The Woodland Muskox *Bootherium bombifrons* (Artiodactyla, Bovidae) from Hebron, Licking County, Ohio, USA and its Paleoecology in the Great Lakes Region

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ABSTRACT. The braincase with horn cores of a male, extinct woodland muskox (*Bootherium bombifrons*) was recovered from a wetland near Hebron, Licking County, Ohio, in 1995. The fossil remains were preserved in sediments associated with a pro-glacial lake on the eastern margin of the Scioto lobe of the Laurentide ice sheet. An 853 cm long sediment core was analyzed, and its pollen record was used to reconstruct changes in the region's late Pleistocene paleoecology, which was barren landscape immediately following deglaciation. This transitioned to a spruce-dominated forest, and finally a deciduous forest. While most previous records of *Bootherium* have been associated with spruce-dominated habitat, the Hebron muskox lived in an environment with forests dominated by deciduous trees with only minor amounts of spruce. A paleoclimatic model—based on multiple records of *Bootherium*—indicates the wide distribution of the species south of the maximum continental ice sheets was due to its lesser cold tolerance and higher warm temperature tolerance than the modern muskox. Based on 2 averaged direct AMS radiocarbon measurements on the muskox skull, its age is 11,086 ± 18 radiocarbon years (13,093 to 12,926 calendar years BP) making it the youngest radiocarbon dated individual of *Bootherium bombifrons*. This date suggests the eventual extinction of the species may be related to the decline of its preferred habitat as climates changed at the end of the Pleistocene.

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INTRODUCTION

The extinct muskox, *Bootherium bombifrons*, first described from Big Bone Lick, Kentucky, was widely distributed across North America from Alaska to Louisiana (McDonald and Ray 1989). While the species has been recovered from a variety of depositional environments, many of them, such as gravel pits, have provided only limited information on the paleoecology of the species. This has been the case for the surviving 4 of the 7 specimens reported from Ohio (McDonald and Davis 1989). The recovery of an in-situ braincase of *Bootherium bombifrons* from near Hebron, Ohio, provides the first detailed information on the environment it inhabited in the state. This is based on an associated pollen profile and is the first occurrence in the state with a direct accelerator mass spectrometry (AMS) radiocarbon date. These associated data are not available for the majority of records of the species and therefore permits this new find to be placed within the context of climatic and environmental change at the end of the Pleistocene. As such, the fossil provides important complementary information to the few previous records of the species with associated pollen data and direct radiocarbon dates and refines our understanding of its ecology.

Licking County is located in central Ohio, 63 km east of Columbus. The western 75% of the county is covered by Late Wisconsinan glacial deposits, while the eastern part of the county is unglaciated. Around the town of Hebron, and extending south into Fairfield County to Buckeye Lake and to the west, the area is mapped as pro-glacial lake deposits formed by runoff from the melting of the Scioto lobe of the Laurentide ice sheet (Goldthwaite et al. 1961). The county contains formerly extensive wetlands that have yielded numerous remains of extinct Pleistocene megafauna, including mastodon, *Mammut americanum*, and the elk-moose, *Cervalces scotti* (McDonald 1989, 1994; Fisher et al. 1994).

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The partial skull of the woodland muskox (*Bootherium bombifrons*) was uncovered on 15 September 1995 by Ohio Department of Transportation highway worker Max Seyfried while using a backhoe to excavate soil for a road project near Hebron. Initial identification of the cranial fragment as *Bootherium bombifrons* was made by Dale Gnidovec, Orton Geological Museum, The Ohio State University. The skull is illustrated in Hansen (1996). Data on the sedimentology and palynology presented in this paper were originally submitted as part of a project report to the Ohio Department of Transportation (ODOT) by Shane and Haskell (2000).

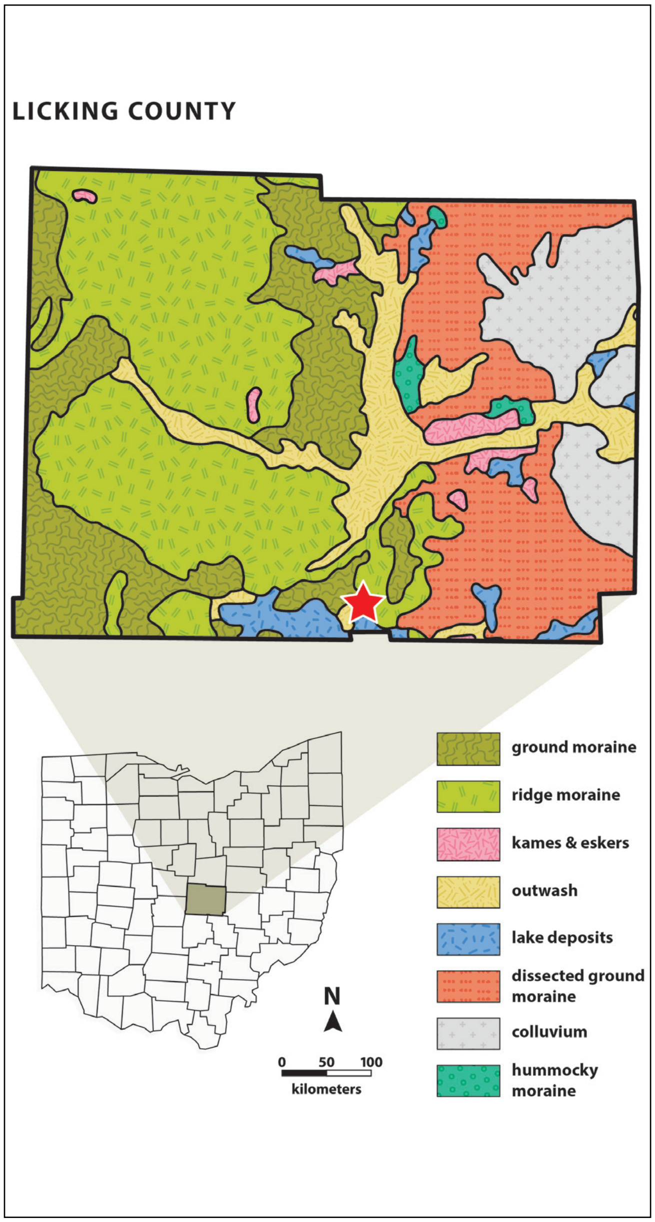

FIGURE 1. Map showing location of Hebron Muskox Site relative to glacial moraines and Pleistocene lake deposits. Modified from Ohio Division of Geological Survey (2005).

MATERIALS AND METHODS

Locality

The Hebron Muskox Site is located in the town of Hebron, Ohio. The specimen was found during the construction of the State Route 79 bypass. The site is on the Thornville, Ohio, 7.5 minute USGS quad in T1N, R13W, approximately 1 km north of US 40 and 0.25 km east of Route 79 (lat 39°58'10"N, long 82°28'22"W, elevation 277 m asl). The entire area has been heavily disturbed during construction of a major industrial park and the bypass. The last remnant of the once extensive wetland is a triangular, 0.4 ha (approximately 1 acre) area bounded by Highway 79 (Hebron Road) on the west, Enterprise Drive to the south, and John Alford Parkway on the eastern and northern margins (Fig. 1).

Description of Specimen

The *Bootherium* skull is housed at the Ohio History Connection (OHC), Columbus, Ohio, under catalog number N 9079 ("N" refers to the Natural History collection). The specimen is the posterior of a skull including a complete braincase with parts of each orbit and both horn cores, each of which lacks its distal tip (Fig. 2). Measurements of the skull (Table 1) were taken by the authors and were similar to other *Bootherium* individuals from Ohio. Measurements were based on those used by McDonald and Davis (1989) in their description of fossil muskoxen from Ohio.

The exostosis (extra bony growth) at the base of the horn cores is mostly complete with only minor breakage of some points along the sharp margins. The exostoses on the dorsal surface of the skull at the medial margin of the horn core have coalesced at the midline of the frontal to form an antero-posteriorly oriented boss with a slightly concave surface. The skull is of a mature male as indicated by the coalesced extososes covering the frontals between the bases of the horn cores. In females, this exostosis does not form, while the frontals are exposed. DNA recovered from the 2 skull morphs has confirmed this morphological difference between the 2 sexes (Bover et al. 2018). A second muskox taxon, the extant *Ovibos moschatus*, is also known from Pleistocene deposits in Ohio (McDonald and Davis 1989). While *O. moschatus* males also develop an exostosis at the dorsal base of the horns, and it extends partially over the frontals, the exostoses do not coalesce and are separated by a prominent furrow.

The left and right frontals of the Hebron muskox are complete and separated anteriorly at the sutures with the lacrimal; the dorsal portions of both orbits are present. A small part of the right frontal is missing at the juncture of the nasal and lacrimal. The occipital is complete except for a portion of the right supraoccipital crest, and the right paracondylar process is missing. The ventral surface of both tympanic bullae is missing. The suture between the basioccipital and basisphenoid is fused.

The condition of the skull is typical of artiodactyl skulls that show a moderate degree of weathering, with separation and loss of the premaxillae, maxillae, nasals, and palatines along their sutures from the denser cranial bones. These sutures fuse much later in life and are weaker than sutures of the braincase. The 5 *Bootherium* specimens described in McDonald and Davis (1989) all show a higher degree of abrasion and erosion than the Licking County specimen because the former were recovered from glacial gravel and fluvial sands. All

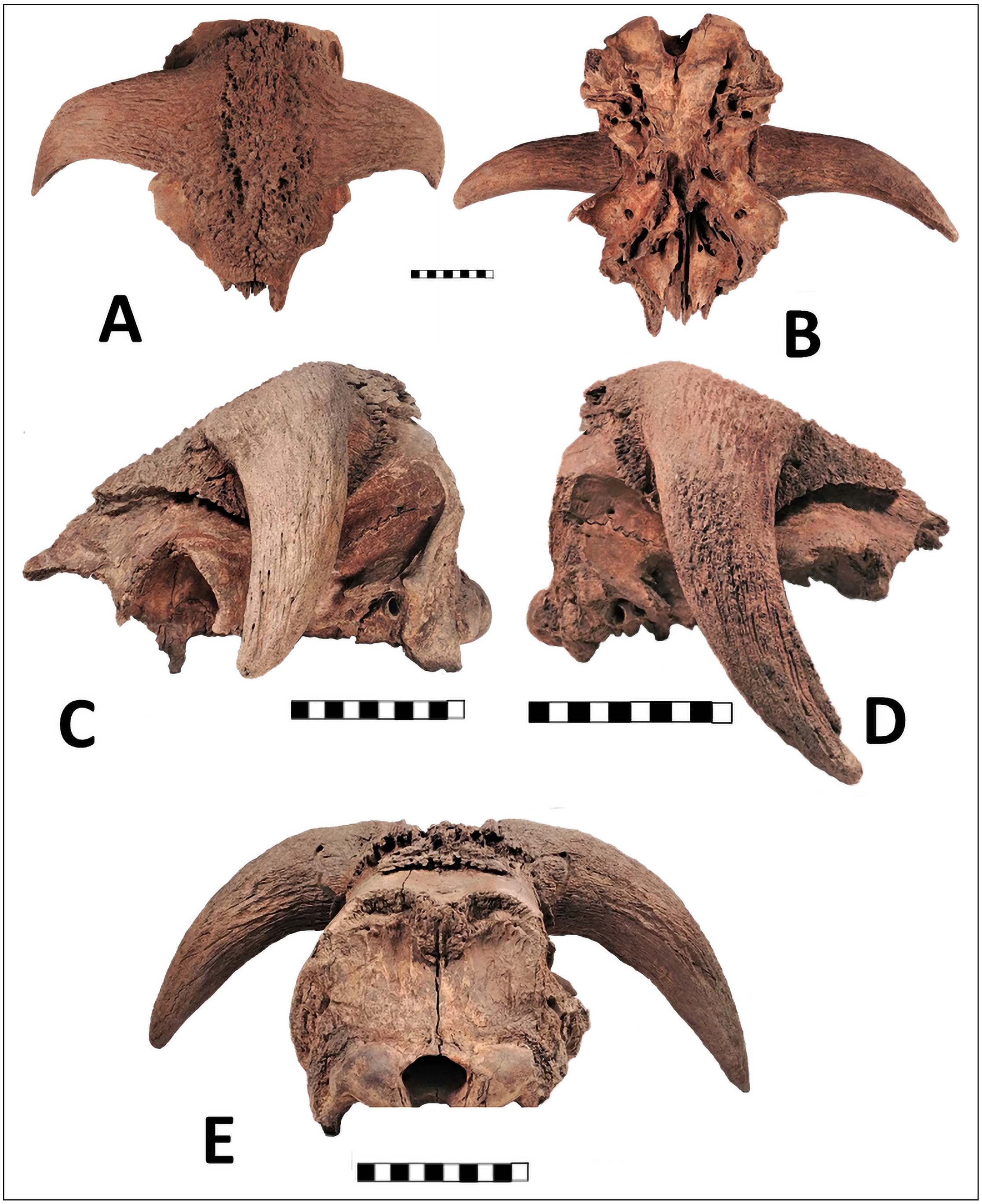

FIGURE 2. Skull of the Hebron muskox, *Bootherium bombifrons*. OHC N 9079. Scale is 10 cm. (A) dorsal view, (B) ventral view, (C) left lateral view, (D) right lateral view, and (E) posterior view. Note: the horn core appears longer in the right lateral view than in the ventral and posterior views due to the requirements of placing the specimen for photography.

6 specimens are represented by only the braincase and all lack the facial portion of the skull. The presence of mostly sharp points on the edges of the exostoses and the general lack of extensive abrasion seen on the other Ohio specimens presumably supports the Licking County skull being found in pro-glacial lake sediments.

McDonald and Davis (1989) described all 7 Ohio *Bootherium bombifrons* specimens, which were all crania. These authors illustrate or describe the 5 specimens preserved in museum collections and 2 additional crania now lost to science. The Licking County skull is more complete than the 5 skulls in McDonald and Davis (1989) and represents the most complete *Bootherium* skull from Ohio.

Currently, all records of *Bootherium* in Ohio are based on the male morph; no skulls of females have been recovered. McDonald and Ray (1989) noted that skulls of females are underrepresented in their review of the genus. Their sample consisted of 51 skulls of the female morph and 171 skulls of the male morph, a ratio of 29% female. Only 3 female skulls are known from the Great Lakes region—the holotype for *Bootherium bombifrons* from Big Bone Lick, Kentucky, a second from Gibson County in southern Indiana, and a third from Muskegon County, Michigan. This Great Lakes sample of *Bootherium* specimens comprises 13% females (3 females and 22 males). McDonald and Ray (1989) noted that female Bovidae skulls are typically smaller, lighter in build, and have less strongly fused sutures than in the males—characteristics that make female crania more susceptible to weathering, abrasion, decomposition, and other taphonomic processes that destroy bone. This observation seems to be supported by the sample in the Great Lakes region.

Table 1
Measurements (mm) of *Bootherium bombifrons* crania from Ohio

Measurement (mm)	OHC[a] N9079	UCGM[b] 37882	CMNH[c] P55	CMNH[c] P54
Anteroposterior diameter of base of horn core	R:127.5 L: 110.3	112.1	108.0	118.1
Dorsoventral diameter of base of horn core	R: 86.0 L: 77.5	96.5	74.0	86.0
Circumference of base of horn core	R:314.0 L: 293.1	350.0	300.0	370.0
Width of cranium posterior of orbits and anterior of horn cores	136.8	148.9	--	148.2
Width of cranium posterior of horn cores	136.7	144.0	139.0	--
Height of occipital from basioccipital to occipital crest	137.4	219.5	200.0	219.4
Height of occipital from top of foramen magnum to occipital crest	103.5	184.9	168.6	185.9
Height from upper edge of foramen magnum to occipital-parietal suture	--	--	109.8	120.5
Exostosis length	245.7	>187	--	262.8
Exostosis width, anterior of horn cores	114.9	99.0	--	120.3
Length basioccipital – basiosphenoid	108.2	108.0	93.4	101.6
Mastoid width	206.7	207.2	--	--
Transverse diameter of occipital condyles	147.1	135.3	123.0	141.9
Transverse internal diameter of foramen magnum	42.5	42.9	39.7	41.8
Dorsoventral internal diameter of foramen magnum	35.4	36.3	33.6	33.6

[a] Ohio History Connection. [b] University of Cincinnati Geology Museum. [c] Cincinnati Museum of Natural History.

Geologic Age of the Site and Fossils

Four radiocarbon measurements were made for the original ODOT report, with a fifth made for the present paper (Table 2). Fossil wood associated with, and inside the muskox skull had ^{14}C ages of 10,110 ± 50 (CAMS-31096) and 10,850 ± 50 (LRC-1157) respectively. The wood inside the skull was collected when sediments were removed from the cranium for pollen analysis. The cranial sediment's pollen spectrum was similar to the pollen profile in Zone 2b (186 to 208 cm BGL), the core interval above the muskox skull.

Spruce (*Picea* cf. *glauca*) needles stratigraphically below the skull dated 12,400 ± 60 RC yr. (LRC-1158). Direct dates on muskox skull bone are 11,150 ± 50 (CAMS-32680) using XAD-2 purified gelatin hydrolyzate measured in 1990, and 11,020 ± 25 RC yr. (UCIAMS-269695) on ultrafiltered (>30 kDa) gelatin measured April 2023 for this paper. The XAD-2 and UF dates were averaged and provide a ^{14}C age for the muskox of 11,086 ± 18 RC yr. and a calibrated date of 13,093 to 12,926 cal BP (Table 2). XAD-2 chemistry is described in Stafford (2014), Ultrafiltration (UF) chemistry is presented in Higham et al. 2006.

The AMS radiocarbon averaged date for the Hebron muskox bone, 11,086 ± 18 RC yr. BP (OxCal v4.4.4) (Bronk Ramsey 2021), is the youngest geologic age for this species in North America. A purportedly younger age of 10,980 ± 90 RC yr. on gelatin (TO-76910) (Table 3) for *B. bombifrons* is from the Wally's Beach Site, St. Mary Reservoir in Alberta, Canada (Waters et al. 2015). This specimen was redated using XAD-2 purification as 11,320 ± 30 RC yr. BP (UCIAMS-127373) (Table 3) (Waters et al. 2015). Consequently, the Hebron muskox remains the youngest *B. bombifrons* presently discovered in North America.

Paleoecologically, the 13,100 to 12,910 cal BP date for the Hebron muskox is when deciduous trees with scattered spruce were the local vegetation, in contrast to an earlier spruce-dominated forest. Based on the vegetation, the climate was sufficiently cool to enable spruce survival, but warming enough to begin deciduous tree forestation. During the muskox's lifetime, the southern edge of the Laurentide ice sheet would have been north of the Great Lakes and approximately 560 km north of Hebron.

Methods of Sediment Analysis

The Hebron Muskox Site was cored on 16 July 1997 by crews from the University of Minnesota Geology Department Limnological Research Center (LRC), Kent State University (KSU), and the Ohio Department of Transportation (ODOT), with help from the Ohio Department of Natural Resources, Cleveland State University, and University of Toledo.

After using a mini-corer to locate the deepest deposits, a single core comprising multiple drives was taken as Core 1997A. Both Vibracore and Wright-Livingston coring techniques were used to obtain a total length of 8.5 m of sediments.

Analysis of the sediments included magnetic susceptibility, and sediment descriptions including smear slides, loss-on-ignition, and pollen identification.

Magnetic Susceptibility. Magnetic susceptibility is a measure of the relative amounts of magnetic particles in the sediments. Allochthonous (clastic) sediments derived from slope wash or stream transport have higher magnetic susceptibility than autochthonous (biological) materials that contain less mineral detritus, high amounts of organic matter, and therefore less magnetic susceptibility than clastic sediments. Cores are passed under a detector that measures the magnetic susceptibility in arbitrary units per cubic centimeter. Measurements were made continuously at 2 cm intervals.

Smear Slides. Sediment samples are placed on slides for direct microscopic observation to determine their mineral content. A small amount of wet sediment is smeared on a microscope slide, air-dried, and embedded under a coverslip with an optically clear epoxy resin. Six slides were made for this study.

Loss-on-ignition. Loss-on-ignition (LOI) determines the percentages of oxidizable organic and inorganic constituents in the sediment. Samples are combusted at increasingly higher temperatures to measure the relative amounts of water, organic carbon, carbonates, and non-carbon components (silicate minerals). Each 1 cm^3 sample is sequentially heated at 100 °C, 500 °C, and 1,000 °C and weighed between each heating stage. Weight losses after heating are a measure of water, organic carbon, carbonate, and mineral content (Dean 1974). Most samples were removed from the cores at 8 cm intervals, except when finer stratigraphic resolution was needed.

Pollen. Forty-five pollen samples were processed using methods modified from Faegri and Iversen (1974). Each 0.5 cc volumetric sample was spiked with a known quantity of *Eucalyptus* pollen to quantitatively determine pollen content. Each sample was treated sequentially with hot 10% KOH to break up colloids, multiple H_2O rinses to remove clays, screening through 160 µm mesh, hot 10% HCl to remove carbonates, screening through 8 µm mesh to continue clay removal, hot 48% HF followed by hot 10% HCl rinses to remove silicates and colloids, dehydration with glacial acetic acid, acetolysis, additional glacial acetic acid rinses, water rinses, and finally dehydration with 100% EtOH and tertiary-butyl alcohol $(CH_3)_3OH$. The residues were transferred to vials and suspended in 2000 CS silicone oil.

Pollen counts were done on all samples. Some levels had a sufficient concentration of pollen to produce counts of 300 to 500 grains. Core depths below 700 cm had too few grains to produce useable counts. Counts were done by scanning transects evenly spaced along 2 different slides from each level using a Leitz® microscope at 490× magnification. Identifications were based on comparison with the pollen reference collection at LRC, University of Minnesota, and published descriptions (Kapp 1969; McAndrews et al. 1973). Because spruce

Table 2
AMS radiocarbon dates from the Hebron Muskox Site, Licking County, Ohio [a]

Sample ID	Material dated	Chemical fraction [b] dated	^{14}C age RC yr. BP ± 1 SD	Calibrated age range 95.4% C.I.[c]	Radio-carbon lab No.	δ^{13}C‰ (VPDB)	δ^{15}N‰ (AIR)	C/N (atomic)	Comment
NSRL-3284	Wood frag. inside skull	ABA	10,110 ± 50	11,930-11,400	CAMS-31096	--	--	--	405-340 cm BGL
OS-22530	Unidentified wood	ABA	10,850 ± 50	12,890-12,720	LRC-1157	--	--	--	347-350 cm BGL
NSRL-3283	Muskox skull bone	XAD-2 purified gelatin hydrolysate	11,150 ± 50	13,170-12,920	CAMS-32680	--	--	--	405-340 cm BGL
SR-9619	Muskox skull bone	UF >30 kDa gelatin	11,020 ± 25	13,070-12,840	UCIAMS-269695	-20.1	4.5	3.3	405-340 cm BGL
OS-22531	*Picea* sp. needles	ABA	12,400 ± 60	14,900-14,180	LRC-1158	--	--	--	407-410 cm BGL
Age ranges									
Averaged muskox ^{14}C date using (CAMS-32680 and UCIAMS-269695)			11,085 ± 18	13,093-12,926	--	--	--	--	405-340 cm BGL
Cal BP age range for Younger Dryas cooling event				12,900-11,700	--	--	--	--	--

[a] Acronyms used in Table 2.
ABA: acid-base-acid; **BGL**: below ground level; **CAMS**: Center for Accelerator Mass Spectrometry, LLNL, CA;
LRC: Limnological Research Center, University of Minnesota, MN; **OS**: National Ocean Science AMS Lab, Woods Hole, MA;
UCIAMS: University of California-Irvine AMS Laboratory, CA; **UF**: Ultrafiltration.

[b] Published chemical purification methods for the following methods:
ABA: https://cpb-us-e2.wpmucdn.com/sites.uci.edu/dist/1/2856/files/2016/12/aba_protocol.pdf ;
Ultrafiltration (>30 kDa gelatin): https://cpb-us-e2.wpmucdn.com/sites.uci.edu/dist/1/2856/files/2016/12/bone_protocol.pdf ;
XAD-2: Stafford 2014.

[c] Rounded to the nearest 10 years using the datasets of Stuiver et al. (1998).

Table 3
***Bootherium* radiocarbon dates from North America**[a]

Locality	Material dated	Chemical fraction dated	^{14}C age, RC yr. BP ± 1 SD	Calendar years range 95.4% C.I.	Radio-carbon lab No.[b]	Reference
St. Mary Reservoir, Alberta	Bone	Gelatin	10,980 ± 90	13,080-12,750	TO-7691	Hills et al. 2014; Waters et al. 2015
Hebron, Ohio	Bone, skull	UF >30kDa Gelatin	11,020 ± 25	13,070-12,840	UCIAMS-269695	Current report
Hebron, Ohio	Bone, skull	XAD-gelatin hydrolysate	11,150 ± 50	13,170-12,920	CAMS-32680	Shane and Haskell 2000
Hebron, Ohio	Bone, skull	Averaged XAD/UF	11,085 ± 35	13,093-12,926	Not available	Current report
Scott's Michigan	Bone, 4th lumbar	Not available	11,100 ± 400	14,000-11,940	M-1402	Semken et al. 1964
St. Mary Reservoir, Alberta	Bone, rib	XAD-gelatin hydrolysate	11,320 ± 30	13,300-13,120	UCIAMS-127373	Waters et al. 2015
Monroc Kearns Gravel Pit, Utah	Bone, left horn core	Collagen	11,770 ± 190	14,070-13,240	Not available	Nelson and Madsen 1980
Kelvin's Cave, Idaho	Bone, humerus	"Collagen"[c]	12,250 ± 60	14,810-14,030	Beta-194532	Henrikson and Long 2007
Coville farm, Climax, Michigan	Bone, 3rd cervical	Not available	13,200 ± 600	17,720-14,040	M-639	Hibbard and Hinds 1960
Saltville, Virginia	Culturally modified tibia of c.f. *Bootherium*	"Collagen"[c]	14,510 ± 80	18,000-17,390	Beta-117541	McDonald 2000
Huntsman Muskox Site, Utah	Bone, unknown	XAD-KOH collagen	15,400 ± 60	18,850-18,360	CAMS-25755	Gillette and Miller 1999
Grass Mesa, Colorado	Bone	Not available	15,970 ± 155	19,600-18,900	SI-6137	McDonald et al. 1987
Kelvin's Cave, Idaho	Bone, sacrum	Collagen	16,260 ± 80	19,870-19,450	Beta-195670	Henrikson and Long 2007

[a] Radiocarbon calibrations: OxCal v4.4.4 Bronk Ramsey (2021); r5; atmospheric data from Reimer et al (2020).

[b] Radiocarbon laboratory abbreviations used in Table 3.
Beta: Beta Analytic, FL; **CAMS:** Center for Accelerator Mass Spectrometry, LLNL, CA; **GX**: Geochron Laboratories, MA; **M**: Michigan Radiocarbon Lab; **SI**: Smithsonian Institution Radiocarbon Lab; **I**: Illinois Geological Survey Radiocarbon Lab, IL; **TO**: Toronto Canada Radiocarbon Lab; **UCIAMS**: University of California-Irvine AMS Lab, CA.

[c] "Collagen" [term in quotes] indicates the assumed material dated was collagen.

(Continued)

Table 3 (continued)
***Bootherium* radiocarbon dates from North America**[a]

Locality	Material dated	Chemical fraction dated	^{14}C age, RC yr. BP ± 1 SD	Calendar years range 95.4% C.I.	Radio-carbon lab No.[b]	Reference
Wetherford Washita, Oklahoma	Bone fragments associated with skeleton	Not available	16,350 ± 190	20,270-19,250	GX-19196	Kirkland and Hilliard 1996
Haystack Cave, Colorado	Bone, left radial carpal	Not available	17,160 ± 90	20,970-20,456	Beta-124332	Emslie and Meltzer 2019
Fairbanks Creek, Alaska	Hair	Not available	17,210 ± 500	22,150-19,610	SI-454	McDonald 1984
Dome Creek, Arkansas	Horn sheath	Not available	17,695 ± 445	22,500-20,445	SI-851	Péwé 1975
Haystack Cave, Colorado	Bone, 1st phalanx	XAD-purified gelatin hydrolysate	18,970 ± 90 19,620 ± 170	23,050-22,570 23,960-23,100	CAMS-1558 AA-4940	Emslie and Meltzer 2019
Lost Chicken Creek, Alaska	Bone	Not available	20,500 ± 390	25,640-23,830	I-10649	Harington 1980
Creek near Fairbanks, Alaska	Horn sheath	Not available	22,540 ± 900	28,950-25,150	SI-292	Péwé 1975
Fairbanks Creek, Alaska	Tissue beneath scalp	Not available	24,140 ± 2,200	36,540-24,200	SI-455	McDonald 1984
Upper Cleary Creek, Alaska	Horn sheath	Keratin	25,090 ± 1,070	31,610-27,340	SI-850	Péwé 1975
Fort Saskatchewan, Alberta	Bone, skull	Not available	30,570 ± 250	35,440-34,470	TO-8973	Hills and Wilson 2003
Livengood, Alaska	Bone, partial skeleton	Ultrafiltration (>30kDa)-gelatin (NaOH/collagen)	41,200 ± 1,500	47,750-42,400	CAMS-120072	Fox-Dobbs et al. 2008
Fairbanks Creek, Alaska	Bone, partial skeleton	Ultrafiltration (>30kDa)-gelatin (NaOH/collagen)	48,000	Out of range	CAMS-120073	Fox-Dobbs et al. 2008

[a] Radiocarbon calibrations: OxCal v4.4.4 Bronk Ramsey (2021); r5; atmospheric data from Reimer et al (2020).

[b] Radiocarbon laboratory abbreviations used in Table 3.
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(End)

pollen was abundant, identification of species was done on 10 levels by Rebecca Teed, following criteria in Hansen and Engstrom (1985). The results of the spruce discrimination analysis are that while both black and white spruce are present in the late glacial, the majority of spruce pollen grains in the Hebron core were white spruce *Picea glauca*.

Relative pollen percentages were calculated using a pollen sum consisting of all upland trees and shrubs (arboreal pollen) (AP) and terrestrial non-arboreal pollen (NAP). Percentages for local aquatic taxa were calculated "outside the sum" by the expedient of adding the count for a particular aquatic taxon (e.g., cattail, *Typha*) to the pollen sum for that level and using the new sum for the denominator.

January and July temperature estimates, plus estimates for mean annual precipitation, are generated from transfer functions (regression equations). The regression equations are derived by relating modern surface sample pollen frequencies to regional weather station data. While the overall results are reasonable for most levels, the reliability is limited for those levels that have no modern pollen analogs. See discussion in Shane and Anderson (1993).

RESULTS

Paleoecological Results of the Sediment Analysis

A key factor in the interpretation of the Hebron Muskox Site (and its paleoecology) is its location within the boundary of a pro-glacial lake and an abrupt sediment change at 454 cm core depth. The lake was sufficiently large that it was mapped by Goldthwaite et al. (1961) and is readily identified on topographic maps as measuring 8 to 10 km east-to-west and 5 to 6.5 km north-to-south. The lake's highest shoreline elevation was 277 m ASL, while the muskox skull was recovered at 271 m ASL. At maximum extent, the lake's water depth was approximately 20 m. As glacial ice retreated and meltwater runoff decreased, the lake changed into a shallow pond and eventually a wetland with standing water. Deposition and vegetation successions determined by pollen analyses are shown in Figure 3.

Description of Pollen Zones in Core 1997A

Zone 1a: 860 to ca. 670 cm; 17,000 ± 1,000 to 15,000 ± 1,000 ^{14}C yr. The basal sediments represent glacial runoff that would have been high energy streams depositing medium-to-coarse clastics. The zone's high magnetic susceptibility

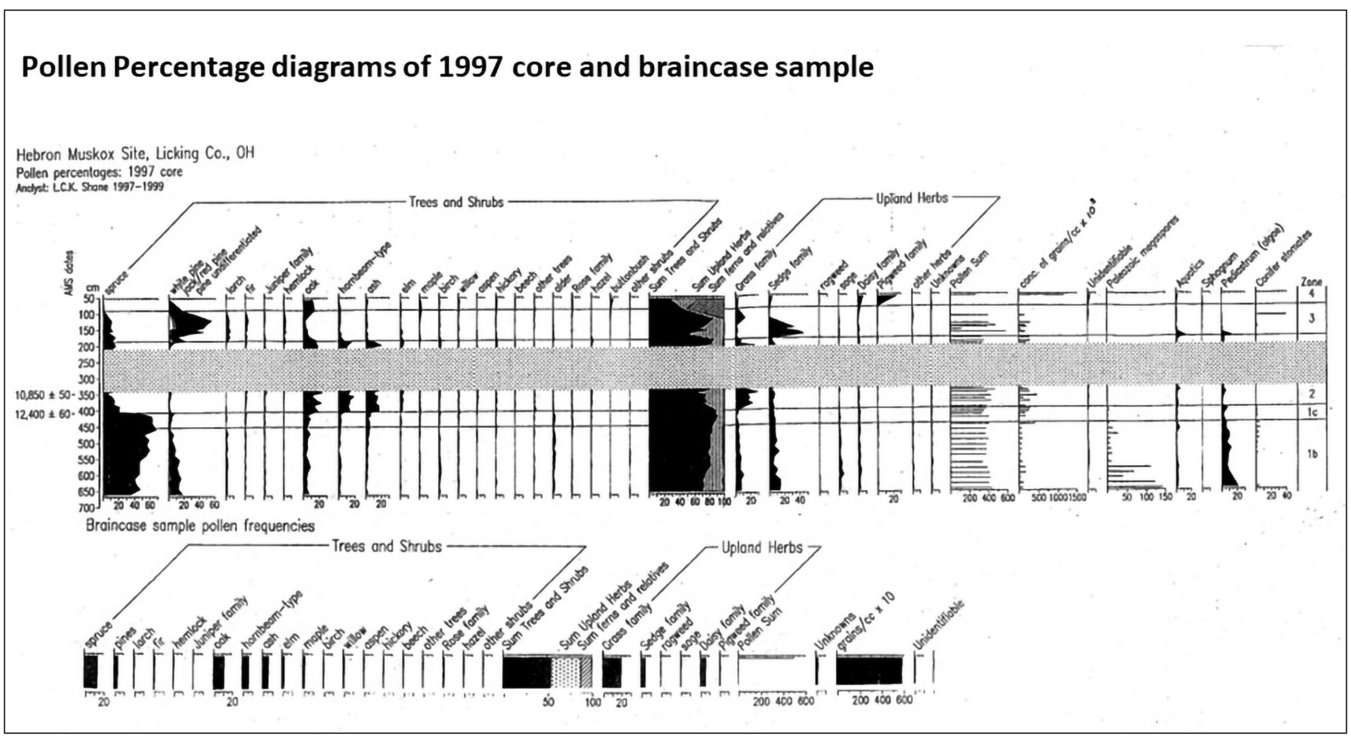

FIGURE 3. Pollen percentage diagrams of 1997 pollen core of the Hebron Muskox Site, Licking County, Ohio, and for sediment removed from the braincase of the muskox

and negligible-to-zero organic carbon content are evidence of a barren, unvegetated landscape. The sediments contain a high amount of redeposited Paleozoic limestone present as "glacial-flour" in the ice. Moraines would have impounded water and sediments between 18,000 and 16,000 ^{14}C years ago. (Shane 1987 and references therein; pers. comm. T. Lowell, University of Cincinnati phone conversation 3 May 2000).

Zone 1b: ca. 670 to 454 cm; 15,000 ± 1,000 to 14,000 ± 500 ^{14}C yr. Zone 1b has a high silt content, low organic matter content, and fluctuating but overall decreasing magnetic susceptibility. The sediments consist of redeposited dolomite containing Paleozoic megaspores. Pleistocene pollen and diatom concentrations are low because the large lake is surrounded by an open, unstable environment that is slowly warming. The pollen assemblage is dominated by spruce with 20% pine, and 30% non-arboreal pollen comprising sage, sedges, and grass that are indicative of cold conditions and sparse vegetation cover. The 20% pine pollen value may not represent the region's true pine tree abundance due to the high pollen production of *Pinus* and its easy redistribution hundreds of kilometers from the source (Jacobson et al. 1987). Therefore, a 20% abundance of pine at Hebron is unlikely. The temperature range during the Zone 1b interval would have been from -16 °C in January to +19 °C in July. Based on the study of the Quillin Site, 110 km north of the Hebron Muskox Site, the July temperature was estimated at +15 °C based on an insect fauna dated at 14,800 ^{14}C (Morgan 1987).

Between approximately 570 and 454 cm, there are indications of a warming climate based on a slight decline in NAP and pine pollen, a decline in magnetic susceptibility, and a slight increase in organic matter in the sediments. The pollen samples also include conifer stomates and eroded needles indicating the presence of trees in the immediate area of the lake. This suggests both the presence of extensive vegetation in the area and a lowering of the lake level.

Zone 1c: 454 to ca. 405 cm; 14,000 to 12,700 ± 300 ^{14}C yr. There is a sharp and pronounced change in sediment lithology at 454 cm, where organic matter increases from approximately 6% to >40%, and magnetic susceptibility decreases over 1 cm. Increased sedimentary organic matter is accompanied by an increase in spruce pollen frequency and a decline in NAP and pine pollen, all indicative of a closed or nearly closed spruce forest surrounding the wetland; however, there is no indication of a significant climate change between Zones 1b and 1c.

This significant change in the lithology is interpreted as the succession of a shallow lake changing into a wetland. The shift was caused by the loss of glacial meltwater as the glacier retreated northward. No material suitable for radiocarbon dating was preserved in this zone and therefore estimates of glacial retreat are not possible.

Zone 2a: 405 to 340 cm; 12,700 ± 300 to 10,600(?) ^{14}C yr. Zone 2a is the 65 cm thick interval within which the muskox skull would have been deposited. The zone is bracketed by 2 radiocarbon dates.

The most conspicuous feature of this zone is the dramatic change from a spruce dominated forest to one dominated by deciduous trees and non-arboreal pollen (NAP). Precipitation would have been minimal, with the July temperature increasing by 3 °C and the January temperature by 7 °C. In Ohio, similar changes in the pollen spectra have been documented to the west in Darke County (Shane 1987), Hardin and Champaign Counties (Shane and Anderson 1993), and to the south in Pickaway County (Shane et al. 2001).

Zone 2b: 186 to 208 cm; 10,300 to 10,100 ± 100 ^{14}C yr. The high organic matter content of Zone 2b is an indication that the basin had been reduced to a small pond or wetland. The pollen assemblage is complex and includes an extensive assemblage of deciduous trees (including oak, ash, elm, and hornbeam-type pollen) with an increasing diversity of conifers (including spruce, larch, fir, and hemlock), along with 25% NAP. This assemblage is similar to the pollen sample recovered from the braincase of the muskox. The climate estimates are comparable to those described for Zone 2a.

Zone 3: 186 to 90 cm; ca. 10,200 to 9,800 ^{14}C yr. The most conspicuous features of this zone are (1) high organic matter content associated with high sedimentation rates and (2) high pine pollen frequencies. Because pine pollen is often overrepresented in pollen spectra, it is not clear if the layer's 60% pine pollen abundance represents the presence of a dense pine forest; however, it is likely that pine was a major component of the local vegetation. Pines are associated with drier environments, and the high frequencies of fern spores at the zone's top indicates a seasonally dry ground surface.

Zone 4: 90 to 30 cm. The sediments of this zone are mixed and oxidized as indicated by the combination of increased siliceous residue in the sample and its low magnetic susceptibility, poor preservation of pollen, and evidence of roots. The identifiable pollen is predominately buttonbush, a shrub that grows on wet soils, while the high fern spore frequencies indicate a lack of standing water. The absence of conifer trees marks the transition into the Holocene and the beginning of today's climate.

Paleoclimatic Model of *Bootherium* Paleoecology

In addition to the inferences on temperature and precipitation based on the pollen record, another approach to examining the paleoecology of *Bootherium* is using climate envelope models (CEMs). CEMs have previously been used to examine the distribution of extant species and infer past and future distribution based on the climatic variables measured at localities across a species' geographic range (Polly and Eronen 2011). Based on the range of values for each climatic variable, the CEMs help predict where and when a species would be expected to occur in the past and how it might have responded (or will respond) to changes in any climatic variable. Currently, this approach is based on extant taxa for which these variables can be directly determined. For an extinct species like *Bootherium*, macrophysical climate modeling (MCM) can be used to approximate some of the climatic parameters that may determine its distribution. One test of the validity of this model is to compare the consistency of the calculated paleoclimatic parameters across multiple sites.

Developed in the mid-1990s by R.A. and R.U. Bryson, macrophysical climate modeling is an alternative to iterative general circulation models (GCMs). The MCM has previously been applied to archeological sites and has been referred to as archaeoclimatology (Bryson and McEnaney DeWall 2007). The MCM utilizes a top-down rather than bottom-up approach to model building, predicated on the following parameters: orbital forcing, variations in atmospheric transparency, and the principles of synoptic climatology. More comprehensive overviews of the model are in Bryson (2005) and Bryson and Bryson (1997, 2000).

The MCM model calculates the climatic parameters in 100-calendar-year intervals. Therefore, in order to compare sites, radiocarbon dates are converted into calendar years. The small number of records of *Bootherium* with radiocarbon dates (Table 3) limits both the number of sites for which the climatic parameters can be modeled and the number of sites from different geographic areas that may be contemporaneous. The model permits an examination and comparison of the climatic parameters for multiple sites containing *Bootherium* and at different times, allowing the creation of a preliminary climatic envelope for this extinct species based on specimens for which there are accurate radiocarbon dates. It has previously been applied to sites with reliable radiocarbon dates for the extinct giant beaver, *Castoroides ohioensis* (McDonald and Bryson 2010) and the paleoecology of the extinct sloth, *Nothrotheriops* (McDonald 2011). Two climatic parameters were examined for this study, the mean average temperature (MAT) and annual precipitation (Fig. 4). The impact of either of these climatic parameters may be direct, depending on the species' physiology, e.g., temperature tolerance, or indirect or secondary, such as changes in rainfall that impacts the quality or quantity of vegetation in the herbivore's diet. While only temperature and precipitation patterns are considered in this paper, other climatic patterns can be determined from the model.

Site specificity is the key component to the MCM model because it permits an examination of climatic parameters at individual sites with extinct fauna and permits a comparison of climatic parameters at multiple sites for an individual species. Calculations from the model are done using 100-year averages, providing the finer time resolution available from AMS radiocarbon dates and permitting the examination of climatic parameters for small increments of time. This allows the calculation of these 2 climatic parameters and changes in those parameters for a species in both time and space. The 2 limitations to the model are the lack of numerous high-resolution radiocarbon AMS dates for extinct Pleistocene species and the limitation of radiocarbon measurements being limited to 48,000 to 50,000 RC years.

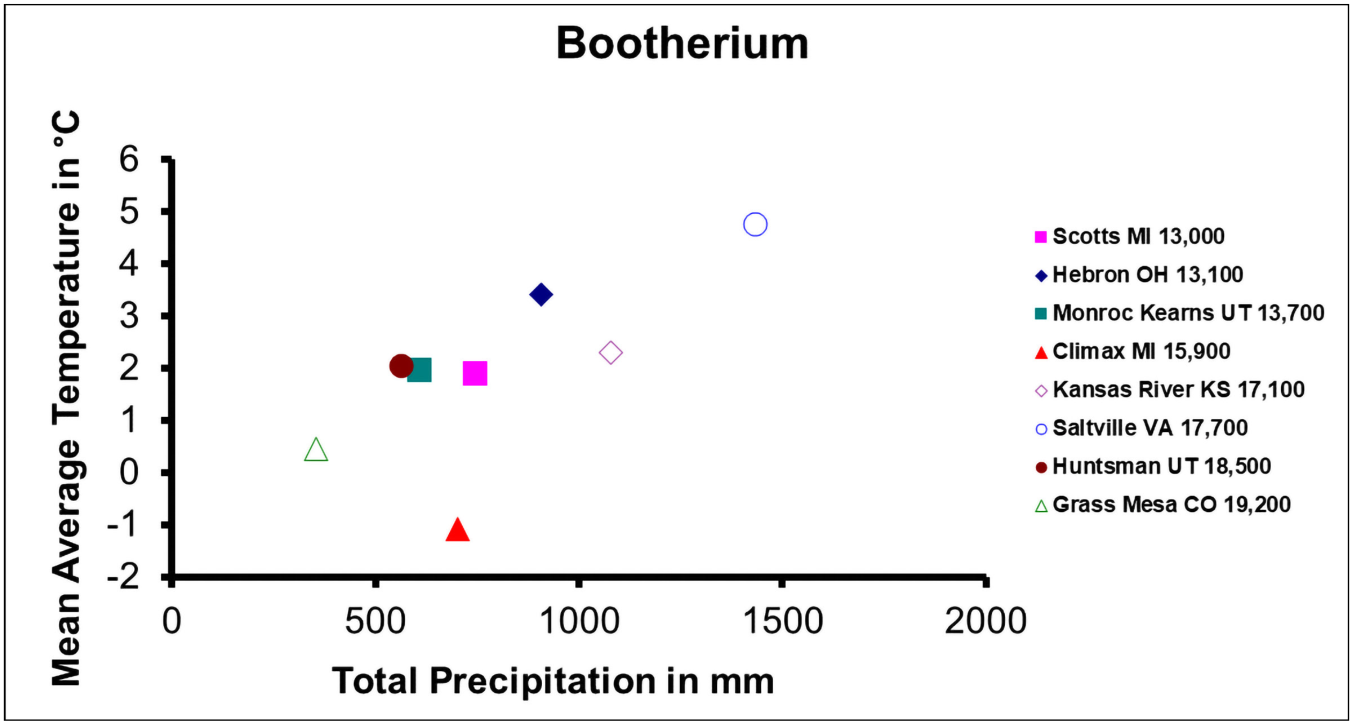

FIGURE 4. Comparison of modeled mean average temperature and total annual precipitation for different sites with *Bootherium* of different ages. Ages given in calendar years BP (cal BP).

Modern local climatic data on monthly mean temperatures and precipitation are obtained from the weather station nearest to the fossil site and are entered into the MCM program. For North America, these climatic values are used to calibrate the program by adjusting the *centers of action*: latitude of the jet stream at 120° west longitude (JET120N), the latitude of the intertropic convergence at 0° longitude (ITC90W), the latitude of the subtropical high axis at 0° west longitude (EUHX), and the latitude of the subtropical high axis at 135° W (NPHX) until the values produced by the model correspond to modern values at the weather station. Once the program has been calibrated to at least 95% accuracy, the program calculates past climatic parameters at 100-year intervals for the past 40,000 years.

Because the MCM is calculated in calendar years, all published radiocarbon dates on extinct species were converted into calendar dates (cal BP) using OxCal. Based on the calendar dates, calculated climatic parameters for the calendar date for the closest 100-year interval in the MCM program were used to estimate the climatic parameters when the animal was alive.

The MAT and total precipitation for the Hebron Muskox Site were compared to 7 other *Bootherium* localities and times, enabling the reconstruction of the species' temperature tolerance and yearly precipitation at each site (Fig. 4). The estimates are that *Bootherium* was cold tolerant with a MAT of -1 °C to +5 °C. The calculated temperature range for the Hebron Muskox Site based on the MCM model was -13 °C to +18 °C, which approximates the range of -9 °C in January to +16 °C in July based on the pollen from Zone 2a, the muskox level. The model predicts that while *Bootherium* was tolerant of cold winter temperatures from -7 °C to -17 °C, it was not as cold tolerant as the extant muskox, *Ovibos moschatus*, which can survive temperatures as low as -70 °C (Tener 1965). *Bootherium* also differed from *Ovibos* in the former's tolerance of higher summer temperatures of +13 °C to +17 °C (Fig. 4). The extant muskox, *Ovibos*, is highly sensitive to high temperature and humidity (Tener 1965). The +10 °C summer isotherm approximates the southern limit of the range of *Ovibos*.

Total annual precipitation at the Hebron Muskox Site at 11,000 RC yr BP (13,000 cal BP) is estimated at 905 mm, the upper end of the range for *Bootherium* based on the available sample. The model also indicates *Bootherium* was tolerant of drier environmental conditions that are indicated by 353 mm estimates for Grass Mesa, Colorado, and 608 mm at Modoc Kearns, Utah.

Given the extensive distribution of *Bootherium* across North America—latitudinally from Utqiagvik (formerly known as Barrow), Alaska (71°23'N), to Bayou Sara, Louisiana (30°57'N), and longitudinally from Anvik, Alaska (160°12'W), to the continental shelf off New Jersey (ca. 74°W) (McDonald and Ray 1989)—it is not surprising that the amount and seasonal patterns of precipitation over its range varied both in total amount as well as seasonal distribution (Fig. 5). *Bootherium* ranged from relatively dry regions in Colorado, with 353 mm of yearly precipitation, to 1,431 mm at Saltville, Virginia. The hypothesized 906 mm of precipitation at the Hebron site is intermediate to values from Colorado and Virginia. While this 906 mm precipitation is higher than the 800 mm estimated from the Hebron pollen record, the value based on the pollen count is still within the range of the other sites. Most of the *Bootherium* sites have their greatest precipitation from late summer to early fall, except Saltville where maximum precipitation occurred from January to April.

DISCUSSION

Prior to the discovery of the Hebron specimen, the extinct muskox *Bootherium bombifrons* was known from 7 records in Ohio—5 from known localities and 2 specimens with no locality information (McDonald and Davis 1989). All specimens are braincases that were previously identified as *Symbos cavifrons* in McDonald and Davis (1989) but which are now considered the male morph of *Bootherium bombifrons* as proposed by McDonald and Ray (1989). This interpretation, based on morphology, was subsequently supported by molecular analysis of the 2 skull morphs (Bover et al. 2018). Currently, the female skull morph has not been recovered from Ohio. The type specimen of *Bootherium* is a female morph from Big Bone Lick, Boone County, Kentucky, 230 km to the southwest of Hebron (Wistar 1818). The distribution of muskox in Ohio extends diagonally across the state from the southwest to the northeast, and all specimens have been found in deposits from the glaciated part of the state (McDonald and Davis

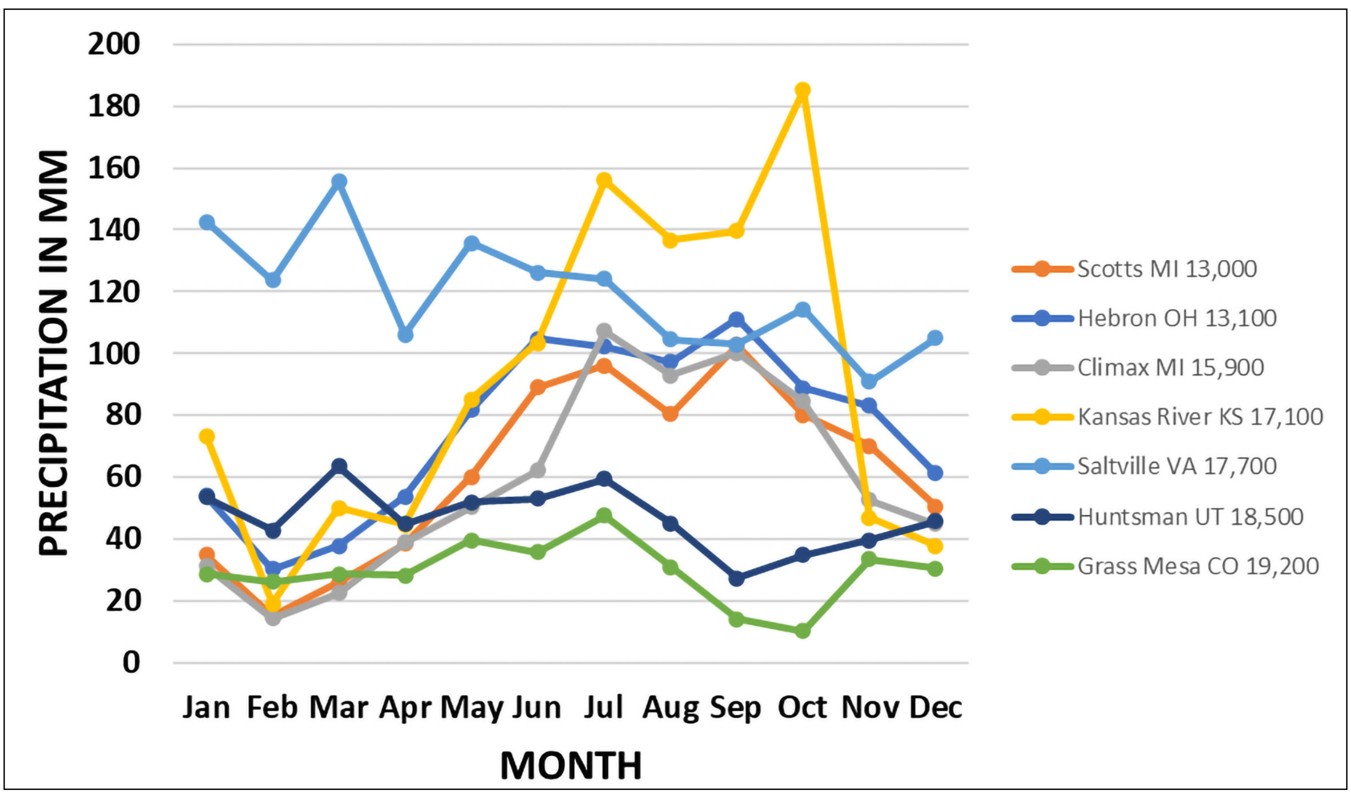

FIGURE 5. Modeled seasonal variation in precipitation at different localities with *Bootherium*. Ages given in calendar years BP (cal BP).

1989). The record from Licking County follows this pattern and fills the gap between the records from Champaign and Mahoning Counties. All previous muskox discoveries in Kentucky have been from glacial outwash sands and gravels that have yielded no organic matter. The Hebron skull has provided the first and only accurate date for this specimen and its local environment.

The geologic age of the Hebron muskox is 11,086 ± 18 ^{14}C yr. (13,093 to 12,926 cal BP); it lived during the deposition of Zone 2a in the sediment core. While the July temperatures at this time are comparable to those of the region today, the winters were colder and reached -9 °C compared to the current January temperature of -2.6 °C. The area was also drier than today and had a mean annual precipitation of 800 mm, compared to the modern 1,000 mm yearly rainfall. The muskox-era vegetation is indicative of very open deciduous woodland, but with some spruce trees still present.

There are a limited number of vegetation records contemporaneous with *Bootherium* in eastern North America. Spruce was associated with a specimen from Kalamazoo County, Michigan (Benninghoff and Hibbard 1961), and St. Josephs County, Michigan (Semken et al. 1964). Spruce and pine were documented at Saltville, Virginia (Ray et al. 1967), although the pine pollen may have been transported from a distance. Both sites are different from the Hebron locality, whose late Pleistocene vegetation was predominately deciduous trees with smaller amounts of spruce.

Farther south, the Pleistocene fauna from Saltville, Virginia, includes *Bootherium* (McDonald and Bartlett 1983) associated with primarily cool, mixed-forests containing pines, spruce, oak, and sedge (Ray et al. 1967). Grass pollen counts are relatively low in this region with relative abundances <10% (Ray et al. 1967; Williams et al. 2000). Two sediment samples analyzed by France et al. (2007) had minimal C_4 vegetation as interpreted from a primarily C_3 plant isotopic signature for both samples.

The Hebron and Saltville *Bootherium* specimens are uncommon examples of fossils having measured $\delta^{15}N$ and $\delta^{13}C$ values. Hebron muskox bone collagen measured $\delta^{15}N$ = +4.5‰ and $\delta^{13}C$ = -20.1‰ (Table 2). The $\delta^{15}N$ and $\delta^{13}C$ values for the Saltville, Virginia, *Bootherium* were $\delta^{15}N$ = 1.99‰ and 5.81‰, and $\delta^{13}C$ = −22.54‰ to −19.91‰ (France et al. 2007). Ruminants (foregut fermenters) generally have protein-rich diets while non-ruminants have a lower protein diet (Stevens and Hume 1995). *Bootherium* is interpreted to have been a ruminant selectively feeding on high protein vegetation.

Stable isotope values of 10 *Bootherium* fossils from Alaska (Fox-Dobbs et al. 2008) had mean $\delta^{15}N$ values of +1.2 ± 1.7‰ and $\delta^{13}C$ values of −20.0 ± 0.9‰, similar to the Saltville *Bootherium*. Radiocarbon dates for 2 individuals in the Alaska sample were 41,200 ± 1,500 and 48,800 RC yr BP (see Table 3), indicating the fossils predated the Last Glacial Maximum. The $\delta^{13}C$ values of the Beringian herbivores, including the muskox, are all within the range of values expected for herbivores with a C_3-dominated plant diet. In contrast to the inferred diet of the species south of the continental ice sheets, Fox-Dobbs et al. (2008) interpreted the diet of *Bootherium* in Alaska as primarily sedges in wetter lowland habitats, lichen-rich tundra vegetation, or a combination of the two. This interpretation of the diet of *Bootherium* contrasts to Guthrie's (1991), as discussed below.

Based on identification of compacted plant fragments in the infundibula of teeth from 6 male *Bootherium* fossils from Alaska, it is possible to more directly determine some components of the animal's diet, at least for that part of its range (Guthrie 1991). Plant cuticles from teeth included *Agropyron*-like, *Bromus*-like, and *Poa*-like grasses, all cool-season taxa. Based on this dental evidence for grasses and woody bark fragments of *Salix* (willow) and *Vaccinium* (heath), *Bootherium* was both a browser and grazer in Alaska.

In counties west and south of Licking County, spruce pollen frequencies had declined to low levels prior to ca. 12,900 years cal BP, but increased afterward. Sites to the north and east have a slower spruce pollen decline from 12,500 to 10,200 ^{14}C years BP, and with no abundance fluctuations (Shane 1987; Shane and Anderson 1993). The difference between these 2 spruce pollen records are attributed to changes in the position of the margin of the spruce ecotone in response to shifting climate systems. This is related to changes in the size and shape of the Laurentide ice sheet to the north. In contrast, the pollen record at the Hebron Muskox Site has a constant spruce frequency, which suggests this area remained environmentally stable and could have served as a small local refugium for megafauna (e.g., *Mammut* (mastodon), *Cervalces* (elk-moose), and *Bootherium*).

The fundamental cause for the late Pleistocene megafauna extinction in North America is debated as either climate change (and its accompanying ecological shifts) or human predation (overkill) (Martin 1967; Meltzer 2015; Surovell et al. 2016) and ecological alterations due to humans expanding into the New World. Although dramatic climate and vegetation changes could explain late Pleistocene megafauna extinctions, the Younger Dryas cooling event at 12,900 to 11,700 cal BP occurred *after* the megafauna extinction—precluding the Younger Dryas event as the cause of megafauna extinctions (Chen et al. 2020).

Robinson et al. (2005) stated the collapse of the megaherbivore fauna in New York was followed by human-caused landscape transformation that began many centuries before the Younger Dryas. However, bone collagen ^{14}C dates for mastodon (*Mammut americanum*) are evidence that some megaherbivores lasted until the beginning of the Younger Dryas, and after the initial megafauna population collapse. Subsequent landscape transformation and climate change may have contributed to a cascade that culminated in the demise of the largest members of North America's mammal fauna. The Hebron muskox, which dates 13,070 to 12,840 cal BP, died immediately before or at the beginning of the Younger Dryas at 12,900 cal BP (Table 2). The mastodon from the Burning Tree Golf Course at Heath, 3.3 km northeast of Hebron, was dated using XAD-purified collagen as 10,860 ± 70 RC BP (Pitt-0830) (Fisher et al. 1994), while an elk-moose (*Cervalces scotti*) from Jersey Township, 23 km northwest of Hebron, has an XAD-purified collagen date of 11,500 ± 130 RC yr BP (Beta-14060) (Dyer et al. 1986). Both records are within the inferred time interval for the spruce-forest refugium proposed by Shane (1987). Three mammoths (*Mammuthus*, not identified to species) are reported from Licking County (McDonald 1994), but none has been radiocarbon dated to determine whether or not they were contemporaneous with the Hebron muskox.

The recovery of additional, AMS-dateable specimens of muskox or other taxa will help determine if this area was a refugium and how late the animals persisted. However, there are 2 younger radiocarbon dates for the species from northwest of Ohio, in Michigan (Semken et al. 1964) and Alberta (Hills et al. 2014). It is possible, therefore, that the final extinction of the woodland muskox did not occur in the Great Lakes Region, although this has been proposed for mastodons (Woodman and Athfeld 2009), which generally utilized a similar habitat. Whether or not similar small areas existed in the state—and served as local refugia for late survival of megafauna—is unknown and will require additional, extensive ^{14}C dating. Alternately, as in the case of the young Michigan date, redate the specimen using AMS to confirm its young age.

Conclusions

The sediments recovered by coring at the Hebron Muskox Site in Licking County, Ohio, accumulated in a pro-glacial lake associated with the Scioto lobe of the Laurentide ice sheet. The deposits record a shift from an open, non-vegetated landscape, followed by water infilling of the lake to create a wetland habitat over approximately 7,000 years. During this time, the surrounding vegetation shifted from barren ground with few trees, to a spruce forest, to a deciduous woodland. Near the top of the stratigraphic sequence there is a short but major change in the forest composition, when pine became the major forest element. The area supported a variety of herbivores, including mastodon, elk-moose, and woodland muskox. The Hebron woodland muskox, represented by a partial cranium, dates to 11,086 ± 18 RC yr BP (13,093 to 12,926 cal BP) and is the youngest occurrence of this species in North America. Pollen extracted from a core at the Hebron site indicates that spruce dominated after deglaciation. While other *Bootherium* sites were associated with similar, spruce-dominated forests, the Hebron muskox lived in an environment with forests dominated by deciduous trees and minor spruce.

During the Younger Dryas, approximately 12,900 to 11,700 cal BP, at sites west and south of Licking County, spruce pollen records indicate glacial conditions and vegetation were constant; however, sites to the north and east record a gradual decline in spruce. In contrast, at the Hebron Muskox Site (and the surrounding area) there is a relatively constant spruce frequency, suggesting this area remained environmentally stable. This stability could have permitted the existence of a small, local refugium for megafauna (e.g., muskox, mastodon, and elk-moose).

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