Journal of Archaeological Science (2000) **27,** 789–798
doi:10.1006/jasc.1999.0502, available online at http://www.idealibrary.com on IDEAL®

Ondatra zibethicus (Arvicolinae, Rodentia) Dental Microwear Patterns as a Potential Tool for Palaeoenvironmental Reconstruction

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(*Received 29 September 1998, revised manuscript accepted 22 September 1999*)

Subfossil muskrat remains are numerous in the lower strata at the Lubbock Lake Landmark, Southern High Plains of Texas, dating from *c.* 11,100 BP to 8500 BP. This period witnessed a significant change in palaeoclimate and habitat at Lubbock Lake and the Southern High Plains. These changes caused the disappearance of many plant and animal species, and the emergence of many others. The muskrat, primarily herbivorous, altered their diet to accommodate these new plants. The scanning electron microscope and qualitative methods were used to analyse differences in dental microwear patterns for the two Lubbock Lake populations most distant temporally. Differential microwear patterns on the enamel of the lower first molars consistent with the changes in vegetation known for Lubbock Lake during the period of muskrat habitation were found.

Keywords: MUSKRAT, DENTAL MICROWEAR, ENVIRONMENTAL RECONSTRUCTION, SCANNING ELECTRON MICROSCOPE.

Introduction

Lubbock Lake Landmark is a well-stratified late Quaternary site in Yellowhouse Draw on the Southern High Plains of Texas (Figure 1). Muskrats (*Ondatra zibethicus*) were prevalent at Lubbock Lake during the late Pleistocene (*c.* 11,100–10,000 BP) and early Holocene (*c.* 10,000–8500 BP), but declined as the palaeoclimate became warmer and drier and surface water became less available (Johnson, 1987*a*; Lewis & Johnson, 1997). By 8500 BP, muskrats were no longer present on the Southern High Plains and do not inhabit the region today (Johnson, 1987*b*; Davis & Schmidly, 1994).

The Landmark (*c.* 120 hectares in areal extent) is situated within valley fill that has been aggrading since the latest Pleistocene. Five major geological strata (each with substrata and facies or local beds) and five principal soils formed in these deposits have been identified in the late Quaternary valley fill (Holliday, 1985, 1995*a*; Holliday & Allen, 1987). An extensive cultural, faunal, and floral record spanning the last 11,500 years is contained within this 8 m thick sequence of sediments and soils (Johnson, 1987*a*). The ages of the substrata, soils, local faunas, and cultural activities are well-controlled with close to 200 radiocarbon determinations (Holliday *et al.*, 1983, 1985; Johnson, 1993, 1995, 1999). Corrections for C^{13}/C^{12} fractionation and calibration for variations in the production of atmospheric C^{14} have been made by the radiocarbon laboratory when appropriate; however, ages have not been dendrocalibrated.

Muskrats inhabited Lubbock Lake during deposition of strata 1 and 2, the deposits of which record extensive sedimentological, faunal, environmental, and climatic changes (Holliday, 1985; Holliday & Allen, 1987; Johnson, 1987*a*, 1987*b*, 1987*c*). These changes, while preserved in detail at the Landmark, are also

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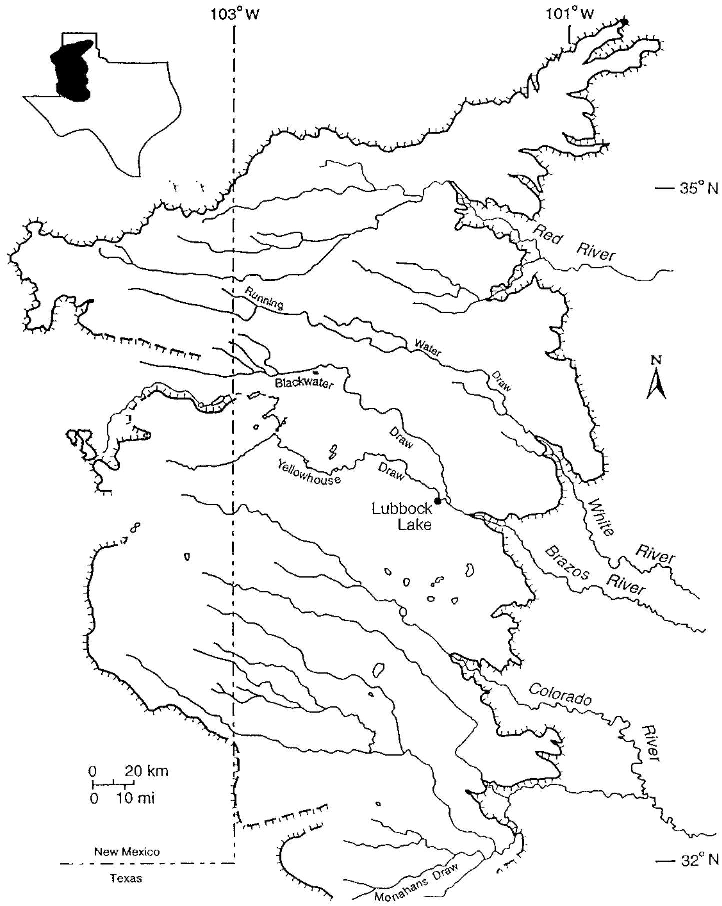

Figure 1. The Southern High Plains with the location of the Lubbock Lake Landmark.

seen on a regional scale (Johnson, 1986; Holliday, 1995*a*; Johnson & Holliday, 1995). Stratum 1, the oldest dated alluvial sediment, is 12,000 to 11,000 years old. During this time, bedded sand and gravel were deposited in most draws, indicative of competent streams flowing in the drainages (Holliday, 1995*a*, 1995*b*). At Lubbock Lake, stratum 1 consists of sands and gravels (substratum 1A), cross-bedded sands (substratum 1B), and clays (substratum 1C). This stratum represents a meandering stream deposit with point bar sediments (1A), and overbank deposits (1B and 1C).

Water ceased to flow and lacustrine deposition of stratum 2, in the form of diatomite and sapropelic mud, began conformably about 11,000 BP in some reaches in a number of draws (Holliday, 1995*a*, 1995*b*). At Lubbock Lake, substratum 2A consists of beds of pure diatomite and inter-bedded peaty muds. Substratum 2B is a homogeneous sapropelic mud. Stratum 2 represents a succession of open to marshy ponds developing into a slowing aggrading freshwater bog with little to no standing water (Holliday, 1985, 1995*a*, 1995*b*; Johnson, 1986; Johnson & Holliday, 1995). The Firstview Soil, formed in the upper part of 2B, began developing about 8500 BP, marking a stable land surface with little deposition or erosion.

Stratum 1 proxy data indicate an equable, humid, maritime palaeoclimate with a lower mean annual temperature than today, and cooler summers and warmer winters that lacked extended freezing conditions. A parkland (grassland interrupted by small stands of trees) existed along the draw. A low gradient stream, with hackberry trees, emergent vegetation, and sedge beds along the banks and margins, meandered through the valley (Johnson, 1986, 1987*b*). An undetermined event altered the course of the stream around 11,000 BP and a ponded environment formed. Water levels in these ponds fluctuated; the water was centimeters to metres deep and was periodically at or below the surface, exposing the floor of the draw. Wet meadow grasses and sedge beds around the ponds graded into better-drained mixed grasslands along the valley floor. An occasional deciduous tree grew on the draw slopes and around the ponds.

By 10,000 BP, the ponds evolved into muddy marshes that by 2B times change into an extensive, shallow wet meadows–marshlands with emergent vegetation and sedge beds. A scrub-grassland dominated the draw. Periodic droughts and disappearing surface-water resources denoted the trend towards modern climatic conditions. Sand sheets formed, mainly on the

Table 1. Data on molars used in microwear study (u2B=upper 2B). Wear categories for each specimen are given (p=pitted, s=striated, +=heavy, − =light)

Specimen	Substratum	Area	Feature	Side	Length (mm)	Width (mm)	Ratio	Wear
TTU-A36673	1B	2	FA2-1	Right	7·4	2·9	2·55	p
TTU-A16838	1B	2	FA2-1	Right	7·5	3	2·5	p+
TTU-A20198	1B	2	FA2-1	Left	7·3	3	2·45	p
TTU-A931	1B	2	None	Left	7·2	2·9	2·52	p −
TTU-A21926	u2B	6	None	Right	6·7	3	2·27	s+
TTU-A20843	u2B	5	FA5-7	Right	7·6	3·3	2·3	s+/p −
TTU-A20824	u2B	5	FA5-7	Left	7·5	3·2	2·32	s
TTU-A23723	u2B	5	FA5-7	Right	7·6	3·2	2·38	s

western half of the Southern High Plains, indicating a regional reduction in vegetative cover (Johnson & Holliday, 1995; Holliday, 1997). Effective precipitation decreased and maximum summer temperatures rose, marking the waning stages of pluvial conditions. The Lubbock Lake freshwater marshland became shallower with the water table at or below the surface. The muskrat that had inhabited it disappeared. Eventually, the marshland turned brackish and, regionally, alkaline marshes began to dominate the floors of the draws (Holliday, 1995*a*). These hydrologic changes resulted both from warming of water and from reduction in effective precipitation that decreased the discharge of springs and seeps (Holliday, 1995*a*). Deposition of aeolian sediments in the draws and the formation of dunes on the uplands became increasingly more common (Holliday, 1997).

At Lubbock Lake, muskrat remains are found in substrata 1B (*c.* 11,100 BP), 2A (10,800 to 10,200 BP), 2B cienega (*c.* 10,000 to 9500 BP), and upper 2B (*c.* 9500 to 8500 BP) (Johnson & Holliday, 1989). During the period of muskrat occupation, the mean annual temperature rose from *c.* 13°C (55°F) to *c.* 19°C (66°F) while the mean annual rainfall fell from *c.* 75 cm per year to *c.* 40 cm per year (Johnson, 1987*b*). This change in climate and habitat caused significant alterations in the flora and fauna at Lubbock Lake (Johnson, 1987*c*; Thompson, 1987). As muskrats are mainly herbivorous, it was hypothesized that the change in vegetation would be accompanied by a concomitant change in microwear on the enamel of their molars. The detailed information on stratigraphy (Holliday, 1982; Holliday & Allen, 1987) and palaeoenvironment (Johnson, 1987*b*) available from Lubbock Lake and for the Southern High Plains (Holliday, 1985, 1995*a*; Johnson, 1986; Johnson & Holliday, 1995) provided an excellent opportunity to view muskrat response to environmental change.

Microwear patterns on the enamel of muskrat lower first molars (M_1) are used to evaluate changes in the plant material processed by the muskrat. The research hypothesis states that microwear patterns that are distinctly different from each other should be found on molars from substrata 1B (N=8) and upper 2B (N=7) and that the patterns are related to differences in the environments of the two muskrat populations. As a test of the hypothesis, eight specimens were analysed: four molars from the oldest (*c.* 11,100 BP) population (1B); and four from the most recent (*c.* 9500–8500 BP) population (upper 2B). Approximately 1500 years separate these two populations, making them the most distant temporally and representative of greatly differing climates and habitats (Johnson, 1987*a*).

Methods

Lower first molars were chosen for this analysis based on four criteria: (1) they are the most abundant element in the Lubbock Lake muskrat collection (N=112 total M_1s); (2) they have been recovered from other Southern Plains Pleistocene deposits (Lundelius, 1972; Dalquest & Schultz, 1992); (3) they are significantly involved in mastication (Gromov & Polyakov, 1992); and (4) they have been well-studied in previous research (Nelson & Semken, 1970; Martin, 1979; Viriot *et al.*, 1993; Lewis & Johnson, 1997; Lewis, 1998). Individual molars were selected based on time period, degree of obvious wear, preservation, and lack of obstructions or damage on the occlusal surface.

As more than one molar from a single individual would bias the results, all molars selected are from different individuals. While independence is an assumption, size, provenience (horizontal and vertical), siding data, and subjectively determined differences in shape and colour of individual molars make it improbable that any two specimens analysed are from the same individual (Table 1). The molars used from 1B and upper 2B are from adult muskrat that had moderate enamel loss from wear typical of modern muskrats 2 to $2\frac{1}{2}$ years old (Galbreath, 1954; Viriot *et al.*, 1993; Lewis, 1998). At this age, the moderate loss of enamel on the anterior loop is due to wear.

The occlusal surfaces were cleaned with reagent-grade acetone to remove any particles adhering to the enamel. Four of the eight molars from 1B were suitable (TTU-A36673, TTU-A16838, TTU-A20198, TTU-A931) and four of the seven from upper 2B

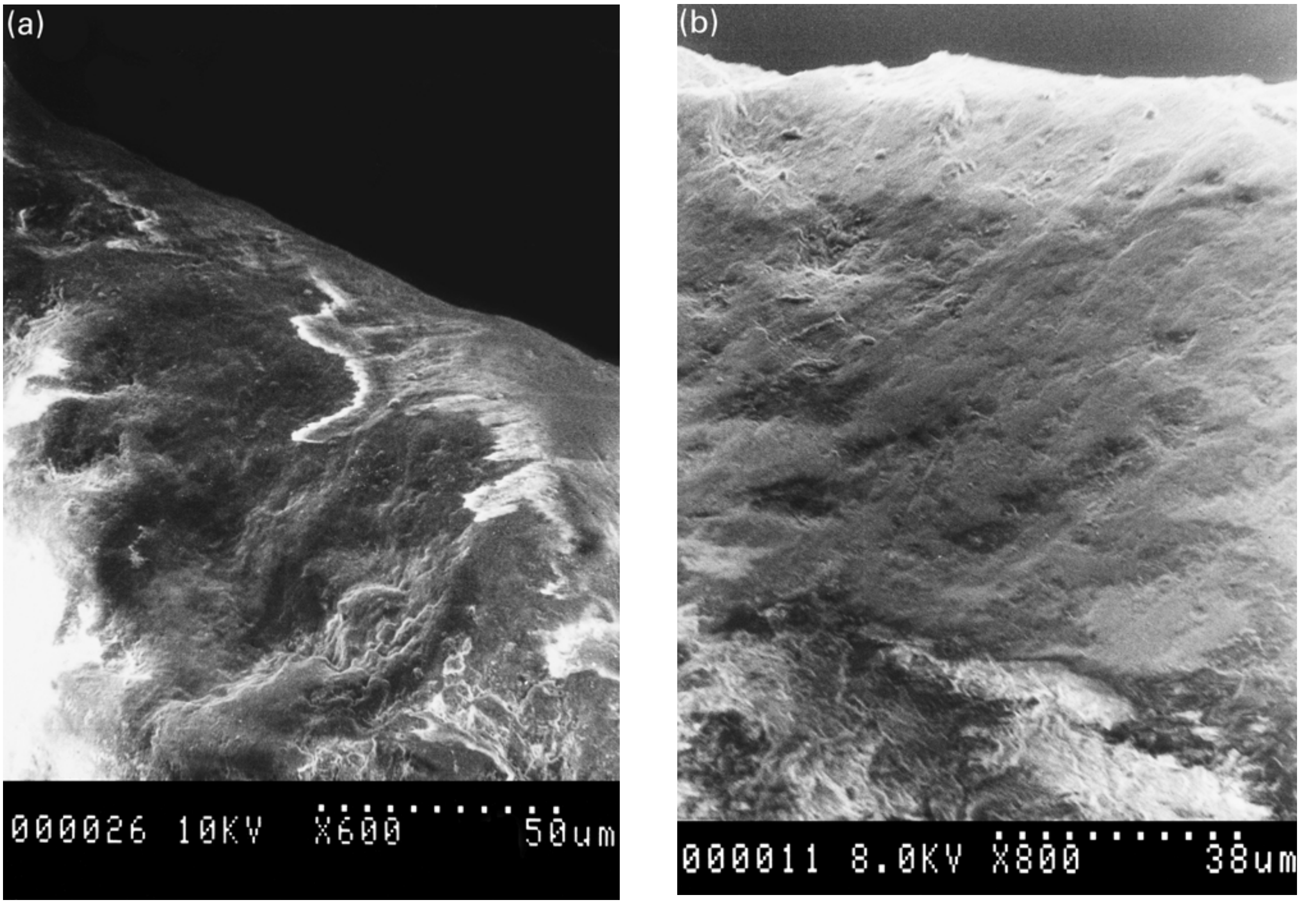

Figure 2. Pitting on the M_1 enamel from 1B muskrat. Note the lack of scratches ((a) at 600 × ; (b) at 800 ×).

(TTU-A21926, TTU-A20843, TTU-A20824, TTU-A23723). These eight molars were placed together and selected randomly for scanning electron microscope (SEM) analysis to avoid any bias in the recording of features or interpretation.

Although SEM specimens generally are coated with a conductive material (such as gold or palladium) that allows dissipation of the electrons (Teaford, 1991), the eight Lubbock Lake molars were not coated. Museum of Texas Tech University policy does not allow coating of original objects because of potential damage to delicate specimens. The teeth were too fragile to take moulds and make replicas that would be coated (e.g. Rose, 1983). While the charging caused poor contrast in many photographs and occasionally affected the colouring of the molars, the microwear features clearly were discernible (Gutierrez *et al.*, 1998) (Figures 2, 3).

The SEM photomicrographs were taken primarily on the buccal side of the anterior loop in order to standardize location, as microwear patterns generally are found in regular patterns and in certain locations on the tooth (Teaford, 1991). Exact placement of the target area on each molar could not be standardized precisely due to equipment limitations. Several positions and magnification levels were used in photographing each molar through the SEM, with microwear patterns best discernible at high magnification levels (700 × to 1000 ×).

Both quantitative and qualitative methods can be used in microwear analysis (Teaford, 1991; Strait, 1993). Due to the inability to duplicate exactly the areas examined for wear on each molar, only qualitative methods have been used with the Lubbock Lake specimens. Qualitative methods focus on the differences in abundance, size, and shape of microwear features and are most reliable when marked differences occur in wear patterns (Teaford, 1991). The most common microwear features are pits and scratches. Scratches are linear depressions, while pits are features exhibiting length to width ratios of 4:1 or below (Strait, 1993). The molars have been classified as having pits, scratches, a combination, or featureless.

Results

Microwear patterns associated with the four molars from 1B show substantial pitting (Figure 2(a), (b)). The

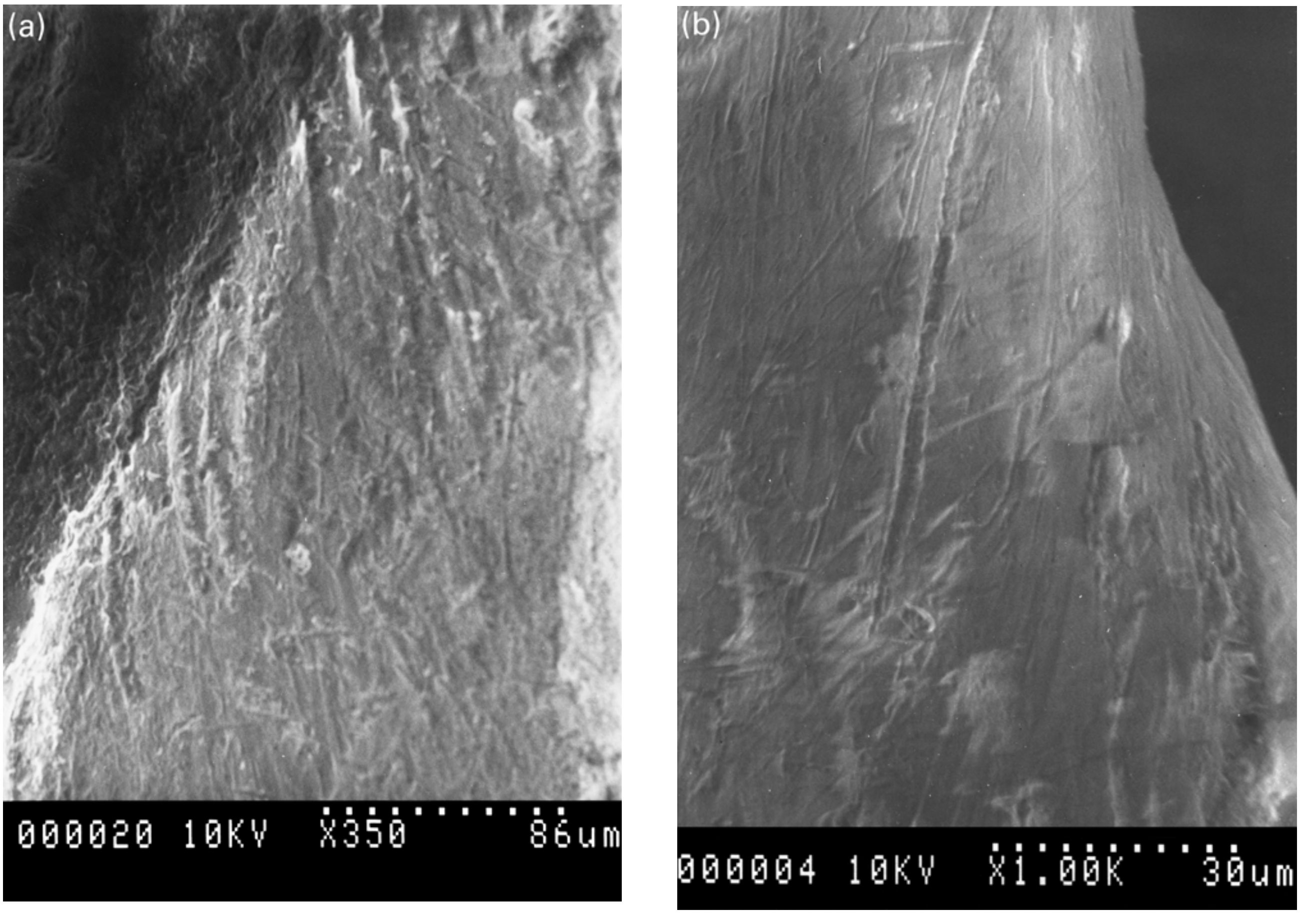

Figure 3. Abundant scratches and lack of pits on the M_1 enamel from upper 2B muskrat ((a) at 350 ×; (b) at 1000 ×).

outer edge of the enamel appears to have the highest amount of wear, and a distinctive lack of discernible patterns is seen over much of the remaining enamel surface. While the molars vary in degree of pitting, few, if any, striations are visible at any magnification. Previous research has determined that hard food items tend to leave pitting rather than scratches (Teaford, 1991; Strait, 1993), suggesting that 1B muskrats included hard food items (i.e. twigs, bark, or vertebrates) in their diet. The pits result from the crushing of hard plant matter or bone (Hillson, 1986).

The microwear patterns on the molars from upper 2B exhibit an abundance of scratches and very little noticeable pitting at all magnification levels (Figure 3(a), (b)). These scratches tend to be long and narrow (10:1 or greater), and frequently cross one another. The pitting along the outer edge of the enamel is reduced greatly compared to the 1B molars, and the quantity of microwear features in general is much higher in the upper 2B sample. The characteristic microwear feature associated with soft material is scratches rather than pits (Teaford, 1991). Scratches are caused by mineral particles such as plant phytoliths, sediment, or dust (Hillson, 1986).

Discussion

Multiple subspecies

Muskrat populations from 1B and upper 2B represent different subspecies diagnosed through an independent morphometric analysis that used all suitable molars from 1B, 2A, and 2B (N=45) (Lewis, 1998; Lewis *et al.*, submitted). The subspecies distinction is due to statistically significant morphological differences in the M_1 occlusal surface at levels exceeding those found between modern subspecies. The diagnosis of the two subspecies is based on analyses of 33 measurements on the occlusal surface of the M_1 using several multivariate methods (Lewis, 1998; Lewis *et al.*, submitted). Modern levels of variation have been estimated based on data from four modern subspecies surrounding the Southern High Plains. These data also demonstrate that the Lubbock Lake specimens were morphologically distinct from nearby modern subspecies (Lewis, 1998). A reversal in the direction of size change in the M_1, the magnitude of morphological change, and a gap in the muskrat fossil record (*c.* 200 years between the most recent 1B and earliest 2A specimens) separating morphotypes all indicate a change in subspecies rather than the evolutionary response of a single subspecies (Lewis, 1998). This microwear analysis, therefore, reveals the differences in wear patterns between two different subspecies rather than changes in a single, evolving subspecies. The acceptance or rejection of the two subspecies, however, is not critical to the findings of this research if it is accepted that muskrat enamel is consistent between subspecies, and no evidence is known that would disallow this assumption.

The occurrence of contemporaneous muskrat subspecies coexisting at Lubbock Lake is not supported. The differences in morphology appear associated with differing, and temporally distinct, hydric environments at Lubbock Lake (Johnson, 1987*a*). Remains of the two subspecies are not found together except in reworked sediments. Two subspecies could not live in close proximity for *c.* 2500 years (spanning first to last appearance) and remain morphologically distinct without an isolating mechanism, and such a mechanism is not apparent at Lubbock Lake. The unfavourable habitat caused by the alteration of the stream prompted the 1B subspecies to disperse, while the formation of ponds provided a new environment for another subspecies to colonize Lubbock Lake.

The exploitation of different niches for these two Lubbock Lake subspecies is supported by the dental microwear patterns and further suggests the presence of two distinct subspecies of muskrat during the late Pleistocene and early Holocene on the Southern High Plains. This condition is found today, among many other locations, in New Mexico where the subspecies *Ondatra zibethicus cinnamominus*, *O. z. osoyoosensis*, and *O. z. ripensis* all coexist in the northeastern quadrant of the state (Willner *et al.*, 1980). *Ondatra zibethicus ripensis* is a river dwelling subspecies, while the other two subspecies more typically are from ponds and lakes. Their distributions do not appear to overlap significantly (Wilner *et al.*, 1980). While modern subspecies living in close proximity to each other presumably have significant gene flow [based on hybridization (Hollister, 1911) and a lack of speciation], unique and predictable molar morphologies persist between them (Lewis, 1998; Lewis *et al.*, submitted).

The effects of the changing palaeoenvironment on muskrat molar morphology are demonstrated further by changing length to width ratios. Molar length/width ratios are large for muskrats in cool climates, while muskrats from warm climates exhibit smaller ratios (Semken, 1966; Nelson & Semken, 1970). Lubbock Lake samples are in agreement with this model as the ratio for the oldest sample of muskrats, those living in the cool climate, are significantly higher than those from subsequent substrata (Lewis & Johnson, 1997). The ratio of the substratum 1B muskrats appears intermediate to those of fossil muskrats of the Wisconsin Period and modern northern muskrats from Michigan (Figure 4). The substratum 2A ratio is near the ratio found in recent muskrat populations from Michigan. This trend towards smaller ratios continues

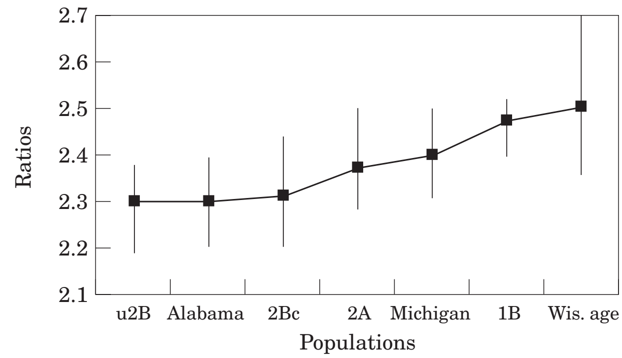

Figure 4. M_1 ratios of muskrat populations from the Wisconsin Period, modern Michigan and Alabama, and the four Lubbock Lake samples (data from Nelson & Semken, 1970; Lewis & Johnson, 1997).

Table 2. Flora found in muskrat-bearing substrata at Lubbock Lake (Bryant & Schoenwetter, 1987; Thompson, 1987)

Common name	Taxon	1B	2A	2B
Netleaf hackberry	*Celtis reticulata*	×		
Chara	*Chara*		×	
Goosefoot	*Chenopodium*		×	
Sedges and rushes	*Cyperaceae*	×	×	
Spikerush	*Eleocharis*	×	×	
Horsetail	*Equisetum*		×	
Bulrush	*Scirpus*	×	×	×
Cattail	*Typha*		×	×

as both of the 2B samples bear a close resemblance to recent muskrats from Alabama and central Texas (Nelson & Semken, 1970; Lewis & Johnson, 1997).

Dietary factors affecting microwear

Muskrats are herbivorous and subsist largely on vegetation in and around water sources (Table 2; Bellrose, 1950). The most abundant and convenient food source ordinarily is used, although cattails (*Typha* spp.) and bulrushes (*Scirpus* spp.) appear to be favoured (Bellrose, 1950). When aquatic and semiaquatic plants are not available, woody plants and the bark of trees also may be eaten (Errington, 1963; Gromov & Polyakov, 1992). Muskrats consume animals such as crayfish, frogs, snails, and fish (Bellrose, 1950; Sather, 1958) during periods of low plant availability (Dauphine, 1965; Gromov & Polyakov, 1992). Food is not stored for winter (Gromov & Polyakov, 1992).

The differences between the diets of modern riverine and pond/marsh populations are unclear due to the lack of research. Studies of muskrat diet have centred on marsh populations due to their prevalence (Bellrose, 1950; Sather, 1958; Errington, 1963), as true riverine populations probably are uncommon. Differing feeding strategies are assumed in this study based on types of plants available in the respective environments and the preferences of muskrats in general. The possible movement between the differing environments in regions where both exist complicates this assumption. For modern *Ondatra zibethicus ripensis* from southwest Texas, the opportunity to utilize both habitats is limited by the relative rarity of year-round ponds and marshes. The movements of 1B muskrats are more uncertain. Microwear patterns, however, change rapidly with any change in diet (Teaford, 1991) and patterns found on 1B molars are assumed to represent wear incurred at Lubbock Lake.

Different habitats and plant communities are associated with substrata 1B and 2B. Substratum 1B is representative of a stream habitat (Johnson, 1987*a*) where woody plants generally would grow on the bank and fewer of the emergent and submergent plants preferred by muskrats would be available (Kozlowski *et al.*, 1991; King, 1997). Upper 2B represents a very shallow freshwater marsh habitat where the emergent and submergent plants are consistent with a marsh environment (Johnson, 1987*a*; Thompson, 1987). Emergent and submergent plants generally are softer, as hard structures are not required for water-dwelling flora (Larcher, 1980; King, 1997). While the plant species consumed by 1B and upper 2B populations would exhibit considerable overlap, the relative percentages of plant species utilized would be different between the two populations.

Plant remains associated with both strata, known from fossil pollen and plant macrofossils (i.e. seeds and molds) (Bryant & Schoenwetter, 1987; Thompson, 1987), are species utilized by modern muskrat as food sources and lodging material (Bellrose, 1950; Sather, 1958; Errington, 1963). For substratum 1B, the netleaf hackberry, a woody plant with leathery leaves associated with watercourses (Petrides & Petrides, 1992), is the tree species found, and was probably utilized by the 1B muskrat. Trees in general are not represented in upper 2B, indicating a significant change in vegetation pattern. The other two plants from 1B deposits are consistent with both riverine and pond/marsh environments (Thompson, 1987). Additional rushes appear in the 2B record, indicating an increasingly varied habitat of emergent vegetation. A difference in diet is suggested due to differing availability of plant species, i.e. woody plants likely made up a higher percentage of the 1B muskrat diet than for upper 2B muskrat.

Muskrats are known to be faunivorous, eating small vertebrates and mollusks, during periods of poor plant food availability (Errington, 1963). Faunivory is known to cause distinctive wear patterns (Strait, 1993). As pitting generally is an indication of hard-object faunivory (Strait, 1993), the pitting of 1B molars suggests that if these muskrat were engaged in faunivorous feeding, their prey may have included hard-body vertebrates. Several muskrat prey species (such as small reptiles, amphibians, and fish) are available at Lubbock Lake during 1B times that could have served as a food source (Johnson, 1987*c*). While the lack of pitting in the upper 2B muskrat population does not support hard-object faunivory, soft-bodied invertebrates present at Lubbock Lake (Johnson, 1987*a*) may have been consumed (Strait, 1993). The lack of pitting supports the increased availability of quality plants in the upper 2B habitat.

Non-dietary impacts on microwear

Muskrats may use their molars in the cutting and moving of lodging material. The two most common types of lodging are burrows dug on high, solid banks near the water's edge, and organic lodges constructed in shallow, marshy areas without suitable banks for burrowing (Sather, 1958; Dauphine, 1965). While incisors and fore- and hindlimbs are used for digging burrows (Errington, 1963; Gromov & Polyakov, 1992), the molars are apparently not. Construction materials normally consist of the dominant emergent plants in the surrounding environment (Sather, 1958). Lodges are typically built on firm substrate. Based on the behaviour of modern muskrat and the palaeoenvironmental conditions at Lubbock Lake, 1B muskrat most likely dug burrows and upper 2B muskrat built lodges. The degree that lodge building affects molar wear is unclear. However, lodge-building populations presumably process more soft plant material than burrowers and this processing may affect microwear patterns. As it is likely that 1B muskrat dug burrows rather than constructed lodges, wear on their molars should principally be the result of foods processed. Wear on upper 2B molars, however, should be the result of processing both food and possibly lodging materials.

Palaeoclimatic and palaeoenvironmental conditions at Lubbock Lake and the Southern High Plains indicate wind-blown dust during upper 2B times (Johnson, 1987*a*; Holliday, 1995*a*, 1997). An increase in amount of dust deposited on food plants may be responsible for increased scratching of enamel (Hillson, 1986). The decrease in pitting, however, is not accounted for with this explanation, but rather indicates either a difference in plant species utilized or an increase in aquatic vegetation being processed. The change from burrows to lodges, increase in abundance of emergent and submergent plant species, and wind-borne transport of dust particles during upper 2B times are all factors that may have increased the quantity of scratches on enamel. These factors probably are working in concert given the dramatic increase in scratches. The decrease in pitting, conversely, is accounted for only by a decline in hard-object processing. This decline most likely is a result of less processing of woody plants and a decrease in hard-object faunivory; both permitted by the abundance of preferred plant species in upper 2B. The addition of C^4 grasses into the diet also could have produced more striations. Given the increase in preferred food plants and the difficulty in processing these tough grasses, this addition seems unlikely.

Modern muskrat in deteriorating (drying) habitats prefer to alter their diets rather than disburse to different locations (Errington, 1939). As the muskrat is a large semi-aquatic rodent, travelling over dry land is perilous due to the threat posed by predators (Errington, 1939, 1963). While muskrats are reluctant to disperse, juveniles may do so at any time and extreme environmental change, such as drought or change in course of the waterway, may induce mass dispersal (Errington, 1939). As annual rainfall amounts fell and temperatures rose during the early Holocene, the Lubbock Lake semi-aquatic fauna (with a spring-fed water supply) became increasingly isolated (Johnson, 1987*b*). This isolation caused overland-travel distances to increase for semi-aquatic species, thereby making travel more precarious and the need to modify diet critical. Changes in molar morphology suggest, however, that 1B muskrat disbursed when the stream disappeared from Lubbock Lake, and the area subsequently was repopulated by 2A muskrat (Lewis, 1998). The 2A muskrat remained at Lubbock Lake and modified their diets with the changing environment until they disappeared *c.* 8500 years ago.

Future research

The analysis of any new specimens from 1B and upper 2B could strengthen the conclusions drawn from this initial study. Although a significant increase in sample size per substratum is unlikely, the use of quantitative methods per molar would allow a more precise and accurate description of the microwear patterns. The exact number of features over a given area could be determined and compared through statistical analyses, such as covariance and regression. More modern SEM equipment would reduce the effects of charging due to the lack of coating and improve the quality of images used in analysis. The inclusion of molars from the intervening substrata would prove valuable in viewing the changing feeding strategies for all muskrat populations at Lubbock Lake and further detailing the environmental change.

The analysis of molars from modern riverine and pond/marsh muskrats eating known plant communities would test the association of particular wear patterns to distinctive habitats and clarify the differences in diet between these populations. In turn, comparison of the microwear patterns of subfossil muskrat from other localities with the Lubbock Lake results would be worthwhile (e.g. Johnson *et al.*, submitted). A correlation between wear pattern and palaeohabitat at other localities would support the conclusions drawn from this initial Lubbock Lake muskrat study. This research has demonstrated the feasibility and potential benefits of such a larger, major undertaking.

Conclusions

The research hypothesis of differential wear between muskrat populations is accepted based on the qualitative data gathered. The change from a cool, maritime climate to an increasingly warm, continental climate, coupled with the change from a stream habitat to a ponded/marsh habitat, had a profound affect on the plant and animal communities at Lubbock Lake (Table 3) (Johnson, 1987*a*). The results of the initial microwear analysis support a change in plants processed between the 1B and upper 2B populations. The transformation in habitat is reflected by a shift from pitting to scratching on the enamel surface of muskrat molars. Based on this initial analysis, a tentative conclusion of a substantial modification in the plant material processed is reasonable. An independent morphometric analysis of muskrat molars indicates disbursement of the 1B subspecies and replacement by the 2A population (Lewis, 1998).

Table 3. Plants commonly eaten and utilized by modern muskrats (Bellrose, 1950; Sather, 1958; Errington, 1963; Neal, 1968; Gromov & Polyakov, 1992)

Common name	Taxon
Sedge	*Carex*
Cattail	*Typha*
Bulrush	*Scirpus*
Bur reed	*Sparganium*
Pondweed	*Potamogeton*
Arrowhead	*Sagittaria*
Duckweek	*Lemna minor*
Smartweed	*Polygonum*
Willow	*Salix lotus*
Reed	*Phragmites*
Wild rice	*Zizania*
Water lily	*Nymphaea*

Data collected from this initial microwear research provide independent support for previous interpretations of the environment, palaeoclimate, and muskrat populations from Lubbock Lake. The methodology used to analyse the Lubbock Lake molars expands on the use of microwear analysis for the purpose of dietary studies into the broader topic of palaeoenvironmental reconstruction. Similar methodology may be employed on other species present during the late Pleistocene and early Holocene to corroborate the conclusions drawn from this initial analysis of the Lubbock Lake muskrat.

Acknowledgements

The authors would like to thank the SEM lab, Biology Department of Texas Tech University, and technician Mark Grimson in particular, for help with this research. Rebecca Lewis (then of the Museum of Texas Tech University) provided the photographic services. The comments of Drs Ernest L. Lundelius Jr (Vertebrate Palaeontology Lab, University of Texas) and Holmes A. Semken Jr (Department of Geology, University of Iowa) and two anonymous reviewers greatly improved the manuscript. Funding for this research was in the form of a graduate research assistantship from the Museum of Texas Tech University provided to the senior and first junior authors and a Summer Thesis Research Grant from the Graduate School of Texas Tech University provided to the senior author. The specimens studied resulted from excavations at the Lubbock Lake Landmark under Texas Antiquities Permit #36 and all specimens and documentation are held-in-trust for the People of the State of Texas at the Museum of Texas Tech University. Those excavations were supported by grants from the National Science Foundation (SOC-14857; BNS76-12006; BNS76-12006-A01), National Geographic Society, Texas Historical Commission (National Register Program), Moody Foundation (Galveston), Center for Field Research (EARTHWATCH), City and County of Lubbock, West Texas Museum Association, Institute of Museum Research, the Museum of Texas Tech University, and the Lubbock Lake Landmark Community Volunteers. This study is part of the ongoing Lubbock Lake Landmark regional research program into late Quaternary climatic and environmental change on the Southern High Plains.

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