Was *Mesopithecus* a seed eating colobine? Assessment of cracking, grinding and shearing ability using dental topography

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A B S T R A C T

Extant colobine monkeys have been historically described as specialized folivores. However, reports on both their behavior and dental metrics tend to ascribe a more varied diet to them. In particular, several species, such as *Pygathrix nemaeus* and *Rhinopithecus roxellana*, are dedicated seasonal seed eaters. They use the lophs on their postcanine teeth to crack open the hard endocarp that protects some seeds. This raises the question of whether the bilophodont occlusal pattern of colobine monkeys first evolved as an adaptation to folivory or sclerocarpic foraging. Here, we assess the sclerocarpic foraging ability of the oldest European fossil colobine monkey, *Mesopithecus*. We use computed microtomograpy to investigate the three-dimensional (3D) dental topography and enamel thickness of upper second molars ascribed to the late Miocene species *Mesopithecus pentelicus* from Pikermi, Greece. We compare *M. pentelicus* to a sample of extant Old World monkeys encompassing a wide range of diets. Furthermore, we combine classic dietary categories such as folivory with alternative categories that score the ability to crack, grind and shear mechanically challenging food. The 3D dental topography of *M. pentelicus* predicts an ability to crack and grind hard foods such as seeds. This is consistent with previous results obtained from dental microwear analysis. However, its relatively thin enamel groups *M. pentelicus* with other folivorous cercopithecids. We interpret this as a morphological trade-off between the necessity to avoid tooth failure resulting from hard food consumption and the need to process a high amount of leafy material. Our study demonstrates that categories evaluating the cracking, grinding or shearing ability, traditional dietary categories, and dental topography combine well to make a powerful tool for the investigation of diet in extant and extinct primates.

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1. Introduction

Colobine monkeys have been historically described as specialized folivores, even to the point of being dubbed "leaf eating monkeys" (Kay and Hylander, 1978). Their anatomy and physiology are indeed adapted to the consumption of leaves and leafy material. They have a multi-chambered stomach with an enlarged forestomach adapted to microbial food fermentation (Kuhn, 1964; Chivers, 1994; Kay and Davies, 1994; Lambert, 1998), which improves the breakdown of cellulose and hemicellulose, but also the detoxification of plant secondary compounds (McKey, 1978; Kay and Davies, 1994). Colobines also possess a reduced anterior dentition but enlarged, bilophodont molars with sharp transverse crests that help

them to shear tough, mature leaves (Lucas and Teaford, 1994; but see; Wright and Willis, 2012). They share robust, deep jaws adapted to the extensive mastication of fibrous material (Ravosa, 1996). Finally, colobines limit energy waste by taking long rests and morning sunbaths (Stanford, 1991; Dasilva, 1992).

Notwithstanding, reports on both their behavior and dental metrics ascribe colobine monkeys a more varied diet. In particular, several species such as *Pygathrix nemaeus* or *Rhinopithecus roxellana* seem to be dedicated seasonal seed eaters (Guo et al., 2007; Koyabu and Endo, 2010; Wright and Willis, 2012; Ehlers-Smith et al., 2013). They use the lophs on their postcanine teeth to crack open the hard or tough endocarp that can protect the seeds (Happel, 1988; Lucas and Teaford, 1994; Butler, 2007). Among mammals however, lophodont morphology is commonly interpreted as an adaptation to the consumption of tough items such as leaves or grass (e.g., Artiodactyla: Harris and Li-Ping, 2007; Perissodactyla: Janis, 2000, 2007).

Concurrently, seed consumption has been suggested to be the evolutionary link leading from fruit consumption to an extensive folivory in primates (Chivers, 1994; Lucas and Teaford, 1994) and other mammals (Dubost, 1984; Bodmer, 1989, 1991). This raises the question whether the bilophodont morphology of colobine molars first evolved as an adaptation to folivory or as an adaptation to sclerocarpic foraging, defined here as the preparation and ingestion of fruit or seeds with a hard protective shell (modified from Kinzey and Norconk, 1993). The answer is likely to be found in the fossil record. Colobines are included in the modern Old World monkey family Cercopithecidae, which forms part of the superfamily Cercopithecoidea. The oldest known members of the Cercopithecoidea are the extinct Victoriapithecidae of the early to early-middle Miocene (19–12.5 Ma; Frost, 2017). They are described as terrestrial, frugivorous primates (Benefit, 2000; Blue et al., 2006). Victoriapithecids do not display the bilophodont molar pattern typical of modern Old World monkeys, i.e., only their inferior molars have lophids in addition to a lower cusp relief and a greater molar flare (Lucas and Teaford, 1994; Benefit, 2000). Cercopithecids appear in the fossil record ~12.5 Ma (Rossi et al., 2013), almost certainly originating in Africa. Mesopithecus, a colobine, is the oldest cercopithecid found outside Africa, with occurrences in Eurasia as early as 8.7–7.4 Ma (Sen et al., 2000; Koufos, 2006), and being represented at sites in south and southwestern Asia, China and Europe (Jablonski et al., 2014; Alba et al., 2015). It is the best represented cercopithecid fossil in Europe, spanning from the late Miocene to the early Pliocene (Delson, 1973; de Bonis et al., 1990; Eronen and Rook, 2004; Koufos, 2009a, 2009b; Alba et al., 2014, 2015), and has been described as a semi-terrestrial primate living in relatively open habitats such as woodland savanna (Delson, 1973; Zapfe, 1991; Youlatos, 1999, 2003; Youlatos and Koufos, 2010). From the results of two-dimensional (2D) dental microwear analysis (Reitz and Benefit, 2001; Reitz, 2002; Merceron et al., 2009a; Solounias et al., 2010) and dental microwear texture analysis (Merceron et al., 2009b) it appears that Mesopithecus was not a leaf eater like its present-day colobine relatives, but could instead be depicted as an opportunistic feeder that often consumed challenging foods such as seeds or nuts.

For most primates, teeth are essential in processing or accessing mechanically challenging foods, which are better digested after comminution or extraction. For instance, primates must remove the protective seed coat and fragment the kernel before digestion and subsequent nutrient extraction (Kinzey and Norconk, 1990, 1993). Mechanical aspects of such tooth-food interactions have been extensively documented (e.g., Kay, 1981; Kinzey and Norconk, 1990, 1993; Lucas and Teaford, 1994; Lucas, 2004; Yamashita, 2008; Wieczkowski, 2009; Daegling et al., 2011; McGraw et al., 2012, 2014). It appears that at least two characteristics define the mechanical action of teeth during mastication: the mechanical properties of the foods themselves, and dental action (or how teeth are used to access or fragment food). How a material behaves under a particular load defines its mechanical properties (Berthaume, 2016). Common food mechanical properties (FMP) described in primate studies include toughness (resistance to crack propagation) and hardness (local resistance to elastic deformation) (Berthaume, 2016), and there is a body of work creating dietary categories from FMPs (Lucas, 1979; Lucas and Luke, 1984; Yamashita, 1996). Dental actions may vary taxonomically, with different species masticating similar foods using different motions or even tooth types. For instance, both mangabeys and pitheciine monkeys are sclerocarpic foragers. However, pitheciines use their anterior teeth to scrape, puncture and pry open seed sclerocarp (Kinzey and Norconk, 1990), while mangabeys use their strong molars to crack the seeds open (McGraw et al., 2012). These feeding actions

(i.e., scraping, puncturing, prying and cracking) imply different kinds of behaviors, motions and loads and consequently different dental morphologies and adaptations (Rosenberger, 1992; Berthaume, 2016).

Investigating how the dental morphology of Mesopithecus was able to cope with mechanically challenging resources, such as seeds, is of primary interest for the understanding of colobine dental evolution. Here, we investigate the sclerocarpic foraging ability of Mesopithecus pentelicus from the late Miocene locality of Pikermi, Greece using a combination of mechanically pertinent variables. We measured both relative enamel thickness and dental topography. Although there is a debate over the significance of food hardness in the evolution of enamel thickness in primates (Sponheimer et al., 2009; Cerling et al., 2011; Ungar et al., 2012; Pampush et al., 2013; Kato et al., 2014), enamel is relatively thicker in several sclerocarpic foragers (Kay, 1981; Dumont, 1995; Shellis et al., 1998; Martin et al., 2003) and it is expected to enhance tooth resistance to stress (Lucas, 2004; Lucas et al., 2008). Dental topography is a promising field of dental morphology that gives a quantitative assessment of tooth shape through three-dimensional (3D) surface parameters, using similar methods to those developed for geographic information systems (Zuccotti et al., 1998; Ungar and Williamson, 2000; M'kirera and Ungar, 2003). Dental topography has been used to characterize the effects of wear on the molars of extant mammals (Ungar and Williamson, 2000; M'Kirera and Ungar, 2003), including Old World monkeys (Ulhaas et al., 2004; Bunn and Ungar, 2009). It has also been used to make inferences about the diets of extinct primates (e.g., Zuccotti et al., 1998; Merceron et al., 2006; Boyer, 2008; Prufrock et al., 2016). To date, a number of dental topographic variables quantifying different aspects of tooth shape have been developed. For instance, variation of relief is generally computed as the ratio between 3D tooth surface area and its 2D projection on the occlusal plane (Ungar and Williamson, 2000; Boyer, 2008). Frugivores are expected to have a lower relief index while folivores and insectivores are expected to present higher values. A variable that complements this is surface curvature. Curvature of the enamel is expected to be higher in folivores and insectivores and is computed either by calculating average angularity (Ungar and Williamson, 2000; Bunn and Ungar, 2009), Dirichlet normal energy (Bunn et al., 2011) or mean curvature of the occlusal surface (Guy et al., 2013). In addition, tooth occlusal complexity, which corresponds to the average number of dental elements, is approximated by counting the number of surface patches with distinct orientations and has been shown to correlate with the amount of herbivory (Evans et al., 2007).

In this article, we combine classic dietary categories with alternative, mechanically pertinent categories. Classic dietary categories such as folivory and frugivory group a wide range of mechanical properties (Coiner-Collier et al., 2016) but emphasize only primary food resources, and neglect secondary dietary resources such as seasonal foods. For instance, almost all extant colobine monkeys are folivorous, but some folivorous species fall back on seeds, which can be expected to influence their dental morphology (e.g., Wright and Willis, 2012). Such secondary or fall back resources might be very challenging to process and are hypothesized to exert a strong selective pressure on dental morphology (Lambert et al., 2004; Laden and Wrangham, 2005; van Schaik and Pfannes, 2005; Marshall and Wrangham, 2007; Lambert, 2009; Cuozzo and Sauther, 2012). It is thus desirable to incorporate additional pertinent dietary factors when examining dental adaptation. Hence, to evaluate sclerocarpic foraging ability in Mesopithecus, we propose alternative categories that score the ability to crack, grind or shear food in terms of hardness and toughness.

2. Materials and methods

2.1. Sample

Our work focused on the slightly worn right upper second molar of a partial palate (Fig. 1A—C) recovered from Pikermi, Greece. Although no magnetostratigraphic or radiometric dates for the locality are available, comparison of the Pikermi fauna with other sites indicates a possible age to be the upper part of middle Turolian (Koufos, 2006) and the site has been correlated with the end of MN12 i.e., ~7.75—7 Ma (de Bonis and Koufos, 1999). The unpublished palatal specimen is currently housed at the Musée des Confluences, Lyon (France), where it has been given the number MHNL-PK-25. In addition, we used casts of four upper second molars from the same locality (Fig. 1D—G). The specimens are stored at the University of Athens. Metrical data on the fossil sample are given in Table 1.

The specimens have quadrate, straight-sided bilophodont upper second molars that display asymmetrical distal margins and sharp longitudinal crests (Fig. 1A—G). Both the distal fovea and the enlarged mesial fovea extend buccally and are relatively shallow. There are basal flares on both buccal and lingual sides, which are more marked on the lingual side of each specimen. The second molars are wider mesially than distally. This morphology closely resembles that of *M. pentelicus*, the type locality of which is Pikermi (Delson, 1973; Zapfe, 1991; Rook, 1997; Jablonski, 2002; Koufos et al., 2004; Koufos, 2006, 2009a, 2009b). In addition, width/length ratios of the fossil sample correspond to those reported for *M. pentelicus* (Table 1). Therefore, we assigned the specimens described in this study to this species.

The comparative sample consisted of 28 upper second molars, from 17 extant Old World monkey species held in the National Museum of Natural History, Paris (France), the iPHEP collections at the University of Poitiers (France) and the Royal Museum of Central Africa, Tervuren (Belgium). We included Asian and African colobine monkeys, as well as some cercopithecines to ensure the comparative sample covered a wide range of dietary preferences (Table 2). Dental wear had to be minimal because we intended to interpret relative enamel thickness. Thus, selected specimens were mostly subadults with slightly worn or unworn second molars, corresponding to wear grades A to B according to the scoring system of Delson (1973).

2.2. Scoring mechanically-pertinent dietary categories

To predict if *Mesopithecus* was able to consume challenging foods, such as seeds, we devised categories based on both FMPs and action range (Table 2). We used a combination of toughness and hardness to delimit the FMP range. We searched the literature for the FMPs of the most challenging foods consumed by every species included in our sample (Table 2). We selected foods that were either heavily consumed or suggested to be a staple fallback food. Resources that were used as only filler fallback foods were ignored, as they can be replaced in the diet by other items and lack the potential to drive the selection of dental structures (Marshall and Wrangham, 2007). In addition, we selected three main action ranges that describe how Old World monkeys use their molars, "cracking", "shearing" and "grinding".

"Cracking" refers to the action of making or propagating a crack into the protective layer of the food by exerting a high orthal crushing load, in the same fashion as a nutcracker. "Grinding" refers to the action of comminuting, crushing into pieces, the bulk of the food item (e.g., one would grind the kernels of a walnut, the flesh of an apple or any non-flat tough food object). "Shearing" refers to the action of cutting relatively flat, tough foods such as leaves or grass. From dietary budgets, behavioral reports and comparable mechanical data, we scored the ability to perform each action.

Three levels of cracking were defined:

1. Soft (s) — an absence of hard food to crack.
2. Hard and brittle (Hb) — the cracking of hard food such as ripe seeds.
3. Hard and tough (H&T) — the cracking of items that were both hard and tough, like the seed casings of *Sacoglottis gabonensis* (Daegling et al., 2011).
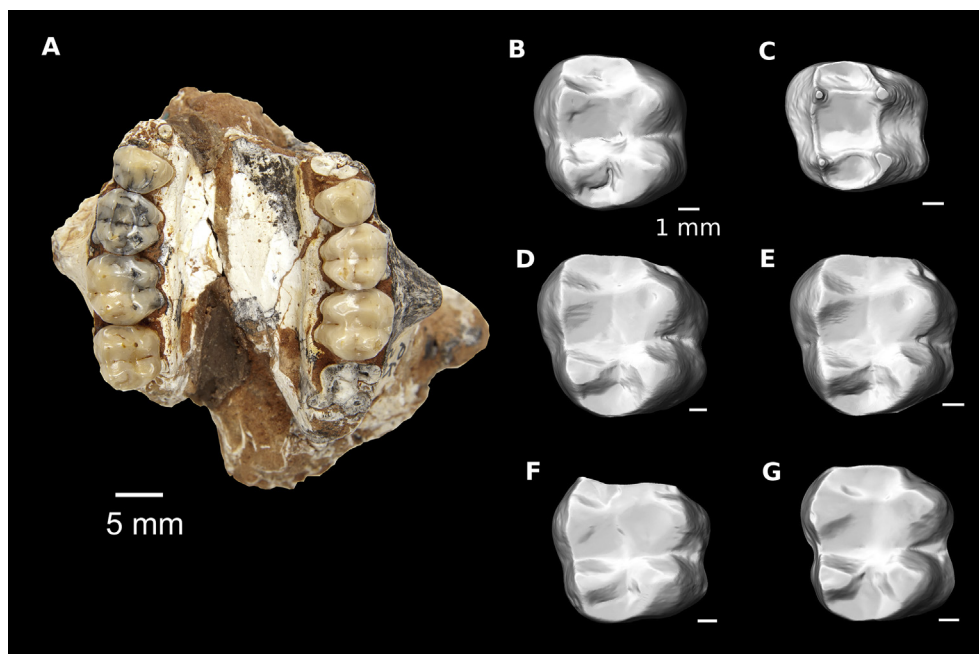

Figure 1. Study sample of *Mesopithecus pentelicus* from Pikermi, Greece. All left-sided tooth surfaces have been mirrored for comparisons (**A**) Maxillary fragment of MHNL-PK-25; (**B**) Outer enamel surface (OES) of the right upper second molar (M2) of MHNK-PK-25; (**C**) Enamel-dentine junction (EDJ) of the right upper M2 of MHNL-PK-25; (**D**) OES of LGPUA-2 (left); (**E**) OES of LGPUA-2 (right); (**F**) OES of LGPUA-4; (**G**) OES of LGPUA-no number; Scale bars, 1 mm.

Table 1
Description and linear measurements of the fossil sample.[a]

Provenance	Specimens	Tooth class	Wear grades	2D variables		
				AW (mm)	L (mm)	AW/L
Lyon, France	MHNL-PK-25	M² right	B	7.28	7.47	0.97
Athens, Greece	LGPUA-2	M² left	C	7.52	7.22	1.04
	LGPUA-2	M² right	C	7.48	7.17	1.04
	LGPUA-4	M² left	C	6.93	7.11	0.97
	LGPUA (no number)	M² left	C	7.28	7.47	0.97
Delson, 1973	M. pentelicus	M²	–	7.60 ± 0.11	7.46 ± 0.09	1.01 ± 0.01
Zapfe, 1991	M. pentelicus (♂)	M²	–	7.74 ± 0.09	7.77 ± 0.08	0.99 ± 0.00
	M. pentelicus (♀)	M²	–	7.65 ± 0.07	7.49 ± 0.05	1.02 ± 0.00

[a] Wear grades follow the classification of Delson (1973), which ranges from A (no wear) to F (contact between the four dentine wells). AW, buccolingual anterior width; L, mesiodistal length.

Four levels of grinding were defined:

1. Soft and brittle (sb) — an absence of hard or tough food to grind.
2. Hard or tough (H|T) — the eating of immature seeds or unripe fruit, which are generally tougher than their ripe counterparts (Kinzey and Norconk, 1993; Kajuna et al., 1997; Soltani et al., 2010; Ledogar et al., 2013).
3. Hard and brittle (Hb) — the consumption of mature seeds.
4. Hard and tough (H&T) — the consumption of both hard and tough foods (i.e., teeth have to handle both FMPs).

Finally, two levels of shearing were defined:

1. Soft and tough (sT) — shearing and eating foods such as the most challenging leaves, flowers (Yamashita, 2008) or soft insects (Lucas and Luke, 1984).
2. Hard (H) — shearing soft and tough items, but cracking and/or grinding hard items as well. This level also includes species, such

as Cercocebus galeritus that do not shear tough items on a regular basis but still process hard foods (Wieczkowski, 2009). Since dealing with hard items might damage sharp enamel crests, we hypothesize that hard food consumption results in dental morphological trade-offs between shearing and cracking/grinding potentials. The "hard" shearing level is designed to test this hypothesis.

2.3. Scanning and 3D surface extraction

The original molars were detailed by x-ray high-resolution micro-computed tomography (HR-μCT). Each molar was scanned at the Centre de Microtomographie of Poitiers using either Viscom X1050 or EasyTom HR-microtomographs at between 10 and 30 μm isovoxel resolution under a voltage of 70–100 kV and an intensity of 100–280 mA, depending on the tooth size. We performed 1000–2500 projections with 10–15 acquisitions per complete rotation. Images were filtered with a Tukey filter set to 80.

Table 2
Dietary categorization of the comparative sample using classical and mechanically-pertinent categories.[a]

Genus	Species	n	Collection	Accession numbers	Cracking scope	Grinding scope	Shearing scope	Classical diet	References
CERCOPITHECIDAE									
Cercocebus	galeritus	1	RMCA	14486	H&b	H&b	H	Frugivore	Rowe, 1996; Wahungu, 1998; Wieczkowski, 2009
Cercocebus	torquatus	1	RMCA	81-07-M-44	H&T	H&T	H	Seed-eater	Mitani, 1989; Daegling et al., 2011; McGraw et al., 2014
Cercopithecus	campbelli	2	RMCA	36280; 80-028-M-24	s	s&b	s&T	Omnivore	Buzzard, 2006
Cercopithecus	cephus	1	RMCA	17507	s	s&b	s&T	Frugivore	Rowe, 1996; Tutin et al., 1997; Tutin, 1999
Cercopithecus	diana	2	iPHEP	Cc1; Cc2	H&T	H&T	H	Seed-eater	Curtin, 2004; Buzzard, 2006
Cercopithecus	nictitans	1	RMCA	15650	H&b	H|T	H	Seed-eater	Brugiere et al., 2002
Cercopithecus	pogonias	1	RMCA	15595; 18273	H&b	H|T	H	Seed-eater	Brugiere et al., 2002
Erythrocebus	patas	1	RMCA	8629	s	s&b	s&T	Omnivore	Isbell, 1998; Nakagawa, 2000
Lophocebus	albigena	4	RMCA, iPHEP	83-006-M-276; 90-042-M-301; 90-042-M-301; Cb4	H&b	H&b	H	Seed-eater	Lambert et al., 2004; McGraw et al., 2012
Papio	anubis	1	iPHEP	Pp4	H&T	H&T	H	Omnivore	Hill and Dunbar, 2002
Papio	cynocephalus	1	iPHEP	Pp3	H&T	H&T	H	Omnivore	Wahungu, 1998; Hill and Dunbar, 2002
COLOBINAE									
Colobus	angolensis	3	RMCA	10308; 10548; 10602	s	s&b	s&T	Folivore	Moreno-Black and Maples, 1977; Lowe and Sturrock, 1998
Colobus	guereza	1	RMCA	1216	s	s&b	s&T	Folivore	Harris and Chapman, 2007
Colobus	polykomos	2	RMCA	38158; 81-07-M174	H&b	H|T	H	Folivore	Dasilva, 1994; Davies et al., 1999
Piliocolobus	badius	2	RMCA	83-042-M77; 91-060-M57	s	s&b	s&T	Folivore	Dasilva, 1994; Davies et al., 1999; Kibaja, 2014
Procolobus	verus	3	RMCA	86-002-M-34; 86-002-M-48; 86-002-M-50	H&b	H|T	H	Folivore	Rowe, 1996; Davies et al., 1999
Semnopithecus	entellus	1	MNHN	1964–1615	H&b	H|T	H	Folivore	Newton, 1992; Rowe, 1996; Sayers and Norconk, 2008

[a] H, hard; H&b, hard and brittle; H&T, hard and tough; H|T, hard or tough; s, soft; s&b, soft and brittle; s&T, soft and tough. Sclerocarpic foragers whose categories are attested by one or several studies measuring FMPs are shadowed in gray. IPHEP, Institut de Paléoprimatologie, Paléontologie Humaine: Evolution, Paléoenvironnements; MNHN, Muséum national d'Histoire naturelle; RMCA, Royal Museum of Central Africa.

Following approaches detailed in earlier publications (Guy et al., 2013, 2015), virtual 3D models were extracted from μCT image stacks. The enamel cap was isolated from the dentine tissue using both automated and manual processing in Avizo 7.0 and was converted into a polygonal surface. This operation allowed the partition of the crown enamel into its inner (enamel-dentine junction [EDJ]) and outer (outer enamel surface [OES]) components. For the purpose of analysis and to minimize the computational load, each EDJ and OES was set to an equivalent amount (55k polygons) by a re-tessellation of the original polyhedral surface with standardization of the polygonal unit area using Geomagic Studio 2013 (Lazzari and Guy, 2014; Guy et al., 2015).

Following Guy et al. (2015), the position and orientation of each OES/EDJ couple was standardized using a best fit procedure applied to the occlusal molar basin (xy alignment) and an alignment of the x axis with the axis formed by the dentine horn tips from the paracone to the protocone. Afterwards, a subsampling procedure was performed separately on OES and EDJ occlusal surfaces, retaining only the regions above a plane parallel to the (xy) reference plane and passing through the lowermost point of the occlusal basin for both the OES and the EDJ (Ulhaas et al., 2004; Guy et al., 2015). All variables were measured from these subsampled occlusal 3D surfaces, because relief index has been shown to correlate better with diet when considering subsampled occlusal surfaces (Allen et al., 2015), as doing this minimizes the influence of tooth elements, such as lateral enamel, that do not participate actively in food comminution.

2.4. Variables measured

Topographic variables are used routinely for dental analysis, although they are generally computed only on OES surfaces (e.g., Ledogar et al., 2013; Winchester et al., 2014; Prufrock et al., 2016). However, the OES may transcribe EDJ morphology to a large extent (Butler, 1956; Skinner et al., 2008a, 2008b, 2009; Morita et al., 2014), especially in thin-enameled primates (although the thicker the enamel, the more the OES topography can differ from that of the EDJ) (Guy et al., 2015). Hence, using the EDJ morphology to assess cracking, grinding or shearing ability of molars that suffered some enamel wear could be helpful, and the predictive power of EDJ topographic analysis will be assessed in this work.

We computed three main topometrics for both OES and EDJ subsampled surfaces.

1. Relief index (RFI) is the natural log of the ratio between the square roots of (a) the OES or EDJ crown surface area and (b) the surface area of the crown's projection into an occlusal plane (Boyer, 2008). It measures how much the tooth surface differs from a flat surface. Both 3D and 2D surfaces were computed using Geomagic Studio 2013.
2. Dirichlet normal energy (DNE) measures the change in normal vectors over the tooth surface (Bunn et al., 2011). It corresponds to the overall degree of surface curvature (Fig. 2A, B). Contrary to other estimators of curvature (see Rugis and Klette, 2006 for a review), DNE is a scale invariant metric, and was calculated following Bunn et al. (2011) using R 3.2.3 (R Core Team, 2015).
3. Occlusal patch count (OPC) is an approximation of tooth complexity, i.e., it indicates the number of structures over the tooth's surface (Evans et al., 2007). It was calculated using R 3.2.3 (R Core Team, 2015) as the number of patches each constituted by a set of >3 contiguous triangles sharing a similar orientation group. Following Guy et al. (2013, 2015), eight orientation groups were defined, as intervals of the xy plane set to 45° (Fig. 2C,D).
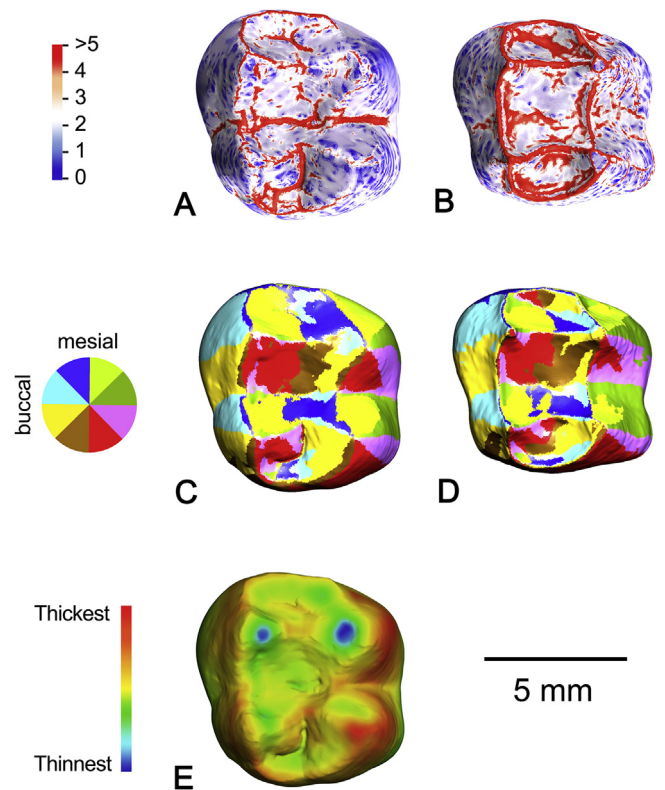

Figure 2. Sharpness, orientation and enamel thickness of MHNL-PK-25 displayed on topographical maps (**A**, **B**) Dirichlet normal energy of OES and EDJ, respectively: (**C, D**) Occlusal orientation of OES and EDJ, respectively; (**E**) Enamel-dentine distance.

In addition, 3D relative enamel thickness (RET) was processed for MHNL-PK-25, and enamel-dentine distance was pictured on topographic maps (Fig. 2E). It was measured as the ratio between the volume of the enamel cap and the surface area of the EDJ, divided by the cube root of coronal dentine volume (Kono, 2004; Olejniczak et al., 2008). Similarly to topographic variables, RET was computed from subsampled occlusal surfaces:

$$RET = \frac{Volume_{enamel}/Area_{EDJ}}{\sqrt[3]{Volume_{dentine}}}$$

All metrics related to RET were computed using Geomagic Studio 2013, and the resulting values, as well as topographic variables of the fossil sample, are available in Table 3.

2.5. Data analysis

The relationship between the variables was evaluated using a phylogenetic generalized least-square analysis (PGLS). Following Winchester et al. (2014), PGLS was preferred because it takes into account the effect of phylogeny on the distribution of data. To perform it, we used the caper (comparative analysis of phylogenetics and evolution in R) package of R version 3.2.3 (R Core Team, 2015), with a phylogenetic tree with branch lengths obtained from the 10kTrees Project (Arnold et al., 2010).

Categories were compared through four different one-way ANOVAs with classic, cracking, grinding and shearing categories as factors. For each ANOVA, we evaluated homoscedasticity with Breusch–Pagan tests and normality with Shapiro–Wilk tests. Afterward, we performed pairwise post-hoc comparisons using Tukey's Honestly Significant Difference (HSD) test.

Table 3
Measurements of RET and topographic variables of *Mesopithecus pentelicus* from Pikermi, Greece.[a]

Specimen	3D variables						
	RFI		DNE		OPC		RET
	OES	EDJ	OES	EDJ	OES	EDJ	
MHNL-PK-25	0.2327	0.2793	175.2071	270.2523	77	82	0.1228
LGPUA-2	0.2436	–	155.8603	–	96	–	–
LGPUA-2	0.2673	–	181.4883	–	82	–	–
LGPUA-4	0.1921	–	125.2922	–	95	–	–
LGPUA (no number)	0.2400	–	126.9620	–	71	–	–

[a] Variable abbreviations defined in main text. RET and data from the EDJ are not available from the cast specimens.

To predict the dietary features of *M. pentelicus*, a set of linear discriminant analyses (LDA) was conducted with several combinations of variables. In particular, variables that were correlated in the PGLS analysis were mutually excluded. We also performed an analysis on each variable alone. Finally, we performed LDAs that included the surface area of OES. For each variable combination, the percentage of correct dietary predictions was evaluated for every categorization system. Afterward, predictions were made from the upper molar of MHNL-PK-25 because it was the only upper molar in our sample for which RET and EDJ variables were available.

3. Results

3.1. Relationships between variables

From the PGLS results (Table 4), it appears that dentine RFI is inversely correlated with RET ($p < 0.01$). Enamel and dentine RFI also strongly correlate with each other ($p < 0.001$). This might be linked to the fact that there is no phylogenetic structuring of the RFI data (lambda = 0). Furthermore, enamel DNE correlates with enamel OPC ($p < 0.001$), again with a null lambda.

3.2. Dietary categories

Seed eating cercopithecids have a lower RFI and thicker enamel than folivorous species ($p < 0.005$), a lower enamel RFI than frugivores ($p < 0.001$) and a non-significantly lower dentine DNE than omnivores ($p > 0.05$). Other classic categories are not separated by post-hoc comparisons (Tables 5 and 6).

While RFI and DNE group *M. pentelicus* with seed-eaters, RET scores clearly group *Mesopithecus* within folivorous taxa (Fig. 3). Concerning LDAs, the highest rate of successful a posteriori

classification corresponds to a combination of variables that includes OES surface area (Table 7). This is consistent with the results of earlier works that involved similar OES topometrics (Winchester et al., 2014). Hence, this variable was selected for inferring the diet of *M. pentelicus*. The LDA conveys a similar signal, classifying *M. pentelicus* with folivorous taxa (Fig. 4A; 70.79%).

3.3. Cracking ability

Monkeys that crack hard and brittle foods have significantly lower RFI for both OES and EDJ ($p < 0.05$) and lower dentine DNE ($p < 0.05$) compared with species that crack soft food. On the other hand, species that crack either hard or tough items (e.g., that fall back on both mature and immature seeds) have a significantly greater enamel DNE and enamel OPC than species that crack either hard and brittle foods ($p < 0.01$) or soft food ($p < 0.05$). Contrary to our expectations, RET is not significantly greater for hard food crackers (Tables 5 and 6).

With relatively low enamel RFI and enamel DNE scores, *Mesopithecus* falls into the morphological space occupied by hard and brittle food crackers (Fig. 5). On the other hand, RET scores do not allow us to characterize its ability to crack hard and brittle food. The LDA performed to evaluate the cracking ability of MHNL-PK-25 gives clearer results, indicating a hard and brittle food (74.55%) cracking morphology slightly leaning towards a soft food (24.60%) cracking morphology (Fig. 4B).

3.4. Grinding ability

Species that grind either soft and brittle food, or have to deal with either hard items or tough items, have significantly lower RFI scores for both OES and EDJ than pure hard and brittle food grinders

Table 4
PGLS correlation between variable pairs, $\alpha = 0.05$.[a]

Variables	Correlation	SE	p	t-value	AIC	AICC	logL	Lambda
RET ~ RFI_EM	−0.4405	0.2128	0.0562	−2.0693	−61.0411	−60.1839	32.5205	0.7491
RET ~ OPC_EM	7.00E-4	6.00E-4	0.2126	1.3019	−58.4366	−57.5794	31.2183	0.5392
RET ~ DNE_EM	1.00E-4	4.00E-4	0.6752	0.4273	−57.0076	−56.1505	30.5038	0.6248
RET ~RFI_DE	−0.5225	0.1659	0.0066	−3.1499	−65.4597	−64.6025	34.7298	0.6504
RET ~ OPC_DE	0	0.001	0.9858	0.0181	−56.8416	−55.9845	30.4208	0.6827
RET ~ DNE_DE	−2.00E-4	2.00E-4	0.2295	−1.2527	−58.4999	−57.6428	31.25	0.729
RFI_EM ~ OPC_EM	7.00E-4	6.00E-4	0.2361	1.2344	−58.7308	−57.8736	31.3654	0.2936
RFI_EM ~ DNE_EM	4.00E-4	2.00E-4	0.0553	2.0784	−60.2491	−59.3919	32.1245	0.5467
RFI_EM ~ RFI_DE	0.7579	0.1171	0	6.4742	−79.6895	−78.8324	41.8448	0
RFI_EM ~ OPC_DE	3.00E-4	0.0011	0.7788	0.286	−57.4509	−56.5937	30.7254	0.1368
RFI_EM ~ DNE_DE	2.00E-4	2.00E-4	0.3358	0.9944	−58.2965	−57.4393	31.1482	0.2474
OPC_EM ~ DNE_EM	0.2841	0.0435	0	6.5325	128.6665	129.5236	−62.3332	0
OPC_EM ~ OPC_DE	0.1768	0.4545	0.7027	0.389	149.3062	150.1633	−72.6531	0.5992
OPC_EM ~ DNE_DE	0.0347	0.0743	0.6466	0.4678	149.2314	150.0886	−72.6157	0.6278
DNE_EM ~ DNE_DE	0.3289	0.1784	0.0851	1.8433	181.325	182.1821	−88.6625	0.9345

[a] AIC, Akaike criterion; AICC, adjusted Akaike criterion; DE, corresponds to the variable measured for EDJ; EM, corresponds to the variable measured for OES; logL, log of the likelihood of the model; SE, standard error. Lambda is a measure of phylogenetic signal, with 1 representing a perfect fit between data and a Brownian motion model of change in values through evolution, and 0 representing no phylogenetic structuring. Pairs of variables that are significantly correlated are shadowed in gray.

Table 5
ANOVAs of the metrics for the four categorization systems, α = 0.05.[a]

Variables	df	MS	F	p-value
Classical categories:				
RET	3	0.0090	5.4230	**0.0054***
RFI (enamel)	3	0.0120	9.3950	**0.0002***
OPC (enamel)	3	552.2	2.3170	0.1010
DNE (enamel)	3	5857	2.0430	0.1350
RFI (dentine)	3	0.0121	5.5910	**0.0047***
OPC (dentine)	3	75.2	0.6370	0.5990
DNE (dentine)	3	11200	3.4760	**0.0316***
Cracking categories:				
RET	2	0.0055	2.4350	0.1080
RFI (enamel)	2	0.0122	7.1930	**0.0034***
OPC (enamel)	2	1123.3	5.4740	**0.0107**
DNE (enamel)	2	16926	8.0560	**0.0019***
RFI (dentine)	2	0.0118	4.5450	**0.0207***
OPC (dentine)	2	189.4	1.7660	0.1920
DNE (dentine)	2	17486	5.7540	**0.0088***
Grinding categories:				
RET	3	0.0096	6.0320	**0.0032***
RFI (enamel)	3	0.0100	6.5910	**0.0020***
OPC (enamel)	3	384.8000	1.4840	0.2440
DNE (enamel)	3	1860	0.5530	0.6510
RFI (dentine)	3	0.0114	5.0500	**0.0074***
OPC (dentine)	3	66.4900	0.5580	0.6480
DNE (dentine)	3	11204	3.4770	**0.0316***
Shearing categories:				
RET	1	0.0091	4.0850	0.0537
RFI (enamel)	1	0.0238	14.4000	**0.0007***
OPC (enamel)	1	0.0500	0.0000	0.9900
DNE (enamel)	1	272	0.0820	0.7770
RFI (dentine)	1	0.0236	9.4540	**0.0049***
OPC (dentine)	1	60.0100	0.5200	0.4770
DNE (dentine)	1	15139	4.1090	0.0530

[a] df, degrees of freedom; F, Fisher's F-ratio; MS, mean square between groups. Significant differences in ANOVAs results in bold. (*) signifies groups with a normal distribution and homogeneous variances. Abbreviations defined in text.

($p < 0.005$). The latter also have lower RET scores ($p < 0.005$) as well as lower DNE scores for EDJ than soft and brittle grinders ($p < 0.05$). Globally, hard and brittle food grinders have rounder, flatter molars with thicker enamel. Other grinding categories are not supported by the ANOVAs (Tables 5 and 6).

Values of OPC and RET for *M. pentelicus* fall within the morphospace of two grinding categories: soft and brittle food grinders, and hard or tough food grinders. By contrast, RFI and DNE values are closer to those of hard and brittle food grinders (Fig. 5). The LDA performed on grinding categories (Fig. 4C) supports the presence of a hard component in the staple diet of *M. pentelicus*, with a dominance of hard and brittle food items (56.88%).

3.5. Shearing ability

Compared to species that shear only soft and tough food, hard food consumers have significantly lower RFI scores ($p < 0.005$). Although hard food consumers seem to have relatively thicker enamel and lower DNE scores (Fig. 5), this observation is not supported by post-hoc comparisons (Tables 5 and 6).

Mesopithecus pentelicus has thin enamel, but very low RFI and DNE scores (Fig. 5). This is consistent with the LDA with the best successful classification rate, which strongly supports (97.82%) the presence of a hard component in its diet (Fig. 4D).

4. Discussion

4.1. Input of mechanically-pertinent categories

Every colobine species used in our comparative sample is ascribed to the same classic category (i.e., folivory). While this categorization admittedly overlooks the diversity of their seasonal behavior, especially regarding seed consumption (Dasilva, 1992; Wright and Willis, 2012), seeds do not average more than 50% of colobine annual diets except in a few species, e.g., *Presbytis rubicunda* (Ehlers-Smith et al., 2013) or *R. roxellana* (Guo et al., 2007). Moreover, the cercopithecine sample exhibits a greater dietary diversity. Because of these obvious contrasts in classic dietary categories, mechanically-pertinent categories were necessary to provide further insights into the dental topography of colobines.

Our categories can be used to make predictions on FMPs for extinct taxa, like *Mesopithecus*, but can also provide information about extant species for which the data are incomplete. For instance, the position of *C. galeritus* on the cracking potential LDA, near hard and tough food crackers (Fig. 5B), contrasts with the FMPs specified for its diet in the literature (Table 2). This most likely indicates that *C. galeritus* is adapted to crack hard and tough items in the manner of *Cercocebus torquatus* (Daegling et al., 2011), despite the fact that this behavior has yet to be documented. Mechanical categories can also give new insights into problems

Table 6
Post-hoc comparisons between factor groups, α = 0.05.[a]

	RET	RFI (enamel)	OPC (enamel)	DNE (enamel)	RFI (dentine)	OPC (dentine)	DNE (dentine)
Classic categories:							
Frugivore ~ Folivore	ns	ns	ns	ns	ns	ns	ns
Omnivore ~ Folivore	ns	ns	ns	ns	ns	ns	ns
Seed ~ Folivore	**0.0048**	**0.0001**	ns	ns	**0.0028**	ns	ns
Omnivore ~ Frugivore	ns	ns	ns	ns	ns	ns	ns
Seed ~ Frugivore	ns	**0.0454**	ns	ns	ns	ns	ns
Seed ~ Omnivore	ns	ns	ns	ns	ns	ns	ns
Cracking:							
H&T ~ H&b	ns	ns	**0.0077**	**0.0013**	ns	ns	**0.0436**
s ~ H&b	ns	**0.0026**	ns	ns	**0.0211**	ns	**0.0204**
s ~ H&T	ns	ns	**0.0334**	**0.0156**	ns	ns	ns
Grinding:							
H&T ~ H&b	ns	ns	ns	ns	ns	ns	ns
H|T ~ H&b	**0.0095**	ns	ns	ns	ns	ns	ns
s&b ~ H&b	**0.0053**	**0.0014**	ns	ns	**0.0042**	ns	**0.0177**
H|T ~ H&T	ns	ns	ns	ns	ns	ns	ns
s&b ~ H&T	ns	ns	ns	ns	ns	ns	ns
s&b ~ H|T	ns	ns	ns	ns	ns	ns	ns
Shearing:							
s&T ~ H	ns	**0.0007**	ns	ns	**0.0049**	ns	ns

[a] Variable abbreviations defined in text; ns, non significant. Significant differences between groups in bold.
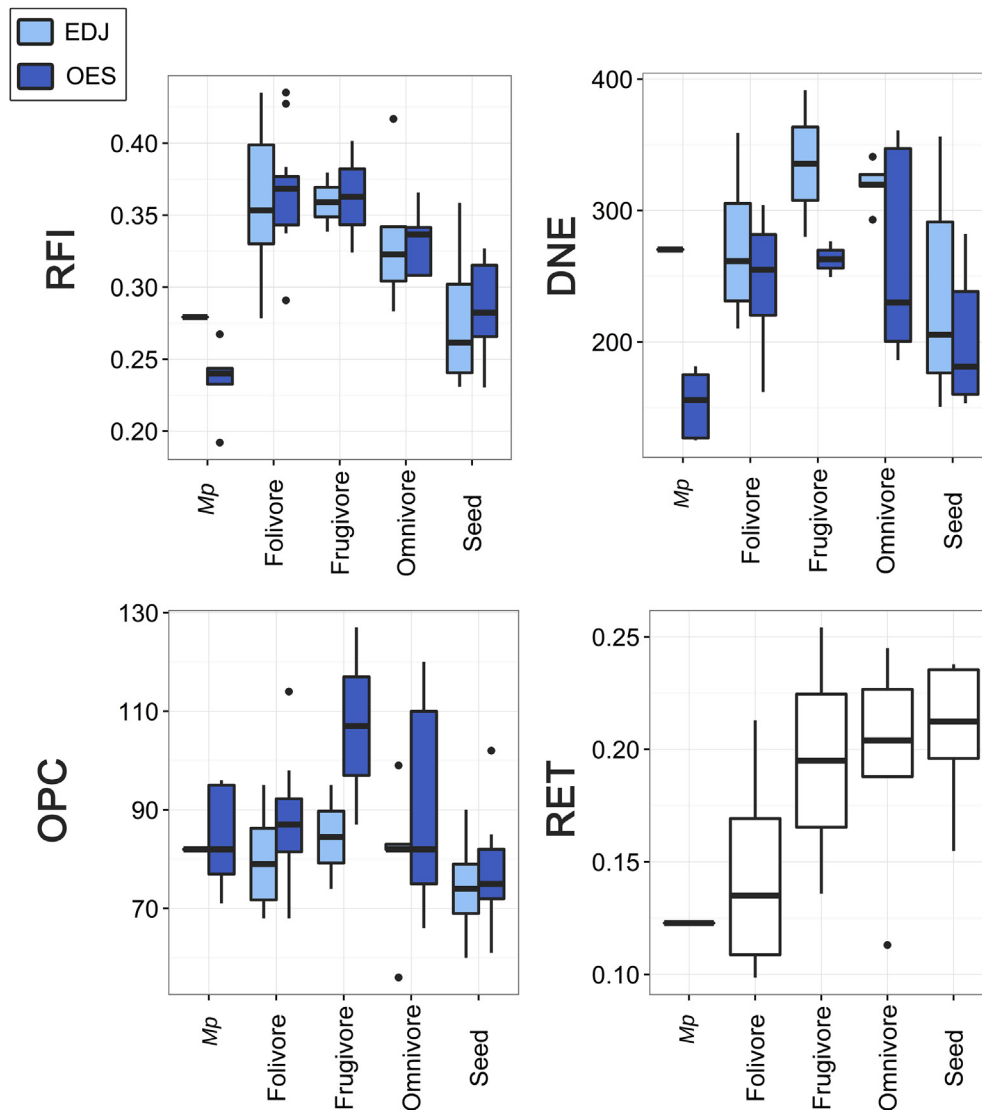
Figure 3. Box plots depicting relief index (RFI), Dirichlet normal energy (DNE), occlusal patch count (OPC) and relative enamel thickness (RET) of both outer enamel (OES) and enamel-dentine junction (EDJ) with classic dietary categories as factors. Middle lines correspond to the median, boxes to the first and third quartiles, and whiskers to the first and ninth deciles. *Mp = Mesopithecus*. Variable abbreviations defined in text.

encountered in previous research. For example, Bunn and Ungar (2009) could not explain the high angularity, defined as the variation of slope, observed in the lower molars of *Cercopithecus campbelli* because Galat and Galat-Luong (1985) reported a fruit consumption of 78% for this species, which corresponds to a frugivorous diet. Departing from the associative approach, we considered the large invertebrate intake of *C. campbelli* (Galat and Galat Luong, 1985; Buzzard, 2006). We interpreted it as having a "soft and tough" food shearing ability, which can explain higher angularity. This is consistent with our results, since high RFI (OES: 0.33 ± 0.03; EDJ: 0.36 ± 0.06) and high dentine DNE scores (334.17 ± 6.77) characterize *C. campbelli*. Finally, mechanical categories brought to light the fact that ability to crack or grind hard food is not necessarily correlated with molar enamel thickening. Assuming that the seeds they consume are indeed protected by a hard pericarp, some colobine monkeys classified as hard food crackers/grinders have relatively thinner enamel than other cercopithecids. In other words, relief, curvature and complexity may compensate for a relatively thin enamel when hard foods represent a staple resource, i.e., when cracking/grinding potential undergoes

a strong selective pressure. This study does not present clear evidence of such compensation, as most studies of colobine diet do not report FMPs. Still, this would be consistent with the suggestion that consumption of abrasive foods could lead to the selection of a thick enamel (Sponheimer et al., 2009; Cerling et al., 2011; Ungar et al., 2012; Pampush et al., 2013). Thus, caution is needed when using this dental variable to investigate the diets of extinct primates.

4.2. Hard food consumption in Mesopithecus

The molars of *M. pentelicus* have been described as very similar to those of extant colobines, with sharp longitudinal crests and deep basins separating two marked lophs and lophids (Jablonski, 2002). Furthermore, the present study found relatively thin enamel compared with that of extant cercopithecids. Many folivorous primates have thin enamel, in part because it creates sharp enamel ridges around dentine pits when the tooth wears (Rosenberger, 1992). Here, the distribution of enamel thickness can be informative. Notwithstanding apical wear, thin enamel in *Mesopithecus* is mostly located within a narrow band along the

Table 7
A posteriori probabilities of successful classification for LDAs using classic, cracking, grinding and shearing categories as factors.[a]

Variables	Success rate of LDA (%)			
	Cracking categories	Grinding categories	Shearing categories	Classical categories
RET	0.5357	0.4643	0.6786	0.6429
RFI_EM	0.6429	0.5000	**0.7857**	0.6786
OPC_EM	0.6429	0.3571	0.5000	0.4643
DNE_EM	0.6071	0.3929	0.5000	0.5000
RFI_DE	0.5357	0.5357	0.7143	0.6429
OPC_DE	0.5714	0.3929	0.4643	0.4286
DNE_DE	0.6071	0.4643	0.6786	0.4643
RET + DNE_EM + DNE_DE	0.6429	0.4643	0.5714	0.6429
RET + OPC_EM + DNE_DE	0.5714	0.4286	0.6071	0.6429
RFI_EM + DNE_EM + DNE_DE	0.6429	**0.5714**	**0.7500**	0.6786
RFI_EM + OPC_EM + DNE_DE	0.6786	**0.5714**	0.7143	0.6786
RFI_DE + DNE_EM + DNE_DE	0.6786	0.4286	0.6429	0.6429
RFI_DE + OPC_EM + DNE_DE	**0.7143**	0.5000	0.6429	0.6429
RET + DNE_EM + DNE_DE + Area_EM	0.6429	0.4643	0.5714	**0.7143**
RET + OPC_EM + DNE_DE + Area_EM	0.6071	0.4643	0.5714	0.6071
RFI_EM + DNE_EM + DNE_DE + Area_EM	0.6786	0.5000	0.7143	0.6786
RFI_EM + OPC_EM + DNE_DE + Area_EM	0.6429	0.5357	0.6786	0.6429
RFI_DE + DNE_EM + DNE_DE + Area_EM	0.6786	0.5000	0.6786	0.6429
RFI_DE + OPC_EM + DNE_DE + Area_EM	0.6429	0.5000	0.6429	0.6071

[a] DE, corresponds to the variables measured for EDJ; EM, corresponds to the variables measured for OES. Success rates corresponding to the best sets of variables in bold. Variable abbreviations defined in text.

longitudinal crests, the preparacrista and postprotocrista (Fig. 2E). This distribution is different from that in hominoid primates, which tend to have thinner enamel over the entire occlusal surface (Kono and Suwa, 2008). It results in emergence of sharp enamel ridges perpendicular to the buccolingual axis, which enhances shearing ability. Therefore the molar morphology of *M. pentelicus* reflects an ability to consume leaves, or other tough foods. This is consistent with the results of the LDA performed on classic dietary categories, which classify *M. pentelicus* as folivorous (Fig. 4A).

Still, 2D dental microwear analysis and 3D dental microwear textural analysis both revealed significant differences between *Mesopithecus* and leaf eating species, with *Mesopithecus* resembling opportunist and seed eating monkeys (Merceron et al., 2009a, 2009b). Using the 2D dental microwear method, Merceron et al. (2009a) found no significant differences between specimens from different late Miocene Eurasian sites where the genus is known. This emphasizes the possibility that challenging foods were a staple resource over the whole geographic range of *M. pentelicus*, and certainly in the Balkans where most of the material is found. In other words, hard foods such as seeds are expected to be more than a filler fallback food for *Mesopithecus* and are expected to represent a staple fallback food, meaning they could have driven dental morphological adaptation to some extent (Marshall and Wrangham, 2007).

The alternative, mechanically-pertinent categories used in this work give us additional insights into the dental adaptations of *Mesopithecus* to deal with hard food. In terms of dental features, *Mesopithecus* shares with hard, brittle food crackers/grinders a low RFI, a low DNE and a moderate enamel OPC. This reduces the shearing potential of the molars, since soft and tough food shearers are characterized by a high relief and a high curvature. It also differs from the molars of hard and tough food consumers such as mangabeys or baboons, which have high OPC scores as well as high DNE. The latter probably results from the development of the wedge-like lophs, which are necessary to fragment hard and tough items (Lucas and Teaford, 1994). On the other hand, *Mesopithecus* retains relatively thin enamel, which ensures an efficient shearing ability in spite of natural dental wear.

In LDAs, a good hard food cracking/grinding ability was predicted for *Mesopithecus*. In fact, its cracking potential is close to *Cercopithecus pogonias* (Fig. 4B), a frugivorous cercopithecine that

preys heavily on seeds (Brugiere et al., 2002) but also to *Colobus polykomos*, a folivorous colobine that falls back on seeds (Dasilva, 1994; Davies et al., 1999). While their diets emphasize different kinds of food, both extant species include a staple portion of possibly hard seeds at least seasonally (Table 2). However, further investigation is required as there is currently no report on the physical properties of the seeds consumed by *C. pogonias* and *C. polykomos*.

In addition, the LDA evaluating the shearing potential of *Mesopithecus* predicts a low ability to process soft, tough foods such as leaves (Fig. 4D). This LDA does not take into account enamel thickness, which might lower the success rate of the discriminant analysis because of the thin enamel of seed eating colobines. Still, two non-exclusive interpretations of this result are possible: (i) *Mesopithecus* may have had this durophagous morphology because it was not as specialized for folivory as expected from its gross dental morphology and the heavy leaf consumption of its extant relatives, or (ii) this may be evidence of a morphological trade-off between an efficient shearing ability (high curvature, high relief, thin enamel) and dental resistance to repeated hard food cracking/grinding (low curvature, low relief and possibly thick enamel).

5. Conclusions

This work provides significant evidence that the dental morphology of *M. pentelicus* was capable of coping with hard, brittle food items such as seeds. This is consistent with existing data on the diet of *Mesopithecus* (Reitz and Benefit, 2001; Reitz, 2002; Merceron et al., 2009a, 2009b). While it shows only a moderate level of ability to hard food cracking/grinding, it is clear that the shearing potential of *M. pentelicus* does not reflect strict folivory. Rather, its dental morphology should be seen as a trade-off between efficient shearing of tough, leaf-like items and resistance to high loads such as seen in extant seed-eaters.

It has been suggested that Old World monkeys could have first evolved molars adapted to seed consumption (Chivers, 1994; Lucas and Teaford, 1994). At this stage, bilophodont morphology could have been selected either for occlusal guiding during mastication or because it provides non-coalescing, concurrent wedges suitable for the fracture of hard and tough food (Lucas and Teaford, 1994). A dietary shift toward seasonal folivory would have subsequently
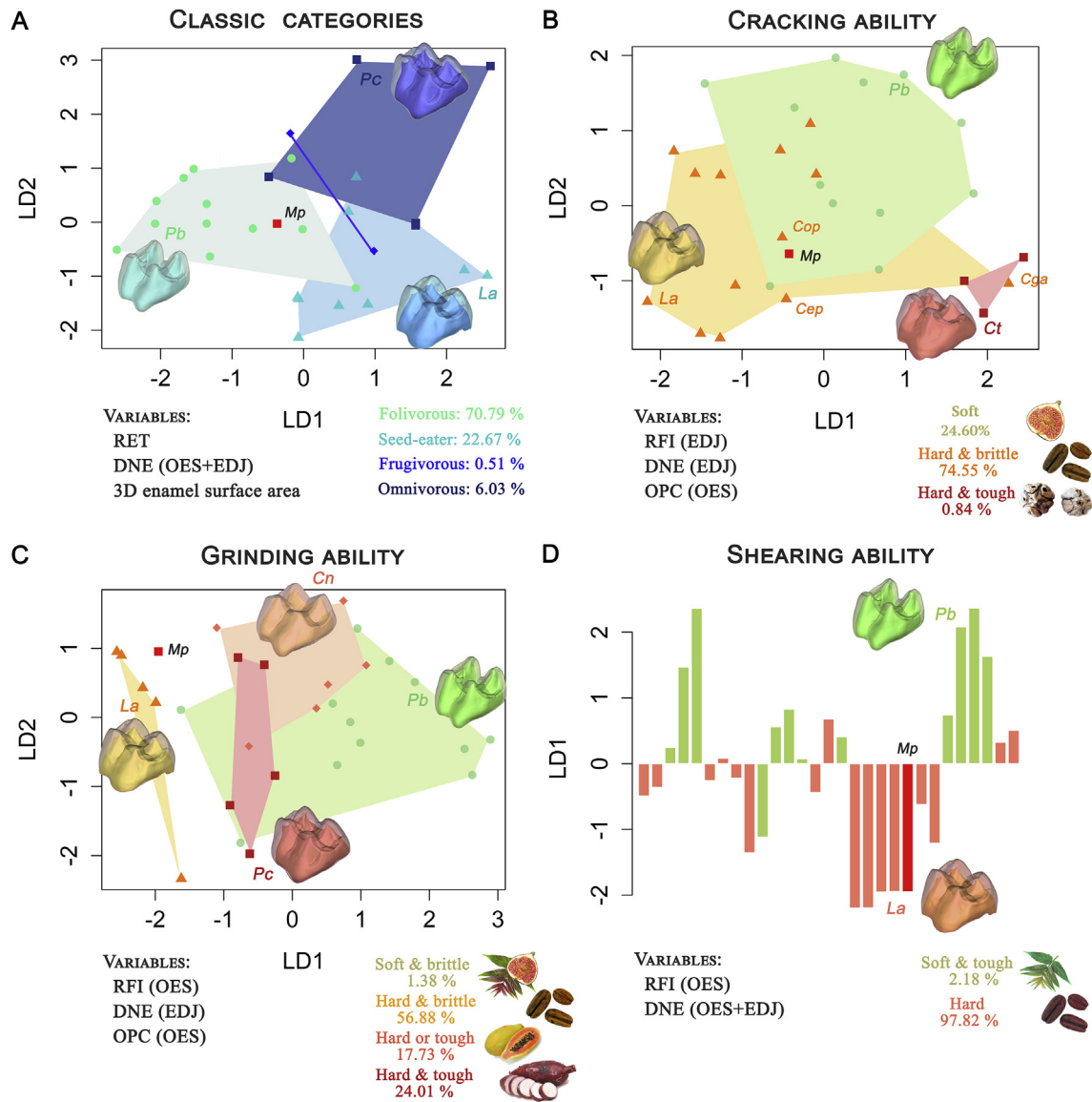
Figure 4. Results of the linear discriminant analyses (LDAs) with the best rate of successful classification inferring the diet as well as the ability to perform cracking, grinding and shearing actions in *Mesopithecus pentelicus*. Percentages correspond to the a posteriori probabilities of classification of *M. pentellicus* in each category. (**A**) Components 1 and 2 of LDA with classic categories as factor; (**B**) Components 1 and 2 of LDA with cracking ability as factor; (**C**) Components 1 and 2 of LDA with grinding ability as factor; (**D**) Component 1 of the LDA with shearing ability as factor. *Cga*, *Cercocebus galeritus*; *Cn*, *Cercopithecus nictitans*; *Cep*, *Cercopithecus pogonias*; *Cop*, *Colobus polykomos*; *Ct*, *Cercocebus torquatus*; *La*, *Lophocebus albigena*; *Mp*, *Mesopithecus pentellicus*; *Pb*, *Piliocolobus badius*; *Pc*, *Papio cynocephalus*. Variable abbreviations defined in text.

occurred during colobine evolution, driving the selection of thinner enamel. Leaves are indeed a common fallback food in primates, being an abundant resource largely available in time of preferred food scarcity, but requiring dental or physiological adaptation (Marshall and Wrangham, 2007). Extant colobine monkeys are also characterized by an early eruption of molars (Schultz, 1935; Harvati, 2000), which has been attributed to an accelerated life history (Smith, 2000) and possibly to their folivorous diet (Leigh, 1994; Dirks, 2000, 2003). Though *Mesopithecus* had a delayed dental eruption of second incisors relative to second molars, this early molar eruption seems to be absent in early colobines, which may indicate that other adaptations to folivory were secondary (Harvati and Frost, 2007).

Being the oldest known colobine in Eurasia, *Mesopithecus* might correspond to a transitional morphotype still preying heavily on hard, brittle food such as seeds but seasonally falling back on leaves. This is consistent with the intermediate morphology of its molars,

as characterized in the present study. While further investigation is needed, this might have been the case for other Mio-Pliocene colobine species. For instance, the Pliocene colobine *Cercopithecoides williamsi* from Africa was also a mixed-feeder (Codron et al., 2005) but retains thin enamel with RET scores comparable to *M. pentelicus* (Beaudet et al., 2016).

One further intriguing finding in our study is the thin enamel of *Mesopithecus*. Two non-exclusive interpretations are possible: (i) thin enamel could be the consequence of a less abrasive diet compared with extant durophagous Old World monkeys, and (ii) it may result from the need to process a reasonable amount of fibrous, tough food, which would have exerted a strong selective pressure favoring thin enamel — at least as strongly as the need to avoid tooth failure. Because *M. pentelicus* was probably a terrestrial species (Youlatos, 2003; Youlatos and Koufos, 2010; but see; Escarguel, 2005), it is unlikely that its diet was less abrasive than that of extant arboreal colobines, which are expected to ingest few abrasive
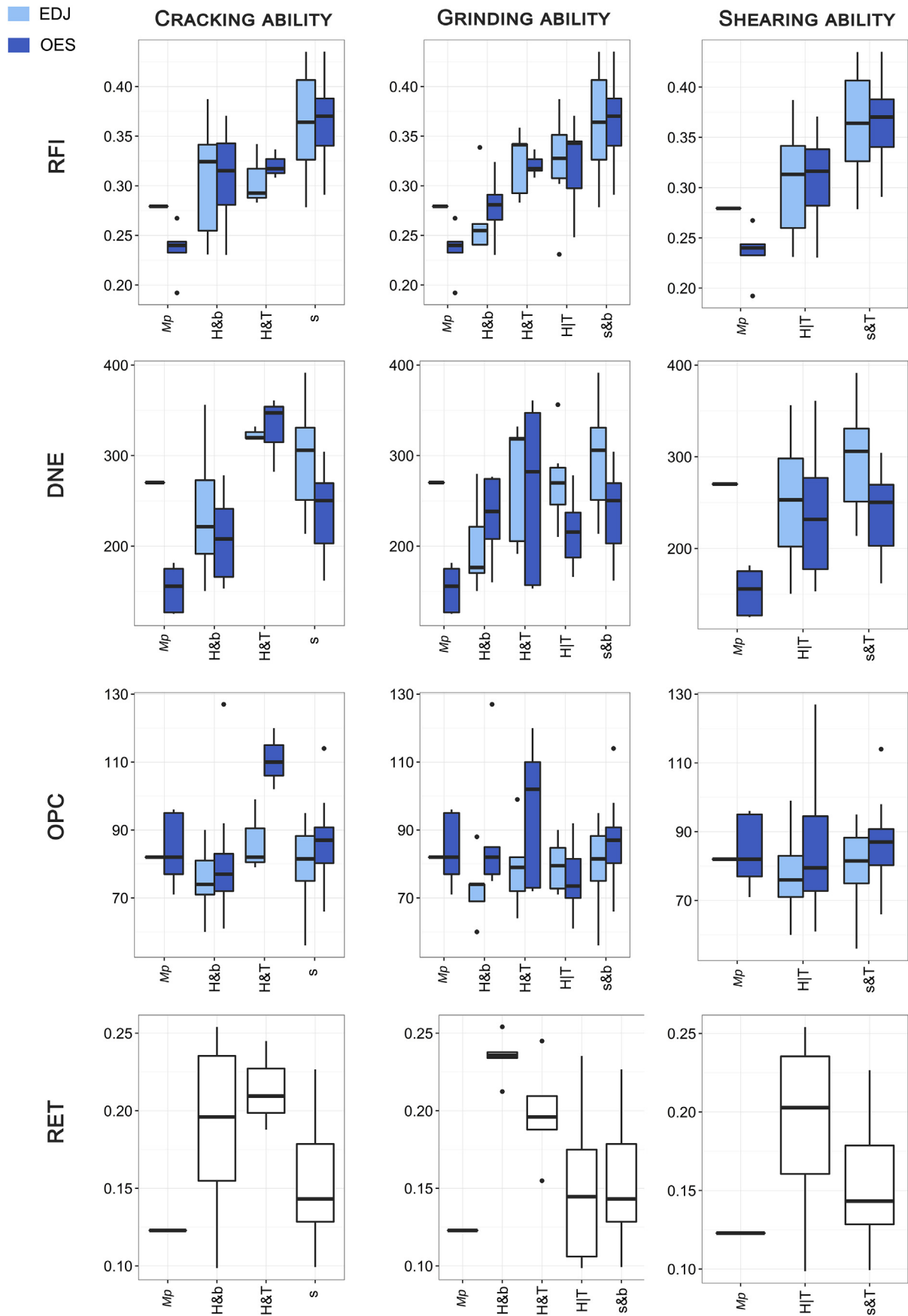
Figure 5. Box plots depicting RFI, DNE, OPC and RET of both enamel (OES) and enamel-dentine junction (EDJ) relative to the ability to crack, grind or shear mechanically challenging food. Middle lines correspond to the median, boxes to the first and third quartiles, and whiskers to the first and ninth deciles. H, hard; H&b, hard and brittle; H&T, hard and tough; H|T, hard or tough; s, soft; s&b, soft and brittle; sT, soft and tough. *Mp* = *Mesopithecus*.

elements like phytoliths or grit (Rabenold and Pearson, 2011). On the other hand, the complex multi-chambered stomach that enables colobine monkeys to digest leaves was probably present in *Mesopithecus* by the late Miocene, because it is shared by both Asian and African extant colobines (Chivers, 1994; Kay and Davies, 1994). It has been suggested that the multi-chambered stomach of colobines could have evolved as an adaptation to toxic secondary compounds, which may be found in seeds with greater concentrations than in mature leaves (McKey et al., 1981). The colobine digestive tract could have originally evolved as an adaptation to seed predation and have been subsequently co-opted as an exaptation to folivory.

In a similar fashion, the bilophodont morphology of *Mesopithecus* appears to have evolved in a context of hard food consumption. This echoes suggestions that seed consumption predates folivory in some mammalian orders (Dubost, 1984; Bodmer, 1989, 1991; Chivers, 1994; Lucas and Teaford, 1994). Applying the methods used in our present study to older Old World monkeys, such as *Microcolobus* (Benefit and Pickford, 1986) or the Victoriapithecidae, might give us additional insights into the evolution of seed predation in mammals. Given the frugivorous diet of Victoriapithecidae and their low shearing quotients compared with extant colobine monkeys (Benefit, 1999; Blue et al., 2006; Teaford et al., 2008), *Mesopithecus* should have a thinner enamel as well as similar relief index and enamel complexity, but a higher curvature because of its marked lophs.

The mechanical approach developed in this work could gain valuable input from other types of functional approaches, based on mathematical modeling such as finite elements analysis (Benazzi et al., 2011, 2013) or empirical testing (Chai et al., 2009). These methods can give us new insights into dental evolution and the feeding biomechanics of fossil taxa (Berthaume et al., 2010). Furthermore they could be used to test some of the major results of this contribution. Nonetheless, the fact that LDAs using dietary categories as a factor predicted a folivorous diet for *Mesopithecus*, despite a probable adaptation to hard, brittle food consumption and the resulting morphological trade-off, reflects how complex dental evolution can be. Being folivorous requires dental traits that are not related to shearing potential alone. Most likely, the mechanical constraints of food mechanical properties are not the only force driving the selection of dental morphology. Hence, classic categories provide important information for the interpretation of dental occlusal topography, and categories evaluating the cracking, grinding or shearing ability should not be seen as a replacement, but as a complementary approach to classic categories.

Acknowledgments

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