

MicroCT-scans of fossil micromammal teeth: Re-defining hypsodonty and enamel proportion using true volume

J.A. van Dam ^{a,*}, J. Fortuny ^a, L.J. van Ruijven ^b

^a Institut Català de Paleontologia Miquel Crusafont (ICP), Campus de la UAB, Mòdul ICP, E-08193 Cerdanyola del Vallès, Spain

^b Academisch Centrum Tandheelkunde Amsterdam (ACTA), Gustav Mahlerlaan 3004 1081 LA Amsterdam, The Netherlands

ARTICLE INFO

Article history:

Received 27 May 2011

Received in revised form 15 August 2011

Accepted 19 August 2011

Available online 30 August 2011

Keywords:

Rodentia

Lipotyphla

Teeth

Hypsodonty

Enamel thickness

X-ray Computed Tomography (CT) scanning

ABSTRACT

Both hypsodonty and proportion of enamel are important measures for reconstructing diets and environments of fossil mammals. Classically, the first is calculated using crude dimensions and the second using specific cross-sections. With the increased availability of three-dimensional imaging techniques such as (micro) CT scanning, an upgrade towards new indices using actual 3D volumes is highly appropriate. Here we present examples from fossil small mammals to illustrate a straightforward and objective protocol to calculate new volume-based indices. Both hypsodonty and enamel proportion are defined in a consistent way with regard to orientation, and both are robust against damage or loss of dentine.

Whereas hypsodonty values in the studied rodents are reduced by more than one third with regard to the older methods, they are lowered by more than a factor two in taxa with a very strong dental relief, such as insectivores. Thus, relative positions of taxa on the continuum between animal and plant consumers change, by using actual dental volume and mean height instead of maximum height. Although enamel proportion and hypsodonty are expected to be positively correlated across rodents in general, the two parameters may easily get decoupled, for instance when thick enamel is needed to break down hard but high-nutrition food items such as seeds or nuts, or when thin enamel blades are needed to cut low-nutrition items, such as grass leaves.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Fossil teeth are highly informative with regard to the ecology and environment of extinct mammals. Not surprisingly, a rich bibliography has been produced correlating ecological and environmental variables with aspects of the dentition such as gross morphology, wear patterns, internal structure and chemical composition (Hershkovitz, 1967; Rensberger and Von Koenigswald, 1980; Janis and Fortelius, 1988; Teaford, 1994; Macho et al., 1996; Kohn and Cerling, 2002; Lucas, 2004; Evans et al., 2007). Hypsodonty, or relative crown height, is the most familiar ecomorphological measure based on teeth (Simpson, 1953; Van Valen, 1960). Interpreted as a measure of dental durability (Fortelius, 1985; Janis and Fortelius, 1988), hypsodonty has functioned as a proxy for diet, feeding habitat, vegetation type and climate. In plant-eating mammals, the correlation to diet is based on the necessary requirement for a sufficient amount of dental material to resist wear by endogenous components such as food particles, and exogenous components such as dust and grit (Janis, 1988; Janis, 1990; Williams and Kay, 2001). Due to the cellulose in their cell walls, endogenous fibrous particles such as green plant parts require extensive pre-processing (shearing, crushing) to

break them down for further chemical processing in the gut. In addition, the associated low nutritional value necessitates bulk consumption, further contributing to crown wear. Moreover, grasses contain extremely hard silica particles (phytoliths) that rapidly wear down tooth enamel (Baker et al., 1959). Ingestion of exogenous dust/grit either as a by-product from feeding close to the surface, or digging, causes additional wear.

Because high abundances of both grasses and dust/grit correlate with the presence of open landscapes, a high hypsodonty values in a fossil mammal community will generally point to an open environment and a more (at least seasonally) arid climate. Because hypsodonty and tooth volume (like length and area) essentially scale isometrically with body size and the number of chews during life are essentially equal for small and large mammals (Fortelius, 1985; Janis, 1988), hypsodonty of large- and small-sized primary consumers can be compared directly without body size correction. This scale-invariance property of teeth allows for straightforward ecomorphological comparisons both *vertically* within smaller and larger clades (radiations), and *horizontally*, between unrelated taxa and even across entire communities (Fortelius et al., 2002; Van Dam, 2002; Eronen et al., 2009).

Enamel thickness represents another widely used paleoecological variable. Because enamel is the hardest organic material known, enamel thickness or enamel proportion is a proxy of dental durability as well. In micromammals as a whole, hypsodonty and enamel thickness or volume appear to be positively correlated, both indicating the bulk consumption of tougher, harder, low-nutritional food and

* Corresponding author.

E-mail address: jan.vandam@icp.cat (J.A. van Dam).

associated grit (e.g., Rensberger, 1975). (Hypsodont forms with thin enamel occur, for instance in voles. In this case, vole species with relatively thin enamel have developed a way of compensation by producing ever-growing molars (Grayson et al., 1990)). In other groups such as primates with a narrower dietary spectrum lacking extreme herbivory and insectivory, the correlation between hypsodonty and enamel thickness will be weaker because other features such as microstructure and food particle size and shape tend to become relatively more important (Kay, 1981; Shimizu and Macho, 2008).

Enamel thickness tends to be variable across individual teeth because it is more functional at some places on the tooth than at others (Von Koenigswald et al., 1994; Kono, 2004). In this paper we focus on gross enamel volume, firstly, because average thickness and overall proportion is supposed to have a general relation to food nutritional value in broad groups such as micromammals, secondly because it is more easy to quantify and thirdly, because it is applicable to almost all types of mammal molars, so that it can easily be averaged across higher taxa and communities.

2. CT scanning

With the increased use of modern three-dimensional recording techniques such as X-ray Computed Tomography (CT), including high-resolution microCT (Ketcham and Carlson, 2001; Tafforeau et al., 2006), and advanced software to manipulate and analyze 3D data structures, the visualization and geometrical analysis of teeth has become more and more straightforward (Jernvall and Selänne, 1999; Kono, 2004; Evans et al., 2007; Lazzari et al., 2008; Olejniczak et al., 2008; Marschallinger et al., 2011). As far as we know, these developments have not yet resulted in an upgrade of the hypsodonty index. Enamel thickness measurements using complete volumes instead of cross-sections have already been realized (Kono, 2004; Olejniczak et al., 2008), but until now have not been applied to fossils except in some hominoids (Bayle et al., 2009; Macchiarelli et al., 2009).

Classically, a hypsodonty index h is calculated by dividing the vertical distance between some unworn cusp tip and a position at the crown base (absolute crown height) by a measure in the plane of the tooth row such as tooth length, width, or the square root of their product (Janis, 1988; Williams and Kay, 2001). Using specific ranges of the hypsodonty index, teeth can be classified as hypsodont, mesodont and brachyodont, and correlated to certain dietary categories such as grazing, browsing, and mixed feeding, respectively (e.g., Janis, 1988 for ungulates). Results may differ depending on which dental element is chosen and if length, width or area are taken as a reference.

In this paper we examine whether relative values of hypsodonty change across taxa, if actual volumes are used instead of combinations of tooth length (or width, area) and maximum tooth height (for example, Webb, 1983; Janis, 1988). This latter, more classical approach leads to an overestimation of dental volume in all forms except a minority of taxa, in which molar shape approaches a columnar body. These latter shapes correspond to what Hershkovitz called coronal hypsodonty, as opposed to tubercular hypsodonty, in which tooth height is related to the presence of pointed tubercles or blades (Hershkovitz, 1967). In fact, here we propose to “reshape” the volume of an irregular body such as a typical molar precisely to such a column, albeit substituting maximum height for mean height. We pay special attention to two aspects that potentially can affect results in an adverse way: orientation of the tooth and the discrimination of enamel and dentine tissues in CT images.

3. Methods

In order to assess differences in dental durability of taxa over a lifetime, unworn specimens of young individuals were used. The samples were scanned with a MicroCT scanner μ CT 40 (Scanco Medical A.G., Bassersdorf, Switzerland) at the Academisch Centrum Tandheelkunde

Amsterdam (ACTA). All the teeth were scanned at 55 kV and 145 μ A, an integration time of 1.75 s, slices of 2048×2048 pixels with a resultant voxel resolution of 6 μ m, and with an inter-slice space of 6 μ m.

We used five isolated molars from extinct lineages recovered from the late Miocene sediments of the Teruel Basin (Spain). The teeth are curated in the department of Earth Sciences, Utrecht University. Three molars are from rodents: *Ruscinomys schaubi* (Cricetodontinae, relatively high-crowned hamsters, Fig. 1), *Occitanomys adroveri* (Murinae, true mice, relatively low-crowned, Fig. 2), and *Spermophilinus turoliensis* (Sciuridae, lower-crowned, supposedly terrestrial squirrel, Fig. 3) (Van de Weerd, 1976). Two molars are from insectivores (van Dam et al., 2001): the non-burrowing mole *Desmanella* sp. (Fig. 4) and the shrew *Miosorex* sp. (Fig. 5). The molar of *Miosorex* sp. originates from the locality Peralejos 5 (10 Ma) and the one of *Spermophilinus turoliensis* from Masada del Valle 2 (7 Ma). The remaining molars are from Los Mansuetos (7 Ma). Four teeth are upper second molars and the *Spermophilinus* tooth is either a first or second upper molar (isolated M1 and M2 are difficult to separate in squirrels). The dentine of the crown and roots is damaged in all teeth by post-mortem processes (Figs. 1–5). The teeth are nearly unworn, except for the one from *Miosorex*, which has lost some enamel at the top part of its highest cusp and other parts of its surface (Fig. 5). This tooth will therefore only be used for a comparison between the classical and the new method to calculate h .

To explore the CT data and create the high resolution 3D models we used the CT software MIMICS (Materialise, Belgium). The 3D models were imported into the CAD modelling software Rhinoceros 4.0 (McNeel, Seattle), which allowed us to calculate reference planes, calculate surfaces and volumes, and perform digital cutting. Because the new method is meant to work across widely different taxa with widely different dental shapes, a proper orientation of the teeth (definition of what is horizontal and vertical) is essential. As our primary reference plane we used the regression plane through the external enamel–dentine junction (also corresponding to the cervix or cementoenamel junction), using a set of points (see subfigures b in Figs. 1–5), which were inserted manually in a pseudo-equally-spaced way. (See later discussion on reference planes). Next, crown volume V_c was defined as the volume of the three-dimensional body above this plane as if it were completely filled, with dentine taking the space between the enamel and the reference plain. By making this choice, the results are unaffected by any absence of dentine due to post-burial processes, and the method can even be used for molars of which only the enamel cap has remained (relatively common in fossil micromammals). Similarly to earlier studies (Kono, 2004; Olejniczak et al., 2008), we ignored the pulp cavity and effectively assumed it to be dentine.

In order to make height relative, we used a surface instead of a distance in the jaw direction (‘length’) or perpendicular to it (‘width’), thereby avoiding arbitrary decisions on measurements of length and width. In line with the use of actual volume, we preferred to use actual area instead of the square root of length and width. Two logical options for the area are: (1) the surface of the cross-section of the tooth in the reference plane, or (2) the surface of the projected area of the complete crown onto the reference plane. Here we use option (2) because it conforms more to how length, width and area are often measured in paleontology (in occlusal view and by taking maximally visible dimensions), but option (1) or another option could be used as well, resulting in slightly different hypsodont indices.

The mean height H_{mean} above the plain is:

$$H_{mean} = V_c/A_{cp} \quad (1)$$

with:

V_c volume above the plain (= re-defined crown volume)
 A_{cp} projection area of the re-defined crown on the horizontal reference plane

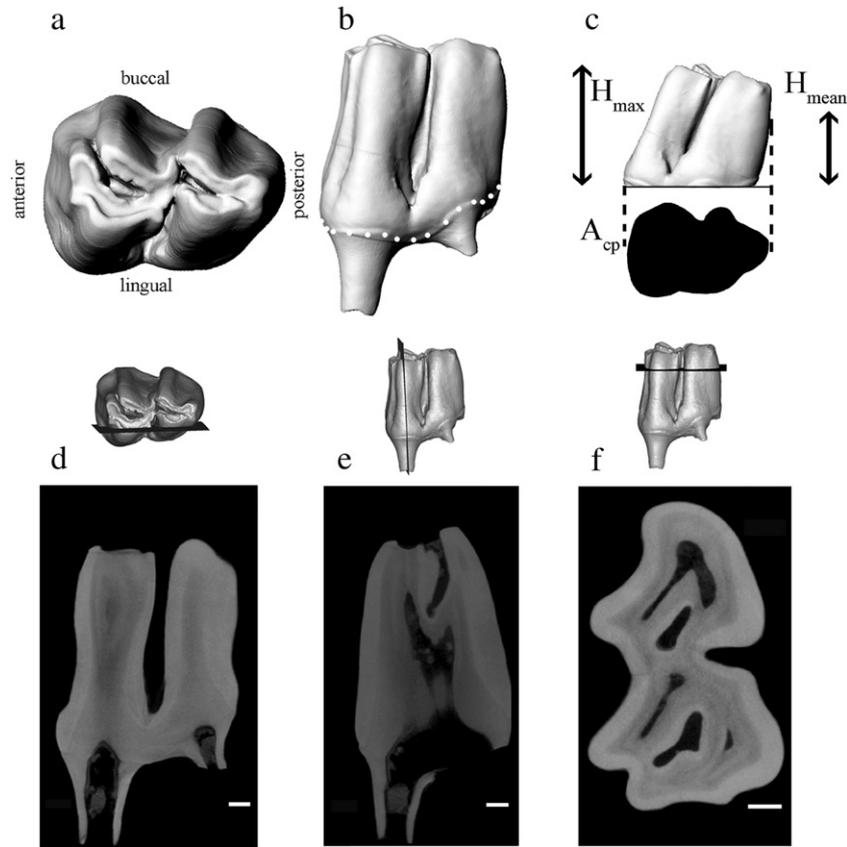


Fig. 1. 3D model, volume-based hypsodonty calculations, and representative cross-sections (unrelated to reference plain, scale bar: 0.3 mm) for right (mirrored) M2 (LM 797) of *Ruscinomys schaubi*. a) occlusal view 3D model, b) lingual view 3D model; points along enamel–dentine boundary used for fitting reference plane, c) above: lingual view of 3D model of crown bounded by reference plane through enamel–dentine boundary; below: reference area resulting from orthogonal projection of crown on reference plane, d) antero-posterior cross-section (lingual view), e) bucco-lingual cross-section (posterior view), f) cross-section parallel to occlusal plane (occlusal view).

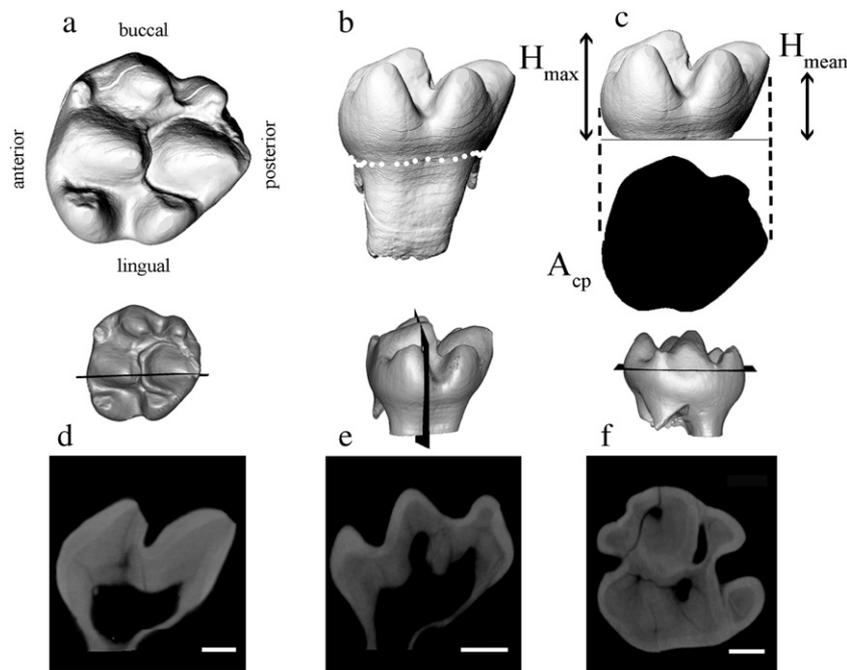


Fig. 2. 3D model, volume-based hypsodonty calculations, and representative cross-sections (unrelated to reference plain, scale bar: 0.3 mm) for right (mirrored) M2 (LM, no number) of *Occitanomys adroveri*. a) occlusal view 3D model, b) lingual view 3D model; points along enamel–dentine boundary used for fitting reference plane, c) above: lingual view of 3D model of crown bounded by reference plane through enamel–dentine boundary; below: reference area resulting from orthogonal projection of crown on reference plane, d) antero-posterior cross-section (lingual view), e) bucco-lingual cross-section (posterior view), f) cross-section parallel to occlusal plane (occlusal view).

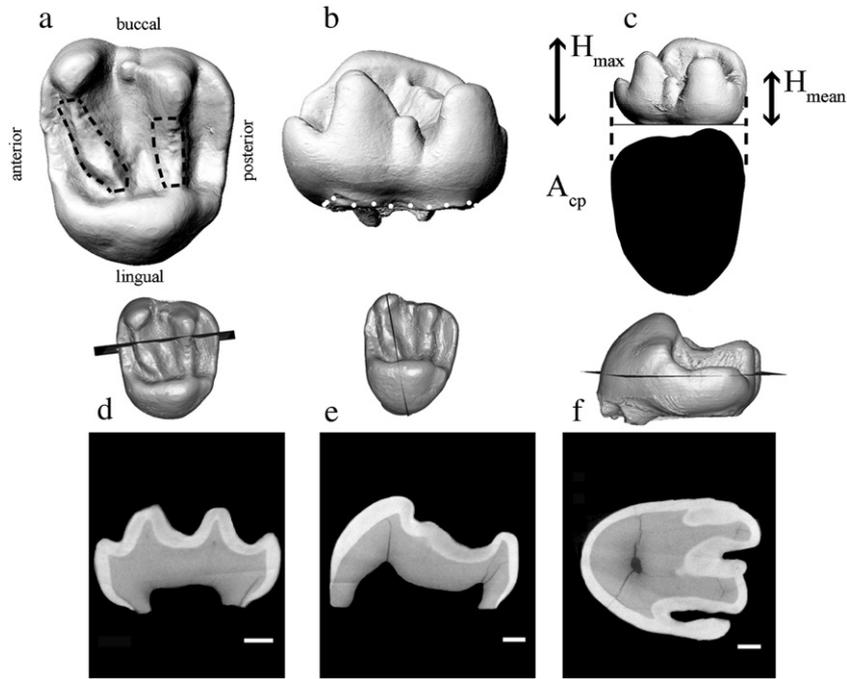


Fig. 3. 3D model, volume-based hypsodonty calculations, and representative cross-sections (unrelated to reference plain, scale bar: 0.3 mm) for right (mirrored) M1-2 (MDV2 1471) of *Spermophilinus turoleus*. a) occlusal view 3D model; two areas enclosed by dashed lines have atypical radiodensity values (see text), b) buccal view of 3D model; points along enamel–dentine boundary used for fitting reference plane, c) above: lingual view of 3D model of crown bounded by reference plane through enamel–dentine boundary; below: reference area resulting from orthogonal projection of crown on reference plane, d) antero-posterior cross-section (lingual view), e) bucco-lingual cross-section (posterior view), f) cross-section parallel to occlusal plane (occlusal view).

As the denominator for the hypsodonty index is chosen to be $A_{cp}^{1/2}$, h_{mean} can be compared to the index h_{max} , which uses maximum height

$$h_{mean} = H_{mean}/A_{cp}^{1/2} = V_c^* A_{cp}^{2/3}$$

$$(2) \quad h_{max} = H_{max}/A_{cp}^{1/2} \quad (3)$$

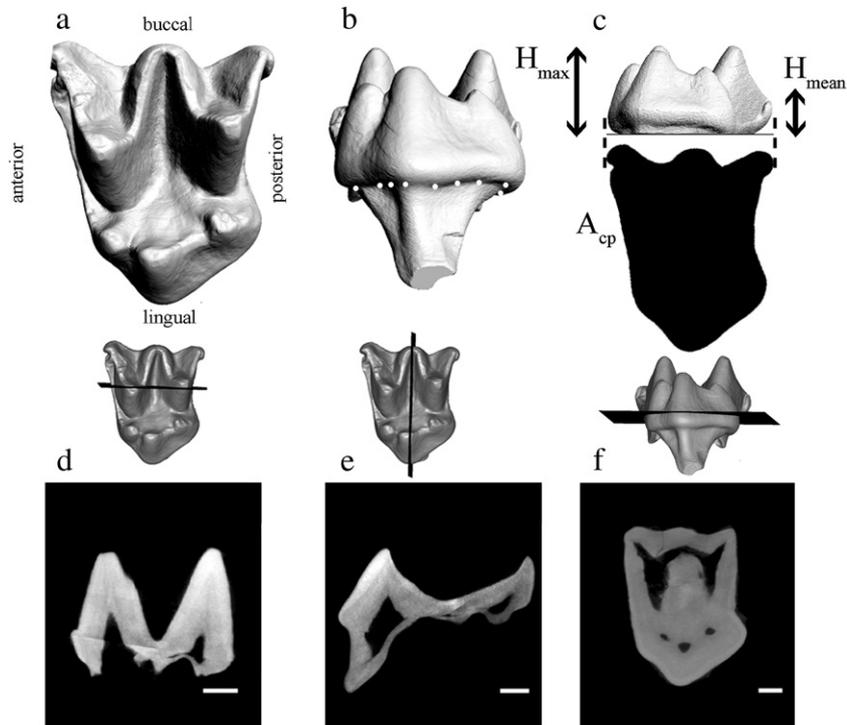


Fig. 4. 3D model, volume-based hypsodonty calculations, and representative cross-sections (unrelated to reference plain, scale bar: 0.3 mm) for left M2 (LM 2259) of *Desmanella* sp. a) occlusal view 3D model, b) lingual view 3D model; points along enamel–dentine boundary used for fitting reference plane, c) above: lingual view of 3D model of crown bounded by reference plane through enamel–dentine boundary; below: reference area resulting from orthogonal projection of crown on reference plane, d) antero-posterior cross-section (lingual view), e) bucco-lingual cross-section (posterior view), f) cross-section parallel to occlusal plane (occlusal view).

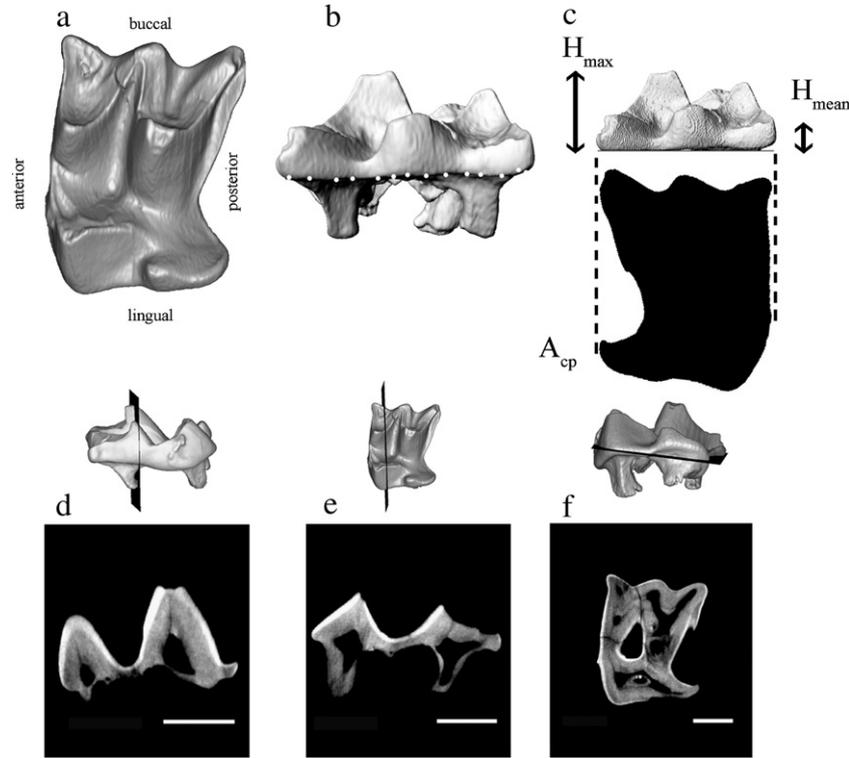


Fig. 5. 3D model, volume-based hypsodontology calculations, and representative cross-sections (unrelated to reference plain, scale bar: 0.3 mm) for left M2 (PER5 330) of *Miosorex* sp. a) occlusal view 3D model, b) buccal view 3D model; points along enamel–dentine boundary used for fitting reference plane, c) above: lingual view of 3D model of crown bounded by reference plane through enamel–dentine boundary; below: reference area resulting from orthogonal projection of crown on reference plane, d) antero–posterior cross-section (lingual view), e) bucco–lingual cross-section (posterior view), f) cross-section parallel to occlusal plane (occlusal view).

Traditionally, enamel thickness (2D AET) is calculated as the area of enamel divided by the length of the enamel–dentine junction in a real or virtual 2D section. To make the measure relative (RET), it is divided by the square of the area of dentine in the same section (Martin, 1985; Smith et al., 2005). (Note that in another type of approach, enamel thickness or relative enamel area has been measured on worn occlusal surfaces (Schmidt-Kittler, 2002)). Here we define a simple 3D measure p_e for the proportion of enamel in a tooth, which is at the same time consistent with the new hypsodontology measure defined above, since the same reference plane and crown volume is used:

$$p_e = V_e/V_c \quad (4)$$

V_e volume of enamel above the plain
 V_c tooth volume

Generally, the digital discrimination of enamel from dentine in regular (micro)CT scans is never perfect, and will involve the setting of

some threshold (e.g., Spoor et al., 1993). Discrimination in fossils may be less perfect than in extant teeth due to diagenesis (secondary mineralizations) homogenizing tooth mineralogy. On the other hand, discrimination may become better because of differential diagenesis in enamel and dentine. Here we test for the effects of different thresholds on the final calculated proportions of enamel, by selecting a lower threshold boundary below which larger unallowable spots of “dentine” appear in the enamel, and an upper boundary with the reversed condition of spots of “enamel” in the dentine. The threshold corresponding to the true enamel–dentine proportion is expected to be within the range defined by these two boundaries.

4. Results

The hypsodontology calculations show a significant reduction in the measurement of hypsodontology (h_{mean}) with regard to the classical method (h_{max}) in all species. The reduction ranges from 36 to 38% for the three rodents, and even to 53–60% for the two insectivores (Table 1,

Table 1
 Hypsodontology and enamel proportion calculations.

Taxon	A_{cp} (mm ²)	V_c (mm ³)	H_{mean} (mm)	H_{max} (mm)	h_{mean}	h_{max}	h_{mean}/h_{max}	Enamel range (Hounsfield units)	V_e (mm ³)	p_e
<i>Ruscinomys schaubi</i>	5.63	9.54	1.69	2.73	0.71	1.15	0.62	115–555	5.24	0.55
<i>Ruscinomys schaubi</i>		9.54						142–555	4.74	0.50
<i>Ruscinomys schaubi</i>		9.54						169–555	4.41	0.46
<i>Occitanomys adroveri</i>	1.53	0.79	0.52	0.81	0.42	0.65	0.64	111–389	0.27	0.34
<i>Occitanomys adroveri</i>		0.79						136–389	0.22	0.28
<i>Spermophilinus turoliensis</i>	3.87	3.25	0.84	1.34	0.43	0.68	0.63	2100–3071; not corrected	1.20	0.37
<i>Spermophilinus turoliensis</i>		3.25						2100–3071; corrected	1.22	0.37
<i>Desmanella</i> sp.	2.65	1.36	0.51	1.08	0.31	0.66	0.47	240–614	0.20	0.15
<i>Desmanella</i> sp.		1.36						250–614	0.18	0.13
<i>Desmanella</i> sp.		1.36						260–614	0.15	0.11
<i>Miosorex</i> sp. (slightly worn)	1.79	0.44	0.24	0.62	0.18	0.46	0.40			

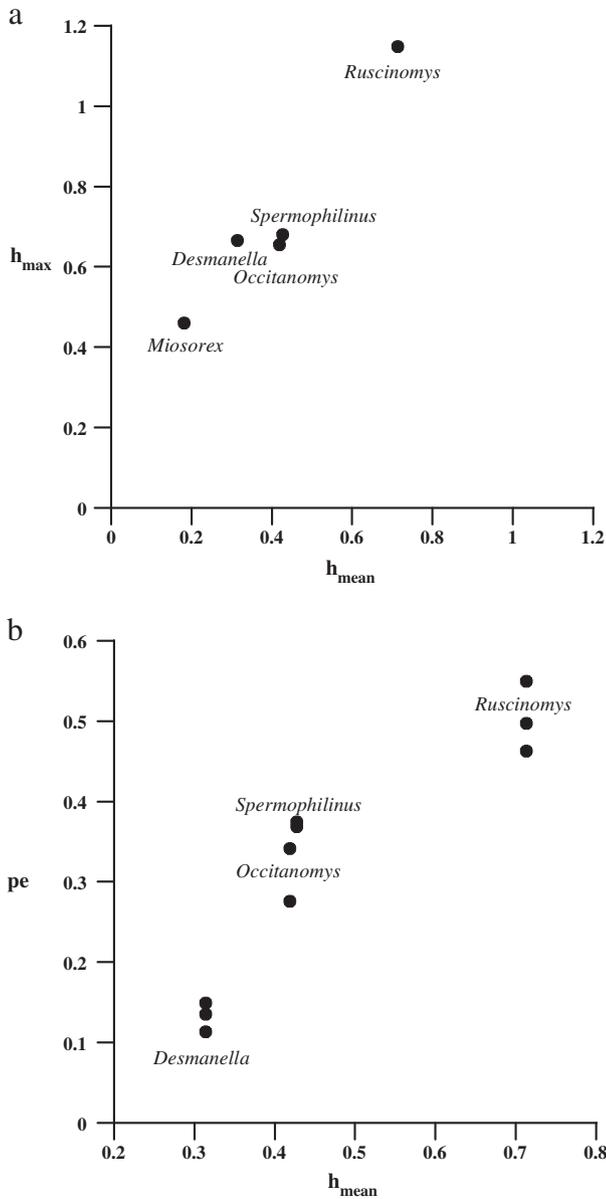


Fig. 6. Plots of volume-based dental indices. Data from Table 1. a) h_{max} against h_{mean} , b) p_e against h_{mean} .

Fig. 6a). The general difference in shape between rodent and insectivores, with the latter having sharp points and blades, is well illustrated by the results for *Occitanomys* and *Desmanella*: their teeth have essentially the same h_{max} , whereas h_{mean} of the insectivore *Desmanella* is 25% smaller.

Although the relative proportion of enamel p_e varies according to the thresholds chosen, these differences are not large (Table 1). The proportion of enamel differs a lot between the taxa: it is very low in the insectivore *Desmanella* (11–15%), and ranges to about 50% in *Ruscinomys*. Because it is slightly worn, we did not calculate the value for the second insectivore *Miosorex*. Nevertheless, as shown by Fig. 5d–f, its enamel is also very thin.

The plot of p_e against h_{mean} suggests a strong relation between the two measures, which is only little affected by the Hounsfield (i.e., measure of radiodensity) threshold values between enamel and dentine (Table 1, Fig. 6b). Although the high Hounsfield numbers for *Spermophilinus turoliensis* from Masada del Valle 2 indicate strong diagenesis, differential reworking of enamel end dentine appears to have resulted in a sharp threshold between the two tissues (Fig. 3). On the other hand, the enamel

of this tooth contains two localized areas of consistently lower density that were mistaken for dentine (Fig. 3a). The effect of this misidentification on p_e appeared to be marginal, however, because after digital correcting this area, a very similar value resulted (Table 1, Fig. 6b).

Although the studied taxa are positioned on an approximately straight line in Fig. 6b, many more taxa and specimens have to be analyzed before any final conclusions can be drawn on the nature of the relationship between micromammal crown height and enamel thickness. Would this relationship turn out to be positive, as already suggested by Rensberger (1975), it would mean that both parameters respond in concert to food item characteristics such as toughness, abrasiveness and nutritional value. The position of *Spermophilinus* above the general trend line could be consistent with the presence of a second selective force acting on enamel thickness, which is the need to break down hard items such as nuts and seeds. Most squirrels appear to parallel primates in this respect (e.g., Kay, 1981), although the former also rely heavily on their incisors for cracking.

5. Discussion

Our approach shows that a standardized way of measuring volume-based hypsodonty and enamel thickness on the basis of CT scans from mammal teeth can be realized using simple conventions, despite a huge variability of complex shapes. Replacing distance-based hypsodonty indices and area-based measures of enamel thickness by volume-based indices is not only theoretically desirable, it also produces different results in terms of the relative scores of taxa on these indices. The next logical step will involve the scanning and analysis of specimens and taxa on a high through-put basis (Evans et al., 2007) enabling comparative analyses across higher taxa and communities. Thus far, the main bottle neck in developing data bases of enamel proportions in fossil teeth has been the very time-consuming task of manually correcting for wrongly identified voxels (enamel to dentine or vice versa) errors. Our analysis suggests that, although such noise occurs, the errors could be too small to bias the basic interpretation in terms of basic dental function and past environments.

Our choice of a reference plane as fitted through the external enamel–dentine junction (=cemento–enamel junction, although cementum has disappeared in most fossil isolated teeth), is an objective one and differs from the ones in earlier studies. For example, in studying extant primates, Kono uses the section through the “lowest height where enamel is continuous around the entire circumference”, with the general orientation of the tooth being such, that the projected area in occlusal view is maximized (Suwa and Kono-Takeuchi, 1998; Kono, 2004). Alternatively, a reference plane has been defined at a slightly lower position as follows “The plane exactly halfway between that containing the most apical continuous ring of enamel and that containing the most apical extension of enamel was taken as the cervical plane, above which coronal measurements were recorded” (Olejniczak et al., 2008). We prefer our own definition, because 1) the maximization of the projected area appears to be a more complicated procedure than fitting a plane, and 2) a fitted plane through the cervix is the optimal planar representation of an undulating crown base. It may be argued that our choice is not perfect, because the reference plane will not always be running parallel to the main direction of the occlusal surface (e.g. Fig. 1). This difference is related to a number of factors including the size of the individual roots around the top of which the cemento–enamel junction (cervix) is running. On the other hand, our solution still fits the definition of what constitutes the crown, namely that part of the tooth that is covered by enamel, as opposed to the root part, which is covered by cementum.

Some groups seem to be excluded by our method when applied too strictly. The possession of enamel-free zones on ever-growing molars, such as those of arvicoline rodents and lagomorphs, confounds the identification of the crown base when using the enamel–dentine boundary. For such groups definition of what constitutes the crown

should be modified. The continuous growth in these small mammals (as well as in some extinct ungulates and in Xenarthra, in which enamel is lacking all together) constitutes an additional problem with regard to the analysis of enamel volume and durability. In such cases we suggest that, when known (e.g., Von Koenigswald and Golenishev, 1979), the additional enamel formed after eruption should be taken into account when estimating volumes.

If the reconstruction of landscape openness and aridity is the study goal, one could opt for the exclusion of non-plant eating animals from the mean hypsodonty calculations. In this case, conventions are necessary with regard to groups with broad dietary spectra. For example, in their calculations of mean large-mammal hypsodonty, Fortelius et al. (2006) included (plant-dominated) omnivores such as pigs, but excluded omnivores who were more carnivorous. However, if the research goal is directed towards reconstructing dietary spectra in general, complete communities should be used. Thus, a large difference between h_{mean} and h_{max} points to the strong development of dental appendices (tubercular hypsodonty), such as spiked cusps and sharp blades, as in insectivores and carnivores. By using h_{mean} this effect is partly eliminated, because the remaining part of the crown is low. In fact, the use of h_{mean} in principle will allow for the positioning of terrestrial mammals on a continuum between animal-consumers and plant-consumers. The generation of such a scale is a highly desirable ecomorphological goal, because it reduces a bewildering diversity of morphologies back to simple underlying functional principles.

As with all paleoecological proxies, ecomorphological interpretations should always be made with care, and should preferably include more taxa from the same site. Firstly, other factors than abrasiveness of food, such as the ingestion of dust and grit (amplified by fossorial habits) and in some cases competition (e.g., Casanovas-Vilar et al., 2011) may select for dental durability. Secondly, it is known that high-crowned taxa may process softer food items as well (see Janis, 1988). Finally, not only other dental features such as microstructure and orientation and degree of complexity of the cusp and ridge pattern (Rensberger and Von Koenigswald, 1980; Jernvall and Selänne, 1999; Evans et al., 2007; Lazzari et al., 2008; Shimizu and Macho, 2008) may compensate for hypsodonty and enamel proportion, but selection for dental features may interfere with selection for other parts of the digestive system as well (Vorontsov, 1967; Webb, 1983; Janis, 1988).

6. Conclusion

Three-dimensional models of teeth based on CT scans can be used to re-define the classical measures of hypsodonty and enamel thickness in a consistent, volume-based way. As shown with examples from fossil micromammals, the definition of the tooth crown as the solid body bounded by a reference plain, such as one through the external enamel–dentine boundary (or cemento-enamel junction) allows for calculation of more objective indices with values being robust to any damage or even absence of dentine. By using mean instead of maximum height, hypsodonty values reflect true dental volume and become independent of dental shape. Although hypsodonty and enamel proportion will often respond to (and therefore indicate) one and the same selectional regime characterized by tough and abrasive food, their correlation will be weaker when the shape and size of food particles requires specific occlusal morphologies, such as sharp edges to cut grass or thick enamel to crack nuts and seeds.

Acknowledgements

We thank Gabriele Macho, Matt Skinner and two anonymous reviewers for giving their comments on versions of the manuscript, and Fred Spoor for discussion. The department of Earth Sciences of Utrecht University is thanked for making available the studied specimens. The study was supported by the Spanish Ministerio de Ciencia e Innovación (project CGL2008–00325/BTE).

References

- Baker, G.L., Jones, H.P., Wardrop, I.D., 1959. Cause of wear in sheep's teeth. *Nature* 184, 1583–1584.
- Bayle, P., Braga, J., Mazurier, A., Macchiarelli, R., 2009. Dental developmental pattern of the Neanderthal child from Roc de Marsal: a high-resolution 3D analysis. *Journal of Human Evolution* 56, 66–75.
- Casanovas-Vilar, I., van Dam, J.A., Moyà-Solà, S., Rook, L., 2011. Late Miocene insular mice from the Tusco-Sardinian palaeobioprovince provide new insights on the palaeoecology of the *Oreopithecus* faunas. *Journal of Human Evolution* 61, 42–49.
- Eronen, J.T., Ataabadia, M.M., Micheels, A., Karme, A., Bernor, R.L., Fortelius, M., 2009. Distribution history and climatic controls of the Late Miocene Pliocene chronofauna. *Proceedings of the National Academy of Sciences of the United States of America* 106, 11867–11871.
- Evans, A.R., Wilson, G.P., Fortelius, M., Jernvall, J., 2007. High-level similarity of dentitions in carnivores and rodents. *Nature* 445, 78–81.
- Fortelius, M., 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. *Acta Zoologica Fennica* 180, 1–76.
- Fortelius, M., Eronen, J., Jernvall, J., Liu, L.P., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z.Q., Zhou, L.P., 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research* 4, 1005–1016.
- Fortelius, M., Eronen, J., Liu, L.P., Pushkina, D., Tesakov, A., Vislobokova, I., Zhang, Z.Q., 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 219–227.
- Grayson, D.K., Maser, C., Maser, Z., 1990. Enamel thickness of rooted and rootless microtine molars. *Canadian Journal of Zoology* 68, 1315–1317.
- Hershkovitz, P., 1967. Dynamics of rodent molar evolution: New World Muridae, family Muridae. *Journal of Dental Research* 46, 829–842.
- Janis, C.M., 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. In: Russell, D.E., Santoro, J.-P., Sigogneau-Russell, D. (Eds.), *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology*, Paris, pp. 367–387.
- Janis, C.M., 1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. In: Boucot, A.J. (Ed.), *Evolutionary Paleobiology of Behavior and Coevolution*. Elsevier Press, New York, pp. 241–259.
- Janis, C.M., Fortelius, M., 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Reviews* 63, 197–230.
- Jernvall, J., Selänne, L., 1999. Laser confocal microscopy and geographic information systems in the study of dental morphology. *Palaeontologia Electronica* 2.
- Kay, R.F., 1981. The nut-crackers — a new theory of the adaptations of the Ramapithecinae. *American Journal of Physical Anthropology* 55, 141–151.
- Ketcham, R.A., Carlson, W.D., 2001. Acquisition, optimization and interpretation of X-ray computed tomographic imagery: applications to the geosciences. *Computers and Geosciences* 27, 381–400.
- Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite. In: Kohn, M.J., Rakovan, J., Hughes, J.M. (Eds.), *Phosphates: Geochemical, Geobiological, and Materials Importance*, pp. 455–488.
- Kono, R., 2004. Molar enamel thickness and distribution patterns in extant great apes and humans, new insights based on a 3-dimensional whole crown perspective. *Anthropological Science* 112, 121–146.
- Lazzari, V., Tafforeau, P., Aguilar, J.-P., Michaux, J., 2008. Topographic maps applied to comparative molar morphology: the case of murine and cricetine dental plans (Rodentia, Muroidea). *Paleobiology* 34, 46–64.
- Lucas, P.W., 2004. *Dental Functional Morphology: How Teeth Work*. Cambridge University Press, Cambridge.
- Macchiarelli, R., Mazurier, A., Illerhaus, B., Zanolli, C., 2009. *Ouranopithecus macedoniensis* (Mammalia, Primates, Hominoidea): virtual reconstruction and 3D analysis of a juvenile mandibular dentition (RPI-82 and RPI-83). *Geodiversitas* 31, 851–863.
- Macho, G., Reid, D., Leakey, M., Jablonski, N., Beynon, A., 1996. Climatic effects on dental development of *Theropithecus oswaldi* from Koobi Fora and Ologorgesailie. *Journal of Human Evolution* 30, 57–70.
- Marschallinger, R., Hofmann, P., Daxner-Höck, G., Ketcham, R.A., 2011. Solid modeling of fossil small mammal teeth. *Computers & Geosciences* 37, 1364–1371.
- Martin, L., 1985. Significance of enamel thickness in hominoid evolution. *Nature* 314, 260–263.
- Olejniczak, A.J., Smith, T.M., Skinner, M.M., Grine, F.E., Feeny, R.N.M., Thackeray, J.F., Hublin, J.J., 2008. Three-dimensional molar enamel distribution and thickness in *Australopithecus* and *Paranthropus*. *Biology Letters* 4, 406–410.
- Rensberger, J.M., 1975. Function in the cheek tooth evolution of some hypsodont geomyoid rodents. *Journal of Paleontology* 49, 10–22.
- Rensberger, J.M., Von Koenigswald, W., 1980. Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. *Paleobiology* 6, 477–495.
- Schmidt-Kittler, N., 2002. Feeding specializations in rodents. *Senckenbergia Lethaea* 82, 141–152.
- Shimizu, D., Macho, G.A., 2008. Effect of enamel prism decussation and chemical composition on the biomechanical behavior of dental tissue: a theoretical approach to determine the loading conditions to which modern human teeth are adapted. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* 291, 175–182.
- Simpson, G.G., 1953. *The Major Features of Evolution*. Columbia University Press, New York, T.M.
- Smith, T.M., Olejniczak, A.J., Martin, L.B., Reid, D.J., 2005. Variation in hominoid molar enamel thickness. *Journal of Human Evolution* 48, 575–592.

- Spoor, C.F., Zonneveld, F.W., Macho, G.A., 1993. Linear measurements of cortical bone and dental enamel by computed tomography: applications and problems. *American Journal of Physical Anthropology* 91, 469.
- Suwa, G., Kono-Takeuchi, R., 1998. A refined method of measuring basal crown and cuspal areas by use of a three-dimensional digitizing system. *Anthropological Science* 106, 95–105 (Supplement).
- Tafforeau, P., Boistel, R., Boller, E., Bravin, A., Brunet, M., Chaimanee, Y., Cloetens, P., Feist, M., Hozzowska, J., Jaeger, J.J., Kay, R.F., Lazzari, V., Marivaux, L., Nel, A., Nemoz, C., Thibault, X., Vignaud, P., Zabler, S., 2006. Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. *Applied Physics A Materials Science & Processing* 83, 195–202.
- Teaford, M.F., 1994. Dental microwear and dental function. *Evolutionary Anthropology* 3, 17–30.
- Van Dam, J.A., 2002. Tracing hypsodonty patterns in Neogene Western Eurasian small mammals. ESF-EEDEN meeting The Middle Miocene crisis, Frankfurt, p. 39.
- Van Dam, J.A., Alcalá, L., Alonzo Zarza, A., Calvo, J.P., Garcés, M., Krijgsman, W., 2001. The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. *Journal of Vertebrate Paleontology* 21, 367–385.
- Van de Weerd, A., 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins Special Publication* 2, 1–217.
- Van Valen, L., 1960. A functional index of hypsodonty. *Evolution* 14, 531–532.
- Von Koenigswald, W.V., Golenishev, F.N., 1979. A method for determining growth rates in continuously growing molars. *Journal of Mammalogy* 60, 397–400.
- Von Koenigswald, W., Sander, P.M., Leite, M.B., Mörs, T., Santel, W., 1994. Functional symmetries in the schmelzmuster and morphology of rootless rodent molars. *Zoological Journal of the Linnean Society* 110, 141–179.
- Vorontsov, N.N., 1967. Evolution of the Alimentary System in Myomorph Rodents. Nauka, Novosibirsk.
- Webb, S.D., 1983. The rise and fall of the Late Miocene ungulate fauna in North America. In: Nitecki, M.H. (Ed.), *Coevolution*. University of Chicago Press, Chicago and London, pp. 267–306.
- Williams, S.H., Kay, R.F., 2001. A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. *Journal of Mammalian Evolution* 8, 207–229.