Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

A late Pleistocene steppe bison (*Bison priscus*) partial carcass from Tsiigehtchic, Northwest Territories, Canada

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ARTICLE INFO

Article history: Received 27 March 2009 Received in revised form 12 June 2009 Accepted 15 June 2009

ABSTRACT

A partial steppe bison (*Bison priscus*) carcass was recovered at Tsiigehtchic, near the confluence of the Arctic Red and Mackenzie Rivers, Northwest Territories, Canada in September of 2007. The carcass includes a complete cranium with horn cores and sheaths, several complete post-cranial elements (many of which have some mummified soft tissue), intestines and a large piece of hide. A piece of metacarpal bone was subsampled and yielded an AMS radiocarbon age of 11,830 \pm 45 ¹⁴C yr BP (OxA-18549). Mitochondrial DNA sequenced from a hair sample confirms that Tsiigehtchic steppe bison (*Bison priscus*) did not belong to the lineage that eventually gave rise to modern bison (*Bison bison*). This is the first radiocarbon dated *Bison priscus* in the Mackenzie River valley, and to our knowledge, the first reported Pleistocene mammal soft tissue remains from the glaciated regions of northern Canada. Investigation of the recovery site indicates that the steppe bison was released from the permafrost during a landslide within unconsolidated glacial outwash gravel. These data indicate that the lower Mackenzie River valley was ice free and inhabited by steppe bison by ~ 11,800 ¹⁴C years ago. This date is important for the deglacial chronology of the Laurentide Ice Sheet and the opening of the northern portal to the Ice Free Corridor. The presence of steppe bison raises further potential for the discovery of more late Pleistocene fauna, and possibly archaeological evidence, in the region.

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1. Introduction

The unglaciated regions of Alaska (USA) and Yukon (Canada) contain some of the most productive Pleistocene vertebrate fossil localities in North America (Guthrie, 1990; Harington, 2003). This area is referred to as "eastern Beringia", the eastern province of the "mammoth-steppe" biome which stretched from England eastward across the entire unglaciated northern hemisphere during Pleistocene cold intervals (Guthrie, 1990). The frigid, arid environment of the mammoth-steppe was a Pleistocene Arctic refugium for the mammoth fauna: the now extinct community of large mammals characterized by woolly mammoths (*Mammuthus primigenius*), steppe bison (*Bison priscus*), and horses (*Equus* sp.). The eastern border of the mammoth-steppe is typically marked by the Richardson and Mackenzie Mountains as suggested by the rarity of

Pleistocene vertebrate fossils from the glaciated terrain in the Northwest Territories (Fig. 1). Although a few Pleistocene mammal fossils have been recovered in the western Canadian Arctic east of the Yukon, little is known about the composition or chronology of these communities.

In this paper we add to the limited data on Pleistocene mammals in northern Canada east of the Yukon, by reporting on a recently discovered partial steppe bison (*Bison priscus*) carcass from Tsiigehtchic near the confluence of the Arctic Red and Mackenzie rivers, Northwest Territories (Fig. 1a). To our knowledge this is the first radiocarbon dated Pleistocene mammal with mummified soft tissue discovered in the glaciated region of northern Canada. Data presented in this paper include an accelerator mass spectrometry (AMS) radiocarbon age, preliminary assessment of the carcass, morphometrics, and mitochondrial DNA sequences that confirm the presence of Pleistocene steppe bison in the Mackenzie River valley during the Lateglacial. These data are considered in light of previously discovered Pleistocene fossils in the Northwest Territories, the glacial chronology of the western





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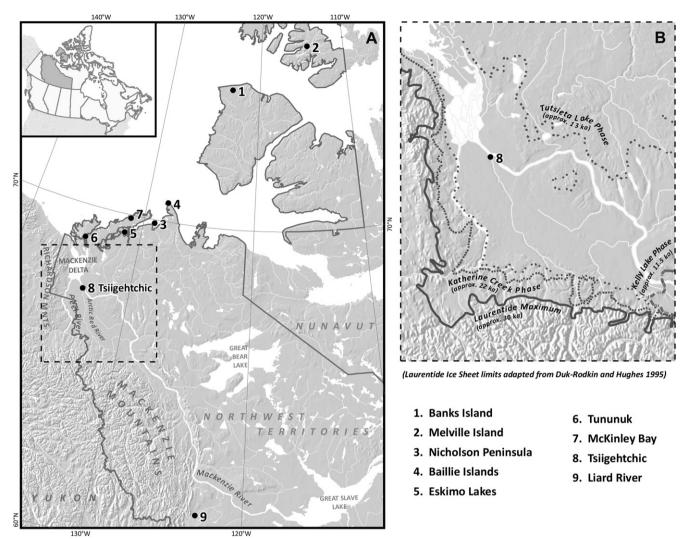


Fig. 1. (A) Map of the lower Mackenzie River valley, Northwest Territories, including location of Tsiigehtchic and other Pleistocene fossil localities; (B) location of Tsiigehtchic in relation to Laurentide Ice Sheet limits after Duk-Rodkin and Hughes (1995).

Canadian Arctic and the northern opening of the "Ice Free Corridor" (IFC) as a mid-continental dispersal route between the Cordilleran and Laurentide Ice Sheets during deglaciation.

2. Regional setting

2.1. Pleistocene fauna of the Northwest Territories

In comparison to the adjacent unglaciated regions of the Yukon, few Pleistocene mammal fossils have been recovered from the Northwest Territories (Harington, 2003; Fig. 1a). The rarity of previous Pleistocene fossil discoveries in the region highlights the significance of the Tsiigehtchic bison for our knowledge of late Pleistocene mammal biogeography. Rare Pleistocene fossils include those recovered from the Mackenzie Delta and Beaufort Coastlands on the mainland, the islands off the Beaufort Sea coast near the Mackenzie Delta (e.g., Summer, Richard's, Garry and Baillie Islands), and Banks and Melville Islands (Harington, 1990). Few Pleistocene fossil vertebrates have been recovered *in situ* or radiocarbon dated, thus often making their stratigraphic and palaeoenvironmental significance difficult to resolve. Until now, the Mackenzie River valley has remained virtually unknown in terms of Pleistocene mammals.

The presence of steppe bison in the Northwest Territories prior to the last glaciation is established by a radiocarbon date of $55,500 \pm 3100$ ¹⁴C yr BP (OxA-1163; Canadian Museum of Nature (CMN) 21096) on a specimen from the Eskimo Lakes area of the Tuktoyaktuk peninsula (Shapiro et al., 2004; Fig. 1a). Gordon (1970) reports an undated Bison antiquus (cf. B. priscus) cranium from the Liard River (Prince of Wales Northern Heritage Center, NWT 984.80.1), further south along the Mackenzie River valley. Harington (2005) reports woolly mammoth specimens from northwestern Banks (CMN 38655) and southwestern Melville Islands (CMN 11833) dating to $20,700\pm270\ ^{14}C$ yr BP (TO-2355) and ~21,000 14 C yr BP (21,000 ± 320, GSC-1760; 21,600 ± 230, GSC-1760-2), respectively. Harington (2005) suggests that these represent animals that moved northwest from the Mackenzie Delta region during the Last Glacial Maximum (LGM). The presence of woolly mammoth during the LGM in the Mackenzie Delta is confirmed by a date of $19,440 \pm 290$ ¹⁴C yr BP (I-8578) on a bone recovered from Tununuk (Rampton, 1988; Harington, 2003). Another woolly mammoth recovered from Nicholson Peninsula dates to 34,000 yr BP (Burns, 2001). The presence of saiga antelope (Saiga tatarica) on the Baillie Islands (NMC 12090) dated to 14,920 \pm 160 ^{14}C yr BP (ETH-3898) provides evidence for a hyperarid environment on the northeastern extremity of Beringia (Harington and Cinq-Mars, 1995). Tooth fragments of Jefferson's ground sloth (*Megalonyx jeffersonii*) and American mastodon (*Mammut americanum*) recovered from Lower Carp Lake near Yellowknife (Stock and Richards, 1949), in addition to three giant moose (*Alces latifrons*) specimens from Portage Point in the Eskimo Lakes area (Harington, 2007a; left scapula, CMN 44623; left humerus, CMN 44624; left radioulna, CMN 44625), represent potential interglacial faunas from the Northwest Territories.

2.2. Bison on the mammoth-steppe

The relative abundance of bison in many North American Quaternary faunas and their eventual importance at archaeological sites across the continent has led to a great deal of research on this taxon (McDonald, 1981; Guthrie, 1990; Wilson et al., 2008). However, literature on the taxonomy and evolution of bison in North America is plagued by often conflicting hypotheses. Guthrie (1990) suggests that steppe bison were the most abundant large mammal during the late Pleistocene in the interior of Alaska and Yukon and estimates that 80% of all fossils recovered from placer mine sites near Fairbanks represent steppe bison. Recently, studies of ancient mitochondrial DNA (mtDNA) suggest that steppe bison populations experienced population decline that commenced around 37,000 years ago, and were eventually extirpated from northwest North America near the terminal Pleistocene around 10,000 yr BP (Stephenson et al., 2001; Harington, 2003; Shapiro et al., 2004). These terminal Pleistocene steppe bison populations in Alaska and Yukon were completely replaced by extant wood and plains bison (Bison bison) during the Lateglacial and early Holocene. However, many questions remain in terms of taxonomic and evolutionary history of late Pleistocene bison, especially in regard to the modes and history of dispersal of various bison morphotypes between Beringia and the mid-continent of North America, possibly through the IFC (Wilson et al., 2008).

2.3. Pleistocene mummified mammals

Over the last century, several nearly complete or partial mummified carcasses (i.e., preserved soft tissues, including hair, skin, muscle, tendons) of Pleistocene large mammals have been recovered from the unglaciated regions of Siberia, Alaska and the Yukon (Guthrie, 1990; Ukraintseva, 1993; Harington, 2007b). These include bison, horse, woolly mammoth, stag moose (Alces latifrons), and helmeted muskoxen (Bootherium bombifrons). The specimen known as Blue Babe dating to \sim 36,000 ¹⁴C yr BP, recovered from a placer gold mine near Fairbanks, Alaska, is the best example of a fossil steppe bison carcass in Beringia (Guthrie, 1990). In the Yukon, the best example of a mummified large mammal carcass is a Yukon horse (Equus lambei) dating to ~26,000 14 C yr BP, including hide and intestinal contents, recovered from Last Chance Creek near Dawson City (Harington and Eggleston-Stott, 1996; Harington, 2002). Most of the mummified fossils in Alaska and Siberia date between \sim 40,000 and \sim 25,000 ¹⁴C yr BP during the interstadial period prior to the LGM (Guthrie, 1990).

3. Discovery of the Tsiigehtchic bison

The partial fossil bison carcass was recovered from a west-facing steep outcrop overlooking the Arctic Red River at the community of Tsiigehtchic, Northwest Territories (67° , 36', 34''N; 133° , 44', 50''W, 32 m a.s.l.) by local resident Shane Van Loon in early September, 2007. Mr Van Loon collected several pieces of the bison carcass after he observed them melting out of permafrost-laden gravel and sand sediments between September 5 and 8, 2007. The bison carcass was released from the frozen sediment during a retrogressive thaw slide near the top of a ~35 m high west-facing outcrop sometime in late

August, 2007. All of the specimens were found at the same site over a narrow time interval, suggesting they together represent one individual animal. After considering the potential significance of his discovery, Mr Van Loon contacted Glen MacKay. Local media reported photographs of Mr Van Loon holding a well-preserved cranium of what was presumed to be a large steppe bison (*Bison priscus*). Considering the rarity of Pleistocene mammal fossils from the Northwest Territories, and the potential for the discovery of more associated remains, MacKay and Grant Zazula visited Tsiigehtchic to examine the fossils and the recovery site between September 13 and 15, 2007.

4. Results

4.1. Site stratigraphy

The site of the fossil bison discovery is locally known as "Church Hill" as it lies directly underneath the Roman Catholic Church grounds and cemetery (Fig. 2). The outcrop is approximately 35 m in height with approximately the upper 8 m representing unconsolidated Quaternary sediments. The exposure of frozen, unconsolidated sand and gravel (with well-rounded cobbles up to \sim 30 cm in diameter) contained a large bowl-shaped retrogressive thaw scar (\sim 18 m in depth into the outcrop) above the contact with underlying sandstone and shale bedrock (Fig. 2). No organic beds within the sediments were observed. Based on previous Quaternary surficial mapping (Duk-Rodkin and Hughes, 1992, 1995) and our field observations, we suggest that the unconsolidated Quaternary sediments which contained the bison carcass are glaciofluvial, and may represent a retreat phase glacial outwash alluvial environment.

4.2. Steppe bison carcass

The fossil specimen recovered at Tsiigehtchic represents a frozen and partially mummified, incomplete carcass of a steppe bison. Along with the complete, well-preserved cranium with horn cores and sheaths (NWT 2008.36.1; Figs. 3 and 4), several postcranial elements were recovered (NWT 2008.36.2), many of which have soft tissues attached (Table 1; Fig. 5). Measurements on the cranium and horns indicate that this specimen represents the extinct steppe bison (Bison priscus) (McDonald, 1981; Guthrie, 1990), rather than that of an extant wood bison (Bison bison), which inhabits areas to the south along the Mackenzie River valley at present (Table 2). Based on several measurements (Table 2), the Tsiigehtchic steppe bison is consistent with the mean size for adult male steppe bison recovered from the interior of Alaska (Skinner and Kaisen, 1947; Harington, 1978; Guthrie, 1990). Conservation efforts are underway to determine the extent of soft tissue preservation on the Tsiigehtchic steppe bison, including the amount and condition of the hide and intestine. As such, the assessment of the carcass as reported in this manuscript is preliminary. Further conservation and research efforts will certainly provide more information on the life and death of this steppe bison. To our knowledge, the fossil steppe bison carcass from Tsiigehtchic is the first reported Pleistocene mummified soft tissue mammal remains from the glaciated regions of northern Canada (Harington, 2007b). This partial carcass raises the potential for discovery of additional mummified Pleistocene mammals in other permafrost regions of northern Canada that were covered by the Laurentide Ice sheet.

4.3. Radiocarbon dating

A subsample of the right metacarpal was submitted to the Oxford Radiocarbon Accelerator Unit to obtain an accelerator mass

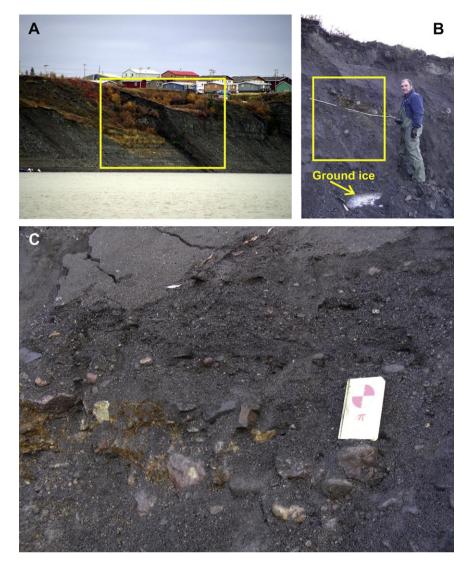


Fig. 2. Photos of the steppe bison recovery site at Tsiigehtchic, Northwest Territories. (A) West-facing outcrop overlooking Arctic Red River with landslide scar; (B) Glen MacKay standing in the landslide scar where steppe bison remains were recovered melting out of the frozen gravel and sand; (C) moderate to well-sorted gravel and sand where steppe bison was recovered.

spectrometry (AMS) radiocarbon date. Prior to analysis the sample underwent an acid-base-acid (ABA) treatment consisting of sequential washes with 0.5 M hydrochloric acid (three washes over approximately 18 h), 0.1 M sodium hydroxide (30 min) and 0.5 M hydrochloric acid (15 min) at room temperature, with thorough rinsing in ultrapure water between each treatment. The resultant crude collagen was gelatinized at 75 °C and pH 3 for 20 h. The gelatin solution was filtered using a 9 µm polyethylene Eezi-filterTM and then ultrafiltered using a Vivaspin[™] 15 30 kD MWCO ultrafilter (Bronk Ramsey et al., 2004; Brock et al., 2007). The gelatin was freeze-dried prior to being combusted and the stable carbon and nitrogen isotope ratios measured on a mass spectrometer, using a Europa ANCA Roboprep interfaced with a Europa 20/20 IRMS operating under continuous-flow mode. CO₂ from the combustion was cryogenically distilled and reduced to graphite over an iron catalyst in the presence of excess H₂ prior to AMS radiocarbon measurement.

The sample yielded a radiocarbon age of 11,830 \pm 45 yr BP (OxA-18549). The collagen yield was 19.6% by weight with a C:N atomic ratio of 3.1, which falls within ORAU's accepted range of 2.9–3.5 (van Klinken, 1999). The collagen had a δ^{13} C value of $-19.9_{\%}^{\circ}$ and

a δ^{15} N value of 2.5‰. The calibrated age for the Tsiigehtchic steppe bison using OxCal 4.05 based on the IntCalO4 dataset (Bronk Ramsey, 2001), falls between 13,565 and 13,811 cal yr BP (at 94.5% probability).

4.4. Mitochondrial DNA analysis

To further confirm the identity of the Tsiigehtchic steppe bison and place it within a phylogenetic framework (Shapiro et al., 2004), a sample of hair from the carcass was sent to the specialized ancient DNA facility at Pennsylvania State University for mitochondrial DNA typing. DNA was extracted from approximately 3 cm of hair using the QiaGen DNEasy tissue kit (Qiagen, USA) according to manufacturers' instructions. Following extraction, a 680-bp fragment of the mitochondrial DNA control region was amplified using a set of five overlapping primers. Primer pairs were selected so that each base was independently amplified twice, thereby minimizing the influence of potentially damaged DNA bases on the recovered sequence (GenBank accession number GQ258703). Amplification was performed using the protocol described in Shapiro et al. (2004). Forward and reverse strands were sequenced using an ABI



Fig. 3. Photos of Tsiigehtchic steppe bison cranium (specimen # NWT 2008.36.1) after preliminary conservation efforts at the Prince of Wales Heritage Center in Yellowknife, Northwest Territories.

Hitachi 3730XL at the Nucleic Acids Facility, University Park, and aligned to a large data set of extinct and living bison (Shapiro et al., 2004). Strict ancient DNA protocols were followed so as to minimize the potential for contamination. All experimental steps involving the ancient specimen (storage, extraction and PCR setup) took place in a dedicated ancient DNA facility, which is physically and geographically isolated from other molecular biology research. In addition, prior to the initiation of this work, no previous steppe bison DNA had been amplified at Pennsylvania State University.

Previous analyses of the mitochondrial DNA control region of steppe bison and both subspecies of extant bison revealed that the extant bison form a single, well-supported cluster within the greater diversity of *Bison* (the *Bison bison* clade 1; Fig. 6). To determine the phylogenetic placement of the Tsiigehtchic bison, we performed an analysis including all previously published North American bison control region sequences and the newly generated sequence from the Tsiigehtchic specimen. Analyses were performed using the Bayesian phylogenetic inference software package BEAST (Drummond and Rambaut, 2007) using the HKY+G model of nucleotide substitution, and the coalescent process

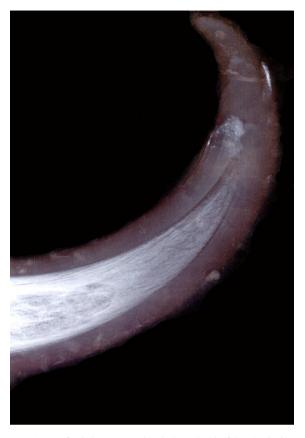


Fig. 4. X-ray image of right horn core within the horn sheath of the Tsiigehtchic steppe bison.

Table 1

Steppe bison elements recovered at Tsiigehtchic, NWT.

Tsiigehtchic bison elements	Number	· Remarks		
Cranium	1	Complete to tip of nasal, with maxillary teeth,		
		horn sheaths, some soft tissue		
Mandible	1	Left side, all teeth present, some soft tissue		
Scapula	2	Both left and right sides complete; right with puncture hole and associated fracture, left with muscle tissue attached		
Femur	1	Left side, complete, soft tissue attached at proximal and distal ends (ligaments?)		
Tibia	1	Left side complete, soft tissue attached at proximal end (ligaments?)		
Naviculo-cuboid	1	Left, complete		
Calcaneum	2	Left and right, complete; right with muscle, skin and hair attached		
Metatarsals and tarsals	2	Left and right complete lower hindlimbs metatarsal-tarsal-phalanges that are articulated, with ligaments, skin, hair		
Metacarpal	1	Right complete (subsampled for ¹⁴ C date)		
Axis	1	Complete		
Cervical vertebra	1	Complete		
Thoracic vertebra	6	Complete		
Lower lumbar vertebra	1	Complete with significant amount of soft tissue attached		
Piece of sacrum?	1	Possible sacrum piece, complete with soft tissue		
Vertebra spinous process fragment	1	Damaged by shovel		
Unidentified bone with flesh (partial tail?)	1	Unidentified bone covered in tissue, possible part of tail?		
Intestines	1	Piece of lower intestine?		
Skin	1	Large bag of skin with substantial sediment attached		
Skin and hair	1	Large bag of skin with long dark brown hair		



Fig. 5. Selected photos of steppe bison taken in Tsiigehtchic, September, 2007. (A) Collection including some of the fossil steppe bison specimens; (B) femur; (C) proximal end of tibia with mummified soft tissue; (D) articulated hindlimb; (E) large clump of frozen hide and hair; (F) piece of frozen intestine.

modeled according to the flexible Bayesian skyline plot (Drummond et al., 2005). Radiocarbon dates were incorporated as prior information to inform a strict molecular clock. Two MCMC chains of 20 million generations were run. The first 10% of generations were discarded from each run and the runs were combined. Mixing and convergence to stationarity were assessed using Tracer (Rambaut and Drummond, 2007).

The maximum clade credibility (MCC) tree from the above analyses is described by Fig. 6. Clade numbers follow Shapiro et al. (2004), where a third clade (clade 3) included bison from Siberia, which are not included in this analysis. Mitochondrial lineages isolated from late Pleistocene bison fossils cluster into two groups: clade 2, and clade 4, although no strong phylogenetic support is found for these major divisions. All modern bison (*Bison bison*), however, fall into a very strongly supported clade (clade 1; Fig. 5) with most of the Holocene steppe bison sampled from specimens recovered in Alberta and British Columbia (Shapiro et al., 2004). The Tsiigehtchic steppe bison falls into a well-supported cluster of individuals within clade 4 (Fig. 6) comprizing one sample from Old Crow, Yukon and another from Black River, Alaska. The phylogenetic position of the Tsiigehtchic steppe bison indicates that it did not belong to the mitochondrial lineage of steppe bison that eventually gave rise to both modern bison subspecies.

5. Glacial retreat, the Ice Free Corridor and Lateglacial palaeoenvironments

The radiocarbon date of 11,830 \pm 45 ¹⁴C yr BP (OxA-18549) from the Tsiigehtchic bison has important implications for the deglacial chronology of the Laurentide Ice Sheet (LIS) (Fig. 1b). The community of Tsiigehtchic, located at the confluence of the Mackenzie and Arctic Red rivers, is situated well within the all-time Late Wisconsinan maximum limit of the LIS (Dyke et al., 2003). According to the glacial chronology of Duk-Rodkin (1999), the LIS advanced across the western Arctic to its maximum position on the eastern flanks of the Richardson and Mackenzie Mountains by ~30,000 yr BP (Duk-Rodkin and Hughes, 1995). This maximum advance of the LIS coalesced with the Cordilleran glaciers to the south along the eastern slopes of the Mackenzie and Rocky mountains (Duk-Rodkin and Hughes, 1995). Eastward retreat of the

Table 2

Size measurements of Tsiigehtchic steppe bison of and comparison with fossil male bison and Blue Babe from interior of Alaska (measurements for comparison based on Guthrie, 1990).

	Tsiigehtchic steppe bison	Fossil male bison from interior Alaska (mean)	Blue Babe
Skull measurements			
Width of cranium between horn cores and orbits (mm)	279	288	273
Spread of horn cores at greatest width (mm)	940 ^a	986	922
Spread of horn sheaths at greatest width (mm)	1010		
Horn sheath length at upper curve (mm)	590	584	565
Total length of skull (mm)	595	598	556
Occipital crest to nasal tip length (mm)	491	491	451
Maximum width of skull at massetric processes at M1 (mm)	190	196	182
Internal diameter of orbit (mm)	74		
Metacarpal measurements			
Maximum length (mm)	223		200
Maximum width at center shaft (mm)	58		52

^a Measurements taken with aid of x-ray image in order to determine position of horn core inside the sheath (Fig. 4).

LIS from the all-time maximum position occurred sometime prior to 22,000 yr BP with retreat phase ice positions, known as the Katherine Creek Phase (\sim 22,000 yr BP), Tutsieta Lake Phase (\sim 13,000 yr BP) and Kelly Lake Phase (\sim 11,500 yr BP) (Duk-Rodkin

and Hughes, 1995; (Fig. 1b). Our new radiocarbon age on the steppe bison indicates that the Tutsieta Lake phase culminated and had retreated eastward beyond the Arctic Red River by $11,830 \pm 45$ ¹⁴C yr BP. This chronology is in concordance with a date on deglaciation

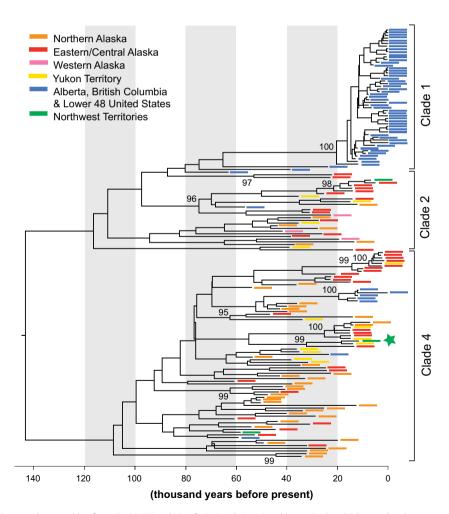


Fig. 6. Maximum clade credibility genealogy resulting from the BEAST analysis of 161 North American bison mitochondrial control region sequences sampled over the last 60 ka. The analysis assumes a molecular clock; a timescale is placed along the bottom of the tree to facilitate interpretation of tip ages and divergence times. Colored rectangles indicate the geographic location of each sampled sequence, and statistical support levels for nodes with >95% Bayesian posterior probabilities are provided. Clade numbers follow Shapiro et al. (2004), and are for convenience (they do not indicate clusters of sequences with high posterior support). All modern bison fall into clade 1. The Tsiigehtchic steppe bison falls into clade 4, and is indicated by a green star.

of 11,530 \pm 170 ^{14}C yr BP (I-3734) from near the Mountain River further southeast along the Mackenzie River valley (Mackay and Mathews, 1973).

The new radiocarbon date from Tsiigehtchic places an important limiting age for the northern opening of the IFC (Mandryk et al., 2001; Arnold, 2002). The IFC is the terrestrial deglaciation corridor that formed with retreat of the Laurentide and Cordilleran glaciers from their maximum, coalesced positions along the Mackenzie River valley and eastern slopes of the Rocky Mountains (Rutter and Schweger, 1980; Jackson and Duk-Rodkin, 1996). This corridor was an important dispersal route for plants, animals, and possibly people between Beringia and the mid-continent (Shapiro et al., 2004; Goebel et al., 2008). However, there has been much controversy surrounding the viability and age estimates for the opening of the IFC during the Lateglacial (Mandryk et al., 2001; Arnold, 2002). Our new data indicate that the northern portion of the IFC in the lower Mackenzie River valley was free from continental glaciers and inhabited by steppe bison by ~ 11,800 ¹⁴C yr BP.

The Lateglacial was a time of significant environmental change in eastern Beringia, with the full-glacial steppe-tundra biome being rapidly replaced by willow (Salix), dwarf birch (Betula) and sedge (Cyperaceae) dominated mesic tundra. The Lateglacial was also a time of abrupt changes for Beringian large herbivore faunas. Woolly mammoth and horse dominated full-glacial faunas were replaced by a resurgence of steppe bison populations, and associated invasion of wapiti (Cervus) and moose (Alces) (Guthrie, 2006). With rapid warming and mesification of the interior of eastern Beringia, steppe bison populations expanded eastward to the periglacial environment in the recently deglaciated Mackenzie River valley. Given that steppe bison inhabited the northern portal to the Ice Free Corridor, data from the Tsiigehtchic bison raises the potential for discovery of terminal Pleistocene archaeological sites in the lower Mackenzie River valley that may be contemporaneous with the Nenana Complex and/or earlier archaeological cultures described for the interior of Alaska and southern Yukon (Hamilton and Goebel, 1999; Holmes, 2001).

6. Summary and conclusions

Our report here of an exceptional partial steppe bison carcass from Tsiigehtchic adds a crucial piece of data to our knowledge on the late Pleistocene faunas and deglacial chronology of the Northwest Territories. This is the first report of mummified soft tissue from a Pleistocene mammal discovered in the area covered by Pleistocene glaciers in northern Canada and is the first radiocarbon dated steppe bison from the Mackenzie River valley. Mitochondrial DNA from the Tsiigehtchic bison carcass confirms its affinity with other late Pleistocene steppe bison from Beringia and indicates that it was not a member of the bison lineage that gave rise to modern bison species. As the Laurentide Ice Sheet commenced its eastward retreat from the Richardson and Mackenzie Mountain front, the newly deglaciated Mackenzie River valley became connected to the Yukon as part of Beringia. Lateglacial environmental changes enabled the resurgence of steppe bison populations in eastern Beringia and their expansion eastward into the formerly glaciated areas of the western Arctic. The radiocarbon date of \sim 11,800 ¹⁴C yr BP (\sim 13,565–13,811 cal yr BP) from the Tsiigehtchic steppe bison provides a reliable age for the deglaciation of the lower Mackenzie River valley and opening of the northern portion of the Ice Free Corridor.

Acknowledgements

We thank Shane van Loon for his keen eyes that led to the steppe bison discovery. We are grateful to: Alestine Andre and Itai Katz for hosting GM and GZ during their stay in Tsiigehtchic and the community of Tsiigehtchic for their interest and support for this research; Ingrid Kritsch, Alestine Andre and Sharon Snowshoe of the Gwich'in Social and Cultural Institute for logistical support; Dean Cluff with ENR-North Slave District for storing the fossil temporarily in Yellowknife. Valerie Tomlinson. ARI for facilitating the transfer of the bison carcass from Tsiigehtchic to Yellowknife: Dale Murphy-Boutilier and Liam Riordan of the Diagnostic Imaging Department of Stanton Territorial Hospital, Yellowknife, for assistance with radiography and CT scans of the bison remains; Ron Morrison of Environment and Natural Resources, GNWT - Inuvik Office for use of the truck; Rosalie Scott, PWNHC for conservation efforts; Joyce de Dios, PWNHC, for map preparation; Susan Irving, PWNHC, for assistance with the photographs of the cranium; and Michael Wilson, Len Hills and Greg Hare for helpful, critical reviews that greatly improved this manuscript.

References

- Arnold, T.G., 2002. Radiocarbon dates from the Ice-Free Corridor. Radiocarbon 44, 437–454.
- Brock, F., Bronk Ramsey, C., Higham, T.F.G., 2007. Quality assurance of ultrafiltered bone dating. Radiocarbon 49, 187–192.
- Bronk Ramsey, C., 2001. Development of the radiocarbon calibration program OxCal. Radiocarbon 43, 355–363.
- Bronk Ramsey, C., Higham, T.F.G., Bowles, A.D., Hedges, R.E.M., 2004. Improvements to the pre-treatment of bone at Oxford. Radiocarbon 46, 155–163.
- Burns, J., 2001. Mammuthus tibia from Canadian Arctic coast, and a review of Pleistocene fossils on Canada's salt shores. Canadian Quaternary Association Meetings, 2001: Program and Abstracts. Occasional Papers in Earth Sciences No. 1. Heritage Branch, Yukon Government, Whitehorse, Yukon, pp. 31-32.
- Drummond, A.J., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolultionary Biology 7, 214.
- Drummond, A.J., Rambaut, A., Shapiro, B., Pybus, O.G., 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. Molecular Biology and Evolution 22, 1185–1192.
- Duk-Rodkin, A. 1999. Glacial limitsmap of Yukon Territory. Geological Survey of Canada, Open File 3694, Yukon Geology Program, Geoscience map, 1999-2.
- Duk-Rodkin, A., Hughes, O.L., 1992. Surficial geology, Arctic Red River, District of Mackenzie, Northwest Territories, Geological Survey of Canada, Map 1746A. scale 1, 250,000.
- Duk-Rodkin, A., Hughes, O.L., 1995. Quaternary geology of the northeastern part of the central Mackenzie valley corridor, District of Mackenzie, Northwest Territories. Geological Survey of Canada Bulletin 458. Natural Resources Canada, Ottawa.
- Dyke, A.S., Moore, A., Robertson, L., 2003. Deglaciation of North America, Geological Survey of Canada Open File 1574. Natural Resources Canada, Ottawa.
- Goebel, T., Waters, M.R., O'Rourke, D.H., 2008. The late Pleistocene dispersal of modern humans in the Americas. Science 319, 1497–1502.
- Gordon, B.C., 1970. Bison antiquus from the Northwest Territories. Arctic 23, 132–133.
- Guthrie, R.D., 1990. Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe. University of Chicago Press, Chicago, IL.
- Guthrie, R.D., 2006. New carbon dates link climate change with human colonization and Pleistocene extinctions. Nature 441, 207–209.
- Hamilton, T.D., Goebel, R., 1999. Late Pleistocene peopling of Alaska. In: Bonnichsen, R., Turnmire, K.L. (Eds.), Ice Age Peoples of North America. Oregon State University Press, Corvalis, OR, pp. 156–199.
- Harington, C.R., 1978. Quaternary vertebrate faunas of Canada and Alaska and their suggested chronological sequence. Syllogeus 15, 1–105.
- Harington, C.R., 1990. Ice Age vertebrates in the Canadian Arctic islands. In: Canada's Missing Dimension, Vol. 1. Canadian Museum of Nature, Ottawa, pp. 138–160.
- Harington, C.R., 2002. Yukon Horse. Beringian Research Note #14. Government of Yukon, Whitehorse.
- Harington, C.R. (Ed.), 2003. Annotated Bibliography of Quaternary Vertebrates of Northern North America – with Radiocarbon Dates. University of Toronto Press, Toronto.
- Harington, C.R., 2005. The eastern limit of Beringia: mammoth remains from Banks and Melville Islands, Northwest Territories. Arctic 58, 361–369.
- Harington, C.R., 2007a. Giant Moose and Moose. Beringian Research Note #18. Government of Yukon, Whitehorse.
- Harington, C.R., 2007b. Late Pleistocene mummified mammals. In: Elias, S.A. (Ed.), Encyclopedia of Quaternary Science. Elsevier, pp. 3197–3202.
- Harington, C.R., Cinq-Mars, J., 1995. Radiocarbon dates on Saiga Antelope (Saiga tatarica) fossils from Yukon and the Northwest Territories. Arctic 48, 1–7.
- Harington, C.R., Eggleston-Stott, M., 1996. Partial carcass of a small Pleistocene horse from Last Chance Creek near Dawson City, Yukon. Current Research in the Pleistocene 13, 105–107.

Holmes, C.E., 2001. Tanana River Valley archaeology circa 14,000 – 9,000 B.P. Arctic Anthropology 38, 154–170.

- Jackson Jr., L.E., Duk-Rodkin, A., 1996. Quaternary geology of the Ice-Free Corridor: glacial controls on the peopling of the New World. In: Azakawa, T., Szathmary, E.J.E. (Eds.), Prehistoric Mongoloid Dispersals. Oxford University Press, New York, pp. 214–227.
- Mackay, J.R., Mathews, W.H., 1973. Geomorphology and Quaternary history of the Mackenzie River Valley near Fort Good Hope, N.W.T. Canada. Canadian Journal of Earth Sciences 10, 26–41.
- Mandryk, C.A.S., Josenhans, H., Fedje, D.W., Mathewes, R.W., 2001. Late Quaternary paleoenvironments of Northwestern North America: implications for inland versus coastal migration routes. Quaternary Science Reviews 20, 301–314.
- McDonald, J.N., 1981. North American Bison: Their Classification and Evolution. University of California Press, Berkeley, CA.
- Rambaut, A., Drummond, A.J. Tracer: v. 1.4 available from http://tree.bio.ed.ac.uk/ software/tracer/.
- Rampton, V.N., 1988. Quaternary geology of the Yukon Coastal Plain. Geological Survey of Canada Bulletin 317. Natural Resources Canada, Ottawa.
- Rutter, N.W., Schweger, C.E. (Eds.), 1980. The Ice-Free Corridor and the peopling of the New World (Special AMQUA Issue). Canadian Journal of Anthropology 1(1).
- Shapiro, B., Drummond, A.J., Rambaut, A., Wilson, M.C., Matheus, P.E., Sher, A.V., Pybus, O.G., Gilbert, M.T.P., Barnes, I., Binladen, J., Willerslev, E., Hansen, A.J.,

Baryshnikov, G.F., Burns, J.A., Davydov, S., Driver, J.C., Froese, D.G., Harington, C.R., Keddie, G., Kosintsev, P., Kunz, M.L., Martin, L.D., Stephenson, R.O., Storer, J., Tedford, R., Zimov, S., Cooper, A., 2004. Rise and fall of the Beringian Steppe bison. Science 306, 1561–1565.

- Skinner, M.F., Kaisen, O.C., 1947. The fossil Bison of Alaska and preliminary revision of the genus. Bulletin of the American Museum of Natural History 89, 123–256.
- Stephenson, R.O., Gerlach, S.C., Guthrie, R.D., Harington, C.R., Mills, R.O., Hare, G., 2001. Wood bison in late Holocene Alaska and adjacent Canada: paleontological, archaeological and historical records. In: Gerlach, S.C., Murray, M.S. (Eds.), People and Wildlife in Northern North America: Essays in Honor of R. Dale Guthrie. BAR International Series 944, Oxford, pp. 124–158.
- Stock, C., Richards, H.G., 1949. A Megalonyx tooth from the Northwest Territories, Canada. Science 110, 709–710.
- Ukraintseva, V.V., 1993. Vegetation cover and environment of the "Mammoth Epoch" in Siberia. Mammoth Site of Hot Springs. South Dakota, Hot Springs, SD. van Klinken, G.J., 1999. Bone collagen quality indicators for palaeodietary and
- radiocarbon measurements. Journal of Archaeological Science 26, 687–695.
- Wilson, M.C., Hills, L.V., Shapiro, B., 2008. Late Pleistocene northward-dispersing Bison antiquus from the Bighill Creek Formation, Gallelli Gravel Pit, Alberta, Canada, and the fate of Bison occidentalis. Canadian Journal of Earth Sciences 45, 827–859.