Investigation of equid paleodiet from Schöningen 13 II-4 through dental wear and isotopic analyses: archaeological implications

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Abstract

The paleodietary traits of the equid population from Schöningen 13 II-4 were investigated through tooth mesowear and microwear analyses, as well as stable isotopic analyses. The mesowear pattern observed on the upper teeth indicates a low abrasion diet with a significant amount of browse in the diet of the horses. The tooth microwear analysis and the isotopic data confirm that the horses from Schöningen 13 II-4 were mixed feeders, like many populations from other Pleistocene localities in Northern and Eastern Europe. Microwear also provides information on seasonal changes in the diet of the horses and offers the possibility to test hypotheses about the presence of one or several horse populations. Our analysis determined that the assemblage of horse remains from Schöningen 13 II-4 resulted from multiple accumulation events, which took place at different periods of time.

Keywords: Horse; Microwear; Mesowear; Stable isotope; Middle Pleistocene; Fossil accumulation; Germany

Introduction

Schöningen is an open lignite mine located in northern Germany, 90 km east of Hannover. Systematic archaeological research has been carried out on a large number of sites at this location since 1983. The Schöningen 13 II site was discovered in 1994 and became famous with the discovery of wooden spears (Thieme, 1997). The stratigraphical (Lang et al., 2012) and the biostratigraphical (van Kolfschoten, 2012, 2014) records of Schöningen 13 II-4 indicate a correlation with Marine Isotope Stage (MIS) 9 and an age of about 300 ka BP (thousands of years before present) (Geyh and Krbetschek, 2012; Sierralta et al., 2012). The pollen assemblage associated with level II-4 is dominated by trees, shrubs, and forbs, with *Pinus* and *Betula* as dominant species (Urban, 2007; Urban et al., 2011). Among the archaeological remains (including the wooden spears), the site has yielded a rich bone assemblage consisting mainly of large mammal remains. In Schöningen 13 II-4 the main large mammal species is the horse (*Equus mosbachensis*), which represents 85% of the large mammal remains in that level (van Kolfschoten, this volume).

Pleistocene horses are usually depicted as obligate grazers, but recent studies using tooth wear and stable isotopes identified mixed feeding or even browsing traits in a number of populations in North America, Africa, and Europe, with some individuals feeding mainly under closed canopy forests (Bocherens et al., 1999; Kaiser and Franz-Odendaal, 2004; Rivals et al., 2009a; Mihlbachler et al., 2011). Horse populations from middle and late Pleistocene localities from Northern and Eastern Europe were found to be browsers or mixed feeders whereas the populations from the Mediterranean area were grazers (Rivals et al., 2009a; Rivals, 2012; Ecker et al., 2013).

In the present paper, we use tooth microwear (microscopic scars produced by the interaction of food items on the occlusal surface of the teeth) and mesowear analyses (cusp relief and shape), as well as stable isotopic analyses, to study the dietary traits of the horse assemblage from Schöningen 13 II-4.

Besides classical uses in dietary interpretations of ungulates, the application of tooth wear analyses on archaeological assemblages offers the possibility of identifying single or multiple depositional events. Part of the horse assemblage from Schöningen 13 II-4 is known to be the result of hominid hunting activities (Thieme, 1997, 2005; Voormolen, 2008; Conard et al., this volume). Some authors have even suggested that the assemblage is the result of a single mass-kill event (Musil, 2007; Thieme, 2007).

On the basis of the data gathered on the dietary traits of the horse assemblage from Schöningen 13 II-4, we test two hypotheses: (1) the horse population(s) had a mixed feeding dietary strategy; and (2) the assemblage is the result of a single accumulation event.

Material and methods

The horse molars analyzed in this study are from the site of Schöningen 13 II-4. Tooth mesowear was examined directly on the fossil specimens and high resolution molds for tooth microwear as well as samples for isotopic analysis were taken in May 2012 at the Faculty of Archaeology at Leiden University. Before analysis, the material was carefully examined to refit the teeth from the same individuals looking at crown height and contact facets between teeth. Only one tooth from each association was sampled.

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 relative amounts of attritive and abrasive dental wear. Mesowear is scored macroscopically from the buccal side of upper molars (Fig. 1), preferably the paracone of M2 (Fortelius and Solounias, 2000). 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 and/or a high rate of soil or dust particle ingestion results in more rounded and blunted buccal cusp apices. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices are omitted from mesowear analyses. Cusp sharpness is sensitive to ontogenetic age among young individuals (who have not yet developed substantial wear facets) and among dentally senescent individuals. However, for intermediate age groups, which typically include the majority of individuals in a fossil collection, mesowear was found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007) and therefore suitable for dietary reconstruction.

Insert Figure 1 approximately here

In this study, the standardized method (mesowear ‘ruler’) introduced by Mihlbachler et al. (2011) is employed (Fig. 2). The method is based on seven modern horse cusps (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). Using the mesowear ruler as a reference, cusps equal to or sharper and higher in relief than reference cusp 0 were assigned a 0. Cusps that were morphologically intermediate between reference cusp 0 and reference cusp 1, or equal to reference cusp 1 were assigned a 1, and so forth. The average value of the mesowear data from a single sample of fossil dentitions corresponds to the ‘mesowear score’ (Mihlbachler et al., 2011).

Insert Figure 2 approximately here

Microwear analysis

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the cleansing, molding, casting, and examination protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). In short, the occlusal surface of each specimen was cleaned using acetone and then 96% alcohol. The surface was molded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. All specimens molded 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 incident 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 in a square area of 0.16 mm^2 using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004) as follows: (1) 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 they are wide, but have straight, parallel sides. (2) Large pits are deeper, less refractive (always dark), generally at least about twice the diameter of small pits, and often have less regular outlines than do small pits. (3) Cross scratches are oriented somewhat perpendicularly to the majority of scratches observed on tooth enamel (Solounias and Semprebon, 2002). In addition, scratch textures were assessed as being either fine (i.e., narrow scratches that appear relatively shallow and have low refractivity), coarse (i.e., wide scratches that are also relatively deep but have high refractivity (relatively shiny)), or a mixture per tooth surface reflecting the most common pattern seen on the two areas where counts were made. The scratch width score (SWS) is obtained by giving a score of '0' to teeth with predominantly fine scratches per tooth surface, '1' to those with a mixture of fine and coarse types of textures, and '2' to those with predominantly coarse scratches. Individual scores for a sample are then averaged to get the SWS.

Scratches and pits were counted in two areas on the paracone and converted to densities (number of features per mm^2). The results were compared with a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002). Using average scratch and pit data, it is possible to discriminate between the dietary categories of browser (i.e., eating woody and non-woody dicotyledonous plants) versus grazer (i.e., eating grass). Mixed feeding ungulates can best be separated from browsers or grazers by calculating the percentage of individuals in a population possessing scratch numbers that fall between 0 and 17 in the 0.16 mm^2 area (0–17%) (Semprebon and Rivals, 2007). Thus, for extant ungulates, the percentages of individuals in the low-scratch range are generally as follows: grazers with 0.0–22.2% of scratches between 0 and 17; mixed feeders with 20.9–70.0% of scratches between 0 and 17; and leaf-dominated browsers with 72.7–100.0% of scratches between 0 and 17 (Semprebon and Rivals, 2007).

Isotopic analysis

Stable oxygen and carbon isotopes of mammalian tooth enamel record ecological conditions and dietary preferences experienced by an individual during the formation of the teeth. Oxygen isotopic values of the mineral phase of dental tissues have been demonstrated to correlate with the δ^{18}O values of meteoric water, and can inform about climate, seasonality or the geographic range of animals (Fricke et al., 1998; Bocherens et al., 2001; Julien et al., 2012; Tütken et al., 2008). The δ^{13}C values of osseous tissues of terrestrial herbivores reflect the δ^{13}C values of dietary plants. The C_3 plants that dominate in Eurasia display different values according to the type of plants and environmental conditions, with plants growing under closed, forested habitats being δ^{13}C depleted in comparison with plants growing in open habitats (Deines, 1980; Tieszen, 1991; Vogel, 1993; Drucker et al., 2008).

In order to avoid the effect of additional fractionation occurring during suckling, we only chose third molars for isotopic analysis (Hoppe et al., 2004). Our sample included three left upper third molars (corresponding to three different individuals) showing a similar stage of development and occlusal wear. The paracone was sampled in the area of thickest enamel. The crown of each sampled tooth was mechanically cleaned to remove the cementum as well as altered enamel (identified by the observation of superficial cracks) and possible contaminants. Fifteen 3 mm thick enamel serial samples were removed with a diamond-studded drill perpendicular to the growing axis of the crown, and 3 cm long bulk enamel samples were taken along the axis of enamel growth (Fig. 3).

Insert Figure 3 approximately here

Powders from each sample were chemically pre-treated with 2.5% NaOCl solution followed by a 0.1M Ca-acetate acetic acid buffer solution to remove organic elements and diagenetic contaminants (Lee-Thorp and van der Merwe, 1991; Koch et al., 1997). Details of the pre-treatment method are provided in Julien et al. (2012). Carbon and oxygen isotopic composition were measured on 1.8 to 2.0 mg of treated powder, with a Finnigan Mat 252 mass spectrometer connected to a Gasbench II, at the Department of Geosciences of the University of Tübingen. Isotopic measurements were calibrated using the international standards NBS-18 and NBS-19, with a reproducibility of ±0.1‰ (1σ). Carbon isotopic values are reported relative to the V-PDB (Vienna Pee Dee Belemnite) international reference standard, whereas oxygen isotopic values are reported relative to the V-SMOW standard (Vienna Standard Mean Ocean Water), with the standard delta notation (δ) in per mil (‰).

Time resolution

Tooth mesowear, microwear, and stable isotopic signals provide information about diet at different temporal scales. Tooth microwear reflects the diet an animal had during the last days or weeks of its life (short temporal scale), and consequently records possible seasonal ecological changes. Tooth mesowear corresponds to a ‘longer’ temporal scale (months–years), which gives a close approximation of overall diet and thus more generalized annual ecological conditions than microwear. Due to the nature and process of formation of horse enamel, stable isotopes analyzed from each horizontal serial sample average the signal of the material formed over a few months, while bulk vertical samples should represent material mineralized during a year of growth (Hoppe et al., 2004).

Tooth microwear as a tool for disentangling single versus multiple events

The method used to detect if the fossil assemblage is the result of a single or multiple death events is based on assumed changes through time in the food resources available to the animals. During each season, a specific set of food resources with a specific microwear signal should be available (plant taxa as well as available plant parts). On the other hand, across seasons, a more diverse range of food should be available. If game animals died during a specific season (i.e., during a short term occupation) then it can be expected that the dental wear signal will show low variation. In contrast, if the animals died in different seasons with a different microwear signal, one would expect more variation. A recent study on modern animals has shown that extant game animals hunted in a single season only have a dental wear signal with low variation (Rivals et al., 2009b). In contrast, game animals hunted during longer periods of time (i.e., long-term or repeated occupations) present a larger variation in their dental wear (Rivals et al., 2009b). This method has been successfully applied to archaeological assemblages of fossil ungulates in Arago Cave in southeastern France (Rivals et al., 2009b) and various Middle Paleolithic localities in Europe (Rivals et al., 2009c; Moncel and Rivals, 2011). At these sites, tooth microwear interpretations were supported by geoarchaeological and zooarchaeological data that permitted the discrimination of various types of occupations.

In this way, microwear patterns in herbivorous ungulates hunted by humans provide a signal used to find differences between samples of animals hunted during a single season and those that were hunted over an entire year (or longer periods). However, this method cannot be applied to assemblages with small sample sizes ($N < 10$).

Statistics

An analysis of variance (ANOVA) was performed to test for significant differences in mesowear and microwear patterns between the different tooth positions (P4 to M3).

Levene's test was used to compare the coefficient of variation (CV) of the scratch densities with reference samples corresponding to short and long occupational events. Levene's test is used as a test for equal relative variation after transforming the raw data to the natural log scale to eliminate the influence of scale (for more details see Rivals et al., 2009b).

Spearman's test was used to test for possible correlations between $\delta^{13}C$ and $\delta^{18}O$ values. All statistical tests were conducted in PAST 3.01 software package (Hammer et al., 2001).

Results and discussion

A total of 111 upper teeth were sampled. From that sample, 98 upper teeth were suitable for mesowear analysis (88.3%), corresponding to a minimum number of 15 individuals (MNI) and 71 teeth for microwear analysis (63.9%) corresponding to a MNI of 12. The teeth discarded from the mesowear analysis had broken cusps, which do not permit the recording of cusp relief and/or shape. The teeth discarded from the microwear study displayed surfaces with taphonomic alterations, which erased the original dietary microwear pattern.

No significant difference was identified between the mesowear scores in P4, M1, M2, and M3 (Table 1). Similar results have been reported by Kaiser and Solounias (2003) and support the use of all four teeth to record mesowear. The same applies for the microwear pattern. Neither the numbers of pits nor the numbers of scratches differs significantly between the individual tooth positions (Table 1). Consequently, all teeth sampled, P4 to M3, have been merged into a single sample (Table 2).

Insert Tables 1 and 2 approximately here

In order to test the possibility of identifying individual differences in the dietary and habitat ecology of the horse sample, we performed stable isotope analysis of carbon (^{13}C) and oxygen (^{18}O) on a selection of 3 specimens (Schö 695/12-24, 715/40-1, and 720/18-1) sampled for meso- and microwear analysis. One of these specimens (Schö 695/12-24) was serially sampled to test the possibility of identifying seasonal changes in diet and habitat recorded during the formation of the tooth enamel.

Dietary traits of the horse population

Mesowear The teeth sampled have predominantly sharp and rounded cusps with high relief, i.e., mesowear scores belonging to categories '1' and '2' (Fig. 1). The average mesowear score (MWS) for the sample from Schöningen 13 II-4 is 1.88, which corresponds to low abrasion and high attrition processes. When compared with the extant ungulates, the MWS is significantly lower than the mesowear score of the two extant zebras, *Equus quagga* (MWS = 4.7) and *E. grevyi* (MWS = 4.5), which are both grazers. The MWS of the Schöningen horses (MWS = 1.88) corresponds to two dietary categories in the extant ungulates, specifically the leaf browsers and the browse dominated mixed feeders (Fig. 2).

The low abrasion observed for the horses from Schöningen 13 II-4 is very unusual among middle and late Pleistocene populations. Horses usually have higher MWS. The horses from Schöningen 13 II-4 were compared with other samples from middle and late Pleistocene localities. The horses from Taubach, Salzgitter-Lebenstedt and Wallertheim level F (Germany), Caune de l'Arago, Le Portel-Ouest, and Payre (France), and Abric Romaní (Spain) all have higher mesowear scores (Rivals et al., 2008, 2009a). Among these, the sample with the lowest abrasion is Wallertheim F with a MWS = 3.0 (Rivals et al., 2009a).

The low MWS recorded for the Schöningen sample indicates an important amount of low abrasion plants, such as shrubs or forbs, in the horse diet. As mesowear provides an average annual signal, it is not possible to determine whether the consumption of low abrasion food was constant over the year, or varied seasonally. The microwear study permits more precise information on possible seasonal changes in the horse diet in this population.

<u>Microwear</u> At Schöningen 13 II-4, enamel surfaces display a large diversity of microwear patterns from low to high densities of pits and scratches (Fig. 4 and 5), with an average value intermediate between the values of the extant leaf browsers and the extant grazers (Table 2). The ‘low-scratch’ value (0–17% is the percentage of individuals with less than 17 scratches in the counting area, i.e., less than 106 scratches per mm^2) is an indicator of the dietary category on a scale from exclusive grazers (0%) to exclusive browsers (100%). At Schöningen, the ‘low-scratch values’ are recorded on 59.2% of the specimens, indicating mixed feeding traits, a result differing slightly from the mesowear data. This discrepancy could be related to seasonal changes in diet.

Insert Figures 4 and 5 approximately here

In comparison with the extant plains zebra (*Equus quagga*) and the Grevy's zebra (*E. grevyi*), the sample from Schöningen 13 II-4 has a density of pits two to three times higher, while the density of scratches is lower (Table 2). The percentage of individuals with cross scratches (%XS), which are more common in grazers, is significantly lower in the fossil sample. Percentages of large pits (%LP) and the scratch width (SWS) are quite similar in the fossil and extant samples and permit us to exclude fruits, seeds and bark in the horse diet (Semprebon et al., 2011). Our results are also consistent with the pollen record indicating the dominance of arboreal pollen in the level Schö 13 II-4 (Urban, 2007; Urban et al., 2011; Urban, this volume).

Stable isotopes

The teeth presented macroscopically well-preserved enamel, with few inclusions providing powder of whitish color, except at the base of the crown where the enamel powder was more greyish (an area avoided for the bulk samples). In comparison with other osseous tissues, due to its high mineral content enamel is less susceptible, but not immune, to diagenetic alteration. The reliability of the isotopic signatures was examined by comparing values obtained from different osseous tissues and by using the trend of intra-tooth variations as well as the proportions of carbonate content (Wang and Cerling, 1994; Koch et al., 1997; Stuart-Williams and Schwarcz, 1997; Kohn et al., 1999; Lee-Thorp and Sponheimer, 2003; Zazzo et al., 2004; Tütken and Vennemann, 2011).

The enamel samples show carbonate content similar to those of fresh enamel, varying between 3.2 and 4.2%. The carbonate content did not correlate with either $\delta^{13}C$ or $\delta^{18}O$ values, and there was no correlation between $\delta^{13}C$ and $\delta^{18}O$ values.Additionally, the sinusoidal pattern of the $\delta^{18}O$ values of the serially sampled specimen is typical of seasonal variations of meteoric values of ^{18}O (Fig. 6), which is unlikely to have been preserved if alterations had affected the biogenic signal. All of these features indicate that the biogenic signal has not been significantly affected by diagenesis.

Insert Figure 6 approximately here

Dentine samples show carbonate content (4.5 and 4.8%) similar to those expected for fresh dentine. Dentine presents similar δ^{13}C values as the enamel from the same tooth, and relatively higher δ^{18}O values (Table 3). A tendency towards more positive δ^{18}O for dentine and cementum in comparison with enamel has been observed for a larger sample from the same collection (cf. Julien et al., this volume). Consequently, the slight difference observed here between dentine and enamel isotopic values likely reflects a limited alteration of the dentine, more susceptible than enamel to diagenetic alterations, and does not challenge the integrity of the enamel samples.

Insert Table 3 approximately here

Enamel bulk δ^{18}O values ranged from 22.8 to 23.6‰. δ^{18}O values ranged from 22.1 to 23.9‰ within the tooth serially sampled (*i.e.* specimen 32). The δ^{18}O curve of this specimen starts with a clear increase of 1.2‰ of the values between samples 32.1 and 32.3 at the top of the crown. Subsequently, the δ^{18}O value decreases by 1.1‰ until sample 32.10, while the last enamel samples present more positive δ^{18}O values (by 1.7‰) forming a plateau near the base of the crown (Fig. 6). This plateau corresponds to a zone of the tooth crown located near the root enamel junction where the enamel is thinner, and could reflect some effect of diagenesis on the seasonal signal or a less attenuated signal reflecting a shorter period of time. However, this might also reflect access to another source of water during the last period of formation of the crown, globally higher temperatures than expected in this part of the sequence, or dispersal to an isotopically different area. Nevertheless, the intra-tooth δ^{18}O values follow a quasi-sinusoidal pattern likely reflecting the seasonal variation of δ^{18}O in local meteoritic water. In lowland temperate regions, δ^{18}O values vary according to temperatures, with lower values corresponding to winter and higher values corresponding to summer temperatures (Fricke and O'Neil, 1996; Fricke et al., 1998).

Enamel δ^{13}C values are very homogeneous, ranging only from -13.0 to -12.1‰ within the specimen 32 and from -12.8 to -12.5‰ in the bulk samples (Table 3). The results correspond to published values for Eurasian Pleistocene ungulates (Bocherens et al., 1995; Ecker et al., 2013; Iacumin et al., 2010). In comparison to the δ^{18}O values, the δ^{13}C values of specimen 32 do not vary in the sequential samples (except at the base of the crown, where the values slightly increase i.e., locations 32.14-32.15 in table 3). This corresponds to the pattern observed in other horse teeth from Schöningen (Julien et al., this volume).

With isotopic fractionation between plants and herbivore bioapatite reaching +14.1‰, Schöningen horse δ^{13}C values are characteristic of the exclusive consumption of C_3 plants growing in a mixed environment composed of patchy light forests, shrubs and grassy areas, or reflect individuals moving regularly between forested land and open grassy areas (Cerling and Harris, 1999; Bocherens, 2003; Drucker et al., 2008). These values are consistent with the Schöningen 13 II-4 pollen record (Urban, 2007; Urban et al., 2011), and with published values of carbon isotopes measured on horse bones and teeth from European temperate Pleistocene and Holocene contexts (Bocherens et al., 1999; Drucker and Bocherens, 2010; Britton et al., 2012).

The lack of variation in the intra-tooth ^{13}C isotopic signatures suggests minimal seasonal variation in the ingested δ^{13}C from plants. This can result from dietary specialization (i.e., low variation in the δ^{13}C of the ingested plants) or from the average of different sources of δ^{13}C in the ingested food. Each sample corresponds to an average value recorded over a relatively long period of time, making it more comparable to the mesowear than to the microwear signal. However, comparing isotopic and micro/mesowear data can be useful for understanding the pattern recorded here.

The mesowear scores of specimens 32 and 55 (MWS = 2) indicate that those individuals were mixed feeders, while molar 56 belonged to a grazer (MWS = 4) (Table 3). This difference in diet recorded in mesowear does not coincide with the enamel $\delta^{13}C$ values, which are very similar for the three individuals. The $\delta^{18}O$ values show a small difference between the grazer (molar 56, 23.6‰) and the mixed feeders (individuals 32 and 55, 22.9 and 22.8‰, respectively). The difference is slight, however, and the sample is too small to infer palaeoecological differences among these individuals. Unfortunately, the microwear pattern of these specimens was taphonomically altered and did not allow a direct comparison between isotopic and microwear data. Nevertheless, considering the large variation of microwear patterns recorded in the fossil assemblage of Schöningen, dietary specialization is very unlikely. The nature and process of hypsodont tooth enamel formation, as well as the sampling procedure, probably dampened the recorded isotopic dietary signal (Balasse, 2002; Passey and Cerling, 2002; Kohn, 2004), averaging a variety of sources of $\delta^{13}C$ from the ingested food (or including different kind of plants of relatively comparable $\delta^{13}C$ values) and mimicking a specialized diet. Therefore, it can be proposed that Schöningen horses were generalists, changing their diet on a regular and/or seasonal basis, a pattern impossible to detect with isotopic sampling methods alone, for the reasons described above.

In contrast with their morphological adaptation for grass-based diets (hypsodonty), the diversity of plants ingested by the Schöningen Pleistocene equids seems to point to a non-selective dietary behavior, intermittently grazing and browsing very likely favored by a mosaic-like vegetation, with woodland patches interspersed with open areas, or open-like vegetation with dispersed trees and bushes. Such a non-strictly grazing feeding behavior has been reported for other Pleistocene horses, as well as late Miocene to Pliocene hypsodont equids, showing that hypsodonty might have resulted from short-time selection pressure, and does not necessarily reflect a dietary specialization (Koch et al., 1998; MacFadden et al., 1999; Mihlbachler et al., 2011; Prado et al., 2011). The dietary plasticity observed in Pleistocene horses can be related to feeding ecology, biogeography, mobility, or resource partitioning within the local environment. Such trophic plasticity is also known in other Pleistocene mammals such as bison or mammoth (Rivals and Semprebon, 2011; Rivals et al., 2012).

Microwear variability: Detecting single versus multiple events

The coefficient of variation (CV) calculated on the scratch values at Schöningen 13 II-4 (CV = 0.28) indicates a relatively high variability (Fig. 7). To estimate the significance of the CV value, the CV of the studied sample was compared with the CV values observed for horse samples from three Pleistocene localities: Arago Cave levels G and P (Rivals et al., 2009b), Payre level F (Rivals et al., 2009c), and Taubach (Moncel and Rivals, 2011). The assemblage from Arago Cave level G corresponds to a thick palimpsest of several occupations at different seasons through the year, with horse remains distributed vertically through the level. By contrast, level P corresponds to a short-term accumulation (Moigne et al., 2006; Rivals et al., 2009b). The sample from Payre (level F) represents a succession of several short occupations during the same season, separated by occupations of the site by cave bear (Daujeard, 2008). The Taubach sequence yielded an undisturbed archaeological horizon represented by a sandy travertine formation with the presence of several hearths (von Stiener, 1976), corresponding to a single and short occupation (Moncel and Rivals, 2011).

Insert Figure 7, Table 4 approximately here

Results from Levene's test (Table 4) indicate significant differences with the short occupation samples from Arago level P ($p = 0.009$; N = 11), Payre level F ($p = 0.016$; N = 10) and Taubach ($p = 0.007$; N = 10) but there is no significant difference with the sample from Arago Cave (level G) corresponding to repeated occupations of the cave over a long period ($p = 0.3853$; N = 38). Compared with an extant plains zebra population from Kenya resulting from a single hunting event (Rivals, Unpublished data), the CV of the Schöningen sample is significantly higher (Fig. 7). Even if taxonomically different, the horse sample from Schöningen was also compared with two extant samples of caribou (*Rangifer tarandus*) representing short and long duration samples, and it appears that the CV of the Schöningen horse sample is very similar to the CV of the long-duration sample of caribou (Fig. 7).

As reported earlier, there is a difference between the mesowear and microwear results. Tooth mesowear indicates a diet dominantly based on browse, while microwear indicates seasonal mixed feeding habits, with some individuals being purely grazers and others purely browsers at the time of death. There is a larger dietary variability based on microwear than on mesowear, and this discrepancy is indicative of the equid behavior at Schöningen. It permits us to rule out the possibility that the population(s) had a variable diet on a daily basis (named meal-by-meal mixed feeders by Solounias and Semprebon, 2002) and indicates that the diet was varying seasonally depending on the availability of resources.

These findings suggest that the assemblage from Schöningen 13 II-4 cannot be the result of a single short event, and thus is the consequence of an accumulation during multiple events, likely occurring during various seasons of the year. These data are supported by a geoarchaeological study (Stahlschmidt et al., this volume), which indicates that the archaeological remains are distributed through distinct geological layers reflecting different lake level stands, with no sedimentary evidence for one single event. Our results are further in agreement with those provided by an inter-individual study of intra-tooth isotopic variation performed on lower cheek teeth of the Schöningen 13 II-4 horse assemblage, which also identified a multi-event accumulation (Julien et al., this volume).

Conclusion

The paleodiet of the horses from Schöningen 13 II-4 was characterized through tooth meso- and microwear analyses as browse-dominated mixed feeding. This result was confirmed by stable isotopic analysis, pointing to a non-selective dietary behavior, with intermittent grazing and browsing in a mosaic-like vegetation habitat, composed of woodland patches interspersed with open areas, or of open vegetation with dispersed trees and bushes. Our results confirm that Pleistocene horse populations from Northern Europe had mixed feeding or browse-dominated dietary traits as observed in other middle and late Pleistocene localities in England, Germany, and Austria, and indicate greater behavioral and ecological flexibility than has been generally assumed for this taxon.

The microwear analysis shows high variability in the microwear pattern for the horse assemblage. The high coefficient of variation, significantly different from localities with short occupations, indicates that the assemblage from Schöningen 13 II-4 is the result of multiple mortality events.

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Figure captions

Figure 1. Horse upper teeth from Schöningen 13 II-4, buccal view. Right M2 Schö 695/51-3 (A) and left P4 Schö 719/13-8 (B). Scale bar = 1 cm

Figure 2. Horse mesowear from Schöningen 13 II-4 compared with extant ungulates (LB = leaf browsers; MF = mixed feeders; G = grazers) and other middle and late Pleistocene horse samples from Western Europe (AR = Abric Romaní; ARA = Caune de l'Arago; LPO = Le Portel-Ouest; PAY = Payre; SL = Salzgitter-Lebenstedt; TAU = Taubach; WAL-F = Wallertheim level F). Extant plains zebra *Equus quagga* (eq) and Grevy's zebra *Equus grevyi* (eg) are plotted among the extant grazers. Abbreviations of the other extant ungulates (Fortelius and Solounias, 2000): **Browsers**: AA = *Alces alces,* AM = *Antilocapra americana,* DB = *Diceros bicornis,* DS = *Dicerorhinus sumatrensis*, GC = *Giraffa camelopardalis,* LW = *Litocranius walleri,* OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni,* OL = *Capreolus capreolus,* OV = *Odocoileus virginianus*, RS = *Rhinoceros sondaicus,* TE = *Tragelaphus euryceros,* TT = *Tragelaphus strepsiceros*; **Grazers**: ab = *Alcelaphus buselaphus,* al = *Sigmoceros lichtensteinii,* bb = *Bison bison,* cs = *Ceratotherium simum,* ct = *Connochaetes taurinus,* dl = *Damaliscus lunatus,* eg = *Equus grevyi,* eq = *Equus quagga*, he = *Hippotragus equinus,* hn = *Hippotragus niger,* ke = *Kobus ellipsiprymnus,* rr = *Redunca redunca*; **Mixed feeders**: Ax = *Axis axis,* Bt = *Budorcas taxicolor,* Ca = *Capricornis sumatraensis,* Cc = *Cervus elaphus canadensis,* Cd = *Rucervus duvaucelii,* Ci = *Capra ibex,* Cu = *Cervus unicolor,* Gg = *Gazella granti,* Gt = *Gazella thomsoni,* Hj = *Hemitragus jemlahicus*, Lv = *Lama vicugna*, Ma = *Antidorcas marsupialis*; Me = *Aepyceros melampus*; Oc = *Ovis canadensis,* Om = *Ovibos moschatus,* Oo = *Ourebia*

ourebi, Op = *Ovis ammon poli*, Pc = *Procavia capensis*, Rf = *Redunca fulvorufula*, Rt = *Rangifer tarandus*, Ru = *Rhinoceros unicornis*, Sc = *Syncerus caffer*, St = *Saiga tatarica*, Ta = *Tragelaphus angasi*, Ti = *Tragelaphus imberbis*, To = *Taurotragus oryx*, Tq = *Tetracerus quadricornis*, Tr = *Boselaphus tragocamelus*.

Figure 3. Sampling procedure of the enamel of horse upper third molar. Bulk samples consist of 3 cm long samples taken along the growing axis of the crown. Serial samples consist of multiple 3 mm thick samples drilled perpendicularly to the axis of enamel growth. Bulk and serial samples were taken on the paracone.

Figure 4. Microwear patterns observed at 35x on the enamel surfaces of horse upper teeth from Schöningen 13 II-4: Schö 693/45-4 (A) and Schö 716/11-4 (B).

Figure 5. Bivariate diagram based on microwear signatures of extant reference species from Solounias and Semprebon (2002) and the ungulate sample from Schöningen. Black dots correspond to individual teeth; the average for the sample is represented with an 'S'. Grey areas indicating Gaussian confidence ellipses ($p = 0.95$) on the centroid of the extant grazer and browser samples adjusted by sample size.

Figure 6. Enamel intra-individual variations of O and C isotope ratios of specimen 32 (upper third molar Schö 695/12-24) from Schöningen 13 II-4. The distance between successive samples is indicated from the root-enamel junction (0 - REJ) to the top of the crown. The arrow indicates the direction of the enamel mineralization process. Lower values of $\delta^{18}O$ correspond to the cold seasons (winter), higher values to the warm seasons (summer).

Figure 7. Coefficient of variation for the horse sample from Schöningen 13 II-4 compared with extant *Rangifer tarandus* (Rivals and Solounias, 2007) and extant and fossil *Equus* samples (Rivals et al., 2009b; Moncel and Rivals, 2011). Red bars indicate high CVs and blue bars low CVs.

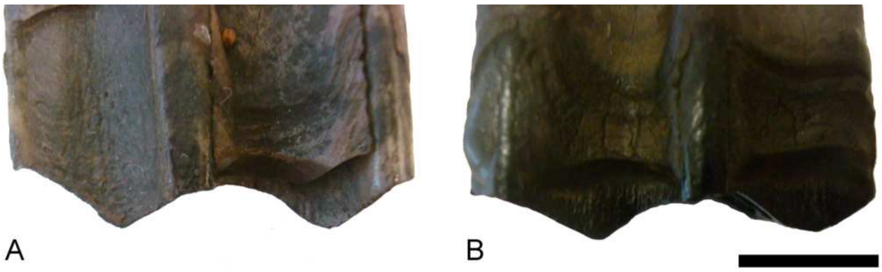

Figure 1

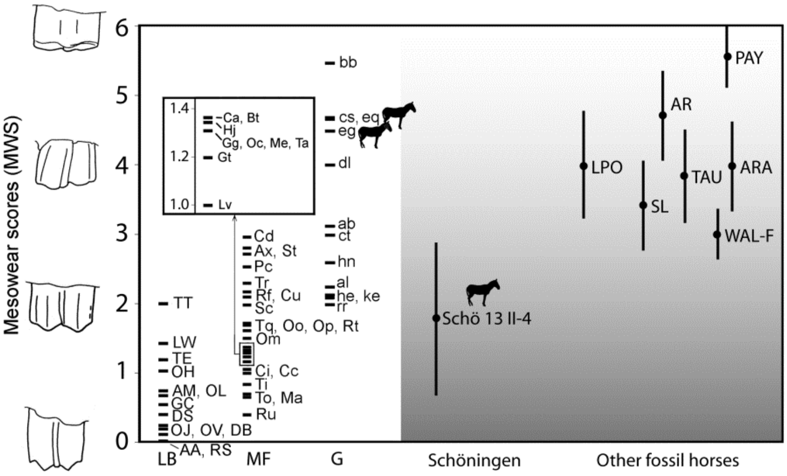

Figure 2

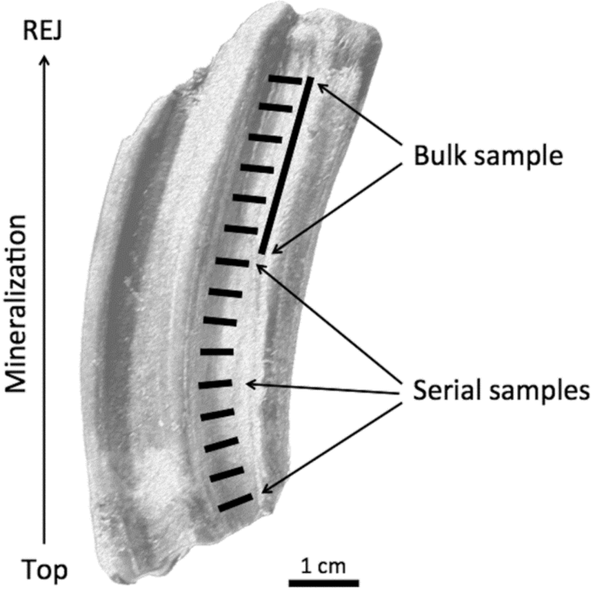

Figure 3

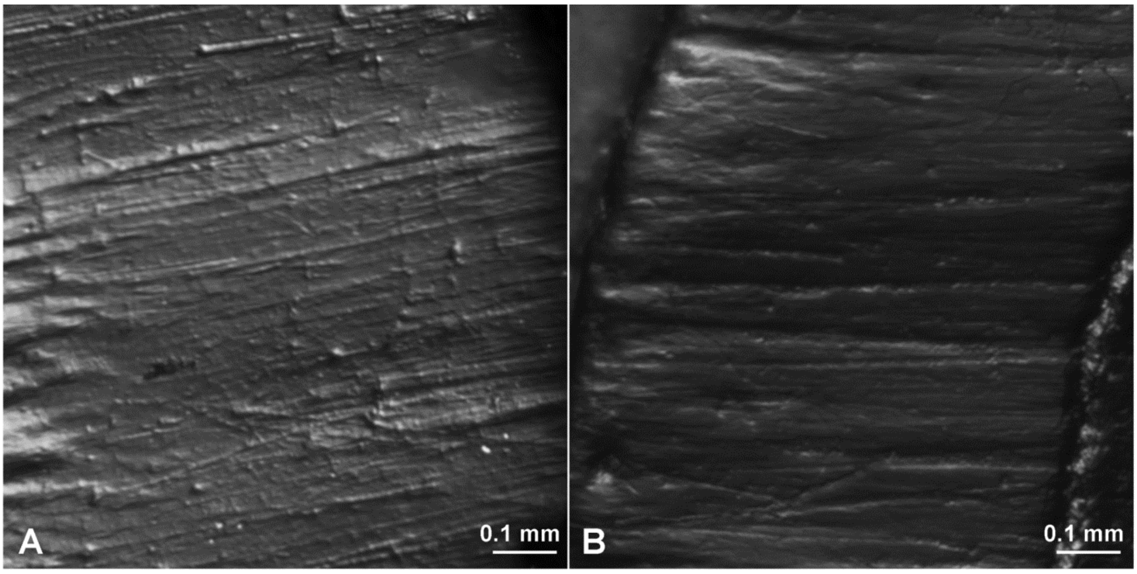

Figure 4

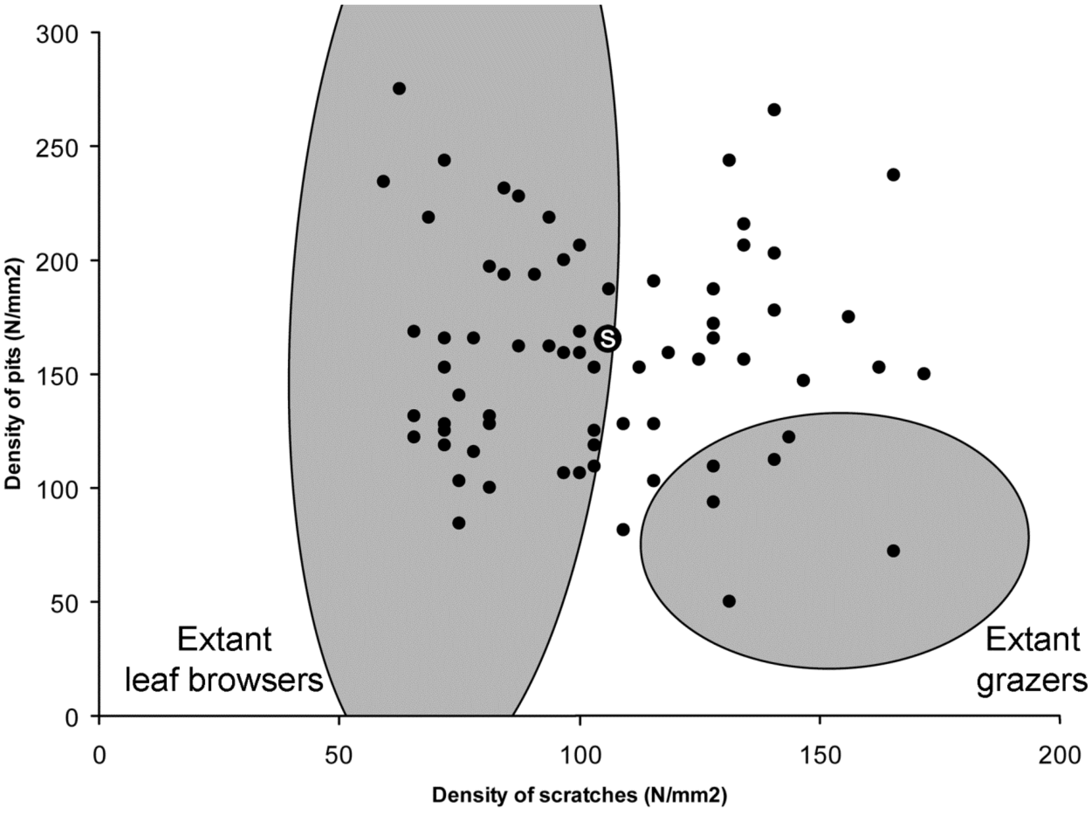

Figure 5

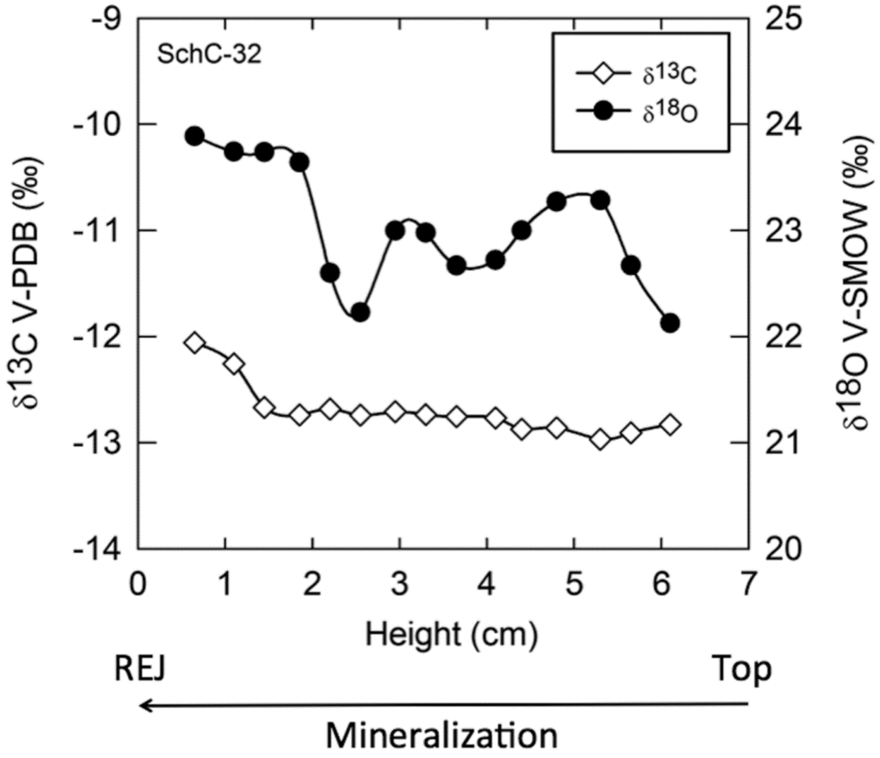

Figure 6

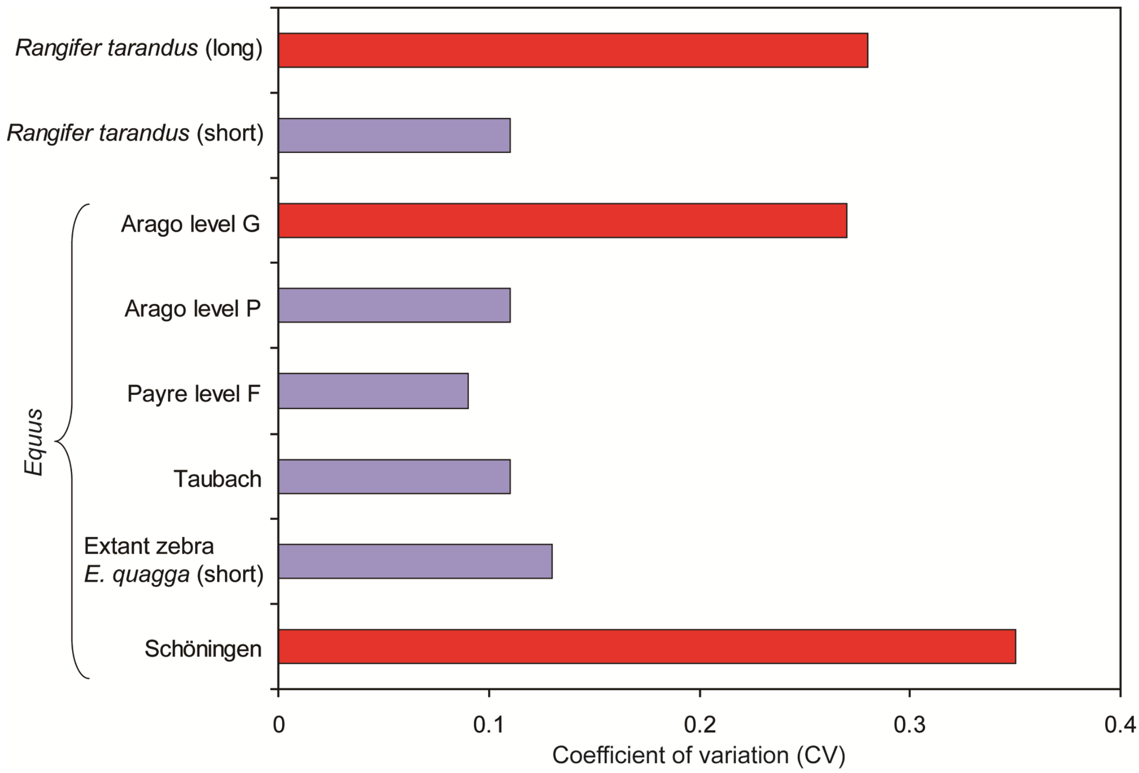

Figure 7

Table 1. ANOVA and Tukey's HSD test results. Abbreviations: df = degrees of freedom; SS = sum of squares; MS = mean square.

Mesowear scores (MWS)

ANOVA results:

Source	df	SS	MS	F-ratio	*p*
Model	3	11.5195	3.839	2.33	0.0822
Residual	67	110.424	1.648		

Pair-wise comparisons – *q* values (Tukey's method); *p*<0.05:

	P4	M1	M2	M3
P4	-			
M1	0.81	-		
M2	1.53	0.72	-	
M3	1.47	2.27	2.99	-

Number of pits (NP)

ANOVA results:

Source	df	SS	MS	F-ratio	*p*
Model	3	86.5011	28.834	0.5208	0.6699
Residual	50	2768.24	55.365		

Pair-wise comparisons – *q* values (Tukey's method); *p*<0.05:

	P4	M1	M2	M3
P4	-			
M1	0.88	-		
M2	0.15	0.73	-	
M3	1.41	0.52	1.26	-

Number of scratches (NS)

ANOVA results:

Source	df	SS	MS	F-ratio	*p*
Model	3	94.41	31.471	1.425	0.2464
Residual	50	1104.07	22.081		

Pair-wise comparisons – *q* values (Tukey's method); *p*<0.05:

	P4	M1	M2	M3
P4	-			
M1	1.76	-		
M2	0.36	1.39	-	
M3	2.34	0.58	1.97	-

Table 2. Mesowear and microwear summary data for the horse sample from Schöningen 13 II-4 and for the extant *Equus quagga* and *E. grevyi* (data from Fortelius and Solounias 2000 and Solounias and Semprebon 2002). Abbreviations: MWS = mesowear score; P = Density of pits (pits/mm^2); S = Density of scratches (scratches/mm^2); %LP = percentage of specimens with large pits; %XS = percentage of specimens with cross scratches; SWS = scratches width score (from 0 = fine scratches only to 2 = coarse scratches only).

	Mesowear		Microwear					
	N	MWS	N	P	S	%LP	%XS	SWS
Schöningen 13 II-4								
Mean	98	1.88	71	158.8	105.2	43.6	4.2	1.09
Coef. of variation		*0.62*		*0.30*	*0.28*			
Extant equids								
Equus quagga	121	4.68	51	72.0	135.8	49.0	60.0	1.10
Equus grevyi	29	4.48	11	49.1	163.1	63.6	66.7	1.33

Table 3. Results of the O and C isotopic measurements and mesowear scores (MWS) of horse third upper left molars from Schöningen 13 II-4. Enamel bulk samples are indicated by a “b”, dentine samples are indicated by a “d”.

Individual	Sample	%CaCO3	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)	MWS
enamel bulk					
695/12-24	32b[a]	3.9	-12.8	22.9	2
715/40-1	55b	3.2	-12.6	22.8	2
720/18-1	56b	3.4	-12.5	23.6	4
enamel serial					
695/12-24	32.1	4.2	-12.8	22.1	
	32.2	4.1	-12.9	22.7	
	32.3	4.1	-13.0	23.3	
	32.4	3.9	-12.9	23.3	
	32.5	4.0	-12.9	23.0	
	32.6	4.0	-12.8	22.7	
	32.7	4.1	-12.8	22.7	
	32.8	3.7	-12.7	23.0	
	32.9	3.8	-12.7	23.0	
	32.10	3.9	-12.7	22.2	
	32.11	3.9	-12.7	22.6	
	32.12	3.9	-12.7	23.6	
	32.13	4.1	-12.7	23.7	
	32.14	4.1	-12.3	23.7	
	32.15	4.1	-12.1	23.9	
dentine					
715/40-1	55d	4.5	-12.9	23.8	
720/18-1	56d	4.8	-12.5	25.8	

[a] In order to compare the isotopic values from the sequentially sampled tooth and the bulk-sampled teeth, a bulk isotopic value was calculated by averaging the isotopic values of 9 serial samples covering a length of 3 cm and located at the same height on the crown than for the bulk samples.

Table 4. Results of the Levene's test for comparisons in *Equus mosbachensis* from Schöningen 13 II-4, and data on short and long occupations from Rivals et al. (2009b) and Moncel and Rivals (2011).

	F-ratio	*p*-value	significance
Comparison Schöningen vs. a long occupation level (Arago Cave level G)			
	F = 253.2	*p* = 0.3853	ns
Comparison Schöningen vs. a short occupation level (Payre level F)			
	F = 3.385	*p* = 0.016	s
Comparison Schöningen vs. a short occupation level (Taubach)			
	F = 7.693	*p* = 0.007	s

Abbreviations: ns = not significant, s = significant.