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LATE QUATERNARY VERTEBRATES AND THE OPENING OF THE ICE-FREE CORRIDOR, WITH SPECIAL REFERENCE TO THE GENUS *BISON*

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The ice-free corridor opened physically in early deglaciation, after 14 ka BP, but at first was not necessarily passable in an ecological sense. One way to gauge the timing of its 'ecological opening' is to establish a chronology for the arrival of immigrant animal species. The bison have excellent potential because of the abundance of their remains. Late Pleistocene and Early Holocene bison finds from western Canada north to the Peace River area extend the known database and provide new insights. Bison of 'southern' appearance (referable to *B. bison antiquus*) were present as far north as the Peace River region until about 10 ka BP. Bison populations in western Canada apparently underwent a rapid change at that time, such that barely 500 years later, bison of 'northern' appearance (referable to *B. bison occidentalis*) were established. The rapidity and pervasiveness of this change seem to defy an evolutionary explanation rooted in punctuated equilibrium or phenotypic change, and could indicate a sudden population influx through the newly opened corridor. Thus far, no late-glacial bison in western Canada have been dated in excess of 11.5 ka BP, with the possible exception of material from Empress, Alberta. If a steppe-tundra was established before that time, the absence of bison with either southern or northern affinities seems inexplicable. Outburst floods have undoubtedly removed part of the record by scouring gravel fills from valleys, but it is doubtful that they completely obliterated the fossil record of a gregarious herbivore such as the bison. Copyright © 1996 INQUA/Elsevier Science Ltd

CORRIDOR HISTORY

The ice-free corridor existed as an ephemeral tract of open land in western Canada between the Laurentide and Cordilleran ice sheets early in Wisconsinan deglaciation. The chronology of its opening is approaching resolution after decades of swings back and forth from a view that it was open throughout the Late Pleistocene to a currently accepted view that it was closed at the height of the last glaciation (Bryan, 1969; Reeves, 1973; Stalker, 1977, 1980; Jackson, 1979; Rutter, 1980, 1984; Mathews, 1980; Clayton and Moran, 1982; Wilson, 1983; Fullerton and Colton, 1986; MacDonald *et al.*, 1987; Catto and Mandryk, 1990; Burns, 1990; Wilson, 1990). Corridors were presumably present both during the Late Wisconsinan advance and during retreat. Most past discussions have centered upon whether the latter corridor was 'open' or 'closed' in a physical sense, as a geographic feature. Few authors have considered in detail the extent to which it was passable as an ecological feature once it was open physically (for exceptions, see MacDonald, 1987b; Pielou, 1991; Schweger and Mandryk, 1986). If the fundamental question is when (and whether or not) humans were able to traverse the corridor in late-glacial times, the compelling issue must be to determine when and to what extent the corridor was ecologically 'open', viable, or passable. What were its ecological, as well as its physical, boundaries? Barriers that existed could have been recently deglaciated substrates of low productivity, extensive proglacial lakes, or areas of particular habitat

type (e.g. forest areas that could not be traversed by obligate grazers).

Dates cited in the following discussion are presented as published. Not all have appeared in date lists and it is not certain that all have been subjected to $\delta^{13}\text{C}$ corrections as was the case for the GSC dates. $\delta^{13}\text{C}$ corrections for bison bone at this time level have tended to be on the order of decades and for the present it is not expected that corrections will alter the broad overall patterns discussed here. However, perturbations and reversals in the correction curve are possible, and will gain importance as investigations become more focused (Wilson, 1993; Fedje *et al.*, 1995). Only one date cited below is an AMS date (RIDDLE-393; Charlie Lake Cave), and all are collagen dates with the exception of the early Saskatchewan laboratory (S), which appear to have been on whole bone.

The C.P.R. pit at Empress, on the Alberta–Saskatchewan border along the South Saskatchewan River, yielded abundant bones, the dates of which seemed to bracket the last glaciation. The fauna includes *Mammuthus primigenius*, *M. imperator*, *Equus conversidens*, *E. sp.*, cf. *E. niobrarenensis*, *Rangifer sp.*, *Camelops sp.*, cf. *C. hesternus*, and *Bison sp.*, cf. *B. occidentalis* (Stalker, 1971; Lowdon and Blake, 1975). Mammoth bone fragments submitted by A. MacS. Stalker were dated to 20,400±320 BP (GSC-1387) and 14,200±1120 BP (GSC-1199; Lowdon and Blake, 1975). Stalker found the dates in conflict and concluded that GSC-1199 might have been contaminated. However, it would be possible for a 13,000 or 14,000-year-old gravel to rest atop, or be inset into, an exhumed 20,000-year-old gravel, much as is

the case with interglacial and postglacial gravels at Edmonton (Burns, 1990). Electron spin resonance (ESR) dating of tooth enamel from the pit indicates a mid-Wisconsinan age (42 ± 2 ka, 34 ± 4 ka BP) and that even older redeposited material is present (Zymela *et al.*, 1988), suggesting that the radiocarbon ages are too young. This aside, there is broad agreement that the Late Wisconsinan glaciation did not reach southern Alberta until after 22 ka BP and possibly after 20 ka BP (Christiansen, 1968; Wilson, 1983; Fulton *et al.*, 1986; Burns, 1990), with its peak extent about 18 ka to 15 ka BP (Dyke and Prest, 1987).

The last area to be opened appears to have been in the southeastern Yukon and southwestern Northwest Territories. The zipper-like opening should be reflected by a gradient of 'earliest' dates from south to north. Dates even in the north are in excess of 11 ka BP and could approach 13.5 ka BP, if shell dates can be accepted (e.g. St-Onge, 1972; Jackson and Pawson, 1984). Ice may have begun to retreat as early as 14 ka BP, though most evidence suggests that ice lingered in northeastern Alberta and central Saskatchewan as late as 11.5 ka BP (Clayton and Moran, 1982). The Kyle Mammoth (*Mammuthus columbi*), Saskatchewan, was dated to $12,000 \pm 200$ BP on bone (S-246; Harington and Shackleton, 1978). Horse bone from the Riddell Local Fauna, Saskatoon, was dated to $15,340 \pm 500$ BP (S-1305), but this date was rejected on the basis of its failure to fit the accepted deglaciation sequence (Skwara-Woolf, 1981). ESR dating of tooth enamel suggests a Sangamon age (Zymela *et al.*, 1988). Bone from the Sutherland gravel pit, near Saskatoon, was dated to $14,040 \pm 465$ BP (S-685). The pit had earlier yielded teeth of *Equus* sp. (Russell, 1943). Christiansen (1979) discounted the reading inasmuch as it did not fit the accepted deglaciation chronology, but left open the possibility that the pit area had been overridden by a Late Wisconsinan readvance. As understood at present, ice retreated to the Lethbridge Moraine position and southern Saskatchewan equivalents about 14 ka BP, with separation of eastern and western ice sheets about 13 ka BP (Dyke and Prest, 1987).

BISON AND THE CORRIDOR

A way to gauge the timing of the ecological opening of the corridor is to establish a chronology for the arrival of immigrant vertebrates through direct radiocarbon dating of bones and associated materials. The bison, in particular, have excellent potential because of their relatively abundant remains. Nevertheless, the issue of biological isolation or non-isolation has clouded discussion of taxonomy and biogeography; the message regarding the corridor has been ambiguous. Bison exhibit so much phenotypic plasticity it is difficult to pick out the phyletic lines. The revision of bison by Skinner and Kaisen (1947) was based largely upon morphology, given only limited stratigraphic controls, leaving the possibility for artificial grouping of phenotypically similar bison of

different ages (Flerov and Zablotski, 1961; Schultz and Hillerud, 1977). By selecting morphotypes, one can give the illusion of limited variability, but this is unprovable without evidence for temporal integrity. Efforts by Wilson (1974) and McDonald (1981) to document well-dated Late Pleistocene and Holocene samples have clarified matters to some extent. The present discussion is less concerned with taxonomic nuances than with the problem of distinguishing northern and southern populations of closely related bison.

Bison originated in Asia, becoming widespread in the form of the Late Pleistocene steppe bison, *Bison priscus*, well known from European cave paintings as well as from skeletal remains. They apparently first crossed the Bering Land Bridge earlier than did humans, arriving 200,000 or more years ago. North American bison evolved, by Illinoian to Sangamonian times, into the giant form *B. latifrons*, but by the Mid-Wisconsinan interval the giants had given way to a smaller form with laterally directed, downswepthorn cores (Guthrie, 1970). The Wisconsinan record south of the ice sheets is dominated by the form *B. bison antiquus*, which probably played a role in the ancestry of the modern bison despite a belief to the opposite by Skinner and Kaisen (1947). North of the ice sheets, *B. priscus* persisted in the Beringian refugium, giving rise to the smaller form *B. bison occidentalis* in late-glacial times. These northern bison had more back-swept horn cores that rose well above the plane of the frontals (Fig. 1).

Part of the legacy of Skinner and Kaisen (1947) was the view that the southern *B. alleni* (= small *B. latifrons* of McDonald, 1981) was the ancestor of *B. bison antiquus*, yet there was a large gap between the smallest *alleni* and the largest *antiquus*. If the phyletic line did exist, there must remain an undescribed intermediary in the midcontinent. Wilson (1969) wondered if the gap could indicate that *B. crassicornis* (= *B. priscus*) was instead the ancestor of *antiquus*, but important differences in horn-core characters seem to exclude such a possibility (Wilson, 1974; McDonald, 1981). It remains noteworthy that any worker trying to fit an isolated mid-sized horn core from a midcontinent locality into a Skinner and Kaisen taxon would have to choose *B. crassicornis* (= *B. priscus*), as was done by Romer (1951) and Lillegraven (1967). The seeming absence of a *latifrons* (*alleni*) to *antiquus* intermediate could therefore be an unintended circularity arising from Skinner and Kaisen's revision.

McDonald (1981), summarizing a variety of paleoecological studies, argued that the Great Plains area and much of the rest of the midcontinent was wooded during the Wisconsinan glaciation, preventing southern grazers from moving northward. A narrow band of tundra existed along the maximum ice front across North America, with shrublands on the western plains and boreal forest on the eastern and central plains (Prest *et al.*, 1987) and large open areas of sand dunes on the plains (Pielou, 1991). The tundra strip need not have been continuous, given that the presence of forest versus tundra was in part determined by the presence and thickness of permafrost; the 'strip' was probably a mosaic of tundra and forest patches (Pielou,

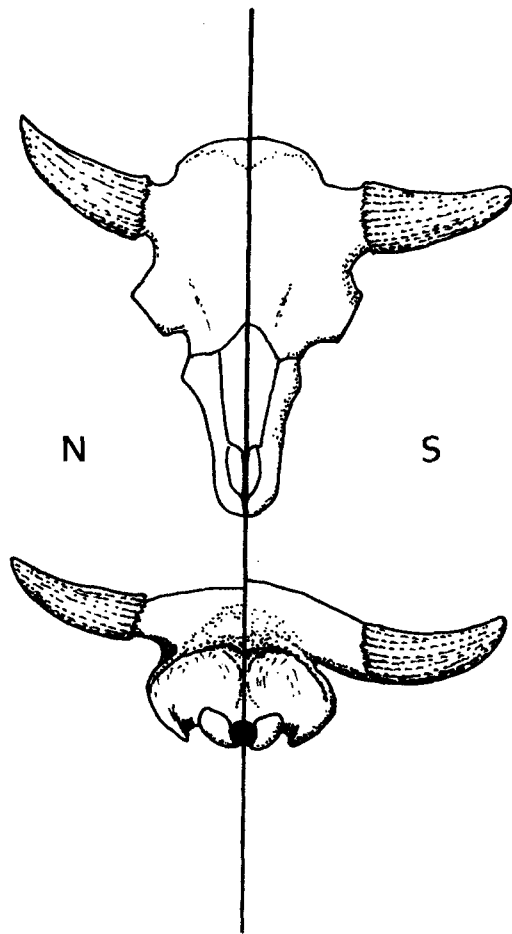


FIG. 1. Idealized diagram showing cranial differences between northern-phenotypic bison (left) and southern-phenotypic bison (right).

1991). As deglaciation proceeded, a continuous corridor of herb- and shrub-dominated vegetation linked Beringia to the Great Plains, to be replaced by spruce forest in the north soon after 10 ka BP (MacDonald, 1987a, b; Ritchie and MacDonald, 1986).

At Lofty Lake, northeast of Edmonton, a pioneering vegetation dominated by *Populus* and *Artemisia* was present between about 11,500 and 10,000 BP (Lichti-Federovich, 1970). This community, which has become widely known as 'steppe-tundra', seems to have no modern analog, which probably reflects the combined influences of freshly deglaciated soils, migrational lag, and different insolation regime from the present (greater insolation in summer, less in winter) (MacDonald and Reid, 1989). Cwynar and Ritchie (1980) argued that the supposed 'steppe-tundra' was in fact only sparse tundra, resembling a fell-field, and of low productivity. However, Guthrie (1985) has countered with detailed arguments in support of a productive 'mammoth steppe' with a firm substrate. The high numbers of grazing mammals, whose body size indicates abundant forage, is suggestive; in addition, their foot morphology indicates a firm steppe-like substrate. Guthrie argued forcefully that the palynologists have misread their own data. The computation of pollen influx values depends upon the rate of sedimentation; it could be that palynologists have been too conservative in their estimates of early sedimentation

rates in the relatively unstable setting of the ice-free corridor.

South of the ice masses between 20 ka and 12 ka BP, bison populations were possibly low and relatively local. Grasslands persisted in the American Southwest, providing a refugium for grazing mammals. The table of ^{14}C dates provided by McDonald (1981) includes only four for bison in this interval, widely scattered geographically (California, New Mexico, Virginia, and Idaho). The contrast with date frequencies for both earlier and later bison is striking. A southern fauna including mammoths, horses, camels, and bison was able to move northward into Alberta as early as 11.5 ka BP (Wilson and Churcher, 1978, 1984). It is accepted that by 11 ka BP a lichen woodland or poplar parkland was established on the northern plains, with shrub tundra in the corridor to the north (Lichti-Federovich, 1972; MacDonald, 1982; Vance, 1986; McAndrews *et al.*, 1987). However, the Guardipee Lake core (Barnosky, 1989) demonstrates that 'a temperate grassland with shrubs growing locally' was present in northern Montana 12 ka BP and shows no evidence of the widespread forest hypothesized by other authors (see discussion in Pielou, 1991). It is likely that grasslands were widespread by that time, allowing southern grazers to move freely northward. The paucity of dated *B. bison antiquus* from the plains area prior to about 12 ka BP is consistent with a forest barrier before that time and indicates that in the Late Wisconsinan there was also an ecological 'opening' of a steppe corridor to the south, analogous to the ice-free corridor to the north. The northward movement of the forest upon ice retreat was controlled by the rate of thawing of permafrost, not simply by the rate at which territory became open (Pielou, 1991). By 10 ka BP, the ice-free corridor itself was bridged by a spruce-poplar forest, closing the pathway for northern grazers (Ritchie and MacDonald, 1986; MacDonald, 1987a, b; McAndrews *et al.*, 1987).

Cool steppe-tundra conditions prevailed for a time, with a megafauna of mammoths, horses, camels, large bighorn sheep, and large *B. bison antiquus*. Barely a millennium later, the mammoths, horses, and camels were extinct in North America, and *B. bison antiquus* had been replaced by the northern form *B. bison occidentalis*. The rapid replacement of one form of bison by another seems to reflect an influx of *occidentalis* through the ice-free corridor from Beringia. The present paper discusses this changeover in western Canada and interprets its significance relative to the history of the corridor. Findings relating to bison populations have relevance also in the understanding of human population movements and adaptive patterns in the ice-free corridor area, though it must not be contended that humans and bison necessarily travelled together.

The author has suggested that there was, for all time periods, a north-south clinal gradient in cranial characteristics of bison (Wilson, 1974). Northern-phenotypic bison had narrow frontal bones and horn cores deflected toward the rear and upswept; while southern-phenotypic bison had broad frontals and horn cores laterally directed and downswept (Fig. 1). In this model, *B. bison*

occidentalis would be the northern counterpart of *B. bison antiquus*, and they would be geographic subspecies linked by a character gradient. Some described populations, such as the 10,000-year-old Casper Site population from Wyoming, seem to display intermediate characteristics. Skinner and Kaisen (1947) had concluded that the two forms, which they considered paleospecies, "...lived contemporaneously, sharing part of a common range during very late Pleistocene, but probably did not interbreed, for no specimens are known that display intermediate characters." Furthermore, *antiquus* in their view did not move northward in the Late Pleistocene, its northern limit remaining southern Montana.

It is not clear to what extent this phenotypic variation was genotypically controlled and to what extent it was an environmental response. The question of hybridization is therefore a particularly vexing one, for it is difficult to postulate what a hybrid would have looked like. Studies of modern deer, *Odocoileus* spp., have shown that unidirectional introgression of genes can occur, with hybrids strongly resembling one source over the other (Carr and Hughes, 1993). Given that morphology was the prime criterion, over stratigraphy, in Skinner and Kaisen's study, and that considerable overlap occurred between the two in measured cranial characters, it is possible that they were simply unable to discern evidence for hybridization or for clinal gradation. Given compelling biogeographic evidence that northern and southern bison populations were physically separated at the height of the last glaciation, along with increasing evidence for temporal differences between *antiquus* and *occidentalis*, it is possible that *occidentalis*, sweeping in through the ice-free corridor, replaced *antiquus* through genetic swamping or other means. Guthrie (1970) suggested that *occidentalis* was coming into a vacated niche, created by the disappearance of *antiquus*. An overlap in dates would not preclude this, given that *antiquus* could have persisted in one area (e.g. the southwest) even as *occidentalis* was populating the northern plains. Certainly the plains bison as now understood has a 'northern' morphology, suggesting a dominantly *occidentalis* ancestry. Yet there remain individuals with *antiquus*-like appearance to the present day. If *antiquus* populations were high, and if the differences reflect genotype, one would expect that it took some time for the *occidentalis* genotype to prevail, and that many intermediate populations should have existed. In effect, the *occidentalis* type would have pushed slowly southward over the plains in a form of genetic overlap (Frison *et al.*, 1976). It is possible that *antiquus* had been on the verge of succumbing to the Pleistocene extinctions, and the incoming *occidentalis* met with very low populations of its relative.

In the second view, then, *antiquus* and *occidentalis* will emerge as temporally distinguishable — a view proposed by Forbis (1956). *B. b. antiquus* would largely predate the opening of the ice-free corridor, and populations of later age would mostly exhibit mixed or *occidentalis* characteristics except where isolation existed (as could possibly have occurred in the American southwest or the intermontane west). This also leaves open the

possibility of successional phenotypic change, in response to climatic change, to account for the sequence, but the apparent rapidity of the transition is more in keeping with a population replacement. A possible relationship between the morphological shift and the sudden terminal Pleistocene climatic change between 11 and 10 ka must be investigated.

A refugium for bison existed in Beringia throughout the Last Wisconsinan glaciation. A bone bed attributed to *B. crassicornis* (= *B. priscus*) at Locality 11, Old Crow Basin, northern Yukon, was dated to 12,460±220 BP (I-3574), 12,275±180 BP (I-7764), and 11,910±180 BP (I-7765; Harington, 1978). Radiocarbon dates on bison bones from Alaska fill the period from 17 to 11 ka BP (Guthrie, 1985) and confirm that a thriving population of bison existed alongside other grazers such as horse and mammoth.

WESTERN CANADIAN EVIDENCE

Southern and Central Alberta

Late Pleistocene gravelly fill units are widespread along Alberta rivers, from the Saskatchewan system in the south to the Peace system in the north. These gravels have been formalized along the Bow River, a South Saskatchewan tributary, as the Bighill Creek Formation. Along the Bow, they have been dated between about 11.5 and 10 ka BP, based upon samples of bone collagen from large vertebrates (Stalker, 1968; Churcher, 1968, 1984).

The gravels form valley trains of montane origin, interpreted as the downstream redistribution of material delivered to valley floors by debris-flows when formerly ice-supported and/or frozen slope deposits became subject to mass-wasting (Jackson *et al.*, 1982). Such a phenomenon must have been time-transgressive and, indeed, dates from the Peace River system are slightly later (11 to 9.5 ka BP), with a comparable duration but a temporal offset of 300–500 years (Wilson and Churcher, 1984). The Bighill Creek Formation was defined by Stalker (1968) at Cochrane, Alberta, where it occurs as a gravel and sand fill exposed in pits on the second terrace above river level. The unit has been traced downstream through Calgary to at least the Carseland Bridge, a river distance of some 100 km (Wilson and Churcher, 1984). Extreme dates for deposition come from two Calgary sites: 11,300±290 BP (RL-757) and 10,200±280 BP (GSC-3065; Wilson and Churcher, 1984). The Cochrane pits have yielded bones of horse (*Equus conversidens*), caribou (*Rangifer tarandus*), large mountain sheep (*Ovis canadensis catclawensis*), and large bison (*B. bison antiquus*), dated to 11,370±170 BP (GSC-613), 11,100±160 BP (GSC-989), and 10,760±160 BP (GSC-612; Stalker, 1968). Fragmentary bison crania were initially referred by (Churcher, 1968, 1975) to *B. bison occidentalis*, but more complete specimens are now available and are clearly referable to *antiquus*. An edentulous mandibular fragment referred by Churcher (1968) to *Cervus canadensis* also resembles that of an old bison, so is here viewed as indeterminate. The Calgary

pits have yielded bones of *Mammuthus* sp., *Equus* sp., *Camelops* sp., cf. *C. hesternus*, and *B. bison antiquus*. Farther downstream, in the Medicine Hat area, bison and horse bones from Lindoe Bluff on the South Saskatchewan River were dated to 11,200±200 BP (GSC-805; Lowdon and Blake, 1968). The bison has been identified as *B. priscus* (Zymela *et al.*, 1988). Bison from Athabasca, Alberta, identified as *occidentalis*, were dated to 10,200±160 rcybp (GSC-1205; St-Onge, 1972). However, this material is fragmentary and subsequently collected isolated horn cores resemble *antiquus* as much as they do *occidentalis*.

The similarities of the *B. bison antiquus* specimens are striking, and are paralleled in the morphology of specimens from U.S. sites far to the south. A specimen from Calgary, like one from Grande Prairie and another from near Fort St John, B.C. (see below), is larger than the maximum recorded by Skinner and Kaisen (1947) and helps to fill the gap between *antiquus* and its probable southern ancestor (Wilson and Hills, *in preparation*). In contrast, all Alberta specimens after ca. 10 ka to 9.5 ka BP are *B. bison occidentalis*. A skeleton from Taber referred to *occidentalis* was thought to date as early as 11 ka BP on the basis of a wood date from the same overall depositional unit (Trylich and Bayrock, 1966). However, the size of the specimen suggests a younger age, and the stratigraphic separation of the skeleton and the underlying beds that yielded the dated wood could easily allow a difference of 1000 or more years in age (Wilson, 1992). Bison from the Milan Site, near Three Hills, are clearly *occidentalis* and have been dated to 9670±160 BP (I-8579) and 9630±300 BP (GSC-1894; Shackleton and Hills, 1977). A sample of crania reliably referred to *B. bison occidentalis* was recovered from the Duffield section, along the North Saskatchewan River west of Edmonton (Hillerud, 1970). Wood from the contact between river gravels and overlying bone-bearing clay and marl with woody peat was dated to 8320±140 BP (GSC-767) and 8150±100 BP (S-106; Lowdon and Blake, 1968).

Peace River Region

For the past several decades at least, vertebrate remains have been turning up in gravel pits in the Peace River region, along the Peace, Smoky, Wapiti, and other rivers.

Much of this material has been found in terrace gravels of Late Pleistocene to earliest Holocene age. Among the remains from these pits are bones of mammoth (*Mammuthus* sp.), horse (*Equus conversidens* and possibly *E. niobrarensis*), wapiti (*Cervus elaphus*), muskox (*Ovibos moschatus*) and bison (*B. bison antiquus*) (Churcher and Wilson, 1979). A heavily abraded tibia referred by these authors to *Hemiauchenia* appears instead referable to wapiti (K. Seymour, *pers. commun.*).

The Peace River region began to be deglaciated more than 13.5 ka BP, on the basis of shell dates (St-Onge, 1972), and certainly more than 11.7 ka BP (White *et al.*, 1985; White and Mathewes, 1986). Areas south of the latitude of Grande Prairie were uncovered about 12 ka BP with the draining of Glacial Lake Iosegun III. Its successor, Glacial Lake Falher I, drained through the Lesser Slave valley about 10.7 ka BP, opening up the area south of the Peace River. Dates on later valley-fill sands and gravels in the region are summarized in Table 1. Dates AECV-272c and S-2614 are on the same wapiti skeleton (Burns, 1986). The dates on bison suggest a duration from 11 ka to 9.75 ka for open country with steppe-like conditions. Bison bones from two levels at the Charlie Lake site, near Fort St John, British Columbia, were dated to 10,770±120 BP (SFU-454) and 9990±150 BP (RIDDL-393; Driver, 1988), indicating precisely the same interval for open woodland or grassland conditions. The pollen record indicates that between about 11.7 and 11.5 ka BP an open poplar woodland was present in the Saddle Hills. From 11.5 to 11.3 ka BP a transition occurred to local coniferous forest; however, the region's modern grasslands probably developed *in situ* out of the early postglacial flora (White and Mathewes, 1986).

In the late 1970s and early 1980s, C.S. Churcher and the author conducted a reconnaissance in this region, concentrating on gravel pits in the Peace River, Watino, and Grande Prairie areas. We visited local museums to examine and describe specimens, and also recovered new specimens from spoil piles or from pit operators (Churcher and Wilson, 1979; Wilson and Churcher, 1984). Among the specimens examined were three measurable mature male crania (Table 2), one from terrace gravels at Watino (N. Boisvert collection, B-1), one from a pit on the Wapiti River south of Grande Prairie (Grand Prairie Pioneer Museum, GPPM-18), and a third from the Lane Pit at Peace River (University of Calgary Archaeology, UC79.53.1). The second and third

TABLE 1. Radiocarbon dates for bone samples from pits in the Peace River region

Pit and location	Date rcybp		Sample
Lower Terrace, Watino	10,975±175	BGS-1016	bison tibia ¹
Gabler Pit, Grande Prairie	10,220±140	AECV-	bison ²
Upper Pucci Pit, Watino	10,200±100	GSC-2895	bison cervical ³
Upper Pucci Pit, Watino	10,200±100	GSC-2902	bison tibia ³
Wakaluk Pit, Watino	9920±220	AECV-272c	wapiti ⁴
Lane Pit, Peace River	9880±130	GSC-2865	bison tibiae ³
Wakaluk Pit, Watino	9075±305	S-2614	wapiti ⁵

¹Wilson, unpublished (courtesy of D. Fedje, Parks Canada). ²J.A. Burns, unpublished. ³Wilson and Churcher (1984). ⁴Driver (1988). ⁵Burns (1986).

TABLE 2. Measurements (in mm) of *B. bison antiquus* crania from Peace River region

Measurement	UC79.53.1	GPPM-18	B-1	CP
1. Spread of horn cores, tip-to-tip	(820)*	935+(990)
2. Greatest spread of cores on outside curve	(820)	(990)
3. Core length, upper curve	(230)	350
4. Core length, lower curve	(265)	410
5. Chord, tip to upper base	(220)	320
6. Vertical diameter of core	(101)	120	126	(125)
7. Basal circumference, core	(300)
8. Greatest width, auditory	(265)	...	297	(310)
9. Width of condyles	130	144	131.5	(150)
10. Depth, occipital crest to top of foramen magnum	109	121	108	115
11. Depth, occipital crest to bottom of foramen magnum	151	157	145	155
12. Transverse diameter, core	(102)	125	...	130
13. Width between core bases	275	262	265	285
14. Width of cranium between horn cores and orbits	340	325	304	316
15. Greatest postorbital width	(370)	(378+)	...	(340++)
16. Anterior orbital width at notch	(260)	(240+)

* Values in parentheses are approximate.

are clearly of *antiquus* morphology; the first is incomplete but consistent with such an assignment. The Wapiti River specimen is remarkable in exceeding the range for *antiquus* as published by Skinner and Kaisen (1947) and therefore provides a link with earlier bison of 'southern' morphology. Its size is consistent with that expected for 11,000-year-old bison on the basis of the chronocline for the northern Great Plains (Wilson, 1980). The Lane Pit specimen, figured by Wilson and Churcher (1984), is heavily abraded but clearly exhibits the broad frontals and laterally directed horn cores of typical *antiquus* (angle of posterior deflection, 83°). Both Lane Pit and Wapiti River specimens show proximal depression of cores and arching of frontals as in *antiquus*; neither has any strong resemblances to *occidentalis*. Two other specimens, one from near Grande Prairie (figured by Wilson and Churcher, 1984) and the other from a pit near Fort St John, B.C. (SFU Archaeology Collections) have horn cores broken away but again exhibit broad, arched frontals and (from basal characteristics) laterally directed horn cores. Measurements for the latter (coded 'CP' for 'Chilly Pit') are given in Table 2; although most can only be estimated they underscore the great size of these bison.

We were unable to locate any specimens from early alluvium that resembled *B. bison occidentalis*. Local museum collections included several specimens in the large *B. b. bison*/small *B. b. occidentalis* range, some of them bleached and apparently of recent vintage. The largest in the Grande Prairie Pioneer Museum (GPPM-20), had a tip-to-tip horn core measurement of 689 mm, while the largest in the Peace River Museum measured

755 mm. The latter could be of Early Holocene age, based upon its size, but all others appear to be of Late Holocene age.

DISCUSSION AND CONCLUSIONS

The abundance of grazing mammals in Alberta and adjacent areas between ca. 11.5 and 9.75 ka BP is consistent with Guthrie's (Guthrie, 1982, 1985) view of a productive "mammoth steppe" at least as far north as the Peace River region. Pollen records suggest that an open poplar woodland with major grassland patches could have been established. The record suggests that a fauna of southern vertebrates arrived first, through a steppe corridor on the plains from refugia to the south. Bison from this early fauna are referable to *B. bison antiquus*, and early bison from the Peace River region appear assignable to this taxon. The 11 ka fauna in southern Alberta, including *Camelops*, has no counterpart in the river gravels of northern Alberta and aside from bison and its members appear to have southern affinities. The presence in western Canada of mammoths, horses, camels, southern-phenotypic bison, and bighorn sheep is consistent with the view that an opening did exist to the south, and that they moved northward through this steppe corridor in the Late Pleistocene. The people who used fluted projectile points at Charlie Lake Cave may have been another element in this northward movement. Pollen records indicate that a continuous steppe-like vegetation was present to the north in the ice-free corridor from ca. 10.5 ka only until about 10 ka BP, after which time this

corridor was locally blocked by spruce forest. An incursion of northern bison (*B. bison occidentalis*) into the northern plains area occurred while this 'window of opportunity' was present. The most parsimonious explanation for the record of bison in western Canada is that very large *antiquus*-like individuals represent in part the 'missing links' between small *B. latifrons* (= *B. alleni*) and smaller *antiquus*; and that the southward pulse of *occidentalis* swamped the remaining population of *antiquus* in a southward genotypic onlap. What happened in the south on the open plains is open to speculation. Both Wilson (1974) and McDonald (1981) have presented evidence that *antiquus* and *occidentalis* interbred on the plains, and some modern bison retain what appear to be southern phenotypic, if not genotypic, characters. The detailed pattern of genotypic onlap remains to be documented through exhaustive study of well-dated Holocene crania from the midcontinent.

Although differences exist between palynologists and vertebrate paleontologists regarding the nature of the 'steppe-tundra', both the palynological and vertebrate records indicate that the ice-free corridor was closed to the passage of large grazers around 10 ka BP as a result of the establishment of a spruce forest barrier.

If the foregoing model is acceptable, it is possible to suggest that areas opened after 10 ka BP (for example, much of southern Manitoba) should yield primarily bison referable to *B. bison occidentalis*. The early bison at Charlie Lake, British Columbia, are most likely to be *B. bison antiquus*. Future collection of material from the corridor and adjacent areas will allow detailed testing of the scenario presented above. Of considerable interest is the likelihood that the incursion of northern bison post-dates the earliest dates available from the southern corridor area, so that southern bison were established in western Canada before the arrival of their northern relatives. Even if bone dates are taken as approximations, the dates establish a pattern that could be of considerable importance in unraveling the history of passability of the corridor and hence of its role in the early peopling of the midcontinent by humans. A bison described by Aplan and Harington (1994) from the Peace River region, if properly identified, may indicate the arrival of *B. bison occidentalis* as early as 10,500 BP; however, the described cranial material (a horn core that disintegrated in the field) appears insufficient for identification.

The rapidity and pervasiveness of the changeover in bison populations seems to defy an explanation rooted in the punctuated equilibrium model of evolution or in phenotypic change as a result of climatic change, and are more consistent with a sudden population influx through the newly opened corridor. Such a sudden incursion of bison could conceivably have caused the extinction of southern forms, through introduction of diseases. If, on the other hand, *antiquus* had disappeared for other reasons barely before arrival of *occidentalis* from north the visibility of such an extinction event might be beyond the resolution of radiometric dating.

Thus far, no late-glacial bison in western Canada have been dated in excess of 11,500 rcybp. If a steppe-tundra

was established before that time, the absence of bison with either southern or northern affinities seems inexplicable. Outburst floods have undoubtedly removed a part of the record by scouring gravel fills from valleys, but it is highly unlikely that they could have completely obliterated the earlier fossil record of a gregarious herbivore such as the bison.

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