

Latest Pleistocene Vertebrates in Western Canada: Northward Dispersal of Late-Glacial to Postglacial Faunas in Two Contrasting Environmental Settings

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This paper discusses the arrival of terrestrial vertebrate faunas in western Canada after the Last-Glacial Maximum (LGM). Two case histories are described, one from the northern Great Plains (in particular, Alberta) and the other from southwestern British Columbia. Special emphasis is placed upon evolutionary change and relationships in bison (particularly *Bison antiquus*), given their occurrence in both areas. Differences in display morphology (horn cores) provide an opportunity to examine the interplay between dispersal and morphology in light of dispersal theory, as elucidated by V. Geist (1971), and in relation to the differing environmental settings.

Laurentide and Cordilleran LGM ice sheets separated northern (Beringian) and southern (midcontinent) North American vertebrate faunas. Evidence had suggested Beringian animals migrated south into the midcontinent as a dispersal corridor opened between retreating ice sheets. Such species would have included giant bison (*Bison priscus*), woolly mammoth (*Mammuthus primigenius*), muskox (*Ovibos moschatus*), caribou (*Rangifer tarandus*), and wapiti (*Cervus elaphus*). It was thought that admixture of Beringian and midcontinent bison between 11,000 and 10,000 ¹⁴C yr BP (~13,000 and 12,000 cal BP) gave rise to the modern bison lineage, through *B. occidentalis* to *B. bison* (see summary of views in Wilson 1996). While some Beringian species appear to be present on the northern plains, evidence is building for a strong northward movement of southern species, especially the bison. Important information is available from the Bighill Creek Formation (BCF), with two faunules (ca. 11,500-10,750 and 10,200-9800 ¹⁴C yr BP, bracketing the Younger Dryas cold climatic episode), and from the coeval Wally's Beach Site, both from southern Alberta. Instead of Beringian *Bison priscus* we see southern *B. antiquus*, confirmed by mtDNA from a BCF specimen as ancestral to modern plains and wood bison (Wilson et al. 2008). BCF and Wally's Beach southern elements also included mammoth (*Mammuthus* sp.), helmeted muskox (*Bootherium bombifrons*), large mountain sheep (*Ovis canadensis catclawensis*), camel (*Camelops* sp., cf. *C. hesternus*), and horse (*Equus* sp., cf. *E. conversidens*), suggesting a steppe environment with riparian woodlands. The mammoth may have been Columbian mammoth (*M. columbi*), well documented to the south, and a second horse species was likely also present. Beringian bison did reach northeast British Columbia before 10,000 ¹⁴C yr BP (Charlie Lake Site) but were blocked, possibly by a forest barrier as is suggested by regional vegetation reconstructions. Although a brief pioneer community of steppe-tundra with *Artemisia* and *Shepherdia* is documented at the base of pollen cores in this region, evidence suggests a narrow, northward-moving band of coniferous forest close to the retreating ice front (Strong and Hills 2007). *C. elaphus*, a versatile grazer-browser, was a late arrival from the north, apparently new to the midcontinent in postglacial times. *R. tarandus* is documented from the BCF but is known to have been already south of the ice sheets in LGM times. Northward movement of southern grassland-adapted species could have been constrained by forested conditions even further southward on the Great Plains until after the Late-Glacial Maximum.

Discoveries of post-LGM *B. antiquus* crania and other skeletal material on the San Juan Islands, Washington, and on southeastern Vancouver Island (SJ-VI) indicate their presence in both areas between ~12,000 and 10,800 ¹⁴C yr BP. A lower relative sea level may have facilitated

their dispersal across a filter corridor, though narrow water barriers likely still remained (Wilson et al. 2009). They represent a community of steppe-adapted species moving northward from Washington as Cordilleran ice retreated, and pollen cores from this time indicate open pine parklands with grassland patches and stands of poplar. Finds from the San Juans also indicate the presence of Jefferson's ground sloth, *Megalonyx jeffersonii*, giant short-faced bear, *Arctodus simus*, and deer, *Odocoileus* sp. *Megalonyx* was likely a riparian zone browser but its wide distribution in North America suggests considerable dietary breadth. Mountain goats (*Oreamnos americanus*) were also present on Vancouver Island, though they do not occur there today, and likely dispersed northward when the ice sheets were still locally disintegrating (~12,500 ¹⁴C yr BP).

Dispersal theory predicts that ungulates moving into newly available, productive environments will increase in body size and will exaggerate the development of energetically costly display morphology, such as horns or antlers. The northern Great Plains sample appears to show this, with *B. antiquus* crania having longer, more massive horn cores than are known from earlier (~LGM) samples such as La Brea, California. Body size was comparable to La Brea bison, if not larger, but body size and horn core size trends were not necessarily directly covariable. Their independence despite linked causation is demonstrated by the SJ-VI *B. antiquus*, which have comparably large bodies but significantly smaller horn cores. Though these bison did move into newly available territory, they soon experienced insular conditions and habitat fragmentation, and horn-core reduction could have been the initial response. The disappearance of SJ-VI bison apparently took place early in the Younger Dryas, at which time the open pine parklands were giving way to mixed coniferous forests, a habitat type unfavorable for grazing ungulates.

It is important to note that a shift in cranial morphology of bison from laterally-directed, downswept horn cores ("classic" *B. antiquus* type) to a more backward-deflected, more upswept pattern ("*B. occidentalis*"- like) took place not only on the Great Plains but also on the San Juans and Vancouver Island. A degree of such change occurred in SJ-VI between 11,750 and 10,900 ¹⁴C yr BP, and that in southern Alberta between 11,300 and 10,000 ¹⁴C yr BP. Given the temporal overlap and the small samples from both areas, there is no clear evidence as yet that it was earlier in one than the other. A synchronous pattern could suggest a widespread environmental cause, of which the onset of the Younger Dryas cold episode and the arrival of humans as predators would be possible candidates. A diachronous pattern could support an evolutionary change followed by gene flow or direct dispersal but seems unlikely given the short timespan.

The northern Great Plains bison record further indicates the onset of body size reduction by or before about 10,000 ¹⁴C yr ago, a possible response to human predation. Predation could have brought adaptive pressure in favor of more rapid growth and earlier maturation to maintain if not improve reproductive success. This would have been reflected in decreased body size, decreased display organs (horn cores), and probably also cranial proportions. Decreasing size is also noted between Late Pleistocene and Holocene bighorn sheep, with the ~10,000 ¹⁴C yr old archaeological sample from the Vermilion Lakes site, near Banff, Alberta, being intermediate in size between BCF and modern bighorns. A camel from the BCF is also of interest in that a recovered metapodial is proportionally shorter than in *C. hesternus* from La Brea, California, though comparably robust. Whether this represents geographic variation or more significant differences is not clear.

Nearby Late Pleistocene finds from Montana document *Bootherium bombifrons*, *Bison antiquus*, *M. columbi* (= *M. imperator*), *O. canadensis*, *Camelops* sp., and *Equus* sp., cf. *E. niobrarensis*. It is likely that two species of horses did co-occur on the northern plains at this time. Northern

plains finds from Canada and Montana also include the carnivores *Arctodus simus*, *Miracinonyx trumani*, and *Panthera atrox*. These have not been directly dated but could be post-LGM. Direct dating of a *B. bombifrons* cranium from post-LGM gravels at Fort Saskatchewan, Alberta, indicates that it was redeposited from pre-LGM (“mid-Wisconsinan”) deposits; so stratigraphic occurrence is not sufficient to indicate antiquity. Finds of *M. primigenius* are known from the northern plains and (if not redeposited) it remains an open question as to whether they represent a post-LGM southward dispersal or populations that moved southward during the LGM advance, becoming isolated from Beringia and persisting along the southern ice margin. Such questions underscore the urgent need for direct dating of all specifically identifiable specimens as well as efforts to recover DNA to facilitate phylogenetic analyses.

It is also noteworthy that these animals must have exerted significant influences in both areas upon the establishment and early succession of vegetation communities. Bison have been portrayed as keystone species for the late Holocene Great Plains grassland and a similar role can be hypothesized for their Late Pleistocene populations. Ungulates were influential in terms of zoochory (importation of plant propagules on the pelage or in the gut). Selective herbivory, grazing intensity, and physical effects such as trampling would have further influenced succession. Large mammalian predators in turn controlled herbivore population levels, indirectly influencing plant communities in a top-down trophic cascade, as has been well documented for modern wolves, elk, and aspen stands in Yellowstone National Park (Ripple and Beschta 2007). Thus I argue that the history of early postglacial vegetation communities must be understood in light of the vertebrates with which they coexisted. Given evidence from human predation on bison and other megafaunal species from ~12,000 or 11,500 ¹⁴C yr BP onward, it is likely that humans also played such a top-down role in influencing Late Pleistocene and Holocene vegetation succession. Thus models of vegetation history that focus upon climate as an explanatory device must be augmented by consideration of top-down trophic influences.

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