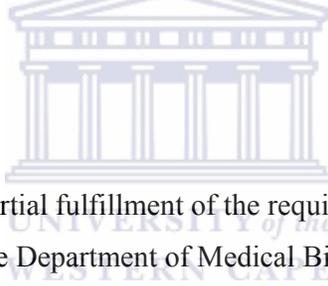


**A COMPARISON OF SOME ASPECTS OF
THE MASTICATORY APPARATUS OF
THE CAPE MOLE-RAT, *Georychus capensis*
WITH THAT OF THE CAPE DUNE MOLE-
RAT, *Bathyergus suillus***

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A thesis submitted in partial fulfillment of the requirements for the degree of
Magister Scientiae in the Department of Medical Biosciences, University of the
Western Cape.

Supervisor: Dr Iona Ismail-Wesso

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Keywords

Angular plate

Bathyergus suillus

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Coronoid process

Comparative anatomy

Digging

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Georychus capensis

Incisors

Mandible

Masticatory apparatus

Masticatory muscles

Masticatory muscles indices

Rodentia

Scratch-digger

Tooth-digger



Abstract

Some African mole-rats of the family Bathyergidae have dramatically different ecological niches which may cause selective anatomical adaptations. *Bathyergus suillus* lives in sandy soil and eats a wide range of food whereas *Georychus capensis* is restricted to the mountainous hard soil and eats mainly geophytes. *Georychus capensis* is considered a chisel-tooth digger in that it uses its incisors to dislodge soil while *Bathyergus suillus* is a scratch-digger that uses both its incisors and large front paws to dislodge soil. The purpose of this study was to compare certain aspects of the masticatory anatomy of *Bathyergus suillus* and *Georychus capensis*. In particular the question that drives this study is: Do the differences in ecology of the two species reflect in the anatomical adaptation of their masticatory apparatus?

Nine whole body specimens of each species were obtained for this study. The masticatory apparatus of each specimen was dissected, examined and analysed. Selected bones of their skulls were investigated to determine their gross morphology. Digitalized images were captured by a high-resolution Olympus digital camera and were analysed by DOCU analysis software, in order to determine the morphometric parameters. In addition, the cleaned skulls of each species were weighed with a chemical balance. In order to make the comparison of the four muscles of mastication more effective than when using only their linear measurements, the mass (in grams) of each skull was divided by the length of each metric traits squared in order to yield their respective indices. Various statistical tests were used.

This study has thus revealed some dissimilarities between the two species. Comparison of the two species reveals that one of the more distinguishing differences between the two is their upper incisors. There are also significant differences in the morphology and dimensions of their angular plates. And the external pterygoid muscle is significantly larger in *Georychus capensis* than in

Bathyergus suillus, there are no significant differences between the others of the masticatory muscles of the two species.

The feeding and foraging activities of *Bathyergus suillus* as well as *Georchus capensis* have close relationship with their lifestyles (digging abilities and adaptations). *Bathyergus suillus* is predisposed to dig with its incisors as well as its large front paws, and the range of food is large, whereas *Georchus capensis* uses its incisors only to dig, and the range of food is limited. Subsequently the skull of *Bathyergus suillus* is bigger than *Georchus capensis*. But, due to the environment of the latter, strong incisors are needed to perform its feeding and digging activities. The investigation thus reveals that the two selected species have successfully adapted their anatomical masticatory elements to their environments.



DECLARATION

I declare that *A comparison of some aspects of the masticatory apparatus of the Cape mole-rat, Georychus capensis with that of the Cape dune mole-rat, Bathyergus suillus* is my own work, that it has not been submitted before for any degree or examination at any other university, and that all the sources I have used or quoted have been indicated and acknowledged as complete references.

Koffi Kouame



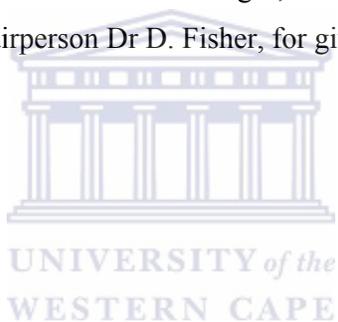
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Signed:

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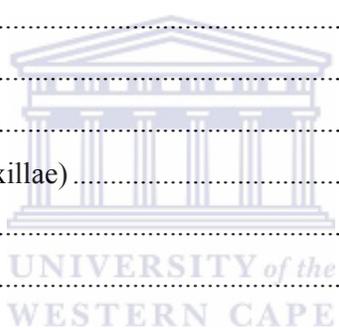
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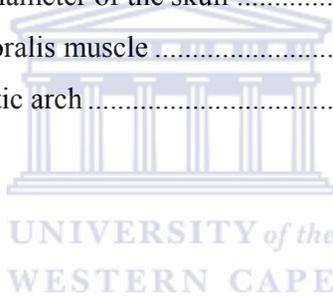
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List of Abbreviations

A = Width of the angular plate
C1 = Width of the condylar process
C2 = Width of the coronoid process
Expt = length of the external pterygoid muscle
It = Index of temporalis muscle
Iexpt = Index of external pterygoid muscle
Iinpt = Index of internal pterygoid muscle
Im = Index of masseter muscle
Inpt = length of the internal pterygoid muscle.....
Ml = length of the masseter muscle
OI = Antero-posterior diameter of the skull
Tl = length of the temporalis muscle
ZA = length of zygomatic arch



Chapter 1

Introduction

[A review of the literature reveals that](#) the gross and functional anatomy of the masticatory apparatus of some rodents has not been completely elucidated. The relative lack of such specific information not only impedes finalization of the generic or systematic classification of these animals, but also the delineation of their presumed natural relationships in terms of [their masticatory apparatus](#).

The masticatory apparatus comprises a variety of structures which operate in unison during chewing and swallowing. Anatomically, the arrangement of these structures does preferably include bones and muscles of the skull to yield adequate, if not superior, functionality.

Although the phylogeny of the order Rodentia is almost fully documented, their classification remains [problematic](#). Suborder is one of the appropriate taxonomic categories available to systematist which derives from the natural or reflects the phylogeny of the forms involved. Some authors divided then the rodents into two suborders *Sciurognathi* and *Hystriognathi* (Carleton, 1984; Chaline & Mein, 1979), while McKenna and Bell (1997) described five suborders of rodents: *Sciuromorpha*, *Myomorpha*, *Omaluromorpha*, *Sciuravida* and *Hystriognatha*.

The evolutionary history of many taxa includes variations in body size and shape. These changes have unequivocal ecological consequences and may have been driven by strong selection pressure (Novacek, 1996; [Schmidt-Nielsen, 1991](#); [Van Valkenburgh, 1994](#)). However, because several anatomical characteristics show allometric relationships in some instances, the emergence of changes in body shape is not necessarily linked to similar phylogenetic forces (Gould, 1974; Harvey & Pagel, 1991; Reeve, 1940). Anatomical features provide a set of important criteria in investigating the many biological aspects of mole-rats, such as classification and behaviour.

It is accordingly imperative to document all such distinctive anatomical traits. This is especially important when characterizing the interrelationships between ontogeny and morphological diversification (Atchley & Hall, 1991). It is now common knowledge that various characteristics when ‘functionally coupled’ usually form biological systems. It has been argued that the evolution of an integrated set of characteristics is highly canalized (Alberch, 1982; Galis, 1993, 1996; Liem, 1973). In other words, it is improbable that a change in one characteristic takes place without a minimum adjustment in another or others, in either a structural or functional sense.

The trophic system of jawed vertebrates is an example of how changes in shape of the jaw system can result in different functional potentialities ([Greaves, 1980](#); Smith & [Savage, 1959](#)). For example, *Ctenomys* (Tuco-tucos) is a highly specious (unique and spectacular) subterranean rodent which has been characterized as a scratch (claw) and tooth-digger (Dubost, 1968; Vassallo, 1998). In rodents, many of the main structural adaptations associated with breaking and removing soil involve changes in osteology and the sites of origin and / or insertion of muscles that improve mechanical efficacy (Casinos, [Quintana & Viladiu, 1993](#); Fernández, Vassallo & Zárate, 2000; Goldstein, 1972; Lessa & Stein, 1992; [Vassallo, 1998](#)). The relationship between in-levers and out-levers has long been recognized as a determinant of functional capabilities (Hildebrand, 1985). This posits the question of how coupled characteristics maintain their function in spite of changes in scale and allometry. In particular, and in addition to its current trophic function, the skull of some *Ctenomys* species itself plays a crucial role as a digging tool during tunnel construction. Moreover, the degree of the anterior projection of incisors in the skull as a characteristic is largely viewed as an adaptation to tooth-digging in several subterranean [rodents](#)’ species (Agrawal, 1967; Hildebrand, 1985; Landry, 1957; Neveu & Gasc, 1999). Furthermore, Lessa and Thaeler (1989) analyzed the structural variation of the digging apparatus in pocket gophers and concluded that these rodents show various degrees of specialization for tooth and claw digging.

Earlier work by Merriam ([1895](#)) led to the proposal of two complementary hypotheses to account for morphological variation among pocket gophers. The

first hypothesis is that the differences in skull shape may relate to distinct modes of mastication. This is borne out by the fact that the skull and jaw shapes are profoundly affected by the size and distribution of jaw muscles. The second hypothesis holds that the different primary directions of jaw movement during chewing may show varying degrees of specialization for digging. In support of the second hypothesis, Merriam (1895) proposed evidence to her findings by describing the development of divergent species of pocket gophers.

African mole-rats of the family Bathyergidae constitute a small category of rodents that spend their entire lives underground. They only come to the surface when their tunnels are flooded, i.e., to search for a new place to burrow or when they are attracted by the smell of food in garbage. A literature search revealed that anatomical information regarding the bathyergids, one of five genera of rodents, is poorly documented. Two members of the family, *Heterocephalus* and *Cryptomys*, are very common to the Western Cape province of South Africa. Due to their unique life histories and ecology, they have received extensive attention and in scientific studies (Bennett & Faulkes, 2000; Lacey, Patton & Cameron, 2000; Nevo & Reig, 1990; Nevo, 1999; Sherman, Jarvis & Alexander, 1991). However, the anatomy of *Bathyergus suillus* and *Georychus capensis* has hardly been reported. But, the feeding behaviour of these two families has been expounded. *Bathyergus suillus* is reported, for example, to prefer to remain in an area where the availability of food is high (Davies & Jarvis, 1985). Davies and Jarvis (1985), also suggested that claw-diggers, such as *Bathyergus suillus* are restricted to sandy soils, whereas modifications for tooth digging allow exploitation of a broad range of soil types.

A comparison of the overall size of the two species indicates that *Bathyergus suillus* is bigger than *Georychus capensis*. However, in considering the sizes of the four main masticatory muscles (masseter, temporalis, external pterygoid and internal pterygoid), it is evident, from earlier observations (Kouame, Leonard & Nyatia, 2006), that the differences between these two species are not so obvious. Likewise, an analysis with regard to the size of some selected components of the

skull did not show conclusively that all the masticatory elements of *Bathyergus suillus* are indeed bigger when compared to those of *Georychus capensis*.

The two selected members of the family Bathyergidae that were selected for this study occupy dramatically different ecological niches (Jarvis & Sale, 1971). *Bathyergus suillus* is limited to soft sandy soil and eats a wide range of food whereas *Georychus capensis* is restricted to the higher rainfall regions of the western and southern Cape. An investigation on the physical characteristics of *Bathyergus suillus* and *Georychus capensis* had shown that these ecological niches would demand different anatomical adaptations to their masticatory apparatus, i.e. features to facilitate efficient feeding (Wood, 1965). *Georychus capensis* is described as a tooth-digger in that it uses its incisors to bite and dislodge the soil, while *Bathyergus suillus* is mainly a scratch-digger that uses both its incisors and large front paws to dislodge soil (Jarvis & Sale, 1971).

One of the aims of this study is to compare the masticatory anatomy of *Bathyergus suillus* and *Georychus capensis*. In particular, it aims to investigate whether there is a correlation between the masticatory apparatus of the two species of the family Bathyergidae and their ecology. The bathyergids that are to be considered here are fossorial (i.e. adapted to digging) and subterranean. As mentioned above. This study aims to establish whether this difference in feeding and foraging behaviour will be reflected in their anatomy – specifically that of their masticatory morphology.

As indicated above the masticatory apparatus of rodents often serve as a criterion for their classification, and information regarding this anatomical feature of the Bathyergidae may therefore be valuable. Another aim of this study is thus to record the distinguishing characteristics of the masticatory elements of *Bathyergus suillus* and *Georychus capensis*. This data could then contribute outstanding data which may assist in the clarification of outstanding taxonomic relationships.

A further aim of this study is to illustrate the comparative masticatory anatomy of the two species. In particular, this study aims to consider whether the differences

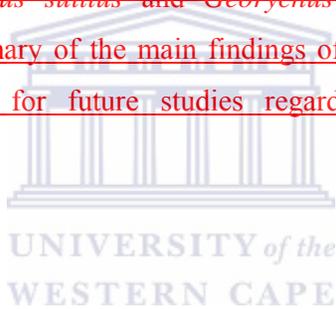
in the masticatory apparatus of the two species, if any, are attributable to their ecology. This study will help us to understand the evolution in small mammals and contribute towards further redesigning and supplementing the classification system of rodents. This investigation links the differences in ecological behaviour to the anatomy of the mandible and further shows how the massive mandibles (45% of skull weight) reflect their biological importance for survival.

In this study, the anatomy of the masticatory apparatus of both species was investigated as follows: Dissection of whole specimens and the identification of specific anatomical features were based on anatomical guides such as that of (Homberger & Walker, 1988; Wahlert, 1974). Morphometric measurements of selected parts of the heads were used to determine the traits of the four main masticatory muscles and the bones directly involved in mastication. These results of of the morphometric analyses of the selected bones and four muscles of mastication were then used to compare the masticatory morphology of the two selected species.

The following description of the thesis chapters indicates how the different aspects related to each phase of the research evolved to achieve the above objectives.

Chapter 2 reviews the classification, distribution, habitat, ecology, feeding and definitely the physical characteristics of rodents in general and mole-rats in particular. It provides an overview of existing literature on the biology and anatomy of *Bathyergus suillus* and *Georchus capensis*. The last part of this chapter focuses onis related to the anatomy of specific some parts of the masticatory apparatus of the Bathyergidea. Chapter 3 outlines the materials that were used and describes the methodologies employed in this study. Eighteen samples were used in total. Fine dissections were performed on each specimen in order to observe the features of the masticatory apparatus. Since the animals of the two species differ in size, and since the masticatory muscles were considered in this study to be those features that may reveal specific adaptations to the ecology of the animals, a new method of calculating 'indices' of individual muscles to accommodate differences in body size, were used. Furthermore, various

~~morphometric and non-morphometric analyses had been applied to some selected muscles and bones of each specimen.~~ In Chapter 4, the selected bones of the skull of each specimen were analyzed separately and described with regard to their anatomical features. In addition, the four main muscles of mastication were depicted in terms of size, origin and insertion. The last part of this chapter covers the descriptive statistics of the measured parameters, metric and non-metric traits of the selected bones of the skull as well as the four main muscles of mastication. Chapter 5 provides a description of the main features of the masticatory bones and muscles of the two species. In addition, it features a comparative ison ~~and~~ discussion of these features; it emphasizes in particular the possible anatomical adaptations each of the two species might have undergone in response to their foraging and feeding behaviour, selected structures of the masticatory apparatus of *Bathyergus suillus* and *Georychus capensis*. This last chapter concludes with a summary of the main findings of this study, a critique thereof and recommendations for future studies regarding *Bathyergus suillus* and *Georychus capensis*.



Chapter 2

Literature Review

2.1 Introduction

Rodents are claimed to be the most numerous species of all mammals. Of the recorded 4206 species of mammals, 1752 (42%) are rodents. Van der Horst (1972) stressed that rodents are not only the direct and indirect vectors of diseases which make them extremely important in medical studies, but they are also important to evolutionary biology, genomics, ecology and agriculture. Although their importance has been recognized by scientists, various aspects of rodents have not been fully recorded and clarified, especially those aspects that are important to taxonomy and details regarding a variety of anatomical features. An important aspect to clarify regarding rodent's anatomy is the jaw structure.

This study focuses firstly, on clarifying and comparing the anatomy of the masticatory apparatus of two rodent's species, of the family Bathyergidae (African mole-rats), viz., *Bathyergus suillus* and *Georchus capensis*. Accordingly, a review of the documented jaw anatomy of rodents will be given here. Secondly, since anatomy of the masticatory apparatus is generally assumed to strongly correlate with behaviour and feeding patterns of rodents in particular, the existing literature pertaining to the habitat, diet and feeding behaviour of rodents will be also reviewed here. To contextualize this information an overview of the classification, distribution, ecology and general anatomy of rodents will first be given.

This chapter concludes with a review of what is currently documented regarding the distribution, anatomy and feeding behaviour of especially the mole-rats *Bathyergus suillus* and *Georchus capensis*.

2.2 Classification and distribution of the Bathyergidae

There are currently five recognized genera of Bathyergidea - four of these genera have relatively low species diversity (Ingram, Burda & Honeycutt, 2003). The Bathyergidea includes the following:

The monotypic genus *Heterocephalus* which is restricted to eastern Africa;

The monotypic genus *Heliophobius* which occurs in eastern and south - eastern Africa;

The monotypic genus *Georychus capensis* which is endemic to South Africa;

The genus *Bathyergus*, which contains two species, namely *Bathyergus suillus* and *Bathyergus janetta*. They are found in Namibia and South Africa and;

The fifth genus, *Cryptomys*, contains 11 recognized species. This group displays a broad, but disjunct distribution extending from Ghana and Nigeria in West Africa to the southern Sudan in east Africa (White, 1983). They also occur from southern Congo and southern Tanzania to the Western Cape Province of South Africa (Bennett & Faulkes, 2000; Burda, 2001; Honeycutt, Allard, Edwards & Schlitter, 1991).

Estimates of the number of families, genera and species of rodents vary. For instance, Vaughan (1972) recorded 34 families, 354 genera and 1685 species while Corbet and Hill (1992) listed 1793 species. By contrast, Tullberg (1899) meticulously split the order into two tribes whereas Gidley and Miller (1918) divided them into five super families.

In some early studies, such as that of Simpson (1945), the classification of rodents was based on differences in skull morphology. These classifications mainly used the size of the zygomatic arch and the origins and insertions of different jaw muscles. For instance Wood (1965) asserted that the difference in origin of various layers of the masseter should serve to distinguish major subgroups of rodents from one another. One should also note that in some mammalian taxonomy, the structure of the masticatory muscles, and particularly the insertion

of the masseter muscle, is used to divide the various rodents into suborders (Brandt, 1855). It is interesting to note that the attachments of the masticatory muscles play an important role in the classification of rodents.

Faulkes, Verheyen, E., Verheyen, W., Jarvis, & Bennett, (2003) emphasized that the classification of the Bathyergidea has been problematic for a long time. Accordingly, there is currently no universal consensus on the the classification of rodents. Faulkes *et al.* (2003) reason that there is now good support for using morphometric parameters and molecular phylogeny for grouping the Bathyergidea with the phiomorph rodents (the Old World lineage of the suborder *Hystricognathi*). The closest relatives of the Bathyergidea are the rock rats (Petromuridae), cane rats (Thyromyidae) and the Old World porcupines (Hystricidae). Faulkes *et al.* (2003) furthermore, observed that the New and Old World *Hystricognathi* probably separated from their common ancestor during the Eocene geological period, 33-49 million years ago. In addition, Faulkes *et al.* (2003) proposed that the Bathyergidae are monophyletic. That is, all taxa can be traced back to a single common ancestor. However, fossil evidence and molecular data indicate an early divergence of *Heterocephalus glaber* from the other genera in the family. Faulkes *et al.* (2003) also observed that the Bathyergidea fossil history is sparse but suggested that they most likely had an ancient African origin. The earliest fossil finds of rodents in east Africa and Namibia, are from the early Miocene—around 25 million years ago (Faulkes *et al.*, 2003)

In another classification done by Faulkes *et al.* (2003), the five modern Bathyergidea genera are grouped into two subfamilies. The one subfamily is the Bathyerginae which contains one genus, *Bathyergus*, with two species, namely *Bathyergus suillus* and *Bathyergus janetta*. They are both characterised by having deeply grooved upper incisors with roots that extend as far as above the molars. They also have enlarged front paws with strong digging - claws which they use for scratch-digging. The other subfamily, the Georychinae contains four genera namely *Georchus*, *Heliophobius*, *Cryptomys*, and *Heterocephalus*. All of these have un-grooved upper incisors and some, like *Bathyergus suillus*, use their front paws for digging. *Georchus capensis*, however has moderately developed weak

claws, and exclusively uses its incisors to dislodge soil. The front paws are used to move earth loosened by the incisors, and the hind feet are broad as *Bathyergus suillus* in most species (Bennett, 1988; Jarvis & sale, 1971).

As seen from above the Bathyergidae family is confined to sub-Saharan Africa. According to Faulkes *et al.* (2003) the Cape dune mole-rats (*Bathyergus suillus*) are endemic to southern Africa. They occur in coastal sandy soils of the south western and Northern Cape and also to southwestern Namibia. The Cape mole-rat (*Georchus capensis*) is endemic to South Africa, mostly occurring in the fynbos vegetation of the southwestern and eastern Cape (Faulkes *et al.*, 2003). The genus *Cryptomys* occur in western, central and southern Africa. The silvery mole-rat (*Heliophobius*) occurs in eastern Africa and the naked mole-rat (*Heterocephalus glaber*) in the arid regions of the Horn of Africa, namely Kenya, Somalia and Ethiopia (Faulkes *et al.*, 2003).

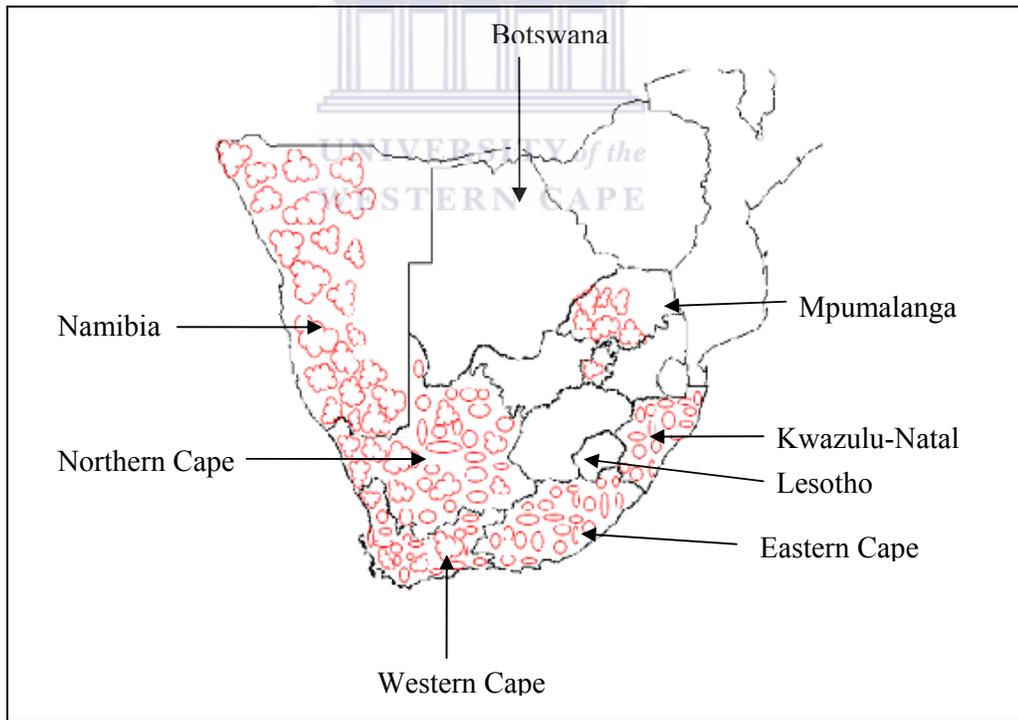


Figure 2.1: A map of Southern Africa indicating the distribution of *Bathyergus suillus* and *Georchus capensis* (*Bathyergus suillus* =  *Georchus capensis* )

2.3 Physical characteristics of the Bathyergidae

Members of Bathyergidae are diggers. Their bodies are fusiform and their size varies from small to medium. Their body mass range from 80 to 600g. Their legs are short and fairly powerful (Bennett & Faulkes, 2000). They have exceptionally loose skin, permitting them to turn around and reverse direction easily in the very narrow spaces of their burrows (Bennett & Faulkes, 2000). Their legs are not as strongly modified as they are in fossorial species such as moles.

The Bathyergidae have small eyes and ears. Bennett and Faulkes (2000) also noted that their vision is poor or not at all (they essentially only differentiate between dark and light). The surface of their eyes may rather serve to detect air movement (as would happen if a normally-sealed burrow entrance were opened). The ears of these rodents lack external pinnae, and their range of hearing is thus more restricted than that of above-ground rodents (Bennett & Faulkes, 2000).

Bennett and Faulkes (2000) analysed the anatomical adaptations of mole-rats and documented that they have various anatomical adaptations for life underground. For instance their limbs are short, their bodies cylindrical in shape, and their heads are robust, ending in flattened pig - like noses. Their streamlined shape and short limbs enable them to move backward and forward with equal ease in the narrow confines of their burrows (Bennett & Faulkes, 2000).

Bennett and Faulkes (2000) also observed that the outer edges of the hind feet of mole - rats are fringed with stiff hairs. These stiff hairs, together with a brush of stiff hairs on their short tails (in all except in the naked mole-rats), help to hold the soil when the animals move it along their burrows (Bennett & Faulkes, 2000).

Because mole-rats live in dark burrows, the sense of touch is important to them. Bennett and Faulkes (2000) offered an explanation about their sensitivity to tactile stimuli. They reckoned that perhaps because these rodents they live in dark environments they seem to rely heavily on their sense of touch. Most bathyergids have a thick and soft pelage which also serves a sensory (tactile) function (Bennett & Faulkes, 2000). In addition, many bathyergids have long sensitive hairs scattered all over their bodies and project above the rest of their hair. These

sensitive hairs are the only hairs present in naked mole-rats (*Heterocephalus glaber*). There are also long, stiff sensory hairs clustered above the eyes and on the front of the face. Bennett and Faulkes (2000) also suggest that rodents (except *Heterocephalus glaber*) use their short tails as tactile organs when they reverse out of their burrows.

The defining characteristics of rodents are (i) a single row of superior chisel-shaped incisors, (ii) inferior incisors that exhibit continuous growth, and (iii) a wide diastema between the incisors and molars which separates the rostral and the caudal portions of the mouth (Feldhamer *et al.*, 1999). The rodents' teeth are uniquely adapted to gnawing and their upper and lower incisors have open roots. The Bathyergidae, as in the case of other burrowing rodents, have their lips close tightly behind their protruding incisors to prevent loose earth from entering the mouth.

Rodents have inherited a distinctive mammalian masticatory apparatus. The masticatory apparatus of mammals is specially designed to aid the ingestion of food and prepare it for swallowing. This is achieved through a fixed upper jaw and moveable mandible that articulates via the TMJ (Anderson & Mathews, 1975). Faulkes *et al.* (2003) described the Bathyergidae as a monophyletic group of subterranean hystricomorph rodents. The masticatory apparatus consists mainly of the temporomandibular joint (TMJ), a zygomatic arch and four muscles of mastication (temporalis, masseter, external and internal pterygoid muscles). The TMJ and associated masticatory elements also come into play in one of the main activities of some mole-rats, viz., burrowing (see below). A detailed review of the rodents' masticatory anatomy appears below under Section 2.6, P.15.

2.4 Habitat and ecology of Bathyergidae

Rodents are only absent from Antarctica and some oceanic islands. Within this large distributional range, rodents have adapted themselves successfully to almost every type of habitat. They display levels of sociality which range from solitary, social, or eusocial, and making them a unique mammalian (Jarvis, Bennett & Spinks, 1998). In this variety of habitats some rodents, such as the mole - rats,

spend their entire lives underground, while others are purely terrestrial, and yet others are almost entirely arboreal.

Bennett and Faulkes (2000) believed that the movement choices that rodents make are influenced by many factors. This includes resource availability which, in turn, can affect whether the rodents search for resources alone or in groups. Subterranean rodents are ideal for examining movement paths because they create burrows that persist for extended periods and thus serve as records of movement. The solitary genera (*Bathyergus*, *Georychus* and *Heliophobius*) tend to be restricted to more mesic areas, whereas the social genera (*Heterocephalus glaber* and some species of *Cryptomys*) can also occur in arid, semi - desert habitats. Their distribution is usually associated with the occurrence of energy rich bulbs, corns and tubers. While these geophytes (plants with underground storage organs) constitute their main food source, they will also eat roots and aerial parts of the plants. The food can either be immediately consumed or stored in a storage area of the burrows.

The naked mole-rat *Heterocephalus glaber* are small, colonial (up to 300 individuals) and eusocial rodents (Jarvis, 1981; Sherman *et al.*, 1991; Sherman, Jarvis, Braude & Grand, 1992). These rats inhabit heavily protected burrows. The large old breeding females make disproportionate, reproductive contributions (Jarvis & Sherman, 2002). That is because evolutionary hypotheses predict that rates of senescence should vary directly with extrinsic mortality and inversely with fecundity. The females thus live much longer (that is, senesce slowly) than would otherwise be expected. Due to this unique life histories and ecology, *Heterocephalus* and *Cryptomys*, have received extensive attention in the literature (Bennett & Faulkes, 2000; Lacey *et al.*, 2000).

Two of the mole-rats' genera, viz., *Cryptomys* appears to be of the most highly social mammal in existence and *Heterocephalus* forming colonies in which most individuals specialize in different tasks, such as defense, digging, food gathering, etc., and forego reproduction (Jarvis & Sale, 1971). Jarvis and Sale (1971), add that different species of mole-rats occur in the same area where they appear segregated by soil type

Mole-rats live in burrow systems that consist of networks of superficial foraging tunnels and a deeper nest complex which contains a toilet area. This physical environment will serve often as food storage area (Bennett & Faulkes, 2000). Burrows are sealed from the surface, and are only opened when excavated soil is disposed on the surface. Consequently, the mole - rats live in a subterranean micro - habitat that is buffered from extremes in temperature and humidity and from predator's small carnivores. In most species (except in *Bathyergus suillus*) the paws are used to loosen the earth (Bennett, 1988; Genelly, 1965; Jarvis & Sale, 1971).

The two largest bathyergids viz., *Bathyergus suillus* and *Georchus capensis* are solitary dwellers. They have relatively shorter burrows than the rest of the family, and in South Africa they are restricted to the higher rainfall regions of the western and southern Cape (Jarvis & Sale, 1971). Their distribution is indicated in Figure 2.1, P.11.

2.5 Feeding adaptations of the Bathyergidae

Nutrition is a central activity of mammals and the methods which they have evolved for catching and processing food, vary. This, according to Rogers (1941), provides a fascinating example of adaptive radiation (that is, the evolutionary diversification of the generalised ancestral form with production of a number of adaptively specialised forms).

Langenbach and Van Eijden (2001) investigated the masticatory systems of mammals and found that the diversity in the morphology of jaw systems is remarkable. Adaptation to diet may play an important role in such morphological variation. For example it contributes to the shape of the jaws and the teeth that the animals bear. Jaws shape differs extensively in groups such as ungulates, carnivores and some other mammals and this relates to feeding (Wolff-Exalto 1951).

Bennett and Faulkes (2000) gave some detailed account of the morphology of skulls of bathyergids. Their findings described the skulls of bathyergids as wide, flat and robustly built, as might be expected in animals that dig with their heads.

The zygomatic arch is heavy, but fairly simple. It also has enlarged angular processes and mandibular fossae. These specialisations may be the result of a need for their enlarged masseters to power the incisors when they are used for digging. Older surveys (Becht, 1953; Kuhlhorn, 1938; Savage & Smith, 1959) of variation in the mammalian jaw system formulated some functional requirements for herbivorous and carnivorous feeding and their consequences for the form of the jaw system. In a major focus and review of morphologies of mammals, Leonard (1985) concluded that: ““morphologies are not distributed randomly in nature, but tend to group in distinctive clusters, correlating phylogenetic relationships””. He posits that: ““similarities may be due to common ancestry or convergent evolution due to adaptation to a similar environment””. The mandibular condyles of mole - rats have various forms and orientations, which permit anterior-posterior and medial-lateral movements of the mandibles relative to the maxillae. It is for these above reasons that mole-rats have a large gape and powerful bite. This arrangement permits a stronger anterior force for gnawing. However, the coronoid process of the jaw is of moderate size.

2.6 Generalised masticatory anatomy of rodents

Scientific studies often compared different species of rodents with regard to their jaw musculature (Gaspard, Liaison & Lautrou, 1976; Fieldler, 1953; Schumacher, 1961; Starck, 1935; Storch, 1968; Turnbull, 1970). Turnbull (1970) also described the function of the anatomy of the masticatory apparatus of 9 diverse rodents. The primary mechanical functions of bones are to provide rigid levers for muscles to pull on and to remain as light as possible to allow efficient locomotion. Turner (1998) states that: ““in order to accomplish these mechanical functions, bones must adapt their shape and construction to make efficient use of material””. Raab and Smith (1990) concurred with the idea that bone mass, shape and strength are regulated by the mechanical forces generated during muscle contraction and physical activity. Due to the tasks performed by the muscles as well as the bones, the masticatory system of mammals has attracted significant attention throughout the 20th century (Langenbach & Van Eijden, 2001). According to Wilhelmus (1980), the masticatory apparatus is a mechanical system, in which muscles

generate forces to cause occlusion, and movement of the mandible.

Thus, the first published studies on the jaw system of rodents focused on the description of the macroscopic morphology of the masticatory muscles and the skull. Myers (1997) mentioned that rodents have large and complex jaw musculature, with modifications to the skull and jaws to accommodate it. This jaw musculature is mainly formed by the four masticatory muscles viz., the temporalis, masseter and external and internal pterygoid muscles. Chewing and gnawing involve all four of these jaw muscles.

Patterns of morphological variation are used by systematists to infer phylogenetic relationships, and by evolutionary morphologists to gain insights into the adaptive significance of particular morphology (Leonard, 1985). Wood (1965) thus presented a synopsis of the evolutionary changes in the masseter muscle of rodents. He stresses that in the earliest and most primitive rodents such as the *Protrogomorphs*, the origin of the masseter muscle was limited to the ventral part of the zygomatic arch, and then the fibres prolonged to insert into the masseteric fossa of the mandible.

Wood (1965) also determined that the arrangement of the masseter as described above, for the most part, pulled the jaw nearly straight up. In concordance with Wood's (1965) axiom, mentioned above, Myers (1997) confirmed that, in rodents, this is done primarily by the masseter muscle. In early studies the masseter was divided into three portions: the masseter superficialis (superficial masseter), the masseter lateralis (lateral masseter), and the masseter medialis or profundus (medial masseter). However, in the current discourse the masseter is divided into a deep masseter muscle and a superficial masseter muscle (Russel, 1994).

All rodents have a particularly large and complex masseter. It not only assists the temporalis muscle in closing the jaw, but also moves the mandible backward and forward during gnawing and grinding. In the course of evolution, different portions of the masseter shifted their origins forward onto the rostrum. Several authors Dominique and Warren (1974) and Wood (1965) emphasized that this change nearly doubled the length of the muscle and greatly augmented the

anterior direction of its pull. This was corroborated by Myers (1997) who affirmed that the masseter muscle of primitive rodents arose near the anterior end of the toothrow. This is indeed the point of origin of the masseter muscle in many rodents, and is referred to as the masseteric tubercle. The fibres of the muscle finish their course by inserting along the lower part of the mandible at the rear. The deep masseter arose from the midportion of the zygomatic arch and is also inserted along the bottom of the mandible towards its rear. The superficial masseter muscle connects the cheekbone with the most posterior lateral part of the mandible.

The pterygoid muscles originate on the sphenoid bone. The muscle fibres run obliquely and laterally to the medial side of the angle of the mandible. The division in rodents of the pterygoid muscles into the external and internal pterygoid muscles was described by Henry and Parson in 1894. These two muscles correspond respectively to the human lateral and medial pterygoid muscles. The contraction of the external pterygoid muscle moves the angle of the mandible to the middle of the upper jaw followed by the sideward movement of the mandible. Bilateral contraction of the internal pterygoid muscles moves the mandibles forward (protraction). This permits chewing (molars grinding against each other). Rodents are unique in that they can chew food on one side only.

In herbivores such as rodents the temporalis muscles and coronoid processes are not very well developed but the ramus of the mandible is. The temporalis muscle originates on the lateral side of the skull and inserts on the coronoid process of the mandible. Jarvis and Sale (1971) analysed the jaw musculature (temporalis, masseter and pterygoid muscles) of several types of mole-rats and found that the heavy jaw musculature fills much of the orbit, and that the strong temporalis muscles are attached to the sagittal crests. The large temporalis muscle, which arises on the cranial roof, inserts on the coronoid process (Vaughan, Ryan, & Czaplewski, 2000). The temporalis generates mainly a vertical force which closes the jaw (Green, 1935). Further selective studies by Sherman *et al.* (1992) revealed that the jaw muscles of *Heterocephalus glaber* (naked mole-rat) constitute 25% of the animal's total muscle mass.

Both the attachment sites and the internal architecture of the jaw elevators (masseter, temporalis and internal pterygoid muscles) were analyzed and a comparison established among the muscles (Turbull, 1970). In addition to the Turbull's findings, Kallen and Gans (1972) stated that: “Such functional comparisons, although typically appropriate to distantly related taxa, has rarely been applied to closely related forms that are phenotypically and ecologically similar”. However, no deep detailed study has been carried out on the masticatory apparatus of rodents. This is especially so for the African mole-rats.

2.7 *Bathyergus suillus*

According to Roberts (1951), *Bathyergus suillus* (see Fig 2. 2 below for representation) belongs to the family Bathyergidae and the subfamily Bathyerginae. The study done by Jarvis and Sale (1971) considered *Bathyergus suillus* (also known as the sand mole) to be the largest of the Bathyergidea (mean mass 933g). In contrast, Roberts (1926) observed that *Bathyergus suillus* is not the only large bathyergids. In addition to Jarvis and Sale's findings of 1971, Davies and Jarvis (1985) revealed that *Bathyergus suillus* is also a large solitary mole - rat. Because of the unique characteristics of *Bathyergus suillus*, some authors suggested that it should be classified as a separate family (Walker, 1964).

An investigation led by Jarvis and Sale (1971), reported that *Bathyergus suillus*, the Cape dune mole-rat inhabits the southern and Western Cape Province of South Africa).

According to the findings of Jarvis and Sale (1971), *Bathyergus suillus* eats and uses as nesting a wide variety of roots, leaves and stems. They however preferentially select certain plant species, such as soft plants and unlignified material (Davies & Jarvis, 1985) which are stored in their burrows. As is the case other mole-rats, micro-organisms in the ceacum aid in the digestion of fibres in their diet. Their digested food is efficiently utilised by their practice of coprophagy, a process in which they eat some of the energy - rich faeces as it is voided (Bennett & Faulkes, 2000).

Bennett and Faulkes (2000) described the limbs of *Bathyergus suillus* as well-

developed with front paws whose digits two, three and four bear well-developed claws. Like all bathyergids they have small eyes and the pinnae of their ears are almost absent. They mainly distinguish between light and dark and their hearing is very restricted (Bennett & Faulkes, 2000). A notable feature of mole-rats is a pair of large, ever-growing, and forwardly-directed incisors which lie outside the mouth (extra-buccal). The bathyergids also have strongly hairs and muscular lips that meet behind the incisors to keep soil out of the mouth during digging. Mole-rats groom their lower incisors against the upper ones to sharpen their incisors. The skull is dorsally flattened and houses strong jaw muscles (masseter and temporalis) that are used in feeding and digging.

One of the information available as far as could be established on the masticatory apparatus of *Bathyergus suillus* is that by Roberts (1926). He mentioned that *Bathyergus suillus* possesses a peculiar characteristic not found in the other genera. This was that they had deeply grooved upper incisors, which are cinnamon in color, and with roots that extend as far back as above the molars.

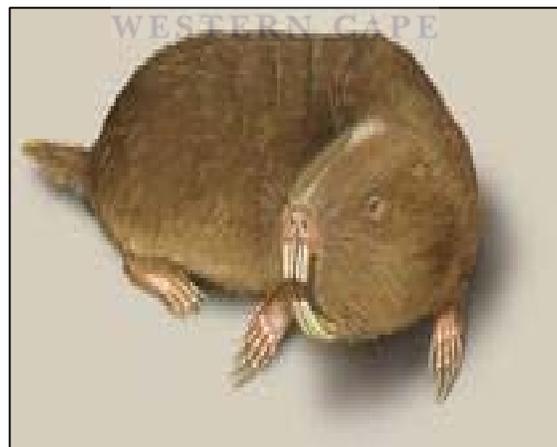


Figure 2.2: *Bathyergus suillus* (Trumpey, 1998)

2.8 *Georchus capensis*

The Cape mole-rat, *Georchus capensis*, is a medium-sized rodent with distinctive white markings on its face and head. It has a short cylindrical body

with a muscular neck that is indistinct from its head and body. It inhabits coastal and mountain fynbos areas of the south - Western Cape regions. These have regions distinct seasonal rainfall pattern (Skinner & Smithers, 1990).

Their pelage is thick, woolly and russet-colored and their bodies are about 150-205 mm in length (with tail) and a body mass of about 193 g. They are strictly burrowers and spend most of their life underground (Jarvis & sale, 1971). Although their diet consists mainly of geophytes, it also includes grass and others above-ground vegetation (Broll, 1981).

The claws of *Georychus capensis* are only moderately developed and relatively weak. However one researcher had focused his study on various features of *Georychus capensis* as follows: Omlin (1998) investigated the optic disc and optic nerve of the blind Cape mole-rat (*Georychus capensis*) and proposed a model for naturally occurring reactive gliosis.

Georychus capensis possesses large chisel shaped incisors that are used for digging. Strongly haired, muscular lips meet behind the incisors to keep soil out of the mouth during digging. Like in all bathyergids, except *Bathyergus suillus*, the roots of the upper incisors extend back to originate behind the molars. The lower jaws of these chisel-tooth diggers can move independently so that their incisors can be splayed apart or brought together, thereby making them a very versatile set of tools. The incisors are cream, un-grooved, and project forward to an unusual degree. The roots of the incisors extend as far as behind the molars.



Figure 2.3: *Georychus capensis* (Abbott, 1986)

Chapter 3

Materials and Methods

3.1 Study population and sampling

This study used nine skulls each of the mole-rats *Bathyergus suillus* and *Georychus capensis*. The nine whole body specimens of each species were obtained from the department of Zoology at the University of Cape Town (UCT). The gender of most of these animals was not known. Six specimens of each species under study were male. The gender of the rest was uncertain. These mole-rat cadavers were stored at – 20°C with the ethical guidelines and regulations of the University. The dissection and processing of the skulls of these whole body specimens is described below. The approximate age of the various animals could unfortunately not be ascertained since their records were missing (Kouame, *et al.*, 2006). However, they appeared to be adults, judging from the following characteristics: (i) The size of the skulls and (ii) the form of the molar teeth. The latter is usually a good indicator of reproductive maturity as an adult. In *Georychus capensis*, for example, if all four of these teeth have erupted, then the animals can be estimated to be between 9-10 months old and therefore adults (Taylor, 1985).

This investigation received ethical approval from the ethics committee of the science faculty of the University of the Western Cape.

3.2 Sources of specimens

Mole-rats have for some time posed a threat to the safety of the runways and underground cables at the Cape Town International Airport. Thus according to O’Riain and Taylor (2003), the Cape dune mole rat (*Bathyergus suillus*), in particular is considered to be a hazard to public safety.

The Cape dune mole-rat is also often used, for scientific research into endemic small mammals (O’Riain & Taylor, 2003). Data generated in this way provides

important information for improving the management of the Cape dune mole within Cape Town International Airport area. In this regard UCT has an agreement with the Airport Company of South Africa (ACSA) which has a contract with an independent company (MOLE Patrol). The latter is a professional mole-rat trappers company, which is contracted to eradicate the mole-rats from the Airport area-especially those of the family Bathyergidae.

The mole-rats were captured by snaring their feet with modified snap-traps that were set below ground at a depth of approximately one metre. The teeth of the traps were wrapped in rubber, which was held in place by two cable-ties, to minimise injuries to the captured animals. To maximise capture success, traps were only placed into burrow systems with recently pushed up mole-hills (a useful sign of recent below-ground activity). Traps were checked no later than 20 minutes after having been set in order to reduce the time that the animals spend in the traps and to be as humane as possible (to minimise the stress of capture). This is the most efficient trapping method since the mole-rats are very sensitive to most types of traps. The live animals were then taken to a processing laboratory at the airport where they were euthenased with chloroform (O’Riain & Taylor, 2003). (Chloroform is relatively inexpensive and can be administered by researchers without requiring the presence of a veterinarian).

3.3 Dissections to expose features of the skulls and gross muscular anatomy

Several anatomical references were used as to guide dissecting and identifying the masticatory structures. These include those published by Donaldson (1926); Greene (1935); Hebel and Stromber (1976); Homberger and Walker (1988); Miller (1964); Rudolf (1976) and Wahlert (1974). In order to facilitate a close examination of isolated skeletal muscles, the dissections were done using the following instruments: (i) Fine and blunt forceps; (ii) Scissors of different sizes with blunt tips; (iii) A pair of small scissors with blunt tips; (iv) Fine scalpels with disposable or fixed blades; (v) A fine strong blunt probe and (vi) A skin pencil, for marking incision lines on the skin (Donaldson, 1926; Homberger & Walker, 1988).

The dissection steps were as follows:

1. A vertical incision of one millimeter was made from the vertex of the skull, down the face to the tip of chin. To avoid damaging the underlying structures only the tip of the scalpel blade was applied. At this junction, an incision was made that followed the inferior border of the mandible as far laterally as the lobule and the tragus of the external ear. From the midline, an incision was made laterally to encircle the eyes and the mouth. Thereafter the skin was removed carefully from the left side of the head, neck and shoulder to extricate the thyroid gland from the anterior surface of the larynx. This also involved the removal of the parotid gland which is situated in a shallow cavity formed by the sternocleidomastoid muscle behind the ramus of the mandible, and in front and superior to the external acoustic meatus and the zygomatic arch. At the same time some muscles were removed. These included the buccinator, zygomaticus major, risorius and the platysma muscles.

2. In order to properly locate the tendon (this attaches the superficial part of the masseter muscle to the zygomatic bone), noticeable excess adipose tissue was removed from the left side of head and neck of the animal to expose the masseter muscle. This dark red muscle characteristically bulges on the angular plate of the mandible.

3. Subsequently, the overlying masseter muscle was cleaned off at its origin/insertion with a sharp scalpel and fine forceps, to remove the connective tissue from the surface of the muscle. This was necessary to identify the borders, insertion and the origin of the masseter muscle. The masseter muscle was then removed carefully to preserve the attachment points of the various muscles in the vicinity (like the digastric and stylohyoid muscles) and the insertion of the temporalis muscle was subsequently exposed.

4. The tendon of the superficial masseter muscle was cut close to the zygomatic bone and the muscle was freed from the angular plate. The fibres of the deep masseter muscle rests under the superficial masseter muscle and run vertically from the zygomatic arch to the mandible. After the superficial masseter muscle

was freed from the angular plate, it was reflected ventrally and the anterior edge of the zygomatic arch was carefully cleaned of tissue. At approximately mid-eye level, part of the deep masseter muscle could be seen entering the orbit underneath the anterior end of the zygomatic arch. This is the infraorbital part of the anterior deep masseter muscle.

5. To free the rest of the masseter muscle down to its insertion on the mandible, the attached fibres were cut to expose the whole masseter muscle.

6. The eyes were removed and all excess tissue was excised to expose the attachment of the masseter muscle in the orbit.

7. To expose the origin of the temporalis muscle, the temporalis muscle was detached from the temporal bone while severing it along the base of the skull. The extension of the muscle down to the ear region and bulging over the posterior end of the zygomatic arch was noted. The temporalis muscle inserts on both sides of the coronoid process, and also further down close to the molar. The muscle was carefully removed from the coronoid process. The animal was placed on its back and the digastric muscle was excised at its occipital end.

8. The larynx and the hyoid apparatus were removed from the floor of the mouth in order to expose the external and the internal pterygoid muscles. Consequently, the internal pterygoid muscle was excised from its point of insertion on the mandible, to expose the external pterygoid muscle between the condyle and the skull.

3.4 Morphometric analysis

The dimensions (lengths) of the four main muscles of mastication and bones involved in mastication were recorded to determine the various metric traits. The four main muscles of masticatory apparatus are the masseter, temporalis, internal pterygoid and external pterygoid. They are attached to several features of the skull viz. the temporal bone, sphenoid bone, zygomatic arch, coronoid process, condyle process and the angular plate.

In addition, individual skulls were weighed (Refer to Section 3.4.2).

3.4.1 Morphometric parameters of bones and muscles

The morphometric parameters refer to the findings of Ribot (2002) which recorded sixty one metric traits in the cranium and the lower jaw. Because the characteristics observed on the human's skull are similar to those of the skulls of the two selected species in this study. However, the lack of agreement for each measurement's definition have been reviewed in various scientific publications of anthropometry, such as the manual of Martin and Saller (1959). Previous studies used instruments such as sliding, spreading caliper, coordinate caliper, and mandible board to measure the vault, base, face of the cranium, as well as the mandible.

In this study, photographic images of the skull specimens were captured with a high-resolution Olympus digital camera. These images were downloaded onto a desktop computer via a scan disk. The different dimensions of the skulls such as (occipital bone to the upper incisors, the zygomatic arch, the coronoid process, the condylar process and the angular plate) which are mainly the points of attachment of the main masticatory muscles, were measured by using the DOCU 9(Document) analysis software (soft imaging system version 3.2). From this, the following distances (in cm) were established on the skull:

ZA = length of zygomatic arch

OI = Antero posterior diameter of the skull

A = Width of the angular plate

C1 = Width of the condylar process

C2 = Width of the coronoid process

TI = length of the temporalis muscle

MI = length of the masseter muscle

Inpt = length of the internal pterygoid muscle

Expt = length of the external pterygoid muscle

The location of each of these metric traits are indicated below in Figs. 3.1 to 3.4.

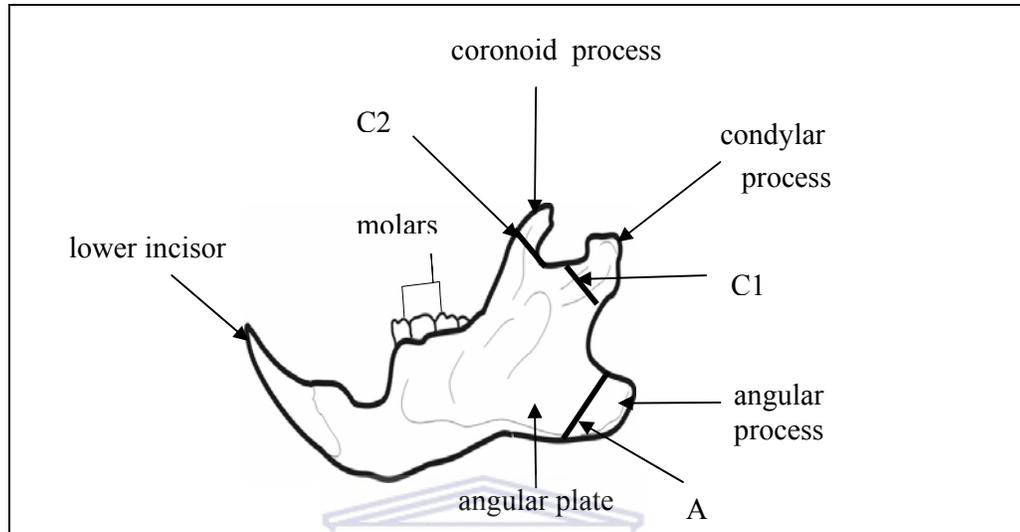


Figure 3.1: Diagram of generalised lateral view of a mole-rat mandible which indicates (i) the width of the condylar process (C1), (ii) the width of the coronoid process (C2) and (iii) the width of the angular plate (A)

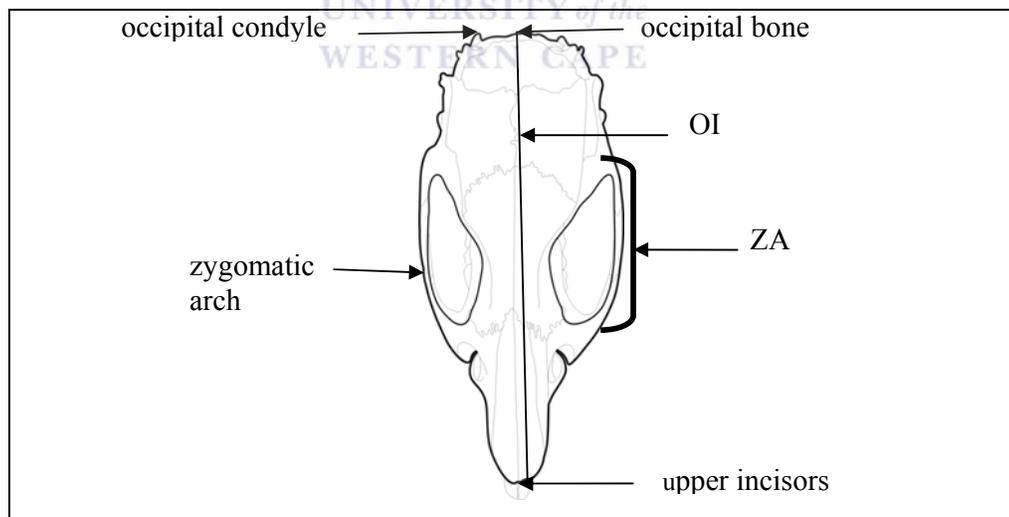


Figure 3.2: Diagram of generalised dorsal view of a mole-rat cranium which indicates (i) the antero-posterior diameter of the skull (OI) and (ii) the length of zygomatic arch (ZA) (from the temporal bone to the zygomatic bone)

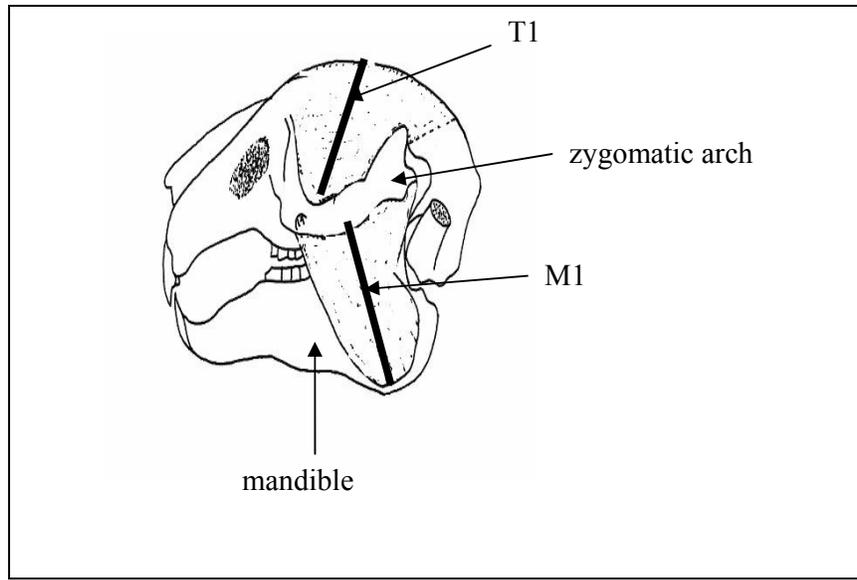


Figure 3.3: Diagram of the generalised lateral view of a mole-rat cranium which indicates (i) the length of masseter muscle (M1) and (ii) the length of the temporalis muscles (T1) (from the sagittal suture to the coronoid process)

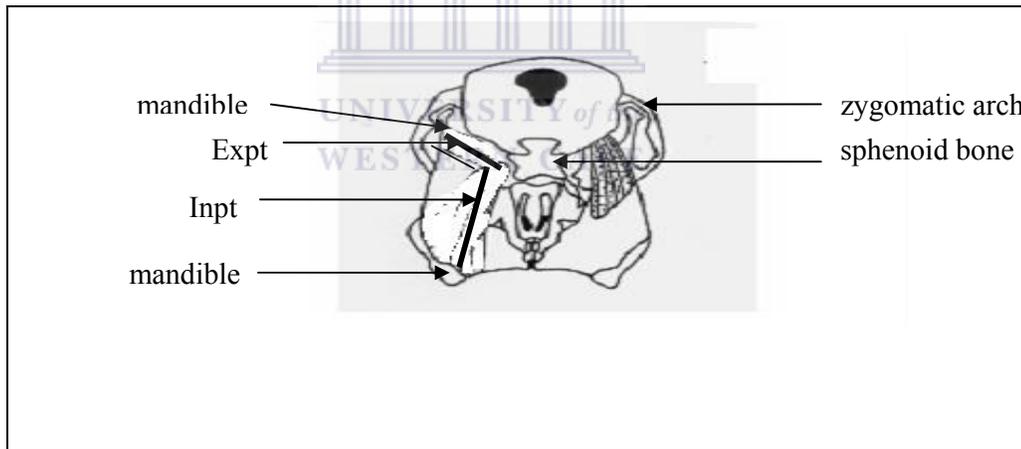


Figure 3.4: Diagram of the generalised posterior view of a mole-rat cranium which indicates (i) the length of internal pterygoid muscle (Inpt) and (ii) the length of external pterygoid muscle (Expt) (Russel, 1994)

3.4.2 Skull mass

The skulls were cleaned of any tissue and were weighed dry after 48 hours, in grams, to provide a rough indication of their overall size (skull mass). This was done with a portable mettler chemical balance, (College 244), the weight of each type of skull was obtained.

3.4.3 Indices of muscles

In order to make the comparison of the various parameters more effective than using only their linear measurements, the mass (in grams) of each skull was divided by the length of each metric trait squared. This yielded the following indices:

Masseter muscle index (I_m) = Mass of skull (g)/length of the masseter, squared (mm^2)

Temporalis muscle index (I_T) = Mass of skull (g)/length of temporalis, squared (mm^2)

External pterygoid muscle index (I_{expt}) = Mass of skull (g)/length of external pterygoid, squared (mm^2)

Internal pterygoid muscle index (I_{inpt}) = Mass of skull (g)/length of internal pterygoid, squared (mm^2)

3.5 Descriptive statistics

Descriptive statistics were used as recommended by Gibbons (2003). to either describe situations or to make various predictions. In this study data was presented as box-whisker plots. These display an exploratory data analysis as the basic statistic of data sets in a visual format (Tukey, Brillinger, Fernholz & Morgenthaler, 1997). On these the first and the third quartiles are marked and the whiskers extend to the range. The median is also marked in the boxes.

3.6 Nonparametric statistical inference

The Wilcoxon-Rank sum test was used to establish the sensitivity to any differences in a position marked by some distinguishing features. In addition, the Ansari-Bradley's method, which is sensitive to differences in scale, was applied. Thereafter, the Kolmogorov-Smirnov test was used to assess the differences about distribution of the recorded values (Gibbons, 2003).

In view of the large number of tests done, it was considered appropriate to consider p as significant at < 0.05 . All statistical tests were done after careful consultation with professional statisticians (Kotze, T., personal communication, May, 2006; Madsen, R., personal communication March, 2007).



Chapter 4

Results

4.1 Introduction

The results reported here focus on three main aspects of the comparison of the masticatory apparatus of *Bathyergus suillus* and *Georychus capensis*. Firstly, it focuses on a comparative description of the general anatomy of the skulls of *Bathyergus suillus* and *Georychus capensis* with special emphasis on the morphology of those individual bones that contribute to the masticatory apparatus. Secondly, it focuses on a comparative description of the morphometric parameters of the four main muscles of mastication and the skull bones directly involved in mastication. This aspect includes the comparison of the masses of the skulls of the two species. Thirdly, it provides a comparative analysis of the indices of the four main muscles of masticatory apparatus of the two species.

4.2 Comparative description of the anatomy of the skulls of *Bathyergus suillus* and *Georychus capensis*

The skulls (generalised dorsal views) of *Bathyergus suillus* and that of *Georychus capensis* are depicted diagrammatically in Figs. 4.1 and 4.2 below. These skulls consist of the occipital, frontal, ethmoid, sphenoid, temporal, parietal, interparietal, nasal, maxilla, incisivum (premaxillae), zygomatic and mandible bones. There is a full set of rodent teeth of which only the incisors will be described below. The temporomandibular joint which is an important component in mechanics of mastication will also be described.

The skull of *Bathyergus suillus* is approximately twice the size as that of *Georychus capensis*. The body sizes of *Bathyergus suillus* and that of *Georychus capensis* are ranged from 1200 g to 1800 g and 300 g to 400 g respectively. This is at least partly due to the bones of the former that are thicker than that of the

latter. A comparison of the mass of the two skulls appears in Section 4.4.3 below. Specific differences in the bones of the two species will be described below.

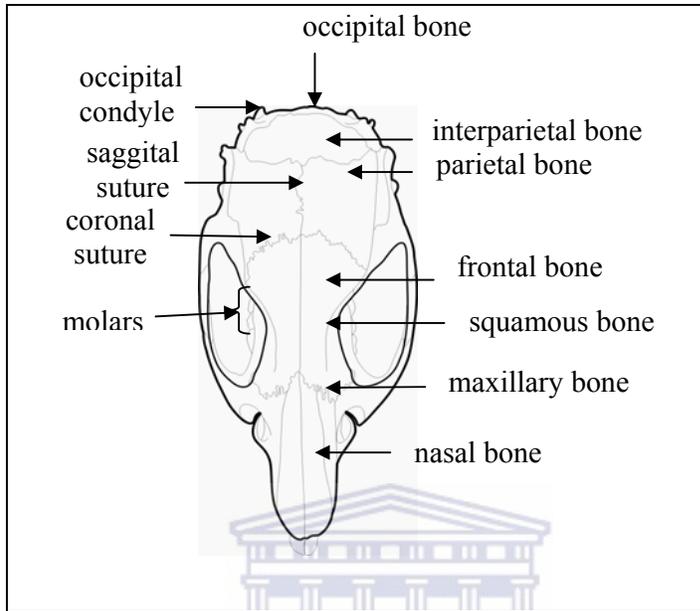


Figure 4.1: A diagrammatic representation of a generalised dorsal view of the cranium of mole-rats

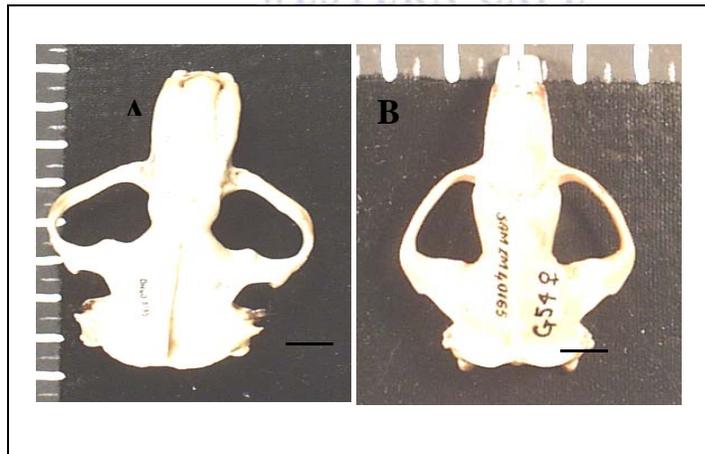


Figure 4.2: A diagrammatic representation of the dorsal view of the craniums of *Georchus capensis* and *Bathyergus suillus*
Key: A = Dorsal view of *Bathyergus suillus*. B = Dorsal view of *Georchus capensis*. Scale bar = 1 cm.

4.2.1 Occipital bone

With regard to both *Bathyergus suillus* and *Georychus capensis*, they both have an oval shape foramen magnum (see Fig. 4.4). On both sides just below this foramen two smooth nut-like projections appear – the occipital condyles (see Fig. 4.1). Below and above the occipital condyles is the area of projection of a strong and voluminous portion of the temporal bone (petrous part). Close to the petrous bones are slight projections which are the mastoid processes. In the case of *Bathyergus suillus*, a prominent crest at the inferior portion of the occipital bone divides the basilar portion into two. Three non prominent external occipital crests divide the occipital bones of both species into four different regions viz. two lateral and two medial regions. In the case of *Georychus capensis* the basilar portion has no crest.

4.2.2 Frontal bone

In the case of *Bathyergus suillus*, the frontal bone (see Fig. 4.2), is narrower than that of *Georychus capensis* and smooth. This narrowness moves downward to meet the molar teeth. From the smooth surface of the frontal bone appears a rough area just before the naso-frontal suture. At this junction a smooth crest lies between the two surfaces. These two crests meet to form a frontal crest which extends caudally across the parietal bone and ends on the nuchal line which separates the occipital bone from the interparietal bone. In the case of *Georychus capensis* the frontal bone is also narrower and smooth and displays the same tapering of *Bathyergus suillus* (see Fig. 4.2). The smooth surface of the frontal bone continues as far as the naso-frontal suture. A frontal crest extends caudally across the parietal bone and ends on the nuchal line which separates the occipital bone from the interparietal bone. A clear coronal suture (see Fig. 4.1) separates the frontal bone from the temporal and parietal bones in both species. The orbital part of the frontal bone forms the main part of the medial wall of the orbit.

4.2.3 Sphenoid bone

The sphenoid bone has similar features in both species and resembles that of other mammals such as rabbit (see Fig. 4.4). This bone is divided into basisphenoid and presphenoid parts. Emerging from the dorsoventrally flattened body of the basisphenoid (see Fig. 4.4), the wing of the sphenoid extends dorsally below the temporal squama. Arising from the base of each wing is an osseous crest which provides an expanded contact with the caudal part of the palatine bone. From the pterygoid plate there originates the internal and external pterygoid muscles originate. The body of the presphenoid (see Fig. 4.4) is widened caudally, tapers rostrally, and ends in a sphenoidal rostrum ventral to the ethmoid bone.

4.2.4 Ethmoid bone

The ethmoid bones of both *Bathyergus suillus* and *Georychus capensis* consist of the crista galli, cribriform plate and the perpendicular plate. From the midline of the cribriform plate the crista galli projects upwards and the perpendicular plate projects downwards.

4.2.5 Temporal bone

The temporal bones of both *Bathyergus suillus* and *Georychus capensis* consist of squamosal, petrosal, tympanic and mastoid parts. The squamosal part begins with a shallow surface and continues via a slight groove as the zygomatic process. The slight groove extends to the mastoid portion. A wide quadrangular zygomatic process arises approximately in the middle of the temporal bone. This process forms the entire bony roof of the mandibular fossa. Ventrally to the base of the zygomatic process lies the narrow, parasagittally oriented, mandibular fossa. It receives the condylar process of the mandible. The strong and oval shaped, closed portion located just below the mastoid process and at the lateral end of the nuchal line is the petrous bone. A clear suture connects the zygomatic process of the temporal bone to the zygomatic arch. The latter continues anteriorly to link to a thin zygomatic bone. Each temporal bone is connected to the parietal bone through a squamosal suture and connected to the interparietal bone via the lambdoid suture.

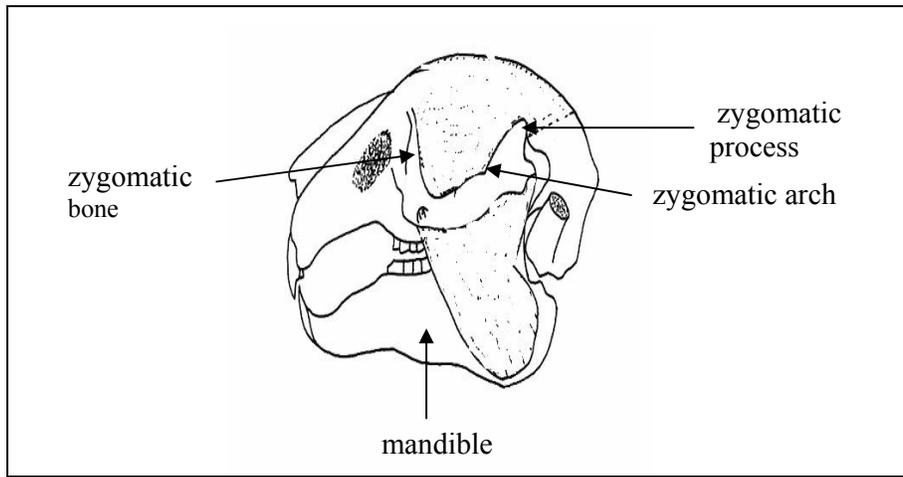


Figure 4.3: A diagrammatic representation of the lateral view of a generalised mole-rat cranium illustrating the zygomatic bone, arch and the zygomatic process

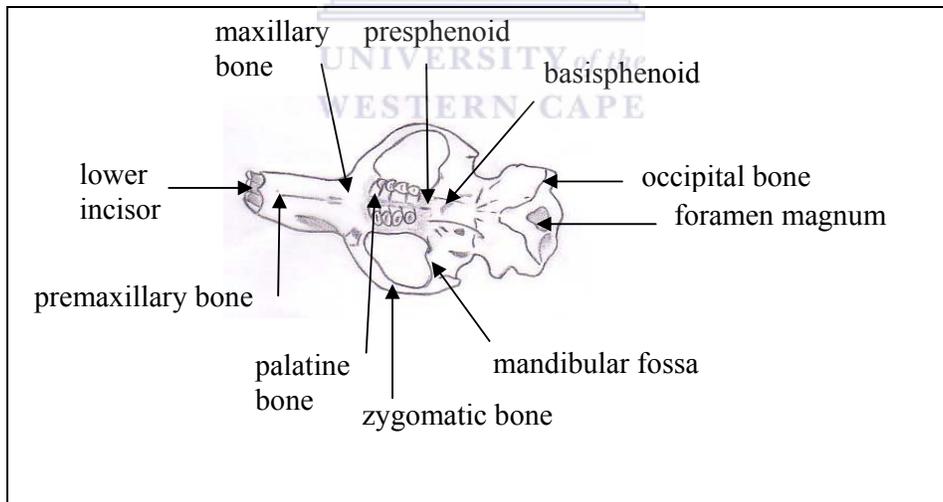


Figure 4.4: A diagrammatic representation of the ventral view of a generalised mole-rat cranium

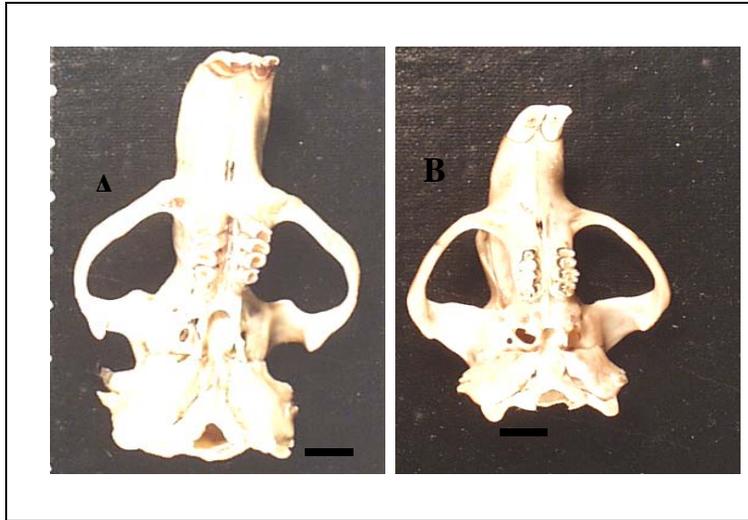


Figure 4.5: A diagrammatic representation of the ventral view of the craniums of *Georychus capensis* and *Bathyergus suillus*
Key: A = Ventral view of *Bathyergus suillus*. B = Ventral view of *Georychus capensis*. Scale bar = 1 cm

4.2.6 Parietal bone

In both *Bathyergus suillus* and *Georychus capensis*, the two parietal bones (see Fig. 4.1) form the upper sides and the roof of the cranium. Each parietal bone is caudally connected to the interparietal bone by means of the interparieto-parietal suture. The parietal bones do not connect directly to the occipital bone. In *Bathyergus suillus* a sagittal suture is visible through the parietal crest, whereas in *Georychus capensis* a prominent parietal crest overlaps the sagittal suture.

4.2.7 Interparietal bone

In both species the interparietal bone (see Fig. 4.1) is a small plate which forms the caudal part of the roof of the cranium. The interparietal bone is separated from the occipital bone by a prominent nuchal line.

4.2.8 Nasal bone

In both species the nasal bone (see Figs. 4.1 and 4.2) forms the dorsal wall of the nasal cavity. The nasal bone is attached laterally to the long naso-frontal process of the incisivum and caudally to the frontal bone (see Figs. 4.1 and 4.2). The

smooth dorsal surface of the bone is flat caudally and curved rostrally. Both nasal bones meet medially at a “false” suture. From the lateral edge of the nasal bone, a thin bony lamina extends ventrally and attaches to the medial side of the incisivum and maxilla. The nasal bone is divided into two distinguishable portions. Each portion is connected to other part by means of a vertical suture. The nasal bone of both species is well separated from other parts of the skull. In *Bathyergus suillus* the nasal bone is smooth and even, whereas in *Georychus capensis* the nasal bone is uneven. The vertical suture (false suture) which connects the two portions of the nasal bone is elevated and uneven.

4.2.9 Incisivum (premaxillae)

The incisivum consists of a body, a palatine process, and a nasofrontal process. Each body contains the alveolus of an upper incisor. The alveolus extends caudally into the rostral part of the maxilla. The palatine aspect of the incisive bodies, together with the palatine processes, forms the rostral part of the hard palate, posterior to the diastema. In *Georychus capensis* the premaxillae has smooth creamed periodontal incisors, whereas in *Bathyergus suillus* those incisors are purely white.

4.2.10 Maxilla

In both species this is the largest facial bone and it takes part in the formation of the nasal and oral cavities as well as the orbit. It consists of a body and zygomatic, alveolar, sphenoid, orbital and palatine processes. The body of the maxilla forms the lateral osseous wall of the maxillary recess. From the dorsal margin of the maxillary body arises a well-developed process, which unites with a vertically oriented bony plate to form the base of the zygomatic process.

4.2.11 Mandible

In both species the two halves of the mandible are firmly united at the cartilaginous symphysis. The body of the mandible consists of an incisive part, housing the root of the incisors (see Fig. 4.6), which sweeps caudally and laterally in a wide curve. Dorsally the molar region of the mandible contains the alveoli for the three molars (see Fig. 4.6). The proximal end of the alveoli of the incisors

forms a lateral elevation of the ramus. The ramus has a hook-shaped coronoid process. In *Bathyergus suillus* the coronoid process is thicker and shorter, whereas in *Georychus capensis* is thinner and longer (see Figs. 4.6 and 4.7). The condyloid process (see Figs. 4.6 and Fig 4.7) is somewhat longer than the coronoid process in both species, and its knob-like articular surface is oriented sagittally. The condyloid process is relatively larger and more oval-shaped in *Georychus capensis* than in *Bathyergus suillus* where it is smaller, thicker, rounded and bending backward – completely away from the ramus. A more pronounced ‘post-condylar notch’ was noted in *Bathyergus suillus* compared to *Georychus capensis*.

The angular process (see Fig. 4.6) in both species is a massive plate of bone that projects laterally from the mandibular ramus. This plate is thicker and longer in *Bathyergus suillus* compared to that of *Georychus capensis*. The outer surface (masseteric fossa) of the angular plate (see Figs. 4.6 and 4.7) is smooth and the inner surface forms a massive angular fossa which accommodates the insertion of the internal pterygoid muscle in both species. The inner part of the angular plate bears a prominent ridge along its margin. The superior portion of the angular plate is covered by an angular crest. This angular crest is wider in *Bathyergus suillus* than in *Georychus capensis*. In *Georychus capensis* the angular plate is shorter and covered by a thin angular crest. This crest runs to the lateral aspect of the body of the mandible. In *Georychus capensis* the angular process (see Figs. 4.6 and 4.7) does not show any projection in contrast that of *Bathyergus suillus* where it projects further backwards.

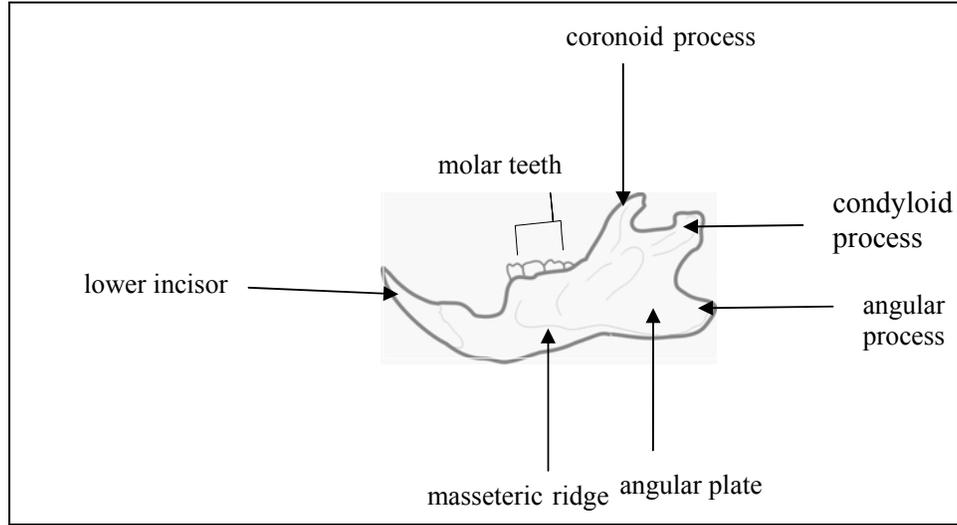


Figure 4.6: A diagrammatic representation of the lateral view of the lower jaw of *Georychus capensis* and that of *Bathyergus suillus*

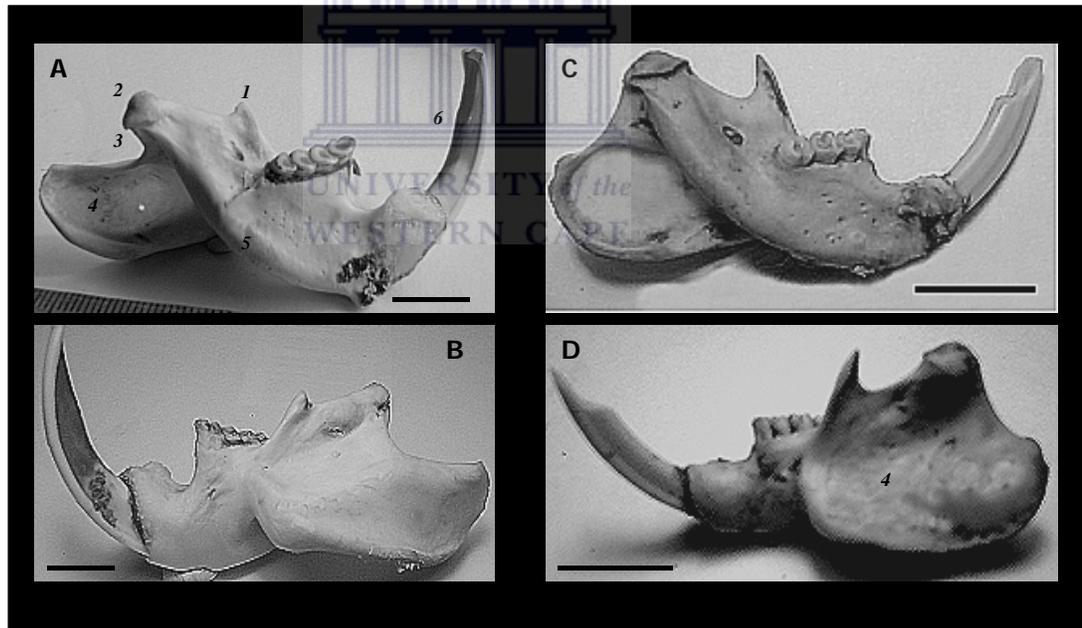


Figure 4.7: A diagrammatic representation of the left mandibles of *Bathyergus suillus* and *Georychus capensis*

Key: A = Medial view of *Bathyergus suillus*. B = Lateral view of *Bathyergus suillus*. C = Medial view of *Georychus capensis*. D = Lateral view of *Georychus capensis*. 1 = Coronoid process of *Bathyergus suillus*. 2 = Condylar process of *Bathyergus suillus*. 3 = post-condylar notch. 4 = Angular plate. 5 = Incisor ridge. 6 = Angle of incisor. Scale bar = 1 cm (Kouame *et al.*, 2006)

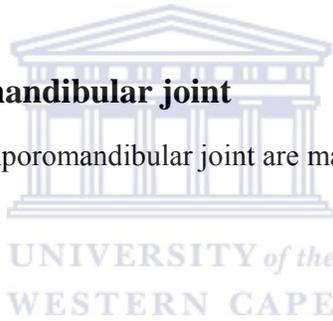
4.2.12 Incisors

The incisors of the two species display several differences. *Bathyergus suillus* and *Georychus capensis* both have hypsodont incisors that allow for continuous growth throughout life and display considerable wear at the masticatory surfaces. The shape of the incisors, with almost geometric precision, is that of a segment of a spiral. The roots of the upper incisors of *Georychus capensis* are long and bend to reach as far back as the molars. With regard to *Bathyergus suillus* the upper incisors are tightly curved and heavily grooved (see Figs. 4.4 and 4.5). These upper incisors do not extend as far back as the molar teeth. The lower incisors of *Georychus capensis* are larger than that of *Bathyergus suillus* (see Figs. 4.6 and 4.7). In both species the roots of the lower incisors curve backward behind the molars and terminate just below the condyles.

4.2.13 Temporomandibular joint

The elements of the temporomandibular joint are mainly:

- (i) mandibular fossa
- (ii) fibrocartilage disc
- (iii) capsule



There are no distinct differences between the temporomandibular joint of the two species.

4.2.13.1 Mandibular fossa

The slightly concave roof of the mandibular fossa is formed by the zygomatic process of the temporal bone. The posterior end of the zygomatic bone deepens this fossa as it fuses ventrally with the lateral margin of the zygomatic process of the temporal bone. The mandibular fossa is located anterior to the external auditory meatus and separated from the tympanic part of the temporal bone by a large gap (post-glenoid fossa). The mandibular fossa forms a deep socket for the condyle of the mandible. The shape of the fossa probably allows free protraction and retraction of the lower jaw since the socket is larger than the condyle. Lateral

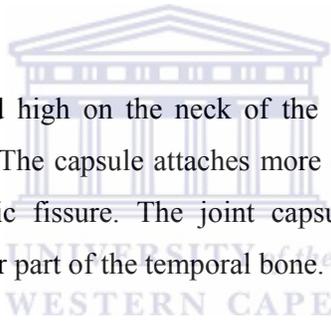
displacement is likely to be limited by the depth, and prominent sidewalls of the fossa.

4.2.13.2 Fibrocartilage disc

The fibrocartilage disc is located between the upper and the lower cavities of the temporo-mandibular joint. This disc is attached around its periphery to the inside of the capsule. Anteriorly this biconcave disc is attached near the condyle, and this part moves forward with the condyle. Posteriorly it is attached to the posterior margin of the zygomatic process of the temporal bone. This limits extreme protraction and retraction. The anterior margin of the disc and adjoining capsule receives the insertion of the upper fibres of the external pterygoid muscle.

4.2.13.3 Capsule

The capsule is attached high on the neck of the mandible around the articular margin of the condyle. The capsule attaches more extensively above the condyle at the squamo-tympanic fissure. The joint capsule encloses the head of the condyle and the articular part of the temporal bone.



4.3 Comparative description of the four main masticatory muscles of *Bathyergus suillus* and *Georchus capensis*

Like in all mammals, the four main muscles of mastication of *Bathyergus suillus* and *Georchus capensis* are: The masseter, temporalis, external pterygoid (equivalent to the lateral pterygoid in humans) and internal pterygoid muscles (equivalent to the medial pterygoid in humans).

4.3.1 Masseter muscle

In both *Bathyergus suillus* and *Georchus capensis* the masseter muscles are large and complex, but distinctly separable into two groups. These are the superficial masseter muscle and the profundus (deep) masseter muscle (see Figs. 4.8 and 4.9). Each of these is in turn subdivided into anterior and posterior portions.

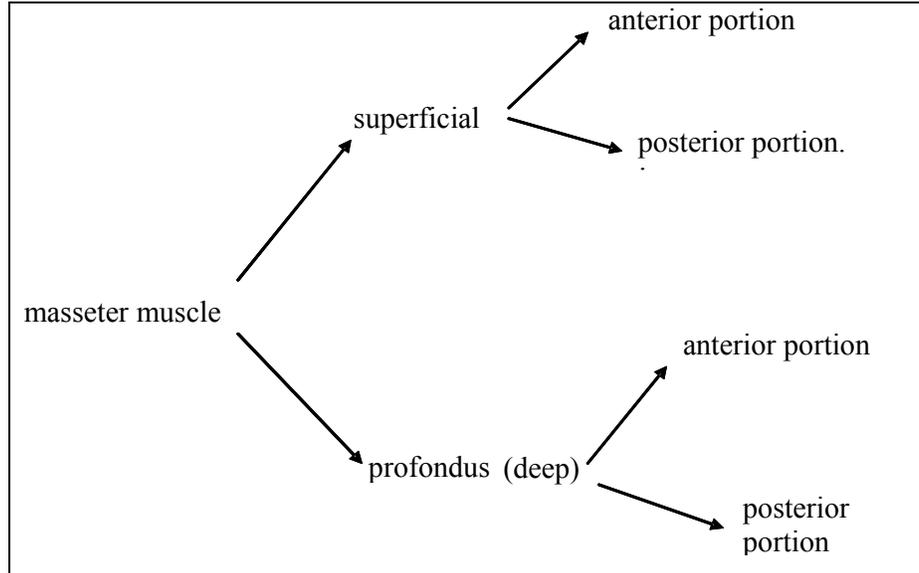


Figure 4.8: Subdivisions of the masseter muscle

4.3.1.1 Superficial masseter

The superficial masseter has similar features in both species which corresponds to that found in others rodents. The **anterior portion** arises by a strong slender tendon. It originates from the lateral surface of the maxilla just posterior to the suture of the maxilla and premaxilla. It inserts along the lower margin and internal surface of the angular plate of the mandible. This happens on the internal surface, which is adjacent to the insertion of the internal pterygoid. Its muscle fibres bundles are oriented more horizontally (see Figs. 4.8 and 4.9).

The **posterior portion** arises from the whole length of the zygomatic arch. It inserts on the lower part of the lateral surface of the angular plate and onto the masseteric ridge. This extends along the lateral surface and lower margin of the angular plate.

The direction of the fibres of the posterior superficial part gives some indications of a possible division into a more superficial posterior portion and a deeper anterior one. This is the main protractor of the jaw (see Fig. 4.9).

4.3.1.2 Profundus (deep) masseter

The profundus masseter has similar features in both *Bathyergus suillus* and *Georychus capensis* (see Fig. 4.9). It consists of the anterior portion and the posterior portion.

The **anterior portion** arises from the fossa just anterior to the infraorbital fissure and converges into a slender muscle. This passes through the infraorbital fissure and inserts upon the lateral surface of the mandible. At the anterior end of the masseteric ridge, nearly covered by the posterior deep masseter.

The **posterior portion** originates from the lower border and the inner surface of the zygomatic arch. It inserts upon the lateral surface of the angular plate of the mandible. The muscle fibres of the deep masseter are almost vertically oriented (see Fig. 4.9).

4.3.2 Temporalis muscle

The temporalis muscle is mainly similar in both species, but there are few dissimilarities. Its fibres arise from the sagittal crest (ridge), which extends along the frontal, parietal and temporal bones. It seems also to arise from the inner surface of the zygomatic arch. As the fibres from the temporal and parietal bones reach the root of the zygomatic arch, they change their course, and with the remaining fibres of the muscle, they insert into the medial surface of the mandible. The groove between the coronoid process and the molars seems to be filled by some fibres of the temporalis muscle (see Fig. 4.9). This muscle is bigger and more powerful than any of the other muscles of mastication.

4.3.2 Pterygoid muscles

Like in all the rodents, the pterygoid muscles appear to be similar in both species (see Fig. 4.10). The pterygoid muscle is grouped into the **internal** and **external pterygoid muscles**.

The external pterygoid arises from the external pterygoid ridge and inserts on the medial surface of the condylar neck of the mandible.

The internal pterygoid is larger than the external pterygoid. The internal pterygoid arises from the lateral surface of the feebly marked internal pterygoid ridge. The insertion is on the medial surface (angular fossa) of the angular plate. The fibres appear to be relatively stronger and larger in *Georychus capensis* than that of *Bathyergus suillus*.

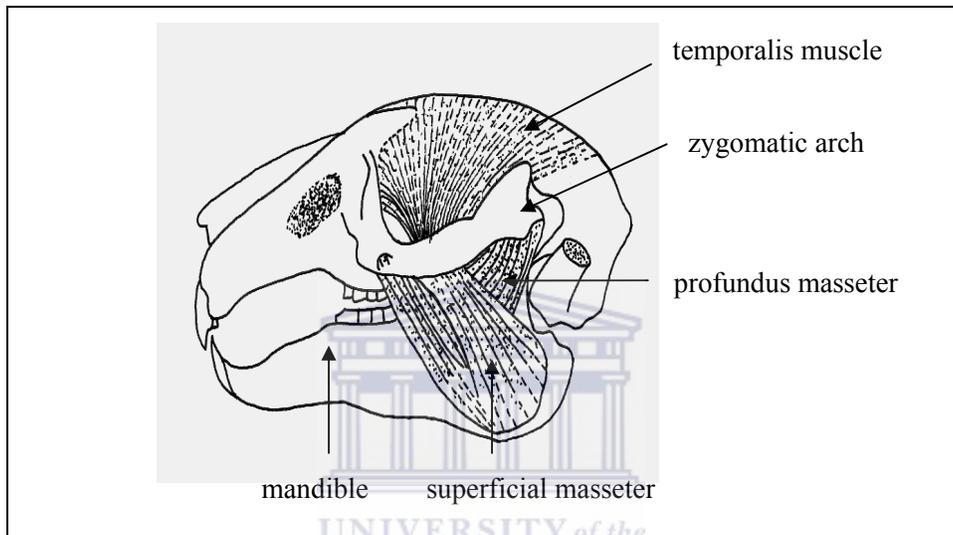


Figure 4.9: A diagrammatic representation of a generalised lateral view of a mole-rat skull illustrating the orientation of the masseter muscles

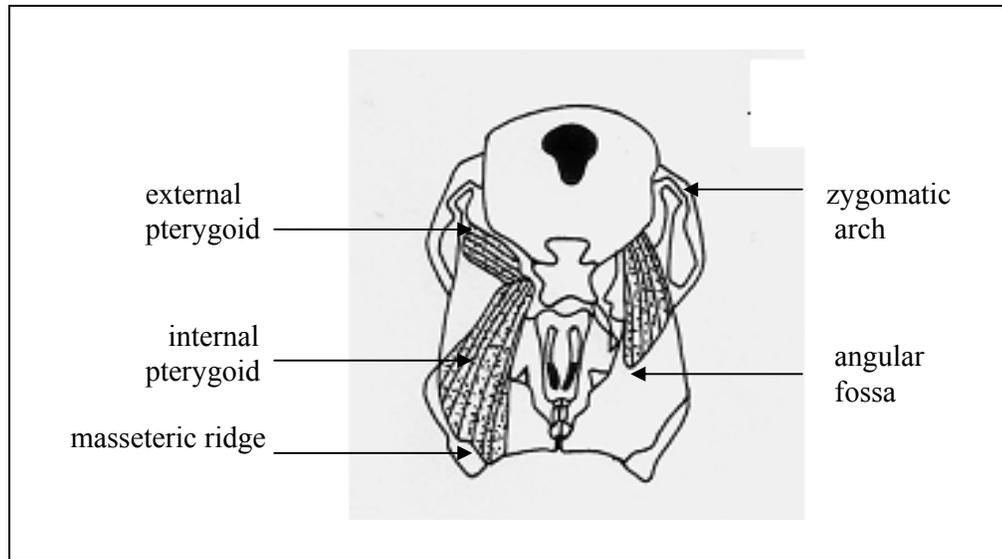


Figure 4.10: A diagrammatic representation of the generalised posterior view of the skull of a mole-rat illustrating the orientation of the pterygoid muscles (Russel, 1994)



4.4 Morphometric analyses of the masticatory apparatus parameters of *Bathyerigus suillus* and *Georychus capensis*

4.4.1 Comparison of the lengths of selected bones of the skulls

n	Bone	Length & Widths mean \pm SD (cm)	Range (cm)	p-value
9	OI _B	5.02 \pm 1.61	3.05 to 7.80	<i>p</i> < 0.05
9	OI _G	2.84 \pm 1.42	1.50 to 5.30	
9	ZA _B	2.64 \pm 0.58	1.90 to 3.50	<i>p</i> > 0.05
9	ZA _G	1.93 \pm 0.69	1.06 to 2.80	
9	A _B	1.59 \pm 1.24	0.43 to 2.90	<i>p</i> > 0.05
9	A _G	1.28 \pm 1.44	0.78 to 2.00	
9	CI _B	0.21 \pm 0.11	0.05 to 0.35	<i>p</i> < 0.05
9	CI _G	0.47 \pm 0.18	0.25 to 0.70	
9	C2 _B	0.17 \pm 0.12	0.05 to 0.47	<i>p</i> > 0.05
9	C2 _G	0.18 \pm 0.060	0.12 to 0.32	

Table 4.1: Comparison of the lengths (mean \pm SD) of selected bones of the skulls of *Bathyerigus suillus* and *Georychus capensis*

Key: OI = Antero-posterior diameter of the skull. ZA = Zygomatic arch length. A = Angular plate width. CI = Condylar process width. C2 = Coronoid process width. The subscripts 'B' and 'G' designate the parameters for *Bathyerigus suillus* and *Georychus capensis* respectively

4.4.1.1 Comparison of the antero-posterior diameter of the skull

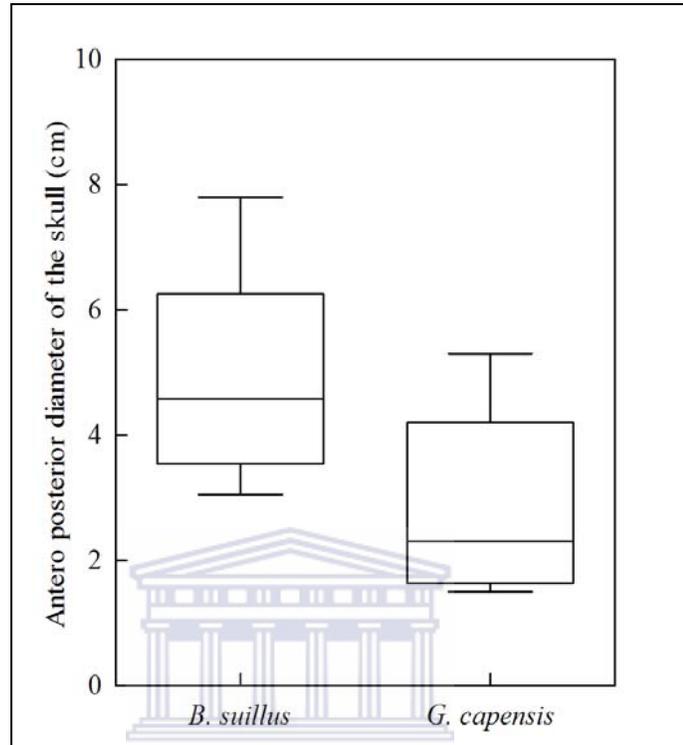


Figure 4.8: Comparison of the antero-posterior diameter of the skull (mean \pm SD) of *Bathyergus suillus* and *Georychus capensis*

Table 4.1 shows that the mean antero-posterior diameter of the skull for *Bathyergus suillus* is 5.02 ± 1.61 cm compared to that of *Georychus capensis* which is 2.84 ± 1.41 cm. Table 4.1 also shows that the distribution of the measured values for *Bathyergus suillus* is 7.75 cm compared to that of *Georychus capensis*. The difference between the mean antero-posterior diameter of the skull of *Bathyergus suillus* and that of *Georychus capensis* is 3.80 cm. The mean diameter of this parameter is 2.18 cm longer in *Bathyergus suillus* than that of *Georychus capensis*. This difference in the mean antero posterior diameter between these two species is statistically significant as estimated with both the Kolmogorov-Smirnov test and Wilcoxon-Rank Sum analysis with $p < 0.05$.

4.4.1.2 Comparison of the lengths of the zygomatic arches

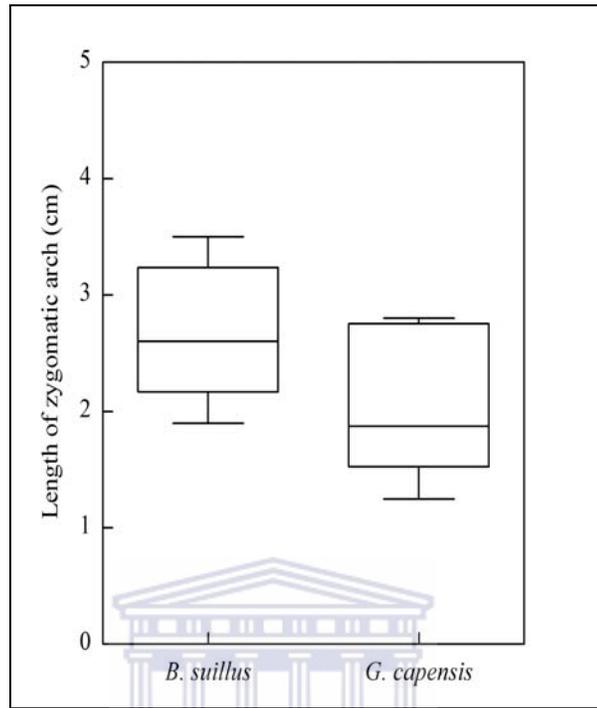


Figure 4.9: Comparison of the lengths (mean \pm SD) of the zygomatic arches of *Bathyergus suillus* and *Georychus capensis*

The mean length of the zygomatic arch for *Bathyergus suillus*, which is 2.64 ± 0.58 cm, differs by 0.71 cm from that of *Georychus capensis* which is 1.93 ± 0.69 cm (see Table 4.1 and Fig. 4.9). The spread of distribution of the recorded values is very similar viz. 1.60 cm for *Bathyergus suillus* and 1.74 cm for *Georychus capensis*. The slight difference of 0.71 cm between the lengths of the zygomatic arches of the two species tested is not statistically significant according to both the Kolmogorov-Smirnov and Ansari-Bradley tests (p value > 0.05) (see Table 4.1).

4.4.1.3 Comparison of the widths of the angular plates

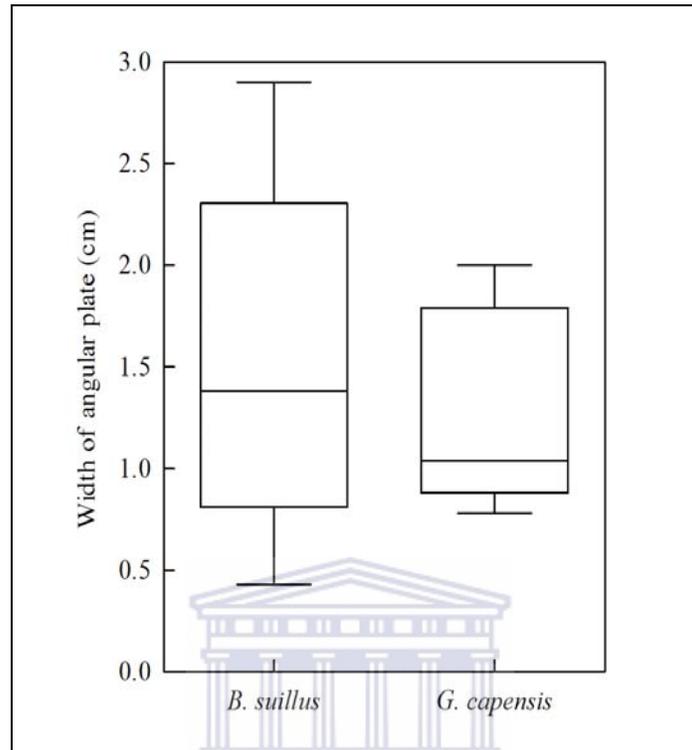


Figure 4.10: Comparison of the widths (mean \pm SD) of the angular plates of *Bathyergus suillus* and *Georychus capensis*

The mean widths of the angular plate for *Bathyergus suillus* is 1.59 ± 1.24 cm compared to that of *Georychus capensis* which is 1.28 ± 1.44 cm (see Table 4.1). The spread of distribution of the recorded values of the angular plate for *Bathyergus suillus* is 2.47 cm compared to the 1.22 cm for *Georychus capensis* as shown in Fig. 4.10. The mean difference of 0.31 cm between the mean widths of the angular plates of the two species is not statistically different. This was demonstrated by both the Kolmogorov-Smirnov and Wilcoxon-Rank Sum statistical analyses, that yielded p -values greater than 0.05 (see Table 4.1).

4.4.1.4 Comparison of the widths of the condylar processes

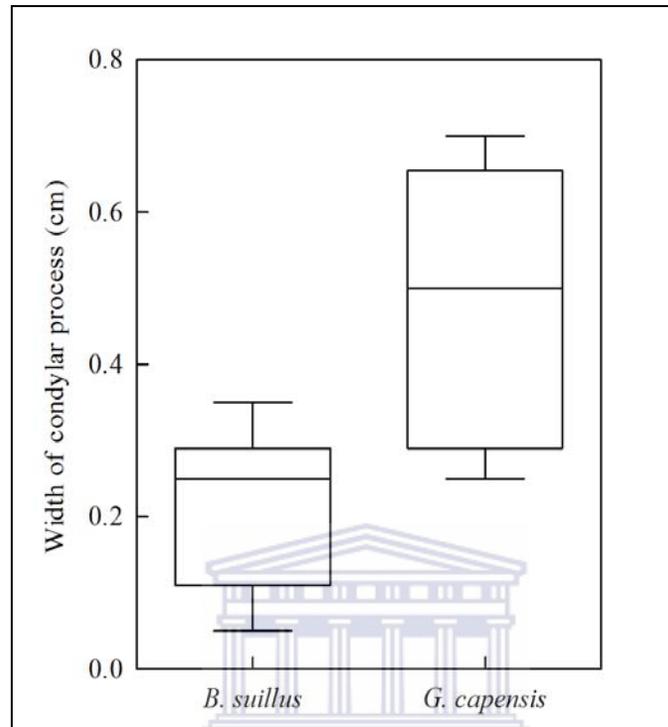


Figure 4.11: Comparison of the widths (mean \pm SD) of the condylar processes of *Bathyergus suillus* and *Georychus capensis*

The mean widths of the condylar process for *Bathyergus suillus* is 0.21 ± 0.11 cm and that of *Georychus capensis* is 0.47 ± 0.18 cm (see Table 4.1). The mean difference in widths of the condylar process of 0.26 cm between these two species is statistically significant (Both the Kolmogorov-Smirnov and Wilcoxon-Rank Sum tests showed a $p < 0.05$). As shown in Table 4.1 the minimum and the maximum values obtained for *Georychus capensis* is 0.25 cm and 0.70 cm (a spread of 0.45 cm), and for *Bathyergus suillus* it is 0.05 cm and 0.35 cm (a spread of 0.30 cm) respectively (see Fig. 4.11).

4.4.1.5 Comparison of the widths of the coronoid processes

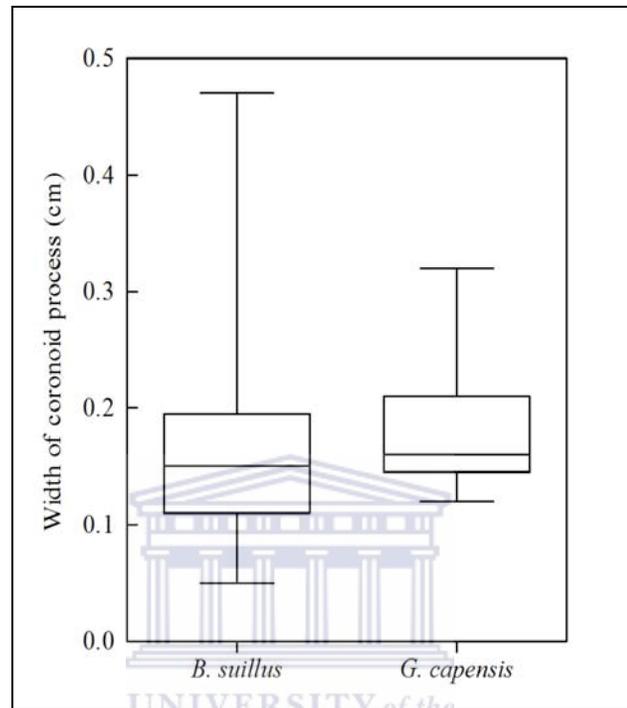


Figure 4.12: Comparison of the widths (mean \pm SD) of the coronoid processes of *Bathyergus suillus* and *Georychus capensis*

The mean widths of the coronoid process of *Bathyergus suillus* is 0.17 ± 0.12 cm compared to that of *Georychus capensis* which is $0.18 \text{ cm} \pm 0.060$ cm (see Table 4.1). The maximum measured value for *Georychus capensis* is 0.32 cm and that of *Bathyergus suillus* is 0.47 cm. While the mean widths of the coronoid processes of the two species are almost identical, the spread of the data for *Bathyergus suillus* is 0.42 cm compared to the 0.20 cm of *Georychus capensis* (see Fig. 4.12). Both the Kolmogorov-Smirnov test and the Wilcoxon-Rank Sum test yielded p values > 0.05 (see Table 4.1). The difference of 0.01 cm of the mean widths between the two species is thus not statistically significant.

4.4.2 Comparison of the lengths of the masticatory muscles

n	Muscle	Length mean \pm SD (cm)	Range (cm)	p-value
9	TI _B	8.54 \pm 3.06	4.80 to 12.90	$p > 0.05$
9	TI _G	5.99 \pm 2.66	2.70 to 10.90	
9	MI _B	7.55 \pm 2.99	3.14 to 13.00	$p > 0.05$
9	MI _G	5.58 \pm 2.51	2.10 to 9.00	
9	Inpt _B	2.20 \pm 0.96	1.00 to 4.00	$p > 0.05$
9	Inpt _G	2.05 \pm 1.89	0.38 to 4.80	
9	Expt _B	0.83 \pm 0.48	0.39 to 2.00	$p < 0.05$
9	Expt _G	1.89 \pm 0.62	0.98 to 3.00	

Table 4.2: Comparison of the lengths (mean \pm SD) of selected masticatory muscles of the skulls of *Bathyergus suillus* and *Georchus capensis*

Key: T1 = length of the temporalis muscle. M1 = length of the masseter muscle. InPt = length of the internal pterygoid muscle. ExPt = length of the external pterygoid muscle. The subscripts 'B' and 'G' designate the parameters for *Bathyergus suillus* and *Georchus capensis* respectively

4.4.2.1 Comparison of the lengths of the temporalis muscles

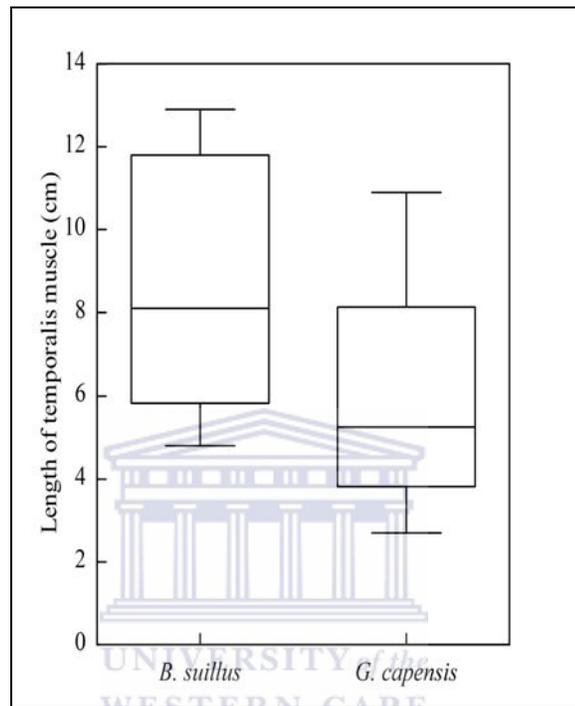


Figure 4.13: Comparison of the lengths (mean \pm SD) of temporalis muscles of *Bathyergus suillus* and *Georychus capensis*

Comparison of the mean lengths of the temporalis muscles shows a mean length of 8.54 ± 3.06 cm for *Bathyergus suillus* and 5.99 ± 2.66 cm for *Georychus capensis* (see Table 4.2 and Fig. 4.13). The maximum values recorded are 10.90 cm and 12.90 cm for *Georychus capensis* and *Bathyergus suillus* respectively while the spread of distribution for the data are almost the same, viz. 8.2 cm and 8.1 cm for the two species respectively. The difference between the mean lengths of the temporalis muscles, of 2.55 cm is, according to both the Kolmogorov-Smirnov and the Wilcoxon-Rank Sum tests, are not statistically significant ($p > 0.05$) (see Table 4.2).

4.4.2.2 Comparison of the lengths of the masseter muscles

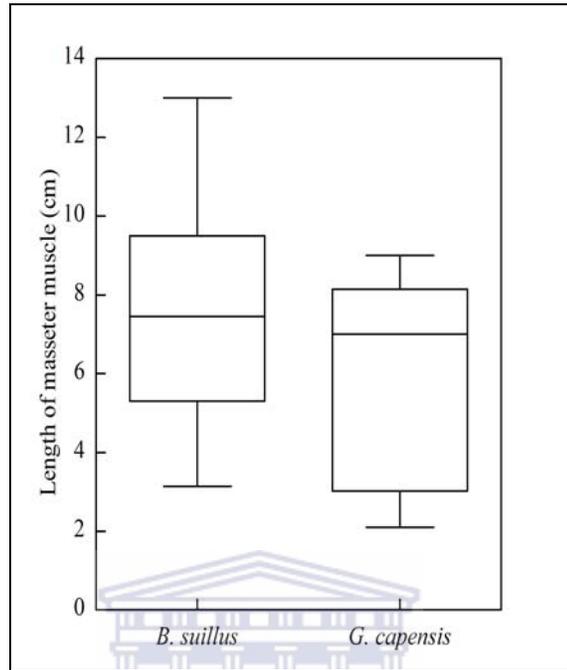


Figure 4.14: Comparison the lengths (mean \pm SD) of masseter muscles of *Bathyergus suillus* and *Georychus capensis*

As can be seen in Table 4.2, the mean length of the masseter muscle recorded for *Georychus capensis* is 5.58 ± 2.51 cm and that of *Bathyergus suillus* is 7.55 ± 2.99 cm – a mean difference of 1.97 cm. The distribution of the data is quite broad viz. 9.86 cm for *Bathyergus suillus* and 6.90 cm for *Georychus capensis* (see also Fig. 4.14). However, the difference in the mean lengths of the masseter muscle of the two species is not statistically significant; considering that the result of Kolmogorov-Smirnov test for this comparison is $p > 0.05$ (see Table 4.2).

4.4.2.3 Comparison of the lengths of the internal pterygoid muscles

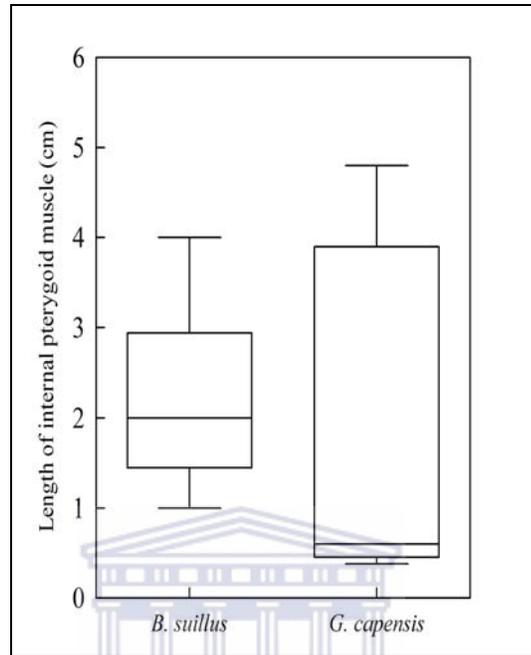


Figure 4.15: Comparison of the lengths (mean \pm SD) of internal pterygoid muscles of *Bathyergus suillus* and *Georychus capensis*

The mean length of the internal pterygoid muscle for *Bathyergus suillus* is 2.20 ± 0.96 cm while that for *Georychus capensis* is 2.05 ± 1.89 cm (see Table 4.2). The values for *Georychus capensis* are spread over 4.42 cm compared to that of *Bathyergus suillus* which is 3.00 cm (see Fig. 4.15). Comparison of the length of this parameter with the Kolmogorov-Smirnov test indicated a p value > 0.05 . These differences in length of the internal pterygoid muscles are thus not statistically significant.

4.4.2.4 Comparison of the lengths of the external pterygoid muscles

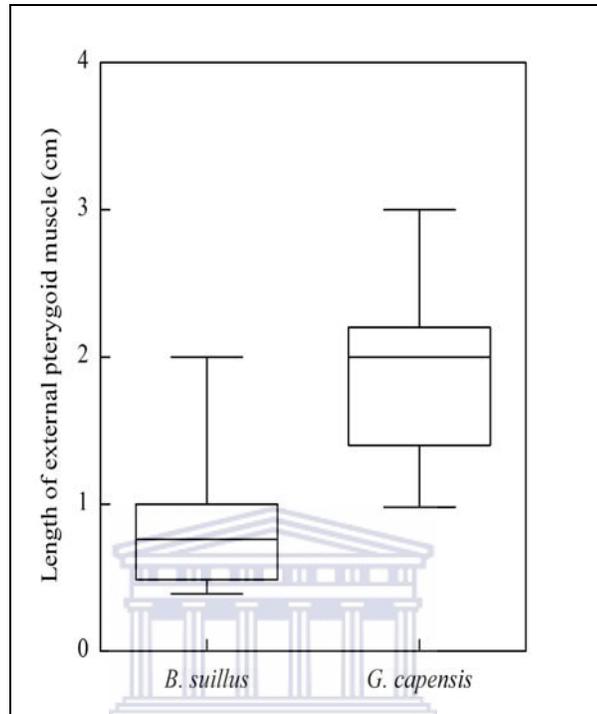


Figure 4.16: Comparison of the lengths (mean \pm SD) of external pterygoid muscles of *Bathyergus suillus* and *Georychus capensis*

The mean length of external pterygoid muscles recorded in Table 4.2 for *Bathyergus suillus* is 0.83 ± 0.48 cm compared to the 1.89 ± 0.62 cm of *Georychus capensis*. The mean length for *Georychus capensis* is being 1.06 cm longer than that of *Bathyergus suillus*, while the spread of data is very similar viz. 2.02 cm and 1.61 cm respectively (see Fig. 4.16). Statistically tests (Kolmogorov-Smirnov and Wilcoxon-Rank Sum) demonstrated that the difference in the lengths of external pterygoid muscles between the two species is statistically significant ($p < 0.05$) (see Table 4.2).

4.4.3 Comparison of the mass of the skulls

	Skull mass (g)	
	<i>Bathyergus suillus</i>	<i>Georychus capensis</i>
n	9	9
Mean ± SD (g)	15.012 ± 10.42	8.50 ± 2.10
Range (g)	12.22 to 46.01	5.24 to 11.99
p-value	$p < 0.05$	

Table 4.3: Comparison of the mass (mean ± SD) of the skulls of *Bathyergus suillus* and *Georychus capensis*

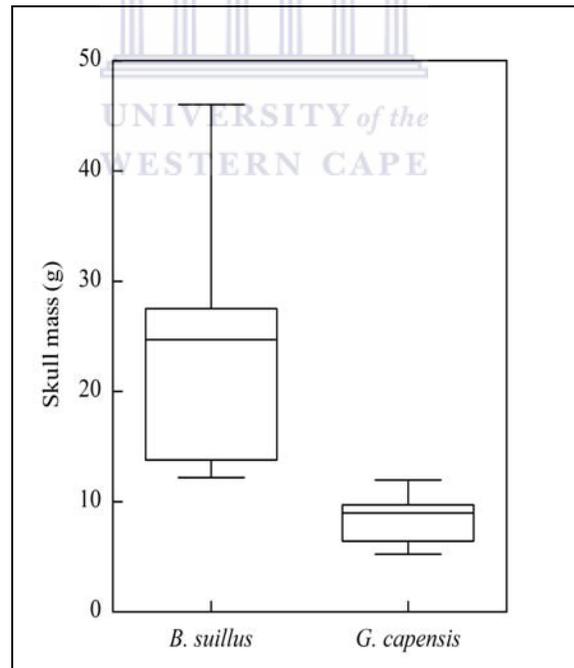


Figure 4.17: Comparison of the mass (g) of the skulls of *Bathyergus suillus* and *Georychus capensis*

Table 4.3 illustrates that the mean skull masses for *Bathyergus suillus* and *Georchus capensis* are 23.78 ± 10.42 g and 8.50 ± 2.10 g respectively. The difference between the mean skull masses of the two species for this parameter is 15.25 g. According to the Wilcoxon-Rank Sum test, this difference is statistically significant ($p < 0.05$). The spread of the data for the two species is demonstrated in Fig. 4.17. The latter shows a broader spread of data for *Bathyergus suillus*, viz. 33.79 g compared to the 6.75 g for *Georchus capensis*.

4.4.4 Comparison of the corresponding indices of the masticatory muscles

n	Index	Index value Mean \pm SD (g/mm ²) ($\times 10^{-3}$)	Range (g/mm ²)	p-value
9	It _B	4.1 \pm 2.5	1.50 to 7.70	$p > 0.05$
9	It _G	3.9 \pm 3.8	0.8 to 79	
9	Im _B	6.6 \pm 7.9	1 to 27	$p > 0.05$
9	Im _G	5.9 \pm 8.4	0.8 to 27	
9	Iinpt _B	75.3 \pm 83.5	16 to 280	$p > 0.05$
9	Iinpt _G	270 \pm 278.1	3.8 to 530	
9	Iexpt _B	535 \pm 361.5	65 to 1120	$p < 0.05$
9	Iexpt _G	57.5 \pm 76.8	9.8 to 94	

Table 4.4: Comparison of the indices (mean \pm SD) of the masticatory muscles of *Bathyergus suillus* and *Georchus capensis*

Key: Im = Index of the masseter muscle. It = Index of the temporalis muscle. Iexpt = Index of the external pterygoid muscle. Iinpt = Index of the internal pterygoid muscle. The subscripts 'B' and 'G' designate the parameters for *Bathyergus suillus* and *Georchus capensis* respectively

4.4.4.1 Comparison of the indices of the temporalis muscles

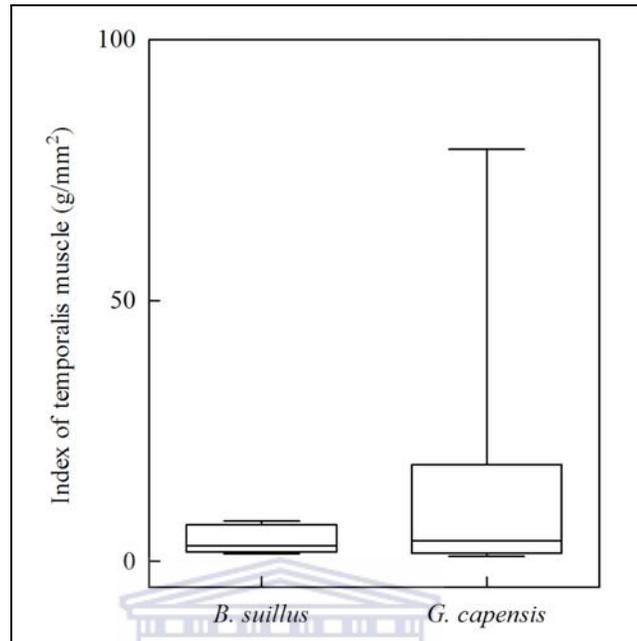


Figure 4.18: Comparison of the temporalis muscles indices of *Bathyergus suillus* and *Georychus capensis*

According to Table 4.4, the mean temporalis index for *Bathyergus suillus* is 4.1 g/mm² and its range of distribution is 6.2 g/mm². The same parameter for *Georychus capensis* is 3.9 g/mm² with a range of distribution of 78.2 g/mm² (see Fig. 4.18). The differences of 0.2 g/mm² between the mean temporalis muscles indices of the two species is not statistically significant ($p > 0.05$) as determined by the Wilcoxon-Rank Sum analysis (see Table 4.4).

4.4.4.2 Comparison of the indices of the masseter muscles

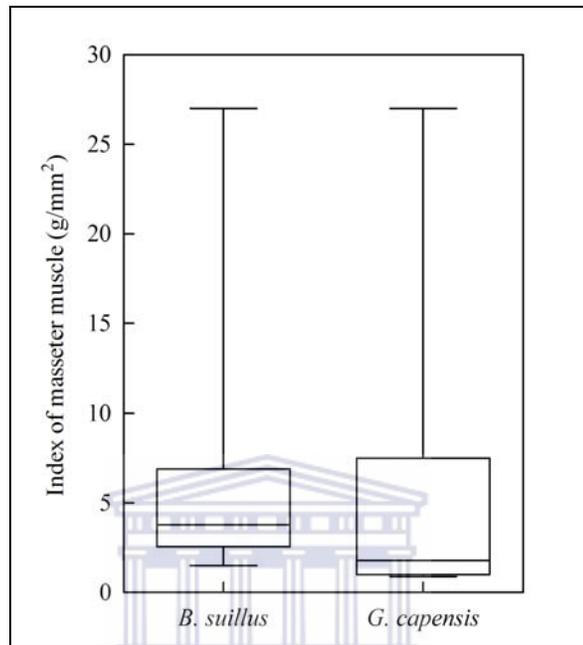


Figure 4.19: Comparison of the masseter muscles indices of *Bathyergus suillus* and *Georychus capensis*

The mean masseter index for *Bathyergus suillus* is $6.6 \pm 7.90 \text{ g/mm}^2$ compared to that of *Georychus capensis* which is $5.9 \pm 8.45 \text{ g/mm}^2$. The differences of 0.67 g/mm^2 between the mean masseter muscles indices of the two species are not statistically significant according to the Kolmogorov-Smirnov test, which yielded $p > 0.05$ (see Table 4.4). The Wilcoxon-Rank Sum test also showed that this difference is not statistically significant (see Table 4.4). Fig. 4.19 reflects the range of data distribution of 26 g/mm^2 for *Bathyergus suillus* compared to 26.2 g/mm^2 for *Georychus capensis*.

4.4.4.3 Comparison of the indices of the internal pterygoid muscles

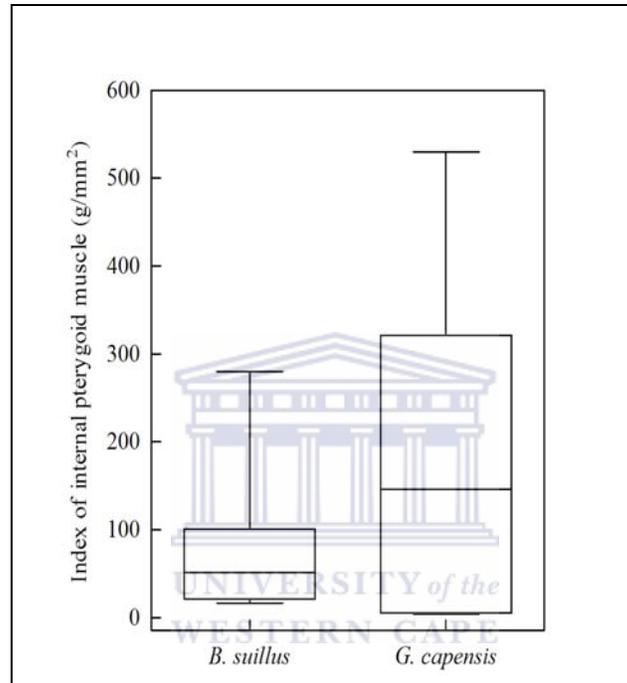


Figure 4.20: Comparison of the internal pterygoid muscles indices of *Bathyergus suillus* and *Georychus capensis*

The mean indices for the internal pterygoid muscles are $75.3 \pm 83.5 \text{ g/mm}^2$ and $270 \pm 278.1 \text{ g/mm}^2$ for *Bathyergus suillus* and *Georychus capensis* respectively. The box plots (see Fig. 4.20) of the mean internal pterygoid muscles indices of the two species show different ranges of distribution of viz. 526.2 g/mm^2 for *Bathyergus suillus* compared to 263.6 g/mm^2 for *Georychus capensis*. In addition, the difference of the mean internal pterygoid muscles indices is 103.41 g/mm^2 . This difference however, according to the Kolmogorov-Smirnov and Wilcoxon-Rank Sum tests, is not statistically significant ($p > 0.05$) (see Table 4.4).

4.4.4.4 Comparison of the indices of the external pterygoid muscles

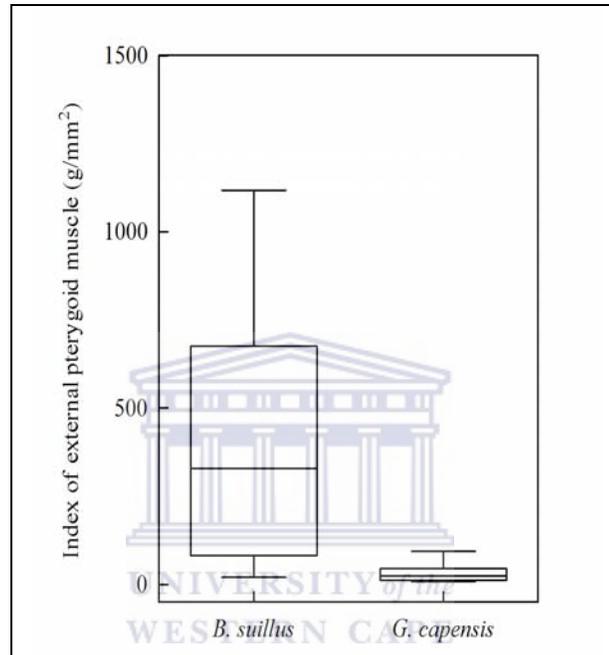


Figure 4.21: Comparison of the external pterygoid muscles indices of *Bathyergus suillus* and *Georychus capensis*

The mean index of the external pterygoid muscle for *Bathyergus suillus* is 535 ± 361.5 g/mm² compared to that of *Georychus capensis* which is 57.5 ± 76.8 g/mm² (Table 4.4). The range of data for *Bathyergus suillus* (1055.00 g/mm²) is much broader than that for *Georychus capensis* (84.2 g/mm²). The difference in the mean indices of the two species of 477.5 g/mm² is however statistically significant ($p < 0.05$) (see Table 4.4) according to the Kolmogorov-Smirnov test.

Chapter 5

Discussion and Conclusion

5.1 Introduction

In order to explore the comparison of some aspects of the masticatory apparatus of *Bathyergus suillus* and *Georychus capensis*, the data presented in this research will be discussed along different routes. Firstly, the morphology of the masticatory apparatus of the two species will be compared with special reference to the individual bones and muscles. Secondly, a comparison of relationship and interaction of the main muscles and bones of mastication will be analysed and discussed. Thirdly, the functional relationship between the skulls and the jaws muscles – in particular during foraging and feeding will be analysed. This section will also address the important question whether differences in feeding and digging behaviour are reflected in the anatomy of the two species. Since the use of indices is a new approach to the comparison of some anatomical parameters between two species, this method warrants a short evaluation. Lastly, the main conclusion of this study will be forwarded.

5.2 Morphological comparison of the two species

One of the objectives of this study is to record the specific features of the morphology of the masticatory apparatus of each of the two species. The purpose of this is two-fold: As far as could be established, little information regarding rodent's general anatomy, and in particular, that of the Bathyergidae. Also, since the taxonomy of the Rodentia is inconclusive, this study could contribute data that could contribute to taxonomic purposes.

5.2.1 Comparison of the osteology of the skulls and the individual bones

Within the Bathyergidae family, the **skull size** of *Bathyergus suillus* is much larger than that of *Georychus capensis* and the largest among the Bathyergidae (Bennett & Faulkes, 2000). This is illustrated by the longer occipital to upper incisor length in *Bathyergus suillus* (OI_B) compared to *Georychus capensis* (OI_G) (see Table 4.1). The larger size of the *Bathyergus suillus* skull is expected, since the mass of *Bathyergus suillus* that is on average about 900 g heavier (Bennett & Faulkes, 2000) than that of *Georychus capensis* (see Table 4.3). With regard to the size of these skulls, Roberts (1913) also reported that in the Bathyergidae family the skull of *Bathyergus suillus* is much broader than that of *Georychus capensis*.

The skull serves as attachment for various muscles – the muscles of mastication being an important group. The surface area available on the skull is generally considered to be a reflection of the attachment area of these muscles. It is also reasoned that the larger the area on the skull where the muscles attach, the larger the relevant muscle will be. Further, one could reason that a larger muscle indicates heightened activity of that muscle. One may thus propose that the larger skull of *Bathyergus suillus* reflects that its muscles engage in more strenuous activity than that of *Georychus capensis*.

Among the mole-rats, *Bathyergus suillus* is known to prefer living in flat areas such as the Cape flats, while *Georychus capensis* lives in mountainous regions (Faulkes *et al.*, 2003). This difference in location may account for the evolutionary difference of a larger skull in *Bathyergus suillus* compared to *Georychus capensis*. Since the two differ in their feeding behaviour (see Section 5.4 below) *Bathyergus suillus* would need larger areas or spaces on their skulls for the attachment of bigger muscles needed for mastication of a particular diet compared to that of *Georychus capensis*. While there are significant differences between the weights of the skulls of the two species, analysis of individual bones of the two reveals that there are also several differences in their skull morphology. A comparison of individual bones follows herewith.

A review of the literature (Hebel & Stromberg, 1976) indicates that the two species do not differ much regarding the morphology of their **occipital bones**. A detailed description of the morphology of this bone appears in Section 4.2.1. Both *Bathyergus suillus* and *Georychus capensis* have **occipital bones** that correspond closely to the general morphology of the Rodentia, and there is only one significant difference between these bones in the two species. This difference relates to the prominent crest at the inferior portion of the occipital bone which divides the basilar portion into two in *Bathyergus suillus*. *Georychus capensis* has no such crest and *Georychus capensis* has demonstrated particular behaviour within its environment (see Section 2.8) which would affect the muscles of the neck, one would expect more force to be applied on the occipital bone, and resultant enlargement thereof. However, this study did not find any evidence of this. This similarity of the occipital bone may be due to the two species being derived from the same ancestor (Faulkes *et al.*, 2003).

The **frontal bone** of *Bathyergus suillus* is narrower than that of *Georychus capensis*. The frontal bone is thus responsible for the broader dimension of the skull in *Georychus capensis* compared to *Bathyergus suillus*. The frontal bone determines the shape of the forebrain. These results correspond to that of Hebel and Stromberg (1976), who revealed that both species have similar features with regard to the frontal bone. Hebel and Stromberg (1976) did not however record the difference in broadness of the bone in the two species. A detailed description of this bone in both species appears in Section 4.2.2.

The **sphenoid bone** (see Section 4.2.3 for a full description) has the same features in both species as that of other rodents, and displays no significant difference between the two species. Since the pterygoid muscles originate on the pterygoid plates of the sphenoid bone, one could consider that because of the grinding and chewing motion predominant in *Georychus capensis*, this bone should be more robust than in *Bathyergus suillus*.

Both species have similar features with regard to the **temporal bone**. The prominent features of this bone are described in Section 4.2.5. This bone is a point

of origin of the temporalis muscle. In *Bathyergus suillus* the temporal muscle is often used compare to that of *Georychus capensis*, due to its diet. In contrary the effect of this diet is not noticed on the morphology and size of the temporal bone.

Although the **parietal bones** of the two species are also very similar in appearance and dimensions in *Georychus capensis* and in *Bathyergus suillus* (see Section 4.2.6 for details) they differ in at least two aspects. The sagittal suture which separates the two parietal bones is more visible in *Bathyergus suillus*, compared to *Georychus capensis*. The latter also has a prominent parietal crest that runs along the sagittal suture. The fascia of the temporalis muscles extends to the crest, the activity of this muscle may be expected to affect the prominence of this crest.

The **interparietal bone** is well developed, as in all Rodentia, and the two species share a similar morphology. In both species it is a small plate which forms the caudal roof of the cranium. A prominent nuchal line separates this bone from the occipital bone.

Generally in mammals and Rodentia in particular, there are two **nasal bones** which form the dorsal wall of the nasal cavity. The naso-frontal process constitutes the nasal process in domestic mammals (Van de Graaf, 1998). A description of the nasal bones of *Bathyergus suillus* and *Georychus capensis* appears in Section 4.2.8 and is illustrated in Figs. 4.1 and 4.2. While these bones are similar in dimensions, they however, differ in at least one aspect. This bone is smooth and even in *Bathyergus suillus*, while in *Georychus capensis* it is coarse and uneven. Like the nasal bone, the incisivum appears uneven in *Georychus capensis* compared to that of *Bathyergus suillus*.

The **maxillae** of the two species are very similar in morphology (see Section 4.2.10 for a detailed description). The incisors of the two species are perhaps that part of the skull morphology where most significant differences are displayed between the two species. Both species have hypsodont incisors that allow for continuous growth. They are spiral-shaped. The **upper incisors** of *Georychus capensis* are cream in color and their roots are long and bent backwards until they

reach the molars. This is not the case in *Bathyergus suillus* where the upper incisors are white, tightly curved, heavily grooved and do not extend as far back as that of *Georychus capensis*. Miller and Gidley back in (1918), also found that there is not any great lengthening of the upper incisor roots, so the upper incisors of *Bathyergus suillus* do not show any inclination to extend to the back of the palate or the pterygoids. The difference in color of the teeth may be caused by many factors, not species difference, probably due to the diet. This finding regarding the upper incisors also corresponds to the findings of Roberts (1926), and is also consistent with that of Jarvis and Sale (1971).

The reason why *Georychus capensis* needs secured upper incisors (far back-ward extending roots) may be because of its feeding habits. In rodents the incisors also play an important function during digging activities. *Georychus capensis* is a tooth-digger compared to *Bathyergus suillus* that is scratch-digger. The role of these teeth in foraging will be explained in Sections 5.5 and 5.6 below.

Several authors (Roberts, 1926; Walker, 1964) found that *Bathyergus suillus* has deep grooved upper incisors with the roots that extend above the molars. Based on these findings they suggested that *Bathyergus suillus* should be classified in a family of its own. To the authors of the findings, although the upper incisors are deeply grooved, their roots do not extend as far back as the molars in *Bathyergus suillus*. However we found that the roots of the upper incisors in *Georychus capensis* extend as far back as the molars. If one thus takes the length of the incisor root as basis for classification, it may therefore be suggested that one could classify *Georychus capensis*, *Bathyergus suillus* in its own family.

The **zygomatic arch** of *Bathyergus suillus* is wider than that of *Georychus capensis* – perhaps to accommodate the large masseter muscle. This muscle is used during mastication only and thus applies forces on the zygomatic arch and affects its size and strength. Meanwhile, the lifestyle of *Georychus capensis* necessitates for this muscle to be used for various purposes, and the zygomatic arch should appear more robust.

Bathyergus suillus is a larger mole-rat compared to *Georychus capensis*. This is not only reflected in the skull, but even more so in the mandible. The **mandibles** house the **lower incisors** in both species. The coronoid process of the mandible in *Bathyergus suillus* is shorter and thicker and the angular process is also longer than that of *Georychus capensis*. *Bathyergus suillus* also has a caudally pointed condylar process which presents a post-condylar notch that lies above a caudally deflected angular plate. On the other hand, the **condylar process** of the mandible in *Georychus capensis* is larger and oval, compared to that of *Bathyergus suillus* which is thicker, rounded and pointed caudally. The *Georychus capensis* mandible lacks a post-condylar notch and has a more pronounced and caudally deflected coronoid process with the condyle pointing dorsally. Both species have grooved lower incisors that extend up to the level of origin of the condyle process.

Georychus capensis as a tooth-digger and utilizes the pterygoid muscle for feeding and digging, since this muscle inserts on the condyloid process. The temporalis muscle, by inserting on the coronoid process, assists in the opening and closing of the jaws. In *Georychus capensis* this muscle is not used often. The reason being so is that why in *Georychus capensis* the coronoid process is thinner and smaller, while the condyloid process is larger. Because of its feeding activity as a tooth-digger, *Bathyergus suillus* applies forces on the coronoid process via its temporalis muscle, than the condyloid process (Jarvis & Sale 1971).

The **angular plates** are massive in both species, but the outer portion is thicker in *Bathyergus suillus* compared to *Georychus capensis*. The masseteric fossa of the angular plate is the insertion of the masseter muscle. In *Bathyergus suillus* the constant impact of this muscle on the angular plate may create its robustness, and elongate its length. *Georychus capensis* intends to keep the original structure of the angular plate. *Georychus capensis* uses the angular plate for other purposes. The angular process has a prominent projection backwards in *Bathyergus suillus*, this is not present in *Georychus capensis*.

According to Brooks, Balmford, Burgess, Moore and Williams (2001), the requirements for different food types will affect the tooth form and arrangement

in different mammals. The **lower incisors** are hypsodont in both species, like in all other rodents-their teeth are not all alike, and are functionally different (Brooks *et al.*, 2001 & Feldhamer *et al.*, 1999). In *Bathyergus suillus*, the lower incisors are white, while in *Georychus capensis* they are cream in colour. In both species these lower incisors bend as far back as the condyloid process. The teeth of these animals are used for holding and chewing food. The processing of food begins in the mouth, so assisting in the maintenance of high metabolic rate of endothermic mammals (Brooks *et al.*, 2001). This means that the teeth must be able to process whatever food is eaten into pieces small enough for effective enzyme action to start.

The comparison above of the bones of the two species did not take into account the relatively larger body size of *Bathyergus suillus*. Neither did it take into account possible gender differences between the two species. However, the data here does provide information regarding the osteology of each of the two species under study, and in that aspect documents data, as far as could be established, that was not available before.

A synopsis of the distinguishing features of *Bathyergus suillus* and *Georychus capensis* is provided below.

5.2.2 Identifying criteria of the skulls of the two species

In Chapter 1 the lack of published scientific data, on particular anatomical descriptions of the mole-rat were argued to be incomplete. Crucial to clarifying the taxonomy of the Bathyergidae family is thus the availability of data which will allow the accurate description of differentiating features of the various species. This study records the features below as distinguishing anatomical characteristics when one compares *Bathyergus suillus* with *Georychus capensis*.

Distinguishing features of the skull *Bathyergus suillus*:

- i. White grooved upper incisors and also white lower incisors
- ii. Even and flat nasal bone
- iii. Non-prominent parietal crest through the sagittal suture

- iv. The coronoid process is short and thick
- v. The condyloid process is small, thick, rounded and facing backward
- vi. The angular plate is massive, thick, and distorted outwards
- vii. A wide angular crest covers the superior portion of the angular plate
- viii. The occipital bone is divided into four small portions
- ix. Caudally deflected condylar process
- x. More pronounced "post-condylar notch"
- xi. The skull of *Bathyergus suillus* is also significantly larger than that of *Georychus capensis*

Distinguishing features of *Georychus capensis*:

- i. Cream colour and un-grooved upper incisors and also cream colour lower incisors
- ii. Nasal bone is uneven and a prominent parietal crest crosses the parietal as well as the frontal bones
- iii. The coronoid process is thin and long
- iv. The condyloid process is large and oval-shaped
- v. The angular plate is thin and short
- vi. A thin angular crest covers the superior portion of the angular plate
- vii. The occipital bone is divided into four small portions
- viii. A dorsally pointed condylar process
- ix. Absence of a condylar notch

5.2.3 Comparison of the four main muscles of mastication between the two species

The major masticatory muscles viz. the temporalis, masseter, internal and external pterygoid muscles are well developed compared to others of non-mole rodents (Jarvis, 1981). The main action of the masticatory muscles, based on the anatomical and the functional literature can be summarized as follow: The **temporalis muscles** function in conjunction with the deep masseter and the pterygoid muscles. In addition, together with the Anterior deep masseter, they elevate the mandible. The temporalis muscle is the prime mover of mandibular retraction. The masseter muscle consists of four parts, one of which, the superficial part functions independently of the others. The deep masseter has essentially the same function as the temporalis muscle. The laterally directed component of the deep masseter tends to evert the mandible and is antagonized by the internal pterygoid. The masseter is the prime mover in gross protraction of the mandible such as occurs in the transition from mastication to incision. It also acts as an elevator. In the protracted position, the superficial masseter, acting

unilaterally, can produce movement of the mandible toward the contra-lateral side (Last, 1978). They are antagonist, with regard to their action.

Like in any other rodent the **masseter muscle** of both species is the most complex and the largest of the masticatory muscles. This muscle is divided into two main components – each of which has two further subdivisions (Russell, 1994) (see Fig. 4.8). A description of this muscle appears in Section 4.3.1. This muscle acts as the main protractor of the jaw and has very similar features in both species. The only difference is that the zygomatic arches of *Bathyergus suillus*, which are the points of origin of the masseter muscles, appear wider compared to those of *Georychus capensis*. Furthermore, the point of insertion of this muscle which is the angular plate in *Bathyergus suillus* appears thicker, wider and pushed outward to accommodate the masseter muscle. This could suggest that the results of this study should then reveal a bigger masseter muscle in *Bathyergus suillus*. However, the findings here revealed that there is a strong similarity in both species with regard to their masseter muscles. The similarities between the two species indicate that both species retained the characteristics of the masseter that is found in their common ancestor, *Heterocephalus*.

The powerful and intricately divided masseter muscles, attached to the jaw and skull in different arrangements, provide most of the power for chewing and gnawing. Based on the feeding behaviour and lifestyle of *Georychus capensis* the masseter muscle is used for two different purposes viz. digging and feeding. In *Bathyergus suillus* the masseter is used mainly for a single only need, viz. feeding. This causes this muscle to raise the mandible against the resistance of the food. It is thus clear from the results of this study that the differences observed about the size with regard to the zygomatic arch and the angular plate as sites of attachments of the masseter muscle in both species do not reflect on the main structure of the masseter muscle. The differences in these elements may be due to the force generated by this muscle in *Bathyergus suillus*. This is the repetitive contraction of the muscle which raises the mandible. (This muscle can be felt at the side of the jaw when the teeth are clenched.)

The **temporalis muscle** is bigger and more powerful than any of the other muscles of mastication in all rodents. It is the major adductor of the jaws. Some authors, such as Russell (1994), described the temporalis muscle in certain rodents to be divided into two: A superficial portion and a deep portion. The findings in this study differ from these authors, in that we found that the temporalis muscles of the mole-rats are not divided. This corresponds to the findings of Hebel and Stromberg (1976) who revealed that the temporalis muscle of rats is not subdivided. A detailed description of this muscle in the two species of this study appears in Section 4.3.2. The orientation of the coronoid process to the molars makes the temporalis the most efficient muscle to crush most objects-as *Bathyergus suillus* would predominantly tend to do. In *Bathyergus suillus*, one may expect the temporalis muscle to be bigger compared to that of *Georychus capensis*, due to differences in utilisation of the masticatory apparatus, but that was not observed here.

Like in any other mammal, the **pterygoid muscles** of rodents are divided into the internal and external pterygoid muscles (Russell, 1994). This study found that it is also the case for the two mole-rat species studied here. Together these muscles are arranged to close the jaws and also to allow transverse jaw motion, which are important during mastication. Both *Bathyergus suillus* and *Georychus capensis* share several similar features with regard to their pterygoid muscles and these are described in detail in Section 4.3.3.

The **external pterygoid** is a jaw depressor muscle in both species. The **internal pterygoid** muscle is the only muscle to have both substantial amplitude of movement and considerable power (Hijemae, 1966). Its orientation suggests that as well as acting with the external pterygoid in producing external movement, it has an important function in antagonizing the tendency of the superficial and deep masseter muscles to evert the angle and lower border of the mandible on contraction (Hijemae, 1966). The internal pterygoid has a constant function in controlling the position of the mandibular angle throughout all masticatory activity as the powerful muscles tend to evert the mandible. In addition, it assists in mandibular elevation and acts as a prime mover in lateral movement.

Investigation of the two pterygoids in this study revealed no significant differences between the two species. The only difference that was found was that, upon observation of the fibres of the internal pterygoid, they appeared to be larger in *Georychus capensis* than in *Bathyergus suillus*. The lack of substantial difference in these muscles between the two species does not correspond to what one would expect from species with different foraging and feeding behaviours. By envisioning the external pterygoid muscle of *Bathyergus suillus* which inserts on the neck of the condyloid process of the mandible, it should appear bigger, because *Bathyergus suillus* is generalist feeder. On other hand, this point of attachment which is the condyloid process is shorter and smaller in *Bathyergus suillus*. This characteristic explains why the external pterygoid muscle is not bigger in *Bathyergus suillus* compared to *Georychus capensis*. In addition the external pterygoid muscle of *Georychus capensis* should appear bigger compared to that of *Bathyergus suillus*, since the site of insertion which is the neck of the condylar process is thicker and larger in *Georychus capensis* (see Section 4.2.11). In addition, the lifestyle (foraging and feeding) of *Georychus capensis* could be expected to increase the activity of the pterygoid muscles, and therefore increase their size, compared to *Bathyergus suillus*. The lifestyle of *Bathyergus suillus* does not require strongly developed pterygoid muscles.

5.3 The functional relationship between the skull and muscles during mastication

The muscular system in a living body performs its functions with the help of the skeletal system. Turner (1998) stressed that the skull provides rigid levers for the masticatory muscles to pull on. Thus the skulls of the mole-rat must adjust its shape and design in order to achieve certain mechanical abilities (Raab & Smith, 1990). The shape of a skull and jaw are profoundly affected by the size and distribution of the jaw muscles. In addition, the powerful action of the four main masticatory muscles has selectively altered the skull morphology (Raab & Smith, 1990).

As in all mammals, the masticatory muscles as well as the jaws of rodents are designed to ensure survival within a specific environment. In this regard Hanney (1975) reasoned for and described various reasons for the evolutionary rapid increase in size of the skull of *Bathyergus suillus*. **Hanney (1975)** refers to the “blue print” that guides the successful survival of rodents. Both *Bathyergus suillus* and *Georychus capensis* are considered to have the same “blue print” for survival. This blue print in rodents, according to Hanney (1975) refers to their heterodont and self-sharpening incisors that are situated in a sturdy skull where an efficient jaw mechanism has evolved. *Bathyergus suillus* finds itself in an environment where it can forage diverse types of food. According to Hanney (1975) these foods provide the large energy requirement needed for its very active foraging lifestyle. This may also account, according to this author, for the larger body size of *Bathyergus suillus*. Regarding *Georychus capensis*, this animal has limited food in its environment, and has to store its food (Jarvis & Sale, 1971). Its feeding activity does thus not require much energy, and the type of food that is available in its environment also does not provide much energy. Consequently these animals do not develop a large body mass.

5.4 Analyses of the interaction between the individual and muscles of the masticatory apparatus of the two species bones

5.4.1 Comparison of the interaction of the angular plate, zygomatic arch and the coronoid process, and the masseter and temporalis muscles in the two species

The **angular plate**, **zygomatic arch** and the **coronoid process**, serve as the main sites of attachment of the masseter and temporalis muscles. The angular plates and the zygomatic arches are points of attachment of the masseter muscles, while the temporalis muscles insert on the coronoid processes. The parameters identified in this study to denote the sizes of these bones are A, ZA, and C2 respectively (see Section 3.4.1 for the legend of these abbreviations). When one compares only the sizes (lengths) of the bones (A, ZA and C2), no difference could be found between the two species as is evidenced in Figs. 3.1 and 3.2 and reported in Table

4.1. This is significant since it is well documented that *Bathyergus suillus* is a larger animal than *Georychus capensis*. It can thus be concluded that the size of the surface areas for attachment of the temporalis and masseter muscles of *Bathyergus suillus* are not different from that of *Georychus capensis*. Also, when one compares the indices of the masseter and temporalis muscles (these indices take into account differences in the sizes of the skulls of the two species (see Table 4.4), no significant differences could be found between these parameters of the two species.

A possible reason why the zygomatic arches, the angular plates and the coronoid processes are similar in size (length measurement) in both species is that they seem to derive, according to Faulkes *et al.* (2003), originally from the same ancestor (*Heterocephalus glaber*). However, from observations in this study, the angular plate of *Bathyergus suillus* does appear thicker and wider than that of *Georychus capensis*. It also appears pushed outward (distorted) to accommodate the masseter muscle in *Bathyergus suillus*. The thickening of the angular plate may be interpreted as the cause of its outwards distortion in *Bathyergus suillus*. These differences in thickness as well as distortion may reflect the idea that the mandible of *Bathyergus suillus* might have been influenced by the stronger actions of the masseter muscles in *Bathyergus suillus*. This finding corresponds to that documented by Miller and Gidley (1918). The masseter muscle acts as a main protractor of the jaw, provides most of the power for chewing and gnawing and is very similar in measurement in the two species. A further difference that was noticed in this study is that the zygomatic arches of *Bathyergus suillus*, which are the point of origin of the masseter muscles, are wider compared to those of *Georychus capensis*.

The deep masseters have essentially the same function as the temporalis muscles. The laterally directed component of the deep masseter tends to evert the mandible and is antagonized by the internal pterygoid (Last, 1978). The masseter is the prime mover in gross protraction of the mandible such as occurs in the transition from mastication to incision. It also acts as an elevator in the protracted position. The superficial masseter acting unilaterally can produce movement of the

mandible toward the contra lateral side. This is antagonized by the internal pterygoid muscle (Last, 1978).

When one considers the feeding behaviour and the lifestyle of *Georychus capensis* and compares it with that of *Bathyergus suillus*, it is apparent that the masseter muscle is used for different needs in the two species. In *Bathyergus suillus* the masseter is used mainly for raising the mandible against the resistance of food and in *Georychus capensis* it is used for elevating the mandible during the digging process. A more complete discussion of this aspect appears in Section 5.4 below.

The **temporalis muscle** function in conjunction with the deep masseter and the pterygoid muscles. In addition, together with the anterior deep masseter they are responsible in the mandibular elevation. The temporalis muscle is also the prime mover of mandibular retraction. This muscle is the major adductor (closer) of the jaws. The orientation of the coronoid process to the posterior teeth makes it the most efficient muscle to crush objects. The sizes of the temporalis muscles of *Bathyergus suillus* and *Georychus capensis* do not exhibit any significant differences as calculated from their actual lengths as well as their indices (see Tables 4.2 and 4.4).

5.4.2 Comparison of the interaction of the condyloid processes and the external pterygoids in the two species

Measurements of the lengths of the **condyloid processes** (C1) (see Table 4.1 and Fig. 3.1) demonstrate that they are significantly smaller in *Bathyergus suillus* (avg. 0.21 cm) than in *Georychus capensis* (avg. 0.47 cm). The **external pterygoid muscles**, via their two heads which lie in a parallel manner, converge and fuse into a short thick tendon that inserts into the pterygoid pit (beneath the medial end of the mandibular condyle). The external pterygoids thus apply force on the condyloid processes. Brooks *et al.* (2001) stated that the external pterygoid muscle is probably the most important muscle in stabilizing and controlling the movement of the condyle in the glenoid fossa. The external pterygoid is a jaw depressor muscle in both species. Together with the internal pterygoids, the

external pterygoids are arranged to close the jaws and also to allow transverse jaw motion. When this muscle contracts it draws the condyle and the disc forwards from the glenoid fossa down the slope of the eminentia articularis (Last, 1978). The external pterygoid muscles must thus be seen to produce a direct force on the condyloid process which may affect its size.

A comparison of the length of the external pterygoid muscles (Table 4.2), as well as the comparison of their indices (Table 4.4), reveals significant differences between that of *Georychus capensis* and *Bathyergus suillus*. The index of the external pterygoid muscle in *Georychus capensis* (I_{ext_G}) (see Table 4.4) is larger by 1.024 g/mm^2 to that of *Bathyergus suillus* (I_{ext_B}). This indicates a larger external pterygoid muscle in *Georychus capensis*. One may thus speculate that in this species this muscle might add other functions to its condyloid process, compared to that in *Bathyergus suillus*. This may for instance, mean that the external pterygoid muscle of *Georychus capensis* allows more intense activity in the type of chewing which is mainly a grinding type rather than vertical chewing. These are side-to-side movements of the temporomandibular joint, with no protraction, retraction and no opening-closing of the mouth. The external pterygoid muscles characteristically elevate the mandible and protract the mandible as well, by pulling the condyles forwards. A more detailed discussion of this follows below.

5.4.3 Comparison of the action of the internal pterygoid muscles during mastication in the two species

Like with the temporalis and masseter of others rodents that no significant difference could be establish between the **internal pterygoid muscles** of the *Bathyergus suillus* and *Georychus capensis* (see Tables 4.2 and 4.4 as well as Figs. 4.15, and 4.20). Both species thus seem to use the three muscles for the same functions. When chewing food, the mouths of these animals does not close like a rat-trap, but the mandible approaches the maxilla with a slewing movement. This grinding between the molars is produced by some antero-posterior as well as lateral excursion of the mandible. The antero-posterior movement of one half of

the mandible is produced by alternate actions of the external and internal pterygoid muscles and the temporalis muscle of the same side – alternately protruding and retruding that side of the mandible. Lateral excursion of the closing of the mandible is produced mainly by the internal pterygoid muscle on the chewing side, pulling the angle of the mandible upwards, forwards and medially. The internal pterygoid muscle antagonizes the unilateral action of the superficial masseter which can produce movement of the mandible toward the contra lateral side.

In both species, like in any other mammals, the internal pterygoid muscle is the only muscle to have both substantial amplitude of movement and considerable power (Hijemae, 1966). Its orientation suggests that, as well as acting with the external pterygoid in producing external movement, it has an important function in antagonizing the tendency of the superficial and deep masseter to evert the angle and lower border of the mandible on contraction (Hijemae, 1966).

In Chapter 2 it was explained that *Bathyergus suillus* and *Georychus capensis* not only find themselves in dissimilar ecological niches, but also display different types of foraging behaviour. One of the objectives of this thesis is to clarify the manner in which the data on the masticatory elements, obtained in this study, relates to these behavioural issues. This will be discussed subsequently.

5.5 The role of the masticatory apparatus during foraging and feeding

Jarvis and Sale (1971) revealed that the differences between Bathyergids are largely attributable to their social structure. This only however refers to only one of the differences among the bathyergids. *Bathyergus suillus* survives on a diet of roots, leaves and the stems of plants that grow above the ground surface. According to Davies and Jarvis (1985), *Bathyergus suillus* is a generalist feeder eating much of what it encounters underground and even pulling the parts of the plants below ground. This group rarely stores food. On the other hand, the diet of *Georychus capensis* consists mainly of geophytes, but they do include grass and other above-ground vegetation in their diet (Broll, 1981). Because *Georychus*

capensis inhabits the mountainous regions of the Western Cape, where food sources are less abundant (Skinner & Smithers, 1990), they have a greatly reduced volume of intake and are regarded as specialist feeders when compared to *Bathyergus suillus* (Davies & Jarvis, 1985).

The feeding behaviour of rodents has a close relationship with their digging abilities and adaptations. Subterranean rodents, like these mole-rats, use both front paws and incisors for digging (Dubost, 1968; Hildebrand, 1985; Nevo, 1979). In their specific environment *Georychus capensis* operates as a tooth-digger. They choose to dig with their teeth because the soil in their environment is harder compared to that of *Bathyergus suillus*. In comparison, *Bathyergus suillus* is predisposed to dig with its teeth and its large front paws because its environment (soil) is softer. According to Brooks *et al.* (2001) the non-feeding functions of the jaws as well as the teeth will affect the shape of the paws and teeth (masticatory elements).

Georychus capensis tends to have relatively smaller front paws and more procumbent and very strong incisors and is like all other mole-rats, unlike *Bathyergus suillus*, a tooth-digger (Jarvis & Sale 1971). The spectrum of soil types that *Georychus capensis* can live in becomes therefore broader than that of *Bathyergus suillus*. Presumably, the chisel-tooth digging reflects in the structural differences in their front paws and incisors compared to *Bathyergus suillus*. The major movement of mastication of *Georychus capensis* is from side to side and the molars can slide across each other because of their complementary surfaces. Their feeding movement is mostly based on grinding because of the coarse contents, like grass, in their diet. In this regard, Brooks *et al.* (2001) emphasises that grass is tough and requires a lot of mastication. Leaves, on the other hand, require less mastication because of their lower fibre content.

Bathyergus suillus appears to have evolved in a rather different way from the remainder of the bathyergids family in that the digging is done not so much with the incisors but rather with the large front paws (Miller & Gidley, 1918). The diet of *Bathyergus suillus* demands active movement of the jaws, like closing and opening in order to perform the chewing. In this way the temporalis and the

masseter muscles are the main active muscles. This is in accordance with (Davies & Jarvis, 1985), who stated that *Bathyergus suillus* is a generalist feeder with a bigger and more powerful temporalis muscle than *Georychus capensis*.

Thus, due to its digging and feeding activities, *Georychus capensis* needs strong incisors where their roots bent as far back as the condyle in order to execute the appropriate actions. *Bathyergus suillus* on the other hand utilizes only its incisors for feeding. This muscle thus provides the necessary force or effort to manage the lower jaw with mainly the assistance of the temporalis and masseter muscles. The lower jaw shall thus act as a rigid lever arm which through the incisors will try to dig the hard soil or move the resisting object. On other hand, during the feeding activity the external pterygoid muscle is needed to apply a force on the condyle, by acting on the lower jaw, in order to chew mainly the tough grass. In addition, Raab and Smith (1990), stressed that the lower jaw, including the condyle, will adapt their shape accordingly. We therefore notice the significant differences of the length of the condyloid process, as well as the length of the external pterygoid muscle between the two species, attributable to the specific masticatory activities of *Georychus capensis*.

In rodents the **incisors** also play an important function during digging. The upper incisors roots of *Bathyergus suillus* do not show any inclination to extend behind the palate and are heavily grooved. These findings are consistent with those of Miller and Gildey (1918), as well as that of Jarvis and Sale (1971). Moreover Miller and Gildey (1918) asserted that there is not any great lengthening of the upper incisors root. So the upper incisors of *Bathyergus suillus* do not show any inclination to extend to the back of the palate or the pterygoids. The findings of this study correspond to those of Roberts (1926) and Walker (1964) who suggested that, since *Bathyergus suillus* has deeply grooved upper incisors with roots that extend above the molars, they should be classified in a family itself. In the contrary my findings mentioned that although the upper incisors are deeply grooved but the roots are not extending below the molars in *Bathyergus suillus*.

5.6 Do the differences in feeding and digging behaviours of *Bathyergus suillus* and *Georychus capensis* reflect in their comparative morphology?

Burrowing in the bathyergids involves an initial excavating period during which the extremely sharp lower incisors are used to dig away at the substratum (Davies & Jarvis 1985; Genelly, 1965). In this study it was noted that the lower incisors of the two species had more deeply grooved incisors that extend as far upwards as the condyle level. However, the lower incisors of *Bathyergus suillus* were relatively smaller in diameter and more curved inward compared to *Georychus capensis* (see Figs. 4.6 and 4.7). This could be attributed to the difference in burrowing method employed by the two species. Both species excavate soil with their lower incisors, but *Bathyergus suillus* uses in addition well-developed claws to burrow the earth. In all African mole-rats, the fore and hind limbs are used to transport the loosened soil of the soil behind the animal.

Although *Bathyergus suillus* is well adapted for feeding on the same type of plant materials like *Georychus capensis* (they belong to the same family), it often inhabits loose sandy soil that have plants with soft roots (Bennett & Faulkes, 2000). They are scratch-diggers, which has led to great enlargement of the claws on the front limbs. They are thus also often reported in residential areas around the Cape Town International Airport where kitchen refuse is dumped. Because of their less tough diet, *Bathyergus suillus* is expected to use more the pterygoid muscles than the temporalis muscles. This facilitates side movements of the jaw along the horizontal plane. *Georychus capensis* on the other hand, has as far as could be established, never been captured near residential areas and live mainly in mountainous areas (Bennett & Faulkes, 2000). These animals are tooth-diggers with very strong upper incisors. They feed on tough plant material and are thus expected to use the temporalis muscle more since a higher percentage of the jaw movements will be vertical rather than horizontal. The investigation thus revealed significant anatomical difference between the two muscles, such as the mean length, under Section 4.4.2.1 and Table 4.2 where the size of temporalis muscle is bigger in *Bathyergus suillus* compared to that of *Georychus capensis*. In Section

4.4.1 and Table 4.4 where the index of the temporalis muscle of *Bathyergus suillus* is shown to be different to that of *Georychus capensis*. These findings are in harmony with those as discussed in the next paragraph.

Davies and Jarvis (1985) mentioned that since *Bathyergus suillus* is a generalist feeder, the temporalis muscle should be bigger. The findings of this study thus concord with the statement of Davies and Jarvis (1985). Langenbach and Van Eijden (2001) added that the variation in the size of the masticatory muscles of Bathyergidae is necessary to adapt to the diet. To defend the more dominant of the two major jaw movements in both species, the structure of the coronoid processes in the two species are notably different. *Georychus capensis* has a longer (above the condyle) and sharper coronoid process (see Figs. 4.6 and 4.7). This serves as attachment for the temporalis muscle. It is possible that the coronoid process could provide a stronger attachment of the temporalis muscle thus favouring the vertical movement of the jaw during mastication.

One can reason that in order to affect a particular foraging behaviour, *Bathyergus suillus* should have more strongly developed masticatory musculature, compared to *Georychus capensis*. These muscles of mastication should fill the large spaces in the broad skull. Due to the type of foraging activities of *Bathyergus suillus* the temporalis and the masseter muscles will be used for constant vertical mastication compared to *Georychus capensis*. Thus these two muscles should be more developed than those of *Georychus capensis*. *Georychus capensis* seems to occasionally use the temporalis and the masseter muscles compared to *Bathyergus suillus* because of its environment. *Georychus capensis* seems to apply an horizontal mastication by using the external pterygoid muscle constantly, in addition to the internal pterygoid muscle, compared to *Bathyergus suillus*. The difference of the mean length of the external pterygoid muscles between the two species is 1.06 cm (see Fig. 4.16), with that of *Georychus capensis* being the greater.

In brief, to answer the question if there are any differences in the anatomy that seem to be adaptive to the contrasting digging methods of *Bathyergus suillus* and *Georychus capensis*, one can summarise that the data obtained here as follow: On

one hand, most of the differences measured can be attributed to the fact that *Bathyergus suillus* is bigger than *Georychus capensis*. On the other hand, there are notable exceptions to this pattern that becomes clearer when the size factor is brought into by creating an index. These exceptions are listed in Section 5.2.2.

5.7 The use of indices to compare anatomical parameters

The anatomical indices proposed and used in this study represent a ratio of measurable value to another value but easily measured. This is similar to the body mass index principle which is calculated as body mass of subject divided by the square of the length of the subject. In human the BMI will give indication about the obesity of the patient. The rationale for using the masticatory muscles indices here was to use it as to compensate for differences in size of the two species. This ratio should confirm the differences observed between the two selected species. One may consider that since *Bathyergus suillus* is a bigger animal than *Georychus capensis* the masticatory muscles indices should be higher. However, in this study this was not found to be the case. The ideal will be to have a recommended range which might assist in the interpretation of our results. Thus the index appears merely as an “indicator” which is subject to many variations due to many factors. Perhaps by putting together the body mass index of each sample and its corresponding masticatory muscles index, one will add value to our new masticatory muscles index.

In our investigation the results about the indices should perhaps serve as a guide, since they do not appear accurate. According to Harvey (2004) we lack equivalent measures for most of animals. He goes on to stress that veterinarians currently rely on charts to determine partly on the basis of look and feel, or whether animals are obese.

In further research design one should consider the mass of the whole head of each sample, in order to obtain perhaps a sufficient masticatory muscle index. Therefore is it advisable to utilise only this new method to confirm or deny differences or similarities in the masticatory muscles between *Bathyergus suillus* and *Georychus capensis*?

5.8 Conclusion

Both neotologists and paleontologists have been trying for the past two hundred years to understand the evolutionary relationships among rodent groups. There have been several attempts to classify these rodents based on different criteria, often based on the morphology and the masticatory apparatus. Thus for example, the classification of Brandt (1855) divided rodents according to the origin and insertion of the masseter muscles, the morphology of the associated infraorbital foramen and the zygomatic arch. Simpson (1945) relied on differences in skull morphology, mainly of the zygomatic arch, and the origin and insertion of the different masticatory muscles. Currently, there is no broad consensus about the detailed classification of rodents. The lack of detailed anatomical studies of the various members of rodents is perhaps a major obstacle to finding a rigorous classification of rodents. While this study does not focus on the classification of rodents, it does attempt to contribute to the body of data that can be used in clarifying the taxonomic relationships between rodent groups – in particular that of the bathyergids' family.

This study provides a record of the osteology and myology of the masticatory apparatus of *Bathyergus suillus* and *Georychus capensis*. The data reported here can thus be added to the pool of taxonomic data currently available on the general anatomy of the rodents, and the bathyergids in particular, and so assist in completing the anatomical records of this vast group of animals.

In addition to recording the above parameters, this study also sheds some light of some comparative aspects of the masticatory apparatus of two mole-rat species. Having recorded this comparative data, this study suggests that, based on the morphology of the incisors, these two species may be separated into different families. More data however is needed to support such a suggestion.

Bathyergus suillus lives among abundant food. It has a well-developed and broad skull compared to *Georychus capensis*. The roots of the grooved upper incisors of *Bathyergus suillus* do not extend far below the molars. However, *Georychus capensis* is a tooth-digger and lives in the mountain, with a limited diet. It has

been shown that although their upper incisors are un-grooved, their roots extend far below the molars. The roots of the lower incisors of both species bend as far as supporting the condyle. Comparisons of the zygomatic arches indicate that they are similar in both species. With regard to the parietal bones there is a more prominent parietal crest that crosses the parietal bone in *Georychus capensis*. The comparison of the coronoid processes revealed that the coronoid process of *Georychus capensis* appears thinner and longer, whereas the coronoid process of *Bathyergus suillus* is shorter. The condyloid process of *Bathyergus suillus* however, is rounded, shorter and deflected, while the condyloid process of *Georychus capensis* is oval-shaped. In addition, the deflection backward and slightly inward bend of this condyle creates a “post-condylar notch” which is unique to *Bathyergus suillus*. The angular plate of *Bathyergus suillus* is also thicker and larger than that of *Georychus capensis*.

The external pterygoid muscle is inserted on the neck of the condyle of the lower jaw and the morphometric analysis here demonstrates that these two parameters (external pterygoid muscle and condyle) of the jaw system of *Georychus capensis* differed from that of *Bathyergus suillus*. These differences (the condyloid process of *Bathyergus suillus* is rounded, shorter and deflected, while that of *Georychus capensis* is larger and oval-shaped) are related to the differences in feeding behaviour of the two species. In addition the calculation of the index of the external pterygoid muscles confirms differences between the two species. Table 4.4 thus shows 68% of the nine observations the external pterygoid muscles indices do not show a significant overlapping. And those observations fall between the intervals mean indices value. On contrary, according to our results the temporalis, masseter, and the internal pterygoid muscles have similar features in both species. This is indicated by the indices given in Table 4.4 which do not show any significant statistical difference.

One of the main questions that drive this study pertains to whether differences in feeding and digging behaviours of *Bathyergus suillus* and *Georychus capensis* reflect in their comparative morphology?

In brief, *Bathyergus suillus* uses its masticatory apparatus mainly for feeding, while *Georchus capensis* uses it for both feeding and digging. Thus, are there subtle differences in the anatomy that seem to be adaptive to the contrasting digging methods. This study records several differences between *Bathyergus suillus* and *Georchus capensis* (see Section 5.2.1). It seems that tooth-digging was an early adaptation in the Bathyergidae. The oldest living bathyergid (4-45 mya) is *Heterocephalus* which is a tooth-digger (Faulkes *et al.*, 2003). Ironically, *Bathyergus suillus* is a scratch-digger, although genetically it seems to be closely related to *Heterocephalus*. It seems the question that should be asked is why is *Bathyergus suillus* different from the other bathyergids? It may be that it is a fairly recent response to their invading sandy habitats where their sharp teeth are not needed for digging through the soft sand (Faulkes *et al.*, 2003). Their size (for energy reasons) and digging method now restricts them to soft sandy soils of coastal habitats. *Georchus capensis*, on the otherhand, can use its teeth to dig through a variety of soil types – not just mountainous habitats.

This study also attempted and suggested a new way to compare anatomical parameters of species that are related but which have significant difference in body size by introducing the concept of the anatomical index of anatomical parts. This method was not very successfully applied in this thesis and the wide range of measurements for individual parameters that were encountered may account for this. Further refinement of this method needs to be done.

In particular, this study needs further explorations about the skull of *Bathyergus suillus* and *Georchus capensis*, in order to elaborate for instance on the breadth of the skulls of both species. On the other hand, the study should further focus on the digging apparatus of one of the selected species, or elaborate only on the feeding behaviour of two selected mole-rats, e.g. (*Bathyergus suillus* and *Georchus capensis*). Ribot (2002) suggested that skull morphology probably reflects not only environmental parameters but historical factors too. The question might be whether changes in both shape and size of the mandible can be the result of biomechanical stresses induced by subsistence shifts. Thus additional studies should explore this aspect. Perhaps, it could be worthwhile to investigate further

analyses on both metric and non metric traits of the skull – especially that of the mandible (Ribot, 2002), as well as with the use of three dimensional methods that are adapted to study complex morphologies (Friess, Marcus, Reddy & Delson, 2001; Hennessy & Stringer, 2002). Further studies may need to consider the measurement of the width of the four muscles of mastication, which might help to obtain the volume of the selected muscles. Although the literature do not mention differences in the masticatory anatomy of African mole-rats based on the gender, we believe that further studies should take into account the problem of the gender of both species.



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