A BISON SKULL FROM LYMAN COUNTY, SOUTH DAKOTA

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ABSTRACT

During August, 1998, a well-preserved bison skull was found in gully fill on the western bank of the Missouri River. The skull was resting upside down near the bottom of a gully incised into the upper part of the Niobrara Formation. The gully was subsequently filled with poorly sorted unconsolidated material consisting of small to large, poorly-rounded chips of Niobrara chalk in a matrix of tan clay. The gully fill also contains a few chips of the Pierre Shale which crops out at the top of the hill. Sediment in the gully fill surrounding the skull resembles sheetwash deposits. A soil profile with vegetation was developed on the gully fill.

The cranium was excavated and jacketed for removal, and later prepared at the New Jersey State Museum. The specimen belongs to a male bison, based on the presence of horn burrs, with a tip-to-tip horn core width (780mm) slightly larger than the published range for *Bison bison bison* horn cores (510-778mm for males). Morphology of the skull is similar to *Bison antiquus occidentalis,* but its radiometric age is only 710±40 ^{14}C years B.P, making it too recent to belong to any fossil species. Horn measurements (length on curve 280mm, straight-line length 250mm) are also slightly larger that those of *Bison bison bison.* Horn measurements and frontal widths (minimum 285mm, maximum 362mm) fall within the overlapping ranges published for *Bison antiquus occidentalis* and *Bison bison athabascae.* Width of the occipital condyles (125mm) and skull length (518mm) fall within the sizes published for *B. a. occidentalis* and the living subspecies of *Bison bison.* Skull morphology and dimensions suggest a closer link with *B. b. athabascae* than with *B. b. bison.*

This specimen retains some horn sheath, preserved near the tips of the horns. The upper cheek teeth are deeply worn, and the animal probably died of old age. There is no evidence of human activity associated with this skull.

INTRODUCTION

During August of 1998 the South Dakota School of Mines and Technology conducted a field paleontology course in central South Dakota. Wet weather kept the crew out of the usual field areas, but it was possible to do a preliminary survey of outcrops along the Missouri River in Lyman County on land belonging to the US Army Corps of Engineers. Outcrops of the Niobrara Formation along the river had been cut by gullies in the past, and the gullies subsequently filled in. One of the authors (B.S.G.) discovered a skull (SDSM 47704) partially exposed in the bottom of one of these sediment-filled gullies. Examination *in situ* suggested that it might be reasonably complete, and appeared to have preserved horn sheaths. The skull was identified in the field as belonging to the genus *Bison*. Excavation was conducted using standard paleontologic field methods. The skull and surrounding sediments were encased in a protective plaster jacket and returned to the lab for preparation.

SDSM 47704 is the skull of one of the shorter-horned *Bison* species. Evolutionary history of *Bison* is still poorly understood (Guthrie, 1990a), and a detailed consideration of *Bison* evolution is beyond the scope of this paper. *Bison* evolution in North America can be briefly summarized as follows. During late Wisconsinan to mid Holocene time two indigenous forms of *Bison* existed in North America. According to McDonald (1981) these were closely related subspecies, *B. antiquus antiquus* Leidy and *B. antiquus occidentalis* Lucas *Bison antiquus antiquus* is the older subspecies, ranging in age from at least 45,000 to around 4000 years BP. *Bison antiquus occidentalis* existed from about 11,000 to 4000 years BP. The two subspecies coexisted for approximately 7000 years, but were adapted to somewhat different environments, with *B. a. antiquus* being adapted to a savanna or wooded steppe environment and *B. a. occidentalis* to a more open prairie environment (McDonald, 1981). McDonald believes that *Bison antiquus occidentalis* evolved from *B. a. antiquus* approximately 11,000 years ago by genetic drift in isolated populations of *B. a. antiquus* during a population bottleneck. This population decline was related to climatic and habitat changes following the last glacial advance, to human hunting, or to both (McDonald, 1981; Kurten and Anderson, 1980; Skinner and Kaisen, 1947). However, Guthrie (1970, 1990a) and Wilson (1969) suggested that there were two *Bison* lineages, a *Bison priscus* - *Bison occidentalis* lineage and a separate *Bison latifrons* - *Bison antiquus* lineage, in North America; although Wilson expressed some doubts about the origin of B. *antiquus*.

McDonald (1981) believes that the two subspecies of *Bison antiquus*, after an initial period of isolation, came back into contact about 9500 years ago, and may have hybridized with one another. Guthrie (1990a) and Wilson (1969) agree that B. *antiquus* and *B. occidentalis* could have hybridized to produce a polyphyletic *Bison bison*, although Wilson (1974) later considered *B. antiquus* and *B. occidentalis* to be conspecific. With or without hybridization, *Bison antiquus occidentalis* eventually evolved into *Bison bison*, possibly in association with the Altithermal event 6500-4000 BP (Wilson, 1974). It is thus a transitional form between *Bison antiquus* and *Bison bison* (McDonald, 1981; Skinner and Kaisen, 1947; Guthrie, 1990a). *Bison bison* incudes the two living subspecies.

Bison bison bison Linneaus is a grazer inhabiting open prairie environments, and *B. b. athabascae* Rhoads inhabits more wooded and upland environments. The two living subspecies originated less than 5000 years ago.

Bison latifrons Harlan is known from South Dakota (Green and Martin, 1960; Pinsof, 1985), as is *Bison* cf. *antiquus* (Pinsof, 1985). Most other cited remains are of postcranials, and are not identified to species (Pinsof, 1985). *Bison antiquus occidentalis* reportedly has been found in archaeological sites currently under study by the state Archaeological Center (Foshe, personal communication). *Bison bison bison* is extant in South Dakota, and is known from prehistoric sites (McDonald, 1981), as is *Bison bison* (subspecies not specified) (Semken and Falk, 1987).

Two species of European *Bison*, *B. priscus* Bojanus and *B. alaskensis* Rhoads, occurred in North America during the Pleistocene. Their ranges extended as far south as Mexico. Both species died out in North America, probably by about 20,000 years BP (McDonald, 1981). While their ranges overlap with that of *B. a. antiquus* they did not coexist with *B. a. occidentalis* or with *Bison bison*. *Bison priscus* may extend into the Holocene in Alaska and northern Canada (Guthrie, 1990a; Wilson, 1969). Pinsof (1991) states that *B. latifrons* and *B. alaskensis* may have survived until very late in the Wisconsinan in Idaho.

Names and classification of *Bison* species and subspecies used in this paper follow McDonald (1981). Guthrie (1966, 1990a, 1990b) differs from McDonald in using *B.antiquus* and *B. occidentalis* as separate species rather than as subspecies. Some authors (Guthrie, 1970; Wilson, 1974; Kurten and Anderson, 1980) have placed *occidentalis*, or even both *antiquus* and *occidentalis*, as subspecies of *Bison bison* (*B.* b. *antiquus* and *B.* b. *occidentalis*). *Bison antiquus* and B. *bison* will be used when referring to forms that predate differentiation of subspecies for each species, or when no distinction is made between subspecies.

GEOLOGIC SETTING

SDSM 47704 was found buried near the bottom of a gully cut into the Niobrara Formation. It was located in the SW1/4 of the NE1/4, section 17, T104N R71W in Lyman County, South Dakota. Its GPS position was 43°48'N, 99°21'W. The skull was covered by about 2m of gully fill. Only the rim of the right orbit and the right premaxilla were exposed in the side of the cliff when the skull was first observed. The gully, as preserved, was some 4m above the current river level, which is elevated because the site is upstream from a dam. Lateral distance from the pre-dam channel is at most about 1km. The gully may have been cut into a terrace formed when river level was higher than it now is. Warren (1952) indicated that terraces are preserved on both sides of the Missouri River in this region. The gully was filled with unconsolidated light tan clay which contained small to large clasts derived from the Niobrara chalk, and a few clasts derived from the Pierre Shale. The clasts were primarily oriented perpendicular to the skull. Their distribution in the jacket was nonrandom. Clasts were sparsely distributed in that portion of the jacket which lay toward the head of the gully, and abundant in the region which lay along the gully bottom under the skull, particularly in that part of the jacketed block on the side closest to the gully mouth.

The skull was upside down when found. It was oriented with its long axis directed S5°E, with the rostral end of the skull directed toward the south. The palatal surface of the skull plunged 31½ degrees to the south. There was an isolated cervical vertebra located about 1m above the skull in the gully fill which might have belonged to the same individual, and a few bone chips in the jacketed sediment on the upgully side of the skull which probably did belong to the same individual. Reexamination of the gully in 1999 did not produce any additional bones.

The gully fill had been penetrated by roots which are presumably mainly of modern age. There were also a few borings in the sediment made by modern beetles. None of these borings penetrated the skull itself.

TAPHONOMY

This skull is exceptionally well preserved. Horn is still present covering the tips of both horn cores and extending much of the length of at least the caudal surface of the left horn core. All bones of the skull are preserved, and all bones are articulated except for the nasals, which are slightly displaced upward. The left horn core is broken near the tip, but does not appear to have been displaced very much following the break. None of the bones appear to have been abraded during transport, and none are broken except for the left horn core and minor damage to the auditory bullae. Even delicate structures of the basicranial surface (the paroccipital processes, muscular processes associated with the auditory tube, and the auditory bullae) are preserved. This skull clearly has undergone only minimal transport. It might have been protected to some degree during transport by remnant soft tissues, but taphonomic evidence suggests the skull was exposed to surface weathering prior to its burial.

Longitudinal cracks are present following the bone fibers, and joint surfaces have undergone mosaic cracking. Slight flaking of the surface layer of bone is evident on the nasals and maxillae, and covers considerably more than 1 cm^2 of the bone surface. Thus, the weathering stage applicable to this skull is early stage 2 of Behrensmeyer (1978). The palatal-basicranial surface of skull, which faced upward at the time of discovery, is less weathered than the naso-maxillary surface. The frontals, which were also directed downward, are less weathered than the nasals or maxillae. Behrensmeyer (1978) observed that bone surfaces in contact with the soil may be more modified than upper surfaces of the same bone, particularly if the bone is in contact with highly alkaline soils where salts such as Na_2CO_3 or NaCl crystallize on the bone surfaces. This skull was enclosed in an adherent layer of caliche, which did not affect the integrity of the bone surface over the frontals, horn cores, or palatal surfaces. It is unlikely that formation of the caliche layer produced greater weathering confined to only a part of the area it covered. It is more likely that the skull lay exposed with its dorsal side up on the surface and was weathered for a period of time before being transported into the gully, probably by sheetwash following an intense storm. Lack of weathering to the frontals and horn cores may mean that they were protected by soft tissues (e.g. the horn sheaths, flesh, or the "hair cap" covering the forehead) for some time prior to burial.

Based on weathering rates that Behrensmeyer (1978) observed in Amboseli, stage 2 weathering implies that the skull may have lain on the surface for 1 or 2 years before being buried. It is likely that the period of exposure was less than one year, since water in the longitudinal cracks would probably have damaged the skull by frost wedging if it had been exposed over the winter (Rothschild and Martin, 1993). Longitudinal cracks in SDSM 47704 remain very narrow. However, Roe (1970) suggested that *Bison* skulls could last 50 years on the ground surface.

The skull was probably buried fairly quickly after being transported into the gully, since the upward facing palatal-basicranial surface remained relatively unweathered. Absence of rodent gnawing on the skull may imply a short period of weathering prior to transport and burial, or may simply mean that relatively few rodents lived in the area at the time the *Bison* died. There was no modification of the skull by carnivores. Rodents, predators, and scavengers can be important agents of bone modification where they are present (Graham, 1993).

The absence of other skeletal elements associated with this skull indicates that the skull had completely disarticulated from the atlas prior to being washed into the gully. Toots (1965) and Hill and Behrensmeyer (1984) found that the skull separated from the atlas relatively soon after death. The lower jaw was not found with the skull. Hill and Behrensmeyer found that mandibles also tended to disarticulate relatively quickly, but Toots found that the lower jaw in large herbivores tended to remain articulated with the skull for a relatively long period. Difference in observed disarticulation patterns might be environmental, since Toots worked on the northern Great Plains and Hill and Behrensmeyer worked in Africa. Absence of postcranial parts of the skeleton could be explained by the fact that skulls act as lag elements (Behrensmeyer, 1975; Voorhies, 1969). Other parts of the skeleton may have washed away, or even been carried off by scavengers. Alternatively, the skull may have become lodged in the gully because its horns hooked into roots or debris on the gully floor. In either case other bones may have washed further down the gully and been deposited in the Missouri River, or in parts of the gully that have subsequently been eroded by the river.

DESCRIPTION

SDSM 47704 is the skull of a very elderly male. The teeth are deeply worn, and are at a very advanced level of the S-4 (old age) stage of Skinner and Kaisen (1947). P^2 has fallen out on both sides, possibly *in vivo*. Both P^3 and P^4 are worn to or below the enamel-dentine junction. M^1 is worn down to the roots on both left and right sides. The styles are worn away on both M^2s and preserved only as a tiny remnant on the right M^3. Fossettes are very reduced on both M^2s, and preserved as a reduced remnant on the left M^3. They remain relatively large on the right M^3. Root canals of P^3 to M^1 are filled in with secondary dentine. There is no sign of decay in these teeth despite their deep wear.

The horn cores have large burrs, indicating that this animal was male. For most of their surfaces they have well-developed longitudinal grooves and ridges. The horn cores are well ossified. The orbits are tubular and extremely protrusive (Table 1). The supraorbital foramen is roofed over. The supraoccipital suture is totally closed, and the frontal suture is closed except for its rostralmost 2.4cm. The lacrimofrontal and lacrimomaxillary sutures are fused at their lateral ends but not at their medial ends, and the nasofrontal sutures are only weakly fused. According to Skinner and Kaisen (1947) these sutures close late in life in *Bison*. The suture between left and right nasals is unfused. Sutures between the zygomatic and the lacrimal and maxilla are completely fused. Fusion of the skull bones is characteristic of mature animals (Skinner and Kaisen, 1947; Shackleton *et al.,* 1975). This skull's appearance agrees best with their plate 10, Figures 3 and 3a.

The left horn core of SDSM 47704 presents an abnormality on its dorsal and rostral surfaces adjacent to the horn pedicle. This portion of the left horn core lacks the ridges and grooves seen elsewhere on the same horn core, and on the right horn core. Ridges and grooves running the length of the horn core are a normal aspect of *Bison* horn cores (Skinner and Kaisen, 1947), and indeed of bovid horns in general (Dyce and Wensing, 1971; Raghaven and Kachroo, 1964). Longitudinal grooves on the horn core may help resist torsional stresses in the horn during male-male combat (Guthrie, 1990a). The horn has an internal blood supply (Bone, 1982) deep to the horn sheath. In bovids branches of the cornual artery run lengthwise along the horn core (Raghaven and Kachroo, 1964). The grooves on the horn core surface are associated in Bos with the rich vascular supply to the corium which generates the horn sheath covering the horn core (Dyce and Wensing, 1971). Absence of the grooves suggests a possible restriction of normal blood supply to that area of the horn.

The bone in this region has a felted texture of crisscrossing bone fibers rather than the normal horn core texture of fibers, grooves, and vascular channels oriented parallel to the long axis of the horn. This region is much less porous than the normal texture seen elsewhere in the horn cores of this spec-

Table 1. Protrusion of the orbits in SDSM 47704 as compared to that in other *Bison* males. Measurements follow McDonald, 1981.

	SDSM 47704	*B. a. antiquus*	*B. a. occidentalis*	*B. b. bison*	*B. b. athabascae*	*B. priscus*	*B. alaskensis*
absolute protrusion	38.5	28.3	25.7	28.8	30.3	28.4	31.9
relative protrusion	0.79	0.85	0.85	0.84	0.85	0.84	0.84

absolute protrusion = (max width frontals _ min width frontals)/2
relative protrusion = min. width frontals / max. width frontals

imen or of other mature *Bison* skulls. The lack of porosity of this region suggests reduction in the number of capillaries passing between the interior and surface of the horn core. Surface appearance of this region is much more similar to that of the horn pedicle or other bones than the normal appearance of a horn core. Disruption of blood supply to this region could have occurred as the result of a traumatic injury during fighting. If so, the injury appears well healed except for restoration of normal vascular supply to the horn corium. Collateral vessels may have compensated for any reduced blood supply, but horn production could have been inhibited in the affected region of the horn. Direct injury to horn cores can cause asymmetries of horn development (Guthrie, 1966). This injury must have occurred after the animal reached maturity, however, since the left and right horn cores are approximately equal in size and only slightly different in orientation (Table 2). Rothschild and Martin (1993) describe several pathologies know to occur in *Bison*, none of which specifically affect the horn cores. Guthrie (1990a) noted damage to horn core fluting which he attributed to fighting between *Bison* bulls.

Table 2. Measurements of SDSM 47704 compared with males of various Bison species. Measurements follow McDonald (1981) and Skinner and Kaisen (1947).

	SDSM 47704	*Bison a. antiquus*	*Bison a. occidentalis*	*Bison b. bison*	*Bison b. athabascae*	*Bison priscus*	*Bison alaskensis*
tip – tip horn core w.	780	765-1067	626-1055	510-778	542-848	751-1064	800-1540
l. core on upper curve	263	203-364	186-392	124-270	165-323	285-416	426-795
l. core on dorsal cord	250	185-330	175-350	120-243	154-277	268-379	294-667
d-v diam. horn base	92.5	81-126	70-114	69-99	81-106	84-116	100-153
min. circ. horn base	263	233-392	237-355	199-324	254-322	293-387	341-493
w. at ext. audit. meatus	265	251-318	238-294	220-270	243-298	248-310	268-340
w. occipital condyles	124.87	132-161	111-151	111-140	118-139	127-165	133-175
d. nuchal line – for. mag	102.85	94-134	89-120	81-115	92-114	91-119	97-134
a-pt diam horn base	98.88	76-129	77-120	67-103	83-109	98-130	122-171
min. width frontals	285	276-352	261-348	237-318	273-313	269-336	281-394
max width frontals	362	338-400	311-394	289-356	326-384	313-415	356-440
M^1-M^3 length (labial side)	l=86.46 r=84.75	105.2-106	90-102	81.8-97.9	--	--	--
max width M^3 (mesial cusp)	l=26.74 r=27.28	29.6-30.0	27.8-29.1	22.3-31.4	--	--	--
total length skull	518	(629.0)	511-606	500-583	562-604	--	602-676
length of frontals	240	260-314	233-287	214-279	240-276	259-286	265-338
< divergence horn core-skull midline	r=68° l=66°	72-86°	63-83°	58-79°	63-77°	63-79°	64-85°
frontal width / length*	1.19	1.11	1.14	1.10	1.15	1.08	1.11
frontal w. / total length*	0.55	0.50	0.53	0.51	0.51	0.48	0.51

*from Skinner and Kaisen (1947)

TAXONOMIC DIAGNOSIS

Measurements of this skull are compared with the published ranges (McDonald, 1981) for various species and subspecies of *Bison* in Table 2. There is significant size overlap between different taxa, even in the horn core character suite (Guthrie, 1966). Only male skulls are included in the diagnosis of this individual to decrease the amount of overlap between species.

Identification of *Bison* skulls usually is based primarily on the horn core character suite (McDonald, 1981), although there may be considerable overlap in these characteristics (Guthrie, 1966). Details of the horn core comparisons are given in Table 3. SDSM 47704 retains horn sheath covering the tips of the horn cores, which means that horn core shape at the tip and presence or absence of a dorsal groove at the tip of the horn core cannot be evaluated. These characters would help to distinguish *Bison antiquus antiquus* and the European species of *Bison* found in North America from *Bison antiquus occidentalis* and the two subspecies of *Bison bison*. Presence of the horn sheath also complicates measurement of horn core length dimensions, which have been estimated from the sheath-covered horn tips.

We refer SDSM 47704 to *Bison bison* cf. *athabascae*. Measurements, horn core characters, and skull shape characters for this specimen are compared with published data for *Bison* species from McDonald (1981) and Skinner and Kaisen (1947) in Tables 2 through 4. The tip-to-tip horn length and individual horn lengths exceed the published size range for *Bison bison bison* but does fall within the known size range for *B. b. athabascae*. The skull is too small to belong to *Bison antiquus antiquus*, specifically in its total and frontal lengths and in width of the occipital condyles. The horn cores are angled backward more than is the case in *B. a. antiquus* and horn core curvature does not fit within the known range of variation for *B. a. antiquus*. Horn cores are depressed below the plane of the frontals, unlike the condition McDonald (1981) described in B. *antiquus occidentalis*. However, Rasmussen (1974) identified a skull with depressed horn cores as *B. a. occidentalis*. Horn shape (posterior margin and long axis shapes and spiraling of the longitudinal grooves) and horn rotation are not consistent with the characteristics found in the European *Bison* species found in North America (B. *priscus* and *B. alaskensis),* and overall size of the specimen is too small for *Bison alaskensis*. Total skull length is smaller than the range known for B. *bison athabascae* but length of the frontals does fall within the range published by McDonald (1981). Most measurements of SDSM 47704 lie within the size range for *Bison bison athabascae*, and also fall within the published size range of *Bison. antiquus. occidentalis* (McDonald, 1981). Many of these measurements also fall within the range known for *Bison bison bison*.

Some aspects of the Lyman County skull have been difficult to evaluate. The molar teeth of SDSM 47704 are smaller than the range McDonald gave for *Bison bison athabascae* or *Bison antiquus occidentalis* (Table 2). McDonald's sample size for these taxa was very small, however (only 1 to 3 individuals), and comparison to our skull would not be meaningful. Tooth dimensions fall within the published range for *Bison bison bison*. Interestingly, M^3 width is identical to that of the one *B. b. athabascae* listed by McDonald (1981). Skinner and Kaisen (1947) indicated that the tooth row shortens with age in *Bison*, and it is possible that our relatively short tooth row would fit within the size range for *Bison bison athabascae* if a larger sample of that subspecies were known. The orbits in SDSM 47704 are unusually protrusive (Table 1) in comparison to McDonald's data for various *Bison* taxa. Protrusion of the orbits is known to increase with the age of an individual *bison* (Skinner and Kaisen, 1947; Wilson, 1974; Shackleton et al., 1975), and our skull belongs to a very elderly individual. The observed orbital protrusion is presumably correlated with the age of this animal, and is also probably not taxonomically significant.

Table 3. Horn core character complex in SDSM 47704 and other male *Bison.*

	SDSM 47704	*Bison a. antiquus*	*Bison a. occidentalis*	*Bison b. bison*	*Bison b. athabascae*	*Bison priscus*	*Bison alaskensis*
base shape: 1 symmetric, 2. asymmetric	1	1	1	1	1	2	2
posterior margin: 1 straight, 2 sinuous, 3. concave	1	1	1 or 3	1 or 3	1 or 3	2	2
long axis: 1 straight, 2 arched, 3 sinuous	2	2	2 or 3	2	2	3	3
growth pattern: 1 spiral, 2 straight	2	2	1 to 2	2	1 to 2	2	2
core rotation: 1 none, 2 forward, 3 backward	3	1	3	3	3	2	2
horn curvature: 1 continuous, 2 base straight, 3 recurved	1	2	1	1	1	1,3	1,3
horn axis rel. frontals: 1 horizontal, 2 downward, 3 upward	2	1 or 2	1 or 3	1 or 2	1 or 2	1 or 2	1 or 2
horn core tip: 1 no twist, 2 post. twist*	1 to 2	2	2	2	2	1	1
index of horn curvature*	132	128-147	121-169	115-182	126-149	107-153	126-152
index of horn compression*	94	83-108	86-104	81-107	84-98	73-103	70-78
index of horn proportion*	106	68-100	85-110	66-104	62-92	100-166	106-134
index of horn length*	98	66-114	88-112	57-92.6	57-90	110-189	109-167

- after Skinner and Kaisen (1947). All others after McDonald (1981)
- index of horn curvature = (length on lower curve / straight line length) x 100
- index of horn compression = (d-v diameter / a-pt diameter) x 100
- index of horn proportion = (upper curve length / base circumference) x 100
- index of horn length = (length on upper curve / min. width of frontals) x 100

Certain aspects of the morphology of SDSM 47704 ally it more closely with the *Bison antiquus* group than the *Bison bison* group (Table 4). The occiput is slightly concave. There is a fairly well developed external occipital protuberance, the rugosity for attachment of the funiculus nuchae (Habel, 1977). The occipital condyles protrude slightly from the occipital plane. The back of the skull tends to be flat in *Bison bison*, but can be slightly to moderately concave in *Bison antiquus*. There is a prominent external occipital protuberance in *Bison antiquus*, but generally *Bison bison* skulls lack a prominent protuberance at the insertion of the funiculus nuchae. The occipital condyles do not protrude from the occipital plane in *Bison bison*, but do protrude slightly in *Bison antiquus*. *Bison bison athabascae* is believed to be relatively less derived from the ancestral B. *antiquus occidentalis* than is *Bison* b. *bison* (Skinner and Kaisen, 1947; Guthrie, 1970), and these morphologic similarities to the *Bison antiquus* group may reflect that closeness.

Table 4. Skull morphology of SDSM 47704 compared with other Bison males (after McDonald, 1981).

	SDSM 47704	***Bison a. antiquus***	***Bison a. occidentalis***	***Bison b. bison***	***Bison b. athabascae***	***Bison priscus***	***Bison alaskensis***
frontal doming?	yes	yes	sometimes	yes	yes	sometimes	sometimes
sheath recurved?	yes	no?	yes?	yes	yes	yes	yes
orbit shape: 1 tubular, 2 faces forward, 3 face to side	1, 2	1, 2	-----	1, 3	1, 3	1, 2	1, 2
occiput: 1 flat, 2 slightly concave, 3 concave	2	1 to 3	2	2	2	3	3
ext. occip. protub.: 1 weak, 2 mod. Prom., 3 prominent	2	3	3	1 to 2	2	2	3
occipital condyles: do not protrude, 2 protrude	2	2	2	1	1	1	2
condyles flanged: 1 no, 2 sometimes, 3 frequently	1	2	2	2	2	2	3
horns thicken distal to burr?	no	no	no	no	no	yes*	yes*

*horn may remain the same thickness distal to burr

DISCUSSION

Radiocarbon dating proved to be critical to identification of this specimen. A small volume of bone fragments from the skull itself was collected during preparation and sent to Geochron Laboratories for analysis (GX-26570-AMS). Care was taken to avoid contaminating the bone during preparation. Because of the small volume of bone fragments available analysis was conducted using accelerator mass spectrometry. The ^{13}C corrected age determined for SDSM 47704 was 710±40 14C years before the reference year (1950). The specimen is therefore too young geologically to fit within the known temporal ranges of any *Bison* species other than *Bison bison*, and SDSM 47704 must belong to one of the two living subspecies.

SDSM 47704 is very well preserved. Fusion of the cranial sutures is nearly complete due to the advanced age of the animal, and this factor undoubtedly contributed to the completeness of this skull. Late fusion of cranial sutures means that *Bison* skulls frequently disarticulate prior to burial (McDonald, 1981). Preservation of delicate processes in the basicranium and relative lack of weathering of the bone surfaces both indicate that the skull is taphonomically immature, which also contributes to its completeness. The recent geologic age of the specimen also is a factor in its excellent preservation.

Based on most dimensions, SDSM 47704 could fall within any of three *Bison* taxa: B. *antiquus occidentalis*, B. *bison bison*, or B. *bison athabascae*. Horn core dimensions would seem to eliminate *Bison bison bison* from consideration. However, horn core dimensions are more variable than those in other parts of the skull (Shackleton *et al.*, 1975; Guthrie, 1966). The large horn cores of this individual might not actually lie outside the normal range of variation in *B.b. bison*, since this skull is only a few millimeters larger than *B. b. bison* for each of the horn core measurements. The short total skull length (dimension OP) would likewise seem to eliminate *Bison bison athabascae* from consideration, but sample sizes for the wood *bison* are very small (7 individuals for this measurement) and this difference may not be significant. The orbits are extraordinarily protrusive, but relative protrusion of the orbits still differs from McDonald's published figures by less than 10% of the average, and this protrusion is probably simply a factor of the age of this particular individual. Wear of the teeth is not only extremely deep, but also relatively level. Level wear is characteristic of grazing habits such as those of *Bison bison bison* rather than browsing habits, and wood *Bison* tend not to have extremely level tooth surfaces (Guthrie, 1990a). Extremely deep wear in old individuals might produce very level teeth even in a browser, however.

The very recent geologic age of the specimen, only about 710 years BP, does serve to eliminate *Bison antiquus occidentalis* from consideration in identifying SDSM 47704. Morphology of the skull actually appears to be somewhat more helpful in identification than do skull dimensions, and suggests greater similarity to *Bison bison athabascae* than to *Bison bison bison*.

Identification of this skull as *Bison bison athabascae* is counter to McDonald's conclusions that the wood *bison* is restricted to northern Canada and Alaska. However, this identification might not be unreasonable. Skinner and

Kaisen (1947), Wilson (1974), Lowery (1974), Guthrie (1970) and Hall and Kelsen (1959) all indicate that wood *bison* were distributed as far south as Colorado in upland areas. Wilson's conclusions were based in part on his study of skulls from upland areas of the Bighorn Mountains in Wyoming. In addition, however, this skull is not modern, but is some 700-800 years old. The Pacific climatic episode, from 800-400 BP, brought cooler conditions to the northern plains (Semken and Falk, 1987). It is possible that the geographic range of wood *bison* extended further south during this climatic episode than it does now, and SDSM 47704 lived during the Pacific climatic episode.

Skinner and Kaisen (1947), in synonomizing *Bison bison septemtrionalis* Figgins with *B. b. bison*, note that some of the skulls described were buried and partly fossilized, and might therefore be expected to differ somewhat from the living population. SDSM 47704 is also a buried skull, whose age is close to one quarter of the entire duration of the living subspecies. It might differ from them to some degree just because it is temporally closer to the ancestral *Bison antiquus occidentalis*, and perhaps morphologically closer as well. Wilson (1969) suggested that earlier chronomorphs of *Bison bison bison* would probably have been similar in both size and cranial characteristics to *Bison bison athabascae*. Distinguishing between the living subspecies in the overlapping portions of their size ranges, and even distinguishing between *Bison bison* subspecies and *Bison antiquus occidentalis*, can be very difficult (Skinner and Kaisen, 1947; Wilson, 1974). It is particularly likely to be difficult to identify a skull which may be morphologically different from the living subspecies because of its geologic age.

SDSM 47704 preserves an apparent pathology of the left horn core. McDonald (1981) documents some unusual morphologies in *Bison* populations which he attributes to inbreeding. These morphological variants include abnormal tooth structure, supernumary teeth, and malformations of the maxillae and nasals. He also indicates that horn core morphology may be altered by genetic drift in isolated populations, for example in "*Bison* scaphoceras" (=*B. antiquus antiquus* fide McDonald). Since the observed pathology in this specimen affects only a limited region of one horn core it is more likely that it results from a traumatic injury than from genetic drift. Injuries to the horn or surrounding tissues could occur during combat between *Bison* males. Horn core damage due to fighting is mentioned by Guthrie (1990a).

CONCLUSIONS

SDSM 47704 probably belongs to *Bison bison athabascae*. It is more similar to the wood *Bison* than to *Bison bison bison*. Morphologically it is very similar to *Bison antiquus occidentalis*, and may indicate persistence of the ancestral morphology into fairly recent times in the northern Great Plains.

Taphonomic evidence suggests that the Lyman County skull lay on the surface only briefly before its burial. The skull does not have any tooth marks to indicate activity by carnivores, and has not been gnawed on by rodents searching for a source of calcium. Duration of its surface exposure is estimated to have been 1-2 years based on weathering of bone in Africa (Behrensmeyer, 1978), but absence of attack by rodents might imply that the skull was exposed for a period of time closer to the minimum. It is also possible that bone weathering is relatively rapid in temperate prairie environments. Surface exposure was not long enough for freeze-thaw cycles to damage the skull (Rothschild and Martin, 1993). Burial probably occurred when the skull was swept into a gully by sheetwash following a heavy rain and incorporated into the poorly sorted, immature sediments accumulating in the bottom of a gully. The gully was later filled in by that or similar sheetwash events.

There is no sign of human activity in connection with this skull. There are no cut marks on the bone surface. No flakes or points were found either during field excavation or preparation of the jacketed skull in the lab. Based on tooth wear it is likely that the animal died as a result of old age.

The great orbital protrusion in this particular individual helps point up the importance of considering the effects of age on skeletal morphology both when attempting to define a species and when attempting to draw conclusions about morphologic variability within a species. It also presents a caution about the care which must be employed when selecting taxonomically significant traits for analysis, as some aspects of morphology will change allometrically with age even after an animal reaches maturity—even in mammals.

More important, SDSM 47704 demonstrates the importance of getting radiometric dates on subfossil materials whenever possible. Without the guidance provided by radiometric dating we would have continued to believe that this was a skull of *Bison antiquus occidentalis*, the taxon with which its dimensions and morphology are in best agreement. It should also serve as a cautionary note about attempting to carry identifications of incomplete remains too far. In this instance a beautifully preserved complete *Bison* skull has proven very difficult to identify even to species, yet fragmentary material may in some cases have been identified to subspecies. This skull suggests that identifications of partial *Bison* skulls can seldom be made with complete confidence.

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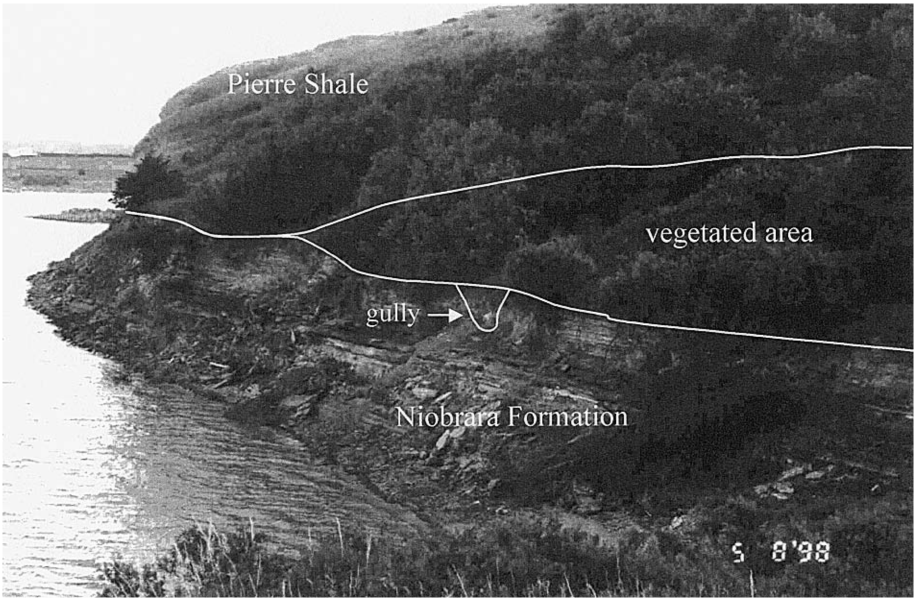

Figure 1. Diagram of Lyman County Bison outcrop.

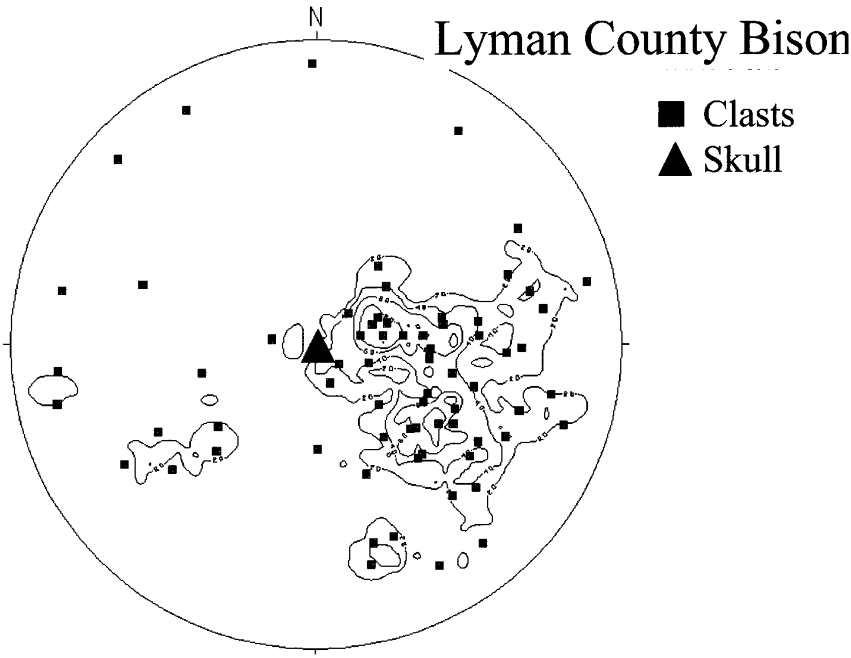

Figure 2. Orientations of pebbles in the Bison skull jacket. Orientations were taken in the lab, and do not reflect true compass orientations of the pebbles. Most clasts strike at high angles to the long axis of the skull. Plot produced using the Stereo program produced by RockWare, Inc.

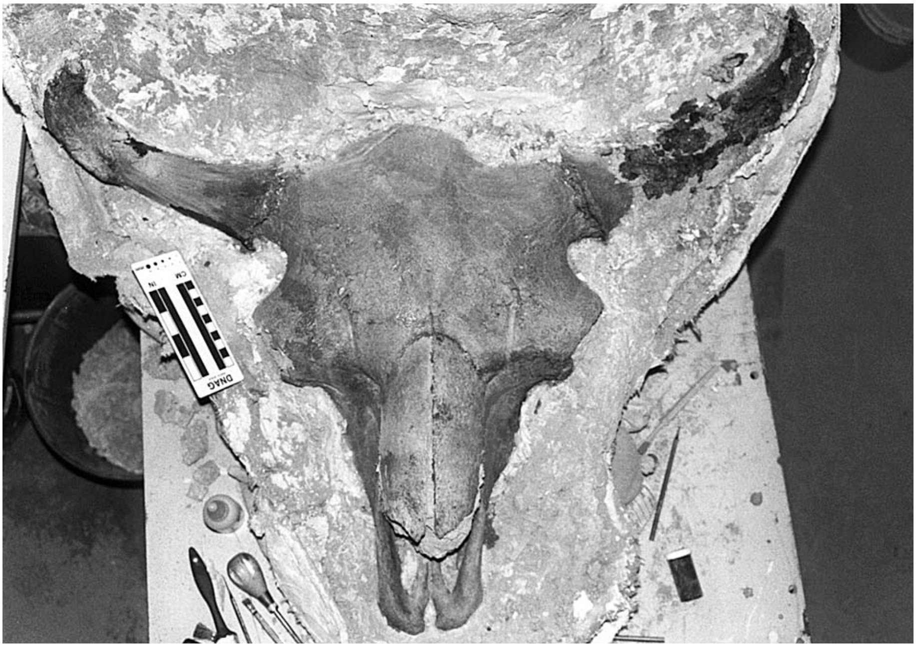

Figure 3. Dorsal view of the Lyman County Bison skull, SDSM 47704. Tips of the horn cores are still covered by sheathing material. Longitudinal grooves can be seen on the right horn core.

Figure 4. Detail of the left horn core base in SDSM 47704. The midline of the skull is toward the left, and the horn tip toward the right. Note the absence of longitudinal grooves and the irregular transverse fabric of the bone in this region of the horn core.