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Masticatory musculature of the African mole-rats (Rodentia: Bathyergidae)

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ABSTRACT

The Bathyergidae, commonly known as blesmols or African mole-rats, is a family of rodents well-known for their subterranean lifestyle and tunnelling behaviour. Four of the five extant bathyergid genera (*Cryptomys*, *Fukomys*, *Georchus* and *Heliophobius*) are chisel-tooth diggers, that is they dig through soil with their enlarged incisors, whereas the remaining genus (*Bathyergus*) is a scratch-digger, only using its forelimbs for burrowing. *Heterocephalus glaber*, the naked mole-rat, is also a chisel-tooth digger and was until recently included within the Bathyergidae (as the most basally branching genus), but has now been placed by some researchers into its own family, the Heterocephalidae. Given the importance of the masticatory apparatus in habitat construction in this group, knowledge and understanding of the morphology and arrangement of the jaw-closing muscles in Bathyergidae is vital for future functional analyses. Here, we use diffusible iodine-based contrast-enhanced microCT to reveal and describe the muscles of mastication in representative specimens of each genus of bathyergid mole-rat and to compare them to the previously described musculature of the naked mole-rat. In all bathyergids, as in all rodents, the masseter muscle is the most dominant component of the masticatory musculature. However, the temporalis is also a relatively large muscle, a condition normally associated with sciuriformous rodents. Unlike their hystricomorphous relatives, the bathyergids do not show an extension of the masseter through the infraorbital foramen on to the rostrum (other than a very slight protrusion in *Cryptomys* and *Fukomys*). Thus, morphologically, bathyergids are protrogomorphous, although this is thought to be secondarily derived rather than retained from ancestral rodents. Overall, the relative proportions of the jaw-closing muscles were found to be fairly consistent between genera except in *Bathyergus*, which was found to have an enlarged superficial masseter and relatively smaller pterygoid muscles. It is concluded that these differences may be a reflection of the behaviour of *Bathyergus* which, uniquely in the family, does not use its incisors for digging.

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INTRODUCTION

The comparative anatomy of the masticatory, or jaw-closing, muscles in rodents has been a well-studied topic over many years (*Wood, 1965; Turnbull, 1970; Woods, 1972;*

Woods & Howland, 1979; Woods & Hermanson, 1985; Ball & Roth, 1995; Thorington & Darrow, 1996; Druzinsky, 2010; Cox & Jeffery, 2011, 2015). Early classifications of rodents were based on masticatory muscle anatomy (Brandt, 1855), although modern phylogenies based on molecular data (Blanga-Kanfi et al., 2009; Fabre et al., 2012; Swanson, Oliveros & Esselstyn, 2019) have shown many of the myological similarities between taxa to be the result of convergent evolution rather than shared evolutionary history. Nonetheless, the highly specialised feeding system in rodents (including enlarged, ever-growing incisors and a lower jaw that can move antero-posteriorly with respect to the cranium) has ensured that the morphology of the jaw adductor muscles remains a relevant research topic in the field of functional morphology.

One group of rodents that is particularly interesting with regard to the jaw-closing muscles is the Bathyergidae, a family of subterranean rodents known as blesmols or African mole-rats. The family comprises at least 21 species (Van Daele et al., 2007; Faulkes et al., 2011, 2017; Burgin et al., 2018; Visser, Bennett & Jansen Van Vuuren, 2019) in five genera—*Bathyergus*, *Cryptomys*, *Fukomys*, *Georychus* and *Heliophobius*—all found in sub-Saharan Africa. A sixth monospecific genus, *Heterocephalus* (the naked mole-rat), was until recently also included within the Bathyergidae. However, it has been proposed (Patterson & Upham, 2014) that *Heterocephalus glaber* should be placed in its own family, the Heterocephalidae (Landry, 1957) based on the depth of the split from other bathyergids (c. 31.2 Ma) and a number of morphological characters. Nevertheless, it is important to note that from an evolutionary perspective the two families are still united as a monophyletic superfamily, the Bathyergoidea (Fig. 1). This division of mole-rats into two families is not universally supported (Visser, Bennett & Jansen Van Vuuren, 2019), but nonetheless has been reflected in a number of recent mammalian taxonomies (Wilson, Lacher & Mittermeier, 2016; Burgin et al., 2018). Accepting this classification, the Bathyergidae first diversified in the early Miocene, around 17.9 Ma (Patterson & Upham, 2014) with the earliest known fossils dating from this time as well (Mein & Pickford, 2008).

African mole-rats are highly specialised for a fossorial lifestyle, spending much of their life underground in complex networks of burrows (Bennett & Faulkes, 2000). Five of the six genera (*Cryptomys*, *Fukomys*, *Georychus*, *Heliophobius* and *Heterocephalus*) are chisel-tooth diggers that dig tunnels with their incisors, whereas the remaining genus, *Bathyergus*, is a scratch digger, only using its limbs for digging (Stein, 2000). Chisel-tooth digging blesmols share a number of morphological adaptations to this behaviour, such as enlarged incisors, taller and wider skulls, enlarged temporal fossae and longer jaws (McIntosh & Cox, 2016a, 2016b; Samuels & Van Valkenburgh, 2009). These modifications have been shown to facilitate the production of high bite forces and wide gapes, both necessary for digging with the incisors (McIntosh & Cox, 2016a).

Despite the well-known osteological adaptations to digging seen in the bathyergid masticatory system, there are comparatively few in-depth studies of the jaw muscle anatomy of blesmols in the published literature. Tullberg (1899), in his large survey of rodent and lagomorph anatomy, illustrated some of the more superficial muscles of *Georychus capensis*, *Cryptomys hottentotus* and *Bathyergus suillus*. Boller (1970) and

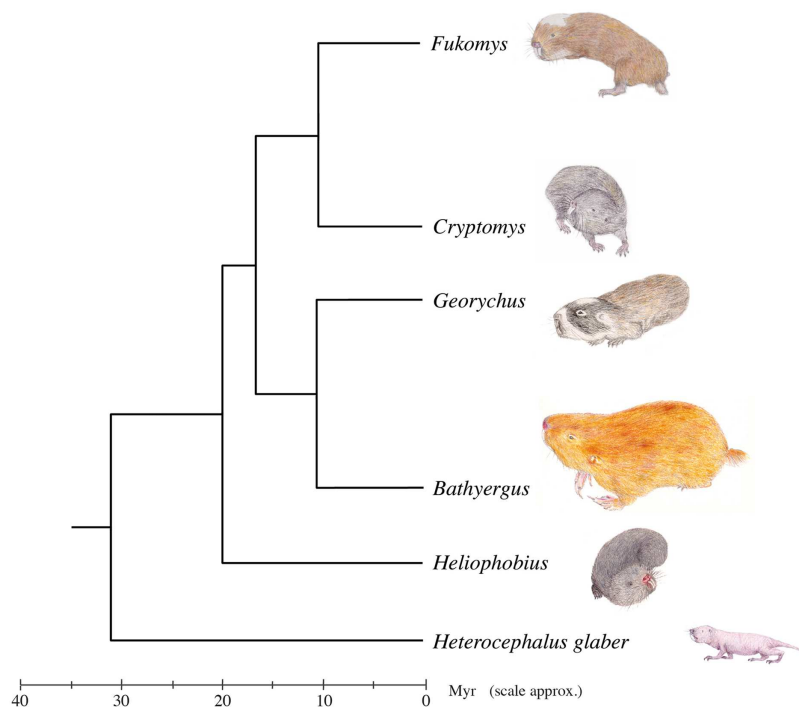


Figure 1 Genus-level phylogeny of the African mole-rats. Tree based on mitochondrial 12S rRNA and cytochrome b sequence data and analysis of 3,999 nuclear genes (Faulkes et al., 2004; Ingram, Burda & Honeycutt, 2004; Davies et al., 2015). A chronologically calibrated scale in millions of years ago is illustrated beneath the tree, estimated using a molecular clock approach and using the bathyergid fossil *Proheliophobius* for calibration of genetic distances. Adapted from Faulkes & Bennett (2013).

Full-size DOI: 10.7717/peerj.8847/fig-1

Van Daele, Herrel & Adriaens (2009) provide more detailed descriptions, but only of *C. hottentotus* and *Fukomys* species respectively. A study of subterranean rodents published by Morlok (1983) has a much broader coverage, including all bathyergid genera except *Fukomys*, which was split more recently from *Cryptomys* (Kock et al., 2006). However, the only detailed descriptions and figures of masticatory musculature in this work are of *Cryptomys*. Most recently, the masticatory musculature of *H. glaber* (now removed from the Bathyergidae as mentioned above) was described by Cox & Faulkes (2014) using digital dissection. That is the jaw-closing musculature was visualised and virtually reconstructed via diffusible iodine-based contrast-enhanced computed tomography (diceCT). This methodology, developed over the last decade (Metscher, 2009; Jeffery et al., 2011; Gignac & Kley, 2014; Gignac et al., 2016), uses iodine staining to increase the radio density of soft tissues and render them visible in CT scans. The technique is a useful complement to physical dissection, particularly when studying small specimens with complex, layered musculature.

The aim of this study is to describe the jaw-closing musculature of all five currently recognised genera of bathyergid mole-rats, in order to facilitate comparisons between them and also with the masticatory musculature of the closely related naked mole-rat. It is hypothesised that all chisel-tooth digging bathyergids have a similar arrangement of jaw adductor muscles, owing to the strong functional constraint of needing to produce a high

bite force at a wide gape (McIntosh & Cox, 2016a). Furthermore, it is hypothesised that the relative proportions of the jaw adductors in chisel-tooth digging bathyergids are similar to those previously described in the naked mole-rat (Cox & Faulkes, 2014), owing to its similar mode of digging and its shared common ancestor with Bathyergidae. Finally, it is hypothesised that blesmols of the genus *Bathyergus* differ from other bathyergid genera in the relative proportions of their jaw-closing muscles, as these taxa are scratch diggers that do not use their incisors to construct burrows (Stein, 2000). In particular, the temporalis has been proposed to be particularly important in chisel-tooth digging (Samuels & Van Valkenburgh, 2009; McIntosh & Cox, 2016a), so this muscle is hypothesised to be relatively smaller in *Bathyergus*.

MATERIALS AND METHODS

Sample and scanning

Five ethanol-preserved heads of bathyergid mole-rats were obtained from collections originating from the University of Pretoria. The work was approved by the animal ethics committee at the University of Pretoria AUCC 030110-002 and AUCC 040702-015. The specimens represented one species from each of the five currently recognised genera of Bathyergidae: *B. suillus*, *C. hottentotus*, *Fukomys mechowi*, *G. capensis* and *Heliophobius argenteocinereus*. As ethanol is known to reduce the efficacy of diceCT (Gignac et al., 2016), the concentration of the preserving fluid was gradually reduced from 70% ethanol down to distilled water over a period of 2 weeks. After another week in distilled water, the specimens were immersed in 4% phosphate-buffered formaldehyde solution. Finally, the specimens were transferred to a 7.5% solution of iodine-potassium iodide in formaldehyde for 3 months. The stained specimens were scanned using microCT at the Cambridge Biotomography Centre, University of Cambridge. The scans were performed at 164 kV and 165 μ A (175 kV and 156 μ A for *B. suillus*), with a 0.5 mm copper filter and a beryllium target. Voxels were isometric with dimensions between 0.026 and 0.046 mm. Further scanning details are given in Table S1. The diceCT stacks are archived and available from www.morphosource.org (the DOI of each stack is given in Table S1).

Digital reconstruction

Scans were imported as stacked TIFF files to Avizo 9.2 Lite (Thermo Fisher Scientific, Waltham, MA, USA) and the jaw adductor muscles of one side of the head were reconstructed. The side of the head chosen for reconstruction differed between specimens and was based on the quality of the staining and scanning in the left and right muscles. The muscles that were digitally reconstructed comprised the superficial masseter, deep masseter, zygomaticomandibularis, temporalis, medial pterygoid and lateral pterygoid, following the nomenclature of Cox & Jeffery (2011) and Cox & Faulkes (2014). Automatic thresholding of masticatory muscles was not possible owing to insufficient contrast difference between bone and muscle, and therefore the muscles were reconstructed using manual painting of selected slices and interpolation between them. Each muscle volume was subjected to a single application of the 'smooth labels' algorithm within the Avizo segmentation editor (size, 4; mode, 3D volume), and the volume of each muscle was

Table 1 Percentage of total masticatory muscle adductor mass occupied by each jaw-closing muscle in each mole-rat genus.

	<i>Bathyergus</i>	<i>Cryptomys</i>	<i>Fukomys</i>	<i>Georchus</i>	<i>Heliophobius</i>	<i>Heterocephalus</i>
Superficial masseter	37.5	24.5	27.4	25.9	19.3	23.4
Deep masseter	23.7	23.8	22.1	22.8	27.7	25.5
Anterior ZM	2.7	1.8	2.2	2.7	5.3	2.9
Posterior ZM	1.8	2.9	4.2	3.6	6.0	2.6
IOZM	3.7	5.6	4.9	7.0	4.8	5.4
Temporalis	26.0	31.8	26.2	28.0	26.1	32.2
Medial pterygoid	3.7	7.7	9.7	7.8	7.2	6.1
Lateral pterygoid	0.9	2.0	3.2	2.3	3.7	2.0

Note:

Values for *Heterocephalus glaber* from Cox & Faulkes (2014). Absolute muscle masses given in Table S2.

recorded. Muscle masses were calculated from volumes assuming a muscle density value of 1.0564 g cm^{-3} (Murphy & Beardsley, 1974), although absolute mass values should be treated with caution as both iodine staining and formalin preservation are known to lead to soft tissue shrinkage (Vickerton, Jarvis & Jeffery, 2013). The percentage contribution of each muscle to total adductor muscle mass was also calculated for each specimen. In addition to the digital dissections, three of the specimens were also physically dissected (*Bathyergus*, *Cryptomys*, *Georchus*). Digital and physical dissections were compared both quantitatively (relative muscles masses) and qualitatively to ensure that muscle attachment sites and boundaries between muscle layers had been correctly identified in the diceCT scans. As congruence between the dissection methods was good (attachment sites correctly identified, relative muscle masses within 4%), digital dissection was deemed to be an accurate reflection of the morphology.

The reconstructed muscles were visualised by aligning them with a virtually reconstructed skull and mandible. Because scans of the unstained specimens were not available, and I_2KI staining renders the reconstruction of bony material very difficult, an individual of the same species, but not the same specimen, was used to create each skull and mandible. A Bookstein warp (Bookstein, 1989) was then used to fit the bony elements to the reconstructed muscles.

RESULTS

The percentage contribution of each muscle to total masticatory muscle mass are given in Table 1 (absolute masses are given in Table S2) and the percentage split between the masseteric complex, temporalis and pterygoid muscles for each specimen is shown in Fig. 2. Overall, it can be seen that the relative proportion of each jaw-closing muscle is largely consistent between *Cryptomys*, *Fukomys*, *Georchus*, *Heliophobius* and *Heterocephalus*, which all have a masseter forming 58–63%, a temporalis contributing 26–32%, and pterygoid muscles accounting for 8–11% of total muscle mass. *B. suillus* differs from the other blesmols somewhat, with a relatively larger masseter (69%) and relatively smaller pterygoids (5%). The morphology of each muscle is described below and shown in Figs. 3–6.

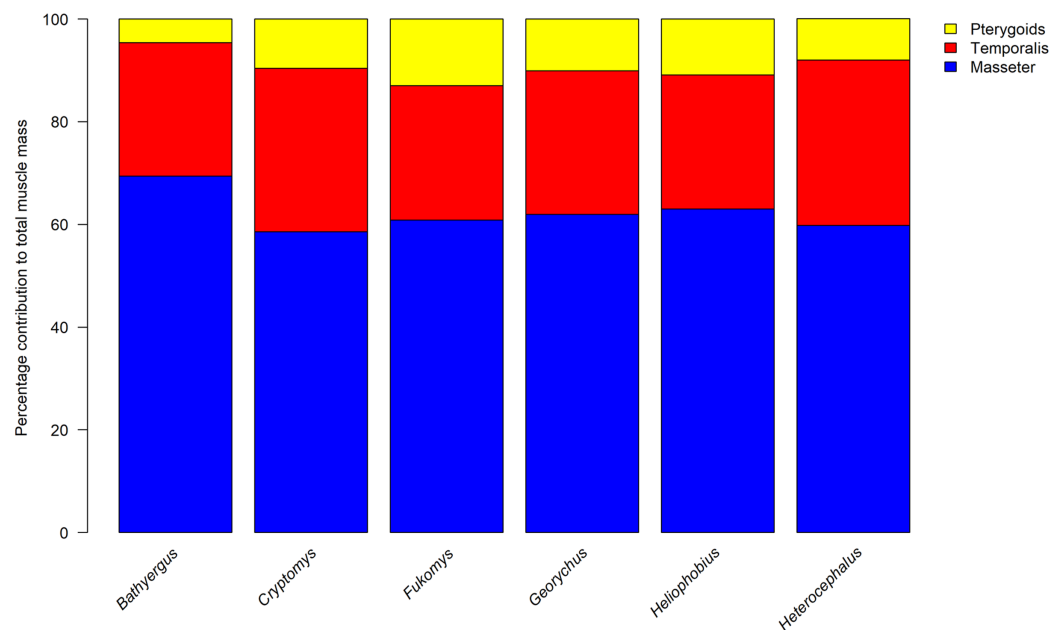


Figure 2 Relative contributions of the masseter, temporalis and pterygoid muscles to total adductor muscle mass in each genus of Bathyergidae and Heterocephalidae. Data for *Heterocephalus* from Cox & Faulkes (2014). Full-size DOI: 10.7717/peerj.8847/fig-2

Superficial masseter

The superficial masseter is a large muscle in all blesmols, although only a small part of it can be seen in lateral view (Fig. 3). It represents about a quarter of the total masticatory musculature in most of the bathyergid genera. However, *Heliophobius* has a slightly reduced superficial masseter of about 19% total muscle mass, and *Bathyergus* has a greatly increased superficial masseter that occupies over 37% of the total musculature. This muscle has a tendinous origin via a small attachment site on the skull on the ventral surface of the zygomatic process of the maxilla. The tendon initially runs antero-medial to the deep masseter, but the muscle itself then wraps around the deep masseter to take a more lateral position. The superficial masseter then inserts along the ventral margin of the masseter all the way to the tip of the angular process. The muscle also wraps around the ventral mandibular margin and extends widely over the medial surface of the mandible, forming a *pars reflexa* (Figs. 4 and 5). This reflected component covers almost the entire medial angular process, leaving just a small area for the insertion of the medial pterygoid muscle.

Deep masseter

The deep masseter is also a large muscle in blesmols, contributing 22–28% of the total adductor muscle mass in all genera. It originates along the entire length of the ventro-lateral surface of the zygomatic arch, from the attachment site of the superficial masseter anteriorly, to the zygomatic process of the squamosal posteriorly. The insertion of the deep masseter is along the lateral mandibular surface just dorsal to the insertion of the superficial masseter. Thus, in lateral view, the deep masseter covers the posterior half of

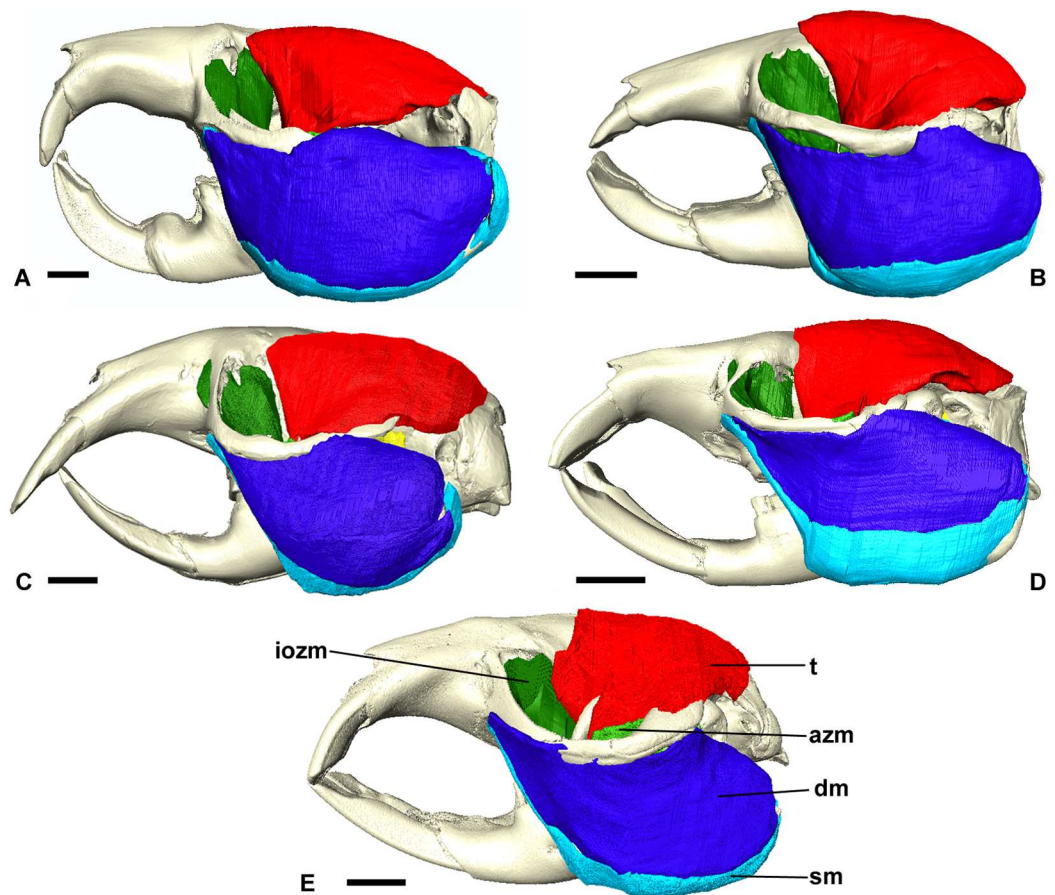


Figure 3 Masticatory muscles of Bathyergidae. Left lateral view of a 3D reconstruction of the cranium, mandible and masticatory muscles of: (A) *Bathyergus suillus*; (B) *Georychus capensis*; (C) *Cryptomys hottentotus*; (D) *Fukomys mechowi*; (E) *Heliophobius argenteocinereus*. Abbreviations: azm, anterior zygomaticomandibularis; dm, deep masseter; iozm, infraorbital portion of the zygomaticomandibularis; sm, superficial masseter; t, temporalis. Scale bars = 5 mm. [Full-size !\[\]\(5fd6ef84f97f42d7f8b34275f1b65312_img.jpg\) DOI: 10.7717/peerj.8847/fig-3](https://doi.org/10.7717/peerj.8847/fig-3)

the mandible (Fig. 3). The separation between the superficial and deep masseter muscles was one of the most difficult aspects of the digital dissection, with these two muscles appearing continuous in some places (Fig. 5). However, the physical dissections of *Bathyergus*, *Cryptomys* and *Georychus* provided confidence that the muscles had been correctly reconstructed. No division of the deep masseter into anterior and posterior sections was identified.

Zygomaticomandibularis

The zygomaticomandibularis or ZM is a small to medium-sized component of the bathyergid masticatory system. It forms 10–13% of the total muscle mass in most genera, although this rises to 16% in *Heliophobius* and drops to 8% in *Bathyergus*. The ZM is divided into three sections—infraorbital, anterior and posterior—that were easily identifiable and separable in all specimens (Fig. 6). The anterior ZM originates from the

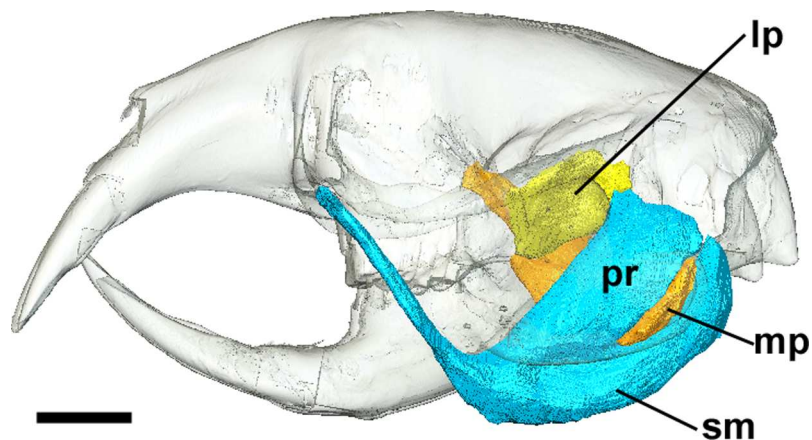



Figure 4 Superficial masseter and pterygoid muscles of *Cryptomys hottentotus*. Left lateral view of a 3D reconstruction of the cranium, mandible, superficial masseter and pterygoid muscles. Cranium and mandible transparent for visualisation of muscles attaching to medial mandibular surface. Abbreviations: lp, lateral pterygoid; mp, medial pterygoid; pr, *pars reflexa* of the superficial masseter; sm, superficial masseter. Scale bar = 5 mm.

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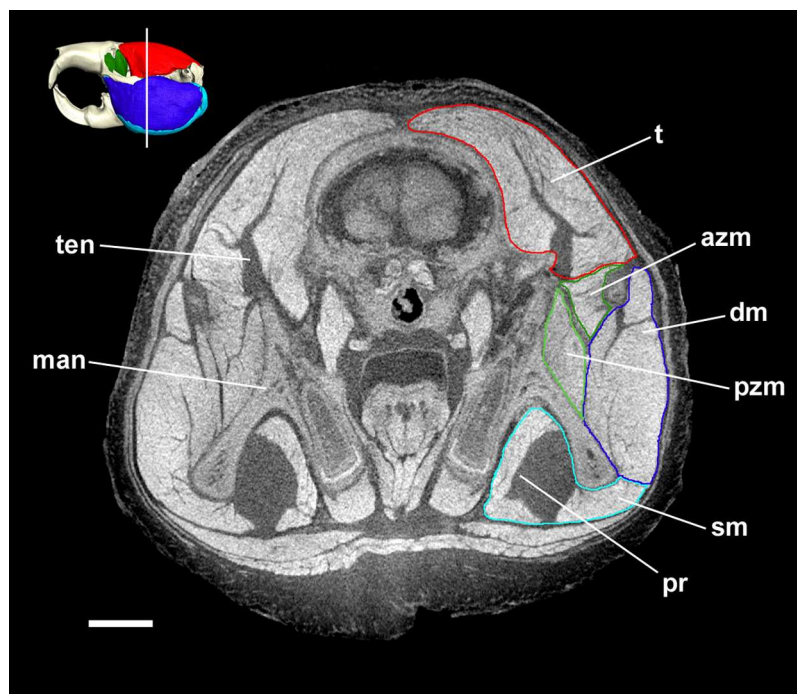


Figure 5 Coronal diceCT slice of *Bathyergus suillus*. MicroCT slice through the head of *Bathyergus suillus* stained with iodine potassium iodide. Abbreviations: azm, anterior zygomaticomandibularis (dark green); dm, deep masseter (dark blue); man, mandible; pr, *pars reflexa* of the superficial masseter (light blue); pzm, posterior zygomaticomandibularis (light green); sm, superficial masseter (light blue); t, temporalis (red); ten, tendon of temporalis. White line on 3D reconstruction shows position of slice. Scale bar = 5 mm.

Full-size  DOI: [10.7717/peerj.8847/fig-5](https://doi.org/10.7717/peerj.8847/fig-5)

medial surface of the zygomatic arch, with the attachment site spanning the posterior half of the jugal bone and the anterior part of the zygomatic process of the squamosal. The origin of the posterior ZM is immediately posterior to that of the anterior ZM and

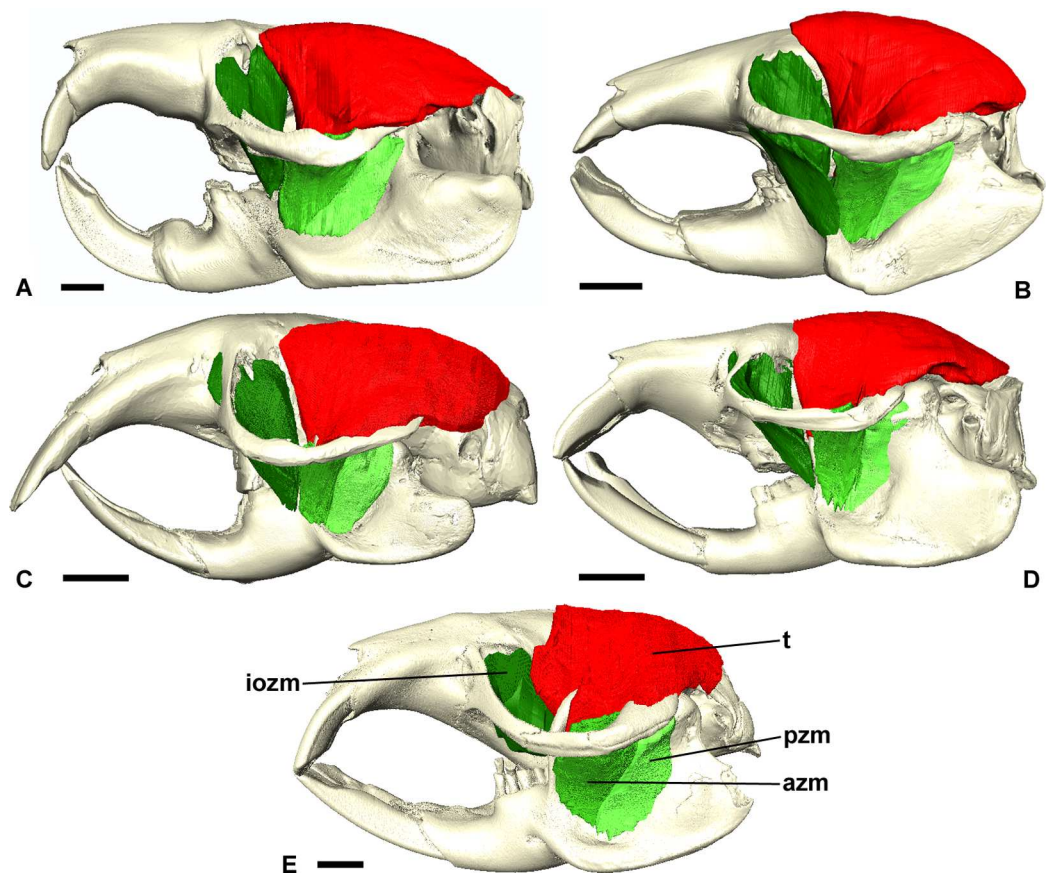


Figure 6 Temporalis and zygomaticomandibularis muscles of Bathyergidae. Left lateral view of a 3D reconstruction of the cranium, mandible, temporalis and zygomaticomandibularis of: (A) *Bathyergus suillus*; (B) *Georychus capensis*; (C) *Cryptomys hottentotus*; (D) *Fukomys mechowii*; (E) *Heliophobius argenteocinereus*. Abbreviations: azm, anterior zygomaticomandibularis; iozm, infraorbital portion of the zygomaticomandibularis; pzm, posterior zygomaticomandibularis; t, temporalis. Scale bars = 5 mm.

Full-size  DOI: [10.7717/peerj.8847/fig-6](https://doi.org/10.7717/peerj.8847/fig-6)

runs medially along the zygomatic arch until it meets the glenoid fossa. Both muscles insert in a fossa on the lateral surface of the mandible, with the anterior ZM having largely ventrally oriented fibres and the posterior ZM running somewhat anteriorly from origin to insertion. The anterior margin of the anterior ZM is at the level of the coronoid process of the mandible. Both muscles are covered by the deep masseter in lateral view.

The infraorbital portion of the ZM (IOZM) is usually the largest division of the ZM (although not in *Heliophobius* where it is smaller than the anterior ZM). It takes a wide origin across the anterior orbital wall and zygomatic process of the maxilla. The fibres then run ventrally and converge to a much narrower insertion area on the lower margin of the coronoid process, next to the attachment site of the anterior ZM. In most bathyergid genera, the IOZM origin is confined to the orbit, but in *Cryptomys* and *Fukomys*, a very small extension of the IOZM can be seen to push through the infraorbital foramen to take its origin on the rostrum (Figs. 6 and 7).

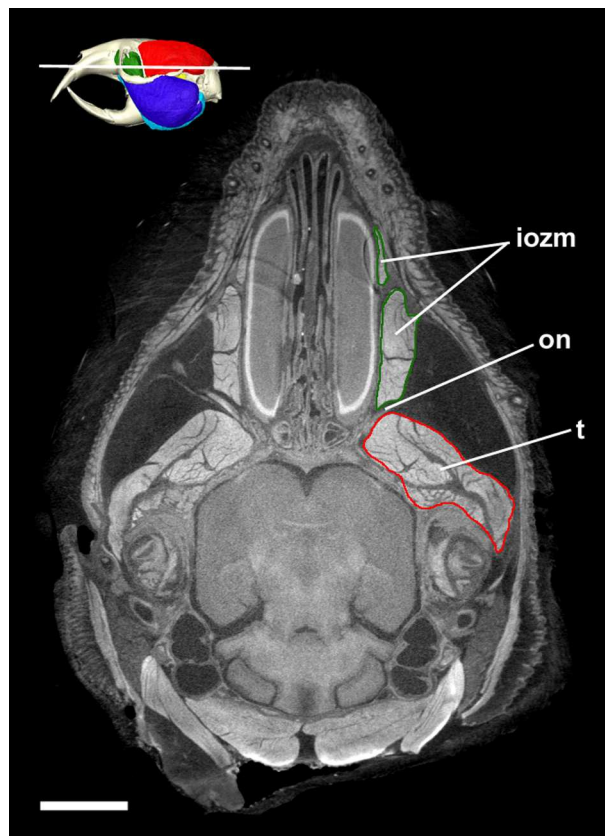


Figure 7 Transverse diceCT slice of *Cryptomys hottentotus*. MicroCT slice through the head of *Cryptomys hottentotus* stained with iodine potassium iodide. Abbreviations: iozm, infraorbital portion of zygomaticomandibularis (dark green); on, optic nerve; t, temporalis (red). White line on 3D reconstruction shows position of slice. Scale bar = 5 mm. [Full-size](#) DOI: 10.7717/peerj.8847/fig-7

Temporalis

The temporalis is large in all bathyergid genera, forming between 26% and 32% of the total muscle mass. It originates on the braincase, covering the parietal and the posterior part of the frontal bone (Fig. 3). The posterior limit of the temporalis on the skull is the nuchal crest, the medial border runs along the midsagittal line and anteriorly it extends into the orbit where it meets the posterior border of the IOZM (Fig. 6). Fibres from all across this wide origin converge on a small insertion on the anterior margin and medial surface of the coronoid process on the mandible. This gives the temporalis a fan-shaped morphology, with fibres from the orbital region running vertically and fibres from the nuchal crest running horizontally over the top of the zygomatic process of the squamosal. A tendon running through the middle of the muscle from the coronoid process upwards appears to divide the ventral part of the muscle into lateral and medial portions, inserting on the lateral and medial surfaces of the coronoid process respectively (Fig. 5). However, these portions come together in the dorsal part of the muscle and it is not possible to subdivide the temporalis here with any certainty. Thus, to avoid introducing errors, the temporalis has been reconstructed as a single component.

Medial pterygoid

The medial pterygoid comprises between 7% and 8% of the total masticatory muscle mass in *Cryptomys*, *Georychus* and *Heliophobius*. It is a little larger in *Fukomys*, representing almost 10% total muscle mass, but is notably smaller in *Bathyergus* occupying only 3% of the adductor musculature. The medial pterygoid has an elongated anterior portion that extends deeply into the pterygoid fossa where it takes its origin. There is also a smaller part of this muscle that originates on the lateral surface of the pterygoid flange that is ventral to the attachment of the lateral pterygoid muscle. From these attachment sites, the medial pterygoid runs ventro-laterally, fanning out somewhat, to insert on the medial surface of the angular process of the mandible, just dorsal to the ventral margin. The insertion site is elongate but narrow and bounded on all sides by the superficial masseter (Fig. 4).

Lateral pterygoid

The lateral pterygoid is a relatively small muscle forming 2–4% of the total adductor muscle mass, except in *Bathyergus* in which it is just under 1% of the total musculature. It takes its origin from the lateral surface of the pterygoid flange, just dorsal to a part of the medial pterygoid. From there, it runs laterally and posteriorly to an insertion site on the medial surface of the condylar process of the mandible.

DISCUSSION

The technique of diceCT was successfully used to reveal the masticatory muscle anatomy of all five extant genera of blesmols. Despite being stored in ethanol for a number of years, which can reduce the contrast differences between soft tissues stained with I₂KI (Gignac et al., 2016), the microCT images produced here were of good quality and allowed the different masticatory muscles to be distinguished from one another (Fig. 5).

The most notable finding from this study is consistency of the relative muscle proportions across the chisel-tooth digging bathyergid genera (*Cryptomys*, *Fukomys*, *Georychus*, *Heliophobius*). This supports our first hypothesis which predicted that the functional demands of needing to produce a high bite force at wide gape (McIntosh & Cox, 2016a) would lead to a constrained configuration of masticatory muscles across the family. In these genera, the masseter complex (including superficial and deep masseters, and all parts of the ZM) forms approximately 60% of adductor muscle mass, the temporalis represents around 30%, and the two pterygoid muscles together make up the final 10%. This distribution of muscle mass, with its dominant masseter, but also relatively large temporalis, has also been reported in a number of rodents, such as the mountain beaver, *Aplodontia rufa*, several members of the Sciuridae (Ball & Roth, 1995; Druzinsky, 2010), and the North American beaver, *Castor canadensis* (Cox & Baverstock, 2016). Notably, all of these rodents are sciuriformous (Wood, 1965), that is they have an extension of the deep masseter on to the rostrum and they are all relatively distantly related to blesmols (Fabre et al., 2012). In contrast, more closely related rodents, from the suprafamilial clade Ctenohystrica to which blesmols belong, generally differ from the bathyergid pattern by having an even more dominant masseter (70% or more of total

muscle mass) and a much reduced temporalis (15% or lower), for example *Hydrochoerus* (Müller, 1933), *Hystrix* (Turnbull, 1970) and *Ctenomys* (Becerra, Casinos & Vassallo, 2013). These rodents are hystricomorphous and have a substantial extension of the IOZM through the infraorbital foramen on to the rostrum. It is notable that the rodent species that more closely resemble bathyergids in the proportions of their jaw-closing muscles are those that require high bite forces at the incisors, either for processing mechanically demanding food items (Smith & Follmer, 1972) or for tree-felling (Rosell et al., 2005). It appears that the demands of chisel-tooth digging may have driven convergent evolution of a similar distribution of muscle mass in blesmols.

The second hypothesis of this study predicted that the chisel-tooth digging bathyergids would resemble *H. glaber* in their masticatory muscle anatomy. This hypothesis is also supported, with the relative proportions of each muscle in the naked mole-rat (Cox & Faulkes, 2014) being very similar to that seen in *Cryptomys*, *Fukomys*, *Georychus* and *Heliophobius*. Given this similarity, it is possible that this muscle arrangement is ancestral for the Bathyergoidea (the superfamily containing Heterocephalidae and Bathyergidae). However, given the strong pressures exerted on morphology by chisel-tooth digging (Lessa, 1990; Samuels & Van Valkenburgh, 2009; Gomes Rodrigues, Šumbera & Hautier, 2016; McIntosh & Cox, 2016a, 2016b), it is also possible that this configuration of adductor muscles evolved independently in the two families, especially given that they appear to have diverged over 30 million years ago (Patterson & Upham, 2014).

The exception to the common arrangement of masticatory muscles in the Bathyergidae is *Bathyergus*, the only genus of scratch-digging blesmols. The distribution of muscles in this genus is 69% masseter, 26% temporalis and 5% pterygoids. Thus, our third hypothesis that *Bathyergus* would differ from the chisel-tooth diggers is supported. However, it should be noted that only one specimen of each genus was available for study, so no statistical test of the difference between scratch and chisel-tooth diggers could be undertaken. We further predicted that the temporalis would be relatively smaller in the scratch digger, owing to the perceived importance of the temporalis in chisel-tooth digging (Samuels & Van Valkenburgh, 2009; McIntosh & Cox, 2016a), but this was not the case. The temporalis muscle in *Bathyergus* forms a similar proportion of total adductor muscle mass as in *Heliophobius* and *Fukomys*; instead the masseter complex in *Bathyergus*, in particular the superficial masseter, is relatively larger and the pterygoid muscles form a smaller part of the masticatory musculature. The lack of difference in the relative temporalis mass may reflect the fact that all bathyergid genera, *Bathyergus* included, have diets that incorporate hard foods such as the roots and tubers of geophytes, many of which are of large size and would require the use of a wide gape. Thus the size of the temporalis may be driven more by diet than by mode of digging.

The function of the superficial masseter has been debated by a number of authors, but it is generally thought to be important in the power stroke of both gnawing and chewing (Gorniak, 1977; Byrd, 1981) as well as being the main protractor of the lower jaw (Hüemae, 1971), based on the antero-posterior orientation of the muscle fibres. Thus, the enlarged superficial masseter in *Bathyergus* may be an adaptation to its diet which incorporates many tough grasses and bulbs (Bennett & Faulkes, 2000). The function of the

expansion of the superficial masseter on the medial mandibular surface, the *pars reflexa*, is less clear. [Satoh & Iwaku \(2004\)](#) have suggested that it may enable a wider gape by increasing the resting length of the muscle fibres. In most bathyergid genera, this would be advantageous as it would facilitate the wide opening of the jaws necessary for chisel-tooth digging. Blesmols of the genus *Bathyergus* do not dig with their teeth ([Stein, 2000](#)) but the males do fight with their incisors ([Bennett & Faulkes, 2000](#)), again requiring a wider gape. Whether or not the fighting behaviour requires a wider gape (and thus larger superficial masseter) than chisel-tooth digging is at present unclear.

The reduced pterygoid muscles in *Bathyergus*, particularly the medial pterygoid, may also be a reflection of scratch digging behaviour. It has previously been noted that the medial pterygoid contracts more strongly during incisor gnawing than molar chewing ([Weijs & Dantuma, 1975](#)). Thus, scratch digging mole-rats may not need such large pterygoid muscles as their chisel-tooth digging counterparts. Alternatively, the reduced medial pterygoid may simply reflect the reduced area for attachment on the medial surface of the angular process, resulting from the increased size of the *pars reflexa* of the superficial masseter in *Bathyergus* ([Satoh & Iwaku, 2004](#)).

In general, the muscle reconstructions presented here are in agreement with the previous descriptions of bathyergid jaw musculature given by [Tullberg \(1899\)](#) and [Morlok \(1983\)](#), but differ in some respects from the anatomy reported by [Boller \(1970\)](#) and [Van Daele, Herrel & Adriaens \(2009\)](#). The main difference arises in the morphology of the superficial masseter, which in [Boller \(1970\)](#) and [Van Daele, Herrel & Adriaens \(2009\)](#) is reported to have a wide expansion across the deep masseter in lateral view and is split into sections known as M1a, M1b and M2. Here, we agree with [Morlok \(1983\)](#) that the main part of the superficial masseter in lateral view is very slender and runs along the ventral margin of the mandible and that most of the muscle attaching to the lateral surface of the mandible is the deep masseter. It is clear that the division between the superficial and deep masseter muscles is quite difficult to determine in some places, but following both digital and physical dissection, we are confident that the morphology presented here is correct and moreover resembles that reported for the naked mole-rat ([Cox & Faulkes, 2014](#)).

The other major difference between the reconstructions here and that of [Boller \(1970\)](#) is with regard to the temporalis. The illustrations of *Cryptomys* in [Boller \(1970\)](#) show the temporalis extending ventrally on to the mandible, between two sections of the ZM muscle. We believe this '*pars zygomatica* of the temporalis' to be a misidentification of the anterior ZM resulting from the close apposition of the two muscles, and the insertion of the temporalis on the mandible to be restricted to the coronoid process.

The virtual reconstructions presented here highlight one well-known peculiarity of bathyergid musculature—the lack of jaw-closing muscles attaching to the rostrum in this family. Species in the Ctenohystrica, which includes the blesmols, are almost all hystricomorphous; that is they have a greatly enlarged infraorbital foramen, through which a portion of the ZM muscle (the IOZM) extends to take its origin on the rostrum ([Hautier, Cox & Lebrun, 2015](#)). In the Bathyergidae, the infraorbital foramen is much smaller and very little, if any, muscle passes through it. This is very similar to the condition known as protrogomorphy, which is believed to be the ancestral state for rodents

(Wood, 1965). Here we have designated the rostral most section of the ZM as the 'IOZM', but only in *Cryptomys* and *Fukomys* does it pass through the infraorbital foramen. In the remaining three genera, the IOZM is confined to the orbit. Maier & Schrenk (1987) noted that some muscle fibres pass through the infraorbital foramen in *Bathyergus* and *Georychus* in early ontogeny, but subsequently retreat and are absent from the rostrum at birth. Similarly, no part of the IOZM was found on the rostrum in the specimens of these two genera in this study.

Despite not extending on to the rostrum, the IOZM is usually the largest part of the ZM in bathyergids and has a wide origin across the anterior part of the orbit. Indeed, in all the specimens studied here, its posterior margin meets the anterior margin of the temporalis in the orbit. Such an arrangement of muscles has likely been made possible by the extreme reduction of the eye in these fossorial species, which has left space into which the muscles have expanded (Fig. 7). The large IOZM also gives a clue to the evolutionary history of the masticatory muscles in Bathyergidae. Although frequently referred to as being 'protrogomorphous' (Tullberg, 1899; Wood, 1965, 1985), the morphology of the bathyergid ZM muscle does not resemble that of the extant protrogomorph, *Aplodontia rufa*, in which the ZM origin is restricted to the zygomatic arch and does not extend dorsally into the orbit. Instead, the bathyergid IOZM more closely resembles that of other hystricomorphs, minus the extension on to the rostrum, a morphology that seems more likely to be secondarily derived than ancestrally retained. This hypothesis is also supported by the phylogenetic position of bathyergids within the otherwise hystricomorph clade Ctenohystrica (Swanson, Oliveros & Esselstyn, 2019), the presence of hystricomorphy in some fossil bathyergids (Lavocat, 1973), and the previously mentioned presence of hystricomorphy in early development of some blesmols (Maier & Schrenk, 1987).

The loss of the rostral extension of the IOZM seems an unusual morphological change, given that this muscle is known to improve the efficiency of molar chewing in rodents (Cox et al., 2012; Cox, 2017). It is possible that it is an adaptation towards increased use of the incisors in digging, as has been suggested for *H. glaber* (Cox & Faulkes, 2014). Shortening the rostrum would decrease the out-lever of incisor biting and would thus increase bite force, but would leave less room for rostral muscle attachment. In addition, the loss of the IOZM from the rostrum could be a strategy for increasing maximum gape, which is also important in chisel-tooth digging (McIntosh & Cox, 2016a). It should be noted that *Bathyergus* also lacks the rostral portion of the IOZM, despite being a scratch digger. This may be a case of phylogenetic inertia and that having lost the rostral IOZM once in its evolutionary history, *Bathyergus* has not re-evolved it.

CONCLUSION

The masticatory musculature of the Bathyergidae is dominated by the masseter muscle, but also has a relatively large temporalis, similar to the condition seen in many sciuriform rodents. The ZM muscle does not extend on to the rostrum (except very slightly in *Cryptomys* and *Fukomys*), a condition that is thought to be secondarily derived from a hystricomorph ancestor. The relative proportions of the jaw-closing muscles are largely

consistent between the chisel-tooth digging blesmols, but the scratch digging genus, *Bathyergus*, differs in having a larger superficial masseter and smaller pterygoid muscles. Despite the deep split between the Heterocephalidae and the Bathyergidae, the jaw adductor musculature of the naked mole-rat is very similar to that of the chisel-tooth digging bathyergids.

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Philip G. Cox is an Academic Editor for PeerJ.

Author Contributions

- Philip G. Cox conceived and designed the experiments, performed the experiments, analysed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Chris G. Faulkes conceived and designed the experiments, analysed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Nigel C. Bennett conceived and designed the experiments, analysed the data, authored or reviewed drafts of the paper, and approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

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Data Availability

The following information was supplied regarding data availability:

All specimens are stored in the PalaeoHub, Department of Archaeology, University of York.

MicroCT stacks are available at Morphosource: [M54784-98703](#), [M54785-98704](#), [M54786-98705](#), [M54787-98706](#), [M54788-98707](#).

The full details of specimens, scanning parameters and microCT stack files are available in [Table S1](#).

Supplemental Information

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REFERENCES

- Ball SS, Roth VL. 1995.** Jaw muscles of new world squirrels. *Journal of Morphology* **224**(3):265–291 DOI [10.1002/jmor.1052240303](#).
- Becerra F, Casinos A, Vassallo AI. 2013.** Biting performance and skull biomechanics of a chisel tooth digging rodent (*Ctenomys tuconax*; Caviomorpha; Octodontidae). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* **319A**(2):74–85 DOI [10.1002/jez.1770](#).
- Bennett NC, Faulkes CG. 2000.** *African mole-rats: ecology and eusociality*. Cambridge: Cambridge University Press.
- Blanga-Kanfi S, Miranda H, Penn O, Pupko T, DeBry RW, Huchon D. 2009.** Rodent phylogeny revised: analysis of six nuclear genes from all major rodent clades. *BMC Evolutionary Biology* **9**(1):71 DOI [10.1186/1471-2148-9-71](#).
- Boller N. 1970.** Untersuchungen an Schädel, Kaumuskulatur und äußerer Hirnform von *Cryptomys hottentotus* (Rodentia, Bathyergidae). *Zeitschrift für wissenschaftliche Zoologie* **181**:7–65.
- Bookstein FL. 1989.** Principal warps: thin-plate splines and the decomposition of deformations. *IEEE Transactions on Pattern Analysis and Machine Intelligence* **11**(6):567–585 DOI [10.1109/34.24792](#).
- Brandt JF. 1855.** Beiträge zur nähern Kenntniss der Säugethiere Russlands. Mémoires de l'Académie Impériale des Sciences de St Pétersbourg. *Sixième Série* **9**:1–375.
- Burgin CJ, Colella JP, Kahn PL, Upham NS. 2018.** How many species of mammals are there? *Journal of Mammalogy* **99**(1):1–14 DOI [10.1093/jmammal/gyx147](#).
- Byrd KE. 1981.** Mandibular movement and muscle activity during mastication in the guinea pig (*Cavia porcellus*). *Journal of Morphology* **170**(2):147–169 DOI [10.1002/jmor.1051700203](#).
- Cox PG. 2017.** The jaw is a second-class lever in *Pedetes capensis* (Rodentia: Pedetidae). *PeerJ* **5**:e3741 DOI [10.7717/peerj.3741](#).
- Cox PG, Baverstock H. 2016.** Masticatory muscle anatomy and feeding efficiency of the American beaver, *Castor canadensis* (Rodentia, Castoridae). *Journal of Mammalian Evolution* **23**(2):191–200 DOI [10.1007/s10914-015-9306-9](#).
- Cox PG, Faulkes CG. 2014.** Digital dissection of the masticatory muscles of the naked mole-rat, *Heterocephalus glaber* (Mammalia, Rodentia). *PeerJ* **2**:e448 DOI [10.7717/peerj.448](#).
- Cox PG, Jeffery N. 2011.** Reviewing the morphology of the jaw-closing musculature in squirrels, rats, and guinea pigs with contrast-enhanced microCT. *Anatomical Record* **294**(6):915–928 DOI [10.1002/ar.21381](#).
- Cox PG, Jeffery N. 2015.** The muscles of mastication in rodents and the function of the medial pterygoid. In: Cox PG, Hautier L, eds. *Evolution of the Rodents: Advances in Phylogeny, Functional Morphology and Development*. Cambridge: Cambridge University Press, 350–372.

- Cox PG, Rayfield EJ, Fagan MJ, Herrel A, Pataky TC, Jeffery N. 2012. Functional evolution of the feeding system in rodents. *PLOS ONE* 7(4):e36299 DOI 10.1371/journal.pone.0036299.
- Davies KT, Bennett NC, Tsagkogeorga G, Rossiter SJ, Faulkes CG. 2015. Family wide molecular adaptations to underground life in African mole-rats revealed by phylogenomic analysis. *Molecular Biology and Evolution* 32:3089–3107.
- Druzinsky RE. 2010. Functional anatomy of incisal biting in *Aplodontia rufa* and sciuriform rodents—Part 1: masticatory muscles, skull shape and digging. *Cells Tissues Organs* 191(6):510–522 DOI 10.1159/000284931.
- Fabre P-H, Hautier L, Dimitrov D, Douzery EJP. 2012. A glimpse on the pattern of rodent diversification: a phylogenetic approach. *BMC Evolutionary Biology* 12(1):88 DOI 10.1186/1471-2148-12-88.
- Faulkes CG, Bennett NC. 2013. Plasticity and constraints on social evolution in African mole-rats: ultimate and proximate factors. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368(1618):20120347 DOI 10.1098/rstb.2012.0347.
- Faulkes CG, Bennett NC, Cotterill FPD, Stanley W, Mgone GF, Verheyen E. 2011. Phylogeography and cryptic diversity of the solitary-dwelling silvery mole-rat, genus *Heliophobius* (family: Bathyergidae). *Journal of Zoology* 285(4):324–338 DOI 10.1111/j.1469-7998.2011.00863.x.
- Faulkes CG, Mgone GF, Archer EK, Bennett NC. 2017. Relic populations of *Fukomys* mole-rats in Tanzania: description of two new species *F. livingstoni* sp. nov. and *F. hanangensis* sp. nov. *PeerJ* 5:e3214.
- Faulkes CG, Verheyen E, Verheyen W, Jarvis JUM, Bennett NC. 2004. Phylogeographical patterns of genetic divergence and speciation in African mole-rats (Family: Bathyergidae). *Molecular Ecology* 13(3):613–629 DOI 10.1046/j.1365-294X.2004.02099.x.
- Gignac PM, Kley NJ. 2014. Iodine-enhanced microCT imaging: methodological refinements for the study of soft-tissue anatomy of post-embryonic vertebrates. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 322B(3):166–176 DOI 10.1002/jez.b.22561.
- Gignac PM, Kley NJ, Clarke JA, Colbert MW, Morhardt AC, Cerio D, Cost IN, Cox PG, Daza JD, Early CM, Echols MS, Henkelman RM, Herdina AN, Holliday CM, Li Z, Mahlow K, Merchant S, Müller J, Orsborn CP, Paluh DJ, Thies ML, Tsai HP, Witmer LM. 2016. Diffusible iodine-based contrast-enhanced computed tomography (diceCT): an emerging tool for rapid, high-resolution, 3-D imaging of metazoan soft tissues. *Journal of Anatomy* 228(6):889–909 DOI 10.1111/joa.12449.
- Gomes Rodrigues H, Šumbera R, Hautier L. 2016. Life in burrows channelled the morphological evolution of the skull in rodents: the case of African mole-rats (Bathyergidae, Rodentia). *Journal of Mammalian Evolution* 23(2):175–189 DOI 10.1007/s10914-015-9305-x.
- Gorniak GC. 1977. Feeding in golden hamsters, *Mesocricetus auratus*. *Journal of Morphology* 154(3):427–458 DOI 10.1002/jmor.1051540305.
- Hautier L, Cox PG, Lebrun R. 2015. Grades and clades among rodents: the promise of geometric morphometrics. In: Cox PG, Hautier L, eds. *Evolution of the Rodents: Advances in Phylogeny, Functional Morphology and Development*. Cambridge: Cambridge University Press, 277–299.
- Hiimae K. 1971. The structure and function of the jaw muscles in the rat (*Rattus norvegicus* L.) III: the mechanics of the muscles. *Zoological Journal of the Linnean Society* 50(1):111–132 DOI 10.1111/j.1096-3642.1971.tb00754.x.
- Ingram CM, Burda H, Honeycutt RL. 2004. Molecular phylogenetics and taxonomy of the African mole-rats, genus *Cryptomys* and the new genus *Coetomys* Gray, 1864. *Molecular Phylogenetics and Evolution* 31(3):997–1014 DOI 10.1016/j.ympev.2003.11.004.

- Jeffery NS, Stephenson R, Gallagher JA, Jarvis JC, Cox PG. 2011. Micro-computed tomography with iodine staining reveals the arrangement of muscle fibres. *Journal of Biomechanics* **44**(1):189–192 DOI [10.1016/j.jbiomech.2010.08.027](https://doi.org/10.1016/j.jbiomech.2010.08.027).
- Kock D, Ingram CM, Frabotta LJ, Honeycutt RL, Burda H. 2006. On the nomenclature of Bathyergidae and *Fukomys* ngen (Mammalia: Rodentia). *Zootaxa* **1142**(1):51–55 DOI [10.11646/zootaxa.1142.1.4](https://doi.org/10.11646/zootaxa.1142.1.4).
- Landry SO. 1957. The interrelationships of the new and old world rodents. *University of California Publications in Zoology* **56**:1–118.
- Lavocat R. 1973. *Les Rongeurs du Miocène d'Afrique orientale. 1, Miocène inférieur, Mémoires et travaux de l'Institut de Montpellier*. Montpellier: École pratique des hautes études, Institut de Montpellier, 1–284.
- Lessa EP. 1990. Morphological evolution of subterranean mammals: integrating structural, functional, and ecological perspectives. In: Nevo E, Reig OA, eds. *Evolution of Subterranean Mammals at the Organismal and Molecular Levels*. New York: Wiley-Liss, 211–230.
- Maier W, Schrenk F. 1987. The hystricomorphy of the Bathyergidae, as determined from ontogenetic evidence. *Zeitschrift für Säugetierkunde* **52**:156–164.
- McIntosh AF, Cox PG. 2016a. Functional implications of craniomandibular morphology in African mole-rats (Rodentia: Bathyergidae). *Biological Journal of the Linnean Society* **117**(3):447–462 DOI [10.1111/bij.12691](https://doi.org/10.1111/bij.12691).
- McIntosh AF, Cox PG. 2016b. The impact of digging on craniodental morphology and integration. *Journal of Evolutionary Biology* **29**(12):2383–2394 DOI [10.1111/jeb.12962](https://doi.org/10.1111/jeb.12962).
- Mein P, Pickford M. 2008. Early miocene rodentia from the northern sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia* **20**:235–290.
- Metscher BD. 2009. MicroCT for comparative morphology: simple staining methods allow high-contrast 3D imaging of diverse non-mineralized animal tissues. *BMC Physiology* **9**(1):11 DOI [10.1186/1472-6793-9-11](https://doi.org/10.1186/1472-6793-9-11).
- Morlok WF. 1983. Vergleichend- und funktionell-anatomische Untersuchungen an Kopf, Hals und Vorderextremität subterranean Nagetiere (Mammalia, Rodentia). *Courier Forschungsinstitut Senckenberg* **64**:1–237.
- Murphy RA, Beardsley AC. 1974. Mechanical properties of the cat soleus muscle in situ. *American Journal of Physiology* **227**(5):1008–1013 DOI [10.1152/ajplegacy.1974.227.5.1008](https://doi.org/10.1152/ajplegacy.1974.227.5.1008).
- Müller A. 1933. Die Kaumuskulatur des *Hydrochoerus capybara* und ihre Bedeutung für die Formgestaltung des Schädels. *Morphologisches Jahrbuch* **72**:1–59.
- Patterson BD, Upham NS. 2014. A newly recognized family from the Horn of Africa, the *Heterocephalidae* (Rodentia: Ctenohystrica). *Zoological Journal of the Linnean Society* **172**(4):942–963 DOI [10.1111/zoj.12201](https://doi.org/10.1111/zoj.12201).
- Rosell F, Bozsér O, Collen P, Parker H. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* **35**(3–4):248–276 DOI [10.1111/j.1365-2907.2005.00067.x](https://doi.org/10.1111/j.1365-2907.2005.00067.x).
- Samuels JX, Van Valkenburgh B. 2009. Craniodental adaptations for digging in extinct burrowing beavers. *Journal of Vertebrate Paleontology* **29**(1):254–268 DOI [10.1080/02724634.2009.10010376](https://doi.org/10.1080/02724634.2009.10010376).
- Satoh K, Iwaku F. 2004. Internal architecture, origin-insertion site, and mass of jaw muscles in Old World hamsters. *Journal of Morphology* **267**(8):987–999 DOI [10.1002/jmor.10443](https://doi.org/10.1002/jmor.10443).
- Smith CC, Follmer D. 1972. Food preferences of squirrels. *Ecology* **53**(1):82–91 DOI [10.2307/1935712](https://doi.org/10.2307/1935712).

- Stein BR. 2000.** Morphology of subterranean rodents. In: Lacey EA, Patton JL, Cameron GN, eds. *Life Underground: The Biology of Subterranean Rodents*. Chicago: University of Chicago Press, 19–61.
- Swanson MT, Oliveros CH, Esselstyn JA. 2019.** A phylogenomic rodent tree reveals the repeated evolution of masseter architectures. *Proceedings of the Royal Society B: Biological Sciences* **286(1902)**:20190672 DOI [10.1098/rspb.2019.0672](https://doi.org/10.1098/rspb.2019.0672).
- Thorington RW, Darrow K. 1996.** Jaw muscles of old world squirrels. *Journal of Morphology* **230**:145–165 DOI [10.1002/\(SICI\)1097-4687\(199611\)230:2<145::AID-JMOR3>3.0.CO;2-G](https://doi.org/10.1002/(SICI)1097-4687(199611)230:2<145::AID-JMOR3>3.0.CO;2-G).
- Tullberg T. 1899.** Über das System der Nagethiere: eine phylogenetische Studie. *Nova Acta Regiae Societatis Scientiarum Upsaliensis Series 3* **18**:1–514.
- Turnbull WD. 1970.** Mammalian masticatory apparatus. *Fieldiana (Geology)* **18**:147–356.
- Van Daele PAAG, Herrel A, Adriaens D. 2009.** Biting performance in teeth-digging African mole-rats (*Fukomys*, Bathyergidae, Rodentia). *Physiological and Biochemical Zoology* **82(1)**:40–50 DOI [10.1086/594379](https://doi.org/10.1086/594379).
- Van Daele PAAG, Verheyen E, Brunain M, Adriaens D. 2007.** Cytochrome b sequence analysis reveals differential molecular evolution in African mole-rats of the chromosomally hyperdiverse genus *Fukomys* (Bathyergidae, Rodentia) from the Zambezi region. *Molecular Phylogenetics and Evolution* **45(1)**:142–157 DOI [10.1016/j.ympev.2007.04.008](https://doi.org/10.1016/j.ympev.2007.04.008).
- Vickerton P, Jarvis J, Jeffery N. 2013.** Concentration-dependent specimen shrinkage in iodine-enhanced microCT. *Journal of Anatomy* **223(2)**:185–193 DOI [10.1111/joa.12068](https://doi.org/10.1111/joa.12068).
- Visser JH, Bennett NC, Jansen Van Vuuren B. 2019.** Phylogeny and biogeography of the African Bathyergidae: a review of patterns and processes. *PeerJ* **7(4)**:e7730 DOI [10.7717/peerj.7730](https://doi.org/10.7717/peerj.7730).
- Weijs WA, Dantuma R. 1975.** Electromyography and mechanics of mastication in the albino rat. *Journal of Morphology* **146(1)**:1–33 DOI [10.1002/jmor.1051460102](https://doi.org/10.1002/jmor.1051460102).
- Wilson DE, Lacher TE, Mittermeier RA. 2016.** *Handbook of the mammals of the world Vol. 6. Lagomorphs and rodents I*. Barcelona: Lynx Edicions.
- Wood AE. 1965.** Grades and clades among rodents. *Evolution* **19(1)**:115–130 DOI [10.1111/j.1558-5646.1965.tb01696.x](https://doi.org/10.1111/j.1558-5646.1965.tb01696.x).
- Wood AE. 1985.** The relationships, origin and dispersal of the hystricognathous rodents. In: Lockett WP, Hartenberger JL, eds. *Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis*. New York: Plenum Press, 475–513.
- Woods CA. 1972.** Comparative myology of jaw, hyoid, and pectoral appendicular regions of New and Old World hystricomorph rodents. *Bulletin of the American Museum of Natural History* **147**:115–198.
- Woods CA, Hermanson JW. 1985.** Myology of hystricognath rodents: an analysis of form, function and phylogeny. In: Lockett WP, Hartenberger JL, eds. *Evolutionary Relationships among Rodents: A Multidisciplinary Analysis*. New York: Plenum Press, 685–712.
- Woods CA, Howland EB. 1979.** Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. *Journal of Mammalogy* **60(1)**:95–116 DOI [10.2307/1379762](https://doi.org/10.2307/1379762).