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1 **TITLE: Mechanical significance of morphological variation in diprotodont incisors**

2

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17 **ABSTRACT**

18 All rodents possess a single pair of enlarged incisors that grow throughout life. This condition
19 (diprotodonty) is characteristic of Rodentia, but is also found in other mammals such as
20 lagomorphs, hyraxes, the aye-aye and common wombat. This study surveyed lower incisor
21 morphology across extant diprotodonts to examine shape variation within and between rodents
22 and other diprotodonts, and to determine if tooth shape varies in a manner predictable from
23 mechanics. Six linear and area variables were recorded from microCT scans of the mandibles
24 of 33 diprotodont mammals. The curvature of the rodent lower incisors, as measured by the
25 proportion of a circle it occupies, was shown to vary between 20% and 45%, with non-Glires
26 taxa falling outside this range. Relative lengths of the portions of the incisor within and external
27 to the mandible were not significantly correlated when overall size was taken into account.
28 Cross-sectional geometry of the incisor was significantly correlated with the external length of
29 the incisor. Overall, incisor morphology was shown to vary in a way predictable from ecology
30 and mechanics, in order to resist bending. Among non-rodents, lagomorph incisors closely
31 resemble those of rodents, and, relative to rodents, hyrax and wombat incisors are somewhat
32 smaller but aye-aye incisors are much more extreme in morphology.

33

34 **KEYWORDS**

35 Incisor; mechanics; morphology; diprotodont; rodents

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42 INTRODUCTION

43 Rodent incisors are some of the most unusual and highly specialised teeth seen in mammals.
44 All rodents have an upper and lower pair of elongated and continually growing incisors. Each
45 incisor grows throughout life in a curved (more specifically helical, based on observation of
46 longer and overgrown incisors) shape, with odontogenesis taking place constantly at the base
47 in order to balance the tooth material continually worn away at the tip through gnawing. The
48 distribution of materials within rodent incisors is also unusual, with enamel being restricted to
49 a layer along the labial surface of the tooth [1,2]. This enables a sharp blade to be maintained
50 constantly at the incisor tip as the harder enamel wears away more slowly than the dentine
51 beneath it [3]. The upper and lower incisors project a long distance posteriorly within both the
52 cranium and mandible. Upper incisors reach as far back as the level of the first cheek tooth in
53 most rodents, and even further back in some chisel-tooth digging mole-rats [4]. Similarly,
54 lower incisors extend well beyond the mandibular premolars and molars, and even stretch into
55 the condyle in some species.

56

57 Such highly specialised incisors, whilst being diagnostic of rodents, are not restricted to that
58 order. The possession of enlarged (often continuously growing) incisors, here referred to as
59 diprotodonty is found in a number of other extant mammals, including the sister-group to
60 rodents, Lagomorpha (hares, rabbits and pikas), and a range of more distantly related taxa
61 including hyraxes (Hyracoidea), the aye-aye (*Daubentonia madagascariensis*) and the
62 common wombat (*Vombatus ursinus*). The lagomorphs likely inherited their enlarged incisors
63 from a shared common ancestor with the rodents [5], but the incisors of hyraxes, the aye-aye
64 and the wombat, whilst similar in morphology to those of rodents, must have evolved
65 independently in each order [3].

66

67 The long, curved incisors of diprotodonts are principally used in food acquisition, and also the
68 processing of hard food objects, such as nuts, seeds and geophytes [6]. However, diprotodont
69 incisors can also be used for a number of other mechanically demanding and specialised tasks
70 e.g. bark-stripping by aye-ayes [7], the felling of large trees by beavers [8], and the digging of
71 burrows through hard soils by mole-rats [9]. Given the range of variation in tooth function in
72 rodents, very little is known about the variation in the mechanically relevant shape (curvature,
73 length, cross-section etc.) and the corresponding mechanical performance of incisors in rodents
74 and other diprotodont mammals. Chisel-tooth digging mole-rats are one of the few rodent
75 groups in which incisor form and function has been well studied. There is a clear positive
76 correlation between the radius of curvature of the incisors and cranial length across rodents in
77 general, but species which dig with their teeth have much larger incisors relative to skull size
78 [10]. In addition, several studies have noted that the angle at which the incisor emerges from
79 the alveolus (incisor procumbency) is greater in chisel-tooth digging rodents [4,9,11-13].

80

81 In biomechanical analyses, biological structures such as long bone diaphyses and mandibular
82 corpora have been frequently modelled as beams owing to their similarity in shape and because
83 of the relative simplicity that this approximation confers on the calculations [14-16]. Given its
84 shape and the nature of the forces to which it is typically exposed, the diprotodont incisor can
85 also be biomechanically approximated as a curved beam subjected to bending. Measures of
86 cross-sectional geometry, particularly cross-sectional area (*CSA*) and second moment of area
87 (*SMA*), are important in understanding the ability of a beam to resist bending [16,17]. *CSA*
88 quantifies the amount of material found at a cross-section, whereas *SMA* indicates how that
89 material is distributed relative to the loaded axis. The cross-sectional geometry of the rodent
90 incisor has been shown to correlate with ecological traits that affect incisor loading such as diet
91 [18] and habitat [10,19,20], and is a good predictor of maximum bite force [21].

92

93 The aim of this study is to determine whether the lower incisors of diprotodont mammals are
94 similar in morphology across a wide range of taxa or if there is substantial shape variation
95 within rodents and between rodents and other mammalian diprotodonts. This study will also
96 assess whether the lower incisors of diprotodonts vary morphologically in a manner predictable
97 from the mechanical loading they experience. Lower incisors were chosen as the focus of this
98 study as they have been the subject of fewer morphological analyses than the upper incisors
99 [4,10]. Three main hypotheses will be tested:

100

101 1. *All lower incisors have the same two-dimensional shape in lateral view.* That is,
102 assuming the curvature of the incisor to be constant along its length and therefore part
103 of a circle (the helix is simplified as a circle for this study), it is expected that all incisors
104 will form the same proportion of a circle (will subtend the same angle). This prediction
105 is based on previous research showing that the upper incisors of rodents were very
106 similar in shape across a wide range of species, all being approximately semicircular
107 [10].

108 2. *There is no correlation between the length of incisor within the mandible and the length*
109 *of the part of the incisor not covered by mandibular bone.* This study assumes the
110 external part of the incisor to act as a cantilever beam that is fixed at the level of the
111 alveolar margin. Under this model, the length of incisor within the bone has no effect
112 on the bending mechanics of the external part of the incisor, and thus the two sections
113 of the incisor will vary independently.

114 3. *There is significant correlation between the length of the external part of the incisor*
115 *and its cross-sectional shape, in particular CSA and SMA.* Both of these measures give

116 an indication of how resistant to bending the incisor is, and so it is hypothesised that
117 both metrics will correlate positively with external tooth length.

118 Each of these hypotheses will also allow differences and similarities in the form-function
119 relationship of the lower incisors to be investigated between the rodent and non-rodent taxa.

120

121 **MATERIALS AND METHODS**

122 **Sample**

123 The sample in this study comprised osteological specimens of the mandibles of 33 diprotodont
124 mammals. These included 27 rodents, chosen to cover the majority of extant families, and six
125 non-rodent diprotodont species: two lagomorphs (*Oryctolagus cuniculus* and *Lepus*
126 *europaeus*), two hyraxes (*Dendrohyrax arboreus* and *Procavia capensis*), one primate
127 (*Daubentonia madagascariensis*) and one marsupial (*Vombatus ursinus*). All specimens except
128 the capybara (*Hydrochoerus hydrochaeris*) were imaged using microCT scanning, resulting in
129 isometric voxels with dimensions ranging between 0.02 and 0.14 mm. Owing to its large size,
130 the capybara skull was imaged on a medical CT scanner with a resulting voxel size of 0.42
131 mm. A full list of specimens, the institutions from which they were borrowed, and the scanning
132 parameters are given in electronic supplementary material, datafile S1.

133

134 A hemi-mandible of each specimen was virtually reconstructed using Avizo 8.0 (FEI,
135 Hillsboro, OR), with the incisor being rendered as a separate object to the mandibular bone. A
136 complete set of reconstructions is given in electronic supplementary material, table S1. Three
137 landmarks were placed along the midline of the labial surface of the incisor (see figure 1): one
138 at the tip, one at the alveolar margin, and one at the posterior extremity (here referred to as the
139 base). These landmarks were used to align all incisor reconstructions to the same orientation
140 and also enabled the calculation of six measurements from each incisor: (1) radius of curvature

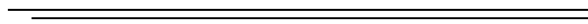
141 (r); (2) total tooth length (TTL); (3) internal tooth length (ITL); (4) external tooth length (ETL);
142 (5) CSA ; and (6) SMA . ‘Internal’ and ‘external’ tooth lengths here refer to the length of the
143 portion of the incisor found within the dentary bone and the length of the portion protruding
144 from the mandible respectively.

145

146 r , TTL , ITL and ETL were derived by treating the three landmarks as the vertices of a triangle
147 and calculating the lengths of its sides a , b and c (see figure 1). r is the radius of the circle that
148 fits the three landmarks and was calculated using a modified version of Heron’s formula as in
149 [4]:

150

151



152

153 TTL is the distance along the curve of the labial surface of the tooth between the tip and the
154 base. It was determined by first calculating the angle subtended by the arc of the tooth (θ):

155



156

157 This angle gave the proportion of the circumference occupied by the tooth, enabling its arc
158 length to be calculated (assuming θ is in radians):

159

160

161 It should be noted that this formula is only correct for angles up to π radians i.e. a tooth that
162 encompasses less than half the circumference of a circle. As a check, the following value,
163 derived from the cosine rule, was calculated (using the side lengths of the triangle in figure 1):

164

165

166 A positive value of X indicated a tooth that encompassed more than half a semicircle, and thus
167 the calculated value of θ had to be corrected by subtracting it from 2π . The proportion of a
168 circle occupied by the lower incisors was compared with that calculated for the upper incisors
169 of a number of rodent species in a previous analysis [10]. Significant differences between the
170 means and the coefficients of variation (CV) of the upper and lower incisors were tested using
171 a t -test and a Fligner-Killeen test respectively. Statistical analyses were carried out in PAST
172 [22].

173

174 *ETL* and *ITL* (arc lengths from tip to alveolar margin, and from alveolar margin to base
175 respectively) were calculated by substituting c with a and b in the calculation of θ . The
176 remaining two measurements, *CSA* and *SMA*, were determined from a cross-sectional slice
177 taken through the incisor at the level of the alveolar margin. The slice was orthogonal to both
178 the long axis of the incisor and the tangent plane at the alveolar margin landmark. The BoneJ
179 module [23] of the ImageJ software [24] was used to calculate the *CSA* and *SMA* of the cross-
180 sectional slice of the incisor.

181

182 The following bivariate plots were generated using the R statistical environment [25]: *TTL* vs
183 r ; *ETL* vs *ITL*; *CSA* vs *ETL*; and *SMA* vs *ETL*. In order to linearise the relationship between
184 variables, the square root of *CSA* and the fourth root of *SMA* were plotted against *ETL*. To
185 control for the confounding effects of size, *ETL* and *ITL* were also plotted against one another
186 as fractions of circle. Phylogenetic generalised least squares (PGLS) regression, implemented
187 in the phytools package in R [26,27], was used to assess the relationship between the variables.
188 A Brownian motion model of evolution was assumed and the underlying phylogeny, compiled
189 using data from [28,29], is shown in figure 2.

190

191 RESULTS

192 *Incisor shape*

193 The plot of r (radius of curvature) against TTL (figure 3) shows a clear positive correlation (a
194 $= 0.43$, $R^2 = 0.65$) between the two variables, which, after phylogenetic correction, is highly
195 significant ($F = 85.11$, $P < 0.001$). However, although r generally increases as TTL increases,
196 it can be seen in table 1 that there is a great deal of variation in the proportion of a circle
197 encompassed by the incisor. Rodent lower incisors vary between 20% and 45% of a circle's
198 circumference, with a mean of 34.2%, which is significantly different ($t = 4.24$, $P < 0.001$)
199 from that of upper incisors (41.6%), as can be seen in Table 2. Variability within the lower
200 incisor sample ($CV = 17.8$) was greater than that of the upper incisor sample ($CV = 14.2$), but
201 not significantly so, as demonstrated by a Fligner-Killeen test. Adding the non-rodents to the
202 lower incisor sample extends the range further to 12% and 51%. Indeed, of the non-rodents,
203 only the lagomorphs fall within the range of the rodents. The wombat and hyraxes have incisors
204 that form a smaller proportion of a circle than rodents, whereas the aye-aye incisor forms a
205 larger proportion. Hypothesis 1, that all lower incisors have the same two-dimensional shape
206 in lateral view, is therefore rejected.

207

208 *External and internal incisor length*

209 The plot of ETL against ITL (figure 4) indicates a relationship between these two
210 measurements, but one that is potentially curvilinear rather than linear. At small sizes, ETL
211 increases as ITL increases with a slope of 0.67. However, above an internal length of around
212 25 mm, the rate of increase of the external length slows dramatically, to a slope of 0.12, and
213 scatter about the trend line increases substantially. Three rodent taxa (coypu, plains viscacha
214 and Cape dune mole-rat) clearly plot above the curve and thus have longer incisors externally

215 than would be predicted from the internal length of their tooth, whereas a rodent and a non-
216 rodent taxa (springhare and aye-aye) are found below the curve, therefore displaying shorter
217 incisors externally than expected. After phylogenetic correction, the log-log relationship
218 between these two variables is highly significant ($F = 60.27, P < 0.001$). *ITL* and *ETL* were
219 converted to fractions of a circle (by dividing by total circumference) and plotted against one
220 another (figure 5). A PGLS model indicated that the relationship between these two variables
221 was not significant ($F = 2.14, P = 0.15$). Hypothesis 2, that there is no correlation between the
222 length of incisor within the mandible and the length of the part of the incisor not covered by
223 mandibular bone, is therefore supported (with the caveat that there are some outliers among
224 the rodent taxa).

225

226 *Cross-sectional geometry*

227 Both *CSA* and *SMA* show clear positive relationships with the *ETL*, as can be seen in figures 6
228 and 7 (*CSA*: $a = 0.18, R^2 = 0.61$; *SMA*: $a = 0.11, R^2 = 0.60$). PGLS models indicate that these
229 correlations are statistically significant (*CSA*: $F = 0.50, P < 0.001$; *SMA*: $F = 0.55, P < 0.001$).
230 Three of the larger taxa (capybara, aye-aye and wombat) have a larger *CSA* and a larger *SMA*
231 than would be predicted from the tooth length. On the other hand, the Cape dune mole-rat has
232 a lower *CSA* and *SMA* than would be predicted from *ETL*. Hypothesis 3, that there is a
233 significant correlation between the length of the external part of the incisor and its cross-
234 sectional shape (as measured by *CSA* and *SMA*), is therefore supported.

235

236 **DISCUSSION**

237 It can be seen from the results here that, on the whole, the lower incisors of diprotodont
238 mammals vary in a predictable manner. There is a close correlation between the length of the
239 incisor and its radius of curvature, between the length of the portion of the incisor within the

240 mandible and the length of the exposed section, and between the cross-sectional morphology
241 and the external length of the incisor.

242

243 *Incisor shape*

244 Previous research [10] found a close correlation between total curved length and radius of
245 curvature of the upper incisor of a sample of rodents. Limited interspecific variation in the
246 relationship between these two variables was previously noted, leading to the conclusion that
247 most upper incisors approach a semicircle in shape [10]. The results here find greater variation
248 in lower incisor shape (CV = 17.8) compared to upper incisors (CV = 14.2), albeit on a different
249 sample of rodents, but indicate that this is not a significant difference. However, the proportion
250 of a circle's circumference occupied by each incisor, given in table 1, does show a significant
251 difference ($P < 0.001$) between upper (mean = 41.6%) and lower incisors (mean = 34.2%)..
252 This shows that, unlike the upper incisors, rodent lower incisors only approach a semicircle in
253 a few taxa, and in most cases are substantially less than that.

254

255 It is not obvious why the shape of the upper incisor forms a greater proportion of the
256 circumference of a circle than that of the lower incisor. One possible explanation is that the
257 upper incisor is constrained to a particular shape because of a need to fit around the other
258 contents of the rostrum – notably the nasal cavity and cribriform plate. Moreover, the upper
259 incisor can, in most rodents, only stretch back as far as the beginning of the molar tooth row,
260 but a relatively large amount of space is available in the dorsal axis, whilst the lower incisor
261 can project backwards as far as, and some cases into, the mandibular condyle, but has limited
262 room to expand dorsally. Thus by forming a semicircle, the upper incisor is maximising its
263 length in the space available and any increase in size will simply result in a larger semicircle,

264 whereas the lower incisor forms a smaller part of a larger circle, and increases in size will tend
265 to increase the proportion of the circle encompassed.

266

267 From examination of the distribution of species within table 1, relative length of the lower
268 incisor appears to be associated with diet and habitat. Those rodents with relatively short
269 incisors (occupying less than 28% of a circle) tend to feed on fruits, leaves and grasses [6,30-
270 32] which, whilst they may require substantial processing by the molar teeth, do not necessitate
271 high incisor bite forces during their ingestion. On the other hand, those rodents with longer
272 incisors, forming 36% of a circle or more, either regularly incorporate hard food items (e.g.
273 roots, nuts, wood) into their diet [8,31,33-36] or live in a fossorial environment [9] which may
274 lead to the ingestion of large amounts of grit. It therefore seems that rodents experiencing
275 greater rates of wear tend to have incisors that form a greater proportion of a circle. This mirrors
276 previous research showing that chisel-tooth digging rodents tend to have relatively larger upper
277 incisors than non-tooth-digging rodents [10]. Further work directly analysing the relationship
278 between diet and mechanically relevant incisor morphology is required. While general, broad
279 dietary categories (e.g. carnivore, insectivore, omnivore, generalist herbivore, specialist
280 herbivore) are available in the literature for most of the taxa in this study, they do not provide
281 information regarding the actual material properties (specifically the geometric and mechanical
282 properties) of the foods and so are not relevant to understanding the mechanics of food
283 acquisition and processing, and could generate misleading results. Unfortunately the detailed
284 information regarding the diets of these taxa, specifically the mechanical properties (e.g.
285 Young's modulus of elasticity; hardness; toughness; fracture strength etc.) and geometric
286 properties (size and shape of the food items, and the implications for gape in the animal),
287 necessary to carry out this analysis is not currently available and would require considerable
288 effort to collect from the field.

289

290 *External and internal incisor length*

291 The second hypothesis of this study predicted that the length of the section of the lower incisor
292 within the alveolus would not covary with the length of the portion external to the mandible.
293 This prediction was based on the biomechanical assumption that the external part of the incisor
294 acts like a cantilever beam fixed at the alveolar margin. As such, the length of the incisor within
295 the mandible does not affect the ability of the external part of the incisor to resist bending. On
296 first inspection, it seems that this hypothesis was not supported. There is a clear positive
297 relationship between the two portions of the incisor (figure 4), although this relationship does
298 not appear to be linear. As *ITL* increases above 25 mm, the rate of increase of *ETL* starts to
299 taper off, and thus the external part of the incisor is much shorter relative to the internal part in
300 larger rodents. This interpretation should be treated with a degree of caution, though, as the
301 trend may be driven by a small number of outliers and may reflect a weakening of the
302 correlation between *ITL* and *ETL* as *ITL* increases.

303

304 It should be noted, however, that the relationship between *ITL* and *ETL* appears to be driven
305 by overall changes in size. As the mandible gets larger, the entire incisor will also increase in
306 size, and thus the correlation between the lengths of the two parts of the incisor may simply
307 reflect this. To account for the confounding factor of size, the *ITL* and *ETL* were converted to
308 fractions of a circle by dividing them by total circumference. Under a PGLS model, it was
309 found that the size-corrected *ITL* and *ETL* were not significantly correlated (figure 5), as
310 predicted by the second hypothesis. It appears that the length of the external portion of the
311 incisor can vary independently of the length of the internal section, and likely has done in
312 response to the external forces experienced by the tooth. For instance, it can be seen that the
313 taxa positioned below the curve in figure 4 tend to be those that engage their incisors in

314 mechanically demanding activities such as gnawing roots and stems (*Pedetes* [36]), wood
315 (*Castor* [8]; *Daubentonia* [7]), or bones (*Hystrix* [37]). These species likely have relatively
316 shorter incisors externally, compared to other rodents, in order to resist the greater bending
317 forces incurred during these activities. This also means that the perceived plateau of *ETL* noted
318 above may be somewhat artefactual and driven by the unusually short external incisors of the
319 beaver and porcupine.

320

321 It is also possible that the presence of the incisor within the mandibular body, in conjunction
322 with the bony adaptations of the mandible, plays a role in the mechanical adaptation of the
323 mandible to resisting bending during incisal biting, particularly in taxa which employ high
324 force incisal biting. This hypothesis is the focus of a separate future study.

325

326 *Cross-sectional geometry*

327 As predicted by the third hypothesis, there is a significant positive correlation between both
328 measures of cross-sectional morphology (*CSA* and *SMA*) and *ETL*. This fits with the
329 biomechanical model of the lower incisor as a curved beam – as the beam gets longer, the
330 bending moment will increase, and this can be resisted by increasing the amount of material in
331 cross-section at the point of bending (the alveolar margin). In particular, the amount of material
332 in the axis of loading (i.e. *SMA*) increases as the external length of the tooth increases. Such a
333 relationship suggests that *ETL* can be estimated from cross-sectional geometry, which could be
334 of particular use for the reconstruction of morphology in extinct rodents. The skulls and
335 mandibles of fossil rodents often have broken or missing incisors (e.g. [38-40]) and it can be
336 important to know their complete length for biomechanical analyses (e.g. [41]). The
337 relationships shown here will enable such length estimations to be made. It should be recalled
338 that the incisor is a composite structure (primarily dentine with a thin layer of enamel and

339 cementum on the labial and lingual surfaces respectively) which has simplified for the purposes
340 of this study as being composed of a single tissue. Additional work would therefore be required
341 to determine if, in addition to facilitating the functional wear of the occlusal (biting) surface of
342 the incisors, the enamel plays a the mechanical role in stiffening the incisors.

343

344 *Non-rodent diprotodonts*

345 Six non-rodent diprotodont species were included in this analysis: two lagomorphs, two
346 hyraxes, an aye-aye and a wombat, to determine if their lower incisors fall within the range of
347 variation of rodent incisors for the metrics measured here. This is certainly the case for the
348 lagomorphs, which fall within the range occupied by rodents for r , TL and the cross-sectional
349 measures (figures 3-7). This is unsurprising as lagomorphs and rodents are united within the
350 clade Glires and are very likely to have inherited their enlarged incisors from a common
351 ancestor [5]. However, it is not clear that the other non-rodents in this analysis are particularly
352 similar to rodents with regard to their lower incisors.

353

354 It was found that hyrax incisors only partially resemble those of rodents. They show rodent-
355 like proportions of the internal and external sections (figure 4), but plot a little way above the
356 line with regard to their CSA and SMA relative to ETL (figures 6 and 7). In addition among the
357 hyrax taxa (figure 3), *Procavia* shows a larger r relative to TTL than other specimens in the
358 analysis, although *Dendrohyrax* is similar to many rodents in this regard. Hyrax incisors are
359 much shorter relative to overall mandible size, compared to the rodents (see reconstructed
360 specimens in electronic supplementary material, table S1) and encompass a smaller proportion
361 of a circle than any rodent in this analysis (less than 20%; see table 1). This shortening results
362 in relatively larger cross-sectional measures in both genera and a slightly enlarged radius of
363 curvature in *Procavia*. Previous research [42] has indicated that hyrax incisors are used very

364 differently to rodent incisors, functionally being more similar to canines, and this appears to be
365 reflected in a somewhat different morphology.

366

367 Despite the large difference in body size, the wombat lower incisors are similar in a number of
368 ways to those of the hyraxes. The arc of the incisor forms only 15% of the circumference of a
369 circle – a value that is lower than any other rodent measured here and that sits between the two
370 hyrax species. This results in the position of the wombat far above the line in the plot of r
371 against TTL in figure 3. The proportion of ETL to ITL is similar to that of many rodents (figure
372 4), but its CSA and SMA are somewhat larger compared to ETL than most rodents (again like
373 hyraxes). The relatively short incisors seen in the hyraxes and wombat are most likely a
374 reflection of the diets of these species which are dominated by grasses and shrubs and do not
375 include a high proportion of hard food objects [43-45].

376

377 The aye-aye is perhaps the most unusual species in this analysis. Its incisor forms just over a
378 semicircle, which is a greater proportion of a circle than any rodent measured here (table 1). It
379 also has a short ETL compared to ITL (figures 4 and 5), which, as mentioned above, is likely
380 an adaptation to minimise bending stresses whilst gnawing into trees to gain access to wood-
381 boring insect larvae [7]. The aye-aye has further strengthened its incisor by increasing the
382 amount of tooth material in the axis of bending so that, in cross-section, the aye-aye incisor is
383 expanded labio-lingually, but reduced mesio-distally (see figure 7b). This can be inferred from
384 figures 5 and 6 which show that the CSA of the aye-aye incisor is relatively large compared to
385 ETL (although no more so than that of the wombat) but that the SMA of the aye-aye incisor is
386 enormous and sits the furthest above the line of all taxa, indicating the increase in size in the
387 axis of bending. Overall, it appears that the highly unusual and specialised dietary ecology of

388 the aye-aye has driven the evolution of an incisor morphology similar to but more extreme than
389 that seen in rodents.

390

391 **CONCLUSIONS**

392 Overall, the lower incisors of rodents vary in a somewhat predictable way. Radius of curvature
393 increases with the total curved length of the tooth, but there is some variation in 2D shape, with
394 rodent incisors varying between 20% and 45% of a circle. Relatively longer incisors are found
395 in species that specialise in hard food items or have a subterranean lifestyle. The lengths of the
396 portions of the incisor within and external to the mandible are also correlated, but this is largely
397 an effect of overall size – when expressed as a fraction of a circle, there is no significant
398 correlation between internal and external incisor length. As predicted by beam mechanics, the
399 cross-sectional geometry is related to the external length of the incisor. Both cross-sectional
400 measures (*CSA* and *SMA*) increase with increasing external length. Amongst non-rodents, only
401 lagomorph incisors resemble those of rodents very closely. Hyrax and wombat lower incisors
402 are somewhat foreshortened compared to rodents, whereas aye-aye incisors are elongated and
403 specialised to resist the high bending forces generated by their bark-stripping behaviour.

404

405

406 **ETHICS** All data were collected from museum specimens with the permission of the
407 respective curators. Full details of specimens and locations are provided in Datafile S1.

408 **DATA ACCESSIBILITY** Surface reconstructions or original microCT scans of all specimens
409 are available from www.morphosource.org (specimen numbers given in Datafile S1).

410 **AUTHORS' CONTRIBUTIONS** P.G.C. and S.N.F.C. conceived the study. P.G.C. collected
411 image data. P.J.R.M. collected and analysed numerical data. P.J.R.M. and P.G.C. drafted the

412 manuscript. All authors interpreted the data, revised the manuscript and gave final approval for
413 publication.

414 **COMPETING INTERESTS** We have no competing interests.

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426

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536

537 **TABLES**

538 **Table 1.** Percentage of a circle encompassed by the lower incisors of rodents and non-rodent
 539 diprotodonts. Non-rodents in bold.

540

Species	%
<i>Procavia capensis</i>	11.74
<i>Vombatus ursinus</i>	14.88
<i>Dendrohyrax arboreus</i>	17.08
<i>Lagostomus maximus</i>	20.36
<i>Oryctolagus cuniculus</i>	21.48
<i>Cavia porcellus</i>	24.54
<i>Laonastes aenigmamus</i>	25.06
<i>Capromys spilorides</i>	25.94
<i>Lepus europaeus</i>	27.49
<i>Hydrochoerus hydrochaeris</i>	28.21
<i>Aplodontia rufa</i>	28.38
<i>Gerbillus watersi</i>	29.10
<i>Dipus sagitta</i>	31.83
<i>Acomys cahirinus</i>	31.99
<i>Myocastor coypus</i>	32.11
<i>Hystrix cristata</i>	32.38
<i>Paralomys gerbillus</i>	33.13
<i>Erethizon dorsatum</i>	34.27
<i>Rattus norvegicus</i>	35.06
<i>Graphiurus nagtglasii</i>	35.31
<i>Castor canadensis</i>	36.93
<i>Sciurus carolinensis</i>	38.05
<i>Georychus capensis</i>	38.17
<i>Pedetes capensis</i>	38.40
<i>Cricetomys gambianus</i>	38.73
<i>Thomomys umbrinus</i>	38.86
<i>Cannomys badius</i>	39.68
<i>Dasyprocta punctata</i>	40.00
<i>Petaurista petaurista</i>	40.42
<i>Ctenomys opimus</i>	40.64

<i>Octodon degus</i>	41.07
<i>Bathyergus suillus</i>	45.04
<i>Daubentonia madagascariensis</i>	50.75

541

542

543 **Table 2.** Summary statistics for percentage of a circle encompassed by the incisors of rodents.

544 Upper incisor data derived from McIntosh & Cox (2016) [10].

545

	Upper incisors	Lower incisors	Significance
Mean	41.61	34.21	$t = 4.24, ***$
SD	5.91	6.08	$F = 1.06, ns$
CV	14.21	17.76	$T = 13.71, ns$

546

547

548 FIGURE LEGENDS

549 **Figure 1. (a)** Reconstruction of beaver lower mandible and incisor in lateral view showing

550 landmarks and length measurements used to calculate incisor variables. Landmarks:

551 red, incisor tip; orange, midpoint on labial incisor surface at alveolar margin; yellow,

552 distalmost extremity of incisor. (b) Lateral view of reconstructions of the lower incisors

553 of: *Daubentonia madagascariensis* (upper); *Rattus norvegicus* (middle); *Sciurus*

554 *carolinensis* (lower), with cross sections taken at the alveolar margin and at halfway

555 along the internal incisor length (not to scale).

556

557 **Figure 2.** Phylogeny of species used in this analysis. Scale bar represents 10 million years.

558

559 **Figure 3.** Scatterplot of radius of curvature against total incisor length. Red circles, rodents;
560 blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing triangles,
561 lagomorphs; open circles, hyraxes; open downward-pointing triangle, wombat.

562

563 **Figure 4.** Scatterplot of external incisor length against internal incisor length. Red circles,
564 rodents; blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing
565 triangles, lagomorphs; open circles, hyraxes; open downward-pointing triangle,
566 wombat.

567

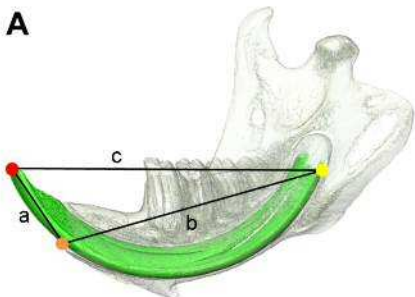
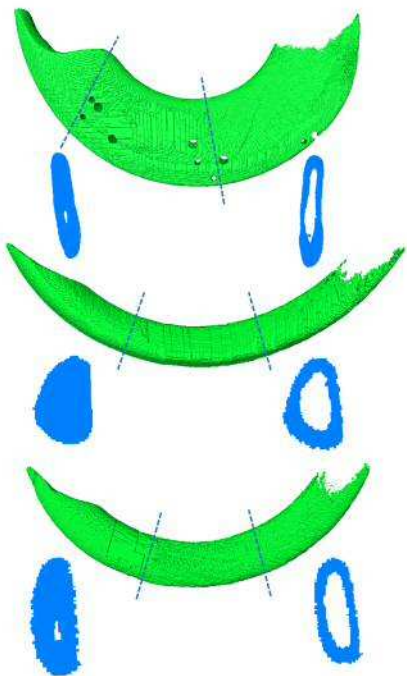
568 **Figure 5.** Scatterplot of external and internal incisor lengths expressed as fractions of a circle.
569 Red circles, rodents; blue symbols, non-rodent taxa; open square, aye-aye; open
570 upward-pointing triangles, lagomorphs; open circles, hyraxes; open downward-
571 pointing triangle, wombat.

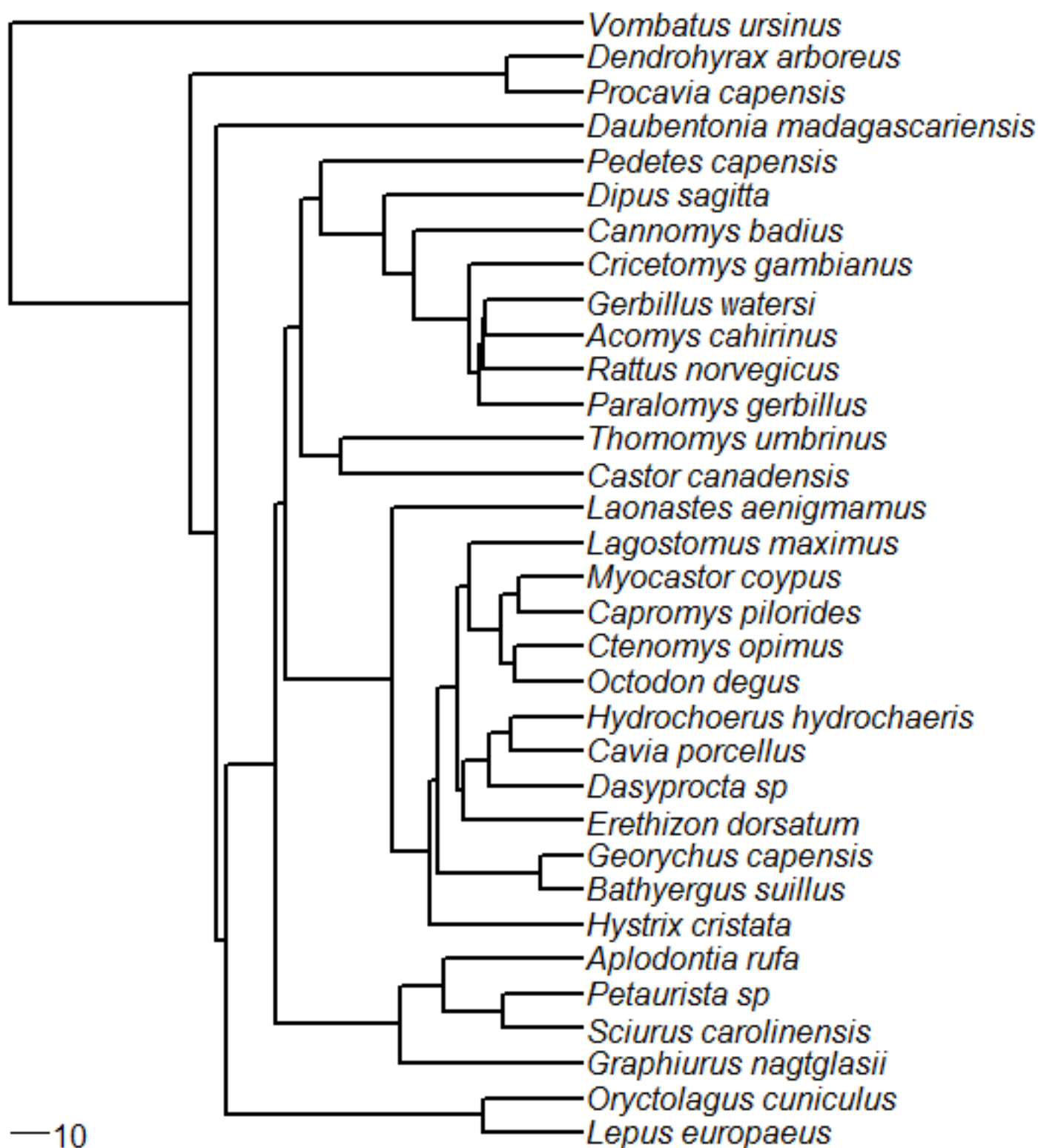
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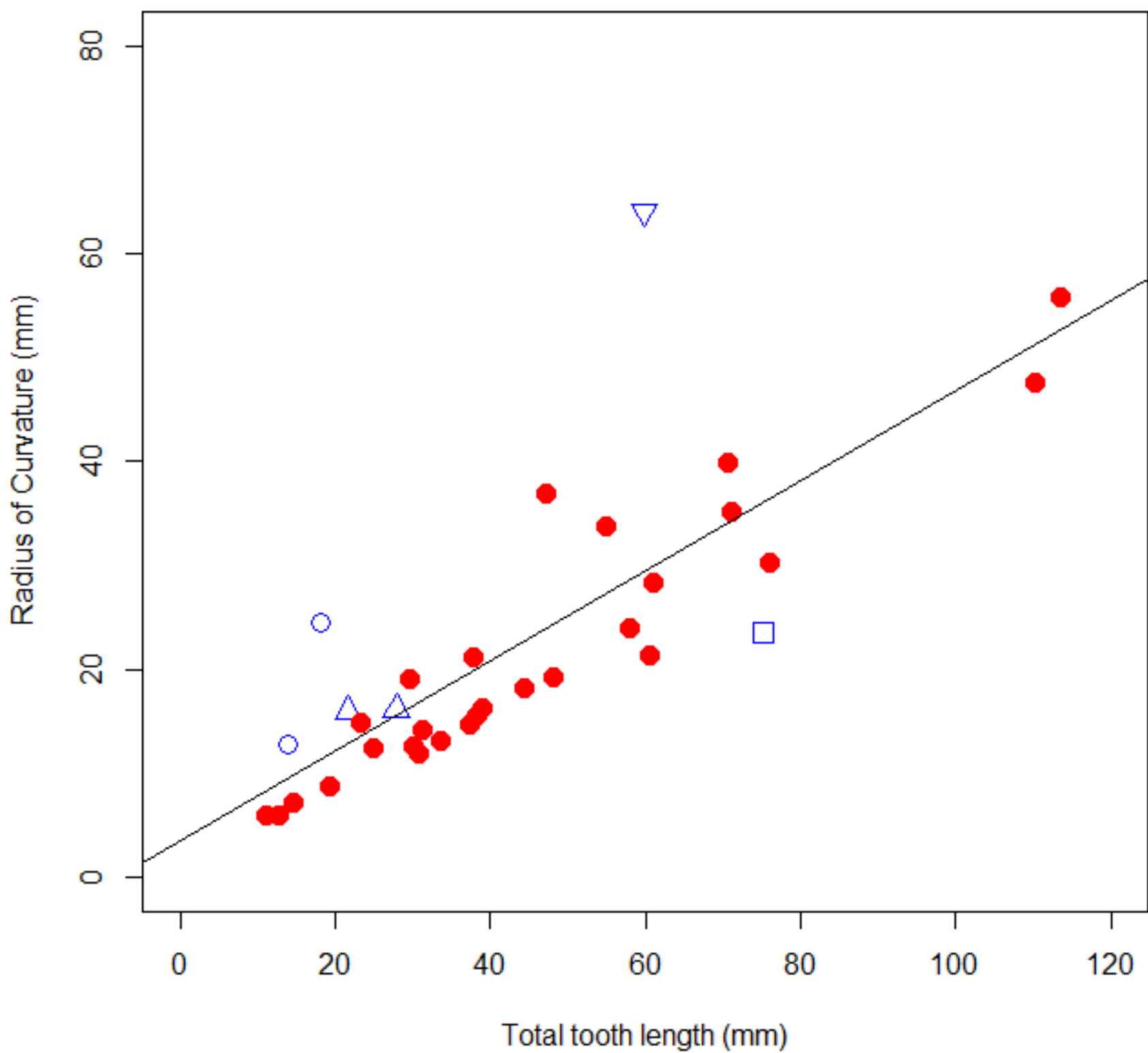
573 **Figure 6.** Scatterplot of square root of CSA against external incisor length. Red circles, rodents;
574 blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing triangles,
575 lagomorphs; open circles, hyraxes; open downward-pointing triangle, wombat.

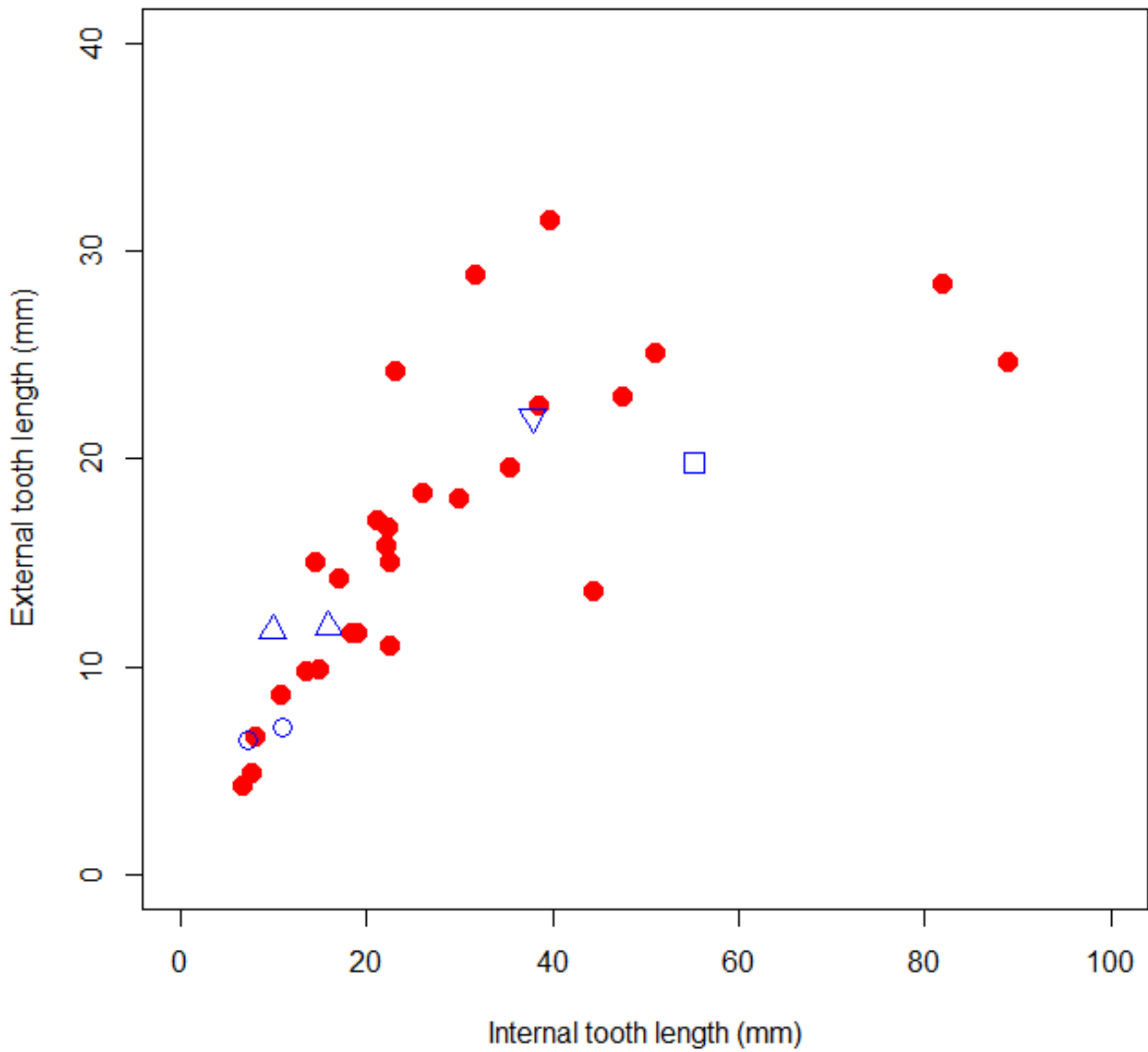
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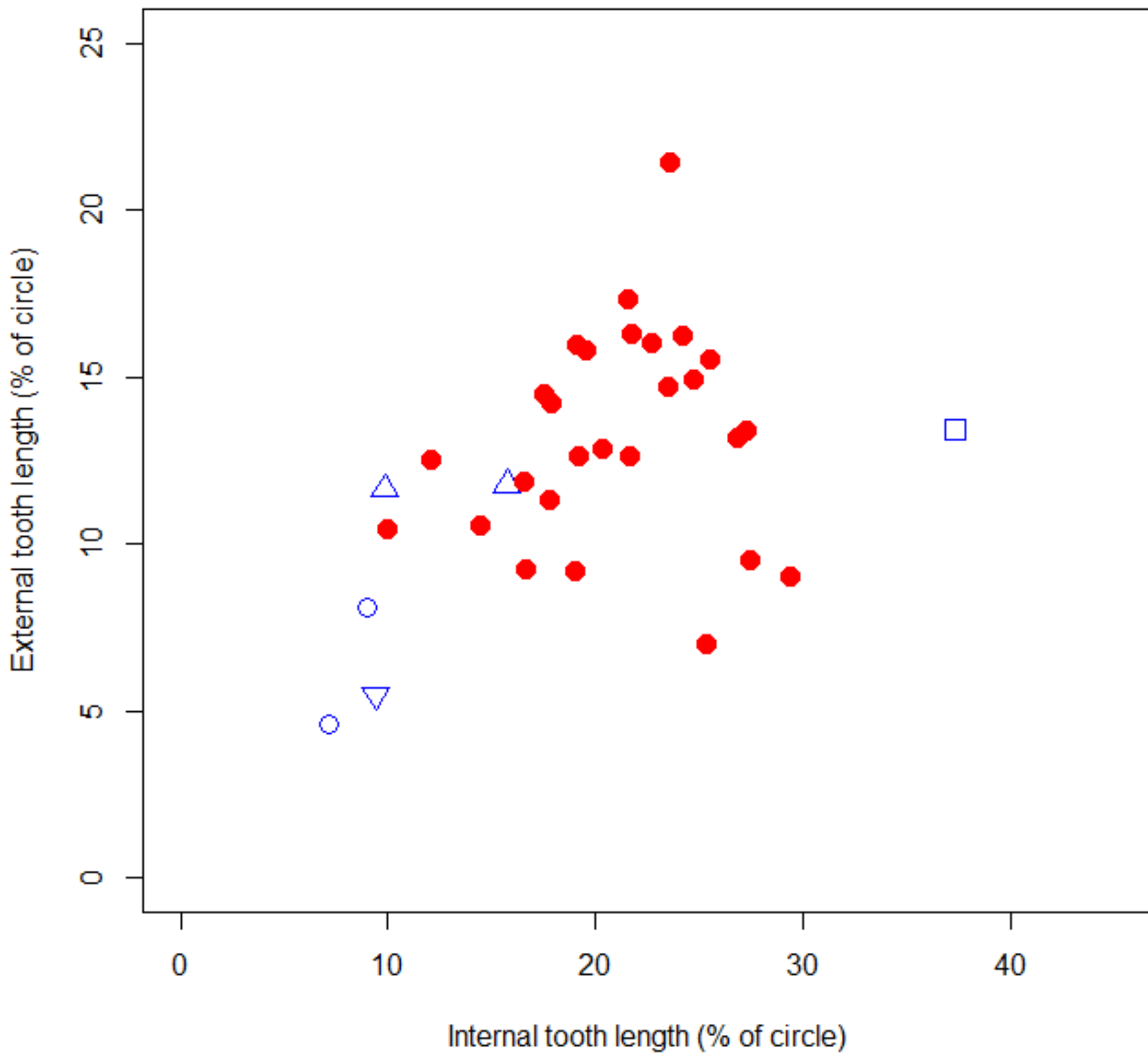
577 **Figure 7.** (a) Scatterplot of fourth root of SMA against external incisor length. Red circles,
578 rodents; blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing
579 triangles, lagomorphs; open circles, hyraxes; open downward-pointing triangle,
580 wombat. (b) CT cross-sections of the incisor close to the alveolar margin illustrating
581 the variation of cross-sectional geometry in the sample (not to scale). Left: *Hystrix*
582 *cristata*; centre: *Aplodontia rufa*; right: *Daubentonia madagascariensis*.

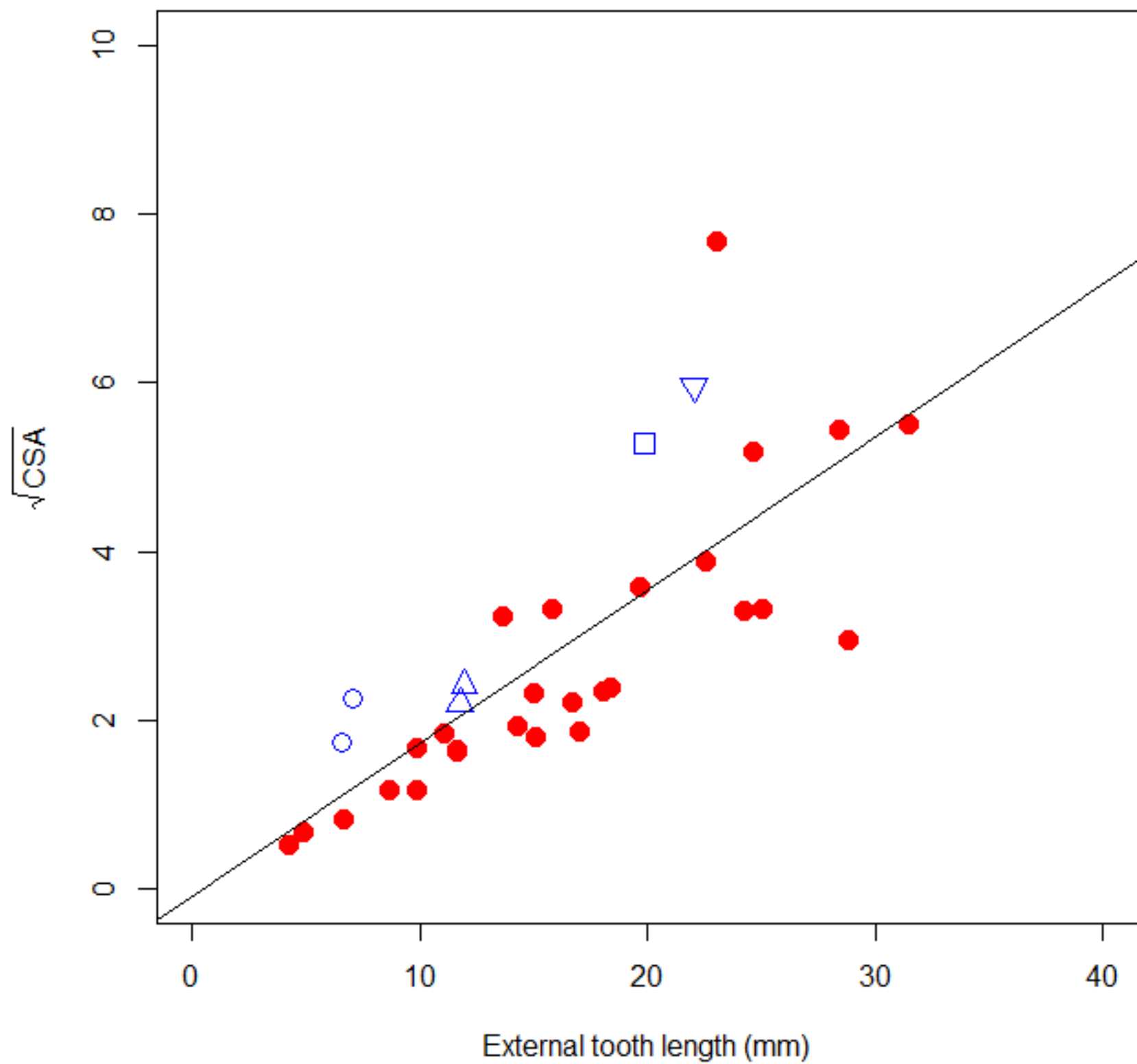
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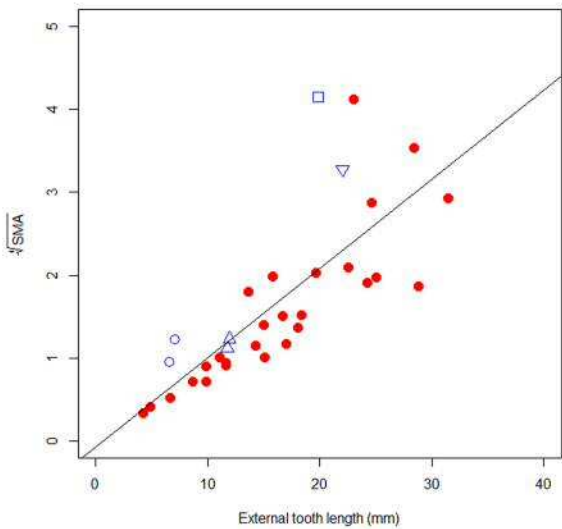




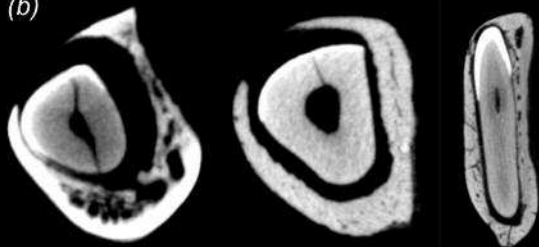


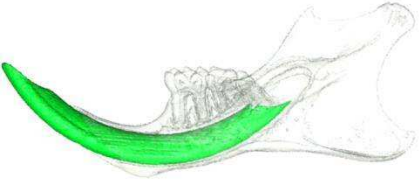
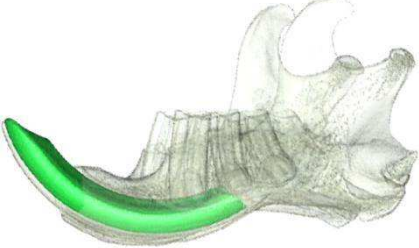
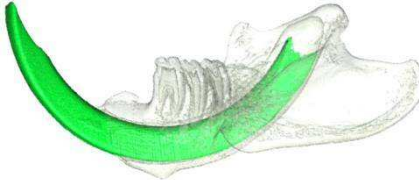
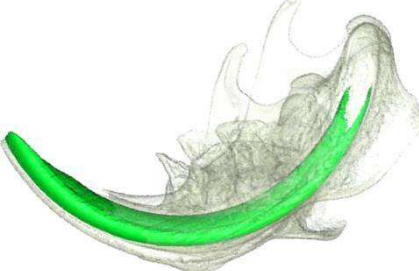
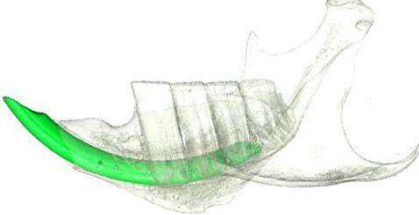
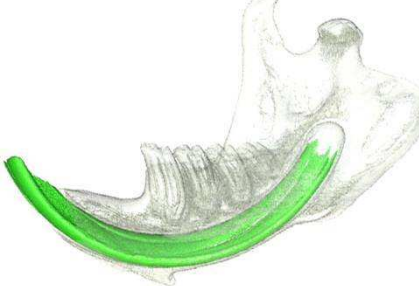


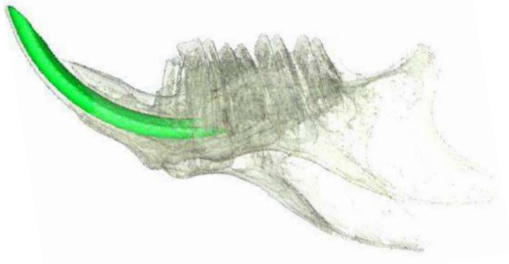
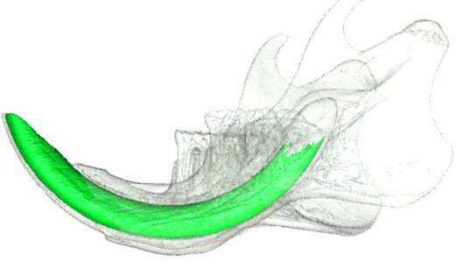
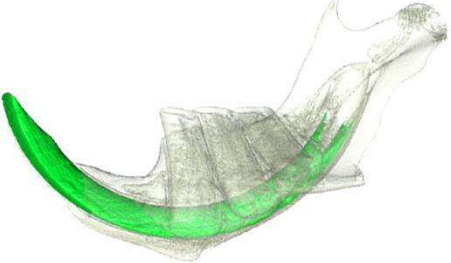
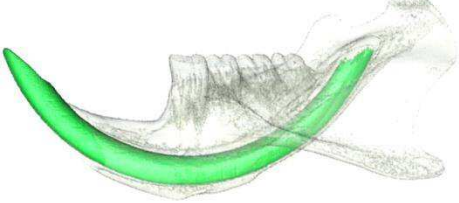
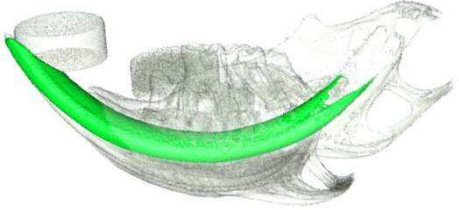
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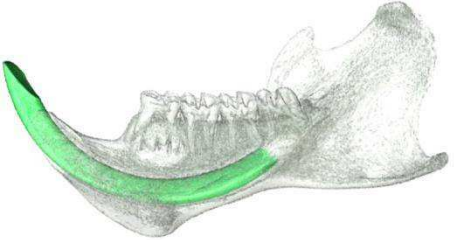
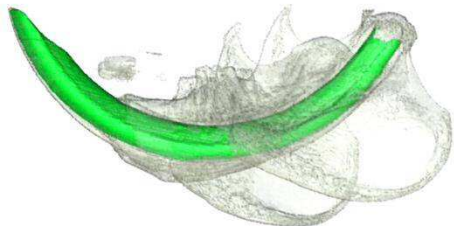
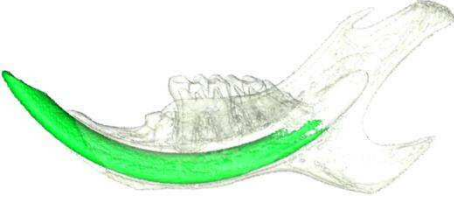
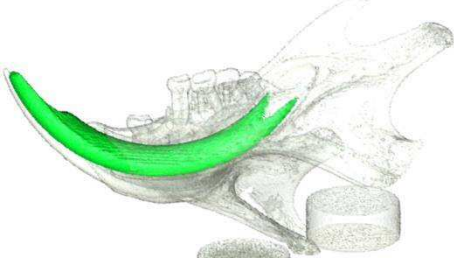
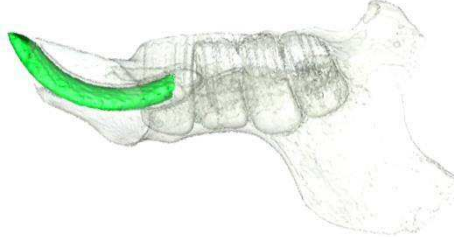
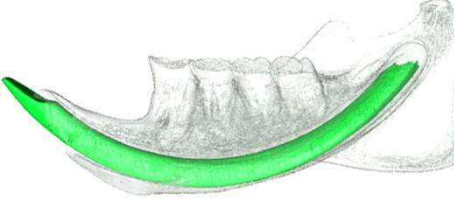


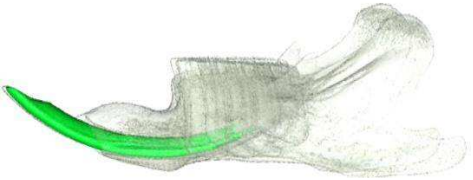
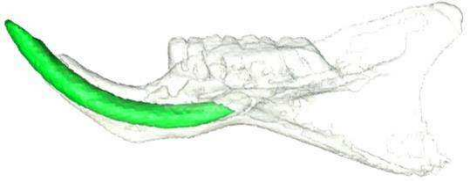
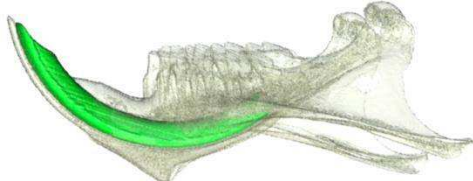
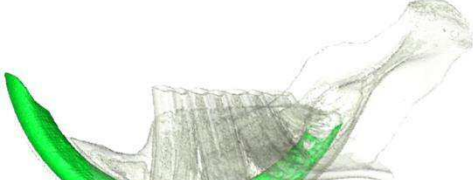
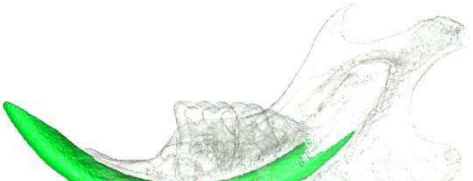

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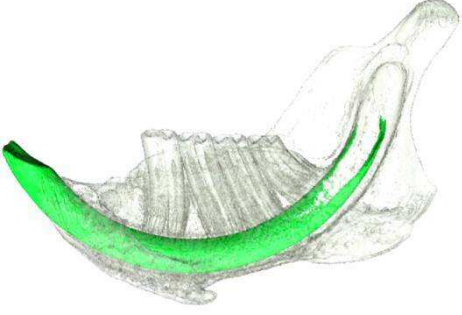
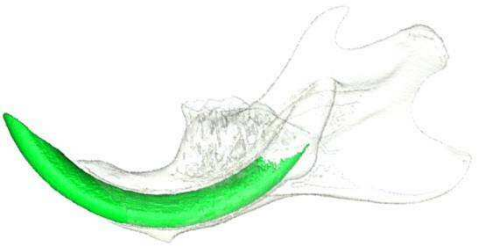
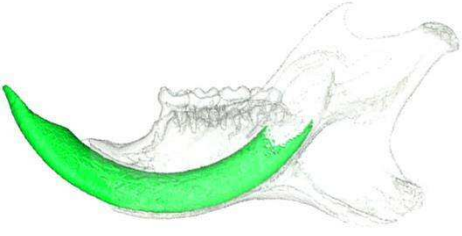
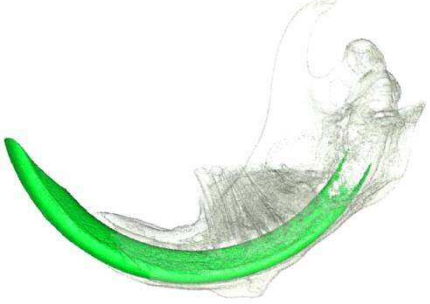


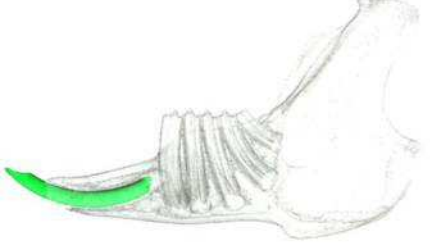
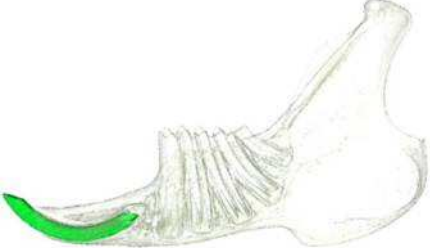
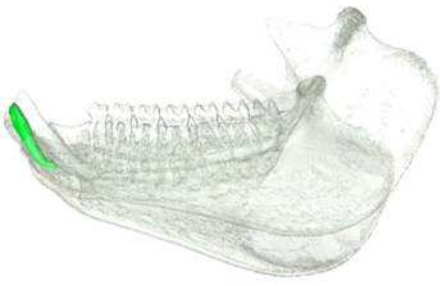
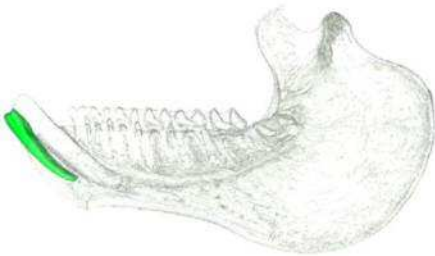
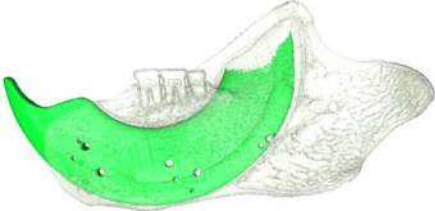
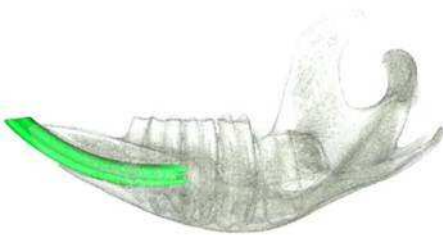
Species	Image of Mandible	Dietary Ecology
<p><i>Acomys cahirinus</i> (Northeast African spiny mouse)</p>		<p>Omnivore – Seeds, fruits, insects, food scavenged from humans, shrubs (green leaves), molluscs, carrion.</p> <p>Omnivore - (Nowak, 1999)</p>
<p><i>Aplodontia rufa</i> (mountain beaver)</p>		<p>Herbivore – forbs, grasses, ferns.</p> <p>Specialised Herbivore – (Samuels, 2009).</p>
<p><i>Bathyergus suillus</i> (Cape dune mole-rat)</p>		<p>Herbivore – grass, sedge, roots, bulbs, tubers.</p> <p>Specialised Herbivore – (Samuels, 2009).</p>
<p><i>Cannomys badius</i> (Lesser bamboo rat)</p>		<p>Herbivore – roots, bamboo, shoots, grasses. Occasional seeds and fruits.</p> <p>Specialised Herbivore – (Samuels, 2009).</p>
<p><i>Capromys pilorides</i> (Desmarest's hutia)</p>		<p>Omnivore – Bark leaves, fruits, small vertebrates, ground and tree level vegetation.</p> <p>Omnivore - (Nowak, 1999).</p>
<p><i>Castor canadensis</i> (North American Beaver)</p>		<p>Herbivore – Leaves, bark, bud and roots, cambium (softer tissue of trees beneath bark).</p> <p>Specialised Herbivore – (Samuels, 2009).</p>

<p><i>Cavia porcellus</i> (Domestic guinea pig)</p>		<p>Herbivore – Leaves, roots and tubers, fruits, flowers, lettuce etc. (rely on humans).</p> <p>Specialised Herbivore (<i>Cavia aperea</i>) - (Samuels, 2009).</p>
<p><i>Cricetomys gambianus</i> (Northern giant pouched rat)</p>		<p>Omnivore – Fruits, vegetables, nuts, insects, molluscs, roots (sweet potatoes etc.).</p> <p>Omnivore – (Nowak, 1999).</p>
<p><i>Ctenomys opimus</i> (Highland tuco-tuco)</p>		<p>Diet for this species has not been extensively documented. Assuming that it is like other tuco-tuco, it is a herbivore – Grasses and roots primarily.</p> <p>Specialised Herbivore (<i>Ctenomys conoveri</i>) - (Samuels, 2009).</p>
<p><i>Dasyprocta</i> (Agouti - species unknown)</p>		<p>Species unknown. Assuming that it is like other Agouti it is primarily a herbivore – Leaves, roots and tubers, seeds, grains and nuts, fruits, occasional crustaceans.</p> <p>Generalist herbivore – (Nowak, 1999) (fruits, vegetables, and various succulent plants)</p>
<p><i>Dipus saggitta</i> (Jerboa)</p>		<p>Assuming the specimen is <i>Dipus saggitta</i>: Herbivore – seeds, green plants. Some occasional use of insects.</p> <p>Generalist herbivore (<i>Dipus [jaculus] aegypticus</i>) – (Samuels, 2009).</p>

<p><i>Erethizon dorsatum</i> (North American porcupine)</p>		<p>Herbivore – Bark, twigs, needles, buds, acorns, grasses, stems, flowering herbs, fruit.</p> <p>Specialised herbivore – (Samuels, 2009).</p>
<p><i>Georychus capensis</i> (Cape mole-rat)</p>		<p>Herbivore – Green plant material and geophyte corms.</p> <p>Specialised herbivore - (Samuels, 2009).</p>
<p><i>Gerbillus watersi</i> (Waters gerbil)</p>		<p>Diet not well documented – if like other gerbillines it tends to be herbivorous or omnivorous – eggs, insects, nuts, seeds, grasses, bulbs.</p> <p>Omnivore (<i>Gerbillus paeba</i>) - (Samuels, 2009)</p>
<p><i>Graphiurus nagtglasii</i> (Nagtglas’s African dormouse)</p>		<p>Diet for this species has not been extensively documented. Assuming that it is like other members of <i>Graphiurus</i> it is an omnivore – grains, fruits, eggs, insects, nuts, small vertebrates.</p> <p>Omnivore - (Nowak, 1999).</p>
<p><i>Hydrochoerus hydrochaeris</i> (Capybara)</p>		<p>Herbivore – primarily grasses and aquatic plants. Occasionally eats bark and fruits. Coprophagy.</p> <p>Specialised Herbivore - (Samuels, 2009).</p>
<p><i>Hystrix cristata</i> (Crested porcupine)</p>		<p>Herbivore – Bark, roots, tubers, rhizomes, bulbs, fruits, crops. Occasional insectivory and carnivory (small vertebrates and carrion – with some bone gnawing to sharpen incisors).</p> <p>Generalist herbivore – (Nowak, 1999) (occasional insectivory).</p>

<p><i>Lagostomus maximus</i> (Argentine plains viscacha)</p>		<p>Herbivore – Seeds and grass. Will consume almost any vegetation when in captivity, however.</p> <p>Generalist herbivore - (Nowak, 1999).</p>
<p><i>Laonastes aenigmamus</i> (Laotian rock rat)</p>		<p>Herbivore – Leaves and fruits of tropical dicotyledonts (maybe also grasses according to its stomach shape).</p> <p>Specialist herbivore – (Scopin, 2011) (primarily leaves).</p>
<p><i>Myocastor coypus</i> (Coypu)</p>		<p>Herbivore – Primarily aquatic vegetation: stems, leaves, roots, bark.</p> <p>Specialised Herbivore – (Samuels, 2009).</p>
<p><i>Octodon degus</i> (Degu)</p>		<p>Herbivore – Grass, bark, leaves and seeds</p> <p>Specialist herbivore – (Nowak, 1999).</p>
<p><i>Paralomys gerbillus</i> (Gerbilline pericote)</p>		<p>Diet for this species has not been extensively documented.</p>
<p><i>Petaurista</i> (species unknown)</p>		<p>Generalist herbivore – (Nowak, 1999) (young leaves, tender shoots, fruits, nuts, flower buds).</p>

<p><i>Pedetes capensis</i> (African springhare)</p>		<p>Herbivore/omnivore – barley, oats, wheat, with some occasional insectivory.</p> <p>Generalist Herbivore – (Samuels, 2009).</p>
<p><i>Rattus norvegicus</i> (Brown rat)</p>		<p>Omnivore – Birds, mammals and other vertebrates, insects and invertebrates, leaves, roots and tubers, fruit, grain, flowers, wood/bark, fungus, detritus.</p> <p>Omnivore – (Samuels, 2009).</p>
<p><i>Sciurus carolinensis</i> (Grey squirrel)</p>		<p>Omnivore – Birds, mammals, amphibians, eggs, carrion, insects, leaves, seeds, grains, nuts, fruit, fungus, bulbs and flowers, occasional cannibalism.</p> <p>Omnivore (<i>Sciurus aberti</i>) - (Samuels, 2009)</p>
<p><i>Thomomys umbrinus</i> (Southern pocket gopher)</p>		<p>Diet for this species has not been extensively documented. If like other members of <i>Thomomys</i> they are generalist herbivores – leaves, roots, tubers, seeds, grains, fruit, grasses.</p> <p>Specialised Herbivore (<i>Thomomys talipoides</i>) - (Samuels, 2009)</p>

Species	Image of Mandible	Dietary Ecology
<p><i>Oryctolagus cuniculus</i> (European rabbit)</p>		<p>Herbivore – Grasses, leaves, buds, bark, roots. In captivity they are noted to eat lettuce cabbage, root vegetables, and grain.</p> <p>Specialised herbivore – (Nowak, 1999; Matrai <i>et al.</i>, 1998).</p>
<p><i>Lepus europaeus</i> (European hare)</p>		<p>Herbivore – Grasses, herbs, field crops, twigs, buds, bark, coprophagia.</p> <p>Specialised herbivore – (Nowak, 1999).</p>
<p><i>Dendrohyrax arboreus</i> (Tree hyrax)</p>		<p>Herbivore – Leaves, twigs, shoots, fleshy fruit, hard seeds.</p> <p>Specialised herbivore - (Nowak, 1999).</p>
<p><i>Procapra capensis</i> (Rock hyrax)</p>		<p>Herbivore – Lots of regional and seasonal vegetation, leaves, wood, bark and stems, fruit, berries, shoots, buds, leaves, bryophytes.</p> <p>Specialised herbivore - (Nowak, 1999).</p>
<p><i>Daubentonia madagascariensis</i> (Aye-aye)</p>		<p>Omnivore – Seeds, nectar, fungus, and insect larvae. Access larvae through gnawing into woods to access xylophagous wood boring insects.</p> <p>Omnivore - (Nowak, 1999).</p>
<p><i>Vombatus ursinus</i> (Common Wombat)</p>		<p>Herbivore – grass, roots and fungi. Prefers fresh seed stems (Nowak, 1999).</p> <p>Specialised herbivore – (Nowak, 1999).</p>

Order	Subgroup	Species	Institution	Specimen number	Voxel dimensions (mm)	Morphosource specimen number
Rodentia	Ctenohystrica	<i>Bathyergus suillus</i>	NML	19.8.75.14	0.0400	M23775
Rodentia	Ctenohystrica	<i>Capromys pilorides</i>	UMZC	E.3371	0.0642	M24093
Rodentia	Ctenohystrica	<i>Cavia porcellus</i>	DMBL	HACB-CP3	0.0671	M23915
Rodentia	Ctenohystrica	<i>Ctenomys opimus</i>	UMZC	E.3261	0.0318	M24071
Rodentia	Ctenohystrica	<i>Dasyprocta punctata</i>	UMZC	E.3621	0.0585	M24091
Rodentia	Ctenohystrica	<i>Erethizon dorsatum</i>	UMZC	E.3506	0.0577	M24132
Rodentia	Ctenohystrica	<i>Georychus capensis</i>	NML	D.300	0.0194	M23721
Rodentia	Ctenohystrica	<i>Hydrochoerus hydrochaeris</i>	UMZC	E.3768	0.4219	M24037
Rodentia	Ctenohystrica	<i>Hystrix cristata</i>	UMZC	E.3406	0.0791	M24114
Rodentia	Ctenohystrica	<i>Lagostomus maximus</i>	UMZC	E.3555	0.0685	M24127
Rodentia	Ctenohystrica	<i>Laonastes aenigmamus</i>	AH	KY213	0.1369	M23942
Rodentia	Ctenohystrica	<i>Myocastor coypus</i>	UMZC	E.3370	0.0764	M24086
Rodentia	Ctenohystrica	<i>Octodon degus</i>	UMZC	E.3288	0.0316	M24074
Rodentia	Mouse-related clade	<i>Acomys cahirinus</i>	UMZC	E.2278	0.0282	M24046
Rodentia	Mouse-related clade	<i>Cannomys badius</i>	UMZC	E.2850	0.0371	M24070
Rodentia	Mouse-related clade	<i>Castor canadensis</i>	UMZC	E.1831	0.0747	M24082
Rodentia	Mouse-related clade	<i>Cricetomys gambianus</i>	UMZC	E.2262	0.0481	M24065
Rodentia	Mouse-related clade	<i>Dipus sagitta</i>	UMZC	E.3165	0.0342	M24073
Rodentia	Mouse-related clade	<i>Gerbillus watersi</i>	UMZC	E.1971	0.0192	M24052
Rodentia	Mouse-related clade	<i>Pedetes capensis</i>	UMZC	E.1446	0.0406	M24076
Rodentia	Mouse-related clade	<i>Phyllotis gerbillus</i>	UMZC	E.2597	0.0282	M24038
Rodentia	Mouse-related clade	<i>Rattus norvegicus</i>	DMBL	HACB-RN4	0.0539	M23930
Rodentia	Mouse-related clade	<i>Thomomys umbrinus</i>	NML	19.8.98.8	0.0341	M23927
						Permission not granted by
Rodentia	Squirrel-related clade	<i>Aplodontia rufa</i>	MNHN	1354	0.0421	museum
Rodentia	Squirrel-related clade	<i>Graphiurus nagtglasii</i>	UMZC	E.1909	0.0340	M24078
Rodentia	Squirrel-related clade	<i>Petaurista petaurista</i>	UMZC	E.1475	0.0367	M24035
Rodentia	Squirrel-related clade	<i>Sciurus carolinensis</i>	DMBL	HACB-SC11	0.0657	M23931
Lagomorpha	Leporidae	<i>Lepus europaeus</i>	DMEH	DMEH-LE1	0.0539	M23932
Lagomorpha	Leporidae	<i>Oryctolagus cuniculus</i>	YZL	YZL017	0.0467	M23910
Primates	Strepsirrhini	<i>Daubentonia madagascariensis</i>	UMZC	E.8201A	0.0518	M24080

Hyracoidea	Procaviidae	<i>Dendrohyrax arboreus</i>	UMZC	H.5281.B	0.0554	M24147
Hyracoidea	Procaviidae	<i>Procavia capensis</i>	UMZC	H.5061.B	0.0596	M24154
Diprotodontia	Vombatiformes	<i>Vombatus ursinus</i>	UMZC	A10.10/3	0.0960	M24207

Abbreviations

AH	Anthony Herrel, Museum National d'Histoire Naturelle, Paris, France
DMBL	Department of Musculoskeletal Biology, University of Liverpool, UK
DMEH	Department of Medical Engineering, University of Hull, UK
MNHN	Museum National d'Histoire Naturelle, Paris, France
NML	National Museums Liverpool, UK
UMZC	University Museum of Zoology Cambridge, UK
YZL	York Zooarchaeology Laboratory, University of York, UK