**Title: Functional implications of craniomandibular morphology in African mole-rats (Rodentia: Bathyergidae)**

**Running head: Bathyergid functional morphology**

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**ABSTRACT**

African mole-rats are subterranean rodents from the family Bathyergidae. The family consists of six genera, five of which (*Cryptomys, Fukomys, Georychus, Heliophobius and Heterocephalus*) are chisel-tooth diggers, meaning they dig underground using procumbent incisors. The remaining genus of mole-rat (*Bathyergus*) is a scratch digger, which digs using its forelimbs. Chisel-tooth digging is thought to have evolved to enable exploitation of harder soils. It was hypothesised that in order to dig successfully using incisors, chisel-tooth digging mole-rats will have a craniomandibular complex that is better able to achieve a large bite force and wide gape compared to scratch digging mole-rats. Linear measurements of morphological characteristics associated with bite force and gape were measured in a number of chisel-tooth digging and scratch digging mole-rats. It was found that chisel-tooth diggers have increased jaw and condyle lengths relative to their size (characteristics associated with larger gape). They also have relatively wider and taller skulls (characteristics associated with larger bite force). The mechanical advantage of three masticatory muscles of each specimen was also calculated. Mechanical advantage of the temporalis muscle was found to be significantly larger in chisel-tooth digging mole-rats compared to the scratch digging genus. Our results demonstrate that chisel-tooth digging bathyergids have a craniomandibular morphology better able to facilitate high bite force and wide gape than scratch digging mole-rats.

**Keywords: Masticatory biomechanics; chisel-tooth digging; scratch digging; Bathyergidae; mole-rats; subterranean rodents**

**INTRODUCTION**

Morphological correlates of digging in subterranean rodents have been well documented (Nevo, 1979) and may be the result of numerous different evolutionary strategies. Lessa and Thaeler (1989) proposed two alternative evolutionary strategies for digging in two genera of pocket gopher: an increase in incisor procumbency to facilitate chisel-tooth digging versus an enlargement of the forearms to enable scratch digging. Scratch digging primarily involves soil removal via enlarged forelimbs, and is used by numerous fossorial mammals, including many rodents (e.g. Dubost, 1968; Hildebrand, 1985; Reichman and Smith, 1990; Nevo, 1999). Chisel-tooth digging, which involves the use of incisors powered by head and jaw muscles to remove compact soil, evolved to allow subterranean species to exploit harder soils (Lessa and Thaeler, 1989) and is associated with many morphological traits such as more procumbent incisors, wider crania, enlarged zygomatic arches, longer rostra and larger temporal fossae (Landry, 1957a; Agrawal, 1967; Lessa, 1990; Samuels and Van Valkenburgh, 2009).

Incisor procumbency, the angle of the incisor protruding from the rostrum or mandible, is a well-studied morphological trait associated with chisel-tooth digging (Lessa, 1990). Stein (2000) notes that, although chisel-tooth digging is accomplished primarily by the lower incisors, with the upper incisors being used to anchor the skull to the soil (Jarvis and Sale, 1971), it is the upper incisors that show greater variability in their procumbency. An example of this exists in the rodent family Bathyergidae (the African mole-rats or blesmols), in which the chisel-tooth diggers *Cryptomys* and *Georychus* have been shown to have significantly greater upper incisor procumbency compared with the scratch digger *Bathyergus*. Lower incisor procumbency however was not significantly different between the three genera (Van der Merwe and Botha, 1998). This association between upper incisor procumbency and chisel-tooth digging is said to allow a more favourable angle of attack for anchoring the head of the rodent to the burrow wall when compared to more recurved upper incisors (Lessa, 1990; Vassallo, 1998; Korth and Rybczynski, 2003). Upper incisor procumbency is influenced by the degree of curvature of the incisor and the position of the incisor in the rostrum (Landry, 1957a; Akersten, 1981). Within the Bathyergidae, the root of the incisor of chisel-tooth diggers extends behind the molar tooth row, a trait unique amongst rodents (Ellerman, 1940). This is in contrast to the scratch digging *Bathyergus*, whose upper incisor is rooted above the first molar. It has been suggested by Van der Merwe and Botha (1998) that the posterior displacement of the upper incisor root in chisel-tooth digging rodents promotes increased procumbency. In addition, Landry (1957a) suggested that an increase in the length of the incisor located within the rostrum would increase the area of contact between tooth and skull, and so would help dissipate biting forces more effectively, thus protecting the region of odontogenesis at the posterior end of the incisor.

Bite force and gape are limiting factors for animals in the context of their feeding and behavioural ecology. For instance, the force at which an animal can bite will limit the range of hardness of food items that the animal can consume, with previous studies showing a correlation between bite force, food mechanical properties and diet (e.g. Kiltie, 1982; Binder and Van Valkenburgh, 2000). In contrast, gape limits the size of food that an animal can ingest (e.g. Gans, 1961; Herring and Herring 1974; Pough and Groves, 1983; Wheelwright, 1985). Although bite force and gape have been widely studied in the context of dietary inferences (Herrel et al, 2001; Dumont and Herrel, 2003; Vinyard, 2003; Taylor and Vinyard 2004; Williams et al, 2009; Santana et al, 2010), very little research has focused on behaviour such as fossorial activity (Van Daele et al, 2009). Furthermore, despite several studies on morphological predictors of bite force and gape, few have combined morphological predictors with biomechanical modelling to show how morphological traits affect the biomechanics of the system.

The main aims of this study were to highlight key morphological traits in the craniomandibular complex that would improve the performance of bite force and/or gape in a particular family of subterranean rodents, the African mole-rats (Bathyergidae). Bathyergids are especially interesting when investigating the morphological correlates of digging because chisel-tooth digging is seen in five of the six genera of bathyergids (*Cryptomys, Fukomys, Georychus, Heliophobius and Heterocephalus*), whereas *Bathyergus* is the only genus to use the scratch digging method (Nowak, 1999; Stein, 2000). Furthermore, recent phylogenies (Figure 1; Faulkes et al, 2004; Seney et al, 2009; Patterson and Upham, 2014) agree that the scratch digging genus *Bathyergus* is nested deep within the crown of Bathyergidae, indicating that chisel-tooth digging is ancestral for the family and has been lost in *Bathyergus*. Despite this, previous research has shown that the cranium of *Bathyergus* is morphologically different from the chisel-tooth digging bathyergids, having more in common with other, more distantly related scratch digging rodents (Samuels and Van Valkenburgh, 2009). Thus, the skull of *Bathyergus* has changed, either by adaptation to a different selection pressure, or by genetic drift owing to the release of the constraint of chisel-tooth digging.

The objective of this study is to ascertain whether the cranial morphology of chisel-tooth digging bathyergids better facilitates high bite force and wide gape than does the cranial morphology of the scratch digging *Bathyergus*. We hypothesise that the change in morphology of *Bathyergus*, whether mediated by selection or drift, will have decreased its tooth digging abilities, which will be manifest in reduced bite force and gape. Based on previous work there are a number of predictions that can be made:

*Morphological predictions related to bite force*

An increase in bite force has been found to be strongly correlated with an increase in head height in *Fukomys* mole-rats (Van Daele et al, 2009) and bats (Dumont and Herrel, 2003). We therefore hypothesise that chisel-tooth diggers will have relatively increased head heights compared to scratch diggers.

Chisel-tooth diggers tend to have broader zygomatic arches and larger temporal fossae to accommodate larger, more powerful masticatory muscles (e.g. Hildebrand, 1985; Stein, 2000; Samuels and Van Valkenburgh, 2009) and so it is hypothesised that chisel-tooth diggers will have relatively wider crania compared to scratch diggers.

An increase in upper incisor procumbency has been shown to be associated with chisel-tooth digging in a number of subterranean rodents (Landry, 1957a; Lessa, 1990; Vassallo, 1998; Samuels and Van Valkenburgh, 2009). This increase in procumbency has also been associated with an increase in rostral length (Lessa and Patton, 1989; Mora et al, 2003). It was therefore hypothesised that chisel-tooth digging rodents will have an increased upper incisor procumbency and a longer rostrum compared to scratch diggers.

*Morphological predictions related to gape*

Gape has been shown to be strongly predicted by jaw length in animals whose masticatory biomechanics have been extensively studied, such as snakes (e.g. Hampton and Moon, 2013). Vinyard and Payseur (2008) also found a significant correlation between maximum gape and jaw length in classical inbred strains of house mice. In addition, the cranium and mandible in rodents strongly co-vary (Hautier et al, 2012). As it has been hypothesised that rostral length increases in chisel-tooth digging rodents, if this covariation occurs in subterranean rodents, then it is also expected that there will be an increase in jaw length combined with that of rostral length in chisel-tooth digging rodents. Thus, it is hypothesised that chisel-tooth diggers will have a relatively longer jaw compared to scratch diggers.

Elongated antero-posterior lengths of articulating joint surfaces are known to increase joint mobility (Ruff, 1988; Hamrick, 1996). An increased antero-posterior length of the condyle articular surface has also been linked to increased gape in primates (Vinyard et al, 2003) and house mice (Vinyard and Payseur, 2008). Gape also increases theoretically in mammals with reduced condyle heights (height of condyle above the molar tooth row) as this reduces stretch in masticatory muscles during gape (Herring and Herring, 1974). Hence, we hypothesise that chisel-tooth digging mole-rats will have lower condyles with longer articulating surfaces than the scratch digging genus *Bathyergus*.

*Biomechanics of a chisel-tooth digger*

The performance of the masticatory apparatus is traditionally assessed by modelling the jaw as a static third class lever and calculating mechanical advantage (MA) of each masticatory muscle (Maynard Smith and Savage, 1959). MA is the ratio of the muscle moment arm to the jaw moment arm and is affected if either moment arm is changed within the system. The jaw moment arm is the distance from the pivot (in mammalian masticatory biomechanics this is equivalent to the temporomandibular joint [TMJ]) to the bite force vector, and the muscle moment arm is the perpendicular distance from the TMJ to the muscle force vector. Movement of the bite point towards the TMJ (assuming constant muscle attachments) will result in a higher MA, as the jaw moment arm has been reduced. This biomechanical definition explains why there is a trade-off between gape and bite force. An increase in jaw length is associated with larger gape (e.g. Hampton and Moon, 2013) but will also increase the jaw moment arm, reducing the MA of the masticatory muscle, and therefore reducing bite force. It is clear that craniomandibular traits that facilitate an increase in gape thus decrease bite force capabilities, and vice versa. Due to this trade-off, animals that need both large gapes and large bite forces, e.g. carnivores, may show unique morphological traits. Animals that must produce high bite forces at large gapes normally have larger temporalis muscles compared to animals that produce larger bite forces with smaller gapes, in which case the masseter dominates (Turnbull, 1970). It was therefore hypothesised that in chisel-tooth digging subterranean rodents, the temporalis muscle would have a higher mechanical advantage compared to that of scratch digging subterranean rodents to enable the production of a high bite force at large gape. It was also hypothesised that MA of temporalis would be maintained at larger gapes in chisel-tooth diggers compared to scratch diggers.

**MATERIALS AND METHODS**

A sample of 47 crania and mandibles from the subterranean rodent family Bathyergidae, representing adult mole-rats of both sexes, were used in this analysis. The sample comprised five species of chisel-tooth digging rodents (*Cryptomys hottentotus*, *Fukomys mechowi*, *Georychus capensis*, *Heliophobius argenteocinereus* and *Heterocephalus glaber*) and one species of scratch digging rodent (*Bathyergus suillus*), representing all six extant genera of bathyergid mole-rats. The specimens were scanned on an X-Tek Metris microCT scanner at the University of Hull (Medical and Biological Engineering Research Group), and the resulting scans had isometric voxels ranging between 0.01-0.07 mm. MicroCT scans were automatically reconstructed in Avizo 8.0 (FEI, Hillsboro, OR) using a predefined grey scale to render a 3D volume of each specimen (Figure 2). From the reconstructions, 3D landmark co-ordinates were recorded to enable the calculation of six linear measurements – three from the cranium (cranial width, head height and rostral length) and three from the mandible (jaw length, condyle length and condyle height). In addition, the procumbency angle of the upper incisor was measured based on the method outlined in Landry (1957a). All measurements taken are detailed in Table 1 and Figure 3. Linear measurements were scaled relative to basilar length (the midline distance along the cranial base from the anterior extremity of the premaxillae to the margin of the foramen magnum). Each linear measurement was also regressed against basilar length to show the effects of allometric scaling. Due to the error contained in the variables and the ambiguity of dependence between variables, a reduced major axis model was fitted (Sokal and Rohlf, 1981). Both variables were logged in order to fit the standard allometric equation, y=axb. The slope, *R*2 and *P* values for each allometric equation are given in Table 2. For visualisation purposes the data were displayed as box plots, with each genus shown separately. However, owing to small sample sizes of *Cryptomys*, *Georychus* and *Heterocephalus*, for statistical testing the specimens were grouped by digging method. Between 10 and 11 specimens of the scratch digging *Bathyergus*, and between 25 and 36 specimens of chisel-tooth digging mole-rats were included in each analysis. Following Ruxton (2006), the unequal variance *t*-test (Welch’s *t*-test) was used to test for significant differences between the scratch digging and chisel-tooth digging groups, except where there was evidence of non-normality in the data, in which case the non-parametric Mann-Whitney *U* test was employed. The normality of the data in each group was tested using the Shapiro-Wilk test. All statistical tests were performed using PAST (Hammer et al, 2001). To check that the over-represented chisel-tooth genera (*Fukomys* and *Heliophobius*) were not unduly influencing the results, the tests were rerun using just five randomly-selected specimens of each; however, the results were unchanged.

In addition to the cranial and mandibular measurements outlined above, the performance of three major masticatory muscles (superficial masseter, deep masseter and temporalis) was measured in each specimen for a comparison between chisel-tooth digging and scratch digging systems. These muscles were selected as together they make up over 80% of the masticatory muscles in mole-rats (Bekele, 1983; Cox and Faulkes, 2014). Performance was measured by calculating the MA of each muscle using moment arms (Figure 4; example using temporalis muscle). Muscle moment arms (MMA) were calculated for the selected muscles, along with the jaw moment arm (JMA) for each specimen. Mechanical advantage was calculated as the ratio between these two variables.

The cranium and mandible of each specimen were re-orientated with respect to one another in Avizo 8.0 to simulate incisal occlusion (Figure 4). Incisal occlusion was defined by the tips of the upper and lower incisor being in contact, and each mandibular condyle being in contact with the articular surfaces of the corresponding glenoid fossa. Following this, a bite force vector (BFV) was defined as a line going directly through the incisor bite point (point of contact between incisors), orthogonal to the occlusal plane of the hemi-mandible. JMA was calculated as the perpendicular distance from the fulcrum (condyle tip) to the BFV (see Figure 4). The incisor was the only bite point chosen in this study as chisel-tooth digging is carried out exclusively by the incisors.

The angle between the jaw moment arm and the line from the fulcrum to the bite point (angle θ, Figure 4) was calculated using trigonometry in 3D. The occlusal plane is defined as the plane on the mandible containing points at the posterior edge of the tooth row and points at the medial and lateral sides of the third mandibular molar. The angle between the occlusal plane and the line connecting the fulcrum and bite point (dashed line in Figure 4) was then calculated using the dot product:

Where **n** is the normal vector to the occlusal plane and **m** is the vector of the line representing the distance from the fulcrum to the incisor bite point. As the occlusal plane runs parallel to the JMA, θ is equivalent to the angle between JMA and the line representing the distance between fulcrum and incisor bite point. The JMA can then be calculated using standard trigonometry.

MMA is calculated as the perpendicular distance from the fulcrum to the muscle force vector (MFV). MFV was defined by a line going through the centre of the origin and insertion of each muscle (see Figure 2). The origin and insertion of each muscle was defined by placing a curve on the dorsal border of each muscle origin on the cranium and the ventral border of each muscle insertion on the mandible. The curve was placed via a B-spline in Avizo 8.0, and automatically divided into 100 equidistant points. Thus the centre of each origin and insertion could be established to represent the directionality of the muscle force. Note that no curve was placed on the insertion of temporalis or the origin of superficial masseter as these muscle attachment areas were small enough to be represented as a single point. MMA was then calculated using standard trigonometry.

In order to evaluate the effect of gape on mechanical advantage, a rotation matrix was used to rotate the co-ordinates lying on the mandible around an axis running through the landmarks representing the dorsal points on the condylar surfaces on the left and right side of the mandible (thus simulating mandibular rotation):

Where) is the point being rotated about the line through with a direction vector of by angle . The direction vector is defined by the tips of the left and right condyles.

It is also worth noting that the theoretical maximum gape of this model was deemed to be the angle where mechanical advantage was a minimum. This assumption originates from the fact that beyond a certain angle of rotation, the mandibular insertion of the muscle will move posterior to the fulcrum, and therefore from that point would operate to open the jaw, not close it. Limitations of this model will also be discussed below.

**RESULTS**

*Morphological predictors of bite force (including upper incisor procumbency)*

The results of the comparisons of head height, cranial width, procumbency angle and rostral length between chisel-tooth and scratch digging bathyergids are displayed in Figure 5. Unequal variance *t*-tests indicated that there are significant differences in relative head height (*t*=-10.37, *P*<0.01) and relative cranial width (*t*=-8.51, *P*<0.01) between chisel-tooth and scratch digging genera. Chisel-tooth digging bathyergids have relatively taller and wider crania than the scratch digging genus, *Bathyergus*. Upper incisor procumbency angle also appeared to be larger in chisel-tooth digging genera compared to *Bathyergus* (*t*=-4.03, *P*<0.01). However, Figure 5C, which represents upper incisor procumbency angles according to each genus, shows that some of the lowest procumbency angles were recorded in specimens of the chisel-tooth digging genus *Heterocephalus*, the naked mole-rat. In comparison, rostral length failed to separate chisel-tooth and scratch diggers. Although *Bathyergus* was predicted, as a scratch digger, to have a relatively shorter rostrum than the chisel-tooth digging genera, no statistically significant difference between the groups was found. Interestingly, *Heterocephalus* also appears to display the shortest rostrum according to Figure 5D, but owing to small sample sizes in some genera, the differences between genera could not be tested statistically.

*Morphological predictors of gape*

The visual comparisons of jaw length, condyle length and condyle height between bathyergid genera are displayed in Figure 6. Chisel-tooth diggers exhibit significant differences in all morphological predictors of gape compared to scratch diggers. A Mann-Whitney *U* test showed that chisel-tooth digging bathyergids have relatively longer lower jaws (*U*=0, *P*<0.01). Unequal variance *t*-tests showed that chisel-tooth diggers have relatively longer condyle articulating surfaces (*t*=-13.58, *P*<0.01) and relatively increased condyle heights (*t*=-2.71, *P*<0.05).

*Allometric relationship of morphological traits*

The allometric equations of the morphological predictors of bite force and gape are displayed in Table 2. All variables were found to strongly correlated with basilar length except for upper incisor procumbency. The mandibular measurements (condyle height, condyle length and jaw length) all scaled with negative allometry (slope<1). Within the cranium, head height and cranial width also scaled with negative allometry. However, rostral length scaled with slightly positive allometry (slope>1). Upper incisor procumbency was not significantly correlated with basilar length (*P*>0.05).

*Biomechanical implications of morphological traits*

Biomechanically modelling the moment arms of the three selected muscles showed the potential impact on the digging/masticatory system from the morphological differences found between chisel-tooth and scratch diggers. At 0° gape, the MA of the temporalis muscle was shown to be significantly different between *Bathyergus* and the chisel-tooth digging bathyergids (*U*=6, *P*<0.01). No such statistical difference was found for the MA of the superficial or deep masseters.

The effect of gape on the mechanical advantage of the three selected masticatory muscles was tested by applying rotation matrices to the landmarks representing muscle insertion points on the mandible. The results (Figure 7) show that for each muscle, increasing gape decreases the mechanical advantage to a minimum point, which varies depending on the genus, beyond which the MA starts to rise again. For example at 0o gape, the mechanical advantage of the temporalis muscle shows a significant difference between chisel-tooth digging and scratch digging genera (see above). However, at around 40o this changes and the mechanical advantage of the scratch digging genus *Bathyergus* begins to increase from its lowest point (Figure 7A). The mechanical advantages of the chisel-tooth digging genera reach their lowest points at higher gape angles, with *Heliophobius* only reaching its lowest MA close to 90o, before increasing.

The effect of gape on the superficial and deep masseters is slightly different compared to the temporalis. Increasing gape decreases mechanical advantage of both masseter muscles at a faster rate compared to the temporalis in all genera. The mechanical advantages of the masseter muscles also reach their lowest values at a larger gape than the temporalis. The lowest MA of the superficial masseter for all genera is in the range of 80-90o before it begins to increase (Figure 7B), and the MA of deep masseter does not seem to reach a minimum for any genus at gapes up to 100o (Figure 7C). It is worth noting at this point that all gape angles are theoretical and may not be achievable in reality. The problems of interpretation of these graphs will be discussed below.

**DISCUSSION**

*Bite force*

Our results indicate that the cranium and mandible of chisel-tooth digging bathyergids are able to produce a larger bite force at the incisors than the scratch digging *Bathyergus*. We found that chisel-tooth diggers had significantly wider crania and taller heads (relative to basilar length) compared with the scratch digger *Bathyergus*. Subterranean rodents tend to have larger skulls than their terrestrial counterparts in order to accommodate larger, more powerful masticatory muscles (Stein, 2000). This trend has accelerated in chisel-tooth diggers, with Samuels and Van Valkenburgh (2009) finding that the skulls of chisel-tooth diggers showed broader rostra, wider zygomatic arches and larger temporal fossae compared to scratch digging rodents, including *Bathyergus*. This supports the results presented in this study, adding to the evidence that chisel-tooth digging is associated with relative enlargement of both the masseter and temporalis muscles (Stein, 2000).

Head height has previously been shown to be a strong indicator of bite force in *Fukomys* by Van Daele et al (2009). However, the authors did not explain exactly how they measured this variable. In our study, head height only included the cranium, from the posterior margin of the palate to the bregma, which may have been different to the measurement reported by Van Daele et al (2009). Nevertheless, head height measured here differentiated the chisel-tooth diggers from the scratch diggers. An increase in the relative head height of chisel-tooth diggers is probably the result of enlarged temporal fossae, as the variable incorporates this region of the skull. The temporalis muscle has been shown to be the dominant masticatory muscle in the chisel-tooth digger *Heterocephalus*, with temporalis accounting for 32% of all masticatory muscles (Cox and Faulkes, 2014). Similar dominance of the temporalis muscle is also seen in *Fukomys*, accounting for a range of around 25% (Van Daele et al, 2009). This proportion of the masticatory muscle is very large in comparison to other hystricognathous rodents e.g. *Cavia* (11%: Cox and Jeffery, 2011), *Hydrochoerus* (5%: Müller, 1933) and *Hystrix* (17%: Turnbull, 1970). Interestingly, temporalis dominance similar to mole-rats is also reported in sciuromorph rodents (25-30%: Druzinsky, 2010) which, like *Fukomys*, have a large bite force for their size (Freeman and Lemen, 2008). Furthermore, a comparative study of the chisel-tooth digger *Georychus* and scratch digger *Bathyergus* found that *Georychus* had a relatively larger temporalis than *Bathyergus* (Kouame et al, 2006). It is clear that the temporalis muscle, along with the other masticatory muscles, is dominant in chisel-tooth digging mole-rats, and may be one of the driving factors behind a relatively increased head height.

The biomechanical impact of this presumed difference in temporalis size was measured by calculating the MA of the muscle (along with that of the superficial and deep masseters). The results show that there is a significant increase in temporalis MA in chisel-tooth diggers compared with the scratch digger. This may be a result of the change in the temporal fossa morphology, which potentially explains why the temporalis takes up a larger proportion of the masticatory muscles in chisel-tooth diggers compared to other rodents. Enlarged temporal fossae are a characteristic that distinguishes the cranial shape of chisel-tooth and scratch digging rodents (Samuels and Van Valkenburgh, 2009). However, Stein (2000) notes that the crania of subterranean rodents are usually dorsally flattened compared to non-subterranean rodents. This study suggests that this flattening is reversed in chisel-tooth diggers in order to increase the size of the temporal fossa and hence produce greater bite forces at the incisors. So then why doesn’t *Bathyergus,* the only scratch digger genus within the Bathyergidae, retain this chisel-tooth digging cranial shape, given that its phylogenetic position within the family (Figure 1) suggests evolution from a chisel-tooth digging ancestor? *Bathyergus* lives in soft soils in Southern Africa, so it is possible that a dorsally flattened skull is an optimum shape to move efficiently through an underground burrow in such a substrate. In order to exploit areas with harder soils, chisel-tooth digging mole-rats have had to adapt their skulls to incorporate a larger temporalis for improved bite force at the incisors. The relaxation of this selection pressure for high bite force may have driven the cranium of *Bathyergus* to revert to the more usual morphology for subterranean rodents.

In addition to changes in muscle attachment areas, there are a number of other potential forces that could have resulted in this increased height height in chisel-tooth diggers. It is possible that variation in head height amongst bathyergids may also be a result of variation in relative brain size. Previous work has indicated that subterranean rodents have relatively small brains (Mace et al, 1981; Vassallo and Echeverría, 2009). However, *Bathyergus* is the largest genus of the Bathyergidae and so its brain is likely to be relatively even smaller owing to the negative allometry between brain and body size. Thus, a relatively smaller brain in *Bathyergus* would require a relatively smaller braincase, which would lead to a reduction in head height. Another alternative is evident in how the upper incisor is positioned within the skull of the bathyergids. Chisel-tooth digging rodents require a longer upper incisor within the skull in order to increase the angle of procumbency. In non-bathyergid chisel-tooth digging rodents (e.g. *Ctenomys* and *Spalacopus*), these large incisors are located in alveolar sheaths that are lateral to the cheek teeth and avoid the internal cranial space (Lessa, 1990). Chisel-tooth digging bathyergids incorporate this enlarged incisor high on the rostrum and orbit, before inserting behind the cheek teeth, as is shown in Figure 2. This configuration may have influenced the overall architecture of the skull by increasing height head in chisel-tooth digging bathyergids. Within *Bathyergus*, the incorporation of an upper incisor is exclusive to the rostrum and inserts anterior to the cheek teeth and so does not require a modification to the rest of the cranium. These explanations and the scenario based on temporalis size are not necessarily mutually exclusive and may all be in operation.

Rostral length did not differentiate between chisel-tooth and scratch digging (Figure 5D), which was rather surprising considering the significant increases found in chisel-tooth digger jaw length (Figure 6A) and the covariation found between the cranium and mandible of hystricognath rodents (Hautier et al, 2012). Samuels and Van Valkenburgh (2009) also found that chisel-tooth diggers have longer rostra compared to scratch diggers, but this pattern has not been found within the context of the bathyergids here. In fact the only notably different rostral length was that of the chisel-tooth digger *Heterocephalus*, which appears to have a shorter rostrum compared to the other bathyergids (Figure 5D). An increase in rostral length has been associated with an increase in incisor procumbency in some subterranean rodents (Lessa and Patton, 1989; Mora et al, 2003). However, such an increase would not be necessary in chisel-tooth digging bathyergids with procumbent incisors owing to the displacement of the incisor roots posteriorly within the skull (Landry, 1957a; Figure 2). Overall, rostral length was shown to be positively allometric in Bathyergidae, which has previously been noted in other mammalian orders (Radinsky, 1985).

*The curious case of the naked mole-rat*

The apparent reduction of rostral length in *Heterocephalus* has previously been proposed to have occurred to shorten the out-lever of the masticatory system and hence increase the mechanical advantage of the masticatory muscles (Cox and Faulkes, 2014). This is probably not the case for two reasons: firstly, the relative reduction in the rostrum would be likely to be seen in the other chisel-tooth digging bathyergids, which it is not; secondly, as chisel-tooth digging is accomplished primarily by the lower incisors (Stein, 2000), a decrease in the out-lever of the masticatory system would require a decrease in lower jaw length, not rostral length. However, lower jaw length has actually increased in all chisel-tooth diggers (see Figure 6A).

The reduced rostrum found in *Heterocephalus* may be partly explained by allometric scaling: rostral length scales with positive allometry (Table 2) and *Heterocephalus* is the smallest species of mole-rat. However, the short rostrum could also be a further adaptation towards chisel-tooth digging, required by this particular species due to its particularly small size. In fact, *Heterocephalus* is one of the smallest subterranean mammals, with a body mass range of 30-50 g (Jarvis and Sherman, 2002). Bite force has been shown to correlate strongly with body mass in rodents (Freeman and Lemen, 2008; Van Daele et al, 2009; Becerra et al, 2014). However, there must be a minimum amount of power produced at the incisors in order to break through the hard soils in which chisel-tooth diggers are known to burrow. Therefore, small rodents such as *Heterocephalus* must modify their chisel-tooth digging apparatus further than larger sized chisel-tooth diggers in order to produce an adequate amount of force at the incisors to break through the soil. Cox and Faulkes (2014) report that the total masticatory muscle mass of *Heterocephalus* is 75% of that reported for the rat (Cox and Jeffery, 2011), despite *Heterocephalus* being only 14-23% of the body mass of the rat specimen used in Cox and Jeffery (2011). These examples show that *Heterocephalus* has evolved a form that can accommodate large masticatory muscles despite its small size.

*Heterocephalus* may have evolved to accommodate these larger masticatory muscles in a number of ways: A reduction of the eyes is a common synapomorphy seen amongst subterranean mammals (Darwin, 1859), with subterranean rodents being no exception (Nevo, 1979; Burda et al, 1990; Stein, 2000). This reduction of the eye has potentially made available space for an anterior expansion of the temporalis into the unoccupied orbit (Lavocat, 1973; Cox and Faulkes, 2014), although this is probably not an adaptation exclusive to *Heterocephalus*.

Secondly, *Heterocephalus* may have evolved these larger masticatory muscles by taking advantage of its unusual cranial musculature. Almost all living rodents can be classified into three (non-phylogenetic) groups, based on their masticatory morphology: sciuromorph (squirrel-like), myomorph (mouse-like) or hystricomorph (porcupine-like) (Brandt, 1855; Wood, 1965). However, the Bathyergidae are unusual as their masticatory morphology does not conform to any of these morphotypes. Unlike most other rodents, no part of the masticatory musculature attaches to the rostrum. This unusual morphology is termed protrogomorph, and is thought to be the ancestral condition of rodents (Wood, 1965), but has probably been secondarily acquired in the Bathyergidae (Landry, 1957b; Maier and Schrenk, 1987; Cox and Faulkes, 2014). The larger mole-rats have retained a long rostrum as there is enough space available in the temporal fossa to accommodate large muscles to provide adequate bite forces; and a reduction of the rostrum would require a reduction in jaw length, which is necessary to produce a large gape (see below). Smaller subterranean rodents such as *Heterocephalus* do not have this luxury; they are constrained by the limited space they have to accommodate muscles that provide a minimum bite force necessary to break through tough soils. They have managed to do so by expanding the zygomatic arches anteriorly, reducing the relative length of the rostrum, and providing more space for the masticatory muscles.

*Incisor procumbency in chisel-tooth digging rodents*

Previous research has suggested that increased upper incisor procumbency is a trait associated with chisel-tooth digging (Lessa, 1990; Van der Merwe and Botha, 1998; Vassallo, 1998; Stein, 2000). This study agrees with the extensive literature as we showed that most chisel-tooth digging bathyergids have a larger upper incisor procumbency angle than the scratch digging *Bathyergus*. However, an examination of Figure 5C shows that some specimens of *Heterocephalus* (a chisel-tooth digger) have a smaller upper incisor procumbency angle than the other chisel-tooth diggers. There was no difference found between the upper incisor procumbency of *Heterocephalus* and the scratch digger *Bathyergus*, despite a significant difference being found between the two digging groups overall. Lessa and Patton (1989) postulated that incisor procumbency is coupled by two main evolutionary mechanisms. First, incisor procumbency has been linked to rostral allometric growth (e.g. Mora et al, 2003), i.e. the longer the rostrum, the higher the incisor procumbency. Second, Landry (1957a) proposed that procumbent incisors require large incisor canals with extended roots at a posterior position within the skull (and procumbency is therefore more of a structural issue rather than a size issue). So, in non-procumbent rodents the incisor root only extends back to a position above the cheek teeth (Landry, 1957a), whereas increased procumbency is found in rodents that have shifted their incisor roots more posteriorly. The incisor root of *Heterocephalus* (like all chisel-tooth digging bathyergids) is positioned as far back in the skull as possible. We therefore hypothesise that, as it appears to have a greatly shortened rostrum, *Heterocephalus* has the most procumbent incisors it can possibly have, given the size of its skull, whereas *Bathyergus* has a relatively reduced procumbency, given its large size (up to 2 kg; Stein, 2000). The varying position of the incisor within the skull has probably led to the lack of clear allometric scaling of incisor procumbency across the Bathyergidae (Table 2).

*Gape*

Our results indicate that the cranium and mandible of chisel-tooth digging bathyergids are able to produce a larger gape than the scratch digging *Bathyergus.* We found that chisel-tooth diggers had significantly greater relative jaw lengths, condyle lengths and condyle heights than *Bathyergus*. Jaw length is a strong predictor of gape in many animals including snakes (Hampton and Moon, 2013), primates (Hylander, 2013) and mice (Vinyard and Payseur, 2008). Functional gapes are typically measured from the tips of the maxillary incisor to tips of the mandibular incisor, and therefore an increased mandible relative to skull length will lead to an increased gape for the same angle of rotation of the mandible. However, it is worth noting that this rule is the case when only considering the geometry of the mandible. Other factors such as muscle stretch of the masseter (Herring and Herring, 1974) have a considerable effect on gape and have not been considered in this study. Masseter fibre lengths taken from the literature however suggest that the chisel-tooth digger *Fukomys* possesses longer masseter muscle fibres (Van Daele et al, 2009) than *Callithrix jacchus,* a common marmoset comparable in size to the mole-rat and with known abilities to produce wide gapes (Eng et al, 2009).

Condyle length has also been found to be associated with increased gape in mice (Vinyard and Payseur, 2008). It is unclear if an increased condyle length relates to an increase in condyle surface area or in condyle curvature, as both these factors can have an effect on joint mobility (Swartz, 1989). Either way, an antero-posteriorly elongated condyle appears to increase potential rotation at the jaw joint, thus facilitating a wider gape. In a number of other chisel-tooth digging rodents in the Ctenomyidae and Spalacidae, this characteristic is correlated with the presence of some kind of postglenoid articulation of the mandible, which provides stability during incisor biting with high forces (Verzi and Olivares, 2006). However, no postglenoid fossa for such an articulation could be identified in the bathyergid species under study here.

Condyle height also differed between chisel-tooth and scratch digging bathyergids, with chisel-tooth digging rodents having larger condyle heights than the scratch digger. This was a rather surprising result as it is contrary to our initial hypothesis, that a low condyle height will facilitate a wider gape by reducing stretch in the masseter muscle (Herring and Herring, 1974). Interestingly, although it was found in primates as a strong morphological predictor of gape, this was not found to be the case in mice (Vinyard et al, 2003; Vinyard and Payseur, 2008). Our result indicates that fibre lengths in the masseter should be greater in order to compensate for the increased stretch of the muscle in chisel-tooth diggers resulting from their high condyles.

It has been well established that increasing gape decreases bite force in mammals with a generalized morphology (Maynard Smith and Savage, 1959; Turnbull, 1970; Herring, 1975; Dumont and Herrel, 2003; Bourke et al, 2008; Williams et al, 2009). In the context of our results, this trade-off is clear when considering that, although it will increase gape, an increased jaw length will also decrease the muscle out-lever, therefore reducing the muscle’s MA. In order to examine how gape theoretically affects the mechanical advantage of each masticatory muscle, the mandible was rotated around the skull of each specimen. The results show that continually increasing gape drastically reduces MA of both the superficial and deep masseter, but that a rather different pattern is found with regard to the temporalis muscle (Figure 7). First, the rate of change (declination) of the temporalis MA is smaller compared to the masseter muscles. This implies that temporalis is better at maintaining MA at increased gapes compared to the masseters. However, it should be noted that the MA of both masseters at low gapes is around a third higher than the temporalis. Second, the temporalis MA decreases as gape increases down to a minimum point, after which it begins to increase again. Interestingly, the point where MA is lowest is different depending on the species; *Bathyergus* reaches its minimum MA at a narrower gape than its chisel-tooth digging relatives. Before anything can be inferred from this result, it is important to discuss what is actually happening at this point of minimum MA. Mathematically, the reason why MA decreases with increasing gape is related to the positioning of the muscle force vector (MFV) relative to the condyle (or the muscle moment arm). Rotating the mandible to mimic jaw opening causes the MFV to change in such a way that the perpendicular distance between the MFV and the condyle is reduced (this distance is the muscle moment arm). As the muscle moment arm is reduced and the jaw moment arm stays the same, the MA of the muscle is reduced (as MA is defined as the ratio between muscle moment arm and jaw moment arm). The minimum MA represents the MFV being as close as possible to the condyle in 3D space. If the mandible is theoretically rotated further after this point, the MA of the muscle will increase again, as the perpendicular distance of the MFV to the condyle increases in the opposite direction. Although this is what happens in theory, this cannot occur in a biologically functional sense because parts of the skull begin to obstruct the path of the muscle. For this reason, the gape at which MA is lowest represents the theoretical maximum gape relevant to each muscle. Looking at the impact of gape on MA of temporalis muscle of the scratch digger *Bathyergus* (Figure 7), it can be seen that MA of temporalis reaches its lowest point around 40°. This is in contrast to the chisel-tooth diggers, who reach their lowest points around 70-80°. This figure for maximum gape is in the *in vivo* range of gape reported for chisel-tooth digger *Fukomys*, which had an average maximum gape of 71° (Heindryckx, 2014). Our model prediction of maximum gape is similar to the *in vivo* result for *Fukomys*, despite only considering the temporalis muscle, and not taking into account other variables such as muscle stretch, which highlights the importance of craniomandibular form in constraining gape.

So why does the temporalis seem to restrict gape in the scratch digger *Bathyergus* more than in chisel-tooth diggers? It appears that a restriction of gape is related to the morphology of the coronoid process, where the temporalis inserts. In the scratch digger *Bathyergus,* the coronoid process has greatly shortened to a level equal to the condyle, creating a shallow mandibular notch. The chisel-tooth digger on the other hand has a much longer fin shaped coronoid process, and displays a much deeper mandibular notch (see Figure 8). In terms of gape constrained by the temporalis, the shape of the coronoid process of the chisel-tooth digger is more advantageous. The long fin shape of the coronoid process means that even at high gape the insertion of the temporalis does not become wrapped around the zygomatic process. The greater length of the coronoid process, along with the larger and deeper temporal fossa, also causes the muscle vector to be more vertical, increasing the muscle moment arm of the temporalis muscle.

*Conclusions*

The results here support previous research indicating that the cranial and mandibular morphology of the scratch digging genus *Bathyergus* is very different to that of chisel-tooth digging members of the Bathyergidae (Samuels and Van Valkenburgh, 2009). It is not possible, with the methods employed in this study, to say if the change in morphology of *Bathyergus* represents selection or genetic drift, but it is possible to test the functional implications of the morphological change. The results show that the morphology seen in the chisel-tooth digging genera better facilitates the production of high bite force and wide gape, thus enabling more efficient digging with the incisors than could be achieved by *Bathyergus*. Clearly as a change in digging behaviour has occurred on the lineage leading to *Bathyergus*, an associated change in morphology has also taken place.

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**TABLES**

**Table 1**. Morphological predictors recorded from the cranium and mandible. All linear measurements were size-adjusted by dividing by basilar length. Measurements shown in Figure 3.

|  |  |  |
| --- | --- | --- |
| **Cranial measurements** | **Definition**  | **Prediction** |
| Head height (HH) | Distance from bregma to posterior margin of the palatine in the midsagittal plane  | Chisel-tooth diggers have greater head heights for increased bite force |
| Cranial width (CW) | Distance between left and right posterior zygomatic arches | Chisel-tooth diggers have wider crania for increased bite force |
| Rostral length (RL) | Distance from upper incisor tip to anterior point of tooth row | Chisel-tooth diggers have longer rostra for more procumbent incisors |
| Upper incisor procumbency (α) | Angle between the incisor and the occlusal plane of the molars | Chisel-tooth diggers have more procumbent incisors |
| Jaw length (JL) | Distance from incisor alveolus to the posterior surface of the mandibular condyle  | Chisel-tooth diggers have longer jaws for increased gape |
| Condyle length (CL) | Anteroposterior length of condylar articular surface  | Chisel-tooth diggers have elongated condyles for increased gape |
| Condyle height (CH) | Height of the condyle above the molar tooth row (perpendicular to occlusal plane) | Chisel-tooth diggers have reduced condyle height for increased gape |

**Table 2.** Allometric equations (y=axb; reduced major axis regression) to assess influence of size (x=basilar length) on morphological variables

|  |  |  |  |
| --- | --- | --- | --- |
| Variable (y) | Equation  | *R*2  | *P* |
| Head height Cranial widthRostral lengthUpper incisor procumbencyJaw lengthCondyle lengthCondyle height | y=-0.01x0.75y=0.22x0.75y=-0.63x1.12y=1.63x0.29y=0.05x0.88y=-0.63x0.84y=-0.630.96 | 0.830.930.980.020.950.710.67 | <0.01<0.01<0.01>0.05<0.01<0.01<0.01 |

**FIGURE LEGENDS**

**Figure 1**. Phylogeny of extant bathyergid mole-rat genera, adapted from Seney et al (2009). Scratch digging genera in bold.

**Figure 2.** Reconstructions of the cranium and mandible of each mole-rat genus in lateral view (left) and of the cranium in dorsal view (right). Muscle force vectors of the superficial masseter (sm), deep masseter (dm), and temporalis (t) shown in lateral view. A. *Fukomys mechowi*. B. *Cryptomys hottentotus*. C. *Bathyergus suillus*. D. *Georychus capensis*. E. *Heliophobius argenteocinereus*. F. *Heterocephalus glaber*.

**Figure 3**. Morphological predictors of bite force (A-C) and gape (D) shown on skull and mandible of *Heliophobius argenteocinereus*. A. Dorsal view of skull. B. Right lateral view of skull. C. Ventral view of skull. D. Medial view of left hemimandible. Abbreviations: BL, basilar length; CL, condyle length; CH, condyle height; CW, cranial width; HH, head height; JL, jaw length; OP, occlusal plane; RL, rostral length; α, incisor procumbency angle. Dashed line represents occlusal plane on mandible. Further details of measurements given in Tables 1 and 2.

**Figure 4**. Calculation of muscle moment arm (MMA) of temporalis and jaw moment arm (JMA) to calculate mechanical advantage of temporalis. Abbreviations: BFV, bite force vector; JMA, jaw moment arm; MFV, muscle force vector; MMA, muscle moment arm; OP, occlusal plane.

**Figure 5**. Box plots showing morphological predictors of bite force and upper incisor procumbency angle. A. Relative head height. B. Relative cranial width. C. Upper incisor procumbency angle. D. Relative rostral length. Chisel-tooth diggers (grey) and scratch diggers (white). Black lines within boxes represent median values. Boundaries of boxes represent 25th and 75th quartiles. Whiskers extend to 1.5 times the interquartile range and white dots represent outliers that fall outside this range.

**Figure 6.** Box plots showing morphological predictors of gape. A. Relative jaw length. B. Relative condyle length. C. Relative condyle height. Chisel-tooth diggers (grey) and scratch diggers (white). Black lines within boxes represent median values. Boundaries of boxes represent 25th and 75th quartiles. Whiskers extend to 1.5 times the interquartile range and white dots represent outliers that fall outside this range.

**Figure 7.** Mechanical advantage of the masticatory muscles at gapes between 0° and 100° in chisel-tooth digging and scratch digging bathyergid genera. A. Temporalis. B. Superficial masseter. C. Deep masseter. Species means are represented.

**Figure 8.** Lateral view of the mandibles of *Heliophobius argenteocinereus* (above) and *Bathyergus suillus* (below). Arrows indicate the coronoid process. Scale bar = 1 cm.