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The Ground Sloth *Megalonyx* from Pleistocene Deposits of the Old Crow Basin, Yukon, Canada

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ABSTRACT. The bear-sized ground sloth *Megalonyx*, endemic to North America, was widespread during the Pleistocene, reaching as far north as Alaska, Yukon, and Northwest Territories. Twenty-two specimens collected from 10 localities in the Old Crow Basin, northern Yukon, include several bones that can be referred to Jefferson's ground sloth (*Megalonyx jeffersonii*) on the basis of the distinctive morphology of the upper and lower caniniform teeth. All of the Yukon specimens are relatively small, suggesting a geological age earlier than Wisconsinan—probably Sangamonian. The Alaskan, Yukon, and Northwest Territories records imply that the species occupied a broad east-west range in northwestern North America during a warm phase of the late Pleistocene.

Key words: Jefferson's ground sloth, *Megalonyx jeffersonii*, late Pleistocene, vertebrate fossils, Yukon

RÉSUMÉ. Le paresseux marcheur *Megalonyx,* de la taille d'un ours, qui était endémique à l'Amérique du Nord, occupait au pléistocène une vaste aire s'étendant au Nord jusqu'en Alaska, au Yukon et aux Territoires du Nord-Ouest. Vingt-deux spécimens recueillis à 10 emplacements dans le bassin de Old Crow (partie nord du Yukon), comprennent plusieurs os que l'on peut attribuer au paresseux marcheur de Jefferson (*Megalonyx jeffersonii*) si l'on se fie à la morphologie particulière des dents supérieures et inférieures en forme de canines. Tous les spécimens du Yukon ont une taille relativement petite, ce qui suggère qu'ils datent d'un âge géologique antérieur au wisconsinien – probablement le sangamonien. Les relevés faits en Alaska, au Yukon et dans les Territoires du Nord-Ouest laissent entendre que l'espèce occupait une vaste aire s'étendant d'est en ouest dans la partie nord-occidentale de l'Amérique du Nord durant une phase de réchauffement du pléistocène tardif.

Mots clés: paresseux marcheur de Jefferson, *Megalonyx jeffersonii,* pléistocène tardif, fossiles vertébrés, Yukon

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INTRODUCTION

Megalonyx, the most widespread North American sloth genus, is known from the late Miocene (Hemphillian ca. 6 Ma) until the end of the Pleistocene (Rancholabrean ca. 10 000 B.P.). The megalonychids represent the earliest members of the South American mammalian fauna to disperse into North America during the late Cenozoic. The earliest representative of the group, *Pliometanastes*, is known from several localities in the southern United States (Hirschfeld and Webb, 1968) and evolved into *Megalonyx* (Hirschfeld, 1981). The latter genus includes a lineage of several species that culminated in *M. jeffersonii*, its largest and most recent representative member (McDonald, 1977).

During this time *Megalonyx* became widely distributed across the North American continent and extended its range as far north as Alaska (Stock, 1942) and the Northwest Territories in Canada (Stock and Richards, 1949). While these two records have at least indicated the presence of *Megalonyx* in the northern parts of the continent, the specimens, each a single tooth, have provided only limited information on the taxon. The first detailed account of Yukon ground sloth remains (Harington, 1977:177–185) comprised descriptions of 12 specimens assigned to *Megalonyx* cf. *M. jeffersonii*. In the Old Crow Basin, C.R. Harington (Canadian Museum of Nature project 1966 to 1987) and W.N. Irving (Northern Yukon Research Programme based at the University of Toronto 1975 to 1983) and their field parties recovered a diverse fauna that includes additional remains of *Megalonyx*. These remains improve our understanding of the northernmost populations of this genus and are the subject of this paper.

LOCALITY DESCRIPTIONS

Megalonyx fossils have been recovered from 10 localities in the Old Crow Basin, Yukon (Fig. 1). Although none of the specimens were found in stratigraphic position except the second phalanx from Locality 44, their possible geological, geochronological and paleoenvironmental context is considered below (see Discussion). Not all

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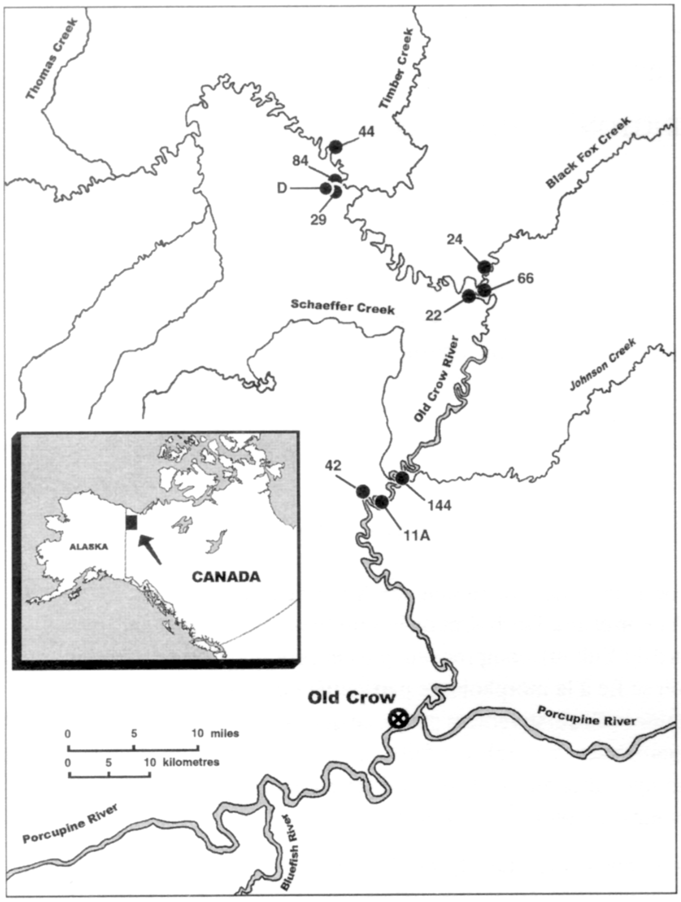

FIG. 1. Map of the Old Crow Basin, Yukon, showing localities where *Megalonyx* remains were found. The numbering of Old Crow fossil localities collected by C.R. Harington began in 1966, his first year in Old Crow Basin, and continued over successive years. Generally, the highest numbers assigned to a locality refer to the latest finds.

FIG. 2. Restoration of Jefferson's ground sloth (*Megalonyx jeffersonii*). From a watercolour by David Brynaert, courtesy of *Canadian Geographic*. The height of the animal standing is about 2.5 m.

recovered material is diagnostic, but those specimens that are diagnostic can be identified as the species *M. jeffersonii* (Fig. 2), and all material is referred to that species. The 22 specimens are listed in Table 1. All are housed in the vertebrate paleontology collections of the Canadian Museum of Nature (CMN).

DESCRIPTION OF SPECIMENS

While all of the specimens listed can be identified as megalonychid sloth and can be referred to the genus *Megalonyx*, only a few specimens can be referred to the species *M. jeffersonii* with any certainty. These specimens will be discussed further below. Measurements of the more diagnostic specimens described below are provided in Table 2.

One of the distinctive dental features of *Megalonyx* is the shape of the enlarged anteriormost tooth, or caniniform. Changes in morphology of the tooth, with the enlargement and increasing prominence of the lingual column in both upper and lower caniniform teeth, permit the chronospecies of *Megalonyx* to be distinguished. In the

TABLE 1. Specimens of *Megalonyx jeffersonii* from the Old Crow Basin, Yukon, Canada.

Locality	Catalog Number	Skeletal Element
11A	CMN 48628	right third metacarpal
11A	CMN 48646	second phalanx digit 4 pes
11A	CMN 24192	molariform
11A	CMN 48661	left upper caniniform
11A	CMN 22567	proximal phalanx
11A	CMN 26193	proximal half ungual digit 3 manus
11A	CMN 48449	second phalanx manus
11A	CMN 24194	proximal right calcaneum
11A	CMN 48656	proximal right calcaneum
22	CMN 14528	molariform
22	CMN 19203	upper fifth molariform
24	CMN 14883	second phalanx
29	CMN 14882	proximal half ungual
42	CMN 33247	molariform
44	CMN 43457	second phalanx
66	CMN 25148	left astragalus
66	CMN 31146	proximal phalanx
66	CMN 24215	left lower caniniform
66	CMN 23042	proximal phalanx digit 3 manus
84	CMN 31778	left upper caniniform
144	CMN 28550	second phalanx digit 3 manus
D	CMN 43284	proximal phalanx

TABLE 2. Measurements of selected specimens of *Megalonyx jeffersonii* from the Old Crow Basin, Yukon. All measurements are in millimetres (mm).

Right Third Metacarpal (CMN 48628) Locality 11A	
Length	95.9
Proximal end, mediolateral width	50.2
Proximal end, dorsoventral width	47.7
Distal end, mediolateral width	39.6
Distal end, length of carina	52.0
Left upper caniniform (CMN 48661) Locality 11A	
Length	31.5
Width	15.4
Left upper caniniform (CMN 31778) Locality 84	
Length	34.4
Width	20.0
Left lower caniniform (CMN 24215) Locality 66	
Length	34.2
Width	14.6
Left astragalus (CMN 25148) Locality 66	
Anteroposterior length	102.2
Width anterior edge trochlea	83.2
Width posterior edge trochlea	71.9
Anteroposterior length of lateral edge of trochlea	80.8
Dorsoventral height navicular process	48.4
Mediolateral width navicular process	69.7

Blancan to earliest Irvingtonian species, *M. leptostomus,* the lingual bulge is the least developed, but is positioned along the midline of the tooth. Longitudinal grooves mesial and distal to the lingual column are generally absent or only incipiently present in the latest members of this species. In *M. wheatleyi,* from the middle Irvingtonian, the lingual column is more prominent, and there are weak grooves along its mesial and distal edge. The mesial and distal grooves along the edge of the lingual column are well developed in *M. jeffersonii.* These characters are seen in the three caniniforms from the Old Crow Basin: a left upper caniniform (CMN 48661) from Locality 11A (Fig. 3c); a left upper caniniform (CMN 31778) from Locality 84 (Fig. 3e); and a left lower caniniform (CMN 24215) from Locality 66 (Fig. 3d). Although the morphology of the upper and lower caniniform teeth conforms to that of *M. jeffersonii*, these teeth fall at the small end of the size range for the species (Figs. 4 and 5).

The sample of *Megalonyx* includes four molariform teeth. The general similarity between the upper and lower molariform teeth makes it difficult to provide more precise identification of isolated teeth. The teeth are triangular in cross section with the mesial and distal lophs of the occlusal surface converging towards the apex of the triangle, a feature characteristic of megalonychid sloth teeth. Like all sloth teeth, they lack roots and have an open pulp cavity.

Heaton and McDonald (1993) described a third metacarpal from the Kuchta Sand Pit locality in South Dakota and documented size differences between Blancan, Irvingtonian, and Rancholabrean species of *Megalonyx.* The graph provided by Heaton and McDonald (1993) has been modified to include the right third metacarpal (CMN 48628) from Locality 11A (Fig. 3a). Morphologically the specimen agrees with other specimens of *Megalonyx,* and

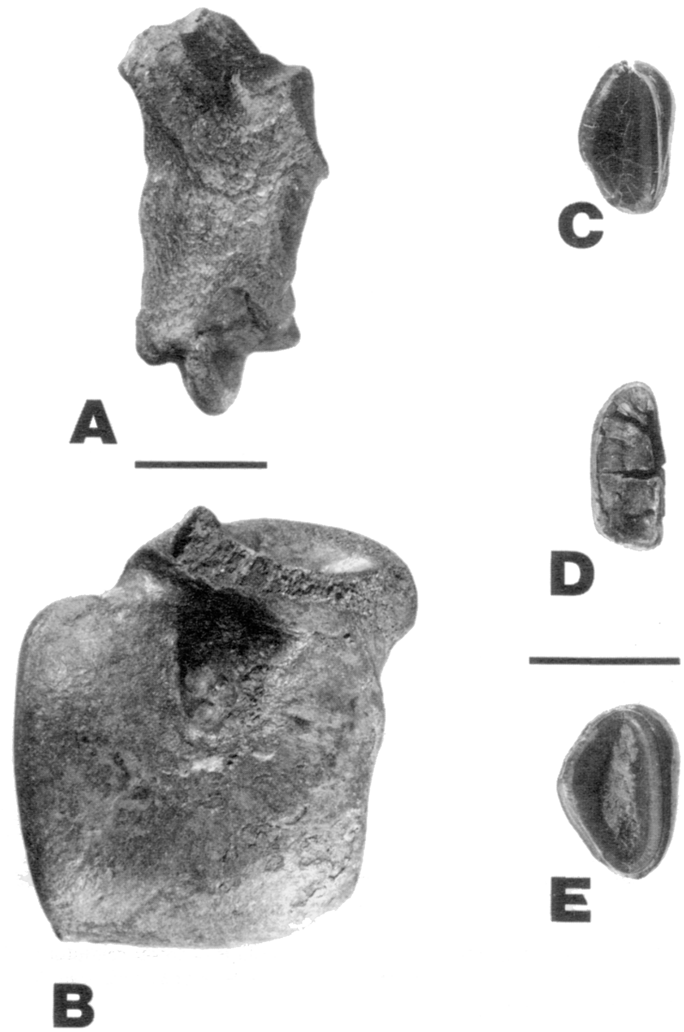

FIG. 3. Diagnostic specimens of *Megalonyx jeffersonii* from the Old Crow Basin, Yukon: a) right third metacarpal (CMN 48628), Locality 11A, anterior view; b) left astragalus (CMN 25148), Locality 66, proximal view; c) left upper caniniform (CMN 48661), Locality 11A, occlusal view; d) left lower caniniform (CMN 24215), Locality 66, occlusal view; e) left upper caniniform (CMN 31778), Locality 84, occlusal view. Scale bars are 30 cm long. The left bar applies to Fig. 3a and c; the right bar applies to Fig. 3b, d, and e.

its size places it at the small end of the size range of *M. jeffersonii* (Fig. 6).

The astragali of megalonychid sloths are distinguished from those of other ground sloths by the absence of the modification of the medial trochlea into an odontoid process. While the lack of this modification gives the astragalus an appearance generally similar to those of carnivores and rodents, the sloth astragalus can readily be distinguished by the concave articular surface on the navicular process. The left astragalus (CMN 25148) from Locality 66 (Fig. 3b) possesses all of the features typical of *Megalonyx* astragali. Like the other specimens, it is from an individual at the small end of the size range for *M. jeffersonii* (Fig. 7).

Many of the *Megalonyx* specimens from the Old Crow Basin are phalanges: four proximal, five second, and two ungual. All members of the order Xenarthra are distinguished

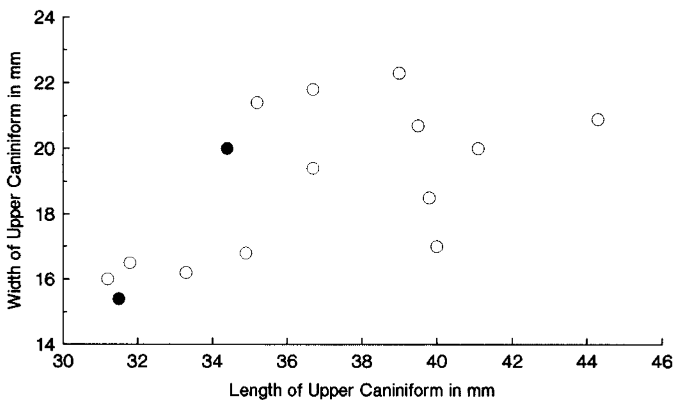

FIG. 4. Scatter diagram showing size relationships of upper caniniform of *Megalonyx* from the Old Crow Basin, Yukon, to those of *M. jeffersonii* from other Rancholabrean sites.

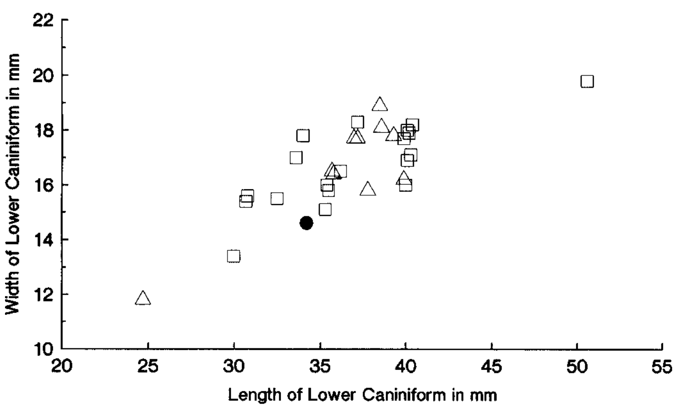

FIG. 5. Scatter diagram showing size relationships of lower caniniform of *Megalonyx* from the Old Crow Basin, Yukon, to those of *M. jeffersonii* from Idaho and other conterminous states.

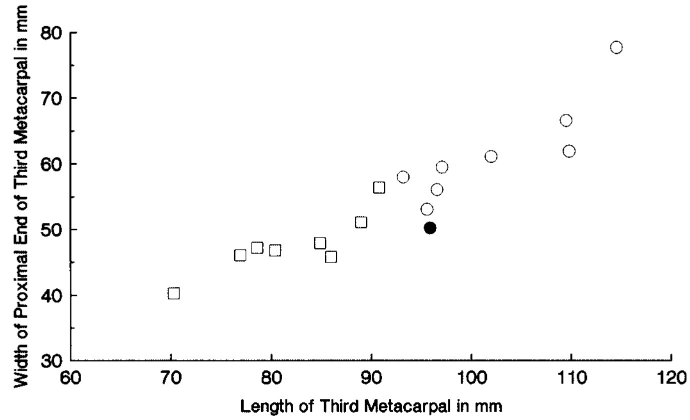

FIG. 6. Scatter diagram showing size relationships of third metacarpal of *Megalonyx* from the Old Crow Basin, Yukon, to those of *M. jeffersonii* and *M. wheatleyi*.

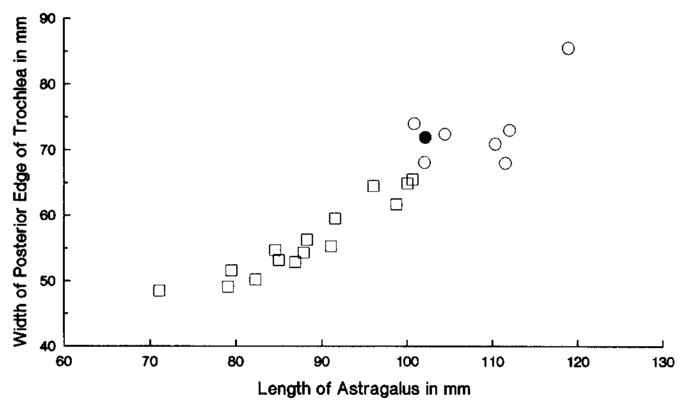

FIG. 7. Scatter diagram showing size relationships of astragalus of *Megalonyx* from the Old Crow Basin, Yukon, to those of *M. jeffersonii* and *M. wheatleyi*, based on the anteroposterior length vs. width of posterior edge of trochlea.

by the proximodistal shortening of the proximal phalanges in both manus and pes. This distinctive feature is seen in the *Megalonyx* proximal phalanges from the Old Crow Basin. The second phalanges are elongated with a distal articular surface that forms almost three-quarters of a circle, reflecting the extreme flexion of the unguals while the sloth is walking. The ungual process of the two unguals has the typical tall, narrow triangular cross section present in megalonychid sloths. Measurements of phalanges from the Old Crow Basin are provided in Table 3.

DISCUSSION

All of the Yukon specimens fall at the small end of the size range for *Megalonyx jeffersonii* and are only slightly larger than the largest individuals of the earlier ancestral species, *Megalonyx wheatleyi* (Figs. 4–7). There are two possible explanations for the small size of the Yukon individuals. One is related to the geological age of the specimens. During its phylogeny, the *Megalonyx* lineage increased in body size through time, so each succeeding species was on the average larger than the preceding species; the terminal species *Megalonyx jeffersonii* is the largest.

The earliest record of *M. jeffersonii* is from the type locality of the Irvingtonian which Repenning (1987) placed in the earlier part of his Irvingtonian II (900 000 to 400 000 ± 25 000 years ago). The small size of the Old Crow Basin specimens may merely be indicative of their Sangamonian age. For example, a substantial vertebrate fauna of possible Sangamonian age has been excavated from Locality 44 (Harington, 1977, 1990), the source of a *Megalonyx* second phalanx (CMN 43457).

Alternatively, the small size of the individuals may indicate a negative Bergmann's response, reflecting an overall trend of a decrease in body size with increasing latitudes. It is not easy to document size trends against latitude for *Megalonyx* in the Sangamonian, since few faunas include the genus; also, the same skeletal element is not always preserved, making direct comparisons difficult. As a preliminary examination of this trend, the sample from Old Crow can be compared with samples from American Falls Reservoir in Idaho and Ingleside Texas. All three faunas are considered Sangamonian in age, reducing the chance that any size trends reflect a change with time as opposed to latitude. Upper and lower caniniforms of *Megalonyx* are known from all three localities and

TABLE 3. Measurements of phalanges of *Megalonyx jeffersonii* from the Old Crow Basin, Yukon. All measurements are in millimetres (mm).

CMN No.	Locality	Mediolateral Width (max.)	Proximodistal Depth (max.)	Anteroposterior Length (max.)
14882	Old Crow Loc. 29			
	(distal half lacking)	29.3	50.5	61.7+
48646	Old Crow Loc. 11A	34.5	42.7	67.2
28550	Old Crow Loc. 144	39.7	52.6	76.2
48449	Old Crow Loc. 11A	27.7	34.0	58.0
31778	Old Crow Loc. 84	36.7	43.8	31.0+
22567	Old Crow Loc. 11A	37.7	53.9	40.0
43284	Old Crow Loc. D	49.3	56.0	34.3
43457	Old Crow Loc. 44	35.6	49.0	63.5
26193	Old Crow Loc. 11A			
	(distal half lacking)	33.3	62.3	73.0+
23042	Old Crow Loc. 66	43.2	55.4	35.9
14883	Old Crow Loc. 29			
	(proximal end damaged)	30.8	28.2+	53.2 (approx.)

permit some comparison. While the overall samples are small (upper caniniform: Old Crow N = 2, American Falls N = 2, and Ingleside N = 1; lower caniniform: Old Crow N = 1, American Falls N = 4, and Ingleside N = 3), a plot of average tooth length against latitude does show a trend. As shown in Figure 8, *Megalonyx* was smaller in the northern part of its range than in the south. This suggests that the overall smaller size of *Megalonyx jeffersonii* from Old Crow compared to other individuals of the species may reflect both its geological age and a pattern of smaller size in the lineage at higher latitudes.

A similar pattern has been observed in the very small Peary caribou *Rangifer tarandus pearyi* of the Canadian Arctic Islands (Banfield, 1961). One explanation for this smaller size in higher latitudes might be that it represents a response to a decrease in the availability of suitable vegetation. Given the low basal metabolism of sloths (McNab, 1985), we might expect that overall body size would increase at higher latitudes, to improve thermal inertia and help maintain a constant body temperature in a cooler environment. Akersten and McDonald (1991) discussed the problems of maintaining body temperature in the sloth *Nothrotheriops,* which lived in desert habitats, and the possible effect on its distribution, so it seems likely that thermal stress would have been a critical factor for *Megalonyx* living at high latitudes as well. Of course, we cannot tell whether the insulation of the pelt in *Megalonyx jeffersonii* varied greatly from south to north. This departure from the expected pattern in size change over the range of the animal points out how much more needs to be learned about the paleophysiology of this extinct group.

Average temperatures during the Sangamonian may have been as much as 3˚C warmer than at present (Karrow, 1990), and this may have been one important factor that permitted *Megalonyx* to expand its range as far north as the Old Crow Basin. Analysis of plant macrofossils and invertebrates of the possible Sangamonian unit at Locality 44 indicates that climate was at least as warm as at present (Harington, 1990). A significant change in climate from cool (dwarf birch) to warmer (spruce-birch) is reflected in

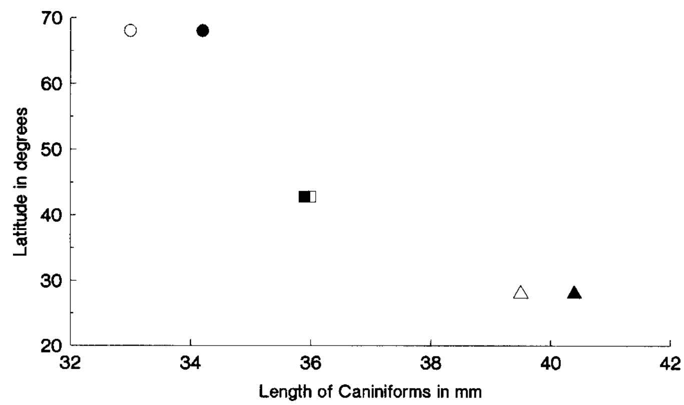

FIG. 8. Size trends in the caniniforms of *Megalonyx* against latitude. Open symbols are for upper caniniform, solid symbols are for lower caniniform.

pollen assemblages extending upward from the reworked Lower Lake clay to the vertebrate fossil–bearing unit (Lichti-Federovich, 1973). Large spruce (*Picea* sp.) logs up to 1.5 m in circumference, along with a nearly equal number of tamarack (*Larix* sp.) logs (identified by J.S. Gonzalez, Forintek Canada Corp., pers. comm. 1986) indicate a period warmer than at present. The tamarack fossils are clearly north of the modern range of the species (Little, 1971; Viereck and Little, 1975). Furthermore, the presence of short-faced skunks *Brachyprotoma obtusata* more than 4300 km north of their known paleo-range (Youngman, 1986)—particularly if they had habitat requirements similar to those of their closest living relatives, the spotted skunks *Spilogale putorius*—may also indicate a warmer phase. In addition, the fossiliferous unit that is the probable source of the ground sloth bones lies between the widespread Lower Lake and Upper Lake beds, considered to be of Illinoian and Wisconsinan ages, respectively (Harington, 1977; Jopling et al., 1981). This fact suggests that the unit is of the last interglacial age.

One taxon found with *Megalonyx* at two localities, 11A and 66, is wolverine, *Gulo gulo* (Bryant, 1987). The modern distribution of this species is circumpolar and corresponds to the boreal zone of the Northern Hemisphere

TABLE 4. Non-Yukon records of *Megalonyx* from Canada.

Specimen	Locality	Reference and Remarks
Alberta		
Right upper cheek tooth fragment (field number MB-68-310)	Medicine Hat (Mitchell Bluff)	Churcher, 1969:154; Stalker and Churcher, 1982. Identified as ?*Megalonyx* sp. Considered to be of Sangamonian age.
Left femur shaft and fragment of shaft (P960.17.40 and 39)	Medicine Hat (Island Bluff)	Confirmed as *Megalonyx* by H.G. McDonald. Both specimens are probably from the same individual (J.A. Burns, pers. comm. 1999).
Right humerus midshaft (P90.6.21)	Edmonton area	Referred to *M. jeffersonii* (J.A. Burns, pers. comm. 1999). See general reference to *Megalonyx* in Burns and Young, 1994.
Right femur midshaft (P98.6.28)	Edmonton area	Referred to *M. jeffersonii* (J.A. Burns, pers. comm. 1999).
First thoracic vertebra (P89.13.68)	Fort Saskatchewan	Referred to *Megalonyx* sp. spinous process (J.A. Burns, pers. comm. 1999).
Left first rib proximal third (P89.13.549)	Fort Saskatchewan	Referred to *M. jeffersonii* (J.A. Burns, pers. comm. 1999).
British Columbia		
Ungual (ROM 3339), cast of missing original	Quesnel Forks	Cowan, 1941; Harington, 1977, 1996. From river gravel.
Northwest Territories		
Lower molariform (ANSP 15208)	Lower Carp Lake	Stock and Richards, 1949. Found with fragments of an American mastodon tooth.
Saskatchewan		
Tooth fragment (ROM 5538)	Saskatoon area (Pike Lake)	Churcher, 1969. Identified as *Megalonyx*. Considered to be late Pleistocene in age.
Condylar region of left mandible (WV-76a)	Stewart Valley (Wellsch Valley fauna)	Churcher, 1969:55; Stalker, 1971. Identified as ?*Megalonyx* sp. Considered to be of Kansan age.

(Kvam et al., 1988). Its possible association with *Megalonyx* might at first suggest that the sloth was capable of surviving in a cooler environment than might be expected. Bryant (1987) did note that the ancestral form *Gulo schlosseri* is associated with decidedly warm faunas in Europe, and early North American *Gulo* may have been adapted to a similar environment. Bryant feels that *Gulo gulo* is not inherently a purely "boreal" or "tundra" species, given that its range extended as far south as Pennsylvania until the mid-1800s.

The southernmost sloth in South America is found at Ultima Esperanza Cave in Chile, at 51.5˚S. This species, *Mylodon darwinii,* has a larger body size than *Megalonyx* from the Old Crow Basin. At 68˚N, within the Arctic Circle, *Megalonyx* from the Old Crow Basin may represent the greatest tolerance to extreme temperatures of any of the extinct ground sloths. Both the southernmost and the northernmost records indicate that some of the extinct sloths may not have been restricted to as narrow a range of environmental temperatures as their modern relatives. Whether this greater tolerance reflected a higher basal metabolism or merely greater body size that provided thermal inertia is unknown at this time.

DISTRIBUTION OF *MEGALONYX* IN CANADA

The Old Crow Basin has produced the best samples of *Megalonyx jeffersonii* from Canada. Previous records included only isolated occurrences of single specimens (Table 4). While *M. jeffersonii* is common in Rancholabrean faunas in the eastern United States (McDonald, 1977), it has not yet been found in any faunas in eastern Canada. Nor is it known from Pleistocene faunas north of the Great Lakes and St. Lawrence River, although many taxa with which it is commonly associated, such as the American mastodon *Mammut americanum*, have been found there. (For example, three mastodon teeth and "elephant" bones—perhaps representing that species too—are known from the Moose River Basin on northern Ontario, as observed by C.R. Harington in 1998; and another mastodon tooth found near Chambord, Lac Saint Jean, Québec, was reported by Piérard and Tremblay, 1980). The presence of *Megalonyx jeffersonii* at higher latitudes in the western part of its range than in the east parallels the distribution seen in the stag-moose *Cervalces scotti*, the giant beaver *Castoroides ohioensis*, and the helmeted muskox *Bootherium bombifrons*. All of these taxa are also closely associated with *Megalonyx* in Pleistocene faunas from the eastern United States. It is worth noting that American mastodon, giant beaver, and helmeted muskox remains are recorded from Pleistocene deposits in the Old Crow Basin, and that the first two species have been found in place in the possible Sangamonian interglacial unit at Locality 44. The FAUNMAP Working Group (1996) found that Pleistocene mammalian faunas followed a Gleasonian model in responding to environmental change: that is, each species responded in accordance with its individual tolerance limits, resulting in range shifts with varying rates, at different times, and in divergent directions. Yet the similarity of these three species in expanding their northernmost ranges into the same general area suggests either a close association with a specific environment or strong similarities in the ecological requirements of these herbivores.

Pinsof (1996) considered 62 faunas in North America as Sangamonian in age. He listed 20 from Canada, 4 from Alaska, 35 from the rest of the United States, and 3 from Mexico. Five of the Canadian faunas include *Megalonyx*, although it should be noted that while Pinsof listed Old Crow as one of the faunas, he did not include *Megalonyx* in the faunal list. Seven of the Sangamonian faunas in Canada are east of Manitoba, and none of these seven include *Megalonyx.* Eleven of the 35 localities in the United States (excluding Alaska) include *Megalonyx*, but except for American Falls Reservoir in Idaho, all are restricted to the southern United States.

The Yukon fossils are important, not only because they constitute the largest samples of ground sloth remains from Canada, but also because they can be identified as Jefferson's ground sloth (*Megalonyx jeffersonii*). Although no specimen has been found in its original stratigraphic context except the specimen from Locality 44, we suggest that the species lived in the proto-Old Crow Basin during the last (Sangamonian) interglacial. Considered together, the Alaskan (Fairbanks area), Yukon (Old Crow Basin), and Northwest Territories (Lower Carp Lake) records suggest that the species occupied a rather broad east-west range in northwestern North America during a warm phase of the late Pleistocene (Harington, 1978, 1993).

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