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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*

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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.

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).

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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.

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

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