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FIRST REPORT OF JEFFERSON'S GROUND SLOTH (*MEGALONYX JEFFERSONII*) IN NORTH DAKOTA: PALEOBIOGEOGRAPHICAL AND PALEOECOLOGICAL SIGNIFICANCE

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A well-preserved ungual of a pes documents the presence of Jefferson's ground sloth (*Megalonyx jeffersonii*) at the end of the Wisconsinan in North Dakota. This is the 1st report of *M. jeffersonii* in North Dakota, and one of few records from the upper Great Plains. An accelerator mass spectrometer radiocarbon age of 11,915 ± 40 years ago was obtained from the specimen, suggesting that the sloth resided in North Dakota during the Rancholabrean Land Mammal Age, just before extinction of the species. Palynological records from sites near the sloth occurrence and of the same age indicate that it resided in a cool, moist, spruce-dominated forest habitat in a riparian setting along the Missouri River. Its presence in that setting corroborates the notion that Jefferson's ground sloth was a browsing inhabitant of gallery forests associated with rivers. It is likely that *M. jeffersonii* used river valleys, such as the Missouri River valley, as migration routes.

Key words: first occurrence, ground sloth, *Megalonyx jeffersonii*, North Dakota, Pilosa, Pleistocene, Rancholabrean, Xenarthra

Few remains of large Ice Age mammals have been found in North Dakota even though about three-quarters of the state is veneered by glacial deposits. The 1st report of Pleistocene mammalian fossils in North Dakota was by Upham (1895), who described mammoth teeth and bones from the base of the Herman Beach ridge of Glacial Lake Agassiz near Absaraka, Cass County, in eastern North Dakota. Harington and Ashworth (1986) suggested that the remains could have been woolly mammoth (*Mammuthus primigenius*), although the specimens are apparently lost (Hay 1924). Ashworth and Cvancara (1983) reviewed the record of Pleistocene vertebrate fossil occurrences in eastern North Dakota and reported a mammoth tooth from Walhalla, Pembina County, along with a tooth of *M. primigenius* from Embden, Cass County. The tooth from Embden was recovered from a Lake Agassiz Herman strandline, believed to have formed 11,500 years ago and was described further by Harington and Ashworth (1986). They also listed occurrences of remains of *M. primigenius* in McKenzie, Stutsman, and Pembina counties and a tooth fragment of the steppe mammoth (*Mammuthus columbi*) from Williams County. The McKenzie County mammoth was 1st reported by Haraldson (1952). Mammoth or mastodon tusk fragments were reported by Clayton (1962) from Logan County. Kihm (1987) noted the scarcity of Ice Age mammalian fossil records in North Dakota and listed mammoth, horse, stag-moose, and bison as being present in the North Dakota Ice Age megafauna. A recently discovered skull of the giant bison (*Bison latifrons*) from Mountrail County near New Town with an age of >47,500 years ago was reported by Hoganson (2003). Hoganson (2006) reviewed the fossil record of Rancholabrean mammalian taxa from North Dakota. An addition to the North Dakota Rancholabrean megaherbivore list occurred in 1999, when Linda and Doug Vannurden discovered an ungual of Jefferson's ground sloth (*Megalonyx jeffersonii*) along the eastern shore of Lake Oahe, Emmons County, near the southwestern margin of the late Wisconsinan Laurentide Ice Sheet (Fig. 1).

First described by Thomas Jefferson and Caspar Wistar in 1799, the endemic North American ground sloth (*Megalonyx*) was widely distributed across the North American continent, ranging as far north as Old Crow Basin in the Yukon (McDonald et al. 2000), south to southern Mexico, and from coast to coast. It is represented by numerous specimens that vary from complete skeletons to isolated bones. Many of the records that have contributed to our understanding of the

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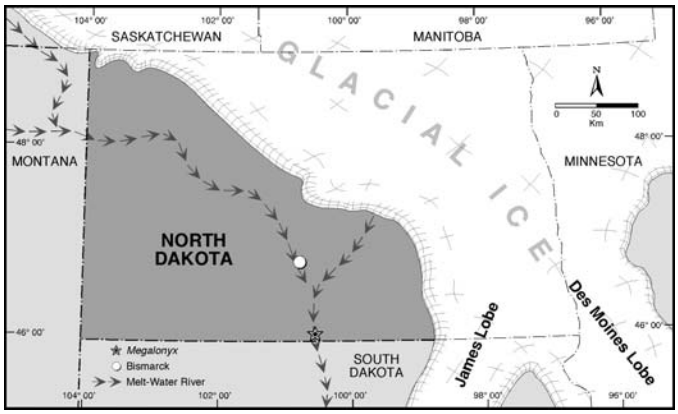

Fig. 1.—Map showing location of the *Megalonyx jeffersonii* (ND 00-10.1) site and position of the continental ice margin during the late Wisconsinan Phase I glacial event about 12,300 years ago. Modified from Clayton and Moran (1982).

distribution of the genus are based on isolated bones. Fortunately, the distinctive skeletal anatomy of the animal makes even single isolated bones readily identifiable and ensures a high degree of reliability in its identification and documentation. The discovery of an ungual of *M. jeffersonii* (Fig. 2) in North Dakota dated at 11,915 ± 40 years ago indicates that just before the animal's extinction it was still widely distributed in North America, including higher latitudes.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Xenarthra Cope, 1889
Family Megalonychidae P. Gervais, 1855
Megalonyx Harlan, 1825
Megalonyx jeffersonii (Desmarest, 1822)
Jefferson's Ground Sloth
(Figs. 2A–F)

Referred specimen.—The referred specimen is a complete ungual of *M. jeffersonii* (catalog number ND 00-10.1). The specimen is curated in the North Dakota State Fossil Collection at the North Dakota Geological Survey Johnsrud Paleontology Laboratory, North Dakota Heritage Center (State Museum), Bismarck.

Locality and age.—The ungual was found as float by Linda and Doug Vannurden along the east shore of Lake Oahe, Emmons County, North Dakota, in 1999 (Fig. 1). They subsequently reported the find to Kent Good, archeologist with the North Dakota Department of Transportation, who brought the specimen to our attention. The site is located in T129N, R79W, SW 1/4, SE 1/4, NW 1/4, SW 1/4, NE 1/4 Sec. 3, 9.4 km south-southeast of Fort Yates. Global positioning system coordinates are latitude 46°1′31.24″N, longitude 100°33′10.5″W.

Very thin and discontinuous late Wisconsinan glacial drift, including river sediments, overlies the Cretaceous Pierre For-

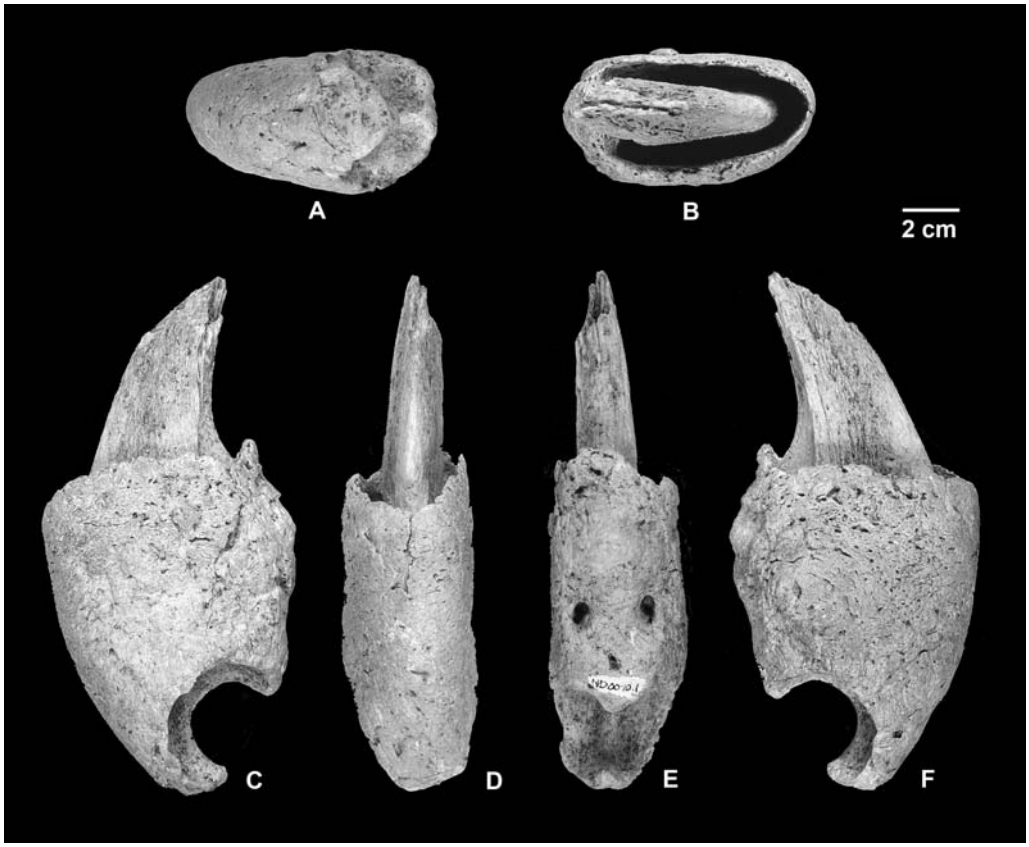

Fig. 2.—Views of *Megalonyx jeffersonii* ungual (ND 00-10.1). A) proximal; B) distal; C) medial; D) dorsal; E) ventral; F) lateral. Height is 166.1 mm.

TABLE 1.—Ungual measurements of *Megalonyx jeffersonii* ND 00-10.1 collected from Emmons County, North Dakota, in 1999 (see Fig. 2).

Measurement	Value (mm)
Greatest length—tip of ungual process to edge of dorsal process of proximal end	166.1
Basal length—tip of ungual process to ventral edge of proximal articular surface	134.6
Maximum height from ventral tendonal insertion to dorsal edge of sheath	80.0
Width of claw at base	41.8

mation at this site. The ungual was found totally exposed on the Lake Oahe beach associated with modern bison and other bones and cultural artifacts weathering out of an Extended Middle Missouri Tradition variant village archeological site referred to as the Havens site (32EM1—Sperry 1995). This site was occupied by ancestral Mandan from about AD 1300 to AD 1425 (Johnson 1999). The possibility that the ungual was collected by an ancestral Mandan elsewhere and transported to the site cannot be ruled out.

An accelerator mass spectrometer age of 11, 915 ± 40 years ago (CAMS-87696) was established for highly purified bone collagen from the specimen by Stafford Research Laboratories, Boulder, Colorado.

Description and comparisons.—In *M. jeffersonii* there are 4 unguals on the manus (digits 1–4) and 3 unguals on the pes (digits 2–4). The unguals of digit 3 in both the manus and pes have an ungual process symmetrical in cross section. In digits 2 and 4 of both the manus and pes the ungual process is asymmetrical with one side relatively straight and the other side slightly convex. The straight side of the ungual process faces digit 3. Specimen ND 00-10.1 is a complete ungual with the nail sheath preserved (Fig. 2; Table 1). The ungual process is triangular in cross section but is asymmetrical when viewed from the distal end. The left side of the ungual process is relatively straight, whereas the right side has a slight convex curvature, indicating it is either from digit 2 of the right pes or digit 4 of the left. These 2 unguals are essentially equal in size in *Megalonyx* and cannot be distinguished in an isolated specimen, so the North Dakota specimen is either from the left digit 4 or right digit 2 of the pes. Reference to an ungual from the pes is based on the relatively stronger ventral curvature and more pronounced robustness for its length than in unguals from the manus.

Although the ungual process in *Megalonyx* has a greater dorsoventral height relative to its width, and so is mediolaterally compressed, the ungual process of *Paramylodon harlani* has a cross section that is semicircular and the dorsoventral and mediolateral dimensions are roughly equal. The cross sections of the ungual processes of the pedal unguals in *Nothrotheriops* generally resemble those of *Megalonyx*, but are not generally as large.

The sheath for the nail is large and well developed and covers about one-half of the ungual. It reflects the generally asymmetry of the ungual process, with one side straight and the other with a slight convex curvature. At the base of the ungual is a pair of large foramina for blood vessels characteristic of sloths. Distal to the pair of foramina is the area for insertion of the tendon of the flexor digitorum profundum. The surface is raised and roughened for attachment of the tendon. Although it is a distinct area, it is not as clearly defined as in *Paramylodon*.

The articular surface for the 2nd phalanx is formed by 2 deep concavities separated by a prominent ridge. The asymmetry of the ungual process is reflected in the articular surfaces, and when viewed proximally, the right articular surface is longer dorsoventrally. The dorsal edge of the articular surface extends farther proximally than the ventral edge and has a slight ventral curvature. The dorsal process of the proximal articular surface would have fit into a small fossa on the dorsal surface of the distal end of the 2nd phalanx and prevented hyperextension of the digit.

PALEOECOLOGICAL SETTING OF *MEGALONYX* IN NORTH DAKOTA

Although the specimen of *M. jeffersonii* was not found in association with other ecologically significant fossils, inferences can be made about the habitat where the ground sloth lived because of geological and paleontological knowledge of the region. Assuming the fossil was found near the place where the animal lived, *M. jeffersonii* inhabited an area about 180 km

FIG. 3.—Map showing locations where remains of *Megalonyx jeffersonii* have been recovered from Wisconsinan sites. Star indicates specimen ND 00-10.1.

Table 2.—Records of *Megalonyx jeffersonii* from the Great Plains (listed from north to south). NA = data not available. AMNH = American Museum of Natural History; BC = Bethany College; HMNS = Houston Museum of Natural Science; KU = University of Kansas; KUVP = University of Kansas; MR = Museum of the Rockies; MSU = Midwestern State University; ND = North Dakota State Fossil Collection, Heritage Center, Bismarck; OMNH = Oklahoma Museum of Natural History; ROM = Royal Ontario Museum; SMVP = Science Museum of Minnesota; TMM = Texas Memorial Museum; UNSM = University of Nebraska State Museum; UOMP = University of Oklahoma Museum of Paleontology; USNM = United States National Museum.

Locality (*n*)	Specimen	Latitude N	Longitude W	Elevation (m)	Reference
Saskatchewan (1)					
Gravel pit, Sutherland, Saskatoon	ROM 5538, molariform fragment	52.2	106.6	490	Skwara 1981
Montana (1)					
Doeden local fauna, Miles City, Custer County	MR 002 tibia, MR 001, proximal end femur, ungula 3rd digit pes	46.4	105.9	763	Wilson et al. 2005
North Dakota (1)					
Lake Oahe, Emmons County	ND 00-10.1, ungula from pes	46.1	100.3	495	This paper
Minnesota (2)					
Minneapolis, Hennepin County	Caudal vertebra (?), location unknown	NA	NA	NA	Hay 1924
Minneapolis, Ramsey County	SMVP P68.40.1, ungula 3rd digit pes	45.0	93.2	280	Erickson 1968
South Dakota (1)					
Philip on Bad River, Haakon County	UNSM 88438, right femur	44	101.7	659	Hay 1924; Pinsof 1985
Nebraska (3)					
Smith Falls local fauna, Cherry County	UNSM 50992, cervical vertebra	42.9	100.3	732	Unpublished
Box Butte Creek, Sheriden County	AMNH 17352, right 3rd metatarsal	42.5	102.6	1,182	Matthew 1918; Schultz 1934
Westpoint Locality B, on Elkhorn River, Cuming County	UNSM 507-42, humerus	41.8	96.7	NA	Unpublished
Kansas (4)					
Lovewell Reservoir, Jewell County	KU uncataloged ungula	39.9	98.1	1,590	Holen et al. 1995
Kansas River Valley, Johnson County	Complete cranium with premaxilla in possession of Edward Yaktine	39	93.3	820	Lillegraven, 1967
Harper Township, McPherson County	BC 996, cranium with zygomatics, type of *M. leidyi*	38.4	97.8	442	Lindahl 1892; Semken 1966
Superior Sand Company Pit, Wichita, Sedgwick County	KUVP 69829, ungual	37.7	97.4	404	Rogers and Martin 1985
Oklahoma (3)					
Deer Creek, Grant County	UOMP 41-4-53, complete mandible, type of *M. jeffersonii oklahomensis*	36.8	97.5	320	Savage 1946
Gould, Harmon County	OMNH 4326, cranium minus zygomatics, type of *M. hogani*	34.7	99.8	488	Stovall 1940
Chickasha local fauna (Bowles Pit), Grady County	OMNH 16511, caudal vertebra	30.1	97.9	343	Smith and Cifelli 2000
Texas (11)					
Quitaque Creek, Motley County	MSU 1605, 1st costal or sternal rib	34.3	100.5	671	Czaplewski, 1993; Dalquest and Schultz 1992; FAUNMAP Working Group 1994
Valley Farms, Navarro County	TMM 31030-10, anterior caudal vertebrae	32.3	96.3	NA	Stovall and McAnulty 1950

TABLE 2.—Continued.

Locality (*n*)	Specimen	Latitude N	Longitude W	Elevation (m)	Reference
Leo Boatwright Gravel Pit, 2.5 miles NE of Trinidad, Henderson County	TMM G-333 (formerly B.E.G 30907-60), cranium with zygomatics, type of *M. brachycephalus*	32.1	96	95	Stovall and McAnulty 1950
Bishop Gravel Pit No. 2, Henderson County	TMM 30893-2, 2nd phalanx digit 3 or 4	32.1	96	NA	Stovall and McAnulty 1950
Hidalgo Falls, Washington County	NA	NA	NA	NA	Hay 1924
Laubach Cave No. 3, Williamson County	TMM 41343-39, phalanx; 41343-42, distal end of humerus; 41343-43, vertebra; 41343-165, lower 1st molariform	30.6	97.6	240	FAUNMAP Working Group 1994; Lundelius 1985
Sour Lake, Hardin County	New York Museum of Natural History, specimen destroyed in fire, upper 1st molariform, type of *M. validus*	30.1	94.1	13	Leidy 1863
Ingleside, San Patricio County	TMM 30967-374, pair of immature mandibular rami; 30967-1843, 1871, pair of lower caniniform teeth; 30967-1673, upper caniniform; 30967-1686, aberrant upper caniniform; 30967-1532, 1687, 1st upper cheek tooth; 30967-1257, 1532, 2088, 1532A, 2nd upper cheek tooth; 30967-1217A, 1491, 1217C, 3rd upper cheek tooth; 30967-1685, 1897, 1623, 4th upper cheek tooth; 30967-909A, 1st lower cheek tooth; 30967-1597, 1290, right and left humeri; 30967-1390, right ulna; 30967-1331, left tibia	28	97.2	0	Lundelius 1972
Livingston, Polk County	HMNS.PV.961, cranium	30.63	95.02	NA	Lundelius and Slaughter 1976; Slaughter 1965
Quinlin, Hunt County	USNM 10836, left 2nd metacarpal	NA	NA	NA	Hay 1924
Thigpen, Falls County	TMM 41335-1, left humerus	NA	NA	NA	Unpublished

southwest of the continental ice margin about 12,000 years ago (Fig. 1). In North Dakota, about 12,300 years, a readvance of the Laurentide ice margin followed ice stagnation and retreat. This readvance is referred to as the late Wisconsinan Phase I glacial event by Clayton and Moran (1982). Apparently the ice did not advance as far to the southwest as the location where the fossil of *M. jeffersonii* was found, although in South Dakota the James Lobe in many areas overrode forests (Fig. 1). Ashworth and Cvancara (1983) suggested that by 12,000 years ago, as glacial ice decayed and Glacial Lake Agassiz began to form, spruce parklands became established in North Dakota interspersed among persistent tundra habitats.

A pollen profile from lacustrine deposits at the Seibold site on the Missouri Couteau, Stutsman County, North Dakota, about 185 km northeast of the *Megalonyx* occurrence, indicates that spruce (*Picea*) forests occupied the Siebold area until about 11,065 years ago (Cvancara et al. 1971; Newbrey and Ashworth 2004). Larch (*Larix*), birch (*Betula*), black ash (*Fraxinus nigra*), juniper (Cupressineae), soapberry (*Shepherdia canadensis*), and aspen or poplar (*Populus*) existed in these spruce-dominated forests, thus indicating cool and moist conditions (Cvancara et al. 1971). The recognition of the widespread occurrence of spruce-dominated forests in the upper Midwest about 12,000 years ago also has been reported at other northern Great Plains sites including the Spiritwood Lake site, North Dakota (McAndrews 1970), the Moon Lake site, South Dakota (Grimm 2001; Laird et al. 1996), the Pickerel Lake site, northeastern South Dakota (Watts and Bright 1968), and the Belmont and Glenboro sites in southern Manitoba (Ritchie and Lichti-Federovich 1968). This suggests that *M. jeffersonii* resided near the Missouri River in a cool, moist, spruce-dominated forest habitat. This is consistent with the observation that *M. jeffersonii* was primarily a browser of forested regions, particularly gallery forests associated with river systems (Gillette et al. 1999; McDonald 1996; McDonald and Anderson 1983; Stock 1925). This is also consistent with another late record of *Megalonyx* associated with a mixed conifer–hardwood habitat in which spruce was dominant, from Illinois dated at 11,405 ± 50 ^{14}C years ago (Schubert et al. 2004).

PALEOBIOGEOGRAPHY OF *MEGALONYX JEFFERSONII*

The genus *Megalonyx* 1st appears in North America in the Hemphillian approximately 5 million years ago (Hirschfeld and Webb 1968). The genus is represented by a series of chronospecies until the terminal species, *M. jeffersonii*, in the late Pleistocene (Rancholabrean), which became extinct around 11,000–10,000 years ago (Schubert et al. 2004). Despite a rich

record in both time and space, the distribution of *Megalonyx* is not uniform across the continent. The fossil record of *Megalonyx* in the Rancholabrean is sufficiently robust (McDonald 1977) that its absence in an area or at least its relative scarcity is probably indicative of aspects of its paleoecology and not necessarily a sampling artifact.

The distribution of *M. jeffersonii* has been published by the FAUNMAP Working Group (1994). Because of the nature of this database and its listing of only specimens with good geological time constraints and the presence of multiple taxa, only 53 localities that met these criteria were utilized. Many records for the species were omitted, particularly single finds similar to the North Dakota record. Although this provides a generalized overview for the distribution of *M. jeffersonii*, the omission of many localities creates artificial gaps in the species' distribution. Our review of both the literature and examination of unpublished specimens in collections has produced a total of 166 localities of *M. jeffersonii*, 27 of which are from the Great Plains (Fig. 3; Table 2). A supplementary distribution map for western records of *M. jeffersonii* is provided by Gillette et al. (1999). Although not necessarily complete, these distribution maps complement each other and demonstrate that although there is a relatively high density of localities on either side of the Great Plains, within the Great Plains the record of *Megalonyx* is relatively sparse. This paucity of records for the genus is reflected by this 1st and only discovery of *Megalonyx* in North Dakota.

Although there are no reviews of Pleistocene faunas for most states in the Great Plains similar to those done for North Dakota (Hoganson 2006), South Dakota (Pinsof 1985), and Oklahoma (Smith and Cifelli 2000), we would argue that based on our examination of both the literature and collections that the small number of records of *Megalonyx* in states located in the Great Plains is a true reflection of the relative rarity of the genus in this region during the late Pleistocene and not merely a sampling artifact. As such, it probably reflects the general absence of preferred habitat for the species in the region. Hoffmann and Jones (1970) noted, as a result of their study of the distribution of recent animals on the northern Great Plains, that many species associated with eastern deciduous forests can only extend their ranges onto the Great Plains by utilizing gallery forests associated with the eastward-flowing tributaries of the Missouri River system, resulting in a dendritic distribution pattern. As a caution, although all of the records from the Great Plains listed here can be referred to *M. jeffersonii*, the lack of precise ages for every site means that although all of the specimens can be considered Rancholabrean in age some may be Sangamonian interglacial or Wisconsinan glacial. Because of this, the occurrence of remains of *M. jeffersonii* can only provide information about general patterns of species distribution and not responses of the species to climatic change.

Conclusions

This 1st reported occurrence of *M. jeffersonii* in North Dakota provides additional documentation that this taxon inhabited the upper Great Plains near the end of the Pleistocene, shortly before extinction of the species. It is also an addition to the meager North Dakota Rancholabrean Land Mammal Age megafaunal list. The population of *M. jeffersonii* south of the Laurentide Ice Sheet in the upper Great Plains was sparse compared to other areas in North America, where the species was widely distributed during Rancholabrean time. *M. jeffersonii* lived in a riparian habitat near the Missouri River in what is now south-central North Dakota about 12,000 years ago. The Missouri River valley was probably a migration route for *Megalonyx*. The Laurentide ice front, which had retreated from the position where the sloth resided, was approximately 180 km to the northeast. Pollen profiles from several lacustrine sites near the *Megalonyx* site indicate that at this time the area was occupied by a spruce-dominated forest in a cool, moist climatic setting.

Acknowledgments

We thank L. and D. Vannurden of Mandan, North Dakota, for discovering the specimen of *M. jeffersonii*, recognizing that it was an important find, and reporting it. We also thank K. Good, North Dakota Department of Transportation, for calling the fossil to our attention. S. Gilbert, United States Army Corps of Engineers, allowed us to study the specimen for which we are grateful to him and the Corps. We are thankful to B. Austin, State Historical Society of North Dakota, for drafting the figures and T. Stafford, Stafford Research Laboratories, for providing the radiocarbon age of the fossil. C. R. Harington and C. Clayton provided useful and insightful comments on how to improve the manuscript. The Evolving Earth Foundation kindly provided funding for the radiocarbon date of the ungula of *M. jeffersonii*.

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