HAL
open science

Feeding ecology of Eucladoceros ctenoides as a proxy to track regional environmental variations in Europe during the early Pleistocene

Émilie Berlioz, Dimitris S Kostopoulos, Cécile Blondel, Gildas Merceron

To cite this version:

Émilie Berlioz, Dimitris S Kostopoulos, Cécile Blondel, Gildas Merceron. Feeding ecology of Eucladoceros ctenoides as a proxy to track regional environmental variations in Europe during the early Pleistocene. Comptes Rendus. Palevol, 2018, 17 (4-5), pp.320-332. 10.1016/j.crpv.2017.07.002 . hal-03907927

HAL Id: hal-03907927

https://hal.science/hal-03907927v1

Submitted on 20 Dec 2022

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.

C. R. Palevol xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General Paleontology, Systematics and Evolution (Vertebrate Palaeontology)

Feeding ecology of *Eucladoceros ctenoides* as a proxy to track regional environmental variations in Europe during the early Pleistocene

*L'écologie alimentaire d'*Eucladoceros ctenoides *: un outil pour suivre les variations environnementales régionales en Europe au Pléistocène inférieur*

Émilie Berlioz[a,*], Dimitris S. Kostopoulos[b], Cécile Blondel[a], Gildas Merceron[a]

[a] *iPHEP–UMR 7262 (CNRS & University of Poitiers), TSA 51106, 86073 Poitiers cedex 9, France*
[b] *Department of Geology, Faculty of Science, School of Geology, 54124 Thessaloniki, Greece*

ARTICLE INFO

Article history:
Received 26 April 2017
Received in revised form 20 July 2017
Accepted after revision 24 July 2017
Available online xxx

Handled by Lorenzo Rook

Keywords:
Dental Microwear Texture Analysis
Villafranchian
Feeding plasticity
Climatic oscillations
Paleoenvironments
Cervidae

Mots clés :
Analyse de la texture de la micro-usure dentaire
Villafranchien
Plasticité alimentaire
Oscillations climatiques
Paléoenvironnements
Cervidae

ABSTRACT

The early Pleistocene is represented by a succession of glacial–interglacial cycles characterized by a general tendency towards global cooling, with increasing aridity and seasonality. The large deer *Eucladoceros* is found in abundance in Europe during this period of faunal dispersions. The dietary plasticity of *Eucladoceros* and how it can mirror early Pleistocene climatic variations will be explored here using Dental Microwear Texture Analysis. The wide range of dental microwear textures for *Eucladoceros* reflects a low selectivity and high plasticity in its diet. It is an appropriate proxy to track vegetal resource availability. Oscillations were identified between a browsing and a grazing signal. This study proposes that a browsing signal is associated with a fossil assemblage deposited during an interglacial event characterized by warmer temperatures and deciduous vegetation. A grazing signal more likely indicates a glacial event with cooler temperatures and a developed herbaceous, bushy layer.

© 2017 Académie des sciences. Published by Elsevier Masson SAS. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

RÉSUMÉ

Le Pléistocène inférieur correspond à une succession de cycles glaciaires–interglaciaires caractérisée par une tendance générale au refroidissement global, avec une aridité et une saisonnalité croissantes. Le cervidé de grande taille *Eucladoceros* est abondant en Europe durant cette période de dispersions fauniques. Grâce à l'analyse de texture de la micro-usure dentaire, nous explorons la plasticité alimentaire d'*Eucladoceros* et la manière dont celle-ci reflète les variations climatiques du Pléistocène inférieur. La large gamme de textures de micro-usure dentaire d'*Eucladoceros* reflète sa faible sélectivité et sa forte plasticité alimentaire. De fait, il constitue un outil approprié pour aborder la disponibilité en ressources

* Corresponding author.
E-mail address: emilie.berlioz@univ-poitiers.fr (É. Berlioz).

http://dx.doi.org/10.1016/j.crpv.2017.07.002
1631-0683/© 2017 Académie des sciences. Published by Elsevier Masson SAS. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

Please cite this article in press as: Berlioz, É., et al., Feeding ecology of *Eucladoceros ctenoides* as a proxy to track regional environmental variations in Europe during the early Pleistocene. C. R. Palevol (2017), http://dx.doi.org/10.1016/j.crpv.2017.07.002

végétales dans le milieu. Nous identifions des oscillations entre un signal brouteur et un signal paisseur. Nous proposons qu'un signal brouteur soit associé à un assemblage fossile déposé lors d'un évènement interglaciaire caractérisé par des températures plus chaudes et une végétation décidue, tandis qu'un signal paisseur correspondrait plutôt à un évènement glaciaire, avec des températures plus froides et la présence d'une strate herbacée et arbustive développée.

© 2017 Académie des sciences. Publié par Elsevier Masson SAS. Cet article est publié en Open Access sous licence CC BY-NC-ND (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

During the early Pleistocene in Europe, flora and fauna were subjected to a general trend towards global cooling, already initiated at the end of the Pliocene with glacial–interglacial cycles characterized by a 41 ky periodicity (Lisiecki and Raymo, 2005). The drop in temperature was accompanied by a progressive increase of aridity and seasonality. This was associated with habitat opening during glacial events, resulting in the progressive development of steppes all over southern Europe (Bonifay and Brugal, 1996; Kahlke et al., 2011; Leroy et al., 2011). The range of this cyclic fluctuation between glacial and interglacial events remains relatively limited in comparison to the climatic variations that occur during more recent periods (Lisiecki and Raymo, 2005). These recurrences had an impact on faunal assemblages, ecology, niche partitioning and geographical dispersion. They represent the very beginning of when the modern Mediterranean climate was established in southern Europe (Suc, 1984). A detailed understanding of the impact of these climatic oscillations on vegetal resources and local environments is necessary to contextualize faunal dispersions occurring during this period. Cervids are particularly abundant and diversified during the early Pleistocene, making them a group of interest that has long been used within the framework of environmental reconstructions. When drawing interpretations of the paleoenvironmental context of a fossil locality, the presence of deer is traditionally interpreted as an indicator of significant tree cover in the habitat (Guérin et al., 2004; Pastre et al., 2015; Rivals and Athanassiou, 2008). However, some studies highlighted the ability of fossil deer to occupy more open habitats or/and include a large proportion of grass in their diets (Alcalde and van den Hoek Ostende, 2015; Curran, 2015; DeMiguel et al., 2008, 2010, 2016; Kaiser and Croitor, 2004; Merceron et al., 2012; Solounias and Moelleken, 1994; Valli and Palombo, 2008). Among cervids, the large deer *Eucladoceros* had a body mass similar to that of extant European *Cervus elaphus*, at 250 kg based on a reconstruction by Kaiser and Croitor (2004). This extinct deer is typically associated with the smaller *Metacervoceros rhenanus* and *Croizetoceros ramosus*. The genus *Eucladoceros* is known in Europe during the Villafranchian, since ca. 2.5 Ma (Croitor, 2009; but also see Lacombat et al., 2008 for an earlier chronology of the taxon).

Dental microwear is the result of the way in which animals masticate, as well as of the physical properties (Lucas, 2004) and inner composition, such as phytoliths, of ingested food items (for detailed reviews, see Calandra and Merceron, 2016; DeSantis, 2016; Ungar, 2015 and references within). The dental microwear of herbivores as direct plant consumers reflects vegetal resource availability in the habitat. This is of particular interest in order to decipher the regional paleoenvironmental context of fossil localities. Dental microwear textures constitute a record of the meals of the last few days or weeks of the life of an animal (Grine, 1986; Teaford and Oyen, 1989) and its analysis proves to be sufficiently efficient to detect subtle seasonal and sexual variations in diet (Bignon-lau et al., 2017; Merceron et al., 2010, 2014).

The goal here is to characterize the vegetation consumed by specimens of *Eucladoceros* from eight middle and late Villafranchian localities (2.6–2.0 Ma and 2.0–1.0 Ma, respectively; Rook and Martínez-Navarro, 2010) and to contextualize this with climatic oscillations across time and space using the dental microwear texture. This would help to better understand the climatic conditions during the time intervals that the fossiliferous sites represent. Firstly, the dietary plasticity of *Eucladoceros* is explored. Variations in the dietary preferences of *Eucladoceros* are then identified. At ca. 250 kg (based on a reconstruction by Kaiser and Croitor, 2004), *Eucladoceros* is expected to present a significant dietary plasticity and therefore to constitute an adequate paleo-habitat proxy.

2. Material and methods

2.1. Dental material

2.1.1. Fossils

A total of 146 dental specimens belonging to *Eucladoceros* from eight fossil localities in Europe are included in the present study. The geographic location of all sites is given in Fig. 1. All but one specimen from Krimni belong to the species *Eucladoceros ctenoides*, as revised by De Vos et al. (1995). Sampled specimens from Saint-Vallier and Senèze ($N = 22$ and 11, respectively) belong to the collections of the "Musée des Confluences de Lyon", France and the Geological Collections of the Laboratoire de Géologie de Lyon - CERESE (UMR CNRS 5276), University Lyon 1, France. Specimens from Chilhac ($N = 78$) are stored in the collections of the "Musée de paléontologie de Chilhac", France. Bulgarian specimens (Varshets, $N = 21$; Slivnitsa, $N = 1$) belong to the collections of the Natural History Museum of Sofia, Bulgaria. Finally, specimens from Greece (Dafnero, $N = 3$; Gerakarou, $N = 9$; and Krimni, $N = 1$) belong

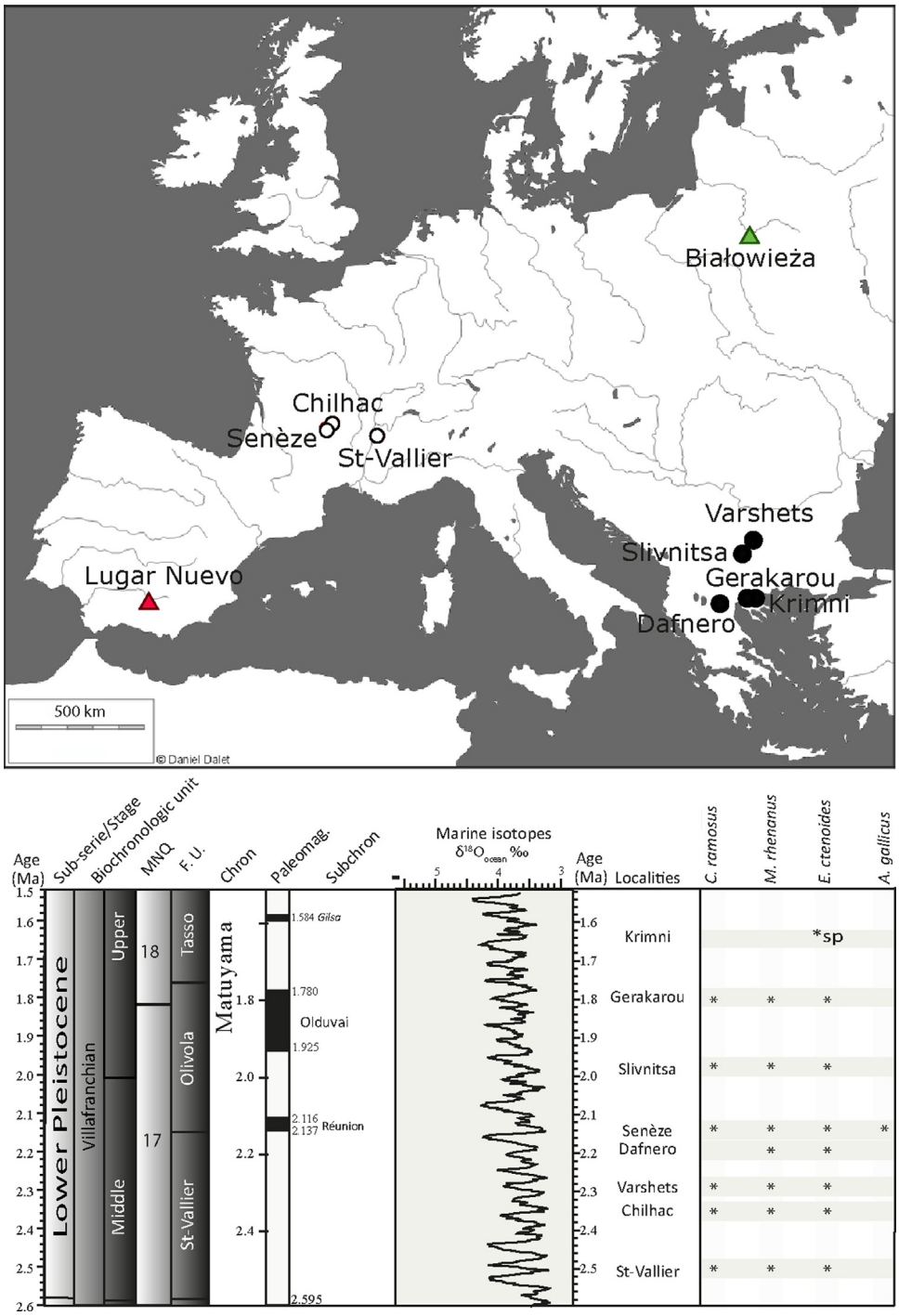

Fig. 1. *Eucladoceros* fossil localities of the early Pleistocene in Europe. Geographical repartition of the eight localities included in the study. The western European localities are represented by white circles and the eastern ones by black circles. The localization of the two reference modern red deer populations are illustrated by triangles. Białowieża is in green and Lugar Nuevo in red. The biochronological scale with localities is presented on the lower part of the figure. Cervid representatives in each locality are presented by stars. MNQ: Mammal Neogene Quaternary biozone. F.U.: Faunal Unit.

Fig. 1. Localités fossilifères à *Eucladoceros* du Pléistocène inférieur d'Europe. Répartition géographique des huit localités incluses dans l'étude. Les localités d'Europe de l'Ouest sont illustrées par des ronds blancs, et les localités d'Europe de l'Est par des ronds noirs. Les deux populations de cerf élaphe moderne de référence sont illustrées par des triangles, vert pour Białowieża et rouge pour Lugar Nuevo. L'échelle biochronologique avec les localités est présentée dans la partie basse de la figure. Les représentants de la famille des cervidés présents dans chaque localité sont présentés par des étoiles. MNQ : biozone mammifère Néogène–Quaternaire. F.U. : Unité Faunique.

Please cite this article in press as: Berlioz, É., et al., Feeding ecology of *Eucladoceros ctenoides* as a proxy to track regional environmental variations in Europe during the early Pleistocene. C. R. Palevol (2017), http://dx.doi.org/10.1016/j.crpv.2017.07.002

to the Geology–Paleontology Museum of the School of Geology of the Aristotle University of Thessaloniki, Greece.

2.1.2. Reference sample

The red deer (*Cervus elaphus*) is well known for its significant dietary plasticity (Gebert and Verheyden-Tixier, 2001). This taxon is widely spread from the Mediterranean forests of the Maghreb to the taiga of Norway and from the Spanish dehesas to Turkey (Lovari et al., 2016). By being strongly adaptable, it occupies various habitats in a large range of environments and is able to cope with diversified abiotic conditions and contrasted vegetal resource availability (Gebert and Verheyden-Tixier, 2001; Geist, 1998).

Two extant populations living in contrasted habitats are included in the present study to be used as reference for dental microwear interpretations.

Firstly, red deer from Lugar Nuevo, southern Spain (Fig. 1), lives in a dehesa, that is a Spanish traditional agro-silvo-pastoral system made up of an understory of open savannah-like grasslands composed of tough abrasive herbaceous monocots and a scattered tree cover (Azorit et al., 2012; Diaz et al., 1997; Joffre et al., 1988; Marañón, 1991; Olea and San Miguel-Ayanz, 2006). This system, results from the management (pastoralism, cultivation, predation) of an initially forested ecosystem (Scarascia-Mugnozza et al., 2000). Based on stomach content analysis (Azorit et al., 2012), the dietary variation of this population throughout the year is well known. Berlioz et al. (in press) explored dental microwear texture and concluded that they indicate a grazing signal. The specimens ($N = 116$) are stored at the Universidad of Jaen, Andalusia (Spain).

In contrast, the red deer population from Białowieża, Poland (Fig. 1), lives in one of the best preserved primeval forests of Europe (Jedrzejewska and Jedrzejewski, 2013). An analysis of dental microwear textures of ruminants in this habitat (Merceron et al., 2014) shows that these deer are engaged in browsing. The mandibles of these specimens ($N = 23$) are housed at the mammal collection of the Mammal Research Institute, Białowieża (Poland).

2.2. Fossil localities

Specimens from the following eight localities were analyzed, presented in chronological order from the earliest to the most recent.

Saint-Vallier (France, Auvergne-Rhône-Alpes, MNQ17) is dated at ca. 2.5 Ma (Nomade et al., 2014). Because of its significant biodiversity, it is considered a reference for the middle Villafranchian (Azzaroli et al., 1988; Guérin, 1990; Guérin et al., 2004; Heintz et al., 1974). The habitat of Saint-Vallier has been described as a mosaic landscape with the presence of steppe, punctuated by a deciduous tree cover typical of a temperate or warm temperate climate and associated with a watering place based on a palynologic study (Argant, 2004). Based on the mammal assemblage, the humidity in the habitat is considered significant and the temperature warm (Argant and Philippe, 2011; Guérin et al., 2004). Cervids are the most abundant family, representing 60% of the faunal assemblage (Valli, 2004). The typical deer assemblage of this period is present in Saint-Vallier, with *Eucladoceros ctenoides vireti* (= *E. senezensis vireti*) together with *Metacervoceros rhenanus (= "Cervus" philisi valliensis*) and *Croizetoceros ramosus medius* (Heintz, 1970; Valli, 2004; Valli and Palombo, 2008).

Chilhac (France, Auvergne-Rhône-Alpes, MNQ17) is radiometrically dated at 2.36 Ma (Nomade et al., 2014) and is a reference site in Europe. *Eucladoceros ctenoides*, *Metacervoceros rhenanus* and *Croizetoceros ramosus* are present in this locality (Boivin et al., 2010; Heintz, 1970). It has been described as a humid site (Boeuf and Gilbert, 1997) and the high proportion of cervids is considered indicative of the significant tree cover in the locality (Guérin et al., 2004).

Varshets (Bulgaria, Province of Montana, MNQ17) is a rich middle Villafranchian karstic locality with similarities to the reference locality of Saint-Vallier (Spassov and Crégut-Bonnoure, 1999). The faunal assemblage is dominated by cervids, represented by *Eucladoceros ctenoides* cf. *vireti, Metacervoceros rhenanus (= "Cervus" philisi valliensis*) and *Croizetoceros ramosus medius* (Guérin et al., 2004). The habitat has been described as a mosaic forest-steppe type of landscape (Bechev and Georgiev, 2016; Spassov and Crégut-Bonnoure, 1999).

Dafnero (Greece, Western Macedonia, MNQ17) is a middle Villafranchian assemblage of three localities with important faunal similarities to Saint-Vallier (Guérin et al., 2004; Koufos, 1993, 2016). Given the balanced ratio of bovids to cervids, the locality is interpreted as a mosaic habitat with forest and savannah areas (Kahlke et al., 2011). Cervids include *E. ctenoides* (= *Eucladoceros senezensis)* and *Metacervoceros rhenanus* (= *"Cervus" philisi*).

Senèze (France, Auvergne-Rhône-Alpes, MNQ18), situated only 10 km from Chilhac, is a reference MNQ18 locality for western Europe (Pastre et al., 2015). It corresponds to a maar deposit. The cervids present in the locality are *Eucladoceros senezensis senezensis* (synonym of *E. ctenoides* according to De Vos et al., 1995), *Metacervoceros rhenanus (= "Cervus" philisi philisi)*, *Croizetoceros ramosus minor* and *Cervalces gallicus* (Azzaroli et al., 1988; Geraads, 1990; Heintz, 1970). *Eucladoceros ctenoides* is among the dominant species of the locality. The environmental context has been described as similar to Saint-Vallier, i.e., mosaic with the presence of open forest and steppe areas. A pollen analysis highlighted the presence of a mesothermophilic vegetation indicative of a temperate climate (Azzaroli et al., 1988; Delson et al., 2006; Guérin et al., 2004; Nomade et al., 2014).

Slivnitsa (Bulgaria, Province of Sofia, MNQ18) is a late Villafranchian cave locality north-west of Sofia. The faunal assemblage presents similarities with the Senèze fauna. The habitat seems to have been more open and the climate more arid than that of Varshets, which would explain the significant proportion of bovids in this locality. Deer are represented by *Eucladoceros* cf. *ctenoides (= E.* cf. *senezensis)* and *Metacervoceros rhenanus* (Spassov, 1998; Spassov and Crégut-Bonnoure, 1999). Despite the significant abundance of fossils in the locality, *Eucladoceros* dental remains are scarce.

Gerakarou (Greece, Central Macedonia, MNQ19) is a rich locality from the beginning of the late Villafranchian (Konidaris et al., 2015; Koufos, 2016), south-east of the Mygdonian Basin, Greece (Koufos et al., 1995). Deer

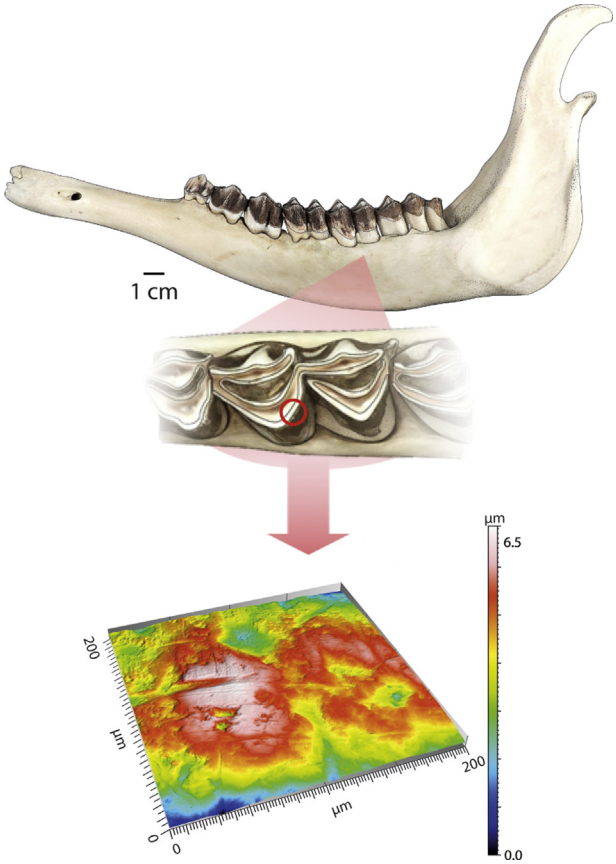

Fig. 2. From red deer mandible (*Cervus elaphus*) to textural surface. Lower tooth row from a modern red deer. We focused on the lingual facet of the protoconid of the lower second molar, circled in red. The resulting surface texture is acquired with a surface profilometer.
Fig. 2. De la mandibule de cerf élaphe (*Cervus elaphus*) à la texture de surface. Rangée dentaire inférieure d'un cerf élaphe actuel. Nous nous sommes concentrés sur la facette linguale du protoconide de la seconde molaire inférieure, entourée en rouge. La texture de surface résultante a été obtenue grâce à un profilomètre surfacique.

from Gerakarou are represented by *Eucladoceros ctenoides*, *Metacervoceros rhenanus ("Cervus" philisi)* and *Croizetoceros ramosus* (Kostopoulos and Athanassiou, 2005; Kostopoulos and Koufos, 1994). When considering faunal composition, no noticeable climatic changes have been observed between Gerakarou and earlier middle Villafranchian localities. Among herbivores, intermediate feeders are considered to be dominant (Kahlke et al., 2011).

Krimni (Greece, Central Macedonia, MNQ19) is a late Villafranchian locality (Koufos, 2016) situated in the Mygdonian Basin, Greece. The material from Krimni is scarce. The faunal assemblage presents similarities with the locality of Gerakarou. There are few fossils from *Eucladoceros* sp. (Kostopoulos, 1996; Koufos et al., 1995) that may not be conspecific with the *Eucladoceros ctenoides* from Gerakarou (Kostopoulos and Koufos, 1994).

3. Methods

The lower second molar of specimens was used whenever available (Fig. 2). Whenever this tooth was unavailable or altered, other lower or upper molars were selected for study. This information is provided for every specimen in the supplementary data (Table S1). Following standard procedures (Ramdarshan et al., 2016), each tooth was carefully cleaned with acetone. The disto-lingual facet of the protoconid was molded with a high-resolution polyvinylsiloxane elastomer (Regular Body President, ref 6015–ISO 4823, medium consistency, polyvinylsiloxane addition type; Coltene Whaledent).

The silicon mold was scanned with a Leica DCM8 white light confocal surface profilometer with a 100 × objective (numerical aperture = 0.90, working distance = 0.9 mm) at the IPHEP lab (CNRS and University of Poitiers, France) in order to avoid the resin-based cast step. For each specimen, a 251 × 333 µm surface (2584 × 1945 points) was scanned at the center of the dental facet. A 200 × 200 µm sub-surface was generated from this surface, leveled and mirrored in Z. A smooth shape replaced the few missing points using an algorithm calculated from the neighboring points. A macro (Merceron et al., 2016) was run in order to automatically erase abnormal peaks. Remaining bigger artifacts and exogenous particles were removed manually and replaced by a smooth shape before proceeding to a final leveling of the surface with Mountains Map Premium 7.3 software.

Surfaces were then analyzed using a Scale Sensitive Fractal Analysis (SSFA) with ToothFrax and Sfrax (Surfract,

Table 1
Mean and standard error of mean for the eight fossil samples of *Eucladoceros* and the two extant reference red deer populations. The last row corresponds to the results of the one-way ANOVAs that test the differences between localities. Fr: France; Bu: Bulgaria; Gr: Greece; Sp: Spain; Po: Poland.
Tableau 1
Moyenne et erreur standard de la moyenne pour les huit échantillons d'*Eucladoceros* et les deux populations de référence de cerfs élaphes actuels. La dernière ligne du tableau correspond aux résultats des ANOVAs à un facteur testant les différences entre localités. Fr : France ; Bu : Bulgarie ; Gr : Grèce ; Sp : Espagne ; Po : Pologne.

Ma	Locality	*N*	Asfc		epLsar ($\times 10^{-3}$)		Smc		HAsfc 9		Tfv	
			Mean	*s.e.m.*	Mean	*s.e.m.*	Mean	*s.e.m.*	Mean	*s.e.m.*	Mean	*s.e.m.*
2.5	**Saint-Vallier (Fr)**	**22**	1.43	*0.13*	4.02	*0.41*	0.53	*0.02*	0.27	*0.04*	30236.0	*3027.6*
2.3-2.4	**Chilhac (Fr)**	**78**	3.25	*0.21*	2.88	*0.18*	5.85	*2.98*	0.39	*0.02*	45103.9	*967.2*
2.3	**Varshets (Bu)**	**21**	2.94	*0.49*	2.71	*0.35*	0.53	*0.07*	0.33	*0.04*	31775.8	*3385.4*
2.1-2.2	**Dafnero (Gr)**	**3**	1.88	*0.46*	6.26	*1.08*	0.34	*0.17*	0.29	*0.05*	41511.8	*8283.7*
2.1	**Senèze (Fr)**	**11**	1.74	*0.50*	5.72	*0.92*	1.57	*0.77*	0.31	*0.06*	42508.5	*2857.6*
1.9-1.8	**Slivnitsa (Bu)**	**1**	1.11	/	7.94	/	0.67	/	0.26	/	41287.7	/
1.9-1.8	**Gerakarou (Gr)**	**9**	3.05	*0.66*	3.32	*0.71*	6.49	*4.06*	0.27	*0.03*	42212.8	*3983.6*
1.7-1.6	**Krimni (Gr)**	**1**	2.36	/	6.30	/	0.13	/	0.31	/	31271.5	/
Extant	**Lugar Nuevo (Sp)**	**116**	1.24	0.05	5.44	0.22	3.41	1.55	0.35	0.02	37549.9	1315.7
Extant	**Białowieża (Po)**	**23**	2.91	0.37	2.81	0.32	2.31	1.50	0.47	0.12	55415.8	12813.6
H0: Difference between localities			*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
			7.771	**<0.001**	4.014	**<0.001**	5.015	**<0.001**	3.040	**0.005**	5.230	**<0.001**

www.surfract.com) software. Five microwear parameters were extracted for each surface (Scott et al., 2006): Complexity (area-scale fractal complexity [Asfc]), anisotropy (exact proportion length-scale anisotropy of the relief [EpLsar]), scale of maximum complexity (Smc), textural fill volume (Tfv) and heterogeneity (Heterogeneity of the area-scale fractal complexity with 9 cells [HAsfc 9]).

Browsing habits result in an intermediate to high complexity coupled with low to intermediate anisotropy. The consumption of hard items like seeds results in higher complexity and textural fill volume (Scott, 2012). Dental microwear textures are more variable for herbivores feeding on a low silica bearing diet (Schulz et al., 2013). Grazers foraging tough and abrasive monocots display high anisotropy coupled with low complexity and less dispersion in dental microwear textural parameters. As the heterogeneity of the complexity is linked to diet diversity, an obligate grazer or leaf browser will show lower values than an herbivore feeding on a wider range of food items. For further details on methods, see Scott (2012) and Scott et al. (2006).

4. Statistics

The analyses were performed with R software (R version 3.2.2, The R Foundation for Statistical Computing), using the "agricolae" package.

Mean and standard error of mean were calculated for each locality included in the study (Table 1). Prior to analyses, the values for each parameter were rank-transformed in order to perform parametric tests on data that traditionally do not fulfill the assumption of normality (Conover and Iman, 1981; Merceron et al., 2010; Scott, 2012). The spatial and temporal heterogeneity, as well as different sample sizes between localities, made it difficult to generate a 3-way analysis of variance (ANOVA). Therefore, one-way ANOVAs were performed in order to identify the significant differences between localities through time and space (Table 1). Finally, post hoc Tukey's Honest Significant Difference tests (HSD tests) and Fisher's Least Significant Difference tests were performed with the adjustment method of Bonferroni (LSD tests) in order to balance the risks of type I and type II errors (Cook and Farewell, 1996).

5. Results

There is an appreciable variation in the dental microwear signals of all *Eucladoceros* specimens included in the analysis. Complexity (Asfc) ranges from 0.6 to a maximum of 10.26 (Supplementary data, Table S1). In the same way, anisotropy varies from 0.105×10^{-3} to 9.08×10^{-3}. When comparing these results with the dental microwear signal of extant red deer from the savannah-like habitat of Lugar Nuevo and from the primeval forest of Białowieża, *Eucladoceros* occupies the wide spectrum included between these two contrasted populations. Two groups are identifiable in Fig. 3. The fossil deer from Chilhac, Varshets and Gerakarou plot among the browsing red deer from Białowieża. Conversely, *Eucladoceros* from Saint-Vallier, Senèze, Dafnero, Slivnitsa and Krimni present a more grazing signal, closer to red deer from Lugar Nuevo. The specimen from Slivnitsa presents an especially high anisotropy coupled with a low complexity while the one from Krimni presents an intermediate complexity with high anisotropy. There are differences in the dispersion of the specimens from one locality to the other, with specimens from Chilhac, Varshets and Gerakarou being more widely spread along the dental microwear spectrum, while *Eucladoceros* from Saint-Vallier, Senèze and Dafnero are restricted to a more limited ecospace.

Results of the one-way ANOVAs performed on each of the five surface parameters indicate significant differences between localities (Table 1). The results of the LSD and HSD tests (Table 2) highlight significant differences among the French localities, with Chilhac presenting higher complexity, heterogeneity of the complexity (HAsfc 9) and Tfv than Saint-Vallier, as well as having higher complexity than

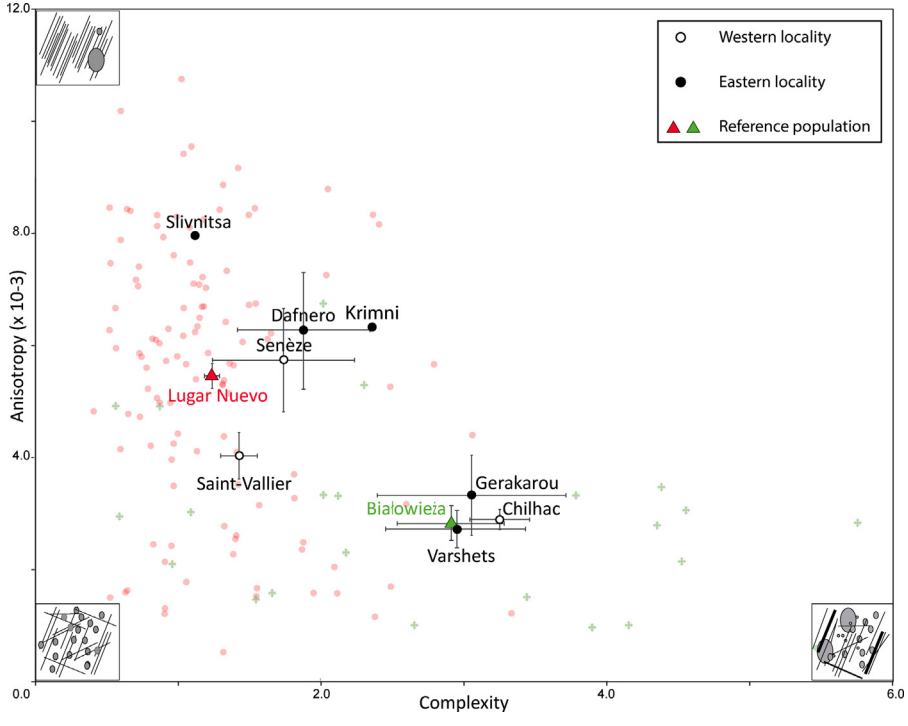

Fig. 3. Distribution (mean and standard error of mean) of *Eucladoceros* from the early Pleistocene European localities depending on the complexity and anisotropy of the dental facets. The extant red deer populations of Lugar Nuevo (Spanish dehesa; red) and of Białowieża (Polish primeval forest; green) are used as references. Transparent red dots and green crosses represent the dispersion of specimens from the two populations. White circles correspond to western European localities, black circles are for eastern localities.

Fig. 3. Distribution (moyenne et erreur standard de la moyenne) des *Eucladoceros* des localités européennes du Pléistocène inférieur en fonction de la complexité et de l'anisotropie des facettes dentaires. Les populations de cerf élaphe actuel de Lugar Nuevo (dehesa espagnole ; rouge) et de Białowieża (forêt primaire polonaise ; vert) sont utilisées comme références. Les ronds rouges et croix vertes transparentes représentent la dispersion des spécimens de ces deux populations. Les cercles blancs correspondent aux localités d'Europe de l'Ouest, les cercles noirs aux assemblages fossiles d'Europe de l'Est.

Please cite this article in press as: Berlioz, É., et al., Feeding ecology of *Eucladoceros ctenoides* as a proxy to track regional environmental variations in Europe during the early Pleistocene. C. R. Palevol (2017), http://dx.doi.org/10.1016/j.crpv.2017.07.002

Table 2
Results of the LSD (lower part of the table) and HSD (upper part of the table) tests. Significant differences between localities are in bold when supported by both LSD (Fisher's Least Significant Differences) and HSD (Tukey's Honest Significant Differences) tests. Otherwise, normal letters are used.
Tableau 2
Résultats des tests LSD (partie basse du tableau) et HSD (partie haute du tableau). Les différences significatives entre localités sont en gras quand elles sont supportées par le LSD de Fisher et par le HSD de Tukey. Dans le cas contraire, une typographie normale est utilisée.

Locality	St-Vallier	Chilhac	Varshets	Dafnero	Senèze	Slivnitsa	Gerakarou	Krimni
St-Vallier	–	**Asfc, Smc, Hasfc 9, Tfv**	Asfc				Asfc	
Chilhac	**Asfc, Hasfc 9, Tfv**	–	**Tfv**		**Asfc**, epLsar, Smc		Smc	
Varshets		**Tfv**	–			epLsar		
Dafnero				–				
Senèze		**Asfc**			–			
Slivnitsa		**Asfc**				–		
Gerakarou							–	
Krimni		Tfv						–

Senèze (Tables 1 and 2; Fig. 3). Chilhac also presents significantly higher Tfv than Varshets. The other differences are not supported by either Tukey's HSD or Fisher's LSD tests. The absence of significant differences between other localities may in part result from their smaller sample size and in part from dispersion differences of the dental microwear texture results between localities. The variation through time of the complexity, anisotropy and heterogeneity of the complexity are presented in Fig. 4.

6. Discussion

6.1. Trophic plasticity of Eucladoceros

The wide range of variation in the dental microwear texture results of *Eucladoceros* illustrates the diversity of the food that this taxon is able to consume and therefore its significant dietary plasticity (Fig. 3).

When comparing the dietary plasticity of *Eucladoceros* with that of the two contrasted modern red deer populations (Fig. 3), it is clear that the dental microwear signal of fossil deer overlaps the signal of both populations and occupies the entire range between the two. This similarity in the dietary plasticity of *Cervus elaphus* and *Eucladoceros ctenoides* is not surprising as it is well known for extant herbivores that a large body mass permits an increased retention time of the digesta in the gut and thereby implies a higher digestive efficiency (Müller et al., 2013). This characteristic means that unlike smaller herbivores, *Eucladoceros* is able to feed on a large range of what is available in its habitat in order to fulfill its energy and nutrient requirements, rather than to select only high-quality food items. This selective behavior is classically found in smaller herbivores such as the extant concentrate feeder *Capreolus capreolus* (Hofmann, 1985) or the intermediate feeder *Dama dama* (Chapman and Chapman, 1980; Hofmann, 1989), which feed on selected foods not necessarily abundant in their habitat (Jackson, 1977; Nugent, 1990; Tixier et al., 1997).

Guérin et al. (2004) consider deer from Saint-Vallier forest inhabitants. Valli and Palombo (2005) concluded, based on a dental microwear, mesowear and skull anatomy analysis of five specimens that the large-sized deer from Saint-Vallier was engaged in browsing. The pollen analysis by Argant and Philippe (2011) highlighted the presence of temperate deciduous tree cover in the locality.

The diatoms and pollen analyses of Senèze (Ehrlich, 1968; Elhaï, 1969) show climatic oscillations between a warm temperate climate with deciduous tree cover and a cool to cold climate with herbaceous monocots and conifers. Pastre et al. (2015) consider the deer from Senèze to be forest inhabitants. Valli and Palombo (2005), based on the analysis of dental microwear, mesowear and skull anatomy of three specimens, concluded that *E. ctenoides* from Senèze was a browser. The abundance of deer in this locality has been interpreted by Bonifay and Brugal (1996) as indicative of "a fresh temperate climate with a constant hygrometry and short cold winters".

With a grazing signal similar to that of the modern reference population from the Dehesa Lugar Nuevo, the feeding ecology of fossil deer from Saint-Vallier and Senèze contrasts highly with interpretations of *Eucladoceros* as being forest inhabitants. This signal somewhat implies the exploitation by these deer of an open habitat with an abundant herbaceous vegetal layer, highlighting the consumption of herbaceous monocots by *Eucladoceros*. Even confronted with mesothermophilic vegetation as in Senèze (Nomade et al., 2014), *Eucladoceros* could have exploited the herbaceous stratum.

Thus, the occurrence of *Eucladoceros* in itself as a proxy for paleoenvironmental reconstructions is flawed.

One could be surprised by the contrasting results on *Eucladoceros ctenoides* from Saint-Vallier and Senèze between the present study and the analysis conducted by Valli and Palombo (2005). In our opinion, such a discrepancy could be the result of a bias linked to a too small sample size ($N = 5$ and 3) in their study (2005). Such sample sizes are not large enough to draw conclusions in terms of diet reconstructions, more specifically when considering dental microwear patterns which may vary on a week to month scale basis. A fact that, by the way, the authors themselves do mention. In their study of the skull anatomy, mesowear and microwear of *Metacervoceros rhenanus* and *Croizetoceros ramosus* from Saint-Vallier, Valli and Palombo (2008) underscored the fact that some taxa, i.e. *Cervus elaphus*, present a huge versatility in their diet while their skull anatomy remains relatively unchanged (See also Berlioz et al., in press; Gebert and Verheyden-Tixier, 2001). In our study, we show that *E. ctenoides* displays a dietary plasticity

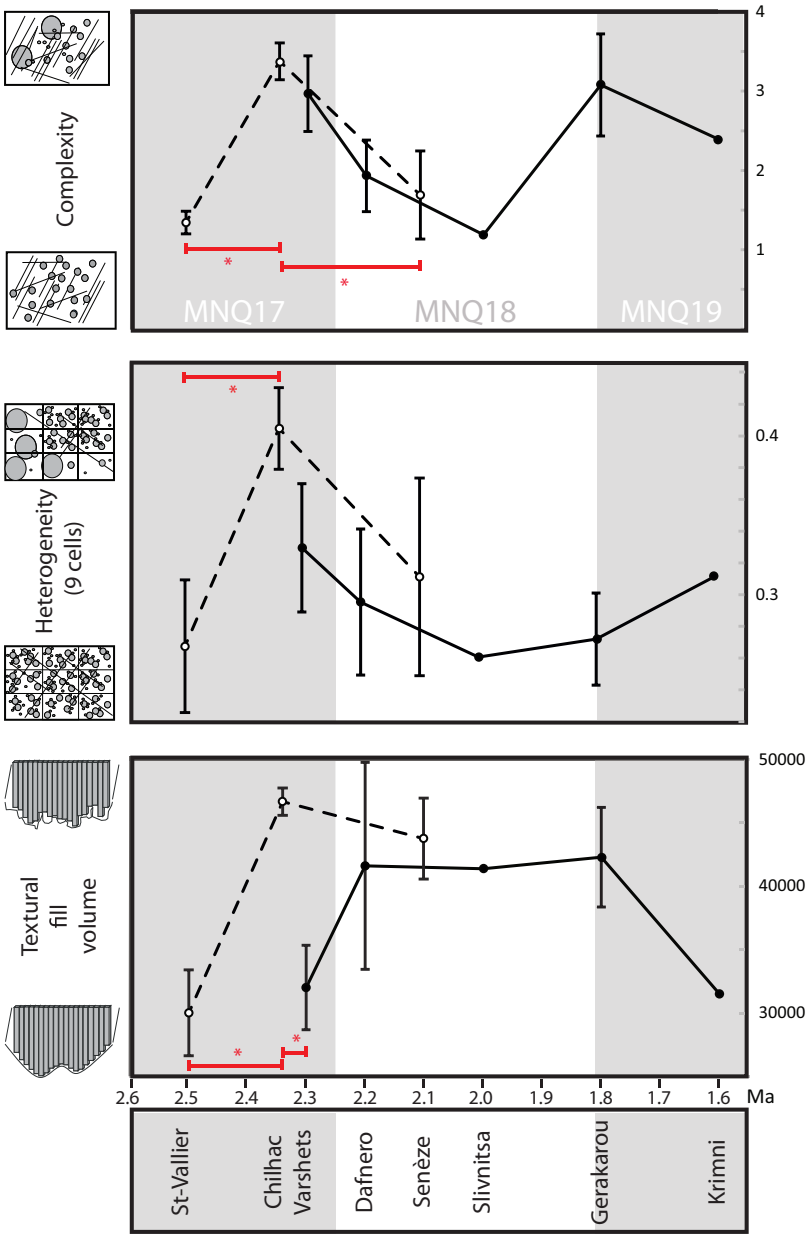

Fig. 4. Evolution through time of the complexity, heterogeneity of the complexity (9 cells) and textural fill volume of the dental surfaces of *Eucladoceros*. Dotted line and white circles correspond to the succession of western European localities through time. In the same way, a black line and black circles are used for eastern European localities. MNQ17, MNQ18 and MNQ19 correspond to the biozones of the localities of interest. Significant differences between localities are identified by red stars.

Fig. 4. Évolution de la complexité, de l'hétérogénéité de la complexité (9 cellules) et du volume de remplissage textural des surfaces dentaires d'*Eucladoceros*. La ligne en tiretés et les cercles blancs correspondent à la succession dans le temps des localités de l'Ouest de l'Europe. De la même manière, une ligne noire et des cercles noirs sont utilisés pour les localités d'Europe de l'Est. MNQ17, MNQ18 et MNQ19 correspondent aux biozones des localités d'intérêt. Les différences significatives entre localités sont identifiées par des étoiles rouges.

similar to that seen in modern *Cervus elaphus* throughout the European continent.

Despite strong similarities in faunal assemblages (Spassov and Crégut-Bonnoure, 1999), *Eucladoceros* from Saint-Vallier differs from the deer from Varshets in its dental microwear signal, the latter being more engaged in browsing. Based on the high proportion and diversity of deer in the faunal assemblage, similar conclusions have been drawn regarding the paleoenvironment of Chilhac (Guérin et al., 2004). Those assumptions are confirmed by dental microwear. Therefore, in a habitat characterized by significant tree cover, *Eucladoceros* present a browsing signal. The same kind of results is supported by dental mesowear for *Eucladoceros* from the Italian locality of Coste San Giacomo. There, the large-sized deer has been found to browse in an environment characterized by a

heterogeneous vegetation providing a large spectrum of food resources (Strani et al., 2015).

While both fossil populations present a browsing signal, *Eucladoceros* from Chilhac and Varshets differ significantly by their textural fill volume results. Ramdarshan et al. (2016) showed that among browsing species, seedeaters tend to have a higher textural fill volume than leaf browsers. Indeed, high values of this parameter are classically interpreted as resulting from the inclusion of hard food items in the diet, leading to the formation of large pits and deep scratches on the dental facet. In addition, the textural fill volume has been shown to be especially high for frugivorous herbivores (Scott, 2012) and higher values for *Eucladoceros* from Chilhac may reflect the ingestion of a larger proportion of hard items such as seeds.

The absence of significative difference between the browsing signal in Chilhac, Varshets and Gerakarou and deer with a more grazing signal results from the fact that deer populations more engaged in browsing have a large spectrum of texture values. This possibly underlines a certain diversity of available food categories in the habitat they occupy either on a spatial range or linked to annual (seasonal) variations in the vegetal phenology. Schulz et al. (2013) have shown that the dispersion of the dental microwear textures is greater when the silica proportion in the diet is low, which is the case for browsing populations like the ones in Chilhac, Varshets and Gerakarou. One could consider these differences in the dental microwear textures between localities as reflecting differences in the season of death. The wide spectrum in Chilhac, Varshets and Gerakarou could alternatively be interpreted as a homogeneous annual mortality rate in comparison with other localities. Biplots considering inter-individual variations in anisotropy and complexity (Supplementary data; Fig. S1) do not highlight any seasonality in the dental microwear textures. Alternatively, no information relative to seasonality based on other proxies (antler shedding, mortality profiles) does allow us to go further into such interpretations for these three localities.

Conversely, Senèze and Saint-Vallier fossil deer are characterized by a low dispersion in their microwear signal that illustrates a vegetal resource availability being more restricted to abrasive food items.

These results concerning fossil deer diet plasticity are of particular interest. The plasticity in dietary habits of extant deer is well understood (Gebert and Verheyden-Tixier, 2001), but the presence of fossil deer in a locality is still too often considered a sufficient paleoenvironmental proxy for drawing conclusions when it comes to the existence of tree cover (e.g., Guérin et al., 2004). This may result in the inaccuracy of paleoenvironmental reconstructions (Alcalde and van den Hoek Ostende, 2015). Yet several studies focusing on early and middle Miocene cervids (DeMiguel et al., 2008, 2010, 2011; Merceron et al., 2007, 2012; Solounias and Moelleken, 1994) stressed the fact that some Miocene deer are already engaged in mixed feeding or even grazing strategies despite presenting a brachydont to mesodont molar morphology. *Procervulus* has even been shown to be highly plastic in its diet, modulating its feeding habits in response to the important Miocene climatic and environmental changes (DeMiguel et al., 2010). Such results are not unexpected when looking at the most recent large ecological studies on modern cervid populations. Indeed, several modern deer taxa also include an important portion of herbaceous monocotyledons in their diet (Berlioz et al., in press; Bugalho and Milne, 2003; Gebert and Verheyden-Tixier, 2001; Geist, 1998 and references therein). For example, the diet of *Cervus elaphus* is composed of up to 90% of herbaceous monocots from March to August in Lugar Nuevo (Azorit et al., 2012).

By being plastic in its diet, the dental microwear textures of *Eucladoceros* might be an adequate proxy to assess paleo-climatic variations during its period of abundance. The picture of vegetal resource availability in the habitat given by such a plastic taxon is much more complete than what could be observed with a deer presenting a selective behavior (e.g. *Capreolus capreolus*).

6.2. Dental Microwear Texture Analysis: through time and space

The dental microwear textures of *Eucladoceros* oscillate over time between a grazing and browsing dietary pole depending on localities. It could reflect an alternation between wooded and open habitats, resulting from climatic fluctuations from glacial to interglacial events following the 41 ky periodicity that occurred during the middle and late Villafranchian (Kahlke et al., 2011; Lisiecki and Raymo, 2005). The microwear signal varies in the same way in western Europe between the deer from Chilhac and Senèze and in eastern Europe between *Eucladoceros* from Varshets and Dafnero. This result may illustrate a certain homogeneity of the environments of southern Europe during the early Pleistocene (Bonifay and Brugal, 1996) (Fig. 4). It is not possible to associate each locality with one specific glacial or interglacial event identified by Lisiecki and Raymo (2005), as most of the fossil sites are only biochronologically dated. However, it is possible to go further into interpretations.

Despite the fact that the differences between eastern European localities are not significant because of a low sample size (Table 1) and the wide dispersion of dental microwear results in woodland habitats, tendencies were identified between 2.3 and 1.6 Ma. As referred to by Bonifay and Brugal (1996), glacial events during the early Pleistocene of southern Europe are characterized by the spread of steppe environments, progressively leading to the reduction of the temperate, mild and humid climate. Hence, observed fluctuations of the dental microwear signal of *Eucladoceros* from browsing in Varshets to grazing in Dafnero and browsing again in the more recent locality of Gerakarou might illustrate climatic oscillations during this period (Fig. 4). Therefore, Dafnero may correspond to a glacial event characterized by a more open habitat compared to Varshets and Gerakarou that may indicate interglacial events. DMTA tends to indicate an increased involvement in browsing for *Eucladoceros* from Gerakarou when compared to earlier representatives, while no noticeable climatic change was observed between Gerakarou and older localities based on the faunal assemblage (Kahlke et al., 2011).

In the western region between 2.5 and 2.2–2.1 Ma, *Eucladoceros* also experiences several significant shifts in its diet that could be superimposed on climatic oscillations occurring during this period. While there is an important abrasive component in the diet of deer from Saint-Vallier that reflects the occupation by *Eucladoceros* of an open habitat, fossil deer from Chilhac present a woodland signal. In Senèze, *Eucladoceros* display dental microwear corresponding to grazing habits. The locality of Saint-Vallier has been described by Guérin et al. (2004) as a mostly open habitat. This could correspond to the description Bonifay and Brugal (1996) made of the Artemisia-Ephedra steppe that developed in southern Europe during glacial recurrences. Conversely, the browsing signal results that are observed in Chilhac may correspond to an interglacial event, with a higher vegetal diversity and tree cover. The signal of Senèze would correspond again to a glacial locality characterized by an open habitat.

The dental microwear signal of *Eucladoceros* from Chilhac and Senèze underlines a good example of climatic variation through time, as the two localities are geographically close to each other (10 km) but are separated by several hundred thousand years if referring to recent age estimations (Nomade et al., 2014; Pastre et al., 2015). This significant shift in the diet of *Eucladoceros* remains in the range of environmental variations that the deer is able to handle.

7. Conclusion

Although the diet of extinct cervids had been the focus of several studies (Kaiser and Croitor, 2004; Strani et al., 2015; Valli and Palombo, 2005), the present study goes further. Indeed, it is the first comprehensive exploration through time and space of the dietary plasticity of *Eucladoceros ctenoides*, an emblematic deer species of the early Pleistocene in Europe. Dental Microwear Texture Analysis shows that *Eucladoceros ctenoides* is as plastic as the extant red deer *Cervus elaphus* in feeding habits. What is striking is the recurrent ability of Cervidae, for Pleistocene as for Miocene forms (DeMiguel et al., 2010), to cope with environmental modifications.

These results are of particular interest because fossil members of the Cervidae are still too often associated in the literature with wooded environments or habitats. Yet, not enough attention is given to several studies that show that Cervidae are able to graze (Azorit et al., 2012; Bugalho and Milne, 2003; Gebert and Verheyden-Tixier, 2001; Geist, 1998; Groot Bruinderink and Hazebroek, 1995; Merceron et al., 2012) and that mixed-feeding habit may be an ancestral feeding strategy for Cervidae (DeMiguel et al., 2008, 2016; Solounias and Moelleken, 1994). Thanks to the present study, deer and notably *Eucladoceros* cannot be considered anymore as strict woody landscape dwellers. *Eucladoceros ctenoides* adapted its diet to the vegetal resource availability in its habitat and is therefore a good paleoenvironmental indicator. From our results, we can conclude that *E. ctenoides* was a browser at Chilhac, suggesting wooded habitats, whereas it fed on high amounts of herbaceous monocotyledons at Saint-Vallier and Senèze, supporting the presence of open habitats. More than characterizing vegetal availability in the habitat, variations in the microwear textures of *Eucladoceros* witness the climatic oscillations (controlling the back and forth balance from open to wooded landscapes) resulting from the glacial–interglacial cycles occurring during the middle and late Villafranchian. Chilhac, with a wooded landscape, may represent a mild episode whereas the vegetation from open habitats in Senèze and Saint-Vallier may be contemporaneous with more arid and cold periods.

Still, *Eucladoceros ctenoides*, by being one element constitutive of the fauna, only represents a window over complex environments from the past. However, contrary to stenotopic species, the trophic plasticity of *E. ctenoides* provides a solid proxy to track global changes in both vegetal context and climatic conditions.

Funding

This project was supported by the "Agence nationale de la recherche" (ANR TRIDENT: grant number: ANR-13-JSV7-0008-01; PI.: Gildas Merceron).

Acknowledgements

We thank S. Ramdarshan (https://srtranslations.wordpress.com/) for corrections of the manuscript and S. Riffaut for help with Fig. 2. For the access to fossil material, we thank E. Robert (Geological Collections, UMR CNRS 5276 Laboratoire de Géologie de Lyon - CERESE, University Lyon 1, France), D. Berthet ("Collection du musée des Confluences", Lyon, France), C. Jacquier, M. Fouché ("Musée paléontologique de Chilhac", France) and N. Spassov (National History Museum of Sofia, Bulgaria). For the access to the reference material, we thank Rafał Kowalczyk (Mammal Research Institute, Polish Academy of Sciences, Białowieża) and Concepción Azorit (University of Jaén, Spain). We also would like to thank the editor Lorenzo Rook, Daniel DeMiguel and two other anonymous reviewers for making constructive comments and suggestions leading to an improvement of the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crpv.2017.07.002.

References

Alcalde, G.M., van den Hoek Ostende, L.W., 2015. Above the hoof: functional morphology of the fossil deer from Tegelen, the Netherlands. Geol. J. 50, 271–289.

Argant, J., 2004. Le gisement pliocène final de Saint-Vallier (Drôme, France) : palynologie. In: Faure, M., Guérin, C. (Eds.), Le gisement pliocène final de Saint-Vallier (Drôme, France), 26. Geobios 37, Mem. Spec., pp. 81–90.

Argant, J., Philippe, M., 2011. L'analyse pollinique des coprolithes : un outil pour la reconstitution du paléoenvironnement. Quat. Hors Ser. 4, 307–318.

Azorit, C., Tellado, S., Oya, A., Moro, J., 2012. Seasonal and specific diet variations in sympatric red and fallow deer of southern Spain: a preliminary approach to feeding behaviour. Anim. Prod. Sci. 52, 720–727.

Azzaroli, A., De Giuli, C., Ficcarelli, G., Torre, D., 1988. Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession

and dispersal events. Palaeogeogr. Palaeoclimatol. Palaeoecol. 66, 77–100.
Bechev, D., Georgiev, D., 2016. Faunistic diversity of Vrachanski Balkan Nature Park. Plovdiv University Press.
Berlioz, E., Azorit, C., Blondel, C., Sierra Tellado Ruiz, M., Merceron, G., in press. Deer in an arid habitat: dental microwear textures track feeding adaptability. Hystrix, doi:10.4404/hystrix-28.2-12048.
Bignon-lau, O., Catz, N., Berlioz, E., Veiberg, V., Strand, O., Merceron, G., 2017. Dental microwear textural analyses to track feeding ecology of reindeer: a comparison of two contrasting populations in Norway. Mamm. Res. 62, 111–120.
Boeuf, O., Gilbert, D., 1997. Présence de thécamoebiens du genre *Trinema*, au Pliocène supérieur, découverte à Chilhac (Haute-Loire, France). C. R. Acad. Sci. Ser. IIa 325, 623–627.
Boivin, P., Barbet, P., Boeuf, O., Devouard, B., Besson, J.C., Hénot, J.M., Devidal, J.L., Constantin, C., Charles, L., 2010. Geological setting of the lower Pleistocene fossil deposits of Chilhac (Haute-Loire, France). Quat. Int. 223, 107–115.
Bonifay, M.-F., Brugal, J.-P., 1996. Biogéographie et biostratigraphie des grandes faunes du Pléistocène inférieur et moyen en Europe du Sud : apport des gisements français. Paleo 8, 19–29.
Bugalho, M.N., Milne, J.A., 2003. The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment: a case of summer nutritional constraint? For. Ecol. Manag. 181, 23–29.
Calandra, I., Merceron, G., 2016. Dental microwear texture analysis in mammalian ecology. Mamm. Rev. 46, 215–228.
Chapman, N.G., Chapman, D.I., 1980. The distribution of fallow deer: a worldwide review. Mamm. Rev. 10, 61–138.
Conover, W.J., Iman, R.L., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am. Stat. 35, 124–129.
Cook, R.J., Farewell, V.T., 1996. Multiplicity considerations in the design and analysis of clinical trials. J. R. Stat. Soc. Ser. A Stat. Soc. 159A, 93–110.
Croitor, R., 2009. In: Bucur, I.I., Săsăran, E., Pop, D. (Eds.), Phylogeny and speciation in Quaternary cervid genera *Eucladoceros* and *Praemegaceros* (Cervidae, Mammalia). Cluj University Press, Cluj-Napoca.
Curran, S.C., 2015. Exploring *Eucladoceros* ecomorphology using geometric morphometrics. Anat. Rec. 298, 291–313.
De Vos, J., Mol, D., Reumer, J.W.F., 1995. Early Pleistocene Cervidae (Mammalia, Artiodactyla) from the Oosterschelde (the Netherlands), with a revision of the cervid genus *Eucladoceros Falconer*, 1868. Deinsea 2, 95–121.
Delson, E., Faure, M., Guérin, C., Aprile, L., Argant, J., Blackwell, B.A.B., Debard, E., Harcourt-Smith, W., Martin-Suarez, E., Monguillon, A., 2006. Franco-American renewed research at the Late Villafranchian locality of Senèze (Haute-Loire, France). In: Kahlke, R.-D., Maul, L.C., Mazza, P. (Eds.), Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations. Vol. I. Proceedings of the 18th International Senckenberg Conference (VI International Palaeontological Colloquium in Weimar), 256. Cour. Forschungsinstitut Senckenberg, pp. 275–290.
DeMiguel, D., Fortelius, M., Azanza, B., Morales, J., 2008. Ancestral feeding state of ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae. BMC Evol. Biol. 8, 13.
DeMiguel, D., Azanza, B., Morales, J., 2010. Trophic flexibility within the oldest Cervidae lineage to persist through the Miocene Climatic Optimum. Palaeogeogr. Palaeoclimatol. Palaeoecol. 289, 81–92.
DeMiguel, D., Azanza, B., Morales, J., 2011. Paleoenvironments and paleoclimate of the middle Miocene of central Spain: a reconstruction from dental wear of ruminants. Palaeogeogr. Palaeoclimatol. Palaeoecol. 302, 452–463.
DeMiguel, D., Azanza, B., Cegoñino, J., Ruiz, I., Morales, J., 2016. The interplay between increased tooth crown-height and chewing efficiency, and implications for Cervidae evolution. Lethaia 49, 117–129.
DeSantis, L.R., 2016. Dental microwear textures: reconstructing diets of fossil mammals. Surf. Topogr. Metrol. Prop. 4, 023002.
Diaz, M., Campos, P., Pulido, F.J., 1997. The Spanish dehesas: a diversity in land-use and wildlife. Farm. Birds Eur. 178, 209.
Ehrlich, A., 1968. Les diatomées fossiles des sédiments villafranchiens de Senèze (Haute-Loire, Massif Central français). Bull. Assoc. Fr. Etud. Quat. 5, 267–280.
Elhaï, H., 1969. La flore sporo-pollinique du gisement Villafranchien de Senèze (Massif-Central-France).
Gebert, C., Verheyden-Tixier, H., 2001. Variations of diet composition of red deer (*Cervus elaphus L.*) in Europe. Mamm. Rev. 31, 189–201.
Geist, V., 1998. Deer of the world: their evolution, behaviour, and ecology. Stackpole books.
Geraads, D., 1990. Contribution des cervidés à la chronologie des débuts de l'occupation humaine en Europe occidentale. Quaternaire 1, 167–174.
Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. J. Hum. Evol. 15, 783–822.
Groot Bruinderink, G., Hazebroek, E., 1995. Ingestion and diet composition of red deer (*Cervus elaphus L.*) in the Netherlands from 1954 till 1992. Mammalia 59, 187–196.
Guérin, C., 1990. Biozones or mammal units? Methods and limits in biochronology. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology. Springer, US, pp. 119–130.
Guérin, C., Faure, M., Argant, A., Argant, J., Crégut-Bonnoure, É., Debard, É., Delson, E., Eisenmann, V., Hugueney, M., Limondin-Lozouet, N., Martin-Suarez, E., Mein, P., Mourer-Chauviré, C., Parenti, F., Pastre, J.-F., Sen, S., Valli, A.M.-F., 2004. Le gisement pliocène supérieur de Saint-Vallier (Drôme, France) : synthèse biostratigraphique et paléoécologique. Geobios 37 (Suppl. 1), 349–360.
Heintz, E., 1970. Les Cervidés villafranchiens de France et d'Espagne. Mem. Museum National Histoire Naturelle Nouvelle Serie, Paris, Serie C, Sciences de la Terre.
Heintz, E., Guérin, C., Martin, R., Prat, F., 1974. Principaux gisements villafranchiens de France : listes fauniques et biostratigraphie. Mem. Bur. Rech. Geol. Min. 78, 169–182.
Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78, 443–457.
Hofmann, R.R., 1985. Digestive physiology of the deer-their morphophysiological specialisation and adaptation. Biology of Deer Production, Proceedings of an International Conference Held at Dunedin, New Zealand, 13–18 February, 1983, pp. 393–407.
Jackson, J., 1977. The annual diet of the Fallow deer (*Dama dama*) in the New Forest, Hampshire, as determined by rumen content analysis. J. Zool. 181, 465–473.
Jedrzejewska, B., Jedrzejewski, W., 2013. Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. Springer Science & Business Media, Berlin.
Joffre, R., Vacher, J., de los Llanos, C., Long, G., 1988. The dehesa: an agrosilvopastoral system of the Mediterranean region with special reference to the Sierra Morena area of Spain. Agrofor. Syst. 6, 71–96.
Kahlke, R.D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. Quat. Sci. Rev. 30, 1368–1395.
Kaiser, T.M., Croitor, R., 2004. Ecological interpretations of early Pleistocene deer (Mammalia, Cervidae) from Ceyssaguet (Haute-Loire, France). Geodiversitas 26, 661–674.
Konidaris, G.E., Tourloukis, V., Kostopoulos, D.S., Thompson, N., Giusti, D., Michailidis, D., Koufos, G.D., Harvati, K., 2015. Two new vertebrate localities from the Early Pleistocene of Mygdonia Basin (Macedonia, Greece): preliminary results. C. R. Palevol 14, 353–362.
Kostopoulos, D.S., 1996. The Plio-Pleistocene artiodactyls of Macedonia (Greece); systematics, palaeoecology, biochronology, biostratigraphy. Tesis Doctoral. Universidad de Salónica.
Kostopoulos, D.S., Athanassiou, A., 2005. In the shadow of bovids: suids, cervids and giraffids from the Plio-Pleistocene of Greece. Quat. Hors Ser. 2, 179–190.
Kostopoulos, D.S., Koufos, G.D., 1994. The Plio-Pleistocene artiodactyls of Macedonia (Northern Greece) and their biostratigraphic significance; preliminary report. C. R. Acad. Sci. Paris, Ser. II 318, 1267–1272.
Koufos, G.D., 1993. Late Pliocene carnivores from western Macedonia (Greece). Palaontol. Z. 67, 357–376.
Koufos, G.D., 2016. Neogene and Quaternary continental biostatigraphy of Greece based on mammals. Bull. Geol. Soc., 50.
Koufos, G.D., Syrides, G.E., Kostopoulos, D.S., Koliadimou, K.K., 1995. Preliminary results about the stratigraphy and the palaeoenvironment of Mygdonia Basin, Macedonia, Greece. Geobios 28, 243–249.
Lacombat, F., Abbazzi, L., Ferretti, M.P., Martinez-Navarro, B., Moulle, P.E., Palombo, M.R., Rook, L., Turner, A., Valli, A.M.F., 2008. New data on the early Villafranchian fauna from Vialette (Haute-Loire, France), based on the collection of the Crozatier Museum (Le Puy-en-Velay, Haute-Loire, France). Quat. Int. 179, 64–71.
Leroy, S.A.G., Arpe, K., Mikolajewicz, U., 2011. Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. Quat. Sci. Rev. 30, 1448–1463.
Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. Paleoceanography 20, PA1003.

Lucas, P.W., 2004. Dental functional morphology: how teeth work. Cambridge University Press.
Lovari, S., Lorenzini, R., Masseti, M., Pereladova, O., Carden, R.F., Brook, S.M., 2016. *Cervus elaphus*. The IUCN Red List of Threatened Species 2016. e.T55997072A22155320.
Marañón, T., 1991. Diversidad en comunidades de pasto mediterraneo: modelos y mecanismos de coexistencia. Ecologia 5, 149–157.
Merceron, G., Schulz, E., Kordos, L., Kaiser, T.M., 2007. Paleoenvironment of *Dryopithecus brancoi* at Rudabánya, Hungary: evidence from dental meso-and micro-wear analyses of large vegetarian mammals. J. Hum. Evol. 53, 331–349.
Merceron, G., Escarguel, G., Angibault, J.-M., Verheyden-Tixier, H., 2010. Can dental microwear textures record inter-individual dietary variations? Plos One 5, e9542.
Merceron, G., Costeur, L., Maridet, O., Ramdarshan, A., Göhlich, U.B., 2012. Multi-proxy approach detects heterogeneous habitats for primates during the Miocene climatic optimum in Central Europe. J. Hum. Evol. 63, 150–161.
Merceron, G., Hofman-Kamińska, E., Kowalczyk, R., 2014. 3D dental microwear texture analysis of feeding habits of sympatric ruminants in the Białowieża Primeval Forest, Poland. For. Ecol. Manag. 328, 262–269.
Merceron, G., Ramdarshan, A., Blondel, C., Boisserie, J.R., Brunetiere, N., Francisco, A., Gautier, D., Milhet, X., Novello, A., Pret, D., 2016. Untangling the environmental from the dietary: dust does not matter. Proc. R. Soc. B. 283 (1838), 1–8.
Müller, D.W., Codron, D., Meloro, C., Munn, A., Schwarm, A., Hummel, J., Clauss, M., 2013. Assessing the Jarman–Bell principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 164, 129–140.
Nomade, S., Pastre, J.F., Guillou, H., Faure, M., Guérin, C., Delson, E., Debard, E., Voinchet, P., Messager, E., 2014. ^{40}Ar/^{39}Ar constraints on some French landmark late Pliocene to early Pleistocene large mammalian paleofaunas: paleoenvironmental and paleoecological implications. Quat. Geochronol. 21, 2–15.
Nugent, G., 1990. Forage availability and the diet of fallow deer (*Dama dama*) in the Blue Mountains. Otago. N. Z. J. Ecol., 83–95.
Olea, L., San Miguel-Ayanz, A., 2006. The Spanish dehesa. A traditional Mediterranean silvopastoral system linking production and nature conservation. Grassl. Sci. Eur. 11, 3–13.
Pastre, J.-F., Debard, É., Nomade, S., Guillou, H., Faure, M., Guérin, C., Delson, E., 2015. Nouvelles données géologiques et téphrochronologiques sur le gisement paléontologique du maar de Senèze (Pléistocène inférieur, Massif central, France). Quat. Rev. Assoc. Fr. Etud. Quat. 26, 225–244.
Ramdarshan, A., Blondel, C., Brunetière, N., Francisco, A., Gautier, D., Surault, J., Merceron, G., 2016. Seeds, browse, and tooth wear: a sheep perspective. Ecol. Evol. 6, 5559–5569.
Rivals, F., Athanassiou, A., 2008. Dietary adaptations in an ungulate community from the late Pliocene of Greece. Palaeogeogr. Palaeoclimatol. Palaeoecol. 265, 134–139.
Rook, L., Martínez-Navarro, B., 2010. Villafranchian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. Quat. Int. 219, 134–144.
Scarascia-Mugnozza, G., Oswald, H., Piussi, P., Radoglou, K., 2000. Forests of the Mediterranean region: gaps in knowledge and research needs. For. Ecol. Manag. 132, 97–109.
Schulz, E., Piotrowski, V., Clauss, M., Mau, M., Merceron, G., Kaiser, T.M., 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. Plos One 8, e56167.
Scott, J.R., 2012. Dental microwear texture analysis of extant African Bovidae. Mammalia 76, 157–174.
Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. J. Hum. Evol. 51, 339–349.
Solounias, N., Moelleken, S.M., 1994. Differences in diet between two archaic ruminant species from Sansan. France. Hist. Biol. 7, 203–220.
Spassov, N., 1998. A new late Villafranchian locality of vertebrate fauna–Slivnitsa (Bulgaria) and the carnivore dispersal events in Europe on the Pliocene/Pleistocene boundary. Hist. Nat. Bulg. 9, 101–113.
Spassov, N., Crégut-Bonnoure, E., 1999. Premières données sur les Bovidae villafranchiens de Bulgarie. C.R. Acad. Sci. Paris Ser. IIa 328, 493–498.
Strani, F., DeMiguel, D., Sardella, R., Bellucci, L., 2015. Paleoenvironments and climatic changes in the Italian Peninsula during the Early Pleistocene: evidence from dental wear patterns of the ungulate community of Coste San Giacomo. Quat. Sci. Rev. 121, 28–35.
Suc, J.P., 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. Nature 307, 429–432.
Teaford, M.F., Oyen, O.J., 1989. In vivo and in vitro turnover in dental microwear. Am. J. Phys. Anthropol. 80, 447–460.
Tixier, H., Duncan, P., Scehovic, J., Yant, A., Gleizes, M., Lila, M., 1997. Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. J. Zool. 242, 229–245.
Ungar, P.S., 2015. Mammalian dental function and wear: a review. Biosurf. Biotribol. 1, 25–41.
Valli, A.M.-F., 2004. Les Cervidae du gisement Pliocène supérieur (Villafranchien moyen) de Saint-Vallier (Drôme, France). In: Faure, M., Guérin, C. (Eds.), Le Gisement Pliocène final de Saint-Vallier (Drôme, France), 26. Geobios 37, Eem. Spec., pp. 191–232.
Valli, A.M.-F., Palombo, M.R., 2005. Le régime alimentaire du Cervidae (Mammalia) *Eucladoceros ctenoides* (Nesti 1841) reconstitué par la morphologie du crâne et par l'usure dentaire. Eclogae Geol. Helvetiae 98, 133–143.
Valli, A.M.-F., Palombo, M.R., 2008. Feeding behaviour of middle-size deer from the upper Pliocene site of Saint-Vallier (France) inferred by morphological and micro/mesowear analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 257, 106–122.

Please cite this article in press as: Berlioz, É., et al., Feeding ecology of *Eucladoceros ctenoides* as a proxy to track regional environmental variations in Europe during the early Pleistocene. C. R. Palevol (2017), http://dx.doi.org/10.1016/j.crpv.2017.07.002