Bison antiquus from Kenora, Ontario, and Notes on the Evolution of North American Holocene *Bison*

Jerry N. McDonald and George E. Lammers

ABSTRACT

An associated skeleton of an adult male *Bison antiquus occidentalis* from Kenora, Ontario, is radiocarbon dated at 4270±65 yrs BP, making it the youngest unequivocal record for the species. It also extends the range 280 km north and 65 km east of the previously documented limits for the genus in the western Great Lakes area. The Kenora bison died in a shallow pond in an oak-pine woodland; it was experiencing nutritional stress at the time of its death. Both halves of the mandible had been fractured by trauma earlier in life.

A review of morphological change in bison during the Holocene shows that later bison, *Bison bison*, were absolutely smaller, had absolutely shorter limbs, and had more robust upper limbs and more gracile lower limbs, relative to length, than did the earlier bison, *Bison antiquus*. Compared with that of *Bison antiquus*, the thoracic limb of *Bison bison* became elongated relative to the pelvic limb, and limb length increased relative to skull size. Relative to the norm in *Bison antiquus*, these traits diverged further in the wood bison, *Bison bison athabascae*, than in the plains bison, *Bison bison bison*. The patterns of pelage development and social behavior in *Bison bison bison*, however, are more distant from parallel patterns postulated for *Bison antiquus antiquus* than are patterns of pelage development and social behavior in *Bison bison athabascae*.

Introduction

The skull, mandible, 14 teeth, and 58 postcranial bones of an adult male bison were collected late in the 1970s during dredging operations in a peat bog near Kenora, Ontario. This bison, now in the collections of the Manitoba Museum of Man and Nature, and cataloged as MMMN V-1914, has been referred to *Bison antiquus occidentalis*, an extinct taxon that was the evolutionary link between the late Pleistocene North American steppe bison, *Bison antiquus*, and the extant North American bison, *Bison bison*. Sediment from within the cranium of the Kenora bison was radiocarbon dated at 4850±60 years before present (yrs BP) (Beta-3779) and ribs of the bison were radiocarbon dated at 4270±65 yrs BP (DIC-3381). Sediment from the site yielded pollen, plant macrofossils, and mollusks, which provided information about the regional environment at the time the bison lived.

The Kenora bison is significant for several reasons. Associated skeletons of *Bison antiquus occidentalis* are uncommon from other than archaeological contexts, and descriptions of the postcranial bones of such associated specimens are rare. The Kenora bison was found farther north and east than any bison previously known in the western Great Lakes region, and it is a rare record of bison in Ontario. The radiocarbon age of 4270± 65 yrs BP is the youngest known for *Bison antiquus*. Pathologies of the face and teeth provide information about the life history of this animal and its biophysical condition at the time of death, and contribute information about patterns of pathology in the taxon. Although most characters of the Kenora bison skull are of average to greater-than-average size for *Bison antiquus occidentalis*, the postcranial bones are smaller than might be expected, a circumstance that raises questions about the pattern of coevolution of the postcranial skeleton and skull in bison during the Holocene.

In this paper we (1) describe the partial bison skeleton, pollen spectrum, and invertebrate remains from the Kenora site; (2) review the zoogeographical, paleoecological, and evolutionary context of the Kenora bison; (3) document the pattern of skull and limb coevolution seen in North American Holocene *Bison*, and, on the basis of the observed pattern of coevolution, (4) comment upon the position of the wood bison, *Bison bison athabascae*, in the evolutionary sequence of North

---

Jerry N. McDonald, Research Associate, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0121; and McDonald & Woodward Publishing Company, 431-B East College Street, Granville, Ohio 43023. George E. Lammers (deceased).

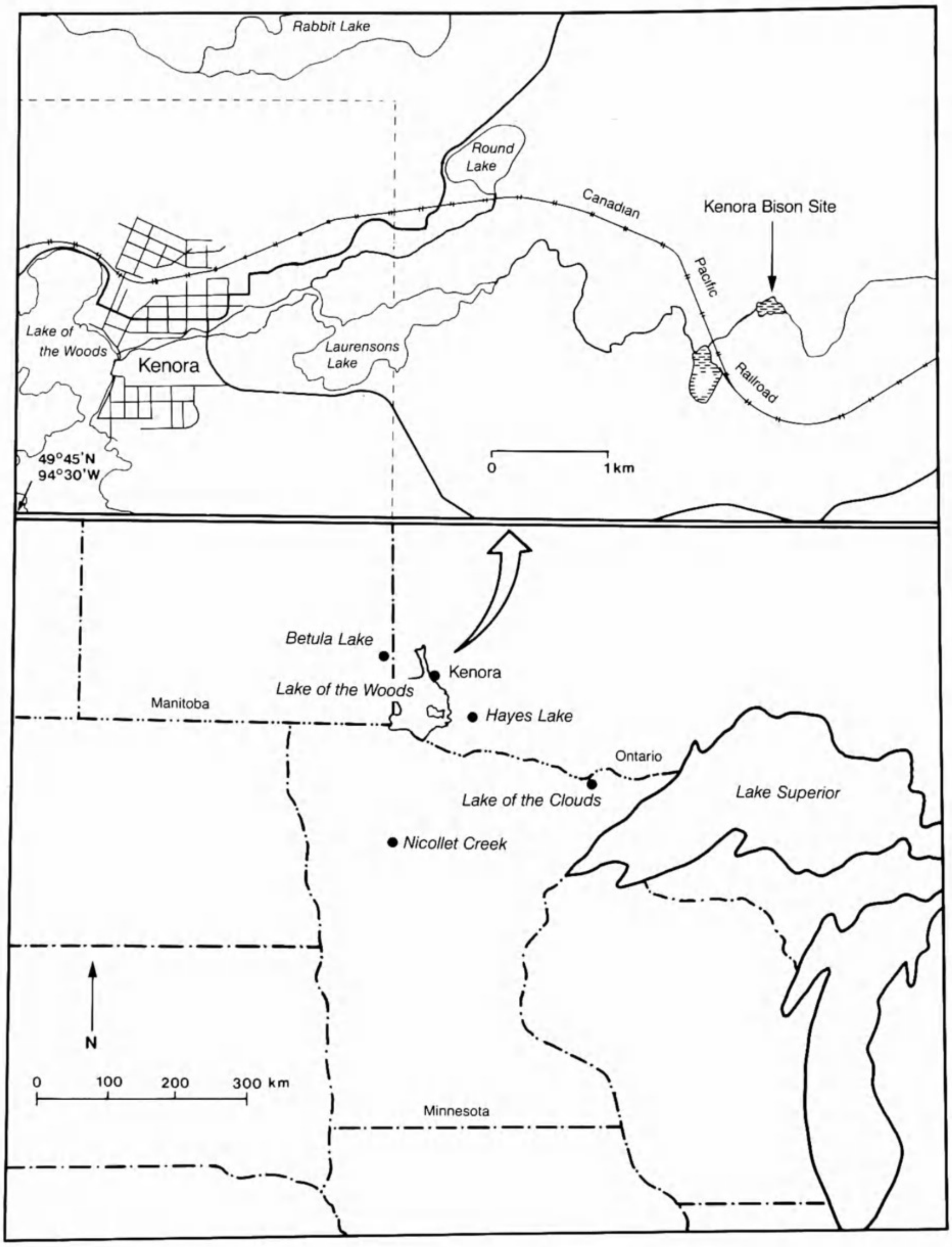

FIGURE 1.—Top: The Kenora, Ontario, area showing the location of the Kenora bison site. Bottom: Southwestern Ontario and adjacent regions showing the Kenora bison site and other places mentioned in the text in regional context.

American *Bison*. All dates are given in uncalibrated radiocarbon years before present.

ACKNOWLEDGMENTS.—We extend our appreciation to Nick Serduletz of Kenora, Ontario, for salvaging the Kenora bison skeleton and donating it to the Manitoba Museum of Man and Nature. Gary Haynes and Clayton E. Ray reviewed this paper and provided many helpful comments, but the authors retain full responsibility for the facts and opinions as finally presented.

ABBREVIATIONS.—The following museum abbreviations are used:

MMMN	Manitoba Museum of Man and Nature, Winnipeg, Manitoba
PIN	Paleontological Institute, Russian Academy of Sciences, Moscow.

The Kenora Bison

LOCATION AND DESCRIPTION OF THE KENORA SITE

The bison skeleton was recovered during a period of several years by Nick Serduletz while dredging a peat bog located in the watershed of Laurensons Creek 3.0 km east of Kenora. The dredging extended to a depth of approximately 4.5 m, at which

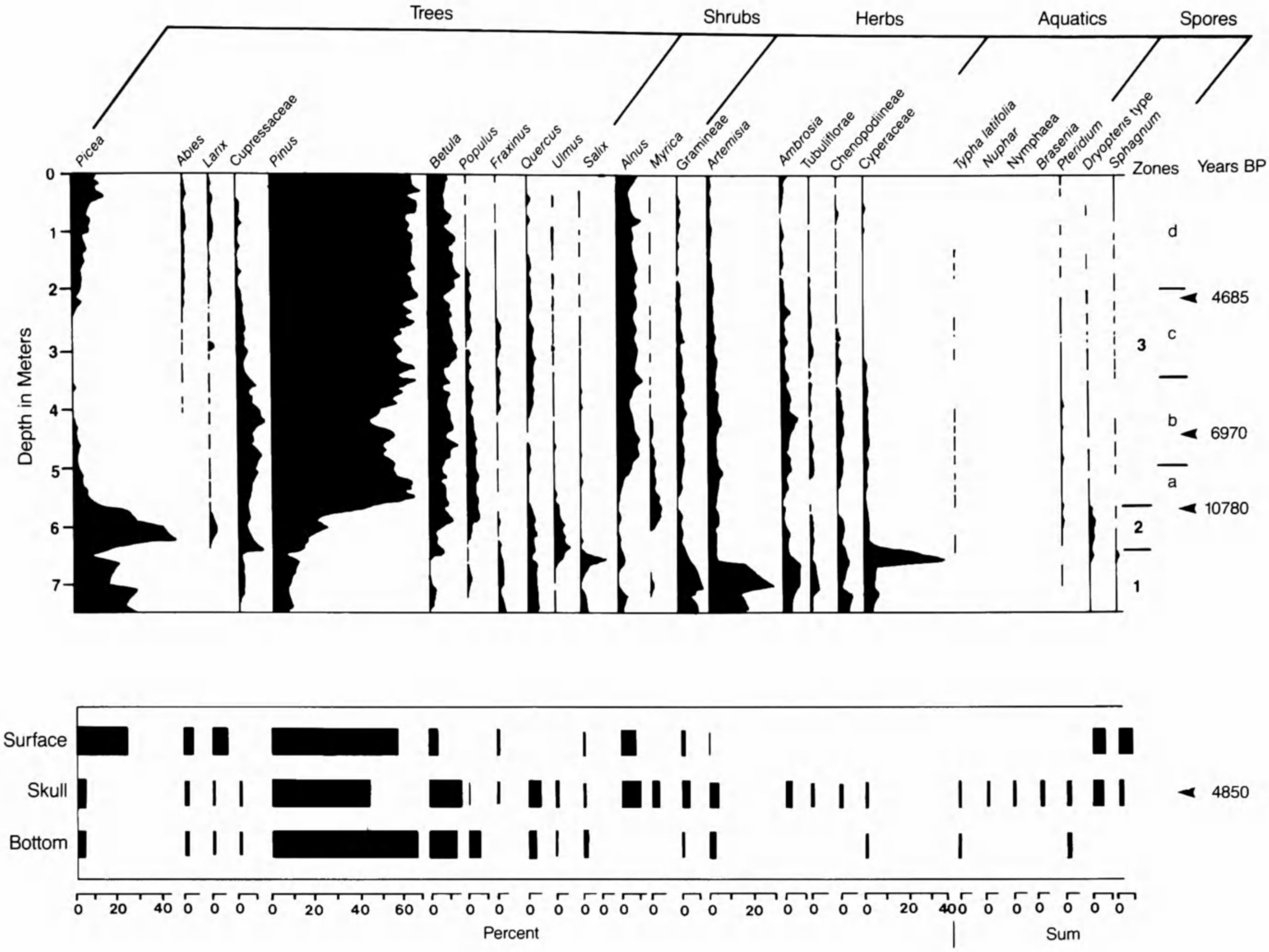

FIGURE 2.—Pollen and spore diagrams for Hayes Lake and the Kenora bison site, Ontario, simplified from McAndrews (1982).

level the skeleton was found. The technical description of the bog location is Lot K101, Concession 4J, Township Jaffray; this site is mapped on the Kenora 52E/16 quadrangle, 1:50,000 series (Figure 1).

PALEOENVIRONMENT OF THE KENORA SITE

McAndrews (1982) analyzed pollen, spores, and plant macrofossils from three samples of sediment from the Kenora bison site. One sample was from the bottom of the bog, another was from within the skull, and the third was from near the upper surface of the bog. McAndrews's analyses indicated that the pattern of vegetation composition and change at Kenora (Figure 2) was similar to patterns at nearby Hayes Lake, Ontario, and the more distant Lake of the Clouds, Minnesota (Figure 1).

The bog began to fill about 10,000 yrs BP, when the regional vegetation was essentially pine forest. Between about 9200 yrs BP and 5000 yrs BP, in response to warming and drying associated with the Boreal and Atlantic climatic episodes, deciduous broadleaf species became more prominent than conifers in the regional forest, and open areas supporting grasses and other herbs presumably reached their maximum. The return of somewhat cooler and more mesic conditions with the onset of the Sub-Boreal climatic episode (ca. 5000–2750 yrs BP), initiated a return to a more closed pine forest. By about 3600 yrs BP this forest was well established (Wendland, 1978; McAndrews, 1982; Webb et al., 1983; Dykev and Prest, 1987; Wendland et al., 1987).

The bison skeleton was entombed in organic-rich mud deposited in a lentic aquatic environment. Sediment from the skull yielded "a variety of marsh shrubs and herbs and pond plants.... This evidence suggests the bison died in a water-lily-

FIGURE 3.—Kenora bison skull in dorsal view. (Scale bar=5 cm.)

covered pond one or two meters deep that was bordered with a marsh dominated by shrubs; wetland conifers (spruce, larch) grew nearby" (McAndrews, 1982:47–48).

Five species of mollusks were collected from within the cranium of the bison. These included the small spire (*Amnicola walkeri*), three-keeled valve (*Valvata tricarinata*), ribbed valve (*Valvata sincera sincera*), modest gyraulus (*Gyraulus parvus*), and shiny pea clam (*Pisidium nitidum*). Although the pond of 4270 yrs BP probably was intimately associated with upper Laurensons Creek, similar to the situation of the depression today, the gastropods from the bison skull suggest that the body of water containing the skeleton was relatively slow moving and pond-like. The Kenora site is within the present range of the five mollusks (Clarke, 1981), and their presence 4270 yrs BP does not require ecological conditions substantially different than exist today. At the same time, these mollusks are widespread today, and their sympatry 4270 yrs BP would have been possible even under environmental conditions somewhat different than those of today.

SKELETAL AND DENTAL MATERIAL COLLECTED

The skull, mandible, 14 teeth, and 58 complete or partial postcranial skeletal elements of the Kenora bison have been recovered. The skull is nearly complete, lacking only the nasals, most of the right premaxilla, and most of the palatine process of the left maxilla (Figures 3–5). Minor fragments are missing from other bones of the skull. Both halves of the mandible are complete (Figures 6–9). Teeth present include RP4–M3, LM2–M3, Rp4–m3, and Lp4–m3. Postcranial elements present include the atlas; axis; cervical vertebrae 3, 5, and 7; thoracic vertebrae (1), 2, 4, 5, ?7, 9, and ?10; lumbar vertebrae (2), (3), (4), and (5); sacrum; ribs R1, (R?2), (R3), (R4), (?R5), R6, R7, (R8), R11, (R12), L1, (L2), (L3), (L4), (L5), L6, L8, L9, L10, L11, L13 or L14; manubrium; (sternebrae); R scapula; R radioulna; R radial carpal; R metacarpal; L scapula; L radioulna; L fused 2+3 carpal; proximal thoracic sesamoid; proximal thoracic first phalanx; medial thoracic phalanx; bony pelvis, R femur, R tibia, R calcaneum; L femur, L tibia, two proximal pelvic phalanges. Specimens in parentheses are incomplete; those not in parentheses are either complete or nearly complete. Cranial, vertebral, and rib measurements are given in Tables 1–3; those for other elements are given in the Appendix.

The bones and teeth of the Kenora bison are well preserved and exhibit no evidence of pre-entombment or diagenetic weathering, abrasion, trampling, crushing, or chew-gnaw damage. The bones do vary in color, ranging from light to dark brown, which suggests exposure during diagenesis to different

FIGURE 4.—Kenora bison skull in lateral view, left side. (Scale bar=5 cm.)

concentrations of decaying organic matter or to groundwater with differing concentrations of oxygen. All breakage of the bones can be attributed to damage during excavation.

AGE AND SEX.—The Kenora bison was approaching senescence at the time of its death. All teeth were in full to advanced wear. The RM1 and both m1s either had lost or were losing, by wear, the enamel fossettes within the dentine field.

Several morphological features identify this specimen as a male. The skull is robust, the frontal and fronto-parietal sutures are obscured by fusion over most of the dorsal surface of the cranium, the supraorbital foramina are bridged by bone at the level of the orbits, the horn cores possess distinct burrs at the base, the horn core growth is spiraled posteriorly around the longitudinal axis, and the anteroposterior plane of the base of the horn cores is rotated rearward relative to the frontal plane. Females of all species of North American bison have relatively gracile skulls. Typically, among the short-horned North American bison, the frontal and fronto-parietal sutures are unfused over most or all of their length, the supraorbital foramina are not bridged by bone at the level of the orbits, the horn cores do not possess burrs at the base, the horn cores grow straight or spiral anteriorly around the longitudinal axis, and the anteroposterior plane of the bases of the horn cores is either rotated forward relative to the plane of the frontals or parallel with the plane of the frontals (McDonald, 1981).

TAXONOMIC IDENTITY.—The Kenora bison is referred to *Bison antiquus occidentalis* on the basis of diagnostic criteria given in McDonald (1981). The horn cores of the Kenora bison are triangular in cross-section and symmetrical about the dorsoventral axis at the base. The tips of the horn cores are ellipti-

FIGURE 5.—Kenora bison skull in caudal view. (Scale bar=5 cm.)

TABLE 1.—Skull (linear measurements in mm, angular measurements in degrees) of Kenora bison (*Bison antiquus occidentalis*) compared with the means of similar measurements for other shorter-horned North American bison. (Data are from McDonald, 1981, except measurements for Banff bison, which are from Harington, 1984; values in single parentheses are estimated dimensions for the complete character; values in double parentheses are for incomplete characters and are provided solely to describe the amount of bone present.)

Measurement	Kenora bison	Banff bison	*B. a. antiquus*[1]		*B. a. occidentalis*[2]		*B. b. bison*[3]		*B. b. athabascae*[4]	
			x̄	*s*	x̄	*s*	x̄	*s*	x̄	s
Spread of horn cores, tip to tip	(850.0)	–	870.0	71.0	779.3	76.9	603.9	44.7	681.2	92.0
Horn core length, upper curve, tip to burr	(315.0)	265.0	279.2	35.1	277.8	39.1	190.7	24.7	235.1	43.9
Straight-line distance, tip to burr, dorsal surface of horn core	275.0	–	249.7	29.2	248.1	31.8	172.4	21.4	207.0	34.4
Dorsoventral diameter, horn core base	88.6	(82.0)	101.9	9.7	94.6	8.4	81.9	6.4	91.5	8.7
Rostro-caudal diameter, horn core base	93.7	85.0	105.6	12.2	98.8	10.0	83.4	6.3	97.2	9.5
Minimum circumference, horn core base	286.0	(260.0)	324.4	32.6	300.3	27.7	255.4	19.5	289.1	22.9
Width of occiput at auditory opening	269.9	–	287.9	18.6	262.0	13.2	243.9	9.7	273.6	15.3
Width of occipital condyles	138.5	–	143.7	8.4	135.0	7.7	126.6	5.7	130.1	6.4
Depth of occiput, nuchal line to dorsal edge of foramen magnum	99.0	–	111.6	9.2	104.0	7.0	98.7	6.2	99.6	6.6
Least width of frontals, between horn cores and orbits	274.1	301.0	314.7	19.4	296.6	16.8	271.1	12.6	293.4	10.5
Greatest width of frontals at orbits	317.0	–	371.3	18.6	348.0	16.7	324.6	12.9	354.0	14.8
Distance, nuchal line to rostral end of premaxillae	545.0	–	629.0*	–	564.3	24.8	535.3	17.0	578.6	15.2
Angle of divergence of horn cores forward from sagittal	70.0	–	72.9	4.8	72.1	5.2	67.7	4.4	71.0	5.0
Angle between foramen magnum and occipital plane	135.0	–	125.4	1.6	129.6	7.3	133.8	7.6	129.4	8.8
Angle between foramen magnum and basioccipital plane	119.0	–	115.6	1.7	113.4	5.6	110.5	5.0	113.8	6.6

[1] Number of specimens measured varies from 1 to 41.
[2] Number of specimens measured varies from 25 to 91.
[3] Number of specimens measured varies from 56 to 142.
[4] Number of specimens measured varies from 7 to 11.
*Denotes sample containing only 1 specimen.

cal in cross-section. Growth along the longitudinal axis is modestly spiraled posteriorly, the posterior margins of the horn cores are slightly concave in dorsal view, and the anteroposterior plane of the horn core is rotated rearward relative to the plane of the frontals. The length along the upper surface of the horn core, tip to burr, is approximately 315 mm, well within the range of 186–392 mm known for the taxon. In *Bison antiquus antiquus,* the tips of the horn cores are typically cordiform to triangular in cross-section and possess a distinct groove on the dorsal surface, growth is straight (not spiraled) around the arched longitudinal axis of the core, the posterior margin is straight, and the anteroposterior plane of the horn cores is parallel with the frontal plane. The horn cores of *Bison bison* grow straight along the longitudinal axis, they are straight along their posterior margins, and they are less slender (i.e., length: basal circumference ratio is less) than in *Bison antiquus occidentalis.*

PATHOLOGIES.—Pathological conditions are apparent in the bones and teeth of the skull and in both halves of the mandible. The RP2 and P3 were missing during at least the later part of the life of the Kenora bison, as evidenced by the ossified alveo-

TABLE 2.—Measurements (in mm) of vertebrae (exclusive of atlas and axis) of Kenora bison. (Measurements conform to those described for bovids in von den Driesch, 1976. Measurements in parentheses are estimated dimensions for the complete character.)

Measurement	C3	C5	C7	T1	T2	T4	T5	?T7	T9	?T10	L2	L3	L4	L5
H	(155.0)	168.0	385.0	–	–		–	–	–	–	158.9	160.5	155.9	148.1
GL	66.0	62.0	57.0	59.0	61.0	62.0	59.0	60.0	61.0	62.0	64.0	65.0	64.0	65.0
GLPa	100.2	89.5	94.3	70.2	66.3	63.7	63.2	63.9	60.7	63.5	99.6	100.6	94.8	96.9
Bpacr	97.0	113.2	109.5	–	–		–	–	–	–	65.6	75.1	78.1	78.2
Bpacd	101.7	102.6	86.3	–	–	–	–	–	–	–	47.6	46.5	49.5	60.1
Bfcr	45.5	41.0	43.0	65.4	58.7	57.1	59.8	48.7	59.2	55.2	48.0	49.1	49.9	50.8
Bfcd	51.1	48.1	79.4	77.5	77.9	74.9	70.2	62.6	77.1	67.3	52.7	53.6	55.8	66.2
Hfcr	53.1	55.1	59.0	51.7	53.5	52.7	49.6	47.2	53.1	47.3	45.9	47.0	47.8	47.1
Hfcd	53.6	57.7	54.8	50.3	51.1	50.1	44.4	45.1	52.2	43.3	43.4	46.3	45.7	42.0
MinBr	59.1	80.1	93.1	67.6	66.9	44.6	43.3	37.2	48.4	43.8	42.8	44.2	52.5	60.9
Bptr	–	–	139.8	129.4	119.0	110.5	110.4	107.8	112.5	107.5	(242.0)	317.0	(358.0)	(369.2)
Height of spine	–	69.9	326.0	–	472.0	—	285.0	214.0	391.0	141.0	(101.0)	93.6	87.4	80.8

FIGURE 6.—Kenora bison mandible in dorsal view. (Scale bar=5 cm.)

lar trough that would have accommodated the roots of these teeth (Figure 6). A hole is present in the dentine fields of LM3. The insertion tubercle for the masseteric muscle on the right mandible is conspicuously larger than the same tubercle on the left mandible (Figure 7). Both the right and left halves of the mandible had been fractured and healed. The fractures were centered approximately below the right p2–p3 and left p4–m1 (Figures 6–9). The right mandibular body contains roughened

FIGURE 7.—Left (top) and right (bottom) halves of Kenora bison mandible in lateral view. (Scale bar=5 cm.)

FIGURE 8.—Left (top) and right (bottom) halves of Kenora bison mandible in medial view. (Scale bar=5 cm.)

FIGURE 9.—Kenora bison mandible in ventral view. (Scale bar=5 cm.)

TABLE 3.—Measurements (in mm) of ribs of Kenora bison. (Measurements in double parentheses are for incomplete elements and are provided solely to describe the amount of the element that is present.)

Rib number	Length	Minimum anteroposterior diameter	Minimum circumference
R1	316	27.6	73.0
?R2	((210))	–	–
R3	360	26.1	64.0
R4	466	26.7	70.0
?R5	((84.9))	–	–
R6	604	27.3	74.0
R7	630	25.1	69.0
R8	((400))	–	–
R11	563	19.6	62.0
R12	((460))	19.9	57.0
L1	309	27.4	74.0
L2	((229))	25.4	63.0
L3	((260))	–	–
L4	((135))	–	–
L5	((224))	29.7	76.0
L6	609	27.6	76.0
L8	644	25.8	69.0
L9	645	21.6	61.0
L10	618	18.2	61.0
L11	568	18.8	61.0
L13	396	17.9	56.0

bone on the lateral, ventral, and medial surfaces of the healed fracture, and a subcircular hole leading to the interior of the bone opens through the ventral surface of the fractured area. Rostral to the level of Rm1, the body of the right ramus of the mandible is conspicuously wider than that of the left, and the diastema is displaced ventral to its normal position. Root canals for the missing Rp2 and Rp3 are present in the alveolar trough, indicating that these teeth were present at, or at least shortly before, the time of death. The medial side of Rm3 was shorn away in life, and the dentine surface thus exposed was worn smooth by use. The surface of the healed left body of the mandible is much smoother than that of the right, and no displacement of the diastema occurred. A circular opening is located between and below Lp4–Lm1; both of these teeth are loosely rooted in the alveolus, and an abnormally long gap separates the two teeth. The bone surrounding the opening is dense and does not appear to have been affected by infection at the time of death. Root canals for the missing Lp2 and Lp3 are present, but they are shallow—a condition that suggests either displacement of the teeth or modification of the roots by the trauma to the mandible or by its subsequent healing. Enamel on the medial surfaces of Lp4, Lm1, and Lm3 had been chipped, part of the medial wall of the rostral cusp of Lm3 is missing, and holes are present in the dentine fields of Lm3 and Lp4. The tooth rows of both halves of the mandible are unusually sinuous, probably reflecting modification of the tooth alignment by the fractures and subsequent healing.

No pathologic conditions were noted in any of the postcranial bones.

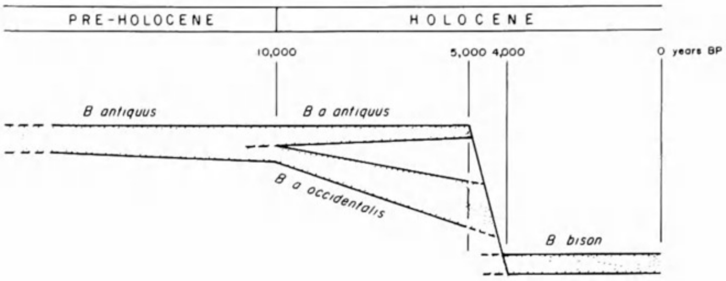

FIGURE 10.—The evolutionary fold of 5000–4000 radiocarbon yrs BP, when the evolution of *Bison bison* from *Bison antiquus* was rapidly completed (from McDonald, 1981).

DISCUSSION

The Kenora bison lived at the time when the nucleus of the North American bison range was anchored on the northern Great Plains and when the final, rapid steps in the evolution of *Bison bison* from *Bison antiquus* were taking place (Figure 10) (McDonald, 1981). The radiocarbon age of 4270±65 yrs BP is the youngest such date of which we are aware for a specimen that can be assigned with confidence to *Bison antiquus occidentalis*. Harington (1984) reported a partial cranium from Banff, Alberta, dated at 3240±90 yrs BP (I-11638), which he referred to *Bison bison occidentalis*, equivalent to *Bison antiquus occidentalis* as used in this paper. Having examined the Banff cranium, we believe that this specimen is referable to *Bison bison*. All measurements that can be obtained from the skull of the specimen are within the range of *Bison bison* (Table 1), and the qualitative aspects of characters still visible on the specimen also are consistent with those typical of *Bison bison*.

Measurements of the Kenora bison skull are all within the range documented for *Bison antiquus occidentalis*, but some are outside the observed ranges for *Bison antiquus antiquus* and *Bison bison* (Table 1; cf. tables 21, 25, 29, and 34 in McDonald, 1981). Most features of the Kenora bison skull conform harmoniously with both qualitative and quantitative attributes of the skull typical of *Bison antiquus occidentalis*. The horn cores are longer and more slender (i.e., long relative to diameter at base), and the dorsal part of the cranium is narrower than typical specimens, however. The breadth of the base of the cranium is near the mean for the taxon.

All measured dimensions of the long bones of the Kenora bison are smaller than the observed means for the limbs of *Bison antiquus occidentalis* except the anteroposterior diameter of the femur, which is slightly larger (within one standard deviation (*s*)) than the observed mean for the taxon (Table 4). The length of the radius is >2*s*, and that of the femur and tibia are between 1*s* and 2*s*, of the mean for *Bison antiquus occidentalis* long bone lengths, whereas the length of the metacarpal in the Kenora bison is smaller than the heretofore-documented minimum for the taxon. The transverse diameters of all four limb

TABLE 4.—Limb measurements (in mm) for shorter-horned North American bison, males only. (For each taxon, top row is mean measurement, bottom row is standard deviation. Data from McDonald, 1981. AP=anteroposterior diameter; TR=transverse diameter; L=rotational length; *=sample with only 1 specimen.)

Species		Humerus			Radius			Metacarpal			Femur			Tibia			Metatarsal		
	n	L	AP	TR	L	AP	TR	L	AP	TR	L	AP	TR	L	AP	TR	L	AP	TR
Bison antiquus	1–28	339.0*	69.7	58.7	343.0	33.7	54.5	222.0	30.7	52.3	429.0	56.2	58.8	412.0	42.5	59.0	273.9	35.2	40.9
antiquus		*S*=–	2.8	0.5	7.7	0.9	1.2	6.6	1.2	3.5	14.0	4.2	2.1	14.7	2.9	3.2	8.3	2.3	2.7
Bison antiquus	38–161	356.9	66.4	55.0	343.8	35.5	58.5	219.8	30.1	51.4	403.7	50.0	49.3	403.5	38.9	53.5	270.3	33.1	39.2
occidentalis		*S*=21.6	4.5	4.2	14.7	2.1	3.3	8.6	1.8	3.7	18.0	3.2	2.3	17.6	2.2	3.0	10.0	1.8	2.9
Kenora bison (MMMN V-1914)	1	–	–	–	309.0	32.0	57.8	190.0	28.2	48.3	383.0	51.8	48.8	370.0	35.0	51.7	–	–	–
Bison bison	37–118	325.9	61.5	50.6	320.5	32.2	53.9	206.3	27.2	45.4	380.7	47.9	47.3	371.9	34.7	49.1	255.2	30.3	35.3
bison		*S*=11.1	3.1	3.1	9.2	1.7	2.8	7.1	1.6	3.4	10.4	2.4	2.4	10.0	1.4	2.2	7.7	1.3	1.9
Bison bison	2–3	354.5	67.5	58.5	341.3	35.0	59.7	228.7	30.3	52.0	421.3	54.0	51.7	414.3	38.0	53.3	275.7	33.0	39.0
athabascae		*S*=6.3	0.7	0.7	14.0	1.0	3.5	4.1	1.1	2.0	11.5	4.3	0.5	12.6	1.7	1.5	5.5	1.0	1.7

bones, and the anteroposterior diameter of the femur, are near the mean for *Bison antiquus occidentalis,* whereas the anteroposterior diameters of the shaft of the radius, metacarpal, and tibia are >1*s* from the observed mean for *Bison antiquus occidentalis*. At the same time, however, the dimensions of the Kenora bison long bones are also within the ranges observed for *Bison bison bison*. The two thoracic limb bones of the Kenora bison are >1*s* shorter than the mean, whereas the two pelvic limb bones are very near the mean for *Bison bison bison*. The diameters of all four bones are near the mean for *Bison bison bison*. All of the long bones of the Kenora bison are smaller than the documented range for equivalent characters in male *Bison bison athabascae*.

The fact that the Kenora bison lived near the end of the *Bison antiquus* lineage, as *Bison antiquus* was changing rapidly into *Bison bison* (Figure 10), suggests that the Kenora bison should be relatively small bodied compared with the mean for *Bison antiquus occidentalis*. Except for the horn cores, which are relatively long for the subspecies, the cranium of the Kenora bison generally conforms to this expectation of small size. The long bones are shorter than might be expected when compared with the size of the skull. If the evolutionary reduction in all skeletal elements were taken to be isometric, these long bones would probably be identified casually as those of *Bison bison bison* had they been found without the associated skull. In general, however, the long bones are broad and robust relative to their length, a condition suggesting that the Kenora bison was more heavily built than *Bison bison bison*. In addition, the bones of the thoracic limb are shorter relative to those of the pelvic limb, a condition resembling more nearly the limb proportions of *Bison antiquus antiquus* than *Bison bison bison*. (The thoracic limb:pelvic limb ratio was lowest (0.81) in *Bison antiquus antiquus,* greater (0.83) in *Bison bison athabascae,* still greater (0.846) in *Bison bison bison*, and greatest (0.854) in *Bison antiquus occidentalis* (i.e., the thoracic limb, relative to the pelvic limb, was shortest in *Bison antiquus antiquus* and longest in *Bison bison occidentalis*). *Bison bison occidentalis* also demonstrated the greatest variation in limb dimensions, which is not unexpected given its dynamic role as a decanalized evolutionary bridge between two relatively canalized species (Tables 5, 6).

ZOOGEOGRAPHIC SIGNIFICANCE.—The Kenora bison is a range record for the subspecies, species, and genus. The nearest known remains of bison from natural contexts are of *Bison antiquus antiquus* from Betula Lake, Whiteshell Provincial Park, Manitoba, and *Bison antiquus occidentalis* from Nicollet Creek, Itasca State Park, Minnesota, respectively 65 km west and 280 km south of Kenora (Figure 1) (Cleland, 1966; Shay, 1971; McDonald, 1981). Prehistoric *Bison bison* remains have been recovered from the Hungry Hall archaeological site along the east side of Rainy River near where it discharges into Lake of the Woods, Ontario (Moore, 1975). Bison from Hungry Hall are north and east of the known natural range of *Bison bison;* they probably were imported by Indians from the nearby bison range.

TABLE 5.—Ratios of anteroposterior and transverse diameters to lengths of long limb bones. (Data from McDonald, 1981, as presented in Table 4. AP=anteroposterior diameter; TR=transverse diameter; L=rotational length; *=sample with only 1 specimen.)

Species		Humerus		Radius		Metacarpal		Femur		Tibia		Metatarsal	
	n	AP:L	TR:L	AP:L	TR:L	AP:L	TR:L	AP:L	TR:L	AP:L	TR:L	AP:L	TR:L
Bison antiquus antiquus	1–28	0.206*	0.173	0.098	0.159	0.138	0.236	0.131	0.137	0.103	0.143	0.129	0.149
Bison antiquus occidentalis	38–161	0.186	0.154	0.103	0.170	0.137	0.234	0.124	0.122	0.096	0.133	0.122	0.145
Kenora bison (MMMN V-1914)	1	–	–	0.104	0.187	0.148	0.254	0.135	0.127	0.095	0.140	–	–
Bison bison bison	37–118	0.180	0.155	0.100	0.168	0.132	0.220	0.126	0.124	0.093	0.132	0.119	0.138
Bison bison athabascae	2–3	0.190	0.165	0.103	0.175	0.132	0.227	0.128	0.123	0.092	0.129	0.120	0.141

TABLE 6.—Ratios between selected cranial and limb biometrics for shorter-horned North American Bison, males only. (Data from McDonald, 1981. FW=least frontal breadth; N-Pm=nasion to premaxilla; BW=breadth across base of skull at mastoid processes; TL=combined rotational length of humerus, radius, and metacarpal; PL=combined rotational length of femur, tibia, and metatarsal; HCL=horn core length.)

Species	FW/N-Pm	BW/N-Pm	TL/PL	HCL/TL	HCL/PL	FW/TL	FW/PL
Bison antiquus antiquus	0.500	0.457	0.811	0.308	0.250	0.348	0.283
Bison antiquus occidentalis	0.526	0.464	0.854	0.302	0.258	0.322	0.275
Kenora bison (MMMN V-1914)	0.503	0.495	–	–	–	–	–
Bison bison bison	0.506	0.455	0.846	0.224	0.189	0.318	0.269
Bison bison athabascae	0.507	0.472	0.832	0.254	0.212	0.317	0.264

PALEOECOLOGICAL SIGNIFICANCE.—During the Atlantic climatic episode (ca. 8500–5000 yrs BP) the regional vegetation of extreme southwestern Ontario was dominated by a mixed forest. Early in the episode, when conditions were cooler and more mesic, conifers dominated. By the end of the episode, when the warming and drying trend reached its maximum, deciduous broadleaf species were more prominent than conifers in the regional forest, and open areas supporting grasses and other herbs presumably reached their maximum. The onset of the Sub-Boreal climatic episode (ca. 5000–2750 yrs BP) brought a cooler, more mesic climate, which led to a closed forest with conifers increasing in importance relative to deciduous broadleaf species.

The parkland vegetation that characterized the Kenora region around 5000 yrs BP, with the deciduous browse and sparse grasses, would have afforded the best local environmental conditions available during the Holocene for supporting populations of bison. This does not mean that the population of bison in the Kenora region was either large or permanent. The Kenora bison does not possess morphological characteristics suggesting inbreeding depression in the population (McDonald, 1981), but it does show evidence of extended nutritional stress.

McAndrews's (1982) interpretation of the death of the Kenora bison—that it died in a shallow pond—is consistent with taphonomic evidence as well as paleobotanic and sedimentary evidence. Similarly, the bones recovered consist of a random array of elements, not the patterned collection that would be expected had the bison been killed by predators or its carcass scavenged, or had flowing water sorted the bones (Voorhies, 1969; Haynes, 1980, 1982; Shipman, 1981). All breakage in the bones appears to be the result of excavation by heavy machinery rather than the result of battering in a high-energy fluvial environment. Some of the elements appear to have weathered after excavation.

INTERPRETATION OF PATHOLOGIES.—Two pathologic conditions appear to be represented in the Kenora bison. A trauma to the face appears to have broken the bodies of both halves of the mandible and dislodged the R/L? P2 and P3. A sharp blow to the right half of the mandible, along or immediately caudal to the diastema, could have produced the fractures that broke the bone completely through, allowing it to become displaced, and bent the body of the left side of the mandible to the left, producing a green-stick fracture that separated the medial and ventral parts but not the dorsolateral part. The incompletely severed left body could have functioned as the splint that held the rostral parts of both halves of the mandible in place while they healed. Healing occurred with slight ventral displacement of the diastema of the right body.

In addition to the pathologic conditions discussed above, the broken teeth conform to a pattern of tooth pathology seen in the dentition of numerous musk oxen (*Ovibos moschatus*) from Greenland, the Arctic islands of Canada, and Alaska (Henrichsen, 1981, 1982; Anne Gunn, pers. comm., 1987; McDonald, unpub. data). The usual pattern of this pathology is that holes exist in the dentine field in correlation with broken teeth. In musk oxen, the enamel walls of teeth are often conspicuously thin in individuals exhibiting the condition. The etiology of this condition is not known, but it is believed to result from inadequate or imbalanced intake of (=access to) essential nutrients, such as calcium or phosphorus. The hypoplastic condition of the dentine and enamel appears to weaken the teeth to the extent that normal use results in tooth breakage. In musk oxen exhibiting hypoplasia and subsequent breakage, irritation of the alveolar bone is common, and teeth frequently are loosely rooted and have nodulated roots.

In the Kenora bison, the medial wall of the Rm3 was broken to below the gum line (Figure 8), but no irritation of the alveolar bone is apparent. Indeed, the alveolar bone is dense and most of the teeth, except those near the fractures, are well rooted. The fact that some teeth exhibit hypoplasia and are chipped or more extensively broken suggests that the Kenora bison was experiencing modest long-term nutritional stress. This stress could have been caused by the inadequate supplies of the requisite nutrients in the formerly glaciated, shallow-soiled Kenora area.

Gross Allometry in Holocene Bison Evolution

The evolution of limb length and proportions in North American Holocene bison is summarized in Tables 4 and 5. The most general tendency was toward absolutely shorter limbs, with more robust (i.e., greater shaft:length ratio) upper limb bones and more gracile (i.e., lesser shaft:length ratio) metapodials, relative to length. Superimposed on this pattern was a trend toward the evolution of longer thoracic limbs relative to pelvic limbs. Both of these observations apply to the derivation of the late Holocene *Bison bison* from the late Wisconsinan *Bison an-*

tiquus. In other ways, the pattern of limb evolution in *Bison bison athabascae* diverged from that in *Bison bison bison*. The latter evolved to absolutely smaller size, with the greatest relative reduction of length taking place in the upper limb bones and the least occurring in the metapodials. In *Bison bison athabascae,* the femur and humerus evolved to be only slightly (1%–3%) shorter than in *Bison antiquus antiquus,* the radius and tibia remained about the same size, and the metapodials became longer.

The skull of bison became smaller during the Holocene, and the proportions of some characters altered, which produced changes in shape. The most obvious changes were those involving the horn cores, which became smaller, directed more caudally, and rotated caudally. The cranium became more domed on the dorsal surface, and the occipital condyles projected less far from the occiput. The skull became shorter and, on the dorsal surface, narrower in nearly equal proportions; but the rate of shortening exceeded the rate at which the base of the cranium narrowed, leaving the ventral side of the cranium proportionately wider in *Bison bison* than it had been in *Bison antiquus*.

When the evolutionary changes in the limbs and skull of bison are correlated, the pattern that emerges is a trend toward a relatively smaller head (with conspicuously allometrically shorter horns) set relatively lower on a body whose limbs, especially the thoracic limbs, were becoming relatively longer (Table 6). Bamforth (1988), drawing upon data in McDonald (1981), observed that limb length in North American bison increased relative to overall body size during the early Holocene.

The relative lengthening of the thoracic limbs and the changes in the robustness of the limb bones are probably associated with the evolution of relatively more cursorial habits in *Bison bison* than characterized *Bison antiquus antiquus*. The musculature of the upper limbs was exaggerated, relative to that of *Bison antiquus antiquus,* paralleling the increased relative robustness of the upper limb bones, and the metapodials developed into support structures carrying absolutely less weight and better equipped for more frequent and versatile mobility than had typified *Bison antiquus antiquus*. The length of the thoracic limb, relative to the pelvic limb, in *Bison bison bison* is greater than in *Bison bison athabascae,* probably because of selection for greater cursoriality, more frequent or specialized agonistic encounters during the rut (which selected for greater forebody strength, focused on the thoracic limb, for delivering and enduring head-to-head clashes and various head-thrusting movements), and the essentially obligatory grazing feeding behavior (requiring regular raising and lowering of the relatively low-slung but massive head) of the former, all as discussed at greater length in McDonald (1981). *Bison bison athabascae,* on the other hand, is less cursorial, probably has less frequent or less specialized agonistic encounters during the rut, and has greater opportunity to browse at higher than ground level with its relatively high-placed head; it has therefore developed a relatively lower hump and shorter thoracic limb.

The Evolutionary Place of *Bison bison athabascae*

The evolutionary position of *Bison bison athabascae* has been a subject of scholarly and practical concern for a century. The existence of a form of extant bison in north-central Canada different from the plains bison, *Bison bison,* has been known to science since at least 1829 (Richardson, 1829; Hind, 1859). Most early writers regarded the northern bison as little more than a phenotypic variant, or merely a marginal population, of the plains bison. Rhoads (1897), however, regarded the northern, or wood, bison to be taxonomically distinct and gave it the name *Bison bison athabascae*. Scientific and political opinion on the taxonomic status of the wood bison has vacillated frequently during the last century. There is no question, however, that the bison native to the parklands of north-central Canada during the nineteenth and twentieth centuries were demonstrably larger than the contemporary plains bison. Here we follow McDonald's (1981) premise that it is scientifically useful and valid to designate the wood bison as taxonomically distinct, a position recently reinforced by van Zyll de Jong and others (1995).

The wood bison became protected by law in 1891, and two years later a preserve was created as a refuge for the remaining populations. The total population of wood bison was about 1500–2000 when, between 1925 and 1928—at a time when wood bison were considered by responsible authorities as not distinct taxonomically from the plains bison—6673 plains bison were introduced into Wood Buffalo National Park. Today, most zoologists familiar with North American bison recognize only a single extant North American species—*Bison bison*—containing the two subspecies *Bison bison bison* (the plains bison) and *Bison bison athabascae* (the wood bison) (e.g., Skinner and Kaisen, 1947; McDonald, 1981; Nowak and Paradiso, 1983; Meagher, 1986; van Zyll de Jong, 1986; van Zyll de Jong et al., 1995). Flerow (1971) considered the wood bison to belong to a separate species, *Bison priscus,* and he identified it as *Bison priscus athabascae*. Geist (1990), however, recently argued that the wood and plains bison are taxonomically identical.

Interpretations of the evolutionary origins of *Bison bison athabascae* have fallen generally into two categories. The first interpretation is that *Bison bison athabascae* represents a descendant (either changed or unchanged) form of bison derived from ancestral populations that originated in eastern Siberia or Beringia and dispersed southward. *Bison bison athabascae* then represents either (1) the evolutionary and geographic endpoint of that parent dispersal or (2) an arrested phase of the evolutionary trajectory that continued as the parent dispersal continued southward to produce, either alone or with introgression with more southerly bison, the plains bison (Skinner and Kaisen, 1947; Guthrie, 1970; Flerow, 1971; Harington, 1984; van Zyll de Jong, 1986). A second interpretation is that *Bison bison athabascae* represents a (changed) descendant form of bison derived from ancestral populations that originated in midlatitude North America and dispersed northward during the early and middle parts of the Holocene (McDonald, 1981).

Elsewhere, McDonald (1981) has argued against the Beringian origin of *Bison bison athabascae* and *Bison bison bison* and for the common origin of both of these subspecies from *Bison antiquus*. McDonald relied upon the dense and continuous factual record documenting both the spatial, temporal, and morphological continuity among midlatitude North American bison throughout the Holocene and the absence of any such spatial and morphological continuity among bison in, or those coming from, Beringia. Quite simply, the vast body of factual evidence still demonstrates that *Bison bison athabascae* is morphologically, temporally, and spatially nearer to *Bison bison bison* than to the late Pleistocene bison of eastern Siberia. Opinions to the contrary are based upon antiquated concepts of either (1) progressive diminution of body size or (2) periodic radiation of new taxa into North America from Siberia, or both (e.g., Allen, 1876; Gromova, 1935; Schultz and Frankforter, 1946; Skinner and Kaisen, 1947; Guthrie, 1970; Wilson, 1975, 1996; Harington, 1986).

Van Zyll de Jong (1986) argued the case for a Beringian origin for *Bison bison athabascae* and supported his thesis with a well-preserved skull (PIN 835-624-39) from the Bolshaya Chukochya River in Siberia. He considered this skull to be representative of "*athabascae*-like bison in eastern Siberia at the close of the last glaciation." "The similarity of this bison to North American *occidentalis* and to *athabascae* is strong evidence of the former existence of an ancestral Beringian population" (van Zyll de Jong, 1986:53). Van Zyll de Jong did not examine the specimen personally, and he provided no absolute age for the specimen or the population it represented. Nor did he figure the specimen, describe any diagnostic characteristics that would allow it to be accepted unequivocally as resembling *Bison bison athabascae* or *Bison antiquus occidentalis* more nearly than a Eurasian form of *Bison,* or provide measurements. To diagnose this specimen, he relied upon linear measurements alone (which were sunk in his quantitative summaries and never presented, in the 1986 paper, as raw data); but measurements alone frequently are insufficient to diagnose most bison specimens, especially those representing taxa that obviously overlap others in size. It is quite possible to obtain identical measurements from two or more bison specimens that possess substantially different qualitative (and genetically controlled) characteristics. It also is theoretically possible for convergent evolution to produce similar phenotypes from generally similar ancestral stock even in the absence of recent genetic unity. The morphological, behavioral, and ecological similarities between *Bison bison* and the Eurasian bison or wisent, *Bison bonasus,* is a case in point. Although these species differ in morphological detail, they evolved generally via pathways that resulted in convergence of size, form, and function; it is obvious from the fossil record that *Bison bonasus* had a larger ancestor that could have passed through a stage during which linear features of its skull morphology resembled those of *Bison bison athabascae*. Lastly, bison collected from along the Bolshaya Chukochya River span nearly 1.7 million years, and most specimens have been collected without stratigraphic context and have not been radiocarbon dated (Sher, 1974, 1986, pers. comm., 1992; McDonald et al., 1991). Thirty years ago, Sher cautioned against the assignment of bison to a given geological age based upon the size and shape of horn cores, noting that this practice "is risky to say the least" (Sher, 1974:207).

Our position is that the weight of factual evidence supports the view that *Bison bison athabascae* originated in North America from the same lineage that gave rise to *Bison bison bison*. McDonald (1981:260–261) was of the opinion that *Bison bison athabascae* could have attained its morphological characteristics by either "(1) suspended equilibrium, in which case *B. b. athabascae* retained large body size as it evolved characters from *B. antiquus* adapted to the new r-type forest/woodland selection regime; or (2) more recent adaptive differentiation, in which case *B. b. athabascae* has increased in body size from *B. b. bison*.... Elements of both alternatives could have operated in the origin and continuation of *B. b. athabascae*, but the second has probably been more important over time...."

Considering the evolutionary trends in the size, shape, and proportions of skeletal elements, as documented for bison during the Holocene, one is left with the realization that *Bison bison athabascae* may be considered the most "advanced" or "furthest evolved" form of Holocene bison in several important respects. When the skull and limb morphology typical of the ancestral *Bison antiquus antiquus* is compared with that of the derivative taxa, *Bison bison bison* and *Bison bison athabascae,* the integrated skeleton of *Bison bison athabascae* is less like that of *Bison antiquus antiquus* than is *Bison bison bison*. Specifically, in *Bison bison athabascae,* the skull is smaller, the upper limb bones are relatively more robust, and the metapodials are relatively more gracile than in *Bison bison bison*. Relative to head size, *Bison bison athabascae* is the most long-limbed of short horned North American bison, whereas *Bison antiquus antiquus* is the shortest limbed.

In other respects, *Bison bison athabascae* is probably not as distant from *Bison antiquus antiquus* as is *Bison bison bison*. The evolutionary lengthening of the front limb relative to the hind limb has progressed further in *Bison bison bison* than in *Bison bison athabascae*. Also, the forebody pelage used to effect social rank and breeding success during the rut is less exaggerated and seasonally pronounced in *Bison bison athabascae* than in *Bison bison bison* (Geist and Karsten, 1977; Lott, 1979). The horns therefore perhaps have relatively greater importance for establishing social rank or dominance in *Bison bison athabascae* than in *Bison bison bison.*

The interpretation of skeletal measurements presented herein suggests that the evolution of the skeleton of *Bison bison athabascae* has, collectively, proceeded further than has that of *Bison bison bison,* whereas the opposite is true for evolution of selected morphological features and behavior of social significance. Claims that *Bison bison athabascae* is more or less far evolved from its ancestral morph should, therefore, indicate exactly which parameter of evolution is being considered. It is not necessary that all parameters evolve the same distance, at the same time, or in the same direction. As environments change, the multitude of selective pressures that act on individual organisms also change. The skeleton of *Bison bison athabascae* appears to have differed allometrically from *Bison antiquus* to a greater extent than has the skeleton of *Bison bison bison,* but behaviorally and ecologically *Bison bison athabascae* might differ less from *Bison antiquus* than from *Bison bison bison.*

Appendix

Measurements (in mm) of limb bones of Kenora Bison

(Measurements and abbreviations follow those given for bovids in von den Driesch, 1976)

1. Atlas: GB=199.9; GL=129.5; BFcd=111.3; BFcr=123.8; H=102.1.
2. Axis: LCDe=122; H=162.1; LAPa=122.6; BFcd=67.7; BPtr=132.8; BPacd=88.5; BFcr=113.6; SBV=75.3.
3. Manubrium: Dorsoventral depth=92.3; length=104.5; breadth at articular surfaces=47.2; minimum breadth=17.5.
4. Sacrum: BFcr=72.0; HFcr=35.3.
5. Scapula (right): Ld=276; HS=504; DHA=487; SLC=79.2; GLP=95.4; LG=75.0; BG=69.8; transverse breadth of neck= 37.9; breadth, lateral border of spine to medial border of neck=76.7.
6. Radius (left): Approximate rotational length=309; GL (radius)=333; GL (radioulna)=452; minimum anteroposterior diameter of diaphysis=32.0; minimum transverse diameter of diaphysis=57.8.
7. Ulna (left): GL=425; DPA=98.9; SDO=68.5; LD=145.7; minimum transverse breadth of diaphysis=21.3.
8. Radial carpal (right): GB=48.2.
9. Fused 2+3 carpal (left): GB=47.4.
10. Metacarpal (right): GL=190.0; SD=48.3; DD=28.2; BD=76.8; anteroposterior diameter, proximal epiphysis=46.0; anteroposterior diameter, distal epiphysis=40.3; Bp=77.5.
11. Proximal sesamoid, thoracic limb: length=26.1; transverse breadth=17.8; anteroposterior depth=15.8.
12. Proximal phalanx, thoracic limb: GLpe=65.3; Bp=39.7; SD=35.8; Bd=39.6.
13. Medial phalanx, thoracic limb: GLpe=43.3; Bp=38.1; SD=31.3; Bd=35.9.
14. Bony pelvis: GL=526; GBTi=279; SBI=180; GBA=268; SB=37.0; GBTc=503; LS=208.6; LA=89.6.
15. Femur (right): GL=436; GLC=405; rotational length=383; Bp=154.1; SD=48.8; Bd=119.3; DC=56.4; anteroposterior diameter of diaphysis=51.8.
16. Tibia (right): Rotational length=370; GL=403; Bp=127.4; Bd=103.4; SD=51.7; minimum anteroposterior diameter of shaft=35.0; Bd=75.7; Dd=53.0.
17. Calcaneum (right): GL=158.9; GB=56.7; transverse breadth of neck=23.0.
18. Proximal phalanx 1, pelvic limb: GLpe=69.7; Bp=34.2; SD=31.6; Bd=35.2.
19. Proximal phalanx 2, pelvic limb: GLpe=70.3; Bp=34.7; SD=31.4; Bd=35.6.

Literature Cited

Allen, J.A.
1876. The American Bisons, Living and Extinct. *Memoirs of the Museum of Comparative Zoology at Harvard College,* 4(10): 246 pages.

Bamforth, D.B.
1988. *Ecology and Human Organization on the Great Plains.* 216 pages. New York: Plenum Press.

Clarke, A.H., Jr.
1981. *The Freshwater Molluscs of Canada.* 446 pages. Ottawa: National Museum of Canada.

Cleland, C.E.
1966. The Prehistoric Animal Ecology and Ethnozoology of the Upper Great Lakes Region. *Anthropological Papers, University of Michigan, Museum of Anthropology,* 29: 294 pages.

Driesch, A. von den
1976. A Guide to the Measurement of Animal Bones from Archaeological Sites. *Bulletin of the Peabody Museum of Archaeology and Ethnology, Harvard University,* 1: x + 138 pages.

Dykev, A.S., and V.K. Prest
1987. *Paleogeography of Northern North America; 18,000–5000 Years Ago* [Map 1703A, scale 1:12,500,000]. Ottawa: Geological Survey of Canada.

Flerov, C.C.
1971. The Evolution of Certain Mammals during the Late Cenozoic. *In* K.K. Turekian, editor, *The Late Cenozoic Glacial Ages,* pages 479–491. New Haven: Yale University Press.

Geist, V.
1990. [Letter to the Editor.] *Conservation Biology,* 4(4):345–346.

Geist, V., and P. Karsten
1977. The Wood Bison (*Bison bison athabascae* Rhoads) in Relation to Hypotheses on the Origin of the American Bison (*Bison bison* Linnaeus). *Zeitschrift für Säugetierkunde,* 42:119–127.

Gromova, V.I.

1935. Pervobtnyi zubr (*Bison priscus* Bojanus) v SSSR. *Trudy Zoological Institute, Academy Nauk SSSR,* 2:77–204.

Guthrie, R.D.

1970. Bison Evolution and Zoogeography in North America during the Pleistocene. *Quarterly Review of Biology,* 45(1):1–15.

Harington, C.R.

1984. Mammoths, Bison and Time in North America. *In* W.C. Mahaney, editor, *Quaternary Dating Methods,* pages 299–309. Amsterdam: Elsevier.

Haynes, G.

1980. Prey Bones and Predators: Potential Ecologic Information from Analysis of Bone Sites. *Ossa,* 7:75–97.

1982. Utilization and Skeletal Disturbances of North American Prey Carcasses. *Arctic,* 35:266–281.

Henrichsen, P.

1981. Dental Anomalies in Muskoxen from Greenland. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening,* 143:113–123.

1982. Population Analysis of Muskoxen, *Ovibos moschatus* (Zimmermann 1780), Based on Occurrence of Dental Anomalies. *Säugetierkundliche Mitteilungen,* 30(4):260–280.

Hind, H.Y.

1859. *Report on the Assiniboine and Saskatchewan Exploring Expedition of 1858.* Toronto: The Legislative Assembly.

Lott, D.F.

1979. Hair Display Loss in Mature Male American Bison: A Temperate Zone Adaptation? *Zeitschrift für Tierpsychologie,* 49:71–76.

McAndrews, J.H.

1982. Holocene Environment of a Fossil Bison from Kenora, Ontario. *Ontario Archaeology,* 37:41–51.

McDonald, J.N.

1981. *North American Bison: Their Classification and Evolution.* 315 pages. Berkeley: University of California Press.

McDonald, J.N., C.E. Ray, and C.R. Harington

1991. Taxonomy and Zoogeography of the Musk Ox Genus *Praeovibos* Staudinger, 1908. *In* J.R. Purdue, W.E. Klippel, and B.W. Styles, editors, Beamers, Bobwhites, and Blue-Points: Tributes to the Career of Paul W. Parmalee. *Illinois State Museum, Scientific Papers,* 23: 285–314.

Meagher, M.

1986. *Bison bison. Mammalian Species,* 266:1–8.

Moore, L.

1975. The Presence of Bison Bones at Hungry Hall Site, Rainy River Northwest Ontario. [Abstract.] In *Eighth Annual Meeting, 1975, Canadian Archaeological Association, Abstracts,* page 24.

Nowak, R.M., and J.L. Paradiso

1983. *Walker's Mammals of the World.* Fourth edition, 1362 pages. Baltimore: Johns Hopkins University Press.

Rhoads, S.N.

1897. Notes on Living and Extinct Species of North American Bovidae. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 49:483–502.

Richardson, J.

1829. *Fauna Boreali-Americana; Or the Zoology of the Northern Parts of British America.* 140 pages. London: John Murray.

Schultz, C.B., and W.D. Frankforter

1946. The Geologic History of the Bison in the Great Plains: A Preliminary Report. *Bulletin of the Nebraska State Museum,* 3:1–10.

Shay, C.T.

1971. *The Itasca Bison Kill Site: An Ecological Analysis.* 133 pages. Saint Paul: Minnesota Historical Society.

Sher, A.V.

1974. Pleistocene Mammals and Stratigraphy of the Far Northeast USSR and North America. *International Geological Review,* 16(7–10): 284 pages. [Original in Russian, published by Nauka Press, Moscow, 1971, 310 pages.]

1986. Olyorian Land Mammal Age of Northeastern Siberia. *Palaeontographica Italica,* 74:97–112.

Shipman, P.

1981. *Life History of a Fossil: An Introduction to Taphonomy and Paleoecology.* 222 pages. Cambridge, Massachusetts: Harvard University Press.

Skinner, M.F., and O.C. Kaisen

1947. The Fossil Bison of Alaska and a Preliminary Revision of the Genus. *Bulletin of the American Museum of Natural History,* 89: 123–256.

van Zyll de Jong, C.G.

1986. A Systematic Study of Recent Bison, with Particular Consideration of the Wood Bison (*Bison bison athabascae* Rhoads 1898). *Publications in Natural Sciences, National Museum of Canada, National Museum of Natural Sciences,* 6: 69 pages.

van Zyll de Jong, C.G., C. Gates, H. Reynolds, and W. Olson

1995. Phenotypic Variation in Remnant Populations of North American Bison. *Journal of Mammalogy,* 76:391–405.

Voorhies, M.R.

1969. Taphonomy and Population Dynamics of the Early Pliocene Vertebrate Fauna, Knox County, Nebraska. *Contributions to Geology* [University of Wyoming], *Special Paper,* 1: 69 pages.

Webb, T., III, E.J. Cushing, and H.E. Wright, Jr.

1983. Holocene Changes in the Vegetation of the Midwest. *In* H.E. Wright, Jr., editor, *Late-Quaternary Environments of the United States, 2: The Holocene,* pages 142–165. Minneapolis: University of Minnesota Press.

Wendland, W.M.

1978. Holocene Man in North America: The Ecological Setting and Climatic Background. *Plains Anthropologist,* 23:273–287.

Wendland, W.M., A. Benn, and H.A. Semken, Jr.

1987. Evaluation of Climatic Changes on the North American Great Plains Determined from Faunal Evidence. *In* R.W. Graham, H.A. Semken, Jr., and M.A. Graham, editors, Late Quaternary Mammalian Biogeography and Environments of the Great Plains and Prairies. *Illinois State Museum, Scientific Papers,* 22:460–472.

Wilson, M.C.

1975. Holocene Fossil Bison from Wyoming and Adjacent Areas. xiv + 276 pages. Master's thesis, University of Wyoming, Laramie, Wyoming.

1996. Late Quaternary Vertebrates and the Opening of the Ice-Free Corridor, with special Reference to the Genus *Bison. Quaternary International,* 32:97–105.

Mcdonald, Jerry N and Lammers, George E. 2002. "Bison antiquus from Kenora, Ontario, and Notes on the Evolution of North American Holocene Bison." *Cenozoic mammals of land and sea : tributes to the career of Clayton E. Ray* 93, 83–97.