Quaternary Science Reviews 188 (2018) 136–142

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

High-resolution paleoenvironmental context for human occupations during the Middle Pleistocene in Europe (MIS 11, Germany)

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ARTICLE INFO

Article history:
Received 27 September 2017
Received in revised form
23 February 2018
Accepted 16 March 2018
Available online 11 April 2018

Keywords:
Paleodiet
Microwear
Mesowear
Large herbivores
Steinheim
Heppenloch
Pleistocene
Western Europe

ABSTRACT

High-resolution paleoecological proxies, such as stable isotopes or tooth microwear in large mammals, are often used for their potential to deliver information about the paleodietary traits of individuals and populations at the time of death. Such proxies are of interest in high resolution sites because they provide accurate data regarding the diet of large herbivores as well as the habitats that were available at the time of formation of the site, and by inference can detect seasonality in the formation of the assemblages. The integration of two techniques, tooth mesowear and microwear, applied to Middle Pleistocene assemblages of large herbivores from Steinheim and Heppenloch did not indicate seasonality at any of the two sites, most likely due to low resolution and time averaging of the dietary signal. However, the combination of the two proxies was highly informative for reconstructing the paleodiets of the large herbivores. The two paleodietary proxies provided consistent results that permitted us to propose a reconstruction of the paleodiets and habitats available at each site.

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1. Introduction

Multi-proxy studies are becoming increasingly common for reconstructing the paleoenvironmental context of human occupations during the Pleistocene. The recent trend in such studies is to integrate a large number of environmental proxies to make paleoenvironmental reconstructions as accurate as possible. A further trend involves the development of high-resolution proxies to improve the quality of data in high-resolution stratigraphic contexts (Vaquero, 2008; Carbonell i Roura, 2012). For example, in recent years, the paleodiets of large mammals (herbivores in particular) have been determined using various proxies for habitat reconstruction at archaeological sites. These proxies range from low temporal resolution (e.g. overall morphology) to high resolution (e.g. dental microwear). Today, in archaeological contexts, the trend is to discard solely morphology-based approaches (e.g. molar hypsodonty) which only give clues about evolutionary trends within a lineage, and to base interpretations on high-resolution proxies such as stable isotopes or tooth microwear which provide a snapshot of the diet and resources exploited by an individual (Davis and Pineda Munoz, 2016). This paper is intended to evaluate a combination of dietary proxies for reconstructing paleoenvironments during the hominin occupation of Europe in the Middle Pleistocene. Multi-proxy approaches are valuable because they take into account differences in scale measured by different proxies including the large temporal and geographical variability inherent in such various methods, which may result in discrepancies in results. Rather than an inconvenience, these discrepancies among proxies reveal the significance of diet at different scales of analysis and their respective potential for comprehensive paleohabitat reconstructions (Davis and Pineda Munoz, 2016; Sánchez-Hernández et al., 2016).

Tooth microwear and mesowear are often used together, as the integration of the two techniques provides information about the habitat exploited at the time of death (Rivals and Semprebon, 2012; Rivals et al., 2015a), but also about the existence of seasonal patterns of occupations at the sites (Rivals et al., 2015b; Sánchez-Hernández et al., 2016).

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https://doi.org/10.1016/j.quascirev.2018.03.026
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The main objective of this paper is to test whether the integrated analysis of tooth mesowear and microwear is able to provide accurate information about habitats and to detect the existence of seasonal patterns in two Middle Pleistocene sites where the temporal resolution is low. The results obtained from the sites selected, Steinheim and Heppenloch, will be compared with data published on coeval assemblages from the UK (Clacton, Hoxne, and Swanscombe) also correlated with MIS 11 (Schreve, 2001; Schreve and Bridgland, 2002; Ashton et al., 2008; Kahlke et al., 2011; van Asperen, 2013; Rivals and Lister, 2016).

2. Materials and methods

2.1. Materials

We studied the large herbivore assemblages from two Middle Pleistocene localities correlated with MIS 11, Steinheim and Heppenloch. The fossil material from these two sites is stored in the collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS) in Germany.

The Steinheim fossil locality, situated on a fluvial terrace of the River Murr, is well known for the discovery of a skull of an ancient hominin in 1933, originally named *Homo steinheimensis*, but often listed as *Homo heidelbergensis*. The Middle Pleistocene fauna was correlated to MIS 11 (Schreve and Bridgland, 2002; van Asperen, 2013). This study is based on the sampling of the assemblage corresponding to one of the four subdivisions defined by Adam (1954) - the *antiquus*-gravels (*antiquus*-Schotter) named after *Palaeoloxodon antiquus*. The large mammal assemblage includes *Palaeoloxodon antiquus*, *Stephanorhinus kirchbergensis*, *Stephanorhinus hemitoechus*, *Equus ferus*, *Bos/Bison*, *Megaloceros giganteus antecedens*, *Cervus elaphus* and *Dama dama*. Two other taxa, *Mammuthus trogontherii* and *Coelodonta antiquitatis*, were sampled but excluded from this analysis because they belong to the upper part of the sequence correlated to the Rissian complex (Saalian) (Ziegler and Dean, 1998; Adam, 1954).

The Heppenloch locality is a cave which infilling has been attributed to the German Holsteinian interglacial (Adam, 1975) and correlated with the MIS 11 (Kahlke et al., 2011). The large mammal assemblage that was sampled in this study includes *Stephanorhinus hemitoechus*, *Equus ferus*, *Bos/Bison*, *Cervus elaphus* and *Capreolus capreolus*.

2.2. Tooth mesowear analysis

Mesowear analysis, first introduced by Fortelius and Solounias (2000), is a method of categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the level of abrasiveness in a species' diet. A diet with low levels of abrasion (high attrition) maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass, results in more rounded and blunted buccal cusp apices. Mesowear was scored macroscopically from the buccal side of upper molars and lingual side of lower molars, preferably the paracone of upper M2 (Fortelius and Solounias, 2000) of all ungulate species. Other molars (both upper and lower M1 and M3) were used to increase sample size. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices were omitted from mesowear analysis (Rivals et al., 2007). In this study, the standardized method introduced by Mihlbachler et al. (2011) was employed. The method is based on seven cusp categories (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). The average value of the mesowear data from a single sample of fossil dentition corresponds to the 'mesowear score' or MWS (Mihlbachler et al., 2011). Dental mesowear analysis was conducted by a single experienced researcher (FR) to reduce inter-observer error, following the recommendations of Loffredo and DeSantis (2014).

2.3. Tooth microwear analysis

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). In the present study, all the data were collected by a single experienced observer (FR). The occlusal surface of each specimen was cleaned using acetone and then 96% alcohol. The surface was moulded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. All casts were carefully screened under the stereomicroscope. Those with badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features made during the collecting process or during storage) were removed from the analysis, following King et al. (1999). Casts were observed under transmitted light with a Zeiss Stemi 2000C stereomicroscope at 35 × magnification using the refractive properties of the transparent cast to reveal microfeatures on the enamel. Microwear scars (i.e., elongated scratches and rounded pits) were quantified on the paracone of the upper teeth or the protoconid of lower teeth in a square area of 0.16 mm^2 using an ocular reticule. We used the classification of Solounias and Semprebon (2002) and Semprebon et al. (2004) which basically distinguishes pits and scratches. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while scratches are elongated microfeatures that are not merely longer than wide, but have straight, parallel sides. Using average scratch and pit data, it is possible to discriminate between the dietary categories of leaf browsers (i.e., eating woody and non-woody dicotyledonous plants), grazers (i.e., eating grass), and mixed feeders.

3. Results

The summary data from the mesowear and microwear analyses are provided in Tables 1 and 2. The raw data have been published in Mendeley Data (Rivals, 2018) and are available at: https://doi.org/10.17632/vkpz5tv84x.2.

3.1. Steinheim

A total of eight species were sampled from the Steinheim fossil assemblage, one proboscidean, three perissodactyls, and four artiodactyls.

The mesowear values (Table 1) ranged from MWS = 1.33 for *Cervus elaphus* to 4.14 for *Stephanorhinus hemitoechus*. Such values cover the dietary spectrum from browsers and browse-dominated mixed feeders to grazers (Fig. 1). The microwear values of pits and scratches (Fig. 2A) show that our 7 samples cover the dietary spectrum from browsers to grass-dominated mixed feeders. There is no pure grazer, only *Stephanorhinus hemitoechus* overlaps slightly with the grazing ecospace. The values also show a significant overlapping among ungulates in terms of microwear patterns (Fig. 2A).

The straight-tusked elephant, *Palaeoloxodon antiquus*, was analysed only through microwear and clearly plots among the extant browsers (Fig. 2A).

The rhinoceroses, *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus*, have similar mesowear values (Fig. 1) but

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