BMSAP (2014) 26:140-146
DOI 10.1007/s13219-014-0099-9

NOTE / *NOTE*

Quantitative three-dimensional topography in taxonomy applied to the dental morphology of catarrhines

Application quantitative de la topographie tridimensionnelle de la morphologie dentaire à la taxonomie des catarrhiniens

V. Lazzari · F. Guy

Received: 30 October 2013; Accepted: 12 February 2014

Abstract This paper presents a new aspect in studies of dental morphology based exclusively on 3D topographical analysis. Our method was applied to a set of 20 unworn upper second molars belonging to seven extant catarrhine genera. From a geometrical analysis of the polygonal grid representing the shape of each tooth, we propose a 3D dataset that provides a detailed characterization of the enamel morphology. In this article, we present a taxonomic application of our method using the example of inclination. Our initial results show intergeneric variation for the selected topographic parameter and its relevance to taxonomic analyses of extinct primates. More generally, our analysis of irregular grid patterns in 3D digital models supplied new parameters and enabled a review of the data classically studied in dental palaeoanthropology, with potential implications for taxonomic, phylogenetic, functional and developmental studies.

Keywords 3D image analysis · Polygonal surface · Dentin · Enamel · Molar · Hominoid · Cercopithecoid

Résumé Nous présentons un nouvel aspect de l'étude de la morphologie dentaire basée exclusivement sur une analyse topographique 3D. Notre méthode a été appliquée à un échantillon de 20 secondes molaires supérieures non usées appartenant à sept genres actuels de catarrhiniens. Au moyen d'une analyse géométrique de maillages polygonaux représentant la forme de la dent, nous proposons un jeu de données 3D permettant de caractériser de manière détaillée la morphologie de la capsule d'émail. Dans ce travail, nous présentons une application taxonomique de notre méthode à travers l'exemple de l'inclinaison. Les résultats préliminaires montrent une variation inter-générique pour le paramètre topographique sélectionné et sa pertinence en termes d'analyse taxonomique chez les primates anciens. Plus généralement, l'analyse du maillage irrégulier des modèles numériques 3D permet d'accéder à de nouveaux paramètres et de revisiter des données classiquement étudiées en paléoanthropologie. Les inférences potentielles sont d'ordre développemental, taxonomique, phylogénétique et fonctionnel.

Mots clés Analyse d'image 3D · Surface polygonale · Dentine · Émail · Molaire · Hominoïde · Cercopithécoïde

V. Lazzari (✉) · F. Guy (✉)
CNRS, INEE, UMR 7262 – Université de Poitiers - Faculté des Sciences – IPHEP Institut de Paléoprimatologie et Paléontologie Humaine, Evolution et Paléoenvironnements, Bât. B35 – TSA 51106, 6, rue Michel Brunet, 86073 Poitiers cedex 9
e-mail : Vincent.lazzari@univ-poitiers.fr, Franck.guy@univ-poitiers.fr

Introduction

Tooth tissue is of central importance to many fields of investigation including anthropology and palaeoanthropology, as a key to taxonomic identification and phylogenetic or biological inferences (e.g. [1-4]). Like any other organs, teeth - as tools contributing to the digestive process in various diets - are a combination of the phylogenetic inheritance of dental traits and adaptive selection of these traits during evolution. However, unlike most other organs, changes in the shape of teeth after their eruption and during the life history of an individual are driven only by wear and not through remodelling (as with bones). Occlusal tooth morphology thus corresponds to the external surface of the enamel cap (EC) as shaped by tooth wear. Therefore, unworn teeth directly reflect the developmental processes governing morphogenesis and are highly suited to evolutionary investigations. However, distinguishing between the adaptive and phylogenetic significance of dental traits has remained a challenge.

Mammals, and therefore primates, have high intra- and inter-species variability in tooth size and shape. Aspects of tooth size and shape have been widely considered by researchers over the last century, from detailed descriptions of occlusal morphology to the characterization of the developmental processes underlying tooth shape (e.g. [5]), including quantification of various dimensional aspects of the teeth through a wide range of descriptors (e.g. [1,4,6-9]).

Recent technological advances in capturing the morphology of objects in three dimensions using non-invasive methods (e.g. CT and μCT-scans) and the improvement of image analysis tools have given a new impetus to tooth studies. Researchers are able not only to consider an extensive set of dental features in their analyses, including crown enamel and the enamel-dentine junction as well as root and pulp canals, but also to study these tissues in all three dimensions.

Analytical tools using 3D imagery now make it possible to perform quantitative appraisals and characterizations of both the morphology and properties of dental tissues [e.g., 10-16]. Tooth form and function can thus be accessed through topographical analyses of the occlusal surface using GIS software (e.g. [13,16]).

In this paper we will focus on data that can be retrieved from 3D topographical analyses of the occlusal enamel surface (EC). While our overall goal is to achieve a comprehensive characterization of tooth occlusal morphology using 3D positioning and distributions of topographical (elevation, inclination, orientation) and material (enamel thickness) descriptors of dental features, we report here on an example of three-dimensional tooth characterization from a taxonomic perspective using one topographical parameter: inclination.

We applied our procedure to a set of unworn to slightly worn left upper second molars of catarrhines.

Data acquisition and analysis

Our sample consisted of molars from two gibbons (*Hylobates sp.*), four gorillas (*Gorilla gorilla*), three chimpanzees (*Pan troglodytes*), five modern humans (*Homo sapiens*) and six cercopithecoids (two *Cercocebus sp.*, two *Cercopithecus sp*. and two *Papio sp.*). All the specimens belong to the osteological collections of iPHEP/University of Poitiers (19th century) and make up a sample with sufficient taxonomic and morphological diversity to assess our protocols. The molars were scanned using a μ-CT VISCOM X8050 (University of Poitiers Microtomography Centre).

The virtual volumes reconstructed from the microtomographic images were processed by automatic segmentation tools with manual correction, using ©Avizo v7 commercial software. A review of concepts and practices in 3D image segmentation is beyond the scope of this paper, but readers may refer to the abundant literature on this topic [e.g. 17,18].

Once segmentation was complete, the EC was isolated from the dentine material and pulp canals. The EC volume data was converted into a polygonal surface (triangular 3D grid) corresponding to a set of three-dimensional points (nodes) connected by their edges. For analysis purposes and in order to minimize the computational load, each EC was set to an equivalent reduced amount of polygons by decimation. The decimation procedure was done by retessellation of the original polyhedral surface with tooth-size standardization of the polygonal unit area (i.e., each surface is made up of polygons of equivalent area, which depends on the tooth size). Following this procedure, all the occlusal EC surfaces together comprised about 22,000 polygons across the sample. Decimation of the original surfaces does not produce any significant alteration of the tooth morphology (Fig. 1) [1,19].

Each surface node and surface triangle is precisely referenced by its Cartesian (x, y, z) coordinates in a virtual 3D space. In order to standardize our result, we chose to orient each molar in its 3D virtual space using a common reference plane and axis. The virtual three-dimensional molar surfaces are aligned to a geometrically constructed plane with no preconceptions as to their biological or functional significance or their future reproducibility in a larger, more heterogeneous sample (*i.e*., including more disparate taxa and molar morphologies). The only prerequisite, for the sake of convenience, was to have the occlusal surface parallel to the viewer plane (e.g. [20]). First, each molar was aligned to a *(xy)* plane (reference plane) defined by the tip of the dentine horns at the protocone, paracone and metacone. The z axis was positively oriented from the cervix to the occlusal relief of the tooth. Secondly, each molar was realigned in the reference plane by having its mesial axis, a line joining the tip of the dentine horns at the protocone and paracone, parallel to the x axis of the virtual 3D space. Finally, again for convenience, the lowest point of each molar cervix was set to *(x, y, 0)* so that crown height is measured on a z-positive scale.

Having oriented all the molars, topographical data were retrieved from EC. The surface geometry of the molar morphology consists of a matrix of 3D point coordinates and their connections. Each triangle of the polygonal surfaces is indexed and can be attached to various signifiers (e.g. enamel thickness at location, elevation, orientation or inclination). Thus, it is possible not only to retrieve individual or average signifier values from the precise location on the molar, but also their entire distribution and all their variations over the whole tooth or a particular region of interest.

Topographical signifier: inclination

A standardized vector field was computed from the triangular 3D molar grid, and the matrix of normal vector coordinates at each individual EC triangle was recorded. The vector

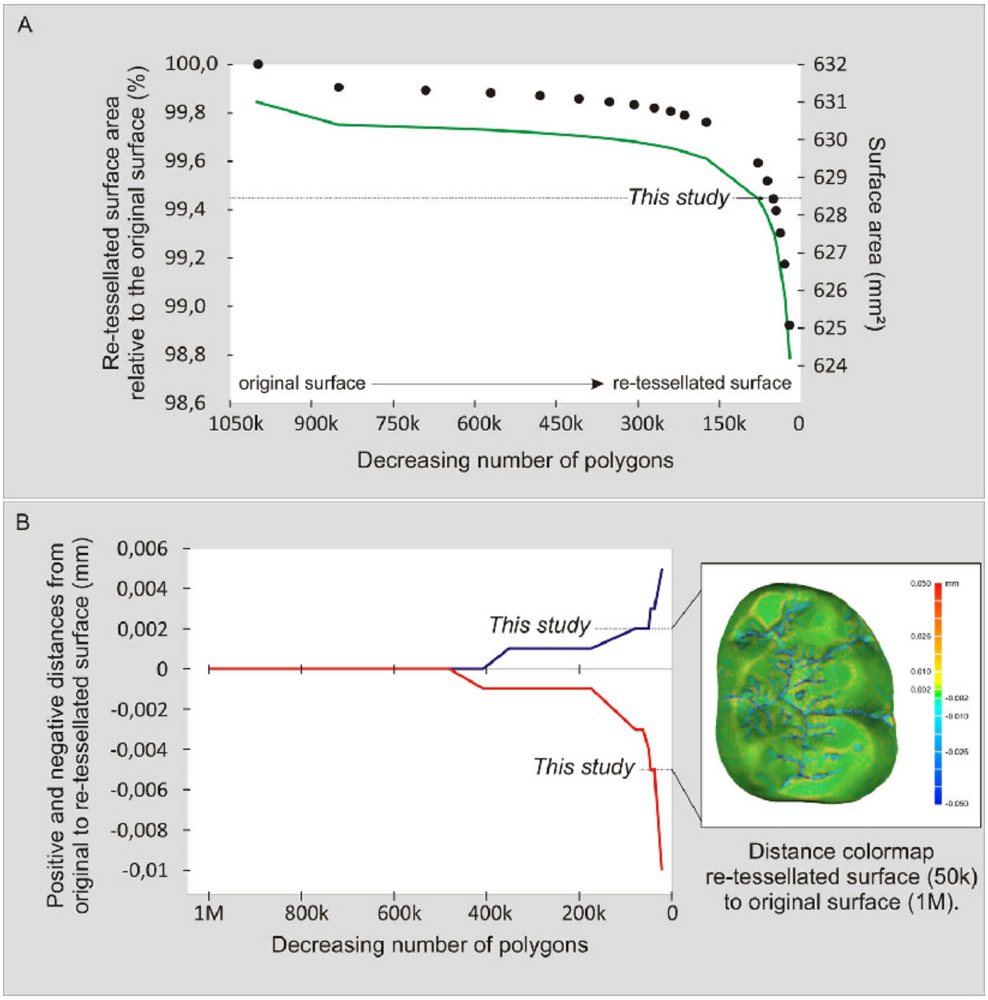

Fig. 1 Surface re-tessellation and tooth morphology. (A) Effect of decimation, here on the enamel surface. Note that in our study, decimation preserves 99% of the original surface. (B) Computed positive (blue line) and negative (red line) distances between decimated surfaces and original surfaces, example of a *Gorilla* lower molar. Note that shape is well preserved by the decimation process, as the alteration mainly concerns the depth of the enamel grooves (less than 50 µm in magnitude) / *Décimation des surfaces et morphologie des molaires. (A) Effet de la décimation, l'exemple de la surface de l'émail. Dans cette étude, 99 % de la surface originale est préservée au cours du processus de décimation. (B) Analyse des distances positives (ligne bleue) et négatives (ligne rouge) entre les surfaces décimées et la surface originale, exemple d'une molaire inférieure de* Gorilla. *La forme originale de la dent est bien préservée au cours du processus de décimation, l'altération observée concerne essentiellement la profondeur des sillons de l'émail (moins de 50 µm en amplitude maximum)*

coordinates are used as raw data for retrieving topographical information on the tooth shape.

Although numerous descriptors may be generated from EC, we selected one simple topographical parameter here that has been proved to be of significant interest in dental studies.

The variable inclination (λ^e) is calculated from EC polygon coordinates and the standardized vector field. All the computations are fully automated using a program developed under R [21]. This topographic variable has been successfully applied, albeit in a different form, to functional and taxonomic studies of rodents and primates (e.g. [23,24]).

Computations

The R program first performs a polygonal indexation before computing the polygon areas (υ), the geometric centre coordinates of the polygon (*i.e.*, its x, y, z position in the virtual 3D space; χ) and the topographical values (*i.e.*, λ in this note). This step allows all subsequent computed values to be precisely associated to their corresponding polygons along with their exact three-dimensional location and their area. The area values are used as a size proxy (using the number of triangles is unreliable) to assess the relative occurrence of the topographic inclination variable.

The inclination is computed for each polygon of EC (λ^e) and is defined as the angle between the polygon tangent vector in the -z direction (in the plane perpendicular to *xy* and carrying the polygon normal vector) and the horizontal plane *xy*. This parameter thus differs from the previously defined *slope* [13] as "the average change in elevation across the surface" ([13] p. 155, see also [16,23,24]). The inclination (λ) is coded over 180°, from 180° for horizontal polygons to 90° for vertical polygons. Inclination values below 90° describe re-entrant angles (surfaces).

The variation in inclination (λ^{ev}), which represents the distribution of horizontal to vertical portions of the tooth, is illustrated, for EC occlusal regions, as the distribution of the relative areas representing particular inclination intervals. In this respect, the range of inclination is divided into eighteen intervals of 10° each, and the corresponding polygonal area is computed within each interval.

The inclination variable was computed for each tooth in our sample. In this paper, the analysis is restricted to the occlusal regions of EC. The EC occlusal region was defined as the region above a plane parallel to the reference plane and passing the lowest point of the occlusal enamel basin for EC.

As an example and to aid visualization, the inclination values were mapped onto EC using a chromatic colour scale and presented for the whole tooth (Fig. 2). The patterns of relative distribution of inclination values in polar coordinates were used as raw data to assess the taxonomic significance of EC occlusal inclination profiles using Procrustes superimpositions from our test sample. The process of polygon reduction did not produce any significant alteration of the tooth shape (Fig. 1). Similarly, decreasing the number of polygons that describe the occlusal topography of the tooth did not produce any significant alteration of the inclination profiles. Decreasing the number of polygons, although this obviously reduces the number of occurrences within each inclination category, does not alter the pattern of relative distribution of inclination values.

Results

The computed inclination maps for a subsample of catarrhine molars are shown in Figure 3A. The results presented in this section provide examples of potential treatments of the data. Using the relative area of expression of inclination intervals describing λ^{ev}, the relative contribution of a particular inclination interval to the tooth surface is illustrated in Figure 3B. For the sake of concision, we chose to focus for this paper on inter-specific rather than intra-specific variability.

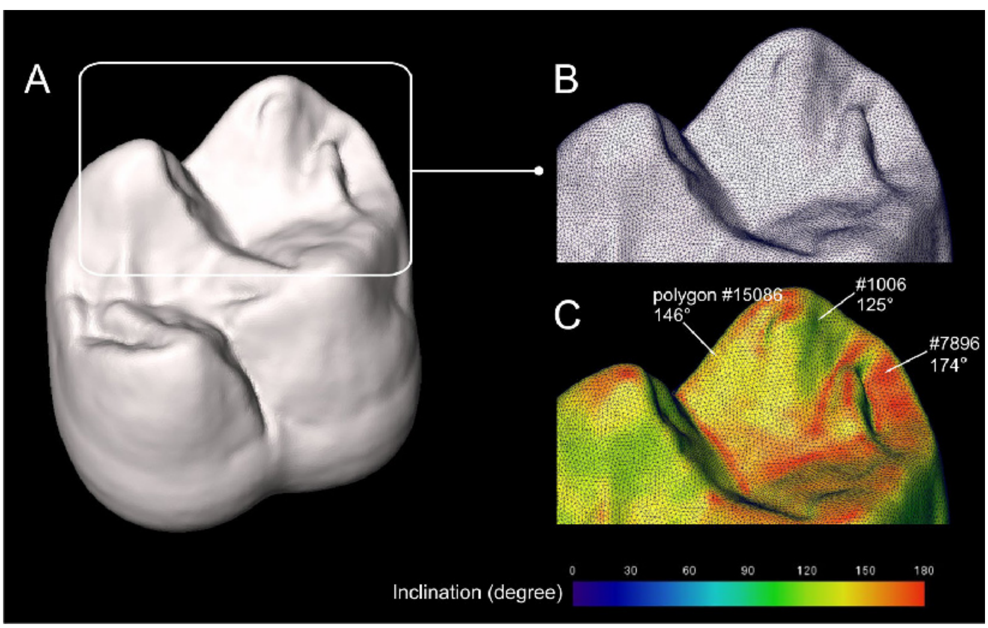

Fig. 2 Surface, grid and topographical parameters. (A) Example of a three-dimensional surface of a second upper *Gorilla* molar; (B) Focus on the polygonal grid of the paracone; (C) Inclination map of polygons for the paracone; each polygon is attached to an inclination value which is colour-coded on a chromatic scale from 0 to 180° / *Surface, maillage et paramètres topographiques. (A). Exemple de surface tridimensionnelle pour une seconde molaire supérieure de gorille; (B). Détail d'un modèle de maillage polygonal, le paracône; (C) Carte d'inclinaison des polygones pour le paracône, chaque polygone est attaché à une valeur d'inclinaison codée par une échelle chromatique variant de 0 à 180°*

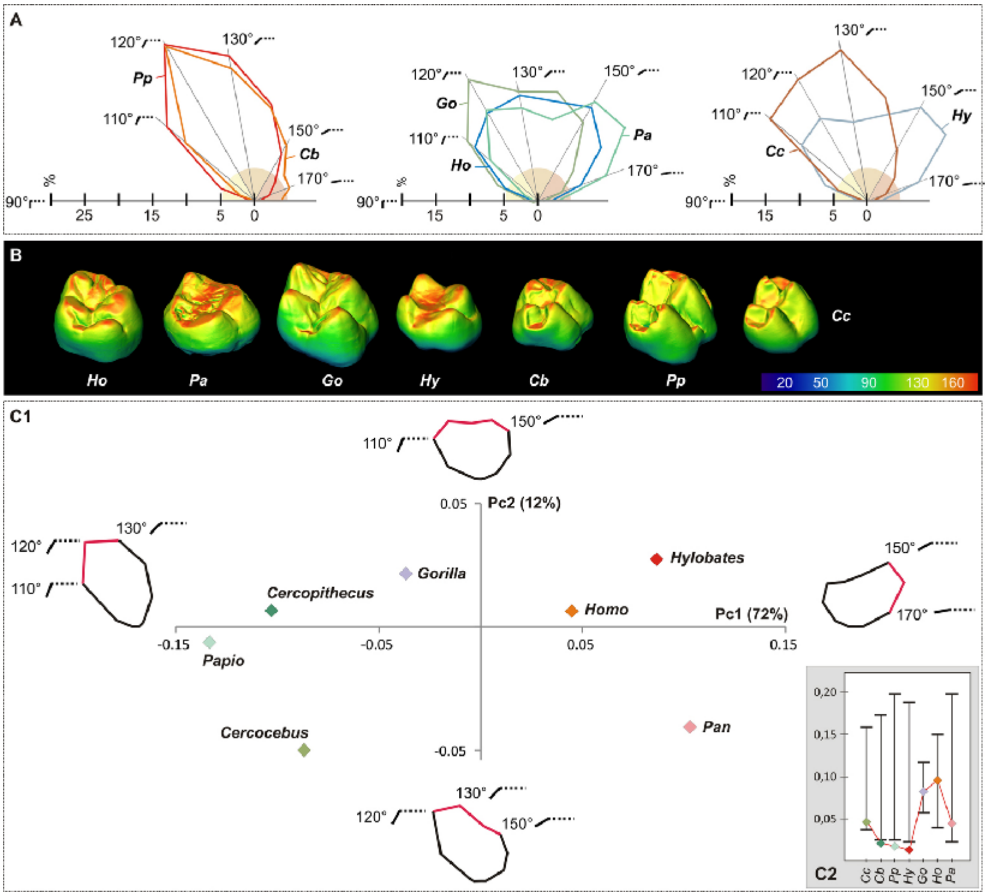

Fig. 3 Variation of inclination in catarrhines. (A) Three-dimensional morphometric maps and associated colour scales of the inclination values (degrees) of EC for a subsample of seven representative individuals of the seven genera studied (relative scale). (B) Inclination profiles of catarrhine molars. The profile corresponds, for each taxon (average data), to the EC relative proportion of area of expression of inclination intervals (increment is 10°). (C1) PCA of the specimens (centroid of each group is shown) according to their inclination values (PC1 and PC2 represent 84% of the total variation). The outlines associated with PC1 and PC2 represent the profile variations in the PCA shape-space, the red colour is for the most frequent inclination intervals. (C2) Comparison of intra-group versus inter-group variations; each variation within a taxon (red line) is defined as the maximum individual distance in the PCA shape space and compared to variation between taxa as the distance (whiskers) from the specimens considered to the centroid of other taxa. Ho, *Homo*; Pa, *Pan*; Go, *Gorilla*; Hy, *Hylobates*; Cb, *Cercocebus*; Pp, *Papio*; Cc, *Cercopithecus* / *Variations de l'inclinaison chez les catarrhiniens. (A) Cartes morphométriques tridimensionnelles et échelles chromatiques associées des valeurs d'inclinaison (degré) de la capsule d'émail pour un sous-échantillon de sept individus représentatifs des sept genres étudiés (échelle relative) ; (B) Profils d'inclinaison de molaires de catarhiniens. Le profil correspond, pour chaque taxon (moyenne), à la proportion surfacique relative des intervalles d'inclinaison (incrément de 10 °) sur la capsule d'émail. (C1) ACP des spécimens (le centroïde de chaque groupe est représenté) en fonction de leurs valeurs d'inclinaison (PC1 et PC2 représentent 84% de la variation totale). Les contours associés à PC1 et PC2 représentent les variations de profil dans l'espace morphologique de l'ACP, la couleur rouge indique les intervalles d'inclinaison les plus représentés. (C2) Comparaison des variations intra-groupe et intergroupes, chaque variation intra-taxon (ligne rouge) est définie comme la distance inter-individuelle maximum dans l'espace morphologique et comparée à la variation inter-taxons (moustaches) i.e., la distance des spécimens considérés aux centroïdes des taxons distincts. Ho,* Homo; *Pa,* Pan; *Go,* Gorilla, *Hy,* Hylobates; *Cb,* Cercocebus; *Pp,* Papio; *Cc,* Cercopithecus

The cercopithecoids have similar inclination profiles that are distinct from other catarrhines in their larger area of expression of rather vertical surfaces (from 90° to 120°). Accordingly, the variance analysis of inclination profiles using shape coordinates shows significant differences between cercopithecoids and hominoids at $p<0.05$. The area of expression is recorded at 120° for *Papio* and *Cercocebus*, and expressed almost similarly in *Cercopithecus* in the 110°-130° range. The distribution of inclination values in hominoids is more homogeneous (Fig. 3B) and distinct from cercopithecoids in the higher proportion of inclination values in the range of 130°-170°. Gorillas are distinct from other hominoids in the high degree of expression of relatively vertical inclination values (*i.e.*, 120°). The chimpanzee profile clearly tends towards a horizontal surface, i.e., represented by the 150°-170° inclination intervals. This morphology is shared with *Hylobates* although the area for the gibbon is smaller with inclination values at 110-130°.

Figure 3C shows the dispersion of the specimens (centroid of each taxon) according to their relative area of expression of inclination intervals (Principal Component Analysis of Procrustes coordinates of superimposed profiles). The distinction between cercopithecoids and hominoids appears clearly along PC1, while PC2 isolates *Cercocebus* and *Pan*, which both display a more heterogeneous distribution of areas of expression of inclination values.

Conclusions and prospects

Our approach has proved to be a useful tool for characterizing tooth shape and is expected to provide new insights into primate taxonomy. The analysis of inclination associated with the size component (*i.e.* surface extent) provides an original approach to quantitative studies of dental shape in three dimensions. The topographic parameter we selected allows a distinction be made between high-ranking (superfamily level) and low-ranking (genus level) catarrhine taxa. Taxon-specific dental morphology could thus be characterized by an inclination profile. This result is to be expected since topographic parameters obviously describe the morphological aspects of the tooth. Thus, bilophodont molars in cercopithecoids display inclination values in accordance with the development of transverse lophs between cusps, contrary to bunodont molars in hominoids. Therefore, our approach should also be able to quantify the emergence and retention of diagnostic dental features such as bilophodonty in Old World monkeys, or the development of accessory cusps in hominins. Since the distribution of inclination approximates the tooth morphology and models the proportion of vertical versus horizontal surfaces, it provides a quantitative proxy to assess dental function (*i.e.* masticatory movements).

Our preliminary results point to topography as a potential taxonomic tool, although this will need be assessed with variously worn specimens given that extreme tooth wear may reduce its potential (but the same would be true whatever the method of investigation used to interpret morphology in terms of taxonomy). It should also be noted that our results could be implemented with additional independent topographical parameters (orientation, curvature) as well as morphological parameters (elevation, enamel thickness), which together would provide a comprehensive three-dimensional characterization of the tooth. The proposed method can also be used to quantify variations in enamel thickness, a key feature in hominin evolution [19], and to relate the patterns of variation in thickness to EDJ morphologies in the context of the generation of novel dental features in the course of our own evolution.

Acknowledgements We thank all the members of iPHEP (UMR 7262) and especially A. Euriat for the virtual preparation of dental specimens. Thanks also to the anonymous reviewers and to A. Balzeau for reading our manuscript and providing helpful comments. This study was made possible by the University of Poitiers Microtomography Centre and supported by the *Agence Nationale de la Recherche* (ANR-09-BLAN-0238) and the Poitou-Charentes Region (Regional Contracts #07/RPC-R-100 & #12/RPC-013).

References

1. Grine FE, Ungar PS, Teaford MF, El-Zaatari S (2006) Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. J Hum Evol 51:297–319
2. Kavanagh KD, Evans RE, Jernvall J (2007) Predicting evolutionary patterns of mammalian teeth from development. Nature 449:427–33
3. Shimizu D (2002) Functional implications of enamel thickness in the lower molars of red colobus (*Procolobus badius*) and Japanese macaque (*Macaca fuscata*). J Hum Evol 43:605–20
4. Suwa G, Kono RT, Katoh S, et al (2007) A new species of great ape from the late Miocene epoch in Ethiopia. Nature 448:921–4
5. Jernvall J, Jung HS (2000) Genotype, phenotype, and developmental biology of molar tooth characters. Ybk Phys Anthrop 43:171–90
6. Bailey SE (2004) A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. J Hum Evol 47:183–98
7. Bunn JM, Boyer DM, Lipman Y, et al (2011) Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. Am J Phys Anthop 145:247–61
8. Evans A, Fortelius M, Jernvall J (2007) How do tooth wear affect dental complexity? Implications for tooth function and dietary reconstruction. J Vert Paleont 27:72A
9. Plyusnin I, Evans AR, Karme A, et al (2008) Automated 3D phenotype analysis using data mining. Plos One 3:e1742 (1-9)
10. Skinner MM, Gunz P, Wood BA, Hublin JJ (2008) Enamel-dentine junction (EDJ) morphology distinguishes the lower molars of *Australopithecus africanus* and *Paranthropus robustus*. J Hum Evol 55:979–88
11. Bernal V (2007) Size and shape analysis of human molars: comparing traditional and geometric morphometric techniques. J Comp Hum Biol 58:279–96
12. Benazzi S, Kullmer O, Grosse IR, Weber GW (2011) Using occlusal wear information and finite element analysis to investigate stress distributions in human molars. J Anat 219:259–72

13. Dennis JC, Ungar P, Teaford MF, Glander KE (2004) Dental topography and molar wear in *Alouatta palliate* from Costa Rica. Am J Phys Anthrop 125:152–61
14. Ungar PS, Grine FE, Teaford MF (2008) Dental microwear and diet of the Plio-Pleistocene Hominin *Paranthropus boisei*. PLoS ONE 3(4):e2044
15. Kullmer O, Schulz D, Benazzi S (2012) An experimental approach to evaluate the correspondence between wear facet position and occlusal movements. Anat Rec 295:846–52
16. Ungar P (2004) Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J Hum Evol 46:605–22
17. Russ JC (2011) The image processing handbook (6th edition). Boca Raton: CRC Press. 885 p
18. Zollikofer CPE, Ponce de León MS (2005) Virtual reconstruction: A primer in computer-assisted paleontology and biomedicine. Hoboken: John Wiley & Sons. 333 p
19. Guy F, Gouvard F, Boistel R, et al (2013) Prospective in (Primate) Dental Analysis through Tooth 3D Topographical Quantification. Plos One 8(6):e66142
20. Benazzi S, Fantini M, De Crescenzio F, Persiani F, Gruppioni G (2009) Improving the spatial orientation of human teeth using a virtual 3D approach. J Hum Evol 56:286–93
21. R Development Core Team (2012) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available: http://www.R-project.org
22. Evans AR, Wilson GP, Fortelius M, Jernvall J (2007) High-level similarity of dentitions in carnivorans and rodents. Nature 445: 78–81
23. Ungar P, Williamson M (2000) Exploring the effects of toothwear on functional morphology: A preliminary study using dental topographic analysis. Palaeontologia Electronica 3:1–18
24. Lazzari V, Charles C, Tafforeau P, et al (2008) Mosaic convergence of rodent dentitions. Plos One 3:e3607 (1-13)