

# Biting Performance in Teeth-Digging African Mole-Rats (*Fukomys*, Bathyergidae, Rodentia)\*

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## ABSTRACT

Phenotypic variation is channeled by adaptation to local environments and phylogenetic constraints. The morphology of the obligatorily subterranean African mole-rats of the genus *Fukomys* has been shaped within the context of their underground habitat, posing particular limits on the animals' morphology. Especially the biting apparatus has likely evolved within severe evolutionary constraints, as it is used for feeding on hard geophytes, for digging complex tunnel systems, and for defensive purposes and social interactions in a colony. We studied interspecific differences in bite performance among three taxa, in relation to their skull anatomy and skull shape. Data on biting performance were gathered by in vivo measurements and compared with model simulations. It is shown that the model simulation is a good proxy for in vivo measurement. Scaling of bite force is positively allometric relative to head size. Moreover, differences in biting performance exist between taxa, which may be linked to differences in their ecology. This study will eventually enable us to analyze the evolutionary pattern behind the variation in structure and performance of the biting apparatus in *Fukomys* mole-rats.

## Introduction

It is generally accepted that an organism's design is a compromise between adaptation to the local environment and phy-

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logenetic constraints (Wainwright 1996; Irschick et al. 1997). For many vertebrate taxa with miscellaneous foraging styles, the relationship between skull design, diet, and feeding performance has been emphasized (Freeman 1984; Zweers et al. 1994; Aguirre et al. 2002; Huber et al. 2005). It is clear from studies on groups with well-established phylogenies that several aspects of an organism's morphology coevolve with foraging behavior (e.g., lizards: Huey and Pianka 1981; Cooper 1997; McBrayer 2004). Evolution toward increased bite capacity, for example, for dietary purposes, may come at the expense of jaw closing speed needed in defensive or in predatory strikes. Thus, evolutionary trade-offs may ultimately constrain the phenotypic radiation of a group (Vanhooydonck et al. 2001; Van Damme et al. 2002).

The subterranean African mole-rats of the genus *Fukomys* (Bathyergidae, Rodentia; a recent split, formerly part of *Cryptomys* [Kock et al. 2006]) have been molded within the context of their underground habitat, posing particular limits on the animals' morphology. Especially the biting apparatus is likely shaped within severe evolutionary constraints, as it is used for feeding on hard geophytes, for digging complex tunnel systems, and for defensive purposes and social interactions in a colony (Bennett and Faulkes 2000). The *Fukomys* radiation is characterized by an overall morphological similarity between the species, despite an impressive variation at the chromosomal and molecular level. Mole-rats of the genus *Fukomys* specifically show differential levels of chromosomal variation and DNA sequence divergence between the main clades that constitute the genus (Van Daele et al. 2007a). Preliminary analyses on the interspecific level show that different cranial morphotypes exist and that there is even considerable shape and size polymorphism among closely related chromosomal races (Van Daele et al. 2006; Murtas et al. 2007).

*Fukomys* are chisel-tooth diggers, using their incisors for tunneling in tropical soils. They spar with opponents by interlocking the incisors, take on defensive postures with wide open jaws, and gnaw on hard bulbs and roots. Therefore, bite force likely is an important aspect of *Fukomys* ecology and offers the potential to gain further insight into the morphological evolution of this group. We first want to answer questions regarding general biting performance in African mole-rats. Do *Fukomys* bite hard in comparison with other mammals, as one would expect on the basis of the skull musculature (Boller 1969)? How is bite force related to body and head size? What is the extent of the variation in bite force between and among *Fukomys* clades? In view of the paucity of empirical data documenting bite force in nonhuman mammals (for an overview, see Dumont and Herrel 2003), the data presented here furthermore allow us to test hypotheses regarding mammalian biting per-

formance. For example, the system may be designed to optimally perform at the incisor while still allowing for bite force to increase toward the molars (Mansour and Reznik 1975; Oyen and Tsay 1991). As tooth digging and foraging on geophytes may require different gape angles, we also wanted to address the effect of gape angle on biting performance. To answer these questions, we assembled two data sets. First, we quantified interspecific variation in bite-force capacity using *in vivo* bite-force measurements. Second, using input data from dissections of the cranial musculature we tested whether static biting simulations from a biomechanical model generate reliable data in comparison with these *in vivo* biting measurements. We then calculated variation in bite performance associated with gape angle and bite point, using the mathematical biting model. Finally, the results were interpreted in the context of known shape variation in the cranium of the three taxa.

## Material and Methods

### Study Specimens

All *Fukomys* specimens used in this study were live-trapped in Zambia or the Democratic Republic of Congo on expeditions between 2002 and 2005. Species boundaries within the genus are currently under debate (Bennett and Faulkes 2000; Van Daele et al. 2007a, 2007b). The study specimens belong to three clades that are all included in the Zambebian group: (1) a basal Zambebian lineage (*Fukomys mechowii* clade—Salujinga chromosomal race; SAL:  $2n = 42$ ), (2) a genetically highly diverged northern Zambebian lineage (*Fukomys whytei* clade—including the West Bangweulu phylogroup from Kasanka;  $2n =$  undetermined and the *Fukomys amatus* phylogroup; Ndeba [NDE]:  $2n = 54$ ), and (3) a derived central Zambebian lineage (*Fukomys micklemei* clade—Kalamba [KAL] and Kataba cytotypes; respectively,  $2n = 56$  and  $2n = 60$ ; Van Daele et al. 2004, 2007b; Fig. 1).

All specimens are adult and belong to the same relative age class (scored on tooth wear and skull characteristics). The animals that were chosen for the dissections are all nonbreeders. Live specimens are housed in an animal care facility at Ghent University (the molarium). The animals are kept at an average temperature of 22°C in dark conditions and receive food *ad lib*. Freshly dead animals were stored in the freezer at  $-20^{\circ}\text{C}$  before fixation. In the dissections, we used three specimens of each of three chromosomal races: SAL, NDE, and KAL.

### *In Vivo* Bite Forces

Individual bite-force measurements were taken with an isometric Kistler force transducer, which was connected to a charge amplifier (for details of the experimental setup, see Herrel et al. 1999). Mole-rats were allowed to bite five times, and the highest bite-force readout was used as an estimator of maximal bite performance. Animals were induced to bite defensively by taking them out of their cages. This immediately resulted in a characteristic threat response with the jaws opened widely. As soon as an object approached the animals they would vigorously

snap at it. All animals were weighed to the nearest 0.1 g, and head length, head width, and head height were measured to the nearest 0.01 mm on pictures of standardized lateral and dorsal views (Table 1). Bite-force measurements were compared with data from the literature on other Mammalia (App. A).

### Morphology

Preserved specimens were dissected using a Wild stereoscope (M5), equipped with a camera lucida. On one side, all muscles were removed separately, and their mass was measured to the nearest 0.01 g. Fiber length was determined following the method of Gans et al. (1989). Ten muscle fibers were selected at random for the calculation of the average fiber length. An estimate of maximal force development of a given muscle was then made on the basis of the physiological cross-sectional area (PCSA). The PCSA was calculated as volume over fiber length, taking pinnation angle into account for the portion M1a and M1b of the masseter muscle only (see below for a description of those portions). Volumes were calculated from mass measurements using a density of  $1.05\text{ g/cm}^3$  (Mendez and Keys 1960). Three-dimensional coordinates of place of origin and insertion of each muscle were taken with a Microscribe (3D-digitizer G2X, Immersion).

### Bite Model

The three-dimensional coordinates and PCSAs were used as the input data (App. B) for a static bite-force model (Cleuren et al. 1995; Herrel et al. 1998a, 1998b). Simulations were run for two gape angles ( $10^{\circ}$  and  $50^{\circ}$ ) and two bite points: at the incisor (incisive bite force: I) and at the first molariform tooth (molar bite force: M1). The orientation or angle of the food reaction forces (AFRF) was set to vary between  $-138$  and  $-54$ . Bite force is then calculated for one side. Bite force is multiplied by two to allow comparison with measurement data. Also for comparative reasons, muscles were set to be maximally active in a first series of trial model runs. Muscles that did not contribute to jaw closing under the given settings were set to zero in a second series of runs, providing the output data presented here.

### Geometric Morphometrics

A landmark-based geometric morphometric analysis using a generalized Procrustes analysis and a thin plate spline algorithm (Rohlf and Slice 1990; Bookstein 1991) allowed to visualize shape differences between shapes of the means calculated in a canonical variates analysis. These analyses were conducted with the TPS suite (Rohlf 2005) and the IMP suite (Zelditch et al. 2004; freeware at <http://life.bio.sunysb.edu/morph/>).

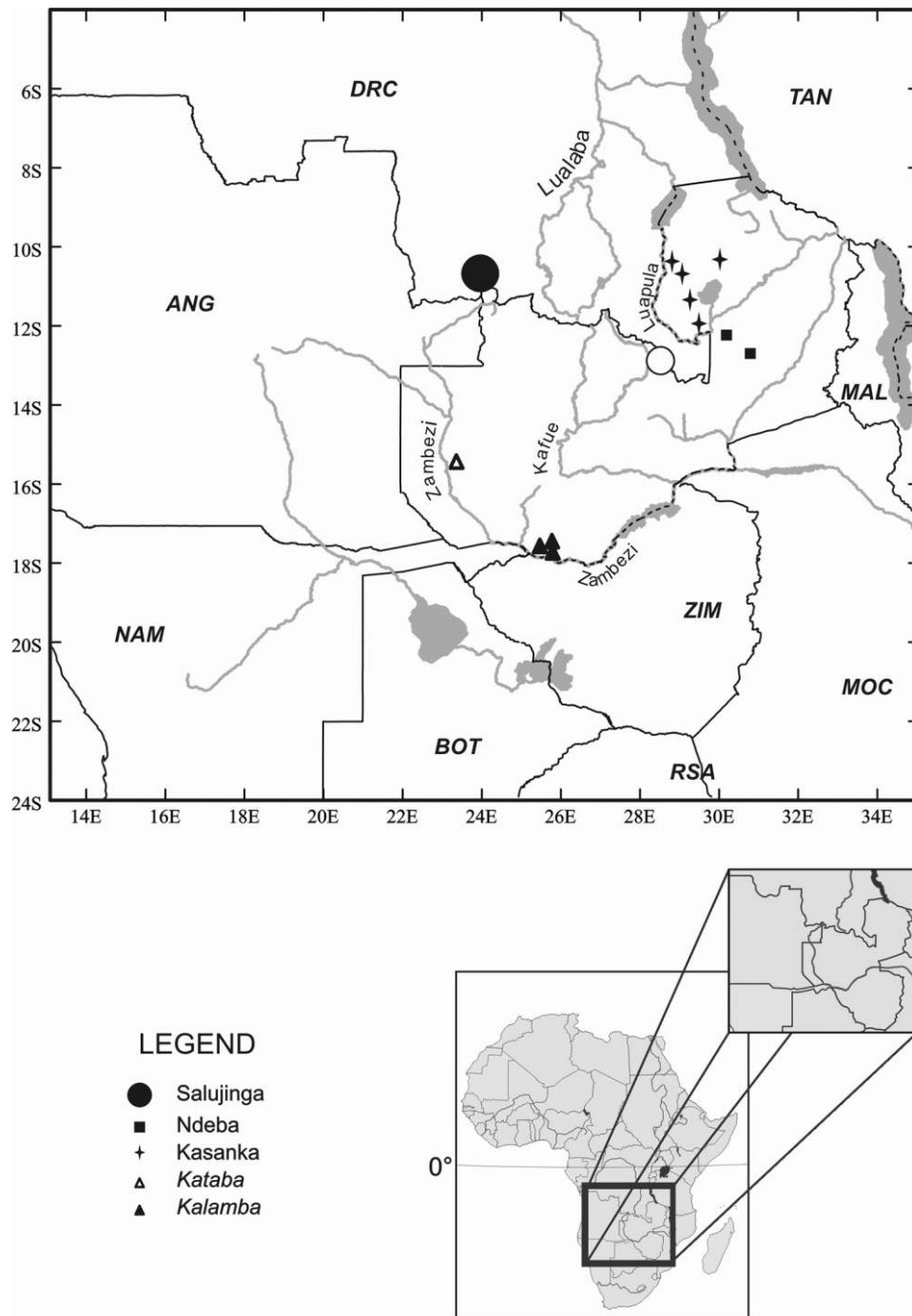


Figure 1. Map showing the sample locations of the different populations used in this study.

## Results

### Myology

The jaw adducting musculature in *Fukomys* can be divided into four main groups, which are similarly structured as in the sister genus *Cryptomys* (Boller 1969; Fig. 2): (1) a pterygoid group (including the musculus pterygoideus medius [PtM] and a smaller m. p. lateralis [PtL]), (2) a musculus temporalis group

(T), (3) a musculus zygomaticus mandibularis group that forms two distinct bundles (m. z. anterior [ZMa] and m. z. posterior [ZMp]), which can be readily separated from the masseter muscle. (4) The musculus masseter can be divided with some difficulty in an m. m. superficialis and an m. m. profundus (Mp), although it is clear on dissecting layer by layer that the two rather comprise a bundle of fibers gradually changing in their orientation. The masseter superficialis is subdivided in three

Table 1: Sample size, body mass ( $M$ ), maximal bite force (BF), head length (HL), head width (HW), and head height (HH) used in the intra- and interspecific analyses of gape angle and bite force (mean  $\pm$  SD)

Clade	Race	Sex	$n$	$M$ (g)	BF (N)	HL (mm)	HW (mm)	HH (mm)
Adults:								
<i>Fukomys micklei</i>	KAL	4F/3M	7	88.93 $\pm$ 14.22	40.53 $\pm$ 8.23	47.74 $\pm$ 5.68	34.83 $\pm$ 2.30	32.94 $\pm$ 2.79
<i>Fukomys</i> sp.	SAL	2F	2	105.60 $\pm$ 16.24	48.25 $\pm$ 22.98	48.39 $\pm$ 5.02	39.13 $\pm$ 2.13	36.59 $\pm$ 4.13
<i>Fukomys whytei</i>	NDE	2F/1M	3	78.90 $\pm$ 28.14	31.44 $\pm$ 13.76	46.45 $\pm$ 3.12	35.25 $\pm$ 1.95	33.39 $\pm$ 4.22
<i>F. whytei</i>	KAS	1F/3M	4	84.73 $\pm$ 15.13	39.55 $\pm$ 24.57	46.12 $\pm$ 5.50	36.97 $\pm$ 4.05	33.99 $\pm$ 5.50
Juveniles:								
<i>F. micklei</i>	KAL	1F/1M	2	9.95 $\pm$ .42	9.95 $\pm$ .21	30.24 $\pm$ .90	23.15 $\pm$ .33	23.90 $\pm$ 1.40

Note. KAL = Kalamba, KAS = Kasanka, NDE = Ndeba, SAL = Salujinga, F = female, M = male.

portions (M1a, M1b, and M2) according to differences in the fiber orientation. These portions can be easily separated where they converge anteriorly at their respective origins, but they are more or less fused near the point of insertion. African mole-rats possess a massive masticatory apparatus in comparison with, for example, *Rattus* (Fig. 2). Masses, fiber lengths, and PCSAs of all muscles used in the simulations are given in Appendix B.

#### In Vivo Bite Forces

To normalize the distribution of the sample values, data were log transformed. Across all taxa studied, there is a clear and significant positive allometric relationship between head size and bite force (Fig. 3). Significant regressions were obtained for all size variables, but head height is the best predictor of bite force (slope = 3.43;  $R^2 = 0.71$ ; compare with a more isometric scaling with head length: slope = 1.97;  $R^2 = 0.45$  and head width slope = 2.57;  $R^2 = 0.45$ ). When taking head height into account, bite forces tended to be different among groups, but differences were not statistically significant (ANCOVA:  $F = 3.01$ ,  $P = 0.09$ ).

#### Bite Forces among Mammalia

Bite forces and body masses were compiled for 43 species (including the *Fukomys* taxa) of Mammalia from the available

literature (see App. A). When all mammals are combined, bite force scaled to body mass with a coefficient of 0.62, that is, with slight negative allometry (Fig. 3B). Making abstraction of the calculated values of Wroe et al. (2005), bite force scaled to body mass with a coefficient of 0.67, close to isometric scaling. For a given body mass, *Fukomys* mole-rats collectively bite harder than all other mammals jointly (ANCOVA:  $F = 8.46$ ,  $P = 0.006$ ; Fig. 3C).

#### Model Calculations versus In Vivo Measurements

The calculated values fall well within the range of in vivo measurement values (Fig. 3A). Taking head height into account, there is no significant difference between simulated bite force at a  $10^\circ$  gape angle (AFRF =  $90^\circ$ ) and in vivo measurements of bite force (ANCOVA:  $F = 3.47$ ,  $P = 0.08$ ). In an analysis that combined in vivo with the model data, significant differences were found in mean bite force between the three taxa (ANCOVA:  $F = 10.00$ ,  $P = 0.002$ ). A Tukey's post hoc test shows that KAL and SAL specimens bite on average significantly harder than the NDE specimens for a given body mass.

#### Effect of Gape Angle, Bite Point, and the Angle of the Food-Reaction Force

In each comparison, we consider the case in which all jaw adductors are maximally active. In Figure 4, the common pat-

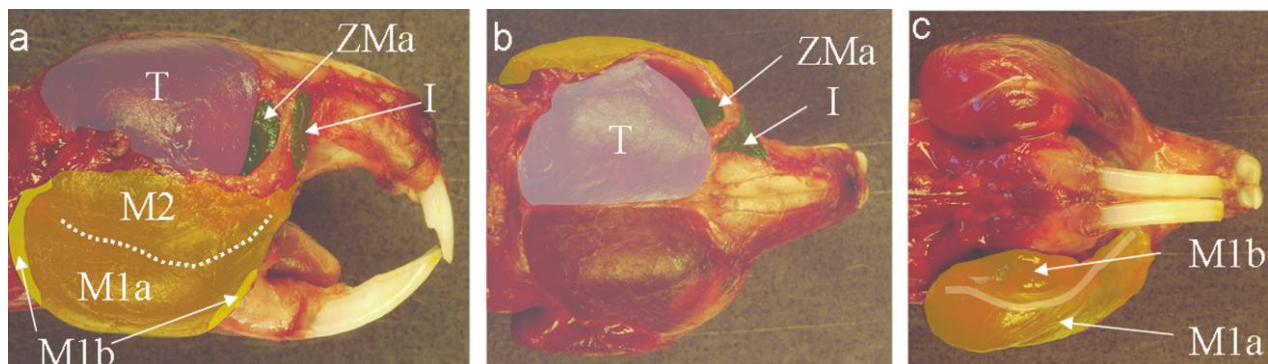


Figure 2. a, Lateral; b, dorsal; and c, ventral views of the masticatory apparatus musculature in *Fukomys*. ZMa = m. zygomaticus mandibularis anterior (I = pars infraorbitalis); M = m. masseter superficialis (parts M1a, M1b, M2); T = m. temporalis.

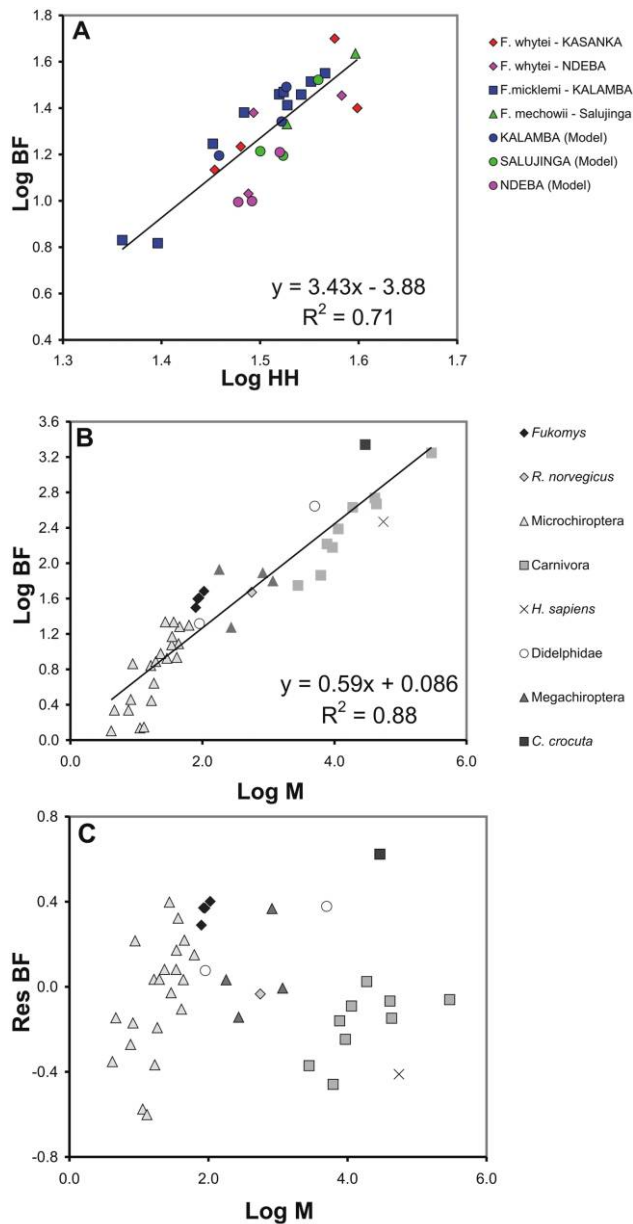


Figure 3. A, Bite force in *Fukomys*. Log<sub>10</sub> bite force against log<sub>10</sub> head height. Simulated bite force at the incisors (circles) is plotted on measured values (squares). Simulated values were taken for an angle of food reaction force of 90° and gape angle of 10°. B, Bite force in *Fukomys* compared with other Mammalia. A, Log<sub>10</sub> bite force plotted against log<sub>10</sub> mass. C, Residuals from regression analysis of log<sub>10</sub> bite force on log<sub>10</sub> mass plotted against log<sub>10</sub> mass.

tern for mammals is retrieved: *Fukomys* bite harder at the occlusal surface of the first molar, where forces are doubled compared with the incisors. Thus, mole-rats are equipped to produce higher forces with the posterior teeth. The KAL and SAL specimens show the highest increase in bite force between incisival and molar bite force. Minimum bite force is generated under rather perpendicular AFRF, depending on taxon and bite point. Similar patterns are found under different gape angles.

Figures 4 and 5 also illustrate the consistently lower biting force in the NDE specimens. Particularly, the KAL and SAL specimens seem to be able to generate considerable higher forces when the AFRF shifts from -90° forward (Fig. 5A, 5B). The ratio of joint force to bite force is more advantageous at the second bite point (M1, Fig. 5C), resulting from a lower joint force for a given bite force.

### Geometric Morphometric Analysis of the Dorsal Cranium

The three taxa can be readily discriminated on the basis of shape differences in the dorsal cranium (Fig. 6A). Relative to the SAL and KAL races, the NDE race is characterized by considerable shape differences associated with the posterior brain case (Fig. 6B, 6C). Notable are the lateral compression in the temporalis area and posteriad displacement of the nuchal crest.

### Discussion

Our results clearly demonstrate that mole-rats have evolved a powerful biting apparatus associated with their unique subterranean lifestyle. Among mammals, they are among the most forceful biters for their body size (Fig. 3). Despite the far-reaching specializations of the cranial apparatus in these animals, our model data suggest that they still follow the basic mammalian design. For example, both gape angle and bite point influence bite-force generation as has been demonstrated for other mammals (e.g., humans: Manns et al. 1979; MacKenna and Turker 1983; Fields et al. 1986; bats: Dumont and Herrel 2003). On the basis of the comparison of the simulations and the in vivo bite-force data, it is clear that the model can be considered a good tool for estimating bite forces in *Fukomys*.

If the jaw system in *Fukomys* operates as in other mammals, as suggested by our data, what explains the apparent selection for increased bite performance? It seems possible that in the case of mole-rats, an increase in bite force would allow them to consume a larger diversity of hard geophytes. However, the

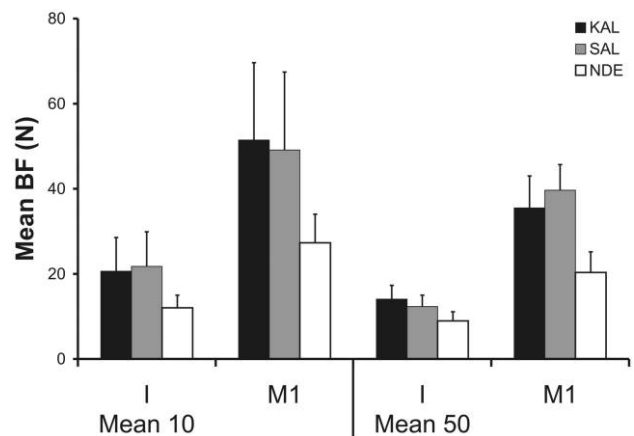


Figure 4. Model output. Mean (+SE) molar and incisival bite force for each group. KAL = Kalamba population, SAL = Salujinga population, NDE = Ndeba population.

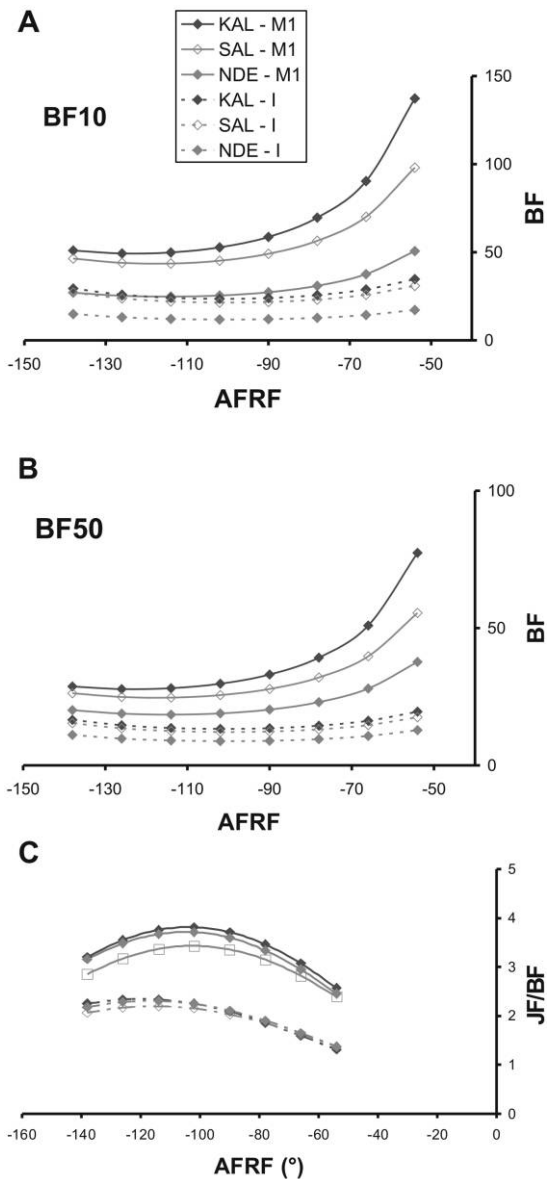


Figure 5. Model output. Mean molar (M1) and incisival (I) bite force (BF) for a given range of angles of the food reaction force (AFRF). *A*, Simulation at gape angle 10°. *B*, Simulation at gape angle 50°. *C*, Ratio of the joint force (JF) to BF for a given range of the AFRF (calculated from the means per taxon).

little data available (Bennett and Faulkes 2000; P. A. A. G. Van Daele, unpublished data) indicate that the animals forage to a large extent on morphologically similar species from the same plant genera. Although the different groups may potentially specialize on different plant parts that differ in hardness, data on the hardness of the different species of food plants are currently lacking. A well-developed jaw musculature will likely also bring a functional advantage during burrowing activities, as this is an energetically high-cost activity (Lessa 1990). However, as mole-rats mainly excavate their tunnel systems during the wet season, when soils are soft, an increase in biting performance may only be useful for extending the time window

that allows economic burrowing. The SAL population is found in the so-called chanas, or dambos (wet grasslands on waterlogged soils), which are partly covered with suffrutices. These are miniature, herblike trees that form dense mats of roots. The observed higher bite forces may therefore be a response to tunneling in what seems to be a challenging subterranean environment. However, this explanation cannot account for the equally high bite forces observed in the KAL specimens, which, on the basis of our observations, occur in more arid habitats that seem to be easier to dig.

Interestingly, our data suggest that the NDE specimens are relative underperformers compared with the SAL and KAL specimens. There are several alternative, not mutually exclusive, explanations for the observed subtle differences in bite force between groups. An important observation in this respect is a trend in the amount of shape difference in line with that of the observed differences in bite force. The NDE taxon is significantly and substantially different from the other two taxa and the two may be causally linked as the compression of the posterior brain case may provide a decreased attachment area for the jaw adductors. Indeed, skull morphology in general is correlated with dietary and performance variation in mammals (Radinsky 1981; Gordon and Illius 1988) and other vertebrates (Lauder 1991; Richman and Price 1992; Wainwright 1996; Barbosa and Moreno 1999a, 1999b; Herrel et al. 2001, 2006; Meyers et al. 2006).

An interesting observation throughout the analyses is the considerable intraspecific variation in many components of the masticatory apparatus, contributing to biting performance. Huge variation in morphological traits was already indicated in early studies on *Fukomys* (formerly part of *Cryptomys*; Boller 1969; De Graaff 1981; Williams et al. 1983). Our previous studies already revealed that intraspecific variation complicates the diagnosis of the different taxa. Here we would like to suggest that the observed intraspecific variation in skull morphology may be related to the high degree of sociality, which mole-rats exhibit. It is well established now that *Fukomys damarensis* is a eusocial mammal with a clear division of labor (Jarvis and Bennett 1993). Consequently, one would expect a morphological distinction between the different casts that make up a colony. The KAL specimens belong to the sister clade of *F. damarensis*, and geometric morphometric studies (Van Daele et al. 2006; Murtas et al. 2007) as well as field studies (P. A. A. G. Van Daele, unpublished data) indicate that at least the members of this clade will qualify as eusocial mammals, as has been suggested by Burda et al. (2000).

In contrast, the *Fukomys mechowii* clade (containing the SAL specimens and the giant mole-rat) and the northern Zambezan *Fukomys whytei* clade (including the Kasanka and NDE populations) seem to exhibit a lower level of social structuring within the colonies. Our field observations indicate that colony size may also be smaller in the SAL and NDE populations. These aspects of sociality would be directly linked with food availability in the different ecogeographic regions in which the animals are found and may thus also affect cranial morphology and performance (Bennett and Faulkes 2000). Whereas *Fukomys micklemei* (containing the KAL population) and *F. da-*

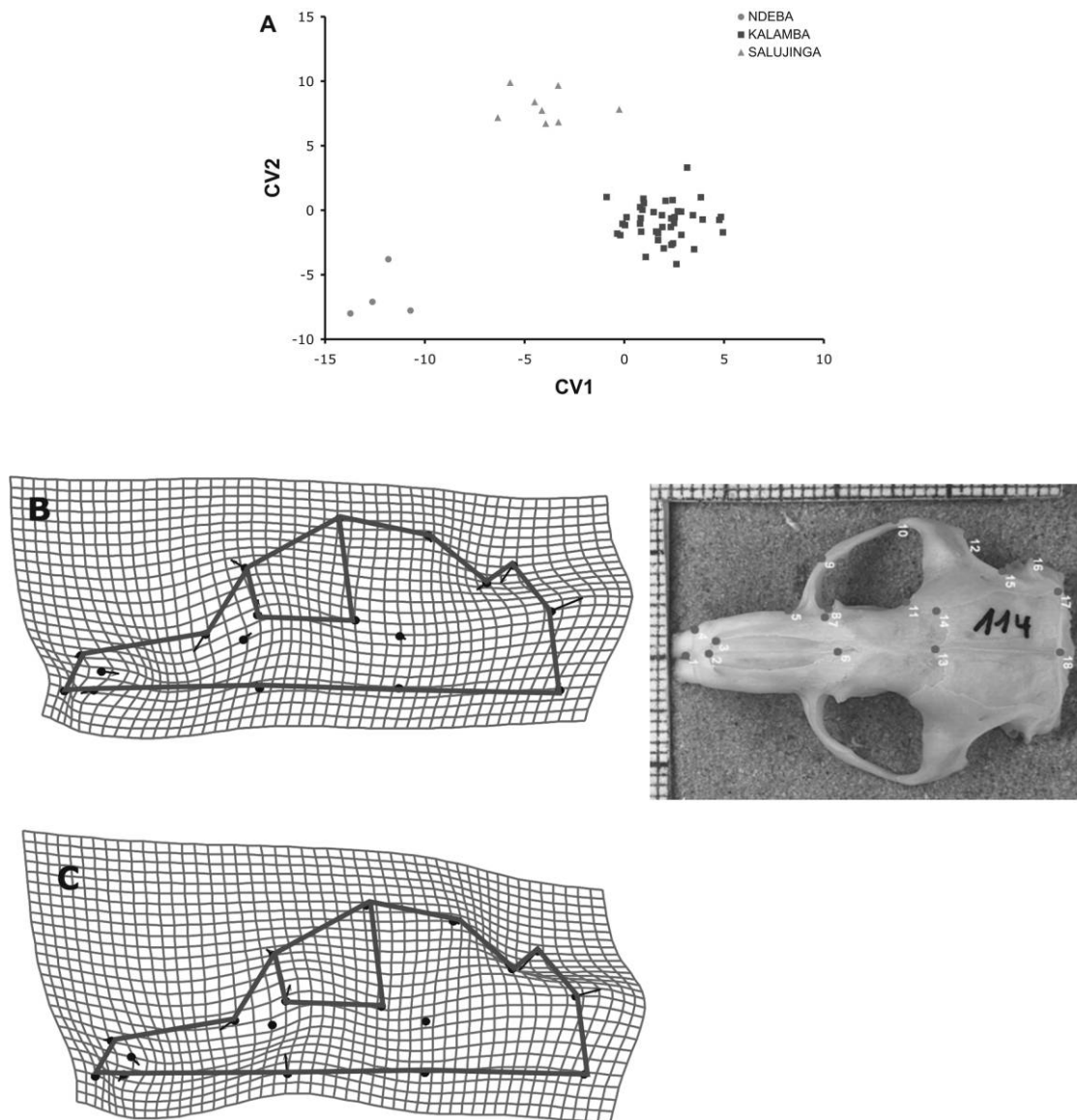


Figure 6. A, Canonical variates plot (ordination of dorsal cranial shape variables). Deformation grids illustrate the discriminating shape differences between (B) the mean shape of Salujinga and Ndeba and (C) Kalamba and Ndeba, shown as a deformation of Salujinga and Kalamba, respectively (exaggerated five times).

*marensis* are found in more arid areas with lower food predictability (consequently requiring a greater energy expenditure for foraging), *F. whytei* and *F. mechowii* tunnel in areas with a higher diversity and abundance of geophytes in more humid conditions. However, virtually nothing is known about morphological variation within colonies and quantifying morphological variation in relation to the presumed differential levels of sociality between clades would require extensive sampling of whole colonies.

Further interpretation of the data and new simulations would benefit from behavioral assessments, including studies on burrowing in relation to social status, intra- and interspecific interactions, dietary studies, and data on colony sizes. In this respect, comparative studies with the sister genus *Cryptomys*

(containing social species) and the solitary genera (*Heliophobius*, *Bathyergus*, and *Georychus*) could be beneficial. If we want to understand the patterns of morphological variation, the key issue will be to gain a better insight into the relation between morphological diversification, colony structure, and the degree of sociality in Zambebian mole-rats.

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## Appendix A

Table A1: Mean maximal bite force (BF), residual bite force (Res BF), and body mass (*M*) for several mammal species

Species	BF (N)	Res BF	<i>M</i> (g)	Source	MV or C <sup>a</sup>
<i>Fukomys micklemi</i> (Kalamba and Kataba; adult)	41	.38	89	This publication	MV
<i>Fukomys</i> sp. (Salujinga)	48	.41	106	This publication	MV
<i>Fukomys whytei</i> (Ndeba)	31	.30	79	This publication	MV
<i>F. whytei</i> (Kasanka)	40	.38	85	This publication	MV
<i>Crocota crocata</i>	2,195	.63	29,200	Binder and Van Valkenburgh 2000	MV
<i>Homo sapiens</i>	294	-.40	55,000	Ringqvist 1973	MV
<i>Rattus norvegicus</i>	47	-.03	555	Robins 1977	MV
<i>Didelphis virginiana</i>	442	.39	5,000	Thomason et al. 1990	MV
<i>Monodelphis domestica</i> (adult)	21	.08	90	Thompson et al. 2003	MV
<i>Canis aureus</i>	165	-.15	7,700	Wroe et al. 2005	C
<i>Felis sylvestris</i>	56	-.36	2,800	Wroe et al. 2005	C
<i>Genetta tigrinum</i>	73	-.45	6,200	Wroe et al. 2005	C
<i>Hyaena hyaena</i>	545	-.06	40,800	Wroe et al. 2005	C
<i>Lycaon pictus</i>	428	.03	18,900	Wroe et al. 2005	C
<i>Meles meles</i>	244	-.08	11,400	Wroe et al. 2005	C
<i>Panthera leo</i>	1,768	-.05	294,600	Wroe et al. 2005	C
<i>Panthera pardus</i>	467	-.14	43,100	Wroe et al. 2005	C
<i>Proteles cristatus</i>	151	-.24	9,300	Wroe et al. 2005	C
<i>Artibeus jamaicensis</i>	19	.23	45	Dumont and Herrel 2003	MV
<i>Carollia perspicillata</i>	4	-.19	18	Dumont and Herrel 2003	MV
<i>Cynopterus brachyotis</i>	12	.04	44	Dumont and Herrel 2003	MV
<i>Eidolon helvum</i>	78	.38	272	Dumont and Herrel 2003	MV
<i>Erophylla sezekorni</i>	3	-.36	17	Dumont and Herrel 2003	MV
<i>Glossophaga soricina</i>	1	-.57	11	Dumont and Herrel 2003	MV
<i>Monophyllus redmani</i>	1	-.59	13	Dumont and Herrel 2003	MV
<i>Pteropus poliocephalus</i>	63	.00	820	Dumont and Herrel 2003	MV
<i>Pteropus vampyrus</i>	85	.04	1,166	Dumont and Herrel 2003	MV
<i>Rousettus egyptiacus</i>	19	-.14	179	Dumont and Herrel 2003	MV
<i>Desmodus rotundus</i>	9	-.10	41	Aguirre et al. 2002	MV
<i>Eptesicus furinalis</i>	7	.22	9	Aguirre et al. 2002	MV
<i>Micronycteris minuta</i>	2	-.26	8	Aguirre et al. 2002	MV
<i>Mimon crenulatum</i>	7	.04	16	Aguirre et al. 2002	MV
<i>Molossus rufus</i>	8	-.02	29	Aguirre et al. 2002	MV
<i>Myotis albescens</i>	2	-.14	5	Aguirre et al. 2002	MV
<i>Myotis nigricans</i>	1	-.35	4	Aguirre et al. 2002	MV
<i>Myotis simus</i>	3	-.16	8	Aguirre et al. 2002	MV
<i>Noctilio leporinus</i>	20	.16	63	Aguirre et al. 2002	MV
<i>Noctilio albiventris</i>	12	.09	34	Aguirre et al. 2002	MV
<i>Phyllostomus elongatus</i>	15	.18	35	Aguirre et al. 2002	MV
<i>Phyllostomus discolor</i>	22	.33	37	Aguirre et al. 2002	MV
<i>Sturnira lilium</i>	8	.04	20	Aguirre et al. 2002	MV
<i>Tonatia sylvicola</i>	22	.41	27	Aguirre et al. 2002	MV
<i>Uroderma bilobatum</i>	10	.09	23	Aguirre et al. 2002	MV

<sup>a</sup> Indicates the origin of the estimates: measurement value (MV) or model calculation (C).



## Appendix B

Table B1: Model input: muscle mass (g), fiber length ( $\mu\text{m}$ ), physiological cross-sectional area ( $\text{cm}^2$ )

	Kalamba				Salujinga				Ndeba			
	Muscle Mass	Fiber Length	$\theta$	PCSA	Muscle Mass	Fiber Length	$\theta$	PCSA	Muscle Mass	Fiber Length	$\theta$	PCSA
SET1:												
T	.59	9,712	0	.58	.88	15,790	0	.53	.61	10,537	0	.55
M1a	.23	8,425	40	.20	.27	21,360	40	.09	.19	8,867	40	.15
M1b	.51	15,139	40	.25	.89	15,991	40	.40	.39	20,325	40	.14
M2	.47	8,836	0	.50	.62	12,687	0	.46	.37	7,620	0	.46
Mp	.67	7,929	0	.80	.50	10,924	0	.43	.22	8,841	0	.24
ZMa	.16	17,771	0	.08	.30	21,720	0	.13	.17	13,383	0	.12
ZMp	.08	10,729	0	.07	.12	7,760	0	.14	.06	10,265	0	.05
Pt med	.19	5,968	0	.31	.24	6,636	0	.34	.21	5,042	0	.40
Pt lat	.07	6,327	0	.11	.13	8,055	0	.15	.07	5,735	0	.12
SET2:												
T	.58	8,732	0	.63	.43	14,303	0	.28	.34	9,316	0	.35
M1a	.26	7,575	40	.25	.11	19,348	40	.04	.13	7,840	40	.12
M1b	.34	13,612	40	.18	.39	14,485	40	.20	.25	17,970	40	.10
M2	.46	7,945	0	.55	.39	11,492	0	.33	.21	6,737	0	.29
Mp	.18	7,129	0	.24	.10	9,895	0	.10	.08	7,817	0	.09
ZMa	.14	15,978	0	.08	.17	19,674	0	.08	.10	11,833	0	.08
ZMp	.07	9,647	0	.07	.07	7,029	0	.09	.07	9,076	0	.07
Pt med	.09	5,366	0	.16	.14	6,011	0	.22	.10	4,458	0	.21
Pt lat	.02	5,689	0	.03	.07	7,296	0	.09	.03	5,071	0	.06
SET3:												
T	.61	8,348	0	.69	.40	12,485	0	.30	.39	9,863	0	.38
M1a	.19	7,242	40	.19	.10	16,890	40	.04	.09	8,300	40	.08
M1b	.37	13,013	40	.21	.37	12,644	40	.21	.26	19,025	40	.10
M2	.31	7,595	0	.39	.37	10,032	0	.35	.24	7,133	0	.33
Mp	.18	6,815	0	.25	.09	8,638	0	.10	.14	8,276	0	.16
ZMa	.11	10,003	0	.10	.16	11,901	0	.12	.08	8,884	0	.08
ZMp	.05	9,222	0	.05	.06	6,136	0	.09	.04	9,609	0	.04
Pt med	.09	5,130	0	.17	.13	5,247	0	.23	.08	4,720	0	.16
Pt lat	.06	5,438	0	.11	.06	6,369	0	.09	.03	5,368	0	.05

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