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

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ABSTRACT

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

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1. Introduction

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

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

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

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

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

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

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

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