Palaeogeography, Palaeoclimatology, Palaeoecology 311 (2011) 103–110

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

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.

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 grid (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).

0031-0182/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2011.08.010

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 μCT 40 (Scanco Medical A.G., Bassersdorf, Switzerland) at the Academisch Centrum Tandheelkunde Amsterdam (ACTA). All the teeth were scanned at 55 kV and 145 μA, an integration time of 1.75 s, slices of 2048 × 2048 pixels with a resultant voxel resolution of 6 μm, and with an inter-slice space of 6 μm.

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:

$$H_{mean} = V_c/A_{cp} \tag{1}$$

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