University of Venda
Creating Future Leaders

Université Fédérale
Toulouse Midi-Pyrénées

THÈSE

En vue de l'obtention du

DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par l'Université Toulouse 3 - Paul Sabatier

Cotutelle internationale : University of Venda

Présentée et soutenue par

Aluwani NENGOVHELA

Le 18 décembre 2018

3D Cranial Morphometry, Sensory Ecology and Climate Change in African Rodents

Ecole doctorale : **BSB - Biologie, Santé, Biotechnologies**

Spécialité : **ANTHROPOBIOLOGIE**

Unité de recherche :
AMIS - Laboratoire d'Anthropologie Moléculaire et Imagerie de Synthèse

Thèse dirigée par
José BRAGA et Peter TAYLOR

Jury
Mme Guila GANEM, Rapporteur
M. Steven GOODMAN, Rapporteur
Mme Sabrina RENAUD, Examinateur
M. José BRAGA, Directeur de thèse
M. Peter TAYLOR, Co-directeur de thèse

This dissertation is dedicated to the late Rod M Baxter and Mukondeleli J Mathivha

ACKNOWLEDGEMENTS

Firstly, I would like to thank the heavenly almighty God for giving me the strength and perseverance to see this through to finalization. I would like to thank my supervisors for their time and guidance: Prof Jose Braga (Université Toulouse III-Paul Sabatier) and Prof Peter J Taylor (University of Venda). I would also like to thank all the institutions, curators and collection managers who provided access to specimens and/or loans: Ditsong National Museum of Natural History, Pretoria (Dr Teresa Kearney), Muséum National d'Histoire Naturelle, Paris (Prof Christiane Denys) and Royal Museum for Central Africa, Tervuren (Prof Emmanuel Gilissen) and access to CT scanners: NECSA (Frikkie de Beer, Lunga Bam, Jakobus W. Hoffman, Mabuti Jacob Radebe) and CIRIMAT, Toulouse (Benjamin Duployer, Christophe Tenailleau). I would also like to offer my gratitude to my thesis advisory committee members (Prof Christiane Denys and Prof Alexandra Riberion). This project would not have been possible without the constant assistance of the Anthropologie Moléculaire et Imagerie de Synthèse (AMIS) lab technician Dr Jean Dumoncel. I would also like to thank my friends and family whom encouraged me and believed in me. Financial support for this work was provided by the Erasmus Mundus: AESOP+ programme and South African National Research Foundation (NRF).

PUBLICATION TIMELINE AND DISCLAIMER

Please note that chapter two to four of this thesis were written as stand-alone papers/chapters (see below), and therefore some repetitions were unavoidable.

Chapter 2: Aluwani Nengovhela, Christiane Denys & Peter J. Taylor. Effect of climate and life history on temporal changes in cranial size in rodents (in preparation).

Chapter 3: Aluwani Nengovhela, José Braga, Christiane Denys, Frikkie de Beer, Christophe Tenailleau, & Peter J. Taylor. 2018. Associated tympanic bullar and cochlear hypertrophy define adaptations to true deserts in African gerbils and laminate-toothed rats (Muridae: Gerbillinae and Murinae). *Journal of Anatomy*, doi: 10.1111/joa.12906 (included at the end of the manuscript)

Chapter 4: Aluwani Nengovhela. Endocranial size and shape in two African rodent subfamilies (Gerbillinae and Murinae) from virtual endocasts (in preparation).

TABLE OF CONTENTS

CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The order Rodentia is the most speciose group of mammals with muroids being the most diverse superfamily. Since they are represented in arboreal, semiaquatic, subterranean and terrestrial niches, rodents may exhibit morphological traits reflecting their adaptations to such diverse environments. This thesis focuses on the morphology of the endocranium, auditory bulla and cochlea in three tribes (Otomyini, Taterillini and Gerbillini) representing 10 species of African rodents, concentrating on their variability, function and adaptability, using micro-CT imaging and 3D shape comparative methods. Additionally, variations in cranial size were also studied in respective of global warming and climatic variables. Morphological changes/variations are a result of environmental change, therefore each chapter in this study details the effect of environmental change (in space and time) on different morphological traits i.e. general cranial size (chapter 2), cochlea and auditory bulla (chapter 3) and endocranial size and shape (chapter 4). With chapter 2 dealing specifically with climate change in its strict sense and the remaining two chapters looking at different environmental gradients.

Chapter 2 tests the applicability of the “third universal response to warming” (i.e. declining body size) and the Resource Rule in two murid subfamilies, Murinae and Gerbillinae. The study shows that the third response is not as universal as only one species conformed to this response. Further, food availability (Resource Rule) was shown to be the more important factor correlated with body size variations in rodent species than Bergmann’s Rule. Chapter 3 looks at the auditory bulla and cochlea, the morphological traits that play a role in hearing capabilities of rodents. I found, with some exceptions, that bulla and cochlea modifications between species could be explained by environment, phylogeny and/or allometry. In addition, I concluded that true desert adapted laminate-toothed rats and gerbils use both bulla and associated cochlea hypertrophy. Chapter 4 shows larger brain size in Taterillini and two species of Otomyini, with life histories and environment being the most probably factors responsible for this. Using a novel method of diffeomorphism (deformation models), there was more variation in endocranial morphology between the gerbils and laminate-toothed rats than within them with olfactory bulb, paraflocculi, and posterior ventral cortex showing the most variability. Overall, this thesis shows that variations in the morphological traits studied are strongly influenced by the environment and function.

CHAPTER ONE: INTRODUCTION

Climate change and rodents

Climate change is a well-known phenomenon worldwide even outside the scientific world with numerous policies proposed and implemented by different countries to lessen the emission of greenhouse gases (Steinitz, 2010). However, even if all the countries adhere to all the "green policies", the process of warming will continue although it may be at a slower and controlled pace (UN secretaty-General-2007). As Lovejoy & Hannah (2005) mentioned "it is now clear that climate change is the major new threat that will confront biodiversity this century". A plethora of studies have looked at the effect of climate change in mammals (Berteaux et al., 2006 and references therein; Hetem et al., 2014; Pacifici et al., 2017, Cianfrani et al., 2018). When faced with climate change, species or animal populations may respond differently; they may either shift their distribution range, adapt (genetic or phenotypic plasticity) or go extinct (global or local) (Parmesan, 2006; Fuller et al., 2010; Hetem et al., 2014). However, the most reported responses include shift in distribution range and phenotypic plasticity (e.g. changes in size or behaviour). An example of climate change consequence by rodents include: the extinction of the Bramble Cay *Melomys* (*Melomys rubicola*) from the Bramble Cay island (Gynther et al., 2016); range shifts in Texas, Senegal, Yosemite National Park, Californian mountains and South Africa to name a few (Cameron & Scheel, 2001; Thiam et al., 2008; Moritz et al., 2008; Rowe et al., 2015; Taylor et al., 2015); morphological evolution and variations (Renaud et al., 2005; Pergams & Lawler, 2009; see Chapter 2). However, the effect of climate change on morphology of rodents is examined in this thesis, climate change in time in its strict sense is investigated in chapter 2 and environmental variations in space and time (climate change) is investigated in chapter 3 and 4.

Rodent ecology

The order Rodentia is the most speciose group of mammals with muroids being the most diverse superfamily (Wilson et al., 2017). Rodents are highly variable in their ecological characters, which include diet, morphology, physiology, locomotion mode, behaviour and habitat (Nowak, 1999; Happold, 2013). Most rodents are terrestrial, with others being fossorial, saltatorial, arboreal, gliding, subterranean and semi-aquatic. Furthermore, they live in most habitats from hyper-arid deserts to hyper-mesic forests and most are habitat specific whilst a few are generalists (Happold, 2013). Rodents are broadly categorized as herbivores, granivores or frugivores with others being omnivorous and a few insectivores (Happold, 2013; Wilson et al., 2017). Rodents show phenomenal levels of morphological diversity that makes them a prime example taxon for the study of morphological variation.

Members of the Otomyini tribe are vole-like African rodents comprising two genera, i.e. *Parotomys* and *Otomys*. This includes our study species: *O. auratus*, *O. angoniensis*, *O. sloggetti*, *O. unisulcatus*, *O. helleri, O. barbouri* and *P. brantsii*. These taxa occupy mesic, montane and sub-montane, alpine, semi-arid and arid habitats and are exclusively herbivorous. They are terrestrial and vary in behaviour, with some being diurnal or crepuscular species and others being active 24 hours (e.g. *O. typus*). Additionally, members of the genus *Parotomys* are burrow-dwellers and they share a large suite of morphological traits with the genus O*tomys* except for their enlarged bulla (Clausnitzer, 2013; Jackson, 2013ab; Taylor, 2013ab; Yalden, 2013; Monadjem et al., 2015).

Among members of the subfamily Gerbillinae, the three studied species (*Desmodillus auricularis*, *Gerbilliscus leucogaster* and *Gerbillus nigeriae*) are endemic to Africa, omnivorous, nocturnal, terrestrial and burrow-dwelling. However, they differ in the size of the auditory bulla with *D. auricularis* having the most inflated (41% of the greatest skull length), *G. nigeriae* and *G. leucogaster* having moderately inflated bulla but the former has a fully pneumatized (air-filled) mastoid chamber, whereas the later has no inflated mastoid (Pavlinov, 2008). *Desmodillus auricularis* occupy arid gravel plains, areas with sparse grass or shrub cover, whilst *G. leucogaster* is associated with savannah habitats and *G. nigeriae* occupy sandy areas, cultivated and fallow lands (Dempster, 2013; Nel, 2013; Sicard, 2013; Monadjem et al., 2015).

In addition to the above species, two more in the subfamily Murinae were also included in the study, *Mastomys natalensis* and *Micalemys namaquensis* (*Aethomys namaquensis sensu lato*). Both species are endemic to Africa with the former being the most abundant and widely distributed. They are both omnivorous, nocturnal and terrestrial, though *M. namaquensis* is also semi-arboreal. *Mastomys natalensis* occupies a vast array of habitats e.g. savannah, grassland, fields, human settlements and it is commensal in West Africa (Fichet-Calvet & Rogers, 2009; Lalis et al., 2015), whilst *M. namaquensis* is mostly associated with savannah and semi-arid areas (Kesner et al., 2013; Leirs, 2013). Besides their negative effects (e.g. agricultural crop pest and reservoirs for zoonotic diseases/pathogens), rodents also have beneficial effects such as seed dispersal (Meerburg et al., 2009; Happold, 2013; Monadjem et al., 2015). These 12 taxa were chosen because they span a wide taxonomic and ecological range, and this provides environmental and phylogenetic gradients against which to test morphological changes in the selected morphological traits.

Phylogeny of Otomyini and Gerbillinae

The Otomyini (suborder: Myomorpha: family: Muridae) is a rodent tribe endemic to Africa, with most of its species occurring in Southern Africa (Musser & Carleton, 2005). The tribe is currently comprised of 33 species (Monadjem et al., 2015) compared to 17 recognized in Happold (2013) that are divided into two genera, i.e. *Otomys* and *Parotomys*. However, the phylogeny of the Otomyini is unresolved due to contradictory results from different types of data (Happold, 2013; Monadjem et al., 2015; Phukuntsi et al., 2016). Some studies have suggested that the genus *Otomys* is polyphyletic because species such as *O. unisulcatus* and *O. sloggetti* are more closely related to *Parotomys* than to *Otomys* (Taylor et al., 2009, 2011, 2014). Furthermore, Pocock (1976) recognized the existence of three genera within Otomyini i.e. *Otomys, Parotomys* and *Myotomys* (which includes *O. sloggetti* and *O. unisulcatus*)*.* Recently, *O. auratus* has been elevated to species level, having been a synonym of *O. irroratus*, following information gathered from molecular, chromosomal and morphometric analyses (Taylor et al., 2009; Engelbrecht et al., 2011).

The subfamily Gerbillinae (suborder Myomorpha and family Muridae) consists of 103 species (16 genera) of murid rodents that primarily inhabit mostly arid, open regions including deserts, grasslands and savannahs, throughout Africa and Asia (Nowak, 1999; Musser & Carleton, 2005). Inflated tympanic bulla is one of the most characteristic features of this subfamily (Lay, 1972). However, the systematics of this subfamily is still intensely debated at various taxonomic levels (Abiadh et al., 2010; Alhajeri et al., 2015; Ndiaye et al., 2016). This family consists of different tribes with Taterillini (e.g. *Gerbilliscus* and *Desmodillus*) and Gerbillini (*Gerbillus*, Pavlinov, 2008) the focus of this study. *Gerbilliscus leucogaster* and *D. auricularis* are more closely related in the phylogenetic tree as opposed to *G. nigeriae*. *Gerbillus* was once considered as one genus, including *Dipodillus*, but then split into distinct genera, on morphological grounds (Musser & Carleton 2005; Pavlinov, 2008). However, molecular studies suggest this distinction should not be maintained (Abiadh et al., 2010; Ndiaye et al., 2012; Alhajeri et al., 2015).

Functional and auditory morphology in rodents

Animals vary in form and their functions and for a long time biologists have been studying this relationship and inferring functions from form (Lauder et al., 1995, and references therein). The most famous example of the relationship between form and function being the Darwin finches, which are characterized by a remarkable variety in beak form and function (Podos & Nowicki, 2004). Morphology in organisms is often assumed to reflect habitat adaptations and phylogenetic history and understanding how these organisms adapt to their environment is important in ecological research (Wainwright & Reilly, 1994; Alhajeri, 2014). Since it is believed that ecological and behavioural factors may influence variations in sensory morphology (Moulton, 1967; Lay, 1972; Jones & Teeling, 2006), it is essential to assess the ecological functions of some of the sensory structures. Therefore, this section will focus on the form and function of the rodent inner ear and auditory bulla (see chapter 3 for a review of functional morphology of the auditory structures).

A hypertrophied bulla, more common in desert rodent species, has been linked to increased auditory sensitivity, which have been hypothesized to help in predator avoidance in open habitats and interspecific communication (Lay, 1972; Webster & Webster, 1975; Dempster, 2018). However, not only has the inflated bulla been correlated with arid environments but also the increased anatomical specialization of middle and inner ear anatomy, hence, increased auditory sensitivity (Lay, 1972; Webster & Webster, 1975). Consequently, studies on the functional morphology of the inner ear, middle ear and auditory bulla in fossorial, subterranean and epigeic rodents have been numerous (Lay, 1972; Webster & Webster, 1975; Lange et al., 2004; Francescoli et al., 2012; Tabatabaei-Yazdi et al., 2015; Mason, 2016), with different causal links proposed/mentioned.

Rationale for the study and structure of thesis

Morphological variation has been observed in plants, invertebrates, amphibians, reptiles, birds, and mammals (Holmes et al., 2016). In rodents, this type of variation is well documented, probably because of their relatively small size, short generation length and life spans, as well as because of the large number of specimens curated in natural history museum collections (Holmes et al., 2016). However, even though studies on variation of polygenic traits, like body size or brain size, are numerous, it is difficult to determine if this variation is genetically and/or plastically controlled (Pergams & Lacy, 2007; Gardner et al., 2011). In any case, the influence of factors such as phylogeny, climatic variables, environmental influences/change, life histories and climate change on morphology is well established (Stumpp et al., 2016). For example, body size variation have been linked to climate change, climatic variables and increased food availability (Yom-Tov & Geffen, 2011; McNab, 2010; Alhajeri et al., 2016; Chapter 2); brain size variation to life history traits, phylogeny, motor/sensory specializations and environment (Mace et al., 1981; Bernard & Nurton, 1993; Hefner & Hefner, 1984; chapter 4); and bulla size, middle and inner ear variation linked to phylogeny, ontogeny and environment (Lay, 1972; Lange et al., 2004; Liao et al., 2007; chapter 3). As mentioned in Albelson (2016) and Sol et al. (2008) variation in brain size can be used in estimating species extinction vulnerability and survival of animals in novel environments. Linzmeier & Ribeiro-Costa (2011) found variation in body size can be used to assess environmental quality (Madliger, 2012), and studying sensory ecology can be useful in understanding how organisms gain information from their environment, and how this information may be interpreted. Thus, integrating information from these kinds of studies may be helpful in management strategies, particularly in Africa where the natural environment is more susceptible to change (Gemeda & Sima, 2015). This kind of information can be used in conservation management (Van Dyck, 2012; Madliger, 2012). Additionally, morphological studies can provide insight into evolutionary theory and processes and can help in tracking climate change.

Interestingly the cranium is one of the most studied structures by anatomists and functional morphologists and a wealth of knowledge has been contributed in order to understand the complex structure that houses the brain, major sensory organs and masticatory apparatus (Hanken & Hall, 1993). Additionally, different skull measurements (e.g. zygomatic breadth, greatest length of the skull, interorbital constriction, length of the upper premolar, skull centroid size and etc.) or combination of measurements has been used to evaluate skull size, which has been used as a proxy for body size (Yom-Tov et al., 2007, 2010; Millien et al., 2017). The skull therefore serves a crucial role and provides a platform to explore hypothesis relating to adaptation (Hanken & Hall, 1993). This thesis is structured into five chapters: the present introductory chapter and a general discussion and conclusion chapter (chapter 5) and the main body, comprising of three chapters (chapters 2 to 4). The main body chapters are written as manuscripts for publication, of which chapters 2 and 3 have been or will be submitted for publication to *Global Ecology and Biogeography* and *Journal of Anatomy*, respectively. Because of the format used, there is some repetition of introductory material and methodological detail. The figures and tables are numbered in sequence for each chapter and not for the complete thesis. The appendices are also grouped based on the chapter they belong. The references for all the chapters are grouped together in the reference section, and the pages of the thesis are numbered sequentially.

Study objectives/main objectives for each chapter/Aim and objectives

The aim of this study was to investigate the effect of environmental change on different morphological traits of African rodent taxa spanning a wide taxonomic and ecological range, using both traditional and advanced 3D morphometric approaches. The results of this thesis are contained in chapters 2, 3 and 4 and each chapter objectives are as follows:

In chapter 2 -- I tested the general morphological responses (cranial size) of several African rodents from different ecological backgrounds over time. A decline in body size has been inferred as the "third universal response to warming" (Gardner et al., 2011), therefore, the general applicability of this response was tested. In addition, I explored body size variation in commensal and non-commensal populations based on the Resource Rule, which posits that "mammalian species will become larger or smaller depending on the size, abundance and availability of resources" (McNab, 2010).

In Chapter 3 -- I examined the hearing capabilities of 10 species of rodents (gerbils and laminate-toothed rats) by investigating the eco-morphological functions of the cochlea and inflated bulla. It has been suggested previously that hypertrophied bulla in desert rodents may be linked to specialized hearing abilities and predictions on the hearing capabilities of mammal species have been proposed from observations on gross features of the cochlea (Lay, 1972; Braga et al., 2015). Therefore, I tested this and other hypotheses by detailing morpho-functional variations in bulla size and cochlea parameters of gerbils and laminate-toothed rats.

In Chapter 4 -- I investigated variation in endocranial size and shape in 10 species of rodents (gerbils and laminate-toothed rats) and inferred eco-morphological functions on the observed variation. Previously, variations in brain size have been associated with habitat type, diet, activity (diurnal/nocturnal) and lifespan with larger brain size correlated with arboreality, omnivorous, nocturnality, longer lifespan (Mace et al. 1981) and high elevation (Sayol et al., 2016). Therefore, I tested environmental variables influence on brain size and infer morpho-functions from the body mass-endocranial volume relationship.

CHAPTER TWO: EFFECT OF CLIMATE AND LIFE HISTORY ON TEMPORAL CHANGES IN CRANIAL SIZE IN RODENTS

SUMMARY

Temporal changes in body size have been documented in a number of rodent species, with different contested mechanisms being suggested to explain these changes. Among these are climate warming (in conjunction with Bergmann’s Rule), the Resource Rule, James Rule, competition, predation risk, human population density, island effects and others. Taking advantage of museum collections spanning the last 100 years, we investigated geographical and temporal variation in cranial size (a proxy for body size) in six African rodent species of varying life history, range size and habitat from two murid subfamilies, Murinae (*Otomys unisulcatus, Parotomys brantsii, Micaelamys namaquensis*, *Mastomys natalensis*) and Gerbillinae (*Gerbilliscus leucogaster, Desmodillus auricularis*). Two species, *M.natalensis* and *O. unisulcatus* showed significant temporal changes in body size, with the former increasing and latter decreasing, in relation with climate warming. Only two species (*M. namaquensis* and *M. natalensis*) showed significant latitudinal and longitudinal trends in skull length linked to rainfall and temperature. As expected from the Resource Hypothesis, commensal (West African) populations of *M. natalensis* were significantly larger-sized than non-commensal (East/Southern Africa), however, non-commensal populationsshowed no temporal response. To text in a general manner the possible effect of different lifehistory predictors on the probability of a temporal response, we incorporated our data into ameta-analysis based on published literature on temporal responses in rodents, resulting in a dataset for 45 species from six families worldwide. Among 45 species tested, 25 showed nosignificant change, seven showed a significant increase in size, and 13 showed a decline insize. Using a binomial logistic regression model, we found that none of our chosen predictorscould significantly explain the probability of a temporal response.

INTRODUCTION

The Intergovernmental Panel on Climate Change (IPCC, 2014) reported a global surface temperature increase of 0.08-0.14°C per decade between 1950 and 2012 and the increases are predicted to rise by 2°C by the year 2100. Africa is believed to be warming faster than the global average (Collier et al., 2008; Gemeda & Sima, 2015) with a predicted increase in temperature by 2-6°C within the next 100 years (Awojobi & Tetteh, 2017). Rainfall is also expected to show several shifts, with certain areas becoming drier and others wetter and experiencing more frequent flooding (Hulme et al., 2001; Collier et al., 2008) The wide spread effects of anthropogenic climate warming on biodiversity and ecosystems is undeniable, with differing observed responses. Global warming can result in phenological changes (e.g. Diamond et al., 2011; Miller-Rushing & Primack, 2008), species distributional range shifts (e.g. Walther et al., 2002; Parmesan & Yohe, 2003; Hickling et al., 2006; Monadjem et al., 2013; Taylor et al., 2015, 2016) and/or decreasing body size (e.g. Daufresne et al., 2009; Gardner et al., 2011; Sheridan & Bickford, 2011). The above-mentioned responses are regarded collectively as the universal ecological response to climate change (Daufresne et al., 2009; Ohlberger, 2013).

Recently, morphological responses to climate change (usually entailing body size) have received growing interest, with changes reported in both aquatic and terrestrial environments (Gardner et al., 2011; Sheridan & Bickford, 2011). Body size varies geographically and temporally within species (Yom-Tov & Yom-Tov, 2004, 2005, 2012; Yom-Tov et al., 2006; McNab, 2010; Yom-Tov & Geffen, 2011; Nengovhela et al., 2015; Alhajeri & Steppan, 2016; Stumpp et al., 2016) in response to environmental variables including ambient temperature and precipitation (Bergmann, 1847; James, 1970; Blackburn et al., 1999; Blois et al., 2008), food availability (Yom-Tov & Yom-Tov, 2004, 2005; Yom-Tov et al., 2003, 2010; McNab, 2010), predation regimes (Gosler et al., 1995), habitat fragmentation (Schmidt & Jensen, 2003) and competition (Raia & Meiri, 2006; Meiri et al., 2007). Different mechanisms have been advanced to explain these effects, most commonly, Bergmann's Rule, which states that individuals under warmer climate should be smaller in body size as compared to individuals in colder climates (Bergmann, 1847; Mayr, 1956). Bergmann's Rule is suggested to apply temporally in the face of global climate warming in a range of animals including insects, birds, rodents and salamanders (Babin-Fenske et al., 2008; McCoy, 2012; Caruso et al., 2014; Blanckenhorn, 2015; Nengovhela et al., 2015). However, its authenticity, general applicability and ultimate causation have been questioned (Calder, 1984; Scholander, 1955; McNab, 1971; 2010; Millien et al., 2006; Yom-Tov & Geffen, 2006; Gardner et al., 2011; Teplitsky & Millien, 2014). Studies contradicting Bergmann's Rule show an increase in size with increasing temperature, either spatially or temporally, e.g. Norwegian and Swedish otters, Alaskan masked shrews (*Sorex cinereus*), Japanese mice (*Apodemus speciosus*) and red foxes (*Vulpes vulpes*) (Yom-Tov & Yom-Tov, 2004, 2005, 2012; Yom-Tov et al., 2006, 2010). Reasons for such increases in size with time could be due to factors such as improved food availability, urbanization and reduced energy expenditure (Yom-Tov et al., 2010; Yom-Tov & Yom-Tov, 2005).

Rodents are considered as ideal model animals because of their small size, short life spans, small dispersal distances and fast generation time as this may cause rapid morphological changes (Poroshin et al., 2010) and adaptive convergence (Samuels, 2009), which may be exacerbated by global environmental changes. Some species of rodents alter their morphology in response to extensive warming, whereas others do not (Koontz et al., 2001). In this study, we used museum collections to investigate the morphological response of six species of African Muridae rodents to global climate warming. These species were chosen because they cover different phylogenetic lineages, habitats and life history attributes to test the importance of these as potential predictors of the occurrence and magnitude of temporal effects on body size (estimated by skull length). We predict that: (1) body size of rodents would decrease with time (year of collection), in accordance with the “third universal response to climate warming”; (2) body size would decrease with increasing temperature and increase with an increase in rainfall; (3) body size of commensal species (in our dataset, West African populations of *Mastomys natalensis*) would firstly have higher mean body size compared to non-commensal populations and secondly, increase with time due to increased human population densities and agricultural production with time, hence increased food availability (i.e. Resource Rule which posits that “mammalian species will become larger or smaller depending on the size, abundance and availability of resources”); (4) differences in the magnitude of the temporal response would be expected between species based on differences in phylogeny and life history attributes such as body mass (hence BMR), litter size, and r versus k-selection. The last prediction is tested both by our choice of African muroid rodents species, as well as by conducting a global meta-analysis of all studies conducted on temporal response of rodents based on an exhaustive literature search.

METHODS

Specimens sampled

A total of 739 skulls of rodents of two murid subfamilies, Murinae (*Otomys unisulcatus, Parotomys brantsii, Micaelamys namaquensis, Mastomys natalensis*) and Gerbillinae (*Gerbilliscus leucogaster, Desmodillus auricularis*) were measured (see Table 2.1 and Table A.1) from the Ditsong National Museum of Natural History (formerly Transvaal Museum: TM) in South Africa, Muséum National d'Histoire Naturelle, Paris, France (MNHN) and Musée Royal de l’Afrique Centrale (Tervuren, Belgium). All specimens were aged based on the lamina wear i.e. for Otomyini individuals were assigned to a relative age class of 1 (youngest) to 5 (oldest) based on tooth wear and skull shape (Taylor & Kumirai, 2001) with class 4 and 5 being adult; as for

Gerbillinae the age classes were also established according to the degree of lamina wear, with classes A-D where A represents the class with the greatest tooth wear following a system of Bates (1985); and a class of I (youngest) to VI (oldest) for *Micaelamys* and *Mastomys*, with class IV-VI being adults (Chimimba & Dippenaar, 1994). The sampling had a fair representation of different periods.

Table 2.1. Composition of samples used in this study and their year of collection interval.

Genus	Species	No of specimens measured	Year of collection interval
Otomys	*unisulcatus*	102	1903-1992
Parotomys	*brantsii*	59	1902-1998
Gerbilliscus	*leucogaster*	132	1905-1997
Desmodillus	*auricularis*	94	1903-1996
Mastomys	*natalensis*	210	1907-2013
Micaelamys	*namaquensis*	142	1906-2003

Morphology

Six cranial variables (mandible and cranium) were taken to measure skull size by AN with the digital callipers to the nearest 0.01 mm: greatest length of skull (GLS), nasal width (NAW), braincase width (BW), zygomatic width (ZYW), interorbital constriction (IOC) and the maxillary tooth row length (MXTRL) (Taylor & Kumirai, 2001; Figure A.1). We used principal component analysis (PCA) to combine the information of the six skull measurements (log transformed for normality) into a single variable for each species (PC.1, Yom-Tov & Yom-Tov, 2012). This is because all our six cranial variables were related to each other and PC.1 show a measure of size as all the variables loaded positive and high (Delcros, 2012; Figure A.2). Therefore, the final analyses were limited to PC.1. The studied species distribution map was constructed using specimen locality data (Figure 2.1).

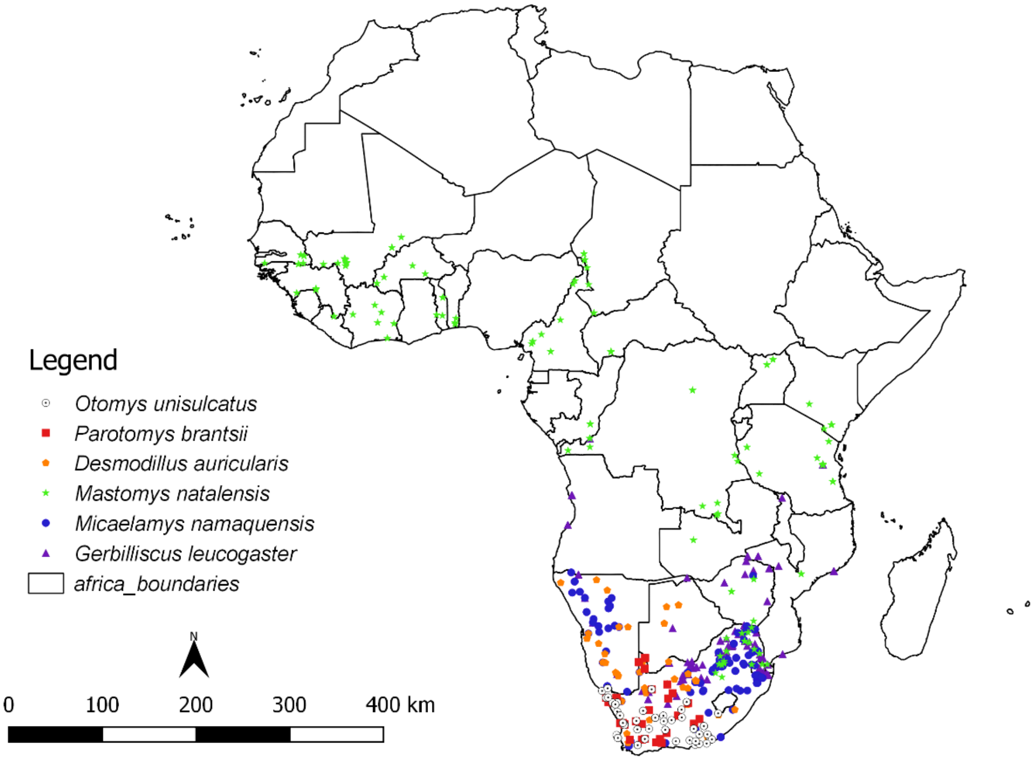


Figure 2.1. Map showing location of collecting localities of the studied species in Africa.

Data analysis

Firstly, sexual size dimorphism was tested using PC.1 as an indicator of size with t-test. None of the analyses showed any sexual size dimorphism, therefore the data for males and females were all pooled together. Regression analyses of PC.1 were performed with R (R Development Core Team, 2012). Both simple and multiple linear models were used to assess the relationship between PC.1 (i.e. proxy for body size) with seven predictor variables i.e. relative age of specimens (tooth-wear class), year of collection, geographical (elevation, latitude and longitude) and environmental (mean annual temperature (Bio1) and annual precipitation (Bio12)) variables. Elevation, Bio1 and Bio12 were obtained from the Worldclim database (Hijmans et al., 2005) and ArcMap was used to extract these variables for each specimen locality. Nine linear models were built for each species with seven involving individual variables a global model that combines all the variables, and the best model determined by ranking all subsets of variables according to their Aikaike information criterion (AIC) values. The model with the lowest AIC score was chosen as the most robust model. The model results showed significant effects of tooth-wear class, latitude and longitude on PC.1; to correct for these effects, the effectof temporal changes (year of collection) on PC.1 residuals obtained after multivariate linearregression on latitude, longitude and tooth-wear class was tested.

Additionally, we also tested body size variation in a partly commensal rodent (*M. natalensis*) by subdividing our data into West and South/East Africa samples. In West Africa tropical forest, *M. natalensis* tends to be commensal (Fichet-Calvet & Rogers, 2009; Lalis et al., 2015). In Eastern and Southern Africa savannas, *M. natalensis* frequently occupies crop fields where it is a crop pest but it seldom enters buildings or becomes commensal (Leirs et al., 1996; Monadjem et al., 2011; Mulungu et al., 2015). Based on these, we used Olson et al. (2001) ecoregions (forests versus savannas) to help us divide localities of the species into two groups: commensal (forest) and non-commensal (savannah), see Figure A.3.

RESULTS

Significant differences in cranial size (PC.1) between relative age classes were documented in all six species, in *Micaelamys namaquensis* (explaining 15% of the variation), *Gerbilliscus leucogaster* (explaining 7% of the variation), *Desmodillus auricularis* (explaining 21% of the variation), *Mastomys natalensis* (explaining 3% of the variation), *Otomys unisulcatus* (explaining 56% of the variation), and *Parotomys brantsii* (explaining 47% of the variation) (Table 2.2). As expected in all the species mean cranial size values increased significantly from younger to older individuals (Figure A.4).

In *M. namaquensis*, latitude, longitude and rainfall were all significantly correlated with PC.1 with latitude and temperature negatively, longitude and rainfall positively. Latitude explained 11%, longitude 26%, temperature 8% and rainfall 25% of the variance in cranial size respectively; cranial size therefore decreased with increasing latitude and temperature and increased with increasing longitude and rainfall (Table 2.2, Figure 2.2).

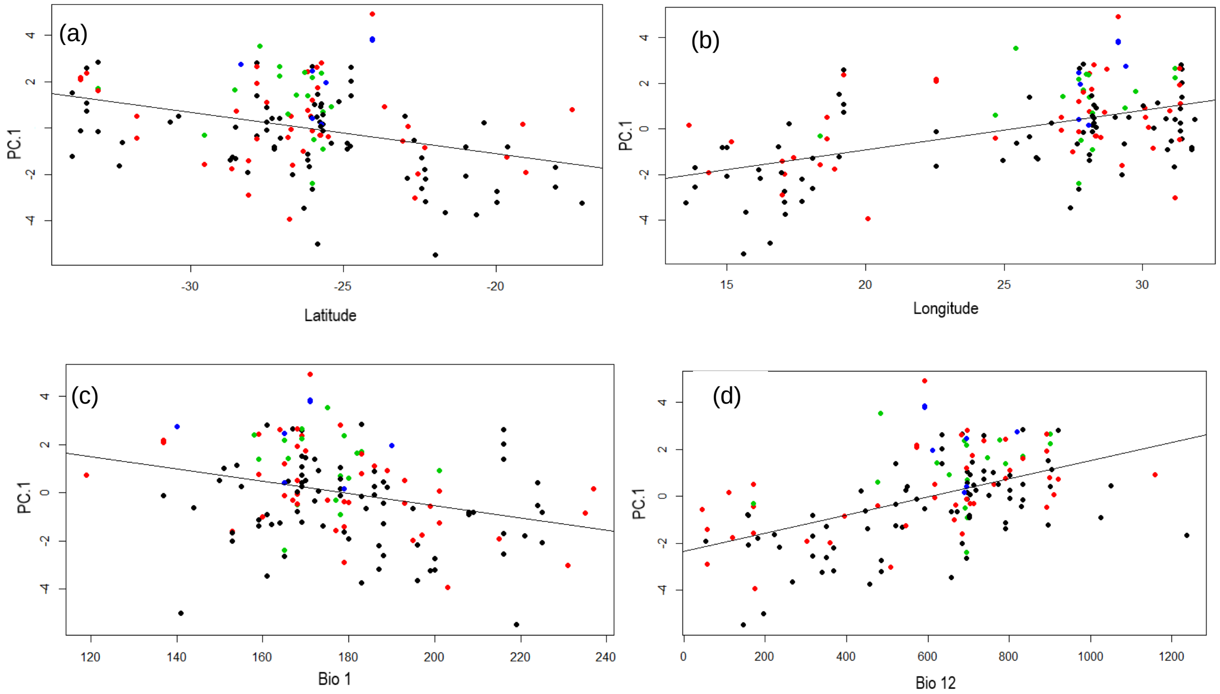


Figure 2.2: Scatterplots and corresponding regression lines between (PC.1) and latitude (a), longitude (b), mean annual temperature (c) and total annual rainfall (d) in *Micaelamys namaquensis*.

Similarly, *M. natalensis* showed a similar trend with latitude, longitude and rainfall significantly correlated with PC.1. Cranial size increased with increasing latitude, and rainfall and decreased with increasing longitude. Latitude explained 7%, longitude 13% and rainfall 8% of the variance in cranial size, respectively (Table 2.2, Figure 2.3). The remaining four species (*D. auricularis, G. leucogaster, O. unisulcatus* and *P. brantsii*) showed no significant correlation with the above variables (p > 0.05) except for *G. leucogaster*, for which rainfall and longitude were positively correlated with PC.1 explaining 10% and 17% of the variance (Table 2.2), respectively. For both *M. namaquensis* and *M. natalensis*, the best model having the lowest AIC value involved all the predictor variables (global), whilst for *D. auricularis*, the best models involved TWCLS only, for *O. unisulcatus* and *P. brantsii* the best model involved five variables (elevation, year, temperature, rainfall and TWCLS) and for *G. leucogaster* the best model involved four variables (latitude, longitude rainfall and TWCLS). The best model considerably out-performed the global model containing all seven predictor variables in all species except *M. namaquensis* and *M. natalensis*.

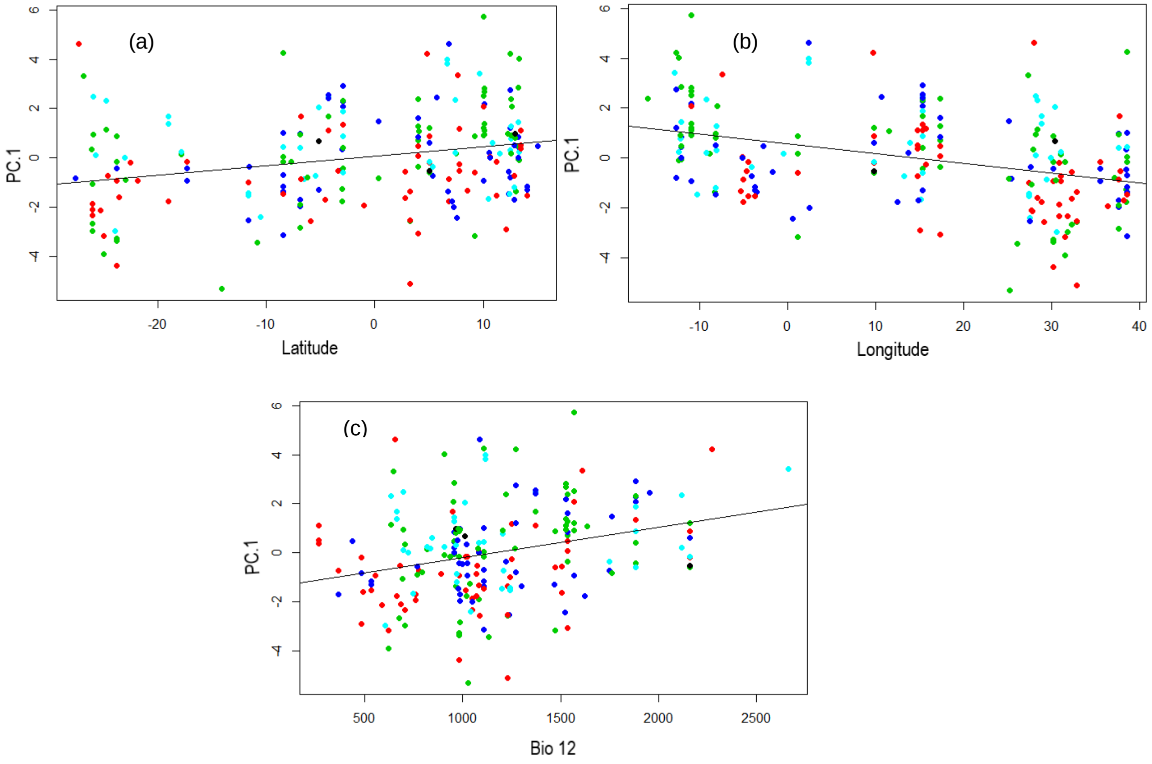


Figure 2.3: Scatterplots and corresponding regression lines between skull size (PC.1) and latitude (a), longitude (b), and total annual rainfall (c) in *Mastomys natalensis*.

In *M. natalensis*, after correcting for TWCLS, latitude and longitude, year of collection was significantly positively correlated with PC.1 ($r^2_{adj} = 0.07$, $p = 0.00006$) (Figure 2.4a) and in *O. unisulcatus*, after correcting for the same variables, year of collection was marginally significantly inversely correlated with PC.1 ($r^2_{adj} = 0.05$, $p = 0.036$) (Figure 2.4b). PC.1 of non-commensal *M. natalensis* population showed no significant change ($p > 0.05$), whilst the commensal populations were significantly positively correlated with year of collection (PC.1 = +0.038(Year) – 75.304, r^2_{adj} = 21%, $p < 0.0001$). Similarly, the t-test comparing adult (toothwear class >5) of West African commensal (Y) and East/Southern African non-commensal (N) populations of *M. natalensis* was also significant (t-value = 3.812, p = 0.0003, Figure A.5).

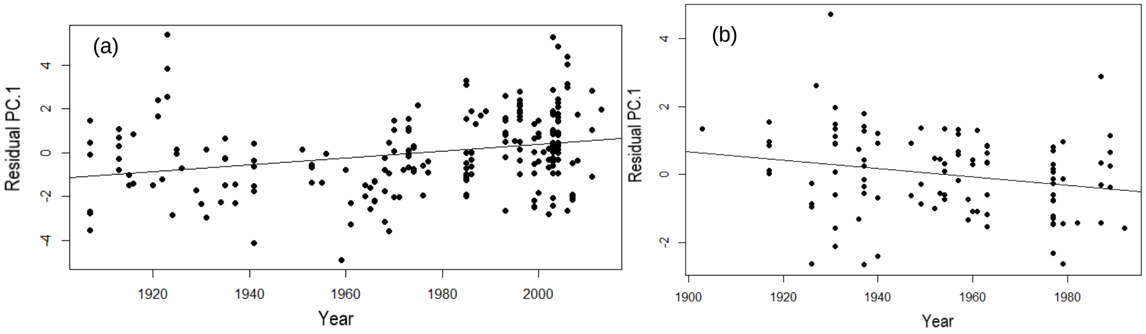


Figure 2.4: Temporal changes in cranial size in *Mastomys natalensis* [y = -30.79+0.016x, (a)] and *Otomys unisulcatus* [y = 23.75-0.012x, (b)]. Scatterplot represent the relationships between year of collection and residuals (corrected for tooth-wear class, latitude and longitude) of skull size (PC.1).

To test generally the possible effect of different life history predictors on the probability of a temporal response, we incorporated our data into a meta-analysis based on published literature of temporal responses in rodents around the world, resulting in a dataset for 45 species from seven families. Among 45 species tested, 25 showed no significant change (mostly from the families Cricetidae and Muridae), seven showed a significant increase in size (families: Muridae, Sciuridae and Spalacidae), and 13 showed a decline in size (families: Muridae and Cricetidae). Using a binomial logistic regression model, we found that none of the several tested predictors (i.e. maximum latitude, range size area, r.k selection, fossoriality, high-elevation, habitat specialist, commensal, desert adapted, mean body mass and mean litter size) could significantly explain the probability of a rodent species to show a temporal effect on skull size or not (Table A.2).

Table 2.2. Akaike's information criterion (AIC) values, coefficients of determination (r^2) and degrees of freedom (df) for nine models per species fitted to explain changes in greatest length of the skull of six species (*Micaelamys namaquensis*, *Gerbilliscus leucogaster*, *Desmodillus auricularis*, *Mastomys natalensis*, *Otomys unisulcatus* and *Parotomys brantsii*). The best model (with the lowest AIC value) is shown in bold for each species. *denotes $p < 0.05$. Climate values were downloaded from the WorldClim database using the software Arc-GIS version 10.1. Elevation was obtained from the GTOPO30 digital elevation model for Africa downloaded on 28 October 2016: http://www.arcgis.com/home/item.html?id=c891f64c13be4a2c96491e386bfed8c5

Model (variables)	**Adj r^2**	**(df)**	**AIC**
Micaelamys namaquensis			
1 Latitude	0.110	(1,140)*	570.510
2 Longitude	0.260	(1,140)*	545.095
3 Year	-0.005	(1,140)	588.430
4 Mean annual temperature	0.080	(1,140)*	575.940
5 Elevation	-0.002	(1,140)	587.980
6 Annual rainfall	0.250	(1,140)*	547.200
7 Tooth-wear class, TWCLS (as factor)	0.150	(3,138)*	566.950
8 Elevation + Year + Mean annual temperature + Annual	0.420	(7,134)*	516.180

rainfall + TWCLS			
9 Global model	**0.430**	**(9,132)***	**515.180**
Gerbilliscus leucogaster			
1 Latitude	-0.004	(1,130)	549.200
2 Longitude	0.170	(1,130)*	523.940
3 Year	0.011	(1,130)	547.150
4 Mean annual temperature	-0.006	(1,130)	549.480
5 Elevation	-0.007	(1,130)	549.570
6 Annual rainfall	0.100	(1,130)*	534.470
7 Tooth-wear class, TWCLS (as factor)	0.074	(2,129)*	539.560
8 Latitude, Longitude, Annual rainfall, TWCLS	**0.290**	**(5,126)***	**506.550**
9 Global model	0.290	(8,123)*	510.750
Desmodillus auricularis			
1 Latitude	-0.007	(1,92)	399.540
2 Longitude	-0.008	(1,92)	399.620
3 Year	-0.011	(1,92)	399.900
4 Mean annual temperature	-0.011	(1,92)	399.910
5 Elevation	-0.005	(1,92)	399.420
6 Annual rainfall	0.009	(1,92)	398.050
7 Tooth-wear class, TWCLS (as factor)	**0.214**	**(2,91)***	**377.280**
8 Elevation + Year + Mean annual temperature + Annual rainfall + TWCLS	0.181	(6,87)	384.870
9 Global model	0.190	(8,85)	385.520
Mastomys natalensis			
1 Latitude	0.068	(1,208)*	856.840
2 Longitude	0.130	(1,208)*	842.370
3 Year	0.160	(1,208)*	8.35.570
4 Mean annual temperature	0.012	(1,208)	868.910
5 Elevation	0.002	(1,208)	871.200
6 Annual rainfall	0.079	(1,208)*	854.330
7 Tooth-wear class, TWCLS (as factor)	0.037	(4,205)*	866.480
8 Elevation + Year + Mean annual temperature + Annual rainfall + TWCLS	0.190	(8,201)*	832.580

9 Global model	**0.240**	**(10,199)***	**821.630**
Otomys unisulcatus			
1 Latitude	-0.008	(1,100)	427.10
2 Longitude	-0.009	(1,100)	427.270
3 Year	0.007	(1,100)	425.620
4 Mean annual temperature	-0.009	(1,100)	427.320
5 Elevation	-0.007	(1,100)	427.060
6 Annual rainfall	-0.010	(1,100)	427.320
7 Tooth-wear class, TWCLS (as factor)	0.550	(2,99)*	344.760
8 Elevation + Year + Mean annual temperature + Annual rainfall + TWCLS	**0.580**	**(6,95)***	**343.470**
9 Global model	0.570	(8,93)*	346.620
Parotomys brantsii			
1 Latitude	-0.005	(1,57)	236.600
2 Longitude	-0.015	(1,57)	237.210
3 Year	-0.006	(1,57)	235.960
4 Mean annual temperature	-0.017	(1,57)	237.290
5 Elevation	-0.012	(1,57)	237.040
6 Annual rainfall	-0.010	(1,57)	236.910
7 Tooth-wear class, TWCLS (as factor)	0.470	(2,56)*	199.550
8 Elevation + Year + Mean annual temperature + Annual rainfall + TWCLS	**0.508**	**(6,52)***	**199.060**
9 Global model	0.500	(8,50)*	200.610

DISCUSSION

Different studies have shown that it is difficult to stipulate which climatic variable exactly influences body size, as most covary. A proposed way to carry this out is to test several climatic factors and assume that the relative effect of each variable tested represents that factors effect on body size (Rosenzweig, 1968; Yom-Tov & Nix, 1986; Yom-Tov & Geffen, 2011). Thus, we tested both temperature and rainfall.

Temperature hypothesis (Bergmann's Rule) – predicts decline in size with increased temperature in space and time

The latitudinal patterns observed in PC.1 of *M. natalensis* and *M. namaquensis* are consistent with the predictions of Bergmann's Rule, reflecting an increase in size away from the equator. A similar trend was observed in laminate-toothed rats (Nengovhela et al., 2015). However, an undisputable demonstration of Bergmann's Rule would require confirmation that temperature is the causal factor in these geographical patterns. Thus, looking at the models of *M. natalensis* and *M. namaquensis*, temperature was only negatively correlated with PC.1 in *M. namaquensis* and not significant in *M. natalensis*. Meaning *M. namaquensis* conforms to the Rule as body size decreased with temperature; however, for *M. natalensis* this scenario did not hold as only rainfall seems to be the factor behind the observed body-size latitudinal trends.

The temporal patterns observed in *O. unisulcatus* are consistent with the predictions of Bergmann's Rule, showing a decrease in size with time and *M. natalensis* contradicts the Rule as an increase in size with time was observed. These findings are congruent to some of the studies mentioned in Table 2.3 (i.e. Smith et al., 1998; Pergams & Lawler 2009; Ozgul et al., 2010; Eastman et al., 2012; Pergams et al., 2015; Nengovhela et al., 2015; Villar & Naya, 2018). However, if the temporal changes in skull size of *O. unisulcatus* and *M. natalensis* are due to temperature change, and if the underlying mechanism is Bergmann's Rule, we expect that the observed latitudinal trends should also be correlated with temperature. However, our models for *O. unisulcatus* and *M. natalensis* showed no correlation of PC.1 with temperature. This study provides some evidence for the idea that a decrease in body size is a “third ecological response to global warming” (Gardner et al., 2011). Although we might conclude that global warming is explaining these temporal trends, mean annual temperature was not a determinant of geographical variation in *O. unisulcatus* and *M. natalensis*. Global warming is not only causing reductions in body size, but it is also causing increases as some studies reported an increase in body size with time (Pergams & Ashley, 1999; Ozgul et al., 2010; Eastman et al., 2012; Pergams et al., 2015) and these were caused by an increase in food availability.

Table 2.3. Studies investigating temporal trends in relation to climate change and Bergmann’s Rule for rodents.

Family	**Genus**	**Species**	**Continent/ Hemisphere**	**Maximum latitude**	**Range size area**	**r-k selection**	**Mean litter size, gestation period, life span, weaning days**	**Mean body mass (g)**	**Fossorial/ not**	**Desert/not**	**high-elevation/ not**	**Habitat specialist/ not**	**Commensal/ pest or not**	**Temporal size trend**	**Predictors**	**Reference**
Cricetidae	*Dicrostonyx*	*groenlandicus*	NA	83.627433662	2561987 km2	k	3.4, 20 days, 3.3 years	66	Yes	No	No	Yes	No	No response	-	Villar & Naya, 2018
Cricetidae	*Lemmus*	*trimucronatus*	NA	74.557830811	5779510 km2	r	3.7, 23 days	80	No	No	No	Yes	No	Decrease	Global warming	Villar & Naya, 2018
Cricetidae	*Microtus*	*longicaudus*	NA	68.1352355920001	40214210 km2	r	5, 20-23 days, 12 months	37	Yes	No	Yes	No	Yes	No response	-	Villar & Naya, 2018
Cricetidae	*Microtus*	*miurus*	NA	70.8893355920001	1431571 km2	r	8.2, 21 days, 12 months	41	Yes	No	Yes	Yes	No	Decrease	Global warming	Villar & Naya, 2018
Cricetidae	*Microtus*	*oeconomus*	Europe, Asia, NA	75.5371462750001	19507729 km2	r	6.9, 20-21 days, 12 months, weaned after 18 days	50	No	No	No	Yes	No	Decrease	Global warming	Villar & Naya, 2018
Cricetidae	*Microtus*	*pennsylvanicus*	NA	70.2534355930001	11963797 km2	r	5.5, 21 days, 16 months, weaned between 12-14 days	44	Yes	No	No	No	Yes	Decrease	Global warming	Villar & Naya, 2018
Cricetidae	*Myodes*	*gapperi*	NA	62.433335593	8370580 km2	r	3.7, 17 to 19 days, 18 months, weaned at 17-21 days	21	Yes	No	Yes	Yes	No	Decrease	Global warming	Villar & Naya, 2018
Cricetidae	*Peromyscus*	*leucopus*	NA	51.1302354630001	5831155 km2	r	4.5, 22-28 days, 12 months	23	No	Yes	Yes	No	No	Decrease	Global warming	Villar & Naya, 2018
Cricetidae	*Peromyscus*	*maniculatus*	NA	65.6470222830001	13316662 km2	r	5, 22-26 days, 12 months, weaned at 25-35 days	20	No	Yes	Yes	No	No	Decrease	Global warming	Villar & Naya, 2018
Cricetidae	*Reithrodontomys*	*megalotis*	NA	50.6100737610001	5116675 km2	r	4, 23-24 days,12 months, weaned at 24 days	11	No	Yes	Yes	No	No	No response	-	Villar & Naya, 2018
Cricetidae	*Sigmodon*	*hispidus*	NA	40.9363846750001	2615709 km2	r	5, 27 days,12 months, weaned at 5-25 days	159	No	Yes	No	No	Yes	No response	-	Villar & Naya, 2018
Cricetidae	*Neotoma*	*albigula*	NA	39.1192465990001	845054 km2	k	2, 30-38 days,17 months,	197	No	Yes	No	No	Yes	Decrease	Climate warming	Smith et al. 1998

							weaned at 62-72 days								
Dipodidae	*Napaeozapus*	*insignis*	NA	54.2319355920001	2009949 km2	k	4.5, 29 days, 2 years, weaned at 34 days	25	No	No	No	Yes	No	No response	-	Villar & Naya, 2018
Dipodidae	*Zapus*	*hudsonius*	NA	65.02594	8737705 km2	r	5, 17-20 days, 1-2 years, weaned at 28-33 days	18	No	No	No	No	Yes	No response	-	Villar & Naya, 2018
Geomyidae	*Thomomys*	*bottae*	NA	42.9594606140001	1541296 km2	k	5.6, 19 days, 2.5 years, weaned at 36-40 days	116	Yes	Yes	Yes	No	No	No response	-	Villar & Naya, 2018
Heteromyidae	*Dipodomys*	*merriami*	NA	40.3870668170001	1423668 km2	k	3, 28-32 days, 1-2 years, weaned at 24-33 days	42	Yes	Yes	No	No	No	No response	-	Koontz et al. 2001
Muridae	*Micaelamys*	*namaquensis*	Africa	14.845464407	3338607 km2	r	3.3, >22 days, 12 months, weaned at 21-26 days	48	No	Yes	No	No	Yes	No response	-	Current study
Muridae	*Desmodillus*	*auricularis*	Africa	12.579564407	1955062 km2	k	3, 21 days, 1-2 years, weaned at 33 days	46	Yes	Yes	No	Yes	No	No response	-	Current study
Muridae	*Gerbilliscus*	*leucogaster*	Africa	4.91946440699996	576523910 km2	r	5, 28 days, 12 months, weaned at 28 days	72.2	No	No	No	Yes	Yes	No response	-	Current study
Muridae	*Mastomys*	*natalensis (sl)*	Africa	16.9106355930001	16655238 km2	r	6.5, 21-22 days, < 12 months, weaned at 21 days	41	No	No	No	No	Yes	Increase	Global warming (rainfall)	Current study
Muridae	*Mus*	*musculus*	Cosmopolitan	73.530334472	151503825 km2	r	5, 21 days, 12 months, weaned at 21 days	21	No	No	No	No	Yes	No response	-	Villar & Naya, 2018
Muridae	*Otomys*	*unisulcatus*	Africa	27.427864407	374311 km2	k	2.09, 37 days	124.5	No	Yes	No	Yes	No	Decrease	Global warming	Current study
Muridae	*Parotomys*	*brantsii*	Africa	23.444364408	679441 km2	k	3.4, 38 days, 1-2 years	95	Yes	Yes	No	Yes	No	No response	-	Current study
Muridae	*Otomys*	*angoniensis*	Africa	1.02173559300007	595014 km2	k	3.1, 37 days,	114.3	No	No	No	Yes	No	Decrease	Global warming	Nengovhela et al. 2015
Muridae	*Otomys*	*auratus*	Africa	18.0354583229999	519018 km2	k	2.8, 35-40 days, 22 months	127.3	No	No	Yes	Yes	No	Decrease	Global warming	Nengovhela et al. 2015
Muridae	*Rattus*	*rattus*	Cosmopolitan	61.7204210090001	43666656 km2	r	8, 21-29 days, 12 months, weaned at 3-4 weeks	200	No	No	No	No	Yes	Increase		Pergams et al. 2015
Sciuridae	*Tamias*	*striatus*	NA	51.6701355930001	4197494 km2	k	4, 31-35 days, 3 years, weaned at	96	Yes	No	No	No	No	No response	-	Pergams & Lawler 2009; Villar & Naya, 2018

							40 days									
Sciuridae	*Tamiasciurus*	*hudsonicus*	NA	67.7819355930001	10363614 km2	k	4, 35 days, 4 years, weaned at 70 days	213	No	No	No	No	Yes	No response	-	Villar & Naya, 2018
Sciuridae	*Urocitellus*	*beldingi*	NA	45.90964	337683 km2	k	5.7, 23-31 days, 3 years, weaned at 27 days	290	Yes	No	Yes	No	Yes	Increase	Temperature & snow melt	Eastman et al. 2012
Sciuridae	*Callospermophilus*	*lateralis*	NA	56.388235593	1704569 km2	k	5, 26-33 days, 4 years, weaned at 29 days,	158	Yes	No	Yes	No	Yes	Increase	Temperature & snow melt	Eastman et al. 2012
Sciuridae	*Otospermophilus*	*beecheyi*	NA	46.9255529760001	467249 km2	k	5, 25-30 days, 4 years, weaned at 6-7 weeks	500	Yes	No	No	No	Yes	No response	-	Eastman et al. 2012
Sciuridae	*Marmota*	*flaviventris*	NA	51.1287355920001	1718209 km2	k	4, 30 days, 5-6 years, weaned at 7 weeks	3350	Yes	No	Yes	Yes	No	Increase	Longer growing season	Ozgul et al. 2010
Cricetidae	*Abrothrix*	*longipilis*	SA	30.294764408	717952.115 km2	r	3.85	36.7	Yes	No	No	No	No	Decrease	Increased temperature	Pergams & Lawler 2009
Cricetidae	*Abrothrix*	*olivaceus*	SA	18.388064408	1085022 km2	r	3.85	39	-	No	No	No	No	No response	-	Pergams & Lawler 2009
Cricetidae	*Abrothrix*	*sanborni*	SA	42.5823798297646	4530.491 km2	r	3.85	25	No	No	No	Yes	No	No response	-	Pergams & Lawler 2009
Cricetidae	*Microtus*	*mexicanus*	NA	37.5773168050001	854502.16 km2	r	2.3	35	No	No	Yes	Yes	No	No response	-	Pergams & Lawler 2009
Geomyidae	*Thomomys*	*umbrinus*	NA	32.862199925	469421.359 km2	k	4, 20 days, 1-2 years	130	Yes	Yes	Yes	No	No	No response	-	Pergams & Lawler 2009
Heteromyidae	*Chaetodipus*	*fallax*	NA	34.3568258450001	46906.768 km2	r	3, 24-26 days, 4-6 months	20	Yes	Yes	No	No	No	No response	-	Pergams & Lawler 2009
Muridae	*Lophuromys*	*flavopunctatus*	Africa	9.94583616700006	1820851.74 km2	r	2.4, 30-31 days	69	No	No	Yes	Yes	No	Decrease	Increased temperature	Pergams & Lawler 2009
Muridae	*Oligoryzomys*	*longicaudatus*	SA	25.901564407	629012.304 km2	r	5	28	No	No	unknown	No	No	Increase	Increased temperature	Pergams & Lawler 2009
Muridae	*Phyllotis*	*xanthopygus*	SA	10.682364407	1499353.412 km2	r	4.7	55	No	No	Yes	No	No	No response	-	Pergams & Lawler 2009
Muridae	*Praomys*	*jacksoni*	Africa	11.114135593	3744033.037 km2	r	3.8, 36 days, weaned at 29 days	41	No	No	Yes	No	No	No response	-	Pergams & Lawler 2009
Muridae	*Rattus*	*tanezumi*	Asia	45.6073355930001	9717373.242 km2	r	8	140	No	No	No	No	Yes	No response	-	Pergams & Lawler 2009
Sciuridae	*Sciurus*	*carolinensis*	NA	53.411035592019	4083837.559 km2	k	3, 44 days, 7-8 years, weaned at 7-10 weeks	540.33	No	No	No	No	Yes	No response	-	Pergams & Lawler 2009
Spalacidae	*Tachyoryctes*	*splendens*	Africa	14.5927355920001	680054.692 km2	k	1.65, 46-49 days, 2-3 years, weaned at 35 days	265.7	Yes	No	Yes	No	Yes	Increase	Increased temperature	Pergams & Lawler 2009

Precipitation/productivity hypothesis – predicts increase in body size with increasing rainfall

Precipitation has been shown to be strongly correlated with primary productivity (Fang et al., 2001; Knapp et al., 2006). The relationship between increased body size and increased precipitation (hence, increased primary productivity) have been observed in a number of studies (Yom-Tov & Yom-Tov, 2005; Yom-Tov & Geffen, 2006). In our study, body size (PC.1) was positively correlated with annual precipitation in *M. natalensis, M. namaquensis* and *G. leucogaster*. This conforms to the productivity hypothesis or what McNab (2010) refers to as Resource Rule, which posits that "mammalian species will become larger or smaller depending on the size, abundance and availability of resources". Our results are consistent with what have been reported in Alhajeri & Steppan (2016), who showed that increased body mass was related to increasing precipitation variables (hence, increased food availability) supporting James (1970) and Yom-Tov & Geffen (2006). Similarly, increased body size was associated with increased food availability brought about by longer growing seasons and earlier green-up (Ozgul et al., 2010; Eastman et al., 2012). However, the relationship between precipitation and primary productivity is not as straight forward as other factors such as temperature, also plays a role in determining primary productivity (Yom-Tov & Geffen, 2006, 2011). Even though precipitation was significantly positively correlated with PC.1 in the three species, it is not clear that the increased precipitation means increased primary productivity as precipitation varies between habitats (Villar & Naya, 2018). These species occur in several different habitats including savannahs, forests, shrublands, semi-arid areas, grasslands, human settlements and agricultural areas (Happold, 2013). Thus, our study does not clearly identify primary productivity as a predictor playing a major role in the pattern of body size variation.

Urbanization/human population density hypothesis – predicts increase in body size with time

Human population density and agricultural practices has increased over the years, offering an augmentation in food availability to commensal species (Yom-Tov, 2003; Yom-Tov & Yom-Tov, 2012). Not only is this increase in food availability linked to increase in body size but also increase in population densities and breeding success (Yom-Tov et al., 2007). Commensal species included in our meta-analysis confirmed the hypothesis of increase in body size through time ($y = -75.304+0.038x$, $p < 0.0001$), a result that is congruent with Yom-Tov (2003), Yom Tov et al. (2003), Pergams & Lawler (2009) and Tomassini et al. (2014). However, caution should be noted as sampling biases through the years may have occurred as most of the so-called commensal regions have not been sampled in places where this species is commensal but have been collected mostly in nature reserves. Similarly, in West Africa (Senegal) the commensality of *M. natalensis* is not as clear cut as it has been shown to live in houses during the dry seasons but go to the fields during crops growing seasons (Granjon & Duplantier, 2009). Similarly, looking at general body size variation between commensal and non-commensal subpopulations of *M. natalensis* in our study, commensal populations are significantly larger in skull size than non-commensal, in agreement with Yom-Tov et al. (2007) where foxes inhabiting agricultural areas were found to be larger than those living elsewhere and were in high densities (Yom-Tov et al., 2007). This is congruent with *M. natalensis*, which is shown to occur in high densities in agricultural areas as compared to human dwellings and natural habitats (Monadjem & Perrin, 2003; Mohr et al., 2007). Similarly, besides precipitation, in Pergams & Ashley (1999) and Pergams et al. (2015) human population density was responsible for positive morphological changes over time in rodents. Therefore, precipitation and commensalism seem to be related (i.e. commensalism is proposed to cause an increase in food availability).

Other factors that may contribute to body size temporal responses

Arid species seem not to respond to any climatic factors even to spatial or temporal variation. Perhaps the absence of temporal responses due to climate warming is the fossoriality of desert-adapted species *D. auricularis* and *P. brantsii* that may lead to less exposure to environmental change due to shielding of temperatures in burrows (Pacifici et al., 2017), however lack of these responses is also observed in savannah species (*G. leucogaster* in part).

Based on our binomial models, we found that none of our chosen predictors could significantly explain the probability of a temporal response. However, looking at each predictor (box/bar plot, r/k selection, litter size and elevation, Figure A.6) shows very marginal non-significant correlation with a temporal response. That is, species with larger litter sizes and higher probability of being r-selected seem to be marginally more likely to show long-term temporal changes in body size. This is expected since species with shorter generation times have higher mutation rates and evolve faster, so would be expected to adapt and respond faster to climate changes over a historical period than longer generation time. Of course, this is highly speculative.

As for the elevation, even though not significant, high altitude species showed a 60% chance of showing temporal changes compared to 30% in low altitude. This might be due the fact that high elevation habitats are more prone to fragmentation (Naya et al., 2017), causing rapid morphological changes. This may be equated to the rapid morphological changes shown on islands (see Pergams & Ashley, 1999; Pergams et al., 2015). The non-significant results in our chosen predictors may be caused by the small sample size, effects of phylogeny, unequal sampling of different rodent families and the subjectivity of scoring some of the predictors. Additionally, litter size can vary much in space and time. Future studies should test these predictors from large samples of species within a single family.

In conclusion, this study shows that the “third universal response to warming” is not universal as only one out of six African species studied showed temporal decrease in body size. Additionally, temperature does not seem to be correlated with body size variations in our study animals on its own. We found significant relationship between body size and climate variables (temperature and rainfall) that are potentially associated with increased food availability and quality. This supports James (1970), in that it is a synergy of factors that best explains body size variations witnessed in different organisms.

CHAPTER THREE: ASSOCIATED TYMPANIC BULLAR AND COCHLEAR HYPERTROPHY DEFINE ADAPTATIONS TO TRUE DESERTS IN AFRICAN GERBILS AND LAMINATE-TOOTHED RATS (MURIDAE: GERBILLINAE AND MURINAE)

SUMMARY

Hearing capabilities in desert rodents such as gerbils and heteromyids have been inferred from both anatomical and ecological points and tested with experiments and theoretical models. However, very few studies have focused on other desert adapted species. In this study, a refined 3D morphometric approach was used on three African rodent tribes (Otomyini, Taterillini and Gerbillini) to describe the cochlea and tympanic bullar morphology. We also explore the role of phylogeny, allometry and ecology to understand better the underlying mechanism of any observed trends of hypertrophy in the bulla and associated changes in the cochlea. As a result, desert adapted species could be distinguished from mesic and semi-arid taxa by the gross cochlea dimensions, particularly the oval window which is larger in desert species. With some exceptions, bulla and cochlea modifications between species could be explained either by environment (bulla and oval window), or phylogeny (cochlea curvature gradient) and/or allometry (cochlea relative length, oval window and bulla). Based on their ear anatomy, we hypothesised that *Desmodillus auricularis* and *Parotomys brantsii* should be sensitive to low frequency sounds, with *D. auricularis* also sensitive to high frequency sounds. This study concludes that desert adapted laminate-toothed rats and gerbils both use bulla and associated cochlea hypertrophy, particularly desert species. Gerbil’s further show tightly coiled cochlea but the significance of this is debatable and may not have anything to do with adaptations to any specific acoustics in the desert environment.

INTRODUCTION

Rodents are the most diverse living mammals, colonizing a vast array of habitats (Wilson et al., 2016, 2017) with the Muridae (or murids) being the most diverse family (Musser & Carleton, 2005). The family consists of species with a wide range of specialization and morphological adaptations (Happold, 2013). Rodents occupying desert habitats/environment are characterized by numerous common features such as inflated tympanic bullae (Prakash, 1959; Lay, 1972; Nikolai & Bramble, 1983; Alhajeri et al., 2015; Tabatabaei-Yazdi et al., 2015; Mason, 2016), long hind feet and bipedal locomotion (Nikolai & Bramble, 1983) with certain subterranean species showing relatively larger bulla (Stein, 2000). Not only is the inflated bulla associated with desert environment but also open micro-habitats (Kotler, 1984) and high elevation (Zhao et al., 2013; Tabatabaei Yazdi et al., 2015). This hypertrophy is said to improve low frequency hearing which is hypothesized to help in both prey localization and predator avoidance (Lay, 1972), as well as interspecific communication (e.g. vocalization, tapping, foot drumming, stomping) in burrows and open mostly desert habitats/environment (Bridelance, 1986; Randall, 1993, 1994, 2014). However, besides the hypertrophied bulla, other aspects of the middle ear morphology as well as the inner ear are also important in improving low-frequency hearing (Dallos, 1970; Lay, 1972; Ravicz et al., 1992; Ravicz & Rosowski, 1997; Salt et al., 2013). Although a plethora of hearing studies (including those inferred from bulla and ear morphology) in desert rodents have been conducted, most of these have focused mainly on Gerbillinae (Lay, 1972; Plassmann et al., 1987; Plassmann & Kadel, 1991; Zhao et al., 2013; Mason, 2016; Tolnai et al., 2017) including *Meriones* (Ryan, 1976; Tabatabaei-Yazdi et al., 2014, 2015), Dipodomyinae (Lay, 1972; Webster & Webster, 1975; Heffner & Masterton, 1980; West, 1985; Shaffer & Long, 2004; Randall, 2014) and various subterranean rodents (Heffner & Heffner, 1992; Lange et al., 2004, 2007; Francescoli et al., 2012; Mason et al., 2016) to name a few. However, no studies have looked at the hearing capabilities of Otomyini in detail despite their adaptation to life in deserts or high altitude. Vocalisation has been studied on two *Parotomys* (whistling rats) species (*brantsii* and *littledalei*; Le Roux et al., 2001ab; Le Roux et al., 2002; Garcia-Navas & Blumstein, 2016) and in gerbils (Dempster & Perrin, 1991, 1994; Dempster et al., 1991; Dempster, 2018). Descriptions of *Otomys* (unknown species, Cockerell et al., 1914) malleus and incus and *Parotomys* middle ears (Oaks, 1967 unpublished cited in Mason, 2015) have been made. The inner ear shows extensive variations across taxa in mammals (Vater & Kossl, 2011) with cochlear function potentially limiting bandwidth of hearing (Ruggero & Temchin, 2002) and semicircular canals responsible for locomotion and balance (Spoor & Zonneveld, 1998; Pfaff et al., 2015; Grohé et al., 2016). The geometry of cochlear features had been said to play a role in determining the limits of high and low frequency hearing and octaval ranges in vertebrates (West, 1985; Manoussaki et al., 2008; Ekdale & Racicot, 2015). However, these functional relationships had been inferred from correlations but not linked to causation.

As ear specialisations are said to be more pronounced in the inner ear because of differing lifestyles (Crumpton et al., 2015), it is of importance to test this on other taxa that have not been studied before to assess whether this is a general/universal or taxon-specific adaptive trend. Studies relating the bulla size to cochlear parameters and the pattern of their covariance in response to environmental variables are very scarce, especially those looking at rodents. The present study used a 3D morphometric approach to describe and compare in detail the cochlea and bullar morphology of African rodent members of three Muridae tribes belonging to two subfamilies (Otomyini in the Murinae and Taterillini and Gerbillini in the Gerbillinae). These taxa are characterised by a wide variation of different life histories and environmental niches, including both desert and non-desert species (see Figure 3.1 and Table 3.1). The classification followed at the tribe level is after Lecompte et al. (2008), Pavlinov (2008) and Wilson et al. (2017). We included the three tribes from two distant murid subfamilies to explore the role of phylogeny, allometry and ecology in an attempt to better understand the underlying mechanism of any observed trends of hypertrophy (if there are any) in the bulla and associated changes in the cochlea. Gerbils are thought to have originated from a desert-adapted ancestor in North Africa (Pavlinov, 2008), while laminate-toothed rats (Murinae: Otomyini) originated 5MYA from *Euryotomys,* a murid occupying the presumably-mesic temperate central plateau of South Africa (Pocock, 1976; Senegas, 2001; Denys, 2003; Monadjem et al., 2015). While gerbils are mostly confined to arid or semi-arid habitats, most Otomyini species are associated with temperate or montane or sub-montane habitats, with the exception of *Otomys unisulcatus*, which is from the semi-arid shrub habitats in the Karoo Desert of South Africa, and two species of whistling rats (*Parotomys brantsii* and *P. littledalei*) from the Karoo, Kalahari and Namib deserts of Southern Africa. The bullae of both desert-dwelling *Parotomys* species are hypertrophic, but not that of *O. unisulcatus* (Pocock, 1976; Taylor et al., 2004). The very wide habitat range within Otomyini offers an excellent opportunity to understand evolutionary responses of the bulla and cochlea to the transition from mesic to desert environments within a closely-related clade of species.

Within Gerbillinae, not only do species differ in the size of the bulla but also in the degree and type of pneumatisation (expansion) of the posteriorly-located mastoid chamber of the bulla. The extreme gerbil desert species (e.g. *Desmodillus auricularis*) is characterized by larger bulla and a two chambered pneumatized mastoid cavity while *Gerbilliscus*, a more semi-arid savannah-associated genus, includes species that typically display a smaller bulla with the mastoid portion hardly expanded, and an intermediate condition of the bulla is found in the genus *Gerbillus* (Lay, 1972; Pavlinov, 2001, 2008; Mason, 2016). Our study included *G. nigeriae,* a species that occupies semi-arid Sahel habitats but has also expanded its range into anthropogenic habitats and therefore is less of a desert specialist than a species such as *D. auricularis*. Our choice of three gerbil taxa for this study therefore includes a range of species representing various bullar morphologies ranging from more generalised (un-inflated mastoid portions of bulla) to more specialised (highly inflated mastoid) adaptations to arid habitats.

The main objectives of this study are: (1) to investigate cochlea morpho-anatomical variation among Otomyini and Gerbillinae focusing on five cochlea features (Braga et al., 2015) that plays a role in hearing capabilities in mammals (West, 1985; Manoussaki et al., 2008; Vater & Kossl, 2011); (2) to test correlation between tympanic bulla size versus cochlea parameters (see material and methods) in three gerbils and ten Otomyini species; (3) to test association of bulla and cochlea parameters with environmental variables (Alhajeri et al., 2015). Following from these objectives we predict that (1) the cochlea should scale with body size and bullar size (i.e. hypertrophy of the bulla means hypertrophy (i.e. enlargement) of the cochlea, or some aspects of it); (2) both the bullar and cochlear morphology should vary because of phylogeny (i.e. a significant phylogenetic signal between the two subfamilies (Gerbillinae and Murinae) and the two tribes within Gerbillinae); body size (i.e. an increase in cochlear and bullar size with body mass) and environmental factors (i.e. a significant inverse correlation between bullar and cochlear measurements with mean annual rainfall due to hypertrophy in species from low rainfall areas associated with deserts and a significant positive correlation of the same measurements with elevational range).

Table 3.1: Brief life history summary of all 10 species included in this study.

Species name	Diet	Habitat	Revised habitat	Mean body mass, g	Life style	Elevation , m
Otomys auratus	Herbivorous[ab]	Montane or highveld plateau grassland[bc]	1 mesic	127[c]	Epigeic[d]	Mid-elevation[cd]
Otomys angoniensis	Herbivorous[ab]	Mesic savannah[bc]	1 mesic	114[c]	Epigeic[ab]	Low-elevation <1000[ab]
Otomys unisulcatus	Herbivorous[ab]	Semi-arid[bc]	2 arid	96[c]	Epigeic[b]	Low-elevation[b]
Otomys helleri	Herbivorous[ab]	Alpine[c]	1 mesic	90[c]	Epigeic[c]	>3000 High-elevation[c]
Otomys sloggetti	Herbivorous[ab]	Alpine[bc]	1 mesic	84[c]	Epigeic[b]	>2000 Mid-elevation[b]
Otomys barbouri	Herbivorous[ab]	Alpine[bc]	1 mesic	112[c]	Epigeic[b]	>3200 High-elevation[c]
Parotomys brantsii	Herbivorous[ab]	Arid[bc]	2 arid	95[c]	Fossorial[b]	<1000 Low-elevation[b]
Gerbilliscus leucogaster	Omnivorous[ab]	Semi-arid (Arid savannah)[ab]	2 arid	72[c]	Fossorial[b]	<1600 Low-elevation[b]
Gerbillus nigeriae	Omnivorous[ab]	Semi-arid Sahel[b]	2 arid	24[c]	Fossorial[b]	Low elevation <1000 (even 500)
Desmodillus auricularis	Omnivorous[ab]	Arid[abc]	2 arid	46.1[c]	Fossorial[b]	<1600 Low-elevation[b]

[a]Skinner & Chimimba, 2005; [b]Happold, 2013; [c]Monadjem et al. 2015; [d]Baxter et al. 2017

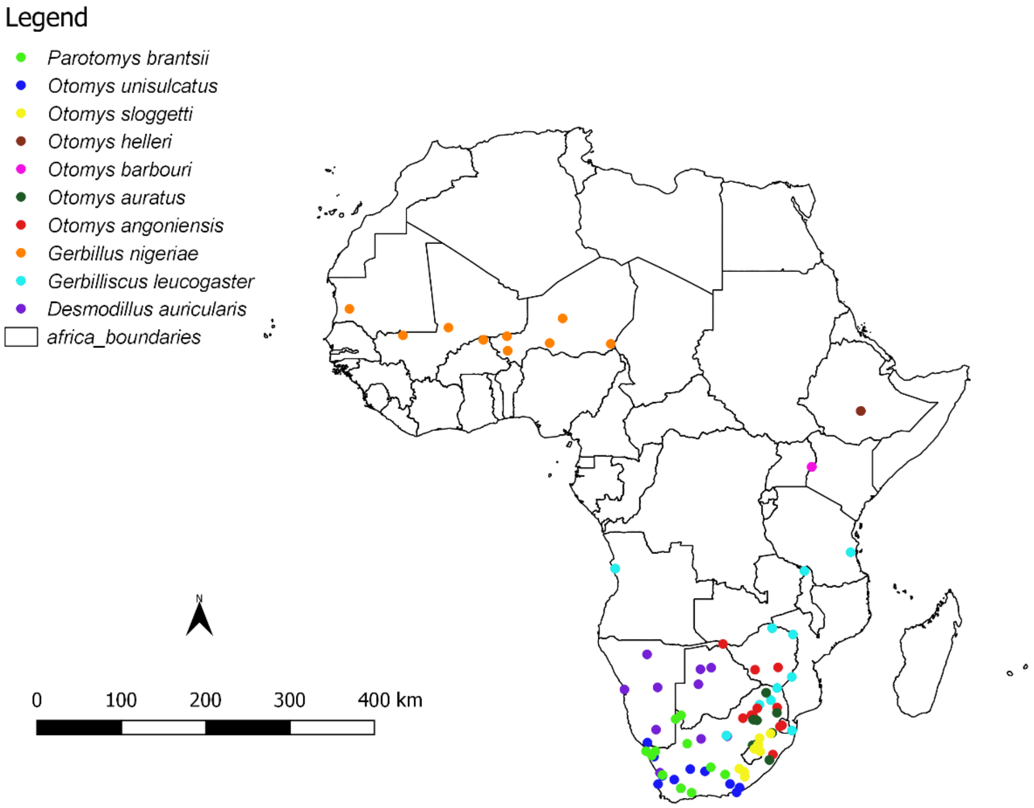


Figure 3.1: Geographic distribution map of all 10 species based on locality coordinates of specimens included in this study. Coordinates were obtained from the specimen labels; where there was none, localities name were used to search for one using Google Earth/Maps and Geonet gazetteer Southern Africa.

MATERIALS AND METHODS

Study samples

The present study is based on micro-focal X-ray computed-tomography (micro-CT) data obtained for 110 dry skulls of known sex (see Table 3.2) representing Otomyini and Gerbillinae curated at the Ditsong National Museum of Natural History (Pretoria) and Muséum National d'Histoire Naturelle (Paris). Most of the specimens were adults, as estimated from their molar lamina wear (Otomyini: Taylor & Kumirai, 2001; Gerbillinae: Bates, 1985). On rare occasions when adult specimens were not available, specimens from younger adult age classes [e.g. Class 3 = subadult (see Taylor & Kumirai, 2001) in Otomyini] were also used. All the specimens housed in the Ditsong National Museum of Natural History in Pretoria, were scanned at the South African Nuclear Energy Corporation (NECSA) tomography centre, using the X-Tek (Metris) H225L industrial micro-XCT scanner. The specimens housed at the Muséum National d'Histoire Naturelle, Paris, France (MNHN) were scanned with the Phoenix Nanotom 180 scanner from the FERMAT Federation at the Centre Inter-Universitaire de Recherche et d'Ingénierie des Matériaux (CIRIMAT) at the University of Toulouse Paul Sabatier. Their isometric voxel size ranged from 19-23 µm. The settings of 100-130 kV and 100-180 µA were used.

Table 3.2: Composition of species and sample size used in this study. N: number of individuals; M: male; F: female.

Species	N	Country (Locality)	Collections	Sex (M, F)
Otomyini				
Otomys angoniensis	11	South Africa, Zimbabwe, Swaziland, Zambia	Ditsong[a]	(6, 5)
Otomys auratus	11	South Africa	Ditsong[a]	(5, 6)
Otomys unisulcatus	11	South Africa	Ditsong[a]	(6, 5)
Otomys helleri	09	Ethiopia	MNHN[b]	(4, 5)
Otomys sloggettii	11	South Africa, Lesotho	Ditsong[a]	(6, 5)
Otomys barbouri	07	Uganda	MNHN[b]	(5, 2)
Parotomys brantsii	11	South Africa	Ditsong[a]	(5, 6)
Gerbillinae				
Gerbilliscus leucogaster	16	Zimbabwe, South Africa, Malawi, Tanzania, Angola	Ditsong[a], MNHN[b]	(8, 8)
Desmodillus auricularus	11	South Africa, Botswana, Namibia	Ditsong[a]	(5, 6)
Gerbillus nigeriae	12	Mauritania, Burkina Faso, Niger, Mali	MNHN[b]	(6,6)

[a]Ditsong National Museum of Natural History, Pretoria; [b]Muséum National d'Histoire Naturelle, Paris

Phylogenetic sampling and analysis

For the seven Otomyini and three Gerbillinae species included in this analysis (see Table 2), the taxonomy followed Wilson et al. (2017) and Pavlinov (2008). Cytochrome b sequences used here were downloaded from GenBank and one sequence per species was used. The sequences were firstly aligned with clustalW and a phylogram tree based on Maximum Composite Likelihood method (Tamura et al., 2004) was generated using MEGA7 (Kumar et al., 2016) software, with an assumption that all the species have been identified correctly (Alhajeri et al., 2015). A Neighbour-joining phylogenetic tree (Saitou & Nei, 1987) was generated in order to test for phylogenetic signal among our samples (Figure B.1).

The phylogenetic signal (i.e. the tendency for related species to resemble one another) was computed by calculating the parameter Lambda λ (Pagel, 1999) under a Brownian model for each trait [cochlear parameters, body mass and bulla centroid size (bullaCS)] separately on the entire sample using "Geiger" package in R (R Development Core Team, 2012). Pagel's λ varies between 0 (traits values independent of phylogeny) and 1.0 (traits values proportional to time of shared evolution under a Brownian model). The phylogenetic signal test is performed under the null hypothesis that $\lambda = 0$ and that $\lambda = 1$ (Table B.2). The entire sample size is selected because it can be difficult to carry out these calculations on small sample size (Braga et al., 2015). For a detailed description of the procedure followed in this analysis, see http://www. anthrotree.info/wiki/projects/pica/The_AnthroTree_Website.html and (Braga et al., 2015).

Bulla data collection

The tympanic bulla semilandmarks, defined as "landmarks on smooth curves/surfaces with positions along the curvature that cannot be identified and that are thus estimated" (Mitteroecker & Gunz, 2009), were digitized from the ventral outer edge of the cranial in 3D with Avizo 8.0 (Visualization Sciences Group, www.vsg3d.com). Semilandmarks were used as the auditory bulla lacks clear homologous landmarks. As most of the skulls were slightly damaged, the whole bulla was then considered, including the bony external auditory meatus. Therefore, we assumed that the relative contribution of bony external meatus to middle ear components in the bulla is the same in each species. The semilandmarks were placed in a clockwise order, starting from the anterior junction between the bulla and the internal pterygoid process (Alhajeri et al., 2015; Figure 3.2). A varying number of points were used by using the "B-Spline" module in Avizo. These points were then saved in “ASCII” format and imported into R 3.2.1 (R Development Core Team, 2015) in order to transform them into a fixed number of points (200) that were equally spaced. Generalized Procrustes Analysis (GPA) was conducted in order to obtain bulla centroid sizes (CS, defined as the sum of the squared distances from the centroid to each individual semilandmark of the bulla (Rohlf & Slice, 1990)) and shape coordinates were discarded. CS obtained from GPA on each specimen was averaged in order to estimate species average size in R (R Development Core Team, 2015; Claude, 2008).

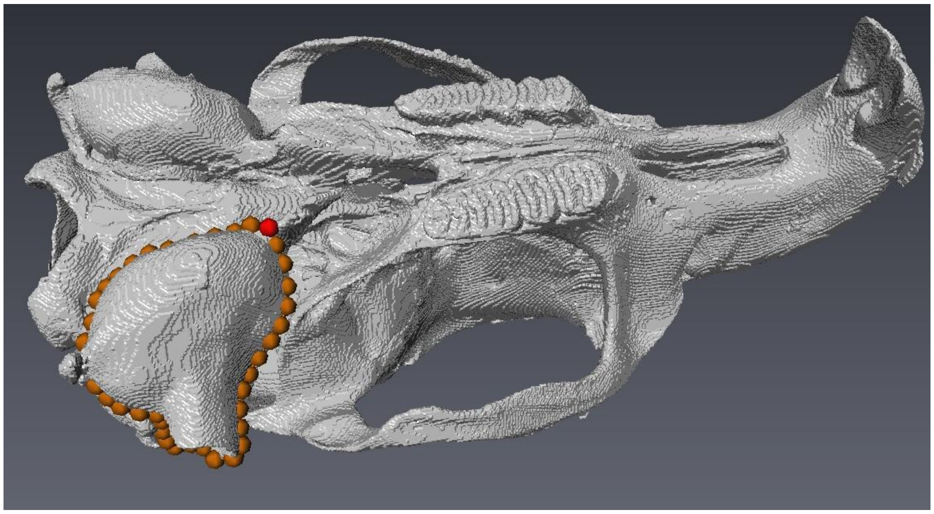


Figure 3.2: Position of bulla semilandmarks used in the geometric morphometric analyses to obtain centroid size of the bulla.

Cochlea and oval window data processing

Avizo 8.0 was also used to segment and reconstruct in 3D the cochlea and oval window fossa. The left bony labyrinth was used; however, in cases it was damaged, the right one was employed. The modelisation of the cochlea and oval window followed of methods of Braga et al. (2013, 2015) and Gunz et al. (2012) (Figure 3.3A). In order to document cochlea variation within our samples, five cochlea parameters were calculated from the semilandmarks coordinates placed on the external length of the cochlea (Figure 3.3A) using MATLAB R2013a v8.1 (Mathworks) software (by J. Dumoncel). These parameters included the external cochlea length (ECL), number of turns (TUR), relative cochlea length (RECL), the curvature gradient (CUR) and oval window area (OWA); see Braga et al. (2013, 2015). The ECL is the length between the apex and the starting point of the basal turn near the bottom margin of the round window (Figure 3.3B). The centre of the cochlear spiral (noted “A”, Figure 3.3B) was computed from the local chords defined by the landmarks placed at its two extremities. Then the radii of the two circles were calculated and denoted respectively R1 for the apical turn and R2 for the basal turn (Figure 3.3B). The ratio between these two radii make it possible to estimate the curvature of the cochlea (CUR = R2 / R1). Two segments joining the point A at both ends of the cochlea noted B (apex) and D (origin of the basal turn) were identified to calculate the number of turns (TUR) which corresponds to the sum of the number of half-turns recorded between B and D and the turn portion between C and D (Figure 3.3B). For the OWA, it was visualized in 3D after extracting an isosurface of its fossa. An oblique slice visually considered to best-fit the complete outline of the oval window was reconstructed. The OWA was then measured from its segmentation on this oblique slice (see Braga et al., 2015). For mean values of each species for these parameters see Table 3.3 and for raw data see Table B.1.

Table 3.3: Species mean and standard deviations for each cochlea parameters and bulla centroid size (CS).

Species names		**RECL (mm)**	**OWA (mm^2)**	**CUR**	**ECL (mm)**	**TUR**	**bullaCS**	**No of measured specimens**
O. angoniensis	Mean	6.08	0.38	1.38	11.78	1.94	50.02414	11
	SD	0.27	0.03	0.06	0.81	0.06	3.04	
O. auratus	Mean	6.48	0.39	1.42	13.23	2.05	51.18687	11
	SD	0.38	0.03	0.09	0.64	0.10	1.63	
O. unisulcatus	Mean	6.30	0.47	1.43	13.32	2.12	56.40981	11
	SD	0.25	0.07	0.10	1.05	0.21	6.96	
O. helleri	Mean	6.03	0.40	1.32	10.66	1.77	52.62486	09
	SD	0.25	0.03	0.06	0.86	0.11	4.62	
O. sloggettii	Mean	6.21	0.47	1.29	11.89	1.91	52.43497	11
	SD	0.37	0.44	0.07	1.07	0.08	2.81	
O. barbouri	Mean	6.00	0.37	1.32	10.96	1.83	48.8853	07
	SD	0.14	0.04	0.06	0.90	0.15	3.74	
P. brantsii	Mean	6.76	0.69	1.29	15.27	2.26	75.10032	11
	SD	0.24	0.05	0.06	0.72	0.10	2.39	
G. leucogaster	Mean	5.36	0.49	1.50	13.13	2.45	60.67969	16
	SD	0.25	0.03	0.11	1.14	0.17	3.24	
G. nigeriae	Mean	5.12	0.37	1.28	10.64	2.08	50.40225	12
	SD	0.16	0.02	0.05	0.79	0.13	2.16	
D. auricularis	Mean	6.02	0.83	1.53	13.75	2.29	75.11491	11
	SD	0.18	0.05	0.14	0.76	0.13	2.53	

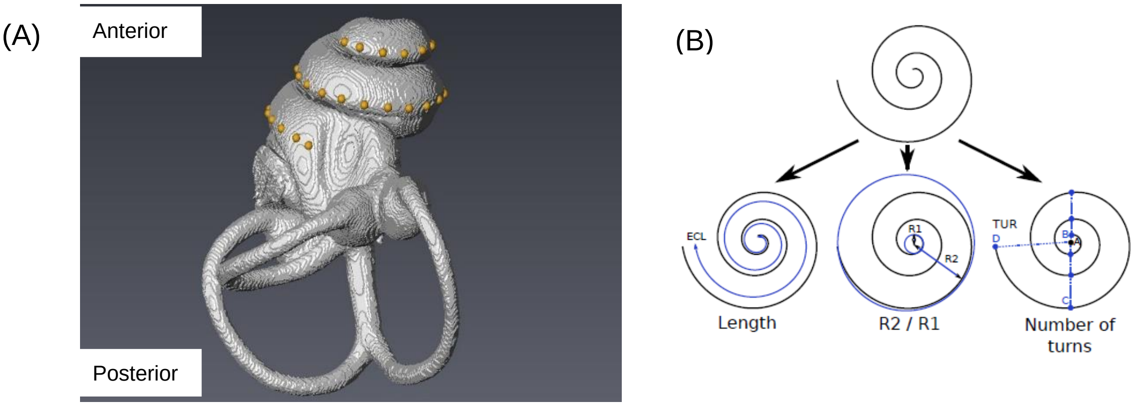


Figure 3.3: Position of cochlea semilandmarks used to calculate five cochlear parameters with the information on the orientation of the inner ear in relation to the position of the skull (A) and graphical representation of five cochlear features expressed as continuous variables (B) taken from Dumoncel (2016, lab tutorial).

Environmental data extraction

Each species habitat was categorized based on its preferred habitat history (see Table 3.1). In order to calculate aridity index, we firstly downloaded Bioclimatic variables from WORLDCLIM (Hijmans et al., 2005) using ArcGIS based on the species geographic distribution. This was done by cross-referencing geographic localities from the range distribution map (see Figure 3.1) of each species with the WORLDCLIM database. We downloaded Bio 1(Annual Mean Temperature), Bio 9 (Mean Temperature of Driest Quarter), Bio 12 (Annual Precipitation), Bio 17 (Precipitation of Driest Quarter) and elevation. The Bio 1,9,12 and 17 were used to calculate the aridity index. Aridity index equation:

$$AI = \frac{\frac{P}{T+10} + \frac{12p}{t+10}}{2}$$

where P is the mean annual rainfall in millimetres, T is the annual mean temperature in degrees Celsius, p is the average rainfall of the driest month in millimetres, and t is the average temperature of the driest month in degrees Celsius (Alhajeri et al., 2015). The aridity index is unitless, with low aridity index value equating to a drier environment (Baltas, 2007).

Statistical Analyses

Principal component analysis (PCA) was used to explore the relationship of cochlea parameters among our samples with R (R Development Core Team, 2012). We used the R “Geiger” and “phytools” packages for phylogenetic bivariate linear regressions (PGLS) and non-phylogenetic (GLS) regressions of log-transformed mean species values for cochlea parameters and body mass in order to account for phylogeny and allometry. The correlation between the bullaCS and cochlea parameters was also tested with non-phylogenetic (GLS) general least squares regression models in R. The relationship of bullaCS and cochlea parameters with aridity index, elevation and habitat was also tested with GLS.

RESULTS

Cochlea variation among our samples (Otomyini and Gerbillinae)

For the variability of the cochlea variables among the species, one-way MANOVA revealed a significant difference between the species (Wilks’ $\lambda = 0.0008$, F (45, 432.5) = 37.36, $p < 0.00001$). The interspecies pair-wise differences using Tukey’s and Mann-Whitney pairwise tests are reported in Table B.4, bonferroni-corrected at $p = 0.001$.

The PCA patterns between species with five (Figure B.2) and three variables (Figure 3.4) was similar and in order to prevent redundancies (as RECL = ECL/TUR), PCA with only three cochlea variables (OWA, RECL and CUR) was performed (Figure 4). In this case, the first two principal components (PC1 and PC2) explained 46.31% and 37.08% of the variation, respectively. The three arid species are separated/isolated from the other species when PC1 and PC2 are considered together. However, there is overlap among the *Otomys* species on PC1; *O. unisulcatus* and *O. barbouri* do not show any overlap (Figure 3.4). The PC loadings show that OWA, RECL and CUR are negatively correlated with PC1, with OWA having the highest correlation (Table B.3). Though OWA shows higher loadings, other parameters loadings are still high meaning it is the general cochlear size that is reflected in PC1. PC2 is a “shape vector” contrasting CUR (positive high loading) with RECL (negative high loading) (Table B.3). Individuals grouping at higher positive scores of PC2 have relatively tightly-coiled cochlea, i.e. a steeper gradient of curvature. Although there is considerable overlap on PC2, the gerbils (*Desmodillus auricularis, Gerbilliscus leucogaster and Gerbillus nigeriae*) group towards the top of the PC plot compared to Otomyini, showing more tightly coiled cochlea (Figure 3.4).

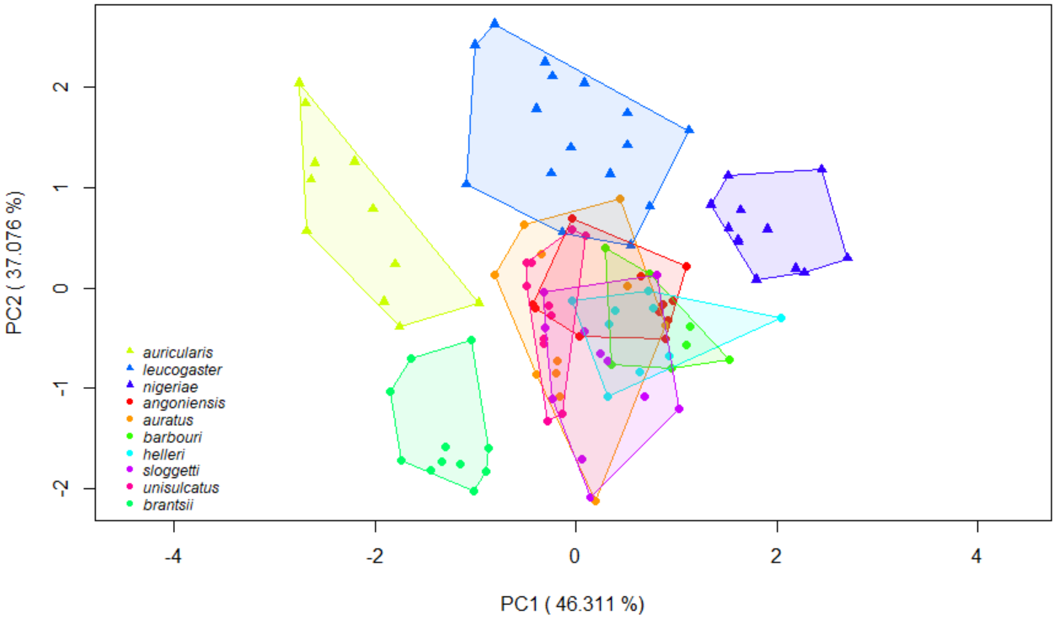


Figure 3.4: Principal Component Analysis of only CUR, OWA and RECL measured among our studied species; triangles = gerbils and circles = laminate-toothed rats.

Phylogenetic signal and allometry

Only for body mass we obtained a high phylogenetic signal that was significantly different from 0 at 5% level (p = 0.0203, Table B.2); this is not surprising as body mass is well known for its high phylogenetic signal in mammals (Blomberg et al. 2003; Kamilar & Cooper, 2013). In our study, the two main clades (Gerbillinae and Murinae) were highly divergent in body mass as gerbils are generally much smaller than Otomyini rodents.

Phylogenetically controlled regressions indicated the absence of any significant allometric associations between cochlea (OWA, CUR and RECL) or bullaCS and body mass ($p > 0.05$, Table 3.4, Figure B.3). For non-phylogenetic GLS regressions, OWA, CUR and bullaCS showed no significant associations with body mass. However, RECL scaled to body mass with a negative allometry ($r^2 = 0.53$, $p = 0.017$, Table 3.4), larger species having relatively shorter cochleae. However, looking at Figure B.3 linear regressions *G. nigeriae* seems to be an outlier, therefore we also ran analysis without this species. After removing *G. nigeriae* RECL and CUR were not significantly correlated with body mass ($p > 0.05$). However, OWA and bullaCS were scaled to body mass with an inverse allometry ($r^2 = 0.61$, $p = 0.013$; $r^2 = 0.48$, $p = 0.038$ respectively, Table 3.4), arid species having relatively larger OWA and bulla. Gerbils are distinctly smaller in size than laminate-toothed rats but have a proportionally larger RECL (Figure B.3A), resulting in significant results when inter-family comparisons were included.

In the case of the remaining variable CUR, phylogenetic correction considerably improved the association and slope between this variable and body mass (although still non-significant). Within each of the two subfamilies, CUR showed an association with body mass, although in both cases, these were non-significant based on separate PGLS analyses (results not shown, Figure B.3C). Since both families display similar ranges of values for CUR, when the data from both families are combined there was an almost horizontal regression line (Figure

B.3C). This is the complete opposite of the situation with respect to RECL where distinct inter-family differences in both body mass and RECL exist (Figure B.3A).

Table 3.4: Results for the non-phylogenetic and phylogenetic bivariate linear regressions to investigate the relationship between log-transformed mean species values for cochlear parameters, body mass (BodyM) and bulla centroid size (bullaCS). *indicates significant correlations (at the 5% level). *G.n. = Gerbillus nigeriae.*

Dep/Indep	**r^2**	**adj r^2**	**p**	**Intercept**	**Slope**	**Equations**
Non-phylogenetic						
OWA/BodyM	0.03	-0.09	0.64	-0.363	-0.09	y = -0.363-0.09x
OWA/BodyM_minus *G.n*	0.61	0.55	0.013*	2.483	-0.715	y = 2.483-0.715x
RECL/BodyM	0.53	0.47	0.017*	1.275	0.119	y = 1.275+0.119x
CUR/BodyM	0.001	-0.12	0.93	0.297	0.004	y = 0.297+0.004x
bullaCS/BodyM	0.03	-0.09	0.6	4.279	-0.056	y = 4.279-0.056x
bullaCS/BodyM_minus *G.n*	0.48	0.41	0.038*	5.769	-0.383	y = 5.769 -0.383x

Phylogenetic

Dep/Indep	**P**	**Intercept**	**Slope**	**Equations**	**AIC**
OWA/BodyM	0.34	-0.625	-0.001	y = -0.625-0.001x	7.423
RECL/BodyM	0.11	1.362	0.096	y = 1.362+0.096x	-23.283
CUR/BodyM	0.29	0.083	0.06	y = 0.083+0.06x	-24.013
bullaCS/BodyM	0.89	4.156	-0.022	y = 4.423-0.022x	-2.733

Associations between bullaCS, cochlea parameters and environmental variables

Although Maximum Likelihood (ML) tests of lambda coefficients showed a lack of phylogenetic signal in the cochlea and bulla variables, in the previous section we noted some differences in the body mass regressions of some bulla/cochlea variables between the Gerbillinae and Murinae (Otomyini). For this reason, we subsequently conducted separate analyses for combined data and for each subfamily separately. GLS showed non-significant correlations of RECL and CUR with bullaCS (Table 3.5, Figure B.4AC). However, the GLS of RECL vs. bullaCS in Otomyini showed a significant correlation (Otomyini, $r^2 = 0.67$, $y = 0.870+0.241x$, $p = 0.024$) (Figure B.4A). For all species and for Otomyini only, there were significant correlations between OWA and bullaCS (all species, $r^2 = 0.94$, $y = -7.386+1.642x$, $p < 0.0001$; Otomyini, $r^2 = 0.94$, $y = -6.476+1.416x$, $p = 0.0003$) (Figure B.4B).

BullaCS was not significantly correlated with either the aridity index ($p > 0.05$) or elevation (Table 3.5, Figure B.5AB), indicating that among our samples neither elevation nor aridity index influence the size of the bulla. However, after removing *G. nigeriae*, the correlation between bullaCS and aridity index becomes significantly inversely correlated ($r^2 = 0.604$, $y = 4.207-0.120x$, $p = 0.01$), indicating that bullae were larger in more arid environments (Figure B.5A). An ANOVA indicated that desert species (in this case both arid and semi-arid, see Table 1) had significantly greater bullaCS than mesic species ($F = 6.652$, $p = 0.033$; Table 3.6, Figure B.5C).

RECL, OWA and CUR were not significantly correlated with aridity index when all species were considered (Table 3.5, Figure B.6). Again removing *G. nigeriae* from all the analysis we only found a significant inverse correlation of OWA with aridity index ($r^2 = 0.56$, $y = -0.476-0.193x$, $p = 0.02$), indicating that OWA was larger in more arid environments (Figure B.6B). A non-significant correlation of RECL, OWA and CUR with elevation (Table 3.6, Figure B.7) was also observed. ANOVA of OWA, RECL and CUR indicated a non-significant association with habitat ($p > 0.05$, Table 3.6, Figure B.8); however, a separate ANOVA of all species minus *G. nigeriae* indicated that arid species had significantly greater OWA than mesic species ($p < 0.05$, Table 3.6).

Table 3.5: Results for the non-phylogenetic bivariate linear regressions to investigate the relationship between cochlear parameters and bulla centroid size (bullaCS); bullaCS and cochlea parameters with environmental variables. *indicates significant correlations (at the 5% level).

Dep/Indep	r^2	adj r^2	p	Intercept	Slope	Equations
OWA/bullaCS	0.94	0.93	<.0001*	-7.386	1.642	$y = -7.386+1.642x$
RECL/bullaCS	0.07	-0.04	0.5	1.239	0.138	$y = 1.239+0.138x$
CUR/bullaCS	0.16	0.06	0.3	-0.321	0.158	$y = -0.321+0.158x$
bullaCS /Arid	0.27	0.18	0.12	4.117	-0.072	$y = 4.117-0.072x$
bullaCS /Elev	0.12	0.01	0.3	4.491	-0.065	$y = 4.491-0.065x$
OWA/Arid	0.20	0.10	0.2	-0.643	-0.105	$y = -0.643-0.105x$
RECL/Arid	0.08	-0.03	0.4	1.772	0.020	$y = 1.772+0.020x$
CUR/Arid	0.05	-0.07	0.5	0.33	-0.012	$y = 0.331-0.012x$
OWA/Elev	0.05	-0.07	0.5	-0.238	-0.075	$y = -0.238-0.075x$
RECL/Elev	0.19	0.09	0.2	1.497	0.043	$y = 1.497+0.043x$
CUR/Elev	0.06	-0.06	0.5	0.441	-0.018	$y = 0.441-0.018x$

Table 3.6: Results for the Anova investigating the relationship between cochlear parameters, bullaCS and habitat, *G.n* = *Gerbillus nigeriae*. *indicates significant correlations (at the 5% level).

Dep/Inde	**F**	**P**
OWA/habitat	3.821	0.09
OWA/habitat_minus *G.n*	9.85	0.02*
RECL/habitat	0.77	0.41
CUR/habitat	0.86	0.38
bullaCS/habitat_with *G.n*	6.652	0.033*

DISCUSSION

Bullar and cochlear co-variation in desert-adapted gerbils and laminate-toothed rats

Morphological variations in the cochlea have been documented in a number of species, with different cochlea features being used to make predictions about hearing capabilities (Braga et al., 2015). West (1985) demonstrated that basilar membrane length (effectively ECL) can be used to predict the values of upper and lower limits of hearing (being inversely correlated with both), while the number of cochlear turns (TUR) can be used to predict octave range (positive correlation). Similar perceptions were confirmed by Vater & Kössl (2011), whilst Manoussaki et al. (2008) showed a strong correlation of CUR with low frequency hearing. Rosowski & Graybeal (1991) and Moggi-Cecchi & Collard (2002) demonstrated that OWA (proxy of stapedial foot plate) is correlated with the range of audible frequencies, with larger OWA correlated with low-frequency and smaller OWA with high-frequency sound detection.

In this study, we assessed the variation of the cochlea in relation to the tympanic bulla of Otomyini and Gerbillinae based on the above-mentioned features, and assessed the effect of environment, phylogeny and body size on the cochlea and bulla. Our analyses show some differences in the morphometry of the cochlea that can shed some light on the hearing capabilities of the investigated species. Two specialist desert-adapted species (*Desmodillus auricularis* and *Parotomys brantsii*) from diverse murid subfamilies are clearly both distinguishable from mesic and semi-arid taxa of both subfamilies by gross cochlea dimensions on PC1 (mostly particularly oval window area), as well as by general bulla size (extreme hypertrophy). Our findings are in line with previous studies that documented the distinctness of the auditory organ (be it tympanic bulla, middle ear and inner ear) of desert, subterranean, fossorial and non-desert rodents (Lay, 1972; Webster & Webster, 1975; Shaffer & Long, 2004; Lange et al., 2004; Alhajeri et al., 2015; Tabatabaei Yazdi et al., 2015; Mason, 2015, 2016). Since a large oval window is strongly correlated with sensitivity to lower frequencies (see above), the strong correlation we obtained between oval window and bullaCS ($r^2 = 0.94$) irrespective of phylogeny/subfamily, provides indirect evidence that bulla hypertrophy in desert rodents is indeed linked to detection of low frequency sounds.

Evolution of tightly coiled cochlea in gerbils (CUR)

Even though our results show no phylogenetic signal in the cochlea and bulla based on ML tests of the lambda coefficient (see Table B.2), the phylogenetic effect on the cochlea of the two subfamilies cannot be entirely excluded. For example, from PCA, we found that all three species of gerbils have a more tightly coiled cochlea (higher CUR) than the laminate-toothed rats, suggesting that not only the gross cochlea size is important in gerbils, but the cochlea curvature gradient may also be important. As mentioned above, the cochlear curvature gradient (CUR) is thought to relate to low-frequency hearing (Manoussaki et al., 2008). Even though both *P. brantsii* and *D. auricularis* are adapted to the same desert environment through bullar and cochlear “hypertrophy”, gerbils may be further adapted through possessing high CUR. These results suggest that *D. auricularis* and other gerbils may use different mechanisms to cope with environmental challenges (including aridity). Gerbillinae is largely characterized by having a hypertrophied bulla (although the degree of hypertrophy varies between species) and occupies mostly arid, open and semi-arid environments (Carleton & Musser, 2013; Alhajeri et al., 2015) as compared to Otomyini whose species are mostly adapted to mesic montane environments (Carleton, 2013; Monadjem et al., 2015; Wilson et al., 2017). The possession of tightly coiled cochlea in gerbils could be a legacy of their evolutionary history, being derived from an arid adapted ancestor as compared to *Otomys*, whose ancestor was from the Highveld of South Africa (Denys, 2003) and possibly only recently entered the desert environment.

However, even though gerbils show a more coiled cochlea than the laminate-toothed rats, it is not clear whether our findings give support to Manoussaki et al. (2008) argument, as no cochlea coiling had been studied in gerbils close-related outgroups.

Evolution of relatively long RECL, enlarged OWA and bulla in gerbils and desert-adapted whistling rats

RECL, OWA and tympanic bulla are thought to be related to lower and higher frequency thresholds, for mammals with longer RECL, enlarged OWA and bulla having sensitivity to lower frequencies and species with smaller size of these parameters having sensitivity to higher frequencies (Lay, 1972; West, 1985; Moggi-Cecchi & Collard, 2002; Braga et al., 2015). Our results show that distinctly smaller gerbils have proportionately longer RECL, enlarged OWA and bulla than larger-sized laminate-toothed rats (negative allometry with body mass). This would suggest that gerbils have higher sensitivity to lower frequencies than laminate-toothed rats. In spite of this, extreme desert-adapted individuals (*D. auricularis* and *P. brantsii*) in both tribes deviate from the predicted relationship by having even longer than expected RECL (Figure B.3A) and larger OWA and bullaCS. Our results therefore suggest that gerbils have the ability to hear lower frequencies than laminate-toothed rats, and over and above this, extreme desert-adapted gerbils, as well as desert-adapted whistling rats (*Parotomys*) have enhanced auditory sensitivity to low frequencies compared to other members of their respective subfamilies.

Association of cochlea morphology and hearing sensitivity

Gerbils have been reported to use high frequency ultrasonic calls in short distance vocalisations (Dempster & Perrin, 1991; Dempster et al., 1991; Holman, 1980; Dempster, 2018) during encounters between individuals. This follows from the observation that to accurately localise sound, smaller mammals having short inter-aural distance need to use higher frequency sounds for communication (Heffner & Heffner, 1992; Heffner et al., 2001). We posit that gerbils (and in particular, extreme desert-adapted gerbils) have good hearing sensitivity in both low frequency sounds (e.g. vibrations and low frequency sounds known to be generated by potential predators like snakes and owls; Dempster, 2018), as suggested by our morphological data, but also high frequency sounds (i.e. ultrasonic sounds used in conspecific communication). This kind of auditory breadth and sensitivity has also been detected in the gerbil *Meriones unguiculatus* (Ryan, 1976) and in *Dipodomys merriami* from the Family Heteromyidae (Heffner & Masterton, 1980). However, it is not clear if the gerbils in our study follow the frequencies trend of *M. unguiculatus* and *D. merriami* (i.e. including broad range of good sensitivity in the middle), as no audiograms are available for these species. The two Heteromyidae rodents are known to use low frequency foot drumming (Randall, 2001), whether this is solely for communication with conspecifics (warning in the presence of predators) or to deter predators or both is still debatable.

All Southern African gerbil species investigated so far use high-frequency ultrasonic vocalisations for short-range conspecific communication; however, while occasional foot drumming was observed in captivity, their functionality has not yet been discussed. Foot-drumming was not observed in *D. auricularis* colonies in captivity, even though it was considered likely for this species to use foot-drumming to communicate over long distances (Dempster & Perrin, 1994; Dempster, 2018). In case of *P. brantsii*, vocal alarm calls are relatively low audible frequencies (Le Roux et al., 2002), and no information about foot-drumming in this species is known. I.e. while foot drumming is known in gerbils (even though not observed in *D. auricularis*) but not for *Parotomys* species, the cochlear adaptation of gerbils to lower frequencies as compared to *Parotomys* might be explained by this.

In conclusion, our data cannot decisively support either the communication and/or the predator avoidance hypothesis, as no conclusive data are known pertaining to low frequency long distance communication of *D. auricularis* and *P. brantsii.* Even though increased CUR is generally associated with lower frequency hearing, it may be, however, that in gerbils increased CUR is not adapted to hearing per se, but it could be a structural constraint of the smaller head size of gerbils compared with laminate-toothed rats, allowing more efficient “packing” of the basilar membrane (West, 1985).

Environmental correlates of cochlea and bulla characters

After correcting for phylogeny and body size, we are left with environmental factors that we predict would impact the morphology of bulla and in turn cochlea. The impacts of aridity, elevation and habitat type on the bullar morphology of rodents has long been recognized, with bulla inflation correlated with deserts, high elevation and open microhabitats (Lay, 1972; Webster & Webster, 1980; Kotler, 1984; Zhao et al., 2013; Tabatabaei Yazdi et al., 2014; Alhajeri et al., 2015). Analysing the above-mentioned relations with regards to bulla and cochlea, specifically in relation with aridity, elevation and habitat, we found some conformation and exceptions. BullaCS and OWA are shown to be correlated with aridity index and desert habitats. Interestingly, the variability in parameter values is shown to be much higher among arid-region species than mesic ones in Figure B.4C & B.7. The plots seem to be strengthening our argument of degree of specialization of cochlea and bulla in arid adapted species. To speculate slightly, it seems like selection is acting on these structures in arid species as it affects hearing and hearing has been shown to be important in arid environments as compared to mesic ones with more closed vegetation. This may be explained by diversifying/disruptive selection.

Inflated bullae (middle ear), and cochlea modification is believed to aid in communication with conspecifics or predators through foot-drumming, hitting, and stomping; however, this observation does not seem to directly apply to our study animals, as no detailed indication of vibrations being produced by the two subfamilies has been documented. However, occasional and unpredictable bouts of foot drumming in captivity have been observed in gerbils (Dempster & Perrin, 1990; Dempster, 2018).

We did not find any correlation between cochlear and bullaCS and elevation, contrary to what has been reported in Zhao et al. (2013, increase of bulla size with altitude in gerbils); Tabatabaei Yazdi et al. (2015, positive correlation of bulla size with elevation in jirds) and Liao et al. (2007, who instead found a decrease in bulla size with increasing altitude in Daurian pikas, Ochotonidae). Our observed trend of no change refutes the prediction that if openness of the environment is a feature of high elevation then alpine environments should show some response in terms of bulla size and cochlea modification, as high elevations are mostly comprised of open habitats similar to desert environments. The increase in bullar size is also said to compensate for a reduction in oxygen partial pressure and strong winds, which are known to impair auditory acuity at high elevations (Zhao et al., 2013). Zhao et al. (2013) proposed that a reduction in oxygen partial pressure (hence hypoxia) and strong winds at high elevation may cause a decrease in auditory sensitivity and sound localisation accuracy, therefore the increase in auditory bulla size with elevation might be a compensatory adaptation against this selective pressure. We included three Otomyini species known to be mostly confined to very high alpine habitats (> 3000m) in Ethiopia (*O. helleri*), Mt Elgon (*O. barbouri*) and the South African high Drakensberg (*O. sloggetti*) and none of these species showed any departure in measured cochlear features and bulla from their congeners found at lower elevations (*O. angoniensis, O. auratus, O. unisulcatus*). The highest elevations experienced by these Afroalpine species may still not be sufficient to induce critical levels of hypoxia or hypothermia in these species. However, the elevational range of the species reported above to have inflated bulla at high elevations is lower and their habitats is mostly in arid regions when compared to that of our *Otomys* species. Alternatively, these species may exhibit behavioural and/or physiological adaptations to hypothermia. Since *Otomys* species are typically relatively large and highly sedentary rodents, their metabolic needs may be reduced such that hypoxia does not pose significant challenge necessitating morphological evolutionary adaptation. An investigation of the extent of possible behavioural or physiological responses to hypothermia in these Afroalpine rodents would be an interesting future study.

Among the gerbils examined here, it seems that *D. auricularis* is the only species that is showing marked bullar and cochlea hypertrophy. Although occurring in sandy semi-arid Sahel habitats in West Africa, *G. nigeriae* does not show predictable response in either bulla or cochlea dimensions. Similarly, with laminate-tooth rats, only *P. brantsii* showed a marked response, while the semi-arid Karoo bush rat *O. unisulcatus* overlaps completely with other mesic species in the tribe. There could be a threshold between arid and semi-arid habitats, whereby only truly arid habitats evoke an adaptive response. This might be related to cover, as in *O. unisulcatus*, where it was suggested to have relative small bulla size due to it occupying elaborate protective stick-nests (Taylor et al., 2004), since true deserts offer no cover compared with more semi-arid habitats where shrubs and ground cover are usually present. However, *P.*

brantsii does occupy semi-arid thickets in the Karoo where it coexists with *O. unisucatus*, suggesting that vegetation cover may not be such a critical factor. A wider sample of species of both subfamilies including more arid and semi-arid species could be instructive. Our sample sizes of specialized desert species were relatively small.

Concluding, this study shows that desert adapted laminate-toothed rats and gerbils both use bulla and associated cochlea hypertrophy, particularly desert species. Gerbils further show tightly coiled cochlea but the significance of this is debatable and may not have anything to do with adaptations to aridity. More work with a larger sample size that covers all habitat types of the three tribes (Taterillini, Gerbillini and Otomyini) needs to be assembled. Attention should focus on the possibility of foot drumming in Southern African gerbils, as our results predict that gerbils should have heightened sensitivity to low frequency sounds.

CHAPTER FOUR: ENDOCRANIAL SIZE AND SHAPE IN TWO AFRICAN RODENT SUBFAMILIES (GERBILLINAE AND MURINAE) FROM VIRTUAL ENDOCASTS

SUMMARY

Relative or absolute brain size is often considered a determining factor in cognitive abilities, behavioural flexibility, and intelligence. The X-ray microtomographic-based 3D virtual imaging and associated analyses were used to investigate endocranial organization and size differences in rodents (Otomyini and Gerbillinae) in order to determine the extent of the endocranial variation. Here we report brain size differences in 10 species of African rodents and test the association of the brain size with different environmental variables. Natural history components such as diet and habitat were proposed to be the probable causes of the size difference. Furthermore, none of the tested environmental variables were significantly correlated with brain size.

In order to compare endocranial morphology a landmark-free registration method based on smooth and invertible surface deformation was used. Our analyses from the deformation-based approach on the variation of endocranial morphology between Otomyini and Gerbillinae indicate that the shape differences of the parafloculli, olfactory bulbs, medial ventral cortex and posterior ventral cortex are more pronounced in laminate-toothed rats than in the gerbils; only three species of gerbils are included in the study, as compared to seven laminate-toothed rats. Furthermore, not much shape variation was seen within each group (Gerbillinae and Murinae).

INTRODUCTION

Relative or absolute brain size variation between and within species has been of interest to scientists studying cognition or behavioural flexibility in animals (Reader & Laland, 2002; Byrne & Corp, 2004; Sol et al., 2008; Møller, 2009). Brain size is reported to be variable across mammals, with certain groups having larger brains or particular regions relative to their body mass and the rate of increase varies between groups (Jerison, 1973). Numerous factors have been shown to explain the variability of brain size, including phylogeny, ecology, basal metabolic rate, behaviour, sensory complexity and life histories (Jerison 1973; Sacher & Stafeldt 1974; Eisenberg & Wilson 1978; Clutton-Brock & Harvey 1980; Eisenberg & Wilson 1981; Harvey & Bennet, 1983; Hoffman, 1983; Sheppey & Bernard 1985; Gittleman, 1986; Bernard et al., 1988; O'Shea & Reep 1990; Pagel & Harvey 1990; Joffe & Dunbar, 1997; Barton, 1998; Isler & Schaik, 2006; Sobrero et al., 2011) or the interaction of these factors. Several hypotheses have been proposed to explain the advantages of larger brains (van Schaik & Deaner, 2003; Dunbar & Shultz, 2007; Sol, 2009), and many of these have assumed that enlarged brains carry cognitive advantages. Amongst other advantages, larger brain has been associated with increased habitat complexity, variety of life styles such as diet, sociality, and nocturnality (Pirlot & Stephan, 1970; Jerison, 1973; Eisenberg & Wilson, 1978; Clutton-Brock & Harvey, 1980; Mace et al., 1981); predation pressure (Kotrschal et al., 2015); life history variables such as longevity, age at maturity and litter size (Sacher, 1975; Sacher & Staffeldt, 1974; Eisenberg & Wilson, 1981). However, even though a large brain has been shown to have potential benefits, brain tissue is said to be extremely energetically costly (Aiello & Wheeler, 1995; Sobrero et al., 2011).

The advantages of larger brains are not limited to the above-mentioned, but it has also been shown to be of advantage at high-altitude environments. Not only are the high-altitude environments characterized by reduced oxygen availability and reduced ambient temperature

(Storz et al., 2010), but also open habitats, intense seasonal changes, longer periods of snow cover, i.e. highest environmental variation (Sayol et al., 2016). All these have been hypothesized to have an impact on brain size and/or cognitive abilities/performance on high altitude adapted organisms. For example, Sayol et al. (2016) showed that birds inhabiting higher altitudes regions tend to have relatively larger brains compared with those living at lower altitudes. Similarly, high altitude Alaskan chickadees (*Poecile atricapilla*) had significantly larger hippocampal volumes, an area of the brain that plays a role in memory, hence, better spatial memory (Pravosudov & Clayton, 2002). Temperature variability has also been reported to shape variations in brain size (Luo et al., 2017). Environmental harshness linked to colder climates was shown to be positively correlated with brain size in birds (Vincze, 2016) and humans (Ash & Gallup, 2007; Naya et al., 2016). Similarly, large-brained parrots were shown to inhabit areas of high degree of seasonal temperature variation (Schuck-Paim et al., 2008). In contrast, temperature variability was found to have no effect on the brain size of *Hylarana guentheri* frog species (Gu et al., 2017) but a decrease in relative brain size with increasing environmental temperature variability has been reported in certain species of frogs (Luo et al., 2017).

As mentioned in the previous chapters, studies focusing on morphological variation in rodents are vast; however, studies that concern changes in morphology and size of the brain are few (Bertrand & Silcox, 2016). Brain size variation has also been shown to be influenced by differing factors in rodents (Pilleri et al., 1984; Mace et al., 1981). For example; enlarged brains has been reported in Heteromyidae kangaroo rats, *Peromyscus leucopus*, *Microtus pennsylvanicus*, Octodontid taxa (*Tympanoctomys, Octodontomys* and *Octomys*), African *Colomys goslingi*, *Spalax ehrenbergi*, and some Southern African Sciuromorpha and Myomorpha, and these were associated with complex auditory-sensory and locomotory functions, urbanization, higher behavioural complexity, habitat and diet type (Mace et al., 1981;

Stephan & Dieterlen, 1982; Hafner & Hafner, 1984; Nevo et al., 1988; Bernard & Nurton, 1993; Monadjem, 1998; Vassallo & Echeverría, 2009; Snell-Rood & Wick, 2013). In contrast smaller brains have also been reported in Bathyergidae, Geomyidae and South African Hystricomorpha and Myomorpha (Mace et al., 1981; Bernard & Nurton, 1993). Kverková et al. (2018) showed that relative brain size was not associated with the social system in the African mole-rats.

Rodents are an ideal group to compare brain size variations because they occupy different niches, differ along several life styles, including habitat, diet and activity period. They can be arboreal, aerial, terrestrial, semiaquatic, burrowing, and even rock-dwelling (Krubitzer et al., 2011). The diet of rodents is also very diverse: some are herbivorous, others omnivorous (Landry, 1970), insectivorous (Pizzimenti & de Salle, 1980), and even fungivorous (Cork & Kenagy, 1989). In this chapter, we describe the endocranial volume (a proxy for brain size [Iwaniuk & Nelson, 2002; Isler et al., 2008]) variations of 10 species of African rodents and test if certain environmental variables/factors may correlate with these variations. Additionally, we compare the endocranial morphology between the two groups (i.e. Gerbillinae and Muridae) and within them and highlight the nature and extent of the differences if there are any. From these objectives, we predict that a) brain size should scale with body size with allometric coefficient of 0.74 (Eisenberg, 1981) or 0.643 (Pilleri et al., 1984); b) brain size should vary with environmental factors (a significant positive correlation between brain size and elevation; the unpredictable open, arid, climatic fluctuating desert environment should select for larger brain size).

MATERIALS AND METHODS

Study samples

This chapter used the same samples (Table 4.1) and 3D scanning procedure reported in Chapter 3 (see Chapter 3 for more details).

Table 4.1: Composition species and sample size used in this study. N: number of individuals; M: male; F: female.

Species	N	Country (Locality)	Collections	Sex (M, F)
Otomyini				
Otomys angoniensis	11	South Africa, Zimbabwe, Swaziland, Zambia	Ditsong[a]	(6, 5)
Otomys auratus	11	South Africa	Ditsong[a]	(5, 6)
Otomys unisulcatus	11	South Africa	Ditsong[a]	(6, 5)
Otomys helleri	09	Ethiopia	MNHN[b]	(4, 5)
Otomys sloggettii	11	South Africa, Lesotho	Ditsong[a]	(6, 5)
Otomys barbouri	07	Uganda	MNHN[b]	(5, 2)
Parotomys brantsii	11	South Africa	Ditsong[a]	(5, 6)
Gerbillinae				
Gerbilliscus leucogaster	16	Zimbabwe, South Africa, Malawi, Tanzania, Angola	Ditsong[a], MNHN[b]	(8, 8)
Desmodillus auricularus	11	South Africa, Botswana, Namibia	Ditsong[a]	(5, 6)
Gerbillus nigeriae	12	Mauritania, Burkina Faso, Niger, Mali	MNHN[b]	(6,6)

[a] Ditsong National Museum of Natural History, Pretoria; [b] Muséum National d'Histoire Naturelle, Paris

Endocast reconstruction

For endocranium extraction and reconstruction (Beaudet, 2015), a specifically developed software for automatic virtual extraction of endocast "Endex" (Subsol et al., 2010) was used. Before importing data to Endex, the surface of the entire skull was generated without smoothing and saved in “obj” format (Figure 4.1A) in Avizo v8.0. This was then imported to Endex and converted into "point cloud". This point cloud was then imported into Endex where a sphere was inserted and positioned at the centre of the intracranial space (Figure 4.1B). The sphere then underwent several phases of expansion until it approached as close as possible the internal surface of the bone. Once the deformation of the sphere was completed (Figure 4.1C), its mesh was exported in “obj” format and then converted to “ply” format by MeshLab v1.3.2 (Figure 4.1D). The final step involved the refinement of the automatic segmentation by converting the surface of the endocrania into 2D slices under Avizo v8.0. with the use of "Scan Surface to Volume" module. These sections are then merged with the segmented bone sections with the module "Arithmetic", which allowed the correction of zones where the automatic segmentation has crossed closed regions (where bone is possibly thin, Figure 4.1E). The slices that were not accessed by the Endex sphere but still part of the endocranium where manually segmented with "Interpolation" module, and thus attributed to the material representing the endocranium.

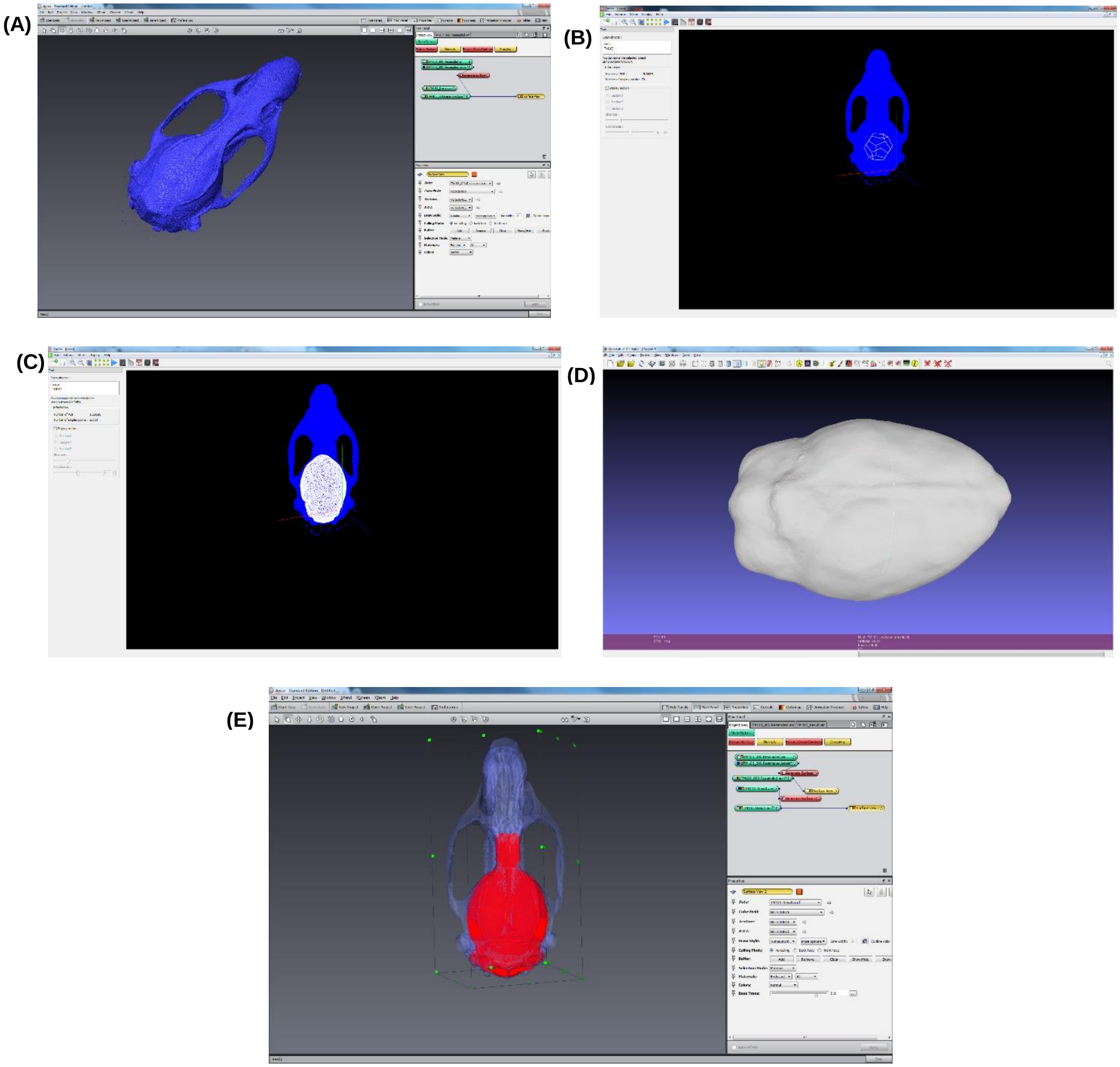


Figure 4.1: The different stages of the automatic segmentation of an endocranium with Avizo, Endex and meshlab. The white and red parts represent the virtual endocasts.

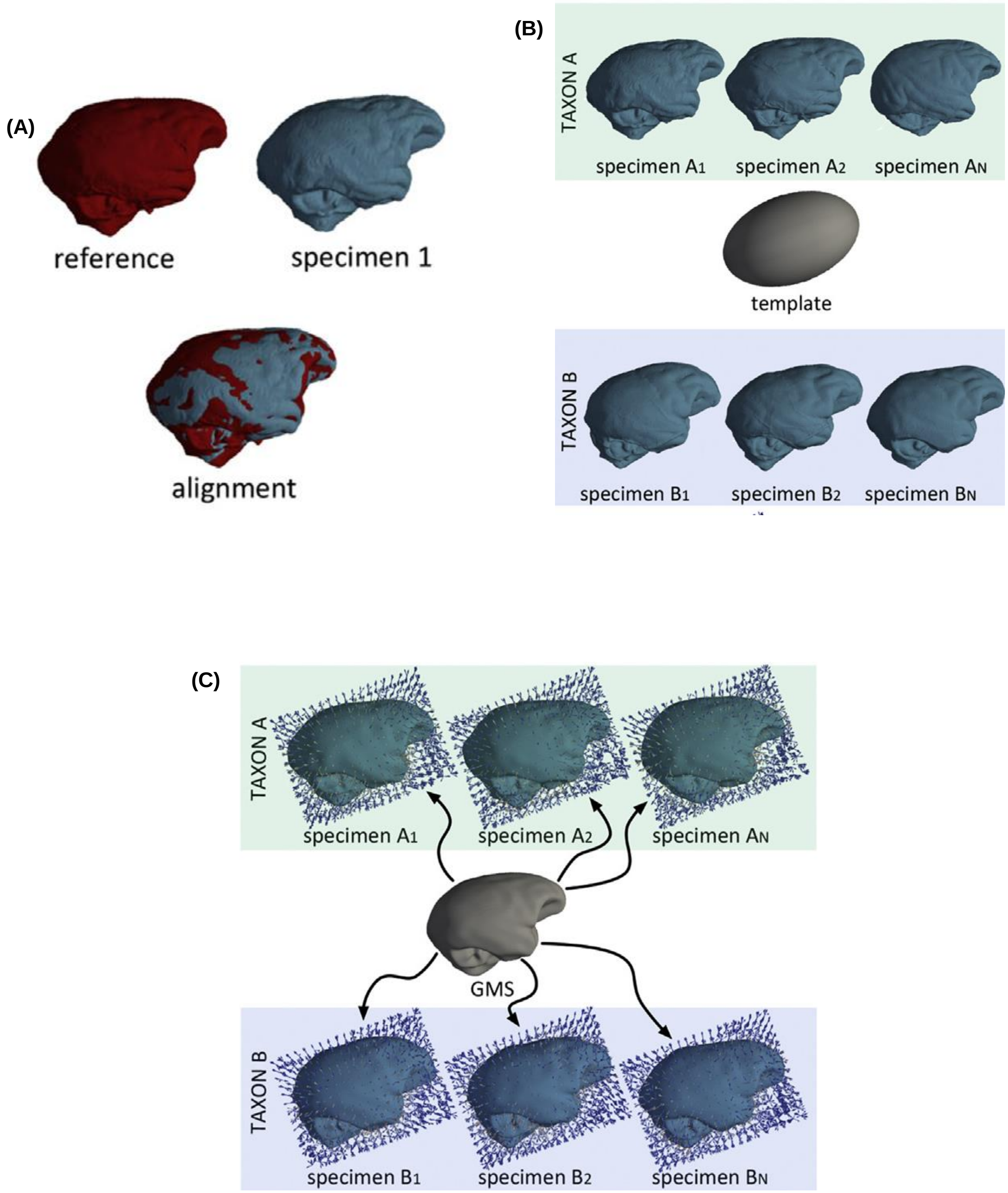
Endocranial volumes

Endocranial volumes (ECV) were measured in 110 specimens of gerbils (39) and laminate-toothed rats (71). Endocranial volume measurements were computed from the unsmoothed 2D segmented surfaces for each specimen with the module “Material statistics” available in Avizo v8.0.

Deformation models

Endocranial morphology between and within the two groups were compared using diffeomorphism, which is a size-independent and landmark-free method based on smooth and invertible surface deformation (Durrleman et al., 2012; Dumoncel et al., 2014; Beaudet et al., 2016, 2018). However, before carrying out deformation models a preprocessing step that involves data preparation was carried out i.e. the endocranial surfaces were resampled to 100,000 faces with the module “Remesh surfaces” in AVIZO to reduce the computation time. From the resampled surfaces, one surface was randomly chosen as a reference surface and all the remaining surfaces were automatically aligned in position, orientation and scale to this reference surface using Iterative Closest Point algorithm (Figure 4.2A; Besl & McKay, 1992).

In order to generate the average shape of our sample, an artificial surface (an ellipsoidal template) was created and aligned to our data surfaces. From the set of aligned surfaces a shape model (called global mean shape, GMS) was computed through the deformation of the template using the software Deformetrica (http://www.deformetrica.org/; Durrleman, 2010; Beaudet et al., 2016; 2018; Figure 4.2BC). In addition to the GMS, the computation also yielded the deformation fields from the GMS to each specimen (Fig. 2C). Based on the results from the third step, the taxon mean shape (TMS) was computed for each species (Figure 4.2D). The magnitude of the displacements of the deformation process was rendered by colour maps from dark blue (lowest displacement values) to red (highest displacement values) on the endocast surfaces (Figure 4.2E; Beaudet et al., 2016, 2018).



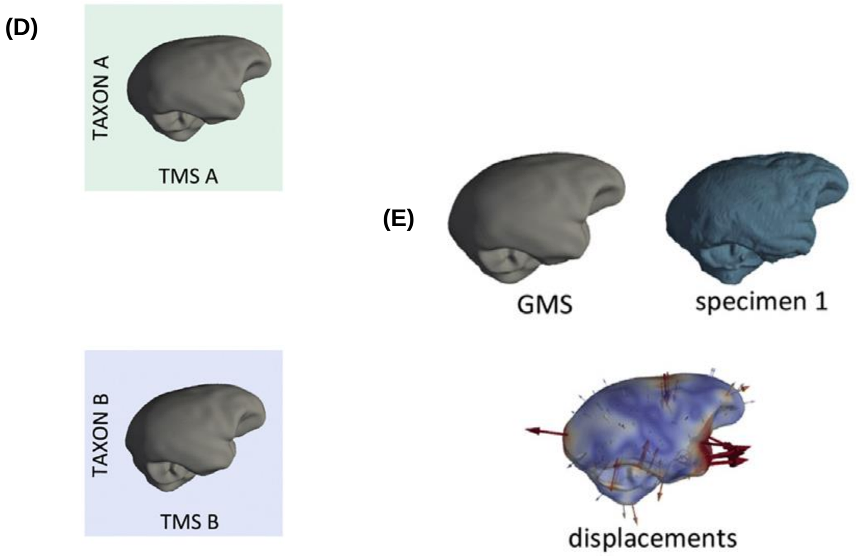


Figure 4.2: Successive processing steps in the deformation-based shape comparisons. First, the surfaces are aligned in position, orientation, and scale with respect to a reference surface (A). From an initial set of aligned surfaces and an ellipsoidal template (B), the deformation fields, the global mean shape (GMS), and the registered surfaces are computed (C) and the taxon mean shapes are generated (TMS) (D). The distances from the GMS to the specimens are rendered by colour maps and vectors (E). In C, the arrows represent the deformations from the GMS to individuals. N indicates the maximum number of specimens included in the sample. Illustration taken from Beaudet et al. (2016).

Statistical Analyses

We used the R “Caper” and “phytools” packages for phylogenetic bivariate linear regressions (PGLS) and non-phylogenetic (GLS) regressions of log-transformed mean species values for endocranial volume and body mass in order to account for phylogeny and allometry. In order to see any endocranial morphology variations between the laminate-toothed rats and gerbils; within the gerbils and laminate-toothed pairwise distance deformation was conducted/computed and the Multidimensional scaling (MDS), which yields a map of items arranged in proximity to others to reflect groupings was used to show this relationship. Deformation displacement maps (with Paraview software) were used to show the variations in endocranial morphology.

RESULTS

Endocranial volumes

The means and standard deviations of endocranial volumes measured for all 10 species are presented in Table C.1. We found a correlation between body mass and endocranial volume (ECV) in our sample. In the non-phylogenetic regression (GLS), there is a significant positive relationship between body mass and ECV ($r^2_{adj} = 0.86$, $y = -1.791+0.476x$, $p < 0.0001$, Figure 4.3) and after correcting for phylogeny (using PGLS), this relationship is still present ($r^2_{adj} = 0.75$, $y = -1.883+0.497x$, $p = 0.001$, Figure 4.3). Larger species have relatively smaller brains, however, *Desmodillus auricularis, Otomys sloggetti*, *Otomys auratus* and *Gerbilliscus leucogaster* have significantly larger brains relative to their body size (Figure 4.3). Figure 4.3 also shows that *Gerbillus nigeriae*, *Otomys helleri*, *Otomys barbouri*, *Otomys angonienis* and *Parotomys brantsii* fall below the regression line and thus have small brains relative to their body size. The allometric exponent describing the functional trend for our rodent species (slope = 0.50) is steeper/shallower and less than the exponent value for brain size: body size scaling across mammals (slope = 0.74; Eisenberg, 1981) and closer to the one for rodents (slope = 0.64; Pilleri et al.,1984).

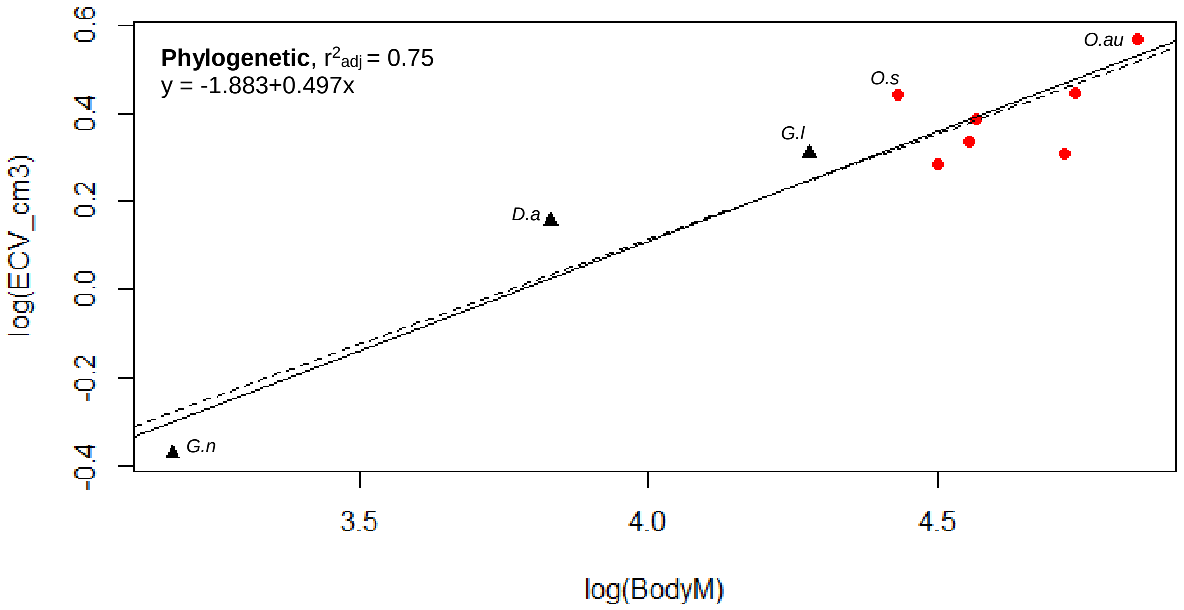


Figure 4.3: Regression plot of log endocranial volume (ECV) versus log body mass for gerbils (black triangles) and laminate-toothed rats (red circles) specimens. PGLS ($r^2_{adj} = 0.75$, $y = -1.883+0.497x$, solid line) and GLS ($r^2_{adj} = 0.86$, $y = -1.791+0.476x$, $p < 0.0001$, dotted line). *G.n* = *Gerbillus nigeriae*, *D.a* = *Desmodillus auricularis*, *G.l* = *Gerbilliscus leucogaster*, *O.s* = *Otomys sloggetti* and *O.au* = *Otomys auratus*.

Associations between endocranial volume and environmental variables

Endocranial volume was tested against aridity index, habitat and elevation for both combined data and Otomyini only, and additionally for individuals per species. The analysis of individuals per species were added based on Gonda et al. (2011, and reference therein) suggestion to also look at brain size variations in populations of the same species. Based on the GLS, none of the previously mentioned variables could explain variations in brain size among our samples when all species and Otomyini (separately) were considered, so the statistical results that will be presented are those that included all the species combined. Brain size (ECV) was not significantly correlated with aridity index ($r^2_{adj} = 0.16$, $y = 0.16785+0.10927x$, $p > 0.05$,

Figure 4.4A); however, when individuals per species were considered only *O. sloggetti* was significantly positively correlated with aridity index ($r^2_{adj} = 0.46$, $y = 0.19225+0.16097x$, $p = 0.01$, Figure 4.4B). Similarly, elevation was not significantly correlated with ECV ($r^2_{adj} = 0.16$, $y = -0.76942+0.15125x$, $p > 0.05$, Figure 4.4C); however, looking at individuals per species elevation was significantly positively correlated with ECV in *O. sloggetti* ($r^2_{adj} = 0.53$, $y = -1.0224+0.1959x$, $p = 0.01$, Figure 4.4D) only. ANOVA did not show any significant correlation between type of habitat and brain size ($F = 8$, $p > 0.05$, Figure 4.4E).

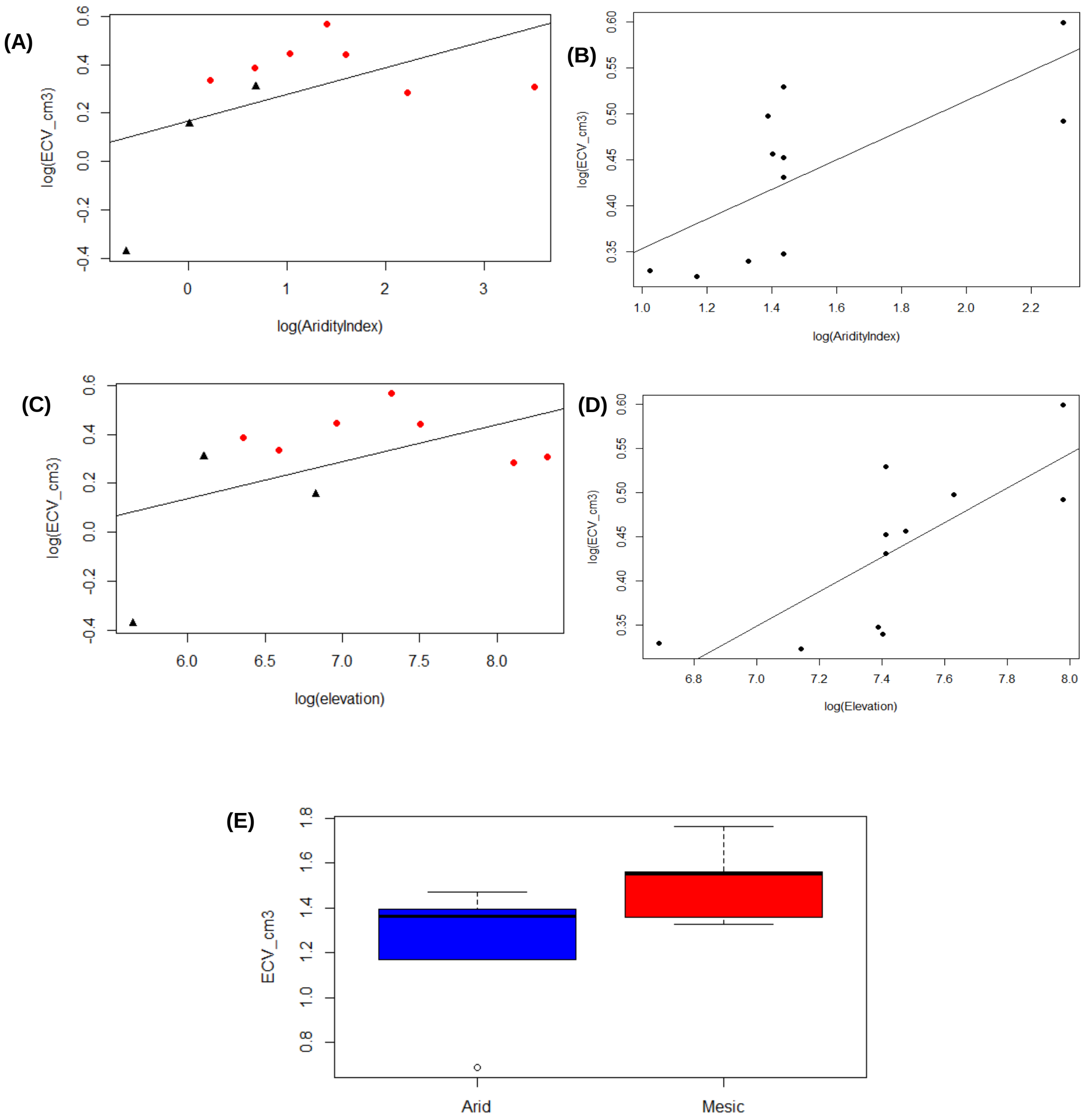


Figure 4.4: Regression plots for the ECV versus aridity index for all species (A, gerbils = black triangles, laminate-toothed rats = red circles) and *Otomys sloggetti* only (B); elevation for all species (C, gerbils = black triangles, laminate toothed rats = red circles), *O. sloggetti* (D); boxplots of ECV versus habitat type for all species combined (E).

Endocranial morphological variations

The endocranial morphology comparisons were made between the 10 species. Pairwise deformation distances are listed in Table S2. To improve the visualization of the results, the pairwise deformations distances are represented in a two-dimensional MDS plot (Figure 4.5). Figure 4.5 shows that the genus *Otomys* species have similar endocranial morphology, whilst all the gerbils and *P. brantsii* have variable morphology compared to the *Otomys* variations. The displacement map of the deformations among our sample shows a more pronounced deformation along the medial ventral cortex (MV) and posterior ventral cortex (PV) in *O. angoniensis, O. auratus, O. barbouri, O. sloggetti, O. helleri* and *O. unisulcatus*; with a more elongated paraflocculi in *O. barbouri, O. helleri, O. sloggetti* and *G. leucogaster*. Only *O. angoniensis* and *O. helleri* show a much elongated olfactory bulb, with *P. brantsii* only showing grooving along the cerebral peduncle. *Gerbillus nigeriae* and *D. auricularis* both show much less elongated paraflocculi (Figure C1,2). However, comparing the laminate-toothed rats with the gerbils, laminate-toothed rats shows elongated paraflocculi, olfactory bulbs and more pronounced deformations along the brainstem, PV and MV. As expected, there is no much endocranial variations within each group, except for *P. brantsii* that is different based on the cerebral peduncle within the Otomyini and *G. leucogaster* on the paraflocculi within Gerbillinae.

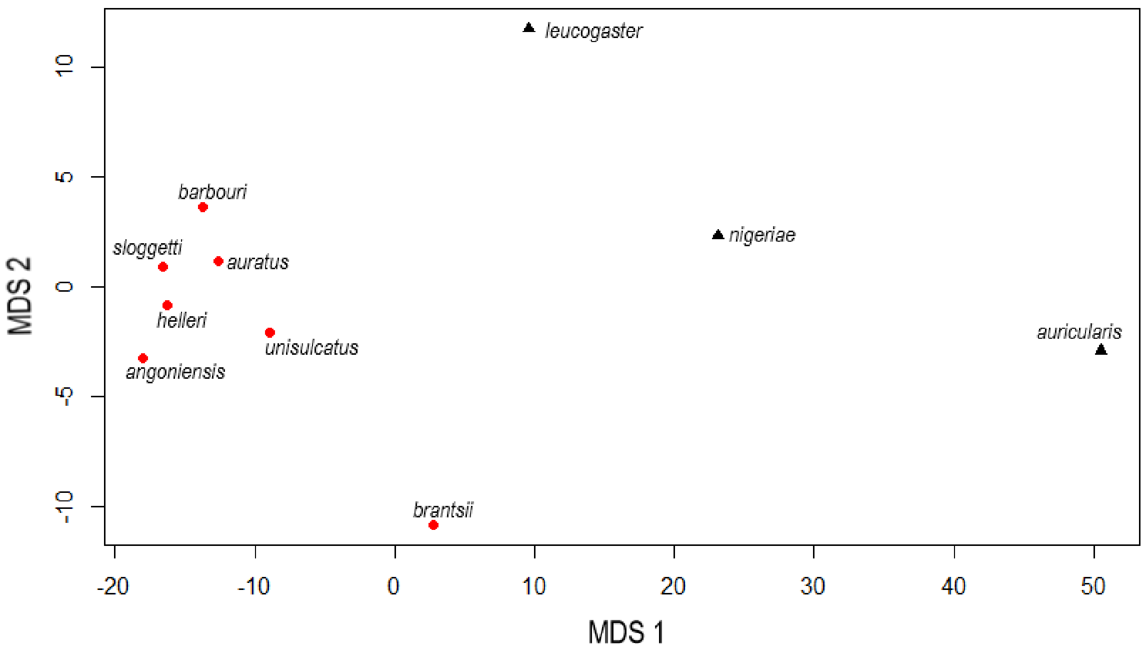


Figure 4.5: Multidimensional Scaling (MDS) map based on the pairwise distance matrix of the GMS deformations, gerbils = black triangles and laminate-toothed rats = red circles. The proximity of the samples to each other indicates how similar they are to each other.

DISCUSSION

Allometry of endocranial volume

When phylogeny is taken into account, brain size and body mass relationship is still significant with body mass explaining 75% of the variation. After correcting for phylogeny and body mass, the residual amount of variation not explained by body size in our sample might be associated with specific species habits as McNab & Eisenberg (1989) concluded that relative brain size is associated with the habits of the species. The results of this study interestingly corroborate those of Monadjem (1998) and Bernard & Nurton (1993), who also found *O. unisulcatus, O. angoniensis* and *P. brantsii* to have smaller relative brain size (Bernard &

Nurton, 1993; Monadjem, 1998) and *G. leucogaster* having a larger one (Monadjem, 1998). However, they both used different methods than the present study, Bernard & Nurton (1993) used cranial volume as a proxy for brain size by filling the cranial cavity with lead shot, which was then weighed, and Monadjem (1998) used the actual brains weights. Activity regimen and diet were said to be the probable cause of smaller brains in these species, but as for *G. leucogaster* its relatively large brain size was hypothesized to be due to its enlarged auditory bullae (Monadjem, 1998); a similar perception shown for the kangaroo (*Dipodomys*) rats where their auditory bulla was positively associated with their brain size (Hafner & Hafner, 1984). However, the eco-ethological hypothesis (which predicts correlation between relative brain size and degree of motor or sensory specialization; Hafner & Hafner,1984) cannot explain the variation in brain size among our species as the more hypertrophied bulla (associated with auditory specialization) species (*P. brantsii*) than *G. leucogaster* has a negative brain size (Figure 4.3). Nonetheless, the kangaroo rats' brain size significant correlation with auditory bulla did not demonstrate any causal links (Hafner & Hafner, 1984).

In general, it is suggested that bigger brains are associated with habitat type (with forest-dwelling species having relatively bigger brains), diet (with omnivores having larger brains than folivores), activity (with nocturnal species having bigger brains than diurnal species), locomotion (arboreal species having larger brains), and longer lifespan (Mace et al., 1981; Mace & Eisenberg, 1982; Meier, 1983; Bernard & Nurton, 1993; Monadjem, 1998; Gonzalez-Lagos et al., 2010). Some of these arguments might be used to explain larger brains in *G. leucogaster, D. auricularis, O. sloggetti* and *O. auratus*. Both *G. leucogaster* and *D. auricularis* share similar ecologies such as diet which is omnivorous and nocturnal activity (Dempster, 2013; Nel, 2013; Taylor, 2013b; Monadjem et al., 2015), these may be influencing their brain size variations; however, *G. nigeriae* shares similar ecology. Mace et al. (1981) mentioned that the above-mentioned ecologies are interrelated and after accounting for other ecological differences diet and habitat were the most distinguishing variables in brain size. Therefore, it is possible that coupled with their diet and activity, habitat may be the determining factor in the two gerbil species. The same can be said about Otomyini species, as they also share similar diet and activity (Carleton, 2013; Monadjem et al., 2015). So, the highly patchy, high-altitude grasslands and alpine habitats in *O. auratus* and *O. sloggetti* (Nengovhela et al., 2015, Monadjem et al., 2015), respectively, may be driving their brain enlargement; however, *O. barbouri* and *O. helleri* are also confined to high altitude. Meaning high altitude per se may not be the determining factor of brain enlargement in this species but the interaction of different factors. However, within Otomyini there was no significant correlation between ECV and body mass (results not shown).

Environmental correlates of brain size

Analyzing the relations (for all species combined) between brain size and aridity, elevation and habitat between species, we see no significant correlation; however, at an individual level there are some correlations. Brain size is shown to be correlated with aridity index and elevation in *O. sloggetti*, respectively. Larger brain size is believed to be of an advantage at high elevation and cooler environments (Ash & Gallup, 2007; Vincze, 2016; Sayol et al., 2016). Two hypotheses of high-altitude environments are proposed as to explain larger brain size at high altitude; i) adaptation to altitude sickness (brain swelling) and ii) adaptation to open environments. Species living in open habitats such as grassland were hypothesized to process more visual information in order to detect potential predators (Kopperud, 2017) and if this task is cognitively demanding, then possibility of larger brain size in species that live in open habitats is more probable. Therefore, *O. sloggetti* with its larger brain size at high altitude maybe an adaptation to detect potential predators based on our prediction that open environment is a feature of high elevation. However, if this adaptation is solely for predator detection, we should expect the same brain size trend in desert adapted species coupled with their auditory specialization as their habitats are also open.

Though not refuting the association of larger brain size with predation pressure, it seems that based on our data, the more probable explanation of larger brain size at high altitudes is either combating altitude sickness (brain swelling) or social brain hypothesis (SBH, for a review see Dunbar & Shultz, 2007; van der Bijl & Kolm, 2016). Hypobaric hypoxia (HBH) is said to be an environmental stressor to vertebrates living at high altitude that cannot be mitigated by behavioral avoidance but by physiological adaptation (Storz et al., 2010). HBH is said to lead to various abnormalities, which include a disruption of cognitive functions/performance (Muthuraju & Pati, 2014). Therefore, *O. sloggetti* may have developed larger brain size at high altitude to compensate for the altitude sickness that might hinder its behavioral flexibility at this demanding and unstable environment. Alternatively, larger brains are said to be important for recognition of group members versus strangers i.e. SBH and *O. sloggetti* is said to live in small groups at high elevation (for huddling and etc) (Neville personal com). Thus, it’s larger brain size at high altitude may be an adaptation to group members recognition or the interaction of both SBH and brain swelling.

However, a concrete conclusion of larger brain size as an adaptation at high altitude cannot be reached as we had insufficient individual data for high altitude adapted species (*O.barbori* and *O. helleri*) collected from different locations to see if indeed larger brain size at highaltitude is an adaptation in rodents. Similarly, physiological experiments on the individuals of thesame rodent species from both low and high altitude are needed to see if indeed this is anadaptation to altitude sickness. Smaller brains at more arid environments, shown by the positivecorrelation of aridity index and brain size might be in accordance with Bergmann’s Rule. Brainsize increases with increasing body size (Seyfarth & Cheney, 2002), though brain size to bodymass ratios differ from one taxonomic group to another (Jerison, 1973). Birds in arid environment were shown to have smaller body size (Nwaogu et al., 2018) in accordance with Bergmann’s Rule.

Variations in endocranial morphology in laminate-toothed rats and gerbils

Our results reveal that there is considerable variation in endocranial morphology between the two groups (gerbils and laminate-toothed rats) than within them. This may be so because the two groups are phylogenetically and ecologically distinct. Though this section will focus on describing the variation in morphology, some of the ecological functions are speculative. Laminate-toothed rats show a well-developed olfactory bulb as compared to the gerbils. The size of the olfactory bulb was said to be a good indication of the acuity of olfaction in an individual (Rombaux et al., 2006). Most of the *Otomys* species included in this study inhabit closed mesic grasslands, savannah habitats where olfaction is an advantage for predator avoidance and foraging as compared to open habitats where vision and hearing might be an advantage. Well-developed olfactory bulbs have been observed in the African giant pouched rat (*Cricetomys gambianus*) and the reason why it has been hypothesized that they can detect landmines and useful in tuberculosis diagnosis (Nzalak et al., 2008; Ibe et al., 2014). Though there is less variation in the olfactory bulb within Otomyini, the arid, semi-arid species showed a less developed olfactory bulb.

Besides the olfactory bulb, the paraflocculi in laminate-toothed rats was also more elongated than in gerbils, especially in *G. nigeriae* and *D. auricularis*, within Otomyini there is a slight variation in the morphology of paraflocculi however the direction of this variation is not as clear. In gerbils, *G. leucogaster* has a more elongated paraflocculus than *G. nigeriae* and *D. auricularis*, the reduction of the paraflocculi in *G. nigeriae* and *D. auricularis* is said to be caused by the process of mastoid pneumatization (Pavlinov, 2008). The paraflocculi are said to regulate functions associated with vision including control of the eye movements, and visual image stabilization in mammals (Zee et al., 1981; Ferreira-Cardoso et al., 2017; Lang et al., 2018). Frugivorous primates exhibited larger paraflocculi than omnivorous (Lang et al., 2018); however, the ecological relevance of this structure is still mostly speculative. Ferreira-Cardoso et al. (2017) found no correlation of paraflocculi with ecology and they suggested that variation in paraflocculi may be due to the anatomical and phylogenetic evolutionary constraints. Therefore, the eco-morphological function of this structure in our samples is unknown. Similarly, the ecological functions of a more protruding posterior ventral cortex in laminate-toothed rats and a grooved cerebral peduncle in *P. brantsii* is unknown, however, the variation in brainstem may be due to segmentation biases. Concluding, this study provides some useful information on the variation in endocranial morphology and relative brain size variations of the African gerbils and laminate-toothed rats where in certain eco-morphological functions are also speculated. However, more samples and physiological experiments are needed to verify some of the proposed brain eco-morphological functions. Similarly, studies looking at eco-morphological functions of certain brain parts that are associated with different sensory systems in rodents are needed.

CHAPTER FIVE: GENERAL DISCUSSION AND CONCLUSION

In this final chapter, I summarize the findings reported in this thesis, discuss their implications and discuss perspectives for future work on the topic.

Climate change and morphological variations

Rapid morphological changes in rodents have been well documented and this has been attributed to environmental changes (Pergams & Lawler, 2009; Pergams et al., 2015; Stumpp et al., 2016), brought about by climate warming, agricultural activities, urbanization, fragmentation, etc. I investigated morphology-phylogeny-environment relationships in rodents by looking at different traits: general cranial size (chapter 2), bulla and cochlea (chapter 3), endocranial size and shape (chapter 4). The analyses showed that climate change, phylogeny and some life history traits have an effect on the morphological variations of cranial size, bulla, cochlea and endocranial volume to an extent. These results together demonstrate the role of the environment in morphological variations of these traits and how evolution has influenced the distribution of those traits. Though based on the results from chapter 2 and 4 it was hard to pinpoint a single environmental or ecological variable, or their synergy in association with reported morphological variations. For example, in chapter 2 the combination of rainfall and temperature was shown to be correlated with cranial size in only three species with the 3rd universal response to warming (decreased body size with climate warming) shown in only one species. In chapter 3 only aridity was associated with bulla and cochlea hypertrophy and in chapter 4 the endocranial volume (ECV) was not associated with any environmental variable (except for *Otomys sloggetti* whose ECV was correlated with elevation) yet a distinction of the elongated olfactory bulb in mesic species was shown by the deformation results.

In a nutshell this study contributes to a better understanding of potential environmental changes impacts on the morphology of rodents in the future. Additionally, inflated auditory bulla has been shown to be one of the morphological traits that have undergone convergence evolution in arid/desert adapted species (Randall, 1994). Interestingly, this study offers the possibility that the hypertrophy in bulla may also have accompanied hypertrophy in the cochlea.

Implications of trait-based ecology for conservation

Traits can determine individual or species performance under given environmental conditions and affect whether a species will be filtered by the environment, as proposed by “assembly rules” (Keddy, 1992). Traits can also reflect how assemblages respond to environmental changes, as driven by “response rules” (Keddy, 1992). For this reason, by investigating species pools or community variation across environmental gradients, trait-based approaches can reveal general rules about the relationship between communities and the environment, which can be particularly useful in predicting climate change effects on communities (McGill et al., 2006). For example, analysis on morphology and climate change or ecological/environmental gradients, showed hotter environments favour small body size in general (Gardner et al., 2011; Yom-Tov & Geffen, 2011; Nengovhela et al., 2015), arid/desert environments favour inflated auditory bulla (Lay, 1972), and larger brain size is associated with high elevated environments, sociality and predation avoidance (Dunbar & Shultz, 2007; Kotrschal et al., 2015; Sayol et al., 2016). This study also looked at the above-mentioned traits by investigating the impacts of environmental change on cranial size (body size), bulla and cochlea and endocranial volume and added important new data from African rodents which contribute to debates about the eco-morphological functions of these traits. This suggests that different ecological/environmental gradients may filter species or alter community structure through these morphological traits.

By investigating rodents from two distinct murid subfamilies across different environmental gradients, I uncovered a pattern that a morphology-environment cline exists across multiple environmental scales. My results also highlighted the importance of evolutionary history in structuring the morphological patterns across habitats. As morphological traits could have significant influence on species sensitivities to environmental change in some rodent groups, the study of morphological variation across environmental gradients should be a priority for understanding climate change vulnerability of species and ecosystems. Furthermore, actual impacts of environmental change on species depends on the extrinsic environmental threats but could be mediated by species specific intrinsic traits, an element often overlooked in recent risk assessments (Garcia et al., 2014). Understanding the influence of traits on species vulnerability could provide a more realistic prediction of their response to environmental changes and would be useful when assessing conservation priority to environmental threats (Lips et al., 2003; Garcia et al., 2014).

Interaction between sensory ecology traits

Chapter 3 and 4 showed a hypertrophied bulla and cochlea in arid species and an elongated olfactory bulb in mesic species respectively. With the former chapter, showing arid/desert species adapted to low frequency sounds and the latter chapter showing mesic species having enhanced acuity of olfaction which is related to the elongated olfactory bulb. However, the eco-functionality of larger brains and elongated paraflocculi are not clear in the present study. Multisensory integration studies in rodents are available with olfactory-auditory interaction reported in lactating mothers and their new born. Olfaction is reported to be one of the central senses by which rodents communicate with each other. Coupled with ultrasonic vocalizations and odours produced by young pups, mothers were shown to use both auditory and olfactory cues to identify and locate their pups (Cohen et al., 2011). However, the integration of these senses can also be used in communication with conspecifics, and not only between the mother and her pup. Individually, both senses are said to be used in communication with conspecifics, predation avoidance, navigation, foraging etc. (Lay, 1972; Amo et al., 2008; Wesson 2015; Dempster, 2018). Thus, integration of olfactory and auditory information is said to have significance for a variety of critical scenarios such as food selection and predator aversion (Wesson & Wilson, 2010). Such arguments, however, cannot be used to explain the specialized audition and olfaction in this study as the results in chapter 3 and 4 shows that those species with specialized audition do not poses specialized olfaction and vice versa. Nevertheless, based on olfactory bulb, perhaps future analysis of nasal structures could show more integration.

Differences in habitat can drive divergence in perception as different environments may vary in how they conceal predators, prey and conspecifics. Additionally, the conspecifics, predators and prey signals may also vary. Moreover, these multiple perceptual demands might favour different perceptual sensitivity for populations/species in different habitats to perform best the specific detection tasks posed by the local environment. Chapter 3 showed that arid/desert species favours a specialized auditory sensitivity in communication with conspecifics and prey avoidance whilst mesic species seems to favour a more specialized olfaction (chapter 4). However, whether the species in this study used both specialized olfaction and audition is not clear as those species showing specialized audition does not seem to use/need specialized olfaction. Although there is ample of research supporting the value of each sense separately, the merging of these senses in a natural context is lacking. This would be an interesting research avenue to look at in the future in the two subfamilies with increased sample size.

Conclusions and future studies

This thesis focused mainly on hypotheses that the environment and life history traits play the most important role in morphological variations of different traits after phylogenetic and allometric corrections. The work presented here aimed to contribute towards increasing knowledge on the functional morphology of different traits in rodents in an African context. First, I have shown that after increasing the dataset from Nengovhela et al. (2015) where both studied species of *Otomys* (*O. auratus* and *O. angoniensis*) conformed to the third universal response; the “third universal response to warming” is not universal given that only two out of six rodent species studied here showed any body size temporal trends. Additionally, temperature (Bergmann’s Rule) on its own did not seem to be influencing body size variations in our samples; but the synergy of temperature and rainfall (hence increased food availability) was the most important mechanism associated with body size variations in rodent species. Our results confirm those of James (1970), Alhajeri & Steppan (2016), Yom-Tov & Geffen (2011, and reference therein). However, as Villar & Naya (2018) concluded less than 0.5% of the extant rodent species have been analyzed to date, therefore more studies with larger sample sizes covering different rodent species (interspecific analyses) are required in order to reach a clear understanding of body size variation patterns that are associated with the environment (chapter 2).

Secondly, I have presented a comparative analysis on bulla and cochlea morphology, and showed that these forms are related to the environment that these animals live in. Additionally, I showed that in extreme desert adapted species bulla hypertrophy is associated with cochlear hypertrophy, possibly auditory specialization. Interestingly, *Desmodillus* showed the possibility of being sensitive to both high and low/middle frequencies; going forward these aspects should be studied further combining morphology studies with hearing sensitivity experiments. This might shed light on whether this species has a bimodal sensitivity like that mentioned in frog-eating bat, *Trachops cirrhosus* (Ryan, 1983), or good sensitivity in the middle (Heffner & Masterton, 1980). As mentioned in chapter 3, more work with a large sample size that covers all habitat types of the three tribes (Taterillini, Gerbillini and Otomyini), still needs to be done and attention should be focused on the possibility of foot drumming in Southern African gerbils.

Thirdly, with the debate of using brain size as proxy for cognition, behavioural flexibility in mammals is rife; different hypotheses have been brought forward to explain variations in brain size e.g. predation, sociality, activity regime, diet, habitat type and habits. Though I did not find any correlation between the ECV and different environmental predictors, I predict that larger brain size seen in our samples may be associated with the species habitat and habits such as diet, sociality and lifestyle or their combination. However, within *O. sloggetti* larger brains were associated with high elevation. Additionally, brain was shown to vary in morphology in our sample with Otomyini having larger sized olfactory bulb, paraflocculi, and a pronounced posterior ventral cortex than the gerbils. Furthermore, larger sized paraflocculi were also seen in *G. leucogaster*. However, even though functions of these structures are known, it is not clear what is their ecological function. Therefore, follow up studies on the brain morphology focusing on different parts of the brain are needed. It would be interesting to study functional morphology of brain in different groups of rodents i.e. wild collected and those raised in laboratory experiments, to establish the non-genetic basis of adaptations.

REFERENCES

Abelson, E.S. (2016). Brain size is correlated with endangerment status in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **283**: 20152772.

Abiadh, A., Chetoui, M., Lamine-Cheniti, T., Capanna, E. & Colangelo, P. (2010). Molecular phylogenetics of the genus *Gerbillus* (Rodentia, Gerbillinae): implications for systematics, taxonomy and chromosomal evolution. *Molecular Phylogenetics and Evolution*, **56**: 513–518.

Aiello, L. & Wheeler, P. (1995). The expensive tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, **36**: 199–221.

Alhajeri, B.H. (2014). Adaptation, diversification, and desert ecology of the most diverse order of mammals (Mammalia, Rodentia). Ph.D. dissertation, Florida State University, Tallahassee, FL.

Alhajeri, B.H., Hunt, O.J. & Steppan, S.J. (2015). Molecular systematics of gerbils and deomyines (Rodentia: Gerbillinae, Deomyinae) and a test of desert adaptation in the tympanic bulla. *Journal of Zoological Systematics and Evolutionary Research,* **53**: 312-330.

Alhajeri, B.H. & Steppan, S.J. (2016). Association between climate and body size in rodents: A phylogenetic test of Bergmann's Rule. *Mammalian Biology*, **81**: 219–225.

Amo, L., Galván, I., Tomás, G. & Sanz, J.J. (2008). Predator odour recognition and avoidance in a songbird. *Functional Ecology*, **22**: 289–293.

Ash, J. & Gallup, G.G. (2007). Paleoclimatic variation and brain expansion during human evolution. *Human Nature*, **18**: 109-124.

Awojobi, O.N. & Tetteh, J. (2017). The impacts of climate change in Africa: A review of the scientific literature. *Journal of International Academic Research for Multidisciplinary*, **5**: 39–52.

Babin-Fenske, J., Anand, M. & Alarie, Y. (2008). Rapid morphological change in stream beetle museum specimens correlates with climate change. *Ecological Entomology*, **33**: 646-651.

Baltas, E. (2007). Spatial distribution of climatic indices in northern Greece. *Meteorological Applications,* **14**: 69-78.

Barton, R.A. (1998). Visual specialization and brain evolution in primates. *Proceedings of the Royal Society B: Biological Sciences,* **265**: 1933-1937.

Bates, P.J. (1985). Studies of gerbils of genus *Tatera*: The specific distinction of *Tatera robusta* (Cretzschmar, 1826), *Tatera nigricauda* (Peters, 1878) and *Tatera phillipsi* (De Winton, 1898). *Mammalia*, **49**: 37–52.

Baxter, R., Taylor, P. & Child, M.F. (2017). *Otomys auratus*. The IUCN Red List of Threatened Species 2017:e.T110662638A110662647. Downloaded on 24 April 2017.

Beaudet, A. (2015). Caracterisation des structures cranio-dentaires internes des cercopithecoïdes et etude diachronique de leurs variations morphologiques dans la sequence Plio-Pleistocene sud-africaine. Ph.D. Dissertation, Universite de Toulouse.

Beaudet, A., Dumoncel, J., de Beer, F., Duployer, B., Durrleman, S., Gilissen, E., Hoffman, J., Tenailleau, C., Thackeray, J.F. & Braga, J. (2016). Morphoarchitectural variation in South African fossil cercopithecoid endocasts. *Journal of Human Evolution*, **101**: 65–78.

Beaudet, A., Dumoncel, J., de Beer, F., Durrleman, S., Gilissen, E., Oettle, A., Subsol, G., Thackeray, J.F. & Braga, J. (2018). The endocranial shape of *Australopithecus africanus*: Surface analysis of the endocasts of Sts 5 and Sts 60. *Journal of Anatomy*, **232**: 296-303.

Bergmann, C. (1847). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, **3**: 595-708.

Bernard, R.T.F., Paton, J. & Sheppey, K. (1988). Relative brain size and morphology of some South African bats. *South African Journal of Zoology*, **23**: 52-58.

Bernard, R.T.F & Nurton, J. (1993). Ecological correlates of relative brain size in some South African rodents. *South African Journal of Zoology*, **28**: 95-98.

Berteaux, D., Humphries, M.M., Krebs, C.J., Lima, M., McAdam, A.G., Pettorelli, N., Réale, D., Saitoh, T., Tkadlec, E., Weladji, R.B. & Stenseth, N.C. (2006). Constraints to projecting the effects of climate change on mammals. *Climate Research*, **32**: 151-158.

Bertrand, O.C. & Silcox, M.T. (2016). First virtual endocasts of a fossil rodent: *Ischyromys typus* (Ischyromyidae, Oligocene) and brain evolution in rodents. *Journal of Vertebrate Paleontology*, **36**: e1095762.

Besl, P.J. & McKay, N.D. (1992). A method for registration of 3-D shapes. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, **14**: 239–256.

Blackburn, T.M., Gaston, K.J. & Loder, N. (1999). Geographic gradients in body size: A clarification of Bergmann's Rule. *Diversity and Distributions*, **5**: 165-174.

Blanckenhorn, W.U. (2015). Investigating yellow dung fly body size evolution in the field: Response to climate change? *Evolution*, **69**: 2227–2234.

Blois, J.L., Feranec, R.S. & Hadly, E.A. (2008). Environmental influences on spatial and temporal patterns of body-size variation in California ground squirrels (*Spermophilus beecheyi*). *Journal of Biogeography*, **35**: 602–613.

Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing the phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution,* **57**: 717-745.

Braga, J., Loubes, J-M., Descouens, D., Dumoncel, J., Thackeray, J.F., Kahn, J-L., de Beer, F., Riberon, A., Hoffman, K., Balaresque, P. & Gilissen, E. (2015). Disproportionate cochlear length in genus *Homo* shows a high phylogenetic signal during apes' hearing evolution. *PLoS One*, **10** : e0127780.

Bridelance, P. (1986). Les podophones de *Psammomys obesus* en milieu naturel : Comparaison avec les podophones de *Meriones* (Gerbillidae, Rodentia). *Mammalia,* **50**: 145-152.

Byrne, R.W. & Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society B: Biological Sciences*, **271**:1693-1699.

Calder, W. (1984). Size, function and life history. Cambridge: Harvard University Press.

Carleton, M.D. (2013). Subfamily Otomyinae Vlei Rats and Whistling Rats. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 571-573. London: Bloomsbury Publishing.

Carleton, M.D. & Musser, G.G. (2013). Subfamily Gerbillinae Gerbils and Jirds. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 260-262. London: Bloomsbury Publishing.

Cameron, G.N. & Scheel, D. (2001). Getting warmer: effect of global climate change on distribution of rodents in Texas. *Journal of Mammalogy*, **82**: 652–680.

Caruso, N.M., Sears, M.W., Adams, D.C. & Lips, K.R. (2014). Widespread rapid reductions in body size of adult salamanders in response to climate change. *Global Change Biology*, **20**: 1751–1759.

Chimimba, C.T. & Dippenaar, N.J. (1994). Non-geographic variation in *Aethomys chrysophilus* (de Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from Southern Africa. *South African Journal of Zoology*, **29**: 107-117.

Cianfrani, C., Broennimann, O., Loy, A. & Guisan, A. (2018). More than range exposure: Global otter vulnerability to climate change. *Biological Conservation*, **221**: 103-113

Claude, J. (2008). *Morphometrics with R*. New York: Springer.

Clausnitzer, V. (2013). *Otomys barbouri* Barbour's Vlei Rat. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 579-580. London: Bloomsbury Publishing.

Clutton-Brock, T.H. & Harvey, P.H. (1980). Primates brains and ecology. *Journal of Zoology London*, **190**: 309-324.

Cockerell, T.D.A., Miller, L.I. & Printz, M. (1914). The auditory ossicles of some African rodents. *Zoologischer Anzeiger,* **44**: 433-440.

Cohen, L., Rothschild, G. & Mizrahi, A. (2011). Multisensory integration of natural odors and sounds in the auditory cortex. *Neuron*, **72**: 357–369.

Collier, P., Conway, G. & Venables, T. (2008). Climate change and Africa. *Oxford Review of Economic Policy*, **24**: 337–353.

Cork, S.J. & Kenagy, G.J. (1989). Nutritional Value of Hypogeous Fungus for a Forest-Dwelling Ground Squirrel*. Ecology*, **70**: 577-586.

Crumpton, N., Kardjilov, N. & Asher, R.J. (2015). Convergence vs. specialization in the ear region of moles (Mammalia). *Journal of Morphology,* **276**: 900-914.

Dallos, P. (1970). Low-frequency auditory characteristics: Species dependence. *Journal of the Acoustical Society of America*, **48**: 489-499.

Daufresne, M., Lengfellner, K. & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, **106**: 12788–12793.

Delcros, G. (2012). The influence of abiotic processes, competition and predation on the community structure of rodents and shrews. Ph. D dissertation, University of KwaZulu-Natal.

Dempster, E.R. & Perrin, M.R. (1990). A preliminary description of body maintenance behaviour of four *Gerbillurus* species. *Madoqua,* **17**: 41-45.

Dempster, E.R. & Perrin, M.R. (1991). Ultrasonic vocalizations of six taxa of Southern African gerbils (Rodentia: Gerbillinae). *Ethology,* **88**: 1-10.

Dempster, E.R., Dempster, R. & Perrin, M.R. (1991). Behaviour associated with ultrasonic vocalizations in six Gerbilline rodent taxa. *Ethol,* **88** : 11-19.

Dempster, E.R. & Perrin, dM.R. (1994). Divergence in acoustic repertoire of sympatric and allopatric gerbil species (Rodentia: Gerbillinae). *Mammalia,* **58**: 93-104.

Dempster, E.R. (2013). *Gerbilliscus leucogaster* Bushveld Gerbil. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 279-281. London: Bloomsbury Publishing.

Dempster, E.R. (2018). Ultrasonic vocalizations in 10 taxa of Southern African Gerbilline rodents. In: *Handbook of Behavioral Neuroscience, Vol. 25*. (eds Brudzynski SM), pp. 207-216. Amsterdam: Academic Press.

Denys, C. (2003). Evolution du genre *Otomys* (Rodentia: Muridae) au Plio-Pléistocène d'Afrique orientale et australe. In: *Advances in Paleontology 'Hent to Pantha'*, volume in Honor of Constatin Radulesca and Petre Mihai Samson. (eds Petculescu A, Stiuca E), pp. 75–84. Bucharest: Romanian Academy.

Diamond, S.E., Frame, A.M., Martin, R.A. & Buckley, L.B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology*, **92**: 1005-1012.

Dumoncel, J., Durrleman, S., Braga, J., Jessel, J-P. & Subsol, G. (2014). Landmark-free 3D method for comparison of fossil hominins and hominids based on endocranium and EDJ shapes. *American Journal of Physical Anthropology*, **153** (Suppl. 56), 110.

Dunbar, R.I.M. & Shultz, S. (2007). Understanding primate brain evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **352**: 649-658.

Durrleman, S. (2010). Statistical Models of Currents for Measuring the Variability of Anatomical Curves, Surfaces and their Evolution. Ph.D. Dissertation, Universite Nice-Sophia Antipolis.

Durrleman, S., Pennec, X., Trouve, A., Ayache, N. & Braga, J. (2012). Comparison of the endocranial ontogenies between chimpanzees and bonobos via temporal regression and spatiotemporal registration. *Journal of Human Evolution*, **62**: 74e88.

Eastman, L.M., Morelli, T L., Rowe, K.C., Conroy, C.J. & Moritz, C. (2012). Size increase in high elevation ground squirrels over the last century. *Global Change Biology*, **18**: 1499–1508.

Eisenberg, J.P. & Wilson, D.E. (1978). Relative brain size and feeding strategies in the Chiroptera. *Evolution*, **32**: 740-751.

Eisenberg. J.F. (1981). The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior. Chicago, IL: University of Chicago.

Eisenberg, J.F. & Wilson, D.E. (1981). Relative brain size and demographic strategies in the didelphid marsupials. *The American Naturalist*, **118**: 1-15.

Ekdale, E.G. & Racicot, R.A. (2015). Anatomical evidence for low frequency sensitivity in an archaeocete whale: Comparison of the inner ear of *Zygorhiza kochii* with that of crown Mysticeti. *Journal of Anatomy,* **226**: 22-39.

Engelbrecht, A., Taylor, P.J., Daniels, S.R. & Rambau, R.V. (2011). Cryptic speciation in the Southern African vlei rat *Otomys irroratus* complex: evidence derived from mitochondrial Cyt b and niche modelling. *Biological Journal of the Linnaean Society*, **104**: 192-206.

Fang, J., Piao, S., Tang, Z., Peng, C. & Ji, W. (2001). Interannual variability in net primary production and precipitation. *Science*, **293**: 1723a-1723.

Ferreira-Cardoso, S., Araújo, R., Martins, N. E., Martins, G.G., Walsh, S., Martins, R.M.S., Kardjilov, N., Manke, I., Hilger, A. & Castanhinha, R. (2017). Floccular fossa size is not a reliable proxy of ecology and behaviour in vertebrates. *Scientific Reports*, **7**(1).

Fichet-Calvet, E. & Rogers, D.J. (2009). Risk maps of lassa fever in West Africa. *PLoS Neglected Tropical Diseases*, **3**: e388.

Francescoli, G., Quirici, V. & Sobrero, R. (2012). Patterns of variation in the tympanic bulla of tuco-tucos (Rodentia, Ctenomyidae, *Ctenomys*). *Acta Theriologica,* **57**: 153-163.

Fuller, A., Dawson, T., Helmuth, B., Hetem, R.S., Mitchell, D. & Maloney, S.K. (2010). Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology*, **83**: 713-20.

Garcia, R.A., Araújo, M.B., Burgess, N.D., Foden, W.B., Gutsche, A., Rahbek, C. & Cabeza, M. (2014). Matching species traits to projected threats and opportunities from climate change. *Journal of Biogeography*, **41**: 724-735.

García-Navas, V. & Blumstein, D.T. (2016). The effect of body size and habitat on the evolution of alarm vocalizations in rodents. *Biological Journal of the Linnean Society,* **118**: 745-751.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology and Evolution*, **26**: 285–291.

Gemeda, D.O. & Sima, A.D. (2015). The impacts of climate change on African continent and the way forward. *Journal of Ecology and the Natural Environment*, **7**: 256–262.

Gittleman, J.L. (1986). Carnivore brain size, behavioral ecology and phylogeny. *Journal of Mammalogy*, **67**: 23-36.

González-Lagos, C., Sol, D. & Reader, S.M. (2010). Large-brained mammals live longer. *Journal of Evolutionary Biology*, **23**: 1064-1074.

Gosler, A.G., Greenwood, J.J.D. & Perrins, C. (1995). Predation risk and the cost of being fat. *Nature*, **377**: 621-623.

Granjon, L. & Duplantier, J-M. (2009). *Les rongeurs de l'Afrique sahelo-soudanienne*. Marseille: Research Institute for Development publishing.

Grohé, C., Tseng, Z.J., Lebrun, R., Boistel, R. & Flynn, J.J. (2016). Bony labyrinth shape variation in extant Carnivora: a case study of Musteloidea. *Journal of Anatomy*, **288**: 366-383.

Gu, J., Li, D.Y., Luo, Y., Ying, S.B., Zhang, L.Y., Shi, Q.M., Chen, J., Zhang, S.P., Zhou, Z.M. & Liao, W.B. (2017). Brain size in *Hylarana guentheri* seems unaffected by variation in temperature and growth season. *Animal Biology*, **67**: 209-225.

Gunz, P., Ramsier, M., Kuhrig, M., Hublin, J-J. & Spoor, F. (2012). The mammalian bony labyrinth reconsidered, introducing a comprehensive geometric morphometric approach. *Journal of Anatomy,* **220**: 529-543.

Gynther, I., Waller, N. & Leung, L.K.P. (2016). Confirmation of the extinction of the Bramble Cay melomys *Melomys rubicola* on Bramble Cay, Torres Strait: results and conclusions from a comprehensive survey in August–September 2014. Unpublished report to the Department of Environment and Heritage Protection, Queensland Government, Brisbane.

Hafner, M.S & Hafner, J.C. (1984). Brain Size, adaptation and heterochrony in geomyoid rodents. *Evolution*, **38**: 1088-1098.

Hanken, J. & Hall, B.K. (1993). The Skull. Chicago: The University of Chicago Press.

Happold, D.C. (2013). Mammals of Africa Volume iii: rodents, hares and rabbits. In D. C. Happold (Ed.). United Kingdom: Bloomsbury Publishing.

Harvey, P.H. & Bennett, P.M. (1983). Brain size, energetics, ecology and life history patterns. *Nature London*, **306**: 314-315.

Heffner, H. & Masterton, B. (1980). Hearing in Glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. *Journal of the Acoustical Society of America,* **68**: 1584-1599.

Heffner, R.S. & Heffner, H.E. (1992). Hearing and sound localization in blind mole rats: *Spalax ehrenbergi*. *Hearing Research,* **62**: 206-216.

Heffner, R.S., Koay, G. & Heffner, H.E. (2001). Audiograms of five species of rodents: Implications for the evolution of hearing and the perception of pitch. *Hearing Research,* **157**: 138-152.

Hetem, R.S., Fuller, A., Maloney, S.K. & Mitchell, D. (2014). Responses of large mammals to climate change. *Temperature*, **1**: 115–127.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C. D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**: 450-455.

Hijmans, R., Cameron, S., Parra, J., Jones, P. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**: 1965–1978.

Hoffman, M.A. (1983). Evolution of the brain in neonatal and adult placental mammals: a theoretical approach. *Journal of Theoretical Biology*, **105**: 317-322.

Holman, S.D. (1980). Sexually dimorphic, ultrasonic vocalizations of Mongolian gerbils. *Behavioral and Neural Biology*, **28**: 183-192.

Holmes, M.W., Hammond, T.T., Wogan, G.O.U., Walsh, R.E., LaBarbera, K., Wommack, E.A., Martins, F.M., Crawford, J.C., Mack, K.L., Bloch, L.M. & Nachman, M.W. (2016). Natural history collections as windows on evolutionary processes. *Molecular Ecology*, **25**: 864-881.

Hulme, M., Doherty, R., Ngara, T., New, M. & Lister, D. (2001). African climate change: 1900-2100. *Climate Research*, **17**: 145–168.

Ibe, C.S., Onyeanusi, B.I. & Hambolu, J.O. (2014). Functional morphology of the brain of the African giant pouched rat (*Cricetomys gambianus* Waterhouse, 1840). *Onderstepoort Journal of Veterinary Research*, **81**(1).

IPCC (Intergovermental Panel on Climate Change). (2014). The synthesis report of the fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC). Available at http://www.ipcc.ch/pdf/assessment-report/ar5/syr/SYR_AR5_ SPMcorr1.pdf [accessed 4 January 2014].

Isler, K. & van Schaik C.P. (2006). Metabolic costs of brain size evolution. *Biology Letters*, **2**: 557–560.

Isler, K., Kirk, E.C., Miller, J.M.A., Albrecht, G.A., Gelvin, B.R. & Martin, R.D. (2008). Endocranial volumes of primate species: Scaling analyses using a comprehensive and reliable dataset. *Journal of Human Evolution*, **55**: 967-978.

Iwaniuk, A.N. & Nelson, J.E. (2002). Can endocranial volume be used as an estimate of brain size in birds? *Canadian Journal of Zoology*, **80**: 16-23.

Jackson, T.P. (2013a). *Otomys unisulcatus* Karoo Vlei Rat (Bush Karoo Rat). *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 594-596. London: Bloomsbury Publishing.

Jackson, T.P. (2013b). *Parotomys brantsii* Brants's Whistling Rat. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 597-600. London: Bloomsbury Publishing.

James, F.C. (1970). Geographic size variation in birds and its relationship to climate. *Ecology*, **51**: 365–390.

Jerison, H. (1973). The evolution of the brain and intelligence. New York: Academic.

Joffe, T.H. & Dunbar, R.I.M. (1997). Visual and socio-cognitive information processing in primate brain evolution. *Proceedings of the Royal Society B: Biological Sciences,* **264**: 1303–1307.

Jones, G. & Teeling, E.C. (2006). The evolution of echolocation in bats. *Trends in Ecology & Evolution*, **21**: 149-156.

Kamilar, J.M. & Cooper, N. (2013). Phylogenetic signal in primate behavior, ecology, and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **368**: 20120341.

Keddy, P.A. (1992). Assembly and response Rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**: 157-164.

Kesner, M.H., Linsey, A.V. & Chimimba, C.T. (2013) *Aethomys namaquensis* Namaqua Veld Rat (Namaqua Aethomys). *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 371-373. London: Bloomsbury Publishing.

Knapp, A.K., Burns, C.E., Fynn, R.W.S., Kirkman, K.P., Morris, C.D. & Smith, M.D. (2006). Convergence and contingency in production–precipitation relationships in North American and South African C4 grasslands. *Oecologia*, **149**: 456-464.

Koontz, T.L., Shepherd, U.L. & Marshall, D. (2001). The effects of climate change on Merriam's kangaroo rat, *Dipodomys merriami*. *Journal of Arid Environments*, **49**: 581-591.

Kopperud, B.T. (2017). Artiodactyl brain-size evolution: A phylogenetic comparative study of brain-size adaptation. MSc Dissertation, University of Oslo.

Kotler, B.P. (1984). Risk of predation and the structure of desert rodent communities. *Ecology,* **65**: 689-701.

Kotrschal, A., Buechel, S.D., Zala, S.M., Corral-Lopez, A., Penn, D.J. & Kolm, N. (2015). Brain size affects female but not male survival under predation threat. *Ecology Letters*, **18**: 646-652.

Krubitzer, L., Campi, K.L. & Cooke, D.F. (2011). All rodents are not the same: A modern synthesis of cortical organization. *Brain, Behavior and Evolution*, **78**: 51-93.

Kumar, S., Stecher, G. & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution,* **33**: 1870-1874.

Kverková, K., Bělíková, T., Olkowicz, S., Pavelková, Z., O'Riain, M.J., Šumbera, R., Burda, H, Bennett, N.C. & Němec, P. (2018). Sociality does not drive the evolution of large brains in eusocial African mole-rats. *Scientific Reports*, **8**(1).

Lalis, A., Evin, A., Janier, M., Koivogui, L. & Denys, C. (2015). Host evolution in *Mastomys natalensis* (Rodentia: Muridae): An integrative approach using geometric morphometrics and genetics. *Integrative Zoology*, **10**: 505-514.

Landry, O. JR. (1970). The Rodentia as omnivores. *The Quarterly Review of Biology*, **45**: 351-372.

Lang, M.M., Bertrand, O.C. & Silcox, M.T. (2018). Scaling patterns of primate paraflocculi: effects of phylogeny and ecology. *American Journal of Physical Anthropology*, **165**: 152.

Lange, S., Stalleicken, J. & Burda, H. (2004). Functional morphology of the ear in fossorial rodents, *Microtus arvalis* and *Arvicola terrestris*. *Journal of Morphology,* **262**: 770-779.

Lange, S., Burda, H., Wegner, R.E., Dammann, P., Begall, S. & Kawalika, M. (2007). Living in a "stethoscope": Burrow-acoustics promote auditory specializations in subterranean rodents. *Naturwissenschaften,* **94**: 134-138.

Lauder, G.V., Huey, R.B., Monson, R.K. & Jensen, R.J. (1995). Systematics and the study of organismal form and function. *BioScience*, **45**: 696–704.

Lay, D.M. (1972). The anatomy, physiology, functional significance and evolution of specialized hearing organs of Gerbilline rodents. *Journal of Morphology,* **138**: 41-120.

Le Roux, A., Jackson, T.P. & Cherry, M.I. (2001a). Does Brants' Whistling Rat (*Parotomys brantsii*) use an urgency-based alarm system in reaction to aerial and terrestrial predators? *Behaviour*, **138**: 757-773.

Le Roux, A., Jackson, T.P. & Cherry, M.I. (2001b). The effect of changing call duration and calling bouts on vigilance in Brants' Whistling Rat, *Parotomys brantsii. Behaviour,* **138**: 1287-1302.

Le Roux, A., Jackson, T.P. & Cherry, M.I. (2002). Differences in alarm vocalizations of sympatric populations of the whistling rats, *Parotomys brantsii* and *P. littledalei* (Rodentia: Muridae). *Journal of Zoology,* **257** : 189-194.

Lecompte, E., Aplin, K., Denys, C., Catzeflis, F., Chades, M. & Chevret, P. (2008). Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a new tribal classification of the subfamily. *BMC Evolutionary Biology,* **8**: 199

Leirs, H., Verheyen, W. & Verhagen, R. (1996). Spatial patterns in *Mastomys natalensis* in Tanzania (Rodentia, Muridae). *Mammalia*, **60**: 545-556.

Leirs, H. (2013) *Mastomys natalensis* Natal Multimammate Mouse (Natal *Mastomys*). *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 468-470. London: Bloomsbury Publishing.

Liao, J., Zhang, Z. & Liu, N. (2007). Effects of altitudinal change on the auditory bulla in *Ochotona daurica* (Mammalia, Lagomorpha). *Journal of Zoological Systematics and Evolutionary Research,* **45**: 151-154.

Linzmeier, A. & Ribeiro-Costa, C.S. (2011). Body size of Chrysomelidae (Coleoptera, Insecta) in areas with different levels of conservation in South Brazil. *ZooKeys*, **157**: 1–14.

Lips, K.R., Reeve, J.D. & Witters, L.R. (2003). Ecological traits predicting amphibian population declines in Central America. *Conservation Biology*, **17**: 1078-1088.

Lovejoy, T.E. & Hannah, L., eds. (2005). Climate change and biodiversity. New Haven & London: Yale University Press.

Luo, Y., Zhong, M.J., Huang, Y., Li, F., Liao, W.B. & Kotrschal, A. (2017). Seasonality and brain size are negatively associated in frogs: evidence for the expensive brain framework. *Scientific Reports*, **7**(1).

Mace, G.M., Harvey, P.H. & Clutton-Brock, T.H. (1981). Brain size and ecology in small mammals. *Journal of Zoology*, **193**: 333–354.

Mace, G.M. & Eisenberg, J.F. (1982). Competition, niche specialization and the evolution of brain size in the genus *Peromyscus*. *Biological Journal of the Linnean Society*,**17**: 243-257.

Madliger, C.L. (2012). Toward improved conservation management: a consideration of sensory ecology. *Biodiversity and Conservation*, **21**: 3277-3286.

Manoussaki, D., Chadwick, R.S., Ketten, D.R., Arruda, J., Dimitriadis, E.K. & O'Malley, J.T. (2008). The influence of cochlear shape on low-frequency hearing. *Proceedings of the National Academy of Sciences USA,* **105**: 6162-6166.

Mason, M.J. (2015). Functional morphology of rodent middle ears. In: *Evolution of the rodents: Advances in phylogeny, functional morphology and development*. (eds Cox PG, Hautier L), pp. 373-404. Cambridge: Cambridge University Press.

Mason, M.J. (2016). Structure and function of the mammalian middle ear. I: Large middle ears in small desert mammals. *Journal of Anatomy,* **228**: 284-299.

Mason, M.J., Cornwall, H.L. & Smith, E.S.J. (2016). Ear structures of the naked mole-rat, *Heterocephalus glaber*, and its relatives (Rodentia: Bathyergidae). *PLoS One*, **11**: e0167079.

Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution*, **10**: 105–108.

McCoy, D.E. (2012). Connecticut birds and climate change: Bergmann's Rule in the fourth dimension. *Northeastern Naturalist*, **19**: 323-334.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**: 178-185.

McNab, B.K. (1971). On the ecological significance of Bergmann's Rule. *Ecology*, 52, 845–854.

McNab, B.K. & Eisenberg, J.F. (1989). Brain size and its relation to the rate of metabolism in mammals. *The American Naturalist*, **133**: 157-167.

McNab, B.K. (2010). Geographic and temporal correlations of mammalian size reconsidered: A resource Rule. *Oecologia*, **164**: 13–23.

Meerburg, B.G., Singleton, G.R. & Kijlstra, A. (2009). Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology*, **35**: 221–270.

Meier, P.T. (1983). Relative brain size within the North American Sciuridae. *Journal of Mammalogy*, **64**: 642-647.

Meiri, S., Yom-Tov, Y. & Geffen, E. (2007). What determines conformity to Bergmann's Rule? *Global Ecology and Biogeography*, **16**: 788-794.

Miller-Rushing, A.J. & Primack, R. B. (2008). Global warming and flowering times in Thoreau's Concord: A community perspective. *Ecology*, **89**: 332-341.

Millien, V., Ledevin, R., Boué, C. & Gonzalez, A. (2017). Rapid morphological divergence in two closely related and co-occurring species over the last 50 years. *Evolutionary Ecology*, **31**: 847-864.

Millien, V., Lyons, S.K., Olson, L., Smith, F.A., Wilson, A.B. & Yom-Tov, Y. (2006). Ecotypic variation in the context of global climate change: Revisiting the rules. *Ecology Letters*, **9**: 853–869.

Mitteroecker, P. & Gunz, P. (2009). Advances in Geometric Morphometrics. *Evolutionary Biology,* **36**: 235-247.

Moggi-Cecchi, J. & Collard, M. (2002). A fossil stapes from Sterkfontein, South Africa, and the hearing capabilities of early hominids. *Journal of Human Evolution,* **42**: 259-265.

Mohr, K., Leirs, H., Katakweba, A. & Machang'u, R. (2007). Monitoring rodents movements with a biomarker around introduction and feeding foci in an urban environment in Tanzania. *African Zoology*, **42**: 294-298.

Møller, A.P. (2009). Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, **159**: 849–858.

Monadjem, A. (1998). Relative brain size of some Southern African myomorph rodents. *South African Journal of Zoology*, **33**: 47-49.

Monadjem, A. & Perrin, M. (2003). Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology*, **38**: 127-137.

Monadjem, A., Mahlaba, T.A., Dlamini, N., Eiseb, S.J., Belmain, S.R., Mulungu, L.S., Massawe, A.W., Makundi, R.H., Mohr, K. & Taylor, P.J. (2011). Impact of crop cycle on movement patterns of pest rodent species between fields and houses in Africa. *Wildlife Research*, **38**: 603–609.

Monadjem, A., Virani, M.Z., Jackson, C. & Reside, A. (2013). Rapid decline and shift in the future distribution predicted for the endangered Sokoke Scops Owl *Otus ireneae* due to climate change. *Bird Conservation International*, **23**: 247-258.

Monadjem, A., Taylor, P.J., Denys, C. & Cotterill, F.P.D. (2015). *Rodents of Sub-Saharan Africa: A biogeographic and taxonomic synthesis*. Berlin, Boston: De Gruyter.

Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite national park, USA. *Science*, **322**: 261-264.

Moulton, D.G. (1967). Olfaction in Mammals. *American Zoologist*, **7**: 421-429.

Mulungu, L.S., Sixbert, V., Ngowo, V., Mdangi, M., Katakweba, A.S., Tesha, P., Mrosso, F.P., Mchomvu, M., Kilonzo, B.S. & Belmain, S.R. (2015). Spatio-temporal patterns in the distribution of the multi-mammate mouse, *Mastomys natalensis*, in rice crop and fallow land habitats in Tanzania. *Mammalia*, **79**: 177–184.

Musser, G.G. & Carleton, M.D. (2005). Superfamily Muroidea. In: *Mammal species of the world: A taxonomic and geographic reference* (3rd edn) (eds Wilson DE, Reeder DM), pp. 894-1531. Baltimore: Johns Hopkins University Press.

Muthuraju, S. & Pati, S. (2014). Effect of hypobaric hypoxia on cognitive functions and potential therapeutic agents. *The Malaysian Journal of Medical Sciences: MJMS*, **21**(Spec Issue): 41-45.

Naya, D.E., Naya, H. & Cook, J. (2017). Climate change and body size trends in aquatic and terrestrial endotherms: Does habitat matter? *PLoS ONE*, **12**: e0183051.

Naya, D.E., Naya, H. & Lessa, E.P. (2016). Brain size and thermoregulation during the evolution of the genus *Homo*. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, **191**: 66-73.

Ndiaye, A., Bâ, K., Aniskin, V., Benazzou, T., Chevret, P., Konečný, A., Sembène, M., Tatard, C., Kergoat, G.J. & Granjon, L. (2012). Evolutionary systematics and biogeography of endemic gerbils (Rodentia, Muridae) from Morocco: an integrative approach. *Zoologica Scripta*, **41**: 11–28.

Ndiaye, A., Chevret, P., Dobigny, G. & Granjon, L. (2016). Evolutionary systematics and biogeography of the arid habitat-adapted rodent genus *Gerbillus* (Rodentia, Muridae): a mostly Plio-Pleistocene African history. *Journal of Zoological Systematics and Evolutionary Research*, **54**: 299–317.

Nel, J.AJ. (2013). *Desmodillus auricularis* Cape Short-tailed Gerbil (Namaqua Gerbil). *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 267-268. London: Bloomsbury Publishing.

Nengovhela, A., Baxter, R.M. & Taylor, P.J. (2015). Temporal changes in cranial size in South African vlei rats (*Otomys*): Evidence for the "third universal response to warming." *African Zoology*, **50**: 233–239.

Nevo, E., Pirlot, P. & Beiles, A. (1988). Brain size diversity in adaptation and speciation of subterranean mole rats. *Journal of Zoological Systematics and Evolutionary Research*, **26**: 467-479.

Nikolai, J.C. & Bramble, D.M. (1983). Morphological structure and function in desert heteromyid rodents. *Great Basin Naturalist Memoirs,* **7**: 91-116.

Nowak, R.M. (1999). Walker's Mammals of the World, 6th edn. Baltimore: The Johns Hopkins University Press.

Nwaogu, C.J., Tieleman, B.I., Bitrus, K. & Cresswell, W. (2018). Temperature and aridity determine body size conformity to Bergmann's Rule independent of latitudinal differences in a tropical environment. *Journal of Ornithology*, **159**: 1053-1062.

Nzalak, J.O., Byanet, O., Salami, S.O., Umosen, A.D., Maidawa, S.M., Ali, M.N. & Imam, J. (2008). Comparative morphometric studies of the cerebellum and forebrain of the African Giant rat (*Cricetomys gambianus*, Waterhouse) and that of grasscutter (*Thryonomys swinderianus*). *Journal of Animal and Veterinary Advances*, **7**: 1090-1092.

Ohlberger, J. (2013). Climate warming and ectotherm body size - from individual physiology to community ecology. *Functional Ecology*, **27**: 991-1001.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *BioScience*, **51**: 933-938.

O'shea, B.T. & Reep, R.L. (1990). Encephalization quotients and life history traits in the Sirenia. *J Mammal*, **71**: 534-543.

Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E., Tuljapurkar, S. & Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change*. Nature*, **466**: 482–485.

Pacifici, M., Visconti, P., Butchart, S.H.M., Watson, J.E.M., Cassola, F.M. & Rondinini, C. (2017). Species' traits influenced their response to recent climate change. *Nature Climate Change*, **7**: 205–208.

Pagel, M.D. & Harvey, P.H. (1990). Diversity in the brain size of newborn mammals. Allometry, energetics, or life history tactics. *BioScience*, **40**: 116-122.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature,* **401**: 877-884.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**: 637-669.

Pavlinov, I.J. (2001). Current concepts of gerbillid phylogeny and classification. In: *African small mammals*. (eds Denys C, Granjon L, Poulet A), pp. 141-149. Paris: Research Institute for Development publishing.

Pavlinov, I.J. (2008). A review of phylogeny and classification of Gerbillinae (Mammalia: Rodentia). Moscow: Moscow University Publishing.

Pergams, O.R.W. & Ashley, M.V. (1999). Rapid morphological change in Channel Island deer mice. *Evolution*, **53**: 1573–1581.

Pergams, O.R.W. & Lacy, R.C. (2007). Rapid morphological and genetic change in Chicago-area *Peromyscus*. *Molecular Ecology,* **17**: 450-463

Pergams, O.R.W. & Lawler, J.J. (2009). Recent and widespread rapid morphological change in rodents. *PLoS One*, **4**: e6452.

Pergams, O.R.W., Byrn, D., Lee, K.L.Y. & Jackson, R. (2015). Rapid morphological change in black rats (*Rattus rattus*) after an island introduction. *PeerJ*, **3**: e812.

Pfaff, C., Martin, T. & Ruf, I. (2015). Bony labyrinth morphometry indicates locomotor adaptations in the squirrel-related clade (Rodentia, Mammalia). *Proceedings of the Royal Society B: Biological Sciences,* **282**: 20150744.

Phukuntsi, M.A., Brettschneider, H., Dalton, D.L., Oosthuizen, M., Goldner, G., Badenhorst, J., Kotze, A. & Kearney, T. (20160. Hidden identities: cryptic species in the *Otomys* genus (Cuvier 1824) (Rodentia: Muridae: Otomyinae) revealed by mitochondrial and nuclear DNA in South Africa. *Journal of Phylogenetics and Evolutionary Biology*, **4**:168.

Pilleri, G., Gihr, M. & Kraus, C. (1984). Cephalization in rodents with particular reference to the Canadian beaver (*Castor canadensis*). In: *Investigations on Beavers*. (ed. Pilleri G), pp. 11–102. Berne, Switzerland: Brain Anatomy Institute.

Pirlot, P. & Stephan, H. (1970). Encepidization in Chiroptera. *Canadian Journal of Zoology*, **48** : 433-444.

Pizzimenti, J.J. & Salle, R. (1980). Dietary and morphometric variation in some Peruvian rodent communities: the effect of feeding strategy on evolution. *Biological Journal of the Linnean Society,*, **13**: 263-285.

Plassmann, W., Peetz, W. & Schmidt, M. (1987). The cochlea in Gerbilline rodents. *Brain Behavior and Evolution,* **30**: 82-101.

Plassmann, W. & Kadel, M. (1991). Low-frequency sensitivity in a gerbilline rodent, *Pachyuromys duprasi*. *Brain Behavior and Evolution,* **38**: 115-126.

Pocock, T.N. (1976). Pliocene mammalian microfauna from Laangebaanweg: A few fossil genus linking the Otomyinae with the Murinae. *South African Journal of Science,* **72**: 58-60.

Podos, J. & Nowicki, S. (2004). Beaks, adaptation, and vocal evolution in Darwin's Finches. *BioScience*, **54**: 501.

Poroshin, E.A., Polly, P.D. & Wójcik, J.M. (2010). Climate and morphological change on decadal scales: Multiannual variation in the common shrew *Sorex araneus* in northeast Russia. *Acta Theriologica*, **55**: 1573-1581.

Prakash, I. (1959). Hypertrophy of the bullae tympanicae in the desert mammals. *Scientific Culture,* **24**: 580-582.

Pravosudov, V.V. & Clayton, N.S. (2002). A test of the adaptive specialization hypothesis: Population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behavioral Neuroscience*, **116**: 515-522.

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

R Development Core Team. 2015. R: A Language and Environment for Statistical Computing. Available from http://cran.r-project.org/.

Raia, P. & Meiri, S. (2006). The Island Rule in large mammals: Paleontology meets ecology. *Evolution*, **60**: 1731-1742.

Randall, J.A. (1993). Behavioural adaptations of desert rodents (Heteromyidae). *Animal Behaviour,* **45**: 263-287.

Randall, J.A. (1994). Discrimination of footdrumming signatures by kangaroo rats; *Dipodomys spectabilis*. *Animal Behaviour,* **47**: 45-54.

Randall, J.A. (2001). Evolution and function of drumming as communication in mammals. *American Zoologist,* **41**: 1143-1156.

Randall, J.A. (2014). Vibrational communication: Spiders to kangaroo rats. In: *Biocommunication of Animals*. (eds Witzany G), pp. 103-133. Dordrecht: Springer.

Ravicz, M.E., Rosowski, J.J. & Voigt, H.F. (1992). Sound-power collection by the auditory periphery of the Mongolian gerbil *Meriones unguiculatus*. I: Middle-ear input impedance. *Journal of the Acoustical Society of America,* **92**: 157-177.

Reader, S.M. & Laland, K.N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences USA*, **99**: 4436-4441.

Renaud, S., Michaux, J., Schmidt, D.N., Aguilar, J.P., Mein, P. & Auffray, J.C. (2005). Morphological evolution, ecological diversification and climate change in rodents. *Proceedings of the Royal Society B: Biological Sciences*, **272**: 609–617.

Rohlf, F.J. & Slice, D. (1990). Extensions of the procrustes method for the optimal superimposition of landmarks. *Systematic Biology,* **39**: 40-59.

Rombaux, P., Mouraux, A., Bertrand, B., Nicolas, G., Duprez, T. & Hummel, T. (2006). Olfactory function and olfactory bulb volume in patients with postinfectious olfactory loss. *Laryngoscope*, **116**: 436-439.

Rosenzweig, M.L. (1968). Net primary productivity of terrestrial communities: Prediction from climatological data. *The American Naturalist*, **102**: 67–74.

Rosowski, J.J & Graybeal, A. (1991). What did *Morganucodon* hear? *Zoological Journal of the Linnean Society,* **101**: 131-168.

Rowe, K.C., Rowe, K.M.C., Tingley, M.W., Koo, M.S., Patton, J.L., Conroy, C.J., Perrine, J.D., Beissinger, S.R. & Moritz, C. (2015). Spatially heterogeneous impact of climate change on small mammals of montane California*. Proceedings of the Royal Society B: Biological Sciences*, **282**: 1857.

Ruggero, M.A & Temchin, A.N. (2002). The roles of the external, middle, and inner ears in determining the bandwidth of hearing. *Proceedings of the National Academy of Sciences USA,* **99**: 13206-13210.

Ryan, A. (1976). Hearing sensitivity of the mongolian gerbil, *Meriones unguiculatis*. *Journal of the Acoustical Society of America,* **59**: 1222-1226.

Ryan, M.J., Tuttle, M.D. & Barclay, R.M.R. (1983). Behavioral responses of the frog-eating bat, *Trachops cirrhosus*, to sonic frequencies. *Journal of Comparative Physiology A*, **150**: 413–418.

Sacher, G.A. & Stafeldt, E.F. (1974). Relation of gestation time and brain weight of placental mammals: implications for the theory of vertebrate growth. *The American Naturalist*, **5**: 593-615.

Sacher, G.A. (1975). Maturation and longevity in relation to cranial capacity in hominid evolution. In: *Primate functional morphology and evolution*. (ed. Tuttle, R.H). The Hague: Morton.

Saitou, N. & Nei, M. (1987). The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, **4**: 406-425.

Salt, A.N., Lichtenhan, J.T., Gill, R.M. & Hartsock, J.J. (2013). Large endolymphatic potentials from low-frequency and infrasonic tones in the guinea pig. *Journal of the Acoustical Society of America*, **133**: 1561-1571.

Samuels, J.X. (2009). Cranial morphology and dietary habits of rodents. *Zoological Journal of the Linnean Society*, **156**: 864-888.

Sayol, F., Maspons, J., Lapiedra, O., Iwaniuk, A. N., Székely, T. & Sol, D. (2016). Environmental variation and the evolution of large brains in birds. *Nature Communications*, **7**: 13971.

Schmidt, N.M. & Jensen, P.M. (2003). Changes in mammalian body length over 175 years-adaptations to a fragmented landscape? *Conservation Ecology*, **7**: 6.

Scholander, P.F. (1955). Evolution of climatic adaptation in homeotherms. *Evolution*, **9**: 15-26.

Schuck-Paim, C., Alonso, W.J. & Ottoni, E.B. (2008). Cognition in an ever-changing world: Climatic variability is associated with brain size in neotropical parrots. *Brain, Behavior and Evolution*, **71**: 200-215.

Sénégas, F. (2001). Interpretation of the dental pattern of the South African fossil *Euryotomys* (Rodentia, Murinae) and origin of otomyine dental morphology. In: *African small mammals*. (eds Denys C, Granjon L, Poulet A), pp. 151-160. Paris: Research Institute for Development publishing.

Seyfarth, R.M & Cheney, D.L. (2002). What are big brains for? *Proceedings of the National Academy of Sciences USA*, **99**: 4141-4142.

Shaffer, L.A. & Long, G.R. (2004). Low-frequency distortion product otoacoustic emissions in two species of kangaroo rats: Implications for auditory sensitivity. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology,* **190**: 55-60.

Sheppey, K & Bernard, R.T.F. (1984) Relative brain size in the mammalian carnivores of the Cape province of South Africa. *South African Journal of Zoology*, **19**: 305-308.

Sheridan, J.A. & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, **1**: 401-406.

Sicard, B. (2013) *Gerbillus nigeriae* Nigerian Gerbil. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 320-321. London: Bloomsbury Publishing.

Skinner, J.D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Sub-region*. Cambridge: Cambridge University Press.

Smith, F.A., Browning, H., Shepherd, U.L. & Low. (1998). The influence of climate change on the body mass of woodrats *Neotoma* in an arid region of New Mexico, USA. *Ecography*, **21**: 140-148.

Snell-Rood, E.C & Wick, N. (2013). Anthropogenic environments exert variable selection on cranial capacity in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **280**: 20131384.

Sobrero, R., May-Collado, L.J., Agnarsson, I. & Hernández C.E. (2011). Expensive brains: “Brainy” rodents have higher metabolic rate. *Frontiers in Evolutionary Neuroscience*, **3**: 2.

Sol, D., Bacher, S., Reader, S.M. & Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *The American Naturalist*, **172**: S63–S71.

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters,* **5**: 130–133.

Spoor, F. & Zonneveld, F. (1998). Comparative review of the human bony labyrinth. *American Journal of Physical Anthropology*, **41**: 211-251.

Stein, B.R. (2000). Morphology of subterranean rodents. In: *Life underground: The biology of subterranean rodents*. (eds Lacey EA, Patton JL, Cameron GN), pp. 19-61. Chicago: University of Chicago Press.

Steinitz, H. (2010). The effects of global climate change on the distribution of terrestrial mammals in Israel. PhD dissertation, Tel-Aviv University.

Stephan, H. & Dieterlen, F. (1982). Relative brain size in Muridae with special reference to *Colomys goslingi*. *Zeitschrift fur Saugetierkunde* ,**47**: 38-47.

Storz, J.F, Scott, G.R. & Cheviron, Z.A. (2010). Phenotypic plasticity and genetic adaptation to high-altitude hypoxia in vertebrates. *The Journal of Experimental Biology*, **213**: 4125-4136.

Stumpp, R., Fuzessy, L. & Paglia, A.P. (2016). Environment drivers acting on rodent rapid morphological change. *Journal of Mammalian Evolution*, **25**: 131–140.

Subsol, G., Gesquière, G., Braga, J. & Thackeray, F. (2010). 3D automatic methods to segment "virtual" endocasts: State of the art and future directions. *American Journal of Physical Anthropolology*, 141, suppl. **50**: 226-227 (résumé).

Tabatabaei-Yazdi, F., Adriaens, D. & Darvish, J. (2014). Cranial phenotypic variation in *Meriones crassus* and *M. libycus* (Rodentia, Gerbillinae), and a morphological divergence in *M. crassus* from the Iranian Plateau and Mesopotamia (Western Zagros Mountains). *European Journal of Taxonomy,* **88**: 1-28.

Tabatabaei-Yazdi, F., Colangelo, P. & Adriaens, D. (2015). Testing a long-standing hypothesis on the relation between the auditory bulla size and environmental conditions: A case study in two jird species (Muridae: *Meriones libycus* and *M. crassus*). *Mammalia,* **79**: 185-200.

Tamura, K., Nei, M. & Kumar, S. (2004). Prospects for inferring very large phylogenies by using the neighbour-joining method. *Proceedings of the National Academy of Sciences USA*, **101**:11030-11035.

Taylor, P.J., Maree, S., Van Sandwyk, J., Baxter, R. & Rambau, R.V. (2009). When is a species not a species? Uncoupled phenotypic, karyotypic and genotypic divergence in two species of South African laminate-toothed rats (Murinae: Otomyini). *Journal of Zoology*, **277**: 317-332.

Taylor, P.J. & Kumirai, A. (2001). Craniometric relationships between the Southern African vlei rat, *Otomys irroratus* (Rodentia, Muridae, Otomyini) and allied species from north of the Zambezi River. *African Small Mammals,* **570**: 161-181.

Taylor, P.J., Kumirai, A. & Contrafatto, G. (2004). Geometric morphometric analysis of adaptive cranial evolution in Southern African laminate-toothed rats (Family: Muridae, Tribe: Otomyini. *Durban Museum Novitates,* **29**: 110-122.

Taylor, P.J., Lavrenchenko, L.A., Carleton, M.D., Verheyen, E., Bennett, N., Oosthuisen, C. & Maree, S. (2011). Specific limits and emerging diversity patterns in east African populations of laminate-toothed rats, genus *Otomys* (Muridae: Murinae: Otomyini): Revision of the *Otomys typus* complex. *Zootaxa*, **3024**: 1–66.

Taylor, P.J. (2013a) *Otomys angoniensis* Angoni Vlei Rat. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 577-578. London: Bloomsbury Publishing.

Taylor, P.J. (2013b) *Otomys sloggetti* Sloggett's Vlei Rat. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 589-591. London: Bloomsbury Publishing.

Taylor, P.J., Maree, S., Cotterill, F.P.D., Missoup, A.D., Nicolas, V. & Denys, C. (2014). Molecular and morphological evidence for a Pleistocene radiation of laminate-toothed rats (*Otomys*: Rodentia) across a volcanic archipelago in equatorial Africa. *Biological Journal of the Linnean Society,* **113**: 320–344.

Taylor, P.J., Nengovhela, A., Linden, J. & Baxter, R.M. (2015). Past, present, and future distribution of Afromontane rodents (Muridae: *Otomys*) reflect climate-change predicted biome changes. *Mammalia*, **80**: 359–375.

Taylor, P.J., Ogony, L., Ogola, J. & Baxter, R.M. (2016). South African mouse shrews (*Myosorex*) feel the heat: using species distribution models (SDMs) and IUCN Red List criteria to flag extinction risks due to climate change. *Mammal Research*, **62**: 149–162.

Teplitsky, C. & Millien, V. (2014). Climate warming and Bergmann's Rule through time: Is there any evidence? *Evolutionary Applications*, **7**: 156–168.

Thiam, M., Bâ, K. & Duplantier, J-M. (2008). Impacts of climatic changes on small mammal communities in the Sahel (West Africa) as evidenced by owl pellet analysis. *African Zoology*, **43**: 135–143.

Tolnai, S., Beutelmann, R. & Klump, G.M. (2017). Exploring binaural hearing in gerbils (*Meriones unguiculatus*) using virtual headphones. *PLoS One,* **12**: e0175142.

Tomassini, A., Colangelo, P., Agnelli, P., Jones, G. & Russo, D. (2014). Cranial size has increased over 133 years in a common bat, *Pipistrellus kuhlii*: A response to changing climate or urbanization? *Journal of Biogeography*, **41**: 944–953.

Van der Bijl, W. & Kolm, N. (2016). Why direct effects of predation complicate the social brain hypothesis. *BioEssays*, **38**: 568–577.

Van Dyck, H. (2012). Changing organisms in rapidly changing anthropogenic landscapes: the significance of the 'Umwelt'-concept and functional habitat for animal conservation. *Evolutionary Application*, **5**: 144-153.

van Schaik, C.P. & Deaner, R.O. (2003). Life history and cognitive evolution in primates. In: Animal social complexity (eds de Waal, F.B.M & Tyack, P.L.), pp. 5-25. Cambridge: Harvard University Press.

Vassallo, A.I. & Echeverría, A.I. (2009). Evolution of brain size in a highly diversifying lineage of subterranean rodent genus *Ctenomys* (Caviomorpha: Ctenomyidae). *Brain, Behavior and Evolution*, **73**: 138-149.

Vater, M. & Kössl, M. (2011). Comparative aspects of cochlear functional organization in mammals. *Hearing Research,* **273**: 89-99.

Villar, C.H. & Naya, D.E. (2018). Climate change and temporal trends in body size: The case of rodents. *Oikos*, **127**: 1186–1194.

Vincze, O. (2016). Light enough to travel or wise enough to stay? Brain size evolution and migratory behavior in birds. *Evolution*, **70**: 2123-2133.

Wainwright, P.C. & Reilly, S.M. (1994). Ecological morphology: integrative organismal biology. Chicago: University of Chicago Press.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O. & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, **416**: 389–395.

Webster, D.B. & Webster, M. (1975). Auditory systems of Heteromyidae: functional morphology and evolution of the middle ear. *Journal of Morphology,* **246***:* 343-376.

Webster, D.M. & Webster, M. (1980). Morphological adaptations of the ear in the rodent family Heteromyidae. *American Zoologist,* **20**: 247-254.

Wesson, D.W. & Wilson, D.A. (2010). Smelling sounds: Olfactory-auditory sensory convergence in the olfactory tubercle. *Journal of Neuroscience*, **30**: 3013–3021.

Wesson, D.W. (2015). Olfactory communication in rodents in natural and semi-natural habitats. *In: Handbook of olfaction and gustation*. (ed Doty, R.L), pp. 579–590. New York: Marcel Dekker, Inc.

West, C.D. (1985). The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. *Journal of the Acoustical Society of America,* **77**: 1091-1101.

Wilson, D.E., Lacher, T.E. Jr. & Mittermeier, R.A. (2016). *Handbook of the Mammals of the World.* Volume. 6. Lagomoprhs and Rodents I. Barcelona: Lynx Edicions.

Wilson, D.E., Lacher, T.E. Jr. & Mittermeier, R.A. (2017). *Handbook of the Mammals of the World*. Volume. 7. Rodents II. Barcelona: Lynx Edicions.

Yalden, D.W. (2013). *Otomys typus* Ethiopian Vlei Rat. *In: Mammals of Africa, Vol. III*. (eds Happold, D.C.D), pp. 592-593. London: Bloomsbury Publishing.

Yom-Tov, Y. & Nix, H. (1986). Climatological correlates for body size of five species of Australian mammals. *Biological Journal of the Linnean Society*, **29**: 245-262.

Yom-Tov, Y. (2003). Body sizes of carnivores commensal with humans have increased over the past 50 years*. Functional Ecology*, **17**: 323–327.

Yom Tov, Y., Yom Tov, S. & Baagoe, H. (2003). Increase of skull size in the red fox (*Vulpes vulpes*) and Eurasian badger (*Meles meles*) in Denmark during the twentieth century: An effect of improved diet? *Evolutionary Ecology Research*, **5**: 1037–1048.

Yom-Tov, Y. & Yom-Tov, S. (2004). Climatic change and body size in two species of Japanese rodents. *Biological Journal of the Linnean Society*, **82**: 263-267.

Yom-Tov, Y. & Yom-Tov, J. (2005). Global warming, Bergmann’s Rule and body size in the masked shrew *Sorex cinereus* Kerr in Alaska. *Journal of Animal Ecology*, **74**: 803–808.

Yom-Tov, Y. & Geffen, E. (2006). Geographic variation in body size: The effects of ambient temperature and precipitation. *Oecologia*, **148**: 213–218.

Yom-Tov, Y., Heggberget, T. M., Wiig, Ø. & Yom-Tov, S. (2006). Body size changes among otters, *Lutra lutra*, in Norway: The possible effects of food availability and global warming. *Oecologia*, **150**: 155-160.

Yom-Tov, Y., Yom-Tov, S., Barreiro, J. & Blanco, J.C. (2007). Body size of the red fox *Vulpes vulpes* in Spain: The effect of agriculture. *Biological Journal of the Linnean Society*, **90**: 729-734.

Yom-Tov, Y., Roos, A., Mortensen, P., Wiig, Ø., Yom-Tov, S. & Heggberget, T.M. (2010). Recent changes in body size of the Eurasian otter *Lutra lutra* in Sweden. *Ambio*, **39**: 496–503.

Yom-Tov, Y. & Geffen, E. (2011). Recent spatial and temporal changes in body size of terrestrial vertebrates: Probable causes and pitfalls. *Biological Reviews*, **86**: 531–541.

Yom-Tov, Y. & Yom-Tov, S. (2012). Observations on variation in skull size of three mammals in Israel during the 20th century. *Zoologischer Anzeiger*, **251**: 331–334.

Zee, D.S., Yamazaki, A., Butler, P.H. & Gucer, G. (1981). Effects of ablation of flocculus and paraflocculus of eye movements in primate. *Journal of Neurophysiology*, **46**: 878-899.

Zhao, L., Wang, Y., Liu, N. & Liao, J. (2013). Effects of Change in Altitude on the Auditory Bulla of Midday Gerbil, *Meriones meridianus*. *Pakistan Journal of Zoology,* **45**: 581-588.

APPENDICES

APPENDIX A

SUPPORTING MATERIAL FOR CHAPTER 2

Table A.1: Raw data of the studied specimens for each species investigated.

Family	Genus	Species	Country	Province	Year	Latitude	Longitude	TWCLS	GLS	MXTRL	NAW	IOC	ZYW	bio_1	bio_12	elevation
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1903	-27.45	23.43333	B	34.18	4.98	4.76	5.78	19.19	176	473	1320
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1926	-31.3833	21.03333	B	38.43	5.12	4.59	6.14	21.27	169	170	1061
Muridae	Desmodillus	auricularis	South Africa	Western Cape	1926	-31.55	18.35	B	35.54	4.26	4.6	5.82	19.77	184	166	47
Muridae	Desmodillus	auricularis	South Africa	Western Cape	1926	-31.7833	18.61667	B	35.34	4.65	4.61	5.96	19.19	193	171	28
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1926	-31.4667	19.78333	C	36.76	5.12	4.74	6.17	21.48	164	216	985
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1927	-28.7833	20.7	A	38.49	5.3	5.11	6.48	21.79	202	137	665
Muridae	Desmodillus	auricularis	South Africa	Western Cape	1927	-33.5783	18.98167	B	36.95	4.58	4.71	6.08	21.17	180	646	99
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1928	-26.95	24.73333	C	31.98	4.23	4.18	5.6	18.52	180	475	1206
Muridae	Desmodillus	auricularis	Namibia	Namibia	1928	-27.15	18.03333	B	35.62	4.75	5	5.93	19.76	201	119	941
Muridae	Desmodillus	auricularis	Namibia	Namibia	1928	-27.15	18.03333	C	34.78	4.76	4.69	5.8	19.52	201	119	941
Muridae	Desmodillus	auricularis	Namibia	Namibia	1928	-27.15	18.03333	B	36.2	5.26	5.04	6.03	20.48	201	119	941
Muridae	Desmodillus	auricularis	South Africa	North West	1928	-27.65	25.51667	C	35.53	4.87	4.88	5.95	19.1	179	485	1233
Muridae	Desmodillus	auricularis	Namibia	Namibia	1929	-27.15	18.03333	A	37.28	4.57	5.17	5.9	20.66	201	119	941
Muridae	Desmodillus	auricularis	Botswana	Botswana	1930	-22.1	22.45	C	36.44	4.28	4.76	5.74	21.43	212	386	1049
Muridae	Desmodillus	auricularis	Botswana	Botswana	1930	-22.1	22.45	C	33.89	4.75	4.49	5.47	18.97	212	386	1049
Muridae	Desmodillus	auricularis	Botswana	Botswana	1930	-22.1	22.45	A	37.26	4.92	5.21	6.7	22.07	212	386	1049
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1932	-26.7833	20.08333	C	35.85	4.62	4.78	5.94	21.21	203	175	835
Muridae	Desmodillus	auricularis	Namibia	Namibia	1932	-18.9092	16.97833	C	33.84	4.22	4.51	5.55	19.32	227	481	1129
Muridae	Desmodillus	auricularis	Namibia	Namibia	1933	-17.9167	15.95	B	33.02	4.55	4.67	5.55	18.43	225	470	1099

Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1937	-29.6	17.9	A	34.6	4.72	4.81	5.75	20.03	164	198	1049
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1937	-29.6	17.9	B	34.43	4.38	4.62	6.15	19.45	164	198	1049
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1937	-30.9667	22.35	C	33.3	4.69	4.51	5.61	19.11	150	254	1451
Muridae	Desmodillus	auricularis	South Africa	Western Cape	1937	-32.7	18.86667	C	32.78	4.7	4.47	6.33	18.78	182	333	110
Muridae	Desmodillus	auricularis	Namibia	Namibia	1937	-25.85	16.55	C	35.47	4.85	4.66	5.86	20.33	141	196	1697
Muridae	Desmodillus	auricularis	Botswana	Botswana	1944	-20.5	22.66667	A	36.03	4.8	4.88	6.36	19.6	223	417	925
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-27.9333	22.73333	B	33.95	4.92	4.51	5.9	20.69	170	357	1267
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-28.85	23.25	B	35.23	4.74	4.39	5.54	19.52	165	321	1303
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-28.85	23.25	C	35.75	4.39	4.73	5.76	19.8	165	321	1303
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-30.9	27.65	B	36.98	4.8	4.72	6.02	21.09	117	692	2048
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-28.25	24.25	C	33.67	4.91	4.8	5.87	19.49	180	433	1171
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-28.3333	24.71667	B	37.15	5.13	5.25	6.32	21.48	183	431	1125
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-27.45	23.4333	B	37.78	5	4.92	6.17	21.38	176	473	1320
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-30.9	27.65	B	35.54	4.9	4.69	6.22	20.07	117	692	2048
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-30.9	27.65	B	36.3	4.73	4.49	5.92	19.49	117	692	2048
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1947	-26.95	24.73333	B	34.12	4.83	4.85	6.09	19.57	180	475	1206
Muridae	Desmodillus	auricularis	South Africa	Eastern Cape	1949	-33.1333	26.61667	B	35.12	4.36	4.55	5.62	19.19	187	504	280
Muridae	Desmodillus	auricularis	Namibia	Namibia	1950	-26.8167	17.78333	B	36.06	4.79	4.86	5.83	20.33	210	105	699
Muridae	Desmodillus	auricularis	Namibia	Namibia	1950	-22.45	18.96667	B	36.76	4.89	5.02	6.42	21.41	193	367	1433
Muridae	Desmodillus	auricularis	Namibia	Namibia	1950	-25.8833	16.81667	B	36.42	4.95	4.82	6.29	21.04	164	171	1394
Muridae	Desmodillus	auricularis	Namibia	Namibia	1951	-25.0167	16.75	B	34.66	4.66	4.78	5.82	19.1	164	155	1383
Muridae	Desmodillus	auricularis	South Africa	North West	1953	-27.5833	25.45	B	34.51	4.6	4.76	5.84	19.34	177	485	1264
Muridae	Desmodillus	auricularis	South Africa	North West	1953	-27.5833	25.45	B	35.36	5.12	4.85	5.96	20.31	177	485	1264
Muridae	Desmodillus	auricularis	South Africa	North West	1953	-27.5833	25.45	B	35.65	4.7	4.56	5.71	20.35	177	485	1264
Muridae	Desmodillus	auricularis	South Africa	North West	1954	-27.5833	25.45	B	33.9	5.02	4.92	5.67	19.52	177	485	1264
Muridae	Desmodillus	auricularis	South Africa	North West	1954	-27.5833	25.45	C	32.78	4.45	4.24	5.56	18.95	177	485	1264
Muridae	Desmodillus	auricularis	South Africa	North West	1954	-27.5833	25.45	B	34.5	4.78	4.7	5.77	19.38	177	485	1264
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1957	-26.45	20.56667	C	35.77	5.05	4.63	6.15	19.7	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1957	-25.7667	20.38333	C	37.35	4.95	4.87	6.27	21	199	229	960
Muridae	Desmodillus	auricularis	South Africa	Eastern Cape	1959	-33.75	25.46667	B	36.43	4.68	4.7	5.63	20.51	179	439	130

Muridae	Desmodillus	auricularis	South Africa	Eastern Cape	1959	-33.75	25.46667	B	37.44	5.04	4.87	5.86	21.33	179	439	130
Muridae	Desmodillus	auricularis	South Africa	Eastern Cape	1959	-33.75	25.46667	B	36.72	5.06	4.95	6.13	20.85	179	439	130
Muridae	Desmodillus	auricularis	South Africa	Eastern Cape	1959	-33.55	25.7	B	34.85	4.7	4.54	6.11	20.37	185	390	55
Muridae	Desmodillus	auricularis	South Africa	Eastern Cape	1960	-30.3833	29.21667	C	36.5	4.69	4.63	5.73	20.68	142	803	1577
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1962	-26.45	20.56667	A	36.1	5.09	4.96	6.59	21.17	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1962	-26.45	20.56667	A	39.76	5.1	5.3	7.62	23.05	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1962	-26.45	20.56667	B	33.7	4.46	4.5	5.91	18.29	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Free State	1962	-29.9107	24.6363	B	35.28	4.98	4.75	6.05	19.97	183	346	1107
Muridae	Desmodillus	auricularis	Namibia	Namibia	1965	-18.1833	12.51667	B	34.35	4.91	4.89	5.61	19.57	180	103	782
Muridae	Desmodillus	auricularis	Botswana	Botswana	1965	-20.3333	23.81667	B	35.74	4.77	4.98	6.38	19.71	221	414	937
Muridae	Desmodillus	auricularis	Botswana	Botswana	1965	-20.3333	23.81667	C	35.73	4.58	4.65	5.73	19.68	221	414	937
Muridae	Desmodillus	auricularis	Botswana	Botswana	1965	-20.3333	23.81667	C	33.95	4.83	4.75	6.01	18.81	221	414	937
Muridae	Desmodillus	auricularis	Namibia	Namibia	1965	-23.55	15.03333	A	37.46	4.99	5.06	5.75	21.5	210	20	406
Muridae	Desmodillus	auricularis	Namibia	Namibia	1965	-23.55	15.03333	A	35.78	4.9	5	6.11	19.15	210	20	406
Muridae	Desmodillus	auricularis	Namibia	Namibia	1965	-23.55	15.03333	A	39.1	4.99	5.21	6.22	20.5	210	20	406
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1966	-26.45	20.56667	B	37.99	4.97	5.03	5.95	22.43	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1966	-26.45	20.56667	C	33.04	4.74	4.89	5.62	19.95	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1966	-26.45	20.56667	B	37.13	4.81	5.15	6.34	20.87	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1966	-26.45	20.56667	B	37.26	4.71	4.52	6.06	21.94	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1966	-26.45	20.56667	C	33.72	4.9	4.61	5.7	19.47	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1966	-26.45	20.56667	C	35.66	4.78	4.92	6.06	20.78	200	217	903
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1970	-25.8167	20.01667	A	36.95	4.72	5.05	6.05	18.72	196	221	974
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1970	-25.8167	20.01667	C	32.1	4.55	4.63	5.64	18.94	196	221	974
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1970	-25.8167	20.01667	B	34.21	4.59	4.72	5.58	19.54	196	221	974
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1977	-29.5833	18.35	A	37.98	4.83	4.76	6.05	21.2	174	180	1033
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1977	-29.5833	18.35	B	34.36	4.87	4.53	6.12	19.53	174	180	1033
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1977	-29.5833	18.35	B	35.79	5.02	4.74	5.78	20.36	174	180	1033
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1977	-29.5833	18.35	B	36.52	5.21	4.41	6.01	20.2	174	180	1033
Muridae	Desmodillus	auricularis	South Africa	Western Cape	1977	-30.95	18.2	B	36.6	4.95	4.91	5.72	21.06	179	176	326
Muridae	Desmodillus	auricularis	South Africa	Western Cape	1977	-30.95	18.2	B	35.79	4.81	4.7	5.9	20.13	179	176	326

Muridae	Desmodillus	auricularis	Namibia	Namibia	1978	-23.0667	15.16667	A	37.78	4.72	5.1	5.94	20.02	199	45	566
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1980	-28.3167	20.56667	C	37.46	5.08	4.81	6.13	21.27	198	174	754
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1980	-28.3167	20.56667	B	34.86	5.05	4.81	5.75	19.47	198	174	754
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1980	-28.3167	20.56667	C	33.11	4.1	4.51	5.72	19.27	198	174	754
Muridae	Desmodillus	auricularis	Namibia	Namibia	1980	-26.95	17.93333	C	33.31	4.44	4.36	5.28	18.61	211	107	708
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1981	-29.5667	18.35	B	34.12	4.57	4.52	5.47	18.93	177	171	1036
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1981	-29.5667	18.35	B	36.82	5.18	4.93	5.99	20.95	177	171	1036
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1981	-29.5667	18.35	B	34.5	4.61	4.68	5.61	19.93	177	171	1036
Muridae	Desmodillus	auricularis	Namibia	Namibia	1984	-22.4333	18.1	B	34.95	5.01	5.02	6.3	19.46	188	350	1550
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1987	-32.2833	19.86667	C	34.06	4.73	4.95	5.85	20.72	186	137	445
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1987	-32.2833	19.86667	C	32.08	4.82	4.41	5.88	18.11	186	137	445
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1987	-32.2833	19.86667	B	36.27	4.63	4.59	5.97	21.05	186	137	445
Muridae	Desmodillus	auricularis	South Africa	Northern Cape	1987	-32.2833	19.86667	B	38.33	4.85	5.12	6.5	21.66	186	137	445
Muridae	Desmodillus	auricularis	Namibia	Namibia	1988	-24.0333	16.15	B	35.56	4.85	5.14	5.94	19.72	174	162	1173
Muridae	Desmodillus	auricularis	South Africa	North West	1996	-25.7869	22.86944	C	32.66	4.72	4.8	5.61	18.96	199	333	992
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Zimbabwe	1895	-17	31	2	38.46	6.27	5.52	6.86	19.05	187	861	1286
Muridae	Gerbilliscus	leucogaster	South Africa	KwaZulu-Natal	1905	-27.0433	32.42306	1	39.38	6.57	5.37	6.24	19.96	226	734	88
Muridae	Gerbilliscus	leucogaster	South Africa	Gauteng	1906	-25.4	28.1	2	36.8	6.75	5.36	6.57	18.34	187	630	1111
Muridae	Gerbilliscus	leucogaster	South Africa	Gauteng	1906	-25.4	28.1	2	37.96	6.71	5.6	6.31	20.69	187	630	1111
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1907	-16.5667	33.41667	1	39.5	7.26	6.1	6.9	18.82	259	607	196
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1907	-23.8	30.16667	1	38.48	6.72	5.65	6.36	19.7	202	983	720
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1907	-23.8	30.16667	1	38.3	7.35	5.64	6.01	19.79	202	983	720
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1911	-25.4333	31.68333	2	39.59	6.79	6.18	6.92	20.1	220	680	279
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1911	-25.4333	31.68333	2	39.1	6.79	5.66	6.48	20.97	220	680	279
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1911	-25.4333	31.68333	1	38.14	6.83	5.46	6.52	18.43	220	680	279
Muridae	Gerbilliscus	leucogaster	South Africa	Gauteng	1912	-25.7167	28.23333	2	36.01	6.58	5.34	6.2	19.31	178	697	1300
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1913	-22.2667	30.1	2	38.98	6.82	5.8	6.04	19.84	234	340	435
Muridae	Gerbilliscus	leucogaster	South Africa	Gauteng	1914	-25.4	28.1	1	38.42	7.16	5.68	6.36	19.35	187	630	1111
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1914	-24.2833	28.95	1	39.04	7.32	5.77	6.58	19.39	189	525	1071
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1915	-24.8833	27.65	1	37.07	6.78	5.83	6.46	18.61	184	671	1361

Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1916	-22.35	30.36667	1	37.34	7.06	5.6	6	19.18	235	395	403
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1917	-23.8667	30.61667	1	38.07	6.83	5.39	5.93	18.98	215	576	541
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1918	-25.4333	31.68333	1	39.4	6.62	6.1	6.73	18.87	220	680	279
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1919	-24.7833	28.41667	1	41.11	7.18	5.8	6.28	21.62	183	636	1255
Muridae	Gerbilliscus	leucogaster	South Africa	Free State	1920	-27.4833	26.55	1	39.37	6.95	5.25	5.92	20.29	169	576	1315
Muridae	Gerbilliscus	leucogaster	South Africa	Free State	1920	-27.4833	26.55	2	38.93	6.58	5.31	5.97	19.15	169	576	1315
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1920	-23.45	30.06667	1	39	6.75	5.4	6.56	18.82	187	1088	951
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1920	-23.45	30.06667	1	39.24	6.63	5.49	6.75	19.43	187	1088	951
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1922	-24.25	30.4	2	37.89	6.66	5.94	6.74	20.5	206	728	818
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1922	-24.25	30.4	2	36.74	6.41	5.49	6.46	19.47	206	728	818
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1924	-25.05	33.8	2	36.31	6.62	5.05	5.98	18.32	229	878	30
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1924	-25.05	33.8	2	34.41	6.07	5.04	5.64	17.41	229	878	30
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1924	-24.2833	28.95	1	37.79	7.18	5.21	6.67	19.43	189	525	1071
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1927	-22.9833	29.88333	1	37.62	6.26	5.18	6.06	19.02	163	1243	1439
Muridae	Gerbilliscus	leucogaster	South Africa	Gauteng	1928	-25.7333	28.18333	2	38.46	6.47	5.47	6.51	20.09	179	697	1307
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1929	-29.0667	23.63333	2	36.08	6.18	5.12	6.01	18.28	188	317	979
Muridae	Gerbilliscus	leucogaster	Botswana	Botswana	1930	-22.55	23.25	1	39.94	7.01	5.81	6.56	20.23	211	365	1011
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1931	-27.1	24.21667	2	38.26	6.6	5.43	5.9	19.02	171	495	1418
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1932	-26.3667	25.21667	2	39.15	6.82	5.23	6.23	19.86	180	491	1293
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1932	-26.1333	24.93333	2	38.09	6.67	5.16	6.15	20.13	186	468	1212
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1935	-22.5	30.83333	1	38.98	6.56	5.41	5.95	19.87	234	485	399
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1936	-23.5167	30.03333	2	37.32	6.62	5.05	5.91	19.02	194	994	805
Muridae	Gerbilliscus	leucogaster	Swaziland	Swaziland	1937	-26.7694	31.93722	2	38.69	6.74	5.59	6.33	20	222	577	119
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1938	-24.0667	31.15	1	37.8	6.52	5.4	6.24	19.32	226	483	331
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Zimbabwe	1938	-19.9667	32.33333	1	36.52	6.35	5.31	6.41	19.01	225	444	498
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Zimbabwe	1938	-19.9667	32.33333	2	37.46	6.78	5.39	6.2	18.44	225	444	498
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1941	-26.05	32.38333	2	36.82	6.53	5.38	6.49	18.84	229	690	8
Muridae	Gerbilliscus	leucogaster	South Africa	Gauteng	1943	-25.6667	28.51667	2	38.37	6.44	5.47	6.01	18.75	167	704	1441
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1947	-26.9833	24.73333	2	37.08	6.55	5.22	5.99	18.84	179	477	1217
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1947	-26.9833	24.73333	2	38.02	6.7	5.3	6.13	20.33	179	477	1217

Muridae	Gerbilliscus	leucogaster	Swaziland	Swaziland	1947	-26.6833	31.68333	2	36.83	6.61	6.09	6.44	19.4	224	621	189
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1947	-23.1333	29.55	2	38.5	6.3	5.71	6.76	19.08	195	488	896
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1947	-28.85	23.25	2	37.13	6.2	5.17	6.26	19.07	165	321	1303
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1947	-28.85	23.25	2	35.4	6.43	4.88	6.02	19.66	165	321	1303
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1947	-28.85	23.25	1	38.42	6.78	5.31	6.12	19.41	165	321	1303
Muridae	Gerbilliscus	leucogaster	South Africa	North West	1948	-26.0833	26.11667	1	39.47	6.9	5.64	6.85	20.88	168	606	1513
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1950	-15.6183	31.44695	1	38.46	6.59	5.45	5.94	18.72	243	716	341
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1950	-15.6183	31.44695	1	39.81	6.68	5.8	6.37	18.67	243	716	341
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1950	-26.9833	24.73333	1	39.4	6.7	5.72	5.92	20.15	179	477	1217
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1950	-22	15.6	1	36.83	6.02	4.89	5.97	19.1	219	146	882
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1951	-24.8	27.86667	2	36.25	5.98	4.84	5.91	17.9	190	631	1224
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1951	-19.6333	14.83333	1	38.09	6.16	5.51	5.96	19.14	209	316	1205
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1952	-28.7	20.96667	2	35.54	5.78	5.14	5.7	18.01	198	155	746
Muridae	Gerbilliscus	leucogaster	South Africa	North West	1953	-27.5833	25.45	2	37.09	6.19	5.1	6.06	18.88	177	485	1264
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1953	-22.9833	31.26667	2	37.7	6.83	5.77	6.14	19.6	229	462	313
Muridae	Gerbilliscus	leucogaster	South Africa	North West	1954	-27.5833	25.45	2	38.39	6.5	5.49	6.08	19.54	177	485	1264
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1955	-27.9333	22.73333	2	36.76	6.48	5.35	6.26	19.12	170	357	1267
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1955	-27.9333	22.73333	1	38.98	6.72	5.73	6.23	19.44	170	357	1267
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1955	-27.9333	22.73333	1	38.5	6.78	5.33	6.54	19.9	170	357	1267
Muridae	Gerbilliscus	leucogaster	South Africa	North West	1957	-27.3167	25.98333	2	37.4	6.6	5.23	6.07	19	173	571	1316
Muridae	Gerbilliscus	leucogaster	Angola	Quissama PanjÃ©	1957	-9.75	13.58333	1	36.79	6.41	5.13	7.32	19.33	242	784	153
Muridae	Gerbilliscus	leucogaster	Angola	Quissama PanjÃ©	1957	-9.75	13.58333	1	37.27	6.03	5.03	6.73	18.98	242	784	153
Muridae	Gerbilliscus	leucogaster	Angola	Quissama Demba	1957	-9.75	13.58333	1	37.36	6.1	5.26	6	19.07	242	784	153
Muridae	Gerbilliscus	leucogaster	Angola	Quissama PanjÃ©	1957	-9.75	13.58333	2	36.83	5.93	5.18	6.69	18.93	242	784	153
Muridae	Gerbilliscus	leucogaster	Angola	Quissama PanjÃ©	1957	-9.75	13.58333	2	35.96	6.02	4.9	6.67	19.04	242	784	153
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1958	-25.4333	31.93333	1	41.12	7.14	5.89	6.98	21.2	230	614	167
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1959	-25.4333	31.68333	2	37.98	6.64	5.68	6.14	19.84	220	680	279
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1961	-25.0833	31.6	1	39.33	6.61	5.61	6.25	18.82	215	668	360
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1961	-24.25	28.58333	2	36.65	6.51	5.5	6.17	19.21	164	676	1539
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1964	-15.6183	30.44695	2	35.96	6.68	5.45	6.25	17.86	256	688	328

Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1964	-15.6183	30.44695	1	37.87	6.77	5.7	6.03	19.73	256	688	328
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1964	-17.3936	14.21694	2	35.4	5.73	5.36	5.88	18.23	228	326	889
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1964	-17.3936	14.21694	2	36.35	6.8	5.16	5.79	17.8	228	326	889
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1964	-17.3936	14.21694	1	37.15	6.33	5.17	5.8	18.11	228	326	889
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1964	-27.4833	24.28333	1	36.78	6.55	5.66	6.2	18.27	169	497	1412
Muridae	Gerbilliscus	leucogaster	South Africa	North West	1964	-25.8333	24.68333	1	40.32	7.27	5.53	6.48	20.07	192	437	1125
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1964	-25.75	25.1	1	38.56	6.94	5.77	6.68	19.91	190	478	1158
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1965	-17.7	24.63333	2	38.07	6.94	5.29	6.22	19.08	220	641	936
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Zimbabwe	1965	-17.3667	30.2	1	37.51	6.65	5.55	5.91	18.81	197	818	1171
Muridae	Gerbilliscus	leucogaster	Angola	Angola	1966	-12.6072	13.19444	2	35.88	5.91	5.08	5.73	18.19	241	254	7
Muridae	Gerbilliscus	leucogaster	Angola	Angola	1966	-12.6072	13.19444	2	35.33	6.16	4.98	6.14	18.79	241	254	7
Muridae	Gerbilliscus	leucogaster	South Africa	Mpumalanga	1967	-24.75	31.41667	2	38.2	6.74	5.68	6	19.06	216	635	395
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1969	-24.1839	29.01278	2	36.43	6.45	5.53	6.03	18.36	195	488	1127
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1970	-28.5911	20.33833	1	35.42	6.14	4.91	5.89	18.7	206	139	623
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1970	-28.5911	20.33833	1	36.69	6.16	5.15	5.66	18.31	206	139	623
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1970	-28.5911	20.33833	1	35.88	6.3	4.93	6.14	18.48	206	139	623
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1970	-25.8167	20.01667	1	37.04	6.26	5.25	5.89	19.2	196	221	974
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1970	-22.8333	29.2411	1	39.4	6.67	5.75	6.57	18.6	206	396	786
Muridae	Gerbilliscus	leucogaster	South Africa	Gauteng	1972	-25.4	28.1	1	40.47	6.51	5.98	6.54	20.69	187	630	1111
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1973	-23.75	27.83333	1	39.17	6.46	5.97	6.71	20.68	207	464	893
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1973	-23.75	27.83333	1	40.29	6.79	5.84	6.42	20.24	207	464	893
Muridae	Gerbilliscus	leucogaster	South Africa	Limpopo	1974	-23.5333	28.41667	2	39.21	6.28	5.77	6.81	19.01	199	490	1009
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1977	-29.8333	22.78333	2	36.17	6.06	5.19	5.8	18.66	167	294	1239
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1977	-29.8333	22.78333	2	35.33	5.89	5.39	6.01	19.05	167	294	1239
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1980	-29.3833	20.9	2	35.2	6.26	5.13	5.52	18.66	189	176	913
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1980	-26.95	17.93333	1	36.64	5.61	5.55	5.51	18.69	211	107	708
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1980	-26.95	17.93333	2	34.5	5.87	5.19	5.61	18.04	211	107	708
Muridae	Gerbilliscus	leucogaster	Namibia	Namibia	1980	-26.95	17.93333	2	36.42	6.3	5.22	5.89	18.76	211	107	708
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Zimbabwe	1981	-18.1667	28.21667	1	38.83	6.41	5.35	6.4	19.35	223	654	874
Muridae	Gerbilliscus	leucogaster	Tanzania	Tanzania	1981	-6.81667	37.66667	2	39.44	6.66	5.53	7.09	20.08	246	935	502

Muridae	Gerbilliscus	leucogaster	Tanzania	Tanzania	1981	-6.81667	37.66667	1	36.79	6.92	5.2	6.88	17.72	246	935	502
Muridae	Gerbilliscus	leucogaster	Tanzania	Tanzania	1981	-6.81667	37.66667	1	38.29	6.96	5.28	6.75	19.5	246	935	502
Muridae	Gerbilliscus	leucogaster	Tanzania	Tanzania	1981	-6.81667	37.66667	2	39.93	6.67	5.44	7.05	20.42	246	935	502
Muridae	Gerbilliscus	leucogaster	DRC	Kinshasa	1981	-4.325	15.32222	2	36.67	6.76	4.9	7.26	18.35	255	1369	281
Muridae	Gerbilliscus	leucogaster	South Africa	KwaZulu-Natal	1982	-26.8833	32.25	2	38.4	6.5	5.54	6.25	19.19	229	627	44
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1982	-26.95	24.73333	2	41.57	7.01	5.79	6.79	21.32	180	475	1206
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1982	-26.3	25.55	2	38.94	7.1	5.68	6.02	20.49	178	538	1373
Muridae	Gerbilliscus	leucogaster	South Africa	Northern Cape	1983	-27.65	24.01667	1	38.51	6.92	5.66	6.08	20.18	166	495	1458
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Kudzwe Dam	1986	-16.7833	32.51667	1	38.16	6.65	5.32	6.86	19.54	228	630	545
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Kudzwe Dam	1986	-16.7833	32.51667	1	37.69	6.33	5	7.2	19.2	228	630	545
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Kudzwe Dam	1986	-16.7833	32.51667	3	34.31	6.11	4.95	6.01	17.28	228	630	545
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Kudzwe Dam	1986	-16.7833	32.51667	3	35.49	6.28	5.15	7	17.43	228	630	545
Muridae	Gerbilliscus	leucogaster	South Africa	KwaZulu-Natal	1987	-27.0667	32.43333	2	41.92	6.74	5.9	6.51	20.31	226	737	73
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Angwa Bridge	1988	-16.1014	30.3077	1	37.94	6.63	5.14	7.22	19.38	236	743	408
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Angwa Bridge	1988	-16.1014	30.3077	1	37.5	6.83	4.91	7.2	18.92	236	743	408
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Angwa Bridge	1988	-16.1014	30.3077	2	35.04	6.4	5.02	6.25	18.62	236	743	408
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Angwa Bridge	1988	-16.1014	30.3077	2	36.85	6.4	5.06	6.72	18.37	236	743	408
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Angwa Bridge	1988	-16.1014	30.3077	2	37.04	6.65	5.26	6.27	19.25	236	743	408
Muridae	Gerbilliscus	leucogaster	Zimbabwe	Angwa Bridge	1988	-16.1014	30.3077	2	35.68	6.6	4.95	6.4	18	236	743	408
Muridae	Gerbilliscus	leucogaster	Swaziland	Swaziland	1995	-26.3667	31.56667	2	39.95	7.08	5.73	6.68	20.39	214	642	376
Muridae	Gerbilliscus	leucogaster	South Africa	North West	1996	-25.8072	22.8875	2	36.25	6.33	5.29	5.85	18.8	198	337	999
Muridae	Gerbilliscus	leucogaster	South Africa	North West	1996	-25.8833	22.93083	2	36.49	6.53	5.52	6.42	19.26	198	344	1009
Muridae	Gerbilliscus	leucogaster	South Africa	North West	1996	-25.8833	22.93083	2	37.47	6.67	5.75	6.52	19.36	198	344	1009
Muridae	Gerbilliscus	leucogaster	Swaziland	Swaziland	1996	-27.0167	31.65	2	38.01	6.5	5.35	6.2	19.48	212	711	358
Muridae	Gerbilliscus	leucogaster	Malawi	Karonga District, Malema	1996	-10	33.75	1	37.36	6.42	5.17	7.21	18.64	230	1315	840
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1997	-17.0631	38.69417	2	41	7.16	6.58	6.46	20.98	254	1261	10
Muridae	Gerbilliscus	leucogaster	Mozambique	Mozambique	1997	-17.0642	38.74389	2	43.79	7.55	6.68	7.32	21.62	254	1253	22
Muridae	Mastomys	natalensis	South Africa	Limpopo	1907	-23.8	30.16667	5	29.62	5.33	5.14	4.29	14.86	202	983	720
Muridae	Mastomys	natalensis	South Africa	Limpopo	1907	-23.8	30.16667	5	29.92	5.71	4.46	4.46	14.6	202	983	720
Muridae	Mastomys	natalensis	South Africa	Limpopo	1907	-23.8	30.16667	4	29.41	5.16	5.01	4.29	13.33	202	983	720

Muridae	Mastomys	natalensis	South Africa	Limpopo	1907	-23.8	30.16667	4	28.66	5.16	5	4.29	14.65	202	983	720
Muridae	Mastomys	natalensis	South Africa	Limpopo	1907	-23.8	30.16667	5	30.05	5.28	4.96	4.14	14.14	202	983	720
Muridae	Mastomys	natalensis	South Africa	Limpopo	1907	-23.8	30.16667	5	32.07	5.69	5.4	4.35	14.51	202	983	720
Muridae	Mastomys	natalensis	South Africa	Limpopo	1907	-23.8	30.16667	6	30.32	5.24	4.82	4.17	14.44	202	983	720
Muridae	Mastomys	natalensis	Kenya	Kenya	1913	-2.98333	38.51667	6	34.03	5.73	5.34	4.86	16.01	254	1001	416
Muridae	Mastomys	natalensis	Kenya	Kenya	1913	-2.98333	38.48333	5	31.74	5.41	4.82	4.24	14.82	254	1020	441
Muridae	Mastomys	natalensis	DRC	DRC	1913	-2.98333	38.46667	5	29.14	5.32	4.4	4.03	13.8	253	1037	452
Muridae	Mastomys	natalensis	Kenya	Kenya	1913	-3.36667	37.78333	4	28.47	5.51	5.01	4.41	14.25	225	681	885
Muridae	Mastomys	natalensis	Kenya	Kenya	1913	-2.98333	38.48333	6	30.92	5.52	4.54	4.34	13.96	254	1020	441
Muridae	Mastomys	natalensis	South Africa	Mpumalanga	1915	-26.05	30.83333	4	29.39	5.44	4.87	4.08	14.37	188	1050	985
Muridae	Mastomys	natalensis	South Africa	Mpumalanga	1915	-26.05	30.83333	4	30.33	5.28	4.83	4.47	13.93	188	1050	985
Muridae	Mastomys	natalensis	South Africa	Gauteng	1916	-26.1	27.96667	5	27.59	5.19	4.17	3.87	13.57	167	704	1514
Muridae	Mastomys	natalensis	South Africa	North West	1916	-25.25	27.81667	4	27.53	5.35	4.4	4.31	13.65	197	589	1018
Muridae	Mastomys	natalensis	DRC	DRC	1920	-5.13333	15.31667	6	30.6	5.02	4.74	4.65	14.57	236	1469	617
Muridae	Mastomys	natalensis	South Africa	Limpopo	1921	-24.7833	28.41667	7	30.48	5.4	5.32	4.29	14.48	183	636	1255
Muridae	Mastomys	natalensis	South Africa	Limpopo	1921	-24.7833	28.41667	5	29.26	5.26	4.59	4.15	14.28	183	636	1255
Muridae	Mastomys	natalensis	DRC	DRC	1922	-5.46667	13.21667	7	31.6	5.51	4.89	4.52	14.36	226	1209	457
Muridae	Mastomys	natalensis	South Africa	Free State	1923	-26.8667	27.36667	5	28.29	4.87	4.84	4	14.3	163	648	1503
Muridae	Mastomys	natalensis	South Africa	Free State	1923	-27.2667	27.98333	4	28.58	5.22	4.4	4.12	14.23	154	655	1577
Muridae	Mastomys	natalensis	South Africa	Gauteng	1923	-25.95	28.2	7	29.21	5.05	4.89	3.87	14.29	167	699	1517
Muridae	Mastomys	natalensis	South Africa	Limpopo	1924	-23.95	30.6	7	30.67	5.63	4.72	4.21	14.71	214	605	574
Muridae	Mastomys	natalensis	South Africa	Limpopo	1925	-24.5833	31.08333	4	28.42	5.37	5.07	4.16	13.72	208	778	632
Muridae	Mastomys	natalensis	Mozambique	unknown	1925	-21.8667	31.01667	4	29.36	5.27	4.72	4.47	14.23	221	554	571
Muridae	Mastomys	natalensis	DRC	DRC	1926	-6.5	29.48333	7	31.95	5.59	4.74	4.2	14.85	241	971	766
Muridae	Mastomys	natalensis	DRC	DRC	1929	-5.93333	29.2	4	27.71	5.49	4.26	4.22	13.34	236	1089	771
Muridae	Mastomys	natalensis	DRC	DRC	1930	-10.5167	27.55	7	30.34	5.47	4.63	4.61	13.97	222	1040	945
Muridae	Mastomys	natalensis	South Africa	Gauteng	1931	-25.75	28.18333	7	30.44	5.54	4.74	4.15	15.3	177	696	1350
Muridae	Mastomys	natalensis	DRC	DRC	1931	-10.8167	26.11667	5	30.54	5.42	4.84	4.09	14.65	203	1135	1307
Muridae	Mastomys	natalensis	DRC	DRC	1934	-11.6667	27.5	6	30.4	5.26	4.69	3.96	14.39	204	1238	1235
Muridae	Mastomys	natalensis	South Africa	Limpopo	1935	-22.9667	30.48333	5	29.6	5.46	4.56	4.1	13.91	217	769	591

Muridae	Mastomys	natalensis	South Africa	Limpopo	1935	-22.5	30.83333	4	28.42	5.23	4.26	4.06	13.43	234	485	399
Muridae	Mastomys	natalensis	DRC	DRC	1935	-11.6833	27.48333	7	31.53	5.72	5.02	4.48	15.54	202	1242	1215
Muridae	Mastomys	natalensis	DRC	DRC	1935	-11.6667	27.46667	4	29.46	5.52	5.1	4.43	14.06	203	1240	1212
Muridae	Mastomys	natalensis	Swaziland	Swaziland	1937	-26.0333	31.85	4	28.01	5.22	4.63	3.98	13.21	222	705	250
Muridae	Mastomys	natalensis	Swaziland	Swaziland	1937	-26.0333	31.85	5	30.31	5.4	4.83	4	14.37	222	705	250
Muridae	Mastomys	natalensis	Uganda	Uganda	1941	3.288889	32.87778	5	33.51	5.65	5	4.8	16.66	243	1230	951
Muridae	Mastomys	natalensis	Uganda	Uganda	1941	3.288889	32.87778	4	31.02	5.16	5.23	4.87	14.8	243	1230	951
Muridae	Mastomys	natalensis	Uganda	Uganda	1941	3.288889	32.87778	4	31.76	5.3	4.64	4.54	14.79	243	1230	951
Muridae	Mastomys	natalensis	Uganda	Uganda	1941	3.288889	32.87778	4	31.71	5.36	5.4	4.92	15.61	243	1230	951
Muridae	Mastomys	natalensis	Uganda	Uganda	1941	2.781667	32.29917	4	33.23	5.74	5.8	5.13	15.86	230	1506	1115
Muridae	Mastomys	natalensis	Uganda	Uganda	1941	2.781667	32.29917	4	32.81	5.61	4.9	4.83	14.78	230	1506	1115
Muridae	Mastomys	natalensis	South Africa	Limpopo	1951	-23.05	29.9	7	30.43	5.61	5.21	4.28	14.33	190	721	932
Muridae	Mastomys	natalensis	South Africa	Gauteng	1953	-26.0167	27.7	5	29.45	5.33	4.32	4.05	13.75	165	695	1494
Muridae	Mastomys	natalensis	South Africa	Gauteng	1953	-26.0167	27.73333	4	26.99	4.96	4.27	3.97	13.42	167	684	1474
Muridae	Mastomys	natalensis	South Africa	North West	1953	-27.5833	25.45	6	31.31	5.08	5.02	4.27	15.32	177	485	1264
Muridae	Mastomys	natalensis	DRC	DRC	1955	-11.6667	27.46667	7	32.93	5.44	4.87	4.32	15.98	203	1240	1212
Muridae	Mastomys	natalensis	DRC	DRC	1956	-11.55	27.61667	6	29.32	5.6	4.55	4.3	14.32	206	1223	1252
Muridae	Mastomys	natalensis	Zambia	Zambia	1959	-14.0833	25.25	5	30.9	5.74	4.93	4.11	14.42	205	1028	1186
Muridae	Mastomys	natalensis	Kenya	Kenya	1960	-1	36.36667	4	29.36	5.31	4.32	4.72	14.17	186	759	1671
Muridae	Mastomys	natalensis	South Africa	Mpumalanga	1961	-24.9833	31.58333	4	29.59	5.4	4.55	4.27	13.26	218	621	272
Muridae	Mastomys	natalensis	South Africa	Mpumalanga	1961	-24.9833	31.58333	5	28.77	5.44	4.4	4.03	13.67	218	621	272
Muridae	Mastomys	natalensis	Mozambique	Mozambique	1964	-26.0417	32.32528	5	29.81	5.7	4.67	4.1	14.62	229	677	42
Muridae	Mastomys	natalensis	Ivory Coast	Ivory Coast	1964	5.33333	-4.11667	7	30.4	5.74	4.78	4.45	15.12	266	1751	15
Muridae	Mastomys	natalensis	TChaD	TChaD	1965	12.11306	15.04917	4	28.26	5.32	4.22	4.9	13.81	281	485	299
Muridae	Mastomys	natalensis	Ivory Coast	Ivory Coast	1965	5.33333	-4.11667	6	30	5.67	4.71	4.62	14.44	266	1751	15
Muridae	Mastomys	natalensis	Ivory Coast	Ivory Coast	1966	6.73333	-3.48333	6	33.55	5.66	5.32	4.65	15.3	264	1301	190
Muridae	Mastomys	natalensis	Burkina Faso	Burkina Faso	1966	12.31667	-1.7	6	31.47	5.54	4.98	4.55	14.32	278	769	340
Muridae	Mastomys	coucha	Cote d'Ivoire	Cote d'Ivoire	1966	6.83333	-5.05	4	27.56	4.95	4.56	4.4	13.12	264	1071	184
Muridae	Mastomys	coucha	Cote d'Ivoire	Cote d'Ivoire	1966	6.83333	-5.05	4	27.88	4.96	4.44	4.3	13.14	264	1071	184
Muridae	Mastomys	natalensis	Togo	Togo	1968	7.58333	0.6	6	30.01	5.31	4.66	4.02	14.61	262	1524	270

Muridae	Mastomys	natalensis	Togo	Togo	1968	9.25	1.2	4	31.46	5.36	4.14	4.51	14.62	244	1474	715
Muridae	Mastomys	natalensis	Togo	Togo	1968	7.51667	1.16667	5	28.08	5.13	4.17	4.44	13.26	265	1266	236
Muridae	Mastomys	natalensis	Ivory Coast	Ivory Coast	1968	8.51667	-5.31667	4	26.77	5.55	4.28	3.98	12.48	270	1084	268
Muridae	Mastomys	natalensis	Togo	Togo	1969	9.25	1.2	5	31.72	5.82	4.73	4.65	14.99	244	1474	715
Muridae	Mastomys	natalensis	Togo	Togo	1969	9.25	1.2	5	28.86	4.95	4.71	4.49	14.23	244	1474	715
Muridae	Mastomys	natalensis	Ivory Coast	Ivory Coast	1969	7.81667	-4.68333	4	29.63	5.31	4.44	4.25	12.26	274	1073	173
Muridae	Mastomys	natalensis	South Africa	Gauteng	1970	-25.95	28.2	5	30.03	5.48	4.7	4.06	14.34	167	699	1517
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1970	4.05	11.55	5	29.36	5.11	4.27	4.35	13.36	242	1636	626
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1970	10.5	15.2	7	33.34	5.45	4.82	4.84	16.02	281	749	319
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1970	10.55	13.68333	6	33.8	5.55	5.52	4.86	16.83	242	956	818
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1971	7.1	12.48333	6	30.95	5.48	4.83	4.68	14.26	225	1625	1052
Muridae	Mastomys	natalensis	Ivory Coast	Ivory Coast	1972	11.53333	-0.48333	7	29.82	5.24	4.48	4.25	13.54	283	836	270
Muridae	Mastomys	natalensis	TChaD	TChaD	1973	7.766667	15.7	4	29.85	4.97	4.37	4.55	14.11	266	1249	458
Muridae	Mastomys	natalensis	TChaD	TChaD	1973	7.766667	15.7	4	29.96	5.11	4.7	4.6	14.16	266	1249	458
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1973	5.03	9.83	5	31	5.4	4.63	5	14.63	161	2159	1977
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1973	5.03	9.83	5	31.68	5.1	4.92	4.6	15.41	161	2159	1977
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1973	5.03	9.83	4	29.06	5	4.33	4.38	13.97	161	2159	1977
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1973	5.03	9.83	3	27.23	5.12	4.24	4.22	12	161	2159	1977
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1973	5.03	9.83	4	28.21	5.26	4.6	4.55	13.7	161	2159	1977
Muridae	Mastomys	natalensis	South Africa	Limpopo	1974	-23.5333	28.41667	4	28.33	5.06	4.16	3.82	14.12	199	490	1009
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1974	5.03	9.83	7	33.17	5.31	5	4.6	15.6	161	2159	1977
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1974	5.03	9.83	6	32.34	5.66	5.03	4.9	15.56	161	2159	1977
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1974	10.86667	13.88333	7	31.7	5.49	4.85	4.3	15.08	263	843	504
Muridae	Mastomys	natalensis	Cameroon	Cameroon	1975	5.7	10.66667	6	31.34	5.46	4.8	4.44	15.75	211	1956	1270
Muridae	Mastomys	natalensis	Burkina Faso	Burkina Faso	1976	11.21667	-4.43333	4	28.16	4.75	4.18	4.03	13.45	273	1014	339
Muridae	Mastomys	natalensis	Burkina Faso	Burkina Faso	1976	11.21667	-4.43333	4	26.47	5.17	4.19	4.09	13.29	273	1014	339
Muridae	Mastomys	natalensis	Burkina Faso	Burkina Faso	1977	10.61667	-5.11667	4	25.91	4.91	4.05	4.09	11.65	273	1081	304
Muridae	Mastomys	natalensis	Burkina Faso	Burkina Faso	1977	10.61667	-5.11667	6	32.42	5.2	4.81	4.41	15.3	273	1081	304
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	13.35	-12.4167	5	30	5.36	5.1	4.66	14.15	281	906	147
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	13.35	-12.4167	5	30.29	5.33	4.88	4.83	13.46	281	906	147

Muridae	Mastomys	natalensis	Senegal	Senegal	1985	13.35	-12.4167	7	33.38	6.26	5.92	5.44	17.14	281	906	147
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	13.2604	-12.1053	5	29.62	5.27	4.54	4.65	14.2	282	957	174
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	13.2604	-12.1053	6	30.39	5.25	4.67	4.6	15.17	282	957	174
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	13.2604	-12.1053	6	32.06	5.36	5.51	4.74	15.15	282	957	174
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	13.2604	-12.1053	5	28.5	4.92	4.88	4.65	14.31	282	957	174
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	12.46667	-12.65	6	32.31	5.14	4.88	4.37	15.19	279	1272	132
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	12.46667	-12.65	6	31.3	5.39	4.57	4.48	15.14	279	1272	132
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	12.46667	-12.65	6	31.71	5.29	4.73	4.71	15.59	279	1272	132
Muridae	Mastomys	natalensis	Senegal	Senegal	1985	12.46667	-12.65	5	29.47	5.18	4.3	5	14.22	279	1272	132
Muridae	Mastomys	natalensis	Tanzania	Morogoro	1985	-6.85	37.63333	6	30.45	5.51	4.88	4.2	14.44	246	986	510
Muridae	Mastomys	natalensis	Tanzania	Morogoro	1985	-6.85	37.63333	5	27.72	5.45	4.39	4.12	13.46	246	986	510
Muridae	Mastomys	natalensis	Senegal	Senegal	1986	13.2604	-12.1053	6	30.2	5.15	4.77	4.73	15.14	282	957	174
Muridae	Mastomys	natalensis	Senegal	Senegal	1986	13.2604	-12.1053	5	29.82	4.74	4.29	4.85	14.1	282	957	174
Muridae	Mastomys	natalensis	Senegal	Senegal	1986	13.2604	-12.1053	7	31.73	5.33	4.41	5.14	14.8	282	957	174
Muridae	Mastomys	natalensis	Senegal	Senegal	1986	12.55	-12.1833	7	32.26	5.48	5.06	4.92	15.6	284	1204	111
Muridae	Mastomys	natalensis	Senegal	Senegal	1986	12.55	-12.1833	5	30.53	5.32	4.54	4.32	13.7	284	1204	111
Muridae	Mastomys	natalensis	Tanzania	Morogoro	1986	-6.85	37.63333	6	29.03	5.42	4.39	4.62	14.05	246	986	510
Muridae	Mastomys	natalensis	Senegal	Senegal	1987	12.56667	-15.8833	5	29.46	5.43	4.44	4.43	14.3	267	1223	28
Muridae	Mastomys	natalensis	Tanzania	Morogoro	1988	-6.85	37.63333	6	26.95	5.44	3.96	3.97	13.011	246	986	510
Muridae	Mastomys	natalensis	Tanzania	Morogoro	1989	-6.85	37.63333	5	24.42	5.34	3.83	4.42	13.3	246	986	510
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	5	29.03	5.11	4.26	4.48	13.83	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	4	28.61	4.63	4.24	4.49	13.2	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	5	29.47	5.12	4.57	4.5	13.58	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	4	28.98	5.18	4.12	4.62	13.1	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	6	30.52	5.61	4.35	4.98	14.48	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	5	29.76	5.2	4.77	4.63	13.57	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	4	29.8	5.08	4.44	4.46	14.2	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	6	32.76	5.52	4.85	5.02	15.02	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	5	29.39	4.98	4.3	4.67	13.86	244	1537	457
Muridae	Mastomys	natalensis	RCA	RCA	1993	4.031944	17.335	5	28.41	4.99	3.98	4.54	13.69	244	1537	457

Muridae	Mastomys	natalensis	Tanzania	Tanzania	1995	-7.7	31.56667	5	27.75	5.27	4.22	3.89	13.39	236	938	869
Muridae	Mastomys	natalensis	Tanzania	Tanzania	1996	-5.15	30.38333	7	31.62	5.27	4.99	4.74	16.22	220	1012	1089
Muridae	Mastomys	natalensis	Tanzania	Tanzania	1996	-5.15	30.38333	3	26.35	5.1	3.8	4.5	12.93	220	1012	1089
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	5	29.95	5.09	4.7	4.4	14.74	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	6	32.2	5.36	4.51	4.69	15.3	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	6	30.71	4.67	4.46	4.86	14.84	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	6	32.6	5.4	4.85	5.06	15.4	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	7	32.51	5.33	4.93	4.9	15.81	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	7	33.74	5.17	4.94	4.83	16.52	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	7	32.58	5.2	4.73	4.98	16.13	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	5	29.74	5.2	4.58	4.76	15.11	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	4	28.86	4.88	4.52	4.38	13.94	232	1882	714
Muridae	Mastomys	natalensis	DRC	DRC	1996	-2.92	15.35	5	28.28	5.22	4.6	4.44	14.29	232	1882	714
Muridae	Mastomys	natalensis	Tanzania	Tanzania	1996	-6.18333	37.11667	5	26.45	5.12	4.27	4.04	12.9	225	793	838
Muridae	Mastomys	natalensis	Mali	Mali	1999	12.50083	-8.09056	7	32.19	5.45	4.6	4.55	15.06	279	964	333
Muridae	Mastomys	natalensis	Mali	Mali	1999	12.88	-8.14222	6	33.68	5.39	4.8	4.9	15.34	272	972	424
Muridae	Mastomys	natalensis	Mali	Mali	1999	12.63917	-8.00278	5	31.42	5.32	4.7	4.45	16.1	278	951	330
Muridae	Mastomys	natalensis	Mali	Mali	1999	12.95222	-8.17306	4	30.65	5.2	4.8	4.55	14.05	269	967	426
Muridae	Mastomys	natalensis	Mali	Mali	1999	12.95222	-8.17306	3	27.21	4.81	4	4.02	12.4	269	967	426
Muridae	Mastomys	natalensis	Mali	Mali	1999	13	-8.23333	5	30.12	5.12	4.55	4.25	15.21	267	967	442
Muridae	Mastomys	natalensis	Mali	Mali	1999	12.31667	-8.13333	6	34.09	5.48	4.9	4.78	15.16	278	978	325
Muridae	Mastomys	natalensis	Mali	Mali	1999	12.88333	-8.13333	7	33.92	5.79	5.41	4.91	17.2	272	969	409
Muridae	Mastomys	natalensis	TChaD	TChaD	2000	12.83701	14.78825	4	28.91	4.93	4.33	4.6	14.34	279	366	288
Muridae	Mastomys	natalensis	TChaD	TChaD	2000	13.46	14.74	4	28.9	5.6	4.01	4.06	13.08	277	266	280
Muridae	Mastomys	natalensis	TChaD	TChaD	2000	13.46	14.74	4	28.62	5.29	4.45	4.46	13.69	277	266	280
Muridae	Mastomys	natalensis	TChaD	TChaD	2000	12.9	14.83333	6	30.53	5.55	4.55	4.98	14.24	281	367	283
Muridae	Mastomys	natalensis	TChaD	TChaD	2000	13.46	14.74	4	29.26	5.23	4.42	4.35	13.4	277	266	280
Muridae	Mastomys	natalensis	Mali	Mali	2001	12.55	-8.05	7	33.78	5.7	5.22	5.06	16.52	279	955	325
Muridae	Mastomys	natalensis	Mali	Mali	2002	12.45	-10.25	7	32.67	5.82	5.52	5	16.42	271	1200	341
Muridae	Mastomys	natalensis	Mali	Mali	2002	15.05	-2.78333	6	32.16	5.33	4.82	4.7	16.01	281	436	324

Muridae	Mastomys	natalensis	Mali	Mali	2002	12.3	-8.13333	5	31.49	5.33	4.91	4.68	14.73	278	978	325
Muridae	Mastomys	natalensis	Mali	Mali	2002	12.55	-8.86667	5	29.48	4.72	4.35	4.41	14.01	259	1079	634
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	6	30.26	5.2	4.21	4.65	14.26	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	6	31.66	5.46	4.63	4.43	14.04	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	6	31.65	5.77	4.51	4.57	14.97	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	7	34.41	5.92	4.99	5.08	17.19	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	5	30.4	5.34	4.36	4.81	14.08	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	5	28.84	5.1	4.24	4.33	13.81	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	5	29.58	5.36	4.5	4.83	14.1	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	6	31.11	5.77	4.77	4.66	16.02	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	6	31.1	5.46	4.38	4.68	14.73	254	1107	159
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-8.44778	38.61556	4	29.73	5.36	4.5	4.42	14.43	254	1107	159
Muridae	Mastomys	natalensis	Guinea	Guinea	2003	10.1	-10.9667	5	31.04	5.5	4.87	4.56	15.3	253	1527	455
Muridae	Mastomys	natalensis	Guinea	Guinea	2003	10.1	-10.9667	5	31.12	5.02	4.6	4.68	14.48	253	1527	455
Muridae	Mastomys	natalensis	Guinea	Guinea	2003	10.1	-10.9667	5	30	5.32	4.63	4.4	13.7	253	1527	455
Muridae	Mastomys	natalensis	Guinea	Guinea	2003	10.1	-10.9667	6	32.1	5.28	4.55	4.1	15.47	253	1527	455
Muridae	Mastomys	natalensis	Guinea	Guinea	2003	10.1	-10.9667	5	30.11	5.5	5.07	4.21	14.9	253	1527	455
Muridae	Mastomys	natalensis	Guinea	Guinea	2003	10.1	-10.9667	5	31.25	5.37	4.61	4.3	14.05	253	1527	455
Muridae	Mastomys	natalensis	Guinea	Guinea	2003	10.00056	-10.9728	6	32.28	5.4	4.88	4.52	16	251	1567	463
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-6.86667	37.65	7	27.95	5.2	4.14	4.36	13.24	235	1081	686
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-6.86667	37.65	5	28.35	5.29	4.62	4.38	14.25	235	1081	686
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-6.83333	37.68333	4	25.31	4.83	3.9	4.06	11.91	242	947	544
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2003	-6.76667	37.66667	4	28.75	4.86	4.5	4	13.84	248	888	474
Muridae	Mastomys	natalensis	Guinea	Guinea	2004	10.00056	-10.9728	5	30.94	5.48	4.74	4.64	14.5	251	1567	463
Muridae	Mastomys	natalensis	Guinea	Guinea	2004	10.00056	-10.9728	5	30.38	5.23	4.92	4.3	14.42	251	1567	463
Muridae	Mastomys	natalensis	Guinea	Guinea	2004	10.00056	-10.9728	5	30.97	5.26	4.66	4.84	14.96	251	1567	463
Muridae	Mastomys	natalensis	Guinea	Guinea	2004	10.00056	-10.9728	5	30.23	5.32	4.76	4.44	14.74	251	1567	463
Muridae	Mastomys	natalensis	Guinea	Guinea	2004	10.00056	-10.9728	4	28.76	4.76	4.26	4.28	13.09	251	1567	463
Muridae	Mastomys	natalensis	DRC	DRC	2004	-4.3	15.3	7	28.6	5.32	4.34	4.28	14.09	255	1370	282
Muridae	Mastomys	natalensis	DRC	DRC	2004	-4.3	15.3	6	32.43	5.26	4.32	4.37	16	255	1370	282

Muridae	Mastomys	natalensis	DRC	DRC	2004	-4.3	15.3	6	31.44	5.27	4.71	4.92	13.84	255	1370	282
Muridae	Mastomys	natalensis	DRC	DRC	2004	-4.3	15.3	5	32.14	5.68	4.68	4.39	16.91	255	1370	282
Muridae	Mastomys	natalensis	DRC	DRC	2004	-4.3	15.3	4	28.4	4.98	4.06	4.33	12	255	1370	282
Muridae	Mastomys	natalensis	Mozambique	Mozambique	2004	-17.3333	35.58333	4	28.4	5.04	4.21	4.05	13.59	234	1026	404
Muridae	Mastomys	natalensis	Zimbabwe	Zimbabwe	2004	-19.0333	28.9	4	29.8	5.86	4.66	4.24	14.26	200	664	1162
Muridae	Mastomys	natalensis	Zimbabwe	Zimbabwe	2004	-19.0333	28.9	7	27.71	5.15	4.53	4.23	13.89	200	664	1162
Muridae	Mastomys	natalensis	Zimbabwe	Zimbabwe	2004	-19.0333	28.9	7	29.47	5.16	4.61	4.29	13.29	200	664	1162
Muridae	Mastomys	natalensis	Zimbabwe	Zimbabwe	2004	-17.85	31.03333	5	28.29	5.2	4.65	3.9	13.94	185	819	1469
Muridae	Mastomys	natalensis	Zimbabwe	Zimbabwe	2004	-17.85	31.03333	7	29.98	5.49	4.64	4	14	185	819	1469
Muridae	Mastomys	natalensis	Mozambique	Mozambique	2004	-17.3333	35.58333	5	31.28	5.27	4.39	4.35	13.8	234	1026	404
Muridae	Mastomys	natalensis	Mozambique	Mozambique	2004	-17.3333	35.58333	6	29.52	5.34	4.43	3.96	13.72	234	1026	404
Muridae	Mastomys	natalensis	Mozambique	Mozambique	2004	-17.3333	35.58333	6	29.12	5.28	4.63	4.11	13.26	234	1026	404
Muridae	Mastomys	natalensis	Cameroon	Cameroon	2006	4.801389	9.708056	4	28.18	5.22	4.58	4.3	13.31	170	2274	1951
Muridae	Mastomys	natalensis	Benin	Benin	2006	6.7	2.38333	7	32.79	5.38	4.97	4.75	14.95	275	1118	13
Muridae	Mastomys	natalensis	Benin	Benin	2006	6.7	2.38333	7	29.98	4.93	5	4.5	14.86	275	1118	13
Muridae	Mastomys	natalensis	Benin	Benin	2006	6.81667	2.36667	6	28.93	5.22	4.34	4.6	13.9	277	1088	11
Muridae	Mastomys	natalensis	Benin	Benin	2006	7.25	2.46667	6	29.36	5.04	4.7	4.43	14.29	280	1050	15
Muridae	Mastomys	natalensis	Mali	Mali	2007	14.06667	-3.68333	6	30.85	5.18	4.48	5.1	14.28	269	532	369
Muridae	Mastomys	natalensis	Mali	Mali	2007	14.06667	-3.68333	4	28.76	5.24	4.3	4.5	12.66	269	532	369
Muridae	Mastomys	natalensis	Mali	Mali	2007	14.06667	-3.68333	6	30.52	5.16	5.4	4.69	14.01	269	532	369
Muridae	Mastomys	natalensis	Tanzania	Tanzania	2007	-4.6	38.23333	4	26.68	5.36	3.87	4.41	12.41	150	762	1944
Muridae	Mastomys	natalensis	DRC	DRC	2008	0.33333	25.16667	5	29.67	5.55	4.21	4.63	14.76	250	1761	446
Muridae	Mastomys	natalensis	DRC	DRC	2008	0.33333	25.16667	6	29.38	5.17	4.65	4.26	13.64	250	1761	446
Muridae	Mastomys	natalensis	Guinea	Guinea	2011	7.442	-9.243	7	32.42	5.73	4.83	4.63	15.45	246	2116	424
Muridae	Mastomys	natalensis	Guinea	Guinea	2011	7.442	-9.243	7	32.7	5.8	5.16	4.83	15.52	246	2116	424
Muridae	Mastomys	natalensis	Guinea	Guinea	2011	7.616667	-7.41667	4	28.58	5.14	4.37	4.61	13	229	1611	751
Muridae	Mastomys	natalensis	Guinea	Guinea	2013	9.690556	-12.8136	7	33.75	5.88	4.97	4.54	16.55	277	2664	119
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1906	-26.1833	28.06667	6	32.54	5.73	5.23	4.7	16.09	159	790	1798
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1906	-26.1833	28.06667	4	30.06	5.1	4.59	4.7	15.67	159	790	1798
Muridae	Micalemys	namaquensis	South Africa	North West	1906	-26.3	27.4	4	28.73	4.5	4.51	4.7	13.93	161	658	1510

Muridae	Micalemys	namaquensis	South Africa	North West	1906	-26.3167	27.46667	5	29.86	5.5	4.78	4.65	14.77	160	664	1516
Muridae	Micalemys	namaquensis	South Africa	North West	1906	-26.7333	27.06667	5	30.71	5.63	4.74	4.98	15.59	168	617	1351
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1907	-26.1833	28.06667	5	30.52	5.26	5.16	5.31	15	159	790	1798
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1907	-26.1833	28.06667	4	30.89	5.51	4.83	4.69	14.7	159	790	1798
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1907	-26.1833	28.06667	5	33.15	5.74	5.07	5	16.2	159	790	1798
Muridae	Micalemys	namaquensis	South Africa	North West	1907	-26.7333	27.06667	5	32.02	5.67	4.89	4.74	15.28	168	617	1351
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1912	-25.6833	28.2	4	31.31	5.42	4.75	4.72	15.29	178	696	1271
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1912	-25.7167	28.23333	4	32.41	5.42	5.06	4.67	15.65	178	697	1300
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1912	-25.7167	28.23333	5	32.88	5.7	4.95	5.11	16.41	178	697	1300
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1912	-25.8667	28.23333	4	31.22	5.59	4.97	4.7	15.35	166	713	1494
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1914	-26.0667	30.1	5	31.71	5.2	5.59	4.55	15.34	150	762	1665
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1915	-24.8833	27.65	4	31.47	5.26	4.88	4.61	14.88	184	671	1361
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1915	-26.05	30.83333	4	31.92	5.45	5.12	4.58	15.01	188	1050	985
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1916	-22.35	30.36667	5	31.05	5.02	5.01	4.63	15.15	235	395	403
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1916	-22.9	30.21667	5	30.05	5.32	5.22	5.07	14.54	201	910	880
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1917	-33.8833	19.05	4	32.09	6.24	4.87	4.9	15.77	169	896	186
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1917	-33.8833	19.05	4	32.18	5.47	4.41	4.63	14.32	169	896	186
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1917	-31.7833	18.61667	5	31.85	5.47	4.58	4.82	15.28	193	171	28
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1917	-31.7833	18.61667	5	31.92	5.87	4.8	4.61	15.49	193	171	28
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1923	-25.7833	28.25	4	30.84	5.77	4.9	4.53	15.22	169	718	1491
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1924	-25.75	28.3	5	32.44	5.58	4.94	4.66	15.02	175	703	1359
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1924	-25.6833	28.2	6	31.07	6.04	4.74	4.32	14.8	178	696	1271
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1924	-25.6833	28.2	6	32.22	5.6	4.9	4.83	15.17	178	696	1271
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1924	-23.6667	30.08333	5	31.89	5.38	5.16	4.92	15.06	189	1158	927
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1925	-25.6833	28.2	4	32.7	5.52	4.87	4.5	15.81	178	696	1271
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1925	-25.6833	28.2	4	30.97	5.55	4.8	4.51	15.35	178	696	1271
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1925	-25.7333	28.05	6	33.1	6.06	5.2	4.9	16	179	689	1411
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1925	-25.7333	28.05	7	31.79	5.83	4.82	4.69	15.18	179	689	1411
Muridae	Micalemys	namaquensis	South Africa	Eastern Cape	1927	-30.6833	26.7	4	31.9	6.11	4.5	4.77	15.1	155	545	1309
Muridae	Micalemys	namaquensis	South Africa	North West	1927	-27.75	25.41667	6	34.09	5.68	5.2	5.16	16.52	175	484	1271

Muridae	Micalemys	namaquensis	South Africa	Western Cape	1929	-33.4167	19.2	4	32.18	5.47	4.8	4.76	15.57	169	738	264
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1929	-33.4167	19.2	5	32.93	5.73	5.29	4.86	16.12	169	738	264
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1929	-33.4167	19.2	4	32.15	5.81	4.71	4.75	15.42	169	738	264
Muridae	Micalemys	namaquensis	South Africa	Eastern Cape	1931	-28.7167	24.96667	4	30.73	5.36	4.43	4.88	14.44	174	452	1275
Muridae	Micalemys	namaquensis	South Africa	Northern Cape	1931	-28.6333	26.15	4	30.18	5.48	4.73	4.5	15.17	164	520	1305
Muridae	Micalemys	namaquensis	South Africa	Northern Cape	1931	-28.5332	26.211	4	30.92	5.71	4.72	4.33	14.93	162	537	1346
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1933	-33.4167	19.2	4	32.8	5.77	4.72	5.2	16.03	169	738	264
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1934	-26.2667	27.96667	6	33.7	5.76	5.3	4.78	16.92	158	777	1725
Muridae	Micalemys	namaquensis	Namibia	Namibia	1937	-19.9833	17.08333	4	29.4	5.26	4.44	4.37	13.75	200	486	1495
Muridae	Micalemys	namaquensis	Namibia	Namibia	1937	-19.9833	17.08333	4	29.9	5.39	4.43	4.62	13.44	200	486	1495
Muridae	Micalemys	namaquensis	Namibia	Namibia	1937	-19.6333	14.83333	4	31.95	5.58	4.76	4.58	14.14	209	316	1205
Muridae	Micalemys	namaquensis	Namibia	Namibia	1937	-22.9167	16.2	4	30.4	5.1	4.51	4.44	14.68	196	235	1283
Muridae	Micalemys	namaquensis	Namibia	Namibia	1937	-25.85	16.55	4	29.16	5.35	4.36	4.05	13.34	141	196	1697
Muridae	Micalemys	namaquensis	Namibia	Namibia	1937	-20.65	17.1	4	30.02	5.3	4.41	4.31	13.87	183	457	1667
Muridae	Micalemys	namaquensis	Namibia	Namibia	1937	-20.4167	17.25	4	31.97	5.35	4.89	4.78	14.96	189	436	1693
Muridae	Micalemys	namaquensis	Namibia	Namibia	1941	-24.7833	16.86667	4	31.29	5.26	4.92	4.71	14.72	168	156	1354
Muridae	Micalemys	namaquensis	Namibia	Namibia	1941	-21.6667	15.66667	4	29.08	5.42	4.53	4.32	13.76	196	267	1374
Muridae	Micalemys	namaquensis	South Africa	Eastern Cape	1947	-33.0286	27.86417	4	33.34	5.36	5.2	4.97	16.21	183	834	105
Muridae	Micalemys	namaquensis	South Africa	Eastern Cape	1947	-33.0286	27.86417	6	33.12	6.22	5.25	4.66	15.07	183	834	105
Muridae	Micalemys	namaquensis	South Africa	Eastern Cape	1947	-33.0286	27.86417	4	31.3	5.6	4.67	4.77	14.95	183	834	105
Muridae	Micalemys	namaquensis	South Africa	Eastern Cape	1947	-33.0286	27.86417	5	33.72	5.87	5.12	4.61	15.3	183	834	105
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1947	-26.0167	27.73333	4	33.72	5.66	5.33	4.96	16.21	167	684	1474
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1947	-30.4	29.01667	4	32.35	5.62	4.82	4.59	14.98	150	773	1542
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1948	-28.5667	29.73333	6	32.56	5.92	5.13	4.65	15.57	182	746	1043
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1948	-28.55	30.41667	4	32.34	5.82	4.78	4.47	15	168	749	1131
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1948	-23	29.5	4	32.13	5.49	4.79	4.87	15.02	170	833	1361
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1949	-28.3667	29.38333	7	33.56	4.69	5.94	4.72	16.7	140	819	1685
Muridae	Micalemys	namaquensis	Namibia	Namibia	1951	-18.0667	13.85	4	31.77	5.12	4.58	4.21	14.82	216	316	1155
Muridae	Micalemys	namaquensis	Namibia	Namibia	1951	-18.0667	13.85	4	30.82	5.31	4.51	4.44	14.3	216	316	1155
Muridae	Micalemys	namaquensis	Namibia	Namibia	1951	-17.19	13.52	4	29.89	5.21	4.56	4.59	13.4	199	340	1264

Muridae	Micalemys	namaquensis	Namibia	Namibia	1951	-19.05	14.35	5	31.61	5.26	4.64	4.18	14.27	215	302	1227
Muridae	Micalemys	namaquensis	Namibia	Namibia	1951	-19.65	17.4	5	32.07	5.91	4.73	4	15.11	201	546	1499
Muridae	Micalemys	namaquensis	Namibia	Namibia	1951	-19.1333	13.61667	5	31.87	5.51	4.44	4.72	15.32	237	110	558
Muridae	Micalemys	namaquensis	South Africa	Northern Cape	1951	-26.7833	20.08333	5	29.92	5.58	4.29	4.32	13.2	203	175	835
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1952	-26.0167	27.7	4	29.15	5.27	4.7	4.55	13.85	165	695	1494
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1952	-26.0167	27.7	6	33.34	5.49	5.13	4.87	16.02	165	695	1494
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1953	-26.0167	27.7	6	29.8	5.36	4.82	4.55	14	165	695	1494
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1953	-26.0167	27.7	5	31.3	5.48	4.82	4.47	15.3	165	695	1494
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1953	-25.9667	27.78333	6	30.95	5.46	4.98	4.49	14.97	168	691	1484
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1953	-26.0167	27.7	5	31.91	5.56	5.12	4.94	15.44	165	695	1494
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1953	-26.0167	27.7	7	32.13	5.19	5.14	4.74	15.12	165	695	1494
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1953	-26.0167	27.7	7	33.05	5.38	5.48	4.94	16.37	165	695	1494
Muridae	Micalemys	namaquensis	Namibia	Namibia	1954	-22.3167	17.7	4	30.63	5.36	4.61	4.44	14.25	187	368	1627
Muridae	Micalemys	namaquensis	Namibia	Namibia	1954	-22.3167	17.7	4	29.88	5.32	4.35	4.38	14.04	187	368	1627
Muridae	Micalemys	namaquensis	South Africa	Free State	1956	-27.8333	25.91667	4	32.27	5.48	4.91	4.78	16.06	172	520	1250
Muridae	Micalemys	namaquensis	South Africa	Free State	1956	-27.8333	25.91667	4	31.52	5.36	4.53	4.52	15.38	172	520	1250
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1957	-26.6667	29.26667	5	30.6	5.7	4.73	4.57	14.51	153	684	1621
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1958	-25.85	28.16667	5	33.29	5.78	5	4.84	15.91	170	709	1433
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1958	-25.85	28.16667	4	32.26	5.46	5	4.75	15.85	170	709	1433
Muridae	Micalemys	namaquensis	Namibia	Namibia	1958	-22	15.6	4	28.79	5.25	4.46	4.01	13.26	219	146	882
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1959	-26.6667	29.26667	4	30.2	5.67	4.3	4.54	14.44	153	684	1621
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1960	-25.4167	29.33333	4	31.6	5.22	4.92	4.28	15.7	195	657	1007
Muridae	Micalemys	namaquensis	South Africa	North West	1964	-26.8333	24.68333	6	32.15	5.75	5.2	4.86	15	180	476	1228
Muridae	Micalemys	namaquensis	South Africa	North West	1964	-26.8333	24.68333	5	31.48	5.73	5	4.63	15.03	180	476	1228
Muridae	Micalemys	namaquensis	Namibia	Namibia	1965	-28.6667	18.88333	5	30.05	5.9	4.69	4.12	15.34	197	120	883
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1966	-25.5833	27.75	7	32.58	5.66	5.36	5.03	15.63	190	611	1154
Muridae	Micalemys	namaquensis	Namibia	Namibia	1966	-21	15	4	31.62	5.42	4.76	4.33	14.9	225	158	814
Muridae	Micalemys	namaquensis	Namibia	Namibia	1966	-21	15	4	30.42	5.5	4.56	4.57	14.2	225	158	814
Muridae	Micalemys	namaquensis	Namibia	Namibia	1966	-22.35	16.13333	4	30.82	5.23	4.43	4.41	14.63	221	181	891
Muridae	Micalemys	namaquensis	Namibia	Namibia	1966	-22.57	17.08361	5	30.46	5.31	4.75	4.42	14.54	195	359	1666

Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1967	-24.75	31.41667	4	31.98	6.1	5.14	4.66	15.24	216	635	395
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1967	-24.75	31.41667	4	31.34	5.95	4.98	5.37	15.12	216	635	395
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1967	-24.75	31.41667	4	32.43	6.37	5.19	5.17	15.2	216	635	395
Muridae	Micalemys	namaquensis	South Africa	Free State	1969	-28.5167	28.61667	5	32.71	5.88	4.62	4.36	16.03	119	921	2068
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1970	-25.75	28.31667	4	31.14	5.24	4.97	4.65	15.47	173	703	1364
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1970	-25.75	28.31667	4	32.43	5.93	5.06	4.63	15.42	173	703	1364
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1970	-24.05	29.11667	5	35.13	5.88	5.96	5.27	16.76	171	592	1362
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1970	-24.05	29.11667	7	35.04	5.75	5.37	5.04	16.65	171	592	1362
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1970	-24.05	29.11667	7	35.98	5.87	5.1	5.11	17.58	171	592	1362
Muridae	Micalemys	namaquensis	South Africa	Eastern Cape	1971	-32.25	25.45	4	32.31	5.32	4.56	4.6	14.56	144	447	1350
Muridae	Micalemys	namaquensis	Namibia	Namibia	1978	-23.0667	15.16667	5	31.15	5.88	4.33	4.61	15.31	199	45	566
Muridae	Micalemys	namaquensis	South Africa	Eastern Cape	1979	-32.3333	22.55	4	30.37	5.8	4.42	4.44	14.71	179	223	874
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1979	-25.5167	28.5	5	31.25	5.82	4.76	4.7	14.57	179	669	1335
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1979	-33.6	22.55	5	33.15	6.28	4.93	4.74	16.1	137	573	895
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1979	-33.6	22.55	4	31.61	5.75	4.56	4.69	15.42	137	573	895
Muridae	Micalemys	namaquensis	South Africa	Western Cape	1979	-33.6	22.55	5	33.23	5.56	5.06	4.72	16.1	137	573	895
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1980	-27.5167	31.35	4	31.86	5.63	4.96	4.64	14.78	186	801	852
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1980	-27.5167	31.35	4	32.72	5.29	5.12	4.9	13.87	186	801	852
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1980	-27.5167	31.35	4	32.64	5.42	4.55	5.01	15.72	186	801	852
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1980	-27.5167	31.35	5	32.4	5.46	5	4.87	15.33	186	801	852
Muridae	Micalemys	namaquensis	South Africa	Northern Cape	1981	-29.5667	18.35	5	31.32	5.8	4.57	4.41	14.3	177	171	1036
Muridae	Micalemys	namaquensis	South Africa	Northern Cape	1981	-29.5667	18.35	6	31.34	5.84	4.8	4.4	15.52	177	171	1036
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1983	-22.6667	31.16667	5	29.86	5.08	4.67	4.79	13.28	231	509	407
Muridae	Micalemys	namaquensis	South Africa	Limpopo	1983	-22.6833	31.03333	4	31.13	5.15	4.88	4.86	14.73	224	592	457
Muridae	Micalemys	namaquensis	Namibia	Namibia	1984	-22.4333	18.1	4	31.06	5.75	4.8	4.34	14.4	188	350	1550
Muridae	Micalemys	namaquensis	Namibia	Namibia	1984	-22.4333	18.1	4	30.05	5.84	4.58	4.06	14.26	188	350	1550
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1987	-27.8333	31.4	4	32.92	5.62	5.36	5.2	15.94	161	921	1225
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1988	-24.8765	30.8888	4	31.87	5.44	4.88	4.67	14.55	161	1025	1465
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1989	-25.4	29.35	6	32.6	5.52	4.76	5.13	15.07	201	652	1039
Muridae	Micalemys	namaquensis	Zimbabwe	Zimbabwe	1989	-17.5167	30.96667	5	32.41	5.64	5.06	4.7	15.17	183	899	1235

Muridae	Micalemys	namaquensis	South Africa	North West	1990	-26.55	27.11667	6	33.37	5.54	5.13	4.74	15.45	166	622	1395
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	1991	-27.3437	31.89041	4	32.16	5.68	5.23	4.56	14.49	224	550	140
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1991	-25.95	30.03333	4	31.86	5.57	5.13	5.03	15.18	151	761	1634
Muridae	Micalemys	namaquensis	South Africa	Gauteng	1992	-25.7833	28.33333	5	31.09	5.2	5.1	4.61	15.31	167	713	1484
Muridae	Micalemys	namaquensis	South Africa	Northern Cape	1992	-28.1303	16.97778	4	30.36	5.54	4.31	4.7	14.24	180	54	329
Muridae	Micalemys	namaquensis	South Africa	Northern Cape	1992	-28.1267	16.98694	5	30.76	5.45	4.35	4.48	14.13	179	57	397
Muridae	Micalemys	namaquensis	South Africa	Northern Cape	1992	-28.1267	16.98694	5	30.52	5.46	4.56	4.63	14.73	179	57	397
Muridae	Micalemys	namaquensis	South Africa	Mpumalanga	1993	-25.1594	30.53778	4	32.14	5.61	4.94	4.68	16.72	154	905	1636
Muridae	Micalemys	namaquensis	Swaziland	Swaziland	1994	-26.1333	31.13333	4	30.7	5.22	4.8	4.57	14.2	153	1237	1498
Muridae	Micalemys	namaquensis	Swaziland	Swaziland	1995	-27.1	31.18333	6	32.73	5.55	5.35	5	15.36	169	900	1110
Muridae	Micalemys	namaquensis	Swaziland	Swaziland	1995	-27.1	31.18333	6	32.93	5.91	5.31	4.89	15.8	169	900	1110
Muridae	Micalemys	namaquensis	Swaziland	Swaziland	1995	-27.1	31.18333	4	30.56	5.4	5.31	4.79	15.06	169	900	1110
Muridae	Micalemys	namaquensis	Swaziland	Swaziland	1996	-27.0667	31.41667	4	31.05	5.83	5.02	4.47	14.75	188	829	673
Muridae	Micalemys	namaquensis	Swaziland	Swaziland	1996	-27.2667	31.76667	4	30.96	5.56	4.98	4.57	15.1	208	702	417
Muridae	Micalemys	namaquensis	Swaziland	Swaziland	1996	-27.2667	31.76667	4	30.06	5.67	4.82	4.56	14.43	208	702	417
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	2002	-27.8426	31.33685	5	33.87	5.51	5.03	4.67	16.13	168	892	1232
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	2002	-27.8426	31.33685	5	33.82	5.59	5.08	4.97	16.07	168	892	1232
Muridae	Micalemys	namaquensis	South Africa	KwaZulu-Natal	2002	-27.8426	31.33685	5	32.03	5.5	4.9	4.77	15.2	168	892	1232
Muridae	Micalemys	namaquensis	South Africa	Gauteng	2003	-25.8833	28.70889	5	33.27	5.75	5.4	4.82	16.21	164	683	1485
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1903	-29.8333	17.71667	4	37.82	9.52	5.73	4.82	17.59	167	169	700
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1917	-31.7833	18.61667	3	33.37	8.72	5.19	4.33	16.78	193	171	28
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1917	-31.7833	18.61667	5	38.7	9.21	6.23	4.38	20.47	193	171	28
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1917	-31.7833	18.61667	4	36.35	9.33	6.13	4.49	18.28	193	171	28
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1917	-31.7833	18.61667	4	35.06	9.16	5.74	4.99	17.87	193	171	28
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1917	-31.7833	18.61667	4	35.23	9.24	5.73	4.8	17.93	193	171	28
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1926	-31.8667	18.61667	5	36.59	9.55	5.97	4.59	18.37	189	189	167
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1926	-31.8667	18.61667	5	36.66	9.14	5.88	5.18	20.08	189	189	167
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1926	-31.8667	18.61667	4	34.5	9.03	5.32	4.7	17.14	189	189	167
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1926	-31.8667	18.61667	5	35.27	8.78	5.75	4.59	17.89	189	189	167
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1927	-31.1386	24.12897	5	39.32	9.5	6.63	5.2	21.03	145	331	1437

Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1926	-31.475	19.77278	5	37.77	9.47	5.61	4.67	18.29	164	214	976
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1931	-31.6667	18.48333	5	38.7	9.77	6.38	4.96	20.92	184	169	33
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.1333	26.83333	5	37.43	9.85	5.97	4.77	20.21	197	431	132
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.1333	26.83333	4	34.82	8.84	5.36	4.59	17.7	197	431	132
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.1333	26.83333	4	32.62	8.65	5.5	4.54	16.42	197	431	132
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.1333	26.83333	5	36.51	9.01	5.88	5.14	18.45	197	431	132
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.1333	26.83333	5	37.04	8.89	5.97	4.05	18.95	197	431	132
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.1333	26.83333	4	36.58	9.25	5.58	4.72	18.62	197	431	132
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.3333	24.88333	4	35.13	9.3	5.67	4.76	18.35	169	376	569
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.1333	26.83333	5	38.62	9.54	6.4	4.76	20.57	197	431	132
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1931	-33.1333	26.83333	5	37.21	9.41	5.91	5.1	19.71	197	431	132
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1936	-30.3833	24.1	5	38	9.53	5.94	4.46	20.22	156	315	1309
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1937	-30.9667	22.35	5	38.5	9.81	6.12	4.98	19.45	150	254	1451
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1937	-29.25	16.86667	5	39.02	10.3	6.13	4.92	19.55	147	74	0
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1937	-29.7	17.95	4	34.64	9.22	5.94	4.67	17.9	178	167	851
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1937	-29.7167	17.48333	3	32.06	8.83	5.09	4.42	16.04	162	147	594
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1937	-29.7167	17.48333	3	33.36	9.21	5.79	4.68	16.48	162	147	594
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1937	-29.7167	17.48333	5	36.83	9.18	5.84	4.92	19.43	162	147	594
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1937	-30.5	20.41667	4	35.59	9.15	5.19	4.74	17.62	174	153	941
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1937	-30.5	20.41667	5	37.44	9.27	6.01	5.18	19.99	174	153	941
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1937	-30.5833	17.93333	5	35.37	9.06	5.78	4.77	17.37	166	203	423
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1936	-32.2333	20.98333	4	34.05	8.81	5.38	4.55	17.55	139	196	1292
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1940	-33.2167	20.58333	4	35.71	8.97	5.9	4.72	18.5	152	185	923
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1940	-33.2167	20.58333	4	34.91	9.16	5.57	4.88	18.1	152	185	923
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1940	-33.4333	23.56667	5	34.55	9.27	5.56	4.72	17.82	142	526	1101
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1940	-33.4333	23.56667	5	37.41	9.35	5.83	4.41	18.31	142	526	1101
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1960	-28.5833	16.48333	4	35.63	9.26	5.58	4.62	19.2	161	50	8
Muridae	Otomys	unisulcatus	South Africa	Free state	1954	-29.65	24.6	4	34.73	8.79	5.7	4.73	17.67	178	369	1170
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1930	-31.6667	18.48333	5	42.88	10.08	6.42	4.98	22.55	184	169	33
Muridae	Otomys	unisulcatus	South Africa	Free state	1954	-29.65	24.6	4	33.42	9	5.64	4.52	17.58	178	369	1170

Muridae	Otomys	unisulcatus	South Africa	Western Cape	1953	-32.8333	17.86667	4	35.09	9.27	5.53	4.61	18.3	157	286	79
Muridae	Otomys	unisulcatus	South Africa	Free state	1954	-29.65	24.6	5	38.76	9.72	6.15	4.82	19.43	178	369	1170
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1963	-32.2333	25.26667	5	36.04	9.2	5.82	4.47	18.25	137	464	1394
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1954	-33.8	19.88333	4	33.86	9.14	5.24	4.82	17.38	175	336	175
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1961	-33.7667	25.41667	4	33.31	8.69	5.38	4.74	17.57	179	437	113
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1959	-33.6833	25.8	5	36.63	8.8	5.53	4.87	19	183	445	21
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1957	-31.9667	26.25	5	36.59	9.63	6.11	4.94	19.15	122	590	1595
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1954	-33.8	19.9	4	35.74	9.16	5.57	4.76	17.78	175	337	189
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1947	-30.75	27.61667	4	34.13	8.48	5.37	4.64	17.33	127	679	1864
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1963	-32.2333	25.26667	5	37.41	9.46	6.12	5.08	18.86	137	464	1394
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1953	-32.8333	17.86667	5	36.43	9.26	5.89	5.06	19.32	157	286	79
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1957	-31.9667	26.25	4	35.92	9.06	5.69	5.2	18.09	122	590	1595
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1957	-31.9667	26.25	4	34.93	9.37	5.66	4.85	17.92	122	590	1595
Muridae	Otomys	unisulcatus	South Africa	South Africa	1960	-32.75	25.81667	4	35.37	8.7	5.42	4.39	17.58	173	487	688
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1957	-31.9667	26.25	5	36.42	8.9	5.86	4.78	19.7	122	590	1595
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1963	-32.75	25.81667	5	38.46	9.29	5.97	4.76	20.74	173	487	688
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1963	-32.2333	25.26667	4	34.79	8.69	5.76	4.41	17.07	137	464	1394
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1949	-33.25	27.0167	4	34.6	8.8	5.62	4.55	16.9	187	514	78
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1949	-32.7667	26.58333	5	36.91	9.4	6.11	5.19	19.78	182	495	462
Muridae	Otomys	unisulcatus	South Africa	South Africa	1961	-32.75	25.81667	4	35.52	8.89	5.75	4.74	19.31	173	487	688
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1949	-33.25	27.0167	5	36.3	8.96	5.86	4.86	18.66	187	514	78
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1960	-33.6483	26.51667	5	37.29	9.3	5.67	5.05	19.3	181	586	125
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1957	-31.9667	26.25	4	33.79	8.87	6.06	4.84	17.55	122	590	1595
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1963	-32.2333	25.26667	5	36.95	9.36	6.08	5.08	19.26	137	464	1394
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1963	-32.2333	25.26667	4	35.3	8.82	5.47	4.8	17.87	137	464	1394
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1963	-32.2333	25.26667	5	36.68	9	5.57	4.6	18.98	137	464	1394
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1963	-32.2333	25.26667	4	35.21	9.25	5.6	4.76	17.34	137	464	1394
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1952	-31.5	22.4	5	37.25	9.12	5.58	4.7	18.51	145	241	1426
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1952	-31.4	23.15	4	35.8	8.91	5.69	4.86	18.14	150	260	1261
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1959	-33.4333	25.46667	5	37.57	8.82	5.65	4.48	19.98	189	341	109

Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1947	-30.75	27.61667	5	37.81	9.45	6.44	4.91	19.05	127	679	1864
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	5	37.34	8.93	6.14	4.51	19.93	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	5	37.46	8.88	5.95	4.78	20.03	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	4	34.08	8.42	5.32	4.76	16.78	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	4	35.04	8.38	5.44	4.48	18.02	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	5	36.12	8.76	6.02	4.72	19.17	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	4	33.98	8.64	5.58	4.77	16.76	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	4	35.8	8.69	5.8	4.59	18.76	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	5	38.4	8.5	5.91	5.11	20.49	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	5	34.67	8.6	5.66	4.94	17.53	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-31.1667	21.58333	5	39.08	9.12	5.95	4.58	20.8	157	225	1302
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-29.8833	17.75	4	35.59	8.57	5.39	4.89	17.5	168	169	724
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-29.8833	17.75	4	34.66	8.46	5.68	5.37	17.12	168	169	724
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-29.8833	17.75	4	35.09	8.88	5.45	4.72	18.25	168	169	724
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-29.8833	17.75	4	33.19	8.51	5.27	4.8	17.1	168	169	724
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1977	-29.8833	17.75	3	32.92	8.75	5.34	4.61	15.7	168	169	724
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1977	-30.95	18.2	3	33.86	8.99	5.52	4.61	16.66	179	176	326
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1979	-32.3333	22.55	3	32.56	8.09	4.93	4.43	16.49	179	223	874
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1979	-32.3333	22.55	5	36.69	9.22	5.67	5.17	18.81	179	223	874
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1979	-32.3333	22.55	5	35.63	8.87	5.58	4.35	17.79	179	223	874
Muridae	Otomys	unisulcatus	South Africa	Eastern Cape	1979	-32.3333	22.55	5	38.39	9.52	5.82	4.9	20.26	179	223	874
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1982	-28.4333	21.23333	4	33.73	8.7	5.21	4.72	18.04	192	182	812
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1987	-29.2167	17.06667	5	36.04	9.42	5.94	5.35	19.02	155	79	183
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1987	-32.2833	19.86667	5	37.03	8.57	5.74	4.92	18.55	186	137	445
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1987	-32.2833	19.86667	5	37.8	8.84	6.63	5.23	21.16	186	137	445
Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1987	-32.2833	19.86667	5	37.3	8.88	5.77	4.96	20.31	186	137	445
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1989	-33.1167	18	4	35.55	9.03	5.74	4.65	18.52	190	310	86
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1989	-33.1167	18	5	38.56	10.03	6.24	4.9	19.45	190	310	86
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1989	-33.1167	18	4	35.63	9.18	5.9	4.86	16.52	190	310	86
Muridae	Otomys	unisulcatus	South Africa	Western Cape	1989	-33.1167	18	4	35.47	9.2	5.72	4.86	17.85	190	310	86

Muridae	Otomys	unisulcatus	South Africa	Northern Cape	1992	-28.3333	17.01667	5	36.07	9.23	5.99	4.66	17.74	169	70	605
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1902	-30.9667	23.7667	4	34.24	8.28	6.25	4.95	18.7	149	309	1383
Muridae	Parotomys	brantsii	South Africa	Eastern Cape	1923	-31.3	25.81667	5	36.31	9.02	6.21	5.13	19.75	144	438	1461
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1926	-31.5	19.71667	4	33.89	8.19	6.59	5.79	19.39	163	223	972
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1926	-31.5	19.71667	4	33.83	8.23	6.42	5.83	19.37	163	223	972
Muridae	Parotomys	brantsii	South Africa	Eastern Cape	1926	-31.7333	25.3	5	38.05	8.72	6.2	6.12	20.83	158	354	1113
Muridae	Parotomys	brantsii	South Africa	Eastern Cape	1926	-31.7333	25.3	4	36.4	7.77	6	5.08	19.33	158	354	1113
Muridae	Parotomys	brantsii	South Africa	Western Cape	1927	-31.7833	18.61667	5	36.28	8.22	5.83	4.67	18.37	193	171	28
Muridae	Parotomys	brantsii	South Africa	Western Cape	1927	-31.8667	18.61667	5	37.64	8.76	6.27	5.03	19.77	189	189	167
Muridae	Parotomys	brantsii	South Africa	Western Cape	1928	-33.2833	19.15	5	36.99	8.35	6.37	5.02	19.32	172	623	173
Muridae	Parotomys	brantsii	South Africa	Western Cape	1929	-31.6667	18.48333	4	33.06	8.06	5.91	4.72	18.16	184	169	33
Muridae	Parotomys	brantsii	South Africa	Western Cape	1931	-31.6667	18.48333	5	39.51	8.92	6.15	5.19	19.66	184	169	33
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1937	-29.25	17.86667	4	38.78	8.22	6.37	4.9	19.49	174	136	879
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1937	-29.25	17.86667	4	36.39	8.33	6.18	4.84	18.79	174	136	879
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1937	-29.25	17.86667	3	34.7	7.7	5.96	4.96	18.48	174	136	879
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1937	-29.25	17.86667	5	34.88	8.45	6.74	4.72	20.06	174	136	879
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1937	-29.25	17.86667	5	40.21	9.05	6.52	5.15	20	174	136	879
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1937	-29.25	17.86667	5	38.37	9.24	6.28	5.28	19.7	174	136	879
Muridae	Parotomys	brantsii	South Africa	Western Cape	1937	-29.7167	17.48333	5	38.5	9.36	6.28	5.04	21.3	162	147	594
Muridae	Parotomys	brantsii	South Africa	Western Cape	1937	-29.7167	17.48333	5	38.69	9.12	6.31	5.32	19.34	162	147	594
Muridae	Parotomys	brantsii	South Africa	Western Cape	1937	-29.7167	17.48333	4	36.29	8.44	6.11	4.72	18.95	162	147	594
Muridae	Parotomys	brantsii	South Africa	Western Cape	1937	-31.7667	20.28333	5	37.97	9.03	6.23	5.22	19.18	156	182	1078
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1937	-30.4333	20.98333	5	37.18	8.67	5.93	4.64	19.75	180	165	962
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1937	-29.3167	22.81667	4	34.66	7.94	5.87	4.86	18.58	178	286	1183
Muridae	Parotomys	brantsii	South Africa	Western Cape	1937	-29.7167	17.48333	4	34.75	7.89	5.92	5.23	18.85	162	147	594
Muridae	Parotomys	brantsii	South Africa	Western Cape	1940	-33.2167	20.58333	3	32.5	7.7	5.88	4.96	19	152	185	923
Muridae	Parotomys	brantsii	South Africa	Western Cape	1940	-33.2167	20.58333	4	33.23	8.18	5.76	4.54	17.98	152	185	923
Muridae	Parotomys	brantsii	South Africa	Western Cape	1941	-33.5833	22.2	5	39.65	8.68	6.19	5.24	19.9	175	262	331
Muridae	Parotomys	brantsii	South Africa	Western Cape	1953	-31.7	18.2	5	36.97	8.43	6.03	5.31	19	180	175	3
Muridae	Parotomys	brantsii	South Africa	Western Cape	1954	-33.2667	20.3	5	39.46	9.1	6.6	5.18	20.62	148	209	977

Muridae	Parotomys	brantsii	South Africa	Western Cape	1954	-33.5333	21.68333	4	36.65	8.7	5.75	5.2	18.75	177	209	224
Muridae	Parotomys	brantsii	South Africa	Western Cape	1954	-33.5333	21.68333	5	37.14	8.17	6.22	5	19.59	177	209	224
Muridae	Parotomys	brantsii	South Africa	Western Cape	1954	-33.2167	22.03333	5	38.94	8.8	6.02	4.88	19.74	159	201	614
Muridae	Parotomys	brantsii	South Africa	Western Cape	1954	-33.5333	21.68333	5	38.8	8.91	6.19	5.07	19.18	177	209	224
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1954	-29.5	17.91667	5	38.19	8.57	6.23	4.76	19.04	162	192	1112
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1956	-27.9667	22.73333	5	35.65	8.64	6.67	5.03	20.16	175	342	1296
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1956	-26.45	20.56667	4	34.25	7.89	6.67	5.13	18.06	200	217	903
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1957	-28.8	23.25	5	39.97	8.44	6.47	5.63	20.3	164	332	1340
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1957	-26.45	20.56667	4	36.5	8.35	6.99	5.75	18.55	200	217	903
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1958	-26.45	20.56667	4	35.32	7.82	6.11	5.4	18.23	200	217	903
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1958	-32.6333	22.66667	4	33.15	8.2	6.06	5.09	18.03	169	247	874
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1958	-28.45	21.25	5	37.29	8.23	6.56	4.8	19.23	193	182	797
Muridae	Parotomys	brantsii	South Africa	Free State	1962	-29.7667	24.71667	5	38.53	8.72	6.07	5.21	20.54	181	371	1174
Muridae	Parotomys	brantsii	South Africa	Free State	1962	-29.7667	24.71667	4	34.54	8.31	6.05	5.53	19.01	181	371	1174
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1962	-25.8167	20.01667	4	34.42	7.81	5.63	5.14	18.21	196	221	974
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1966	-26.45	20.56667	5	38.49	8.89	6.66	5.86	20.36	200	217	903
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1966	-26.45	20.56667	4	37.31	8.7	6.45	5.08	19.33	200	217	903
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1966	-26.45	20.56667	4	36.6	8.62	6.43	4.87	19.28	200	217	903
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1966	-26.45	20.56667	4	35.47	8.35	6.36	5.15	19.15	200	217	903
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1966	-26.45	20.56667	4	35.06	8.45	6.32	5.23	18.97	200	217	903
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1970	-25.8167	20.01667	3	33.44	8.13	6.07	4.92	18.33	196	221	974
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1970	-25.8167	20.01667	5	37.29	8.58	6.69	5.17	20.13	196	221	974
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1970	-25.8167	20.01667	5	36.88	8.67	6.71	4.86	20.16	196	221	974
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1970	-25.8167	20.01667	5	37.78	9.15	6.92	5.68	19.18	196	221	974
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1970	-25.4167	20.6	5	36.76	8.7	6.54	5.07	19.33	204	239	966
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1970	-25.8167	20.01667	4	36.83	8.61	6.72	5.29	19.67	196	221	974
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1970	-25.4167	20.6	5	38.68	8.68	6.87	5.34	19.11	204	239	966
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1971	-25.4167	20.6	4	35.11	8.53	6.3	5.3	18.05	204	239	966
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1976	-29.25	16.86667	5	37.78	9.14	6.02	5.27	20.2	147	74	0
Muridae	Parotomys	brantsii	South Africa	Northern Cape	1998	-29.6667	17.08333	5	37.14	8.77	6.52	4.46	19.26	160	93	47

Table A.2: Results for the binomial regressions to investigate the relationship between temporal effect and life history parameters. None of the regressions were significant.

Dep/Indep	p	Intercept	Slope	AIC	r^2 ML	Equations
Temporal effect/maximum latitude	0.6	-0.627	0.0083	65.62	0.005	y = -0.627+0.0083x
Temporal effect/range size area	0.96	-0.109	-0.008	65.82	0.0001	y = -0.109-0.008x
Temporal effect/r.k selection	0.9	-0.318	0.077	64.16	0.0372	y = -0.318+0.077x
Temporal effect/fossorial	1	-0.223	4.079e-16	65.83	0.00000	y = -0.223+4.079e-16x
Temporal effect/elevation	0.1	-0.693	1.049	61.41	0.096	y = -0.693+1.049x
Temporal effect/habitat	0.08	-0.493	0.744	64.43	0.031	y = -0.493+0.744x
Temporal effect/commensal	0.7	-0.143	-0.214	65.71	0.003	y = -0.143-0.214x
Temporal effect/Desert	0.23	-2.030e-16	-0.811	64.41	0.031	y = -2.030e-16-0.811x
Temporal effect/mean body mass	0.4	-0.372	0.0001	64.46	0.03	y = -0.372+0.0001x
Temporal effect/mean litter size	0.5	-0.772	0.127	65.42	0.009	y = -0.772+0.127x

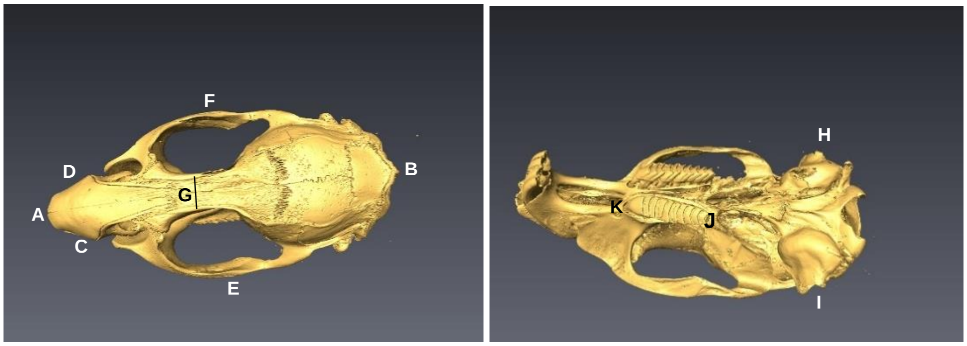


Figure A.1: Landmarks used for skull measurements. See text for descriptions.

GLS - Greatest length of skull measured dorsally (A-B)

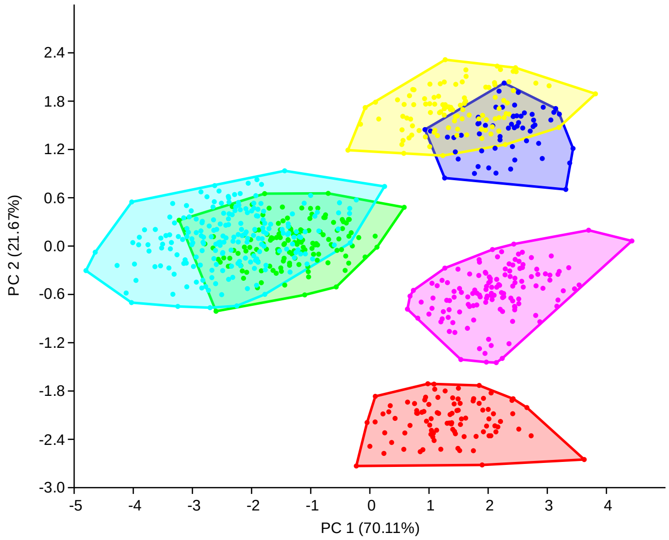
NAW - Nasal width, greatest width across nasals (C-D)

ZYW- Zygomatic width, greatest distance between the outer margins of the zygomatic arches (E-F)

IOC - Interorbital constriction, least distance dorsally between the orbits (G)

BW – Braincase width (H-I)

MXTRL - Maxillary tooth row length, distance from anterior edge of first maxillary tooth to posterior edge of last maxillary tooth (J-K)



Variables	PC 1	PC2
GLS	0.97	-0.01
MXTRL	0.59	0.77
NAW	0.78	0.54
IOC	0.78	-0.53
ZYW	0.96	-0.16
BW	0.89	-0.34

Figure A.2: Plot of component scores of the six species and the associated variable loadings of the first two principal components (PC 1 and PC 2); red = *Desmodillus auricularis*, blue = *Parotomys brantsii*, pink = *Gerbilliscus leucogaster*, green = *Micalemys namaquensis*, turquoise = *Mastomys natalensis*, yellow = *Otomys unisulcatus*.

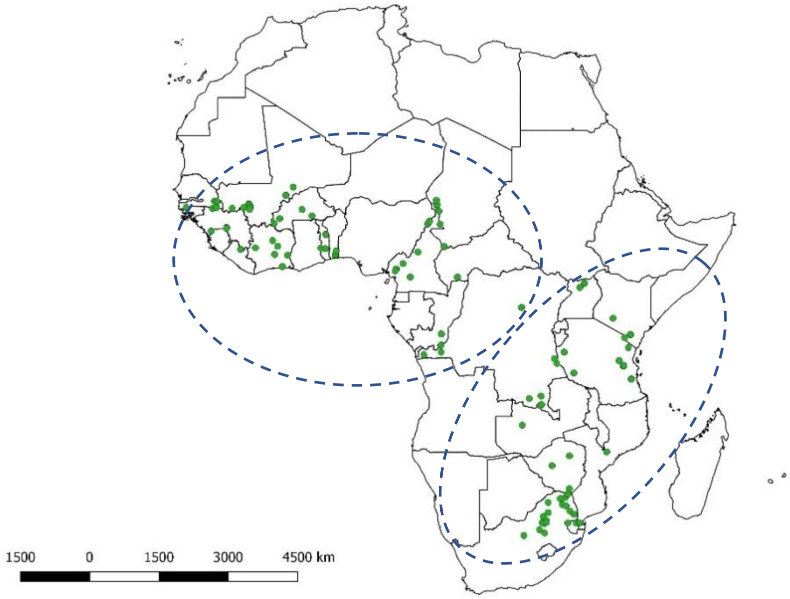


Figure A.3: Map of *Mastomys natalensis* records showing approximate delimitation of presumed-commensal populations from West and Central African Congolean, Guinea, Sudanian and Sahel savannah-rainforest mosaics, and non-commensal populations from eastern and Southern African Miombo, Zambezian, Mopane and *Acacia commiphora* savannahs and Highveld grasslands (based on terrestrial ecoregions; Olson et al., 2001). Based on studies of lassa fever outbreaks in West Africa, these are associated with the commensal nature of *Mastomys natalensis* (Fichet-Calvet & Rogers 2009) so we used their risk map of lassa fever for west/central Africa to define the limits of commensal populations for our study. Studies of *M. natalensis* from east Africa (e.g. Leirs et al., 1996; Mulungu et al., 2015) and Southern Africa (Monadjem et al., 2011) show that *M. natalensis* frequently occupies crop fields where it is a crop pest; however, it seldom enters buildings or becomes commensal. In such agricultural systems, cropping and food availability is highly seasonal and *M. natalensis* populations are also highly seasonal, compared with commensal populations which are presumable provisioned year-round on human food stores in houses. Crop productivity (as well as productivity of natural habitats) would increase with higher rainfall.

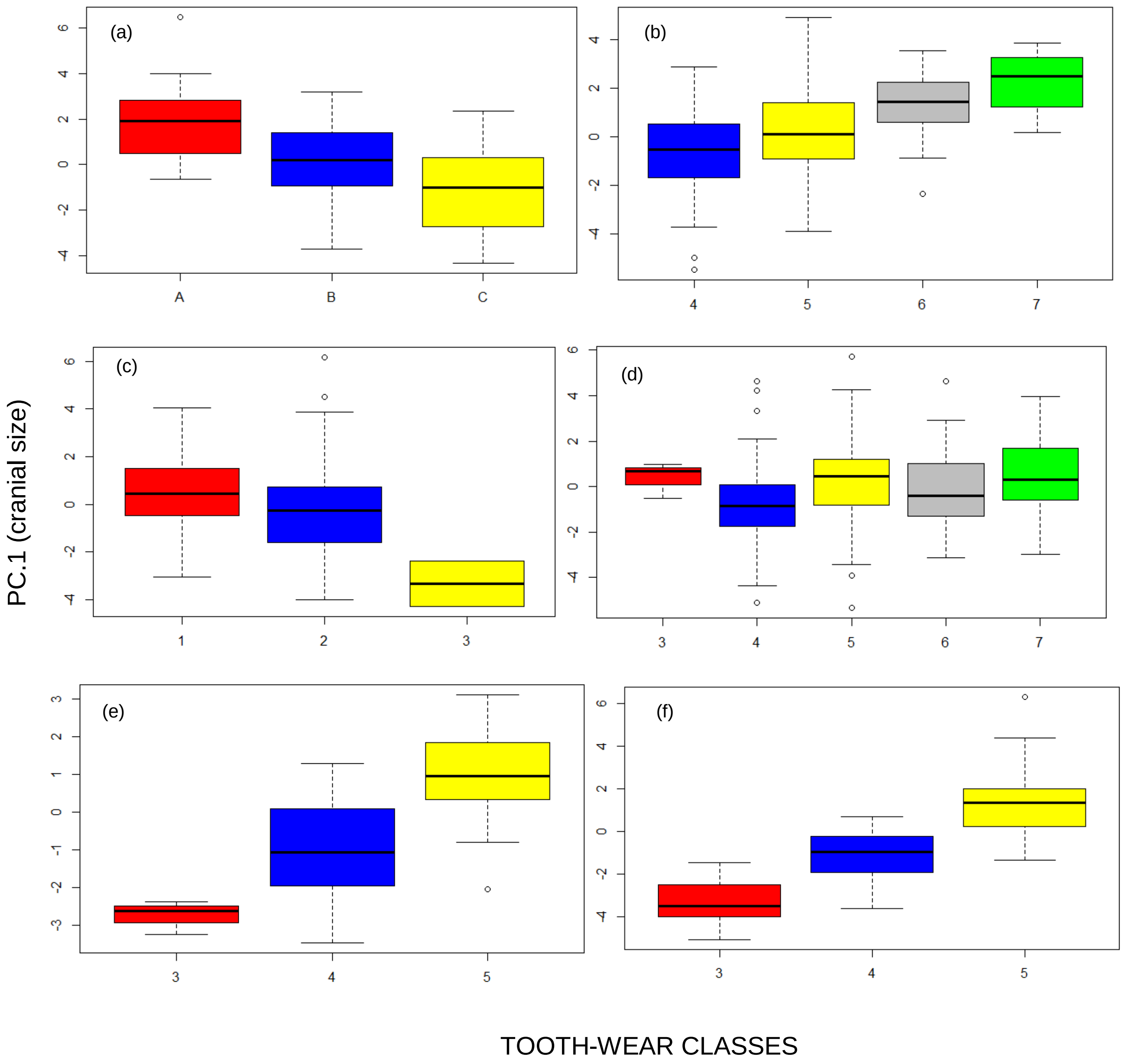


Figure A.4: Box-and-whisker plots describing differences in greatest length of the skull (PC.1) between tooth-wear classes of *Desmodillus auricularis* (a), *Micaelamys namaquensis* (b), *Gerbilliscus leucogaster* (c), *Mastomys natalensis* (d), *Parotomys brantsii* (e), and *Otomys unisulcatus* (f).

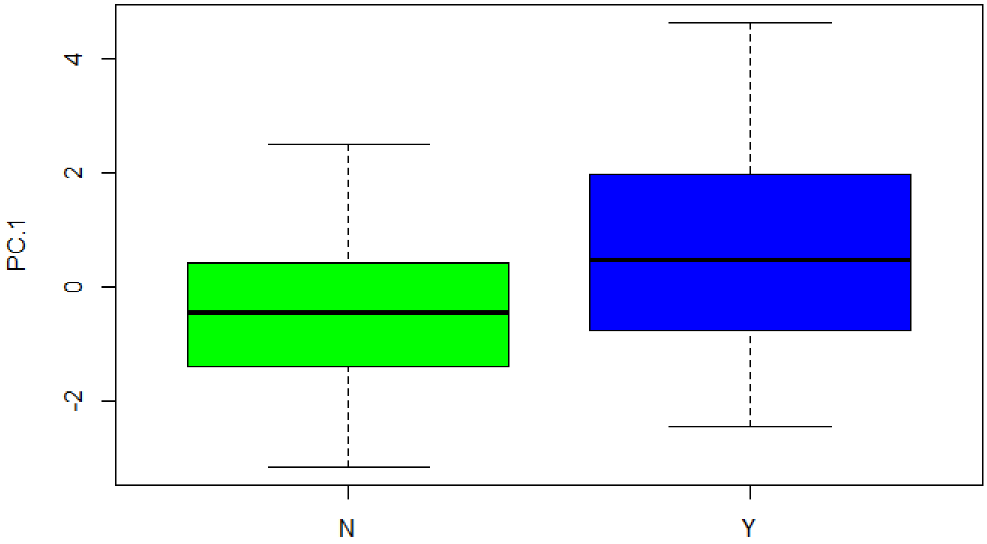


Figure A.5: Boxplots comparing adult West African commensal (Y) and East/Southern African non-commensal (N) populations of *Mastomys natalensis*.

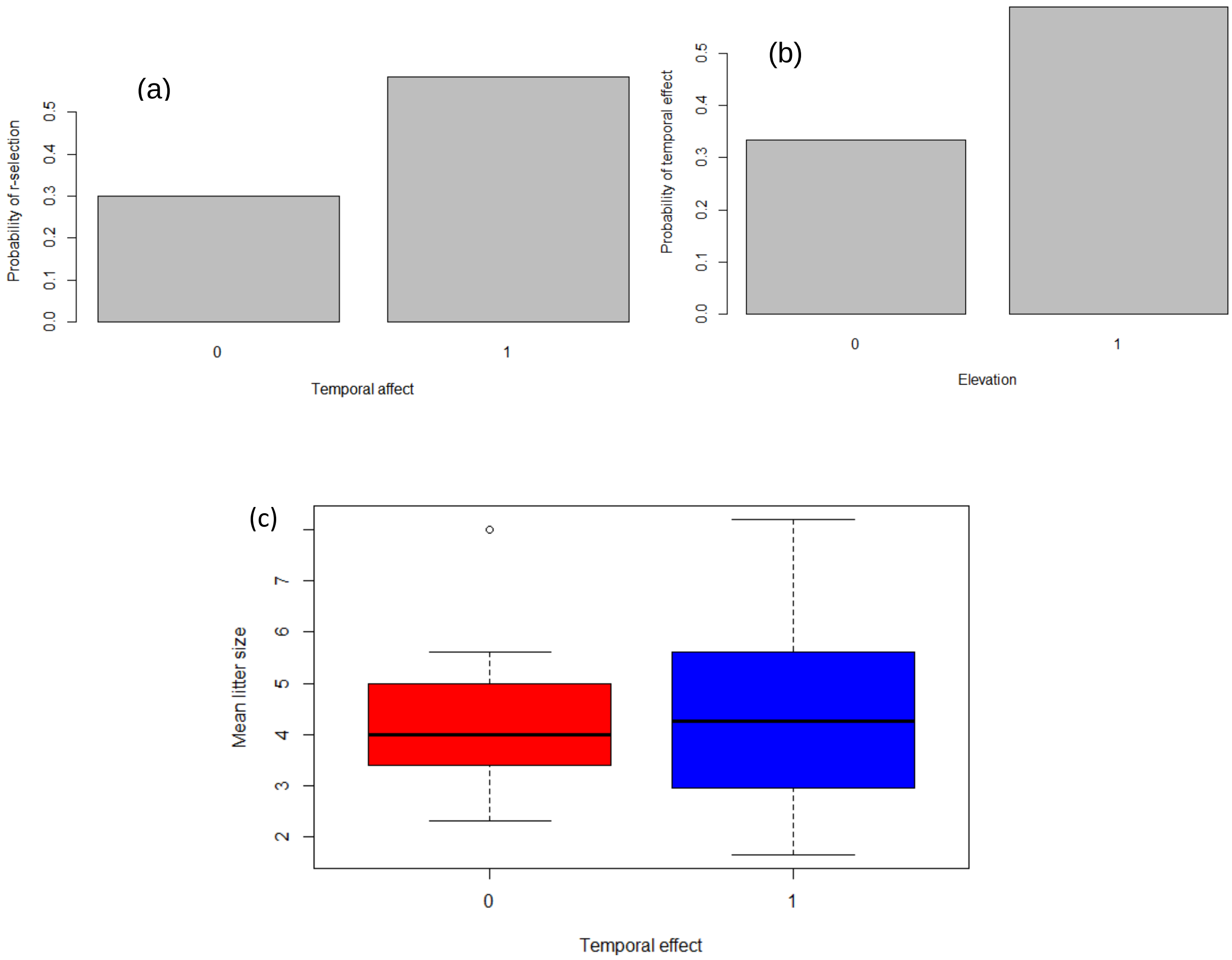


Figure A.6: Barplots of temporal effect versus r-selection (a) with 0 showing no effect and 1 showing yes effect, elevation with 0 showing low elevations and 1 high elevations (b) and boxplots of mean litter size (c) with 0 showing no effect and 1 showing yes effect.

APPENDIX B

SUPPORTING MATERIAL FOR CHAPTER 3

Table B.1. Raw data of the studied specimens with individual sex, cochlear micro-ct measurements, body mass (BodyM) and bulla centroid size (bullaCS).

FILENAME	GENUS	SPECIES	SEX	RECL, mm	CUR	OWA, mm²	ECL, mm	TUR	BodyM, g	bullaCS
TM13610	*Desmodillus*	*auricularis*	F	5.77	1.71	0.86	14.71	2.55	46.1	72.05029
TM22976	*Desmodillus*	*auricularis*	F	6.20	1.53	0.93	13.58	2.19	46.1	74.4604
TM23012	*Desmodillus*	*auricularis*	M	5.99	1.61	0.75	13.96	2.33	46.1	76.73254
TM23036	*Desmodillus*	*auricularis*	F	6.08	1.63	0.82	14.42	2.37	46.1	76.0306
TM32588	*Desmodillus*	*auricularis*	M	6.23	1.37	0.83	13.71	2.20	46.1	70.52641
TM37519	*Desmodillus*	*auricularis*	F	6.02	1.43	0.82	13.37	2.22	46.1	74.42082
TM4329	*Desmodillus*	*auricularis*	F	5.85	1.69	0.84	13.98	2.39	46.1	76.68003
TM4744	*Desmodillus*	*auricularis*	F	6.13	1.61	0.84	14.15	2.31	46.1	78.02452
TM5387	*Desmodillus*	*auricularis*	M	6.22	1.41	0.83	13.68	2.20	46.1	74.28502
TM6371	*Desmodillus*	*auricularis*	M	6.03	1.53	0.77	13.93	2.31	46.1	79.12399
TM7620	*Desmodillus*	*auricularis*	M	5.71	1.30	0.81	11.76	2.06	46.1	73.92939
1958-742	*Gerbiliscus*	*leucogaster*	F	5.97	1.56	0.54	14.81	2.48	72	66.04022
1958-743	*Gerbiliscus*	*leucogaster*	M	5.70	1.41	0.51	12.99	2.28	72	64.75632
1969-64	*Gerbiliscus*	*leucogaster*	M	5.13	1.53	0.48	12.11	2.36	72	59.80813
1990-340	*Gerbiliscus*	*leucogaster*	M	5.30	1.59	0.47	13.84	2.61	72	56.48836
1990-616	*Gerbiliscus*	*leucogaster*	M	4.96	1.40	0.42	11.17	2.25	72	56.83054
1990-617	*Gerbiliscus*	*leucogaster*	F	5.45	1.45	0.44	13.35	2.45	72	60.68751
1990-620	*Gerbiliscus*	*leucogaster*	F	5.26	1.35	0.47	13.09	2.49	72	58.03407
1990-626	*Gerbiliscus*	*leucogaster*	M	5.48	1.46	0.53	12.6	2.30	72	59.7778
1996-573	*Gerbiliscus*	*leucogaster*	M	5.13	1.42	0.48	11.6	2.26	72	60.34655
1996-574	*Gerbiliscus*	*leucogaster*	F	5.44	1.33	0.49	11.96	2.20	72	56.54395
1999-72	*Gerbiliscus*	*leucogaster*	F	5.11	1.47	0.45	12.31	2.41	72	57.25886
2007-1135	*Gerbiliscus*	*leucogaster*	M	5.38	1.55	0.51	13.24	2.46	72	63.67492
TM13659	*Gerbiliscus*	*leucogaster*	F	5.17	1.58	0.51	13.35	2.58	72	64.37561
TM1432	*Gerbiliscus*	*leucogaster*	F	5.47	1.70	0.51	14.72	2.69	72	62.8095
TM32	*Gerbiliscus*	*leucogaster*	F	5.46	1.5	0.47	13.98	2.56	72	62.763
TM7501	*Gerbiliscus*	*leucogaster*	M	5.29	1.69	0.51	14.96	2.83	72	66.04022
1943-102	*Gerbillus*	*nigeriae*	F	5.24	1.31	0.38	10.85	2.07	24	52.84867
1962-4220	*Gerbillus*	*nigeriae*	M	5.23	1.29	0.38	10.78	2.06	24	52.55021
1980-293	*Gerbillus*	*nigeriae*	F	4.87	1.18	0.35	8.96	1.84	24	48.12395
1980-346	*Gerbillus*	*nigeriae*	M	5.28	1.24	0.38	9.88	1.87	24	51.10348
1987-383	*Gerbillus*	*nigeriae*	M	4.78	1.29	0.33	9.85	2.06	24	48.03581

1987-386	*Gerbillus*	*nigeriae*	F	5.25	1.31	0.33	10.93	2.08	24	46.53813
1990-905	*Gerbillus*	*nigeriae*	M	5.05	1.20	0.37	10.04	1.99	24	51.56148
1997-1476	*Gerbillus*	*nigeriae*	M	5.21	1.34	0.39	10.95	2.10	24	48.7289
2004-1117	*Gerbillus*	*nigeriae*	F	5.16	1.23	0.35	11.50	2.23	24	49.48695
2004-1120	*Gerbillus*	*nigeriae*	F	5.10	1.36	0.37	11.23	2.20	24	51.00813
2004-983	*Gerbillus*	*nigeriae*	M	5.08	1.30	0.39	11.02	2.17	24	53.17291
2004-987	*Gerbillus*	*nigeriae*	F	5.20	1.28	0.39	11.65	2.24	24	51.66834
TM103	*Otomys*	*angoniensis*	F	6.05	1.34	0.35	11.68	1.93	114	51.14102
TM123	*Otomys*	*angoniensis*	F	6.38	1.43	0.45	13.21	2.07	114	54.73533
TM22700	*Otomys*	*angoniensis*	M	5.94	1.49	0.41	11.93	2.01	114	49.92039
TM22876	*Otomys*	*angoniensis*	M	5.93	1.34	0.37	11.39	1.92	114	48.22569
TM24415	*Otomys*	*angoniensis*	M	6.53	1.41	0.38	12.86	1.97	114	50.18055
TM25623	*Otomys*	*angoniensis*	M	5.90	1.38	0.38	11.45	1.94	114	49.30879
TM35027	*Otomys*	*angoniensis*	M	6.10	1.32	0.36	11.71	1.92	114	47.16786
TM44987	*Otomys*	*angoniensis*	F	5.90	1.34	0.36	10.85	1.84	114	51.4746
TM4504	*Otomys*	*angoniensis*	M	5.94	1.33	0.38	11.40	1.92	114	43.64898
TM45584	*Otomys*	*angoniensis*	F	5.69	1.35	0.36	10.58	1.86	114	53.74636
TM6485	*Otomys*	*angoniensis*	F	6.50	1.46	0.42	12.55	1.93	114	50.71592
TM10282	*Otomys*	*auratus*	F	6.75	1.39	0.43	13.17	1.95	127	48.18751
TM15012	*Otomys*	*auratus*	F	6.19	1.36	0.33	13.00	2.10	127	49.96258
TM19287	*Otomys*	*auratus*	M	6.53	1.52	0.44	13.20	2.02	127	50.22489
TM2916	*Otomys*	*auratus*	F	5.80	1.49	0.36	12.58	2.17	127	51.72409
TM35182	*Otomys*	*auratus*	M	6.78	1.36	0.41	13.70	2.02	127	51.75141
TM3611	*Otomys*	*auratus*	M	6.02	1.39	0.38	11.74	1.95	127	52.88281
TM3614	*Otomys*	*auratus*	F	6.45	1.54	0.37	13.62	2.11	127	49.22943
TM41608	*Otomys*	*auratus*	M	6.25	1.55	0.41	14.07	2.25	127	51.02863
TM46864	*Otomys*	*auratus*	F	6.79	1.40	0.39	13.30	1.96	127	52.39796
TM7597	*Otomys*	*auratus*	M	6.69	1.40	0.40	13.64	2.04	127	53.49452
TM9052	*Otomys*	*auratus*	F	7.03	1.24	0.41	13.56	1.93	127	52.17177
1933-2758	*Otomys*	*barbouri*	F	5.95	1.31	0.35	11.42	1.92	112	45.22757
1933-2759	*Otomys*	*barbouri*	F	6.23	1.30	0.35	11.33	1.82	112	52.69945
1933-2760	*Otomys*	*barbouri*	M	6.15	1.29	0.45	10.77	1.75	112	48.72887
1933-2762	*Otomys*	*barbouri*	M	5.91	1.43	0.40	11.65	1.97	112	broken
1933-2764	*Otomys*	*barbouri*	M	5.88	1.38	0.37	11.47	1.95	112	broken
1933-2765	*Otomys*	*barbouri*	M	5.86	1.24	0.35	9.03	1.54	112	broken
1933-2766	*Otomys*	*barbouri*	M	6.05	1.30	0.35	11.08	1.83	112	broken
1972-218	*Otomys*	*helleri*	M	6.28	1.42	0.41	11.99	1.91	90	49.85414
1972-220	*Otomys*	*helleri*	M	5.93	1.26	0.41	11.09	1.87	90	53.19018
1972-221	*Otomys*	*helleri*	M	6.35	1.28	0.44	11.05	1.74	90	56.10628
1972-223	*Otomys*	*helleri*	F	6.21	1.29	0.40	9.62	1.55	90	52.06238
1972-224	*Otomys*	*helleri*	F	5.87	1.35	0.39	9.74	1.66	90	53.33326
1972-225	*Otomys*	*helleri*	F	6.00	1.35	0.37	10.8	1.80	90	52.63067
1972-226	*Otomys*	*helleri*	F	6.02	1.35	0.42	11.26	1.87	90	53.78809
1972-227	*Otomys*	*helleri*	F	5.50	1.23	0.33	9.46	1.72	90	46.89101
1972-228	*Otomys*	*helleri*	M	6.08	1.34	0.43	10.95	1.80	90	54.84596
TM1203	*Otomys*	*sloggetti*	M	5.97	1.19	0.44	10.86	1.82	84	51.37335
TM12915	*Otomys*	*sloggetti*	F	5.61	1.32	0.43	9.76	1.74	84	54.42251
TM13730	*Otomys*	*sloggetti*	F	6.48	1.30	0.50	12.77	1.97	84	52.16358

TM16519	*Otomys*	*sloggetti*	M	6.15	1.35	0.52	11.93	1.94	84	52.11853
TM22664	*Otomys*	*sloggetti*	M	5.86	1.24	0.54	11.36	1.94	84	56.5382
TM22670	*Otomys*	*sloggetti*	F	6.71	1.25	0.46	13.01	1.94	84	50.18285
TM22676	*Otomys*	*sloggetti*	F	6.21	1.32	0.44	11.92	1.92	84	57.4588
TM22684	*Otomys*	*sloggetti*	M	6.08	1.23	0.45	11.25	1.85	84	59.29027
TM7606	*Otomys*	*sloggetti*	M	6.01	1.38	0.52	11.71	1.95	84	54.83523
TM7780	*Otomys*	*sloggetti*	M	6.38	1.39	0.40	12.96	2.03	84	56.28088
TM7781	*Otomys*	*sloggetti*	F	6.87	1.22	0.45	13.26	1.93	84	54.12049
TM2247	*Otomys*	*unisulcatus*	M	6.30	1.45	0.46	13.54	2.15	96	55.16288
TM22768	*Otomys*	*unisulcatus*	F	6.37	1.43	0.43	13.19	2.07	96	50.0304
TM22782	*Otomys*	*unisulcatus*	M	6.48	1.39	0.45	12.63	1.95	96	56.38046
TM22794	*Otomys*	*unisulcatus*	F	6.61	1.29	0.50	12.43	1.88	96	75.62706
TM27359	*Otomys*	*unisulcatus*	F	5.86	1.44	0.43	13.19	2.25	96	51.81354
TM39371	*Otomys*	*unisulcatus*	M	6.06	1.44	0.49	13.03	2.15	96	58.12217
TM43864	*Otomys*	*unisulcatus*	F	6.34	1.37	0.48	12.75	2.01	96	55.37782
TM4754	*Otomys*	*unisulcatus*	M	6.03	1.49	0.40	13.14	2.18	96	52.83469
TM6734	*Otomys*	*unisulcatus*	M	6.35	1.41	0.44	13.47	2.12	96	58.58904
TM75	*Otomys*	*unisulcatus*	F	6.06	1.44	0.50	13.02	2.15	96	55.65355
TM9057	*Otomys*	*unisulcatus*	M	6.71	1.32	0.44	12.81	1.91	96	50.91629
TM16845	*Parotomys*	*brantsii*	F	6.8	1.26	0.68	15.77	2.32	95	76.53325
TM22628	*Parotomys*	*brantsii*	M	6.81	1.25	0.63	15.11	2.22	95	76.81687
TM22630	*Parotomys*	*brantsii*	M	6.94	1.31	0.64	15.69	2.26	95	71.38595
TM27543	*Parotomys*	*brantsii*	F	7.00	1.30	0.75	16.3	2.33	95	77.13138
TM4750	*Parotomys*	*brantsii*	F	6.54	1.38	0.72	15.11	2.31	95	77.39622
TM4799	*Parotomys*	*brantsii*	M	6.24	1.35	0.66	14.84	2.38	95	78.10408
TM5088	*Parotomys*	*brantsii*	M	6.55	1.24	0.68	15.01	2.29	95	74.51233
TM66	*Parotomys*	*brantsii*	F	6.89	1.39	0.70	16.41	2.38	95	72.25011
TM7902	*Parotomys*	*brantsii*	F	7.04	1.29	0.68	15.14	2.15	95	75.89446
TM7912	*Parotomys*	*brantsii*	F	6.66	1.24	0.78	14.06	2.11	95	74.06579
TM9069	*Parotomys*	*brantsii*	M	6.87	1.23	0.67	14.49	2.11	95	72.01311

Table B.2. Phylogenetic signal calculated for each cochlear trait and body mass. *indicates a phylogenetic signal not significantly different from λ = 1 but significantly different from λ = 0 (at 5%).

	Pagel's λ	**aic**	**ML vs λ = 0 p-value**	**aic**	**ML vs λ = 1 p-value**	**aic**
OWA	0.000	7.144	1.000	5.144	0.680	5.316
RECL	1.000	-20.340	0.080	-19.245	1.000	-22.341
CUR	0.9768	-24.420	0.540	-24.419	0.980	-24.792
ECL	0.000	-8.740	0.999	-10.737	0.084	-7.752
TUR	0.592	-12.700	0.450	-14.137	0.514	-14.273
BodyM	1.000	13.650	0.020 *	17.037	1.00	13.362
bullaCS	0.000	-3.280	0.990	-5.280	0.460	-4.730

Table B.3. Variable loadings from PCA of three cochlea parameters for our data.

Cochlea variables	PC 1	PC 2
OWA	-0.7503	-0.0086
RECL	-0.4550	-0.7190
CUR	-0.4798	0.6950

Table B.4. Interspecies RECL and OWA ; CUR; TUR and ECL differences using a pairwise t-tests applied to each pair of rodent species. Da, *Desmodillus auricularis*; Gl, *Gerbilliscus leucogaster*; Gn, *Gerbillus nigeriae*; Oa, *Otomys angoniensis*; Oau, *Otomys auratus*; Ob, *Otomys barbouri*; Oh, *Otomys helleri*; Os, *Otomys sloggetti*; Ou, *Otomys unisulcatus*; and Pb, *Parotomys brantsii.* *indicates significant bonferroni-corrected p-values at p = 0.001.

OWA										
	D.a	*G.l*	*G.n*	*O.a*	*O.au*	*O.b*	*O.h*	*O.s*	*O.u*	*P.b*
RECL *D.a*		33.84*	42.89*	40.52*	39.6*	36.48*	37.02*	32.79*	33.87*	12.54*
G.l	9.091*		12.17*	10.26*	39.6*	9.675*	8.119*	1.859	3.034	20.2*
G.n	11.55*	3.302		1.505	2.438	0.5556	2.87	9.393*	8.29*	30.09*
O.a	0.7195	9.874*	12.29*		0.9133	0.7531	1.418	7.721*	5.729*	27.07*
O.au	5.768	15.37*	17.44*	5.048		1.559	0.5513	6.808*	5.729	27.07*
O.b	0.1842	7.661*	9.951*	0.8188	5.271		1.987	7.563*	6.611*	25.43*
O.h	0.0686	8.62*	11*	0.614	5.403	0.2379		5.907	4.883	25.13*
O.s	2.398	11.7*	14*	1.679	3.369	2.299	2.207		1.079	20.26*
O.u	3.358	12.75*	14.98*	2.638	2.41	3.146	3.117	0.9594		21.34*
P.b	9.263*	19.17 *	21.01*	8.543*	3.495	8.353*	8.719*	6.864*	5.905	

CUR										
	D.a	*G.l*	*G.n*	*O.a*	*O.au*	*O.b*	*O.h*	*O.s*	*O.u*	*P.b*
D.a										
G.l	1.298									
G.n	10.31*	9.942*								
O.a	5.947	5.176	4.239							
O.au	4.305	3.389	5.916	1.642						
O.b	7.35*	6.72*	1.581	2.105	3.553					
O.h	8.003*	7.413*	1.606	2.361	3.919	0.08624				
O.s	9.595*	9.148*	0.5124	3.648	5.29	1.112	1.1			
O.u	4.925	4.064	5.283	1.022	0.6202	3.006	3.33	4.67		

P.b	9.413*	8.949*	0.6988	3.466	5.108	0.9515	0.9268	0.1824	4.488	

TUR										
	D.a	*G.l*	*G.n*	*O.a*	*O.au*	*O.b*	*O.h*	*O.s*	*O.u*	*P.b*
ECL *D.a*		40	18	1*	8*	0*	0*	0*	11	56
G.l	54.5		2.5*	0*	1.5*	0*	0*	0*	1.5*	34.5
G.n	0*	4*		24	53	6	5*	18	64.5	14
O.a	4*	28	20.5		17	20	6*	59.5	23	0*
O.au	25	80	0*	9*		6	0*	15.5	51.5	8*
O.b	0*	5*	28.5	19	0*		20	26	7.5	0*
O.h	1*	4*	52.5	17	1*	22		11.5	1.5*	0*
O.s	6*	36	21	54	14	18	17		19.5	0*
O.u	13	83	0*	14	36	0*	0*	20		16.5
P.b	4*	7*	0*	0*	1*	0*	0*	0*	0*	

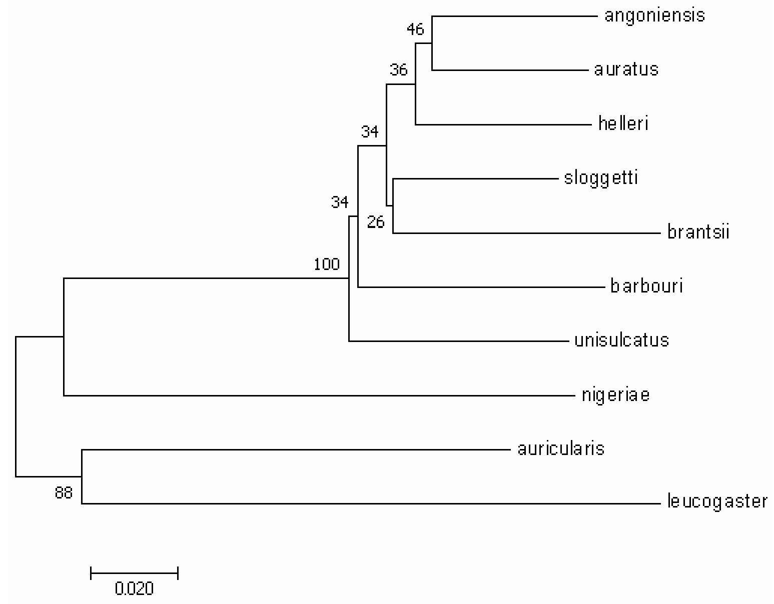


Figure B.1. Phylogram tree produced by Neighbour-Joining method with branch length.

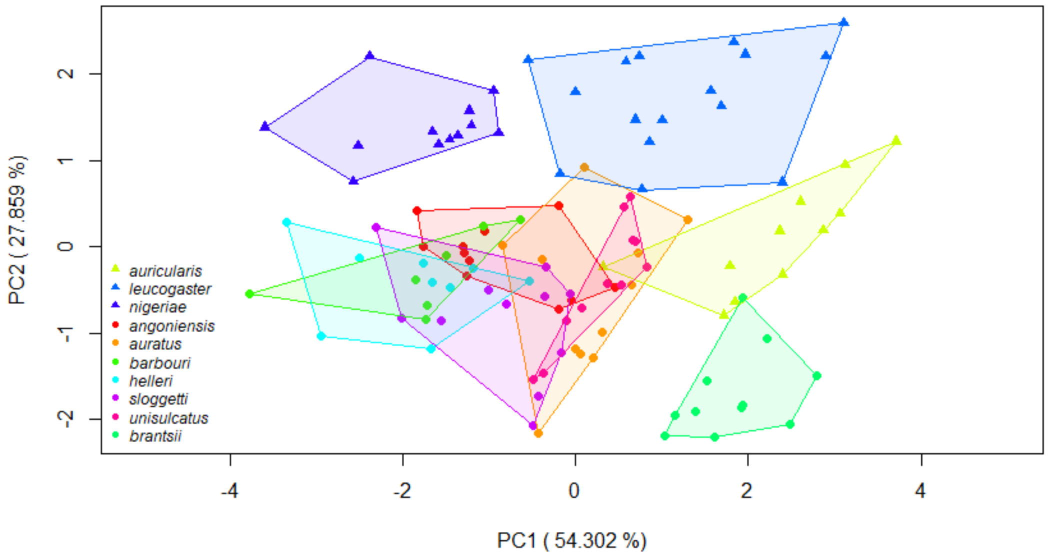
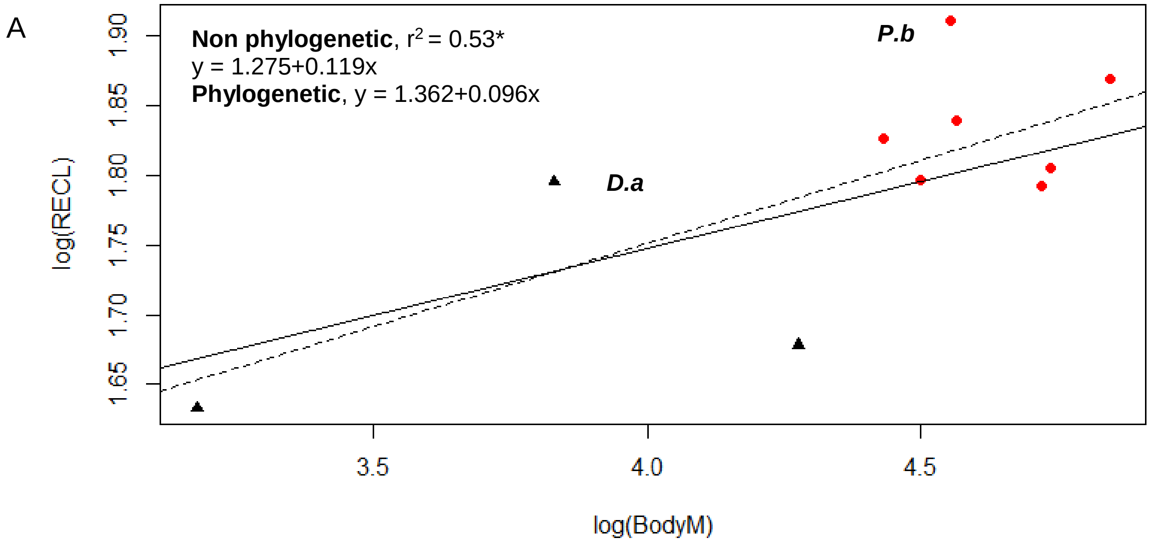
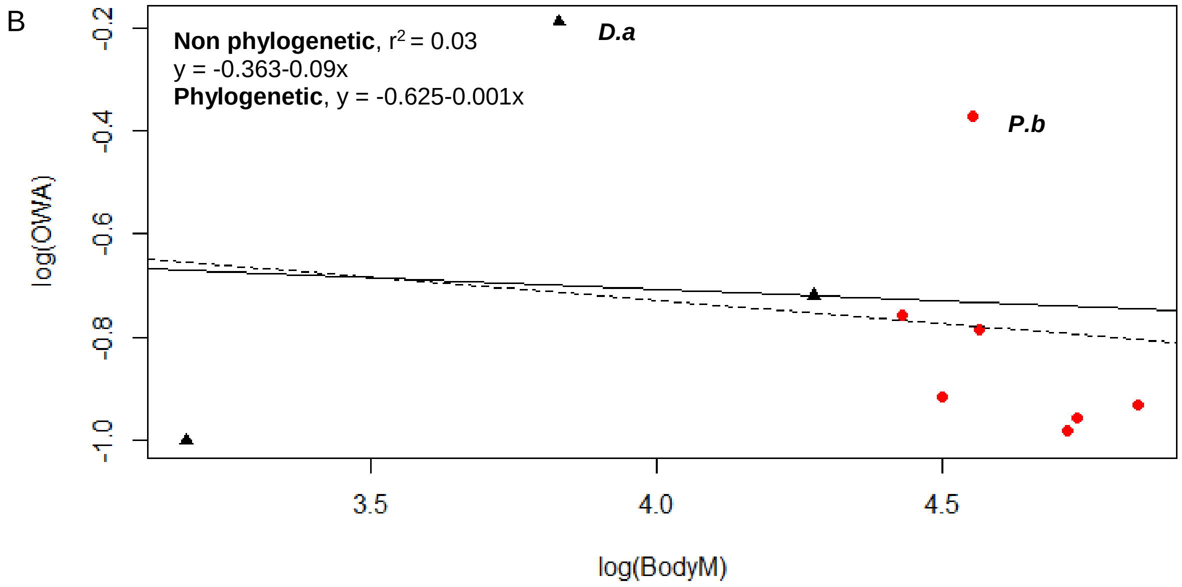
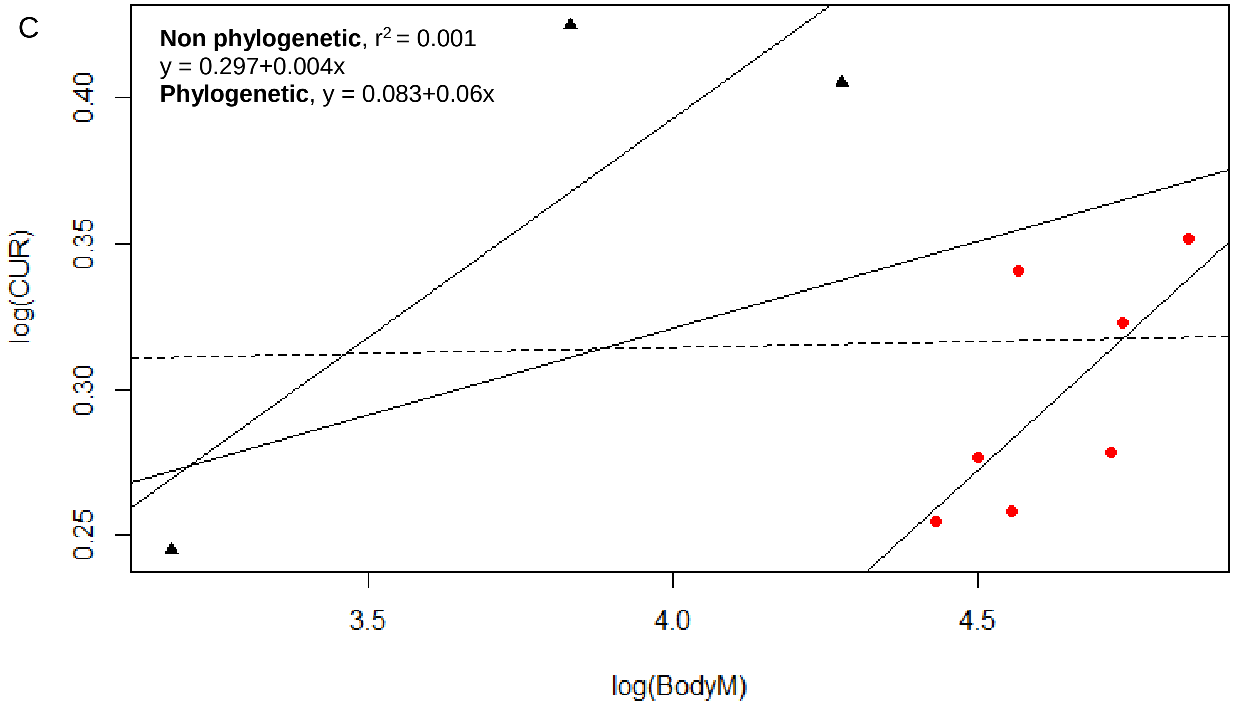


Figure B.2. Principal Component Analysis of all five cochlear features (OWA, RECL, CUR, TUR, ECL) investigated in this study, gerbils (triangles) and laminate-toothed rats (circles).




B
Non phylogenetic, $r^2 = 0.03$
y = -0.363-0.09x
Phylogenetic, y = -0.625-0.001x
D.a
P.b
log(OWA)
-0.2
-0.4
-0.6
-0.8
-1.0
3.5
4.0
4.5
log(BodyM)


C
Non phylogenetic, $r^2 = 0.001$
y = 0.297+0.004x
Phylogenetic, y = 0.083+0.06x
log(CUR)
0.40
0.35
0.30
0.25
3.5
4.0
4.5
log(BodyM)

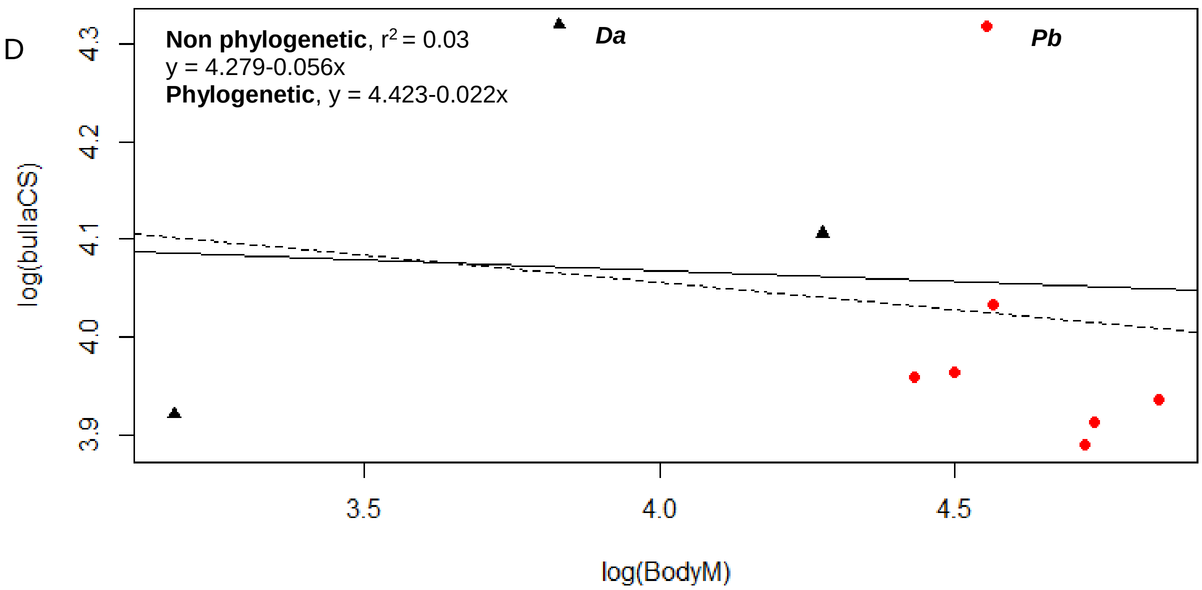
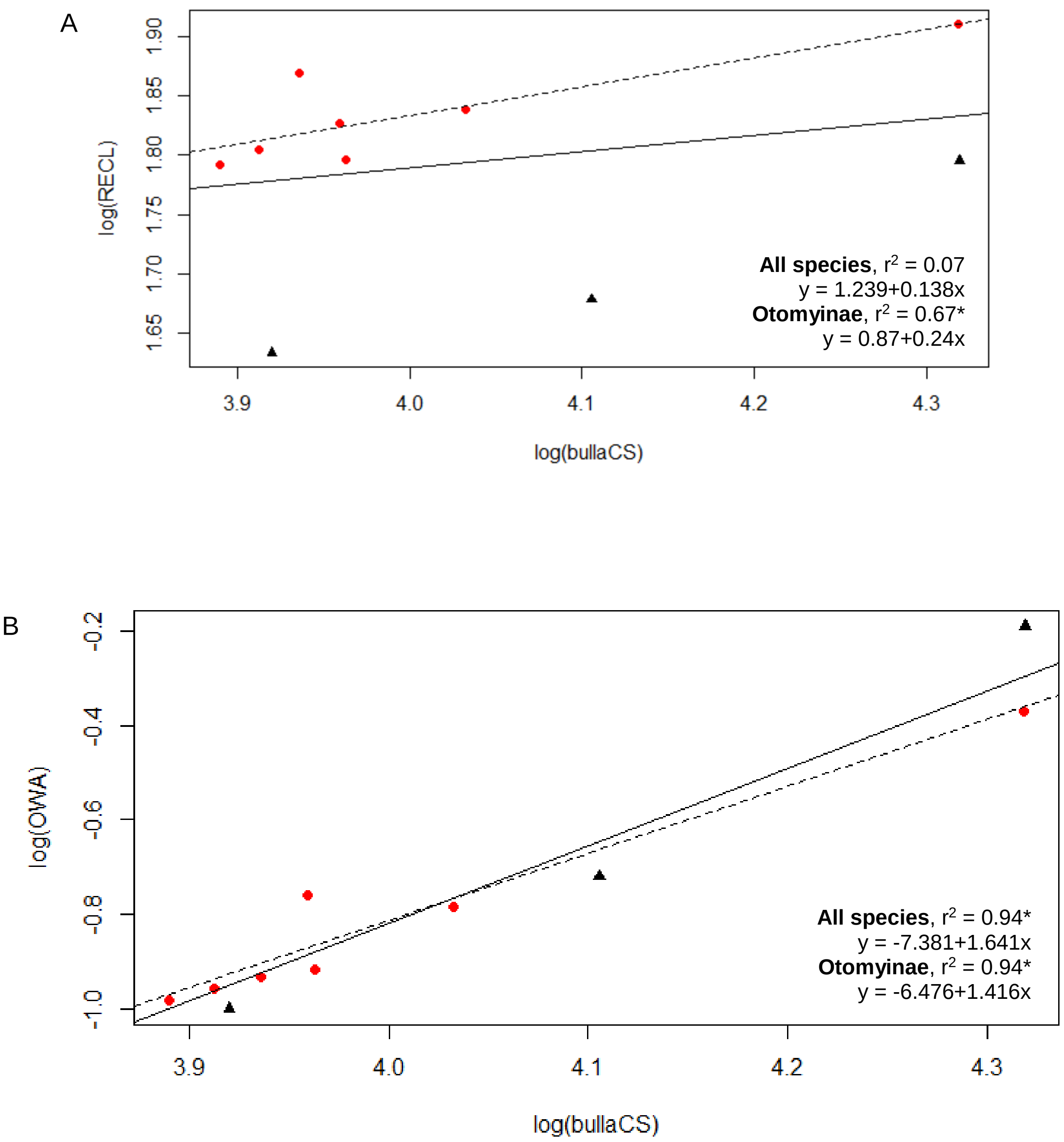


Figure B.3. Non-phylogenetic and phylogenetic controlled linear regressions between RECL, OWA, CUR, bulla and body mass. (A) RECL for gerbils (black triangles) and Otomyini (red circles) with dashed line (non-phylogenetic) and solid line (phylogenetic) regressions. (B) OWA for gerbils (black triangles) and Otomyini (red circles) with dashed line (non-phylogenetic) and solid line (phylogenetic) regressions. (C) CUR for gerbils (black triangles) and Otomyini (red circles) with dashed line (non-phylogenetic) and solid line (phylogenetic) regressions. (D) Bulla for gerbils (black triangles) and Otomyini (red circles) with dashed line (non-phylogenetic) and solid line (phylogenetic) regressions. *indicates significant level of 5%.


A
log(RECL)
1.65
1.70
1.75
1.80
1.85
1.90
3.9
4.0
4.1
4.2
4.3
log(bullaCS)
All species, r^2 = 0.07
y = 1.239+0.138x
Otomyinae, r^2 = 0.67*
y = 0.87+0.24x
B
log(OWA)
-1.0
-0.8
-0.6
-0.4
-0.2
3.9
4.0
4.1
4.2
4.3
log(bullaCS)
All species, r^2 = 0.94*
y = -7.381+1.641x
Otomyinae, r^2 = 0.94*
y = -6.476+1.416x

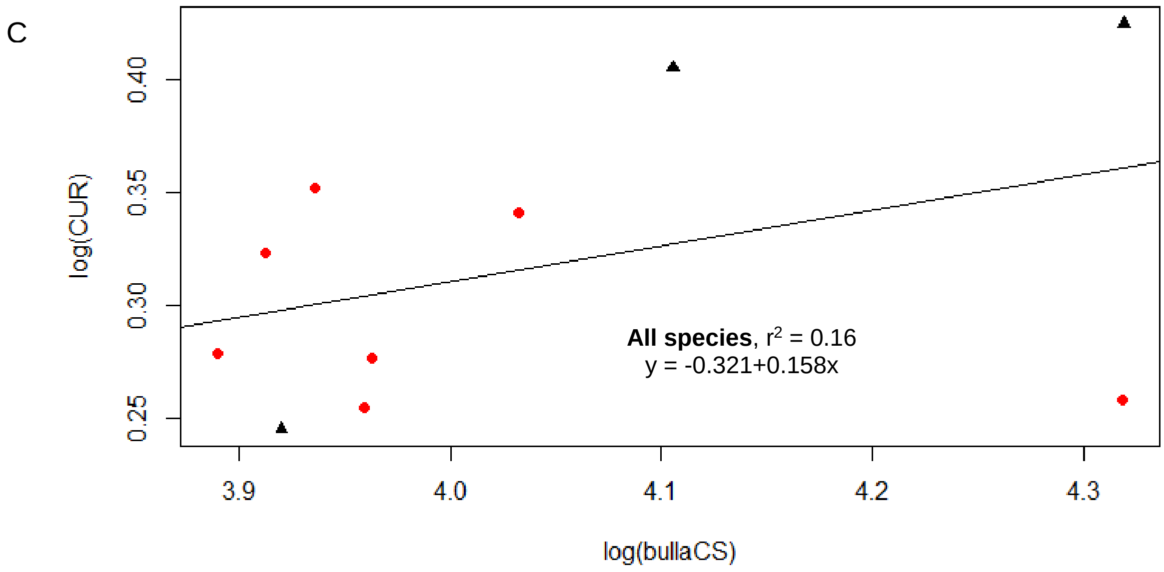
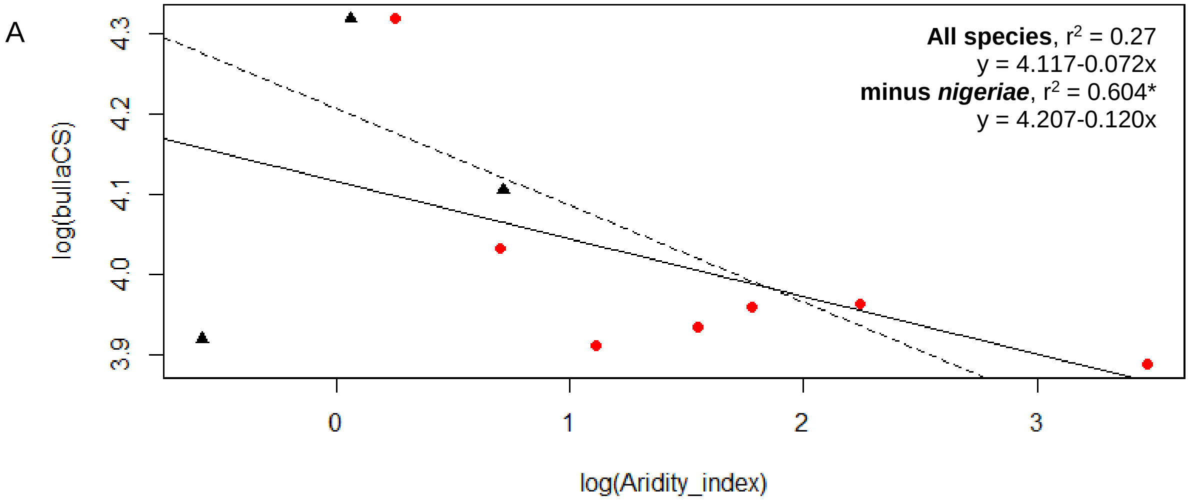


Figure B.4. Association between bulla CS and (A) RECL; with solid line (all species included) and dashed line (Otomyini only), (B) OWA; with solid line (all species included) and dashed line (Otomyini only), (C) CUR. Gerbils (black triangle) and laminate-toothed rats (red circles). *indicates significant level of 5%.



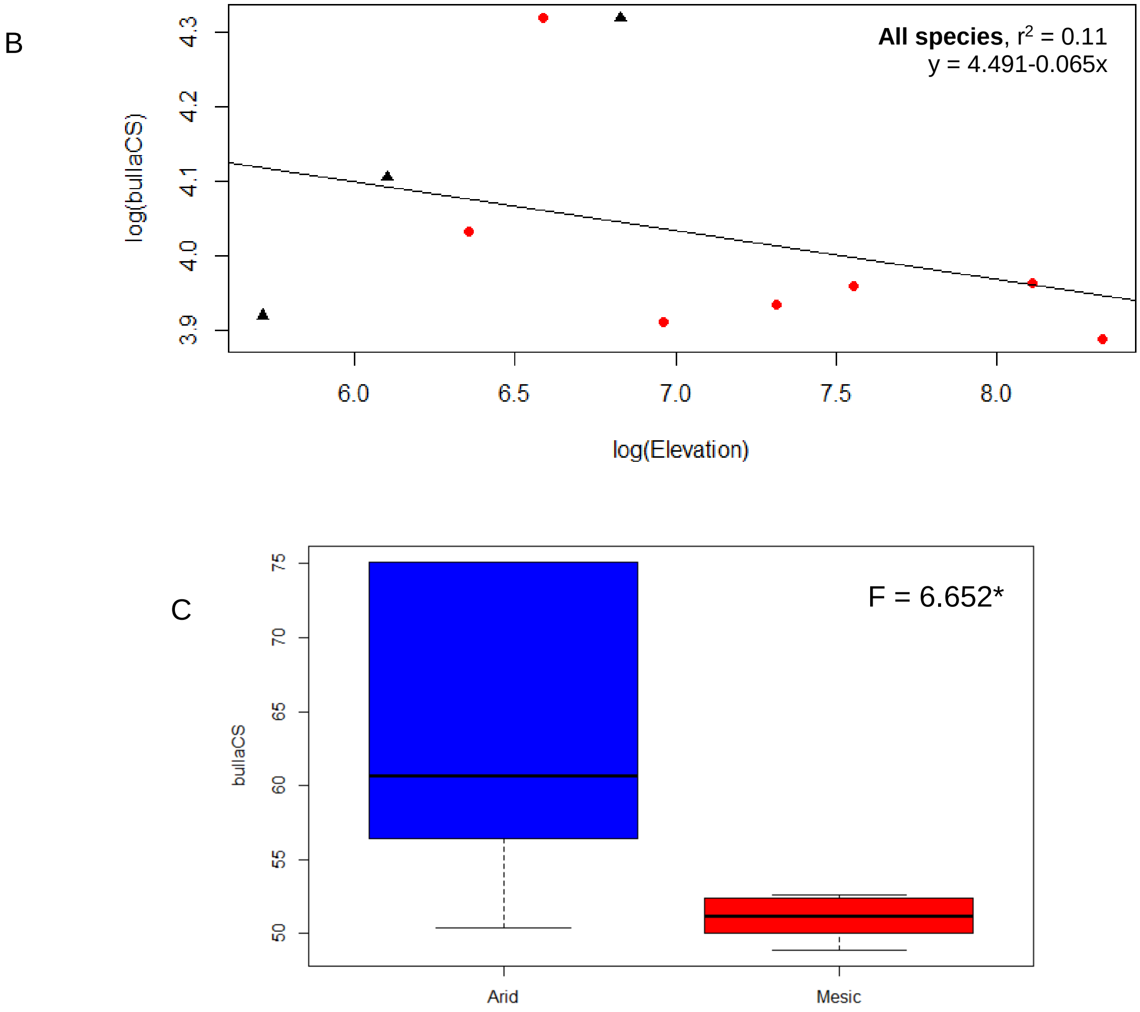
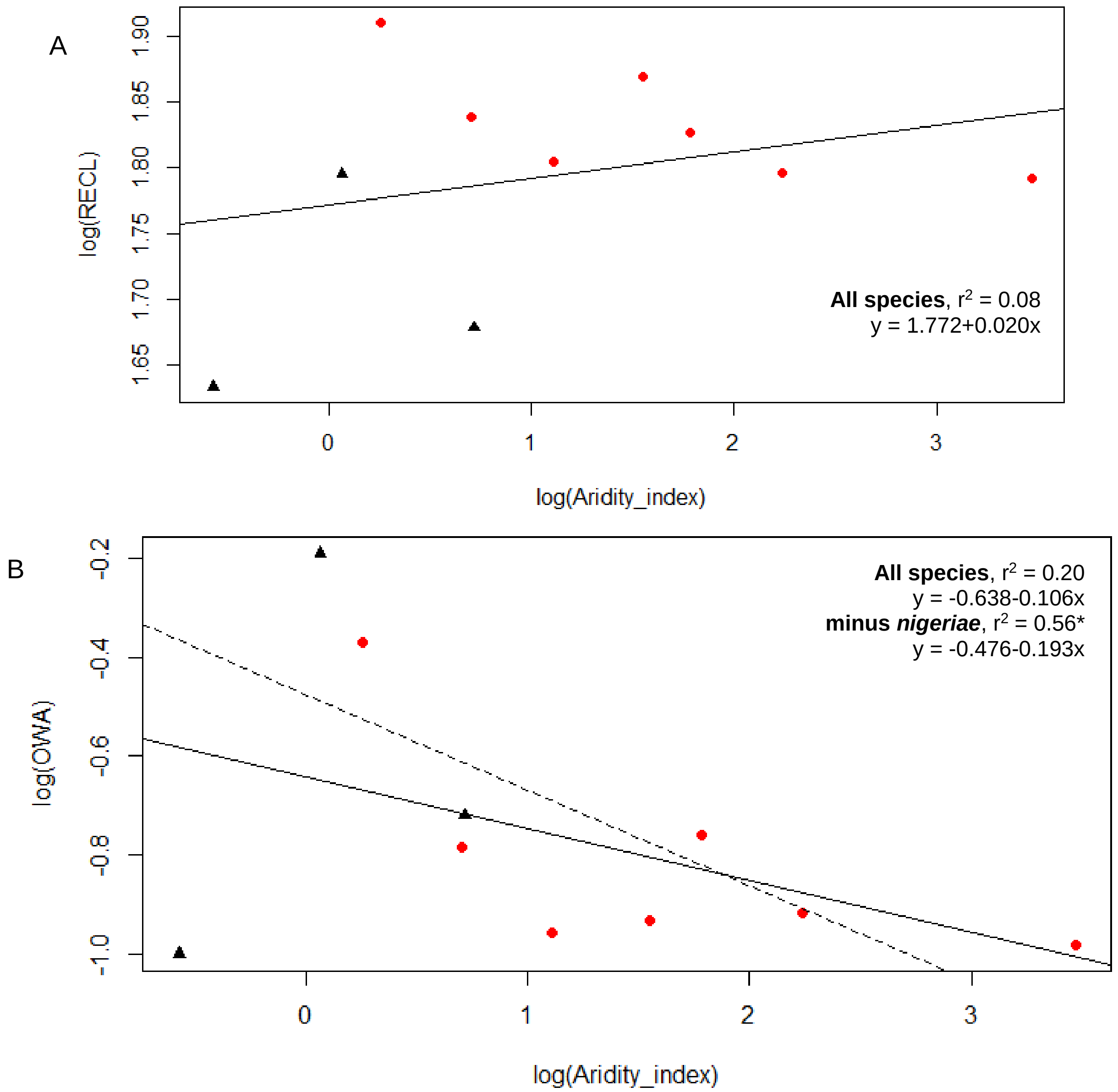


Figure B.5. Association between bulla CS and environmental variables (A) aridity index; with solid line (all species included) and dashed line (*Gerbillus nigeriae* removed) (B) elevation, (C) habitat. Gerbils (black triangle) and laminate-toothed rats (red circles). *indicates significant level of 5%.


A
log(RECL)
1.90
1.85
1.80
1.75
1.70
1.65
0
1
2
3
log(Aridity_index)
All species, r² = 0.08
y = 1.772+0.020x
B
log(OWA)
-0.2
-0.4
-0.6
-0.8
-1.0
0
1
2
3
log(Aridity_index)
All species, r² = 0.20
y = -0.638-0.106x
minus *nigeriae*, r² = 0.56*
y = -0.476-0.193x

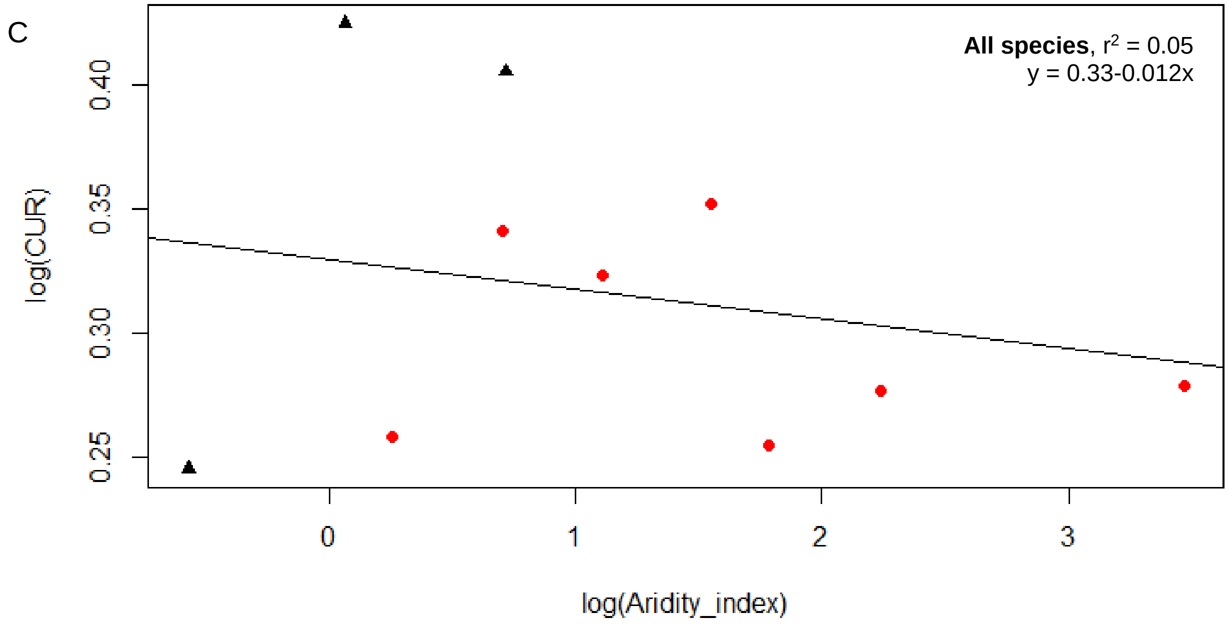
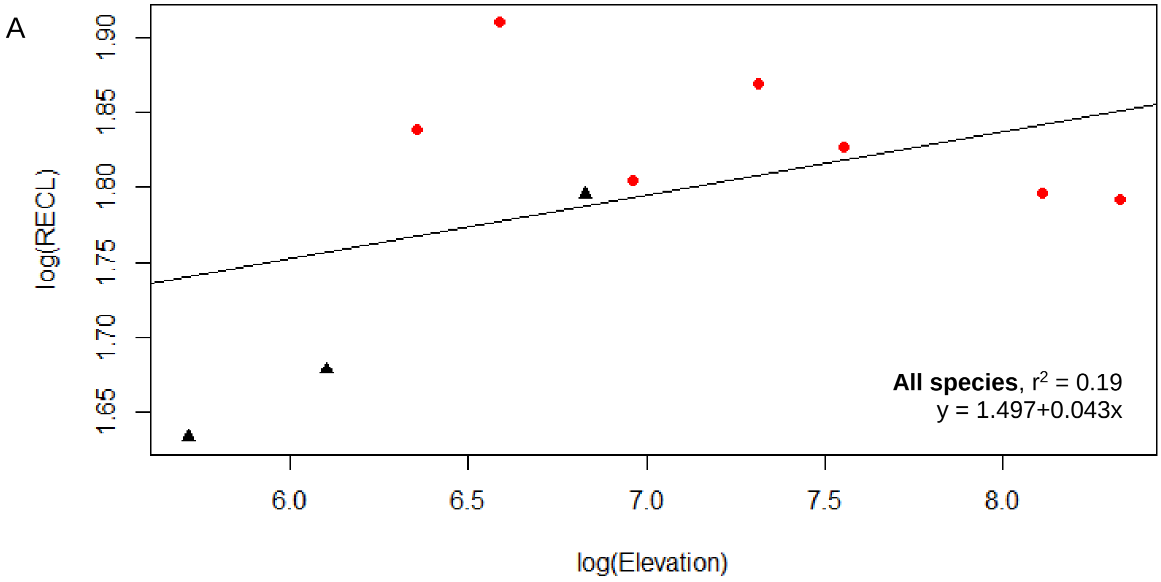


Figure B.6. Association between aridity index and cochlea parameters (A) RECL, (B) OWA; with solid line (all species included) and dashed line (*Gerbillus nigeriae* removed) (C) CUR. Gerbils (black triangle) and laminate-toothed rats (red circles). *indicates significant level of 5%.



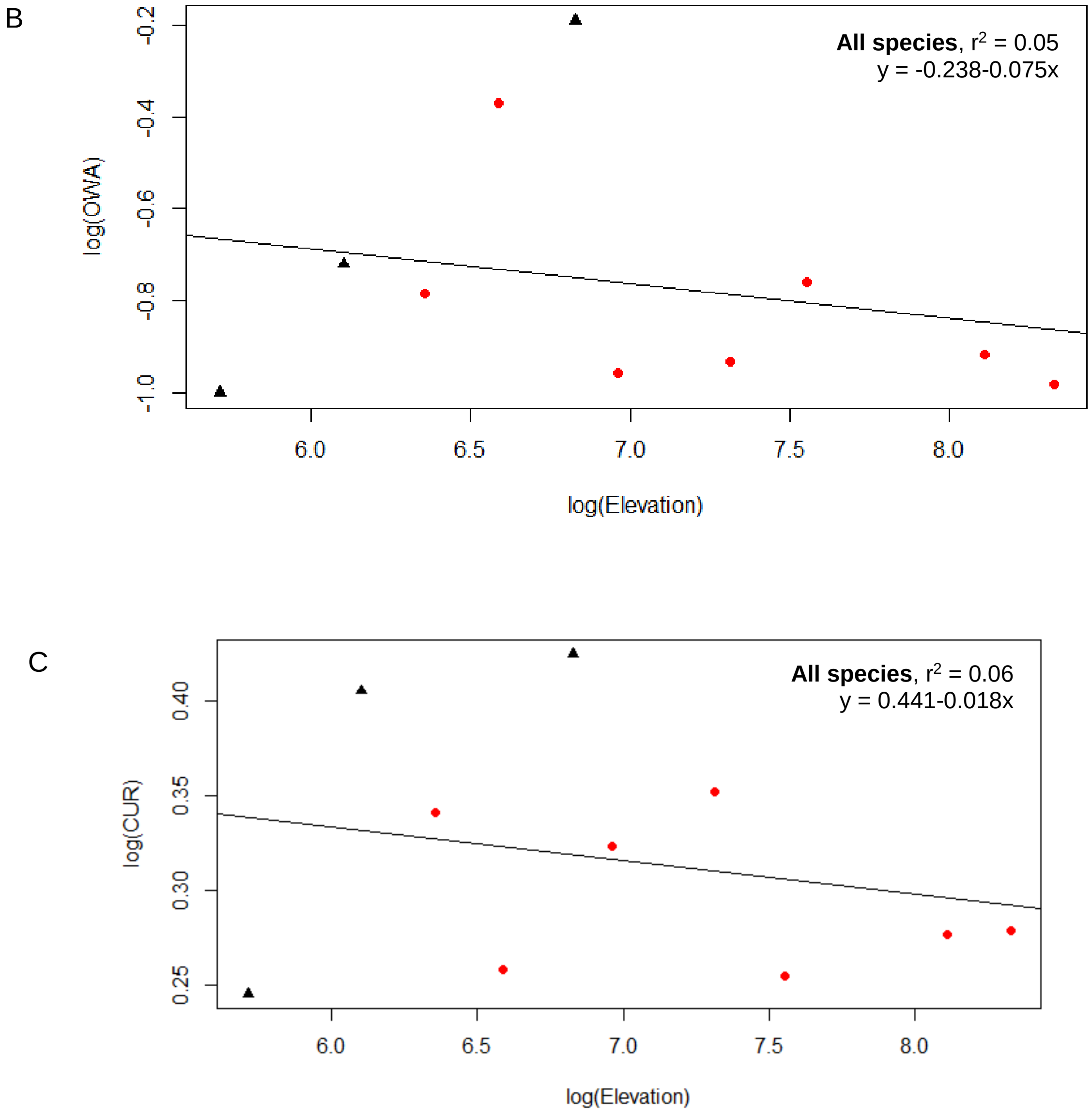


Figure B.7. Association between elevation and cochlea parameters for all species (A) RECL, (B) OWA (C) CUR. Gerbils (black triangle) and laminate-toothed rats (red circles).

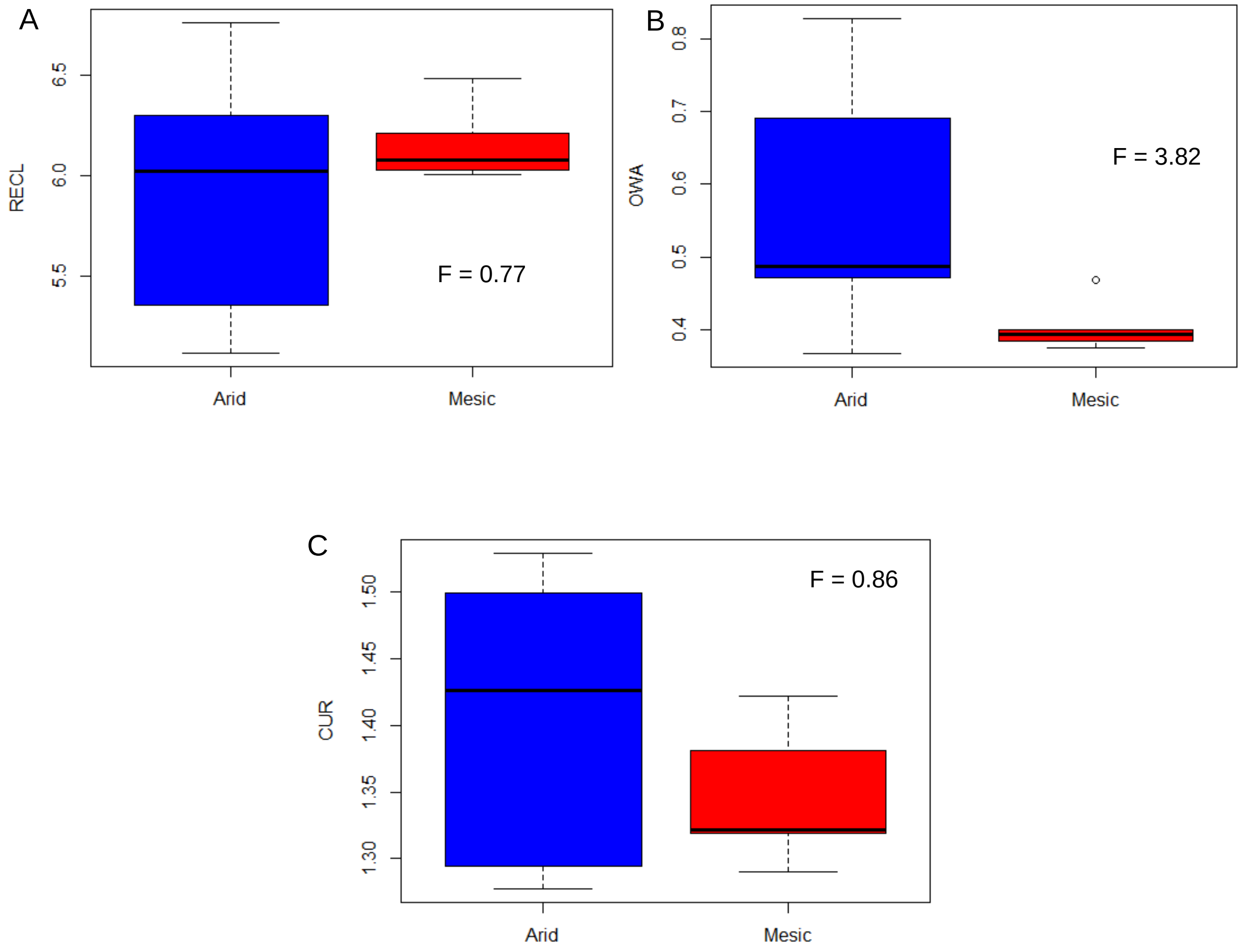


Figure B.8. Association between habitat and cochlea parameters for all species (A) RECL, (B) OWA, (C) CUR.

APPENDIX C

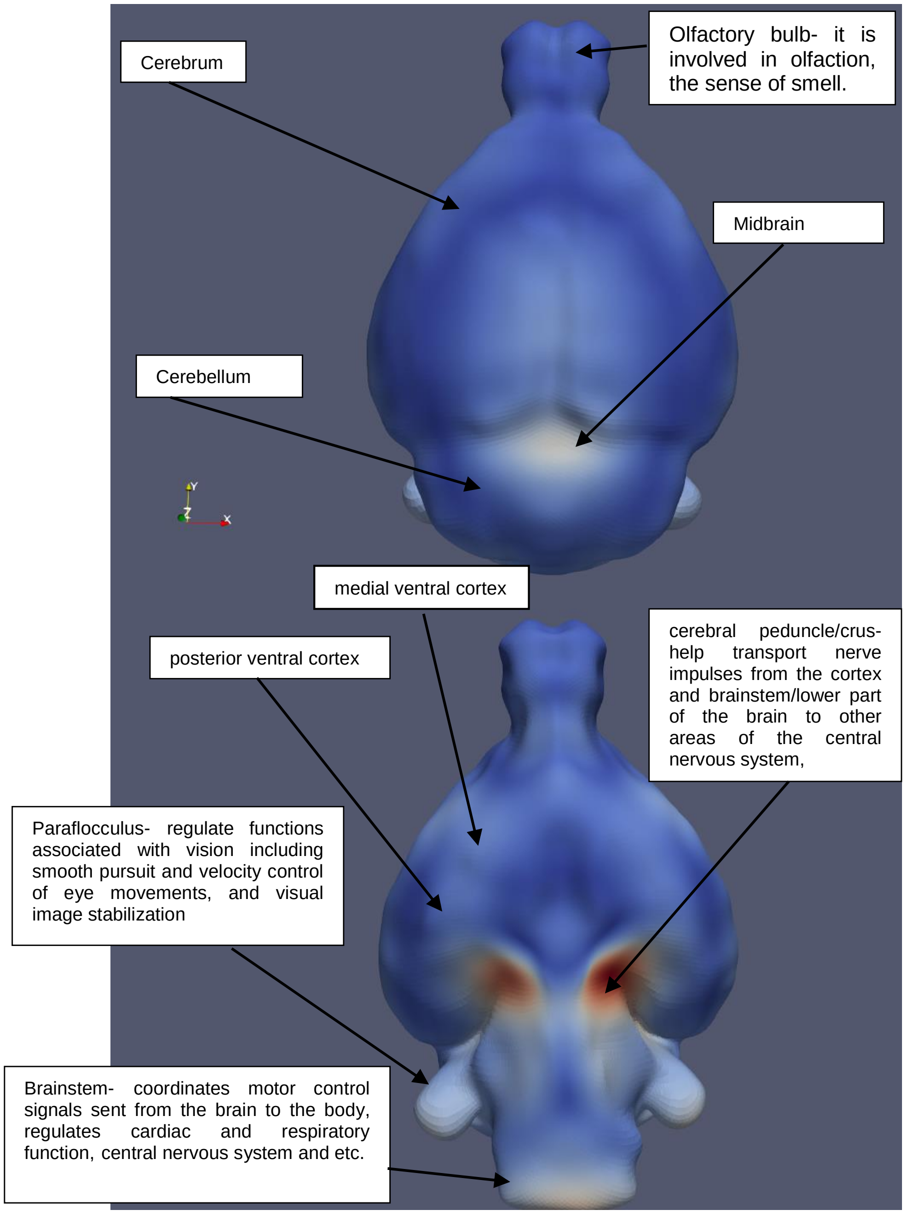
SUPPORTING MATERIAL FOR CHAPTER 4

Table C.1: Species mean and standard deviations for the endocranial volume.

Species names		**ECV (cm^3)**
O. angoniensis	Mean	1.561
	SD	0.26
O. auratus	Mean	1.765
	SD	0.113
O. unisulcatus	Mean	1.47
	SD	0.15
O. helleri	Mean	1.33
	SD	0.12
O. sloggettii	Mean	1.55
	SD	0.144
O. barbouri	Mean	1.36
	SD	0.14
P. brantsii	Mean	1.396
	SD	0.06
G. leucogaster	Mean	1.36
	SD	0.113
G. nigeriae	Mean	0.69
	SD	0.044781542
D. auricularis	Mean	1.1678
	SD	0.081121889

Table C.2: Pairwise distance matrix of the GMS deformations.

	D. auricularis	*G. leucogaster*	*G. nigeriae*	*O. angoniensis*	*O. auratus*	*O. barbouri*	*O. helleri*	*O. sloggetti*	*O. unisulcatus*	*P. brantsii*
D. auricularis	0	46.6314	18.1481	64.4147	58.8218	68.7442	71.9035	74.2141	59.0689	47.9921
G. leucogaster	46.6314	0	12.8403	36.6276	27.0419	21.4390	27.0690	26.1156	22.4935	24.0298
G. nigeriae	18.1481	12.8403	0	43.6654	34.2837	34.8592	40.9253	37.2014	28.7234	24.0442
O. angoniensis	64.4147	36.6276	43.6654	0	4.6211	7.1134	3.0282	4.9442	6.7498	24.1080
O. auratus	58.8218	27.0419	34.2837	4.6211	0	2.9003	4.2615	5.4291	4.7798	24.2707
O. barbouri	68.7442	21.4390	34.8592	7.1134	2.9003	0	3.0652	5.2714	6.4128	23.2787
O. helleri	71.9035	27.0690	40.9253	3.0282	4.2615	3.0652	0	3.2317	5.2988	19.6532
O. sloggetti	74.2141	26.1156	37.2014	4.9442	5.4291	5.2714	3.2317	0	4.6738	20.8894
O. unisulcatus	59.0689	22.4935	28.7234	6.7498	4.7798	6.4128	5.2988	4.6738	0	9.5206
P. brantsii	47.9921	24.0298	24.0442	24.1080	24.2707	23.2787	19.6532	20.8894	9.5206	0



Cerebrum

Olfactory bulb- it is involved in olfaction, the sense of smell.

Midbrain

Cerebellum

medial ventral cortex

posterior ventral cortex

cerebral peduncle/crus- help transport nerve impulses from the cortex and brainstem/lower part of the brain to other areas of the central nervous system,

Paraflocculus- regulate functions associated with vision including smooth pursuit and velocity control of eye movements, and visual image stabilization

Brainstem- coordinates motor control signals sent from the brain to the body, regulates cardiac and respiratory function, central nervous system and etc.

Figure C.1: Virtual endocast of *Parotomys brantsii* in (a) dorsal and (b) ventral view, with brain parts labels and functions of some of those mentioned in the manuscript.

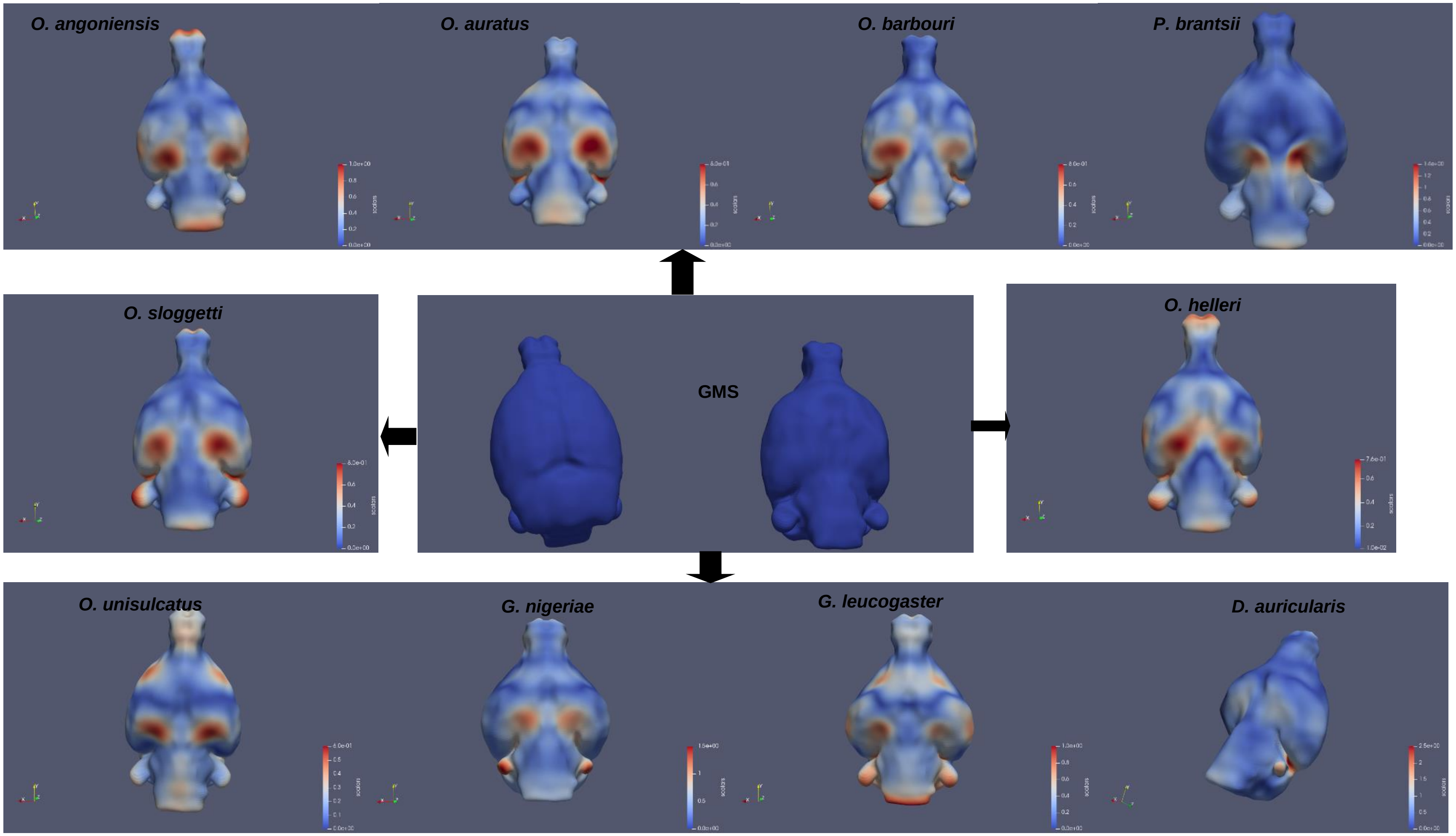


Figure C.2: Colour maps illustrating changes from the overall mean shape to the taxon mean shape. Cumulative displacement variations are rendered by a pseudo-colour scale ranging from dark blue (lowest values) to red (highest values) at the individual surface.

Journal of Anatomy

J. Anat. (2019) **234**, pp179–192 doi: 10.1111/joa.12906

Associated tympanic bullar and cochlear hypertrophy define adaptations to true deserts in African gerbils and laminate-toothed rats (Muridae: Gerbillinae and Murinae)

Aluwani Nengovhela,[1,2] José Braga,[1,3] Christiane Denys,[4] Frikkie de Beer,[5] Christophe Tenailleau[6] and Peter J. Taylor[2,7,8]

[1]*Laboratoire d'Anthropologie Moléculaire et Imagerie de Synthèse, UMR 5288 CNRS, Université de Toulouse (Paul Sabatier), Toulouse, France*
[2]*South African Research Chair in Biodiversity and Change and Centre for Invasion Biology, School of Mathematical and Natural Sciences, University of Venda, Thohoyandou, South Africa*
[3]*Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa*
[4]*Institut de Systématique, Evolution, Biodiversité, UMR 7205, CNRS, MNHN, UPMC, EPHE, Sorbonne Universités, Paris, France*
[5]*South African Nuclear Energy Corporation, Pelindaba, North West Province, South Africa*
[6]*Centre Inter-Universitaire de Recherche et d'Ingénierie des Matériaux, UMR 5085 CNRS, Université de Toulouse (Paul Sabatier), Toulouse, France*
[7]*Core Team Member of the Centre of Invasion Biology, Stellenbosch University, Stellenbosch, South Africa*
[8]*School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa*

Abstract

Hearing capabilities in desert rodents such as gerbils and heteromyids have been inferred from both anatomical and ecological aspects and tested with experiments and theoretical models. However, very few studies have focused on other desert-adapted species. In this study, a refined three-dimensional morphometric approach was used on three African rodent tribes (Otomyini, Taterillini and Gerbillini) to describe the cochlear and tympanic bullar morphology, and to explore the role of phylogeny, allometry and ecology to better understand the underlying mechanism of any observed trends of hypertrophy in the bulla and associated changes in the cochlea. As a result, desert-adapted species could be distinguished from mesic and semi-arid taxa by the gross cochlear dimensions, particularly the oval window, which is larger in desert species. Bullar and cochlear modifications between species could be explained by environment (bulla and oval window), phylogeny (cochlear curvature gradient) and/or allometry (cochlear relative length, oval window and bulla) with some exceptions. Based on their ear anatomy, we predict that *Desmodillus auricularis* and *Parotomys brantsii* should be sensitive to low-frequency sounds, with *D. auricularis* sensitive to high-frequency sounds, too. This study concludes that in both arid and semi-arid adapted laminate-toothed rats and gerbils there is bulla and associated cochlea hypertrophy, particularly in true desert species. Gerbils also show tightly coiled cochlea but the significance of this is debatable and may have nothing to do with adaptations to any specific acoustics in the desert environment.

Key words: adaptation; cochlea; CT scans; hearing capabilities; Muridae; semi-landmarks; three-dimensional morphometrics.

Introduction

Rodents are the most diverse living mammals, colonising a vast array of habitats (Wilson et al. 2016, 2017), with Muridae (or murids) being the most diverse family (Musser & Carleton, 2005). The family consists of species with a wide range of specialisation and morphological adaptations (Happold, 2013). Rodents occupying desert habitats/environment are characterised by numerous common features such as inflated tympanic bullae (Prakash, 1959; Lay, 1972; Nikolai & Bramble, 1983; Alhajeri et al. 2015; Tabatabaei-Yazdi et al. 2015; Mason, 2016), long hind feet and bipedal locomotion (Nikolai & Bramble, 1983), with certain subterranean species showing relatively larger bulla (Stein, 2000). The inflated bulla is not only associated with desert

---

Correspondence
Aluwani Nengovhela, Laboratoire d'Anthropologie Moléculaire et Imagerie de Synthèse, UMR 5288 CNRS-Université de Toulouse (Paul Sabatier), 37 Allées Jules Guesde, 31000 Toulouse, France. E: aluwani.nengovhela@univ-tlse3.fr

Accepted for publication *11 October 2018*

environments but also with open micro-habitats (Kotler, 1984) and high elevation (Zhao et al. 2013; Tabatabaei-Yazdi et al. 2015). This hypertrophy is said to improve low-frequency hearing, which is hypothesised to help in both prey localisation and predator avoidance (Lay, 1972), and interspecific communication (e.g. vocalisation, tapping, foot drumming, stomping) in burrows and open, mostly desert habitats/environment (Bridelance, 1986; Randall, 1993, 1994, 2014). However, besides the hypertrophied bulla, other aspects of the middle ear morphology as well as the inner ear are also important in improving low-frequency hearing (Dallos, 1970; Lay, 1972; Ravicz et al. 1992; Ravicz & Rosowski, 1997; Salt et al. 2013). Although a multitude of hearing studies (including those inferred from bulla and ear morphology) in desert rodents have been conducted, these have mainly focused on Gerbillinae (Lay, 1972; Plassmann et al. 1987; Plassmann & Kadel, 1991; Zhao et al. 2013; Mason, 2016; Tolnai et al. 2017), including *Meriones* (Ryan, 1976; Tabatabaei-Yazdi et al. 2014, 2015), Dipodomyinae (Lay, 1972; Webster & Webster, 1975; Heffner & Masterton, 1980; West, 1985; Shaffer & Long, 2004; Randall, 2014) and various subterranean rodents (Heffner & Heffner, 1992; Lange et al. 2004, 2007; Francescoli et al. 2012; Mason et al. 2016) to name a few.

However, no studies have looked at the hearing capabilities of Otomyini in detail despite their adaptation to life in deserts or high altitude. Vocalisation has been studied in two desert-dwelling *Parotomys* (whistling rats) species, *brantsii* and *littledalei* (Le Roux et al. 2001a,b, 2002; García-Navas & Blumstein, 2016) and in gerbils (Dempster & Perrin, 1991, 1994; Dempster et al. 1991; Dempster, 2018). *Otomys* (unknown species, Cockerell et al. 1914) malleus and incus and *Parotomys* middle ears (Oaks, 1967, unpublished cited in Mason, 2015) have been described.

The inner ear shows extensive variations across taxa in mammals (Vater & Kössl, 2011), with cochlear function potentially limiting the hearing bandwidth (Ruggero & Temchin, 2002) and semicircular canals responsible for locomotion and balance (Spoor & Zonneveld, 1998; Pfaff et al. 2015; Grohé et al. 2016). The geometry of cochlear features has been said to play a role in determining the limits of high- and low-frequency hearing and octaval ranges in vertebrates (West, 1985; Manoussaki et al. 2008; Ekdale & Racicot, 2015). However, these functional relationships had been inferred from correlations but not linked to causation.

As ear specialisations are said to be more pronounced in the inner ear because of differing lifestyles (Crumpton et al. 2015), it is of importance to test this on other taxa that have not been studied before to see whether this is a general/universal or taxon-specific adaptive trend. Studies relating the bulla size to cochlear parameters and the pattern of their covariance in response to environmental variables are very scarce, especially those looking at rodents. The present study used a three-dimensional (3D) morphometric approach to describe and compare in detail the cochlear and bullar morphology of African rodent members of three Muridae tribes belonging to two subfamilies (Otomyini in the Murinae, and Taterillini and Gerbillini in the Gerbillinae). These taxa are characterised by a wide variation of different life histories and environmental niches, including both desert and non-desert species (see Table 1 and Fig. 1). Our tribe classification follows Lecompte et al. (2008), Pavlinov (2008) and Wilson et al. (2017). We included the three tribes from two distant murid subfamilies to explore the role of phylogeny, allometry and ecology in an attempt to better understand the underlying mechanism of any observed trends of hypertrophy in the bulla and associated changes in the cochlea. Gerbils are thought to have originated from a desert-adapted ancestor in North Africa (Pavlinov, 2008), and laminate-toothed rats (Murinae: Otomyini) originated 5 MYA from *Euryotomys*, a murid occupying the presumably mesic temperate central plateau of South Africa (Pocock, 1976; Sénégas, 2001; Denys, 2003; Monadjem et al. 2015). Whereas gerbils are mostly confined to arid or semi-arid habitats, most Otomyini species are associated with temperate or montane or sub-montane habitats, with the exception of *Otomys unisulcatus*, which is from the semi-arid shrub habitats in the Karoo desert of South Africa, and two species of whistling rats (*Parotomys brantsii* and *Parotomys littledalei*) from the Karoo, Kalahari and Namib deserts of southern Africa. The bullae of both desert-dwelling *Parotomys* species are hypertrophic but not that of *O. unisulcatus* (Pocock, 1976; Taylor et al. 2004). The very wide habitat range within Otomyini offers an excellent opportunity to understand evolutionary responses of the bulla and cochlea to the transition from mesic to desert environments within a closely related clade of species.

Within Gerbillinae, species differ not only in the size of the bulla but also in the degree and type of pneumatisation (expansion) of the posteriorly located mastoid chamber of the bulla. Extreme desert species (e.g. *Desmodillus auricularis*) are characterised by larger bulla and a two-chambered pneumatised mastoid cavity; *Gerbilliscus*, a more semi-arid savannah-associated genus, includes species that typically display a smaller bulla with the mastoid portion hardly expanded; and an intermediate condition of the bulla is found in the genus *Gerbillus* (Lay, 1972; Pavlinov, 2001, 2008; Mason, 2016). Our study included *Gerbillus nigeriae*, a species that occupies semi-arid Sahel habitats but has also expanded its range into anthropogenic habitats and therefore is less of a desert specialist than a species such as *D. auricularis*. Our choice of three gerbil taxa for this study therefore includes a range of species representing various bullar morphologies ranging from more generalised (un-inflated mastoid portions of bulla) to more specialised (highly inflated mastoid) adaptations to arid habitats.

The main objectives of this study are (1) to investigate cochlear morpho-anatomical variation among Otomyini and Gerbillinae, focusing on five cochlea features (Braga et al. 2015) that play a role in hearing capabilities in

Table 1 Brief life history summary of all 10 species.

Species name	Diet	Detailed habitat	Simplified habitat	Mean body mass (g)	Life style	Elevation (m)
Otomys auratus	Herbivorous*[†]	Montane or highveld plateau grassland[†‡]	Mesic	127[‡]	Epigeic[§]	Mid-elevation[‡§]
Otomys angoniensis	Herbivorous*[†]	Mesic savannah[†‡]	Mesic	114[‡]	Epigeic*[†]	Low elevation < 1000*[†]
Otomys unisulcatus	Herbivorous*[†]	Semi-arid[†‡]	Arid	96[‡]	Epigeic[†]	Low elevation[†]
Otomys helleri	Herbivorous*[†]	Alpine[‡]	Mesic	90[‡]	Epigeic[‡]	> 3000 High elevation‡
Otomys sloggetti	Herbivorous*[†]	Alpine[†‡]	Mesic	84[‡]	Epigeic[†]	> 2000 Mid-elevation[†]
Otomys barbouri	Herbivorous*[†]	Alpine[†‡]	Mesic	112[‡]	Epigeic[†]	> 3200 High elevation‡
Parotomys brantsii	Herbivorous*[†]	Arid[†‡]	Arid	95[‡]	Fossorial[†]	< 1000 Low elevation[†]
Gerbilliscus leucogaster	Omnivorous*[†]	Semi-Arid (Arid savannah)*[†]	Arid	72[‡]	Fossorial[†]	< 1600 Low elevation[†]
Gerbillus nigeriae	Omnivorous*[†]	Semi-arid Sahel[†]	Arid	24[‡]	Fossorial[†]	Low elevation < 1000
Desmodillus auricularis	Omnivorous*[†]	Arid*[†‡]	Arid	46.1[‡]	Fossorial[†]	< 1600 Low elevation[†]

*Skinner & Chimimba (2005).

[†] Happold (2013).

[‡] Monadjem et al. (2015).

[§] Baxter et al. (2017).

mammals (West, 1985; Manoussaki et al. 2008; Vater & Kössl, 2011); (2) to test the correlation between tympanic bulla size vs. cochlear parameters (see Material and methods) in three gerbils and seven Otomyini species; and (3) to test the association of bullar and cochlear parameters with environmental variables (Alhajeri et al. 2015). Following on from these objectives, we predict that the cochlea should scale with body size and bulla size (i.e. hypertrophy of the bulla means hypertrophy (i.e. enlargement) of the cochlea, or some aspects of it). In addition, we predict that both the bullar and cochlear morphology should vary because of phylogeny [i.e. a significant phylogenetic signal between the two subfamilies (Gerbillinae and Murinae) and the two tribes within Gerbillinae], body size (i.e. an increase in cochlea and bulla size with body mass) and environmental factors (i.e. a significant inverse correlation between bullar and cochlear measurements with mean annual rainfall due to hypertrophy in species from low rainfall areas associated with deserts and a significant positive correlation of the same measurements with elevational range).

Materials and methods

Study samples

The present study is based on micro-focal X-ray computed tomography (micro-CT) data obtained for 110 dry skulls of known sex (see Table 2) representing Otomyini and Gerbillinae curated at the Ditsong National Museum of Natural History (Pretoria) and Muséum National d'Histoire Naturelle (Paris). Most of the specimens were adults, as estimated by their molar lamina wear (Otomyini: Taylor & Kumirai, 2001; Gerbillinae: Bates, 1985). On rare occasions where no other specimens were available, specimens from younger adult age classes [e.g. Class 3 = subadult (see Taylor & Kumirai, 2001) in Otomyini] were also used. All the specimens housed in the Ditsong National Museum of Natural History in Pretoria were scanned at the South African Nuclear Energy Corporation (NECSA) tomography centre, using the X-Tek (Metris) H225L industrial micro-XCT scanner. The specimens housed at the Muséum National d'Histoire Naturelle, Paris, France (MNHN), were scanned with the Phoenix Nanotom 180 scanner from the FERMAT Federation at the Centre Inter-Universitaire de Recherche et d'Ingénierie des Matériaux (CIRIMAT) in the University of Toulouse Paul Sabatier. Their isometric voxel size ranged from 19 to 23 μm. Scanner settings of 100–130 kV and 100–180 μA were used.

Phylogenetic sampling and analysis

For the seven Otomyini and three Gerbillinae species included in this analysis (see Table 2) the taxonomy followed Wilson et al. (2017) and Pavlinov (2008). Cytochrome b sequences used here were downloaded from GenBank and one sequence per species was used. The sequences were first aligned with CLUSTALW and a phylogram tree based on the maximum composite likelihood method (Tamura et al. 2004) was generated using MEGA7 (Kumar et al. 2016) software, with an assumption that all the species have been identified correctly (Alhajeri et al. 2015). A neighbour-joining phylogenetic tree (Saitou & Nei, 1987) was generated to test for

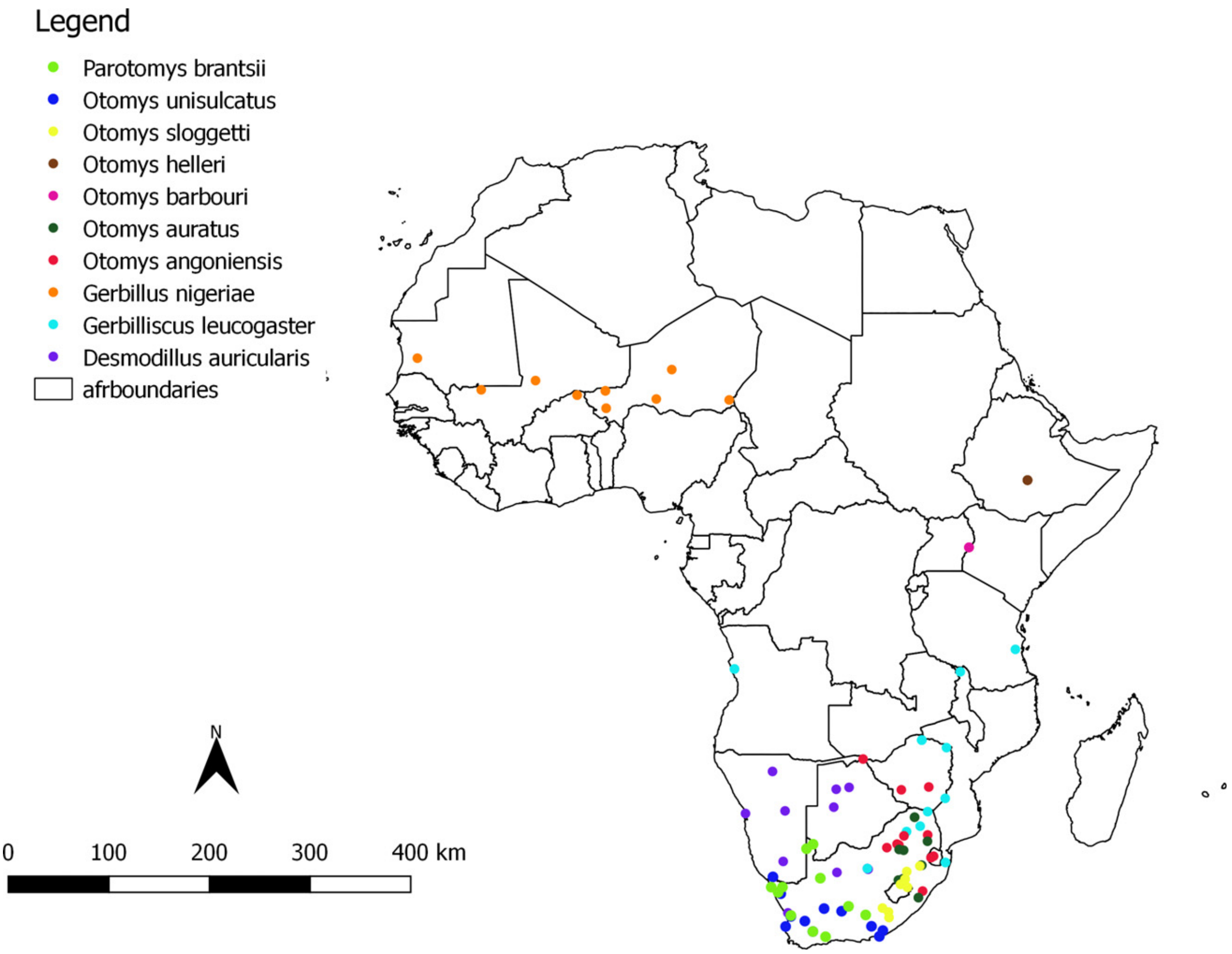


Fig. 1 Geographical distribution map of all 10 species based on locality coordinates of specimens included in this study and another related study employing linear cranial measurements (A. Nengovhela unpubl. data). Coordinates were obtained from the specimen labels; where there none, locality names were used to search for one using Google Earth/Maps and Geonet gazetteer Southern Africa.

phylogenetic signal among our samples (Supporting Information Fig. S1).

The phylogenetic signal (i.e. the tendency for related species to resemble one another) was computed by calculating the parameter lambda (λ; Pagel, 1999) under a Brownian model for each trait [cochlear parameters, body mass and bulla centroid size (bullaCS)] separately on the entire sample using the 'Geiger' package in R (R Development Core Team, 2015). Pagel's λ varies between 0 (trait values independent of phylogeny) and 1.0 (trait values proportional to time of shared evolution under a Brownian model). The phylogenetic signal test is performed under two possible null hypotheses that $\lambda = 0$, or that $\lambda = 1$ (Supporting Information Table S2). The entire sample was selected because it can be difficult to carry out these calculations on small samples (Braga et al. 2015). For a detailed description of the procedure followed in this analysis, see http://www.anthrotree.info/wiki/projects/pica/The_AnthroTree_Website.html and Braga et al. (2015).

Bulla data collection

The tympanic bulla semi-landmarks, defined as landmarks on smooth curves or surfaces positioned along the curvature that cannot be identified and that are thus estimated (Mitteroecker & Gunz, 2009), were digitised from the ventral outer edge of the cranial in 3D with Avizo 8.0 (Visualization Sciences Group, www.vsg3d.com). Semi-landmarks were used, as the auditory bulla lacks clear homologous landmarks. As most of the skulls were slightly damaged, the whole bulla was then considered, including the bony external auditory meatus. Therefore, we assumed that the relative contribution of bony external meatus to middle ear components in the bulla is the same in each species. The semi-landmarks were placed in a clockwise order, starting from the anterior junction between the bulla and the internal pterygoid process (Alhajeri et al. 2015; Fig. 2). A varying number of points were used with the 'B-Spline' module in Avizo. These points were then saved in 'ASCII' format and imported into R 3.2.1 (R Development Core Team, 2015) in order to transform them into a fixed number of equally spaced points (200). Generalised Procrustes analysis (GPA) was conducted to obtain bulla centroid sizes (CS, defined as the sum of the squared distances from the centroid to each individual semi-landmark of the bulla; Rohlf & Slice, 1990) and shape coordinates were discarded. CS obtained from GPA on each specimen was averaged to estimate the average species size in R (R Development Core Team, 2015) (Claude, 2008).

Table 2 Composition of samples used in this study.

Species	*n*	Country (locality)	Collections	Sex (M, F)
Otomyini				
Otomys angoniensis	11	South Africa, Zimbabwe, Swaziland, Zambia	Ditsong*	(6, 5)
Otomys auratus	11	South Africa	Ditsong*	(5, 6)
Otomys unisulcatus	11	South Africa	Ditsong*	(6, 5)
Otomys helleri	09	Ethiopia	MNHN†	(4, 5)
Otomys sloggettii	11	South Africa, Lesotho	Ditsong*	(6, 5)
Otomys barbouri	07	Uganda	MNHN†	(5, 2)
Parotomys brantsii	11	South Africa	Ditsong*	(5, 6)
Gerbillinae				
Gerbilliscus leucogaster	16	Zimbabwe, South Africa, Malawi, Tanzania, Angola	Ditsong*, MNHN†	(8, 8)
Desmodillus auricularus	11	South Africa, Botswana, Namibia	Ditsong*	(5, 6)
Gerbillus nigeriae	12	Mauritania, Burkina Faso, Niger, Mali	MNHN†	(6, 6)

n, number of individuals; M, male; F, female.
*Ditsong National Museum of Natural History, Pretoria.
†Muséum National d'Histoire Naturelle, Paris.

Cochlea and oval window data processing

Avizo 8.0 was also used to segment and reconstruct in 3D the cochlea and oval window fossa. The left bony labyrinth was used; in cases where it was damaged, the right one was used instead. The modelisation of the cochlea and oval window followed methods used in Braga et al. (2013, 2015) and Gunz et al. (2012) (Fig. 3). To document the cochlea variation within our samples, five cochlea parameters were calculated from the semi-landmark coordinates placed on the external length of the cochlea (Fig. 3) using matlab r2013a v8.1 (Mathworks) software. These parameters included the external cochlea length (ECL), number of turns (TUR), relative cochlea length (RECL), the curvature gradient (CUR) and oval window area (OWA); see Braga et al. (2013, 2015) for an illustration. For species values means of these parameters, see Table 3 and for raw data see Table S1.

Environmental data extraction

Each species habitat was categorised based on its distribution and preferred habitat history (see Table 1). To calculate aridity index, we first downloaded bioclimatic variables from WORLDCLIM (Hijmans et al. 2005) using arcgis based on the species geographical distribution. This was done by cross-referencing geographical localities from the range distribution map (see Fig. 1) of each species with the WORLDCLIM database. We downloaded Bio 1 (Annual Mean Temperature), Bio 9 (Mean Temperature of Driest Quarter), Bio 12 (Annual Precipitation), Bio 17 (Precipitation of Driest Quarter) and elevation. Bio 1, 9, 12 and 17 were used to calculate the aridity index using the following equation:

$$\mathrm{AI} = \frac{\frac{P}{T+10} + \frac{12p}{t+10}}{2}$$

where P is the mean annual rainfall in millimetres, T is the annual mean temperature in degrees Celsius, p is the average rainfall of the driest month in millimetres, and t is the average

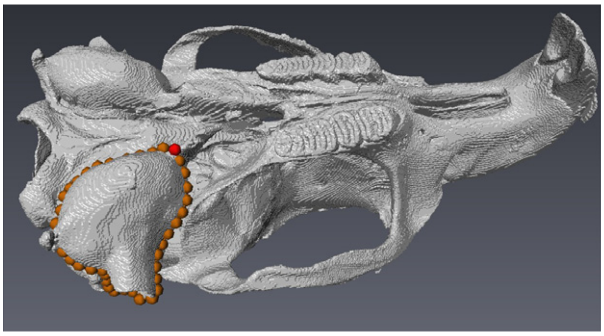


Fig. 2 Position of bulla semi-landmarks used in the geometrical morphometric analyses, to obtain centroid size of the bulla.

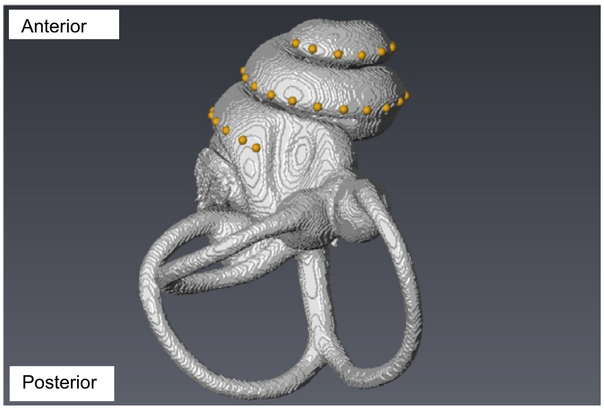


Fig. 3 Position of cochlea semi-landmarks used to calculate five cochlear parameters with the information on the orientation of the inner ear in relation to the position of the skull.

Table 3 Species mean and standard deviations for each cochlear parameter and bulla centroid size.

Species names	RECL (mm)	OWA (mm^2)	CUR	ECL (mm)	TUR	bullaCS
O. angoniensis						
Mean	6.08	0.38	1.38	11.78	1.94	50.02414
SD	0.27	0.03	0.06	0.81	0.06	3.04
O. auratus						
Mean	6.48	0.39	1.42	13.23	2.05	51.18687
SD	0.38	0.03	0.09	0.64	0.10	1.63
O. unisulcatus						
Mean	6.3	0.47	1.43	13.32	2.12	56.40981
SD	0.25	0.07	0.1	1.05	0.21	6.96
O. helleri						
Mean	6.03	0.4	1.32	10.66	1.77	52.62486
SD	0.25	0.03	0.06	0.86	0.11	4.62
O. sloggettii						
Mean	6.21	0.47	1.29	11.89	1.91	52.43497
SD	0.37	0.44	0.07	1.07	0.08	2.81
O. barbouri						
Mean	6.00	0.37	1.32	10.96	1.83	48.8853
SD	0.14	0.04	0.06	0.9	0.15	3.74
P. brantsii						
Mean	6.76	0.69	1.29	15.27	2.26	75.10032
SD	0.24	0.05	0.06	0.72	0.1	2.39
G. leucogaster						
Mean	5.36	0.49	1.5	13.13	2.45	60.67969
SD	0.25	0.03	0.11	1.14	0.17	3.24
G. nigeriae						
Mean	5.12	0.37	1.28	10.64	2.08	50.40225
SD	0.16	0.02	0.05	0.79	0.13	2.16
D. auricularis						
Mean	6.02	0.83	1.53	13.75	2.29	75.11491
SD	0.18	0.05	0.14	0.76	0.13	2.53

temperature of the driest month in degrees Celsius (Alhajeri et al. 2015). The aridity index is unitless, with low aridity index value equating to a drier environment (Baltas, 2007).

Statistical analyses

Principal component analysis (PCA) was used to explore the relationship of cochlear parameters among our samples with R (R Development Core Team, 2012). We used the R 'Geiger' and 'phytools' packages for phylogenetic bivariate linear regressions (PGLS) and non-phylogenetic (GLS) regressions of log-transformed mean species values for cochlea parameters and body mass to account for phylogeny and allometry. The correlation between the bullaCS and cochlear parameters was also tested with non-phylogenetic (GLS) general least-squares regression models in R. The relationship of bullaCS and cochlear parameters with aridity index, elevation and habitat was also tested with GLS.

Results

Cochlear variation among our samples (Otomyini and Gerbillinae)

For the variability of the cochlear variables among the species, one-way multivariate analysis of variance (MANOVA) revealed a significant difference between the species (Wilks' $\lambda = 0.0008$, $F_{45,432.5} = 37.36$, $P < 0.00001$). The interspecies pairwise differences using Tukey's and Mann–Whitney pairwise tests are reported in Supporting Information Table S4, Bonferroni-corrected at $P = 0.001$.

The PCA patterns between species with five (Supporting Information Fig. S2) and three variables (Fig. 4) were similar, and to prevent redundancies (as RECL = ECL/TUR), PCA with only three cochlear variables (OWA, RECL and CUR) was performed (Fig. 4). In this case, the first two principal components (PC1 and PC2) explained 46.31 and 37.08% of the variation, respectively. The three arid species are separated/isolated from the other species when PC1 and PC2 are considered together. Although there is overlap of the *Otomys* species on PC1; *O. unisulcatus* and *O. barbouri* show no overlap (Fig. 4). The PC loadings show that OWA, RECL and CUR are negatively correlated with PC1, with OWA having the highest correlation (Supporting Information Table S3). Though OWA shows higher loadings, other parameter loadings are still high, meaning it is the general cochlear size that is reflected in PC1. PC2 is a 'shape vector' contrasting CUR (positive high loading) with RECL (negative high loading; Table S3). Individuals grouping at higher

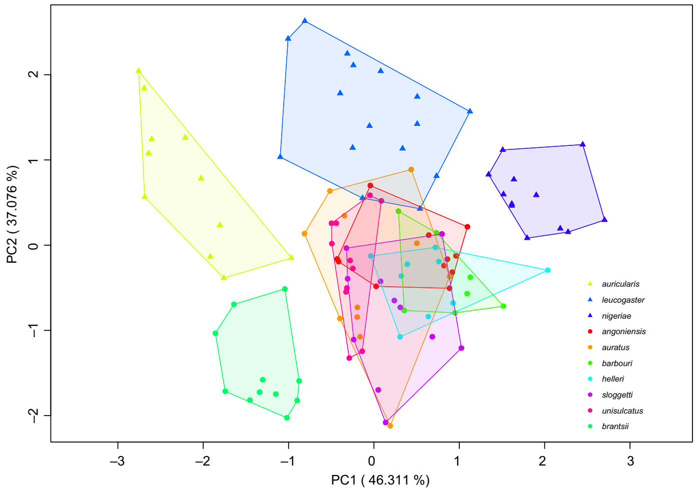


Fig. 4 Principal component analysis of only CUR, OWA and RECL measured among our studied species. Triangles = gerbils; circles = laminate-toothed rats.

positive scores of PC2 therefore have relatively tightly coiled cochlea, i.e. a steeper gradient of curvature. Although there is considerable overlap on PC2, the gerbils (*D. auricularis*, *G. leucogaster* and *G. nigeriae*) group towards the top of the PC plot compared with Otomyini, showing more tightly coiled cochlea (Fig. 4).

Phylogenetic signal and allometry

Only for body mass did we obtain a high phylogenetic signal that was significantly different from 0 at 5% level ($P = 0.0203$, Table S2); however, this is not surprising as body mass is well known for its high phylogenetic signal in mammals (Blomberg et al. 2003; Kamilar & Cooper, 2013). In our study, the two main clades (Gerbillinae and Murinae) were highly divergent in body mass, as gerbils are generally much smaller than Otomyini rodents.

Phylogenetically controlled regressions indicated the absence of any significant allometric associations between cochlea (OWA, CUR and RECL) or bullaCS and body mass ($P > 0.05$, Table 4, Fig. S3). For non-phylogenetic GLS regressions, OWA, CUR and bullaCS showed no significant associations with body mass. However, RECL scaled to body mass with a negative allometry ($r^2 = 0.53$, $P = 0.017$, Table 4), larger species having relatively shorter cochleae. However, looking at Fig. S3 linear regressions, *G. nigeriae* seems to be an outlier; therefore, we also ran an analysis without this species. After removing *G. nigeriae,* RECL and CUR were not significantly correlated with body mass ($P > 0.05$). However, OWA and bullaCS were scaled to body mass with a negative allometry ($r^2 = 0.61$, $P = 0.013$; $r^2 = 0.48$, $P = 0.038$, respectively; Table 4), larger species having relatively smaller OWA and bulla. Gerbils are distinctly smaller than laminate-toothed rats but have a proportionally larger RECL (Fig. S3A), bigger OWA and bulla, resulting in significant results when inter-family comparisons were included.

In the case of the remaining variable CUR, phylogenetic correction considerably improves the association and slope between this variable and body mass (although still non-significant). Within each of the two subfamilies, CUR shows an association with body mass, although in both cases, these were non-significant based on separate PGLS analyses (results not shown; Fig. S3C). As both families display similar ranges of values for CUR, when data from both families are combined there is an almost horizontal regression line (Fig. S3C). This is the complete opposite of the situation with respect to RECL, where distinct inter-family differences in both body mass and RECL exist (Fig. S3A).

Associations between bullaCS, cochlear parameters and environmental variables

Although maximum likelihood (ML) tests of lambda coefficients showed lack of phylogenetic signal in cochlea and bulla variables, we noted the above differences in the body mass regressions of some bullar/cochlear variables between the Gerbillinae and Murinae (Otomyini). For this reason, thereafter we conducted separate analyses for combined data and for each subfamily. GLS showed non-significant correlations of RECL and CUR with bullaCS (Table 5, Fig. S4AC). However, the GLS of RECL vs. bullaCS in Otomyini showed a significant correlation (Otomyini, $r^2 = 0.67$, $y = 0.870 + 0.241x$, $P = 0.024$; Supporting Information Fig. S4A). For all species and for Otomyini only, there were significant correlations between OWA and bullaCS (all species, $r^2 = 0.94$, $y = -7.386 + 1.642x$, $P < 0.0001$; Otomyini, $r^2 = 0.94$, $y = -6.476 + 1.416x$, $P = 0.0003$; Fig. S4B).

BullaCS was not significantly correlated with either the aridity index ($P > 0.05$) or elevation (Table 5, Supporting

Table 4 Results for the non-phylogenetic and phylogenetic bivariate linear regressions to investigate the relationship between log-transformed mean species values for cochlear parameters, body mass (BodyM) and bulla centroid size (bullaCS). *G.n.* = *Gerbillus nigeriae*.

Non-phylogenetic

Dep/Indep	r^2	Adj r^2	P	Intercept	Slope	Equations
OWA/BodyM	0.03	−0.09	0.64	−0.363	−0.09	$y = -0.363 - 0.09x$
OWA/BodyM_minus *G.n*	0.61	0.55	0.013*	2.483	−0.715	$y = 2.483 - 0.715x$
RECL/BodyM	0.53	0.47	0.017*	1.275	0.119	$y = 1.275 + 0.119x$
CUR/BodyM	0.001	−0.12	0.93	0.297	0.004	$y = 0.297 + 0.004x$
bullaCS/BodyM	0.03	−0.09	0.6	4.279	−0.056	$y = 4.279 - 0.056x$
bullaCS/BodyM_minus *G.n*	0.48	0.41	0.038*	5.769	−0.383	$y = 5.769 - 0.383x$

Phylogenetic

Dep/Indep	P	Intercept	Slope	Equations	AIC
OWA/BodyM	0.34	−0.625	−0.001	$y = -0.625 - 0.001x$	7.423
RECL/BodyM	0.11	1.362	0.096	$y = 1.362 + 0.096x$	−23.283
CUR/BodyM	0.29	0.083	0.06	$y = 0.083 + 0.06x$	−24.013
bullaCS/BodyM	0.89	4.156	−0.022	$y = 4.423 - 0.022x$	−2.733

*Significant correlations (at the 5% level).

Table 5 Results for the non-phylogenetic bivariate linear regressions to investigate the relationship between cochlear parameters and bulla centroid size (bullaCS); bullaCS and cochlear parameters with environmental variables.

Dep/Indep	r^2	Adj r^2	P	Intercept	Slope	Equations
OWA/bullaCS	0.94	0.93	<.0001*	−7.386	1.642	$y = -7.386 + 1.642x$
RECL/bullaCS	0.07	−0.04	0.5	1.239	0.138	$y = 1.239 + 0.138x$
CUR/bullaCS	0.16	0.06	0.3	−0.321	0.158	$y = -0.321 + 0.158x$
bullaCS/Arid	0.27	0.18	0.12	4.117	−0.072	$y = 4.117 - 0.072x$
bullaCS/Elev	0.12	0.01	0.3	4.491	−0.065	$y = 4.491 - 0.065x$
OWA/Arid	0.20	0.10	0.2	−0.643	−0.105	$y = -0.643 - 0.105x$
RECL/Arid	0.08	−0.03	0.4	1.772	0.020	$y = 1.772 + 0.020x$
CUR/Arid	0.05	−0.07	0.5	0.33	−0.012	$y = 0.331 - 0.012x$
OWA/Elev	0.05	−0.07	0.5	−0.238	−0.075	$y = -0.238 - 0.075x$
RECL/Elev	0.19	0.09	0.2	1.497	0.043	$y = 1.497 + 0.043x$
CUR/Elev	0.06	−0.06	0.5	0.441	−0.018	$y = 0.441 - 0.018x$

*Significant correlations (at the 5% level).

Information Fig. S5AB), indicating that among our samples neither elevation nor aridity index influences the size of the bulla. However, after removing *G. nigeriae* the correlation between bullaCS and aridity index becomes significantly inversely correlated ($r^2 = 0.604$, $y = 4.207 - 0.120x$, $P = 0.01$), indicating that bullae were larger in more arid environments (Fig. S5A). Analysis of variance (ANOVA) indicated that desert species (in this case both arid and semi-arid, see Table 1) had a significantly greater bullaCS compared with mesic species ($F = 6.652$, $P = 0.033$; Table 6; Fig. S5C).

RECL, OWA and CUR were not significantly correlated with aridity index when all species were considered

Table 6 Results for the ANOVA investigating the relationship between cochlear parameters, bullaCS and habitat. *G.n.* = *Gerbillus nigeriae*.

Dep/Inde	F	P
OWA/habitat	3.821	0.09
OWA/habitat_minus *G.n.*	9.85	0.02*
RECL/habitat	0.77	0.41
CUR/habitat	0.86	0.38
bullaCS/habitat_with *G.n.*	6.652	0.033*

*Significant correlations (at the 5% level).

(Table 5, Supporting Information Fig. S6). Again removing *G. nigeriae* from all the analyses, we only found a significant inverse correlation of OWA with aridity index ($r^2 = 0.56$, $y = -0.476 - 0.193x$, $P = 0.02$), indicating that OWA was larger in more arid environments (Fig. S6B). A non-significant correlation of RECL, OWA and CUR with elevation (Table 6, Supporting Information Fig. S7) was also observed. The ANOVA of OWA, RECL and CUR indicated a non-significant association with habitat ($P > 0.05$, Table 6; Supporting Information Fig. S8); however, a separate ANOVA of all species minus *G. nigeriae* indicated that arid species had significantly greater OWA compared with mesic species ($P < 0.05$, Table 6).

Discussion

Bullar and cochlear covariation in desert-adapted gerbils and laminate-toothed rats

Morphological variations in the cochlea have been documented in a number of species, with different cochlear features being used to make predictions about hearing capabilities (Braga et al. 2015). West (1985) demonstrated that basilar membrane length (effectively ECL) can be used to predict the values of upper and lower limits of hearing (being inversely correlated with both), and the number of cochlear turns (TUR) can be used to predict octave range (positive correlation). Similar observations were confirmed by Vater & Kössl (2011), and Manoussaki et al. (2008) showed a strong correlation of CUR with low-frequency hearing. Rosowski & Graybeal (1991) and Moggi-Cecchi & Collard (2002) demonstrated that OWA (proxy of stapedial foot plate) is correlated with the range of audible frequencies, with larger OWA correlated with low-frequency and smaller OWA with high-frequency sound detection.

In this study, we assessed the variation of the cochlea in relation to the tympanic bulla of Otomyini and Gerbillinae based on the above-mentioned features, and assessed the effect of environment, phylogeny and body size on the cochlea and bulla. Our analyses show some differences in the morphometry of the cochlea that can shed some light on the hearing capabilities of the investigated species. Two specialist arid-adapted species (*D. auricularis* and *P. brantsii*) from diverse murid subfamilies are clearly distinguishable from mesic and semi-arid taxa of both subfamilies both in their gross cochlea dimensions on PC1 (mostly particularly oval window area) and in general bulla size (extreme hypertrophy). Our findings are in line with previous studies that documented the distinctness of the auditory organ (be it tympanic bulla, middle ear and inner ear) of desert, subterranean, fossorial and non-desert rodents (Lay, 1972; Webster & Webster, 1975; Lange et al. 2004; Shaffer & Long, 2004; Alhajeri et al. 2015; Mason, 2015, 2016; Tabatabaei-Yazdi et al. 2015). As a large oval window is strongly correlated with sensitivity to lower frequencies (see above), the strong correlation we obtained between oval window and bullaCS ($r^2 = 0.94$) irrespective of phylogeny/subfamily provides indirect evidence that bullar hypertrophy in desert rodents is indeed linked to detection of low-frequency sounds.

Evolution of tightly coiled cochlea in gerbils (CUR)

Even though our results show no phylogenetic signal in the cochlea and bulla based on ML tests of the lambda coefficient (see Table S2), the phylogenetic effect on the cochlea of the two subfamilies cannot be entirely excluded. For example, from PCA, we found that all three species of gerbils have a more tightly coiled cochlea (higher CUR) than the laminate-toothed rats, suggesting that not only is the gross cochlea size important in gerbils, but the cochlear curvature gradient may also be important. As mentioned above, the cochlear curvature gradient (CUR) is thought to relate to low-frequency hearing (Manoussaki et al. 2008). Even though both *P. brantsii* and *D. auricularis* are adapted to the same desert environment through bullar and cochlear ‘hypertrophy’, gerbils may be further adapted through possessing high CUR. These results suggest that *D. auricularis* and other gerbils may use different mechanisms to cope with environmental challenges (including aridity). Gerbillinae is largely characterised by having a hypertrophied bulla (although the degree of hypertrophy varies between species) and occupies mostly arid, open and semi-arid environments (Happold, 2013; Alhajeri et al. 2015), in contrast to Otomyini, whose species are mostly adapted to mesic montane environments (Happold, 2013; Monadjem et al. 2015; Wilson et al. 2017). The possession of tightly coiled cochlea in gerbils could be a legacy of their evolutionary history, being derived from a desert-adapted ancestor, as compared with *Otomys*, whose ancestor was from the Highveld of South Africa (Denys, 2003).

However, even though the cochlea of gerbils is more coiled than that of the laminate-toothed rats, it is not clear whether our findings support Manoussaki et al.’s (2008) argument, as no cochlear coiling had been studied in closely related outgroups of gerbils to see whether the coiling has increased or decreased evolutionarily.

Evolution of relatively long RECL, enlarged OWA and bulla in gerbils and desert-adapted whistling rats

RECL, OWA and tympanic bulla are said to be related to lower and higher frequency thresholds, with mammals with longer RECL, enlarged OWA and bulla being sensitive to lower frequencies and species with smaller sizes of these attributes being sensitive to higher frequencies (Lay, 1972; West, 1985; Moggi-Cecchi & Collard, 2002; Braga et al. 2015). Our results show that distinctly smaller gerbils have proportionately longer RECL, enlarged OWA and bulla compared with larger-sized laminate-toothed rats (negative allometry with body mass). This would suggest that gerbils have a higher sensitivity to lower frequencies than laminate-toothed rats do. In spite of this, extreme desert-adapted individuals (*D. auricularis* and *P. brantsii*) in both tribes deviate from the predicted relationship by having even longer than expected RECL (Fig. S3A) and larger OWA and bullaCS. Our results therefore suggest that gerbils have a greater ability to hear lower frequencies than laminate-toothed rats and, over and above this, extreme desert-adapted gerbils, as well as desert-adapted whistling rats (*Parotomys*), have enhanced auditory sensitivity to low frequencies compared with other members of their respective subfamilies.

Association of cochlear morphology and hearing sensitivity

Gerbils have been reported to use high-frequency ultrasonic calls in shorter distance vocalisations (Holman, 1980; Dempster & Perrin, 1991; Dempster et al. 1991; Dempster, 2018) during encounters between individuals. This follows from the observation that, to accurately localise sound, smaller mammals having short inter-aural distance need to use higher frequency sounds for communication (Heffner & Heffner, 1992; Heffner et al. 2001). We posit then that gerbils (in particular extreme desert-adapted gerbils) have good hearing sensitivity in both low-frequency sounds (e.g. vibrations and low-frequency sounds known to be generated by potential predators such as snakes and owls; Dempster, 2018), as suggested by our morphological data, and also in high-frequency sounds (i.e. ultrasonic sounds used in conspecific communication). This kind of auditory sensitivity has also been detected in the gerbil *Meriones unguiculatus* (Ryan, 1976) and in *Dipodomys merriami* from the family Heteromyidae (Heffner & Masterton, 1980). However, it is not clear whether the gerbils in our study follow the *M. unguiculatus* and *D. merriami* frequency trends (i.e. including a broad range of good sensitivity in the middle), as no audiograms are available for our species. The two Heteromyidae rodents are known to use low-frequency foot drumming (Randall, 2001); however, whether this is solely for communication with conspecifics (warning in the presence of predators) or is used to deter predators or both is still debatable.

All southern African gerbil species investigated so far use high-frequency ultrasonic vocalisations for short-range conspecific communication; however, while occasional foot drumming was observed in captivity, their functionality has not yet been discussed. Foot drumming was not observed specifically in *D. auricularis* colonies that have been observed in captivity, even though it was considered likely for this species to use foot drumming to communicate over long distances (Dempster & Perrin, 1994; Dempster, 2018). In the case of *P. brantsii*, vocal alarm calls are in relatively low audible frequencies (Le Roux et al. 2002) and no information about foot drumming in this species has been found. Thus, as foot drumming is known for gerbils (even though not observed in *D. auricularis*) and not for *Parotomys* species, this could explain the cochlear adaptation of gerbils to lower frequencies as compared with *Parotomys*.

In conclusion, our data cannot decisively support either the communication or the predator avoidance hypothesis as no conclusive data exist pertaining to low-frequency long-distance communication of *D. auricularis* and *P. brantsii.* Even though increased CUR is generally associated with lower frequency hearing, it may be that in gerbils, increased CUR is not adapted to hearing *per se* but could be a structural constraint of the smaller head size of gerbils compared with laminate-toothed rats, allowing more efficient 'packing' of the basilar membrane (West, 1985).

Environmental correlates of cochlear and bullar characters

After correcting for phylogeny and body size, we are left with environmental factors that we predict would impact the morphology of bulla and, in turn, cochlea. The impacts of aridity, elevation and habitat type on the bullar morphology of rodents has long been recognised, with bullar inflation correlated with deserts, high elevation and open microhabitats (Lay, 1972; Webster & Webster, 1980; Kotler, 1984; Zhao et al. 2013; Tabatabaei-Yazdi et al. 2014; Alhajeri et al. 2015). Analysing the above-mentioned relations with regard to bulla and cochlea; aridity, elevation and habitat, we can see that there are some conforming data and some exceptions. BullaCS and OWA are shown to be correlated with aridity index and desert habitats. Interestingly, the variability in parameter values is shown to be much higher among arid-region species than among mesic ones in Figs S4C and S7. The plots seem to strengthen our argument for a degree of specialisation of cochlea and bulla in arid-region adapted species. To speculate slightly, it is as if selection is acting on these structures in arid-region species by affecting hearing, and hearing has been shown to be important in arid environments as compared with mesic ones whose vegetation is closed. This may be explained by diversifying/disruptive selection.

Inflated bullae, the middle ear, and cochlear modification are believed to aid in communication with conspecifics or predators through foot drumming, hitting and stomping; however, this observation doesn't seem to apply to our study animals, as no detailed indication of vibrations being produced by the two subfamilies has been documented. However, occasional and unpredictable bouts of foot drumming in captivity have been observed in gerbils (Dempster & Perrin, 1990; Dempster, 2018).

We did not find any correlation between cochlear and bullaCS and elevation, contrary to what has been reported in Zhao et al. (2013; increase of bulla size with altitude in gerbils); Tabatabaei-Yazdi et al. (2015; positive correlation of bulla size with elevation in jirds) and Liao et al. (2007; who instead found a decrease in bulla size with increasing altitude in Daurian pikas, Ochotonidae). Our observed trend of no change refutes our prediction that if openness of the environment is a feature of high elevation, then alpine environments should show some response in terms of bullar size and cochlear modification, as high elevations are mostly composed of open habitats similar to desert environments. The increase in bullar size is also said to compensate for a reduction in oxygen partial pressure and strong winds, which are known to impair auditory acuity at high elevations (Zhao et al. 2013). Zhao et al. (2013) believed that a reduction in oxygen partial pressure (hence hypoxia) and strong winds at high elevation may cause a decrease in auditory sensitivity and sound localisation accuracy, therefore the increase in auditory bullar size with elevation is a compensatory adaptation against this selective pressure. We included three Otomyini species known to be mostly confined to very high alpine habitats (> 3000 m) in Ethiopia (*Otomys helleri*), Mt Elgon (*Otomys barbouri*) and the South African high Drakensberg (*Otomys sloggetti*) but none of these species showed any departure in measured cochlear features and bulla from their congeners found at lower elevations (*Otomys angoniensis*, *Otomys auratus*, *Otomys unisulcatus*). It is possible that the highest elevations experienced by these Afroalpine species may still not be sufficient to induce critical levels of hypoxia or hypothermia in these species. However, the elevational range of the species reported above to have inflated bulla at high elevations is lower and their habitats is mostly in arid regions when compared to that of our *Otomys* species. Alternatively, these species may exhibit behavioral and/or physiological adaptations to hypothermia. Since *Otomys* species are typically relatively large and highly sedentary rodents, their metabolic needs may be reduced such that hypoxia does not pose a significant challenge necessitating morphological evolutionary adaptation. An investigation into the extent of possible behavioural or physiological responses to hypothermia in these Afroalpine rodents would be an interesting future study.

Among the gerbils examined here, it seems like *D. auricularis* is the only species that is showing marked bullar and cochlear hypertrophy. Although occurring in sandy semi-arid Sahel habitats in West Africa, *G. nigeriae* does not show a predictable response in either bullar or cochlear dimensions. Similarly, with laminate-toothed rats, only *P. brantsii* shows a marked response, while the semi-arid Karoo bush rat *O. unisulcatus* overlaps completely with other mesic species in the tribe. There could be a threshold between arid and semi-arid habitats, whereby only truly arid habitats evoke an adaptive response. This might be related to cover, as in the case of *O. unisulcatus*, where it was suggested to have relative small bulla size due to it occupying elaborate protective stick-nests (Taylor et al. 2004), as true deserts offer no cover compared with more semi-arid habitats where shrubs and ground cover are usually present. However, *P. brantsii* does occupy semi-arid thickets in the Karoo, where it coexists with *O. unisucatus*, suggesting that vegetation cover may not be such a critical factor. A wider sample of species of both subfamilies including more arid and semi-arid species could be instructive. Our sample sizes of specialised desert species were relatively small.

Concluding remarks

This study concludes that desert-adapted laminate-toothed rats and gerbils both use bullar and associated cochlear hypertrophy, particularly extreme desert species. Gerbils further show tightly coiled cochlea but the significance of this is debatable and may have nothing to do with adaptations to aridity. More work with a large sample size that covers all habitat types of the three tribes (Taterillini, Gerbillini and Otomyini) still needs to be done. Much attention should be focused on the possibility of foot drumming in southern African gerbils, as our results predict that gerbils should have heightened sensitivity to low-frequency sounds.

Acknowledgements

We are grateful to museum curators at the Ditsong National Museum of Natural History, Pretoria (Dr Teresa Kearney) and Muséum National d'Histoire Naturelle, Paris (Prof. Christiane Denys), for allowing access to their collections. We also thank L. Bam, K. Hoffman (NECSA, Pretoria) and B. Duployer (CIRIMAT, Toulouse) for tomographic micro-X-ray acquisitions. This research has been supported by the Erasmus Mundus Programme (AESOP+ project) and National Research Foundation of South Africa (NRF). We acknowledge the NRF, Department of Science and Technology (DST) of South Africa, and the French research federation FERMaT for providing micro-X-ray tomography facilities. Apart from supporting A.N.'s PHD study, the NRF and the DST are acknowledged for their support of the SARCHI Chair on Biodiversity Value and Change hosted by the University of Venda and co-hosted by the Centre for Invasion Biology at Stellenbosch University.

Author contributions

A.N. designed research, collected measurements from the μCT data, performed data analysis/interpretation and drafting of the manuscript. J.B. designed research and provided critical revisions of the manuscript. C.D. provided critical revision of the manuscript and approval of the article. F.d.B. and C.T. helped with the scanning of CT data. P.J.T. designed the research, assisted in data analysis/interpretation and provided critical revisions of the manuscript.

References

Alhajeri BH, Hunt OJ, Steppan SJ (2015) Molecular systematics of gerbils and deomyines (Rodentia: Gerbillinae, Deomyinae) and a test of desert adaptation in the tympanic bulla. *J Zool Syst Evol Res* **53**, 312–330.

Baltas E (2007) Spatial distribution of climatic indices in northern Greece. *Meteorol Appl* **14**, 69–78.

Bates PJJ (1985) Studies of gerbils of genus *Tatera:* the specific distinction of *Tatera robusta* (Cretzschmar, 1826), *Tatera nigricauda* (Peters, 1878) and *Tatera phillipsi* (De Winton, 1898). *Mammalia*, **49**, 37–52.

Baxter R, Taylor P, Child MF (2017) *Otomys auratus*. The IUCN Red List of Threatened Species 2017: e.T110662638A110662647. https://doi.org/10.2305/iucn.uk.2017-2.rlts.t110662638a110662647.en (accessed 24 April 2017).

Blomberg SP, Garland T, Ives AR (2003) Testing the phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.

Braga J, Thackeray JF, Dumoncel J, et al. (2013) A new partial temporal bone of a juvenile hominin from the site of Kromdraai B (South Africa). *J Hum Evol* **65**, 447–456.

Braga J, Loubes J-M, Descouens D, et al. (2015) Disproportionate cochlear length in genus homo shows a high phylogenetic signal during apes' hearing evolution. *PLoS ONE* **10**, e0127780.

Bridelance P (1986) Les podophones de *Psammomys obesus* en milieu naturel: comparaison avec les podophones de *Meriones* (Gerbillidae, Rodentia). *Mammalia* **50**, 145–152.

Claude J (2008) *Morphometrics with R*. New York: Springer.

Cockerell TDA, Miller LI, Printz M (1914) The auditory ossicles of some African rodents. *Zool Anz* **44**, 433–440.

Crumpton N, Kardjilov N, Asher RJ (2015) Convergence vs. specialization in the ear region of moles (Mammalia). *J Morphol* **276**, 900–914.

Dallos P (1970) Low-frequency auditory characteristics: species dependence. *J Acoust Soc Am* **48**, 489–499.

Dempster ER (2018) Ultrasonic vocalizations in 10 taxa of Southern African Gerbilline rodents. In: *Handbook of Behavioral Neuroscience*, vol. **25** (ed. Brudzynski SM), pp. 207–216. Amsterdam: Academic Press.

Dempster ER, Perrin MR (1990) A preliminary description of body maintenance behaviour of four *Gerbillurus* species. *Modoqua* **17**, 41–45.

Dempster ER, Perrin MR (1991) Ultrasonic vocalizations of six taxa of Southern African gerbils (Rodentia: Gerbillinae). *Ethology* **88**, 1–10.

Dempster ER, Perrin MR (1994) Divergence in acoustic repertoire of sympatric and allopatric gerbil species (Rodentia: Gerbillinae). *Mammalia* **58**, 93–104.

Dempster ER, Dempster R, Perrin MR (1991) Behaviour associated with ultrasonic vocalizations in six Gerbilline rodent taxa. *Ethology* **88**, 11–19.

Denys C (2003) Evolution du genre *Otomys* (Rodentia: Muridae) au Plio-Pléistocène d'Afrique orientale et australe. In: *Advances in Paleontology 'Hent to Pantha'*, volume in Honor of Constatin Radulesca and Petre Mihai Samson (eds. Petculescu A, Stiuca E), pp. 75–84. Bucharest: Romanian Academy, Institute of Speleology.

Ekdale EG, Racicot RA (2015) Anatomical evidence for low frequency sensitivity in an archaeocete whale: comparison of the inner ear of *Zygorhiza kochii* with that of crown Mysticeti. *J Anat* **226**, 22–39.

Francescoli G, Quirici V, Sobrero R (2012) Patterns of variation in the tympanic bulla of tuco-tucos (Rodentia, Ctenomyidae, *Ctenomys*). *Acta Theriol* **57**, 153–163.

García-Navas V, Blumstein DT (2016) The effect of body size and habitat on the evolution of alarm vocalizations in rodents. *Biol J Linnean Soc* **118**, 745–751.

Grohé C, Tseng ZJ, Lebrun R, et al. (2016) Bony labyrinth shape variation in extant Carnivora: a case study of Musteloidea. *J Anat* **288**, 366–383.

Gunz P, Ramsier M, Kuhrig M, et al. (2012) The mammalian bony labyrinth reconsidered, introducing a comprehensive geometric morphometric approach. *J Anat* **220**, 529–543.

Happold DCD (2013) *Mammals of Africa. Volume iii: Rodents, Hares and Rabbits*. London: Bloomsbury Publishing.

Heffner RS, Heffner HE (1992) Hearing and sound localization in blind mole rats: *Spalax ehrenbergi*. *Hear Res* **62**, 206–216.

Heffner H, Masterton B (1980) Hearing in Glires: domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. *J Acoust Soc Am* **68**, 1584–1599.

Heffner RS, Koay G, Heffner HE (2001) Audiograms of five species of rodents: implications for the evolution of hearing and the perception of pitch. *Hear Res* **157**, 138–152.

Hijmans RJ, Cameron SE, Parra JL, et al. (2005) Very high-resolution interpolated climate surfaces for global land areas. *Int J Clim* **25**, 1965–1978.

Holman SD (1980) Sexually dimorphic, ultrasonic vocalizations of Mongolian gerbils. *Behav Neural Biol* **28**, 183–192.

Kamilar JM, Cooper N (2013) Phylogenetic signal in primate behavior, ecology, and life history. *Philos Trans R Soc B* **368**, 20120341.

Kotler BP (1984) Risk of predation and the structure of desert rodent communities. *Ecology* **65**, 689–701.

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Mol Biol Evol* **33**, 1870–1874.

Lange S, Stalleicken J, Burda H (2004) Functional morphology of the ear in fossorial rodents, *Microtus arvalis* and *Arvicola terrestris*. *J Morphol* **262**, 770–779.

Lange S, Burda H, Wegner RE, et al. (2007) Living in a 'stethoscope': burrow-acoustics promote auditory specializations in subterranean rodents. *Naturwissenschaften* **94**, 134–138.

Lay DM (1972) The anatomy, physiology, functional significance and evolution of specialized hearing organs of Gerbilline rodents. *J Morphol* **138**, 41–120.

Le Roux A, Jackson TP, Cherry MI (2001a) Does Brants' Whistling Rat (*Parotomys brantsii*) use an urgency-based alarm system in reaction to aerial and terrestrial predators? *Behaviour* **138**, 757–773.

Le Roux A, Jackson TP, Cherry MI (2001b) The effect of changing call duration and calling bouts on vigilance in Brants' Whistling Rat, *Parotomys brantsii*. *Behaviour* **138**, 1287–1302.

Le Roux A, Jackson TP, Cherry MI (2002) Differences in alarm vocalizations of sympatric populations of the whistling rats, *Parotomys brantsii* and *P. littledalei* (Rodentia: Muridae). *J Zool Lond* **257**, 189–194.

Lecompte E, Aplin K, Denys C, et al. (2008) Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a new tribal classification of the subfamily. *BMC Evol Biol* **8**, 199.

Liao J, Zhang Z, Liu N (2007) Effects of altitudinal change on the auditory bulla in *Ochotona daurica* (Mammalia, Lagomorpha). *J Zool Syst Evol Res* **45**, 151–154.

Manoussaki D, Chadwick RS, Ketten DR, et al. (2008) The influence of cochlear shape on low-frequency hearing. *Proc Natl Acad Sci USA* **105**, 6162–6166.

Mason MJ (2015) Functional morphology of rodent middle ears. In: *Evolution of the Rodents: Advances in Phylogeny,* *Functional Morphology and Development* (eds. Cox PG, Hautier L), pp. 373–404. Cambridge: Cambridge University Press.

Mason MJ (2016) Structure and function of the mammalian middle ear. I: Large middle ears in small desert mammals. *J Anat* **228**, 284–299.

Mason MJ, Cornwall HL, Smith ES (2016) Ear structures of the naked mole-rat, *Heterocephalus glaber*, and its relatives (Rodentia: Bathyergidae). *PLoS ONE* **11**, e0167079.

Mitteroecker P, Gunz P (2009) Advances in geometric morphometrics. *Evol Biol* **36**, 235–247.

Moggi-Cecchi J, Collard M (2002) A fossil stapes from Sterkfontein, South Africa, and the hearing capabilities of early hominids. *J Hum Evol* **42**, 259–265.

Monadjem A, Taylor PJ, Denys C, et al. (2015) *Rodents of Sub-Saharan Africa: A Biogeographic and Taxonomic Synthesis*. Berlin: De Gruyter.

Musser GG, Carleton MD (2005) Superfamily Muroidea. In: *Mammal Species of the World: A Taxonomic and Geographic Reference*. 3rd edn (eds. Wilson DE, Reeder DM), pp. 894–1531. Baltimore: Johns Hopkins University Press.

Nikolai JC, Bramble DM (1983) Morphological structure and function in desert heteromyid rodents. *Great Basin Nat Memoirs* **7**, 91–116.

Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884.

Pavlinov IJ (2001) Current concepts of gerbillid phylogeny and classification. In: *African Small Mammals* (eds. Denys C, Granjon L, Poulet A), pp. 141–149. Paris: IRD.

Pavlinov IJ (2008) *A Review of Phylogeny and Classification of Gerbillinae (Mammalia: Rodentia)*. Moscow: Moscow University Publishing.

Pfaff C, Martin T, Ruf I (2015) Bony labyrinth morphometry indicates locomotor adaptations in the squirrel-related clade (Rodentia, Mammalia). *Proc R Soc B* **282**, 20150744.

Plassmann W, Kadel M (1991) Low-frequency sensitivity in a gerbilline rodent, *Pachyuromys duprasi*. *Brain Behav Evol* **38**, 115–126.

Plassmann W, Peetz W, Schmidt M (1987) The cochlea in Gerbilline rodents. *Brain Behav Evol* **30**, 82–101.

Pocock TN (1976) Pliocene mammalian microfauna from Langebaanweg: a few fossil genus linking the Otomyinae with Murinae. *S Afr J Sci* **72**, 58–60.

Prakash I (1959) Hypertrophy of the bullae tympanicae in the desert mammals. *Sci Cult* **24**, 580–582.

R Development Core Team (2015) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available from http://cran.r-project.org/.

Randall JA (1993) Behavioural adaptations of desert rodents (Heteromyidae). *Anim Behav* **45**, 263–287.

Randall JA (1994) Discrimination of footdrumming signatures by kangaroo rats; *Dipodomys spectabilis*. *Anim Behav* **47**, 45–54.

Randall JA (2001) Evolution and function of drumming as communication in mammals. *Am Zool* **41**, 1143–1156.

Randall JA (2014) Vibrational communication: spiders to kangaroo rats. In: *Biocommunication of Animals* (ed. Witzany G), pp. 103–133. Dordrecht: Springer.

Ravicz ME, Rosowski JJ (1997) Sound-power collection by the auditory periphery of the Mongolian gerbil *Meriones unguiculatus*: III. Effect of variations in middle-ear volume. *J Acoust Soc Am* **101**, 2135–2147.

Ravicz ME, Rosowski JJ, Voigt HF (1992) Sound-power collection by the auditory periphery of the Mongolian gerbil *Meriones unguiculatus*. I: middle-ear input impedance. *J Acoust Soc Am* **92**, 157–177.

Rohlf FJ, Slice D (1990) Extensions of the procrustes method for the optimal superimposition of landmarks. *Syst Biol* **39**, 40–59.

Rosowski JJ, Graybeal A (1991) What did *Morganucodon* hear? *Zool J Linn Soc* **101**, 131–168.

Ruggero MA, Temchin AN (2002) The roles of the external, middle, and inner ears in determining the bandwidth of hearing. *Proc Natl Acad Sci USA* **99**, 13206–13210.

Ryan A (1976) Hearing sensitivity of the Mongolian gerbil, *Meriones unguiculatis*. *J Acoust Soc Am* **59**, 1222–1226.

Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol Biol Evol* **4**, 406–425.

Salt AN, Lichtenhan JT, Gill RM, et al. (2013) Large endolymphatic potentials from low-frequency and infrasonic tones in the guinea pig. *J Acoust Soc Am* **133**, 1561–1571.

Sénégas F (2001) Interpretation of the dental pattern of the South African fossil *Euryotomys* (Rodentia, Murinae) and origin of otomyine dental morphology. In: *African Small Mammals* (eds. Denys C, Granjon L, Poulet A), pp. 151–160. Paris: IRD.

Shaffer LA, Long GR (2004) Long low-frequency distortion product otoacoustic emissions in two species of kangaroo rats: implications for auditory sensitivity. *J Comp Physiol A* **190**, 55–60.

Skinner JD, Chimimba CT (2005) *The Mammals of the Southern African Sub-Region*. Cambridge: Cambridge University Press.

Spoor F, Zonneveld F (1998) Comparative review of the human bony labyrinth. *Am J Phys Anthropol* **41**, 211–251.

Stein BR (2000) Morphology of subterranean rodents. In: *Life Underground: The Biology of Subterranean Rodents* (eds. Lacey EA, Patton JL, Cameron GN), pp. 19–61. Chicago: University of Chicago Press.

Tabatabaei-Yazdi F, Adriaens D, Darvish J (2014) Cranial phenotypic variation in *Meriones crassus* and *M. libycus* (Rodentia, Gerbillinae), and a morphological divergence in *M. crassus* from the Iranian Plateau and Mesopotamia (Western Zagros Mountains). *Eur J Taxon* **88**, 1–28.

Tabatabaei-Yazdi F, Colangelo P, Adriaens D (2015) Testing a long-standing hypothesis on the relation between the auditory bulla size and environmental conditions: a case study in two jird species (Muridae: *Meriones libycus* and *M. crassus*). *Mammalia* **79**, 185–200.

Tamura K, Nei M, Kumar S (2004) Prospects for inferring very large phylogenies by using the neighbour-joining method. *Proc Natl Acad Sci USA* **101**, 11030–11035.

Taylor PJ, Kumirai A (2001) Craniometric relationships between the southern African vlei rat, *Otomys irroratus* (Rodentia, Muridae, Otomyini) and allied species from north of the Zambezi River. *Afr Small Mammals* **570**, 161–181.

Taylor PJ, Kumirai A, Contrafatto G (2004) Geometric morphometric analysis of adaptive cranial evolution in southern African laminate-toothed rats (Family: Muridae, Tribe: Otomyini). *Durban Mus Novit* **29**, 110–122.

Tolnai S, Beutelmann R, Klump GM (2017) Exploring binaural hearing in gerbils (*Meriones unguiculatus*) using virtual headphones. *PLoS ONE* **12**, e0175142.

Vater M, Kössl M (2011) Comparative aspects of cochlear functional organization in mammals. *Hear Res* **273**, 89–99.

Webster DB, Webster M (1975) Auditory systems of Heteromyidae: functional morphology and evolution of the middle ear. *J Morphol* **246**, 343–376.

Webster DM, Webster M (1980) Morphological adaptations of the ear in the rodent family Heteromyidae. *Am Zool* **20**, 247–254.

West CD (1985) The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. *J Acoust Soc Am* **77**, 1091–1101.

Wilson DE, Lacher TE Jr, Mittermeier RA (2016) *Handbook of the Mammals of the World.* Volume 6. Lagomorphs and Rodents I. Barcelona: Lynx Edicions.

Wilson DE, Lacher TE Jr, Mittermeier RA (2017) *Handbook of the Mammals of the World*. Volume 7. Rodents II. Barcelona: Lynx Edicions.

Zhao L, Wang Y, Liu N, et al. (2013) Effects of change in altitude on the auditory bulla of midday gerbil, *Meriones meridianus*. *Pak J Zool* **45**, 581–588.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Raw data of the studied specimens with individual sex, cochlear micro-CT measurements, body mass (BodyM) and bulla centroid size (bullaCS).

Table S2 Phylogenetic signal calculated for each cochlear trait and body mass. * Phylogenetic signal not significantly different from $\lambda = 1$ but significantly different from $\lambda = 0$ (at 5%).

Table S3 Variable loadings from PCA of three cochlear parameters for our data.

Table S4 Interspecies RECL and OWA; CUR; TUR and ECL differences using a pairwise *t*-tests applied to each pair of rodent species. Da, *Desmodillus auricularis;* Gl, *Gerbilliscus leucogaster;* Gn, *Gerbillus nigeriae;* Oa, *Otomys angoniensis;* Oau, *Otomys auratus;* Ob, *Otomys barbouri;* Oh, *Otomys helleri;* Os, *Otomys sloggetti;* Ou, *Otomys unisulcatus*; Pb, *Parotomys brantsii.* *Significant Bonferroni-corrected *P*-values at $P = 0.001$.

Fig. S1 Phylogram tree produced by neighbour-joining method with branch length.

Fig. S2 Principal component analysis of all five cochlear features (OWA, RECL, CUR, TUR, ECL) investigated in this study, gerbils (triangles) and laminate-toothed rats (circles).

Fig. S3 Non-phylogenetic and phylogenetic controlled linear regressions between RECL, OWA, CUR, bulla and body mass. (A) RECL for gerbils (black triangles) and Otomyini (red dots) with dashed line (non-phylogenetic) and solid line (phylogenetic) regressions. (B) OWA for gerbils (black triangles) and Otomyini (red dots) with dashed line (non-phylogenetic) and solid line (phylogenetic) regressions. (C) CUR for gerbils (black triangles) and Otomyini (red dots) with dashed line (non-phylogenetic) and solid line (phylogenetic) regressions. (D) Bulla for gerbils (black triangles) and Otomyini (red dots) with dashed line (non-phylogenetic) and solid line (phylogenetic) regressions. * Significant level of 5%.

Fig. S4 Association between bulla CS and (A) RECL; with solid line (all species included) and dashed line (Otomyini only), (B) OWA; with solid line (all species included) and dashed line (Otomyini only), (C) CUR. Gerbils (black triangle) and laminate-toothed rats (red dots). * Significant level of 5%.

Fig. S5 Association between bulla CS and environmental variables (A) aridity index; with solid line (all species included) and dashed line (*nigeriae* removed) (B) elevation, (C) habitat. Gerbils (black triangle) and laminate-toothed rats (red dots). * Significant level of 5%.

Fig. S6 Association between aridity index and cochlear parameters (A) RECL, (B) OWA; with solid line (all species included) and dashed line (*nigeriae* removed), (C) CUR. Gerbils (black triangle) and laminate-toothed rats (red dots). * Significant level of 5%.

Fig. S7 Association between elevation and cochlear parameters for all species (A) RECL, (B) OWA, (C) CUR. Gerbils (black triangle) and laminate-toothed rats (red dots).

Fig. S8 Association between habitat and cochlea parameters for all species (A) RECL, (B) OWA, (C) CUR.