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**The impact of gape on the performance of the skull in  
chisel-tooth digging and scratch digging mole-rats  
(Rodentia: Bathyergidae)**

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SCHOLARONE™  
Manuscripts

1  
2  
3 Responses to reviewers  
4

5 We thank the reviewers for their positive comments on the manuscript. We have addressed the  
6 outstanding issues as follows:  
7

- 8
- 9 1. The spelling of the species name of *Fukomys mechowii* has now been corrected throughout  
10 the manuscript.
  - 11 2. The Barciová et al paper on the relationship between soil type and cranial morphology has  
12 now been discussed and cited in both the introduction (line 70) and conclusions (line 335).
  - 13 3. Apologies for giving the wrong Figshare link – I'm still getting to grips with the site. The  
14 correct link has been added to the manuscript and is  
15 [https://figshare.com/articles/Mole\\_rat\\_FEA/3188830](https://figshare.com/articles/Mole_rat_FEA/3188830)  
16  
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18  
19 Regards,  
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21 Andrew McIntosh & Phil Cox  
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1 **Title: The impact of gape on the performance of the skull in chisel-tooth digging and**  
2 **scratch digging mole-rats (Rodentia: Bathyergidae)**

4 **Running head: Bathyergid cranial performance**

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26 **ABSTRACT**

27 The African mole-rats (Bathyergidae) are a family of rodents highly adapted for life  
28 underground. Previous research has shown that chisel-tooth digging mole-rats (which use  
29 their incisors to dig burrows) are clearly distinguishable from scratch diggers (which only use  
30 the forelimbs to tunnel) on the basis of morphology of the skull, and that the differences are  
31 linked to the production of high bite forces and wide gapes. We hypothesised that the skull of  
32 a chisel-tooth digging mole-rat would perform better at wider gapes than that of a scratch  
33 digging mole-rat during incisor biting. To test this hypothesis, we created finite element  
34 models of the cranium of the scratch digging *Bathyergus suillus* and the chisel-tooth digging  
35 *Fukomys mechowii*, and loaded them to simulate incisor bites at different gapes. Muscle loads  
36 were scaled such that the ratio of force to surface area was the same in both models. We  
37 measured three performance variables: overall stress across the cranium; mechanical  
38 efficiency of biting; and degree of deformation across the skull. The *Fukomys* model had a  
39 more efficient incisor bite at all gapes, despite having greater average stress across the skull.  
40 In addition, the *Fukomys* model deformed less at wider gapes, whereas the *Bathyergus* model  
41 deformed less at narrower gapes. These properties of the cranial morphology of *Fukomys*  
42 and *Bathyergus* are congruent with their respective chisel-tooth and scratch digging  
43 behaviours and, all other factors being equal, would enable the more efficient production of  
44 bite force at wider gapes in *Fukomys*. However, *in vivo* measurements of muscle forces and  
45 activation patterns are needed to fully understand the complex biomechanics of tooth digging.

46  
47 **Keywords: Cranial biomechanics; finite element analysis; chisel-tooth digging; scratch**  
48 **digging; Bathyergidae**

## 51 INTRODUCTION

52 The African mole-rats, or blesmols, are a family of rodents (Bathyergidae) comprising 25-30  
53 species, all of which spend a large proportion of their life underground [1]. Of the six extant  
54 genera, five are chisel-tooth diggers, that is, they dig tunnels with their enlarged rodent  
55 incisors. Just one genus (*Bathyergus*) is a scratch digger, tunnelling with only its forelimbs  
56 and claws [2]. Chisel-tooth digging is a specialised form of tunnel construction that has also  
57 evolved independently in several other families of subterranean and fossorial rodents [3]. It is  
58 thought to have evolved in order to exploit harder soils as incisors are covered in hard enamel  
59 and fixed within the cranium and mandible. This is in contrast to the claws, which are made  
60 up of softer keratin and have more flexibility [4].

61  
62 A number of morphological characteristics in the cranium have been associated with chisel-  
63 tooth digging. These include: more procumbent incisors, wider crania, enlarged zygomatic  
64 arches and larger temporal fossae [5-9]. Chisel-tooth digging mandibles are also convergent  
65 across rodents and show higher coronoid processes, reduced condyle heights and deep incisor  
66 roots [6,10,11]. Such traits have been linked to the requirement for chisel-tooth diggers to  
67 produce high bite force at the incisors at wide gape [5,6,10], and have also been found in  
68 carnivorans with similar functional requirements [12-14]. Within chisel-tooth digging  
69 species, variation in cranial morphology has been suggested to correlate with soil type,  
70 indicating that digging has a major influence on skull shape [15,16].

71  
72 To understand how morphological traits can impact biomechanical function in extant and  
73 extinct vertebrates, many researchers have turned to the engineering technique finite element  
74 analysis (FEA) over the decade or so [17-26]. FEA allows stress, strain and deformation to be  
75 predicted in a complex 3D object subjected to a load, by dividing that object into a large

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3 76 number of smaller, simpler elements (usually cubes or tetrahedra) connected at nodes [27].  
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5 77 As a modelling technique, the results of FEA, and the conclusions that can be drawn from  
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7 78 them, are necessarily limited by the accuracy of the model inputs. In particular, parameters  
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9 79 such as material properties, constraints and loads are often unknown or can only be roughly  
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11 80 estimated in biological models. Indeed, some validation studies have indicated that outputs  
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13 81 from FEA (e.g. strain values) do not always match *ex vivo* or *in vivo* measurements in  
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15 82 absolute terms [18,28,29]. However, these studies also indicate that the relative values are  
16  
17 83 generally correct (e.g. areas of high strain and low strain predicted by FEA match those  
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19 84 measured *in vivo*). Thus, whilst comparisons of absolute values between different unvalidated  
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21 85 FE models can be difficult to interpret, comparisons between different loading scenarios in  
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23 86 the same model (i.e. where one parameter is varied but all others are held constant) are  
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25 87 justified.  
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34 89 The aim of this study is to predict the performance of the skull of two bathyergid mole-rats,  
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36 90 one chisel-tooth digger and one scratch digger, when loaded at the incisors over a number of  
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38 91 different gapes. It is hypothesised that the shape of the cranium of the chisel-tooth digging  
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40 92 species will lead to improved performance at the incisors compared to the scratch digging  
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42 93 species, particularly at wide gapes. FEA will be used to simulate masticatory muscle loading  
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44 94 at different gape angles, and the patterns of stress distribution across the cranium will be  
45  
46 95 predicted, as well as bite force at the incisors. By integrating geometric morphometrics  
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48 96 (GMM) with FEA [22,30], it will also be possible to quantify and visualise the differences in  
49  
50 97 overall deformations of the cranium between the two species. Following Dumont *et al.* [20],  
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52 98 biomechanical performance will be measured in three ways. We predict that, compared to the  
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54 99 scratch digging species, the chisel-tooth digging cranial model at wide gapes will: (1) exhibit  
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56 100 lower stress (and thus be more resistant to structural failure); (2) be more efficient at  
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3 101 converting muscle forces to bite forces; and (3) experience less deformation. These  
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5 102 predictions are based on the hypothesis that the cranial morphology of the chisel-tooth  
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7 103 digging mole-rat will be adapted to both generate high forces at the incisors and withstand the  
8  
9 104 reaction forces. It should be noted that this analysis seeks only to understand the impact of  
10  
11 105 the difference in cranial morphology between *Fukomys* and *Batherygus*. Many other factors  
12  
13 106 can influence digging biomechanics, such as muscle physiology, muscle activation patterns  
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15 107 and bone material properties, but data on these is scant in mole-rats and they are beyond the  
16  
17 108 focus of this study.  
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## 22 110 **MATERIALS AND METHODS**

### 23 111 *Model construction*

24  
25 112 Finite element (FE) models were created from microCT scans of two adult African mole-rat  
26  
27 113 skulls: the chisel-tooth digging *Fukomys mechowii* (Muséum National d'Histoire Naturelle,  
28  
29 114 Paris, ZM-MO-1911-664) and the scratch digging *Batherygus suillus* (Specimen 631,  
30  
31 115 Professor Nigel Bennett, University of Pretoria). The specimens were scanned in an X-Tek  
32  
33 116 Metris microCT scanner at the University of Hull (Medical and Biological Engineering  
34  
35 117 Research Group). The scans had isometric voxels of 0.0417 mm (*Fukomys*) and 0.0532 mm  
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37 118 (*Batherygus*). Using Avizo 8.0 (FEI, Hillsboro, OR) the scans were resampled to double their  
38  
39 119 original voxel sizes to ensure a reasonable processing time during FE model creation and  
40  
41 120 solving stages. 3D volume reconstructions of the skulls were created by a combination of  
42  
43 121 automated and manual thresholding of materials. Bone, teeth, and incisor pulp cavity were  
44  
45 122 segmented as separate volumes, with all bone was modelled as cortical bone. The  
46  
47 123 reconstructions were then converted to an 8-noded cubic mesh directly from voxels using  
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49 124 VOX-FE, in-house custom-built FEA software [31]. The *Fukomys* and *Batherygus* models  
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51 125 comprised 9481075 and 6796670 elements, respectively.  
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5 127 Based on previous nano-indentation work on rodents [21,32] and other mammals [19], bone  
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7 128 and teeth were assigned Young's moduli of 17 and 30 GPa, respectively. Pulp was assigned a  
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9 129 Young's modulus of 2 MPa [33]. All materials were modelled as homogeneous and isotropic  
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11 130 with a Poisson's ratio of 0.3 being assigned to bone and teeth and a ratio of 0.45 to pulp [33].  
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13 131 No data is available for material properties of bathyergids. However, it was considered  
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15 132 appropriate to use these properties as this study is primarily concerned with the relative  
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17 133 digging performance between two species, and therefore is less concerned with absolute  
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19 134 output values.  
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25 136 In order to model chisel-tooth digging, the models were constrained at the point of contact of  
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27 137 the incisor tip with the substrate in the direction of the bite (i.e. orthogonal to the occlusal  
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29 138 plane). Forty nodes were constrained at each temporo-mandibular joint (TMJ) in all three  
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31 139 axis. Loads were added to the model representing the following muscles: temporalis;  
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33 140 superficial masseter; deep masseter; zygomaticomandibularis (ZM: infraorbital, anterior and  
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35 141 posterior parts); lateral pterygoid; and medial pterygoid (Figure 1). The masseter muscle was  
36  
37 142 divided into 3 parts (superficial; deep and ZM) following [34,35]. Muscle attachment sites  
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39 143 were assigned based on previously published dissections [36-38] and virtual muscle  
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41 144 reconstructions [39] of bathyergids. Equal loads were applied to each side of the model as  
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43 145 many rodents have demonstrated a bilateral muscle activation pattern when biting at the  
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45 146 incisors [40,41].  
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52 148 The direction of pull of each muscle (i.e. muscle directional vector) was determined by  
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54 149 placing a reconstruction of the specimen's mandible in a position of incisor occlusion (0°)  
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56 150 with the cranial reconstruction using Avizo. Landmarks were placed at the centroid of each  
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3 151 muscle attachment site on the mandible. These landmarks were then uploaded into VOX-FE  
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5 152 to provide end points for the muscle direction vectors. The *Bathyergus* and *Fukomys*  
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7 153 mandibles were automatically segmented in Avizo from microCT scans (0.0481 and 0.0350  
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9 154 mm isometric voxel sizes, respectively). To calculate muscle magnitudes, PCSA values for  
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11 155 *Fukomys mechowii* were taken from Van Daele *et al.* [38] and then multiplied by an intrinsic  
12  
13 156 muscle stress value of 0.3 Nmm<sup>-2</sup> [42]. No PCSA data was available for *Bathyergus*, so the  
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15 157 *Fukomys* muscle forces, scaled to model size, were used instead (the details and limitations of  
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17 158 this are discussed below). Muscle loads for each model are given in Table 1. To replicate  
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19 159 different angles of gape, muscle directional vectors were rotated about an axis running  
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21 160 between the left and right TMJ (see [6] for further details of method). Condyle translation has  
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23 161 been shown to occur in the terrestrial rodent, *Pedetes capensis* during different stages of  
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25 162 mastication [40]. However, condyle movement during digging at the incisors has been shown  
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27 163 to be stable in *Ctenomys*, a South American subterranean rodent [11]. For this reason,  
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29 164 condyle translation has not been included in the model, and the mandible has been simply  
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31 165 rotated around an axis (TMJ).  
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### 38 167 *Analysis*

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40 168 In this study, von Mises (VM) stress was used as a key indicator of performance. Structures  
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42 169 which exhibit overall lower VM stresses in a comparative context are less likely to fail under  
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44 170 a given loading. If two models of the same shape but of different sizes have equal loads, the  
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46 171 larger model will exhibit less stress (as stress equals force applied over the area of the  
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48 172 model). To consider the effect of difference in shape on stress between two models, the effect  
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50 173 of size must be controlled for, which can be achieved by keeping the ratio of force to surface  
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52 174 area constant between the two models [43]. As PCSA values were not available for  
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54 175 *Bathyergus*, surface areas for both models were calculated in Avizo, and the ratio of the two  
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3 176 surface areas was used to scale forces applied to the *Bathyergus* model. Thus the impact of  
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5 177 cranial morphology on VM stress values for each model could be directly compared without  
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7 178 the confounding influence of size. In order to quantify VM stress across the skull, the VM  
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9 179 stress of each element from each model was extracted and the median VM stress for both  
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11 180 models was calculated. Using the median, rather than the mean, to compare VM stress  
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13 181 prevents outlying values that can arise from modelling artifacts from exaggerating the  
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15 182 average stress value.  
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21 184 The mechanical efficiency of incisor biting in each model was also calculated to assess the  
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23 185 performance of both models. Mechanical efficiency is the ratio of predicted bite force to total  
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25 186 muscle input force and provides a single value, independent of size, to assess the efficiency  
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27 187 of the masticatory system in transforming muscle to bite force [20,21]. Absolute bite force  
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29 188 was not reported in this study as the muscle forces and geometry of the *Fukomys* model were  
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31 189 gleaned from separate specimens. Therefore, there is no expectation that the bite force will be  
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33 190 biologically accurate. However, dividing bite force by input muscle force to produce  
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35 191 mechanical efficiency produces a meaningful performance parameter for comparison  
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37 192 between FE models.  
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43 194 Geometric morphometrics (GMM) was used to analyse variation in deformations between the  
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45 195 FE models, following [22,23,26,30,31,44]. A set of 3D landmarks (Figure 2 and Table S1)  
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47 196 were recorded from the unloaded and loaded models. The landmarks were then subjected to a  
48  
49 197 generalised Procrustes analysis and scaled to centroid size. The residual differences between  
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51 198 the loaded and unloaded models were then added to the mean landmark configuration of the  
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53 199 unloaded *Fukomys* and *Bathyergus* models. The mean and loaded configurations were  
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55 200 subjected to a second Procrustes analysis without scaling or tangent projection [44], to  
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3 201 represent the multivariate data on a graph. Cranial deformations were visualised via surface  
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5 202 rendering of a hybrid of the two unloaded models warped along the vectors of deformation.  
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7 203 Deformations were magnified 500 times to aid visual interpretation of transformation grids.  
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10 204 All GMM analyses were carried out using the EVAN toolbox ([www.evan-society.org](http://www.evan-society.org)).  
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12 205 Further details of the GMM methods and the theory underlying them are given in electronic  
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14 206 supplementary material, text S1.  
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19 208 It should be noted that because no muscle PCSA data was available for the individuals from  
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21 209 which the model geometries were constructed, the resulting data should not be treated as  
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23 210 reflecting biological reality. The scaling of the muscle forces instead allows us to draw  
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25 211 conclusions on the relative impact of changing muscle orientations in species with different  
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27 212 cranial morphologies.  
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## 31 32 214 **RESULTS**

33  
34 215 Figure 3 shows the distribution of VM stress across the crania of the two models. As might be  
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36 216 expected, at occlusion both models show areas of high stress around the constraints (glenoid  
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38 217 fossae and incisor tips), and some of the muscle attachment sites (zygomatic arch and  
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40 218 pterygoid fossa). Beyond these areas, both models also show high stresses in the postero-  
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42 219 ventral part of the rostrum. In addition, the *Fukomys* cranium has high stresses in the dorsal  
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44 220 rostrum and in the incisor itself. As gape increases, stress tends to decrease in the rostrum and  
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46 221 anterior zygomatic arch, and increase in the temporal region and posterior orbital region.  
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48 222 Studying median VM stresses (Table 2) shows that increasing gape reduces the overall stress  
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50 223 in the cranium, and that *Fukomys* experiences higher VM stress in the cranium at each  
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52 224 pairwise gape compared to *Bathyergus*.  
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3 226 The mechanical efficiency of biting (the ratio of predicted bite force to input muscle force) at  
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5 227 each gape in the two species is given in Table 2. *Fukomys* is more efficient than *Bathyergus*  
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7 228 at converting input forces to output forces at all gape angles. As gape increases, mechanical  
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9 229 efficiency decreases in both specimens, but at different rates. Specifically, *Fukomys* is half as  
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11 230 efficient at 60° as at 0° whereas the mechanical efficiency of *Bathyergus* at 60° is only a  
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13 231 quarter of its efficiency at occlusion. It should be noted that the mechanical efficiency (and  
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15 232 thus bite force) of *Bathyergus* at 90° gape is negative. This is a result of many of the muscle  
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17 233 vectors rotating so far around that they now exert an upward rather than downward force on  
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19 234 the skull model, and is clearly a biologically unrealistic situation.  
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236 Figure 4 shows the size and shape deformations between the two model types at varying  
237 degrees of gape. PC1 represents 76.27% variance and PC2 13.33%. PC1 is dominated by the  
238 differences between the loaded models at differing angles of gape whilst PC2 shows the  
239 difference between the unloaded mean and the loaded models. *Bathyergus* in occlusion and  
240 *Fukomys* at 90° gape are the least deformed from the mean unloaded model; whereas  
241 *Bathyergus* at 90° gape and *Fukomys* in occlusion are the most deformed from the mean  
242 unloaded model. Figures 5A-C show the deformation between the mean unloaded model and  
243 the two models at occlusion using thin plate splines. The main difference between the mean  
244 unloaded model and the loaded models at occlusion is the ventral deflection of the zygomatic  
245 arch. Figures 5D and E show cranial deformations from unloaded mean to 90° gape in both  
246 models. The deformations between the two models are shown to be rather similar, with  
247 increasing gapes being associated with dorsoventral bending.  
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249

## 250 **DISCUSSION**

251 *Von Mises stress*

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3 251 The results of the FEA allow us to compare the biomechanical performance of the skull  
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5 252 between gapes within each model. Three performance metrics were studied: median VM  
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7 253 stress across the model; the ratio of predicted bite force to total input adductor muscle force;  
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9 254 and overall deformation of the model (following [20]). In both models, average VM stress  
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11 255 decreases as gape increases (Table 2). In particular, VM stress is reduced in the anterior part  
12  
13 256 of the skull (Figure 3), likely as a result of the muscle vectors being oriented in a more  
14  
15 257 posterior, rather than ventral, direction. At each gape, the *Bathyergus* model experiences a  
16  
17 258 lower median stress than the *Fukomys* model, suggesting that the morphology of the  
18  
19 259 *Bathyergus* cranium is better able to resist the forces applied to it in this analysis. This is  
20  
21 260 counter to the first hypothesis that suggested the chisel-tooth digging species would exhibit  
22  
23 261 lower stresses at wider gapes. However, we urge caution in interpreting this result as,  
24  
25 262 although the muscle forces were scaled to surface area to enable direct comparisons of stress  
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27 263 values [43], it only indicates how the cranial morphology responds to forces. In reality, there  
28  
29 264 are likely to be large differences in the muscle force to surface area ratio, as well as potential  
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31 265 differences in the relative proportions of the muscles and the bone material properties  
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33 266 between the two taxa.  
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41 268 It is unclear whether VM stress values really matter in an evolutionary context, as long as  
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43 269 they are below the yield strength of bone, and there is little evidence of cranial bone naturally  
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45 270 loading to failure [20]. Thus, assuming cranial stress is within a suitable safety factor, its  
46  
47 271 precise value may not be important. Previous work has suggested that bats adapt their crania  
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49 272 in favour of mechanical efficiency of biting, whereas adaptation to cranial strength (i.e. low  
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51 273 VM stress) is not as strongly selected for [45].  
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56 275 *Mechanical efficiency of biting*  
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3 276 From Table 2, it can be seen that the *Fukomys* model has a greater mechanical efficiency of  
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5 277 biting than the *Bathyergus* model at all simulated gapes, not just at wider gapes as predicted  
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7 278 in our second hypothesis. As would be expected from simple mechanics, bite force (and thus  
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9 279 mechanical efficiency) decreased with increasing gape in both models [46-49]. However, the  
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11 280 relative decrease with increasing gape was much greater in the *Bathyergus* model. That is, the  
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13 281 cranial morphology of *Fukomys* is better able to maintain mechanical efficiency as the  
14  
15 282 muscle forces rotate posteriorly. A higher mechanical efficiency can be partly achieved by  
16  
17 283 having masticatory muscles that have increased moment arms around the TMJ. Previous  
18  
19 284 work has indicated that the temporalis muscles of chisel-tooth digging bathyergids have  
20  
21 285 increased moment arms compared to *Bathyergus* [6] and therefore this could be the muscle  
22  
23 286 driving improved mechanical efficiency at increased gapes in the *Fukomys* model presented  
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### 31 *Cranial deformation*

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34 290 The GMM analysis shows that the relative deformation of the models at different gapes  
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36 291 follows an almost symmetrical pattern (Figure 4). The main difference between the two  
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38 292 models is that, as gape increases, the *Fukomys* model deforms less (plots closer to the  
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40 293 unloaded model) and the *Bathyergus* model deforms more (plots further from the unloaded  
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42 294 model). This result is as predicted by the third hypothesis and fits with the digging behaviour  
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44 295 of these two species. It appears that in *Fukomys* the morphology of the cranium leads to  
45  
46 296 reduced deformation at the wide gapes necessary for chisel-tooth digging [6,10]. *Bathyergus*,  
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48 297 as a scratch digger [2], does not employ such wide gapes as frequently, and thus its cranial  
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50 298 morphology deforms least at narrower gapes.  
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3 300 When comparing the two models at occlusion, it can be seen that the main difference in  
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5 301 deformation occurs at the zygomatic arch, which is more ventrally deflected in *Fukomys* than  
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7 302 *Bathyergus* (Figures 5B and C). As the models have been scaled to the same muscle  
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9 303 force:surface area ratio, it is unlikely that the greater zygomatic deformation is a product of  
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11 304 greater muscle force in *Fukomys*; rather, it is differences in the direction of muscle pull that  
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13 305 appear to be leading to this result. It can be seen in Figure 1 that the deep masseter of  
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15 306 *Bathyergus* has a greater posterior component to its line of action than does that of *Fukomys*.  
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17 307 Thus the forces acting on the zygomatic arch of *Fukomys* are likely to produce a greater  
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19 308 ventral deflection than is seen in *Bathyergus*.  
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25 310 Figures 5D and E represent how the models deform at large gape angles. Both models seem  
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27 311 to experience dorsoventral bending of the cranium. As gape increases, the arrangement of the  
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29 312 most dominant muscles (Figure 1), the temporalis (which attaches to the posterior area of the  
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31 313 cranium) and masseters (which attach to the zygoma), will cause dorsoventral bending of the  
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33 314 cranium around the TMJ constraints. Less bending will occur at the incisor as the muscle  
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35 315 vectors rotate with the mandible as gape increases. This results in the muscle vectors  
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37 316 directing more force towards the posterior part of the skull, and less force towards the  
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39 317 anterior portion (this is also demonstrated by VM stress patterns in Figure 3 where cranial  
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41 318 stress is concentrated at the posterior areas of the cranium as gape increases). Interestingly,  
42  
43 319 the *Fukomys* model does not experience as much deformation or dorsoventral bending at 90°  
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45 320 gape compared to *Bathyergus* (Figures 4 and 5D,E). This implies that the *Fukomys* cranium is  
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47 321 stiffer than the *Bathyergus* cranium, which is to be expected from a cranium that has higher  
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49 322 mechanical efficiency (Table 2). The stiffer the cranium is during mastication, the less energy  
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51 323 it will waste in deforming, making it more efficient at converting muscle forces into bite  
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53 324 forces.  
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326 *Conclusions*

327 The results here demonstrate that the cranial morphology of *Fukomys* performs better during  
328 incisor biting at wide gapes than does *Bathyergus*. That is, the *Fukomys* model had a greater  
329 mechanical efficiency of biting than *Bathyergus* and was able to maintain it to a greater  
330 degree as gape increased. In addition, deformations of the *Fukomys* cranial model were  
331 smaller at larger gapes, whereas in *Bathyergus* deformations were smaller at narrower gapes.  
332 The relative performance of the models is congruent with the known digging behaviour of the  
333 two species under study here i.e. chisel-tooth digging in *Fukomys* and scratch digging in  
334 *Bathyergus* [2]. Previous studies of subterranean rodents have indicated that digging  
335 behaviour has a major impact on cranial morphology [15,16] and that chisel-tooth digging  
336 species have adaptations for high bite force and wide gape [6,10]. The cranial morphology of  
337 the chisel-tooth digger in this analysis is clearly able to function well at wide gapes, and,  
338 although absolute bite force cannot be predicted with any degree of confidence by our  
339 unvalidated models, increasing the efficiency of the masticatory system would necessarily  
340 increase bite force. It should be emphasised that the conclusions drawn here relate only to the  
341 morphology of the cranium. To understand the biomechanics of digging more thoroughly  
342 would require a much more complex model incorporating data on muscle physiology, bone  
343 material properties, behaviour, and many other factors, which we feel would be a very fruitful  
344 avenue of research.

345

346 **DATA ACCESSIBILITY.** Surface reconstructions, FE models and displacement files  
347 available from [https://figshare.com/articles/Mole\\_rat\\_FEA/3188830](https://figshare.com/articles/Mole_rat_FEA/3188830).

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3 348 **AUTHOR CONTRIBUTIONS.** PGC conceived the study. AFM built and solved the  
4  
5 349 models and analysed the data. Both authors interpreted the data. AFM drafted the manuscript.  
6  
7 350 Both authors revised the manuscript and gave final approval for publication.  
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11  
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32 361 **REFERENCES**

- 33  
34 362 1. Faulkes CG, Bennett NC. 2013 Plasticity and constraints on social evolution in  
35  
36 363 African mole-rats: ultimate and proximate factors. *Phil. Trans. R. Soc. B* **368**,  
37  
38 364 20120347.  
39  
40 365 2. Jarvis JUM, Bennett NC. 1991 Ecology and behaviour of the family Bathyergidae. In  
41  
42 366 *The biology of the naked mole-rat* (eds PW Sherman, JUM Jarvis, RD Alexander), pp.  
43  
44 367 66-96. Princeton, NJ: Princeton University Press.  
45  
46 368 3. Stein BR. 2000 Morphology of subterranean rodents. In *Life underground: the*  
47  
48 369 *biology of subterranean rodents* (eds EA Lacey, JL Patton, GN Cameron), pp. 19-61.  
49  
50 370 Chicago: University of Chicago Press.  
51  
52 371 4. Lessa EP, Thaler CS. 1989 A reassessment of morphological specializations for  
53  
54 372 digging in pocket gophers. *J. Mammal.* **70**, 689-700.  
55  
56  
57  
58  
59  
60

- 1  
2  
3 373 5. Samuels JX, Van Valkenburgh B. 2009 Craniodental adaptations for digging in  
4  
5 374 extinct burrowing beavers. *J. Vert. Paleo.* **29**, 254-268.  
6  
7 375 6. McIntosh AF, Cox PG. 2016 Functional implications of craniomandibular  
8  
9 376 morphology in African mole-rats (Rodentia: Bathyergidae). *Biol. J. Linn. Soc.* **117**,  
10  
11 377 447-462.  
12  
13 378 7. Landry SO. 1957 Factors affecting the procumbency of rodent upper incisors. *J.*  
14  
15 379 *Mammal.* **38**, 223-234.  
16  
17 380 8. Agrawal V. 1967 Skull adaptations in fossorial rodents. *Mammalia* **31**, 300-312.  
18  
19 381 9. Lessa EP, Stein BR. 1992 Morphological constraints in the digging apparatus of  
20  
21 382 pocket gophers (Mammalia: Geomyidae). *Biol. J. Linn. Soc.* **47**, 439-453.  
22  
23 383 10. Gomes Rodrigues H, Šumbera R, Hautier L. 2016 Life in burrows channelled the  
24  
25 384 morphological evolution of the skull in rodents: the case of African mole-rats  
26  
27 385 (Bathyergidae, Rodentia). *J. Mamm. Evol.* **23**, 175-189.  
28  
29 386 11. Verzi DH, Olivares AI. 2006 Craniomandibular joint in South American burrowing  
30  
31 387 rodents (Ctenomyidae): adaptations and constraints related to a specialized  
32  
33 388 mandibular position in digging. *J. Zool.* **270**, 488-501.  
34  
35 389 12. Wroe S, McHenry C, Thomason J. 2005 Bite club: comparative bite force in big  
36  
37 390 biting mammals and the prediction of predatory behaviour in fossil taxa. *Proc. R. Soc.*  
38  
39 391 *B* **272**, 619-625.  
40  
41 392 13. Wroe S, Milne N. 2007 Convergence and remarkably consistent constraint in the  
42  
43 393 evolution of carnivore skull shape. *Evolution* **61**, 1251-1260.  
44  
45 394 14. Figueirido B, Tseng ZJ, Martín-Serra A. 2013 Skull shape evolution in durophagous  
46  
47 395 carnivorans. *Evolution* **67**, 1975-1993.  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 396 15. Barčiová L, Šumbera R, Burda H. 2009 Variation in the digging apparatus of the  
4  
5 397 subterranean silvery mole-rat *Heliophobius argenteocinereus* (Rodentia,  
6  
7 398 Bathyergidae): the role of ecology and geography. *Biol. J. Linn. Soc.* **97**, 822-831.  
8  
9  
10 399 16. Beolchini F, Corti M. 2004 The taxonomy of the genus *Tachyoryctes*: a geometric  
11  
12 400 morphometric approach. *It. J. Zool.* **71**, 35-43.  
13  
14 401 17. Rayfield EJ. 2004 Cranial mechanics and feeding in *Tyrannosaurus rex*. *Proc. R. Soc.*  
15  
16 402 *B* **271**, 1451-59.  
17  
18 403 18. Strait DS, Wang Q, Dechow PC, Ross CF, Richmond BG, Spencer MA, Patel BA.  
19  
20 404 2005 Modeling elastic properties in finite-element analysis: how much precision is  
21  
22 405 needed to produce an accurate model? *Anat. Rec.* **283A**, 275-287.  
23  
24 406 19. Kupczik K, Dobson CA, Fagan MJ, Crompton RH, Oxnard CE, O'Higgins P. 2007  
25  
26 407 Assessing mechanical function of the zygomatic region in macaques: validation and  
27  
28 408 sensitivity testing of finite element models. *J. Anat.* **210**, 41-53.  
29  
30 409 20. Dumont ER, Davis JL, Grosse IR, Burrows AM. 2011 Finite element analysis of  
31  
32 410 performance in the skulls of marmosets and tamarins. *J. Anat.* **218**, 151-162.  
33  
34 411 21. Cox PG, Rayfield EJ, Fagan MJ, Herrel A, Pataky TC, Jeffery N. 2012 Functional  
35  
36 412 evolution of the feeding system in rodents. *PLoS ONE*, **7**, e36299.  
37  
38 413 22. O'Higgins P, Fitton L, Phillips R, Shi J, Liu J, Gröning F, Cobb S, Fagan MJ. 2012  
39  
40 414 Virtual functional morphology: novel approaches to the study of craniofacial form  
41  
42 415 and function. *Evol. Biol.* **39**, 521-535.  
43  
44 416 23. Cox PG, Kirkham J, Herrel A. 2013 Masticatory biomechanics of the Laotian rock  
45  
46 417 rat, *Laonastes aenigmamus*, and the function of the zygomaticomandibularis muscle.  
47  
48 418 *PeerJ* **1**, e160.  
49  
50 419 24. O'Hare LMS, Cox PG, Jeffery N, Singer ER. 2013 Finite element analysis of stress in  
51  
52 420 the equine proximal phalanx. *Equine Vet. J.* **45**, 273-277.  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 421 25. Cox PG, Rinderknecht A, Blanco RE. 2015 Predicting bite force and cranial  
4  
5 422 biomechanics in the largest fossil rodent using finite element analysis. *J. Anat.* **226**,  
6  
7 423 215-223.  
8  
9  
10 424 26. Fitton LC, Prôa M, Rowland C, Toro-Ibacache V, O'Higgins P. 2015 The impact of  
11  
12 425 simplifications on the performance of a finite element model of a *Macaca fascicularis*  
13  
14 426 cranium. *Anat. Rec.* **298**, 107-121.  
15  
16 427 27. Rayfield EJ. 2007 Finite element analysis and understanding the biomechanics and  
17  
18 428 evolution of living and fossil organisms. *Ann. Rev. Earth Planet. Sci.* **35**, 541-576.  
19  
20  
21 429 28. Bright JA, Rayfield EJ. 2011 Sensitivity and *ex vivo* validation of finite element  
22  
23 430 models of the domestic pig cranium. *J. Anat.* **219**, 456-471.  
24  
25 431 29. Porro LB, Metzger KA, Iriarte-Diaz J, Ross CF. 2013 *In vivo* bone strain and finite  
26  
27 432 element modelling of the mandible of *Alligator mississippiensis*. *J. Anat.* **223**, 195-  
28  
29 433 227.  
30  
31  
32 434 30. O'Higgins P, Cobb SN, Fitton LC, Gröning F, Phillips R, Liu J, Fagan MJ. 2011  
33  
34 435 Combining geometric morphometrics and functional simulation: an emerging toolkit  
35  
36 436 for virtual functional analyses. *J. Anat.* **218**, 3-15.  
37  
38 437 31. Liu J, Shi J, Fitton L, Phillips R, O'Higgins P, Fagan MJ. 2012 The application of  
39  
40 438 muscle wrapping to voxel-based finite element models of skeletal structures.  
41  
42 439 *Biomech. Model. Mechanobiol.* **11**, 35-47.  
43  
44  
45 440 32. Cox PG, Fagan MJ, Rayfield EJ, Jeffery N. 2011 Finite element modelling of squirrel,  
46  
47 441 guinea pig and rat skulls: using geometric morphometrics to assess sensitivity. *J.*  
48  
49 442 *Anat.* **219**, 696-709.  
50  
51  
52 443 33. Williams KR, Edmundson JT. 1984 Orthodontic tooth movement analysed by the  
53  
54 444 finite element method. *Biomaterials* **5**, 347-351.  
55  
56  
57  
58  
59  
60

- 1  
2  
3 445 34. Turnbull WD. 1970 Mammalian masticatory apparatus. *Fieldiana (Geol.)* **18**, 147-  
4  
5 446 356.  
6  
7 447 35. Cox PG, Jeffery N. 2011 Reviewing the morphology of the jaw-closing musculature  
8  
9 448 in squirrels, rats, and guinea pigs with contrast-enhanced microCT. *Anat. Rec.* **294**,  
10  
11 449 915-928.  
12  
13 450 36. Boller N. 1970 Untersuchungen an Schädel, Kaumuskulatur und äußerer Hirnform  
14  
15 451 von *Cryptomys hottentotus* (Rodentia, Bathyergidae). *Z. wiss. Zool.* **181**, 7-65.  
16  
17 452 37. Morlok WF. 1983 Vergleichend- und funktionell-anatomische Untersuchungen an  
18  
19 453 Kopf, Hals und Vorderextremität subterranean Nagetiere (Mammalia, Rodentia). *Cour.*  
20  
21 454 *Forsch. Inst. Senck.* **64**, 1-237.  
22  
23 455 38. Van Daele P, Herrel A, Adriaens D. 2009 Biting performance in teeth-digging  
24  
25 456 African mole-rats (*Fukomys*, Bathyergidae, Rodentia). *Physiol. Biochem. Zool.* **82**,  
26  
27 457 40-50.  
28  
29 458 39. Cox PG, Faulkes CG. 2014 Digital dissection of the masticatory muscles of the naked  
30  
31 459 mole-rat, *Heterocephalus glaber* (Mammalia, Rodentia). *PeerJ* **2**, e448.  
32  
33 460 40. Offermans M, de Vree F. 1990 Mastication in springhares, *Pedetes capensis*: a  
34  
35 461 cineradiographic study. *J. Morphol.* **205**, 353-367.  
36  
37 462 41. Satoh K. 1998 Balancing function of the masticatory muscles during incisal biting in  
38  
39 463 two murid rodents, *Apodemus speciosus* and *Clethrionomys rufocanus*. *J. Morphol.*  
40  
41 464 **236**, 49-56.  
42  
43 465 42. Weijjs W, Hillen B. 1985 Cross-sectional areas and estimated intrinsic strength of the  
44  
45 466 human jaw muscles. *Acta Morphol. Neerl. Scand.* **23**, 267-274.  
46  
47 467 43. Dumont ER, Grosse IR, Slater GJ. 2009 Requirements for comparing the performance  
48  
49 468 of finite element models of biological structures. *J. Theor. Biol.* **256**, 96-103.  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 469 44. O'Higgins P, Milne N. 2013 Applying geometric morphometrics to compare changes  
4  
5 470 in size and shape arising from finite elements analyses. *Hystrix* **24**, 126-132.  
6  
7 471 45. Dumont ER, Samadevam K, Grosse I, Warsi OM, Baird B, Davalos LM. 2014  
8  
9 472 Selection for mechanical advantage underlies multiple cranial optima in new world  
10  
11 473 leaf-nosed bats. *Evolution* **68**, 1436-1449.  
12  
13 474 46. Herring SW, Herring SE. 1974 The superficial masseter and gape in mammals. *Am.*  
14  
15 475 *Nat.* **108**, 561-576.  
16  
17 476 47. Dumont ER, Herrel A. 2003 The effects of gape angle and bite point on bite force in  
18  
19 477 bats. *J. Exp. Biol.* **206**, 2117-2123.  
20  
21 478 48. Bourke J, Wroe S, Moreno K, McHenry C, Clausen P. 2008 Effects of gape and tooth  
22  
23 479 position on bite force and skull stress in the dingo (*Canis lupus dingo*) using a 3-  
24  
25 480 dimensional finite element approach. *PLoS ONE*, **3**, e2200.  
26  
27 481 49. Williams SH, Peiffer E, Ford S. 2009 Gape and bite force in the rodents *Onychomys*  
28  
29 482 *leucogaster* and *Peromyscus maniculatus*: does jaw-muscle anatomy predict  
30  
31 483 performance? *J. Morphol.* **270**, 1338-1347.  
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38 485 **FIGURE LEGENDS**

39  
40 486 **Figure 1.** Attachment sites and vectors of pull of the masticatory muscles in models of  
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42 487 *Bathyergus suillus*, in (A) right lateral and (B) ventral view, and *Fukomys mechowii*, in (C)  
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44 488 right lateral and (D) ventral view. Colours of muscle origins and vectors: temporalis, red;  
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46 489 superficial masseter, cyan; deep masseter, royal blue; IOZM, green; anterior ZM, purple;  
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48 490 posterior ZM, yellow; lateral pterygoid, brown; medial pterygoid, orange.  
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54 492 **Figure 2.** Landmark configuration represented on *Fukomys mechowii* in (A) dorsal, (B)  
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56 493 ventral, and (C) left lateral view. Text definitions of landmarks given in Table S1.  
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5 495 **Figure 3.** Predicted von Mises stress distributions across the skulls of *Fukomys* (left column)  
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7 496 and *Bathyergus* (right column) during incisor biting at four different gape angles.

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11 498 **Figure 4.** PCA plot representing the differences of deformations between the two models  
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13 scaled to force:area ratio. Key: cross, mean unloaded model; blue shapes, *Fukomys* models;  
14 499 red shapes, *Bathyergus* models; circles, occlusion; triangles, 30° gape; squares, 60° gape;  
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16 500 diamonds, 90° gape.  
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23 503 **Figure 5.** Transformation grids and surface warps associated with PCA plot (Figure 4)  
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25 504 representing the differences of deformation between the two models scaled to force:area  
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27 505 ratio. Arrows represent the change in size and shape between unloaded mean model and  
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29 506 target. A, unloaded mean model; B, size and shape change from unloaded model to *Fukomys*  
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31 507 model in occlusion; C, size and shape change from unloaded model to *Bathyergus* model in  
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33 508 occlusion; D, size and shape change from unloaded model to *Fukomys* model at 90° gape; E,  
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35 509 size and shape change from unloaded model to *Bathyergus* model at 90° gape.

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#### 42 512 **TABLE CAPTIONS**

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45 513 **Table 1.** Muscle loads applied to each side of the finite element models of *Fukomys*  
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47 514 *mechowii* and *Bathyergus suillis*.

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52 516 **Table 2.** Median von Mises stress and mechanical efficiency of biting in *Fukomys mechowii*  
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54 517 and *Bathyergus suillis* at increasing gape.

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**Table 1.** Muscle loads applied to each side of the finite element models of *Fukomys mechowii* and *Bathyergus suillus*.

Muscle	Force (N)	
	<i>Fukomys</i>	<i>Bathyergus</i>
Temporalis	20.7	24.1
Superficial masseter	6.3	7.3
Deep masseter	11.7	13.6
Anterior ZM	1.5	1.7
Posterior ZM	1.5	1.7
Infraorbital ZM	3.0	3.5
Medial pterygoid	5.1	6.0
Lateral pterygoid	3.3	3.8

**Table 2.** Median von Mises stress and mechanical efficiency of biting in *Fukomys mechowii* and *Bathyergus suillis* at increasing gape.

Gape angle (°)	Median VM (MPa)		Mechanical efficiency	
	<i>Fukomys</i>	<i>Bathyergus</i>	<i>Fukomys</i>	<i>Bathyergus</i>
0	1.06	0.88	0.18	0.13
30	1.04	0.76	0.15	0.08
60	0.85	0.52	0.09	0.03
90	0.63	0.59	0.02	-0.03

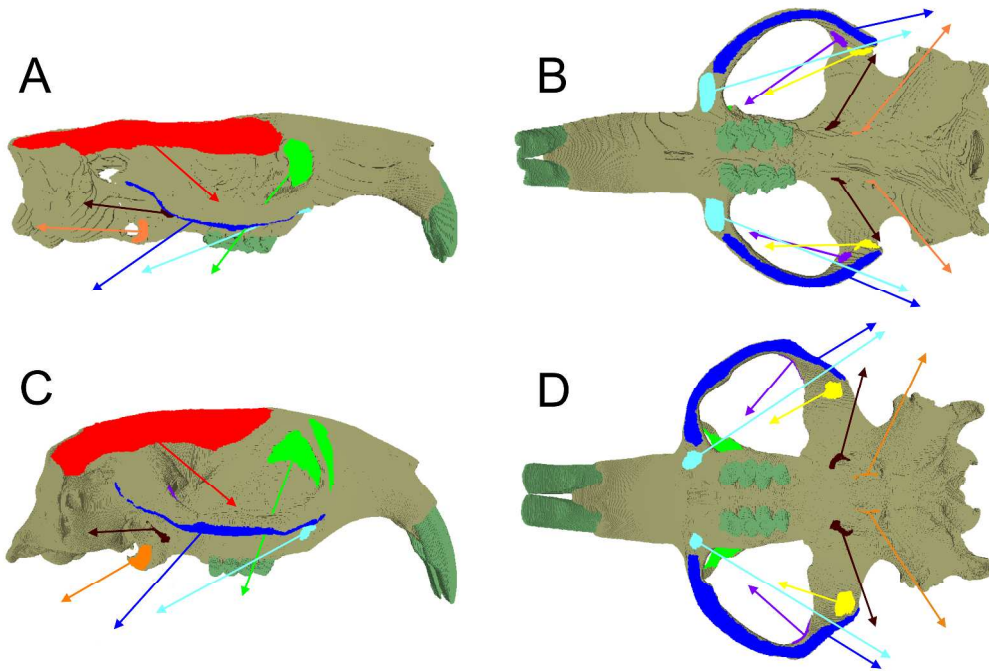


Figure 1. Attachment sites and vectors of pull of the masticatory muscles in models of *Bathyergus suillus*, in (A) right lateral and (B) ventral view, and *Fukomys mechowii*, in (C) right lateral and (D) ventral view. Colours of muscle origins and vectors: temporalis, red; superficial masseter, cyan; deep masseter, royal blue; IOZM, green; anterior ZM, purple; posterior ZM, yellow; lateral pterygoid, brown; medial pterygoid, orange.

170x116mm (600 x 600 DPI)

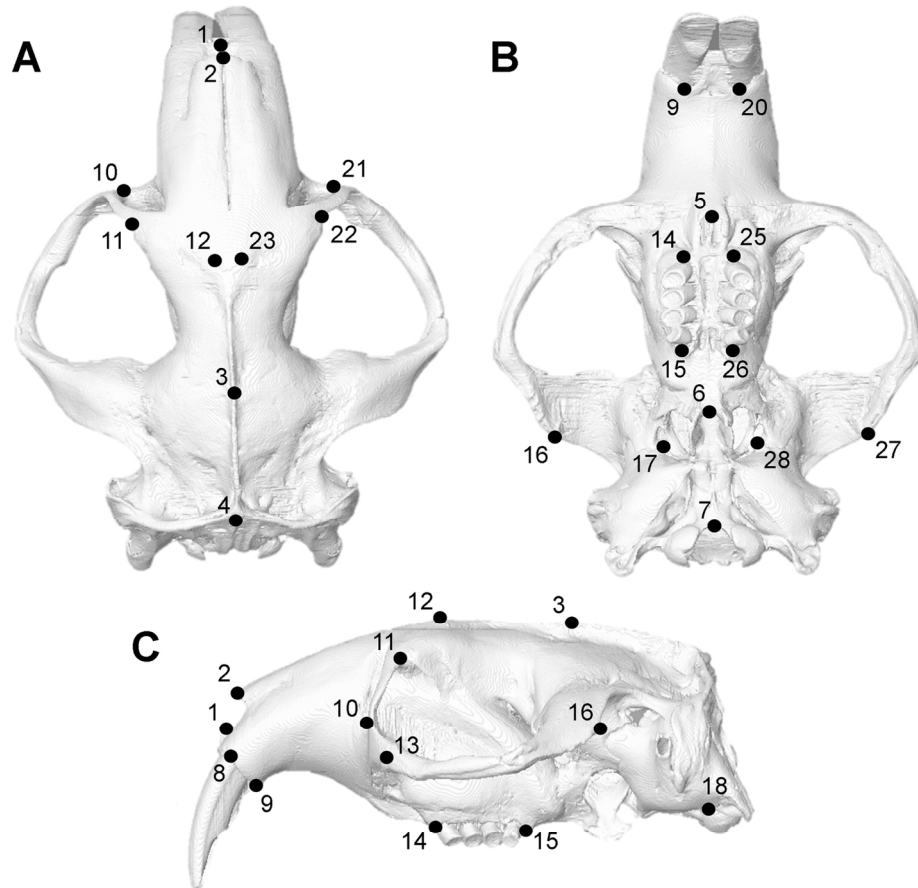


Figure 2. Landmark configuration represented on *Fukomys mechowii* in (A) dorsal, (B) ventral, and (C) left lateral view. Text definitions of landmarks given in Table S1.

140x131mm (300 x 300 DPI)

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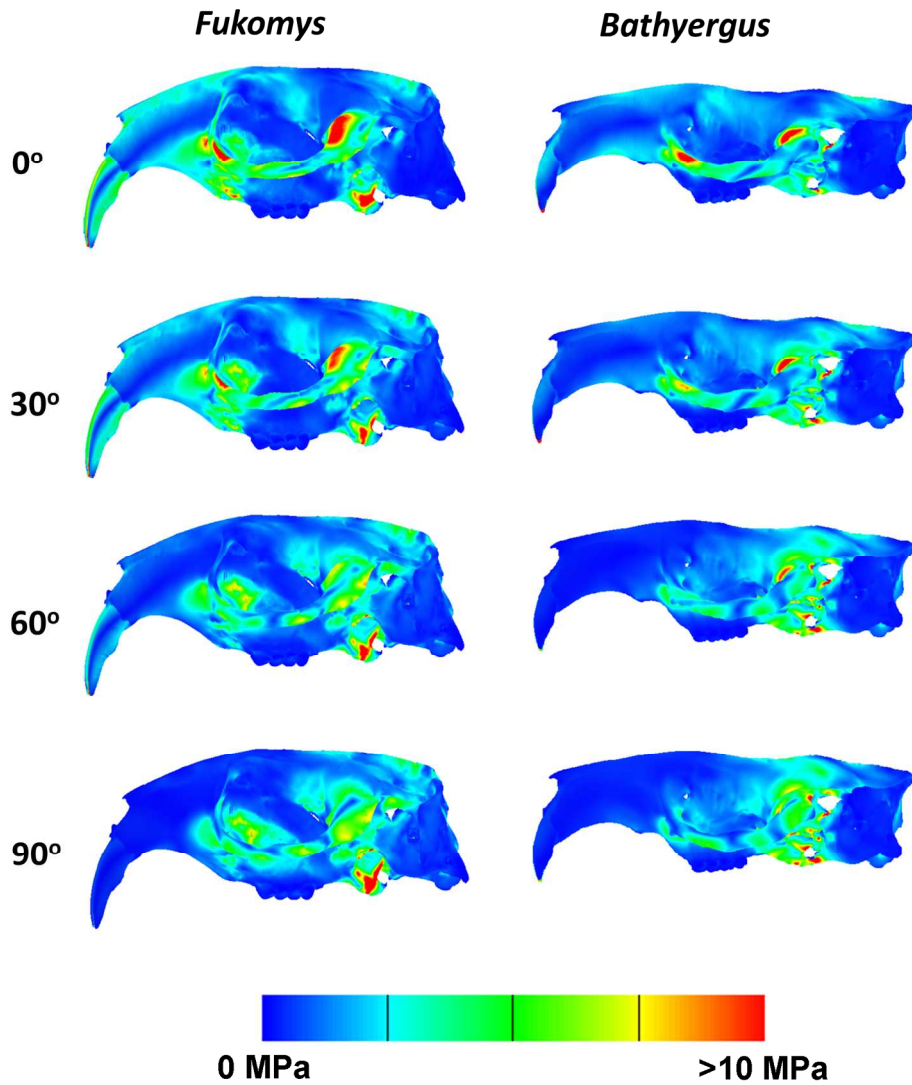


Figure 3. Predicted von Mises stress distributions across the skulls of *Fukomys* (left column) and *Bathyergus* (right column) during incisor biting at four different gape angles.

174x207mm (283 x 283 DPI)

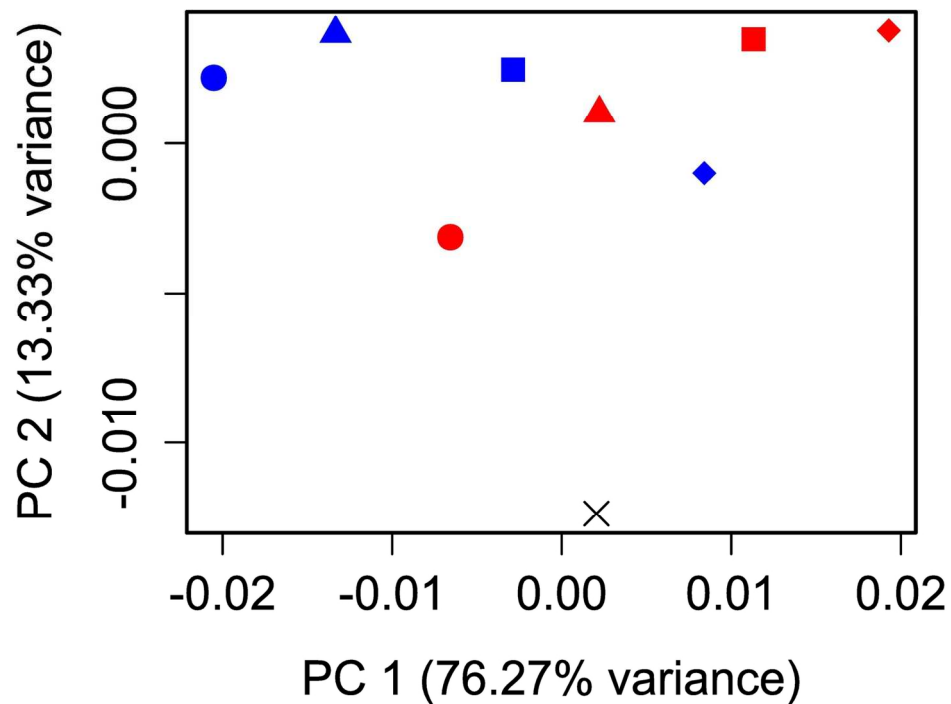


Figure 4. PCA plot representing the differences of deformations between the two models scaled to force:area ratio. Key: cross, mean unloaded model; blue shapes, *Fukomys* models; red shapes, *Bathyergus* models; circles, occlusion; triangles, 30° gape; squares, 60° gape; diamonds, 90° gape.

143x114mm (300 x 300 DPI)

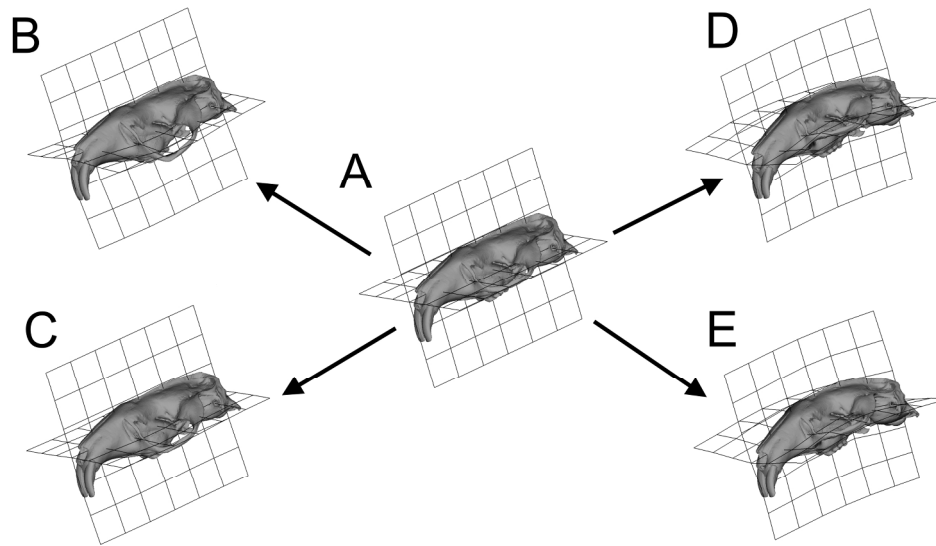


Figure 5. Transformation grids and surface warps associated with PCA plot (Figure 4) representing the differences of deformation between the two models scaled to force:area ratio. Arrows represent the change in size and shape between unloaded mean model and target. A, unloaded mean model; B, size and shape change from unloaded model to *Fukomys* model in occlusion; C, size and shape change from unloaded model to *Bathyergus* model in occlusion; D, size and shape change from unloaded model to *Fukomys* model at 90° gape; E, size and shape change from unloaded model to *Bathyergus* model at 90° gape.