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Microwear patterns on the teeth of northern high latitude hadrosaurs with comments on microwear patterns in hadrosaurs as a function of latitude and seasonal ecological constraints

Anthony R. Fiorillo

ABSTRACT

Dental microwear studies have value in qualitatively addressing patterns of food use in both extinct and extant vertebrates. This study has examined dental microwear patterns on the teeth of Campanian/Maastrichtian hadrosaurs from northern Alaska to western Texas. The primary parameters examined were the incidence of pitting and the orientation of linear features on the occlusal surfaces of the teeth. The results of the examination have shown similar patterns of tooth wear independent of geographic location. Thus it may be that hadrosaurs all along western North America were consuming food items with similar hardness.

The dominant food consumed by hadrosaurs is considered to be conifers, although it is unlikely that conifers constituted the entire diet of the high latitude forms given the constraints imposed by a highly seasonal annual cycle. Further, given the similarity of food items consumed along such a large latitudinal gradient, combined with the deciduous nature of the food items in Alaska, it seems likely that northern hadrosaurs reduced their metabolic rates during the winter months, in a manner similar to many modern terrestrial Arctic vertebrates. This reduction in metabolic rate during the winter months may have been facilitated if these animals were inertial homeotherms (i.e., of a low surface: mass ratio) or ectotherms rather than full endotherms.

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KEY WORDS: hadrosaurs; Cretaceous; microwear; Alaska; food use; polar latitudes

INTRODUCTION

One of the basic handicaps of the fossil record is that it is incomplete and biased. With respect to the record of dinosaurs it is clear from the literature that there is a strong bias toward fossil remains found in the lower latitudes while the higher latitudes, relatively speaking, are underrepresented (Weishampel et al. 2004). Now that a growing number of dinosaur discoveries have come to light in the higher latitudes (de Lapparent 1962; Heintz 1963; Roehler and Stricker 1984; Brouwers et al.

PE Article Number: 14.3.20A

Submission: 15 June 2007. Acceptance: 11 March 2011

Fiorillo, Anthony R. 2011. Microwear patterns on the teeth of northern high latitude hadrosaurs with comments on microwear patterns in hadrosaurs as a function of latitude and seasonal ecological constraints. *Palaeontologia Electronica* Vol. 14, Issue 3; 20A:‘7p;
palaeo-electronica.org/2011_3/7_fiorillo/index.html

1987; Davies 1987; Parrish et al. 1987; Nelms 1989; Clemens and Nelms 1993; Pasch and May 1997; Gangloff 1995; 1998; Gangloff et al. 2005; Rich et al. 2002; Fiorillo and Gangloff 2000; 2001; Fiorillo and Parrish 2004; Fiorillo 2004; 2006a; Fiorillo et al. 2009; Fiorillo et al. 2010) it is also clear that rather than these remains representing oddities from remote, often cold places, these discoveries provide insights into the dynamics of life in ancient high-latitude terrestrial ecosystems.

The first discoveries of dinosaurs from high latitudes presented challenges to our understanding of dinosaur physiology (de Lapparent 1962; Heintz 1963). To accommodate this apparent paradox some workers have invoked migration models for high-latitude dinosaurs (Heintz 1963; Hotton 1980; Brouwers et al. 1987; Parrish et al. 1987; Currie 1989), with modern caribou (*Rangifer tarandus*) most commonly used as the modern analog. A more thorough evaluation of the caribou migration model revealed several problems resulting in Fiorillo and Gangloff (2001) rejecting the analogy based on biomechanical grounds and arguing instead that Arctic hadrosaurs lived year-round in the high latitudes. Similarly, southern hemisphere dinosaurs are also now considered year-round residents of the southern high latitudes (Bell and Snively 2008).

If prey did not migrate, their predators need not have either. Examination of the theropod fauna from the Late Cretaceous of northern Alaska showed that one small theropod, *Troodon formosus*, a taxon that is rare in the more southern latitudes, is overwhelmingly abundant in Alaska (Fiorillo and Gangloff 2000; Fiorillo 2008). Following the work of Russell and Seguin (1982) in which they suggested the taxon was a crepuscular or nocturnal predator, Fiorillo and Gangloff (2000) suggested *Troodon formosus* was well adapted to thrive in the extremely seasonal light régime present in the Cretaceous high latitudes. Further, this adaptive advantage may have resulted in an increase in overall body size for Alaskan forms of *Troodon* (Fiorillo 2008).

From this earlier work it now appears that Alaska dinosaurs lived year- round in the high latitudes, and that at least some aspects of the fauna adapted to life in the ancient Arctic. Numerous studies have suggested higher mean annual temperatures in the Cretaceous high latitudes compared to the modern Arctic (Otto-Bliesner and Upchurch 1997; Parrish and Spicer 1988; DeConto et al. 1999; Takashima et al. 2006) but there remains the issue of an extremely seasonal light régime (Spicer 1987, 2003; D'Oro 2006). Further, given that many of the plants of northern Alaska are thought to be deciduous (Spicer 1987, 2003), it is reasonable to assume that there were times of food scarcity. Hence, it is a basic principle in ecology that consumers eat a broader diet when food is scarce, and that consumers specialize when food is abundant (Schoener 1971; MacArthur 1972; Pianka 1978; Emlen 1984; Krebs and Davies 1987; Ricklefs and Miller 2000).

Thus, this paper addresses the issue of dietary preferences of high-latitude dwelling hadrosaurs in relation to the dietary preferences of hadrosaurs found in lower latitudes. The Alaskan form of hadrosaur has traditionally been referred to as *Edmontosaurus* (Nelms 1989; Gangloff and Fiorillo, 2010). If this identification is correct, this taxon, during the Late Cretaceous, occupied a geographic range extending from modern northern Alaska (Nelms 1989, Gangloff and Fiorillo, 2010) to Baja, Mexico (Weishampel et al. 2004). One modern terrestrial vertebrate has a comparable latitudinal range, the mountain sheep *Ovis*. *Ovis* has a geographic range in North America from the Brooks Range in Alaska, extending south through western Canada and the United States to northwestern Mexico (Valdez and Krausmann 1999). *Ovis*, therefore, provides an analog for how hadrosaurs may have utilized food resources.

Given the extensive area inhabited by sheep, there is a great variety of potential plant species available as food. Nichols and Bunnell (1999), however, identify one feeding generality for the northern Dall and Stone's Sheep; they consume more lichens and mosses than other North American sheep species. Lichens have a high digestibility (amount of food absorbed during consumption) yet they have a low nutritional value (amount of nutrition provided). The harsh environment then forces the sheep to consume food items less than optimal for their needs. In their study of habitat selection for lambing ewes, Rachlow and Bowyer (1998) similarly showed that given the nutritional needs for nursing during lambing, Dall Sheep choose lambing sites that had reduced quantities of moss and lichens, further emphasizing the expanded range of food use during at least non-lambing parts of the annual cycle.

From *Ovis* one can suggest that northern hadrosaurs may have had a more varied diet than hadrosaurs found in the more southern latitudes. One tool, which has shown tremendous value for inferring dietary patterns in extinct animals, is the analysis of microwear on teeth. The application of this tool to the teeth of hadrosaurs found in Alaska, Alberta, Wyoming, and Texas forms the basis for this discussion.

MICROWEAR STUDIES BACKGROUND

It is widely recognized in biology that acquisition of food is a basic determinant in the behavior of an organism. Patterns of food acquisition and use provide insight into the behavior of extant and extinct organisms. The tool of choice for many students interested in this aspect of the paleobiology of vertebrates is the study of dental microwear.

George Gaylord Simpson (1933), in his landmark study, used teeth to determine variation in jaw movements among Jurassic mammals, differences thought to reflect inferred food differences. Wear features are ultimately produced by the movement between upper and lower teeth, and linear features provide a record of the pattern of chewing (Fiorillo and Weishampel 1997). Numerous workers have examined microwear on teeth, using light microscopy or scanning electron microscopy as a tool to determine patterns of food use (Kay and Covert 1983; Teaford and Walker 1984; Teaford 1985; Teaford and Byrd 1989; Walker and Teaford 1989; Walker et al. 1978; Taylor and Hannam 1987; Ungar 1990, 1994, 1998; Maas 1991; Merceron et al. 2004; Rivals and Deniaux 2003; Hotton et al. 1997; Fiorillo 1998, 2006b; King et al. 1999; Goswami et al. 2005; Schubert and Ungar 2005; Solounias and Moelleken 1992, 1993; Solounias and Hayek 1993). Ungar et al. (2008) have provided an excellent overview of the history of the study of microwear, and interested students of microwear are referred to it for further details.

Broadly speaking, striae and pits are the commonly analyzed features of microwear. Some authors have defined pits as having length to width ratios of less than 2:1 while others have used a ratio of 4:1. The presence of pits is generally associated with the consumption of hard food items. The development of striae, their length, depth, and density, can be used to infer qualitatively the food hardness consumed between animals with only scratches on their wear facets. Microwear patterns in modern animals can change with seasonal variation in diet.

Whereas most of these studies have focused on diets in mammals, either extant or extinct, relatively little attention has been directed toward non-mammalian studies. However, some studies focus on critical moments in non-mammalian evolution and use results to determine behavior in early vertebrate history. For example, Purnell (2001, 2002) used microwear patterns on a variety of conodonts and heterostracan fishes to develop feeding models in early vertebrates. Additionally, Hotton et al. (1997) used microwear in the teeth of early amniotes to discern omnivory versus high-fiber herbivory.

Other studies have focused on patterns of food use within single paleoecosystems. In a study of microwear in sympatric Jurassic sauropods from western North America, specifically *Diplodocus* and *Camarasaurus*, it was demonstrated that there was niche partitioning between these taxa, and that they had distinctively different diets (Fiorillo 1998). Similarly, Goswami et al. (2005) used microwear to make dietary inferences about two cynodonts and a prosauropod from the Triassic of Madagascar. Their study also showed aspects of difference in food use patterns. In contrast, food partitioning could not be demonstrated for Late Cretaceous small theropods, either within a paleoecosystem or between ancient ecosystems separated geographically (Fiorillo 2006b, 2008). Schubert and Ungar (2005) studied the wear facets of tyrannosaurids and determined wear facets in this group to be the result of tooth-to-tooth contact between the maxillary teeth and the dentary teeth. Similarly, Rybczynski and Vickaryous (2001) used patterns of microwear in the teeth of the ankylosaurid *Euoplocephalus* to propose a more complex pattern of mastication than had been previously been appreciated.

MATERIALS AND METHODS

This study is based on samples of hadrosaur teeth representing a latitudinal gradient that extends from northern Alaska to west Texas (Figure 1). The sample of dinosaur teeth was gathered from the Kikak-Tegoseak Quarry in northern Alaska (Fiorillo and Gangloff 2003; Fiorillo et al. 2010). This quarry is within the Prince Creek Formation, a largely fluvial rock unit that is based on biostratigraphy and radiometric dating and straddles the Campanian-Maastrichtian boundary (see discussions in Fiorillo 2006a; Fiorillo and Gangloff 2000, 2001; Gangloff et al. 2005; Fiorillo et al. 2009; Fiorillo et al. 2010), though the quarry itself is considered to be Early Maastrichtian in age (Fiorillo et al. 2010). These specimens are housed at the Museum of Nature and Science (formerly the Dallas Museum of Natural History).

Wear patterns on these Alaskan hadrosaur teeth were compared to wear patterns on samples of hadrosaur teeth found in more southern latitudes and include samples from southern Alberta, Wyo-

FIGURE 1. General map showing relationship of the four geographic areas that provided specimens for this study. The base map is for the Late Cretaceous (75Ma) from R. Blakey, Northern Arizona University. jan.ucc.nau.edu/~rcb7/namK75.jpg

ming, and west Texas. These southern samples are from Campanian, Maastrichtian, or Campanian/Maastrichtian aged rock units. Thus they are broadly correlative with the Prince Creek Formation (Table 1).

These southern samples were gathered from specimens housed at the Museum of Nature and Science, the Texas Natural Science Center (formerly the Texas Memorial Museum), and the Denver Museum of Nature & Science. Despite the institutional name changes for the first two organizations, the historic acronym has been retained in each case. Given that both the Museum of Nature and Science and the Denver Museum of Nature & Science both use the acronym DMNH, in this paper specimens from these two institutions are differentiated by the Denver Museum of Nature and Science specimens are listed here as DMNH [Denver]. The acronyms for specimens from these three institutions, respectively, are DMNH, TMM, and DMNH [Denver]. Table 1 is a list of taxa used in this study, the rock unit from which they were collected, and their general locality.

Horner et al. (2004) noted that wear is virtually continuous across the dental battery of hadrosaurs, thus providing the prediction that there would be little variance in microwear patterns among the teeth of a single tooth row. Specimens were obtained so that teeth could be examined across hadrosaurian tooth batteries (TMM 42314-1, TMM 40484-15, TMM 42315-1). These specimens are from southern Alberta and housed at the Texas Natural Science Center. Each tooth battery was examined to determine variation in microwear patterns across individual batteries to validate the use of isolated teeth as a proxy for microwear of individual hadrosaurs. Because adult hadrosaur maxillae do not fit into the chamber of scanning electron microscopes, epoxy replicas had to be generated. The tooth batteries were molded using Coltene Whaledent, and the subsequent casts were made using Tap Plastics 4 to 1 epoxy. Twelve teeth from three maxillae were examined.

Twenty-three isolated, unassociated teeth were examined. The lack of association among teeth provides a maximum number of individuals represented in the sample. These isolated teeth were collected from sites in Alaska, Wyoming, and Texas.

The LEO (now part of Zeiss) scanning electron microscope, model 1450 VPSE, housed in the Department of Geosciences at Southern Methodist University was used for this study. The wear surfaces of the teeth were examined at magnifications up to 1000X. The scanning electron microscope typically employed the backscatter detector. The parameters used to examine specimens are shown in Table 2. Analysis of patterns was facilitated by using Microware 4.02 developed by Ungar (2002).

TABLE 1. Geographic and lithostratigraphic data of samples of hadrosaur teeth used in this study.

Taxon	Institution	Site Location	Rock unit
Edmontosaurus	Museum of Nature and Science	Alaska	Prince Creek Fm.
Edmontosaurus	Museum of Nature and Science	Wyoming	Lance Fm.
Hadrosauridae	Texas Natural Science Center	Alberta	Oldman Fm
Hadrosauridae	Texas Natural Science Center	Texas	Aguja Fm.
Hadrosauridae	Texas Natural Science Center	Texas	Javelina Fm.
Hadrosauridae	Denver Museum of Nature and Science	Wyoming	Lance Fm.

TABLE 2. Scanning electron microscope parameters used in this study.

	Resin replicas	Actual specimens
Beam current (micro amps)	10 µA	10 µA
Beam energy (kilovolts)	20 kv	20 kv
Working distance (millimeters)	18 – 28 mm	18 – 28 mm
Chamber pressure (Pascal's)	30 Pa	15 – 30 Pa

Many parameters for assessing the significance of microwear are focused on patterns found in various mammal teeth where tooth structure is more clearly understood. The significance of some features is sometimes interpreted in relation to mammalian enamel microstructure (Maas 1991). The scale of magnifications used approached those used to study dental microstructure (Sander 1999; Maas 1991). Therefore regular patterns that appeared in either the dentine or the enamel were attributed to microstructure and were not included in the microwear analysis (Figures 2 and 3).

Two parameters used effectively in determining resource partitioning in dinosaurs are the presence of pits, and scratch or striation orientation (Fiorillo 1998). In addition to the presence of pits, I examined the percent incidence of pits (*sensu* Ungar 1994), which is the number of pits divided by the total number of features multiplied by one hundred. Microware 4.02 (Ungar 2002) provides the length of the mean striation vector, which is a measure of the concentration of the orientations of the long axis of each linear feature. Shorter vectors indicate more random distributions of features (where r = 0 or approaches 0), and longer vectors indicate more preferred distribution (where r = 1 or approaches 1).

Comparative studies of microwear have focused on patterns of enamel wear (Kay and Covert 1983; Teaford and Walker 1984; Teaford 1985; Teaford and Byrd 1989; Walker and Teaford 1989; Walker et al. 1978; Taylor and Hannam 1987; Rivals and Deniaux 2003; Hotton et al. 1997; Fiorillo 1998, 2006b, 2008; King et al. 1999; Goswami et al. 2005; Schubert and Ungar 2005). Wear on the enamel and dentine of the ornithischian teeth is considered here in detail. Although comparable studies are lacking for wear patterns on dentine surfaces, wear patterns preserved on the dentine are discussed here in the context of associated wear on the enamel of the teeth. With respect to relative wear on dentine versus enamel in the teeth of small theropods, it was noted that the softer dentine exhibited relatively coarser wear (Fiorillo 2006b, 2008). A similar pattern of relative wear was expected with these hadrosaur teeth.

It was not a prerequisite for individual teeth to have fully developed wear facets to be included in this study. All scanning electron microscope images were taken with the wear surface approximately perpendicular to the electron beam.

DISCUSSION OF MICROWEAR PATTERNS

The pattern of microwear along each of the three maxillae examined was consistent (Figures 4 and 5). Independently, Vincent Williams, a Postgraduate Researcher currently at the University of Leicester, examined a hadrosaur maxillary from the Belly River Formation of Alberta and noted a similar pattern for that specimen (www.le.ac.uk/gradschool/festival/pdf/WhatDidDinosaursEat.pdf). Therefore, the prediction implied by Horner et al. (2004) bears out regarding microwear patterns, and the use of isolated teeth as a proxy for individual animals is valid.

Given that dentine and enamel are of different hardness it is expected that each material will show a different pattern of wear. Indeed, for theropod teeth it was noted that dentine microwear patterns were more developed than microwear patterns observed in the enamel of similar theropod teeth (Fiorillo 2006b, 2008). Such a pattern holds true as well for the hadrosaur teeth used in this study. Figure 6 shows wear on a tooth from the Aguja Formation of west Texas. This tooth is representative of the discussion here. The dentine is the lighter gray area to the left of the image and shows an abundance of scratches compared to the nearly vertical band of darker gray enamel. Further, there is a broad scratch near the top of the image that is prominent in the dentine but loses definition in the enamel. Therefore, although somewhat intuitive given the softer nature of dentine compared to enamel, it is only appropriate in further comparisons to use either dentine wear or enamel wear to compare between teeth.

Pits are considered to indicate the consumption of harder food items (Teaford 1985; Taylor and

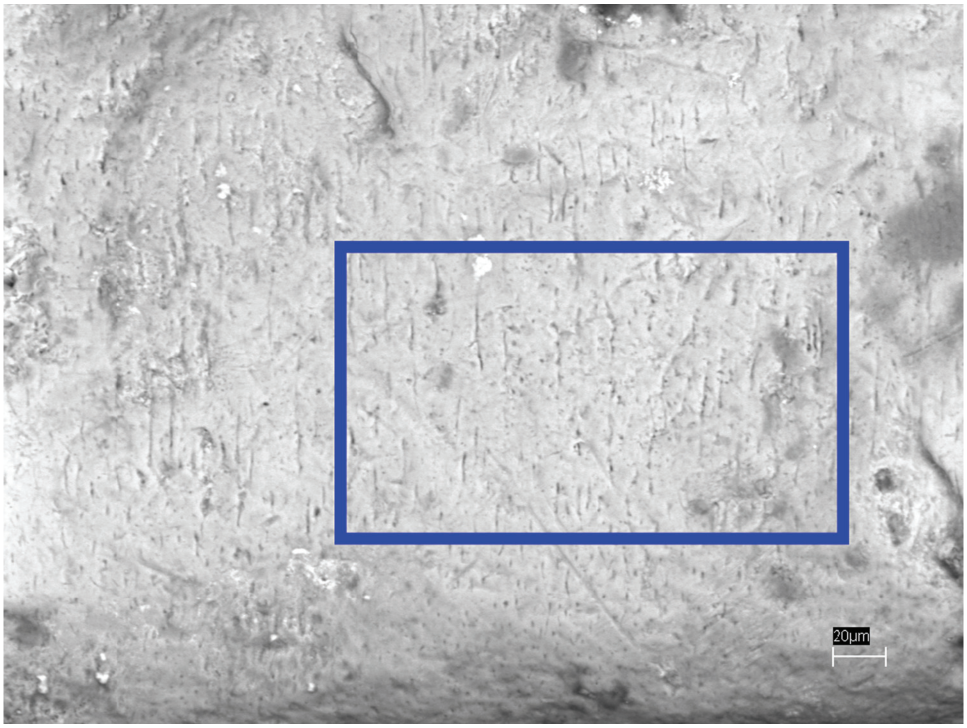

FIGURE 2. Photograph of the dentine wear surface of a hadrosaur tooth from the Lance Formation, Wyoming (DMNH[Denver]20378A) exhibiting the linear microstructure of the tooth expressed on the wear surface, outlined by rectangle.

Hannam 1987; Walker and Teaford 1989; Ungar 1994; Fiorillo 1998). Pits were not commonly observed on the teeth examined (Figures 4-10; Table 3). As predicted given the relative softness of dentine compared to enamel, the incidence of pitting was higher on dentine surfaces than on enamel surfaces. Further, the incidence of pitting remained relatively consistent independent of locality. Hence, this analysis suggests that hadrosaurs were consuming food items of similar hardness independent of latitude. In addition, scratch and pit density per tooth showed some variation within localities (e.g., compare Figure 7 with Figure 10). Such a variation may indicate either additional time chewing or the consumption of the occasional food item of a different hardness. Valdez and Krausman (1999) point out that given the wide geographic range of *Ovis*, it is reasonable to expect a great deal of breadth in food items consumed. The variations in wear observed here may likewise be attributed to a function of the broad geographic area occupied by these hadrosaurs.

A good deal of attention has been directed at scratch orientations in microwear studies to understand aspects of jaw mechanics and dietary preferences. When scratches predominate it is typically inferred to indicate a degree of jaw translation in the power stroke. With respect to hadrosaurs, tooth wear parameters have been shown to be best predicted by a hinge-like articulation between the maxilla and associated elements against the premaxilla and skull roof (Weishampel 1984). This mechanism, termed pleurokinesis (Norman 1984), provides a transverse power stroke through the lateral rotation of the maxillae in concert with the continuous upward movement of the lower jaws. Weishampel (1984) noted microstriae have a transverse orientation along inclined occlusal surfaces in hadrosaurs, that the wear was mirrored on both sides of maxillary and dentary teeth, and that wear striae are oriented approximately 79°-82° distally from the transverse axis of the tooth. Table 3 includes the length of the mean striation vector, which is a measure of the concentration of the orientations of the long axis of each linear feature of 10 representative teeth in the sample. The values in the table are less than conclusive regarding a preferred orientation for the striae examined on each tooth. This discrepancy may reflect that at higher magnifications (1000 X) the inclusion of very small striae obscures the more dominant pattern discussed by others (Weishampel 1984; Horner et

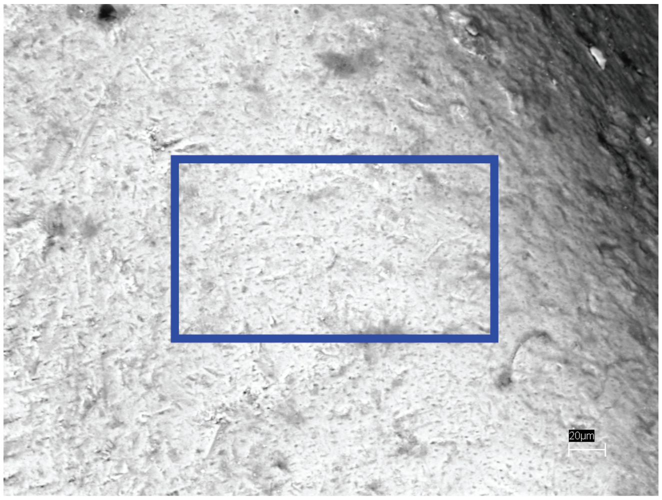

FIGURE 3. Photograph of the dentine wear surface of a hadrosaur tooth from the Lance Formation, Wyoming (DMNH[Denver]20378B) exhibiting the porous aspect of the microstructure of the tooth expressed on the wear surface, outlined by rectangle.

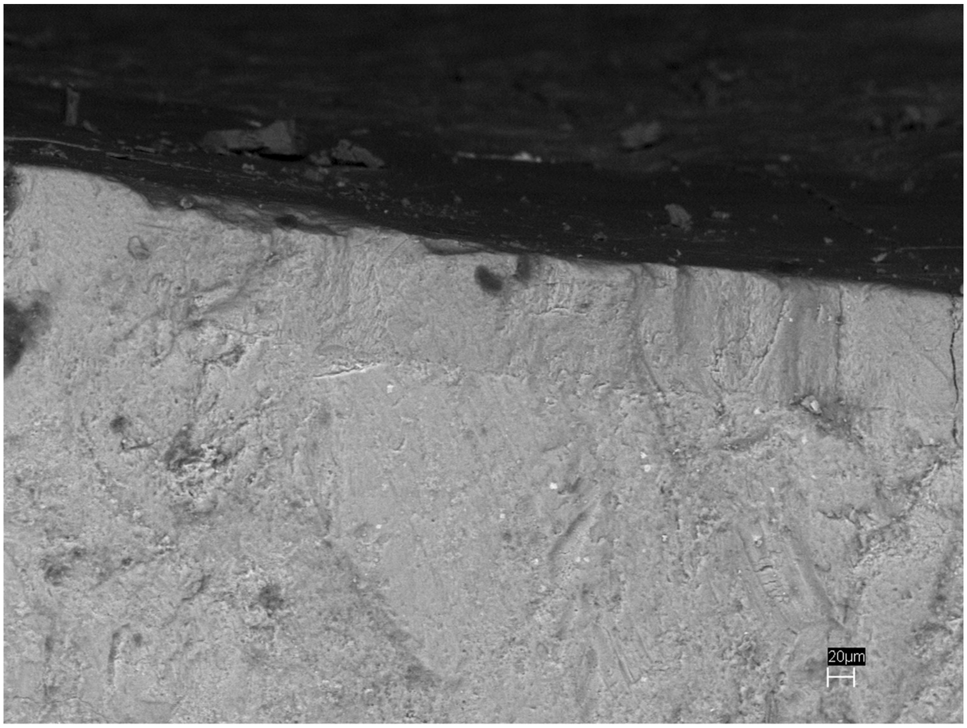

FIGURE 4. Photograph of the wear surface on a hadrosaur tooth from Alberta (TMM 42315-1D). Compare to wear in Figure 5.

al. 2004). Regardless of the cause of this discrepancy, there seems to be little difference between the geographic regions to justify further discussion.

DISCUSSION OF DIET

In correspondence with me, C.A. Repenning, the person who first correctly identified the dinosaur bones originally found along the Colville River, speculated that “the hadrosaurs had fed on root mats of *Equisetum* in the shallow water of the Arc-

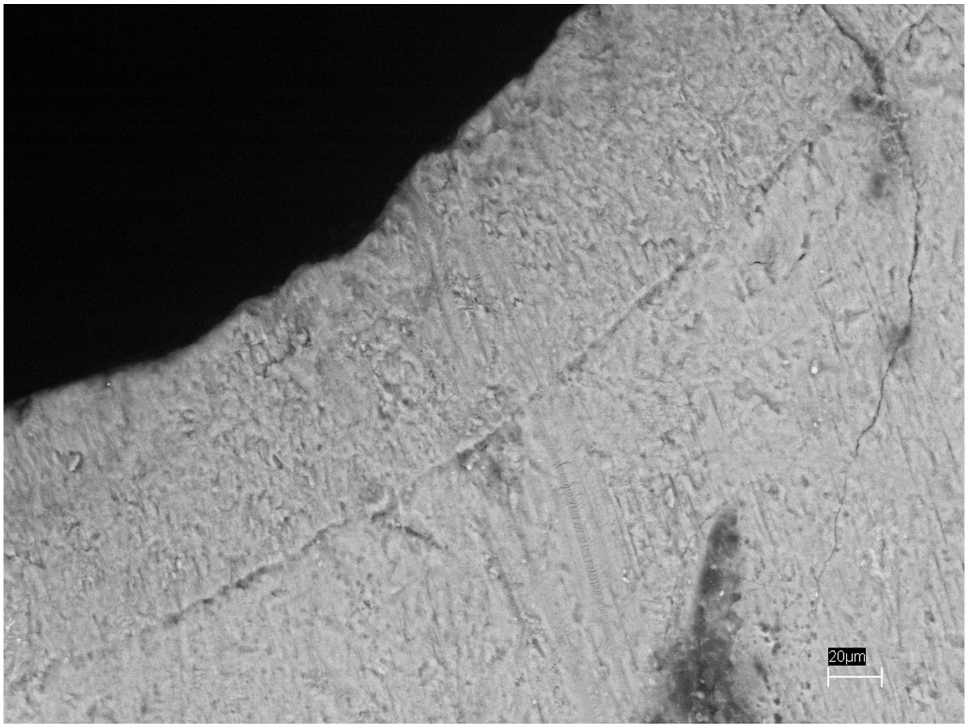

FIGURE 5. Photograph of the wear surface on a hadrosaur tooth from Alberta (TMM 42315-1B). Note the similarity to wear in Figure 4.

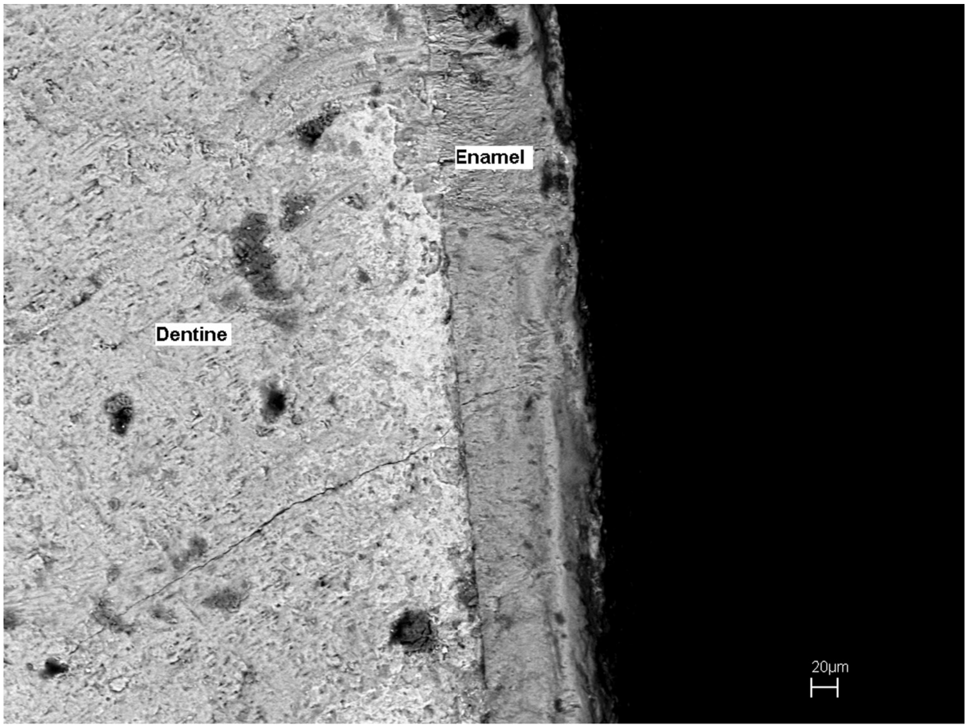

FIGURE 6. Photograph of the wear surface of a hadrosaur tooth from the Aguja Formation, Texas (TMM 42335-68C) showing the expression of coarser wear on the relatively softer dentine compared to that exhibited on the harder enamel. Notice the prominent, broad scratch in the dentine near the top of the image compared to the diminished scale of the same feature in the corresponding enamel.

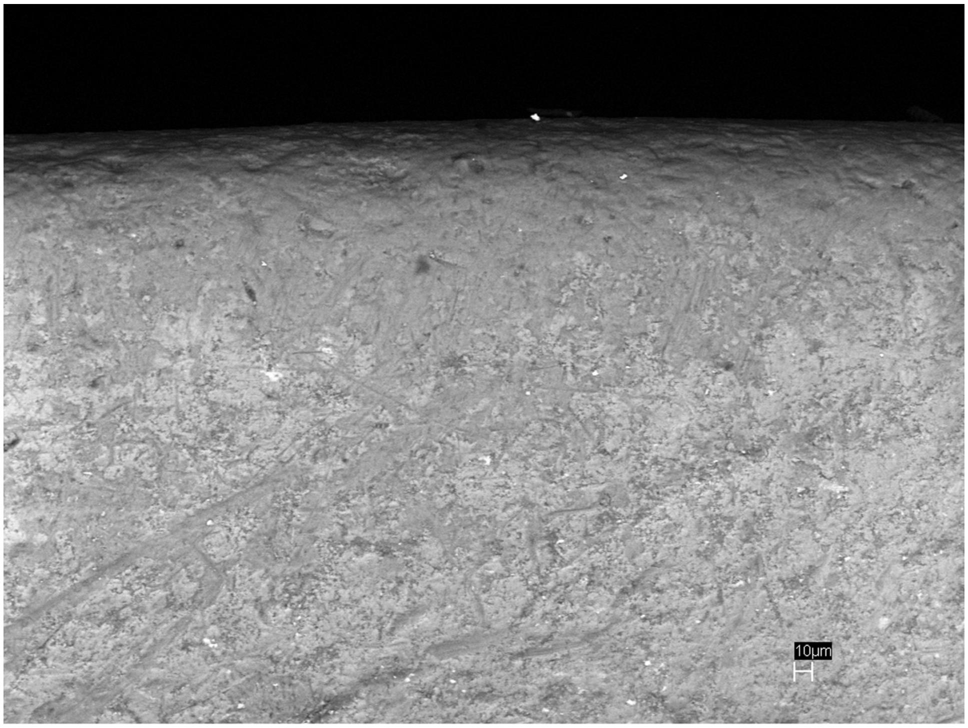

FIGURE 7. Photograph of the wear surface on a hadrosaur tooth from the Prince Creek Formation, Alaska (DMNH 22141). This wear surface is dentine only and shows an abundance of shallow scratches.

tic Ocean and kept alive because the ocean was not frozen and would have been relatively warmer than the air" (Repenning, personal comm., 2004). As an intriguing attempt to understand the biology of Alaskan dinosaurs, it is in the spirit of this speculation that I will review possible specific food types for these animals.

Teaford and Oyen (1989) suggested that coarse wear on teeth indicated that more time was spent chewing. Hadrosaurs, however, have the most efficient tooth batteries of any dinosaurian group (Weishampel 1984; Horner et al. 2004). Further, many heavily worn teeth attributable to hadrosaurs are often found as components of Late Cretaceous microvertebrate assemblages. So despite the fine wear patterns observed on the teeth used in this study, hadrosaurs must have spent significant time chewing food items.

In her study of potential food items for the sauropod *Brachiosaurus*, Weaver (1983) estimated the range of caloric values for Jurassic plants based on their modern relatives. Horsetails and ferns had the lowest caloric values; ginkgos were intermediate, cycads the highest, with conifers ranging from high to intermediate in value. Ginkophytes and cycadophytes are present in the warmest part of the middle of the Cretaceous but have been squeezed out by the Campanian on the North Slope (Spicer 1987; Spicer 2003), and therefore cannot be considered further as a potential food source. Ferns, however, are present as part of the floral assemblages of the North Slope.

The author discounts longterm use of either ferns or horsetails by Alaskan hadrosaurs for three reasons. First is the low caloric value of either plant group as illustrated by Weaver (1983). Secondly, horsetails commonly include siliceous granules in their cuticle. Siliceous particles, because they are abrasive, would leave a much coarser wear pattern than that observed on the teeth here. Similarly, the last reason is that given the short stature of ferns and horsetails, such plants are almost assuredly coated to some degree with grit, which would also serve as an abrasive and leave a coarser wear pattern on teeth.

Given the abundance of conifer remains from the Cretaceous rocks of northern Alaska, conifers would seem to be the dominant food source for hadrosaurs on the North Slope (Spicer 1987, 2003). Conifers seem to have the presumed needed caloric value as shown by Weaver (1983), and they have been found in hadrosaurian coprolites to the south in Montana (Chin and Gill 1996). The similarity in wear patterns supports similarity in

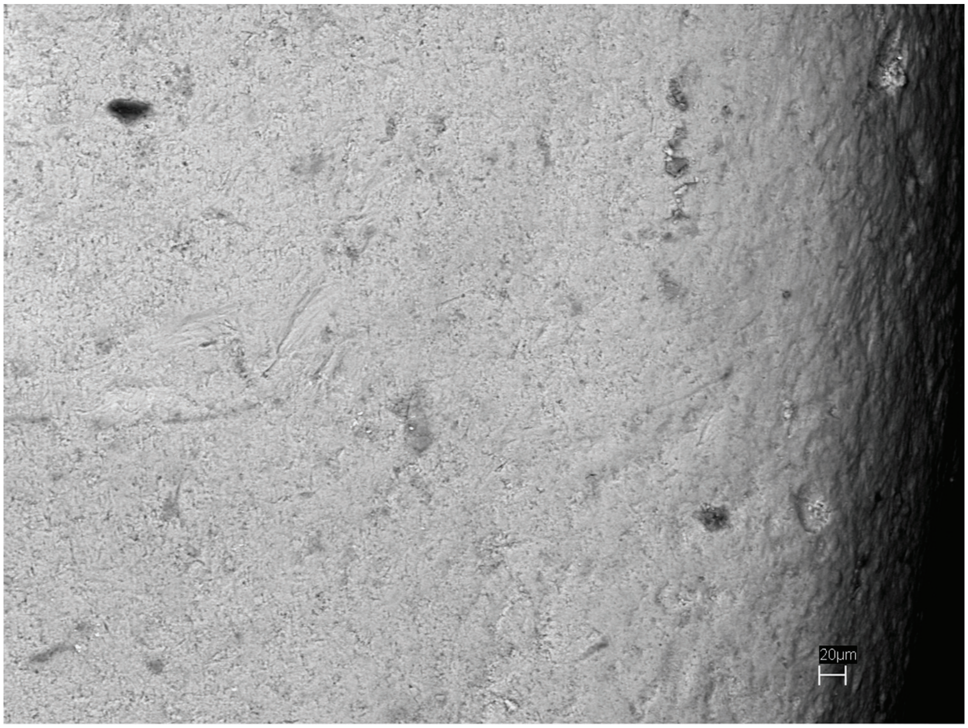

FIGURE 8. Photograph of the wear surface on a hadrosaur tooth from the Lance Formation, Wyoming (DMNH 22160). This wear surface is dentine only and shows an abundance of shallow scratches similar to that in Figure 7.

diet among hadrosaurs in these two general geographic regions, and similar wear among all populations of teeth examined suggests likewise.

The Cretaceous North Slope conifers are dominantly deciduous (Spicer 2003). Given the obliquity of light in the high latitudes during the Cretaceous (Spicer 1987; Fiorillo and Gangloff 2001; Fiorillo and Parrish 2004), the deciduous nature of the leafy part of the primary food source additional food sources should be considered.

Dead trees delignify and decay. Delignification with modern woods is brought on by wood-rot fungi (Tuor et al. 1995). Once delignification has occurred, wood, particularly conifer wood, has been recognized as a nutritious food source for domesticated ruminants (Orth and Orth 1977). Chin (2007) has recently described an intriguing specimen identified as a hadrosaur coprolite. The specimen contains small coniferous wood fragments. She attributes the appearance of partial decomposition to wood-rot fungi delignifying the wood prior to ingestion by this particular hadrosaur. Therefore, the author submits that it may be that during those parts of the annual cycle when deciduous plants lose their leaves, arctic hadrosaurs may have survived by consuming delignified wood, perhaps in combination with other adaptations (see next section).

Whereas delignified wood, in all likelihood, would be available all year, likely in limited quantities, given the deciduous nature of the vegetation, an additional food source during the Cretaceous spring of the ancient north may have been the buds and new wood. Anecdotally it has been observed along the Yukon River in central Alaska that black bears (*Ursus americanus*), after leaving hibernation, preferentially seek the new buds of trees because of the high nutritive value (O’Neill 2006).

To summarize, based on physical evidence found elsewhere such as coprolites, and nutritional inference from modern plants, a primary source of food for northern hadrosaurs was conifers. However, given the profound seasonality of light régimes, but not so much temperature seasonality during the Cretaceous, it seems likely other food resources were also utilized. These additional resources at this point can only be speculated upon. The only constraint provided by this study is that those foods qualitatively had a similar hardness. Further, the original prediction based on comparison to the dietary range of *Ovis* seems to be inconclusive for hadrosaurs as this study has

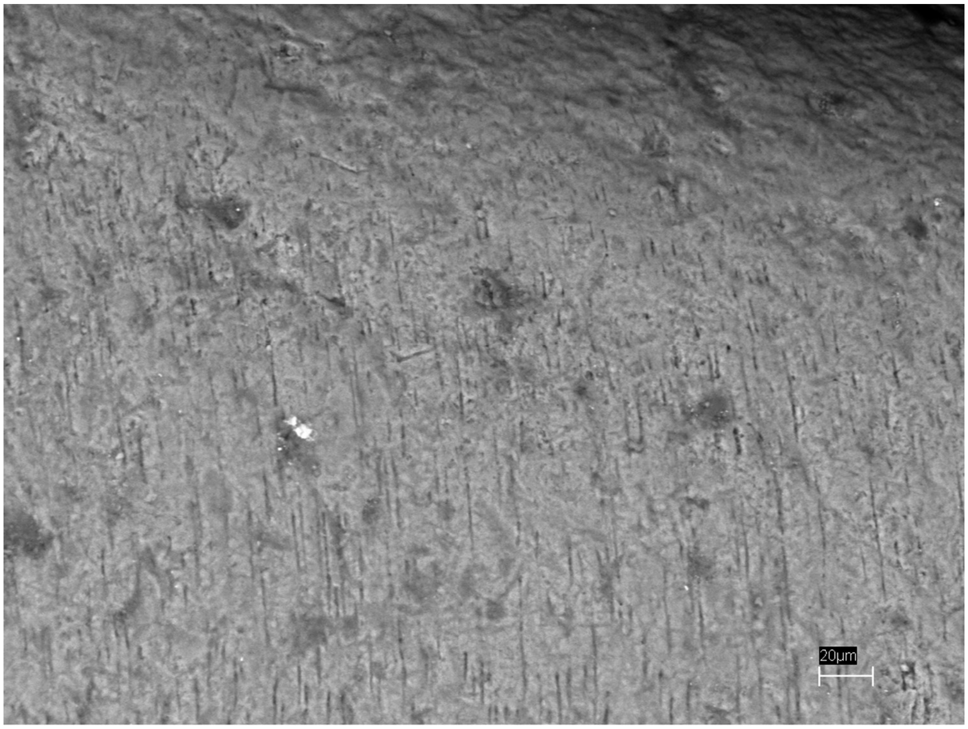

FIGURE 9. Photograph of the wear surface on a hadrosaur tooth from the Aguja Formation, Texas (TMM 43057-439D).

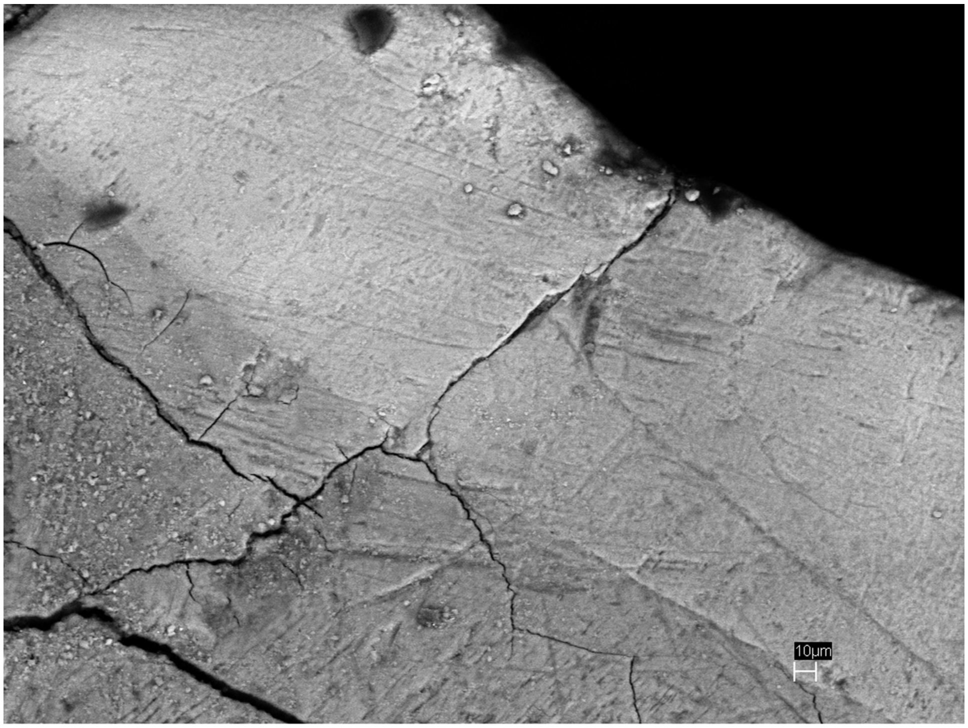

FIGURE 10. Photograph of the wear surface on a hadrosaur tooth from the Prince Creek Formation, Alaska (DMNH 22143). Note the higher density of microwear features on this tooth compared to those observed in Figure 7.

TABLE 3. Frequency of scratch marks and pits on a representative sample of teeth used in this study. DIP represents dentine incidence of pitting. EIP represents Enamel incidence of pitting. DIP and EIP expressed as percentages. Note the consistent pattern of higher incidence of pitting on the dentine surfaces. The open entries in the table reflect the dental surface was not preserved well enough to reliably discern features. Vector length refers to the length of the mean scratch vector and is a measure of the concentration of the orientations of the long axis of each scratch. More random distributions approach 0 and more preferred distributions approach 1 (see Ungar 1994, 2002).

Specimen number	Geography	DIP	EIP	Vector Length
DMNH 22143	Alaska	--	09	0.441
DMNH 22142	Alaska	--	11	0.356
DMNH 22141	Alaska	18	--	0.171
TMM 42315-1D	Alberta	14	0	0.295
TMM 42315-1B	Alberta	18	0	0.499
TMM 40484-21A	Alberta	--	13	0.283
DMNH 22160	Wyoming	17	--	0.398
DMNH [Denver] 20378D	Wyoming	15	13	0.293
TMM 43057-439D	Texas	17	--	0.397
TMM 42335-68C	Texas	13	11	0.442

pointed out a similarity in food hardness across the latitudinal range but an understanding of specific different food types remains ambiguous.

DISCUSSION OF ADAPTATION TO HIGH LATITUDES

When most people think of the modern high latitudes they think of the extreme temperatures. Most of those people however do not live in the Arctic. Those people that do live there tend to think of the annual cycle in terms of extreme changes in the light regime (D'Oro 2006). Therefore, despite a generally milder Cretaceous polar environment compared to that of today's high latitude (Otto-Bliesner and Upchurch 1997; Parrish and Spicer 1988; DeConto et al. 1999; Takashima et al. 2006), the annual variance in light regime should also be considered in discussing the Cretaceous Arctic.

Modern arctic organisms are remarkably complex and demonstrate high levels of adaptation (Irving 1960; 1972; Prestud 1991; Gray 1993; Pielou 1994). With vertebrates those adaptations are either structural such as issues related to insulation, behavioral such as use of shelter, body orientation or posture, or metabolic. Irving (1960 p. 345) noted, for example, in arctic birds that contour feathers differed from those birds farther south, with the net result being that arctic feathers retained more air than feathers on birds from warmer areas. Arctic hares (*Lepus arcticus*) use posture and body orientation to adapt to extreme changes in Arctic climate (Gray 1993). And arctic foxes (*Alopex lagopus*) adjust their metabolic rates to survive periods of low temperature and food scarcity (Prestud 1991), a strategy also employed by some arctic birds (Pielou 1994) and caribou (*Rangifer tarandus*, Jeffries et al. 1992). In *Rangifer*, it is now recognized that, due to the lighting conditions of the northern high latitudes, commonly but mistakenly referred to as six months of darkness and six months of sunlight (e.g., Bell and Snively 2008), that circadian activity is suppressed within this group (van Oort et al. 2005). Further, van Oort et al. (2005) speculate that a reduction in circadian organization may be an adaptative response for all resident polar vertebrates. This adaptation may also be advantageous in assisting animals with adjusting to the variation in the light/dark cycle. The breakdown in dependence on circadian rhythms may contribute to an animal's ability to reduce its metabolic rates during the winter.

I speculate further regarding the significance of the similarity in microwear patterns across all assemblages, independent of latitude, and the implication of similar food use. To accommodate similar food use in the dark part of the year in the northern latitudes hadrosaurs may have dropped their metabolic rates much as has been observed in modern vertebrates during times of food scarcity. Given that most of the conifers of Cretaceous Alaska are thought to be deciduous (Spicer 1987, 2003), this reduction in metabolic rates in northern hadrosaurs would allow them to survive periods of food scarcity. This reduction in metabolic rate may not have ultimately led to hibernation as it is difficult to imagine these animals living in such large numbers burrowing. Rather, this reduction may have been more similar to torpidity often seen in birds.

If the conifers of Cretaceous Alaska were deciduous (sensu Spicer 1987, 2003), thereby making food extremely scarce, the pattern of food use may provide insight into the metabolism of hadrosaurs in Alaska. In reviewing reptile life history strategies, Shine (2005) explored the question of how ectothermy may have shaped life history evolution in reptiles. A key point in reptilian ectothermy is the ability to decouple the time of energy acquisition (feeding) from energy expenditure (reproduction), allowing reptiles to withstand months or years of starvation. In contrast, within endotherms these parameters are intimately linked, providing the need for example for most migrating birds to refuel to complete the journey for breeding. If hadrosaurs ate the same type of foods, independent of latitude, then the source of calories was the same even if the quantity fluctuated seasonally for arctic hadrosaurs. Alaskan hadrosaurs may have essentially starved during the winter and reproduced during the short summer. In contrast to the trend in thinking that dinosaurs were endotherms, perhaps dinosaurs as reptiles represent the large-bodied end members of this ectothermic life history phenomenon.

Van Valkenburgh and Molnar (2003) put forth a supportive discussion for high-latitude dinosaurs' physiology. They recognized the compaction of niche space in small theropod guilds throughout western North America during the Cretaceous in comparison to modern ecosystems. They argued that this niche compression in high-latitude sympatric theropods implied reduced metabolic rates for these taxa, or in other words that high-latitude small theropods may have been ectothermic.

It should be clear from this discussion that high-latitude dinosaurs present intriguing challenges to what we think we know about dinosaur physiology and behavior. It is so often stated in paleontological studies that more work and more specimens are needed to resolve the specific topics of discussion in those studies. It is repetitive to suggest that more work and more specimens will add further insight into the discussion of the paleobiology of high-latitude dinosaurs, but with respect to this paleontological problem, it is appropriate to repeat what has been so commonly been stated before. That said however, given that the most important question regarding high-latitude dinosaur faunas remains, how they survived the long periods of darkness during the winter, potentially the most important aspect of further work would be to determine if there are patterns of seasonal variation in food use.

CONCLUSIONS

Dental microwear studies are valuable in qualitatively addressing patterns of food use in both extinct and extant vertebrates. This study has examined dental microwear patterns on the teeth of Campanian/Maastrichtian hadrosaurs from northern Alaska to western Texas. The results of the examination have shown similar patterns of tooth wear independent of geographic location, suggesting that hadrosaurs all along western North America were consuming food items with similar hardness.

The dominant food is considered to be conifers, although it is unlikely that conifers constituted the entire diet of high latitude hadrosaurs given the constraints imposed by a highly seasonal annual cycle, that cycle largely defined by variation in light regime. Further, given the similarity of food items consumed along such a large latitudinal gradient, combined with the deciduous nature of the food items in Alaska, it seems likely that northern hadrosaurs reduced their metabolic rates during the winter months, in a manner similar to many modern terrestrial arctic vertebrates. This reduction in metabolic rate during the winter months may have been facilitated if these animals were large-bodied ectotherms rather than endotherms.

ACKNOWLEDGMENTS

I thank D. Norton for his willingness to share his experiences and ideas about modern polar animal biology. I thank R. Tykoski and B. Hong of the Museum of Nature and Science for preparation of specimens used in this study, and K. Morton, also of the Museum of Nature and Science, for help with illustrations. I thank P. Ungar for providing access to Microware 4.02 and his willingness to share his thoughts and in press manuscript. I thank T. Rowe for access to the collections at the Texas Natural Science Center and L. Ivy for access to specimens at the Denver Museum of Nature and Science. I also thank E. Taylor for bringing to my attention the recent discussion regarding reindeer and circadian rhythms. And I also thank Rep for freely exchanging his thoughts on the paleobiology of Alaskan dinosaurs. I also thank R. Beavers for providing support for the Scanning Electron Microscope component of this study. Two anonymous reviewers provided insightful comments that greatly improved this manuscript. And, I appreciate the help of Dr. Federico Fanti for the Italian translation of the abstract.

The National Science Foundation grant OPP 0424594 and the Jurassic Foundation provided financial support for research on the North Slope. I also gratefully acknowledge the support of the Museum of Nature and Science, American Airlines, Whole Earth Provision Company, Arco Alaska, Inc., Phillips Petroleum, Inc., Alyeska Pipeline Service Company, Inc., and the Arctic Management Unit of the Bureau of Land Management for additional support in the field.

Lastly, this paper is dedicated to C.A. Repenning, first for his contributions to vertebrate paleontology in the northern high latitudes and secondly for being the first person to recognize the significance of Alaskan dinosaurs and starting the rush north for more.

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