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

Gildas Merceron, Marc Colyn, Denis Geraads

► To cite this version:

Gildas Merceron, Marc Colyn, Denis Geraads. Browsing and non-browsing extant and extinct giraffids Evidence from dental microwear textural analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2018, 505, pp.128-139. 10.1016/j.palaeo.2018.05.036 . hal-01834854v2

HAL Id: hal-01834854

<https://hal-univ-rennes1.archives-ouvertes.fr/hal-01834854v2>

Submitted on 6 Sep 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Browsing and non-browsing extant and extinct giraffids: evidence from dental microwear
textural analysis.

Gildas MERCERON¹, Marc COLYN², Denis GERAADS³

¹ Palevoprim (UMR 7262, CNRS & Université de Poitiers, France)

² ECOBIO (UMR 6553, CNRS & Université de Rennes 1, Station Biologique de Paimpont,
France)

³ CR2P (UMR 7207, Sorbonne Universités, MNHN, CNRS, UPMC, France)

¹Corresponding author: gildas.merceron@univ-poitiers.fr

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 History 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, Frankfurt, Germany; UP Paleoprimate lab, University of Poitiers, France; KNM National Museums of Kenya, Nairobi, Kenya; MNHN Muséum National d'Histoire 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-

locus DNA analysis recognizes the existence of four species (Fennessy et al., 2016): *G. giraffa* (southern giraffe), *G. tippelskirchi* (Masai giraffe), *G. reticulata* (reticulated giraffe) and *G. camelopardalis* (northern giraffe). The geographical distribution of the giraffe and its genetic diversity were even higher until the Holocene since subfossil remains and glyph representations in caves and rock shelters attest to its presence 4,000 years ago in north-western Africa and along the Nile Valley (Le Quellec, 1999). Because of these taxonomic uncertainties, we made the choice to group all modern giraffes under *Giraffa* sp. Our purpose here is to have an ecologically homogeneous milestone to represent the leaf-dominant browsing ecospace. None of the specimens of modern species used in this study were captive before death, they were shot in the wild decades ago.

The fossil specimens belong to six genera: *Bohlinia*, *Helladotherium*, *Palaeogiraffa*, *Palaeotragus* and *Samotherium*. The material comes from a dozen upper Miocene (Vallesian and Turolian) localities in Greece, Bulgaria, Turkey, Afghanistan, Iran and Tunisia (Table 1, Fig. 1). *Helladotherium duvernoyi* comes from the turolian faunas of Southern Bulgaria (Geraads et al., 2005; Spassov, 2002), continental Greece (Kostopoulos et al., 1996; Solounias, 1981), and southern Tunisia (but the identification there is less secure). The specimens attributed to *Bohlinia attica* (Giraffinae) come from Nikiti-1 in Greece dated to close to the Vallesian-Turolian transition (Kostopoulos, 2016) and from Kalimantsi (K), Bulgaria (Geraads et al., 2005). Among the Palaeotraginae, the specimens assigned to *Samotherium major* come from turolian sites: Mytilini-A, Mytilini-B (MTLA and MTLB; two sites from the Mytilini ravines in Samos Island, Greece; Kostopoulos, 2009), Vathylakkos-3 (VAT) in the Axios Valley (Geraads, 1978), Salihpasalar (MYS) and Irefköy-1 (MYSe-1) in the Mu la Yata an Basin of Turkey (Kaya et al., 2012), and from the Turolian of Mahmutgazi (MA) in Turkey (Sickenberg, 1975). The specimens of *S. boissieri* do not come 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 (RPI; 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), erefköy-1 and erefköy-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 (RPI) 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 Yulafl, in Turkish Thrace.

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

reflect the dietary bolus from the last few weeks, one might fear that the signal from such small samples is meaningless, but Purnell *et al.* (2012) have shown that significant differences in textural parameters can be detected even for small samples ($N < 5$) of fishes (see also Purnell *et al.*, 2013). Besides, the analysis of several scans per individual, as proposed by Purnell and Darras (2016) and as done in the present study, mitigates the effects of the small sample size..

2.2. Methods

DMTA is a method quantifying tooth abrasion (for detailed reviews of intra- and inter-observer errors, see DeSantis *et al.*, 2013; Galbany *et al.*, 2005; Grine *et al.*, 2002; Mihlbachler *et al.*, 2012; Calandra and Merceron, 2016; Mihlbachler and Beatty, 2012; Scott, 2012; Scott *et al.*, 2006). Tooth wear reflects individual senescence and physical properties of foods; thus, it is correlated with the availabilities of food resources and can be used to explore niche partitioning among sympatric species of mammals (Calandra and Merceron, 2016). From the scale of a whole tooth to the micrometric scars on dental facets, differences in dietary preferences are mirrored by tooth wear. DMTA has proved to be a particularly useful methodology free of (inter- and intra-)observer measurement errors at least at the analytic step (for detailed reviews of intra- and inter-observer errors, see DeSantis *et al.*, 2013; Galbany *et al.*, 2005; Grine *et al.*, 2002; Mihlbachler *et al.*, 2012; Mihlbachler and Beatty, 2012) in assessing diets of fossil as well as modern taxa (Calandra and Merceron, 2016).

The analysis was performed preferentially on second upper or lower molars (Figs. 2 and 3). However, third or first molars were considered when the second molars are weathered, too much worn or too recently erupted. Following standard procedures, replicas of dental facet were produced with a silicone (medium consistency) polyvinylsiloxane (Coltène Whaledent, President Regular Body, ISO 4823). Scans ($320 \times 280 \mu\text{m}$) were produced on

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

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

an intermediate complexity (Asfc) between the hartebeest and the yellow-backed duiker (Tables 1 and 3; Figs. 2 and 5). The differences in dental microwear textures between the two browsing species reflect the ingestion of fruits and seeds by the duiker (Ramdarshan et al., 2016). The dental microwear textures (intermediate complexity and anisotropy) of the red deer (*Cervus elaphus*) reflect its mixed feeding habits that involve both browsing and grazing (Tables 1 and 3; Figs. 2 and 5). The third variable, heterogeneity of complexity (HAsfc), provides a significant complement. The giraffe and the hartebeest foraging mostly on a homogeneous source of vegetation (tree leaves and herbaceous monocotyledons, respectively; Estes, 1991, Gagnon and Chew, 2000; Leuthold, 1978; Parker et al., 2003) over long time span (over a year) have lower values than the red deer and the yellow-backed duiker whose diets are mechanically diverse and variable from a day to another or from a season to another (Tables 1 and 3; Figs. 2 and 5; Estes, 1991; Gebert and Verheyden-Tixier, 2001; Gagnon and Chew, 2000; Gauthier-Hion et al. 1980; Lumpkin and Kranz, 1984).

The modern okapi (*Okapia johnstoni*) has a wide distribution across the dental microwear textural ecospace. It differs from the giraffe in having higher anisotropy (epLsar) and from the yellow-backed duiker in having lower complexity (Asfc; Tables 1 and 3; Figs. 3 and 5). The okapi also differs from the hartebeest and the giraffe in having higher heterogeneity of complexity (HAsfc). It does not differ from the red deer when the two most discriminating variables (Asfc and epLsar) are considered (Tables 1 and 3; Figs. 3 and 5). These results for the present-day okapi assumed to be a browser can be discussed in light of the ecological data. Hitherto, only one single study dealt with the feeding ecology of the okapi in the wild (Hart and Hart, 1989). It was conducted at Epulu, Ituri forest, a lowland forest located at the far north eastern of the Congo basin. The authors tracked eight collared individuals for several months and recorded from direct observations browse signs on vegetation but only those ranging from 0.5 to 2.0 meters in height because *õthis is the forest*

260 *layer most frequently browsed by okapiö* (Hart and Hart, 1989: 35). There is indeed no record
261 regarding lower vegetal layers. Hart and Hart (1989) identified shade- and light-tolerant plant
262 species, all of them being dicotyledonous trees or bushes, constituting the staple food
263 spectrum of the okapi. However, one of these two authors from the pioneer study mentions in
264 Kingdon et al. (2013: in vol. VI, p. 110-115) that herbaceous monocotyledons are part of the
265 okapi diet but does not provide details regarding their abundance. Hart and Hart (1989) had
266 actually made mention that the okapi favors tree-fall gaps where it leaves the highest density
267 of browse signs. These tree-fall gaps are also hotspots of biodiversity in the Central African
268 forest where the herbaceous vegetation (mostly monocotyledons) reaches its highest diversity
269 and density. These plant resources are known to be critical in dense forested habitats for other
270 mammals such as buffaloes (Blake, 2002), gorillas, and pygmy chimpanzees (Blake et al.,
271 1995; Malenky and Wrangham, 1994; Williamson et al., 1990). For instance, these apes feed
272 on herbaceous stems (sometimes only the soft inner pith) of monocotyledonous plants such as
273 Marantacea and Zingiberacea (Malenky and Wrangham, 1994; Williamson et al., 1990;
274 Wrangham et al., 1991). Monocotyledonous plants have generally higher silica content than
275 dicotyledonous plants (Hodson et al., 2005). Besides, the herbaceous stems that are eaten are
276 tougher than most fruits (Elgart-Berry, 2004). Therefore, on the basis of the dental microwear
277 textures of the okapis analyzed in the present study and the information provided by Hart and
278 Hart (1989) and Hart in Kingdon et al. (2013), we hypothesize that the okapi does include
279 some terrestrial herbaceous vegetation in its diet, especially when its home range overlaps tree
280 fall gaps. Our hypothesis needs to be tested in the future through alternative direct or non
281 direct dietary proxies and new material. It is worth mentioning that Clauss et al. (2006) had
282 described the digestive tract of two captive okapis as similar to that of modern selective
283 browsers with the exception that the parotid glands were found to be small, a feature shared
284 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

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

Bohlinia attica was a giraffine weighting about a ton; it was likely able to reach foliage as high as the modern giraffe, from 4 to 6 m above ground (Table 4, Fig. 6; Leuthold, 1978; O'Connor et al., 2015). The dental microwear textures attest that *B. attica* fed mostly on soft foliages, as modern giraffes do (Figs. 5 and 6). The body traits found in *Bohlinia* and *Giraffa* and their similarities in tooth wear both suggest that the ecological niche of leaf-dominated browsers targeting the highest tree foliages was shared by the common ancestor.

Among large giraffids, the sivatheriine *Helladotherium duvernoyi* weighted as much as two tons; the low values for the three textural parameters depict it as a likely leaf-dominant browser (Fig. 5). Thus, *H. duvernoyi* shared similar feeding habits with *B. attica*, in spite of its distinctly higher molar crowns (Table 4), but could not reach foliages as high as this species, which was less stoutly built, but taller (Table 4, Fig. 6). *Palaeogiraffa* is represented in this study by three species. They were less tall than *B. attica*, and thus had reduced competition with it to exploit tree foliages (Fig. 6). *Palaeogiraffa pamiri* from Thrace was likely a leaf-dominant browser while the contemporaneous *P. macedoniae* and *P. major* from the lower Axios valley in Greece may have incorporated herbaceous monocotyledons in their diet. Such contrasted differences between species of the same genus (Figs. 5 and 6) might reflect differences in food resources between the two regions (woody landscapes in the Thracian site and floodplain grasslands along the Axios).

In the late Miocene of the Mediterranean region, palaeotragines were more diverse than sivatheriines and giraffines, but the height range at which they could browse is far smaller than their species diversity and body mass range suggest. The palaeotragine *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

that *H. duvernoyi* and *Samotherium* spp. browsed (Table 4, Fig. 6). A more versatile diet than that of *H. duvernoyi* could explain their coexistence at some sites, and thus the probable overlap of their home ranges. *Palaeotragus coelophrys* was stouter than *P. rouenii*, but based on their metacarpal lengths, they could reach the same foliages. A fifth species of palaeotragine, *Samotherium neumayri*, is represented by a single individual whose body mass was similar to that of the modern giraffe but with a height at the withers similar to that of other palaeotragines; its dental microwear texture suggests that this specimen fed on soft foliages the few weeks before its death.

3.3 Dietary adaptation and Phylogeny

A recent study based on new material challenges the phylogeny of the giraffids (Ríos et al., 2017). Giraffines are represented by the modern giraffes and the species of the genus *Bohlinia*. The elongation of the cervical vertebrae and the extreme elongation of the metacarpal allowing them to forage on the highest arboreal stratum may be seen as an autapomorphy of the Giraffinae (Ríos et al., 2017). Our data strongly support such dietary adaptations. Besides, the monophyly of the paleotragines is challenged. According to their study, the genus *Samotherium*, previously thought to be close to *Palaeotragus*, actually shares a set of derived features with the Sivatherinae. The species of the genus *Palaeotragus* compose the sister group of a monophyletic group including the modern okapi, *Decennatherium*, *Palaeogiraffa* (assumed to be close to the former genus according to these authors) and *Samotherium* in which the sivatherines (including *Helladotherium*) are rooted. More versatile feeding habits might have been the ancestral conditions for this second clade. In view of this phylogeny proposed by Ríos et al. (2017), we may consider that either browsing or mixed feeding habits were the ancestral ecological conditions for giraffids. The 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 C₄ plants, i.e. herbaceous monocots,
413 in their diet.

414

415 **4. Conclusions**

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

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

437

5. Acknowledgments

The authors thank C. Sagne and P. Tassy (Muséum National d'Histoire Naturelle, Paris, France), E. Robert (Geological Collections, UMR CNRS 5276 Laboratoire de Géologie de Lyon - CERES, University Lyon 1), N. Spassov and the late D. Kovatchev (National Museum of Natural History, Sofia, Bulgaria), D.S. Kostopoulos and G.D. Koufos (Aristotle University of Thessaloniki, Greece), S. Mayda and T. Kaya (Natural History Museum, Ege University, Izmir, Turkey), W. Wendelen (RMCA, Tervuren, Belgium), L. Costeur (Naturhistorisches Museum at Basel, Switzerland), and W. Munk (Staatliches Museum für Naturkunde, Karlsruhe, Germany), for giving access to collections. We are grateful to A. Souron (University of Bordeaux-1) who contributed to the sampling of okapis.

A significant part of the fossil material was sampled in various European institutions thanks to the International Research Collaborative Grant "*Environmental Dynamics of Western Eurasian Hominids during the Late Miocene*" (PIs: R. S. Scott and T. Kaya) funded by the Wenner-Gren Foundation. G.M. thanks his colleagues of the Wenner-Gren International Research Collaborative Grant group: R.S. Scott (Rutgers University, USA), D.S. Kostopoulos (Aristotle University of Thessaloniki, Greece), T. Kaya and S. Mayda (Ege University, Izmir, Turkey) as well as G. Reynaud and S. Riffaut (Paleovprim). We also thanks the associate editor I. Montanez and four reviewers including N. Spassov for their helpful comments that greatly improve the manuscript. This study was funded by the Project TRIDENT (ANR-13-JSV7-0008-01, PI: G. Merceron, France; <http://anr-trident.prd.fr/>).

6. Data availability

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

6. References

- Blake, S., 2002. Forest buffalo prefer clearings to closed-canopy forest in the primary forest of northern Congo. *Oryx* 36, 81686.
- Blake, S., Rogers, E., Fay, J.M., Ngangoué, M., Ebéké, G., 1995. Swamp gorillas in northern Congo. *Afr. J. Ecol.* 33, 2856290. <https://doi.org/10.1111/j.1365-2028.1995.tb00809.x>
- Bonis, L. de, Bouvrain, G., 2003. Nouveaux Giraffidae du Miocène supérieur de Macédoine (Grèce). *Adv. Vertebr. Paleontol.* 5616.
- Brown, D.M., Brenneman, R.A., Koepfli, K.-P., Pollinger, J.P., Milá, B., Georgiadis, N.J., Louis, E.E., Grether, G.F., Jacobs, D.K., Wayne, R.K., 2007. Extensive population genetic structure in the giraffe. *BMC Biol.* 5, 1.
- Brunet, M., Heintz, E., 1983. Interprétation paléoécologique et relations biogéographiques de la faune de vertébrés du Miocène supérieur de l'Iraq. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 44, 2836293.
- Calandra, I., Merceron, G., 2016. Dental microwear texture analysis in mammalian ecology: DMTA in ecology. *Mammal Rev.* 46, 2156228. <https://doi.org/10.1111/mam.12063>
- Clauss, M., Hummel, J., Völlm, J., Lorenz, A., Hofmann, R.R., 2006. The allocation of a ruminant feeding type to the okapi (*Okapia johnstoni*) on the basis of morphological parameters. *Zoo Anim. Nutr.* 3, 2536270.
- Colbert, E.H., 1938. The relationships of the okapi. *J. Mammal.* 19, 47664.
- Conover, W.J., Iman, R.L., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* 35, 1246129.
- Danowitz, M., Hou, S., Muhlbachler, M., Hastings, V., Solounias, N., 2016. A combined-mesowear analysis of late Miocene giraffids from North Chinese and Greek localities of the Pikermian Biome. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 449, 1946204.

485 DeSantis, L.R.G., Scott, J.R., Schubert, B.W., Donohue, S.L., McCray, B.M., Van Stolk,
 486 C.A., Winburn, A.A., Greshko, M.A., O'Hara, M.C., 2013. Direct Comparisons of 2D and 3D
 487 Dental Microwear Proxies in Extant Herbivorous and Carnivorous Mammals. PLoS ONE 8,
 488 e71428. <https://doi.org/10.1371/journal.pone.0071428>
 489 Elgart-Berry, A., 2004. Fracture toughness of mountain gorilla (*Gorilla gorilla beringei*) food
 490 plants. Am. J. Primatol. 62, 275-285. <https://doi.org/10.1002/ajp.20021>
 491 Estes, R.D., 1991. Behavior Guide to African mammals. The University of California Press,
 492 Los Angeles.
 493 Fennessy, J., Bidon, T., Reuss, F., Kumar, V., Elkan, P., Nilsson, M.A., Vamberger, M., Fritz,
 494 U., Janke, A., 2016. Multi-locus Analyses Reveal Four Giraffe Species Instead of One. Curr.
 495 Biol. <https://doi.org/10.1016/j.cub.2016.07.036>
 496 Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. J. Mammal. 8,
 497 490-511.
 498 Galbany, J., Martínez, L.M., López-Amor, H.M., Espurz, V., Hiraldo, O., Romero, A., de
 499 Juan, J., Pérez-Pérez, A., 2005. Error rates in buccal-dental microwear quantification using
 500 scanning electron microscopy. Scanning 27, 23-29. <https://doi.org/10.1002/sca.4950270105>
 501 Gauthier-Hion, A., Emmons, L.H., Dubost, G., 1980. A comparison of the diets of three major
 502 groups of primary consumers of Gabon (Primates, Squirrels and Ruminants). Oecologia 45,
 503 182-189.
 504 Gebert, C., Verheyden-Tixier, H., 2001. Variations of diet composition of red deer (*Cervus*
 505 *elaphus* L.) in Europe. Mammal Rev. 31, 189-201.
 506 Geraads, D., 1989. Vertébrés fossiles du Miocène supérieur du Djebel Krechem El Artsouma
 507 (Tunisie centrale). Comparaisons biostratigraphiques. Géobios 22, 777-801.
 508 Geraads, D., 1986. Remarques sur la systématique et la phylogénie des Giraffidae
 509 (Artiodactyla, Mammalia). Geobios 19, 465-477.

510 Geraads, D., 1978. Les Paleotraginae (Giraffidae, Mammalia) du Miocène supérieur de la
511 région de Thessalonique (Grèce). Géologie Méditerranéenne V, 269-276.

512 Geraads, D., Spassov, N., Kovachev, D., 2005. Giraffidae (Artiodactyla, Mammalia) from the
513 Late Miocene of Kalimantsi and Hadjidimovo, Southwestern Bulgaria. Geol. Balc. 35, 11-18.

514 Grine, F.E., Ungar, P.S., Teaford, M.F., 2002. Error rates in dental microwear quantification
515 using scanning electron microscopy. Scanning 24, 144-153.
516 <https://doi.org/10.1002/sca.4950240307>

517 Groves, C., Grubb, P., 2011. Ungulate taxonomy. JHU Press.

518 Hart, J.A., Hart, T.B., 1989. Ranging and feeding behaviour of okapi (*Okapia johnstoni*) in
519 the Ituri Forest of Zaire: food limitation in a rain-forest herbivore, in: Symposium of the
520 Zoological Society of London. pp. 31-50.

521 Hassanin, A., Ropiquet, A., Gourmand, A.-L., Chardonnet, B., Rigoulet, J., 2007.
522 Mitochondrial DNA variability in *Giraffa camelopardalis*: consequences for taxonomy,
523 phylogeography and conservation of giraffes in West and central Africa. C. R. Biol. 330, 265-
524 274.

525 Hodson, M.J., White, P.J., Mead, A., Broadley, M.R., 2005. Phylogenetic variation in the
526 silicon composition of plants. Ann. Bot. 96, 1027-1046.

527 Kaya, T.T., Mayda, S., Kostopoulos, D.S., Alcicek, M.C., Merceron, G., Tan, A., Karakutuk,
528 S., Giesler, A.K., Scott, R.S., 2012. Irefköy-2, a new late Miocene mammal locality from
529 the Yatağan Formation, Muğla, SW Turkey. Comptes Rendus Palevol 11, 5-12.

530 Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., Kalina, J., 2013.
531 Mammals of Africa. A&C Black.

532 Kostopoulos, D.S., 2016. Palaeontology of the upper Miocene vertebrate localities of Nikiti
533 (Chalkidiki Peninsula, Macedonia, Greece): Artiodactyla. Geobios 49, 119-134.

534 Kostopoulos, D.S., 2009. The Late Miocene mammal faunas of the Mytilinii Basin, Samos
 535 Island, Greece: new collection. 13. Giraffidae. Beitr. Zur Paläontol. 31, 299-343.
 536 Kostopoulos, D.S., Koliadimou, K.K., Koufos, G.D., 1996. The giraffids from the Late
 537 Miocene mammalian localities of Nikiti (Macedonia, Greece). Palaeontogr. Abt. -Stuttg.- 239,
 538 61-688.
 539 Kostopoulos, D.S., Sen, S., 2016. Suidae, Tragulidae, Giraffidae, and Bovidae. Geodiversitas
 540 38, 273-298.
 541 Koufos, G.D., 2009. The Late Miocene mammal faunas of the Mytilinii Basin, Samos Island,
 542 Greece: new collection. 1. History of the Samos Fossil Mammals. Beitr. Zur Paläontol. 31, 1-
 543 12.
 544 Koufos, G.D., 2006. The Neogene mammal localities of Greece: faunas, chronology and
 545 biostratigraphy. Hell. J. Geosci. 41, 183-214.
 546 Le Quellec, J.-L., 1999. Répartition de la grande faune sauvage dans le nord de l'Afrique
 547 durant l'Holocène. Anthropol.-PARIS- 103, 161-176.
 548 Leuthold, B.M., 1978. Ecology of the giraffe in Tsavo East National Park, Kenya. East Afr.
 549 Wildl. J. 16, 1-20.
 550 Lumpkin, S., Kranz, K.R., 1984. *Cephalophus sylvicultor*. Mamm. Species 225, 1-7.
 551 Malenky, R.K., Wrangham, R.W., 1994. A quantitative comparison of terrestrial herbaceous
 552 food consumption by *Pan paniscus* in the Lamako forest, Zaire, and *Pan troglodytes* in the
 553 Kibale forest, Uganda. Am. J. Primatol. 32, 1-12.
 554 Mecquenem, R. de, 1924. Contribution à l'étude des fossiles de Maragha. Ann. Paléontol.
 555 Vertébrés 13/14, 135-160.
 556 Merceron, G., Ramdarshan, A., Blondel, C., Boissérie, J.-R., Brunetiere, N., Francisco, A.,
 557 Gautier, D., Milhet, X., Novello, A., Pret, D., 2016. Untangling the environmental from the
 558 dietary: dust does not matter. Proceeding R. Soc. Lond. B 283, 20161032.

559 Mihlbachler, M.C., Beatty, B.L., 2012. Magnification and resolution in dental microwear
560 analysis using light microscopy. *Paleontol Electron.* 15, 25A.

561 Mihlbachler, M.C., Beatty, B.L., Caldera-Siu, A., Chan, D., Lee, R., 2012. Error rates and
562 observer bias in dental microwear analysis using light microscopy. *Palaeontol. Electron.* 15,
563 12A.

564 O'Connor, D.A., Butt, B., Fofopoulou, J.B., 2015. Foraging ecologies of giraffe (*Giraffa*
565 *camelopardalis reticulata*) and camels (*Camelus dromedarius*) in northern Kenya: effects of
566 habitat structure and possibilities for competition? *Afr. J. Ecol.* 53, 1836193.
567 <https://doi.org/10.1111/aje.12204>

568 Parker, D.M., Bernard, R.T.F., Colvin, S.A., 2003. The diet of a small group of extralimital
569 giraffe. *Afr. J. Ecol.* 41, 245.

570 Purnell, M., Seehausen, O., Galis, F., 2012. Quantitative three-dimensional microtextural
571 analyses of tooth wear as a tool for dietary discrimination in fishes. *J. R. Soc. Interface* 9,
572 222562233.

573 Purnell, M.A., Crumpton, N., Gill, P.G., Jones, G., Rayfield, E.J., 2013. Within-guild dietary
574 discrimination from 3-D textural analysis of tooth microwear in insectivorous mammals. *J.*
575 *Zool.* 291, 2496257.

576 Purnell, M.A., Darras, L.P.G., 2016. 3D tooth microwear texture analysis in fishes as a test of
577 dietary hypotheses of durophagy. *Surf. Topogr. Metrol. Prop.* 4, 014006.
578 <https://doi.org/10.1088/2051-672X/4/1/014006>

579 Ramdarshan, A., Blondel, C., Brunetière, N., Francisco, A., Gautier, D., Surault, J., Merceron,
580 G., 2016. Seeds, browse, and tooth wear: a sheep perspective. *Ecol. Evol.* 6, 555965569.

581 Ríos, M., Sánchez, I.M., Morales, J., 2017. A new giraffid (Mammalia, Ruminantia, Pecora)
582 from the late Miocene of Spain, and the evolution of the sivathere-samotherium lineage. *PLOS*
583 *ONE* 12, e0185378. <https://doi.org/10.1371/journal.pone.0185378>

584 Ríos, M., Sánchez, I.M., Morales, J., 2016. Comparative anatomy, phylogeny, and
 585 systematics of the Miocene giraffid *Decennatherium pachecoi* Crusafont, 1952 (Mammalia,
 586 Ruminantia, Pecora): State of the art. J. Vertebr. Paleontol. 36, e1187624.
 587 <https://doi.org/10.1080/02724634.2016.1187624>
 588 Scott, J.R., 2012. Dental microwear texture analysis of extant African Bovidae. Mammalia 76,
 589 1576174.
 590 Scott, K.M., 1990. Postcranial dimensions of ungulates as predictors of body mass. Body Size
 591 Mamm. Paleobiology Estim. Biol. Implic. 30, 16335.
 592 Scott, R.S., Ungar, P., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A.,
 593 2006. Dental microwear texture analysis: technical considerations. J. Hum. Evol. 51, 3396
 594 349.
 595 Sen, S., 1998. The age of the Molayan mammals locality, Afghanistan. Geobios 31, 3856391.
 596 Senyürek, M.S., 1954. A study of the remains of *Samotherium* found at - Recherche Google.
 597 Rev. Fac. Lang. Hist. Géographie Univ. Ank. 12, 1632.
 598 Sickenberg, O., 1975. Die Gliederung des höheren Jungtertiärs und Altquartärs-in der Türkei
 599 nach Vertebraten und ihre Bedeutung für die-internationale Neogen-Gliederung. Geol. Jahrb.
 600 Reihe B 16167.
 601 Sokal, S.R., Rohlf, F.J., 1969. Biometry. W. E. Freeman and Company, New York.
 602 Solounias, N., 1988. Evidence from horn morphology on the phylogenetic relationship of the
 603 Pronghorn (*Antilocapra americana*). J. Mammal. 69, 1406143.
 604 Solounias, N., 1981. Mammalian fossils of Samos and Pikermi. Part 2. Resurrection of a
 605 classic turolian fauna. Ann. Carnegie Mus. 50, 2316269.
 606 Solounias, N., Danowitz, M., 2016. The Giraffidae of Maragheh and the identification of a
 607 new species of *Honanotherium*. Palaeobiodiversity Palaeoenvironments 96, 489-506.

608 Solounias, N., Dawson-Saunders, B., 1988. Dietary adaptations and paleoecology of the late
609 Miocene ruminants from Pikermi and Samos in Greece. *Palaeogeogr. Palaeoclimatol.*
610 *Palaeoecol.* 65, 149-172.

611 Solounias, N., Mac Graw, W.S., Hayek, L.-A., Werdelin, L., 2000. The paleodiet of the
612 Giraffidae, in: Vrba, E.S., Schaller, G.B. (Eds.), *Antelopes, Deer, and Relatives*. Yale
613 University Press, New Haven, pp. 84-95.

614 Solounias, N., Rivals, F., Semprebon, G.M., 2010. Dietary interpretation and paleoecology of
615 herbivores from Pikermi and Samos (late Miocene of Greece). *Paleobiology* 36, 113-136.
616 <https://doi.org/10.1666/0094-8373-36.1.113>

617 Solounias, N., Teaford, M.F., Walker, A., 1988. Interpreting the diet of extinct ruminants : the
618 case of a non-browsing giraffid. *Paleobiology* 14, 287-300.

619 Spassov, N., 2002. The Turolian Megafauna of West Bulgaria and the character of the Late
620 Miocene -Pikermian biome. *Bull. Della Soc. Paleontol. Ital.* 41, 69-81.

621 Thenius, E., 1992. Das Okapi (Mammalia, Artiodactyla) von Zaire - šlebendes Fossilö oder
622 sekundärer Urwaldbewohner? *J. Zool. Syst. Evol. Res.* 30, 163-179.
623 <https://doi.org/10.1111/j.1439-0469.1992.tb00166.x>

624 Williamson, E.A., Tutin, C.E.G., Rogers, M.E., Fernandez, M., 1990. Composition of the diet
625 of lowland gorillas at Lopé in Gabon. *Am. J. Phys. Anthropol.* 21, 265-277.

626 Wilson, D.E., Reeder, D.M., 2005. *Mammal species of the world: a taxonomic and*
627 *geographic reference*. JHU Press.

628 Wrangham, R.W., Conklin, N.L., Chapman, C.A., Hunt, K.D., 1991. The significance of
629 fibrous foods for Kibale forest chimpanzees. *Philos. Transl. R. Soc. Lond.* 334, 171-178.

630

631

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

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

	<i>df</i>	SS	MS	F	<i>p</i>
Asfc	14	115848.3	8274.9	3.1334	0.0002
	176	464791.7	2640.9		
	<i>df</i>	SS	MS	F	<i>P</i>
epLsar	14	176760.3	12625.7	5.5020	0.0000
	176	403878.7	2294.8		
	<i>df</i>	SS	MS	F	<i>P</i>
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).

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

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

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

649 Metacarpal length (in mm), body mass (in kg) based upon humerus distal articular width (in mm) following the
650 equation of Scott (1990) for Ruminants (body mass = $10^{(2.5518 \cdot \log(\text{Humerus W}) + 0.4093)}$), indexes of upper and lower
651 premolar/molar rows of modern and extinct giraffids. Most data are our own, with a few additions from Bohlin
652 (1926⁽¹⁾), Kostopoulos (2009⁽²⁾, 2016⁽³⁾) and Senyürek (1954⁽⁴⁾).

653

654

655 **Figure captions**

656

657

658

659

660

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 photomicrographs 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).

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

Cervus elaphus
UP - Chat-9-4168-scan D
Asfc = 2.28
epLsar = 0.0066

Alcelaphus buselaphus
UP-ART 8-21-scan B
Asfc = 1.34
epLsar = 0.0079

Cephalophus silvicultor
NHMB-319-scan C
Asfc = 2.29
epLsar = 0.0047

Giraffa camelopardalis
NHMB-Z553-scan D
Asfc = 2.21
epLsar = 0.0017

Okapia johnstoni
NHMB-Z1085-scan A
Asfc = 1.22
epLsar = 0.0074

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.

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

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

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

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

State	Species	Individual	Asfc	epLsar 1.8 μ m	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 silivictor	NHMB-Csilv-14	8.18	0.00175	0.504
Extant species	Cephalophus silivictor	NHMB-Csilv-1611	2.96	0.00607	0.289
Extant species	Cephalophus silivictor	NHMB-Csilv-1612	2.65	0.00101	0.520
Extant species	Cephalophus silivictor	NHMB-Csilv-1616	2.11	0.00290	0.497
Extant species	Cephalophus silivictor	NHMB-Csilv-1617	3.51	0.00428	0.467
Extant species	Cephalophus silivictor	NHMB-Csilv-319	4.11	0.00288	1.325
Extant species	Cephalophus silivictor	NHMB-Csilv-366	2.21	0.00615	0.384
Extant species	Cephalophus silivictor	NHMB-Csilv-578	3.32	0.00256	0.813
Extant species	Cephalophus silivictor	NHMB-Csilv-878	6.06	0.00139	1.089
Extant species	Cephalophus silivictor	NHMB-Csilv-924	2.07	0.00426	0.317
Extant species	Cephalophus silivictor	NHMB-Csilv-DIE-1	17.03	0.00063	0.605
Extant species	Cephalophus silivictor	NHMB-Csilv-GM4	3.06	0.00211	0.975
Extant species	Cephalophus silivictor	NHMB-Csilv-R12923	1.45	0.00223	0.156
Extant species	Cephalophus silivictor	NHMB-Csilv-R16753	2.66	0.00191	0.427
Extant species	Cephalophus silivictor	NHMB-Csilv-SN-DIB-95	1.52	0.00454	0.318
Extant species	Cephalophus silivictor	NHMB-Csilv-Z2039-2	2.62	0.00209	0.280
Extant species	Cephalophus silivictor	NHMB-Csilv-Z3048	7.53	0.00153	0.283
Extant species	Cephalophus silivictor	NHMB-Csilv-Z3344	2.15	0.00460	0.359
Extant species	Cephalophus silivictor	NHMB-Csilv-Z3347	3.43	0.00460	0.623
Extant species	Cephalophus silivictor	NHMB-Csilv-Z352	1.95	0.00476	0.338
Extant species	Cephalophus silivictor	NHMB-Csilv-Z3669	2.11	0.00312	0.334
Extant species	Cephalophus silivictor	NHMB-Csilv-Z3916	5.29	0.00355	0.749
Extant species	Cephalophus silivictor	NHMB-Csilv-Z3918	3.53	0.00476	0.344
Extant species	Cephalophus silivictor	NHMB-Csilv-Z404	6.10	0.00140	1.063
Extant species	Cephalophus silivictor	NHMB-Csilv-Z464	3.07	0.00170	0.455

706

707

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	LGPU-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	LGPU-NKT-148-UM2	1.44	0.00097	0.432	Greece	Nikiti-1
Extinct species	Bohlinia attica	LGPU-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	LGPU-NIK 1804	2.27	0.00555	0.298	Greece	Nikiti-2
Extinct species	Helladotherium duvernoyi	LGPU-NIK 1057	2.32	0.00472	0.250	Greece	Nikiti-2
Extinct species	Helladotherium duvernoyi	LGPU-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	LGPU-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	LGPU-PNT 137	2.00	0.00150	0.329	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPU-PNT 328	2.01	0.00682	0.357	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPU-PNT 136	2.33	0.00669	0.194	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPU-PNT 112	2.75	0.00346	0.488	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPU-PNT 111A	2.86	0.00376	0.220	Greece	Pentalophos
Extinct species	Palaeogiraffa macedoniae	LGPU-PNT 121	3.72	0.00851	0.545	Greece	Pentalophos
Extinct species	Palaeogiraffa major	LGPU-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	LGPU-RPL104	1.32	0.00592	0.304	Greece	Ravin de la Pluie
Extinct species	P. coelophrys	LGPU-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	LGPU-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	LGPU-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	LGPU-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	LGPU-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