

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*

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Received 25 January 2007

Abstract

During the late Pleistocene and early Holocene, *Bison* was widely dispersed across North America and occupied most regions not covered by ice sheets. A dietary study on *Bison* paleopopulations from Alaska, New Mexico, Florida, and Texas was performed using two methods that relate dental wear patterns to diet, mesowear analysis and microwear analysis. These data were compared to a mixed sample of extant *Bison* from the North American central plains, extant wood *Bison* from Alberta (Canada) and a variety of other modern ungulates. Mesowear relates macroscopic molar facet shape to levels of dietary abrasion. The mesowear signature observed on fossil *Bison* differs significantly from the hyper-abrasive grazing diet of extant *Bison*. Tooth microwear examines wear on the surface of enamel at a microscopic scale. The microwear signal of fossil samples resembles to modern *Bison*, but the fossil samples show a greater diversity of features, suggesting that fossil *Bison* populations regularly consumed food items that are texturally inconsistent with the short-grass diet typical of modern plains *Bison*. Mesowear and microwear signals of fossil *Bison* samples most closely resemble a variety of typical mixed feeding ungulates, all with diets that are substantially less abrasive than what is typical for modern plains *Bison*. Furthermore, statistical tests suggest significant differences between the microwear signatures of the fossil samples, thus revealing geographic variability in Pleistocene *Bison* diets. This study reveals that fossils are of value in developing an understanding of the dietary breadth and ecological versatility of species that, in recent times, are rare, endangered, and occupy only a small remnant of their former ranges.

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Keywords: Paleodiet; Mesowear; Microwear; *Bison*; Pleistocene; Paleoecology

Introduction

Several species of *Bison* inhabited large parts of North America during the Wisconsinan glaciation (McDonald and Lammers, 2002). Numerous archaeological kill sites in North America suggest that *Bison* were important for Paleo-Indian subsistence strategies (Hofman and Todd, 2001; Frison, 2004). Modern *Bison* are primarily grazers (Reynolds et al., 1978). During the Pleistocene and early Holocene, *Bison* were much

more widely distributed in North America and occupied habitats ranging from semi-desert to boreal forest (McDonald, 1981). Although suitable grazing was probably available in all of these different habitats (McDonald, 1981), the more widespread prehistoric distribution of *Bison* suggests that populations exhibited a greater degree of dietary variance than that of the range restricted populations of recent times, reflecting a greater variety of occupied habitats. To explore this idea, we investigated the diet of four *Bison* populations from late Pleistocene and early Holocene localities and compared our results to a sample of modern plains *Bison* from North America and a sample of modern wood bison from Alberta (Canada), in addition to a wide variety of other extant ungulates.

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Materials and methods

Fossil samples

We studied four large samples of *Bison* in the Frick Collection at the American Museum of Natural History in New York. The samples come from (1) Fairbanks Area, Alaska, (2) Folsom Quarry, Union County, New Mexico, (3) Dalhart Sideroad Pit, Channing, Hartley County, Texas, and (4) Seminole Field Station B, Pinellas County, Florida (Fig. 1). (1) The Alaska sample of *Bison priscus* and was recovered from frozen deposits (Wilkerson, 1932) that have been radiocarbon dated to $11,990 \pm 135$ ^{14}C yr B.P. (Stephenson et al., 2001). The associated ungulates are *Rangifer tarandus*, *Alces alces*, *Cervus elaphus*, *Equus lambei*, *Ovibos moschatus*, *Ovis dalli*, and *Mammuthus primigenius* (Guthrie, 1968; Yesner, 2001). (2) The New Mexico sample is identified as *Bison antiquus*. The site includes an artifact of undoubtedly human manufacture (a Folsom fluted point) that was found in unambiguous association with the remains of *Bison* (Figgins, 1927). Radiocarbon assays on bone amino acids from different individuals in the bison sample indicated an average age of approximately 10,500 ^{14}C yr B.P. (Meltzer et al., 2002). *Odocoileus hemionus* is an additional ungulate species from this locality (Hay and Cook, 1930; McDonald, 1981). (3) The Texas sample of *Bison* sp. is labeled as late Pleistocene in the archives at the AMNH but no other data is available. (4) Finally, *Bison* sp. from Seminole Field Station B, Pinellas County, Florida, is associated with *Mammuthus columbi*, *Mammuth americanum*, *Tapirus veroensis*, *Equus complicatus*, *Equus leidyi*, *Platygonus compressus*, *Mylohyus fossilis*, *Hemiauchenia macrocephala*, *Paleolama mir-*

ifica, and *Odocoileus virginianus* indicating a Rancholabrean land mammal age (Webb, 1974) (~160–10 ka).

Dietary analysis

We used two methods, dental mesowear and dental micro-wear, to analyze paleodiet. Both methods are found to be relatively insensitive to interobserver error and relatively small samples of approximately 8 are sufficient for making at least generalized inferences about the diet of a particular fossil sample (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Semprebon et al., 2004a; Kaiser et al., 2000). Even with small sample sizes, these methods can significantly discriminate between browsing and grazing diets in a wide variety of species including both ungulates (Fortelius and Solounias, 2000) and primates (Semprebon et al., 2004a). For ungulates, as a matter of convention, species whose diets are less than 10% grass are classified as browsers; species whose diets are more than 90% grass are grazers, and species who consume a more balanced mixture of browse and graze are considered mixed feeders.

A more detailed description of the mesowear method is provided by Fortelius and Solounias (2000) and further discussion of its application towards extinct species are exemplified by Kaiser et al. (2000), Kaiser and Solounias (2003), Kaiser and Fortelius (2003), Franz-Odenaal and Kaiser (2003), Semprebon et al. (2004b), and Mihlbachler and Solounias (2006). Mesowear is based on physical properties of ungulate foods as reflected in the relative amounts of attritive (tooth-on-tooth) wear and abrasive (food-on-tooth) wear on the dental enamel of the occlusal surfaces (Fortelius and Solounias,

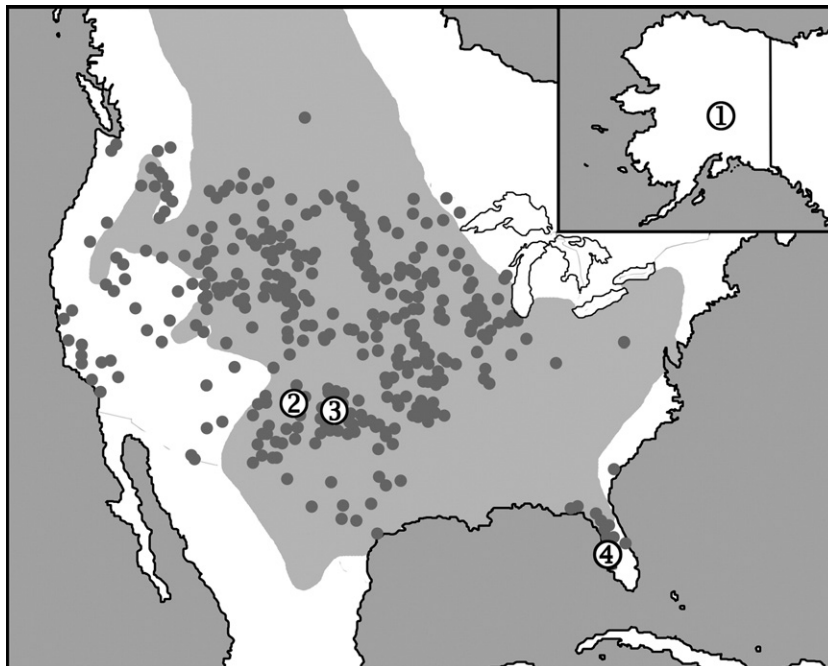


Figure 1. Pleistocene localities with *Bison* in United States (dots). The dark grey area represents a possible modern distribution. Data and map after FAUNMAP Working Group (1994), modified. Localization of the studied sites: (1) Fairbanks area, Alaska; (2) Folsom Quarry, New Mexico; (3) Dalhart Sideroad Pit, Texas; (4) Seminole Field Station B, Florida.

2000). Essentially, low abrasion diets, such as those of browsers, result in the maintenance of precise occlusion between the upper and lower teeth because dental wear is primarily attritional (tooth-on-tooth), thus generating an attritional or honing (sharpening) relationship between the upper and lower cusps. In contrast, abrasion-dominated (food-on-tooth) wear, associated with grazing diets, results in more rounded and blunted wear facets and less precise occlusion. Mesowear was scored on the paracone of the M2 for the *Bison* samples. Obviously, unworn (and marginally worn) teeth, extremely worn teeth (where the crown has worn nearly to or below the dentinoenamel junction), and those with broken or damaged cusp apices are omitted from mesowear analysis (Rivals et al., 2007). Resulting sample sizes for the fossil *Bison* samples are as follows: Alaska ($N=251$), New Mexico ($N=16$), Arizona ($N=15$), Florida ($N=14$).

In the original formulation of the method, mesowear was recorded macroscopically by characterizing the buccal apices of molar cusps as sharp, rounded or blunt, and the valleys between the cusps as high or low (Fortelius and Solounias, 2000). We converted the original data of Fortelius and Solounias (2000) on extant ungulates and the data on fossil bison 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). Intermediate stages of mesowear consisting of more rounded cusp apices with higher and lower levels of cusp relief were assigned 1 and 2, respectively. To summarize mesowear data for a large number of species (Fig. 2), the average score for a particular sample or species is represented as a single data-point.

The microwear analysis was performed following methods described by Solounias and Semperebon (2002) and Semperebon et al. (2004a). Further discussion of this methodology and its application toward dietary reconstruction can also be found in Godfrey et al. (2004), Merceron et al. (2004), Palombo et al. (2005). Microwear features were identified and quantified on

high resolution epoxy tooth casts at $35\times$ magnification using an Olympus SZH10 stereomicroscope. Most microwear features can be categorized as pits and scratches of various sizes and textures. Pits are circular or subcircular microwear scars. Small pits are relatively shallow, refract light easily, and appear bright and shiny. Large pits are deeper, wider, and less refractive. They are generally twice the diameter of small pits, or larger. Scratches are elongated microfeatures with straight, parallel sides and can be subcategorized as fine or coarse. Scratch texture is evaluated on the basis of general appearance and light refractive properties. Fine scratches are narrow and barely etched into the enamel surfaces. Coarse scratches are wider and more obviously etched into the enamel surface. Cross scratches are oriented somewhat perpendicularly to the majority of scratches observed on dental enamel (Solounias and Semperebon, 2002). Small pits and scratches tend to be the most common microwear features. To approximate their frequency, they are counted in a standard 0.4×0.4 mm square area on the lingual (inner) band of enamel on the paracone of the upper second molar. Specimens were further categorized by the texture of the scratches (0=fine scratches only; 1=mixture of fine and coarse, 2=only coarse scratches). Large pits are recorded qualitatively as being present or absent on the wear surface of the tooth.

Results

Mesowear

The mesowear scores of a large number of modern ungulate species from data in Fortelius and Solounias (2000) are shown in Figure 2. There are clear trends in the mesowear data related to diet. Leaf browsers have the lowest mesowear scores, grazers have higher mesowear scores, while mixed feeders and fruit browsers have intermediate scores that overlap the ranges of browsers and grazers. Much of the overlap in the mesowear data for these dietary categories is attributable to the fact that abrasion levels in diets are not only related to the intrinsic properties of the plants themselves, but also variable amounts of extrinsic grit (dust and sand) that is incidentally consumed along with the plants (Williams and Kay, 2001; Muhlbacher and Solounias, 2006).

The predominant mesowear pattern among all of the fossil *Bison* samples is high cusp relief and rounded cusp apices (Table 1). More than 90% of the specimens from the Alaska, Texas, and Florida samples have both high cusp relief and rounded apices with overall mesowear scores (MS) ranging from 1.05–1.10 (Table 1). These mesowear scores are on the low end for grazers and overlap with the upper extremes for mixed feeders and fruit browsers. The mesowear of modern plains *Bison* differs dramatically. The vast majority of the cusps are completely worn flat, giving an overall MS of 2.73, the highest for any ungulate for which there is mesowear data, indicating extreme levels of dietary abrasion. The mesowear of modern wood *Bison* is very similar to the mesowear signal observed for the fossil samples. With an overall MS of 1.00, it is the lowest score recorded for modern grazing species.

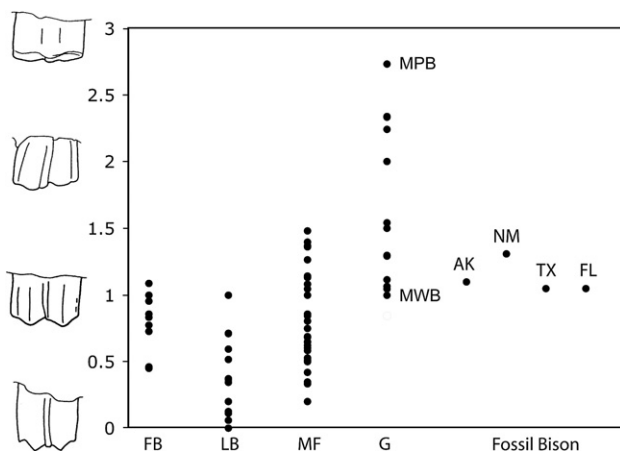


Figure 2. Mesowear scores for the fossil *Bison* samples compared to modern plains *Bison* (MPB) and other modern ungulates (black dots) (data transformed into mesowear scores from Fortelius and Solounias, 2000). Abbreviations: FB=fruit browsers, LB=leaf browsers, MF=mixed feeders, G=Grazers, AK=Alaska *Bison*, TX=Texas *Bison*, NM=New Mexico *Bison*, FL=Florida *Bison*, MPB=modern plains bison, MWB=modern wood bison.

Table 1
Summary statistics of the mesowear data

| Locality | N | Mesowear stage frequencies | | | | Mesowear score |
|---|-----|----------------------------|-----|----|----|----------------|
| | | 0 | 1 | 2 | 3 | |
| Fairbanks Area, Alaska | 251 | 9 | 215 | 21 | 6 | 1.10 |
| Folsom Quarry, New Mexico | 16 | 1 | 9 | 6 | 0 | 1.31 |
| Dalhart Sideroad Pit, Texas | 15 | 0 | 14 | 1 | 0 | 1.05 |
| Seminole Field Station B, Florida | 14 | 0 | 13 | 1 | 0 | 1.05 |
| Modern plains bison (<i>Fortelius</i> and <i>Solounias</i> , 2000) | 15 | 0 | 0 | 4 | 11 | 2.73 |
| Modern wood bison | 11 | 3 | 7 | 1 | 0 | 1.00 |

Microwear

Microwear patterns observed for the fossil samples are shown on Figure 3. The average numbers of pits and scratches found in the 0.4 × 0.4 mm² sampling area for fossil and modern *Bison* are plotted in Figure 4, along with average values for a number of extant browsing, fruit browsing, grazing, and mixed feeding species using data from Solounias and Semprebon (2002). Some taxa, such as camels (the two highest points on the plot), have atypical wear patterns for browsers, but for the most part microwear data forms a sort of trophic triangle. Grazers have the highest numbers of scratches and the lowest number of pits, typical leaf browsers have lower numbers of scratches and more disparate numbers of pits, while fruit-

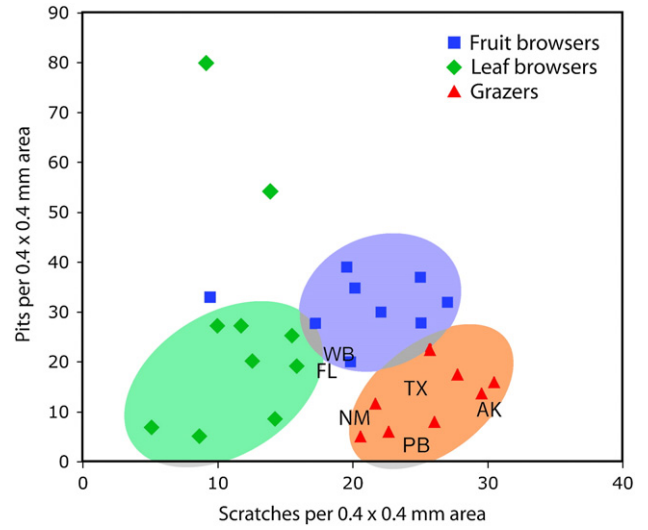


Figure 4. Bivariate plot for average numbers pits and scratches for extant fruit browsers, leaf browsers, and grazers (from Solounias and Semprebon, 2002), modern plains bison (PB), modern wood bison (WB), and the Pleistocene *Bison* samples (AK=Alaska, TX=Texas, NM=New Mexico, FL=Florida). Ellipses correspond to the 95% confidence. MB=modern plains bison, WB=modern wood bison.

dominated browsers tend to have intermediate numbers of scratches and pits. The average values for mixed feeders (not shown in Fig. 4) extensively overlap the grazer, and to a lesser

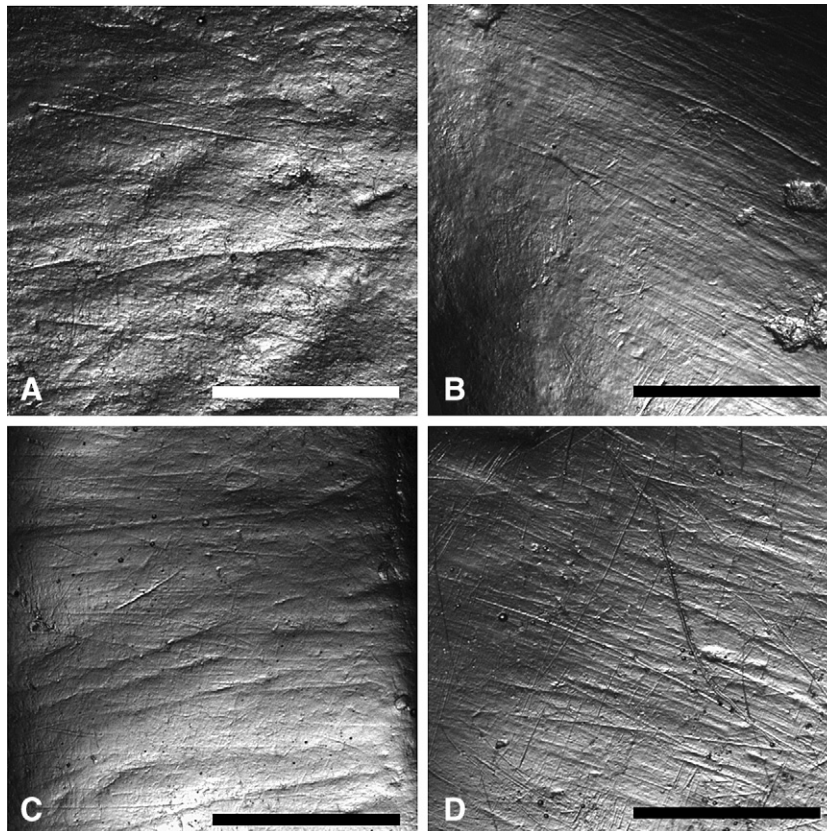


Figure 3. Microwear pictures at 35× for the fossil *Bison* from Florida (A), Texas (B), New Mexico (C), and Alaska (D). Specimen numbers: (A) AMNH 23579 C, (B) AMNH 25749 A, (C) AMNH 131564, and (D) AMNH 4003489. Scale bar=0.4 mm.

extent, the browser area. The microwear patterns in all of the *Bison* samples are characterized by high densities of scratches and low densities of pits (Table 2).

Three of the fossil samples (NM, TX, and AK) plotted with modern *Bison* in the grazer area. The Florida sample, on the other hand, was somewhat unusual and plotted nearer to the browsers. Using an analysis of variance (ANOVA), highly significant differences among the average numbers of pits and scratches of the four samples were found (one-way ANOVA, $p < 0.0001$). Despite statistically significant differences, the sheer number of pits and scratches are not all that different from modern wood and plains bison (Fig. 5). Samples from Alaska, Texas, and New Mexico plot close to the modern plains bison, while the sample from Florida has a microwear pattern similar to the wood bison. Moreover other aspects of the microwear data suggest more dietary variability. The modern *Bison* specimens mostly show a mixture of fine and coarse scratches, while the scratches on the Alaska specimens are generally much finer. On the other hand, the Texas and Florida samples show very few cross scratches, in contrast to the modern sample. The New Mexico sample most closely resembles the modern sample with both relatively coarse scratches and a high frequency of cross scratches. The significance of these microwear differences is further considered in the following section.

Multivariate analysis

The microwear and mesowear analyses give similar results concerning the overall diet of the fossil *Bison* samples, with signals that are consistent with either grazing or perhaps grass-dominated mixed feeding. However, the mesowear and microwear analyses offer different pictures regarding how the diets of fossil *Bison* compare to modern *Bison*. However, the disparity in these results does not mean that either of these methods is flawed. Microwear and mesowear offer clues to diet on very different time scales. Mesowear requires a substantial amount of dental wear to form. Mesowear reflects the cumulative effect of diet, thus having an ecologically significant signal (Fortelius and Solounias, 2000). Microwear, however, is the result of single occlusal events and can change with the mastication of every food item. Thus, microwear reflects diet on a time frame of days or hours before the death of the animal. In conclusion, mesowear and microwear can give somewhat different signals.

Table 2
Summary statistics of the microwear data

| Locality | N | #P | SD | #S | SD | %LP | STS | %CS |
|---|----|------|-----|------|-----|-------|------|-----|
| Fairbanks Area, Alaska | 27 | 11.4 | 2.9 | 27.9 | 4.0 | 7.41 | 0.11 | 100 |
| Folsom Quarry, New Mexico | 12 | 10.8 | 1.7 | 20.1 | 2.3 | 41.67 | 0.83 | 100 |
| Dalhart Sideroad Pit, Texas | 14 | 16.9 | 2.2 | 25.3 | 3.1 | 57.14 | 1 | 7 |
| Seminole Field Station B, Florida | 13 | 20.0 | 2.5 | 17.5 | 1.8 | 21.43 | 1 | 15 |
| Modern plains bison (Solounias and Semprebon, 2002) | 18 | 3.5 | 1.3 | 24.8 | 5.7 | 38.89 | 1.06 | 94 |
| Modern wood bison | 8 | 21.3 | 3.9 | 24.8 | 2.8 | 0 | 0.50 | 0 |

#P=average number of pits; #S=average number of scratches; SD=standard deviation; %LP=percent of specimens with >4 large pits; STS=scratch texture score; %CS=percent of specimens with cross scratches.

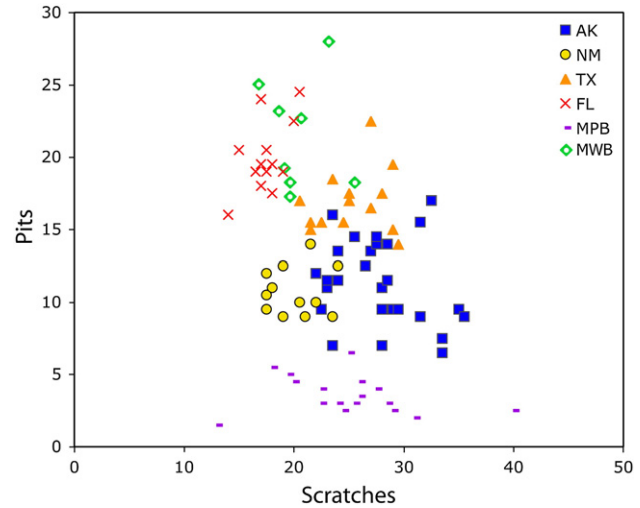


Figure 5. Bivariate plot for raw data of numbers pits and scratches for modern plains bison (MPB), modern wood bison (MWB), and the Pleistocene *Bison* samples (AK=Alaska, TX=Texas, NM=New Mexico, FL=Florida).

Bearing in mind that mesowear and microwear offer dietary signals on different time scales, we attempted to combine 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 five microwear variables (Table 3). Modern ungulate species included in the analysis are those for which there is both mesowear and microwear data (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). At least the first three principle components explained significant amounts of variation in the data. Plots of the loadings for PC1, PC2, and PC3 can be found in Figures 6A and B. The mesowear score (MS) and variables relating to the number of scratches (#S) and widths of scratches (STS) loaded most heavily on PC1, while variables relating to the number of pits (#P) and the sizes of pits (%LP) loaded more heavily on PC2. In the plot of PC1 and PC2, all of the fossil *Bison* samples plotted outside of the area occupied by modern grazers and fall into intermediate areas occupied by modern mixed feeders. The Florida and Texas samples of fossil *Bison* are well removed

Table 3
Eigenvalues and eigenvectors resulting from PCA of mesowear and microwear variables

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---------------------|-------|-------|-------|-------|-------|-------|
| Eigenvalue | 2.06 | 1.61 | 1.02 | 0.50 | 0.42 | 0.39 |
| Percent | 34.3 | 26.9 | 17.0 | 8.3 | 7.1 | 6.5 |
| CumPercent | 34.3 | 61.2 | 78.2 | 86.5 | 93.5 | 100.0 |
| <i>Eigenvectors</i> | | | | | | |
| MS | 0.47 | -0.39 | -0.16 | 0.56 | -0.12 | 0.52 |
| #P | -0.02 | 0.61 | 0.47 | 0.08 | 0.02 | 0.59 |
| #S | 0.56 | -0.20 | 0.13 | -0.35 | 0.71 | -0.07 |
| %LP | 0.39 | 0.51 | -0.09 | 0.53 | 0.06 | -0.55 |
| STS | 0.55 | 0.18 | 0.10 | -0.48 | -0.64 | 0.03 |
| %CS | -0.02 | -0.36 | 0.85 | 0.23 | -0.16 | -0.28 |

MS=mesowear score; #P=average number of pits; #S=average number of scratches; %LP=percent of specimens with large pits; STS=scratch texture score; %CS=percent of specimens with cross scratches.

Microwear variability in fossil *Bison*

The microwear analysis revealed significant geographical differences during the Pleistocene. The four bison samples studied show clear differences in terms of abrasiveness of their diet. We observed a gradient from high average numbers of scratches for the bison from Alaska and then decreasing numbers for the samples from Texas to New Mexico and Florida. This corresponds to a highly abrasive diet for the bison from Alaska and then decreasing abrasiveness from the samples from Texas to New Mexico and Florida. Pit numbers does not show such tendencies, except for the sample from Florida, which display the highest number of pits of all fossil samples, similar to the number observed on the modern wood bison. Habitat and the composition of the vegetation would have an influence on the feeding behavior of the bison. This behavior can explain the dietary diversity observed in the Pleistocene. Because of human activities, modern *Bison* populations have a more restricted range and a less diverse diet.

Results of the PCA revealed that Alaska and New Mexico samples have high frequencies of specimens in those samples with cross scratches. The Florida and Texas samples, on the other hand, have low percentages. Comparing with data from (Solounias and Semprebon, 2002), we observed that high percentages of cross scratches reflect a more abrasive diet. Thus, we observe an east–west trend in diet for the Pleistocene bison.

The scratches observed for the extinct Alaska *Bison* were mainly fine scratches which might be explained by the fact that C₃ grasses may produce such very fine microwear scratches (Solounias and Semprebon, 2002). There are similarities at high altitudes and longitudes for the C₃ grasses. High numbers of fine scratches were observed in some high-altitude animals such as *Capricornis sumatraensis*, *Budorcas taxicolor*, and *Lama glama* as well as in some forest animals (Solounias and Semprebon, 2002). The fine scratches observed on the Alaska sample may suggest this extinct bison population was feeding on C₃ grasses. On the Great Plains, increases in the biomass of C₃ grasses are correlated with increasing latitude (Cannon, 2001). This is consistent with the high latitude of Alaska and the lower Pleistocene temperatures.

Stable isotope data reveal different climatic and environmental conditions during the Pleistocene in the areas of the contiguous United States we investigated in this study (Connin et al., 1998; Koch et al., 1998; Feranec and MacFadden, 2000; Holliday, 2000; Nordt et al., 2002; Balakrishnan et al., 2005). From our results, and data on vegetation and stable isotopes, we can infer that fossil *Bison* had access to different and more diverse habitats than modern plains *Bison*. Present bison distribution and diets do not mirror the Pleistocene adaptations and the principle of uniformitarianism does not apply.

Using comparisons with modern ungulates, a better understanding can be obtained of the diets of the four *Bison* samples analyzed in the PCA. Most of the fossil samples we analyzed plot close to mixed feeders (graze dominated mixed feeders in particular) and few of them plot near the strict grazers. There is clearly more variation in the diet of fossil *Bison* than in modern

Bison. It is interesting that such variation in the diet is known for a large number of modern ungulates living in non disturbed environments (Estes, 1991). The reduction of variability in the modern plains *Bison* diet may be the result either of the impact of humans on these populations or of the Pleistocene extinctions. Restriction in dietary variation could be used in other studies to understand this type of changes.

Using modern *Bison* as ecological models

Modern plains *Bison* is often used as a typical model for modern *Bison* ecology (Meagher, 1978, 1986; Knapp et al., 1999; Irby et al., 2002; Lott, 2002) and more importantly for fossil *Bison* ecology (Guthrie, 1970, 1990; Hanson, 1984; Cannon, 2001; Johnson et al., 2005). For example, in an archeological context, Johnson et al. (2005) analyzed organic material from 'stomach contents' from a *Bison bison* in Nevada. Vegetal material consisted mostly of twigs rather than forbs and grasses, and this was deemed unusual because *Bison* is expected to graze. Because of this difference, they suggested that it could be the result of differential preservation and not representative of the entire diet. These studies have to be considered with caution due to our findings. This idea of *Bison* as an animal adapted for extreme short grass grazing in plains life has to change for *Bison sensu lato*.

Modern populations of plains *Bison* are diminished and anthropogenically disturbed with altered genetics (Lott, 2002), population dynamics, ecology, and behavior (Berger and Cunningham, 1994). Our study is a start in the development of a better model for the adaptation and diet of fossil *Bison*. The data we collected for four samples from North America from the late Pleistocene and perhaps early Holocene show that diets of fossil *Bison* were consistently different from modern plains *Bison* diet. Plains *Bison* ecology is on the fringes because of anthropogenic factors, and the results suggest that mixed feeding diets or lower abrasive grazing diets might be more typical for *Bison*.

Conclusion

Combining the two methods of diet analysis on four samples of fossil *Bison* from North America yielded two important results. Firstly, the mesowear analysis shows that Pleistocene *Bison* had a different diet than the modern plains bison (a less abrasive diet). Secondly, a combined analysis of mesowear and microwear revealed important diet differences at the geographical level. Our study reveals the importance of a diet analysis in the understanding of the change of *Bison* diet from the late Pleistocene–Holocene to the modern species. The results show geographically variable diets for the extinct *Bison*. The diversity in diets of our samples of *Bison* is suggestive that some difference must have existed in their habitats or different species behavior, compared to the habitat of the modern bison in North America. Finally, we can assume that modern plains bison has an atypical diet in comparison to the fossils. Our analysis begins to show the importance of diet and also the breadth of diet in the evolution of a species. By focusing our investigation on the

reaction of *Bison* populations to past climate change, our study can be useful in the management of *Bison* herds, as well as in the understanding of the relationship between past and future climate changes.

Acknowledgments

We acknowledge the curators for access to the specimens, in particular we are grateful to J. Flynn, J. Meng, C. Norris, J. Galkin (Department of Vertebrate Paleontology, American Museum of Natural History, New York), and E. Westwig (Department of Mammalogy, American Museum of Natural History, New York). We also thank R. Dale Guthrie and two anonymous reviewers for their comments and Renata Trister for critical review and editing. This research was supported by a Lavoisier grant from the French ministry of Foreign Affairs to FR.

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