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A middle Holocene steppe bison and paleoenvironments from the Versleuce Meadows, Whitehorse, Yukon, Canada

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Abstract: A partial skeleton of a bison was recovered during residential house construction in Whitehorse, Yukon, Canada. The specimen represents a young (estimated 6 year old) bison individual that died, was partially scavenged by carnivores, and subsequently buried by calcareous silt sediment in a pond or small lake during the middle Holocene, ~5400 years ago. Palaeoenvironmental data, including molluscs, pollen, vascular plant, and bryophyte macrofossils demonstrate that the small waterbody was surrounded by white spruce dominated boreal forest. Morphometric analysis of the skeleton reveals that its taxonomic affinity is ambiguous, likely owing to it representing an ontogenetically young individual, though it does share some cranial and horn core characteristics of named species such as *Bison occidentalis* or *Bison priscus*. Mitochondrial genomic data confirm that this bison belongs to Clade 2A (northern clade), which represents Pleistocene steppe bison (*B.* cf. *priscus*) in Beringia through the Holocene and is not represented in living bison species. These data further demonstrate that northern steppe bison population survived the late Pleistocene extinction event, persisted locally in southern Yukon into the Holocene, and are best characterized as a species with a high degree of morphological variability and ecological flexibility.

Résumé : Le squelette partiel d'un bison a été récupéré durant la construction d'immeubles résidentiels à Whitehorse (Yukon, Canada). Le spécimen représente un unique jeune bison (d'âge estimé à 6 ans) qui est mort, a été partiellement dévoré par des carnivores pour ensuite être enseveli sous du silt calcareux dans un étang ou un petit lac durant l'Holocène moyen, il y a ~5400 ans. Des données paléoenvironnementales, dont des mollusques, du pollen, des plantes vasculaires et des macrofossiles de bryophytes, démontrent que le petit plan d'eau était entouré d'une forêt boréale où dominait l'épinette blanche. L'analyse morphométrique du squelette révèle que son affinité taxonomique est ambiguë, probablement en raison du fait qu'il représente un individu jeune sur le plan ontogénétique, bien qu'il partage avec des espèces nommées comme *Bison occidentalis* ou *Bison priscus* des caractéristiques communes du crâne et des cornillons. Des données génomiques mitochondriales confirment que ce bison appartient au Clade 2A (clade septentrional), qui représente le bison des steppes pléistocène (*B.* cf. *priscus*) en Béringie jusqu'à l'Holocène et n'est pas représenté parmi les espèces actuelles de bisons. Ces données démontrent également que la population septentrionale de bisons des steppes a survécu à l'extinction du Pléistocène tardif, a persisté localement dans le sud du Yukon jusque durant l'Holocène et qu'il s'agit d'une espèce caractérisée par un haut degré de variabilité morphologique et de souplesse écologique. [Traduit par la Rédaction]

Introduction

Bison (*Bison*) dominate Pleistocene mammal faunas from the unglaciated regions of interior and northern Alaska and Yukon, the area commonly referred to as eastern Beringia (Guthrie 1990; Harington 2011). Fossil records suggest that once bison initially dispersed from Asia across the exposed Bering Isthmus 195–135 thousand years ago (Froese et al. 2017), they subsequently established themselves as the most abundant, large Pleistocene ungulate in many parts of North America (Guthrie 1970, 1990; McDonald 1981). Estimates suggest that typical late Pleistocene mammal faunas in eastern Beringia are composed of over 80% steppe bison (*B. priscus*) remains (Guthrie 1990). In contrast, remains of bison dating to the Holocene in glaciated regions of northern North America are relatively rare, often poorly preserved, and generally lack the morphologically diagnostic cranial characteristics that are often used

to make taxonomic identifications (Stephenson et al. 2001). As such, there is limited information on eastern Beringian bison populations following deglaciation in comparison to more common subarctic ungulates such as caribou (*Rangifer tarandus*) (Farnell et al. 2004). Coupled with generally poor preservation conditions in subarctic soils, cultural practices such as fracturing long bones to remove marrow likely resulted in significant underrepresentation of identified bison remains from Holocene zooarchaeological assemblages.

Because of their ubiquity and abundance in the fossil, archaeological, and historical records, bison are one of the most extensively studied North American Quaternary mammal species (Skinner and Kaisen 1947; McDonald 1981; Guthrie 1990). However, their formal taxonomy is rather confusing because of numerous named, but likely nominal species, largely defined based

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on inconsistent cranial and horn core metrics and morphology. However, there has been a trend towards informal taxonomic lumping, especially in regards to Pleistocene bison from eastern Beringia which are now generally considered to all represent the Holarctic species *B. priscus* (Bojanus 1827) sensu lato (Guthrie 1970, 1990). Further, some have suggested, based on morphological criteria, that Holocene-aged bison in Alaska and Yukon represent the extant wood bison (*B. bison athabascae*; Stephenson et al. 2001).

Genetic studies based on mitochondrial DNA from Quaternary bison have shown that extant bison, *B. bison*, arose during the last glacial maximum from ancestors situated south of the continental ice sheets, and that *B. bison* mitochondrial variation falls within a much more diverse bison complex (including the steppe bison, *B. priscus*) that occurred both north and south of the ice sheets during the late Pleistocene (Shapiro et al. 2004; Heintzman et al. 2016; Froese et al. 2017). As mitochondrial DNA sequences can distinguish *B. bison* from other bison taxa, they can be used to infer the systematic status and phylogeographic history of enigmatic bison specimens. The mitochondrial north–south differentiation between Pleistocene bison species is loosely supported by morphological data as well, with *B. priscus* found in the north and *B. antiquus* in the south (Shapiro et al. 2004; Wilson et al. 2008). The integration of both morphological and genetic data for ancient bison are key to resolving questions about bison dispersal history and phylogenetics especially regarding the dramatic changes following the Pleistocene–Holocene transition (Wilson et al. 2008). In Yukon and Alaska, there are relatively few well-preserved Holocene bison specimens to address questions related to the taxonomy, evolution, and spatial–temporal distribution of bison in this region. Although it is beyond the scope of the present paper to resolve, studies of North American bison are clearly hindered by the inconsistency of morphological and genetic data and future work should attempt to address the numerous species names that are presently recognized in the literature.

This paper reports a well-preserved partial skeleton of a bison including the cranium and many of the post-cranial elements from the Versleuce Meadows site in the formerly glaciated region of Whitehorse, southern Yukon, Canada (Fig. 1). The specimen is described, identified, radiocarbon dated, and placed into a mitochondrial genome-based phylogenetic context. We also evaluate associated palaeoenvironmental proxies to further shed light on the palaeoecological context of this post-glacial bison in northern Canada. The primary topics addressed in this paper are the following:

(1) Can morphometric data be used to confidently assign this specimen into one of the previously defined species of Quaternary bison?

(2) What is the mitochondrial genetic affinity of the Versleuce Meadows bison?

(3) When and how did this bison die and become preserved at Versleuce Meadows?

(4) What was the environment surrounding Versleuce Meadows when this bison died?

(5) What is its significance for bison taxonomy and history in the north?

Materials and methods

Study site and regional context

The study site (Fig. 1) is located within the city of Whitehorse, Yukon, in an area known locally as "Versleuce Meadows" (60°46′21.9″N, 135°08′26.3″W) in the neighbourhood of Porter Creek. Historically, this shallow low-lying area (elevation: 715 m a.s.l.) consisted of agricultural hayfields surrounding a small ephemeral pond or slough. In recent decades, extensive topsoil mining in the meadow has removed the surface substrate for local gardener usage. The fossil discovery site is on the periphery of a low-lying meadow, immediately downslope from a ridge that forms the northern edge of a small basin. The entire area was glaciated

during the McConnell Glaciation of the northern Cordilleran ice sheet (Fig. 1), and became ice free after ~11 000 years ago (Bond 2004).

The study site is situated in the Yukon Southern Lakes ecoregion (Yukon Ecoregions Working Group 2004), generally characterized by rounded montane summits and broad valleys resulting from the effects of Pleistocene glaciation. The vegetation in the region is dominated by open coniferous and mixed forests, with lodgepole pine (*Pinus contorta*) dominating dry and recently burned sites, whereas white spruce (*Picea glauca*) forests are more common on active floodplains, other mesic to moist sites, and serally advanced sites. Mixed aspen (*Populus tremuloides*) and white spruce are common on sites with fine soils with variable ground shrubs and lichen. Open areas and steep south and west facing slopes at low elevation commonly include grasslands, while depressions have alkaline ponds and small lakes. Black spruce (*Picea mariana*) on permafrost soils are rare in the region at low elevation.

Paleoecological data from southern Yukon demonstrate the changes in vegetation cover following the retreat of the Cordilleran ice sheet after 11 000 years ago (Cwynar and Spear 1995; Gajewski et al. 2014). Immediately after deglaciation, the landscape was covered by a herb tundra vegetation with abundant grass (Poaceae), sage (*Artemisia*), and forbs, transitioning to a more shrub-dominated tundra environment with abundant birch (*Betula*), some trembling aspen (*Populus tremuloides*), and juniper (*Juniperus* spp.) in the understory, and which dominated until around 10 000 or 9000 years ago (Gajewski et al. 2014). White spruce forests were abruptly established after this time and continued to be abundant for much of the Holocene. Significant changes in regional vegetation composition occurred between roughly 6000 and 5000 years ago, with a shift towards a predominance of black spruce over white spruce and with major increases in alder (*Alnus crispa*). Pine trees replaced spruce as the dominant tree of open woodlands around Whitehorse by around 2000 years ago, following dispersal from the south and east (Cwynar 1988; Cwynar and Spear 1995).

The composition of the present-day large mammal fauna in the region is the result of the dramatic changes during the Pleistocene–Holocene transition, which included the extirpation of many species of the "mammoth-steppe" such as woolly mammoth (*Mammuthus primigenius*), horses (*Equus* spp.), and saiga antelope (*Saiga tatarica*). This period of faunal turnover also saw the initial dispersal of Asian migrants such as elk (*Cervus elaphus*), moose (*Alces alces*), and people (*Homo sapiens*) into North America (Guthrie 2006). Populations of elk, bison, and caribou locally survived in Yukon through this period of dramatic ecological turmoil and remained in the Subarctic and Arctic through much of the Holocene. Fossil and ethnohistorical evidence demonstrates that native bison populations in Yukon were regionally extirpated roughly 400 years ago (Stephenson et al. 2001; Heintzman et al. 2016). Present day populations of elk and wood bison (*B. bison athabascae*) are now common in the boreal forest of southern Yukon and are the result of human-mediated reintroductions during the mid-20th century.

Field excavation

On the morning of 26 April 2012, Whitehorse resident Craig Duncan encountered several large mammal bones, while excavating with heavy equipment to construct a basement on his residential property. He gathered these bones and brought them to the Government of Yukon, Heritage Resources Unit office. The bones were all readily identified as those from a bison. This small collection included a cervical vertebra, a thoracic vertebra, left metacarpal, right metatarsal, and fragments of both a left and right tibia. Since it appeared that all these elements belonged to a single individual, were well-preserved, and discovered in approximate anatomical position, a small crew was immediately assembled to further investigate the site.

Fig. 1. Map of Yukon Territory including the late Pleistoene McConnell and Laurentide ice sheet limits (after Westgate et al. 2000). Inset is the Versleuce Meadows study site in relation to the City of Whitehorse and Yukon River.
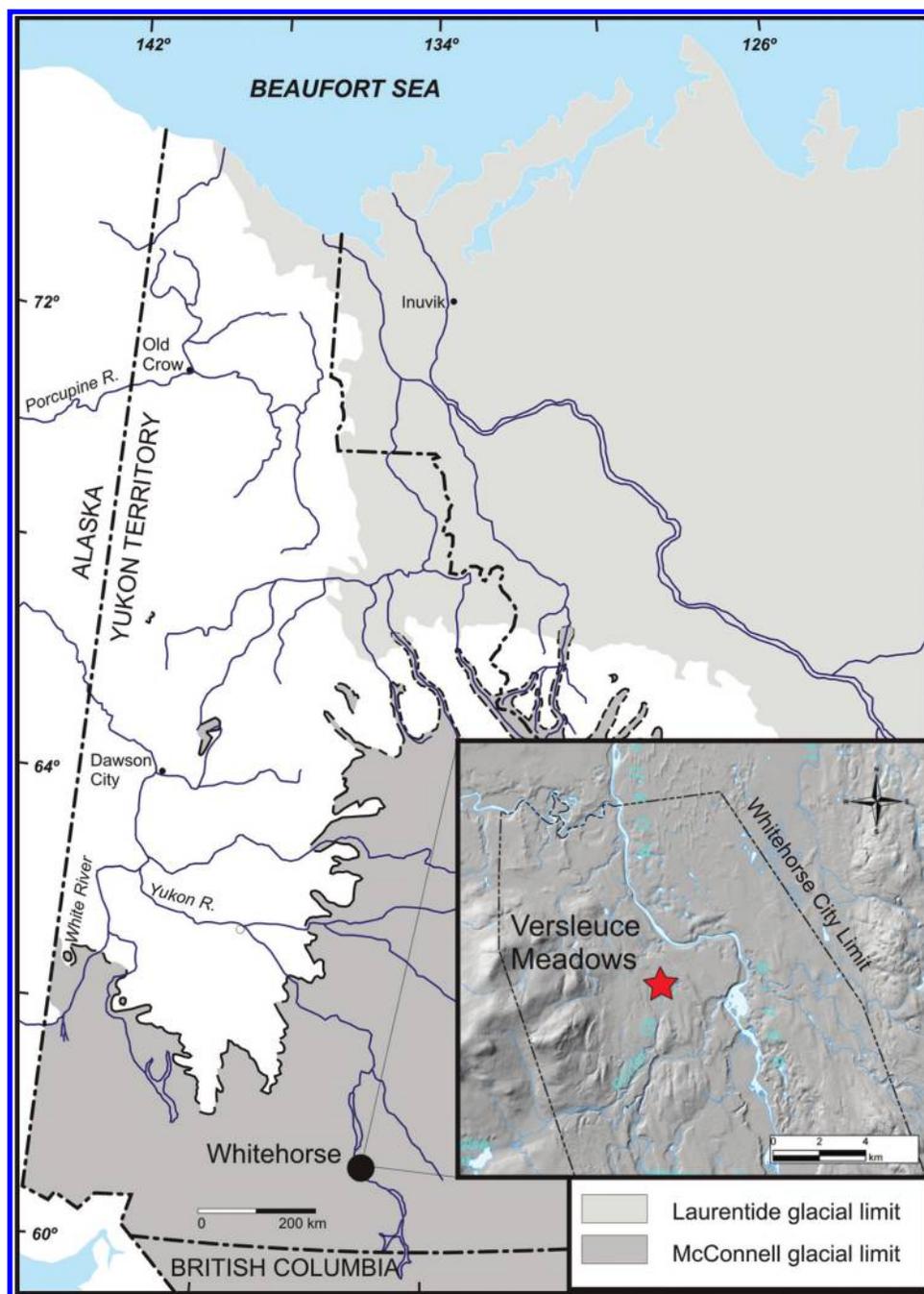
After initial investigation in the afternoon of 26 April 2012, it became evident the area being excavated on the periphery of Versleuce Meadow (Fig. 2a) was part of an ancient lacustrine environment. The initial trenches and excavation conducted by the equipment revealed fine-grained, horizontally bedded tan colored silt (Fig. 2b) with abundant mollusks at depth (Fig. 2c). The excavated and disturbed areas were examined by a small group of palaeontologists and archaeologists in an attempt to recover more faunal material and determine the extent of the fossil site. A number of other elements were discovered immediately, including a pair of unfused bison innominates found together, upside down. A large-scale salvage excavation then commenced, employing the use of a backhoe that was available on site, to further

reveal the site stratigraphy and look for more of the bison remains. The backhoe was used to slowly excavate a large area until a bone bed was discovered at a depth of approximately 150 cm below the surface (Fig. 2d). Excavation of the remaining elements of the bison skeleton was conducted with shovel and trowel the next day with the assistance of local community volunteers. As the salvage excavation had brought construction activities to a halt it was determined that the priority was to recover as much of the faunal material as quickly as possible, with less emphasis on details of skeletal element provenience and detailed site recording. This excavation resulted in the recovery of a partial skeleton of an individual bison and an abundance of palaeoecological samples. When shovel and trowel excavations were concluded, a

Fig. 2. Photographs from the Versleuce Meadows site. (*a*) Area with trenches where the initial accidental discovery of bones was made and where further excavation was focused; (*b*) tan-colored silty-marl sediments exposed by the excavation; (*c*) mollusc-rich silt sediment; (*d*) in situ partial bison skeleton found roughly 150 cm below the surface.

much larger area was subsequently excavated by backhoe to ensure that no other bones had been missed.

Due to time constraints of the field project, only one day of hasty salvage excavation was performed at the Versleuce Meadows site. Excavation of the partial skeleton was focussed on the bone bed that occurred roughly 150 cm below the surface. The skeleton was largely confined to a horizontal plane, roughly 550 cm in length. The skeleton was roughly orientated in anatomical position with the cranium upside down. After removal of fossils, further reconnaissance was performed with the backhoe below and laterally, but failed to yield any further remains. Samples of the sediments associated with the bison skeleton were collected at the site for subsequent analysis. All the faunal material was taken back to the Yukon Government Heritage Resource Unit offices for further study.

Metric osteological analysis

Mensurational data were taken on the bison fossils using digital calipers and following the methods of van den Driesch (1976) and Skinner and Kaisen (1947) with others from McDonald (1981) and Wilson et al. (2008). Age-of-death estimation for the bison was established following the methods of Duffield (1973).

Radiocarbon analysis

A subsample of cortical bone from the diaphysis of the right tibia, specimen YG 422.21, was submitted to the KECK University of California Irvine Accelerator Mass Spectrometer (UCIAMS) laboratory for radiocarbon dating. Procedures used in the preparation of the ultrafiltered (>30 kD) bone collagen gelatin are detailed in Beaumont et al. (2010). Detailed description of the combustion and graphitization protocols and the operation of the UCIAMS instrument are described in Beverly et al. (2010).

Phylogenetic analysis of mitochondrial genomes

To diagnose the taxonomic identity of the Versleuce Meadows bison and place it within a mitochondrial phylogenetic framework (Shapiro et al. 2004; Heintzman et al. 2016), a sample of specimen YG 422.21 (right tibia shaft) was sent to the specialized ancient DNA facility at the University of California, Santa Cruz. DNA extraction, library preparation, mitochondrial genome target enrichment, and sequencing were all performed during a previous study using the approach of Heintzman et al. (2016). We constructed a consensus sequence following Heintzman et al. (2016), except that we retained the entire mitochondrial genome (GenBank accession number MF134653). We compared the Versleuce Meadows bison mitogenome sequence to a previously published alignment (Froese et al. 2017), which consists of mitochondrial genome sequences from 46 North American or Siberian bison and four yak. We performed a phylogenetic timetree analysis using BEAST (v1.8.1; Drummond et al. 2012) utilizing parameters outlined in Froese et al. (2017). Briefly, we partitioned the data, used a strict molecular clock informed by radiocarbon or stratigraphic data (with independent rates for each partition), and a skygrid coalescent prior (Gill et al. 2013). We ran two analyses of 60 million iterations each, sampling trees every 3000 iterations, and discarding the first 10% as burn-in. Sampled trees from both analyses were combined and summarized as a maximum clade credibility (MCC) tree.

Paleoecological analyses

Two samples of calcareous lake sediment in association with the bison skull were analyzed for pollen, spores, and algal remains to help assess the local paleoenvironment. Subsamples of 5 mL were treated by standard processing techniques (Faegri et al. 1989), involving HCl, HF, KOH, and acetolysis after adding exotic *Eucalyptus* marker pollen grains (1 tablet, 16 180 ± 1460 grains) to each sample to calculate palynomorph concentrations. Residues were mounted in glycerine jelly and identified and counted at 400× magnification. Pollen sums are 540 and 571 grains for percent calculations. As expected, the sediment analyzed was strongly calcareous, and reacted violently with dilute HCl. Most of the volume, however, was siliceous and needed two HF treatments and hot HCl to dissolve. White and black spruce pollen types were separated using the morphological criteria of Hansen and Engstrom (1985).

For other macrofossil analyses, sediments collected in association with the bison fossils were soaked in water to disaggregate the material and washed through a 425 μm mesh sieve. The retained material was picked through under a dissecting microscope. Vascular plant macrofossils were identified with the aid of comparative modern plant material at the Yukon Heritage Resources Unit, as well as publications such as Lévesque et al. (1988). Taxonomic nomenclature follows Cody (1996).

Bryophyte macrofossils were dispersed and separated from detrital material (unidentifiable rootlets and degraded graminoid tissue), then examined initially in water under a dissecting microscope. Bryophyte fragments were then compiled into distinct taxa, further examined with the aid of a compound microscope,

and identified using Hedenäs (2014*a*, 2014*b*). Species determinations were confirmed with comparison to extant material available in the Cryptogamic Herbarium (ALTA), Department of Biological Sciences, University of Alberta. Exceptional preservation was noted for all species determined. Vouchers are deposited in the Cryptogamic Herbarium (ALTA).

Sieved gastropods and bivalves were brought to the malacology laboratory at the Canadian Museum of Nature (CMN), in Gatineau, Québec, where the national mollusc collections are located. The specimens were examined using a stereomicroscope and identification was conducted using Clarke (1981) and the national mollusc collection at the CMN. Specimens are generally well-preserved, with the surface texture of the shell intact, thus facilitating the identification. Nomenclature and taxonomical authority follow the Integrated Taxonomical Information System (ITIS 2016).

Results

Site stratigraphy

Excavation with the backhoe and shovels revealed a consistent stratigraphic profile across the site (Fig. 2). Considering the area underwent extensive removal of surficial sediments and soil at various times in the past, it is difficult to assess the nature of the uppermost sediments. The observed stratigraphy is as follows:

0–20 cm (below surface): highly disturbed modern sod and organic rich soil;

20–70 cm: well-sorted tan-colored silt, no clasts, rare gastropods and bivalves, modern roots from the surficial vegetation;

70–100 cm: well-sorted tan-colored silt with some grey beds of clay, increasing abundance of mollusc shells with depth, sediments reacted vigorously to HCl;

100–170 cm: tan-colored silt with grey clay beds, beds of marl consisting of dense concentrations of mollusc shells, increasing shell content with depth in the sediment, rare clasts, sediments reacted vigorously to HCl. This is the level that contained the bison fossils.

A partial skeleton of a bison (Fig. 3; Tables 1, 2) was recovered from within the silty-marl sediments approximately 150–170 cm below the surface. The bison was in approximate death position. All skeletal material is accessioned in the collections of the Yukon Palaeontology Program (specimen acronym YG) in Whitehorse, Yukon. Description of the skeletal remains are as follows:

Systematic vertebrate palaeontology

Order   Artiodactyla
Family   Bovidae

Bison sp.

CRANIUM: Referred specimens: YG 422.1 with both horn cores, LM1–3, LPM2–4, RM1–3, RPM3.

The cranium from the Versleuce Meadows bison is largely complete (Fig. 4; Table 1), though much of the maxilla is broken into numerous small pieces. The maxillary teeth were recovered in the sediment surrounding the cranium. The cranium has a relatively narrow, flat frontal and slightly domed, broad nasal. The orbits are roughly parallel to the frontal plan. The horn core bases are triangular in cross section, and slightly rotated rearward. The horn cores have a dorsal groove on the proximal half and they taper gradually toward the tip which are elliptical in cross section. The anterior–posterior margin of the horn cores are weakly concave and proximally downswept with tips rising about 60 mm above the frontal plane. The horn cores are directed laterally with the distal halves backswept and with tips terminating slightly behind the occipital plan. The growth of the horn cores is relatively straight on an arched axis with negligible distal twist. The rugose burrs at the base of the horn cores have weakly developed

Fig. 3. An idealized skeleton of a bison showing parts that we recovered at the Versleuce Meadows site shaded in gray. Precise anatomical position of some elements, such as rib fragments, were not determined but are illustrated here for interpretive purposes. Illustration after Gilbert (1990).

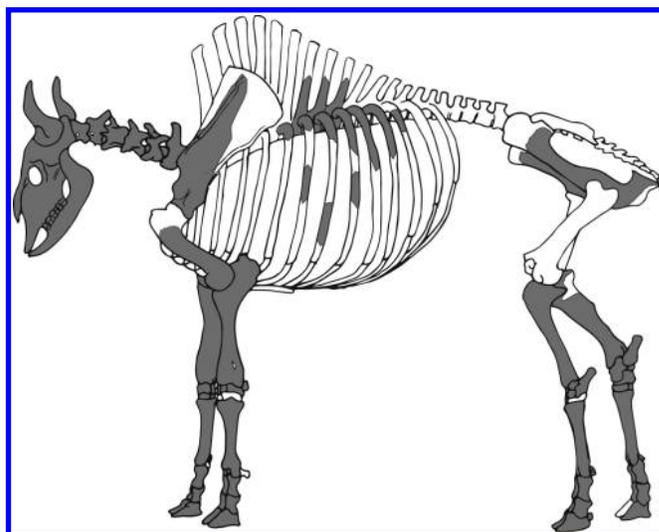exosteses and the frontal midline suture of the cranium is not fused, suggesting a young individual.

MANDIBLES: Referred specimens: YG 422.2 (R) with m1–3, i1–3, c1 and pm4 (Fig. 5*a*); YG 422.3 (L) with m1–3 and pm2–3.

Both mandibles halves were recovered near to the cranium and are largely complete, though are not fused at the symphysis. The incisor teeth were found in the sediment next to the mandibles.

VERTEBRAL COLUMN AND RIBS: Referred specimens: *atlas*: YG 422.4; *axis*: YG 422.5; *cervical vertebra*: YG 422.24 (3rd cervical: complete though centrum epiphysis is not fused to body; Fig. 5*b*), YG 422.7 (4th cervical: transverse processes broken on distal ends), YG 422.8 (5th cervical: complete), YG 422.6 (6th cervical: complete), YG 422.9 (7th cervical: complete); *thoracic vertebra*: YG 422.25 (unfused portion of posterior centra epiphysis), YG 422.26 (spinous process broken on distal end, anterior epyphysis of centra missing; Fig. 5*c*), YG 422.27 (spinous process broken on distal end), YG 422.85 (fragment of unfused distal centrum epiphysis); *innominates* (Fig. 5*d*): YG 422.32 (L: incomplete and broken in five pieces), YG 422.31 (R: incomplete and broken in four pieces); *ribs*: (Fig. 5*e*) YG 422.12, YG 422.13, YG 422.14, YG 422.15, YG 422.16, YG 422.17, YG 422.17, YG 422.18, YG 422.19, YG 422.22, YG 422.13.

The vertebral elements are consistent in that they exhibit only partial fusion of the centra or in some, no fusion at all. The lack of complete fusion in the vertebra further suggests this was a young individual. Only 11 individual broken rib fragments were recovered. The ribs were all recovered in situ immediately below the left ulna and radius. The innominates are not fused and broken in several pieces, with both ilia showing evidence of carnivore gnawing. The innominates were recovered approximately 4 m from the rest of the skeleton.

FORELIMBS: Referred specimens: *metacarpal* (Fig. 5*f*): YG 422.33 (R) and YG 422.40 (L); *proximal phalanx* (pairs): YG 422.47 (R) – YG 422.48 (L) and YG 422.45 (R) – YG 422.46 (L); *medial phalanx* (pairs): YG 422.51 (R) – YG 422.52 (L) and YG 422.49 (R) – YG 422.50 (L); *distal phalanx* (pairs): YG 422.55 (R) – YG 422.46 (L) and YG 422.53 (R) – YG 422.54 (L); *magnum*: YG 422.34 (R) and YG 422.41 (L); *unciform*: YG 422.35 (R); *scaphoid*: YG 422.36 (R) and YG 422.42 (L); *lunar*: YG 422.37 (R) and YG 422.42 (L); *cuneiform*: YG 422.38 (R) and YG 422.38 (L); *trapezoid*: YG 422.39 (R); *radius* (Fig. 5*g*): YG 422.85 (L) and YG 422.30 (R); *ulna*: YG 422.84 (L) and YG 422.29 (R); *humerus*: YG 422.10 (L; (Fig. 5*h*)) and YG 422.11 (R); *scapula*: YG 422.28 (L; Fig. 5*i*).

Table 1. Mensurational data from Versleuce Meadows bison cranium YG 422.1 with comparative metrics from other Quaternary bison species (after McDonald 1981).

Description of metric	Skinner and Kaisen (1947) metric	van den Driesch (1976) metric (fig. 8, *Bos taurus*)	YG 422.1	*Bison antiquus*			*Bison occidentalis*			*Bison priscus*			*Bison bison athabascae*			*Bison alaskensis*		
				Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
Spread of horn cores, tip to tip	#1	#42	802	765	870	1067	626	779	1055	751	888	1064	542	681	848	800	1151	1540
Greatest spread of cores on outside curve	#2	#43	810	—	—	—	735	782	892	—	—	—	—	—	—	—	—	—
Core length on upper curve, tip to burr	#3	—	282	203	279	364	186	278	392	285	362	416	165	235	323	426	553	795
Core length on lower curve, tip to burr	#4	#47	332	280	336	395	275	340	405	—	—	—	—	—	—	—	—	—
Straight line length, tip of core to upper base at burr	#5	—	253	185	250	330	175	249	350	268	318	379	154	207	277	294	459	667
Vertical (or least) diameter of horn core at base (at burr)	#6	—	93	81	102	126	70	95	114	84	98	116	81	92	106	100	117	153
Greatest (transverse) diameter of horn core at base	—	#45	96	76	106	129	77	99	120	98	115	130	83	97	109	122	142	171
Circumference of core at base (at burr)	—	#44	313	233	324	392	237	300	355	293	330	387	254	289	322	341	397	493
Greatest width of auditory opening	#8	#25	273	251	288	318	238	262	294	248	276	310	243	274	298	268	302	340
Width of condyles	#9	#26	145	132	144	161	111	135	151	127	141	165	118	130	139	133	152	175
Depth from occipital crest to top of foramen magnum	#10	#41	94	94	112	134	89	104	120	91	103	119	92	100	114	97	111	134
Depth from occipital crest to bottom of foramen magnum	#11	#40	135	—	—	—	136	158	177	—	—	—	—	—	—	—	—	—
Greatest width between bases of horn cores	#13	—	340	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Least width between horn cores	#31	—	335	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Width of cranium between horn cores and orbits	#14	#32	280	276	315	352	261	297	348	269	294	336	273	293	313	281	332	394
Maximum internal width of orbit	—	#23	80	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Greatest breadth across the orbits—greatest frontal breadth	#15	#33	331	346	353	360	311	348	394	313	350	415	326	354	384	356	396	440
Least breadth between the orbits	#16	#34	252	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Facial breadth	#17	#35	n/a	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rostral width at maxillary–premaxillary suture	#18	—	n/a	—	—	102	115	125	—	—	—	—	—	—	—	—	—	—
Least occipital breadth	—	#30	163	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Greatest breadth across nasals	—	#36	94	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Condylobasal length	O-P		573	—	—	—	505	573	630	—	—	—	562	579	604	602	650	676
Basal length	F-P	#3	548	520	545	560	467	516	582	—	—	—	—	—	—	—	—	—
Breadth across the premaxillae on the oral protruberences	—	#37	n/a	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Greatest palatal breadth measured across outer borders of alveoli	—	#38	n/a	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Length of cheek tooth row	#19	#20	n/a	—	—	—	137	147	160	—	—	—	—	—	—	—	—	—
Length of molar row	#20	#21	n/a	105.2	105.6	106	84	91	102	—	—	—	—	—	—	—	—	—
Length of premolar row	—	#22	n/a	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Length of nasal bone	N-T	#12	219	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Length, occipital crest to nasal-frontal suture	O-N	#8	244	240	295	350	229	259	273	254	272	286	240	256	276	265	298	338
Length, beyond P2 to tip of premaxilla	M-P	—	n/a	—	—	143	153	168	—	—	—	—	—	—	—	—	—	—
Short upper cranium length—occipital crest to tip of nasals	O-T	#10	454	482	510	527	471	493	543	—	—	—	—	—	—	—	—	—
Angle of posterior divergence of horncore	#A21	—	74°	72°	79°	86°	63°	72°	83°	63°	71°	79°	63°	71°	77°	64°	74°	85°
Angle of proximal horncore depression	#A22	—	12°	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Note: Measurements reported for YG 422.1 horn cores are taken from the left side. Values are in millimeters, unless defined otherwise.

Table 2. Post cranial measurements (in millimeters) from Versleuce Meadows bison.

Metacarpal (YG 422.40)	
Overall length	225.2
Proximal breadth	83.4
Midshaft breadth	49.7
Distal breadth	83.2
Midshaft depth	31.6
Proximal depth	47.2
Distal depth	44.4
Min. shaft depth	29.9
Min. shaft breadth	49.1
Metatarsal (YG 422.57)	
Overall length	275.2
Proximal breadth	62
Midshaft breadth	39
Distal breadth	71.1
Midshaft depth	37.1
Proximal depth	61.2
Distal depth	43.4
Min. shaft depth	34.3
Min. shaft breadth	38.1
Humerus (YG 422.10)	
Smallest breadth of shaft	56.3
Greatest breadth of trochlea	112.4
Greatest breadth of distal end	120.2
Radius (YG 422.30)	
Greatest length	376.4
Smallest breadth of shaft	58.2
Greatest breadth of proximal end	109.4
Greatest breadth of proximal articular facies	99
Breath of distal end	99.7
Breadth of distal articular facies	94.9
Greatest proximal depth	59.6
Ulna (YG 422.84)	
Greatest length	440.2
Smallest depth of olecranon	74.8
Greatest depth across the processus anconaeus	104.3
Smallest depth across the processus anconaeus	66.7
Tibia (YG 422.20)	
Greatest length	453.9
Medial length	439.4
Proximal depth	127.1
Min. breadth of shaft	43.2
Min. depth of shaft	38.5
Greatest distal breadth	84.1
Greatest depth of distal end	54.7
Breadth at midshaft	49.6
Depth at midshaft	55.2
Mandible (YG 422.2)	
Length from the angle: Gonion caudale—infradentale	423
Length from the condyle: aboral border of the condyle process—infradentale	453
Length: Gonion caudale—aboral border of the alveolus of M_3	133
Length of the horizontal ramus: aboral border of the alveolus of M_3—infradentale	291
Length: Gonion caudale—oral border of the alveolus of P_2	287
Length: Gonion caudale—the most aboral indentation of the mental foramen	360
Length of the cheektooth row, measured along the alveoli on the buccal side	158
Length of the molar row, measured along the alveoli on the buccal side	101
Length of the premolar row, measured along the alveoli on the buccal side	58
Length (L) and breadth (B) of M_3, measured near the biting surface	44 (L), 16 (B)
Length of the diastema: oral border of the alveolus of P_2—aboral border of the alveolus of I_4	125
Aboral height of the vertical ramus: Gonion ventrale—highest point of the condyle process	202
Middle height of the vertical ramus: Gonion ventrale—deepest point of the mandibular notch	183
Oral height of the vertical ramus: Gonion ventrale—coronion	232
Height of the mandible behind M_3 from the most aboral point of the alveolus on the buccal side	71
Height of the mandible in front of M_1	50
Height of the mandible in front of P_2	39

Fig. 4. Versleuce Meadows Bison cranium (YG 422.1). [Colour online.]

The distal forelimb elements are complete, except for missing unciform and trapezoid on the left side. The radius and ulna are not fused; both radii are complete, the left ulna is complete, while the right ulna has been broken into three pieces postmortem. Both humerii are largely complete though substantial carnivore gnawing has completely eliminated the proximal end of the right humerus, while the proximal end of the left humerus is partially removed. Several broken portions of the left scapula were recovered and the distal margins seem to have been removed by carnivores.

HINDLIMBS: Referred specimens: *metatarsal* (Fig. 5j): YG 422.58 (R) and YG 422.57 (L); *proximal phalanx* (pairs): YG 422.66 (R) – YG 422.67 (L) and YG 422.68 (L); *medial phalanx*: YG 422.69 (R) – YG 422.70 (L) and YG 422.71 (R) – YG 422.72 (L); *distal phalanx*: YG 422.73 (L) and YG 422.74 (R) – YG 422.75 (L); *naviculo-cuboid*: YG 422.62 (R) and YG 422.59 (L); *lateral malleolus*: YG 422.63 (R) and YG 422.60 (L); *astragalus*: YG 422.64 (R); *calcaneum*: YG 422.65 (R) and YG 422.61 (L); tibia: YG 422.20 (L) and YG 422.21 (R; Fig. 5k).

The distal hindlimb elements are complete, except for missing right distal (3rd) phalanx, a left proximal (1st) phalanx, and a left astragalus. Both femora are missing. Both tibias are mostly complete, though there is substantial evidence of carnivore gnawing on the right tibia, and minimal gnawing marks on the left. Mid-shaft breakage on the left tibia seems to be from excavation by heavy equipment, though the pattern of breakage on the right tibia seems to suggest natural postmortem damage as warping of the bone prevented the broken pieces from fitting back together smoothly.

OTHER ELEMENTS: Referred specimens: *sesamoids*: YG 422.76, YG 422.77, YG 422.78, YG 422.79, YG 422.80, YG 422.81, YG 422.82, YG 422.83.

Ontogeny

Several skeletal features enable an age estimation for this bison based on known skeletal development of extant European bison (*B. bonasus*) (Duffield 1973). The distal epiphyses of the radius are fused (Fig. 5g), and the proximal head of the humerus is fused

Fig. 5. Versleuce Meadows bison skeletal elements. Scale bar is in 1 cm increments. (*a*) Right mandible; (*b*) 3rd cervical vertebra showing unfused epiphysis of the centrum; (*c*) thoracic vertebra lacking anterior epiphysis of centra and broken spinous process; (*d*) innominates; (*e*) various rib fragments; (*f*) metacarpal with complete set of phalanges; (*g*) left radius; (*h*) left humeus with substantial carnivore gnawing of proximal end; (*i*) left scapula with substantial carnivore gnawing on the periphery; (*j*) metatarsal with complete set of phalanges; (*k*) right tibia which is heavily carnivore gnawed on proximal end and fractured on distal part of the shaft, radiocarbon sample removed from the middle shaft. [Colour online.]
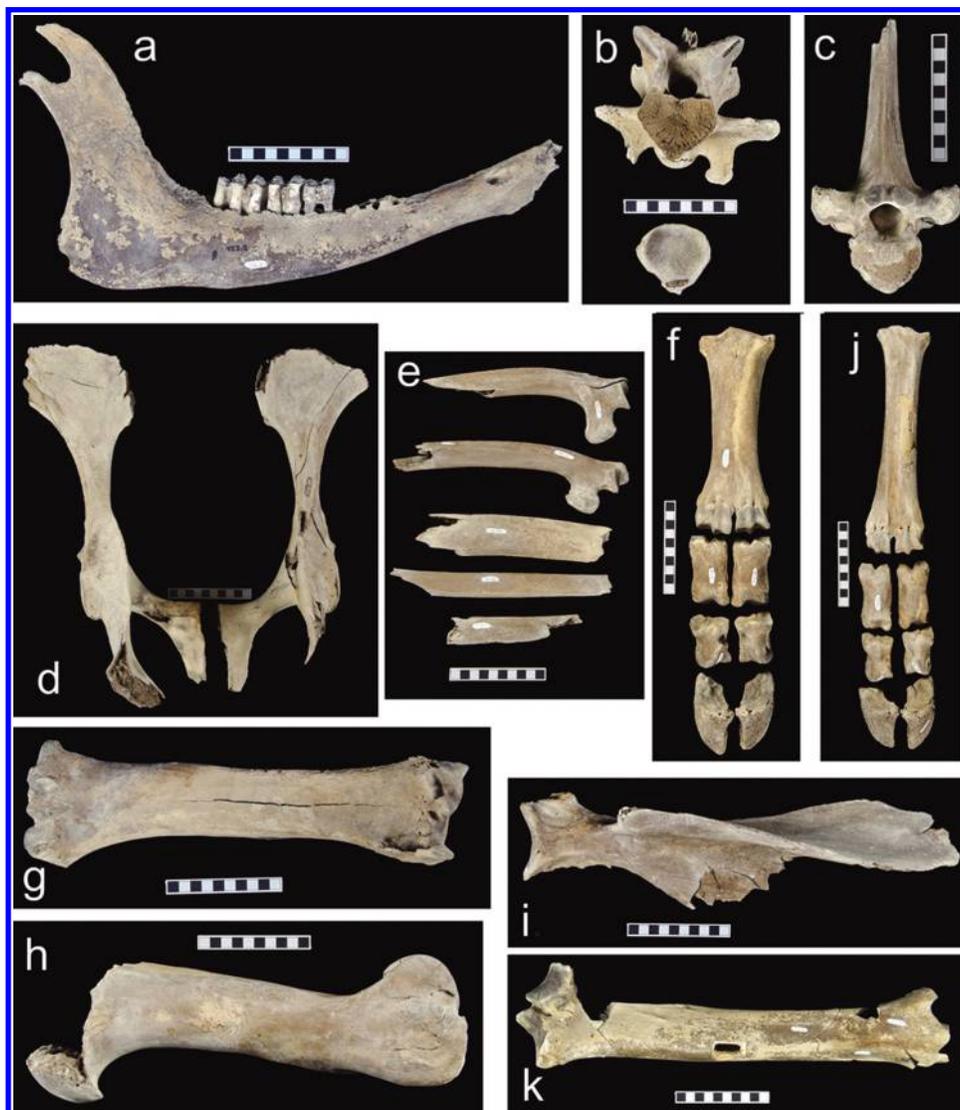
(Fig. 5*h*), which generally occurs early in the sixth year. Since some of the vertebral epiphyses are in early stages of fusion, especially in the cervicals, though the thoracics remain largely fused, it is likely the animal died before the start of its seventh year. This assessment is supported by the lack of frontal fusion on the cranium (Fig. 4), and minimal development of exosteses on the rugose burrs of the horn core bases. We also heed Duffield's (1973) cautions with determination of sex since this is an immature individual and there may be considerable overlap in several measurement indices between young males and females.

Radiocarbon date

Ultrafiltered collagen from the bone sample yielded a radiocarbon age of 4710 ± 15 ^{14}C yr BP (UCIAMS 114030; Heintzman et al. 2016). Calibration of this radiocarbon date using the IntCal13 dataset (Reimer et al. 2013 Radiocarbon) places the bison between 5578 and 5327 cal. yr BP (midpoint = 5452 cal. yr BP) at 95.4% confidence.

Phylogenetic analysis

Separate analyses of bison mitochondrial genomes confirm that both subspecies of extant bison (*B. bison*) form a single, well-supported cluster (Clade 1A) within the greater diversity of North American bison (Shapiro et al. 2004; Heintzman et al. 2016; Froese et al. 2017; Fig. 6). To confirm the phylogenetic placement of the Versleuce Meadows bison, we added this newly generated complete mitochondrial genome sequence to a previously published data set of North American and Siberian bison mitochondrial genomes (Froese et al. 2017) and constructed a new phylogeny. The Versleuce Meadows bison clusters with a Clade 2A bison from Edmonton (PH027). This is consistent with a previous analysis that included only a ~600 base pair sequence of the mitochondrial control region (Heintzman et al. 2016) and confirms the placement of the Versleuce Meadows bison within Clade 2A. This phylogenetic position indicates that the Versleuce Meadows bison did not belong to the mito-

Fig. 6. A Bayesian timetree of bison mitochondrial genomes, with three well-supported Clades (1A, 2A, 2B; Heintzman et al. 2016) highlighted in grey. The Versleuce Meadows bison (VersMead) is highlighted in bold and belongs to Clade 2A. All living bison in North America are members of Clade 1A. For this study, we refer to all bison outside of Clade 1A as *Bison* c.f. *priscus* regardless of their morphology. Four yak outgroup sequences have been removed. Branch support values are given for deep nodes and those shallower nodes with posterior probability values >0.95. Light grey node bars are 95% highest posterior density intervals for node heights and are shown for nodes with posterior probability values >0.95.
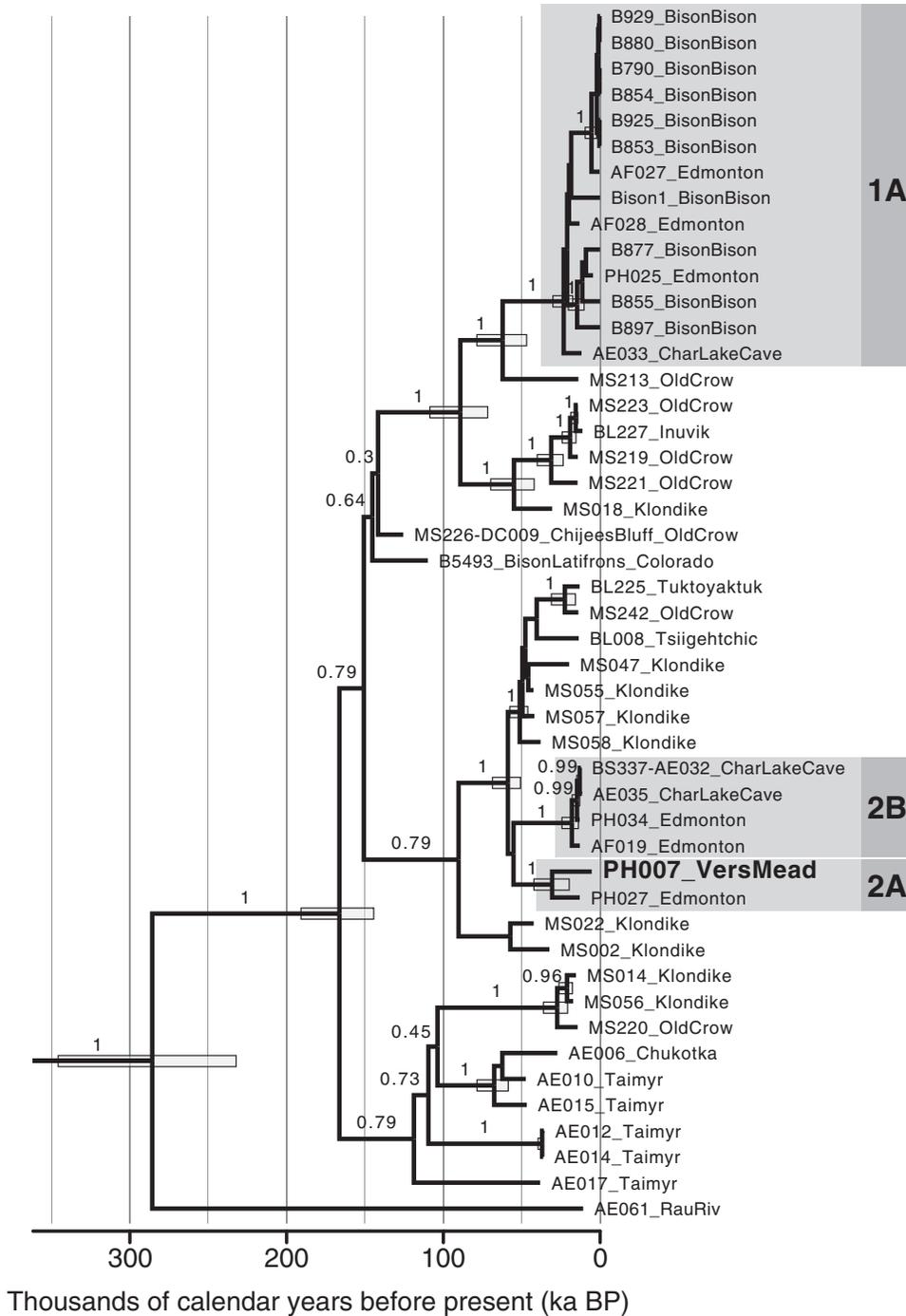
chondrial lineage of bison that eventually gave rise to extant bison subspecies.

Paleoenvironmental data

Palynomorph concentrations are very low (Table 3) but preservation was generally good. The pollen spectra are dominated by arboreal taxa such as white and black spruce, birch, and alder shrubs, while sedges (Cyperaceae) dominate the herb component.

Plant seeds, fruits, and vegetative parts from vascular plants are not abundant within the silt sediments, though are generally well-preserved (Fig. 7). The plants are dominated by aquatic plants that presently inhabit littoral edges of ponds and lakes in the region at present, such as pondweeds (*Potamogeton* sp.; Fig. 7a) and common mare's tail (*Hippuris vulgaris*; Fig. 7b), and nearshore sedges (*Carex* spp.; Figs. 7c, 7d) with rare *Elocharis* sp. (Fig. 7e). Moderate amounts of spruce (*Picea* sp.; Fig. 7f) needles were recov-

Table 3. Fossil palynomorphs from the Versleuce Meadows site.

Taxon	Sample A (%) (sum = 540)	Sample B (%) (sum = 571)
Trees total (AP)	60.7	67.1
Picea glauca type	38.1	42.1
Picea mariana type	9	13.9
Pinus contorta type	0.8	0
Betula	12.3	10.6
Shrubs		
Alnus viridis type	11.5	8.5
Salix	2	5.6
Shepherdia canadensis	0.8	0.2
Herbs		
Cyperaceae	22	16.7
Poaceae	0.8	0
Artemisia	2.3	1.8
Potamogeton type	0.4	0.2
Spores		
Filicales undiff.	0.6	1.1
Equisetum	0.2	0
Lycopodium	0.4	0
Algae		
Botryococcus	2.2	1.4
Pediastrum	1.1	0.2
Palynomorph concentration	25 300 per mL	15 500 per mL

ered, most being charred. Rare terrestrial herbaceous taxa were recovered as well, including goosefoot (*Chenopodium* sp.; Fig. 7g), buttercup (*Ranunculus aquatilis* type), and knotweed (*Polygonum* sp.). In addition to vascular plants, remains of the charophyte algae (*Chara* sp.) and statoblasts of the acquatic bryozoan *Cristatella mucedo* (Fig. 7h) were common.

The bryophyte macrofossils recovered from the Versleuce Meadows sediments include three species (Figs. 7i, 7j, 7k). Excellent preservation included intact leaves with leaf habit and attachment to stems clearly visible, in addition to detached leaves or denuded stems. *Scorpidium scorpioides* (Hedwig) Limpricht (Fig. 7i)—a submerged to emergent hydric taxon—often had leaves with shredded apices, yet the ovate leaf shape (linear, smooth leaf cells, entire margins and lack of a costa and differentiated alar cells) are diagnostic of this common circumpolar arctic–boreal wetland taxon. *Calliergon giganteum* (Schimper) Kindberg (Fig. 7j) is a common circumpolar arctic–boreal emergent wetland species that had broad, strongly concave leaves with well-preserved, abruptly inflated alar cells reaching the costa and a single unbranched costa that reaches the apical region of the leaf. The rounded apex and linear, smooth leaf cells help to determine this taxon. *Drepanocladus longifolius* (Wilson ex. Mitten) Brotherus ex. Paris (Fig. 7k) is one of the most common taxa preserved in sediments at northern sites (as *Drepanocladus crassicostatus* Janssens in Janssens 1983). This is a distinct taxon determined by its long excurrent and stout costa. It has alar cells that form 1–2 rows along the leaf base. Its preferred habitat also includes nutrient-rich waters of pools, lake margins, oxbows, or depressions of wet meadows (Hedenäs 2014a; Janssens 1983). Within the subsample, *Scorpidium scorpioides* was the most abundant taxon (50%–100%) followed by *Drepanocladus longifolius* (25%–50%) and *Calliergon giganteum* (0%–25%).

An abundance of well-preserved molluscan taxa, including at least 10 species of freshwater bivalves and gastropods (Table 4; Figs. 7l, 7m, 7n), were recovered from the silty marl collected in association with the bison skeleton. All species of bivalves and gastropods found are currently found in Canada and are typical of a pond or lake environment—although some of those species also currently inhabit running water.

The largest molluscan species found is the frigid lymnaea (sometimes called Alaskan lymnaea), *Lymnaea atkaensis*, which is restricted at present to British Columbia, the Northwest Territories, and the Yukon Territory (Clarke 1981). It prefers cold, oligotrophic lakes and appears to have similar habitat characteristics as *Sphaerium nitidum*. Many complete and unbroken large adult specimens of *Lymnaea atkaensis* were recovered, suggesting that deposition of the shell material in the pond or lake occurred with little reworking of the sediment or mixing of the sediments. All the gastropods belong to species that are typically found in the littoral or sublittoral zone of ponds or lakes. They are known to crawl on submerged macrophytes, sometimes on the fine sediment (sand, silt, mud), occasionally crawling on sunken debris, and less frequently or rocks or stones. Among the bivalves, the two species of *Pisidium* (Fig. 7m) and the one species of *Sphaerium* collected (Table 4) belong to the family Sphaeridae and are commonly found in small or large ponds, or lakes. They live normally just below the surface of the sediment on the bottom of the pond or lake, and they are capable of moving through the sediment, using their muscular foot. These little clams use their long siphonal tubes, feeding on microscopic plants and detritus deposited on the bottom (deposit feeders). Many or most of the mollusc species found are usually associated with cold, hard waters, although some, especially *Pisidium casertanum*, occur in a wide range of pH (5.50–8.34), total alkalinity (0–280 mg $CaCO_3$/L), total hardness (10–332 mg $CaCO_3$/L), and Ca hardness (Mackie and Flippance 1983).

Discussion

Bison taxonomy

Bison taxonomy has focused traditionally on adult male cranial and horn core characteristics and measurements (Skinner and Kaisen 1947), while the post-cranial skeleton is largely considered to be unreliable for taxonomic assignments (McDonald 1981). The relative completeness of the Versleuce Meadows bison cranium (Fig. 4) enables comparison with other reported bison fossils, to help resolve the taxonomy of this individual. However, caution must be taken with this assessment, because cranial and post-cranial features demonstrate this is a young individual. Horn core measurements on a young bison are not directly comparable to published data from mature adults and may preclude any definitive taxonomic assignment (sensu McDonald 1981). Even with a complete adult cranium, there are few diagnostic characters that can be used to positively distinguish one named bison taxon from another, and there is demonstrated mensurational overlap between most of the recognized species.

Superficially, the cranial characters and measurements (Table 1; Fig. 4) from the Versluce Meadows bison demonstrate a possible morphological affinity with a variety of named bison species, including *B. occidentalis* and *B. priscus* (Skinner and Kaisen 1947; McDonald 1981). Some of the characters considered important are the triangular horn core bases that gradually taper toward the tip which are elliptical in cross section, a dorsal groove along the proximal part of the horn core, proximally down-swept and distally rear-swept horn cores, relatively flat frontal, and low lying orbits. Considering overall size, the Versleuce Meadows bison fits within the lower size ranges reported for *B. priscus*, and is well below the range for the highly curved and robust horned *B. alaskensis* (McDonald 1981). Based purely on cranial measurements, the Versleuce Meadows specimen also fits within the range reported for large-sized extant wood bison (McDonald 1981). In recognition that this specimen represents a sub-adult, and the inherent problems with bison taxonomy, inconsistency in morphological species diagnoses, and substantial inter-species mensurational overlap, we remain conservative in our approach and are hesitant to commit to any assignment apart from *Bison* sp. based purely on morphological or mensurational grounds.

Fig. 7. Macrofossils recovered from sediment associated with the bison skeleton. (*a*) *Potameogeton* nutlet; (*b*) *Hippuris* seed; (*c*) *Carex* perigynia; (*d*) *Carex* achene; (*e*) *Eleocharis* achene; (*f*) *Picea* needle; (*g*) *Chenopodium* seed; (*h*) *Cristatella mucedo* statoblast; (*i*) *Scorpidium* scorpioides stem with leaves; (*j*) *Calliergon giganteum* stem with leaves; (*k*) *Drepanocladus longifolius* stem with leaves; (*l*) *Stagnicola arctica* shell; (*m*) *Valvata sincera* bivalve shell; (*n*) *Pisidium casertanum* shell.
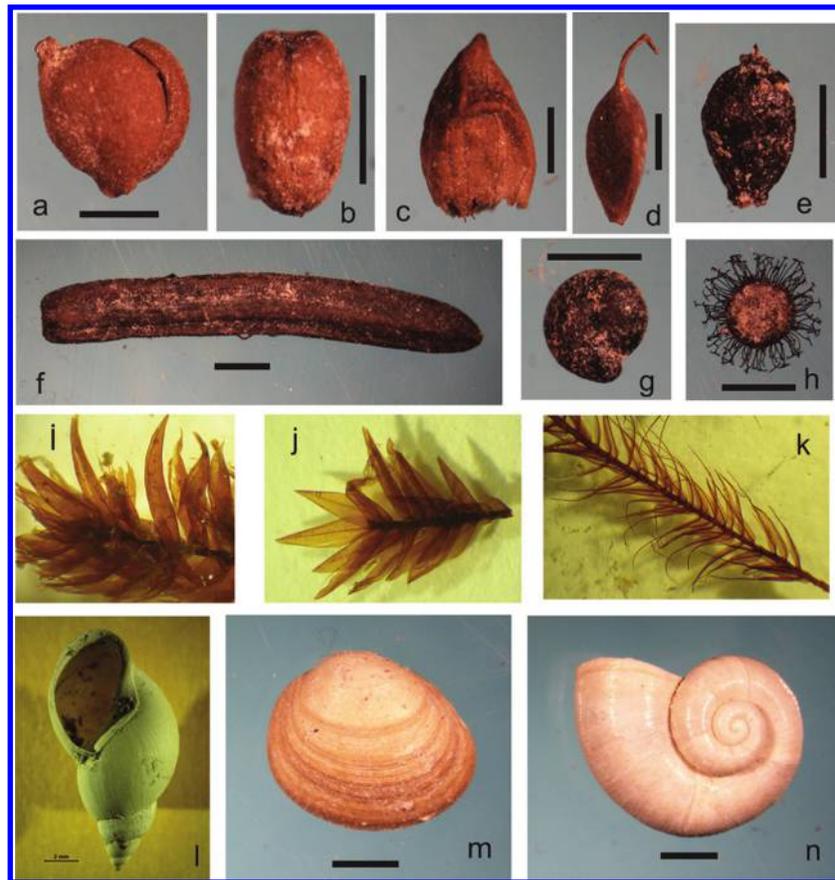
However, genomic data enable us to place this specimen within a phylogenetic model that includes numerous other ancient bison from this region, assisting greatly in a taxonomic assignment (Shapiro et al. 2004; Heintzman et al. 2016; Froese et al. 2017). Mitochondrial genomic data from the Versleuce Meadows bison confirm that it belongs to Clade 2A, which includes Pleistocene *B.* cf. *priscus* from Beringia and northwest Canada through the Holocene and is not represented in living bison species (Shapiro et al. 2004; Heintzman et al. 2016). For this study, we refer all North American bison outside of Clade 1A as *B.* cf. *priscus* regardless of morphological affinity, but acknowledge that more work needs to be done to further resolve the inconsistency between morphological and genetic data in the study of North American bison. Given the combination of genomic data placing the Versleuce Meadows specimen in the Clade 2A, while recognizing that some of the cranial characteristics and measurements of this young individual are similar to descriptions reported for steppe bison, a taxonomic assignment of *B.* c.f. *priscus* is warranted.

Importantly, the Versleuce Meadows bison did not belong to the lineage that gave rise to present-day wood and plains bison (Fig. 6). All living bison have mitochondrial haplotypes within Clade 1A. The geographical origins of Clades 2A and 2B are of interest, as this is relevant to the timing and direction of bison dispersal between Beringia and the North American midcontinent after the recession of glacial ice (Heintzman et al. 2016). While the location of origin of the common ancestor of Clade 2B cannot be determined with confidence, phylogeographic models provide strong support for a northern or Beringian origin of Clade 2A, to which the Versleuce Meadows bison and other Holo-

cene steppe bison from Beringia belong. We acknowledge that in the absence of nuclear genetic data, the degree of breeding between resident bison from Beringia and northward dispersing bison during post-glacial times after the opening of the ice-free corridor remains unknown (Heintzman et al. 2016). While it is not possible to know how long this lineage of steppe bison persisted into the Holocene, the young radiocarbon age on the Versleuce Meadows specimen makes it one of the last surviving members.

Versleuce Meadows bison skeleton taphonomy

The sediments, stratigraphy, and radiocarbon age from the Versleuce Meadows site suggests that the animal died in a small lake ~5400 years ago. With much of the skeleton recovered in partially articulated death position, there was minimal post-mortem movement of many of the bones. Considering the presence and excellent preservation of the distal limb elements, including metatarsals, metacarpals, carpals sesamoids, and phalanges, it is possible that the animal's lower limbs became mired in the lake bottom mud immediately prior to its death (Figs. 4, 5). The breakage on the distal tibia shafts perhaps occurred as the animal struggled to free itself and collapsed. Much of the anterior half of the skeleton was recovered in situ in a confined area that seemingly was the location of the animal's death (cranium, mandible, radii, ulnae, cervical and thoracic vertebrae, rib fragments, metacarpals, and carpals), while much of the posterior parts of the skeleton (pelvis, tibia, metatarsals) were discovered a few meters away from the main skeleton and accidentally discovered and recovered during the initial construction and trenching at the site. Carnivores clearly were able to scavenge the more proximal parts

Table 4. Mollusks from the Versleuce Meadows site.

Class	Family	Common name	Species	Habitat
Gastropoda	Lymnaeidae	Frigid lymnaea, Alaskan lymnaea	*Lymnaea atkaensis* (Dall, 1884)	Restricted to BC, NWT, and Yukon Territory. Clarke (1981) reports it from cold, oligotrophic lakes and appears to have similar habitat characteristics as *Sphaerium nitidu.*
Gastropoda	Valvatidae	Mossy valvata (subspecies)	*Valvata sincera sincera* (Say, 1824)	Widely spread and very common when found. Most common in littoral and sublittoral zones on substrates of mud and organic debris.
Gastropoda	Valvatidae	Mossy valvata (subspecies)	*Valvata sincera helicoidea* (Dall, 1905)	A northern species (subspecies) in shallow ponds, lakes, rivers, streams, and bogs, on a variety of substrates in littoral and sublittoral zones.
Gastropoda	Planorbidae	Ash gyro	*Gyraulus parvus* (Say, 1817)	Common in vegetation zones of permanent ponds and lakes, and in organic to mud substrates.
Gastropoda	Lymnaeidae	Arctic pondsnail	*Stagnicola arctica* (Lea, 1864)	A northern species in shallow ponds, lakes, rivers, streams, and bogs.
Gastropoda	Lymnaeidae	Marsh pondsnail ?	*Stagnicola elodes* ? (Say, 1821)	—
Gastropoda	Lymnaeidae	Modest fossaria	*Fossaria modicella* (Say, 1825)	Very common everywhere, in temporary and permanent aquatic habitats. A littoral/sublittoral species common in muddy, organic substrates
Gastropoda	Lymnaeidae	Boreal fossaria ?	*Fossaria decampi* ? (Streng, 1896) (syn. *Galba galbana)*	Cold water species, most common in large lakes in southern Canada, streams and shallow lakes in northern parts of its range.
Bivalvia	Sphaeriidae	Ubiquitous peaclam	*Pisidium casertanum* (Poli, 1791)	The most ubiquitous fingernail clam, and probably freshwater mollusc in all parts of the world. Found in oligotrophic to eutrophic lakes, deep and shallow waters, sandy to muddy organic ooze, temporary and permanent aquatic habitats.
Bivalvia	Sphaeriidae	—	*Sphaerium nitidum*	Cold water species, most common in oligotrophic lakes, in shallow depths in the north but hypolimnial depths in southern parts of Canada.
Bivalvia	Sphaeriidae	—	*Pisidium ventricosum*	Found principally in lakes and large rivers (never in ephemeral aquatic habitats). Large populations of the species are uncommon, but when found they are usually in fine sand or mud.

of the post-cranial skeleton as demonstrated by substantial gnawing and removal of bone on the proximal humeri and tibiae. These scavengers seemingly could not access the fairly complete distal limb elements (metapodials, phalanges) because they were buried in the lake mud, while other parts of the torso and proximal limbs were exposed. The highly fragmented nature of the ribs and limited preservation of the vertebral column suggests heavy scavenging of the internal organs and guts within the abdominal cavity. Since we were not able to recover some elements such as the femurs, while the pelvis was recovered some distance from the rest of the skeleton, this suggests that much of the carcass decomposed in situ while the forelimbs were stuck in the lake mud, and the posterior parts were scattered by carnivores or floated away. There is no evidence of human hunting or butchering on the bison remains or at the site.

Paleoenvironment

Paleoecological data recovered from sediments in association with the bison skeleton provides details of the plant communities, molluscs, and limnological conditions in and around Versleuce Meadow ~5400 years ago. The calcareous silty sediments exposed during the excavation demonstrate that a substantial body of water occupied the site during the middle Holocene. The diverse and well-preserved gastropod and bivalve assemblage supports this interpretation, as 10 species recovered are presently known to inhabit permanent ponds or lakes. Recovery of the bivalve *Pisidium ventricosum* is particularly relevant as it is not presently known to live in ephemeral aquatic habitats.

Vascular plant and bryophyte macrofossils and pollen also document the plant community within and immediately surrounding the pond. An aquatic environment is indicated by the abundance of pondweed (*Potamogeton*) seeds (and rare pollen), mare's tail, and *Chara* macrofossils, in addition to palynomorphs of algae *Botryococcus* and *Pediastrum*. Sedges were probably very common along the marshy areas along the lake margin as revealed by the abundance of *Carex* spp. achenes and pollen. However, some sedge and sage pollen might come from open meadows, such as surrounding dry, south facing slopes around the lake basin. The hydric bryophyte species typify an in situ minerotrophic, marl-rich fen, wet meadow, or still oxbow pool type of aquatic environment similar to those at present in the circumpolar Arctic and boreal regions.

Palynological results support previous studies and reveal a boreal forest dominated by white spruce, with lesser amounts of black spruce, birch, and shrub alder, with a conspicuous absence of lodgepoll pine. Rare, highly fragmentary, spruce needles confirm that spruce trees were locally present, and their pollen was not transported to Versleuce Meadows from long-distance sources. The lack of lodgepoll pine in the southern Yukon as revealed in this and previous studies provides a stark contrast to the forest community at present.

Based on paleoecological data from southern Yukon, Cwynar and Spear (1995) suggests the period between 6000 and 5400 years ago was characterized by relatively cooler and wetter climates than times before and after. Data recovered from Versleuce Meadows supports that interpretation and suggests that a sizable pond or small lake existed at this site during that period. A shallow lake in open spruce woodlands would have likely been an attractive focal point for a variety of fauna, including bison. This paleoecological reconstruction, however, is seemingly at odds with the interpretation of data from nearby alpine non-glacial ice patches. Analysis of three representative Holocene alpine ice patches suggests there was little or no accumulation of alpine ice between 6700 and 4700 years ago, suggesting increased temperatures and (or) reduced precipitation during this time period (Farnell et al. 2004). These differences may reflect differences associated with lowland versus upland paleoenvironmental records.

Holocene steppe bison in Beringia

The Versleuce Meadows bison skeleton is important for our understanding post-glacial bison in the north as it may be the best preserved middle Holocene specimen that has yielded both comprehensive morphometric and mtDNA data from the region. The combined morphometric and genetic data are a further demonstration that there is considerable morphological variation within and between previously defined species. Morphological and mensurational characteristics may not be adequate alone to make taxonomic assignments for bison fossils, or useful in distinguishing species from one another. As such, it is critical to recover genomic data to determine whether bison from the Subarctic represent a lineage that includes steppe bison from the north or the lineage that gave rise to extant bison species from the south (Clade 1A). At least for bison that lived in Beringia, steppe bison *B. priscus* (sensu lato) may be best interpreted as representing a single, morphologically variable species that dominated late Pleistocene mammal communities and persisted through the Holocene in southern Yukon until their relatively recent extirpation ~400 years ago (Shapiro et al. 2004; Heintzman et al. 2016). Further, the common name "steppe bison" may be misleading as Holocene records of Clade 2A bison in the Subarctic represent populations that inhabited boreal forests. As such, this expands our interpretation of *B. priscus* ecology that has traditionally been thought of as grazers of the open, largely treeless, "mammoth steppe" biome (Guthrie 1990). Rather, steppe bison should be considered to have been a species that had a high degree of ecological flexibility, which could occupy a wide range of open and forested habitats across the Arctic and Subarctic, during both glacial and interglacial time periods of the Quaternary. This ecological flexibility may be the major factor that led to the high degree of morphological variability exhibited in horn cores and crania clearly found in the paleontological record.

Conclusions

The Versleuce Meadows bison, a juvenile, is likely the most complete Holocene bison reported from the Subarctic of northern Canada. The animal died roughly 5400 years ago after being mired down in a pond or small lake that was surrounded by a white spruce dominated forest. Exposed parts of the carcass were scavenged by carnivores, though most of the distal limbs and crania were left unscathed. The rest of the animal was buried in silty-marl sediment.

Combined morphometric and mitochondrial genomic data support the assignment of this specimen to *Bison* cf. *priscus* and reveal it was a member of Clade 2A, which in Beringia are considered to represent steppe bison. This bison was not a member of the lineage of present-day extant plains and woods bison (Clade 1A), which are descended from populations that were restricted to the southern part of the continent during the last glaciation. Steppe bison were a morphologically variable and ecologically flexible species of bison that dominated late Pleistocene landscapes of Beringia, and survived locally through the Holocene interglaciation.

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