

## Differences in Tooth Microwear of Populations of Caribou (*Rangifer tarandus*, Ruminantia, Mammalia) and Implications to Ecology, Migration, Glaciations and Dental Evolution

Florent Rivals · Nikos Solounias

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**Abstract** Tooth microwear was analyzed for a large sample of wild-shot barren-ground caribou (*Rangifer tarandus groenlandicus*) from the Kaminuriak population of eastern Canada. This sample was compared to the microwear of specimens from three Pleistocene localities in North America (Alaska) and western Europe (Caune de l’Arago in France and Salzgitter in Germany). The results show that the extant samples from eastern Canada have seasonal variation in microwear and presumably in diet. The differences in microwear between the various seasons may reflect a cyclic migration of the population within a year. The extinct population from Alaska has extremely blunt teeth (mesowear), as blunt as those of modern zebras and bison. This observation is corroborated by the lowest number of microwear pits. The findings are untypical, as most typical caribou teeth have sharper apices, and we interpret this as an indication of a local habitat that was different with animals feeding on non-typical vegetation. The combination of *Rangifer* from Caune de l’Arago and Salzgitter reveals a pattern in microwear variability. The Salzgitter is interglacial and shows a greater diversity of browsing (broad spectrum on average number of pits) than the glacial Caune de l’Arago. The interglacial population from Salzgitter is interesting because it shows several different types of browsing. Collectively all the *Rangifer* teeth show that diet of a brachyodont taxon can vary across most of the dietary morphospace of ungulates as represented by tooth microwear. The three Pleistocene samples exhibit microwear that is different from the extant population in question. This observation implies that the recent diet of *Rangifer* has changed from the typical caribou diet in the past. This indicates dietary change within a species. This is important because it represents dietary evolution without changes in tooth morphology.

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F. Rivals (✉)

ICREA—IPHES, Àrea de Prehistòria, Universitat Rovira i Virgili, Plaça Imperial Tàrraco 1, 43005 Tarragona, Spain  
e-mail: florent.rivals@icrea.es

N. Solounias

Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, NY 11568-8000, USA

N. Solounias

Division of Vertebrate Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

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## Introduction

Scientists are interested in finding out how the diet of ungulate herbivores is affected by glaciation cycles. In addition there is concern with how evolution works on a small scale. Does dietary behavior precede dental morphology or is evolutionary morphologic change imperceptibly synchronized to behavioral change? We were interested to see how tooth microwear relates to seasonal fluctuations in diet. We were fortunate to have obtained samples of caribou from different Pleistocene localities as well as a large sample of recent caribou. These samples and the microwear analysis enabled us to address the questions listed above.

Microwear analysis has been used since the late 1970s to predict the diet of extinct animals (Rensberger 1978; Walker et al. 1978). Since then it has been successfully applied to a wide variety of mammals in both paleontological and archaeological contexts (e.g. Solounias et al. 1988; Solounias and Moelleken 1992, 1994; Solounias and Semprebon 2002). Currently only a few analyses have attempted to correlate microwear with seasonality, climate and diet on modern or fossil animals (Merceron et al. 2004; Rivals and Deniaux 2005).

We used a large sample of wild-shot barren-ground caribou (*Rangifer tarandus groenlandicus*) from the Kaminuriak population of eastern Canada. The sample was compared to specimens from three Pleistocene localities in North America (Alaska) and western Europe (France and Germany). The wild-shot barren-ground caribou was used as a comparative database. The Canadian sample is extraordinary because sex and age of the individual specimens are known, the season of death was recorded, and the stomach contents were analyzed (Miller 1974, 1976). Using specimens from the same caribou population, significant variation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in teeth were found by Drucker et al. (2001). The measured isotopic signatures with high  $\delta^{13}\text{C}$  values strongly support winter lichen consumption and  $\delta^{15}\text{N}$  variations result from mechanisms related to seasonal environment and diet changes. The Kaminuriak population of caribou was used in this study to test whether dental microwear can detect a sexual and/or a seasonal signal in the diet. The two Pleistocene European localities (France and Germany) were selected because of large samples of *Rangifer* and because animals were seasonally hunted (Gaudzinski and Roebroeks 2000; Rivals et al. 2004). The third sample, from Alaska is not from an archaeological locality. Seasonal death is not evidenced there.

## Material

*Modern sample* The sample used in this study is a large assemblage of wild-shot barren-ground *Rangifer tarandus groenlandicus* from the Kaminuriak population of eastern Canada. The population ranges over the southeastern District of Keewatin, in the Northwest Territories, and northern Manitoba and northeastern Saskatchewan. Caribou from the Kaminuriak population were killed across all seasons and collected by Canadian Wildlife Service biologists from March 1966 to July 1968 (Miller 1974). The collection's teeth are currently housed in the Department of Anthropology at New York University. The collection used in this study consists of lower right mandibular teeth of 66 individuals of all age classes, and both sexes. This sample is extraordinary because the sex and age of the individual specimens are known—

all caribou specimens had been tagged early in the calving season allowing us to attribute an age at death (Miller 1974, 1976). The season of death was recorded (Miller 1974) and the stomach contents were preserved and analyzed for 545 individuals (Miller 1976). Dentition was examined for age and sex determination (Miller 1974), for skeletochronology study (Pike-Tay 1995), for studying the relationship between dental crown height and age (Pike-Tay et al. 2000), for stable isotopes (Drucker et al. 2001), and for dental mesowear analysis (Rivals et al. 2007a).

Their diet and environment are presented in publication for an entire year (Miller 1974). From November to April, Kaminuriak caribou stay in open boreal forest and consume great quantity of lichen especially when other plants are not available. In spring, they move to the tundra where they search for high protein and high fat content plants. Caribou are gregarious animals and so individuals belonging to the same herd are presumed to share the same food sources.

*Fossil samples* Four samples of *R. tarandus* were used to compare with the modern caribou. Samples come from three Pleistocene localities: Fairbanks (Alaska, USA), Caune de l'Arago (France), and Salzgitter (Germany).

The Alaska sample of *R. tarandus* was recovered from frozen deposits located in the Fairbanks area (Wilkerson and Kaisen 1932) that have been radiocarbon dated to  $11,990 \pm 135$   $^{14}\text{C}$  year B.P. (Stephenson et al. 2001). The associated ungulates are *Bison priscus*, *Alces alces*, *Cervus elaphus*, *Equus lambei*, *Ovibos moschatus*, *Ovis dalli*, and *Mammuthus primigenius* (Guthrie 1968; Yesner 2001).

The Caune de l'Arago cave is a middle Pleistocene archaeological site located in southern France. The deposits cover a period from 690,000 to 100,000 years and various climatic changes (de Lumley et al. 1984). Ungulates associated with *R. tarandus* are *Ovis ammon antiqua*, *Hemitragus bonali*, *Bison priscus*, *Praeovibos priscus*, *Equus ferus mosbachensis*, and *Stephanorhinus hemitoechus*. We selected two large samples from this locality from two stratigraphical units (CM1 and CM3). Stratigraphical unit 1 or CM1 is dated to OIS 14 (about 570,000 to 530,000 years). In this unit the population of *Rangifer* is composed of 2/3 females and only 1/3 males. The estimated hunting season, autumn, corresponds to the end of the breeding period and the beginning of winter migrations (Rivals et al. 2004). Stratigraphical unit 3 or CM3 is dated to OIS 12 (about 480,000–400,000 years).

The middle Paleolithic site Salzgitter Lebenstedt in northern Germany is well known because of its well-preserved faunal remains, dominated by adult *R. tarandus* (Gaudzinski and Roebroeks 2000). The archaeological assemblage accumulated in an arctic setting in an earlier part of the last glacial period (OIS 5 or 3). The results of the zooarchaeological analysis indicate autumn hunting of reindeer by middle Paleolithic hominids (Gaudzinski and Roebroeks 2000).

## Methods

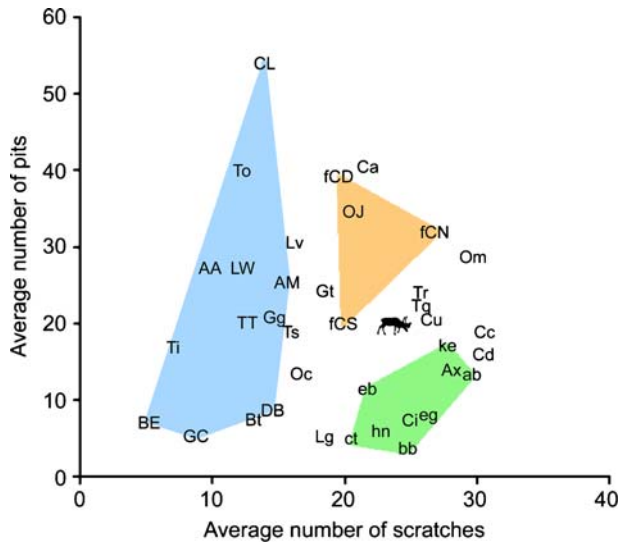
We used the light microscope tooth microwear method to analyze paleodiet (Solounias and Semprebon 2002; Semprebon et al. 2004). Further discussion of this methodology and its application toward dietary reconstruction can also be found in Godfrey et al. (2004), Merceron et al. (2004), and Palombo et al. (2005). For preparation of teeth, cleaning casting and counting features see the previous studies (Solounias and Semprebon 2002; Semprebon et al. 2004).

Microwear features were identified and quantified on high resolution epoxy tooth casts at 35x 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 sub-circular 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 microwear scars 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. In ungulate teeth most scratches reflect the direction of jaw motion. Hence it is certain that they are not erosional. Cross scratches are oriented somewhat anteroposteriorly in the mouth and are probably produced as stems are stripped off by the animal. Cross scratches are perpendicular to the majority of scratches observed on dental enamel (Solounias and Semprebon 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 band of enamel on the protoconid of the lower 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. Overall, 66 extant *Rangifer* specimens were suitable for microwear analysis: 41 females and 25 males. Four periods of the year are represented: June, September, November, and April. The Student's *t* test was used to compare the male and female data. We used an analysis of variance (ANOVA) with Tukey's post hoc test for Honestly Significant Differences (HSD) to test for significant differences in microwear between each season. Statistical analyses were run on SYSTAT 11.0 with significance set at  $p < 0.05$ .

**Table 1** Microwear data for the modern caribou (*Rangifer tarandus*)

	Number	Average number of pits	Average number of scratches	% large pits	% gouges	Scratch texture score	% cross scratches
Total	66	20.07	23.53	62.1	69.7	0.97	53.0
Sex							
Females	41	19.90	23.85	61.0	68.3	1.00	58.5
Males	25	20.34	23.00	64.0	72.0	0.92	44.0
Season							
June	21	15.36	28.45	47.6	57.1	1.10	38.1
September	9	17.17	21.44	77.8	66.7	1.00	77.8
November	13	24.96	21.31	92.3	100.0	1.00	69.2
April	23	22.74	21.11	52.2	65.2	0.83	47.8

Average numbers of pits and scratches, percentages of specimens with large pits, gouges and cross scratches in the sample, and scratch texture score (averaged for each sample from 0=fine scratches; 1=mixture of fine and coarse scratches; 2=coarse scratches only)



**Fig. 1** Bivariate plot of the average number of pits versus average number of scratches in extant ungulates and *Rangifer tarandus* at 35x magnification (extant data from Solounias and Semprebon 2002). Convex hulls are drawn around leaf browsing taxa, fruit browsing taxa, and grazing taxa for ease of comparison. Abbreviations: Leaf-browsers—AA, *Alces alces*; AM, *Antilocapra americana*; BE, *Boocercus euryceros*; CL, *Camelus dromedarius*; DB, *Diceros bicornis*; GC, *Giraffa camelopardalis*; LW, *Litocranius walleri*; OJ, *Okapia johnstoni*; TT, *Tragelaphus strepsiceros*; Fruit-Browsers—fCD, *Cephalophus dorsalis*; fCN, *Cephalophus natalensis*; fCS, *Cephalophus silvicultor*; Grazers—ab, *Alcelaphus buselaphus*; bb, *Bison bison*; ct, *Connochaetes taurinus*; eb, *Equus burchelli*; eg, *Equus grevyi*; hn, *Hippotragus niger*; ke, *Kobus ellipsiprymnus*; Mixed-feeders—Ax, *Axis axis*; Bt, *Budorcas taxicolor*; Ca, *Capricornis sumatraensis*; Cc, *Cervus canadensis*; Cd, *Cervus duvauceli*; Ci, *Capra ibex*; Cu, *Cervus unicolor*; Gg, *Gazella granti*; Gt, *Gazella thomsoni*; Lg, *Lama glama*; Oc, *Ovis canadensis*; Om, *Ovibos moschatus*; Ti, *Tragelaphus imberbis*; To, *Taurotragus oryx*; Tq, *Tetracerus quadricornis*; Tr, *Boselaphus tragocamelus*; Ts, *Tragelaphus scriptus*; Lv, *Lama vicugna*.

## Results

### Comparison of caribou microwear to other extant ungulates

Microwear data are presented in Table 1. Bivariate plot in Fig. 1 shows the relative position of tooth microwear in *Rangifer* in comparison to other ungulates. The sample we analyzed falls between browsers and grazers, in an area occupied by mixed feeders. The microwear signal is close to the one recorded by Solounias and Semprebon (2002) for *Tetracerus quadricornis*, *Boselaphus tragocamelus*, and *Cervus unicolor* (three mixed feeders). *T. quadricornis* is a mixed feeder living in closed or open habitats; its diet may include more than 50% grass (Schaller 1967; Nowak 1999). *B. tragocamelus* is a browse dominated mixed feeder and lives in dry closed habitats. The diet of this species consists of less than 50% grass (Schaller 1967) and the use of browse may vary from 56% during the monsoon to 100% in summer (Khan 1994). Finally, *C. unicolor* may use grassland or forest habitats (Ngampongsai 1987; Johnsingh and Sankar 1991). The diet of this species includes 86% grass in grassland habitats, and leaves from trees (57%) and shrubs (36%) in forest habitats (Ngampongsai 1987). The dietary habits of these three ungulates are characterized by seasonal and/or geographical variation similar to that known for caribou in North America. Most of these populations also live in dry forested habitats.

Caribou feed on a broad range of plants, eating a wider variety of plants than other deer species (Skoog 1968; Bergerud 1972, 1978; Miller 1982). Their diet includes lichens, fungi,

sedges, grasses, forbs, twigs and leaves of woody plants (Miller 1982; Klein 1992; Larter and Nagy 1997). However, caribou show a preference for green vascular plants and mushrooms. When these plants cannot be secured, caribou are opportunistic and will eat whatever plants are available (Bergerud 1972, 1978). Feeding on lichens is the key to caribou survival in many areas. Foliose lichens dominate the diet in the fall and winter (Miller 1982). As the snow melts, caribou seek exposed sites to feed on leaves and graminoids, which tend to dominate the diet and lead to the exclusion of lichens as summer progresses (Skoog 1968; Miller 1982). Rumen contents analyzed by Miller (1976) from the same individuals that were used for microwear show a diet comprised of bryophytes, lichens, conifer needles, woody angiosperms and grasslike plants (*Equisetum* spp.).

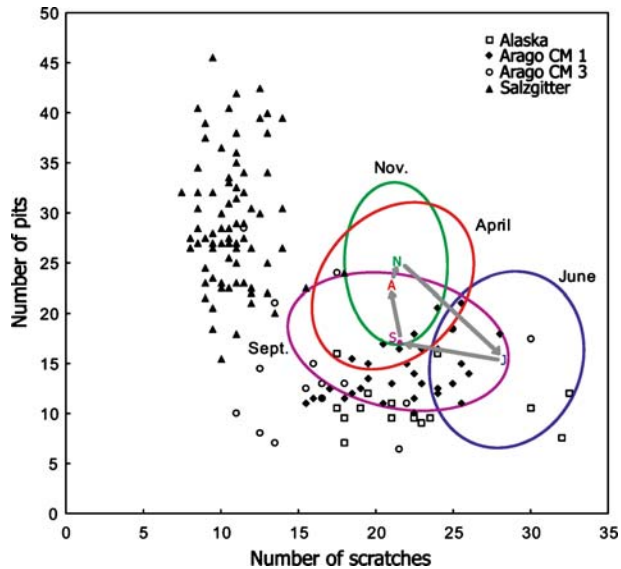
The observed microwear signal clearly reflects a diet comprised of a large variety of plants with very different abrasive properties (browse and grasses). Caribou may be defined by their microwear results as mixed feeders. The position of our sample close to the grazing morphospace may be due to either sexual differences or to differences in the number of individuals killed in the various seasons.

The summary statistics for males and females are presented in Table 1. No significant differences in the number of pits (Student's *t* test,  $t=0.281$ ,  $df=64$ ,  $p=0.7795$ ) and scratches (Student's *t* test,  $t=0.723$ ,  $df=64$ ,  $p=0.4722$ ) were detected. The previous analysis of the rumen contents of caribou from this population revealed no differences in forage classes used between sexes (Miller 1976).

#### Comparison of modern caribou microwear samples from various seasons

Figure 2 is a plot of the average number of pits versus average number of scratches for modern and fossils samples. The figure shows that the extant samples from eastern Canada have variation in microwear and presumably in diet. The samples vary by month and the variation may be cyclic as is indicated by the arrows. From June to September the average number of scratches decreases but the number of pits does not change significantly. Compared to September, the November and April samples show an increase in the number of pits but no real change in

**Fig. 2** Bivariate plot of the average number of pits versus average number of scratches in extant and fossil population of caribou (*Rangifer tarandus*). For the modern caribou, the 95% confidence ellipses are drawn for ease of comparison.



**Table 2** ANOVA and Tukey’s HSD test results

Statistical results					
Pits					
ANOVA results					
Source	<i>df</i>	SS	MS	<i>F</i> -ratio	<i>P</i>
Model	3	1,017.21	339.10	15.08	<0.001
Residual	62	1,393.74	22.48		
Pair-wise comparisons— <i>q</i> values (Tukey’s method); <i>p</i> <0.05					
	June	Sept	Nov	April	
June	–				
Sept	ns	–			
Nov	5.187	2.367	–		
April	3.604	0.651	ns	–	
Scratches					
ANOVA results					
Source	<i>df</i>	SS	MS	<i>F</i> -ratio	<i>p</i>
Model	3	747.02	249.01	23.77	<0.001
Residual	62	649.42	10.47		
Pair-wise comparisons— <i>q</i> values (Tukey’s method); <i>p</i> <0.05					
	June	Sept	Nov	April	
June	–				
Sept	3.604	–			
Nov	4.129	ns	–		
April	4.765	ns	ns	–	

*df* degrees of freedom; *SS* sum of squares; *MS* mean square

scratches. Then moving to June, the number of scratches increases whereas the number of pits decreases. The microwear statistics for each sub-sample corresponding to various seasons are given in Table 1. We tested for statistical differences in the seasons for both pits and scratches (Table 2). For pits, the one-way ANOVA revealed highly significant differences among seasons ( $F=15.08$ ;  $p<0.001$ ). Tukey’s HSD test revealed significant differences in the number of pits between all seasons except between June and September, and between November and April

**Table 3** Microwear data for the fossil samples of caribou (*Rangifer tarandus*)

Locality	Number	Average number of pits	Average number of scratches	% large pits	% gouges	Scratch texture score	% cross scratches
Fairbanks	15	10.67	22.60	0.00	0.00	0.00	13.33
Caune de l’Arago CM I	32	14.19	21.75	15.63	0.00	0.88	18.75
Caune de l’Arago CM III	17	14.15	17.41	11.76	5.88	0.88	35.29
Salzgitte	82	29.28	10.75	48.78	37.80	0.94	3.66

Average numbers of pits and scratches, percentages of specimens with large pits, gouges and cross scratches in the sample, and scratch texture score (averaged for each sample from 0=fine scratches; 1=mixture of fine and coarse scratches; 2=coarse scratches only)

(Table 2). For scratches, the ANOVA also revealed highly significant differences among seasons ( $F=23.77$ ;  $p<0.001$ ). Tukey's HSD test revealed significant differences between June and all other seasons. There were no significant differences between September, November, and April (Table 2). Combining both pits and scratches suggests that the only samples without significant differences were November and April.

The 1 year cycle is clear and is drawn as a counterclockwise trend with arrows. Thus the diet of the same population varies seasonally. When compared to the diet of modern caribou (Miller 1976, 1982; Bergerud 1978), the cycle can be broadly interpreted as an alternation from willow and sedges to lichens and mushrooms and then back to willow and sedges and so on.

#### Comparison of the fossil caribou samples

Microwear data for the fossil samples are presented in Table 3. In Fig. 2, for the fossil samples, each point represents a specimen and is the average of two counts (two counts per specimen). The fossil sample from Alaska shows the lowest number of pits. An explanation of this difference may be approached by looking at dental wear on another scale, via a different method. Figure 3a shows typical teeth (on a lower jaw) from this Alaska population. The teeth are worn down and are blunt, similar to those of zebra and bison (Fortelius and Solounias 2000). This observation is part of a tooth mesowear evaluation, not a microwear one. Blunt teeth in terms of mesowear reflect grazing (Fortelius and Solounias 2000). Figure 3b also shows the more typical *Rangifer* teeth with the high rounded (or sometimes sharp) apices. The contrast between these two is remarkable.

The Caune de l'Arago samples, which are from a glacial cycle of the Pleistocene, also have low numbers of pits. Mesowear observation on these samples also revealed low relief, very similar to the pattern recorded for the Alaska sample.

The interglacial population from Salzgitter is interesting because it shows a breadth of types of browsing, low and high averages of pits. The data all fall in the morphospace of browsers. In these individuals the number of scratches is low. This observation is suggestive of diverse opportunities of browsing within the same interglacial habitat.



**Fig. 3** Lower teeth of caribou (*Rangifer tarandus*). **a** Mandible from the fossil Alaska sample (AMNH 3258-1958). **b** Lower M2 from the Kaminuriak caribou population (individual number 795).



## Discussion

The results show that the extant samples from eastern Canada have variation in microwear and presumably diet. The significant differences observed in microwear between the various seasons may reflect a cyclic migration of the population. However, the sample collected over 2 years is not sufficient to currently establish this with certainty. The apparent cycle shown in Fig. 2 is tight, in that the clusters touch each other on the plot. Larger samples from more years are needed to show regularities and effects of geography and climate. These two concepts are closely interrelated, and there is a good chance that our 2 year data did pick up a migrating herd through slightly different habitats. It is difficult to find such well-documented samples in museum collections. These results are significant due to climatic deterioration and can be used to detect changes in time and trends in the future of some species as humans alter their habitats.

The extinct species from Alaska have extremely blunt teeth (mesowear), as blunt as those of modern zebras and bison. Such heavy occlusal wear for young and adult animals reflects a very abrasive diet which is unusual for brachyodont species. Blunt teeth represent extreme wear as in some types of grazing (Fortelius and Solounias 2000). When considering microwear, it can therefore be assumed that low number of pits reflects somehow the drastically altered diet. Explanation of the exact microwear data cannot, however, be derived from the observed mesowear of blunt cusps. Many species have low number of pits, which do not correlate with blunt cups in mesowear. The mesowear observation is corroborated by the lowest number of pits of all the samples we analyzed. These findings indicate that the diet of these animals was very different from that of the typical caribou as a species. The data do not definitely imply that the stress factor of the Alaska teeth was grazing. For grazing, a higher number of scratches would be expected.

Some questions can be asked at present. What was the dietary habitat during the Pleistocene? As the ice melted and retreated, did the ruminants follow the ice margin? Did they migrate south during the colder season? The combination of the two localities (Caune de l'Arago and Salzgitter) reveals a pattern. The Caune de l'Arago samples, which are from Pleistocene glacial cycles, have low number of pits. Mesowear observation on this sample also revealed low relief very similar to the pattern recorded for the Alaska sample. The data suggest that the Caune de l'Arago sample was subjected to diets different from the typical modern caribou. Salzgitter is from an interglacial cycle of the Pleistocene and shows a broad spectrum of browsing diets (high variation in pit counts). The dietary signal is different from the one observed for the glacial Caune de l'Arago.

A confined number of pits shows diet focused onto a few types of vegetation. This means that the diversity in browse utilized by *Rangifer* was very low. The data are suggestive that this population was affected by the local environmental conditions, which perhaps came from near the ice margin. The interglacial population from Salzgitter is interesting because it shows a breadth of types of browsing. This may mean that migrations occurred to different habitats during the interglacial. It may also mean that the vegetation available was very diverse and hence the diverse type of pit averages. Again this species does not feed substantially on grasses (Miller 1976, 1982; Bergerud 1978, 2000). The data are not rich, but they suggest that glaciations affected the diet of this species. In other words, the diet had to be changed drastically due to climate. This is contrary to the notion that as the amount of ice changed, animals gradually drifted north or south and vegetation passively followed the slow change from a glacial to an interglacial period retaining an unchanging dietary adaptation (Huntley and Webb 1989; Vrba 1992).

Collectively all the teeth from all samples show that diet of a brachyodont taxon can vary across most of the dietary morphospace of ungulates. This dietary variability was already

observed for plains bison during the late Pleistocene (Rivals et al. 2007b). Examination of the Pleistocene samples shows that all three are different in diet from a typical extant population. They fall to the left and below a typical extant population on the microwear plot (Fig. 2). This implies the diet of *Rangifer* has changed since the end of the Pleistocene. This observation in our data shows dietary change within a species. This is important as it shows a dietary evolution without change in tooth morphology. In other words, tooth morphology has remained the same despite dietary changes.

We add results on caribou from a different study as a supplement because it corroborates our findings. Merceron and Madelaine (2006) analyzed four *Rangifer* specimens from La Berbie (France) using confocal microscopy. Because microscopic methods are different, the results cannot be directly compared to ours. In that study the number of pits is high. La Berbie was also dated from an interglacial period of the Pleistocene and microwear results confirm our observation that populations from interglacial cycles feed on a broad range of plants unlike those from glacial cycles.

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