

Dietary flexibility and niche partitioning of large herbivores through the Pleistocene of Britain

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Abstract

Tooth wear analysis techniques (mesowear and microwear) are employed to analyse dietary traits in proboscideans, perissodactyls and artiodactyls from 33 Pleistocene localities in Britain. The objectives of this study are to examine the variability in each taxon, to track dietary shifts through time, and to investigate resource partitioning among species.

The integration of mesowear and microwear results first allowed us to examine dietary variability. We identified differences in variability among species, from more stenotopic species such as *Capreolus capreolus* to more eurytopic species such as *Megaloceros giganteus* and *Cervus elaphus*. Broad dietary shifts at the community level are seen between climatic phases, and are the result of species turnover as well as dietary shifts in the more flexible species. The species present at each locality are generally spread over a large part of the dietary spectrum, and resource partitioning was identified at

most of these localities. Mixed feeders always coexist with at least one of the two strict dietary groups, grazers or browsers. Finally, for some species, a discrepancy is observed between meso- and microwear signals and may imply that individuals tended to die at a time of year when their normal food was in short supply.

Keywords: tooth wear, microwear, mesowear, proboscideans, ungulates, Quaternary

1. Introduction

The objective of this study is to use tooth wear (mesowear and microwear) to analyze dietary traits in a wide range of herbivorous mammals, using samples from Pleistocene localities in Britain. We examine the variability in each taxon, track dietary changes through time, and investigate niche partitioning among species.

Tooth microwear and mesowear techniques are powerful tools for gaining insight into local and global environmental trends (Merceron et al., 2004; Merceron et al., 2007; Rivals et al., 2010; Semprebon et al., 2004a). Ungulate tooth mesowear and microwear in particular have served as useful proxies for geographical and/or temporal variability in diet and vegetation structure through the Cenozoic (Mihlbachler et al., 2011; Semprebon and Rivals, 2007, 2010; Semprebon et al., 2016). Improvements in these techniques have revealed correlations with vegetation and climate as well as aspects of niche utilization (Calandra et al., 2008; Rivals et al., 2012). Over the past decade, integrated studies of microwear and mesowear have been undertaken for the inference of paleodiets (Rivals and Semprebon, 2006; Rivals et al., 2007a); the

combination of the two techniques provides dietary information on two different timescales: mesowear averages the diet over few months (Fortelius and Solounias, 2000), while microwear reveals the diet in the last days of an animal's life (Grine, 1986). While the results obtained from the two methods are usually in agreement (Semperebon and Rivals, 2007, 2010), discrepancies are sometimes observed (Rivals, 2012; Rivals et al., 2009a). Such differences, related to the temporal resolution of each method (Davis and Pineda Munoz, 2016) are not limitations but are informative of temporal (often seasonal) variation in diet (Sánchez-Hernández et al., 2016). The value of combining various dietary proxies has recently been highlighted by Loffredo and DeSantis (2014), who recommend caution when interpreting dietary traits based on dental mesowear alone. The same must also be valid for microwear because it is sensitive to short-term shifts in diet.

We focus on large mammals in Britain because of their rich fossil record and secure stratigraphic framework (Schreve, 2001a; Currant and Jacobi, 2011; Preece and Parfitt, 2012; Penkman, 2013). Details of the localities and dating evidence are given in the references cited in Table 1. The geographical position of the British Isles also made its fauna particularly sensitive to climatic changes, with repeated taxic turnovers of mammals between cold and warm phases. Together these factors provide considerable potential for examining dietary shifts and niche partitioning among herbivorous mammal species.

2. Material and methods

2.1. Material

The material studied was selected from 33 Pleistocene localities in Britain spanning the last 2.6 Myr (Fig. 1; Table 1). We analysed large herbivorous mammals among the Proboscidea (Gomphotheriidae and Elephantidae), Perissodactyla (Rhinocerotidae, Equidae, Tapiridae), and Artiodactyla (Cervidae and Bovidae). In addition, we studied the mammal assemblage from the Red Crag Nodule Bed, of Late Pliocene age (ca. 3.0-2.6 Ma).

Specimens were sampled in 2010 and 2012 from the following collections: Natural History Museum (London), British Geological Survey (Keyworth), Colchester and Ipswich Museums Service (Ipswich), Torquay Museum, Norfolk Museums Service (Norwich), and the Cruickshanks private collection.

A total of 1491 specimens were moulded and screened to assess their suitability for tooth wear analyses. After excluding teeth where both buccal cusps were broken or damaged, 910 original specimens were suitable for mesowear analysis. After an examination of the epoxy casts under the stereomicroscope, specimens with taphonomic alterations which damaged the original microwear pattern were discarded, leaving a total of 815 specimens suitable for microwear analysis.

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 relative amounts of attritive and abrasive dental wear (due to tooth-tooth and tooth-food-tooth contact, respectively). Mesowear is scored macroscopically from the buccal side of upper molars, 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, 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 analysis. Cusp sharpness is sensitive to ontogenetic age among young individuals (which have not yet developed substantial wear facets) and among dentally senescent individuals. However, for intermediate age groups, which usually comprise the majority of individuals in a fossil collection, mesowear is found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007b) and therefore suitable for dietary reconstruction.

In this study, the standardized method (mesowear ‘ruler’) introduced by Mihlbachler et al. (2011) is 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). Using the mesowear ruler as a reference, cusps equal to or sharper and higher in relief than reference cusp 0 were assigned a value of 0. Cusps that were morphologically intermediate between reference cusp 0 and reference cusp 1, or equal to reference cusp 1 were assigned a value of 1, and so forth. The average value of the mesowear data from a single sample of fossil dentitions corresponds to the ‘mesowear score’ or MWS (Mihlbachler et al., 2011). Dental mesowear analysis was conducted by a single experienced researcher to reduce inter-observer error, corresponding to the recommendations of Loffredo and DeSantis (2014).

Mesowear was applied to Rhinocerotidae, Equidae, Cervidae, and Bovidae because of their suitable tooth morphology when using the Fortelius and Solounias (2000) method. Recently, Saarinen et al. (2015) has developed a new approach to

analysing proboscidean tooth surfaces and his data on British Pleistocene proboscideans complements that of the present study (Saarinen and Lister, in prep).

2.3. Tooth microwear analysis

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the cleaning, moulding, casting, and examination protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004b). The low-magnification microwear technique has been questioned in relation to repeatability and inter-observer error (DeSantis et al., 2013; Mithlbackler et al., 2012). Such problems may arise when observers are not properly trained in the microwear method or when comparing data that were collected by different researchers. To avoid this problem, 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 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 mm² using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004b) 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 they are wide, but have straight, parallel sides. These categories are subdivided as follows:

Pits are classified as small pits, large pits, or puncture pits. Large pits are deeper, less refractive (always dark), generally at least twice the diameter of small pits, and often have less regular outlines than do small pits. Puncture pits are large and very deep pits with crater-like features with regular margins, and they appear dark due to low refractivity.

Scratches are divided into fine scratches (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), and hypercoarse (i.e., very deep and trenchlike features which are wider than the other types of scratches).

The presence of some other features is recorded qualitatively. Cross scratches are oriented approximately perpendicularly to the majority of scratches observed on the enamel (Solounias and Semprebon, 2002). Gouges are features which have ragged, irregular edges and are much larger (approximately 2–3 times as large) and deeper than large pits. They are relatively dark features with low refractivity. The presence or absence of these features in a microscope field was recorded.

In addition, scratch textures were assessed using the scratch width score (SWS) which is obtained by giving a score of '0' to a tooth with predominantly fine scratches, '1' to one with a mixture of fine and coarse types of textures, and '2' to one with

predominantly coarse scratches. Individual scores for a sample of teeth are then averaged to get the SWS.

In artiodactyls and perissodactyls, scratches and pits were counted in two areas on the paracone of the upper molars and the protoconid of the lower molars. In proboscideans, the area was selected on a loph in the center of the worn part of the occlusal surface. The results were compared with a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002; Rivals et al., 2010). 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 mm² 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 have 0.0–22.2% of individuals with scratches between 0 and 17; mixed feeders have 20.9–70.0% of individuals with scratches between 0 and 17; and leaf-dominated browsers have 72.7–100.0% of individuals with scratches between 0 and 17 (Semprebon and Rivals, 2007).

3. Results

3.1 Species' dietary traits

Dietary traits in Proboscidea, Rhinocerotidae, Equidae, Cervidae, and Bovidae are here examined by combining tooth mesowear and microwear analyses. Mesowear and microwear results for each locality and species are summarized in Table 1. Raw data for all the specimens sampled are given in the Supplementary Online Data.

3.1.1. Proboscidea

Proboscidea are represented in the British Pleistocene fossil record by one species of Gomphotheriidae (*Anancus arvernensis*) and five species of Elephantidae (*Mammuthus rumanus*, *M. meridionalis*, *M. trogontherii*, *M. primigenius*, and *Palaeoloxodon antiquus*).

The gomphothere *Anancus arvernensis* is present in the Early Pleistocene Red Crag and Norwich Crag Formations. Tooth microwear patterns are different between the two samples. In the Red Crag, all individuals have low numbers of scratches and quite high numbers of pits and, thus, fall within the range of extant leaf browsers based on these two variables alone (Fig. 2A). They also show the presence of large pits, puncture pits, and gouges, suggesting that they may have included seeds and fruits in their diet (Rivals et al., 2015a). In the Norwich Crag, *A. arvernensis* has a higher number of scratches but an intermediate number of pits (Fig. 2A). The scratch numbers (%0-17) classify the sample as grass-dominated mixed feeders (Fig. 3). It also has somewhat more gouging present which might again be related to fruit and seed consumption. This microwear pattern has also been observed in Early Pleistocene *Anancus* from Chilhac (France) and the Eastern Scheldt in the Netherlands (Rivals et al., 2015a). In Africa, *Anancus* was also reported to be opportunistic and to feed both on browse and grass (Zazzo et al., 2000; Lister, 2013).

The earliest member of the mammoth lineage in Europe, *Mammuthus rumanus* from the Red Crag proper, has a microwear pattern similar to that of the co-occurring

gomphothere (*Anancus arvernensis*), with low numbers of scratches and quite high numbers of pits, indicating leaf browsing (Fig. 2B). Large pits most likely indicate the presence of grit ingested together with the plants (Semperebon and Rivals, 2007), which would indicate that it frequented open habitats (Rivals et al., 2015a).

Early Pleistocene *Mammuthus meridionalis* samples show a relatively high variability in microwear pattern, although most are identified as grass-dominated mixed feeders. Some samples have high numbers of scratches which plot in the grazing morphospace, such as at Overstrand, West Runton, and East Runton (Fig. 2B). The samples from Norwich Crag and Mundesley are intermediate in terms of scratches; their low-scratch percentage indicates grass-dominated mixed feeding (Table 1). Finally, the sample from Bacton shows low numbers of scratches which indicates browse-dominated mixed feeding (Fig. 2B and 3).

Mammuthus trogontherii and *Mammuthus primigenius* show microwear patterns with intermediate to high numbers of scratches (Fig. 2B), indicating a range from mixed feeding to grazing. None of our samples of *M. trogontherii* or *M. primigenius* was found to have exclusive browsing traits, although *M. trogontherii* from West Runton, Overstrand and Sidestrand (early Middle Pleistocene) and Ilford (MIS 7) are identified as browse-dominated mixed feeders (Fig. 2B). At West Runton, the tooth microwear results are supported by paleoenvironmental evidence for mixed environments with woodland as well as open grassland areas (Lister and Stuart, 2010).

Palaeoloxodon antiquus, present at nine Middle Pleistocene localities, shows microwear patterns with sample means ranging from 13.4 to 19.5 scratches in the 0.16 mm² area (Fig. 2A). The %0-17 values range from 33.3 to 83.3% (Table 1). Such values indicate diets ranging from the mixed feeders to leaf browsers (Fig. 3). These

observations are in agreement with the association of the species with temperate, forested or mixed vegetational, conditions (Stuart 1982). The absence of grazing *P. antiquus* is consistent with the finding that in Britain it is absent from cold stages with generally open habitat (Schreve, 2001a; Stuart, 1982). Nonetheless, grass-dominated mixed feeding habit was identified previously in microwear analysis of *P. antiquus* from the Middle Pleistocene of Megalopolis in Greece (Rivals et al., 2012).

3.1.2. Rhinocerotidae and Tapiridae

The Rhinocerotidae are represented in the British Pleistocene by four species of *Stephanorhinus* (*S. etruscus*, *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*) and, in the late Middle to Late Pleistocene, by *Coelodonta antiquitatis*.

The low-crowned *Stephanorhinus etruscus* from the Red Crag Nodule Bed and East Runton, show low mesowear scores (MWS = 1.3) and low numbers of scratches (Table 1). At the two localities, the mesowear and microwear patterns both indicate that *S. etruscus* had dominant browsing habits (Fig. 4 and 5). In the Red Crag Nodule Bed it shows a higher number of pits and most of the individuals have large pits, while at East Runton average number of pits is lower and no individuals have large pits (Table 1). Considering that higher numbers of pits indicate grit consumption (Hoffman et al., 2015) the rhinoceros population from the Red Crag Nodule Bed occupied more open environments on average than at East Runton.

In the early Middle Pleistocene, *S. hundsheimensis* shows higher mesowear scores (MWS between 1.8 and 4.0) than *S. etruscus*. It also shows intermediate and low

numbers of scratches (Table 1). Both proxies suggest browsing and mixed-feeding dietary habits. The mesowear scores show that *S. hundsheimensis* was restricted to the mixed-feeding ecospace, varying from browse-dominated to graze-dominated mixed feeding (Fig. 5). Tooth microwear supports a similar pattern for the samples from Pakefield and Boxgrove. However there is a discrepancy at West Runton and Westbury, where microwear suggests a browsing diet. This is presumably linked to different levels of temporal resolution into diet afforded by each technique, with mesowear providing a long term perspective and microwear seasonal and/or episodic dietary trait(s), and assuming also correlated (probably seasonal) mortality of the sample. In any case it is clear that *S. hundsheimensis* was a highly flexible feeder. This generalist adaptation has already been evidenced in the Middle Pleistocene of Germany, where dental mesowear indicated the presence of both grazing and browsing populations (Kahlke and Kaiser, 2011).

Merck's rhinoceros, *S. kirchbergensis*, and the narrow-nosed rhinoceros, *S. hemitoechus*, co-occurring during the late Middle Pleistocene, show different tooth-wear patterns.

S. kirchbergensis shows low mesowear scores, low numbers of scratches (and high %0-17), and higher percentages of individuals with large pits (over 57 %) (Table 1). They also tend to have wider scratches as reflected by the scratch width score (SWS), and most of them have more gouging. According to mesowear scores and number of scratches, *S. kirchbergensis* was browser or mixed feeder (Figs. 4 and 5). The presence of large pits and gouges, as well as larger scratches, suggests the consumption of fruits and seeds (Semprebon et al., 2004a; Semprebon et al., 2011). The sample from Grays Thurrock stands out because of its higher number of pits (Fig. 4). It

plots among the extant “dirty browsers” (sensu Semprebon and Rivals, 2007), which are species that feed on dicotyledonous plants whose leaves are coated with dust and grit, or animal that feed plant parts very close to the ground.

S. hemitoechus shows high mesowear scores and high numbers of scratches (and low %0-17) compared to *S. kirchbergensis* (Table 1). It shows low percentages of individuals with large pits (below 33.3%). The mesowear and microwear patterns indicate grazing and mixed feeding dietary traits (Fig. 5), both indicating an adaptation to more open habitats than *S. etruscus* or *S. hundsheimensis*.

Throughout the Middle Pleistocene, *S. kirchbergensis* and *S. hemitoechus* show clear dietary differences: *S. kirchbergensis* has more browsing dietary traits, while *S. hemitoechus* has more grazing traits (Fig. 5). Nonetheless, each of these two species maintains a certain degree of dietary flexibility, as also reported in Germany and some localities in the UK for these two species, based on dental mesowear (van Asperen and Kahlke, 2015). In *S. hemitoechus* we observed a difference between the two proxies for the sample from Clacton (MIS 11), where mesowear suggests longer-term grazing while microwear indicates shorter-term browse-dominated mixed-feeding.

Finally, the woolly rhinoceros *Coelodonta antiquitatis*, at Crayford and Slade Green (MIS 7-6), shows a high mesowear score pointing toward a high proportion of grass in its diet (Fig. 5). The microwear pattern, however, with intermediate number of scratches, suggests a mixed-feeding diet with the inclusion of browse, at least during parts of the year (Figs. 4 and 5). At Kent’s Cavern (MIS 3), *C. antiquitatis* has the highest mesowear scores of all the rhinoceros samples analysed, and also high numbers of scratches (and low %0-17). Here, both mesowear and microwear patterns provide evidence of a strict grazing diet (Figs. 4 and 5).

Considering the Rhinocerotidae as a whole, and its history during the British Quaternary, we observe a broad temporal shift into more abrasive diets. This was achieved largely by taxonomic replacement, with the more specialized grazing species, *Stephanorhinus hemitoechus* and later *Coelodonta antiquus*, appearing during the Middle Pleistocene.

Tapiridae are present at the oldest locality, Red Crag Nodule Bed (Late Pliocene). Because tooth mesowear cannot be applied to bunodont teeth, the samples from these two groups were examined exclusively through microwear analysis. The sample of tapir (*Tapirus* sp.) shows a microwear pattern with low number of scratches and high number of pits, characteristic of browsers. Moreover, this sample shows that all individuals have large pits and gouges, as well as high numbers of puncture pits, indicating fruit-eating (Table 1).

3.1.3. Equidae

All the species of Equidae available in the collections were sampled: *Hipparion* sp. in the Red Crag Nodule Bed, the Early Pleistocene horses *Equus bressanus* and *E. stenonis*, the early Middle Pleistocene *E. altidens*, and the Middle and Late Pleistocene *E. ferus* (including *E. mosbachensis*). However, at some localities some species could not be included in this study because of small sample size (few specimens, or specimens discarded for taphonomic reasons). *Equus suessenbornensis* is not included at all for the same reasons.

Hipparion sp. from the Red Crag Nodule Bed shows a mesowear score indicating grazing. However, it is one of the lowest mesowear scores recorded for all the Equidae sampled in this study (Table 1). The microwear pattern, with low numbers of scratches, indicates leaf browsing at the time of death (Figs. 6 and 7). Microwear analysis on various species has shown that hipparions were not exclusively grazers, but had broad dietary traits (Hayek et al., 1992) which is supported by the discrepancy between mesowear and microwear in this study.

Tooth microwear and mesowear patterns indicate intra- and inter-specific variability in horse feeding traits (Figs. 6 and 7). Mesowear scores of all samples are relatively high ($MWS > 3.5$), indicating high abrasiveness and hence grazing (Fig. 7). Tooth microwear shows a trend toward more grazing through the Pleistocene, from browser-dominated mixed-feeding traits in the Early Pleistocene horses from East Runton, to mixed-feeding and grazing traits in the Middle and Late Pleistocene populations. However, this shift across most of the microwear dietary spectrum needs to be viewed in the context of the temporal resolution of the microwear method. Tooth microwear only reflects the diet of the last days or week, consequently it is more sensitive to short-term changes in diet than mesowear. The biggest differences between meso- and microwear are found in the oldest sample at East Runton, mesowear suggesting a mostly grazing diet but microwear revealing that *Equus bressanus* could also browse.

Microwear patterns in Middle Pleistocene horses show a diversity of dietary traits, from browse-dominated mixed-feeding to grazing. The discrepancy with the mesowear data indicates a difference in diet at the time of death, especially from the populations from West Runton and Boxgrove (early Middle Pleistocene), as well as

Brundon, Stoke Tunnel, and Stutton (MIS 7), all of interglacial age. Finally, the strongest grazing signal is found at the Late-glacial interstadial locality of Gough's Cave (MIS 2), where both mesowear and microwear indicate an almost exclusive focus on grass in the horses' diet.

In sum, tooth mesowear confirms the largely grazing habit of horses through the Pleistocene in Britain, but microwear suggests a frequent browsing element, especially for Early Pleistocene and some Middle Pleistocene populations. Browse-dominated mixed-feeding horses are known from tooth wear in Middle Pleistocene assemblages at Schöningen in Germany (Kuitens et al., 2015; Rivals et al., 2015b) and Deutsch-Altenburg 1 in Austria (Rivals, 2012). It is not possible to distinguish if this is low herbaceous browse or tree/shrub browse. DNA analysis of stomach contents of one horse (*E. ferus*) from Late Pleistocene Siberia revealed a high proportion of forbs (low-growing browse) in this animal's last food, with subsidiary grass, but no shrub or tree browse (Willerslev et al., 2014).

3.1.4. Cervidae

Pleistocene cervids have a high taxonomic diversity in Britain. Eleven taxa of cervids were sampled and examined.

In the Red Crag Nodule Bed, the cervids are attributed to three size categories (Lister, 1999): most specimens belong to a medium-sized deer (cf. *Cervus pardinensis*), a few to a large-sized deer (cf. *C. perrieri*) and one to the small-sized cf. *Procapreolus cusanus*. *P. cusanus* was discarded from the study because of its small sample size. For

the two other size categories, the dietary proxies are internally consistent (Fig. 8A and 9A). For the medium-sized deer (cf. *Cervus pardinensis*), mesowear score is intermediate (MWS = 2.14) and microwear pattern is also characterized by intermediate number of scratches. The two proxies suggest mixed-feeding traits. The large-sized deer (cf. *C. perrieri*) has a lower mesowear score (MWS = 1.50) and lower number of scratches; it is categorized as browse-dominated mixed feeder.

At East Runton, the dietary signal is shifted towards more browsing, as indicated by lower mesowear scores and higher numbers of scratches in *Cervalces gallicus* and *Eucladoceros* spp. (Figs. 8C and 9B). It is important to note that the sample of *Eucladoceros* from East Runton includes three species (Lister, 1996) which cannot be morphologically separated on teeth on our current understanding. Few studies are available for comparison, but mesowear analysis on *Eucladoceros* sp. from the Early Pleistocene of Italy also indicates browsing habits (Strani et al., 2015).

In the Middle Pleistocene, cervids are diverse and abundant at most of the localities (Table 1), especially during the early Middle Pleistocene. Some of the genera persist into a less diverse Late Pleistocene cervid assemblage.

Among the Megacerini, early Middle Pleistocene jaws and maxillae from West Runton have provisionally been allocated to three species (Lister et al., 2010): ‘species A’ (cf. *Megaloceros savini*), ‘species B’ (cf. *Praemegaceros verticornis*) and ‘species C’ (cf. *P. dawkinsi*). Among the teeth we sampled, only two specimens could provisionally be attributed to one of these species. The other specimens were not identifiable (isolated teeth) or not suitable for microwear. The two specimens allocated to ‘species B’ (NHM M17538 and M17741) belong to different individuals (Lister et

al., 2010). Their microwear patterns show the same average number of scratches (see raw data available in the online Supplementary Material), suggesting a similar browsing diet for the two individuals. Among the unidentified megacerine specimens from West Runton, some have a similar pattern to ‘species B’ and others are different. Considering the West Runton megacerine sample as a whole, it plots among the browse-dominated mixed feeders (Fig. 8C).

At Pakefield, all megacerine material was provisionally referred to ‘species A’ (cf. *M. savini*) (Lister et al., 2010) and all specimens fit within the browsing ecospace (Fig. 8C). For the unidentified megacerine in correlated deposits at Kessingland, mesowear indicates grazing dietary traits while microwear suggests the incorporation of some browse during parts of the year. At Boxgrove, the specimens were referred to ‘species B’ (cf. *Praemegaceros verticornis*) and plot among the browse-dominated mixed feeders. The inter-individual variation observed at these localities does not permit us to detect any pattern among the three species found in the early Middle Pleistocene.

In the late Middle to Late Pleistocene, *Megaloceros giganteus* has tooth-wear patterns indicating a wide range of dietary behaviour including grazing, leaf browsing and mixed feeding, but generally tending toward mixed feeding and grazing (Figs. 8C and 9B). The samples of *M. giganteus* from Grays Thurrock (MIS 9) and Ilford (MIS 7) show an average annual signal corresponding to mixed feeding, but microwear suggests a shift toward more grass at the time of mortality.

The Middle and Late Pleistocene red deer (*Cervus elaphus*) shows a wide range of mesowear and microwear values (Fig. 8A and 9A) compared to other cervids, corresponding to significant dietary plasticity (Lister, 1984). Globally, the two proxies

point toward a preference for mixed feeding and leaf browsing. However some discrepancies between the mesowear and microwear data indicate periodic shifts in individual diet, in particular at Boxgrove, Grays Thurrock, and Gough's Cave. Previous tooth microwear and mesowear analyses on red deer from European localities of the same age range revealed a similar pattern, with high variability in dietary traits (Rivals et al., 2009b).

The Middle and Late Pleistocene fallow deer, *Dama roberti* (Breda and Lister 2013) and *Dama dama* (including *D. d. clactoniana* and *D. d. dama*) have tooth wear patterns pointing toward browsing. *Dama* cf. *roberti* from the early Middle Pleistocene of Westbury sub Mendip, and *Dama dama* from Swanscombe (MIS 11) are the only two *Dama* samples which provide a mixed-feeding signal from mesowear, but the tooth microwear indicates pure leaf browsing. This would suggest seasonal mixed feeding for those samples. A similar result, showing mixed feeding from mesowear and leaf browsing from microwear, has been reported for *D. d. clactoniana* from the Middle Pleistocene of Caune de l'Arago in France (Rivals et al., 2008). All the other populations of *D. roberti* and *D. dama* have consistent mesowear and microwear patterns indicating leaf browsing (Figs. 8B and 9A) and are likely to be related to foraging in closed habitats as suggested by studies of stable isotopes at various localities in the Middle Pleistocene of Atapuerca, Spain (García García et al., 2009).

The Middle Pleistocene roe deer (*Capreolus capreolus*) has very low mesowear scores (between 0 and 0.5) and low numbers of scratches at West Runton, Boxgrove and Grays Thurrock. The two proxies, tooth mesowear and microwear, are in agreement

and both indicate that the roe deer was a strict browser (Fig. 9C). It seems that *C. capreolus* had dietary habits which were not subject to seasonal changes.

Finally, the reindeer (*Rangifer tarandus*), which is represented in our samples only at Kent's Cavern, shows a mixed feeding habit (Figs. 8C and 9B) which may be related to seasonal migration as seen in last-glacial and extant populations, and reflected in antler shedding (Aaris-Sorensen et al., 2007), microwear (Rivals and Solounias 2007) and stable isotopes (Britton et al., 2009, 2011; Drucker et al. 2012).

3.1.5. Bovidae

Bovidae are represented by the Late Pliocene *Parabos* sp., the Early Pleistocene *Leptobos* sp., and by two genera that are present in the Middle and Late Pleistocene: *Bos* and *Bison*. The separation of teeth of the latter two can be problematic, especially when both genera are present at a locality. In such cases, the samples are labelled here as *Bos/Bison*. Diagnostic specimens were identified as belonging to *Bos primigenius*, *Bison schoetensacki*, and *Bison priscus*.

The late Pliocene *Parabos* sp., from the Red Crag Nodule Bed, has a mesowear score plotting at the boundary between browsers and grazers (MWS=2) and a tooth microwear pattern with low number of scratches (and high %0-17) that indicates browsing habits (Figs. 10 and 11). The discrepancy between the two proxies suggests general mixed feeding traits but a more browsing diet at the time of death.

The Early Pleistocene *Leptobos* sp. from East Runton shows mesowear similar to *Parabos* sp., indicating mixed feeding (Fig. 11). Only one tooth was suitable for microwear at that locality; its microwear pattern is consistent with mixed feeding.

The early Middle Pleistocene *Bison schoetensacki* from Mundesley, West Runton, Pakefield and Westbury-sub-Mendip plot into the graze-dominated mixed feeding range of mesowear (Fig. 11). Microwear data are only available at West Runton and indicate grazing traits, at least at the time of death (Fig. 10 and 11), suggesting periodic shifts towards the consumption of more grass.

In the Middle and Late Pleistocene, where *Bos* and/or *Bison* are present, the mesowear shows a narrow range of variation ($MWS = 2$ to 3.28) while the microwear data cover the complete dietary spectrum, from grazing to browsing. To explore further, unidentified *Bos/Bison* samples were excluded and only the localities with identifiable *Bos primigenius* or *Bison priscus* were considered. In the interglacial assemblages of Ilford and Aveley (MIS 7), Grays Thurrock (MIS 9), and Clacton (MIS 11), the large bovid is *Bos primigenius*, which is notably a mixed feeder to browser. *Bison priscus*, scorable here only in Late Pleistocene localities, tends towards mixed feeding and grazing (Fig. 11). Tooth microwear confirms these patterns but the higher intraspecific ranges of variation suggest temporal variability in both *Bos primigenius* and *Bison priscus* diets.

4. Discussion

4.1. Resource partitioning

Resource partitioning was examined at a selection of localities where tooth wear from at least three species was sampled and provided suitable data. Following this criterion, 12 localities were selected for a comparison of meso- and microwear patterns among all ungulates (Fig. 12).

4.1.1. General patterns

At all sites selected, mixed feeders are always present together with at least one of the two strict dietary groups, grazers and/or browsers (Fig. 12). The species present at each locality are spread over a large part of the dietary spectrum. In general, species at a locality are separated in their diets, i.e. there is evidence of resource partitioning among species. This is very clearly seen, for example, at Kent's Cavern (MIS 3), where six species do not, with one exception, overlap in either microwear or mesowear scores.

There are exceptions, however, e.g., the clustering of three cervids and two rhinos at Grays Thurrock (MIS 9), or various cervid species at Boxgrove (cf. MIS 13). However, the discrepancy often observed between the two proxies (as described in section 3) suggests that resource partitioning could occur on a temporal or spatial basis. For example, the two rhinoceros species from Grays Thurrock have a very similar mesowear pattern indicating mixed feeding, while tooth microwear indicates that the preserved samples of the species represent animals which had different diets at the time of death. The same occurs at West Runton (cf. MIS 17) between *Bison schoetensacki* and *Stephanorhinus hundsheimensis*, at Ilford and Aveley (MIS 7) between *Megaloceros giganteus* and *Bos primigenius*, and at Kent's Cavern (MIS 3) between *Cervus elaphus* and *Bison priscus*.

In a few cases, species have very similar tooth-wear patterns both in meso- and microwear, suggesting competition for the use of similar resources. In some case, competition could have been mitigated by grazing succession, although in the African test case (Fortelius and Solounias, 2000) tooth-wear differences were observed, as successive species take different plant parts. This pattern occurs at Boxgrove and West Runton between *Capreolus capreolus* and *Dama roberti*. It should be recognized, however, that the relatively coarse categorization into browsers and grazers may conceal differences of detail in the combination of plant taxa consumed by different mammal species.

4.1.2. Intra-group patterns

Some interesting patterns are evidenced among species in the main taxonomic groups when they occur both at a locality.

Among Proboscidea, *Palaeoloxodon antiquus* is always found to be mixed-feeding to browsing. (Fig. 12). *Mammuthus primigenius* is strongly grazing in the last cold stage of Kent's Cavern, as is its predecessor *M. trogontherii* in the early Middle Pleistocene of Pakefield. Very interestingly, however, remains attributed (Lister et al., 2005) to late *M. trogontherii* at Ilford (MIS 7), appear mixed-feeding. At this site, where both *P. antiquus* and *M. trogontherii* are present in the same horizon (Schreve 1997), the former is more browse-dominated and the latter more graze-dominated (Fig. 12). See also discussion about Crayford, below.

For the Rhinocerotidae, as reported earlier, *S. kirchbergensis* shows lower mesowear scores and lower numbers of scratches (and higher %0-17) than *S. hemitoechus* at all localities where they co-occur (Table 1 and Fig. 12). The two species always plot in the expected direction, i.e. *S. hemitoechus* more grazing, *S. kirchbergensis* more browsing.

At most localities *S. kirchbergensis* plots among the cervids (such as *Cervus elaphus* or *Dama dama*) while *S. hemitoechus* is often closer to *Equus ferus* (e.g. at Ilford and Aveley (MIS 7) and at Grays Thurrock (MIS 9); see comment about Crayford below).

Among cervids, *Capreolus capreolus*, *Dama robertii* and *D. dama* (as well as the unidentified megacerines where present) always display a strong browsing signal, while *Cervus elaphus* and *Megaloceros giganteus* tend more towards mixed-feeding (Fig. 12). When *Dama* and *Cervus* co-occur in the same assemblage, microwear and mesowear consistently indicate a more browsing diet for *Dama* than *Cervus*. This pattern is evidenced in the single assemblages sampled at West Runton, Boxgrove, Grays Thurrock and Joint Mitnor Cave (Figs. 9 and 12).

At East Runton, even though its widespread antlers suggest open habitat, *Cervalces gallicus* appears as a browser, as proposed on the basis of the low-crowned teeth (Lister, 1981). Considering all these data, the paleoecology of *C. gallicus* can be proposed as an open-ground soft-leaf feeder (like the reindeer), although a lightly-wooded habitat, as proposed by Breda (2008), cannot be ruled out.

4.2. Implication for paleoecological interpretation at selected localities

The dietary spectrum of a herbivore community as a whole contributes to our understanding of the vegetational environments at a given locality, especially where direct palaeobotanical evidence is limited or lacking. Some examples, from sites with three or more species, are given below.

The Red Crag Nodule Bed or Basement Bed (ca. 3.0-2.7 Ma) is characterized by an exotic fauna including *Tapirus arvernensis*, *Hipparion* sp., *Mammut borsoni*, and at least three species of deer. All examined species are mixed feeders or browsers, except the hipparions which have a mesowear signal typical of grazers, although the microwear indicates periodic browsing (Fig. 12). This browse-dominated community corresponds to pollen evidence for temperate forest (Head, 1998a).

At West Runton, all scorable species fit into the mixed feeding and browsing categories, corresponding to temperate climatic conditions during the Cromerian interglacial with an ecosystem dominated by forest, but also with some open areas (Lister and Stuart, 2010). No pure grazers are evidenced: even the stenonid horse *Equus altidens* has a browsing microwear signature, but its mesowear could not be scored, nor could that of the larger *E. suessenbornensis*.

At Swanscombe, where palaeobotanical evidence is limited, micro- and mesowear show that the fauna was mainly mixed-feeding. Notably, the horse has the lowest mesowear value (i.e., the least exclusively grass-eating diet) of all *Equus ferus* samples analysed here (Fig. 12). This corresponds to the correlation of the lower levels at Swanscombe to the first half of the Hoxnian interglacial, MIS 11 (Ashton et al 2008)

and the attribution of the fauna to predominantly forested conditions (Schreve, 2001b), though some grassy areas were available to the mixed-feeders.

Based on the composition of the mammalian assemblage, Schreve (1997) suggested that Grays (MIS 9) was more strongly wooded than Ilford and Aveley (MIS 7), where the faunas is characterized by a predominance of open-habitat or parkland species. The browsing to browse-dominated mixed-feeding clustering of the mesowear values for all species except horse at Grays Thurrock supports this conclusion.

Interpretation of the Crayford sites is complicated by uncertainty over the stratigraphic provenance of the material; mammalian fossils were recovered from underlying gravels and overlying brickearths, but the origin of individual fossils is not always clear. Curren (1986) suggested that the cold elements of the fauna (*Coelodonta antiquitatis* and *Ovibos moschatus*) came from later (MIS 6) deposits than the main MIS 7 fauna, although accounts from the time of excavation report the former species from the underlying gravel and the latter from the overlying brickearth (Schreve, 1997). The tooth wear data indicate mixed-feeding or grazing for all species, suggesting a relatively open phase even in MIS 7. *Equus ferus* and *Stephanorhinus hemitoechus* both have a remarkably similar dietary profile to *Coelodonta antiquitatis*, and since the former two species are not doubted to have occurred in MIS 7, the attribution of the Crayford *C. antiquitatis* to MIS 7 cannot be excluded on dietary grounds. As discussed above, microwear in *C. antiquitatis* at Crayford suggests a mixed-feeding diet with the inclusion of browse, at least during parts of the year. This indicates the availability of significant numbers of trees or shrubs at that time, which confirms that the Crayford and Slade Green deposits may belong at least in part to the interglacial MIS 7 rather than to

the cold stage MIS 6 (cf. Scott et al., 2011). *Stephanorhinus hemitoechus* and *Equus ferus* are very similar in both meso- and microwear to *C. antiquitatis*, which may even suggest competition for the use of similar resources if all three species came from the Crayford Gravels as indicated in contemporary reports (Schreve, 1997). *S. kirchbergensis*, conversely, is reported only from the brickearth, and shows the same dietary differentiation from *S. hemitoechus* as at other localities (including those of MIS 7 age). *Mammuthus trogontherii* and *Palaeoloxodon antiquus* are graze-dominated and browse-dominated mixed feeders, respectively, as at Ilford (see above); both species apparently co-occurred in the Crayford Gravel although *M. trogontherii* also extended into the brickearth (Schreve, 1997).

Kent's Cavern is a celebrated last cold stage site; the main cave-earth fauna is dated to ca. 40-20 ka (Higham et al., 2011). In Britain in general this period has been reconstructed as an open steppe-tundra, but there is also evidence for growth of boreal trees, at least at times (West, 2000), and this seems especially plausible for southern hilly country such as the vicinity of Kent's Cavern where, however, direct palaeobotanical evidence is poor. The browse component in the mixed-feeding diets of *Cervus elaphus* and *Megaloceros giganteus*, and even *Bison priscus* from the Kent's Cavern main cave earth supports the presence of trees, shrubs and/or dicotyledonous herbs the area. The presence of some wooded areas around Kent's Cavern is supported rather negative bone collagen $\delta^{13}\text{C}$ values observed in *Cervus elaphus* remains (Bocherens and Fogel, 1995). It is an interesting and unanswered question whether the development of these plant types, and the animals that depended on them, was a permanent feature in this region or dates only to the short MIS 3 interstadials. The reindeer (*Rangifer tarandus*) has a strong browsing to browse-dominated mixed-feeding

signature which indicates a diet of dicotyledonous plants. The scratch width and the proportion of large pits and gouges fits with extant caribou populations (Rivals and Solounias, 2007) which feed on low plants, including lichens and mosses, confirming the reindeer from Kent's Cavern as an open-country animal.

5. Conclusion

The combination of mesowear and microwear provides a powerful tool for examining dietary flexibility and resource partitioning at different temporal scales. Mesowear provides a dietary signal integrated over several months at least, and allows us to contrast more eurytopic species (e.g. *Megaloceros giganteus*, ranging from grazing to browse-dominated mixed-feeding) to more stenotopic (e.g. *Capreolus capreolus*, always browsing). Broad dietary shifts in the faunas as a whole are also evident between climatic phases (Section 4.2 above; Fig. 12), and result from both species turnover and dietary shifts in flexible species common to the sites.

Dental microwear provides an independent proxy that records relatively short-term diet. For stenotopic species (e.g. the browser *Capreolus capreolus* or the grazer *Coelodonta antiquitatis*) the two proxies tend to match. For other species, however, there is commonly a discrepancy between meso- and microwear signals that is clearly informative but not always easy to interpret. The discrepancy is not systematic in direction, e.g. *M. giganteus* shows a more grazing signal in mesowear than microwear at Kent's Cavern (MIS 3), but a more browsing signal in mesowear than microwear at Ilford and Aveley (MIS 7) and Grays Thurrock (MIS 9). The differences can be extreme, e.g. *Stephanorhinus kirchbergensis* at Swanscombe shows graze-dominated

692 mixed-feeding in mesowear but 100% browsing in microwear. The microwear signal is
693 clearly capturing one part of the individual's mixed diet in the weeks leading up to the
694 time of death. Since the microwear signal for a fossil sample is averaged over all
695 available individuals, a consistent difference from the mesowear average implies that
696 individuals tended to die at a time when they were eating mainly one element of their
697 mixed diet. This is most easily interpreted as a seasonal effect, and since the model
698 requires mortality to be concentrated in the season when a particular food was being
699 taken, it may be that this food, or its level of productivity, was suboptimal and was
700 taken at that season only because the optimal food was not available. In other words, the
701 animals tended to die at a time of year when their normal food was in short supply so
702 they were forced to eat suboptimal food. In rare cases, the microwear signal appears to
703 be a small minority of the total diet indicated by mesowear. An example is the
704 *Hipparion* from the Red Crag Basement Bed, whose diet is grazing on the basis of
705 mesowear, but whose microwear indicates browsing around the time of death.

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References

- Aaris-Sørensen, K., Mühldorff, R., Brinch Petersen, E., 2007. The Scandinavian reindeer (*Rangifer tarandus* L.) after the last glacial maximum: time, seasonality and human exploitation. *Journal of Archaeological Science* 34, 914-923.
- Andrews, P., Cook, J., Currant, A., Stringer, C., 1999. Westbury Cave: The Natural History Museum excavations 1976-1984. Western Academic & Specialist Press, Bristol.
- Ashton, N., Lewis, S.G., Parfitt, S.A., Penkman, K.E.H., Russell Coope, G., 2008. New evidence for complex climate change in MIS 11 from Hoxne, Suffolk, UK. *Quaternary Science Reviews* 27, 652-668.
- Bocherens, H., Fogel, M.L., 1995. Trophic structure and climatic information from isotopic signatures in Pleistocene cave fauna of Southern England. *Journal of Archaeological Science* 22, 327-340.
- Breda, M., 2008. Palaeoecology and palaeoethology of the Plio-Pleistocene genus *Cervalces* (Cervidae, Mammalia) in Eurasia. *Journal of Vertebrate Paleontology* 28, 886-899.
- Breda, M., Lister, A.M., 2013. *Dama roberti*, a new species of fallow deer from the early Middle Pleistocene of Europe, and the origins of modern fallow deer. *Quaternary Science Reviews* 69, 155-167.
- Bridgland, D.R., 1995. The Quaternary sequence of the eastern Thames basin: problems of correlation, in: Bridgland, D.R., Allen, P., Haggart, B.A. (Eds.), *The Quaternary of the Lower Reaches of the Thames*. Field Guide, Quaternary Research Association, Durham, pp. 35-52.
- Britton, K., Grimes, V., Dau, J., Richards, M.P., 2009. Reconstructing faunal migrations using intra-tooth sampling and strontium and oxygen isotope analyses: a case study of modern caribou (*Rangifer tarandus granti*). *Journal of Archaeological Science* 36, 1163-1172.
- Britton, K., Grimes, V., Niven, L., Steele, T.E., McPherron, S., Soressi, M., Kelly, T.E., Jaubert, J., Hublin, J.-J., Richards, M.P., 2011. Strontium isotope evidence for migration in late Pleistocene *Rangifer*: Implications for Neanderthal hunting strategies at the Middle Palaeolithic site of Jonzac, France. *Journal of Human Evolution* 61, 176-185.
- Calandra, I., Göhlich, U.B., Merceron, G., 2008. How could sympatric megaherbivores coexist? Example of niche partitioning within a proboscidean community from the Miocene of Europe. *Naturwissenschaften* 95, 831-838.
- Campbell, J.B., Sampson, C.G., 1971. A new analysis of Kent's Cavern, Devonshire, England. *Univ. Oregon Anthrop. Papers* 3, 1-40.
- Currant, A.P., 1986. Man and Quaternary interglacial faunas of Britain, in: Collcutt, S.N. (Ed.), *The Palaeolithic of Britain and its nearest neighbours*. University of Sheffield, Sheffield, pp. 50-52.

- Currant, A.P., Jacobi, R., 2011. The mammal faunas of the British late Pleistocene, in: Ashton, N., Lewis, S.G., Stringer, C. (Eds.), *The Ancient Human Occupation of Britain*. Elsevier, Amsterdam, pp. 165-180.
- Davis, M., Pineda Munoz, S., 2016. The temporal scale of diet and dietary proxies. *Ecology and Evolution* 6, 1883-1897.
- DeSantis, L.R.G., Scott, J.R., Schubert, B.W., Donohue, S.L., McCray, B.M., Van Stolk, C.A., Winburn, A.A., Greshko, M.A., O'Hara, M.C., 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivorous and carnivorous mammals. *PLoS ONE* 8, e71428.
- Drucker, D.G., Hobson, K.A., Münzel, S.C. and Pike-Tay, A., 2012. Intra-individual variation in stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in mandibles of modern caribou of Qamanirjuaq (*Rangifer tarandus groenlandicus*) and Banks Island (*Rangifer tarandus pearyi*): Implications for tracing seasonal and temporal changes in diet. *International Journal of Osteoarchaeology* 22, 494-504.
- Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* 3301, 1-36.
- García García, N., Feranec, R.S., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Isotopic analysis of the ecology of herbivores and carnivores from the Middle Pleistocene deposits of the Sierra de Atapuerca, northern Spain. *Journal of Archaeological Science* 36, 1142-1151.
- Gibbard, P.L. & Stuart, A.J., 1975. Flora and vertebrate fauna of the Barrington Beds. *Geological Magazine* 112, 493-501.
- Gibbard, P.L., Zalasiewicz, J.A., Mathers, S.J., 1998. Stratigraphy of the marine Pliocene Pleistocene crag deposits of East Anglia. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen* 60, 239-262.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *Journal of Human Evolution* 15, 783-822.
- Hayek, L.-A.C., Bernor, R.L., Solounias, N., Steigerwald, P., 1992. Preliminary studies of hipparionine horse diet as measured by tooth microwear. *Annales Zoologici Fennici* 28, 187-200.
- Head, M.J., 1998a. Pollen and dinoflagellates from the Red Crag at Walton-on-the-Naze, Essex: evidence for a mild climatic phase during the early Late Pliocene of eastern England. *Geological Magazine* 135, 803-817.
- Head, M., 1998b. Marine environmental change in the Pliocene and early Pleistocene of eastern England: the dinoflagellate evidence reviewed. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen* 60, 199-226.
- Higham, T., Compton, T., Stringer, C., Jacobi, R., Shapiro, B., Trinkaus, E., Chandler, B., Groning, F., Collins, C., Hillson, S., O'Higgins, P., FitzGerald, C., Fagan, M., 2011. The earliest evidence for anatomically modern humans in northwestern Europe. *Nature* 479, 521-524.
- Hoffman, J.M., Fraser, D., Clementz, M.T., 2015. Controlled feeding trials with ungulates: a new application of in vivo dental molding to assess the abrasive factors of microwear. *The Journal of Experimental Biology* 218, 1538-1547.
- Jacobi, R.M., Higham, T.F.G., 2009. The early Lateglacial re-colonisation of Britain: new radiocarbon evidence from Gough's Cave, southwest England. *Quaternary Science Reviews* 28, 1895-1913.
- Kahlke, R.-D., Kaiser, T.M., 2011. Generalism as a subsistence strategy: advantages and limitations of the highly flexible feeding traits of Pleistocene *Stephanorhinus*

- 812 *hundsheimensis* (Rhinocerotidae, Mammalia). Quaternary Science Reviews 30,
813 2250-2261.
- 814 Kennard, A.S., 1944. The Crayford brickearths. Proceedings of the Geologists'
815 Association 55, 121-169.
- 816 Kerney, M.P., Gibbard, P.L., Hall, A.R., Robinson, J.E., Coope, G.R., 1982. Middle
817 Devensian river deposits beneath the 'Upper Floodplain' terrace of the River
818 Thames at Isleworth, West London. Proceedings of the Geologists' Association
819 93, 385-393.
- 820 King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental
821 microwear. American Journal of Physical Anthropology 108, 359-373.
- 822 Kuitens, M., van der Plicht, J., Drucker, D.G., Van Kolfschoten, T., Palstra, S.W.L.,
823 Bocherens, H., 2015. Carbon and nitrogen stable isotopes of well-preserved
824 Middle Pleistocene bone collagen from Schöningen (Germany) and their
825 paleoecological implications. Journal of Human Evolution 89, 105-113.
- 826 Lewis, S.G., Ashton, N., Jacobi, R., 2011. Testing human presence during the Last
827 Interglacial (MIS 5e): a review of the British evidence. Developments in
828 Quaternary Science 14, 125-164.
- 829 Lister, A.M., 1981. Evolutionary Studies on Pleistocene Deer. University of Cambridge,
830 Cambridge, p. 350.
- 831 Lister, A.M., 1984. Evolutionary and ecological origins of British deer. Proceedings of
832 the Royal Society of Edinburgh 82B, 205-229.
- 833 Lister, A.M., 1992. Mammalian fossils and Quaternary biostratigraphy. Quaternary
834 Science Reviews 11, 329-344.
- 835 Lister, A.M., 1993. The stratigraphical significance of deer species in the Cromer
836 Forest-bed Formation. Journal of Quaternary Science 8, 95-108.
- 837 Lister, A.M., 1996. The stratigraphical interpretation of large mammal remains from the
838 Cromer Forest-bed Formation, in: Turner, C. (Ed.), The Early Middle Pleistocene
839 of Europe. Balkema, Rotterdam, pp. 25-44.
- 840 Lister, A.M., 1997. The evolutionary response of vertebrates to Quaternary
841 environmental change, in: Huntley, B., Cramer, W., Morgan, A.V., Prentice, H.C.,
842 Allen, J.R.M. (Eds.), Past and future rapid environmental changes: the spatial and
843 evolutionary responses of terrestrial biota. Springer-Verlag, Berlin, pp. 287-302.
- 844 Lister, A.M., 1998. The age of early Pleistocene mammal faunas from the 'Weybourne
845 Crag' and Cromer Forest-bed Formation (Norfolk, England). Mededelingen
846 Nederlands Instituut voor Toegepaste Geowetenschappen 60, 271-280.
- 847 Lister, A.M., 1999. The Pliocene deer of the Red Crag Nodule Bed (UK). Deinsea 7,
848 215-221.
- 849 Lister, A.M., 2013. The role of behaviour in adaptive morphological evolution of
850 African proboscideans. Nature 500, 331-336.
- 851 Lister, A.M., Parfitt, S.A., Owen, F.J., Collinge, S.E., Breda, M., 2010. Metric analysis
852 of ungulate mammals in the early Middle Pleistocene of Britain, in relation to
853 taxonomy and biostratigraphy: II: Cervidae, Equidae and Suidae. Quaternary
854 International 228, 157-179.
- 855 Lister, A.M., Sher, A.V., van Essen, H., Wie, G., 2005. The pattern and process of
856 mammoth evolution in Eurasia. Quaternary International 126-128, 49-64.
- 857 Lister, A.M., Stuart, A.J. (eds.), 2010. The West Runton Freshwater Bed and the West
858 Runton Mammoth, Quaternary International, pp. 1-248.
- 859 Loffredo, L.F., DeSantis, L.R.G., 2014. Cautionary lessons from assessing dental
860 mesowear observer variability and integrating paleoecological proxies of an

- extreme generalist *Cormohipparion emsliei*. Palaeogeography, Palaeoclimatology, Palaeoecology 395, 42-52.
- Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., Heintz, E., 2004. The Late Miocene paleoenvironment of Afghanistan as inferred from dental microwear in artiodactyls. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 143-163.
- Merceron, G., Blondel, C., Viriot, L., Koufos, G.D., de Bonis, L., 2007. Dental microwear analysis of bovids from the Vallesian (late Miocene) of Axios Valley in Greece: reconstruction of the habitat of *Ouranopithecus macedoniensis* (Primates, Hominoidea). Geodiversitas 29, 421-433.
- Mihlbachler, M.C., Beatty, B.L., Caldera-Siu, A., Chan, D., Lee, R., 2012. Error rates and observer bias in dental microwear analysis using light microscopy. Palaeontologia Electronica 15, 12A, 22p.
- Mihlbachler, M.C., Rivals, F., Solounias, N., Semprebon, G.M., 2011. Dietary change and evolution of horses in North America. Science 331, 1178-1181.
- Parfitt, S.A., Barendregt, R.W., Breda, M., Candy, I., Collins, M.J., Coope, R.G., Durbidge, P., Field, M.H., Lee, J.R., Lister, A.M., Mutch, R., Penkman, K.E.H., Preece, R.C., Rose, J., Stringer, C.B., Symmons, R., Whittaker, J.E., Wymer, J.J., Stuart, A.J., 2005. The earliest record of human activity in northern Europe. Nature 438, 1008-1012.
- Parfitt, S.A., Ashton, N.M., Lewis, S.G., Abel, R., Coope, G.R., Field, M.H., Gale, R., Hoare, P.G., Larkin, N.R., Lewis, M.D., Karloukovski, V., Maher, B.A., Peglar, S.M., Preece, R.C., Whittaker, J.E., Stringer, C.B., 2010. Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. Nature 466, 229-233.
- Penkman, K.E.H., Preece, R.C., Bridgland, D.R., Keen, D.H., Meijer, T., Parfitt, S.A., White, T.S., Collins, M.J., 2011. A chronological framework for the British Quaternary based on *Bythnia* opercula. Nature 476, 446-449.
- Penkman, K.E.H., Preece, R.C., Bridgland, D.R., Keen, D.H., Meijer, T., Parfitt, S.A., White, T.S., Collins, M.J., 2013. An aminostratigraphy for the British Quaternary based on *Bythnia* opercula. Quaternary Science Reviews 61, 111-134.
- Preece, R.C., Parfitt, S.A., 2012. The Early and early Middle Pleistocene context of human occupation and lowland glaciation in Britain and northern Europe. Quaternary International 271, 6-28.
- Richards, A.E., Gibbard, P.L., Pettit, M.E., 1999. The sedimentology and palaeoecology of the Westleton Member of the Norwich Crag Formation (Early Pleistocene) at Thorington, Suffolk, England. Geological Magazine 136, 453-464.
- Rivals, F., 2012. Ungulate feeding ecology and middle Pleistocene paleoenvironments at Hundsheim and Deutsch-Altenburg 1 (eastern Austria). Palaeogeography, Palaeoclimatology, Palaeoecology 317-318, 27-31.
- Rivals, F., Semprebon, G., 2006. A comparison of the dietary habits of a large sample of the Pleistocene pronghorn *Stockoceros onusrosagris* from the Papago Springs Cave in Arizona to the modern *Antilocapra americana*. Journal of Vertebrate Paleontology 26, 495-500.
- Rivals, F., Solounias, N., 2007. Differences in tooth microwear of populations of caribou (*Rangifer tarandus*, Ruminantia, Mammalia) and implications to ecology, migration, glaciations and dental evolution. Journal of Mammalian Evolution 14, 182-192.

- Rivals, F., Solounias, N., Mithlacher, M.C., 2007a. Evidence for geographic variation in the diets of late Pleistocene and early Holocene *Bison* in North America, and differences from the diets of recent *Bison*. *Quaternary Research* 68, 338-346.
- Rivals, F., Mithlacher, M.C., Solounias, N., 2007b. Effect of ontogenetic-age distribution in fossil samples on the interpretation of ungulate paleodiets using the mesowear method. *Journal of Vertebrate Paleontology* 27, 763-767.
- Rivals, F., Schulz, E., Kaiser, T.M., 2008. Climate-related dietary diversity of the ungulate faunas from the middle Pleistocene succession (OIS 14-12) at the Caune de l'Arago (France). *Paleobiology* 34, 117-127.
- Rivals, F., Schulz, E., Kaiser, T.M., 2009a. A new application of dental wear analyses: estimation of duration of hominid occupations in archaeological localities. *Journal of Human Evolution* 56, 329-339.
- Rivals, F., Schulz, E., Kaiser, T.M., 2009b. Late and middle Pleistocene ungulates dietary diversity in Western Europe indicate variations of Neanderthal paleoenvironments through time and space. *Quaternary Science Reviews* 28, 3388-3400.
- Rivals, F., Mithlacher, M.C., Solounias, N., Mol, D., Semprebon, G.M., de Vos, J., Kalthoff, D.C., 2010. Palaeoecology of the Mammoth Steppe fauna from the late Pleistocene of the North Sea and Alaska: Separating species preferences from geographic influence in paleoecological dental wear analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 286, 42-54.
- Rivals, F., Semprebon, G., Lister, A., 2012. An examination of dietary diversity patterns in Pleistocene proboscideans (*Mammuthus*, *Palaeoloxodon*, and *Mammot*) from Europe and North America as revealed by dental microwear. *Quaternary International* 255, 188-195.
- Rivals, F., Mol, D., Lacombe, F., Lister, A.M., Semprebon, G.M., 2015a. Resource partitioning and niche separation between mammoths (*Mammuthus rumanus* and *Mammuthus meridionalis*) and gomphotheres (*Anancus arvernensis*) in the Early Pleistocene of Europe. *Quaternary International* 379, 164-170.
- Rivals, F., Julien, M.-A., Kuitens, M., Van Kolfschoten, T., Serangeli, J., Drucker, D.G., Bocherens, H., Conard, N.J., 2015b. Investigation of equid paleodiet from Schöningen 13 II-4 through dental wear and isotopic analyses: Archaeological implications. *Journal of Human Evolution* 89, 129-137.
- Roberts, M.B., Parfitt, S.A., 1999. Boxgrove: A Middle Pleistocene hominid site at Eartham Quarry, Boxgrove, West Sussex. London: English Heritage Archaeological Report 17, 1-456.
- Saareinen, J., Karme, A., Cerling, T., Uno, K., Säilä, L., Kasiki, S., Ngene, S., Obari, T., Mbua, E., Manthi, F.K., Fortelius, M., 2015. A new tooth wear-based dietary analysis method for Proboscidea (Mammalia). *Journal of Vertebrate Paleontology* 35, e918546.
- Sánchez-Hernández, C., Rivals, F., Blasco, R., Rosell, J., 2016. Tale of two timescales: Combining tooth wear methods with different temporal resolutions to detect seasonality of Palaeolithic hominin occupational patterns. *Journal of Archaeological Science: Reports* 6, 790-797.
- Schreve, D.C., 1997. Mammalian biostratigraphy of the later Middle Pleistocene in Britain. University College London, London, p. 776.
- Schreve, D.C., 2001a. Differentiation of the British late Middle Pleistocene interglacials: the evidence from mammalian biostratigraphy. *Quaternary Science Reviews* 20, 1693-1705.

- 958 Schreve, D.C., 2001b. Mammalian evidence from the Middle Pleistocene fluvial
959 sequences for complex environmental change at the oxygen isotope sub-stage
960 level. *Quaternary International* 79, 65-74.
- 961 Schreve, D. (ed.) 2004. *The Quaternary Mammals of Southern and Eastern England:*
962 *Field Guide*. Quaternary Research Association, London.
- 963 Scott, B., Ashton, N., G. Lewis, S., Parfitt, S., White, M., 2011. Technology and
964 landscape use in the early Middle Palaeolithic of the Thames Valley, in: Ashton,
965 N., Lewis, S.G., Stringer, C. (Eds.), *The Ancient Human Occupation of Britain*.
966 Elsevier, Amsterdam, pp. 67-89.
- 967 Semprebon, G.M., Rivals, F., 2007. Was grass more prevalent in the pronghorn past?
968 An assessment of the dietary adaptations of Miocene to recent Antilocapridae
969 (Mammalia: Artiodactyla). *Palaeogeography, Palaeoclimatology, Palaeoecology*
970 253, 332-347.
- 971 Semprebon, G.M., Rivals, F., 2010. Trends in the paleodietary habits of fossil camels
972 from the Tertiary and Quaternary of North America. *Palaeogeography,*
973 *Palaeoclimatology, Palaeoecology* 295, 131-145.
- 974 Semprebon, G., Janis, C., Solounias, N., 2004a. The diets of the Dromomerycidae
975 (Mammalia: Artiodactyla) and their response to Miocene vegetational change.
976 *Journal of Vertebrate Paleontology* 24, 427-444.
- 977 Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L.,
978 2004b. Can low-magnification stereomicroscopy reveal diet? *Journal of Human*
979 *Evolution* 47, 115-144.
- 980 Semprebon, G., Sise, P., Coombs, M., 2011. Potential bark and fruit browsing as
981 revealed by stereomicroscopy analysis of the peculiar clawed herbivores known as
982 chalicotheres (Perissodactyla, Chalicotherioidea). *Journal of Mammalian*
983 *Evolution* 18, 33-55.
- 984 Semprebon, G.M., Rivals, F., Solounias, N., Hulbert Jr, R.C., 2016. Paleodietary
985 reconstruction of fossil horses from the Eocene through Pleistocene of North
986 America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 442, 110-127.
- 987 Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate
988 ecomorphology with application to early fossil equids. *American Museum*
989 *Novitates* 3366, 1-49.
- 990 Strani, F., DeMiguel, D., Sardella, R., Bellucci, L., 2015. Paleoenvironments and
991 climatic changes in the Italian Peninsula during the Early Pleistocene: evidence
992 from dental wear patterns of the ungulate community of Coste San Giacomo.
993 *Quaternary Science Reviews* 121, 28-35.
- 994 Stuart, A.J., 1976. The history of the mammal fauna during the Ipswichian/Last
995 Interglacial in England. *Philosophical Transactions of the Royal Society of*
996 *London B* 276, 221-250.
- 997 Stuart, A.J., 1982. *Pleistocene vertebrates in the British Isles*. Longman, London.
- 998 Stuart, A.J., 1996. Vertebrate faunas from the Early Middle Pleistocene of East Anglia,
999 in: Turner, C. (Ed.), *The Early Middle Pleistocene in Europe*. Balkema,
1000 Rotterdam, pp. 9-24.
- 1001 Stuart, A.J., Lister, A.M., 2001. The mammalian faunas of Pakefield/Kessingland and
1002 Corton, Suffolk, UK: evidence for a new temperate episode in the British early
1003 Middle Pleistocene. *Quaternary Science Reviews* 20, 1677-1692.
- 1004 Stuart, A.J., West, R.G., 1976. Late Cromerian fauna and flora at Ostend, Norfolk.
1005 *Geological Magazine* 113, 469-473.
- 1006 Stuart, A.J., Wolff, R.G., Lister, A.M., Singer, R., Egginton, J.M., 1993. Fossil
1007 vertebrates, in: Singer, R., Gladfelter, B.G., Wymer, J.J. (Eds.), *The Lower*

1008 Paleolithic Site at Hoxne, England. University of Chicago Press, Chicago, pp.
 1009 163-206.
 1010 Sutcliffe, A.J., 1960. Joint Mitnor Cave, Buckfastleigh, Transactions of the Torquay
 1011 Natural History Society 13, 3-28.
 1012 van Asperen, E.N., Kahlke, R.-D., 2015. Dietary variation and overlap in Central and
 1013 Northwest European *Stephanorhinus kirchbergensis* and *S. hemitoechus*
 1014 (Rhinocerotidae, Mammalia) influenced by habitat diversity. Quaternary Science
 1015 Reviews 107, 47-61.
 1016 West, R.G., 1980. The Pre-glacial Pleistocene of the Norfolk and Suffolk Coasts.
 1017 Cambridge University Press, Cambridge.
 1018 West, R.G., 2000. Plant Life of the Quaternary Cold Stages: Evidence from the British
 1019 Isles. Cambridge University Press, Cambridge.
 1020 Willerslev, E., Davison, J., Moora, M., Zobel, M., Coissac, E., Edwards, M.E.,
 1021 Lorenzen, E.D., Vestergard, M., Gussarova, G., Haile, J., Craine, J., Gielly, L.,
 1022 Boessenkool, S., Epp, L.S., Pearman, P.B., Cheddadi, R., Murray, D., Brathen,
 1023 K.A., Yoccoz, N., Binney, H., Cruaud, C., Wincker, P., Goslar, T., Alsos, I.G.,
 1024 Bellemain, E., Brysting, A.K., Elven, R., Sonstebo, J.H., Murton, J., Sher, A.,
 1025 Rasmussen, M., Ronn, R., Mourier, T., Cooper, A., Austin, J., Moller, P., Froese,
 1026 D., Zazula, G., Pompanon, F., Rioux, D., Niderkorn, V., Tikhonov, A., Savvinov,
 1027 G., Roberts, R.G., MacPhee, R.D.E., Gilbert, M.T.P., Kjaer, K.H., Orlando, L.,
 1028 Brochmann, C., Taberlet, P., 2014. Fifty thousand years of Arctic vegetation and
 1029 megafaunal diet. Nature 506, 47-51.
 1030 Zazzo, A., Bocherens, H., Brunet, M., Beauvilain, A., Billiou, D., Mackaye, H.T.,
 1031 Vignaud, P., Mariotti, A., 2000. Herbivore paleodiet and paleoenvironmental
 1032 changes in Chad during the Pliocene using stable isotope ratios of tooth enamel
 1033 carbonate. Paleobiology 26, 294-309.
 1034

Figure captions

Figure 1. Geographic position of the localities sampled.

Figure 2. Bivariate plots of the average numbers of pits and scratches in (A) *Anancus arvernensis* and *Palaeoloxodon antiquus* and (B) the *Mammuthus* lineage. Bars correspond to standard error of the mean (± 1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semperebon (2002) and Rivals et al. (2010).

Figure 3. Low scratch percentages (%0-17) and dietary changes in (A) *Anancus arvernensis* and *Palaeoloxodon antiquus* and (B) the *Mammuthus* lineage through geological time. The gray areas correspond to the range of values for the extant mixed feeders.

Figure 4. Bivariate plot of the average numbers of pits and scratches in Rhinocerotidae. Bars correspond to standard error of the mean (± 1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semperebon (2002) and Rivals et al. (2010).

Figure 5. Low scratch percentages (%0-17), mesowear scores (MWS), and dietary changes in Rhinocerotidae through geological time. For mesowear, the dotted line indicates the limit between extant browsers and extant grazers (MWS=2). The grey area

indicate the range of values for extant mixed feeders, which overlap both with extant grazers and browsers.

Figure 6. Bivariate plot of the average numbers of pits and scratches in Equidae. Bars correspond to standard error of the mean (± 1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002) and Rivals et al. (2010).

Figure 7. Low scratch percentages (%0-17), mesowear scores (MWS), and dietary changes in Equidae through geological time. The grey areas correspond to the range of values for the extant mixed feeders (see Fig. 5).

Figure 8. Bivariate plot of the average numbers of pits and scratches in Cervidae. (A) *Cervus* and *Dama*. (B) Other species. Bars correspond to standard error of the mean (± 1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002) and Rivals et al. (2010).

Figure 9. Low scratch percentages (%0-17), mesowear scores (MWS), and dietary changes in Cervidae through geological time. (A) *Cervus* and *Dama*. (B) Other species. The grey areas correspond to the range of values for the extant mixed feeders (see Fig. 5).

Fig. 10. Bivariate plot of the average numbers of pits and scratches in Bovidae. Bars correspond to standard error of the mean (± 1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002) and Rivals et al. (2010).

Figure 11. Low scratch percentages (%0-17), mesowear scores (MWS), and dietary changes in Bovidae through geological time. The grey areas correspond to the range of values for the extant mixed feeders (see Fig. 5).

Figure 12. Low scratch percentages (%0-17), mesowear scores (MWS), and dietary changes for all taxa in selected localities. Abbreviations: Aa = *Anancus arvernensis*; B/B = *Bos/Bison*; Bo = *Bos primigenius*; Bp = *Bison priscus*; Bs = *Bison schoetensacki*; Ca = *Coelodonta antiquitatis*; Cc = *Capreolus capreolus*; Ce = *Cervus elaphus*; Cpa = *Cervus pardinensis*; Cpe = *Cervus perrieri*; Cg = *Cervalces gallicus*; C? = deer indet. *Cervus?*; Dd = *Dama dama*; Dr = *Dama roberti*; Ea = *Equus altidens*; Eb = *Equus bressanus*; Ef = *Equus ferus*; Es = *Equus stenonis*; Eucl. = *Eucladoceros* sp.; Ha = *Hippopotamus amphibius*; Hi = *Hipparion* sp.; Lep. = *Leptobos*; m = megacerine sp.; Mb = *Mamut borsoni*; Mg = *Megaloceros giganteus*; Mm = *Mammuthus meridionalis*; Mp = *M. primigenius*; Mt = *M. trogontherii*; Pa = *Palaeoloxodon antiquus*; Par. = *Parabos*; Pp = *Propotamochoerus provincialis*; Rt = *Rangifer tarandus*; Sa = *Sus arvernensis*; Se = *Stephanorhinus etruscus*; Sh = *S. hemitoechus*; Sk = *S. kirchbergensis*; Su = *S. hunsheimensis*; T = *Tapirus* sp.