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TITLE: Mechanical significance of morphological variation in diprotodont incisors

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ABSTRACT

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

KEYWORDS

Incisor; mechanics; morphology; diprotodont; rodents

INTRODUCTION

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

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

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

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

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

1. *All lower incisors have the same two-dimensional shape in lateral view.* That is, assuming the curvature of the incisor to be constant along its length and therefore part of a circle (the helix is simplified as a circle for this study), it is expected that all incisors will form the same proportion of a circle (will subtend the same angle). This prediction is based on previous research showing that the upper incisors of rodents were very similar in shape across a wide range of species, all being approximately semicircular [10].
2. *There is no correlation between the length of incisor within the mandible and the length of the part of the incisor not covered by mandibular bone*. This study assumes the external part of the incisor to act as a cantilever beam that is fixed at the level of the alveolar margin. Under this model, the length of incisor within the bone has no effect on the bending mechanics of the external part of the incisor, and thus the two sections of the incisor will vary independently.
3. *There is significant correlation between the length of the external part of the incisor and its cross-sectional shape, in particular CSA and SMA*. Both of these measures give

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

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

MATERIALS AND METHODS

Sample

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

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

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

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

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

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

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

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

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

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

RESULTS

Incisor shape

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

External and internal incisor length

The plot of *ETL* against *ITL* (figure 4) indicates a relationship between these two measurements, but one that is potentially curvilinear rather than linear. At small sizes, *ETL* increases as *ITL* increases with a slope of 0.67. However, above an internal length of around 25 mm, the rate of increase of the external length slows dramatically, to a slope of 0.12, and scatter about the trend line increases substantially. Three rodent taxa (coypu, plains viscacha and Cape dune mole-rat) clearly plot above the curve and thus have longer incisors externally than would be predicted from the internal length of their tooth, whereas a rodent and a non-rodent taxa (springhare and aye-aye) are found below the curve, therefore displaying shorter incisors externally than expected. After phylogenetic correction, the log-log relationship between these two variables is highly significant ($F = 60.27$, $P < 0.001$). *ITL* and *ETL* were converted to fractions of a circle (by dividing by total circumference) and plotted against one another (figure 5). A PGLS model indicated that the relationship between these two variables was not significant ($F = 2.14$, $P = 0.15$). Hypothesis 2, that there is no correlation between the length of incisor within the mandible and the length of the part of the incisor not covered by mandibular bone, is therefore supported (with the caveat that there are some outliers among the rodent taxa).

Cross-sectional geometry

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

DISCUSSION

It can be seen from the results here that, on the whole, the lower incisors of diprotodont mammals vary in a predictable manner. There is a close correlation between the length of the incisor and its radius of curvature, between the length of the portion of the incisor within the mandible and the length of the exposed section, and between the cross-sectional morphology and the external length of the incisor.

Incisor shape

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

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

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

External and internal incisor length

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

It should be noted, however, that the relationship between *ITL* and *ETL* appears to be driven by overall changes in size. As the mandible gets larger, the entire incisor will also increase in size, and thus the correlation between the lengths of the two parts of the incisor may simply reflect this. To account for the confounding factor of size, the *ITL* and *ETL* were converted to fractions of a circle by dividing them by total circumference. Under a PGLS model, it was found that the size-corrected *ITL* and *ETL* were not significantly correlated (figure 5), as predicted by the second hypothesis. It appears that the length of the external portion of the incisor can vary independently of the length of the internal section, and likely has done in response to the external forces experienced by the tooth. For instance, it can be seen that the taxa positioned below the curve in figure 4 tend to be those that engage their incisors in mechanically demanding activities such as gnawing roots and stems (*Pedetes* [36]), wood (*Castor* [8]; *Daubentonia* [7]), or bones (*Hystrix* [37]). These species likely have relatively shorter incisors externally, compared to other rodents, in order to resist the greater bending forces incurred during these activities. This also means that the perceived plateau of *ETL* noted above may be somewhat artefactual and driven by the unusually short external incisors of the beaver and porcupine.

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

Cross-sectional geometry

As predicted by the third hypothesis, there is a significant positive correlation between both measures of cross-sectional morphology (*CSA* and *SMA*) and *ETL*. This fits with the biomechanical model of the lower incisor as a curved beam – as the beam gets longer, the bending moment will increase, and this can be resisted by increasing the amount of material in cross-section at the point of bending (the alveolar margin). In particular, the amount of material in the axis of loading (i.e. *SMA*) increases as the external length of the tooth increases. Such a relationship suggests that *ETL* can be estimated from cross-sectional geometry, which could be of particular use for the reconstruction of morphology in extinct rodents. The skulls and mandibles of fossil rodents often have broken or missing incisors (e.g. [38-40]) and it can be important to know their complete length for biomechanical analyses (e.g. [41]). The relationships shown here will enable such length estimations to be made. It should be recalled that the incisor is a composite structure (primarily dentine with a thin layer of enamel and cementum on the labial and lingual surfaces respectively) which has simplified for the purposes of this study as being composed of a single tissue. Additional work would therefore be required to determine if, in addition to facilitating the functional wear of the occlusal (biting) surface of the incisors, the enamel plays a the mechanical role in stiffening the incisors.

Non-rodent diprotodonts

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

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

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

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

CONCLUSIONS

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

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

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

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

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

COMPETING INTERESTS We have no competing interests.

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TABLES

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

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

Octodon degus	41.07
Bathyergus suillus	45.04
Daubentonia madagascariensis	**50.75**

Table 2. Summary statistics for percentage of a circle encompassed by the incisors of rodents. Upper incisor data derived from McIntosh & Cox (2016) [10].

	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

FIGURE LEGENDS

Figure 1. (a) Reconstruction of beaver lower mandible and incisor in lateral view showing landmarks and length measurements used to calculate incisor variables. Landmarks: red, incisor tip; orange, midpoint on labial incisor surface at alveolar margin; yellow, distalmost extremity of incisor. (b) Lateral view of reconstructions of the lower incisors of: *Daubentonia madagascariensis* (upper); *Rattus norvegicus* (middle); *Sciurus carolinensis* (lower), with cross sections taken at the alveolar margin and at halfway along the internal incisor length (not to scale).

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

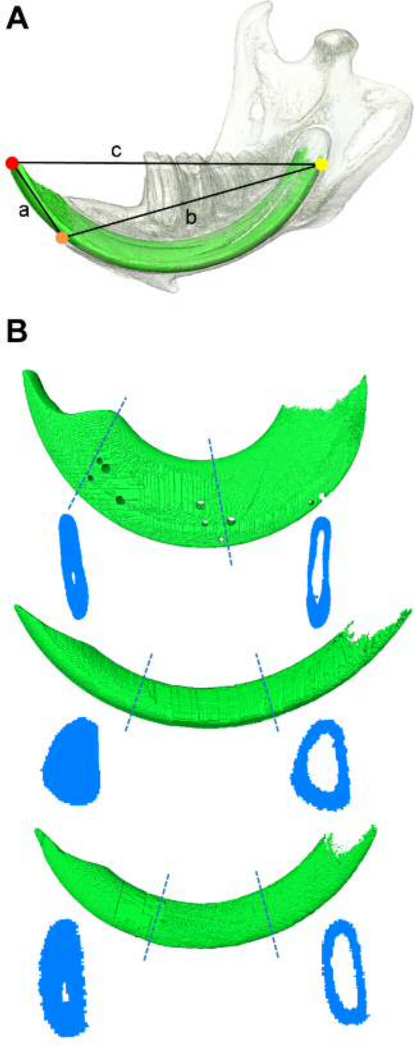
Figure 3. Scatterplot of radius of curvature against total incisor length. Red circles, rodents; blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing triangles, lagomorphs; open circles, hyraxes; open downward-pointing triangle, wombat.

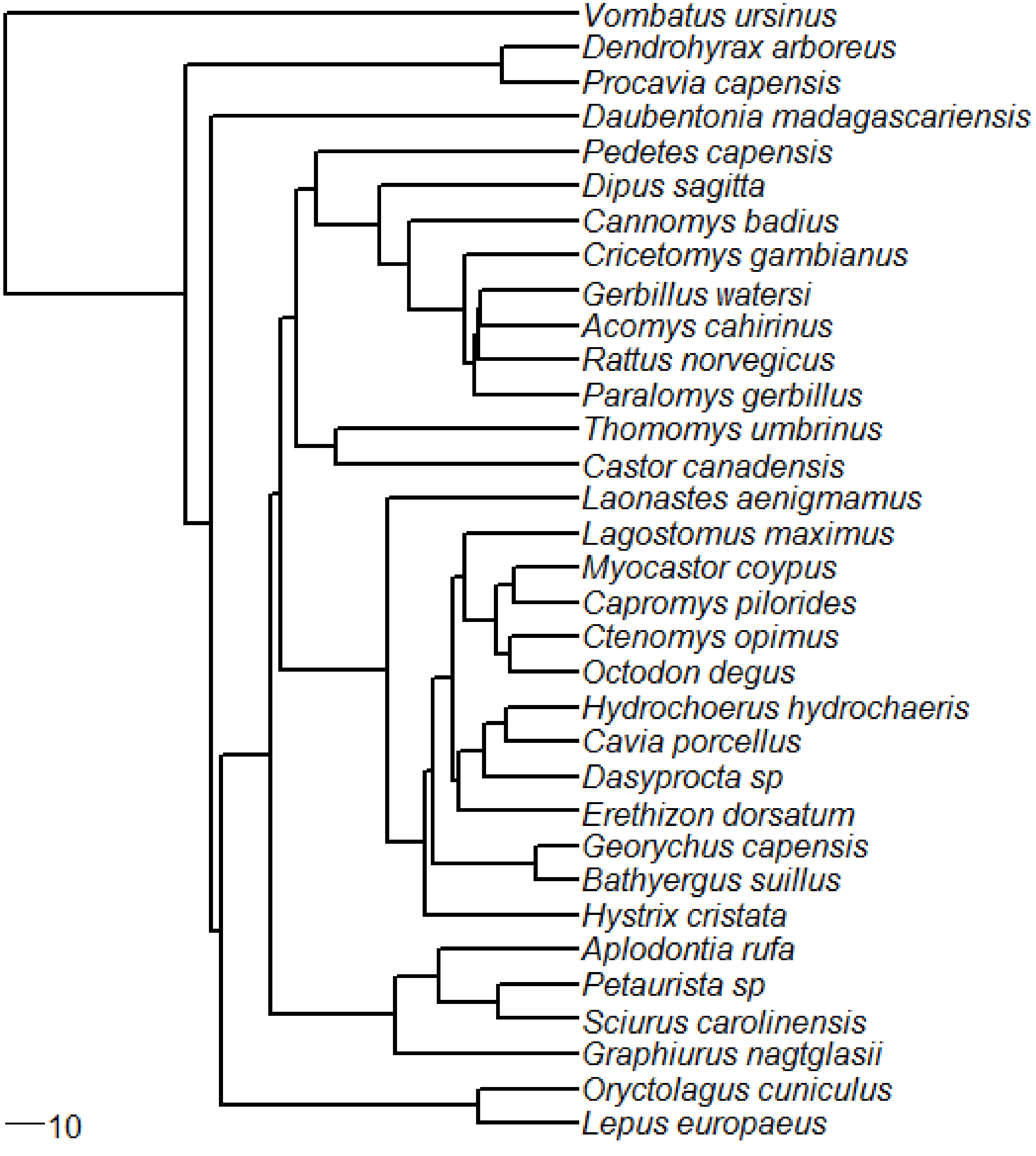
Figure 4. Scatterplot of external incisor length against internal incisor length. Red circles, rodents; blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing triangles, lagomorphs; open circles, hyraxes; open downward-pointing triangle, wombat.

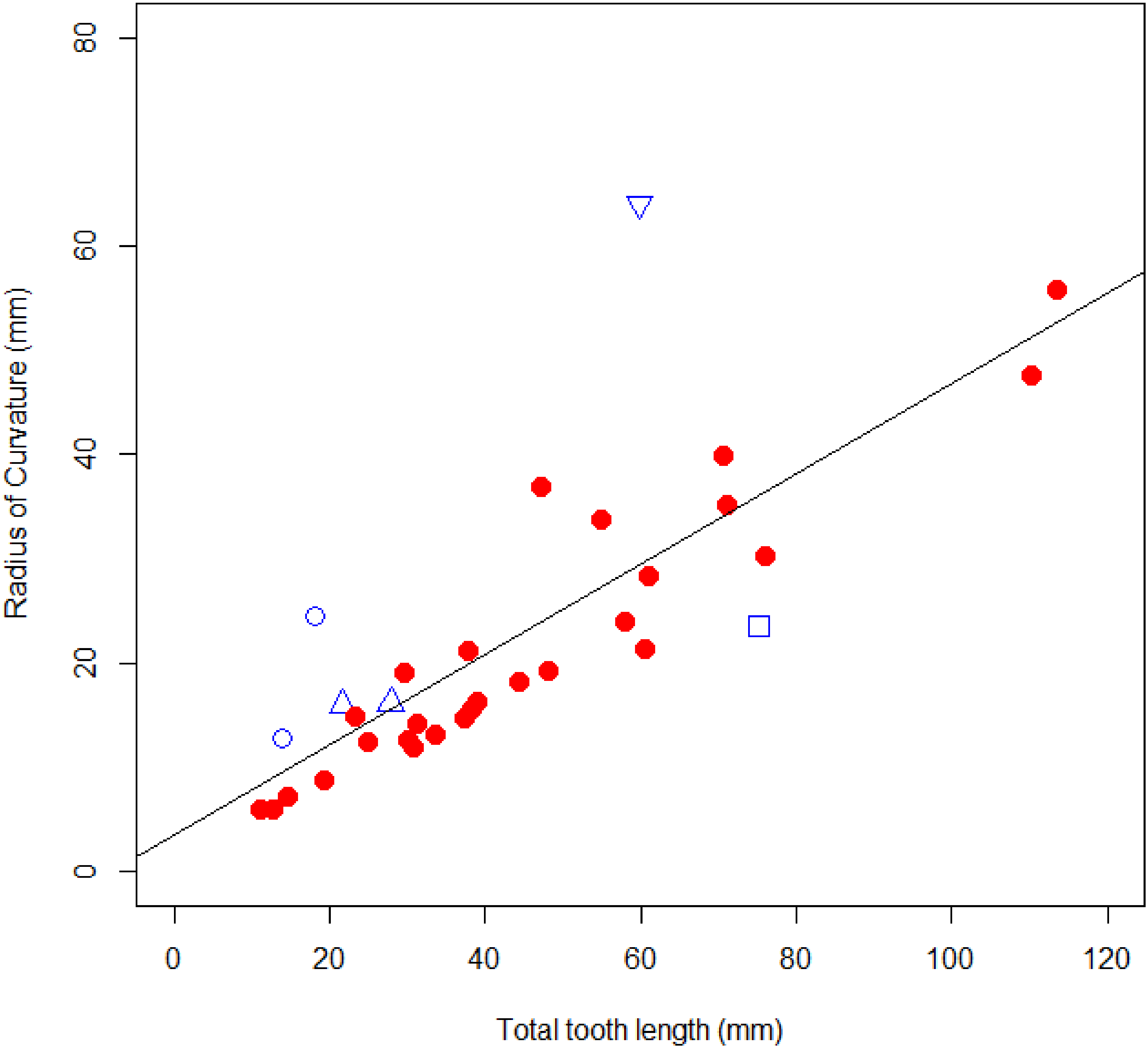
Figure 5. Scatterplot of external and internal incisor lengths expressed as fractions of a circle. Red circles, rodents; blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing triangles, lagomorphs; open circles, hyraxes; open downward-pointing triangle, wombat.

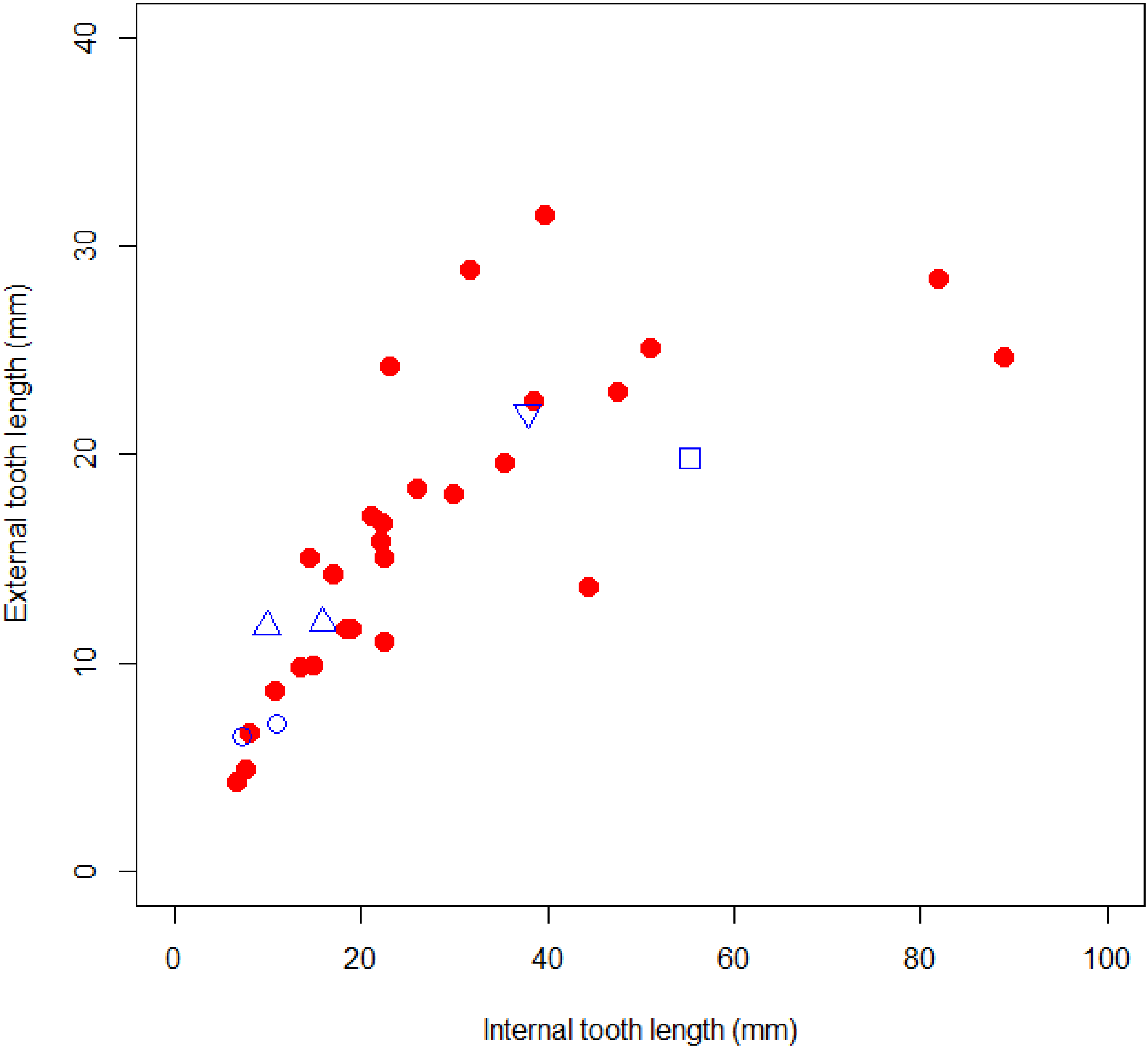
Figure 6. Scatterplot of square root of CSA against external incisor length. Red circles, rodents; blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing triangles, lagomorphs; open circles, hyraxes; open downward-pointing triangle, wombat.

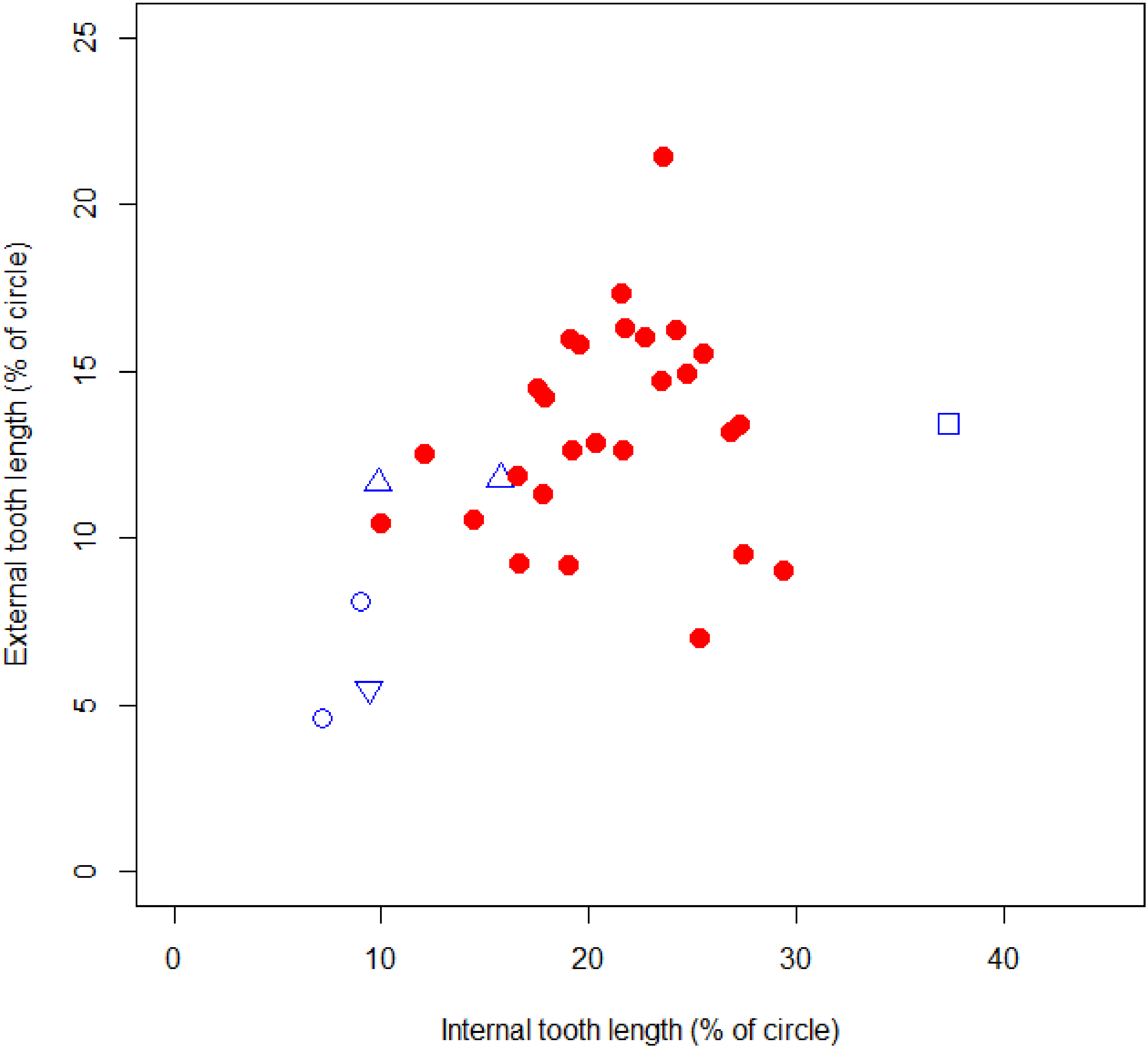
Figure 7. (a) Scatterplot of fourth root of SMA against external incisor length. Red circles, rodents; blue symbols, non-rodent taxa; open square, aye-aye; open upward-pointing triangles, lagomorphs; open circles, hyraxes; open downward-pointing triangle, wombat. (b) CT cross-sections of the incisor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

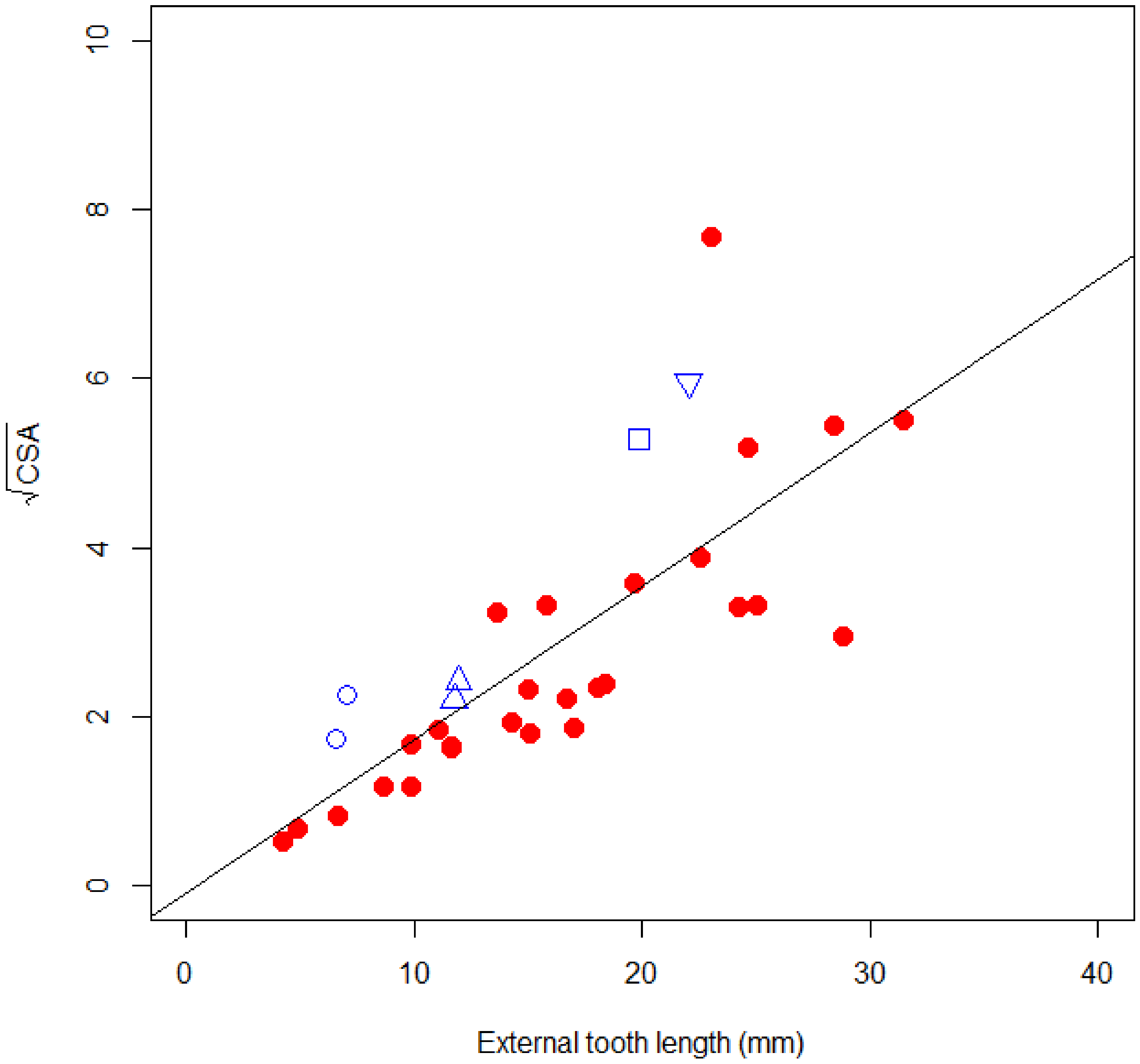

A
c
a
b
B


Vombatus ursinus
Dendrohyrax arboreus
Procavia capensis
Daubentonia madagascariensis
Pedetes capensis
Dipus sagitta
Cannomys badius
Cricetomys gambianus
Gerbillus watersi
Acomys cahirinus
Rattus norvegicus
Paralomys gerbillus
Thomomys umbrinus
Castor canadensis
Laonastes aenigmamus
Lagostomus maximus
Myocastor coypus
Capromys pilorides
Ctenomys opimus
Octodon degus
Hydrochoerus hydrochaeris
Cavia porcellus
Dasyprocta sp
Erethizon dorsatum
Georychus capensis
Bathyergus suillus
Hystrix cristata
Aplodontia rufa
Petaurista sp
Sciurus carolinensis
Graphiurus nagtglasii
Oryctolagus cuniculus
Lepus europaeus
10

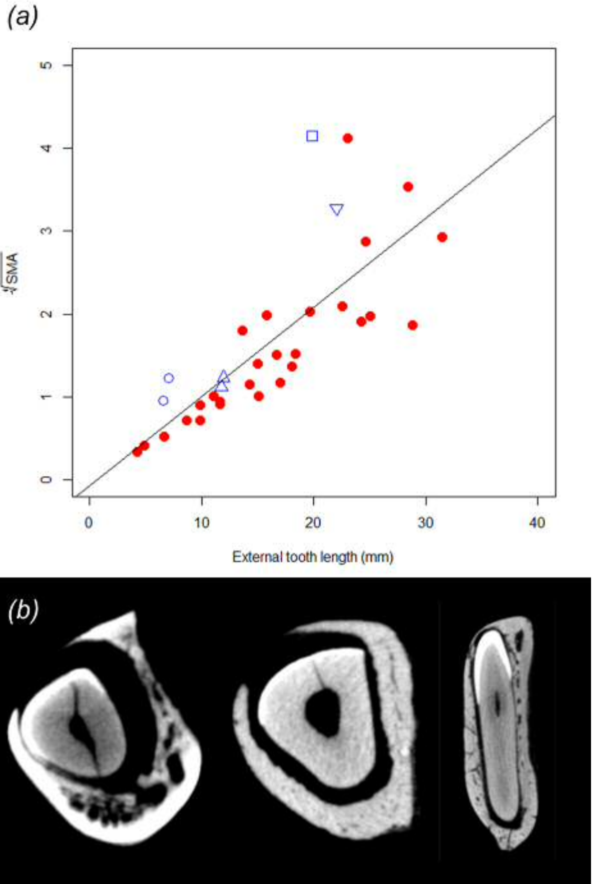

Radius of Curvature (mm)
0
20
40
60
80
Total tooth length (mm)
0
20
40
60
80
100
120

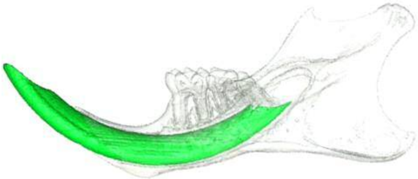
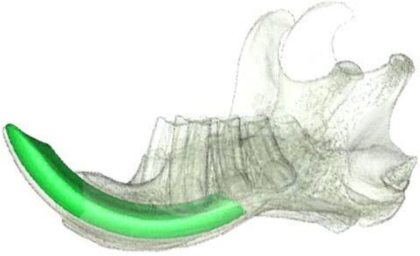
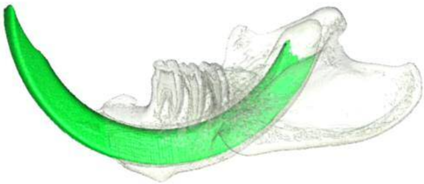
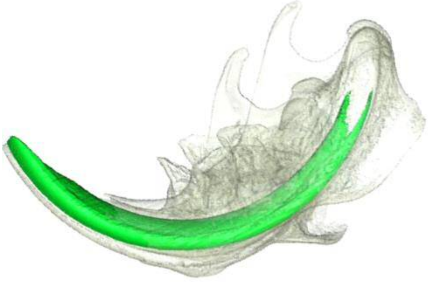
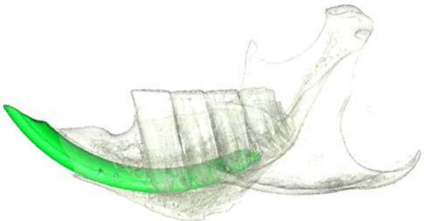
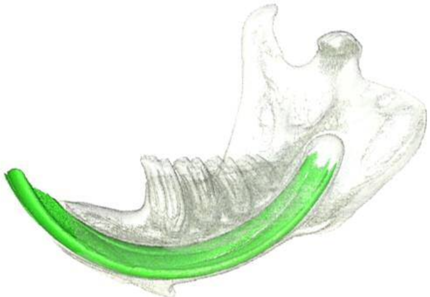

External tooth length (mm)
0
10
20
30
40
Internal tooth length (mm)
0
20
40
60
80
100

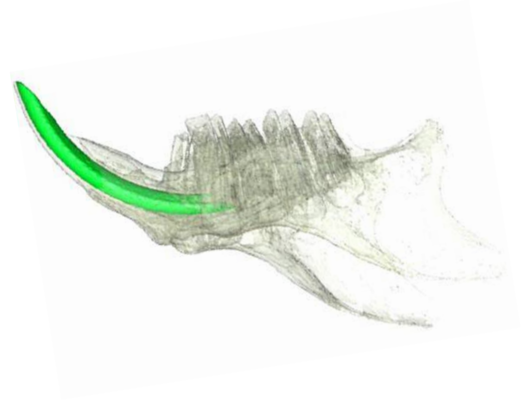
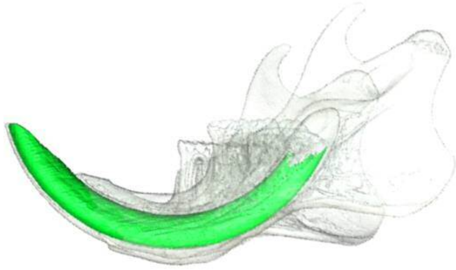
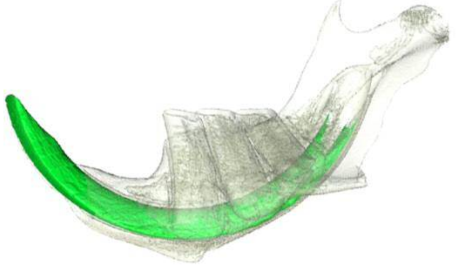
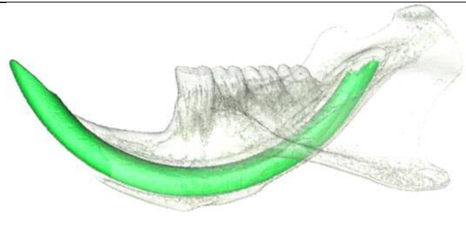
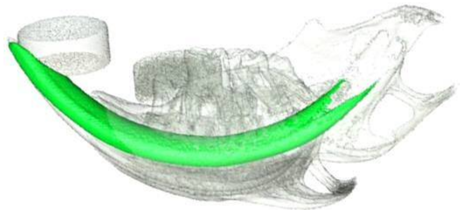

External tooth length (% of circle)
0
5
10
15
20
25
0
10
20
30
40
Internal tooth length (% of circle)

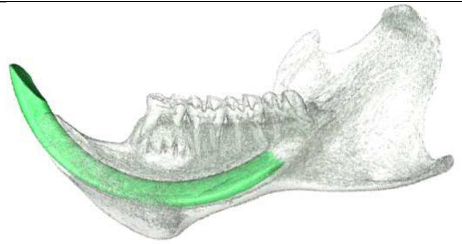
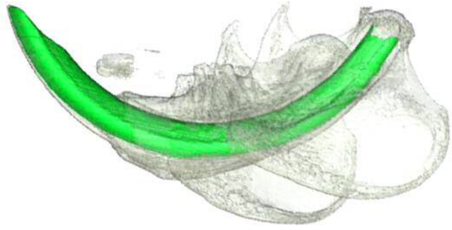
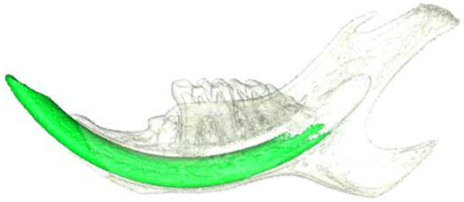
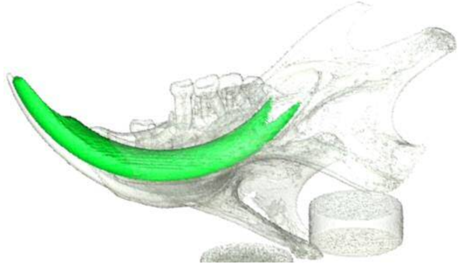
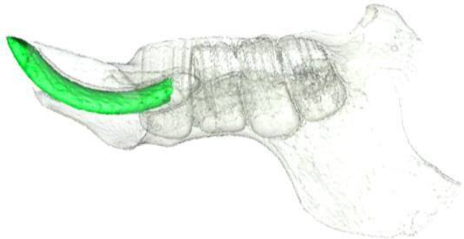
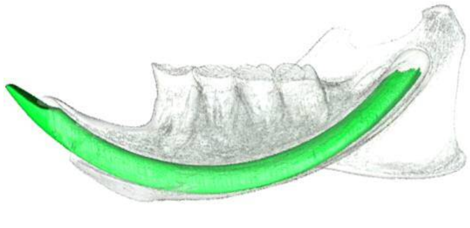


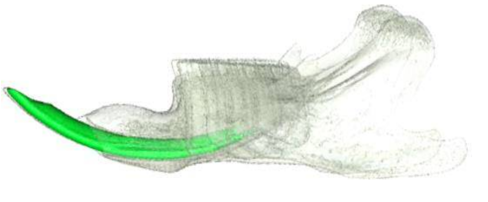
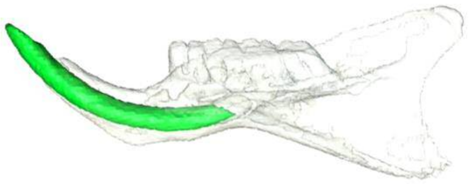
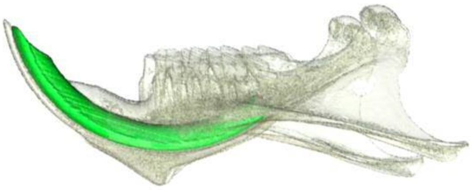
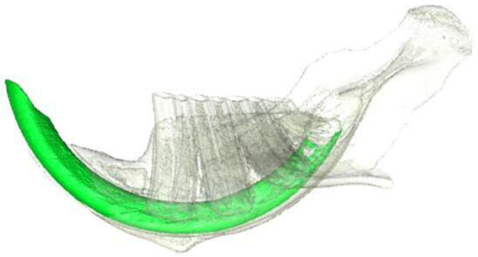
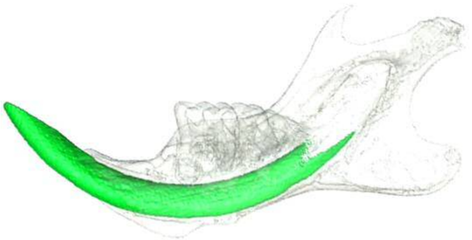
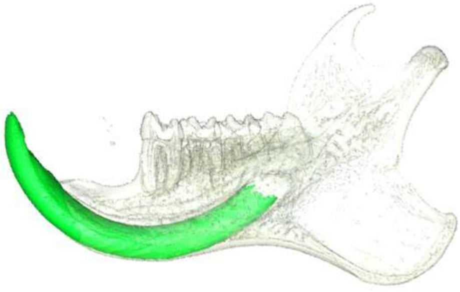
0
2
4
6
8
10
√CSA
0
10
20
30
40
External tooth length (mm)

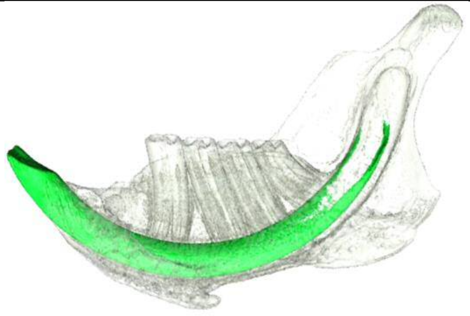
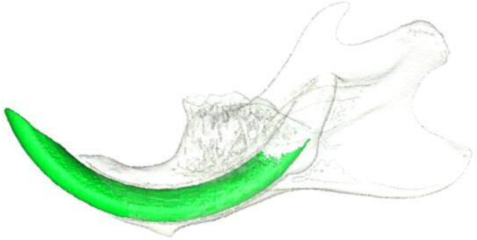
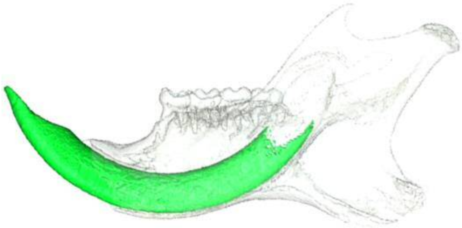
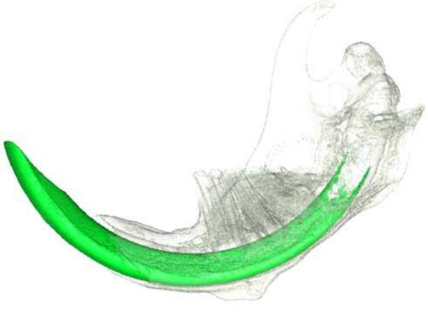

(a)
∜SMA
0
1
2
3
4
5
0
10
20
30
40
External tooth length (mm)
(b)

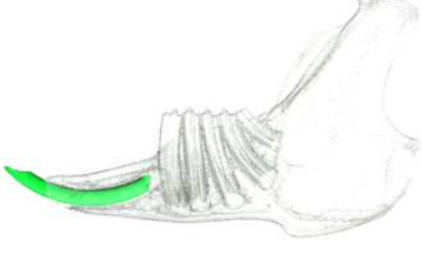
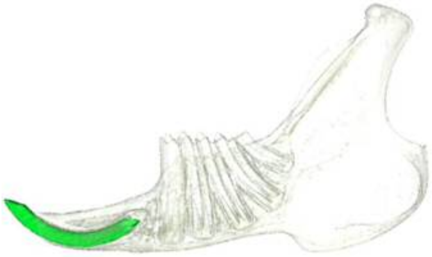
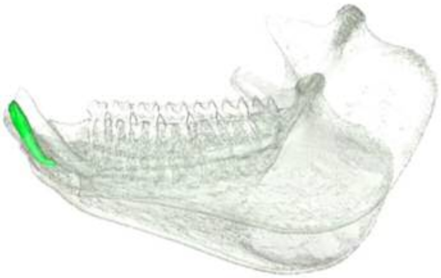
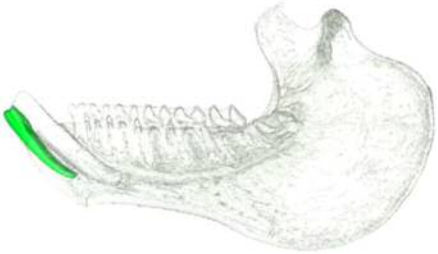
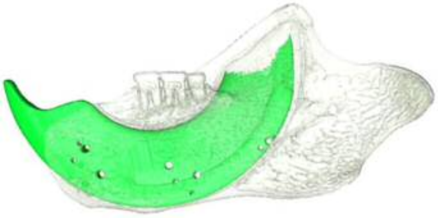
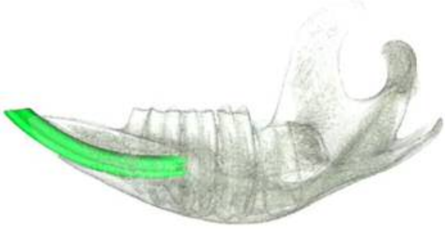
Species	Image of Mandible	Dietary Ecology
Acomys cahirinus **(Northeast African spiny mouse)**		Omnivore – Seeds, fruits, insects, food scavenged from humans, shrubs (green leaves), molluscs, carrion. Omnivore - (Nowak, 1999)
Aplodontia rufa (mountain beaver)		Herbivore – forbs, grasses, ferns. Specialised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

***Cavia porcellus* (Domestic guinea pig)**		Herbivore – Leaves, roots and tubers, fruits, flowers, lettuce etc. (rely on humans). Specialised Herbivore (*Cavia aperea*) - (Samuels, 2009).
***Cricetomys gambianus* (Northern giant pouched rat)**		Omnivore – Fruits, vegetables, nuts, insects, molluscs, roots (sweet potatoes etc.). Omnivore – (Nowak, 1999).
***Ctenomys opimus* (Highland tuco-tuco)**		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. Specialised Herbivore (*Ctenomys conoveri*) - (Samuels, 2009).
***Dasyprocta* (Agouti - species unknown)**		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. Generalist herbivore – (Nowak, 1999) (fruits, vegetables, and various succulent plants)
***Dipus saggitta* (Jerboa)**		Assuming the specimen is *Dipus sagitta:* Herbivore – seeds, green plants. Some occasional use of insects. Generalist herbivore (*Dipus [jaculus] aegypticus*) – (Samuels, 2009).

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

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

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

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

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

Hyracoidea	Procaviidae	*Dendrohyrax arboreus*	UMZC	H.5281.B	0.0554	M24147
Hyracoidea	Procaviidae	*Procavia capensis*	UMZC	H.5061.B	0.0596	M24154
Diprotodontia	Vombatiformes	*Vombatus ursinus*	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