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Investigating the dietary niches of fossil Plio–Pleistocene European macaques: The case of *Macaca majori* Azzaroli, 1946 from Sardinia

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Abstract

The genus *Macaca* includes medium to large-bodied monkeys and represents one of the most diverse primate genera, also having a very large geographic range. Nowadays, wild macaque populations are found in Asia and Africa, inhabiting a wide array of habitats. Fossil macaques were also present in Europe from the Late Miocene until the Late Pleistocene. Macaques are considered ecologically flexible monkeys that exhibit highly opportunistic dietary strategies, which may have been critical to their evolutionary success. Nevertheless, available ecological information regarding fossil European species is very sparse, limiting our knowledge of their evolutionary history in this geographic area. To further our understanding of fossil European macaque ecology, we investigated the dietary ecology of *Macaca majori*, an insular endemic species from Sardinia. In particular, we characterized the dental capabilities and potential dietary adaptations of *M. majori* through dental topographic and enamel thickness analyses of two M²s from the Early Pleistocene site of Capo Figari (1.8 Ma). We also assessed its diet through dental microwear texture analysis, while the microwear texture of *M. majori* was also compared with microwear textures from other European fossil macaques from mainland Europe. The dental topographic and enamel thickness analyses suggest that *M. majori* frequently consumed hard/mechanically challenging and/or abrasive foods. The results of the dental microwear analysis are consistent with this interpretation and further suggest that *M. majori* probably exhibited more durophagous dietary habits than mainland Plio–Pleistocene macaques. Overall, our results indicate that *M. majori* probably occupied a different dietary niche compared to its mainland fossil relatives, which suggests that they may have inhabited different paleoenvironments.

Keywords: Macacina; Dental microwear; Texture analysis; Dental topography; Enamel thickness; Paleoeecology

1. Introduction

The genus *Macaca* represents one of the most successful extant primate genera, exhibiting the second largest geographic distribution among primates, surpassed only by the genus *Homo*. Currently, macaques comprise multiple species and subspecies (Fooden, 1982; Thierry, 2017; Roos et al., 2019). Extant macaque species are mostly found in Asia and occupy a broad range of habitats (Lehman and Fleagle, 2006). However, macaques are also represented in Africa by a single species, *Macaca sylvanus*, which is restricted to isolated temperate forests of Algeria and Morocco (Fooden, 2007). In Asia, the genus is widely distributed from northern Japanese coniferous forests to Sumatran equatorial forests and shows high species diversity (e.g., Fooden, 1982; Fa, 1989; Goldstein and Richard, 1989; Riley, 2008; Tsuji, 2010; Roos et al., 2019). With the sole exception of a semi free-ranging colony of *M. sylvanus* in Gibraltar introduced by humans in historical times (Modolo et al., 2005), macaques are nowadays absent from Europe and Western Asia. Regardless, the fossil record indicates that macaques were widespread in Europe during the Plio–Pleistocene (e.g., Delson, 1980; Alba et al., 2021 and references therein).

1.1. *The fossil record of the genus Macaca in Europe*

According to the fossil record and more recent molecular evidence, the last common ancestor of macaques is dated to around 7.0–6.7 Ma in the Late Miocene of Africa (Szalay and Delson, 1979; Delson, 1980; Thomas and Petter, 1986; Benefit, 2008; Roos et al., 2019). As a result, the genus *Macaca* is the oldest cercopithecine found in Europe where it probably dispersed from Africa by the latest Miocene (Köhler et al., 2000; Alba et al., 2014) in the context of faunal exchanges associated with the Messinian Salinity Crisis (Gibert et al., 2013). Around that time, the level of the Mediterranean Sea fluctuated and eventually desiccated, most likely facilitating the dispersal of the genus from North Africa (Alba et al., 2014; Roos et al., 2019). Nevertheless, macaque remains from the Late Miocene of Europe are scarce, with only two fossil sites reported, Almenara-Casablanca M in Spain (Köhler et al., 2000) and Moncucco

Torinese in Italy (Alba et al., 2014). By the Early Pliocene, macaques were distributed along southern Europe, including eastern France and all the way to the modern Black Sea region (Delson, 1974; Alba et al., 2018). During the earliest Pleistocene, fossil representatives of *Macaca* reached as far as north as Tegelen in the Netherlands (van den Hoek Ostende and de Vos, 2006). Toward the end of the Early Pleistocene, macaques maintained their broad distribution from northern to southern mainland Europe where they persisted into the Middle Pleistocene (Elton and O'Regan, 2014; Konidaris et al., 2022). By the early Late Pleistocene (0.2–0.1 Ma), most of the European macaque fossil sites are found in Spain, but macaque remains are not solely restricted to the Iberian Peninsula as they have been recovered from a wider range of contemporary European sites (see Elton and O'Regan, 2014).

Plio–Pleistocene European macaques are represented by several taxa that belong to the lineage of *Macaca sylvanus*, the extant barbary macaque from North Africa (Szalay and Delson, 1979; Delson, 1980; Alba et al., 2008, 2011, 2018; Roos et al., 2019). Overall, three extinct subspecies of *M. sylvanus* are tentatively distinguished (Alba et al., 2008, 2018): *Macaca sylvanus prisca*, from the Pliocene of Europe, sometimes found associated with other fossil cercopithecids (i.e., *Dolichopithecus* and *Mesopithecus*; Eronen and Rook, 2004; Alba et al., 2014, 2018); *Macaca sylvanus florentina*, from the Late Pliocene to the Early Pleistocene of southern and central Europe (Alba et al., 2011; Rook et al., 2013; Marigó et al., 2014); and *Macaca sylvanus pliocena*, from the Middle Pleistocene of Europe plus Caucasus and Israel (Delson, 1980; Tchernov and Volokita, 1986; Maschenko and Baryshnikov, 2002). In turn, macaque remains from the Early to Middle Pleistocene of Sardinia are usually assigned to a distinct species, *Macaca majori* Azzaroli, 1946 (Gentili et al., 1998; Rook and O'Higgins, 2005; Zoboli et al., 2016).

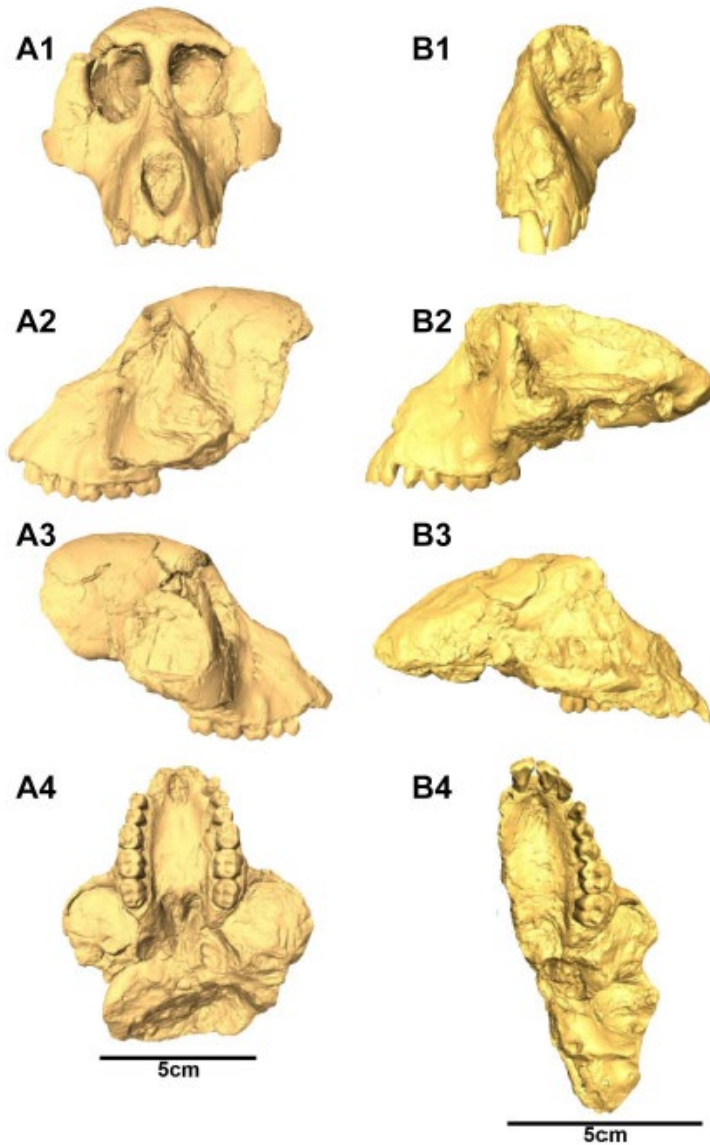


Figure 1. Virtual reconstruction of the fossil specimens Ty5199 (A) and Ty5203 (B) of *Macaca majori* from Capo Figari, in frontal (A1, B1), left lateral (A2, B2), right lateral (A3, B3), and basal (A4, B4) views. The scanning resolution of Ty5199 and Ty5203 is 60.0 and 48.0 μm , respectively.

1.2. *The Sardinian fossil macaque*

Macaca majori was described on the basis of a large fossil sample found in Capo Figari fossil site (Golfo Aranci, northeastern Sardinia; Azzaroli, 1946). Additional fossil remains were recovered from other fossil sites, such as Is Oreris (Fluminimaggiore) in southwestern Sardinia and more recently from

fissure fillings at Monte Tuttavista (Orosei) in southwestern and eastern Sardinia respectively (Abbazzi et al., 2004; Palombo, 2006; Zoboli et al., 2016). Its overall smaller size compared to other contemporaneous fossil macaques from mainland Europe along with a series of craniodental differences support the presence of an endemic dwarfed distinct species in Sardinia (Rook and O’Higgins, 2005; Zoboli et al., 2016).

The chronostratigraphic range of *M. majori* remains uncertain (Sondaar, 1987; Sondaar and Van der Geer, 2005; Abbazzi et al., 2008; Palombo and Rozzi, 2014). *Macaca majori* was undoubtedly present in Sardinia during the Early to Middle Pleistocene (Van der Made, 1999), yet the time of arrival of the genus *Macaca* to Sardinia is unclear (see Palombo, 2006 and references therein). The absence of *M. majori* from the fossil record of Sardinia after the Middle Pleistocene suggests that the species became extinct by then, although the causes remain unknown (Abbazzi et al., 2004).

1.3. *Dietary ecology of fossil European Plio–Pleistocene macaques*

The dietary ecology of modern macaque species has been extensively studied (e.g., Maruhashi, 1980; Fooden, 1982; Fa, 1989; Krishnamani, 1994; Agetsuma, 1995; Hill, 1997; Menard and Vallet, 1997; O’ Brien and Kinnaird, 1997; Hanya et al., 2003; Pombo et al., 2004; O’Regan et al., 2008; Hanya et al., 2011; Albert et al., 2013; Sengupta et al., 2014; Richter et al., 2015; Tsuji et al., 2015). In general, extant macaques are usually regarded as opportunistic and highly eclectic feeders exploiting a wide variety of food items available in their habitats (Fa, 1989; Thierry, 2011). They primarily depend on plant matter for food, even though they may supplement their diet with faunal resources like insects, invertebrates, eggs, fish, gastropods, and crustaceans (Fooden, 2000; O’Regan et al., 2008; Stewart et al., 2008; Pal et al., 2018). However, dietary information for fossil macaques is sparse (Ramírez-Pedraza et al., 2023) and there is a lack of information for fossil macaque species from Europe.

The presumed closest extant relative of fossil European macaques is *Macaca sylvanus sylvanus* from North Africa, which appears to prefer fruit and/or seeds such as acorns when available but also includes large amounts of leaves in its diet (Ménard and Vallet, 1997; Ménard, 2002). This seems to be a common dietary strategy in macaque species found in temperate habitats, such as *Macaca fuscata* from Japan and some *Macaca mulatta* populations found in high altitudes in China (Hanya et al., 2011; Sengupta and Radhakrishna, 2016; Cui et al., 2019, 2020). By contrast, species found in tropical habitats, such as *Macaca nemestrina* and *Macaca nigra*, apparently consume more fruits than do those in temperate and marginal zones (O'Brien and Kinnaird, 1997; Hanya et al., 2013; Ruppert et al., 2018). In addition, geographical and regional factors that affect the availability of vegetal resources may also influence the dietary choices of some macaque species (e.g., Agetsuma and Nakagawa, 1998; Hanya et al., 2003, 2004; Hanya, 2004). Since European Plio–Pleistocene macaques probably dwelled in temperate and marginal habitats, it may be assumed that they followed dietary strategies similar to those seen in extant temperate species (e.g., Elton and O'Regan, 2014). However, it must be noted that behaviors observed in modern species are not always equivalent to those of extinct taxa, especially when considering the anthropogenic effects on present-day ecosystems.

This work examines the dietary niches of fossil Plio–Pleistocene European macaques, focusing on *M. majori* from Sardinia. Previous research revealed that *M. majori* possesses some unique dental anatomical traits (overall more robust dentition with molars having a more 'inflated' morphology) compared with other species of the genus *Macaca* (Szalay and Delson, 1979; Zanaga, 1998). It has been previously assumed that these derived features might reflect specific dietary adaptations (e.g., Rook and O'Higgins, 2005), potentially towards an overall more durophagous dietary niche. Here, we evaluate this hypothesis by examining the molar morphology of *M. majori* along with its dental microwear texture. We assume that, if its molars possess some distinctive morphological features that could be suggestive of an overall more durophagous diet compared to other cercopithecids, this will also be reflected in its dental

microwear textures. To that end, we first assess the molar morphology of *M. majori* (i.e., via enamel thickness and dental topography) using two fossil molars from two specimens from Capo Figari (Ty5199 and Ty5203; Fig. 1) and compare these with a broad sample of modern cercopithecids which includes folivorous, fruit/seed and mixed feeding species. We then assess the microwear textures of *M. majori* by comparing them with a series of modern cercopithecids with folivorous, fruit/seed eating and mixed feeding dietary habits. Furthermore, in the dental microwear comparative sample we included two extant macaques found in temperate habitats (*M. sylvanus* and *M. fuscata*) and one in more tropical (*M. nemestrina*) and other European mainland *Macaca* fossil specimens (here assigned to *M. s. florentina*). As previously mentioned, due to the opportunistic dietary nature of the extant macaques usually there are distinct differences in the dietary composition of macaques found in temperate habitats compared to macaques found in tropical habitats (Ménard, 2002, Hanya et al., 2011, 2013), that could be reflected in their microwear textures. Therefore, differences and/or similarities in the microwear textures between extant macaque species will allow us to better comprehend ecological factors that may have influenced the diet of the fossil European species (i.e., *M. majori* and *M. s. florentina*). In addition, as previous research suggests inter-population differences in the dietary choices and feeding behavior of some temperate macaque species most likely associated with habitat differences (e.g., Maruhashi, 1980; Agetsuma and Nakagawa, 1995; Ménard and Qarro, 1999), it is possible that this also applied to European mainland fossil macaques and *M. majori*. To evaluate this possibility, we also explore microwear texture differences among three extant populations of a temperate macaque species in our microwear sample, *M. fuscata*, found in northern (Aomori), central (Nagano) and southern (Yakushima) Japan, assuming that potential microwear texture differences will enable us to better understand the dietary ecology of extant and fossil macaques found in temperate environments. Our results have important implications for understanding the diversity of the genus *Macaca* in Europe, its paleoecology during the Plio–Pleistocene and the dietary strategies of extant macaque species. If *M. majori* potentially occupies a dietary niche

relatively distinct from the modern cercopithecids compared here and its European mainland fossil macaques, this may suggest that ecological differences among paleohabitats (e.g., European mainland and Sardinian insular) may have promoted different dietary strategies that favored certain feeding adaptations. This further implies that the opportunistic and generalist dietary nature of macaques may have been a key trait for their extensive geographic distribution and ecological success (e.g., Elton and O'Regan, 2014).

2. Material and methods

2.1. Studied material

Enamel thickness and dental topography The fossil sample of *M. majori* consists of two virtual models of M²s (Fig. 2) from Capo Figari (Sardinia, Italy) housed in the Naturhistorisches Museum Basel (Switzerland). These molars are slightly to moderately worn; following Delson (1973) Ty5203 scores as wear grade B and Ty5199 as wear grade C.

The extant comparative sample consists of 44 M²s belonging to 23 cercopithecoid species, including papionins, cercopithecins and Asian and African colobines (Supplementary Online Material [SOM] Table S1). All teeth are derived from dry skulls housed in museums and other public institutions. Following previous standard approaches, only individuals with unworn or minimally worn M²s were selected, corresponding to grades A to B according to the scoring system of Delson (1973), to ensure that no macroelements were significantly altered by wear (e.g., Olejniczak et al., 2008; Guy et al., 2015; Thiery et al., 2017c).

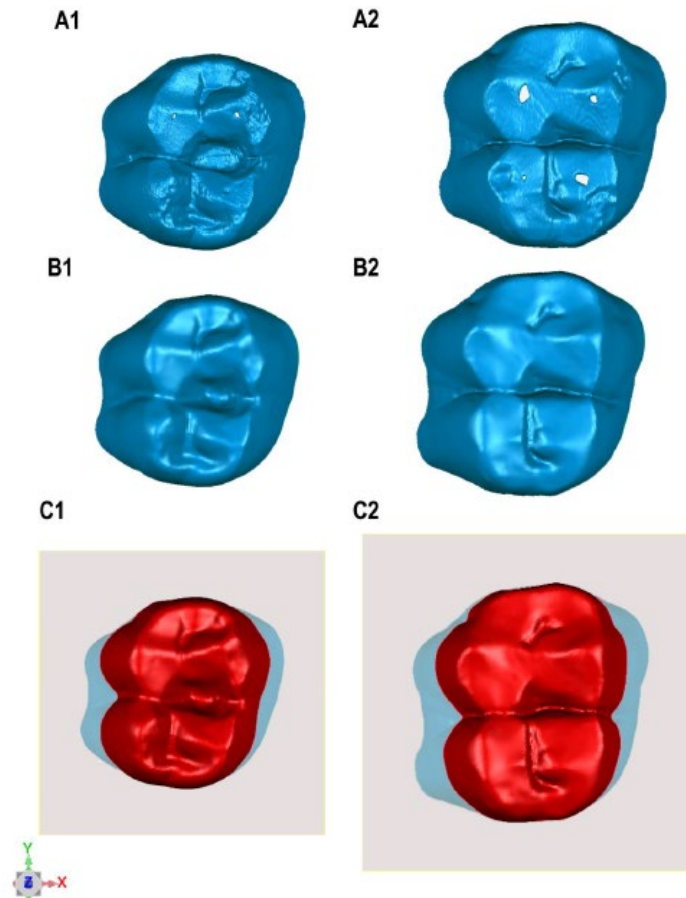


Figure 2. Virtual reconstructions of the M²s of the *Macaca majori* specimens after segmentation from μ CT images (A1: Ty5203; A2: Ty5199), after using the surface preparation and orientation protocol (B1: Ty5203; B2: Ty5199) and the subsampled enamel surfaces (in red; C1: Ty5203; C2: Ty5199). The scanning resolution of the Ty5199 and Ty5203 fossil molars is 20.0 μ m.

Dental microwear texture analysis The macaque fossil material included in the dental microwear texture analysis (DMTA) consists of 39 molars from fossil sites in Italy and Spain (SOM Table S2): 30 belong to *M. majori* from Capo Figari (Sardinia), five to *M. s. florentina* from the Upper Valdarno fossil localities, one to *Macaca s. cf. prisca* from Villafranca d' Asti–Fornace RDB, and three to *Macaca s. cf. florentina* from Cal Guardiola and Vallparadís fossil sites (see Alba et al., 2008). As sample sizes are too small to explore dental microwear texture differences among extinct macaque subspecies or fossil sites of mainland Europe, here we pool the fossil specimens at the species level (SOM Table S2). The fossil specimens from the Cal

Guardiola and Vallparadís localities are housed in the Institut Català de Paleontologia Miquel Crusafont (Spain), and those from Capo Figari, Upper Valdarno and Villafranca d' Asti–Fornace RDB are housed in the Naturhistorisches Museum Basel (Switzerland). The extant comparative sample includes only individuals from wild/natural populations of eight cercopithecoid species with dietary behaviors that we assume that brackets the extremes of food mechanical properties (i.e., soft–tough, hard–brittle, and more diverse; see SOM Table S3): six species of papionins (*Macaca fuscata*, $n = 67$ [Aomori population, $n = 26$; Nagano population, $n = 27$; Yakushima population, $n = 14$]; *Macaca nemestrina*, $n = 11$; *Macaca sylvanus*, $n = 9$; *Lophocebus albigena*, $n = 14$; *Papio hamadryas*, $n = 39$; *Mandrillus sphinx*, $n = 33$), a cercopithecine (*Chlorocebus aethiops*, $n = 36$), and a colobine (*Colobus guereza*, $n = 20$).

2.2. Dietary categorization

Following Plastiras et al. (2022), all species used in this study were assigned to one of three general dietary categories: folivory, mixed feeding or fruit/seed consumption. This classification is based on dietary information from previously published studies on wild populations (SOM Table S3 and citations therein). Some extant species were used only in enamel thickness and dental topographic analyses, while others only in dental microwear analysis, because there were not available data for both methodologies for all extant species shown in SOM Table S3. However, it is important to note the dietary categorization used here was not based on the actual mechanical properties of the foods ingested and masticated, with studies showing that broad dietary categorization may not always accurately track the food material properties (e.g., Vogel et al., 2008, 2014; McGraw et al., 2012; Smith et al., 2012; Coiner-Collier et al., 2016). Even if that is the case and these dietary categories may be relatively broad, we expect them to reflect dental morphological and microwear differences among primates with contrasting dietary

preferences (e.g., folivores vs. fruit/seed-eaters), as well as intermediate morphologies and microwear textures associated with mixed diets (Plastiras et al., 2022).

2.3. *Data collection*

Dental topographic and enamel thickness analyses The fossil and extant M²s were scanned using the EasyTom XL duo μ CT (Plateforme PLATINA, PALEVOPRIM, University of Poitiers, France) with a voxel resolution ranging from 19.0 to 40.0 micrometers (μ m). The μ CT scans were processed in Avizo v. 7.0 (Visualization Sciences Group, 2011, Berlin). Each enamel cap was isolated from the dentine tissue using automatic segmentation tools and then was smoothed using the 'smoothing labels' command (size = 3, 3D volume). Each resulting enamel cap surface was extracted using the 'generate surface' module with the unconstrained smoothing type (smoothing extent = 3). The resulting enamel caps then were separated into two components, the outer enamel surface (OES) and the enamel-dentine junction surface (EDJ), using Geomagic studio 2013 (3D Systems Inc., Rock Hill). After removing potential artifacts (e.g., small holes, intersecting triangles produced by the tessellation procedure), the resulting surfaces were set to an equivalent number of polygons (55,000) by a re-tessellation of the original polyhedral surface, with each polygon retaining an equivalent size. This procedure has been previously shown to have no significant affect any macroscopic features present on the tooth crown (Guy et al., 2015; Thiery et al., 2017c, 2021; Plastiras et al., 2022). The position and orientation of all OES/EDJ couples were standardized using a reference plane, created by a best-fit plane procedure applied on the occlusal basin of the EDJ surface, which represents the virtual space xy axis. The x-axis was then aligned with an axis formed by connecting the dentine horn tips of the paracone and protocone. Lastly, the lowermost point of each molar cervix was set to x, y, 0 so that the crown height could be measured on a z positive scale (see Guy et al., 2015; Thiery et al., 2017c; Plastiras et al., 2022).

Topographic and enamel thickness variables are usually measured on either subsampled surfaces (i.e., cropped OES and EDJ on their lowermost point) or the entire enamel cap (Ulhaas et al., 2004; Boyer, 2008; Bunn and Ungar, 2009; Ledogar et al., 2013; Guy et al., 2013; Winchester et al., 2014; Allen et al., 2015; Guy et al., 2015; Pampush et al., 2016; Zanolli et al., 2016; Thiery et al., 2017c; Berthaume et al., 2018, 2020; Plastiras et al., 2022). However, only few studies have incorporated both cropped and uncropped dental crown surfaces (Prufrock et al., 2016; Winchester, 2016; Berthaume et al., 2019), with some suggesting that some topographic measures better correlate with diet when considering subsampled occlusal 3D surfaces (e.g., Allen et al., 2015) because the subsampling process minimizes the influence of some tooth elements that may not actively participate in food processing. Nevertheless, so far to our knowledge there has been no quantitative investigation on the relationship between the two sampling methods with respect to diet. In this work, all enamel thickness and dental topographic variables (see below) were measured using both sampling methods; the 'basin cut off' (BCO) and 'entire enamel cap' (EEC; sensu Berthaume et al., 2019). We did this because we wanted to explore the differences between sampling methods in the studied variables, the relationship between their resulting values and diet, and to provide a baseline for comparisons for future studies.

Seven variables were measured on each molar (SOM Table S1). We used three variables that characterize enamel thickness. Two of these variables estimate 3D relative enamel thickness—the volumetric variable, which measures the volume of the enamel cap (3DRETvol; Martin, 1985; Kono, 2004; Olejniczak et al., 2008), and the geometric variable, which assesses and depicts the 3D spatial distribution of enamel on the tooth crown as the shortest normal distance from the 3D polygonal meshes of the outer enamel surface to the enamel dentine junction surface (3DRETgeo; Thiery et al., 2017b, 2019). Additionally, we measured absolute crown strength (ACS; Schwartz et al., 2020), a linear measure of average enamel thickness modeled as a hemisphere assuming a uniform distribution, that is used to assess the resistance of teeth to fracture (see Schwartz et al., 2020: SOM Fig. S1). Furthermore,

we measured three variables that characterize aspects of molar topography. Dental relief was assessed by relief index (LRFI) and inclination (Boyer, 2008; Guy et al., 2013, 2015) whereas curvature/sharpness was assessed by the area-relative curvature (ARC; Guy et al., 2017; Thiery et al., 2021; Plastiras et al., 2022). The latter curvature-based measure corresponds to the mean curvature normalized by the size of the tooth using a theoretical linear model (see SOM S1). Compared to previous estimates (e.g., Dirichlet normal energy, Bunn et al., 2011), it provides a quantitative and more detailed assessment of curvature, a notion further advocated by later similar metrics (e.g., Pampush et al., 2022). Nevertheless, topographic variables may be considered as abstract expressions of dental form that may be able to discriminate different morphologies but do not necessarily capture only functionally relevant information (Pampush et al., 2022). Lastly, we considered the two-dimensional projection of the occlusal enamel surface (OES 2D) of each specimen as an estimate of the area of the molar crown. Calculations for 3DRETgeo, ACS, LRFI, inclination, ARC, and OES 2D were performed using the beta version of the 'Doolkit' package (Thiery et al., 2021) in R v. 3.6 (R Core Team, 2013), while 3DRETvol was calculated using Geomagic studio 2013 (3D Systems Inc., 2013).

Dental microwear texture analysis Data for DMTA were collected on molar Phase II (crushing) and Phase I (shearing) facets (Maier, 1977). In this analysis, we include both Phase I and II facets, as both facet types bear dietary signals (Louail et al., 2021; Merceron et al., 2021; Plastiras et al., 2022). Analyses were preferentially based on upper and lower M2s in extant species, but the fossil sample also includes some M1s and M3s. Experimental work has shown no significant variation along the upper and lower molar sequences (Ramdarshan et al., 2017).

Following standard protocols, teeth were cleaned and then molded with a silicone dental molding material (polyvinyl siloxane Coltene Whaledent, President Regular Body). Each dental facet was isolated from the silicon molds and then scanned with 'TRIDENT', a confocal DCM8 Leica Microsystems surface profilometer housed at the PALEVOPRIM lab (CNRS and University of Poitiers) using a 100× lens

(see details in Merceron et al., 2016: Supplementary Information). The scanned surfaces were mirrored and automatically freed from any abnormal peaks, and a 200 × 200 μm area was then extracted and saved as a digital elevation model to be used for DMTA. The resulting data were analyzed in Toothfrax v. 1.0, Sfrax software (Surfract, www.surfract.com) and LeicaMap 7.4 (Leica Microsystems). Four variables were used to characterize microwear surface textures (Scott et al., 2006): complexity (Asfc; dimensionless), anisotropy (epLsar at 1.8 μm; dimensionless), heterogeneity (Hasfc with 81 cells; dimensionless), and textural fill volume (Tfv at the scale of 2.0 μm; in μm³).

2.4. *Statistical analysis*

Dental topographic and enamel thickness analyses Similar dental traits among closely related species (e.g., thick/thin enamel, high/low dental relief) may be due to phylogenetic relatedness, while other factors may have also influenced their evolution (e.g., diet). Estimating the phylogenetic signal may provide some insights into how particular traits possibly evolved (see Symonds and Blomberg, 2014). Hence, we assessed the relationships among the six topographic and enamel thickness variables (e.g., 3DRETvol, 3DRETgeo, ACS, LRFI, inclination, ARC) for both sampling methods (i.e., BCO and EEC) using phylogenetic generalized least squares (PGLS) regression analysis on species averages, which allowed us to evaluate the potential effects of phylogeny on the distribution of the data (see also Winchester et al., 2014; Boyer et al., 2015; Pampush et al., 2016; Thiery, et al., 2017c; Plastiras et al., 2022). The effect of phylogeny was measured using Pagel's lambda (λ ' Pagel, 1994, 1999; Freckleton et al., 2002), which is a measure of phylogenetic signal that ranges from 0 to 1 (0 representing no phylogenetic structuring, 1 representing a perfect fit between data and a Brownian motion model of evolutionary change). A phylogeny for the 23 cercopithecoid species included in this study was generated using a consensus tree (100 iterations) downloaded from the 10k Trees Project website v. 3 (Arnold et al., 2010). We also

included OES 2D in our PGLS regression to investigate the effect of size on the distribution of data. To perform the PGLS regression we used the 'caper' package v. 1.0.1 (Orme et al., 2013) in R v. 3.6 (R Core Team, 2013).

To explore the dental traits of the fossil molars of *M. majori* with respect to diet, we first examined the morphological differences among the proposed dietary categories using both sampling methods (BCO and EEC). This was done in SPSS v. 22.0 (IBM Corp, 2013) by comparing the variables among the dietary categories (3DRETvol, 3DRETgeo, ACS, LRFI, inclination, and ARC) using the nonparametric Kruskal-Wallis test, followed by Dunn's post-hoc tests with Bonferroni correction for multiple comparisons, and a significance level set to 0.05. Visualizations were performed using R v. 3.6 (R Core Team, 2013). Lastly, two principal component analyses (PCAs) were performed, one for each sampling method, to summarize group differences and to determine where the fossil molars fell with respect to the range of variation of the comparative sample. Computations and visualizations for the PCAs were performed using PAST v. 3.22 (Hammer et al., 2001).

Dental microwear texture analysis To identify microwear texture differences associated with diet, nonparametric Kruskal-Wallis tests were performed on extant species and the fossil macaques (i.e., *M. majori* and *M. s. florentina*) to determine which variables differ significantly among species for each dental facet type (i.e., Phase II and Phase I). Lastly, two nonparametric Kruskal-Wallis tests were performed among the extant populations of *M. fuscata* (i.e., from Aomori, Nagano and Yakushima) to explore potential inter-population differences in dental microwear textures. For all Kruskal-Wallis tests, post-hoc pairwise comparisons were performed for both dental facet types using Dunn's post-hoc tests with Bonferroni correction for multiple comparisons, with a significance level set to 0.05. All computations were performed using SPSS v. 22.0 (IBM Corp, 2013).

3. Results

3.1. Dental topographic and enamel thickness analyses

The descriptive statistics of all enamel thickness and dental topographic variables of each dietary category are given in Table 1, while the results of the PGLS analysis are summarized in Table 2. The PGLS analysis reveals significant correlations between pairs of variables, with some suggesting that they are influenced by the phylogenetic structure of the comparative sample (Table 2). It is worth noting that measures of 3D relative enamel thickness (3DRETvol and 3DRETgeo) are strongly correlated with both relief estimates (LRFI and inclination) with a relatively low phylogenetic effect, although the phylogenetic signal varies depending on the sampling method. For instance, 3DRETvol is significantly correlated with inclination and LRFI in both sampling methods, yet based on BCO there seems to be no phylogenetic effect, whereas based on EEC there is some ($\lambda = 0.204$ and $\lambda = 0.273$ respectively; see Table 2). On the other hand, ACS is correlated with inclination only when considering EEC and with no phylogenetic effect. Furthermore, some significant correlations among variable pairs seem to be influenced by the sampling method, some being significantly correlated based on the BCO method, others based on the EEC method (Table 2). In addition, size (e.g., OES 2D) is significantly correlated with ACS, 3DRETvol, 3DRETgeo and inclination, yet with 3DRETvol and 3DRETgeo only in BCO method, whereas with inclination only in EEC (Table 2).

Table 1

Descriptive statistics for dental topographic and enamel thickness variables of the dietary categories proposed (i.e., folivores, fruit/seed eaters, mixed feeders) for both sampling methods (BCO and EEC).

Diet	n_{sp}	n_{ind}		BCO						EEC						
				3DRETvol	3DRETgeo	ACS	ARC	LRFI	inclination	3DRETvol	3DRETgeo	ACS	ARC	LRFI	inclination	
Folivores	8	18	Mean	0.189	0.177	1.227	1.804	0.347	119.432	0.119	0.103	105.347	2.153	0.562	105.347	
			sd	0.028	0.026	0.162	0.106	0.038	2.623	0.013	0.010	1.641	0.124	0.029	1.641	
			95%	Upper	0.203	0.190	1.308	1.857	0.366	120.737	0.126	0.108	106.195	2.216	0.547	106.195
				Lower	0.174	0.164	1.146	1.751	0.328	118.127	0.112	0.098	105.378	2.091	0.576	105.378
Fruit/seed eaters	8	13	Mean	0.291	0.280	1.405	1.51	0.278	124.572	0.146	0.125	108.118	1.895	0.524	108.118	
			sd	0.055	0.053	0.204	0.12	0.044	3.357	0.021	0.016	2.261	0.113	0.036	2.261	
			95%	Upper	0.325	0.312	1.528	1.583	0.305	126.601	0.160	0.135	109.485	1.963	0.546	109.485
				Lower	0.258	0.248	1.408	1.437	0.251	122.543	0.133	0.115	106.751	1.826	0.502	106.751
Mixed feeders	8	13	Mean	0.229	0.228	1.897	1.617	0.3	122.766	0.152	0.126	108.112	1.982	0.528	108.112	
			sd	0.036	0.026	0.611	0.111	0.043	3.542	0.022	0.012	3.246	0.149	0.042	3.246	
			95%	Upper	0.251	0.244	2.267	1.685	0.326	124.907	0.166	0.133	110.074	2.072	0.553	110.074
				Lower	0.207	0.212	1.527	1.55	0.274	120.625	0.139	0.118	106.151	1.891	0.502	106.151

Abbreviations: n_{sp} = number of species; n_{ind} = number of individuals of all species; BCO = basin cut off cropping method (after Berthaume et al., 2019); EEC = entire enamel cap method (after Berthaume et al., 2019); sd = standard deviation; 95% = 95% confidence interval; 3DRETvol = 3D volumetric relative enamel thickness; 3DRETgeo = 3D geometric relative enamel thickness; ACS = absolute crown strength; LRFI = relief index; ARC = area-relative curvature.

Table 2

Phylogenetic generalized least squares correlations on species averages between dental topographic and enamel thickness variables for both sampling methods.

Variables ^b	Pagel's λ ^a			Slope		Std. error	t-value	AIC	logL	BIC	Multiple r^2 ^c	Adjusted r^2 ^c
	Value	Bounds	p-value	Value	p-value							
3DRETvol-LRFI (BCO)	0	1 0	0.019 1	-1.153	<0.001	0.252	-4.566	-17.316	10.658	-15.045	0.498	0.474
3DRETvol-LRFI (EEC)	0.204	1 0	0.327 0.737	-1.558	0.001	0.419	-3.717	-30.814	17.407	-28.543	0.396	0.368
3DRETgeo-LRFI (BCO)	0.514	1 0	0.051 0.363	-1.092	<0.001	0.239	-4.562	-26.644	15.322	-24.373	0.497	0.473
3DRETgeo-LRFI (EEC)	0.272	1 0	0.676 0.598	-1.275	0.002	0.362	-3.52	-38.085	21.042	-35.814	0.371	0.341
3DRETvol-inclination (BCO)	0	1 0	0.016 1	6.320	<0.001	1.362	4.638	-17.679	10.839	-15.408	0.506	0.482
3DRETvol-inclination (EEC)	0.273	1 0	0.082 0.536	4.633	<0.001	1.153	4.016	-33.173	18.586	-30.902	0.434	0.407
3DRETgeo-inclination (BCO)	0.596	1 0	0.032 0.272	5.638	<0.001	1.31	4.301	-26.054	15.027	-23.783	0.468	0.443
3DRETgeo-inclination (EEC)	0.324	1 0	0.193 0.434	3.960	<0.001	0.991	3.994	-40.932	22.466	-38.661	0.431	0.404
ACS-inclination (BCO)	0.972	1 0	0.578 0.006	0.338	0.870	2.048	0.165	-5.034	4.517	-2.763	0.001	-0.046
ACS-inclination (EEC)	0	1 0	1 1	8.603	<0.001	1.582	5.435	-12.576	8.288	-10.305	0.584	0.564
OES 2D-3DRETvol (BCO)	1	1 0	1 <0.001	-1.308	0.001	0.367	-3.56	15.771	-5.885	18.042	0.376	0.346
Variables ^b	Value	Pagel's λ ^a Bounds	p-value	Slope Value	p-value	Std. error	t-value	AIC	logL	BIC	Multiple r^2 ^c	Adjusted r^2 ^c
OES 2D-3DRETvol (EEC)	0.975	1	0.628	0.158	0.812	0.657	0.240	23.998	-9.999	26.269	0.002	-0.044

		0	0.058									
OES 2D–3DRETgeo (BCO)	0.996	1 0	0.914 0.001	-1.163	0.021	0.469	-2.478	20.595	-8.297	22.866	0.226	0.189
OES 2D–3DRETgeo (EEC)	0.979	1 0	0.649 0.030	0.158	0.832	0.744	0.213	24.002	-10.001	26.273	0.002	-0.045
OES 2D–ACS (BCO)	0.938	1 0	0.466 0.001	1.908	<0.001	0.102	18.607	-39.588	21.794	-37.317	0.942	0.940
OES 2D–ACS (EEC)	0.845	1 0	0.253 0.188	1.877	<0.001	0.109	17.219	-37.095	20.547	-34.824	0.933	0.930
OES 2D–inclination (BCO)	0.955	1 0	0.427 0.030	-1.760	0.667	4.041	-0.437	25.966	-10.983	28.237	0.008	-0.038
OES 2D–inclination (EEC)	0	1 0	0.271 1	12.908	<0.001	3.228	3.998	20.128	-8.109	22.489	0.432	0.405
3DRETvol–3DRETgeo (BCO)	0	1 0	0.009 1	0.942	<0.001	0.059	15.934	-60.608	32.304	-58.337	0.923	0.920
3DRETvol–3DRETgeo (EEC)	0	1 0	<0.001 1	1.158	<0.001	0.044	25.753	-95.231	49.615	-92.960	0.969	0.967
ARC–LRFI (BCO)	0.924	1 0	0.482 0.016	1.160	<0.001	0.193	5.998	-55.321	29.660	-53.050	0.631	0.613
ARC–LRFI (EEC)	0.473	1 0	0.037 0.346	0.343	0.062	0.174	1.969	-66.270	35.135	-63.999	0.1555	0.115
RETvol–ACS (BCO)	1	1 0	1 0.001	-0.413	0.032	0.180	-2.286	-13.300	8.650	-11.029	0.199	0.161
RETvol–ACS (EEC)	0.474	1 0	1 0.292	0.301	0.020	0.120	2.501	-27.990	15.995	-25.719	0.229	0.192
Variables^b	Value	Page's λ^a	p-value	Slope	Std.	t-	AIC	logL	BIC	Multiple	Adjusted	
ARC–RETgeo (BCO)	0.52	1	0.008	-1.637	<0.001	0.390	-4.190	-24.837	14.814	-22.567	0.455	0.429

		0	0.231									
ARC–RETgeo (EEC)	0.72	1 0	0.178 0.148	-0.711	0.052	0.346	-2.053	-34.834	19.417	-32.563	0.167	0.127
ARC–RETvol (BCO)	0	1 0	0.005 1	-1.713	< 0.001	0.375	-4.562	-17.296	10.648	-15.025	0.497	0.473
ARC–RETvol (EEC)	0.951	1 0	0.517 0.026	-0.602	0.116	0.367	-1.638	-29.088	16.544	-26.817	0.113	0.071
OES 2D–ARC (BCO)	0.936	1 0	0.419 0.017	0.562	0.621	1.123	0.501	25.960	-10.980	28.231	0.011	-0.035
OES 2D–ARC (EEC)	0.966	1 0	0.552 0.003	0.519	0.653	1.141	0.455	23.872	-9.936	26.143	0.009	-0.037
OES 2D–LRFI (BCO)	0.959	1 0	0.463 0.050	0.206	0.793	0.206	0.265	26.091	-11.045	28.362	0.003	-0.044
OES 2D–LRFI (EEC)	0.992	1 0	0.865 0.054	-1.138	0.401	1.328	-0.856	23.309	-9.654	25.580	0.033	-0.012
LRFI–inclination (BCO)	0.371	1 0	0.015 0.348	-5.320	<0.001	0.199	-	-	57.808	-109.346	0.971	0.969
LRFI–inclination (EEC)	0.383	1 0	1 1	-2.586	<0.001	0.299	-8.636	-96.883	50.441	-94.612	0.780	0.769
ARC–inclination (BCO)	0.821	1 0	0.272 0.075	-0.236	<0.001	0.035	-6.662	-	69.467	-132.664	0.678	0.663
ARC–inclination (EEC)	0.771	1 0	0.030 0.006	-0.160	0.003	0.048	-3.328	-	64.653	-123.035	0.345	0.314
RETgeo–ACS (BCO)	1	1 0	1 <0.001	-0.216	0.213	0.169	-1.282	-16.383	10.191	-14.112	0.072	0.028
Variables ^b	Value	Page's λ ^a	p-value	Slope	Std.	t-	AIC	logL	BIC	Multiple	Adjusted	
RETgeo–ACS (EEC)	0.402	1	1	0.249	0.024	0.103	2.414	-34.24	19.12	-31.969	0.217	0.180

		0	0.280									
ARC-ACS (BCO)	0.980	1 0	0.744 0.001	-0.155	0.776	0.539	-0.287	-5.070	4.535	-2.799	0.003	-0.043
ARC-ACS (EEC)	0.994	1 0	0.891 <0.001	0.012	0.982	0.541	0.022	-7.447	5.723	-5.176	< 0.001	-0.047
LRFI-ACS (BCO)	0.74	1 0	0.611 0.012	-0.152	0.702	0.393	-0.388	-5.166	4.583	-2.895	0.007	-0.040
LRFI-ACS (EEC)	1	1 0	1 0.007	-0.888	0.183	0.646	-1.375	-9.409	6.704	-7.138	0.082	0.038

Abbreviations: BCO = basin cut off cropping method (after Berthaume et al., 2019); EEC = entire enamel cap method (after Berthaume et al., 2019); 3DRETvol = 3D volumetric relative enamel thickness; 3DRETgeo = 3D geometric relative enamel thickness; ACS = absolute crown strength; LRFI = relief index; ARC = area-relative curvature; OES 2D = 2D occlusal enamel surface; std. error = standard error of the slope; AIC = Akaike information criterion; LogL = Log likelihood; BIC = Bayesian information criterion; r^2 = coefficient of determination.

^a Pagel's λ is a measure of phylogenetic signal, with 1 representing a perfect fit between the data and a Brownian motion model of change in values through evolution, and 0 representing no phylogenetic structuring.

^b Pairs of variables that are significantly correlated are in bold (alpha = 0.05).

^c Multiple r^2 measures the variation that is explained by the regression model (values range from 0 to 1) and it increases or remains the same as new predictors are added to the multiple regression model. The adjusted r^2 measures the variation for a multiple regression model and helps determine the how well it fits, while it takes into account the number of independent variables in the model in order to avoid overestimating the impact of adding independent variables to the model.

^d The degrees of freedom for each correlation are 2.

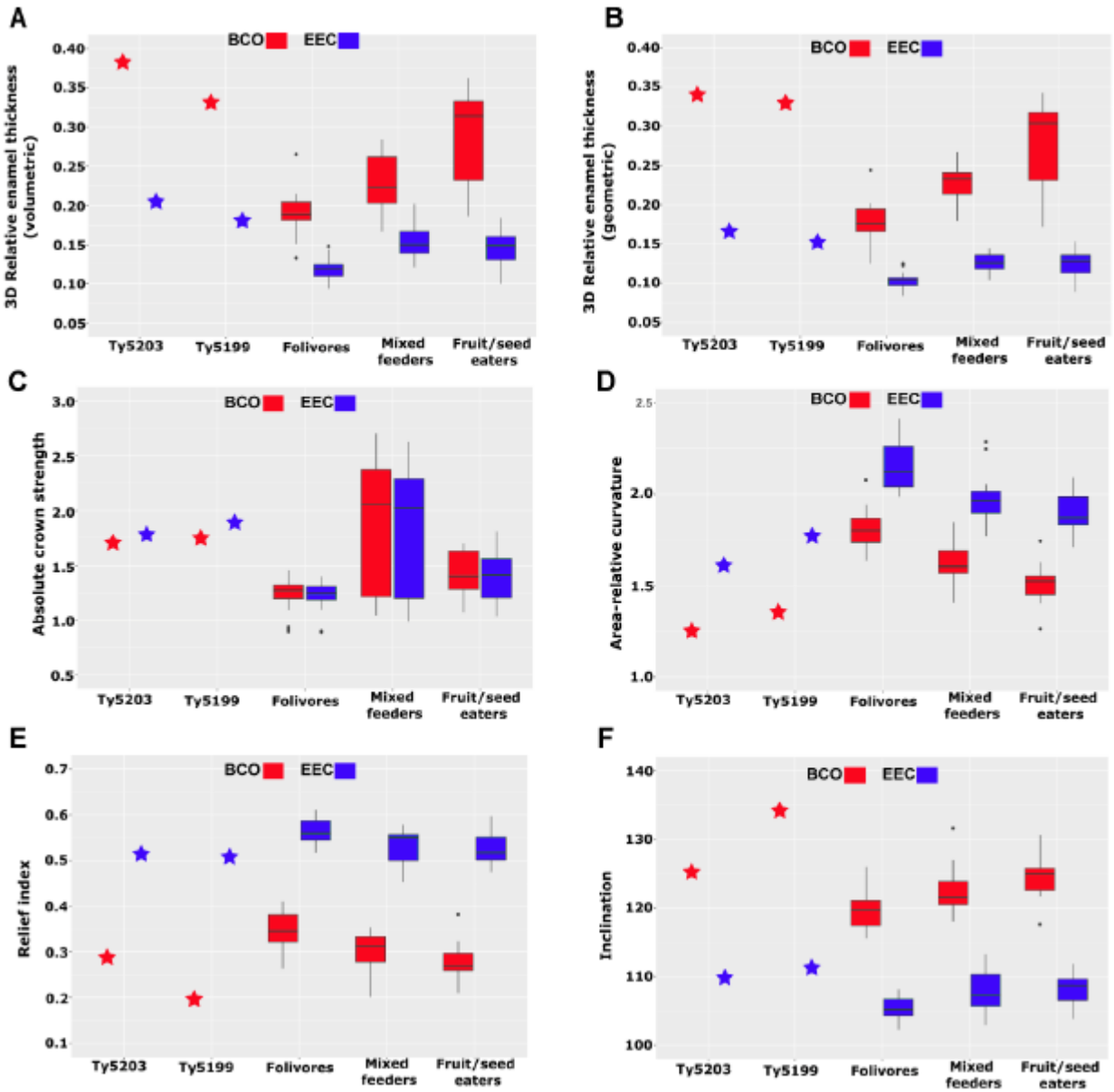


Figure 3. Boxplots showing the results of the dental topographic and enamel thickness analyses. A) three-dimensional relative enamel thickness (volumetric); B) three-dimensional relative enamel thickness (geometric); C) absolute crown strength (ACS); D) area-relative curvature (Guy et al., 2017); E) relief index (Boyer, 2008); F) inclination. Data for the dietary categories represented in the sample of extant cercopithecids and *Macaca majori* (Ty5199 and Ty5203) are represented for both BCO (basin cut off, in red) and EEC (entire enamel cap, in blue) sampling methods. The horizontal center line marks the median, the lower and upper bounds of the box mark the 25th and 75th percentiles, whiskers represent the minimum and maximum interquartiles (1.5*interquartile range), and filled (black) circles represent outliers.

Table 3. Kruskal Wallis tests on enamel thickness and dental topographic variables among the proposed dietary categories (i.e., folivores, fruit/seed eaters, mixed feeders) for the two sampling methods (BCO and EEC).

Variables	df	χ^2	p-value
BCO			
3DRETvol	2	22.765	<0.001
3DRETgeo	2	25.181	<0.001
ACS	2	7.946	0.019
ARC	2	26.754	<0.001
LRFI	2	15.735	<0.001
inclination	2	16.603	<0.001
EEC			
3DRETvol	2	19.755	<0.001
3DRETgeo	2	19.773	<0.001
ACS	2	7.239	0.026
ARC	2	20.728	<0.001
LRFI	2	8.654	0.013
inclination	2	10.606	0.004

Abbreviations: df = degrees of freedom; BCO = basin cut off cropping method (after Berthaume et al., 2019); EEC = entire enamel cap method (after Berthaume et al., 2019); 3DRETvol = 3D volumetric relative enamel thickness; 3DRETgeo = 3D geometric relative enamel thickness; ACS = absolute crown strength; ARC = area-relative curvature; LRFI = relief index.

The results of the Kruskal-Wallis tests indicate significant differences in all variables (3DRETvol, 3DRETgeo, ACS, LRFI, inclination and ARC) among dietary categories, consistent for both sampling methods (Table 3). Concerning the BCO method, the pairwise comparisons with Bonferroni adjustment reveal that folivores have significantly lower values of 3DRETvol compared to the fruit/seed eaters (Fig. 3A; Table 4), whereas in terms of 3DRETgeo folivores have significantly lower values compared to both fruit/seed eaters and mixed feeders (Fig. 3B; Table 4). Furthermore, folivores also possess significantly lower values of ACS compared to mixed feeders (Fig. 3C; Table 4), while they also possess significantly higher values of ARC, LRFI and significantly lower values of inclination compared to both fruit/seed eaters and mixed feeders (Fig. 3D–F; Table 4). Concerning the EEC method, the pairwise comparisons with Bonferroni adjustment reveal that the folivores exhibit significantly lower values of 3DRETvol and 3DRETgeo compared to fruit/seed eaters and mixed feeders (Fig. 3A; Table 4). Moreover, the folivorous species have significantly lower values of ACS compared mixed feeders (Fig. 3C; Table 4). Lastly, folivores also exhibit significantly higher and lower values of ARC and inclination, respectively, compared to both

fruit/seed eaters and mixed feeders, while they also exhibit significantly higher values of LRFI compared only to the fruit/seed eaters (Fig. 3D–F; Table 4).

The results of PCAs based on the values of the enamel thickness and dental topographic variables of the M²s from the extant sample of cercopithecids and the two fossil specimens (Ty5199 and Ty5203) for both sampling methods are shown in Figure 4. The cumulative variance of the first two principal components (PC1 and PC2) is 86.04% of the total variance for the BCO sampling method and 83.350% for EEC (SOM Table S4). The proposed dietary categories show less overlap for the BCO method compared to EEC (Fig. 4A, B).

Table 4 . Dunn’s post-hoc tests among the proposed dietary categories (i.e., folivores, fruit/seed eaters, mixed feeders) with *p*-values (before and after Bonferroni correction for multiple comparisons) for the enamel thickness and dental topographic variables for both sampling methods. Significant differences following the Bonferroni correction are highlighted in bold.

Variables	Comparisons between dietary categories		<i>p</i> -values	
			Significance ^a	Adjusted significance ^b
BCO				
3DRETvol	folivores	mixed feeders	0.017	0.051
	folivores	fruit/seed eaters	<0.001	<0.001
	mixed feeders	fruit/seed eaters	0.028	0.085
3DRETgeo	folivores	mixed feeders	0.001	0.004
	folivores	fruit/seed eaters	<0.001	<0.001
ACS	folivores	mixed feeders	0.006	0.017
ARC	folivores	mixed feeders	0.001	0.003
	folivores	fruit/seed eaters	<0.001	<0.001
LRFI	folivores	mixed feeders	0.014	0.042
	folivores	fruit/seed eaters	<0.001	<0.001
inclination	folivores	mixed feeders	0.014	0.043
	folivores	fruit/seed eaters	<0.001	<0.001
EEC				
3DRETvol	folivores	mixed feeders	<0.001	<0.001
	folivores	fruit/seed eaters	0.001	0.002
3DRETgeo	folivores	mixed feeders	<0.001	<0.001
	folivores	fruit/seed eaters	<0.001	0.001
ACS	folivores	mixed feeders	0.008	0.023
ARC	folivores	mixed feeders	0.002	0.006
	folivores	fruit/seed eaters	<0.001	<0.001
LRFI	folivores	mixed feeders	0.022	0.065
	folivores	fruit/seed eaters	0.008	0.025
inclination	folivores	mixed feeders	0.009	0.028
	folivores	fruit/seed eaters	0.004	0.012

Abbreviations: BCO = basin cut off cropping method (after Berthaume et al., 2019); EEC = entire enamel cap method (after Berthaume et al., 2019); 3DRETvol = 3D volumetric relative enamel thickness; 3DRETgeo = 3D geometric relative enamel thickness; ACS = absolute crown strength; ARC = area-relative curvature; LRFI = relief index. ^a Asymptotic significances (two-sided tests) are displayed with

significance level set at 0.05. ^b Significance values have been adjusted by the Bonferroni correction for multiple tests.

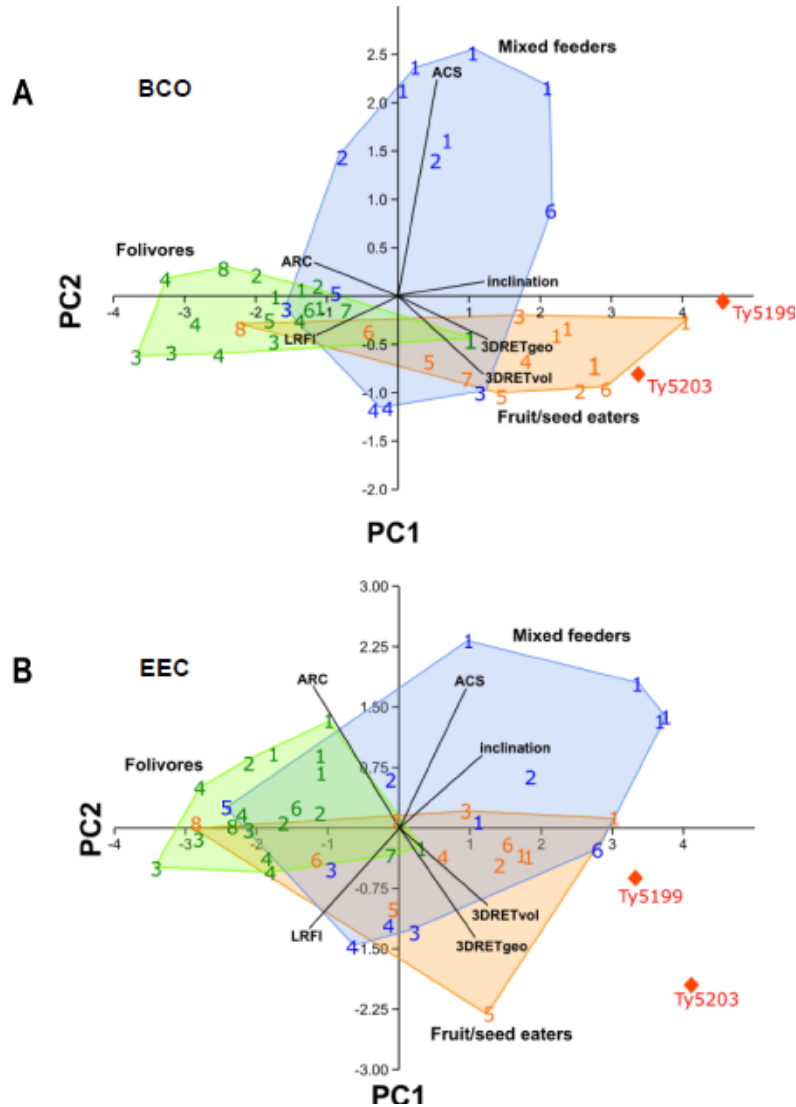


Figure 4. Results of the principal component analyses (PCAs) as bivariate plots of the first and second principal components (PC1 and PC2, respectively) based on enamel thickness and dental topographic variables of the three dietary categories with convex hulls using both BCO (A) and EEC (B) including the fossil M²s (Ty5199 and Ty5203). Blue = mixed feeders (1 = *Papio*; 2 = *Mandrillus*; 3 = *Cercopithecus campbelli*; 4 = *Chlorocebus aethiops*; 5 = *Erythrocebus patas*; 6 = *Macaca sylvanus*); orange = fruit/seed eaters (1 = *Lophocebus albigena*; 2 = *Lophocebus atterimus*; 3 = *Cercocebus torquatus*; 4 = *Cercocebus galeritus*; 5 = *Cercopithecus diana*; 6 = *Cercopithecus pogonias*; 7 = *Cercopithecus nictitans*; 8 = *Cercopithecus cephus*); green = folivores (1 = *Colobus polykomos*; 2 = *Colobus guereza*; 3 = *Procolobus verus*; 4 = *Ptilocolobus badius*; 5 = *Colobus satanas*; 6 = *Trachypithecus cristatus*; 7 = *Semnopithecus entellus*; 8 = *Nasalis larvatus*).

In the PCA using the data acquired with the BCO method (Fig. 4A), PC1 accounts for 70.86% of the total variance and is primarily explained by 3DRETgeo (19.03%), LRFI (18.61%), and inclination (18.53%), followed by ARC (17.74%), 3DRETvol (17.48%), and ACS (8.57%). All variables except LRFI and ARC have positive loadings (SOM Tables S4 and S5). In turn, PC2 accounts for 15.71% of the total variance and is mostly explained by ACS (52.71%) followed by 3DRETvol (17.32%), 3DRETgeo (10.10%), ARC (9.06%), LRFI (7.62%), and inclination (3.17%). In this case, 3DRETvol, 3DRETgeo and LRFI have negative loadings while the remaining variables (ACS, inclination, ARC) have positive loadings (SOM Table S5). In the PCA using the data acquired with the EEC method (Fig. 4B), PC1 accounts for 69.93% of the total variance and is primarily explained by inclination (18.39%), followed by 3DRETvol (17.82%), 3DRETgeo (17.21%), LRFI (16.68%), ARC (14.92%), and ACS (14.59%). In this case, ARC and LRFI have negative loadings whereas the remaining variables (3DRETvol, 3DRETgeo, ACS, and inclination) have positive loadings (SOM Table S5). The second PC accounts for 13.41% of the total variance and is mainly explained by ACS (24.72%) and ARC (23.20%), followed by 3DRETgeo (18.17%), LRFI (16.97%), inclination (13.56%), and 3DRETvol (13.05%). In this case, 3DRETvol, 3DRETgeo, and LRFI have negative loadings, while the rest of the variables (i.e., ACS, ARC, and inclination) have positive loadings (SOM Table S5). In both cases, the fossil M²s of *M. majori* (5199 and Ty5203) are situated in the PC1–PC2 shape space closer to the fruit/seed eating cercopithecids (Fig. 4A, B).

Table 5. Descriptive statistics for microwear texture variables on phase II and phase I facets of fossil *Macaca* and extant species.

Taxa	n		Phase II				n	Phase I			
			Asfc	epLsar (x10 ³)	Tfv	Hasfc ₈₁		Asfc	epLsar (x10 ³)	Tfv	Hasfc ₈₁
Fossil											
<i>M. majori</i>	24	Mean	4.47	2.19	59797.1	0.69	26	3.59	2.30	45167.9	0.78
		SD	2.49	1.28	58453.2	0.23		1.75	1.33	23059.2	0.16
<i>M. s. florentina</i>	7	Mean	1.98	3.27	37623.9	0.53	9	0.98	3.55	35055.1	0.48
		SD	1.37	1.45	10320.7	0.12		0.24	1.20	24136.9	0.16
Extant											
<i>M. fuscata</i>	54	Mean	2.32	3.38	34228.4	0.43	40	1.63	3.78	37793.2	0.42
		SD	1.22	1.58	15233.2	0.24		1.68	2.05	8724.5	0.18
(Aomori, North)	23	Mean	1.99	3.31	31811.6	0.37	14	1.17	3.57	37797.5	0.38
		SD	0.86	1.45	15465.5	0.19		0.52	2.51	9849.2	0.19
(Nagano, Central)	12	Mean	2.39	3.65	43267.0	0.54	6	2.02	2.70	36591.4	0.44
		SD	1.44	2.09	11479.5	0.40		0.81	1.95	9014.4	0.07
(Yakushima, South)	19	Mean	2.68	3.23	31445.4	0.44	20	1.83	4.24	41789.1	0.45
		SD	1.394	1.44	15501.2	0.13		0.81	1.64	2786.6	0.19
<i>M. nemestrina</i>	11	Mean	3.94	3.24	45674.5	0.68	11	2.55	4.76	39465.0	0.91
		SD	2.92	2.94	9339.2	0.17		1.68	1.55	9086.0	0.33
<i>M. sylvanus</i>	9	Mean	4.15	2.59	40469.6	0.71	6	2.10	2.99	29646.2	1.02
		SD	2.20	1.41	8567.9	0.29		1.11	1.10	15384.2	1.05
<i>P. hamadryas</i>	39	Mean	1.72	2.87	33919.2	0.56	39	1.25	3.33	34473.0	0.48
		SD	1.06	1.51	13966.4	0.20		0.71	1.67	13618.7	0.14
<i>L. albigena</i>	14	Mean	2.61	3.03	45212.5	0.73	14	1.97	3.29	38618.2	0.67
		SD	1.33	1.89	11685.8	0.27		1.07	1.44	10588.1	0.26
<i>Ma. sphinx</i>	33	Mean	1.81	4.20	47838.5	0.56	33	1.53	3.60	46883.1	0.51
		SD	0.78	1.75	11093.8	0.35		0.85	1.94	8567.6	0.19
<i>Co. guereza</i>	20	Mean	0.92	4.34	32070.2	0.56	20	0.70	3.95	30219.3	0.49
		SD	0.48	1.76	12007.4	0.14		0.38	2.53	11067.7	0.22
<i>Ch. aethiops</i>	36	Mean	2.60	2.93	36365.6	0.65	36	1.72	3.72	34857.5	0.67
		SD	1.80	1.64	13901.2	0.73		1.56	1.92	9954.0	0.62

Abbreviations: Asfc = area-scale fractal complexity; epLsar = exact proportion length-scale anisotropy of relief; Hasfc₈₁ = heterogeneity of area-scale fractal complexity on 81 cells; Tfv = textural fill volume; CI = 95% confidence intervals.

3.2. Dental microwear texture analysis

The descriptive statistics for each microwear texture variable are given in Table 5 and the results of the Kruskal-Wallis tests in Table 6. Results for both Phase II and I facets showed significant differences among species in Asfc, epLsar, Hasfc₈₁, and Tfv (Table 6). The post-hoc pairwise comparisons that revealed significant differences between the extinct macaques (i.e., *M. majori* and *M. s. florentina*) and extant species are given in Table 7, whereas the post-hoc pairwise comparisons that showed significant differences among all extant species are shown in SOM Table S6. The pairwise comparisons that were not significant before and after Bonferroni correction are not reported.

In Phase II dental facets, the pairwise comparisons with Bonferroni correction indicate that *Co. guereza* exhibits significantly lower values of Asfc compared to *M. fuscata*, *Ch. aethiops*, *L. albigena*, *M. nemestrina*, and *M. sylvanus* (Fig. 5; SOM Table S6), while *P. hamadryas* also exhibits significantly lower values of Asfc compared to *M. sylvanus*. Furthermore, *M. fuscata* possess significantly lower values of Hasfc compared to *P. hamadryas*, *M. sylvanus*, *L. albigena*, and *M. nemestrina* (SOM Table S6). Lastly, *Ma. sphinx* possess significantly higher values of Tfv compared to *Co. guereza*, *P. hamadryas*, *M. fuscata*, and *Ch. Aethiops* (SOM Table S6). In Phase I dental facets, *Co. guereza* exhibits significantly lower values of Asfc compared to *Ch. aethiops*, *Ma. Sphinx*, *M. fuscata*, *L. albigena*, and *M. nemestrina* (SOM Table S6). Moreover, *M. nemestrina* possess significantly higher values of Hasfc compared to *Co. guereza*, *P. hamadryas*, and *M. fuscata*, with the latter taxon also exhibiting significantly lower values compared to *L. albigena* (SOM Table S6). Lastly, *Ma. Sphinx* possess significantly higher values of Tfv compared to *Co. guereza*, *P. hamadryas*, *Ch. aethiops*, and *M. fuscata* (SOM Table S6).

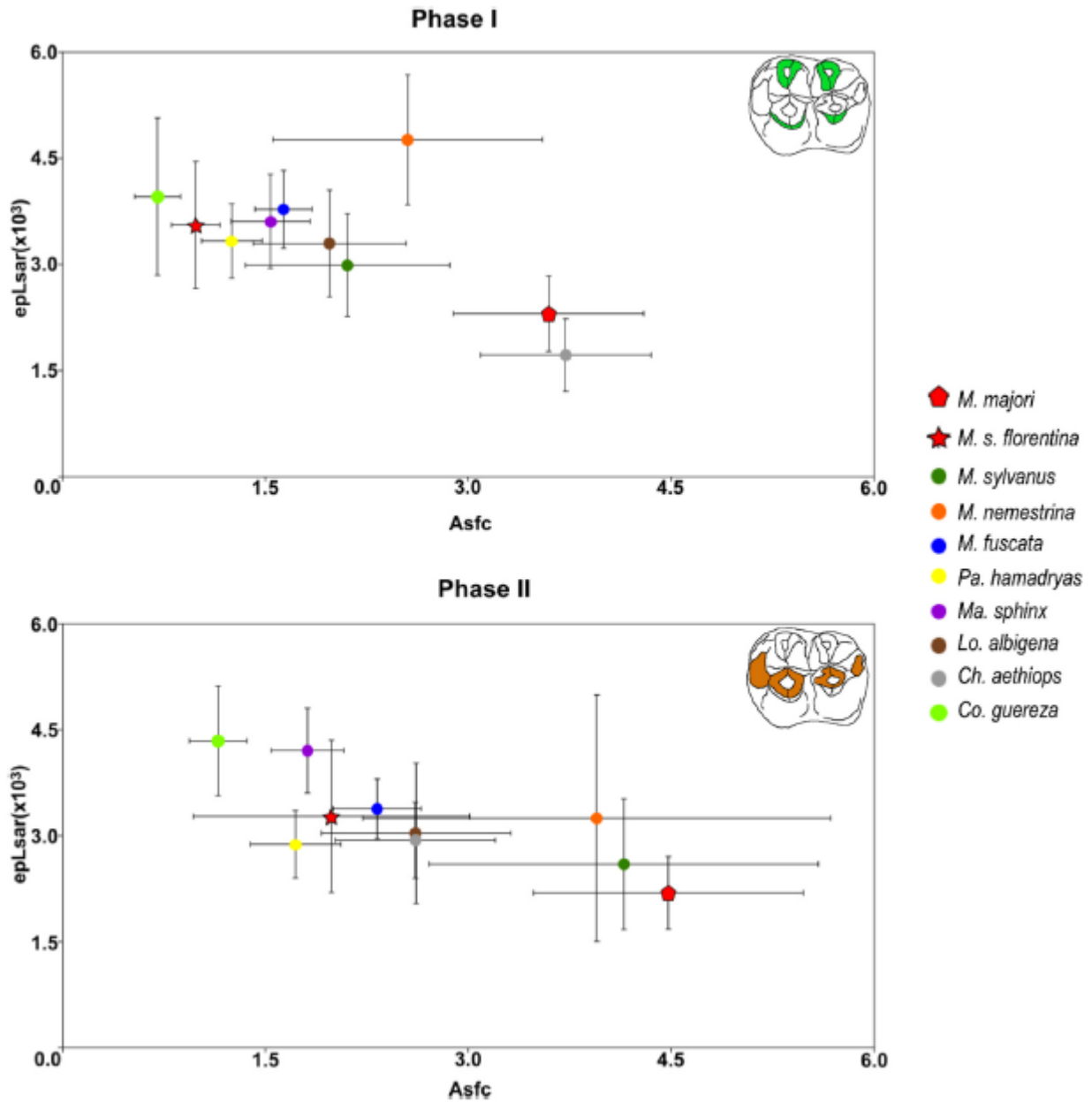


Figure 5. Bivariate plots (means with 95% confidence intervals) of complexity (Asfc) and anisotropy (epLsar) on phase I and phase II facets. The fossil sample of *Macaca majori* occupies a space suggestive of an overall more durophagous diet compared with *Macaca sylvanus florentina*.

Table 6. Results of Kruskal-Wallis tests between the fossil *Macaca* (*M. majori*, *M. s. florentina*) and extant species (*Co. guereza*, *M. fuscata*, *M. nemestrina*, *M. sylvanus*, *P. hamadryas*, *Ma. sphinx*, *L. albigena*, *Ch. aethiops*) and) on both phase I and phase II facets with species as factor. Significant differences are highlighted in bold.

Facets	Variable	df	χ^2	p-value
Phase II	Asfc	9	70.179	<0.001
	epLsar	9	32.925	<0.001
	Hasfc ₈₁	9	50.525	<0.001
	Tfv	9	40.793	<0.001
Phase I	Asfc	9	70.676	<0.001
	epLsar	9	20.056	0.018
	Hasfc ₈₁	9	47.174	<0.001
	Tfv	9	43.750	<0.001

Abbreviations: df = degrees of freedom; Asfc = area-scale fractal complexity; epLsar = exact proportion length-scale anisotropy of relief; Hasfc₈₁ = heterogeneity of area-scale fractal complexity on 81 cells; Tfv = textural fill volume.

Table 7. Dunn's post-hoc tests among the fossil *Macaca* (*Macaca majori*, *Macaca s. florentina*) and extant species with significant differences (before^a and after^b Bonferroni correction for multiple comparisons) in dental microwear texture variables for both phase II and phase I facets. Significant differences after Bonferroni adjustment are shown in bold.

Variables	Comparisons among extant species		p-value	
			Significance ^a	Adjusted significance ^b
Phase II				
Asfc	<i>Macaca majori</i>	<i>Colobus guereza</i>	<0.001	<0.001
	<i>Macaca majori</i>	<i>Papio hamadryas</i>	<0.001	<0.001
	<i>Macaca majori</i>	<i>Mandrillus sphinx</i>	<0.001	<0.001
	<i>Macaca majori</i>	<i>Macaca fuscata</i>	<0.001	0.004
	<i>Macaca majori</i>	<i>Chlorocebus aethiops</i>	0.001	0.029
	<i>Macaca majori</i>	<i>Lophocebus albigena</i>	0.036	1.000
	<i>Macaca s. florentina</i>	<i>Macaca sylvanus</i>	0.029	1.000
	<i>Macaca s. florentina</i>	<i>Macaca majori</i>	0.001	0.063
epLsar	<i>Macaca majori</i>	<i>Mandrillus sphinx</i>	<0.001	0.001
	<i>Macaca majori</i>	<i>Colobus guereza</i>	<0.001	0.001
	<i>Macaca majori</i>	<i>Macaca fuscata</i>	0.003	0.131
Hasfc ₈₁	<i>Macaca majori</i>	<i>Macaca fuscata</i>	<0.001	<0.001
	<i>Macaca majori</i>	<i>Mandrillus sphinx</i>	0.002	0.083
Tfv	<i>Macaca majori</i>	<i>Chlorocebus aethiops</i>	0.005	0.206
	<i>Macaca majori</i>	<i>Colobus guereza</i>	0.002	0.105
	<i>Macaca majori</i>	<i>Papio hamadryas</i>	0.009	0.406
	<i>Macaca majori</i>	<i>Macaca fuscata</i>	0.009	0.417
	<i>Macaca s. florentina</i>	<i>Mandrillus sphinx</i>	0.024	1.000

Table 7 (continued)

Variables	Comparisons among extant species		p-value	
			Significance ^a	Adjusted significance ^b
	Phase I			
Asfc	<i>Macaca majori</i>	<i>Macaca s. florentina</i>	<0.001	0.001
	<i>Macaca majori</i>	<i>Colobus guereza</i>	<0.001	<0.001
	<i>Macaca majori</i>	<i>Papio hamadryas</i>	<0.001	<0.001
	<i>Macaca majori</i>	<i>Chlorocebus aethiops</i>	<0.001	<0.001
	<i>Macaca majori</i>	<i>Mandrillus sphinx</i>	<0.001	0.002
	<i>Macaca majori</i>	<i>Macaca fuscata</i>	<0.001	0.005
	<i>Macaca majori</i>	<i>Lophocebus albigena</i>	0.037	1.000
	<i>Macaca s. florentina</i>	<i>Lophocebus albigena</i>	0.021	0.943
	<i>Macaca s. florentina</i>	<i>Macaca nemestrina</i>	0.012	0.559
epLsar	<i>Macaca majori</i>	<i>Macaca fuscata</i>	0.001	0.044
	<i>Macaca majori</i>	<i>Macaca nemestrina</i>	<0.001	0.004
	<i>Macaca majori</i>	<i>Macaca s. florentina</i>	0.038	1.000
	<i>Macaca majori</i>	<i>Papio hamadryas</i>	0.014	0.623
	<i>Macaca majori</i>	<i>Colobus guereza</i>	0.010	0.441
	<i>Macaca majori</i>	<i>Chlorocebus aethiops</i>	0.002	0.083
Hasfc ₈₁	<i>Macaca majori</i>	<i>Macaca fuscata</i>	<0.001	<0.001
	<i>Macaca majori</i>	<i>Colobus guereza</i>	0.001	0.033
	<i>Macaca majori</i>	<i>Papio hamadryas</i>	0.001	0.026
	<i>Macaca majori</i>	<i>Macaca s. florentina</i>	0.019	0.833
	<i>Macaca majori</i>	<i>Mandrillus sphinx</i>	0.002	0.070
	<i>Macaca s. florentina</i>	<i>Macaca nemestrina</i>	0.007	0.320
	<i>Macaca majori</i>	<i>Chlorocebus aethiops</i>	0.016	0.738
Tfv	<i>Macaca majori</i>	<i>Colobus guereza</i>	0.001	0.037
	<i>Macaca s. florentina</i>	<i>Mandrillus sphinx</i>	<0.001	0.016
	<i>Macaca s. florentina</i>	<i>Macaca majori</i>	0.025	1.000
	<i>Macaca majori</i>	<i>Macaca sylvanus</i>	0.049	1.000
	<i>Macaca majori</i>	<i>Chlorocebus aethiops</i>	0.008	0.382
	<i>Macaca majori</i>	<i>Papio hamadryas</i>	0.032	1.000

Abbreviations: Asfc = area-scale fractal complexity; epLsar = exact proportion length-scale anisotropy of relief; Hasfc₈₁ = heterogeneity of area scale fractal complexity on 81 cells; Tfv = textural fill volume.

^a Asymptotic significance (two-sided tests) are displayed with significance level set at 0.05.

^b Significance values have been adjusted by the Bonferroni correction for multiple tests.

When extant species and fossil macaques are compared, the pairwise comparisons with Bonferroni correction indicate that *M. majori* exhibits significant texture differences in both dental facet types

(Table 7). In Phase II dental facets, *M. majori* possess significantly higher values of Asfc compared to *Co.*

guereza, *P. hamadryas*, *Ma. sphinx*, *M. fuscata*, and *Ch. aethiops*, while it also exhibits significantly lower values of epLsar compared to *Ma. sphinx* and *Co. guereza* (Fig. 5; Table 7). Lastly, *M. majori* possess significantly higher values of Hasfc compared to *Ma. sphinx* (Table 7). Concerning Phase I dental facets, *M. majori* possess significantly higher values of Asfc compared to *M. s. florentina*, *Co. guereza*, *P. hamadryas*, *Ch. aethiops*, *Ma. sphinx*, and *M. fuscata*, and significantly lower values of epLsar compared to *M. fuscata* and *M. nemestrina* (Fig. 5; Table 7). Moreover, *M. majori* exhibits significantly higher values of Hasfc compared to *M. fuscata*, *Co. guereza* and *P. hamadryas* (Table 7), while in terms of Tfv, *M. majori* exhibits significantly higher values compared to *Co. guereza* and *M. s. florentina*, and significantly lower values compared to *Ma. sphinx* (Table 7).

Table 8. Results of Kruskal-Wallis tests among the wild populations (Aomori, Nagano, Yakushima) of *Macaca fuscata* for both phase I and phase II facets with locality as factor. Significant differences are highlighted in bold.

Facets	Variable	df	χ^2	p-value
Phase II	Asfc	2	1.921	0.382
	epLsar	2	0.249	0.890
	Hasfc ₈₁	2	6.251	0.042
	Tfv	2	5.570	0.056
Phase I	Asfc	2	8.632	0.013
	epLsar	2	3.796	0.150
	Hasfc ₈₁	2	3.868	0.145
	Tfv	2	1.716	0.458

Abbreviations: df = degrees of freedom; Asfc = area-scale fractal complexity; epLsar = exact proportion length-scale anisotropy of relief; Hasfc₈₁ = heterogeneity of area-scale fractal complexity on 81 cells; Tfv = textural fill volume.

The Kruskal-Wallis tests applied to microwear textures of the wild populations of *M. fuscata* suggested some potential significant differences in the values of Hasfc and Asfc among populations depending on the dental facet type (Table 8). However, it was significant in only one case following Bonferroni correction. In Phase I dental facets, the northern population from Aomori exhibits significantly lower values of Asfc compared to the central from Nagano (Table 9).

Table 9. Dunn’s post-hoc tests showing significant differences among the wild populations (Aomori, Nagano, Yakushima) of *Macaca fuscata* (before^a and after^b Bonferroni correction for multiple comparisons) for both phase II and phase I facets. Significant differences are highlighted in bold.

Variables	Comparisons among populations		<i>p</i> -value	
			Significance ^a	Adjusted significance ^b
	Phase II			
Hasfc ₈₁	Aomori (Northern)	Nagano (Central)	0.043	0.130
	Aomori (Northern)	Yakushima (Southern)	0.030	0.089
	Phase I			
Asfc	Aomori (Northern)	Nagano (Central)	0.010	0.029
	Aomori (Northern)	Yakushima (Southern)	0.019	0.057

Abbreviations: Asfc = area-scale fractal complexity; Hasfc₈₁ = heterogeneity of area-scale fractal complexity on 81 cells.

^a Asymptotic significance (2-sided tests) are displayed with significance level set at 0.05.

^b Significance values have been adjusted by the Bonferroni correction for multiple tests.

4. Discussion

The results of this study provide novel information regarding the dietary ecology of the Sardinian fossil macaque (*M. majori*) and indicate that its typical dietary habits may have differed from those of contemporaneous fossil macaques from mainland Europe (i.e., *M. s. florentina*). Below we address the implications of our results in relation to the potential dietary niches of fossil European macaques.

4.1. Molar morphology of *Macaca majori* relative to diet as evidenced by dental topography and enamel thickness

Our comparisons of dental topographic measures support their utility in investigating dental morphology relative to the main dietary preferences of each proposed dietary category. More specifically, the values of ARC, LRFI, and inclination of the folivorous species generally differ significantly from both fruit/seed eating and mixed feeding cercopithecids with both sampling methods (Tables 3 and

4). Nevertheless, the significant differences are more marked between folivores and fruit/seed eaters, as mixed feeders display an intermediate condition (Fig. 3D–F). This is not surprising given that the mixed feeding category includes species with highly variable diets in terms of composition and presumed food material/geometric properties, which may be more effectively processed by a versatile molar morphology.

The comparisons of 3D enamel thickness (3DRETvol, 3DRETgeo) show that folivorous species tend to exhibit significantly lower values of 3DRETvol and 3DRETgeo compared to the fruit/seed eating and mixed feeding species. Likewise, the ACS comparisons also reveal significant differences between the folivores and the mixed feeders (Table 4). However, the observed differences in ACS between folivores and mixed feeders may also reflect molar size differences between species as this metric is directly influenced by overall tooth size, as shown by the significant correlation between ACS and OES 2D (Table 2; see also Schwartz et al., 2020; Guatelli-Steinberg et al., 2022; Plastiras et al., 2022).

The overall results of the dental topographic and enamel thickness analyses suggest that both Ty5199 and Ty5203 fossil molars of *M. majori* from Sardinia exhibit a combination of morphological features (e.g., shorter and more blunt molar cusps with very thick enamel) consistent with previous suggestions (e.g., Szalay and Delson, 1979; Zanaga, 1998), resembling those of fruit/seed eating cercopithecids which primarily rely on mechanically challenging food resources. In fact, both Ty5199 and Ty5203 fossil molars fall outside of the shape space occupied by the proposed dietary categories mostly due to their high 3D relative enamel thickness (volumetric and geometric) values (Fig. 4A, B). The thick enamel observed in Ty5199 and Ty5203 may reflect an adaptation that allowed *M. majori* molars to maintain structural integrity in the presence of high bite forces related to hard-object feeding (e.g., Kay, 1981; Lambert et al., 2004), and/or it could mean that *M. majori* had an overall more abrasive diet (e.g., Molnar and Gantt, 1977; King et al., 2005) and/or a broader diet in terms of food material properties. However, previous research on enamel thickness in the genus *Macaca* revealed that temperate

macaque species exhibit overall thicker molar enamel compared to tropical macaques, suggesting that thick enamel may be adaptive in seasonal environments (e.g., Kato et al., 2014). Nevertheless, enamel thickness seems to be an evolutionarily plastic trait, meaning that factors in addition to diet may promote changes (e.g., Hlusko et al., 2004; Kelly and Swanson, 2008; Pampush et al., 2013). Furthermore, several studies have demonstrated that broad characterizations of primate diets (e.g., folivore/fruit/seed eaters) fail to capture the fact that not all leaves are tough and not all fruits are soft while not all seeds are hard and/or actually masticated (e.g., Martin et al., 2003; Vogel et al., 2008, 2014; McGraw et al., 2012; Smith et al., 2012; Coiner-Collier et al., 2016). This means that not all foods within a given class (e.g., fruits, leaves, seeds etc.) are necessarily correlated with the material properties that would be expected to relate to specific dental morphological features, and the ingestion of certain food items does not necessarily provide information related to feeding behavior (i.e., seeds may be chewed or swallowed whole, etc.). This further implies that categorizing primate diets is indeed complex, as multiple factors may influence the dietary habits of primate species (Guillotin et al., 1994; Tutin et al., 1997; Stevenson et al., 2000; Brugiere et al., 2002; Worman and Chapman, 2006; Taylor et al., 2008, 2018; Schreier et al., 2009; Vinyard et al., 2009; Kamilar and Ledogar, 2011; Ross et al., 2012; McGraw et al., 2014; Hartstone-Rose et al., 2015, 2018; Coiner-Collier et al., 2016; Thiery et al., 2017c).

Additional studies would be required to test whether some of the observed molar morphological features (i.e., low curvature and relief), enamel thickness, as well as additional aspects of dental microstructure that were not investigated here (e.g., enamel prism decussation), are related to specific dietary requirements (i.e., abrasive diet and/or durophagy) of *M. majori*, and if *M. majori* differs (i.e., in molar features and/or in diet) from extant macaques (see Kato et al., 2014), as well as contemporaneous fossil species from mainland Europe (e.g., *M. s. florentina*). Lastly, studies on food material properties of extant macaques will undoubtedly be beneficial as currently there absence of

information regarding the mechanical properties of the foods ingested, bit, and/or chewed by macaques.

4.2. *Dietary habits of Macaca majori as evidenced by dental microwear texture analysis*

Dental microwear analysis is one of the most widely used dietary proxies, with several studies demonstrating its ability to track dietary patterns between primates with contrasting diets (e.g., leaf eaters and hard object foragers), but also to identify more subtle dietary differences (Teaford and Walker, 1984; Teaford, 1985; Teaford and Glander, 1991; El Zaatari et al., 2005; Teaford, 2007; Merceron et al., 2005, 2009, 2021; Scott et al., 2005, 2006, 2012; Ragni et al., 2017; Percher et al., 2018; Plastiras et al., 2022). Most of the previous dental microwear analyses in primates have been focused on occlusal dental facets, Phase II dental facets, as it has been suggested that they better discriminate among primate species with contrasting dietary habits (e.g., Krueger et al., 2008). However, more recent analyses suggest that incorporating Phase I dental facets may also be useful in primate dietary investigations (e.g., Merceron et al., 2021; Plastiras et al., 2022). As Phase I and II dental facets contribute to the shearing and crushing/grinding of food items respectively, it may be assumed that variation in textures on Phase I facets would reflect the abundance and availability of tough vegetal resource, whereas texture differences on Phase II facets would reflect other more mechanically challenging food resources. Nevertheless, this requires further investigation. Even if that is the case, our results support the potential of Phase I dental facets in primate dietary discriminations, and further highlight the overall more durophagous dietary habits of *M. majori*, in agreement with the limited available evidence from isotopic analysis (e.g., Chenery et al., 2008).

When evaluating the dietary signals of both dental facet types, the microwear texture of *M. majori* differs from that of some of the extant cercopithecids analyzed in ways which are suggestive of a more durophagous and/or abrasive diet (Table 7). For instance, it exhibits differences with *Co. guereza*,

a highly folivorous species, but also with mixed feeding species such as *P. hamadryas*, *Ma. sphinx*, *M. fuscata*, and *Ch. aethiops* in the values of *Asfc* in both dental facet types. In primates, higher values of *Asfc* are indicative of rough and complex dental surfaces, which are typically associated with durophagy, whereas higher values of *epLsar* are commonly associated with more frequent consumption of tough foliage (Scott et al., 2006, 2012; Merceron et al., 2009; Calandra and Merceron, 2016; Ragni et al., 2017; Plastiras et al., 2022). In fact, *M. majori* possess the highest values of *Asfc* and one the lowest values of *epLsar* in our comparative sample (Fig. 5; Table 5). Furthermore, the high values of *Hasfc* and *Tfv* of *M. majori* in both dental facet types are indicative of a more heterogeneous and rougher dental microwear texture, likely resulting from a more heterogeneous diet in terms of food wear particle size and food composition (e.g., Krueger et al., 2008; Scott et al., 2012; Ragni et al., 2017). Setting aside its differences with the extant species, *M. majori* also has significantly higher values of *Asfc* compared to *M. s. florentina*, at least on Phase I dental facets (Table 7), which may also be suggestive of a harder and/or more abrasive dietary component in the diet of the former compared to the latter.

Although extant macaques seem to primarily feed on fruit and/or seeds if/when available (Hanya et al., 2004; Krishnadas et al., 2011; Hanya et al., 2011; Richter et al., 2013, 2015; Sengupta et al., 2014), their dietary choices are heavily dependent on resource availability in their habitat (Hanya et al., 2011, 2013). For instance, *M. nemestrina*, which is mostly found in tropical habitats of southeast Asia, primarily relies on fruits and/or seeds throughout the year (Krishnamani, 1994; Albert et al., 2013; Sengupta and Radakrishna, 2016 and references therein). In contrast, species occupying temperate habitats with higher seasonality, such as *M. sylvanus* and *M. fuscata*, exhibit a broader dietary spectrum overall (e.g., Hanya et al., 2013; Tsuji et al., 2015). Furthermore, there seem to be dietary differences even among populations of the same species from different latitudes (e.g., Agetsuma and Nakagawa, 1998; Tsuji et al., 2015), as supported by the intraspecific variation of microwear textures revealed here among populations of *M. fuscata* (Table 8).

In particular, the central (Nagano) population of *M. fuscata* exhibits significantly higher Asfc in Phase I dental facets compared to the population from Aomori in North Japan (Table 9). These differences might be indicative of a more constrained dietary spectrum for the northern population in terms of vegetal resources, as reflected by food material properties (Rosenzweig, 1995; Zhou et al., 2011; Tsuji et al., 2015). Such differences may also be associated with the diversity of available vegetal resources which decreases towards northern latitudes in Japan (Maruhashi, 1980; Takasaki, 1981), and potentially other environmental and geographical factors that influence their availability (Hanya et al., 2003; Enari and Sakamaki-Enari, 2013; Tsuji et al., 2015). Regardless, these assumptions require further investigation as we need to better understand how such factors may influence macaque diets and, consequently, their microwear textures, while the inclusion of additional extant macaque species would undoubtedly enable more refined inferences. Notwithstanding these limitations, our results highlight the potential of dental microwear texture analysis in primate dietary investigations (e.g., Scott et al., 2012; Teaford et al., 2017; Martin et al., 2018; Percher et al., 2018; Ungar, 2019; Ungar et al., 2020; Merceron et al., 2021), as well as the potential of the genus *Macaca* for exploring further complex ecological questions, such as the relationship between diet, habitat, and environment.

4.3. *The dietary niche of Macaca majori*

The results of our analysis suggest that the analyzed M²s of *M. majori* (Ty5199 and Ty5203) display a morphology that more closely resembles durophagous cercopithecoid species (i.e., very high values of enamel thickness as well as low relief and curvature), implying that they were adapted to process mechanically challenging food resources on a regular basis. In addition, the dietary behavior of *M. majori*, as evidenced by its microwear texture properties, is consistent with the observed molar morphology.

The complementary patterns of molar topography, enamel thickness, and dental microwear textures suggest that the Sardinian fossil macaque probably occupied a more durophagous dietary niche than did its fossil relatives, which might explain some of the previously observed craniodental differences; palate reduced in length, robust dentition with reduced diastemas, very short upper and lower P3s and molars with 'inflated' morphology (e.g., Szalay and Delson, 1979; Zanaga, 1998; Rook and O'Higgins, 2005). The dietary niche of *M. majori* could potentially reflect paleoecological/paleoenvironmental differences between mainland European and Sardinian paleohabitats (e.g., Rook and O'Higgins, 2005). Indeed, factors such as food resource variation, limitation and abundance, water availability, as well as population densities may differ between mainland and insular habitats (Sondaar, 1977; Sara and Morand, 2002; Palombo, 2008). As a result, insular endemic mammals are sometimes confronted with more mechanically challenging foods and/or abrasive ones (Schüle, 1993; Alcover et al., 1999; Ménard and Qarro, 1999; Hautier et al., 2009). Such an environmental pressure can select dental phenotype (Smith et al., 2011, 2012), and insular endemic mammals tend to have enlarged teeth relative to their body mass (van der Geer, 2014). Our results suggest that *M. majori* probably used mechanically challenging and/or abrasive food resources as diet staples, which could have been relatively abundant in Sardinian paleohabitats.

Sardinia, in particular, was home to megadont lagomorphs (Ochotonidae, Lagomorpha) of the genus *Prolagus* (Moncunill-Solé et al., 2021). Their enlarged cheek teeth (premolars and molars) are currently interpreted as an adaptation to chew large amounts of abrasive food (Moncunill-Solé et al., 2021; but see Angelone, 2005), although this matter has yet to be investigated. A putative consumption of more abrasive foods is consistent with the thick enamel of *M. majori*, as observed in other extant primates (Molnar and Gantt, 1977; Rabenold and Pearson, 2011). While extant macaques do not occupy the same niche as extant ochotonids, Sardinian macaques may have been confronted with the same abrasive resources because of low food abundance. Another explanation for a more abrasive diet is the

higher intake of adherent soil particles, possibly related to ingesting strategies such as rooting, overgrazing and near-surface browsing (Damuth and Janis, 2011). Again, this is consistent with the uniformly high complexity of dental microwear observed on both phase I and phase II facets in *M. majori*. Indeed, a higher intake of grit may have also contributed in the complex and rough microwear texture of *M. majori*, although, it is more likely that it was not the sole wear causing agent (Xia et al., 2015; Daegling et al., 2016; Merceron et al., 2016; Ungar et al., 2016; Hedberg and DeSantis, 2017; Adams et al., 2020; Hua et al., 2020; Schulz-Kornas et al., 2020; Teaford et al., 2021; but see Lucas et al., 2013; Van Casteren et al., 2018, 2019, 2020).

Alternatively, the dental phenotype of *M. majori* might be related to life history traits, such as an extended life span, because enamel thickness is also strongly correlated with longevity in extant primates (e.g., Molnar and Gantt; King et al., 2005; Pampush et al., 2013). Many insular endemic mammals are indeed characterized by a slower life history (Clauss et al. 2014; Köhler et al., 2021) and a slower life history has been associated with enlarged teeth and/or hypsodonty in extinct insular mammals (Alcover et al., 1999; Angelone, 2005; Köhler & Moyà-Solà 2010; Jordana et al., 2012). This interpretation does not exclude an effect of paleohabitat nor food properties. More likely, the dental morphology of *M. majori* (e.g., low relief and curvature and thick enamel) is the result of a complex interplay between ecological factors that influence the abundance, availability and distribution of food resources, their mechanical properties (e.g., abrasiveness, hardness, but also nutrient contents) and life history traits. Nevertheless, such assumptions require further investigation ideally with a larger dataset of fossil and extant macaque species.

5. Conclusions

The results of this work provide novel information regarding the dietary ecology of European fossil macaques, which enables a better understanding of their paleoecological context during the Plio–Pleistocene. We combined dental topographic, enamel thickness, and dental microwear texture analyses to characterize the dietary ecology of *M. majori* from Sardinia and draw inferences regarding the dietary niches of fossil European Plio–Pleistocene macaques. Our results indicate that the molar morphology of *M. majori* resembles durophagous cercopithecoid species, implying that it probably consumed hard/mechanically challenging and/or abrasive food resources on a frequent basis. This interpretation is consistent with the results of microwear texture analysis, which indicate a highly durophagous dietary behavior. It is possible that mechanically challenging food and/or abrasive food resources, such as some fruits, seeds, and nuts may have been consumed frequently by *M. majori*. However, the contribution of adherent soil particles in its overall very rough dental microwear texture due to certain ingesting strategies (e.g., exploitation of underground storage organs), is also possible. Furthermore, the comparisons of microwear textures between *M. majori* and its fossil mainland relative, *M. s. florentina*, suggest that these macaques may have occupied different dietary niches. Although adequately understanding such differences would require additional investigation, such differences hint at paleoenvironmental differences between European mainland and Sardinian paleohabitats during the Plio–Pleistocene.

Data availability statement

The data that support the findings of this study were generated at the University of Poitiers (France), and access to the data is subject to regulations and approval of the original and governing institutions. These archives will be deposited in a national server that adheres to regulations of the original and governing institutions and will be made accessible once ongoing research programs are complete (within 1 to 3 years of the publication of the current paper). However, 3D meshes are still accessible upon reasonable request,

directly to authors of this study (F. G., and C.-A. P.), upon the authorization of the institutions holding the rights.

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Supplementary Online Material (SOM):

Investigating the dietary niches of fossil Plio-Pleistocene European macaques: The case of *Macaca majori* from Sardinia

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SOM S1

Supplementary methods

Technical note: Area-relative curvature (ARC)

Measuring the sharpness of dental occlusal surfaces is the core objective of several dental topography variables, including angularity (Ungar and Williamson, 2000), sharpness index (Karme, 2008; Ungar et al., 2018), mean curvature (Guy et al., 2013), Dirichlet normal energy (DNE; Bunn et al., 2011; Pampush et al., 2016), and a robustly implemented algorithm for Dirichlet normal energy (ariaDNE; Shan et al., 2019). Some of these variables rely on abstract measurements that are difficult to connect with sharpness, or to interpret in terms of dental morphology. For instance, angularity is the derivative of the slope (Ungar and Williamson, 2000), while DNE is the deformation of the normal space (Bunn et al., 2011). Other variables are size-dependent, such as mean curvature (Thiery, 2016:67). Some of these variables are also characterized by a strong dependence on the orientation of the xy plane (angularity, sharpness index) or must be calculated on dental elevation models (sharpness index).

Area-relative curvature (ARC) is an attempt to measure curvature using a measurement that is independent from the aforementioned factors, but also easy to interpret from a morphological perspective. It has been used to characterize the dental morphology of primates in a handful of works (Thiery, 2016; Guy et al., 2017; Thiery et al., 2021; Plastiras et al., 2022), but it has yet to be comprehensively described in a peer-reviewed study. We define ARC as the ratio between the mean curvature of a structure over the mean curvature of a theoretical structure that would have the same 3D surface area, but would have the shape of a hemisphere. The curvature of a hemisphere is related to its surface area by the following equation:

$$(1) H_{\text{Hemisphere}} = 2.4481 * 1 / \sqrt{A_{\text{Hemisphere}}}$$

where $H_{\text{Hemisphere}}$ is the mean curvature and $A_{\text{Hemisphere}}$ the surface area of the hemisphere (see SOM Fig. 1 for a graphical representation of this relationship).

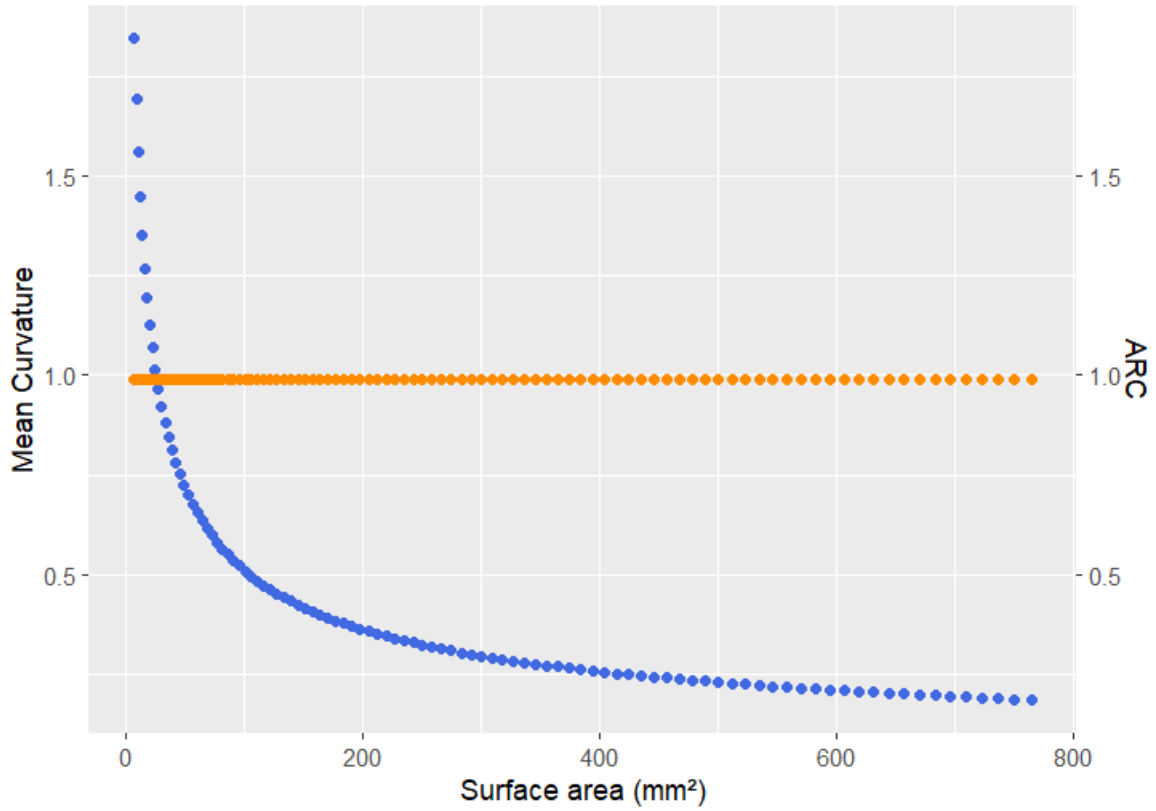
Then, for a given structure, ARC is computed as follows:

$$(2) \text{ARC}_{\text{structure}} = H_{\text{structure}} / H_{\text{Hemisphere}}$$

$$(3) \text{ARC}_{\text{structure}} = H_{\text{structure}} * \sqrt{(A_{\text{Hemisphere}}) / 2.4481}$$

Based on the classification of (nondental) topographic variables proposed by Delahaye (2005), ARC falls into the category of 'shape indices', which “determine the degree of resemblance between an object and another reference object” (Thiery, 2016:15, our translation from the French original). For ARC, the reference object is a hemisphere, and the ARC approximates how much the mean curvature of a tooth surface differs from that of a hemisphere. A hemisphere's average ARC will equal 1; by contrast, most dental surfaces would have average ARC higher than 1. The higher the ARC, the sharper the tooth and, reciprocally, the lower the ARC, the blunter the tooth.

Area-relative curvature is strongly correlated with the recently described convex DNE (Pampush et al., 2022); this is to be expected, as both variables were designed to quantify surface sharpness—and, in fact, authors of the current study also found a high correlation with total DNE. However, contrary to convex DNE—which only takes into account the positive curvature areas—average ARC takes into account the entire crown (positive, negative, and null curvature, i.e., flat areas). Furthermore, convex DNE computes the sum of sharp Dirichlet energies divided by the associated triangle area, whereas average ARC is a comparison between the average curvature of the surface and that of a hemisphere. In short, both variables measure the same aspect of tooth shape (sharpness), but they were designed following completely different approaches, meaning that 1) their applications can differ and 2) they might behave differently depending on the investigated organisms.



SOM Figure S1. Relationship between mean curvature and surface area in hemispheres of growing sizes. Blue = mean curvature (no dimension); orange = area-relative curvature (ARC; no dimension).

SOM Table S1

Enamel thickness, crown strength, and dental topographic variables for *Macaca majori* and the modern sample.

Species	ID	Institution	3DRETvol		3DRETgeo		ACS		ARC		LRFI		inclination		OES 2D	
			BCO	EEC	BCO	EEC	BCO	EEC	BCO	EEC	BCO	EEC	BCO	EEC	BCO	EEC
<i>Macaca majori</i>	Ty5203	NHMB	0.383	0.206	0.340	0.169	1.718	1.794	1.260	1.612	0.286	0.514	125.156	109.918	42.336	49.316
<i>Macaca majori</i>	Ty5199	NHMB	0.333	0.181	0.332	0.154	1.75	1.896	1.361	1.767	0.199	0.508	134.32	111.296	48.277	58.882
<i>Cercocebus galeritus</i>	14486	RMCA	0.336	0.140	0.308	0.121	1.466	1.514	1.552	1.845	0.302	0.542	122.564	108.43	35.805	46.765
<i>Cercocebus torquatus</i>	81-07-M-44	RMCA	0.295	0.129	0.283	0.113	1.677	1.649	1.417	1.764	0.291	0.521	123.232	109.724	49.206	61.244
<i>Cercopithecus cephus</i>	17507	RMCA	0.186	0.100	0.172	0.089	1.228	1.153	1.744	2.093	0.382	0.597	117.601	103.818	35.093	39.362
<i>Cercopithecus diana</i>	Cc1	PALEVOPRIM	0.229	0.136	0.227	0.119	1.177	1.158	1.484	1.812	0.294	0.551	123.306	106.552	27.672	30.644
<i>Cercopithecus diana</i>	Cc2	PALEVOPRIM	0.295	0.184	0.296	0.153	1.298	1.247	1.454	1.832	0.297	0.563	122.427	105.914	26.884	30.143
<i>Cercopithecus nictitans</i>	15650	RMCA	0.232	0.130	0.231	0.113	1.076	1.039	1.451	1.986	0.267	0.493	125.737	107.377	23.062	27.101
<i>Cercopithecus pogonias</i>	15595	RMCA	0.224	0.131	0.207	0.113	1.284	1.206	1.612	2.061	0.323	0.56	121.687	104.985	33.187	35.39
<i>Cercopithecus pogonias</i>	18273	RMCA	0.314	0.149	0.304	0.128	1.289	1.253	1.401	1.845	0.233	0.477	128.787	109.201	28.607	33.821
<i>Lophocebus albigena</i>	83006-M276	RMCA	0.327	0.160	0.318	0.135	1.404	1.413	1.525	1.901	0.230	0.501	127.332	109.747	31.274	39.272
<i>Lophocebus albigena</i>	90042-M-301	RMCA	0.338	0.163	0.318	0.138	1.633	1.570	1.552	1.904	0.270	0.513	124.923	109.561	41.831	47.893
<i>Lophocebus albigena</i>	90042-M-301	RMCA	0.333	0.160	0.314	0.136	1.634	1.561	1.553	1.872	0.260	0.512	125.815	109.628	42.236	48.421
<i>Lophocebus albigena</i>	Cb4	PALEVOPRIM	0.321	0.159	0.328	0.136	1.701	1.81	1.264	1.711	0.210	0.475	130.679	111.856	50.561	65.979
<i>Lophocebus aterrimus</i>	14113	RMCA	0.362	0.167	0.343	0.139	1.403	1.448	1.628	2.01	0.259	0.517	125.357	108.743	31.798	40.015
<i>Colobus satanas</i>	33512	RMCA	0.206	0.113	0.186	0.100	1.246	1.22	1.798	1.986	0.351	0.55	118.648	107.064	35.309	38.619
<i>Ptilocolobus badius</i>	9201	RMCA	0.189	0.121	0.168	0.105	1.094	1.096	1.753	2.074	0.392	0.582	116.446	105.045	28.273	31.743
<i>Ptilocolobus badius</i>	91-060-M57	RMCA	0.184	0.126	0.171	0.107	1.228	1.199	1.857	2.276	0.403	0.584	116.188	104.177	34.096	36.517
<i>Ptilocolobus badius</i>	91-060-M76	RMCA	0.18	0.120	0.166	0.104	1.309	1.255	2.079	2.413	0.389	0.587	116.396	103.098	41.971	43.737
<i>Ptilocolobus badius</i>	83-042-M77	RMCA	0.215	0.131	0.2	0.113	1.322	1.306	1.813	2.135	0.351	0.600	118.836	103.956	36.564	40.018
<i>Colobus guereza</i>	1216	RMCA	0.192	0.117	0.167	0.101	1.375	1.333	1.873	2.319	0.349	0.56	119.584	104.641	47.476	50.89
<i>Colobus guereza</i>	3800	RMCA	0.208	0.121	0.195	0.105	1.368	1.304	1.804	2.117	0.321	0.568	120.654	104.776	40.332	43.196
<i>Colobus polykomos</i>	10307	RMCA	0.265	0.148	0.244	0.125	1.287	1.24	1.637	2.026	0.264	0.517	126.014	107.184	33.908	36.371
<i>Colobus polykomos</i>	10548	RMCA	0.206	0.131	0.194	0.112	1.291	1.307	1.819	2.287	0.319	0.536	121.873	106.117	39.346	43.789
<i>Colobus polykomos</i>	10602	RMCA	0.157	0.104	0.150	0.093	1.248	1.194	1.673	2.038	0.342	0.517	119.803	107.581	40.709	43.614

<i>Colobus polykomos</i>	8107-M174	RMCA	0.189	0.109	0.178	0.095	1.352	1.342	1.706	2.131	0.329	0.518	120.004	108.167	41.396	51.242
<i>Colobus polykomos</i>	38158	RMCA	0.189	0.117	0.178	0.101	1.189	1.188	1.875	2.297	0.323	0.544	121.263	106.207	33.096	37.021
<i>Nasalis larvatus</i>	5042	SMF	0.185	0.12	0.174	0.106	1.453	1.4	1.885	2.223	0.378	0.599	117.571	103.429	49.522	51.47
<i>Procolobus verus</i>	86-002-M48	RMCA	0.165	0.109	0.149	0.096	0.918	0.898	1.942	2.22	0.382	0.61	117.408	102.264	23.536	24.386
<i>Procolobus verus</i>	86-002-M34	RMCA	0.133	0.094	0.125	0.084	0.897	0.89	1.801	2.037	0.41	0.587	115.602	105.072	23.115	24.559
<i>Procolobus verus</i>	86-002-M50	RMCA	0.151	0.104	0.148	0.092	0.941	0.902	1.736	2.046	0.313	0.552	121.642	105.253	23.815	24.531
<i>Semnopithecus entellus</i>	1964-1615	MNHN	0.2	0.144	0.202	0.122	1.317	1.312	1.685	2.03	0.317	0.546	121.695	106.888	35.906	39.595
<i>Trachypithecus cristatus</i>	1085	SMF	0.191	0.119	0.199	0.104	1.259	1.251	1.741	2.116	0.328	0.559	120.159	105.898	34.462	39.658
<i>Chlorocebus aethiops</i>	1972-302	MNHN	0.262	0.15	0.233	0.126	1.047	0.991	1.602	1.971	0.334	0.567	121.473	104.82	21.155	22.343
<i>Chlorocebus aethiops</i>	1972-328	MNHN	0.284	0.152	0.241	0.129	1.14	1.114	1.606	1.963	0.353	0.552	119.975	105.714	25.186	27.808
<i>Cercopithecus campbelli</i>	80-028-M-24	RMCA	0.167	0.131	0.179	0.114	1.218	1.202	1.703	2.016	0.338	0.556	119.841	105.05	34.43	36.712
<i>Cercopithecus campbelli</i>	36280	RMCA	0.279	0.144	0.267	0.125	1.214	1.171	1.46	1.809	0.294	0.55	124.186	106.548	26.315	29.217
<i>Erythrocebus patas</i>	8629	RMCA	0.203	0.121	0.191	0.104	1.368	1.295	1.703	2.286	0.315	0.578	121.152	102.909	41.189	44.844
<i>Mandrillus leucophaeus</i>	2002-105	RMCA	0.219	0.125	0.212	0.109	2.204	2.182	1.692	1.96	0.352	0.577	118.038	107.292	97.255	113.701
<i>Mandrillus leucophaeus</i>	1893-269	RMCA	0.185	0.15	0.241	0.13	2.055	2.027	1.599	1.921	0.278	0.511	123.855	110.044	66.709	84.468
<i>Papio anubis</i>	80-44-M-101	RMCA	0.223	0.167	0.214	0.142	2.659	2.61	1.568	1.874	0.322	0.474	120.52	112.052	130.242	146.785
<i>Papio anubis</i>	Pp4	PALEVOPRIM	0.267	0.162	0.252	0.136	2.394	2.291	1.664	1.999	0.312	0.557	121.559	106.378	97.785	108.067
<i>Papio anubis</i>	90-042-M226	RMCA	0.199	0.202	0.215	0.118	2.285	2.201	1.567	1.897	0.201	0.453	131.65	113.256	101.673	119.993
<i>Papio anubis</i>	C2	PALEVOPRIM	0.219	0.139	0.217	0.119	2.372	2.382	1.847	2.247	0.278	0.5	123.007	108.966	112.51	137.571
<i>Papio hamadryas</i>	97-020-M004	RMCA	0.226	0.169	0.241	0.144	2.704	2.629	1.614	2.054	0.28	0.476	123.688	112.1	121.057	139.309
<i>Macaca sylvanus</i>	T150kV	MNHN	0.246	0.173	0.264	0.142	2.007	2.026	1.406	1.771	0.249	0.513	127.022	110.339	70.369	80.341

Abbreviations: RMCA = Royal Museum of Central Africa, Tervuren (Belgium); MNHN = Muséum National d'Histoire Naturelle, Paris (France); MHNPN = Muséum d'Histoire Naturelle, Perpignan (France); PALEVOPRIM = Laboratoire Paléontologie, Evolution Paléoécosystèmes, Paléoprimatologie UMR CNRS 7262 - Université de Poitiers (France); SMF = Senckenberg Museum of Frankfurt, (Germany), BCO = basin cut off cropping method (after Berthaume et al., 2019); EEC = entire enamel cap method (after Berthaume et al., 2019); 3DRETvol = 3D volumetric relative enamel thickness (dimensionless); 3DRETgeo = 3D geometric relative enamel thickness (dimensionless); ACS = absolute crown strength; ARC = area-relative curvature (dimensionless); LRFI = relief index (dimensionless); OES 2D = 2D occlusal enamel surface.

SOM Table S2

Fossil *Macaca* (*Macaca majori*, *Macaca sylvanus florentina*) raw dental microwear data.

ID	Tooth	Species	Phase	Facet	Locality	Asfc	epLsar*1000	Hasfc ₈₁	Tfv
Ty12456	M ²	<i>M. majori</i>	II	f9	Capo Figari	3.107	1.684	0.857	40050.927
Ty12458	M ²	<i>M. majori</i>	II	f9	Capo Figari	3.150	1.303	0.702	50172.447
Ty12460	M ₂	<i>M. majori</i>	II	f9	Capo Figari	4.385	2.313	0.833	37233.637
Ty12462	M ²	<i>M. majori</i>	II	f9	Capo Figari	3.040	0.760	1.002	42805.837
Ty12464	M ²	<i>M. majori</i>	II	f9	Capo Figari	11.865	2.286	0.694	43647.665
Ty12469	M ₃	<i>M. majori</i>	II	f9	Capo Figari	2.216	2.211	1.099	23349.728
Ty12470	M ₃	<i>M. majori</i>	II	f9	Capo Figari	5.126	2.374	0.628	35190.093
Ty12499	M ₂	<i>M. majori</i>	II	f9	Capo Figari	6.555	2.519	0.577	49167.380
Ty12502	M ³	<i>M. majori</i>	II	f9	Capo Figari	3.863	1.719	0.548	18120.040
Ty12514	M ₃	<i>M. majori</i>	II	f9	Capo Figari	1.956	5.544	0.554	254809.860
Ty5209	M ₂	<i>M. majori</i>	II	f9	Capo Figari	7.328	2.440	0.948	50773.059
Ty5210	M ₂	<i>M. majori</i>	II	f9	Capo Figari	7.604	1.792	0.457	43386.387
Ty5211	M ₃	<i>M. majori</i>	II	f9	Capo Figari	2.539	4.025	1.309	56952.860
Ty5213	M ₃	<i>M. majori</i>	II	f9	Capo Figari	3.166	0.562	0.526	18555.083
Ty5215	M ₃	<i>M. majori</i>	II	f9	Capo Figari	5.350	3.177	0.446	34518.138
Ty5216	M ₃	<i>M. majori</i>	II	f9	Capo Figari	2.873	5.444	0.935	36768.227
Ty5217	M ₃	<i>M. majori</i>	II	f9	Capo Figari	3.543	1.133	0.610	43480.752
Ty5218	M ₂	<i>M. majori</i>	II	f9	Capo Figari	6.599	1.301	0.629	33147.042
Ty5221	M ₁	<i>M. majori</i>	II	f9	Capo Figari	8.272	1.972	0.827	56310.013
Ty5223	M ¹	<i>M. majori</i>	II	f9	Capo Figari	1.520	1.440	0.414	43031.019
Ty5226	M ¹	<i>M. majori</i>	II	f9	Capo Figari	1.937	1.425	0.537	39392.814
Ty5229	M ¹	<i>M. majori</i>	II	f12	Capo Figari	3.153	0.673	0.496	70380.953
Ty5302	M ₂	<i>M. majori</i>	II	f9	Capo Figari	3.012	2.054	0.539	232205.771
Ty5304	M ₃	<i>M. majori</i>	II	f9	Capo Figari	5.327	2.489	0.574	81683.004
IPS14955	M ²	<i>M. s. florentina</i>	II	f12	Cal Guardiola	2.468	0.886	0.557	58357.367
IPS35016	M ₁	<i>M. s. florentina</i>	II	f11	Cal Guardiola	1.734	4.772	0.575	33822.806

VA1088	M ₂	<i>M. s. fiorentina</i>	II	f9	Valdarno	4.877	3.507	0.689	40249.550
VA1415	M ₂	<i>M. s. fiorentina</i>	II	f9	Valdarno	0.912	5.189	0.309	39551.038
VA2075	M ₁	<i>M. s. fiorentina</i>	II	f9	Valdarno	1.324	2.281	0.448	31852.933
EVT24036	M ²	<i>M. s. fiorentina</i>	II	f9	Vallparadis	1.628	3.196	0.553	33468.781
Vj88	M ²	<i>M. s. fiorentina</i>	II	f12	Villafranca D' Asti	0.969	3.096	0.587	26065.226
Ty12456	M ²	<i>M. majori</i>	I	f3	Capo Figari	3.604	0.759	1.055	42599.156
Ty12457	M ²	<i>M. majori</i>	I	f3	Capo Figari	3.027	3.053	0.533	45768.416
Ty12458	M ²	<i>M. majori</i>	I	f3	Capo Figari	3.180	1.924	0.998	37587.168
Ty12460	M ₂	<i>M. majori</i>	I	f6	Capo Figari	4.871	1.489	0.574	30903.175
Ty12462	M ²	<i>M. majori</i>	I	f3	Capo Figari	5.199	1.723	1.549	35216.651
Ty12469	M ₃	<i>M. majori</i>	I	f6	Capo Figari	4.181	1.365	1.453	43024.167
Ty12470	M ₃	<i>M. majori</i>	I	f6	Capo Figari	1.577	4.657	0.644	39795.789
Ty12472	M ²	<i>M. majori</i>	I	f4	Capo Figari	6.632	1.795	0.593	45567.600
Ty12493	M ₁	<i>M. majori</i>	I	f5	Capo Figari	1.404	1.403	0.399	34603.047
Ty12502	M ³	<i>M. majori</i>	I	f3	Capo Figari	1.145	4.294	0.410	41987.033
Ty12514	M ₃	<i>M. majori</i>	I	f5	Capo Figari	1.985	1.499	0.704	13870.699
Ty5203	M ²	<i>M. majori</i>	I	f4	Capo Figari	4.531	0.703	1.651	36644.399
Ty5207	M ²	<i>M. majori</i>	I	f4	Capo Figari	4.158	1.052	1.233	41671.927
Ty5209	M ₂	<i>M. majori</i>	I	f6	Capo Figari	1.250	3.759	0.414	39909.367
Ty5210	M ₂	<i>M. majori</i>	I	f6	Capo Figari	3.307	3.591	0.794	35585.366
Ty5211	M ₃	<i>M. majori</i>	I	f6	Capo Figari	3.684	1.320	0.784	53355.904
Ty5213	M ₃	<i>M. majori</i>	I	f6	Capo Figari	3.528	0.045	0.529	51379.673
Ty5214	M ₃	<i>M. majori</i>	I	f5	Capo Figari	1.702	2.375	0.769	30071.381
Ty5215	M ₃	<i>M. majori</i>	I	f6	Capo Figari	6.053	2.511	0.478	42891.514
Ty5217	M ₂	<i>M. majori</i>	I	f5	Capo Figari	2.752	4.623	0.937	48613.744
Ty5218	M ₂	<i>M. majori</i>	I	f5	Capo Figari	4.479	2.995	0.660	50127.526
Ty5221	M ₁	<i>M. majori</i>	I	f6	Capo Figari	4.292	1.392	0.914	42710.760
Ty5223	M ¹	<i>M. majori</i>	I	f4	Capo Figari	6.822	4.614	0.623	42351.089
Ty5229	M ¹	<i>M. majori</i>	I	f4	Capo Figari	2.614	2.600	0.918	37502.260
Ty5302	M ₂	<i>M. s. fiorentina</i>	I	f5	Capo Figari	0.931	1.158	0.280	61133.820

Ty5304	M ₃	<i>M. s. fiorentina</i>	I	f6	Capo Figari	6.563	3.224	0.518	149495.309
IPS14955	M ²	<i>M. s. fiorentina</i>	I	f3	Cal Guardiola	1.052	3.996	0.510	26362.106
IPS35016	M ₁	<i>M. s. fiorentina</i>	I	f5	Cal Guardiola	1.261	3.526	0.682	40698.434
VA1088	M ₂	<i>M. s. fiorentina</i>	I	f5	Valdarno	0.606	4.208	0.362	31307.274
VA1415	M ₂	<i>M. s. fiorentina</i>	I	f6	Valdarno	0.923	1.772	0.524	92676.370
VA2058	M ₂	<i>M. s. fiorentina</i>	I	f5	Valdarno	1.067	2.795	0.343	16840.979
VA2075	M ₁	<i>M. s. fiorentina</i>	I	f6	Valdarno	1.355	4.420	0.455	10125.905
VA352	M ₂	<i>M. s. fiorentina</i>	I	f5	Valdarno	0.990	5.558	0.291	33349.831
EVT24036	M ²	<i>M. s. fiorentina</i>	I	f4	Vallparadis	0.919	1.983	0.805	43137.114
Vj88	M ²	<i>M. s. fiorentina</i>	I	f4	Villafranca D' Asti	0.679	3.767	0.405	20997.929

Abbreviations: Asfc = area scale fractal complexity; epLsar = exact proportion length-scale anisotropy of relief; Hasfc₈₁ = heterogeneity of area-scale fractal complexity on 81 cells; Tfv = Textural fill volume.

SOM Table S3

The extant species used in each methodology, with average body mass for males (M) and females (F) and the dietary categorization used in this study with the respective sources for dietary information (modified from Plastiras et al., 2022).

Taxon	Methodology	Diet	Body mass (kg) ^a		References
			M	F	
<i>Lophocebus albigena</i>	Dental topographic and enamel thickness Dental microwear texture analysis	Fruit/seed eater	8.25	6.02	Olupot (1988); Poulsen et al. (2001); Brugiére et al. (2002); McGraw et al. (2012); McGraw (2017)
<i>Lophocebus aterrimus</i>	Dental topographic and enamel thickness	Fruit/seed eater	7.84	5.76	Horn (1987); McGraw et al. (2012)
<i>Cercocebus torquatus</i>	Dental topographic and enamel thickness	Fruit/seed eater	9.47	5.50	Mitani (1989); McGraw et al. (2012); McGraw (2017)
<i>Cercocebus galeritus</i>	Dental topographic and enamel thickness	Fruit/seed eater	9.61	5.26	Wieczkowski (2004, 2009, 2013)
<i>Mandrillus leucophaeus</i>	Dental topographic and enamel thickness	Mixed feeder	17.50	12.50	Astaras et al. (2008, 2011); Owens et al. (2015)

<i>Mandrillus sphinx</i>	Dental microwear texture analysis	Mixed feeder	31.6	12.9	Hoshino (1985); Kudo and Mitani (1985); Lahm (1986); Norris (1988); Nsi Akoue et al. (2017); Hongo et al. (2018); Percher et al. (2018)
<i>Papio anubis</i>	Dental topographic and enamel thickness	Mixed feeder	25.10	13.30	Harding (1976); Morris and Goodall (1977); Hill and Dunbar (2002); Newton-Fisher and Okecha (2006); Akosim et al. (2010); Johnson et al. (2012)
<i>Papio hamadryas</i>	Dental topographic and enamel thickness	Mixed feeder	16.90	9.90	Pochron (2000); Swedell et al. (2008); Henzi et al. (2011); Schreier et al. (2019)
<i>Macaca sylvanus</i>	Dental topographic and enamel thickness Dental microwear texture analysis	Mixed feeder	~16.0	~11.0	Fa (1986); Ménard and Vallet (1997), (2002); El Alami et al. (2012); Maibeche et al. (2015)
<i>Macaca fuscata</i>	Dental microwear texture analysis	Mixed feeder	11.0	8.03	Maruhashi (1980); Iguchi and Izawa (1990); Agetsuma (1995); Hill (1997); Hanya et al. (2011); Enari and Sakamaki-Enari (2013); Tsuji et al. (2015)
<i>Macaca nemestrina</i>	Dental microwear texture analysis	Mixed feeder	11.2	6.5	Crocket and Wilson (1980); Caldecott (1986)
<i>Cercopithecus diana</i>	Dental topographic and enamel thickness	Fruit/seed eater	5.20	3.90	Oates and Whitesides (1990); Curtin (2004); Buzzard (2006); Kane and McGraw (2018)
<i>Cercopithecus nictitans</i>	Dental topographic and enamel thickness	Fruit/seed eater	6.67	4.26	Brugiere et al. (2002)

<i>Cercopithecus pogonias</i>	Dental topographic and enamel thickness	Fruit/seed eater	4.26	2.90	Brugiere et al. (2002)
<i>Cercopithecus cephus</i>	Dental topographic and enamel thickness	Fruit/seed eater	4.29	2.88	Brugiere et al. (2002)
<i>Cercopithecus campbelli</i>	Dental topographic and enamel thickness	Mixed feeder	4.50	2.70	Buzzard (2006)
<i>Chlorocebus aethiops</i>	Dental topographic and enamel thickness Dental microwear texture analysis	Mixed feeder	4.26	2.98	Kavanagh (1978); Whitten (1983); Pruetz and Isbell (2000); Nakagawa (2003); Barrett (2005)
<i>Erythrocebus patas</i>	Dental topographic and enamel thickness Dental microwear texture analysis	Mixed feeder	12.40	6.50	Isbell (1998); Nakagawa (2000); Isbell and Young (2007)
<i>Colobus guereza</i>	Dental topographic and enamel thickness Dental microwear texture analysis	Folivore	13.50	9.20	Oates et al. (1977); Fashing (2001); Harris and Chapman (2007); Harris (2010)
<i>Colobus polykomos</i>	Dental topographic and enamel thickness	Folivore	9.90	8.30	Dasilva (1994); Davies et al. (1999); Daegling and McGraw (2001); McGraw et al. (2016)
<i>Colobus satanas</i>	Dental topographic and enamel thickness	Folivore	10.40	7.42	McKey et al. (1981); Tutin et al. (1997); Brugiere et al. (2002)

<i>Ptilocolobus badius</i>	Dental topographic and enamel thickness Dental microwear texture analysis	Folivore	8.36	8.21	Marsh (1981); Dasilva (1994); Mowry et al. (1996); Davies et al. (1999); Daegling and McGraw (2001); Shimizu (2002)
<i>Procolobus verus</i>	Dental topographic and enamel thickness	Folivore	4.70	4.20	Oates and Whitesides (1990); Davies et al. (1999); Daegling and McGraw (2001)
<i>Nasalis larvatus</i>	Dental topographic and enamel thickness Dental microwear texture analysis	Folivore	20.40	9.82	Salter et al. (1985); Bennett and Sebastian (1988); Yeager (1989); Boonratana (1993); Matsuda et al. (2009)
<i>Semnopithecus entellus</i>	Dental topographic and enamel thickness Dental microwear texture analysis	Folivore	13.00	9.89	Newton (1992); Rowe et al. (1996); Punekar (2002); Sayers and Norconk (2008)
<i>Trachypithecus cristatus</i>	Dental topographic and enamel thickness	Folivore	6.61	5.76	Kool (1992); Caton (1999); Wright et al. (2008)

^a Body mass estimates given here represent the average body mass for each species taken from Smith and Jungers (1997) and references therein.

SOM Table S4

Amount of explained variance for every principal component of the PCAs for both sampling methods (i.e., BCO and EEC) using the enamel thickness (3DRETvol, 3DRETgeo, ACS) and dental topographic variables (ARC, LRFI, inclination) among the proposed dietary categories (i.e., folivores, mixed feeders, fruit/seed eaters).

PC	Eigenvalue	Variance (%)
BCO		
1	4.251	70.864
2	0.910	15.176
3	0.535	8.916
4	0.266	4.441
5	0.235	0.392
6	0.012	0.210
EEC		
1	4.196	69.934
2	0.804	13.416
3	0.601	10.032
4	0.303	5.069
5	0.063	1.061
6	0.029	0.496

Abbreviations: BCO = basin cut off cropping method (after Berthaume et al., 2019); EEC = entire enamel cap method (after Berthaume et al., 2019); 3DRETvol = 3D volumetric relative enamel thickness; 3DRETgeo = 3D geometric relative enamel thickness; ACS = absolute crown strength; ARC = area-relative curvature; LRFI = relief index.

SOM Table S5

Loadings of the principal components of the PCAs for both sampling methods (i.e., BCO and EEC).

Variables	PC1	PC2	PC3	PC4	PC5	PC6
BCO						
3DRETvol	0.418	-0.300	0.524	0.257	0.410	-0.473
3DRETgeo	0.455	-0.175	0.367	0.183	-0.482	0.600
ACS	0.205	0.913	0.331	-0.083	0.081	-0.005
ARC	-0.424	0.157	0.051	0.887	0.002	0.066
LRFI	-0.445	-0.132	0.461	-0.254	0.505	0.500
inclination	0.443	0.055	-0.513	0.200	0.580	0.399
EEC						
3DRETvol	0.436	-0.283	0.348	0.315	0.709	-0.070
3DRETgeo	0.421	-0.394	0.378	0.202	-0.678	0.147
ACS	0.357	0.536	0.487	-0.536	-0.030	-0.242
ARC	-0.365	0.503	0.468	0.575	-0.034	0.246
LRFI	-0.408	-0.368	0.426	-0.489	0.161	0.500
inclination	0.450	0.294	-0.311	-0.044	0.090	0.776

Abbreviations: BCO = basin cut off cropping method (after Berthaume et al., 2019); EEC = entire enamel cap method (after Berthaume et al., 2019); 3DRETvol = 3D volumetric relative enamel thickness; 3DRETgeo = 3D geometric relative enamel thickness; ACS = absolute crown strength; ARC = area-relative curvature; LRFI = relief index.

SOM Table S6

Dunn's post-hoc tests among the extant species with significant differences (before^a and after^b Bonferroni correction for multiple comparisons) in dental microwear texture variables for both phase II and phase I facets. Significant differences are highlighted in bold.

Variables	Comparisons among extant species		p-value	
			Significance ^a	Adjusted significance ^b
	Phase II			
Asfc	<i>Colobus guereza</i>	<i>Macaca fuscata</i>	<0.001	0.001
	<i>Colobus guereza</i>	<i>Chlorocebus aethiops</i>	<0.001	0.002
	<i>Colobus guereza</i>	<i>Lophocebus albigena</i>	<0.001	0.005
	<i>Colobus guereza</i>	<i>Macaca nemestrina</i>	<0.001	0.001
	<i>Colobus guereza</i>	<i>Macaca sylvanus</i>	<0.001	<0.001
	<i>Colobus guereza</i>	<i>Papio hamadryas</i>	0.049	1.000
	<i>Colobus guereza</i>	<i>Mandrillus sphinx</i>	0.009	0.410
	<i>Papio hamadryas</i>	<i>Macaca sylvanus</i>	0.001	0.035
	<i>Papio hamadryas</i>	<i>Macaca fuscata</i>	0.008	0.375
	<i>Papio hamadryas</i>	<i>Chlorocebus aethiops</i>	0.008	0.351
	<i>Papio hamadryas</i>	<i>Lophocebus albigena</i>	0.009	0.416

	<i>Papio hamadryas</i>	<i>Macaca nemestrina</i>	0.002	0.098
	<i>Mandrillus sphinx</i>	<i>Macaca nemestrina</i>	0.015	0.669
	<i>Mandrillus sphinx</i>	<i>Macaca sylvanus</i>	0.006	0.249
epLsar	<i>Macaca sylvanus</i>	<i>Mandrillus sphinx</i>	0.020	0.903
	<i>Macaca sylvanus</i>	<i>Colobus guereza</i>	0.016	0.712
	<i>Macaca nemestrina</i>	<i>Mandrillus sphinx</i>	0.019	0.859
	<i>Macaca nemestrina</i>	<i>Colobus guereza</i>	0.015	0.690
	<i>Papio hamadryas</i>	<i>Mandrillus sphinx</i>	0.002	0.070
	<i>Papio hamadryas</i>	<i>Colobus guereza</i>	0.002	0.099
	<i>Chlorocebus aethiops</i>	<i>Mandrillus sphinx</i>	0.002	0.103
	<i>Chlorocebus aethiops</i>	<i>Colobus guereza</i>	0.003	0.133
	<i>Lophocebus albigena</i>	<i>Mandrillus sphinx</i>	0.032	1.000
	<i>Lophocebus albigena</i>	<i>Colobus guereza</i>	0.026	1.000
	<i>Macaca fuscata</i>	<i>Mandrillus sphinx</i>	0.048	1.000
	<i>Macaca fuscata</i>	<i>Colobus guereza</i>	0.042	1.000
HasfC81	<i>Macaca fuscata</i>	<i>Papio hamadryas</i>	<0.001	0.011
	<i>Macaca fuscata</i>	<i>Macaca sylvanus</i>	0.001	0.023
	<i>Macaca fuscata</i>	<i>Lophocebus albigena</i>	<0.001	<0.001
	<i>Macaca fuscata</i>	<i>Macaca nemestrina</i>	<0.001	0.003
	<i>Macaca fuscata</i>	<i>Chlorocebus aethiops</i>	0.014	0.637

	<i>Macaca fuscata</i>	<i>Mandrillus sphinx</i>	0.046	1.000
	<i>Macaca fuscata</i>	<i>Colobus guereza</i>	0.001	0.050
	<i>Mandrillus sphinx</i>	<i>Macaca sylvanus</i>	0.031	1.000
	<i>Mandrillus sphinx</i>	<i>Lophocebus albigena</i>	0.005	0.240
	<i>Mandrillus sphinx</i>	<i>Macaca nemestrina</i>	0.011	0.475
	<i>Chlorocebus aethiops</i>	<i>Lophocebus albigena</i>	0.011	0.496
	<i>Chlorocebus aethiops</i>	<i>Macaca nemestrina</i>	0.020	0.894
Tfv	<i>Lophocebus albigena</i>	<i>Colobus guereza</i>	0.007	0.301
	<i>Macaca nemestrina</i>	<i>Colobus guereza</i>	0.003	0.124
	<i>Mandrillus sphinx</i>	<i>Colobus guereza</i>	<0.001	<0.001
	<i>Mandrillus sphinx</i>	<i>Papio hamadryas</i>	<0.001	0.001
	<i>Mandrillus sphinx</i>	<i>Macaca fuscata</i>	<0.001	<0.001
	<i>Mandrillus sphinx</i>	<i>Chlorocebus aethiops</i>	<0.001	0.020
	<i>Lophocebus albigena</i>	<i>Papio hamadryas</i>	0.024	1.000
	<i>Macaca nemestrina</i>	<i>Papio hamadryas</i>	0.010	0.448
	<i>Lophocebus albigena</i>	<i>Macaca fuscata</i>	0.027	1.000
	<i>Macaca nemestrina</i>	<i>Macaca fuscata</i>	0.011	0.496
	<i>Chlorocebus aethiops</i>	<i>Macaca nemestrina</i>	0.041	1.000
		Phase I		
Asfc	<i>Colobus guereza</i>	<i>Chlorocebus aethiops</i>	0.001	0.033

	<i>Colobus guereza</i>	<i>Mandrillus sphinx</i>	<0.001	0.003
	<i>Colobus guereza</i>	<i>Macaca fuscata</i>	<0.001	<0.001
	<i>Colobus guereza</i>	<i>Lophocebus albigena</i>	<0.001	0.001
	<i>Colobus guereza</i>	<i>Macaca nemestrina</i>	<0.001	<0.001
	<i>Colobus guereza</i>	<i>Papio hamadryas</i>	0.004	0.166
	<i>Colobus guereza</i>	<i>Macaca sylvanus</i>	0.002	0.074
	<i>Papio hamadryas</i>	<i>Lophocebus albigena</i>	0.022	0.970
	<i>Papio hamadryas</i>	<i>Macaca nemestrina</i>	0.012	0.560
	<i>Chlorocebus aethiops</i>	<i>Macaca nemestrina</i>	0.040	1.000
epLsar	<i>Papio hamadryas</i>	<i>Macaca nemestrina</i>	0.022	1.000
Hasfc ₈₁	<i>Macaca nemestrina</i>	<i>Colobus guereza</i>	0.001	0.024
	<i>Macaca nemestrina</i>	<i>Papio hamadryas</i>	0.001	0.027
	<i>Macaca nemestrina</i>	<i>Macaca fuscata</i>	<0.001	<0.001
	<i>Macaca fuscata</i>	<i>Lophocebus albigena</i>	<0.001	0.011
	<i>Macaca fuscata</i>	<i>Chlorocebus aethiops</i>	0.003	0.119
	<i>Macaca fuscata</i>	<i>Macaca sylvanus</i>	0.021	0.967
	<i>Macaca fuscata</i>	<i>Mandrillus sphinx</i>	0.042	1.000
	<i>Papio hamadryas</i>	<i>Lophocebus albigena</i>	0.024	1.000
	<i>Colobus guereza</i>	<i>Lophocebus albigena</i>	0.017	0.753
	<i>Mandrillus sphinx</i>	<i>Lophocebus albigena</i>	0.039	1.000

	<i>Mandrillus sphinx</i>	<i>Macaca nemestrina</i>	0.001	0.054
	<i>Chlorocebus aethiops</i>	<i>Macaca nemestrina</i>	0.008	0.351
Tfv	<i>Mandrillus sphinx</i>	<i>Colobus guereza</i>	<0.001	<0.001
	<i>Mandrillus sphinx</i>	<i>Papio hamadryas</i>	<0.001	0.001
	<i>Mandrillus sphinx</i>	<i>Chlorocebus aethiops</i>	<0.001	<0.001
	<i>Mandrillus sphinx</i>	<i>Macaca fuscata</i>	<0.001	0.009
	<i>Colobus guereza</i>	<i>Macaca fuscata</i>	0.030	1.000
	<i>Macaca sylvanus</i>	<i>Mandrillus sphinx</i>	0.002	0.091
	<i>Colobus guereza</i>	<i>Lophocebus albigena</i>	0.042	1.000
	<i>Macaca nemestrina</i>	<i>Mandrillus sphinx</i>	0.028	1.000
	<i>Lophocebus albigena</i>	<i>Mandrillus sphinx</i>	0.017	0.750

Abbreviations: Asfc = area-scale fractal complexity; epLsar = exact proportion length-scale anisotropy of relief; Hasfc₈₁ = heterogeneity of area-scale fractal complexity on 81 cells; Tfv = textural fill volume.

^a Asymptotic significance (two-sided tests) are displayed with significance level set at 0.05.

^b Significance values have been adjusted by the Bonferroni correction for multiple tests.

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