

End of the Pleistocene: elk-moose (*Cervalces*) and caribou (*Rangifer*) in Wisconsin

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Fossils of caribou (*Rangifer tarandus*) and elk-moose (*Cervalces scotti*) were found in a Wisconsinan–Holocene outwash bog on Kluck Farm, near Bevent, Marathon County, Wisconsin. These caribou fossils are the northernmost records for the state, and the extinct *Cervalces* the 1st known from the state and northernmost record for the species. The site is located at the mapped ice front of the Green Bay Lobe of the late Wisconsinan Valder's Readvance, which was present between 12,500 and 11,500 years before present. Examination of accelerator mass spectrometry ^{14}C data indicated that the elk-moose was older than the caribou by 1,600–1,700 years. Matching the radiocarbon dates with those of nearby sites and to their pollen records helps to clarify the nature of climatic conditions and corresponding plant communities at the upper Pleistocene boundary. The pattern of replacement of taiga forest southward and westward of the Green Bay Lobe to warmer, open-range conditions, with invading prairie, pine (*Pinus*), and deciduous trees, resembles changes that took place earlier, when glaciers and cool climate occurred south of the late Wisconsinan ice fields. Perhaps cursorial carnivores preyed on the large cervids, which were made more visible in openings of the taiga and grassland and by the typical succession expected of boreal wetlands to dry prairie or park-like savanna copses of spruce (*Picea*), oak (*Quercus*), and pine.

Key words: *Cervalces*, Green Bay Lobe, megafauna, Pleistocene–Holocene boundary, *Rangifer*, Wisconsinan glaciation

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Establishment of the Pleistocene and subsequently the modern mammal fauna in what today is Wisconsin and Upper Michigan resulted from the dispersal of mammals from southward, eastward, and westward of this heavily glaciated region following deglaciation. In the last but not least extensive of the major glacial events documented in Wisconsin the Wisconsinan ice covered most of the state, except in the center and southwestern Coulee region. Beyond the ice fronts, indicated by the moraines of accumulated gravel, boulders, and sand outwash, mostly boreal woodlands—taiga: spruce (*Picea*), tamarack (*Larix*), and fir (*Abies*), and probably aspen (*Populus*) and willow (*Salix*)—were present. As the glacial ice receded westward, northward, and eastward (see Aber and Apolzer 2004) due to climatic warming a dramatic replacement, near retreating ice masses, of boreal trees from spruce and tamarack to white pine (*Pinus strobus*) and eventually oak (*Quercus*) and other deciduous trees (West 1961) occurred in central Wisconsin. Eventually, some brush and wooded savanna and arid grasslands appeared, with extensive marshes and scattered local peat bogs created by glacial melting.

The known Pleistocene vertebrate fossils (Fig. 1) of what now is Wisconsin, ranging from about 12,500 to perhaps 9,500

^{14}C years before present, were arctic or boreal species adapted to tundra and arcticlike climate, prevalent in the region during Wisconsinan glaciation. The end of the Pleistocene Epoch, defined as when and where the Wisconsinan ice vanished altogether in Wisconsin (Clayton and Moran 1982; Faith and Surovell 2009), was marked by the deposition of fresh sediments of clean outwash sands, some subsequently buried by organic deposits of decaying plants in bogs and marshes that developed along the ice front. In these stream deposits and wetland assemblages some large mammals also were buried and preserved (West and Dallman 1980). The late- and post-Wisconsin fauna of Wisconsin included large boreal mammoths (*Mammuthus*) and mastodons (*Mammut*; Fig. 1) and the giant beaver (*Castoroides*—West and Dallman 1980). Large-bodied caribou (*Rangifer tarandus*) ranged through bogs and marshes at that time (Long 1986; West 1978).

We report a new record of caribou northward of all other Wisconsin records and the 1st record of the elk-moose



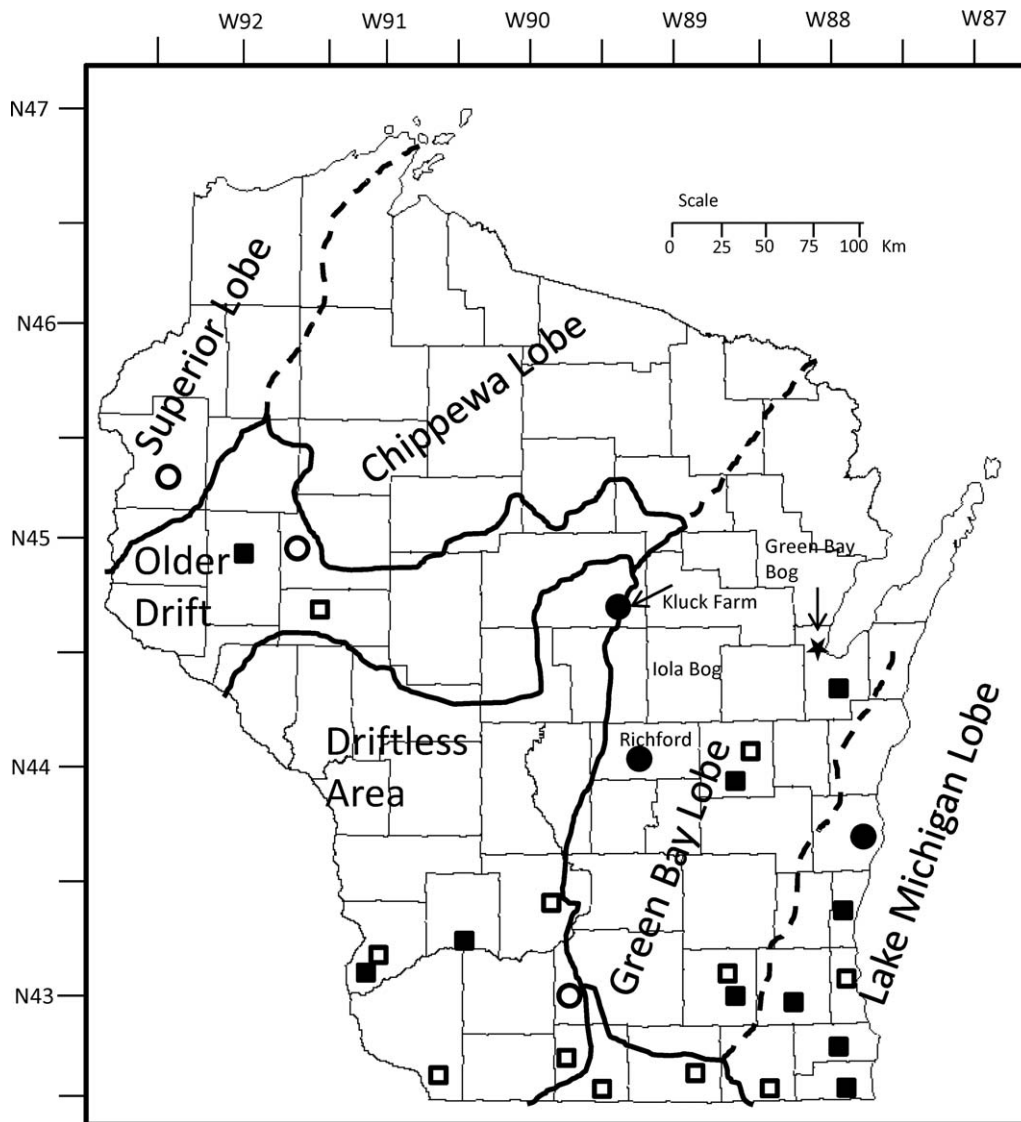


FIG. 1.—Map of the caribou (*Rangifer tarandus*) and elk-moose (*Cervalces scotti*) Pleistocene boundary site in Marathon County, Wisconsin, and the Wisconsin counties showing important fossil sites and the extent of glacial Wisconsinan ice fronts. Megafauna sites in Wisconsin: black circles = caribou, open circles = bison, black squares = woolly mammoth, open squares = mastodon. Kluck Farm site for elk-moose and caribou. Iola Bog and Two Creeks Forest site (labeled Iola Bog; creeks are Peter's Quarry and Duck Creek) provide vegetation successions where the glacial ice was wasting and had receded.

Cervalces for the state. We compared these cervid fossils with those of other dated sites, including nearby deposits from near Green Bay and from western Waupaca County, and to a caribou record 60 km south, extracted from a bog in Waushara County. Our objective was to place these fossils within the associated habitats that existed along the wasting glacial front.

MATERIALS AND METHODS

The fossil cervid specimens, now housed in the University of Wisconsin–Stevens Point (UWSP) Museum of Natural History mammal collection (*Cervalces* UWSP 8440, *Rangifer* large UWSP 8441, and *Rangifer* small UWSP 8442), were excavated with a dragline during creation of a small pond where brush and grasses covered a depression of higher

ground. These remains were recovered from the Kluck Farm near Bevent (44°45.55'N, 89°26.10'W, elevation 368 m) in eastern Marathon County, Wisconsin. The caribou and elk-moose were buried in the same shallow sediments that accumulated in a bog now overgrown with grasses, forbs, and brush, located beneath the mapped western ice front of the former Green Bay Lobe of the Laurentide ice sheet (Aber and Apolzer 2004; Syverson and Colgan 2004). This grand glacial expanse extended southward along Lake Michigan and was confluent eastward with the great mass of ice in Lake Michigan extending westward of the lake basin (i.e., the Lake Michigan Lobe). The Green Bay Lobe did not cover central Wisconsin, extending at the maximum of the Valder's Readvance a little beyond the vicinity of the Kluck Farm site. The specimens were compared with modern specimens

TABLE 1.—Accelerator mass spectrometry (AMS) radiocarbon dates on *Cervalces* and *Rangifer* from the Kluck Farm site, Marathon County, Wisconsin.

Specimen	Lab no.	AMS date, ¹⁴ C years before present ± 1 σ	δ ¹³ C value (‰)	2-σ range, calendar years before present (IntCal04) ^a
<i>Cervalces</i>	Beta-237597	10,850 ± 60	−20.0	12,920–12,790
<i>Rangifer</i>	Beta-237598	9,790 ± 50	−18.8	11,260–11,170
Difference		1,060 years		1,660–1,620 years

^a Reimer et al. 2004.

of moose and caribou in the UWSP mammal collection. Measurements were made in millimeters with dial calipers or a flexible meter rule. We define the morphology of an antler as follows. Proximally a pedicel and its burr arise on each side of the skull. The beam is the main trunk (called a pedicel by Scott [1885]). The tines or spikes are expanded (flattened) somewhat on a moose antler, and the large palmate portion of a moose antler is the massive (and heavy) bony expanse from which the small expanded tines develop.

Approximately 10–15 g of bone material (antler) was removed from the *Cervalces* (UWSP 8440) and 1 of the *Rangifer* specimens (UWSP 8442) for accelerator mass spectrometry ¹⁴C dating. The accelerator mass spectrometry ¹⁴C analysis was done by Beta Analytic Radiocarbon Dating Laboratory (Miami, Florida). During pretreatment material was 1st tested for friability to determine quality of the collagen fraction. Each sample was then washed in deionized water, and the surface was scraped free of the outermost layers and then gently crushed. The samples then were treated with dilute, cold HCl, and this was applied repeatedly and replenished until the mineral fraction was eliminated. The collagen fraction then was dissected and inspected for rootlets to reduce contamination from modern material. Finally, the collagen material was extracted with NaOH to ensure absence of secondary organic acids. Each sample provided sufficient carbon for accurate measurements. Accelerator mass spectrometry results were derived from reduction of sample carbon to graphite (100% C), which was then detected for ¹⁴C content in an accelerator mass spectrometer (National Electrostatics Corp., Middleton, Wisconsin).

The uncalibrated conventional radiocarbon age (radiocarbon years before present, with “present” = 1950 AD) was reported with a standard error of ± 1 sigma (σ; >68% probability) and was based on combined measurements of the sample, background, and modern reference standards. Because of fluctuations in atmospheric ¹⁴C, radiocarbon dates were calibrated using IntCal04 data sets (Reimer et al. 2004). The Pretoria Calibration Procedure program (Talma and Vogel 1993) was applied to convert years before present results to calendar years. This procedure uses splines through hundreds of samples from known-age tree rings of oak, sequoia, and fir up to about 10,000 years before present. The spline calibration allows adjustment of the average curve by a quantified closeness-of-fit parameter to the measured points. A single spline is used for the precise correlation data available back to 9,900 year before present for terrestrial samples. Beyond that, splines are taken on the error limits of the correlation curve to

account for the lack of precision in the data points. The reported calendar age ranges represent a 2-δ calibrated result (95% probability).

We followed the precedent of defining the upper boundary of the Pleistocene as the end of the Wisconsinan glaciation, and specifically the end of deglaciation particularly of the Green Bay Lobe. Glaciers might have lingered in northern Wisconsin and Upper Michigan, within the lake basin for a time, and in montane climates in the Rocky Mountains (where many are present today). Likewise, northern remnants existed in Canada of the melting and retreating Laurentide ice sheet. However, the Wisconsinan was the last grand ice age or glacial epoch, and its termination in Wisconsin about 11,300 years before present (Clayton and Moran 1982), and the 10,000 years accepted for final wasting of all the ice, is a useful demarcation or pragmatic stratigraphical boundary between Pleistocene or the Wisconsinan and Recent or Holocene time. Pollen records in the state are numerous and provide the most accurate depiction of plant communities for this region following deglaciation (Jacobson et al. 1987; West 1961).

RESULTS

Caribou (Rangifer tarandus).—Two caribou antlers were excavated at the Kluck Farm site. A small caribou specimen (UWSP 8442) was found at a depth of 3 m and could be from a young animal or a female. The antler was partly damaged and appears to be a shed spike. The accelerator mass spectrometry ¹⁴C data estimated age of this specimen was 9,790 ± 50 years before (Beta-237597). Calibrated dates calculated because of fluctuations in atmospheric ¹⁴C were 11,260–11,170 cal years before present (Table 1). The larger caribou was excavated at a depth of 3.3 m. The larger caribou specimen (UWSP 8441; Fig. 2) was a shed antler consisting of the pedicel, part of the brow tine, and main beam. Measurements of this specimen were as follows. From the burr to the tip of the broken main beam the length was 502 mm, and from the burr to the broken-off brow tine length was 241 mm (Fig. 2). The bone was somewhat mineralized, and clay had invaded the spongy bone area. The larger caribou antler differed somewhat from other Wisconsin antlers in its absence of a 2nd palmate extension jutting forward over the forehead and away from the main beam. Caribou can have 1 or 2 brow tines extending forward. Distally, a broken, flat extension existed where the main beam curves upward, and 30 mm beyond that was a sharp, thornlike point (length = 35 mm). Curvature of the antler was inward,

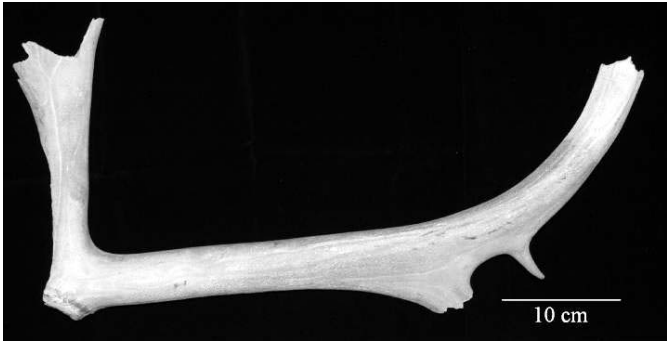


FIG. 2.—Caribou antler (UWSP 8441) from the Kluck Farm site. This fossil was collected in September 2002 at a depth of approximately 3.3 m.

and that of the brow tine was on the left. We have no radiocarbon data for this specimen, but it was in close proximity and depth to the smaller record.

Scott's elk-moose (*Cervalces scotti*).—The elk-moose (UWSP 8440) was the 1st record of this species for Wisconsin. The specimen was dark brown and more heavily mineralized than the tan (large) and bone-white (small) caribou remains. The accelerator mass spectrometry ¹⁴C data estimated age of this specimen was 10,770 ± 60 years before present (Beta-237598). Calibrated dates calculated because of fluctuations in atmospheric ¹⁴C were 12,920–12,790 cal years before present (Table 1). A large part of the cranium was preserved (Figs. 3 and 4). Separate from the cranium was part of the left palmate antler (Fig. 3) and a shorter segment of the right antler. We measured the left antler using the dimensions in Churcher and Pinsof (1987) and compared our specimen with those of McDonald (1989). We also provided measurements from the basicranium (Table 2).

Although preserved parts of the cranium resembled modern moose (*Alces americanus*) skulls, the resemblance was not diagnostic because this rare species more closely resembled moose in the posterior than anterior of the skull. The only obvious character that differed from *Alces* in our specimen was the long beam leading to the palmate part of the antler. A few *Alces* do show elongate beams (Cory 1912). The form and position of our antler are important diagnostic characters of



FIG. 3.—Left antler and ventral aspect of basicranium of *Cervalces* (UWSP 8440). Note the tubercles on the basioccipital and basisphenoid bones. This fossil was collected in May 2006.

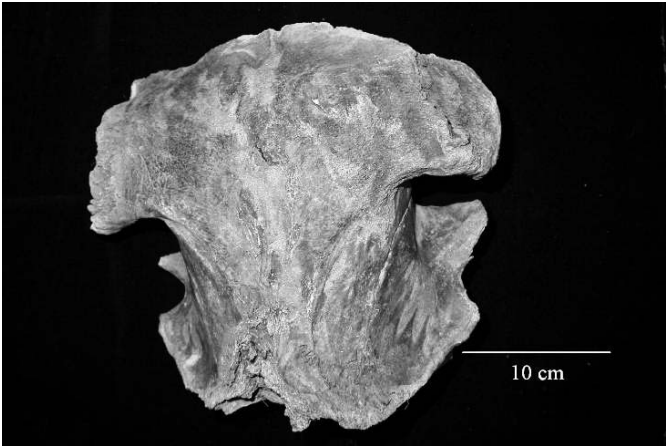


FIG. 4.—Dorsal aspect of the cranium of *Cervalces* (UWSP 8440) showing smoothly rounded frontals, parietals, and supraoccipital. Note the lack of a raised superiminent crest, as found in *Alces*.

Cervalces scotti (Fig. 3). The drawing of a *Cervalces* skeleton from New Jersey, called *C. americanus* (Scott 1885), is the best description available of a preserved specimen and provides evidence that the fossil from Wisconsin is *Cervalces*.

TABLE 2.—Measurements (mm) of the antler beam of *Cervalces* (UWSP 8440) from this study compared to those from specimens from McDonald (1989). Dimensions after Churcher and Pinsof (1987). The last 3 measurements pertain to the cranium.

Dimension	DMNH G-28338	G-28378	UWSP 8440
Maximum diameter of burr	67.9	59.5	84.5
Minimum diameter of burr	61.6	47.5	75.7
Maximum diameter of beam at 50 mm	55.9	45.2	57.0
Minimum diameter of beam at 50 mm	48.7	41.4	54.9
Maximum diameter of beam at 100 mm	53.0	44.3	53.5
Minimum diameter of beam at 100 mm	46.4	40.1	52.5
Length of beam at anterior margin			
Maximum	270	245	290
Minimum	220	190	210
\bar{X}	245	217.5	250
Length of beam at posterior margin	340	—	320
Circumference of burr	205	170	255
Circumference of beam at 50 mm	175	140	180
Circumference of beam at 100 mm	160	137	172
Diameter above the pedicel break		59	
Basioccipital length from posterior to anterior tubercles			63.4
Width across tubercles of <i>musculus rectus capitis ventralis minor</i>			56.0
Width across tubercles of <i>musculus rectus capitis ventralis major</i>			26.1

Our left antler differed from *Alces* by the longer cylindrical beam (Fig. 3), which was longer than Scott's (1885) elk-moose. Both antler beams are cylindrical, which suggests that the palmate portion of the antler in *Cervalces* was not as heavy as in modern *Alces* (i.e., short, circular beam). Our left fossil antler was better preserved than the right. It conjoined perfectly with the broken pedicel of the left frontal, indicating that the antler still was attached to the cranium at the time the animal died. When the antler and frontal were conjoined, the entire structure, with horizontal beam and antler thrusting upward but also flaring back and becoming palmate, further indicated *Cervalces* (Fig. 3). The antler closely resembled the left antler of an elk-moose from Ohio (McDonald 1989). Although our *Cervalces* seemed larger in its cranial bones, the burr of the antler seemed slightly smaller than in large modern moose. Measuring to the inflection point of curvature of expansion, after proceeding along the elongate cylinder, distance was 275 mm toward development of the 1st tine, and toward the palmate expansion a distance greater than 310 mm (Fig. 3). In our modern moose the distance toward the 1st tine was <200 mm, and as short as 130 mm in one large moose.

Ends of the true pedicels were not well preserved, but the frontals leading to the pedicels, and the pedicels themselves, were inclined less than the upward-directed pedicels of modern moose. This also suggests that the antlers were positioned more horizontally relative to the skull, as in *Cervalces* (Fig. 3). When the bones were conjoined, the interantler width was about 81 mm. In a large modern moose the same distance was approximately 10% less. The cranium of our specimen was larger than those of modern moose from central Wisconsin and southern Ontario but not as large as in some Alaskan moose. We compared the fossil with our specimens of *Alces* expecting to find some subtle, but significant differences, especially in the ear region. However, we found no differences in this region; the external auditory meatus, alisphenoid, glenoid fossa of the squamosal, sutures of parietals, frontals, and basioccipital were similar. The lambdoidal crest was more pronounced in our *Cervalces* specimen, but this was an age-related character.

The modern moose resembled *Cervalces* in the posterior parts of the skull, but the anterior was adapted more for browsing in marshes and along streams, particularly with respect to elongation of the anterior portion of the maxillae and premaxillae and the shortening of the nasals in *Alces*, characters not present in *Cervalces*. The antlers of *Alces* are elevated and shortened, for moving through brush, but the antlers of *Cervalces* are low and sweeping, seemingly a better defense against pack carnivores in more-open habitats. The ventral portion of the cranium in *Cervalces* was different from the *Alces* in our collection. Both McDonald (1989) and Schubert et al. (2004) thought that morphological differences in tubercles located on the basioccipital and basisphenoid might reflect differences between the genera. These paired tubercles provide muscle attachment of the *musculus rectus capitis ventralis minor*, located on the posterior end of the basioccipital bone, and the *musculus rectus capitis ventralis*

major, extending from the anterior end of the basioccipital onto the basisphenoid (Fig. 3). In the Kluck Farm *Cervalces* the tubercles for the *m. r. c. v. minor* were more equidimensional in orientation than the same tubercles in *Alces*, which were narrow and more pronounced. Although Scott (1885) found these structures similar to those in *Alces*, our observations corroborated McDonald (1989) and Schubert et al. (2004) in supporting the utility of this character in distinguishing the 2 taxa. We also noted that although the length from the posterior margin of the paired tubercles of the *m. r. c. v. minor* forward to the anterior margin of the paired tubercles of the *m. r. c. v. major* was about the same in *Alces* (UWSP 70) and *Cervalces* (63.4 mm and 63.2 mm, respectively), the width across the tubercles narrowed more dramatically posterior to anterior in *Alces* (from 66.4 mm to 18.8 mm) than in *Cervalces* (56 mm to 26.1 mm; Table 2). The top of the cranium in the Kluck Farm *Cervalces* (Fig. 4) was indistinguishable from both Lang Farm (Schubert et al. 2004) and Wildcat Swamp (McDonald 1989) specimens. The top of our fossil skull was rounded gently and smoothly from one side to the other. In *Alces* the top of the skull is markedly raised middorsally and developed into a supereminent crest.

DISCUSSION

Caribou (Rangifer tarandus).—The Kluck Farm site is situated in a small, shallow depression with brush and grass cover and is situated midway between the courses of the Little Eau Claire and Plover rivers, which drain south into the Wisconsin River. The Richford Township site, located 80 km south of the Iola Bog, was in sandy till south of the moraines. Both caribou sites were located near the western front of the Green Bay Lobe. West (1978) determined the age of another caribou from a few kilometers farther south of the Richford site, from peat eastward of the Green Bay Lobe, at 12,500 ¹⁴C years before present. The older age of the southern Wisconsin compared to those of the 2 northern sites reflects its occurrence beyond the wasting ice margin. Both the Kluck Farm site and the Richford site were within the mapped range of the former glacial ice of the Green Bay Lobe. Therefore, time of burials of the northernmost caribou occurred when the ice was receding from eastern Wisconsin and places the age of these specimens at 12,000–11,200 ¹⁴C years before present, and similar to those indicated by dates for climatic warming recorded from pollen profiles from the Iola Bog, Peter's Quarry, and Duck Creek, near Green Bay (at the Two Creeks Forest site). These sites date to 11,640–11,850 ¹⁴C years before present, just after the Valder's glacial advance (Syverson and Colgan 2004). Black spruce (*Picea mariana*) and tamarack (*Larix laricina*) forest, likely with aspens and willow near water, were augmented later by white pine, oak, many composites, and prairie grasses as the overall climate warmed following the Cary and later Valder's readvances of the Green Bay Lobe (Schweger 1969). Nonglaciated open vistas of prairie, probably with some persisting taiga, represented a dramatic change from persisting conifer forests

TABLE 3.—Representative late-glacial records of *Cervalces scotti* from states in the United States (State) arranged from youngest to oldest based on radiocarbon age. Material from the animal or associated material was used in ¹⁴C dating. Samples denoted with an asterisk (*) used accelerated mass spectrometry technology. Co. = county.

State ^a	Site name	Age, ¹⁴ C years before		Lab no.	Material dated	Latitude (°N)	Reference
		present ± 1 σ					
OH	Carter, Darke Co.	10,230 ± 150		UGA-666	Wood above bone	40.2	Mills and Guilday (1972)
WI	Kluck Farm, Marathon Co.	10,850 ± 60		Beta-237598	Bone collagen*	44.7	This study
NY	Dewey Parr, Orange Co.	10,950 ± 150		I-4016	Bone collagen	41.2	Buckley and Willis (1970)
MI	Shelton Site, Oakland Co.	10,970 ± 130		Beta-10303	Wood with tooth	42.6	Shoshani and Smith (1996)
MI	Powers, Van Buren Co.	11,220 ± 310		Beta-9482	Bone collagen	42.2	Garland and Cogswell (1985)
NJ	Columbia, Warren Co.	11,230 ± 160		I-11335	Bone collagen	41.0	Harington (1984)
IL	Lang Farm, Bureau Co.	11,405 ± 50		CAMS-82932	Bone collagen*	41.5	Schubert et al. (2004)
IN	Kendallville, Noble Co.	11,420 ± 70		CAMS-14809	Bone collagen*	41.4	Farlow and McClain (1996)
OH	Licking Co.	11,500 ± 130		Beta-14060	Bone collagen	40.1	Dyer et al. (1986)
MI	Shelton Site, Oakland Co.	11,770 ± 130		Beta-14266	Wood with jaw	42.6	Shoshani and Smith (1996)
IL	Biddle Farm, Kane Co.	12,070 ± 100		ISGS-2080	Humus	42.1	Graham and Graham (1989)
NY	Pawelski Farm, Orange Co.	12,180 ± 160		Beta-141061	Bone collagen*	41.2	Robinson et al. (2005)
IA	Brayton, Audubon Co.	12,420 ± 420		I-8015	Plant macrofossils	41.7	Baker et al. (1980)
OH	Sheriden Cave, Wyandot Co.	12,520 ± 170		Beta-127907	Dentin collagen	40.8	Tankersley (1999)
IL	Tonica Thermokarst, LaSalle Co.	13,480 ± 120		ISGS-1921	Wood	41.3	Graham and Graham (1989)
NJ	Manasquan Inlet	23,530 ± 170		GX-26619	Bone collagen*	39.4	Becker et al. (2010)

^a State abbreviations are as follows: OH = Ohio, WI = Wisconsin, NY = New York, MI = Michigan, NJ = New Jersey, IL = Illinois, IN = Indiana, IA = Iowa.

growing on moraines left by the Cary and Valder’s advances, which became confluent communities (Schweger 1969). This scenario fits well with caribou from the Richford site (Long 1986; West 1978) and the Kluck Farm site (9,790 ± 50 years before present). The caribou probably followed the retreating boreal habitats northward and subsequently emigrated northward from what is now Wisconsin. The aforementioned specimens of caribou comprise all the Pleistocene–Holocene records from Wisconsin, except probably a human-transported bone from Polk County (Eddy and Jenks 1935) and a poorly documented record from the shore of Lake Michigan (West 1978). According to the genetics work on extant populations of *Rangifer* (Flagstad and Roed 2003), the fossil caribou records from central Wisconsin likely represent part of a distinct refugial area consisting of more southerly distributed woodland caribou. The extant woodland ecotype, which has been seen in nearby northern Minnesota in recent years (Hazard 1982; Long 2008), is characterized by larger body size, long legs, and short and heavy antlers (Flagstad and Roed 2003).

Scott’s elk-moose (Cervalces scotti).—*Cervalces* also is known from other midwestern states, including Michigan (Garland and Cogswell 1985; Hibbard 1958; Shoshani and Smith 1996), Indiana (Farlow and McClain 1996), Ohio (McDonald 1989; Mills and Guilday 1972; Tankersley 1999), Illinois (Schubert et al. 2004), and Iowa (Baker et al. 1980), and several eastern and southern states (see Churcher and Pinsof 1987). Because the ice lasted longer in central Wisconsin than farther southward, a later occurrence of *Cervalces* in Wisconsin would not be surprising. A specimen from central Illinois dated between 13,830 and 13,480 years before present (Graham and Graham 1989) was from farther southward, but one (CAMS-82932) of comparable age (11,405 ± 50 ¹⁴C years before present) was found at Lang Farm, Illinois (Schubert et al. 2004; Table 3). The latest record from a peat bog in Darke County, Ohio, was 10,230 ± 150 ¹⁴C years before present, based on

wood taken from a slightly higher level than where a vertebra was recovered (Table 3). This compares with our record of 10,770 ± 60 ¹⁴C years before present, shortly before wasting of the Green Bay Lobe, the front of which is mapped as extending over the outwash bog from which the *Cervalces* was recovered.

These fossils help clarify the chronologic and geographic relationships of the megafauna relative to the retreating ice front. The *Cervalces* remains seem to be somewhat more mineralized and peat-stained than the caribou and were situated in the lowest sediments (marl and sand) excavated—that is, immediately above pure sand deposited by meltwater—indicating that the animal was living close to the glacial edge. The Green Bay Lobe ice mass was still melting when the *Cervalces* was buried, and meltwater was continuously filling the bog and supporting peat accumulation at least for a period of about 2,000 years, somewhat earlier and below the accepted 10,000-year age boundary. In contrast, the caribou specimens were found higher in the site and were younger than the elk-moose by about 1,600–1,700 years (Table 1). By this time the terminus of the Green Bay Lobe glacial front would have been farther from the bog. Both species at other sites far eastward and southward are interpreted as associated with spruce and periglacial climatic conditions, and our record shows the same preference, during the deglaciation, despite the time difference and relative distance from the glacial front of the specimens.

In proximity to the Kluck Farm site excellent and contemporary geological and palynological localities were available for comparison and provided evidence for the dramatic ecological succession that took place in Wisconsin following deglaciation, with spruce, fir, tamarack, and aspen giving way to white pine, then oak forest and other deciduous woods that transition to dry grasslands, marshy sedge meadows, and composites that were becoming abundant in dry prairies and wetlands. This ecological transformation resembled that found at similar glacially influenced sites, some much earlier in time

and farther southward. The lag of climatic warming as indicated by the glaciers' gradual retreat northward, often interrupted by readvancing, clearly shows that even at the end of their existence glaciers were affecting the flora and fauna in the Lake Michigan and Lake Superior regions.

Although some spruce remains in the region, pollen records from multiple sites show that over the entire Pleistocene of the region the deglaciation period brought a peak of dramatic change in plant communities. White pine was established in the new boreal forests at the expense of spruce and *Ostrya-Carpinus* (West 1961). As the Valder's ice readvanced to its greatest extent, to the Bevent bog (Kluck Farm site), cold and dry climate permitted the arrival of sage (*Artemisia*) and many other forbs and grasses at the expense of abundant sedges. Eventually oak arrived, along with hickory (*Carya*) and other deciduous trees, establishing the climax plant associations familiar in Wisconsin today.

The habitats for *Cervalces* were probably marshes and peat bogs, but these animals also were associated with the spruce-taiga floral community, which corresponds with the *Symbos-Cervalces* faunal province (Martin and Neuner 1978). McDonald (1989) indicated an ecological preference of *Cervalces* for taiga and declining spruce persisting near the wasting Wisconsin Glacier as the reasonable explanation for their association geographically and temporally. Schubert et al. (2004) discussed an Illinois elk-moose from a peat bog dated at $11,405 \pm 50$ ^{14}C years before present from Lang Farm, thought to be the youngest reliably dated elk-moose (Faith and Surovell 2009), with surroundings ranging from tundra-mixed conifer to deciduous woodland, and with spruce abundance in decline. The specimens from Darke County, Ohio (Table 3), might be contemporary with the Kluck Farm specimen taken at the terminus of the Valder's Glaciation, where the Pleistocene ended. Spruce wood, tamarack pollen, and *Populus* wood have been found with other fossils of elk-moose (Dyer et al. 1986; Mills and Guilday 1972). How does our elk-moose match specimens of these other localities relative to its habitat preference? It is currently the northernmost occurrence and occurred during deglaciation of the Valder's ice. Peat staining of bone indicated decaying *Sphagnum* mosses and other plants common in glacial bogs. No study has suggested that the elk-moose or caribou fed on any of these plants, but sedges and willows associated with this type of habitat were likely major food items.

Most of the North American megafauna perished during the rather brief but dynamic episode of warming and wasting ice, with the consequential radical alterations in some plant communities that provided herbivores food and perhaps cover. Faith and Surovell (2009) concluded that 35 genera of Pleistocene mammals vanished in a chronologically synchronous event between 12,000 and 10,000 ^{14}C years before present. *Cervalces* was one such casualty, and the distribution of caribou was altered radically. One of the shortcomings of their work was the paucity of highly reliable radiocarbon dates that could be used to model Pleistocene extinctions. Using the criteria outlined by Pettitt et al. (2003), our samples yielded a

score of 29 of 36, with 27 being their cutoff to be considered highly reliable. With this specimen we move the last appearance date for *Cervalces* from $11,405 \pm 50$ ^{14}C years before present (Faith and Surovell 2009; Schubert et al. 2004) to $10,850 \pm 60$ ^{14}C years before present. Both of these latest records for the species were radiocarbon dated using a similar bone-collagen accelerator mass spectrometry method.

Of the 35 genera of extinct Pleistocene mammals discussed by Faith and Surovell (2009), 6 are known from fossil records from what is now Wisconsin. Their disappearance is coincident with the phenomenon of final deglaciation and disappearance of the Wisconsin ice and the advent of new communities of plants and animals. Although no evidence exists that humans played a role in the decline of elk-moose in Wisconsin, Redmond and Tankersley (2005) found Paleo-Indian tools associated with *Cervalces* fossils at the Sheriden Cave site in Ohio. More plausible was competition among the several herbivorous artiodactyls, between established and invading species, including the appearance of *Bison* from the south and west with the appearance of grassland habitat replacing spruce forest and spruce parkland. A time hiatus stands between the elk-moose and moose (*Alces americanus*) in Wisconsin. Although the modern moose likely arrived in North America 14,000–11,000 years ago, prior to the flooding of Beringia (Hundertmark and Bowyer 2004; Hundertmark et al. 2003), the oldest reliable radiocarbon date, from an antler recovered near Fairbanks, Alaska, was $8,740 \pm 70$ ^{14}C years before present (DIC-2414—Guthrie 1990). Fossil moose from this region of the Great Lakes are most common in the late Holocene between 450 and 4,500 years ago (Faunmap Working Group 1996). Furthermore, the 1st Wisconsin appearance of elk (*Cervus*) and white-tailed deer (*Odocoileus*) also was during the late Holocene (Faunmap Working Group 1996), and thus, these 2 artiodactyl assemblages seem temporally and ecologically exclusive. The close association of caribou and elk-moose with the ice front, and its nearby taiga, bogs, and marshes, surely indicates ecological isolation, enhanced by the invaders' association (as known today) with grasslands, oak forest, and composites that were replacing tundra, taiga, sedge meadows, and willow-lined lakes and streams. Change in the artiodactyl fauna in Wisconsin from *Cervalces* and *Rangifer* in the Pleistocene to that of the Holocene *Alces*, *Cervus*, and *Odocoileus* seems to be closely related to change in vegetation as driven by climatic warming that characterized the Pleistocene–Holocene transition.

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LITERATURE CITED

- ABER, J. S., AND K. APOLZER. 2004. Pre-Wisconsinan glacial database and ice limits in the central United States. Pp. 83–88 in Quaternary glaciations extent and chronology part II: North America (J. Ehlers and P. L. Gibbard, eds.). Elsevier B.V., Amsterdam, The Netherlands.
- BAKER, R. G., K. L. VAN ZANT, AND J. L. DULIAN. 1980. Three Late-glacial pollen and plant macrofossil assemblages from Iowa. *Palynology* 4:197–203.
- BECKER, M. A., J. A. CHAMBERLAIN, JR., AND R. B. CHAMBERLAIN. 2010. Probable cervical vertebrae of an extinct elkmoose dredged from the inner continental shelf of central New Jersey, USA. *Atlantic Geology* 46:7–18.
- BUCKLEY, J. D., AND E. H. WILLIS. 1970. Isotopes' radiocarbon measurements VIII. *Radiocarbon* 12:87–129.
- CHURCHER, S. S., AND J. D. PINSOFF. 1987. Variation in the antlers of North American *Cervalces* (Mammalia: Cervidae): review of new and previously recorded specimens. *Journal of Vertebrate Paleontology* 7:373–397.
- CLAYTON, L., AND S. R. MORAN. 1982. Chronology of Late Wisconsinan glaciation in middle North America. *Quaternary Science Reviews* 1:55–82.
- CORY, C. B. 1912. The mammals of Illinois and Wisconsin. Field Museum of Natural History, Zoology Series 11:1–502.
- DYER, D. L., C. R. HARRINGTON, R. L. FERNANDEZ, AND M. C. HANSEN. 1986. A Pleistocene stag-moose (*Cervalces scotti*) from Licking County, Ohio. *Ohio Journal of Science* 86:7.
- EDDY, S., AND A. E. JENKS. 1935. A kitchen midden with bones of extinct animals in the Upper Lakes area. *Science* 81:535.
- FAITH, J. T., AND T. A. SUROVELL. 2009. Synchronous extinction of North American Pleistocene mammals. *Proceedings of the National Academy of Sciences* 106:20641–20645.
- FARLOW, J. O., AND J. MCCLAIN. 1996. A spectacular specimen of the elk-moose *Cervalces scotti* from Noble County, Indiana, U.S.A. Pp. 322–330 in *Paleoecology and paleoenvironments of late Cenozoic mammals: tributes to the career of C. S. (Rufus) Churcher* (K. M. Stewart and K. L. Seymour, eds.). University of Toronto Press, Toronto, Ontario, Canada.
- FAUNMAP WORKING GROUP. 1996. Faunmap: an electronic database documenting late Quaternary distributions of mammal species. Illinois State Museum, Springfield.
- FLAGSTAD, O., AND K. H. ROED. 2003. Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. *Evolution* 57:658–670.
- GARLAND, E., AND J. COGSWELL. 1985. The Powers mastodon site, Van Buren County, Michigan. *Michigan Archeologist* 31:3–39.
- GRAHAM, R. W., AND M. A. GRAHAM. 1989. Taphonomy and paleoecology of stag-moose (*Cervalces scotti*) from thermokarst deposits, Tonica, north-central Illinois. Geological Society of America, North-central Section, Annual Meeting, April 20–21, 1989, Abstract 20064:12.
- GUTHRIE, R. D. 1990. New dates in Alaskan Quaternary moose, *Cervalces-Alces*: archeology, evolutionary, and ecological implications. *Current Research in the Pleistocene* 7:111–112.
- HARRINGTON, C. R. 1984. Quaternary marine and land mammals and their paleoenvironmental implications—some examples from northern North America. Carnegie Museum of Natural History, Special Publication 8:511–525.
- HAZARD, E. D. 1982. The mammals of Minnesota. University of Minnesota Press, Minneapolis.
- HIBBARD, E. A. 1958. Occurrence of the extinct moose *Cervalces*, in the Pleistocene of Michigan. *Michigan Academy of Science, Arts and Letters* 43:33–37.
- HUNDERTMARK, K. J., AND R. T. BOWYER. 2004. Genetics, evolution, and phylogeography of moose. *Alces* 40:103–122.
- HUNDERTMARK, K. J., R. T. BOWYER, G. G. SHIELDS, AND C. C. SCHWARTZ. 2003. Mitochondrial phylogeography of moose (*Alces alces*) in North America. *Journal of Mammalogy* 84:718–726.
- JACOBSON, G. L., T. WEBB III, AND E. C. GRIMM. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. Pp. 277–288 in *North America and adjacent oceans during the last deglaciation. The geology of North America* (W. F. Ruddiman and H. E. Wright, Jr., eds.). Geological Society of America, Boulder, Colorado. Vol. K-3.
- LONG, C. A. 1986. Pleistocene caribou in central Wisconsin. *Transactions of the Wisconsin Academy of Science, Arts and Letters* 78:12–13.
- LONG, C. A. 2008. The wild mammals of Wisconsin. University of Wisconsin—Stevens Point, Museum of Natural History, Reports on the Fauna and Flora of Wisconsin, Publication No. 56. Pensoft Publishers, Sofia, Bulgaria.
- MARTIN, L. D., AND A. M. NEUNER. 1978. The end of the Pleistocene in North America. *Nebraska Academy of Sciences* 6:117–126.
- MCDONALD, H. G. 1989. New records of the elk-moose *Cervalces scotti* from Ohio. *American Midland Naturalist* 122:349–356.
- MILLS, R. S., AND J. E. GUILDAY. 1972. First record of *Cervalces scotti* (Ledekker) from the Pleistocene of Ohio. *American Midland Naturalist* 88:255–256.
- PETTITT, P. B., W. DAVIES, C. S. GAMBLE, AND M. B. RICHARDS. 2003. Palaeolithic radiocarbon chronology: quantifying our confidence beyond two half-lives. *Journal of Archaeological Science* 30:1685–1693.
- REDMOND, B. G., AND K. B. TANKERSLEY. 2005. Evidence of early Paleoindian bone modification and use at the Sheriden Cave site (33WY252), Wyandot County, Ohio. *American Antiquity* 70:503–526.
- REIMER, P. J., ET AL. 2004. IntCal04 terrestrial radiocarbon age calibration, 0–26 cal kyr BP. *Radiocarbon* 46:1029–1058.
- ROBINSON, G. S., L. P. BURNEY, AND D. A. BURNEY. 2005. Landscape paleoecology and megafaunal extinction in southeastern New York State. *Ecological Monographs* 75:295–315.
- SCHUBERT, B. W., R. W. GRAHAM, H. G. MCDONALD, E. C. GRIMM, AND T. W. STAFFORD, JR. 2004. Latest Pleistocene paleoecology of Jefferson's ground sloth (*Megalonyx jeffersonii*) and elk-moose (*Cervalces scotti*) in northern Illinois. *Quaternary Research* 61:231–240.
- SCHWEGER, C. E. 1969. Pollen analysis of Iola Bog, and paleoecology of the Two Creeks Forest Bed, Wisconsin. *Ecology* 50:859–868.
- SCOTT, W. B. 1885. *Cervalces americanus*, a fossil moose, or elk, from the Quaternary of New Jersey. *Proceedings of the Academy Natural Sciences of Philadelphia* 1:181–202.
- SHOSHANI, J., AND G. R. SMITH. 1996. Late Pleistocene fishes from the Shelton Mastodon site (Oakland County, Michigan) and their ecological context. *Contributions from the Museum of Paleontology, University of Michigan* 29:419–433.
- SYVERSON, K. M., AND P. M. COLGAN. 2004. The Quaternary of Wisconsin: a review of stratigraphy and glaciation history. Pp. 295–311 in *Quaternary glaciations extent and chronology part II: North America* (J. Ehlers and P. L. Gibbard, eds.). Elsevier B.V., Amsterdam, The Netherlands.

- TALMA, A. S., AND J. C. VOGEL. 1993. A simplified approach to calibrating ^{14}C dates. *Radiocarbon* 35:317–322.
- TANKERSLEY, K. B. 1999. Sheriden: a stratified Pleistocene–Holocene cave site in the Great Lakes region of North America. Pp. 67–76 in *Zooarchaeology of the Pleistocene/Holocene boundary* (J. C. Driver, ed.). BAR International Series 800. Archaeopress, Oxford, United Kingdom.
- WEST, R. G. 1961. Late- and postglacial vegetational history in Wisconsin, particularly changes associated with the Valder's Readvance. *Journal of American Science* 259:766–783.
- WEST, R. M. 1978. Late Pleistocene (Wisconsinan) caribou from southeastern Wisconsin. *Transactions of the Wisconsin Academy of Science, Arts and Letters* 66:50–53.
- WEST, R. M., AND J. E. DALLMAN. 1980. Late Pleistocene and Holocene vertebrate fossil record of Wisconsin. *Geoscience Wisconsin* 4:25–45.
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