Browsing and non-browsing extant and extinct giraffids Evidence from dental microwear textural analysis

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Abstract:

Today, the family Giraffidae is restricted to two genera endemic to the African continent, *Okapia* and *Giraffa*, but, with over ten genera and dozens of species, it was far more diverse in the Old World during the late Miocene. We attempt to describe here how several species may have shared feeding resources in the Eastern Mediterranean. Dietary preferences were explored by means of Dental Microwear Textural Analysis in combination with estimation of body mass and the maximum height at which the various species were able to browse.

One of our main results concerns the modern okapi, *Okapia johnstoni*. It is a forest dweller usually regarded as a browser, but we show that it might also forage on tough plants, possibly herbaceous monocots. Such feeding habits including portions of herbaceous monocotyledons were also found for some extinct species, especially the genera *Samotherium* and *Palaeotragus*. *Palaeogiraffa* shows a contrasted pattern: the specimens of *P. pamiri* from a site in Thrace were leaf-dominant browsers whereas those belonging to *P. major* and *P. macedoniae* from the Axios valley in Greece ingested herbaceous monocotyledons. *Helladotherium duvernoyi*, the only sivatheriine analyzed here is described as a leaf-dominant browser. The giraffine *Bohlinia attica* also falls within the leaf-dominant browser category but could browse on higher foliages than *H. duvernoyi*. On the whole, the reconstructed diets confirm the relationship between more grazing habits and smaller premolars, but not with higher dental crown height.

Keywords: Tooth, Ruminant, Neogene, Diet, Ecology

1. Introduction

Today, giraffids are poorly diverse with only two genera, *Okapia* and *Giraffa* (Agaba et al., 2016), both endemic to the African continent. The okapi *Okapia johnstoni* is endemic to the north east of the Democratic Republic of Congo in the Congo Basin. There, the okapi is confined to dense equatorial forest, which explains why its anatomical description in a scientific journal dates back only to the early 20th century. *Okapia johnstoni* is unknown as a fossil, but its discovery has generated several hypotheses regarding its relationships with the giraffe and the many species of extinct giraffids (Colbert, 1938; Thenius, 1992). The modern giraffe has a wide range of distribution in subsaharan Africa. The genus dates back to the early Pliocene. A large part of the evolutionary history of the Giraffidae did not take place in Africa but in Eurasia during the Neogene (Solounias et al., 2010). With over 10 genera and dozens of named species that can be conveniently grouped in three subfamilies (Sivatheriinae, Giraffinae, Palaeotraginae), the family reached its highest diversity during the late Miocene. They share with modern taxa a small set of synapomorphies such as large body size, bilobate canine, and a molariform fourth premolar, but their skin-covered cranial appendages are not exclusive to the family (Geraads, 1986). A phylogenetic analysis of giraffids based upon new material from the late Miocene of Spain confirmed the monophylies of the two subfamilies Sivatheriinae and Giraffinae. However, the Sivatheriinae appear as the sister-group of the genus *Samotherium* and are thus rooted within the Palaeotraginae, whose paraphyletic status is thus emphasized (Ríos et al., 2017, 2016).

The present study aims at determining the feeding ecology of the extinct giraffids from the late Miocene of Eastern Mediterranean in regard to their differences in morphology mirroring the phylogeny. We use dental microwear textural analysis (DMTA, hereafter) to specify the dietary habits. First, we discuss the relations between dietary habits and dental microwear textural parameters on extant species of ruminants. This allows us to interpret and

discuss the dental microwear textural parameters of species with unknown feeding habits. Before applying these parameters to extinct species of giraffids to identify their feeding type, we question the dietary habits of the present-day okapi, a species assumed to be a browser on the basis of a single field ecological survey (Hart and Hart, 1989). Second, we discuss the dietary reconstruction of these extinct species in relation to the morphology, and notably the body mass estimates and the length of the metacarpal bone, the latter feature being a proxy to assess the maximum height at which a given species can access the food resources. We may expect that smaller species with shorter forelimbs are more prone to include herbaceous vegetation than large species of giraffids. This permits us to evaluate the ecological niche partitioning when species co-occurred in the fossil record, suggesting an overlap of their home-range, such as at Pikermi (Greece) and Hadjidimovo (Bulgaria). Besides, considering that none of these giraffids displayed post canine hypsodont cheekteeth, we may expect that none of these giraffids included herbaceous vegetation in its diet. However, an early pioneer study on dental abrasion (Solounias et al., 1988) challenged the hypothesis of browsing habits among all extinct giraffids. These authors depicted *Samotherium boissieri*, a late Miocene giraffid from Samos Island (Greece) as a mixed feeding species incorporating silica-bearing herbaceous monocotyledons in its diet. Previous dental wear analysis on material from historical collections of Samos and Pikermi also found out differences between giraffids species (Danowitz et al., 2016; Solounias, 1988; Solounias et al., 2000). We here go further in significantly increasing the sample with new material from northern Greece, Bulgaria and Turkey.

2. Material and Methods

2.1. Material

The dental microwear textures of extinct giraffids are compared with those of present-day species of ruminants with known differences in diet (housed in the following museum and institutions: AMNHS Aegean Museum of Natural Histry of Samos, Greece; NHMEU Natural History Museum of the Ege University of Izmir, Turkey; NHML Natural History Museum of London, UK; NHMB Naturhistorisches Museum Basel, Switzerland; SMNS Staatliches Museum für Naturkunde Stuttgart, Germany; SMNK Staatliches Museum für Naturkunde Karlsruhe, Germany; SNG Senckenberg Museum, Franckfort, Germany; UP Palevoprim lab, University of Poitiers, France; KNM National Museums of Kenya, Nairobi, Kenya; MNHN Muséum National dôHistoire Naturelle, Paris, France; MRAC Central African Royal Museum of Tervuren, Belgium; FSL Collection de Géologie de la Faculté des Sciences de l'Université de Lyon, France; AM-NHNMS Assenovgrad Museum; a division of the National Museum of Natural History of Sofia, Bulgaria). Instead of selecting a large dataset covering the whole spectrum of feeding habits, we chose here to focus on four taxa representing four different dietary poles (Table 1). These taxa are the hartebeest (*Alcelaphus buselaphus*, grazer; Estes, 1991; Gagnon and Chew, 2000), the red deer (*Cervus elaphus*, generalist; Gebert and Verheyden-Tixier, 2001), the giraffe (*Giraffa* sp., leaf-dominant browser; Estes, 1991; Leuthold, 1978; Parker et al., 2003) and the yellow-backed duiker (*Cephalophus silvicultor*; fruit-dominant browser; Estes, 1991; Gagnon and Chew, 2000; Gauthier-Hion et al., 1980; Lumpkin and Kranz, 1984). These ruminants share a common occlusal molar pattern. A fifth modern species is included in this study: *Okapia johnstoni*, the okapi, assumed to be a browser (Hart and Hart, 1989).

The taxonomy of the modern giraffe is currently under debate among zoologists. Several subspecies of *Giraffa camelopardalis*, differing in their horns and coat ornamentations had been identified (Brown et al., 2007; Groves and Grubb, 2011; Hassanin et al., 2007; Kingdon et al., 2013; Wilson and Reeder, 2005) but a recent study based on multi-

111 locus DNA analysis recognizes the existence of four species (Fennessy et al., 2016): *G.*
112 *giraffa* (southern giraffe), *G. tippelskirchi* (Masai giraffe), *G. reticulata* (reticulated giraffe)
113 and *G. camelopardalis* (northern giraffe). The geographical distribution of the giraffe and its
114 genetic diversity were even higher until the Holocene since subfossil remains and glyph
115 representations in caves and rock shelters attest to its presence 4,000 years ago in north-
116 western Africa and along the Nile Valley (Le Quellec, 1999). Because of these taxonomic
117 uncertainties, we made the choice to group all modern giraffes under *Giraffa* sp. Our purpose
118 here is to have an ecologically homogeneous milestone to represent the leaf-dominant
119 browsing ecospace. None of the specimens of modern species used in this study were captive
120 before death, they were shot in the wild decades ago.
121 The fossil specimens belong to six genera: *Bohlinia*, *Helladotherium, Palaeogiraffa,*
122 *Palaeotragus* and *Samotherium*. The material comes from a dozen upper Miocene (Vallesian
123 and Turolian) localities in Greece, Bulgaria, Turkey, Afghanistan, Iran and Tunisia (Table 1,
124 Fig. 1). *Helladotherium duvernoyi* comes from the turolian faunas of Southern Bulgaria
125 (Geraads et al., 2005; Spassov, 2002), continental Greece (Kostopoulos et al., 1996;
126 Solounias, 1981), and southern Tunisia (but the identification there is less secure). The
127 specimens attributed to *Bohlinia attica* (Giraffinae) come from Nikiti-1 in Greece dated to
128 close to the Vallesian-Turolian transition (Kostopoulos, 2016) and from Kalimantsi (K),
129 Bulgaria (Geraads et al., 2005). Among the Palaeotraginae, the specimens assigned to
130 *Samotherium major* come from turolian sites: Mytilini-A, Mytilini-B (MTLA and MTLB; two
131 sites from the Mytilini ravines in Samos Island, Greece; Kostopoulos, 2009), Vathylakkos-3
132 (VAT) in the Axios Valley (Geraads, 1978), Salihpasalar (MYS) and ķerefköy-1 (MYSe-1) in
133 the Muĵ la Yataĵ an Basin of Turkey (Kaya et al., 2012), and from the Turolian of
134 Mahmutgazi (MA) in Turkey (Sickenberg, 1975). The specimens of *S. boissieri* do not come
135 from recent excavations but belong to historical collections from Samos for which site

provenance is not guaranteed (see Koufos, 2009 for a historical review of the paleontological surveys and studies in Samos). A single specimen attributed to *Samotherium neumayri* comes from Maragha (MAR), Iran (Solounias and Danowitz, 2016, as *Alcicephalus neumayri*). The genus *Palaeotragus* is represented by two taxa. A single specimen of *Palaeotragus rouenii* from the vallesian site of Ravin de la Pluie (RPl; Geraads, 1978; Koufos, 2006) has been analyzed but the species is widespread and abundant in the turolian sites of Hadjidimovo (HD; Geraads et al., 2005), Dytiko-3 (DIT), Pikermi (PIK; Koufos, 2006), Mytilini-B (MTLB; Kostopoulos, 2009), ķerefköy-1 and ķerefköy-2 (MYSe-1 and MYSe-2; Kaya et al., 2012) and Molayan (MOL; Afghanistan; Brunet and Heintz, 1983; Sen, 1998). Specimens that belong to *Palaeotragus coelophrys* or to a closely related species come from the vallesian sites of Ravin de la Pluie (RPl) and Pentalophos (PNT) in Greece (Koufos, 2006) and from Maragha (MAR) in Iran (Mecquenem, 1924; Solounias and Danowitz, 2016). *Palaeogiraffa pamiri* comes from the vallesian sites of Küçükçekmece (KUC) in Turkish Thrace (Kostopoulos and Sen, 2016). The only specimen of *Palaeogiraffa major* comes from the vallesian site of Ravin de la Pluie (Koufos, 2006). A third species of *Palaeogiraffa, P. macedoniae* is known from the vallesian site of Pentalophos (PNT), also in the Axios Valley (Koufos, 2006). Ríos *et al.* (2016, 2017) synonymized *Palaeogiraffa* and *Decennatherium* (a genus assumed to be the sister group of a clade composed notably by sivatherines and *Samotherium major* and *S. boissieri*), a view which is not shared by Bonis & Bouvrain (2003). Pending agreement on this taxonomic issue, we keep using *Palaeogiraffa* as genus name for specimens from the vallesian sites from Axios, in northern Greece and from Yulaflē in Turkish Thrace.

For some of the species, the number of specimens is large enough (N=>10) to generate robust interpretations regarding their dietary habits. However, for several taxa, the number is moderate (5=<N<10) and even low (5<N). Taking into account that dental microwear textures

161 reflect the dietary bolus from the last few weeks, one might fear that the signal from such
162 small samples is meaningless, but Purnell *et al.* (2012) have shown that significant differences
163 in textural parameters can be detected even for small samples (N<5) of fishes (see also
164 Purnell et al., 2013). Besides, the analysis of several scans per individual, as proposed by
165 Purnell and Darras (2016) and as done in the present study, mitigates the effects of the small
166 sample size..
167
168 *2.2. Methods*
169 DMTA is a method quantifying tooth abrasion (for detailed reviews of intra- and inter-
170 observer errors, see DeSantis et al., 2013; Galbany et al., 2005; Grine et al., 2002;
171 Mihlbachler et al., 2012; Calandra and Merceron, 2016; Mihlbachler and Beatty, 2012; Scott,
172 2012; Scott et al., 2006) . Tooth wear reflects individual senescence and physical properties of
173 foods; thus, it is correlated with the availabilities of food resources and can be used to explore
174 niche partitioning among sympatric species of mammals (Calandra and Merceron, 2016).
175 From the scale of a whole tooth to the micrometric scars on dental facets, differences in
176 dietary preferences are mirrored by tooth wear. DMTA has proved to be a particularly useful
177 methodology free of (inter- and intra-)observer measurement errors at least at the analytic step
178 (for detailed reviews of intra- and inter-observer errors, see DeSantis et al., 2013; Galbany et
179 al., 2005; Grine et al., 2002; Mihlbachler et al., 2012; Mihlbachler and Beatty, 2012) in
180 assessing diets of fossil as well as modern taxa (Calandra and Merceron, 2016).
181 The analysis was performed preferentially on second upper or lower molars (Figs. 2
182 and 3). However, third or first molars were considered when the second molars are weathered,
183 too much worn or too recently erupted. Following standard procedures, replicas of dental
184 facet were produced with a silicone (medium consistency) polyvinylsiloxane (Coltène
185 Whaledent, President Regular Body, ISO 4823). Scans (320 x 280 µm) were produced on

186 replicas using a surface profilometer confocal DCM8 Leica Microsystems with a 100× lens
187 (Leica Microsystems; NA = 0.90; working distance = 0.9 mm) at the Palevoprim, CNRS and
188 University of Poitiers, France. Lateral resolution is 0.129 µm and vertical spacing is 0.002
189 µm. Up to four surfaces (140 × 100 µm; 1088 × 776 pixels) were generated from the original
190 scans and saved as .Plµ files (Figs. 2 and 3; details on surface preparation are given in
191 Merceron et al. 2016).

192 The DMTA was performed using the Scale-Sensitive Fractal Analysis using Toothfrax
193 and Sfrax software (Surfract, http://www.surfract.com) following Scott et al. (2006). The
194 individual values of surface parameters for extinct and extant species are given in Appendix 1.
195 Three variables were extracted from the surface: complexity (Asfc), anisotropy (epLsar), and
196 heterogeneity of complexity (HAsfc calculated with a 9-cell mesh; Table 1). Scott et al.
197 (2006) detailed the variables used here. Complexity (Asfc or Area-scale fractal complexity) is
198 a measure of the roughness at a given scale. Anisotropy (epLsar or exact proportion of length-
199 scale anisotropy of relief) measures the orientation concentration of surface roughness.
200 Heterogeneity of complexity (HAsfc or heterogeneity of area-scale fractal complexity),
201 quantifies the variation of complexity within scan. All of these three textural parameters are
202 dimensionless (see Scott et al., 2006). Scanned surfaces display dental microwear but also, for
203 some of the teeth, structural reliefs such as growth lines or perikemata reflecting the
204 intersection between Retzius lines with the enamel surface. One may argue that such enamel
205 structural relief influences the parameter values, and notably the anisotropy of the dental
206 microwear textures. Although the perikemata are more or less preferentially orientated, they
207 do not interfere with the anisotropy calculation, because the height amplitudes of these
208 perikemata are lower than topographic variations due to the microwear on enamel surfaces
209 (Fig. 4).

As the distribution of textural parameters violates conditions for parametric tests, variables were rank-transformed before analysis (Conover and Iman, 1981; Sokal and Rohlf, 1969). One-way factorial ANOVAs with post-hoc tests for each parameter were used to determine the sources of significant variation (Tables 2 and 3). Any potential difference was then highlighted using the combination of the conservative HSD test (Tukeyôs Honest Significant Differences) together with the less conservative LSD test (Fisherôs Least Significant Differences).

Body mass (calculated according Scott, 1990) and height at the withers are two body traits that can be used in combination with DMTA to explore the partitioning of food resources between sympatric species. Here we use metacarpal length as a proxy of height at the withers and the height at which a species can gather its resources. This certainly suffers exceptions, but the length of the metacarpals is a good proxy for the height at which the animal can browse (for a given metacarpal length, if the animal is heavier, height at the withers will be higher, but neck will be shorter). We also noted classic parameters of dental morphology, notably the premolar/molar ratio that is distinctly lower for hyper-grazing bovids (Table 4).

3. Results and Discussion

3.1. Dental microwear textures and diet

The four modern species used as milestones differ from each other in all three surface textural parameters (Tables 1-3). The hartebeest (*Alcelaphus buselaphus*), a grazing alcelaphine, has the lowest enamel surface complexity (Asfc) and the highest anisotropy (epLsar) of dental microwear textures (Tables 1 and 3; Figs. 2 and 4). The yellow-backed duiker (*Cephalophus silvicultor*) displays the highest complexity (Asfc) and low values of anisotropy (epLsar) whereas the giraffe (*Giraffa* sp.) has the lowest anisotropy (epLsar) and

235 an intermediate complexity (Asfc) between the hartebeest and the yellow-backed duiker
236 (Tables 1 and 3; Figs. 2 and 5). The differences in dental microwear textures between the two
237 browsing species reflect the ingestion of fruits and seeds by the duiker (Ramdarshan et al.,
238 2016). The dental microwear textures (intermediate complexity and anisotropy) of the red
239 deer (*Cervus elaphus*) reflect its mixed feeding habits that involve both browsing and grazing
240 (Tables 1 and 3; Figs. 2 and 5). The third variable, heterogeneity of complexity (HAsfc),
241 provides a significant complement. The giraffe and the hartebeest foraging mostly on a
242 homogeneous source of vegetation (tree leaves and herbaceous monocotyledons, respectively;
243 Estes, 1991, Gagnon and Chew, 2000; Leuthold, 1978; Parker et al., 2003) over long time
244 span (over a year) have lower values than the red deer and the yellow-backed duiker whose
245 diets are mechanically diverse and variable from a day to another or from a season to another
246 (Tables 1 and 3; Figs. 2 and 5; Estes, 1991; Gebert and Verheyden-Tixier, 2001; Gagnon and
247 Chew, 2000; Gauthier-Hion et al. 1980; Lumpkin and Kranz, 1984).
248 The modern okapi (*Okapia johnstoni*) has a wide distribution across the dental
249 microwear textural ecospace. It differs from the giraffe in having higher anisotropy (epLsar)
250 and from the yellow-backed duiker in having lower complexity (Asfc; Tables 1 and 3; Figs. 3
251 and 5). The okapi also differs from the hartebeest and the giraffe in having higher
252 heterogeneity of complexity (HAsfc). It does not differ from the red deer when the two most
253 discriminating variables (Asfc and epLsar) are considered (Tables 1 and 3; Figs. 3 and 5).
254 These results for the present-day okapi assumed to be a browser can be discussed in light of
255 the ecological data. Hitherto, only one single study dealt with the feeding ecology of the okapi
256 in the wild (Hart and Hart, 1989). It was conducted at Epulu, Ituri forest, a lowland forest
257 located at the far north eastern of the Congo basin. The authors tracked eight collared
258 individuals for several months and recorded from direct observations browse signs on
259 vegetation but only those ranging from 0.5 to 2.0 meters in height because ñ*this is the forest*

*layer most frequently browsed by okapi*ò (Hart and Hart, 1989: 35). There is indeed no record regarding lower vegetal layers. Hart and Hart (1989) identified shade- and light-tolerant plant species, all of them being dicotyledonous trees or bushes, constituting the staple food spectrum of the okapi. However, one of these two authors from the pioneer study mentions in Kingdon et al. (2013: in vol. VI, p. 110-115) that herbaceous monocotyledons are part of the okapi diet but does not provide details regarding their abundance. Hart and Hart (1989) had actually made mention that the okapi favors tree-fall gaps where it leaves the highest density of browse signs. These tree-fall gaps are also hotspots of biodiversity in the Central African forest where the herbaceous vegetation (mostly monocotyledons) reaches its highest diversity and density. These plant resources are known to be critical in dense forested habitats for other mammals such as buffaloes (Blake, 2002), gorillas, and pygmy chimpanzees (Blake et al., 1995; Malenky and Wrangham, 1994; Williamson et al., 1990). For instance, these apes feed on herbaceous stems (sometimes only the soft inner pith) of monocotyledonous plants such as Marantacea and Zingiberacea (Malenky and Wrangham, 1994; Williamson et al., 1990; Wrangham et al., 1991). Monocotyledonous plants have generally higher silica content than dicotyledonous plants (Hodson et al., 2005). Besides, the herbaceous stems that are eaten are tougher than most fruits(Elgart-Berry, 2004). Therefore, on the basis of the dental microwear textures of the okapis analyzed in the present study and the information provided by Hart and Hart (1989) and Hart in Kingdon et al. (2013), we hypothesize that the okapi does include some terrestrial herbaceous vegetation in its diet, especially when its home range overlaps tree fall gaps. Our hypothesis needs to be tested in the future through alternative direct or non direct dietary proxies and new material. It is worth mentioning that Clauss et al. (2006) had described the digestive tract of two captive okapis as similar to that of modern selective browsers with the exception that the parotid glands were found to be small, a feature shared with ruminants feeding on monocotyledons.

All fossil giraffids but *Samotherium boissieri* (and the only specimen of *Palaeogiraffa major*, see Table 1) significantly differ from the grazing hartebeest in having either higher complexity (Asfc) or lower anisotropy (epLsar) or the combination of the two conditions (Tables 2 and 3; individual values are provided in table S1 in supplementary material). Like the modern giraffe, *Helladotherium duvernoyi* has lower anisotropy (epLsar) than the red deer and the hartebeest, and lower complexity (Asfc) than the yellow-backed duiker; it also has lower values in heterogeneity of complexity (HAsfc) than the red deer and the duiker, supporting a monotypic diet for this sivatheriine (Tables 1 and 3; Figs. 3 and 5; table S1). There is little doubt that *Helladotherium* (N= 15) was a leaf-dominant browser. The five specimens of *Bohlinia attica* all have low values of both anisotropy (epLsar) and complexity (Asfc) suggesting that these individuals fed on soft browse (Tables 1 and 3; Figs. 3 and 5; table S1). The specimens of *Palaeogiraffa pamiri* from Turkish Thrace show low values in all three textural parameters (Tables 1 and 3; Figs. 3 and 5; table S1), showing that they were undoubtedly leaf-dominated browsers. By contrast, *Palaeogiraffa macedoniae* and the specimen of *P. major* from the Axios Valley sites in northern Greece display a sharply different pattern (Tables 1 and 3; Fig. 3; table S1). They have higher anisotropy (epLsar) than the sample from Thrace, the modern giraffe and the yellow-backed duiker. When complexity (Asfc) is also considered, such dental microwear textures suggest mixed feeding habits for *Palaeogiraffa* from the lower Axios Valley (Tables 1 and 3; Fig. 5; table S1). One may argue that differences in windblown dust deposit on vegetation could be the key factor controlling differences in dental microwear textures. However the only study that actually tested these hypotheses on living captive domesticated animals concludes that differences in (dust-free) diet generates significant differences in dental microwear textures (Merceron et al., 2016). Moreover, the effects on foods of dust simulating the Western Africa Harmattan windblown dust are not significant enough to hide the dietary signal (Merceron et al., 2016). *Samotherium*

also displays a wide range of values (Tables 1 and 3; Figs. 3 and 5; table S1). *Samotherium major* differs from the modern giraffe in having higher anisotropy (epLsar), from the hartebeest in having a higher complexity (Asfc) and from the red deer, the yellow-backed duiker, and the okapi in its lower heterogeneity of complexity (HAsfc; Tables 1 and 3; Figs. 3 and 5; table S1). *Samotherium boissieri* also has higher anisotropy (epLsar) than the giraffe and the yellow-backed duiker. It is worth noting that there is no significant difference between *S. boissieri* and the grazing and mixed feeding species. The sample of *Palaeotragus rouenii* displays higher anisotropy (epLsar) than the modern giraffe and lower complexity (Asfc) than the yellow-backed duiker. This species covers the whole spectrum. cf. *P. coelophrys* shares the same pattern. On the whole, mixed feeding habits seem to be prevalent for all palaeotragines.

3.2. Morphology, diet, and niche partitioning

Modern giraffids constitute a relic of a diverse group that became impoverished during Pliocene and Pleistocene times, but during the late Miocene, their species and ecomorphological diversities were far greater than today. Body mass and heights at which they could gather food resources differed from one species to another (Table 4, Fig. 6). *Helladotherium duvernoyi* was likely the heaviest giraffe in Europe, weighting perhaps as much as two tons, whereas *Palaeotragus rouenii* was not larger than the modern okapi, at about 500 kg. The length of their metacarpals, approximating height at the withers, and the height at which each species could reach its food, covered the whole range of the modern forms, from the okapi to the giraffe. The relative proportions of the premolar / molar rows are not very variable in the Giraffidae, which suggests that there were probably no huge differences in diets. On the basis of the index (Table 4, Fig. 6), and given low sample size, most fossil giraffes do not significantly differ from their modern relatives, except the

335 paleotragines that have smaller premolars. This is in agreement with the dental microwear
336 textural analysis that suggests more versatile feeding habits for paleotragines than other
337 extinct giraffids.

338 *Bohlinia attica* was a giraffine weighting about a ton; it was likely able to reach
339 foliage as high as the modern giraffe, from 4 to 6 m above ground (Table 4, Fig. 6; Leuthold,
340 1978; OôConnor et al., 2015). The dental microwear textures attest that *B. attica* fed mostly on
341 soft foliages, as modern giraffes do (Figs. 5 and 6). The body traits found in *Bohlinia* and
342 *Giraffa* and their similarities in tooth wear both suggest that the ecological niche of leaf-
343 dominated browsers targeting the highest tree foliages was shared by the common ancestor.
344 Among large giraffids, the sivatheriine *Helladotherium duvernoyi* weighted as much
345 as two tons; the low values for the three textural parameters depict it as a likely leaf-dominant
346 browser (Fig. 5). Thus, *H. duvernoyi* shared similar feeding habits with *B. attica*, in spite of
347 its distinctly higher molar crowns (Table 4), but could not reach foliages as high as this
348 species, which was less stoutly built, but taller (Table 4, Fig. 6). *Palaeogiraffa* is represented
349 in this study by three species. They were less tall than *B. attica*, and thus had reduced
350 competition with it to exploit tree foliages (Fig. 6). *Palaeogiraffa pamiri* from Thrace was
351 likely a leaf-dominant browser while the contemporaneous *P. macedoniae* and *P. major* from
352 the lower Axios valley in Greece may have incorporated herbaceous monocotyledons in their
353 diet. Such contrasted differences between species of the same genus (Figs. 5 and 6) might
354 reflect differences in food resources between the two regions (woody landscapes in the
355 Thracian site and floodplain grasslands along the Axios).
356 In the late Miocene of the Mediterranean region, palaeotragines were more diverse
357 than sivatheriines and giraffines, but the height range at which they could browse is far
358 smaller than their species diversity and body mass range suggest. The palaeotragine
359 *Samotherium major* has a body mass similar to that of the sivatheriine *H. duvernoyi* (Table 4,

Fig. 6). These two species could reach the same foliage heights. Based on tooth morphology, we would have expected more grazing habits for the large palaeotragine compared to the sivatheriine, because small premolars compared to molars are usually taken as indicating more grazing habits in ruminants (Solounias and Dawson-Saunders, 1988), but no significant difference in the present study seems to distinguish the species with the larger premolars (*H. duvernoyi*) from the similar-sized species with the smaller premolars (*S. major;* Table 4, Figs. 5 and 6). However, using dental microwear analysis on a larger sample, Solounias et al. (2010) regarded *S. major* as a mixed feeder. Based on a dental mesowear scoring approach, Danowitz et al. (2016) depicted it as a browser or a mixed feeder. To sum up, although the present study fails to discriminate *S. major* from *H. duvernoyi*, previous studies supported the view that *S. major* included herbaceous monocotyledons in its diet, as suggested by its dental morphology.

Samotherium boissieri differs from *S. major* in its lighter body mass and in being less tall at the withers. Besides, the slight differences in the morphology of the premaxilla (but not in the teeth) between these co-generic species (Fig. 7) suggest that *S. boissieri* might have ingested more herbaceous monocotyledons than *S. major*, although according to our own observation, the specimen NHMUK M 4215 has a distinctly less squarish premaxilla than typical grazers. Although our study fails to detect any significant differences between these two species of *Samotherium*, it is worth mentioning that, in contrast to *S. major*, *S. boissieri* has significantly higher values of anisotropy than modern browsing species (yellow-backed duiker and giraffe) and the three most presumably leaf browsing extinct giraffids (*B. attica*, *H. duvernoyi*, *P. pamiri;* Table 4, Figs. 5 and 6). Solounias et al. (1988) had also shown that *S. boissieri* includes herbaceous monocotyledons in its diet.

The genus *Palaeotragus* is represented by two species. *Palaeotragus rouenii* has a body mass similar to that of the modern okapi but could reach vegetal layers as high as those

385 that *H. duvernoyi* and *Samotherium* spp. browsed (Table 4, Fig. 6). A more versatile diet than
386 that of *H. duvernoyi* could explain their coexistence at some sites, and thus the probable
387 overlap of their home ranges. *Palaeotragus coelophrys* was stouter than *P. rouenii*, but based
388 on their metacarpal lengths, they could reach the same foliages. A fifth species of
389 palaeotragine, *Samotherium neumayri*, is represented by a single individual whose body mass
390 was similar to that of the modern giraffe but with a height at the withers similar to that of
391 other palaeotragines; its dental microwear texture suggests that this specimen fed on soft
392 foliages the few weeks before its death.
393
394 *3.3 Dietary adaptation and Phylogeny*
395 A recent study based on new material challenges the phylogeny of the giraffids (Ríos
396 et al., 2017). Giraffines are represented by the modern giraffes and the species of the genus
397 *Bohlinia*. The elongation of the cervical vertebrae and the extreme elongation of the
398 metacarpal allowing them to forage on the highest arboreal stratum may be seen as an
399 autapomorphy of the Giraffinae (Ríos et al., 2017). Our data strongly support such dietary
400 adaptations. Besides, the monophyly of the paleotragines is challenged. According to their
401 study, the genus *Samotherium*, previously thought to be close to *Palaeotragus*, actually shares
402 a set of derived features with the Sivatherinae. The species of the genus *Palaeotragus*
403 compose the sister group of a monophyletic group including the modern okapi,
404 *Decennatherium*, *Palaeogiraffa* (assumed to be close to the former genus according to these
405 authors) and *Samotherium* in which the sivatherines (including *Helladotherium*) are rooted.
406 More versatile feeding habits might have been the ancestral conditions for this second clade.
407 In view of this phylogeny proposed by Ríos et al. (2017), we may consider that either
408 browsing or mixed feeding habits were the ancestral ecological conditions for giraffids. The
409 adaptation to leaf browsing occurred twice, first among Giraffines and then at least in

410 *Helladotherium* within the Sivatherines. It is worth mentioning that the African sivatheres
411 show a shortening of the forelimbs in the course of the Pliocene, a morphological trend
412 correlated with the incorporation of a greater amount of C_4 plants, i.e. herbaceous monocots,
413 in their diet.

4. Conclusions

The present study explores the ecological diversity of the diverse radiation of giraffids that took place during the late Miocene of the Eastern Mediterranean. In combination with body traits such as wither heights, and thus estimation of the height at which these extinct ruminants may have foraged, DMTA detects differences in feeding preferences. As expected, several of these extinct giraffids were leaf-dominant browsers but foraging at different heights. The modern giraffe can be consider as an appropriate model for understanding the ecology of *Bohlinia*. *Helladotherium duvernoyi* browsed at lower heights. Our study supports previous views that regarded the species of *Samotherium* as engaged in both browsing and grazing. *Palaeogiraffa* from the Axios valley in Greece undoubtedly included high amounts of tough plants, most likely tall herbaceous monocots, in its diet. The present study enlarges our knowledge of the ecology of this diversified group and emphasizes the importance of considering megaherbivores to faithfully depict past ecosystems and available resources. Indeed, together with proboscideans, rhinocerotids and chalicotheriids, giraffids compose a guild of megaherbivores with no analog in the modern ecosystems.

In addition, the present study provides surprising results regarding the okapi. Its dental microwear textures significantly differ from those of the leaf-eating giraffes as well as from those of the fruit-eating yellow-backed duikers. They show similarities with those of the red deer, a species eating both monocots and dicots. Here, we hypothesize that the okapi is not a browser *sensu stricto*. This giraffid feeds on a wider dietary spectrum than previously thought and likely forages on tough plants, possibly tall herbaceous monocotyledons when exploiting resources in tree fall gaps.

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6. Data availability

The dental microwear texture parameters for each fossil specimen are given in Appendix 1.

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630
631

Table 1. Descriptive statistics of dental microwear textural parameters of modern ruminants and extinct species of giraffids.

			Asfc*		epLsar ($\times 10^{-3}$)		HAsfc	
	Taxa	*N*	m	sd	m	sd	m	sd
Modern species	*Cephalophus silvicultor*	25	4.03	3.25	3.07	1.58	0.54	0.30
	Giraffa sp.	12	2.51	1.48	2.10	1.57	0.35	0.12
	Cervus elaphus	29	2.12	0.80	4.59	1.91	0.55	0.25
	Okapia johnstoni	25	2.46	1.46	4.07	2.07	0.52	0.27
	Alcelaphus buselaphus	28	1.60	0.77	5.80	1.64	0.39	0.12
Extinct species	*Bohlinia attica*	5	1.47	0.73	2.47	0.94	0.49	0.11
	Helladotherium duvernoyi	15	2.46	1.23	2.99	1.37	0.43	0.52
	Palaeogiraffa macedoniae	6	2.61	0.65	5.13	2.63	0.36	0.14
	Palaeogiraffa major	1	2.87	-	6.41	-	0.38	-
	Palaeogiraffa paimiri	6	1.68	0.93	1.92	0.97	0.51	0.29
	Samotherium neumayri	1	0.66	-	1.99	-	0.15	-
	Palaeotragus rouenii	21	2.30	1.06	3.80	1.63	0.35	0.11
	cf. *P. coelophrys*	3	1.84	0.93	3.60	2.43	0.34	0.07
	Samotherium boissieri	5	2.43	1.33	4.97	2.10	0.37	0.14
	Samotherium major	9	2.89	1.63	3.70	1.63	0.37	0.25

* all of these three parameters are dimensionless (see Scott et al., 2006); m: mean; sd: standard deviation; Asfc: complexity; epLsar: anisotropy (calculated at the 1.8 µm scale); HAsfc: Heterogeneity of complexity (calculated with a 9-cell mesh).

638 **Table 2**. Analysis of variance on rank-transformed variables.

639

	df	SS	MS	F	*p*
Asfc	14	115848.3	8274.9	3.1334	0.0002
	176	464791.7	2640.9		
	df	SS	MS	F	*P*
epLsar	14	176760.3	12625.7	5.5020	0.0000
	176	403878.7	2294.8		
	df	SS	MS	F	*P*
HAsfc	14	109086.9	7791.9	2.9082	0.0005
	176	471552.1	2679.3		

640 Asfc: complexity; epLsar: anisotropy (calculated at the 1.8 µm scale); HAsfc: Heterogeneity of complexity

641 (calculated with a 9-cell mesh). ; SS: sum of squares; MS: mean of squares; F: F statistic; p: p-value

642

643 Table 3. Post-hoc test of comparisons (the Fisher Least Significant Differences and the

644 conservative Tukey Honest Significant Differences test).

	C. silvicultor	*C. elaphus*	*Giraffa* sp.	*O. johnstoni*	*A. buselaphus*	*B. attica*	*H. duvernoyi*	*P. paimiri*	*P. macedoniae*	*P. major*	*S. neumayri*	*P. rouenii*	cf. *P. coelophrys*	*S. boissieri*
Cervus elaphus	Asfc epLsar													
Giraffa sp.	HAsfc	HAsfc **epLsar**												
Okapia johnstoni	Asfc epLsar		HAsfc epLsar											
Alcelaphus buselaphus	**Asfc epLsar**	HAsfc Asfc epLsar	Asfc **epLsar**	HAsfc Asfc **epLsar**										
Bohlinia attica	**Asfc**	epLsar	HAsfc		**epLsar**									
Helladotherium duvernoyi	HAsfc Asfc	**HAsfc** epLsar		HAsfc	Asfc **epLsar**	HAsfc								
Palaeogiraffa paimiri	Asfc	**epLsar**		epLsar	**epLsar**									
Palaeogiraffa macedoniae	epLsar	HAsfc	epLsar		Asfc	Asfc epLsar	epLsar	epLsar						
Palaeogiraffa major			epLsar			epLsar		epLsar						
Samotherium neumayri	HAsfc Asfc	HAsfc		HAsfc	epLsar	HAsfc			Asfc					
Palaeotragus rouenii	HAsfc Asfc	**HAsfc**	epLsar	HAsfc	Asfc **epLsar**	HAsfc		epLsar						
cf. *Palaeotragus coelophrys*	Asfc				epLsar									
Samotherium boissieri	epLsar		epLsar			epLsar	epLsar	epLsar						
Samotherium major	HAsfc	HAsfc	epLsar	HAsfc	Asfc epLsar	Asfc		epLsar			Asfc			

645 Variables were rank-transformed before analysis. When both LSD and HSD detect significant differences, the

646 variable is underlined and in bold.

647

Table 4. Body anatomical traits of modern and extinct giraffids.

	Metacarpal length		Body mass estimate			Pm/M index (upper teeth)	Pm/M index (lower teeth)
Species	N	L	N	Humerus W	body mass		
Giraffa sp.	33	701	26	116	1362	75 (mean)	68 (mean)
Okapia johnstoni	2	307	2	75	441	74, 75	60, 65, 70
Bohlinia attica	6	704	7	107	1118	73, 76, 78	-
Helladotherium duvernoyi	20	435	15	141	2201	77, 79, 81	63, 65, 67[(3)]
Palaeogiraffa macedoniae	1	465	2	115	1324	72, 73, 75	65
Palaeogiraffa pamiri	4	469	1	115	1324	76 ?	68
Palaeotragus coelophrys	4	370	-	-	-	70, 71, 73, 74	68
Palaeotragus rouenii	5	409	6[(2)]	75	439	70, 74	63, 67, 68
Samotherium boissieri	14[(2)]	357	4[(2)]	104	1022	67.5 (mean of 7)[(1)]	57, 59, 60, 60
Samotherium major	32[(2)]	417	7[(2)]	141	2185	65, 67, 68[(4)]	63, 66
Samotherium neumayri	11	382	4	116	1341	65	58, 67

Metacarpal length (in mm), body mass (in kg) based upon humerus distal articular width (in mm) following the equation of Scott (1990) for Ruminants (body mass = $10^{(2.5518*\log(\text{Humerus W})+0.4093)}$), indexes of upper and lower premolar/molar rows of modern and extinct giraffids. Most data are our own, with a few additions from Bohlin (1926[(1)]), Kostopoulos (2009[(2)], 2016[(3)]) and Senyürek (1954[(4)]).

Figure captions

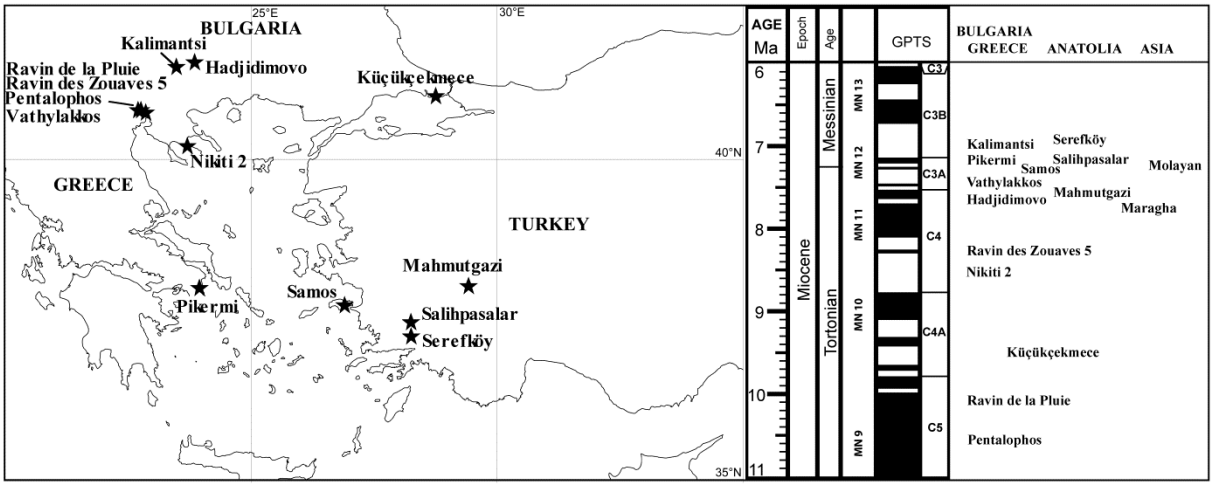


Figure 1. Geographic and chronostratigraphic distribution of the main localities considered in this study. A few specimens come from Asian (Maragha in Iran and Molayan in Afghanistan) and North African (Douaria in Tunisia) localities outside the map.

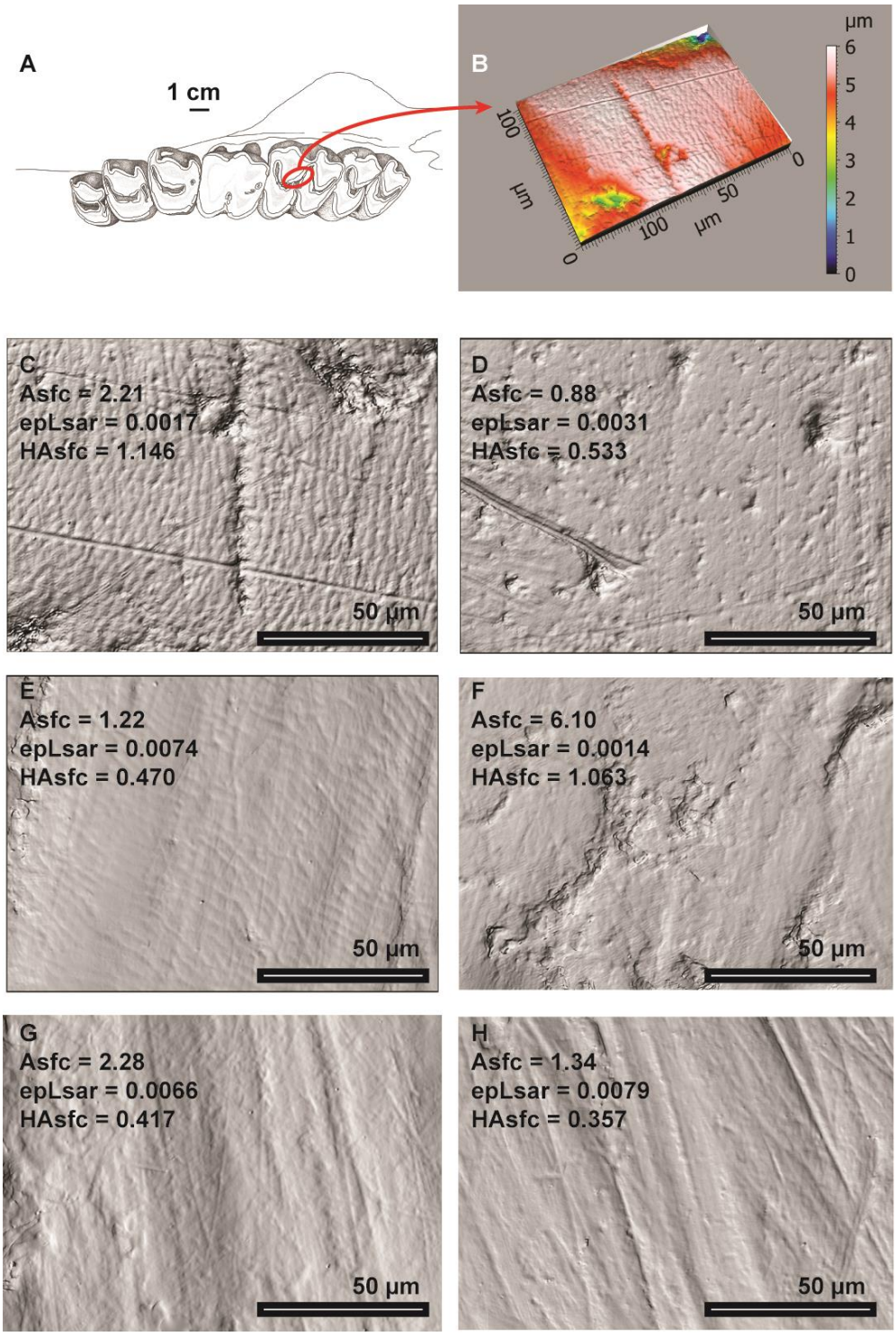
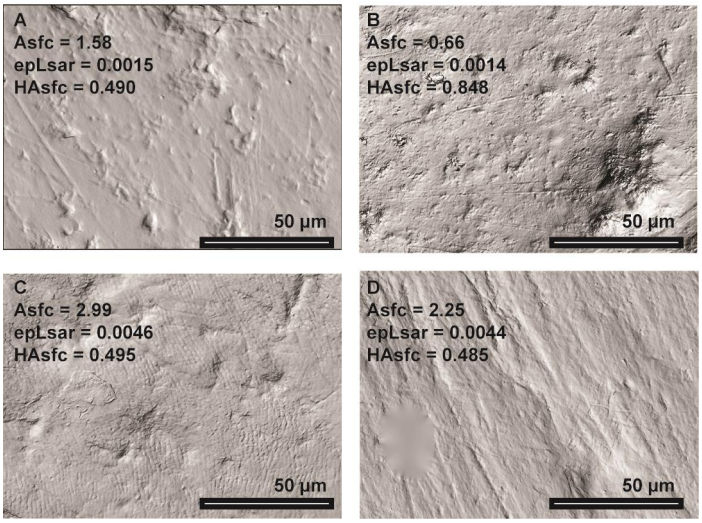


Figure 2. Occlusal view of left upper molar of a modern giraffe, *Giraffa* sp. (A; UP-M10-5-001-A) and 3D surface simulation on shearing dental facet (B; NHMB-Z553). The photosimulations C-H were generated through the LeicaMap 7.0: *Giraffa* sp. (C: NHMB-Z553), *Okapia johnstoni* (D: NHMB-Z245; E: NHMB-Z1085), *Cephalophus silvicultor* (F: NHMB-1611), *Cervus elaphus* (G: UP-Chat-9-4168) and *Alcelaphus buselaphus* (H: UP-ART8-21).



669

670 **Figure 3**. The photosimulations A-D were generated through the LeicaMap 7.4:
671 *Helladotherium duvernoyi* from Kalimansti, Bulgaria (A; K5159), *Palaeogiraffa pamiri* from
672 Küçükçekmeçe, Turkey (B; MNHN-TRQ-430), *Palaeotragus rouenii* from Pikermi, Greece
673 (C; MNHN-PIK-1672), and *Samotherium major* from Salihpasalar, Turkey (D; MTA-MYS-
674 843).
675

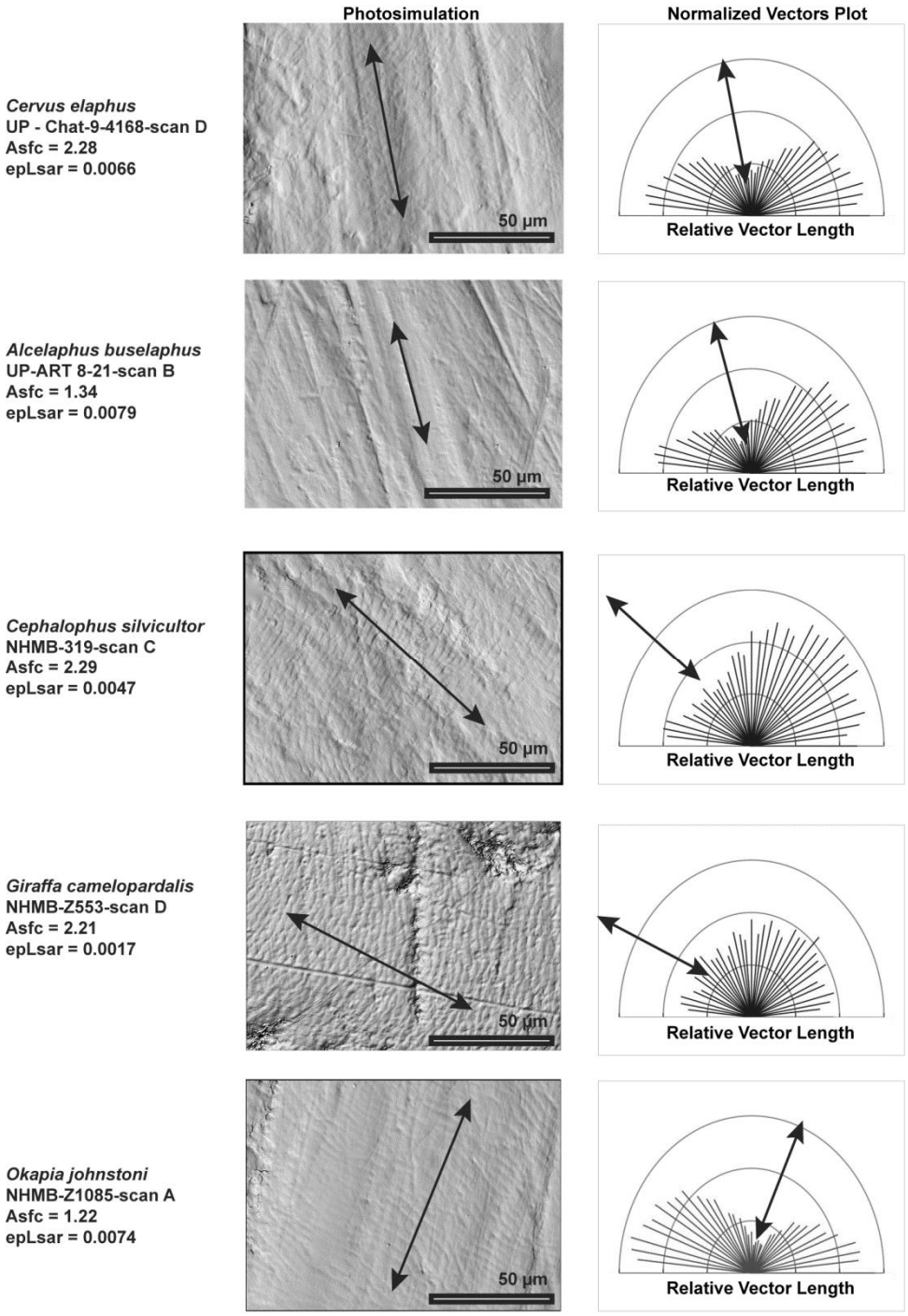
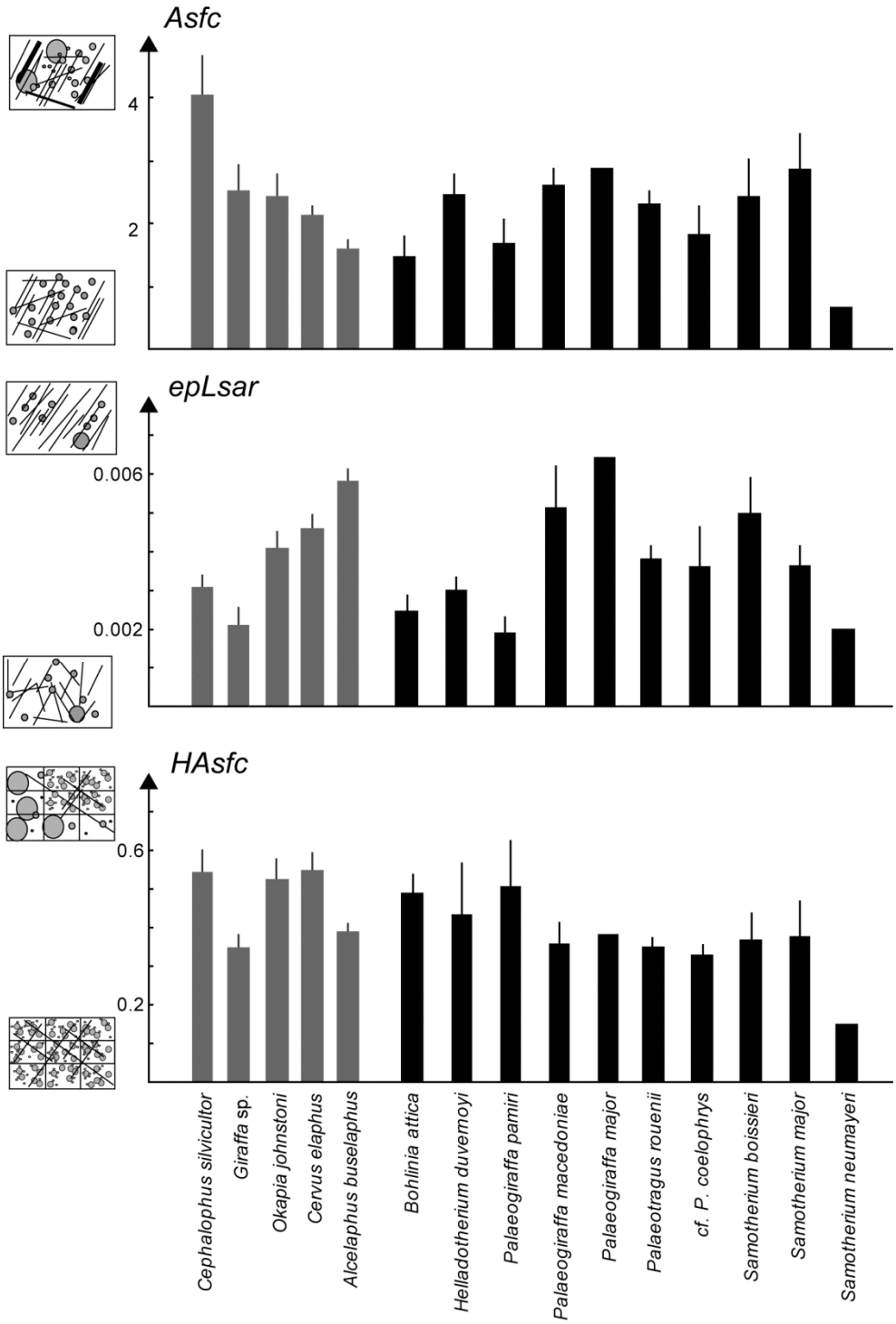


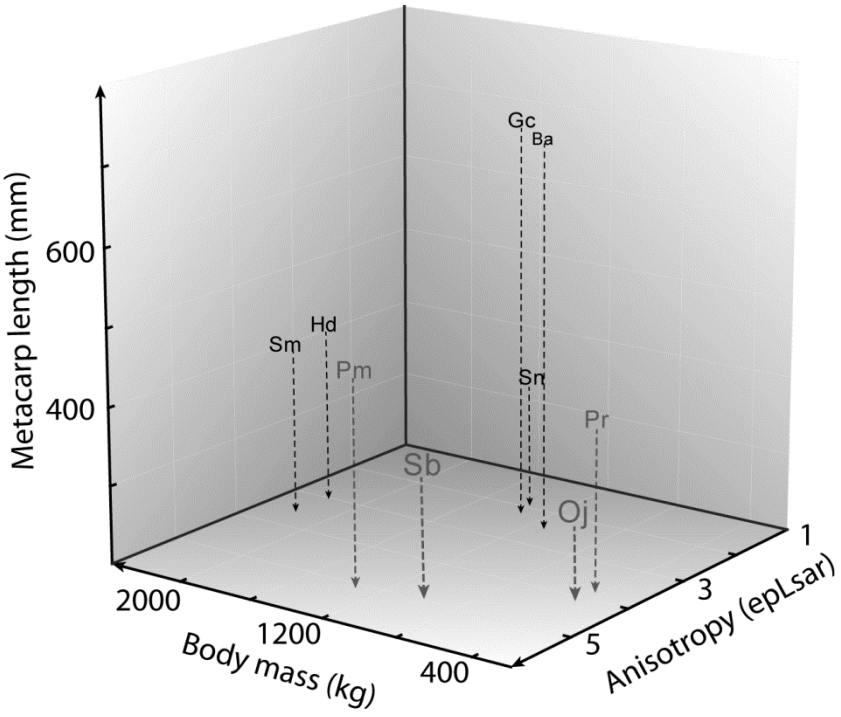
Figure 4. Photosimulations of dental microwear textures of modern ruminants with values in complexity (Asfc) and anisotropy (epLsar) and the corresponding rosette plot of relative lengths taken at 36 different orientations. The two first surfaces (*Cervus elaphus* and *Alcelaphus buselaphus*) display low relative length correlated with the main microwear textural orientation (here the main directionality is highlighted with the black arrows). The last three surfaces (*Cephalophus silvicultor*, *Giraffa camelopardalis* and *Okapia johnstoni*) display a main orientation of dental microwear textures disconnected from the perikemata direction, meaning that anisotropy does not reflect the perikemata directionality, but the dental microwear texture one.



687

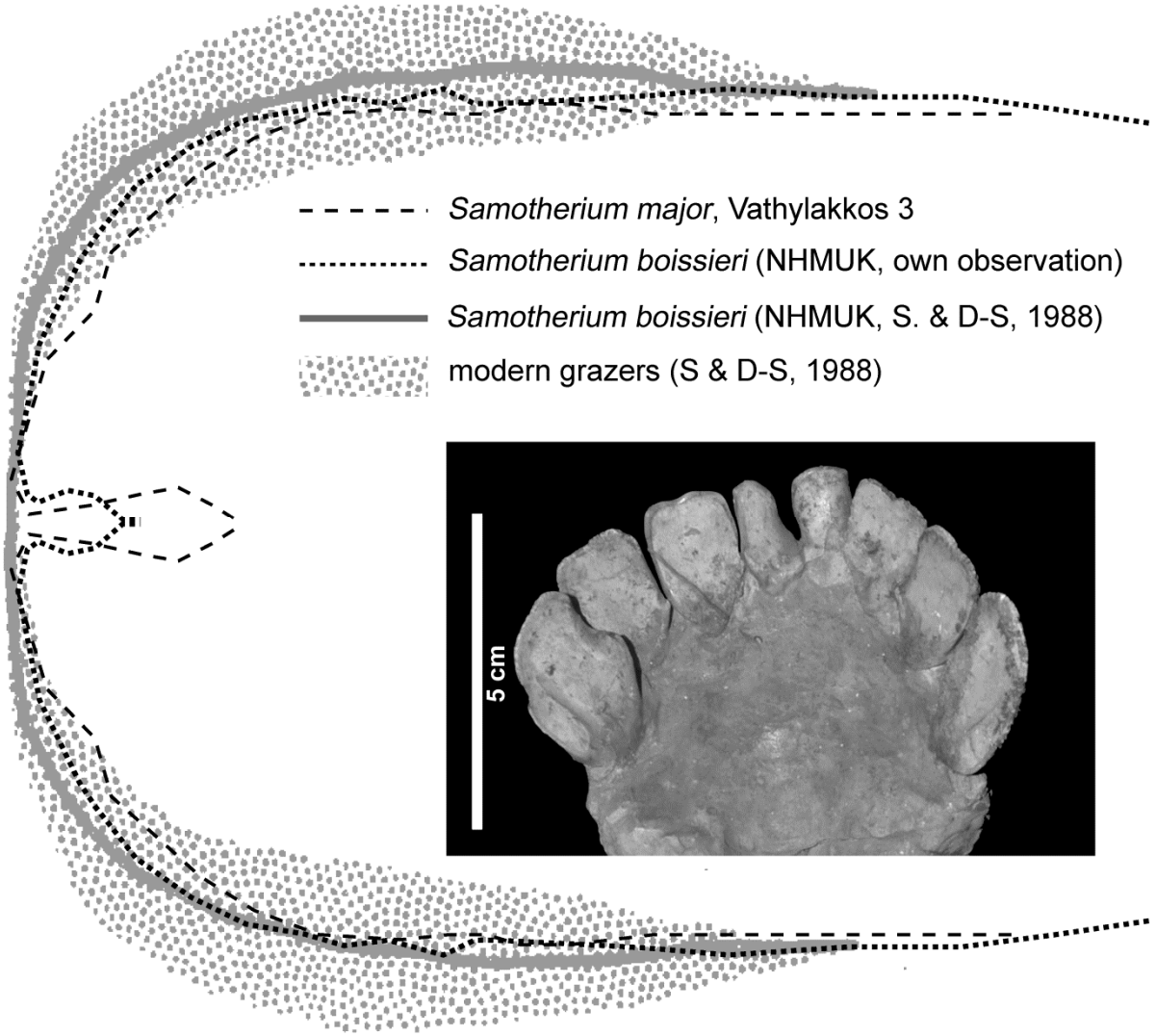
688 **Figure 5.** Bar plots (mean and standard error of the mean) of dental microwear textural
689 parameters Asfc: complexity; epLsar: anisotropy calculated at the 1.8 µm scale; HAsfc:
690 Heterogeneity of complexity (calculated with a 9-cell mesh) for modern ruminants (in gray)
691 and extinct giraffids (in black).

692



693

694 **Figure 6**. 3D plot of the average of anisotropy (epLsar) of the dental microwear textures vs.
695 averages of body mass (in kg) and length of metacarpal bone (in mm), which approximates
696 the height at the withers. Note that specimens used for body traits and dental microwear
697 analysis are not the same (see Table 4).
698



699

700 **Figure 7**. Outlines of the premaxilla in *Samotherium*. Square outline denotes grazers. S & D-
701 S: Solounias and Dawson-Saunders (1988); outline of *S. major* based upon the specimen from
702 Vathylakkos 3 (Geraads, 1978); outlines of *S. boissieri* based upon NHMUK M4215.
703

704

Appendix 1 - List of extant and extinct specimens with surface parameters

State	Species	Individual	Asfc	epLsar 1.8 µm	Hasfc 9 cells
Extant species	Alcelaphus buselaphus	MNHN-1894-1524	1.56	0.00480	0.381
Extant species	Alcelaphus buselaphus	MNHN-1913-39	0.52	0.00166	0.491
Extant species	Alcelaphus buselaphus	MNHN-1913-744	0.87	0.00339	0.297
Extant species	Alcelaphus buselaphus	MNHN-1965-1099	1.52	0.00736	0.272
Extant species	Alcelaphus buselaphus	MNHN-1965-1101	0.73	0.00398	0.405
Extant species	Alcelaphus buselaphus	MNHN-1965-1104	1.16	0.00545	0.519
Extant species	Alcelaphus buselaphus	MNHN-1965-1105	1.02	0.00491	0.199
Extant species	Alcelaphus buselaphus	MNHN-1965-1107	1.08	0.00525	0.270
Extant species	Alcelaphus buselaphus	MNHN-1970-31	1.97	0.00709	0.366
Extant species	Alcelaphus buselaphus	MNHN-1970-34	1.94	0.00740	0.312
Extant species	Alcelaphus buselaphus	MNHN-1970-35	1.76	0.00517	0.424
Extant species	Alcelaphus buselaphus	MNHN-1974-211	1.19	0.00564	0.329
Extant species	Alcelaphus buselaphus	MNHN-BUB-6	0.87	0.00360	0.249
Extant species	Alcelaphus buselaphus	MNHN-BUB-8	2.40	0.00417	0.446
Extant species	Alcelaphus buselaphus	SMNK-1027	1.14	0.00507	0.302
Extant species	Alcelaphus buselaphus	SMNK-1206	1.29	0.00680	0.791
Extant species	Alcelaphus buselaphus	SMNK-1207	1.18	0.00796	0.333
Extant species	Alcelaphus buselaphus	SMNK-126	0.94	0.00706	0.339
Extant species	Alcelaphus buselaphus	SMNK-2358	2.40	0.00759	0.401
Extant species	Alcelaphus buselaphus	SMNK-47	1.72	0.00673	0.345
Extant species	Alcelaphus buselaphus	UP-ART-8-22	3.53	0.00622	0.344
Extant species	Alcelaphus buselaphus	UP-ART-8-26	2.57	0.00529	0.608
Extant species	Alcelaphus buselaphus	UP-ART-8-27	3.69	0.00555	0.561
Extant species	Alcelaphus buselaphus	UP-ART-8-20	1.48	0.00610	0.400
Extant species	Alcelaphus buselaphus	UP-ART-8-21	1.34	0.00796	0.357
Extant species	Alcelaphus buselaphus	UP-ART-8-23	1.24	0.00650	0.358
Extant species	Alcelaphus buselaphus	UP-ART-8-24	2.05	0.00913	0.399
Extant species	Alcelaphus buselaphus	UP-ART-8-25	1.71	0.00466	0.361
Extant species	Cephalophus silivicultor	NHMB-Csilv-14	8.18	0.00175	0.504
Extant species	Cephalophus silivicultor	NHMB-Csilv-1611	2.96	0.00607	0.289
Extant species	Cephalophus silivicultor	NHMB-Csilv-1612	2.65	0.00101	0.520
Extant species	Cephalophus silivicultor	NHMB-Csilv-1616	2.11	0.00290	0.497
Extant species	Cephalophus silivicultor	NHMB-Csilv-1617	3.51	0.00428	0.467
Extant species	Cephalophus silivicultor	NHMB-Csilv-319	4.11	0.00288	1.325
Extant species	Cephalophus silivicultor	NHMB-Csilv-366	2.21	0.00615	0.384
Extant species	Cephalophus silivicultor	NHMB-Csilv-578	3.32	0.00256	0.813
Extant species	Cephalophus silivicultor	NHMB-Csilv-878	6.06	0.00139	1.089
Extant species	Cephalophus silivicultor	NHMB-Csilv-924	2.07	0.00426	0.317
Extant species	Cephalophus silivicultor	NHMB-Csilv-DIE-1	17.03	0.00063	0.605
Extant species	Cephalophus silivicultor	NHMB-Csilv-GM4	3.06	0.00211	0.975
Extant species	Cephalophus silivicultor	NHMB-Csilv-R12923	1.45	0.00223	0.156
Extant species	Cephalophus silivicultor	NHMB-Csilv-R16753	2.66	0.00191	0.427
Extant species	Cephalophus silivicultor	NHMB-Csilv-SN-DIB-95	1.52	0.00454	0.318
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z2039-2	2.62	0.00209	0.280
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z3048	7.53	0.00153	0.283
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z3344	2.15	0.00460	0.359
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z3347	3.43	0.00460	0.623
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z352	1.95	0.00476	0.338
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z3669	2.11	0.00312	0.334
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z3916	5.29	0.00355	0.749
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z3918	3.53	0.00476	0.344
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z404	6.10	0.00140	1.063
Extant species	Cephalophus silivicultor	NHMB-Csilv-Z464	3.07	0.00170	0.455

State	Species	Individual	Asfc	epLsar 1.8 µm	Hasfc 9 cells
Extant species	Cervus elaphus	UP-Chat9-1023	1.65	0.00263	1.127
Extant species	Cervus elaphus	UP-Chat9-1024	1.02	0.00388	0.594
Extant species	Cervus elaphus	UP-Chat9-1025	1.54	0.00400	1.229
Extant species	Cervus elaphus	UP-Chat9-1035	2.72	0.00063	1.055
Extant species	Cervus elaphus	UP-Chat9-1037	3.17	0.00491	0.595
Extant species	Cervus elaphus	UP-Chat9-1038	1.98	0.00646	0.311
Extant species	Cervus elaphus	UP-Chat9-1039	1.71	0.00835	0.584
Extant species	Cervus elaphus	UP-Chat9-2054	2.92	0.00531	0.527
Extant species	Cervus elaphus	UP-Chat9-2057	3.17	0.00523	0.742
Extant species	Cervus elaphus	UP-Chat9-3105	1.18	0.00457	0.516
Extant species	Cervus elaphus	UP-Chat9-3132	2.69	0.00057	0.380
Extant species	Cervus elaphus	UP-Chat9-3133	1.65	0.00391	0.486
Extant species	Cervus elaphus	UP-Chat9-4152	1.14	0.00451	0.451
Extant species	Cervus elaphus	UP-Chat9-4157	0.95	0.00596	0.199
Extant species	Cervus elaphus	UP-Chat9-4159	1.57	0.00567	0.196
Extant species	Cervus elaphus	UP-Chat9-4161	1.70	0.00373	0.510
Extant species	Cervus elaphus	UP-Chat9-4167	2.49	0.00715	0.457
Extant species	Cervus elaphus	UP-Chat9-4168	2.28	0.00655	0.417
Extant species	Cervus elaphus	UP-Chat9-4180	1.80	0.00411	0.290
Extant species	Cervus elaphus	UP-Chat9-4189	2.79	0.00557	0.578
Extant species	Cervus elaphus	UP-Chat9-4190	1.42	0.00511	0.467
Extant species	Cervus elaphus	UP-Chat9-4264	2.87	0.00169	0.824
Extant species	Cervus elaphus	UP-Chat9-4271	1.86	0.00402	0.486
Extant species	Cervus elaphus	UP-Chat9-4278	1.57	0.00688	0.589
Extant species	Cervus elaphus	UP-Chat9-4295	1.45	0.00153	0.320
Extant species	Cervus elaphus	UP-Chat9-4302	3.69	0.00291	0.477
Extant species	Cervus elaphus	UP-Chat9-4319	3.96	0.00547	0.551
Extant species	Cervus elaphus	UP-Chat9-4339	2.06	0.00654	0.602
Extant species	Cervus elaphus	UP-Chat9-4354	2.43	0.00518	0.283
Extant species	Giraffa sp.	KNM-no#-Z7	1.43	0.00234	0.241
Extant species	Giraffa sp.	KNM-OM-2087	1.31	0.00190	0.401
Extant species	Giraffa sp.	KNM-OM-2275	2.70	0.00141	0.190
Extant species	Giraffa sp.	MNHN-1928-307	2.90	0.00179	0.446
Extant species	Giraffa sp.	NHMB-Z-1086	1.46	0.00613	0.254
Extant species	Giraffa sp.	NHMB-Z-553	2.21	0.00171	0.300
Extant species	Giraffa sp.	SMNS-30171	3.06	0.00192	0.481
Extant species	Giraffa sp.	SNG-35595	1.82	0.00066	0.311
Extant species	Giraffa sp.	SNG-36628	1.76	0.00126	0.298
Extant species	Giraffa sp.	SNG-497	2.98	0.00043	0.350
Extant species	Giraffa sp.	SNG-498	1.76	0.00415	0.279
Extant species	Giraffa sp.	SNG-501	6.75	0.00149	0.606
Extant species	Okapia johnstoni	MRAC-1025	3.10	0.00226	0.474
Extant species	Okapia johnstoni	MRAC-1192	3.93	0.00461	0.381
Extant species	Okapia johnstoni	MRAC-1193	4.48	0.00174	0.371
Extant species	Okapia johnstoni	MRAC-2904	1.38	0.00608	0.433
Extant species	Okapia johnstoni	MRAC-3074	3.19	0.00427	0.483
Extant species	Okapia johnstoni	MRAC-3075	2.82	0.00151	0.375
Extant species	Okapia johnstoni	MRAC-3076	2.37	0.00454	0.260
Extant species	Okapia johnstoni	MRAC-4051	1.32	0.00762	0.636
Extant species	Okapia johnstoni	MRAC-6293	1.99	0.00246	1.302
Extant species	Okapia johnstoni	MRAC-705B	4.49	0.00061	0.442
Extant species	Okapia johnstoni	MRAC-8358	1.82	0.00542	0.445
Extant species	Okapia johnstoni	MRAC-8663	3.36	0.00127	0.552
Extant species	Okapia johnstoni	MRAC-9726	2.23	0.00634	0.230
Extant species	Okapia johnstoni	MRAC-9727	1.81	0.00537	0.774
Extant species	Okapia johnstoni	NHMB-Z-1085	1.22	0.00738	0.470
Extant species	Okapia johnstoni	NHMB-Z-243	1.69	0.00346	0.603
Extant species	Okapia johnstoni	NHMB-Z-245	0.88	0.00311	0.533
Extant species	Okapia johnstoni	NHMB-Z-2908	0.74	0.00472	0.208
Extant species	Okapia johnstoni	NHMB-Z-329	2.36	0.00268	1.019
Extant species	Okapia johnstoni	NHMB-Z-576	4.42	0.00288	0.133
Extant species	Okapia johnstoni	NMHB-C3899	0.44	0.00192	0.603
Extant species	Okapia johnstoni	NMHB-C3900	0.56	0.00279	0.533
Extant species	Okapia johnstoni	NHMB-Z-2308	1.32	0.00749	0.276
Extant species	Okapia johnstoni	NHMB-Z-244	6.27	0.00544	0.534
Extant species	Okapia johnstoni	NHMB-Z-3686	3.26	0.00585	0.887

State	Species	Individual	Asfc	epLsar 1.8 µm	Hasfc 9 cells	Region	Site
Extinct species	Bohlinia attica	LGPUT-NKT-147-UM2	0.91	0.00211	0.343	Greece	Nikiti-1
Extinct species	Bohlinia attica	AM-NMNHS-K 5206	1.07	0.00317	0.533	Bulgaria	Kalimantsi
Extinct species	Bohlinia attica	AM-NMNHS-K 5209	1.23	0.00301	0.518	Bulgaria	Kalimantsi
Extinct species	Bohlinia attica	LGPUT-NKT-148-UM2	1.44	0.00097	0.432	Greece	Nikiti-1
Extinct species	Bohlinia attica	LGPUT-NKT-145-UM2	2.72	0.00307	0.618	Greece	Nikiti-1
Extinct species	Palaeogiraffa paimiri	MNHN TRQ-430	0.66	0.00142	0.259	Turkey	Küçükçekmece
Extinct species	Palaeogiraffa paimiri	MNHN TRQ-428	0.78	0.00215	0.433	Turkey	Küçükçekmece
Extinct species	Palaeogiraffa paimiri	MNHN TRQ-424	1.10	0.00103	0.317	Turkey	Küçükçekmece
Extinct species	Palaeogiraffa paimiri	MNHN TRQ-422	2.36	0.00131	0.533	Turkey	Küçükçekmece
Extinct species	Palaeogiraffa paimiri	MNHN TRQ-425	2.56	0.00187	0.427	Turkey	Küçükçekmece
Extinct species	Palaeogiraffa paimiri	MNHN TRQ-432	2.62	0.00372	1.068	Turkey	Küçükçekmece
Extinct species	Helladotherium duvernoyi	AM-NMNHS-HD 5157	0.88	0.00343	0.645	Bulgaria	Hadjidimovo
Extinct species	Helladotherium duvernoyi	AM-NMNHS-K 5198	1.06	0.00290	0.207	Bulgaria	Kalimantsi
Extinct species	Helladotherium duvernoyi	MNHN-PIK1501	1.08	0.00278	0.267	Greece	Pikermi
Extinct species	Helladotherium duvernoyi	AM-NMNHS-K 5159	1.58	0.00146	0.490	Bulgaria	Kalimantsi
Extinct species	Helladotherium duvernoyi	AM-NMNHS-HD 5200	1.69	0.00471	0.747	Bulgaria	Hadjidimovo
Extinct species	Helladotherium duvernoyi	FSL16753-M1	2.12	0.00137	0.249	Algeria	Douaria
Extinct species	Helladotherium duvernoyi	AM-NMNHS-K 5161	2.23	0.00187	0.106	Bulgaria	Kalimantsi
Extinct species	Helladotherium duvernoyi	LGPUT-NIK 1804	2.27	0.00555	0.298	Greece	Nikiti-2
Extinct species	Helladotherium duvernoyi	LGPUT-NIK 1057	2.32	0.00472	0.250	Greece	Nikiti-2
Extinct species	Helladotherium duvernoyi	LGPUT-NIK 1	2.34	0.00362	0.152	Greece	Nikiti-2
Extinct species	Helladotherium duvernoyi	AM-NMNHS-K 5156	2.50	0.00138	0.221	Bulgaria	Kalimantsi
Extinct species	Helladotherium duvernoyi	LGPUT-RZO189	3.52	0.00128	0.177	Greece	Ravin des Zouaves-5
Extinct species	Helladotherium duvernoyi	AM-NMNHS-HD 5204	4.01	0.00292	0.239	Bulgaria	Hadjidimovo
Extinct species	Helladotherium duvernoyi	AM-NMNHS-K 5197	4.55	0.00421	2.179	Bulgaria	Kalimantsi
Extinct species	Helladotherium duvernoyi	MNHN-MNHN-PIK1500	4.77	0.00280	0.264	Greece	Pikermi
Extinct species	Palaeogiraffa macedoniae	LGPUT-PNT 137	2.00	0.00150	0.329	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPUT-PNT 328	2.01	0.00682	0.357	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPUT-PNT 136	2.33	0.00669	0.194	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPUT-PNT 112	2.75	0.00346	0.488	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPUT-PNT 111A	2.86	0.00376	0.220	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPUT-PNT 121	3.72	0.00851	0.545	Greece	Pentalophos
Extinct species	Palaeogiraffa major	LGPUT-RPL 734	2.87	0.00641	0.381	Greece	Ravin de la Pluie
Extinct species	P. coelophrys	MNHN-MAR-669	1.30	0.00108	0.419	Iran	Maragheh
Extinct species	P. coelophrys	LGPUT-RPL104	1.32	0.00592	0.304	Greece	Ravin de la Pluie
Extinct species	P. coelophrys	LGPUT-PNT113	2.91	0.00379	0.287	Greece	Pentalophos
Extinct species	Palaeotragus rouenii	MNHN-MOL-4211	0.68	0.00400	0.341	Afghanistan	Molayan
Extinct species	Palaeotragus rouenii	MNHN-MOL-4201	0.78	0.00488	0.363	Afghanistan	Molayan
Extinct species	Palaeotragus rouenii	LGPUT-DIT-2-UM2-a.sur	1.15	0.00554	0.175	Greece	Dytiko
Extinct species	Palaeotragus rouenii	NHML-PIK-M11453#5	1.39	0.00131	0.284	Greece	Pikermi
Extinct species	Palaeotragus rouenii	LGPUT-RPI-91b-UM2	1.40	0.00650	0.422	Greece	Ravin de la Pluie
Extinct species	Palaeotragus rouenii	NHML-PIK-M11419#7	1.46	0.00235	0.271	Greece	Pikermi
Extinct species	Palaeotragus rouenii	NHML-PIK-M11419#3	1.78	0.00338	0.429	Greece	Pikermi
Extinct species	Palaeotragus rouenii	AMNHS-MTLB52	1.80	0.00483	0.232	Greece	Mytilinii B
Extinct species	Palaeotragus rouenii	MTA-MYS351	1.81	0.00573	0.299	Turkey	Serefköy-2
Extinct species	Palaeotragus rouenii	MNHN-MOL-4212	1.93	0.00266	0.732	Afghanistan	Molayan
Extinct species	Palaeotragus rouenii	LGPUT-DIT-3-UM2	2.04	0.00342	0.221	Greece	Dytiko
Extinct species	Palaeotragus rouenii	MNHN-PIK1671	2.19	0.00277	0.371	Greece	Pikermi
Extinct species	Palaeotragus rouenii	AM-NMNHS-HD 5190	2.43	0.00228	0.372	Bulgaria	Hadjidimovo
Extinct species	Palaeotragus rouenii	NHMEU-PV-1598	2.58	0.00493	0.299	Turkey	Serefköy-2
Extinct species	Palaeotragus rouenii	NHMEU-PV-1629	2.69	0.00610	0.348	Turkey	Serefköy-2
Extinct species	Palaeotragus rouenii	MNHN-PIK1672	2.99	0.00464	0.388	Greece	Pikermi
Extinct species	Palaeotragus rouenii	AMNHS-MTLB128	3.53	0.00457	0.378	Greece	Mytilinii B
Extinct species	Palaeotragus rouenii	NHML-PIK M11419#9	3.66	0.00493	0.298	Greece	Pikermi
Extinct species	Palaeotragus rouenii	MTA-MYS-299	3.75	0.00144	0.457	Turkey	Serefköy-1
Extinct species	Palaeotragus rouenii	MNHN-PIK1674	3.77	0.00225	0.366	Greece	Pikermi
Extinct species	Palaeotragus rouenii	NHML-PIKM11419#4	4.40	0.00129	0.282	Greece	Pikermi
Extinct species	Samotherium boissieri	NHMB-Sam29	0.76	0.00651	0.408	Greece	Samos
Extinct species	Samotherium boissieri	NHML-Samos-M-4226	1.39	0.00658	0.179	Greece	Samos
Extinct species	Samotherium boissieri	NHML-Samos-M-4235	2.67	0.00418	0.418	Greece	Samos
Extinct species	Samotherium boissieri	NHML-Samos-M4234d-No14	3.41	0.00163	0.559	Greece	Samos
Extinct species	Samotherium boissieri	NHML-Samos-M-4241	3.93	0.00596	0.302	Greece	Samos
Extinct species	Samotherium major	LGPUT-VAT-157-lm2	1.41	0.00481	0.178	Greece	Vathylakkos
Extinct species	Samotherium major	AMNHS-MTLA-540	1.59	0.00530	0.429	Greece	Mytilinii A
Extinct species	Samotherium major	AMNHS-MTLA-311	1.79	0.00545	0.228	Greece	Mytilinii A
Extinct species	Samotherium major	MTA-MYS-843	2.25	0.00441	0.279	Turkey	Salihpasalar
Extinct species	Samotherium major	AMNHS-MTLB95	2.71	0.00479	0.336	Greece	Mytilinii B
Extinct species	Samotherium major	MTA-MYS-848	4.63	0.00089	0.562	Turkey	Salihpasalar
Extinct species	Samotherium major	MTA-MYS-620	4.95	0.00238	0.939	Turkey	Serefköy-1
Extinct species	Samotherium major	MTA-MYS-847	5.21	0.00198	0.159	Turkey	Salihpasalar
Extinct species	Samotherium major	SMNK-MA3	1.16	0.00325	0.254	Turkey	Mahmut Ghazi
Extinct species	Samotherium neumayeri	MNHN-MAR-528	0.66	0.00199	0.149	Iran	Maragheh