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# From leaves to seeds? The dietary shift in late Miocene colobine monkeys of southeastern Europe

**Running title:** Dietary shift in late Miocene colobines

**Authors:** Ghislain Thiery<sup>1\*</sup>, Corentin Gibert<sup>1</sup>, Franck Guy<sup>1</sup>, Vincent Lazzari<sup>1</sup>, Nikolaï Spassov<sup>2</sup>, Denis Geraads<sup>3</sup>, Gildas Merceron<sup>1\*</sup>

1. Paleovoprim UMR 7262 CNRS, Université de Poitiers, France

2. National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria

3. UMR 7207, Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, France

\* **Corresponding authors:**

• Ghislain Thiery ([ghislain.thiery@univ-poitiers.fr](mailto:ghislain.thiery@univ-poitiers.fr))

• Gildas Merceron ([gildas.merceron@univ-poitiers.fr](mailto:gildas.merceron@univ-poitiers.fr))

**Author contributions:**

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• data acquisition: GT, FG, VL, GM

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## Conflicts of interest:

The authors have no conflict of interest to declare.

## Data accessibility:

The R code is available in its entirety as online supplementary material, along with all data used for the preparation of this manuscript [<https://dx.doi.org/10.13140/RG.2.2.13861.42722>]. When it was possible, surface meshes of the specimens used in the topographic analysis have been uploaded on Morphosource [<https://www.morphosource.org>].

39 **From leaves to seeds? The dietary shift in late Miocene colobine monkeys of southeastern**  
40 **Europe**

41 **Abstract**

42 Extant colobine monkeys are specialized leaf eaters. But during the late Miocene, western Eurasia  
43 was home to colobines which were less efficient at chewing leaves than they were at breaking  
44 seed shells. To understand the link between folivory and granivory in this lineage, the dietary  
45 niche of *Mesopithecus delsoni* and *M. pentelicus* was investigated in southeastern Europe, where a  
46 major environmental change occurred during the late Miocene. We combined dental topographic  
47 estimates of chewing efficiency with dental microwear texture analysis of enamel wear facets. *M.*  
48 *delsoni* was more efficient at chewing leaves than *M. pentelicus*, the dental topography of which  
49 matches an opportunistic seed eater. Concurrently, microwear complexity increases in *M.*  
50 *pentelicus*, especially in the northernmost localities corresponding to present-day Bulgaria. This is  
51 interpreted as a dietary shift towards hard foods such as seeds or tubers, which is consistent with  
52 the savanna and open mixed forest biomes that covered Bulgaria during the Tortonian. The fact  
53 that *M. delsoni* was better adapted to folivory and consumed a lower amount of hard foods than *M.*  
54 *pentelicus* suggests that colobines either adapted to folivory before their dispersal to Europe, or  
55 evolved adaptations to leaf consumption in multiple occurrences.

56 **Keywords:** Balkans; Colobinae; Dental microwear texture analysis; Dental topography;  
57 *Mesopithecus*; Paleoecology.

## 58 **Background**

### 59 *Climate change, plant communities and the adaptive answer of plant eaters*

60 Climate change can have drastic and long-term effects on the structure and the diversity of  
61 terrestrial plant communities. Plenty of examples can be found in the fossil record, such as the  
62 collapse of the ‘Coal Forest’ in Europe and North America following the greenhouse-gas forced  
63 aridification at the end of the Carboniferous (Montañez et al. 2007), or the replacement of C<sub>3</sub>  
64 carbon fixation plants by C<sub>4</sub> carbon fixation plants in the intertropical zone at the end of the  
65 Miocene, triggered among other factors by global aridification in a cooling context (Osborne and  
66 Beerling 2006; Osborne 2008). Such major changes in plant communities can dramatically affect  
67 the ability of contemporaneous fauna to feed on their preferred food resources, hence impacting  
68 both taxonomic diversity and ecological disparity of animals. For instance, the collapse of the  
69 Carboniferous rainforest resulted in a large faunal turnover in tetrapods as well as the emergence  
70 of new dietary strategies, such as carnivory or tree fern browsing (Sahney et al. 2010). Similarly,  
71 the expansion of C<sub>4</sub> plants during the late Miocene resulted in the diversification of grazing  
72 mammals in North America (Janis et al. 2000; Osborne 2008), Asia (Behrensmeyer et al. 2007)  
73 and Africa (Cerling et al. 2005).

74 Still, the consequences of the global climatic events can have different outcomes, depending on  
75 the regional context. For instance, the global aridification which took place at the end of the  
76 Miocene did not result in the expansion of C<sub>4</sub> plants in Western Eurasia, even though they could  
77 have been locally abundant (Böhme et al. 2017); instead, it induced the shrinking of the Paratethys

78 and then, the disappearance of the Central European Wet Zone (van Dam 2006; Utescher et al.  
79 2011; Pound et al. 2012). At the same time, a quasi-continuous biome of woodland/savanna and  
80 open mixed forest arose from western China to eastern Europe (Böhme et al. 2017; Kaya et al.  
81 2018; but see Denk et al. 2018), associated with the Pikermian and Baodean chronofaunas adapted  
82 to these new environments (Kostopoulos 2009; Ataabadi et al. 2013). Concurrently, one likely  
83 consequence of this aridification trend was the rise and fall of successive primate families in  
84 Europe (Fig. 1). The Miocene epoch is indeed characterized by a radiation of hominoid primates  
85 in Eurasia, with more than 10 genera ranging from Spain to south-eastern Asia (Moyà-Solà et al.  
86 2009; Casanovas-Vilar et al. 2011; Begun 2015; DeMiguel et al. 2021). At the end of the Middle-  
87 Miocene Climatic Transition (MMCT), the taxonomic diversity of European primates reached a  
88 peak for hominoids and the now extinct pliopithecoids (Fig. 1). This high specific diversity  
89 mirrors a wide ecological disparity, with species foraging on both soft and hard foods (Ungar and  
90 Kay 1995; King et al. 1999; Merceron et al. 2005; DeMiguel et al. 2013, 2014), occupying  
91 different types of habitats (Eronen and Rook 2004; Merceron et al. 2007, 2012, 2013, 2016;  
92 Sukselainen et al. 2015; DeMiguel et al. 2021). Afterwards, the fossil record progressively  
93 decreased for both pliopithecoids (Harrison 2005; Begun 2016) and hominoids (Casanovas-Vilar  
94 et al. 2011), and the cercopithecids started occurring in Eurasia during the early Turolian (de  
95 Bonis et al. 1990; Koufos 2009), where they persisted until Pleistocene times (Elton and O'Regan  
96 2014).

97 The fossil record can translate how biodiversity is impacted by a global and/or regional  
98 environmental changes, but it can also help exploring the adaptive answer of species to the local  
99 effects of these environmental changes (Davis and Pineda-Munoz 2016). When faced with climate

100 change and its influence on primary production, species can avoid extinction either (i) by tracking  
101 their preferred environment or (ii) by adapting to their new environmental conditions. Comparing  
102 the dietary niches of extinct species at different localities, but within a constrained spatial and  
103 temporal framework, could give important insights into the mechanisms underlying adaptation and  
104 how they ultimately result in macroevolution.

### 105 *When colobine monkeys roamed the Balkans*

106 Colobine monkeys are a subfamily of catarrhines feeding principally on leaves. But back in the  
107 late Miocene, the oldest colobine, *Microcolobus tugenensis* from Kenya, had low-cusped molars  
108 compared to extant colobines (Benefit and Pickford 1986) and was thus unlikely to have been as  
109 folivorous as extant species. This raises the issue of the evolutionary origins of folivory in  
110 colobines. Following the terminology of Gould and Vrba (1982), it has been suggested that the  
111 aptitudes of extant colobines for leaf consumption, such as their multi-chambered stomach or their  
112 dental morphology, could in fact be exaptations co-opted from adaptations for seed consumption  
113 (Chivers 1994; Lucas and Teaford 1994). For instance, the multi-chambered stomachs of  
114 colobines are interpreted by Chivers (1994) as exaptations to folivory, which would have been co-  
115 opted from an adaptation to digest high concentration of toxic carbon chains in seeds. . Similarly,  
116 dental tools used during leaf chewing (i.e. lophs) could have been co-opted from an adaptation to  
117 process tough seed shells (Happel 1988; Lucas and Teaford 1994). Still, it is not known when such  
118 dietary shift to folivory would have occurred, and what could have caused it.

119 Today, colobines are restricted to inter-tropical biomes of Asia and Africa, with the notable  
120 exceptions of three species of snub-nosed monkeys living in the temperate forests of China

121 (Nüchel et al. 2018) and at least two species of gray langurs living in the Himalayas (Groves  
122 2001). But from the late Miocene to the Pliocene, they also thrived in western Eurasia. The earliest  
123 reliable occurrence of a Eurasian colobine is *Mesopithecus delsoni* found in the Greek locality of  
124 Ravin des Zouaves-5 (de Bonis et al. 1990; Koufos 2009); magnetostratigraphic estimations date  
125 the site to ~ 8.2 Ma, while relative datation, based on the faunal assemblage, have assigned the site  
126 to the Mammalian Neogene zone (MN; see Guérin 1980, 1982; Van Dam et al. 2001) MN11 (~  
127 8.7 to 7.75 Ma; de Bonis et al. 1990; Koufos 2009). The status of *M. delsoni* is debated and  
128 regarded either as a bona fide species (Koufos et al. 2004; Koufos 2009) or as a subspecies of the  
129 later species *M. pentelicus* (Alba et al. 2015), which spans the second half of the MN12 (the  
130 Pikermian event ~ 7.43 to 7.27 Ma; De Bonis and Koufos 1999; Böhme et al. 2018; Spassov et al.  
131 2018) and possibly later at the beginning of the Messinian (Spassov et al. 2012). *Mesopithecus*  
132 *delsoni* differs from *M. pentelicus* in its less inclined mandible planum alveolare, larger teeth, a  
133 large honing facet on the lower third premolar, and a large hypoconulid on the lower third molar  
134 with a deep groove on the distal face (de Bonis et al. 1990; Koufos 2009; Spassov et al. 2018).  
135 Given these differences, we consider *M. delsoni* as a separate species.

136 From the analysis of its dental microwear texture (Merceron et al. 2009b), *M. pentelicus* has been  
137 described as an opportunistic forager feeding occasionally on stress-limited food such as hard  
138 seeds, having a high microwear complexity (Asfc) and a low anisotropy (EpLsar), as expected  
139 from crushing wear facets with a high count of pits (Merceron et al. 2009a). A similar pattern was  
140 observed in *M. delsoni* fossils from Ravin des Zouaves-5 and Hadjidimovo (Merceron et al.  
141 2009b). The upper second molars of *M. pentelicus* have thin enamel combined with a low relief,  
142 which indicates a moderate ability to crush hard foods, such as seeds, tubers or the exocarp of

143 some fruit, as well as a low ability to shear tough and pliant foods, such as leaves (Thiery et al.  
144 2017). Compared to their extant relatives, these monkeys may have ingested a larger proportion of  
145 sturdy, seed-like foods and a smaller proportion of tough, leaf-like foods.

146 The present study aims to explore how the dietary niche of the genus *Mesopithecus* changed  
147 during the late Miocene in the Balkans (Fig. 1). This time and geographic location are especially  
148 interesting because of the environmental change that occurs there at the end of the late Miocene.  
149 Indeed, by the end of the MN11, the dominating evergreen broadleaf forest which occurred in  
150 southeastern Europe had lost ground to forest savanna and open woodlands, particularly east of  
151 longitude 28°E (Eastern border of Romania/Bulgaria; Pound et al. 2012). This aridification and  
152 landscape opening then continued during the Pikermian event (MN12; Böhme et al. 2017).

### 153 ***Multi-scale analysis of the dietary niche***

154 Dietary estimates can only track the diet at a given temporal scale (Davis and Pineda-Munoz  
155 2016). For instance, the dietary niche of a species can be inferred from cranial and dental  
156 morphology, which reflect adaptations to ingest and process a range of foods at a large organismal  
157 extent i.e., metapopulations. Since cranio-dental evolution may take thousands of years,  
158 morphological estimates operate at a large temporal scale. At the same time, the food eaten by  
159 individuals can leave a trace in the isotopic composition of the enamel (Ben-David and Flaherty  
160 2012) or at the surface of the enamel wear facets, in the form of microscopic wear marks (Teaford  
161 and Oyen 1989; Merceron et al. 2016; Ramdarshan et al. 2016; Teaford et al. 2017); but in  
162 contrast with cranio-dental morphology, stable isotopes and dental microwear work to small  
163 organismal extents i.e., the individuals, and operate at a small time scale (from weeks in dental

164 microwear to years in stable isotopes of the enamel; Davis and Pineda-Munoz 2016 and references  
165 therein).

166 This work combines dental estimates from (i) dental topography and (ii), dental microwear texture  
167 analysis. Dental topography measures the three-dimensional geometry of the tooth surface (Ungar  
168 and Williamson 2000; Guy et al. 2013). Like cranio-dental morphology, the topography of the  
169 teeth (before any significant modification by dental wear) is the result of selection over multiple  
170 generations (Davis and Pineda-Munoz 2016). Dental topographic variables measure several  
171 aspects of the tooth surface geometry. First, dental relief i.e., height variation over the tooth  
172 surface can be estimated using slope (Ungar and Williamson 2000) and relief indices such as RFI  
173 (Ungar and Williamson 2000; Boyer 2008; Thiery et al. 2019). The sharpness of the dental tools  
174 can be estimated using Dirichlet normal energy (DNE: Bunn et al. 2011) and other curvature-  
175 based indices, such as the area-relative curvature (ARC) introduced therein (see also Guy et al.  
176 2017). Lastly, dental complexity is estimated using variables based on the heterogeneity of  
177 exposure, such as orientation patch count rotated (OPCR; Wilson et al. 2012; Guy et al. 2013).  
178 Leaf-eating cercopithecids tend to have higher relief and sharper teeth compared to more  
179 frugivorous species (Bunn and Ungar 2009). Based on Thiery et al. (2017), the topography of *M.*  
180 *pentelicus* and *M. delsoni* is expected to match with cercopithecids consuming a large proportion  
181 of hard food i.e., we expect their molars to have a low-to-medium relief and a low sharpness.

182 In contrast, dental microwear texture analysis (DMTA) investigates texture changes of enamel  
183 wear facets caused by daily contacts with food and other ingested particles (Scott et al. 2006,  
184 2012). Experimental data and modern datasets confirm that hard food eaters have higher texture  
185 complexity (Asfc) values (Scott et al. 2012; Ramdarshan et al. 2016). The heterogeneity of texture

186 complexity quantifies the variation of texture complexity observed within a scan (Asfc) and is  
187 expected to be higher for animals with a versatile diet compared for instance to species with a  
188 specialized diet (Scott et al. 2012; Ramdarshan et al. 2016; Merceron et al. 2018). The anisotropy  
189 of the microwear texture (epLsar) measures the orientation concentration of surface roughness,  
190 which is expected to be more directional (higher epLsar) for leaf eating species, notably when  
191 their diet includes tough foliages and silica-bearing plants (Scott et al. 2012; Merceron et al.  
192 2021). Finally, the textural fill volume (Tfv) is the result of an algorithm that fills a surface with  
193 square cuboids of different volumes. Tfv does not depend on the surface shape but on its finer  
194 texture. We expect a higher Tfv to be associated with higher Asfc values (Scott et al. 2012). Based  
195 on earlier works on 2D microwear analysis (Merceron et al. 2009a) and DMTA (Merceron et al.  
196 2009b), the texture complexity of *M. pentelicus* and *M. delsoni* is expected to reflect the  
197 opportunistic inclusion of hard foods, with regional and possibly temporal variations in response  
198 to local differences in environmental conditions (Kostopoulos 2009).

## 199 Results

### 200 *Dental topography*

201 Average slope is significantly higher in colobine monkeys than in the other catarrhines examined  
202 here (Kruskall-Wallis' chi squared test:  $K = 13.601$ ,  $p < 0.001$ ). However, both *Trachypithecus*  
203 *auratus* and *T. cristatus* have a noticeably lower slope than other colobines. In addition,  
204 *Erythrocebus patas* has a higher slope than other non-colobine monkeys (Fig. 2A). Similarly,  
205 ARC is significantly higher in colobines (Kruskall-Wallis' chi squared test:  $K = 18.652$ ,  $p <$   
206  $0.001$ ). Again, *T. auratus* shows noticeably lower ARC values than other colobines, while *E. patas*  
207 shows higher ARC values than other non-colobines (Fig. 2B).

208 Both *M. aff. delsoni* from Hadjidimovo and *M. pentelicus* from Pikermi have low slope values  
209 grouping them with the most granivorous catarrhines, although *M. pentelicus* has an even lower  
210 slope than the granivorous *Lophocebus albigena*. Similarly, the ARC of *M. pentelicus* is as low as  
211 the ARC of *Chlorocebus aethiops* and *L. albigena*. In *M. aff. delsoni* however, ARC is visibly  
212 higher, being similar to that of *T. auratus*. In contrast, *M. cf. pentelicus* (noted *M. sp.* on Fig. 2)  
213 from Azmaka shows high slope values for a colobine, comparable to *Ch. Aethiops* or *T. auratus*,  
214 and intermediate ARC values between *M. aff. delsoni* and *M. pentelicus*. Regarding other  
215 estimates, the higher relief in *M. cf. pentelicus* is confirmed by relief index (RFI, Fig. 3B) sensu  
216 Ungar and Williamson (2000) but not by relief index sensu Boyer (2008; LRFI, Fig. 3C). Both  
217 variables do not separate *M. delsoni* from *M. pentelicus*. Concerning dental sharpness, DNE values  
218 confirm that *M. delsoni* had sharper molars than *M. pentelicus* (Fig 3E). Finally, *M. delsoni* had

219 lower OPCR values indicating that its molars were less complex than the molars of *M. pentelicus*  
220 (Fig. 3F).

### 221 ***Dental microwear texture analysis***

222 Complexity Asfc on phase II (crushing/grinding molar facets) is significantly higher in the  
223 omnivorous *Chlorocebus aethiops* and *Erythrocebus patas*, and in the seed-eating mangabeys *C.*  
224 *atys* (*Cercocebus* sp. on Fig. 2) and *L. albigena* than in the African colobines and in *T. auratus*  
225 (post-hoc LSD-test, p-value < 0.05). The mangabeys also have significantly higher Asfc values  
226 than *S. entellus*. In contrast, *Nasalis larvatus* shows a broad range of Asfc values overlapping with  
227 mangabeys, and *T. cristatus* has Asfc values exceeding mangabeys' (Fig. 2A, B).

228 The Asfc of *Mesopithecus* ranges over most of the spectrum observed in extant species (Fig. 2A-  
229 B). However, *Mesopithecus delsoni* from Ravin des Zouaves-5 and *M. pentelicus* from Pikermi  
230 have low Asfc values (Fig. 2C). The highest Asfc values are observed in the northernmost  
231 population of *M. pentelicus*, from Gorna Sushitsa (N = 4). They are significantly higher than what  
232 is measured for Ravin des Zouaves-5 and Pikermi (post-hoc LSD-test, p-value < 0.05) and range  
233 as high as the values observed for *T. cristatus* (Fig. 2A-B). In addition, Asfc values are  
234 significantly higher in *M. pentelicus* from the Bulgarian locality of Kalimantsi than in Pikermi  
235 (post-hoc LSD-test, p-value < 0.05). Lastly, specimens from Vathylakkos-2 (N = 1) and Perivolaki  
236 (N = 4) attributed to *M. delsoni/pentelicus* (noted M. sp on Fig. 2) only differ significantly from  
237 Gorna Sushitsa (post-hoc LSD-test, p-value < 0.05).

238 The heterogeneity of Asfc (Hasfc) shows a contrasting picture in extant species and does not  
239 reflect dietary categories and phylogeny (Table 1). In extinct species however, it is worth noting

240 that the dispersion of data is much larger in Pikermi compared to the other sites (Fig. 4B).  
241 Regarding epLsar, African colobines and *T. auratus* all have a significantly higher anisotropy than  
242 the frugivorous and seed-eating cercopithecids, together with *T. cristatus* (Table 1). The  
243 anisotropy is also significantly lower in the MN12 locality of Kalimantsi (*M. pentelicus*) than in  
244 the MN11 locality of Hadjidimovo (*M. delsoni*), denoting a lower reliance on leaves (Fig. 4C).  
245 Still, other MN12 localities do not mirror this difference. Again, the epLsar variance is the largest  
246 at the MN12 locality of Pikermi, indicating a wide range of behaviors. Finally, the textural fill  
247 volume (Tfv) does not separate extinct species or their localities (Fig. 4D; see also Table S8).

## 248 **Discussion**

### 249 *Fundamental niche predicted from dental topography*

250 Caution is needed when interpreting dental topography, as morphology is strongly constrained by  
251 phylogeny, and what seems like an adaptation may be the remnants of an ancestral morphology  
252 (Davis and Pineda-Munoz 2016). Still, a large number of studies have shown that folivorous  
253 primates are characterized by high-relief molars which are on average sharper (Boyer 2008; Bunn  
254 and Ungar 2009; Bunn et al. 2011; Winchester et al. 2014; see also Kay and Hiiemae 1974; Kay  
255 1975, 1977). This is most likely related to the selective pressure exerted by flat, tough and pliant  
256 foods such as leaves, which are displacement-limited foods and usually take more chewing  
257 motions to be comminuted (Lucas 2000). The higher the molar relief, the sharper the tooth, and  
258 the more displacement-limited food can be comminuted in a single chewing motion.

259 Apart from *T. auratus*, all colobine monkeys have high slope and ARC values, which indicates a  
260 high leaf-chewing efficiency (Fig. 2A, 1B). The three species of African colobines forages  
261 primarily on leaves even though *Co. polykomos* has been reported to fall back on seeds (protected  
262 by pods) in several locations (Dasilva 1994; Davies et al. 1999). It is worth noting that colobine  
263 monkeys usually remove the pods' shell using their anterior teeth i.e., incisors and canines and do  
264 not use their molars for that purpose (Oates 1994; McGraw et al. 2016). Moreover, Fashing (2001)  
265 reports on two populations of *Co. guereza* in western Kenya spending 40% to 60% of their  
266 foraging time on fruits for 6 month a year. This degree of frugivory represents exceptions driven  
267 by local environmental conditions and is most likely undetectable by dental topography due to the  
268 scale of evolutionary biological changes through time. That being said, the consumption of seed-  
269 like foods would have probably affected the dental topography of worn teeth even on a short-term,  
270 local scale, as hinted by several studies (Ungar and Williamson 2000; Yamashita et al. 2012; Li et  
271 al. 2020).

272 The four species of Asian colobines are also known to favor leaves. However, *T. auratus* has been  
273 reported to target seeds as well (Kool 1993). This is consistent with their average slope, which is  
274 the lowest among colobines. In addition, some populations of *N. larvatus* devote 15-20% of their  
275 feeding time to seeds (Bennett and Sebastian 1988; Yeager 1989), and the most terrestrial colobine  
276 monkey *S. entellus* also relies on fruits, seeds and even underground storage organs (USOs),  
277 depending on resource availability (Hladik 1977; Sayers and Norconk 2008). This is consistent  
278 with their lower ARC scores compared to other colobines. Both *Ch. aethiops* and *E. patas* have  
279 intermediate slope scores, but the former has very low ARC scores, denoting a low leaf-chewing  
280 ability, whereas *E. patas* has ARC scores comparable to *N. larvatus* or *T. auratus*. Again, this is

281 consistent with their diet, as vervets feed frequently on fruits and seeds (Wrangham and Waterman  
282 1981; Whitten 1983), whereas patas feed more on tough but soft foods such as arthropods (Isbell  
283 1998; Isbell et al. 1998). In contrast, the mangabeys have low slope and ARC values, pointing to a  
284 poor leaf-chewing efficiency. Their molars better suit the grinding and crushing of sturdy hard  
285 food such as seeds (Lambert et al. 2004; McGraw et al. 2014).

286 Given its low-relief and relatively dull molars, the theoretical dietary niche of *Mesopithecus*  
287 *pentelicus* can be inferred as more versatile than extant colobines (Fig. 2A-B). It was probably  
288 able to masticate or crack sturdy, hard foods such as seeds, seed shells or tubers without damaging  
289 its molars, as suggested in previous studies (Merceron et al. 2009a,b; Thiery et al. 2017). The low  
290 leaf-chewing ability of *M. pentelicus*, similar to that of *Ch. aethiops*, also indicates that it would  
291 have experienced difficulties to thrive from leaves alone (because of longer chewing times, lower  
292 digestibility, etc.). In addition, the thin enamel of *M. pentelicus*, which differs from the thick  
293 enamel of both mangabey species, would have mitigated its ability to crack the hardest foods,  
294 while improving the natural sharpening of enamel crests as tooth wears down (Thiery et al. 2017).  
295 Having sharper molars, *M. delsoni* appears to have been slightly more efficient at chewing  
296 leathery, leaf-like foods. However, the topography of only one specimen of *M. aff. delsoni* was  
297 measured, so this interpretation remains highly hypothetical. Lastly, *M. cf. pentelicus* from  
298 Azmaka (AZM-6) have intermediate ARC values between *M. delsoni* and *M. pentelicus*, but a  
299 higher slope which reminds the molar topography of *Cercocebus*. This suggests a decent aptitude  
300 to crush hard foods such as seeds, but also some underground storage organs e.g., tubers (Dominy  
301 et al. 2008).

302 ***Realized niche inferred from dental microwear texture***

303 High Asfc on phase II molar facets is correlated with the consumption of USOs and any other food  
304 which may carry grit and dust on their surface. However, and despite the fact that quartz grains  
305 present on food do contribute to tooth wear, experiments which emulated natural conditions  
306 concluded that dust loads do not obliterate the dietary signal (Merceron et al. 2016; Schulz-Kornas  
307 et al. 2019). The complexity (Asfc) of crushing/grinding molar facets is also higher for primates  
308 consuming hard, sturdy food items, such as fruits with hard exocarp or hard seeds (Scott et al.  
309 2012; this study). This relationship has been shown experimentally on captive primates (Teaford  
310 and Oyen 1989; Teaford et al. 2017) and on captive ewes (Ramdarshan et al. 2016). The two  
311 mangabeys *C. atys* and *L. albigena* have high Asfc values (Fig. 2), while all colobines except *N.*  
312 *larvatus* and *T. cristatus* have low to moderate Asfc values. Because they occupy one of the  
313 wettest dense forest around the world, dusty sandstorms are unlikely to have affected dental  
314 microwear of *N. larvatus* and *T. cristatus*, and their higher Asfc is more likely to result from the  
315 seasonal inclusion of small seeds, as observed in *N. larvatus* (Yeager 1989; Matsuda et al. 2013).  
316 During MN11, *M. delsoni* and *M. aff. delsoni* present Asfc scores within the range of *S. entellus*  
317 and *N. larvatus*. Like these species, the dietary niche of *M. delsoni* was probably restricted to a  
318 relatively narrow range of foods, likely fruit and leaves – albeit wider than other colobine  
319 monkeys such as African colobines, the dietary niche of which is even narrower. In contrast, there  
320 is a significant increase in the range of complexity (Asfc) between *M. delsoni* during MN11 and  
321 *M. pentelicus* during MN12. While the complexity (Asfc) of *M. pentelicus* at the southern Greece  
322 locality of Pikermi and to some extent in Vathylakkos-2 and Perivolaki) remains comparable to  
323 the complexity of *M. delsoni*, it is similar to *C. atys* in the Bulgarian locality of Kalimantsi (N =

324 16) and it is even higher in Gorna Sushitsa (N = 4), pointing to the consumption of harder foods  
325 such as seeds or tubers.

326 It is unlikely that this dietary shift would have resulted from interspecific competition with other  
327 primates. The extinction of Pliopithecidae after the Middle Miocene Climatic Transition (Fig. 1),  
328 and the progressive extinction of European hominoids during the late Miocene (Merceron et al.  
329 2010; Casanovas-Vilar et al. 2011) before the genus *Macaca* disperses to Europe from Africa  
330 (Alba et al. 2014), could have instead left dietary niches open to colobines, although hominoids  
331 might have co-existed with *Mesopithecus pentelicus* in a different site of Azmaka (respectively  
332 found in AZM-4 and AZM-6, Spassov et al. 2012; Böhme et al. 2017). More likely, the dietary  
333 shift that we observe (Fig. 2C; Fig. 4) is the consequence of the environmental changes which  
334 occurred in southeastern Europe during the late Miocene. The opening of landscapes, especially  
335 east of longitude 23°E (Western border of Romania/Bulgaria; Pound et al. 2012) after MN11  
336 benefited species with broader dietary niches. This was probably the case for *M. pentelicus* which  
337 displays a broad geographic range, from the Iberian peninsula (Alba et al. 2015) to China  
338 (Jablonski et al. 2011; Dong and Qi 2013), and was likely able to disperse and inhabit a wide  
339 range of habitats, including woodland/savanna environments (Clavel et al. 2012; Pound et al.  
340 2012; Kaya et al. 2018).

341 Periods of environmental change are prone to select more generalist species at the expense of  
342 specialized ones. *Mesopithecus delsoni* joins the cohort of species affected by the great  
343 environmental change which occurs in southeastern Europe between the early/mid-Miocene and  
344 the late Miocene, coinciding with the extinction of Moschidae and the decrease in richness of  
345 Cervidae as well as forest-affiliated small taxa (Casanovas-Vilar et al. 2005). At the same time,

346 the richness of Bovidae, Equidae, Giraffidae and rodents adapted to open environments increase as  
347 the global climate cools and Eurasia aridifies (Merceron et al. 2005, 2010; Fortelius et al. 2014;  
348 Cano et al. 2015). It will not be until MN13 and the decline of the evergreen forest in southern  
349 Europe (Casanovas-Vilar et al. 2005; Cano et al. 2015) that *M. pentelicus* disperses from eastern  
350 Europe to Italy (Pradella and Rook 2007) and then to the Iberian basin (Alba et al. 2015), denoting  
351 its high dispersal capacity in a landscape opening context.

### 352 *Implications for the evolutionary origins of folivory in colobines*

353 While our results do not contradict the general assumption that adaptation to folivory would have  
354 emerged from granivory in colobine monkeys (Chivers 1994; Lucas and Teaford 1994), they show  
355 that *M. delsoni* during MN11 was less prone to the consumption of hard foods than *M. pentelicus*  
356 during MN12 (Fig. 2C; Fig. 3A). Regarding dental topography, much caution is needed, as only a  
357 single unworn molar of *M. delsoni* could be examined. Still, its higher average ARC indicates a  
358 higher leaf-shearing ability and most likely a lower ability to process hard foods (Fig. 2B).  
359 Together, these data indicate that *M. delsoni* was less likely to consume seeds than the later  
360 colobine *M. pentelicus*.

361 If a shift from a seed-rich diet towards folivory did actually occur in colobines, two evolutionary  
362 scenarios come to mind. On the one hand, folivory could have already emerged in colobines  
363 before the dispersal of *Mesopithecus* to Eurasia; *M. pentelicus* would have then adapted to a  
364 broader dietary niche, including the consumption of hard foods (Thiery et al. 2017). In fact, the  
365 oldest colobine monkeys could have been folivorous to some extent, and colobine monkeys might  
366 have evolved sharper molars later as their body size increased, thus resulting in higher nutritional

367 needs (Rossie et al. 2013). A thorough analysis of both dental topography and microwear of  
368 *Microcolobus tugenensis* and other early African colobine monkeys is required to test whether  
369 folivory was the ancestral dietary niche of European colobines or not.

370 On the other hand, folivorous colobines might have emerged several times, each time when a  
371 favorable environmental context occurred. While it seems like a costly hypothesis, the early  
372 presence of key physiological adaptations to seed consumption (Happel 1988) might have been  
373 co-opted as exaptations to folivory and facilitated the multiple rises of convergent folivorous  
374 lineages. As a matter of fact, existing differences in physiology and gut anatomy within extant  
375 colobines are not connected to phylogeny but rather reflect the importance of seasonal fruit and  
376 seed consumption (Matsuda et al. 2019) which supports the hypothesis of a multiple emergence of  
377 the folivory. In addition, the whole-genome sequencing of the golden snub-nosed monkey  
378 (*Rhinopithecus roxellana*) revealed that Asian colobines have evolved early on an enhanced  
379 ability to derive energy from fatty acids and to degrade xenobiotics (Zhou et al. 2014), which  
380 would have directly improved their ability to digest seeds and at the same time facilitated the  
381 digestion of low-energy food such as lichens or leaves. Lastly, folivory is hypothesized to have  
382 evolved from seed consumption in many mammalian orders, including primates, rodents and  
383 marsupials (Cork 1996). Rumination (chewing after microbial pre-digestion into a forestomach)  
384 could have also evolved in artiodactyls in order to digest hard seeds too hard to break with the  
385 teeth, by directly swallowing them and softening them into the forestomach before re-chewing  
386 them, as proposed by Bodmer (1989) while studying the feeding behavior of the brocket deer  
387 (*Mazama americana*) in Amazonia. Further comparison is required in order to identify key

388 adaptations which would have enabled the convergent evolution of folivory in early colobines and  
389 other potential seed-eating mammals.

### 390 **Conclusions**

391 This work finds that dental microwear complexity within the genus *Mesopithecus* increased  
392 between MN11 and MN12 in southeastern Europe. This observed increase was more important in  
393 northern regions corresponding to present Bulgaria, which were then covered by savanna and open  
394 mixed forests, whereas in southern regions (notably Pikermi) corresponding to present Greece,  
395 there was no increase despite a more open biome. We interpret this result as a dietary niche shift  
396 towards a more challenging diet, with the likely inclusion of hard foods such as seeds or  
397 underground storage organs, especially in the northernmost populations of *M. pentelicus*. This  
398 ecological shift is concurrent with a change in dental topography, the molars of *M. pentelicus*  
399 showing lower slopes and sharpness scores compared to *M. delsoni*, which attests of its large scale  
400 occurrence, at least at the specific level.

401 While our results do not contradict the assumption that adaptation to folivory would have emerged  
402 from granivory in colobine monkeys, they show that *M. delsoni* was more likely to eat leaves  
403 during MN11 than *M. pentelicus* during MN12, albeit to a lesser extent than extant colobines. This  
404 indicates that colobine monkeys either evolved folivory before their dispersal to Eurasia, or re-  
405 evolved folivory in multiple occurrences, likely because of key adaptations to seed predation  
406 which would have been co-opted for the consumption of leaf-like foods. This may have included  
407 bilophodont molars, but also multi-chambered stomach, rumination strategy or physiological

408 adaptations such as enzymes improving the digestion of fatty acids and the degradation of  
409 xenobiotics.

410 This work illustrates how the analysis of the fossil record within a constrained temporal and  
411 geographic scale can give insights into the mechanisms underlying adaptation and  
412 macroevolution. Here, combining dietary estimates operating on populations at a large timescale,  
413 such as dental topography, with estimates operating on single individuals at a small timescale,  
414 such as dental microwear textures, allowed us to characterize change in behavior driven by  
415 environmental change, and how it ultimately resulted in the emergence of dietary adaptations. This  
416 multi-scale approach could be applied to multiple evolutionary discussions related to  
417 environmental change and how it can drive dietary evolution in terrestrial tetrapods.

418

## 419 **Material and methods**

### 420 *Material*

421 Dental microwear texture analysis: One hundred sixty nine extant specimens belonging to four  
422 African species of cercopithecines and seven of Asian and African colobines were considered. The  
423 colobines are represented by *Colobus guereza*, *C. polykomos*, *Piliocolobus badius* and  
424 *Semnopithecus entellus*, *Nasalis larvatus*, *Trachypithecus cristatus*, *T. auratus*. The  
425 cercopithecines are represented by *Lophocebus albigena*, *Cercocebus atys*, *Chlorocebus aethiops*

426 and *Erythrocebus patas*. The complete list of the specimens can be found in supplementary  
427 materials (Table S9).

428 Sixty six specimens of the extinct genus *Mesopithecus*, coming from Bulgarian and Greek late  
429 Miocene sites, were considered. Fifteen specimens are attributed to *Mesopithecus delsoni* from  
430 Ravin des Zouaves-5 (type-locality, Greece, N = 3) and to *Mesopithecus aff. delsoni* from  
431 Hadjidimovo (Bulgaria, N = 12). Ravin des Zouaves-5 is dated from MN11 (de Bonis et al. 1990)  
432 while Hadjidimovo is located at the end/second half of MN11 (Li and Spassov 2017; Spassov et  
433 al. 2018). Forty-six specimens are attributed to *M. pentelicus* from Pikermi (type-locality, Greece,  
434 N = 26), Kalimantsi (Bulgaria, N = 16), and Gorna Sushitsa (Bulgaria, N = 4; Spassov et al. 2019).  
435 Koufos (2009) considered specimens from Perivolaki (Greece, N= 4) and Vathylakkos-2 (Greece,  
436 N = 1) as intermediate forms between *M. delsoni* and *M. pentelicus*.

437 Dental topographic analysis: The skulls of twenty seven specimens were selected from the same  
438 species as the microwear sample. The list of the specimens can be found in supplementary  
439 materials (Table S2). Dental topography and especially dental relief and complexity can be greatly  
440 affected by dental wear (Ungar and Williamson 2000; Bunn and Ungar 2009; Pampush et al.  
441 2018; Li et al. 2020). In order to mitigate this effect, only the relatively unworn second molars of  
442 subadults were selected following previous works (Guy et al. 2013, 2015; Thiery et al. 2017)  
443 hence the limited sample size. Scans of extant specimens were combined with scans of molar row  
444 casts. In addition, nine specimens of the genus *Mesopithecus* coming from Bulgarian and Greek  
445 late Miocene sites were considered. Five previously investigated specimens (Thiery et al. 2017)  
446 are attributed to *M. pentelicus* from Pikermi (type-locality, Greece), two specimens from Azmaka  
447 (Bulgaria) which are under study will be considered here as *M. cf. pentelicus*, one specimen is

448 attributed to *M. pentelicus* from Gorna Sushitsa (Bulgaria; Spassov et al. 2019) and one to *M. aff.*  
449 *delsoni* from Hadjidimovo (Bulgaria).

#### 450 **Methods**

451 Dental Microwear Texture Analysis: Methods for dental microwear texture analysis have been  
452 discussed in detail by Scott et al., (2006, 2012; see also Calandra and Merceron 2016). Molars  
453 were cleaned with cotton swabs soaked in alcohol in order to remove grit, dust, and glue residues.  
454 After cleaning, dental impressions were made with a silicone material (polyvinyl siloxane ISO  
455 4823, President Regular Body, Coltène-Whaledent Corp.). Scans were made directly from the  
456 silicon molds with the "TRIDENT" Leica DCM8 white-light scanning confocal microscope (Leica  
457 Microsystems) with a  $\times 100$  long-distance lens (Numerical Aperture=0.90; working  
458 distance=0.9mm), housed at the PALEVOPRIM laboratory. For each specimen, one Phase II facet  
459 (Facets 9 to 13) was scanned on either the upper or lower molars (M1, M2, M3). The scanning  
460 process generates  $350 \times 264 \mu\text{m}$  point clouds with a vertical sampling lower than  $0.002 \mu\text{m}$  and a  
461 lateral sampling (x, y) of  $0.129 \mu\text{m}$ . The resulting surfaces were then imported in the LeicaMap  
462 software (Mountain technology, Leica Microsystems) to remove aberrant peaks with automatic  
463 operators including a morphological filter. The surfaces were also leveled and a  $200 \times 200 \mu\text{m}$  area  
464 was selected and saved as a Digital Elevation Model (Merceron et al. 2016).

465 Complexity (Asfc), heterogeneity of complexity (HASfc) and anisotropy (epLsar) were calculated  
466 with Toothfrax software, while textural fill volume (Tfv) was calculated with Sfrax software  
467 ([www.surfract.com](http://www.surfract.com)). Hasfc is obtained by subdividing the surface to a  $9 \times 9$  grid, hence 81 cells,  
468 in which texture complexity is calculated. Textural fill volume is the result of an algorithm that

469 fills a surface with square cuboids of different volumes (10 and 2  $\mu\text{m}$  - side cuboids). All DMTA  
470 data can be found in supplementary materials (Table S6-9). Inter-group differences were tested  
471 after Box-Cox transformation using an ANOVA (Table S7), followed by post-hoc LSD-test (Table  
472 S8). Only the most discriminant variable was retained to be compared with topographic variables  
473 (Asfc, Table. 2; see supplementary material for details on the evaluation of the discriminant power  
474 of variables).

475 Dental topography: Outer enamel surfaces were scanned using high-resolution microtomography  
476 at the Centre de Microtomographie de Poitiers. Dental surfaces were segmented and exported as  
477 three-dimensional polygonal meshes using Avizo. The meshes were then oriented, smoothed and  
478 re-tesselated using Geomagic Studio as in Guy et al., (2015) except that surfaces were re-  
479 tessellated to an amount of 10,000 triangles instead of 50,000. Afterwards, the surfaces have been  
480 cropped above the lowermost point of the occlusal basin (Ungar and Williamson 2000; Bunn and  
481 Ungar 2009).

482 Topographic variables were measured in R 4.0.0 (R Core Team 2021) using the beta version of the  
483 package doolkit 0.9.9. Among the variables currently supported by the package, we compared  
484 three-dimensional area, occlusal patch count rotated 'OPCR' (Wilson et al. 2012; Guy et al. 2013),  
485 Dirichlet normal energy 'DNE' (Bunn et al. 2011), as well as all relief estimates presented in  
486 Thiery et al., (2019), notably the average slope (Ungar and Williamson 2000; Bunn and Ungar  
487 2009), the relief index 'RFI' (Ungar and Williamson 2000) and the linearized relief index (Boyer  
488 2008). We also use an original estimate of tooth sharpness, the area-relative curvature 'ARC' (Guy  
489 et al., 2017).

490 In contrast with dental microwear data, the sample size for the topographic analysis was too small  
491 for performing a parametric test to compare species. Therefore, we compared the ability of  
492 topographic variables to separate colobine monkeys from other cercopithecids using Wilcoxon's  
493 rank-sum test (Table 2). Only the most discriminant variables were retained for comparisons with  
494 microwear variables (average slope and average ARC, Fig. 2A-B; see supplementary materials for  
495 details on the evaluation of the discriminant power of variables). Average ARC and average slope  
496 are correlated (Pearson's  $r = 0.8$ ,  $p\text{-value} < 0.001$ ; see supplementary materials: Table S4). Other  
497 variables were correlated, such as RFI, LRFI and DNE, but since they measure the same aspect as  
498 slope and ARC, they were only represented for fossil taxa (Fig. 3B, 3C, 3E). In contrast, variables  
499 which were not correlated to ARC nor slope, such as OPCR (see supplementary materials: Fig. S2;  
500 Table S3-S4), were not able to discriminate colobines from other cercopithecids. Nevertheless,  
501 OPCR was represented for fossil taxa because it is a widely used variable (Fig. 3F).

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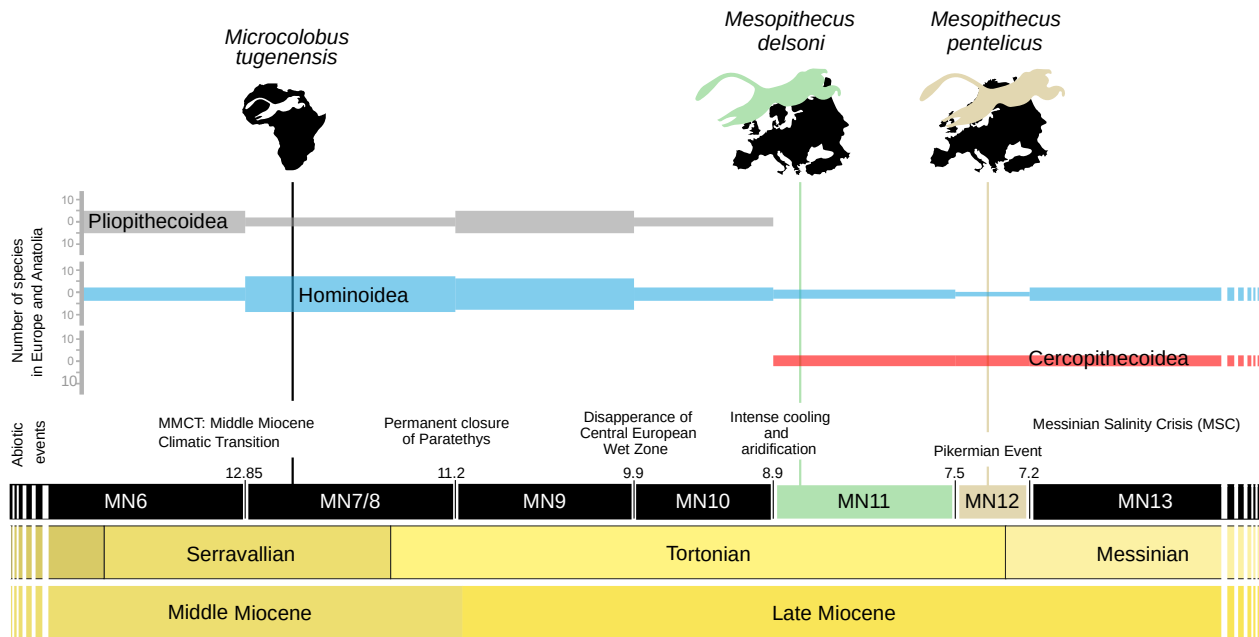
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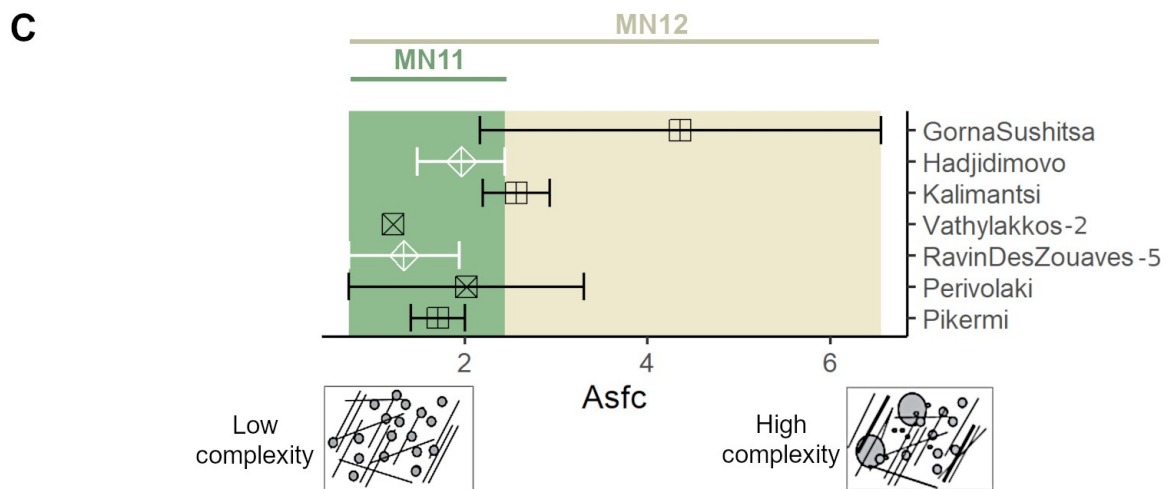
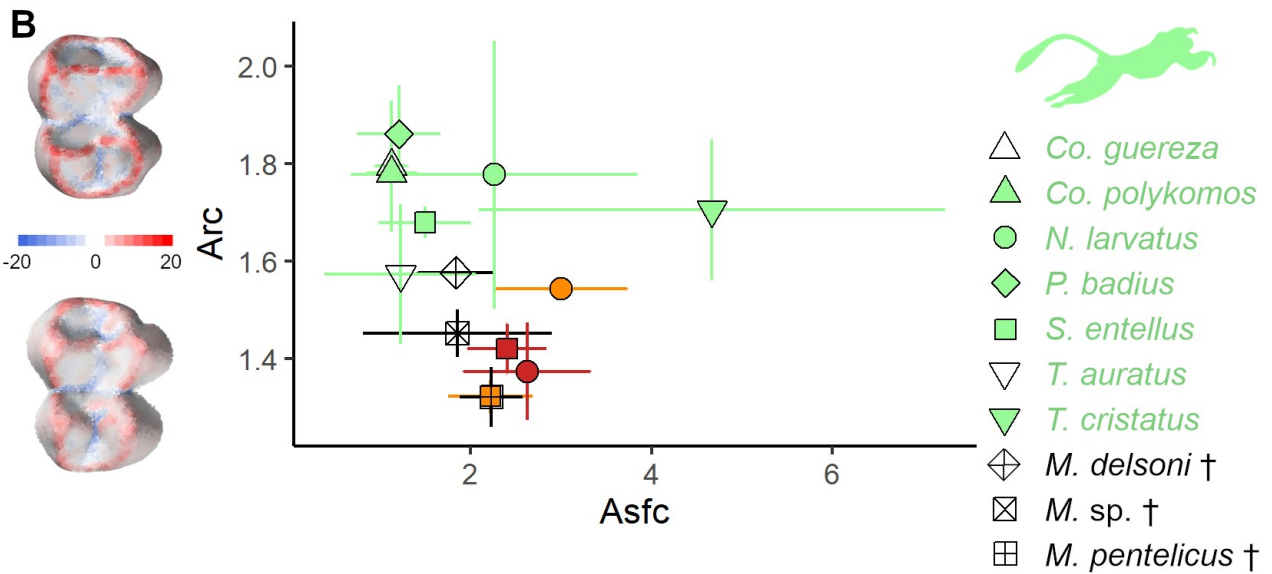
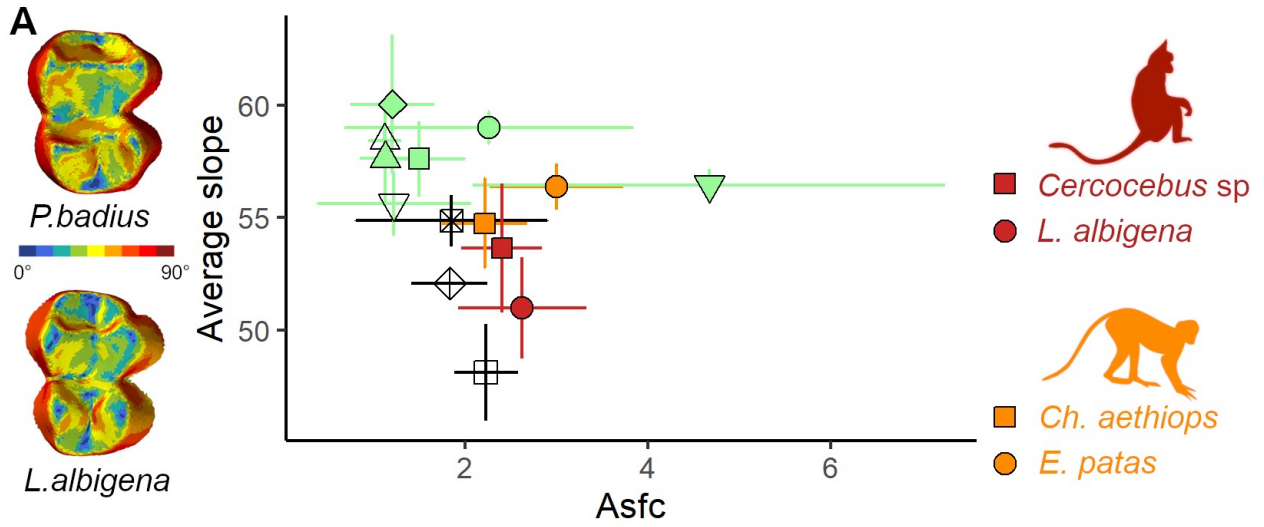
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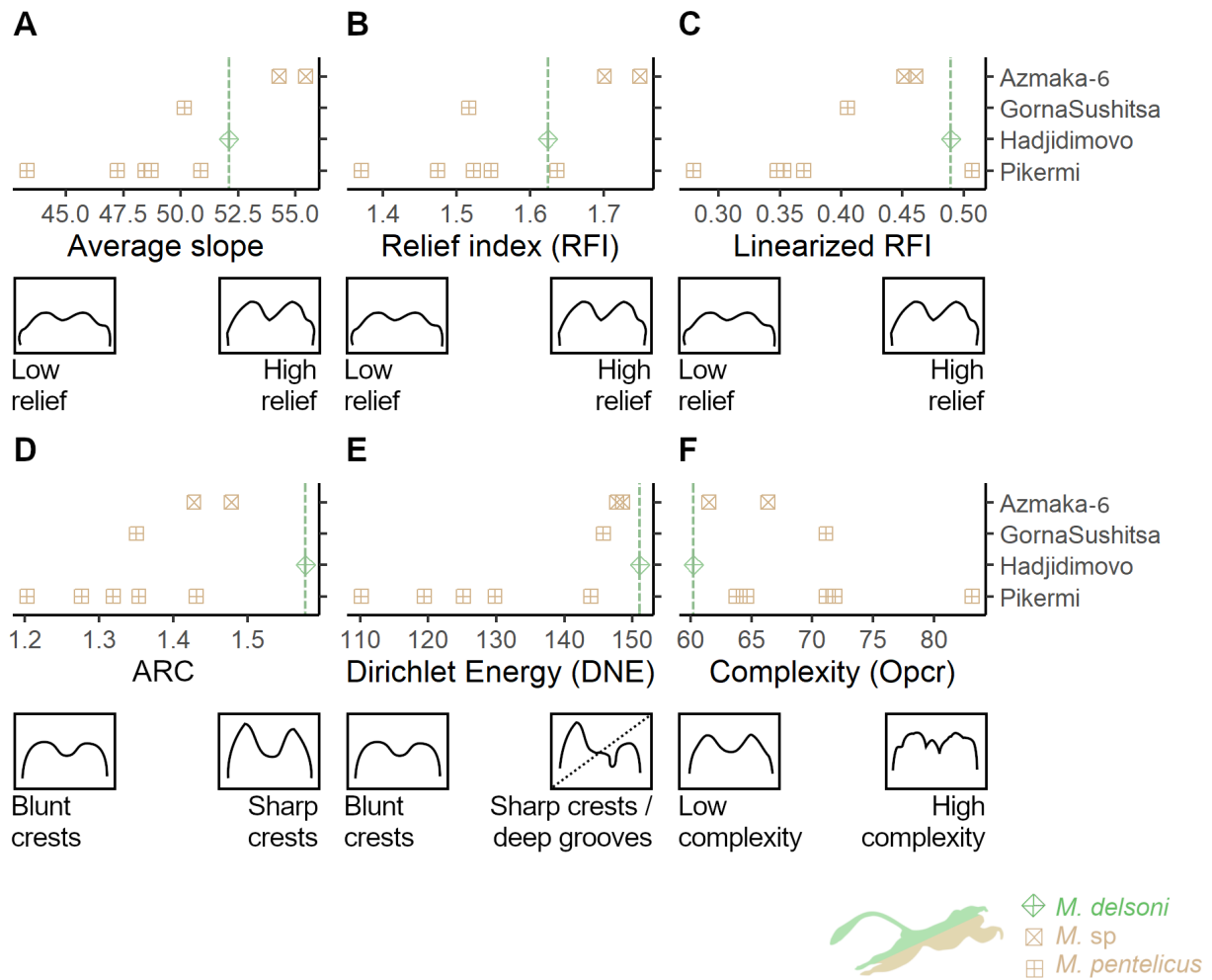
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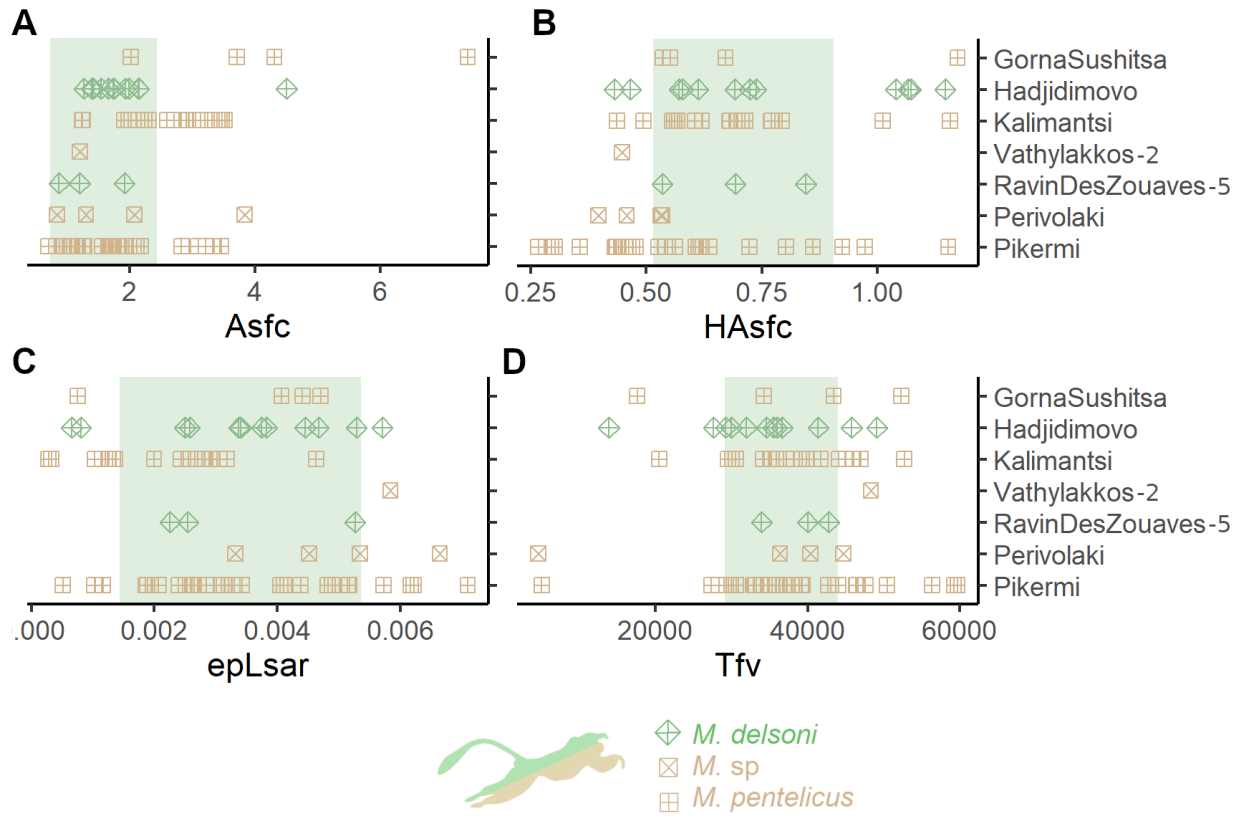
503 Figure 1. Chronology of the successive primate radiations that took place in western Eurasia  
 504 during the Miocene (see Table S1). The progressive disappearance of the Central European Wet  
 505 Zone (Utescher et al. 2011) coincides with a decrease in biodiversity of European pliopithecoids  
 506 (gray) and hominoids (blue). Although the first part of the evolutionary history of cercopithecids  
 507 took place in Africa, they appear in the fossil record of Europe during the late Miocene with the  
 508 genus *Mesopithecus* (red). This study compares *M. delsoni* and *M. pentelicus* specimens found in  
 509 the Balkans within MN11 and MN12 Mammal Neogene zones (Guérin, 1980, 1982), with  
 510 populations from the MN12 sharing features with both *M. delsoni* and *M. pentelicus*.  
 511



513 Figure 2. The dietary niches of *M. delsoni* and *M. pentelicus* compared to extant catarrhines.  
514 *Mesopithecus* sp. groups specimens that are similar to *M. pentelicus* but whose taxonomic  
515 affinities are not clear (*M. cf. pentelicus* from Azmaka and *M. delsoni/pentelicus* from Perivolaki  
516 and Vathylakkos-2). Data points correspond to specific means with error bars marking confidence  
517 intervals (standard error of the mean with  $\alpha = 0.05$ ). (A) Bivariate plot of the complexity of  
518 enamel wear facets (Asfc) versus molar average slope. (B) Bivariate plot of Asfc versus average  
519 molar area-relative curvature (ARC). (C) Asfc of extinct specimens ordered by site, from the  
520 northernmost (Gorna Sushitsa) to the southernmost location (Pikermi).



521 Figure 3. Dental topographic analysis of *Mesopithecus* from the Balkans. Variables are ordered by  
 522 site, from the northernmost (Gorna Sushitsa) to the southernmost location (Pikermi). Dental relief  
 523 estimated from (A) average slope; (B) relief index sensu Ungar and Williamson (2000); and (C)  
 524 relief index sensu Boyer (2008); dental sharpness estimated from (D) average area-relative  
 525 curvature (ARC) and (E) Dirichlet normal energy (DNE). (F) Complexity estimated from  
 526 Orientation Patch Count Rotated (OPCR).



527 Figure 4. Dental microwear texture analysis of *Mesopithecus* from the Balkans. Variables are  
 528 ordered by site, from the northernmost (Gorna Sushitsa) to the southernmost location (Pikermi).  
 529 (A) Textural complexity (Asfc). (B) Heterogeneity of Asfc (HASfc). (C) Anisotropy (epLsar). (D)  
 530 Textural fill volume (Tfv). The green area shows the confidence interval for *M. delsoni* values  
 531 (standard error of the mean with  $\alpha = 0.05$ ).

532 Table 1. Results of post hoc LSD tests on texture parameters obtained from Phase II facets of  
 533 extant cercopithecids.

	<i>L.a.</i>	<i>C.a.</i>	<i>Ch.a.</i>	<i>E.p.</i>	<i>Co.g.</i>	<i>Co.p.</i>	<i>P.b.</i>	<i>N.l.</i>	<i>S.e.</i>	<i>T.a.</i>	<i>T.c.</i>
<i>L. albigena</i>	■										
<i>C. atys</i>	Hasfc	■									
<i>Ch. aethiops</i>	Hasfc		■								
<i>E. patas</i>			Hasfc	■							
<i>Co. guereza</i>	Asfc epLsar Tfv	Asfc epLsar Tfv	Asfc epLsar Tfv	Asfc epLsar Tfv	■						
<i>Co. polykomos</i>	Asfc epLsar Tfv	Asfc epLsar Tfv	Asfc, epLsar Tfv	Asfc epLsar Tfv		■					
<i>P. badius</i>	Asfc epLsar	Asfc epLsar	Asfc epLsar	Asfc epLsar		Tfv	■				
<i>N. larvatus</i>		Hasfc	Hasfc	Asfc	epLsar	EpLsar Tfv		■			
<i>S. entellus</i>	Asfc	Asfc		Asfc					■		
<i>T. auratus</i>	Asfc epLsar	Asfc epLsar	Asfc epLsar	Asfc epLsar		Tfv		Asfc epLsar		■	
<i>T. cristatus</i>			Hasfc		Asfc epLsar Tfv	Asfc epLsar Tfv	Asfc epLsar	Asfc	Asfc	Asfc epLsar	■

534 Only variables with a significant P-value for the LSD test are shown ( $\alpha = 0.05$ ). Comparison  
 535 between extant colobines and cercopithecines is highlighted in grey. See supplementary materials  
 536 (Table S8) for more details.

537 Table 2. Ability of topographic variables to separate colobines from other cercopithecids,  
538 evaluated using Wilcoxon's rank-sum test. Variables classified from the most discriminant (top) to  
539 the least discriminant (bottom).

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Wilcoxon		
Variable	U	P-value
Average Arc	2	0.000
Average slope	15	0.000
Rfi	21	0.000
Dne	41	0.014
Lrfi	49	0.043
Area	50	0.048
Opcr	81	0.645

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540