Ruminant diets and the Miocene extinction of European great apes

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The successful evolutionary radiations of European hominoids and pliopithecoids came to an end during the Late Miocene. Using ruminant diets as environmental proxies, it becomes possible to detect variations in vegetation over time with the potential to explain fluctuations in primate diversity along a NW–SE European transect. Analysis shows that ruminants had diverse diets when primate diversity reached its peak, with more grazers in eastern Europe and more browsers farther west. After the drop in primate diversity, grazers accounted for a greater part of western and central European communities. Eastwards, the converse trend was evident with more browsing ruminants. These opposite trends indicate habitat loss and an increase in environmental uniformity that may have severely favoured the decline of primate diversity.

Keywords: biodiversity; hominoids; Neogene; environmental dynamics; ungulates

1. INTRODUCTION

During the Miocene epoch, the Eurasian continent was home to a great radiation of hominoid primates that pre-dated the radiation of hominids in Africa. Records show more than 10 genera ranging from Spain to south-eastern Asia (Begun 2007; Moyà-Solà *et al.* 2009). The pliopithecoids, a catarrhine superfamily with no known descendants, were also taxonomically and ecologically diverse. In Europe, they appear even more diverse than hominoids, with more than 10 species representing five genera and two families (Begun 2002). While pliopithecoids became uniformly extinct in Eurasia, hominoid evolution was presumably continuous in southeastern Asia, as they are still diverse there (Rowe 1996). A different pattern characterizes the western part of the continent, and especially Europe. Indeed, hominoids and pliopithecoids went gradually extinct there during the Late Miocene, in all likelihood with a west–east trend, after a dramatic drop during the Late Tortonian (11.2–7.1 Ma) and more specifically around the Vallesian/Turolian mammalian age boundary (i.e. around 8.7 Ma; Andrews *et al.* 1996). At the same time, as both European hominoids and pliopithecoids became less diverse before their extinction, a distinct dispersal of colobine cercopithecoids took place throughout Europe. However, their diversity remained restricted to only one genus, *Mesopithecus* (Andrews *et al.* 1996).

Recent studies demonstrate that environmental heterogeneity, coupled with stable climatic conditions, is a major factor in maintaining high specific diversity (Griffin

et al. 2009). We may therefore hypothesize that the drop in diversity among European primates was a direct response to habitat loss and more homogeneous environmental conditions. Previous authors concluded that the faunal changes in Europe during the Late Miocene are the result of the climate change that comes with the development of higher seasonality (de Bonis *et al.* 1992; Eronen & Rook 2004; Fortelius *et al.* 2006; Eronen *et al.* 2009). An eastward trend towards drier conditions has also been noted. All of these studies were actually based either on faunal composition or on ecomorphological proxies. The former approach is limited by the fact that faunal events such as species dispersal are strongly constrained by geomorphological contexts (Fortelius *et al.* 1996; Costeur & Legendre 2008; Kostopoulos 2009). Thus, it is difficult to reliably detect which faunal events carry an environmental and climatic signal. For instance, the dispersion of hipparionines in Eurasia, thought to be synonymous with grassland expansion, actually postdates their development in Anatolia (Strömberg *et al.* 2007). The ecomorphology-based studies are also limited. Indeed, certain features used as environmental and/or climate proxies do not actually reflect ecology, and therefore blur the environmental signal. For instance, some taxa retain high-crowned cheek teeth as a plesiomorphic condition thought to be associated with grazing feeding habits, even though they may have a wider spectrum of feeding traits (MacFadden *et al.* 1999; Rivals & Semperebon 2006).

In view of this, spatial and temporal changes in environmental conditions are herein quantified using a taxon-free proxy: the diet of extinct ruminants. These ungulates constitute an excellent model because: (i) in Neogene and modern environments, they dominate the large herbivore guild; (ii) they have experienced

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Figure 1. Dental wear patterns of Late Miocene ruminants track the drop in primate diversity. 848 extant ruminants, such as (a) the roe deer (*Capreolus capreolus*), involved either in grazing or browsing are used as comparative datasets. Their dental (b) mesowear (MwS) and (c) microwear (MiC) signatures displayed by mean and confidence interval of the mean (95%) actually reflect their feeding styles. (d) The dental mesowear (MwS) and microwear (MiC) pattern of 552 extinct ruminants clustered in community show significant variations depending on location (Germany, Hungary, Greece) before and after the Vallesian (square)/Turolian (triangle) mammalian age limit (approx. 8.7 Ma). The dietary signals strongly differ from one community to another, while hominoids and pliopithecoids were still diverse during the Vallesian period. Conversely, a trend towards more homogeneous conditions is detected during the early Turolian interval during which primate diversity drops.

important evolutionary radiations, expanding into a great variety of ecological niches ranging from the arctic tundra to closed canopy; and (iii) their dietary habits are closely related to the local environments, since they are vegetarians. Combining two taxon-free approaches for dietary reconstruction, both based on the cheek teeth as the very first constituents of the digestive tract, allows us to estimate changes in past vegetation and consequently environmental dynamics. While the dental mesowear score (MwS) provides a long-term signal of dietary abrasiveness (Fortelius & Solounias 2000), the dental microwear signal reflects the physical properties of foods before death and is therefore more likely to be indicative of diet in a shorter term (Walker *et al.* 1978). Both the dental mesowear and microwear signatures of every specimen were condensed into two synthetic variables as dietary estimators: MwS and microwear coordinate (MiC; figure 1; electronic supplementary material, tables S1 and S2). Two inter-community disparities, d_1 and d_2 , are then computed to quantify spatial and temporal differences between communities, respectively. A third index, d_3 , is also calculated to quantify the 'within-community' disparity (for details, see §2).

The sampling strategy employed here is geographically focused on three geographical spots along a northwest–southeast European transect (figure 1), and restricted to the Vallesian and Early Turolian mammal ages (electronic supplementary material, table S3), during which time the highest decline in primate diversity took place. Six

communities are here defined: the Vallesian ruminants from Germany, Hungary and Greece that coexisted with hominoids and possibly pliopithecoids, and the Turolian ones that existed after the last occurrence of hominoids in the same three regions. The Vallesian hominoid record related to the investigated sites includes three taxa: cf. *Dryopithecus* in Germany, *Dryopithecus branchoi* in Hungary and *Ouranopithecus macedoniensis* in Greece (Begun 2007). Pliopithecoids co-occurred with hominoids in western and central Europe (Begun 2002). Although they may have persisted after the Vallesian mammalian age in eastern Europe (Spassov & Geraads 2008), hominoids—and pliopithecoids as well—are actually absent from the three investigated spots during the Early Turolian.

2. MATERIAL AND METHODS

(a) Material

The material studied belongs to several European Late Miocene localities. Ravin de la Pluie in Greece, Rudabánya in Hungary, and Höwenegg and Deinother Sand localities (Esselborn and Eppelsheim) in Germany comprise the Vallesian samples (MN zones 9–10; electronic supplementary material, table S4). These regions have yielded hominoid remains: *O. macedoniensis* in Greece (de Bonis & Melentis 1977; de Bonis *et al.* 1990), *D. branchoi* in Hungary (Kretzoi 1975) and a hominoid assigned to the genus *Dryopithecus* in Germany (Franzen *et al.* 2003). Ravin des Zouaves-5 in

Table 1. Summary statistics (number of specimens *n*, mean *m* and standard deviation s.d.) for the dietary estimators (A; microwear coordinate MiC and mesowear score MwS) and the three inter- and intra-community disparities (B, C and D).

			MwS		MiC	
A						
age	spot	<i>n</i>	<i>m</i>	s.d.	<i>m</i>	s.d.
Vallesian	Germany	40	0.46	0.30	−1.71	1.63
	Hungary	71	0.56	0.27	−0.50	2.10
	Greece	115	1.09	0.52	1.38	1.46
Early Turolian	Germany	165	0.59	0.48	−0.20	1.28
	Hungary	96	0.61	0.41	0.77	1.39
	Greece	95	0.98	0.58	0.41	1.42
B			disparity <i>d</i> ₁			
age	inter-spot couples	<i>n</i>	<i>m</i>	s.d.		
Vallesian	all	15 605	2.92	1.74		
	Hungary–Greece	8165	2.82	1.63		
	Germany–Greece	4600	3.45	1.77		
	Germany–Hungary	2840	2.33	1.78		
Early Turolian	all	40 635	1.75	1.31		
	Hungary–Greece	9120	1.72	1.31		
	Germany–Greece	15 675	1.74	1.31		
	Germany–Hungary	15 840	1.78	1.31		
C			disparity <i>d</i> ₂			
inter-age couple	spots	<i>n</i>	<i>m</i>	s.d.		
Vallesian–Turolian	Germany	6600	2.21	1.42		
	Hungary	6816	2.37	1.58		
	Greece	10 925	2.01	1.27		
D			disparity <i>d</i> ₃			
age	spots	<i>n</i>	<i>m</i>	s.d.		
Vallesian	Germany	40	1.29	1.02		
	Hungary	71	1.67	1.29		
	Greece	115	1.17	1.01		
Early Turolian	Germany	165	1.02	0.90		
	Hungary	96	1.09	0.95		
	Greece	95	1.09	1.07		

Greece, Csakvar in Hungary and Dorn Dürkheim-1 in Germany are correlated to the Early Turolian mammalian age (MN zone 11) and have yielded neither hominoids nor pliopithecoids (electronic supplementary material, table S3). The cercopithecoid *Mesopithecus* is known in Ravin des Zouaves-5 with many cranial remains (de Bonis *et al.* 1997).

Bovids, cervids, tragulids and moschids compose the investigated guild of medium-sized herbivorous mammals (Gentry 2005; Kostopoulos 2006). The feeding traits of 552 specimens of fossil ruminants were identified by combining microwear with mesowear analysis (electronic supplementary material, tables S1 and S2). The mesowear pattern of fossil species was investigated through comparisons with a database composed of living species whose feeding preferences and behaviours are well known (electronic supplementary material, table S1). All extant species and specimens used here for comparisons came from the database published by Fortelius & Solounias (2000). This database was originally composed of 64 species of herbivorous mammals representing 2200 adult individuals. However, the number of specimens and species was here deliberately limited compared with the original publication.

Fortelius & Solounias (2000) have indicated that phylogenetic history obviously influences tooth morphology and the way occlusal relief and cusp shape are worn. Therefore, the database was here restricted to the ruminant species that share common dental structure and phylogenetic history. Ultimately, the original database is further truncated to the two dietary spectrum extremities: grazers and browsers. Yet the database was still composed of 443 wild-shot specimens representing 13 extant species of ruminants (electronic supplementary material, table S1). Following the same procedures, the extant species used for comparative data were limited to ruminant species from the two dietary spectrum poles (grazers and browsers). Therefore, the microwear comparative database was here composed of 405 wild-shot individuals belonging to 18 ruminants (electronic supplementary material, table S2; Merceron *et al.* 2007).

(b) Methods

(i) Mesowear analysis

The mesowear signal was evaluated at the buccal cutting edges of the upper second molars using two discrete variables (occlusal relief and cusp shape). We followed here the scoring

shown in Kaiser *et al.* (2009). The dental mesowear pattern is scored as follows: 0 for high relief with sharp cusps, 1 for high relief with round cusps, 2 for low relief with sharp cusps, 3 for low relief with round cusps and 4 for low relief with blunt cusps. Thus, MwSs indicate the overall abrasiveness of the diet a species had to cope with (table 1A; electronic supplementary material, table S1).

(ii) Microwear analysis

The digital capture and the dental microwear analysis are conducted following the procedures shown in Merceron *et al.* (2005). The microwear pattern is composed of nine variables: length of scratches, numbers of fine and wide scratches, numbers of small and large pits, total numbers of microwear of pits, scratches and microwear scars, and percentage of pits (electronic supplementary material, table S2). These variables were integrated into a model set-up on extant ruminants clustered in two dietary groups (grazers and browsers) using a Fisher's or simple discriminant analysis (also named canonical variate analysis; electronic supplementary material, table S4). Because discriminant analysis is sensitive to the normality conditions, the skewed variables were first log-transformed prior to the discriminant analysis. The discriminant analysis generates a unique discriminant function of variables that maximizes the differences between clusters (grazers versus browsers; Legendre & Legendre 1998; Gotelli & Ellison 2004). As Legendre & Legendre (1998) suggest, all variables are integrated. However, different trials were executed on different sets of microwear variables known in the literature to discriminate dietary groups. The better ratios of overall and group misclassifications are obtained when all the nine variables are included in the discriminant analysis model (electronic supplementary material, table S4). The misclassification is 10.86 per cent overall, and 4.92 per cent for browsers and 21.98 per cent for grazers. Subsequently, a Student's *t*-test was run on individual coordinates along the discriminant function to test the significance of differences between grazers and browsers. Because normality and homogeneity of variances were not respected, the variable 'coordinate along the axis' was first log-transformed. As expected, results showed significant differences between grazers and browsers (electronic supplementary material, table S4). The Fisher discriminant function set up with the two groups of extant grazing and browsing ruminants is then used as a predictive model for fossil specimens. The values for the nine variables of each specimen are integrated in the discriminant function. The feeding habits of every fossil taxon in every community are therefore identified by their position average within the factor space of the browsing or the grazing kernels in the actualistic model (figure 1). The dental microwear pattern for fossil ruminants is summarized by a new synthetic variable: the microwear coordinate, MiC (table 1; electronic supplementary material, table S2).

(iii) Combining microwear with mesowear signals

The coordinates MiC and MwS of fossil communities are plotted along the axes of a bivariate diagram (figure 1). Missing values (either MiC or MwS) for a given individual are replaced with the species average to which the specimen belongs. Based only on MiC and MwS variables (table 1A), three differential new variables are calculated. The inter-community disparity d_1 is estimated as the mean of pairwise distances between individuals from two distinct

contemporaneous communities (table 1B). The inter-age disparity d_2 is the mean of the pairwise distance between individuals from two age-distinct communities (Vallesian and Turolian) from the same location (table 1C). Finally, the intra-community disparity d_3 is calculated as the distance between individuals and the centroid from a given community (table 1D).

(iv) Statistical procedures

The differences among the groups are investigated through different sets of multivariate analyses of variances (table 2; electronic supplementary material, table S5). Sources of significant variation were determined by univariate analyses of variances and Tukey's honestly significant difference with Fisher's least significant difference multiple comparison tests (table 2; electronic supplementary material, table S5; Sokal & Rohlf 1969). Results for pairwise tests are presented to balance risks of type I and type II errors given the large number of comparisons. Because distributions of variables are very diverse owing to a high number of groups (species, communities and age factors), it is difficult to determinate which transformation is more appropriate for the variables. Therefore, we decided to rank-transform all variables before applying parametric MANOVAs and ANOVAs (Conover & Iman 1981).

3. RESULTS

(a) Ruminant diets and hominoid habitats during the Vallesian period

When applied to the two dietary estimators (MwS and MiC), a nested MANOVA reveals significant differences among species of ruminants and between the communities to which they belong (tables 1A and 2A). The nested ANOVAs indicate that the two variables vary significantly for the two hierarchical levels: ruminants and communities (tables 1A and 2A). The inter-taxa variations were actually expected since they describe the ecological niche partitioning among species. Assuming that a given ruminant community mainly involved in grazing indicates open landscapes, whereas the prevalence of browsing signatures supports the presence of bushy and woody vegetation, the distribution of palaeocommunities along the bivariate plot (figure 1) reveals significant differences in vegetation.

Based on significant differences in dietary preference between ruminant communities (tables 1A and 2A; electronic supplementary material, tables S5A), *Ouranopithecus* in Greece inhabited more open landscapes compared with other Vallesian primates in Hungary and Germany (figure 1). These habitats were characterized by the prevalence of grasses in a widespread herbaceous formation. Also, findings show the ruminants in Germany to be shifted more towards the browsing end of the dietary spectrum than the Hungarian ruminants (figure 1; tables 1A and 2A; electronic supplementary material, table S5A). It is thus demonstrated that primate habitats were probably more open in Hungary than in Germany during the Vallesian (figure 1). This is also emphasized by the inter-community disparities d_1 , which are significantly higher between the Greek community and the two other Vallesian ones than they are between these two (figure 2a; tables 1B and 2B; electronic supplementary material, table S5B). The Hungarian community

Table 2. Multivariate and univariate analyses of variances (MANOVAs and ANOVAs) on the dietary estimators (A; microwear coordinate MiC and mesowear score MwS) and the three inter- and intra-community disparities (B, C and D). d.f., degree of freedom; SS, sum of squares; MS, mean of squares; *F*, Fisher statistics; *p*, probability.

		d.f.	SS	MS	<i>F</i>	<i>p</i>
A. analyses on dietary estimators MiC and MwS						
nested MANOVA						
species (community)		26, 1124	Wilk's lambda = 0.6459		10.561	<0.001
communities		10, 1124	Wilk's lambda = 0.5919		33.687	<0.001
nested ANOVAs						
MwS	species (community)	13	3 134 846	241 142	14.216	<0.001
	communities	5	2 227 958	445 592	26.269	<0.001
	residuals	563	9 550 128	16 963		
MiC	species (community)	13	1 659 495	127 653	7.368	<0.001
	communities	5	3 816 883	763 377	44.064	<0.001
	residuals	563	9 753 555	17 324		
B. analysis on inter-community disparity d_1						
nested ANOVA						
communities (age)		4	2.40×10^{11}	6.00×10^{10}	260.0	<0.001
age		1	1.21×10^{12}	1.21×10^{12}	5230.5	<0.001
residuals		56 234	1.30×10^{13}	2.31×10^8		
C. analysis on inter-community disparity d_2						
one-way ANOVA						
spot		2	1.01×10^{10}	5.06×10^9	103.35	<0.001
residuals		24 338	1.19×10^{12}	4.89×10^7		
D. analysis on inter-community disparity d_3						
two-way factorial ANOVA						
age		1	420 079	420 079	15.446	<0.001
spot		2	278 173	139 086	5.114	<0.01
age $\times$ spot		2	57 564	28 782	1.058	0.347
residuals		576	15 665 293	27 197		

also displays a significantly higher intra-community disparity d_3 than the Greek assemblage, as well as to the German one to a lesser extent (figure 2c; tables 1D and 2D; electronic supplementary material, table S5A). On the other hand, there is no significant difference between the Greek and the German Vallesian communities in the intra-community disparity d_3 (figure 2c; tables 1D and 2D; electronic supplementary material, table S5A). These results imply that Vallesian habitats differ from each other also by an apparent inequality in ecological niche availabilities for ruminants.

(b) Changes in ruminant diets during the Early Turolian period

Although there is still ecological diversity among the Early Turolian communities, the pattern is significantly different compared with the Vallesian one (figure 1; tables 1A and 2A; electronic supplementary material, table S5A). First of all, the inter-community disparities d_1 are significantly lower (figure 2a; tables 1B and 2B; electronic supplementary material, table S5B). Indeed, in contrast to Vallesian samples, there are no more significant differences between the inter-community Greece–Germany and Greece–Hungary disparities d_1 (figure 2a; tables 1B and 2B; electronic supplementary material, table S5B). This is due to significant shifts in MiC and MwS variables towards more grazing for ruminants in Germany and more browsing in Greece (figure 1; tables 1A and 2A; electronic supplementary material, table S5A). In Hungary, a shift towards more grazing traits in the ruminant diet is also detected by

MiC shift at the passage between Vallesian and Turolian (figure 1; tables 1A and 2A; table S5A). The largest inter-age disparity d_2 seen in the Hungarian communities indicates that central European ruminant communities experienced the greatest shift in dietary preferences during the Late Miocene (figure 2b; tables 1C and 2C; electronic supplementary material, table S5C). Besides this, the intra-community disparities d_3 also significantly differ between the two periods, since in contrast to the Vallesian there is no more difference for the Turolian period (figure 2c; tables 1D and 2D; electronic supplementary material, table S5A). All variables thus reveal a change in ruminant dietary habits that reflect changes in vegetation towards more homogeneous conditions. Thus, it appears that the Vallesian–Turolian transition saw the landscapes in Germany and Hungary become more open while there was an increase in bushy vegetation in Greece.

4. DISCUSSION

The hominoid extinction from Spain to Pakistan reflects the high impact of global climatic changes, such as the succession of Antarctic glaciations between 13.5 and 8.5 Ma (Miller & Feigenson 1991; Zachos *et al.* 2001) or the impacts of Tibetan elevation phases on atmospheric circulations (Kutzbach *et al.* 1993; Harris 2006; Wang *et al.* 2008). However, regional factors also had an important impact since the changes in vegetal composition were dissimilar. In central Europe, the Alps uplift contributed to the shrinking of the Pannonian Lake,

Figure 2. Variations in inter- and intra-community disparities (mean and confidence interval of the mean at 95%) reflect environment and ecosystem dynamics throughout Europe before and after the Vallesian/Turolian boundary (approx. 8.7 Ma). (a) The inter-space disparity d_1 is estimated as the pairwise distance between individuals from different contemporaneous communities. (b) The inter-age disparity d_2 is determined as the pairwise distance between Vallesian and Turolian communities from the same location, whereas (c) the intra-community disparity d_3 is calculated as the distance between individuals and the community centroid.

with oscillations during the Late Miocene (Harzhauser *et al.* 2007; Böhme *et al.* 2008; Jiménez-Moreno *et al.* 2008). Consequently, the lowland mega-thermophileous vegetation issued from the middle Miocene climatic optimum in western and central Europe was gradually replaced by mid-latitude and higher altitudinal elements (Jiménez-Moreno *et al.* 2008). In southern latitudes, the drastic decreases in the Mediterranean–Atlantic water exchange, especially at 8.5 Ma, driven by major tectonic events (Seidenkrantz *et al.* 2000), had severe impacts on vegetation. It is worth noting that this is contemporaneous with the first occurrence of *Mesopithecus* in the Balkans. Indeed, the increase in xeric dicotyledons, noted after the Vallesian crisis in Spain and in eastern Europe (Agustí *et al.* 2003; Jiménez-Moreno *et al.* 2007), supports the hypothesis that changes in dietary preference among ruminants may be associated with the development of Mediterranean-like climaxes along the northern Mediterranean ridge. Such vegetal climaxes include scrubby, bushy and even arboreal settings with trees and bushes spread wide enough to leave space for the development of an extended herbaceous vegetal formation (White 1986). These conditions, with the co-occurrence of bushy/shrubby xeric vegetation and herbaceous formations including annual dicotyledons and C_3 metabolic pathway grasses, were actually known in Anatolia since the Middle Miocene (Strömberg *et al.* 2007). Such Mediterranean-like vegetation requires climates with a pronounced drought period in the summer and cool winters with periods of prolonged rainfall (White 1986). If such changes in both structure and composition of vegetation in western Eurasia can be seen as a key factor in controlling the loss of primate diversity, they may also have driven the increase in ruminant and equid diversities (Gentry & Heinzman 1996; Koufos 2003). These ungulates are likely to have

diversified their available food resources by including items from the herbaceous, shrubby and bushy vegetal formations in response to the opening of the arboreal layer. In contrast, primates, at least in western and central Europe, seem to have been affected by the loss of vertical niche distribution (i.e. the arboreal vegetation). However, the situation is quite different along the Axios River where arboreal cover was most probably not dense while hominoids were present. The disappearance of hominoids in eastern Europe, or at least along the Axios River in Greece, cannot be linked to a decrease in tree cover but instead could be associated to an increase in bushy vegetation, as our results on ruminant diets demonstrate. The possible presence of *Ouranopithecus* in Turolian deposits in Bulgaria (Spassov & Geraads 2008) implies the conclusion that environmental changes in eastern Europe were not so drastic in comparison to those in western and central Europe. Farther east, the extinction of *Sivapithecus* during the Late Miocene, about 8.5 Ma, is also tied to sharp environmental changes towards more open and drier conditions. Contrary to western Eurasia, changes in southern Asia are associated with C_4 grass expansion as evidenced by thorough faunal, dental microwear and stable isotope data (Nelson 2003).

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