

Ouranopithecus macedoniensis **(Mammalia, Primates, Hominoidea): virtual reconstruction and 3D analysis of a juvenile mandibular dentition (RPI-82 and RPI-83)**

Roberto MACCHIARELLI

Muséum national d'Histoire naturelle,
Département de Préhistoire, UMR 7194 CNRS,
1 rue René Panhard, F-75013 Paris (France),
and Université de Poitiers, Département Géosciences,
40 av. du Recteur Pineau, F-86000 Poitiers (France)
roberto.macchiarelli@mnhn.fr

Arnaud MAZURIER

Société Études Recherches Matériaux, CRI-BIOPOLE,
4 rue C. Heitz, F-86000 Poitiers (France)
arnaud.mazurier@erm-poitiers.fr

Bernhard ILLERHAUS

Federal Institute for Materials Research and Testing (BAM),
Richard-Willstätter-Str. 11, G-12478 Berlin (Germany)
bernhard.illerhaus@bam.de

Clément ZANOLLI

Muséum national d'Histoire naturelle,
Département de Préhistoire, UMR 7194 CNRS,
1 rue René Panhard, F-75013 Paris (France)
clement.zanolli@mnhn.fr

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 (4): 851-863.

ABSTRACT

Dental enamel thickness is commonly listed among the diagnostic features for taxonomic assessment and phylogenetic reconstruction in the study of fossil hominids, and is widely used as an indicator of dietary habits and palaeoenvironmental conditions. However, little quantitative information is currently available on its topographic variation in deciduous crowns of fossil primates. By means of high-resolution microtomography, we investigated the inner structural morphology of the mixed lower dentition of *Ouranopithecus macedoniensis*, a late Miocene large-bodied ape from Macedonia, Greece. With respect to the extant African apes and *Homo*, *O. macedoniensis* shows a significant difference in occlusal enamel thickness between the relatively thin deciduous second molar and the absolutely thick-enamelled permanent first molar.

KEY WORDS

Mammalia,
Primates,
Ouranopithecus,
hominid,
Miocene ape,
mixed dentition,
microtomography,
tooth inner structure,
3D reconstruction,
enamel thickness.

RÉSUMÉ

Ouranopithecus macedoniensis (Mammalia, Primates, Hominoidea): reconstruction virtuelle et analyse 3D d'une denture inférieure juvénile (RPL-82 et RPL-83).

L'épaisseur de l'émail dentaire est couramment incluse parmi les traits diagnostiques pour l'attribution taxinomique et la reconstruction phylogénétique dans l'étude des hominidés fossiles, et elle est aussi utilisée comme indicateur d'habitudes alimentaires et de conditions paléoenvironnementales. Cependant, peu d'informations quantitatives sont disponibles à ce jour concernant sa variation topographique dans les couronnes déciduales des primates fossiles. Grâce à la microtomographie à haute résolution, nous avons exploré la morphologie structurale interne de la denture inférieure mixte d'*Ouranopithecus macedoniensis*, un grand singe du Miocène supérieur de Macédoine, Grèce. Par rapport aux grands singes africains actuels et à *Homo*, *O. macedoniensis* montre une différence significative dans l'épaisseur de l'émail occlusal entre la deuxième molaire déciduale, relativement fine, et la première molaire permanente, très épaisse.

MOTS CLÉS

Mammalia,
Primates,
Ouranopithecus,
hominidé,
Miocène,
denture mixte,
microtomographie,
endostructure dentaire,
reconstruction 3D,
épaisseur de l'émail.

INTRODUCTION

Ouranopithecus macedoniensis (Bonis & Melentis, 1977) is a late Miocene large-bodied ape currently known from three localities in Macedonia, Greece: Ravin de la Pluie (RPL) and Xirochori (XIR), in the valley of the Axios River, and Nikiti-1 (NKT), in the Chalkidi peninsula, east of Thessaloniki (Bonis & Koufos 2001). The associated mammalian fauna, which globally indicates an open environment (Bonis *et al.* 1999; Merceron *et al.* 2005a, 2007), suggests a late Vallesian age (MN 10). More precisely, the magnetostratigraphic record available for the two northern sites of the Axios valley indicates the interval 9.6–9.3 Ma (Sen *et al.* 2000), while the faunal assemblage from Nikiti points to a slightly younger age, within the interval 9.3–8.7 Ma (Koufos 2000).

Firstly discovered in 1973 in the Axios valley (Bonis *et al.* 1974), *Ouranopithecus* Bonis & Melentis, 1977 is currently represented by cranial and mandibular remains and, mostly, from a large sample of isolated permanent teeth (Bonis *et al.* 1975, 1990, 1998; Koufos 1993, 1995; Bonis & Koufos 1993; Koufos & Bonis 2006). The mandibular remains of a young individual from the *c.* 9.3 Ma site of Ravin de la Pluie, bearing a partial mixed dentition, have been discovered for the first time in 2001 and reported in 2004 (Koufos & Bonis 2004).

The individual, likely a male whose age at death has been estimated between 3.5 and 6 years (Koufos & Bonis 2004), is represented by two fragments, RPL-82 (left partial ramus) and RPL-83 (right partial ramus). According to its original description, the left fragment preserves *in situ* three erupted deciduous teeth, all in occlusion: the lateral incisor (Li2), the canine (Lc), and the first molar (Lm1). On radiographic ground, the presence of the third premolar crown (LP3) has been also reported (Koufos & Bonis 2004). On the larger RPL-83 right fragment, the following deciduous and permanent erupted elements are visible: the deciduous canine (Rc), both deciduous molars (Rm1 and Rm2), and the fully erupted, unworn first permanent molar (RM1). In addition, partially embedded in a hard matrix, the permanent crowns of the permanent central incisor (RI1), of both lateral incisors (LI2 and RI2), and of the canine (RC) can be traced. On the same specimen, the presence of both permanent premolars (RP3 and RP4) has been recorded through radiography and cross-sectional computed tomography images (Koufos & Bonis 2004).

Specimens bearing a mixed dentition are rare in the non-human hominid and, to a lesser extent, hominin fossil record (see review in Hartwig 2002; Schwartz & Tattersall 2005; for the largest sample of deciduous teeth for any species of fossil ape, see Mortzou & Andrews 2008), and the information

currently available on dental inner structural organization, including tissue proportions and enamel thickness topographic variation of fossil primate taxa mostly concerns permanent teeth (see Olejniczak *et al.* 2008a, b).

Here we present preliminary evidence on the structural morphology of deciduous and permanent front and cheek crowns of *Ouranopithecus macedoniensis* based on the three-dimensional (3D) reconstruction and quantitative analysis of the high-resolution microtomographic record of the two mandibular portions from Ravin de la Pluie (Koufos & Bonis 2004). More specifically, we comparatively assess enamel thickness topography and proportions in its second deciduous and first permanent molars.

METHODS

The microtomographic (μ CT) acquisition and reconstruction of RPL-82 and RPL-83 have been performed in 2002 at the Bundesanstalt für Materialforschung und -prüfung (BAM) of Berlin (<http://www.ct.bam.de/>). A high-resolution 3D-tomograph equipped with a unique bipolar 320 kV micro focal X-ray tube combined with a flat panel detector of 1024×1024 pixels has been used. Scans parameters were as follow: 240 kV tube voltage; 0.05 mA tube current; 0.25 mm Sn V-filter; 1200 (each 0.3°) and 900 (each 0.4°) respectively for RPL-82 and RPL83. Reconstructions of the final volumes (isotropic voxel size of 50 μ m) have been done with Advanced Visualization Software v6.1 (AVS, Inc.). Virtual cross-sections 3D rendering were done at ERM, Poitiers (<http://www.erm-poitiers.fr>) by means of AVIZO v.5 (Mercury Computer Systems Inc.) 64-bit version.

In the case of dental elements from highly fossilized specimens, there is no single automatic solution to the problem of segmentation (isolation and digital extraction), the most effective algorithms being usually obtained by running various combinations of components and methods (Macchiarelli *et al.* 2008a; Bondioli *et al.* 2009). For the purposes of the present study, we carried out a semi-automatic segmentation of the μ CT record with manual corrections by means of AMIRA v.3.1 and v.4.0

(Mercury Computer Systems Inc.) and Artcore v.1.0 (Nespos Society). Threshold values between segmented components were found according to the methodology of Spoor *et al.* (1993).

The assessment of the relative developmental stages of RPL-82 and RPL-83 deciduous and permanent dental elements are based on the scoring systems established by Demirjian *et al.* (1973) and by Liversidge and Molleson (2004), recently revised and integrated by Bayle *et al.* (2009a).

For individual measurements, crowns were digitally isolated from roots following Olejniczak *et al.* (2008c), and surface rendering was performed using triangulation and constrained smoothing from the volumetric data (Lorensen & Cline 1987). In the case of the right deciduous second molar (Rm2) and of the permanent first molar (RM1), enamel thickness variation was assessed on the buccolingual (BL) mesial section through metaconid-protoconid (BLm), the BL distal section through entoconid-hypoconid (BLd), the mesiodistal (MD) lingual section through metaconid-entoconid (MDl), and the MD buccal section through protoconid-hypoconid (MDb) (see Macchiarelli *et al.* 2004). The following linear, surface, and volumetric variables have been measured on 2-3D reconstructions: total crown surface area; surface area of the enamel-dentine junction (EDJ); volume of the enamel cap; volume of the coronal dentine (including the coronal aspect of the pulp chamber); average enamel thickness (AET; total volume of the enamel/EDJ surface area); average of minimum enamel thickness (average of the minimum thickness between each outer enamel surface element and all the elements representing the EDJ); maximum radial enamel thickness (maximum value of the minimum enamel thickness); scale-free relative enamel thickness (RET; AET/cubic root of crown "dentine" *100) (for methodological issues, see Martin 1985; Kono 2004; Macchiarelli *et al.* 2006; Olejniczak *et al.* 2008c; Bayle *et al.* 2009b).

Linear measurements were taken on cross-sections using the software package MPSAK v.2.9 (available in Dean & Wood 2003). The volumes have been automatically extracted by counting the number of voxels contained in a segmented component and multiplying it by the size of a single voxel.

Intra- and inter-observer tests for accuracy of the measurements were run by two observers. Recorded differences are less than 5%, which is compatible with previous results (e.g., Suwa & Kono 2005; Olejniczak & Grine 2006; Bayle *et al.* 2009b).

For the purposes of this preliminary descriptive study, the results of *O. macedoniensis* have been compared to the evidence from three cases (all unworn or poorly worn dentitions) available in our files illustrating the “average” condition shown by modern humans, chimpanzee (*Pan troglodytes*), and gorilla (*Gorilla gorilla*), obtained by means of high-resolution ($45.5 \times 45.5 \times 45.7 \mu\text{m}^3$) synchrotron radiation microtomography (SR- μCT) at the beamline ID 17 of the European Synchrotron Radiation Facility of Grenoble (Macchiarelli *et al.* 2006, 2007, 2008a; Mazurier *et al.* 2006).

RESULTS AND DISCUSSION

Besides the three erupted deciduous teeth (Li2, Lc, and Lm1) and the LP3 originally observed on radiographs (Koufos & Bonis 2004), the μCT -based virtual reconstruction of the RPI-82 left mandibular portion (Fig. 1) also reveals the previously unreported crown of the permanent canine (LC). Additionally, the 3D buccal projection in semi-transparency of the RPI-83 right specimen permits to clarify the relative position assumed by the residual crown fragment corresponding to the RI1 (cf. Koufos & Bonis 2004: 700, 706), and also to visualize the two displaced lateral permanent incisors (Macchiarelli *et al.* 2008a). In sum, with respect to the external appearance and the preliminary radiographic and tomographic record of these two specimens, the 3D virtual rendering extends to 15 (six deciduous and nine permanent) the number of dental elements borne by the two *Ouranopithecus* juvenile mandibular fragments (Li2, Lc and Rc, Lm1 and Rm1, Rm2, RI1, LI2 and RI2, LC and RC, LP3 and RP3, RP4, RM1).

RELATIVE MATURATIONAL PATTERN

With regards to developmental timing, the analysis of several histological sections of a lower third molar suggests a crown formation time for this Miocene

ape similar to *Pan* Oken, 1816 and greater than reported for modern humans (Smith *et al.* 2004). A detailed report of the *Ouranopithecus* dental developmental pattern is out of the goals of the present study. Nonetheless, even if the preservation condition and degree of fossilization of the two mandibular specimens, the resolution of the available microtomographic record, and the slight physical displacement shown by some dental elements (likely due to multi-axial compression towards the right side having affected the original mandible) do not allow any conclusive statement on this matter, some remarks are possible on the relative maturational stage reached in this juvenile individual by its partially hidden dental elements.

Notably, the deciduous lateral incisor and molars seem having started the process of root resorption (stage *r*), thus showing a more advanced developmental stage than the deciduous canine (more likely in stage *h1*, i.e. root length complete with apical walls converging, but still open apex [in Bayle *et al.* 2009a]). While the evaluation of the permanent central incisor is not reliable, crown formation in the lateral one seems to be completed down to the cement-enamel junction (stage *D*). In the permanent canine and both premolars, approximal edges of forming crown have reached future contact areas, and the beginning of a dentinal deposit is seen (at least, stage *C*); crown formation in the third premolar likely reached completion down to the cement-enamel junction (stage *D*). In the only preserved permanent molar, root length is greater than crown height and, midway towards the apex, root wall is thinner than root canal (stage *F*).

ENAMEL THICKNESS DISTRIBUTION

According to Koufos & Bonis (2004), in *Ouranopithecus* there appears to be a marked proportional difference in enamel thickness between the deciduous and the permanent teeth, being the lower M1 very thick relative to its size. These preliminary evaluations, which based on medical CT imaging, are fully supported by our high-resolution μCT investigation.

The buccolingual (BL) virtual sections of six deciduous and eight permanent erupted and unerupted *Ouranopithecus* tooth crowns are shown in Figure 2.

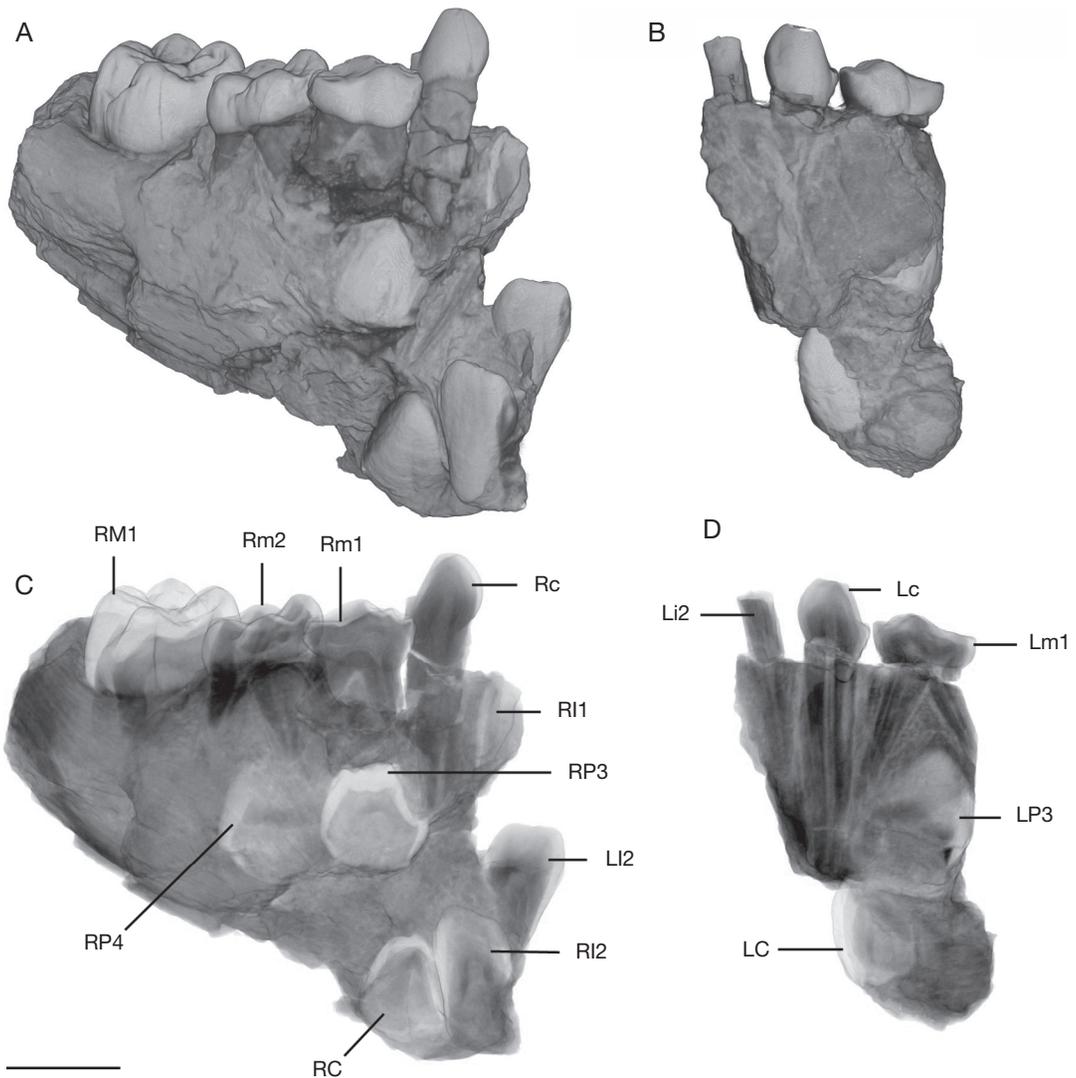


FIG. 1. — μ CT-based 3D virtual reconstruction of the juvenile *Ouranopithecus* Bonis & Melentis, 1977 partial mandible bearing a mixed dentition from the late Miocene site of Ravin de la Pluie (Macedonia, Greece). The two portions, RPI-82 (left partial ramus) and RPI-83 (right partial ramus), are here shown in frontal view: **A**, RPI-83; **B**, RPI-82; **C**, **D**, RPI-83 and RPI-82 rendered in semi-transparency with indication of the deciduous and permanent dental elements preserved *in situ*. Abbreviations: see text. Scale bar: 10 mm.

In the case of the deciduous second right molar (Rm2) and of the permanent first molar (RM1), BL sections are provided through the mesial (BLm) and the distal (BLd) cusps, and two additional mesiodistal (MD) sections are provided through the lingual (MDl) and the buccal (MDb) sides, respectively. While occlusal wear affects the de-

ciduous crowns (notably, Li2 and both canines), some observations on their enamel thickness radial variation are possible along the crown walls. On the deciduous molars, dentine is exposed on the tip of some cusps, but lateral wall enamel is intact; conversely, the enamel is finely preserved on the fully erupted M1.

TABLE 1. — μ CT-based comparative dental measures based on 3D reconstructions for the deciduous lower second molar (m2) and the permanent lower first molar (M1) in *O. macedoniensis* Bonis & Melentis, 1977, *H. sapiens* Linnaeus, 1758, *P. troglodytes* (Blumenbach, 1775), and *G. gorilla* (Savage & Wyman, 1847). All taxa are represented by a single tooth. Only three variables have been considered for m2 because of occlusal wear in *Ouranopithecus* Bonis & Melentis, 1977. Parentheses bracket values affected by cuspal wear and represent minimal estimations. RET is adimensional.

		<i>O. macedoniensis</i>	<i>H. sapiens</i>	<i>P. troglodytes</i>	<i>G. gorilla</i>
Total crown surface area (mm ²)	M1	482.94	273.61	302.25	503.93
Surface area of EDJ (mm ²)	m2	163.96	144.12	122.12	241.96
	M1	265.63	165.73	199.48	370.38
Volume of the enamel cap (mm ³)	M1	571.51	212.57	210.18	344.65
Volume of the coronal dentine (mm ³)	M1	430.66	186.82	261.20	706.09
Average enamel thickness (mm)	M1	2.15	1.28	1.05	0.93
Average of minimal enamel thickness (mm)	m2	(0.69)	0.64	0.45	0.43
	M1	1.65	1.06	0.87	0.83
Maximum radial enamel thickness (mm)	m2	(1.32)	1.12	0.74	0.75
	M1	2.87	1.89	1.36	1.40
Relative enamel thickness (RET)	M1	28.49	22.40	16.40	10.50
Average of minimal enamel thickness ratio m2/M1*100		41.82%	60.38%	51.72%	51.81%
Maximum radial enamel thickness ratio m2/M1*100		45.99%	59.26%	54.41%	53.57%

In *Ouranopithecus*, the enamel is thicker on the deciduous canine than on the deciduous lateral incisor, especially buccally (thickest values: 0.66 vs. 0.22 mm, respectively). While this pattern is shared also by *Homo* Linnaeus, 1758 and *Gorilla* Saint-Hillaire, 1853, for example, its extent is greater in the late Miocene ape. Conversely, the quantitative contrast usually observed on the deciduous lateral incisor of extant hominids between thicker buccal and thinner lingual enamel is virtually absent in *Ouranopithecus*, even if it is found on the deciduous canine (0.66 mm buccally vs. 0.40 mm lingually). Differences in enamel topography between the lower m1 and m2 mostly concern the buccolingual section through the mesial cusps, which in *Ouranopithecus* is thicker on the second molar (1.05 vs. 0.73 mm, on average). On m2, the thickest radial enamel (1.53 mm) is found on the mesial aspect of the metaconid.

Preliminary estimates on the unerupted permanent crowns show that the thickest radial enamel is buccal on both the lateral incisor (0.96 vs. 0.73 mm on the lingual aspect) and the canine (1.20 vs. 0.83 mm). A quantitative assessment

on P3 shows thicker enamel on the lingual side (2.33 mm), while on P4 the maximum radial thickness (2.66 mm) is found buccally.

With special reference to the contrast for the non-cuspal enamel between the m2, which is occlusally worn, and the unworn M1, it can be noted that, on both crowns, the lateral enamel is thicker distally than mesially (1.29 vs. 1.0 mm on m2 and 3.22 vs. 2.51 mm on M1). On the permanent molar, enamel is thicker buccally (2.27 mm) than lingually (1.54 mm). According to our comparative record, this pattern is also shown by *H. sapiens* Linnaeus, 1758, *Pan* and *Gorilla*, but the quantitative contrast between the two teeth specifically displayed by this juvenile *Ouranopithecus* is more marked.

On M1, *Ouranopithecus* cuspal enamel thickness follows the relative decreasing pattern hypoconid (2.61 mm) > hypoconulid (~2.5 mm) > entoconid (2.4 mm) > protoconid (2.04 mm) > metaconid (1.85 mm). In the comparative record considered for this study, while M1 hypoconid and metaconid show the thickest and the thinnest radial enamel, respectively, the protoconid is relatively thicker

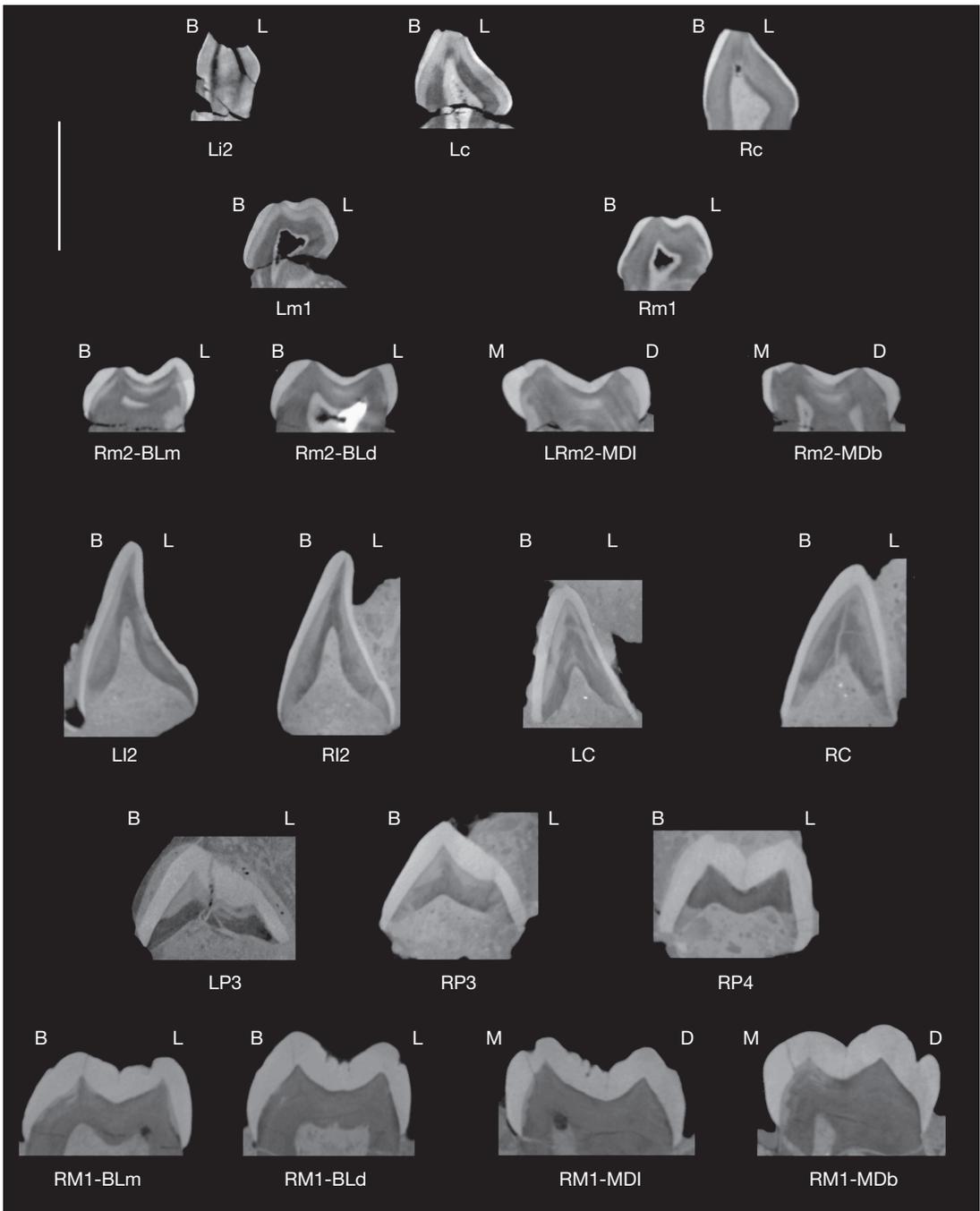


FIG. 2. — μ CT-based virtual sections of six deciduous (Li2, Lc, Rc, Lm1, Rm1, Rm2) and eight permanent tooth crowns (LI2, RI2, LC, RC, LP3, RP3, RP4, RM1) from the juvenile *Ouranopithecus* Bonis & Melentis, 1977 partial mandible (RPI-82 and RPI-83). Abbreviations: see text; **BL**, buccolingual; **BLm**, buccolingual through the mesial cusps; **BLd**, buccolingual through the distal cusps; **MD**, mediobuccal; **MDI**, mediobuccal through the lingual cusps; **MDb**, mediobuccal through the buccal cusps. Scale bar: 1 cm.

than observed in *Ouranopithecus*, notably in *Homo* (see Kono *et al.* 2002; Kono 2004; Suwa & Kono 2005; Smith *et al.* 2005; Olejniczak *et al.* 2007). In *Ouranopithecus*, the thickest radial enamel of the lower M1 (3.29 mm) is found laterally to the distobuccal cusp.

Quantitative comparisons among various taxa for a number of selected variables virtually assessed on m2 and M1 are shown in Table 1. Unfortunately, the degree of occlusal wear displayed by the *Ouranopithecus* deciduous second molar limits the extent of the analysis. Nonetheless, it is evident that, notably lingually, the lateral wall of deciduous enamel, but not the occlusal one, is significantly thicker in the Miocene ape than in the extant hominids considered in the analysis, including thick-enamelled *Homo* (Olejniczak *et al.* 2008d).

As shown by both the average of minimum enamel thickness and the maximum radial enamel thickness, *Ouranopithecus* also evidences the relatively and absolutely most marked quantitative differences in the contrast m2/M1 (cf. Koufos & Bonis 2004). Despite the current absence in the literature of comparable data on fossil apes, the extent of this discrepancy in *Ouranopithecus* clearly results from the percent ratio, estimated for the two variables, between the respective values of the deciduous and the permanent molars. For both ratios, an opposite pattern in our comparative sample is shown by *Homo*, while the extant African apes display an intermediate condition (Table 1). Conversely, the proportions recorded for the surface area of the enamel-dentine junction indicate a closer resemblance among all the investigated taxa, but extant humans (for the slightly different Neanderthal condition, see Olejniczak *et al.* 2008c).

As a whole, *Ouranopithecus* relative and absolute enamel thickness exceed the values typical of extant hominids, including *Pongo* Lacépède, 1799 (Grine 1991; Kono 2004; Gantt *et al.* 2006; Olejniczak *et al.* 2008b). For the M1, this is shown by the scale-free value of the relative enamel thickness (RET, in Table 1). These results confirm previous observations provided on histological ground by Smith *et al.* (2004). Following the analysis of an isolated lower permanent M3 from the same site (RPI-641), the authors noted that *Ouranopithecus* has the thickest relative and absolute molar enamel of any Miocene hominid reported so far,

but has relatively and absolutely thinner molar enamel than *Paranthropus* Broom, 1938 (Smith *et al.* 2004; Lacruz *et al.* 2008; but see Olejniczak *et al.* 2008a) and absolutely thinner enamel than *Gigantopithecus* von Koenigswald, 1935 (Dean & Schrenk 2003; Smith *et al.* 2004; Olejniczak *et al.* 2008b).

Preliminary estimates for the lower M1 in the late Miocene (MN 11-12) ape *Oreopithecus bambolii* Gervais, 1872 (Macchiarelli *et al.* 2008b; Zanolli *et al.* 2009) indicate an “intermediate” (*sensu* Martin 1985) enamel thickness (RET = 18.8), close to the values reported for *Sivapithecus parvada* Kelley, 1988 (18.9) and *Griphopithecus* sp. (17.2) (as summarized in Smith *et al.* 2006). Finally, among the fossil hominins, while only a single *Ardipithecus ramidus* White, Suwa & Asfaw, 1994 permanent molar crown (the left upper M1 ARA-VP-1/3288) has been measured so far by micro-computed tomography for average (AET) and relative (RET) enamel thickness (Suwa *et al.* 2009), its values (0.96 and 14.8, respectively) barely reach *c.* 50% of those found in *Ouranopithecus*, but overlap the extant African apes figures (Table 1).

A 3D virtual perspective in occlusal, lingual, and buccal views of the topographic variation of the enamel thickness assessed on the lower deciduous second molar (m2) and the permanent first molar (M1) of *Ouranopithecus* is rendered in Figure 3, where crowns have been digitally isolated from roots. In order to facilitate the comparison with *Homo*, *Pan*, and *Gorilla*, the grey scale of enamel thickness is relative to each specimen.

This visualization technique, which maps the local enamel thickness on the outer enamel surface, permits to appreciate the contrast in the relative amount of occlusal enamel volume between the permanent and the deciduous crowns which characterizes the fossil with respect to the extant apes considered in the present analysis, as well as the overall trans-taxic variation (Macchiarelli *et al.* 2008a). In fact, while the M1 occlusal enamel is much thicker in *Ouranopithecus* than in extant apes, that of the deciduous second molar is thicker in *Homo*, the only taxon among those considered in the present analysis where the enamel is proportionally thicker on m2 than on M1. However, together with relatively poorly contrasted occlusal enamel topography, compared to *Homo*, *Ouranopithecus* m2 has absolutely thicker enamel

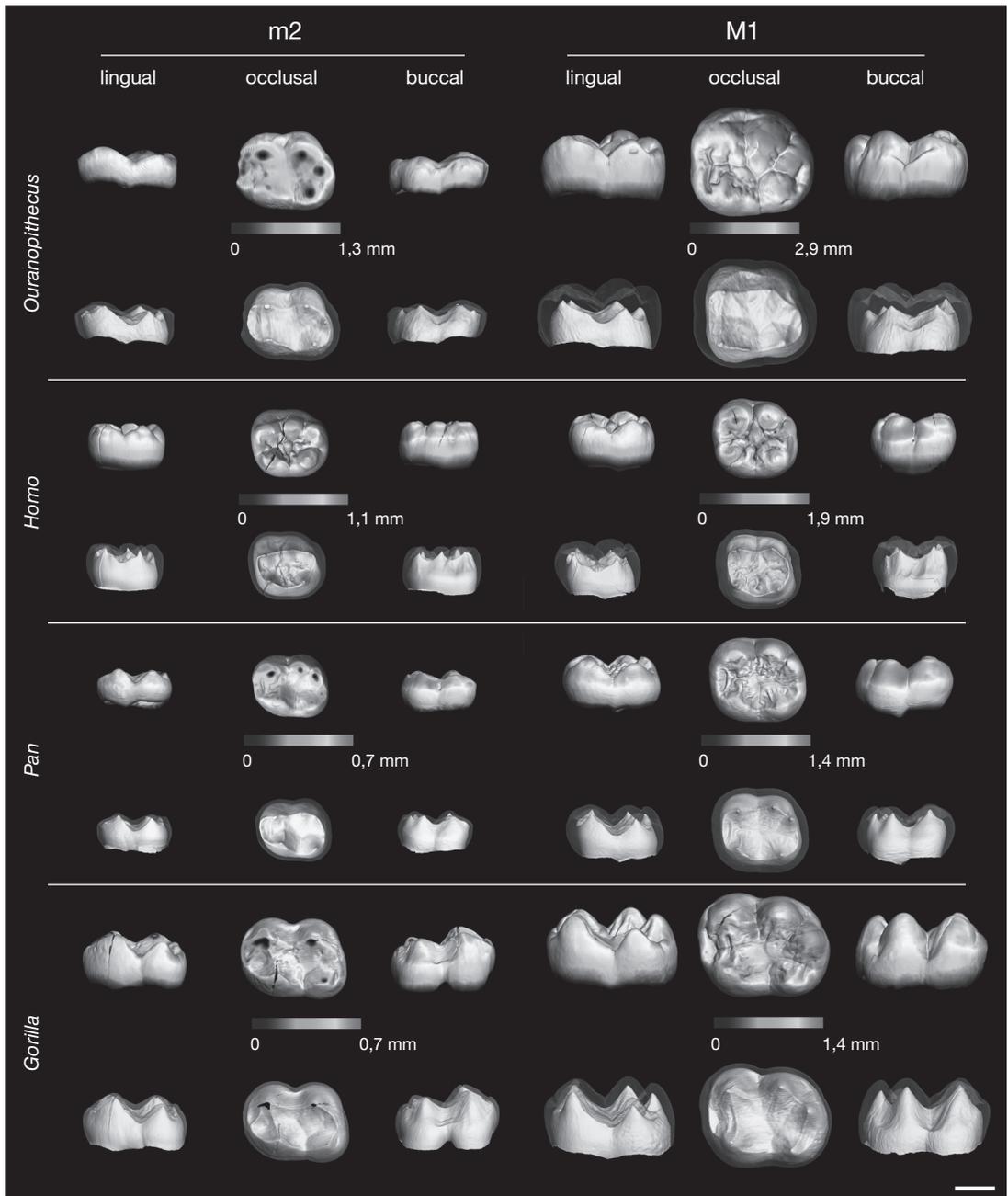


Fig. 3. — μ CT-based comparative enamel thickness and dentine shape variation of the lower deciduous second molar (m2) and permanent first molar (M1) in *Ouranopithecus* Bonis & Melentis, 1877, *Homo* Linnaeus, 1758, *Pan* Oken, 1816, and *Gorilla* Saint-Hillaire, 1853. Crowns have been digitally isolated from roots and are shown in lingual, occlusal, and buccal views. The enamel thickness topographic variation (upper row for each taxon) is rendered by a thickness-related grey scale (ranging from “thin” light to “thick” dark), specific for each investigated tooth. Isolated dark spots correspond to cuspal dental wear. Dentine partial volume (lower rows) is virtually rendered by enamel transparency. Scale bar: 5 mm.

lingually and buccally. Also, while partially affected by wear, occlusal enamel in *Ouranopithecus* seems distributed more evenly across the deciduous than the permanent crown.

The topographic rendering of this feature allows the qualitative and quantitative appreciation not only of the cuspal-related occlusal variation, but also of the differences existing between the crown walls (Schwartz 2000; Kono *et al.* 2002; Kono 2004; Olejniczak *et al.* 2008b). Notably, while in M1 the enamel is systematically thicker buccally than lingually, a similar contrast is not found on the m2 in *Ouranopithecus* and, to a minor extent, also in *Gorilla*.

In the same image (Fig. 3), m2 and M1 dentine partial volumes are virtually rendered for each taxon by enamel transparency. Besides the occlusal profile, the lingual and buccal perspectives show the relatively short dentine horns of *Ouranopithecus*, a feature associated to a low-cusped occlusal surface, notably on the RPI-83 lower first permanent molar. Among the fossil hominids investigated so far in a high-resolution 3D perspective, a similar pattern has been observed in *Gigantopithecus* (Olejniczak *et al.* 2008b).

A full account of the relationships between tooth form, structure and function in primates remains out of reach (Ungar 2008). However, a hyper-thick-enamelled lower M1 crown displaying a relatively large occlusal surface related to short dentine horns indicates that, differently from extant African apes but similarly to other extinct hominid taxa (e.g., Martin 1985; Grine & Martin 1988; Andrews & Martin 1991; Macho & Thackeray 1992; Smith *et al.* 2003, 2004; Macchiarelli *et al.* 2004, 2008a; Olejniczak *et al.* 2008b), *Ouranopithecus* developed a hyper-masticatory adaptation to grind very tough food (for its microwear pattern, see Ungar 1996; Merceron *et al.* 2005b).

In describing the inner dental features of the late Miocene *Chororapithecus abyssinicus* Suwa, Kono, Katoh, Asfaw & Beyene, 2007, from Ethiopia, Suwa *et al.* (2007) noted that its thick enamel “functional” side cusps and the extremely low EDJ topography seen in one of its upper molars indicate that this large-bodied ape is probably too derived to represent a direct ancestral condition of the modern gorilla. Accordingly, whenever enamel thickness variation by itself is used for assessing phylogenetic relationships among extinct

taxa, uniquely based on the present results, a direct ancestry of *Ouranopithecus* to the earliest putative members of the hominin clade seems unlikely because of its highly specialized condition.

Conversely, the functional/adaptative reasons for the striking discrepancy in relative occlusal enamel thickness between the deciduous and the permanent molars characterizing the Vallesian ape with respect to the fossil and extant apes, including *Homo*, and its specific patterning in thickness distribution at each tooth position within the dental arcade (Smith *et al.* 2008) and between the deciduous and the permanent dentition (Aiello *et al.* 1991) deserve additional research.

CONCLUDING REMARKS

During the last decade, advances in dental anthropology have shown that critical information for assessing evolutionary pathways and phylogenetic relationships, adaptive strategies, growth rates and developmental timing, and age- and sex-related variation patterns in extinct primate taxa is hidden within the dental crown and root(s) (see review in Bailey & Hublin 2007; Irish & Nelson 2008). In addition/alternative to histomorphometry, the increasing use of noninvasive analytical techniques capable to virtually explore, to extract, to “clean”, and to render in a 3D perspective at varied resolutions the subtle endo-microstructural signature imprinted in dental tissues have recently opened new promising research tracks, mostly in the analysis and interpretation of the fossil record (e.g., Smith & Tafforeau 2008; Macchiarelli *et al.* 2008a; Tafforeau & Smith 2008). Accordingly, it is likely that the currently in progress comparative characterization of the mixed dentition of *Ouranopithecus macedoniensis*, notably of the 3D topography of its enamel-dentine junction, will shed new light on the still open question of its taxonomy and phylogenetic relationships (Koufos & Bonis 2005; Kunitatzu *et al.* 2007).

Acknowledgements

We are indebted to S. Peigné and G. Merceron for their kind invitation to contribute this special volume

in honour of Prof. L. de Bonis. R. M. acknowledges that, since his early arrival at the University of Poitiers, in 2001, L. de Bonis provided him generous and competent support in teaching and research activities. We thank L. de Bonis and G. Koufos for having granted access to the fossil specimens discussed in this paper. Comparative data used in this study come from microtomographic analyses of modern and fossil primate teeth realized during the last years at: the ESRF beamline ID 17 of Grenoble, the Dept. of Physics at the Univ. of Bologna, the BAM of Berlin, the Centre de Microtomographie (CdMT) at the University of Poitiers. For technical and scientific collaboration, we acknowledge P. Bayle, A. Bergeret, L. Bondioli, J. Braga, A. Bravin, F. Casali, C. Dean, B. Maureille, C. Nemoz, L. Rook, M. Rossi, P. Sardini, P. Tafforeau, V. Volpato. Researches supported by the French CNRS, the EUTNT Project, the ESRF, the Univ. of Poitiers (to R.M.), the GDR 2152 (to R. M. and A. M.), the Région Poitou-Charentes (to A. M.).

REFERENCES

AIELLO L. C., DEAN M. C. & MONTGOMERY C. 1991. — The natural history of deciduous tooth attrition in hominoids. *Journal of Human Evolution* 21: 397-412.
 ANDREWS P. & MARTIN L. 1991. — Hominoid dietary evolution. *Philosophical Transactions of the Royal Society of London, Serie B* 334: 199-209.
 BAILEY S. E. & HUBLIN J.-J. (eds) 2007. — *Dental Perspectives on Human Evolution. State of the Art Research in Dental Paleoanthropology*. Springer, Berlin, 409 p.
 BAYLE P., BRAGA J., MAZURIER A. & MACCHIARELLI R. 2009a. — Dental developmental pattern of the Neanderthal child from Roc de Marsal: a high-resolution 3D analysis. *Journal of Human Evolution* 56: 66-75.
 BAYLE P., BRAGA J., MAZURIER A. & MACCHIARELLI R. 2009b. — High-resolution assessment of the dental developmental pattern and characterization of tooth tissue proportions in the late Upper Paleolithic child from La Madeleine, France. *American Journal of Physical Anthropology* 138: 493-498.
 BONDIOLI L., BAYLE P., DEAN C., MAZURIER A., PUYME-RAIL L., RUFF C., STOCK J. T., VOLPATO V., ZANOLLI C. & MACCHIARELLI R. 2009. — Morphometric maps of long bone shafts and dental roots for imaging topographic thickness variation. *American Journal of Physical Anthropology*.
 BONIS L. DE & KOUFOS G. D. 1993. — The face and the mandible of *Ouranopithecus macedoniensis*: description of new specimens and comparisons. *Journal*

of Human Evolution 24: 469-491.
 BONIS L. DE & KOUFOS G. D. 2001. — Phylogenetic relationships of *Ouranopithecus macedoniensis* (Mammalia, Primates, Hominoidea, Hominidae) of the late Miocene deposits of central Macedonia (Greece), in BONIS L. DE, KOUFOS G. D. & ANDREWS P. (eds), *Hominoid Evolution and Climate Change in Europe. Phylogeny of the Neogene Hominoid Primates of Eurasia*. Cambridge University Press, Cambridge: 254-268.
 BONIS L. DE & MELENTIS J. 1977. — Un nouveau genre de Primates hominoïde dans le Vallésien (Miocène supérieur) de Macédoine. *Comptes rendus de l'Académie des Sciences de Paris* 284: 1393-1396.
 BONIS L. DE, BOUVRAIN G., GERAADS D. & MELENTIS J. 1974. — Première découverte d'un primate hominoïde dans le Miocène supérieur de Macédoine (Grèce). *Comptes rendus de l'Académie des Sciences de Paris* 278: 3063-3066.
 BONIS L. DE, BOUVRAIN G. & MELENTIS J. K. 1975. — Nouveaux restes de primates hominoïdes dans le Vallésien de Macédoine (Grèce). *Comptes rendus de l'Académie des Sciences de Paris* 281: 379-382.
 BONIS L. DE, BOUVRAIN G., GERAADS D. & KOUFOS G. D. 1990. — New hominid skull material from the late Miocene of Macedonia in Northern Greece. *Nature* 345: 712-714.
 BONIS L. DE, KOUFOS G. D., GUY F., PEIGNÉ S. & SYL-VESTROU I. 1998. — Nouveaux restes du primate hominoïde *Ouranopithecus* dans les dépôts du Miocène supérieur de Macédoine (Grèce). *Comptes rendus de l'Académie des Sciences de Paris* 327: 141-146.
 BONIS L. DE, BOUVRAIN G. & KOUFOS G. D. 1999. — Palaeoenvironments of late Miocene Primate localities in Macedonia, Greece, in AGUSTÍ J., ROOK L. & ANDREWS P. (eds), *Hominoid Evolution and Climate Change in Europe. The Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge: 413-435.
 DEAN M. C. & SCHRENK F. 2003. — Enamel thickness and development in a third permanent molar of *Gigantopithecus blacki*. *Journal of Human Evolution* 45: 381-387.
 DEAN M. C. & WOOD B. 2003. — A digital radiographic atlas of great apes skull and dentition, in BONDIOLI L. & MACCHIARELLI R. (eds), *Digital Archives of Human Paleobiology*. ADS Solutions, Milano (CD-ROM).
 DEMIRJIAN A., GOLDSTEIN H. & TANNER J. M. 1973. — A new system of dental age assessment. *Human Biology* 45: 211-227.
 GANTT D. G., KAPPELMAN J., KETCHAM R. A., ALDER M. E. & DEAHL T. H. 2006. — Three-dimensional reconstruction of enamel thickness and volume in humans and hominoids. *European Journal of Oral Sciences* 114: 360-364.
 GRINE F. E. 1991. — Computed tomography and the measurement of enamel thickness in extant hominoids: implications for its paleontological application.

- Palaeontologica Africana* 28: 61-69.
- GRINE F. E. & MARTIN L. B. 1988. — Enamel thickness and development in *Australopithecus* and *Paranthropus*, in GRINE F. E. (ed.), *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York: 3-42.
- HARTWIG W. C. (ed.) 2002. — *The Primate Fossil Record*. Cambridge University Press, Cambridge, 530 p.
- IRISH J. D. & NELSON G. C. (eds) 2008. — *Technique and Application in Dental Anthropology*. Cambridge University Press, Cambridge, 456 p.
- 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.
- KONO R. T., SUWA G. & TANIJIRI T. 2002. — A three-dimensional analysis of enamel distribution patterns in human permanent first molars. *Archives of Oral Biology* 47: 867-875.
- KOUFOS G. D. 1993. — A mandible of *Ouranopithecus macedoniensis* from a new late Miocene locality of Macedonia (Greece). *American Journal of Physical Anthropology* 91: 225-234.
- KOUFOS G. D. 1995. — The first female maxilla of the hominoid *Ouranopithecus macedoniensis* from the late Miocene of Macedonia (Greece). *American Journal of Physical Anthropology* 91: 225-234.
- KOUFOS G. D. 2000. — New material of Vallesian late Miocene hipparions (Mammalia, Perissodactyla) from the lower Axios Valley, Macedonia, Greece. *Senckenbergiana Lethaea* 80: 231-255.
- KOUFOS G. D. & BONIS L. DE 2004. — The deciduous lower dentition of *Ouranopithecus macedoniensis* (Primates, Hominoidea) from the late Miocene deposits of Macedonia, Greece. *Journal of Human Evolution* 46: 699-718.
- KOUFOS G. D. & BONIS L. DE 2005. — The late Miocene hominoids *Ouranopithecus* and *Graecopithecus*. Implications about their relationships and taxonomy. *Annales de Paléontologie* 91: 227-240.
- KOUFOS G. D. & BONIS L. DE 2006. — New material of *Ouranopithecus macedoniensis* from late Miocene of Macedonia (Greece) and study of its dental attrition. *Geobios* 39: 223-243.
- KUNIMATSU Y., NAKATSUKASA M., SAWADA Y., SAKAI T., HYODO M., HYODO H., ITAYA T., NAKAYA H., SAE-GUSA H., MAZURIER A., SANEYOSHI M., TSUJIKAWA H., YAMAMOTO A. & MBUA E. 2007. — A new late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. *Proceedings of the National Academy of Sciences USA* 104: 19220-19225.
- LACRUZ R. S., DEAN M. C., RAMIREZ-ROZZI F. & BROMAGE T. G. 2008. — Megadontia, striae periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins. *Journal of Anatomy* 213: 148-158.
- LIVERSIDGE H. M. & MOLLESON T. 2004. — Variation in crown and root formation and eruption of human deciduous teeth. *American Journal of Physical Anthropology* 123: 172-180.
- LORENSEN W. E. & CLINE H. E. 1987. — Marching cubes: a high-resolution 3D surface construction algorithm. *Computer Graphics* 21: 163-169.
- MACCHIARELLI R., BONDIOLI L., FALK D., FAUPL P., ILLERHAUS B., KULLMER O., RICHTER W., SAID H., SANDROCK O., SCHÄFER K., URBANEK CH., VIOLA B. T., WEBER G. W. & SEIDLER H. 2004. — Early Pliocene hominid tooth from Galili, Somali Region, Ethiopia. *Collegium Antropologicum* 28: 65-76.
- MACCHIARELLI R., BONDIOLI L., DEBÉNATH A., MAZURIER A., TOURNEPICHE J.-F., BIRCH W. & DEAN C. 2006. — How Neanderthal molar teeth grew. *Nature* 444: 748-751.
- MACCHIARELLI R., MAZURIER A. & VOLPATO V. 2007. — L'apport des nouvelles technologies à l'étude des Néandertaliens, in VANDERMEERSCH B. & MAUREILLE B. (eds), *Les Néandertaliens. Biologie et Cultures*. Comité des Travaux Historiques et Scientifiques (C.T.H.S.), Paris: 169-179.
- MACCHIARELLI R., BONDIOLI L. & MAZURIER A. 2008a. — Virtual dentitions: touching the hidden evidence, in IRISH J. D. & NELSON G. C. (eds), *Technique and Application in Dental Anthropology*. Cambridge University Press, Cambridge: 426-448.
- MACCHIARELLI R., ZANOLLI C., MAZURIER A., BONDIOLI L., ROOK L. & DEAN C. 2008b. — *Oreopithecus bambolii*: virtual reconstruction and noninvasive (SR- μ CT), high-resolution characterization of its deciduous and permanent inner molar structure, with comparisons to *Ouranopithecus*. *Colloquium on European Fossil Primates*, Siena-Grosseto (abstract).
- MACHO G. A. & THACKERAY J. F. 1992. — Computed-tomography and enamel thickness of maxillary molars of Plio-Pleistocene hominids from Sterkfontein, Swartkrans, and Kromdraai (South-Africa): an exploratory study. *American Journal of Physical Anthropology* 89: 133-143.
- MARTIN L. 1985. — Significance of enamel thickness in hominoid evolution. *Nature* 314: 260-263.
- MAZURIER A., VOLPATO V. & MACCHIARELLI R. 2006. — Improved noninvasive microstructural analysis of fossil tissues by means of SR-microtomography. *Applied Physics A, Materials Science & Processing* 83: 229-233.
- MERCERON G., BONIS L. DE, VIRIOT L. & BLONDEL C. 2005a. — Dental microwear of the late Miocene bovids of northern Greece: Vallesian/Turolian environmental changes and disappearance of *Ouranopithecus macedoniensis*? *Bulletin de la Société géologique de France* 176: 475-484.
- MERCERON G., BLONDEL C., BONIS L. DE, KOUFOS G. D. & VIRIOT L. 2005b. — A new method of dental microwear analysis: application to extant primates and *Ouranopithecus macedoniensis* (late Miocene of Greece). *Palaios* 20: 551-561.
- MERCERON G., BLONDEL C., VIRIOT L., KOUFOS G. D. &

- BONIS L. DE 2007. — Dental microwear analysis of bovids from the Vallesian (late Miocene) of Axios Valley in Greece: reconstruction of the habitat of *Ouranopithecus macedoniensis* (Primates, Hominoidea). *Geodiversitas* 29 (3): 421-433.
- MORTZOU G. & ANDREWS P. 2008. — The deciduous dentition of *Griphopithecus alpani* from Paşalar, Turkey. *Journal of Human Evolution* 54: 494-502.
- OLEJNICZAK A. J. & GRINE F. E. 2006. — Assessment of the accuracy of dental enamel thickness measurements using microfocal x-ray computed tomography. *Anatomical Record* 288 A: 263-275.
- OLEJNICZAK A. J., GRINE F. E. & MARTIN L. B. 2007. — Micro-computed tomography of primate molars: methodological aspects of three-dimensional data collection, in BAILEY S. E. & HUBLIN J.-J. (eds), *Dental Perspectives on Human Evolution. State of the Art Research in Dental Paleoanthropology*. Springer, Berlin: 103-115.
- OLEJNICZAK A. J., SMITH T. M., SKINNER M. M., GRINE F. E., FEENEY R. N. M., THACKERAY J. F. & HUBLIN J.-J. 2008a. — Three-dimensional molar enamel distribution and thickness in *Australopithecus* and *Paranthropus*. *Biology Letters* 4: 406-410.
- OLEJNICZAK A. J., SMITH T. M., WEI W., POTTS R., CIOCHON R., KULLMER O., SCHRENK F. & HUBLIN J.-J. 2008b. — Molar enamel thickness and dentin horn height in *Gigantopithecus blacki*. *American Journal of Physical Anthropology* 135: 85-91.
- OLEJNICZAK A. J., SMITH T. M., FEENEY R. N. M., MACCHIARELLI R., MAZURIER A., BONDIOLI L., ROSAS A., FORTEA J., RASILLA M. DE LA, GARCIA-TABERNERO A., RADOV I. J., SKINNER M. M., TOUSSAINT M. & HUBLIN J.-J. 2008c. — Dental tissue proportions and enamel thickness in Neandertal and modern human molars. *Journal of Human Evolution* 55: 12-23.
- OLEJNICZAK A. J., TAFFOREAU P., FEENEY R. N. M. & MARTIN L. B. 2008d. — Three-dimensional primate molar enamel thickness. *Journal of Human Evolution* 54: 187-195.
- SCHWARTZ G. T. 2000. — Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. *American Journal of Physical Anthropology* 111: 221-244.
- SCHWARTZ J. H. & TATTERSALL I. 2005. — *The Human Fossil Record. Volume Four. Craniodental Morphology of Early Hominids (Genera Australopithecus, Paranthropus, Orrorin), and Overview*. Wiley-Liss, Hoboken, 561 p.
- SEN S., KOUFOS G. D., KONDOPOULOU D. & BONIS L. DE 2000. — Magnetostratigraphy of the late Miocene continental deposits of the lower Axios valley, Macedonia, Greece. *Bulletin of the Geological Society of Greece* 9: 197-206.
- SMITH T. M. & TAFFOREAU P. 2008. — New visions of dental tissue research: tooth development, chemistry, and structure. *Evolutionary Anthropology* 17: 213-226.
- SMITH T. M., MARTIN L. B. & LEAKEY M. G. 2003. — Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *Journal of Human Evolution* 44: 283-306.
- SMITH T. M., MARTIN L. B., REID D. J., BONIS L. DE & KOUFOS G. D. 2004. — An examination of dental development in *Graecopithecus freybergi* (= *Ouranopithecus macedoniensis*). *Journal of Human Evolution* 46: 551-577.
- 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.
- SMITH T. M., OLEJNICZAK A. J., REID D. J., FERRELL R. J. & HUBLIN J. J. 2006. — Modern human molar enamel thickness and enamel-dentine junction shape. *Archives of Oral Biology* 51: 974-995.
- SMITH T. M., OLEJNICZAK A. J., REH S., REID D. J. & HUBLIN J. J. 2008. — Enamel thickness trends in the dental arcade of humans and chimpanzees. *American Journal of Physical Anthropology* 136: 237-241.
- 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* 91:469-484.
- SUWA G. & KONO R. T. 2005. — A micro-CT based study of linear enamel thickness in the mesial cusp section of human molars: reevaluation of methodology and assessment of within-tooth, serial, and individual variation. *Anthropological Science* 113: 273-289.
- SUWA G., KONO R. T., KATOH S., ASFAW B. & BEYENE Y. 2007. — A new species of great ape from the late Miocene epoch in Ethiopia. *Nature* 448: 921-924.
- SUWA G., KONO R. T., SIMPSON S. W., ASFAW B., LOVEJOY C. O. & WHITE T. D. 2009. — Paleobiological implications of the *Ardipithecus ramidus* dentition. *Science* 326: 94-99.
- TAFFOREAU P. & SMITH T. M. 2008. — Nondestructive imaging of hominoid dental microstructure using phase contrast X-ray synchrotron micro-tomography. *Journal of Human Evolution* 54: 272-278.
- UNGAR P. 1996. — Dental microwear of European Miocene catarrhines: evidence for diets and tooth use. *Journal of Human Evolution* 31: 335-366.
- UNGAR P. 2008. — Strong teeth, strong seeds. *Nature* 452: 703-705.
- ZANOLLI C., BONDIOLI L., DEAN C., MAZURIER A., ROOK L. & MACCHIARELLI R. 2009. — Evolution in isolation: the dentition of *Oreopithecus bambolii* revised. *13th Congress on Earth System Evolution and the Mediterranean Area from 23 Ma to the Present. Paleontology: Hominid Evolution and Climate*, Naples (abstract).

Submitted on 27 September 2008;
accepted on 15 November 2009.