

# Late Pleistocene northward-dispersing *Bison antiquus* from the Bighill Creek Formation, Gallelli Gravel Pit, Alberta, Canada, and the fate of *Bison occidentalis*

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**Abstract:** Late Pleistocene bison skeletal remains from the Gallelli Gravel Pit in the Bighill Creek Formation at Calgary, Alberta, document at least two individuals, including the largest postglacial bison reported from North America south of Beringia. Two partial crania, dated to 11 290 and 10 100 <sup>14</sup>C years BP, are referred to the southern species *Bison antiquus* Leidy, indicating northward movement from the midcontinent as ice retreat opened a corridor between Laurentide and Cordilleran ice. Their large size suggests a dispersal phenotype exploiting newly available territory. DNA evidence links the 11 290-year-old bison to Clade 1, which includes modern *B. bison*. This supports in situ evolution of *B. bison* from *B. antiquus* through the intermediate usually called *B. "occidentalis"*. Bison of *B. "occidentalis"* character appeared in Alberta about 10 ka BP, and the DNA evidence counters the suggestion of a migratory wave from Beringia. The *B. occidentalis* type specimen is from Alaska, so this name may be inappropriate for southern populations. Radiocarbon dates suggest that the Bighill Creek Formation paleofauna comprises two faunules separated in time by the Younger Dryas climatic episode.

**Résumé :** Les restes de squelettes de bisons datant du Pléistocène tardif trouvés dans la gravière Gallelli dans la Formation de Bighill Creek à Calgary, en Alberta, représentent au moins deux individus, dont le plus gros bison postglaciaire trouvé en Amérique du Nord au sud de la Béringie. Deux crânes partiels, datés à 11 290 et 10 100 années <sup>14</sup>C avant le présent correspondraient à l'espèce méridionale *Bison antiquus* Leidy, indiquant un mouvement vers le nord à partir du milieu du continent alors que le retrait de la glace ouvrait un corridor entre la glace laurentidienne et la glace de la Cordillère. Leur grande taille suggère un phénotype de dispersion exploitant un territoire récemment disponible. Les preuves fournies par l'ADN relie le bison de 11 290 ans au Clade 1, lequel comprend le *B. bison* moderne. Cela soutient l'évolution in situ du *B. bison* à partir de *B. antiquus* en passant par l'intermédiaire habituellement appelé *B. « occidentalis »*. Un bison *B. « occidentalis »* s'est retrouvé en Alberta il y environ 10 ka avant le présent et les preuves d'ADN opposent la suggestion d'une vague migratoire à partir de la Béringie. Le spécimen de type *B. occidentalis* provient de l'Alaska; ce nom ne conviendrait donc pas aux populations du sud. Selon les datations au radiocarbone, la paléofaune de la Formation de Bighill Creek comprendrait deux faunules séparées dans le temps par l'épisode climatique du Dryas récent.

[Traduit par la Rédaction]

## Introduction

For decades, vertebrate fossils have been collected from Bighill Creek Formation (BCF) gravels and sands at Calgary and Cochrane on the Bow River in Alberta, including important remains described here of *Bison antiquus* Leidy, 1852 from the Gallelli Pit, Calgary (Fig. 1). The BCF is a widespread alluvial unit along the Bow and other Alberta

rivers, associated with the most prominent postglacial terrace (Figs. 2, 3). Bone collagen radiocarbon dates range from about 11 500 to 10 000 <sup>14</sup>C years BP (Table 1; Lowdon et al. 1967; Stalker 1968; Wilson and Churcher 1984), equivalent to about 13 300 to 11 700 or 11 300 cal (calibrated) years BP (Bard 1998; Stuiver et al. 1998; CALIB 5.0.1). Thus the fauna has relevance as to the timing and character of deglaciation, Late Pleistocene environmental change, Beringian–midcontinental faunal relationships, and opening of an “ice-free corridor” between Laurentide and Cordilleran ice sheets. Bones of large ungulates at Calgary and Cochrane (25 km upstream) include some with little abrasion, a few being articulated. Calgary and Cochrane paleofaunas differ slightly, suggesting ecological differences. Large bison (*Bison antiquus*), Mexican ass (*Equus conversidens*), and mammoth (*Mammuthus* sp.) are present in both, but pits at Cochrane also yield caribou (*Rangifer tarandus*) and large mountain sheep (*Ovis canadensis catclawensis*), whereas pits at Calgary also yield camel (*Camelops* sp., cf. *C. hesternus*) (Churcher 1968, 1975; Wilson 1983, 1987; Wilson and Churcher 1978, 1984; J.A.

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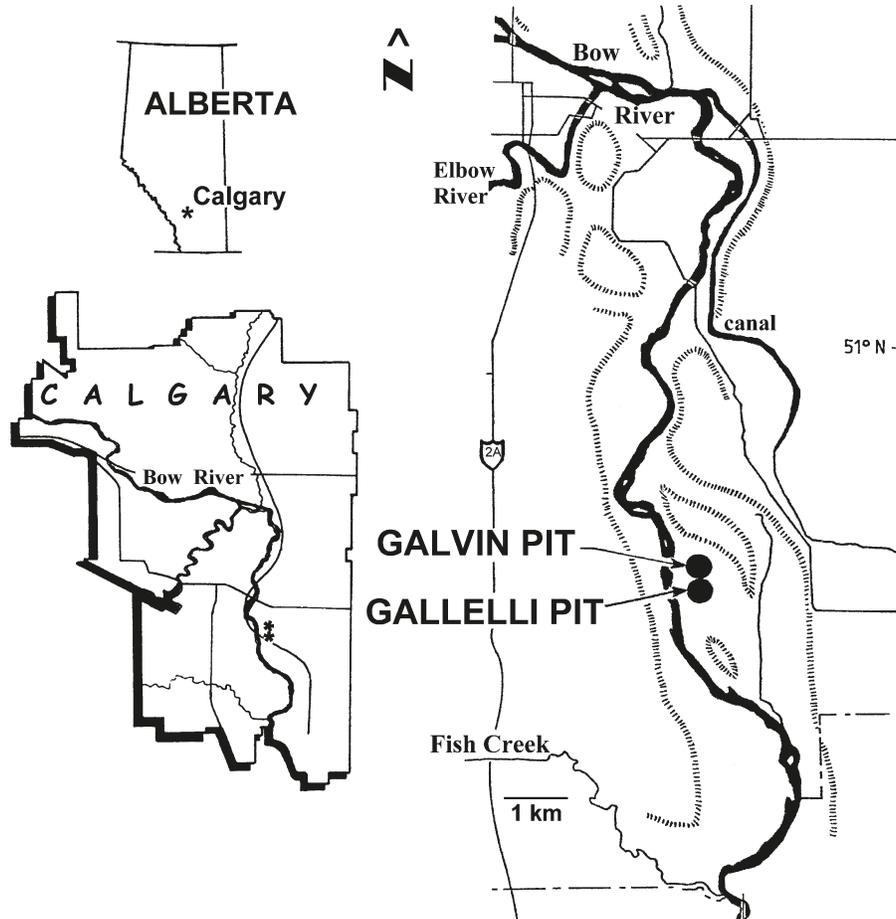
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**Fig. 1.** Map showing location of Gallelli and Galvin pits along the Bow River valley in Calgary, Alberta, Canada.



**Fig. 2.** Oblique aerial view of Bow River valley immediately west of Calgary, looking northwest to town of Cochrane (right distance), type locality of the Bighill Creek Formation (BCF). The broad alluvial terrace surface in the middle foreground comprises the BCF filltop and minor inset units of Holocene age.



**Fig. 3.** Bighill Creek Formation exposure at Bonnycastle Pit, southeast of Calgary, Alberta (Wilson 1983); thickness of exposed section (at right, not including covered interval at base) is  $\sim 4.5$  m. Note pebble and cobble gravels with sandy interbeds. A *Bison* metatarsal lies on displaced cobbles on the footslope (arrow).



Burns, personal communication, 2001). There may also be two temporally distinct faunules within the overall BCF paleofauna, spanning the time of the Late Pleistocene extinctions (Barnosky et al. 2004; Grayson and Meltzer 2002; Guthrie 2006). All dates in the ensuing discussion are in  $^{14}\text{C}$  years or  $^{14}\text{C}$  ka BP unless specifically indicated as cal years.

Calgary and Cochrane are in the plains to foothills grassland zone today, with local riparian stands of Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), and poplars (*Populus tremuloides* and *P. balsamifera*) along the Bow River valley (Sherrington 1975). The BCF paleofauna, rich in grazers, suggests steppe grasslands or steppe-tundra with local bush or parkland tracts (Wilson and Churcher 1978, 1984). No coeval pollen cores are available from Calgary, but regional information supports that interpretation and reveals that vegetational zones migrated northward with ice retreat. Palynological studies show that a narrow band of spruce-dominated (*Picea glauca* and *P. mariana*) forest with tamarack (*Larix laricina*), poplars (*Populus tremuloides* and *P. balsamifera*), and birch (*Betula* sp., tree form, including *B. papyrifera*) existed south of Laurentide

ice ca. 14  $^{14}\text{C}$  ka BP, preceded by pioneer steppe-tundra (Strong and Hills 2005). South of the forest band, temperate grasslands with shrubs in mesic settings were established on the Montana plains before 11 ka BP (Barnosky et al. 1987; Barnosky 1989). As glaciers retreated, spruce-birch forests expanded northwestward in Alberta, replacing pioneer steppe-tundra (Ritchie and MacDonald 1986; Strong and Hills 2005). In northeastern Alberta, a pioneer sagebrush (*Artemisia*) – grass community was replaced by spruce forest about 10.5 ka BP (Hutton et al. 1994). By about 12 ka BP grasslands invaded southern Alberta nearly to their modern northward extent, replacing forests, but Laurentide ice and fringing forests persisted in Saskatchewan and Manitoba. An ice-free corridor may have not opened between the Yukon and northwest Alberta until as late as 11  $^{14}\text{C}$  ka, although an earlier date is possible (see discussion later in this paper). Ice retreat from the southern Alberta plains before 11.5 ka BP is confirmed by limiting bone and wood dates and by Glacier Peak tephra (ca. 11.2 ka BP) in loess at Lethbridge (Vreeken 1989). By 10 ka BP grasslands expanded to or beyond modern limits in all three provinces, with *Picea–Betula* or *Picea* forests in northern Alberta (Strong and Hills 2005). Forests need not always have formed an unbroken, moving band across the region, but evidence suggests that a forest barrier rapidly succeeded steppe-tundra in the northern ice-free corridor, blocking migration of grazing ungulates (MacDonald and McLeod 1996; Wilson 1996). In the foothills southwest of Calgary a shrub and herb-dominated community with local *Populus* was established by 10 ka BP, with coniferous forests at higher elevations in nearby mountains. Forests replaced steppe-tundra before 10 ka BP in the Rocky Mountain Front Ranges 30 km west of Cochrane and invaded the foothills between 9.4 and 8 ka BP (MacDonald 1982, 1989). More deeply in the mountains, pine forest replaced tundra at Wilcox Pass, near Columbia Icefield in Jasper National Park, before 9.6 ka BP (Beaudoin and King 1990). The BCF paleofauna postdates the northwestern movement of spruce forest and expansion of plains grasslands.

Late Pleistocene large bison are best identified from crania with relatively complete frontals. Isolated BCF horn cores were initially assigned to *B. occidentalis* Lucas, 1898 (Churcher 1968, 1975), but more complete crania indicate that only the morphospecies *B. antiquus* was present (Wilson and Churcher 1984; = *B. a. antiquus* of McDonald 1981). We here describe *B. antiquus* specimens from the Gallelli Pit, including crania and postcranial bones of the largest bison recovered from midcontinent postglacial deposits, and which have yielded mitochondrial DNA.

There are morphological and genetic distinctions between bison that were south of the ice sheet in last glacial times (classic *Bison antiquus* as at Rancho La Brea, California) and bison that occupied Beringia, *B. priscus* (Bojanus, 1827), sensu lato. Linkage of Beringian populations with Asia and the diversity of east Asian Quaternary bison suggest a greater variety of species in Beringia, as reflected by higher DNA clade diversity, than in the North American midcontinent (Shapiro et al. 2004). However, both areas have seen taxonomic “lumping,” reducing the numbers of accepted morphospecies (Guthrie 1970; McDonald 1981;

**Table 1.** Radiocarbon dates from the Bighill Creek Formation, Bow River valley.

Sample No.	Date <sup>a</sup> and technique	Material and reference
GSC-613	11 370±170; conventional, collagen	bone, species not reported, Cochrane; (Lowdon et al. 1967); (Stalker 1968)
RL-757	11 300±290; conventional, collagen	<i>Bison</i> bone; (Wilson and Churcher 1978) and this paper (Gallelli tibia)
TO-7694	11 290±80; AMS, collagen	<i>Bison</i> cranium UCG 4066; this paper
GSC-989	11 100±160; conventional, collagen	bone, species not reported, Cochrane; Stalker 1968
GSC-612	10 760±160; conventional, collagen	bone, species not reported, Cochrane; (Lowdon et al. 1967; Stalker 1968)
GSC-3065	10 200±280; conventional, collagen	<i>Bison</i> cranium, Aquitaine Pit; (Wilson 1983; Blake 1986)
TO-7695	10 090±70; AMS, collagen	<i>Bison</i> cranium UCG 6125; this paper

**Note:** Laboratory designations: GSC, Geological Survey of Canada, Ottawa, Ontario; RL, Radiocarbon Limited, Lampasas, Texas; TO, IsoTrace Laboratory, Toronto, Ontario. AMS, accelerator mass spectrometry; UCG, University of Calgary, Department of Geoscience, Calgary, Alberta. Species of animal not identified in Stalker (1968) or Lowdon et al. (1967) but likely bison.

<sup>a</sup>Dates in radiocarbon years BP. Quoted errors represent 1 standard deviation (68% probability).

**Fig. 4.** Oblique aerial view of Gallelli Pit (right) and Galvin Pit (lower left), southeast Calgary, Alberta, prior to reclamation; Gallelli Pit margin (centre) marks the east wall of the Bow Valley. See Wilson and Churcher (1978) for details of Gallelli Pit stratigraphy and geomorphic setting.



Skinner and Kaisen 1947; Wilson 1969, 1974a). Beringian populations were hypothesized to have given rise to the Late Pleistocene – early Holocene morphospecies *B. occidentalis* Lucas, identified from its type material in Alaska as well as from Great Plains archaeological bison kills (Fuller and Bayrock 1968; Skinner and Kaisen 1947; Wilson 1974a). Late Pleistocene southern forms originating from an earlier migration, the *B. latifrons* (Harlan, 1825) to *B. antiquus* line, came to exhibit broad, arched frontals with downswept, laterally directed horn cores. Forms of hypothesized northern origin (*B. priscus* to *B. occidentalis* line) exhibited narrow, flat frontals with upswept and backswept horn cores, their tips well behind the occipital plane (Skinner and Kaisen 1947; Wilson 1996). Midcontinent *B. antiquus* finds tend to predate 10 ka BP, whereas *B. occidentalis* finds largely postdate that time (Forbis 1956; Guthrie 1970, 1990; McDonald 1981; Wilson 1974a,

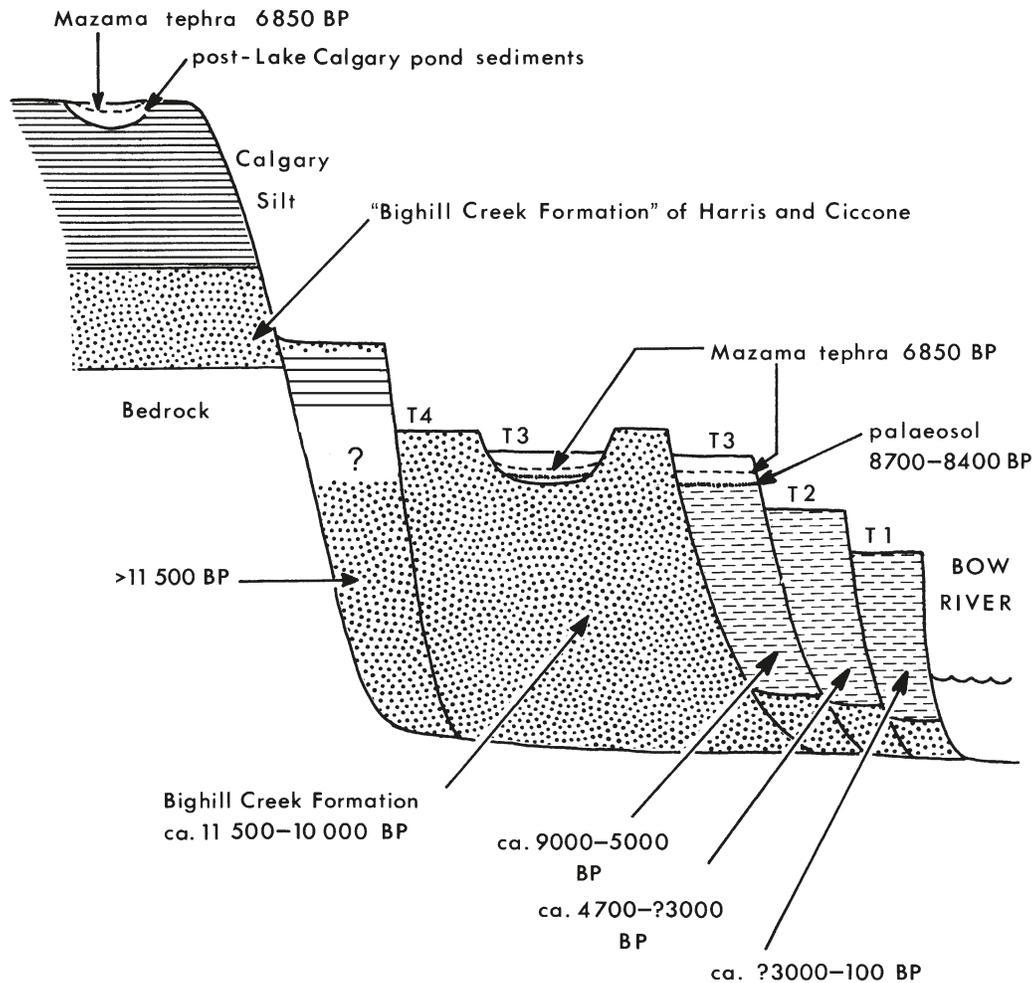
1974b). Remaining in question is whether replacement in the midcontinent was through

1. in situ evolutionary change;
2. introgressive hybridization, with northern forms genetically “swamping” southern forms; or
3. full replacement, with southern forms having become extinct upon or just before the arrival of northern forms (Wilson 1996).

These alternatives can only be tested through documentation and dating of bison from the “ice-free corridor” area in western Canada and in postulated reservoir areas to the north and south. The Gallelli Pit sample, allowing both morphological and DNA diagnoses, is vital in this context.

Laurentide and Cordilleran ice sheet coalescence produced a continuous ice mass at the last glacial maximum (LGM), and ice retreat opened an intervening “ice-free cor-

**Fig. 5.** Schematic diagram showing simplified relationships of Bighill Creek Formation with older and younger deposits in the Cochrane–Calgary area. Local bedrock is the Paleocene Porcupine Hills Formation. Gravels identified by Harris and Ciccone (1983) as belonging to the BCF represent a stratigraphically distinct, older unit. The terrace shown here above T4 conflates a number of local features, including a major unit of glaciolacustrine silts at Cochrane (Fisher 1999; Wilson and Churcher 1984). Oetelaar (2002) labels our T4 as T3 and fails to note that at Cochrane his T3 includes glaciolacustrine silts related to Lake Calgary.



ridor" no earlier than 14 or 13  $^{14}\text{C}$  ka BP, and possibly as late as 11.0 ka BP (Arnold 2002; Burns 1996; Dyke 2004; Dyke et al. 2002; Jackson et al. 1997, 1999; Mandryk et al. 2001; Rutter 1980; Schweger 1989; Stalker 1980; Young et al. 1994). Use of the term "corridor" here in the context of animal and human migrations follows the biogeographic corridor concept: that of a pathway by which biological colonization occurred (McKenna 1973). Its *effective width* and *opening time* were distinctive for each species, depending upon presence of conditions adequate for their support (MacDonald and McLeod 1996; Wilson 1996). An "opening" event was thus not only physical but also biotic, and the initial physical opening was probably accompanied by climatic extremes, as well as blockage by ephemeral ice-frontal meltwater lakes. Any biotic opening that allowed bison to disperse southward must have been brief because an ice barrier between Beringia and the midcontinent was rapidly replaced by a forest barrier, with perhaps only 500 years

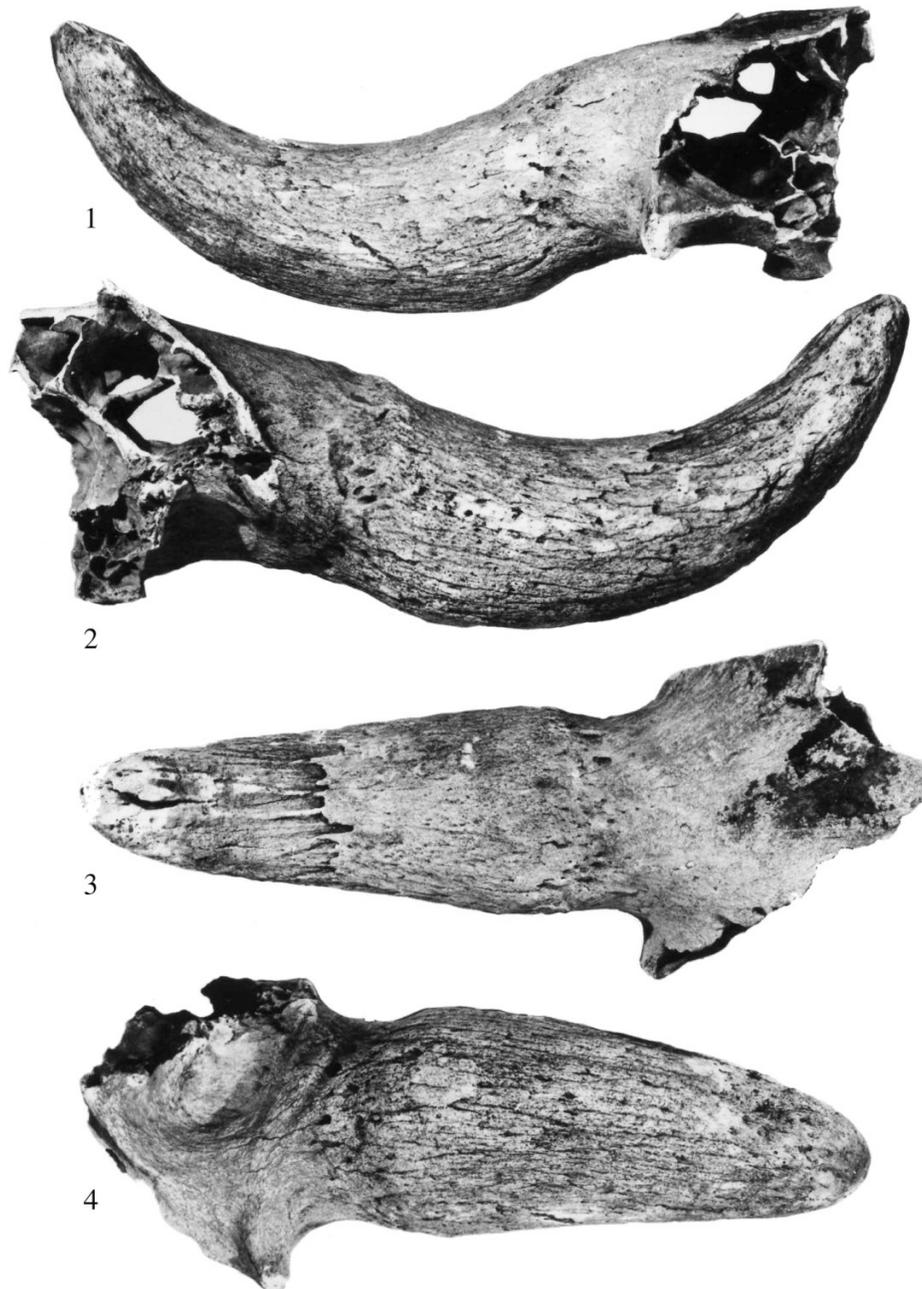
during which a steppe or steppe-tundra corridor existed (MacDonald and McLeod 1996).

Fundamental issues addressed here include

1. whether BCF bison are of "southern" or "northern" morphology and DNA affinities;
2. if they are "southern," whether or not they conform with dispersal theory expectations for a population expanding into newly open territory; and
3. on this basis, their significance for bison taxonomy.

Dispersal theory suggests that individuals in such a population would increase in size compared with their ancestors, particularly in energetically costly display characters, such as horn cores (Geist 1971, 1999). As for the third issue, it has been unclear whether *B. antiquus* and *B. occidentalis* are valid as sympatric paleospecies, given the possibilities that they interbred upon contact of northern and southern populations in latest Pleistocene times or that one evolved

**Fig. 6.** The larger *Bison antiquus* cranial fragment, including right horn core, from Gallelli Pit, UCG 4066. (1) anterior view, (2) posterior view, (3) dorsal view, (4) ventral view.



into the other (McDonald 1981; Wilson 1974a, 1996). If they represent biological subspecies or simply individual variation, it would still remain to be decided if the species reference would be to the modern descendant form, *B. bison* or to the first-named fossil form, *B. antiquus*.

### Regional geologic context and paleoenvironment

The contiguous Gallelli and Galvin Pits (Figs. 1, 4), east of the Bow River in southeast Calgary ( $50^{\circ}57'45''\text{N}$  latitude,  $114^{\circ}01'\text{W}$  longitude), were excavated until the 1970s and reclaimed (Wilson 1983; Wilson and Churcher 1978). The

BCF at Cochrane and Calgary is inset into Glacial Lake Calgary silts, glacial till, or bedrock (Fisher 1999; Oetelaar 2002; Wilson 1983; Wilson and Churcher 1984). Pre-Lake Calgary gravels referred by Harris and Ciccone (1983) to the BCF are older but also Late Pleistocene (Fig. 5). Stalker (1968) interpreted the BCF (ca. 11.5–10 ka; Table 1) as outwash from Cordilleran ice stalled near the mountain front, but upper Bow River basin dates indicate that ice had retreated to cirques by 11.5 ka, with only a minor readvance not far beyond the cirques (Crowfoot glacial advance) at the time of BCF gravel deposition (Luckman and Osborn 1979; Osborn and Luckman 1988; Osborn and Gerloff 1997; Osborn et al. 2001). Dates on charcoal from Vermilion

**Fig. 7.** The smaller *Bison antiquus* cranium from Gallelli Pit, UCG 6125. (Above), dorsal view; (below), posterior (occipital) view.



Lakes, near Banff, range as early as 11.1 ka BP; and post-glacial sedimentation began before 11.5 ka BP at Copper Lake, near Banff, and before 11.1 ka BP at Crowfoot Lake, near the head of the Bow Valley (Fedje et al. 1995; Reasoner et al. 1994; Reasoner and Huber 1999; White and Osborn 1992). Jackson et al. (1982) reinterpreted the BCF as a paraglacial fill emplaced after ice retreat when rapid warming mobilized previously frozen hillslopes, resulting in deposition of till-like debris-flow diamicts in the upper Bow Valley (Church and Ryder 1972; Ballantyne 2002). At Vermilion Lakes in the floor of Bow Valley, there was frequent debris-flow activity before 10.8 ka and again between about 10.3 and 9.5 ka BP; but none between about 10.8 and 10.3 ka BP (Fedje et al. 1995).

BCF radiocarbon dates (Table 1) fall into “early” (11 370 to 10 760 BP) and “late” (10 200 to 10 090 BP) groups, correlating with depth. A partial bison cranium from the upper third (3 m depth) of the BCF at the Aquitaine Pit, Calgary, was dated to 10 200 ± 280 BP (GSC-3065; Blake

1986; Wilson 1983). The cranium, smashed by backhoe, included the fragile rostral area, indicating minimal transport. The Gallelli Pit, excavated through the full gravel unit to till and bedrock, gave both early (11 300 BP) and late (10 090 BP) dates (see later in the text). A bone from Cochrane dated to 10 760 ± 160 BP (GSC-612) was found stratigraphically higher than others dated to 11 100 ± 160 (GSC-989) and 11 370 ± 170 BP (GSC-613) (Stalker 1968).

The BCF timespan straddles the cool Younger Dryas (YD) climatic interval, which began between 10.8 and 10.6 <sup>14</sup>C ka BP and ended between 10.05 and 10.0 <sup>14</sup>C ka BP (Alley et al. 1993; Broecker 2003; Edwards et al. 1993; Fairbanks 1989; Muscheler et al. 2008; Teller et al. 2002). Given a radiocarbon plateau reflecting exchange-rate changes in the global carbon cycle, the YD was longer than these dates suggest (Bard 1998), spanning about 1100 to 1300 years, from ~12 800 to 11 600 cal BP (Hughen et al. 1998, 2000; Muscheler et al. 2008). The Crowfoot glacial advance is dated between ca. 11.3 and 10.1 <sup>14</sup>C ka BP, ice having pre-

**Fig. 8.** Right lateral view of Gallelli Pit bison cranium UCG 6125, rotated slightly from the correct anatomical position to highlight details of horn core.



**Table 2.** Comparison of measurements of fossil bison crania from Gallelli Pit with criteria for *Bison antiquus*.<sup>a</sup>

Standard measurement	Gallelli Pit		<i>Bison antiquus</i>		
	UCG 4066	UCG 6125	Minimum	Mean	Maximum
1. Spread of horn cores, tip to tip	(860)	(838)	765	870	1067
2. Greatest spread of cores on outside curve	(890)	(840)	—	—	—
3. Core length on upper curve, tip to burr	(280)	224	203	279	364
4. Core length on lower curve, tip to burr	(345)	274	280	336	395
5. Length, tip of core to upper base at burr	(270)	215	185	250	330
6. Vertical diameter of horn core at base	105	106	81	102	126
7. Circumference of core at base	365	303	233	324	392
8. Greatest width at auditory openings	—	294	251	288	318
9. Width of condyles	—	132.5	132	144	161
10. Depth, occipital crest to top of foramen magnum	—	100.5	94	112	134
11. Depth, occipital crest to bottom of foramen magnum	—	148	—	—	—
12. Transverse diameter of horn core at base	118	100.5	76	106	129
13. Width between bases of horn cores	(260?)	(296)	—	—	—
14. Width of cranium between horn cores and orbits	(320)	(324)	276	315	352
Angle 1. Angle of posterior divergence of horn core	(80°)	80°	72°	79°	86°
Angle 2. Angle of proximal depression of horn core	(20°)	15°–20°	—	—	—

<sup>a</sup>Measurements after Skinner and Kaisen (1947), as expanded by McDonald (1981). Estimated Gallelli Pit measurements are in parentheses. Measurements for 1–14 are in mm.

viously receded from Crowfoot Lake basin shortly before 11 330 <sup>14</sup>C years BP. About 11.1 ka BP ice spilled out of cirque basins but not far enough to coalesce into valley glaciers, then retreated before about 10 ka BP (Osborn and Gerloff 1997; Reasoner et al. 1994; Reasoner and Huber 1999; Reasoner and Jodry 2000). The Vermilion Lakes debris-flow hiatus spans much of the YD, suggesting reestablishment of slopes by freezing (Fedje et al. 1995). The BCF paleofauna, dominated by grazers, and the enclosing alluvium date to the latest part (ca. 13 200 to 12 700 cal-years

BP) of the Bølling–Allerød warm interval and near the end of the YD. Considering lag factors, BCF alluvium likely reflects (i) Bølling–Allerød warming (Bighill Creek I) and (ii) renewed warming after YD times (Bighill Creek II), each with debris-flow activity and downstream redistribution. The intervening paucity of dated specimens need not represent an absence of fauna; rather, it could represent a time of non-deposition, a taphonomically driven absence of specimens. However, given the climatic impact of the YD, the faunal hiatus could have other significance.

**Table 3.** Comparison of measurements of fossil bison crania from Gallelli Pit with criteria for *Bison occidentalis*.<sup>a</sup>

Standard measurement	Gallelli Pit			<i>Bison occidentalis</i>	
	UCG 4066	UCG 6125	Minimum	Mean	Maximum
1. Spread of horn cores, tip to tip	(860)	(838)	626	779	1055
2. Greatest spread of cores on outside curve	(890)	(840)	735	782	892
3. Core length on upper curve, tip to burr	(280)	224	186	278	392
4. Core length on lower curve, tip to burr	(345)	274	275	340	405
5. Length, tip of core to upper base at burr	(270)	215	175	249	350
6. Vertical diameter of horn core at base	105	106	70	95	114
7. Circumference of core at base	365	303	237	300	355
8. Greatest width at auditory openings	—	294	238	262	294
9. Width of condyles	—	132.5	111	135	151
10. Depth, occipital crest to top of foramen magnum	—	100.5	89	104	120
11. Depth, occipital crest to bottom of foramen magnum	—	148	136	158	177
12. Transverse diameter of horn core at base	118	100.5	77	99	120
13. Width between bases of horn cores	(260+)	(296)	—	—	—
14. Width of cranium between horn cores and orbits	(320)	(324)	261	297	348
Angle 1. Angle of posterior divergence of horn core	(80°)	80°	63°	72°	83°
Angle 2. Angle of proximal depression of horn core	(20°)	15°–20°	—	—	—

<sup>a</sup>After Skinner and Kaisen (1947) and McDonald (1981). Ranges for measurements 2, 4, 11, and 13 after Skinner and Kaisen. *B. occidentalis* sample is dominated by referred specimens from the midcontinent. Measurements for 1–14 are in mm.

**Fig. 9.** Right lateral view of 5th thoracic vertebra (left), and right lateral and posterior views of 7th cervical vertebra (middle and right) of *Bison antiquus* from Gallelli Pit (grouped as UCA 74.33.7). Note asymmetry of C7 postzygapophyses.

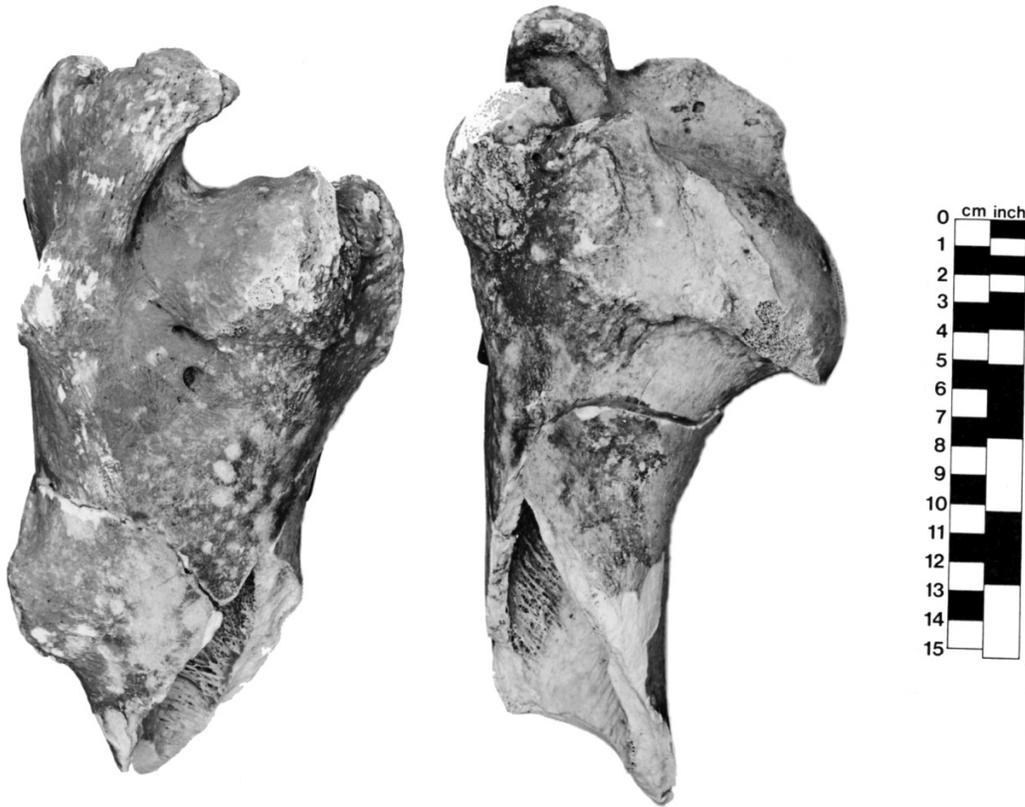


### Radiocarbon dates from Gallelli Pit

Two bone collagen <sup>14</sup>C dates were originally obtained from Gallelli Pit: 11 300 ± 290 years BP (RL-757; Wilson and Churcher 1978) for the unabraded left tibia of the articulated bison skeleton described here, and 8145 ± 320 years BP (GX-2104; B.O.K. Reeves, personal communication,

1977; Wilson and Churcher 1978) for the horn core of the smaller of two bison crania (UCG 6125). Wilson and Churcher (1978) speculated that the smaller cranium came from a thin capping gravel layer observed in the pit; however, doubts remained as to validity of the date. A new accelerator mass spectrometry (AMS) reading of 10 090 ± 70 years BP (TO-7695) for this specimen is consistent with

**Fig. 10.** Proximal end of right humerus, anterior (left) and medial (right) views, of *Bison antiquus* from Gallelli Pit (UCA 74.33.3). Difference in apparent length results from slight rotation in photography.



**Fig. 11.** Right metacarpal (anterior view) of *Bison antiquus* from Gallelli Pit (UCA 74.33.2).



other BCF dates, as well as with its size, so the date of 8145 BP is rejected. Collagen from the larger cranium (UCG 4066) was also submitted and yielded an AMS date of  $11\,290 \pm 80$  years BP (TO-7694).

### Gallelli Pit Bison material

Twelve bison elements and additional fragments were recovered from the Gallelli Pit, eight from an unabraded partial, articulated skeleton, including two vertebrae and bones from one forelimb and both hind limbs, obtained from a loader operator. This specimen is by several measurements the largest postglacial specimen yet recorded from the mid-continent. A comparably large partial frontal with horn core, collected at about the same time, is nearly identical in date but shows abrasion. An isolated radius fragment is comparably large. A second cranium with horn cores, although smaller than the first, is larger than early Holocene counterparts. The specimens are deposited at the University of Calgary, Department of Geoscience (UCG) and Department of Archaeology (UCA; partial skeleton 74.33). Approximate values for abraded specimens appear in measurement tables in parentheses.

### Cranial material

The larger cranium (UCG 4066) exhibits considerable abrasion, especially of the horn core tip. The specimen includes the massive right horn core and much of the posterior half of the frontal tables (Fig. 6). The parietal-occipital mass and anterior half of the frontal were broken away in exposure, leaving only a small portion of the braincase. A

**Fig. 12.** Right femur: anterior (left), medial (middle), and posterior (right) views of *Bison antiquus* from Gallelli Pit (UCA 74.33.5).



small remnant of the sagittal suture shows that it was unfused, so given horn core burr development the individual was in middle maturity at death. Cortical abrasion exposed longitudinal cavities on the distal superior surface of the core. The core is strongly keeled ventrally and proximally depressed, its tip not rising above the frontal plane. A sub-circular 5 cm indentation with vascular grooves, in the anterior half of the superior aspect of the basal burr, suggests a healed depressed fracture.

The second, more complete, cranium (UCG 6125) is a lightly abraded frontlet with both horn cores (one, already detached, sacrificed for dating) and intact occipitals and basicranium (Figs. 7, 8). It has broad frontals and relatively straight, proximally downswept horn cores with tips rising moderately above the frontal plane. The cores are directed

laterally with minor backward deflection, their tips just reaching the occipital plane, and are subcircular in cross-section and weakly keeled, with a negligible distal twist. The rugose burrs have knobby exostoses and frontal midline fusion has progressed about one-quarter of the way forward, suggesting middle maturity (Wilson 1980a).

#### Dentition

A right M<sub>3</sub> (third lower molar; UCA 83.47.2) with freshly broken hypoconulid shows broadly arcuate fossetids without infolds, like many Late Pleistocene bison. Its occlusal breadth is ~15 mm and metaconid height 57.4 mm. Light postfossetid wear indicates an individual <3 years old at death, so the tooth does not belong with either cranium (see Reher and Frison 1980).

**Fig. 13.** Right tibia: lateral (left), anterior (middle), and medial (right) views of *Bison antiquus* from Gallelli Pit (UCA 74.33.6).



### Vertebral column

Two vertebrae from the articulated skeleton, a 7th cervical and a 5th thoracic (grouped as UCA 74.33.7), had neural spines snapped away and eminences freshly abraded in exposure (Fig. 9). Both are large, with rugose muscle attachment areas. The left postzygapophysis of the cervical is deformed and twice the articular area of the right. A hypertrophic area lateral to the normal articular facet has an uneven surface with minor reactive tissue and small marginal osteophytes. Both vertebral centra exhibit incomplete fusion of anterior and posterior epiphyses, indicating an individual in middle maturity but not old age. In modern European bison, *B. bonasus* (L.), vertebral fusion occurs in about the 7th year, proceeding from anterior to posterior (Duffield 1973; Koch 1935); however, epiphyseal fusion in *B. antiquus* did not agree with the schedule for the European bison, with

several other *B. antiquus* bones fusing at an earlier age (Bement and Basmajian 1996).

### Forelimb

A right humerus (UCA 74.33.3) and right metacarpal (UCA 74.33.2) came from the articulated skeleton. A partial left radius (UCA 83.47.1), an isolated find likely representing a different individual, is similarly massive and rugose. The humerus (proximal one-third; Fig. 10) and metacarpal are unrolled but freshly damaged. The radius shows light abrasion from transport and an old spiral fracture just below the proximal end. Light polish and spalling around the point of this break on the posterior face might reflect scavenger activity or, less likely, human tool-use (see Binford 1981 for discussion of factors). The metacarpal (Fig. 11) has an ovoid lump on the anterior aspect proximal to the lateral distal con-

**Fig. 14.** Left metatarsal: anterior (left) and posterior (right) views of *Bison antiquus* from Galleli Pit (UCA 74.33.1).



dyle, possibly a healed local impact injury. A midshaft block was removed from the metacarpal for DNA recovery.

### Hind limb

Hind limb material includes a right femur (UCA 74.33.5) (Fig. 12), two tibiae (left, UCA 74.33.4, and right, UCA 74.33.6) (Fig. 13), and left metatarsal (UCA 74.33.1) (Fig. 14), all well preserved with no evidence of transport and slight damage in recovery. The tibiae were clearly from the same individual, so the left was submitted for conventional radiocarbon dating.

### Morphological comparisons

The crania differ in size but both possess proximally depressed horn cores, directed laterally to differing degrees. These characters and measurements agree with those presented by Skinner and Kaisen (1947) and McDonald (1981) for *Bison antiquus* (Tables 2, 3), though UCG 6125 shows some characters reminiscent of *B. occidentalis*. *B. occidentalis* (including Alaskan type and referred mid-continent specimens) had more upswept and backswept horn cores than did *B. antiquus*. A few Galleli measurements fall slightly outside the range given by Skinner and Kaisen for *B. antiquus* but are within the limits redefined by McDonald (1981). In UCG 4066 basal horn core meas-

urements are near the upper limit documented by Skinner and Kaisen, whereas in UCG 6125 horn core length is near the lower limit, the low measurement 4 (length on lower curve) value reflecting the core's relative straightness. Width of the cranium at auditory openings (measurement 8) for UCG 6125 is at the maximum documented for *B. occidentalis* and is more typical of the broader *B. antiquus* cranium (McDonald 1981).

Postcranial comparative data are compiled from many Late Pleistocene and earliest Holocene samples (site references, Table 4). Galleli postcranial measurements fall within the range for *B. antiquus* as documented by Miller (1971) and McDonald (1981). The 7th cervical vertebra (Fig. 9) is close in size to California specimens assigned by Miller (1971) to the giant *B. latifrons* (Table 5). In four of five measurements of the centrum, the Galleli specimen meets or exceeds maxima for Rancho La Brea *B. antiquus*. In length, it even exceeds Costeau Pit *B. latifrons*, but in the others it falls near the sample minima. The thoracic vertebra is similarly large (Table 6) but comparative data are few. Unfused epiphyses show that large Galleli dimensions are not due to age-dependent remodelling.

The massive Galleli humerus (UCA 74.33.3; Fig. 10), missing its distal two-thirds, cannot be compared with published Rancho La Brea and Costeau measurements. In most respects, it is decidedly larger than latest Pleistocene and

**Table 4.** Comparative samples for postcranial measurements.<sup>a</sup>

Site locality	Age (ka BP)	Taxon	References
Costeau Pit, Calif.	42	<i>Bison latifrons</i>	(Miller 1971)
Chuchi Lake, B.C.	35	<i>Bison</i> sp., cf. <i>B. latifrons</i>	(Harington et al. 1996)
American Falls, Idaho	>32–21	<i>B. latifrons</i>	(Stevens 1978)
Gold Run Creek, Y.T.	32–22	<i>B. crassicornis</i> (= <i>B. priscus</i> , sensu lato)	(Harington and Clulow 1973)
Rancho La Brea, Calif.	30–13	<i>B. latifrons</i> (earlier) and <i>B. antiquus</i> (later)	(Miller 1971)
Lost Chicken Cr., Alaska	>40–7	<i>B. crassicornis</i> (= <i>B. priscus</i> , sensu lato)	(Harington 1980; Porter 1986)
Old Crow locality 11, Y.T.	~ 12	<i>B. priscus</i>	(Cinq-Mars et al. 1991)
U.P. Mammoth site, Wyo.	11.2?	<i>Bison</i> sp.	(Irwin et al. 1962; Wilson 1974b)
Plainview site, Tex.	ca. 10.5	<i>Bison</i> sp.	(Lorrain 1968)
Agate Basin 1, Wyo.	10.7	<i>B. antiquus</i>	(Walker 1982; Zeimens 1982)
Agate Basin 2, Wyo.	10.5	<i>B. antiquus</i>	(Walker 1982; Zeimens 1982)
Jones-Miller site, Colo.	10.3	<i>Bison</i> sp.	(Zeimens 1982)
Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	(Wilson 1983)
Olsen-Chubbuck site, Colo.	10.1	<i>Bison</i> sp.	(Bedord 1974)
Casper site, Wyo.	10	<i>B. antiquus</i>	(Wilson 1974a)
Horner II site, Wyo.	10	<i>B. antiquus</i>	(Todd 1987a)
Hubbell Creek, Man.	10.3–9.5	<i>Bison</i> sp.	(Nielsen et al. 1984)
Hudson-Meng site, Nebr.	9.8	<i>Bison</i> sp.	(Agenbroad 1978)
Milan site, Alta.	9.6	<i>Bison occidentalis</i>	(Shackleton and Hills 1977)
Finley site, Wyo.	9.0?	<i>Bison antiquus</i>	(Bedord 1974; Haspel and Frison 1987)
Horner I site, Wyo.	9	<i>Bison antiquus</i>	(Zeimens 1982)

<sup>a</sup>Data for *B. occidentalis* in this and subsequent tables are from the midcontinent and their relationship to the Alaskan type specimen remains open to question given mtDNA evidence.

**Table 5.** Measurements of 7th cervical vertebrae of *Bison* spp.

Measurement	<i>N</i>	Costeau Pit					Gallelli Pit			Rancho La Brea			
		<i>N</i>	Minimum	Mean	Maximum	<i>S</i>	UCA 74.33.7	<i>N</i>	Minimum	Mean	Maximum	<i>S</i>	
1 AntPost	5	82	84.6	87	2.4	(89.4)	22	69	73.1	76	2.1		
2 GWidth	3	88	94	98	5.3	(88.5)	22	69	74.5	79	3		
3 GHeight	3	68	68.7	69	0.6	(66.5)	21	49	53.5	56	1.5		
4 GWHead	5	50	51.2	53	1.3	46.9	22	35	38.7	49	1.5		
5 APSpine	4	58	61.3	67	4	(55)	20	45	51.7	55	2.8		
6 GLArch						119							
7 GBPrezy						(131)							
8 GBPostz						(105.5) <sup>a</sup>							
9 BrTran						(195)							
10 GHHead						62.9							

**Note:** Measurements: (1) greatest anteroposterior length of centrum; (2) greatest width of centrum; (3) greatest height of centrum; (4) greatest width of head (cranial articular surface); (5) anteroposterior diameter at base of spine; (6) greatest length, arch; (7) greatest breadth across prezygapophyses; (8) greatest breadth across postzygapophyses; (9) breadth across transverse processes; (10) greatest height of head. Measurements 1 to 5 after Miller (1971); 6 to 10 after von den Driesch (1976). *N*, number of measurements; *S*, standard deviation.

<sup>a</sup>Measurement 8 is anomalously large due to zygapophyseal deformity.

early Holocene samples from Bonfire Shelter, Horner II, and Finley (Table 7). The radius (UCA 83.47.1) is much smaller than Costeau Pit, Chuchi Lake, and American Falls male *B. latifrons* but is comparable with female *B. latifrons* from American Falls. It groups with Rancho La Brea *B. antiquus* and is larger than Horner II *B. antiquus* and early Holocene Canadian plains *B. occidentalis* (Table 8). An even more massive bison radius from the U.P. Mammoth site, Wyoming (Irwin et al. 1962; Wilson 1974b) is not directly dated but a mammoth tusk from that site was dated to 11 280 ± 350 BP (I-449; Trautman and Willis 1966).

Metacarpal UCA 74.33.2 (Fig. 11) exceeds all Holocene and some Late Pleistocene samples in breadth (Bedord

1974; Hughes 1978), indicating a male of great anterior mass (Table 9). A temporal trend to shorter metacarpals is weak, so comparably long specimens persisted as late as 7000 years BP. Standard deviations (*S*) of compared samples provide insights into the integrity of the data. For radii, known-sex *S* values tend to be about one-half to three-quarters of those for both sexes combined (Table 8). Metacarpal lengths typically range in *S* between 6.0 and 9.5 mm, including samples where both sexes are clearly present (Table 9). That for Lost Chicken Creek, Alaska, is 11.5 mm, suggesting that the sample is temporally if not taxonomically composite. This agrees with the spread of dates obtained for that site (Harington 1980; Porter 1986), although none were

**Table 6.** Measurements of 5th thoracic vertebra from Gallelli Pit.<sup>a</sup>

	Measurement	UCA 74.33.7
1	Physiological length of centrum (PL)	—
2	Greatest zygapophyseal length of neural arch (GLPa)	(63.7+)
3	Breadth across prezygapophyses (BPacr)	40
4	Breadth across postzygapophyses (BPacd)	39
5	Greatest breadth across transverse processes (BRtr)	(111)
6	Greatest breadth of head (cranial articular surface) (BFcr)	65
7	Greatest breadth of caudal articular surface (BFcd)	(90.2+)
8	Greatest height of cranial articular surface (HFcr)	60.7
9	Greatest height of caudal articular surface (HFcd)	61.2

<sup>a</sup>Measurements after von den Driesch (1976, pp. 72–73); letter codes are those assigned by her. Measurements are in mm.

**Table 7.** Measurements of fossil bison humeri.<sup>a</sup>

Measurement	Sample, specimen	Age (ka)	Sex	N	Minimum	Mean	Maximum	S
HM4 ProxBr	Gallelli, Alta. UCA 74.33.3	11.3	M	1	—	(147)	—	—
	Bonfire 2, Tex.	10.2	(M)–F	3	80.0	85.5	95.6	8.8
	Horner II, Wyo.	10	M	1	—	106.0	—	—
F			10	92.0	97.7	101.0	3.2	
HM9 ProxAP	Finley, Wyo.	9.0?	M–F	6	105	127.3	142	12.8
	Gallelli, Alta.	11.3	M	1	—	165.0	—	—
			M	3	137.0	141.7	145.0	4.2
Horner II, Wyo.	10	F	9	113.0	120.9	127.0	3.9	
		M–F	7	113	131.4	146	11	
HM9a ProxAP	Gallelli, Alta.	11.3	M	1	—	156	—	—
HM12 SagitD	Gallelli, Alta.	11.3	M	1	—	81.3	—	—
			M	2	96.0	96.5	97.0	0.7
	Horner II, Wyo.	10	F	10	74.0	77.9	88.0	4.3
M–F			7	76	86.6	95	7.2	
HM13 ArtBr	Gallelli, Alta.	11.3	M	1	—	103.6	—	—
	Horner II	10	M	3	88.0	91.0	96.0	4.4
			F	12	70.0	77.6	84.0	4.1
Finley, Wyo.	9.0?	M–F	5	76	86.8	97	9.3	

**Note:** HM4, greatest proximal breadth; HM9, greatest depth of proximal end; HM9a (new, this paper), greatest depth of proximal end perpendicular to shaft; HM12, greatest sagittal depth of head; HM13, greatest breadth of articular surface of head. Decimal accuracy varies as to source. Mature individuals selected if tables included all age groups. N, number of measurements; S, standard deviation.

<sup>a</sup>Measurements after Todd (1987b). Measurements are in mm.

on bison metacarpals. The Gallelli specimen falls within the length range for Lost Chicken Creek *B. crassicornis* Richardson, 1852–1854 (= *B. priscus*, sensu lato) metacarpals but is more massive than any in that sample. The high S for the Horner I (Princeton) sample also suggests a composite sample, perhaps comprising latest Pleistocene and early Holocene populations.

Femur UCA 74.33.5 (Fig. 12) is much larger than any in the Horner II sample (Table 10). Head diameter and proximal breadth are within the range of Rancho La Brea *B. antiquus* and close to *B. latifrons*. The tibia (Fig. 13) is much larger compared with *B. crassicornis* (Gold Run Creek, Lost Chicken Creek), latest Pleistocene and Holocene *B. antiquus*, and midcontinent specimens referred to *B. occidentalis* (Table 11). Measurements place below, with, or above those of *B. latifrons* from American Falls, Chuchi Lake, and Costeau Pit, and at the middle to the top of the range for Rancho La Brea *B. antiquus*. Metatarsal

length (Table 12; Fig. 14) is greater than *B. crassicornis* from Gold Run Creek and Lost Chicken Creek and in mid-range for the Alaskan sample described by Skinner and Kaisen (1947). It falls in mid-range for Rancho La Brea *B. antiquus* but near the maxima for latest Pleistocene and Holocene *B. antiquus* and midcontinent *B. occidentalis*. A female BCF bison metatarsal from the Aquitaine Pit, Calgary, Alberta, associated with a cranium dated to 10 200 years BP (Table 1; Wilson 1983), is the same length as the Gallelli Pit metatarsal but is more slender. In breadth and anterior–posterior diameter, the Gallelli metatarsal is larger than *B. crassicornis* and latest Pleistocene to Holocene samples, being closest to large Rancho La Brea *B. antiquus*. Compared with American Falls and Costeau Pit *B. latifrons*, it is in mid-range or near the top in anterior–posterior diameter, but below the range in minimum transverse diameter. Rotational lengths are only estimated for these elements because McDonald (1981) did not clearly de-

**Table 8.** Measurements of fossil bison radii.<sup>a</sup>

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S
RD3 ProxTr	Costeau Pit, Calif.	42	<i>Bison latifrons</i>	M-F	3	(120)	123	125	2.7
	Chuchi Lake, B.C.	35	<i>Bison sp.</i> , cf. <i>B. latifrons</i>	M	1		124		
	American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	9	131	136.1	144	3.9
				F	6	109	114.2	124	5.3
	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M-F	3	86.7	95.9	111	13.5
	Lost Chicken, Alaska	>40–7	<i>B. crassicornis</i>	M-F	1		121.6		
	U.P. Mammoth site, Wyo.	11.2?	<i>Bison sp.</i>	M	1		129.2		
	Rancho La Brea, Calif.	30–13	<i>B. antiquus</i>	M-F	13	100	107.7	122	5.8
	Gallelli Pit, Alta.	11.3–10.1	<i>B. antiquus</i>	M	1		112.3		
	Bonfire 2, Tex.	10.2	<i>Bison sp.</i>	M-F	6	91	103.3	124	
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	1	98	103.7	111	4.1
				F	718	83	88.5	93	2.8
	Hudson-Meng, Nebr.	9.8	<i>Bison sp.</i>	M-F	?		87.3		
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	36	85	102.5	113	7.6
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M-F	6	88	102.3	109	7.5
RD4 ProxAr	American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	9	118	120.4	124	2.0
	Gallelli Pit, Alta.	11.3 or 10.1	<i>B. antiquus</i>	M	1		110.8		
	Jones-Miller, Colo.	10.3	<i>Bison sp.</i>	M	1	100.9	105.5	111.7	3.4
				F	918	84.3	90.4	97.7	3.1
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	1	94	98.7	104	3.2
				F	719	82	85	89	2.4
Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	34	80	96.7	107	6.3	
RD9 ProxAP	Chuchi Lake, B.C.	35	<i>Bison sp.</i> , cf. <i>B. latifrons</i>	M	1		63.2		
	American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	9	65	69.1	73	2.7
				F	6	50	56.5	61	4.5
	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M-F	4	42.3	50	55.4	5.9
	Lost Chicken, Alaska	>40–7	<i>B. crassicornis</i>	M?	1		65.7		
	Gallelli Pit, Alta.	11.3 or 10.1	<i>B. antiquus</i>	M	1		66.4		
	Jones-Miller, Colo.	10.3	<i>Bison sp.</i>	M	1	54	57.9	63.1	2.8
				F	916	41.6	50.2	56.7	2.4
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	18	53	57	61	2.8
				F	19	45	48.7	52	2.3
	Hudson-Meng, Nebr.	9.8	<i>Bison sp.</i>	M-F	?		46.2		
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	38	36	54.9	65	5.6

**Note:** RD3, greatest proximal transverse diameter; RD4, transverse breadth of proximal articular facet; RD9, greatest proximal anteroposterior diameter. Decimal accuracy varies as to source. Mature individuals selected if tables included all age groups. *N*, number of measurements; *S*, standard deviation.

<sup>a</sup>Measurements (after Todd 1987b). Measurements are in mm.

fine “approximate rotational length” with specific landmarks; hence it is not readily replicable by others. From his diagrams, it appears that the Gallelli Pit tibia rotational length is proportionally longer in relation to the femur (~425 and 428 mm, respectively) than is typical for *B. antiquus*. This gives a summed “limb length” of ~1130 mm for the three hind limb elements, longer than the *B. antiquus* mean (1114.9 mm) but much shorter than that for *B. latifrons* (1243.4 mm; McDonald 1981).

## DNA analysis

A midshaft block from the Gallelli metacarpal was successfully sampled at the Henry Wellcome Ancient Biomolecules Centre, University of Oxford, for mitochondrial DNA (mtDNA). It was included in an mtDNA analysis of 405 bison remains ranging in age from >60 ka BP through modern, using analytical techniques developed for ancient DNA

to sequence a 685-base pair (bp) fragment of the mitochondrial control region (Shapiro 2003; Shapiro et al. 2004 and online supplement; Drummond et al. 2005). Stringent laboratory protocols included replication at a DNA facility in Copenhagen, Denmark, minimizing opportunities for cross-contamination. Bayesian and Maximum Likelihood analyses were used to reconstruct the recent phylogenetic and demographic history of bison in North America and eastern Asia. They demonstrated extensive genetic diversity in Late Pleistocene bison populations, which can be roughly subdivided into four major and several minor clades. Few of the deep nodes in the tree were strongly supported, suggesting that all bison sequences are very closely related and not indicative of multiple, independent species. The majority of bison diversity (3 of 4 clades) is not represented in modern bison; only the surviving clade (Clade 1, Fig. 15) has strong statistical support for monophyly, indicating a recent shared common ancestor. This clade consists only of bison <11.5 ka BP

**Table 9.** Measurements of fossil bison metacarpals.<sup>a</sup>

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S	
MC1 length	Alaska	Pleistocene	<i>Bison</i> spp.	M	21	191	218.7	249	19	
				F	20	186	213.6	247	16	
	American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	15	239	248.6	264	7.25	
				F	8	234	246.3	258	8.05	
	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	2	232	232.5	233	0.7	
	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	23	203	217.1	228	7.1	
	Rancho La Brea, Calif.	30–13	<i>?B. latifrons</i>	M–F	7		228.3		5.4	
				<i>B. antiquus</i>	M–F	69		220.5		6.8
				combined	M–F	76	205	221.2	235	7
	Lost Chicken, Alaska	>40–7	<i>B. crassicornis</i>	M–F	7	202	218.4	235	12	
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M–F	6	217	223.9	230		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		226			
	Blackwater Draw, N.Mex.	11.2	<i>B. antiquus</i>	M	1		(224.–5)			
	Plainview, Tex.	~10.5	<i>B. antiquus</i>	M–F	16	200	221.5	238	—	
	Agate Basin 1, Wyo.	10.7	<i>B. antiquus</i>	M–F	7	205	216.3	230	8.9	
	Agate Basin 2, Wyo.	10.5	<i>B. antiquus</i>	M–F	56	196	216	235	8.9	
	Bonfire 2, Tex.	10.3	<i>Bison</i> sp.	M–F	10	208	216.9	232	—	
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M–F	36	201	215.7	229	8.9	
	Casper, Wyo.	10	<i>B. antiquus</i>	M–F	58	200	213.4	224	6.5	
	Horner II, Wyo.	10	<i>B. antiquus</i>	M–F	60	199	214.3	228	6.5	
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		209.9			
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	12	201	213	230	8.3	
	Finley, Wyo.	?9.0	<i>B. antiquus</i>	M–F	67	201	215.7	230	7.1	
	Horner I, Wyo.	9	<i>Bison</i> sp.	M–F	24	195	211.2	240	11	
	MC2 ProxBr	Alaska	Pleistocene	<i>Bison</i> spp.	M	21	72.5	85.9	97.5	8.4
					F	20	62.2	70.3	78.3	4.7
		American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	16	92	99.4	106	4.4
					F	8	84	86.6	88	1.3
		Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	25	65.7	77.6	83.2	6.5
		Lost Chicken, Alaska	>40–7	<i>B. crassicornis</i>	M–F	6	67.3	77.5	89	—
		Rancho La Brea, Calif.	30–13	<i>?B. latifrons</i>	M–F	7		86		4.5
					<i>B. antiquus</i>	M–F	69		76.1	
					combined	M–F	76	65	77	94
Old Crow Loc. 11, Y.T.		~12	<i>B. priscus</i>	M–F	6	67.7	77.4	84.8		
Gallelli Pit, Alta.		11.3	<i>B. antiquus</i>	M	1		92.9+			
Blackwater Draw, N.Mex		11.2	<i>B. antiquus</i>	M	1		83.6			
Plainview, Tex.		?10.5	<i>B. antiquus</i>	M–F	16	67	78.5	97	—	
Agate Basin 1, Wyo.		10.7	<i>B. antiquus</i>	M–F	11	63	74.8	86	—	
Agate Basin 2, Wyo.		10.5	<i>B. antiquus</i>	M–F	54	54	75.5	92	—	
Bonfire 2, Tex.		10.3	<i>Bison</i> sp.	M–F	7	67	74.2	88	—	
Olsen-Chubbuck, Colo.		10.1	M–F	M–F	33	64	73.3	85	6	
Casper, Wyo.		10	<i>B. antiquus</i>	M–F	64	65	71.7	85	4.3	
Horner II, Wyo.		10	<i>B. antiquus</i>	M–F	57	66	76	89	—	
Hudson-Meng, Nebr.		9.8	<i>Bison</i> sp.	M–F	?		66.3			
Finley, Wyo.		9.0?	<i>B. antiquus</i>	M–F	59	64	75.2	88	6.4	
Horner I, Wyo.		9	<i>Bison</i> sp.	M–F	17	58	71.4	84	—	
Milan, Alta.		9.6	<i>B. occidentalis</i>	M–F	14	67.9	78.4	86	4.4	
MC3 MidsBr		Alaska	Pleistocene	<i>Bison</i> spp.	M	21	48.2	56.4	67.2	4.7
					F	20	35.7	40.9	45.7	3.3
		Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	25	35.3	50.4	59.4	6.8
		Lost Chicken, Alaska	>40–7	<i>B. crassicornis</i>	M–F	8	38.9	48.2	62.8	8.8
		Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M–F	6	38.9	47.3	57.9	
		Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		62.9		
		Blackwater Draw, N.Mex.	11.2	<i>B. antiquus</i>	M	3		54.3		
		Agate Basin 1, Wyo.	10.7	<i>B. antiquus</i>	M–F	7	42	48.1	54	—
		Agate Basin 2, Wyo.	10.5	<i>B. antiquus</i>	M–F	36	38	47.3	58	—

Table 9 (continued).

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M-F	35	37	44	56	5.6
	Casper, Wyo.	10	<i>B. antiquus</i>	M-F	65	36	43	55	3.9
	Horner II	10	<i>B. antiquus</i>	M-F	52	36	45.4	52	—
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M-F	?		40.5		
	Engigstciak, Y.T.	9.77	<i>Bison</i> sp.	M-F	1		(52.8)		
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M-F	19	40.3	48.7	55.8	3.4
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	71	32	46.3	54	5.2
	Horner I, Wyo.	9	<i>Bison</i> sp.	M-F	19	35	43.4	53	—
MC4 DistBr	Alaska	Pleistocene	<i>Bison</i> spp.	M	21	76.2	88.5	98.2	7.2
				F	20	63.9	73.8	84	5
	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M-F	3	96	100	106	5.3
	Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	24	68.3	81	89.7	7.2
	Rancho La Brea, Calif.	30-13	? <i>B. latifrons</i>	M-F	7		88.6		4.7
			<i>B. antiquus</i>	M-F	69		78.1		3.6
			combined	M-F	76	70	79	94	4.8
	Lost Chicken, Alaska	>40-7	<i>B. crassicornis</i>	M-F	8	69.6	78.6	90.9	8
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M-F	6	73.9	81.3	94.3	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		93.5		
	Blackwater Draw, N.Mex.	11.2	<i>B. antiquus</i>	M	1		84.6		
	Plainview, Tex.	10.5?	<i>B. antiquus</i>	M-F	15	68	82.8	96	—
	Agate Basin 1, Wyo.	10.7	<i>B. antiquus</i>	M-F	11	71	82.2	96	—
	Agate Basin 2, Wyo.	10.5	<i>B. antiquus</i>	M-F	65	69	78.17	92	—
	Bonfire 2, Tex.	10.3	<i>Bison</i> sp.	M-F	8	71	78.4	88	—
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M-F	34	68	76.3	90	5.6
	Casper, Wyo.	10	<i>B. antiquus</i>	M-F	58	70	75.5	91	4.9
	Horner II, Wyo.	10	<i>B. antiquus</i>	M-F	59	67	78.6	88	—
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M-F	?		71.3		
	Engigstciak, Y.T.	9.77	<i>Bison</i> sp.	M-F	1		(85.5)		
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M-F	11	75.5	79.6	85.5	2.6
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	60	66	78.8	88	6.3
	Horner I, Wyo.	9	<i>Bison</i> sp.	M-F	19	64	76.7	89	—
MC5 APMids	Alaska	Pleistocene	<i>Bison</i> spp.	M	21	30.4	35.8	40.8	3.1
	Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	25	27.2	32.2	35.3	2.9
	Lost Chicken, Alaska	>40-7	<i>B. crassicornis</i>	M-F	8	26.7	30.5	35.6	3.6
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M-F	6	28	31.6	36.3	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		36.7		
	Blackwater Draw, N.Mex.	11.2	<i>B. antiquus</i>	M	2	35	35.1	35.1	0.1
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M-F	35	26	29.9	35	2.5
	Casper, Wyo.	10	<i>B. antiquus</i>	M-F	64	26	29.6	35	2
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M-F	?		28		
	Engigstciak, Y.T.	9.77	<i>Bison</i> sp.	M-F	1		(28.5)		
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M-F	16	25	29	31.8	1.9
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	72	24	31	37	3
MC7 ProxAP	American Falls, Idaho	>32-21	<i>B. latifrons</i>	M	15	50	56	62	3.4
				F	8	45	49.1	52	2.1
	Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	23	37.7	45.2	53	3.9
	Rancho La Brea, Calif.	30-13	? <i>B. latifrons</i>	M-F	7		49		4
			<i>B. antiquus</i>	M-F	69		44.6		2.4
			combined	M-F	76	39	45	57	2.9
	Lost Chicken, Alaska	>40-7	<i>B. crassicornis</i>	M-F	6	39	44.9	51	4.6
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M-F	6	41.6	46.5	50.5	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		53.9		
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M-F	34	40	44.2	51	3.2
	Casper, Wyo.	10	<i>B. antiquus</i>	M-F	61	38	42.8	51	2.8
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M-F	?		39.7		
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	54	37	46	52	3.9

**Table 9** (concluded).

Measurement	Sample	Age (ka)	Taxon	Sex	<i>N</i>	Minimum	Mean	Maximum	<i>S</i>
MC8 DistAP	Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	13	34.4	41.3	45.3	2.4
	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	21	36.4	42	46.7	3.1
	Rancho La Brea, Calif.	30–13	<i>?B. latifrons</i>	M–F	7		46.9		1.4
			<i>B. antiquus</i>	M–F	69		41.7		5.4
			<i>B. antiquus</i>	M–F	69		41.7		5.4
			Combined	M–F	76	37	42.7	49	2.3
			<i>B. crassicornis</i>	M–F	7	36.3	41.8	46.5	3.6
	Lost Chicken, Alaska	>40–7	<i>B. priscus</i>	M–F	6	40.5	43.3	47.5	
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M–F	6				
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		48+		
	Blackwater Draw, N.Mex.	11.2	<i>B. antiquus</i>	M	1		(44.5)		
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M–F	37	37	40.9	49	2.7
	Casper, Wyo.	10	<i>B. antiquus</i>	M–F	59	34	39.7	46	2.1
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		37.1		
	Engigstciak, Y.T.	9.77	<i>Bison</i> sp.	M–F	1		43.9		
MC9 MinAP	Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	9	40.2	41.9	43.5	1.1
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	58	36	41.1	46	2.7
	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	3	34	35.7	38	2.1
		>32–21	<i>B. latifrons</i>	M	19	33	36	39	1.9
	Rancho La Brea, Calif.	30–13	<i>?B. latifrons</i>	M–F	7		32	33	1.2
			<i>B. antiquus</i>	M–F	69		33.1		1.9
			combined	M–F	76	27	29.9	36	1.1
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		30.2		1.6
	Blackwater Draw, N.Mex.	11.2	<i>B. antiquus</i>	M	1		34.6		
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M–F	36	25	28	33	1.9
	Casper, Wyo.	10	<i>B. antiquus</i>	M–F	63	23	27.7	32	1.7
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		26.6		
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	58	24	28.6	32	2
	Hawken, Wyo.	6.5	<i>B. occidentalis</i>	M–F	28	23	26.8	32	2.3
	MC10 MinTra	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	2	61	61	61
American Falls, Idaho		>32–21	<i>B. latifrons</i>	M	19	61	66.4	73	3.4
				F	9	48	52.1	58	3.1
Rancho La Brea, Calif.		30–13	<i>?B. latifrons</i>	M–F	7		54		3
			<i>B. antiquus</i>	M–F	69		46.9		2.7
			combined	M–F	76	38	47.6	59	2.9
Gallelli Pit, Alta.		11.3	<i>B. antiquus</i>	M	1		62.6		
Blackwater Draw, N.Mex.		11.2	<i>B. antiquus</i>	M	2	52.9	53.3	53.6	0.5
Olsen-Chubbuck, N.Mex.		10.1	<i>Bison</i> sp.	M–F	35	37	43.6	56	5.6
Casper, Wyo.		10	<i>B. antiquus</i>	M–F	64	36	43	55	3.8
Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		40			
Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	52	36	45.9	54	5.2	

**Note:** MC1, overall length; MC2, transverse diameter, proximal end; MC3, transverse diameter at midshaft; MC4, transverse diameter, distal end; MC5, anteroposterior diameter, midshaft; MC7, anteroposterior diameter, proximal end; MC8, anteroposterior diameter, distal end; MC9, minimum anteroposterior diameter of shaft; MC10, minimum transverse diameter of shaft. Decimal accuracy varies as to source. Mature individuals selected if tables included all age groups. *N*, number of measurements; *S*, standard deviation.

<sup>a</sup>Measurements (after Bedord 1974). Measurements are in mm.

and includes all sampled Holocene bison from south of Beringia, including all modern and historic specimens of plains bison (*B. b. bison* [L.]) and pre-admixture wood bison (*B. b. athabasca* Rhoads, 1897), except for a single Holocene Clade 4 bison skull from Banff National Park. Placement of *B. b. athabasca* in Clade 1, including tissue specimens from individuals born before the 1925–1928 introduction of plains bison, negates suggestions that wood bi-

son are linked instead to a Beringian origin and confirms its southern origin (see summary of views in McDonald and Lammers 2002). The level of genetic diversity in Clade 1 suggests a much older genetic history south of the ice sheets (Shapiro et al. 2004 and online supplement). The Gallelli specimen belongs with Clade 1, indicating a close relationship between *B. antiquus* and *B. bison*. This result was confirmed by independent extraction and amplification of

**Table 10.** Measurements of fossil bison femora.<sup>a</sup>

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S
FM1 Length	Gold Run Cr., Y.T.	32–22	<i>Bison crassicornis</i>	M–F	1		480		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		489++		
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	6	441	448.3	476	13.7
FM2 LatLen	Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	1		428		
				M	1		482++		
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	7	435	444	468	13
				F	2	403	407	411	5.7
FM3 MedLen	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		467		
	Bonfire 2, Tex.	10.3	<i>Bison sp.</i>	M–F	2	314	346.3	379	45.6
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	11	408	420.8	440	11.6
F				11	369	383.8	395	9.2	
FM5 LMedC	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		(80)		
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	5	67	68.6	71	1.5
F				6	60	62.7	65	1.8	
M				6	71	73.2	76	2.2	
FM6 LLatC	Horner II, Wyo.	10	<i>B. antiquus</i>	M	6	62	65.8	68	2.1
				F	6	62	65.8	68	2.1
				M	6	71	73.2	76	2.2
FM7 ProxBr	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	2	172	173.5	(175)	2.1
	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	F?	1		134.3		
	Rancho La Brea, Calif.	30–13	<i>B. antiquus</i>	M–F	11	155	163	184	8.6
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		168++		
	Bonfire 2, Tex.	10.3	<i>Bison sp.</i>	M–F	3	146	151.7	156	5.1
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	8	145	158	168	6.7
				F	4	128	134.5	142	6.2
FM8 DepHd	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	4	66	67.5	69	1.3
	Rancho La Brea, Calif.	30–13	<i>B. antiquus</i>	M–F	12	61	63.5	69	2.5
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		66.4		
	Bonfire 2, Tex.	10.3	<i>Bison sp.</i>	M–F	4	53.2	57.3	61.2	—
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	13	57	58.6	61	1.5
F				13	52	54.2	57	1.5	
FM10 MinSBr	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	3	42.3	43.8	44.8	1.3
	Lost Chicken, Alaska	>40–7	<i>B. crassicornis</i>	M–F	1		52.4		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		57.2		
	Bonfire 2, Tex.	10.3	<i>Bison sp.</i>	M–F	1		44.2		
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	11	44	48.8	52	2.3
				F	6	40	43.2	46	2.2
FM12 DistBr	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	1		117.2		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		136		
	Bonfire 2, Tex.	10.3	<i>Bison sp.</i>	M–F	6	86	98.7	115	—
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	4	116	118.3	123	3.3
				F	2	106	107.5	109	2.1
FM17 MinAP	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	3	42.6	45.7	49.1	3.3
	Lost Chicken, Alaska	>40–7	<i>B. crassicornis</i>	M–F	1		45.8		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		58.8		
	Bonfire 2, Tex.	10.3	<i>Bison sp.</i>	M–F	2	41.4	41.7	42	0.4
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	10	45	49.6	53	2.3
				F	5	42	44.6	49	3
FM18 DistDep	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	1		139.4		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		144+		
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	7	140	146.4	155	5.6
F				5	130	134	139	3.2	

**Note:** FM1, greatest overall length; FM2, length, lateral, from major trochanter to lateral condyle; FM3, length, medial, from head to medial condyle; FM5, greatest length of medial condyle; FM6, greatest length of lateral condyle; FM7, greatest breadth of proximal end; FM8, greatest anteroposterior diameter of head; FM10, minimum transverse diameter of shaft (= transverse diameter at midshaft); FM12, greatest breadth of distal end; FM17, minimum anteroposterior diameter at location of FM10 (= anteroposterior diameter at midshaft). Decimal accuracy varies as to source. Mature individuals selected if tables included all age groups. N, number of measurements; S, standard deviation.

<sup>a</sup>Measurements (after Todd 1987b). Measurements are in mm.

**Table 11.** Measurements of fossil bison tibiae.<sup>a</sup>

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S	
TA1 Length	Gold Run Cr., Y.T.	32–22	<i>Bison crassicornis</i>	M–F	1		452			
	Lost Chicken Cr., Alaska	>40–7	<i>B. crassicornis</i>	M–F	1		447.6			
TA2 MedL	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M–F	5	413	424.1	437		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		465			
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	8	418	431.1	443	9.6	
				F	9	370	385.8	399	12	
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	2	399	414.5	430	22	
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	11	395	436.3	453	23	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		449			
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	3	404	416	424	11	
				F	8	354	370.4	382	10	
		Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	6	380	421.8	437	23
TA4 ProxBr	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	1		152			
	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	1		126.5			
	Rancho La Brea, Calif.	30–13	<i>B. antiquus</i>	M–F	20	121	132.4	151	7.2	
	Lost Chicken Cr., Alaska	>40–7	<i>B. crassicornis</i>	M–F	1		125.0+			
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M–F	5	110	122.8	134		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		141.6			
	Bonfire 2, Tex.	10.3	<i>Bison sp.</i>	M–F	1		117			
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	7	108	125.6	134	8.2	
				F	9	103	110.3	121	5.9	
		Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	1		122.5		
TA6 MinBr	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	17	102	120.9	134	10	
	American Falls, Idaho	>32–21	<i>B. latifrons</i>	M–F	2	46	50	54	5.7	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		62.5			
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	5	52	53	54	1	
				F	7	41	44.1	46	1.8	
TA7 DistBr	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	18	43	50.1	56	4.1	
	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	2	(86)	90	94	5.7	
	Chuchi Lake, B.C.	35	<i>Bison sp., cf. B. latifrons</i>	M	1		93.8			
	Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	2	67	74.5	81.9	11	
	Rancho La Brea, Calif.	30–13	<i>B. antiquus</i>	M–F	22	76	82.3	93	4	
	Lost Chicken Cr., Alaska	>40–7	<i>B. crassicornis</i>	M–F	3	73.1	80.6	85.7	6.6	
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M–F	6	72	76.9	82.5		
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		89.4			
	Bonfire 2, Tex.	10.3	<i>Bison sp.</i>	M–F	7	70	74.9	85.2	—	
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	8	77	79.4	81	1.4	
TA9 MinDep				F	9	69	71.2	74	1.6	
	Engigstciak, Y.T.	9.87	<i>Bison sp.</i>	M–F	1		(75.8)			
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	3	75	77	79	2	
	Finley, Wyo.	9	<i>B. antiquus</i>	M–F	15	63	76.7	85	6.9	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		45.6			
	Horner II, Wyo.	10	<i>B. antiquus</i>	M	5	39	40.2	41	1.1	
				F	7	34	35.7	37	1.1	
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	18	31	37.3	41	3.2	
	TA10 DistDep	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	1		66		
		Chuchi Lake, B.C.	35	<i>B. sp., cf. B. latifrons</i>	M	1		71.2		
Gold Run Cr., Y.T.		32–22	<i>B. crassicornis</i>	M–F	1		56.5			
Rancho La Brea, Calif.		30–13	<i>B. antiquus</i>	M–F	21	59	61.9	69	2.5	
Lost Chicken Cr., Alaska		>40–7	<i>B. crassicornis</i>	M–F	3	58.2	62.6	68.3	5.2	
Old Crow Loc. 11, Y.T.		~12	<i>B. priscus</i>	M–F	6	54	59.3	62.6		
Gallelli Pit, Alta.		11.3	<i>B. antiquus</i>	M	1		69.2			

**Table 11** (concluded).

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S
TA15 PrxDep	Horner II, Wyo.	10	<i>B. antiquus</i>	M	8	58	59.5	61	0.9
				F	9	48	52.9	56	2.3
	Engigstciak, Y.T.	9.87	<i>Bison</i> sp.	M-F	1		55.3		
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	15	46	55.4	65	5.2
	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M-F	1		145		
	Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	1		126.4		
	Rancho La Brea, Calif.	30-13	<i>B. antiquus</i>	M-F	20	117	126.5	143	6.3
	Lost Chicken Cr., Alaska	>40-7	<i>B. crassicornis</i>	M-F	1		116.5		
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M-F	5	105	115.2	123	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		(125)		
TA20 MidSBr	Horner II, Wyo.	10	<i>B. antiquus</i>	M	7	108	109.9	112	1.8
				F	6	84	93	98	5
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M-F	2	123	124.5	127	2.8
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	15	91	109.5	118	9.3
	Chuchi Lake, B.C.	35	<i>Bison</i> sp., cf. <i>B. latifrons</i>	M	1		62.4		
	Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	2	45.9	50.1	54.2	5.9
	Lost Chicken Cr., Alaska	>40-7	<i>B. crassicornis</i>	M-F	2	47.3	52.9	58.4	7.8
	Old Crow Loc. 11, Y.T.	~12	<i>B. priscus</i>	M-F	6	45.4	51.2	58.6	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		66.4		
	Engigstciak Y.T.	9.87	<i>Bison</i> sp.	M-F	1		(55)		
TA21 MidSDp	Chuchi Lake, B.C.	35	<i>Bison</i> sp., cf. <i>B. latifrons</i>	M	1		48.4		
	Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	2	39.5	42.7	45.8	4.5
	Lost Chicken Cr., Alaska	>40-7	<i>B. crassicornis</i>	M-F	2	39.2	44.2	49.1	7
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		56		

**Note:** TA1, greatest length; TA2, medial length; TA4, greatest breadth, proximal end; TA6 minimum breadth of diaphysis; TA7, greatest distal breadth; TA9, minimum depth (anterior-posterior) of diaphysis; TA10, greatest depth of distal end; TA15, depth of proximal end; (not after Todd) TA20, breadth at midlength of shaft; TA21, depth at midlength of shaft. Decimal accuracy varies as to source. Mature individuals selected if tables included all age groups. N, number of measurements; S, standard deviation.

<sup>a</sup>Measurements (after Todd 1987b). Measurements are in mm.

mtDNA from the Gallelli specimen using a second sample sent to Oxford more than two years after the original sequence was produced.

The demographic analyses suggest that all North American and Siberian bison shared a common maternal ancestor some 160 000 years ago (Shapiro et al. 2004). While the genetic evidence does not support the co-existence of reproductively isolated bison species in Beringia (at least in the Late Pleistocene), the patterns of mtDNA diversity suggest that formation and coalescence of Laurentide and Cordilleran ice sheets did serve as a barrier to gene flow between bison populations isolated to the north in Beringia and to the south in the midcontinent. A severe population bottleneck around the end of the Pleistocene to early Holocene is documented by a dramatic reduction in genetic diversity across the range of bison in Asia and North America, followed by an increase in population size throughout the Holocene (Drummond et al. 2005).

DNA does not survive well in non-permafrost environments, and this prevented a comprehensive analysis of Late Pleistocene bison genetic diversity in North America south of Beringia. However, while the number and geographic range of specimens from which mtDNA was successfully characterized was small, it is still feasible to reconstruct pat-

terns of bison dispersal into newly deglaciated habitat following retreat of the Laurentide and Cordilleran ice sheets. The distribution of mitochondrial haplotypes among bison with radiocarbon dates older than the LGM suggests that there was no restriction to gene flow between Beringia and the North American midcontinent at this time (Fig. 15). However, when considering only bison with radiocarbon dates younger than 13.0 <sup>14</sup>C ka BP, a clear genetic distinction is observed between bison originating from the north and from the south. Nearly all bison remains found fully south of the ice sheets fall into Clade 1 in Fig. 15 and share a common ancestor around 13 000 years ago. This is consistent with the timing of the ice barrier, suggesting that the appearance of Clade 1 bison in the region of the ice-free corridor resulted from post-LGM northward dispersal of bison that had been isolated south of the ice sheets during the LGM.

While mtDNA evidence indicates northward movement of Clade 1 following initial retreat of the ice sheets, none of the previously extensive mitochondrial diversity in Beringia is observed farther south than northeastern British Columbia, except for one late Holocene Banff National Park specimen (Clade 4, Fig. 15; Shapiro et al. 2004). The small group of Clade 4 finds suggests a minor southward movement with

**Table 12.** Measurements of fossil bison metatarsals.<sup>a</sup>

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S	
MT1 Length	Alaska	Pleistocene	<i>Bison</i> spp.	M	13	236	271.3	304	23	
	American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	16	290	303.1	314	6.3	
				F	2	287		287		
		Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	1		275		
		Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	11	255.8	264.1	277	6.6
		Rancho La Brea, Calif.	30–13	? <i>B. latifrons</i>	M–F	5		271.5		6.3
				<i>B. antiquus</i>	M–F	59		271.4		6.8
				combined	M–F	64	258	271.5	287	6.7
		Lost Chicken Cr., Alaska	>40–7	<i>B. crassicornis</i>	M–F	3	268.2	273.3	277	4.5
		Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		279		
		Plainview, Tex.	10.5?	<i>B. antiquus</i>	M–F	10	244	264	280	—
		Agate Basin 1, Wyo.	10.7	<i>B. antiquus</i>	M–F	2	259	259.5	260	0.7
		Agate Basin 2, Wyo.	10.5	<i>B. antiquus</i>	M–F	35	242	264.7	283	—
		Bonfire 2, Tex.	10.3	<i>Bison</i> sp.	M–F	2	(260)	263.5	267	4.9
		Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	F	1		279.5		
		Olsen-Chubbuck, Tex.	10.1	<i>Bison</i> sp.	M–F	25	247	265.2	280	9.2
		Casper, Wyo.	10	<i>B. antiquus</i>	M–F	43	242	261.2	276	7.9
		Horner II, Wyo.	10	<i>B. antiquus</i>	M–F	44	252	264.4	284	—
		Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		257.8		
		Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	3	252.8	262	269	8.2
		Finley, Wyo.	9	<i>B. antiquus</i>	M–F	41	253	268.8	284	7
		Horner I, Wyo.	9	<i>Bison</i> sp.	M–F	1		249		
	MT2 ProxBr	Alaska	Pleistocene	<i>Bison</i> spp.	M	13	60	66.8	73.2	5.1
		Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	3	72	72.3	73	0.6
		American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	17	72	77.4	82	3.3
					F	4	61	63.5	66	2.4
			Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	12	48	57.6	68.9
		Rancho La Brea, Calif.	30–13	? <i>B. latifrons</i>	M–F	5		65.2		2.7
				<i>B. antiquus</i>	M–F	59		60.1		2.8
				combined	M–F	64	55	60.6	69	3.2
		Lost Chicken Cr., Alaska	>40–7	<i>B. crassicornis</i>	M–F	4	61.7	62.7	64.4	1.2
		Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		72.7		
		Plainview, Tex.	10.5?	<i>B. antiquus</i>	M–F	8	55	61	66	—
		Agate Basin 1, Wyo.	10.7	<i>B. antiquus</i>	M–F	5	53	57	60	—
		Agate Basin 2, Wyo.	10.5	<i>B. antiquus</i>	M–F	46	46	58.2	71	—
		Bonfire 2, Tex.	10.3	<i>Bison</i> sp.	M–F	2	(53)	56.3	59.5	4.6
		Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	F	1		56.5		
		Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M–F	20	51	58.7	65	4.4
		Casper, Wyo.	10	<i>B. antiquus</i>	M–F	45	52	57.2	67	3.8
		Horner II, Wyo.	10	<i>B. antiquus</i>	M–F	50	50	59.2	68	—
		Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		53.2		
		Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	8	51.4	57.7	61	3.6
		Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	51	52	60.2	67	4.1
		Horner I, Wyo.	9	<i>Bison</i> sp.	M–F	3	49	53.7	57	—
MT3 MidBr		Alaska	Pleistocene	<i>Bison</i> spp.	M	13	38	43.6	50	4
		Gold Run Cr., Y.T.	32–22	<i>B. crassicornis</i>	M–F	13	30.9	37.2	44.5	4.7
		Lost Chicken Cr., Alaska	>40–7	<i>B. crassicornis</i>	M–F	4	39.1	39.8	41.2	1
		Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		46.6		
		Agate Basin 1	10.7	<i>B. antiquus</i>	M–F	3	37	37.7	39	1.1
	Agate Basin 2	10.5	<i>B. antiquus</i>	M–F	30	32	36.5	46	—	
	Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	F	1		38.2			
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M–F	25	30	37	42	4.4	
	Casper, Wyo.	10	<i>B. antiquus</i>	M–F	43	31	35.2	41	3	
	Horner II, Wyo.	10	<i>B. antiquus</i>	M–F	40	28	36.8	43	—	
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		33.7			

Table 12 (continued).

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S	
MT4 DistBr	Milan, Alta.	9.6	<i>B. occidentalis</i>	M-F	11	29.9	36.9	43.8	3.9	
	Finley, Wyo.	9	<i>B. antiquus</i>	M-F	60	32	38.7	47	3.4	
	Horner I, Wyo.	9	<i>Bison</i> sp.	M-F	1		33			
	Alaska	Pleistocene	<i>Bison</i> spp.	M	13	70.5	77.5	85.2	5.2	
	Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	10	62.2	69.1	76.1	5.1	
	Rancho La Brea, Calif.	30-13	<i>?B. latifrons</i>	M-F	5		79.7		3.7	
			<i>B. antiquus</i>	M-F	59		72.3		2.8	
	Lost Chicken Cr., Alaska	>40-7	combined	M-F	64	67	73	83	3.7	
			<i>B. crassicornis</i>	M-F	4	71.7	74.8	76.8	2.3	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		82.5			
	Plainview, Tex.	10.5?	<i>B. antiquus</i>	M-F	7	67	72	77	—	
	Agate Basin 1, Wyo.	10.7	<i>B. antiquus</i>	M-F	8	66	70.6	74	—	
	Agate Basin 2, Wyo.	10.5	<i>B. antiquus</i>	M-F	68	54	69.9	81	—	
	Bonfire 2, Tex.	10.3	<i>Bison</i> sp.	M-F	3	66	70.5	74	4.1	
	Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	F	1		74			
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M-F	25	61	70.8	77	4.6	
	Casper, Wyo.	10	<i>B. antiquus</i>	M-F	47	63	68.5	79	4.1	
	Horner II, Wyo.	10	<i>B. antiquus</i>	M-F	48	60	70	77	—	
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M-F	?		65.6			
Milan, Alta.	9.6	<i>B. occidentalis</i>	M-F	3	70.8	72.1	74	1.7		
Englstciak, Y.T.	9.4	<i>Bison</i> sp.	M-F	1		68.1				
Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	47	60	71.4	79	4.7		
MT5 MidAP	Horner I, Wyo.	9	<i>Bison</i> sp.	M-F	2	66	69	72	4.2	
	Alaska	Pleistocene	<i>Bison</i> spp.	M	13	35.529.5	41.9	46.5	3.5	
	Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	13	32	36.2	41.6	3.1	
	Lost Chicken Cr., Alaska	>40-7	<i>B. crassicornis</i>	M-F	4	37.2	39.8	41.5	1.8	
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		43.4			
	Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	F	1		39.5			
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M-F	24	33	37.3	41	2.6	
	Casper, Wyo.	10	<i>B. antiquus</i>	M-F	44	31	34.3	42	2.4	
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M-F	?		33.6			
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M-F	11	28.6	30.9	33.3	1.4	
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M-F	54	31	36.6	41	2.9	
	MT6 PrxAP	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M-F	3	53	60.3	65	6.4
		American Falls, Idaho	>32-21	<i>B. latifrons</i>	M	17	69	74.2	78	2.7
					F	4	61	64	68	3.2
		Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	10	46.3	55.6	64.2	7.5
		Rancho La Brea, Calif.	30-13	<i>?B. latifrons</i>	M-F	5		67.2		
				<i>B. antiquus</i>	M-F	59		60.7		
		Lost Chicken Cr., Alaska	>40-7	combined	M-F	64	54	61.3	74	3.8
				<i>B. crassicornis</i>	M-F	4	57.8	60.5	62.2	1.9
Gallelli Pit, Alta.		11.3	<i>B. antiquus</i>	M	1		63.9			
Aquitaine Pit, Alta.		10.2	<i>Bison</i> sp.	F	1		56			
Olsen-Chubbuck, Colo.		10.1	<i>Bison</i> sp.	M-F	21	53	59.4	66	4.3	
Casper, Wyo.		10	<i>B. antiquus</i>	M-F	44	49	55.2	62	2.9	
Hudson-Meng, Nebr.		9.8	<i>Bison</i> sp.	M-F	?		52.2			
Milan, Alta.		9.6	<i>B. occidentalis</i>	M-F	6	50.4	55.7	58.8	3.1	
Finley, Wyo.		9.0?	<i>B. antiquus</i>	M-F	44	51	57	63	3.5	
MT8 DistAP		Hawken, Wyo.	6.5	<i>B. occidentalis</i>	M-F	29	47	53.3	59	3.6
		Gold Run Cr., Y.T.	32-22	<i>B. crassicornis</i>	M-F	9	34.8	39.7	45.3	3.5
		Rancho La Brea, Calif.	30-13	<i>?B. latifrons</i>	M-F	5		44.7		2
				<i>B. antiquus</i>	M-F	59		43		2
	Lost Chicken Cr., Alaska	>40-7	combined	M-F	64	39	43.1	49	2	
			<i>B. crassicornis</i>	M-F	4	41.7	44.3	45.9	1.8	

**Table 12** (concluded).

Measurement	Sample	Age (ka)	Taxon	Sex	N	Minimum	Mean	Maximum	S
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		49.5		
	Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	F	1		45.5		
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M–F	25	34	41.4	47	2.8
	Casper, Wyo.	10	<i>B. antiquus</i>	M–F	46	33	40.3	46	2.3
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		37.2		
	Milan, Alta.	9.6	<i>B. occidentalis</i>	M–F	5	35	40.2	43	3.1
	Engigstciak, Y.T.	9.4	<i>Bison</i> sp.	M–F	1		39.8		
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	54	36	40.9	46	2.5
MT9 MinAP	American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	18	39	41.3	44	1.5
	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	2	34	39	44	7.1
	Rancho La Brea, Calif.	30–13	? <i>B. latifrons</i>	M–F	5		37		1.3
			<i>B. antiquus</i>	M–F	59		35.9		1.6
			combined	M–F	64	34	36	40	1.6
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		39.4		
	Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	F	1		35		
	Olsen-Cubbuck, Colo.	10.1	<i>Bison</i> sp.	M–F	25	30	32.2	35	1.5
	Casper, Wyo.	10	<i>B. antiquus</i>	M–F	44	27	31	35	1.8
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		30.4		
	Finley, Wyo.	9.0?	<i>B. antiquus</i>	M–F	48	28	31.9	35	1.8
MT10 MinBr	American Falls, Idaho	>32–21	<i>B. latifrons</i>	M	18	48	52.2	57	2.7
	Costeau Pit, Calif.	42	<i>B. latifrons</i>	M–F	3	47	49	50	1.7
	Rancho La Brea, Calif.	30–13	? <i>B. latifrons</i>	M–F	5		43.3		4
			<i>B. antiquus</i>	M–F	59		38.9		2.5
			combined	M–F	64	33	39.3	48	3
	Gallelli Pit, Alta.	11.3	<i>B. antiquus</i>	M	1		45.4		
	Aquitaine Pit, Alta.	10.2	<i>Bison</i> sp.	F	1		36.3		
	Olsen-Chubbuck, Colo.	10.1	<i>Bison</i> sp.	M–F	25	30	36	42	3.9
	Casper, Wyo.	10	<i>B. antiquus</i>	M–F	43	30	33.9	40	3
	Hudson-Meng, Nebr.	9.8	<i>Bison</i> sp.	M–F	?		32.5		
	Finley, Wyo.	9	<i>B. antiquus</i>	M–F	47	30	36.2	44	3.3

<sup>a</sup>Measurements as for metacarpals, and after Bedord (1974). Decimal accuracy varies as to author. Mature individuals selected if tables included all age groups. Measurements are in mm.

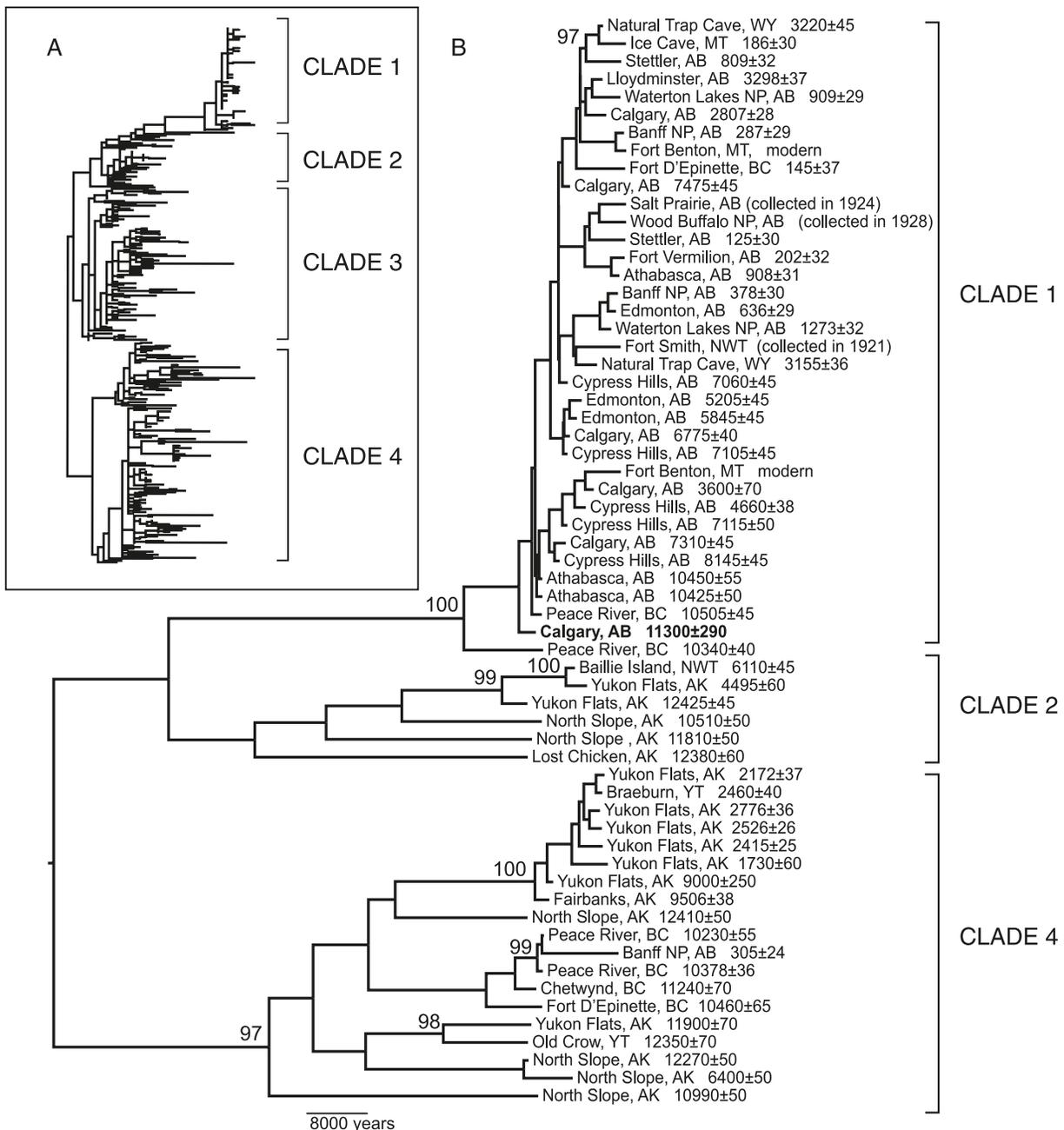
no modern descendants (Fig. 15). Following the LGM, the majority of the diversity outside of Clade 1 appears to have been restricted to present-day Alaska, where non-Clade 1 bison persisted until at least 1730 BP before becoming extinct.

## Discussion: taxonomy and evolutionary trends

Cranial and postcranial measurements and other characters identify the Gallelli Pit sample as *B. antiquus* and document the largest post-LGM bison yet recorded from the northern Great Plains. Many postcranial measurements exceed documented ranges for latest Pleistocene and Holocene *B. antiquus* and midcontinent specimens referred to *B. occidentalis*, though cranial measurements fall within the range for *B. antiquus* when earlier samples are included. The breadth of the smaller cranium is at the maximum for *B. occidentalis*. On the other hand, the material varies from being comparable to, to smaller than, the ranges for *B. latifrons*, the putative ancestor of *B. antiquus*. The Gallelli Pit sample extends the definition of *B. antiquus* from that of Skinner and Kaisen (1947) but in regard to crania falls within the range redefined by McDonald (1981). Indeed, the larger Gallelli Pit horn core was first referred tentatively to

*B. alleni* Marsh, 1877 (= late, small *B. latifrons*), the precursor of *B. antiquus* in the south, because it exceeded the Skinner and Kaisen maxima for *B. antiquus*. The timing of the *B. latifrons* – *B. alleni* to *B. antiquus* transition is not clear, but were it a Late Pleistocene (Wisconsinan) event, even larger bison would have immediately preceded the form exemplified at the Gallelli Pit. Comparably small (*antiquus*-sized) bison do date to the mid-Wisconsinan (ca. 30 000 – 20 000 <sup>14</sup>C years BP) but appear distinctive in possessing a marked distal twist to the horn cores (McDonald and Anderson 1975). If they were ancestral to postglacial *B. antiquus*, the evolutionary pattern was not a simple trend to diminution, as suggested by some analysts (for historical summaries of views, see McDonald 1981; Wilson 1974a, 1975). A partial skeleton of a large bison, found near Chuchi Lake in central British Columbia, had much larger horn cores than the Gallelli Pit specimens. It was tentatively referred to *B. latifrons* on the basis of partial horn cores and gave bone AMS dates of 35 480 ± 1080 (Beta-78574), 34 800 ± 420 (Beta-78573/CAMS 17566), and 30 740 ± 220 <sup>14</sup>C years BP (TO-3653; Harington et al. 1996). More samples are needed from south of the ice sheets of bison from between 20.0 and 12.0 <sup>14</sup>C ka BP. At present, there are few dated specimens from this interval aside from the La Brea sample, all but

**Fig. 15.** (A) Neighbor-joining tree (dendrogram) describing the relationships between 405 mitochondrial control region DNA sequences (680 base pairs) of Late Pleistocene and Holocene bison from North America and eastern Asia, with diversity loosely divided into four clades (adapted from original in Shapiro et al. 2004 and online supplement). The tree was created using the software Phylogenetic Analysis Using Parsimony (PAUP) v4b10 (Swofford 2002). Only Clade 1 bison have survived to the present in North America. (B) Coalescent phylogeny showing relationships among 61 post-LGM bison in North America. Specimens older than 13 ka BP are excluded here to simplify the figure. Bayesian probabilities >97% are given at the nodes as a measure of statistical support for the shape of the tree. Tissue specimens from Salt Prairie and Wood Buffalo National Park, Alberta, and Fort Smith, Northwest Territories, represent adult wood bison (*B. b. athabascae*) born before introduction of plains bison to Wood Buffalo National Park.



one cranium of which are smaller than *B. alleni*, so the evolutionary linkages of mid-Wisconsinan and latest Pleistocene bison remain incompletely understood.

The Gallelli material agrees broadly with Rancho La Brea *B. antiquus*, which spans a long time interval from about 30.0 to 13.0 <sup>14</sup>C ka BP (Marcus and Berger 1984; earliest dates may apply to *B. latifrons* – *alleni*). Many Gallelli

measurements fall at or near Rancho La Brea maxima. Given the Clade 1 mtDNA affinity, these early southern Alberta bison were part of a southern (midcontinent) faunal community migrating northward in the wake of ice retreat. Their large size is consistent with expectations from dispersal theory for a population moving into newly opened territory with relatively high productivity. Dispersal theory

suggests that such animals would tend to become larger and to develop more elaborate, energetically expensive display apparatus. These developments would be coupled with a longer growth period and late maturation and would also depend upon a long period of nutrient availability during the growing season (Geist 1971; Guthrie 1984). The even longer, albeit less robust, horn cores of the Casper site, Wyoming, *B. antiquus* (10.1 ka BP; Wilson 1974a) are also consistent with this model. The long limbs of the Gallelli specimen suggest a strongly cursorial animal, and would also have contributed to the display morphology by exaggerating body size in frontal and lateral views.

Most Gallelli Pit postcranial elements are also larger compared with *B. crassicornis* (*B. priscus*) material from pre-LGM sites in the Yukon and Alaska. The large size of the articulated specimen is significant in that it is an animal in middle maturity without extensive arthritic overgrowths to influence measurements. It was not at the upper extreme for BCF bison; a water-rolled metatarsal (UCA, unnumbered) from the Bonnycastle Pit, downstream from the Gallelli Pit on the Bow River in southern Calgary, is another 5 mm longer. The fauna from this pit, which includes horse, camel, and bison, is under study by the first author (MCW).

Bison specimens of comparable antiquity examined by the first author from Clovis archaeological sites (Murray Springs, Arizona; Blackwater Draw, New Mexico; U.P. Mammoth site, Wyoming; all between 11.5 and 11.0 ka BP) are also large. More detailed study of these samples will likely show that the large size of the Gallelli bison was not unusual for early postglacial populations dispersing in the expanding plains steppe-grassland habitat, although they were at the large extreme for the slightly earlier La Brea population. Table 9 includes new, unpublished measurements of paired bison metacarpals from the El Llano excavations at Blackwater Draw (Hester 1972) associated with remains of Mammoth III (specimens BI MIII Unc and BI MIII 101:63).

Size trends over the preceding few millennia are not clear in the absence of temporally restricted samples. Based on data assembled here, the rate of bison diminution over the past 12 000 years was probably not matched in the preceding 12 000 years. Dispersal theory suggests that opening of newly deglaciated territory for colonization by bison should have favoured a trend to increased size and disproportionately larger horn cores (Geist 1971) opposite to the well-documented Holocene trend to diminution (McDonald 1981; McDonald and Lammers 2002; Wilson 1974a, 1980b). If a trend to increased size began prior to 12 ka BP south of the ice sheets, it could have escaped detection thus far because of the paucity of samples.

In the perspective of dispersal theory, the subsequent Holocene trend to decreased size (Wilson 1978) is counter-intuitive given that ice retreat continued to open up new territory; however, the sweep of spruce forests across the northern plains in western Canada placed limits on grassland expansion as early as 11 ka BP. Further insight as to the pressures facing late Quaternary bison comes from the possibility that Holocene diminution was also influenced by human predation. Bison life expectancy at the Casper site was only 12 to 15 years, whereas in modern managed herds bison cows can produce offspring into their third decade (Reher 1974). High frequencies of dental anomalies in early

postglacial bison have been suggested to reflect genetic drift in small, relatively isolated populations for which reduced life expectancy lowered the selective pressure for third-molar morphology (Wilson 1974a). This possibility is supported by mtDNA evidence that suggests bison populations in both Beringia and the midcontinent declined from a maximum ca. 45–30 ka BP to a minimum with a severe genetic bottleneck ~10 ka BP, possibly caused by hunting pressures (Shapiro et al. 2004; Drummond et al. 2005). The bottleneck occurred at about the same time as the last of the Late Pleistocene megafaunal extinctions (Barnosky et al. 2004; Grayson and Meltzer 2002; Guthrie 2006). Yet bison populations rebounded and were particularly high in the late Holocene at the very time when bison jumps were being operated on a near-industrial scale (Kehoe 1978). This suggests that bison responded to selective pressures in such a way as to offset the effects of this predation. By shortening lifespan, human predation would have introduced selective pressure favoring more rapid maturation and hence smaller body size and reduced display organs—the opposite of the dispersal phenotype. More rapid maturation, if expressed in terms of cranial suture fusion rates, could have caused morphological changes in terms of frontal breadth and hence horn core orientation as well as size. Bison population numbers increased on the Great Plains during the Holocene and it could be argued that this increased intraspecific competition, favoring size decrease; however, the decrease appears to have happened in all environments, not simply on the productive plains. The scenario just presented suggests that population increase in the face of intensified predation was a correlate rather than a causative mechanism for the size decrease. Another evolutionary strategy in response to hunting could have involved intensification of migratory habits, a documented ungulate strategy to minimize predatory pressures (Fryxell et al. 1988). Seasonal mortality evidence at La Brea indicates that *B. antiquus* was already migratory (Jefferson and Goldin 1989), and this pattern could have intensified during the Holocene (e.g., Peck 2004).

In terms of traditional morphospecies, replacement of *B. antiquus* by *B. occidentalis* began on the northern Great Plains near or just after the close of BCF deposition. BCF bison specimens, therefore, have important ramifications regarding the overall history of latest Pleistocene and Holocene bison on the Great Plains. Formerly, it appeared possible that *B. occidentalis* was in southern Alberta as early as 11 300 <sup>14</sup>C years BP, based on identification of the Cochrane material as that form. Reidentification of the Cochrane and Calgary material places *B. antiquus* on the Canadian plains between 11.5 and 10.0 ka BP (Wilson and Churcher 1984). The Wally's Beach site (DhPg-8), an archaeological and paleontological locality on St. Mary Reservoir, southern Alberta, has yielded a similar fauna to that of the BCF, dated between 11.4 and 10.9 ka BP, with bones of *Equus conversidens*, *B. antiquus*, *Rangifer tarandus*, and *Bootherium bombifrons* (Harlan's muskox), as well as trackways of mammoth, camel, and horse (Kooyman et al. 2001; McNeil et al. 2004). A partial skull from Wally's Beach is nearly as large as the older Gallelli Pit specimen and appears closely similar; it is also identified as *B. antiquus* and has been dated to 11 130 ± 90 <sup>14</sup>C years BP (Tolman 2001). Its basal horn-core circumference of 346 mm falls between

the two Gallelli values. A skull and partial skeleton from Taber, Alberta, was referred to *B. occidentalis* (Trylich and Bayrock 1966) and interpreted as Late Pleistocene, but wood dated to 11 000 and 10 500  $^{14}\text{C}$  years BP was not closely associated, so the bison is not reliably dated. A large bison skull with arched frontals and laterally directed, downswept horn cores was recovered from an excavation in Bellevue, Crowsnest Pass, southwestern Alberta (site DjPo-81). From photographs the specimen appears assignable to *B. antiquus*. It was dated to  $9860 \pm 320$   $^{14}\text{C}$  years BP (RL-360) and had a horn-core spread of close to 900 mm (Reeves 1975; Decoux 1974). Specimens from the Milan site, near Three Hills, Alberta, dated to  $9630 \pm 300$   $^{14}\text{C}$  years BP (GSC-1894 and  $9670 \pm 160$  years BP (I-8579; Shackleton and Hills 1977), fully resemble *B. occidentalis* with upswept and backswept horns and narrower frontals.

If these findings are representative, and in light of the DNA findings, it appears that *B. antiquus* gave rise to, and possibly gave way to, bison resembling the *B. occidentalis* type on the Canadian plains about 10.0  $^{14}\text{C}$  ka BP. At 2S the Bellevue specimen could date as early as 10 500 BP or as young as 9220 BP. The overall 2S range for the Milan site *B. occidentalis* would be from 10 230 to 9030 BP, suggesting that the morphological transition was rapid, though without a dramatic change in overall size (Wilson 1980b). The transition occurred at the time of the genetic bottleneck documented by Drummond et al. (2005). A previous hypothesis explaining this has been that an influx of bison from the north through the ice-free corridor gave rise to midcontinent *B. occidentalis*, based upon horn-core similarities with the Alaskan type specimen (Fuller and Bayrock 1968; Guthrie 1970; Harington 1984; Skinner and Kaisen 1947; Wilson 1996). Wilson (1969, 1974a), further raised the possibility that these were not biospecies and that introgressive hybridization occurred between the new arrivals and southern bison to produce the modern species. He, therefore, designated the two as chronosubspecies of the modern bison: *B. bison antiquus* and *B. b. occidentalis*, the latter after Fuller and Bayrock (1968). McDonald (1981) argued instead for derivation of *B. occidentalis* primarily from *B. antiquus* through in situ change; given their differing selective regimes and morphology he viewed the two forms as the subspecies *B. antiquus antiquus* and *B. a. occidentalis* (see also McDonald and Lammers 2002).

The mtDNA findings for the Gallelli specimen and other southern bison provide new insights unavailable from the morphological studies. There is no mtDNA evidence for a post-LGM southward movement of bison through the corridor beyond northeastern British Columbia (unless only males were involved), and Holocene plains bison appear to have been derived directly from *B. antiquus*; therefore, *B. "occidentalis"* of the midcontinent is a chronomorph (sensu Martin et al. 2002) within that lineage (Clade 1). Impassable lake barriers, muskeg, and forest tracts could have served as barriers to southward movement of Beringian bison without impeding other species, including humans. Even for humans, however, the corridor may have been impassable until as late as 11.0 ka (Arnold 2002). Bison belonging to both northern and southern mtDNA clades have been documented at the Charlie Lake Cave site in northeastern British Columbia (10.5 ka), marking the Late Pleisto-

cene range extremes for both groups (Driver 1988; Driver et al. 1996; Shapiro et al. 2004; Vallières 2004). Bison appear to have been rare in this region, and, if they were migratory, the two groups could even have been present in different seasons, so it is difficult to interpret the small sample. Bison persisted in the Yukon into early Holocene times; for example, three bones from the "Buffalo Pit" at Engigstciak on the Arctic coast gave AMS dates between 9900 and 9400 BP. Preliminary study indicates a large bison, which Cinq-Mars et al. (1991) suggested was closer to *B. priscus* than to *B. occidentalis*.

If Holocene plains bison were derived directly from *B. antiquus*, one would expect occasional, persistent occurrence of bison with arched frontals and downswept horn cores in Holocene populations. This is the case, even with skulls from the Historic period: photographs of skulls piled up by "bone-pickers" in the late 19th century show many such specimens. A large horn core from the Assiniboine valley, Manitoba, dated to  $6300 \pm 100$  years BP (BGS-1019), resembled cores of *B. antiquus* (Wilson 2000). McDonald and Lammers (2002) argued for the persistence of *B. a. antiquus* alongside *B. a. occidentalis* as late as 5.0 ka BP.

The mtDNA findings add significance to the observation that no clearly ancestral members of the supposed southward-migrating *B. "occidentalis"* line have been documented from the southern Yukon or Alberta from the 12.0–10.0  $^{14}\text{C}$  ka BP interval. A fragmentary skull from northeastern British Columbia, dated to 10 550 BP, was identified as possibly *B. occidentalis* (Apland and Harington 1994) and could be such a migrant. However, bison postcranial remains from northern British Columbia sampled for mtDNA included some linked to Beringian clades and others representing the northern extreme of southern Clade 1 (Shapiro et al. 2004). The *B. occidentalis* holotype was collected from Fort Yukon, Alaska, and disjunct material from the Great Plains was soon referred to this species on the basis of horn-core similarities (Lucas 1898, 1899a, 1899b). Such geographic spread, with discontinuity, raises concerns about possible ecophenotypic convergence in a character-set as plastic as horn-core form and direction. The distinction between Beringian and midcontinent bison mtDNA clades (Shapiro et al. 2004) now indicates that careful reassessment of *B. occidentalis* is necessary. If the type specimen and referred material prove to belong to different mtDNA clades, use of the name *B. "occidentalis"* for midcontinent populations would be spurious and an alternative would have to be sought among other existing names.

In situ derivation of Holocene plains bison from Late Pleistocene *B. antiquus* raises the expectation that forms intermediate between *B. antiquus* and *B. "occidentalis"* (or intermediate populations with variable morphology) should be found in the interval from about 10 500 to 9 000  $^{14}\text{C}$  years BP. Two large male skulls were recovered from the ~10 100 years old Casper site, Wyoming, one of which closely resembled *B. antiquus*, whereas the other exhibited upswept and backswept horns more reminiscent of *B. occidentalis*. This was taken as possible evidence of hybridization between *B. antiquus* and incoming northern-derived *B. occidentalis* (Wilson 1974a), but in light of the Gallelli mtDNA and morphological findings, it now appears

consistent with the in situ evolutionary transition between the two. The small differences between the two Gallelli Pit specimens are also consistent with such a view, the more recent specimen being more *occidentalis*-like. Given the similarity of isolated horn cores and postcranial elements of *B. antiquus* and *B. occidentalis*, identifications of latest Pleistocene and early Holocene bison from the Great Plains should be made with caution.

The Gallelli Pit sample and others from Alberta indicate that bison of southern affinities were established on the extreme northern Great Plains by about 11 500 <sup>14</sup>C years BP. This agrees with palynological evidence for open grasslands in Montana (Barnosky 1989) and establishes that a steppe dispersal corridor linked these areas biogeographically with the southern plains, where *B. antiquus* has been well documented. Earlier postglacial or LGM finds are few on the Great Plains and suggest that bison just before and at the LGM were restricted to areas even farther south, from California to Florida (Chandler 1916; Dalquest and Hughes 1965; Graham 1981; Kirkland et al. 1991; Robertson 1974; Webb et al. 1984).

The Bighill Creek Formation sample and coeval paleofaunas on the Canadian plains have played an important role in clarifying the relationships of *B. antiquus* and *B. occidentalis*, much as the southern Alberta area will continue to yield important information about species of other genera, such as *Camelops* and *Equus*. Given that the BCF appears to span much of the time of the Late Pleistocene extinctions, as well as apparently bracketing the Younger Dryas climatic episode, its samples will also continue to serve as the basis for hypotheses that can be applied and tested more widely on the Great Plains and elsewhere in North America.

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