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# The jaw is a second-class lever in *Pedetes capensis* (Rodentia: Pedetidae)

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The mammalian jaw is often modelled as a third-class lever for the purposes of biomechanical analyses, owing to the position of the resultant muscle force between the jaw joint and the teeth. However, it has been proposed that in some rodents the jaws operate as a second-class lever during distal molar bites, owing to the rostral position of the masticatory musculature. In particular, the infraorbital portion of the zygomatico-mandibularis (IOZM) has been suggested to be of major importance in converting the masticatory system from a third-class to a second-class lever. The presence of the IOZM is diagnostic of the hystricomorph rodents, and is particularly well-developed in *Pedetes capensis*, the South African springhare. In this study, finite element analysis (FEA) was used to assess the lever mechanics of the springhare masticatory system, and to determine the function of the IOZM. An FE model of the skull of *P. capensis* was constructed and loaded with all masticatory muscles, and then solved for biting at each tooth in turn. Further load cases were created in which each masticatory muscle was removed in turn. The analyses showed that the mechanical advantage of the springhare jaws was above one at all molar bites and very close to one during the premolar bite. Removing the IOZM or masseter caused a drop in mechanical advantage at all bites, but affected strain patterns and cranial deformation very little. Removing the ZM had only a small effect on mechanical advantage, but produced a substantial reduction in strain and deformation across the skull. It was concluded that the masticatory system of *P. capensis* acts as a second class lever during bites along almost the entire cheek tooth row. The IOZM is clearly a major contributor to this effect, but the masseter also has a part to play. The benefit of the IOZM is that it adds force without substantially contributing to strain or deformation of the skull. This may help explain why the hystricomorphous morphology has evolved multiple times independently within Rodentia.

1 **The jaw is a second-class lever in *Pedetes capensis* (Rodentia: Pedetidae)**

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32 **ABSTRACT**

33 The mammalian jaw is often modelled as a third-class lever for the purposes of biomechanical  
34 analyses, owing to the position of the resultant muscle force between the jaw joint and the teeth.  
35 However, it has been proposed that in some rodents the jaws operate as a second-class lever  
36 during distal molar bites, owing to the rostral position of the masticatory musculature. In  
37 particular, the infraorbital portion of the zygomatico-mandibularis (IOZM) has been suggested to  
38 be of major importance in converting the masticatory system from a third-class to a second-class  
39 lever. The presence of the IOZM is diagnostic of the hystricomorph rodents, and is particularly  
40 well-developed in *Pedetes capensis*, the South African springhare. In this study, finite element  
41 analysis (FEA) was used to assess the lever mechanics of the springhare masticatory system, and  
42 to determine the function of the IOZM. An FE model of the skull of *P. capensis* was constructed  
43 and loaded with all masticatory muscles, and then solved for biting at each tooth in turn. Further  
44 load cases were created in which each masticatory muscle was removed in turn. The analyses  
45 showed that the mechanical advantage of the springhare jaws was above one at all molar bites  
46 and very close to one during the premolar bite. Removing the IOZM or masseter caused a drop in  
47 mechanical advantage at all bites, but affected strain patterns and cranial deformation very little.  
48 Removing the ZM had only a small effect on mechanical advantage, but produced a substantial  
49 reduction in strain and deformation across the skull. It was concluded that the masticatory system  
50 of *P. capensis* acts as a second class lever during bites along almost the entire cheek tooth row.  
51 The IOZM is clearly a major contributor to this effect, but the masseter also has a part to play.  
52 The benefit of the IOZM is that it adds force without substantially contributing to strain or  
53 deformation of the skull. This may help explain why the hystricomorphous morphology has  
54 evolved multiple times independently within Rodentia.

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## 63 INTRODUCTION

64 The mammalian jaw is frequently treated as a lever for the purposes of biomechanical analysis  
65 (e.g. Crompton, 1963; Bramble, 1978; Greaves, 1978, 1982, 2000; Gingerich, 1979; Thomason,  
66 1991; Satoh, 1998; 1999; Spencer, 1998, 1999; Satoh & Iwaku, 2006, 2009; Davis et al., 2010;  
67 Druzinsky, 2010; Cornette et al., 2012; Becerra et al., 2013; Santana, 2015). More specifically, it  
68 is frequently considered to be a third-class lever i.e. one in which the input force sits between the  
69 fulcrum and the output force (Kerr, 2010). In mammals, the resultant masticatory muscle force  
70 (the input force) is usually situated between the jaw joint (fulcrum) and the biting tooth (output  
71 force) and thus the comparison with a third-class lever is generally accurate. The advantage of  
72 positioning muscle force posterior to the teeth is that relatively wide gapes can be achieved and  
73 high tensile forces at the temporo-mandibular joint, which could lead to dislocation of the jaws,  
74 are avoided (Greaves, 2000, 2012). However, the trade-off is that the mechanical advantage of a  
75 third-class lever is always less than one – that is, the output bite force will always be less than the  
76 effective muscle force.

77

78 It has occasionally been proposed that mammalian jaws do not always operate as third-class  
79 levers (Davis, 1955; Turnbull, 1970), and can in certain circumstances act as second-class levers  
80 with the output force between fulcrum and input force. In his classic work on the mammalian  
81 masticatory system, Turnbull (1970) suggested that the relative size and position of the masseter  
82 in many rodents (and a few ungulates) can shift the resultant of the masticatory musculature  
83 anterior to the distal cheek teeth, converting the masticatory system into a second-class lever  
84 during distal molar biting. Such an effect has even been claimed to occur in humans, with the  
85 jaw operating as a second-class lever during bites on the second and third molars (Mansour &  
86 Reynik, 1975). Alternatively, other authors have argued that although some parts of the muscle  
87 mass attach far forward on the jaws in rodents, the resultant muscle force is still located towards  
88 the posterior end of the jaw (Greaves, 2012).

89

90 In rodents, one muscle in particular has been identified as contributing to the jaw operating as a  
91 second-class lever. The infraorbital portion of the zygomatico-mandibularis (IOZM) is an  
92 anterior expansion of the deepest layer of the masseter, the zygomatico-mandibularis (ZM),  
93 which passes through the enlarged infraorbital foramen to take its origin on the lateral surface of

94 the rostrum. The IOZM, also referred to as the maxillo-mandibularis (Becht, 1953; Turnbull,  
95 1970) or medial masseter (Wood, 1965; Woods, 1972), is the one of the defining characters of  
96 hystricomorph rodents, but is also present in a somewhat smaller form in myomorphs, where it is  
97 found in combination with a rostral expansion of the deep masseter (Wood, 1965; Cox & Jeffery,  
98 2011). Given its rostral origin on the skull and its mandibular insertion at the level of the  
99 premolar, Becht (1953) believed the function of the IOZM was to convert the jaw from a third-  
100 class lever to a second-class lever during molar biting.

101

102 This study seeks to understand the lever mechanics of the skull in the South African springhare,  
103 *Pedetes capensis* – a rodent species in which the IOZM is notably well-developed (Offermans &  
104 De Vree, 1989). *P. capensis* is a nocturnal, bipedal, saltatorial rodent that inhabits arid and semi-  
105 arid areas of southern Africa (Peinke & Brown, 2003). It is large for a rodent (3-4 kg) and feeds  
106 principally on grasses, especially the rhizomes of *Cynodon dactylon* and the tubers of *Cyperus*  
107 *esculentus* (Peinke & Brown, 2006). *P. capensis* and its sister-species *P. surdaster* are the only  
108 two extant members of the Pedetidae (Wilson & Reeder, 2005), a family which molecular  
109 analyses place as sister-group to the Anomaluridae (scaly-tailed flying squirrels) in the  
110 Anomaluromorpha, which itself is part of the mouse-related clade (Fabre et al., 2012). Given the  
111 presence of the IOZM muscle, the pedetids (and anomalurids) have been identified as being  
112 hystricomorphous (Wood, 1965). However, the hystricomorphy seen in the Anomaluromorpha  
113 has evolved independently from that seen in three other groups of rodents: the Ctenohystrica, the  
114 Dipodidae, and some members of the Gliridae (Hautier, Cox & Lebrun, 2015). Thus, the  
115 function of the IOZM is of prime interest to understanding the evolution of the rodents – why has  
116 this muscle arisen independently so many times throughout rodents?

117

118 The aim of this study is to model the masticatory system of *P. capensis* to determine if it  
119 functions as a second or third-class lever, and to assess the function of the masticatory muscles,  
120 particularly the IOZM. There are two specific hypotheses that will be tested:

- 121 1. It is hypothesised that a model of the skull of *P. capensis* will demonstrate the  
122 masticatory system operating as a second-class lever along most of the molar tooth row.  
123 This is expected based on previous dissection work by Offermans and De Vree (1989)  
124 who showed that a great deal of the masticatory musculature is situated alongside or

125 anterior to the cheek teeth. The masticatory system will be determined to be a second-  
126 class lever when the bite force exceeds the effective muscle force, i.e. when the  
127 mechanical advantage is greater than one, and when the reaction force at the temporo-  
128 mandibular joint is negative.

129 2. It is hypothesised that the IOZM muscle has a major role in converting the masticatory  
130 system from a third to a second-class lever in *P. capensis*. This hypothesis was previously  
131 proposed by Becht (1953) and is also expected owing to the large size and rostral position  
132 of the IOZM (Offermans & De Vree, 1989, 1993). The function of the IOZM will be  
133 determined by virtual ablation analyses i.e. removing it and other muscles from the  
134 models to elucidate the effect on the biomechanical performance of the system, as  
135 determined by mechanical advantage, principal strains and the overall deformation of the  
136 skull during biting.

137

138 Previous studies of the lever mechanics of the mammalian masticatory system have tended to  
139 focus on the mandible (Greaves, 1978; 1982, 2000; Spencer, 1998, 1999), owing to its relatively  
140 simple shape and because its function is largely limited to feeding. However, in this study, the  
141 skull will be analysed, because of the interest in the IOZM, which is a particularly unusual fan-  
142 shaped and convergent muscle, originating on the rostrum. To address the hypotheses and to  
143 study the function of the springhare skull during biting, finite element analysis (FEA) will be  
144 employed. FEA is an engineering technique for predicting stress, strain and deformation in an  
145 object during loading (Rayfield, 2007), and is now frequently applied to reconstructions of skulls  
146 and other skeletal elements in order to analyse vertebrate biomechanics (e.g. Richmond et al.,  
147 2005; Kupczik et al., 2007; Dumont et al., 2011; Ross et al., 2011; Cox et al., 2012; Cox,  
148 Kirkham & Herrel, 2013; O'Hare et al., 2013; Porro et al., 2013; Figueirido et al., 2014; Cuff,  
149 Bright & Rayfield, 2015; Sharp, 2015; McIntosh & Cox, 2016; McCabe et al., 2017; Tsouknidas  
150 et al., 2017). As well as simulating stress and strain distributions, FEA is also able to predict  
151 reaction forces, and so will be used here to estimate bite force, jaw joint reaction force and  
152 mechanical advantage. Although these metrics could in theory be estimated via simple 2D lever  
153 models, it has been shown that such simplification leads to inaccuracies in muscle attachment  
154 areas, force magnitudes and directions of pull (Davis et al., 2010; Greaves, 2012). The advantage  
155 of FEA is that muscle forces can be distributed across the whole attachment site rather than being

156 modelled as originating from a single centroid point, and muscle force vectors can act in three  
157 dimensions rather than two.

158

## 159 **MATERIALS AND METHODS**

### 160 **Sample and model creation**

161 The cranium and mandible of an adult specimen of *Pedetes capensis*, the South African  
162 springhare, were obtained from the University Museum of Zoology, Cambridge (catalogue  
163 number E.1446). The sex of the specimen was unknown, but sexual dimorphism has not been  
164 reported in this species (Offermans & De Vree, 1989; López-Antoñanzas, 2016). The specimen  
165 was microCT scanned on the X-Tek Metris system in the Medical and Biological Engineering  
166 group, University of Hull. Voxels were isometric with dimensions of 0.052 mm and 0.041 mm  
167 for the cranium and mandible respectively.

168

169 A virtual reconstruction of the cranium was created from the scan using Avizo 8 (FEI, Hillsboro,  
170 OR). Bone and teeth were segmented as separate materials, but no differentiation was made  
171 between cortical and trabecular bone, nor between different materials within the teeth. These  
172 simplifications of the model geometry were felt to be justified as several previous studies have  
173 indicated that, whilst absolute strain magnitudes are impacted by the presence or absence of  
174 trabecular bone and different tooth materials, the large-scale patterns of deformation are  
175 relatively insensitive to such changes (Fitton et al., 2015; Toro-Ibacache et al., 2016). In order to  
176 reduce solution times and allow effective manipulation of the model in the FE software, the  
177 reconstruction was down-sampled to a voxel size of 0.21 x 0.21 x 0.21 mm. The cranial  
178 reconstruction was then converted into a mesh of 2,310,268 eight-noded, cubic (first-order)  
179 elements via direct voxel conversion, implemented in VOX-FE, custom-built open-source FE  
180 software (Liu et al., 2012). The Avizo reconstruction and VOX-FE model are both available for  
181 download at [https://figshare.com/articles/Springhare\\_FEA/5082598](https://figshare.com/articles/Springhare_FEA/5082598).

182

### 183 **Material properties, constraints and loads**

184 Material properties were assigned to the model based on previous nano-indentation work on  
185 rodent skulls (Cox et al., 2012). Both bone and teeth were assumed to be linearly elastic isotropic  
186 with Young's moduli of 17 and 30 GPa respectively and a Poisson's ratio of 0.3 for both. The



187 model was constrained at both temporo-mandibular joints as well as the biting tooth. The jaw  
188 joints were constrained in all three dimensions, whilst the bite points were only constrained in  
189 the bite direction (i.e. orthogonal to the occlusal plane). This configuration of constraints is  
190 somewhat conservative (it restricts the jaw to simple hinge movements), but has been used by a  
191 number of other authors previously (Porro et al., 2013; Cuff, Bright & Rayfield, 2015; Cox,  
192 Rinderknecht & Blanco, 2015) and provides robust conclusions with regard to mechanical  
193 advantage. The number of nodes constrained at each location varied between 158 and 332.

194

195 Loads were applied to both sides of the model to simulate the following jaw-closing muscles (see  
196 Figure 1) based on previous published data (Offermans & De Vree, 1989, 1993): masseter  
197 (combining the superficial and deep layers), posterior masseter, ZM, IOZM, temporalis, medial  
198 pterygoid and lateral pterygoid. Unfortunately, the superficial and deep masseters could not be  
199 modelled separately, because they were recorded as a single entity in Offermans & De Vree  
200 (1993). Muscle attachment sites were determined based on the detailed descriptions and figures  
201 in Offermans & De Vree (1989). Muscle directions of pull (assuming a gape angle of  $0^\circ$ , i.e.  
202 teeth in occlusion) were assigned using landmarks recorded from the insertion areas on a  
203 reconstruction of the springhare mandible, created from the previously gathered microCT scans.  
204 Muscle forces were calculated by multiplying the physiological cross-sectional areas (PCSA)  
205 given in Offermans & De Vree (1993) by an intrinsic muscle stress value of  $0.3 \text{ Nmm}^{-2}$  (van  
206 Spronsen et al., 1989; Sharp, 2015; Tseng & Flynn, 2015). These muscle forces were then  
207 modified based on the maximum percentage activations recorded by electromyography during  
208 incision and mastication of groundnuts (Offermans & DeVree, 1993). Thus the relative  
209 proportions of total muscle force provided by each muscle were different in incisor biting to  
210 premolar/molar biting. Applied muscle forces for incision and mastication are given in Table 1.  
211 In order to ascertain the function of the masticatory muscles, versions of the model were created  
212 without each of the muscles in turn. The loaded FE model is shown in Figure 1.

213

### 214 **Model solution and analysis**

215 The model was solved for biting at each tooth along the dental arcade. Based on experimental  
216 work by Offermans & De Vree (1990), all bites were modelled as bilateral i.e. the muscles on  
217 both sides of the skull were active with identical forces and the same tooth was loaded on each

218 side of the dental row. Reaction forces at the biting tooth and at the jaw joints were calculated for  
219 each loadcase. Bite forces were divided by the effective muscle force (equal to the sum of the  
220 bite force and joint reaction forces) to calculate the mechanical advantage of the masticatory  
221 system at each tooth. As a ratio, the mechanical advantage provides a useful metric for  
222 comparing loadcases with different input muscle forces. It should be noted that it is a different  
223 measure to the mechanical efficiency of biting used in other studies (Dumont et al., 2011; Cox et  
224 al., 2012; Cox, Kirkham & Herrel, 2013), which divides the bite force by the total adductor  
225 muscle force, but does not take into account the orientation of muscle vectors. The distribution of  
226 maximum ( $\epsilon_1$ : predominantly tensile) and minimum ( $\epsilon_3$ : predominantly compressive) principal  
227 strains across the skull were examined using contour maps. Geometric morphometric methods  
228 were used to analyse deformation patterns across the skull (Cox et al., 2011; Cox, Kirkham &  
229 Herrel, 2013; O'Higgins et al., 2011; McIntosh & Cox, 2016). A set of 46 3D landmark co-  
230 ordinates (described in Figure 2 and Table S1), based on that used in Cox, Kirkham & Herrel  
231 (2013), was recorded from each solved model as well as from the original unloaded model. As  
232 changes in size are of equal significance to changes in shape during mechanical loading, the  
233 landmark sets were subjected to a Procrustes size and shape analysis (O'Higgins & Milne, 2013),  
234 not a Procrustes form analysis, which gives a lower weighting to size (Fitton et al., 2015). This  
235 was followed by a principal component analysis (PCA). All analyses were implemented in the  
236 EVAN toolbox software ([www.evan-society.org](http://www.evan-society.org)).

237

## 238 RESULTS

239 The absolute bite forces and joint reaction forces predicted by the model during biting at each  
240 tooth in *P. capensis* are given in Table 2. In addition, the mechanical advantage of the jaws at  
241 each bite has been calculated. It can be seen that joint reaction forces are negative and  
242 mechanical advantage exceeds one at all three molar teeth. In addition, the mechanical advantage  
243 is almost one (0.99) and the joint reaction force is close to zero (2.8 N) at the premolar.

244

245 The effect of removing each of the masticatory muscles on the overall mechanical advantage is  
246 given in Table 2 and shown in Figure 3. Removal of either the IOZM or the masseter causes a  
247 decrease in mechanical advantage during both incision and mastication, with removal of the  
248 IOZM leading to the greatest decrease. Removal of the medial pterygoid muscle leads to an

249 increase in mechanical advantage across all cheek teeth, but little effect is seen during incisor  
250 biting. Removal of the ZM causes a substantial drop in bite force at all teeth, but has little effect  
251 on the mechanical advantage of the system, except at the incisor where mechanical advantage  
252 increases in the absence of the ZM. Removal of the posterior masseter, temporalis or lateral  
253 pterygoid results in very little change in either bite force or mechanical advantage at any of the  
254 teeth, and hence the results of the models lacking these muscles have not been illustrated in  
255 Figure 3 (although the numerical data is still available in Table 2).

256

257 The contour maps of principal strain distribution across the cranium of *P. capensis* during biting  
258 on the incisor and first molar are shown in Figure 4. It can be seen that the highest maximum and  
259 minimum principal strains are concentrated in similar areas of the skull – along the zygomatic  
260 arch and up its wide ascending ramus, and across the orbital wall, especially the anterior part.  
261 However, there are some differences between the strain distributions. The ascending ramus of  
262 the zygomatic arch is subject to greater  $\epsilon_1$  strains than  $\epsilon_3$  strains, and thus is predominantly under  
263 tension, whereas the orbital wall seems to be experiencing greater  $\epsilon_3$  strains and is likely mostly  
264 in compression. Strains are generally greater during molar biting than incision, and there is an  
265 overall caudal shift of the most highly strained regions away from the rostrum towards the orbit  
266 as the bite point moves posteriorly along the tooth row.

267

268 Figure 4 also shows the effect of removing three of the masticatory muscles (IOZM, masseter  
269 and ZM) on principal strain distributions. Despite being relatively large muscles, the impact of  
270 removing the IOZM or the masseter appears to be minimal. There are very few differences  
271 between models with all masticatory muscles applied and those without the IOZM, except for a  
272 slight reduction in strain on the rostrum and in the posterior part of the orbit during incisor and  
273 molar biting. Removal of the masseter has little effect on the strains generated by incisor biting,  
274 but reduces strains across the zygomatic arch and in the anterior part of the orbit during molar  
275 biting. Elimination of the ZM from the model, however, leads to a substantial reduction in  $\epsilon_1$  and  
276  $\epsilon_3$  strains across the skull during bites at all teeth.

277

278 The geometric morphometric analysis highlights differences in the magnitude and mode of  
279 deformation between the different loadcases solved in this study. Figure 5 shows the scatter plot

280 of the first two principal components. The first principal component encompasses 90% of the  
281 variation, and the second principal component 9% of the variation. It should be noted that to be  
282 able to visualise change across PC2, the axes have not been shown to the same scale. As  
283 demonstrated by the warped reconstructions in Figure 5, the shape change along PC1 is mainly  
284 bending of the zygomatic arch, and this axis mostly separates loaded models from the unloaded  
285 skull, incisor bites from bites on other teeth, and models with different muscles excluded from  
286 one another. In general, incisor bites result in smaller deformations than cheek tooth bites (that  
287 is, the incisor bites are found closer to the unloaded model on PC1), whereas premolar and molar  
288 bites produce very similar deformations. Models lacking the IOZM, temporalis, medial pterygoid  
289 or lateral pterygoid deform in a very similar manner to the models with all masticatory muscles,  
290 whereas removal of the posterior masseter reduces the magnitude of deformation very slightly.  
291 Removal of the masseter causes a greater reduction in cranial deformation and elimination of the  
292 ZM (the largest masticatory muscle) causes the largest reduction in deformation. Shape change  
293 along PC2 represents dorso-ventral bending of the skull and separates the four different bites  
294 along the cheek tooth row.

295

## 296 **DISCUSSION**

297 The results of this study support both of the hypotheses proposed here. The skull of *Pedetes*  
298 *capensis* operates as a second-class lever during biting along almost all of the cheek teeth (first  
299 hypothesis), and this effect can be largely ascribed to the presence of the IOZM muscle (second  
300 hypothesis), although the masseter is important in this regard as well.

301

### 302 *Second-class vs third-class lever*

303 The FE model of *P. capensis* indicates that the mechanical advantage of the masticatory system  
304 is greater than one and the reaction forces at the temporo-mandibular joints are negative during  
305 bites on all three molars. Furthermore, the mechanical advantage is almost one and the joint  
306 reaction force is very close to zero during premolar biting. Thus, as the bite point moves distally  
307 along the tooth row, the system switches from a third-class to a second-class lever somewhere  
308 between the premolar and first molar. In an analysis of the mandibles of two murid species,  
309 *Apodemus speciosus* and *Clethrionomys rufocanus*, such an effect was calculated to occur  
310 between the first and second molars (Sato, 1999). The more anterior position of the effective

311 muscle force in the springhare may be driven in large part by its unusual cranial morphology. In  
312 most hystricomorph rodents, the anterior root of the zygomatic arch arises from the skull  
313 approximately at the level of the first cheek tooth, but in *P. capensis* it is much further forward,  
314 attaching to the shortened rostrum just posterior to the upper incisor (Offermans & De Vree,  
315 1989). Thus, the masticatory musculature, as a whole, is more rostrally positioned than in most  
316 other rodents, and so the jaw becomes a second-class lever at more anterior position along the  
317 tooth row.

318

319 The prediction of large tensile forces at the jaw joints of the springhare is a result that is at odds  
320 with some published work on mammalian masticatory biomechanics. It has been argued that the  
321 capsule and ligaments of the mammalian jaw joint are poorly suited to resisting high tensile  
322 forces (Greaves, 2000, 2012), and that the mammalian masticatory system has evolved to  
323 maintain the resultant muscle force within the posterior third of the jaw ramus in order to prevent  
324 instability and dislocation of the jaws (Greaves, 1978, 1982, 2000; Spencer, 1998, 1999). The  
325 mismatch between the results presented here and this earlier work may be the product of  
326 insufficient knowledge of muscle recruitment in springhare mastication and also the limitations  
327 of static FE models. Although the muscle forces were based on *in vivo* work that measured the  
328 degree to which each muscle was activated during biting (Offermans & De Vree, 1993), a single  
329 set of values was used for all molar bites; the only variation in muscle recruitment was between  
330 incisor and cheek teeth bites. It has been shown that muscle recruitment can vary a great deal  
331 from tooth to tooth, and even between bites on the same tooth (Cleuren, Aerts & De Vree, 1995).  
332 Furthermore, the percentage activations used to calculate muscle force are the maximum applied  
333 at any point during the masticatory cycle. Obviously, the recruitment of each muscle changes as  
334 the teeth are brought into and out of occlusion, but a static model cannot reflect this. Thus, the  
335 results here indicate that jaw is a second-class lever in molar biting, but this only holds true for  
336 the muscle recruitment pattern applied to the model. In reality, the springhare may modulate  
337 fibre recruitment within its complex set of muscles to maintain the jaws as a third-class lever  
338 even at the distal molars. For instance, the external pterygoid may increase in activation during  
339 distal molar biting to resist dislocation of the jaws as has been suggested to occur in murids  
340 (Sato, 1999).

341

342 Even after taking the limitations of the model into consideration, it is clear that the springhare  
343 has the potential to generate very high bite forces at its molar teeth. Moreover, even if not quite a  
344 second-class lever these bites are very efficient, so high bite forces can be produced without  
345 having to massively increase the overall adductor muscle mass. It is likely that *P. capensis* has  
346 evolved this highly efficient feeding system in order to cope with the demands of the arid  
347 environment in which it lives (Peinke & Brown, 2003). Springhares are herbivorous, feeding  
348 almost exclusively on grasses (Peinke & Brown, 2006). Although they are known to eat the  
349 leaves, springhares tend to favour underground storage organs, such as rhizomes and tubers,  
350 particularly during autumn and winter when nutritional reserves are transferred away from leaves  
351 and into the leaf bases and roots (Peinke & Brown, 2006). These storage organs tend to be  
352 mechanically demanding to eat, requiring a great deal of mastication to break down, which may  
353 have driven the evolution of the highly efficient masticatory system of springhares. The  
354 disadvantage of the masticatory arrangement seen in *P. capensis* is that the rostral position of  
355 many of the jaw-closing muscles is likely to severely limit maximum gape. However, given their  
356 preferred diet of grasses, these limitations are not likely to impact the ability of springhares to  
357 feed effectively.

358

### 359 *Function of the masticatory muscles*

360 The virtual ablation experiments, in which masticatory muscles were sequentially removed from  
361 the FE model, show that the IOZM is the most important muscle in converting the masticatory  
362 system from a third-class to second-class lever in molar biting, as predicted by the second  
363 hypothesis. When the IOZM is removed, the mechanical advantage decreases, indicating that  
364 more force is being directed towards the jaw joints. This has the effect that the point at which the  
365 system switched from operating as a third-class to a second-class lever moves back to  
366 somewhere between the first and second molars. Thus, this result supports the idea proposed by  
367 Becht (1953) that the function of the IOZM is to convert the masticatory system to a second-  
368 class lever during molar biting, at least in *P. capensis*. Removal of the IOZM had very little  
369 impact on the distribution and magnitudes of strain across the skull (Figure 4), nor did it greatly  
370 change the overall deformation of the skull during biting (Figure 5), as has also been noted in  
371 another species of rodent, *Laonastes aenigmamus* (Cox, Kirkham & Herrel, 2013). Thus, it  
372 appears that the increase in mechanical advantage gained by the presence of an IOZM muscle

373 does not come at the cost of greatly increased strain or deformation, either in the region of the  
374 IOZM origin or elsewhere on the skull. In addition, the development of the IOZM in *P. capensis*  
375 may be a response to the need to generate large forces at the incisors, such as during the cracking  
376 of nutshells (Offermans & De Vree, 1990) or gnawing of roots and tubers (Peinke & Brown,  
377 2006). The anterior position of the IOZM on the skull means that improvements in incisor bite  
378 force can be achieved without an excessive increase in muscle size.

379

380 The ZM is one of the largest masticatory muscles in the springhare (Offermans & De Vree,  
381 1993), which is unusual among rodents; usually the ZM is smaller than the superficial and deep  
382 masseters and the IOZM (Turnbull, 1970; Woods, 1972; Cox & Jeffery, 2011; Baverstock,  
383 Jeffery & Cobb, 2013; Becerra et al., 2014). Despite its large size, the removal of the ZM from  
384 the FE model had very little effect on the efficiency of the masticatory system i.e. the mechanical  
385 advantage and joint reaction force remained largely the same. Thus, by virtue of being large, the  
386 ZM is an important muscle for increasing overall bite force, but its presence does not alter the  
387 efficiency of the system a great deal. However, the ZM does have a large effect on the  
388 deformation of the springhare skull during biting. The GMM analysis showed that elimination of  
389 the ZM greatly reduces the magnitude of deformation experienced by the skull (Figure 5), much  
390 more so than any other masticatory muscle. This appears to be a consequence of the attachment  
391 site of the ZM on the zygomatic arch. As has been found in other FEA studies of mammal skulls  
392 (Bright, 2012; Cox et al., 2012; Fitton et al., 2012), the morphology of the zygomatic arch makes  
393 it susceptible to larger deformations than other parts of the skull. Indeed, in this study,  
394 deformations of the zygoma overwhelm deformations in all other parts of the skull, as can be  
395 seen from the warped reconstructions in Figure 5. The large size and location of the ZM in *P.*  
396 *capensis* leads to it being the principal generator of zygomatic strain and deformation. This can  
397 be seen in Figure 4, where removal of the ZM vastly reduces strain in the zygomatic arch.

398

399 It has been suggested that the large zygomatic strains seen in many FEA studies of mammalian  
400 skulls may be artificial and the result of a failure to incorporate important soft tissue structures  
401 into the models. In particular, the temporal fascia has been shown to resist inferior bending of the  
402 zygomatic arch in an FE model of a macaque (Curtis et al., 2011). This is unlikely to be the case  
403 here as no temporal fascia was reported by Offermans & De Vree (1989) in their dissection of a

404 springhare. Furthermore, the temporalis is extremely small in *P. capensis*, and the temporal  
405 region is positioned distinctly caudal the zygomatic arch, which would reduce the ability of a  
406 temporal fascia to counteract ventral deflection of the zygomatic arch. However, there is an  
407 aponeurosis attached extensively around the margin of the infraorbital fossa (Offermans & De  
408 Vree, 1989), which may have the potential to resist some bending in the anterior part of the  
409 zygomatic arc and its ascending ramus. Further work, both *ex vivo* dissection and *in silico*  
410 modelling, is necessary to understand the biomechanical consequence of this aponeurosis.

411

412 The masseter has been shown to have a similar effect to the IOZM with regard to bite force,  
413 although not quite to the same extent. It, too, appears to shift the resultant masticatory muscle  
414 force anteriorly along the rostrum, thus directing force towards the biting tooth and away from  
415 the jaw joints. Removal of the masseter has much the same effect as removing the IOZM – the  
416 mechanical advantage is decreased and the point at which the system becomes a second-class  
417 lever is shifted posteriorly along the tooth row. Unfortunately for this study, Offermans &  
418 DeVree (1993) did not separate the superficial and deep masseter when measuring PCSA, so the  
419 two muscles could not be modelled separately in the FEA. However, the illustrations in  
420 Offermans & DeVree (1989) indicate that the fibres of the superficial masseter have a more  
421 horizontal alignment than those of the deep masseter (as in most rodents, e.g. Turnbull, 1970), so  
422 it is likely that the superficial masseter is the more important division of the masseter with regard  
423 to the operation of the jaw as a second-class lever. In terms of cranial deformations, the masseter  
424 has a similar, but lesser, effect to the ZM. Owing to its attachment to the zygomatic arch, the  
425 action of the masseter generates inferior bending of the arch, and thus its removal tends to reduce  
426 global deformation of the springhare cranium (Figure 5). It can also be seen that that removal of  
427 the masseter causes a slight reduction in zygomatic and orbital strains during molar biting  
428 (Figure 4).

429

430 The medial pterygoid, because of its posterior line of action, tends to direct muscle force away  
431 from the teeth and towards the jaw joints, unlike the IOZM and masseter. Thus removal of the  
432 medial pterygoid increased the mechanical advantage of the masticatory system. Overall, the  
433 presence of the medial pterygoid increases bite force because it increases the total input adductor  
434 muscle force, but it does so in a somewhat inefficient manner. Thus, although the medial



435 pterygoid has a relatively large PCSA, it has a relatively small effective muscle force owing to  
436 its orientation. However, it has been shown that the medial pterygoid is important in other  
437 aspects of masticatory biomechanics, notably as a counterbalance to the lateral pull of the  
438 masseter, thereby preventing wishboning of the mandible (eversion of the lower border and  
439 angular process) and reducing tensile strains at the symphysis (Hiemae, 1971; Satoh, 1998; Cox  
440 & Jeffery, 2015).

441

442 The posterior masseter, temporalis and lateral pterygoid are very small compared to the other  
443 masticatory muscles in *P. capensis*, each providing less than 11% of the total adductor muscle  
444 force. Hence, the impact of their removal on bite force and mechanical advantage was minimal.  
445 Similarly, removal of these muscles had a very limited impact on the overall deformation of the  
446 skull (Figure 5). The models without the temporalis and lateral pterygoid can barely be  
447 distinguished from the models with all masticatory muscles. The models without a posterior  
448 masseter show a very slight reduction in the magnitude of cranial deformation. This is because  
449 the posterior masseter attaches to the caudal part of the zygomatic arch and thus is able to cause a  
450 small amount of posterior deflection. It is likely that these muscles contribute to aspects of the  
451 masticatory process other than bite force generation, especially the antero-posterior movements  
452 of the mandible relative to the skull that are common to rodents. The temporalis, whilst clearly  
453 too small to be a powerful elevator of the jaw as in myomorphs (Hiemae, 1971; Gorniak, 1977),  
454 may have a braking role during the power stroke of chewing (Byrd, 1981), and the lateral  
455 pterygoid may be important in protraction of the mandible (Weijs & Dantuma, 1975; Gorniak,  
456 1977) or in resisting tensile forces at the temporo-mandibular joint as mentioned above (Satoh,  
457 1999).

458

## 459 CONCLUSIONS

460 The masticatory system of *P. capensis* has been shown to have the potential to act as a second-  
461 class lever along the majority of the cheek tooth row and, as predicted by Becht (1953), the  
462 IOZM is a particularly important muscle in the switch from third-class to second-class lever  
463 mechanics. It should be noted that masseter also plays an important role in this regard. This  
464 analysis of muscle function is, of course, specific to *P. capensis* and further analyses of other  
465 species are necessary to determine whether the conclusions hold true for other rodents. However,

466 the position of the IOZM, far forward on the rostrum, makes it likely that it will have some role  
467 to play in increasing the mechanical advantage of the masticatory system in most hystricomorph  
468 rodents (the exact scale of the effect being dependent on the size of the IOZM relative to the  
469 other masticatory muscles). Previous research has suggested that, amongst rodents, sciuriforms  
470 are adapted for efficient gnawing at the incisors, whereas hystricomorphs are adapted to efficient  
471 grinding at the molars (Cox et al., 2012). Druzinsky (2010) determined that of all the masticatory  
472 muscles, it is the anterior deep masseter that confers efficacious incisor bites in sciuriforms.  
473 Here, it is indicated that the IOZM provides efficiency in molar bites in hystricomorphs, without  
474 substantially increasing strains across the skull or the magnitude of cranial deformation. This  
475 may go some way to explaining why hystricomorphy has evolved convergently at least four  
476 times within the rodents.

477

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484

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657

## 658 **FIGURE LEGENDS**

659 **Figure 1. FE model showing muscle attachment sites and vectors.** Skull of *Pedetes capensis*  
660 shown in (A) lateral and (B) dorso-lateral view. Key: blue, masseter; brown, posterior  
661 masseter; dark green, ZM; light green, IOZM; red, temporalis; orange, medial pterygoid;  
662 yellow, lateral pterygoid.

663

664 **Figure 2. Landmarks used in GMM analysis of skull deformations.** Reconstruction of skull  
665 of *Pedetes capensis* in (A) dorsal, (B) ventral and (C) left lateral view. Landmarks 11-28  
666 recorded on both sides of the skull. Landmark descriptions are given in Table S1.

667

668 **Figure 3. Mechanical advantage at each tooth predicted by FE model.** Abbreviations: I,  
669 incisor; PM, premolar; M1, first molar; M2, second molar; M3, third molar. Data for  
670 models with posterior masseter, temporalis and lateral pterygoid removed available in  
671 Table 2 but not illustrated here.

672

673 **Figure 4. Predicted principal strains across the skull of *Pedetes capensis* during incisor and**  
674 **first molar biting.** A-H: maximum ( $\epsilon_1$ ) principal strains during incisor (A-D) and M1 (E-  
675 H) biting; I-P: minimum ( $\epsilon_3$ ) principal strains during incisor (I-L) and M1 (M-P) biting.  
676 A,E,I,M: model with all masticatory muscles included; B,F,J,N: model with IOZM  
677 excluded; C,G,K,O: model with masseter excluded; D,H,L,P: model with ZM excluded.



678

679 **Figure 5. GM analysis of cranial deformations in *Pedetes capensis*.** Plot of the first two  
680 principal components from a GM analysis of 46 landmarks and 41 models. Axes not to  
681 scale. Cranial reconstructions indicate shape changes (x400) along axes.

**Table 1** (on next page)

Muscle forces applied to each side of the model.

PCSA and percentage activations of each muscle from Offermans & De Vree (1993).

1 **Table 1.** Muscle forces applied to each side of the model. PCSA and percentage activations of each  
2 muscle from Offermans & De Vree (1993).

3

	PCSA (cm <sup>2</sup> )	Maximum force (N)	% activation		Applied force (N)	
			Incision	Mastication	Incision	Mastication
<b>Masseter</b>	2.886	86.58	20	70	17.32	60.61
<b>Posterior masseter</b>	0.654	19.62	0	40	0.00	7.85
<b>ZM</b>	3.360	100.80	60	100	60.48	100.80
<b>IOZM</b>	2.244	67.32	100	60	67.32	40.39
<b>Temporalis</b>	0.516	15.48	0	30	0.00	4.64
<b>Medial pterygoid</b>	1.130	33.90	15	90	5.09	30.51
<b>Lateral pterygoid</b>	0.519	15.57	60	70	9.34	10.90

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**Table 2** (on next page)

Bite force, joint reaction force and mechanical advantage of each model.

1 **Table 2.** Bite force, joint reaction force and mechanical advantage of each model.

2

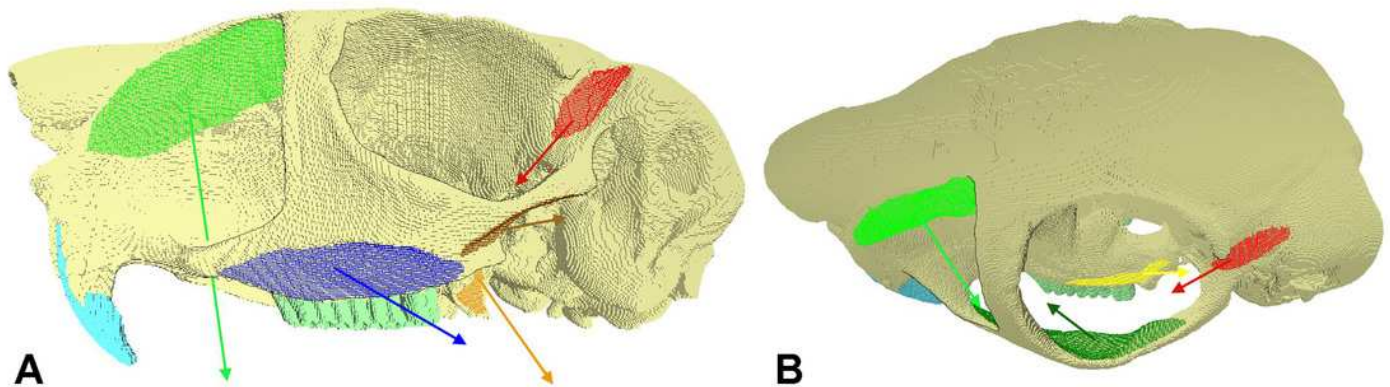
	All muscles	No masseter	No posterior masseter	No ZM	No IOZM	No temporalis	No medial pterygoid	No lateral pterygoid
<b>Bite force</b>								
I	154.6	138.3	154.3	122.5	49.9	154.3	152.0	154.3
PM	347.5	244.4	345.7	247.4	232.5	346.6	319.9	348.7
M1	395.6	279.0	393.5	280.7	265.7	394.6	362.5	397.4
M2	457.7	323.0	455.2	324.7	307.8	456.4	418.8	459.8
M3	539.6	380.8	536.7	382.9	362.7	538.1	494.1	541.9
<b>Joint reaction force</b>								
I	85.9	83.0	86.2	39.8	56.0	86.2	79.3	154.3
PM	2.8	29.2	3.4	-2.3	38.8	-0.4	-26.9	9.3
M1	-45.3	-5.4	-44.4	-35.7	5.5	-48.3	-69.6	-39.5
M2	-107.3	-49.4	-106.1	-79.7	-36.4	-110.2	-125.9	-102.0
M3	-189.2	-107.1	-187.5	-137.9	-91.3	-191.8	-201.1	-184.0
<b>Mechanical advantage</b>								
I	0.64	0.62	0.64	0.75	0.47	0.64	0.66	0.50
PM	0.99	0.89	0.99	1.01	0.86	1.00	1.09	0.97
M1	1.13	1.02	1.13	1.15	0.98	1.14	1.24	1.11
M2	1.31	1.18	1.30	1.33	1.13	1.32	1.43	1.28
M3	1.54	1.39	1.54	1.56	1.34	1.55	1.69	1.51

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## Figure 1

FE model showing muscle attachment sites and vectors.

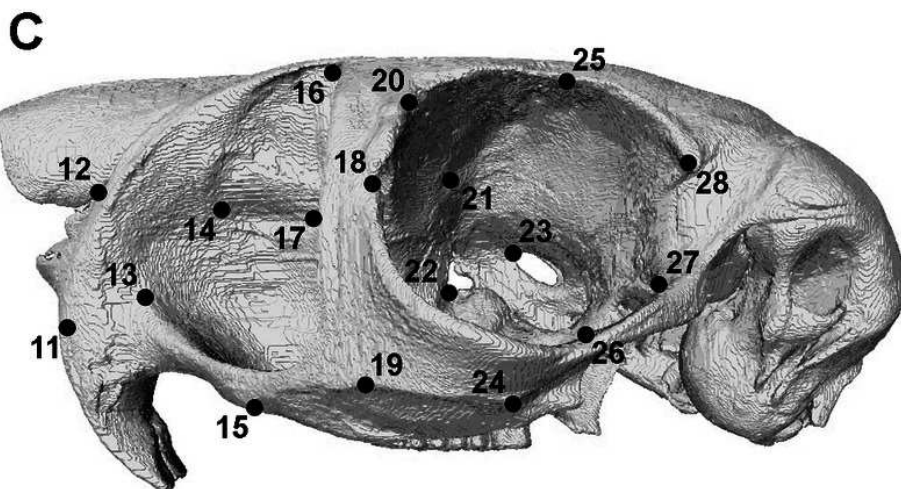
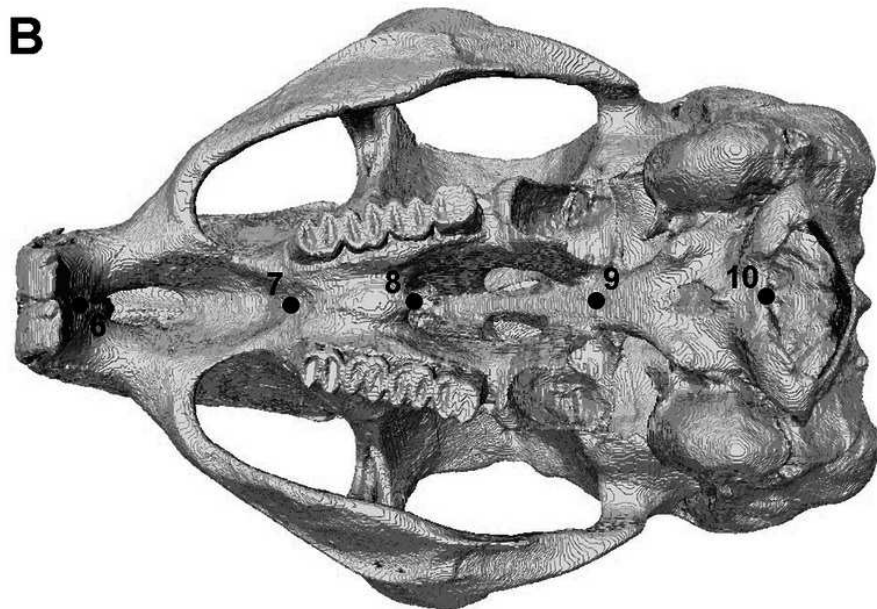
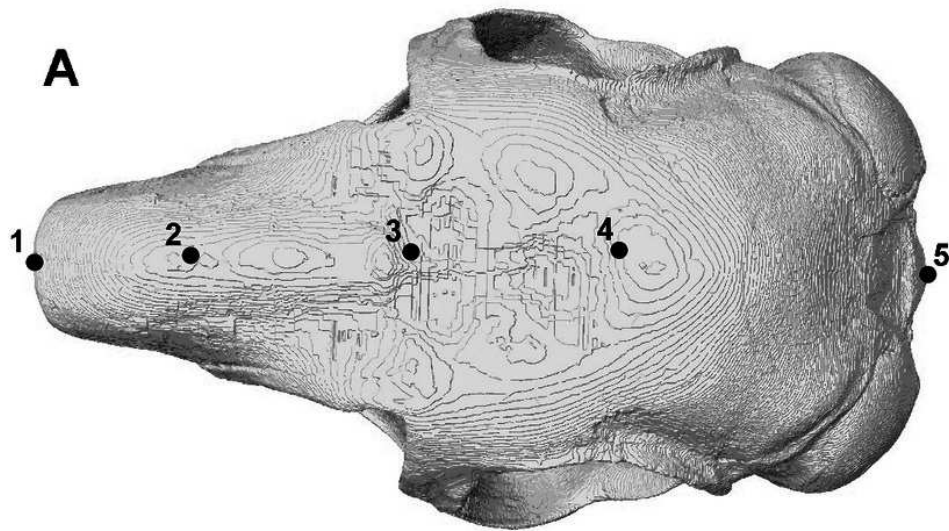
Skull of *Pedetes capensis* shown in (A) lateral and (B) dorso-lateral view. Key: blue, masseter; brown, posterior masseter; dark green, ZM; light green, IOZM; red, temporalis; orange, medial pterygoid; yellow, lateral pterygoid.



## Figure 2

Landmarks used in GMM analysis of skull deformations.

Reconstruction of skull of *Pedetes capensis* in (A) dorsal, (B) ventral and (C) left lateral view. Landmarks 11-28 recorded on both sides of the skull. Landmark descriptions are given in Table S1.

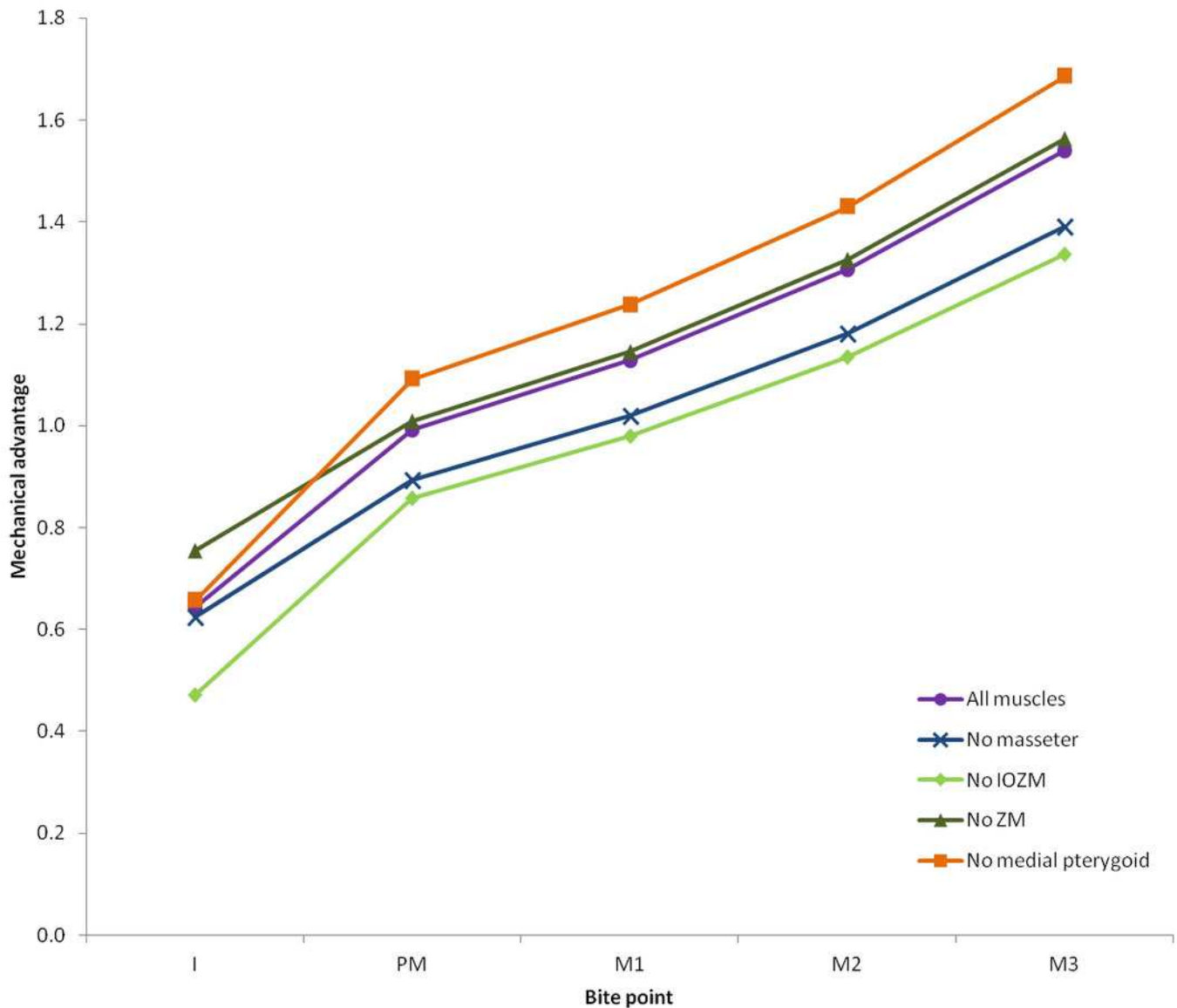




## Figure 3

Mechanical advantage at each tooth predicted by FE model.

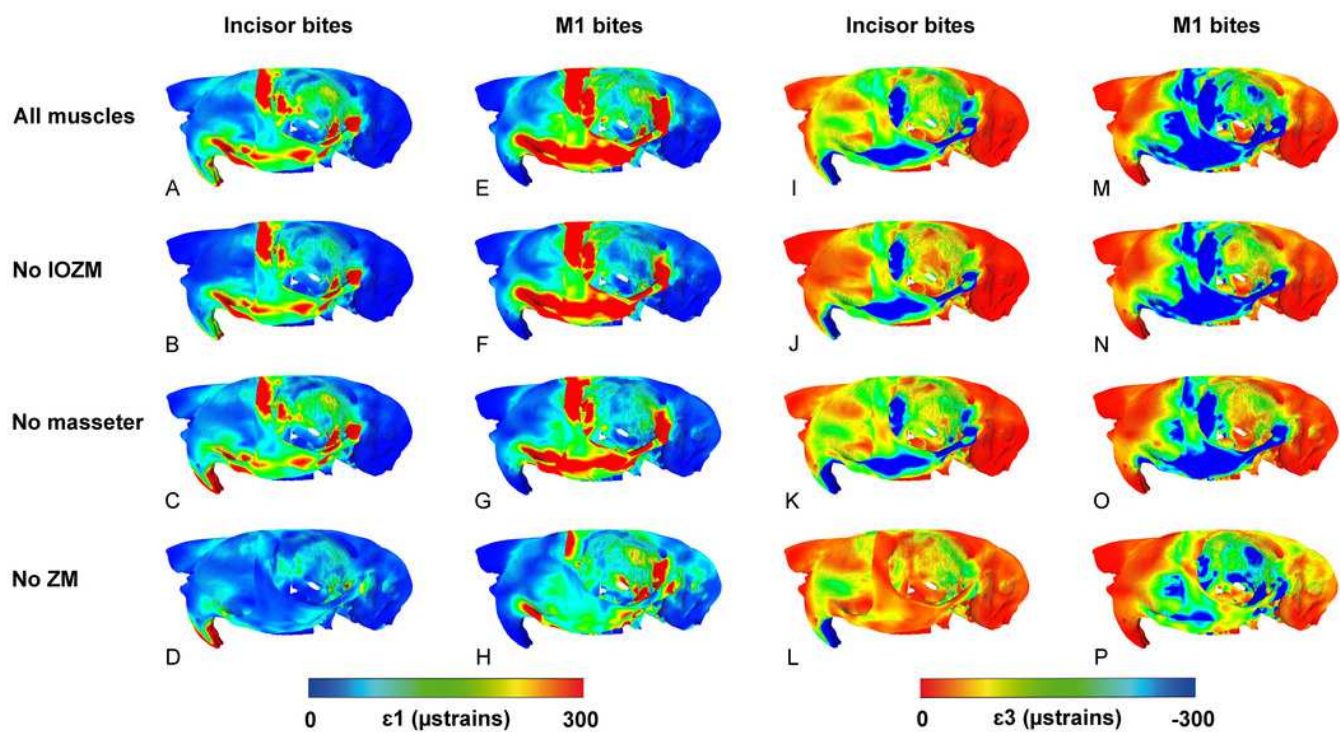
Abbreviations: I, incisor; PM, premolar; M1, first molar; M2, second molar; M3, third molar. Data for models with posterior masseter, temporalis and lateral pterygoid removed available in Table 2 but not illustrated here.



## Figure 4

Predicted principal strains across the skull of *Pedetes capensis* during incisor and first molar biting.

A-H: maximum ( $\epsilon_1$ ) principal strains during incisor (A-D) and M1 (E-H) biting; I-P: minimum ( $\epsilon_3$ ) principal strains during incisor (I-L) and M1 (M-P) biting. A,E,I,M: model with all masticatory muscles included; B,F,J,N: model with IOZM excluded; C,G,K,O: model with masseter excluded; D,H,L,P: model with ZM excluded.



## Figure 5

GM analysis of cranial deformations in *Pedetes capensis*.

Plot of the first two principal components from a GM analysis of 46 landmarks and 41 models.

Axes not to scale. Cranial reconstructions indicate shape changes (x400) along axes.

