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

Florent Rivals [a,*], Matthew C. Mihlbachler [b,c], Nikos Solounias [b,c], Dick Mol [d], Gina M. Semprebon [e], John de Vos [f], Daniela C. Kalthoff [g]

[a] ICREA and Institut Català de Paleoecologia Humana i Evolució Social, Plaça Imperial Tarraco 1, 43005 Tarragona, Spain
[b] Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, NY 11568, USA
[c] Department of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA
[d] Natural History Museum Rotterdam, P.O. Box 23452, 3001 KL Rotterdam, The Netherlands
[e] Bay Path College, 588 Longmeadow St., Longmeadow, MA 01106, USA
[f] National Museum of Natural History Naturalis, P.O. Box 9517, 2300 RA Leiden, The Netherlands
[g] Naturhistoriska riksmuseet, Paleozoologi, Box 50007, SE-104 05 Stockholm, Sweden

ARTICLE INFO

ABSTRACT

The paleodietary ecology of Late Pleistocene ungulate faunas of the Mammoth Steppe ecosystem was investigated at Fairbanks (Alaska) and Brown Bank (North Sea) through dental mesowear and microwear analysis. The purpose of the study is to address questions concerning the paleoecology of the Mammoth Steppe, an ecosystem that has no extant analog. Dental wear patterns indicate that the niche partitioning at Brown Bank (BB) region was consistent with ecosystem dynamics found in diverse ungulate faunas in recent time. In contrast, despite the lower numbers of extinct taxa, the Fairbanks (FB) fauna is ecologically bizarre. In general, the microwear of this fauna includes excessive numbers of very (narrow) fine scratches that are atypical for extant mixed feeders and grazers. Moreover, the mesowear signal suggests unusual paleodiets (niche dynamics), where low-crowned mixed-feeding cervids, *Rangifer* and *Cervus*, adopted diets that are similar to *Equus* in terms of mesowear (abrasion) and much more abrasive than the diets of either *Bison* or *Ovis*. We suggest that the anomalies may relate to unique, possibly disharmonious, ecosystem dynamics during the Pleistocene–Holocene transition. In addition to these findings, it was discovered (found) that dental wear patterns, particularly microwear variables such as scratch frequency and scratch width are strongly affected by geographic region, irrespective of species-specific dietary preferences.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

The end of the Late Pleistocene was the time when species such as giant deer, woolly mammoth and woolly rhinoceros became extinct after having survived many climatic changes during several hundreds of thousands of years (Lister and Sher, 1995; Stuart et al., 2004; Solow et al., 2006; Buck and Bard, 2007; Nogués-Bravo et al., 2008). The latest Pleistocene is also the period during which humans spread into Northern Siberia and crossed Beringia into America (Hoffecker et al., 1993; Yesner, 2001; Dixon, 2001). During the Late Pleistocene, the environments of the middle and northern parts of Europe, northern Asia, and northern North America were generally open, tending toward steppic (Vereschagin and Baryshnikov, 1982; Guthrie, 1982, 1990, 2001; van Andel and Tzedakis, 1996). The steppe biome is a dry,

cold, grassland which may be semi-desert, or covered with grass or shrubs or both, depending on the season and latitude. The term is also used to denote the climate in regions too dry to support a forest, but not dry enough to be a desert. Steppe is characterized by a continental and semi-arid climate. The Mammoth Steppe (Guthrie, 1980) is an extinct biotope remarkable for its unusual combination of mammal species when compared to the present-day distribution of their modern relatives. The ecosystem of the Mammoth Steppe collapsed during the period that marks the Pleistocene–Holocene transition and was replaced by the modern tundra, taiga, and steppe belts of Eurasia and North America (Zimov et al., 1995; Guthrie, 1995). The Mammoth Steppe was characterized by a diverse flora and fauna. During the collapse of the steppe biome, the geographical ranges of several species shrank and many were regionally extirpated, whereas others went extinct.

The purpose of this study is to analyze the paleodietary ecology of two fossil ungulate assemblages from Alaska and the North Sea using two methods of dental wear analysis (dental mesowear and dental

* Corresponding author. Tel.: +34 977 25 78 82.
  E-mail address: florent.rivals@icrea.es (F. Rivals).

microwear). In addition to the unique paleoenvironment of the Mammoth Steppe, the (Mammoth Steppe) faunas contain associations of extinct and extant species as well as associations of extant species that do not occur today. These unique faunal associations may have created interspecies niche dynamics that are not analogous to modern faunas from the same regions.

We propose to address the following questions:

(1) Is the dietary ecology of Mammoth Steppe faunas predictable, given our current understanding of the autecologies of the constituent species? For instance, are the dietary ecologies of extant species in the Mammoth Steppe similar to those today, or do they differ due to the unique faunal and floral associations?
(2) Was the dietary ecology and interspecific niche dynamics of the ungulates of the Mammoth Steppe homogeneous in every region? or was it diverse with a significant regional effect?
(3) Is there any evidence that terminal Pleistocene faunas are "disharmonious" or show ecologically anomalous interspecies niche dynamics in comparison to earlier or later faunas?

2. Material

We analyzed material from two regions selected for their richness in fossil ungulates, the Fairbanks (FB) area of Alaska, and the Brown Bank (BB) in the North Sea (Fig. 1).

2.1. Fairbanks area, Alaska

We examined samples of late Pleistocene ungulates from open-pit gold mines near Fairbanks (FB), Alaska (Fig. 1), housed in the Division of Vertebrate Paleontology at the American Museum of Natural History, New York. Massive dredges and extensive water pipelines moved millions of cubic meters of late Pleistocene silts to expose gold-bearing gravels buried just above bedrock. The frozen deposits consist of muck, gravels, sands, peat and other vegetation, volcanic ash and ice (Wilkerson, 1932). The miners used powerful jets of water to thaw and erode deposits. They reshaped entire valleys in this search for gold and exposed innumerable fossil bones and several frozen mummies (Guthrie, 1968a).

Seven species from this region were analyzed: *Mammuthus primigenius* (woolly mammoth), *Equus ferus* (horse), *Cervus elaphus* (red deer), *Alces alces* (moose), *Rangifer tarandus* (caribou), *Bison priscus* (bison), and *Ovis dalli* (Dall sheep). Large mammal fossils from these beds have been dated to the Wisconsin (most recent) glacial period (110 to 12 kyr BP), from Marine Isotopic Stage (MIS) 3-2 (60 to 12 kyr BP) i.e. to the last glacial maximum (Guthrie, 2006). The specimens sampled are from three basic collecting areas: Engineer Creek, Cripple Creek, and Gold Hill. Radiocarbon dates for those areas range from ca. 14 to 12 kyr BP (Guthrie, 2006), i.e. the end of the very cold and dry period of the Mammoth Steppe and the beginning of a transitional period, warmer and more humid, with abundant graminoids and woody plants (Anderson et al., 1991; Bigelow and Powers, 2001). However, radiocarbon dates for *Alces alces* are consistently younger than those of the other ungulates. *Alces* dates range from 12 to 9 kyr BP (Guthrie, 2006). *Alces* is also reported to be a Holocene component of the fauna at other localities in Alaska, like at Lost Chicken Creek (Porter, 1988). Those remains occur after the transition of the Mammoth Steppe to the tundra and taiga vegetation (Guthrie, 2006). This ungulate assemblage does not result from a single depositional event, but, with the exception of *Alces*, the radiocarbon range through a relatively short interval of time that has been treated as an essentially contemporaneous latest Pleistocene fauna (Guthrie, 1968a, 2003, 2004, 2006; Porter, 1988).

2.2. Brown Bank area, North Sea

In glacial times, the southern North Sea was above sea level and contained abundant rivers and lakes. Many thousand fossil bones of Pleistocene age mammals, both terrestrial and marine, have been recovered from the bottom of the North Sea by fishermen using beamtrawls in the Brown Bank (BB) area, between Great Britain and The Netherlands (Fig. 1). Nine species were analyzed: *Mammuthus primigenius* (woolly mammoth), *Coelodonta antiquitatis* (woolly rhinoceros), *Equus ferus* (horse), *Megaloceros giganteus* (Irish elk), *Alces alces* (elk/moose), *Cervus elaphus* (red deer), *Rangifer tarandus* (reindeer), *Bos primigenius* (aurochs), and *Bison priscus* (bison).

Seventeen AMS radiocarbon dates were obtained from BB and range from ca. 45,000 to 34,000 BP (Mol et al., 2006). This range corresponds to the MIS 3 (interstade during the last glacial period) and more specifically to the Middle Pleniglacial (ca. 28,000–50,000 BP), during which three interstadials can be discerned. During the cold periods the land was a steppe–tundra; during the interstadials, it was mostly covered in low growth and birch (Mol et al., 2006). Glimmerveen et al. (2006) suggested reindeer probably inhabited the area only during the colder stadials. The fossil assemblage does not result from a single depositional event (van Kolfschoten and Laban, 1995; Mol et al. 2006), like at FB, but it gives an overall view of the species and their dietary breadth of the late Pleistocene interval for this region. The teeth were sampled in the collections from Naturalis (National Museum of Natural History) at Leiden (Netherlands).

It is evident that the samples from the two areas selected are significantly separated in space (about 7000 km) and time (20 to 30 kyr). It is also important to note that the two fossil assemblages do not result from a single depositional event and that all the taxa analyzed may not be exactly contemporaneous. However, the results would provide an overall view of the dietary traits for these species and the breadth of their dietary habits during the late Pleistocene.

3. Methods

3.1. Mesowear

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 has been successfully used to assign paleodiets to extinct species and test hypotheses of dental/diet coevolution (Kaiser et al., 2000; Kaiser and Solounias, 2003; Mihlbachler and Solounias, 2006; Semprebon and Rivals, 2007). Mesowear analysis is applicable to selenodont and lophodont ungulates with a predominantly transverse direction of shearing mastication, which includes many artiodactyls and perissodactyls. The mesowear technique is inapplicable to Proboscidea, such as *Mammuthus*, and other mammal groups with functionally different types of masticatory apparati. It is scored macroscopically from the buccal side of upper molars, preferably the paracone of M2 (Fortelius and Solounias, 2000). Among taxa with the appropriate masticatory apparatus, a diet with low levels of abrasion, such as the browsing diet of the moose, 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, such as the coarse grazing diets of African zebra, 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 (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
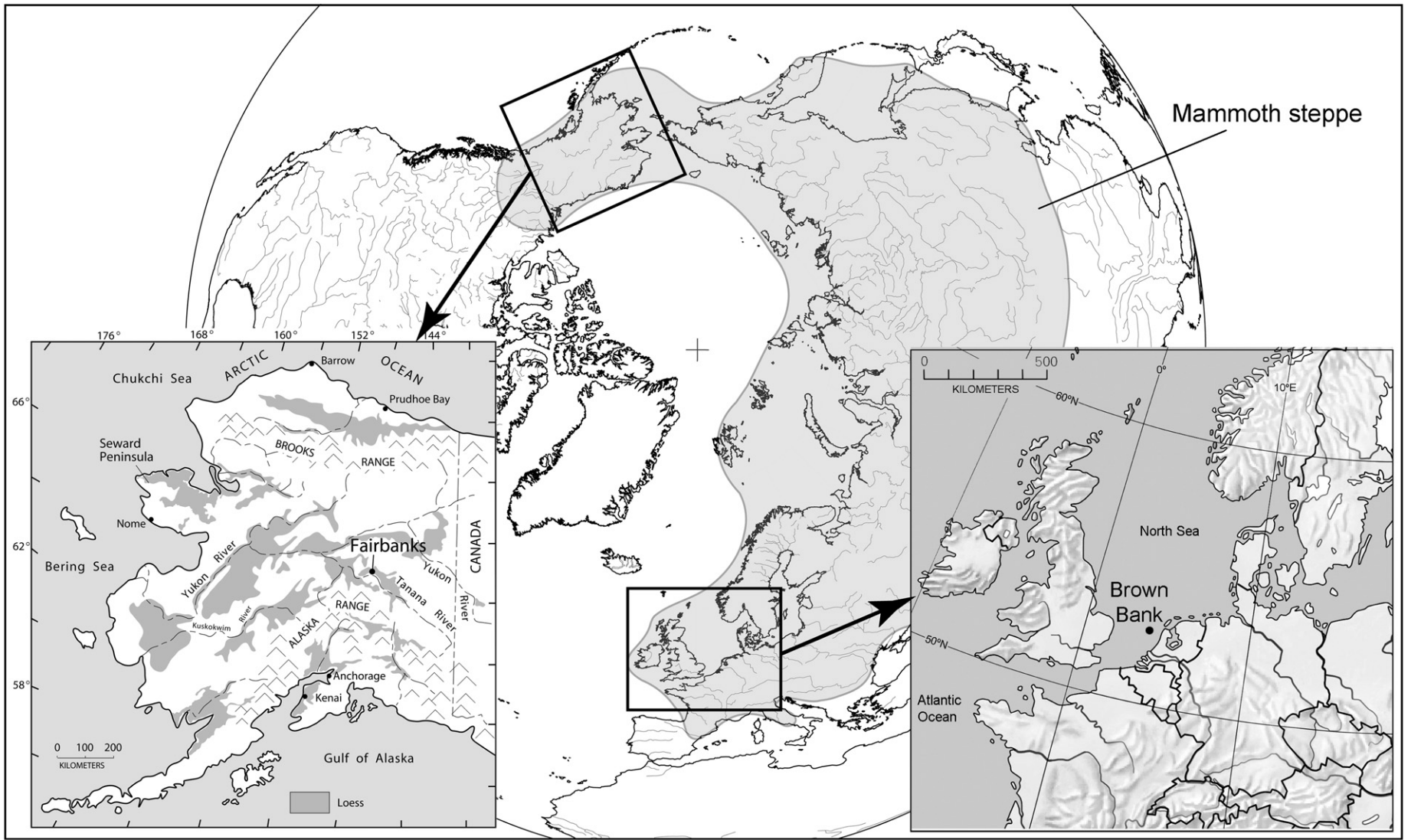
Fig. 1. Map showing the suspected extension of the Mammoth Steppe in Eurasia and North America (from Guthrie, 1990) and the location of Fairbanks and Brown Bank. The map of Alaska indicates the loess deposits compiled by Muhs and Budahn (2006) from Hopkins (1963) and Sainsbury (1972) for the Seward Peninsula, and Péwé (1975) for all other parts of the region.

less insensitive to age and more strongly related to diet (Rivals et al., 2007a). To exclude potential interobserver error, mesowear was scored by one investigator (FR).

In the original formulation of the method, mesowear was treated as a bivariate phenomenon. Apices of molar cusps were scored as sharp, rounded, or blunt, and the relief of the cusps as high or low (Fortelius and Solounias, 2000). However, the two variables, sharpness and relief, are strongly interdependent. For instance, sharpened cusps have high relief and completely blunted cusps have zero relief. Therefore, at least in most instances, mesowear is more appropriately treated as a univariate phenomenon (Mihlbachler and Solounias, 2006). Here, the original data of Fortelius and Solounias (2000) on extant ungulates were converted into a more simplified univariate score representing a continuum of mesowear stages from the highest and sharpest cusps (0) to cusps that are completely blunted with little or no relief (3) (Rivals et al., 2007b). Intermediate stages of mesowear consisting of more rounded cusp apices with higher and lower levels of cusp relief were assigned 1 and 2, respectively.

3.2. Microwear

All available upper and lower second molars (M2 or m2) of dentally adult individuals, whether isolated or in tooth rows were sampled, following the methodology of Solounias and Semprebon (2002). The occlusal surface of each tooth was molded using polyvinylsiloxane dental impression material. Each mold was cast with clear epoxy resin. Postmortem processes may affect dental surfaces (taphonomic alterations, damages during the collection of the specimens, or by the storage in the collections). All specimens were carefully screened and those with badly preserved enamel or extensive taphonomic defects (features with unusual morphology and size, or fresh features made during collecting process or during storage) were removed from the analysis (King et al., 1999). At BB (North Sea), from the 532 molded specimens, 137 specimens were discarded from the microwear analysis, i.e. 25.7% of the total number of specimens. The percentage of specimens excluded is quite high, probably due to the taphonomic conditions of preservation but also to the collecting process. At FB (Alaska), 174 casts of fossil ungulates were collected, out of which 24 specimens were discarded, i.e. 13.8% of the total number of specimens.

Microwear analysis was performed using low-mag stereomicroscopy following methods outlined by Solounias and Semprebon (2002), and Semprebon et al. (2004). Further discussion of this methodology

and its application toward dietary reconstruction can also be found in Godfrey et al. (2004) and Palombo et al. (2005). High-resolution epoxy casts of the teeth were examined at 35x magnification using a Leica MZ16 stereomicroscope. Light was shone onto surface of the casts, i.e. by adjusting the angle of incident light beam and its intensity. Examination of microwear was done on the enamel band of the paracone of the upper second molar or alternatively the protoconid of the lower second molar. Microwear features are identified, counted and classified on the basis of differential light refraction properties as outlined by Solounias and Semprebon (2002) and Semprebon et al. (2004) and assigned to four categories: small pits, large pits, fine (narrow) scratches and coarse (wide) scratches. Counts of microwear features were made on a standard 0.16 mm² square area on each tooth. Using modern species of known diets, counts of the numbers of pits and scratches in the counting area at a constant magnification of 35x are capable of discriminating three main recognized dietary categories within the herbivore dietary continuum, fruit browser, woody browser, and grazer (Solounias and Semprebon, 2002; Semprebon et al., 2004).

To minimize interobserver error, the microwear data were collected by a single investigator (FR), except for those of the horse from Alaska (collected by GMS). Moreover, our fossil data were superimposed over previously published microwear data from Solounias and Semprebon (2002). We also included additional microwear data on modern European and Asian ungulates species for better comparison including, *Alces alces*, *Cervus elaphus*, *Ovis ammon*, and *Bison bonasus* (Table 1). Those specimens were molded from the collections of the Natural History Museum in Vienna and microwear was recorded for these species by FR.

Because some of our data were collected by different individuals, this brings about the possibility that some of the patterns in the data may be an artifact of interobserver error. Semprebon et al. (2004) have suggested that intra-observer and interobserver errors are low using the low-magnification stereomicroscopy microwear method. We consider the microwear data collected from the FB and BB regions to be to be equivalent and statistically comparable.

3.3. Statistical methods

Statistical tests were performed on SPSS v14.0. For analyses involving two independent samples of species (either from different regions or within the same region) we used non-parametric Mann–Whitney U test. We used Kruskal–Wallis tests for intra-regional tests when three or more independent samples of species were included.

Table 1

Mesowear and microwear summary data for the modern ungulates. Abbreviations: n = number of specimens; MWS = mesowear score; NP = average number of pits; NS = average number of scratches; %LP = percentage of specimens with large pits; %CS = percentage of specimens with cross scratches; %G = percentage of specimens with gouges; SWS = scratches width score (from 0 = fine scratches only to 2 = coarse scratches only); %0–17 = percentage of specimens with between 0 and 17 scratches; and n.d. = new data (unpublished).

Species		Mesowear			Microwear								
		n	MWS	Ref.	n	NP	NS	%LP	%CS	%G	SWS	%0–17	Ref.
Alces alces — North America	AA-na	30	0.00	(1)	10	13.2	10.9	20.0	10.0	40.0	1.00	100	(2)
Alces alces — Europe	AA-eu	10	0.25	n.d.	10	25.9	10.4	0.0	40.0	0.0	0.70	100	n.d.
Bison bison athabascae	Bba-m	11	1.00	(3)	8	21.3	19.8	0.0	0.0	0.0	0.50	12.5	(3)
Bison bison bison	Bbb-m	15	2.73	(1)	18	3.5	24.8	38.9	94.4	5.6	1.06	5.6	(2)
Bison bonasus	Bbo-m	7	1.57	n.d.	7	23.2	18.7	71.4	14.3	57.1	1.14	28.6	n.d.
Ceratotherium simum	Cs-m	24	2.33	(1)	10	95.9	18.6	40.0	40.0	30.0	0.3	30.0	n.d.
Cervus canadensis	CE-na	19	0.53	(1)	28	18.6	30.6	42.9	96.4	21.4	0.36	10.7	(2)
Cervus elaphus	CE-eu	33	0.86	n.d.	28	13.3	13.4	32.1	25.0	35.7	1.46	89.3	n.d.
Diceros bicornis	Db-m	34	0.06	(1)	10	88.6	11.5	90.0	50.0	40.0	0.2	90.0	n.d.
Elephas maximus	Em-m		NA		7	9.9	28.1	71.4	85.7	71.4	1.71	0.0	(2)
Equus burchelli	Eqb-m	121	2.34	(1)	51	11.5	21.7	49.0	60.0	52.9	1.10	16.3	(2)
Equus grevyi	Eqg-m	29	2.24	(1)	11	7.9	26.1	63.6	66.7	54.5	1.33	1.6	(2)
Ovis ammon darwini	Oad-m	12	0.54	n.d.	11	14.1	16.7	90.9	0.0	91.0	1.09	45.5	n.d.
Ovis ammon poli	Oap-m	16	1.09	n.d.	22	13.3	26.3	22.7	4.5	9.1	0.86	0.0	n.d.
Ovis canadensis	Oc-m	29	0.62	(1)	19	13.2	16.7	42.1	31.6	47.4	1.53	47.4	(2)
Rangifer tarandus	Rt-m	102	0.80	(4)	66	26.9	23.3	62.1	0.0	69.7	0.96	9.1	(4)

(1) Fortelius and Solounias (2000); (2) Solounias and Semprebon (2002); (3) Rivals et al. (2007b); (4) Rivals and Solounias (2007).
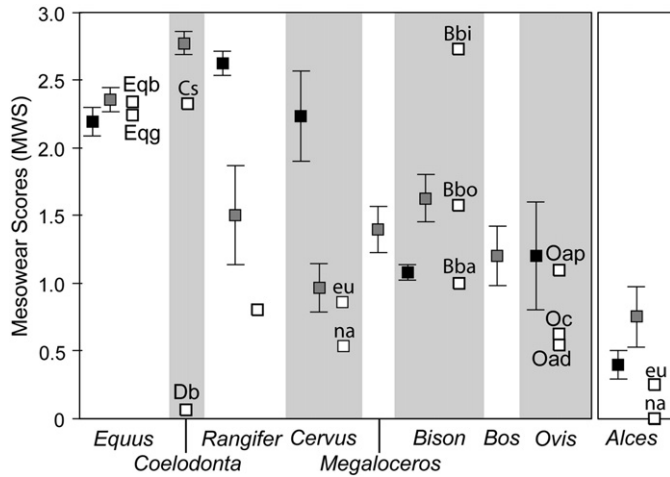
Fig. 2. Mesowear scores (MWSs) for Fairbanks, Alaska (black squares) and Brown Bank, North Sea (grey squares) compared to their modern relatives (white squares). Abbreviations: eu: Europe; na: North America; Bbi: *Bison bison athabascae*; Bbi: *Bison bison bison*; Bbo: *Bison bonasus*; Cs: *Ceratotherium simum*; Db: *Diceros bicornis*; Eqb: *Equus burchelli*; Eqg: *Equus grevyi*; Oad: *Ovis ammon dalli*; Oap: *Ovis ammon poli*; and Oc: *Ovis canadensis*. Error bars = standard error of the mean.

Because of their small size, the turnover rate of microwear features is very high (hours to days), whereas mesowear requires more dental wear and represents a longer-term diet signal (months to years). Keeping in mind that mesowear and microwear provide clues to diet on different time scales, we combined the results of both methods by running a principal components analysis (PCA) on the correlation matrix of six variables, including the mesowear score and the six microwear variables.

Comparisons with modern ungulates are realized using the databases from Fortelius and Solounias (2000) and Solounias and Semprebon (2002). We selected the extant relatives for each fossil species at FB and BB, and we exclusively choose specimens from restricted geographic areas, others were excluded.

4. Results

4.1. Mesowear

The mesowear data from the FB and BB collecting areas reveal a seemingly unpredictable variety of similarities and dissimilarities to each other and to modern samples (Fig. 2, Tables 1–3). Among the five taxa shared by FB and BB for which mesowear is applicable, *Alces* and *Equus*, do not show region-specific differences ($p = 0.053$ and 0.311 respectively). *Rangifer*, *Bison* and *Cervus* have significantly different mesowear between regions ($p = 0.000$ for the three species). At FB *Bison* have sharper cusp apices than at BB, whereas *Rangifer* and *Cervus* show the opposite pattern with blunter apices at FB and sharper apices at BB.

The fossil cervid samples exhibit a very broad range of abrasion from low to high (low-abrasion and high abrasion types of dental wear). *Alces* has substantially sharper cusp apices than other cervids and values of fossil and modern samples are similar. The cusp apices of *Cervus*, and *Rangifer* from FB (Table 2) are extremely blunt compared to modern cervids. With the exception of *Alces*, the BB cervids, *Cervus*, *Rangifer* and the extinct *Megaloceros*, tend to be somewhat blunter than modern samples, but not to the same extreme as the Fairbanks cervids. *Equus* mesowear from both fossil regions is blunted and not unusual compared to modern *Equus*. *Bison* from both fossil regions show rounded mesowear unlike the more excessive blunted cusps of the North American plains bison (*Bison bison bison*) and more like the rarer woodland bison taxa, *Bison bison athabascae* and *Bison bonasus*. *Ovis* cusps are rounded and not much different from modern samples of the same genus.

4.2. Microwear

Comparisons of microwear data for six taxa common to FB and BB indicate substantial region-specific differences for nearly every microwear variable between these two collecting regions (Figs. 3 and 4A and B; Table 4). Scratch frequency and scratch width, in particular, are strongly affected by region regardless of the dietary preferences of each species (Fig. 5). The FB species consistently have more scratches and finer (narrower) scratches compared to BB. Other variables differ within taxa between the two regions, but lack the consistent region-specific trend seen in the scratch data. For example, large pits occur are more frequent on the teeth of the BB samples. At FB, large pits are completely absent in some taxa, but occur frequently in others. Large pitting is generally indicative of either fruit consumption or encroachment of grit on food items. In the context of the Mammoth Steppe open habitat, fruit browsing is not likely to occur. Large pitting is seen more frequently in open habitat taxa that feed close to the ground and related to grit encroachment.

Diet is often inferred from microwear data via a scratch vs. pit plot such as those in Figs. 3 and 4, where modern species form a "trophic triangle" of browsers, grazers, and fruit browsers (Semprebon et al., 2004). While most of the FB taxa (except *Alces*) plot near modern grazers in a scratch versus pit plot in Fig. 3, other aspects of the microwear are dissimilar to the microwear of many modern grazers. Modern grazers tend to have a higher frequency of wide coarse-natured scratches, whereas those of the FB fauna are narrower and have a finer appearance (Fig. 5).

Superposition of the BB microwear data over those of extant species in a scratch vs. pit plot (Fig. 4) suggests a greater diversity of microwear patterns within the BB fauna compared to the FB fauna. *Alces*, again is an outlier, with low numbers of scratches and excessive numbers of pits. Most other BB species samples have pit and scratch frequencies clustering in a portion of the plot between browsers and grazers, with some slight overlap with the modern browser and modern grazer areas, predominantly suggesting various degrees of mixed-feeding diets for the BB species (except *Alces*). There is also an

Table 2
Mesowear and microwear summary data for the samples from Fairbanks, Alaska. Abbreviations see Table 1, and DW = dental wear (i.e. dietary category resulting from dental wear analysis); B = leaf browser; BMF = browse-dominated mixed feeder; G = grazer; GMF = grass-dominated mixed feeder; and MF = mixed feeder.

Species		Mesowear		Microwear								Dietary category	
		n	MWS	n	NP	NS	%LP	%CS	%G	SWS	%0–17	Expected	From DW
Alces alces	AA	89	0.39	25	42.7	12.5	96.0	12	0	1.0	93	B	B
Bison priscus	BI	251	1.10	27	11.4	27.9	7.4	100	3.7	0.1	0	G	G?
Cervus elaphus	CE	13	2.23	8	14.6	21.7	75.0	37.5	0	0.8	12.5	MF	GMF?
Equus ferus	EF	228	2.18	14	17.0	26.3	0	7.1	0	0.1	20	G	G?
Mammuthus primigenius	MP	–	n/a	32	10.1	26.4	0	93.8	12.5	0.4	0	G	G?
Ovis dalli	OD	5	1.20	5	12.9	28.0	0	60	0	0.4	0	G	G?
Rangifer tarandus	RT	193	2.62	15	10.7	22.6	0	13.3	0	0	0	MF	G?

Table 3

Mesowear and microwear summary data for the samples from Brown Bank, North Sea. Abbreviations see Table 1, and DW = dental wear (i.e. dietary category resulting from dental wear analysis); B = leaf browser; BMF = browse-dominated mixed feeder; G = grazer; GMF = grass-dominated mixed feeder; and MF = mixed feeder.

Species		Mesowear		Microwear								Dietary category	
		n	MWS	n	NP	NS	%LP	%CS	%G	SWS	%0–17	Expected	From DW
Alces alces	AA	6	0.8	6	43.4	8.2	0	33.3	0	1.8	100	B	B
Bison priscus	BI	24	1.6	22	12.7	22.5	4.5	0	0	0.6	0	G	GMF
Bos primigenius	BO	10	1.2	10	17.2	14.8	50.0	0	40.0	1.2	90.0	G	MF, BMF
Cervus elaphus	CE	13	1.0	9	14.4	15.4	55.6	11.1	0	1.0	77.8	MF	MF
Coelodonta antiquitatis	CA	46	2.8	64	17.1	14.0	54.7	25.0	0	1.2	89.1	G	GMF
Equus ferus	EF	98	2.4	96	18.1	22.2	34.4	3.1	7.3	1.0	5.2	G	G
Mammuthus primigenius	MP	–	n/a	127	13.3	18.6	11.0	60.6	0.8	1.1	31.5	G	GMF
Megaloceros giganteus	MG	24	1.4	28	13.6	13.0	78.6	53.6	39.3	1.4	100	MF	BMF
Rangifer tarandus	RT	6	1.5	6	20.6	15.3	50.0	0	0	1.2	100	MF	GMF

overall higher frequency of wide coarse scratches in the BB microwear data. In this respect, the microwear of this region is more similar to microwear of modern species, unlike the fine narrow scratches found on FB teeth that are unusual compared to modern grazing and mixed-taxa.

4.3. Principal component analysis

Multiple components are necessary to account for all of the significant variation in the mesowear and microwear data. PC1 explains 32.26% of the variance, PC2 19.11%, PC3 17.88%, and PC4 12.04%. PC1 is most heavily influenced by the scratch width and, negatively, by the number of scratches (Table 5). However, most of the other variables also load fairly highly on PC1, so high scores also suggest a tendency for high percentages of gouges, high percentages of large pits, high number of pits, and low number of scratches, low percentages of cross scratches, and low mesowear scores. On PC2, high scores indicate a tendency for low numbers of pits and higher values for all the other variables. On the plot of PC1 and PC2 (Fig. 6), PC 2 best separates modern examples of browsers, grazers and mixed feeders. Modern equids and bison are on the right and modern browsers such as *Alces* and *Diceros* are on the left.

The PCA clearly illustrates the unique and homogenous nature of dental wear within the FB fauna. Most of the FB samples, including *Equus*, *Ovis*, *Rangifer*, and *Bison* form a tight cluster and score lower on the first component than any extant samples. *Cervus* and *Alces* from FB exhibit more normal overall wear patterns and plot more closely to extant samples of the same taxa. The BB samples tend to cluster more

centrally within the region of the plot surrounded by extant samples, indicating overall dental wear patterns similar to mixed feeders.

5. Discussion

5.1. Summary of results

The following patterns in the data are most compelling: (1) Most of the statistical comparisons of microwear and mesowear data are significant in separating the various species and the two regions. Differences between species within a single region relate to species-specific dietary preferences and dietary behaviors within that region. (2) We find that each region has a characteristic local vegetational
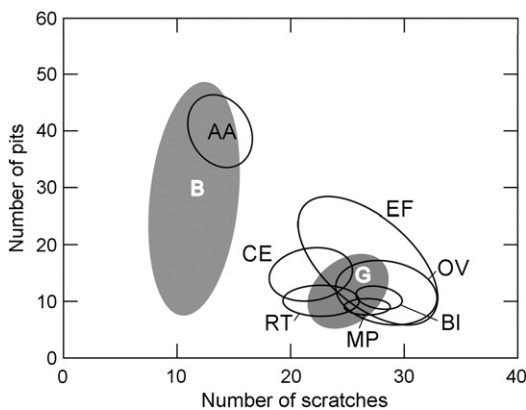

Fig. 4. Bivariate plot of the average number of pits versus average number of scratches for the cervids (A) and the other ungulates (B) from Brown Bank. Gaussian confidence ellipses (*p* = 0.95) on the centroid are indicated for the fossil species (black circles) and the extants browsers (B) and grazers (G) (grey areas) adjusted by sample size (extant data from Solounias and Semprebon, 2002). Abbreviations: AA: *Alces alces*; BI: *Bison priscus*; BO: *Bos primigenius*; CA: *Coelodonta antiquitatis*; CE: *Cervus elaphus*; EF: *Equus ferus*; MG: *Megaloceros giganteus*; MP: *Mammuthus primigenius*; and RT: *Rangifer tarandus*.

Fig. 3. Bivariate plot of the average number of pits versus average number of scratches for the ungulates from Fairbanks. Gaussian confidence ellipses (*p* = 0.95) on the centroid are indicated for the fossil species (black circles) and the extants browsers (B) and grazers (G) (grey areas) adjusted by sample size (extant data from Solounias and Semprebon, 2002). Abbreviations: AA: *Alces alces*; BI: *Bison priscus*; CE: *Cervus elaphus*; EF: *Equus ferus*; MP: *Mammuthus primigenius*; OV: *Ovis dalli*; and RT: *Rangifer tarandus*.
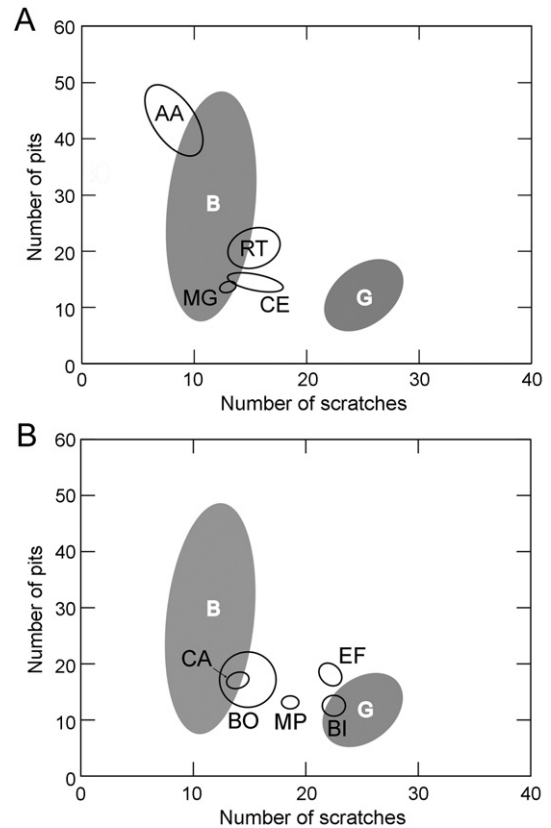
Table 4

P values for non-parametric Mann–Whitney U test (for differences between two samples) and Kruskal–Wallis test (for tests with 3 or more samples). Bold indicates significant differences. Abbreviations see Table 1.

	MWS	NP	NS	%LP	%CS	%G	SWS
Inter-region comparisons							
Alces vs. *Alces*	0.053	0.803	**0.000**	**0.000**	0.209	1.000	**0.000**
Rangifer vs. *Rangifer*	**0.000**	**0.000**	**0.000**	**0.004**	0.359	1.000	**0.000**
Bison vs. *Bison*	**0.000**	0.212	**0.000**	0.681	**0.000**	0.367	**0.000**
Cervus vs. *Cervus*	**0.000**	0.923	**0.003**	0.417	0.214	1.000	0.121
Mammuthus vs. *Mammuthus*	NA	**0.000**	**0.000**	0.050	**0.000**	**0.001**	**0.000**
Equus vs. *Equus*	0.311	0.346	**0.027**	**0.009**	**0.000**	0.299	**0.000**
Intra-region comparisons							
All North Sea	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
North Sea (without *Alces*)	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
North Sea cervids (without *Alces*)	**0.007**	**0.000**	**0.001**	0.231	**0.010**	**0.021**	**0.041**
All Alaska	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.184	**0.000**
Alaska (without *Alces*)	**0.000**	**0.020**	**0.005**	**0.000**	**0.000**	0.297	**0.000**
Alaska cervids (without *Alces*)	**0.009**	**0.010**	0.974	**0.000**	0.191	1.000	**0.000**

Table 5

Loadings of each variable of the PCA on the components.

	Components			
	1	2	3	4
MWS	−0.479	0.410	−0.073	0.741
NP	0.312	−0.781	0.297	0.354
NS	−0.749	0.298	0.413	−0.027
LP	0.678	0.191	0.473	0.300
CS	−0.355	0.087	0.665	−0.265
G	0.621	0.343	0.474	−0.053
SWS	0.632	0.556	−0.311	−0.063

signature and the diet of species from that region is affected by the local vegetation independently to what an ideal expectation for each species would be. There are consistent differences between samples of the same species between the region, suggesting that localized environmental conditions exerted strong influences on feeding behaviors and/or diet. In particular, some aspects of the microwear appear to have a strong regional influence, such as the number and widths of scratches, suggesting there localized environmental conditions are influencing at least these aspects of dental wear regardless of species-specific food preferences. (3) Despite having a greater number of extinct taxa, the BB fauna exhibits mesowear and microwear patterns that more closely match dietary predictions and more closely resemble microwear patterns that are typical of modern grazers and mixed feeders. This finding suggests that the ecology of this ungulate fauna is more comparable to modern ecosystems, at least in terms of dental wear. (4) On the other hand, the FB ungulate fauna is peculiar, with unique and atypical microwear and mesowear patterns in many species, that renders dietary interpretation difficult. Scratch numbers and widths are atypical in comparison to extant grazers and mixed feeders. Mesowear patterns are inconsistent with modern ecological systems, where normally browsing and mixed-feeding deer (*Rangifer* and *Cervus*)
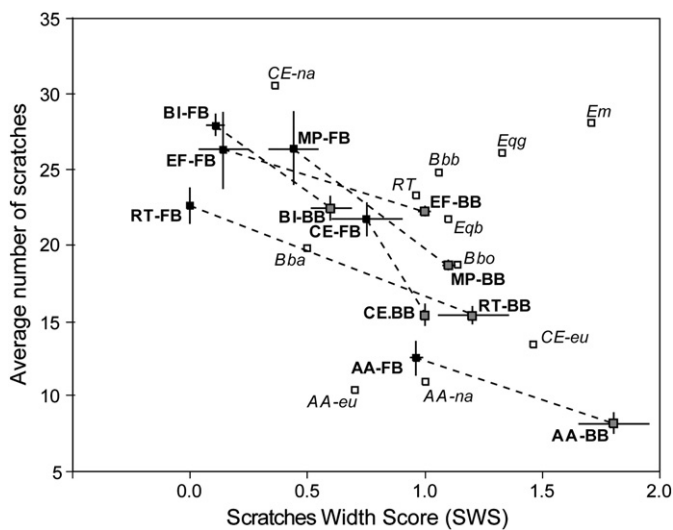
have excessively blunted cusps, indicating levels of dietary abrasion that are similar to or exceed those of species known to be grazing specialists, such as *Equus* and *Bison*. It is interesting to compare our data with the analysis of stable isotopes by Fox-Dobbs et al. (2008) which also identified *Rangifer* as having a different isotopic signature than *Equus*, *Bison* and *Mammuthus*. This study (Fox-Dobbs et al., 2008) interpreted the diet of *Rangifer* in terms of the consumption of mostly tundra plants including lichen and mosses, whereas *Equus*, *Bison*, and *Mammuthus* were portrayed as most likely focusing primarily upon grasses, sedges, and herbaceous plants. Consequently, feeding on tundra plants near the ground with a concomitant ingestion of soil particles or the ingestion of a very coarse browse (i.e., *Equisetum*) may explain the high abrasive mesowear pattern observed for the cervids at FB (which have an extreme and abrasive mesowear pattern) rather than feeding on grasses which is more likely for *Equus* and *Bison*.

5.2. Interpretation of the diets of steppe ungulates via dental wear

We did find significant statistical differences in the dental wear patterns for each taxa at both FB and BB, suggesting the dental wear
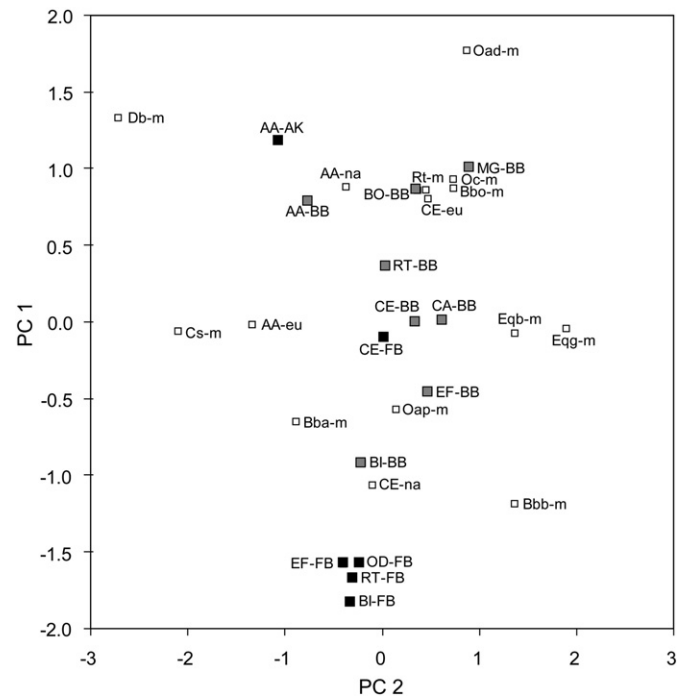

Fig. 5. Average number of scratches vs. scratches width scores (SWSs) for Fairbanks (FB), Alaska (black squares) and Brown Bank (BB), North Sea (grey squares) compared to their modern relatives (white squares). Abbreviations: eu: Europe; na: North America; Bbi: *Bison bison athabascae*; Bbi: *Bison bison bison*; Bbo: *Bison bonasus*; Eqb: *Equus burchelli*; and Eqg: *Equus grevyi*. Error bars = standard error of the mean. Dashed lines connect pairs of species from the two localities.

Fig. 6. PCA on mesowear scores (MWSs) and the six microwear variables for Fairbanks, Alaska (black squares) and Brown Bank, North Sea (grey squares) compared to their modern relatives (white squares). Proboscideans were excluded because lacking mesowear data. Abbreviations: eu: Europe; na: North America; Bbi: *Bison bison athabascae*; Bbi: *Bison bison bison*; Bbo: *Bison bonasus*; Cs: *Ceratotherium simum*; Db: *Diceros bicornis*; Eqb: *Equus burchelli*; Eqg: *Equus grevyi*; Oad: *Ovis ammon dalli*; Oap: *Ovis ammon poli*; and Oc: *Ovis canadensis*.

patterns are not homogeneous within these two areas and that species were partitioning their diets. In order to derive ecological interpretations from the microwear data it is worth reviewing what is known of the habitats and dietary preferences of these species and then to compare them to the microwear and mesowear data. *Equus* and *Bison* are known to be grazing specialists, based on their morpho-physiological adaptations, recent habitats, and apparent dietary preferences (Meagher, 1986; Eisenmann, 1998; Nowak, 1999; Cannon; 2001). However, both exhibit some degree of dietary plasticity that allows them to incorporate various quantities of browse in their diets, particularly during colder seasons, when grass is in shorter supply. Some modern *Bison* forage on forbs and woody browse although they generally prefer low-growth grasses in open habitats (Meagher, 1986; Guthrie, 1990). *Bison* introduced into Alaska in the 1930s eat predominantly grass although some populations seasonally consume 50%–75% browse (Waggoner and Hinkes, 1986; Guthrie, 1990). Rivals et al. (2007b) previously examined the microwear and mesowear patterns of late Pleistocene *Bison* from several regions of North America and found dental wear patterns that are roughly consistent with primarily grazing, but with degrees of dietary abrasion much lower than recent *Bison* on the Great Plains of North America, suggestive of mixed feeding.

The microwear of the BB *Bison* sample is consistent with a primarily grazing diet (or perhaps grass-dominated mixed feeding), with a degree of dietary abrasion lower than North American plains *Bison* and more similar to the European *Bison* (*Bison bonasus*). The European *Bison* is primarily a grazer, but will browse if that resource is available (Borowski et al., 1967; Borowski and Kossak, 1972; Pucek, 2004) which supports the diet observed for the European fossil *Bison* at BB. In contrast, the fossil *Bison* from FB have somewhat rounder cusps and abnormally fine scratches in comparison to modern grazers and other fossil *Bison* samples (Rivals et al., 2007b). This microwear pattern suggests a finer and less abrasive diet, and although we find it difficult to interpret this wear pattern (see below), histological examination of plant fragments trapped in the infundibulum of *Bison* teeth of FB fossil bison suggest a grass-dominated mixed-feeding diet, 80% composed of graminoids; the remaining 20% are dicot forbs, woody plants, and cryptogams (Guthrie, 1990).

Wild horses and zebras prefer grass, but are known to broaden their diet to include many species of forbs and woody browse (including roots) when grass is scarce (Grubb, 1981; Houpt, 2006; St-Louis and Côté, 2009). Free-ranging horses have been observed to consume up to 50% browse during seasons when grasses are in short supply (Putman, 1996). The dental wear patters of the BB *Equus* sample are consistent with a predominantly grazing or grass-dominated mixed-feeding diet similar to that observed in modern *Equus*. The blunted cusps of the FB *Equus* sample suggest a highly abrasive diet, like modern *Equus*. However, like *Bison*, the microwear of the FB *Equus* sample is characterized by exceedingly fine narrow scratches that are not common among modern grazing specialists. At FB, the horse, with large confidence ellipse, has a microwear more variable than the other species at the same area (Fig. 3). However, this is because two specimens have very low scratches numbers that fall in the browsing range. The others have a microwear signal typical of regular grazers or hyper-grazers. Was the horse more opportunist than the others ungulates and was feeding on any kind of vegetation available? That could be related to high competition with other species for vegetal resources. It is also possible that some specimens, in particular the two browsing specimens, are from Holocene age (as the *Alces*) and would feed on more browse than during the Late Pleistocene.

Although *Mammuthus* is extinct, stomach contents of mummies (Guthrie, 1990; van Geel et al., 2008) of *Mammuthus primigenius* and other studies of dental microwear and stable carbon isotopes suggest a grass-dominated diet for *Mammuthus*, but with small amounts of browsing (Olivier, 1982; Vereschagin and Baryshnikov, 1982; Mead et al., 1986; Bocherens et al., 1996; Koch et al., 1998; Bocherens,

2003). *Mammuthus* from BB has as relatively high frequency of coarse scratches, a microwear pattern that resembles many extant grazers, although the density of scratches appears to be rather low, suggesting the possibility of a more mixed-feeding diet for *Mammuthus* in this particular region. Again, at FB, fine scratches are unusually abundant, coarse scratches are relatively uncommon and atypical for modern grazers.

Compared to FB, the BB fauna is the more diverse and likely includes taxa that were grazing specialists. These include both *Coelodonta* and *Bos*. Less is known of the paleoecology of *Coelodonta*, although the hypsodont and complex nature of its cheekteeth suggest a grazing preference. Stomach contents and plant remains pulled from the infundibula of molars suggest a diet largely composed of grass (Guthrie, 1990). In comparison to extant African rhinos, the mesowear of the BB *Coelodonta* sample suggest a high abrasion diet, similar to the grazing white rhino. However, in the microwear plots, *Coelodonta* appears to plot closer to the browsers, suggesting a more mixed diet.

Species of *Bos* show preferences for grass and consume lesser amounts of other plants (Leslie and Schaller, 2009). The cusps or BB *Bos* are less blunt than *Bison* from the same region, and microwear scratches are less frequent, strongly suggesting a less abrasive mixed feeding, possibly even browse-dominated, diet. Both mesowear and microwear point out more browsing for the extinct *Bos primigenius* than its modern relatives. Using mesowear, Holocene populations of extinct *Bos* from Scandinavia were found to be grazers or mixed feeders indicating an ecological plasticity for that species (Schulz and Kaiser, 2007).

Ovis dalli and *Ovis canadensis*, the two extant North American sheep species, are mixed feeders or grass-dominated mixed feeders. They mainly select grass, use forbs when available, and shrubs can be seasonally important (Kasworm et al., 1984; Shackleton, 1985; Bowyer and Leslie, 1992). The fossil species, *O. dalli*, from FB is found to be probably a grazer. However the sample is small and the population sampled may reflect a seasonal diet, when *Ovis* was grazing in the area.

Despite their brachydont dentitions, cervids adopt a diverse variety of diets spanning the browser-grazer continuum although they lack the extreme grazing adaptations seen in *Equus* and *Bison* (Geist, 1998). *Alces* is a dedicated woody browser that favors highly nutritious low-toxin foliage and browse including submerged plants (Franzmann, 1981; Geist, 1998). Microwear and mesowear of *Alces* from both the FB and BB areas are consistent with a strictly non-abrasive browsing diet. The dental wear of *Alces* is very different from the remainder of the cervids in these two faunas. *Alces* from FB was also found to have a different diet based on the analysis of stable isotopes. Bocherens (2003) reported lower δ^{15}N values which are consistent with a diet of leaves identified by microwear for the moose from the FB area. The discrepancy in microwear results between *Alces* and the other ungulates studied here may possibly be explained by the fact that at the two areas, *Alces* is not contemporaneous with the other ungulates and existed during a time when these areas more readily supported browsing specialists.

Rangifer tarandus is a mixed feeder with highly variable diets with preferences for forbs, shrubs, and lichens (White and Trudell, 1980; Geist, 1998; Ihl and Klein, 2001; Bjørkvoll et al., 2009). The mesowear of the BB sample suggests a higher abrasion diet than our modern sample although the microwear suggests a mixed diet. The microwear of the FB sample seems to suggest a grass-dominated diet, although like many of the other FB taxa, it also has unusually fine scratches, complicating dietary interpretation. Additionally, the mesowear of FB *Rangifer* is extreme, suggesting a very highly abrasive diet, similar to *Equus* and modern North American Plains *Bison*. However, such highly abrasive diet in *Rangifer* is different from that of *Equus* or *Bison*, and might be related to the ingestion of soil particles when feeding on tundra plants or coarse plants such as *Equisetum*, rather than feeding on grass.

Cervus elaphus is a browse-dominated mixed feeder that favors forbs, foliage, and browse, while grasses make up a lesser part of its diet (Geist, 1998; Gebert and Verheyden-Tixier, 2001). The microwear and mesowear of the BB *Cervus* sample are consistent with a mixed-feeding diet. The FB *Cervus* sample is less unusual than the other fauna from this area because wide coarse scratches are more frequent. However, the mesowear is unusual, with exceedingly blunt cusps, similar to hypergrazing taxa such as *Equus*.

Megaloceros only occurs at BB. Based on numerous lines of evidence, Geist (1998) suggests that *Megaloceros* was primarily a concentrate selector, perhaps similar to *Cervus*, feeding on foliage and browse, although aspects of its dental morphology suggest some grazing. Mesowear and microwear of this taxon from BB are consistent with this interpretation, suggesting a browsing or browse-dominated type of mixed-feeding diet.

5.3. Explaining dental wear patterns of the Mammoth Steppe

At the two regions, *Alces* is probably not a contemporaneous member of the Mammoth Steppe fauna, thus it will not be considered below.

5.3.1. Brown Bank

The BB assemblage is older than FB, it was dated around 45 to 34 kyr BP (Mol et al., 2006). With the exception of *Alces*, the ungulate faunas from both regions appear to have been a mixture of mixed feeders and grazers, with little evidence of highly concentrated browsing diets. However, the dental wear patterns at BB are more readily interpreted than those of FB. Plots of pit versus scratch counts suggest a greater ecological diversity at BB. Moreover, the dental wear patterns are more or less consistent with niche partitioning expectations. For instance, many of the hypsodont grazing specialists such as *Bison*, *Equus*, and *Mammuthus* have dental wear patterns that are considerably more grazing-like than the cervids of this fauna. The cervids all have cusps of intermediate sharpness and microwear patterns indicative of mixed feeding. Grazing specialists have microwear and mesowear patterns that are indicative of a more abrasive grazing diet.

Both *Equus* and *Coelodonta* have the bluntest cusps in the BB fauna, suggesting a highly abrasive diet. Both *Equus* and *Coelodonta* are perissodactyls and, consequently, they are hindgut fermenters. They are metabolically suited to a less selective diet, consuming higher quantities of the toughest, most abundant, and most accessible plants or plant parts, whereas ruminants, such as *Bison*, must feed more selectively on plants or plant parts with higher protein content (Stevens and Hume, 1995). The more hyper-abrasive nature of the diets of *Equus* and *Coelodonta* are likely to be a consequence of less selective feeding strategies. The mesowear suggests that *Bison* and other ruminants may have selectively grazed on less abrasive plants or plant parts. For instance, in the African savanna, zebra consume the tougher upper strata of the foraging layer, while other ruminants feed from lower to the ground vegetation (strata). Mesowear was actually found to mirror the grazing succession of the African savanna, where zebras have the bluntest cusps, large ruminants have considerably rounder cusps, and the smallest most selective ruminant have the sharpest cusps (Fortelius and Solounias, 2000). The fact that the two hindgut fermenters of the BB fauna show more blunted mesowear in comparison to the ruminants suggest a similar type of grazing succession at BB.

Unlike mesowear, the microwear data of the BB fauna does separate the hindgut fermenters from the ruminants. However, microwear reflects diet on a much shorter time scale (weeks, days, or hours) while mesowear, due to its gross nature, reflects diet over longer intervals of time (months to years). Therefore, while mesowear represents something closer to an annual average, microwear represents diet near the time of death. In highly seasonal environments, two factors will contribute to mesowear–microwear disagreement. (1) Diets are likely to fluctuate seasonally in terms of both type of food available and amount of food available. Microwear is more sensitive to such short-term fluctuations than mesowear. (2) Natural deaths are most concentrated in the harshest season (winter) (Post and Stenseth, 1998; Uno et al., 1998; Forchhammer et al., 1998; Forchhammer et al., 2002). Therefore, microwear will more strongly represent winter diet, where as mesowear will represent something closer to an annual average. Despite having very different mesowear, *Bison* and *Equus* have very similar microwear patterns, suggesting that their diets have converged in times of food shortage, when grass was more limited and diets were less selective overall.

There are other noteworthy discrepancies between the mesowear and microwear data from BB. For instance, the dental wear patterns of *Bos primigenius* from BB appear to be more indicative of mixed feeding, though *Bos* is generally known to be a grazing specialist. *Coelodonta* mesowear is extremely blunt, suggesting a grazing diet, although its microwear is more suggestive of browsing or mixed feeding. It is entirely possible that the inconsistencies between the mesowear and microwear of *Coelodonta* are a consequence of seasonal dietary fluctuation. When grass is seasonally available, animals that otherwise prefer grass, such as horses and bison, are known to utilize woody browse during times of shortage, particularly in the colder months. If deaths are seasonally concentrated, typically during the colder months, it is likely that the microwear will more strongly reflect a browsing or mixed-feeding type of diet, whereas mesowear will suggest a greater concentration of grass. The very blunt mesowear observed in *Coelodonta* molars suggest levels of dietary abrasion indicative of primarily grazing while the microwear suggest the use of more browse. This discrepancy suggests one or more of the following possibilities: (1) that *Coelodonta* deaths were more highly seasonal than other species, (2) that *Coelodonta* was more sensitive to seasonal fluctuations in food availability, (3) or that *Coelodonta* occupied the region during time(s) when grass availability was more seasonally limited.

5.3.2. Fairbanks

The dental wear patterns of the FB fauna are more perplexing and difficult to interpret. In a plot of scratch and pit frequency, the microwear of the FB fauna, with the exception of *Alces*, is more homogenous than the BB microwear data. Generally, the pits and scratch frequencies of the FB ungulates overlap with modern grazers in terms of scratch and pit density. Stable isotopes results on the Fairbanks ungulates (Fox-Dobbs et al., 2008) suggest the existence of dietary niche overlap among some herbivores, like *Equus* and *Bison*. Based on the frequency of scratches and pits, it is probable that these species were either grazers or grass-dominated mixed feeders. However, other aspects of the microwear and mesowear data are perplexing, rendering dietary interpretation difficult. The majority of the FB ungulates have a much higher frequency of finer scratches, an aspect of the microwear that is unusual. The microwear patterns of the majority of modern grazers are characterized by coarser scratches or a more heterogeneous mixture of coarse and fine scratches that are probably caused by a combination of contributing factors, including a high concentration of plant phytoliths and/or soil, sand, dust, and other incidental particles that are ingested when feeding low to the ground. Browsers, on the other hand, experience fewer and finer scratches either due to the less abrasive nature of the plant parts they consume and/or the higher cleaner feeding conditions. The combination of a high frequency of fine scratches and very few coarse scratches appears to be rare among extant ungulates (see data in Solounias and Semprebon, 2002) but is the pervasive pattern at FB. Extant grazers and mixed feeders with mostly fine scratches and high scratch frequencies include *Tetracerus quadricornis* (four-horned antilope), *Cervus canadensis* (wapiti), *Capricornis sumatrensis* (serow), and *Llama glama* (llama). These species inhabit forest, forest edges, and/or mountainous environments (Harper et al., 1967;

Schaller, 1977; Nowak, 1999; Krishna et al., 2009), although we are not certain if it is some shared characteristics of these habitats that produce the microwear similarities or if some other shared aspect of the dietary preferences of this species is the cause. The microwear suggests that the majority of the species, with the possible exception of *Cervus*, which has a somewhat higher frequency of coarse scratches, adopted a fairly homogenous diet containing a high concentration of an unknown fine-grained abrasive.

The finer, more homogenous nature of the microwear scratches in the majority of the FB fauna seem to suggest cleaner feeding conditions and reduced consumption of soil or dust. However the mesowear patterns found at FB strongly contradict this interpretation and suggest that the diets of most of these species were actually much more abrasive. Unlike BB, the mesowear patterns at FB are not consistent with niche partitioning expectations where hypergrazing specialists, such as *Equus* and *Bison* would be expected to have blunter cusps than mixed-feeding cervids. The most unusual mesowear patterns are the excessively blunt mesowear patterns of the two cervids, *Rangifer* and *Cervus*. *Rangifer* cusps are actually blunter than *Equus*. *Cervus* mesowear is similar to that of *Equus*, but other ruminants, *Bison* and *Ovis*, have more intermediate mesowear values. The FB mesowear seems to show a greater degree of dietary diversity, at least in terms of abrasion, than the microwear, which is fairly homogenous. The mesowear, being a more long-term dietary average, may reveal overall roughly annual differences in the average diets of these species. On the other hand, the microwear, which is relatively homogeneous, suggests that diet was more homogenous during the winter, and that animals may have less selectivity during this season, probably due to greater food limitations. Even if seasonal fluctuation in dietary selectivity explains the comparatively homogeneous nature of the microwear in comparison to the mesowear, the mesowear itself, is very difficult to explain. As noted above, the dental wear patterns of this fauna are inconsistent with niche partitioning expectations. There is apparently no relationship of the dental wear with the apparent adaptation of these species or the different digestive physiologies of horses and ruminants. Mesowear values for *Equus* and *Bison* from FB are not much different from the BB sample or modern samples. However, the excessively blunted cusps of the two cervids, *Rangifer* and *Cervus* are at odds with their ruminant physiology, dental morphology, and feeding patterns of modern populations; they are expected to have less abrasive diets than *Bison* or *Equus*. However, if stable isotopes data are considered (Fox-Dobbs et al., 2008), the dental wear data for *Rangifer* are consistent with feeding on tundra plant (which may include high quantities of dirt and grit) or coarse vegetation.

In a graphic sense (Fig. 2), based on the mesowear, the dietary ecology of the FB ecosystem appears to be nearly inverted, with suspected brachydont mixed-feeding specialists having coarser, more abrasive diets than the grazing specialists. However, the causes of these dental wear patterns are uncertain, but because the microwear of the FB fauna is nearly homogeneous, the extremely blunt mesowear is likely due to some aspect of diet that did not necessarily occur during the winter-kill season because it does not appear to be recorded by the microwear. The hyper-abrasive nature of their mesowear is not necessarily indicative of extreme grazing, and we find it unlikely that these cervids would have adopted coarser more unselective grazing diets than either *Equus* or *Bison*, nor do we believe that a high rate of soil or dust ingestion would have been the cause, because that would also have affected the mesowear of the other taxa to an equal degree. A variety of other possible explanations exists. For instance, competition may have forced these two cervids to feed on very low-quality browse. For instance, Takahashi et al. (1999) reported that dental wear rates increased in a population *Cervus nippon* (sika deer) as the population overexploited grasses and began feeding on greater quantities of low-quality browse. Interestingly, some herbs are known to have very high amounts of phytoliths, such

as the horsetail (*Equisetum*). It contains the highest amount of silica of all known herbs (Bonnett, 1972) and was very common in the Pleistocene in Alaska and the North Sea habitats (Guthrie, 1968b; Muhs et al., 2001; Oswald et al., 2003; Matheus et al., 2003; Mol et al., 2006). Modern cervids, like *Rangifer* for example (Veiberg et al., 2007), are reported to use such plants in their diet. Such plants are known in the environment at both regions and could be part of the resources used by the cervids. If there was competition for food and habitat among the herbivores, it would result in resource partitioning where cervids may have been forced to feed on large amounts of those very abrasive plants. While we do not fully understand the cause of the excessively worn cervid dentitions at FB, it is certainly noteworthy that, among this fauna, the two species to survive the Pleistocene extinctions show the most extreme response to ecological conditions in the latest Pleistocene, whereas two species that went extinct (*Bison latifrons* and *Equus ferus*), show essentially no response to the unusual ecological conditions. Several fossil species were found to have had highly variable feeding habits, reflecting broad ecological tolerances. It is the case for the Late Pleistocene *Rangifer tarandus* in Western Europe (Rivals and Solounias, 2007), *Bison priscus* in Northern America (Rivals et al., 2007b), or *Bos primigenius* in Northern Europe (Schulz and Kaiser, 2007). Those species survived the Pleistocene–Holocene transition, and *Rangifer* is still present today. Species with broad ecological tolerances will not be as prone to extinction as species with narrow requirements (Maurer, 1999; Alroy, 1999).

5.3.3. Regional effects on microwear

Dental wear patterns are biased pictures of food availability filtered through the differential selective preferences of species. In that sense, they tell us both about the environment and the selective preferences of species. Miscellaneous non-dietary factors, such unavoidable ingestion of dust or pathological teeth grinding (e.g. cribbing in horses) are contributing factors that are also ecologically relevant. However, teasing apart the influence of animal and environment is not easy, though in this case, regional effects are separable from species' effects to some extent. Significant differences were found between the species within each fauna. Assuming that these species were contemporaneous (which is questionable in the case of *Alces*), these intrafaunal dental wear differences within both the FB and BB faunas are a strong indicator that some aspects of dental wear are influenced by species-specific behaviors, even if we are uncertain, as is the case with FB, what behaviors or diets those specific wear patterns represent. However, comparisons of the shared taxa between the two regions suggest that some of the variation in the data, particularly microwear, appears to be strongly related to localized environmental influences, regardless of species-specific preferences or behaviors. Microwear scratches appear to be more sensitive to regional environment than pits. There is not a consistent difference in the density of size of pits among species shared between these regions. On the other hand, the frequency and width of scratches has a clear and consistent regional effect. For taxa common to both regions, including *Alces*, the FB sample has an increased number of scratches and much lower frequency of wide coarsely textured scratches. This effect is clearly regional in nature and not temporal, because *Alces* shows the same effect, despite the fact that it is occurs later than the other FB ungulates and probably occurs earlier than the other BB fauna. As noted above, the microwear of the BB fauna is more consistent with that of extant grazers and mixed feeders, while the FB microwear has a distinct texture that is rare among modern extant grazers and mixed feeders.

At this point we do not understand the cause, but it appears that something about the FB region has a consistent influence on the microwear of different species, independent of their species preferences. This suggests that the effect is environmental in nature, but without further investigation we cannot say what is the cause. However, this clear and consistent regional effect on the microwear

signals of FB fossil samples suggests that microwear is a complex process, affected by both animal and environmental influences. Microwear data are most frequently used to interpret the paleodiets of species, typically by directly comparing fossil microwear data to the microwear of extant species from a variety of habitats. It is normally presumed that variations in the microwear data are a result of dietary differences and/or differences in the abrasive nature of other material. However, comparison of the FB and BB data demonstrate quite clearly that regional influences can have a highly significant impact on microwear. Simply superimposing such data over extant microwear data, or statistically analyzing raw microwear data (such as a hierarchical cluster analysis, where extant and extinct species from variable regions are included), does not give the whole picture where dietary reconstruction is concerned.

6. Conclusion

Two conclusions can be made: (1) concerning the comparative ecologies of the FB and BB faunas and ecological dynamics in Mammoth Steppe in the late Pleistocene, and secondly (2) concerning regional effects on dental wear, and their bearing on the interpretation of diet from microwear data.

(1) Dental wear patterns in the BB and FB steppe faunas offer two ecologically contrasting regions of the late Pleistocene Mammoth Steppe ecosystem. The BB region is the taxonomically and ecologically more diverse of these two faunas, with a range of dental wear patterns that are typical for a variety of mixed-feeding and grazing diets. Despite the greater diversity of extinct taxa, ecosystem dynamics are not unusual compared to modern ungulate-rich ecosystems. The dental wear of the BB fauna is consistent with a feeding succession such as that of the African savanna, where larger hindgut fermenting species adopt less abrasive diets than ruminants. Among the ruminants, cervids appear to adopt more diverse mixed-feeding diets in comparison to the more grass-dominated *Bison* diets. In contrast, despite the lower numbers of extinct taxa, the FB fauna is ecologically unusual. In general, the microwear of this FB fauna includes excessive numbers of very narrow scratches that are atypical for mixed feeders and grazers. Additionally, the mesowear suggests unusual niche dynamics, where low-crowned mixed-feeding cervids, *Rangifer* and *Cervus*, adopted diets that are similar to *Equus* in terms of abrasion and much more abrasive than the diets of either *Bison* or *Ovis*. Although we do not know specifically what aspects of diet created these unusual dental wear patterns at FB, we suggest that the anomalies may relate to unique, possibly disharmonious, ecosystem dynamics during the Pleistocene–Holocene transition. While we would have expected Pleistocene survivors to have been less dramatically affected than extinct taxa by the transitional ecological conditions of the terminal Pleistocene, we note that two surviving species, *Rangifer* and *Alces*, appear to show the strongest and most peculiar dietary response. On the contrary taxa that suffered extinction, *Bison* and *Equus*, appear to have had normal dental wear patterns and continued with their expected diet during the transition whereas *Rangifer* and *Cervus* did not. Perhaps that is why the former went extinct at the terminal Pleistocene.

(2) In addition to these findings, it was found that dental wear patterns, particularly microwear variables such as scratch frequency and scratch width are strongly influenced by environment. The microwear patterns of all species shared by these two faunas shows the identical trends of more scratches and narrower scratches at FB. The consistency of this trend among species and its very strong regional correlation suggests that this aspect of variation in the microwear data is not tied to a specific trophic habit, such as grazing or browsing. It could

reflect the nature of food items available, i.e. C_3 grasses or a different type of grasses and browse. We do not know the specific cause of this regional effect, although it might relate to different varieties or different quantities of extrinsic dust or soil particles at each locality that are involuntarily ingested by all species. Microwear data are most frequently used to interpret paleodiets, either by (1) plugging the raw data into a cluster analysis with numerous extant species, or (2) plotting raw numbers of pits and scratches over a "trophic triangle" of modern fruit browsers, woody browsers, and grazers. It is clear in our data that region-specific causes of dental wear can have substantial effects on microwear data and could lead to misinterpretation of diet. It is becoming increasingly clear that microwear is the result of a variety of dietary and non-dietary factors and interpretation of paleodiet from microwear data is not necessarily a simple process. Examination of dental microwear patterns within faunas and between faunas is necessary to understand regional non-dietary effects on microwear data, and any paleodietary interpretations made of fossil species much consider the possibility of such effects.

References

Alroy, J., 1999. Putting North America's end–Pleistocene megafaunal extinction in context: large scale analyses of spatial patterns, extinction rates, and size distributions. In: MacPhee, R.D.E. (Ed.), Extinctions in Near Time: Causes, Contexts, and Consequences. Plenum Press, New York, pp. 105–143.

Anderson, P.M., Bartlein, P.J., Brubaker, L.B., Gajewski, K., Ritchie, J.C., 1991. Vegetation–pollen–climate relationships for arcto-boreal region of North America and Greenland. Journal of Biogeography 18, 565–582.

Bigelow, N.H., Powers, W.R., 2001. Climate, vegetation, and archaeology 14,000–9,000 cal yr B.P. in Central Alaska. Arctic Anthropology 38, 171–195.

Bjørkvoll, E., Pedersen, B., Hytteborn, H., Jonsdottir, I.S., Langvatn, R., 2009. Seasonal and interannual dietary variation during winter in female Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Arctic, Antarctic, and Alpine Research 41, 88–96.

Bocherens, H., 2003. Isotopic biogeochemistry and the paleoecology of the mammoth steppe fauna. Deinsea 9, 57–76.

Bocherens, H., Pacaud, G., Lazarev, P.A., Mariotti, A., 1996. Stable isotope abundances (^{13}C, ^{15}N) in collagen and soft tissues from Pleistocene mammals from Yakutia: implications for the palaeobiology of the mammoth steppe. Palaeogeography, Palaeoclimatology, Palaeoecology 126, 31–44.

Bonnett, O.T., 1972. Silicified Cells of Grasses: A Major Source of Plant Opal in Illinois. University of Illinois at Urbana-Champaign, Urbana.

Borowski, S., Kossak, S., 1972. The natural food preference of the European bison in seasons free of snow cover. Acta Theriologica 17, 151–169.

Borowski, S., Krasinski, Z., Milkowski, L., 1967. Food and role of the European bison in forest ecosystems. Acta Theriologica 12, 367–376.

Bowyer, R.T., Leslie, D.M., 1992. *Ovis dalli*. Mammalian Species 393, 1–7.

Buck, C.E., Bard, E., 2007. A calendar chronology for Pleistocene mammoth and horse extinction in North America based on Bayesian radiocarbon calibration. Quaternary Science Reviews 26, 2031–2035.

Cannon, K.P., 2001. What the past can provide: contribution of prehistoric bison studies to modern bison management. Great Plains Research 145–174.

Dixon, E.J., 2001. Human colonization of the Americas: timing, technology and process. Quaternary Science Reviews 20, 277–299.

Eisenmann, V., 1998. Folivores et tondeurs d'herbe : forme de la symphyse mandibulaire des équidés et des tapiridés (Perissodactyla, Mammalia). Geobios 31, 113–123.

Forchhammer, M.C., Stenseth, N.C., Post, E., Langvatn, R., 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. Proceedings of the Royal Society B 265, 341–350.

Forchhammer, M.C., Post, E., Stenseth, N.C., Boertmann, D., 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. Population Ecology 44, 113–120.

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.

Fox-Dobbs, K., Leonard, J.A., Koch, P.L., 2008. Pleistocene megafauna from eastern Beringia: Paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records Palaeogeography. Palaeoclimatology, Palaeoecology 261, 30–46.

Franzmann, A.W., 1981. *Alces alces*. Mammalian Species 154, 1–7.

Gebert, C., Verheyden-Tixier, H., 2001. Variation of diet composition in red deer (*Cervus elaphus* L.) in Europe. Mammal Review 31, 189–201.

Geist, V., 1998. Deer of the World: Their Evolution, Behavior, and Ecology. Stackpole Books, Mechanicsburg, PA.

Glimmerveen, J., Mol, D., van der Plicht, H., 2006. The Pleistocene reindeer of the North Sea — initial palaeontological data and archaeological remarks. Quaternary International 142–143, 242–246.

Godfrey, L.R., Semprebon, G.M., Jungers, W.L., Sutherland, M.R., Simons, E.L., Solounias, N., 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. Journal of Human Evolution 47, 145–169.

Grubb, P., 1981. *Equus burchelli*. Mammalian Species 157, 1–9.

Guthrie, R.D., 1968a. Paleoecology of a Late Pleistocene small mammal community from interior Alaska. Arctic 21, 223–244.

Guthrie, R.D., 1968b. Paleoecology of the large-mammal community in interior Alaska during the late Pleistocene. The American Midland Naturalist 79, 346–363.

Guthrie, R.D., 1980. Bison and man in North America. Canadian Journal of Anthropology 1, 55–73.

Guthrie, R.D., 1982. Mammals of the mammoth steppe as paleoenvironmental indicators. In: Hopkins, D.M., Matthews, J.W., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 307–326.

Guthrie, R.D., 1990. Frozen Fauna of the Mammoth Steppe. The Story of Blue Babe. The University of Chicago Press, Chicago.

Guthrie, R.D., 1995. Mammalian evolution in response to the Pleistocene–Holocene transition and the break-up of the mammoth steppe: two case studies. Acta Zoologica Cracoviensia 38, 139–154.

Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. Quaternary Science Reviews 20, 549–574.

Guthrie, R.D., 2003. Rapid body size decline in Alaskan Pleistocene horses before extinction. Nature 426, 169–171.

Guthrie, R.D., 2004. Radiocarbon evidence of mid-Holocene mammoths stranded on an Alaskan Bering Sea island. Nature 429, 746–749.

Guthrie, R.D., 2006. New carbon dates link climatic change with human colonization and Pleistocene extinctions. Nature 441, 207–209.

Harper, J.A., Ha, J.H., Bentley, W.W., Yocum, C.F., 1967. The Status and Ecology of the Roosevelt Elk in Canada. Wildlife Monographs, vol. 16. The Wildlife Society, Washington.

Hoffecker, J.F., Powers, W.R., Goebel, T., 1993. The colonization of Beringia and the peopling of the new world. Science 259, 46–53.

Hopkins, D.M., 1963. Geology of the Imuruk Lake area, Seward Peninsula, Alaska. US Geological Survey, Bulletin 1141-C.

Houpt, K.A., 2006. Mastication and feeding in the horse. In: Bels, V. (Ed.), Feeding in Domestic Vertebrates: From Structure to Behaviour. CABI, Oxfordshire, pp. 195–209.

Ihl, C., Klein, D.R., 2001. Habitat and diet selection by muskoxen and reindeer in western Alaska. Journal of Wildlife Management 65, 964–972.

Kaiser, T.M., Solounias, N., 2003. Extending the tooth mesowear method to extinct and extant equids. Geodiversitas 25, 321–345.

Kaiser, T.M., Solounias, N., Fortelius, M., Bernor, R.L., Schrenk, F., 2000. Tooth mesowear analysis on *Hippotherium primigenium* from the Vallesian Dinotheriensande (Germany) — a blind test study. Carolinea 58, 103–114.

Kasworm, W.F., Irby, L.R., Ihsle Pac, H.B., 1984. Diets of ungulates using winter ranges in Northcentral Montana. Journal of Range Management 37, 67–71.

King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. American Journal of Physical Anthropology 108, 359–373.

Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America. Part 1. Florida. Chemical Geology 152, 119–138.

Krishna, Y.C., Clyne, P.J., Krishnaswamy, J., Kumar, N.S., 2009. Distributional and ecological review of the four horned antelope, *Tetracerus quadricornis*. Mammalia 73, 1–6.

Leslie, D.M., Schaller, G.B., 2009. *Bos grunniens* and *Bos mutus* (Artiodactyla; Bovidae). Mammalian Species 836, 1–17.

Lister, A.M., Sher, A.V., 1995. Ice cores and mammoth extinction. Nature 378, 23–24.

Matheus, P., Begét, J., Mason, O., Gelvin-Reymiller, C., 2003. Late Pliocene to late Pleistocene environments preserved at the Palisades Site, central Yukon River, Alaska. Quaternary Research 60, 33–43.

Maurer, B.A., 1999. Untangling Ecological Complexity. University of Chicago Press, Chicago.

Mead, J.I., Agenbroad, L.D., Davis, O.K., Martin, P.S., 1986. Dung of *Mammuthus* in the arid Southwest, North America. Quaternary Research 25, 121–127.

Meagher, M., 1986. *Bison bison*. Mammalian Species 266, 1–8.

Mihlbachler, M.C., Solounias, N., 2006. Coevolution of tooth crown height and diet in oreodonts (Merycoidodontidae, Artiodactyla) examined with phylogenetically independent contrasts. Journal of Mammalian Evolution 13, 11–36.

Mol, D., Post, K., Reumer, J.W.F., van der Plicht, J., de Vos, J., van Geel, B., van Reenen, G., Pals, J.P., Glimmerveen, J., 2006. The Eurogeul — first report of the palaeontological, palynological and archaeological investigations of this part of the North Sea. Quaternary International 142–143, 178–185.

Muhs, D.R., Budahn, J.R., 2006. Geochemical evidence for the origin of late Quaternary loess in central Alaska. Canadian Journal of Earth Sciences 43, 323–337.

Muhs, D.R., Ager, T.A., Begét, J.E., 2001. Vegetation and paleoclimate of the last interglacial period, central Alaska. Quaternary Science Reviews 20, 41–61.

Nogués-Bravo, D., Rodríguez, J., Hortal, J., Batra, P., Araújo, M.B., 2008. Climate change, humans, and the extinction of the woolly mammoth. PLoS Biology 6, e79.

Nowak, R.M., 1999. Walker's Mammals of the World. John Hopkins University Press, Baltimore.

Olivier, R.C.D., 1982. Ecology and behavior of living elephants: bases for adaptations concerning the extinct woolly mammoths. In: Hopkins, D.M., Matthews, J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 281–290.

Oswald, W.W., Brubaker, L.B., Hu, F.S., Gavin, D.G., 2003. Pollen–vegetation calibration for tundra communities in the Arctic Foothills, northern Alaska. Journal of Ecology 91, 1022–1033.

Palombo, M.R., Filippi, M.L., Iacumin, P., Longinelli, A., Barbieri, M., Maras, A., 2005. Coupling tooth microwear and stable isotope analyses for palaeodiet reconstruction: the case study of Late Middle Pleistocene *Elephas* (*Palaeoloxodon*) *antiquus* teeth from Central Italy (Rome area). Quaternary International 126–128, 153–170.

Péwé, T.L., 1975. Quaternary geology of Alaska. U.S. Geological Survey Professional Paper 835.

Porter, L., 1988. Late Pleistocene fauna of Lost Chicken Creek, Alaska. Arctic 41, 303–313.

Post, E., Stenseth, N.C., 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. Journal of Animal Ecology 67, 537–543.

Pucek, Z., 2004. European Bison. Status Survey and Conservation Action Plan. IUCN, Gland.

Putman, R.J., 1996. Competition and Resource Partitioning in Temperate Ungulate Assemblies. Chapman & Hall, London.

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., Mihlbachler, M.C., Solounias, N., 2007a. 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., Solounias, N., Mihlbachler, M.C., 2007b. 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.

Sainsbury, C.L., 1972. Geologic Map of the Teller Quadrangle, Western Seward Peninsula, Alaska. US Geological Survey, Miscellaneous Geologic Investigations, Map I-685, Scale 1:250,000.

Schaller, G.B., 1977. Mountain Monarchs. The University of Chicago Press, Chicago.

Schulz, E., Kaiser, T.M., 2007. Feeding strategy of the Urus *Bos primigenius* Bojanus, 1827 from the Holocene of Denmark. Courier Forschungsinstitut Senckenberg 259, 155–164.

Semprebon, G.M., Rivals, F., 2007. Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to recent Antilocapridae (Mammalia: Artiodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology 253, 332–347.

Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? Journal of Human Evolution 47, 115–144.

Shackleton, D.M., 1985. *Ovis canadensis*. Mammalian Species 230, 1–9.

Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. American Museum Novitates 3366, 1–49.

Solow, A.R., Roberts, D.L., Robbirt, K.M., 2006. On the Pleistocene Extinctions of Alaskan Mammoths and Horses. Proceedings of the National Academy of Sciences 103, 7351–7353.

St-Louis, A., Côté, S.D., 2009. *Equus kiang* (Perissodactyla; Equidae). Mammalian Species 835, 1–11.

Stevens, C.E., Hume, I.D., 1995. Comparative Physiology of the Vertebrate Digestive System. Cambridge University Press, Cambridge.

Stuart, A.J., Kosintsev, P.A., Higham, T.F.G., Lister, A.M., 2004. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. Nature 431, 684–689.

Takahashi, H., Kaji, K., Koizumi, T., 1999. Molar wear rates in Sika deer during three population phases: increasing versus decline and post-decline phases. Mammal Study 24, 17–23.

Uno, H., Yokoyama, M., Takahashi, M., 1998. Winter mortality pattern of Sika deer (*Cervus nippon yesoensis*) in Akan National Park, Hokkaido. Mammalian Science 77, 233–246 in Japanese, with English abstract.

van Andel, T.H., Tzedakis, P.C., 1996. Palaeolithic lanscapes of Europe and environs, 150,000–25,000 years ago: an overview. Quaternary Science Reviews 15, 481–500.

van Geel, B., Aptroot, A., Baittinger, C., Birks, H.H., Bull, I.D., Cross, H.B., Evershed, R.P., Gravendeel, B., Kompanje, E.J.O., Kuperus, P., Mol, D., Nierop, K.G.J., Pals, J.P., Tikhonov, A.N., van Reenen, G., van Tienderen, P.H., 2008. The ecological implications of a Yakutian mammoth's last meal. Quaternary Research 69, 361–376.

van Kolfschoten, T., Laban, C., 1995. Pleistocene terrestrial mammal faunas from the North Sea. Mededelingen Rijks Geologische Dienst 52, 135–151.

Veiberg, V., Mysterud, A., Bjørkvoll, E., Langvatn, R., Loe, L.E., Irvine, R.J., Bonenfant, C., Couweleers, F., Stenseth, N.C., 2007. Evidence for a trade-off between early growth and tooth wear in Svalbard reindeer. Journal of Animal Ecology 76, 1139–1148.

Vereschagin, N.K., Baryshnikov, G.F., 1982. Paleoecology of the mammoth fauna in the Eurasian Arctic. In: Hopkins, D.M., Matthews, J.W., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 267–278.

Waggoner, V., Hinkes, M., 1986. Summer and fall browse utilization by an Alaskan bison herd. Journal of Wildlife Management 50, 322–324.

White, R.G., Trudell, J., 1980. Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Research 12, 511–529.

Wilkerson, A.S., 1932. Some frozen deposits in the goldfields of interior Alaska. A study of the Pleistocene deposits of Alaska. American Museum Novitates 525, 1–22.

Yesner, D.R., 2001. Human dispersal into interior Alaska: antecedent conditions, mode of colonization, and adaptations. Quaternary Science Reviews 20, 315–327.

Zimov, S.A., Chuprynin, V.I., Oreshko, A.P., Chapin, F.S., Reynolds, J.F., Chapin, M.C., 1995. Steppe–tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. American Naturalist 146, 765–794.