

Pleistocene Bison Skeleton (*Bison bison* cf. *occidentalis*) from Clayhurst Crossing, British Columbia

Découverte d'un squelette de bison datant du Pléistocène (*Bison bison* cf. *occidentalis*) de Clayhurst Crossing, en Colombie-Britannique

Ein Bison-Skelett (*Bison bison* cf. *occidentalis*) aus dem Pleistozän bei Clayhurst Crossing, British Columbia

Brian Apland and Charles R. Harington

Volume 48, Number 2, 1994

URI: <https://id.erudit.org/iderudit/032998ar>

DOI: <https://doi.org/10.7202/032998ar>

[See table of contents](#)

Publisher(s)

Les Presses de l'Université de Montréal

ISSN

0705-7199 (print)

1492-143X (digital)

[Explore this journal](#)

Cite this article

Apland, B. & Harington, C. R. (1994). Pleistocene Bison Skeleton (*Bison bison* cf. *occidentalis*) from Clayhurst Crossing, British Columbia. *Géographie physique et Quaternaire*, 48(2), 213–233. <https://doi.org/10.7202/032998ar>

Article abstract

Remains of a large old male bison skeleton from a gravel pit near Clayhurst Crossing are tentatively referred to the extinct western bison (*Bison bison* cf. *occidentalis*). It is the most complete late Pleistocene "medium-horned" bison so far reported from Canada, and is therefore described in detail. Four accelerator mass spectrometry (AMS) radiocarbon dates on bone from the specimen provide a weighted average age of 10,500±90 yr BP, supporting an earlier suggestion that river terraces in the mid-Peace area began developing before 10,000 years ago. Evidently *Bison bison antiquus* occurred in southern Alberta about 11,000 years ago, and both it and *Bison bison occidentalis* occupied the Peace River area shortly before 10,000 years ago. It is hypothesised that by at least 9700 BP, *B. b. occidentalis* had spread southern Alberta. These data suggest that biotic interchange between the former Beringian refugium and the southern interior Plains of North America occurred prior to 10,500 years ago.

PLEISTOCENE BISON SKELETON (*Bison bison* cf. *occidentalis*) FROM CLAYHURST CROSSING, BRITISH COLUMBIA

Brian APLAND and Charles R. HARRINGTON, Archaeology Branch, Government of British Columbia, Victoria, British Columbia V8V 1X4 and Paleobiology, Canadian Museum of Nature, Ottawa, Ontario K1P 6P4.

ABSTRACT Remains of a large old male bison skeleton from a gravel pit near Clayhurst Crossing are tentatively referred to the extinct western bison (*Bison bison* cf. *occidentalis*). It is the most complete late Pleistocene "medium-horned" bison so far reported from Canada, and is therefore described in detail. Four accelerator mass spectrometry (AMS) radiocarbon dates on bone from the specimen provide a weighted average age of $10,500 \pm 90$ yr BP, supporting an earlier suggestion that river terraces in the mid-Peace area began developing before 10,000 years ago. Evidently *Bison bison antiquus* occurred in southern Alberta about 11,000 years ago, and both it and *Bison bison occidentalis* occupied the Peace River area shortly before 10,000 years ago. It is hypothesised that by at least 9700 BP, *B. b. occidentalis* had spread southern Alberta. These data suggest that biotic interchange between the former Beringian refugium and the southern interior Plains of North America occurred prior to 10,500 years ago.

RÉSUMÉ Découverte d'un squelette de bison datant du Pléistocène (*Bison bison* cf. *occidentalis*) de Clayhurst Crossing, en Colombie-Britannique. Les restes du squelette d'un vieux bison de grande taille, découverts dans une carrière près de Clayhurst Crossing, appartiennent probablement à l'espèce éteinte des bisons occidentaux (*Bison bison* cf. *occidentalis*). Quatre datations au ^{14}C sur les os, réalisées par spectrométrie de masse par accélérateur, indiquent un âge moyen, après ajustement, de $10\,500 \pm 90$ ans BP. Cet âge appuie l'hypothèse selon laquelle les terrasses fluviales dans la région centrale de Peace commencent à se développer il y a plus de 10 000 ans. De toute évidence, *Bison bison antiquus* vivait au sud de l'Alberta, il y a environ 11 000 ans. Ce dernier et *Bison bison occidentalis* occupaient le territoire de la rivière de la Paix il y a un peu plus de 10 000 ans BP. On croit qu'à 9700 BP, tout au moins, *B. b. occidentalis* s'est propagé au sud de l'Alberta. Les données laissent supposer que l'échange biotique entre l'ancien refuge de la Béringie et la partie intérieure sud des plaines de l'Amérique du Nord était possible il y a plus de 10 500 ans.

ZUSAMMENFASSUNG Ein Bison-Skelett (*Bison bison* cf. *occidentalis*) aus dem Pleistozän bei Clayhurst Crossing, British Columbia. Reste eines grossen, alten, männlichen Bison-Skeletts, gefunden in einer Kiesgrube bei Clayhurst Crossing, werden versuchsweise der ausgestorbenen Art des westlichen Bison (*Bison bison* cf. *occidentalis*) zugeschrieben. Es handelt sich um den vollständigsten Bison aus dem späten Pleistozän, über den bisher in Kanada berichtet wurde, und deshalb wird er im Detail beschrieben. Vier mit Teilchen-Beschleuniger gewonnene ^{14}C -Daten von den Knochen des Exemplars zeigen ein durchschnittliches Alter von $10,500 \pm 90$ Jahren v.u.Z. und stützen so eine frühere Hypothese, derzufolge die Flussterrassen im mittleren Peace-Gebiet sich vor 10.000 Jahren zu entwickeln begannen. Offensichtlich gab es *Bison bison antiquus* im südlichen Alberta vor etwa 11.000 Jahren, und letzterer sowie *Bison bison occidentalis* bewohnten das Gebiet des Peace River vor etwas mehr als 10.000 Jahren. Man nimmt an, dass spätestens 9700 v.u.Z. *Bison bison occidentalis* sich über Süd-Alberta ausgebreitet hatte. Diese Daten lassen vermuten, dass der biotische Austausch zwischen dem ehemaligen Bering-Zufluchtsort und den inneren südlichen Ebenen von Nordamerika vor mehr als 10.500 Jahren stattfand.

INTRODUCTION

In 1984, the most complete skeletal remains of a late Pleistocene bison so far reported in Canada were discovered in a gravel pit on the northern bank of the Peace River near Clayhurst Crossing, British Columbia (Fig. 1). Remains of fossil bison, including two specimens with some articulated hind limb bones, had previously been found on several occasions at that locality.

The purpose of this paper is to provide information regarding: the geographic, stratigraphic and geological setting of the Clayhurst Crossing site; the description, and measurements, of the bison skeletal remains recovered in 1984; the results of radiocarbon analyses of bone from the specimen; and a discussion of the significance of the finds.

THE SITE

LOCATION

The Clayhurst gravel pit complex (56°07'40"N, 120°05'00"W; Fig. 1) is situated on the north bank of Peace River approximately 2.5 km west of the confluence of Peace and Alces rivers and ca. 5 km west of the Alberta border, in northeastern British Columbia. The site lies at an elevation of 544 m above sea level (determined by Thommen TX handheld altimeter set at the Fort St. John Airport). In 1984, active gravel quarrying was concentrated near the western end of the site; more easterly parts, including the section containing the bison skeleton, were less actively worked.

HISTORY OF FINDS

The first recorded find from the Clayhurst Crossing gravel pit was an eroded bison cervical vertebra (BCPM 723A) collected at the site by O.W.H. Roberts about 1955. Catalogue information states: ... "from gravel pit about 300' (91.5 m) above river level on the North bank of the Peace River on the Clayhurst Ferry Road" (CRH, field notes, 1978).

In 1965, A.B. Sanderson of Victoria donated a posterior thoracic vertebra (BCPM 723B) of a bison from the same locality. This specimen is also stream-rounded, and lacks the posterior plate of the centrum (CRH, field notes, 1978).

In 1966, Vaso Jankovic collected four articulating bones of a right hind leg [calcaneum (NMC 11311), astragalus (NMC 11313), naviculocuboid (NMC 11310), metatarsal (NMC 11309, Table I), as well as the proximal end of a left tibia (NMC 11314) and a left calcaneum (NMC 11312). That left calcaneum, like NMC 11311, is similar size and reddish brown colour, and is also damaged at the proximal end (Table I, Fig. 2). On the basis of epiphyseal fusion, large size and well-developed surface sculpture, these bones are considered to have been derived from a single adult animal.

In 1974, during a preliminary survey of the area for the then proposed "Site E" hydro-electric reservoir, Fladmark (1975) recorded the east end of the gravel pit as a paleontological locality registered in the B.C. provincial archaeological site registry as HaRa 15. The site record form (1974) states that a local resident of Clayhurst Flats had reported "... quantities of bones came out of here earlier", and later, that this

was .. "one of several paleontological localities on the Peace — This is highest in elevation and perhaps therefore, the earliest."

During the summer of 1982, Frank Wilde collected three bones, apparently from the right hind leg of another adult bison larger than the 1966 specimen [distal half of a femur (NMC 38181), distal two-thirds of a tibia (NMC 38182), and a metatarsal (NMC 38180, Table I, Fig. 3). These bones came from a sandy layer about 6.2 m below the surface and, like the 1966 collection, are stained reddish brown. Both lots of specimens were referred to *Bison* sp. by the second author, and are deposited in the Quaternary Zoology Collection, Canadian Museum of Nature (NMC) in Ottawa.

In August 1983, the second author revisited the Clayhurst Crossing gravel pit to collect additional materials. Unfortunately, only four rather fragile, reddish-brown stained bison rib fragments were recovered. Gravel quarrying was not in progress at the time.

In the spring of 1984, the bison skeletal remains described in this paper were discovered by a local child whose parents informed the North Peace Historical Association (NPHA) in Fort St. John. At the request of the NPHA, the first author and Knut R. Fladmark visited the site on June 15, 1984 and recorded the specimen.

More recently, during the summer of 1991 while conducting geological studies in the area, Peter Bobrowsky, of the British Columbia Geological Survey Branch, collected a bison scapula several hundred metres west of the 1984 find.

GEOLOGICAL SETTING

Studies of Quaternary deposits in the region (St-Onge, 1972; Mathews, 1978, 1980; Rutter, 1984) show that, after the Laurentide ice retreated following 13,500 yr BP, a series of proglacial lakes was established in the Peace River valley. The bison remains reported here were situated at an elevation 116 m lower than the local minimum strandlines of the Clayhurst stage of Glacial Lake Peace, as reported by Mathews (1980). Indeed, they were at least 86 m lower than the last major phase of Glacial Lake Peace, the Indian Creek Stage.

Radiocarbon dates from the bison skeleton (see Radiocarbon Dating Section), combined with the elevation of the find, tend to support White's (1983) contention that there may have been a brief proglacial pondage recession lower than the Clayhurst Stage before 10,400 yr BP. The presence of cross-bedded micaceous sand members lying stratigraphically above the bones (see Stratigraphic Setting section) might imply a renewed ponding subsequent to the death of the bison, if those members represent a period of foreset bed development.

Parallel evidence from Charlie Lake Cave near Fort St. John, which is similar in elevation to the Clayhurst Stage, suggests that the glacial lake level had dropped below the Clayhurst site by 10,500 BP, allowing glaciofluvial deposition and terrace formation to take place (Liverman, 1989). About that time too, Glacial Lake Fahler I drained through the Lesser Slave valley opening the area south of Peace River for

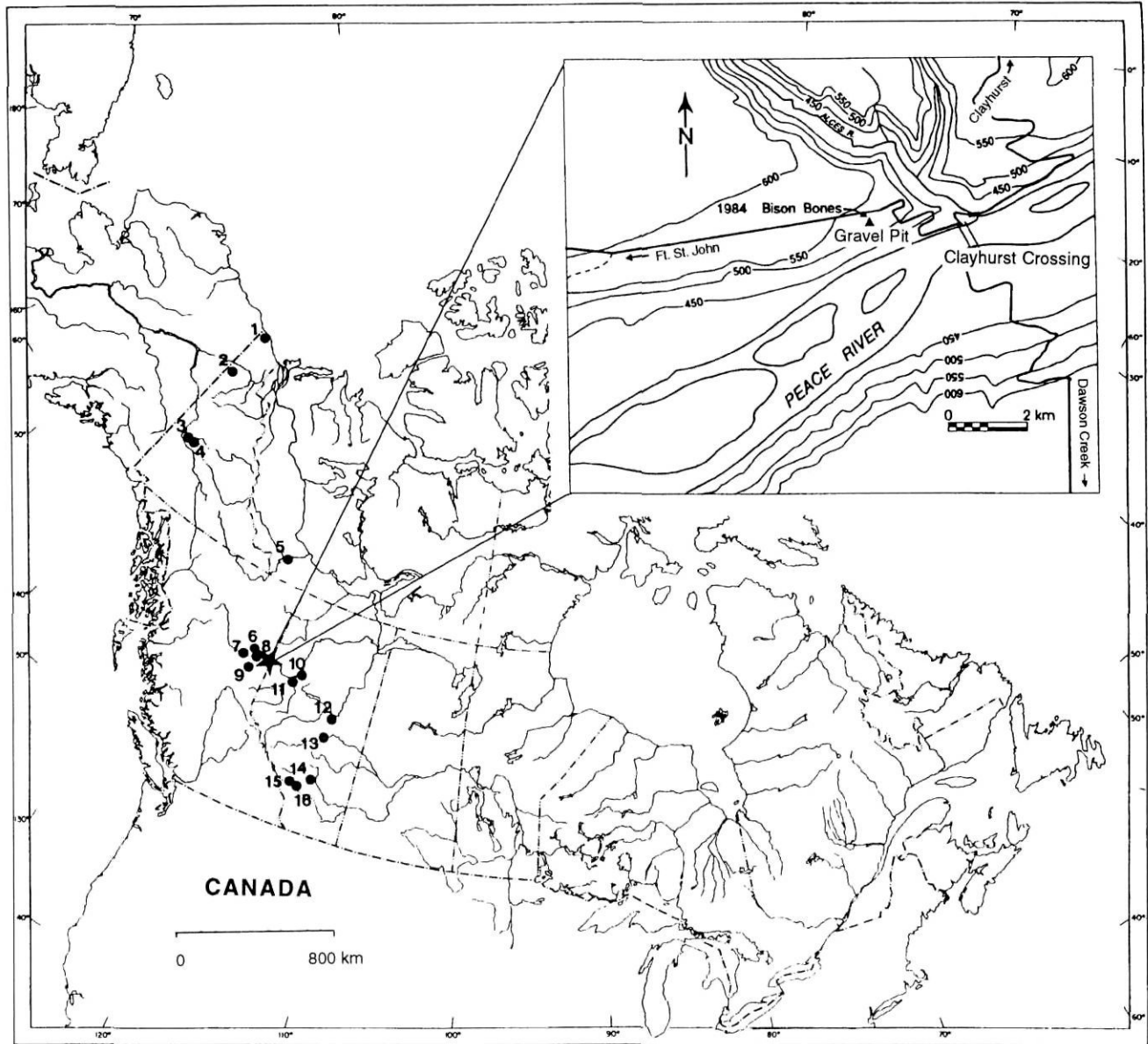


FIGURE 1. Map of Canada showing locations (see Table IV for numbering key) from which referenced bison remains have been reported. Inset map: Clayhurst Crossing area of British Columbia showing location of Clayhurst Pit from which partial bison skeleton (FSJM 984.195.01) was recovered.

Carte du Canada montrant la localisation des sites (voir tabl. IV) où on a rapporté la présence de restes de bison. Le carton montre la carrière de Clayhurst (Clayhurst Crossing, Colombie-Britannique) d'où a été recueilli le squelette partiel d'un bison (FSJM 984.195.01).

TABLE I
Comparative measurements of bison metatarsals from Clayhurst Crossing gravel pit, British Columbia

Measurements (mm)	FSJM 984.195.01q (left)	FSJM 984.195.01bb (right)	NMC 38180	NMC 11309
Total length	269.1	269.3	281.2*	275.1
Proximal width	69.0	69.6	61.2	61.4
Proximal depth	65.6	66.2	60.9	57.4
Midshaft width	41.6	42.9	39.2	39.9
Midshaft depth	41.1	49.6	38.7	39.0
Distal width	80.0	80.8	73.0	66.5*
Distal depth	45.8	45.7	43.5	40.2

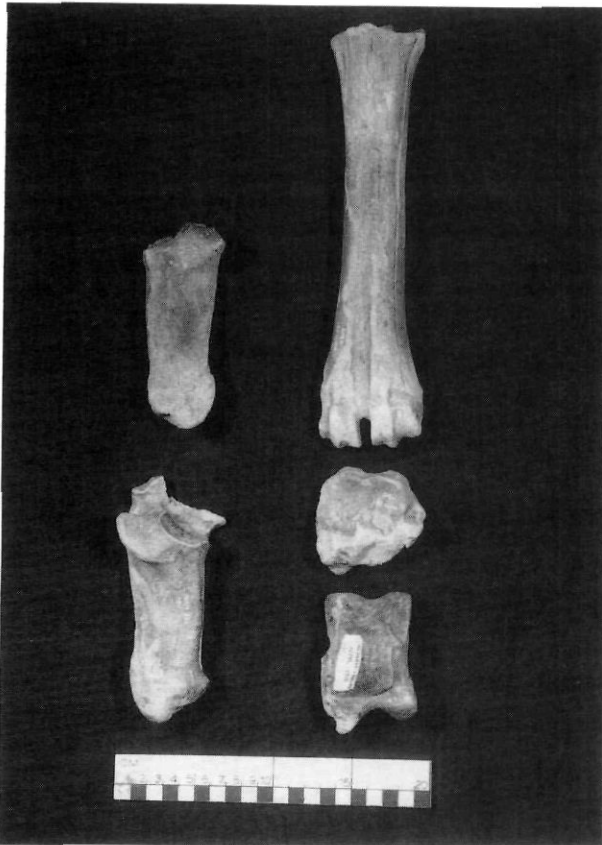


FIGURE 2. Articulating bones (NMC 11309-11314) of a right hindleg and left calcaneum of a bison collected at the Clayhurst gravel pit in 1966 (left: fragmentary calcaneum; right top to bottom: metatarsal, naviculocuboid, astragalus).

Os articulés (NMC 11309-11314) de la patte postérieure droite et tarse gauche d'un bison recueillis dans la carrière de Clayhurst, en 1966 (à gauche: tarse fragmenté; à droite, de haut en bas: métatarse, naviculaire, astragale).

occupation by terrestrial plants and animals (Churcher and Wilson, 1979).

White (1983) suggested that the "ice free corridor" could have been open by 12,220 yr BP, or minimally by 11,600 yr BP. This would have allowed terrestrial plants and animals to have established themselves through the study area by at least 11,500 yr BP. Perhaps the open grassland habitats suitable for bison survival were well established by 11,000 yr BP, and were being rapidly replaced by boreal forests approximately 10,000 years ago (MacDonald, 1987; White and Mathews, 1986).

Bobrowsky and Rutter (1990, 1992) argue that there is no clear evidence of ice-sheet coalescence in the Peace River area, during the Late Wisconsinan. They suggest that sporadic coalescence may have occurred east of the Rocky Mountains in various areas south of the Peace River valley, but dating of those events is still uncertain. They propose that deglaciation during the Late Wisconsinan started as early as 14,000 BP south of the Peace, and only slightly later in the north.



FIGURE 3. Right hindleg bones (NMC 38180-38182), apparently from an individual bison, collected at the Clayhurst gravel pit in 1982 (left to right: distal half of femur, distal two-thirds of tibia, metatarsal).

Os de la patte postérieure droite (NMC 38180-38182) apparemment d'un seul individu, recueilli dans la carrière de Clayhurst, en 1982 (de gauche à droite: moitié distale d'un fémur, deux-tiers distaux d'un tibia, métatarse).

STRATIGRAPHIC SETTING

The stratigraphy at the site is not entirely clear as the surface area or upper part of the sedimentary sequence may have been disturbed or removed by heavy equipment in preparation for excavating the gravel. Mathews (1978) mapped the area as "Terrace Deposits: gravel, sand, minor silt".

The exposure of sediments containing the bison skeleton consists of 1 to 1.5 m of well-rounded medium gravel interbedded with micaceous sand, overlying at least 1 m of coarse, rounded pebbles. The sand strata directly above the bones exhibit cross-bedding which dips approximately 40° to the east (090°; downstream). The bones were embedded in strata containing two thin layers of small to medium pebbles on top of a coarse gravel layer. The freshly exposed elements evidenced a 2 to 5 mm coating of silty clay containing many fine root hairs which suggested an organically rich, sedimentary environment existed prior to the deposition of the overlying sands.

The base of the coarse gravels, upon which the bones rested, was obscured by slump (Fig. 4). However, some 12 m west of the fossils, the same gravel layer ranges from 30 to 50 cm in thickness, and is underlain by 30 cm of horizontally bedded fine sand, which separates the bone-bed gravels from the coarse basal gravels.

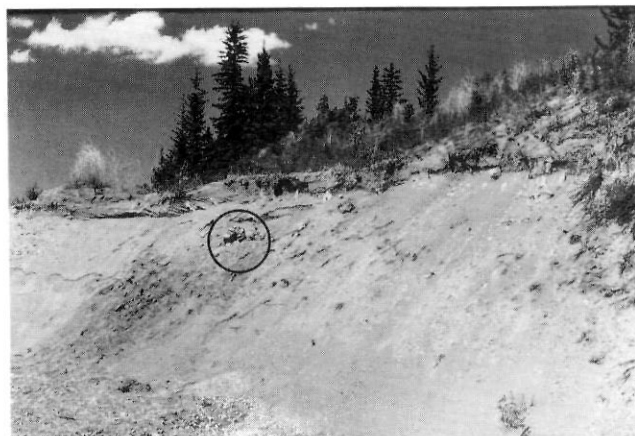


FIGURE 4. Position of partial skeleton (FSJM 984.195.01, circled area illustrated in Fig. 5), approximately *in situ* at the Clayhurst gravel pit, June 15, 1984.

Emplacement du squelette partiel (FSJM 984.195.01, partie encadrée illustrée à la fig. 5), approximativement in situ dans la carrière de Clayhurst, le 15 juin 1984.

The sequence of sediments surrounding the bison remains is tentatively interpreted as river channel and/or point bar deposits of possible glaciofluvial origin.

COLLECTING THE SKELETON

When initially seen by B. Apland and K. Fladmark, the skeleton appeared to be little disturbed with most large bones being firmly *in situ* (Figs. 4,5). Except for the cranium and horncores, a right tibia fragment (evidently from another individual) and a few ribs, the skeletal remains were in good condition. There was no evidence of prehistoric cultural association.

The skeletal remains were scattered over an area of approximately 1.5 m along the face of the exposure. The skeleton, with head upstream, was aligned parallel to the flow of the present Peace River, and presumably the paleostream flow as well. The cranium lay upside down, lacked several teeth, was damaged in the nasal region, and the right horncore was broken off at the base. Although the left horncore was excavated carefully *in situ* (Fig. 6), it disintegrated when removal was attempted. Fortunately, its general dimensions were recorded, and measurements critical for identification of the specimen (*e.g.*, upper horncore length and horncore circumference at base) could be estimated using two clear, scaled photographs, allowing for foreshortening (Table II).

Two vertebrae were found near the east end of the bone bed. A humerus and femur were found directly east of the cranium indicating relative displacement of some of the bones. However, a set of hindfoot bones (astragalus, calcaneum and metatarsal) just east of the femur were in their natural articulated position reminiscent of earlier finds at the site.

The bones were initially stored at the Fort St. John Museum, and later sent to the Royal British Columbia Museum for temporary storage. In 1991, they were shipped to the second author at the Canadian Museum of Nature for study before being returned to the NPHA for permanent storage at the Fort St. John Museum.



FIGURE 5. Bones of bison (FSJM 984.195.01) as seen June 15, 1984. Left to right: radio-ulna, tibia, cranial fragment (upside down with posterior end to right, right horncore broken off at base, left horncore buried), humerus, femur, articulated hindleg elements (calcaneum, astragalus, metatarsal), loose bones (rib fragments, tibia, calcaneum, metatarsal, etc.).

Os de bison (FSJM 984.195.01) tels qu'observés le 15 juin 1984. De gauche à droite: radio-ulna, tibia, fragment de crâne (à l'envers, la partie postérieure étant à droite, corne brisée à la base, corne gauche enterrée), humérus, fémur, parties articulées de la patte postérieure (tarse, astragale, métatarse), os libres (fragments de côte, tibia, tarse, métatarse, etc.).



FIGURE 6. Left horncore of bison (FSJM 984.195.01) as excavated. Note roughly triangular shape of base, relatively great length and robustness compared to modern bison horncores, marked curvature and backward twist at the tip.

Corne gauche de bison (FSJM 984.195.01) déterrée. Noter la forme grossièrement triangulaire de la base, la longueur et la robustesse de la corne plus grandes que celles du bison moderne, ainsi que la courbe accusée et la torsion de la pointe vers l'arrière.

RADIOCARBON DATING

The stratigraphic position of the bison skeletal remains in terrace gravels of the proto-Peace River, and the rather large horncore dimensions recorded for this animal, suggested that it was of Late Wisconsinan or early Holocene age. This view has been corroborated by four AMS radiocarbon dates from the left tibia. One date was processed by Erle Nelson of the Radio Isotopes Direct Detection Laboratory (RIDDL, Simon Fraser University, Burnaby, British Columbia). The other

TABLE II
Cranial measurements (mm)^a of the Clayhurst bison in relation to some other North American bison living near the close of the last glaciation

Specimens	Approx. age (yr BP)	1	2	3	4	5	6	7
<i>Bison bison</i> cf. <i>occidentalis</i> Ad. male, FSJM 984.195.01 Clayhurst Crossing Site, B.C.	10,500	330 ^b est.	119 ^b	315 ^c est.	377	316	100.2	263
<i>"Bison antiquus occidentalis"</i> (McDonald, 1981, Table 25)								
Males								
M	11,500	277.8	98.8	300.3	348	296.6	97.3	259.5
OR	-5,000	186-392	77-120	237-355	311-394	261-348	90-102	233-287
N		86	91	89	64	74	3	57
<i>"Bison occidentalis"</i> (Skinner & Kaisen, 1947, Table 12)								
M	-	279	98	290	351	299	91	259
OR		222-330	85-114	253-336	328-400	277-340	84-102	229-273
N		12	16	16	8	12	5	8
<i>"Bison antiquus antiquus"</i> (McDonald, 1981) Ad. male, NMC 12442 Athabasca, Alberta (measurements from Harington, 1977, Table 12)								
	-	275	104	318	348	294	-	-
<i>"Bison occidentalis"</i> (Shackleton & Hills, 1977, Table 6) cf. Ad. male, UC 3417 Three Hills area, Alberta								
	9,700	320	97.2	298	373.2 est.	297.5	-	271
<i>Bison priscus</i> (Harington, 1977, Table 87) Ad. males, Old Crow Loc.11 (1)								
M	12,000	396	102	309	377	274	92	267
OR		384-410	94-110	290-330	333-340	272-276	-	-
N		4	4	4	2	2	1	1

^a 1. Upper horncore length. 2. Transverse diameter of horncore base. 3. Horncore circumference at base. 4. Greatest width of frontals at orbits. 5. Least width of frontals between horncores and orbits. 6. Alveolar length (M^1-M^3). 7. Length from occipital crest to naso-frontal suture.

^b Estimated using two scaled photographs showing left horncore "cast", accounting for foreshortening.

^c Estimated using measurement 2 as a scale on a photograph of the horncore base seen end on.

three dates were arranged by D.E. Nelson as independent age determinations from other laboratories using differing collagen extraction techniques (Arizona Accelerator, Tucson, Arizona [aa]; Center for Accelerator Mass Spectrometry, Livermore, California [CAMS]).

According to D.E. Nelson (personal communication, 1991), protein preservation in the bone was excellent, and it has been used as a test sample in several experiments on radiocarbon dating procedures. Carbon/nitrogen and amino acid ratios of the extracted protein material were indistinguishable, within the limits of measurement uncertainty, from material similarly extracted from a modern domestic cow. Further, the measured stable carbon isotopic ratio for the whole protein was $\delta^{13}C = -19.4\%$, which is that expected for terrestrial animals of the region.

The four radiocarbon analyses yielded the following dates: $10,750 \pm 180$ yr BP (RIDDL-220); $10,600 \pm 160$ yr BP (AA-1219); $10,580 \pm 210$ yr BP (CAMS-398); and $10,340 \pm 150$ yr BP (CAMS-150) (Nelson, 1991, Table 1 PRB). These dates are concordant, and provide a weighted average age for the bison of $10,550 \pm 90$ yr BP.

Peter Bobrowsky (personal communication, 1992) reported to us that the bison scapula he collected in 1991 was dated at the Alberta Environmental Centre at Vegreville, yielding an age determination of $10,230 \pm 140$ yr BP (AECV-1558c). A bison tibia found at the Ostero gravel pit near Taylor, British Columbia produced a similar radiocarbon date of $10,240 \pm 160$ yr. BP (AECV-1206c) (Bobrowsky *et al.*, 1991).

DESCRIPTION

Bison bison cf. *occidentalis* (western bison)

The skeleton represents the most complete late Pleistocene bison so far reported in Canada which adds to its significance and makes it worth describing and measuring in some detail. The specimens reported below (Tables I-III) are referenced to the Fort St. John Museum catalogue (FSJM 984.195.01), and are illustrated in Figs. 4 to 6. All measurements are in millimetres and follow von den Driesch (1976), except where her letters do not appear. Additional comparative measurements of the cranium and major limb bones are recorded in Tables II and III.

Skull

Right facial fragments (.01a) of cranium from orbit to tip of right premaxilla, with palatal region and some teeth (partial roots of RM¹, RM²–RM³ — heavily worn and therefore representing an old individual). Alveoli for premolars are present but show damage. Measurements: alveolar length (P²-M³) 164.4; alveolar length (M¹-M³) 100.2; length from anterior of P² alveolus to tip of premaxilla 146.3; lateral length of premaxilla 188.1; short lateral facial length (posterior of infraorbital foramen to tip of premaxilla) 168.4.

Vertebrae

A posterior thoracic vertebra lacking most of the neural spine (.01b) and two caudal vertebrae (.01c,d) are preserved.

Ribs

A complete right rib (.01e) measured 605 mm along the outer surface. Several other rib fragments are too incomplete to warrant further description.

Forelimbs

Left humerus (.01e): GLL (greatest length, lateral side) 414; GLC (greatest length from head) 369; SD (least shaft width) 61.8; BT (greatest trochlear width) 113.8; DD (maximum distal depth) 113.5. Left radio-ulna (.01f). Ulna — GL (greatest length) 471.0; LO (olecranon length) 150.5; DPA (minimum anconal depth) 109.9; SDO (minimum depth of olecranon) 81.8; BPC (greatest width of articular surface) 67.2. Radius — GL (greatest length) 365.0; BP (greatest proximal width) 122.1; SD (minimum shaft width) 65.8; BD (maximum distal width) 113.9. Left ulnar carpal (.01f). Left scaphoid or radial carpal (.01g). First phalanx (.01h): TL (total length) 76.7; PW (proximal width) 47.2; PD (proximal depth) 48.7; MW (minimum shaft width) 42.5; MD (minimal shaft depth) 30.4; DW (distal width) 50.7; DD (distal depth) 36.7. Second phalanx (.01i): TL 60.8; PW 48.8; PD 46.8; MW 39.2; MD 34.7; DW 41.8; DD 42.3. Distal sesamoid (.01j). Third phalanx (.01k) with slightly damaged anterior tip: TL 88.5+; MH (maximum height) 58.6.

Hindlimbs

Left femur (.01 l): GL (greatest length) 457.0; GLC (greatest length from head) 449.0; BP (greatest proximal width) 163.0; DC (depth of head) 62.1; SD (minimum shaft width) 55.6; CD (minimum circumference of shaft) 179.0; BD (greatest distal width) 134.7; DD (maximum distal depth on medial side) 162.8. Left patella (.01 m): GL (greatest length) 88.9; BP (minimum width) 77.2. Left tibia (uncatalogued; sacrificed for radiocarbon dating). Left lateral malleolus (fibula) (.01 n). Left astragalus (.01 o): GLL (greatest length on lateral side) 84.6; GLM (greatest length on medial side) 81.9; DL (greatest depth on lateral side) 49.6; DMC (greatest depth on medial side) 53.4; BD (greatest distal width) 60.2. Pathological indications, perhaps consonant with old age, are seen in several parallel score

marks on the medial articular surface and faceted bone on the distolateral surface. Left calcaneum (.01 p): GL (greatest length) 176.8; GBS (greatest breadth at sustentaculum) 56.0. Groove marks on the articular surface correspond to those on the opposing surface of the left astragalus. Left metatarsal (.01 q): see Table I for measurements. Left lateral first phalanx (.01 r): TL (total length) 78.1; PW (proximal width) 43.8; PD (proximal depth) 47.9; MW (minimum shaft width) 37.9; MD (minimum shaft depth) 25.5; DW (distal width) 40.6; DD (distal depth) 29.3. Left lateral second phalanx (.01 s): TL 59.3; PW 41.4; PD 43.3; MW 32.8; MD 30.9; DW 35.1; DD 37.9. Left lateral third phalanx (.01t): TL total (length) 83.3; MH (maximum height) 56.8. Two proximal sesamoids, not designated to side, are present (.01 u) and (.01 v). Right femur (.01 w): GL (greatest length) 462.0+ (end of greater trochanter damaged); GLC (greatest length from head) 450.0; BP (greatest proximal width) 170.2; DC (depth of head) 61.8; SD (minimum shaft width) 55.3; CD (minimum circumference of shaft) 178.5; BD (greatest distal width) 134.2; DD (maximum distal depth on medial side) 163.9. Right tibia (.01x): GL (greatest length) 449.0; BP (greatest proximal width) 140.5; SD (minimum shaft width) 58.2; BD (greatest distal width) 89.7; DD (distal depth) 63.2. Right lateral malleolus (.01 y). Right astragalus (.01 z): GLL (greatest length on lateral side) 85.7; GLM (greatest length on medial side) 81.4; DL (greatest depth on lateral side) 49.4; DM (greatest depth on medial side) 51.6; BD (greatest distal width) 61.0. Right calcaneum (.01 aa): GL (greatest length) 173.4; GBS (greatest breadth at sustentaculum) 56.0. Right metatarsal (.01 bb): see Table I for measurements. Right medial first phalanx (.01 cc): TL 79.8; PW 42.1; DD 47.0; MW 35.6; MD 24.9; DW 41.0; DD 29.9. Right medial second phalanx (.01 dd): TL 60.5; PW 42.3; PD 43.5; MW 31.4; MD 29.3; DW 35.9; DD 37.9. Right medial third phalanx (.01 ee): TL (total length) 79.4+ (tip slightly worn); MH (maximum height) 53.3. Right lateral first phalanx (.01 ff): TL 78.2; PW 43.2; PD 47.3; MW 37.3; MD 25.5; DW 40.6; DD 30.0.

DISCUSSION

CLASSIFICATION

Although bison horncores can be highly variable, they are probably the best available taxonomic indicators. Since the estimated horncore length of FSJM 984.195.01 (see below) clearly places it in the "medium-horned" (Shackleton and Hills, 1977) or "*occidentalis-antiquus* complex" (Harington, 1984) range, the main character we use here in differentiating *Bison bison occidentalis* from *Bison bison antiquus* is the apparent extension of the horncore rearward, often behind the occipital plane of the cranium, rather than perpendicular to the main axis of the skull (Skinner and Kaisen, 1947; Shackleton and Hills, 1977; McDonald, 1981).

Fortunately, scaled photographs, and some characteristics and approximate measurements of the left horncore were recorded in the field before it disintegrated. The estimated upper horncore length of about 330 mm lies well above the mean for "*Bison occidentalis*" (Skinner and Kaisen, 1947) and "*B. a. occidentalis*" (McDonald, 1981) (Table II), whereas the transverse diameter at the horncore base and the estimated horncore circumference are closer to the mean for *Bison priscus* than *B. b. occidentalis*. The field sketch and photograph (Fig. 6) of the left horncore suggest it was relatively robust and had a marked backward twist considered characteristic of both *B. b. occidentalis* and *B. priscus*. The horncore base was roughly in the shape of an isosceles

TABLE III

Comparative measurements of Clayhurst bison (*Bison bison cf. occidentalis*) limb bone with those of "*Bison antiquus occidentalis*" (McDonald, 1981, methods of taking bone measurements from Table 12, Figs. 9, 10)

Measurements (mm)	Humerus	Radius	Femur	Tibia	Metatarsal
Approximate rotational length					
FSJM 984.195.01	363	337	428	410	263
NMC 11309					264
NMC 33180					276
" <i>Bison antiquus occidentalis</i> " (McDonald, 1981, Table 26)					
Males M	356.9	343.8	403.7	403.5	270.3
OR	326-402	306-381	362-448	372-464	248-300
N	39	82	38	63	150
Anteroposterior diameter of shaft					
FSJM 984.195.01	74.0	45.0	55.2	43.4	35.4
NMC 11309					32.4
NMC 33180					34.4
" <i>Bison antiquus occidentalis</i> "					
Males M	66.4	35.5	50.0	38.9	33.1
OR	58-76	30-39	44-62	34-45	29-38
N	41	83	40	64	161
Transverse minimum of shaft					
FSJM 984.195.01	62.2	64.4	54.6	58.8	40.8
NMC 11309					37.7
NMC 33180					39.0
" <i>Bison antiquus occidentalis</i> "					
Males M	55.0	58.5	49.3	53.5	39.2
OR	48-66	52-69	44-55	49-61	32-48
N	41	83	40	64	156

triangle — considered to be a characteristic of males in most North American fossil bison (McDonald, 1981, Table 43).

Cranial measurements of FSJM 984.195.01 are above the means for *B. b. occidentalis* (McDonald, 1981, Table 25; Skinner and Kaisen, 1947, Table 12), as well as being generally larger than some of the latest surviving Yukon steppe bison (*B. priscus*) dating to about 12,000 yr BP (Harington, 1977, Table 87). Exceptions to this observation are the estimated upper horncore length and length from occipital crest to naso-frontal suture. Omitting horncore length and degree of backsweep, the Clayhurst specimen is perhaps best matched (Table II) by a *B. b. antiquus* cranium (NMC 12442) from Athabasca, Alberta (Harington, 1977, Table 92; McDonald, 1981, Table 23).

Limb bones of FSJM 984.195.01 (Table III) are generally longer than the means for *B. b. occidentalis* (McDonald, 1981, Table 26). However, exceptions occur in radius and metatarsal lengths. The metatarsal (NMC 33180) collected from the Clayhurst site in 1982 is slightly longer than that of FSJM 984.195.01.

Considering these factors, we conclude that the skeleton best represents an old male of the western bison (*B. b. occidentalis*). However, because the horncores were not preserved and measurements for the left horncore are approximate, it seems best to designate the Clayhurst specimen as

Bison bison cf. occidentalis. We hope that additional crania with intact horncores of similar age will be found at Clayhurst in order to verify our conclusion.

EVOLUTION OF *BISON BISON OCCIDENTALIS*

Students of fossil bison disagree on many points such as classification, dispersal history and the geological age of specimens older than about 40,000 yr BP (e.g., Skinner and Kaisen, 1947; Wilson, 1974; Flerov, 1979; McDonald 1981). Although McDonald's (1981) view of bison evolution differs from most, pertinent points should be outlined because it is the most recent comprehensive North American study published. He infers that the large *Bison latifrons* and smaller *Bison antiquus* stemmed from Eurasian *Bison sivalensis* about the time of the penultimate (Illinoian) glaciation. He attributes the presence of the subspecies *Bison antiquus occidentalis* to genetic drift (from *Bison antiquus antiquus*) and interbreeding as a result of small populations isolated by human hunters. Further, he thinks that *B. a. occidentalis* probably evolved directly from *B. a. antiquus* in the mid-latitude grasslands of North America rather than having a Eurasian or Beringian origin (e.g., Skinner and Kaisen, 1947; Guthrie, 1970; Geist, 1971; Wilson, 1974; Harington, 1977).

McDonald's study, and all other published work on the subject, suffers from a lack of the thorough quantitative analysis of Eurasian fossil bison that would be necessary to

TABLE IV
Data on some bison specimens from western Canada that may relate to the Clayhurst bison

Map Number (fig. 1)	Locality	Taxon	Remarks
1	Engigstciak, Yukon Territory	<i>Bison</i> sp.	Postcranial remains of large bison. Three bison limb bones showing evidence of butchering have yielded radiocarbon dates of 9870±180 yr BP (RIDDL-362), 9770±180 yr BP (RIDDL-281) and 9400±230 yr BP (RIDDL-319) (Cinq-Mars <i>et al.</i> , 1991).
2	Bluefish Caves, Yukon Territory	<i>Bison</i> sp.	Postcranial remains. A metacarpal from Cave 2 yielded a radiocarbon date of 10,230±140 yr BP (RIDDL-561) (Cinq-Mars <i>et al.</i> , 1991).
3	Eldorado Creek, Dawson City Area, Loc. 5, Yukon Territory	" <i>Bison bison occidentalis</i> "	An undated posterior cranial fragment that may be of Late Wisconsinan age (Harington, 1977). It is worth noting that the holotype of <i>occidentalis</i> (USNM 4157) is from Fort Yukon, Alaska, near the Yukon border.
4	Dominion Creek, Dawson City area, Yukon Territory	" <i>Bison bison occidentalis</i> "	An undated posterior cranial fragment with horncores (NMC 2242). The horncores are not strongly backswept, being like <i>B. b. antiquus</i> in this feature (Harington, 1977).
5	Liard River (near Black-stone River confluence) N.W.T.	" <i>Bison antiquus</i> "	An undated partial cranium with horncores perpendicular to the cranial axis (Gordon, 1970).
6	Charlie Lake Cave, British Columbia	<i>Bison</i> sp.	Postcranial remains that date to about 10,500 yr BP. The site may have been covered by Glacial Lake Peace before that time (Driver, 1988; Driver and Hobson, 1992).
7	Site C locality, Fort St. John, British Columbia	" <i>Bison bison occidentalis</i> "	An undated cranium with horncores from a gravel pit overlooking the proposed "Site-C" dam-site (K.R. Fladmark, pers. comm., 1990).
8	Taylor, British Columbia	" <i>Bison bison cf. occidentalis</i> "	A left horncore and part of the adjoining frontal region (NMC 35807, identified by C.R. Harington) from the Ostero gravel pit located on a high terrace. A <i>Bison</i> sp. tibia from this pit yielded a radiocarbon date of 10,240±160 yr BP (AECV-1206c) (Bobrowski, 1991, Plate 4-7-7).
9	Tumbler Ridge, British Columbia	<i>Bison</i> sp. (<i>occidentalis-antiquus</i> complex)	A skull radiocarbon dated to approximately 10,400 yr BP (K. Woolf, pers. comm., 1991) from a gravel pit.
10	Peace River, Alberta	<i>Bison</i> sp.	Two bison tibiae from the municipal gravel pit (about 340 m a.s.l.) yielded a radiocarbon date of 9880±130 yr BP (GSC-2865) (Lowdon and Blake, 1979; Jackson and Pawson, 1984, Table II).
11	Watino, Alberta	<i>Bison</i> sp.	Radiocarbon dates on a large bison cervical vertebra and a tibia were both 10,200±100 yr BP (GSC-2895, GSC-2902) (Lowdon and Blake, 1979; Jackson and Pawson, 1984, Table II).
12	Athabasca, Alberta	" <i>Bison antiquus antiquus</i> "	An undated cranial fragment with complete horncores (NMC 12442) found 4.6 m below the surface of terrace gravels (Harington, 1977). It was referred to <i>Bison antiquus antiquus</i> by McDonald (1981). Two bison (<i>Bison</i> sp.) tibiae from a gravel pit in a high-level river terrace, 0.6 km north of Athabasca at an elevation of about 545 m yielded a radiocarbon date of 10,200±160 yr BP (GSC-1205).
13	Edmonton, Alberta	" <i>Bison bison occidentalis</i> "	Two undated cranial fragments with horncores (UA 600, UA 619) probably derived from early Holocene gravels at the Beverly pits in eastern Edmonton (Fuller and Bayrock, 1965). At least one of the specimens has horncores perpendicular to the cranial axis, like <i>B. b. antiquus</i> .
14	Three Hills, Alberta	" <i>Bison occidentalis</i> "	Two cranial fragments with horncores (UC 3417, UC 3418) and more than 200 postcranial bones from the Milan site. Bison rib fragments yielded radiocarbon dates of 9630±300 yr BP (GSC-1894) and 9670±160 yr BP (I-8579).
15	Cochrane, Alberta	" <i>Bison bison antiquus</i> " or " <i>Bison antiquus</i> " (formerly referred to " <i>Bison (Bison) occidentalis</i> ")	A right horncore (NMC 11579 -sacrificed for dating) from gravels at the Griffin North Pit. Bones from that pit yielded a radiocarbon date of 10,760±160 yr BP (GSC-612) (Churcher, 1968). Other cranial fragments with horncores referred to <i>Bison occidentalis</i> (ROM 13044, ROM 13048) were reported later from the nearby Clarke's Pit (Churcher, 1975). More complete crania with horncores are now referred to <i>antiquus</i> (Wilson and Churcher, 1984; Graham <i>et al.</i> , 1987; Wilson, 1992)
16	Calgary, Alberta	<i>Bison bison antiquus</i>	Bone (<i>Bison</i> sp.) was radiocarbon dated at 10,200±280 yr BP (GSC-3065) (Wilson, 1981). Since then, vertebrae from a partial bison skeleton and parts of a bison cranium from the Gallelli/Galvin pits (Bow River Gravels) have yielded radiocarbon dates of 11,300±290 yr BP (RL-757) and 8145±320 yr BP (GX-2104), respectively (Wilson and Churcher, 1978; Graham <i>et al.</i> ; 1987; Wilson, 1992).

These specimens are mentioned since they may relate to the Clayhurst bison skeleton in type (*i.e.*, part of the "*occidentalis-antiquus* complex") or in geological age (Late Wisconsinan to early Holocene).

provide a better perspective on North American bison. It also lacks thorough statistical treatment of morphological data on both Eurasian and North American specimens required to assess the most likely choices among possible phylogenies, and a rigorous stratigraphic and geochronological framework for bison evolution.

In contrast to McDonald (1981), and emphasizing the similarity in horncore conformation, relative closeness of apparent northern source regions, and the progressive sequence in time of appearance of *B. priscus*, *B. b. occidentalis* and *B. b. athabascae*, we prefer to view western bison (*B. b. occidentalis*) as stemming from steppe bison (*B. priscus*) which may have survived in the northern Yukon until about 12,000 yr BP (Harington, 1977). We feel that sometime toward the close of the last (Wisconsin) glaciation, western bison spread southward via the Peace River region of British Columbia and along the eastern flanks of the Cordillera. These bison could then have interbred with other small-horned bison (*B. b. antiquus*) derived from southern stocks (Guthrie, 1970) creating a genetically mixed population, "the *occidentalis-antiquus* complex" (Harington, 1984).

Whatever their evolutionary history, western bison seem to have reached maximum numbers about 9000 to 8000 yr BP in western North America, and can be recognized in deposits as late as 6500 yr BP in Wyoming (Wilson, 1974) and approximately 5600 yr BP in Iowa (Hall, 1972).

APPEARANCE AND HABITAT OF *BISON BISON OCCIDENTALIS*

Western bison were probably similar in appearance to modern wood bison, albeit having larger horns. It is also probable that western bison were adapting to life in moister, more heavily wooded regions than the terrain occupied by their steppe bison ancestors — terrain similar to the current margins of subalpine forests, open forest and parkland. Such habitat may have developed following the reopening of Bering Strait and a marked northward shift of easterly moving storm tracks producing warmer, wetter conditions in Northwestern North America toward the close of the Pleistocene (Harington, 1977).

Like other bison, western bison probably fed mainly on grasses, forbs and sedges, in an environment similar to that proposed for the upper Peace River region (White *et al.*, 1984), and likely established as early as 11,700 yr BP. If these hypotheses can be confirmed, such bison fossils could be useful paleoenvironmental indicators of rather moist, partly wooded terrain.

RELATIONSHIPS WITH OTHER BISON OF SIMILAR AGE AND TYPE

Clearer understanding of the place of the Clayhurst specimen in the evolution and dispersal history of bison in northwestern North America can be gained by more thorough morphological and geochronological studies of other bison specimens from nearby sites in British Columbia, the Yukon, the Northwest Territories and Alberta (Table IV). Such a project is beyond the scope of this paper, but we feel the information presented here might help focus future research.

Considering evidence in Table IV, apparently *B. a. antiquus* flourished in southern Alberta (*e.g.*, Calgary and Cochrane sites) about 11,000 years ago; *B. a. antiquus* and *B. b. occidentalis* (the former from the south and the latter from the north) both occupied the Peace River area shortly before 10,000 years ago (*e.g.*, Athabasca, Taylor and possibly Clayhurst sites); and *B. b. occidentalis* evidently had spread to southern Alberta (Three Hills) by about 9700 years ago. Wilson (1992) has advanced several dispersal hypotheses that bear on this subject.

SUMMARY

1. The Clayhurst bison, an old male, is the most complete late Pleistocene, "medium-horned" bison so far reported from Canada. It is also the most thoroughly radiocarbon-dated specimen of its kind in Canada. Four AMS dates from three different laboratories provide a weighted average age of $10,550 \pm 90$ yr BP.

2. Evidently the specimen represents an extinct western bison (*Bison bison cf. occidentalis*) of larger than average size. It is probably closely related to bison of similar geological age from Charlie Lake Cave and Tumbler Ridge (Kevin Woolf, 1992, personal communication). Following regional inundation by a series of glacial lakes, the first bison entered the area prior to 10,500 years ago, when the Clayhurst bison died and its bones were incorporated by the proto-Peace River into high terrace gravels.

3. Apparently *Bison bison antiquus* occurred in southern Alberta about 11,000 years ago; both *antiquus* and *occidentalis* occupied the Peace River area shortly before 10,000 years ago; and *B. b. occidentalis* had spread to southern Alberta by at least 9,700 years ago. More detailed work is required to refine or correct this general outline.

4. The solid dating of the Clayhurst Crossing bison further substantiates a growing body of data suggesting that the Peace River region of Northwestern British Columbia was open and habitable for late Pleistocene flora and fauna (including people), to travel between the Beringian refugium and the southern interior Plains of North America prior to 10,500 yr BP.

ACKNOWLEDGEMENTS

We are grateful to Knut R. Fladmark and Jon Driver (Simon Fraser University), as well as Peter Bobrowsky (British Columbia Geological Survey Branch), for their advice on the manuscript. We are particularly appreciative to Knut Fladmark for his assistance in collecting the specimens and providing us with his field notes; and to Peter Bobrowsky for supplying two pertinent radiocarbon dates on bone from the Clayhurst and Taylor (Ostero) gravel pits. We also thank those who have collected and donated specimens from the Clayhurst site: O.W.H. Roberts, A.B. Sanderson, Vaso Jankovic, Frank Wilde, and members of the North Peace Historical Association. Erle Nelson (Simon Fraser University) arranged for all the AMS radiocarbon dates on the bone. C. Coates provided the map and K. Woolf (Simon Fraser

University) provided information on a bison skull with horncores from Tumbler Ridge that is of similar geological age to the Clayhurst specimen. We are also grateful to reviewers C. Churcher and J. A. Burns for their useful suggestions.

REFERENCES

- Bobrowsky, P.T., Catto, N. and Levson, V., 1991. Reconnaissance Quaternary geological investigations in Peace River District, British Columbia (93P, 94A). British Columbia Geological Survey Branch, Geological Fieldwork 1990, Paper 1991-1: 345-358.
- Bobrowsky, P.T. and Rutter, N., 1990. Geologic evidence for an ice-free corridor in northeastern British Columbia, Canada. *In Current Research in the Pleistocene*, 7: 133-135.
- 1992. The Quaternary geologic history of the Canadian Rocky Mountains. *Géographie physique et Quaternaire*, 46(1): 5-50.
- Churcher, C.S., 1968. Pleistocene ungulates from the Bow Rivergravels at Cochrane, Alberta. *Canadian Journal of Earth Sciences*, 5(6): 1467-1488.
- 1975. Additional evidence of Pleistocene ungulates from the Bow River gravels at Cochrane, Alberta. *Canadian Journal of Earth Sciences*, 12: 68-76.
- Cinq-Mars, J., Harington, C.R., Carlson, D.E. and NacNeish, R.S., 1991. Engistciak revisited: A note on early Holocene AMS dates from the "Buffalo Pit", p. 33-44. *In Cinq-Mars and J.L. Pilon, eds., NOGAP archaeology project: An integrated archaeological research and management approach.* Canadian Archaeological Association Occasional Paper No. 1: 33-44.
- Driver, J.C., 1988. Late Pleistocene and Holocene vertebrates and paleoenvironments from Charlie Lake Cave, northeast British Columbia. *Canadian Journal of Earth Sciences*, 25: 1545-1553.
- Driver, J.C. and Hobson, K.A., 1992. A 10,500-year sequence of bird remains from the southern boreal forest region of western Canada. *Arctic*, 45(2): 105-110.
- Fladmark, K.R., 1975. Peace past: A report on the archaeological reconnaissance of the Peace River basin, 1974 field season. Unpublished report to the Heritage Conservation Branch, Victoria, British Columbia.
- Flerov, C.C., 1979. European bison: Morphology, systematics, evolution, ecology. Nauka, Moscow, 495 p.
- Fuller, W.A. and Bayrock, L.A., 1965. Late Pleistocene mammals from central Alberta, Canada, p. 55-63. *In C.R. Stelck, ed., Vertebrate paleontology in Alberta.* University of Alberta, Department of Geology, Edmonton.
- Geist, V., 1971. The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the Old World deer and the genus *Bison*. *Quaternary Research*, 1: 283-315.
- Gordon, B.C., 1970. *Bison antiquus* from the Northwest Territories. *Arctic*, 23: 132-133.
- Graham, M.A., Wilson, M.C. and Graham, R.W., 1987. Paleoenvironments and mammalian fauna of Montana, southern Alberta, southern Alberta, and southern Saskatchewan. *In R.W. Graham, H.A. Semken, Jr. and M.A. Graham, ed., Late Quaternary Mammalian Biogeography and Environments of the Great Plains and Prairies.* Illinois State Museum Scientific Papers 22: 410-459.
- Guthrie, R.D., 1970. Bison evolution and zoogeography in North America during the Pleistocene. *Quarterly Review of Biology*, 45(1):1-15.
- Hall, S.A., 1972. Holocene *Bison occidentalis* from Iowa. *Journal of Mammalogy*, 53: 604-606.
- Harington, C.R., 1977. Pleistocene mammals of the Yukon Territory. Ph.D. thesis, University of Alberta, Edmonton, 1060 p.
- 1984. Mammoths, bison and time in North America, p. 299-309. *In W.C. Mahaney, edit., Quaternary Dating Methods.* Elsevier Science Publishers, Amsterdam.
- Jackson, L.E., Jr., and Pawson, M., 1984. Alberta radiocarbon dates. Geological Survey of Canada, Paper 83-25: 1-27.
- Liverman, D.G., 1989. The Quaternary geology of the Grande Prairie area, Alberta. Ph.D. Thesis, University of Alberta, Edmonton.
- Lowdon, J.A. and Blake, W., Jr. 1979. Geological Survey of Canada Radiocarbon Dates XIX. Geological Survey of Canada, Paper 79-7: 1-57.
- MacDonald, G.M., 1987. Postglacial development of the subalpine- boreal transition forest of western Canada. *Journal of Ecology*, 75: 303-320.
- Mathews, W.H., 1978. Quaternary stratigraphy and geomorphology of Charlie Lake (94A) map area, British Columbia. Geological Survey of Canada, Paper 76-20.
- 1980. Retreat of the last ice sheets in northeastern British Columbia and adjacent Alberta. Geological Survey of Canada, Bulletin 331.
- McDonald, J.N., 1981. North American bison: Their classification and evolution. University of California Press, Berkeley and Los Angeles, 316 p.
- Nelson, D.E., 1991. A new method for carbon isotopic analysis of protein. *Science*, 251: 552-554.
- Rutter, N.W., 1984. Pleistocene history of the western Canadian ice-free corridor. *In R.J. Fulton, ed., Quaternary stratigraphy of Canada. A Canadian contribution to IGCP Project 24.* Geological Survey of Canada, Paper 84-10.
- Shackleton, D.M. and Hills, L.V., 1977. Post-glacial ungulates (*Cervus* and *Bison*) from Three Hills, Alberta. *Canadian Journal of Earth Sciences*, 14: 963-986.
- Skinner, M.F. and Kaisen, O.C., 1974. The fossil *Bison* of Alaska and preliminary revisions of the genus. *Bulletin of the American Museum of Natural History*, 89: 123-256.
- St-Onge, D.A., 1972. Sequence of glacial lakes in north-central Alberta. Geological Survey of Canada, Bulletin 213.
- von den Driesch, A., 1976. A guide to the measurement of animal bones from archaeological sites. Peabody Museum Bulletin, 1: 1-135.
- White, J.M., 1983. Late Quaternary Geochronology and Paleoecology of the Upper Peace River District, Canada. Ph.D. thesis, Simon Fraser University, Burnaby.
- White, J.M. and Mathewes, R.W., 1986. Postglacial vegetation and climatic change in the upper Peace River district, Alberta. *Canadian Journal of Botany*, 64: 2305-2318.
- White, J.M., Mathewes, R.W. and Mathews, W.H., 1985. Late Pleistocene chronology and environment of the "Ice-Free Corridor" of northwestern Alberta. *Quaternary Research*, 24: 173-186.
- Wilson, M., 1974. The Casper local fauna and its fossil bison, p. 125-171. *In G.C. Frison, ed., The Casper site: A Hell Gap bison kill on the High Plains.* Academic Press, New York.
- 1981. Once upon a river: Archaeology and geology of the Bow River valley at Calgary, Alberta. Ph.D. thesis, University of Calgary.
- 1992. Bison in Alberta: Paleontology, evolution and relations with humans, p. 1-17. *In J.E. Foster, D. Harrison and I.S. MacLaren, ed., Buffalo.* Alberta Nature and Culture Series, University of Alberta Press.
- Wilson, M.C. and Churcher, C.S. 1984. The Late Pleistocene Bighill Creek Formation and its equivalents in Alberta: Correlative potential and vertebrate paleofauna, p. 169. *In W.C. Mahaney, ed., Correlation of Quaternary Chronologies.* Geo Book, Norwich.