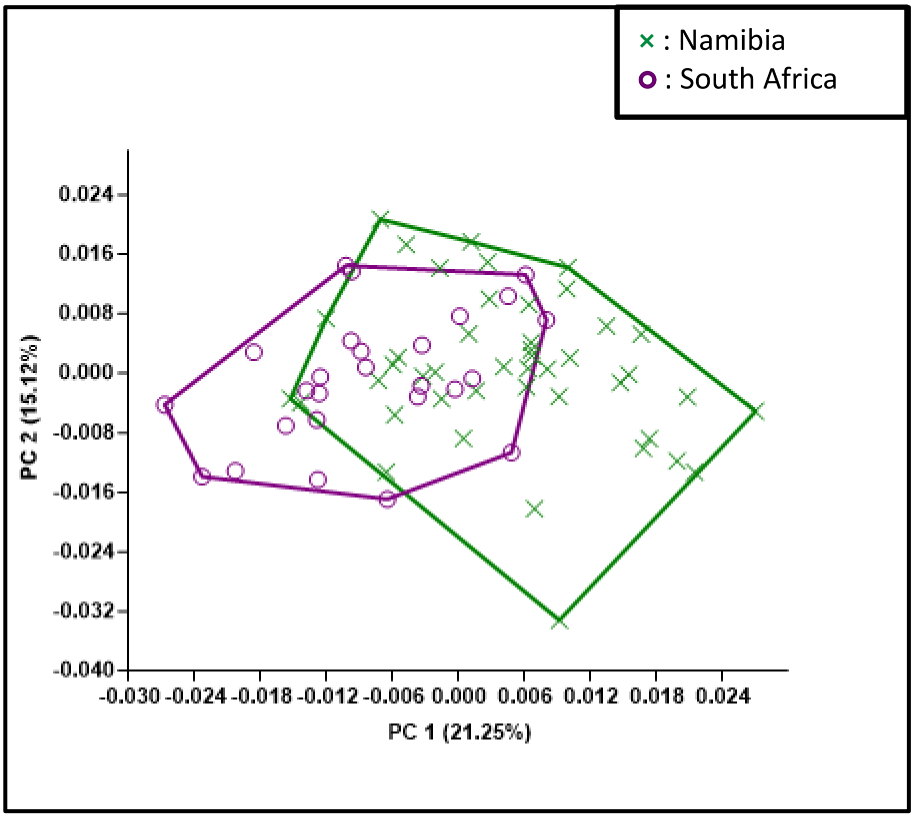


Figure 3.20. The first two axes from Relative warps analyses used to assess geographic variation within samples of *M. natalensis*, from ventral side of skull

All species- ventral view

Centroid size differences between the three species from Namibia are indicated in **Fig. 3.21.** Specimens of *M. shortridgei* are slightly larger on average than specimens of *M. natalensis* and *M. coucha* (**Fig. 3.21**).

The two principal components (PC1 and PC2) due to ventral skull shape (**Fig. 3.22)** indicate that there are no clear differences between specimens of the three species *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia.

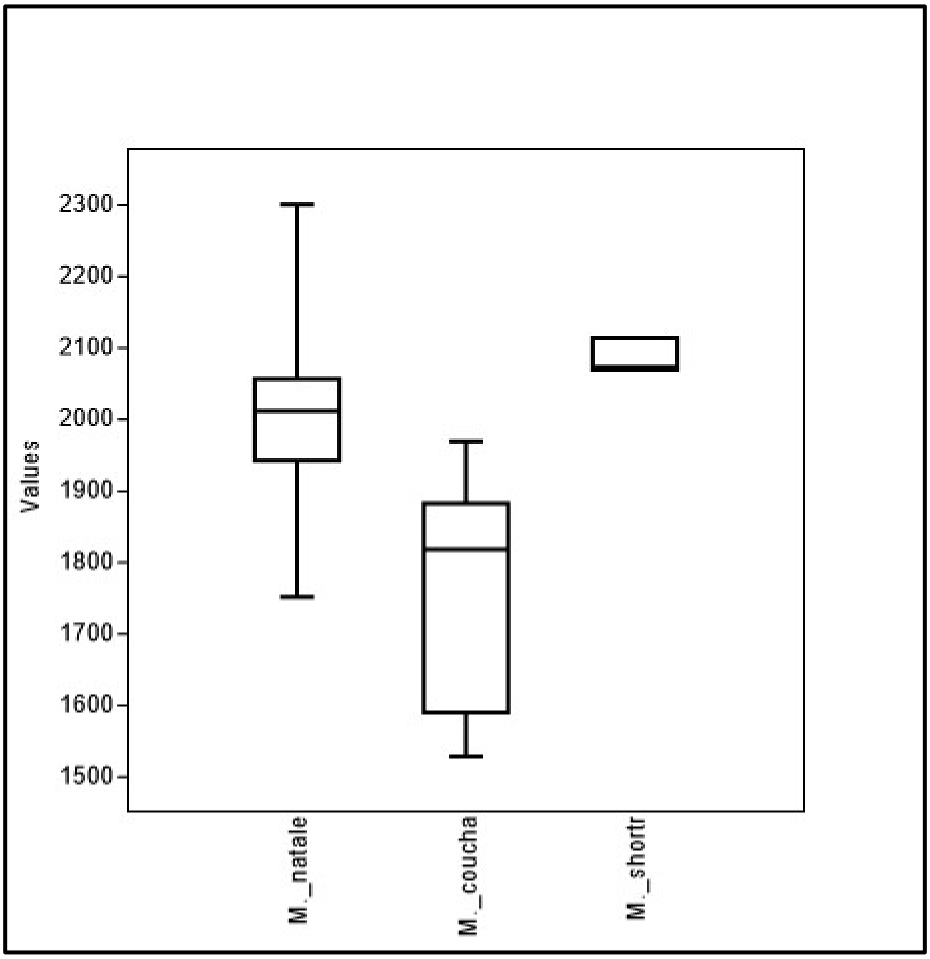


Figure 3.21. Centroid size differences between populations of *M. coucha*, *M. natalensis* & *M. shortridgei* from Namibia, for ventral side of the skull

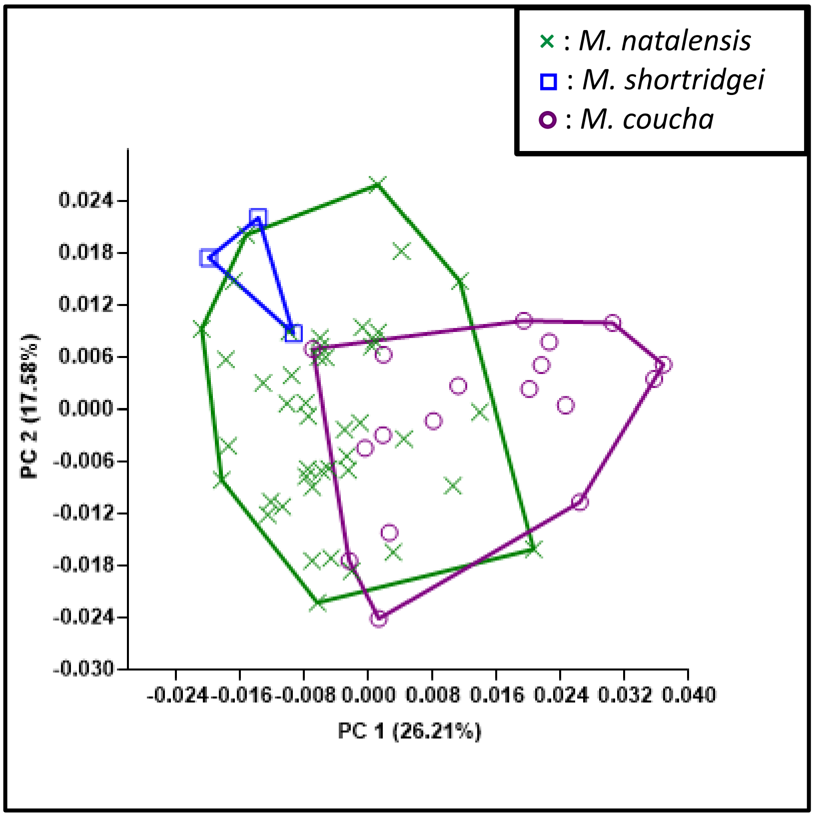
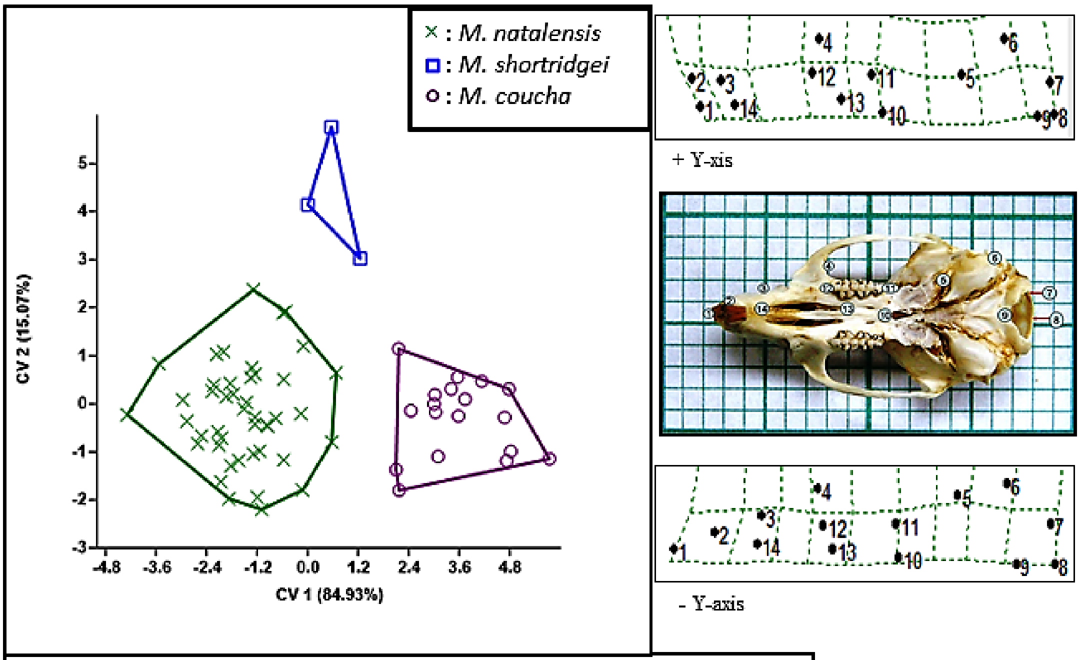


Figure 3.22. The first two axes from Relative warps analyses used to assess variation among samples of *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia, for ventral side of skull

Results from One-way MANOVA (Multivariate Analysis of Variance) of the three species *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia revealed statistically significant differences between group partial weight matrices of OTU's (Wilk's $\Lambda = 0.081$, $F(48, 78) = 4.07$, $p < 0.0005$). **Figure 3.23** shows a plot of the first and second canonical variates axes. The first axis (CV1), explaining 84.93% of the variation, suggests generally that *M. shortridgei* specimens are distinct from *M. coucha* and *M. natalensis* specimens.

On the visualizations of ventral view, the cranial shape of *M. natalensis* appeared to be longer and more elongated than that of *M. coucha* and *M. shortridgei* (**Fig. 3.23**). Both *M. coucha* and *M. shortridgei* have a much shorter and broader skull than *M. natalensis* (**Fig. 3.23**). This was affected probably by the larger bullae of *M. coucha* and *M. shortridgei* than that of *M. natalensis* as shown in the grid deformation visualization of ventral view (**Fig. 3.23**). The distinctive shape difference exhibited by *M. shortridgei* is a much longer- longest palatal foramen (LPF) than that of *M.*

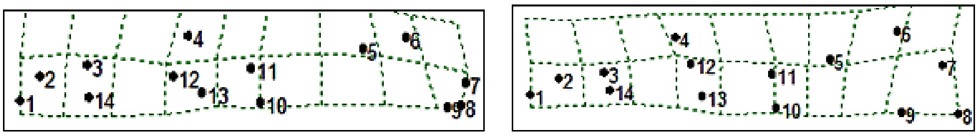
coucha and *M. natalensis*, as is indicated by the distance between landmarks 14 and 13 (**Fig. 3.23**, deformation grid + Y-axis).



+ Y-xis

- Y-axis

Figure 3.23. The first two axes from canonical variates analyses used to assess variation among samples of *M. coucha*, *M. natalensis* and *M. shortridgei* from Namibia, for ventral side of skull. Thin plate splines depict deformations at the relevant landmarks (magnified 3x).



- X-axis

+ X-axis

3.2. Cytogenetics

A total of 353 *Mastomys* specimens were trapped and collected throughout the three countries (**Appendices Four, Five and Six**). From these specimens, a total of 64 were karyotyped. The results of the chromosome counts, diploid number (2n) and the chromosome arm number (aFN) are given in **Table 3.11**.

Table 3.11. Summary of results of chromosome counts and morphological divisions of chromosomes

Locality	**Country**	**Number of specimens**	**Diploid number (2n)**	**Chromosome arms number (aFN)**
Windhoek	Namibia	5	36	60/60
Omatjene	Namibia	6	36	60/60
Uniab	Namibia	5	36	60/60
Namutoni	Namibia	2	32	57/58
Namutoni	Namibia	2	36	60/60
Etunda	Namibia	2	32	57/58
Etunda	Namibia	2	36	60/60
Omatako-Kavango rivers confluence	Namibia	8	32	57/58
Shamvura village	Namibia	2	32	57/58
Shamvura camp	Namibia	2	32	57/58
Popa Falls	Namibia	5	32	57/58
Shakawe	Botswana	2	32	57/58
Shakawe	Botswana	2	36	51/52
Sepopa	Botswana	6	32	57/58
Maun	Botswana	2	32	57/58
Lubango	Angola	4	32	57/58
Mbalanondolo village	Angola	4	32	57/58
Longa village	Angola	4	32	57/58

Three different chromosome numbers for *Mastomys* was found in this study, the first karyomorph having 2n = 32 (aFN = 57/58), the second having 2n = 36 (aFN = 60/60) and the third having 2n = 36 (aFN = 51/52). **Figures 3.24 & 3.25** are karyotypes of male and female *Mastomys* with the diploid number of 2n = 32 (aFN = 57/58). Within this karyomorph specimens from northern Namibia, Botswana and Angola had similar karyotypes with 7 pairs of submetacentric autosomes, 5 pairs of metacentric autosomes and 3 pairs of acrocentric autosomes plus a large metacentric X and a large acrocentric Y chromosome. The current study assigns this karyomorph to species: *M. natalensis*.

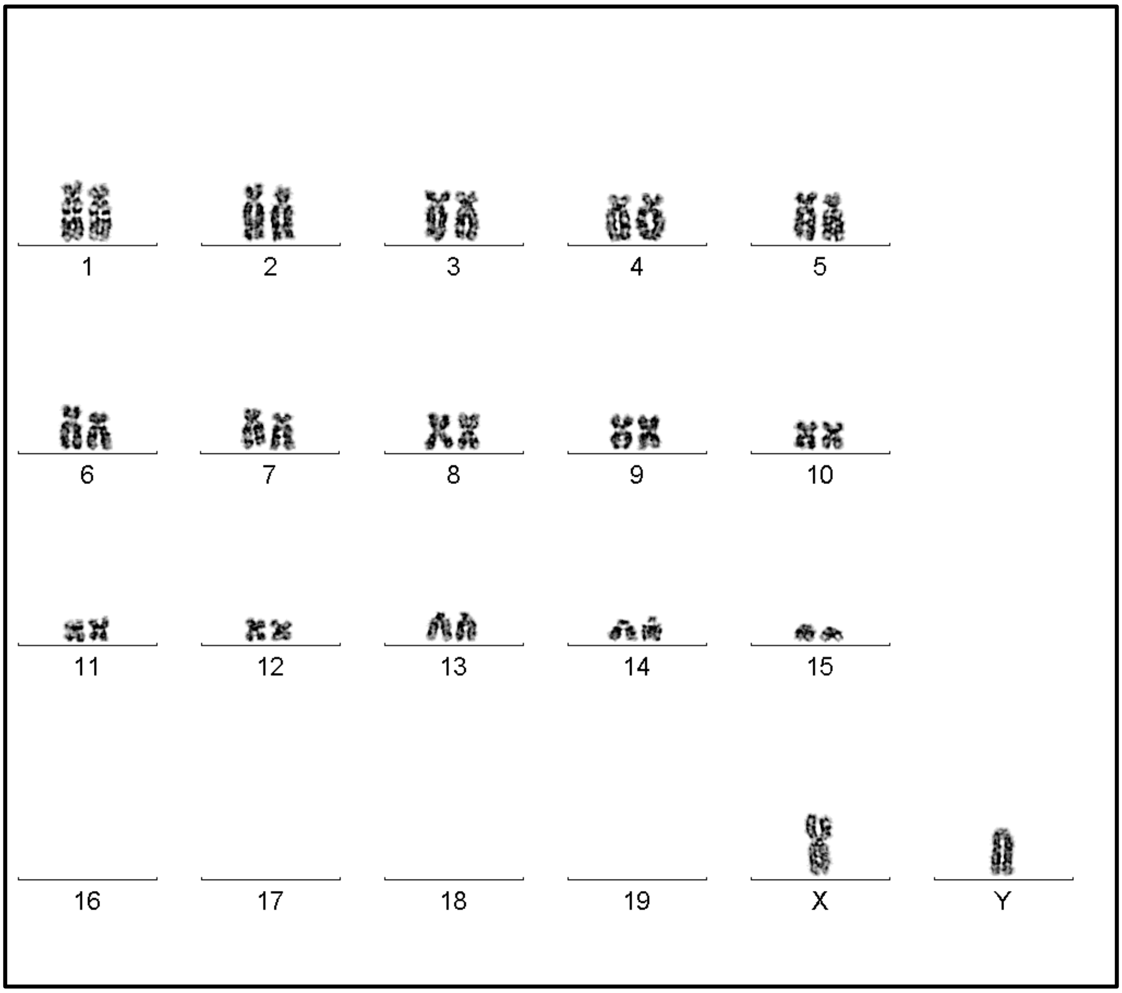


Figure 3.24. Karyogram of male 2n=32, aFN = 57/58 *Mastomys natalensis*

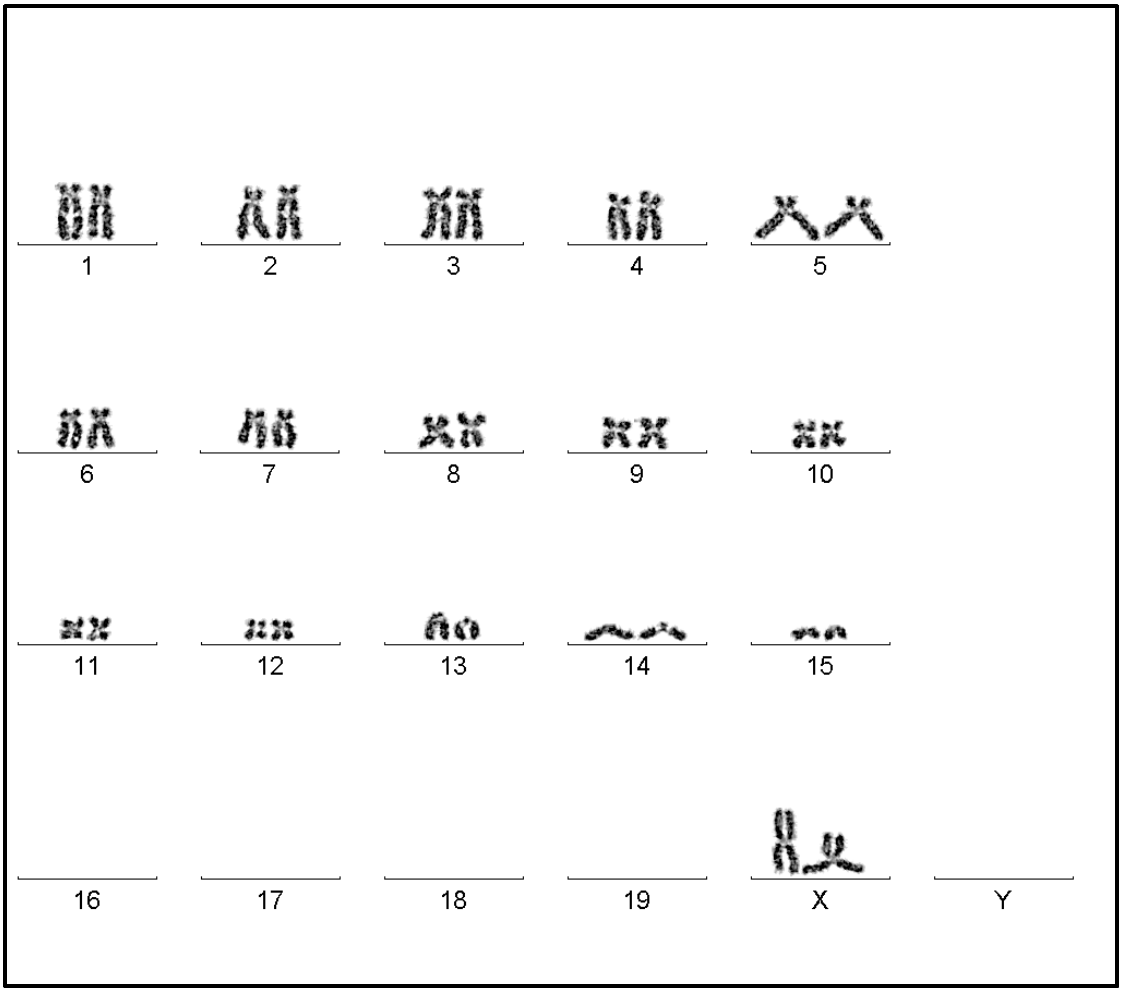


Figure 3.25. Karyogram of female 2n=32, aFN = 57/58 *Mastomys natalensis*

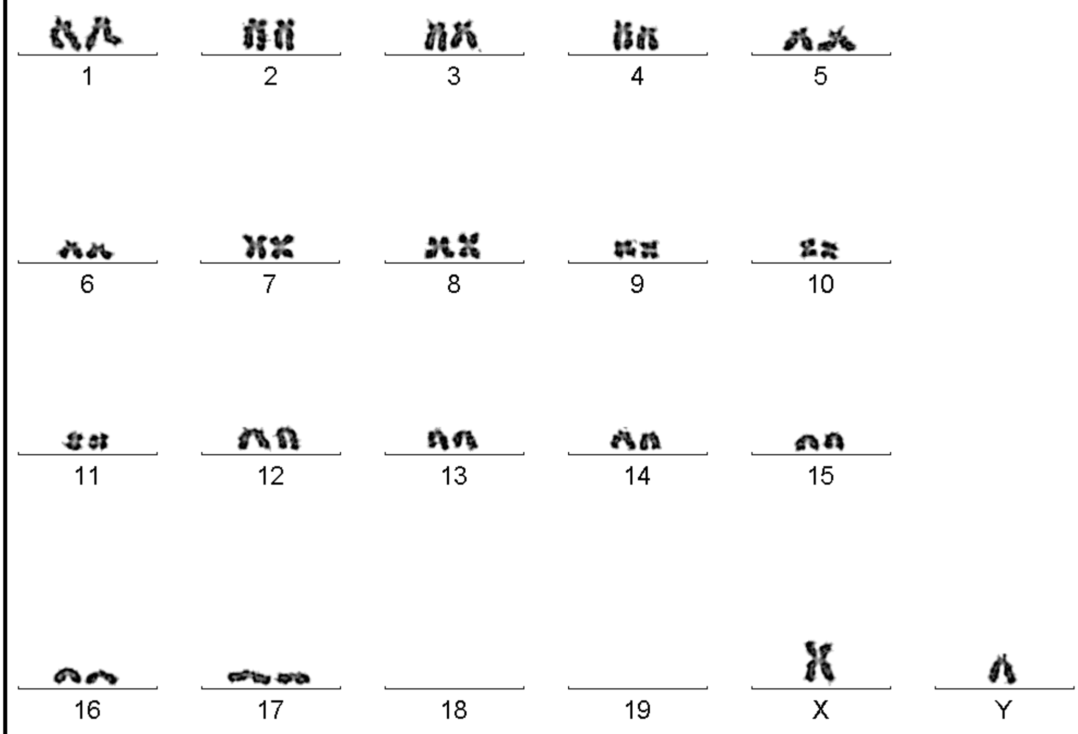


Figure 3.26. Karyogram of male 2n=36, aFN = 60/60 ***Mastomys coucha***

Figures 3.26 & 3.27 are karyotypes of male and female *Mastomys* with the higher diploid number of 2n = 36 (aFN = 60/60). Within this karyomorph, specimens from Windhoek to Namutoni and Etunda in central-north areas had similar karyotypes with 6 pairs of submetacentric autosomes, 5 pairs of metacentric autosomes, 6 pairs of acrocentric autosomes, plus a large metacentric X chromosome and a large submetacentric Y chromosome. The current study assigns this karyomorph to species: *M. coucha*.

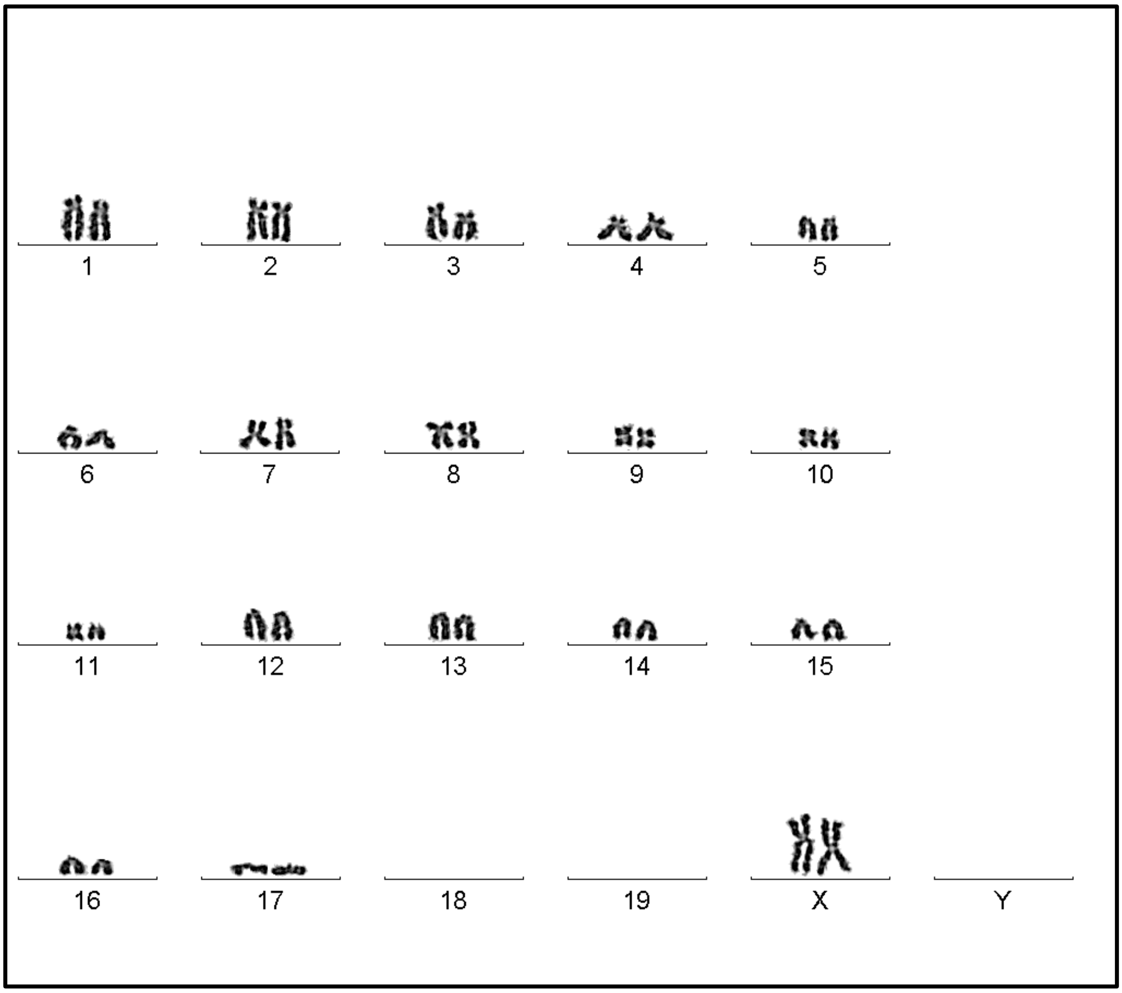


Figure 3.27. Karyogram of female 2n=36, aFN = 60/60 *Mastomys coucha*

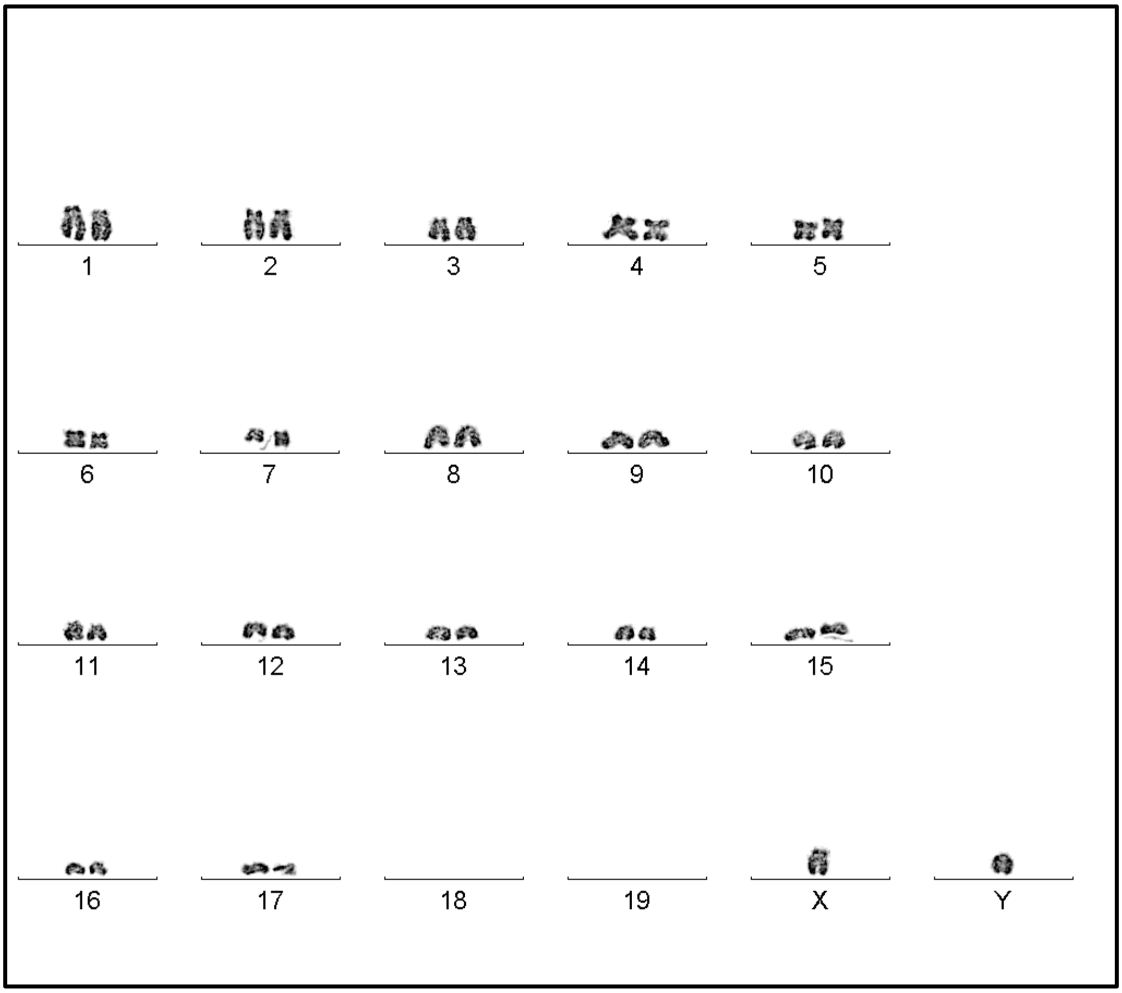


Figure 3.28. Karyogram of male 2n=36; aFN = 51/52 *Mastomys shortridgei*

Figure 3.28 is karyotypes of male *Mastomys* with the diploid number of 2n = 36 (aFN = 51/52). This karyomorph was only recorded from one specimen that was collected at the Okavango River swamps in Shakawe, Botswana. The karyotype consists of three pairs of submetacentric autosomes, four pairs of metacentric autosomes, ten pairs of acrocentric autosomes, plus a small submetacentric X chromosome and a small acrocentric Y chromosome. The current study assigns this karyomorph to species: *M. shortridgei*.

The results indicates that the 2n = 32 (aFN = 57/58) karyomorph is more widespread in the three countries than that of the 2n = 36 (aFN = 60/60 and aFN = 51/52) karyomorphs (**Fig. 3.29**) and that the 2n = 32 (aFN = 57/58) karyomorph is absent from central Namibia. It is also clear that two karyomorphs 2n = 32 (aFN = 57/58) and 2n = 36 (aFN = 60/60) occur sympatrically at Namutoni and Etunda in Namibia.

Whereas two karyomorphs 2n = 32 (aFN = 57/58) and 2n = 36 (aFN = 51/52) occur sympatrically at Shakawe, Botswana.

Figure 3.29. Collecting localities of *Mastomys* across Namibia, Angola and Botswana indicating chromosome diploid numbers per locality

3.3. Molecular study

A total of 141 *Mastomys* specimens were processed for DNA extraction, amplification and sequencing. The final set of sequences used was: 128 from this study as well as additional set of 35 sequences obtained from the Genbank.

3.3.1. Data Statistics

Results indicate that 80% of the sequence data is made up of conserved sites, as opposed to variable sites that made up 20% of the sequence data (refer **Table 3.12**). Parsimony informative sites consist of 12% of the sequence data as opposed to singleton sites that consists 8.3% of the sequence data (refer **Table 3.13**).

Table 3.12. Number of conserved, variable, parsimony informative and singleton sites out of 755 nucleotides found in the cytochrome b sequence data.

Variables (out of 755 nucleotides)	All samples included
Conserved sites	80%
Variable sites	20%
Parsimony informative sites	11.7%
Singleton sites	8.3%

Table. 3.13. Nucleotide composition for OTU's

OTU's	%T(U)	%C	%A	%G	Total
M. natalensis	29.6	24.2	32	14.1	742.3
M. coucha	28.1	25.3	33.2	13.4	745.4
M. shortridgei	28	24.9	33	14	649.5
M. sp.	30.5	23.7	31.8	14.0	688.0

Sequences did not differ by more than 2.5% in nucleotide composition frequency. The *Mastomys* mitochondrial cytochrome b strand is characterized by a low percentage of guanine relative to other nucleotides, as is expected for vertebrate mtDNA (**Table 3.13**).

3.3.2. Phylogenetic Analysis

3.3.2.1. Genetic Distances

From **Table 3.14**, it can be seen that the largest divergence (32.1%) exists between OTU's *M. pernanus* and *M. kollmannspergeri*. The smallest divergence (1.3%) exists between OTU's *M. shortridgei* and *M. coucha*.

Table 3.14. Average interspecific genetic divergence for *Mastomys* samples only

	M. awashensis	***M. coucha***	***M. erythroleucus***	***M. huberti***	***M. kollmannspergeri***	***M. natalensis***	***M. pernanus***
M. awashensis							
M. coucha	**0.101**						
M. erythroleucus	**0.085**	**0.107**					
M. huberti	**0.106**	**0.111**	**0.103**				
M. kollmannspergeri	**0.163**	**0.176**	**0.169**	**0.165**			
M. natalensis	**0.086**	**0.101**	**0.081**	**0.101**	**0.176**		
M. pernanus	**0.238**	**0.201**	**0.246**	**0.217**	**0.321**	**0.212**	
M. shortridgei	**0.111**	**0.013**	**0.116**	**0.113**	**0.196**	**0.091**	**0.182**

3.3.2.2. NJ, ML & Bayesian Analyses

Among the 128 in-group sequences (755 bp), 84 different haplotypes were identified and 35 haplotypes identified from the 35 out-group sequences. The trees obtained by the NJ (**Fig. 3.30**), ML (**Fig. 3.31**) and Bayesian (**Fig. 3.32**) analyses have a similar topology. *Mastomys natalensis* (Clade: A1) and *M. coucha* (Clade: B2) form two distinct highly supported genetic clades, and these clades are not sister clades. These results confirm that they are two distinct species, and both occurring in Namibia.

The Clade: A1 represent haplotypes that were sampled in northern Namibia, northern Botswana and southern Angola.

At least two lineages can be identified within *M. coucha* (Clade: B), these are representing *M. coucha* (Clade: B2) and *M. shortridgei* (Clade: B1). The Clade: B1, consists of haplotypes (No. 44, 48 & 50) that were sampled along the Okavango

River swamps in Namibia and Botswana as well as 1 specimen sampled along the Cuito River swamps in southern Angola. The haplotypes of Clade: B1, were confirmed as belonging to the karyotype ($2n = 36$; $aFN = 51/52$). The Clade: B2 represent haplotypes that were sampled within drier parts of central Namibia, and these were confirmed as belonging to *M. coucha* by the use of karyotype data ($2n = 36$; $aFN = 60$).

According to the phylogenetic trees the split between *M. coucha* and *M. shortridgei* could be more recent than the split between *M. natalensis* and the two other species.

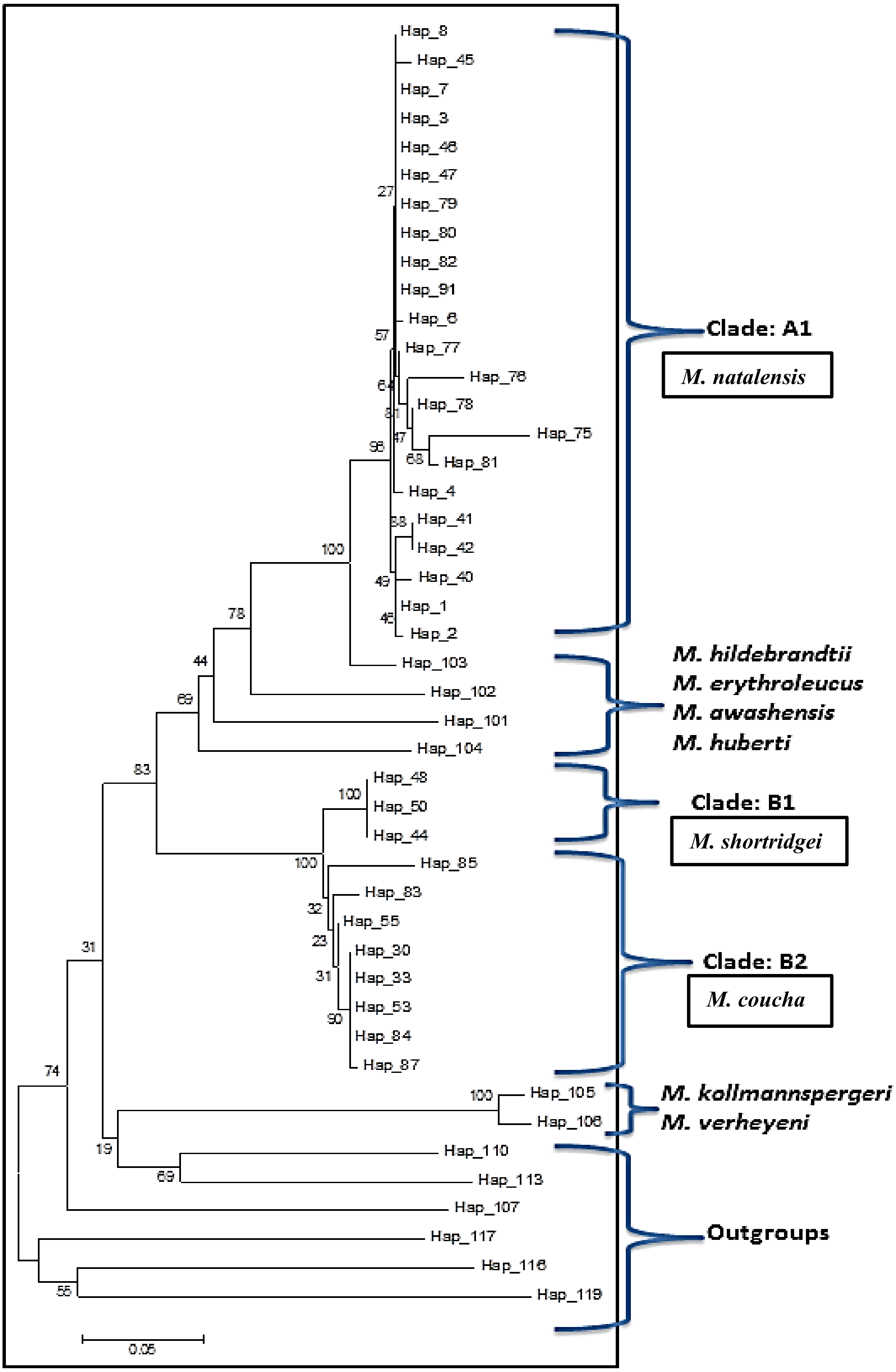


Figure 3.30. Phylogeny of cytochrome b haplotypes resulting from neighbour-joining (NJ) analysis (HKY + G model). Numbers at nodes represent NJ bootstrap support (1000 replications)

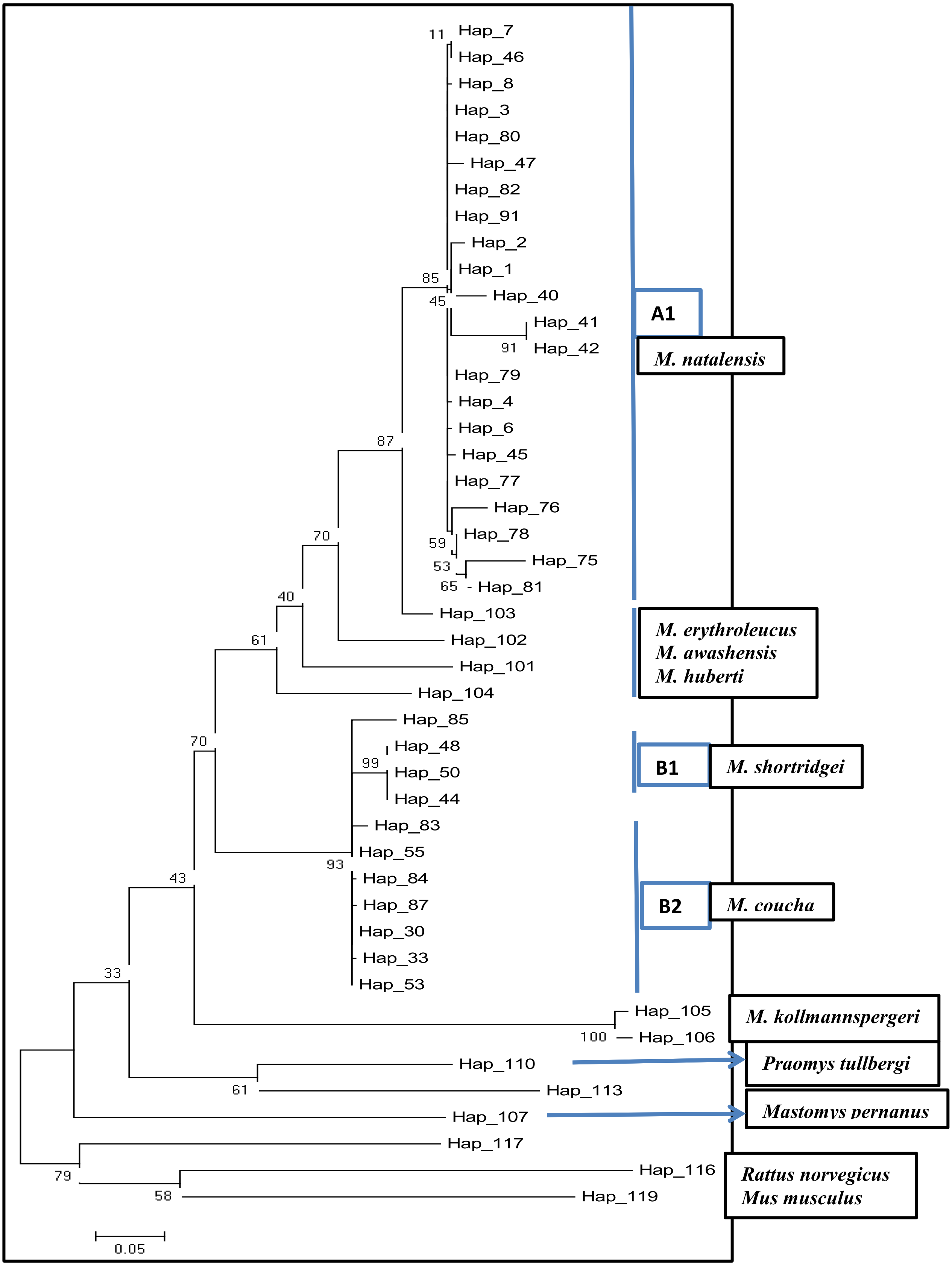


Fig. 3.31. Phylogeny of cytochrome *b* haplotypes resulting from maximum-likelihood (ML) analysis (HKY + G model). Numbers at nodes represent ML bootstrap support (1000 replications).

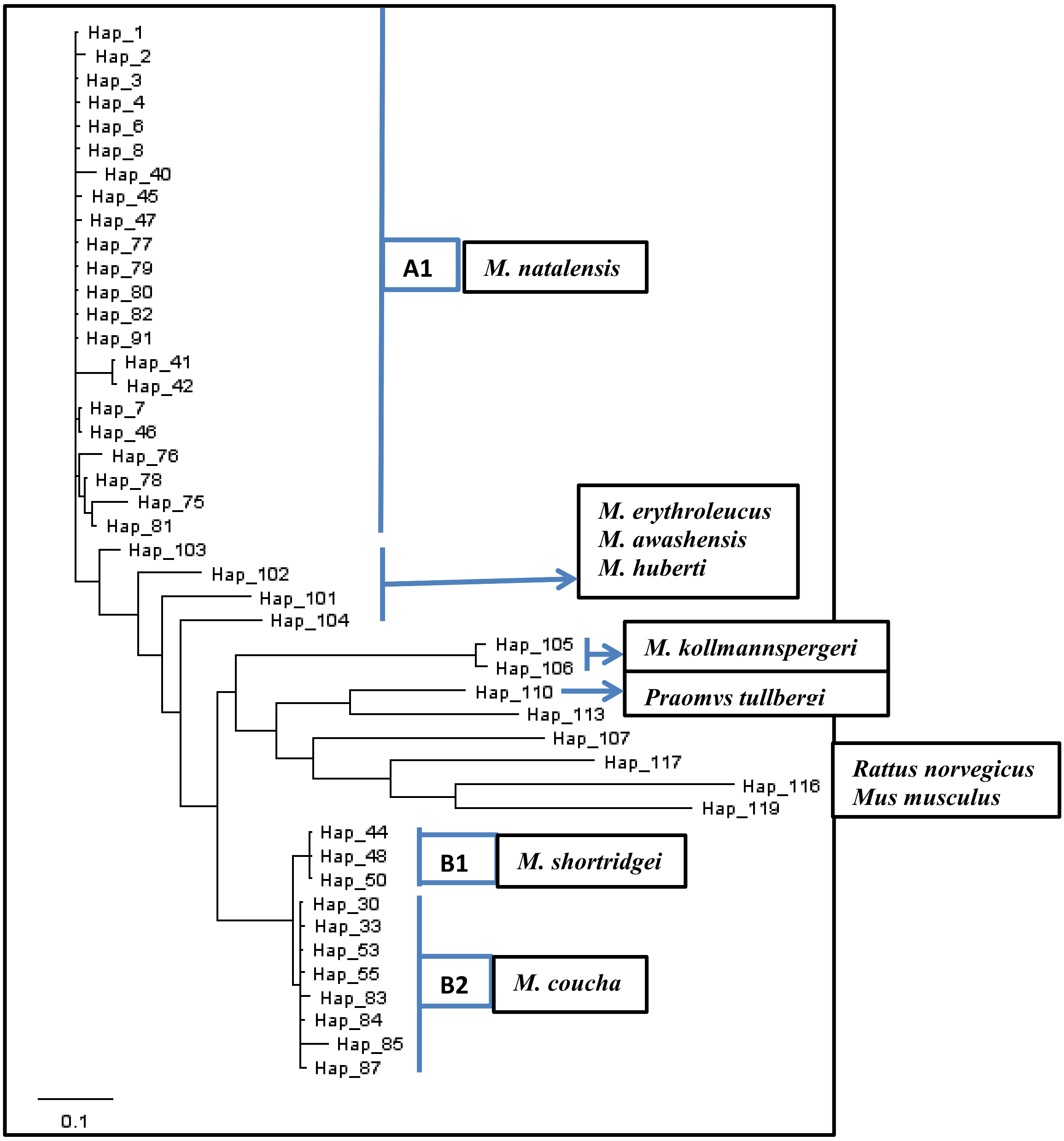


Fig. 3.32. Phylogeny of cytochrome *b* haplotypes resulting from Bayesian analysis (HKY + G model).

The genus *Mastomys* is paraphyletic due to the species *M. pernanus* that appears quite divergent from others. The other species (*M. awashensis*, *M. coucha*, *M. erythroleucus*, *M. huberti* and *M. natalensis*) form a highly supported clade of closely related species, a finding consistent with the NJ, ML and Bayesian analyses based on amino acids. *Mastomys pernanus* is the first species to diverge, followed by *M. kollmannspergeri* and *M. coucha*, whereas *M. natalensis* and *M. erythroleucus* are sister groups.

3.3.3. Phylogeography

A total of 84 haplotypes (**Table 3.15**) were identified from the in-group. Haplotype diversity (Hd) was 0.986.

Table 3.15. Haplotypes excluding out-groups

Locality	**Country**	**Number of samples**	**Haplotype number**
1. Omatako-Kavango rivers confluence	Namibia	2, 1, 3, 1, 1, 1, 5	1, 3, 4, 5, 6, 7, 8
2. Divundu Irrigation Scheme; Popa Falls	Namibia	2, 1, 7, 1, 1, 1, 1, 1, 1, 1	1, 2, 3, 8, 9, 10, 11, 12, 13, 39
3. Ngalla village	Namibia	1, 2, 1, 4, 1, 1	4, 14, 15, 16, 17, 18
4. Swamps at Shamvura village	Namibia	7	45, 46, 47, 48, 49, 50, 51
5. Etunda Irrigation Scheme	Namibia	1, 2, 1, 1, 1, 1, 1, 1, 1	17, 19, 23, 24, 25, 26, 27, 28, 29
6. Etosha National Park	Namibia	1, 1, 1, 1	19, 20, 21, 22
7. Uniab River Mouth	Namibia	8, 1, 1	30, 31, 32
8. Omatjene Research Station	Namibia	5, 1, 1, 1, 1, 1	30, 33, 35, 36, 37, 38
9. Waterberg Plateau Park	Namibia	1, 1	30, 34
10. Windhoek	Namibia	1, 4	30, 33
11. Shakawe	Botswana	5	52, 53, 54, 55, 56
12. Sepopa Swamp	Botswana	18	57, 58, 59, 60, 61, 62,

Stop			63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74
13. Maun	Botswana	9	75, 76, 77, 78, 79, 80, 81, 82
14. Konakry Hills	Botswana	2	83, 84
15. Lubango	Angola	3	40, 41, 42
16. Mbalanondolo village	Angola	1	43
17. Longa village	Angola	1	44
Totals		**128**	**84**

The haplotype network (**Fig. 3.33**) shows the grouping of haplotypes according to different species, as seen in the NJ, ML and Bayesian trees. Haplotypes representing *M. shortridgei* are also grouped together with haplotypes representing *M. coucha* (**Fig. 3.33**).

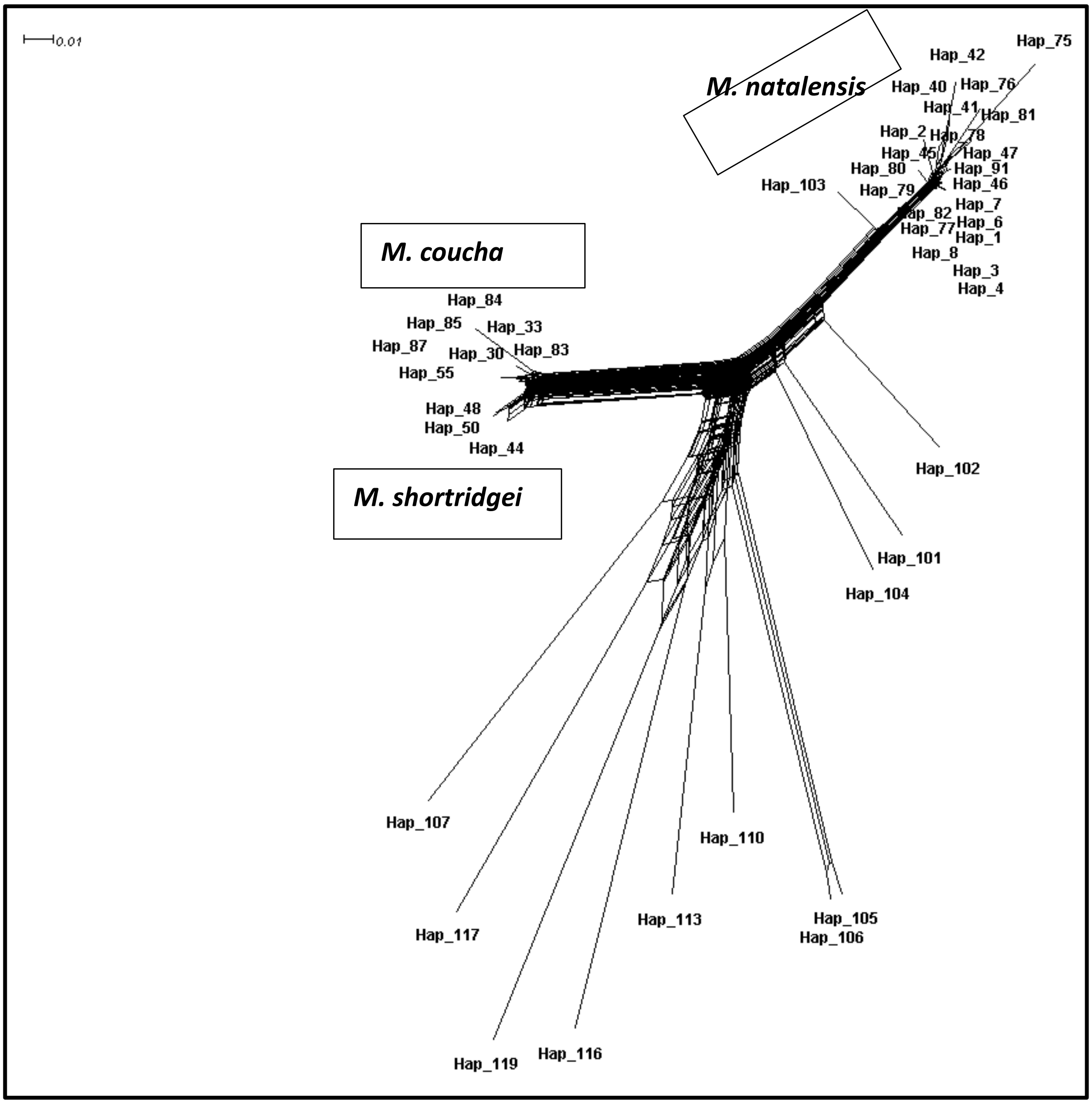


Fig. 3.33. Neighbour-net network generated by SplitsTree, illustrating evolutionary relationships among *Mastomys* lineages in Namibia.

3.3.4. Divergence Time Estimates

The most recent common ancestor (TMRCA) for all *Mastomys* haplotypes was estimated to be 5.55 Mya (range 5.2 – 8.0). The molecular clock estimates (**Fig. 3.34**) suggest that the split between *M. coucha* and *M. natalensis* occurred about 2.97 Mya. Additionally, the split of *M. shortridgei* from *M. coucha* is estimated to be 0.71 Mya (**Fig. 3.34**).

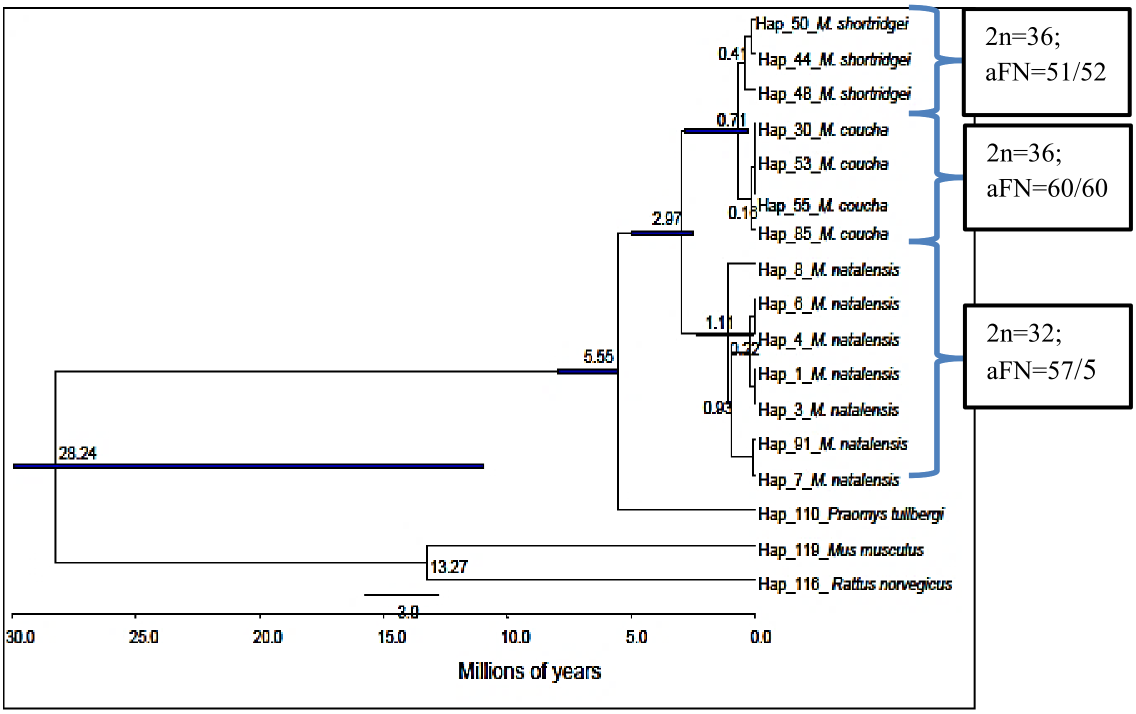


Fig. 3.34. Chronogram illustrating the evolution of *Mastomys* clades in Namibia. The scale is in millions of years. Bars represent the 95% confidence limits.

CHAPTER 4. GENERAL DISCUSSION

4.1. Morphometrics

4.1.1. Error Measurement & Character Selection

The present investigation was based on a measurement selection procedure in *Aethomys* (Rodentia: Muridae) from southern Africa (Chimimba & Dippenaar, 1995) and vesper bats of the genera *Eptesicus*, *Hypsugo*, *Neoromicia*, and *Pipistrellus* (Mammalia: Chiroptera: Vespertilionidae) from southerm Africa (Kearney & Taylor, 2011).

The procedure applied attempted to identify a reduced number of measurements that could summarize morphometric variation in the overall cranial and mandibular configuration in the multimammate mice (Chimimba & Dippenaar, 1995; Richards, 2007; Rotherham, 2007; Kearney & Taylor, 2011).

The selection of the final set of characters was based on: (1) relative ease of measurement; (2) measuring points associated with frequently damaged areas of the skull; and (3) previous use, particularly in original descriptions (Chimimba & Dippenaar, 1995; Richards, 2007; Rotherham, 2007; Kearney & Taylor, 2011). A suite of 12 characters (GLS, ZAL, ZYW, IOB, NAS, PAL, LPF, MAW, HOR, UTR, GML & MAF) with %ME levels of 10% and lower, and which were normally distributed were used in the final analyses.

For error measurement investigation within the geometric morphometrics technique, individuals were clearly differentiated from one another and landmark data did not overlap (**Fig. 3.9**), indicating that the placement of landmarks was easily repeatable, consistent and precise.

4.1.2. Non-geographic Variation

Both the univariate (ANOVA) and multivariate analyses (PCA) undertaken in this study clearly showed the presence of statistically significant age variation, but a lack of sexual dimorphism. The younger age classes (I-III) are shown to be morphologically different than the older age classes (IV-VI). All these results justify the pooling of sexes and the recording and analyses of older age classes (IV-VI) in subsequent revision of *Mastomys* from Namibia and adjacent countries.

The results in the present study are similar to those found in the African rock rats, *Aethomys* (Chimimba & Dippenaar, 1994), multimammate mice, *M. coucha* & *M. natalensis* occurring in South Africa (Bronner *et al*., 2007), the water rat, *Dasymys incomtus* (Mullin *et al*., 2001) and the spring hare, *Pedetes capensis* (Matson & Blood, 1996), that generally there is a lack of sexual dimorphism in rodents. Smithers & Wilson (1979) showed by using body measurements in *M. natalensis* of Zimbabwe, that males were larger than females; however, the statistical results obtained in that study were not significant. The present study clearly shows lack of sexual dimorphism in *Mastomys* populations.

According to Ralls (1977), rodents display little or only moderate sexual dimorphism in body size. In mammals, sexual size dimorphism is usually attributed to contest among individuals in polygynous mating systems, in which larger males achieve greater reproductive success (Shine, 1978; Lu *et al*., 2014).

For small mammals, evidence from some genera of rodents indicates that there is non-significant difference in body size between males and females based on the fact that individuals choose their mates by olfaction rather than contests (Eisenberg & Kleiman, 1972; Blaustein, 1981; Sun & Zhu, 2008).

4.1.3. Geographic & Taxonomic Variation

Mayr (1963, 1970) defined geographic variation as: “the occurrence of differences, in both gene frequencies and morphology, among spatially segregated populations of species”. Intra- and interspecific geographical variation in morphology is almost universal among mammals, and often complex, showing a wide range of patterns such as clinal, categorical, mosaic etc. (Thorpe, 1987).

The study of geographic variation is of considerable importance to evolutionary theory and systematics (Thorpe, 1976). A researcher may relate geographic variation in the phenotype or genotype to environmental variables in an attempt to gain insight into selection pressures and microevolution. The researcher may, also, be concerned with assessing the degree of genetic or phenetic similarity between spatially segregated populations of a single species and/or among different species of the same genus (Thorpe, 1976).

In this study, skull (cranial, mandibular and dental) characters were used to explore morphological geographical variation among *M. coucha*, *M. natalensis* and *M. shortridgei*. Multivariate analyses, within the Traditional Morphometrics, indicated that cranial size (i.e. greatest length of skull- PC1 loading = 69%) is the most important factor contributing to morphometric variation within populations of *M. coucha* (PC1 = 73.14%) and within populations of *M. natalensis* (PC1 = 86.86%). It was found within this study that *M. coucha* and *M. natalensis* individuals from South Africa were, on average, larger than individuals from Namibia.

Despite the lack of well-defined isolated clusters for all the three species from Namibia, within the results produced by the Traditional Morphometrics approach, the results from the Geometric Morphometrics analyses did detect geographical trends/differences among the populations of *M. coucha*, *M. natalensis* and *M. shortridgei*, especially in the CVA scatter plots. This clear separation of the three species from Namibia was exhibited by large differences in skull shape, both dorsal and ventral views.

The main shape changes between the three species concerned the length of the nasal bone (*M. natalensis*), increased width of the braincase and size of bullae (*M. coucha*), as well as the length of the longest palatal foramen (LPF) – longer in *M. shortridgei* compared with the other two species.

Taylor *et al.* (2004) demonstrated ecological adaptations in skull shape and size in laminate-toothed rats (Family: Muridae, Tribe: Otomyini) associated with increasing aridity and/or high altitude (e.g. smaller size, bullar expansion and narrowing of nasal bones in arid-adapted *Parotomys* species). Larger nasal bone, as observed in *M.*

natalensis, appears to be an adaptation for enhanced sense of smell, since *M. natalensis* occupies more mesic environments. Enlarged bullae and reduced nasal bone size, as observed in *M. coucha*, appears to be an adaptation for the more arid environments that is inhabited by *M. coucha*, in Namibia.

It has been suggested that changes in bulla shape and volume amongst taxa may correspond to adaptive differences in sound frequency sensitivity and recognition (Schleich & Vassalo, 2003; Colangelo *et al*., 2010). Large bullae could imply an enhanced sense of hearing, which could be as an adaptation for predator avoidance in open (arid) vegetation less habitats (Taylor *et al*., 2004; Richards *et al*., 2012).

Results analysed in the present study has shown that morphometrics (especially geometric morphometrics) is valuable in exploring geographical and taxonomic variation within and between *M. coucha*, *M. natalensis* and *M. shortridgei*. It was found, in other studies done on sibling species, that cranial characteristics as utilized in geometric morphometrics was sufficient to be a valid identification criterion (Dobigny *et al*., 2002; Cordeiro-Estrela *et al*., 2008; Lalis *et al*., 2009a, 2009b).

4.1.4. Distinguishing Morphological Characters

Dippenaar *et al*. (1993) showed that the two species *M. natalensis* and *M. coucha* differ diagnostically in cranial configuration, by using traditional morphometrics method. They showed, by using a principal component analysis (PCA), that there was clear separation of samples of the two species in the scatter plot. The characters with high measurement loadings on first PC component were: GLS- greatest length of skull (0.929), MDL- greatest length of mandible (0.918), ROST- width of rostrum (0.847) and DOP- greatest depth of braincase (0.883). It was possible to positively identify specimens of both species by using the results of a discriminant function analysis (Dippenaar *et al*., 1993). They could identify correctly 91% of specimens by the use of the discriminant function results (Dippenaar *et al*., 1993).

The results from the present study suggest that the three species: *M. coucha*, *M. natalensis* and *M. shortridgei* can be differentiated owing to their skull shapes with a probability of 100% in both dorsal (**Fig. 3.18**) and ventral views (**Fig. 3.23**). A study carried out by Lalis *et al.* (2009b) by using geometric morphometrics method, indicated that they could differentiate between the three species: *M. erythroleucus*, *M. huberti* and *M. natalensis* with a high probability (90%).

4.1.5. Effectiveness of Traditional & Geometric Morphometrics

In the present study, results obtained from the traditional morphometrics method could not clearly separate the three species in well-defined groups. This was, however, possible with the analyses of shape variation by using the geometric morphometrics method.

At lower taxonomic levels, morphological divergence can be subtle and traditional morphometrics is sometimes insufficient to differentiate groups, while geometric morphometrics performs better (Cordeira-Estrela *et al*., 2008; Evin *et al*., 2008; Lalis *et al*., 2009b; Breno, 2011). Thus, geometric morphometrics is especially well suited when investigating the evolution of forms among and within species (Monteiro, 1999; Cordeiro-Estrela *et al.,* 2006; Lalis *et al*., 2009b) as well as to address problems of functional morphology and ecological divergence (McKinnon *et al*., 2004; Lalis *et al*., 2009b).

4.1.6. Taxonomic Conclusions

Analyses of geometric morphometric (dorsal and ventral landmark) data revealed clear morphological divisions amongst *Mastomys* individuals from Namibia. Multivariate analyses of landmark data as well as deformation grids for shape change provided strong support for three geographically distinct species corresponding to the cytogenetic lineages as described within the present study; and these are *M. coucha*, *M. natalensis* and *M. shortridgei*.

Under the Morphological Species Concept (Cronquist, 1978; Mayden, 1997), *M. coucha*, *M. natalensis* and *M. shortridgei* will be regarded as separate species based on results obtained within the present study. This species concept uses anatomical or physiological features (characters) and/or some precise degree of phenotypic similarity to delimit taxa (Cronquist, 1978; Mayden, 1997).

4.2. Cytogenetics

An unquestionable discrimination of the sibling species in *Mastomys* remains a difficult task & requires the systematic use of cytogenetic and molecular analyses. The karyotype appeared as the most reliable diagnostic character for this group of rodents (Granjon *et al.,* 1996; Volobouev *et a*l., 2002).

This study has revealed three forms of *Mastomys* with different karyotypes in Namibia, Botswana and Angola. These were assigned to species *M. coucha* (2n = 36, aFN = 60/60), *M natalensis* (2n = 32, aFN = 57/58) and *M. shortridgei* (2n = 36, aFN = 51/52). The karyotypes of *M. coucha* and *M. natalensis* are congruent with recorded karyotypes from elsewhere in the southern African region (Hallett, 1979; Green *et al*., 1980; Lyons *et al*., 1980; Dobigny *et al*., 2008).

A third karyomorph does exist - *M. shortridgei* (Gordon, 1985). It shares same diploid number (2n = 36) with *M. coucha* but differs in autosomal fundamental number: *M. shortridgei* (aFN = 51/52) & *M. coucha* (aFN = 60/60) (Gordon, 1985). Variation in the number of chromosome arms in a karyotype (aFN) is usually the result of pericentric rearrangements (Aguilar, 1993; Britton-Davidian *et al*., 1995). Pericentric inversions are the most probable rearrangements involved in the process of differentiation (Aguilar, 1993).

According to Volobouev *et al*. (2002), pericentric inversions are predominant in genus *Mastomys*, making up > 60% of rearrangements scored. This study recorded that the karyotype of *M. shortridgei* has a large number of acrocentric autosomes. It could be that the metacentric chromosomes from *M. coucha* were converted to acrocentric types via pericentric inversions (Hallett, 1979; Kirkpatrick & Barton, 2006). An inversion occurs when a chromosome breaks at two points and the segment bounded by the breakpoints is reinserted in the reversed orientation (Kirkpatrick, 2010). This rearrangement brings about a reduction by 2 in the number of major chromosome arms in the homozygote (Aguilar, 1993; Britton-Davidian *et al*., 1995; Kirkpatrick, 2010).

The current habitat (swamps, reeds, high precipitation) where *M. shortridgei* occurs does not form suitable natural habitat for *M. coucha* (Shortridge, 1934; De Graaff, 1981). Therefore, this study hypothesizes that a geographic isolation event occurred in the past, which isolated the current *M. shortridgei* from *M. coucha* populations after which chromosomal rearrangements (i.e. pericentric inversions) occurred in ancestral populations of *M. shortridgei* peripheral to the main distribution range of *M. coucha*. Over time *M. shortridgei* population become adapted to the local swampy conditions.

According to Kirkpatrick (2010), local adaptation is the situation in which different genes are favoured in different environments. An inversion that captures two or more alleles that are adapted to the local environmental conditions has a selective advantage that can cause it to spread. This effect results from suppressed recombination: the new inversion carries only the locally adapted alleles, while the ancestral rearrangement carries mixtures of adapted and maladapted alleles. No epistasis (gene interaction) is needed for the inversion to gain an advantage, which means that this local adaptation mechanism can operate even when the loci are adapting to different environmental variables. Inversions spread because they prevent recombination from breaking apart sets of alleles that work well in an ecological or sexual setting (Kirkpatrick *et al*., 2006; Kirkpatrick, 2010).

Rieseberg (2001) argue that chromosomal rearrangements (i.e. pericentric inversions) reduce gene flow more often through their effects on recombination rates than through their effects on fitness. Chromosomal differences that have accumulated between the neospecies (e.g. *M. shortridgei*) and its progenitor(s) (e.g. *M. coucha*) are assumed to impair the fertility or viability of interspecific hybrids, thereby reducing gene flow (Rieseberg, 2001; Kirkpatrick *et al*., 2006; Kirkpatrick, 2010).

4.3. Molecular study

The phylogenetic analysis of cytochrome b revealed two well-defined clades within the genus *Mastomys* from Namibia and adjacent countries. These two clades representing the two species: *M. coucha* and *M. natalensis*. This result corroborates previous records of systematics of *Mastomys* in southern Africa (Granjon *et al*., 1997; Van der Straeten & Robbins, 1997). However, the *M. coucha* clade is further sub-divided into two smaller clades, representing *M. coucha* and *M. shortrigei.* The *M. shortridgei* haplotypes were positively identified by using cytogenetic markers in the present study. The mtDNA divergence between the species *M. coucha* and *M. shortridgei* was relatively low (1.3%); additionally the molecular clock estimated *M. shortridgei* to be a recent off-shoot of *M. coucha* (0.71 Mya).

A species is typically separated from other taxonomic units by a genetic distance indicative of genetic isolation (Baker & Bradley, 2006; Lamb *et al*., 2014). Baker & Bradley (2006) reports a mean intraspecific genetic distance of 1.50% (range 0.0-4.7%) and a mean distance between sister species of 7.3% (range 1.3-13.0%). *Mastomys shortridgei* will be considered as being part of the *M. coucha* complex, based on the Genetic Species Concept (Baker & Bradley, 2006).

Individuals representing the species *M. shortridgei* were collected within swamps along the Okavango River in Namibia and Botswana. One specimen that was positively identified as *M. shortridgei* was collected along the Longa River in southern Angola. The Longa River is a small tributary of the Cuito River which forms part of the main Okavango River drainage system.

The current habitat (swamps, reeds, high precipitation) where *M. shortridgei* occurs is does not form suitable natural habitat for *M. coucha* (Venturi *et al*., 2004). Smit *et al*. (2001) noted that *M. natalensis* seems to occupy the warm, moist savannah regions, in South Africa, while the grassland regions appear to predominantly support *M. coucha*. In the present study, it was clearly shown that more arid areas are suitable for *M. coucha*.

Therefore, this study hypothesizes that a geographic isolation event occurred in the past (0.71 Mya), which isolated the current *M. shortridgei* populations from *M. coucha* populations. This isolation event could have facilitated peripatric speciation (Mayr, 1963). Mayr (1963) observed that geographical isolation may commonly occur rapidly in small peripheral isolates, populations at the margin of the range of the ancestral species. Speciation can occur because, in a newly founded small population, rapid genetic evolution can be caused by the combined effects of genetic drift and strong natural selection under new environmental conditions, what Mayr called "genetic revolutions" (Mayr, 1963)

Peripatric speciation is similar to allopatric speciation in that populations are isolated and prevented from exchanging genes (Barraclough & Nee, 2001). However, peripatric speciation, unlike allopatric speciation, proposes that one of the populations is much smaller than the other (Barraclough & Nee, 2001). One possible consequence of peripatric speciation is that a geographically widespread ancestral species becomes paraphyletic, thereby becoming a paraspecies. The concept of a paraspecies is therefore a logical consequence of the Evolutionary Species Concept (Simpson, 1961) by which one species give rise to a daughter species.

A Model of Drainage Evolution in south-central Africa since the Mesozoic (Moore & Larkin, 2001; Cotterill, 2003, 2004) may elucidate the events leading up to the eventual divergence of *M. shortridgei* from *M. coucha*. A series of floodplains and shallow lakes consisted of the largest components in the wetland archipelago on the south-central African plateau. They included the shallow basins of Bangweulu, Barotse, Busanga, Kafue, Lukanga, and Okavango (Cotterill, 2003, 2004). These large wetlands shared a complex history of links with major rivers that are today parts of either the Congo or Zambezi drainage systems (Cotterill, 2003, 2004). These wetlands were interconnected, and then broken up, to eventually forge the modern composition of the Congo and Zambezi systems.

According to Cotterill (2003, 2004), particularly dramatic events occurred after the Pliocene, notably when the mid-Zambezi captured the Cuando, Upper Kafue and Upper Zambezi rivers as its major tributaries. The wetland that formerly interlinked all these rivers was the Palaeo-Lake Makgadikgadi situated in the present country of

Botswana. It is estimated that the Palaeo-Lake Makgadikgadi covered much of the eastern Kalahari basin, and at its largest extent covered an area of 120 000 km^2 (Cotterill, 2004). It could be that the peripheral ancestral population of *M. shortridgei* came in contact with the Palaeo-Lake Makgadikgadi and were isolated with the shrinking Palaeo-Lake Makgadikgadi during the End-Pleistocene to Early Holocene. Over time the *M. shortridgei* ancestral population become adapted to the local swampy environmental conditions.

Cotterill (2003) further states that, over the past few million years the history of drainage evolution has involved the creation of a shifting mosaic of wetlands. These changes to wetlands and associated landforms have influenced mammal biogeography and evolution through two different mechanisms. Firstly, these wetlands have contained and focused dispersals by organisms. The biotic habitats in wetlands restricted dispersal of some populations, but abetted dispersal of others. Secondly, wetlands have been fragmented frequently - disrupting established lakes and river channels, with the creation of new water bodies. Schilthuizen (2001) stated that fluctuating lake levels have driven rapid divergence in cichlid fishes in the Great Lakes of East Africa, with new species evolving within thousands and even hundreds of years.

For populations that have remained isolated for long periods of time, climate-driven vicariant events may be sufficient for reproductive isolation to evolve by drift alone (mutation-driven speciation) (Plana, 2004). Adaptation to local ecological conditions in different refuges may accelerate divergence and finally lead to ecological speciation. According to Schluter (2009) ecological speciation refers to the evolution of reproductive isolation between populations or subsets of a single population by adaptation to different environments or ecological niches. The present study does hypothesise that this scenario could have been carried out to the initially isolated population of ancestral *M. shortridgei*.

Owing to the broad geographic sampling, the present study is able to determine the precise distributional range of each species in Namibia. Contrary to prior reports of *Mastomys sp*. distributions in Namibia which were unclear (e.g. Granjon *et al*., 1997; Skinner & Chimimba, 2005; Wilson & Reeder, 2005); *M. coucha* & *M. natalensis* have distinct geographical distributions influenced by precipitation. *M. coucha* occurs in low rainfall areas of central Namibia, also with isolated populations within dry riverbeds that transgress the Namib Desert. Whereas *M. natalensis* occur along higher rainfall areas of north-central and north-eastern Namibia, extending into Angola and northern Botswana.

CHAPTER 5. SYNTHESIS

5.1. Introduction

The current study is the first to detail cranial morphometrics, using both traditional and geometric morphometric techniques, cytogenetics and molecular approaches in the study of *Mastomys* from southern Africa. The investigation examined patterns of intra-population and inter-population morphological variation, cytogenetics and molecular study.

Prior to the main analyses to assess the nature and extent of geographic variation within southern African *Mastomys*, a few preliminary considerations were examined. It included the selection of meaningful taxonomic characters for use in assessing the nature and extent of craniometric variation within *Mastomys*. This method was previously applied in a wide range of studies on animals: mongooses (Taylor & Meester, 1993), mice (Chimimba & Dippenaar, 1995), hedgehogs (Rotherham, 2007), bats (Richards, 2007; Kearney & Taylor, 2011) and weevils (Janse van Rensburg *et al.*, 2003). The measurement selection procedure adopted in the present study reduced an initial set of 61 measurements to 12.

This chapter provides an overview of the study and synthesis of findings presented in previous portions of this dissertation.

5.2. Nongeographic variation of genus *Mastomys* occurring in Namibia and adjacent countries

This included the analyses of nongeographic variation at the level of sexual dimorphism and age variation using traditional and geometric morphometric analyses of the cranium. Sexual dimorphism and age variation was undertaken with the aim of establishing whether sexes should be treated together or separately, and which specimens have reached adult dimensions, and, therefore, suitable for measurement recording and analyses in the subsequent assessment of the nature and extent of variation in southern African *Mastomys*.

The results obtained showed a lack of sexual dimorphism but variation between juveniles (Age Classes I to III) and adults (Age Classes IV to VII). The results in the present study are similar to those found in the African rock rats, *Aethomys* (Chimimba & Dippenaar, 1994), multimammate mice, *M. coucha* & *M. natalensis* occurring in South Africa (Bronner *et al*., 2007), the water rat, *Dasymys incomtus* (Mullin *et al*., 2001) and the spring hare, *Pedetes capensis* (Matson & Blood, 1996), in that these studies also recorded no sexual dimorphism but variation between juveniles and adults. According to Ralls (1977), rodents display little or only moderate sexual dimorphism in body size.

5.3. Geographic and taxonomic variation of genus *Mastomys* occurring in Namibia and adjacent countries

Multivariate analyses, based on traditional morphometrics, indicated that cranial size (i.e. greatest length of skull) is the most important factor contributing to morphometric variation among individuals from different populations of *M. coucha* (73.14% variation) and *M. natalensis* (86.86% variation). It was found within this study that *M. coucha* and *M. natalensis* individuals from South Africa were, on average, larger than individuals from Namibia.

Despite the lack of well-defined isolated clusters for all the three species from Namibia based on traditional approach, the results from geometric morphometrics did detect geographical trends/differences among the populations of *M. coucha*, *M. natalensis* and *M. shortridgei*, especially in the CVA scatter plots. This clear separation of the three species from Namibia was exhibited by large differences in skull shape based on, both dorsal (**Fig. 3.17**) and ventral views (**Fig. 3.22**). The main shape changes between the three species concerned the length of the nasal bone (*M. natalensis*), increased width of the braincase and size of bullae (*M. coucha*), as well as the length of the longest palatal foramen (LPF) – longer in *M. shortridgei* compared with the other two species.

5.4. Concordance between morphology, cytogenetic and molecular data

This study has revealed three forms of *Mastomys* with different karyotypes in Namibia, Botswana and Angola. These were assigned to species *M. coucha* (2n = 36, aFN = 60/60), *M natalensis* (2n = 32, aFN = 57/58) and *M. shortridgei* (2n = 36, aFN = 51/52). The karyotypes of *M. coucha* and *M. natalensis* are congruent with recorded karyotypes from elsewhere in southern African region (Hallett, 1979; Green *et al.*, 1980; Lyons *et al.*, 1980; Dobigny *et al.*, 2008). The third karyomorph *M. shortridgei* shares the same diploid number (2n = 36) with *M. coucha* but differs in autosomal fundamental number: (*M. shortridgei* 51/52; *M. coucha* 60/60) (see also Gordon, 1985). Variation in the number of chromosome arms in a karyotype (aFN) is usually the result of pericentric rearrangements and this was probably the case in this study although G-banding of molecular cytogenetic (FISH) data were not available to confirm this (Aguilar, 1993; Britton-Davidian *et al.*, 1995).

The molecular results indicated the existence of two distinct clades *M. coucha* and *M. natalensis*. The third karyomorph, *M. shortridgei*, was represented within the *M. coucha* clade based on cytochrome-b gene data. The divergence between the species *M. coucha* and *M. shortridgei* was relatively low (1.3%), additionally the molecular clock estimated *M. shortridgei* to be a recent off-shoot of *M. coucha* (0.71 Mya).

5.5. Distribution, dispersal and speciation of genus *Mastomys* occurring in Namibia and adjacent countries

The earliest records of murines in Africa are in the late Miocene, ca 11-10 Mya (Winkler *et al.*, 2010). In northern Africa, now extinct *Progonomys* is reported from several sites in Algeria, Libya, Egypt and Morocco (Winkler *et al.*, 2010). The split between the genera *Praomys* and *Mastomys* was estimated as 5.5-6.0 Mya, based on the earliest fossil of *Praomys* found in Lissasfa, Morocco (Geraads, 2002). Colangelo *et al.* (2013), stated that the fossil record of the genus *Mastomys* is scarce, and that the earliest record of *Mastomys cinereus*, which is closely related to *M. huberti*, *M. coucha* and *M. natalensis*, was dated to between 3.7 – 2.5 Mya (Denys, 1987).

In the present study, the most recent common ancestor (TMRCA) for all *Mastomys* haplotypes was estimated to be 5.55 Mya (range 5.2 – 8.0). The molecular clock estimates (**Fig. 3.34**) suggest that the split between *M. coucha* and *M. natalensis* occurred about 2.97 Mya. Additionally, the split of *M. shortridgei* from *M. coucha* is estimated to be 0.71 Mya (**Fig. 3.34**). The current habitat (swamps, reeds, high precipitation) where *M. shortridgei* occurs is restrictive and does not form suitable natural habitat for *M. coucha* (Venturi *et al*., 2004). Smit *et al*. (2001) noted that *M. natalensis* seems to occupy the warm, moist savannah regions, in South Africa, while the grassland regions appear to predominantly support *M. coucha*.

Since distinct skull shape differences indicative of adaptive divergence could be distinguished between the three species, this study hypothesizes that a geographic isolation event occurred in the past (0.71 Mya), which isolated the current *M. shortridgei* populations from ancestral *M. coucha* populations. This isolation event probably constitutes peripatric speciation. Mayr (1963) described peripatric speciation as occurring in a population or incipient species with a distribution that is located at the periphery of the main species distribution. Mayr (1963) observed that geographical isolation may also commonly occur in small peripheral isolates, populations at the margin of the range of the ancestral species. Speciation can occur because, in a newly founded small population, rapid genetic evolution can be caused by the combined effects of genetic drift and strong natural selection under new environmental conditions, what Mayr called “genetic revolutions” (Mayr, 1963).

A model of drainage evolution in south-central Africa since the Mesozoic (Moore & Larkin, 2001; Cotterill, 2003, 2004) may elucidate the events leading up to the eventual divergence of *M. shortridgei* from *M. coucha*. A series of floodplains and shallow lakes consisted of the largest components in the wetland archipelago on the south-central African plateau. They included the shallow basins of Bangweulu, Barotse, Busanga, Kafue, Lukanga, and Okavango (Cotterill, 2003, 2004). These large wetlands shared a complex history of links with major rivers that are today parts of either the Congo or Zambezi drainage systems (Cotterill, 2003, 2004). These wetlands were interconnected, and then broken up, to eventually forge the modern composition of the Congo and Zambezi systems.

According to Cotterill (2003, 2004), particularly dramatic events occurred after the Pliocene, notably when the mid-Zambezi captured the Cuando, Upper Kafue and Upper Zambezi rivers as its major tributaries. The wetland that formerly interlinked all these rivers was the Palaeo-Lake Makgadikgadi situated in the present country of Botswana. It is estimated that the Palaeo-Lake Makgadikgadi covered much of the eastern Kalahari basin, and at its largest extent covered an area of 120 000 km^2 (Cotterill, 2004). It could be that the peripheral ancestral population of *M. shortridgei* came in contact with the Palaeo-Lake Makgadikgadi and were isolated with the shrinking Palaeo-Lake Makgadikgadi during the End-Pleistocene to Early Holocene. Over time the *M. shortridgei* ancestral population become adapted to the local swampy environmental conditions.

5.6. Summary of study findings and areas of future research

This study confirms the existence of three species of *Mastomys* in Namibia: *M. coucha*, *M. natalensis* and *M. shortridgei*. There is a clear pattern of distribution of the three species in Namibia, whereby *M. coucha* occurs in drier areas of central Namibia and one isolated population at the Namibian coast. *Mastomys natalensis* is distributed from north-central to the far north-eastern areas of Namibia and spreads into northern Botswana and Angola. The third species, *M. shortridgei*, was trapped along the Okavango river swamps and has a restricted distribution range.

Only few individuals were trapped of the species *M. shortridgei* from eight localities along the Okavango River. This is a very low return after approximately 4480 trap-nights. Ecologically specialized organisms, such as *M. shortridgei*, are vulnerable to habitat disturbances and thus relatively more susceptible to extinction. Human impacts on wetlands of the Okavango River drainage system might have influenced the low density that was observed for *M. shortridgei*. It is proposed by this study that the IUCN should review the conservation status of species *M. shortridgei*.

Areas of future research should be to karyotype few individuals of *M. shortridgei* to produce G-banded and C-banded chromosomes. Comparisons of chromosome banding patterns can confirm evolutionary relationships between species and also reveal changes in karyotype that may have been important in speciation.

CHAPTER 6. REFERENCES

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Diese Studie repräsentiert die eigenstaendige Arbeit des Autors und ist nicht in irgendeiner Form für einen Abschluss oder ein Diplom einem anderen Institut vorgelegt worden. Wo aus anderen Arbeiten zitiert wurde ist dies entsprechend gekennzeichnet worden.

Windhoek, Namibia, den 24 März 2015.

Seth Johannes Eiseb

APPENDIX ONE

SPECIMENS UTILISED IN CRANIOMETRICS CHARACTER SELECTION ANALYSES

Thirty-four specimens examined from the Hwange National Park in Zimbabwe, housed in the Natural History Museum of Zimbabwe in Bulawayo. S = Sex; M = Male; F = Female; TWC = Tooth wear class.

Museum no:	**Species**	**Locality**	**Grid/Ref**	**S**	**TWC**	**Collector**
NM75256	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM75270	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM64839	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	IV	V. Wilson
NM64840	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	IV	V. Wilson
NM75335	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75333	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75331	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	VI	V. Wilson
NM75332	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75330	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75329	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	V	V. Wilson
NM75325	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM75324	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	VI	V. Wilson
NM75322	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	V	V. Wilson
NM75321	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	VI	V. Wilson
NM75320	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	VI	V. Wilson
NM75318	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	IV	V. Wilson
NM75223	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM75387	*M. natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	V	V. Wilson
NM18122	*M. natalensis*	Headquarters, Hwange National Park, Zimbabwe	1826Dd	F	IV	
NM18123	*M. natalensis*	Headquarters, Hwange National Park, Zimbabwe	1826Dd	F	VII	
NM73587	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM73904	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	U	VI	V. Wilson
NM75346	*M. natalensis*	Shumba, Hwange National	1826Cd	M	VI	V. Wilson

		Park, Zimbabwe				
NM75347	*M. natalensis*	Shumba, Hwange National Park, Zimbabwe	1826Cd	M	IV	V. Wilson
NM75360	*M. natalensis*	Makalowa, Hwange National Park, Zimbabwe		F	IV	V. Wilson
NM18161	*M. natalensis*	Headquarters, Hwange National Park, Zimbabwe	1826Dd	M	IV	
NM73162	*M. natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	V	V. Wilson
NM75036	*M. natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	VII	V. Wilson
NM75038	*M. natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	V	V. Wilson
NM75046	*M. natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	V	V. Wilson
NM75049	*M. natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	VI	V. Wilson
NM75051	*M. natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	VI	V. Wilson
NM75054	*M. natalensis*	114 miles to Plumtree from Bulawayo, Zimbabwe		F	III	V. Wilson
NM75055	*M. natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	IV	V. Wilson

APPENDIX TWO

SPECIMEN CRANIA EXAMINED AND UTILISED IN TRADITIONAL MORPHOMETRIC ANALYSES

This table provides details of *Mastomys* specimen crania examined from museum collections (see below for museum abbreviations). The sex, toothwear class, geographic locality and museum catalogue number of each specimen are listed. Museum Abbreviations: TM = Transvaal Museum (*now* Ditsong National Museum of Natural History); BM = Natural History Museum, London; DM = Durban Natural Science Museum; SMM = State Museum, Namibia (*now* National Museum of Namibia); KM = Kaffrarian Museum (*now* Amathole Museum). NM = Natural History Museum (Zimbabwe). Type specimen names in bold.

Museum no.	Species	Locality	Coordinates	S	TWC	Collector
TM388	***Mus coucha (coucha)***	Potchefstroom, South Africa	26°42'S; 27°05'E	M	U	J. Ayres
TM389	***Mus socialis (coucha)***	Wonderfontein Limeworks, Ventersdorp, South Africa	26°19'S; 27°28'E	F	IV	H. L. Jameson
TM1341	***Mus limpopoensis (coucha)***	Limpopo and Sand rivers confluence, South Africa	22°19'S; 30°08'E	M	IV	Austin Roberts
TM1463	***Mus breyeri (coucha)***	Moorddrift, Potgietersrus, South Africa	24°17'S; 28°58'E	M	VI	Austin Roberts
TM1794	***Mus limpopoensis komatiensis (natalensis)***	Arnhemburg, carolina district, TVL, South Africa	26°03'S; 30°50'E	M	V	Austin Roberts
TM2454	***Mastomys coucha ovamboensis***	Namutoni, ENP, Namibia	15°44'S; 26°36'E	M	V	J. Breyer
TM3554	***Mastomys coucha bradfieldi***	Quickborn, Okahandja district, Namibia	21°08'S; 17°07'E	M	IV	R. D. Bradfield
BM412362	***Mastomys microdon zuluensis (coucha)?***	Umfolozi station, Zululand, South Africa		F	V	C. W, Rudd & P. Grant
BM457319	***Mus coucha***	Botswana		F	IV	A. Smith
BM457320	***Mastomys natalensis***	Natal, South Africa		U	III	A. Smith
BM457325	***Mus marikuensis mariquensis***	Marikura, South Africa		U	VI	A. Smith
BM331111	***Myomys shortridgei (shortridgei)***	Okavango-Omatako confluence, Namibia		F	U	G. C. Shortridge
SMM15849	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15798	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo

SMM15857	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15862	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15859	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15823	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15852	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM16150	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15817	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15812	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15829	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15799	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15832	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15855	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15820	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15811	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15831	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15803	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15794	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15833	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15815	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15850	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15789	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15861	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15825	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15864	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15787	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15835	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15843	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15807	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo

SMM15810	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15805	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
TM37769	*Mastomys natalensis*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	V	D. H. Gordon
TM37791	*Mastomys natalensis*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	F	IV	D. H. Gordon
TM37793	*Mastomys natalensis*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	F	V	D. H. Gordon
TM37795	*Mastomys natalensis*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	F	V	D. H. Gordon
TM37794	*Mastomys natalensis*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	F	V	D. H. Gordon
DM246	*Mastomys natalensis*	Sinjemba, Kavango region, Namibia	17°56'S; 21°18'E	M	IV	G. C. Shortridge
DM256	*Mastomys natalensis*	Ssanukannu village, Grootfontein district, Namibia	19°34'S; 18°06'E	F	VI	G. C. Shortridge
SMM1707	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	M	V	C. G. Coetzee
SMM1709	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	F	IV	C. G. Coetzee
SMM1710	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	M	V	C. G. Coetzee
SMM1711	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	F	V	C. G. Coetzee
SMM1712	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	F	IV	C. G. Coetzee
SMM1714	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	F	IV	C. G. Coetzee
SMM1717	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	M	V	C. G. Coetzee
SMM3469	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	U	IV	C. G. Coetzee
SMM3470	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	U	IV	C. G. Coetzee
SMM4336	*Mastomys natalensis*	Kapaku village, Kavango region, Namibia	1719Dc	M	V	C. G. Coetzee
SMM15938	*Mastomys natalensis*	Ngalla village, Caprivi region, Namibia	17°57'14.2''S 24°25'37.8''E	M	III	S. Eiseb, U. Zeller & G.

						Shihepo
SMM15924	*Mastomys natalensis*	Ngalla village, Caprivi region, Namibia	17°57'14.2''S 24°25'37.8''E	F	IV	S. Eiseb, U. Zeller & G. Shihepo
NM75249	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM75256	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM75265	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	IV	V. Wilson
NM75270	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM75276	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM64839	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	IV	V. Wilson
NM64840	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	IV	V. Wilson
NM75335	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75333	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75331	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	VI	V. Wilson
NM75332	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75330	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75329	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	V	V. Wilson
NM75325	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM75324	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	VI	V. Wilson
NM75322	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	V	V. Wilson
NM75321	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	VI	V. Wilson
NM75320	*Mastomys*	Robins, Hwange	1825Db	M	VI	V. Wilson

	natalensis	National Park, Zimbabwe				
NM75318	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	IV	V. Wilson
NM75223	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	IV	V. Wilson
NM75387	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	V	V. Wilson
NM18122	*Mastomys natalensis*	Headquarters, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM18123	*Mastomys natalensis*	Headquarters, Hwange National Park, Zimbabwe	1826Dd	F	VII	V. Wilson
NM73587	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM73904	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	U	VI	V. Wilson
NM75346	*Mastomys natalensis*	Shumba, Hwange National Park, Zimbabwe	1826Cd	M	VI	V. Wilson
NM75347	*Mastomys natalensis*	Shumba, Hwange National Park, Zimbabwe	1826Cd	M	IV	V. Wilson
NM75360	*Mastomys natalensis*	Makalowa, Hwange National Park, Zimbabwe		F	IV	V. Wilson
NM75250	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	III	V. Wilson
NM18161	*Mastomys natalensis*	Headquarters, Hwange National Park, Zimbabwe	1826Dd	M	IV	V. Wilson
NM75336	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	M	III	V. Wilson
NM75327	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	III	V. Wilson
NM75326	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	III	V. Wilson
NM75319	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	IV	V. Wilson
NM75317	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	III	V. Wilson
NM75316	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	III	V. Wilson

NM75315	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	III	V. Wilson
NM75198	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	M	III	V. Wilson
NM75202	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	III	V. Wilson
NM75203	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	III	V. Wilson
NM75204	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	III	V. Wilson
NM75205	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	III	V. Wilson
NM75211	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	III	V. Wilson
NM75213	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	M	III	V. Wilson
NM75218	*Mastomys natalensis*	Robins, Hwange National Park, Zimbabwe	1825Db	F	III	V. Wilson
NM75391	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	III	V. Wilson
NM75389	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	III	V. Wilson
NM75388	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	M	III	V. Wilson
NM73591	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	M	III	V. Wilson
NM73162	*Mastomys natalensis*	Main Camp, Hwange National Park, Zimbabwe	1826Dd	F	IV	V. Wilson
NM75036	*Mastomys natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	VII	V. Wilson
NM75038	*Mastomys natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	V	V. Wilson
NM75046	*Mastomys natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	V	V. Wilson
NM75049	*Mastomys natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	VI	V. Wilson
NM75051	*Mastomys natalensis*	6 miles on Figtree road from Bulawayo,		F	VI	V. Wilson

		Zimbabwe				
NM75054	*Mastomys natalensis*	114 miles to Plumtree from Bulawayo, Zimbabwe		F	III	V. Wilson
NM75055	*Mastomys natalensis*	6 miles on Figtree road from Bulawayo, Zimbabwe		F	IV	V. Wilson
DM864	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	M	V	E. Rzepecka
DM863	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	M	V	E. Rzepecka
DM871	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	V	Gavin Pretorius
DM872	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	U	IV	Gavin Pretorius
DM876	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	V	Gavin Pretorius
DM869	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	M	IV	E. Rzepecka
DM875	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	U	IV	Gavin Pretorius
DM1285	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	M	VII	P. Taylor & M. Rall
DM1284	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	VII	P. Taylor & M. Rall
DM1282	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	IV	P. Taylor & M. Rall
DM1281	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	VI	P. Taylor & M. Rall
DM1274	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	IV	P. Taylor & M. Rall
DM1271	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	M	IV	P. Taylor & M. Rall
DM1270	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	VI	P. Taylor & M. Rall
DM1269	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	VI	P. Taylor & M. Rall
DM1268	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	F	VI	P. Taylor & M. Rall
DM1267	*Mastomys*	Kranzkloof Nature	29°49'S; 30°50'E	F	VII	P. Taylor & M.

	natalensis	Reserve, Kwazulu Natal, South Africa				Rall
DM1264	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	M	VI	P. Taylor & M. Rall
DM1263	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	M	IV	P. Taylor & M. Rall
DM237	*Mastomys natalensis*	Mfongosi, Kwazulu Natal, South Africa	28°43'S; 30°48'E	M	VI	W. E. Jones
DM228	*Mastomys natalensis*	Mfongosi, Kwazulu Natal, South Africa	28°43'S; 30°48'E	F	V	W. E. Jones
DM222	*Mastomys natalensis*	Mfongosi, Kwazulu Natal, South Africa	28°43'S; 30°48'E	M	VI	W. E. Jones
DM252	*Mastomys natalensis*	Mfongosi, Kwazulu Natal, South Africa	28°43'S; 30°48'E	F	IV	W. E. Jones
DM795	*Mastomys natalensis*	Hawaan Forest Nature Reserve, Kwazulu Natal, South Africa	29°48'S; 31°02'E	M	IV	K. Willan
DM859	*Mastomys natalensis*	Umhlanga Reserve, Kwazulu Natal, South Africa	29°44'S; 31°05'E	F	IV	M. Jacobs
DM866	*Mastomys natalensis*	Kranzkloof Nature Reserve, Kwazulu Natal, South Africa	29°49'S; 30°50'E	M	IV	E. Rzepecka
DM952	*Mastomys natalensis*	Mbumbazi Nature Reserve, Kwazulu Natal, South Africa	30°48'10''S; 30°16'45''E	M	VII	M. R. Heywood
DM836	*Mastomys natalensis*	Vernon Crooks Nature Reserve, Kwazulu Natal, South Africa	30°17'S; 30°36'E	M	VII	K. Willan
DM837	*Mastomys natalensis*	Vernon Crooks Nature Reserve, Kwazulu Natal, South Africa	30°17'S; 30°36'E	F	IV	K. Willan
DM838	*Mastomys natalensis*	Vernon Crooks Nature Reserve, Kwazulu Natal, South Africa	30°17'S; 30°36'E	M	IV	K. Willan
DM839	*Mastomys natalensis*	Vernon Crooks Nature Reserve, Kwazulu Natal, South Africa	30°17'S; 30°36'E	F	IV	K. Willan
DM840	*Mastomys natalensis*	Vernon Crooks Nature Reserve, Kwazulu Natal, South Africa	30°17'S; 30°36'E	F	IV	K. Willan
DM841	*Mastomys natalensis*	Vernon Crooks Nature Reserve, Kwazulu Natal, South Africa	30°17'S; 30°36'E	M	IV	K. Willan
DM842	*Mastomys natalensis*	Hillcrest, Kwazulu Natal, South Africa	29°46'S; 30°46'E	M	IV	K. Willan
DM843	*Mastomys*	Hillcrest, Kwazulu	29°46'S; 30°46'E	M	IV	K. Willan

	natalensis	Natal, South Africa				
DM844	*Mastomys natalensis*	Hillcrest, Kwazulu Natal, South Africa	29°46'S; 30°46'E	M	IV	K. Willan
DM845	*Mastomys natalensis*	Hillcrest, Kwazulu Natal, South Africa	29°46'S; 30°46'E	M	IV	K. Willan
DM846	*Mastomys natalensis*	Hillcrest, Kwazulu Natal, South Africa	29°46'S; 30°46'E	M	IV	K. Willan
DM847	*Mastomys natalensis*	Hillcrest, Kwazulu Natal, South Africa	29°46'S; 30°46'E	F	IV	K. Willan
DM1154	*Mastomys natalensis*	Farm Clearwater, Kwazulu Natal, South Africa	31°02'S; 30°10'E	M	V	M. Rall, P. Taylor, D. van Dyk
DM1155	*Mastomys natalensis*	Farm Clearwater, Kwazulu Natal, South Africa	31°02'S; 30°10'E	F	V	M. Rall, P. Taylor, D. van Dyk
DM1159	*Mastomys natalensis*	Farm Clearwater, Kwazulu Natal, South Africa	31°02'S; 30°10'E	M	V	M. Rall, P. Taylor, D. van Dyk
DM1160	*Mastomys natalensis*	Farm Clearwater, Kwazulu Natal, South Africa	31°02'S; 30°10'E	F	V	D. van Dyk
DM1168	*Mastomys natalensis*	Farm Clearwater, Kwazulu Natal, South Africa	31°02'S; 30°10'E	M	V	M. Rall, P. Taylor, D. van Dyk
DM1169	*Mastomys natalensis*	Farm Clearwater, Kwazulu Natal, South Africa	31°02'S; 30°10'E	M	VI	M. Rall, P. Taylor, D. van Dyk
DM1179	*Mastomys natalensis*	Farm Clearwater, Kwazulu Natal, South Africa	31°02'S; 30°10'E	M	VI	P. Taylor, M. Rall, D. van Dyk
DM1180	*Mastomys natalensis*	Farm Clearwater, Kwazulu Natal, South Africa	31°02'S; 30°10'E	F	V	P. Taylor, M. Rall, D. van Dyk
DM1206	*Mastomys natalensis*	Allerriver Valley, Kwazulu Natal, South Africa	29°50'S; 30°56'E	M	VI	John Watson
DM1207	*Mastomys natalensis*	Farm Cato Ridge, Kwazulu Natal, South Africa	29°44'S; 30°36'E	F	IV	P. Paul
DM1211	*Mastomys natalensis*	Farm Cato Ridge, Kwazulu Natal, South Africa	29°44'S; 30°36'E	F	V	P. Paul
DM1212	*Mastomys natalensis*	Allerriver Valley, Kwazulu Natal, South Africa	29°50'S; 30°56'E	M	VI	John Watson
DM1213	*Mastomys natalensis*	Allerriver Valley, Kwazulu Natal, South Africa	29°50'S; 30°56'E	M	V	John Watson
DM1215	*Mastomys natalensis*	Pietermaritzburg, Kwazulu Natal, South Africa	29°36'S; 30°24'E	M	V	E. Rzepecka
DM1217	*Mastomys natalensis*	11 Highgates ave., Westville, Kwazulu Natal, South Africa	29°50'S; 30°56'E	M	VI	S. Copley
DM1218	*Mastomys natalensis*	11 Highgates ave., Westville, Kwazulu	29°50'S; 30°56'E	M	VI	S. Copley

		Natal, South Africa				
DM999	*Mastomys natalensis*	Futululu, Kwazulu Natal, South Africa	28°25'S; 32°16'E	M	V	R. Nanni
DM1000	*Mastomys natalensis*	Futululu, Kwazulu Natal, South Africa	28°25'S; 32°16'E	M	V	R. Nanni
KM4113	*M. shortridgei*	Ssannukanu, Groot fontein district, Namibia		M	IV	G. C. Shortridge
KM4112	*M. shortridgei*	Ssannukanu, Groot fontein district, Namibia		M	IV	G. C. Shortridge
KM4111	*M. shortridgei*	Ssannukanu, Groot fontein district, Namibia		F	IV	G. C. Shortridge
KM4122	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		M	IV	G. C. Shortridge
KM4123	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		F	V	G. C. Shortridge
KM4124	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		F	V	G. C. Shortridge
KM4125	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		F	IV	G. C. Shortridge
KM4126	*M. shortridgei*	Mbambi, Kavango region, Namibia		F	VI	G. C. Shortridge
KM4127	*M. shortridgei*	Mbambi, Kavango region, Namibia		M	IV	G. C. Shortridge
KM4137	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		F	IV	G. C. Shortridge
KM4138	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		U	IV	G. C. Shortridge
KM4139	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	IV	G. C. Shortridge
KM4140	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	IV	G. C. Shortridge
KM4115	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		F	IV	G. C. Shortridge
KM4116	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		M	IV	G. C. Shortridge
KM4117	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		M	III	G. C. Shortridge
KM4118	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		F	IV	G. C. Shortridge
KM4119	*M. shortridgei*	Omatako-Kavango rivers confluence,		M	IV	G. C. Shortridge

		Namibia				
KM4120	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		M	V	G. C. Shortridge
KM4121	*M. shortridgei*	Omatako-Kavango rivers confluence, Namibia		M	VI	G. C. Shortridge
KM4128	*M. shortridgei*	Mahango drift, Kavango region, Namibia		M	V	G. C. Shortridge
KM4130	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	IV	G. C. Shortridge
KM4131	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	IV	G. C. Shortridge
KM4132	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	V	G. C. Shortridge
KM4133	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	IV	G. C. Shortridge
KM4134	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	IV	G. C. Shortridge
KM4135	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	IV	G. C. Shortridge
KM4136	*M. shortridgei*	Diwai, Bagani drift, Kavango region, Namibia		M	IV	G. C. Shortridge
TM37751	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	IV	D. H. Gordon
TM37754	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	IV	D. H. Gordon
TM37755	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	V	D. H. Gordon
TM37756	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	IV	D. H. Gordon
TM37757	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	VI	D. H. Gordon
TM37762	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	IV	D. H. Gordon
TM37764	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	IV	D. H. Gordon
TM37796	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	F	IV	D. H. Gordon
TM37797	*M. shortridgei*	Mahango Nature	18°10'S; 21°43'E	F	IV	D. H. Gordon

		Reserve, Kavango region, Namibia				
TM38834	*M. shortridgei*	Mahango Nature Reserve, Kavango region, Namibia	18°10'S; 21°43'E	M	VI	D. H. Gordon
KM15881	*Mastomys natalensis*	Nokaneng, Ngami land, Botswana	1922Ca	F	VI	
KM15876	*Mastomys natalensis*	Nokaneng, Ngami land, Botswana	1922Ca	M	III	
KM15882	*Mastomys natalensis*	Tsau, Ngamiland, Botswana	2022Ab	M	V	
TM21730	*Mastomys natalensis*	Shakawe, Botswana	1821Bd	F	IV	P. J. Geldenhuys
TM31166	*Mastomys natalensis*	Sepopa riverbank, Botswana	1822Cc	F	V	S. W. Goussorch
TM21851	*Mastomys natalensis*	Bodipeng, Lake Ngami, Botswana	2022Da	M	VI	
TM21864	*Mastomys natalensis*	Nokaneng village, Botswana	1922Cb	F	IV	P. J. Geldenhuys
TM31167	*Mastomys natalensis*	Shakawe, Botswana	1821Bd	M	III	J. N. Liversedge
TM31165	*Mastomys natalensis*	Shakawe, Botswana	1821Bd	F	III	J. N. Liversedge
TM31164	*Mastomys natalensis*	Shakawe, Botswana	1821Bd	M	III	J. N. Liversedge
TM6398	*Mastomys coucha*	Maun, Botswana	1923Cd	M	VI	Vernay-Lang Kalahari Expedition
TM6399	*Mastomys coucha*	Maun, Botswana	1923Cd	M	IV	Vernay-Lang Kalahari Expedition
TM6400	*Mastomys coucha*	Maun, Botswana	1923Cd	F	VI	Vernay-Lang Kalahari Expedition
TM6401	*Mastomys coucha*	Maun, Botswana	1923Cd	M	III	Vernay-Lang Kalahari Expedition
TM6402	*Mastomys coucha*	Maun, Botswana	1923Cd	M	IV	Vernay-Lang Kalahari Expedition
TM6403	*Mastomys coucha*	Maun, Botswana	1923Cd	F	IV	Vernay-Lang Kalahari Expedition
TM6407	*Mastomys coucha*	25 miles East of Maun, Botswana	2023Aa	F	V	Vernay-Lang Kalahari Expedition
TM6409	*Mastomys coucha*	25 miles East of Maun, Botswana	2023Aa	M	III	Vernay-Lang Kalahari Expedition
TM5204	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	V	Meyer
TM5209	*Mastomys natalensis*	Moombola, Angola	1114Cb	F	IV	Meyer
TM5210	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	IV	Meyer
TM5211	*Mastomys*	Moombola, Angola	1114Cb	M	IV	Meyer

	natalensis					
TM5212	*Mastomys natalensis*	Moombola, Angola	1114Cb	F	IV	Meyer
TM7653	*Mastomys natalensis*	Angola		U	VI	D. L. Fourie
TM11876	*Mastomys natalensis*	Pereira De EGA, Angola	1714Ba	M	IV	C. K. Brain
TM5215	*Mastomys natalensis*	Moombola, Angola	1114Cb	F	VII	Meyer
TM5216	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	IV	Meyer
TM5217	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	IV	Meyer
TM5218	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	IV	Meyer
TM5220	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	V	Meyer
TM5223	*Mastomys natalensis*	Moombola, Angola	1114Cb	F	III	Meyer
TM5224	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	III	Meyer
TM5231	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	IV	Meyer
TM5232	*Mastomys natalensis*	Moombola, Angola	1114Cb	M	V	Meyer
SMM15868	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	F	V	S. Eiseb & G. Shihepo
SMM16158	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	F	V	S. Eiseb & G. Shihepo
SMM15847	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	F	V	S. Eiseb & G. Shihepo
SMM15797	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	F	V	S. Eiseb & G. Shihepo
SMM15792	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	F	VI	S. Eiseb & G. Shihepo
SMM15843	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	M	IV	S. Eiseb & G. Shihepo
SMM15844	*Mastomys coucha*	Omatjene Research Station, Namibia	20°24'53.1''S 16°28'44.5''E	U	IV	S. Eiseb & G. Shihepo
SMM15826	*Mastomys coucha*	Waterberg Plateau Park, Namibia	20°25'35.2''S 17°21'14.6''E	M	IV	S. Eiseb & G. Shihepo
SMM15824	*Mastomys coucha*	Waterberg Plateau Park, Namibia	20°25'35.2''S 17°21'14.6''E	M	IV	S. Eiseb & G. Shihepo
SMM15785	*Mastomys coucha*	Waterberg Plateau Park, Namibia	20°25'35.2''S 17°21'14.6''E	U	IV	S. Eiseb & G. Shihepo
SMM3383	*Mastomys coucha*	Waterberg 416, Namibia	20°25'35.2''S 17°21'14.6''E	M	IV	P. J. Buys
SMM3384	*Mastomys coucha*	Waterberg 416, Namibia	20°25'35.2''S 17°21'14.6''E	F	IV	P. J. Buys
SMM3388	*Mastomys coucha*	Waterberg 416, Namibia	20°25'35.2''S 17°21'14.6''E	M	IV	P. J. Buys
SMM3389	*Mastomys coucha*	Waterberg 416, Namibia	20°25'35.2''S 17°21'14.6''E	F	IV	P. J. Buys
SMM3390	*Mastomys coucha*	Waterberg 416, Namibia	20°25'35.2''S 17°21'14.6''E	M	IV	P. J. Buys
SMM3395	*Mastomys*	Waterberg 416,	20°25'35.2''S	F	IV	P. J. Buys

	coucha	Namibia	17°21'14.6''E			
SMM3399	*Mastomys coucha*	Waterberg 416, Namibia	20°25'35.2''S 17°21'14.6''E	F	V	P. J. Buys
SMM3402	*Mastomys coucha*	Waterberg 416, Namibia	20°25'35.2''S 17°21'14.6''E	F	V	P. J. Buys
SMM3404	*Mastomys coucha*	Waterberg 416, Namibia	20°25'35.2''S 17°21'14.6''E	M	VI	P. J. Buys
SMM12673	*Mastomys coucha*	Waterberg Plateau Park, Namibia	20°25'35.2''S 17°21'14.6''E	M	V	M. Griffin
SMM12675	*Mastomys coucha*	Waterberg Plateau Park, Namibia	20°25'35.2''S 17°21'14.6''E	F	V	M. Griffin
SMM12676	*Mastomys coucha*	Waterberg Plateau Park, Namibia	20°25'35.2''S 17°21'14.6''E	M	VI	M. Griffin
SMM12677	*Mastomys coucha*	Waterberg Plateau Park, Namibia	20°25'35.2''S 17°21'14.6''E	U	IV	M. Griffin
SMM12693	*Mastomys coucha*	Waterberg Plateau Park, Namibia	20°25'35.2''S 17°21'14.6''E	U	IV	M. Griffin
SMM5818	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	M	VI	C. Grobler
SMM5822	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	M	VI	C. Grobler
SMM5823	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	M	VI	C. Grobler
SMM5824	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	M	VII	C. Grobler
SMM5825	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	C. Grobler
SMM5826	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	C. Grobler
SMM5827	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	VI	C. Grobler
SMM5828	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	IV	C. Grobler
SMM5829	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	C. Grobler
SMM5830	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	M	VII	C. Grobler
SMM5831	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	C. Grobler
SMM5845	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	M	V	C. Grobler
SMM5846	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	C. Grobler

SMM5854	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	M	V	C. Grobler
SMM5855	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	C. Grobler
SMM5856	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	C. Grobler
SMM5857	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	C. Grobler
SMM7786	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	M	V	A. P. Simoes
SMM7787	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	A. P. Simoes
SMM7788	*Mastomys coucha*	Elshorst 91, Otjiwarongo dist., Namibia	2016Cd	F	V	A. P. Simoes
SMM7789	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	M	IV	A. P. Simoes
SMM7790	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	M	III	A. P. Simoes
SMM7791	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	M	III	A. P. Simoes
SMM7792	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	M	III	A. P. Simoes
SMM7793	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	M	III	A. P. Simoes
SMM7794	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	M	III	A. P. Simoes
SMM7795	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	F	III	A. P. Simoes
SMM7806	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	F	IV	A. P. Simoes
SMM7807	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	M	IV	A. P. Simoes
SMM7808	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	F	III	A. P. Simoes
SMM7809	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	F	III	A. P. Simoes
SMM7812	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist.,	2016Cd	F	IV	A. P. Simoes

		Namibia				
SMM7818	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	M	IV	A. P. Simoes
SMM7819	*Mastomys coucha*	Etaneno 44, Otjiwarongo dist., Namibia	2016Cd	F	IV	A. P. Simoes
SMM7822	*Mastomys coucha*	Geduld 111, Outjo dist., Namibia	2015Bc	F	IV	A. P. Simoes
SMM7823	*Mastomys coucha*	Klein Okombahe 18, Omaruru dist., Namibia	2015Dc	F	VII	A. P. Simoes
SMM2238	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	F	V	C. G. Coetzee
SMM2269	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	F	IV	C. G. Coetzee
SMM2272	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	F	VI	C. G. Coetzee
SMM2273	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	M	VI	C. G. Coetzee
SMM2312	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	F	VI	C. G. Coetzee
SMM15932	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	M	IV	S. Eiseb & G. Shihepo
SMM16047	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	M	III	S. Eiseb & G. Shihepo
SMM15927	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	M	III-IV	S. Eiseb & G. Shihepo
SMM16027	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	M	IV	S. Eiseb & G. Shihepo
SMM16011	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	M	VII	S. Eiseb & G. Shihepo
SMM16031	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	F	VI	S. Eiseb & G. Shihepo
SMM15984	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	F	IV	S. Eiseb & G. Shihepo
SMM15750	*Mastomys coucha*	Uniab River mouth, Namibia	20°13'00.8''S 13°12'30.8''E	M	IV	S. Eiseb & G. Shihepo
SMM16234	*Mastomys natalensis*	Popa Falls Resort, Kavango, Namibia	18°07'17.4''S 21°35'03.1''E	M	IV	S. Eiseb & A. Mbangu
SMM16248	*Mastomys natalensis*	Popa Falls Resort, Kavango, Namibia	18°07'17.4''S 21°35'03.1''E	M	V	S. Eiseb & A. Mbangu
SMM16245	*Mastomys natalensis*	Popa Falls Resort, Kavango, Namibia	18°07'17.4''S 21°35'03.1''E	M	V	S. Eiseb & A. Mbangu
SMM16240	*Mastomys natalensis*	Popa Falls Resort, Kavango, Namibia	18°07'17.4''S 21°35'03.1''E	F	V	S. Eiseb & A. Mbangu
SMM16237	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	V	S. Eiseb & A. Mbangu
SMM16252	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	V	S. Eiseb & A. Mbangu
SMM16250	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	V	S. Eiseb & A. Mbangu
SMM16247	*Mastomys*	5km S. Omatako-	17°58'45.0''S	M	V	S. Eiseb & A.

	natalensis	Kavango rivers confluence, Namibia	20°27'26.0''E			Mbangu
SMM16254	*Mastomys natalensis*	Omatako-Kavango rivers confluence, Namibia	17°57'06.0''S 20°28'26.9''E	F	V	S. Eiseb & A. Mbangu
SMM16242	*Mastomys natalensis*	Omatako-Kavango rivers confluence, Namibia	17°57'06.0''S 20°28'26.9''E	M	IV	S. Eiseb & A. Mbangu
SMM16241	*Mastomys natalensis*	Omatako-Kavango rivers confluence, Namibia	17°57'06.0''S 20°28'26.9''E	M	IV	S. Eiseb & A. Mbangu
SMM16249	*Mastomys natalensis*	Omatako-Kavango rivers confluence, Namibia	17°57'06.0''S 20°28'26.9''E	F	IV	S. Eiseb & A. Mbangu
SMM16238	*Mastomys natalensis*	Omatako-Kavango rivers confluence, Namibia	17°57'06.0''S 20°28'26.9''E	M	IV	S. Eiseb & A. Mbangu
SMM12681	*Mastomys shortridgei*	Mahango Nature Reserve, Namibia	1821Ba	F	III	D. H. Gordon
SMM12682	*Mastomys natalensis*	Mahango Nature Reserve, Namibia	1821Ba	F	IV-V	D. H. Gordon
SMM12686	*Mastomys shortridgei*	Mahango Nature Reserve, Namibia	1821Ba	U	III	D. H. Gordon
SMM12687	*Mastomys shortridgei*	Mahango Nature Reserve, Namibia	1821Ba	U	III	D. H. Gordon
SMM12688	*Mastomys natalensis*	Mahango Nature Reserve, Namibia	1821Ba	M	III	D. H. Gordon
BOT028	*Mastomys natalensis*	Thamalakane River, Maun, Botswana	19°56'29.2"S, 23°29'40.5"E	M	IV	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT001	*Mastomys natalensis*	Drotsky's Cabin, Shakawe, Botswana	18°24'58.8"S, 21°53'22.1"E	M	IV	S. Eiseb, A. Serogwe & J. Haradoes
BOT016	*Mastomys natalensis*	Sepopa Swamp Stop, Botswana	18°44'41.4"S, 22°11'48.7"E	M	IV	S. Eiseb, A. Serogwe & J. Haradoes
BOT017	*Mastomys natalensis*	Sepopa Swamp Stop, Botswana	18°44'41.4"S, 22°11'48.7"E	F	V	S. Eiseb, A. Serogwe & J. Haradoes
BOT018	*Mastomys natalensis*	Sepopa Swamp Stop, Botswana	18°44'41.4"S, 22°11'48.7"E	M	IV	S. Eiseb, A. Serogwe & J. Haradoes
SMM15777	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15770	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15763	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15780	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15782	*Mastomys*	5km S. Omatako-	17°58'45.0''S	M	IV	S. Eiseb & U.

	natalensis	Kavango rivers confluence, Namibia	20°27'26.0''E			Zeller
SMM15759	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15755	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15779	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15769	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15781	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	F	V	S. Eiseb & U. Zeller
SMM15762	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	F	IV	S. Eiseb & U. Zeller
SMM15776	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15765	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15766	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15754	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	M	IV	S. Eiseb & U. Zeller
SMM15784	*Mastomys natalensis*	5km S. Omatako-Kavango rivers confluence, Namibia	17°58'45.0''S 20°27'26.0''E	F	VI	S. Eiseb & U. Zeller
SMM16266	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata, Angola	14°58'47.2"S, 13°26'19.9"E	M	IV	S. Eiseb & L. Nghilundilua
SMM16283	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata, Angola	14°58'47.2"S, 13°26'19.9"E	F	V	S. Eiseb & L. Nghilundilua
SMM16275	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata, Angola	14°58'47.2"S, 13°26'19.9"E	M	IV	S. Eiseb & L. Nghilundilua
SMM16271	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata, Angola	14°58'47.2"S, 13°26'19.9"E	M	IV	S. Eiseb & L. Nghilundilua
SMM16265	*Mastomys kollmannspergeri*	Mbalanondolo village on banks of Rio Cubango, Angola	12°44'15.8"S, 16°18'00.2"E	M	IV	S. Eiseb & L. Nghilundilua
SMM16267	*Mastomys shortridgei*	Longa village; on road between Menongue & Cuito Cuanavale,	14°35'29.2"S, 18°27'43.4"E	F	IV	S. Eiseb & L. Nghilundilua

		Angola				
SMM16260	*Mastomys natalensis*	Swamps at Shamvura village, Kavango, Namibia	18°02'10.5''S 20°50'37.4''E	F	IV	S. Eiseb & V. Mughongora
SMM16256	*Mastomys natalensis*	Swamps at Shamvura village, Kavango, Namibia	18°01'57.2''S 20°51'39.2''E	M	IV	S. Eiseb & V. Mughongora
SMM16261	*Mastomys natalensis*	Swamps at Shamvura village, Kavango, Namibia	18°01'57.2''S 20°51'39.2''E	M	IV	S. Eiseb & V. Mughongora
SMM16258	*Mastomys shortridgei*	Swamps at Shamvura village, Kavango, Namibia	18°01'57.2''S 20°51'39.2''E	F	IV	S. Eiseb & V. Mughongora
SMM16259	*Mastomys shortridgei*	Swamps at Shamvura village, Kavango, Namibia	18°01'57.2''S 20°51'39.2''E	M	IV	S. Eiseb & V. Mughongora
SMM16257	*Mastomys natalensis*	Swamps at Shamvura village, Kavango, Namibia	18°01'57.2''S 20°51'39.2''E	F	IV	S. Eiseb & V. Mughongora
SMM16272	*Mastomys shortridgei*	Close to Shakawe Police Station, Shakawe, Botswana	18°23'42"S, 21°51'13.7"E	F	V	S. Eiseb, A. Serogwe & J. Haradoes
SMM16268	*Mastomys natalensis*	Close to Shakawe Police Station, Shakawe, Botswana	18°23'42"S, 21°51'13.7"E	F	III	S. Eiseb, A. Serogwe & J. Haradoes
SMM16274	*Mastomys natalensis*	Close to Shakawe Police Station, Shakawe, Botswana	18°23'42"S, 21°51'13.7"E	M	III	S. Eiseb, A. Serogwe & J. Haradoes
SMM16264	*Mastomys shortridgei*	Close to Shakawe Police Station, Shakawe, Botswana	18°23'42"S, 21°51'13.7"E	M	IV	S. Eiseb, A. Serogwe & J. Haradoes
SMM16273	*Mastomys natalensis*	Close to Shakawe Police Station, Shakawe, Botswana	18°23'42"S, 21°51'13.7"E	F	III	S. Eiseb, A. Serogwe & J. Haradoes

APPENDIX THREE

SPECIMEN CRANIA EXAMINED AND UTILISED IN GEOMETRIC MORPHOMETRIC ANALYSES

This table provides details of *Mastomys* specimen crania examined from museum collections (see below for museum abbreviations). The sex, toothwear class, geographic locality and museum catalogue number of each specimen are listed. Museum Abbreviations: TM = Transvaal Museum (*now* Ditsong National Museum of Natural History); SMM = State Museum, Namibia (*now* National Museum of Namibia).

Museum no:	**Species**	**Locality**	**Coordinates**	**S**	**TWC**	**Collector**
SMM3362	*Mastomys coucha*	Uris 590	1917Bc	F	V	P. J. Buys
SMM3378	*Mastomys coucha*	Uris 590	1917Bc	M	III	P. J. Buys
SMM3375	*Mastomys coucha*	Uris 590	1917Bc	M	V	P. J. Buys
SMM3346	*Mastomys coucha*	Uris 590	1917Bc	M	VII	P. J. Buys
SMM3360	*Mastomys coucha*	Uris 590	1917Bc	M	IV	P. J. Buys
SMM16034	*Mastomys natalensis*	Andoni, Etosha National Park	18°30'03.6''S 16°44'38.9''E	F	III	S. Eiseb & G. Shihepo
SMM16048	*Mastomys natalensis*	Andoni, Etosha National Park	18°30'03.6''S 16°44'38.9''E	F	III	S. Eiseb & G. Shihepo
SMM16001	*Mastomys natalensis*	Andoni, Etosha National Park	18°30'03.6''S 16°44'38.9''E	M	III	S. Eiseb & G. Shihepo
SMM16036	*Mastomys natalensis*	Andoni, Etosha National Park	18°30'03.6''S 16°44'38.9''E	M	III	S. Eiseb & G. Shihepo
SMM16042	*Mastomys natalensis*	Andoni, Etosha National Park	18°30'03.6''S 16°44'38.9''E	M	IV	S. Eiseb & G. Shihepo
SMM16024	*Mastomys*	Oshigambo village	17°51'17.6''S 16°05'10.2''E	M	IV	S. Eiseb & G. Shihepo
SMM15989	*Mastomys*	Namutoni, Etosha National Park	18°48'25.9''S 16°56'22.3''E	F	V	S. Eiseb & G. Shihepo
SMM16020	*Mastomys*	Namutoni, Etosha National Park	18°48'25.9''S 16°56'22.3''E	F	V	S. Eiseb & G. Shihepo
SMM16026	*Mastomys*	Namutoni, Etosha National Park	18°48'25.9''S 16°56'22.3''E	M	IV	S. Eiseb & G. Shihepo
SMM15987	*Mastomys*	Namutoni, Etosha National Park	18°48'25.9''S 16°56'22.3''E	M	IV	S. Eiseb & G. Shihepo
SMM15988	*Mastomys*	Namutoni, Etosha National Park	18°48'25.9''S 16°56'22.3''E	F	IV	S. Eiseb & G. Shihepo
SMM15752	*Mastomys*	Namutoni, Etosha National Park	18°48'25.9''S 16°56'22.3''E	U	I	S. Eiseb & G. Shihepo
SMM15932	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	V	S. Eiseb & G. Shihepo
SMM15927	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	IV	S. Eiseb & G. Shihepo
SMM16027	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	III	S. Eiseb & G. Shihepo

SMM16059	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	I	S. Eiseb & G. Shihepo
SMM16023	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	III	S. Eiseb & G. Shihepo
SMM16004	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	II	S. Eiseb & G. Shihepo
SMM16031	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	F	VI	S. Eiseb & G. Shihepo
SMM15750	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	IV	S. Eiseb & G. Shihepo
SMM15984	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	F	IV	S. Eiseb & G. Shihepo
SMM16045	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	F	I	S. Eiseb & G. Shihepo
SMM16027	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	IV	S. Eiseb & G. Shihepo
SMM15928	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	F	III	S. Eiseb & G. Shihepo
SMM16051	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	III	S. Eiseb & G. Shihepo
SMM16047	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	IV	S. Eiseb & G. Shihepo
SMM16052	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	F	I	S. Eiseb & G. Shihepo
SMM16016	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	III	S. Eiseb & G. Shihepo
SMM16011	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	M	VII	S. Eiseb & G. Shihepo
SMM15999	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	F	VII	S. Eiseb & G. Shihepo
SMM16065	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	M	IV	S. Eiseb & G. Shihepo
SMM15610	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	F	IV	S. Eiseb & G. Shihepo
SMM15948	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	F	III	S. Eiseb & G. Shihepo
SMM16008	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	M	III	S. Eiseb & G. Shihepo
SMM15997	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	F	III	S. Eiseb & G. Shihepo
SMM16085	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	F	III	S. Eiseb & G. Shihepo
SMM16044	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	M	III	S. Eiseb & G. Shihepo
SMM15992	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	F	III	S. Eiseb & G. Shihepo
SMM15019	*Mastomys*	Etunda	17°25'34.6''E	M	V	S. Eiseb & G.

		Irrigation Project	14°31'52.0''E			Shihepo
SMM15751	*Mastomys*	Etunda Irrigation Project	17°25'34.6''E 14°31'52.0''E	M	III	S. Eiseb & G. Shihepo
SMM15826	*Mastomys coucha*	Waterberg Plateau Park	20°25'35.2''S 17°21'14.6''E	M	III	S. Eiseb & G. Shihepo
SMM15824	*Mastomys coucha*	Waterberg Plateau Park	20°25'35.2''S 17°21'14.6''E	M	III	S. Eiseb & G. Shihepo
SMM15785	*Mastomys coucha*	Waterberg Plateau Park	20°25'35.2''S 17°21'14.6''E	U	III	S. Eiseb & G. Shihepo
SMM12693	*Mastomys coucha*	Waterberg Plateau Park	2017Ad	U	VI	M. Griffin
SMM12676	*Mastomys coucha*	Waterberg Plateau Park	2017Ad	M	VI	M. Griffin
SMM12673	*Mastomys coucha*	Waterberg Plateau Park	2017Ad	M	V	M. Griffin
SMM12677	*Mastomys coucha*	Waterberg Plateau Park	2017Ad	U	IV	M. Griffin
SMM12675	*Mastomys coucha*	Waterberg Plateau Park	2017Ad	F	V	M. Griffin
SMM3383	*Mastomys coucha*	Waterberg Plateau Park	2017Cb	M	III	P. J. Buys
SMM3395	*Mastomys coucha*	Waterberg Plateau Park	2017Cb	F	IV	P. J. Buys
SMM3388	*Mastomys coucha*	Waterberg Plateau Park	2017Cb	M	III	P. J. Buys
SMM3389	*Mastomys coucha*	Waterberg Plateau Park	2017Cb	F	III	P. J. Buys
SMM3399	*Mastomys coucha*	Waterberg Plateau Park	2017Cb	F	V	P. J. Buys
SMM3384	*Mastomys coucha*	Waterberg Plateau Park	2017Cb	F	III	P. J. Buys
SMM3390	*Mastomys coucha*	Waterberg Plateau Park	2017Cb	M	III	P. J. Buys
SMM15729	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	F	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15944	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15726	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15935	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15913	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15938	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15923	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	F	IV	S. Eiseb, U. Zeller & G. Shihepo

SMM15725	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15943	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15735	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15931	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	F	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15945	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15926	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15924	*Mastomys natalensis*	Ngalla village, Caprivi	17°57'14.2''S 24°25'37.8''E	F	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM12147	*Mastomys natalensis*	Lupala Island, Caprivi	1823Bc	F	III	A. S. Samahiya
SMM12154	*Mastomys natalensis*	Nkasa Station, Caprivi	1823Bc	M	III	B. S. Lishumi
SMM12558	*Mastomys natalensis*	Balelwa Station, Caprivi	1823Ad	F	V	B. S. Bede
SMM12556	*Mastomys natalensis*	Balelwa Station, Caprivi	1823Ad	M	V	B. S. Bede
SMM12157	*Mastomys natalensis*	Lupala Island, Caprivi	1823Bc	M	III	C. M. Kakambi
SMM13570	*Mastomys natalensis*	Omega, Caprivi	1822Ab	M	III	J. Pallett
SMM13534	*Mastomys natalensis*	Buffalo Camp, Caprivi	1821Ba	M	V	J. Pallett
SMM5305	*Mastomys*	Capangombe, Angola	1513Aa	U	VI	C. G. Coetzee
SMM6414	*Mastomys*	Alto De Chela Tchivinguira, Angola	1513Ab	U	VI	C. G. Coetzee
SMM5287	*Mastomys*	Tchivinguira, Angola	1513Aa	U	VI	C. G. Coetzee
SMM6413	*Mastomys*	Alto De Chela Tchivinguira, Angola	1513Ab	U	V	C. G. Coetzee
SMM5302	*Mastomys*	Capangombe, Angola	1513Aa	U	IV	C. G. Coetzee
SMM5304	*Mastomys*	Capangombe, Angola	1513Aa	U	IV	C. G. Coetzee
SMM5480	*Mastomys*	Vila Ariaga, Angola	1413Cb	U	VI	C. G. Coetzee
SMM5483	*Mastomys*	Vila Ariaga, Angola	1413Cb	U	VI	C. G. Coetzee
SMM5484	*Mastomys*	Vila Ariaga, Angola	1413Cb	U	V	C. G. Coetzee
SMM5306	*Mastomys*	Capangombe,	1513Aa	U	IV	C. G.

		Angola				Coetzee
SMM5303	*Mastomys*	Capangombe, Angola	1513Aa	U	V	C. G. Coetzee
SMM5479	*Mastomys*	Vila Ariaga, Angola	1413Cb	U	IV	C. G. Coetzee
SMM5481	*Mastomys*	Vila Ariaga, Angola	1413Cb	U	V	C. G. Coetzee
SMM5482	*Mastomys*	Vila Ariaga, Angola	1413Cb	U	V	C. G. Coetzee
SMM1712	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	F	V	C. G. Coetzee
SMM1709	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	F	V	C. G. Coetzee
SMM1714	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	F	IV	C. G. Coetzee
SMM1707	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	M	V	C. G. Coetzee
SMM1710	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	M	VI	C. G. Coetzee
SMM3469	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	U	III	C. G. Coetzee
SMM1717	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	M	V	C. G. Coetzee
SMM1724	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	M	VI	C. G. Coetzee
SMM1711	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	F	V	C. G. Coetzee
SMM4336	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	M	VI	C. G. Coetzee
SMM3470	*Mastomys natalensis*	Kapaku, Kavango	1719Dc	U	IV	C. G. Coetzee
SMM1998	*Mastomys natalensis*	Andara, Kavango	1821Ab	M	IV	C. G. Coetzee
SMM2009	*Mastomys natalensis*	Andara, Kavango	1821Ab	M	IV	C. G. Coetzee
SMM12688	*Mastomys natalensis*	Mahango Nature Reserve	18°10'S; 21°43'E	M	III	D. H. Gordon
SMM12682	*Mastomys natalensis*	Mahango Nature Reserve	18°10'S; 21°43'E	F	V	D. H. Gordon
SMM12686	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	U	III	D. H. Gordon
SMM12687	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	U	III	D. H. Gordon
SMM12681	*Mastomys natalensis*	Mahango Nature Reserve	18°10'S; 21°43'E	F	III	D. H. Gordon
SMM16245	*Mastomys natalensis*	Popa Falls, Kavango	18°07'17.4''S 21°35'03.1''E	M	V	S. Eiseb & A. Mbangu
SMM16240	*Mastomys natalensis*	Popa Falls, Kavango	18°07'17.4''S 21°35'03.1''E	F	V	S. Eiseb & A. Mbangu
SMM16248	*Mastomys natalensis*	Popa Falls, Kavango	18°07'17.4''S 21°35'03.1''E	M	V	S. Eiseb & A. Mbangu
SMM16234	*Mastomys natalensis*	Popa Falls, Kavango	18°07'17.4''S 21°35'03.1''E	M	IV	S. Eiseb & A. Mbangu
SMM16251	*Mastomys natalensis*	Popa Falls, Kavango	18°07'17.4''S 21°35'03.1''E	M	III	S. Eiseb & A. Mbangu
SMM16233	*Mastomys*	Popa Falls,	18°07'17.4''S	M	III	S. Eiseb & A.

	natalensis	Kavango	21°35'03.1''E			Mbangu
SMM2030	*Mastomys natalensis*	Popa Falls, Kavango	1821Ba	M	VI	
SMM2020	*Mastomys natalensis*	Popa Falls, Kavango	1821Ba	M	V	
SMM2036	*Mastomys natalensis*	Popa Falls, Kavango	1821Ba	M	III	
SMM15738	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15724	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	VI	S. Eiseb, U. Zeller & G. Shihepo
SMM15731	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15939	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15730	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15914	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15732	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15942	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15725	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15728	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15930	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	VI	S. Eiseb, U. Zeller & G. Shihepo
SMM15946	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15936	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15929	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15941	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	IV	S. Eiseb, U. Zeller & G. Shihepo
SMM15933	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	V	S. Eiseb, U. Zeller & G. Shihepo
SMM15937	*Mastomys*	Divundu	18°06'49.7''S	M	IV	S. Eiseb, U.

	natalensis	Irrigation Project	21°34'42.3''E			Zeller & G. Shihepo
SMM15912	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15904	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15981	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15922	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	F	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15906	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15934	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15917	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SEG125	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15915	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM15909	*Mastomys natalensis*	Divundu Irrigation Project	18°06'49.7''S 21°34'42.3''E	M	III	S. Eiseb, U. Zeller & G. Shihepo
SMM16241	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	M	IV	S. Eiseb & A. Mbangu
SMM16249	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	F	V	S. Eiseb & A. Mbangu
SMM16238	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	M	V	S. Eiseb & A. Mbangu
SMM16254	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	F	V	S. Eiseb & A. Mbangu
SMM16242	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	M	V	S. Eiseb & A. Mbangu
SMM15756	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	F	III	S. Eiseb & U. Zeller
SMM15758	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	III	S. Eiseb & U. Zeller
SMM15783	*Mastomys*	5km south of	17°58'45.0''S	M	III	S. Eiseb & U.

	natalensis	Omatako-Kavango rivers confluence	20°27'26.0''E			Zeller
SMM15768	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	F	III	S. Eiseb & U. Zeller
SMM15764	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	F	III	S. Eiseb & U. Zeller
SMM15772	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	III	S. Eiseb & U. Zeller
SMM15771	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	III	S. Eiseb & U. Zeller
SMM15757	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	III	S. Eiseb & U. Zeller
SMM15775	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	III	S. Eiseb & U. Zeller
SMM15778	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	III	S. Eiseb & U. Zeller
SMM16247	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	VI	S. Eiseb & A. Mbangu
SMM16237	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	VI	S. Eiseb & A. Mbangu
SMM16250	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	VI	S. Eiseb & A. Mbangu
SMM16252	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	M	VI	S. Eiseb & A. Mbangu
SMM15813	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM16158	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	F	VI	S. Eiseb & G. Shihepo
SMM15847	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	F	VI	S. Eiseb & G. Shihepo

SMM15863	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	V	S. Eiseb & G. Shihepo
SMM15814	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	IV	S. Eiseb & G. Shihepo
SMM15812	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15820	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15827	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15854	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15803	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15843	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	V	S. Eiseb & G. Shihepo
SMM15828	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15797	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	F	V	S. Eiseb & G. Shihepo
SMM15792	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	F	VI	S. Eiseb & G. Shihepo
SMM15844	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	VI	S. Eiseb & G. Shihepo
SMM15861	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15850	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15868	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	F	VI	S. Eiseb & G. Shihepo
SMM15866	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15790	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15787	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15846	*Mastomys coucha*	Omatjene Research	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo

		Station				
SMM15807	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM16150	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15811	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15856	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15867	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	F	III	S. Eiseb & G. Shihepo
SMM15835	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15834	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15839	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15786	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	F	III	S. Eiseb & G. Shihepo
SMM15793	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15857	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15842	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15852	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15809	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15831	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15804	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15862	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15869	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15864	*Mastomys coucha*	Omatjene	20°24'53.1''S	M	III	S. Eiseb & G.

		Research Station	16°28'44.5''E			Shihepo
SMM15816	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15825	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15799	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15805	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15855	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15849	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15794	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15865	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15815	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15795	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15821	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15823	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15836	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15802	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15845	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15791	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15869	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15822	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo

SMM15840	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15871	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15798	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15860	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15833	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15841	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15837	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15859	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15789	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
SMM15853	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SMM15848	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	U	III	S. Eiseb & G. Shihepo
SEG416	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	M	III	S. Eiseb & G. Shihepo
TM38834	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	M	VI	D. H. Gordon
TM37797	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	F	IV	D. H. Gordon
TM37796	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	F	IV	D. H. Gordon
TM37764	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	M	V	D. H. Gordon
TM37762	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	M	IV	D. H. Gordon
TM37755	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	M	IV	D. H. Gordon
TM37751	*Mastomys shortridgei*	Mahango Nature Reserve	18°10'S; 21°43'E	M	IV	D. H. Gordon
TM31167	*Mastomys legerae*	Shakawe, Botswana	1821Bd	M	IV	D. H. Davis
TM31165	*Mastomys legerae*	Shakawe, Botswana	1821Bd	F	IV	D. H. Davis
TM31164	*Mastomys legerae*	Shakawe, Botswana	1821Bd	M	IV	D. H. Davis

TM5204	*Mastomys angolensis*	Moombola, Angola	1114Cb	M	V	Mayer
TM6401	*Mastomys coucha*	Maun, Botswana	1923Cd	M	IV	Vernay-Lang Kalahari Expedition
TM6402	*Mastomys coucha*	Maun, Botswana	1923Cd	M	IV	Vernay-Lang Kalahari Expedition
TM6403	*Mastomys coucha*	Maun, Botswana	1923Cd	F	IV	Vernay-Lang Kalahari Expedition
TM6404	*Mastomys coucha*	Motlhatlogo, Botswana	2022Bd	F	V	Vernay-Lang Kalahari Expedition
TM6405	*Mastomys coucha*	Motlhatlogo, Botswana	2022Bd	M	IV	Vernay-Lang Kalahari Expedition
TM6406	*Mastomys coucha*	Kwai, Botswana	1923Ba	M	V	Vernay-Lang Kalahari Expedition
TM6408	*Mastomys coucha*	28 mile east of Maun, Botswana	2023Aa	M	III	Vernay-Lang Kalahari Expedition
TM6409	*Mastomys coucha*	25 mile east of Maun, Botswana	2023Aa	M	III	Vernay-Lang Kalahari Expedition
TM21682	*Mastomys*	Xwe, 30 miles on Tsau-Nonkaneng road, Botswana	1922Cd	M	V	
TM21710	*Mastomys*	Xwe, 30 miles on Tsau-Nonkaneng road, Botswana	1922Cd	F	VI	
TM21721	*Mastomys*	Kachikau Police Camp, Botswana	1824Ba	F	IV	
TM21723	*Mastomys*	Linyanti	1824Aa	M	V	P. J. Geldenhuys
TM21724	*Mastomys*	Linyanti	1824Aa		V	P. J. Geldenhuys
TM21730	*Mastomys*	Shakawe, Botswana	1821Bd	F	IV	P. J. Geldenhuys
TM21732	*Mastomys*	Xwe, 30 miles on Tsau-Nonkaneng road, Botswana	1922Cd	F	IV	
TM21760	*Mastomys*	Nonkaneng	1922Cb	F	III	R. Upton
TM21762	*Mastomys*	Nonkaneng	1922Cb	F	III	R. Upton
TM21851	*Mastomys*	Bodibeng, Lake Ngami, Botswana	2022Da	M	V	
TM21853	*Mastomys*	Danega, Botswana	1922Ac	F	V	P. J. Geldenhuys
TM21855	*Mastomys natalensis*	Kachikau, Botswana	1824Ab	F	IV	P. J. Geldenhuys

TM21857	*Mastomys*	Rakops, Botswana		M	IV	
TM21858	*Mastomys*	Danega, Botswana	1922Ac	M	V	P. J. Geldenhuys
TM21861	*Mastomys natalensis*	Kachikau, Botswana	1824Ab	M	IV	P. J. Geldenhuys
TM21864	*Mastomys*	Nokaneng village	1922Cb	F	III	P. J. Geldenhuys
TM21865	*Mastomys*	Mosetse 62 miles of Francis Town-Nata road, Botswana	2027Ca	F	IV	
TM21866	*Mastomys*	Gweta, Botswana	2025Aa	M	V	
TM21867	*Mastomys*	Gomare, Botswana	1922Ad	F	IV	P. J. Geldenhuys
TM21868	*Mastomys*	Komo, Botswana	2124Ba	F	V	
TM21870	*Mastomys*	Gweta, Botswana	2025Aa	F	V	
TM21871	*Mastomys*	Toteng, Botswana	2022Bd	M	VI	P. J. Geldenhuys
TM21872	*Mastomys*	Gweta, Botswana	2025Aa	M	IV	
TM21876	*Mastomys*	Bodibeng, Lake Ngami, Botswana	2022Da	M	V	
TM21877	*Mastomys*	Lothlokone, Botswana	2125Bc	M	IV	
TM21882	*Mastomys*	Gomare, Botswana	1922Ad	M	V	P. J. Geldenhuys
TM21883	*Mastomys*	Danega, Botswana	1922Ac	F	V	P. J. Geldenhuys
TM21885	*Mastomys natalensis*	Kachikau, Botswana	1824Ab	F	IV	P. J. Geldenhuys
TM21888	*Mastomys*	Danega, Botswana	1922Ac	F	IV	P. J. Geldenhuys
TM21905	*Mastomys*	Tsau, Ngamiland, Botswana	2022Ab	M	IV	R. Upton
TM21906	*Mastomys*	Toteng, Botswana	2022Bd		VI	P. J. Geldenhuys
TM21907	*Mastomys*	Namibia	1919Ac	F	VI	
TM33220	*Mastomys natalensis*	Popa Camp, Kavango, Namibia		F	VI	D. H. Gordon
TM33225	*Mastomys natalensis*	Mahango village, Kavango, Namibia	1821Ba	M	IV	D. H. Gordon
TM33226	*Mastomys natalensis*	Mahango village, Kavango, Namibia	1821Ba	F	IV	D. H. Gordon
TM33227	*Mastomys natalensis*	Mahango village, Kavango, Namibia	1821Ba	M	IV	D. H. Gordon
TM33229	*Mastomys*	Mahango	1821Ba	M	V	D. H. Gordon

	natalensis	village, Kavango, Namibia				
TM33233	*Mastomys natalensis*	Mahango village, Kavango, Namibia	1821Ba	M	III	D. H. Gordon
TM29002	*Mastomys coucha*	Vaalharts, South Africa	2724Da	M	IV	South African Health Department
TM29011	*Mastomys coucha*	Vaalharts, South Africa	2724Da	M	III	South African Health Department
TM29013	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	III	South African Health Department
TM29014	*Mastomys coucha*	Vaalharts, South Africa	2724Da	M	IV	South African Health Department
TM29021	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	III	South African Health Department
TM29022	*Mastomys coucha*	Vaalharts, South Africa	2724Da	M	III	South African Health Department
TM29026	*Mastomys coucha*	Vaalharts, South Africa	2724Da		IV	South African Health Department
TM29028	*Mastomys coucha*	Vaalharts, South Africa	2724Da	M	IV	South African Health Department
TM29185	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	IV	South African Health Department
TM29187	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	IV	South African Health Department
TM29198	*Mastomys coucha*	Vryburg, South Africa	2724Da	M	III	South African Health Department
TM29201	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	IV	South African Health Department
TM29183	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	V	South African Health Department

TM29186	*Mastomys coucha*	Vaalharts, South Africa	2724Da	M	IV	South African Health Department
TM29188	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	III	South African Health Department
TM29189	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	IV	South African Health Department
TM29192	*Mastomys coucha*	Kolhaarfarm, South Africa	2624Ab	F	V	
TM29194	*Mastomys coucha*	Hoogmoed, Vryburg, South Africa	2624Ad	F	VII	M. Gregor
TM29195	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	F	III	Wantenaar
TM29196	*Mastomys coucha*	Vaalharts, South Africa	2724Da	F	IV	South African Health Department
TM29199	*Mastomys coucha*	Vaalharts, South Africa	2724Da	M	IV	South African Health Department
TM29202	*Mastomys coucha*	De Noor, Vryburg, South Africa	2624Ac	F	IV	South African Health Department
TM29204	*Mastomys coucha*	Backhouse C. P., South Africa	2923Bb		IV	South African Health Department
TM29207	*Mastomys coucha*	Courans drift C. P., South Africa	3325Ad		IV	South African Health Department
TM29208	*Mastomys coucha*	Belvedere C. P., South Africa	2523Db		III	South African Health Department
TM29210	*Mastomys coucha*	Vryburg, South Africa	2624Ab	M	III	South African Health Department
TM29214	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	M	III	South African Health Department
TM29215	*Mastomys coucha*	De Bad C. P., South Africa	2824Cc		IV	South African Health Department
TM29219	*Mastomys coucha*	Vryburg, South Africa	2624Ab	F	III	South African

						Health Department
TM29220	*Mastomys coucha*	Kolhaarfarm, South Africa	2624Ab	F	IV	Wantenaar
TM29221	*Mastomys coucha*	Vryburg, South Africa	2624Ab		III	South African Health Department
TM29226	*Mastomys coucha*	Vaalharts, South Africa	2724Da	M	IV	South African Health Department
TM29232	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	M	IV	Wantenaar
TM29236	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	M	III	Wantenaar
TM29238	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	F	III	Wantenaar
TM29235	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	M	III	
TM29229	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	F	IV	Wantenaar
TM29230	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E		IV	Wantenaar
TM29234	*Mastomys coucha*	Kimberley, South Africa	27°28'S; 23°28'E		III	South African Health Department
TM29239	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	M	IV	Wantenaar
TM29240	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	F	III	Wantenaar
TM29242	*Mastomys coucha*	Kuruman, South Africa	27°28'S; 23°28'E	F	V	Wantenaar
TM32319	*Mastomys coucha*	2km north of Dordrecht, South Africa	3127Ac	F	V	South African Institute of Medical Research
TM32318	*Mastomys coucha*	Sterkstroom, South Africa	3126Da			
TM32320	*Mastomys coucha*	15km south of Dordrecht, South Africa	3126Bd	F	V	South African Institute of Medical Research
TM32323	*Mastomys coucha*	2km north of Dordrecht, South Africa	3127Ac	M	III	South African Institute of Medical Research
TM32326	*Mastomys coucha*	2km north of Dordrecht, South Africa	3127Ac	M	III	
TM29247	*Mastomys coucha*	Kimberley, South Africa	28°43'S; 24°46'E		IV	South African

						Health Department
TM33146	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	IV	Smithsonian Institution
TM33147	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	IV	Smithsonian Institution
TM33148	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	F	IV	Smithsonian Institution
TM33149	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	IV	Smithsonian Institution
TM33150	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	IV	Smithsonian Institution
TM33151	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	IV	Smithsonian Institution
TM33152	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	F	III	Smithsonian Institution
TM33153	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	F	V	University of Natal
TM33154	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	F	IV	University of Natal
TM33155	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	F	IV	University of Natal
TM33157	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	III	University of Natal
TM33165	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	V	Smithsonian Institution
TM33166	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	V	Smithsonian Institution
TM33167	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	V	Smithsonian Institution
TM33168	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	F	IV	Smithsonian Institution
TM33164	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	IV	Smithsonian Institution
TM33169	*Mastomys natalensis*	Darvill sewage works, Pietermaritzburg, South Africa	29°35'S; 30°25'E	F	IV	Smithsonian Institution
TM33170	*Mastomys natalensis*	Darvill sewage works,	29°35'S; 30°25'E	F	IV	Smithsonian Institution

		Pietermaritzburg, South Africa				
TM33163	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	F	IV	University of Natal
TM33308	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	V	D. H. Gordon
TM33310	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	IV	D. H. Gordon
TM33311	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	IV	D. H. Gordon
TM33312	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	F	IV	D. H. Gordon
TM33313	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	F	V	D. H. Gordon
TM33314	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	F	IV	D. H. Gordon
TM33316	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	IV	D. H. Gordon
TM33317	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	V	D. H. Gordon
TM33318	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	F	V	D. H. Gordon
TM33319	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	F	III	D. H. Gordon
TM33320	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	VII	D. H. Gordon
TM33321	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	F	V	D. H. Gordon
TM33322	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	V	D. H. Gordon
TM33323	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	IV	D. H. Gordon
TM32382	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	F	IV	DW143
TM32388	*Mastomys natalensis*	Umlalazi Nature Reserve, South Africa	2831Dd	M	IV	DW74
TM33424	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	F	V	D. H. Gordon
TM33425	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	F	V	D. H. Gordon
TM33426	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	V	D. H. Gordon
TM33427	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	V	D. H. Gordon
TM33428	*Mastomys natalensis*	Durban, South Africa	29°49'S; 31°01'E	M	V	D. H. Gordon
TM43112	*Mastomys natalensis*	Van Reenen, Wyford farm, South Africa	28°25'S; 29°26'E	M	IV	G. Bronner
TM43341	*Mastomys natalensis*	Van Reenen, Wyford farm, South Africa	28°25'S; 29°26'E	F	IV	G. Bronner
TM43345	*Mastomys*	Van Reenen,	28°25'S; 29°26'E	F	IV	G. Bronner

	natalensis	Wyford farm, South Africa				
TM43346	*Mastomys natalensis*	Van Reenen, Wyford farm, South Africa	28°25'S; 29°26'E	M	VI	G. Bronner
TM44376	*Mastomys natalensis*	Hluhluwe G. R., Natal, South Africa	28°04'62''S; 32°02'64''E	M	IV	G. Bronner
TM44377	*Mastomys natalensis*	Hluhluwe G. R., Natal, South Africa	28°04'62''S; 32°02'64''E	F	III	G. Bronner
TM44378	*Mastomys natalensis*	Hluhluwe G. R., Natal, South Africa	28°04'62''S; 32°02'64''E	F	IV	G. Bronner
TM44379	*Mastomys natalensis*	Hluhluwe G. R., Natal, South Africa	28°04'62''S; 32°02'64''E	F	IV	G. Bronner
TM44437	*Mastomys natalensis*	Van Reenen, Wyford farm, South Africa	28°25'S; 29°26'E	M	IV	G. Bronner
TM44438	*Mastomys natalensis*	Van Reenen, Wyford farm, South Africa	28°25'S; 29°26'E	F	III	G. Bronner
TM44439	*Mastomys natalensis*	Van Reenen, Wyford farm, South Africa	28°25'S; 29°26'E	M	IV	G. Bronner
TM44441	*Mastomys natalensis*	Van Reenen, Wyford farm, South Africa	28°25'S; 29°26'E	F	IV	G. Bronner
TM44440	*Mastomys natalensis*	Van Reenen, Wyford farm, South Africa	28°25'S; 29°26'E	M	V	G. Bronner
TM388	*Mastomys*	Potchefstroom, South Africa	26°41'S; 27°07'E		V	
TM389	*Mastomys*	Wonderfontein Lime Works, North-West Province, South Africa			V	
TM1341	*Mastomys*	Sandriver near Messina, South Africa	22°18’50”S; 30°7’41”E		V	
TM1463	*Mastomys*	Moord drift, Limpopo Province, South Africa	24°16'60"S; 28°57'0"E		V	
TM1794	*Mastomys*	Arnhemburg, Mpumalanga, South Africa	26°1'60"S; 30°49'60"E		V	
TM2454	*Mastomys*	Namutoni, Etosha National Park	18°48’S; 16°59’E		V	
TM3554	*Mastomys*	Quickborn, Okahandja district, Namibia	2117Aa		IV	

APPENDIX FOUR

SPECIMENS TRAPPED AND PROCESSED IN NAMIBIA

Fld no.	**Museum no.**	**Species**	**Locality**	**GPS coordinates**	**S**	**Age**	**Collector**
SE003	SMM15758	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE004	SMM15777	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE005	SMM15770	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE006	SMM15763	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE007	SMM15773	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE010	SMM15780	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE011	SMM15783	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE012	SMM15771	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE013	SMM15772	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE014	SMM15778	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller

SE015	SMM15775	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE026	SMM15764	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	f	a	S. Eiseb & U. Zeller
SE027	SMM15756	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	f	a	S. Eiseb & U. Zeller
SE028	SMM15757	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller
SE029	SMM15753	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller
SE030	SMM15782	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller
SE031	SMM15768	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	f	juv	S. Eiseb & U. Zeller
SE032	SMM15759	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller
SE033	SMM15755	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE034	SMM15779	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE035	SMM15769	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE036	SMM15781	*Mastomys natalensis*	5km south of Omatako-	17°58'45.0''S 20°27'26.0''E	f	a	S. Eiseb & U. Zeller

			Kavango rivers confluence				
SE037	SMM15762	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	f	a	S. Eiseb & U. Zeller
SE038	SMM15776	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & U. Zeller
SE039	SMM15765	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller
SE040	SMM15767	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	f	juv	S. Eiseb & U. Zeller
SE041	SMM15766	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller
SE042	SMM15774	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	f	a	S. Eiseb & U. Zeller
SE043	SMM15754	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller
SE044	SMM15896	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller
SE045	SMM15760	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	f	juv	S. Eiseb & U. Zeller
SE046	SMM15784	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	f	a	S. Eiseb & U. Zeller
SE047	SMM15761	*Mastomys natalensis*	5km south of Omatako-Kavango rivers	17°58'45.0''S 20°27'26.0''E	m	juv	S. Eiseb & U. Zeller

			confluence					
SEG068	SMM15724	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG069	SMM15933	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG070	SMM15738	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG071	SMM15905	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG073	SMM15904	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG074	SMM15930	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG075	SMM15909	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG076	SMM15728	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG077	SMM15937	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG079	SMM15939	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG080	SMM15745	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG082	SMM15934	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG083	SMM15929	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG084	SMM15911	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG085	SMM15981	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG086	SMM15903	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG087	SMM15740	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG088	SMM15731	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG089	SMM15925	*Mastomys*	Divundu	18°06'49.7''S	m	juv	S. Eiseb, U.

		natalensis	Irrigation Scheme	21°34'42.3''E			Zeller & G. Shihepo
SEG090	SMM15914	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG091	SMM15916	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG094	SMM15732	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG095	SMM15942	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG096	SMM15906	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG097	SMM15912	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG098	SMM15737	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG101	SMM15736	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG102	SMM15915	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG104	SMM15910	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG105	SMM15739	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG106	SMM15749	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG107	SMM15746	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG108	SMM15747	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG109	SMM15743	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG110	SMM15908	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG111	SMM15725	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG112	SMM15744	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo

SEG113	SMM15941	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG114	SMM15919	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG115	SMM15920	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG116	SMM15742	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG117	SMM15741	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG118	SMM15922	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG119	SMM15940	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG120	SMM15748	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG121	SMM15946	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG122	SMM15917	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG123		*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG124	SMM15730	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG125		*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG126	SMM15936	*Mastomys natalensis*	Divundu Irrigation Scheme	18°06'49.7''S 21°34'42.3''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG127	SMM15735	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG128	SMM15938	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG130	SMM15924	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG131	SMM15918	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG132	SMM15923	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	f	a	S. Eiseb, U. Zeller & G.

							Shihepo
SEG133	SMM15921	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	f	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG134	SMM15931	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG136	SMM15913	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG137	SMM15943	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG138	SMM15727	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG139	SMM15729	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	f	a	S. Eiseb, U. Zeller & G. Shihepo
SEG140	SMM15944	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG142	SMM15733	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG143	SMM15907	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG144	SMM15726	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG145	SMM15734	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	juv	S. Eiseb, U. Zeller & G. Shihepo
SEG146	SMM15926	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG147	SMM15935	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG148	SMM15945	*Mastomys natalensis*	Ngalla village	17°57'14.2''S 24°25'37.8''E	m	a	S. Eiseb, U. Zeller & G. Shihepo
SEG156	SMM16034	*Mastomys natalensis*	Andoni Plains, Etosha	18°30'03.6''S 16°44'38.9''E	f	a	S. Eiseb & G. Shihepo
SEG157	SMM16036	*Mastomys natalensis*	Andoni Plains, Etosha	18°30'03.6''S 16°44'38.9''E	m	a	S. Eiseb & G. Shihepo
SEG168	SMM16048	*Mastomys natalensis*	Andoni Plains, Etosha	18°30'03.6''S 16°44'38.9''E	f	juv	S. Eiseb & G. Shihepo
SEG169	SMM16001	*Mastomys natalensis*	Andoni Plains, Etosha	18°30'03.6''S 16°44'38.9''E	m	juv	S. Eiseb & G. Shihepo
SEG170	SMM16042	*Mastomys*	Andoni	18°30'03.6''S	m	a	S. Eiseb & G.

		natalensis	Plains, Etosha	16°44'38.9''E			Shihepo
SEG173	SMM15987	*Mastomys natalensis*	Namutoni, Etosha	18°48'25.9''S 16°56'22.3''E	m	a	S. Eiseb & G. Shihepo
SEG177	SMM15989	*Mastomys natalensis*	Namutoni, Etosha	18°48'25.9''S 16°56'22.3''E	f	a	S. Eiseb & G. Shihepo
SEG181	SMM15752	*Mastomys natalensis*	Namutoni, Etosha	18°48'25.9''S 16°56'22.3''E	U	juv	S. Eiseb & G. Shihepo
SEG182	SMM15988	*Mastomys natalensis*	Namutoni, Etosha	18°48'25.9''S 16°56'22.3''E	f	a	S. Eiseb & G. Shihepo
SEG185	SMM16026	*Mastomys natalensis*	Namutoni, Etosha	18°48'25.9''S 16°56'22.3''E	m	a	S. Eiseb & G. Shihepo
SEG186	SMM16028	*Mastomys natalensis*	Namutoni, Etosha	18°48'25.9''S 16°56'22.3''E	f	a	S. Eiseb & G. Shihepo
SEG187	SMM16020	*Mastomys natalensis*	Namutoni, Etosha	18°48'25.9''S 16°56'22.3''E	f	a	S. Eiseb & G. Shihepo
SEG188	SMM16024	*Mastomys natalensis*	Oshigambo village	17°51'17.6''S 16°05'10.2''E	m	a	S. Eiseb & G. Shihepo
SEG208	SMM15999	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	f	a	S. Eiseb & G. Shihepo
SEG209	SMM15751	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	m	juv	S. Eiseb & G. Shihepo
SEG211	SMM16044	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	m	juv	S. Eiseb & G. Shihepo
SEG212	SMM16008	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	m	juv	S. Eiseb & G. Shihepo
SEG214	SMM16065	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	m	a	S. Eiseb & G. Shihepo
SEG215	SMM15997	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	f	a	S. Eiseb & G. Shihepo
SEG217	SMM15019	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	m	a	S. Eiseb & G. Shihepo
SEG218	SMM15610	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	f	a	S. Eiseb & G. Shihepo
SEG219	SMM15948	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	f	a	S. Eiseb & G. Shihepo
SEG220	SMM15992	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	f	juv	S. Eiseb & G. Shihepo
SEG221	SMM16085	*Mastomys natalensis*	Etunda Irrigation Scheme	17°25'34.6''E 14°31'52.0''E	f	a	S. Eiseb & G. Shihepo
SEG222	SMM16016	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	a	S. Eiseb & G. Shihepo
SEG223	SMM16004	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	a	S. Eiseb & G. Shihepo
SEG224	SMM15932	*Mastomys*	Uniab river	20°13'00.8''S	m	a	S. Eiseb & G.

		coucha	mouth	13°12'30.8''E			Shihepo
SEG225	SMM15928	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	f	juv	S. Eiseb & G. Shihepo
SEG226	SMM16047	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	juv	S. Eiseb & G. Shihepo
SEG227	SMM16027	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	juv	S. Eiseb & G. Shihepo
SEG229	SMM15927	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	juv	S. Eiseb & G. Shihepo
SEG230	SMM16027	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	juv	S. Eiseb & G. Shihepo
SEG235	SMM16011	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	a	S. Eiseb & G. Shihepo
SEG240	SMM16031	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	f	a	S. Eiseb & G. Shihepo
SEG241	SMM15984	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	f	a	S. Eiseb & G. Shihepo
SEG242	SMM16051	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	juv	S. Eiseb & G. Shihepo
SEG255	SMM15750	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	juv	S. Eiseb & G. Shihepo
SEG265	SMM16023	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	juv	S. Eiseb & G. Shihepo
SEG266	SMM16059	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	m	juv	S. Eiseb & G. Shihepo
SEG267	SMM16045	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	f	juv	S. Eiseb & G. Shihepo
SEG268	SMM16052	*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	f	juv	S. Eiseb & G. Shihepo
SEG270		*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	f	a	S. Eiseb & G. Shihepo
SEG271		*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	f	a	S. Eiseb & G. Shihepo
SEG272		*Mastomys coucha*	Uniab river mouth	20°13'00.8''S 13°12'30.8''E	f	juv	S. Eiseb & G. Shihepo
SEG274	SMM15956	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG275	SMM15964	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	f	a	S. Eiseb & S. Hegarty
SEG276	SMM15949	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG277	SMM15960	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG278	SMM15893	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	f	a	S. Eiseb & S. Hegarty
SEG279	SMM15967	*Mastomys*	Gammams	20°32'01.7''S	m	a	S. Eiseb & S.

		coucha	sewerage works, Windhoek	17°01'53.1''E			Hegarty
SEG280	SMM15950	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG281	SMM15900	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG282	SMM15959	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG283	SMM15958	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG285	SMM15954	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	f	a	S. Eiseb & S. Hegarty
SEG286	SMM15957	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E			S. Eiseb & S. Hegarty
SEG287	SMM15955	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG288		*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG289	SMM15894	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	f	a	S. Eiseb & S. Hegarty
SEG290	SMM15899	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG291		*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG292	SMM15892	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG293	SMM15969	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG294	SMM15891	*Mastomys coucha*	Gammams sewerage	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty

			works, Windhoek				
SEG295	SMM15897	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG301	SMM15961	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG302	SMM15970	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG306	SMM15882	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG308	SMM15883	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG309	SMM15884	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	f	a	S. Eiseb & S. Hegarty
SEG310	SMM15885	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG311	SMM15872	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E			S. Eiseb & S. Hegarty
SEG312	SMM15873	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG313	SMM15874	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG314	SMM15875	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	a	S. Eiseb & S. Hegarty
SEG315	SMM15876	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	m	juv	S. Eiseb & S. Hegarty
SEG316	SMM15877	*Mastomys coucha*	Gammams sewerage works, Windhoek	20°32'01.7''S 17°01'53.1''E	f	a	S. Eiseb & S. Hegarty
SEG321	SMM15826	*Mastomys coucha*	Waterberg Plateau Park	20°25'35.2''S 17°21'14.6''E	m	a	S. Eiseb & G. Shihepo

SEG322	SMM15824	*Mastomys coucha*	Waterberg Plateau Park	20°25'35.2''S 17°21'14.6''E	m	a	S. Eiseb & G. Shihepo
SEG327	SMM15785	*Mastomys coucha*	Waterberg Plateau Park	20°25'35.2''S 17°21'14.6''E		juv	S. Eiseb & G. Shihepo
SEG338	SMM15849	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG339	SMM15798	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG341	SMM15857	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG342	SMM15862	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG343	SMM15859	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG344	SMM15823	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	juv	S. Eiseb & G. Shihepo
SEG345	SMM15852	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG346	SMM15868	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	f	a	S. Eiseb & G. Shihepo
SEG347	SMM15866	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E			S. Eiseb & G. Shihepo
SEG348	SMM15867	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	f	a	S. Eiseb & G. Shihepo
SEG353	SMM16150	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG358	SMM16158	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	f	a	S. Eiseb & G. Shihepo
SEG359	SMM15817	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG361	SMM15812	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG362	SMM15829	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG363	SMM15822	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG364	SMM15799	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG365	SMM15818	*Mastomys*	Omatjene	20°24'53.1''S	f	juv	S. Eiseb & G.

		coucha	Research Station	16°28'44.5''E			Shihepo
SEG366	SMM15832	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG367	SMM15855	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG368	SMM15820	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG369	SMM15811	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG370	SMM15831	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG371	SMM15803	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	juv	S. Eiseb & G. Shihepo
SEG372	SMM15794	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG373	SMM15833	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG374	SMM15815	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG375	SMM15850	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG376	SMM15789	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG377	SMM15861	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG378	SMM15825	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG379	SMM15864	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	juv	S. Eiseb & G. Shihepo
SEG380	SMM15847	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	f	a	S. Eiseb & G. Shihepo
SEG381	SMM15871	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG382	SMM15797	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	f	a	S. Eiseb & G. Shihepo
SEG383	SMM15788	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo

SEG384	SMM15790	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E			S. Eiseb & G. Shihepo
SEG385	SMM15841	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG386	SMM15869	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG387	SMM15863	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG388	SMM15802	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG389	SMM15792	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	f	a	S. Eiseb & G. Shihepo
SEG392	SMM15813	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG394	SMM15828	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG395	SMM15851	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG397	SMM15838	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG398	SMM15801	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG400	SMM15819	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG401	SMM15853	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E			S. Eiseb & G. Shihepo
SEG404	SMM15787	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG405	SMM15835	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG406	SMM15843	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG407	SMM15830	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG408		*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG409	SMM15836	*Mastomys coucha*	Omatjene Research	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo

			Station				
SEG410	SMM15800	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG411	SMM15844	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG412	SMM15865	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG413	SMM15807	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG414	SMM15810	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	juv	S. Eiseb & G. Shihepo
SEG415	SMM15805	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG416		*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG417	SMM15840	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG418	SMM15809	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG419	SMM15869	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG420		*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E			S. Eiseb & G. Shihepo
SEG421	SMM15796	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG422	SMM15846	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E			S. Eiseb & G. Shihepo
SEG423	SMM15860	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG424	SMM15804	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG425	SMM15827	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG426	SMM15854	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG429	SMM15808	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG433	SMM15821	*Mastomys*	Omatjene	20°24'53.1''S	m	a	S. Eiseb & G.

		coucha	Research Station	16°28'44.5''E			Shihepo
SEG435	SMM15856	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG438	SMM15834	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG439	SMM15806	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG440	SMM15837	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		a	S. Eiseb & G. Shihepo
SEG442	SMM15814	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG443	SMM15791	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG444	SMM15795	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	juv	S. Eiseb & G. Shihepo
SEG447	SMM15793	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG448	SMM15786	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	f		S. Eiseb & G. Shihepo
SEG449	SMM15816	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG450	SMM15845	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG451	SMM15842	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG452	SMM15858	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E	m	a	S. Eiseb & G. Shihepo
SEG453	SMM15848	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEG454	SMM15839	*Mastomys coucha*	Omatjene Research Station	20°24'53.1''S 16°28'44.5''E		juv	S. Eiseb & G. Shihepo
SEA003	SMM16251	*Mastomys natalensis*	Popa Falls Resort	18°07'17.4''S 21°35'03.1''E	m	a	S. Eiseb & A. Mbangu
SEA004	SMM16233	*Mastomys natalensis*	Popa Falls Resort	18°07'17.4''S 21°35'03.1''E	m	a	S. Eiseb & A. Mbangu
SEA005	SMM16234	*Mastomys natalensis*	Popa Falls Resort	18°07'17.4''S 21°35'03.1''E	m	a	S. Eiseb & A. Mbangu
SEA006	SMM16248	*Mastomys natalensis*	Popa Falls Resort	18°07'17.4''S 21°35'03.1''E	m	a	S. Eiseb & A. Mbangu
SEA007	SMM16245	*Mastomys*	Popa Falls	18°07'17.4''S	m	a	S. Eiseb & A.

		natalensis	Resort	21°35'03.1''E			Mbangu
SEA008	SMM16240	*Mastomys natalensis*	Popa Falls Resort	18°07'17.4''S 21°35'03.1''E	f	juv	S. Eiseb & A. Mbangu
SEA015	SMM16237	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & A. Mbangu
SEA016	SMM16252	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & A. Mbangu
SEA017	SMM16250	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & A. Mbangu
SEA018	SMM16247	*Mastomys natalensis*	5km south of Omatako-Kavango rivers confluence	17°58'45.0''S 20°27'26.0''E	m	a	S. Eiseb & A. Mbangu
SEA019	SMM16254	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	f	a	S. Eiseb & A. Mbangu
SEA020	SMM16242	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	m	a	S. Eiseb & A. Mbangu
SEA021	SMM16241	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	m	a	S. Eiseb & A. Mbangu
SEA022	SMM16249	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	f	a	S. Eiseb & A. Mbangu
SEA023	SMM16238	*Mastomys natalensis*	Omatako-Kavango rivers confluence	17°57'06.0''S 20°28'26.9''E	m	a	S. Eiseb & A. Mbangu
SEV002	SMM16260	*Mastomys natalensis*	Swamps at Shamvura village	18°02'10.5''S 20°50'37.4''E	f	a	S. Eiseb & V. Mughongora
SEV004	SMM16256	*Mastomys natalensis*	Swamps at Shamvura camp fence	18°01'57.2''S 20°51'39.2''E	m	a	S. Eiseb & V. Mughongora
SEV005	SMM16261	*Mastomys natalensis*	Swamps at Shamvura camp fence	18°01'57.2''S 20°51'39.2''E	m	a	S. Eiseb & V. Mughongora
SEV006	SMM16258	*Mastomys shortridgei*	Swamps at Shamvura camp fence	18°01'57.2''S 20°51'39.2''E	f	a	S. Eiseb & V. Mughongora
SEV007	SMM16259	*Mastomys*	Swamps at	18°01'57.2''S	m	a	S. Eiseb & V.

		shortridgei	Shamvura camp fence	20°51'39.2''E			Mughongora
SEV008	SMM16257	*Mastomys natalensis*	Swamps at Shamvura camp fence	18°01'57.2''S 20°51'39.2''E	f	a	S. Eiseb & V. Mughongora

APPENDIX FIVE

SPECIMENS TRAPPED AND PROCESSED IN BOTSWANA

Fld no.	Museum no.	Species	Locality	Coordinates	S	Age	Collector
BOT001		*Mastomys natalensis*	Drotsky's Cabins, Shakawe	18°24'58.8"S, 21°53'22.1"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT004	SMM16272	*Mastomys shortridgei*	Close to Shakawe Police Station, Shakawe	18°23'42"S, 21°51'13.7"E	F	Adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT005	SMM16268	*Mastomys natalensis*	Close to Shakawe Police Station, Shakawe	18°23'42"S, 21°51'13.7"E	F	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT006	SMM16274	*Mastomys natalensis*	Close to Shakawe Police Station, Shakawe	18°23'42"S, 21°51'13.7"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT007	SMM16264	*Mastomys shortridgei*	Close to Shakawe Police Station, Shakawe	18°23'42"S, 21°51'13.7"E	M	Adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT008	SMM16273	*Mastomys natalensis*	Close to Shakawe Police Station, Shakawe	18°23'42"S, 21°51'13.7"E	F	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT009		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT010		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT011		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	F	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT012		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	F	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT013		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Juv	S. Eiseb, A. Serogwe & J. Haradoes
BOT014		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT015		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT016		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT017		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	F	Adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT018		*Mastomys*	Sepopa	18°44'41.4"S,	M	Sub-	S. Eiseb, A.

		natalensis	Swamp Stop, Sepopa	22°11'48.7"E		adult	Serogwe & J. Haradoes
BOT019		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	F	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT021		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT022		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT023		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT024		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT025		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Sub-adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT026		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	M	Adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT027		*Mastomys natalensis*	Sepopa Swamp Stop, Sepopa	18°44'41.4"S, 22°11'48.7"E	F	Adult	S. Eiseb, A. Serogwe & J. Haradoes
BOT028		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT029		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT030		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT031		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT032		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	F	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT033		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Sub-adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT034		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	F	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT035		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J.

							Haradoes
BOT036		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT037		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Sub-adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT038		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT039		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Sub-adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT040		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT041		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT042		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT043		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	F	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT045		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT046		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	F	Adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT047		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT048		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	F	Adult	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT049		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT050		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J.

							Haradoes
BOT051		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT052		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT053		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes
BOT054		*Mastomys natalensis*	Thamalakane river, Maun	19°56'29.2"S, 23°29'40.5"E	M	Juv	S. Eiseb, M. Tswiio, A. Serogwe & J. Haradoes

APPENDIX SIX

SPECIMENS TRAPPED AND PROCESSED IN ANGOLA

Fld no.	Museum no.	Species	Locality	Coordinates	S	A	Collector
ANG003	SMM16280	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata	14°58'47.2"S, 13°26'19.9"E	F	A	S. Eiseb & L. Nghilundilua
ANG004	SMM16266	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata	14°58'47.2"S, 13°26'19.9"E	M	A	S. Eiseb & L. Nghilundilua
ANG005	SMM16281	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata	14°58'47.2"S, 13°26'19.9"E	M	J	S. Eiseb & L. Nghilundilua
ANG006	SMM16283	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata	14°58'47.2"S, 13°26'19.9"E	F	A	S. Eiseb & L. Nghilundilua
ANG008	SMM16282	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata	14°58'47.2"S, 13°26'19.9"E	M	A	S. Eiseb & L. Nghilundilua
ANG010	SMM16275	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata	14°58'47.2"S, 13°26'19.9"E	M	A	S. Eiseb & L. Nghilundilua
ANG011	SMM16271	*Mastomys natalensis*	Humpata Poligona Florestal; 4km W of Lubango on road to Humpata	14°58'47.2"S, 13°26'19.9"E	M	A	S. Eiseb & L. Nghilundilua
ANG016	SMM16265	*Mastomys kollmannspergeri*	Mbalanondolo village on banks of Rio Cubango; south of town Cahiungo	12°44'15.8"S, 16°18'00.2"E	M	A	S. Eiseb & L. Nghilundilua
ANG023	SMM16269	*Mastomys natalensis*	Longa village; on road between Menongue and Cuito Cuanavale	14°35'29.2"S, 18°27'43.4"E	F	J	S. Eiseb & L. Nghilundilua
ANG026	SMM16267	*Mastomys shortridgei*	Longa village; on road between Menongue and Cuito Cuanavale	14°35'29.2"S, 18°27'43.4"E	F	A	S. Eiseb & L. Nghilundilua