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April 3, 2012

Ken Salazar, Secretary
Department of the Interior
1849 C Street, N.W.
Washington, D.C. 20240

U.S. Fish and Wildlife Service
Interim Director
1849 C Street, N.W.
Washington, D.C. 20240

Re: Petition to Delist Wood Bison

Dear Sirs:

Enclosed please find a petition to delist the Wood Bison from the Endangered Species Act list. This petition is filed pursuant to 16 U.S.C. § 1533. The wood bison was listed as an endangered species in 1970 under the Endangered Species Conservation Act, the predecessor to the Endangered Species Act. For the reasons set forth in the attached petition, this species should be delisted.

For further information regarding this petition, please do not hesitate to contact:

W. Michael Gear and Kathleen O'Neal Gear
Wind River Archeological Consultants
Red Canyon Ranch
P.O. Box 1329
Thermopolis, WY 82443

or

John Painter
President, Western Bison Association
P.O. Box 61
Tres Piedras, NM 87577

Should you have additional questions, please do not hesitate to contact me.

Sincerely,

Karen Budd-Falen
BUDD-FALEN LAW OFFICES, LLC

KBF:vld

Enclosure

xc w/o encl: John Painter
Michael and Kathleen Gear

Western Bison Association
ON THE MOVE...

Western Bison Association
4610 E Lane Park Rd. • Mead, WA 99021 • 509-467-0158

March 20, 2012

Mr. Ken Salazar, Secretary
U.S. Department of the Interior
1849 C Street, NW
Washington, D.C. 20240

Dear Secretary Salazar,

Please consider the attached petition to remove Wood Bison from administration under the provisions of the Endangered Species Act 1973, as amended. Recent scientific studies have documented that Wood Bison and Plains Bison are not significantly different with respect to their genetic compositions, and Wood Bison recovery efforts for the ecotype have been successful. Wood Bison should, therefore, be delisted.

Thank you for your consideration of this important matter.

Sincerely,

John Painter, President
For the Board of Directors, Western Bison Association

Co-submitters:

W. Michael Gear and Kathleen O'Neal Gear
Wind River Archaeological Consultants
Red Canyon Ranch
P.O. Box 1329
Thermopolis, Wyoming, 82443

Rocky Mountain Buffalo Association
11806 Elk Head Range Rd.
Littleton, CO. 80127-3705

Minnesota Buffalo Association
22627 Buffalo Ridge Road
Winona, MN. 55987

Oklahoma Bison Association
P.O. Box 113
Ft. Lupton, CO. 80321

North Dakota Buffalo Association
National Buffalo Museum
500 17th St. SE
Jamestown, ND 58401

Northwest Bison Association
720 Stephens Blvd.
Nyssa, OR. 97913

Missouri Buffalo Association
2201 E. 203rd St.
Belton, MO. 64012-9676

Kansas Buffalo Association
409 W. 5th St.
Longton, KS 67352-9103

PETITION TO REMOVE WOOD BISON FROM ADMINISTRATION UNDER THE PROVISIONS OF THE ENDANGERED SPECIES ACT

SUMMARY: We petition the USFWS to remove Wood Bison (*Bison bison athabascae*) from administration under the Endangered Species Act of 1973 (ESA), as amended. Wood Bison and Plains Bison are not significantly different genetically, and should be managed as a single species, *Bison bison*. In addition, Wood Bison recovery efforts have been successful in increasing both the number and distribution of Wood Bison so that ESA listing for the ecotype is no longer necessary.

BACKGROUND

The scientific discussion regarding the differences between Wood Bison and Plains Bison has a long history dating back to Allen, 1876, who, because of contradictory reports, decided not formalize a subspecies designation for Wood Bison. Hornaday similarly declined to formalize such a designation in 1887. However, in 1897, Rhoads established the *Bison bison athabascae* taxon based on "second-hand descriptions of *one* specimen, which he did not examine" (Geist, 1991). Since that time, evidence documenting the subspecies has been elusive,

and challenged by many (Burton, 1962; Corbet, 1978; van Gelder, 1977; Bork, et al. 1991: Peden and Kraay, 1979; Wilson and Reeder, 1993; Wilson and Strobeck, 1999; Douglas, et al. 2011). To understand the development of the idea of Wood Bison as a subspecies, an historical overview is necessary. The major scientific studies regarding Wood Bison fall into three categories:

(1) Studies based on morphology, and the more quantitative, morphometry: Skinner and Kaisen, 1947; Bayrock and Hillerud, 1964; Guthrie, 1970; Shackelton, et al. 1975; McDonald, 1981; Meagher, 1986; van Zyll de Jong, 1986; Berger and Peacock, 1988; Guthrie, 1990; Geist, 1991; van Zyll de Jong, et al. 1995. Morphometric studies included archaeological and historical attempts to establish the geographical boundaries of subspecies of bison, several of which demonstrated that the range of bison meeting diverse *Bison bison athabascae* morphometric criteria extended widely across the U.S. and Canada, extending as far south as Wyoming, Utah, Colorado, (Cannon, 2004; Cannon, 2007), and perhaps even to New Mexico (Skinner and Kaisen, 1947), suggesting overlapping ranges and gene flow between populations: Lotenberg, 1996; Cannon, 1997a; Cannon, 2001; Cannon, 2004. Also, several studies demonstrated that morphological and morphometric data were unreliable, because criteria regarding measurements of the skull, horn, dentition, osteology, and elements like pellage showed a high degree of variability based upon age-related differences, health, diet, time of year, and geographical location, (McHugh, 1972; Berger and Peacock, 1988; Geist, 1991). However, in many cases the only evidence we have to distinguish between bison species or subspecies is morphological or morphometric.

(2) Biochemical studies, including protein electrophoretic studies which utilized heterozygosity to quantify genetic variation in *Bison bison,* and stable carbon and nitrogen isotope studies attempting to establish diet and migration patterns among prehistoric and historic bison: Stormont, 1960; Ying and Peden, 1977; Peden and Kraay, 1979; Widga, 2006; Cannon, 2007.

(3) Genetic studies: Bork, et al. 1991; Cronin and Cockett, 1993; Polziehn, et al. 1996; Wilson and Strobeck, 1999; Shapiro, et al. 2004; McFarlane, et al. 2006; Halbert and Derr, 2007; Decker, et al. 2009; Pertoldi, et al. 2010; Douglas, et al. 2011.

Please see full critical articles in Addendum I, II, and III.

In the information that follows, we provide an historical presentation of the major landmark studies, both positive and negative, that have generated our current understanding of Wood Bison and Plains Bison. These documents come from a variety of scientific disciplines, and often can be seen to build upon and supersede earlier research. By showing the evolution of thought regarding Wood Bison and Plains Bison, we delineate our reasons for requesting de-listing.

SCIENTIFIC RATIONALE FOR DE-LISTING WOOD BISON:

The Wood Bison taxon was first significantly challenged in 1991, when Geist wrote "...neither subspecies of bison is a well-defined taxon," and suggested that Wood Bison was only an ecotype (*Arctic:* 44(4): 283-300). His article was entitled: "Phantom Subspecies: The Wood Bison." Since then, numerous studies have supported Geist's hypothesis, including Strobeck (1992), who concluded that wood and plains bison "do not form distinct phylogenetic groups and are not genetically distinct subspecies." Cronin and Cockett (1993; Kappa casein): "No fixed allelic differences were observed...among bison herds or subspecies," and Polziehn et al. (1996), who determined that neither subspecies of bison: "...is a well-defined taxon," and added, "While many approaches have been taken to find characters that can separate bison subspecies, not one diagnostic character has been found," (p. 740).

As well, Wilson and Strobeck's 1999 study, "Genetic Variation Within and Relatedness among Wood and Plains Bison

Populations," concluded that while "Genetic differences between the sampled populations were generally larger between than within the two bison subspecies," Wood Bison and Plains Bison had interbred in the past, and said, "All wood bison herds existing today, either inside or outside the Wood Buffalo National park, contain some plains bison genetic material in their gene pool," (*Genome*: 42: 488, 1999; see also, Hedrick, 2009, and Wilson, 2011). They also suggested that, "If the bison inhabiting North America before their near-extinction were essentially acting as a single metapopulation, with gene flow occurring between all areas, genetic distances between areas would be low."

The idea of gene flow across the continent was suggested in 1947 Skinner and Kaisen when they conducted the first quantitative study of museum bison specimens—primarily crania—and presented metric data that argued for an overlap in the ranges, and interbreeding, of *B. b. athabascae* and *B. b. bison* along the eastern slopes of the Rocky Mountains.

As well, in 1974, M. Wilson documented that morphological characteristics demonstrated by 10,000 year old bison at the Casper Site in Wyoming could be best explained by the interbreeding *Bison bison antiquus* and *Bison bison occidentalis.* Wilson suggested gene flow between the two populations in the chapter entitled, "History of the bison in Wyoming with particular reference to Early Holocene forms," published in *Applied Geology and Archaeology: the Holocene History of Wyoming* (Wyoming Geological Survey. Reports of Investigations, 10:91-99).

Ancient gene flow between bison populations was also studied by Shapiro, et al., in their *Science* article, "Rise and Fall of the Beringian Steppe Bison" (Vol. 306, November, 2004). Based upon the analyses of mitochondrial DNA extracted from 442 bison fossils from Alaska, Canada, Siberia, China, and the lower 48 United States, Shapiro determined that between 60 thousand years ago and 25 thousand years ago, gene flow occurred between "bison populations in Beringia and central

North America" (p. 1563), and concluded: "This suggests that late Pleistocene bison from the Ural Mountains to northern China are descendants of one of more dispersals from North America. Several North American lineages fall within the Eurasian clade, indicating subsequent asymmetric genetic exchange, predominantly from Asia to North America." In addition, Wilson and Strobeck (1999) suggested that all modern North American bison are a relatively recent evolutionary product, dating to only about 4,000 to 5,000 years ago.

The 2003 discovery by archaeologists of a partial bison skull in the Ashley National Forest gave further credence to the hypothesis that gene flow among bison populations was relatively constant. Kenneth Cannon, discussing this find in his chapter, "They Went as High as they Choose: What an Isolated Skull can Tell Us about the Biogeography of High-Altitude Bison," published in *Arctic, Antarctic, and Alpine Research* (2007(39):44-56), noted that between 1725-1778 bison demonstrating phenotypic Wood Bison characteristics had inhabited areas as far south as the Uinta Mountains in Utah, saying, "The Gilbert Peak skull horn core morphology is more similar to *B. bison athabascae*, being larger than either the high-altitude or the *B. bison bison* populations." Table 2, page 48, of this same article provides a list of bison specimens found in the United States during the historic and prehistoric periods that fall into the morphometric ranges of *B. bison athabascae*.

Additional evidence of gene flow was provided by Pertoldi, et al. in their 2010 article, "Genome variability in European and American bison detected using the BovineSNP50 BeadChip," (*Conservation Genetics* 11:627-634). This study genotyped bison and cattle samples for approximately 54,000 single nucleotide polymorphisms (SNPs) across the entire bovine genome. Their samples included 50 European bison, 25 Wood Bison from Wood Buffalo National Park, Canada, and 26 Plains Bison from Elk Island National Park, Canada. The North American populations had previously been determined to be among the most diverse of their "subspecies" (Wilson and

Strobeck, 1999). This genetic diversity is important because in Post-hoc tests Pertoldi et al. found (p. 631) that average observed individual heterozygosity between Plains and Wood bison "did not differ significantly from each other."

More recent evidence for de-listing Wood Bison from the ESA can be found in the January, 2011, article in the journal *Mitochondrion*, by Douglas, et al., entitled, "Complete Mitochondrial DNA Sequence Analysis of *Bison bison* and Bison-Cattle hybrids: Function and Phylogeny." On page 173, the authors write: "...wood bison haplotypes do not form a single clade (wHap14, 15) and are mixed with plains bison haplotypes...the fact that both of these haplotypes fall into a clade with plains bison suggests that wood bison may never have been a genetically distinct subspecies" and, "...current populations of *B. bison bison* and *B. bison athabascae* are not significantly different with respect to their mitochondrial genomic sequences and should not be considered subspecies," (*Mitochondrion* 11: 2011: 166-175).

As you will see in Addenda I, II, and III, earlier research suggesting MRCAs for Wood and Plains bison has been superseded by later research.

CURRENT STATUS OF WOOD BISON

Historically, Wood Bison, ranged throughout the boreal forest of northern Alberta, northeastern British Columbia, northwestern Saskatchewan, the southwestern Northwest Territories, and much of Yukon and Alaska, and archaeological evidence indicates they may have roamed as far south as Utah in the United States. By the late 1800s only a few hundred animals remained. In 1957, Canada estimated that Wood Bison numbers were around 200, and a recovery program was established. In 1978, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessed Wood Bison as Endangered. As a result of an active recovery program, Wood Bison were reassessed as Threatened by COSEWIC in

2000. Since then numbers have continued to increase. In 2008-2009, the Canadian government established a hunt of surplus animals in the Greater Wood Buffalo National Park region (IUCN report, p. 36). Presently, there are approximately 11,000 Wood Bison in conservation herds in Canada (Environment Canada, 2011. See Addendum III). In addition to conservation herds, there are over 1,800 Wood Bison in private herds. There are also approximately 1,000 Wood Bison in captive conservation and research herds (Letter from the Canadian Bison Association to Gary Edwards, Deputy Director, US Fish and Wildlife, dated July 26, 2010.)

In addition, Environment Canada and Parks Canada Agency have been managing Wood Bison by providing surplus animals to other conservation initiatives. In Canada, Wood Bison have been relocated to British Columbia, Alberta, Saskatchewan, Ontario, and Yukon Territory. Internationally, Wood Bison have been relocated to both the United States and Russia. In 2006, 30 Wood Bison were transferred to Lenskie Stolby Nature Park in the Republic of Sakha, and another 30 Wood Bison were transferred in 2011. These animals are reproducing and increasing in number. In 2008, 54 Wood Bison were transferred to Alaska to complement a herd of 33 Wood Bison that were already being held at the Alaska Wildlife Conservation Center south of Anchorage. That herd has since grown to 103 animals. In total, Elk Island National Park has successfully relocated 855 Wood Bison to conservation programs in Alaska, Russia, and other parts of Canada.

Wood Bison were moved from CITES Appendix 1, to Appendix II in 1997, and import is currently regulated under permit by CITES authorities within member nations. Offspring from Wood Bison have been shipped widely across Canada, and offspring of Wood Bison crossed with Plains Bison, have been shipped across both Canada and to the United States, thereby distributing Wood Bison genetics across North America.

CONCLUSIONS

Wood Bison genetics are not markedly different from Plains Bison. No pure Wood Bison have been documented. Current studies indicate that "pure" Wood Bison may never have existed, and they are, in fact, an ecotype. Wood Bison populations are not bounded by international borders or restricted to unique ecological settings. Significant hybridization has occurred, so that all Wood Bison today contain some Plains Bison genetics, and cattle introgression has been detected in both the Elk Island and Wood Buffalo National Park populations (Schnabel, et al. unpublished, see Wilson, 2011--Addendum III). Therefore, Wood Bison do not meet either the "discreteness" or the "significance" criteria of the DPS policy. As a result, it is unclear what is being protected by the Endangered Species Act listing of Wood Bison.

Morphological, morphometric, biochemical, and genetics studies verify that over the past 130,000 years, bison populations have often shared ranges, interbreeding as they moved. There is no evidence to verify that any impenetrable geographic barriers existed to prevent gene flow between bison populations during the Holocene, especially over the past 5,000 years. The archaeological evidence suggests there was never a period of long-term population separation that would have allowed the formation of bison subspecies. The distinctive phenotypic differences that we see today between Wood Bison and Plains Bison can be accounted for by the interaction of gene flow, epigenetics, ecological adaptation, behavioral factors, and natural selection. As well, Wood Bison recovery programs for the ecotype have been successful in increasing the number of animals and their distribution across North America and Russia.

Finally, the purpose of the ESA is to prevent the extinction of imperiled plants and animals and work toward recovery of such species. The best scientific evidence indicates that recovery programs have been successful. It would be inconsistent with the purposes of the ESA to continue administering Wood Bison

under the provisions of the Endangered Species Act of 1973, as amended.

Therefore, we petition USFWS to remove Wood Bison from the Endangered Species list.

Supplementary Information: Historical Presentation of Scientific Efforts to document the existence of *Bison bison athabascae.*

Addendum I: Morphological and Morphometric studies
Addendum II: Biochemical Studies
Addendum III: Genetic Studies

Addendum I

MORPHOLOGICAL AND MORPHOMETRIC STUDIES

This occurred on the Doddieburn Ranch of Henderson and Sons (Pvt.), Ltd. in the lowveld of Southern Rhodesia. A large adult waterbuck bull walked into view at 36 yards and saw me standing motionless. He could be seen as well as heard to give a call. In my notes it is described as follows, "Snort is low (in pitch) and somewhat prolonged and loud—a bit like a bronx cheer." He then moved out of sight fairly rapidly. The other animals seemed only moderately disturbed. This work was supported by a research grant provided under the Fulbright Act and sponsored by the National Museum of Southern Rhodesia.—ARCHIE S. MOSSMAN, *Div. of Nat. Resources, Humboldt State College, Arcata, California.* *Received 10 July 1963.*

NEW DATA ON *BISON BISON ATHABASCAE* RHOADS

E. W. Rowan of the Department of Zoology, University of Alberta, killed two old bison bulls on 10 and 16 September 1925, in Wood Buffalo Park in northern Alberta and found a skull of a bison bull in the park. The 2 killed animals were both *B. bison athabascae*, as they were old animals and as only young specimens of *B. bison bison*, all branded on the hoof, had been introduced into the park in 1925 to 1928. The skull found on the ground surface was also definitely that of *B. bison athabascae*. Rowan's catalog numbers of the three skulls are as follows: D 233—animal killed on 10 September 1925; D 234—skull of old bull found on surface; D 235—animal killed on 16 September 1925.

As the number of *B. bison athabascae* skulls existing in collections is small, the authors believe that a description of Rowan's skulls is desirable. Body measurements made by Rowan on the 2 killed *B. bison athabascae* specimens are given in Table 1. The dimensions of the skulls according to the system of standard measurements used by Skinner and Kaisen (Am. Mus. Nat. Hist. Bull., Vol. 83, pp. 131–256, 1947) are given in Table 2. Measurement of the width between horn-cores as given by Skinner and Kaisen (1947, pp. 144–145) was omitted because too great a spread in repeated measurements was obtained.

It is of interest that the 3 skulls have some measurements greater and some less than the maxima and minima listed by Skinner and Kaisen (1947). The skulls show marked differences from one another and also have variations greater than recorded by Skinner and Kaisen (1947). The skull D 233 is the largest of the group and it has 6 measurements larger than the maximum for *B. bison athabascae* as given by Skinner and Kaisen (1947, p. 164). These measurements all relate to the horn-cores, indicating that this particular animal had very large horns. However, this same skull also has 3 measurements below the minimum for *B. bison athabascae* (*ibid.*, p. 164), thus indicating a very short skull length. The second skull, D 234, has 7 measurements that are larger than the maximum (*ibid.*). These measurements indicate a very long skull, large horns and a wide

TABLE 1.—*Some body measurements on* B. bison athabascae *Rhoads killed in 1925 (two specimens, from Rowan)*

Measurement	SPECIMEN NUMBER	
	D 233	D 235
Standing height	177 cm	169 cm
Length	279 cm	264 cm
Tail	50 cm	48 cm
Track (front foot)	15 cm	13.5 cm
Weight (dry)	2,011 lb	1,821 lb
Weight and estimate for liquids	2,150 to 2,200 lb	2,000 lb

TABLE 2.—*Skull measurements of* Bison bison athabascae *Rhoads skulls collected by E. Rowan (all measurements in mm)*

Measurement	SPECIMEN NUMBER		
	D 233	D 234	D 235
Spread of horn-cores, tip to tip	770[a,b]	682[a]	658
Greatest spread of cores on outside curve	780[a,b]	715[a]	688[a]
Core length on upper curve, tip to burr	254[a]	235	215
Core length on lower curve, tip to burr	288	299[b]	270
Length, tip of core to upper base of burr	234[a,b]	213[a,b]	187
Vertical diameter of horn-core at right angles to longitudinal axis	101[a,b]	90	80[c]
Circumference of horn-core at right angles to longitudinal axis	304[a,b]	288[a]	254
Greatest width at auditory openings	290[a]	298[a,b]	274
Width of condyles	133	136[a]	114
Depth, occipital crest to top of foramen magnum	93	101	100
Depth, occipital crest to lower border of foramen magnum	148	152	145
Transverse diameter of core at right angle to longitudinal axis	109[a,b]	95	80[c]
Width of cranium between horn-cores and orbits	302[a]	293[a]	283
Greatest postorbital width	358[a]	361[a]	361[a]
Anterior orbital width at notch	278	288	274
Width of skull at masseteric process above M^1	196	207[b]	196
Rostral width at maxillary–premaxillary suture	116	125[a]	120[a]
P^2–M^3 alveolar length	143	142[c]	159[a,b]
M^1–M^3, alveolar length	87[c]	94[b]	101[a,b]
Length, overall, occipital crest to tip of premaxilla	562	604[a,b]	—
Length, basilar, foramen magnum to tip of premaxilla	510[a,c]	542[a]	—
Length, occipital crest to nasal frontal suture	241[c]	276[a,b]	257
Length, beyond P^2 to tip of premaxilla	151	152[a]	—
Length, occipital crest to tip of nasals	—	—	457
Length of nasal bone	—	—	207

[a] Measurements greater than the maximum for *B. bison bison* as listed by Skinner and Kaisen (1947, p. 162).
[b] Measurement greater than the maximum for *B. bison athabascae* as listed by Skinner and Kaisen (1947, p. 164).
[c] Measurement less than the minimum for *B. bison athabascae* as listed by Skinner and Kaisen (1947, p. 164).

occipital bone. The third skull, D 235, is average or a little below average in size for *B. bison athabascae* (*ibid.*), but the alveolar length of the molars and premolars is unusually long.

The 2 skulls of male wood buffaloes described by Banfield and Novakowski (National Mus. Canada, Nat. Hist. Papers No. 8, 1960) show similar features to the 3 skulls discussed in this report. One skull (No. 24026) has 2 measurements above the maxima and 2 below the minima recorded for the subspecies by Skinner and Kaisen (1947). The second skull (No. 24027) has 2 measurements longer than the maxima and 3 smaller than the minima (*ibid.*). Also, individual differences between the 2 skulls are significant in that although skull No. 24026 is generally larger than skull No. 24027, the latter has a much more curved horn-core (length of horn on lower curve, tip to burr, being 255 mm and 300 mm

for Nos. 24026 and 24027, respectively), and a much longer alveolar length of the molars and premolars (No. 24026—228 mm, No. 24027—247 mm). This variability is in accord with the 3 skulls described in this report.

The number of wood buffalo skulls available to Skinner and Kaisen (1947) was small and because of this they were not able to define the true range of variability of this subspecies. The extension of the range of dimensions indicated in this paper may lead to problems in subspecific differentiation on the basis of skull size. In particular, small or incomplete skulls of *B. bison athabascae* may not be separable on the basis of standard measurements as defined by Skinner and Kaisen (1947) from those of *B. bison bison*.

Acknowledgments.—The author expresses thanks to Messrs. G. C. Ford, J. S. MacKenzie, J. N. MacKenzie, D. R. Salhub and Miss C. A. Horrocks, all from Jasper Place Composite High School, who helped greatly in measuring the skulls. Drs. W. A. Fuller and R. Green (University of Alberta and Research Council of Alberta) read the manuscript critically. The University of Alberta made the bison skulls available for study.

Three new *Bison bison athabascae* Rhoads skulls are described. Two skulls are of bulls killed by E. W. Rowan, University of Alberta, in Wood Buffalo Park in 1925, and the third was found by him in the park at that time. Two of the skulls have from 6 to 7 standard measurements (of Skinner and Kaisen, 1947) greater than the maximum for the subspecies, and also have some standard measurements below the minimum (*ibid.*). The third skull is a little below average in size.—L. A. Bayrock, *Research Council of Alberta, Edmonton, Alberta* and J. M. Hillerud, *Jasper Place Composite High School, Edmonton, Alberta.* *Received 4 August 1963.*

BAIT PREFERENCES OF SOME SMALL MAMMALS

Many baits have been used to attract small mammals to traps but only a few attempts have been made to evaluate the success of these baits. Townsend (Roosevelt Wildlife Annals, 4(1): 1–120, 1935) tested peanuts, raisins and bacon and found that peanuts gave the best results for *Sorex* and *Clethrionomys*, and bacon for *Blarina*. *Peromyscus*, *Microtus* and *Zapus* appeared to take the baits indiscriminately. Fowle and Edwards (J. Wildl. Mgmt., 18(4): 503–508, 1954) tested cheese, bacon fat and rolled oats. Their results suggested that *Blarina* preferred cheese but since only 33 animals of 5 species were taken definite conclusions could not be made. Stickle (J. Wildl. Mgmt., 12(2): 211–212, 1948) tested a mixture of peanut butter and rolled oats against unbaited traps and found that the catch of *Peromyscus* was increased by about 150% by using this bait.

In the present study 12 baits, which could be easily used on large numbers of traps, were chosen for evaluation. These included simple baits of peanut butter, bacon, rolled oats, limburger cheese, ground raisins, berry jam, hamburger (raw), canned sardines and walnut meats, as well as mixtures of peanut butter and rolled oats; peanut butter, rolled oats, ground raisins and bacon fat; and anise oil in a cooking oil carrier. The first 2 mixtures were composed of about equal parts of each component. The anise oil was used at a rate of about 6 drops to 100 g of cooking oil.

The traps used were new Victor break-back traps with wood treadles. With the exception of rolled oats, which was sprinkled over the trap, the baits were smeared onto the treadle of the trap.

The baits were tested 4 at a time against an unbaited control. The trapping was set up in units of 5 stations with 3 traps at each station. One station contained only unbaited traps while each of the other stations contained traps with a single bait. A single bait was used at a station to eliminate the possibility of one bait drawing an animal from a distance and its selecting another bait when in the vicinity of the station. The sequence of baits used for each unit was based on a random numbers table. Ten units of 5 stations placed at 30-foot intervals were set out in a line. The traps at each station were placed without

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THE QUARTERLY REVIEW of BIOLOGY

BISON EVOLUTION AND ZOOGEOGRAPHY IN NORTH AMERICA DURING THE PLEISTOCENE

BY R. D. GUTHRIE

Department of Biological Sciences, University of Alaska, College, Alaska 99701

ABSTRACT

The fossil record and information about contemporary forms provide evidence that the evolutionary pattern of bison cannot be interpreted as either a unidirectional decrease in horn size or as a series of successive invasions to the New World from the Old. Rather, some species have persisted and remained relatively unchanged for long periods of time, while elsewhere other contemporaneous species were changing quite rapidly. Although the trends in the evolution of bison horn size have been remarkably regular, major reversals have taken place.

Bison arose in Eurasia and have had a much longer history there than in North America. In spite of this longer history in the Old World, bison have undergone greater evolutionary changes in North America. This can be explained by a different mode and intensity of competition in the New World.

The major points presented are the following: (1) The giant-horned B. latifrons *was a New World product. (2)* B. priscus (= B. crassicornus) *appeared early as a holarctic northern species and remained in that niche until the late Wisconsin (Würm). (3) Most of the other bison species in the late Pleistocene were derived indirectly or directly from this widespread northern species. (4) Middle and Late Pleistocene bison can be placed into four species:* B. priscus, *which can be dated at least as far back as early mid-Pleistocene;* B. latifrons, *which extends back at least to late Illinoian (Riss) time (it is possible that* B. latifrons *gave rise to* B. antiquus; *if so the species* B. alleni *should be maintained);* B. antiquus, *which originated during the early to middle part of the Wisconsin (Würm) glaciation; and* B. bison, *which was a late Wisconsin product. (5)* B. latifrons *became extinct, at least over most of its range, in pre-Wisconsin time.* B. priscus *and* B. antiquus *became extinct in the late Wisconsin, and* B. bison *still exists in relict populations. (6) Two or more species of bison have not occurred sympatrically for extended periods of time. (7) Neither the "orthogenetic" nor the "wave" theory adequately accounts for the evolution of bison in North America; rather, the fossils can only be explained by a combination of invasions from Siberia and evolutionary changes that occurred in the new environment.*

INTRODUCTION

PLEISTOCENE stratigraphers in North America have shown more than usual interest in the history of bison, presumably because some of the phylogenetic lines have undergone comparatively rapid evolution and these fossils may thus be used as sensitive stratigraphic indicators. Unfortunately, bison chronology has not been plotted with such precision that one can always key the fossil by the stratigraphic unit or the unit by the fossil, nor has there been complete agreement on the phylogenetic pattern. Bison evolution has been an area of heated controversy among many Pleistocene paleontologists and no doubt will continue to be for some time. In spite of, or perhaps because of, these disagreements, something of a synthesis is beginning to emerge. I have undertaken here the task of bringing this synthesis up to date. No doubt this version will undergo considerable refinement in the future and perhaps major revisions, as records of phylogenies become more complete and chronologies more refined.

In general, paleontological studies emphasizing stratigraphy are characterized by a tendency to subdivide taxa, for obvious utilitarian purposes. As interest shifts to the biology of the organism, taxa become more inclusive. This phenomenon can be attributed to the fact that the concepts of interpopulational and intrapopulational variation, both vertical and horizontal, were introduced into paleontology from biology, although these concepts suffered long from malnutrition, even there, under the burden of their typological predecessors. Since paleontology has been a subdiscipline of geology rather than biology, paleontologists have been, by tradition, taxonomic "splitters." The study of bison evolution in North America has been approached primarily from a geologist's viewpoint and interests. In this analysis, I have attempted to unite the varied interests of both geology and biology.

One of the main factors which has frustrated bison phylogenists is the nature of characters available for tracing evolutionary patterns. Bison post-cranial structures have differed little through time or spatially. With the exception of the horns, almost the same can be said of the skull. Flerov (1965) has illustrated several cranial differences among living bison groups, but these character differences appear to be mainly adaptations to local environments. If bison had no horns, some paleontologists would consider placing all of the fossil and recent bison into one morphological species. This is the crux of the difficulty. Horns appear to be the most variable character among taxa, yet, used alone, horns have growth and variational characteristics which make mapping of phylogenies hazardous. Some of these difficulties have been reviewed elsewhere (Guthrie, 1966a). Horns show a tremendous variational lability. As well as having an additive ontogenetic growth pattern, they are responsive to changes in nutrition, hormonal imbalance, physical accidents, and the overall health of the animal. In addition to this great spatial intrapopulational and interpopulational variation, the fact that horns are important as a secondary sexual characteristic makes them very responsive to natural selection. Horn size and shape have undergone rapid changes, including apparent evolutionary regressions.

In using horns as a taxonomic character we are dealing with a quasi-indeterminate growth form; the concept of average size or shape borders on being meaningless, since all individuals of all species begin life with no horns at all and thereafter develop horns which vary in size and shape throughout ontogeny. Although techniques are available for use on characters exhibiting indeterminate growth patterns, these are as yet essentially inapplicable to bison because adequate samples of age structure, variation within and between age classes, sexual variation, and the nature and extent of intersubspecific variations for each of the groups being compared are not available. Thus, parameters such as *means* are of questionable value, except when taken in a general way. Also, one cannot expect the standardized variation parameters based on a normal distribution to be applicable.

During the late Pleistocene the bison of Eurasia were basically a northern genus. Bison apparently are a northern homologue of cattle, *Bos*, both phylogenetically and ecologically. Both genera have a long history in Eurasia that extends back to the early Pleistocene (Zeuner, 1945). Cattle and bison are so closely

related in their morphology that many postcranial skeletal elements are easily confused unless examined in detail (Olsen, 1960). The two are also very similar serologically (Stormont, Miller, and Suzuki, 1961). They have occupied the large-bovid grazing niche across Eurasia, *Bison* to the north and *Bos* in the south. In the far south other closely related large bovids, the buffalo, occupied a similar habitat. Intermediate zones between these three subhabitats existed and harbored both genera; thus bison co-existed with *Bos*, and *Bos* with buffalo (Zeuner, 1963). The chief osteological differences between these three bovid forms are in the horns. There are other major differences, such as the length of neural spines and the degree of orbital extension. The length of the neural spines is taxonomically distinct, but evolutionary studies have not, as yet, made use of this character. Unlike the cattle and buffalo, the orbits of bison protrude (telescope out) from the skull. This may be a compensation for the thick mass of wooly hair on the face of the bison (Guthrie, 1966b).

Several studies (Larson, 1940; Szaniawski, 1960) have shown that *Bos* and *Bison* are predominately herb eaters, particularly of grass and grass-like plants, and differ little in their dietary preferences. Thus, during the middle and late Pleistocene *Bos* probably served as a biotic barrier to the expansion of *Bison* southward and *Bison* as a barrier to the northward expansion of *Bos*. However, in the highlands of Asia *Bos* gave rise to a cold-adapted form, the yak, which managed to penetrate into the far northern latitudes. This latter line, or a closely related form, crossed into North America and their remains are found in Alaska (Frick, 1937).

This entire group of large bovids probably began as an auroral-crepuscular park feeder, eating in open grass clearings during twilight and dawn and then retreating to the protection of the forests to ruminate. Running in a northward cline, from the buffalo to cattle and then to bison, there is an increasing tendency to remain in the open areas throughout the day and to rely on flight or the protection of the herd, rather than seclusion, for safety.

Thus in Eurasia the grazing habitat was geographically partitioned between these three forms. (It is not completely valid to treat all the buffalo and subtropical cattle as one ecological form; however, to go into more detail here is beyond the scope of our specific interest.) *Bison* did not expand to the south because of competitive exclusion, and likewise *Bos* was able to penetrate northward only in a single limited case. In the colonization of North America, however, no such limitations were placed on the southern extensions of *Bison*. The other two groups were not able to successfully colonize the New World, leaving bison as the only large bovid to compete with the native plains grazers. In this new environment the bison were free to undergo considerable range expansion and phylogenetic change. The various features of bison evolution are thus more dramatic in the New World, where it was able to invade the habitats of less efficient inhabitants. It is within this ecological setting that bison evolution is here re-examined.

THEORIES OF BISON EVOLUTION

Most of the taxonomic studies of fossil bison have been done on American forms, because, for reasons just noted, the greatest interspecific variation is found there. It is due to the apparent lesser degree of diversification in Eurasia, and perhaps to some degree to a different taxonomic orientation of paleontologists, that bison have not presented the same problems in Eurasia as they have in North America. Thus, concern with bison evolution has historically been heavily weighted in favor of Nearctic forms.

During the early history of Pleistocene paleontology in America it was not uncommon to give any horn core the status of a new species if it was slightly different from any other type that had been described; consequently, the literature abounds with forms such as *Bison regius, B. angularis, B. oliverhayi, B. rotundus, B. californicus, B. ferox, B. texanus, B. taylori, B. pacificus, B. sylvestris,* and *B. kansensis,* which have since been lost in the sea of synonomy.

Although fossil bison are referred to in the literature in hundreds of cases, there have been only two papers in the past several decades which have dealt in detail with bison evolution in North America. The first of these was a preliminary study by Schultz and Frankforter

(1946) and, a short time later, a more elaborate review by Skinner and Kaisen (1947). These two works have profoundly affected later concepts of bison evolution and Pleistocene stratigraphy as well.

Although Skinner and Kaisen speak of the chronologies in more general terms, they are in basic agreement with the major tenet of Schultz and Frankforter's work, which is, essentially, that the oldest bison in North America have the biggest horn cores, the later ones horn cores of medium size, and the latest ones small horn cores. Both state that this sequence of horn core dimunition corresponds, respectively, to early mid-Pleistocene, late Pleistocene, and Holocene.

Although they are in agreement on the above point many major differences exist between the two works. Schultz and Frankforter conceived of the early large-horned invaders as becoming successively smaller horned in a gradation from *B. latifrons* to *B. bison* in one phylogenetic sequence. I will call this concept the *orthogenetic theory*. Almost at the opposite extreme, Skinner and Kaisen visualized little phylogenetic change in the North American forms. Instead, they explained the diversity as successive waves of migration from Eurasia. I will later refer to this as the *wave theory*.

According to Schultz and Frankforter the phylogeny follows the sequence, *B. latifrons, B. alleni, B. antiquus,* and *B. bison*. The primary character used is horn-core size. Skinner and Kaisen, as well as having a vertical (chronological) species differentiation, constructed a model of several species existing in a given place at one time. Also, in addition to size, they based their phylogenies on the degree of dorsoventral horn compression and the degree of curvature or twisting. According to their model, the first wave of bison came over into North America via the Bering land bridge in the early or mid-Pleistocene. These species were *B. latifrons, B. chaneyi,* and *B. alleni*. The second wave, following the same route, consisted of *B. crassicornis, B. preoccidentalis, B. alaskensis,* and *B. geisti*. The very late Pleistocene saw the occurrence of two other new forms: *B. antiquus,* derived from *B. alleni* of the first migration, and *B. occidentalis,* an even later form derived from the Alaskan *B. preoccidentalis*. *B. occidentalis* then gave rise to *B. bison* in recent times. Skinner and Kaisen thus accounted for the diversity of North American forms primarily by immigration from Eurasia in the middle to late Pleistocene followed by some degree of phylogenetic change in the very late Pleistocene and Recent.

In a more recent paper, Fuller and Bayrock (1965) interpret the late Wisconsin and recent bison phylogeny as a late branching of *B. bison occidentalis* from *B. crassicornis,* which in turn gave rise to *B. bonasus* and the two living subspecies of *B. bison*. According to their phylogeny, *B. bison occidentalis* and *B. crassicornis* lived contemporaneously with the form also found in the earlier Pleistocene, *B. latifrons*.

Dalquest (1961) suggests a general picture similar to the pattern presented by Schultz and Frankforter (1946) and Skinner and Kaisen (1947), except that he follows Hibbard (1955a) in his later date of bison invasion into central North America. He indicates three major horn size groups. The first group, *B. latifrons, B. chaneyi,* and *B. alleni* were found during the Illinoian glacial and Sangamon interglacial. These giant-horned forms were replaced by the medium horned forms, *B. occidentalis* and *B. antiquus,* during the Wisconsin glacial, and these in turn were replaced by the modern *B. bison*. He does not indicate the source or origin of these species, but does imply that they do not represent a phylogenetic gradation.

Allen (1876) also proposed a type of orthogenetic theory of bison evolution when he stated that both the New World and Old World medium horned bison, *B. antiquus* and *B. priscus* developed from the large horned *B. latifrons*. The species *B. americanus* (*B. bison*) subsequently arose from *B. antiquus,* and in the other independent line *B. priscus* gave rise to *B. bonasus*.

The theory presented by Flerov and Zablotski (1961) pictures *B. latifrons* colonizing North America in the mid-Pleistocene and decreasing in horn size into the late Pleistocene as *B. antiquus*. Then there was a recolonization in the very late Pleistocene by *B. bison,* which replaced *B. antiquus*. In a later study Flerov (1967) proposed that the northern bison species, *B. priscus,* gave rise to both *B. bonasus* and *B. bison athabascae*. The latter he classified as *B. priscus athabascae*. He also suggested

that *B. alleni*, which came from *B. latifrons*, developed into *B. antiquus* (he reclassifies *B. antiquus* as *B. bison antiquus*). He thus proposed, like Allen (1876) and Schultz and Frankforter (1946), that the New World bison evolved in a gradation from *B. latifrons* through *B. antiquus* to *B. bison*. He differs from other authors by separating *B. bison bison* and *B. bison athabascae* (his *B. priscus athabascae*) into two different species with quite different origins.

Hillerud (1966) has followed the orthogenetic model of Schultz and Frankforter. He derived *B. bison* from *B. antiquus* and *B. antiquus* from *B. alleni*. The unique aspect of his theory is that he places *B. occidentalis* as a subspecies of *B. antiquus* and calls it *B. antiquus occidentalis*. This subspecies arose from *B. crassicornis*.

These are at present the major theories of bison evolution. Although they represent most of the possible permutations, there are some common threads that unite them, and they also contain numerous inconsistencies that can be resolved.

CRITIQUE OF THEORIES

Strangely enough, from the beginning there has been an unquestioned assumption by paleontologists concerned with bison evolution in North America that *B. latifrons*, the gigantic-horned form found in mid-Pleistocene deposits from the Great Plains, was an invader from Eurasia. This idea has persisted in spite of the fact that no comparably large horned forms have ever been found in Alaska or in Eurasia. A more tenable explanation is that *B. latifrons* was a New World product, evolving from an Eurasian immigrant with medium-sized horns, as Flerov (1967) has recently observed. Contrary to the concepts of bison evolution as a continual stage of horn reduction, the overall pattern of bison horn evolution in North America, as in Eurasia, is characterized by increasing size, followed by an irregular trend of size decrease. The bison of the early Pleistocene of Eurasia did not have extremely large horns (Fischer, 1963).

Although records from the Great Plains show a gradual decrease in horn size from mid-Pleistocene to the living bison (Schultz and Frankforter, 1946), this pattern is not commonly observed in other regions in the holarctic. The general picture of decrease in horn size from very large horned forms is surely a correct interpretation, but the diverse faciations, migrations, and replacements seem to be more complex than the orthogenetic model indicates. The orthogenetic theory also fails to take into account the living Eurasian bison and the problem of its New World affinities, as well as the relationships of the now extinct northern *B. priscus* (= *B. crassicornis*). The close relationship of living Old World and New World bison indicate the necessity of finding a fairly recent common ancestor, which is most difficult to do within the orthogenetic theory. *B. priscus*, a species with medium-sized horns, occurred in Alaska and northern Eurasia and existed almost unchanged at least throughout the latter half of the Pleistocene and only became extinct (either by rapid evolution or elimination) as recently as the late Wisconsin.

Synonomizing the Alaskan *B. crassicornis* specimens with the Siberian and other Eurasian *B. priscus* seems appropriate since there is a morphological gradient across the Holarctic. Skinner and Kaisen (1947) recognized this continuum when they referred some of the Siberian specimens to *B. crassicornis*.

The phylogenetic pattern presented by the Alaskan fossils directly affects the plausibility of the wave theory with even more fatal consequences than it does the orthogenetic theory. The ubiquitous northern species, *Bison priscus* (= *B. crassicornis*), is present in Alaskan and Siberian deposits dating from Illinoian to late Wisconsin, and has been recorded in Pre-Illinoian sediments (Péwé and Hopkins, 1967). Even though thousands of medium-horned bison fossils have been found in northern Eurasia and in Alaska there is still good reason to believe that these represent just one species. If one considers all the factors that influence horn size, the variations within this series fall well within the range of variability of a comparable modern species. All other medium-horned species described from the latter half of the Pleistocene of Northern Eurasia and Alaska fall within the expected variation of this one species which, because of priority, should be referred to as *B. priscus*. Not unexpectedly, this synonomy fits into the general pattern found in northern ungulate communi-

ties which, apparently without exception, involve only one variable species per genus; for example, *Equus caballus, Alces alces, Rangifer tarandus, Ovibos moschatus, Saiga tatarica, Cervus elaphus* and *Elephas (Mammuthus) primigineus* were all monotypic species. Along with *B. priscus* these comprise almost the entirety of Illinoian- and Wisconsin-age ungulate assemblages throughout the northern part of the holarctic.

There are two species, *B. alleni* and *B. chaneyi*, recognized from post-*B. latifrons* and pre-*B. antiquus* sediments in the great plains. Most paleontologists who have worked recently with bison assume that one of these was a degenerate (in horn size) descendant of the *B. latifrons* line, or that both were. Although there is support for this assumption, there is also some evidence to the contrary. Actually, the published distinction between *B. alleni* and *B. chaneyi* is so nebulous that the two are operationally inseparable (Dalquest, 1957). Moreover, all the horn measurements referred to in the literature as being diagnostic of *B. alleni* (and/or *B. chaneyi*) show considerable overlap with the large samples of *B. priscus* from Alaska. The *means* of the measurements of these characters are obviously not the same for *B. alleni* and *B. priscus*, but on face value they are not different enough to give the former "species" a taxonomic distinction above that of a chronological or geographical subspecies. Some of the Alaskan *B. priscus* have even been referred to *B. alleni* (Hay, 1913). The chief difference between *B. priscus* and those specimens now referred to as *B. alleni* is not in the horn cores but in the cranium. The crania of the *B. alleni* specimens are more like *B. latifrons*, i.e., large and robust with less protruding oribts. However, the published indices of horn length of *B. alleni* are almost half those of *B. latifrons* with no overlap (Skinner and Kaisen, 1947; Brophy, 1965). Compared to *B. priscus* (= *B. crassicornis*), on the other hand, *B. alleni* shows considerable overlap in every index of horn size or shape (Brophy, 1965). Thus, one is confronted with the decision of either thinking of the *B. alleni* line as a continuation of *B. latifrons* that has converged upon the *B. priscus* horn characters, or as a side branch of the *B. priscus* line that has converged on the *B. latifrons* type of crania. The evidence is still inconclusive. Since there is such a great size discrepancy between the adult male horn cores of *B. alleni* and *B. latifrons*, however, it would appear that the specimens referred to as *B. alleni* came from the *B. priscus* line and replaced *B. latifrons*, acquiring in the process some of the characteristics of the displaced species. Orbital protrusion and skull size may well be directly related to the particular demands of the immediate environment (Guthrie, 1966b). However, the hiatus between *B. alleni* and *B. latifrons* may simply be due to incompleteness of the fossil record.

The fossils now considered to be *B. alleni* would have had to undergo few changes from *B. priscus* ancestors, in fact so few that specific recognition for the former is difficult to justify. This phylogenetic scheme would account for the several specimens far to the south of Alaska which are referred to as *B. priscus* (= *B. crassicornis*) (Romer, 1951; Fuller and Bayrock, 1965).

There is little argument that *B. antiquus* descended from the line represented by the specimens that have been referred to as *B. alleni* or *B. chaneyi*. On this point most agree, since there seems to be a gradation, through time, into *B. antiquus*.

Both Skinner and Kaisen (1947) and Schultz and Frankforter (1946) have interpreted *B. bison* as a species of North American origin. This poses some difficulty in accounting for the origin of the Eurasian *B. bonasus*, which, because of its morphological similarity and ability to interbreed freely with *B. bison*, has been considered distinct by some only at the subspecific level or at least as a closely related species. If one classified *B. bonasus* as a completely separate line the difficulty still remains because of the fossil remains, *B. bison athabascae* (= *B. occidentalis* = *B. bison occidentalis* = *B. priscus diminutus*), found in northern Asia (Flerov, 1967).

Fuller and Bayrock (1965) attack the problem by suggesting that *B. bonasus, B. bison athabascae* and *B. bison bison* branched from *B. bison occidentalis* at approximately the same time [less than 8,000 years Before Present (= B.P.)]. Their interpretation could only be possible if they classified some Asiatic forms as *B. bison occidentalis*, and pushed their date for the

branching back earlier. It is difficult to postulate that *B. bison* of North America gave rise to *B. bonasus* of Eurasia at such a late date, because the land bridge between the two continents was probably not available then for large ungulate interchange (Hopkins, 1959).

If one assumes that the New World *B. bison* could not have given rise to the Old World *B. bonasus* then there are two alternative positions to choose between. The first alternative is to postulate a Eurasian origin for *B. bison* (Flerov and Zablotski, 1961). There is a good fossil sequence in Northern Russia from a medium-horned form (*B. priscus*) to smaller-horned form (*B. bison occidentalis*). The *B. bison* in North America would then be considered a post-glacial immigrant. Skinner and Kaisen (1947) essentially had *B. bison* colonizing North America from Eurasia, except they called the immigrants *B. preoccidentalis* and *B. occidentalis.*

Fossils of small-horned bison are found in late Wisconsin and post-glacial deposits of northeastern Siberia and central Alaska. (These have been variously called *B. priscus diminutus, B. priscus athabascae, B. occidentalis,* and *B. bison athabascae.*) This is the route the invaders would have had to take, and at the right time for colonization through the Cordilleran Corridor. The early *B. bison* forms were slightly larger in horn size than living subspecies. This size reduction seems to have taken place concurrently in all modern forms, both in Eurasia and North America. There is an unresolved minor sub-argument within this Old World origin theory as to whether *B. bison occidentalis* arose from *B. priscus* in Alaska as it did in Siberia, or replaced the Alaskan *B. priscus* after the latter had become extinct. Since the large mammals of Alaska were really a part of the Siberian community, the first alternative seems more plausible.

The future validity of either form of the Old World origin theory of *B. bison,* as in the case of the next alternative, will depend upon the accumulation of more material and dates from the critical area of Alaska and Siberia. Although the explanation invoking a Eurasian origin is made unappealing by the late date required for such an extensive North American invasion, it has considerably more appeal after the other alternative is evaluated.

To take the second position, that *B. bison* originated in North America, one must contend that the living North American bison and the living and extinct Eurasian small-horned bison evolved independently. Continental correlations and cross comparisons of the origins and chronologies of the small-horned bison prove to be no encumbrance to this theory, although a more basic problem does develop: As was pointed out above, one must explain the morphological similarities between the Eurasian and North American bison. This general type of problem could be entitled *Coon's Dilemma,* as it has appeared elsewhere in another context (Coon, 1963). The dilemma originates from the general doubt about the existence of *polyphyletic species* (without hybridization). If one is to support rigorously the extreme orthogenetic theory, it means that starting from a large-horned form, the North American *B. bison bison,* the living Eurasian *B. bison bonasus* (= *B. bonasus*) and the extinct *B. bison occidentalis* of Siberia, originated independently through a long succession of reductions in horn core size which resulted in subspecies which, as some contend, are not sufficiently distinct to warrant the status of separate morphological species. The less orthodox supporter of the orthogenetic theory may indicate a later separation than the mid-Pleistocene. However, one escapes the dilemma only when he grades into the preceding alternative, which specifies a common ancestor of Eurasian, or perhaps amphiberengian, orgin (*B. bison occidentalis*) from which came both the Eurasian and North American small-horned bison during late Wisconsin times.

The phenomenon of range extension outward from the Great Plains, even in recent times (Roe, 1951), by *B. bison* argues for the Eurasiatic invasion theory of the species' origin. The fact that *B. bison* apparently failed to penetrate the eastern and western mountain ranges which bound North America, or at most, did so only to a very limited degree, also suggests a late arrival. *B. antiquus,* however, which according to some theories gave rise to *B. bison,* was able to establish itself on the west coast where it did not grade into *B. bison* phylogenetically, but became extinct without being replaced.

Flerov and Zablotski (1961) have argued that the differences between the two North American subspecies can be explained by the interbreeding of the early *B. bison* immigrants with the native species *B. antiquus*. Since this occurred on the more southern boundary the result of these hybridizations was *B. bison bison*. They contended that the forms to the north, *B. bison athabascae*, did not have occasion to interbreed with *B. antiquus*, and consequently remained more similar to *B. bonasus*. Some interbreeding could have been possible between *B. bison* and *B. antiquus;* however, the difference between the modern subspecies can also be explained by direct adaptation. Elsewhere, Flerov (1967), in order to explain the differences between living bison groups, has suggested that *B. bonasus* (=*B. bison bonasus*) and *B. bison athabascae* arose from *B. priscus* and that *B. bison* arose from *B. antiquus*. The differences between *B. bison bison* and the other living representatives of the genus need not be due to such separate phylogenetic histories, however; rather, they can be explained easily by a moderate rate of adaptation to the environment each occupies. Flerov (1965) reviews these adaptations in detail. Schultz and Frankforter (1946) and later Hillerud (1966) have visualized *B. antiquus antiquus* giving rise to the modern *B. bison bison*. The evidence against this position is derived from the fact that replacement of the former by the latter is rather abrupt (Wendorf, 1961). Dalquest (1961) has even reported an instance of the two species occuring contemporaneously at the same locality. Published radiocarbon dates from the *occidentalis* and *athabascae* material indicate a post-glacial occurrence in North America throughout the Wisconsin glaciation. Actually, no dates on *occidentalis* have ever been established that would pre-date man's arrival into the New World. Hillerud also courts *Coon's Dilemma* when he says that his *B. antiquus occidentalis* was derived from *B. crassicornis* (=*B. priscus*) while *B. antiquus antiquus* came from the *B. alleni* line.

Thus far I have discussed mainly the controversies involved in tracing phylogenies. There is also the problem of vertical separation of species. Unlike the real questions of "where did species X originate and how long ago did the existing species Z separate from the existing species Y?," the decision as to how many species one phylogenetic line has included is, in a sense, rather arbitrary. The source of the difficulty is that our taxonomic conceptualizations and nomenclature are geared to one slice of time or a very incomplete phylogenetic sample. When we begin to get numerous specimens from transitional periods the system must incorporate, or at least tolerate, the idea of a "process" or "continuum." Bison horn evolution has been comparatively rapid and horns changed at a time most likely to be well-documented. The combination of these two factors has resulted in the problem of where to delimit the species in one phylogenetic sequence. For example, if *B. bison* came from the larger-horned *B. priscus*, are the intermediates to be given separate specific rank? Rather than attempt to manage the many difficulties that would result in too many separations, I feel that it is more prudent to label, as species, the forms which represent ends of continuums that were relatively stable for extended periods but to consider the intermediates simply as transitional stages. Yet, one can retain the subspecific designation for the utilitarian purposes of Pleistocene stratigraphers in such sequences as *B. bison occidentalis* ⟶ *B. bison athabascae* ⟶ *B. bison bison*.

SYNTHESIS

The following discussion presents a more or less reconstituted theory of bison evolution and zoogeography in North America that embodies parts of several theories as well as some new features.

Looking first to Eurasia, we see smaller-horned bison (Fisher, 1963), sometimes called *B. schoetensacki*, becoming larger-horned in the early to mid-Pleistocene, at which time they are called *B. priscus*. During this time the species became widespread with many local variants. Other similar bovids were present, and characteristic distributional patterns arose as ecological separations became more mature. Buffalo occupied the southern-most part of Eurasia, particularly the humid southeast. The true cattle specialized in exploiting the temperate climatic belt, while bison became associated with the irregularly expanding northern environment.

This species of bison, *B. priscus*, is found in deposits dating from early to late Pleistocene throughout most of northern Eurasia and in middle Pleistocene deposits from Alaska. *B. priscus* seems to have flourished in the northern niche. If the thousands of fossil ungulate remains removed from the Alaskan late Pleistocene muck deposits are used as an index, one can only conclude that bison must have been the dominant ungulate in this northern habitat (Guthrie, 1968).

The major expansion of bison into the interior of North America appears to have taken place in late Yarmouth or Illinoian. The presence of bison is used as an indicator of Nearctic Rancholabrean mammalian faunas (see Repenning 1967, for an excellent review of the Palearctic-Nearctic mammalian dispersal). There is evidence that *B. priscus* did reach Alaska in Kansan times, but as Repenning points out, the concept of a North American Rancholabrean fauna is really not applicable to Alaskan faunas since Alaska was more a part of Asia than North America during the glaciations. When the *B. priscus* in Alaska extended their range southward to the central part of the North American continent (Figs. 1 and 2) they found a large complex ungulate community, but apparently not one competitive enough to prevent their colonization. In Eurasia, bison were subject to keen competition on their southern periphery by a closely related species. They met with no similar species in North America. The native grazing community in North America had been dominated chiefly by horses, *Equus*, a genus with which bison had sympatrically evolved and competed in Eurasia. In their new habitat, this line of bison increased considerably in body and horn size, as is common in many ungulate species during the early phases of the exploitation of a more suitable habitat.

This giant-horned species, *B. latifrons*, persisted at least during a glacial age and part of an interglacial, then became extinct. During its existence *B. latifrons* must have affected the evolutionary patterns of the native grazers — increasing their capacity to offer more effective competition even though their numbers may have been reduced in the process. Although it is difficult to support on a quantitative basis because of the lack of population studies, the percent of *Equus* fossils in North America seems to decline in the late Pleistocene. The expansion of bison may have been responsible for this decline. If so, this type of replacement is consistent with the general pattern, beginning in the mid-Tertiary of artiodactyl increase at the expense of the perissodactyls.

Radical increases and decreases in horn size

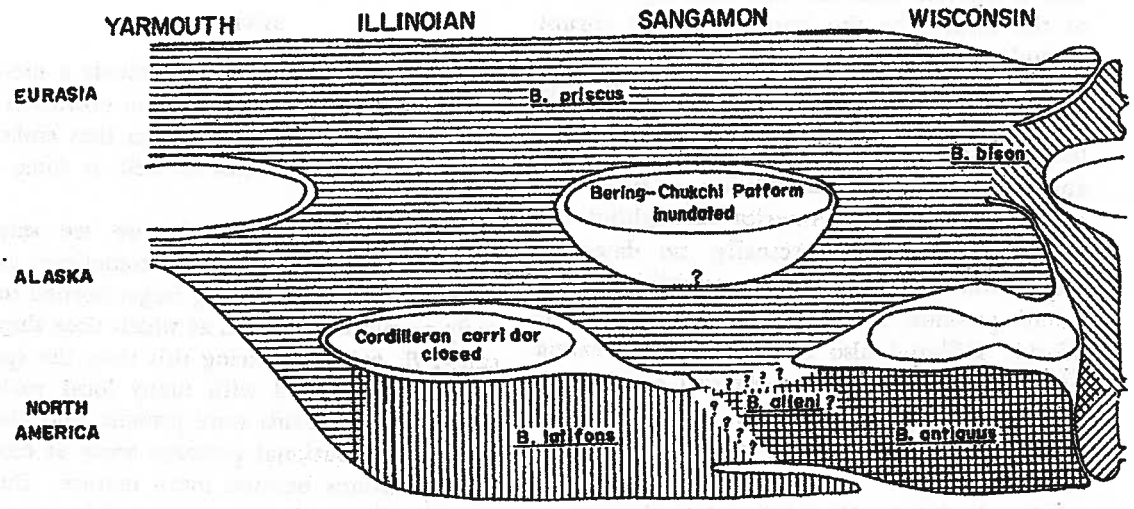

FIG. 1. THE RELATIONSHIP BETWEEN THE BISON OF EURASIA, ALASKA (ACTUALLY THE AMPHIBERINGIAN REGION), AND CENTRAL NORTH AMERICA

The periodic isolation of Eurasia and Alaska is due to flooding of the Bering-Chukchi Platform during Interglacials; the isolation of Alaska from the rest of North America during the glacials is a result of the continental ice sheet. *B. Bison* is illustrated here as having an Amphiberingian origin.

such as are found in the *B. latifrons* line have long presented an unsolvable problem to paleontologists. However, recent studies on the biology of horns and horn-like organs (Geist, 1966a) have given us a much better foundation to understand evolutionary changes in horns. Geist has shown that there is an intimate relationship between horn size and the nature of the intraspecific aggression patterns. Like several other bovids, the bison use a semi-broadside stance (fronto-lateral display) when confronting other members of the species in an intimidating manner. Unlike the short-haired cattle groups which use only the dewlaps (skin hanging from the neck) and elongated neural spines in the lumbar area such as in the gaur (*Bos gaurus*) to present a more massive image, the bison have, in addition, a thick woolly mat of hair covering the forequarters and head, which performs much the same function. The evolutionary "choice" of using thick fur in addition to skeletal changes for display functions was perhaps a product of the genus' long history in the north where thick fur would not be much of a detriment, and might even be an asset to survival.

But as was proposed above, in colonizing North America the bison could move far into the south, an area that was equivalent to the *Bos* niche in Eurasia. In the south the heavy coat of hair used for display was probably reduced, as I indicated in an earlier study of bison orbital protrusion (Guthrie, 1966b), which is directly correlated with the amount of facial hair. Geist (1966b) also has shown that in several ungulate groups (sheep are the classic example) the extent of body display paraphernalia is inversely correlated with horn size. He found that large horns, in addition to their role as weapons, are also used for display, replacing such structures as manes and ruffs. The two lines of evidence are: (1) an indication of hair reduction in *B. latifrons,* and (2) large horns in known cases always being used as display organs. These suggest that *B. latifrons* shifted emphasis from body wool to horns for display. The shifting of the display organs toward the head is a trend Geist found in a number of artiodactyl lines and is generally accompanied by a more frontal display posture. The rudiments of this trend can be seen in short-horned bison (Fuller, 1960). Geist (1966b) mentions that the increased use of horns as display organs in sheep seems to be correlated with the colonization of new habitats which have not yet been exploited.

Such may also have been the case with *B. latifrons.* The increased supply of nutrients increased the survival of the larger individuals and those with larger horns, allowing them to contribute more to future generations (it is the larger-horned males which do most of the breeding in a population which uses horns as a means of social ranking). Increased intrapopulational competition between ungulates generally results in a heritable decrease in individual size (Foster, 1965). By the same mechanism, but perhaps independently, a lowered nutritional level tends to result in a genetic decrease in horn or antler size. The reverse also presumably holds, i.e., an increase in the mean horn size requires an increase in available nutrition. Some of these forces will have to be considered if we are to understand the evolutionary causes of horn change in bison. The theory of bison horn evolution presented in this paper is illustrated in Fig. 3.

Unlike the conditions when *B. latifrons* arrived, future bison in the Great Plains were never again to experience a situation which enabled them to reach this large size, and were, moreover, to undergo a general trend in horn reduction into recent times. It is probable that before its extinction *B. latifrons* also underwent some horn reduction at least over part of its range. The chronological distribution of *B. latifrons* is still in question, although convincing arguments have been presented (Hibbard, 1955a; Green, 1962) for an Illinoian and Sangamon age in the midwest. There is a possibility that *B. latifrons* may have existed into early Wisconsin as relic populations in restricted refugia (e.g., Savage, 1950).

The bison of California provide examples of extinction both by, and without, interspecific competition. If Savage (1950) is correct in saying that *B. latifrons* existed during the Wisconsin glaciation in California, it indicates that the extinction of *B. latifrons* in other areas was due to competition. *B. antiquus* was able to invade the west coast during the Wisconsin, and probably resulted in the demise of the *B. lati-*

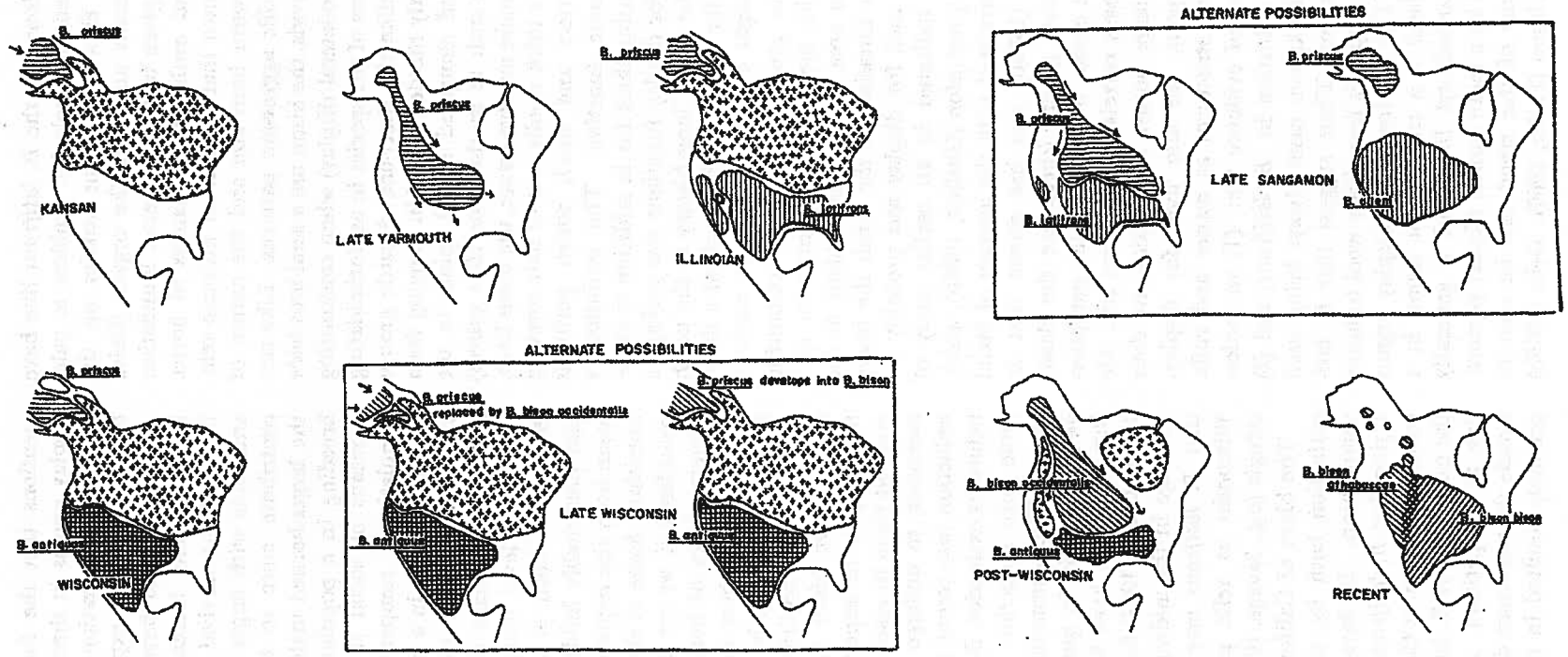

FIG. 2. DIAGRAMMATIC SEQUENCE OF BISON EVOLUTION IN NORTH AMERICA

The scattered checks represent continental glaciation. Note that one species, *B. priscus,* persists in the Amphiberingian Region through most of the mid and late Pleistocene, while there is much variety in the Great Plains during this time. Although there are several features still open to question, the data seem particularly incomplete in two cases. These are presented as alternate possibilities.

frons there. West of the Rocky Mountains *B. antiquus* also eventually became extinct, apparently without other bison being present.

It is probable that the demise of *B. latifrons* in the great plains came about when confronted with the reinvasion of the northern *B. priscus* during an interglacial or interstadial; either that, or an evolutionary change of *B. latifrons* into *B. alleni* took place. Thus, one would expect to find somewhat smaller-horned forms both predating and postdating *B. latifrons*. If *B. priscus* replaced *B. latifrons*, it apparently underwent a small increase in horn size (although it may be difficult to separate these from the earlier intermediates between *B. priscus* and *B. latifrons*). Quite a few of those specimens that have been placed in the species *B. alleni* or *B. chaneyi* may have been representatives of the *B. priscus* invaders that underwent a slight increase in horn size, or *B. latifrons* could have evolved rapidly into a smaller-horned form. If the latter alternative is correct, *B. alleni* should be retained as a species. The Wisconsin age representative of this line was rather different from its ancestors because of its smaller horns, and is given the name *B. antiquus*. It is this species that the late Paleoindians used as the mainstay of their hunting economy. *Bison antiquus* became extinct at the close of the Wisconsin glaciation. The fossils with the most recent radiocarbon dates are between 8–9,000 years B.P. (Wendorf, 1961).

Before, or shortly after, man's invasion of the new world — while *B. antiquus* was the dominant member of the great plains grazing ungulate community — a small-horned form was differentiating from *B. priscus* in Eurasia and possibly Alaska. Flerov and Zablotski (1961) have contended that *B. priscus* in Alaska and Siberia developed into *B. bison* (*B. bison occidentalis*) directly. Although there is moderately good evidence of this transition in Siberia, the exact placement of the Alaskan fossils in time is only beginning. One adult male *B. priscus* (= *B. crassicornis*) from Alaska was dated by radiocarbon as about 31,400 (i.e., 29,585–33,440) years B.P. and a female at 11,950 ± 135 years B.P. (Péwé, 1965). Another adult male horn core was dated (Guthrie, unpubl.) at greater than 39,900 years B.P. (I-2246).

The Asiatic or "amphiberingian" origin of the North American *B. bison* must have taken place in the late Wisconsin. With the opening of the Cordilleran Corridor which followed soon afterward, this small-horned species moved southward into North America and there replaced the dominant *B. antiquus*. Folsom points of the same character are found with remains of *B. antiquus* and *B. bison*, with only a short interval separating the two (Wendorf, 1961). The replacement of *B. priscus* in Europe and *B. antiquus* (and perhaps the Alaskan *B. priscus*) in North America by the present species may have been an active biotic replacement, in which case the contender eliminated the occupant through direct competition, or by a more passive replacement, in which the indigenous form became extinct and the niche was immediately reoccupied by the new form, or perhaps even a replacement pattern involving both types.

The fact that *B. antiquus* became extinct in areas such as California where *B. bison* has never been able to invade, suggests that the replacement in the Great Plains involved the invasion of a vacated niche rather than the direct competitive elimination by an invading species. However, according to the various dates listed in the journal, *Radiocarbon*, over the past 15 years it appears that there was some temporal overlap between *B. antiquus* and *B. bison* (see Hester, 1967, for review). This overlap does not necessarily negate the concept of the reoccupation of a vacated niche.

It is doubtful that, within the genus *Bison*, sufficient specialization has taken place to allow a stabilized sympatric distribution of two or more species for any great length of time. The fossil record essentially supports this idea. The contradictory evidence may represent transitional situations where one species is in process of replacing another (see Hibbard, 1955b, for possible example); or they may be situations in which species with different chronologies occur in one heterogeneous reworked deposit and are described as contemporaneous, as appears to be the case in the instance of *B. latifrons*, *B. crassicornis*, and *B. bison occidentalis* horn cores found in a single gravel terrace in Alberta, Canada (Fuller and Bayrock, 1965).

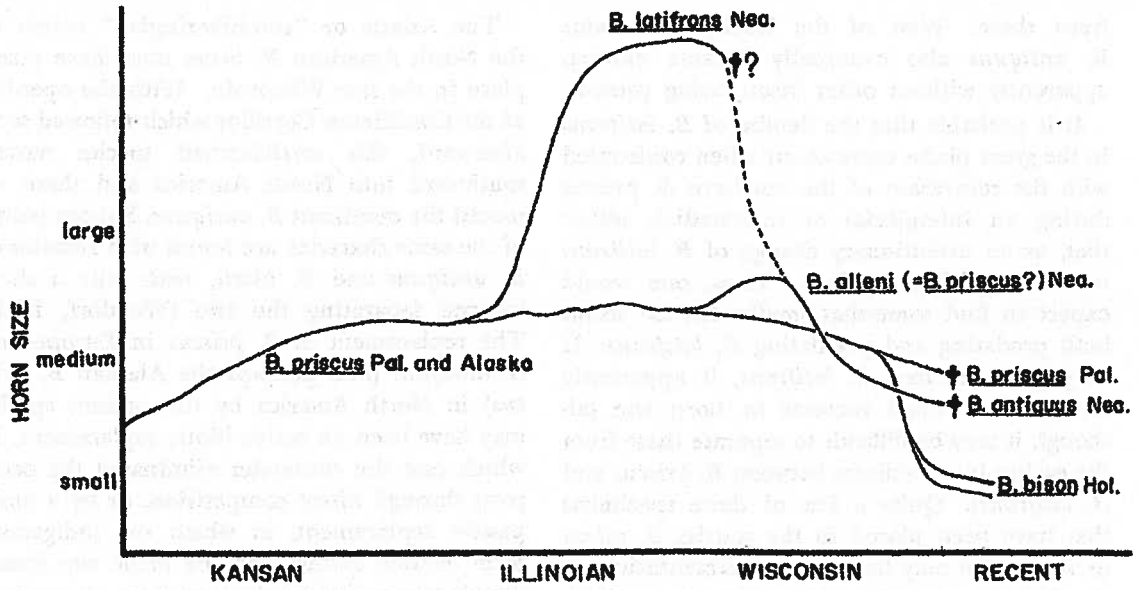

FIG. 3. AN ILLUSTRATION OF THE CHANGE IN BISON HORN SIZE DURING THE LATTER HALF OF THE PLEISTOCENE

At this time only the general features can be presented, and even these must be considered as only a preliminary outline. Nea = Nearctic, Pal. = Palarctic, Hol = Holarctic.

The usual condition of apparent sympatry, however, is the situation where one species is taxonomically partitioned into several. The previously discussed studies of fossil Alaskan bison serve as an excellent example.

If the extinction of many of the plains ungulates and their predators can be traced to the cultural development of the big-game hunting societies, as some have suggested (Martin, 1958), man may have worked inadvertently with *B. bison* to eliminate the other larger-horned bison species. As man reduced the numbers of the larger bison (*B. antiquus* and *B. priscus*), the smaller form, which was adapted to the mode and magnitude of predation pressure exerted by Paleolithic (and/or Paleoindian) cultures, took over the vacated niche. The fact that *B. bison* not only survived this time of widespread extinction, but extended its range and established itself as a dominant grazer over large areas in both northern continents, supports this idea. The replacement theories, of course, still apply even if *B. priscus* and *B. antiquus* became extinct by forces other than man's predation.

Both the recent Eurasian and American bison have undergone horn reduction from the late Wisconsin ancestral species, *B. bison occidentalis*. The two subspecies, *B. bison bonasus* and *B. bison athabascae*, seem to be more closely related to *B. bison occidentalis* than does *B. bison bison* (Flerov, 1965). However, *B. bison bison* has become farther removed from its earlier habitat. It has become more of a resident of the open plains than the other subspecies, which are park-woodland or savanna inhabitants.

Although there are several characters other than overall horn size which change in the phylogeny of bison, the main feature of bison evolution is the quite extreme changes in their horns (Fig. 3). There are certainly many factors that regulate horn shape and size, some of which we know moderately well; however, we know much less about their interaction. The evolutionary mechanics of secondary sex-ornamentation offer many intriguing problems. These characters are generally among the more labile ones, both ontogenetically and phylogenetically, with a great deal of feedback between the two. An animal nutritionist, or behaviorist, or morphologist concerned with horn variations is just as handicapped without an historical perspective as a paleontologist is without

the knowledge of the factors affecting intrapopulational variation. Understanding of horn variations and their phylogenetic change must be a product of interdisciplinary cooperation.

It will be some time before our knowledge of bison evolution will be resolved to the point that most investigators will agree on the major features. Bison evolution will continue to be vigorously studied for a long time to come, but gradually a general image is beginning to form, albeit still a blurred one.

ACKNOWLEDGMENTS

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ASPECTS OF VARIATION IN CRANIAL CHARACTERS OF PLAINS BISON (*BISON BISON BISON* LINNAEUS) FROM ELK ISLAND NATIONAL PARK, ALBERTA

D. M. Shackleton, L. V. Hills, and D. A. Hutton

Abstract.—A sample of 157 known age skulls from a population of plains bison (*Bison bison bison*) were examined following the taxonomic measurements described by Skinner and Kaisen (1947). Lower jaws were also examined following the characters defined by Butler *et al.* (1971). Tables of these data are presented against which samples from other studies may be compared. Cranial characters could be used to estimate the age of individuals within certain limits, and sexes were readily distinguishable from these parameters. Lower jaws, however, were found unsuitable for clear discrimination of age and sex unless teeth were present. The importance of the measurements for archaeological studies, and the need for a revision of the genus *Bison*, are also discussed.

In their revision of the North American members of the genus *Bison*, Skinner and Kaisen (1947) relied mainly upon subjective comparisons of the means and ranges of various craniometric characters. Unfortunately, no standard statistical measures of variability were provided in this study for comparisons between the assigned species, nor for comparisons with other samples. Further, the main morphological characters used to separate species of this genus were those of the horn-cores (Skinner and Kaisen, 1947). Use of horn-cores for taxonomic purposes has been questioned by Guthrie (1966*a*) on the grounds that secondary sex characters such as these would be expected to show high individual and interpopulation variation, induced by environmental differences. Variability of this type could easily confuse our understanding of the taxonomic status of individuals, if normal levels of intra- and interpopulation variation are not known (Guthrie, 1966*a*). Indeed, where sources of craniometric variation have been studied in other ungulates, the degree of difference between populations and between individuals has led to a reduction of taxonomic trinomials (Cowan and McCrory, 1970; Hutton, 1972).

Only one study of bison has appeared which provides statistical measures of variability, and from these data Bohlken (1967) revised the living bison reducing the two species with two subspecies each to a single species with four subspecies. The examination of material from recent finds of extinct bison has led to similar questions of the validity of morphologically and temporally similar species from both the Old (Flerov, 1965) and the New Worlds (Lorrain, 1968; Guthrie, 1970; Butler, 1971; Butler *et al.*, 1971).

North American and European taxonomists differ in the degree of emphasis which they place on horn-core variability in separating species of bison. According to Kurtén (1968) three species of bison are recognized in Eurasia during the post-Villafranchian to Recent period. The horn-cores of these

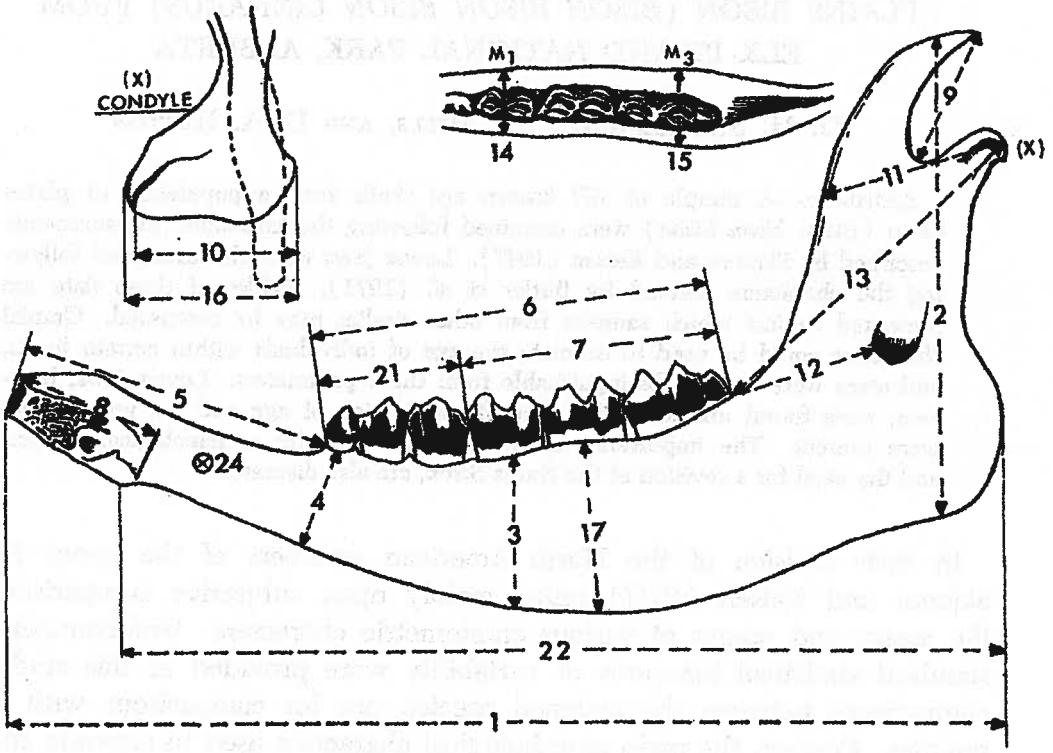

FIG. 1.—Lingual view of left mandible showing majority of measurements taken during present study. Measurements 1 to 21 follow Butler *et al.* (1971), and measurements 22 to 24 taken in addition are described in the text.

three species range in size from the small horned *Bison bonasus* (= *B. bison bonasus* of Bohlken, 1967) to the medium to large horned *Bison priscus*. In contrast, Skinner and Kaisen (1947) recognize nine North American species, included in three subgenera, whose combined horn-core range is similar to that of the three Eurasian species (see Degerbol and Iverson, 1945). A tenth North American species, *Bison latifrons*, is recognized and placed in a fourth subgenus by Skinner and Kaisen (1947). This species has considerably larger horn-cores than any other North American or Eurasian bison described to date.

The purpose of this paper is 1) to make available craniometric data for certain age classes of male and female plains bison, against which other samples may be compared, and 2) to present standard statistical measures of the craniometric characters described by Skinner and Kaisen (1947) and Butler *et al.* (1971) to initiate a re-evaluation of the choice of taxonomic characters used in this genus (Guthrie, 1966*a*).

MATERIAL AND METHODS

A total of 157 skulls of modern plains bison were obtained from a reduction program at Elk Island National Park, Alberta, during the early winter of 1971. This population originated from animals purchased by the Canadian Government from the Pablo-Allard herd,

TABLE 1.—*Skull measurements of adult male bison from Elk Island National Park.*

Measurements*	N**	Mean	SD	CV	Range
(1) Spread of horns, tip to tip	75	594.5	46.69	7.85	486 – 695
(2) Greatest spread of cores on outside curve	75	612.8	43.44	7.09	521 – 707
(3) Core length on upper curve, tip to burr	80	196.4	19.54	9.95	152 – 250
(4) Core length on lower curve, tip to burr	80	244.0	24.05	9.86	197 – 300
(5) Length, tip of core to upper base of burr	80	176.2	17.72	10.06	139 – 220
(6) Vertical diameter of horn-core at right angles to longitudinal axis	81	73.6	5.42	7.36	63 – 87
(7) Circumference of horn-core at right angles to longitudinal axis	81	232.7	16.51	7.11	204 – 278
(12) Transverse diameter of core at right angles to longitudinal axis	83	78.2	6.34	8.12	68 – 94
(13) Width between bases of horn-cores	70	223.3	10.89	4.86	200 – 245
(8) Greatest width at auditory openings	78	255.9	8.78	3.43	229 – 276
(9) Width of condyles	77	123.4	5.19	4.21	116 – 138
(10) Depth, occipital crest to top of foramen magnum	74	99.2	6.04	6.09	84 – 119
(11) Depth, occipital crest to lower border of foramen magnum	72	140.2	5.58	3.98	129 – 154
(14) Width of cranium between horn-cores and orbits	82	265.0	8.82	3.33	246 – 289
(15) Greatest postorbital width	81	318.1	12.23	3.84	282 – 352
(16) Anterior orbital width at notch	82	240.6	13.57	5.64	214 – 274
(17) Width of skull at masateric process above M^1	83	189.8	9.10	4.79	160 – 206
(18a) Rostral width at maxillary-premaxillary suture	83	118.9	6.16	5.18	103 – 132
(18b) Rostral width as in 18a, see text for description	83	101.7	4.65	4.57	86 – 118
(19) PM^2–M^3, alveolar length	83	150.3	5.31	3.53	131 – 162
(20) M^1–M^3, alveolar length	83	94.0	3.90	4.14	80 – 103
(O–P) Length, overall, occipital crest to tip of premaxilla	81	534.7	15.74	2.94	476 – 570
(F–P) Length, basilar, foramen magnum to tip of premaxilla	77	486.6	12.24	2.52	450 – 520

TABLE 1.—*Continued.*

Measurements*	N**	Mean	SD	CV	Range
(O–T) Length, occipital crest to tip of nasals	81	435.1	14.30	3.29	382 – 465
(O–N) Length, occipital crest to nasal-frontal suture	81	242.8	11.46	4.72	210 – 269
(M–P) Length, beyond PM^2 to tip of premaxilla	83	136.1	5.01	3.68	124 – 148
(N–T) Length of nasal bone	83	203.7	9.17	4.50	177 – 225
	Indices				
Horn-core curvature	80	138.9	10.79	7.77	115.0 – 163.6
Horn-core compression	81	94.4	5.16	5.47	80.5 – 107.4
Horn-core proportion	80	84.5	6.63	7.85	71.7 – 101.4
Horn-core length	79	74.1	6.74	9.10	61.1 – 92.6
Toothrow proportion	77	30.9	.94	3.04	27.3 – 32.6

* Measurements after Skinner and Kaisen (1947), key numbers and letters follow their format.
** N = sample size; SD = standard deviation; CV = coefficient of variability, expressed as a percentage.

Kalispell, Montana, which were held at Elk Island National Park before shipment to Wainwright National Park, Alberta, in the early 1900's (Garretson, 1938).

The skulls were cleaned by boiling and cranial measurements described by Skinner and Kaisen (1947) were taken to the nearest millimeter (mm). Measurements of the mandibles followed those of Butler *et al.* (1971) and are illustrated in Fig. 1. Three additional measurements were made and are also illustrated in Fig. 1 and are described as follows: substitute total length—greatest distance between posterior margin of ramus and the projection of posterior edge of symphyseal surface (22); substitute diastema length—least distance between posterior border of incisive foramen and anterior edge of alveolus of PM_2 (23); diastema width—least width of diastema at point shown in Fig. 1 (24).

The age and sex of most of the skulls were determined from tag and brand data collected by National Park personnel during the reduction program. Skulls not having such data were aged by tooth wear and eruption sequence as outlined by Frison and Reher (1970). This aging method was checked against the known age specimens from Elk Island, and showed closer agreement than did other methods (Hogben, no date, cited by Taber, 1963; Fuller, 1959). All specimens 5.5 years of age and older were classed as adult, and separated by sex. This class would be equivalent to the "fully mature-S3 class" described by Skinner and Kaisen (1947).

RESULTS AND DISCUSSION

Cranial Dimensions and Taxonomic Characters

The cranial dimensions following Skinner and Kaisen (1947) are given in Tables 1 to 4 inclusive, for the four age-sex classes examined. A comparison of these data for adult bulls (Table 1) with those given by Skinner and Kaisen (1947) for *B. b. bison* show very close agreement for means and ranges. Only measurement 11 (Table 1) differs consistently in mean and

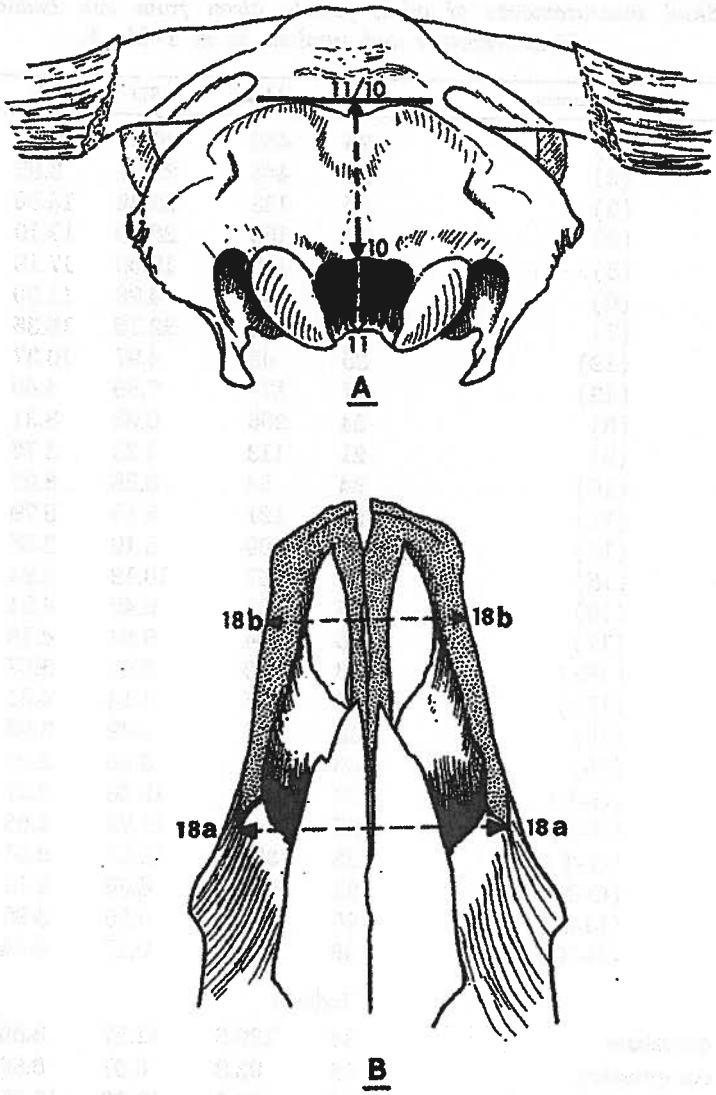

FIG. 2.—Reference points used in present study which may differ from those of Skinner and Kaisen (1947), for measurements (A) of occipital depth, and (B) of rostral width (premaxillae shown stippled). Measurement 18b taken across junction of premaxillae with lower anterior portions of maxillae.

range values, and this together with measurement 10 (Table 1), have poorly defined reference points (see Fig. 2A). Similar difficulty was encountered in interpreting measurement 18 (Skinner and Kaisen, 1947) of rostral width. This was not originally defined clearly and consequently two measurements of rostral width were made here as shown in Fig. 2B. It is felt that measurement 18b (Fig. 2B, Table 1) may be the better measurement because it is easily defined and has a lower coefficient of variability (Tables 1 to 4).

In comparison to Bohlken's (1967) data for *B. b. bison*, the Elk Island adult males show differences in a number of their cranial dimensions. Al-

TABLE 2.—*Skull measurements of adult female bison from Elk Island National Park. Measurements and symbols as in Table 1.*

Measurements	N	Mean	SD	CV	Range
(1)	25	438	40.89	9.33	359 – 517
(2)	25	445	39.57	8.82	359 – 525
(3)	34	123	23.22	18.90	63 – 162
(4)	34	150	28.59	19.10	68 – 203
(5)	34	115	19.69	17.19	63 – 145
(6)	35	44	4.98	11.30	30 – 52
(7)	34	148	22.76	15.35	100 – 248
(12)	35	48	4.97	10.37	32 – 56
(13)	27	179	7.86	4.40	165 – 195
(8)	24	205	6.98	3.31	189 – 220
(9)	21	113	4.23	3.76	102 – 120
(10)	24	84	6.98	8.65	76 – 107
(11)	22	121	8.10	5.79	112 – 141
(14)	34	209	8.10	3.88	190 – 222
(15)	35	257	10.13	3.94	237 – 275
(16)	35	191	9.45	4.94	174 – 211
(17)	36	164	6.82	4.16	153 – 179
(18a)	36	99	5.64	5.67	83 – 110
(18b)	36	85	4.10	4.81	76 – 93
(19)	36	147	4.49	3.06	137 – 158
(20)	36	92	3.36	3.64	84 – 99
(O–P)	33	478	12.28	2.57	452 – 500
(F–P)	25	443	11.79	2.66	415 – 468
(O–T)	33	389	10.91	2.81	366 – 406
(O–N)	33	209	8.66	4.14	184 – 225
(M–P)	36	124	4.95	3.98	115 – 135
(N–T)	36	190	9.17	4.84	168 – 205
	Indices				
Horn-core curvature	34	130.6	11.57	8.86	104.8 – 148.0
Horn-core compression	35	92.0	6.07	6.60	76.0 – 110.3
Horn-core proportion	34	83.2	13.18	15.85	51.1 – 103.4
Horn-core length	32	59.2	10.37	17.51	31.2 – 76.1
Toothrow proportion	25	33.2	1.04	3.13	30.7 – 34.9

though possibly of limited validity, statistical comparisons by Student's *t*-test of eight of the measurements showed that five of these were significantly different ($P < 0.05$). All but measurement 8 (Table 1) were smaller than Bohlken's (1967) samples. In fact, the data from Elk Island resembled more closely Bohlken's (1967) samples of *B. bonasus* than they did the *B. b. bison* sample. Similar differences between Bohlken's samples and the Elk Island data were found in females.

If data for three of the living bison described by Bohlken (1967) together with the Elk Island sample and data from Skinner and Kaisen (1947) are arranged in order of increasing size, the cline runs as follows: *B. bonasus*

(= *B. bison bonasus*, Bohlken, 1967); *B. b. bison* (Skinner and Kaisen, 1947; Elk Island sample); *B. b. bison* (Bohlken, 1967); *B. b. athabascae* (Skinner and Kaisen, 1947; Bayrock and Hillerud, 1965). It must be noted that many of the specimens in Bohlken's (1967) sample of *B. b. bison*, came from zoological gardens. Presumably they had lived under conditions of less bioenergetic stress than experienced by the specimens collected at Elk Island and in the sample of Skinner and Kaisen (1947). Differences of similar magnitude in these cranial characters have been found between populations of mountain sheep (*Ovis canadensis canadensis*) by Shackleton (1973) and between populations of wapiti (*Cervus elaphus nelsoni*) by Hutton (1972). In these latter studies the observed differences were attributed to nutritional and other environmental variation, similar to those discussed by Klein (1964, 1965) for variation in postcranial elements of black-tailed deer (*Odocoileus hemionus sitkensis*) populations.

The coefficients of variability of horn core dimensions and indices show that these characters are the most variable of the craniometric measurements (Tables 1 to 4). Thus Guthrie's (1966*a*) hypothesis that this region of the skull would be expected to show high variability is supported. Whether this degree of variability invalidates the use of horn core dimensions for taxonomic purposes cannot be adequately examined with data from only one population. Similar studies of other populations of plains bison should be made before conclusions are drawn.

Samples representing other types, designated as distinct species by Skinner and Kaisen (1947) should also be examined for their degree of variation. It is very likely that a revision of the genus will prove necessary, and that the number of species of North American bison will be substantially reduced from the present ten. Data from prehistoric archaeological sites have already begun to raise doubts as to the distinctness of *B. antiquus* and *B. occidentalis* (Lorraine, 1968; Butler *et al.*, 1971).

Cranial Dimensions and Age-Sex Differences

For animals up to the age of 4.5 years the sequence of tooth eruption and wear described by Frison and Reher (1970) agrees with that observed in the majority of specimens from Elk Island. Variation of tooth eruption and wear, however, was noted in our samples, and was also found by Wenchell (1963) for a sample of known aged bison collected at the National Bison Range, Montana. Variability of tooth eruption sequence has been found in other species (Keiss, 1969; Cowan, 1940; Taylor, 1962), and may reflect environmentally induced differences between both individuals and populations (Geist, 1971*b*). The sequence described by Fuller (1959), and substantiated by Novakowski (1965), is in agreement with the description of Frison and Reher (1970) for animals up to the age of 2.5 years. After this age discrepancies of up to 12 months difference appear depending upon whose criteria are followed (Reher, 1973). The bison studied by Fuller (1959) and Novakowski

TABLE 3.—*Skull measurements of 4.5-year-old male bison from Elk Island National Park. Measurements and symbols as in Table 1.*

Measurements	N	Mean	SD	CV	Range
(1)	8	572.0	48.26	8.44	505 – 650
(2)	8	597.0	46.72	7.83	540 – 682
(3)	8	198.5	18.39	9.26	178 – 235
(4)	8	256.4	18.14	7.08	239 – 296
(5)	8	169.6	10.32	6.09	156 – 188
(6)	8	68.9	2.85	4.14	66 – 74
(7)	8	218.0	6.05	2.77	207 – 225
(12)	8	72.0	2.51	3.48	69 – 75
(13)	8	223.0	12.78	5.73	200 – 240
(8)	9	246.6	12.35	5.01	222 – 262
(9)	9	123.9	8.62	6.96	113 – 141
(10)	9	96.2	3.83	3.98	90 – 101
(11)	9	135.6	5.57	4.11	125 – 144
(14)	9	260.3	11.94	4.59	248 – 282
(15)	9	301.6	13.32	4.42	277 – 324
(16)	9	219.1	10.69	4.88	205 – 242
(17)	9	182.8	8.77	4.80	173 – 199
(18a)	9	120.0	7.04	5.86	112 – 132
(18b)	9	97.7	5.34	5.47	90 – 106
(19)	9	154.9	4.17	2.69	148 – 160
(20)	9	93.0	2.24	2.33	93 – 99
(O–P)	9	520.2	20.10	3.86	493 – 545
(F–P)	9	477.7	11.78	2.47	146 – 179
(O–T)	9	420.1	15.20	3.62	399 – 439
(O–N)	9	236.1	12.94	5.48	216 – 251
(M–P)	9	132.9	4.57	3.44	125 – 139
(N–T)	9	195.7	8.65	4.42	182 – 213
		Indices			
Horn-core curvature	8	151.1	4.70	3.11	145.5 – 157.5
Horn-core compression	8	95.8	6.46	6.74	88.0 – 105.7
Horn-core proportion	8	91.2	9.35	10.26	79.1 – 107.8
Horn-core length	8	76.3	5.59	7.33	70.6 – 85.1
Toothrow proportion	9	32.4	.78	2.41	31.5 – 35.1

(1965) came from Wood Buffalo National Park, Alberta, and probably represented a hybrid population of the indigenous *B. b. athabascae* and the introduced *B. b. bison*. These animals suffer from brucellosis, tuberculosis, and arthritis, with occasional epizootics of anthrax (Fuller, 1961), and these diseases may result in a depression of population quality and effect a delay in eruption of the dentition (Geist, 1971*b*).

Tooth wear characteristics have been suggested for aging bison of 5.5 years of age and older (Frison and Reher, 1970). However, the accuracy of this method is subject to serious error when applied to other ungulates (Erikson *et al.*, 1970; Gilbert and Stolt, 1970).

TABLE 4.—*Skull measurements of 3.5-year-old male bison from Elk Island National Park. Measurements and symbols as in Table 1.*

Measurements	N	Mean	SD	CV	Range
(1)	10	553.3	31.96	5.78	510 – 585
(2)	10	580.6	24.66	4.25	548 – 615
(3)	12	198.8	14.72	7.40	172 – 225
(4)	12	263.2	18.29	6.94	233 – 305
(5)	12	166.8	16.44	9.85	139 – 198
(6)	12	68.8	4.78	6.95	61 – 76
(7)	12	220.8	12.57	5.70	199 – 240
(12)	12	71.8	3.61	5.03	67 – 79
(13)	10	211.6	10.06	4.75	195 – 225
(8)	9	223.1	7.08	3.17	212 – 234
(9)	9	118.6	2.65	2.24	116 – 123
(10)	10	93.0	3.59	3.86	86 – 97
(11)	10	131.1	4.04	3.08	122 – 137
(14)	13	251.5	10.65	4.24	232 – 268
(15)	13	271.4	9.58	3.53	255 – 286
(16)	13	192.3	9.86	5.13	176 – 212
(17)	12	163.3	8.88	5.44	146 – 180
(18a)	11	108.4	6.67	6.15	99 – 123
(18b)	12	89.8	5.59	6.23	82 – 100
(19)	13	154.0	6.07	3.94	145 – 168
(20)	13	97.0	3.96	4.08	91 – 105
(O–P)	12	494.6	10.84	2.19	478 – 515
(F–P)	10	448.6	9.38	2.09	436 – 463
(O–T)	12	403.6	9.69	2.40	386 – 418
(O–N)	12	227.7	8.64	3.79	216 – 245
(M–P)	13	127.2	3.83	3.01	120 – 135
(N–T)	12	187.4	6.63	3.54	177 – 199
	Indices				
Horn-core curvature	12	158.3	8.26	5.22	148.0 – 175.0
Horn-core compression	12	95.8	4.76	4.97	90.3 – 104.4
Horn-core proportion	12	90.1	4.23	4.70	82.0 – 95.5
Horn-core length	12	79.5	5.23	6.59	69.4 – 86.5
Toothrow proportion	10	34.3	1.23	3.59	33.1 – 37.1

In light of aging techniques used for a number of ungulates, counts of the annual cementum rings would appear to be a relatively accurate method (Taber, 1963) free from the above mentioned problems. Wenchell (1963) using incisor teeth in this technique, could draw no useful conclusions as to its validity for aging bison, whereas Novakowski (1965) found that cementum layers of the fourth premolar were valuable criteria for aging bison 5.5 years and older.

The major limitation of relying on criteria of the teeth for aging individuals is that for fossil and many Recent specimens the alveolar region is rarely complete or even partially intact. The cranial region most frequently pre-

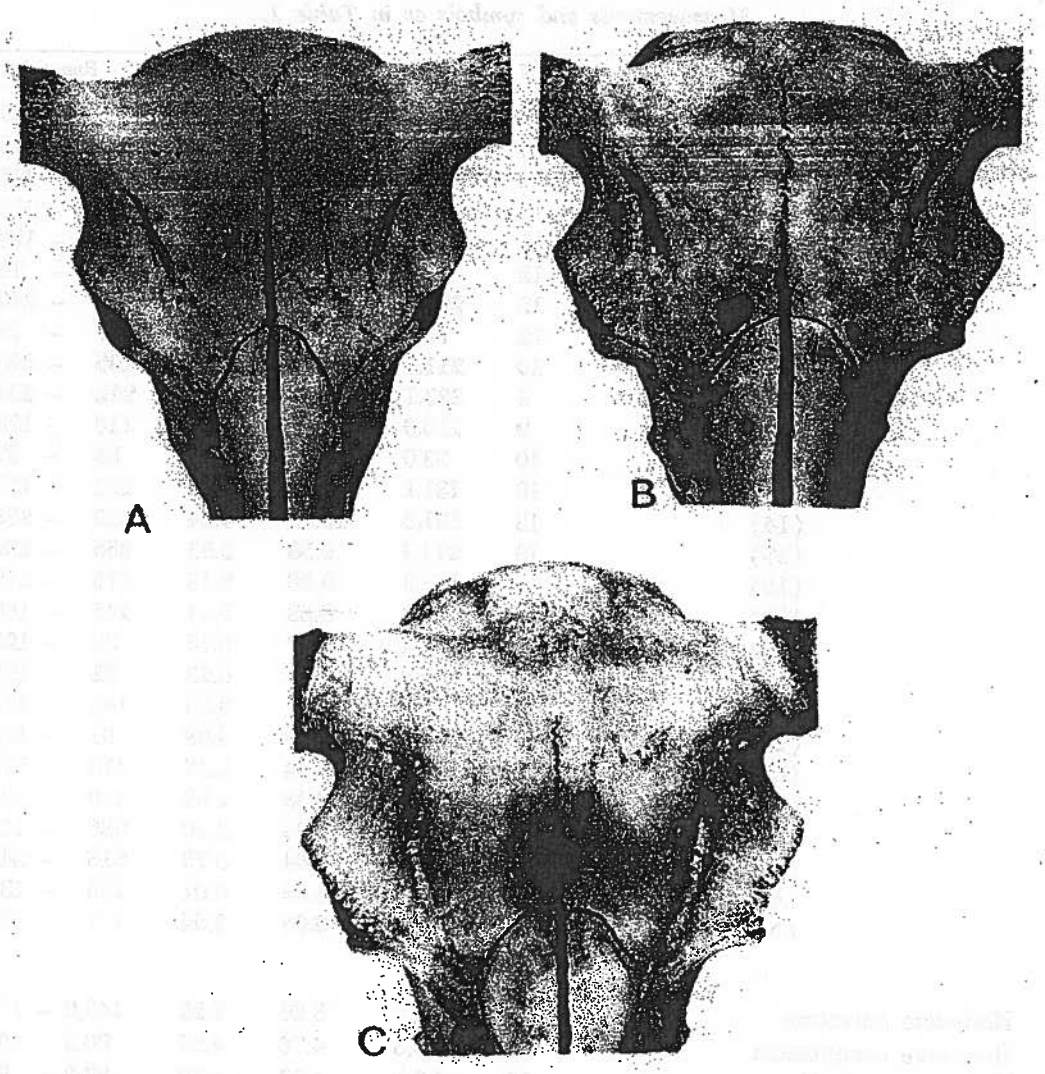

FIG. 3.—Dorsal views of skulls of 3.5-year-old male (A) showing unfused parietofrontal and frontal sutures, and smooth orbital rims, 4.5-year-old male (B) with partial fusion of parietofrontal suture, unfused frontal suture, and roughened orbital rims, and 8.5-year-old (adult) male (C) with fusion of parietofrontal and frontal sutures, and orbital rugosities. (All photographs to same scale).

served is that portion comprised of frontals, occipital region, and horn-cores. Our data indicate that two of the characters used by Skinner and Kaisen (1947) to describe the "fully mature—S3 class," proved very useful in separating adult (5.5 years and older) males from subadults. These were the degrees of fusion of the parietofrontal sutures and the frontal suture. Fusion of the former sutures began in a number of 4.5-year-old males from Elk Island, but did not extend along the common frontal suture until the males were 5.5 years of age (Fig. 3). These would appear to be useful criteria for

separating adult-subadult males when teeth are missing. Other cranial dimensions show too great an overlap in their ranges for distinctly separating males (Tables 1, 3, and 4).

As shown in Tables 3 and 4, no distinct separations occur between 3.5 and 4.5 year-old males, although one of these plus a qualitative character, may have some use in separating these age groups. The ranges of measurement 15 (Tables 3 and 4) for these two age classes showed the least amount of overlap, and the degree of orbital rim rugosity differed markedly. This difference in the smooth orbital rim of 3.5 year males compared to the roughened rims of the 4.5 year males is shown in Fig. 3.

The differences in orbital protrusion for subadult and adult males supports Guthrie's (1966*b*) hypothesis regarding orbital protrusion and amount of facial hair. Orbital protrusion increases with increasing age (Table 1, 3 and 4) in males, and during ontogeny the amount of facial hair increases, reaching a maximum at 6 or 7 years of age (McHugh, 1972). At this stage the hair on the front face between the orbits may reach a length of over 30 centimeters, and higher on the skull may be sufficient to almost completely hide the horns.

Fusion of sutures was not as useful a criteria for separating female age classes. Fusion of the parietofrontal and frontal sutures is varied between females and does not appear to start until the animal is at least 5.5 years of age. For the archaeologist wishing to age kill-site samples to estimate the season of the kill, the biological importance of separating females older than 3.5 years may be limited. If one considers reproductive activity as a measure of maturity in females, this begins around 3.5 years of age, whereas males do not actively participate in the rut until they are at least 6.5 years of age (McHugh, 1958; Fuller, 1960; Shackleton, 1968).

Sexing the Elk Island sample by cranial dimensions proved straightforward. If the ranges of measurements 6, 12, and 14 are compared (Tables 1 to 4), it is clear that the two sexes show no overlap. These measurements are particularly useful because they occur in that portion of the skull most frequently preserved. Bulls of 2.5 years, though probably resembling adult females in a number of dimensions may still have larger horn cores, and will also undoubtedly differ in certain qualitative characters indicative of their "youth."

Lower Jaw Measurements

Measurements of the lower jaws are given for the four age-sex classes in Tables 5 to 8. The measurements made in addition to those of Butler *et al.* (1971) are included for comparative purposes with other studies, and for use with fragmentary material. For example, measurement 22 shows a high correlation ($r = 0.93$) with measurement 1, and may be useful as a substitute measure of the length of the lower jaw, when the fragile anterior region is damaged.

TABLE 5.—*Lower jaw measurements of adult female bison from Elk Island National Park. Symbols as in Table 1.*

Measurements*	N	Mean	SD	CV	Range
(1) Total length	35	386.0	11.39	2.95	352 – 405
(2) Total height	35	206.1	7.29	3.54	190 – 218
(3) Height at M_1	35	49.4	2.52	6.78	44 – 54
(4) Height at PM_2	35	41.5	2.81	6.78	36 – 49
(5) Length of diastema	35	119.5	5.53	4.63	108 – 130
(6) PM_2 to M_3, alveolar length	35	155.0	4.71	3.04	145 – 167
(7) M_1 to M_3, alveolar length	35	101.1	3.27	3.23	94 – 108
(8) Length of symphyseal surface	35	67.4	4.23	6.28	56 – 74
(9) Height of coronoid process	35	54.3	2.69	4.95	48 – 61
(10) Width of coronoid process at mandibular notch	35	44.7	1.51	3.37	41 – 47
(11) Width of articulating process at mandibular notch	35	74.1	3.01	4.06	69 – 81
(12) Posterior of M_3 to mandibular foramen	35	60.7	5.51	9.08	44 – 70
(13) Posterior of M_3 to posterior edge of articulating process	35	149.4	6.37	4.27	130 – 162
(14) Width of ramus at posterior of M_3	35	28.5	1.60	5.60	26 – 34
(15) Width of ramus at posterior of M_3	35	28.9	1.51	5.23	26 – 33
(16) Width of mandibular condyle	35	47.0	2.11	4.48	42 – 50
(17) M_2 alveolar to base height	35	59.8	3.02	5.05	54 – 68
(18) Width M_3	35	17.4	1.31	7.54	15 – 20
(19) Width M_2	35	18.1	1.32	7.31	15 – 20
(20) Width M_1	35	17.1	.95	5.56	15 – 19
(21) PM_2 to M_1	35	52.8	2.35	4.45	49 – 58
(22) Substitute total length	35	336.2	11.17	3.32	310 – 365
(23) Substitute diastema length	35	61.1	5.96	9.75	47 – 70
(24) Diastema width	35	15.9	1.18	7.36	14 – 19

* Measurements and numbers follow Butler *et al.* (1971).

Unfortunately, no useful comparisons can be made between the Elk Island material and the lower jaw data presented by Butler *et al.* (1971), because the latter authors believed that they had a mixed sample of *B. b. bison*, *B. antiquus*, and *B. occidentalis*, which they were unable to separate.

TABLE 6.—*Lower jaw measurements of adult male bison from Elk Island National Park. Measurements as in Table 5 and symbols as in Table 1.*

Measurements	N	Mean	SD	CV	Range
(1)	76	415.2	10.00	2.41	390 – 435
(2)	76	222.6	7.51	3.37	200 – 245
(3)	76	53.0	3.03	5.71	45 – 60
(4)	76	46.3	2.62	5.66	39 – 52
(5)	76	130.6	5.80	4.45	117 – 145
(6)	76	158.0	5.54	3.48	144 – 170
(7)	76	103.1	4.09	3.97	92 – 112
(8)	76	77.0	5.28	6.87	67 – 95
(9)	76	58.7	3.43	5.84	52 – 67
(10)	76	47.9	3.11	6.49	40 – 59
(11)	76	82.6	3.83	4.64	76 – 92
(12)	76	74.9	5.18	6.92	62 – 87
(13)	76	174.0	6.38	3.67	160 – 190
(14)	76	30.0	1.61	5.41	26 – 34
(15)	76	30.5	1.53	5.0	26 – 35
(16)	76	50.9	2.93	5.76	43 – 57
(17)	76	62.9	2.98	4.74	56 – 70
(18)	76	18.3	1.25	6.80	15 – 21
(19)	76	19.0	1.23	6.50	16 – 22
(20)	76	17.7	.87	4.94	16 – 20
(21)	76	54.9	2.92	5.32	48 – 61
(22)	76	361.1	7.32	2.03	342 – 375
(23)	76	65.8	5.04	7.67	54 – 76
(24)	76	19.2	1.76	9.16	17 – 29

As shown in Tables 5 to 8, the lower jaws, unlike the crania, provide no clear criteria for separating the sexes. Only measurement 13 (Table 5) showed almost no overlap in the ranges of the two adult sexes (Tables 5 and 6). Five individuals fell in the zone of overlap of this dimension, which ranged from the minimum value for adult males of 160 mm to the maximum value for adult females of 162 mm. If measurement 13 had been used to distinguish sexes of adult plains bison, only 4.5 percent would have been incorrectly identified. This error may be acceptable where no other criteria are available, or as a check of separation by metapodial dimensions. Although this measurement, along with others, are similar in magnitude between adult females and subadult males (3.5 years and older) (Tables 5, 7, and 8), the sexes may still be distinguished. Where a specimen is similar in size to the values for measurement 13 of adult females, but lacks adult dentition, it would be classed as a subadult male older than 3.5 years. Subadult females would be smaller. Specific age of specimens, after sexing, would then obviously be determined by tooth wear and eruption sequence.

Both correlations and discriminant function analyses were applied to the lower jaw data in an attempt to identify more useful criteria for separating

TABLE 7.—*Lower jaw measurements of 4.5-year-old male bison from Elk Island National Park. Measurements as in Table 5 and symbols as in Table 1.*

Measurements	N	Mean	SD	CV	Range
(1)	8	406.5	11.94	2.94	390 – 424
(2)	8	215.3	7.65	3.55	205 – 227
(3)	8	49.8	2.82	5.66	46 – 53
(4)	8	42.9	2.53	5.91	40 – 47
(5)	8	125.9	5.14	4.08	117 – 132
(6)	8	163.9	3.44	2.10	160 – 168
(7)	8	104.6	2.72	2.60	101 – 108
(8)	8	71.3	6.48	9.09	60 – 78
(9)	8	57.5	3.42	5.95	52 – 63
(10)	8	48.8	1.39	2.85	47 – 50
(11)	8	81.4	3.50	4.30	76 – 85
(12)	8	68.4	7.25	10.60	59 – 82
(13)	8	163.4	11.49	7.03	149 – 184
(14)	8	29.5	.54	1.81	29 – 30
(15)	8	30.1	1.46	4.83	28 – 32
(16)	8	49.8	1.83	3.68	47 – 53
(17)	8	62.8	3.24	5.16	58 – 67
(18)	8	16.9	.84	4.94	16 – 18
(19)	8	17.5	1.20	6.83	16 – 20
(20)	8	17.1	.64	3.74	16 – 18
(21)	8	58.1	2.42	4.16	54 – 62
(22)	8	358.1	7.40	2.07	346 – 370
(23)	8	63.5	5.66	8.91	57 – 74
(24)	8	17.3	1.04	6.00	16 – 19

the lower jaws of the various age-sex classes. Neither of these methods added to the precision provided by measurement 13 alone. When butchered material from archaeological sites are considered (Brumley, 1971), the fragmentation of the lower jaws adds complication to the problem.

Comparative data are obviously required from other populations of both modern plains bison and extinct forms, but it appears from the present study that the large number of measurements of the lower jaw may be unnecessary and may be reduced. Factor analysis may be a useful method to select the most valuable dimensions.

CONCLUSIONS

It was apparent from the material examined in the present study of a single population of plains bison that the horn-cores, traditionally used to separate North American bison, show the highest degree of variability. This therefore supports the feelings of Guthrie (1966*a*) with regard to their value as taxonomic characters. However, before any judgment can be made as to the value of horn-core characters, further studies are required to investigate

TABLE 8.—*Lower jaw measurements of 3.5-year-old males from Elk Island National Park. Measurements as in Table 5 and symbols as in Table 1.*

Measurements	N	Mean	SD	CV	Range
(1)	13	387.6	10.26	2.65	374 – 413
(2)	13	209.9	8.84	1.17	190 – 223
(3)	13	53.9	2.81	5.22	50 – 58
(4)	13	42.5	1.71	4.03	39 – 45
(5)	13	122.5	6.08	4.96	111 – 136
(6)	13	165.2	9.04	5.47	156 – 190
(7)	13	100.8	4.36	4.33	94 – 108
(8)	13	67.9	5.44	8.01	58 – 76
(9)	13	56.5	3.46	6.11	50 – 62
(10)	13	44.9	2.27	5.06	40 – 49
(11)	13	76.4	2.82	3.68	71 – 81
(12)	13	59.9	4.25	7.10	51 – 65
(13)	13	147.7	5.51	3.73	140 – 161
(14)	13	28.5	1.20	4.20	27 – 30
(15)	13	28.9	1.38	4.78	26 – 31
(16)	13	46.8	2.65	5.67	41 – 51
(17)	13	66.4	3.62	5.45	59 – 70
(18)	13	15.9	1.12	7.01	14 – 18
(19)	13	16.8	.73	4.32	15 – 18
(20)	13	16.5	1.05	4.38	15 – 18
(21)	13	61.6	3.38	5.49	57 – 66
(22)	13	341.6	9.05	2.65	330 – 360
(23)	13	61.9	5.71	9.22	49 – 72
(24)	13	16.6	1.33	7.97	15 – 19

both interpopulation and interspecific variability of these and other cranial characters.

Although the data presented here appear comparable to the sample described by Skinner and Kaisen (1947), evidence presented by Bohlken (1967) suggest a revision of the genus is required. This need is further supported by the data available for some extinct forms found in association with archaeological sites (Lorraine, 1968; Butler *et al.*, 1971), and is also suggested in the recent hypotheses of bison evolution presented by Guthrie (1970) and Geist (1971*a*).

Sexing fragmentary cranial material would appear to present little problem, and adequate aging of such material lacking teeth would also seem practical within limits. When lower jaw material is used, sexing is adequate only if teeth are present, because an estimate of age is necessary. Where natural or man-made fragmentation of the lower jaws occurs (Brumley, 1971), the problem becomes complicated. Until adequate comparative studies of other forms of bison are made, problems will also arise where separation of different types of bison is difficult (Butler *et al.*, 1971).

Acknowledgments

The authors wish to express their thanks to the Superintendent, the Chief Park Warden, and to other personnel of Elk Island Park, to Mr. B. Rottenfusser for his assistance in preparing the skulls, to Ms. E. Earle for assistance in data collection, and to Dr. V. Geist for his criticisms. This study was supported by an NRC Grant to Dr. L. V. Hills.

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NORTH AMERICAN BISON

THEIR CLASSIFICATION AND EVOLUTION

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UNIVERSITY OF CALIFORNIA PRESS
Berkeley Los Angeles London

MORPHOLOGICAL VARIATION AND VARIABILITY

Genotypic and phenotypic variation are qualities of sexually reproducing populations and the source material for the evolution of species. This chapter presents information on selected facets of phenotypic variation and variability observed among bison skulls and limb bones, including patterns of continuous variation within each sex of each taxon, sexual dimorphism, allometry, variability of characters, and chroroclines, in order to illustrate generalized patterns of variation.

This chapter presents data on all specifically identified skulls that yielded biometric information and selected postcranial samples. The taxonomic identity of postcranial samples has been determined for historic period collections (Homaday, Richardson and Elliot, Rowan, and so on) and numerous archeologic samples with associated horn cores and good provenience information, as well as a few individual fossil bison found with skull and limb bones articulated. Many postcranial samples have not, however, been positively identified. These samples are of two types: those which probably contain bones predominantly, if not entirely, of one taxon (Rancho La Brea, Big Bone Lick, Dows Bog, Minnesota bogs); and those that predominantly contain bones representing two or more taxa (American Falls region, Fairbanks area, Dawson area).

The *B. b. bison* limb sample used in this chapter consists of the Homaday, Richardson and Elliot, Buffalo Creek, Dows Bog, Glenrock, Rocky Ford, Bonfire (bed 3), Sitter Ranch, Lubbock Lake (Archaic and late Prehistoric levels), Southern Plains Archaic, and Big Bone Lick collections. The *B. b. athabascae* limb sample has been assembled from several individual specimens. *B. a. antiquus* limbs are from Rancho La Brea, Blackwater Draw, and Big Bone Lick. *B. a. occidentalis* limbs are from Lindenmeier, Jones-Miller, Bonfire (bed 2), Lubbock Lake (Clovis and Folsom levels), Folsom, Olsen-Chubbock, Des Moines, Casper, Agate Basin, Finley, Jurgens, Hudson-Meng, Plainview, James Allen, Wasden and Hawken archeological sites, and Minnesota bogs and Interstate Park Bog sites.

Few *B. latifrons* limb bones have been positively identified (tables 44 and 45). Many skulls and isolated limb bones have been found around American Falls Reservoir in southeast Idaho. A majority of the identifiable skulls found here (25 of 34; cf. tables 19, 23, 39, and 41) belongs to *B. latifrons*. The majority of limb bones probably also belongs to *B. latifrons*, although limbs of all other species (especially *B. alaskensis*) are also probably present. The

Table 44

Measurements of *Bison latifrons* Skulls with Articulated Limb Bones

Standard measurement	IMNH VP 27[a]	IMNH VP 26594	IMNH VP 26602[a]	UF VP 7559[b]
Spread of horn cores, tip to tip	1888 mm	.....	1830 mm	(1342 mm)
Horn core length, upper curve, tip to burr	870 mm	519 mm	930 mm	(795 mm)
Straight line distance, tip to burr, dorsal horn core	.....	506 mm	890 mm	.....
Dorso-ventral diameter, horn core base	.....	107 mm	175 mm	145 mm
Minimum circumference, horn core base	.....	316 mm	560 mm	(414 mm)
Width of occipital at auditory opening	330 mm	.....	.....	.....
Width of occipital condyles	.....	.....	155 mm	.....
Antero-posterior diameter, horn core base	160 mm	97 mm	175 mm	(126 mm)
Least width of frontals, between horn cores and orbits	330 mm	.....	.....	368 mm
Greatest width of frontals at orbits	.....	.....	.....	430 mm
$M^1 - M^3$, inclusive alveolar length	.....	.....	.....	.....
M^3, maximum width, anterior cusp	.....	.....	.....	.....
Distance, nuchal line to tip of premaxillae	.....	.....	.....	.....
Distance, nuchal line to nasal-frontal suture	340 mm	.....	.....	.....

Sources:
[a]John A. White, field notes, August 9, 1975;
[b]Robertson, 1974.
Note: Figures in parentheses are estimates. UF VP 7559 is not fully mature.

Table 45
Measurements of *Bison latifrons* Limb Bones Articulated with Skull Material

Standard measurement	IMNH VP 27[a]	IMNH VP 26594	IMNH VP 26602[a]	UF VP 7559[b]
Humerus:				
Approximate rotational length of bone	394 mm	.....	.....	379 mm
Antero-posterior diameter of diaphysis	86 mm	.....	.....	73 mm
Transverse minimum of diaphysis	68 mm	.....	.....	60 mm
Radius:				
Approximate rotational length of bone	384 mm	(366 mm)	.....	362 mm
Antero-posterior minimum of diaphysis	46 mm	37 mm	.....	41 mm
Transverse minimum of diaphysis	72 mm	64 mm	.....	65 mm
Metacarpal:				
Total length of bone	249 mm	.....	.....	241 mm
Antero-posterior minimum of diaphysis	37 mm	.....	.....	35 mm
Transverse minimum of diaphysis	69 mm	.....	.....	58 mm
Femur: (no articulated specimens available)				
Tibia:				
Approximate rotational length of bone	464 mm	.....	.....	459 mm
Antero-posterior minimum of diaphysis	54 mm	.....	.....	46 mm
Transverse minimum of diaphysis	69 mm	.....	.....	63 mm
Metatarsal:				
Total length of bone	302 mm	.....	310 mm	286 mm
Antero-posterior minimum of diaphysis	40 mm	.....	42 mm	37 mm
Transverse minimum of diaphysis	54 mm	.....	52 mm	48 mm

Sources:
[a]John A. White, field notes, August 9, 1975;
[b]Robertson, 1974.
Note: The figure in parentheses is an estimate. Robertson (1974) provides measurements for other postcranial bones of UF VP 7559 (which is not fully mature).

American Falls Reservoir area sample (which does not include specimens from Minidoka County) represents the closest approximation to *B. latifrons* limb size and variation possible at this time. True *B. latifrons* limb dimensions would possibly average slightly larger than the mean dimensions reported in the American Falls area sample.

B. priscus and *B. alaskensis* limb bones have not been positively identified from North America, but limb bones of both species (and hybrid individuals) are certainly present in the various Beringian samples. Here limb bones from the sexable Old Crow River and Lost Chicken Creek collections are grouped into a single sample. This sample is probably representative of *B. priscus* limb size. The Fairbanks and Yukon areas samples could not be adequately sexed because there was no bimodal clustering of cases within these samples. Both of these samples probably contain undifferentiable limb bones of *B. priscus*, *B. alaskensis*, and hybrid bison, but the samples do provide some indication of the overall range of limb sizes which occurred in Beringia and can therefore be used to approximate the upper and lower limits of limb bone variation among the various species known to have inhabited the region.

CONTINUOUS VARIATION

Continuous variation among phenotypes is characteristic of mammalian populations. Usually, phenotypic characters are normally or near normally distributed within populations and usually, skull characters are more variable than postcranial characters (Olsen, 1964; Yablokov, 1974). I will discuss the nature of case distribution within samples, the relationship between sample

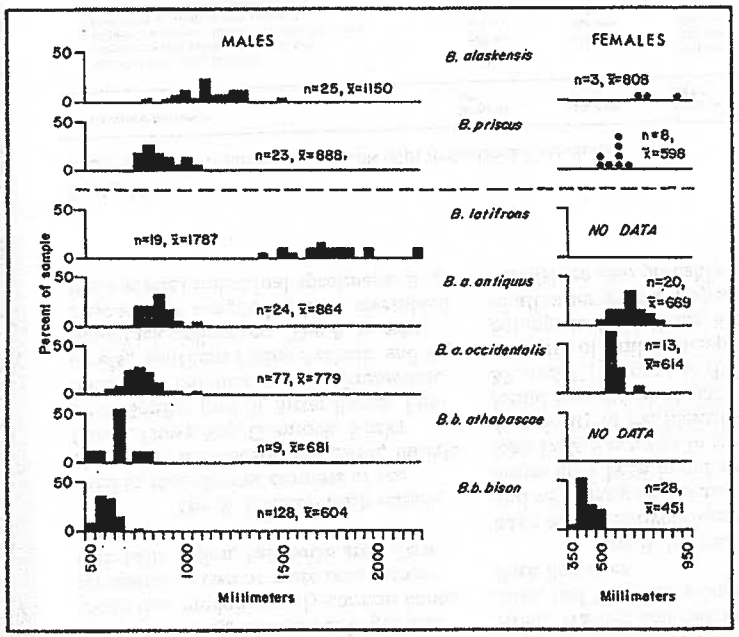


FIGURE 30 Frequency distribution: spread of horn cores, tip to tip.

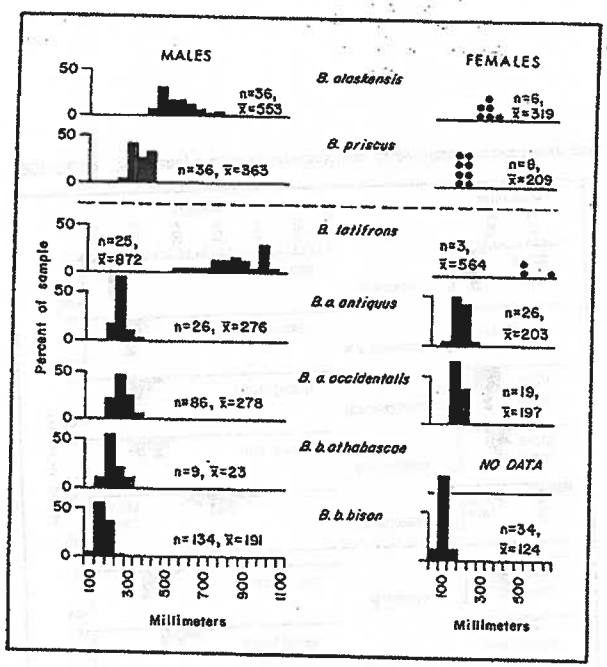


FIGURE 31 Frequency distribution: horn core length, upper curve, tip to burr.

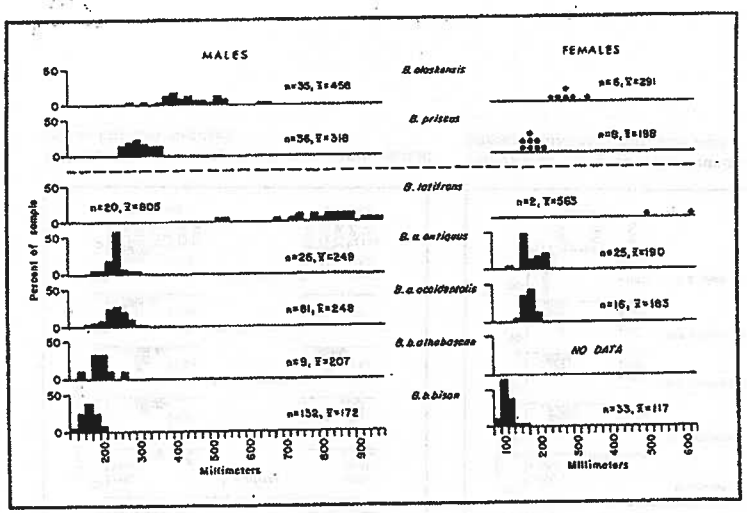


FIGURE 32 Frequency distribution: horn core length, straight line, tip to burr.

means and absolute ranges, and the direction and magnitude of skew. Patterns of variation observed in *B. b. bison*, both sexes of which are represented by large sample sizes, are useful as reference standards. Patterns of variation in other taxa need not, however, be identical to those observed for *B. b. bison*, and the small sample size for some characters needs to be kept in mind when evaluating variation.

Frequency distributions of linear skull variates are illustrated in figures 30 to 44. Most samples are normally or near normally distributed, although variations in the degree and direction of kurtosis and skew are apparent. Generally, the larger the character, the greater is the observed range of variation (fig. 57). The greater the range, the lower is the observed kurtosis. Both positive and negative skewing are evident in figures 30 to 44.

Frequency distributions of limb lengths are illustrated in figures 45 to 50. Limb bone lengths are usually normally or near normally distributed and show less kurtotic variation and skew than do skull variates. As was true for skulls, the larger the character the greater the observed range (fig. 58). *B. a. occidentalis*, however, is conspicuously more variable, skewed, and kurtotic than the preceding generalizations suggest should be the case. This pattern of distribution is probably due in great part to the evolutionary role of this taxon as the adaptive transition from *B. a. antiquus* to *B. bison*.

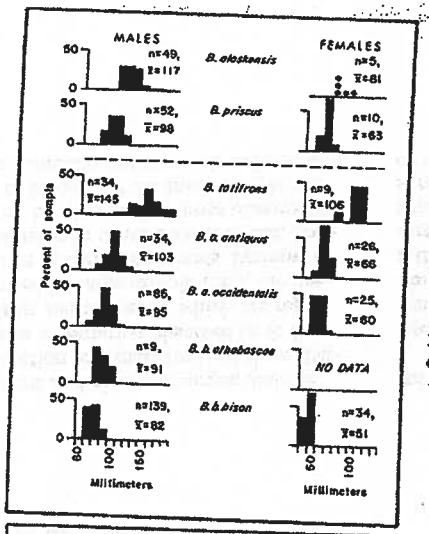


FIGURE 33 Frequency distribution: dorso-ventral diameter, horn core base.

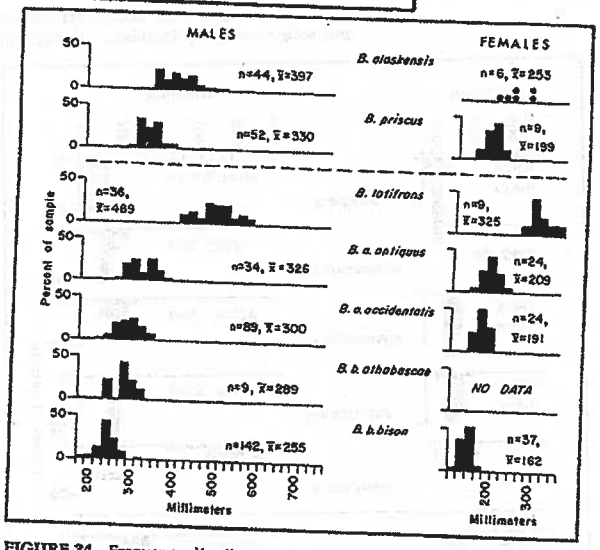


FIGURE 34 Frequency distribution: minimum circumference, horn core base.

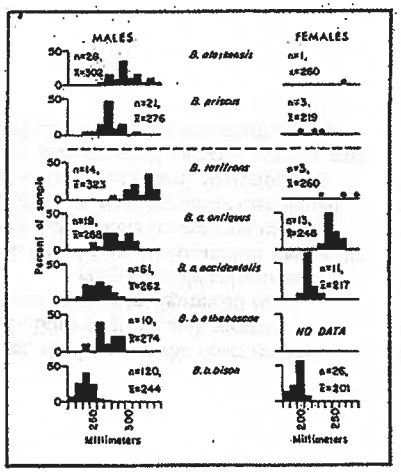


FIGURE 35 Frequency distribution: width of occipital at auditory openings.

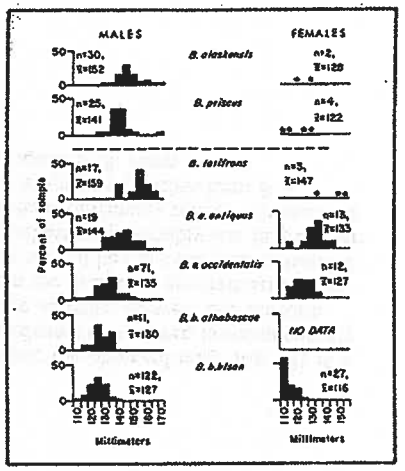


FIGURE 36 Frequency distribution: width of occipital condyles.

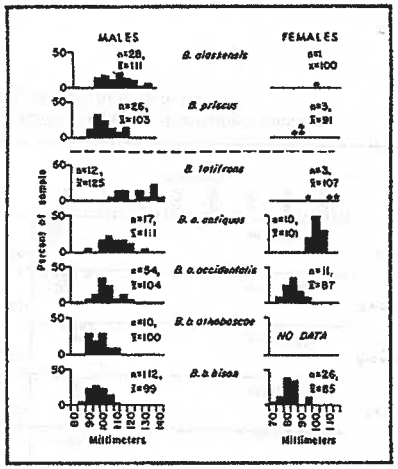


FIGURE 37 Frequency distribution: depth, nuchal line to foramen magnum.

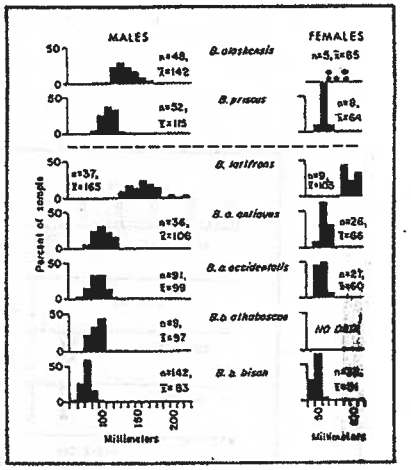


FIGURE 38 Frequency distribution: antero-posterior diameter, horn core base.

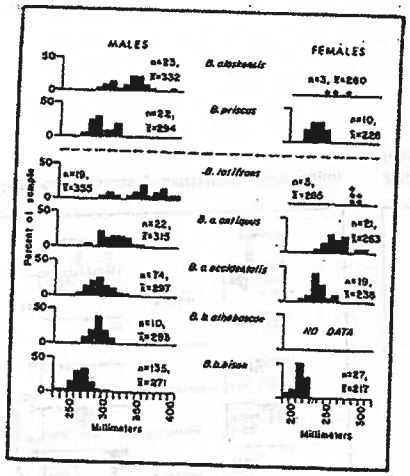


FIGURE 39 Frequency distribution: least width of frontals.

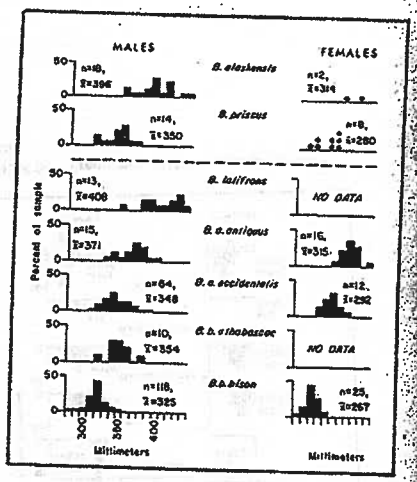


FIGURE 40 Frequency distribution: greatest width of frontals.

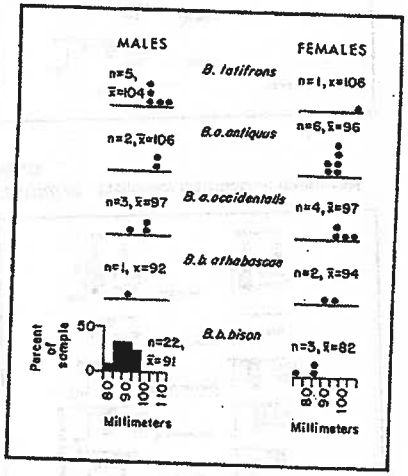


FIGURE 41 Frequency distribution: superior molar alveolar length.

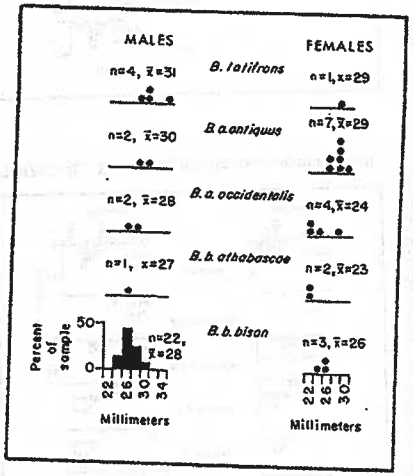


FIGURE 42 Frequency distribution: anterior M^3 cusp width.

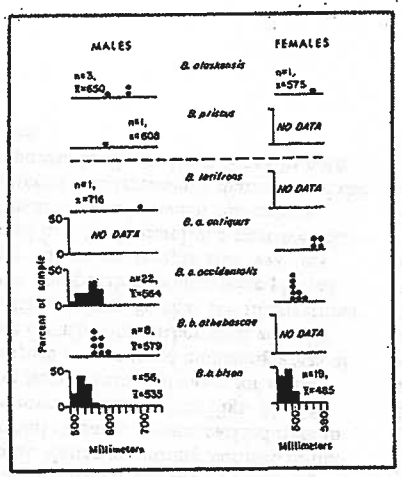


FIGURE 43 Frequency distribution: distance, nuchal line to tip of premaxillae.

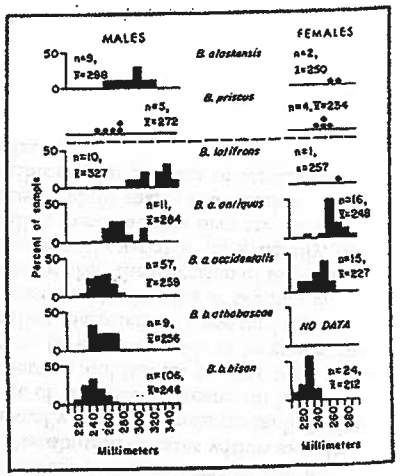


FIGURE 44 Frequency distribution: distance, nuchal line to nasal-frontal suture.

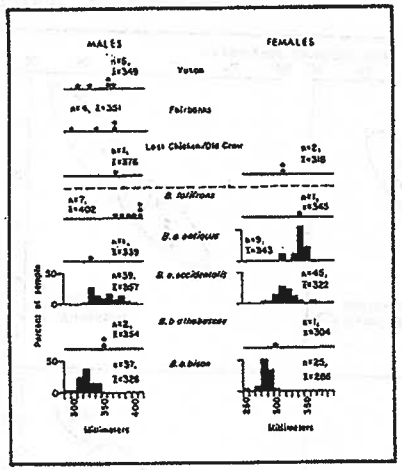


FIGURE 45 Frequency distribution: humerus length.

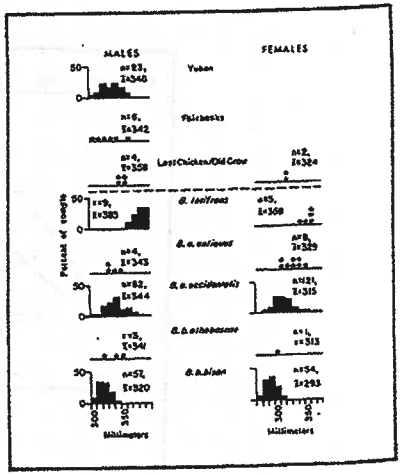


FIGURE 46 Frequency distribution: radius length.

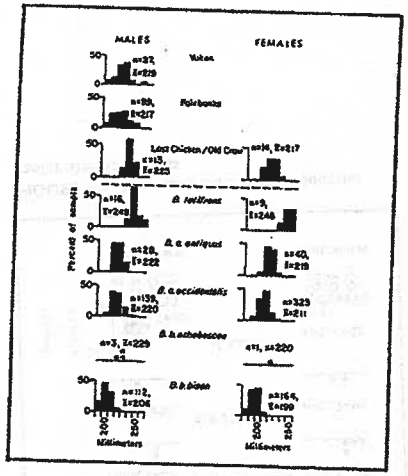


FIGURE 47 Frequency distribution: metacarpal length.

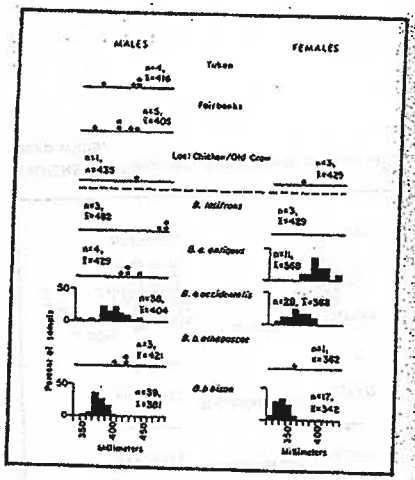


FIGURE 48 Frequency distribution: femur length.

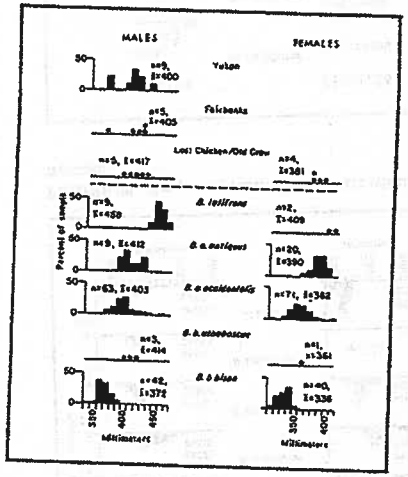


FIGURE 49 Frequency distribution: tibia length.

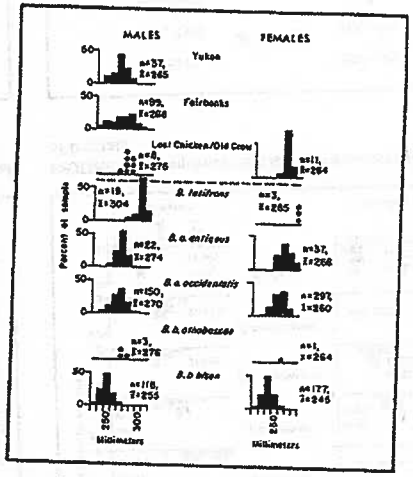


FIGURE 50 Frequency distribution: metatarsal length.

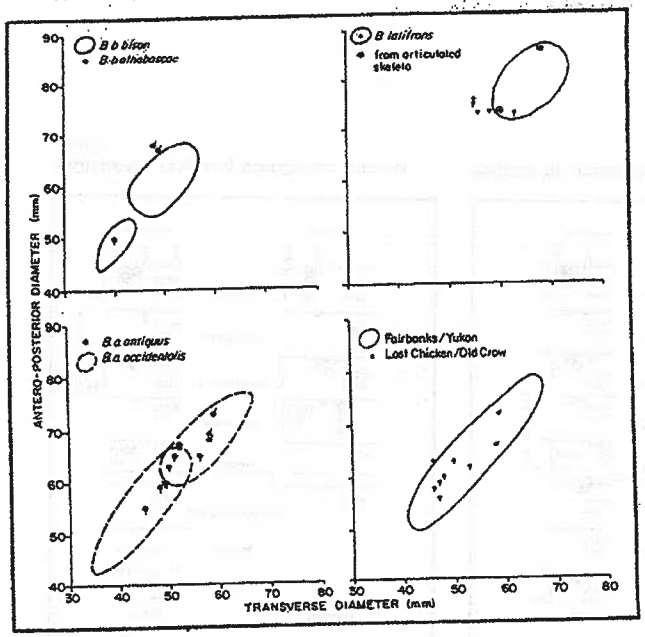


FIGURE 51 Bivariate distribution: humerus diaphysis.

Absolute variation among limb diaphysial variates is relatively small. Variation among samples of diaphysial variates is summarized here in the form of scatterplots (figs. 51–56). The large number of cases for some samples necessitated enclosing areas of case distribution rather than actually plotting points. So that the illustrations were comparable, points were plotted only where the sample size was very small ($n < 9$). Generally, a positive relationship exists between the antero-posterior and transverse diameters of the diaphysis in all six limb bones in both sexes.

Continuous variation among linear variates of bison skulls and limb bones may be summarized as follows: (1) Distribution of cases within samples is usually normal or near-normal; (2) the range of variation is greater for larger characters and less for smaller characters; (3) kurtosis tends to be greater for smaller characters and less for larger characters; (4) skewing of samples is common, but the direction of skew is unpredictably variable; (5) generally, the skull is more variable than are the limb bones; and (6) males and females exhibit similar patterns of continuous variation.

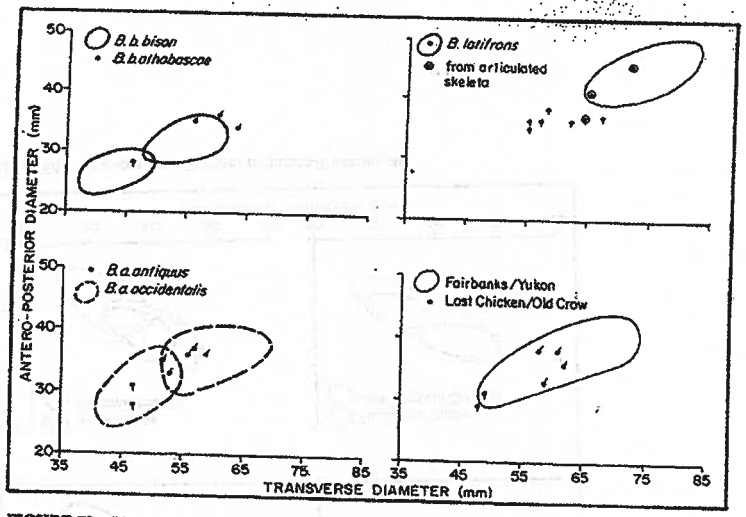


FIGURE 52 Bivariate distribution: radius diaphysis.

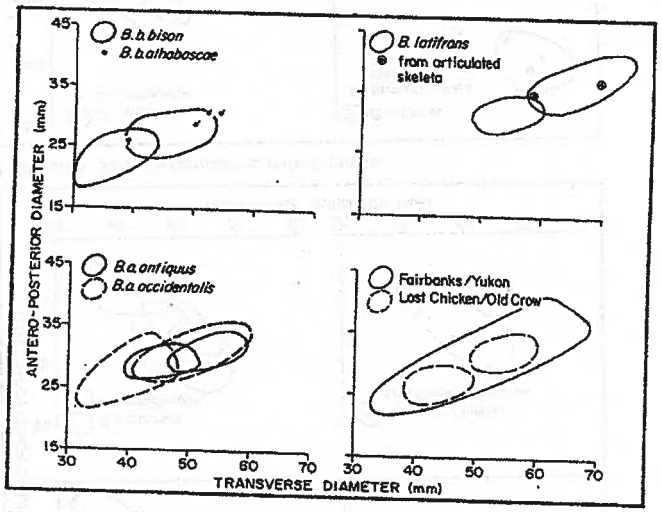


FIGURE 53 Bivariate distribution: metacarpal diaphysis.

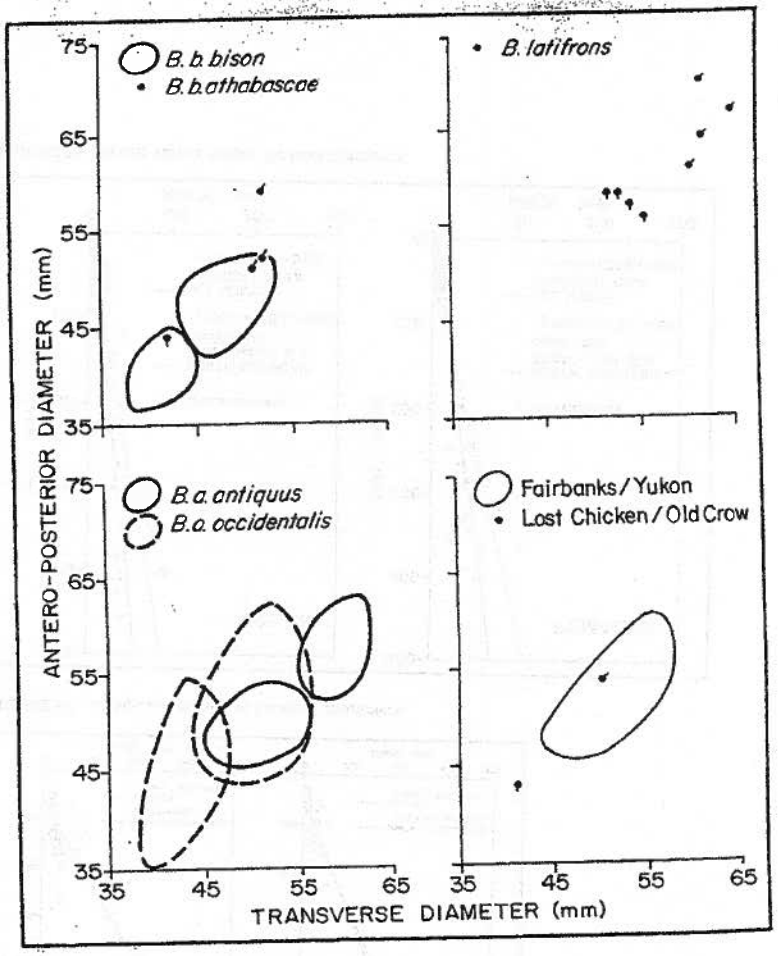


FIGURE 54 Bivariate distribution: femur diaphysis.

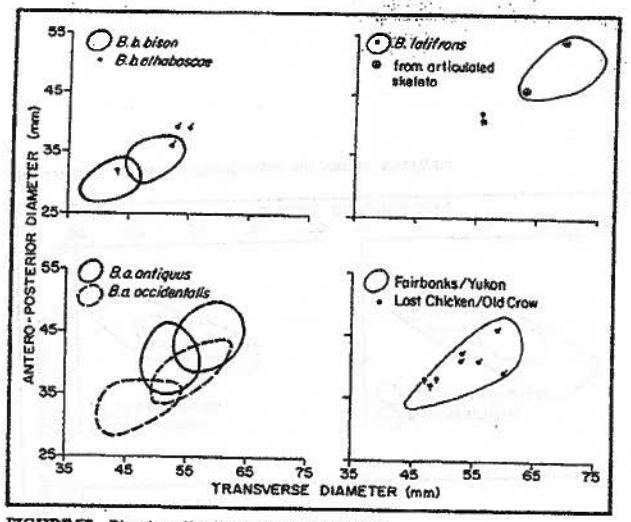


FIGURE 55 Bivariate distribution: tibia diaphysis.

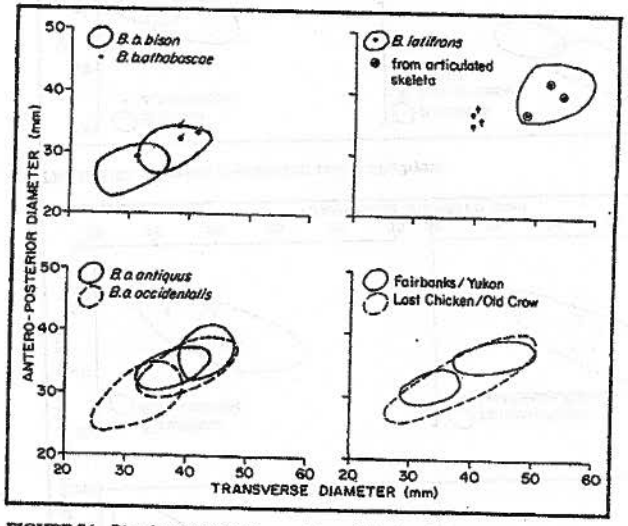


FIGURE 56 Bivariate distribution: metatarsal diaphysis.

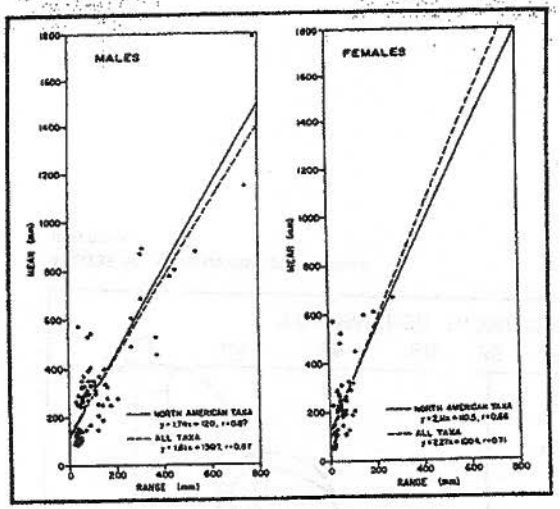


FIGURE 57 Means versus ranges for skull characters.

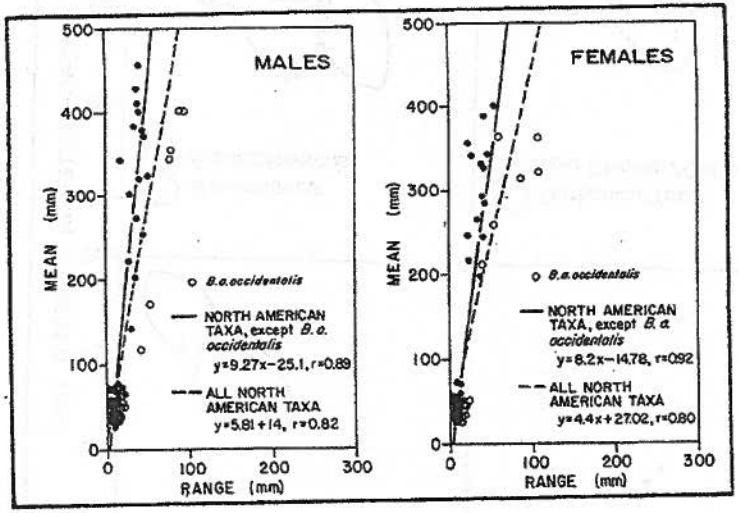


FIGURE 58 Means versus ranges for limb characters.

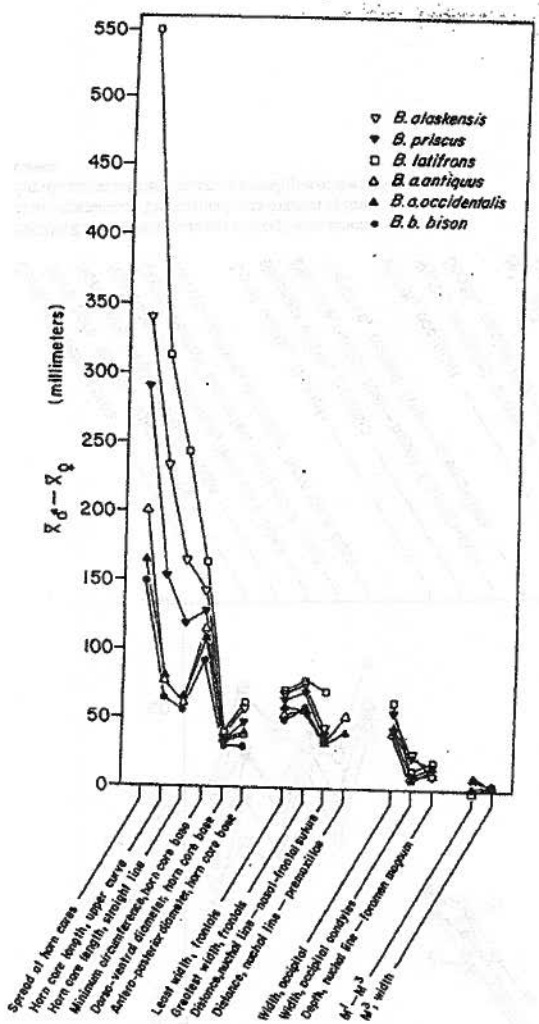


FIGURE 59 Absolute sexual dimorphism among skull characters.

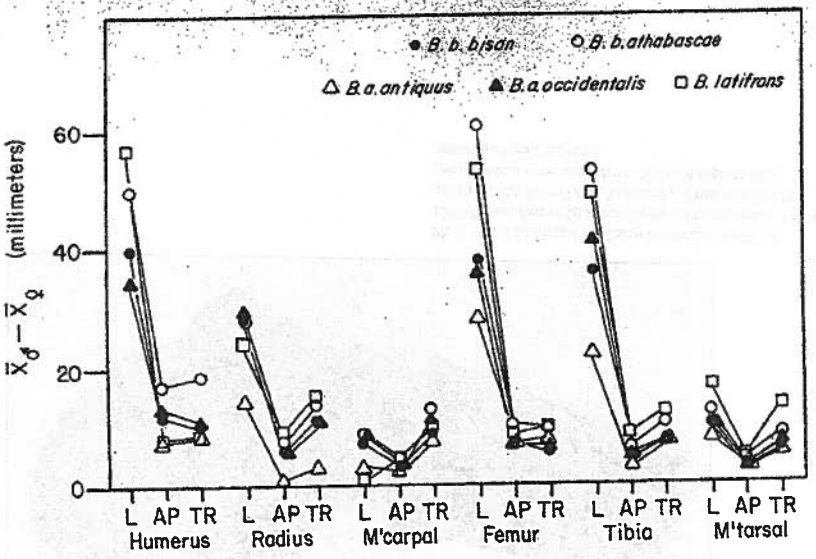


FIGURE 60 Absolute sexual dimorphism among limb characters.

SEXUAL DIMORPHISM

Sexual dimorphism is a usual characteristic of sexually reproducing organisms. The magnitude of both absolute and relative sexual dimorphism in characters of bison differs among characters within a taxon and among the various taxa. Absolute dimorphism in linear skull characters is generally greatest among horn core characters, less among facial and frontal characters, and least among occipital characters (fig. 59). Absolute dimorphism in limb bones is greatest for length and less for the two diaphysial diameters (fig. 60). In both limbs the most proximal bone shows greatest dimorphism and the most distal bone shows least dimorphism (figs. 45–56 and 60). Generally, in both skulls and limb bones the larger the character the greater the absolute dimorphism.

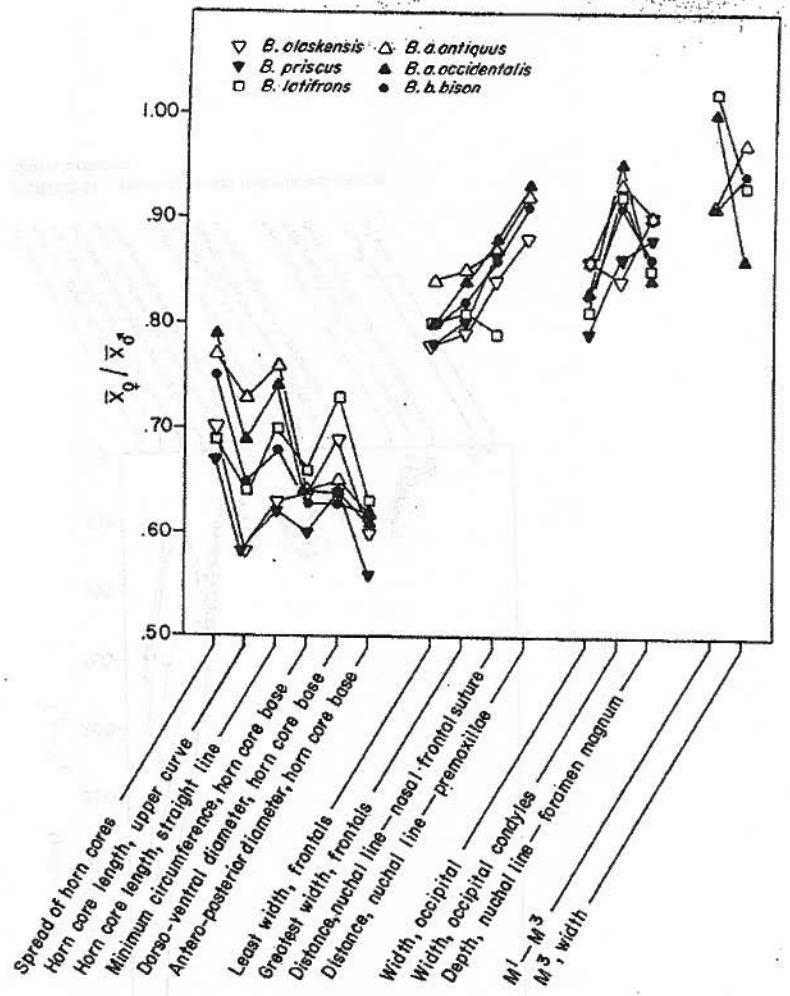
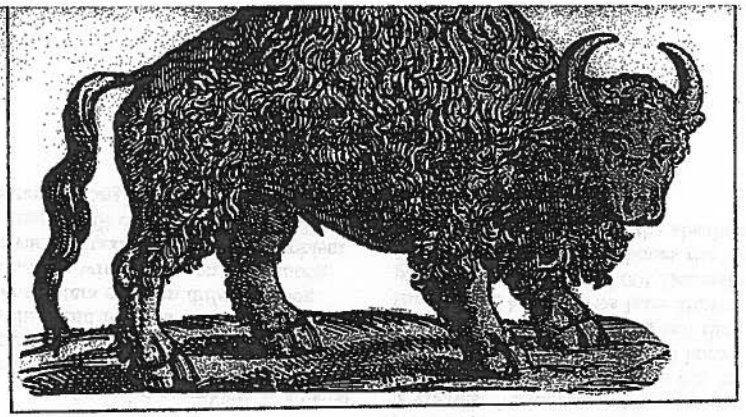
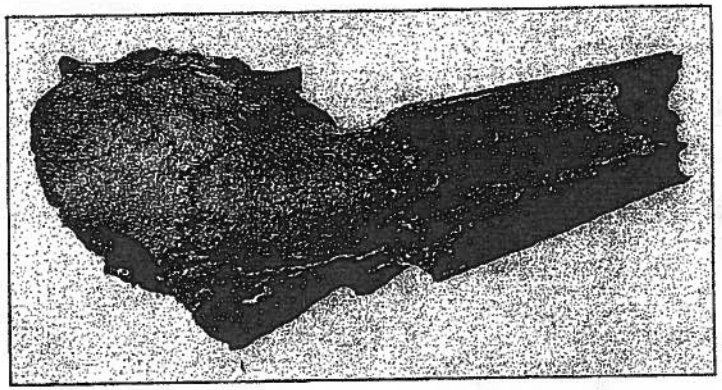


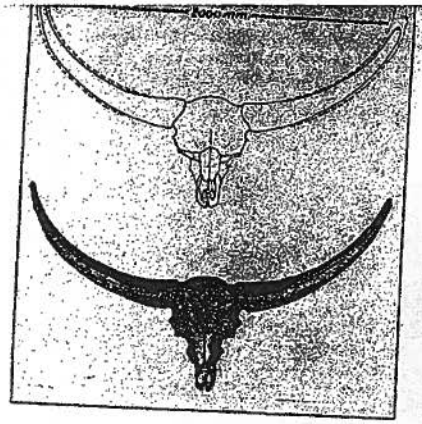
FIGURE 61 Relative sexual dimorphism among skull characters. The vertical axis expresses the female mean for each taxon as a multiple of the male mean.



Pl. 1 The Mexican bull, "*Taurus Mexicanus*," as pictured in Dr. Francisco Hernandez's natural history of Mexico (1651). Linnaeus used Hernandez's description as the type description for *Bos bison*, now *Bison bison*. *Bison bison* is the type species for the genus.

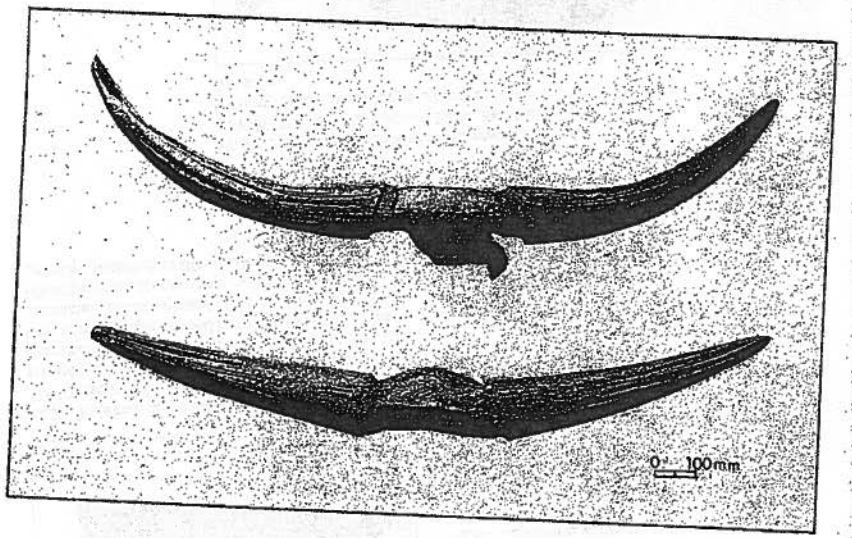


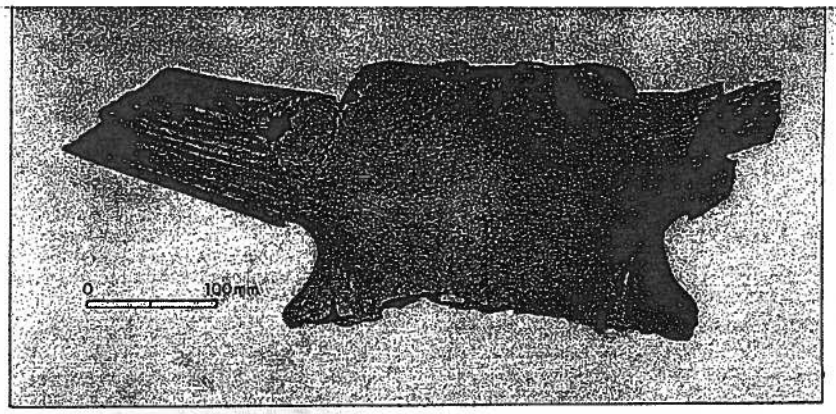
Pl. 2 The holotype of *Bison latifrons* (ANSP G 12993) was found in a small creek about twelve miles north of Big Bone Lick, Kentucky. This was the first fossil bison specimen from North America to be described and figured.



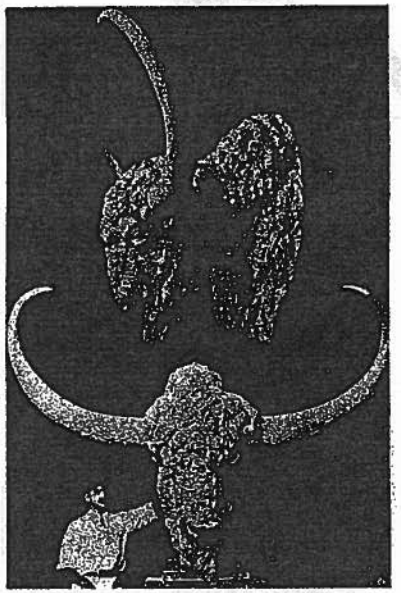
...known likeness of a *Bison latifrons* horn sheath occurred as a sand cast in association with this skull. This cast provided important information on the shape of the horn sheath and placement of the horn tips relative to other skull characters.

Pl. 4 Male *Bison latifrons* horn cores (AMNH VP 26828) from the Bradenton Canal, Manatee County, Florida, show typical horn core, frontal, and occipital characters.

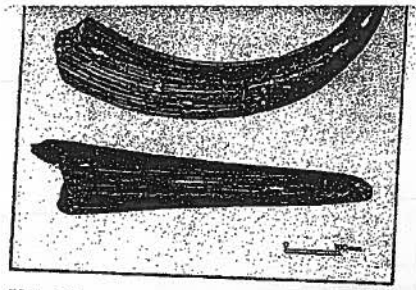




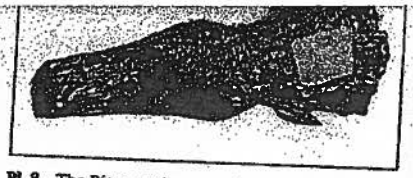
Pl. 5 Female *Bison latifrons* have more robust skulls and well defined burrs on the dorsal horn core than do females of other species. These characters show clearly on this skull (IMNH VP 17536) from the American Falls Reservoir in southeast Idaho.



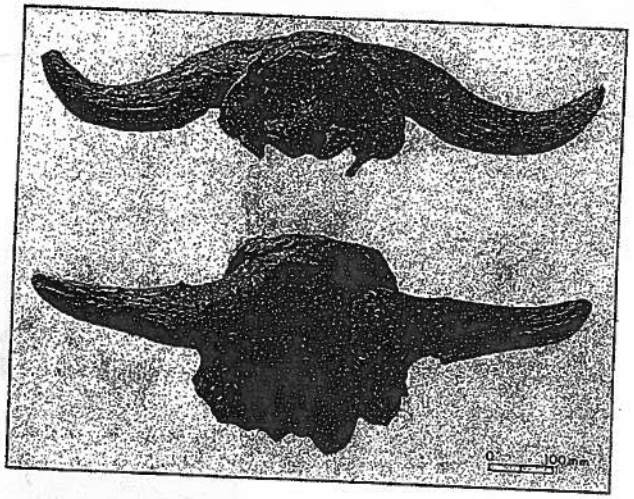
Pl. 6 This life size restoration of a *Bison latifrons* head was based on the MacArthur, California, skull (UCMP 4067) and associated horn sheath cast. *Bison bison* was used as a guide for this restoration, a circumstance which probably resulted in a model with more body hair and rearward rotation of the horns than was actually characteristic of *Bison latifrons*.



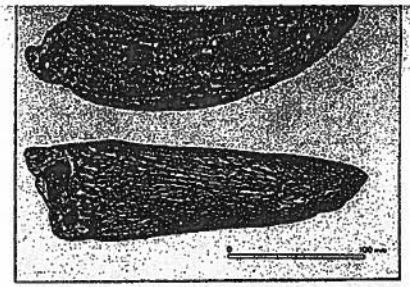
Pl. 7 This cast of the *Bison alleni* holotype (YPM VP 10910) shows typical *Bison latifrons* characters—straight posterior margin of horn cores, mildly spiraled growth around an arched axis, and an isosceles triangle shaped basal cross section. These characters are not typical of *Bison alaskensis* or *Bison priscus*, specimens of which have been frequently identified as *Bison alleni*.



Pl. 8 The *Bison antiquus antiquus* holotype (ANSP G 12990) is from Big Bone Lick, Kentucky. This specimen is actually atypical of the taxon. It possibly represents a *Bison antiquus* X *Bison priscus* hybrid, but *Bison antiquus* characters are dominant.

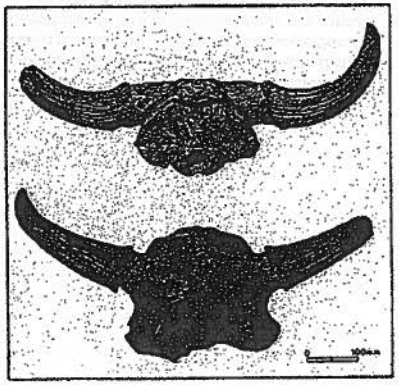


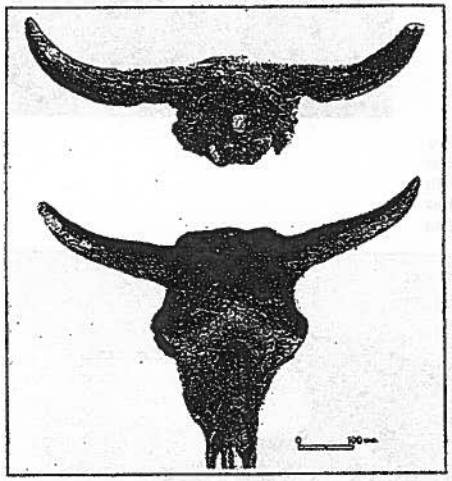
Pl. 9 This male *Bison antiquus antiquus* (TMM 30967-423) from the Tedford Farm, San Patricio County, Texas, is more typical of the taxon than is the holotype.



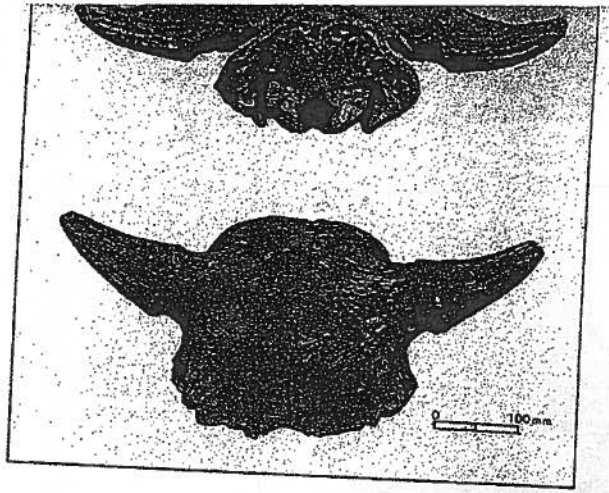
Pl. 11 The *Bison antiquus occidentalis* holotype (USNM P 4157) was found near Fort Yukon, Alaska, a fact that has contributed to the notion that "*Bison occidentalis*" originated in Alaska and thereafter dispersed southward into midlatitude North America. The model presented here maintains that *Bison antiquus occidentalis* originated in central North American and spread northward as far as Alaska during the early and middle Holocene.

specifically identifiable specimen of North American bison. Lucas (1899) thought this was the horn core of a sheep (*Ovis*), but it is actually an abnormal bison horn core not unlike other bison horn cores from tropical North America.

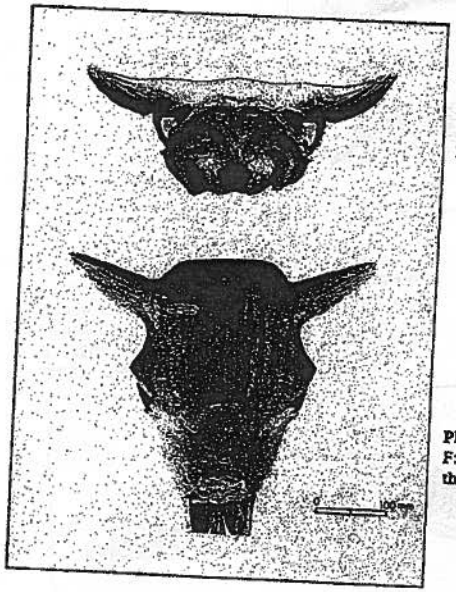




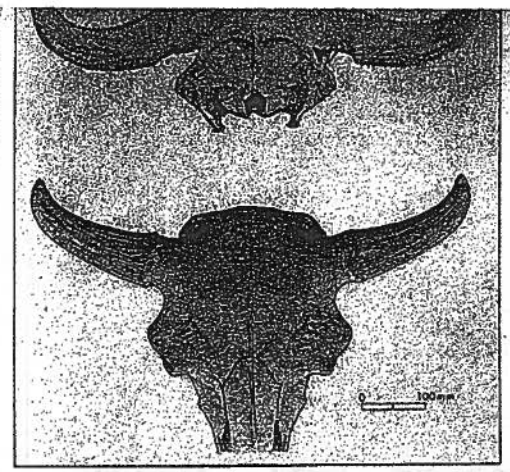
Pl. 12 A female *Bison antiquus occidentalis* (UNSM VP 30809) from the Scottsbluff archeological site, Nebraska.



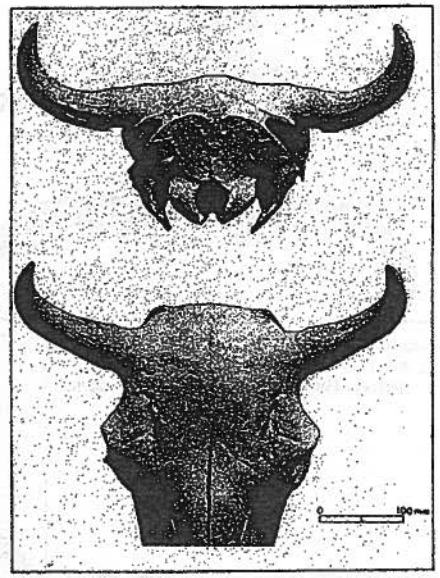
Pl. 13 *Bison bison bison* from the southern Great Plains were characterized by somewhat smaller body size and distinctly smaller horn cores than northern populations. This specimen (PPHM 619–14) is from Tierra Blanca Creek in the Texas panhandle, and shows horn core characters which might now be lost as a result of the commercial hunting during the 1870s which destroyed the southern plains population.



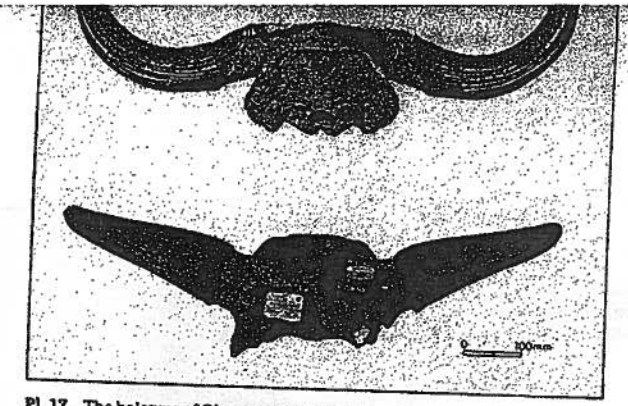
Pl. 14 A female *Bison bison bison* skull (AMNH VP F:AMSD109–2181) from Rocky Ford, a crossing of the White River, in Shannon County, South Dakota.



Pl. 15 The *Bison bison athabascae* holotype (NMC M 625) was shot in 1892 by an Indian about 50 miles southwest of Fort Resolution, Northwest Territories.

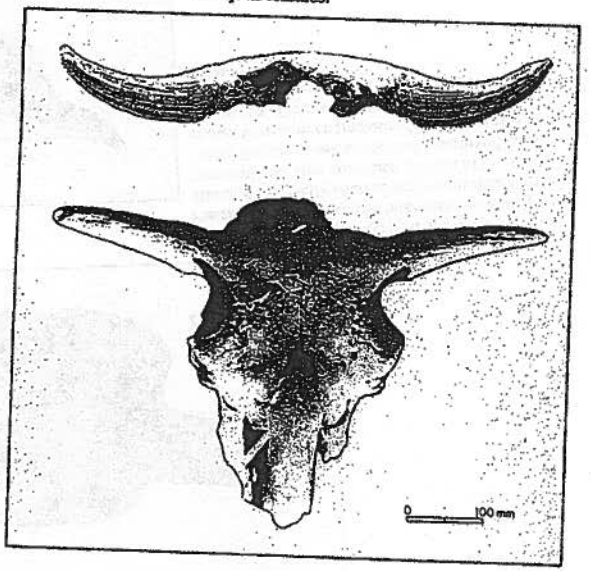


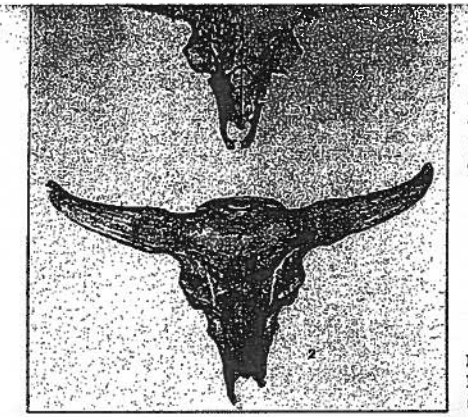
Pl. 16 More than 6,000 plains bison were released into Wood Buffalo National Park between 1925 and 1928, and most bison in the park are now considered plains X woods bison hybrids. This skull (AMNH M 98954) of an assumed hybrid female probably shows characters near those of true *Bison bison athabascae* females.



Pl. 17 The holotype of *Bison geisti* (AMNH VP F:AM46893), found near Fairbanks, Alaska, clearly shows characters typical of *Bison priscus*, with which it is here synonymized. *Bison priscus* is well represented in eastern Beringia, but specimens also occur in midlatitude and tropical North America.

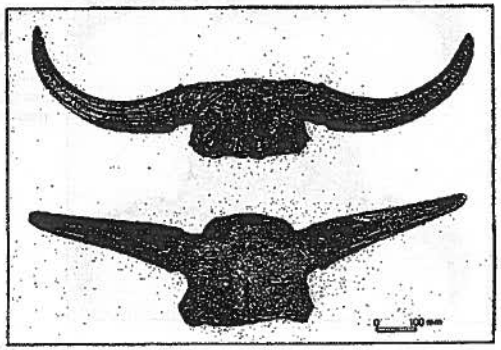
Pl. 18 This female *Bison priscus* (SMP 272-74-z) from Cherokee County, Iowa, is the most southerly female specimen of this taxon studied. The forward rotation and sinuous posterior profile of the horn cores differentiate this specimen from *Bison antiquus* females.

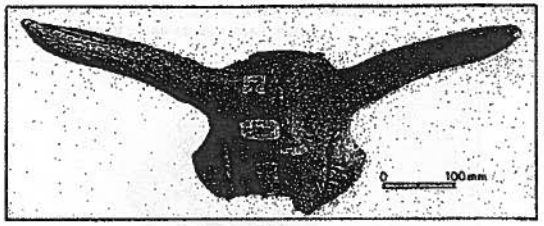




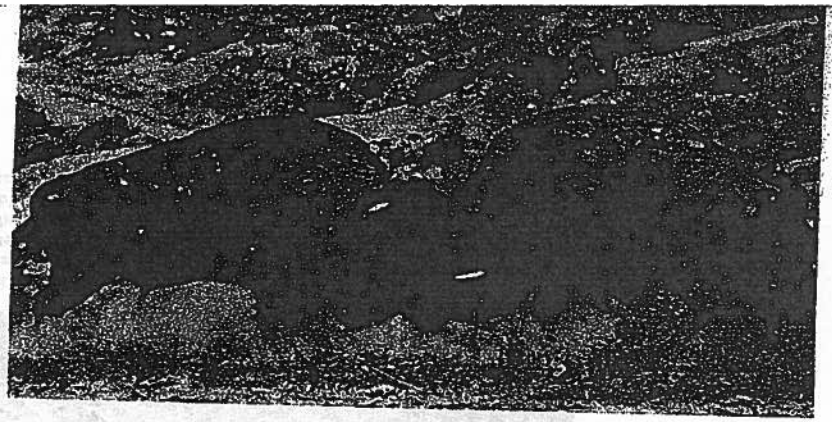
accept Cuvier's 1828 figure as the type illustration for the taxon. Cuvier indicated that the figured specimen was in the University of Pavia. Vialli attempted to identify the figured specimen from among the Pavia bison and selected the top specimen shown above. The bottom skull, however, in the University of Turin, more strongly resembles Cuvier's figure and is here considered more likely the lectotype if, in fact, Cuvier's figure was based on a single specimen.

Pl. 20 The *Bison alaskensis* holotype (FMNH P 25226) was found near Point Barrow, Alaska. This specimen is typical of larger Eurasian autochthons.

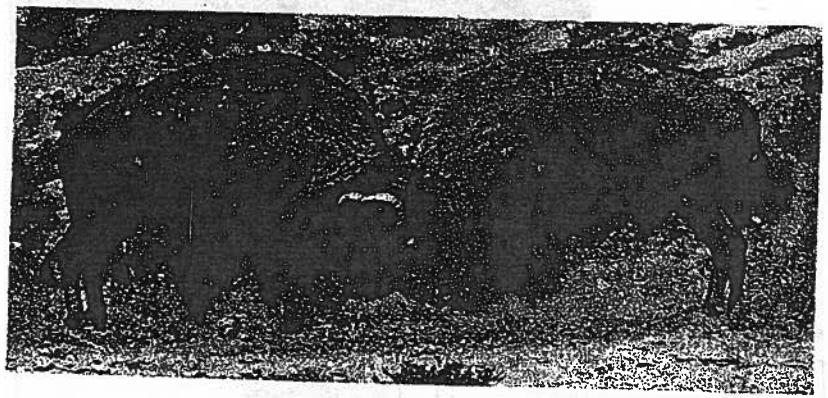




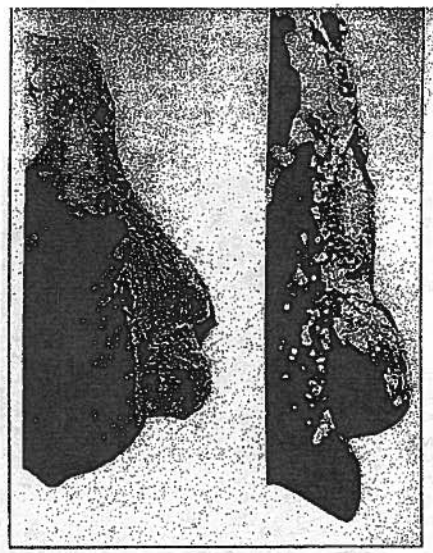
Pl. 21 This female *Bison alaskensis* (UNSM VP F:AM46972) from Goldstream, Alaska, shows horn core characters typical of Eurasian bison—sinuous posterior margin, sinuous axis with obviously spiraled growth, and forward rotation of the antero-posterior axis.



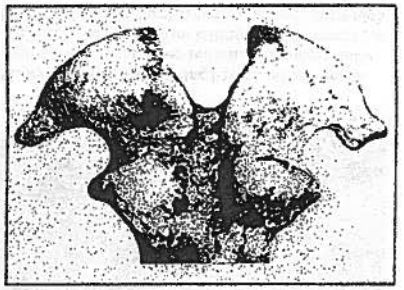
Pl. 22 Escalated fighting between two male *Bison bison bison* during the summer rut. These bulls have just collided head-to-head, culminating a mutual charge of several yards toward each other. The wool-covered frontals were the surfaces of impact in both cases. The individual on the right was reeled as a result of the collision. (Photo by S. L. Woodward; used with permission.)



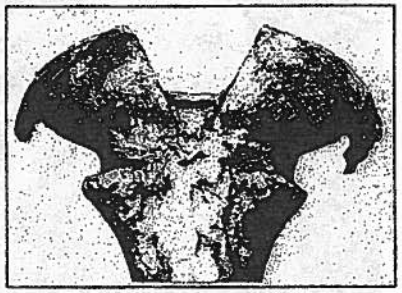
Pl. 23 Head wrestling following the collision in plate 22. Pushing and rolling of the head against that of the opponent is often punctuated by deliberate, sudden hooking motions in which the horn tips are thrust toward the opponent's head. (Photo by S. L. Woodward; used with permission.)



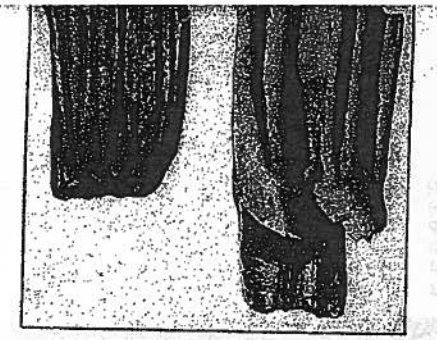
holotype (ANSP G 12993) shows the exaggerated protrusion of the ventral occipital and the resulting proximal displacement of the occipital condyles and concavity of the occipital surface. A similar profile of a *Bison bison bison* occipital (AMNH VP F:AMSD110–2210) shows the more planar surface typical of smaller bodied bison.



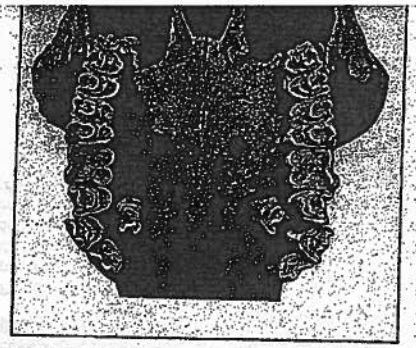
Pl. 25 The occipital condyles of larger bodied bison tend to have strongly flanged ventro-labial margins that might function to more securely fix the condyles of the large, heavy, flexible head into the articular cup of the atlas.



Pl. 26 The occipital condyles of smaller bodied bison are usually not flanged, although weak flanging is found in some specimens. *Bison bison* condyles show less flanging than those of any other taxon, probably because the smaller, lighter, and less flexible head precludes the necessity of such nonslippage characters.

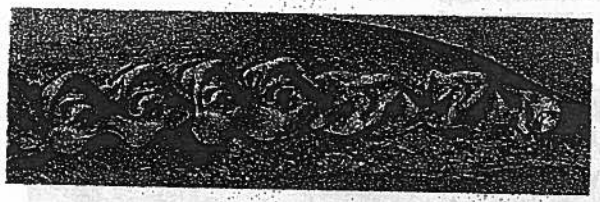


Pl. 31 The labial enamel surface of superior molars is normally characterized by three narrow and two wide alternating ridges. Occasionally, distinct auxiliary styles occur on the labial surface opposite the normal lingual style. These abnormal labial characters might also possibly identify populations experiencing inbreeding or genetic drift, especially when they occur in high frequencies or in conjunction with other abnormal characters. (Specimens are in the American Museum of Natural History and the Museum of Arid Lands Biology.)

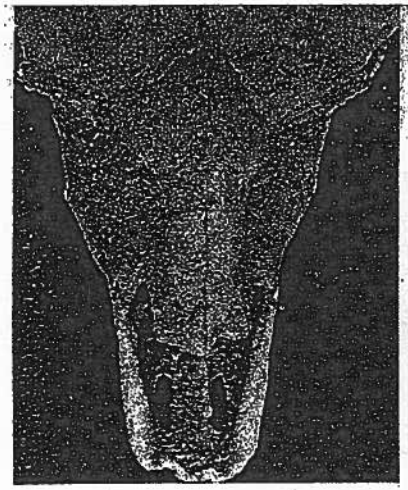


Pl. 32 Supernumerary teeth occasionally appear in bison. The holotype of *Bison bison oregonus* (USNM M 250145) contains an extra pair of premolars, and over 15% of the superior molars examined from the Malheur Lake sample had abnormal fosset borders. The Lake Malheur population possibly represents a small, inbred population from the western periphery of the *Bison bison* range.





Pl. 33 The Casper archeological site, excavated near the town of Casper, Natrona County, Wyoming, yielded a bison deme possessive of numerous abnormalities—some probably genetic, others probably developmental. The incompletely formed third molar (top) pictured here is probably a genetic-based abnormality, whereas the case of "lumpy jaw" (bottom) is probably a developmental pathology, but a condition that suggests that the probably inbred population might have been abnormally susceptible to somatic traumas.



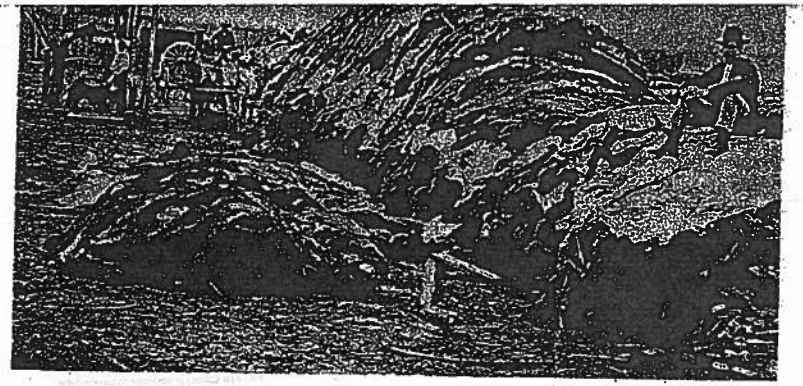


actors. A mature female (UW NC2560) from the Casper archeological site illustrates nasal-maxillae competition. In this case the nasals have been pinched inward at the nasal-maxilla sutures, forming them into the shape of an hourglass.



Pl. 35 Radiocarbon dating has provided dependable evidence that paleo-Indians had successfully implemented methods for killing herds of bison by at least 11,000 BP in North America. The relatively high frequency of skeletal abnormalities which are found in bison dating from the 11,000–9,000 BP period suggests that human hunting might have been sufficient to cause enough isolation of populations to initiate widespread inbreeding and genetic drift. The Hudson-Meng archeological site, in Sioux County, Nebraska, shown here during the 1975 excavation, represents the early Holocene period of presumably heavy predation on bison by paleo-Indians. For further information on this site, see Agenbroad (1978).

Pl. 36 The Vore archeological site, located on the edge of the Black Hills in northeastern Wyoming, provides a two hundred fifty year record of late prehistoric (ca. A.D. 1500–1750) bison procurement on the northwestern Great Plains. For further information on this site see Reher (1978). (Photo by C. A. Reher; used with permission.)



Pl. 37 Millions of bison were slaughtered on the Great Plains of the United States during the two decades following the Civil War, primarily for their hides. The commercial extermination of the plains bison started in the central plains, then shifted to the southern plains in the mid-1870s, and concluded in the early 1880s in the northern plains. Dodge City, Kansas, came into existence in the early 1870s as a rail station from which bison hides from Indian Territory and the Texas panhandle were shipped to eastern tanneries. This view of the Dodge City hide yard is reproduced with permission of the Kansas State Historical Society.

Pl. 38 Perhaps only a few hundred wild bison survived the slaughter of the nineteenth century, but enough were saved and protected to allow the establishment of the many private and public herds which now exist. With but few exceptions, however, modern bison exist in artifical selection regimes and are subject, in great part, to human influence upon their continued evolution. Pictured here is a portion of the herd at Fort Niobrara-Valentine National Wildlife Refuge Complex, Nebraska, where herd size, range, composition, and predation are more or less human controlled.



Relative sexual dimorphism in linear variates of the skull and limb bones follows a generally similar pattern among all taxa, yet significant differences in degrees of dimorphism are apparent for many characters. Among skull characters, the horn cores are most dimorphic, whereas the occipital-frontal-facial characters are considerably less so (fig. 61; table 46). Horn core characters collectively show the greatest range of dimorphism among the taxa and occipital characters show the least dimorphism. Among limb bones, lengths are less dimorphic than diaphysial diameters and, usually, the antero-posterior diaphysial diameters are less dimorphic than the transverse diameters (fig. 62, table 47). The magnitude of relative dimorphism in both skull and limb characters is not directly correlated with the absolute size or the absolute dimorphism of the characters.

No single taxon is unquestionably more or less sexually dimorphic in all characters than are the other taxa, yet some taxa do show tendencies toward greater or lesser relative dimorphism (figs. 61 and 62). *B. a. antiquus* is least dimorphic in more skull and limb characters than is any other taxon. *B. priscus* is most dimorphic in more skull characters than any other taxon (this observation may be biased by the small female *B. priscus* sample size). Among North American autochthons, *B. bison* is more dimorphic in more skull and limb characters than *B. latifrons* or *B. antiquus*. The great limb dimorphism observed for *B. b. athabascae* may be biased by the small sample size.

Table 46
Relative Sexual Dimorphism in Skulls

Standard measurement	*B. b. bison*	*B. b. occidentalis*	*B. a. antiquus*	*B. latifrons*	*B. priscus*	*B. alaskensis*
Spread of horn cores, tip to tip	.76	.79	.77	.59	.67	.70
Horn core length, upper curve, tip to burr	.65	.71	.73	.64	.58	.58
Straight line distance, tip to burr, dorsal horn core	.58	.74	.76	.70	.62	.63
Dorso-ventral diameter, horn core base	.63	.64	.65	.73	.64	.69
Minimum circumference, horn core base	.63	.64	.64	.66	.60	.64
Width of occipital at auditory openings	.83	.83	.86	.81	.78	.86
Width of occipital condyles	.91	.94	.93	.92	.86	.94
Depth, nuchal line to dorsal margin of foramen magnum	.86	.84	.90	.85	.88	.90
Antero-posterior diameter, horn core base	.62	.61	.62	.63	.56	.60
Least width of frontals, between horn cores and orbits	.80	.80	.84	.80	.76	.78
Greatest width of frontals at orbits	.82	.84	.85	.81	.80	.79
$M^1 - M^3$, inclusive alveolar length	.91	1.00	.91	1.02	...	...
M^3, maximum width, ectarior cusp	.94	.96	.97	.93	...	...
Distance, nuchal line to tip of premaxillae	.91	.93	.92	...	...	.88
Distance, nuchal line to nasal-frontal suture	.86	.88	.87	.76	.86	.84

Note: The male mean for each character in each taxon = 1.00. Values given in the table are multiples of the male mean.

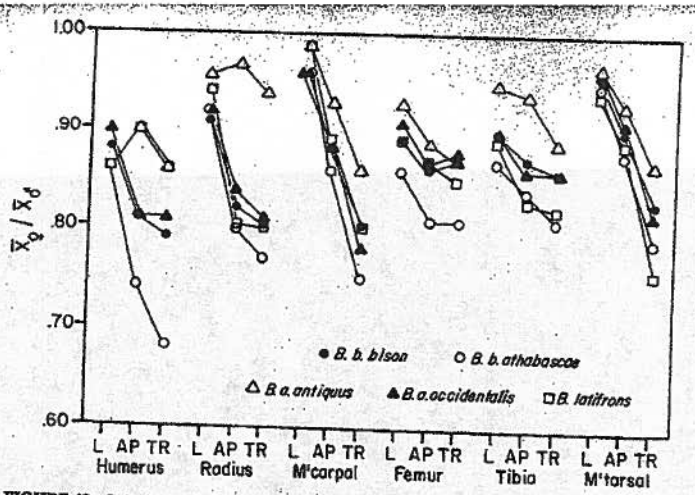


FIGURE 62 Relative sexual dimorphism among limb characters. The vertical axis expresses the female mean for each taxon as a multiple of the male mean.

Table 47

Relative Sexual Dimorphism in Limb Bones

Standard measurement	*B. b. bison*	*B. b. athabascae*	*B. a. occidentalis*	*B. a. antiquus*	*B. latifrons*
Humerus:					
Approximate rotational length of bone	.88	.86	.90	...	.86
Antero-posterior diameter of diaphysis	.81	.74	.81	.90	.90
Transverse minimum of diaphysis	.78	.68	.81	.86	.86
Radius:					
Approximate rotational length of bone	.91	.92	.92	.96	.94
Antero-posterior minimum of diaphysis	.82	.80	.84	.97	.80
Transverse minimum of diaphysis	.80	.77	.81	.94	.80
Metacarpal:					
Total length of bone	.96	.96	.96	.99	.99
Antero-posterior minimum of diaphysis	.88	.86	.88	.93	.88
Transverse minimum of diaphysis	.80	.75	.76	.86	.80
Femur:					
Approximate rotational length of bone	.89	.86	.91	.93	.89
Antero-posterior diameter of diaphysis	.86	.81	.87	.89	.87
Transverse minimum of diaphysis	.87	.81	.88	.87	.85
Tibia:					
Approximate rotational length of bone	.90	.87	.90	.95	.89
Antero-posterior minimum of diaphysis	.87	.84	.86	.94	.83
Transverse minimum of diaphysis	.86	.81	.86	.89	.82
Metatarsal:					
Total length of bone	.96	.96	.96	.97	.94
Antero-posterior minimum of diaphysis	.90	.88	.91	.93	.89
Transverse minimum of diaphysis	.83	.79	.82	.87	.76

Note: The male mean for each character in each taxon = 1.00. Values given in the table are multiples of the male mean.

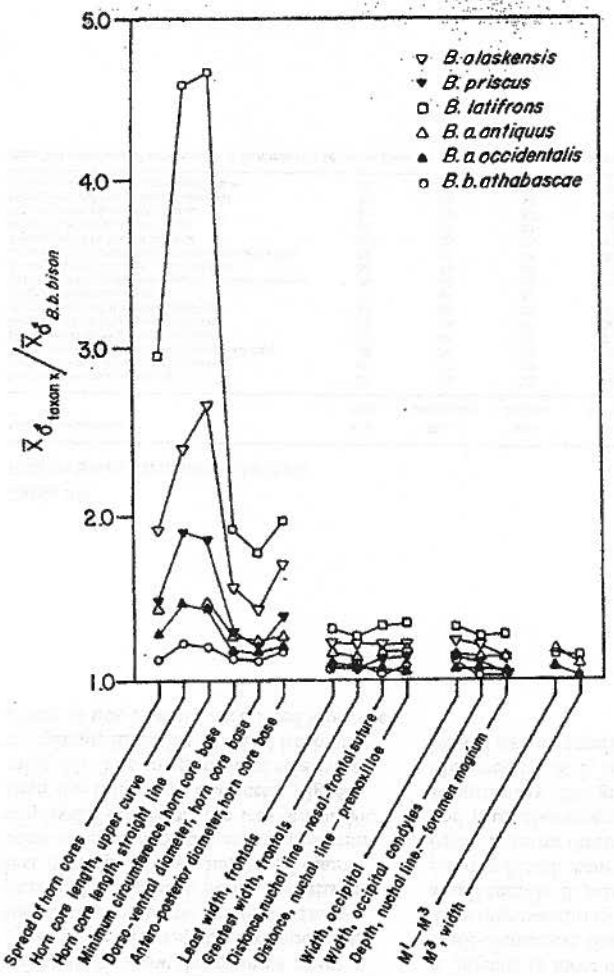


FIGURE 63 Skull allometries relative to *Bison bison bison*: males. The vertical axis expresses the male mean for each taxon as a multiple of the *Bison bison bison* male mean.

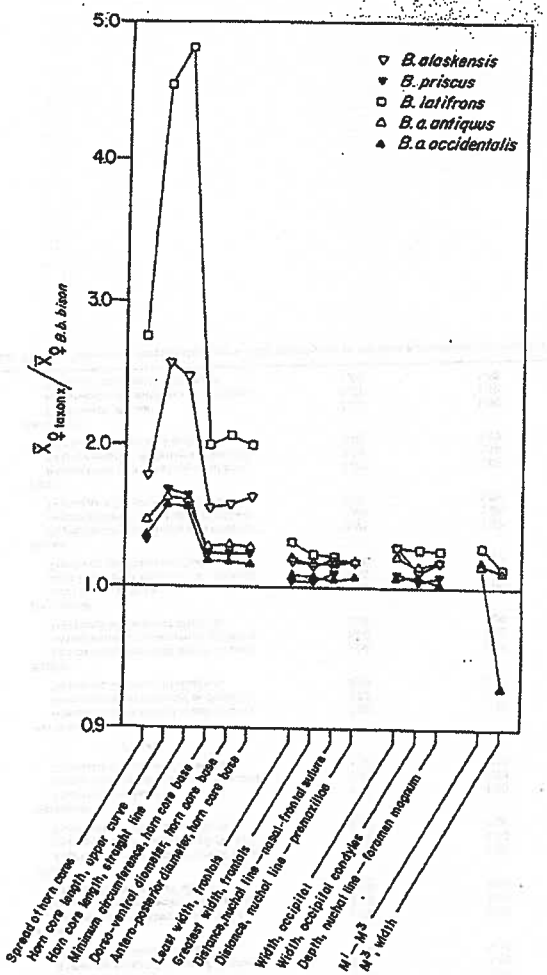


FIGURE 64 Skull allometries relative to *Bison bison bison:* females. The vertical axis expresses the female mean for each taxon as a multiple of the *Bison bison bison* female mean.

Table 48
Skull Allometries Relative to *Bison bison bison*

Standard measurement	*B. b. athabascae*	*B. a. occidentalis*	*B. a. antiquus*	*B. latifrons*	*B. priscus*	*B. alaskensis*
Males						
Spread of horn cores, tip to tip	1.13	1.29	1.44	2.96	1.47	1.91
Horn core length, upper curve, tip to burr	1.23	1.46	1.46	4.89	1.90	2.90
Straight line distance, tip to burr, dorsal horn core	1.20	1.44	1.45	4.67	1.85	2.66
Dorso-ventral diameter, horn core base	1.12	1.16	1.24	1.77	1.20	1.43
Minimum circumference, horn core base	1.13	1.18	1.27	1.92	1.29	1.56
Width of occipital at auditory openings	1.12	1.07	1.18	1.32	1.13	1.24
Width of occipital condyles	1.02	1.07	1.14	1.26	1.11	1.20
Depth, nuchal line to dorsal margin of foramen magnum	1.01	1.05	1.13	1.27	1.04	1.13
Antero-posterior diameter, horn core base	1.17	1.18	1.27	1.97	1.38	1.70
Least width of frontals, between horn cores and orbits	1.08	1.09	1.16	1.31	1.08	1.22
Greatest width of frontals at orbits	1.09	1.07	1.14	1.28	1.08	1.22
$M^1 - M^3$, inclusive alveolar length	....	1.07	1.17	1.15	....	....
M^3, maximum width, anterior cusp	....	1.03	1.08	1.14	....	....
Distance, nuchal line to tip of premaxillae	1.08	1.05	1.18	1.34	1.14	1.21
Distance, nuchal line to nasal-frontal suture	1.04	1.06	1.16	1.33	1.11	1.21
Females						
Spread of horn cores, tip to tip	....	1.36	1.48	2.75	1.33	1.79
Horn core length, upper curve, tip to burr	....	1.59	1.63	4.54	1.68	2.57
Straight line distance, tip to burr, dorsal horn core	....	1.56	1.62	4.81	1.69	2.49
Dorso-ventral diameter, horn core base	....	1.18	1.30	2.07	1.24	1.59
Minimum circumference, horn core base	....	1.18	1.29	2.00	1.23	1.56
Width of occipital at auditory openings	....	1.08	1.22	1.29	1.09	1.29
Width of occipital condyles	....	1.10	1.15	1.27	1.05	1.11
Depth, nuchal line to dorsal margin of foramen magnum	....	1.03	1.19	1.26	1.08	1.18
Antero-posterior diameter, horn core base	....	1.17	1.28	2.00	1.24	1.64
Least width of frontals, between horn cores and orbits	....	1.10	1.21	1.32	1.05	1.20
Greatest width of frontals at orbits	....	1.09	1.18	1.24	1.06	1.17
$M^1 - M^3$, inclusive alveolar length	....	1.19	1.17	1.29	....	....
M^3, maximum width, anterior cusp	....	0.93	1.11	1.13	....	....
Distance, nuchal line to tip of premaxillae	....	1.08	1.19	....	....	1.19
Distance, nuchal line to nasal-frontal suture	....	1.07	1.17	1.21	1.10	1.18

Note: The *B. b. bison* mean for each character = 1.00. Values given in the table are multiples of the *B. b. bison* mean.

ALLOMETRY

Most characters are to a greater or lesser degree allomorphic among bison taxa. The magnitude of allometry among skull characters, relative to *B. b. bison* (an arbitrarily selected norm), is illustrated in figures 63 and 64 and quantified in table 48. Horn core characters show the greatest allomorphosis among taxa, whereas occipital-frontal-facial characters show considerably less allomorphosis. Both males and females exhibit similar patterns of skull allometry.

Limb characters are less allometric than skull characters (table 49). Limb length is usually, but not always, less allomorphic than are the diaphysial diameters. There is no strong tendency for either of the diaphysial diameters to be more or less allomorphic than the other. Both sexes show similar patterns of limb allometry.

Table 49

Limb Allometries Relative to *Bison bison bison*

Standard measurement	*B. b. athabascae*	*B. a. occidentalis*	*B. a. antiquus*	*B. latifrons*
Males				
Humerus:				
Approximate rotational length of bone	1.08	1.09	....	1.23
Antero-posterior diameter of diaphysis	1.09	1.07	1.13	1.30
Transverse minimum of diaphysis	1.15	1.08	1.16	1.32
Radius:				
Approximate rotational length of bone	1.06	1.07	1.07	1.20
Antero-posterior minimum of diaphysis	1.08	1.10	1.04	1.41
Transverse minimum of diaphysis	1.10	1.08	1.01	1.40
Metacarpal:				
Total length of bone	1.10	1.06	1.07	1.21
Antero-posterior minimum of diaphysis	1.11	1.10	1.12	1.33
Transverse minimum of diaphysis	1.14	1.13	1.15	1.45
Femur:				
Approximate rotational length of bone	1.10	1.06	1.12	1.27
Antero-posterior diameter of diaphysis	1.12	1.04	1.17	1.37
Transverse minimum of diaphysis	1.09	1.04	1.24	1.33
Tibia:				
Approximate rotational length of bone	1.11	1.08	1.10	1.23
Antero-posterior minimum of diaphysis	1.09	1.12	1.22	1.43
Transverse minimum of diaphysis	1.08	1.08	1.20	1.39
Metatarsal:				
Total length of bone	1.08	1.05	1.07	1.19
Antero-posterior minimum of diaphysis	1.08	1.09	1.16	1.35
Transverse minimum of diaphysis	1.10	1.11	1.15	1.49
Females				
Humerus:				
Approximate rotational length of bone	1.06	1.12	1.19	1.21
Antero-posterior diameter of diaphysis	1.00	1.08	1.26	1.45
Transverse minimum of diaphysis	0.99	1.10	1.25	1.42
Radius:				
Approximate rotational length of bone	1.06	1.07	1.12	1.23
Antero-posterior minimum of diaphysis	1.06	1.12	1.24	1.38
Transverse minimum of diaphysis	1.06	1.09	1.18	1.40
Metacarpal:				
Total length of bone	1.10	1.06	1.10	1.25
Antero-posterior minimum of diaphysis	1.08	1.10	1.18	1.34
Transverse minimum of diaphysis	1.08	1.10	1.22	1.44
Femur:				
Approximate rotational length of bone	1.05	1.07	1.17	1.25
Antero-posterior diameter of diaphysis	1.06	1.05	1.21	1.39
Transverse minimum of diaphysis	1.01	1.04	1.23	1.29
Tibia:				
Approximate rotational length of bone	1.07	1.07	1.16	1.22
Antero-posterior minimum of diaphysis	1.05	1.10	1.32	1.37
Transverse minimum of diaphysis	1.02	1.09	1.24	1.33
Metatarsal:				
Total length of bone	1.07	1.05	1.08	1.16
Antero-posterior minimum of diaphysis	1.05	1.10	1.19	1.33
Transverse minimum of diaphysis	1.05	1.09	1.20	1.36

Note: The *B. b. bison* mean for each character = 1.00. Values given in the table are multiples of the *B. b. bison* mean.

VARIABILITY OF CHARACTERS

Pearson's coefficient of variation (V) is a measure of relative variation within samples. Higher Vs indicate greater variation among cases relative to the sample mean and imply greater variability of the respective character. Lower Vs indicate the opposite. Normally, Vs for mammalian characters are between about three and ten (Olson and Miller, 1958; Simpson, 1953; Yablokov, 1974).

The Vs for bison skull characters are greatest for horn cores and less for other characters (figs. 65 and 66; table 50). Limb Vs are higher for diaphysial diameters than for length (figs. 67 and 68; table 51). There is no correlation between Vs and absolute size of characters. Patterns of variability in skull and limb bone characters are similar for both males and females.

No single taxon shows distinctly greater or less variability than other taxa in all characters. With the exception of some horn core variates the mean coefficients of variation for all linear skull and limb variates studied fall within the general limits of variation expected in mammals (i.e., between three and ten). Coefficients of variation for horn core length characters average somewhat larger than ten (table 52). Limb character Vs range from 3.0 to 8.0 (table 53).

CHOROCLINES

Choroclines can be demonstrated among all North American bison. The *B. bison* sample represents a shorter span of geologic time than any other available sample and can, therefore, best illustrate the nature of choroclinal variation among bison. Six skull characters show different clinal gradients along the north-south axis of the primary *B. bison* range (fig. 69). Northern bison are larger than southern bison in all characters included in figure 69, but they are decidedly larger in horn core characters than in others. Also, some characters decrease in size continuously from north to south, whereas other characters increase in size from the Canadian prairies southward. Front limb bones of *B. bison* also generally decrease in length from north to south (fig. 70). Female and male limbs show parallel clinal gradients. (Female *B. bison* skull character clines are not figured because of inadequate southern plains, northern plains, and boreal samples.)

Character clines for other North American taxa are presented in figure 71. These clines reinforce the observations made from *B. bison* clines that clinal gradients vary from character to character. North-south trending clines for Pleistocene and early-to-middle Holocene bison show generally larger phenotypes to the south and smaller phenotypes to the north, whereas later Holocene *B. bison* show larger phenotypes to the north and smaller phenotypes to the south. *B. latifrons* characters (especially horn cores) are generally larger to the west and smaller to the east, whereas *B. a. antiquus* characters are larger in the east and smaller in the west. When evaluating choroclines in fossil bison, however, the fact must be kept in mind that the samples probably represent a relatively longer period of geologic time, and reflect the consequences of greater environmental fluctuations and perturbations of gene flow than does the *B. bison* sample.

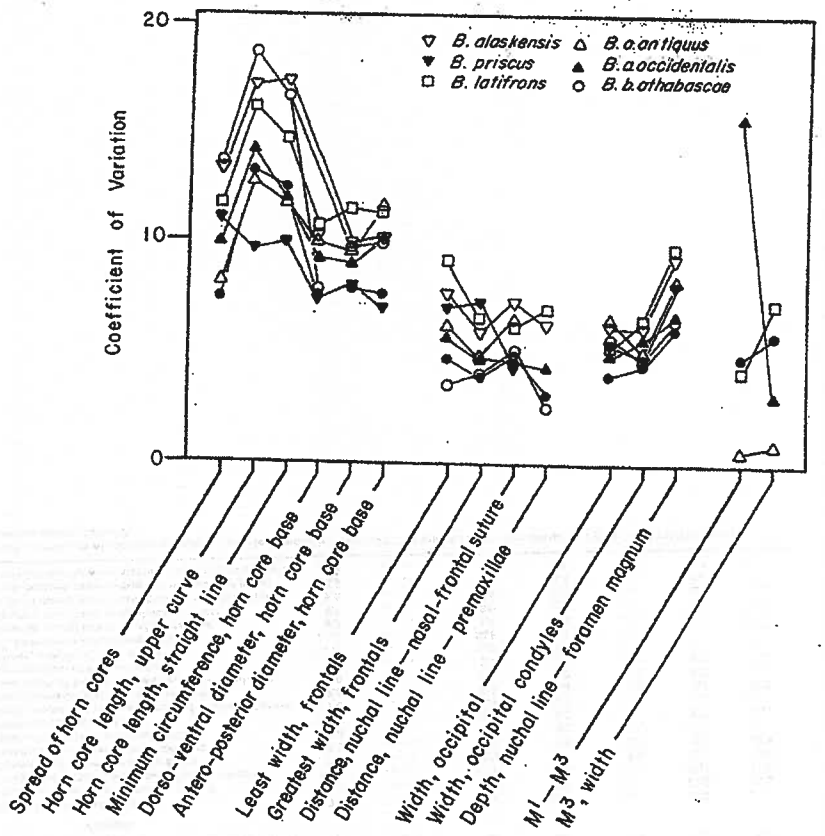


FIGURE 65 Coefficients of variation, skull characters: males.

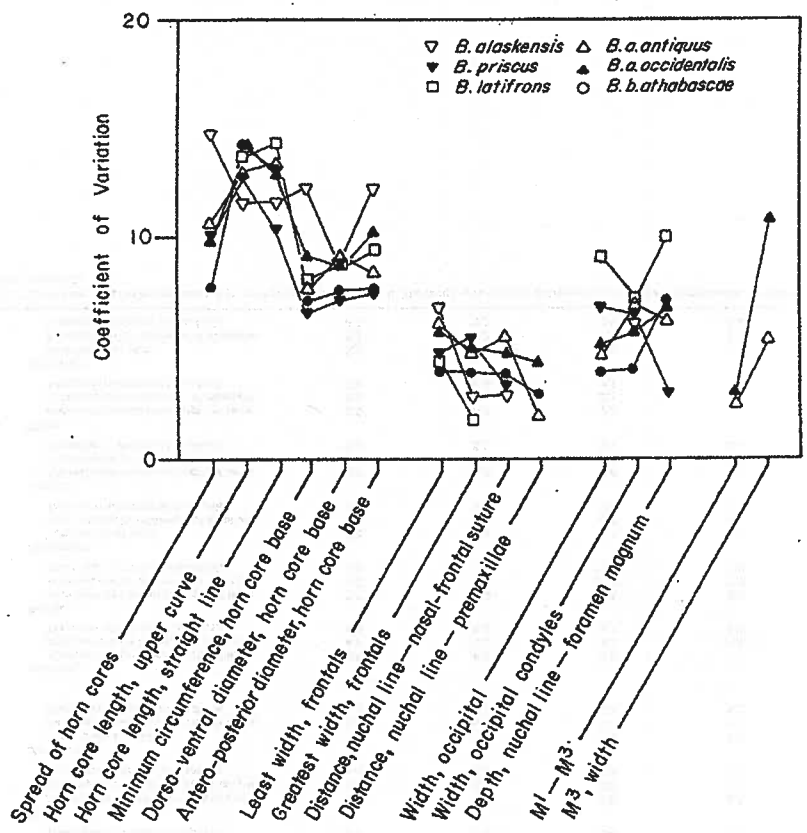


FIGURE 66 Coefficients of variation, skull characters: females.

Table 50
Coefficients of Variation: Skull Characters

Standard measurement	*B. b. bison*	*B. b. athabascae*	*B. a. occidentalis*	*B. a. antiquus*	*B. latifrons*	*B. priscus*	*B. alaskensis*
Males							
Spread of horn cores, tip to tip	7.4	13.5	9.9	8.2	11.7	11.0	13.3
Horn core length, upper curve, tip to burr	13.0	16.7	14.1	12.6	16.1	9.7	17.1
Straight line distance, tip to burr, dorsal horn core	12.4	16.6	12.8	11.7	14.6	9.9	17.4
Dorso-ventral diameter, horn core base	7.9	9.5	8.9	9.5	11.4	8.4	9.7
Minimum circumference, horn core base	7.6	7.9	9.2	10.0	10.7	6.4	10.2
Width of occipital at auditory openings	4.0	5.6	5.0	6.5	5.3	5.1	6.3
Width of occipital condyles	4.5	4.9	5.7	5.9	6.4	4.9	6.2
Depth, nuchal line to dorsal margin of foramen magnum	6.2	6.6	6.7	8.3	9.7	8.1	9.2
Antero-posterior diameter, horn core base	7.6	9.8	10.1	11.5	11.3	7.0	10.1
Least width of frontals, between horn cores and orbits	4.7	3.6	5.7	6.2	9.1	7.0	7.7
Greatest width of frontals at orbits	4.0	4.2	4.8	4.8	6.6	7.3	8.9
M^1–M^3, inclusive alveolar length	4.8	.....	.....	.....	4.0	....	....
M^3, maximum width, anterior cusp	5.9	.....	.....	.....	7.2	....	....
Distance, nuchal line to tip of premaxillae	3.2	2.8	4.4	.....	.....	....	....
Distance, nuchal line to nasal-frontal suture	5.0	5.2	4.7	6.6	6.3	4.6	7.3
Angle of divergence of horn cores, forward from sagittal	6.6	7.0	7.2	6.1	7.0	5.7	7.9
Angle between foramen magnum and occipital planes	5.6	6.8	6.7	5.3	7.1	6.7	6.5
Angle between foramen magnum and basioccipital planes	4.5	5.8	4.9	6.1	6.4	5.0	6.5
Females							
Spread of horn cores, tip to tip	7.9	.....	8.4	10.6	....	10.0	....
Horn core length, upper curve, tip to burr	14.1	.....	9.6	12.8	....	12.8	11.5
Straight line distance, tip to burr, dorsal horn core	13.1	.....	77.7	13.2	....	10.4	11.5
Dorso-ventral diameter, horn core base	7.5	.....	8.0	9.1	8.6	7.1	8.6
Minimum circumference, horn core base	7.1	.....	7.0	7.7	8.1	6.6	12.1
Width of occipital at auditory openings	3.8	.....	3.7	4.7	....	....	....
Width of occipital condyles	4.0	.....	5.5	6.9	....	6.5	....
Depth, nuchal line to dorsal margin of foramen magnum	7.0	.....	6.8	8.1	....	....	....
Antero-posterior diameter, horn core base	7.6	.....	9.3	8.3	9.4	7.5	12.1
Least width of frontals, between horn cores and orbits	4.0	.....	5.2	6.0	4.3	4.7	....
Greatest width of frontals at orbits	3.3	.....	3.7	4.7	....	5.4	....
M^1–M^3, inclusive alveolar length	....	.....	3.0	2.5	....	....	....
M^3, maximum width, anterior cusp	.....	.....	10.8	5.4	....	....	....
Distance, nuchal line to tip of premaxillae	2.8	.....	3.4	1.9	....	....	....
Distance, nuchal line to nasal-frontal suture	3.7	.....	6.0	5.5	....	3.4	....
Angle of divergence of horn cores, forward from sagittal	5.5	.....	5.9	6.5	....	8.8	....
Angle between foramen magnum and occipital planes	5.5	.....	5.4	3.8	....	4.0	....
Angle between foramen magnum and basioccipital planes	4.4	.....	4.9	5.8	....	5.7	....

Note: Coefficients of variation are reported only for samples in which n≥4. The sample size for each character is given in the skull biometric summary tables, chapter 2.

Table 51
Coefficients of Variation: Limb Characters

Standard measurement	*B. b. bison*	*B. a. occidentalis*	*B. a. antiquus*	*B. latifrons*
Males				
Humerus:				
Approximate rotational length of bone	3.4	5.9	...	3.7
Antero-posterior diameter of diaphysis	5.1	6.8	...	4.9
Transverse minimum of diaphysis	6.2	7.7	...	5.5
Radius:				
Approximate rotational length of bone	2.8	4.2	2.2	2.8
Antero-posterior minimum of diaphysis	5.2	5.8	2.8	5.9
Transverse minimum of diaphysis	5.2	5.6	2.3	5.7
Metacarpal:				
Total length of bone	3.4	3.9	3.0	3.3
Antero-posterior minimum of diaphysis	6.1	6.0	4.0	5.9
Transverse minimum of diaphysis	7.5	7.2	6.8	7.5
Femur:				
Approximate rotational length of bone	2.7	4.4	3.2	...
Antero-posterior diameter of diaphysis	5.1	6.5	7.4	5.2
Transverse minimum of diaphysis	5.1	4.7	3.6	3.0
Tibia:				
Approximate rotational length of bone	2.7	4.3	3.5	2.4
Antero-posterior minimum of diaphysis	4.2	5.8	6.9	4.6
Transverse minimum of diaphysis	4.4	5.6	5.9	5.0
Metatarsal:				
Total length of bone	3.0	3.7	3.0	2.2
Antero-posterior minimum of diaphysis	4.6	5.5	6.7	4.1
Transverse minimum of diaphysis	5.4	7.6	6.7	5.7
Females				
Humerus:				
Approximate rotational length of bone	3.0	6.6	4.0	...
Antero-posterior diameter of diaphysis	4.6	8.3	6.7	4.8
Transverse minimum of diaphysis	4.4	8.2	6.1	5.2
Radius:				
Approximate rotational length of bone	3.1	5.2	4.5	2.5
Antero-posterior minimum of diaphysis	5.2	7.0	10.7	2.6
Transverse minimum of diaphysis	5.8	7.2	11.2	7.6
Metacarpal:				
Total length of bone	3.4	3.5	3.1	2.5
Antero-posterior minimum of diaphysis	6.7	6.8	6.5	3.8
Transverse minimum of diaphysis	6.3	7.3	7.8	5.7
Femur:				
Approximate rotational length of bone	2.9	4.6	3.8	...
Antero-posterior diameter of diaphysis	6.0	8.3	4.3	1.7
Transverse minimum of diaphysis	6.0	5.3	5.7	3.9
Tibia:				
Approximate rotational length of bone	3.0	5.2	2.6	...
Antero-posterior minimum of diaphysis	5.8	6.4	6.1	...
Transverse minimum of diaphysis	5.1	6.6	4.1	...
Metatarsal:				
Total length of bone	3.2	3.6	3.2	...
Antero-posterior minimum of diaphysis	5.5	6.2	7.3	3.5
Transverse minimum of diaphysis	6.7	8.2	9.5	2.4

Note: Coefficients of variation are reported only for samples in which n≥ 4. The sample size for each character is given in the limb biometric summary tables, chapter 2.

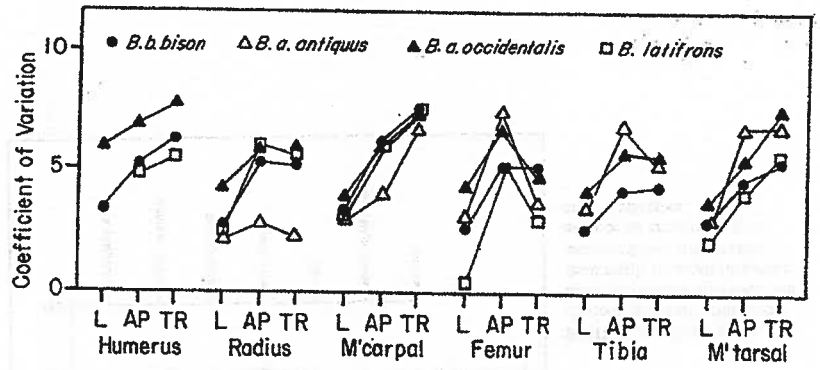


FIGURE 67 Coefficients of variation, limb characters: males.

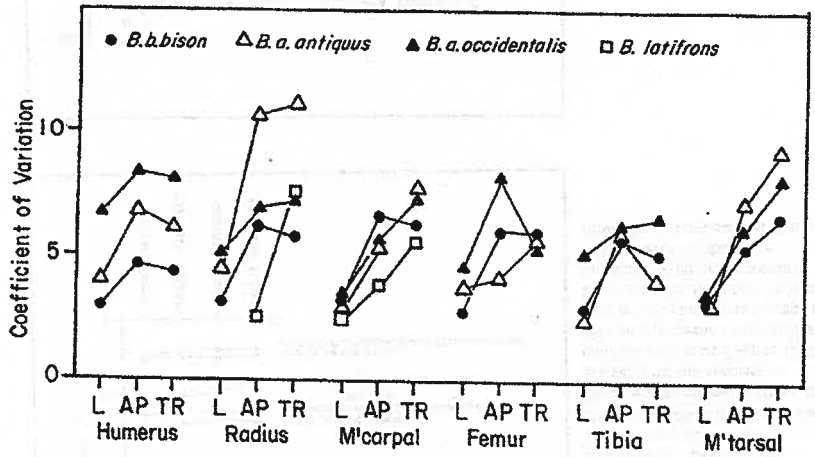


FIGURE 68 Coefficients of variation, limb characters: females.

Table 52
Mean Coefficients of Variation: Skull Characters

Standard measurement	Males	Females
Spread of horn cores, tip to tip	10.7	9.2
Horn core length, upper curve, tip to burr	14.5	12.2
Straight line distance, tip to burr, dorsal horn core	13.6	11.2
Dorso-ventral diameter, horn core base	9.3	8.2
Minimum circumference, horn core base	8.9	8.1
Width of occipital at auditory openings	5.4	4.1
Width of occipital condyles	5.5	5.7
Depth, nuchal line to dorsal margin of foramen magnum	7.8	6.6
Antero-posterior diameter, horn core base	9.6	9.0
Least width of frontals, between horn cores and orbits	6.3	4.8
Greatest width of frontals at orbits	5.4	4.4
$M^1 - M^3$, inclusive alveolar length	4.4	2.8
M^3, maximum width, anterior cusp	6.6	8.1
Distance, nuchal line to tip of premaxillae	3.4	2.7
Distance, nuchal line to nasal-frontal suture	5.6	4.7
Angle of divergence of horn cores, forward from sagittal	6.8	6.7
Angle between foramen magnum and occipital planes	6.2	4.7
Angle between foramen magnum and basioccipital planes	5.6	5.2

Note: These data have been calculated from the coefficients of variation presented in table 50.

Table 53
Mean Coefficients of Variation: Limb Characters

Standard measurement	Males	Females
Humerus:		
Approximate rotational length of bone	4.3	4.5
Antero-posterior diameter of diaphysis	5.6	6.1
Transverse minimum of diaphysis	6.5	6.0
Radius:		
Approximate rotational length of bone	3.0	3.8
Antero-posterior minimum of diaphysis	5.0	6.6
Transverse minimum of diaphysis	4.7	8.0
Metacarpal:		
Total length of bone	3.4	3.1
Antero-posterior minimum of diaphysis	5.5	5.5
Transverse minimum of diaphysis	7.2	6.8
Femur:		
Approximate rotational length of bone	3.4	3.8
Antero-posterior diameter of diaphysis	6.0	5.1
Transverse minimum of diaphysis	4.1	5.2
Tibia:		
Approximate rotational length of diaphysis	3.2	3.6
Antero-posterior minimum of diaphysis	5.4	6.1
Transverse minimum of diaphysis	5.1	5.3
Metatarsal:		
Total length of bone	3.0	3.3
Antero-posterior minimum of diaphysis	5.2	5.6
Transverse minimum of diaphysis	6.3	6.7

Note: These data have been calculated from the coefficients of variation presented in table 51.

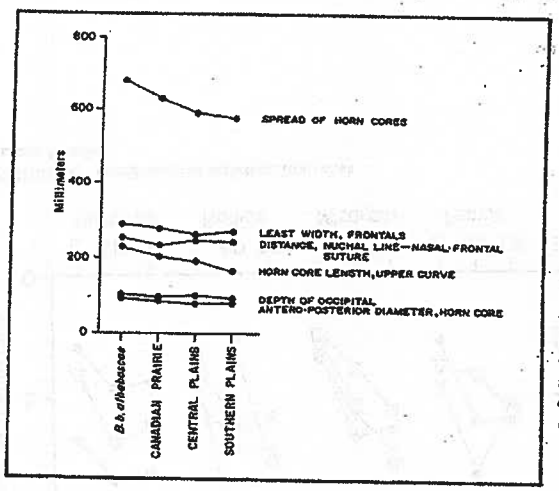


FIGURE 69 *Bison bison* choroclines: male skull characters. Six character clines document a general north–south gradient for the species, as claimed earlier by Figgins (1933). The data presented here indicate that not all characters change at the same rate, undergo the same amount of change, or continuously change in the same direction throughout the cline.

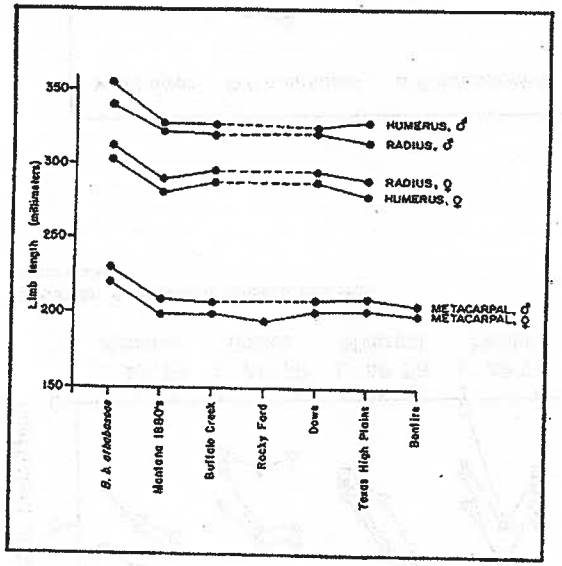


FIGURE 70 *Bison bison* choroclines: limb characters. Limb characters also decrease from north to south through the primary *Bison bison* range, but not as continuously as skull characters.

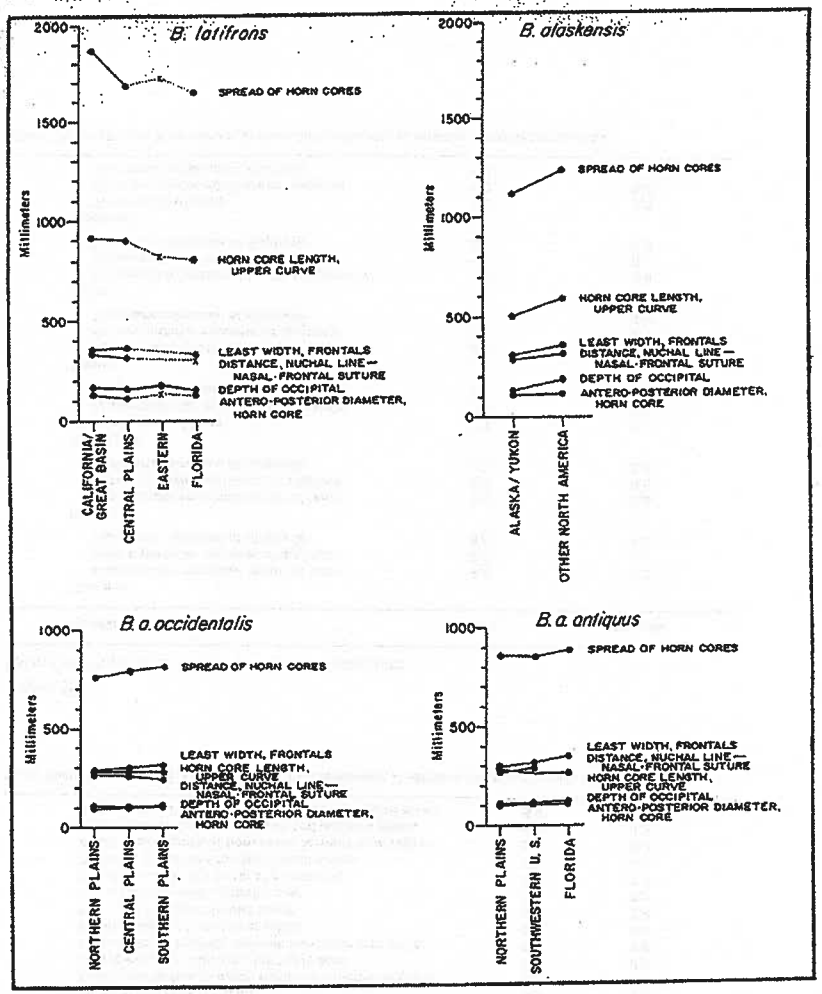


FIGURE 71 Choroclines in taxa other than *Bison bison*. These chorolines are oriented so as to represent the major axis of each taxon's range. Two axes are presented for *Bison antiquus antiquus* (southwest Florida and southwest–northern plains).

PERSPECTIVE

General aspects of variation in the bison skeleton have been documented and illustrated above. The range of variation, the distribution of cases, skewing, and the relative variability of characters are each important qualities of bison populations. These qualities are also of substantial evolutionary importance. The range over which cases within a variate sample are distributed is an unweighted measure of the phenotypic potential of a population. The pattern of case distribution is a weighted measure of relative phenotypic fitness within the population. The positive and negative tendencies (skewing) of a sample may, if the sample is truly representative of the natural population, serve as a weighted measure of (1) the taxon's adaptive potential, should a shift in selection factors occur; and (2) the direction from which an adaptive shift came, if a shift in selection factors occurred in the geologically recent past (fig. 72).

Pearson's coefficient of variation is a weighted measure of a character's plasticity. Theoretically, more variable characters will more easily respond to new forces of selection than will less variable characters. Accordingly, characters with high Vs should most readily (and extensively?) respond to differing selective forces, whereas the least variable characters should respond most slowly to differing selective forces. Less variable characters, therefore, should act as a brake on the extent of evolution (and the rate of adaptation). In newly ordered selection regimes, then, a dual phenotypic response may be envisioned where highly variable characters respond more rapidly and extensively to selection at the same time that less variable characters respond more slowly and less extensively. The intensity of new selection forces and the capacity of bison populations to respond to these forces determine whether or not adaptation will be possible and, if so, the rate at which that adaptation will take place.

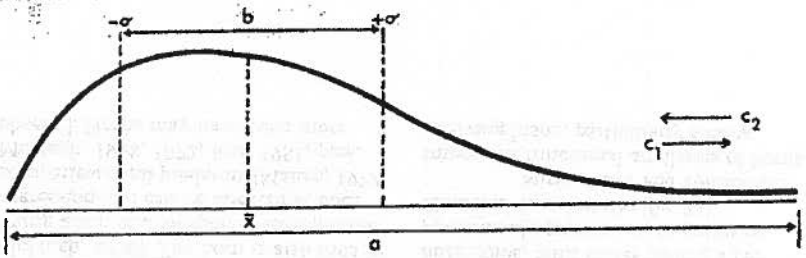


FIGURE 72 Measures of adaptive potential.

a. Range of variation: an unweighted measure of a population's potential for generating a character of such magnitude.

b. Mean and standard deviation of case distribution within the sample: a weighted measure of the population's fitness (i.e., the fitness of any given character).

c. 1. Skew indicating adaptive potential: an indicator of a population's phenotypic potential to shift toward a larger or smaller character should a shift in selective factors occur which favored a larger or smaller character.
2. Skew indicating recent adaptive shift: an indicator of a recent phenotypic shift from a larger or smaller character to the current mean character, following upon a change in selective factors which effected the phenotypic shift.

4

ADAPTIVELY DIFFERENTIATED SKELETAL CHARACTERS

The operation of different selection regimes (= environments) on populations of bison resulted, over relatively brief periods of geologic time, in the evolution of adaptively differentiated, biologically homeostatic bison species. This chapter identifies what appear to be adaptively significant morphological differences among bison taxa.

The bison skeleton, in general, changed very little during the Pleistocene and Holocene except for size. Characters that show significant shape differences among taxa are restricted to the skull and primarily consist of social organs or adjustments to feeding and visual communication in different habitat types. Accordingly, the social and ecological significance of specialized skull characters receive most attention here. Adaptation, however, comprises the complete organism, not merely isolated characters, and reflects an integrated coevolution of morphology, behavior and ecology, not a stepwise progression of one of these categories followed sequentially by others. Also, the phyletic distinctiveness of the North American and Eurasian lineages must be kept in mind; similar environments selected for parallel adaptations (= convergence) in both lineages, but exact duplication of form among vicariant taxa did not result.

HORN CORES

Living bison are dominance organized and the horns are important display paraphernalia that function in the nonfighting dominance and threat behavior of male bison. When alternate less violent forms of dominance behavior fail to establish relative ranking among competing males, actual fighting normally ensues. Fighting consists of two elements: the head-on clash, which terminates in a push, lunge, or charge directly at the opponent's head, and a hooking motion in which the horns are normally thrust upward and inward toward a vulnerable region of the opponent's body. Use of the horns in fights is normally (but not exclusively) confined to the head region where offensive and defensive maneuvering are centered. Infrequently, however, the defense maneuvering fails and injurious (sometimes fatal) wounds are delivered to the body of an opponent (Herrig and Haugen, 1969; Lott, 1972*a*, 1972*b*, 1974; McHugh, 1958). The horn is also used in living bison as a weapon of interspecific aggression and can be directed at both competitors and predators (Mahan, 1977; McHugh, 1958, 1972; Roe, 1951; pers. observ.). Horns may have been more important to earlier bison than to modern bison, considering the probability that body hair (which also functions as a dominance organ in living bison) may have been less prominent, that hooking may have been relatively more important than clashing in fighting behavior, and that interspecific competition may have been more intense in earlier than later bison.

Horn cores present the most obvious and extreme morphological difference among bison taxa (figs. 63 and 64). The most critical aspects of functional horn core morphology are overall horn size and tip placement. The size of horns probably determines their relative effectiveness in various types of dominance encounters. Tip placement is probably the ultimate measure of horn morphology fitness in actual fights and is also probably instrumental in determining the relative viability of fighting techniques. The length, surface area, weight (or volume), configuration, and tip placement are considered here as adaptively significant qualities of horn core morphology.

Horn core length is an important attribute of horn core size and a determinant of tip placement. The basal circumference of the horn core is strongly correlated with horn core length in both sexes, but the ratio between circumference and length is consistently greater in males than in females (fig. 73). Sexual dimorphism is also evident in the basal diameters of male and female horn cores, with males having a proportionately greater antero-posterior diameter than females (fig. 74).

Surface area and volume are important functional attributes of horns in living bison, particularly among

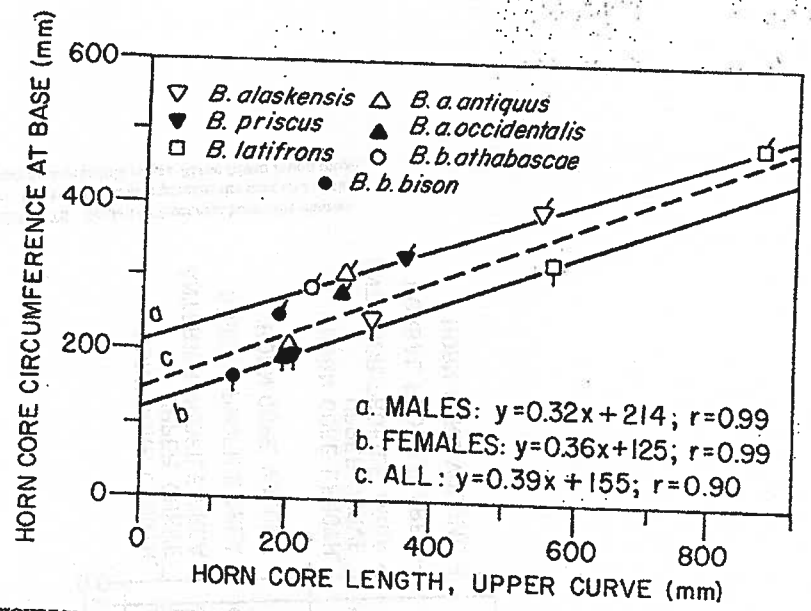


FIGURE 73 Horn core length versus basal circumference. The proportionately greater circumference: length ratio among male horn cores imparts greater surface area, volume, and weight to the male than female horn core.

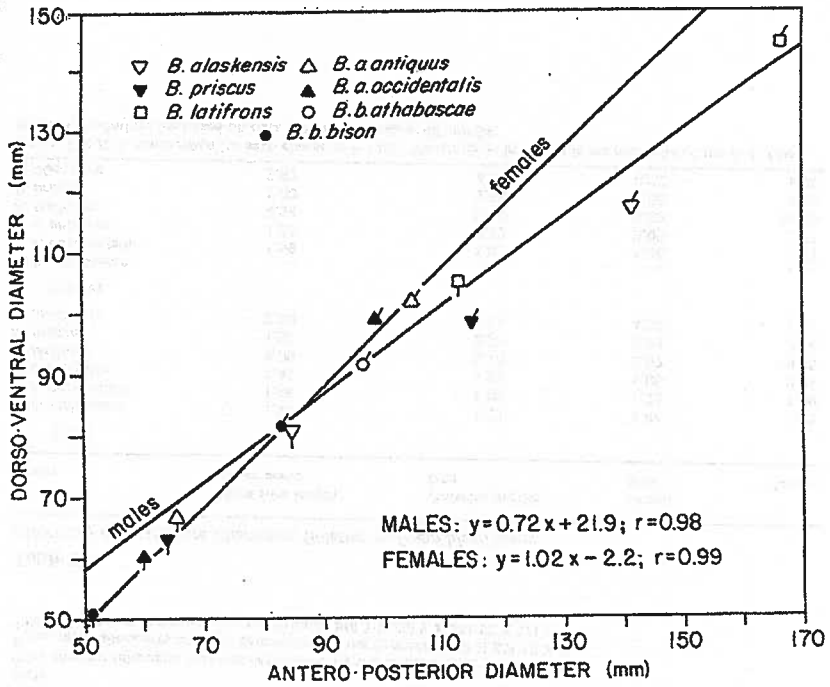


FIGURE 74 Covariation among horn core basal diameters. The proportionately greater antero-posterior diameter for males imparts relatively greater dorsal surface area to the horn.

males who use horns much more frequently and damagingly than females in dominance and aggressive activities. Area, particularly profile area, can conceivably function in dominance and aggression activities in two important ways. First, horn core area conveys an impression of relative size (ideally, an impression of greater than actual size), and hence relative dominance of the organism. Second, both the anterior and dorsal profile areas block, deflect, or absorb blows from an opponent's horns.

Greater horn core volume (hence weight) is an advantage in dominance and aggression activities because it presents greater surface area and can contribute to greater absolute force of delivery with a hooking blow. Larger horns, however, impose certain costs to the organism in excess of those required of bison with smaller horns. Added energy demands and specialized skeletal requirements can be envisaged stemming from such routine activities as raising and lowering the head to feed, water, or check for the presence of competitors or predators; walking or running; and fighting. Smaller horns would substantially reduce the cost to the organism engaging in the activities just mentioned, but would present less surface area to intercept an opponent's offensive hooks, less weight with which to strike an opponent, and less reach with which to stab an opponent. Figure 75 illustrates the differences of scale among linear, areal, and volumetric dimensions for horn cores, and tables 54 and 55 compare the areas, volumes, and allometries of horn core characters.

Horn tips are the critical offensive attribute, so the orientation of the horns and placement of the horn

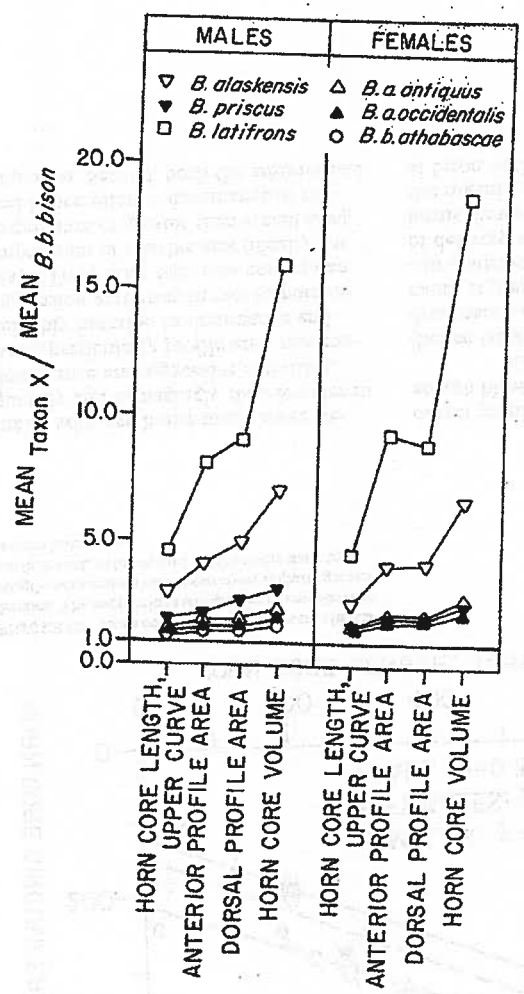


FIGURE 75 Scaled differences: horn core characters. The vertical axis expresses the mean for each taxon as a multiple of the *Bison bison bison* mean.

Table 54
Comparative Horn Core Biometrics: Areas and Volumes

Taxon	Anterior profile area (mm^2)[a]	Dorsal profile area (mm^2)[b]	Volume (mm^3)[c]
Males			
B. b. bison	7,809	7,952	341,012
B. b. athabascae	10,756	11,426	547,405
B. a. occidentalis	13,140	13,723	679,750
B. a. antiquus	14,225	14,742	786,542
B. latifrons	63,466	72,139	5,473,117
B. priscus	17,827	20,837	1,072,481
B. alaskensis	32,345	39,201	2,401,471
Females			
B. b. bison	3,177	3,195	85,668
B. b. athabascae	.....	.....	.....
B. a. occidentalis	5,952	6,943	187,936
B. a. antiquus	6,746	6,676	232,433
B. latifrons	29,864	29,046	1,610,575
B. priscus	6,622	6,684	221,910
B. alaskensis	12,960	13,502	574,060

Note: Calculations are based on data presented in skull biometric summary tables, chapter 2. The mean value for selected standard measurements (SMs) for each taxon have been used to determine the values presented in this table.
[a]The anterior silhouette area was determined by the formula SM 3 X SM 6 X ½.
[b]The dorsal silhouette area was determined by the formula SM 3 X SM 12 X ½.
[c]The volume was determined by the formula SM 3 X SM 6 X SM 12 X 1/12.

Table 55
Allometry of Horn Core Characters Relative to *Bison bison bison*

Taxon	Horn core length, upper curve	Anterior profile area	Dorsal area	Volume
Males				
B. b. athabascae	1.23	1.37	1.44	1.61
B. a. occidentalis	1.46	1.68	1.73	1.99
B. a. antiquus	1.46	1.82	1.85	2.31
B. latifrons	4.59	8.13	9.07	16.05
B. priscus	1.90	2.28	2.62	3.14
B. alaskensis	2.90	4.14	4.93	7.04
Females				
B. b. athabascae	....	....	....	.....
B. a. occidentalis	1.59	1.87	1.86	2.19
B. a. antiquus	1.63	2.12	2.09	2.71
B. latifrons	4.54	9.40	9.09	18.80
B. priscus	1.68	2.08	2.09	2.59
B. alaskensis	2.57	4.08	4.23	6.70

Note: The *B. b. bison* mean for each character = 1.00. Values given in the table are multiples of the *B. b. bison* mean. Calculations are based on data presented in tables 48 and 54.

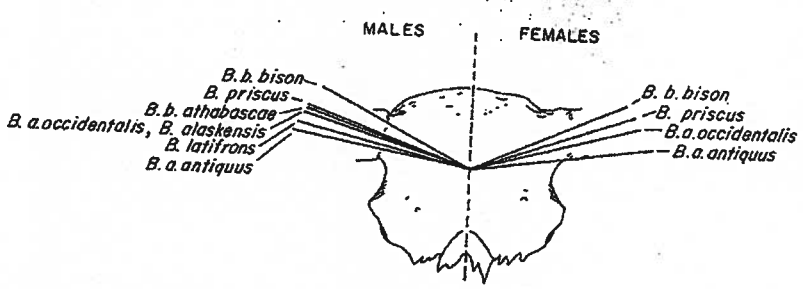


FIGURE 76 Horn core divergence forward from the sagittal plane. Longer horned taxa have greater forward divergence of horn cores than do shorter horned taxa in both the Eurasian and North American lineages.

tips is very important in determining the fitness of horn morphology and the mode of fighting behavior involving use of the horns. Three characteristics of horn tip placement are considered here, including (1) the angle at which horn cores emanate from the frontals relative to the sagittal plane; (2) the placement of the horn core tip relative to the occipital plane; and (3) the placement of the horn core tip relative to the frontal plane. The mean angle of horn core divergence forward from the sagittal for both sexes of each taxon is illustrated in figure 76, and the strong similarity of this divergence between both sexes of each taxon is illustrated in figure 77. These figures show that the angle of horn core divergence strongly affects the placement of the horn tips relative to the occipital plane, and, usually, in both the North American and Eurasian lineages the longer the horn core, the greater is the angle of divergence forward from the sagittal plane. Male *B. latifrons* and *B. a. antiquus* do not exactly fit this pattern, but both have horn cores oriented far forward, probably near the maximum functional forward orientation for horns that are deflected outward and upward.

The placement of the horn tips relative to the occipital and frontal planes is illustrated in figures 78 and 79. In the living animal the horn core would be covered with a keratin sheath, which would have a threefold effect on the placement of the horn tips relative to the horn core tips. (1) In all cases, the horn tips would be positioned rearward from the horn core tips. The extent of this rearward extension generally varies in proportion to the length of the horn core. Rearward rotation of the horn cores and posterior deflection of the horn core tips would further accentuate this rearward extension. (2) The horn tips would be positioned higher than the horn core tips. (3) The distance between the tips of the (recurved) horns would be

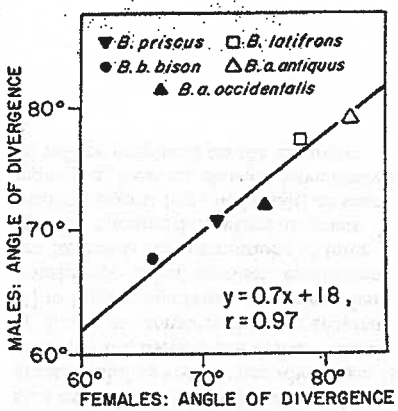


FIGURE 77 Correspondence between sexes of horn core divergence forward from sagittal. Males tend to have a slightly more posterior orientation of horn cores than do females.

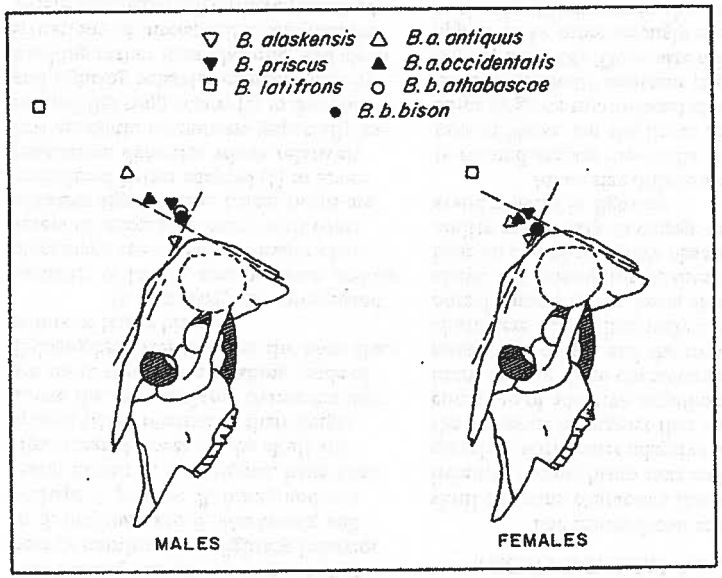


FIGURE 78 Horn core tip placement relative to the frontal plane: lateral view. Male horn core tips are placed higher and further to the rear than are female tips.

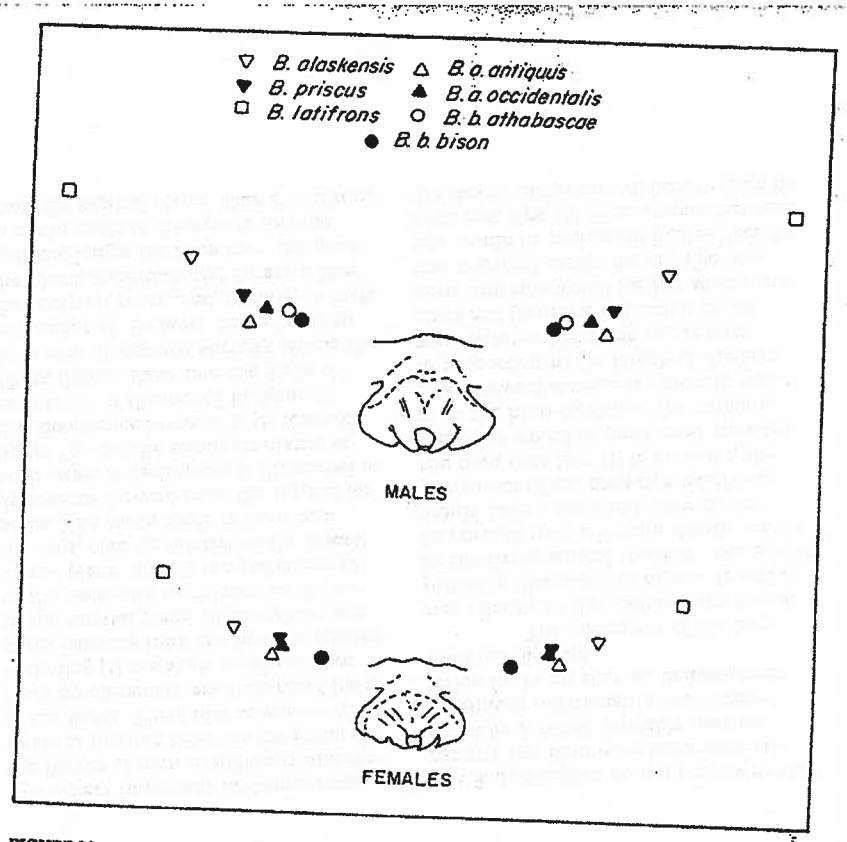


FIGURE 79 Horn core tip placement relative to the frontal plane: sagittal view. Male horn core tips are placed higher than are female tips. There is also a correlation between horn core length and height of tip placement above the frontal plane.

less than that between the tips of the horn cores. The net effect of the sheath relative to the horn cores, therefore, is to place the horn tips further above and behind the frontal-occipital region and to reduce the functional distance between the tips. The combined effects of recurved tips situated high above the frontals in larger horned bison suggests that butting was not an important aspect of dominance or fighting behavior in *B. latifrons* and *B. alaskensis*, and perhaps *B. priscus*. *B. bison*, and to a lesser extent *B. a. antiquus*, have horn tips situated lower on the skull and spaced wider relative to their height above the frontal plane, characters that are more suited to a clashing mode of fighting behavior than are the horn characters of larger bison.

In summary, the interrelated variables of length, area, volume, and tip placement are considered major characters of bison horn cores with overt adaptive significance. Larger horns are considered better adapted (1) to lower population densities where relatively few agonistic encounters (especially escalated fighting) occur; (2) to dominance and fighting behavior characterized by hooking rather than clashing; and (3) to situations of interspecific competition where size (especially where perceived size exceeds actual size) and actual aggressive ability convey net advantages in resource acquisition and defense. Smaller horns are considered better adapted (1) to higher population densities where dominance linked agonistic encounters are frequent; (2) to situations of interspecific competition where alternate ranking organs (e.g., body hair) or strategies (e.g., head-on clashes) have evolved to reduce emphasis on the ultimate and more lethal or damaging use of horns as weapons; and (3) to environments with more abundant resources and reduced absolute competition (thus less need for direct aggression between competitors).

FRONTO-FACIAL REGION

The fronto-facial region of the skull contains characters that differ sufficiently among bison taxa and which correlate with other adaptive features of the skeleton to suggest that the differences are of adaptive significance. Prominent among these characters are the nasals, the orbits, and the frontals—characters that collectively compose the dorsal surface of the bison skull. The shape and orientation of these characters bear on the phenotype's observational ability and ability to engage in and withstand clashes in fighting.

Mean size differences obviously existed among the skulls of different taxa of bison, but the linear relationships of gross fronto-facial characters remained generally constant (figs. 63 and 64, 80; table 48). These size differences appear to be more strongly correlated with size differences in the overall phenotype than to represent specific adaptive differences as such. Between sexes, the frontals of males are absolutely and proportionately wider and shorter than those of females (table 56.)

Differences in the shape of characters are the most important adaptations of the fronto-facial region. The frontals are more strongly domed transversely between the horn cores in shorter horned taxa (*B. bison* and *B.*

Table 56
Comparative Skull Biometrics: Indexes, Areas, and Volumes

Taxon	Frontal breadth: frontal length[a]	Frontal breadth: skull length[b]	Frontal area (mm^2)[c]	Dorsal skull area (mm^2)[d]	Occipital area (mm^2)[e]	Skull volume (mm^3)[f]	Molar occlusal area (mm^2)[g]	Molar occlusal area: frontal breadth[h]
Males								
B. b. bison	1.10	.51	68,609	72,590	37,814	3,371,718	2,509	9.25
B. b. athabascae	1.15	.51	75,110	84,880	42,806	4,127,837	2,558	8.72
B. a. occidentalis	1.14	.53	76,868	83,686	42,801	4,025,440	2,763	9.31
B. a. antiquus	1.11	.50	89,343	98,973	50,468	5,280,846	3,147	10.00
B. latifrons	1.09	.50	116,011	127,126	63,685	7,596,146	3,273	9.22
B. priscus	1.08	.48	80,003	89,285	44,859	4,525,620	.....	.....
B. alaskensis	1.11	.51	99,098	107,982	52,786	5,721,128	.....	.....
Females								
B. b. bison	1.02	.45	46,027	52,517	26,750	2,161,005	2,132	9.84
B. b. athabascae	.....	.....	.....	.....	.....	.....	.....	.....
B. a. occidentalis	1.05	.46	54,143	62,349	28,662	2,588,003	2,364	8.92
B. a. antiquus	1.06	.46	66,200	75,818	38,994	3,745,087	2,770	10.50
B. latifrons	1.12	...	73,298	.....	43,750	.....	3,116	10.93
B. priscus	.97	...	53,583	.....	31,304	.....	.....	.....
B. alaskensis	1.07	.46	65,026	74,750	40,841	3,913,901	.....	.....

Note: Calculations are based upon data presented in skull biometric summary tables, chapter 2. The mean value for selected standard measurements (SMs) for each taxon have been used to determine the values presented in this table.
[a]This index was determined by the formula SM 14÷SM ON.
[b]This index was determined by the formula SM 14÷SM OP.
[c]The frontal silhouette area was determined by the formula SM 14 X SM ON.
[d]The dorsal skull silhouette area was determined by the formula SM 14 X SM OP X ½.
[e]The occipital silhouette area was determined by the formula SM 8 X SM 10 X π/2.
[f]The skull volume was determined by the formula SM 8 X SM 10 X SM OP X π/12.
[g]The molar occlusal silhouette area was determined by the formula SM 20 X SM 20a.
[h]This index was determined by the formula (SM 20 X SM 20a) ÷ SM 14.

antiquus) than in larger horned taxa (*B. priscus, B. alaskensis* and *B. latifrons*) (fig. 81). Doned frontals are usually more strongly and completely fused along the frontal and fronto-parietal sutures than are flatter frontals, and the supraorbital nutriment foramen is usually more completely covered in doned than in flatter frontals. The pneumatic sinus protection of the brain may also be greater in skulls with doned frontals than those with flatter frontals. Relative flattening of the nasals (i.e., broadening in relation to height above the maxillae), which correlates with doming, may constitute another adaptation of the dorsal skull of shorter horned bison.

The adaptive significance of the frontal doming, nasal broadening tendency can be related to head-to-head clashes and subsequent head wrestling and hooking between fighting males (plates 22 and 23). Doming reinforces the frontal region against potentially damaging consequences of fighting in several ways. Relative to flatter frontals, doned frontals provide greater durability against the impact of clashing, more efficient dissemination of the force of impact away from the point of impact, greater cushioning of impact by allowing the skull to rotate forward a short distance after initial impact as deceleration takes place, greater protection of the brain, and greater resistance to the hooking blows of an opponent's horn tips. The reinforced dome allows an aggressor to put relatively more force behind a charge when intending to collide with an opponent head-on, and to concentrate that force into more of a point than could be possible with flat frontals. The relatively flattened nasals are able

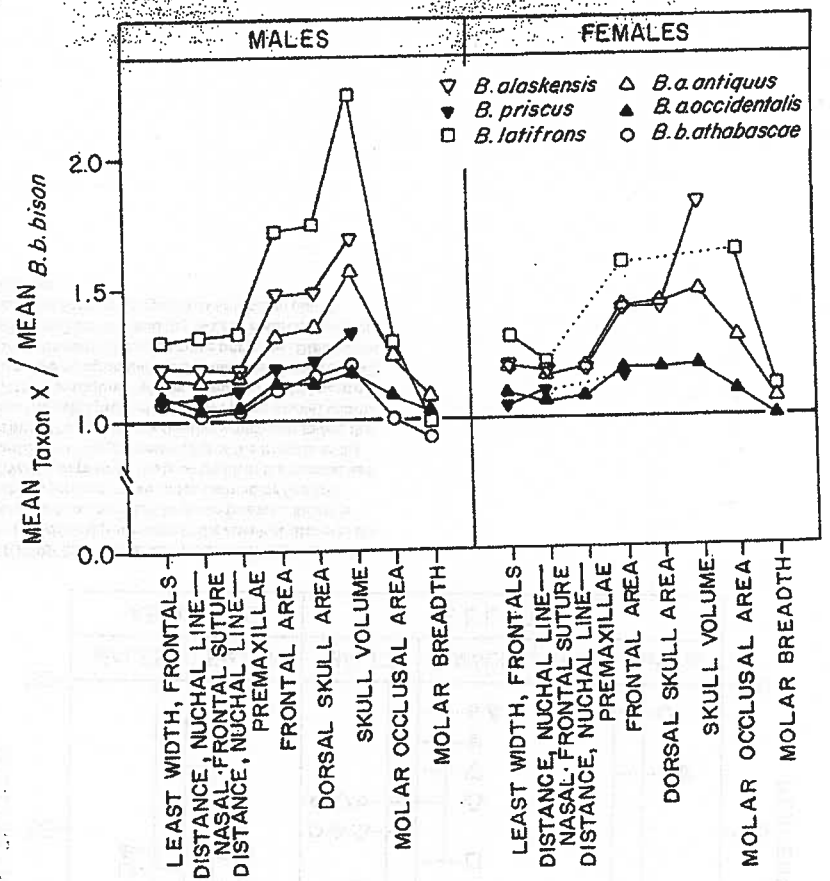


FIGURE 80 Scaled differences: fronto-facial characters. The vertical axis expresses the mean for each taxon as a multiple of the *Bison bison bison* mean.

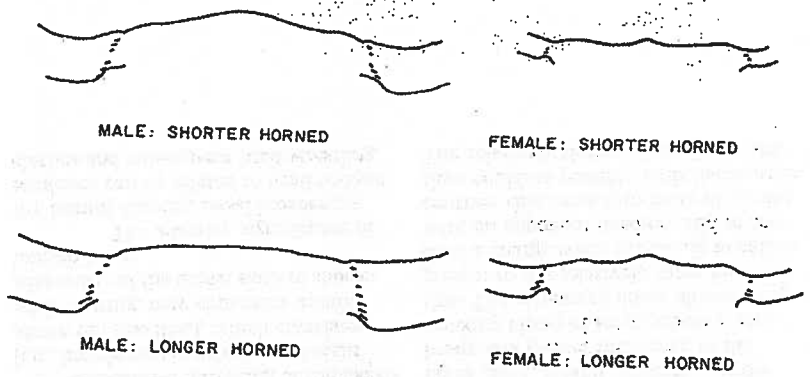


FIGURE 81 Frontal shapes: transverse profiles. The differences among frontal profiles are especially great between longer and shorter horned male bison.

to more effectively sustain the impact of collisions and deflect the hooking horns characteristic of the clashing mode of fighting behavior than are higher, narrower nasals.

Both domed frontals and lowered, broadened nasals occasionally occur in larger horned bison. Consequently, these characters have been available in all taxa and subject to selection. The extreme development of these characters in *B. bison*, and the infrequency of their occurrence in *B. latifrons* suggests that domed frontals and lowered, broadened nasals may represent adaptive differences that accompanied differences in fighting behavior which probably existed between longer and shorter horned bison.

Differences in orbital orientation were observed in skulls. In pre-Holocene bison and many *B. a. occidentalis* skulls the orbits tended to be placed higher (i.e., dorsally) on the cranium and to be directed more forward than is true for *B. bison*. This observation generally concurs with Flerow's (1971) observation on evolutionary change in relative orbital orientation. This observation suggests that pre-Holocene bison had relatively forward-oriented vision and vision requirements, whereas *B. bison* has more laterally oriented vision and vision requirements.

Differences in the absolute and relative protrusion of the orbits also occur among bison taxa. Absolute orbital protrusion is the maximum distance the posterior orbit margin extends laterally from the frontal region. Relative orbital protrusion expresses the narrowest distance across the frontals (standard measurement 14) as a multiple of the greatest width of the frontals at the posterior orbits (standard measurement 15). The greater the relative orbital protrusion, the less protruding are the orbits relative to the frontal width.

Mean absolute and relative orbital protrusion values for each taxon

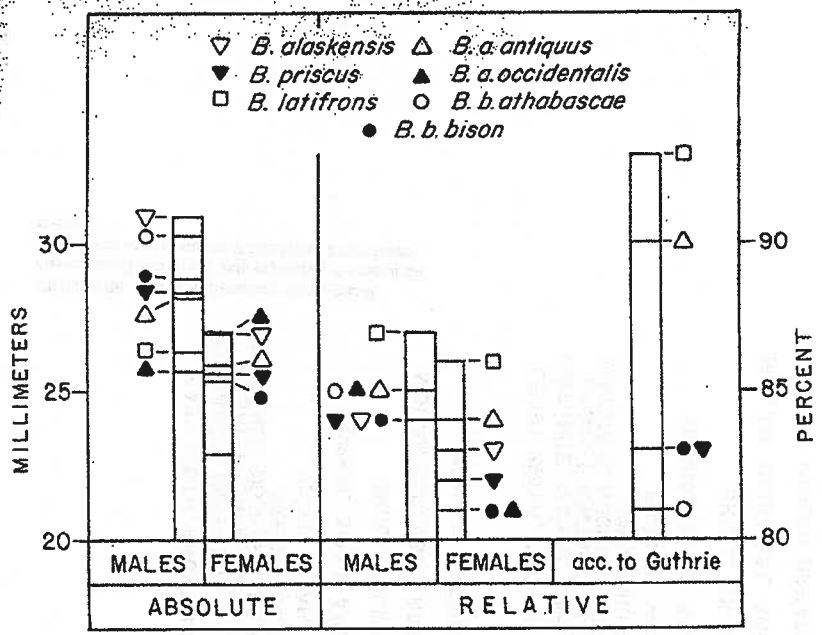


FIGURE 82 Actual and relative orbital protrusion. Actual orbital protrusion is the absolute distance the orbits extend outward from the frontals. Relative orbital protrusion, an index defined by Guthrie (1966*b*), expresses the least width of the frontals as a multiple of the greatest width of the frontals at the orbits. The greater the relative protrusion index, the less the orbit protrudes relative to the frontal width. Guthrie's original indices of relative orbital protrusion, based upon data in Skinner and Kaisen (1947), are presented for comparative purposes. Differences between Guthrie's and my indices result from differences in sample composition and bison classification.

Table 57
Absolute and Relative Orbital Protrusion

Taxon	Absolute Protrusion[a]	Relative Protrusion[b]
Males		
B. b. bison	28.8 mm	.84
B. b. athabascae	30.3 mm	.85
B. a. occidentalis	25.7 mm	.85
B. a. antiquus	28.3 mm	.85
B. latifrons	26.4 mm	.87
B. priscus	28.4 mm	.84
B. alaskensis	31.9 mm	.84
Females		
B. b. bison	25.4 mm	.81
B. b. athabascae	.....	...
B. a. occidentalis	27.1 mm	.81
B. a. antiquus	25.9 mm	.84
B. latifrons	22.9 mm	.86
B. priscus	25.6 mm	.82
B. alaskensis	27.0 mm	.83

Note: Calculations are based on data presented in skull biometric summary tables, chapter 2.
[a]The absolute distance the orbit extends outward from the skull was determined by the formula (SM 15 − SM 14) X 1/2.
[b]The relative protrusion of orbits is determined by the formula SM 14 ÷ SM 15. The larger the index, the less the protrusion (see Guthrie, 1966*b*).

are listed in table 57 and illustrated in figure 82. No special adaptive meaning is apparent in the order of absolute protrusion observed among the various taxa (i.e., absolute protrusion does not correlate with mean body size, inferred behavioral clines, or inferred habitat associations). Differences in relative orbital protrusion among the taxa, however, are ordered in what appears to be an adaptively meaningful way. There is distinct ordering according to mean body size, inferred behavioral clines, and inferred habitat associations. There is no correlation between relative orbital protrusion and latitude, thus no chorocline is represented. At least four explanations can be put forth to account for differences in orbital protrusion.

1. Guthrie (1966*b*) first considered the adaptive significance of relative orbital protrusion and concluded that relative orbital protrusion could serve as an index of the length of pelage on the head, with a lower index indicating longer hair, and a higher index indicating shorter hair; that northern species had a lower index, and therefore longer facial pelage, than did southern species; and that this difference in pelage was due to climatic differences, where northern bison had evolved more pelage with which to withstand the northern climate than was required by southern bison to withstand the southern climate. Guthrie's ordering of taxa, based on data from Skinner and Kaisen (1947), is illustrated in figure 82. *B. bison*, the obvious anomally in Guthrie's model, was considered by him to have only recently evolved from northern bison and to have not yet completely adapted to the more mild southern climate.
2. Geist (1971*a*) has suggested that there exists an inverse relationship between horn size (which is correlated with body size in *Bison*) and body hair. The magnitudes of relative orbital protrusion indices in bison correlate very well with horn and body size as predicted by Geist. Only the male *B. alaskensis* index is anomalous, equaling, but not exceeding, that of *B. priscus*. This anomally is of minor importance. Although females have proportionately lower indices than males, males have wider frontals and both sexes must accommodate a species specific (yet sexually dimorphic) amount and length of hair. In this explanation body (including facial) hair is viewed as a social organ in addition to a thermoregulatory organ, and selection for body hair is considered a social, as well as extra-social, process. Smaller bodied, shorter horned bison in which body hair is strongly selected for (perhaps as a surrogate for actual body size) would expectedly have lower relative orbital protrusion indices than larger bodied, longer horned bison in which the length of body hair, as a social organ, was probably less and may have been a consequence of stronger selection for larger body size or longer horns.
3. A third explanation for differences in relative orbital protrusion indices results from the possibility that patterns of facial hair development did not vary significantly from taxon to taxon. Assuming that the extent of orbital protrusion is causally related to the amount of facial hair present, there should be little or no meaningful difference in absolute orbital protrusion if the amount of facial hair did not vary from taxon to taxon. According to this view, larger bodied bison should have higher relative orbital protrusion indices than smaller bison, but all taxa should have about the same absolute orbital protrusion.
4. A final explanation results from shifts in the orientation of the orbits from higher, more forward directed orbits in pre-Holocene bison to lower, more laterally directed orbits in Holocene bison. The lateral shifts of the orbits, in conjunction with decreasing overall body size, could exaggerate the relative and absolute orbital protrusion in smaller bison vis-à-vis larger bison.

Any one of the foregoing explanations could conceivably account for the differences in absolute and relative orbital protrusion. All were possibly instrumental in producing the observed pattern, although the third explanation is here considered unlikely. Biometric and distribution data, however, suggest that social selection for greater or lesser body hair and morphological changes in orbital placement and orientation were the most important factors influencing orbital protrusion.

In summary, major adaptive differences in the fronto-facial region exist among bison taxa. Longer horned taxa tend to have relatively flatter and less robust frontals, higher and narrower nasals, more forward and dorsally oriented orbits, and higher relative orbital protrusion indices (i.e., less protruding orbits) than do shorter horned taxa.

MOLAR DENTITION

Molar teeth apparently differ among bison taxa only by size. The data presented here indicate that mean body

size and molar occlusal area are correlated in both sexes (table 56: molar occlusal area). The ratio in males between molar occlusal area and the width of the frontals (a rough index of body size) suggests, however, that the occlusal area in larger forest/woodland taxa (*B. latifrons, B. b. athabascae*) is proportionately less than in contemporary smaller savanna/grassland taxa (*B. a. antiquus, B. b. bison*). This is not indicated for females. In all taxa the molar occlusal area:width of frontals is greater in females than males, suggesting that females have greater occlusal area per unit of body weight than males.

The differences between contemporary male forest/woodland and savanna/grassland taxa can be explained as different adaptations to the available forage. Forest/woodland bison would likely feed on less abrasive vegetation than would savanna/grassland bison, and their dentition would therefore wear less rapidly than would the dentition of the savanna/grassland bison. Less molar surface area per unit of body weight would be required in the forest/woodland bison than the savanna/grassland bison. Fossil species were probably longer lived (see chapter 5) than recent bison and therefore possessed a greater occlusal area:body weight ratio as one adaptation permitting longer functional dentition life. More data are needed to support or refute this interpretation based on admittedly limited information. The greater molar occlusal area:body size ratio in females than males can perhaps be attributed to the fact that pregnant and/or nursing females have relatively greater nutritional needs than males and simply need more food per unit of body weight to sustain these critical functions.

OCCIPITAL REGION

The occipital region consists of the posterior wall of the skull, extending from the nuchal line to the basioccipital bones. This region consists of surfaces with which the head is suspended from the neck. Interspecific differences in the contours and alignment of the occipital features appear to have adaptive significance, although some may result from direct selection for other characters. Differences in the shape of the occipital condyles and the angles formed by the occipital plane and the basioccipital axis with the foramen magnum plane are of probable adaptive significance. Intertaxa differences in the occipital area, the relative concavity or flatness of the occipital and the extent of development of the nuchal line and external occipital protuberance are probably evolutionary responses to selection for other characters, such as overall body size and head weight.

The relationship between occipital linear dimensions and area, and overall skull volume is summarized in figure 83 and tables 56, 58, and 59. Larger bodied taxa do tend to have more concave occipitals than smaller taxa, a characteristic resulting from the relatively greater development of the nuchal line/external occipital protuberance and the protrusion of this muscle/ligament attachment crescent and the occipital condyles beyond the occipital plane (plate 24). The greater development of the nuchal line and external occipital protuberance in larger bodied bison taxa indicates that muscles and ligaments normally attached along this line were more extensive than in smaller bodied

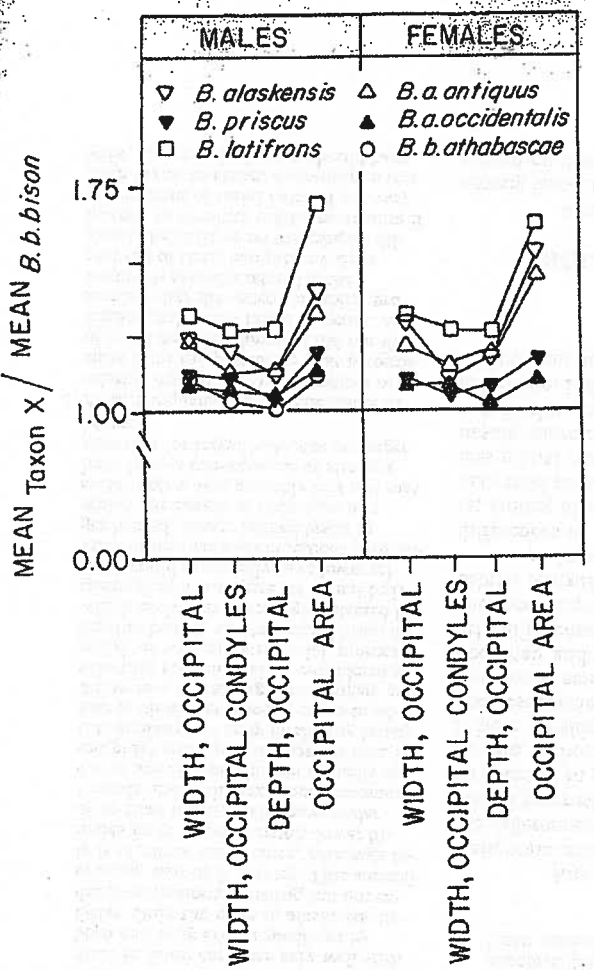


FIGURE 83 Scaled differences: occipital characters. The vertical axis expresses the mean for each taxon as a multiple of the *Bison bison bison* mean.

Table 58

Allometry of Skull Characters Relative to *Bison bison bison*: Areas and Volumes

Taxon	Molar area	Frontal area	Dorsal area	Occipital area	Skull volume
Males					
B. b. athabascae	1.02	1.13	1.17	1.13	1.22
B. a. occidentalis	1.10	1.16	1.15	1.13	1.19
B. a. antiquus	1.25	1.34	1.36	1.33	1.57
B. latifrons	1.30	1.74	1.75	1.68	2.25
B. priscus	....	1.20	1.23	1.18	1.34
B. alaskensis	....	1.49	1.49	1.40	1.70
Females					
B. b. athabascae	....	....	....	....	....
B. a. occidentalis	1.11	1.18	1.19	1.11	1.20
B. a. antiquus	1.30	1.42	1.44	1.46	1.73
B. latifrons	1.46	1.59	....	1.64	....
B. priscus	....	1.16	....	1.17	....
B. alaskensis	....	1.41	1.42	1.53	1.81

Note: The *B. b. bison* mean for each character = 1.00. Values given in the table are multiples of the *B. b. bison* mean. Calculations are based on data presented in table 56.

Table 59

Comparative Biometrics: Skulls with Horn Cores

Taxon	Overall volume (mm^3)	Horn core volume (% total volume)	Allometry relative to *B. b. bison*
Males			
B. b. bison	4,053,743	16.8	1.00
B. b. athabascae	5,222,647	21.0	1.29
B. a. occidentalis	6,384,940	25.2	1.33
B. a. antiquus	6,883,930	22.9	1.69
B. latifrons	18,542,382	59.0	4.57
B. priscus	6,670,482	32.2	1.65
B. alaskensis	10,524,070	45.6	2.60
Females			
B. b. bison	2,332,341	7.3	1.00
B. b. athabascae	.....	....	....
B. a. occidentalis	2,963,875	12.7	1.27
B. a. antiquus	4,209,953	11.0	1.81
B. latifrons	.....	....	....
B. priscus	.....	....	....
B. alaskensis	5,062,021	22.7	2.17

Note: The overall volume is the sum of the mean skull volume and horn core volume for each taxon. The horn core volume is here expressed as a percentage of the overall volume. Allometry here expresses the overall volume as a multiple of the *B. b. bison* mean, where the *B. b. bison* mean = 1.00. Calculations are based on data presented in tables 54 and 56.

bison. This phenomenon is logically explained by the probability that more muscle and ligament mass was necessary to hold and maneuver the head. Protruding occipital condyles direct the weight of the head into more of a point at the atlas than do condyles situated more nearly flush with the occipital plane. The protruding condyles of larger bison, therefore, suggest that these species had a more maneuverable head (laterally and dorso-ventrally) than did smaller bison.

The ventro-lateral margins of occipital condyles characteristically differ in degree of development between larger and smaller bison. In larger bison, and most clearly in *B. latifrons*, the condyle margins are characteristically flanged outward, downward and backward (plate 25). In smaller bison, and most clearly in *B. bison*, the condyle margins are weakly or not at all flanged (plate 26). This flange is interpreted as an adaptation that reduced lateral slippage of the condyles in the cup of the atlas. This would be an obvious advantage to larger bodied, heavier headed bison, considering the relative weight vectors constantly imposed by the long heavy horns and the periodic torque developed when the head was moved quickly, as when startled or in fighting.

Variations in the angles that separate the foramen magnum plane from the basioccipital axis and the occipital plane among bison taxa are also of probably adaptive significance. Within both the North American and Eurasian lineages, the angle between the basioccipital axis and the foramen magnum plane (∠BF) increases with increasing body size, whereas the angle between the occipital plane and the foramen magnum plane (∠OF) decreases with increasing body size (fig. 84; table 60). The differing relationships among the basioccipital, foramen magnum and occipital in different taxa result in differences in the alignment of the vertebral axis (as oriented at the atlas-occipital articulation) with the skull. Smaller bison have heads rotated further downward relative to the vertebral axis than do larger bison (fig. 85). These ordered differences in alignment of the skull with the vertebral column are not easily explained by size, but they do appear to correlate with inferred differences in ecology, social organization, and dominance behavior of bison taxa. A head oriented higher relative to the vertebral column would be better suited for eye-level browsing, whereas a head oriented lower relative to the vertebral column would be better suited for grazing. The vertebral axis is more nearly perpendicular to the frontals in smaller bison than larger bison, a characteristic that would conceivably render the smaller bison better fit than larger bison for fighting with head-to-head clashes. In smaller bison with lower placed heads, the impact of collision would be more directly transferred into the postcranial skeleton and less likely to inflict injury to the neck ligaments and muscles than would be true for larger bison with higher placed heads (fig. 86).

In summary, the occipital region contains characters with probable adaptive significance which vary interspecifically, but mainly by degree. The difference in these characters can be explained in part by direct selection favoring their differential development and in part by indirect selection differentially favoring other characters with which the

Table 60
Occipital Angles

Taxon	Angle between basioccipital and foramen magnum ♂♂	Angle between basioccipital and foramen magnum ♀♀	Angle between occipital and foramen magnum ♂♂	Angle between occipital and foramen magnum ♀♀
B. b. bison	110.5°	109.7°	133.8°	131.8°
B. b. athabascae	113.8°	.....	129.4°	.....
B. a. occidentalis	113.4°	110.2°	129.6°	131.7°
B. a. antiquus	115.6°	115.0°	125.4°	123.8°
B. latifrons	127.4°	119.0°	128.5°	124.0°
B. priscus	117.2°	110.3°	133.2°	134.8°
B. alaskensis	120.5°	112.0°	129.6°	134.0°

Note: Data are from skull biometric summary tables, chapter 2.

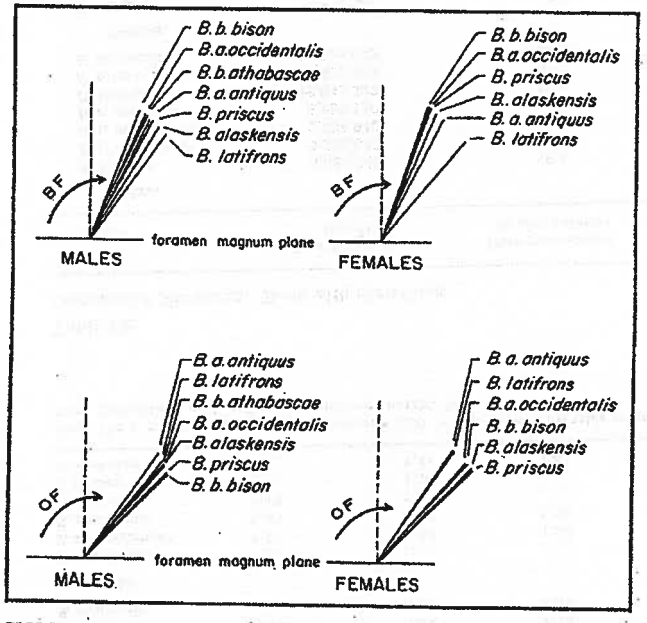


FIGURE 84 Interspecific differences in occipital angles. Top: mean angle separating the foramen magnum and basioccipital planes for each taxon. Bottom: mean angle separating the foramen magnum and occipital planes for each taxon.

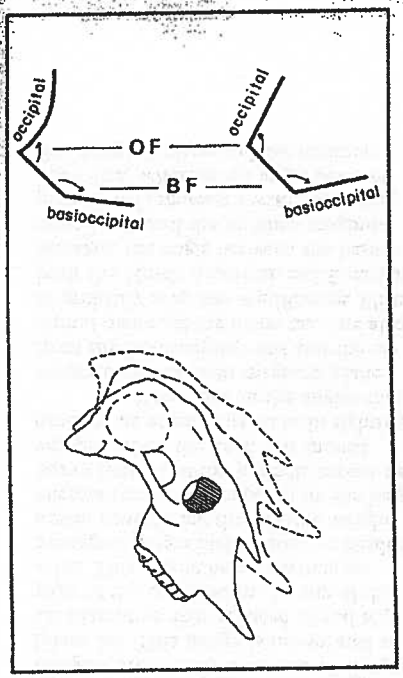


FIGURE 85 Occipital angles and placement of the skull. Top: differences in the relationship among the foramen magnum, basioccipital, and occipital planes between larger, longer horned taxa (left) and smaller, shorter horned taxa (right). Bottom: downward rotation of the head, relative to the vertebral axis, and associated changes in the shape of the occipital. The highest head position is associated with the larger, longer horned taxa while the lowest head is associated with the smaller, shorter horned taxa. The intermediate position represents the relative head placement for smaller pre-Holocene savanna/wooded steppe taxa. Notice the more concave occipital profile for larger taxa and the less concave profile for smaller taxa.

occipital characters are functionally integrated. Differences in the shape of the occipital condyles and the angular arrangement of occipital characters are probably of direct adaptive significance. Species with larger skulls have more strongly developed nuchal lines, external occipital protuberances, protruding occipital condyles, flanged occipital condylar surfaces, greater occipital areas, and heads oriented higher relative to the vertebral axis than do species with smaller skulls. These features are most strongly developed in *B. latifrons*, but they are also well developed in *B. alaskensis* and, to a lesser extent, in *B. priscus* and *B. a. antiquus*. Some of these features, such as the nuchal line and external occipital protuberance, are always obviously present and well developed, even in smaller bison, whereas other features, such as the flanged and protruding occipital condyles, are not usually present in smaller bison.

LIMBS

Limbs are the organs of mobility and elevation in ungulates. Limb length is a determinant of an organism's elevation above the ground or low growing vegetation; feeding strategy; visibility to conspecifics, competitors and

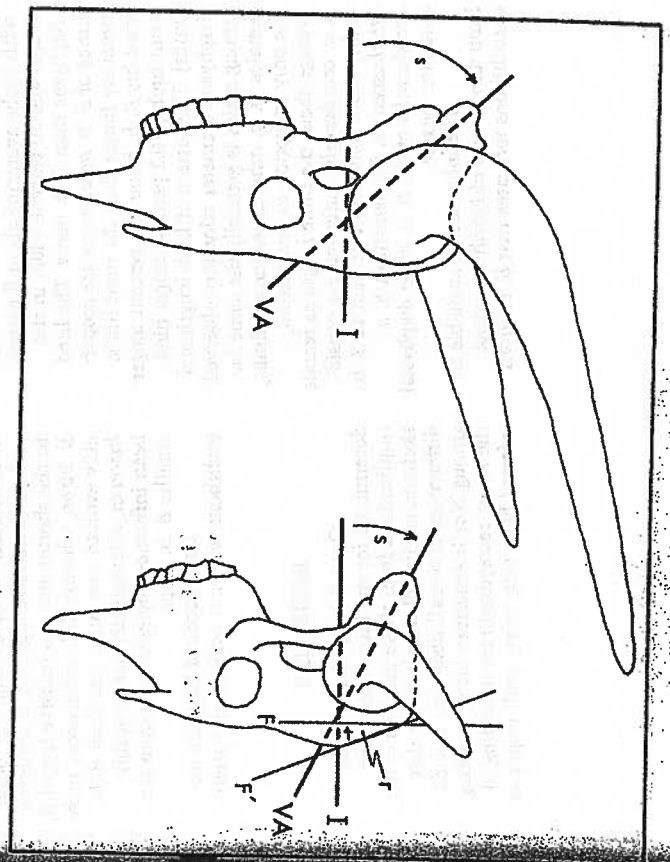


FIGURE 86 Shear and rotation angles of impact. The shear angle (∠s) separates the vertebral axis (VA) and the impact vector (I) resulting from head-to-head collisions. The greater shear angle indicates that greater torque would result from head-to-head collisions and that the energy of impact would less efficiently be transmitted to the postcranial skeleton. A larger shear angle would increase the likelihood of neck injuries resulting from head-to-head collisions. The rotation angle (∠r) is the maximum angle through which the skull can rotate, as deceleration occurs, while the combatants' skulls maintain frontal contact. This rotation, which would be opposed by the elastic ligaments and muscles of the neck, would absorb some of the energy of impact, thereby reducing the total energy transmitted to the skeleton. Notice the large shear angle and the absence of a rotation angle in the larger horned bison, characteristics which render the large bison less suited for head-to-head collisions than smaller bison. (Compare Schaffer [1968] and Stanley [1974] for related discussions of functional differences in skull structure among closely related taxa.)

predators; and mobility, including agility, acceleration and stride length. Limb massiveness is a gross index of the relative weights of organisms.

Among autochthonous North American bison, longer limbed taxa generally have more massive limbs than shorter limbed taxa (tables 49 and 61). *B. latifrons* has the longest limbs and *B. b. bison* has the shortest limbs among

Table 61
Mean Limb Lengths, North American Autochthons

Taxon	Humerus	Radius	Metacarpal	Total front limb	Femur	Tibia	Metatarsal	Total rear limb	Rear limb total: front limb total	Allometry relative to *B. b. bison*	
										Front limb	Rear limb
Males											
B. b. bison	325.9 mm 38.2%	320.6 mm 37.6%	206.3 mm 24.2%	852.7 mm	380.7 mm 37.8%	371.9 mm 36.9%	255.2 mm 25.3%	1007.8 mm	1.18	1.00	1.00
B. b. athabascae	364.5 mm 38.4%	341.3 mm 36.9%	228.7 mm 24.7%	924.5 mm	421.3 mm 37.9%	414.3 mm 37.3%	276.7 mm 24.8%	1111.3 mm	1.20	1.08	1.10
B. a. occidentalis	356.9 mm 38.8%	343.8 mm 37.3%	219.8 mm 23.9%	920.5 mm	403.7 mm 37.5%	403.8 mm 37.4%	270.3 mm 25.1%	1077.5 mm	1.17	1.08	1.07
B. a. antiquus	(355.0 mm) (38.2%)	343.0 mm 37.0%	222.0 mm 23.9%	(927.0 mm)	428.0 mm 38.5%	412.0 mm 36.9%	273.9 mm 24.6%	1114.9 mm	(1.20)	1.09	1.11
B. latifrons	401.7 mm 38.9%	383.2 mm 37.1%	248.6 mm 24.0%	1033.6 mm	491.7 mm 38.7%	456.1 mm 36.8%	303.6 mm 24.4%	1243.4 mm	1.20	1.21	1.23
Females											
B. b. bison	288.3 mm 36.8%	293.0 mm 37.7%	198.9 mm 25.5%	778.2 mm	342.2 mm 37.1%	336.9 mm 36.4%	245.2 mm 26.5%	923.3 mm	1.19	1.00	1.00
B. b. athabascae	304.0 mm 36.3%	313.0 mm 37.4%	220.0 mm 26.3%	837.0 mm	362.0 mm 36.7%	361.0 mm 36.6%	264.0 mm 26.7%	987.0 mm	1.18	1.08	1.07
B. a. occidentalis	321.7 mm 38.0%	318.2 mm 37.1%	211.2 mm 24.9%	848.1 mm	367.6 mm 37.1%	362.2 mm 36.6%	259.9 mm 26.3%	989.7 mm	1.17	1.09	1.07
B. a. antiquus	343.5 mm 38.5%	329.0 mm 36.8%	219.5 mm 24.6%	892.0 mm	400.7 mm 37.9%	390.2 mm 36.9%	266.0 mm 25.2%	1056.9 mm	1.18	1.15	1.14
B. latifrons	346.0 mm 36.2%	359.2 mm 37.7%	248.1 mm 26.1%	952.3 mm	428.7 mm 38.2%	409.5 mm 36.4%	285.3 mm 25.4%	1123.5 mm	1.18	1.22	1.22

Note: Calculations are based on data presented in limb biometric summary tables, chapter 2. Values in parentheses are estimates. Percentage figures beneath mean lengths for each element indicate the percentage of the three-bone total represented by that element.

North American autochthons. The front limb of male *B. latifrons* averages 21 percent longer than the front limb in *B. b. bison;* the hind limb averages 23 percent longer in male *B. latifrons* than in male *B. b. bison* (table 61). Diaphysial diameters of the *B. latifrons* limbs are proportionately much larger than limb lengths vis-à-vis these same characters in *B. b. bison.* Diaphysial diameters range from 18 percent to 43 percent, and average about 30 percent, greater in male *B. latifrons* than *B. b. bison.* Male *B. a. antiquus* have proportionately shorter and less massive limbs than do *B. latifrons,* averaging only about 9 percent longer and 15 percent wider in the diaphyses than *B. b. bison.* Male *B. a. occidentalis* are smaller yet, averaging about 7 percent longer and 9 percent wider in the diaphyses than *B. b. bison.* Male *B. b. athabascae* have larger limbs than *B. a. occidentalis,* with limbs averaging about 9 percent longer and 10 percent wider in the diaphyses than *B. b. bison.* The hind limbs of *B. b. athabascae* are proportionately longer than the front limbs vis-à-bis *B. b. bison* (8.4 percent longer front limbs, 10.2 percent longer hind limbs). The pattern of limb length and diaphysial diameter allometry observed among males is generally the same for females. *B. b. athabascae* female limbs, the only exception to this pattern, average about the same length as female *B. a. occidentalis* limbs but are considerably more slender (4.1 percent in *B. b. athabascae* vs. 8.8 percent in *B. a. occidentalis* of the *B. b. bison* diaphysial diameter means).

The information available for limb dimensions of North American autochthons indicates that *B. latifrons* was a tall and heavy bison not built for sudden movements or prolonged running. The long and massive legs suggest that *B. latifrons* was probably primarily an eyelevel browser, well adapted to feed on shrubs and smaller trees. *B. a. antiquus* was about midway between *B. b. bison* and *B. latifrons* in limb size. The relatively shorter and less massive legs suggest that *B. a. antiquus* was more adapted to feeding on lower growing vegetation (herbs and shrubs), running and agile movements. *B. b. bison,* with the shortest and most slender limbs, appears best adapted of all North American bison to grazing, agile movements, rapid acceleration, and prolonged running. The relative differences of limb length and massiveness between *B. a. occidentalis* and *B. b. athabascae* are probably consequences of their phyletic ancestry and evolutionary directions. *B. a. occidentalis* evolved from the longer and more massive legged *B. a. antiquus* to the shorter and less massive legged *B. b. bison,* whereas *B. b. athabascae* probably evolved to a larger size from *B. b. bison* or, alternatively, has probably been influenced by gene flow from the smaller *B. b. bison.*

Limb bones of Eurasian autochthons were not available for study.

BODY SIZE

Overall body size was not determined for any bison taxon, but implications from those portions of the skeleton studied clearly indicate that differences of overall body size existed among North American bison. Ranking the seven recognized taxa according to inferred body size, using skull length as a guide, *B. latifrons* was largest followed by *B. alaskensis, B. priscus, B. a. antiquus, B. a. occidentalis, B. b. athabascae,* and *B. b. bison.* Difference in body size is of adaptive significance itself, but it also correlates with other adaptive differences, especially differences in longevity, maturation rates, and reproductive potential (Western, 1979).

Generally predictable differences exist between larger bodied and smaller bodied mammals, especially within a closely related and behaviorally similar taxonomic group. Larger-bodied taxa generally live longer, mature more slowly, have fewer offspring per unit of time, have greater absolute energy requirements, consume absolutely more forage (if equalized for nutrition and energy), and have larger space requirements per individual than do smaller bodied taxa (Crandall, 1964; Estes, 1974; Gould, 1977; Hediger, 1964; Morris, 1965; Western, 1979; E. Wilson, 1975). Large body size can be considered adaptive when prolonged sexual maturation, low biotic potential, and available resources combine successfully to maintain population viability in any given selection regime. Larger body size can convey a competitive advantage in the acquisition of food, water, and space; dominance; and defense; and can be considered adaptive so long as the advantages of large body size exceed the disadvantages. Smaller body size can be considered adaptive if more rapid sexual maturation, greater biotic potential, and greater specialization in resource use combine to successfully maintain the species population.

The adaptive significance of differences in maturation rates is closely tied to the nature of selection regimes operating upon populations. The extremes in maturation rates vis-à-vis their adaptiveness to environments are commonly termed r-selected and K-selected (E. Wilson, 1975). Generally speaking, K-selected maturation rates characterize populations that inhabit relatively stable environments and have relatively slow maturation rates and lower biotic potential. These characteristics can result in larger bodied, longer lived individuals with lower overall numbers and lower population densities maintained at or near carrying capacity. R-selected maturation rates characterize populations that inhabit relatively unstable environments and have relatively fast maturation rates and higher biotic potential. These characteristics result in smaller bodied, shorter lived individuals with higher population numbers and densities maintained well below carrying capacity. The significances of r-selected adaptations are that rapidly maturing individuals can potentially contribute to the reproductive effort sooner than more slowly maturing individuals, rapidly expanding populations gain access to available resources before more slowly expanding populations, and the more fecund population can better absorb and rebound from periodic decimation by environmental catastrophies, including predation. Both K- and r-selected maturation rates are, of course, extremes along a continuum and represent only one level of the overall adaptation hierarchy.

6

UNUSUAL MORPHOLOGIES: POSSIBLE EVIDENCE OF HYBRIDIZATION AND GENETIC DRIFT

Many species of large mammals are composed of numerous demes distributed throughout the species' range. Some demes exist on the periphery of the species' range, and individuals from these peripheral demes are likely to disperse into new habitats or regions when dispersal is permitted by environmental changes or instigated by population pressures. Such dispersal has several potential consequences besides range expansion, including hybridization with individuals of other species or isolation from the species' gene pool and the subsequent development of unbalanced polymorphism as a result of genetic drift and inbreeding. Isolation of demes within an established range can also occur if surrounding demes are destroyed or if barriers to interdemic gene flow develop.

Both hybridization and genetic drift are known or inferred to exist among natural populations (e.g., R. Doughty, written comm., August 12, 1979; Heptner, Nasimovitsch, and Bannikov, 1961; Lande, 1976, 1979; McDonnell, Gartside, and Littlejohn, 1978; Palmieri, 1968; Patton, 1973; Schaller, 1977; Schueler and Rising, 1976; Valdez, Nadler, and Bunch, 1978; E. Wilson, 1975; Wint, 1960; Woodruff, 1973; pers. observ.). These processes have received little attention insofar as their roles in accounting for variation in bison morphology are concerned, but hybridization between *B. b. bison* and *B. b. athabascae* has been assumed for bison in Wood Buffalo National Park since the large-scale introduction of *B. b. bison* into the park after 1924, and Wilson (1969, 1974*b*) has invoked both hybridization and genetic drift to explain the high variability and morphological abnormalities that characterize late Wisconsin-early Holocene bison from the western Great Plains. Both processes are important considerations in assessing morphological variation in bison; they simply and logically account for some of the most enduring problems in the study of bison taxonomy and morphological variation, including intermediate phenotypes, abnormal specimens, and the origin of *B. a. occidentalis*.

HYBRIDS AND HYBRIDIZATION

I consider horn cores possessing characters diagnostic of both North American and Eurasian autochthons to be hybrid specimens. Hybrids of only North American (e.g., *B. latifrons* X *B. a. antiquus*) or only Eurasian (e.g., *B. alaskensis* X *B. priscus*) autochthons were not recognized among fossil specimens although such hybrid specimens undoubtedly exist. Adult *B. b. athabascae* collected after 1928 are considered to represent *B. b. athabascae* X *B. b. bison* hybrids. Here I will present information on the nature of variation characterizing what are considered hybrid populations, document the distribution of hybrid specimens, and designate hybrid zones which appear to have existed in the past.

B. b. athabascae X B. b. bison

B. b. athabascae had been nearly exterminated when it was protected by law in 1891. Wood Buffalo reserve was created in 1893 as a refuge for the remaining population. By the early 1920s the *B. b. athabascae* population numbered about 1500 animals. From 1925 to 1928, however, 6,673 *B. b. bison* were released in the Wood Buffalo National Park (Banfield and Novakowski, 1960). The introduced bison freely interbred with the numerically fewer *B. b. athabascae* and, as a result, few true wood bison now remain. Most bison in Wood Buffalo National Park are assumed to be *athabascae* X *bison* hybrids, although a pure population survived in one remote portion of the park (Banfield and Novakowski, 1960). Available biometric data support the contention that widespread hybridization occurred. Bison from Wood Buffalo National Park collected after 1928 are phenotypically intermediate between *B. b. bison* from south of the boreal forest and pre-1929 adult *B. b. athabascae* (tables 64–68).

Table 64

Summary of *Bison bison athabascae* (Post-1928 Adults) Skull Biometrics

Standard measurement	n	Range	Mean ± SE	σ	V
Males					
Spread of horn cores, tip to tip	8	555 – 778 mm	636.1 ± 24.0 mm	67.9 mm	10.6
Horn core length, upper curve, tip to burr	8	183 – 249 mm	218.3 ± 7.0 mm	20.0 mm	9.1
Straight line distance, tip to burr, dorsal horn core	8	167 – 230 mm	195.4 ± 6.2 mm	17.6 mm	9.0
Dorso-ventral diameter, horn core base	8	81 – 109 mm	91.5 ± 3.3 mm	9.5 mm	10.4
Minimum circumference, horn core base	8	233 – 336 mm	280.3 ± 10.2 mm	29.0 mm	10.3
Width of occipital at auditory openings	11	243 – 276 mm	266.2 ± 2.8 mm	9.4 mm	3.5
Width of occipital condyles	10	117 – 142 mm	131.1 ± 2.0 mm	6.5 mm	5.0
Depth, nuchal line to dorsal margin of foramen magnum	10	96 – 114 mm	106.2 ± 1.6 mm	5.0 mm	4.8
Antero-posterior diameter, horn core base	8	77 – 112 mm	91.5 ± 3.6 mm	10.2 mm	11.1
Least width of frontals, between horn cores and orbits	11	264 – 303 mm	284.7 ± 4.0 mm	13.4 mm	4.7
Greatest width of frontals at orbits	11	311 – 365 mm	345.4 ± 5.9 mm	19.6 mm	5.6
M^1–M^3, inclusive alveolar length	0	.....	.....	.....	....
M^3, maximum width, anterior cusp	0	.....	.....	.....	....
Distance, nuchal line to tip of premaxillae	11	512 – 602 mm	565.6 ± 8.6 mm	28.6 mm	5.1
Distance, nuchal line to nasal-frontal suture	11	233 – 268 mm	251.8 ± 3.5 mm	11.9 mm	4.7
Angle of divergence of horn cores, forward from sagittal	7	64° – 69°	66.8° ± 0.9°	2.4°	3.6
Angle between foramen magnum and occipital planes	10	115° – 135°	125.4° ± 2.3°	7.3°	5.8
Angle between foramen magnum and basioccipital planes	10	109° – 127°	117.8° ± 1.8°	5.8°	4.9
Females					
Spread of horn cores, tip to tip	3	429 – 457 mm	440.0 ± 8.6 mm	14.9 mm	3.3
Horn core length, upper curve, tip to burr	3	131 – 177 mm	156.0 ± 13.4 mm	23.2 mm	14.9
Straight line distance, tip to burr, dorsal horn core	3	127 – 144 mm	137.6 ± 5.3 mm	9.2 mm	6.7
Dorso-ventral diameter, horn core base	3	53 – 56 mm	54.3 ± 0.8 mm	1.5 mm	2.8
Minimum circumference, horn core base	3	164 – 180 mm	171.3 ± 4.6 mm	8.0 mm	4.7
Width of occipital at auditory openings	3	205 – 220 mm	213.7 ± 4.4 mm	7.7 mm	3.6
Width of occipital condyles	3	109 – 123 mm	115.3 ± 4.0 mm	7.0 mm	6.1
Depth, nuchal line to dorsal margin of foramen magnum	3	93 – 100 mm	95.3 ± 2.3 mm	4.0 mm	4.2
Antero-posterior diameter, horn core base	3	53 – 59 mm	56.0 ± 1.7 mm	3.0 mm	5.3
Least width of frontals, between horn cores and orbits	3	227 – 232 mm	228.6 ± 1.6 mm	2.8 mm	1.2
Greatest width of frontals at orbits	3	275 – 280 mm	277.0 ± 1.5 mm	2.6 mm	0.9
M^1–M^3, inclusive alveolar length	0	.....	.....	.....	....
M^3, maximum width, anterior cusp	0	.....	.....	.....	....
Distance, nuchal line to tip of premaxillae	3	495 – 514 mm	501.3 ± 6.3 mm	10.9 mm	2.1
Distance, nuchal line to nasal-frontal suture	3	210 – 221 mm	214.0 ± 3.5 mm	6.0 mm	2.8
Angle of divergence of horn cores, forward from sagittal	3	61° – 70°	66.3° ± 2.7°	4.7°	7.1
Angle between foramen magnum and occipital planes	3	124° – 131°	128.0° ± 2.0°	3.6°	2.8
Angle between foramen magnum and basioccipital planes	3	109° – 113°	111.3° ± 1.2°	2.0°	1.8

Note: The above sample was collected after 1928 and is assumed to represent *B. b. athabascae* X *B. b. bison* hybrids.

Table 65

Skull Allometries in *Bison bison athabascae* (Post-1928 Adults)

Standard measurement	Relative to *B. b. bison* ♂♂	Relative to *B. b. bison* ♀♀	Relative to *B. b. athabascae* ♂♂	Relative to *B. b. athabascae* ♀♀
Spread of horn cores, tip to tip	1.05	0.98	0.93	....
Horn core length, upper curve, tip to burr	1.15	1.26	0.93	....
Straight line distance, tip to burr, dorsal horn core	1.13	1.18	0.94	....
Dorso-ventral diameter, horn core base	1.12	1.06	1.00	....
Minimum circumference, horn core base	1.10	1.05	0.97	....
Width of occipital at auditory openings	1.09	1.06	0.97	....
Width of occipital condyles	1.04	1.00	1.00	....
Depth, nuchal line to dorsal margin of foramen magnum	1.08	1.13	1.08	....
Antero-posterior diameter, horn core base	1.10	1.09	0.94	....
Least width of frontals, between horn cores and orbits	1.05	1.05	0.97	....
Greatest width of frontals at orbits	1.06	1.04	0.97	....
M^1 – M^3, inclusive alveolar length	1.00	1.15	0.99	....
M^3, maximum width, anterior cusp	0.98	1.00	0.98	....
Distance, nuchal line to tip of premaxillae	1.04	1.03	0.97	....
Distance, nuchal line to nasal-frontal suture	1.02	1.01	0.98	....

Note: Calculations are based on data presented in tables 29, 34, and 64. The *B. b. athabascae* (post-1928 adults) mean for each character = 1.00. Values reported in this table are multiples of the *B. b. athabascae* (post-1928 adults) mean for each character. Here, post-1928 adult *B. b. athabascae* are synonymous with *B. b. athabascae* X *B. b. bison* hybrids.

Table 66

Summary of *Bison bison athabascae* (Post-1928 Adults) Limb Biometrics

Standard measurement	n	Range	Mean ± SE	σ	V
Males					
Humerus:					
Approximate rotational length of bone	4	324 – 357 mm	346.0 ± 7.5 mm	15.0 mm	4.3
Antero-posterior diameter of diaphysis	4	60 – 65 mm	63.3 ± 1.1 mm	2.3 mm	3.7
Transverse minimum of diaphysis	4	48 – 56 mm	52.3 ± 1.5 mm	3.1 mm	5.9
Radius:					
Approximate rotational length of bone	4	318 – 348 mm	336.3 ± 7.1 mm	14.2 mm	4.2
Antero-posterior minimum of diaphysis	4	32 – 36 mm	34.0 ± 0.9 mm	1.8 mm	5.3
Transverse minimum of diaphysis	4	53 – 59 mm	57.5 ± 1.5 mm	3.0 mm	5.2
Metacarpal:					
Total length of bone	5	205 – 230 mm	220.0 ± 4.1 mm	9.3 mm	4.2
Antero-posterior minimum of diaphysis	5	27 – 31 mm	29.2 ± 0.6 mm	1.4 mm	5.0
Transverse minimum of diaphysis	5	44 – 52 mm	48.6 ± 1.2 mm	2.9 mm	6.1
Femur:					
Approximate rotational length of bone	4	372 – 433 mm	409.3 ± 13.0 mm	26.1 mm	6.3
Antero-posterior diameter of diaphysis	4	47 – 55 mm	51.0 ± 1.8 mm	3.6 mm	7.1
Transverse minimum of diaphysis	4	48 – 51 mm	49.5 ± 0.5 mm	1.2 mm	2.6
Tibia:					
Approximate rotational length of bone	4	362 – 411 mm	389.8 ± 10.4 mm	20.9 mm	5.3
Antero-posterior minimum of diaphysis	4	36 – 38 mm	37.0 ± 0.4 mm	0.8 mm	2.2
Transverse minimum of diaphysis	4	48 – 53 mm	51.0 ± 1.0 mm	2.1 mm	4.2
Metatarsal:					
Total length of bone	4	256 – 279 mm	268.0 ± 5.4 mm	10.8 mm	4.0
Antero-posterior minimum of diaphysis	5	30 – 35 mm	32.6 ± 0.8 mm	1.9 mm	5.9
Transverse minimum of diaphysis	6	34 – 39 mm	37.5 ± 0.8 mm	2.0 mm	5.5
Females					
Humerus:					
Approximate rotational length of bone	1	.....	303.0 mm	.....	...
Antero-posterior diameter of diaphysis	1	.....	48.0 mm	.....	...
Transverse minimum of diaphysis	1	.....	41.0 mm	.....	...
Radius:					
Approximate rotational length of bone	1	.....	310.0 mm	.....	...
Antero-posterior minimum of diaphysis	1	.....	26.0 mm	.....	...
Transverse minimum of diaphysis	1	.....	45.0 mm	.....	...
Metacarpal:					
Total length of bone	2	210 – 218 mm	214.0 ± 3.9 mm	5.6 mm	2.6
Antero-posterior minimum of diaphysis	2	24 – 25 mm	24.5 ± 0.4 mm	0.7 mm	2.8
Transverse minimum of diaphysis	2	37 – 40 mm	38.5 ± 1.4 mm	2.1 mm	5.5
Femur:					
Approximate rotational length of bone	1	.....	360.0 mm	.....	...
Antero-posterior diameter of diaphysis	1	.....	43.0 mm	.....	...
Transverse minimum of diaphysis	1	.....	41.0 mm	.....	...
Tibia:					
Approximate rotational length of bone	1	.....	348.0 mm	.....	...
Antero-posterior minimum of diaphysis	1	.....	30.0 mm	.....	...
Transverse minimum of diaphysis	1	.....	42.0 mm	.....	...
Metatarsal:					
Total length of bone	2	256 – 260 mm	258.0 ± 1.9 mm	2.8 mm	7.1
Antero-posterior minimum of diaphysis	2	.....	28.0 mm	.....	...
Transverse minimum of diaphysis	2	29 – 33 mm	31.0 ± 1.9 mm	2.8 mm	9.1

Note: The above sample was collected after 1928 and is assumed to represent *B. b. athabascae* X *B. b. bison* hybrids.

Table 67

Limb Bone Allometries in *Bison bison athabascae* (Post-1928 Adults) Relative to True *Bison bison bison* and *Bison bison athabascae*

Standard measurement	Relative to *B. b. bison*		Relative to *B. b. athabascae*	
	♂♂	♀♀	♂♂	♀♀
Humerus:				
Approximate rotational length of bone	1.06	1.06	.98	.99
Antero-posterior diameter of diaphysis	1.03	.96	.93	.96
Transverse minimum of diaphysis	1.03	1.02	.89	1.02
Radius:				
Approximate rotational length of bone	1.05	1.06	.98	.99
Antero-posterior minimum of diaphysis	1.06	.98	.97	.92
Transverse minimum of diaphysis	1.07	1.04	.96	.97
Metacarpal:				
Total length of bone	1.07	1.08	.96	.97
Antero-posterior minimum of diaphysis	1.07	1.02	.96	.94
Transverse minimum of diaphysis	1.07	1.05	.93	.98
Femur:				
Approximate rotational length of bone	1.07	1.05	.97	.99
Antero-posterior diameter of diaphysis	1.06	1.04	.94	.98
Transverse minimum of diaphysis	1.05	1.01	.96	1.00
Tibia:				
Approximate rotational length of bone	1.05	1.04	.97	.96
Antero-posterior minimum of diaphysis	1.06	.99	.97	.94
Transverse minimum of diaphysis	1.04	1.00	.95	.98
Metatarsal:				
Total length of bone	1.05	1.05	.97	.98
Antero-posterior minimum of diaphysis	1.08	1.02	.98	.97
Transverse minimum of diaphysis	1.07	1.06	.96	1.00

Note: Calculations are based on data presented in tables 30, 35, and 66. The *B. b. athabascae* (post-1928 adults) mean for each character = 1.00. Values reported in the table are multiples of the *B. b. athabascae* (post-1928 adults) mean for each character. *B. b. athabascae* (post-1928 adults) are assumed to be *B. b. athabascae* X *B. b. bison* hybrids.

Table 68

Bison bison athabascae (Post-1928 Adults): Referred Specimens

Institution and identification number		Sex	Provenience
AMNH	M 86950	♂	Wood Buffalo National Park (1935)
AMNH	M 98228	♂	10 miles from Slave River, Alberta (1935)
AMNH	M 98229	♂	10 miles from Slave River, Alberta (1935)
AMNH	M 98953	♂	Salt Lick, Five Acre Wallow, Wood Buffalo National Park (1936)
AMNH	M 98954	♀	Salt Plain, 7 mile camp, Alberta (1934)
AMNH	M 98957	♀	Salt Plain, 7 mile camp, Alberta (1934)
AMNH	M 130171	♂	Salt River, Wood Buffalo National Park (1936)
NMC	M 11436	♂	Cabin 7, Murdock Creek, Wood Buffalo National Park
NMC	M 24026	♂	Nyarling River, Frying Pan Lake, Wood Buffalo National Park
NMC	M 39876	♀	Needle Lake Area, Wood Buffalo National Park (1968)
PMA	Z 68.31.1	♂	Wood Buffalo National Park (1930s)
PMA	Z 73.82.1	♂	Elk Island National Park, Alberta (1973)
PMA	Z 74.86.1	♂	Alberta Game Farm, Alberta (1974)
USNM	M 263390	♂	Fort Fitzgerald, Alberta (1936-7)

Note: These specimens were collected after 1928; known dates of collection are given in parentheses.

Male *athabascae* X *bison* hybrids average about 5 percent larger than *B. b. bison* in frontal and occipital characters, but about 11 percent larger than *B. b. bison* in horn core characters (table 65). *Athabascae* X *bison* hybrids average about 1.5 percent smaller than pre-1929 adult *B. b. athabascae* in frontal and occipital characters, but almost 5 percent smaller than true *B. b. athabascae* in horn core characters (table 65). The limbs of crosses are about 6 percent larger than *B. b. bison* and about 4 percent smaller than true *B. b. athabascae* (tables 66 and 67). Female crosses show similar size differences. *Athabascae* X *bison* crosses are, therefore, phenotypically intermediate between *B. b. bison* and true *B. b. athabascae*, but they are nearer *B. b. athabascae* than *B. b. bison* in size. Male horn cores are proportionately larger than other skeletal characters in the crosses, which suggests the nature of selection in the parkland environment. The numerical superiority of *B. b. bison* to *B. b. athabascae* immediately following the releases of plains bison into Wood Buffalo National Park during the late 1920s could have resulted in the complete swamping of wood bison by plains bison. The fact that *athabascae* X *bison* crosses are nearer true *B. b. athabascae* than *B. b. bison* in size suggests that selection has been relatively stronger than simple genotypic frequency (in late 1920s) in determining the resultant phenotypic characters of hybrids. The forest/woodland adaptation model presented in chapter 5 emphasized the intensity of selection characteristic of these habitat types and the adaptive value of both larger body size and exaggerated dominance organs. Larger horns and larger body size would predictably convey greater competitive and dominance fitness than would smaller characters. Larger phenotypes, with emphasis on larger horns, would, therefore, be selectively favored by the relatively wooded environment of Wood Buffalo National Park.

In contrast, size increase, especially of horn cores, has been attributed to an abundance of nutritious forage (Geist, 1971*a*, oral comm., September 2, 1978; Guthrie, 1966*a*; 1970; 1978). If environmental benevolence alone were the determinant of organic and character size, however, the *athabascae* X *bison* hybrids should be as large as true *B. b. athabascae*; they are not.

Bison "crassicornis"

The term *B. crassicornis* was introduced by Richardson (1852–1854) as the name for a new species of heavy horned bison from Alaska. Skinner and Kaisen (1947) recognized *B. crassicornis* as a species in their revision, and the term is still used in publications, although normally as a subspecies or synonym of *B. priscus*. Herein, *B. "crassicornis"* is used in reference to all hybrids of North American X Eurasian autochthons from the Beringian region regardless of the species involved (which in most cases can only be guessed anyway). Specimens identified as *B. "crassicornis"* constitute a majority of the skulls studied from Beringia. The fact that many specimens from Beringia show diagnostic characters of both North American and Eurasian autochthons, that these specimens occur in the most likely zone of contact between dispersing populations from both continents (fig. 90), and that dispersals of taxa

into Beringia from both continents have been confirmed by nonhybrid specimens collected from Beringia, lead to the conclusion that the specimens that possess shared characters can reasonably be considered hybrids.

B. "crassicornis" averages smaller than other pre-Holocene North American bison in most skull characters, but the minimum observed size for most characters in *B. "crassicornis"* is usually very near or greater than the minima observed for the same characters in other pre-Holocene North American bison. Horn core characters in *B. "crassicornis,"* however, tend to be either larger than, or intermediate to, those of *B. priscus* or *B. a. antiquus*, the two pre-Holocene taxa most nearly resembling *B. "crassicornis"* and the two taxa that, probably, most frequently interbred to give rise to these hybrids. Limb evidence from Old Crow River and Lost Chicken Creek suggests that *B. "crassicornis"* was about the same size as *B. a. antiquus* (figs. 45–56) or perhaps a little smaller, considering that the smaller limb elements from the Fairbanks and Dawson areas probably represent *B. "crassicornis"* as well as *B. priscus* (and, perhaps, *B. a. antiquus* and *B. bison* as well). The distribution of cases within character samples is normal or near normal for both sexes and the ranges of variation for samples are about what is expected (fig. 57; table 69). Sexual dimorphism is somewhat greater than is observed in other samples (tables 46 and 70), and the coefficients of variation tend to be lower than those observed in other samples (tables 50 and 69).

The fact that *B. "crassicornis"* horn cores are larger than, or intermediate to, those of *B. a. antiquus* or *B. priscus*, and that other skull characters average smaller than those of *B. a. antiquus* or *B. priscus*, presents a problem that can be resolved to a degree by consulting the analyses of variation among bison (chapter 3) and the various adaptation models developed earlier (chapter 5). Mean coefficients of variation for bison skull and limb characters (tables 52 and 53) show that horn cores are more variable than other skeletal characters. The differences between r- and K-selection regimes were noted in chapter 5. Beringia was probably characterized by a relatively r-type selection regime for large herbivores during the transition to glacial or stadial periods. This occurred because available habitat and carrying capacity increased as ocean levels dropped and interglacial/interstadial forests and woodlands withdrew to more suitable environments or disintegrated. At other times the subaerial Beringian environment was probably characterized by a K-type selection regime. This is because once the habitat made available by the onset of glacial/stadial conditions became completely occupied by the megaherbivores, populations would tend to approximate the region's carrying capacity.

The small mean size of *B. "crassicornis"* is explained by the spread of *B. a. antiquus* and *B. priscus* populations into Beringia during the onset of glacial/stadial conditions. Dispersal through this relatively r-type selection regime permitted greater representation of small phenotypes in the population as the formerly dominant K-type selection regimes, prevailing on both sides of Beringia, were relaxed. Smaller phenotypes, then, would characterize the r-type, or

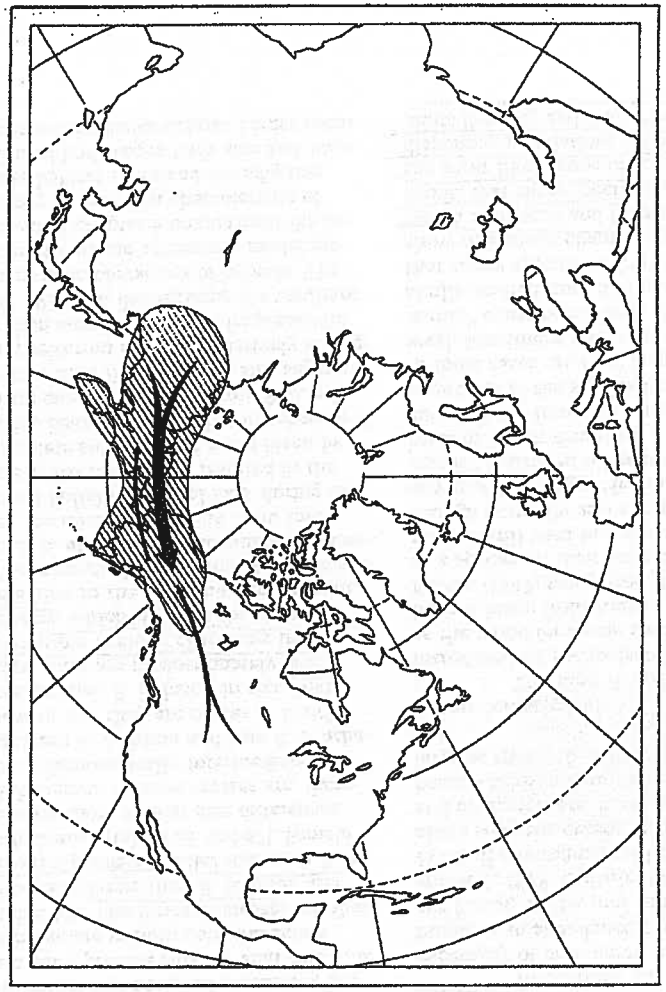


FIGURE 90 The Beringian hybrid zone. The heavy arrow represents the strong dispersal of Eurasian bison into glacial/stadial eastern Beringia. The lighter arrows represent the moderate dispersal of North American bison into (a) interglacial/interstadial Alaska and (b) glacial/stadial Siberia.

Table 69

Summary of *"Bison crassicornis"* Skull Biometrics

Standard measurement	n	Range	Mean ± SE	σ	V
Males					
Spread of horn cores, tip to tip	46	535 – 1192 mm	928.8 ± 17.4 mm	118.4 mm	12.7
Horn core length, upper curve, tip to burr	63	292 – 512 mm	390.8 ± 5.9 mm	47.0 mm	12.0
Straight line distance, tip to burr, dorsal horn core	63	282 – 458 mm	350.7 ± 5.1 mm	40.8 mm	11.6
Dorso-ventral diameter, horn core base	73	90 – 133 mm	102.1 ± 0.9 mm	7.8 mm	7.6
Minimum circumference, horn core base	73	297 – 375 mm	325.2 ± 2.3 mm	20.4 mm	6.2
Width of occipital at auditory openings	50	252 – 292 mm	271.6 ± 1.3 mm	9.6 mm	3.5
Width of occipital condyles	55	126 – 161 mm	139.8 ± 0.8 mm	6.1 mm	4.4
Depth, nuchal line to dorsal margin of foramen magnum	57	96 – 115 mm	101.1 ± 0.8 mm	6.2 mm	6.1
Antero-posterior diameter, horn core base	73	96 – 135 mm	110.1 ± 0.8 mm	8.4 mm	7.6
Least width of frontals, between horn cores and orbits	60	251 – 311 mm	286.3 ± 1.8 mm	14.0 mm	4.9
Greatest width of frontals at orbits	46	320 – 397 mm	346.0 ± 2.1 mm	14.6 mm	4.2
M^1–M^3, inclusive alveolar length	0	.....	.....	.....	...
M^3, maximum width, anterior cusp	0	.....	.....	.....	...
Distance, nuchal line to tip of premaxillae	8	582 – 629 mm	600.1 ± 5.9 mm	16.8 mm	2.8
Distance, nuchal line to nasal-frontal suture	16	248 – 313 mm	274.8 ± 4.0 mm	15.8 mm	5.7
Angle of divergence of horn cores, forward from sagittal	20	64° – 81°	73.1° ± 0.6°	4.1°	5.6
Angle between foramen magnum and occipital planes	59	115° – 150°	133.2° ± 0.9°	7.4°	5.5
Angle between foramen magnum and basioccipital planes	59	108° – 130°	116.2° ± 0.7°	5.4°	4.7
Females					
Spread of horn cores, tip to tip	14	517 – 667 mm	591.6 ± 10.6 mm	397.7 mm	6.7
Horn core length, upper curve, tip to burr	13	171 – 275 mm	217.9 ± 7.9 mm	28.8 mm	13.2
Straight line distance, tip to burr, dorsal horn core	13	165 – 251 mm	208.5 ± 6.7 mm	24.4 mm	11.7
Dorso-ventral diameter, horn core base	19	57 – 72 mm	63.0 ± 0.8 mm	3.5 mm	5.6
Minimum circumference, horn core base	18	183 – 223 mm	198.9 ± 2.4 mm	10.5 mm	5.2
Width of occipital at auditory openings	3	218 – 225 mm	220.7 ± 2.1 mm	3.7 mm	1.7
Width of occipital condyles	8	120 – 134 mm	125.5 ± 1.6 mm	4.8 mm	3.8
Depth, nuchal line to dorsal margin of foramen magnum	4	86 – 91 mm	87.7 ± 1.9 mm	3.9 mm	4.5
Antero-posterior diameter, horn core base	15	57 – 89 mm	62.6 ± 0.7 mm	3.4 mm	6.4
Least width of frontals, between horn cores and orbits	18	202 – 242 mm	222.4 ± 2.1 mm	9.4 mm	4.2
Greatest width of frontals at orbits	14	254 – 308 mm	277.9 ± 3.5 mm	13.7 mm	4.9
M^1–M^3, inclusive alveolar length	0	.....	.....	.....	....
M^3, maximum width, anterior cusp	0	.....	.....	.....	....
Distance, nuchal line to tip of premaxillae	1	.....	561.0 mm	.....	....
Distance, nuchal line to nasal-frontal suture	5	218 – 240 mm	232.0 ± 3.8 mm	8.6 mm	3.7
Angle of divergence of horn cores, forward from sagittal	19	61° – 77°	68.8° ± 1.0°	4.4°	6.3
Angle between foramen magnum and occipital planes	6	123° – 132°	127.0° ± 1.3°	3.3°	2.6
Angle between foramen magnum and basioccipital planes	7	107° – 116°	111.6° ± 1.3°	3.6°	3.3

Table 70

Absolute and Relative Sexual Dimorphism in *"Bison crassicornis"* Skulls

Standard measurement	Absolute (mm)	Relative[a]
Spread of horn cores, tip to tip	337	.63
Horn core length, upper curve, tip to burr	173	.55
Straight line distance, tip to burr, dorsal horn core	142	.59
Dorso-ventral diameter, horn core base	39	.61
Minimum circumference, horn core base	126	.61
Width of occipital at auditory openings	51	.81
Width of occipital condyles	14	.89
Depth, nuchal line to dorsal margin of foramen magnum	13	.86
Antero-posterior diameter, horn core base	47	.56
Least width of frontals, between horn cores and orbits	64	.77
Greatest width of frontals at orbits	68	.80
M^1 – M^3, inclusive alveolar length	...	...
M^3, maximum width, anterior cusp	...	...
Distance, nuchal line to tip of premaxillae	39	.93
Distance, nuchal line to nasal-frontal suture	43	.84

[a]The male mean for each character = 1.00. Values given are multiples of the male mean.

Note: Calculations are based on data presented in table 69.

colonization, phase of the megaherbivore occupation of glacial/stadial Beringia. (See Geist [1971*b*, 1974], for a sharply contrasting point of view.) The meeting of eastward dispersing Eurasian autochthons and westward dispersing North American autochthons (fig. 90) would result in hybridization between the two.

Once the available habitat was completely occupied and a more K-selection regime had developed, selection for large size would again occur. Presumably, the most variable characters would be the first to respond to selection, and the least variable characters would be the last to respond to selection. Thus, according to this reasoning, K-selection would result in larger horns appearing in phenotypes before other, less variable characters showed size increases. Also, with the passing of time, the K-selected *B. priscus* population would probably expand into Beringia and swamp the hybrid populations.

An alternate point of view, and the traditional one, maintains that what is here considered *B. "crassicornis"* was ancestral to Holocene North American bison. According to this point of view Beringian bison became smaller near the end of the Wisconsin and some populations of these dwarfing bison dispersed southward into midlatitude North America and there gave rise to *B. occidentalis* (= *B. a. occidentalis* of this classification) and *B. bison*. Evidence presented in chapters 3 and 5, however, suggests that horn cores should perhaps be the first and most obvious of characters to change, not the last. A further difficulty is that the *B. "crassicornis"* sample (table 71) probably represents a longer period of time than just the late Wisconsin, and it probably overlaps with *B. priscus*, *B. a. antiquus*, and *B. alaskensis* samples as well. *B. "crassicornis"* is better considered a hybrid than a discrete regional taxon because it is not morphologically distinct from *B. priscus* and *B. a. antiquus*, but it is instead generally intermediate, and the environment of late Quaternary Beringia was too dynamic, habitats were too varied over several glacial and interglacial oscillations, and other species of bison were too frequently present to convincingly argue that *B. "crassicornis"* was specifically distinct and homeostatic. Beringia was probably much more important as a megafaunal crossroad and mixing tank than a source area for new taxa.

Hybrid Zones

Eurasian autochthons occur widely over Beringia and midlatitude North America (figs. 26 and 27). So, too, do specimens that possess diagnostic characters of both North American and Eurasian autochthons, and, although these are relatively rare south of Beringia, they serve to identify zones where hybridization seems to have taken place between North American and Eurasian autochthons.

The most intense zone of hybridization was Beringia, which alternated between being an easterly extension of the Palearctic during glacial/stadial periods and a Nearctic outlier during interglacial/interstadial periods. Over half of the skulls studied from Alaska and northwest Canada shared North American and Eurasian characters. This zone probably formed as eastern Siberian bison dispersed eastward into Beringia during the onset of

Table 71

"Bison crassicornis": Referred Specimens

Institution and identification number	Sex	Provenience
AMNH VP F:AM13721	♂	Fox Gulch, Yukon Territory
AMNH VP F:AMA173-8103	♀	Ester Creek, Alaska
AMNH VP F:AMA256-7389	♀	Goldstream at Fox, Alaska
AMNH VP F:AMA284-6594	♀	Goldstream at Fox, Alaska
AMNH VP F:AMA284-6595	♀	Goldstream at Fox, Alaska
AMNH VP F:AMA284-6600	♀	Goldstream at Fox, Alaska
AMNH VP F:AMA437-1348	♂	Fairbanks area, Alaska
AMNH VP F:AMA449-1041	♀	Fairbanks Creek, Alaska
AMNH VP F:AMA502-1013	♀	Fairbanks Creek, Alaska
AMNH VP F:AMA579-2034	♀	Fairbanks Creek, Alaska
AMNH VP F:AMA579-2036	♀	Fairbanks Creek, Alaska
AMNH VP F:AMA580-2037	♀	Fairbanks Creek, Alaska
AMNH VP F:AMA580-2040	♀	Goldstream at Fox, Alaska
AMNH VP F:AMA605-1003	♂	Fairbanks Creek, Alaska
AMNH VP F:AMA605-1022	♀	Fairbanks Creek, Alaska
AMNH VP F:AMA605-3002	♂	Dome Creek, Alaska
AMNH VP F:AMA606-1082	♂	Fairbanks Creek, Alaska
AMNH VP F:AMA606-1103	♀	Fairbanks Creek, Alaska
AMNH VP F:AMA683-3244	♂	Dome Creek, Alaska
AMNH VP F:AMA683-3251	♂	Dome Creek, Alaska
AMNH VP F:AMA683-3256	♂	Dome Creek, Alaska
AMNH VP F:AMA683-8090	♂	Chatam Creek, Alaska
AMNH VP F:AMA684-3253	♀	Dome Creek, Alaska
AMNH VP F:AMA685-3262	♀	Dome Creek, Alaska
AMNH VP F:AMA685-3265	♂	Dome Creek, Alaska
AMNH VP F:AMA698-2026	♂	Fairbanks Creek, Alaska
AMNH VP F:AMA698-2031	♀	Fairbanks Creek, Alaska
AMNH VP F:AMA862-	♀	Cleary Creek, Alaska
AMNH VP F:AMA863-	♀	Cleary Creek, Alaska
AMNH VP F:AM30512	♂	Cleary Creek, Alaska
AMNH VP F:AM30517	♂	Fairbanks area, Alaska
AMNH VP F:AM30523	♂	Goldstream, Alaska
AMNH VP F:AM30524	♂	Fairbanks area, Alaska
AMNH VP F:AM30526	♂	Fairbanks area, Alaska
AMNH VP F:AM30529	♂	Fairbanks area, Alaska
AMNH VP F:AM30530	♂	Cleary Creek, Alaska
AMNH VP F:AM30533	♂	Fairbanks area, Alaska
AMNH VP F:AM30541	♂	Fairbanks area, Alaska
AMNH VP F:AM30551	♂	Lillian Creek, Alaska
AMNH VP F:AM30558	♂	17 miles north of Fairbanks, Alaska
AMNH VP F:AM30567	♂	Cleary Creek, Alaska
AMNH VP F:AM30571	♂	Cleary Creek, Alaska
AMNH VP F:AM30582	♂	Cleary Creek, Alaska
AMNH VP F:AM30583	♂	Cleary Creek, Alaska
AMNH VP F:AM30588	♂	Goldstream, Alaska
AMNH VP F:AM30595	♂	Cleary Creek, Alaska
AMNH VP F:AM30601	♂	Goldstream, Alaska
AMNH VP F:AM30617	♂	Cleary Creek, Alaska
AMNH VP F:AM30618	♂	Cleary Creek, Alaska
AMNH VP F:AM30622	♂	Gilmore Creek, Alaska
AMNH VP F:AM30629	♂	Fairbanks area, Alaska

Table 71

"Bison crassicornis": Referred Specimens (Continued)

Institution and identification number	Sex	Provenience
AMNH VP F:AM30631	♂	Goldstream, Alaska
AMNH VP F:AM30644	♂	Goldstream, Alaska
AMNH VP F:AM30648	♂	Upper Cleary Creek, Alaska
AMNH VP F:AM30651	♂	Cleary Creek, Alaska
AMNH VP F:AM30653	♂	Goldstream at Fox, Alaska
AMNH VP F:AM32761	♂	Alder Creek, Seward Peninsula, Alaska
AMNH VP F:AM46884	♂	Goldstream, Alaska
AMNH VP F:AM46886	♂	Upper Cleary Creek, Alaska
AMNH VP F:AM46888	♂	Goldstream, Alaska
AMNH VP F:AM46889	♂	Upper Cleary Creek, Alaska
AMNH VP F:AM46890	♂	El Dorado Creek, near Fairbanks, Alaska
AMNH VP F:AM46891	♂	Cripple Creek, Alaska
AMNH VP F:AM46892	♂	Engineer Creek, Alaska
AMNH VP F:AM46894	♂	Cripple Creek, Alaska
AMNH VP F:AM46895	♂	Ester Creek, Alaska
AMNH VP F:AM46908	♂	Ester Creek, Alaska
AMNH VP F:AM46911	♂	Upper Cleary Creek (?), Alaska
AMNH VP F:AM46914	♂	Upper Cleary Creek, Alaska
KU VP 8348	♂	Fairbanks area, Alaska
NMC VP 7700	♂	Last Chance Creek, Yukon Territory
NMC VP 8145	♂	Bonanza Creek, Yukon Territory
NMC VP 10468	♂	Hunker Creek, Yukon Territory
NMC VP 10459	♂	Hunker Creek, Yukon Territory
NMC VP 10460	♂	Hunker Creek, Yukon Territory
NMC VP 11674	♂	Gold Bottom Creek, Yukon Territory
NMC VP 11683	♂	Brewer Creek, Yukon Territory
NMC VP 12098	♂	Aklavik (?), Northwest Territories
NMC VP 13510	♂	Gold Run Creek, Yukon Territory
NMC VP 17687	♀	Locality 11, Old Crow River, Yukon Territory
NMC VP 17689	♂	Porcupine River, Yukon Territory
NMC VP 20634	♂	Locality 11, Old Crow River, Yukon Territory
NMC VP 24200	♂	Locality 11A, Old Crow River, Yukon Territory
NMC VP 25219	♂	Bonanza Creek, Yukon Territory
NMC VP 26026	♂	Quartz Creek, Yukon Territory
PPHM 1407-1	♂	Fairbanks Creek, Alaska
PPHM 1407-2	♂	Fairbanks Creek, Alaska
TTM 962-1	♂	Livengood, Alaska
TTM 962-2	♂	Head of Ester Creek, Alaska
USNM P 2643	♂	Old Crow River, Yukon Territory
USNM P 8584	♂	Kolyma River, Siberia
YPM VP 5938	♂	Ketchum Creek, Alaska
YPM VP 33873	♂	Upper Cleary Creek, Alaska

Note: Only those specimens which appeared to have diagnostic characters of both North American and Eurasian autochthons, and are from the Beringian area, are included in this table. Other probable hybrids are identified in table 72.

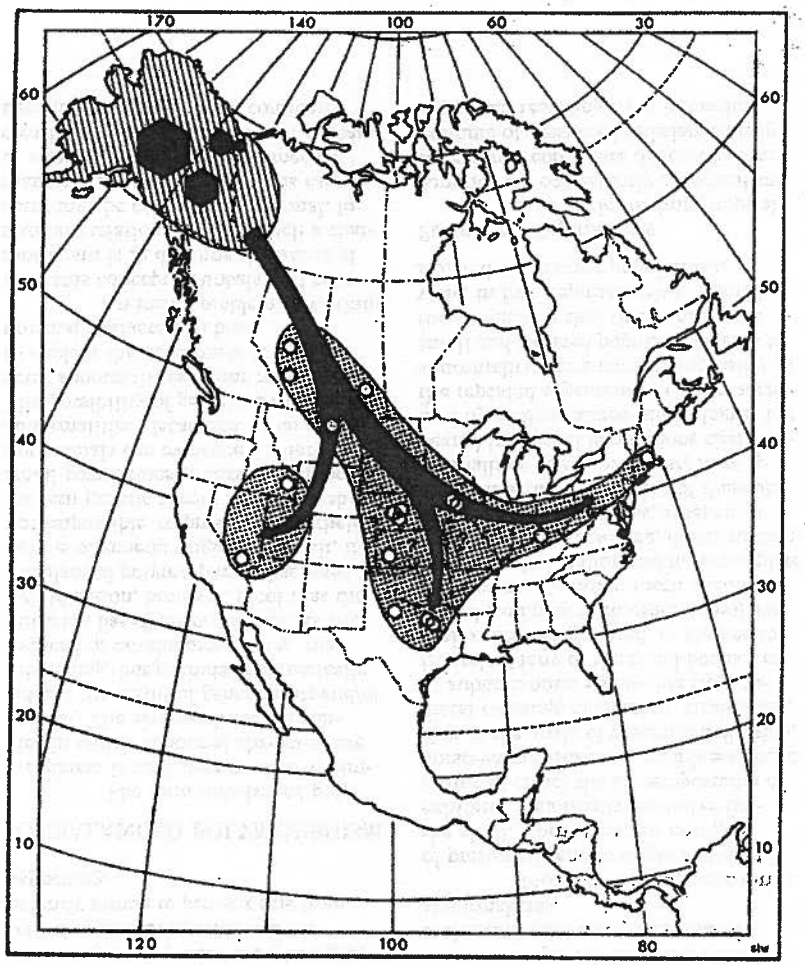


FIGURE 91 North American bison hybrid zones. Three hybrid zones are represented: (1) the eastern Beringian zone, which was probably the most strongly developed; (2) the periglacial arc—Great Plains zone, and (3) the Great Basin zone. Hexagons represent hybrid specimens, and arrows indicate dispersal salients of Eurasian bison entering midlatitude North America.

glacial/stadial periods and thereupon came into contact with North American bison that had dispersed northward during the preceding interglacial/interstadial. The Eurasian *B. priscus* and North American *B. a. antiquus*, being ecological vicars, alternately reinvaded Beringia in phase with the climatic oscillations, and thereby allowed *B. "crassicornis"* to periodically recur. Probably, hybridization was most intense during the early phases of each stadial.

Eighteen specimens studied from midlatitude North America were identified as hybrids (table 72). These specimens are distributed in regions where southward dispersing *B. priscus* or *B. alaskensis* populations probably met and interbred with northward dispersing or resident *B. latifrons* or *B. a. antiquus* populations (fig. 91). This interbreeding took place, apparently, along the periglacial zone and along the axes of two salients of Eurasian autochthon dispersal which penetrated midlatitude North America. One of these salients extended southward across the Great Plains and one crossed the Rocky Mountains and entered the Great Basin. (Many additional specimens that appear to be hybrids are in the collections of the University of Nebraska's Division of Vertebrate Paleontology. I was not able to study these specimens, but they are unusually well represented in the Nebraska Collections, a fact that supports the midlatitude hybrid zone concept presented here.)

In summary, this discussion has attempted to present information that establishes hybridization as a logical explanation for the occurrence of certain specimens that do not conform

Table 72
Probable Hybrid Specimens

Institution and identification number		Sex	Provenience
AMNH	VP F:AM30052	♂	Clark County, Nevada
AMNH	VP F:AM39412	♂	American Falls Reservoir, southeast Idaho
ANSP	G 12990	♂	Big Bone Lick, Boone County, Kentucky
KU	VP 390	♂	Near Garden City, Kansas
KU	VP 7388	♂	Kansas (?)
MCZ	VP 4425	♂	Harvard, Massachusetts
PPHM	2797/1	♂	Montana
SM	60317	♂	Seale Pit, near Dallas, Texas
SM	61363	♀	Moore Pit, near Dallas, Texas
SMNH	P100(?)	♂	Ft. Qu'appelle, Saskatchewan
SMP	158-56-z	♂	Polk County, Iowa
SMP	159-56-z	♂	Polk County, Iowa
TMM	31041	♂	Stonewall County (?), Texas
UAI	627	♂	Dale Brothers Gravel Pit, Alberta
UCy	G A*	♂	Near Calgary, Alberta
UMo	VP 766	♂	Missouri (?)
UNSM	VP 30310	♂	Devils Gap, southwest of Gothenburg, Dawson County, Nebraska
UNSM	VP 30357	♂	Near Broken Bow, Custer County, Nebraska

*No identification number was found for this specimen.

phenotypically to species' or subspecies' norms. The argument for hybridization was based on the use of specific criteria (shared diagnostic traits) to identify hybrid specimens. Hybrid zones are identified in Beringia and midlatitude North America. Either the frequency and intensity of hybridization was insufficient to cause the breakdown or alteration of typical species' morphologies, or selection against hybrids was sufficiently strong to prevent this from happening.

UNBALANCED POLYMORPHISM

The term unbalanced polymorphism is used here to refer to samples in which abnormal characters are present. The abnormalities are considered the result of genetic drift and/or inbreeding, but excludes traumatically induced or developmental (e.g., malnutrition based) abnormalities. As with hybridization, however, proof that the unbalanced polymorphism discussed here is of genetic origin is difficult, if not impossible, to provide. Nonetheless, modern genetic theory recognizes that small populations of sexually reproducing animals can evidence phenotypic abnormalities (decanalized characters). The possibility of genetically based character abnormalities seems most simply to explain the occurrence of several unusual characters in bison.

An initial problem in working with this concept of unbalanced polymorphism is in deciding the limits of normal variation, beyond which a character may be considered abnormal. In many instances this decision is easy—if, after studying many specimens, a clearly unique or rare character appears, then it may reasonably be considered abnormal. When only a few specimens have been examined and expected variation is poorly defined, or when the particular characteristic is only marginally abnormal, a problem arises, however. The distribution, frequency, and intensity of abnormal characters must be considered in evaluating abnormalities. Frequent and patterned occurrences permit the most reliable and meaningful interpretations of abnormalities.

Most observed abnormalities of presumed genetic origin appeared in the skull. Horn cores, for example, exhibited abnormally excessive flattening of either the antero-posterior or dorso-ventral surfaces, roundness, reduction of the angle of posterior deflection, distal twisting, elongation, diminution, or subhorizontal emanation from the frontals. Many of the facial bones were malformed, exaggerated, or seemed to crowd (compete with other bones) during growth. Common tooth abnormalities included malformation, incomplete formation, overcrowding, disorientation, structural abnormalities, absence, or supernumerary teeth. Any of these abnormalities could, of course, have appeared in normal populations characterized by well-canalized mophologies, but the repeated appearance of many such abnormalities in a context suggestive of small and isolated populations leads to the conclusion that these specimens were, in fact, representative of small, isolated, inbreeding populations.

Peripheral Populations

B. a. antiquus from tropical America are consistently abnormal and collectively constitute the best-known example of presumed unbalanced polymorphism resulting from inbreeding within peripheral populations of North American bison (fig. 92). The holotype of *B. scaphoceras* (plate 10) from Nicaragua is diminutive and has a distorted shape. The "*B. occidentalis*" described and photographed by Hibbard (1955*b*) from locality 7, Barranca de Acatlan, Tequixquiac (IG 49–76), appears to be a *B. a. antiquus* with diminutive, posteriorly oriented, distorted, distally twisting horn cores. With but one exception, a suite of seven partial skulls, mostly horn cores from the Barranca de Caulapan near Valsequillo, Puebla, all show deviant characters: all deviant cores are flattened dorso-ventrally to a greater or lesser degree, two are especially diminutive, and one skull has exaggerated facial characters. A color transparency taken by Donald Brand of a *B. a. antiquus* (?) skull in a Morelia, Michoacan, museum shows that this specimen apparently had unusually shaped horns. These specimens probably represent small populations of *B. a. antiquus* which were probably typical of this taxon in tropical North America. Further north a medial section of what is probably a *B. a. antiquus* horn core (UALP no #) from near Tecoripa, Sonora, is abnormally flattened.

The relatively frequent occurrence of abnormal characters in some other regional samples suggests that these abnormalities too may have represented small isolated populations. *B. a. antiquus* from the Wacissa River, Florida (RO 5; UF VP 11861); Beaumont, California (AMNH VP 31070); and Contra Costa, California (UCMP 37615) are abnormal (fig. 92). Isolated teeth from numerous pre-Holocene localities, but especially Alaska and highland Mexico (table 73), show frequent malformations (plates 30 and 31). *B. b. bison* from the Malheur Valley, Oregon, show considerable dental abnormalities. The holotype of *B. b. oregonus* has an extra pair of premolars and 15 percent of all molar fossets in the Malheur Valley sample contain reentering enamel folds (table 73; plate 32). Females in the Malheur Valley sample are unusually large and robust. *B. b. bison* from Big Bone Lick, Kentucky, show abnormal doming of the fronto-parietal sutures. Specimen MCZ VP 2047 from Big Bone Lick shows unequal wear on the upper dentition which may be the result of malocclusion. The holotype of *B. b. athabascae* (NMC M 299), collected in 1892 at a time when the wood bison population was very much reduced, has extremely exaggerated lacrymal salients that completely separate the nasals and maxillae. These patterns suggest that the abnormal characters of tropical *B. a. antiquus* specimens and of similar abnormalities in other regions of North America may be the result of genetic drift and inbreeding in small, isolated populations.

The Latest Wisconsin-Early Holocene Bottleneck

Late Wisconsin and early Holocene bison populations from the western Great Plains show extremely unbalanced polymorphism. The Casper archeological site in Natrona County, Wyoming—a paleo-Indian bison kill site radiocarbon dated at about 10,000 BP—has yielded the best-known and most extreme example of a population evidencing excessive morphological abnormalities probably attributable to the direct or indirect effects of genetic drift

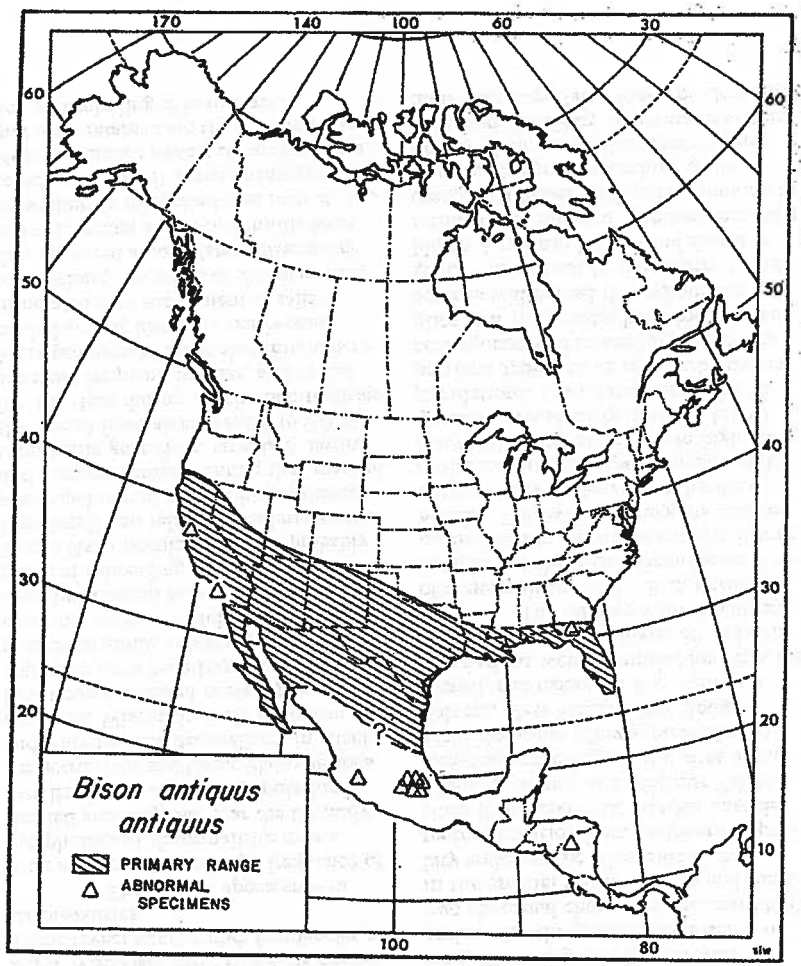


FIGURE 92 The distribution of abnormal *Bison antiquus antiquus* specimens, relative to the primary range of the taxon.

and inbreeding. Many of the abnormalities found in this deme have been described by Wilson (1974*b*), from whose study the following list of abnormalities is taken, supplemented by my own observations. Horn core deviations in the Casper sample consist of relative elongation, flattening, posterior orientation, and posterior rotation of the core tips. Dentition deviations include one case of shear mouth, unerupted premolars, overcrowding in the tooth row with associated disorientation of individual teeth, malformed and incompletely formed teeth, excessive development of cement, inadequate enamel formation, and malocclusion (plate 33). Three adult females show a single mode of nasal-maxillae deformation, although in differing degrees. In one specimen the maxillae are drawn inward toward the sagittal at the nasals, pinching the nasals into the shape of an hourglass (plate 34). In a second the pinching effect is present but less apparent. In the third the right maxilla has a scar-like mass at the nasal suture line. The extreme genetic debilitation probably rendered the Casper population (and others like it) more susceptible to somatic pathologies than would be true of a less inbred population (plate 33).

Bison from other archeological sites dating from the latest Wisconsin to middle Holocene (ca. 12,000–6,000 BP) reveal similar abnormalities (fig. 93), although these are less severe and frequent than in the Casper sample. Bison from the Clovis, New Mexico, area show a high frequency of dental abnormalities (table 73). Folsom, New Mexico, bison have elongate horns and deviant dentition. Rex Rodgers, Texas, bison have elongate horns with slight distal twist and upward orientation, deviant dentition, and crowding between the maxillae and nasals. Olsen-Chubbock, Colorado, bison skulls have horn

Table 73
Frequency of Selected Abnormalities in Molar Dentition

Sample	n	Abnormal fosset pattern (n)	Auxiliary labial styles (n)
Bison antiquus antiquus[a]	13	0	0
Bison bison bison:			
Central and northern Great Plains	48	5	0
Malheur Valley, Oregon	75	12	0
Bison antiquus occidentalis:			
Rex Rodgers archeological site, Texas	8	6	0
Specifically unidentified samples:			
Clovis area, New Mexico	12	6	1
Fairbanks area, Alaska	78	39	6
Folsom, New Mexico	10	4	0
Lago de Chapala, Jalisco	39	21	...

[a]The specimens providing this information are from various localities in California and Florida.

cores which emanate upward, are rotated rearward, and have distal twists. Hawken, Wyoming, bison show excessively developed maxillae along the nasal suture, and abnormal dentitions have been reported elsewhere for this population (Frison, Wilson, and Wilson, 1976). Detailed examination of other bison populations representative of the latest Wisconsin-early Holocene period might reveal similar high frequencies of abnormalities.

The sudden appearance of such a wide array and high frequency of morphological abnormalities over a limited area suggests that the formerly canalized *B. a. antiquus* population in the southwest and Great Plains regions suddenly became decanalized. In effect, the latest Wisconsin-early Holocene bison populations of these regions appear to have been fragmented into numerous small, relatively isolated populations, most of which probably developed unbalanced polymorphisms because of inbreeding and genetic drift. These bison populations were probably kept small and relatively isolated over a prolonged period of time by continuous and intense human hunting that reduced interdemic gene flow, especially during the period from about 11,000 to 9,000 BP, the time during which abnormalities are most frequent, intense, and varied. Most genetically based abnormalities recorded among bison did not become integrated into subsequent canalized populations, but some of the characters that appeared among latest Wisconsin-early Holocene *B. a. occidentalis* were subsequently integrated into later *B. a. occidentalis* and *B. bison* phenotypes. Most prominent among these characters that were retained are the rearward rotation and spiraling of horn cores.

Dental Abnormalities

A systematic survey of the frequencies of two abnormal dental characters was made in order to compare the abnormality rate in a population of known geologic age and normal gene flow with similar rates in other populations. The upper molars of nineteenth-century *B. b. bison* from Montana, Wyoming, and Kansas were examined for the presence or absence of two abnormal characters: reentrant folds in the enamel fosset margins and auxiliary styles on the labial side of the teeth. Dentition from peripheral populations (Fairbanks area, Alaska; Lago de Chapala, Jalisco; and Malheur Valley, Oregon); archeological kill sites of the early Holocene (Clovis, New Mexico; Folsom, New Mexico; Rex Rodgers, Texas); and canalized *B. a. antiquus* populations were examined for the same characters (table 73; plates 30 and 31).

The relatively low incidence of abnormalities in the *B. a. antiquus* sample and the higher frequencies of abnormalities in the other samples is noteworthy. The evidence suggests that reentrant folds in the enamel border of molar fossets and supernumerary styles can result from, and when in high frequencies can identify, isolated inbred populations. Crenulated fosset border patterns appear to be rather ubiquitous consequences of inbreeding, which implies that the genetic basis for the character is widespread throughout the genus—or at least in the shorter horned North American bison—and that it is rather easily released. The fact that such crenulated fosset borders are common in *Bos* may bespeak something of the antiquity of the genetic basis for the phenomenon. Auxiliary styles are less common than crenulated fosset borders, but nonetheless do occur with some frequency. This fact suggests that auxiliary styles, too, may be controlled by recessive genes widespread among bison and easily released in inbred populations.

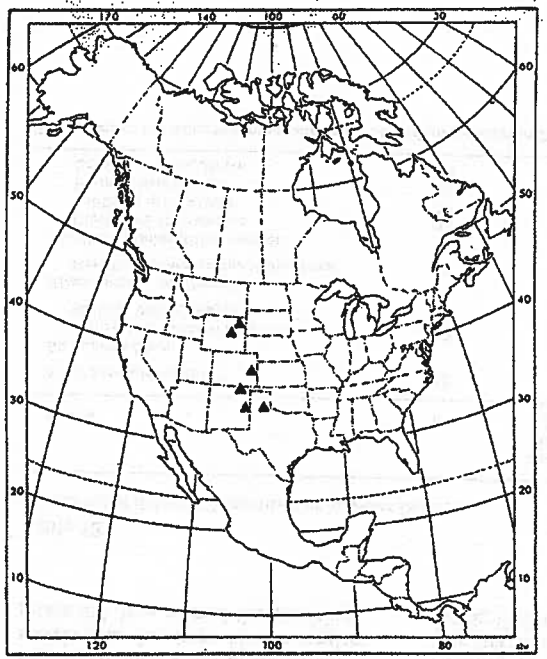


FIGURE 93 The distribution of abnormal *Bison antiquus occidentalis* during the latest Wisconsin to middle Holocene. The localities represented are, from north to south, Hawken (ca. 6,370 BP); Casper (ca. 9,946 BP); Olsen-Chubbock (ca. 10,150 BP); Folsom (ca. 10,000 BP); Clovis, New Mexico, area (probably spans entire period, with greater representation from earlier part of the period); and Rex Rodgers, Texas (ca. 9,391 BP). The abnormalities found in bison from these localities are probably the result of inbreeding and genetic drift, brought about by heavy human hunting.

Unusual Morphologies and Evolution

The distinction between the chance appearance of a character and active selection for a character must be kept in mind when evaluating both adaptations and unique characters. Normally, the appearance of a unique character in a phenotype as a result of genetic drift or inbreeding does not indicate that that character has been, or will be, adaptively favored, and such abnormal characters have little or no real evolutionary significance. Only after a character has become integrated into subsequent, canalized populations can it be considered adaptive.

old of sustained yield for the continent's megafauna was crossed between 12,000 and 11,000 BP, and population levels of most genera declined sharply thereafter. The relatively high number of conventional radiocarbon dates between 11,000 and 9,000 BP (fig. 95) is considered a reflection of greater hunting pressure on bison resulting from the demise or extinction of alternate game species.

Less information is available for the eastern Beringian region than for midlatitude North America, but accumulating evidence indicates that human hunting of the region's megafauna was taking place throughout the late Wisconsin (Dixon, 1975; Müller-Beck, 1967; Péwé, 1975). The pressures imposed on the region's megafauna by human hunting and environmental changes, from habitats more suitable to habitats less suitable for sustaining viable populations of large herbivores, probably resulted in the extinction of much of the region's late Pleistocene megafauna by the onset of the Holocene (Dixon, 1975; R. Guthrie, 1968; Péwé, 1975). The extinction of the eastern Beringian megafauna during the late Wisconsin-early Holocene constitutes the final disappearance of Eurasian *Bison* from North America.

In summary, the late Wisconsin megafaunal populations oscillated according to available land area and suitable habitat, and the carrying capacity of that habitat. A general decrease in megafaunal populations in midlatitude North America followed the middle Wisconsin interstade, whereas the megafaunal population of eastern Beringia probably increased during this time. A period of climatic amelioration (between ca. 16,000 and 14,000 BP) was accompanied by an increase in midlatitude megafaunal populations, but was possibly followed by a decrease in populations immediately thereafter. The final midlatitude megafaunal rebound of the late Wisconsin commenced after ca. 14,000 BP. About 11,000 BP there occurred a population crash involving most large bodied genera in midlatitude North America. A similar crash occurred in *Mammut* ca. 9,000 BP. These population crashes, which occurred at a time when populations should have actually been increasing, considering the nature of habitat changes which were then taking place (chapter 1), are interpreted as a result of excessive hunting pressure by man. The two genera that survived this hunting pressure and habitat change (*Bison* and *Ovibos*) apparently did so because they were better adapted to occupy expansive, open, and physiognomically simple habitats, and to utilize them to a greater extent than man.

THE SURVIVAL OF LATE PLEISTOCENE BISON

Bison barely survived the late Pleistocene-early Holocene extinctions. The point has already been made that a crash in bison numbers occurred after about 11,000 BP and that bison did not rebound until after about 9,000 BP. The high rate of unbalanced polymorphism (chapter 6) which existed in bison during the 11,000 to 9,000 BP period is empirical evidence that supports this theorized reduction in numbers. How and why, then, did bison survive?

Much of the explanation rests with the chance coincidence of (1) location; (2) reproductive potential; (3) direction of environmental change; and (4) adaptive potential. The principal range of late Wisconsin *B. a. antiquus* was southwestern North America and, perhaps, the Great Basin (fig. 97). This principal range habitat became steadily drier during the transition from glacial to interglacial environments but, simultaneously, the central North American grasslands were developing where glacial forests, woodlands, and savannas had previously existed. The structural and compositional simplification of habitat which occurred during the transition from late Wisconsin to Holocene should have resulted in increased populations of most large herbivore species and, simultaneously, a more distinct partitioning of the habitat due to greater specialization in feeding behavior among these species. Human hunting also increased during this period. As a result, the potential for population increase afforded by vegetation changes was nullified by the proportionately more adverse selective factors operating against most of the genera in the form of human hunting. (The counter argument that loss of habitat was responsible for most megafaunal extinctions is weakened by two facts. Similar habitat changes took place earlier during the Pleistocene but were not characterized by catastrophic megafaunal simplification. Also, most if not all large bodied late Wisconsin mammals were euryecious and, practically speaking, many habitats they occupied at that time remained throughout the Holocene.)

The transition from woody to herbaceous vegetation on the Great Plains resulted in an abundance of resources which could be utilized by fully grazing species. The formation of this grassland was synchronous with the desiccation of the savanna, and in a region generally contiguous to what was then the main bison range. Basic herding tendencies and the capability to forage largely, if necessary, by grazing were established parts of the *B. a. antiquus* behavior and ecology. The development of grasslands provided impetus to bison population growth in two ways—it segregated bison from previous competitors that might have been unable to adapt to the grassland environment and it provided less diverse but more fully utilizable food resources than were available in the savanna habitat. Hunting pressure against bison, however, not only continued but probably intensified as other genera became extinct. As a bison population increased and herding tendencies strengthened, because of either adaptively increased social tendencies or simply greater opportunity to aggregate in the wake of decreased competition and habitat diversity, humans apparently evolved specialized hunting methods that were able to more efficently exploit the newly organized resource. The period from about 11,000 to 9,500 BP, therefore, was a time of both expanding suitable habitat for bison and increased hunting pressure on bison imposed by man during which time the bison range was minimal and bison populations appear (on the basis of unbalanced polymorphisms) to have been kept small and relatively isolated by the human hunting (fig. 98). It was during this period that the widespread effects of genetic drift and inbreeding brought about the appearance of *B. a. occidentalis*, a highly variable taxon in apparent disequilibrium with its environment. Populations of *B. a. antiquus* continued to exist, however, until the middle Holocene.

After about 9,500 BP bison populations appear to have rebounded and expanded their range (fig. 99). Extinction was probably avoided, ultimately, because bison were able to adapt to the open grasslands more completely than was man. This point is simple—bison depended primarily on the grasses, forbs, and water of the grasslands for survival. Man, an omnivore, required more shelter and regularly utilized a greater variety of diet items than the open grassland provided in abundance. Bison populations on the open plains, away from the plains margins where human hunters regularly and effectively cropped bison, were able to increase in numbers rapidly. Indeed, one of the most important factors in the survival of the bison might have been the relatively high reproductive potential and relatively short maturation period which probably characterized late Wisconsin-early Holocene bison vis-à-vis those genera that became extinct.

During and following the early Holocene bison rebound, environmental changes were occurring which resulted in a major expansion and shift of the bison range. The onset of the Atlantic climatic episode ca. 8,500 BP initiated the desiccation of the southern plains and a consequent reduction in the region's carrying capacity. At the same time the grasslands and the bison range were expanding northward and eastward (figs. 100 and 101). The boreal forest to the north was relatively permeable because of retarded succession over the recently glaciated terrain. Human hunting of bison continued during this period, probably strongest on the northern, eastern, and western periphery of the range, but the net effect of hunting was probably greater in the southern and central plains where it, together with reduced carrying capacity, virtually eliminated bison from the region (Dillehay, 1974; McDonald, 1974, 1976). One salient of this early Holocene range change extended eastward into the midwestern prairie peninsula, whereas another extended north along the western lowland corridor toward Alaska.

A gradual southward expansion of the bison range began after 6,000 BP but accelerated after about 5,000–4,000 BP, coinciding with the dispersal of the newly evolved late Holocene grassland bison, *B. b. bison*. The principal environmental factors that contributed to these range dynamics were a slight cooling trend and correlated decrease in the aridity of the southern plains. The boreal forest was also probably becoming less penetrable as succession proceeded. The cumulative effects of these habitat changes on bison were to reduce dispersal northward and eastward, but to increase dispersal southward and (less so) westward. The primary and generally historic *B. bison* range was established by about 3,000–2,000 BP (figs. 102 and 103).

HOLOCENE DWARFING OF BISON

Bison diminished in body size during the period from about 11,000 BP until about 5,000–4,000 BP, after which time the reduction generally terminated for most characters (table 75). The terminal Wisconsin-early and middle Holocene may be considered the transitional phase in the evolution of *B. antiquus* to *B. bison*, the period during which late Wisconsin savanna bison were adapting

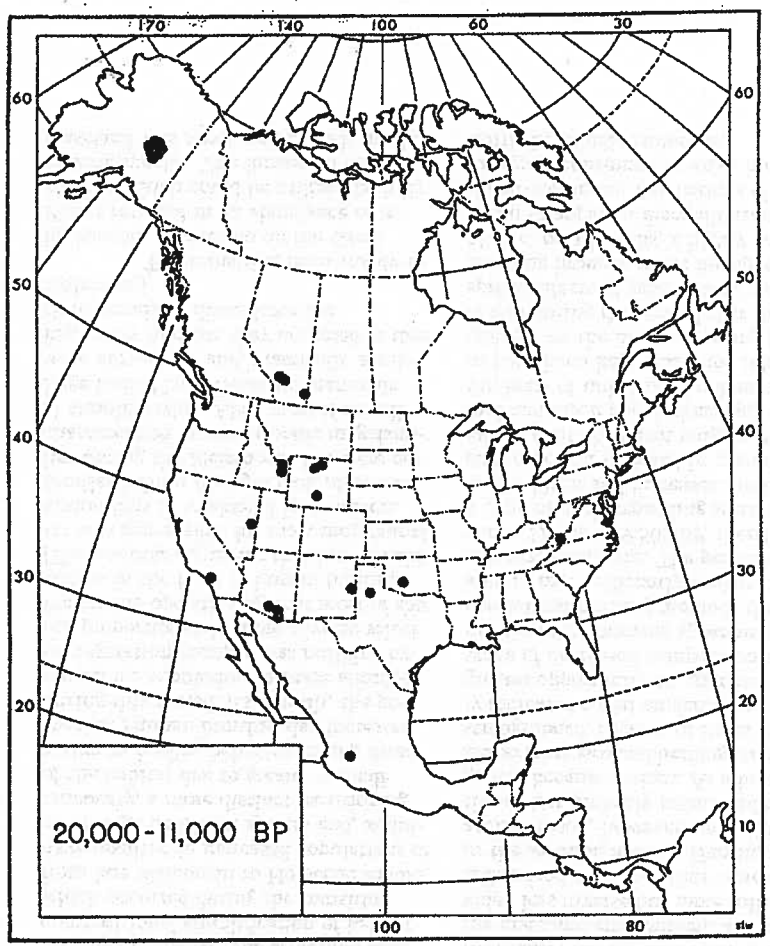


FIGURE 97 Radiocarbon dated bison distribution: 20,000–11,000 BP. Although southwestern North American was the primary bison range during the late Wisconsin period, populations were nonetheless widely distributed throughout nonglaciated North America. *Bison antiquus* was the dominant, and perhaps only, taxon in midlatitude and tropical North America; its range possibly extended northward into Beringia. Eurasian bison were present in Beringia during at least part of the late Wisconsin.

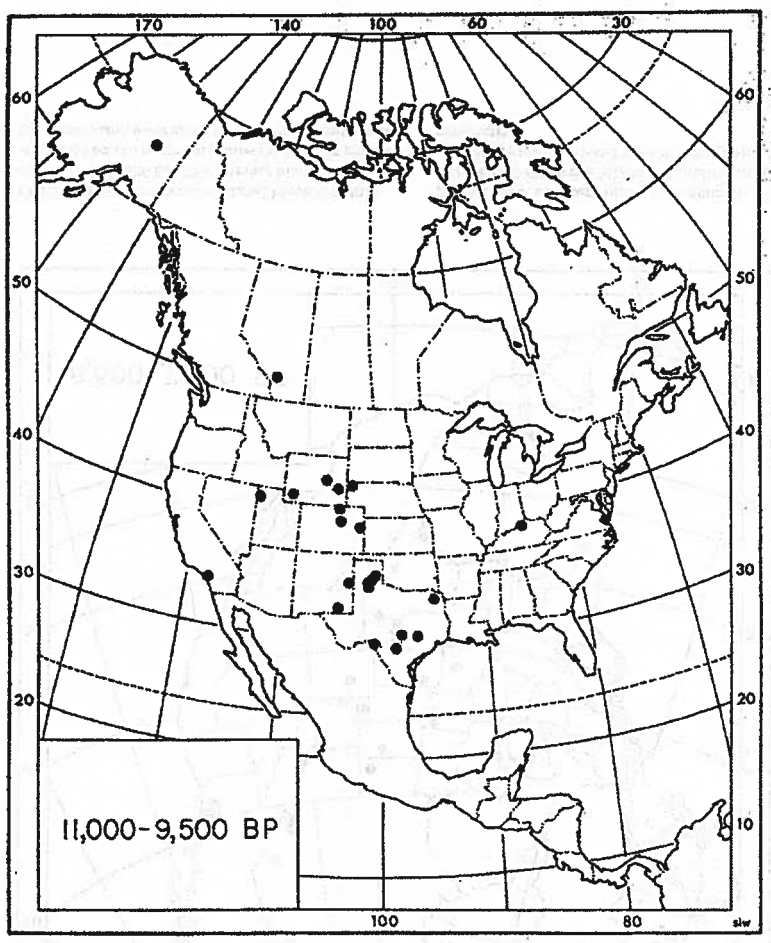


FIGURE 98 Radiocarbon dated bison distribution: 11,000–9,500 BP. The primary range is now shifting northeastward onto the Great Plains as the central grassland develops. The most intense, varied and widespread instances of abnormal specimens also date from this period, suggesting that the bison population probably came nearer the threshold of extinction at this time than at any other time prior to the nineteenth century. Bison became extinct in Alaska during this period.

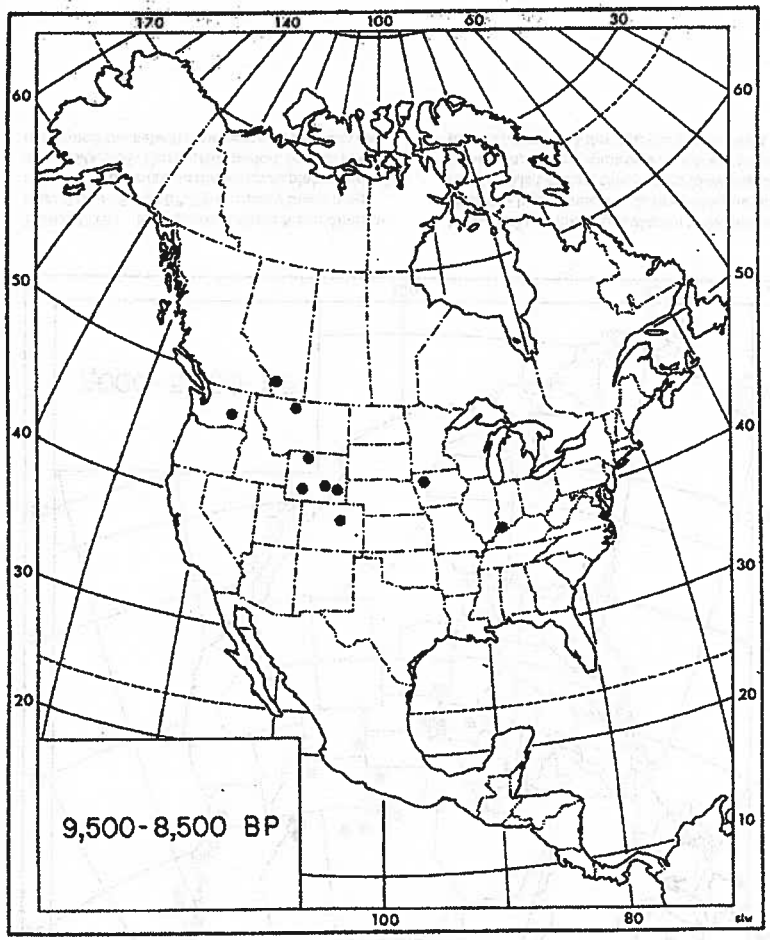


FIGURE 99 Radiocarbon dated bison distribution: 9,500–8,500 BP. The primary bison range has now shifted onto the northern Great Plains and adjacent prairie margins. A slight decrease in abnormal specimens from this period suggests that gene flow is becoming reestablished and the species' population might be increasing modestly, probably away from the plains margins where human hunting would have been generally heaviest.

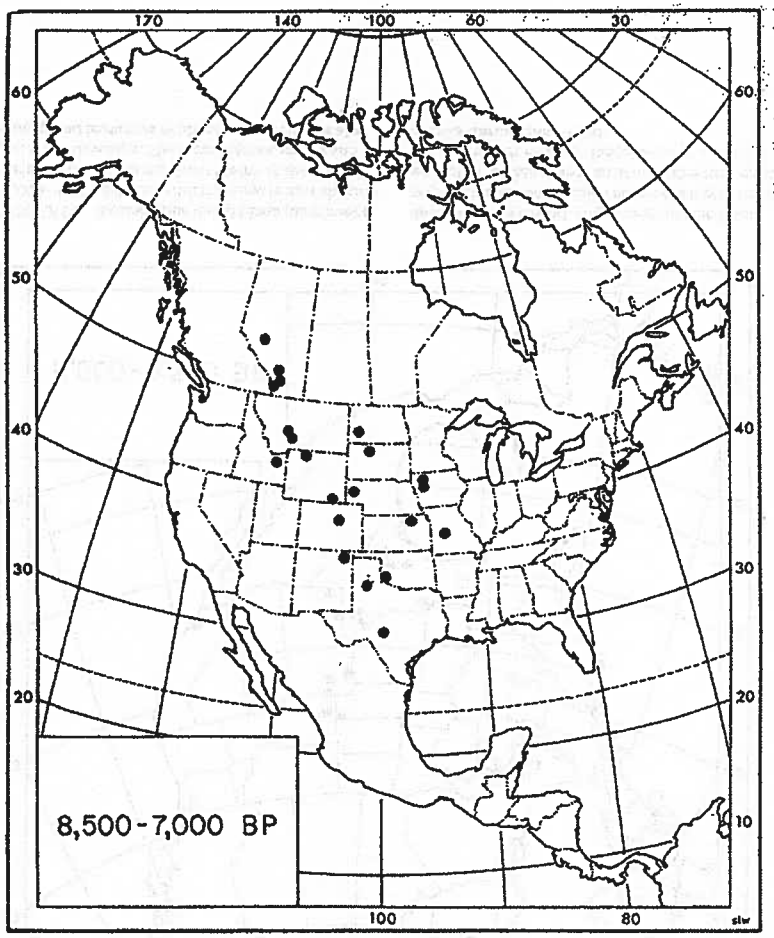


FIGURE 100 Radiocarbon dated bison distribution: 8,500–7,000 BP. The primary bison range remained on the northern plains during this period, but some bison were also on the southern and central plains. Most southern bison were gone by, or soon after, 8,000 BP as the Atlantic climatic episode got under way and rendered the southern plains less productive.

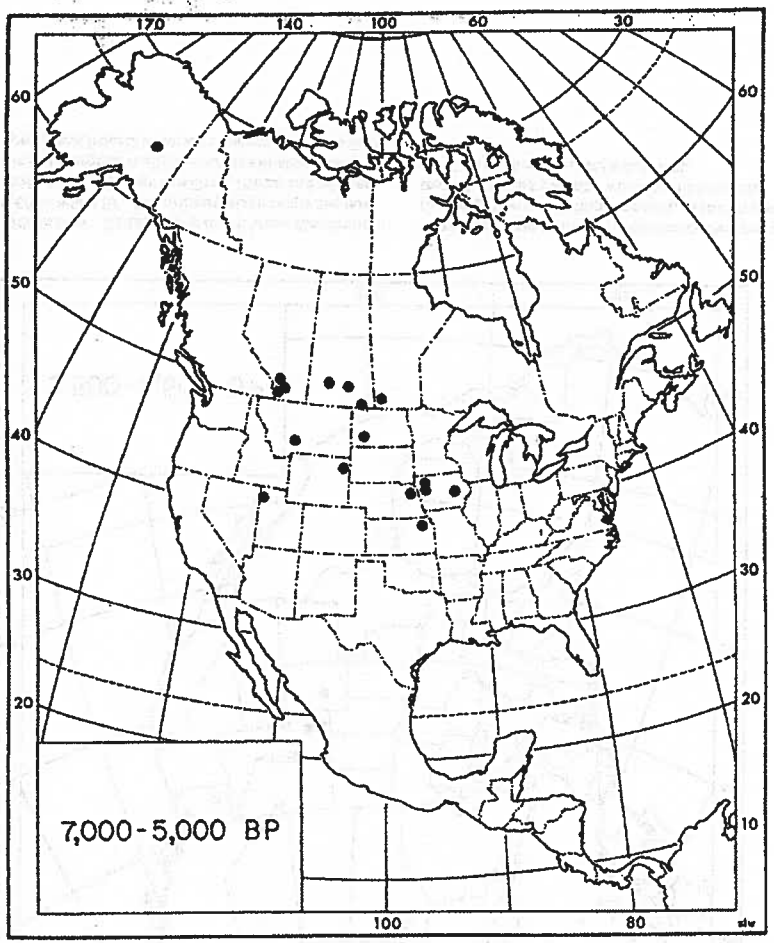


FIGURE 101 Radiocarbon dated bison distribution: 7,000–5,000 BP. The primary bison range remained anchored on the northern plains until after about 5,000 BP. During this period, human predation continued the selective pressure upon bison and brought the regional population to the verge of a new adaptive homeostasis with the Holocene selective regime. Also during this period, bison again appear in Alaska, some populations apparently having dispersed northward through the boreal forest filter.

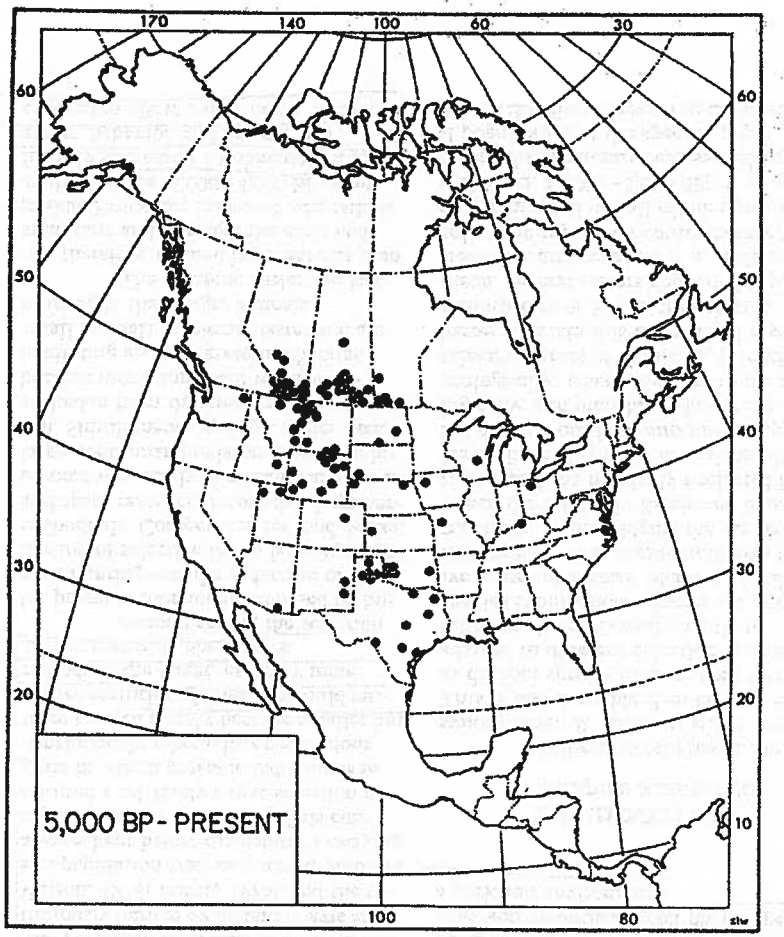


FIGURE 102 Radiocarbon dated bison distribution: 5,000—present. The bison population started expanding its range southward after about 5,000 BP as the central and southern plains habitat improved as a result of regional climatic changes, and as a new phenotype, *Bison bison*, appeared. The southward expansion apparently accelerated around 3,000 BP and, by about 2,000 BP, the species maximum range had probably been achieved.

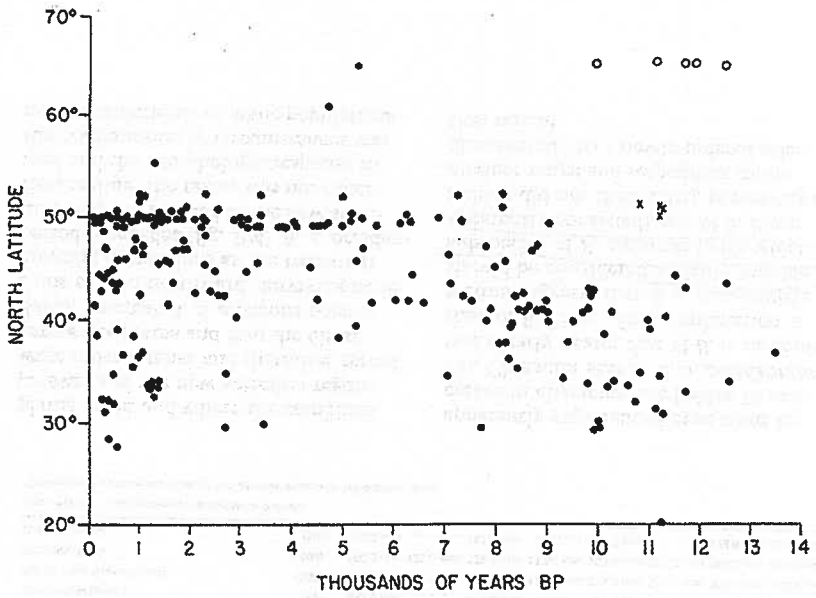


FIGURE 103 Radiocarbon dated bison distribution: years BP vs. latitude. Shown here are dated occurrences of midlatitude and tropical bison (dots), periglacial bison (x's), and eastern Beringian bison (circles). Notice especially (a) the northward shift in the midlatitude bison range which occurred between about 10,000 and 7,000 BP; (b) the virtual absence of bison on the southern Great Plains during the period from about 8,000 to 3,500 BP; and (c) the range expansion which occurred after about 5,000 BP. The Beringian and periglacial populations are assumed to have become extinct during the latest Wisconsin—earliest Holocene.

to the new Holocene environment and its reordered selection regime.

The progressive diminution of bison has been documented for horn cores and metapodials (Bedord, 1974; Hillerud, 1970; Hughes, 1978; McDonald, 1978*a*; M. Wilson, 1975). Not all characters, however, diminished in size at the same rate (table 75). In fact, the size of some characters in some populations actually increased during the early part of this transitional period, soon after disequilibrium was established.

Usual explanations given for the net size reduction in Holocene bison include density-dependent stress or resource limitations, low nutritional levels, or climatic conditions (e.g., Geist, 1971*a*; Guthrie, 1970, 1978; Wilson, 1974*b*). Of these explanations the first is nonadaptive, whereas the second and third are environmentally deterministic

but not adaptive. The dwarfing was, of course, general—but it also included qualitative structural changes and was, ultimately, a genetically based phenomenon.

Possibly the simplest and most meaningful explanation for Holocene size reduction in North American bison lies in the selective advantage of accelerated maturation and increased biotic potential. Holocene bison were continuously hunted by Indians (Davis and Wilson, 1978; Frison, 1975), and the bison population was, as a result, probably always kept below the habitat's carrying capacity (plates 35 and 36). This constituted a relatively r-type selection regime in which progenic individuals in continuously rebounding populations were favored simply because smaller but earlier maturing phenotypes could outreproduce the larger, probably more slowly maturing phenotypes.

Accompanying the selection for progenic individuals imposed by human hunting was the reduction or elimination of selective forces favoring larger individuals. Competition for food, water, and space resources from other large herbivores was nearly eliminated and fewer large nonhuman predators preyed on bison. Simultaneously, flight rather than seclusion from threatening situations became more important to bison inhabitating an open grassland habitat; small animals accelerate faster and are more agile than larger animals.

The combined selective factors, therefore, favored largeness less than smallness and, through the early and middle Holocene, improved adaptations evolved. By ca. 5,000–4,000 BP, a sufficently successful combination of characters, behavior, and ecology had evolved to allow a new taxon, *B. bison*, to reach adaptive homeostasis with its environment and to undergo an increase in numbers and expand across the post-Atlantic central grasslands. The selective environment has remained sufficiently stable since the end of the Sub-Boreal climatic episode (table 4) to maintain general phenotypic equilibrium throughout the *B. b. bison* population. *B. b. athabascae*, however, may have undergone, or may be undergoing, selection favoring a larger phenotype in a parkland environment.

THE IDENTITY OF *B. antiquus occidentalis*

Wilson (1974*b*) has recently synonymized *B. antiquus* and *B. bison*. This is less desirable than keeping them as distinct species because both were adapted to different selection regimes at different times. Considering these species synonymous ignores the adaptive aspect of species' identity and differentiation. *B. a. occidentalis* was the transition taxon bridging the gap between the relatively K-selected *B. a. antiquus* and the relatively r-selected *B. bison*. Even though *B. a. occidentalis* did depart from *B. a. antiquus* morphologically, and probably behaviorally and ecologically, when subjected to the new selective forces of the times, it is still better to retain this transitional taxon as a subspecies of *B. antiquus* than *B. bison*. Several factors support this position. *B. a. antiquus* and *B. a. occidentalis* were apparently contemporaneous during much if not all of the transition period (ca. 11,000–5,000 BP). *B. a. occidentalis* apparently represented regional populations of the species; populations that first appeared on the western plains when and where the combined pressures of the new selection regime were most intense and thereafter spread across the plains and into the Great Basin, whereas *B. a. antiquus* populations shifted northward, surviving in decreasing proportions as the transition period proceeded (fig. 104). *B. a. occidentalis* was not adapted to the new selection regime, the taxon was not canalized and the morphologic response to the combination of circumstances was not unidirectional as some populations apparently experienced even some increase in character size (tables 73 and 75). Character size in *B. a. occidentalis* was clearly nearer that of *B. a. antiquus* than of *B. bison*. This combination of factors suggests that *B. a. occidentalis* should be considered a highly variable subspecies of *B. antiquus* (with which it apparently coexisted), not of *B. bison* (which did not then exist), possessing a distinct range and responding multidirectionally to a newly ordered selection regime.

Table 75
Character Dwarfing During the Holocene

Sample	Radiocarbon age (years BP)	Horn core length, dorsal curve (SM 3) ♂♂	Horn core length, dorsal curve (SM 3) ♀♀	Width of occipital condyles (SM 9) ♂♂	Width of occipital condyles (SM 9) ♀♀	Least width of frontals (SM 14) ♂♂	Least width of frontals (SM 14) ♀♀	Length of metatarsal ♂♂	Length of metatarsal ♀♀
Rancho la Brea, California	> 12,000	287.0 mm	208.0 mm	144.7 mm	136.4 mm	322.2 mm	264.0 mm	277.3 mm	271.3 mm
Lindenmeier, Colorado	10,990*	292.0 mm	.....	148.0 mm	.....	330.0 mm	.....	280.8 mm	.....
Lubbock Lake, Texas (Clovis/Folsom)	10,155*	.....	.....	.....	.....	.....	.....	276.9 mm	.....
Olsen-Chubbock, Colorado	10,150	240.0 mm	197.0 mm	148.0 mm	.....	309.6 mm	243.0 mm	265.7 mm	262.2 mm
Folsom, New Mexico	(10,000)	267.0 mm	166.0 mm	143.6 mm	.....	.....	.....	280.2 mm	267.8 mm
Bonfire, Texas (Bed 2)	10,083*	.....	.....	.....	.....	.....	.....	.....	269.5 mm
Casper, Wyoming	9,945*	381.0 mm	206.0 mm	147.0 mm	124.0 mm	310.0 mm	250.0 mm	.....	.....
Hudson-Meng, Nebraska	9,820	.....	.....	.....	.....	.....	.....	274.6 mm	255.1 mm
Plainview, Texas	9,800	303.0 mm	214.0 mm	143.0 mm	.....	329.0 mm	.....	268.0 mm	263.7 mm
Rex Rodgers, Texas	9,391	351.0 mm	215.0 mm	151.0 mm	.....	327.0 mm	221.0 mm	270.0 mm	.....
Wasden, Idaho	(8,000)	.....	.....	.....	.....	.....	.....	273.5 mm	263.9 mm
James Allen, Wyoming	7,900	.....	.....	.....	.....	.....	.....	.....	268.0 mm
Zap, North Dakota	7,840	330.0 mm	.....	125.0 mm	.....	270.0 mm	.....	.....	.....
Duffield, Alberta	7,750*	269.1 mm	188.6 mm	131.3 mm	117.0 mm	288.2 mm	232.6 mm	.....	.....
Hawken, Wyoming	6,370*	262.1 mm	190.0 mm	140.0 mm	124.0 mm	300.5 mm	232.0 mm	263.1 mm	252.4 mm
Hughes Bog, Iowa	5,640	315.0 mm	.....	130.0 mm	.....	293.0 mm	.....	.....	.....
Zap, North Dakota	5,440	253.0 mm	.....	145.0 mm	.....	280.0 mm	.....	.....	.....
Scoggin, Wyoming	4,540	.....	.....	126.0 mm	.....	285.0 mm	.....	.....	.....
Southern plains Archaic sites, Texas	(2,500 – 3,500)	.....	141.0 mm	.....	.....	.....	.....	249.3 mm	242.5 mm
Sitter, Texas	(2,500 – 3,500)	.....	.....	.....	.....	.....	.....	.....	245.0 mm
Bonfire, Texas (Bed 3)	2,795	.....	106.4 mm	.....	.....	.....	.....	255.8 mm	248. 6 mm
Buffalo Creek, Wyoming	2,530	206.0 mm	129.0 mm	128.0 mm	113.0 mm	270.0 mm	227.0 mm	256.0 mm	247.1 mm
Glenrock, Wyoming	245*	202.0 mm	.....	131.0 mm	.....	281.0 mm	.....	254.2 mm	244.6 mm
Rocky Ford, South Dakota	(200)	202.0 mm	123.0 mm	129.8 mm	114.5 mm	275.7 mm	212.1 mm	263.0 mm	248.0 mm
Montana, 1880s	(100)	190.5 mm	125.3 mm	128.4 mm	118.0 mm	264.6 mm	220.3 mm	254.6 mm	247.5 mm
B. b. athabascae	(90±)	248.7 mm	.....	192.5 mm	.....	295.7 mm	.....	275.6 mm	264.0 mm

Note: Figures in parentheses are estimates or historic.
*Designates the arithmetic mean of two or more acceptable radiocarbon dates.

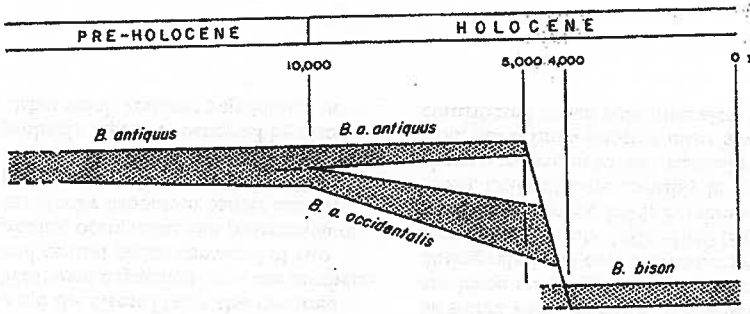


FIGURE 104 This model illustrates several important facets of the evolution of *Bison bison* from *Bison antiquus*. Until about 11,000 BP, *Bison antiquus* was a monotypic, well canalized species, but at that time a sudden increase in abnormal specimens occurred. Some populations (*B. a. antiquus*) remained unchanged throughout the early and perhaps middle Holocene, but the highly variable and still uncanalized populations (*B. a. occidentalis*) became more numerous as the Holocene progressed. During the millenium between 5,000 and 4,000 BP, while the primary bison range was still largely anchored on the northern plains, adaptive homeostasis was reached and *Bison bison*, a smaller, then-and-thereafter canalized taxon adapted to the selective regime then prevailing in North America, appeared.

Bison bison

Bison bison represents the current stage of North American bison evolution. More information is available on morphological variation, population dynamics, behavior, ecology, and range dynamics for *B. bison* than any other species. This provides an opportunity to evaluate these characteristics in greater detail than is possible for other species. Such a detailed examination, however, is beyond the scope of the present study. Here only three specific aspects of *B. bison* range and phenotypic variation of evolutionary significance will be briefly discussed. These are (1) differences between *B. b. athabascae* and *B. b. bison;* (2) the retention of an r-selection regime throughout the species existence; and (3) range oscillations and population distribution within the species range.

B. b. athabascae occupied the boreal parklands and woodlands at the northern end of the primary *B. bison* range. *B. b. athabascae* is larger than *B. b. bison* because of the selective forces operating in the forest opening/woodland environment, although the *B. b. athabascae* selection regime has more of an r-selection character than was true for pre-Holocene North American bison. The greater body size of *B. b. athabascae* could have been reached by either, or both, of two methods: (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* as populations of the latter dispersed from the grasslands and adapted to the forest/woodland environment. 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 in influencing the nature of *B. b. athabascae*. The *B. b. athabascae* gene pool has probably been regularly supplemented by gene flow from *B. b. bison* populations to the south. Periodic, and perhaps continuous, contact between grassland and parkland bison probably occurred for as long as *B. bison* has existed, or at least until Euroamerican instigated hunting of bison accelerated the decline of bison numbers (plate 37) and isolated many regional populations. Moodie and Ray (1976) have documented annual movements of *B. b. bison* into the boreal parkland during the historic period, this after hunting pressure had increased. The seasonal movement was probably even greater before the Euroamerican impact, and gene flow between both subspecies probably regularly occurred as individuals periodically joined and remained with herds dominated by members of other subspecies.

The differentiation of *B. b. athabascae* from *B. b. bison* is somewhat analogous to the speciation of *B. alaskensis* from *B. priscus*, although the time over which *B. b. athabascae* has differentiated is much shorter, and the area and the bison population involved are much smaller than were probably true for *B. alaskensis*. *B. b. athabascae*, therefore, has been in a tension situation between the selection for larger body size by intraspecific resource competition and hierarchal dominance organization in small, presumably socially organized (although numerically unstable) herds, and the selection for more rapid maturation imposed by regular hunting by man. *B. b. athabascae*, then, probably existed in a forest/woodland mode r-selection regime in which human hunting probably kept population levels below the habitat's carrying capacity. Many aspects of the distribution, behavior, and ecology of *B. b. athabascae* are described by Allen (1900), Fuller (1950, 1960), Roe (1951), Seton (1885–1886), and Soper (1941).

B. b. bison also remained under a relatively r-type selection regime after adapting to the late Holocene grassland environment. This was because adverse environmental factors were sufficiently strong to keep the overall population below the carrying capacity of its environment. Drought, fire, winter storms, and other environmental phenomena all probably functioned to periodically reduce regional populations, but human hunting was probably the single most important and widespread process that kept the overall population level below its potential (plate 36). As with paleo-Indians, however, neo-Indians appear to have hunted primarily and most consistently along, or from, the margins of the main bison range, although they did, of course, hunt in the interior of the bison range as well, both before and after their acquisition of the horse and displacement toward or onto the plains by the Euroamerican advance. This hunting, in effect, minimized or prevented the peripheral expansion of the bison range. Hunting in or outward from the ecotonal periphery of the Great Plains

grassland may have been the most influential factor separating the *B. b. athabascae* and *B. b. bison* gene pools, to the extent that they were, in fact, separated.

Range and population oscillations did occur for *B. b. bison*; the Great Plains were not completely or uniformly occupied by populations of *B. b. bison*. Within the main range regional droughts caused displacements in the distribution of bison, and severe snow and ice storms destroyed or reduced local populations (Allen, 1876, 1877; Cole, 1954; McHugh, 1972; Meagher, 1971; Roe, 1951; see also Bryson, 1974). Alternatively, improved conditions brought regional population increases, such as apparently occurred in the northwestern Great Plains during the "Little Ice Age" of the sixteenth to nineteenth centuries (Reher, 1978). Unrestricted hunting by Indians often dislodged bison populations from an area, whereas contested hunting in intertribal buffer zones (i.e., regions that experienced intergroup conflict over hunting rights) appears to have provided relative security and temporary refuges for some bison populations. Within the main bison range there was, then, a regular ebb and flow of bison populations locally (see, e.g., Davis and Wilson, 1978; Roe, 1951), resulting in a mosaic of areas with and without bison at any given time.

Periodic range expansions beyond the Great Plains also occurred. Westward expansion from the northern and central plains consisted of two phases, occupation and penetration of the Rocky Mountain barrier and dispersal across the Great Basin. The Rocky Mountain valleys and parks were probably regularly occupied by bison, either small resident populations or immigrants from the western Great Plains. The carrying capacity of these habitats was relatively low because of their small area, and occupation was largely seasonal, especially at higher altitudes (Christman, 1971; Meagher, 1973; Reeves, 1978*a*). Penetration of the Rocky Mountain barrier was, therefore, minimized by environmental circumstances and probably accompanied by selection for larger phenotypes (chapter 5).

Populations of *B. b. bison* had filtered through the Rocky Mountain barrier and become well established in the northern Great Basin steppes and brushlands by about 2,500 BP (Schroedl, 1973). Between that time and the early nineteenth century, this regional population was seriously reduced, probably by a combination of drought (such as that of the late thirteenth century) and human hunting (Jennings, 1957; Jennings and Norbeck, 1955; Schroedl, 1973). Euroamerican accounts indicate that bison were present but only in small numbers in the Great Basin in the midnineteenth century, and were soon thereafter hunted to extinction (Hornaday, 1889; Roe, 1951; Schroedl, 1973).

The great southwestern salient of bison probably reached its maximum extent by about 2,000 BP, although more information, especially from Mexico, is needed before this can be stated with certainty. The southwestern bison range apparently expanded during relatively cool and moist periods between about A.D. 1100–1460 (Agenbroad and Haynes, 1975; P. Johnson, 1974). Drier climate probably brought about a reduction in the regional population, but human hunting must have contributed to the reduction also. Euroamerican explorers in the southwest during the sixteenth to eighteenth centuries encountered evidence that bison either then existed, or had recently existed, in the area from Zacatecas to northern Arizona. Bison were, however, relatively rare throughout the region south and west of the Rio Grande even in the early sixteenth century, and by the late eighteenth century most, if not all, had disappeared from the region. The last population of any significance probably existed in northeastern Arizona (Brand, 1967, oral comms., 1972–1976; Gunnerson, 1974; Reed, 1955; Roe, 1951).

Bison probably dispersed into the humid, generally forested eastern United States regularly, just as they dispersed into the Rocky Mountains, although the human barrier in the east was probably more difficult to penetrate. Little evidence is available to determine how early or how rapidly dispersal eastward occurred, but bison (identified as *B. bison*) are known from the Atlantic Coast of North Carolina by at least 2,610 BP (Painter, 1978), and occurred from Florida to New York and Ontario at or near the time of European contact (i.e., sixteenth century). Accounts from the sixteenth to the eighteenth centuries indicate that bison were widely distributed throughout the east during this time, although in relatively dispersed and small populations. The displacement of eastern Indians westward and the westward advance of Euroamerican settlement resulted in the elimination of bison from most of the humid east by the early nineteenth century (see, e.g., Allen, 1876; Dunbar, 1962; Goodwin, 1936; Griffin and Wray, 1945; Hays, 1871; Hornaday, 1889; Jakle, 1968; Painter, 1978; Roe, 1951; Rostlund, 1960; Sherman, 1954).

The main bison range was steadily reduced from the early seventeenth through the middle nineteenth centuries by both Euroamerican and Indian hunting (Allen, 1876; Dary, 1974; Hornaday, 1889; Newcomb, 1950; Roe, 1951). The major range reduction and near extinction of *B. b. bison*, however, occurred between the late 1860s and early 1880s when millions of bison were killed, primarily by Anglo-American hunters supplying the meat and robe trade (plate 37). Very few individual bison were saved from this slaughter, but from that small sample several thousands now exist, although mainly as quasi-domesticates (plate 38). The overall effect of this second Holocene bottleneck and subsequently established new selection regime has not yet been systematically assessed, but it does appear that some morphological changes have occurred (e.g., the southern Great Plains phenotype may have been completely lost), and probably behavioral changes as well. The bison range, of course, has been fragmented and gene flow seriously reduced and artificially regulated. Lastly, new selective factors have replaced those of the pre-nineteenth century late Holocene; general and semiselective hunting have been replaced by selective removal or retention of individual bison, and idiosyncratic human preferences control the distribution, composition, and density, and in many ways the behavior and ecology, of *B. bison*.

8

CONCLUSIONS AND PERSPECTIVE

The preceding chapters have presented information and developed models that attempt to fulfill the objectives identified in the preface. In addition, the information and models developed earlier can usefully be compared with existing theories of bison evolution to better ascertain their reliability. Lastly, the accumulated, organized, and evaluated information, and the models derived from this, provide some insight into informational deficiencies and needs. A useful way to close this book might, therefore, be to summarize the previous chapters vis-à-vis the stated objectives, to comment on the findings of this study vis-à-vis other current theories, and to indicate some areas in which more information seems to be especially needed.

The revised classification presented here recognized five species of North American bison. Three of these—*B. latifrons*, *B. antiquus*, and *B. bison*—are considered to be North American autochthons. *B. priscus* and *B. alaskensis* are considered to be Eurasian autochthons that periodically dispersed into North America through Beringia. The North American and Eurasian lineages probably both developed from *B. sivalensis*. Two subspecies are recognized for *B. antiquus* (*B. a. antiquus* and *B. a. occidentalis*) and *B. bison* (*B. b. bison* and *B. b. athabascae*). Each species included in this classification is considered to have been adapted to a distinct selection regime. *B. a. occidentalis* is considered the transitional phase leading from *B. antiquus* to *B. bison*.

Measures of variation are given for selected skeletal characters of both sexes of each taxon. These measures provide insight into the absolute, relative, and statistical nature of continuous variation, sexual dimorphism, allometry, and variance. Clinal gradients for some characters are also provided. The data presented in chapter 3 indicate that not all characters vary identically between sexes, among taxa, or in space, and that not all characters are equally plastic and equally responsive to evolutionary pressures.

Interspecific differences among selected characters and character complexes are identified and described in chapter 4, and their adaptive significances (i.e., functions) are considered. The horns, fronto-facial region, superior molars, occipital region, limbs, and overall body size were evaluated for various adaptive qualities of size, shape, placement, and articulation. Skull characters were shown to have the greatest interspecific differences, a fact that underscores the socially and ecologically adaptive functions of the head and its elements.

Bison occupying forest openings or woodlands are larger than those occupying open grasslands. This fundamental difference forms the basis for the adaptation models presented in chapter 5. Generally, pre-Holocene forest opening/woodland and savanna/wooded steppe bison were both adapted to relatively K-type selection regimes in which selection favored large body size, longevity, and competitiveness, but the forces of selection peculiar to each habitat type differentially emphasized certain characters. Holocene bison are adapted to a relatively r-type selection regime that favors high biotic potential as a result of the recurrent significant catastrophic reduction of their populations. Even within the general r-type selection regime of the Holocene, however, the differential selection of forest/woodland and grassland environments is evident in both North American and Eurasian bison, with the forest/woodland taxa (*B. b. athabascae* and *B. b. bonasus*) being larger than the savanna/grassland taxa (*B. b. bison* and *B. b. caucasicus*).

Hybridization, genetic drift, and inbreeding were considered possible mechanisms by which certain problematic phenotypes could be explained. Hybridization is assumed for most bison in Canada's Wood Buffalo National Park since the late 1920s, and morphological characteristics of post-1928 adults indicate some of the phenotypic responses to be expected in hybrids. It was not possible to identify hybrid *B. latifrons* X *B. antiquus* or *B. priscus* X *B. alaskensis* (but see the East Asia/Beringia data in fig. 24) because their qualitative diagnostic characters are identical. Some specimens studied shared Eurasian and North American characters, however,

and these were considered hybrid specimens. *B. priscus* X *B. antiquus* and *B. latifrons* X *B. alaskensis* hybrids would probably not be competitively disadvantaged vis-à-vis pure individuals of either taxon because both species of each pair were essentially vicarious. This helps to explain the relatively high frequency of hybrid specimens. *B. priscus* X *B. latifrons* or *B. antiquus* X *B. alaskensis* hybrids would, however, probably be competitively disadvantaged (as would *B. antiquus* X *B. latifrons*). Hybridization appears to have occurred in well-defined zones, strongest in Beringia and less frequently in periglacial and central North America.

Genetic drift and inbreeding are probably responsible for several types of phenotypic abnormalities which appear in bison, including numerous types of dental abnormalities, facial abnormalities, deviant horn cores, and, less frequently, occipital and limb abnormalities. Some inbred populations were probably also more susceptible to pathologies than were less inbred populations. Some of the dental pathologies of the Casper bison and the rapid tooth wear evident in some early Holocene southern plains populations might be attributable to the debilitating consequences of inbreeding. Two general situations were probably especially conducive to genetic drift and inbreeding: isolated populations on the periphery of the main bison range (e.g., the tropical American bison) and bottlenecking (e.g., the very late Wisconsin-early Holocene bison).

An attempt to integrate bison chronology and phylogenesis with environmental patterns and regulatory processes of the Quaternary resulted in the synthetic model of bison evolution presented in chapter 7. Drawing on environmental information presented in chapter 1 and systematic information presented in chapters 2–6, the origin, dispersal, distribution, differentiation, and extinction of taxa was described as a systematic process occurring through time and space, given detail and direction by the dynamic Quaternary environment.

The most important points made in this study insofar as the current theories of bison evolution are concerned are that (1) *B. latifrons* survived, and apparently in significant numbers, into the mid- and possibly late Wisconsin; (2) *B. latifrons* and *B. antiquus* were apparently synchronous; and (3) *B. bison* evolved from *B. antiquus*, not a Beringian taxon. Other important relevant elements of this study include findings that (4) *B. latifrons* and *B. antiquus* were largely if not completely allopatric, with *B. antiquus* located south of *B. latifrons*; (5) Eurasian taxa dispersed into North America and these taxa were not, therefore, phases of North American bison phylogenesis; (6) some early Holocene bison actually experienced an increase in character size, including horn size; (7) the mainstream of Holocene bison shifted from a generally southwestern location northward to a northern plains location during the early to middle Holocene, and then expanded southward to occupy its present range by about 3,000–2,000 BP; and (8) forest/woodland taxa are typically larger than savanna/grassland taxa.

Five of the six theories identified in the preface are based, ultimately, on the notion that North American bison horn core size diminished regularly (either step-wise or continuously) over time, following the establishment of the "original" North American species, *B. latifrons*. The Horn Core Theory (Allen, 1876) appears invalid, however, because *B. latifrons* and *B. antiquus* were contemporaries (which they should not have been if the larger had evolved into the smaller), were allochthonous (which implies adaptive differentiation, not sequential occupance of the same general range), and their horn cores are differentiated by a decided morphological gap (which should not be the case if they were phyletically sequential). Inserting the two Eurasian taxa into the horn core gradation observed for North American bison requires that *B. latifrons* evolve into a taxon like Eurasian taxa, and this or these in turn evolve into a subsequent taxa showing typical North American characters (i.e., *B. antiquus*). This is an unlikely and unnecessarily complex arrangement, and is otherwise incompatible with the findings of this study. If the Horn Core Theory is invalid, so too is the Orthogenetic Theory (Schultz and Frankforter, 1946), and the Wave Theory (Skinner and Kaisen, 1947), Synthetic Theory (Guthrie, 1970), and Cline Theory (Wilson, 1974*a*) are seriously weakened.

The Wave Theory is probably accurate in that it recognizes multiple immigrations into Alaska from Siberia, but there were probably more than two such immigrations (immigration probably took place with each exposure of the Bering land bridge); the bison immigrating were probably not typical North American autochthons and, with the exception of the earliest immigrants, they probably did not give rise to early North American autochthons; and they were probably not strictly allopatric until the Holocene.

The Synthetic Theory contains three essential elements: North American bison species each evolved from a Beringian taxon, each successive species evolved horns smaller than the previous species, and each North American species, except for the last (*B. bison*), evolved horns larger than the parent species (*B. priscus* as a result of higher quality forage available at lower latitudes. The first two elements are variants of the Horn Core and Wave theories, discussed above. The third elements introduces a new consideration—the idea that phenotypic development is dependent on the quality of forage. The quality of forage must certainly be recognized as an important element in phenotypic development, but I doubt that this parameter alone is sufficient to generate the degree of phenotypic difference which exists among North American bison. Two problems with the nutrition-based explanation for differences among bison are the failure of subsequently evolving taxa (1) to attain the size of previous taxa (when bison chronology is viewed according to the Synthetic Theory model); or (2) to duplicate the pre-Holocene spatial pattern of larger versus smaller horned bison. Another problem is that this view subordinates, excessively I think, the genotype's role in phenotypic development. The Dispersal Theory (Geist, 1971*a*) is based on the same notion that forage quality, coupled with social changes, associated with the spread of

peripheral populations into an unoccupied range is responsible for phenotypic development. Here, too, the same criticism applies—too much emphasis is placed on forage quality and too little on genotype influence. Beyond this fundamental objection, I have differed quite strongly with the specifics of the Dispersal Theory in my interpretation of bison adaptation to different environments. Although both the Synthetic and Dispersal theories attempt to establish an environmental basis for observed differences among bison taxa, both rely on a deterministic role of environment, rather than treating the environment as a source of stimuli influencing adaptive differentiation among bison.

The Cline Theory is weakened by the general synchroneity and allopatry of *B. antiquus* and *B. latifrons* during the pre-Holocene, and *B. b. bison* and *B. b. athabascae* during the late Holocene (both of which are exactly opposite of the pattern predicted by the Cline Theory); the northward shift of early Holocene bison (which is exactly the opposite predicted by the Cline Theory); and the invalidity of the Horn Core Theory.

The specific objectives and tests of current theories have been accomplished with varying degrees of completeness and confidence. Much additional information is needed to either disprove or support the conclusions reached here, as well as to press ahead with new investigations into bison evolution. The following seem to me to be especially critical needs:

1. More evidence is needed on the origin of the genus *Bison* in Asia. I have here noted the close association between *Leptobos* and *Bison*, and acknowledged Gutherie's information that current work on bovids from China has yielded a more likely ancestor for *Bison* than *Leptobos*. Also, *B. sivalensis* must actually be regarded as a tentative taxon only. A "primitive" species is not to be unexpected at or soon after the origin of a new genus, and *B. sivalensis* fills this position. Both specmens identified herein have nonetheless been identified by others as females and they could, in fact, be female *B. priscus*, although they are too large and too male-like, vis-à-vis the early, small *B. priscus* males, to convince me that they are females. We have here the possibility that early males might simply resemble later females. Additional information bearing on the time and place of origin, the phyletic pathway, and the morphology, behavior, and ecology of early bison is sorely needed.

2. Systematically derived information on the morphology and chronology of Eurasian bison is needed. Information describing morphological variation and the geochronology of Eurasian bison is essential to an understanding of the *B. priscus-B. alaskensis* problem and to an assessment of the role of Eurasian bison in the origin and evolution of bison in North America. Information on Eurasian bison morphology is available, but in limited quantities only. Good chronology, ideally based on absolute measurements, is also available only in limited quantities. These data are needed for the entire Eurasian bison range, but especially for the Siberian area insofar as North American-Eurasian bison relations are concerned.

3. The temporal and spatial relations between *B. latifrons* and *B. antiquus* need to be better documented. Radiocarbon measurements are gradually providing reliable resolution of the time of disappearance of these two species, but the time and place of their origin is still very poorly known. Careful attention to the interpretation of the age of new-found specimens, preferably employing some absolute dating technique, would be extremely helpful.

4. Many additional radiocarbon measurements for late Pleistocene megafauna are needed. Radiocarbon dates have provided important chronological control for the examination and assessment of late Pleistocene bison specimens and populations, and their relations to other faunal elements. Available radiocarbon dates have permitted a reasonably clear picture of the rate and direction of Holocene bison evolution, but much greater temporal resolution would be possible if additional dates were available. This is especially true for bison occurrences on the margins of the main bison range, and for regions in the Great Plains not yet well represented by adequate dates.

5. Certain geographic regions need additional attention. Mexico is probably the region for which additional information on the presence of bison is most needed, but more information is also needed from the Great Basin and the southwestern United States for the period before 12,000 BP. Good chronology for eastern Beringia is also needed to help clarify what is, in fact, still a relatively confusing history of bison in that region.

6. Additional biometric analyses of populations are needed. Much more information on the nature of variation among populations, especially on other than (but certainly not excluding) skull and metapodial characters, is necessary to better understand all aspects of morphological variation. The measures of variation presented in chapter 3 need to be supplemented, perhaps with the use of additional quantitative techniques. New data for females of taxa represented here by only small samples would be very useful. Studies of the nature of ontogeny could be especially useful, as would investigations of evolutionary differences in nonskeletal characters (see, e.g., Smiley, 1978; M. Wilson, 1975).

7. Further empirical work is needed on the physiology, ethology, and ecology of bison and other ungulates. This serves the immediate function of providing a better understanding of modern populations, but it also provides baselines for making inferences about past behavior and ecology and to influence predictions and management decisions for future behavior and ecology. Bison evolution is continuing, and the more completely we understand the present needs and responses of modern bison, the better will we be able to evaluate its future needs and evolutionary directions in this human dominated and directed world.

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LARGE MAMMALS ARE GENETICALLY LESS VARIABLE?

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Estimates of genetic variability, based on electrophoretic studies, indicate a large disparity among organisms within various taxonomic assemblages (Powell, 1975; Nevo, 1978). One hypothesis forwarded to account for some of these differences suggests that large, mobile animals generally have lower levels of genetic variability than smaller, less mobile ones (Selander and Kaufman, 1973). These authors proposed, following logically Levins' (1968) work, that larger animals perceive their environments as fine grained or more predictable. An organism's perception of its environment as fine grained suggests a dampening of internal metabolic responses due to environmental perturbations. The ability to be buffered from environmental fluctuations is a definite advantage of large size. Smaller, less mobile organisms experience a coarser grained environment and, theoretically, maintain higher genetic variability as a result of varying selection pressures in different microhabitats. Although Selander and Kaufman (1973) were specifically referring to differences observed between vertebrate and invertebrate species, their arguments can justifiably be extended as possible explanations of within-class observations.

Recent electrophoretic studies involving mammalian species (Bonnell and Selander, 1974; Allendorf et al., 1979; Manlove et al., 1980; Ryman et al., 1980; Simonsen, 1982; Simonsen et al., 1982*a*, 1982*b*; O'Brien et al., 1983) have reported heterozygosity (H) values for large mammals which are generally lower than the class average (H for all mammals = 0.0359; Nevo, 1978). Somewhat conflicting findings have been reported for other large mammals (Baccus et al., 1983). For three genera of Ceropithecines, Kawamoto et al. (1982) found a mean H of 0.05 (averaged from their Table 3). Simonsen et al. (1982*b*) indicated that Atlantic walruses (*Odobenus rosmarus*) exhibited reduced variability, but their reported estimate ($H = 0.033$) is quite similar to Nevo's (1978) mammalian value. Nei and Roychoudhury (1982) reported a mean H of 0.30 (averaged from their Table 4) for eight human Caucasian populations, as well as similar values within other racial divisions. In addition, for a large mammal, white-tailed deer (*Odocoileus virginianus*) appear to exhibit exceptional variability ($H = 0.074$; Baccus et al., 1983).

Our purpose was to examine the relationship between body size and genetic variability (heterozygosity) in mammals. Our null hypothesis was that no relationship exists between these two variables. Selander and Kaufman's (1973) prediction would be positively demonstrated by a significant negative correlation (or by a negative slope on a line of best fit). To test the hypothesis, data were extracted from the available electrophoretic literature using studies that contained estimates of mammalian heterozygosity and that involved 13 or more loci. When more than one value was available, the estimates were averaged to obtain one value per species. All heterozygosity values were direct count averages or adjusted equivalents. In five cases, expected heterozygosity values were given in the literature. These estimates were adjusted by a least squares linear regression equation ($r_p^2 = 0.94$, $P < 0.0001$) to pre-

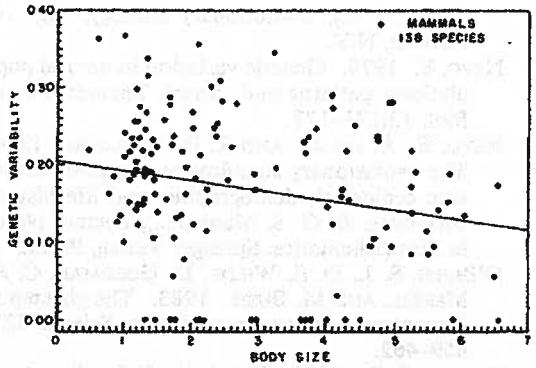

FIG. 1. Plot of common log transformed gram body weight estimates (BODY SIZE) against arcsine square root transformed direct count heterozygosity values (GENETIC VARIABILITY) for 138 mammalian species. The solid line represents a line of best fit through the data points as determined by least squares regression.

dicted direct count values. Data from a total of 138 mammalian species (mean $H = 0.039$) were obtained. Body weight was taken to represent a general measure of overall size. These values were obtained from the literature and converted to gram equivalents. Heterozygosity values were arcsine square root transformed following the recommendations of Sokal and Rohlf (1981). A plot of these values with the associated line of best fit is presented in Figure 1. A common log transformation was applied to each body weight. Pearson product-moment correlation analyses were performed using both transformed and nontransformed variables. For completeness, Spearman correlation coefficients were also calculated. All statistical comparisons produced negative correlation coefficients. Pearson correlation values (r_p) were -0.13 ($P = 0.11$) between the nontransformed weight and heterozygosity estimates and -0.20 ($P = 0.02$) between the transformed values. Spearman rank correlations produced similar results ($r_s = -0.22$, $P < 0.01$). These correlations are considerably lower than that reported by Baccus et al. (1983; $r_s = -0.60$) for ranked variables in a similar study across 10 mammalian species, but they exhibit the same negative relationship.

Recognizing that the heterozygosity values presented in Figure 1 were derived from a diverse group of studies, several attempts were made to standardize the data base. First, all species represented by a single population were excluded and the correlations recalculated. Next, analysis of covariance (ANCOVA) procedures (Huitema, 1980) were used to adjust each value by the number of individuals, the number of populations, and the number of loci sampled, and the values retested. Finally, ANCOVA procedures were again used to remove the effects of sampling different loci. All loci were classified into one of three groups (Group 1—glucose metabolizing and single substrate, Group 2—variable substrate, and Group 3—non-enzymatic proteins). This method produced 110 testable values. In several of the comparisons, data adjustment did increase the predictability of the relationship between heterozygosity and body size, but in no case did r_p^2 exceed 0.13. Therefore, the conclusions obtained from comparisons of the unadjusted data appear to be robust. Because the results from all comparisons were consistent, only correlation values for unadjusted data are presented and discussed. Interested readers may contact the authors for actual results from the various comparisons of adjusted values and/or for a complete listing by species of the raw data and all associated references.

Because our analysis produced correlation coefficients which were consistently negative (with significance indicated at the $P = 0.01$ level for two of the comparisons), we must reject the null hypothesis that no relationship exists between body size and genetic variability in mammals. Analyses support a pattern of reduced genetic variability with increased body size as hypothesized by Selander and Kaufman (1973). However, the predictive power for the relationship between size and heterozygosity is quite low ($r_p^2 = 0.017$–0.040). Whereas the body size hypothesis exhibits statistical validity, its contribution to our understanding of the overall pattern of genetic variability among mammalian species is quite limited. This hypothesis must be included in any comprehensive discussion of mammalian genetic variation, but other avenues should be explored in the search for an answer to the question of cause and effect relationships underlying the large interspecific variation in heterozygosity.

One possible way of enhancing our understanding of the underlying causes would be the examination of genetic variability among smaller groups of species. Nevo (1978) used this approach by separating *Drosophila* from other insects when comparing heterozygosity values. He reported that insects (excluding *Drosophila*) are not significantly higher in heterozygosity than most vertebrate classes. In fact, this finding casts doubt on the basic premise upon which Selander and Kaufman (1973) based their original size-genetic variability argument.

Using available data, we calculated Pearson product-moment and Spearman rank correlations between transformed heterozygosity and body weight for three rodent families abundantly represented in Figure 1 (Geomyidae: $N = 18$ species; Heteromyidae: $N = 17$ species; Muridae: $N = 28$ species). None of the six correlation coefficients was found to be statistically significant from zero. The Heteromyidae exhibited the greatest negative correlation ($r_p = -0.45$; $r_s = -0.39$) and the Geomyidae the most positive ($r_p = 0.24$; $r_s = 0.29$). Essentially no relationship at all exists for the best represented family (Muridae: $r_p = -0.05$; $r_s = -0.11$). These data do not support the size-genetic variability argument. Using different biological subdivisions, Nevo (1984) reported similar conclusions and argued that mammalian heterozygosity levels may be derived not from size but from other

causal forces. Findings of this type suggest that we may need to examine the relationships within families or at a lower level of biological organization (population?) to understand the relevance of available data.

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ON THE EVOLUTION OF HANDLING TIME

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In a study designed to assess the evolutionary impact of a predator on its prey, Livdahl (1979) analyzed the functional response of a predatory mosquito to varying density of its prey, another mosquito. His goal was to determine the evolutionary impact of the predator on the prey, as ex-

MAMMALIAN SPECIES No. 266, pp. 1–8, 4 figs.

Bison bison.

By Mary Meagher

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Bison (Hamilton-Smith, 1827)

Bison Hamilton-Smith, 1827:373. Type species *Bison bison* (Linnaeus, 1758). Proposed as subgenus, recognized as genus by Knight, 1849:408.

CONTEXT AND CONTENT. Order Artiodactyla, Family Bovidae, Tribe Bovini. The genus *Bison* includes two extant species, *B. bonasus*, the European bison or wisent, and *B. bison*, the late Holocene bison of North America.

Bison bison (Linnaeus, 1758)

Bison

Bos bison Linnaeus, 1758:72. Type locality earlier considered to be "Mexico" (Thomas, 1911); subsequently considered to be the "Quivira Region," (central Kansas; Hershkovitz, 1957); redesignated as the Canadian River Valley of eastern New Mexico, United States (McDonald, 1981).

Bison americanus Brisson, 1762:56. Type locality America.

Bison occidentalis Lucas, 1898:678. Type locality Fort Yukon, Alaska.

Bison sylvestris Hay, 1915:515. Type locality Huron Co., Ohio.

Bison bison Jordan, 1888:337. First use of present name combination.

CONTEXT AND CONTENT. Context as given above. Two subspecies are recognized (McDonald, 1981; Skinner and Kaisen, 1947). Synonomy for both subspecies follows Skinner and Kaisen (1947):

B. b. athabascae Rhoads, 1897:498. Type locality, within 50 miles southwest of Fort Resolution, Mackenzie District, Northwest Territories, Canada (*occidentalis* Lucas, *oregonus* Bailey, and *haningtoni* Figgins are synonyms).

B. b. bison (Linnaeus, 1758). Type locality, see above (*americanus* Brisson, *sylvestris* Hay, *pennsylvanicus* Shoemaker, and *septemtrionalis* Figgins are synonyms).

DIAGNOSIS. The following applies to the genus and species: horn cores in cross section at the base more or less triangular (males) or elliptical to circular (females), cores extend outward laterally from frontals forward of the occipital plane; frontals quadrate, flat to convex between the horn cores, never bossed; parietals on or about the same plane as the frontals, parietal plane forming an obtuse angle with occipital plane; occipital broad; orbits tubular (more so in males), protruding anterolaterally; nasals broad, short, triangular; premaxilla triangular, nasal process of premaxilla not reaching nasals (Figs. 1 and 2). *B. bison* includes specimens dating 5,000 BP and less (McDonald, 1981; Wilson, 1975).

GENERAL CHARACTERS. The body is massive, tall but proportionately narrow in transverse profile (Fig. 3). Both massiveness and height are accentuated by the shoulder hump formed by elongation of the neural processes of thoracic vertebrae and musculature of the shoulder and thoracic girdle. The hindquarters are lighter than the frontquarters; this disproportion is further accented by marked pelage differences between front and rear. Pelage is brown, long over the forehead, neck, hump, and frontquarters, short over the rear and tail. The tail is relatively short, with tufted tip. The head is large and carried low on the short, thick neck. Both sexes have short, black horns that curve upward and inward and taper to a circular, relatively sharp tip. Eyes are placed anterolaterally; ears are well buried in the long pelage of the head. The legs are relatively short and stout. Hooves are black with a nearly circular print.

Sexes are dimorphic with females similar to males but generally presenting a smaller, slighter appearance (Fig. 3). External measurements (in mm) for males and females, respectively (Hall, 1981; Meagher, 1973; Seton, 1929), are: total length, 3,040 to 3,800, 2,130 to 3,180; tail length, 330 to 910, 300 to 510; hindfoot, 580 to 680, 500 to 530; height at shoulder, 1,670 to 1,860, 1,520 to 1,570; body mass (in kg), 544 to 907, 318 to 545. Maximum recorded mass is 1,724 kg for a semidomestic bull (Hebbring, 1978). Males are about 9.1% heavier than females of equal girth (Kelsall et al., 1978). Males have proportionately stouter, more evenly curving horns, with horn cores burred at the base. Their hump structure is much larger and the neck is relatively stouter. They have longer pelage on the forehead, chin, ventral mane, and chaps of the forelegs, and a more pronounced line of demarcation between the longer hair of the forequarters and the shorter hair of flanks and rear.

B. b. athabascae and *B. b. bison* closely resemble each other. *B. b. athabascae* is generally larger but there is overlap. Selected measurements (in mm) of male skulls for *B. b. athabascae* and *B. b. bison*, respectively (McDonald, 1981), are as follows: maximum length, 562 to 604, 500 to 583; spread of horn cores, 542 to 848, 510 to 778; least width at frontals between horn cores and orbits, 273 to 313, 237 to 318.

DISTRIBUTION. Bison formerly were widespread in North America from Alaska and western Canada across the United States and into northern Mexico (Fig. 4). Occupation of marginal areas may have been intermittent (McDonald, 1981). McDonald (1981) believes the maximum geographic distribution of *B. b. bison* occurred in the late prehistoric period because of the many historical accounts of bison presence near the margins of the indicated maximum range (Christman, 1971; Reed, 1955; Roe, 1970; Rostland, 1960). The distribution of *B. b. athabascae* is less well known (McDonald, 1981). They apparently disappeared from Alaska before historic times but there are unfossilized specimens (Skinner and Kaisen, 1947).

Today bison occur as geographically isolated population units in parks, preserves, and other public lands, and on private ranches and small holdings throughout and external to the maximum known geographic distribution (Fig. 4). Major free-ranging populations occur in Canada (Mackenzie Sanctuary, Wood Buffalo National Park and adjacent Slave River lowlands) and the United States (Yellowstone National Park); a few smaller units also exist (Reynolds et al., 1982).

Altitude does not appear to have limited bison distribution. Evidence of past bison occupation was reported from about 3,903 m in Colorado (Beidelman, 1955), from 2,897 m to about 3,659 m in Wyoming (Fryxell, 1928), and at approximately 3,200 m in Montana (Pattie and Verbeek, 1967).

FOSSIL RECORD. Although the time and place of origin of the ancestors of *B. bison* are obscure, the earliest dated remains of the genus occur from the late Pliocene of Central Asia, with possible early Pleistocene occurrences from northern India and northern China (McDonald, 1981). Bison seemingly were confined to temperate and upland east Asia until after the early Pleistocene. Thereafter they appeared in southeastern and central Europe, becoming relatively common as fossils and in later cave paintings throughout much of Europe. Bison reached northern Eurasia during the middle Pleistocene and spread across the Palearctic into Alaska, but survived in northern Eurasia until the very late Pleistocene (McDonald, 1981). They first appeared in the fossil record south of Beringia in North America in early late Pleistocene faunas (Guthrie, 1980; McDonald, 1981). Most specimens of bison are known from the late Pleistocene of North America and higher latitude Eurasia, and the Holocene steppes and adjacent forests of Eurasia and North America (McDonald, 1981).

The evolutionary line leading to *B. bison* remains controversial although there seems to be general agreement on many elements. *Proleptobos* from the early Pliocene may be the ancestor of the

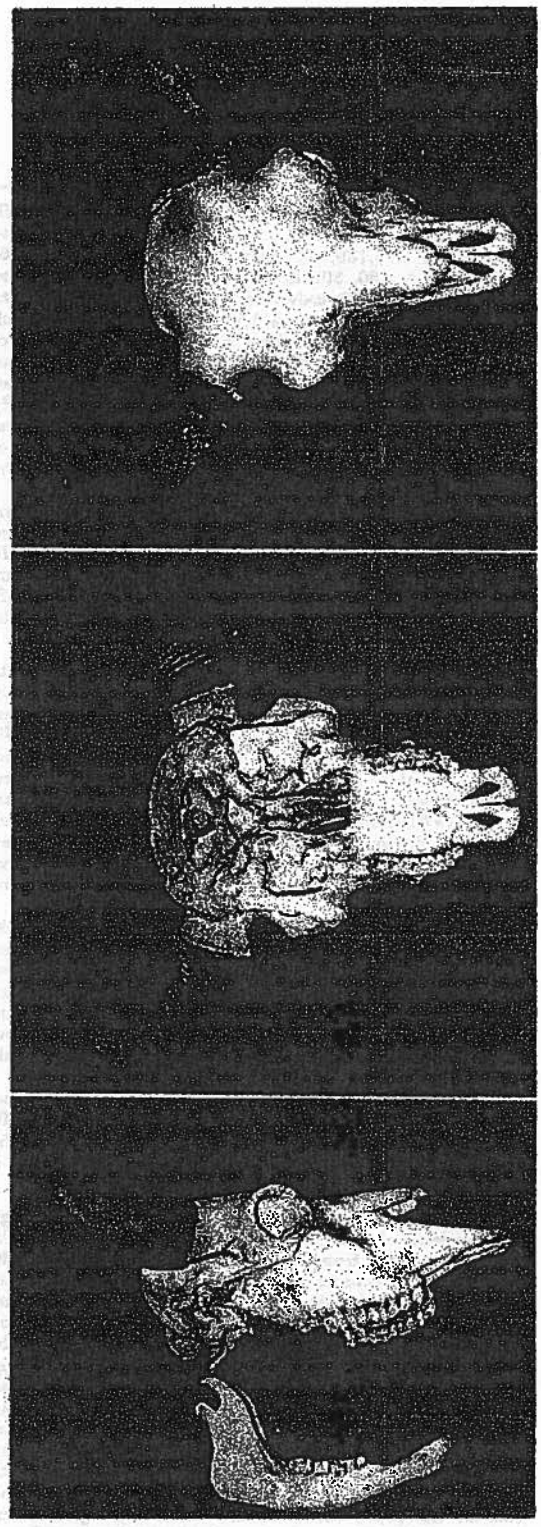

FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of adult male bison (YNP 11661) Condylobasal length, 519 mm. Photographs by A. Vanderbilt.

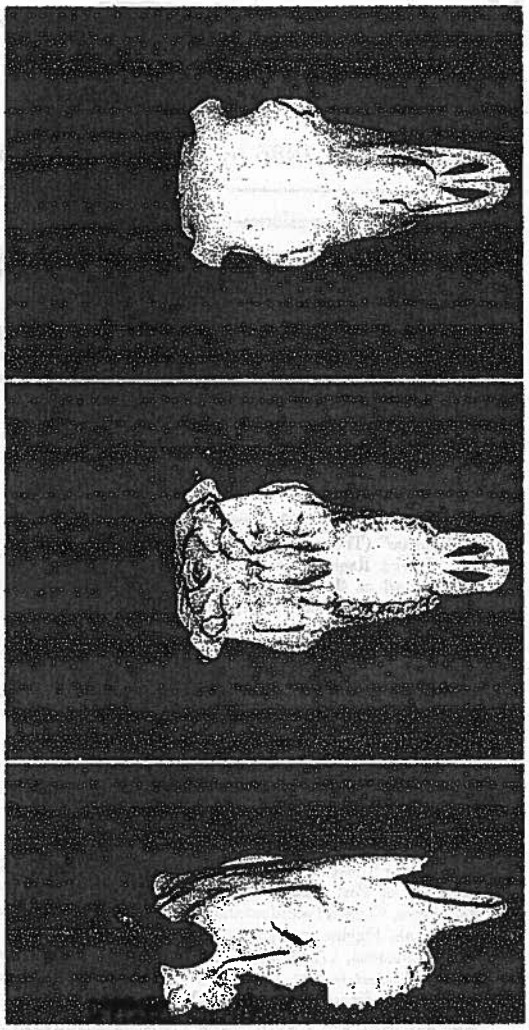

FIG. 2. Dorsal, ventral, and lateral views of cranium of adult female bison (YNP 12050). Condylobasal length, 460 mm. Photographs by A. Vanderbilt.

Bos–Bison group of Bovini (McDonald, 1981). *Leptobos*, appearing later in the Pliocene and widely distributed in central and southern Eurasia during both the Pliocene and Pleistocene, may be either a common ancestor (Guthrie, 1980; McDonald, 1981) or a closely related taxon (McDonald, 1981). *B. sivalensis*, the earliest known species and possible ancestor of later lineages of bison, dispersed northward into Siberia by the middle Pleistocene or earlier (McDonald, 1981). This species and another poorly known early form, *B. paleosinensis*, seem to have been small bodied, small horned, and more cattle-like compared to later bison, and were probably adapted to a woodland–parkland environment (Guthrie, 1980).

Early in the middle Pleistocene the so-called steppe bison, *B. priscus* appeared (Guthrie, 1980). This larger bodied, larger horned bison apparently was the dominant form during the rest of the Pleistocene and may be ancestral to the North American forms (Guthrie, 1980; Wilson, 1975).

By the late Illinoian to early Sangamon the large steppe bison seems to have spread into the grasslands of central North America where they became even larger, with enormous horn cores reaching 2 m tip to tip (Guthrie, 1980). This form, *B. latifrons* or *B. priscus latifrons*, occurred in much of unglaciated North America but seems to have been most common from Alberta to Texas along the east front of the Rocky Mountains and the intermontane basins. Guthrie



FIG. 3. Photographs of a fully mature male (top) during rut and female (bottom) bison showing contrast in head and horn shape. Photographs courtesy of A. Stephen Johnson.

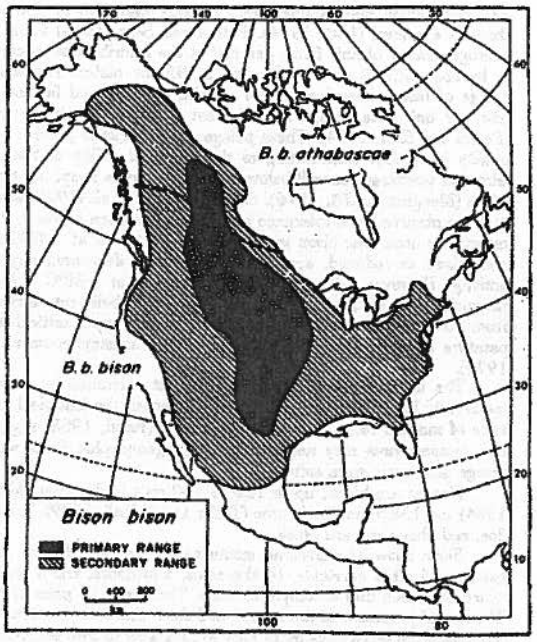

FIG. 4. Map illustrating probable maximum distribution of *B. bison* during late prehistoric times with the north-south axis of the primary range coincident with the central North American grasslands. The maximum extent of the range of *B. b. athabascae* is not as well known as that of *B. b. bison*. Map is fig. 23 from McDonald (1981) courtesy of University of California Press (scale added).

(1980) and Wilson (1975) believed this line decreased in size during the Wisconsin, grading eventually into the smaller *B. antiquus*.

About 13,000–12,000 BP, a gradual diminution in size of *B. priscus* seems to have occurred in the far north (Guthrie, 1980) leading to *B. occidentalis* (Guthrie, 1980; Wilson, 1975). At the end of the Wisconsin, this northern line of *B. occidentalis* may have reinvaded the grasslands of the Great Plains to contact and interbreed with the more southern line of *B. antiquus* (Wilson, 1975). At this time the two lines may have been similar in size although somewhat different in cranial and horn-core morphology (Guthrie, 1980). During the Holocene, North American bison seemingly continued to diminish in body size while at the same time increase in numbers (Guthrie, 1980).

Guthrie (1980) pointed out that the rapid rate of bison evolution led to a bewildering assortment of taxonomic designations. The trend in recent years has been to synonymity (Guthrie, 1980; McDonald, 1981; Skinner and Kaisen, 1947; Wilson, 1975), but temporal and spatial trends seem to warrant subepecific status for resulting differences of form. In this view, then, the evolution of North American bison led to two Holocene species, the earlier *B. priscus*, and the extant *B. bison*, with their subspecies (Guthrie, 1980; Wilson, 1975).

FORM AND FUNCTION. The annual pelage molt begins late winter to early spring. Tattered patches of bleached winter hair may cling to the forequarters well into August. New growth is short, somewhat stiff, and nearly black. By late fall the winter coat of woolly underfur with overlying coarse guard hairs is essentially full grown. Head, underparts, flanks, and rear are dark brown, appearing black at a distance. The long woolly hair across the forequarters commonly lightens to bleached tan, most pronounced on older bulls. Usually there is a dark streak down the front of the hump, suggesting a mane, although the hair is scarcely longer than that over the shoulders.

Length of hair (in mm) has been estimated as follows: flanks and rear, 25; rump and hips, 50 to 90; shoulders and hump, 65 to 160; chaps, 150 to 190; and beard, 300 mm (Meagher, 1973; Soper, 1941). On bulls, the hair of the forehead may be 150 to

210 mm, which may compact into a frizzy mat 100 to 130 mm thick at eye level (Lott, 1974). Peters and Slen (1964) found an average density of hair fibers per cm^2 at the midrib of bison calves to be about 2,992 for females and 2,182 for males. The winter pelage of bison showed a greater weight, density, and fineness of hair per unit area compared with that of three breeds of cattle (Peters and Slen, 1964). These pelage characteristics provide high quality insulation, contributing to the observed ability of bison to winter at temperatures well below zero and in areas swept by strong winds (Meagher, 1973, 1976). Christopherson et al. (1979) attributed the observed cold tolerance of 6-month-old bison calves to their heavy hair coat. The bison metabolic rate in still air at −30°C was maintained or reduced, apparently because of decreased physical activity. However, with the addition of wind at −30°C a lower thermally critical zone was reached with a metabolic rate increase from 700 KJ/kg to 950 KJ/kg. In winter, the upper critical temperature apparently was exceeded at 10°C (Christopherson et al., 1979).

The upper limits of physiological heat tolerance in summer apparently have not been determined. However, the historical presence of modern bison in Texas and Mexico (Reed, 1955) suggests that temperatures may not have imposed geographic limits where forage and water were suitable.

Hooves are black, up to 120 to 130 mm in diameter (Murie, 1954) and 133.5 cm^2 insole area (Telfer and Kelsall, 1979). Tongue, lips, and rhinarium are black.

Bison have 31 vertebrae exclusive of the caudals: the atlas, axis, and 5 other cervicals, 14 thoracics, 5 lumbars, and 5 sacrals, which are fused into a composite bone. There are 14 pairs of ribs. The neural processes of the second and third thoracic vertebrae are the longest; in large bulls these may extend 450 to 500 mm (Olsen, 1960).

The dental formula is: i 0/3, c 0/1, p 3/3, m 3/3, total 32 (Hall, 1981). Molariform teeth are hypsodont and selenodont. At birth all deciduous teeth are present and covered by a semitransparent membrane that sloughs off during the first days of life (Fuller, 1959). The first permanent tooth, m1, erupts during the first year; by age 5 all teeth are permanent (Fuller, 1959). Age estimates based on wear thereafter are approximate and subjective.

Four inguinal mammae are present. Milk analysis showed 8.9% nonfat solids, 6.3% protein, 2.9% anhydrous lactose, 6.3% fat, 0.3% calcium (Hebbring, 1983).

Bison bulls yielded dressed carcass weights (without hide, head, and entrails) of 52 to 54%, adult cows yielded 54 to 58% (Halloran, 1957). Analysis of muscle from various body parts showed 28 to 35% protein and 0.8 to 5% fat (Johnson and Deethardt, 1980).

Values for selected cellular constituents of adult bison blood ($n = 163$) were: hemoglobin, 16.99 ± 1.43 g%; hematocrit (packed cell volume, PCV), 47.11 ± 4.06%; erythrocytes, 10.08 ± 1.43 $10^6/mm^3$; and leucocytes, 8.03 ± 1.41 $10^3/mm^3$ (Mehrer, 1976). The leucocyte component varied according to diet and season (Keith et al., 1978), and was significantly different between bison under 2 years of age and adults (Marler, 1975). Oxygen-carrying capacity for seven adult bison was 22.2 ml/100 ml; oxygen tension at half saturation (P_50) was 32 m at pH 7.4 and 37°C (Haines et al., 1977). Haines et al. (1977) related this comparatively great oxygen carrying capacity and low oxygen affinity to the frequently observed prolonged running ability of bison.

Values for selected blood chemistry components of adult bison serum ($n = 6$) were: total protein, 8.0 ± 0.6 g/100 ml; globulin, 4.9 ± 0.2 g/100 ml; bilirubin, 0.7 ± 0.2 mg/100 ml; blood urea nitrogen, 16.3 ± 4.1 mg/100 ml; creatinine 2.3 ± 0.6 mg/100 ml; glucose, 77.5 ± 9.7 mg/100 ml; cholesterol, 76.0 ± 8.2 mg/100 ml; calcium, 10.4 ± 1.0 mg/100 ml; chloride, 113.3 ± 5.9 meq/l; phosphorus, 5.8 ± 1.0 mg/100 ml; potassium, 4.2 ± 0.6 meq/l; sodium, 145.0 ± 1.8 meq/l; alkaline phosphate, 21.0 ± 8.6 U/l; lactic dehydrogenase, 545.8 ± 149.5 U/l; and serum glutamic oxalacetic transaminase, 57.0 ± 24.8 U/l (Keith et al., 1978). Schaefer et al. (1978) found mean plasma T_3 and T_4 levels of 45.5 μg/100 ml and 5.42 ug/100 ml, respectively. Blood urea nitrogen was 20.63 mg/dl and 12.33 mg/dl on high-N and low-N diets, respectively (Keith et al., 1981). High- (D > 1.063) and low-density (D < 1.063) lipoproteins comprised 64 and 36%, respectively, of bison serum total lipids from two heifers (Evans, 1964). Most serum components showed significant variation according to diet quality and time of year (Keith et al., 1978).

Mean heart rate for bison was 89 beats/min; rate fluctuated as much as 50% within 30 sec (Hawley and Peden, 1982). Mean body temperature was 38.7°C (Hawley and Peden, 1982). Christopherson et al. (1979) recorded mean respiration rates that ranged from 11.2 ± 2.9 to 20.0 ± 8.8/min.

Bison have the ruminant digestive system with a four-compartment stomach consisting of the rumen, reticulum, omasum, and abomasum. Voluntary feed intake in kg kg body $mass^{-1}day^{-1}$ by bison was 0.009 on sedge and 0.011 on grass (Richmond et al., 1977).

During rumination a bolus may be chewed 38 to 70 times at a rate of about one chew/s (Fischer, 1967). Pearson (1967) found that rumen microorganisms included eight species of ciliate protozoa and five morphological types of bacteria, with average total counts of 0.58 × 10^6/ml and 7.14 × 10^9/ml, respectively. Rumen content lipids contained 4, 16, 17, 22, and 33%, respectively, of monoglycerides, triglycerides, sterols, phospholipids, and nonesterified fatty acids (Evans, 1964). Apparent digestibility in percent of a sedge hay diet was: dry matter, 51.3; crude protein, 38.3; crude fat, 64.2; neutral detergent fiber, 54.7; acid detergent fiber, 47.0; hemicellulose, 67.1; lignin, 25.2; and gross energy, 50.6 (Hawley et al., 1981*a*). On this diet, bison showed an average daily gain in kg/day of 0.42 and 0.04 for summer and winter, respectively. When compared with cattle, digestibility coefficients for all nutrients in low quality (low protein, high fiber) diets were higher, as were digestibilities of various native forages (Hawley et al., 1981*b*). Rumen ammonia concentrations and urinary urea levels appeared to be proportional to dietary N levels (Keith et al., 1981). Apparent absorption of N from the gastrointestinal tract was 3.50 g/100 g of dry matter; retention time of digesta in feeding trials was 78.8 h (Schaefer et al., 1978).

Droppings are similar to those of cattle. On succulent feed, a flat mass of 30 cm diameter is common; with drier feed a more rounded, layered mass forms (Murie, 1954). Defecation rates of approximately once per h were observed in bulls (Herrig and Haugen, 1969).

The mean brain weight for four subadult males and two mature females was 458 g. Mean forebrain measurements (in mm) were: length, 114.3; width, 93.3; height, 64.1. Mean cerebellum measurements were: length, 44.8; height, 38.7 (Harper and Maser, 1976).

In 4.5-year-old bison the mean chest height for males ($n = 95$) was 677 ± 3.3 mm and for females ($n = 23$) was 643 ± 7.0 mm; the mean foot load, in gm/cm^2, was 884.1 ± 8.02 and 672.4 ± 9.47 for males and females, respectively (Telfer and Kelsall, 1979). These authors suggested that males might cope more successfully with increased snow depth, but that females might have a greater advantage when walking on hard or dense snow. The musculature of the neck and shoulders allows bison to forage by swinging the head from side to side to clear feeding areas. Mixed groups regularly foraged in snows 600 mm deep, bulls to 900 mm deep (Houston, 1982). McHugh (1958) observed some bison to forage at 1,200 mm.

ONTOGENY AND REPRODUCTION. A few precocious female bison first conceive as yearlings but sexual maturity most commonly occurs at 2 to 4 years of age (Fuller, 1962; Halloran, 1968; Meagher, 1973). Sexual maturity in males is similar. A few show sperm in the epididymis as yearlings; by age 3 most males are sexually mature (Fuller, 1962; Shult, 1972). Although Halloran (1968) found that 2-year-old males might perform effectively as sires in the absence of older males, bulls usually do not breed cows until age 6 (Herrig and Haugen, 1969; Lott, 1981; McHugh, 1958).

The breeding season may extend from late June or early July through September (McHugh, 1958; Meagher, 1973; Shult, 1972) but actual breeding is more strongly seasonal. Lott (1981) reported that about 90% of copulations occurred in a 2-week period with 17 of 37 observed occurring 30–31 July and 1–2 August. Haugen (1974) calculated that most conceptions occurred between 21 July and 19 August with a peak about 1 August. In the north, at Wood Buffalo National Park, breeding activity may begin later (Soper, 1941) and peak between 10 and 20 August (Fuller, 1962).

Gestation was estimated at 285 days (Haugen, 1974). The calving season generally extends from mid-April through May with births often concentrated from the end of April through the first two weeks of May (Lott and Galland, 1985; McHugh, 1958; Meagher, 1973; Rutberg, 1984; Shult, 1972). Out-of-season births are

recorded in most herds, usually later in summer (Fuller, 1962; Lott and Galland, 1985; McHugh, 1958; Meagher, 1973).

Bison cows have one calf; twins are known but are rare (Engelhard, 1970; Fuller, 1962; Halloran, 1968, Haugen, 1974; McHugh, 1958; Roe, 1970). At birth, the calf may weigh 15 to 25 kg (Rutberg, 1984). The fetal sex ratio usually favors males (Fuller, 1962; Haugen, 1974; McHugh, 1958; Meagher, 1973).

Calves are usually bright reddish tan, although Engelhard (1970) recorded some calves with atypical dark streaking and areas of gray. Calves begin to darken to a brownish black at about 2.5 months (McHugh, 1958); darker hair appears first on the head, then the shoulders and back, but calves are not uniformly dark until 4 months (Engelhard, 1970). Sexes are alike in appearance at birth, with no apparent hump. There is a tendency for males to develop slightly larger body size, larger hump, and longer more conical horns by the end of the first year (Engelhard, 1970). Calves usually weigh between 135 and 180 kg by 8 to 9 months of age; yearlings (20 to 22 months) weigh between 225 and 315 kg (Meagher, 1973).

Calves are precocious; average times for 10 calves to first stand and first nurse were 10.9 min and 32.2 min, respectively (Lott and Galland, 1985). They may try to graze by 5 days of age (Shult, 1972) and will drink water after the first week (Engelhard, 1970; Shult, 1972). Engelhard (1970) noted a 1-month-old calf with partly digested grass in the abomassum; calves orphaned at 7 to 8 weeks of age have survived (Shult, 1972). Cows nurse their calves for at least 7 to 8 months (McHugh, 1958), but most calves apparently are weaned by the end of the first year (Halloran, 1968; McHugh, 1958; Shult, 1972; Van Vuren, 1979).

Age of physical maturity in bison apparently differs between the sexes. Bulls appear to attain near-maximum mass by age 5 or 6 with small increments thereafter (McHugh, 1958). Average mass of 237 known-age bulls suggests that maximum was reached at age 10 to 12; similar data for cows suggests that maximum size might be attained by 3 years of age (Halloran, 1968). Horn development provides a rough estimate of maturity for bulls; mature curve and thickness was attained by 7 to 8 years (Fuller, 1959). Cows attain full curvature by 3 to 5 years of age (McHugh, 1958).

Females may be seasonally polyestrus, with a cycle of approximately 3 weeks (Fuller, 1962). Estrus may last 9 to 28 h (Haugen, 1974).

Average longevity in bison has not been documented. Fuller (1959, 1962) placed the onset of old age at 12 to 15 years. In the wild, a few bison apparently survive more than 20 years (Meagher, 1973); records of a few known-age cows of 40+ years were cited by McHugh (1958).

ECOLOGY. An estimated 30 million bison inhabited North America about the time modern man arrived (McHugh, 1972). Subsequently, bison nearly were exterminated through overhunting. Various writers have chronicled this exploitation (Dary, 1974; Haines, 1970; McHugh, 1972; Roe, 1970). By 1903, a known 1,644 bison existed (Carretson, 1938), mostly in zoos and privately owned herds. They survived near extermination as a wild species in two areas: Wood Buffalo National Park, Canada (Soper, 1941), and Yellowstone National Park, Wyoming (Meagher, 1973). Through establishment of additional public preserves and privately owned herds, bison numbered an estimated 75,000 in 1983 (Jennings and Hebring, 1983).

Prehistoric distribution occurred primarily on the central grasslands and northern parklands of North America, but habitats used ranged from semidesert to boreal forest where suitable grazing was available (McDonald, 1981). Bison are grazers at all seasons, taking mostly grasses and sedges (*Carex* spp.). Use of warm season grasses predominated in shortgrass pasture (Peden et al., 1974); cool season grasses including some sedges composed 79 to 96% of the diet of herds on mixed prairie (Popp, 1980). In a shrub-steppe habitat, 96% of the summer diet was grasses (Van Vuren, 1984). Sedges were selected throughout the year in montane and northern areas where sedge-grass meadows are a major habitat component (Meagher, 1973; Reynolds et al., 1978; Soper, 1941; Telfer and Cairns, 1979). Bison ingest an average of 7.4 kg of sedge hay/day (Hawley et al., 1981*b*), or a mean daily dry matter intake of 1.6% of body mass both summer and winter (Hawley et al., 1981*a*). Most apparently ingest water or snow daily (McHugh, 1958).

Where bison coexist with other ungulates, interspecific competition apparently is minimized through differences in habitat use and food habits (McCullough, 1980), and morphology (Houston, 1982; Telfer and Kelsall, 1984). In a shrub-steppe habitat, bison were frequently at higher elevations, generally moved further from water, and grazed steeper slopes than cattle (Van Vuren, 1979). Bison and pronghorn showed spatial overlap but quite different food habits (McCullough, 1980; Wydeven and Dahlgren, 1985). The existence of prairie dog (*Cynomys* sp.) towns apparently facilitated bison habitat selection for a shortgrass successional state in a mixed-grass community (Coppock et al., 1983). Among four species of ungulates on a shortgrass pasture, bison were the least selective and ingested the lowest quality forage (Rice et al., 1974; Schwartz and Ellis, 1981). In montane habitat in winter, bison appeared more restricted than elk (*Cervus elaphus*) to highly productive wet meadows where they could forage in deeper snow while obtaining a large quantity of food (Houston, 1982). In boreal forest–aspen–meadows of Elk Island National Park, elk and bison in winter overlapped most in habitat use but least in food habits; the reverse was true in summer (Telfer and Cairns, 1979). Telfer and Kelsall (1984) developed a morphological index in combination with behavioral information to evaluate snow-coping ability of eight species of ungulates; bison ranked below all but pronghorn (*Antilocapra americana*).

Use of forested areas appears limited except occasionally for shade, for escape from insects and other disturbances (Fuller, 1962; Meagher, 1973; Soper, 1941), and for shelter during severe winter storms (Fuller, 1962; Soper, 1941). Foraging in more open forest may be relatively frequent (Fuller, 1962; Soper, 1941) or incidental (Meagher, 1973). Extensive forests were traversed between open foraging areas and on seasonal migrations (Fuller, 1962; McHugh, 1958; Meagher, 1973; Soper, 1941).

Most free-ranging bison appear to be seasonally migratory; movements are directional and also altitudinal in some regions (McHugh, 1958; Meagher, 1973; Soper, 1941; Van Vuren, 1983). They moved distances of about 14 to 40 km in montane habitat (McHugh, 1958), and as much as about 240 km in boreal forest-parkland habitat (Soper, 1941). Travel was usually along well-defined travel routes in montane areas from elevations of 1,828 to 3,049 m (Meagher, 1973). In boreal forest–parklands, movements were more fan-like from winter to summer ranges (Soper, 1941). Apparent influences on seasonal migrations included supply and accessibility of forage (Soper, 1941), spring weather conditions and temperatures, and fall snow storms at higher elevations (Meagher, 1973).

In smaller preserves, bison may have individual but overlapping home ranges. On Santa Catalina Island, 16 bison cows had average home ranges of 56.1 km², ranging from 26.9 to 70.5 km² (Lott and Minta, 1983*a*); in the Henry Mountains, Utah, six cows had average home ranges of 52 km² (Van Vuren, 1983). Factors which appeared to influence home-range size were plant productivity (Lott and Minta, 1983*a*; Van Vuren, 1983), environmental homogeneity, and size of preserve (Lott and Minta, 1983*a*).

Daily movements of bison herds between foraging sites in summer are usual (McHugh, 1958). These averaged 3.2 km in a montane valley (McHugh, 1958) and 2.8 km in coastal scrub-grassland on Santa Catalina Island (Lott and Minta, 1983*a*). In shrub-steppe habitat the average stay in one area was 1.9 days (Van Vuren, 1979). Apparent influences on summer range movements are seasonal vegetation changes, interspersion and size of forage sites, the rut, and the presence of biting insects in large numbers (Meagher, 1973). Size of preserve and availability of water may be additional influences (McHugh, 1958).

Population structures for free-ranging herds of Wood Buffalo National Park, Henry Mountains (Utah), and Yellowstone National Park, respectively, were: calves, 16, 21, and 22%; yearlings, 9, 13, and 17%; 2- and 3-year olds, 15, no data, and 16%; cows, 39, 36, and 28%; and bulls, 21, 30, and 16% (Fuller, 1960; Meagher, 1973; Van Vuren, 1979). Productivity for females 2.5 years and older was 53, 60, and 52%, respectively. A sub-population with a relatively younger age structure showed productivity of 76% (Fuller, 1962). The proportion of calves in mixed herds in a stable population may be 18 to 20%; 25% may be more usual in a population undergoing increase (Meagher, 1973). Percent composition of calves may be consistent during the first year of life (Meagher, 1973), or may decline June to December at about 2% per month (Fuller, 1962). Recruitment may occur as yearlings (Fuller, 1962), or after the second year (Meagher, 1973). In all three of the foregoing populations, adult males appeared to outnumber adult females.

Mortality in most herds is man-caused through commercial and sport harvest, or subsistence hunting. The wolf (*Canis lupus*) is apparently a competent predator of free-ranging bison. Bison contributed about 65% to the winter diet of wolves in Wood Buffalo National Park, but wolves did not appear to have a negative impact on the bison population (Fuller, 1962). However, wolf and human predation may be additive. On the Slave River lowlands a severe winter coupled with the combined predation apparently triggered a decline in bison numbers from 1,900 to 1,250; bison declined further to about 750 (Reynolds et al., 1982). Bison separated from herds appeared to be the primary targets of attack (Haynes, 1982).

Periodically, severe winter weather is the primary mortality agent in Yellowstone National Park; winterkill to some degree occurs every year with differential mortality among age and sex classes (Meagher, 1973). Unusually severe spring storms may cause both high calf mortality and increase adult mortality (Meagher, 1976). Winterkill also occurs frequently in and adjacent to Wood Buffalo National Park (Reynolds et al., 1982). Accidents are usually insignificant but several thousand bison have drowned in single occurrences (Reynolds et al., 1982).

At least 31 endoparasites have been reported from bison, mostly from captive herds where confinement may enhance occurrence. Effects in wild bison appear insignificant; only 2 of 26 species of nematodes were reported from free-ranging herds: the lungworm, *Dictyocaulus* sp., and the coelomic worm, *Setaria* sp. (Reynolds et al., 1982).

Anthrax outbreaks cause sporadic but appreciable mortality in northern bison. Tuberculosis may affect as much as 50% of the bison of Wood Buffalo National Park but effects of the disease on the population remain obscure. Brucellosis occurs at varying rates, sometimes more than 50% (Reynolds et al., 1982); it may cause abortions but does not appear to prevent population increases (Meagher, 1973). Economic concerns of the cattle industry dictate that most bison herds are maintained brucellosis-free. Chronic fluoride toxicosis is prevalent in geothermally active parts of Yellowstone National Park (Shupe et al., 1984). Other pathological conditions occur infrequently (Reynolds et al., 1982).

BEHAVIOR. Bison are gregarious, forming herds according to sex, age, season, foraging conditions, and habitat. Females of all ages, calves, most males 2 to 3 years old, and one to a few older males form mixed (sometimes called cow) groups throughout the year (Fuller, 1960; McHugh, 1958). Older males join these groups in increasing numbers as rut approaches (McHugh, 1958), but are afterwards found singly, in pairs, or in bull groups containing as many as 30 individuals (Fuller, 1960). Mixed herds are fluid and variable in size but tend to be larger during rut (Lott, 1981) and in more open habitat (Van Vuren, 1983). In spring, cows with calves tend to cluster (Rutberg, 1984). Solitary bulls sometimes rejoin mixed herds (Fischer, 1967; Herrig and Haugen, 1969). Fuller (1960) found that only 34% of lone bulls were 7 years or older. Mixed groups show a high degree of cohesion, and bulls, low levels (McHugh, 1958). However, the cow-calf bond appears to be the only stable relationship (Lott and Minta, 1983*b*; Van Vuren, 1983).

Cows usually give birth in isolation where vegetation provides cover; where cover is lacking, isolation is infrequent (Lott and Galland, 1985). Parturition for 16 cows averaged 68 min after the amnion became visible (Lott and Galland, 1985). At first the cow-calf association is close with cows often keeping themselves between the newborn and other bison (McHugh, 1958), but by 2 to 3 weeks of age calves often cluster in groups of 2 to 15 (Engelhard, 1970; McHugh, 1958). Mothers commonly defend young calves from perceived danger; bulls were not observed to do so (McHugh, 1958). Adoptions have occurred, but are rare (Engelhard, 1970).

Lott (1981) classified bison as promiscuous but breeding occurs in a one-to-one relationship termed tending, which is initiated by the bull. Copulation is brief. Interaction among mature bulls during the rut is intense; much of it is stylized with threat displays and signals of submission (Lott, 1974; McHugh, 1958). Fights tend to occur in clusters which Lott (1974) termed fighting storms: such fights often terminate without damage but injuries and occasional fatalities occur. Wallowing and tree horning, more commonly done by bulls, increase during rut.

Dominance between bulls generally is linear but reversals may occur (Lott, 1979*b*). Aggressive interactions between bulls, rather than age and weight, apparently confer status, and bulls with high status have higher breeding rates (Lott, 1979*b*). The copious display hair of head, beard, and chaps of mature bulls apparently decreases from physiological changes after rut; this may decrease postrut aggression and attendant energy costs (Lott, 1979*a*). Cows also show linear dominance but reversals are rare; Rutberg (1983) suggested that female status is established early between individuals and seldom contested during their lifetimes.

Bison are primarily diurnal, with several grazing periods interspersed with loafing and ruminating (McHugh, 1958; Shult, 1972). Grazing occurs in a loose grouping that Shult (1972) termed a wave pattern, but travel is usually in line and is influenced by terrain and habitat conditions. Leadership is usually by an adult cow, but not necessarily by the same individual on all occasions (McHugh, 1958).

McHugh (1958) described gaits as walking, trotting, galloping, and bounding. Speeds of nearly 60 km/h may be attained in spurts. Bison are strong swimmers; Fuller (1960) noted that bison regularly swam rivers approximately 1 km wide with currents of perhaps 3 to 6 km/h.

Smell is acute and appears to be important in detecting danger (Fuller, 1960; McHugh, 1958). Flehmen (lip curl) occurs generally but is most commonly seen in mature bulls during rut, when it may facilitate identification of a cow in estrus (Lott, 1981). Hearing is acute. Bison may visually distinguish large objects such as a horse with rider at about 1 km, and moving objects at nearly 2 km (McHugh, 1958). Vocalizations commonly consist of grunts and snorts audible at short distances; the distinctive roar or bellow of rutting bulls may carry nearly 5 km (McHugh, 1958).

GENETICS. The diploid number is 60; there are 29 pairs of acrocentric autosomes, a metacentric X- and a small acrocentric Y-chromosome (Basrur and Moon, 1967; Bhambani and Kuspira, 1969). Ying and Peden (1977) indicated that at least 20 pairs of autosomes and the sex chromosomes of *B. b. athabascae* and *B. b. bison* are homologous. The autosomes and the X-chromosome of *B. bison* are indistinguishable from those of *Bos taurus*. Crossbreeding experiments between bison and cattle date back apparently to the 1700's (Dary, 1974; Haines, 1970; McHugh, 1972; Roe, 1970) and continue to the present. Bison bull matings with cattle females generally result in fatalities to cow and calf because of excess amniotic fluid. Female hybrids are fertile, males are not.

Polymorphism in components of bison blood has been distinguished as follows: hemoglobin, two (Harris et al., 1973); 6-phosphogluconate-dehydrogenase, three (Naik and Anderson, 1970); and carbonic anhydrase, five (Sartore et al., 1969). Albinism occurs in bison, but rarely (McHugh, 1958; Roe, 1970).

REMARKS. The taxonomic status of *B. b. athabascae* and *B. b. bison* remains somewhat controversial. The differences in shape and pelage described by Geist and Karsten (1977) may be modified as larger samples are compared. Studies of chromosomes (Ying and Peden, 1977) and blood characteristics (Peden and Kraay, 1979) have not resolved the issue.

Additional research needs on bison include further anatomical and physiological descriptions and comparisons with wisent and cattle, further studies of adaptive strategies and interspecific relationships, and long-term analyses of the population dynamics and factors that naturally regulate the different free-ranging populations. Additional behavioral studies that compare various populations would be useful. Researchers and non-researchers alike would benefit from further studies of the evolutionary history and more recent forms of bison that might allow a consensus on nomenclature and the species and subspecies represented.

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VARIABILITY IN SIZE-WEIGHT RELATIONSHIPS OF *BISON BISON*

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Relationships among body weight, size, and morphological traits have been described for numerous large mammals, but most data are based on dead animals (Cowan, 1950; Saether and Haagenrud, 1983; Stelfox et al., 1985). This prevents study of the extent to which size may affect a number of life-history traits. It also obscures differences that arise from changes within individuals rather than from differences among individuals. Although weight data in relation to behavior and reproduction in live animals are available for at least three large live mammals (bison, *Bison bison*; Lott, 1979; Rutberg, 1983; red deer, *Cervus elaphus*; Clutton-Brock et al., 1982; and feral horses, *Equus caballus*; Berger, 1986), the logistic difficulties of acquiring such information are enormous. Nevertheless the recent surge in functional interpretations of mammalian life-histories (Eisenberg, 1981; Georgiadis, 1985; Western, 1979) and behavior (Clutton-Brock et al., 1982; Geist, 1971; Hrdy, 1977) underscores the utility of readily available data on size as related to body weight. In this paper we report information in five areas of size-weight relationships in bison: 1) head, chest, and body length of males and females; 2) inbred and noninbred animals; 3) weights from different geographical areas; 4) differences in size-weight relationships between dead and live bison; and 5) possible sources of variation and bias.

In numerous areas of North America, bison occur in disjunct populations. At Badlands National Park, South Dakota, they were extirpated about 1860 (M. Knowles, in litt.); they were reintroduced twice since then. In 1963, 25 animals arrived from Theodore Roosevelt Memorial National Park, North Dakota, and three from Fort Niobrara National Wildlife Refuge, Nebraska; these 28 founders originated from the isolated population at Fort Niobrara that has been there since at least 1913. In 1983, 20 additional animals arrived from Colorado National Monument. These latter animals stem from three founders (two cows and a bull) secured from a private collection in the Denver, Colorado, area and transferred in 1925 to Colorado National Monument. Because of the small number of founders ($n = 3$) from which the 1983 immigrants were derived, we designate them "inbred" bison.

Animals stemming from the 1963 reintroduction are referred to as "noninbred" bison because of the greater number of founders ($n = 28$). We recognize that the animals from North Dakota must to some extent also be inbred but refer to the inbred and noninbred dichotomy simply for convenience as these terms highlight relative differences in expected gene frequencies based on founder number.

Data on live bison were secured during capture and immobilization operations during 1985 and 1986 in Badlands National Park where animals roam freely throughout the approximately 250-km^2 Sage Creek Wilderness Area. Bison were captured by baiting with alfalfa during later winter; by leaving gates to traps open, but subsequently closing them after animals entered (in late summer); or immobilizing animals with narcotic drugs (Kock and Berger, 1987). More than 200 animals were captured by use of the first two methods, 28 by employing the third.

TABLE 1.—*Correlation matrix of morphological characters for male (n = 64) and female (n = 56) bison.*

Sex and character	Character					
	Age	Body weight	Body length	Head length	Head width	Chest girth
Males						
Age	1.000					
Body weight	0.784	1.000				
Body length	0.670	0.849	1.000			
Head length	0.683	0.827	0.860	1.000		
Head width	0.750	0.861	0.821	0.862	1.000	
Chest girth	0.708	0.777	0.795	0.732	0.745	1.000
Females						
Age	1.000					
Body weight	0.714	1.000				
Body length	0.678	0.790	1.000			
Head length	0.711	0.864	0.756	1.000		
Head width	0.679	0.756	0.756	0.794	1.000	
Chest girth	0.434	0.585	0.656	0.545	0.533	1.000

Standard measurements were obtained after animals had been chased into cattle chutes modified for bison, restrained in squeeze cages, and weighed on cattle scales. In not every case could the same data be obtained for all animals. For instance, weight was not recorded for some animals when the scale jammed. Therefore, in the analysis we used to predict weight we relied only on actual weights recorded from scales. Such weights were distinguished from those predicted from body measurements. Ages were either known from animals tagged as calves, or estimated by tooth wear (Fuller, 1959). Because bison have been under observation for more than 3,700 h, reproductive histories and social relationships for some animals are known for a 3-year period.

We examined relationships between morphological traits and body weight by multiple regressions employing all variables, correlation matrices demonstrating the relationships between all single variables, and simple regressions using single independent variables.

Because bison are sexually dimorphic and the sexes differ in their body proportions (Reynolds et al., 1982), males and females were analyzed separately. Multiple regression explained about 96% of the variation in weight for males and 69% for females. However, as stated earlier, several variables were not simultaneously available for all animals. Hence, we used simple regressions employing single variables to predict weights (Table 1). Because all traits were intercorrelated, when only single variables are available they can be used to predict weight.

To examine the relationship between body weight and single morphological characters several regression equations were generated using data for 64 male and 56 female bison: linear regression ($Y = A + BX$), exponential ($Y = A^{BX}$), natural log transformation of X ($Y = A + B \log X$), and a power function ($Y = AB^X$). The amount of variation explained in body size-weight relationships for both males and females using single variables in simple regressions is about equal regardless of which of four methods is used (Table 2). However, the R^2 values for the power function were somewhat higher in most cases for all single variables.

The best individual predictor of weight for males was body length ($R^2 = 0.81$) and head length was best for females ($R^2 = 0.76$; Table 2). Cannon-bone length was the poorest predictor, explaining no variance in either sex, whereas chest girth accounted for 64% of the variation in males and 33% in females.

Information on live weights of native large mammals in relation to genetic lines is rare. Although our samples are small, data on sex and seasonal differences in weight are presented for our outbred and inbred animals 4 years of age or older (Table 3). Seasonal weight changes were noticeable in males and females in both lineages; the greatest mean increases occurred among inbred bulls and the smallest mean increases occurred among inbred cows.

Because both lineages of bison now have access to the same foods, wander over the same habitats, and occur in sympatry, it is tempting to suggest that inbreeding in itself is responsible for the reported weight differences. Yet this would be premature because the inbred animals arose from xeric regions where food may be limiting in western Colorado (C. H. Wasser, in litt.), whereas the noninbred line stemmed from animals that previously inhabited more productive prairie environments. Hence, smaller sizes and lower weights in the inbred line might be a result of nutritional constraints in the area from which they originated.

TABLE 2.—*Coefficients of determination (R^2) for regression equations used to predict body weight from morphological characters, and Y-intercepts and regression coefficients for the power relationships.*

	Linear $Y = A + BX$	Exponential $Y = A^{BX}$	Logarithmic $Y = A + B \log X$	Power $Y = AB^X$	Y-intercept	Regression coefficient
Males						
Body length	0.72	0.81	0.68	0.81	$1.67\ 10^{-4}$	2.78
Head length	0.68	0.78	0.66	0.80	$2.09\ 10^{-2}$	2.42
Head width	0.74	0.76	0.71	0.79	2.00	1.52
Chest girth	0.60	0.64	0.57	0.64	$1.57\ 10^{-4}$	2.72
Females						
Body length	0.62	0.65	0.61	0.66	$1.48\ 10^{-4}$	2.80
Head length	0.74	0.75	0.74	0.76	0.025	2.39
Head width	0.57	0.60	0.58	0.62	0.78	1.87
Chest girth	0.34	0.34	0.33	0.33	$5.45\ 10^{-4}$	2.46

At the National Bison Range in Montana, Fort Niobrara in Nebraska, and Wichita Mountains National Refuge in Oklahoma, bison weights generally are recorded on an annual basis during routine capture operations. In Figs. 1 and 2, yearly variation in weight at both the National Bison Range and Fort Niobrara and variation between these two areas and those at Wichita Mountains Refuge are presented for both sexes. Because the data from the latter area were available only as means lumped over an 8-year period (Halloran, 1961), they could not be analyzed statistically for yearly differences; however, they were included for general comparison of mean weights with those of bison of the other areas.

Before investigating the relationship among years, geographical area, and weight, the relationship between weight and age was defined. A number of regression equations were generated to determine the best fit between weight (Y) and age (X): linear, exponential, natural-log transformation of X, and a power function. When weight is regressed upon the natural-log transformation of age, 94% of the variation in weight is explained for males and 76% for females. Natural-log transformed age then was used as one factor in a two-factor completely randomized analysis of variance (Wilkinsin, 1986), with year as the second factor. This analysis was used to determine if differences between years within areas and differences between areas were present.

In bison at both the National Bison Range and Fort Niobrara significant differences were found among years (at National Bison Range males, $F = 5.026$, females, $F = 7.115$; at Fort Niobrara males, $F = 5.387$, females, $F = 9.698$, $P < 0.01$) but not between areas (males, $F = 3.750$, females, $F = 1.201$, $P > 0.05$). Annual data at each site were averaged separately so that mean weight could be contrasted with the Wichita Mountains bison; these weights were significantly different (males, $F = 48.617$, females, $F = 20.497$, $P < 0.001$) from bison at both the National Bison Range and Fort Niobrara. Because these data were collected during different years (National Bison Range, 1978–1984; Fort Niobrara, 1963–1972; Wichita Mountains, 1953–1960) we can only say that variation among areas exists but it could be caused by many factors.

Previous investigators of extant ungulates have not used cranial measurements to estimate body weight. This is not surprising given that other ways are available, some (Franzmann et al., 1978; Rideout and Worthen, 1975; Seip and Bunnell, 1984; Talbot and McCullogh, 1965) of which demonstrated superior

TABLE 3.—*Seasonal weights (kg) of inbred and noninbred bison 4 years of age or older in Badlands National Park. Weights of inbred animals were obtained from actual (scale-derived) weights and regression equations in Table 2, whereas weights of noninbred animals are from scales only.*

	Winter			Fall		
	$\bar{X}$	SD	n	$\bar{X}$	SD	n
Males						
Inbred	508.8	24.0	4	628.3	50.2	3
Noninbred	615.4	123.6	23	682.0	94.3	6
Females						
Inbred	357.0	18.0	2	386.5	53.8	4
Noninbred	410.3	66.7	10	469.8	104.7	13

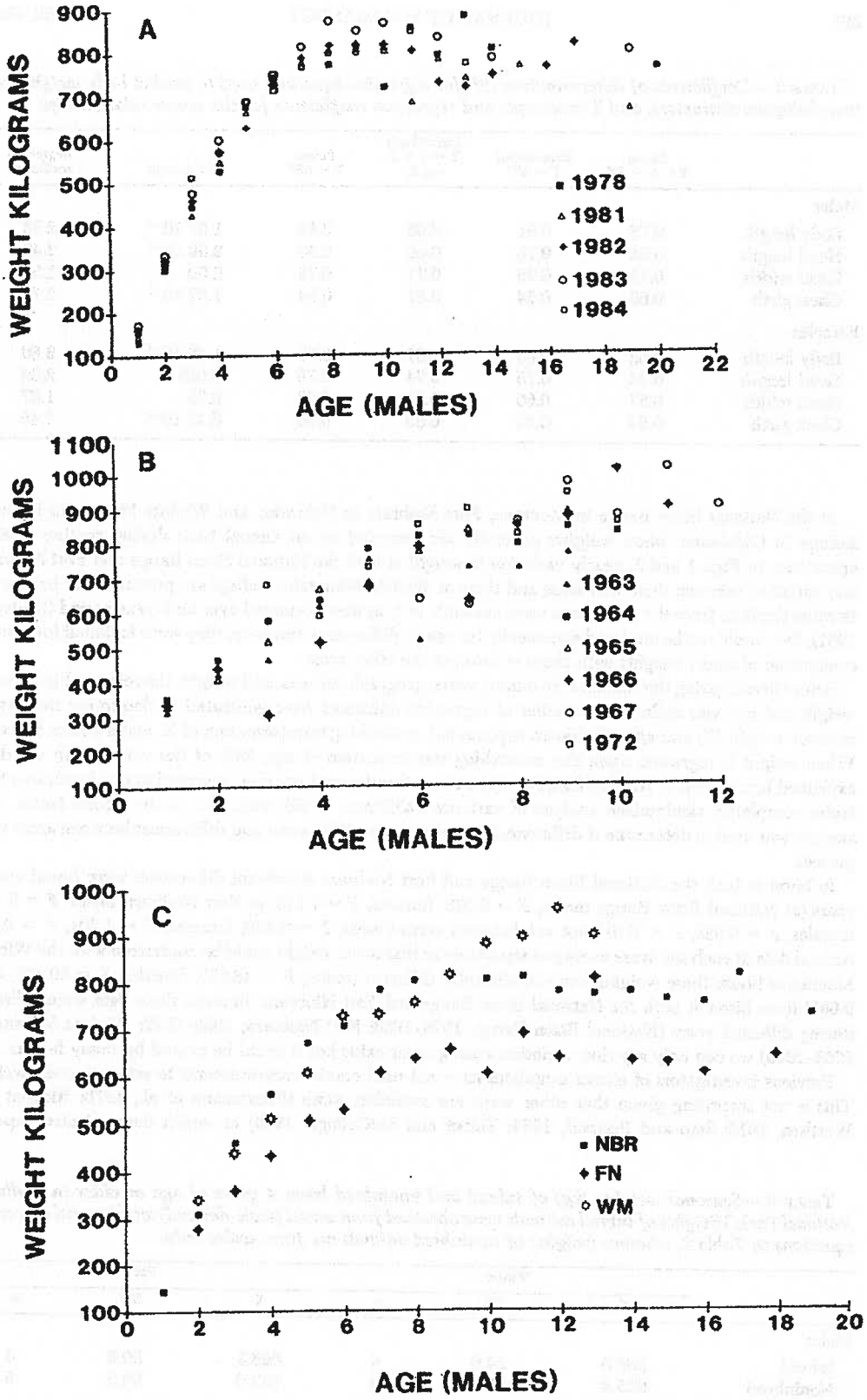

FIG. 1.—Relationships between age and body weight in bison males: A) National Bison Range (NBR) by year; B) Fort Niobrara (FN) by year; C) mean weights at National Bison Range, Fort Niobrara, and Wichita Mountains (WM).

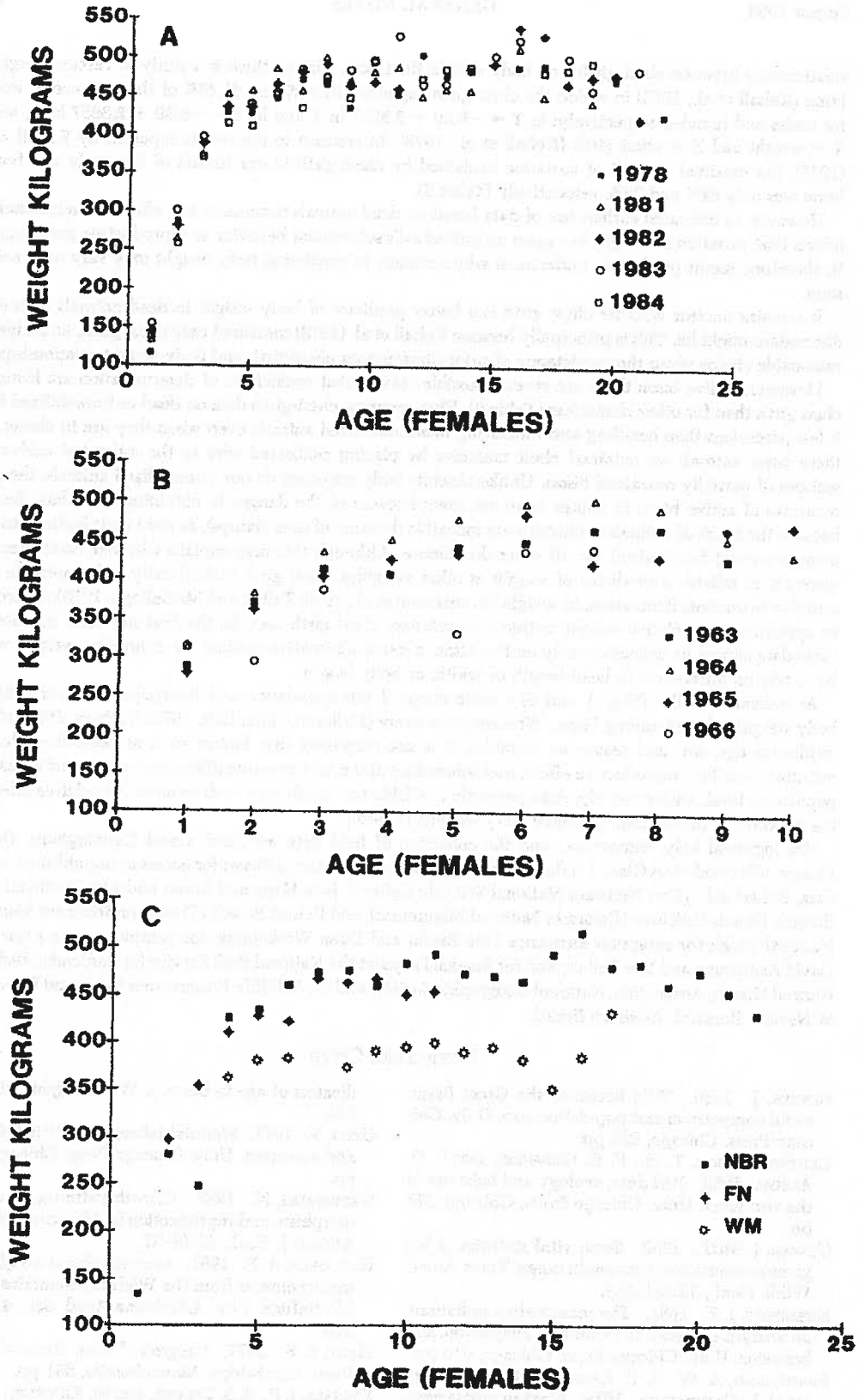

FIG. 2.—Relationships between age and body weight in bison females: A) National Bison Range (NBR) by year; B) Fort Niobrara (FN) by year; C) mean weights at National Bison Range, Fort Niobrara, and Wichita Mountains (WM).

relationships between chest girth and body weight than ours. Among these is a study of carcass weight of bison (Kelsall et al., 1978) in which the chest girth explained 81.97% and 61.43% of the variance in weight for males and females, respectively: ln Y = −6.30 + 2.3257 ln X and ln Y = −6.39 + 2.3257 ln X, where Y = weight and X = chest girth (Kelsall et al., 1978). In contrast to the results reported by Kelsall et al. (1978), the maximal amount of variation explained by chest girth in our studies of live male and female bison was only 64% and 33%, respectively (Table 2).

However, as indicated earlier, use of data based on dead animals terminates any effort to understand the effects that variation in weight has upon an individual's subsequent behavior or reproductive performance. It, therefore, seems prudent to understand why accuracy in predicting body weight may vary with animal state.

It remains unclear whether chest girth is a better predictor of body weight in dead animals than other dimensions might be. This is principally because Kelsall et al. (1978) measured only chest girth, an eminently reasonable choice given the consistency of prior literature on chest-girth and body-weight relationships.

However, in live bison there are several possible reasons that coefficients of determination are lower for chest girth than for other characters (Table 2). First, securing chest-girth data on dead or immobilized bison is less precarious than handling and measuring nonimmobilized animals even when they are in chutes. For these latter animals we obtained chest measures by placing calibrated wire to the estimated midventral sections of partially restrained bison. Unlike absolute body measures on our immobilized animals, the chest measures of active bison in chutes were not exact because of the danger in obtaining such data. Second, because the heads of animals in chutes were inflexible (because of nose clamps), as were their bodies, absolute measures could be obtained for all other dimensions. Although this may explain why our chest measures were not as reliable a predictor of weight as other variables, chest girth undoubtedly is the measure most sensitive to seasonal fluctuations in weight (Franzmann et al., 1978; Talbot and McCullogh, 1965). Therefore, in approximating relative weight within a population, chest girth may be the best measure, but because these data cannot be collected easily on live bison, a sound alternative method for estimating weights would be to rely on differences in head length or width, or body length.

As indicated earlier (Figs. 1 and 2) a wide range of intrapopulation and interpopulation variability in body weight is found among bison. Whereas prior study (Halloran, 1961; Lott, 1979; Rutberg, 1983) clearly implicates age, sex, and season as variables, it is not surprising that factors such as population density, nutrition, weather, reproductive effort, and inbreeding also might promote differences at the individual and population level. Unfortunately, data presently available are insufficient to determine the relative effects of the majority of factors that influence body weights of bison.

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SELECTION OF TREES FOR RUBS BY WHITE-TAILED DEER IN MAINE

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Considerable research has been conducted on scent-marking behaviors of ungulates (Bowyer and Kitchen, 1987; Eisenberg and Kleiman, 1972; Ewer, 1968; Graf, 1956; Leuthold, 1977; Peters, 1980; Ralls, 1971; Walther, 1984). Information on these behaviors has been especially well documented for *Odocoileus*. One type of scent mark, the "buck rub," is made by male deer debarking small trees and shrubs with their antlers then rubbing the frayed area with their glandular foreheads (Marchinton and Hirth, 1984).

Moore and Marchinton (1974) and Kile and Marchinton (1977) reported that deer did not rub trees primarily to remove antler velvet; rubbing behavior continued long after velvet shedding was completed. Rather, rubbing of trees by *Odocoileus* sp. often was associated with aggressive interactions between males (Bowyer, 1986; Geist, 1981; Hirth, 1977; Kile and Marchinton, 1977; Kucera, 1978; Moore and Marchinton, 1974), and most likely functioned to express dominance (Marchinton and Hirth, 1984; Peters, 1980). Some data on chemical composition of pheromones released and histology of glands used in scent marking are available (Atkeson and Marchinton, 1982; Muller-Schwarze, 1971, 1972; Muller-Schwarze et al., 1978; Quay, 1959; Quay and Muller-Schwarze, 1970; Volkman et al., 1978), as well as information on timing, location, and types of trees rubbed by deer (DeVos, 1967; Kile and Marchinton, 1977; Moore and Marchinton, 1974; Nielsen et al., 1982).

Rubs made by white-tailed deer (*O. virginianus*) typically were concentrated at trail junctions, along old roadbeds, and in woods adjacent to open areas (Moore and Marchinton, 1974). Kile and Marchinton (1977) reported that rubs were not distributed randomly, but were most frequent in areas with many small saplings. The physical characteristics of trees (Kile and Marchinton, 1977; Nielsen et al., 1982) and the aromatic qualities of some woody species (Kile and Marchinton, 1977) were important in determining trees that deer selected to rub.

We observed that deer rubs along forested edges of fields in central Maine did not correspond well with findings of Kile and Marchinton (1977) that aromatic trees were selected for scent marking. Thus, the purpose of this study was to test whether white-tailed deer in Maine used particular woody species for rubbing and to compare the physical characteristics of plants they rubbed with those available.

FROZEN FAUNA OF THE MAMMOTH STEPPE

The Story of Blue Babe

R. DALE GUTHRIE



The University of Chicago Press
Chicago and London

4

RECONSTRUCTING BLUE BABE'S APPEARANCE

Vertebrate paleontologists work mostly with bones. Reconstructions of extinct animals rely on our anatomical understanding of modern animals to make analogous decisions concerning the form of an animal for which we may have only a handful of bones. Often times, however, a strong dose of fancy is also added. The fossil record rarely preserves details of external appearance. The skin and hair preserved in a mummy such as Blue Babe provide a unique view into the past.

Some groups of mammals have relatively conservative coloration and body form, for example field mice (*Microtus*). A frozen Pleistocene-aged *Microtus miurus* carcass has been found near Fairbanks; the little mummy simply looks like a gray mouse. Because the appearance of *Microtus* has changed so little over time, mummies of this genus are unlikely to yield many surprises. Bison, however, are quite different. The two living species, *Bison bonasus* or wisent (fig. 4.1) in Eurasia and *Bison bison* (fig. 4.2) in North America, differ from each other in general body form and color. Additionally, Pleistocene steppe bison (*Bison priscus*) drawn on European cave walls (fig. 4.3) and portrayed in mobilary art are unlike either extant bison species. I use the term *species* advisedly, as late Pleistocene and living bison seem to form a single species complex.

Studies of fossil bones had already told us much about steppe bison before Blue Babe was found. By reconstructing skeletal shape, we could see that bison in Beringia were different from living bison (Guthrie 1980). Beringian bison were a little larger overall than extant bison (Skinner and Kaisen 1947), with disproportionately larger horns. But these subtle skeletal differences may be a poor clue to external appearances. For example, living bison species show much more variation in their coat patterns and hair color than in their skeletons. Within a related group, such as a genus, skeletons are comparatively similar. A bison mummy with hair provides much



Fig. 4.1. Wisent or European bison (*Bison bonasus*). This species is found in Po and the Soviet Union.

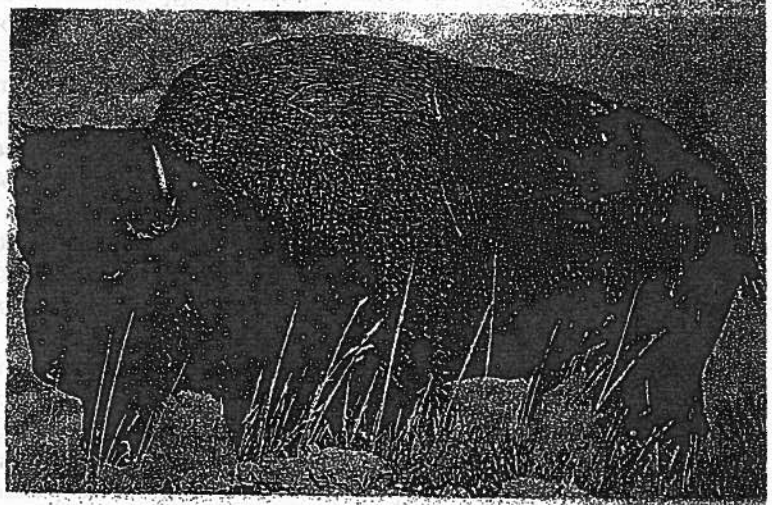

Fig. 4.2. American bison (*Bison bison*). This species is quite variable. The individ pictured here is a typical plains bison (*Bison bison bison*) with large hair bonnet pantaloons.

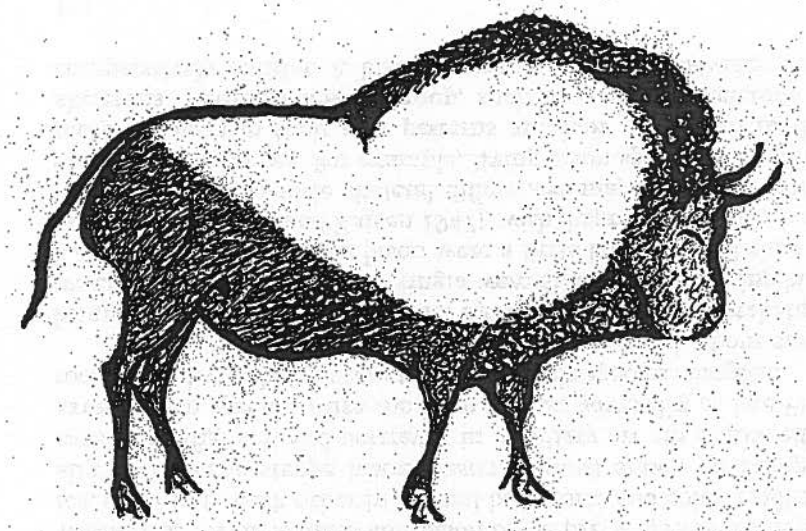

Fig. 4.3. Late Pleistocene steppe bison (*Bison priscus*). Many bison portrayed in Paleolithic art are exquisitely rendered. From this artwork we get a good idea of the appearance of the steppe bison. This picture is from Santimamine in Spain.

more information about overall appearance than one can ever get from a skeleton alone.

Woolly Bison, Woolly Mammoths, Woolly Rhinos, and Unwoolly People

We characterize the northern, Pleistocene rhino and mammoth as "woolly" because their nearest analogue, living in more temperate regions have short hair. If bison were extinct and all we had for comparison were extant forms like cattle and Asian and African buffalo, we certainly would be talking about woolly bison too. Bison are part of modern natural history, so the adjective *woolly* is unnecessary, but they are one of the Pleistocene woollies. If the bison and musk-ox had become extinct 11,000 years ago, along with the mammoth and northern rhino, the title of this book would have been different and I would have been writing about a mummy of the extinct woolly bison.

In fact, northern horses were also woollies. Some horses portrayed in Paleolithic art have long "beards," thick belly hair, and "feathered feet," woolier than domestic horses raised at northern latitudes. Likewise, lions would have been very thickly coated, as are other felines adapted to northern climates. That northern subgroup could legitimately be referred to as Pleistocene woolly lions.

This train of thought about the woolly bison and its compatriots on the Mammoth Steppe is not all facetious. Pleistocene northern large mammals were adapted to extraordinarily low temperatures: wind chill factors must have regularly brought effective winter temperatures down to −60° F and lower. The animals' tails and ears were short and well furred. Mammoths, rhinos, and horses had long hair even on their lower limbs.

The balance of the amount of energy taken in over the amount lost is central to the equation of whether a northern animal lives or dies each winter. Energy input can be reduced if the animal is more capable of conserving energy. Pelage is not simply a coat needed to keep warm. Heat is produced as a by-product of body metabolism, and in the case of a large herbivore, heat is a product of food composting by microorganisms. Most food we consume goes into maintaining our body temperature rather than meeting other basic requirements. Reducing heat loss, for a northern-adapted animal, directly affects use of fat reserves. Effective pelage can extend a little further the meager calories in winter food, which invariably are below maintenance. Woolliness can mean the difference between life and death.

The woolly pelt and runty tails and ears of these Pleistocene creatures are a signpost to us as we try to imagine what kind of ecological limit could have prevailed for about 20,000 years prior to the Holocene and probably why unwoolly humans did not inhabit Alaska until the "warmer" time during the end of the last glacial, as discussed in chapter 10. But pelage does more than retain warmth. It is an amalgam of a variety of functions that include the trappings of stature and social position.

Hair Length

When Walter Roman first discovered Blue Babe, only the posterior portion of the carcass was showing. Hair was not attached to the exposed skin, but tufts of black hair were found in the surrounding silt. By contrast, when the bison's anterior end was excavated, we found the hair had slipped but was still held in place by frozen muck on the head and in patches over the forequarters and forelegs. I had often wondered how Pleistocene steppe bison must have looked, so finding hair preserved with the frozen carcass was really exciting for me; we carefully sampled and mapped this hair before the carcass was moved. Concurring with Geist (1971b), I had often observed

(Guthrie 1980) that hair patterns of European Pleistocene bison (as portrayed on cave walls) were unlike either species of living bison.

Living bison from different geographic areas exhibit considerable differences in hair patterns. For example, "wood buffalo" (an unfortunate name because it suggests deep woodlands instead of the parkland clearings characteristic of their Canadian habitats), *B. bison athabascae*, have a high hump, small hair bonnet, and almost no chaps on the forelegs (Geist and Karsten 1977). Bison from the Caucasus, *B. bonasus caucasicus*, were different from Polish and Russian subspecies (Flerov 1977). Since Beringian bison occurred across such a vast area during the Pleistocene, it is likely they had geographic variations in hair color and pattern comparable to those of extant bison. Thus we could expect that Alaskan Blue Babe would resemble bison portrayed thousands of miles away by French and Spanish Paleolithic artists, but differ in certain details. Today ungulates occupying that geographic span exhibit subtle differences east and west. For example red deer, *Cervus elaphus*, moose, *Alces alces*, and caribou, *Rangifer tarandus*, vary between western Europe and eastern Asia, but are still justifiably considered members of their respective species.

Hair pattern among the three bison species *B. bonasus*, *B. bison*, and *B. priscus* differs most on certain parts of the body: the head, beard or ventral manes, foreleg pantaloons or chaps, and the hump. Fortunately these are located on the anterior part of the body—the very portion preserved on Blue Babe. But since our bison carcass was eaten from the dorsal side, skin and hair on the hump region were torn away. Likewise, thoracic vertebrae and their long neural arches were removed from the carcass and were not preserved. These parts would have told us about the hump. Eurasian *B. bonasus*, *B. priscus*, and North American *B. bison* all differ in neural arch contours and in hump hair patterns (Poplin 1984). We can use other steppe bison fossils to reconstruct the underlying bony part of the hump, and indeed this is the subject of chapter 5, but for now I confine my interest to hair and compare the hair contours of Blue Babe's forelegs, head, beard, and tail with that of other bison.

Blue Babe retained sufficient hair to show that he lacked well-developed chaps or leggings. In this regard he is similar to the wood bison, *B. bison athabascae*, and the Eurasian *B. priscus* (fig. 4.4). Geist (1971b) pointed out that bison in cave paintings do not have long hair on the forelegs. The living European bison, *B. bonasus*, does not have pendulous leggings but does have long hair on the forelegs, which exaggerates the apparent thickness of the upper leg

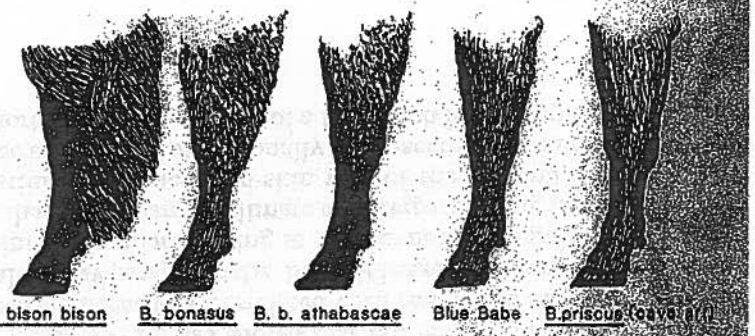

Fig. 4.4. Variations of "leggings" or "pantaloons" among bull bison. A comparison of pantaloon development shows Blue Babe is closest to the European Pleistocene steppe bison (*B. priscus*), which had negligible pantaloons. American plains bison (*B. bison bison*) has the largest. Both the European bison (*B. bonasus*) and the wood bison (*B. bison athabascae*) have traces of pantaloons.

(fig. 4.5). Hair on the posterior side of the leg down from the olecronon process is 30 mm on the Alaskan mummy, compared to the much longer hair (up to 300 mm) of mature plains bison bulls.

The length of Blue Babe's bonnet and forelock, hair over the frontal and parietal bones, is comparatively short for bison (fig. 4.6). It is about the same length as hair found on *B. bonasus* and, judging from cave paintings (fig. 4.7), must have been similar to the Eurasian *B. priscus*. North American bison have long hair above the eyes, producing a large bonnet. However, as first pointed out by Geist and Karsten (1977), *B. bison athabascae* has a smaller bonnet than plains bison, *B. bison bison*, and it is a rather different shape. The Alaskan bison mummy is quite unlike either extant American subspecies in this regard.

Only two parts of Blue Babe's beard were preserved—just behind the lower lip and, farther posterior, just forward of the jaw angle. Both are short in comparison to *B. bison bison* and resemble other bison with short beards, especially *B. priscus* in cave art (fig. 4.7). There was simply not enough hair on Blue Babe to determine the overall shape of the ventral mane.

Blue Babe emerged without a tail. His tail (bones and skin) was later found attached to a patch of rump skin. Tail hair also differs among living bison (fig. 4.8), but unfortunately Blue Babe's tail was hairless, so no comparisons of hair length are possible. We can evaluate color, however, because the broken bases of coarse black hairs can be seen embedded in the skin.

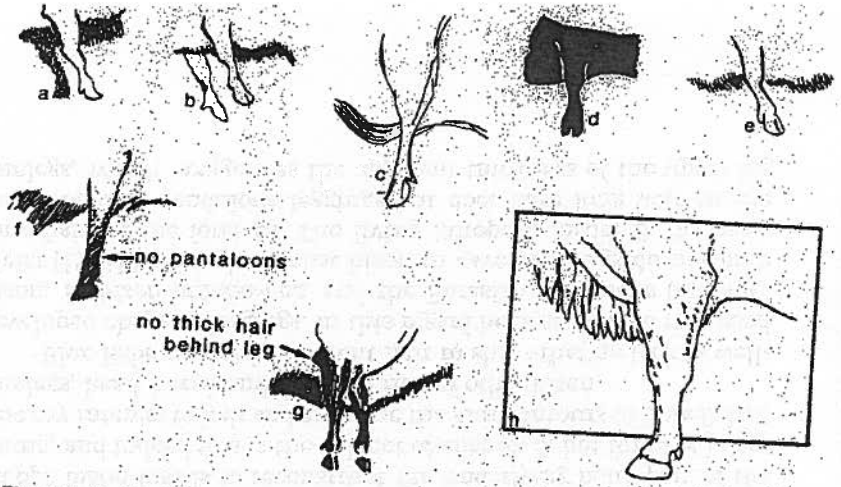

Fig. 4.5. Foreleg hair patterns of steppe bison from Paleolithic art. All living bison have some degree of hairy pantaloons on the foreleg, especially on the posterior part of the radius-ulna region (below the elbow). Pictures of steppe bison painted by Paleolithic artists show no indications of foreleg pantaloons. These examples of Paleolithic art are from (*a* and *b*) Niaux, (*c*) Candamo, (*d*) Le Portel, (*e*) Les Trois Frères, (*f*) Font-de-Gaume, and (*g*) Altamira. The hair on Blue Babe's forelegs was similar to the pattern shown in these Paleolithic pictures of steppe bison.

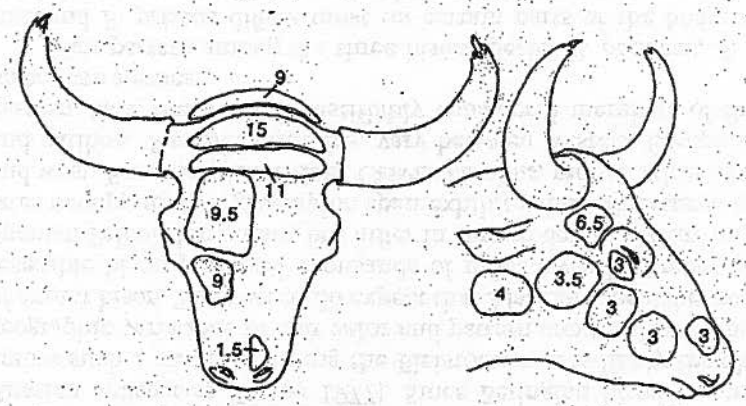

Fig. 4.6. Head and facial hair. The hair removed from Blue Babe's face and head was mapped and measured. The hair had "slipped" its attachment from the underlying skin but was still held in place by the surrounding wet silt. Hair length is shown in centimeters.

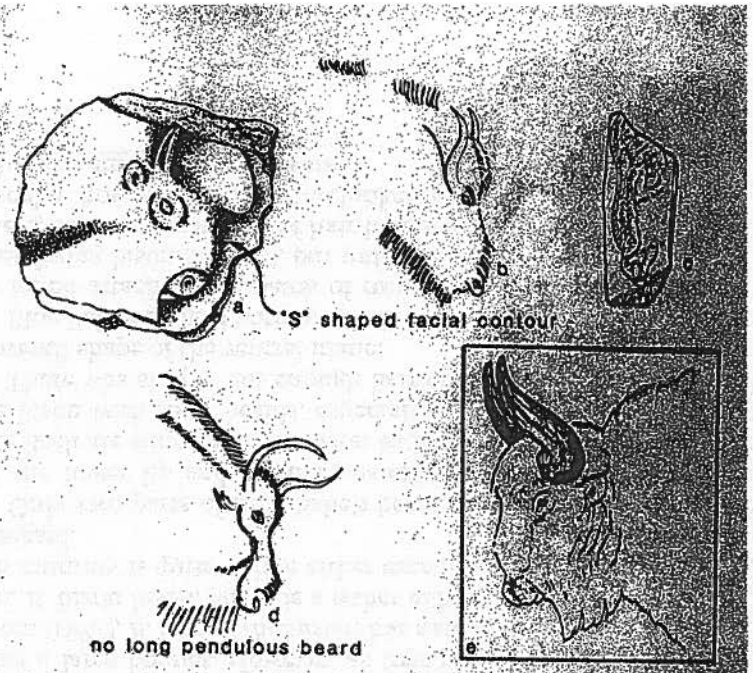

Fig. 4.7. Reconstructed face of steppe bison from Paleolithic art. Unlike Ameri plains bison, steppe bison in Paleolithic art are pictured with short facial hair, an shaped profile, and a shorter beard. These Paleolithic bison portraits are from Angles-sur-l'Anglin, (*b*) Le Puy de Lacan, (*c*) Isturitz, and (*d*) Les Trois Frères. Rem nants of facial hair on Blue Babe (*e*) show a similar pattern.

Blue Babe's tail without hair is around 20 cm long, much smaller than *B. bison's* tail. Van Zyll de Jong (1986) shows that the mean length of tail, without tassel, for *B. bison bison* was 42 cm and that that of *B. bison athabascae* was 50 cm (both male samples). Tails of living European bison are much longer (Flerov 1979 illustrates the bison from the Caucasus as having a small tail). Flerov (1977) estimates the tail of a female Siberian bison mummy at 80 cm, longer than Blue Babe's but shorter than living European bison.

Geist (1971a) has shown that tail length is important socially and seems negatively correlated with the degree of cephalization of social display paraphernalia. But tail length is also related to severity of winter. Ungulates living in the far north generally have shorter tails than their warmer climate counterparts. Long tails (speaking of the structural bone-blood-skin part of the tail and not hair) are a source of heat loss. Additionally the insect season in the far north is so short that the advantage of a fly switch for hind quarters is small.

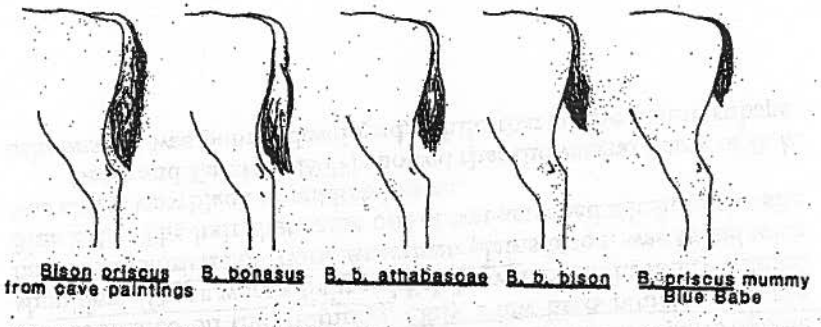

Fig. 4.8. Bison tail lengths. Tail length varies among bison groups. European *B. bonasus* have the largest tails and plains bison (*B. bison bison*) have the shortest of living bison. However, Blue Babe's tail was even shorter. No full-length hairs remained on the tail, so the tail pictured here is a tentative reconstruction based on bone and skin remains. The steppe bison in cave art have long, well-furred tails like European bison. Presumably tail length varied from west to east across the Mammoth Steppe because the continental climatic effects in the east produced (and still produce) colder winters.

Northern ungulates all have short tails—just enough to cover the ano-vulvar area as an insect-proof seal and an insulating cap. Consistent with this, the woolly mammoth and woolly rhino pictured in Paleolithic art have smaller tails than their living analogues in more southern latitudes.

Although Blue Babe was a steppe bison (*B. priscus*), his tail was shorter than tails of European steppe bison (*B.. priscus*) shown in Paleolithic art (fig. 4.8), probably due to the milder winters European steppe bison experienced, especially during the warm and wet Pleistocene interstadials. Winters were never warm for Alaskan and Siberian bison, even during the interstadials, so those bison have short tails. American bison, *B. bison*, which are derived from native Beringian bison, seem to have retained short tails as they moved south. Winters on the High Plains are not as severe as those in Alaska, but they are not mild.

In addition to these hair patterns, other areas on the bison mummy were not preserved. For example, lack of hair on the shoulders did not allow us to assess whether a shoulder mantle was present, as in *B. bison bison*, or almost absent, as in *B. bonasus*, *B. bison athabascae*, or Eurasian *B. priscus* (in Paleolithic art). Also missing from the specimen was the penile tuft, which is most developed in the plains bison, *B. bison bison*, and least developed in the European bison, *B. bonasus*.

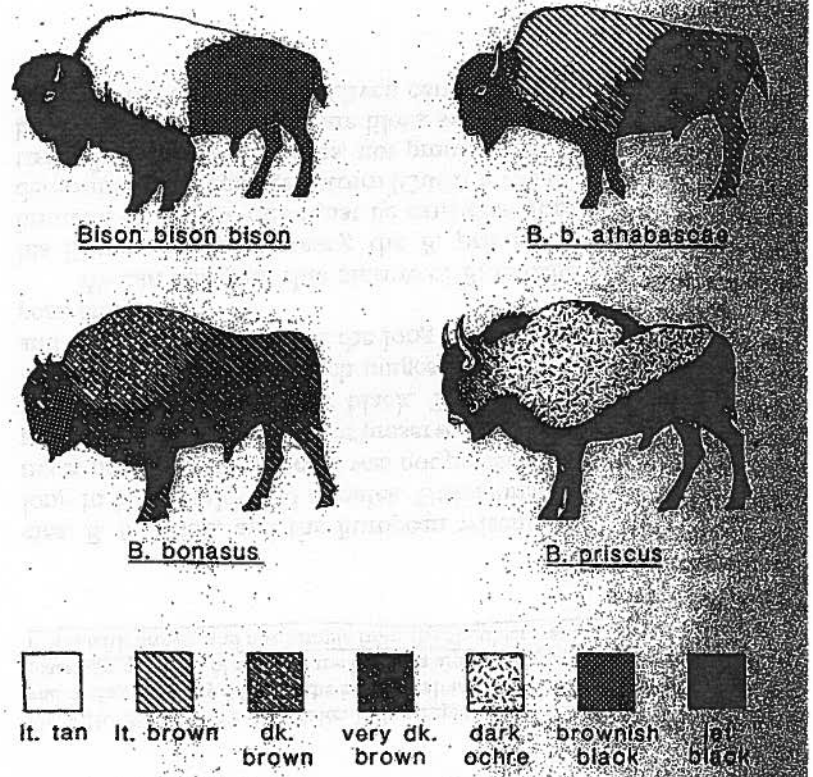

Fig. 4.9. Bison color patterns. A bull typical of each "species" is shown here along with a reconstruction of steppe bison from Paleolithic art.

Blue Babe and Bison of Other Colors

The color patterns of Blue Babe and subspecific variants of living bison species are compared in figure 4.9. There is some variability in pelage within bison populations as well as some geographic variability, so these comparisons are of the more typical forms. Coat color is a fairly labile character among mammals, unlike teeth or feet. The evolution of teeth and feet are tied to conservative and exacting environmental constraints, but external appearance is linked more closely with less conservative traits such as social behavior; as a consequence, external appearance is one of the more variable characters between groups. Just as external appearance is the character that differs most among living bison, so it would be expected to differ on an

...gradient. Because the mummy is an adult bull, I compare him only with adult bulls from other bison species.

European bison, *B. bonasus*, are the most homogenously colored bison. Their coat is a uniformly dark rusty brown. The hump area is subtly lighter and the face forward of the ear a darker brown. Among bison I observed in the Prioksko-Terransny Reserve on the Oka River, USSR, there were some bulls with black faces. Skins I have seen from Caucasian subspecies had a similar homogenous color, but were darker than Russian and Polish bison. Flerov (1977) also pictures Caucasian *B. bonasus* as uniformly dark.

American plains bison are more dramatically colored; they are, overall, a deep rust brown. Most bulls have jet black hair on the head, neck, and foreleg (a few individuals are more "cow" colored, with a very dark brownish tone in these parts). A stripe of dark hair runs down the central part of the hump, in contrast with the light sand of the hump itself. This sandy hair extends ventrally to the elbow, or olecronon process, as part of a thick mantle of hair covering the shoulders. Although European bison bulls have a shoulder mantle, it is not exaggerated, nor does it have a discreet posterior border as in American bison. Posterior to this shoulder mantle, hair on American bison bulls is much shorter and quite dark, ranging from black to dark brown. These contrasting tones produce a striking late-autumn appearance before the pelage is bleached by sun and weather. Geist and Karsten (1977) have shown that the wood bison subspecies (*B. b. athabascae*) is not so dramatically colored as the plains subspecies: wood bison have a darker, more reddish hump that is less dramatically colored than that of the plains bison.

In contrast to these variants of living bison, Blue Babe looked like a dark bay horse; he was mainly a rich dark brown with black "points" on his face, legs, and tail. His forelegs were dark brown, but hair on the lower leg, from metacarpals to the hoof, was so dark it was almost black. The face, or anterior part of the head, was black, reaching posterior only to the eyes and dorsally toward the frontals on a line between the anterior edges of the horn bases (fig. 4.10). The rest of the head, bonnet, cheeks, and ears was a rusty brown. The beard or ventral mane was black, at least on its anterior parts (where hair remained on the mummy). Only a few hairs remained on the shoulders. These were a light reddish brown. No light sandy-colored hair, characteristic of living American plains bison, was found with Blue Babe. The hair that came out of wet-screened silt from the site was either very black or reddish brown.

Geist and Karsten (1977) showed that the ventral name of *B. b. athabascae* was poorly developed, while that of the plains subspe-

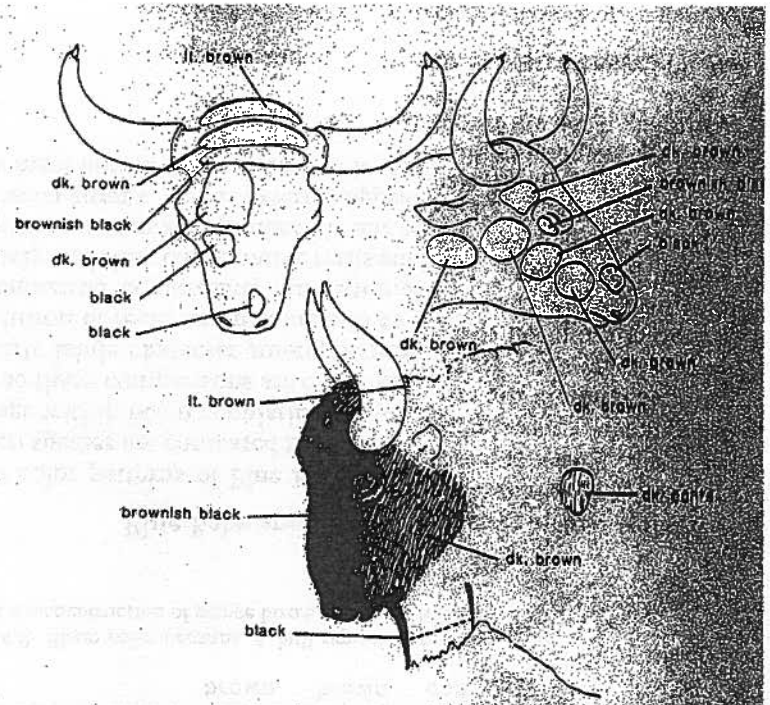

Fig. 4.10. Blue Babes's head color. Hair samples were collected as the bison emerg and during necropsy. Most of the hair had already slipped, but some facial hair was place. On the front of the face the hair was almost jet black. On the sides of the he it was dark brown, and one sample from the shoulder was a reddish brown.

cies, *B. b. bison*, and the European wisent, *B. bonasus*, was quit long in both males and females. Unfortunately Blue Babe's ventra mane posterior to the beard was not preserved. As already noted, th mummy's tail hairs were not preserved, but broken bases of hair stil in the tail skin were very black. This tail hair resembles that o American bison tails (which ranges from black to very dark brown and is quite different from the long reddish brown tail hair of Euro pean bison.

We can compare this picture of Blue Babe with the images o his European contemporary, the *B. priscus*, drawn by Paleolithic hunters. Of course one must be cautious when using art works to determine actual pelage pattern (Guthrie 1984c), just as a single portrait offers only suggestions, not proof, about details of appearance But cave pictures of bison are like a set of portraits done by different artists of the same model. Given certain caveats, one can argue that

if a general pattern exists, it very likely relates to what was actually seen.

Although bison are among the most common animal portrayed in Paleolithic art (Leroi-Gourhan 1982), only a few of these drawings and paintings are fully colored (figs. 4.11 and 4.12); most bison are drawn in outline and lack body tones or color. Also, there is a wide variability in the pictures which surely did not correspond to an actual variability in nature. The bison are always positioned laterally in the paintings, and the interior of the body usually has the same color. Among the bison that are fully colored, the body interior is dark reddish, while the periphery, particularly the cervical and posterior thoracic hump, the tail, legs, and face are regularly darkened or painted black. This coloration differs from living bison, but is very similar to Blue Babe's, at least to the portions for which we have hair.

Flerov (1977) discussed hair color and hair length of a two-and-a-half-year-old female Pleistocene bison mummy found on the Indi-

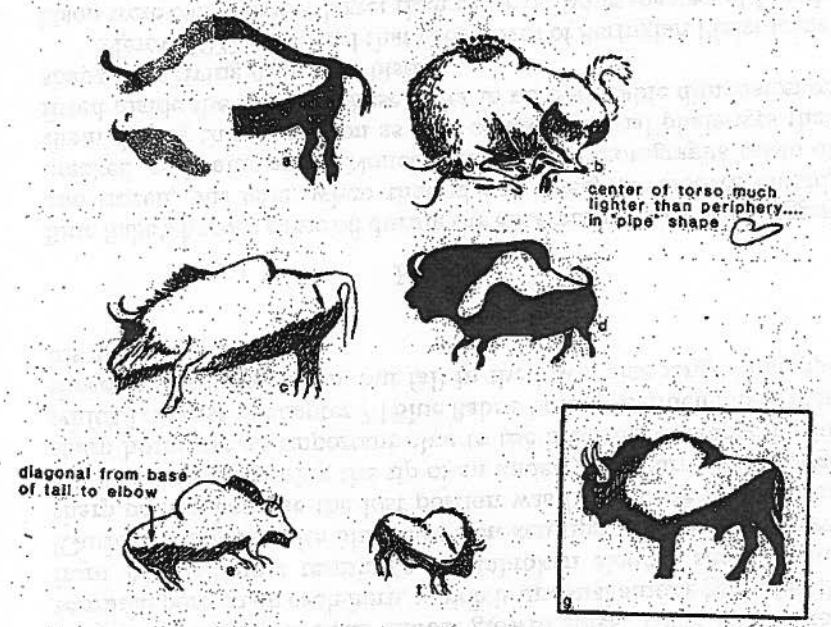

Fig. 4.11. Color pattern of steppe bison in Paleolithic art. A dark wedge runs from rump to elbow, and a smaller dark wedge appears at the posterior base of the hump. A dark mane, legs, and head leave a light side panel in the shape of a tobacco pipe. These samples are from (*a*) Le Portel, (*b*) Altimira, (*c*) Niaux, (*d*) Lascaux, and (*e* and *f*) Santamamine.

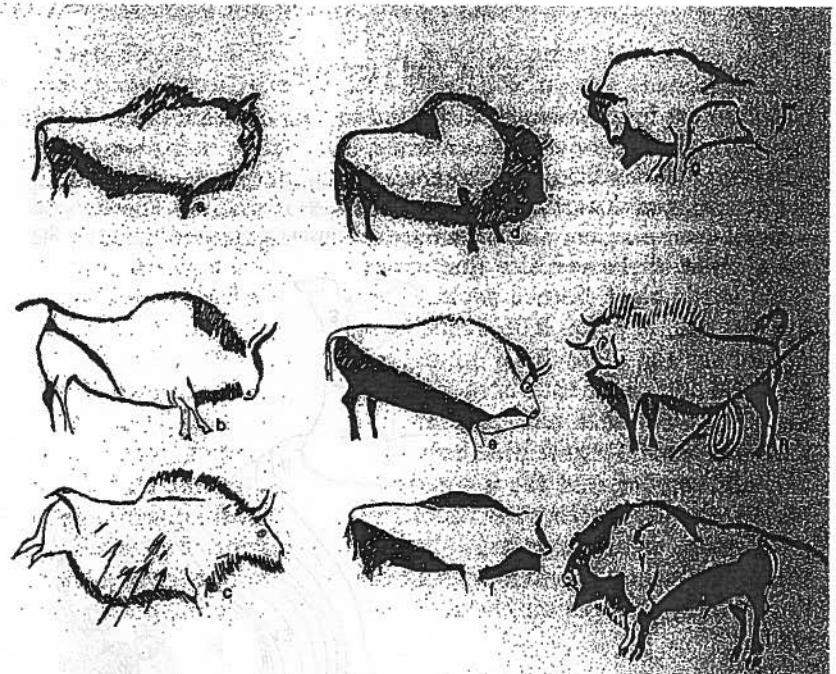

Fig. 4.12. Steppe bison in Paleolithic art. (See also those of fig. 4.11.) Further examples from (*a*) Fontanet, (*b* and *c*) Les Trois Frères, (*d*) Le Portel, (*e* and *f*) Niaux, (*g*) Font-de-Gaume, (*h*) Lascaux, and (*i*) Altimera.

girka, USSR. Unfortunately, females have different color patterns than males among living American bison, and this dimorphism probably held true for Beringian bison as well. The color patterns Flerov reports are roughly similar to those I have described for Blue Babe except his are lighter in every individual area. The most notable difference is a very light leg coloration ("light yellow ochre") of Flerov's female mummy; no living bison has lightly colored legs. This could be the color in life, or the leg hair could have been bleached in a manner I described earlier.

Flerov (1977) also describes a slightly different pattern of hair length from that of Blue Babe. Unfortunately he does not directly describe the hair length for the young female, but uses her to reconstruct how bulls must have looked. He proposes short pantaloons on the rear of the forelegs; there is no trace of these in Blue Babe. Flerov does describe the "rusty-ochre" and "rusty-cherry" color of the neck and shoulders that I saw on Blue Babe.

Horns and Hooves

Unlike most fossil bison skulls found in Alaska, which have poorly preserved sheaths on their horn cores, Blue Babe's horns were in almost original condition. Horn keratin had undergone some chemical deterioration and was brittle, but the surface remained, appearing as it must have in life. The horns are a deeply pigmented black and show none of the porosity that appears as a white frosting among some living black-horned bovids, including some individual bison. The tip end, or distal half, of the horns is highly polished, and one cannot see the more distal annual growth rings. There is a broken terminal portion on each horn, which is unusual among bison fossils from Alaska, most terminate in unbroken slender sharp points (Guthrie 1980). Despite Blue Babe's broken tips, the horns still have sharp points, because the lost portion was like a cone pulled from the distal end, exposing the tip of an underlying sharp cone. (Large sharp horns are an important clue to the behavior of steppe bison, which I discuss in chapter 7.) Blue Babe's horns are much larger than those of any living bison, but fall in the lower size range of steppe bison.

Hooves

Blue Babe's hooves came off during the excavation. They were bagged and frozen, but later, when thawed and dried, the hooves curled, cracked, and came apart. Nonetheless, I have photographs taken of them during the excavation as well as the terminal phalanges that fitted inside the hooves. These differ in no noticeable dimension or shape from living American bison.

Flerov (1977) proposed that the hooves of Beringian Pleistocene bison were considerably larger than those of living species, although Vereshchagin and Baryshnikov (1984) disagreed. Flerov shows the forehoof of an old European bison bull, *Bison bonasus*, and compares it with a two-and-a-half-year-old Pleistocene cow. The cow has hooves the exact appropriate size and shape for an American bison of that age (Murie 1954), but Flerov's illustration of the foot of the European bison bull does not fit my photographs of *B. bonasus* feet. Either Flerov mistakenly used a hind foot of a European bison (which has the same size and shape as the one shown by Flerov), or the European bison he used had dramatically different-shaped hooves than ones I have examined. From a search of many slides of European bison the latter does not seem to be the case.

I think that in fact the slightly overlapping, inward-curved hooves Flerov describes (1977) as being adaptive for swampy environments, are simply late winter hooves showing lack of wear, as occurs in winter among living bison. Bison on snow-covered ground do not wear down their hooves, nor do they regularly use their hooves as horses do to dig through snow for food. I have seen musk-oxen (*Ovibos moschatus*) with similar, and even more extreme, overlapping hooves in the spring. Hoof shape and size are very important in understanding an animal's adaptation to different substrates; they are discussed in chapters 8 and 9.

Skin Thickness

Although skin thickness is not directly related to Blue Babe's appearance, it tells part of the story of how behavior affects external anatomy. Geist (1971a) noted that patterns of skin thickness vary considerably from one ungulate species to another and, further, that skin thickness is correlated with mode of combat. Geist compared sheep (*Ovis canadensis*) with Rocky Mountain goats (*Oreamnos americanus*) and found that while sheep have thick skin around the head

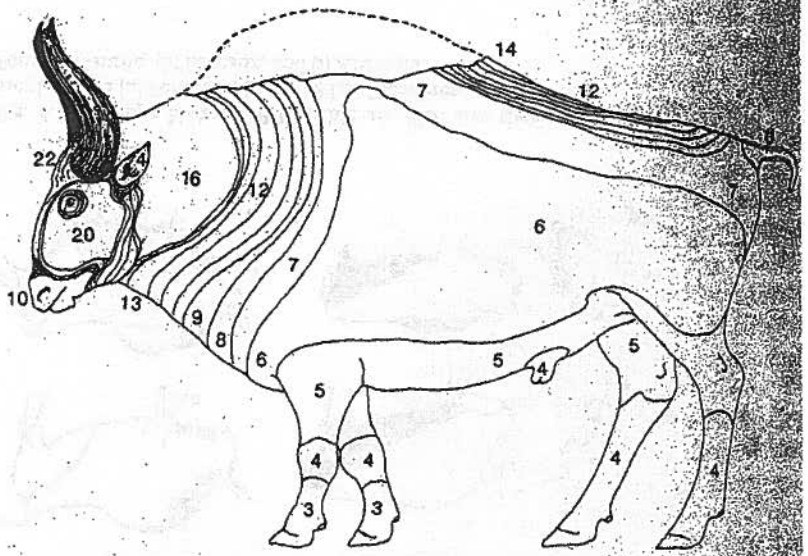

Fig. 4.13. Skin thickness. Presumably the thick skin, especially around the head and neck, was a defensive armor against an opponent's sharp horns. The thinner torso and leg skin allowed supple movement. (Thickness shown in millimeters.)

and thin skin on the posterior of the body, this pattern is reversed in Rocky Mountain goats. Their face and shoulder skin is thin, while the skin on their flanks and posterior is thickest. Sheep are head clashers, and occasionally their horns slip onto the forward part of the opponent's body. Rocky Mountain goats fight standing side by side, facing opposite directions, and dig their sharp horns into one another's flanks. For both sheep and goats, thick skin thus acts as defensive armor, decreasing the damage of an opponent's blow.

Even when the mummy's neck and head were first exposed during the excavation, it was obvious that skin in this area was unusually thick. I have plotted skin thickness in figure 4.13. Skin around the distal part of the legs is 3–4 mm thick, and over the lateral part of the body skin averages 6 mm. Along the dorsal surface, over the sacrum and lumbar area, it is thicker, ranging between 8 and 16 mm. Skin on Blue Babe's head is by far the thickest, 22 mm—measuring nearly one inch.

Age

Much of Blue Babe's appearance would have been determined by his sex and age. We know from horn size and the presence of male genitals that Blue Babe was a male. I used several methods to determine Blue Babe's age because age at death is so critical to other elements in the analysis. For instance age is the key to estimating rates of tooth wear, which, in turn, has important ecological repercussions.

Determining the age of a mummy is rather easy, like finding a freshly killed bison. However, aging techniques are approximations. Northern mammals have an obligate period of dormancy during winter. All northern ungulates will not grow—cannot grow—even when ample food is present; they "turn off" growth for the winter. The horns and teeth leave an annulus of this period of dormancy, so the growth segments represent summer only. Thus on the basis of tooth and horn aging, it would probably have more meaning to speak in terms of an animal being so many summers old.

There are five well-delimited growth zones (including the last, which makes up the proximal edge of the horn base) near the base, but annuli in the middle and distal parts of the horn are obscured, a common phenomenon even among living bison (Fuller 1959). Listed from the base distally, these growth segments measure, on their dorsal surfaces, 22, 26, 35, and 46 mm, and a long 430 mm from the last segment until the distal tip. The tip is "broomed" somewhat, so there was an additional missing length beyond this. Judging from those measurements, and comparisons with horn sheaths of other Pleistocene bison, I estimated Blue Babe's age to be 8 or 9 years. The large horns with their annuli are probably the best evidence that the bison is in the 8-year range. They assure us that Blue Babe is not a young six-year-old, nor is he a ten-year-old.

Teeth cementum annuli can also be informative, but they too are approximate. When the bison was excavated the incisors fell out and were preserved. The first incisor (I1) was sent to a commercial tooth-sectioning laboratory in Montana. While not necessarily the best indicator tooth in bison, the first incisor was available before the bison had been rethawed and necropsied. This tooth erupts at about 2 years of age (Fuller 1959); bison do not normally lay down root annuli on the incisors until about 4 years of age (Novakowski 1965). The lab read the first incisor's annuli as four, thus the annuli reading would make the bison about 8 years old.

Among populations with the same rate of tooth wear, degree of wear can be a rough indicator of age. Fuller's sample of 1,800 bison from Wood Buffalo Park showed that at age 8 the lower canine has more than 2 mm of wear. That tooth in Blue Babe appears to have at least 2 mm of wear, but not much more, which would place it at about 8 years of age according to Fuller's sample.

Skinner and Kaisen (1947) constructed wear stages of 1,322 mandibles from interior Alaskan Pleistocene sediments, including some from Pearl Creek. Blue Babe corresponds to S-2 in their diagram. At that stage the enamel of the first lower molar (M1) is worn about halfway down its vertical height. Their measurements and mine on Alaskan material indicate that a bison from age 14 to 16 shows complete wear of the M1 enamel. Also their increase in mortality due to senility begins with age class S-3, which is to say that death from aging debilitation begins in bison at around 10 years of age. So age estimation (just prior to S-3) also points to the 7- to 9-year range.

Epiphyses, which usually fuse in an age-related sequence, have been mapped for European bison (*Bison bonasus*) by Duffield (1973). He found that vertebral epiphyses fuse during the seventh year, during the eighth year those of the pelvis, ribs, and scapula fuse. All of the epiphyses of this mummy seem to be well fused, again suggesting it is at least 8 or 9 years old.

At 8 to 9 years old Blue Babe would have been at his prime, having reached his maximum body size, social station, and full pelage development. In fact, his age is probably one notch past that point, just past the break in slope of the mortality curve, when older males begin to be lost from the population. In short, Blue Babe is a fine specimen of his ilk.

5

TRACKING DOWN BLUE BABE'S MISSING HUMP

Hump shape may sound like an esoteric issue, but dorsal contours of different species relate in important ways to their behavior and ecology. Living bison and fossil Eurasian steppe bison all have subtly different hump shapes; I propose that this is because humps are a structural adaptation to the environments in which different bison groups live or lived. For this reason, I think that the hump shape of the Alaskan Pleistocene bison is significant and that it can be compared with humps of other bison for clues to behavior, locomotion, diet, and a whole suite of biological features. What sort of hump Blue Babe had is important.

I was unable to reconstruct hump contour directly from the mummy because critical thoracic vertebrae were missing. There are, nevertheless, hundreds of fossil bison vertebrae from Alaskan deposits, and, although few of these have been dated, we know most bones are from the latest Pleistocene, well within radiocarbon-dating range (see dates listed for Alaskan Pleistocene bison in chapter 10). Because there was only one phylogenetic line of bison in Alaska during the late Pleistocene (Guthrie 1970, 1980), I argue that vertebrae and other postcranial material should be relatively similar, which is not to say that Pleistocene bison did not evolve. One would expect differences between bison living tens of thousands of years apart, but bison seem to exhibit a continuity of body shape within the late Pleistocene throughout Eurasia. Working on that assumption, I used bison vertebrae from other Alaskan late Pleistocene deposits to reconstruct Blue Babe's hump profile. And although there were sexual and individual variations, the fossil bison vertebrae I examined followed a similar pattern.

Most morphological, evolutionary, and systematic studies of bison are based on male skulls (e.g., Skinner and Kaisen 1947; Guthrie 1970; McDonald 1981). Thoracic vertebrae needed to reconstruct dorsal contours are among the most poorly preserved elements of fossil skeletons. Thoracic vertebrae are not conservative characters and, taken singly, they are not very diagnostic. As a result, biologists and paleontologists have given hump shape little thought. Dorsal contour is actually the net outcome of a suite of physical features, including manes, bulging muscles, and connective tissue humps. But neural processes, or spines on vertebrae, are the key factor. Relative to body size, these rise higher in bison than in any other mammal, making a bison skeleton appear almost like the Permian reptile *Dimetrodon*.

Functionally, an ungulate's neural spines are comparable to the uprights in a suspension bridge. As in the Golden Gate Bridge in San Francisco Bay, truss members reaching skyward are attached to cables (tendons in the case of neural spines), which carry the long span between piers (legs) that reach to the bottom of the bay (fig. 5.1).

In mammals this structure of uprights and cables does something more than provide a stationary support. Muscles combine with bones and tendons so that half the body can be cantilevered without leg support from the other end, like a cantilever bridge. This is exactly what happens in the gallop; the body is supported alternately from first the pectoral (front) end and then from the pelvic (rear) end. Although little is known about hump function, I can begin with the hypothesis that the most important role of shoulder humps is increasing the efficiency of the gallop. This role can be seen (1) as a cantilever for a phase of the gallop, (2) as a girder to aid in the length of foreleg stride, and, probably most important, (3) as a structure to add leverage, allowing an efficient use of the stretch tendon of the neck.

At this point, to appreciate the function of hump shape we must approach it in a roundabout way, taking a close look at the physical demands of different gaits. The *walk* of a quadruped is analogous to two people walking in tandem, carrying a short pole across their shoulders, "out of step" with each other. A *trot* can be pictured as these same two people running, still out of step with one another. The advantage of a walk or trot is its efficiency. The body is always directly supported on both ends (anterior and posterior) and from alternate sides at the same time, so it does not tend to fall left or

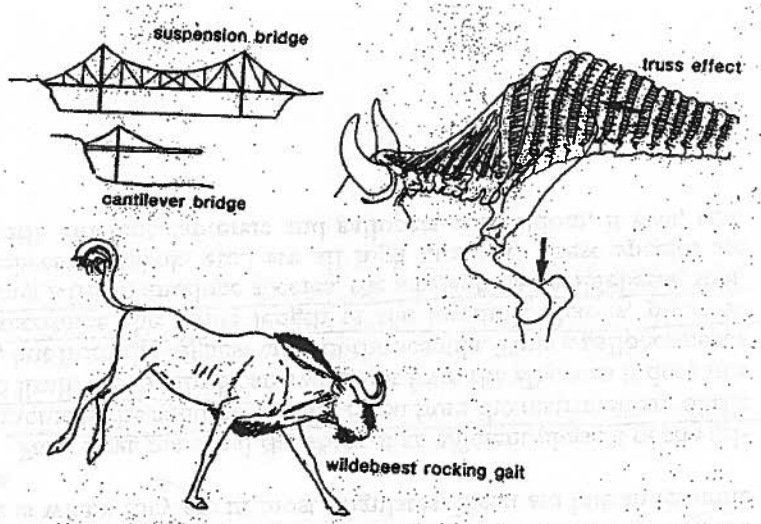

Fig. 5.1. Hump engineering. The construction and action of neural spines have been likened to the upright trusses of a suspension bridge, but during the gallop they are, in fact, part of a cantilever system. Weight is supported from below by forequarters or hindquarters, while the alternate end is held aloft by a cantilever effect. A strongly developed hump thus contributes to an efficient gallop, as seen in black wildebeest (pictured here) and bison.

right. Because of the energetic efficiency of a trot, most quadrupeds use that gait at moderate speeds. Unlike an upright biped, a walking quadruped has to step twice over the same ground, once with the fore feet and once with the hind feet, which makes the gait easy to model with two bipeds walking in tandem. The main disadvantage of a walk or trot is that each stride, hind and front, must be the same length, just as two people carrying a pole on their shoulders should walk in cadence and have the same stride length. A quadruped's hind foot cannot overstep the front foot in a walk or trot.

Camels and giraffes have developed a gait that avoids this problem but produces others. Instead of moving front and hind limbs out of step, they stride in step in a *pace* or *rack*. The problem with this gait is that the entire weight of the body is alternately thrown left and right, which is why camel riding can make a person seasick. The special build of a camel's legs and its broad feet are accommodations to this inherent instability.

Trotting is energetically efficient but has an inherent maximum speed limit. A trot cannot make full use of the flexible fore-

limb's potentially greater stride length. As a trotting animal gains speed, the stretch of the front leg is limited by the stride length of the hind limb. Unlike the more freely attached forelegs, rear legs have a fixed radius, being securely anchored in the pelvic girdle. To gain greater speed an animal must shift into a *canter* or *gallop*.

While a walk or trot can be modeled by two bipeds with a pole, and we can see that a walking or trotting quadruped does twice the work as two bipeds, it is not easy to model a gallop. To gallop our bipeds would have to alternately throw and pull each other forward by the pole while running. A gallop enables a small quadruped, a squirrel weighing a half kilogram to outrun an 80-kilogram bipedal human. A canter or gallop loses the support efficiency of a walk or a slow trot where the nonsupporting leg has only to move forward to catch the body as it falls. Canters and gallops are energetically more costly, in theory, because they have a greater vertical component; that is, the body is thrown into space, unsuspended, for substantial periods of the gait. However, a gallop has a different kind of efficiency because the hind and fore limbs do not duplicate each others' work.

To understand how a gallop works we look at it in four beats or phases (fig. 5.2), one of which discloses the anatomical importance of humps. A galloping animal hurtles through the air unsupported after it pushes from the hind legs (phase 1) and after it pushes from its fore feet (phase 3). The other phases are the steps on the ground of the forelegs (phase 2) and between both stretched hind legs (phase

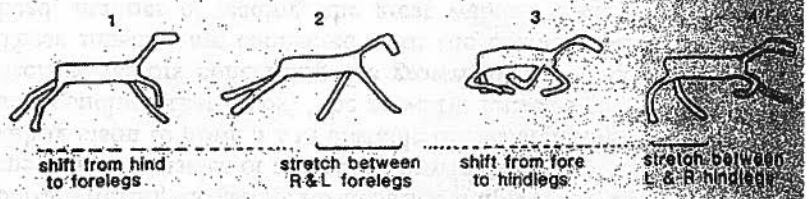

Fig. 5.2. Four phases of the gallop. I divide the gallop into four units relating to suspension and distance traveled. The *first* phase marks the shift from hind legs to forelegs. European and American bison differ, as the latter seems not to leave the ground during this phase. The *second* phase is the distance gained as one fore foot steps ahead of the other. Animals vary considerably in this phase, but bison excel, taking an extremely wide foreleg step. Their tall hump is especially important in phase two. The *third* phase marks the shift from forelegs to hind legs. Most gallopers leave the ground during this phase, even a one-ton bull bison. The *fourth* phase marks the length of step from one hind leg to the other. This is especially short in bison, related to this bison hindquarters are rather low and their hams relatively small.

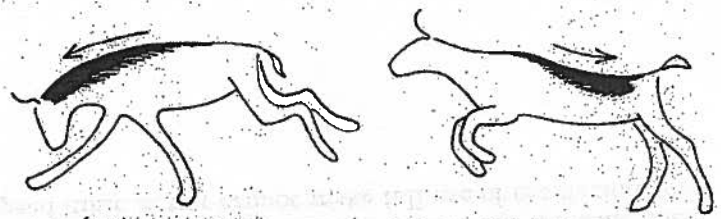

Fig. 5.3. Cantilevers and gallops. During phase two and phase three, one end of the quadruped is suspended by the other via a cantilever system of muscles, tendons, and bony struts. Bison have accentuated phase two more than phase four; consequently, the forequarters used in phase two are more exaggerated than the hindquarters.

4). So the complete four-phase cycle of a gallop can be measured and classified by the footfalls or tracks. Phase 2 is where the hump becomes important. Normally the forelegs do not land simultaneously; rather, one hits the ground, taking the whole weight of the animal, and pushes backward at the same time that the second foreleg is reaching forward and making contact. That second leg then carries the animal's weight and pushes backward, whereupon the entire body is projected forward through the air. The hind legs repeat this left-right sequence, again propelling the animal through space until it lands on its first fore foot (called the lead foot).

This shifting suspension of a galloping animal between anterior and posterior ends emphasizes the importance of the cantilever system of tall neural spines and tendon cables (fig. 5.3). Unlike some other large mammals, bison do not leave the ground in phase 1. Rather, the forelegs carry the center of gravity for an exceptionally long time (extended phase 2). Since the hindquarters are suspended out in space for a longer time than the forequarters, the main cantilever struts would logically be located in the shoulder area. Indeed that is where they are in most ungulates; bison are but an extreme case.

For a large mammal the story of an efficient phase 2 of the gallop includes the shoulder hump. Freed from the restricted arc of the hind limb, the forelimb can swing not from the elbow as it does in a trot, but from the highest crest of the scapula. Thus a galloper needs to maximize the stride length of the forelimb, that is, phase 2. Among African antelope species, the alcelaphines (wildebeest, topi, hartebeest, blesbok, etc.) are all high humped. These species are smooth, efficient canterers and gallopers and seldom, if ever, trot.

Bison are a bovine version of an alcelaphine. Wildebeest and bison can maintain their rocking, distance-eating canter for hours and days. Today they are here in the thousands; tomorrow they are gone to some distant pasture. This mobility is, I believe, the ecological significance of humps.

Fortunately, Swiezynski (1962) has done a careful study of bison musculature that helps us understand how bison humps work. The high neural spines near the anterior portion of the thorax are the major origins for the *splenius* muscle, which inserts on the head and neck. These spines are also the origin of the powerful extensor muscle of the pectoral limb, the *rhomboideus*. The *rhomboideus pars thoracalis et pars cervicalis* attach to the dorsal portion of the tall scapula, acting as a powerful lever to pull it forward during the backstroke of the foreleg (fig. 5.4). These muscles are especially important during the gallop. Roskosz and Empel (1961) argue that these specialized muscles of the hump provide agility and flexibility, enabling bison to jump a 2 m obstacle from a standing start, but they also conclude that (p. 69) "the powerful muscles of the withers are decisive factors concerning the growth of the spinous processes. These muscles are connected with the characteristic pose of the head, manner of feeding, the great weight of the body, and the strongly developed anterior part of the European bison. The specific gait and great activity of this animal is not without importance."

As I said earlier, the second phase of the gallop is one of the most important for bison. The tall scapula hinges from its apex, allowing a wide stretch between forelegs, even for such a heavy creature as a bison. But the spines of the anterior thoracic vertebrae are tall in all bison species, and so are those near the posterior end of the thorax, but these latter are proportionally and absolutely much larger in the steppe bison.

Unfortunately, we need the muscles, tendons, and ligaments to say for certain how the steppe bison's unique hump functioned, and we do not have those because they were removed from the Blue Babe specimen by predators and scavengers. We can, however, make a good guess. Perhaps the *rhomboideus* extended more posteriorly; we know from the shape and size of the anterior neural spines that it had a different shape in steppe bison. But another muscle, the *spinalis*, is a series of bellies that originate on the distal ends of each thoracic vertebrae and that travel posteriorly, inserting toward the lumbar vertebrae. These bellies act in synchrony to arch the back convexly (dorsally), and because of their size and origination height they provide a powerful mechanism by which the back can add push

to the hind limbs for greater distance during the first beat or phase of the gallop.

This same enlarged *spinalis* muscle originating from a higher angle would also have given the males more power in fighting, as the back comes from a collected convex to an extended concave position when the head is forced upward during pushing bouts. There seems to have been a difference in fighting mode between America bison

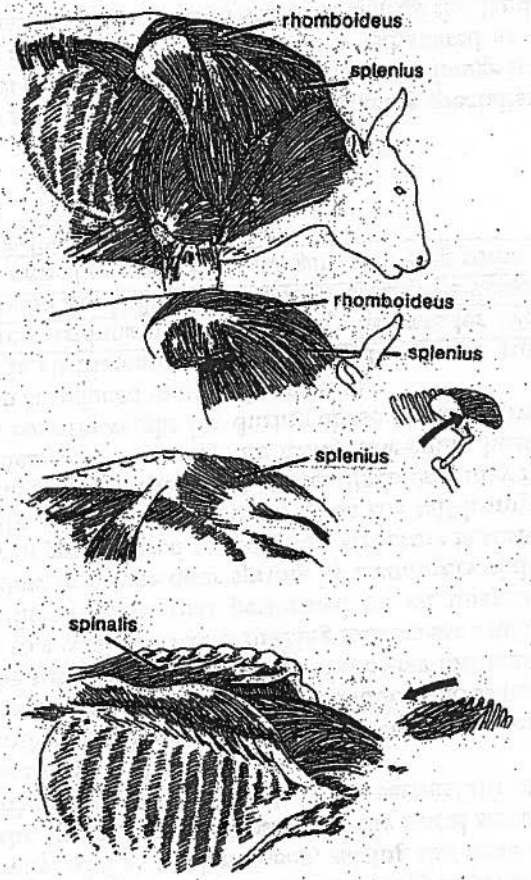

Fig. 5.4. Thoracic muscles of European bison. Some shoulder muscles used in the suspension process are portrayed in this anatomical dissection redrawn from Swieczynski (1962). The rhomboideus and splenius pull the scapula forward, rotating the foreleg backward (the main strength of the bison's gait). The spinalis pulls the neural spines backward, using that leverage to arch the vertebral column in phase one, as well as supporting the rear quarters in phase two.

and the large-horned Pleistocene steppe bison (Guthrie 1980, and reviewed elsewhere in this book). So in addition to its differences in locomotion the steppe bison may have had a muscle-lever system which accompanied a different adaptation in fighting strategy and style.

The long neural spines of a bison's hump are also important as girders or struts for the attachment of the elastic neck ligament, or nucal ligament. This is a thick elastic yellow cable which allows energy to be stored as the head is lowered by gravity (for example, when the animal grazes). Stretch ligaments make it less costly to return the head to its natural position (fig. 5.5). The nucal ligament originates from the tips, or distal ends, of the neural spines and in-

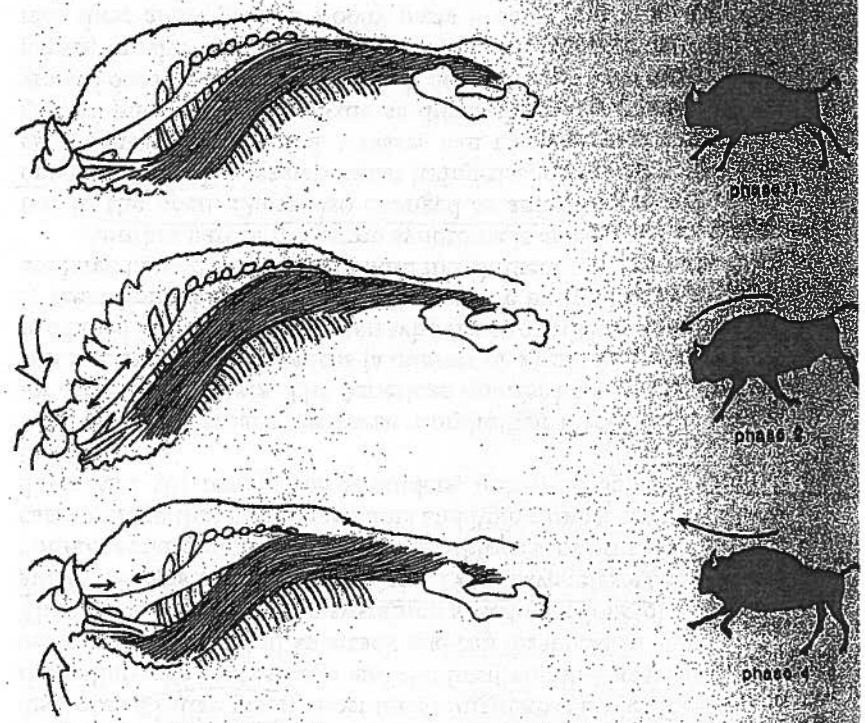

Fig. 5.5. Role of stretch ligament in gallop of European bison. The neural spines in the hump act as girders to which the nucal ligaments attach. The tall spines provide leverage as the head bobs up and down during the gallop. During phase two the head is lowered by gravity and by the pull of the muscles attached to the rearward-moving foreleg, providing a counterweight to the suspended hindlegs. The nucal ligament aids in raising the head, decreasing the expenditure of energy otherwise required.

serts onto the back, or occiput, of the skull. But this ligament may have another function.

To my knowledge, no one has mentioned the nucal ligament's importance in galloping. A galloping animal alternately lifts its head up and down (a novice horse rider must learn to move the taut rein in this rhythm). The down thrust of the galloping animal's head comes during phase 2 (fig. 5.5); it seems to act as a counterweight in the suspension of the cantilevered rear end. The tall trusses of the hump increase that mechanical advantage. The nucal ligament seems to be the main cable of energy transmission in that process. The lowering of the head requires little energy expenditure because it uses gravity. And as we have seen, raising the head is greatly assisted by the energy storage capacity of the nucal stretch ligament. The upward spring of the head aids in the vertical lift of the forelegs during phase 4 (fig. 5.5).

A familiar analogue to this energy storage process in stretch ligaments is the pogo stick, where one bounces along on a stick with springs. The spring stores the energy of the gravitational descent and converts it to a vertical ascent, making movement much more energetically efficient than that performed on an unsprung stick. A heavy window or garage door sprung by a counterweight is similar. The energy of gravity used to lower the structure is stored, allowing one to easily raise the garage door. Thus the tall hump of a bison, acting as the origin of the nucal stretch ligament, may increase galloping efficiency by allowing the heavy low-slung head to be employed as a counterweight lift during phase 2 and recovered to normal position at reduced metabolic expense.

There is an increasing awareness in locomotor studies of the role of stretch tendons in energy storage (Alexander 1984; Alexander, Dimery, and Ker 1985). These energy-storage devices make a gallop a comparatively energy efficient gait, allowing some animals to use it in long-distance travel.

The Ecology of Humps

High humps are the mark of open-plains grazing specialists. In areas where grasses grow thinly and the sward is short, forage is limited in volume and any one area can be quickly exhausted as rangeland. Likewise, quality forage is often scattered across the landscape in a mosaic—rains may come ten kilometers away. The phenological peak of plant quality also occurs at different altitudes and at different aspects of slope at different times of year. A plains-adapted social creature traveling with a herd must keep on the move. An animal adapted to fibrous forage cannot go very long without water, yet the highest quality of range is often quite distant from water and frequent trips must be made between the two. An efficient and fast gait is important on the plains.

Humps are often part of another set of traits. As animals moved away from the forest where thick vegetation afforded protection from predators, many species resorted to sociality as a substitute "cover." The presence of a hundred other animals dilutes a predator's focus on one's self. Forest ungulates are built for great speed over very short distances. Unlike bison, most forest ungulates emphasize phase 1 of the gallop; the rear is large and the front small. Forest antelope accelerate quickly to foil an attack and can disappear in dense habitat. Thus they do not require sustained speed over long distances. Ungulate biologists (Estes 1974; Geist 1974) have referred to this as the "duiker syndrome," named after small forest- or brush-adapted African antelope that have large hams and high rumps, giving the body a downward tilt toward the shoulders, quite the opposite of wildebeest.

One can actually see these morphological traits in horses bred for different purposes. The American quarter horse has been bred to run fast over short distances (a quarter of a mile or about 400 m). It is a breed favored by cattlemen who have to quickly cut off a cow as it veers from the herd. Quarter horses are built like dragsters, they are large hamed and slope forward like duikers.

Another part of the hump syndrome is an adaptation to grazing out in the open. Diets also changed as animals moved into more open country. Grasses have most living-tissue and energy storage organs beneath the ground. Grasses can treat their seasonal, above-ground photosynthetic tissue as disposable. As such, tissue above ground does not have to be so well defended from herbivores. Woody plants, on the other hand, usually produce toxic chemicals to protect their above-ground woody parts because these parts are more costly to grow. The open sun-drenched plains can have excellent forage part of the year when grasses are abundant and high in nutrient quality and calories. But forage on the plains is more seasonal than in shade-buffered woodlands. Seasonal plenty alternates with lean, inhospitable times, when the only food available to a herbivore is standing dead grasses which offer abundant empty calories, but lack other essential nutrients. A plains-adapted animal weathers this bleak period by having the ability to use poor food (many woodland species cannot survive on such undigestible material). Most north-

ern plains species also rely on fat reserves gained during earlier seasons of plenty. To live year-round on the open plains a species must make full use of available resources. Mobility that is both rapid and efficient is a critical part of survival.

American bison are like wildebeest in their adaptations to grasslands. American bison have large shoulder humps, and they frequently use a rocking canter. But because their body mass is bovine in scale, they have different problems in locomotion. Bison humps are unusually large, the largest of all ungulates in their size range or smaller. When one examines photos of galloping bison, the span between the fore feet in the second phase of the gallop is enormous. A high hump allows bison scapula to be quite tall, it is a feature of

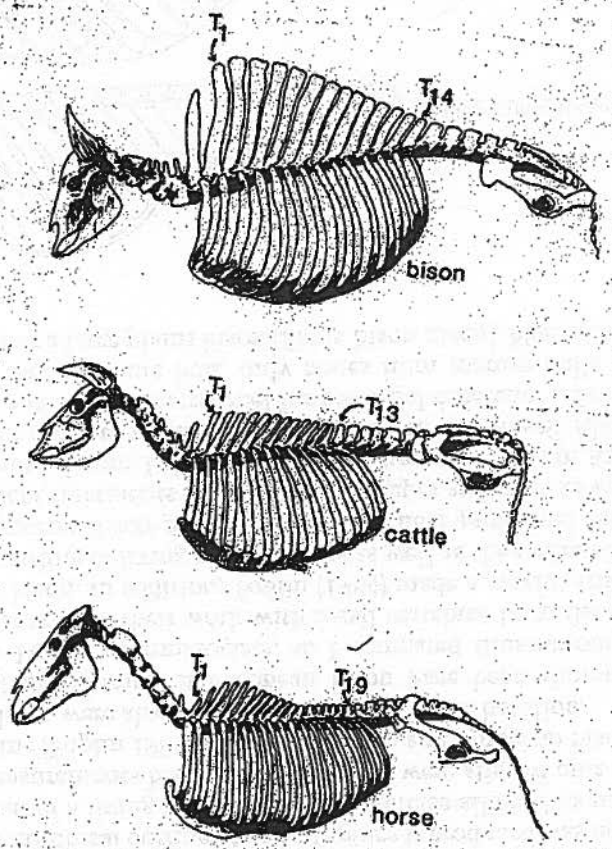

Fig. 5.6. Partial skeletons of bison, cattle, and horse. Note dramatic differences in neural spines.

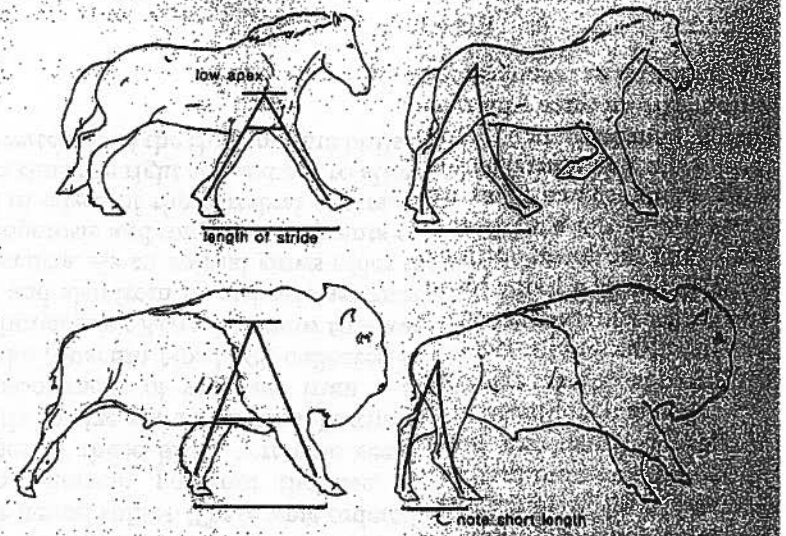

Fig. 5.7. Relative stride lengths of galloping horse and bison. Even though bison are short-legged, they travel about the same distance in phase two (distance between right and left fore feet) as horses, because their high shoulder raises the apex of the arcle of foreleg rotation. In phase four (the span of hind feet), bison travel a shorter distance than horses.

bison osteology that easily separates (fig. 5.6) bison from cattle (*Bos*) and buffalo (*Bubalus, Syncerus*) or even equids. As I pointed out earlier, a tall scapula increases the height of the arc through which the forelegs can travel and hence the potential length of stride, making a bison's gallop exceptionally efficient (fig. 5.7).

It was once thought that humps related to heavy heads or big horns (Koch 1932), but there seems to be very little correlation. The open-ground grazing niche is a better predictor of who is humped. Among bovines, bison are the most well adapted to life on open grasslands, and bison have by far the tallest humps. Cattle, in comparison, are small humped; they are woodland edge or parkland creatures. Even among cattle breeds with heavy heads and immense horns, for instance, Watusi cattle and Ankol cattle of Africa, the "withers," as cattlemen call the hump, are low (Roskosz and Empel 1961), that is, the neural spines of the thoracic vertebrae are short. In America we do not think of cattle as adapted to the woodland edge, but associate them with cowboys on the open plains. But cattle on the plains must be fed hay for a big part of the year. Compared to bison, cattle are not well adapted to living wild in these habitats.

Blue Babe's Hump

My first step in reconstructing Blue Babe's hump was to assemble vertebrae from three American bison, in a long band down three pine boards, using one-inch (25mm) strips of clay about four inches (100 mm) wide. The ventral part of the centrum was pushed into the clay, with neural spines pointing dorsally (see fig. 5.8). Of course the board provided a base quite unlike the complex contour of a living bison, and the dorsal outline of neural spines it produced was not the same as that of a living bison. Still, this exercise allowed us to take precise measurements because all vertebrae were aligned on a common baseline (Poplin 1984). Other American and European bison, as discussed later, were also compared using this same baseline.

Vertebral columns of European bison have been thoroughly studied by Polish mammalogists, so I compared illustrations and measurements from their work with fossil vertebrae from the Alaskan steppe bison. In addition, Poplin (1984) made a careful study of the dorsal outline of living bison species as well as the extinct European Pleistocene *Bison priscus*. Although these published studies were excellent treatments of neural spine shapes and sizes as well as vertebral musculature, I chose to examine three skeletons of American bison in order to make direct comparisons with fossil Alaskan specimens and to get a better feel for potential differences. Because Blue Babe was a mature bull, only bones from mature bulls were used. One was a large plains bison (*Bison bison bison*), National Museum of Canada No. 45632, from Montana. The second was a wood bison (*B. b. athabascae*), National Museum of Canada No. 32628, from an introduced bison population in Elk Island Park, Alberta. The third, also a wood bison subspecies, National Museum of Canada was from Wood Buffalo National Park, taken before plains bison were introduced to that area (table 5.1).

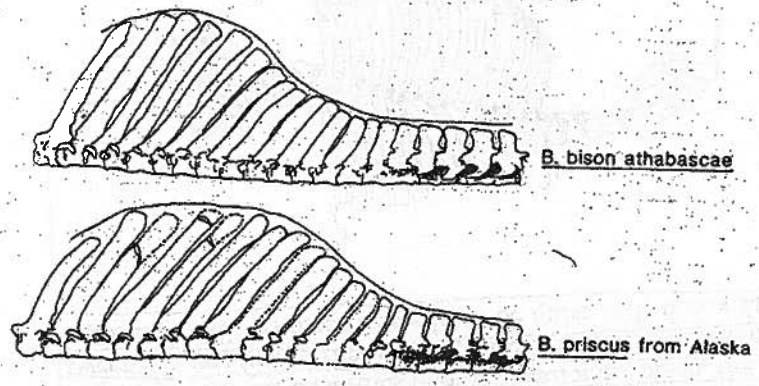

Fig. 5.8. Thoracic and lumbar vertebrae. Vertebrae are assembled on a flat base to illustrate differences in hump contour. The highest point of the steppe bison hump is far posterior to that of plains bison. Also, the neural spines of plains bison fall smoothly to the rear; in steppe bison this contour is more abrupt.

Table 5.1 Bison Neural Spine Length

		B. priscus	*B. b. bison*[a]	*B. b. athabascae*[b]	*B. b. athabascae*[c]
Cervical	no. 7	15.5	14.75	15.5	13.0
Thoracic	no. 1	16.5	16.0	18.5	13.75
Thoracic	no. 2		15.75	18.5	13.75
Thoracic	no. 3	17.0	14.75	18.0	17.25
Thoracic	no. 4		13.0	18.0	16.0
Thoracic	no. 5	18.75	11.25	18.0	14.25
Thoracic	no. 6	17.5	10.0	16.25	12.0
Thoracic	no. 7	16.25	9.0	13.0	10.5
Thoracic	no. 8		8.0	11.50	9.5
Thoracic	no. 9	12.0	7.0	9.25	8.25
Thoracic	no. 10	11.0	6.25	7.50	7.25
Thoracic	no. 11	9.25	5.5	7.25	6.0
Thoracic	no. 12	6.25	4.5	6.25	5.25
Thoracic	no. 13	4.75	4.0	5.0	4.0
Thoracic	no. 14	4.25	3.75	4.5	3.75

Note: All measurements are taken from the posterio-dorsal rim of the neural canal in a straight line to the most distal part of the neural spine, to the nearest 0.25 cm.
a. National Museum of Canada No. 45632 mature male.
b. National Museum of Canada Wood Buffalo Park mature male.
c. National Museum of Canada No. 32628 mature male.

Several hundred vertebrae of Pleistocene Alaskan bison at the University of Alaska Museum were sorted for specimens with complete neural spines. These were ordered in categories of cervical, anterior thoracic, posterior thoracic, and lumbar. The individual shapes of these bison vertebrae seemed similar, but they varied greatly in size and robustness. Fortunately the collection contained an assortment of vertebrae from a single animal, University of Alaska Museum No. 1178, collected in 1956 at the Utica Mine on the Imnachuck River. We know this was an old bull, judging from its size and also from its arthritic asymmetry and the pearling around the centra. As an animal grows older the vertebrae exhibit arthritic osteoporosis and roughness at points of muscle origin and insertion and in edges of the vertebral centra. The Utica Mine bison bones were thus the right sex and age to allow for a good comparison with the vertebrae of the three mature bulls from Canada. Using vertebrae

from a single steppe bison avoided the problem of assembling vertebrae from individuals of slightly different age and size.

The vertebrae of this steppe bison from the Utica Mine could be ordered in sequence by using the recent bison vertebrae as a comparison. In addition, we were able to cross-check our identifications and vertebral ordering because the articulations showed many unique patterns and asymmetry which had to match exactly. No two articulation facets of the anterior and posterior zygopophyses were alike in this regard, so our identifications were certain.

Noting specific features of these different vertebrae help us reconstruct Blue Babe's hump. Cervical vertebrae of steppe bison and the two subspecies of modern American bison differed mostly in the steppe bisons' greater robustness of muscle and ligament attachments, attributable, I think, to their massive horns which increased the weight of the head. The last cervical vertebra, C7, however, was quite different in shape as well as size. This cervical vertebra is incorporated in the thoracic series and can be thought of as thoracic in shape and function. It is immediately identifiable in any jumble of vertebrae because it has no demifacets for rib attachments, yet it has a very long neural spine, like the thoracic vertebrae.

The shape of steppe bison vertebra C7 is very different from that of a living American plains bison. In steppe bison the C7 is tightly arched posteriorly, that is, it has a convex surface all along its anterior face. The C7 neural spines of plains bison rise from the base in the same posterior bend but reverse themselves halfway in an anterior bend (concave on the anterior face). Also the anterior-posterior width of the neural spine base is greater in steppe bison than in plains bison. From this wide base the spine tapers gradually to a narrow distal end. American plains bisons' C7 spine keeps much of its anterior-posterior width instead of narrowing to a point. Unfortunately, few terminal portions of C7 are present among fossils, as this part is quite edible and is usually scavenged.

In contrast, the C7 neural spine of the Canadian wood bison more closely resembles that of the steppe bison, but is not so wide at the base. Wood bison are in between plains bison and steppe bison, but more akin to the latter. One specimen of wood bison, NMC 32628, had a longer C7 spine (390 mm) than plains bison (355 mm); the other wood bison, NMC 45632, had a much smaller neural spine (330 mm). The C7 of European bison measured by Roskosz (1962) seems smaller than that of both American bison and steppe bison. Roskosz pictured only the C7 of female bison. These were straight in profile and tapered in width to the distal tip, like those of steppe bison, but were not arched posteriorly.

The first thoracic vertebrae, the T1, evidences another difference. Two subspecies of living American bison have a more smoothly curved concave anterior border to their neural spines, whereas the neural spine anterior border of steppe bison is convex on the proximal half and slightly concave only on the distal half. The T1 neural spine of wood bison is longer than any of the other neural spines. The wood bison neural spine lengths of the T1 were 470 mm and 485 mm. The T1 length of the American plains bison was 400 mm and the steppe bison's was 415 mm. These measurements and those that follow are from the dorsal-anterior point on the neural arch to the distal end of the neural spine, along the anterior face.

Thoracic neural spines were more convex on their anterior borders among steppe bison than among either modern American bison subspecies. Both wood bison and plains bison spines almost always started from a concave sweep as they rose from their bases and arched more convexly on their distal half. Comparing neural spine lengths within individuals, both plains bison and wood bison had longer T1 and T2 spines than any other vertebrae. They differed subtly in pattern in that wood bison tended to have longer absolute length than plains bison. I had only one mature male plains bison for comparison, so perhaps some individuals reach lengths comparable to wood bison, but in general a higher forward portion of the hump is characteristic of wood bison (Geist and Karsten 1977).

A striking difference between Alaskan steppe bison and the above specimens is that in steppe bison, the longest neural spine is T5. As can be seen in figure 5.8, the thoracic hump of steppe bison is located farther back than in wood or plains bison. For example, in contrasting the two, the wood bison had longer neural spines from T1 through about T4; the steppe bison had larger spines between T5 and T12.

A comparison of neural spines of vertebrae T4, T5, and T6 (fig. 5.9) highlights thoracic hump placement. Those of the plains bison (T4, T5, and T6) are short relative to other vertebrae. These same neural spines are longer in the wood bison. Among steppe bison these neutral spines are longer than in either living American bison species, and they are set differently, being bent posteriorly in a more acute angle. A similar pattern can be seen in T8, T9, and T10 (fig. 5.10). Neural spines of steppe bison are also broader anterior-posteriorly than the others. Posterior to T10, neural spines among all of the bison are rather similar, including those of the lumbar vertebrae. Among both female and male European bison pictured by Roskosz (1962), the thoracic vertebrae had concave anterior surfaces to their neural spines, more like those of American plains bison.

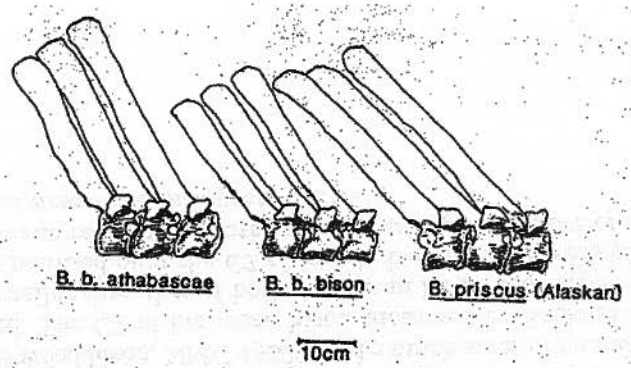

Fig. 5.9. Lengths and angles of the fourth, fifth, and sixth thoracic vertebrae. These are longest in fossil steppe bison, and they emerge from the centrum at a lower angle, bending more posteriorly.

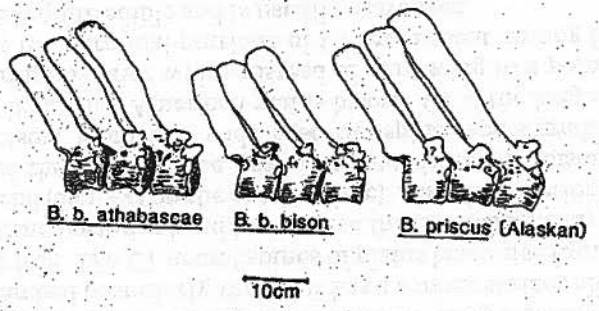

Fig. 5.10. The neural spines of thoracic vertebrae eight, nine, and ten. These are located at the posterior "stop" or drop-off of the hump of steppe bison, *B. priscus*, and, as a consequence, differ from their homologues in wood bison, *B. b. athabascae*, and plains bison, *B. b. bison*. Those of the steppe bison are broader (anterior-posteriorly) and longer.

All this means that the hump shape produced by thoracic vertebrae of Pleistocene Alaskan specimens differed considerably from that of living plains and wood bison. Wood bison have a high hump that is straighter in profile from the saddle of the back (lumbar area) forward to the neck. In wood bison, the forward edge of the hump drops abruptly, almost vertically. In plains bison, the hump is high in front but drops less abruptly to the neck. Overall the plains bison has a slightly concave profile to the highest point of the hump.

As reconstructed from Alaskan fossils, steppe bison had a more gently ascending hump from the front which reached a high point well posterior to that of both American bison subspecies. Posterior to the scapula, the hump arched upward then dropped rather abruptly in a convex arch. The steppe bison's hump was more similar to that of the living European bison, *B. bonasus*, but the former's hump was much more exaggerated in height and contour.

Although he did not have access to Alaskan fossil material, Poplin (1984) examined bones of American *(B. bison)* and European *(B. bonasus)* bison, comparing the dorsal contour of the neural spines. Poplin did not distinguish the two subspecies of American bison in his work. However, I wanted to use the subspecies differences because I felt the geographic proximity of wood bison to Alaskan Pleistocene bison might be significant. Poplin compared many individual bison, both females and males; a diagrammatic summary of his findings is presented in figure 5.11. Poplin was primarily concerned with testing the idea that European cave artists drew bison with a dorsal contour different from that of now living bison. He

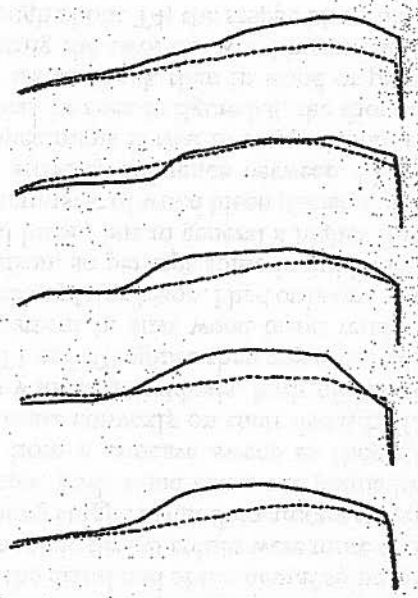

Fig. 5.11. Male bison dorsal skeletal contours. When Poplin (1984) compared dorsal contours of vertebrae from different bison groups, he was able to show there were differences in hump shape. Humps of living bison and extinct European steppe bison (*B. priscus*) have diagnostic shapes. The dashed base-line contour is that of an American female bison; solid-line comparisons are different males. The lower three are fossil steppe bison. (After Poplin 1984)

because of artistic style but because of a biological difference in their model. Fortunately, he was able to find two almost complete specimens of European steppe bison, *B. priscus*, the same species that, on the basis of other evidence, I have argued lived in Alaska, the species to which Blue Babe belonged.

In length of neural spines, Poplin found that among American bison the first thoracic, T1, is normally the longest. Among European bison it is T2, and for European Pleistocene steppe bison it is T3. Remember that Alaskan Pleistocene steppe bison had the longest neural spine of T5, even farther posterior than European steppe bison. More important, Poplin was able to show that, unlike living bison, Pleistocene steppe bison had a dorsal hump placed posterior to the shoulder and, furthermore, that the hump's posterior edge was strikingly convex. As I have shown, this pattern is identical to that of steppe bison from Alaska.

Functional Significance of Steppe Bison Humps

As our comparison showed, the biggest difference in hump shape is between the humps of the steppe bison and the American plains bison. The crest of the American plains bison hump is located in front of the scapula, while the steppe bison's crest is behind the scapula; a possible difference in function may be the humps' mechanical relationship to the nucal ligament. Let me propose a new theory.

The low-slung character of the American bison's head is, I believe, derived from its specialized adaptation to the thin sward of the American shortgrass plains. Not only is the grass normally low in growth form after being grazed, but it readily regrows into a very short "lawn" pattern in an especially thin sward. To get sufficient quantities of grass, American bison must spend many hours grazing with their heads almost touching the ground. There is a dearth of midheight forage.

As a direct product of this adaptation, the entire anatomy of the American plains bison has located the normal position of the head lower than in other bovids (like a lawn mower set low to the ground). This changes the optimum mechanical arrangement of the nucal ligament for head raising and lowering to a more forward emphasis on the hump, its point of origin (fig. 5.12). Additionally, the lower head position changes the optimum mechanical angle for the neck ligament to a more forward or anterior location. Thus the hump of the American plans bison may be part of a network of adaptations to a lowered-head position as a lawn grazer, quite unlike the environmental adaptations of other large bovines. If that is correct, their hump would be an evolutionarily derived trait from a more steppe bison–like hump.

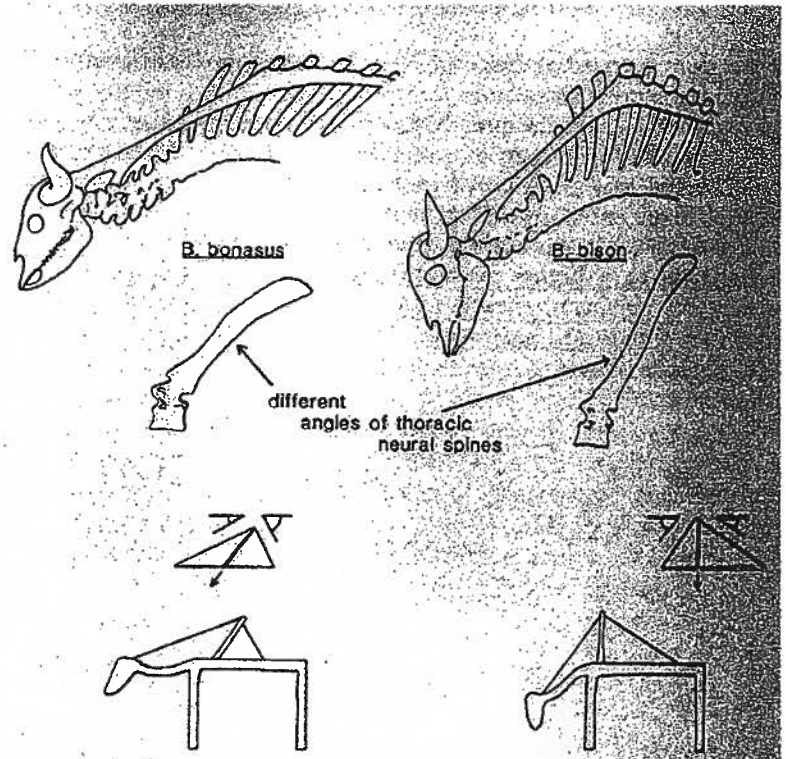

Fig. 5.12. Arrangement of nucal ligaments in living European (*B. bonasus*) and American bison (*B. bison*). Normal head carriage is lower in American bison, necessitating a more vertical alignment of the neural spines and a more forward location of the longest neural spines.

Steppe bison seem to have held their heads higher, at rest, than do American plains bison—more like fossil and recent European bison. This can be seen in Paleolithic art. Steppe bison probably did not occur in vast enough herds to promote a lawn system of grazophilic grass species, as do wildebeest and plains bison. Rather, modest densities on a relatively cold-arid grassland would have necessitated considerable mobility. The larger shoulder hump apparently enhanced the ability of these large creatures to move rapidly across the landscape. Not only did Pleistocene bison have to move great distances to find fresh ranges and water, but they also had to run

away from predators. This necessitates seeing predators before they come dangerously close.

On the generally open Mammoth Steppe landscape, approaching lions could be seen at considerable distances by a bison with head raised to a position of modest height. Among small herds of steppe bison, predation alert would have been a selective pressure countering a permanently lowered-head arrangement. Given some advantage to a higher resting head position, the location of the steppe bison's hump crest behind the scapula may be the optimum pattern to maintain both speed and galloping efficiency of this large and powerful bison.

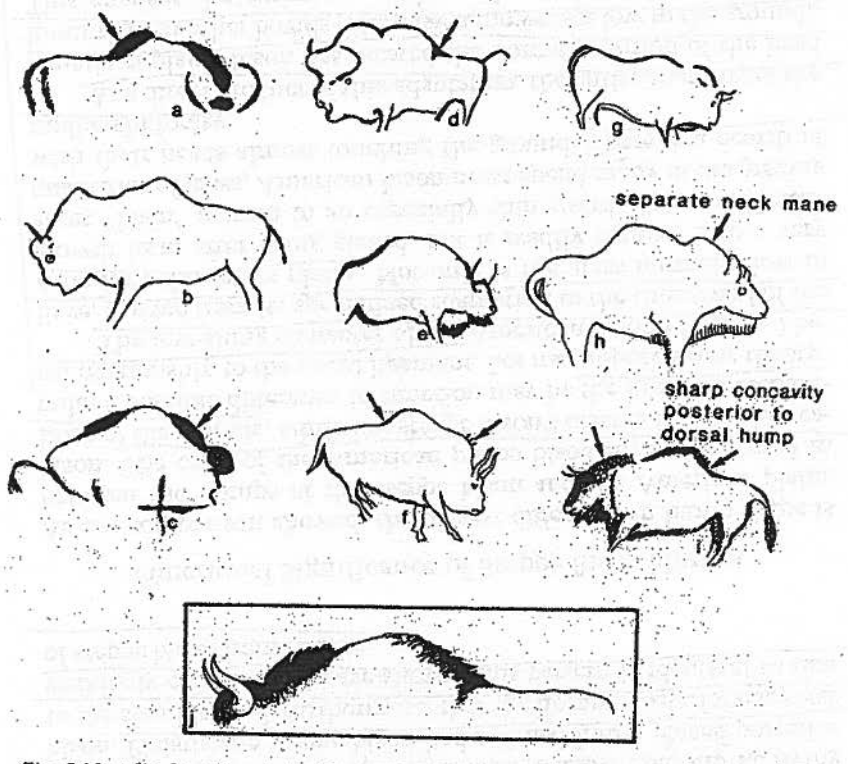

Fig. 5.13. The dorsal contour of steppe bison from Paleolithic art. Numerous drawings of steppe bison in Paleolithic art show an abrupt "stop" just posterior to the hump which seems to have been a darker color as well. A distinct neck mane is shown which is also dark. This mane is not present in American plains bison (*B. bison*), but there are slight traces of it in European bison (*B. bonasus*). These bison are drawn from (*a*) Marcenac, (*b*) Etchberriko-Karbia, (*c*) Santimimine, (*d*) La Pasiega, (*e*) Le Portel, (*f*) Pindel, (*g*) El Castillo, (*h*) Le Tuc d'Audoubert, and (*i*) Niaux.

Despite the absence of Blue Babe's hump, we have successfully reconstructed it indirectly. Given that Blue Babe's hump is similar in structure to the hump of Pleistocene European bison, it is likely that the pelage of Blue Babe's dorsal line was also more similar to European steppe bison than to any other bison. European Paleolithic art provides many drawings of steppe bison (fig. 5.13). In these drawings the stop in the posterior thorax is emphasized by a contrasting, dark-colored hair patch; the dorsal neck hackles also form a hump and are of a contrasting dark color. These appear as two humps.

Working on the ethology of extinct species may strike most ethologists as a strange enterprise, but most ethological studies rely heavily on the literature, that is, on others' earlier observations. In many ways, Paleolithic works of art are very old references that recently uncovered. While they do not always tell us exactly what we want to know, they provide a wealth of information, some of it obviously incorrect, as indeed in the case of older scientific literature. But we can see by their work that Paleolithic artists were empirically oriented, drawing mainly from observation rather than copying some stylized icon form.

6

STEPPE BISON ETHOLOGY

Social Organs and the Art of Spying on Ice Age Behavior

Many aspects of an animal's appearance are "social" in function; the wattles, stripes, manes, horns, and color patterns shown in an illustrated field guide, for example, are usually social organs. Social organs distinguish the sex, age, and social stature of the bearer; they are flaunted in displays of aggression, submission, sexual attraction, or social bonding. Of course, much of a species' social behavior is shaped by environmental adaptations that also affect anatomy, and thus appearance is an interacting composite of social garb and environmental adaptations. Too brilliant a coat can be dangerous, so while an individual concerns himself with winning stature and females he must also worry about predation. Likewise, features that make an individual stronger among peers (large horns, muscles, and heavy bones) may also make him slow and less agile in defending against predators. Social anatomy and survival have to strike an evolutionary compromise, but the balance of this compromise should theoretically vary with environment.

Estes (1974) outlined the interaction of behavior and environment among African bovids in a gradient from woodland edge to savanna and fully exposed plains. I retailored these (fig. 6.1) to describe evolutionary trends in northern bovines (Guthrie 1980). I think that Pleistocene bison living in an open steppe experienced increases in agonistic behavior, nonlethal fighting apparatuses and techniques, group size, class hierarchies, and gaudy social display organs. In addition to the above changes, homeland fidelity probably declined and was replaced by more migratory or nomadic tendencies. Feeding in a steppe environment became more unselective, and wintertime diets included a high percentage of fiber.

Animals living on the Mammoth Steppe experienced a highly seasonal environment: the quality, abundance, and digestibility of

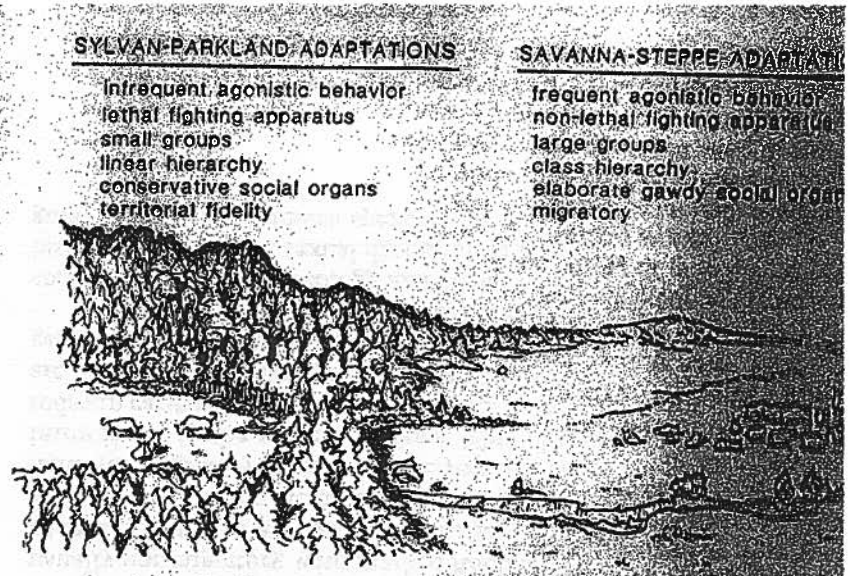

Fig. 6.1. Woodland versus steppe adaptations. Early bovines originally were adapt to wooded habitats. The expansion of open grasslands created a potentially rich nich but the move to more seasonally variable grasslands involved new demands and in duced different adaptations. Behavioral and morphological traits characteristic o woodland and plains bovines are summarized in this illustration.

their food changed markedly throughout the year. Monocotyledo and nonwoody forbs were relatively rich and abundant during t short summer, but each fall, as growth stopped, these plants move most nutrients to their roots, leaving poorer quality dead tissu above ground. Pleistocene bison depending on this low-nutrie winter forage required a large rumen to incubate quantities of th high-fiber, poor-quality food. Severe northern winters and attendan mortality would have kept bovine populations well below summe carrying capacity, thus reducing competition for resources durin the growth season. Abundance and quality of food in the growin season gave each animal the resources to attain its full genetic po tential for horn and body size. I have proposed (Guthrie 1980, 1982 1984a, 1984b) that such strong seasonality shifts selection optim and favors a larger body size.

The larger group size characteristic of plains ungulates (Este 1974) generally precludes a linear social hierarchy. Linear hierarchie are common in feral cattle (Schloeth 1961; Frazer 1968) as long a the cattle are in small groups. Hierarchies in large dairy herds of fift or more often include such subgroupings as "triads" (Brantas 1968)

Both American bison (McHugh 1958; Lott 1974) and European bison (Jaczewski 1958) have rank hierarchies, but the former tend toward a class ranking system, particularly when studied in more natural situations in large parks (Shult 1972; Petersburg 1973). Holocene bison of Europe inhabited parkland openings in a forested landscape and probably experienced selection pressures for homogeneity of color and reduced display organs. The reverse is true of American plains bison on expanding Holocene grasslands. These grasslands had no counterpart in Holocene Eurasia. American plains bison developed extreme display paraphernalia, weapon morphology (short stubby upward-oriented horns), and fighting styles (head clashing). Along with wildebeest, American bison are at the farthest end of Estes' (1974) spectrum of plains-adapted bovines that live in large herds (fig. 6.1).

Migratory species living in highly seasonal plains environments sometimes do not form reproductive territories; instead, males display *themselves*, and outside the brief reproductive period, mature bulls form separate herds. Sexual dimorphism is most exaggerated among these animals. During the breeding season, males join the female bands where they seek out and "tend" females in estrus, fending off an array of contenders, then move on to the next estrus female. Intense selection pressures favor males sporting the most extreme display paraphernalia. These social organs are used for only a brief period, but without them bulls are reproductively neutered (Petersburg 1973).

In other plains ungulate species (e.g., *Oryx*), where both sexes live most or all of the year in mixed herds, there is little marked sexual dimorphism (Estes 1974). Presumably, this sexual similarity is due to both sexes experiencing similar resource availability (fig. 6.2).

In some situations (e.g., wildebeest and plains bison) large herds feed so intensively in one area that they keep grasses clipped short like a lawn. Grasses respond to this "mowing" by ungulates and reshoot laterally. The resulting lawn is highly productive and provides quality grazing, but with keen competition from other herd members. The main advantage to herding has to do with predation, not improved forage, although grass "lawns" can be maintained in highly productive condition by large herds and hence benefit individual animals. The antipredator advantages of herd life are usually accompanied by a decrease in forage quality. Ungulates select their food from an array of plants that are not equally desirable. The "cafeteria" selections in any one area differ in quality and digestibility,

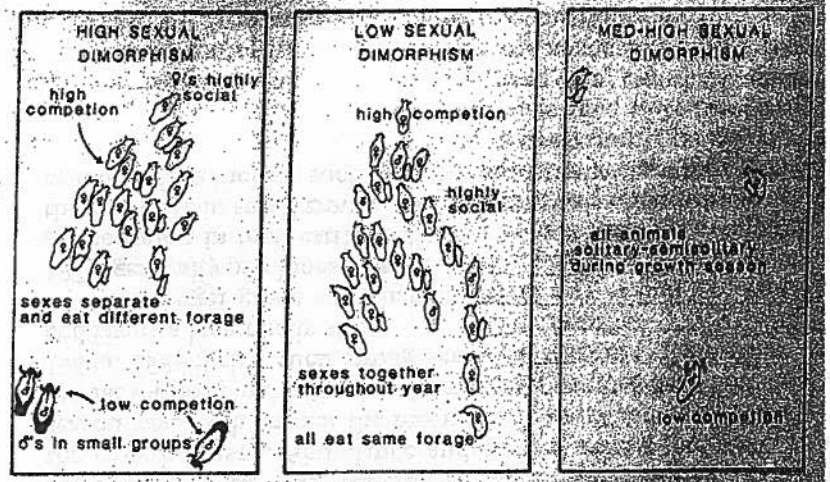

Fig. 6.2. Ethology and sexual dimorphism. Competition for resources is the accepted explanation for radical sexual dimorphism in certain ungulate species. In a polygamous social structure, there is a selective premium for large, powerful bulls; dietary resources become the main limit on their body size and social paraphernalia. If males and females live more solitary lives, as do moose, sexual dimorphism is modest. Sexual dimorphism is most pronounced when females live in herds and males live a solitary life or exist in small herds, as do bison.

and less choice vegetation normally dominates. Single animals can afford to take the "cream," but members of large herds must necessarily duplicate others' routes and feed on second-choice plants or plant parts.

American plains bison are flexible in their response to opportunities offered by different environments. Small bison herds are usually nonmigratory, with marked fidelity to their home range. On such ranges the sexes live apart for most of the year. On the Great Plains, where bison herds built to enormous numbers, the entire herd was migratory for most of the year and sexes remained in proximity if not in the same subgroups. This phenomenon can be seen today in caribou. Small herds of caribou, numbering in the hundreds, are local and move little, whereas the long-distance migratory herds generally number in the tens of thousands.

Thus we can look at sexual differences in social organs to learn something about the ecology and social behavior of extinct steppe bison. We know that sexual dimorphism is greatest among herd ungulates when adult males spend most of the growing season apart

from the herd, foraging in small groups or solitarily. Today's American male bison behave in this way. As bulls do not have to share resources with a large herd, they can select better-quality food, thus sustaining large body size.

Sexual dimorphism in body size of *B. priscus* was great, greater in fact than that of any other bison species (McDonald 1981). While the mature bulls had a gigantic skull with long robust horns, the females were very gracile horned, with a skull more like that of cattle. Also steppe bison cows did not have heavy protruding eye orbits like males. The extreme sexual dimorphism of the steppe bison (fig. 6.3) suggests that (1) bulls remained separate from cows throughout the growth season, at least, and (2) herds of steppe bison may not have been so large as bison herds on the Great Plains. The Beringian steppe landscape probably favored moderate-sized groups of bison and a class hierarchy in an "open" social system oriented toward frequent display to many individually unrecognized herd members.

Not only are male-to-female differences important in reconstructing social behavior, but so too are differences between adults and young. American plains bison differ from living European bison with regard to color of the young. The young of American bison (which normally live in large herds) are very light, contrasting with darker adults, while the young of European bison (a species that lives in small groups) are similar in color to their mothers: a medium monotone brown. This pattern conforms to the general rule that highly social species, living in open environments, generally have contrastingly colored young. This is true, for example, of baboons, wildebeest, reindeer, and others. Theoretically, the contrasting color gives the young special social distinction, protecting them from the full brunt of adult aggression. In large groups, individuals are often not known personally and must wear badges of rank, age, and sex.

Paleolithic art is uninformative on the color of steppe bison calves (fig. 6.4), and we have, as yet, no mummified ones. I would expect, based on other plains-adapted features we have been able to reconstruct, that young steppe bison were light colored, in contrast to the dark adults.

The size and shape of Blue Babe's horns can also tell us about steppe bison behavior. Clutton-Brock and Harvey (1976) have proposed an association between larger horns (fighting and display paraphernalia) and environments where bulls can accumulate more females. Since extant bison have much smaller horns than steppe bison, their reproductive behaviors are probably different as well. I have used morphological features of fossil Beringian steppe bison to reconstruct their fighting behavior (Guthrie 1980): (1) Wound damage on the frontals indicates the animals received sharp forceful blows. (2) Moderately developed shock-absorbant frontal sinuses also indicate the use of frontal concussion blows. (3) The complex oval pattern on the horns of adult bulls makes it experimentally difficult to articulate the horns simply and smoothly with those of an oppo-

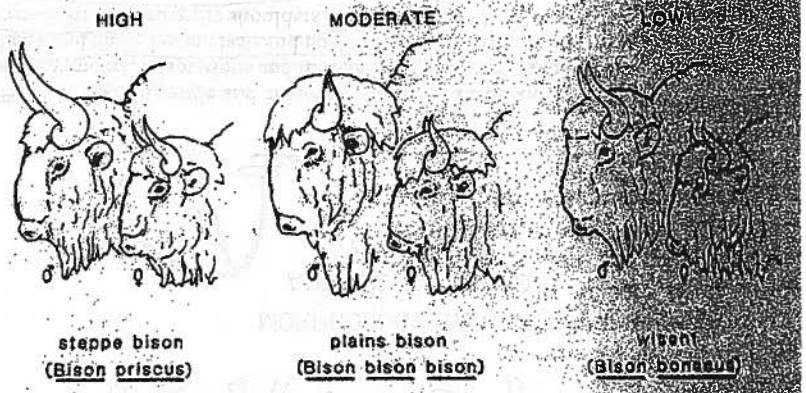

Fig. 6.3. Sexual dimorphism. Size and shape differences between sexes of plains ungulates are associated with the degree of separation of males and females throughout the year. Sexual dimorphism in skull size in steppe bison was extreme, suggesting that male and female steppe bison lived quite separately.

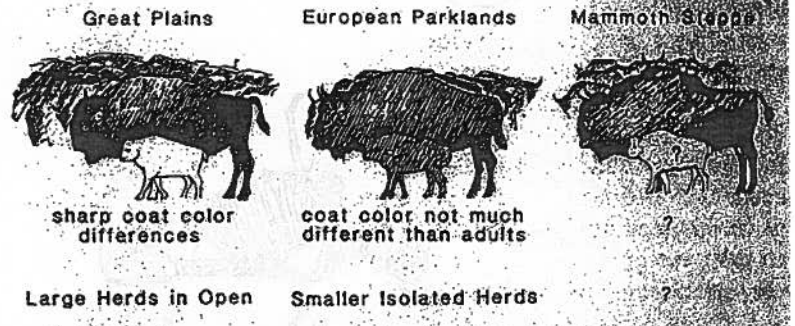

Fig. 6.4. Calf-adult coat color differences. The young of ungulates living in large herds on open plains are usually distinctly colored, for example, plains bison calves are light reddish in contrast to the much darker adults. European bison in less open situations have young that are almost the same shade as adults. The color of young steppe bison is unknown.

nent. (4) The rarity of broken horn tips in older males, compared with this occurrence in living bison, is striking. Most horn tips of older Beringian bison bulls are gracile and sharp. (5) Antitorsion fluting or louvering between horn sheath and core suggests substantial torsion in horn engagement during fighting. And (6) construction of thoracic suspension of the head points to an ability to exert great (lift) force upward.

In early bison the horns were deflected backward or outward, eye orbits were telescoped, and the frontal sinuses were expanded. As bison evolved, these trends continued to increase in an irregular fashion. The element that links these changes in skull and horn morphology and makes them intelligible is a shift in fighting—from a more cattlelike, pushing of foreheads to the sharp impact of forehead clashing (fig. 6.5).

Other ungulates have shifted to a clashing form of fighting, using the horn base as the contact surface. Sheep (*Ovis*) and goats (*Capra*) catch the leading edge of an opponent's horns in the V of the inner horn crotch. In African buffalo (*Syncerus*) and musk-oxen (*Ovibos*) a flattened horn bos evolved as a catching or butting plate. Unlike the above animals, bison use the frontal bone as a clashing platform.

Cattle engage their frontals and then push one another (Haféz 1975), while horns are interlocked. In the bison line this pushing or punching must have graded into violent butting and later into clashing. The horn cores, covered by a relatively thin horny sheath ending in a sharp tip, were adapted for "hooking" in the bovines. They were thus relatively fragile and susceptible to damage. The shift toward a more violent butting-clashing confrontation was apparently accompanied by a backward movement of the horns, moving them out of the way of the clashing plane.

Associated with the above changes, the frontal sinus in bison expanded to a large-domed pneumatic cavity separated from the brain encasement by an elaborate strut complex (fig. 6.6). This cavity extended into both horn cores which are also hollow. The double wall separated by struts seems to have served as a bumper—a device to disperse and dampen the opponent's blow away from the brain tissue (Schaffer and Reed 1972).

In an earlier study (Guthrie 1980), I concluded that steppe bison displayed more and fought less violently than living plains bison and that horn size was a significant aspect of that display. Unlike the horns of living bison, those of steppe bison continued to grow longer even into old age, more like those of wild mountain sheep. Steppe

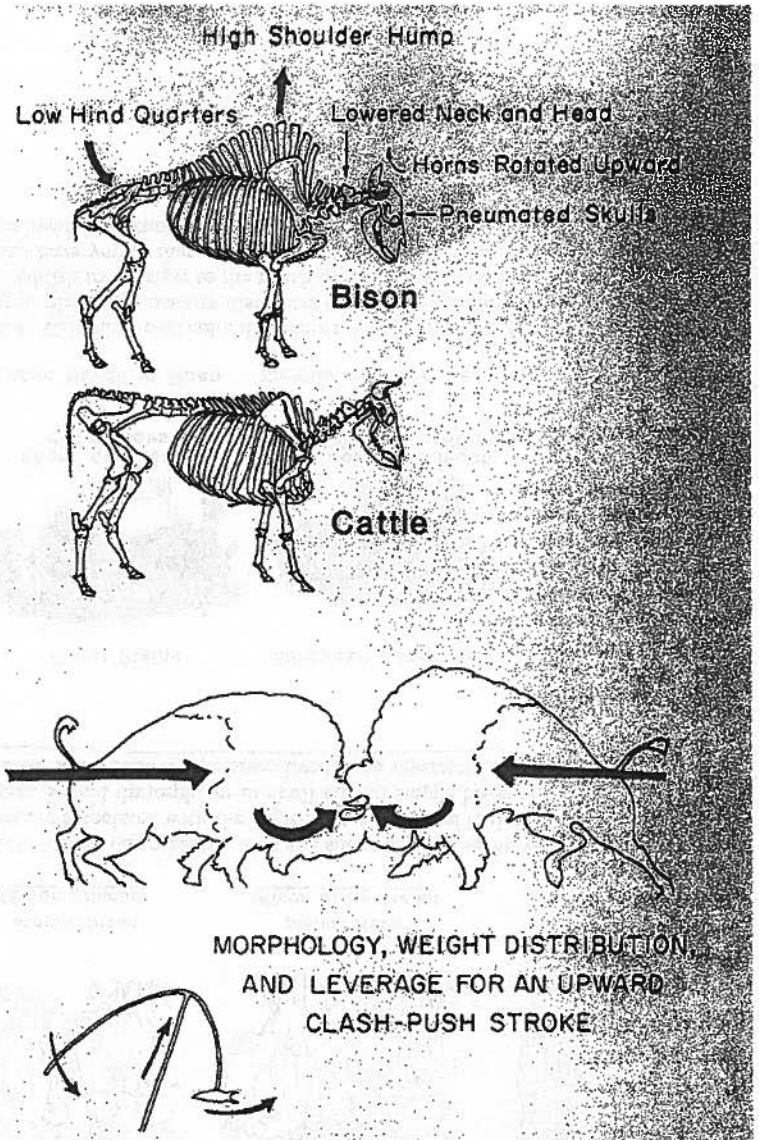

Fig. 6.5. Fighting style and anatomy. Bison and cattle are at opposite ends of bovine environmental adaptations and morphology. They fight in quite different ways: cattle hook and push; bison clash and push upward, lowering their hindquarters as a counterweight and using the shoulders as a fulcrum.

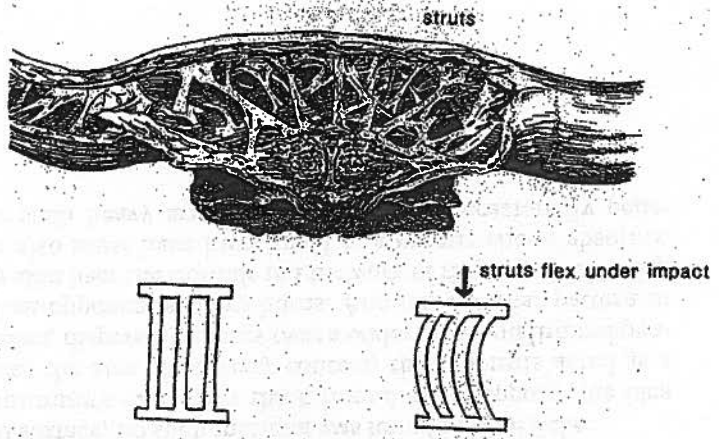

Fig. 6.6. Cranial shock absorbers. Bison fight with their heads, clashing frontals against frontals, in violent concussions which create a dangerous shock to the brain. Bison skulls have a structure that reduces this shock by smoothing the transmission wave and by carrying the blow away from the brain. An intricate network of struts separates the inner and outer walls of the skull. Though appearing to be rigid, these flex on impact, absorbing some of the peak of the shock wave. The above drawing is taken from a naturally broken fossil steppe bison skull from the Fairbanks area. The brain is small, lying behind the convoluted olfactory "chestnut-appearing" structures in the lower medial portion of the skull.

bison horns are oriented forward. Horns of American plains bison are shorter and point upward. The smaller hair bonnet and the more forward-oriented long sharp horns suggest that the steppe bison "must have engaged from a close distance, with the horns slightly occluded diagonally but most of the pressure carried on the frontals, each trying to lift upward" (Guthrie 1980: 60).

Soft tissue on the bison mummy supports information I collected from skeletons of other Beringian bison bulls which suggested that they fought frequently. Ubiquitous damage on the frontals and the antitorsion fluting (fig. 6.7) of the horn sheaths and cores suggest that Beringian bison engaged with considerable force (Guthrie 1980). However, the flattened-oval shape of the horn cross section and the frequency of sharp horn tips indicate a fighting mode unlike American plains bison.

Modern plains bison bulls run full speed toward an opponent, clashing heads, with contact primarily on the parietals. The horns of American plains bison are blunted and broomed, and the large

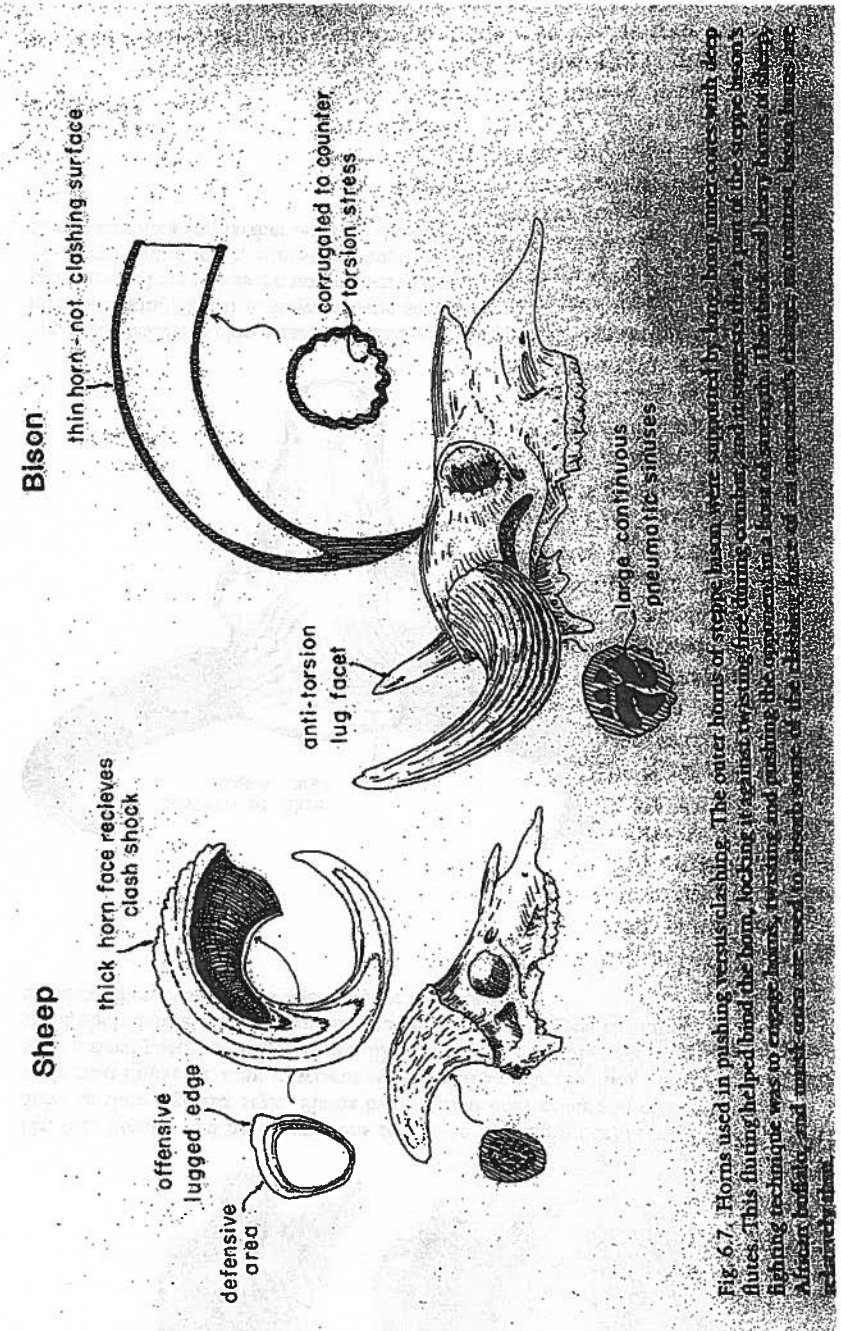

Fig. 6.7. Horns used in pushing versus clashing. The outer horns of steppe bison were apparently large, heavy, interlocked with deep flutes. This fluting helped bind the horn sheaths to the cores and strengthened the horns for clashing rather than pushing. The sharp tips of the steppe bison's horns were also more suitable for piercing than the blunted horns of the modern plains bison. The sheep's horn is shown for comparison. Sheep rams butt heads, and the thick horn face recieves the shock. The defensive area is the part of the horn that is presented to the opponent. The offensive lugged edge is used to gouge the opponent's flank.

bonnet of hair serves as a shock-absorbing cushion for the head-on clash, which is followed by a head-to-head pushing contest.

The basic Bovini threat posture is a high head with chin pulled down (Sinclair 1977). Basic fighting technique is a head-to-head pushing contest. Among the Bovini, American plains bison and African buffalo are unique in that they clash. The former uses a clash prior to the pushing contest and the latter just clashes, like sheep; the pushing phase has been eliminated (Sinclair 1977). From clues present on steppe bison fossils, both bones and mummies, we know that they clashed, probably as a prefix to a typical Bovini head-push fight. This behavior has ties to the living bison of the American Great Plains and not to European bison, which have a poorly defined clash at best (Flerov 1977).

The development of a full-blown, noninjurious head clash in American plains bison shifted emphasis from large horns to the upper forehead area (parietals) and led to the development of a padded-hair-bonnet clashing organ. Large horns of Pleistocene bison served to catch and hold an opponent while both pushed. The width of these sweeping horns essentially guaranteed protection from an aggressor slipping by to gore an opponent. By contrast, the short horns of plains bison allow an opponent to slip by, and wounds on the fore quarters after the rut are frequent (Petersburg 1973). I suggest that the forequarters of American plains bison have such a heavy coat of curly hair to act as a protective mantle.

The shock-absorbing hair bonnet (fig. 6.8) in American plains bison is more appropriate for concussion, whereas thick skin on the face of the Alaskan bison mummy acts as a protective shield against horn puncture (fig. 6.9). These traits are correlated with horn size and shape differences in the two species, but they are more a difference of degree than of kind. Although Blue Babe did have facial hair padding, it was not as well developed as that of plains bison; likewise, while plains bison have thick skin on the face (Petersburg 1973), it is not as thick as Blue Babe's. Beneath the facial skin of American bison is a thick layer of elastic connective tissue attached to the skull surface; no such material was found in Blue Babe.

The mummy's extremely thick frontal skin supports the idea that this was the area of primary contact; thick dermis acted as a shock absorber, dispersing energy over a wider area, and limited penetration of an opponent's sharp horns. Another peculiar pattern in Blue Babe's skin over the frontals is a network of ridges and folds (fig. 6.9). These also must have functioned as a unique shock absorber. Yet despite such heavy armor, some horn tips occasionally pene-

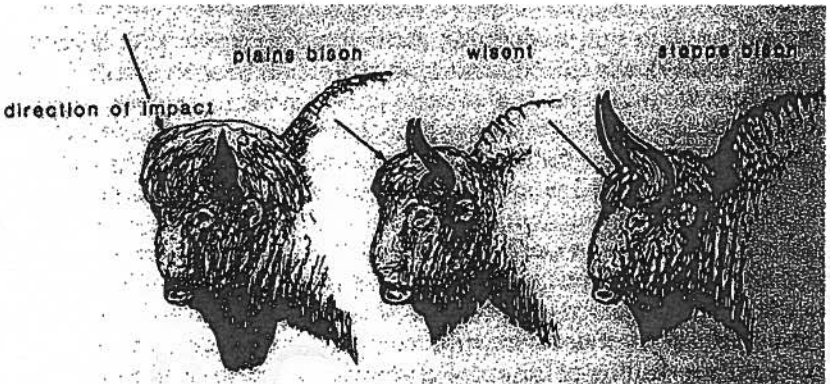

Fig. 6.8. Bonnet and horn variations related to fighting mode. Living bison species differ in their fighting style. Plains bison run at each other and clash head to head with great impact. European wisent are more like cattle, hooking horns and pushing from a fixed position. Steppe bison, like Blue Babe, probably used neither mode. Instead, their cranial anatomy and healed head wounds suggest clashing from a distance, then pushing and wrestling for advantage.

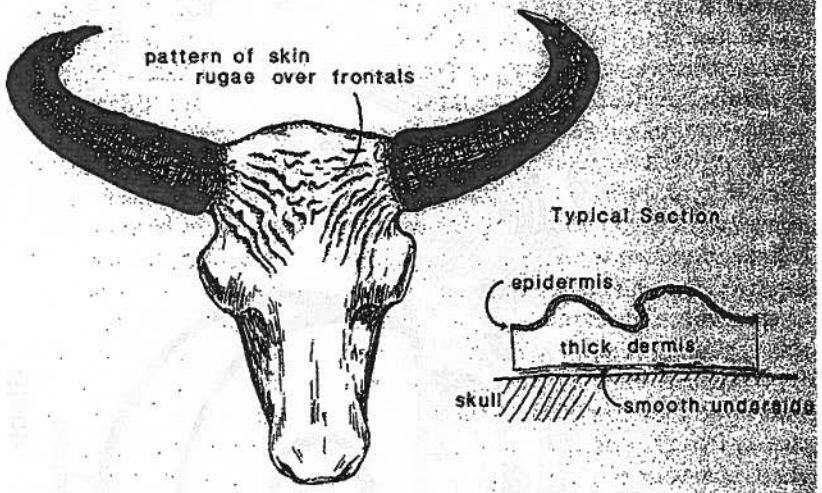

Fig. 6.9. Defensive skin armor over frontals. Blue Babe had strange folds in his thick forehead skin. (*Right*) A diagrammatic section of these folds shows the flat base on the dermis. These folds are not known to occur in living bison. American bison bulls (*B. bison*) have a thick, almost gelatinous, layer of connective tissue beneath the dermis in this area and farther out into the orbits and nasals.

trated the skin and underlying skull roof. We know this because many bison skulls from Pleistocene sediments near Fairbanks have puncture wounds with healed bone growth on the periphery. Fighting between Beringian bison probably began with a hard punch from a standing position, followed by a pushing contest in which each bull tried to reach his opponent's most vulnerable spots with his sharp horns.

In the course of working with Blue Babe and other steppe bison fossils I have developed what I believe is a significant new insight about antler and horn use; this new theory applies not only to steppe bison but to the majority of antlered and horned ungulates. Our current understanding of horn and antler use has developed from models first proposed by Walther (1966) and Geist (1966), which seem fundamentally correct. Walther and Geist focused on the ritualized behavior that occurs prior to fighting, tracking through comparative ethology, and the evolutionary origins and forms of horn and antler displays. This emphasis on ritualization and displays influences their models of actual combat activity by deemphasizing its bloody nature and the damage-producing design of antler and horn weaponry.

Walther and Geist proposed that early ungulate groups had stiletto horns and antlers and mainly attacked the opponent's flanks, while standing facing opposite directions. The goal of fighting among these ungulates was apparently inflicting lethal abdominal punctures or debilitating damage of locomotor muscles. From this early stage, ungulates began to limit injury by catching and holding an opponent's horns with their own, preventing access to more vulnerable body parts. Horns and antlers took on a more defensive design: lugs, hooks, and forks developed to more easily lock onto the other's offensive weaponry. Geist (1966) proposed that the long arching hook of a bison's horn is one of the first steps in this stage; the shape evolved to hook an opponent as it tried to get by the defensively padded head.

Once the level of defense reaches the point where rivals can seldom get by the more elaborately shielding horns or antlers to strike, fighting takes on a new form. Geist, Walther, and others argued that very social ungulates, instead of attempting to injure an opponent, first use ritualized displays to convince a rival of its lower rank; then, if equally matched, noninjurious but sometimes painful tests of skill and strength ensue. These formalized fights involve pushing or wrestling contests with locked horns or antlers; other phylogenetic lines have evolved a head-clashing technique. But all these fights accomplish the same thing: nondamaging combat which settles hierarchy disputes. Until recently this has also be my view, but now I think the emphasis on conventionalized comb formality is somewhat askew.

The skew is consistent with the pervading mood of the la 1960s when our understanding of ritualized behavior in etholo first blossomed. Social signals, or expressive behaviors, as Walth called them, were seen as a means of ritualizing or conventionali ing agonistic behavior. This new awareness of formalized conve tions for aggression largely supplanted the previous image of "natu red in tooth and claw." Although theoretically independent from this ethological understanding emerged concurrently with the no discredited, but then popular, "epidectic display" (Wynne-Edwar 1962; proposal that many behaviors consisted of a rechanneling violent, individually oriented competition toward ritualized resol tion, for the best interests of the group). It is not too farfetched al to see ethological thinking of that time in the context of the cou terculture peace movement in the United States. Remember, ecol gists and ethologists (such as Paul Erhlich and Desmond Morr played a prominent role in the newly developing generational Zeitg ist.

Whatever its exact history, the trend of the time was to env sion social evolution as generally culminating in noninjurious ago istic forms. We saw the horn and antler structures of more soci ungulate species as devices to hold an opponent, thus convertin potentially deadly fights into noninjurious tests of strength. Evol tion had transferred the spearheads of early horns and antlers into multitude of shielding shapes that were now used in ritualiz dances of aggression and dominance.

I realize now that the spearheads are still there, mounted the shield itself. And they are there because they are in active use propose that the horns and antlers of most social species consist two main portions: a defensive apparatus, as defined by Geist (196 and other structures specifically formed to breach this same d fense—to inflict as much damage as possible given the effective d fenses. The offensive aspects of horn and antler form are structur to injure a rival by reaching (1) *through*, such as with the oryx's lon sharp horns, (2) *under*, for example, with the long, upward-hookin brow and bez tines of the wapiti, (3) *over*, such as with the hig upward-reaching antlers of reindeer and caribou, and (4) *around*, in the widely hooked horns of steppe bison.

During my sabbatical year in Africa, I watched a fighting gem bok (*Oryx*) reach through the horns of a rival and thrust his lon rapiers with total energy, obviously intent on skewering the oth

male, who responded with (sometimes incompletely successful) parries. I examined freshly shot older impala males, just after rut, with deep gouges in their head and neck, their ears in fringes from violent tears. Living in Alaska, I have watched dozens of caribou rutting battles, both in the flesh and on film; these are not just formalized pushing battles but are in deadly earnest. Those long beams reach over and catch an opponent's strained shoulder and neck muscles between inwardly pointing tines and, like giant claws, dig and scratch, hair tufts flying, with the full weight of the body thrown into every gouge. I think the majority of horned and antlered ungulates that lock head to head have in their armory specially adapted offensive structures used to injure their rivals by breaching his defenses.

This behavior and horn structure I had watched in African antelope and saw afresh in Alaskan ungulates caused me to rethink the image of fighting behavior I had reconstructed for steppe bison. Two important pieces of evidence from Alaskan fossil steppe bison show that the male's long, widely arching, hooked horn had an offensive role—to cause injury. One was the frequent skull damage seen in Pleistocene bison bulls from a sharp-pointed "instrument," undoubtedly another bull's horns, and the second was the unusually thick neck skin noted in Blue Babe, which dispersed the pressure of the pointed horn tip and thus decreased its damage. Steppe bison horns were not horns for clean wrestling, but were used to protect the animal while at the same time allowing him to reach around the opponent's defenses and stab the dickens out of him.

I propose that steppe bison horns work this way: The broad forward-facing cross section of the horn's trunk, discussed previously, acted as a defensive blocking device, engaging the corresponding portion of an opponent's horns, above or below his horns, or in an offset rotation with one above and one below (fig. 6.10). The slightly flattened trunk of the horn reached well out, away from the skull, and would have added leverage to keep an opponent from swinging around to the side. The rough annuli on the forward surface probably assisted the defensive holding process. Occasionally, the broad, telescoped orbits of these bison may also have helped hold an opponent's head from rotating. The occiput of steppe bison is especially broad from left to right (fig. 6.10), providing more leverage to hold the skull from a lateral twist. The bison's fighting strategy must have been to keep parallel to his own body the sharp forward-pointing horntips of an opponent. As long as the animals were standing horn to horn on a line, the match was a "draw," that is, the fight was stalemated. In a serious fight, one bison would try to push the

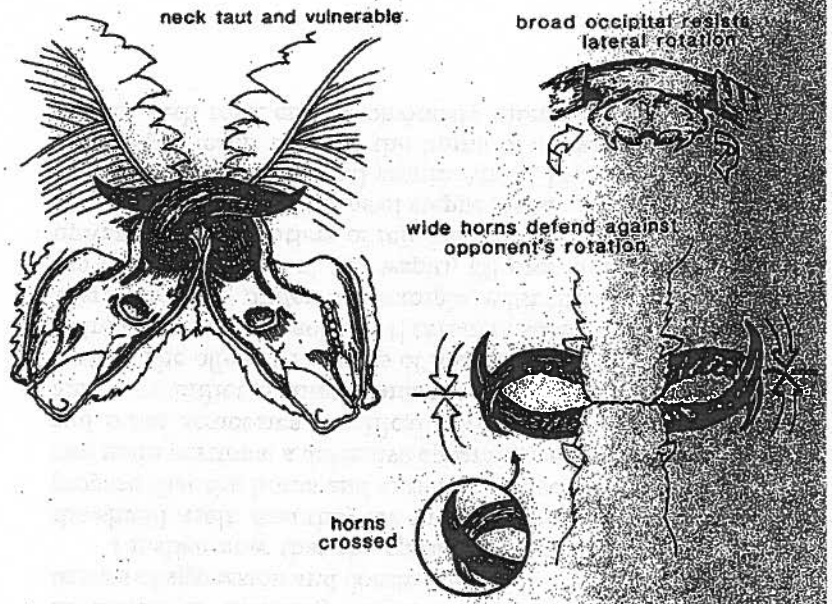

Fig. 6.10. Pattern of horn engagement. The horn and head structures of Blue Babe and other steppe bison show that their horns engaged well away from the face. This holding structure would have added leverage to keep an opponent from swinging around to the side.

other backward faster than it could retreat and still keep its body in alignment. The greater strength of one bison would thus cause the body of the other to rotate while their heads remained locked and held rigid. This would have protected the body of the advancing bison, while the twisted neck and shoulders of the retreating bison would be within range of the advancing bison's sharp horns (fig. 6.11).

The inward curve of horn tips found among many fossil specimens can be better explained by this strategy than as a hooking device to keep opponents from slipping by. An inward-pointing hook decreases the angle an opponent's body must rotate before horns can be dug into his neck. When bison had their heads lowered and horns locked in place, the taut neck and shoulder muscles would not be far from the inwardly pointing horn tips (fig. 6.10).

When two bulls with the same-sized and -shaped horns twist symmetrically, their horns contact each other's neck at the same time and to the same degree. If one animal has a significantly longer outward reach of the horn trunk, or a longer forward-pointing horn

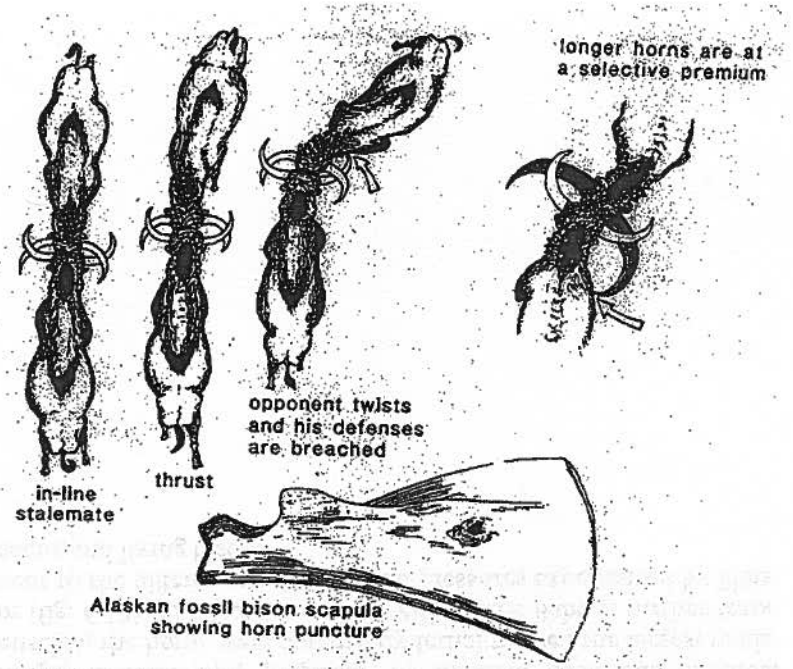

Fig. 6.11. Horn shape and defense breaching strategy. The widely arching sharp horns of steppe bison were curved so that they could reach through an opponent's defense and puncture the opponent's neck or shoulder. The scapula shown, UA-V-54803, was punctured all the way through by a horn stab and has healed.

tip, it will cause proportionally greater damage (fig. 6.11). This is probably one of the selective forces that created the long and sharply pointed hooked horns in steppe bison.

I propose that evidence of horn shape, preserved skeletal wounds on fossil steppe bison skulls, and Blue Babe's thick protective head and neck skin suggest that the hooked shape of steppe bison horns functioned as a breaching device. Once locked with the opponent's horns, this form allowed the stronger bison with the larger horns to ultimately breach or circumvent his opponent's holding defenses by reaching around and stabbing into his body.

For steppe bison the initial display of social stature would have been concentrated more toward the anterior body than it is now in European bison. The length of the tail characterizes this difference: Blue Babe's tail is only half the length of the European bison's, both living (*B. bonasus*) and extinct (judging from cave art). A long tail can be used to express emotion if the opponent is watching the en-

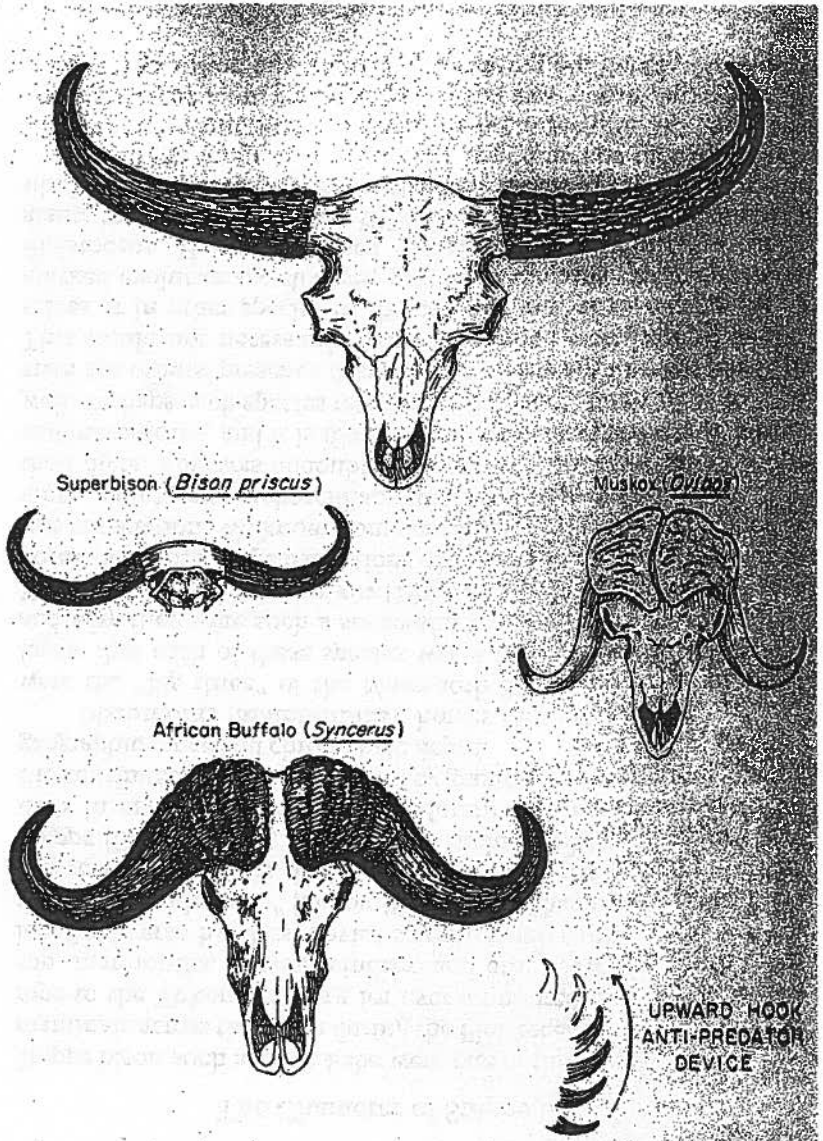

Fig. 6.12. Steppe bison horns as an antipredator device. African buffalo and musk oxen have a sharp hook on their horns which seems to be used primarily against predators and has little or no role in interactions within the species, unlike bison.

tire body. Among the European *B. priscus*, the height of the neural spines, hence hump, was larger and extended more posteriorly than that in *B. bison* (Poplin 1984). Also, this posterior hump had contrastingly colored hair (Geist 1971b; Guthrie 1980). As I showed in the last chapter, Alaskan steppe bison were similar to European Pleistocene bison in hump shape. Likewise, the beard was relatively short, but the ventral mane running down onto the sternum was moderately well developed. Yet display paraphernalia of steppe bison in Paleolithic art are not as cephalized as in plains bison. The latter has an enlarged head bonnet and elongated beard. Foreleg pantaloons also add mass to the anterior end of plains bison, *B. bison bison*, as part of their exceptionally developed anterior display. Plains bison swing these pantaloons in their threat displays, exaggerating the movements of the forelegs (Petersburg 1973; Lott 1974).

Compared to living plains bison, the focus of display among steppe bison was subtly more posterior. The darker peripheral coloration of Alaskan steppe bison would have focused an opponent's attention toward the center of the body, but perhaps farther forward than with Pleistocene and Holocene European bison. However, unlike all living bison, Pleistocene bison had massive horns, which no doubt formed a central part of their social display.

Unlike Holocene bison, which had no predator larger than wolves, steppe bison faced lions (*Panthera leo*) and other large predators. Their horns, therefore, were not only a social organ, but also a major antipredator defense. Like musk-oxen (*Ovibos moschatus*) and African buffalo (*Syncerus cafer*), steppe bison had horns with sharply hooked tips, propelled by massive neck and shoulder muscles; the horns were potentially lethal to even the largest predator (fig. 6.12). The fact that a lion killed Blue Babe is further testament to the different environmental pressures experienced by Pleistocene and living bison.

7

STEPPE BISON ECOLOGY AND PHYLOGENY

The Character of Steppe Bison

Steppe bison such as Blue Babe were one of the most common large mammals across the north during the Pleistocene. From western Europe to the Yukon Territory, for over a hundred thousand years, bison, mammoths, horses, reindeer, and others occupied a blend of locally diverse habitats. Soviet scientists refer to these animals as the "mammoth fauna" (Flerov 1977; Vereshchagin 1959; Sher 1971). I have expanded this designation and used the name *Mammoth Steppe* (Guthrie 1980, 1982, 1985), including both plants and animals in my discussions. I think *Mammoth Steppe* fairly describes the continued presence of these key grazing species over a truly vast geographic range and chronologic depth.

Mammoths (*Mammuthus*), horses (*Equus*), and bison (*Bison*) were the "big three" of the Mammoth Steppe (Guthrie 1982). We know that each of these species was a grazing specialist, but how and why they were such a successful team is not completely clear. Vereshchagin and Baryshnikov (1982) and I (Guthrie 1982) have proposed theoretical specializations that would have accommodated this association. We know from contemporary studies that large herbivines, equids, and proboscidians tolerate different degrees of fiber in their diets. This was undoubtedly true of Pleistocene bison, horses, and mammoths, and it is likely that other specializations existed as well. Perhaps each species retained specializations that let them tolerate the others' presence despite changes with time and geography. This would not necessarily exclude evolutionary change in themselves or in other species in the community. If fact, all underwent marked evolutionary changes, particularly in the latter part of the Pleistocene. Horses increased and then diminished in size, from giants to petite ponies (Sher 1971). Mammoths also changed, particularly with regard to cheek-tooth complexity (Sher 1971), to the ex-

tent that some paleontologists have wanted to give the later mammoth separate generic stature. Bison changed too. Bison fossils record changes in horn core size and shape and subsequent cranial effects (Guthrie 1980).

The large-horned steppe bison found in western Beringia (Flerov 1977, 1979; Sher 1971; Vereshchagin and Baryshnikov 1982) and eastern Beringia (Guthrie 1970, 1980) are interpreted as chronological representatives of the same species. McDonald (1981) separated Beringian fossil bison into two phylogenetically separate species and proposed that these alternated in appearance during interglacials and glacials throughout the Pleistocene. But this seems to be a misinterpretation of the data (Walker and Boyce 1984). Rather, Beringian fossil bison seem to be one variable species; such variation within a species is comparable to that found today among reindeer-caribou (*Rangifer tarandus*). Morphological differences between northern steppe bison and bison farther south, as well as changes in steppe bison over time, probably represent adaptive tuning within the context of the far north and events there. At least this would be a logical start in accounting for changes within *Bison priscus*—its similarity to and differences from other bison. I use these different specific names for bison groups, knowing that in reality they are all closely related and are better thought of as one species complex.

We know that during much of the last hundred thousand years Beringia has been herbaceous steppe (Hopkins et al. 1982). Such conditions would have favored grazing species. During most of this time we can document the presence of bison in Alaska and, in fact, know that bison were the dominant large mammal (Guthrie 1968). A comparison of equids, proboscidians, and bison remains from central Alaska showed that bison were overall the most numerus and especially predominated in the uplands (Guthrie 1968). My observations since that time have supported those earlier studies. Among the large numbers of Pleistocene bones collected at Pearl Creek, where Blue Babe was found, over 80% are from bison. These include stratigraphically dated bison bones from the interstadial and undated fossils emerging from all other parts of the section.

In Alaska, dozens of male steppe bison skulls have been collected which still have the entire horny sheath attached to the horn cores. At least the proximal annuli are very marked, unlike many living bison, and some sense can be gained as to life expectancy and perhaps maximum life span. I have plotted age against length around the outside horn curve (fig. 7.1). Although the sample is too small for a precise look at survivorship, we can conclude that steppe bison had a life expectancy similar to that of American plains bison.

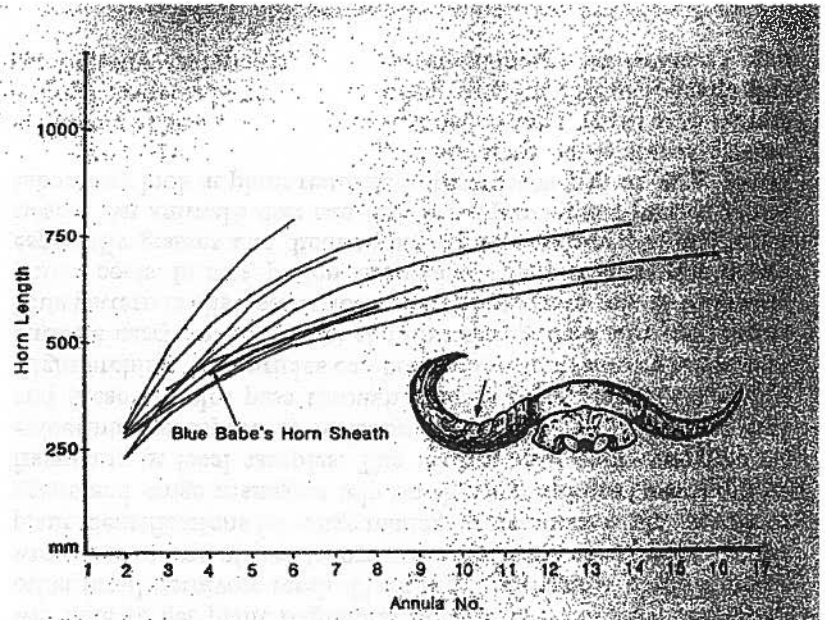

Fig. 7.1. Cumulative length of male Alaskan steppe bison horns. Bison horns grow only during the summer, leaving an annulus, a construction between the segments of summer growth. Among bovids the first summer's segment is often worn away, so this was not measured. The cumulative lengths of horns from eight Alaskan (only) steppe bison are shown for comparison with Blue Babe. The first three annular rings are not visible in Blue Babe's horns, but the plots of later annuli show its growth rate is in the lower range of this sample. These plots show that maximum horn length is reached at 8 or 9 years (Blue Babe's age). Variations in individual horn lengths seem to depend mainly on growth rate of the early segments.

Diet of Steppe Bison

We can determine what Blue Babe ate, or more generally, what steppe bison ate, by looking at diets of extant bison and examining the anatomy of fossil bison. Extant bison are eclectic foragers. Yet despite this apparent versatility, bison are actually adaptive specialists and prefer low-growth herbs, particularly grasses (Guthrie 1980, 1982). I think this was also true for steppe bison (*Bison priscus*). Vereshchagin and Baryshnikov (1982) have argued on the basis of hypsodont molars and cochleariform incisors that the steppe bison was a grazer. Gut contents of a steppe bison mummy from the Siberian Kolyma Basin were analyzed, along with pollen from surrounding sediments, by Korobkov and Filin (1982). All plant macrofossils they found in the gut were grasses, and pollen showed a predominance of Graml-

nae, Compositae, Chenopodiaceae, and Cruciferae. Anatomically and physiologically modern bison are grazing specialists (Hofman and Stewart 1972). They consume some forbs and woody browse, but browse seems to be their lowest choice (Soper 1941). Grass comprises 80% to 90% of the diet of American plains bison studied under natural conditions (Meagher 1971, Peden et al. 1974; Hansen 1976; Hubbard and Hansen 1976; Hansen, Clark, and Lawhorn 1977; Olsen and Hansen 1977; Vavra and Sneva 1978; Van Vuren 1984). However, at the margins of their range or on poor range they can subsist on other plants. For example, bison in Wood Buffalo Park rely on sedges. European bison now confined to atypical dense woodland habitats consume a lot of browse (Borowski, Kra, and Milkowski 1967).

Bison, which were introduced to Alaska in the 1930s, provide an interesting sample. There are several populations; all are confined to windswept riverine areas within or adjacent to mountain passes where wind keeps snow cover to a minimum depth, allowing the bison to reach winter food. Campbell and Hinkes (1983) found that the *Fairwell* bison eat grasses and sedges through the winter (browse contributed to just over 1% of the bison's diet). Bison in the *Delta herd* take some browse and *Equisetum* but mainly eat riverbar grasses and farmer's barley (Gipson and McKendrick 1981). Two smaller herds at *Chitna* and the *Copper River* are on very poor range (Miquelle 1985). There are about fifty bison in the Chitna herd, and they consume considerable summer browse, about 50% willow and 50% graminoids (based on five fecal droppings that were analyzed). The winter diet was about 75% browse and the rest graminoids (from a sample of four droppings).

I use this dietary information (see table 1) from living northern bison to address two issues. The first is an argument used by some ecologists—that if bison can survive today in Alaskan boreal forests on browse, their presence in the fossil record cannot be taken to indicate a steppe environment (Colinvaux and West 1984). However, steppe bison are only part of a large community of grazers. The inability of reintroduced bison to spread from small special habitats argues, if anything, against their adaptive ability to cope in the north without widespread graminoids. I return to this point later in the context of arguments against the Mammoth Steppe.

During the time I've spent thinking about Blue Babe and writing this book, I've also been working on several other projects which turned out to be relevant to the Blue Babe study. In one of these I investigated the diets of Mammoth Steppe fauna by picking small plant fragments from the infundibula of teeth in fossil skulls (fig.

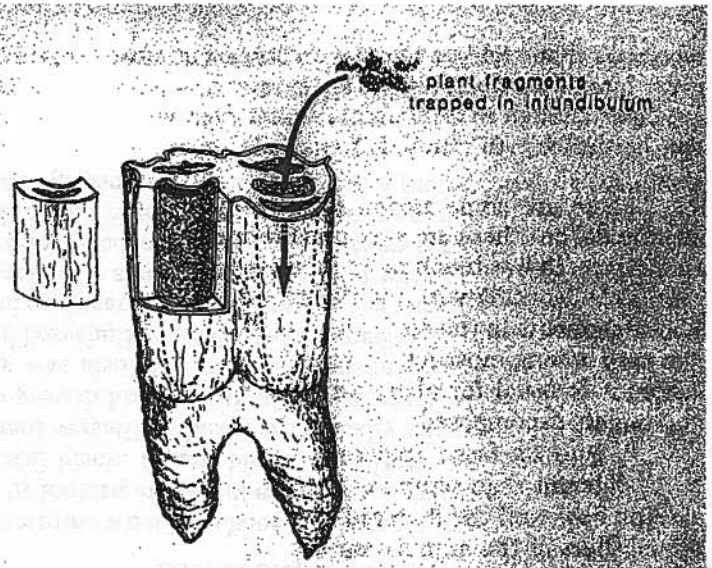

Fig. 7.2. Plant fragments compacted in molar infundibula. Histological structure allows even tiny pieces to be identified to plant group. Decay is so limited in frozen soils that plant fragments taken from Pleistocene-aged Alaskan fossil teeth can be identified.

7.2). In part this work was a response to proposals that the dominant Mammoth Steppe animals—bison, horses, mammoths, saigas, and others—were not grazers at all but simply ate sedges or willow as moose, caribou, and musk-oxen do today. Fossil steppe bison skulls were especially numerous from the Fairbanks mining district, and I was able to get plant fragments from these bison as well as from other fossil herbivore teeth. Plant fragments taken from the molars were sent to one of two laboratories that now do most histological plant identifications for range managers and wildlife biologists. Biologists and range managers rely on these two labs to identify plant fragments in fecal samples. The waxy cuticles covering the plant epidermis are especially resistant to digestive enzymes and acids, and these cuticles pass through the gut undamaged. Except for a slight etching, the cuticles can be readily identified in the lab. Plant cuticles carry an imprint of the underlying epidermal cell pattern. This pattern is characteristic of each plant group, even more so than pollen coats. In fact, pollen is undiagnostic for many plant groups, especially grasses and dicot forbs, whereas cuticles are quite diagnostic. An animal's diet can thus be approximated by this kind of laboratory look at plant remains in their feces. This approach is less

laborious than trying to follow an animal at close range, observing every bite; often observations are simply impossible. It is difficult to get close enough to wild animals, and even when rather tame they can be difficult to study. For example, many deer feed mainly at night.

There are some frozen feces of Alaskan Pleistocenen large mammals, but these are very uncommon. Studying diets via plants in fossil teeth was much more promising, and I was especially fortunate to be working with fossils preserved in frozen ground because plant fragments in the teeth were usually well preserved. This is not the case among most fossils from temperate and tropical climates, where it is usual for plant parts trapped between the cusps to be thoroughly decomposed.

Relying on fossil epidermal fragments in teeth was, however, quite different than sampling feces; I needed a modern analogue to tell me how well the material I took from fossil teeth reflected the actual diets of the animals on the Mammoth Steppe. In 1985–86, while on sabbatical in Africa, I was able to collect tooth samples from a number of large mammal skulls, including animals that had died naturally and ones that had been culled by wildlife managers.

I sampled strict grazers, like the Alcelaphines (wildebeest, blesbok, etc.), mixed feeders (for example, springbok and impala), and browsers (such as eland and kudu). Fortunately, I was able to sample in areas where the diets of these species and the plant fragments found in the molars had already been studied. Correspondence between the natural diets of these species and the plant fragments found in the molars was almost complete. This information from African analogues allows us to say that the plants we find in the teeth of Pleistocene large mammal fossils probably indicate their usual diets. I report on this study in greater detail elsewhere, but the general conclusion is that grass fragments were the predominant food found in the teeth of steppe bison, horses, and woolly rhinos. Data summarized in table 7.1, based on plant material taken from 44 steppe bison, are especially relevant to questions about Blue Babe's diet.

Histological studies of bison known to be eating a grass diet show that their feces contain only 80–90% grass fragments. There are two reasons for this. First, a big-bite grazer is not selective enough to eat only grass; dicot forbs and moss grow in between grass stems and are ingested with the grass. Although more toxic than grass parts, small amounts of these dicot forbs from diverse species actually cause little metabolic harm. In fact, small doses of them can add greatly to overall nutrition because dicots normally are

Table 7.1 Plant Cuticle Fragments Taken from First Molar of 44 Fossil Steppe Bison from Interior Alaska

Gramindoids	Number	Percentage
Agropryon	224	5
Bromus	153	3
Carex	7	—
Poa	480	11
Glume	107	2
Unidentified grass	2540	58
		80%
Dicot forbs		
Dicot seed	335	8
Dicot stem	68	2
		10%
Woody plants		
Wood	124	3
Bark	200	4
Vaccinium	17	—
		7%
Cryptogams		
Moss	123	3
		3%

higher in protein than are grasses, which is why dicots are so well protected with pharmacologically active defense compounds. Second, woody plants such as willows and some other shrubs can be quite digestible, even for grazers, if they are eaten in the spring. These shrubs' new growth tissue is fairly high in protein and low in toxic defense compounds.

A second dietary issue is rate and pattern of toothwear. Bison vary tremendously from area to area and through time in the rate at which they wear their teeth (Reher 1974, 1977; Frison and Reher 1970; Haynes 1984). The lower M1 crown height (enamel height of the metaconid) has been chosen to quantify differences in wear. It is the first permanent cheek tooth to erupt and thus wears out first, giving the most dramatic index of tooth wear.

Frison and Reher (1970) calculated wear rate for Holocene bison from the late Pleistocene Vore Site to be 3.5–3.8 mm per year. They point out that tooth wear rate changes with geological time among plains bison. Haynes (1984), however, observed that plains bison teeth always wear faster than those of extant bison in Wood Buffalo

National Park located at the border of Alberta and the Northwest Territories.

Haynes found Wood Buffalo Park bison have unusually low rates of tooth wear, almost half that of plains bison (Haynes 1984). The northern Canadian bison averaged 1.7 mm per year of enamel attrition on the lower M1, using the same measurement of metaconid height as Frison and Reher did. Additionally, the occlusal surface of their teeth is different. It wears in a deeply furrowed pattern, creating a "steepling" effect. Most young bovines have this pattern, but with age it is smoothed into low ridges. This steepling is characteristic of an unabrasive diet and is common among browsers such as moose (*Alces*), which eat vegetation that is very low in phytoliths.

Haynes (1984) attributes this pattern and slow rate of tooth wear to the diet of the Wood Buffalo National Park animals, which consists mainly of sedges growing there in dry pans of Pleistocene lake beds. Unlike grasses, sedges have less biomass in opaline phytoliths. These bison therefore consume fewer abrasive particles per volume of forage. Haynes proposed that amounts of phytoliths in the diet and the amount of dust on leaf surfaces are the main factors in tooth wear. The differences between the teeth of bison Haynes studied and those of the Great Plains bison offer the opportunity to assess teeth of fossil bison in light of these ecological differences.

There has been considerable controversy over the nature of Pleistocene vegetation in Beringia (which I discuss in detail in chapter 9). Several botanists (Cwynar and Ritchie 1980; Colinvaux 1980) have argued that Beringian vegetation was more alpinelike mesic tundra, not very different from today's high-arctic tundras. These present-day tundras are dominated by sedges with few grasses, and the grasses that do grow there tend to be more mesic adapted. If Beringian vegetation was more tundralike, one would expect fossil Alaskan bison, particularly those living during the interstadials when conditions were even more mesic, to be mainly sedge eaters and would show tooth wear rates and patterns similar to those studied by Haynes.

We can figure how rapidly Blue Babe was wearing his teeth. The metaconid height was 16.2 mm. Haynes uses 41.71 mm as the crown height for a newly erupted lower M1 in a 3-year-old animal. Assuming Blue Babe was 8 years old at death, we can calculate rate of tooth wear to be 5.1 mm per year. This rate is much more rapid than Haynes found among his Canadian bison; in fact it is among the more rapid rates of tooth wear observed in bison anywhere. Reher (1974) calculated that the average enamel height of an 8.5-year-old

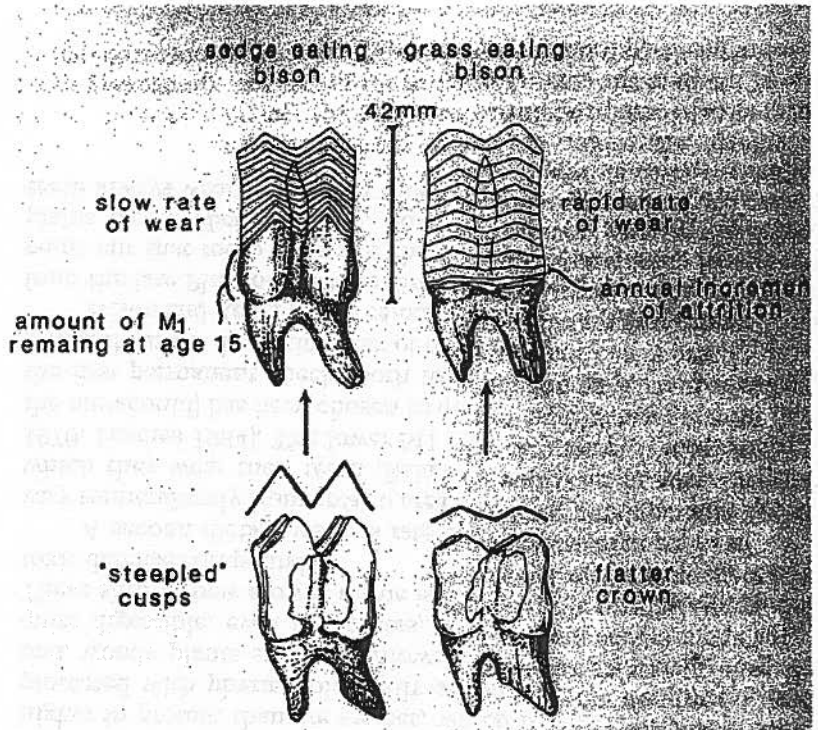

Fig. 7.3. Bison diets as indicated by tooth wear. Teeth are a rough indicator of diet. Sedge-eating bison in Wood Buffalo Park have peculiar teeth; they wear down at less than half the normal rate and show a pattern of high steepled cusps like teeth of a browser. Steppe bison teeth are worn more like those of grass-eating bison on the Great Plains.

bison, at the 10,000-year-old Casper Site in Wyoming where the tooth wear rate was considered rapid, to be 20.5 mm (in contrast to the 16.2 mm of Blue Babe).

The wear pattern on the mummy's cheek-tooth occlusal surface is more similar to that of living plains bison and quite unlike that of the Wood Buffalo Park bison (fig. 7.3). This suggests Blue Babe's diet was more like that of open plains bison, which are obligate grazers.

Age tables of Pleistocene Alaskan bison made by Skinner and Kaisen (1947) on the basis of mandibular tooth wear clearly show wear classes and attritional survivorship curves similar to those from plains bison and dramatically unlike the sedge-eating Wood Buffalo Park bison. From a sample of 1,322 individual Alaskan Pleis-

tocene bison, Skinner and Kaisen showed that the majority, that is, those dying in the senility mode of the curve, had almost exhausted or had exhausted the entire crown of M1. In their sample, 14–16 years represents a very old animal (Skinner and Kaisen 1947), judged by horn sheath annuli; this corresponds well with the rate of tooth wear in Blue Babe (8 years for half-worn M1). Skinner and Kaisen's first age-class (S-4) identified an extreme degree of crown wear with an almost completely worn M1. This age class contained more individuals than any other (40% of the 1,322 mandibles).

Examining the same hundreds of mandibles studied by Skinner and Kaisen, I also found flatter patterns of tooth wear than those Haynes observed among his nongrazing bison; rather, the steppe bison molars were similar to those of Blue Babe and Holocene Great Plains bison. I did not find teeth with extreme furrowing or steepling characteristic of the Wood Buffalo Park bison. These data suggest a grassy arid habitat in Beringia.

In addition to studying bison cheek teeth to determine patterns and rates of wear, the shape and size of the nipping incisors and the premaxillary plate against which they "occlude" can tell us something about steppe bison ecology. There are considerable differences in these characters among different bison groups. Like cattle, European bison have narrow premaxillary widths and American plains bison have the broadest, while steppe bison have intermediate widths. The question is why.

Generally speaking, grazers have very broad incisor batteries and premaxillary widths, and those of browsers are quite narrow. Actually, the story behind these differences is that selective feeders must have a more refined "forcep" because they choose to eat very specific foliage, high in energy and nutrients, but often adjacent to other plants or plant parts which are to be avoided because of their antiherbivory defenses. Some grazers are also quite selective, like roan and sable antelopes (*Hippotragus*); these have pointed snouts and comparatively narrow premaxillary widths. So only certain kinds of grazers have these traits exaggerated. When one examines grazers more carefully, the anatomically wide nippers are the ones that graze on a sward of shortgrasses. More important, these species are large herd animals which often regraze the same area several times during the same growth season. Many grasses are adapted to this kind of repeated grazing and respond by shifting away from a tall-growth form and sexual reproduction to a more prostrate growth form and vegetative reproduction by tillers. This low-growth vegetation makes grazing not only difficult for a large grazer but reduces the "take" of each bite. In response, the "lawn grazers" have expanded the width of their biting apparatus—the premaxillary plate and incisor battery—not to be less selective but to increase the volume intake of each bite such that these regrazed lawn growth forms can be exploited. This is not to say that wildebeest or plains bison always or regularly needed this broad nipper, just that they have met with those requirements sufficiently frequently in the past to be able to exploit and survive those situations when they occur.

Whatever the character of the Mammoth Steppe rangeland across northern Eurasia, the mammoth fauna probably never were so numerous that they resorted to lawn-forming kinds of grazing behavior. This is not true of American plains bison. We know from early records that herds of millions of bison did regraze. Likewise, the kinds of grasses growing on the shortgrass plains were adapted to lawn formation. Some of the grasses, like the ones eaten by wildebeest in Africa, are cultivated today as commercial lawn species because these grasses are already adapted to "mowing."

Although the premaxillary and incisor width of Blue Babe and other northern steppe bison, *B. priscus*, is not as wide as that of the American plains bison, *B. bison*, it is quite wide (figs. 7.4 and 7.5). These bison are very unlike the living European wisent, *B. bonasus*, which has the narrow nipping arrangement of a more selective grazer indicative of either thicker grasses or a more eclectic diet, and a diet higher in dicots.

We can say that Blue Babe and steppe bison in general were grazers; that these bison chose bites from a thin to modest sward but were not well adapted to using and reusing law-forming grass species to the extent of modern bison on the American Great Plains. We have assumed that the steppe bison did little browsing because for tens of thousands of years during the full glacials there was little browse. There were few trees on the mammoth steppe. The anatomy of steppe bison incisors and premaxillaries supports this assumption. During the interstade, when some woody vegetation reinvaded the Mammoth Steppe, bison probably utilized the leafy parts of dicots, especially during the summer, as a dietary supplement.

I found compacted plant matter in Blue Babe's first molars. Cheek teeth of large herbivores have small infundibular pits between the cusps which become permanently filled with plant fragments from the food being chewed. Leaf and stem cuticles are very resistant to both chemical destruction and decomposition, as they form the outer protective coating or seal of the plant against parasites or infection. Because of this durability they preserve quite well. Also, they

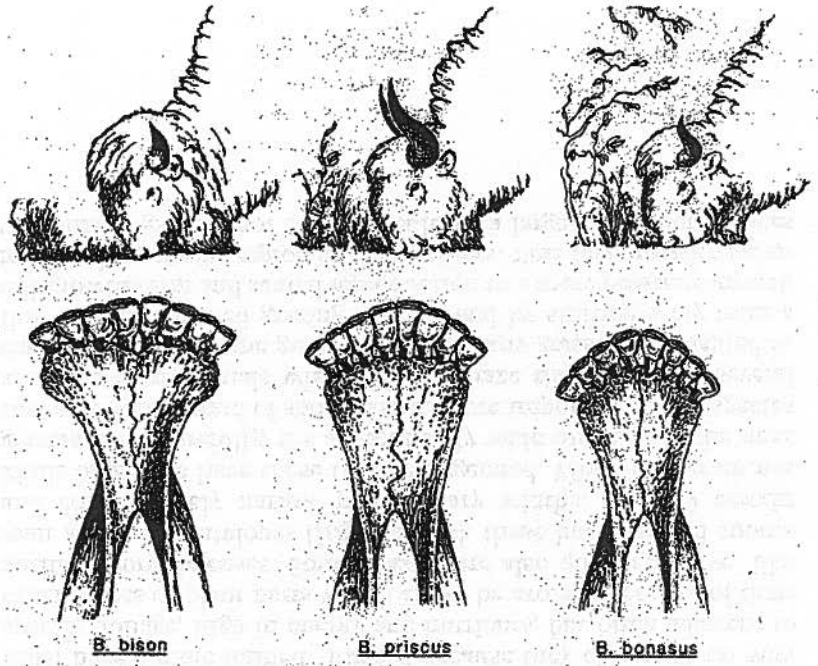

Fig. 7.4. Incisor width and diet. Among grazers the width of lower incisors (the lower canine is incorporated into this row in incisiform pattern) is associated with adaptation to grazing on short grasses. The incisor row is widest in American plains bison (*left*) and intermediate in steppe bison (*middle*). European bison have the narrowest incisor row (*right*).

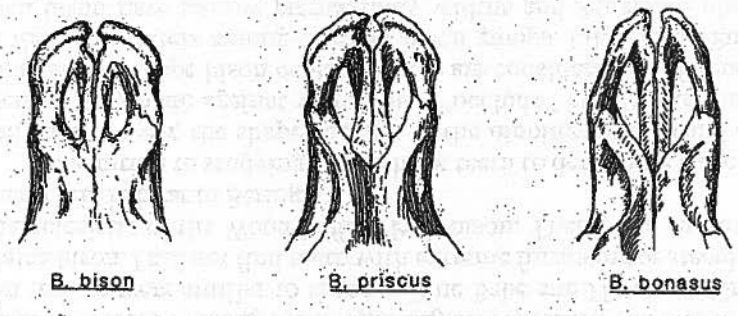

Fig. 7.5. Premaxillary width and diet. The "breadth of bite" among ungulates is a general indication of dietary selectivity; species with narrow mouths can be very selective about each bite. Browsers are normally more selective and hence have narrower biting structures than grazers. Bite width among grazers also corresponds to the volume of sward regularly available in one bite. Animals that feed on very short, previously grazed "lawns" tend to have wider mouths. Premaxillary bones which underly the biting pad are widest in American bison (*left*), intermediate in steppe bison (middle), and narrowest in European bison (*right*).

form an imprint or "fingerprint" of the underlying epidermal cells which tend to be very characteristic for each plant group. So, not only do epidermal fragments preserve well, but they are very informative as to which plants were eaten. Many studies have used epidermal fragments from fecal pellets or stomach contents to reconstruct diets of grazing mammalian herbivores.

Blue Babe's tooth contents were sent to a commercial histological laboratory (at the Department of Range Management, Colorado State University, Fort Collins, Colorado) for identification, where the cuticles mentioned earlier in this chapter were analyzed. Only about 20% of the cuticle fragments were identifiable, and then only to genus. Two grasses were the most common. Wheatgrass or *Agropyron* was one of them. There are several species of wheatgrass in Alaska today. They are somewhat "weedy," that is, they are found on disturbed gravel bars and riverbanks or high alpine meadows. They all occur in rather dry habitats (Hultén 1968).

The other kind of grass cuticle in Blue Babe's teeth was *Danthonia*, a grass that is moderately common at mid latitudes in the plains states, but does not now occur in central Alaska. There are some specimens collected from the Matanuska Valley and Seward Peninsula, and it is possible that these are introduced from farther south. From Hultén's (1968) map this genus seems to be especially widespread in the southern Yukon Territory.

In addition to these grasses, a willow (*Salix*) twig tip was found among the cuticle remains, so the presence of grass and some dicots is consistent with the dietary portrayal of steppe bison predicted by its morphology. This would be especially true of the interstadial time, in which Blue Babe lived, when more willows would have been available.

Interstadial Bison in Alaska

Discussions about the ecology of large mammal species on the Mammoth Steppe have more or less been limited to glacial episodes (see articles and references in Hopkins et al. 1982). We know much less about Beringian mammals during interglacials, primarily because the depositional and preservational environment was better during glacials (Guthrie 1985a). More acid soils and complete vegetational mat characteristic of warmer and wetter peak interglacials left a peaty deposit relatively devoid of bones. However, some specimens, including Blue Babe, date from the last interstadial (Hopkins's Boutellier Interval); these can tell us something about interstadial conditions.

Strangely enough, most of the Mammoth Steppe fauna continued throughout the last interstadial (from about 60,000 to 28,000 years ago), in roughly the same proportions. Three species (bison, horse, and mammoth) dominate most faunal assemblages reported from that time (as an example see the radiocarbon dates listed from the articles in Hopkins et al. 1982). What is odd about the persistence of bison, horse, and mammoth during the interstadial is that this was a time when trees recolonized much of Beringia, approximately reaching their present distribution. Hamilton (1979) described spruce stumps 41,000 years old found on the Chandalar River, near the present northern limit of spruce. However, the presence of Mammoth Steppe fauna during the last interstadial suggests that the climate and landscape must have been rather dry, unlike that of today. The continued presence of bison, horse, and mammoth indicates an arid, grassy environment, with facies not too different from those occurring during glacials over a wide area in all kinds of topographic terrain. Yet tree species that now characterize the boreal forest were present (Schweger and Janssens 1980). Such a combination is strange to consider because it is not comparable to our experience with the present boreal forest or with an arid and treeless steppe. This picture reflects what Andersen found in the pollen around Blue Babe (Appendix B).

Today, both the northern and altitudinal limits to the boreal forest are apparently controlled by warmth, that is, by degree days. Since the present amount of moisture throughout the north is so meager, we might assume it represents a minimum quantity, but in fact it can be reduced. The southern border of the boreal forest is controlled by aridity, at least in the southwestern part. Picture for a moment a combination of these factors: aridity controlling treeline from below, so to speak, and summer warmth controlling the upper reaches of treeline. We can better imagine the interstadial as a combination of warmth allowing trees to expand northward to their present altitudinal and latitudinal extent, but under more arid conditions. Trees would then grow only in well-watered locations, particularly along streams, like the way trees penetrated more arid southern grasslands (Wells 1970). To empty Beringia of trees, as occurred during glacial peaks, by cold alone would have required very acute changes. But increased aridity in conjunction with cold would be a severe challenge to trees. The interstadial climate then was an unusual mixture of warmth, with a little less than the same degree days as present, and considerably less moisture. This allowed woodlands to grow along valley bottoms, with restricted accumulation of peats, at the same time extensive grasslands marked better-drained environments and probably much of the broad lowlands away from stream arteries.

Several fragments of information point to this interpretation. One is the presence of saiga antelope (*Saiga tatarica*) on the north slope of Alaska and in the Yukon Territory around 37,000 years ago, about the same time that Blue Babe lived in the Fairbanks region (Harington 1981). Today, these areas have over twice as much snow as saigas can tolerate. And in summer our ubiquitous tussock meadows would be totally unnegotiable. Nelson (1982) identified an assortment of insect fossils from interstadial deposits (Boutellier interval) on the north slope. He found a number of species that do not occur there today and are found only in very dry conditions elsewhere. Yet these insects from arid habitats occur in deposits with other species still found in the north slope that are now limited to moist habitats. Pollen from this same Boutellier Interval found in Siberia and parts of eastern Beringia suggests that although spruce, larch, birch, cottonwood, and aspen were present, they grew much more sparsely than today (Hopkins et al. 1982). Unfortunately we have no pollen cores from interior Alaskan lakes which reach so far back into the past.

As in Alaska and Siberia, Europe was without trees during the full glacial episodes. However, the European interstadial (isotope stage 3, in the deep-sea cores) was not characterized by a reinvasion of oak hardwood forests as occurred in the early Holocene. European interstadial pollen continues a pattern of herbaceous dominance with some pine (Bowen 1981). In that regard Europe was probably more like interior Alaska during the interstadial, as indeed it was similar to Alaska during the peak glacial.

How did these glacial and interstadial changes affect steppe bison? Does Blue Babe, our interstadial (Boutellier) bison, differ from his glacial counterparts? We know that the Holocene profoundly affected bison all across the Holarctic, markedly reducing body size and changing horn size and shape (Sher 1971; Wilson 1975, 1978; Guthrie 1970, 1980). Did a similar thing occur during the last interstadial? Unfortunately our data are not good enough to make a detailed comparison, but we can gather some ideas from Blue Babe.

Natural Trap Cave in northern Wyoming contains many bones that provide a long record of large mammals during the late Pleistocene. Gilbert and Martin (1984), who have worked with these fossils, found no reduction in body size during the last interglacial among sheep (*Ovis*), pronghorns (*Antilocapra*), bison (*Bison*), wolves

(*Canis*), and wolverines (*Gulo*). They argue that this is a general pattern and that the dramatic dwarfing at the beginning of the Holocene is unique to that time. I agree with Gilbert and Martin and have argued (Guthrie 1984b) that Holocene changes indeed appear unique when viewed from biotic evidence, even though physical climatic data are not striking. From this we would expect the interstadial bison to be as large as a full glacial bison, but was it?

Blue Babe and other interstadial bison remains collected from Pearl Creek are much larger horned than living bison, one would never mistake these large thick horns for those of a modern bison. However, the interstadial bison are somewhat smaller than most full

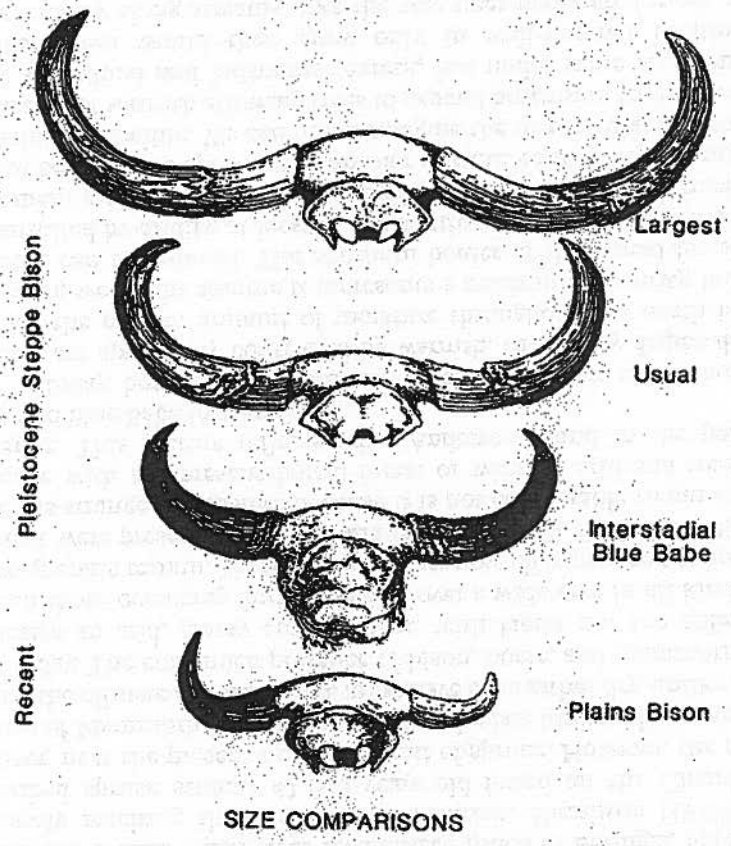

Fig. 7.6. Male skulls. The horn size of Alaskan Pleistocene steppe bison is quite variable. Intrapopulational differences probably account for much of this. Blue Babe's horns are smaller than most steppe bison but larger than horns of living bison.

Table 7.2 Size Comparisons of Blue Babe with Fossil Male Bison from Interior Alaska

	Blue Babe	Minimums	Mean	Maximum
Width of cranium between cores and orbits	273	255	288	339
Width of skull at masseteric processes at M^1	182	177	196	213
Greatest postorbital width	332	307	349	405
Horn sheath length on upper curve	565	410	584	810
Greatest spread of horn cores on outside curve	922	790	986	1372
M^1-M^3 alveolar length	92	72	92	115
P^2-M^3 alveolar length	144	131	147	166
Total length of skull	556	558	598	642
Occipital crest of tip of nasals	451	473	491	503

Sources: Skinner and Kaisen 1947.
Note: Measured in mm.

glacial bison (see comparisons in figs. 7.1 and 7.6, and table 7.2). Blue Babe and the other interstadial bison from Pearl Creek fall within the lower range of Skinner and Kaisen's (1947) size distributions of Alaskan Pleistocene bison (fig. 7.7).

I have discussed body size among Alaskan Pleistocene large mammals in detail elsewhere (Guthrie 1984a). In that context, contrary to Gilbert and Martin's (1984) finding, the same processes that caused Holocene dwarfing in Beringian bison were at work to a lesser extent during the interstadial. During the Holocene, the grassland environment was reduced and bison range in Alaska was limited to small islands of habitat. Usually this habitat was adjacent to mountains where windswept river outwash plains provided early succession herbs. Winter winds kept these herbs exposed. These would have been survival habitats but not dependably rich ranges with generous peaks of protein availability. Judging from the smaller size of interstadial bison, invading trees and shrubs as well as changes in the herbaceous community, reduced range quality, and poorer quality range led to smaller bison.

We can make other comparisons between Blue Babe and extant bison. We can measure hoof phalanges to see if foot structure changed commensurate with the more moist, soft substrate we now have in the north. Today ungulates that use interior Alaskan lowlands (e.g., moose and caribou) have specially adapted feet to spread

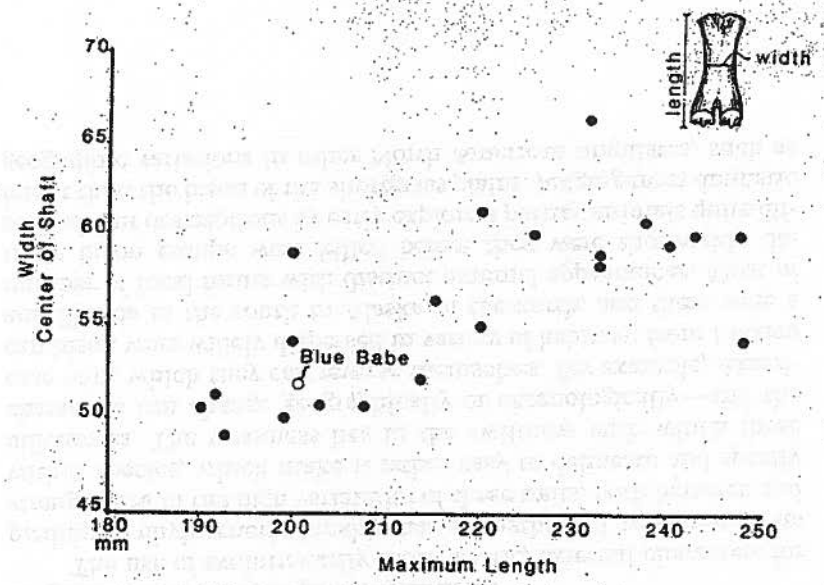

Fig. 7.7. Alaskan Pleistocene male bison metacarpi. In this plot of metacarpal size of Alaskan bison, Blue Babe is near the lower end of the range. Any bone could be used in such a comparison, but metacarpi are particularly good because weight loading more or less determines the size of this particular bone.

their weight, thus decreasing weight loading (kg/cm^2). Sinclair (1977) observed that water buffalo (*Bubalus*) have broad hoofs which allow them to traverse swampy country, whereas bison have comparatively small feet for their size, being adapted to dry grasslands. Vereshchagin and Baryshnikov (1982) have measured the hooves of Beringian bison and concluded that they were much the same size as living bison. The hooves of Blue Babe were also similar to those of living bison, so the interstadial seems not to have affected hoof size significantly.

Fossil evidence indicates that the main characters of the Mammoth Steppe fauna (bison, horse, and mammoth) continued throughout interstadials. Yet at the end of the last glacial, most of the Mammoth Steppe fauna became extinct or severely reduced in their distribution and were supplanted by the boreal forest fauna of today—black bear, moose, and so forth. By this fact alone one would say that the interstadial large mammal community had a different climate than today exists in those same areas. Bison cannot live in Pearl Creek or the Fairbanks area now. In addition to forage insufficient for winter survival, forage that is there is frequently made inaccessible by deep snows a meter in depth undrifted, and occasionally well over a meter, far too deep for bison to survive the winter.

The paleoenvironment of the last interstadial in interior Alaska is ripe for more study. It is an interesting time, a mixture of the Mammoth Steppe and the boreal forest. It must have been a rather unique period, with many internal variations over the several tens of thousands of years it lasted. Matthews (1982) proposes that the interstadial might have been the critical period when eastern and western steppe faunas and floras intermingled.

Phylogenetic Kinship

Some studies of bison phylogeny and biogeography propose multiple coexisting species across the north (Skinner and Kaisen 1947; Geist 1971b; McDonald 1981). Others see only a central line with considerable geographic and chronological diversity (Flerov 1967, 1977; Guthrie 1970, 1980; Wilson 1975, 1978). If the former is correct, bison are unique among artiodactyls in the far north in having had more than one species per genus at any one time and place in the last half of the Pleistocene. One characteristic of far northern artiodactyls (*Ovibos, Alces, Rangifer, Ovis,* and *Saiga*), proboscidians (*Mammuthus*), equids (*Equus*, caballids, and hemionids), rhinos (*Coelodonata*), or even most larger carnivores—brown bears (*Ursus*), wolves (*Canis*), and lions (*Panthera*)—is that they lived in a community with no other closely related species. This is understood if we see that in the continuous habitat of northern environments there is (and was) little home fidelity, which encourages high variability and social systems that foster large-scale genetic mixing. Thus, I think it unlikely that two or more species of bison coexisted for any length of time. Although placed in the same genus, hemionids and true horses (caballids) are quite distantly related and may have occupied different habitats in Beringia (hemionids the uplands and horses the lowlands).

The ungulate community in the north is comparatively simple and species are widespread, although individuals exhibit considerable variation in body size and social paraphernalia throughout their geographic ranges. Most if not all northern species show dramatic evolutionary changes when lineages are traced through time (Guthrie 1984a). Social paraphernalia can change rapidly, in either direction. Although Geist (1971b) implies a unidirectional colonization process and McDonald (1981) proposes a semipermanent "stasis" picture of artiodactyl populations moving through time and space,

we can document rapid evolution in these populations even since the beginning of the Holocene. Wilson (1975, 1978) showed that Great Plains bison change from a large-horned form to the modern small-horned species in 9,000 years. Contrary to colonization or stasis models, most northern species have decreased in body size and in horn and antler size during the Holocene (Guthrie 1984a). Moose, *Alces alces*, for example, seem to have colonized the New World late in the last glacial or early Holocene, yet southern moose populations are now morphologically different from those that colonized the far north.

Like other artiodactyl lines in the north, bison are a rather plastic and broadly adapted species, readily responding to selection pressures of local environments, both geographically or chronologically. In fact, bison seem especially sensitive in their evolutionary refinement to new environmental conditions and attendant changes in social organization. Wilson's (1975) documentation of body size reductions in Holocene bison on expanding grasslands in the Great Plains is a case in point.

Although Gentry (1967), and Groves (1980) link all the Bovini (cattle, bison, and buffalo) within a narrow evolutionary radiation (they wish to submerge bison within the genus *Bos*), the variety of social behaviors and anatomy within the group shows that similar environments can quickly override old phylogenetic ties, strongly modifying these characters. The use of rutting wallows by African buffalo, *Syncerus*, and American plains bison, *B. bison*, extreme sexual dimorphism in body size and horn size, and the clashing form of combat used by these two species are not an indication of their phylogenetic proximity but rather a product of a parallel behavioral adaptation to more open plains situations.

The use of evolutionarily more plastic, external characters for predicting phylogenetic kinship has strengths and weaknesses. Its strength lies in the high variability of these traits, both between and within species, which make it rather easy to delineate and specify differences. The weakness lies in the swiftness with which these characters can change geographically or chronologically—and the ease with which they can reverse themselves. For example, American bison were widely dispersed in variety of habitats: from Mexico and Florida in the south to Alaska in the north, and there were a number of local forms with distinct external appearances. Most of these bison groups were killed before they were thoroughly described, but descriptions by early explorers portray animals quite different than the bison of the shortgrass plains. Judging from dramatic geographic variations in other North American ungulates, such as white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), we would expect the same range in appearance among American bison. Although island and coastal populations of mule deer in the northwest are easily distinguished from their counterparts in the Rocky Mountains, phylogenetically both forms are undoubtedly quite close. The point is that differences between steppe bison of western Europe and of Alaska are within the range one would expect in a species of such wide distribution and diverse habitats. These differences are less than those of mule deer subspecies referred to above, and for that matter are in the same range as differences between wood bison (*B. b. athabascae*) and plains bison (*B. b. bison*) which were contiguously distributed and interbreeding on the Continent.

Strangely enough the confusing variety of fossil bison names is mainly an American phenomenon. Eurasians have placed most of the large, middle-to-late Pleistocene bison into a catchall species called the steppe bison (*Bison priscus*), although they have acknowledged that it varied chronologically and geographically. European systematists prefer a broad identity, much the same as in the brown bear, *Ursus arctos*, or reindeer, *Rangifer tarandus*, which show analogous temporal and spatial variations. They have given the various forms of *B. priscus* subspecific status, for example, *B. priscus dimenutus*, *B. priscus longicornis*, and so forth.

There are several reasons for Eurasian conservatism in naming late Pleistocene bison; one is philosophical, but another must be the comparative paucity of bison in the Old World. Although bison are not an uncommon fossil in the Old World, they occur in far greater quantities in the American Great Plains sites. It is relatively safe to say that herds of millions of bison were unique to the Holocene Great Plains.

Unfortunately, in North America there is still no unanimous agreement as to which bison species were present when and where nor the place of their origins. However, a general pattern is emerging of the overall features of the zoogeography of various "forms." The exact systematic placement is yet to be agreed on, but that is not my main concern at present. My choice of nomenclature does not necessarily imply agreement with a particular taxonomic status, but is rather a reference to a commonly recognized form.

Bison origins remain obscure. There are a number of bison or bisonlike skulls from the late Pliocene–early Pleistocene of southern Asia—a relatively important center of bovine evolution and diversification. At first they were quite cattlelike, with none of the swollen frontals or orbital protrusion of later bison. The horns began

even this early to swing laterally instead of forward as in most cattle groups. *Probison dehmi* and *Bison sivalensis* have been described from India, and *B. paleosinensis* from China. (See Wilson 1975 and McDonald 1981 for further discussions involving the controversy of bison origins.) Very early in the Quaternary these small, somewhat lightly built bison spread throughout Eurasia and were seen in Europe as forms variously called *B. tamanensis, B. voigtstedtensis, B. langenocomis,* and *B. schotensacki.* There may be problems with too fragmentary remains and sexual identification, however, this is currently a focus of interest to several paleontologists and a clearer picture may soon emerge.

Whatever the exact lineage, the generalization of a more cattle-like ancestor seems to hold, as does a stem form that was small bodied and small horned in comparison to some later bison. This early diversification probably still centered around a woodland-parkland environment through temperate Eurasia. However, early in the Pleistocene another form arose that was considerably larger and had long stout horns—the steppe bison, *B. priscus;* it persisted throughout the rest of the Pleistocene, disappearing only at the beginning of the Holocene. *B. priscus* existed as far eastward as England and westward into North America. It was even found northward as far as Novaya Zemlya, 75° N latitude, and southward into Spain and the Caucasus, 40° N latitude. *B. priscus* was the dominant form throughout Eurasia during most of the Pleistocene, and it seems to have been virtually ubiquitous in semiopen and open country. During the glacials it can be found everywhere in the Mammoth Steppe (the Arctic grasslands spreading across northern Eurasia and Beringia) and during the interglacials along the central belt of temperate Eurasian steppes. Interestingly, *B. priscus,* although common, seldom dominates any Eurasian Pleistocene faunal assemblage.

Because of the chronological persistence and ubiquity of *B. priscus,* an understanding of its paleobiology is perhaps a key to an understanding of bison evolution. This is particularly true as it becomes apparent that *B. priscus* probably gave rise to the North American lineages.

The colonization of central North America by bison is also a controversial issue. However, debate has narrowed the time of first arrival from late Illinoian to early Sangamon. (It is central North America which is the area critical to our interest, as Alaska and the Yukon Territory are zoogeographically linked more closely to northeastern Asia.)

Whatever the exact date of colonization, it is agreed that these already large Old World bison, *B. priscus,* became even larger in central North America. In fact, they became enormous, with horn cores reaching 2 m from tip to tip; this New World giant has been given a separate species category, *B. latifrons.* Their bones are found throughout much of unglaciated North America from California to Florida, but the greatest concentrations seem to be along a line from Alberta to Texas, just east of the Rocky Mountains, and in the intermontane basins just to the west.

As with its origins, the disappearance of *B. latifrons* is also controversial. It seems to be the Sangamon bison and probably decreased in size at the onset of the Wisconsinan or soon after, throughout all or most of its range.

There is a smaller form of bison occurring after *B. latifrons* (the chronology of which is again disputed). The main point is that there are enough transitional forms to conclude that the gigantic *B. latifrons* was not a "terminal" line but graded into a comparatively smaller (but still quite large) Wisconsinan form, called *B. antiquus.* This line continued to decrease somewhat in body size throughout the Wisconsinan. Like *B. latifrons* its distributional abundance falls along the line from Alberta to Texas, although it too has a scattered occurrence from Florida to California.

This "*B. latifrons–B. antiquus*" line exhibits decreased horn size and increased doming of the frontals. Also the orbitals are less telescoped outward. The horn cores extend outward in more of a straight line from the central axis of the skull. There is less hook in the horns, and the bases are thick in comparison to northern bison. Wilson (1975) separates these northern and southern "types" in relation to the Holocene bison, a point to which I return later.

In northern Eurasia, in Alaska, and in the Yukon Territory, the large *B. priscus* decreases in size as it continues through to the Holocene. It passes through forms Sher (1971) has called *B. priscus diminutus–B. bison athabascae* in Siberia; in Alaska, Skinner and Kaisen (1947) have called the forms *B. crassicornis–B. preoccidentalis–B. occidentalis–B. bison athabascae.* Whatever names one uses to label the change, there seems to be a diminution of body size in the far north, starting about or slightly earlier than 13,000–12,000 B.P.

Europe is more of a puzzle. Vereshchagin (1959) proposes that in the Caucasus, *B. priscus* decreased in size toward the small-living *B. bonasus* of Europe well before the Holocene. The fate of central and northern European *B. priscus* is unclear, whether it was replaced by a smaller bison from elsewhere (Kowalski 1967a) or whether it experienced a size decrease (Degerbol and Iverson 1945; Gromova 1965) is unknown. The living European bison, *B. bonasus,* seems to be an evolutionary regression toward the woodland-edge cattle adap-

tation. Like cattle, *B. bonasus* even marks its territory (Zablocki 1967).

Thus during the Holocene (and perhaps earlier in some areas), we have a picture of Eurasian bison rapidly decreasing in body size. There was also a decrease in numbers and in distributional extent (Vereshchagin 1959).

The picture in North America, however, is different. There Holocene bison were becoming more abundant while also decreasing in body size. At the end of the Wisconsinan, evidence shows that the northern small form of *B. priscus* (called *B. occidentalis*) reinvaded the Great Plains and came in contact with the line of *B. latifrons* (called *B. antiquus*) from the south (Wilson 1975). The northern forms, having decreased in size independent from the more southern

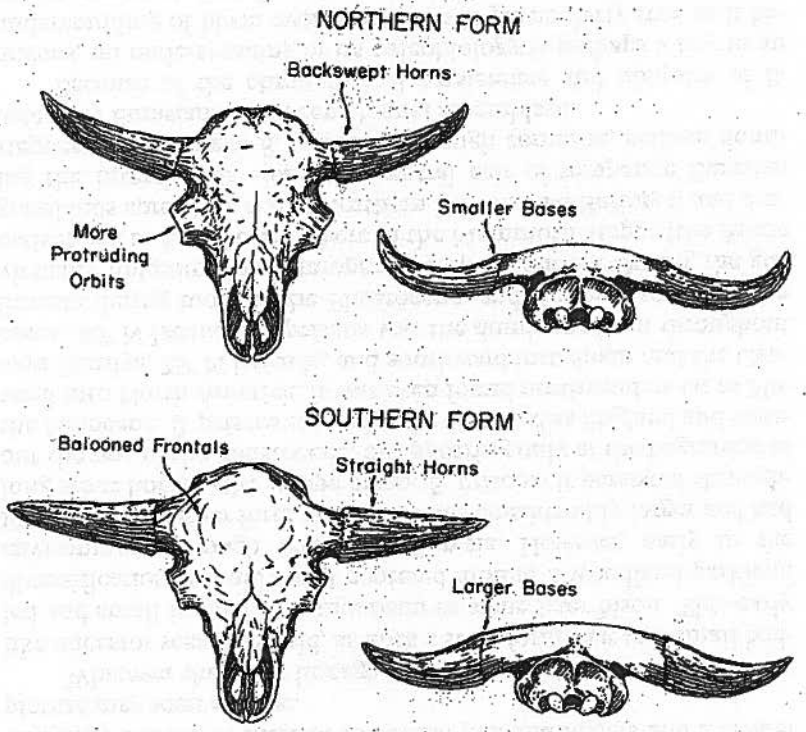

Fig. 7.8. Ancestors of plains bison. Two late Pleistocene-Holocene bison groups are given a variety of names because their biological relationships are as yet unclear. The northern form is referred to as *B. occidentalis* and the southern form *B. antiquus*. One, or both, of these gave rise to the living plains bison, *B. bison*.

forms, were then not very dissimilar in body size at the time of the early Holocene contact, although they differed somewhat in cranial and horn characters (fig. 7.8).

Wilson (1975, and elsewhere), in a study of bison from well-dated archaeological sites, has presented a convincing model of the southern movement of the northern *Bison occidentalis* displacing *B. antiquus*. Additionally, he found several sites in which there were mixtures of the *occidentalis* and *antiquus* skull patterns (fig. 7.8) in various combinations. He interpreted this as strong evidence for genetic remixing of the two lines.

The only thread of information running contrary to this interpretation of *B. priscus–B. occidentalis* is the data about hump shape (chapter 5). All of the fossil bison humps from Alaska and the Yukon Territory have a definite *B. priscus* dorsal arc, which shows a definite concavity in the dorsal contour in the region of T10–T13 neural spines; *B. bonasus* shows a similar contour. However, both *B. bison bison* and *B. bison athabascae* show a rather straight dorsal contour (van Zyll de Jong 1986). The nominal species, *B. antiquus* and *occidentalis*, show a slight concavity like *B. priscus*, but the anterior thoracic neural spines are very similar to *B. bison* (fig. 7.9), so the most appropriate specific designation is unclear.

All this controversy over bison nomenclature seems unnecessary. If we had referred all late Pleistocene and living bison to one species as we have done with caribou or African buffalo, as some have suggested (Bohlken 1967; van Zyll de Jong 1986), bison phylogeny would not have clouded the important issues of bison paleobiology and biogeography. Many things, such as horn-size reduction, are obviously parallel adaptations, and multivariate techniques used to show nearest neighbor groups must incorporate biological and paleontological information into their models to give us much real insight.

In figure 7.10 I have summarized this brief history in relation to body size, geography, and chronology. I have emphasized body size because it is conveniently pictured, but size is correlated with a number of other traits such as frontal sinus development, horn size and many horn characteristics, such as ventral rugae or flutes on the horn core. I have tried to be both abstract and conservative. There are a few "outliers" which do not fit this portrayal and several controversies involving placement of the hatched lines. I think, overall, it is an accurate summary.

Ancestral interaction of these groupings is, however, a different matter. The most logical route is to derive a later from an earlier one in the same region; we know this does not always happen, but it is

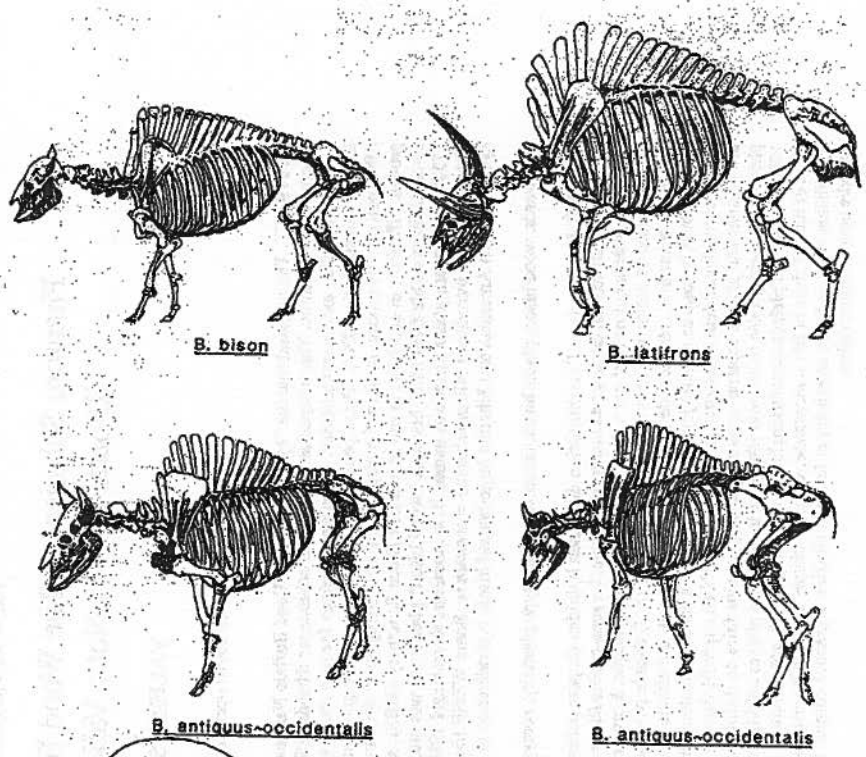

Fig. 7.9. Hump shape in American bison. Bison humps can be seen in these mounted skeletons of *B. bison* (*upper left*), Smithsonian, National Museum of Natural History; *B. latifrons* (*upper right*), Idaho State Museum; *B. antiquus ~ occidentalis* (*lower left*), Nebraska State Museum; *B. antiquus ~ occidentalis* (lower right), American Museum of Natural History. Though the fossil specimens are not identical to those of recent *B. bison*, they all have a more forward hump than the Eurasian steppe bison, *B. priscus* (compare with fig. 5.8). (Drawn from photos)

the usual case. Therefore my phylogenetic connections are vertical unless there is some evidence to believe otherwise (fig. 7.10).

In previous chapters I have shown that Blue Babe is virtually identical to Pleistocene bison in Siberia, known as steppe bison, *B. priscus*. The Alaskan Pleistocene mummy is also closely related to European Pleistocene steppe bison. Steppe bison ranged from Alaska to western Europe, where they were important figures in Paleolithic art. The Blue Babe mummy allows us to compare the easternmost steppe bison with its counterpart two continents away in Europe. Although *B. priscus* seems rather conservative compared to many large mammals, the species did change some, both geographically

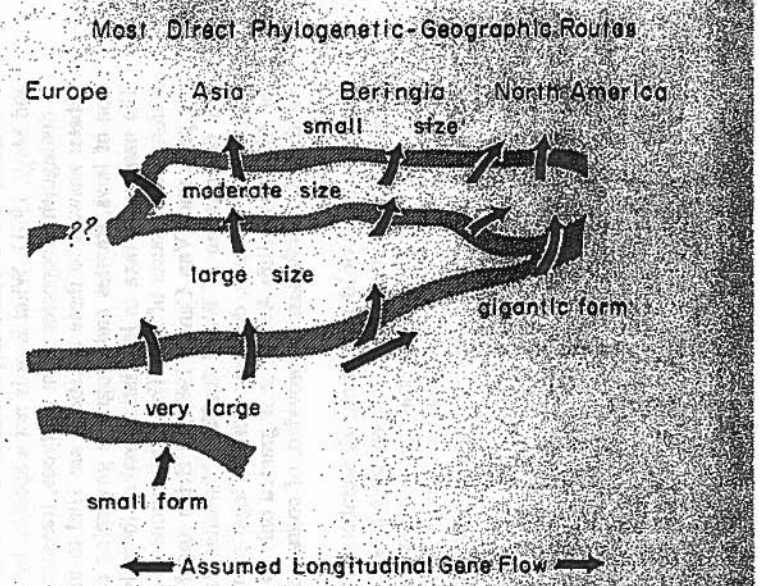

Fig. 7.10. Schematic pattern of bison body size changes throughout the Quaternary. The course of bison evolution is not simple, but it appears that earlier forms were small (there are some exceptions) and that bison increased in size in the mid Pleistocene. There was a late Pleistocene reduction in size among all bison, and this accelerated during the Holocene. Horn size followed the same pattern.

and over time. Blue Babe also allows us to better compare northern steppe bison with their more southern relatives in the rest of North America.

While different from his Pleistocene contemporaries in Europe and his later relatives in North America, Blue Babe resembles both. In basic color, in pelage length and in hump shape he seems more closely connected to European *B. priscus*, yet, his tail length is more like living American bison. In almost all traits he is more similar to *B. bison athabascae*, the northern subspecies of American bison, than to the more southern subspecies, *B. bison bison*.

These characteristics, both in time and from west to east, seem to follow general social-anatomical patterns first seen by Geist (1971a, 1971b) in ungulates. They include shortening of the tail, concentration of social display into the forward part of the body, and a richer, more contrasting pelage pattern. These trends apparently reversed during the European Holocene, as the earlier European *B. priscus* is much more dramatically adorned than its Holocene descendant, European *B. bonasus*.

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Phantom Subspecies: The Wood Bison *Bison bison "athabascae"* Rhoads 1897 Is Not a Valid Taxon, but an Ecotype

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ABSTRACT. The proposal that the "hybrid bison" of Wood Buffalo National Park (WBNP) be exterminated and replaced with "wood bison" has no taxonomic justification. The subspecies *Bison bison athabascae* Rhoads 1897 is based on inadequate descriptions and taxonomically invalid criteria — i.e., body size and morphometrics. Its accepted pelage features are based on studies of the same herd of Nyarling River (NR) bison from Elk Island National Park (EINP). These pelage features, assumed to be genetically fixed, are ecotypic confinement effects, which NR bison share with EINP bull elk and moose. In bison the display hair acts analogous to deer antlers, which reflect their bearers' access to high-quality food during their growth. NR bison in captivity, in the Mackenzie Bison Sanctuary (MBS), and the original wood bison are "northern plains bison." Nor are WBNP bison distinguishable from MBS bison. A "wood bison" phenotype was also described as diagnostic for southern plains bison *(B. b. bison* Linnaeus 1758); the northern plains bison was named *B. b. montanae* Krumbiegel 1980. Consequently, *B. b. athabascae* = *B. b. bison*, as the latter has priority. Yet captive and introduced NR *athabascae* = *montanae*. Some WBNP bison resemble *B. priscus*, supporting the view that *B. bison* evolved as a hybrid between American and Siberian large-horned bison. Hybridization in large mammals need not be a tragedy for conservation.

Key words: wood bison, plains bison, taxonomy, phenotype plasticity, ecotype, display organs, morphometry, subspecies, conservation

RÉSUMÉ. Le plan visant l'extermination du «bison hybride» du parc national Wood Buffalo (PNWB) et son remplacement par le «bison des bois» n'a aucune justification du point de vue taxonomique. La sous-espèce *Bison bison athabascae* Rhoads 1897 se fonde sur des descriptions inadéquates et sur des critères qui ne sont pas valides du point de taxonomique, à savoir la taille et la morphométrie. Les attributs reconnus du pelage s'appuient sur des études du même troupeau de la rivière Nyarling (RN) dans le parc national Elk Island (PNEI). Ces attributs du pelage, que l'on suppose génétiquement déterminés, résultent de la limitation des écotypes, qui affecte le bison de la RN tout comme le caribou et l'orignal mâle du PNEI. Chez le bison, la hure (pelage de parade) joue un rôle analogue à celui des andouillers chez le cerf, tous deux reflétant l'accès des animaux à une alimentation très nutritive durant leur croissance. Le bison de la RN en captivité dans la Réserve de bisons Mackenzie (RBM) et le bison des bois d'origine sont des «bisons des plaines septentrionales». On ne peut plus faire de distinction entre le bison du PNWB et le bison de la RBM. On a aussi décrit un phénotype de «bison des bois» pour identifier le bison des plaines méridionales (*B. b. bison* Linnaeus 1758); on a appelé *B. b. montanae* Krumbiegel 1980 le bison des plaines septentrionales, ce qui fait que *B. b. athabascae* = *B. b. bison*, vu que ce dernier a priorité. Cependant le *athabascae* en captivité et relâché dans la RN = *montanae*. Certains bisons du PNWB ressemblent à *B. priscus*, ce qui confirme l'idée que *B. bison* est le produit d'une hybridation entre le bison américain et le bison sibérien à grandes cornes. L'hybridation chez les grands mammifères ne devrait pas constituer une tragédie pour la conservation.

Mots clés: bison des bois, bison des plaines, taxonomie, plasticité des phénotypes, écotype, organes de parade, morphométrie, sous-espèce, conservation

Traduit pour le journal par Nésida Loyer.

"Change is not made without inconvenience, even from worse to better." — Dr. Samuel Johnson (1709-1784), quoting Richard Hooker.

INTRODUCTION

Taxonomy has become important in conservation (O'Brian and Mayr, 1991). What is or is not a species, by what criteria to distinguish subspecies from ecotypes, transcends academic debate: answers to these questions are vital to the interpretation of laws, treaties and programs governing conservation. The naming of taxa in legislation makes them legal entities, actionable in courts of law. The implications to conservation are profound (Van Camp, 1989; O'Brian and Mayr, 1991). The designation of Wood Buffalo National Park bison as hybrids, for instance, deprives them of legal protection under the Alberta Wildlife Act. Such is granted only to bison designated as *B. b. athabascae*, provided, of course, that such can be identified.

For purposes of identification, *all* members of a subspecies listed in legislation must be *recognizable* as such or lose the protection of the law. Consequently, a subspecies has to be defined as a collection of populations whose individuals share common taxonomic — that is, hereditary (genetic) — traits. This would make into polymorphisms taxonomic characteristics not shared by all individuals, though one can designate as a subspecies all populations containing one polymorphism or another. Put another way, subspecies are distinguished by at least one consistent taxonomic difference. Geographic location as an integral part of the definition of subspecies (O'Brian and Mayr, 1991), however, has drawbacks legally, since geographic origin is never a material part of a specimen and must be normally accepted on faith (Geist, 1991a).

The species can be defined as all subspecies not genetically segregated by reproductive barriers in nature (see O'Brian and Mayr, 1991) or as all subspecies sharing one or more taxonomic characteristics (e.g., species of *Ovis* are recognized by chromosome numbers linked to specific morphological features; see Nadler *et al.*, 1973) — that is, as the next cladistic level above the subspecies. If taxonomy is to reflect evolution, then taxonomic criteria must be hereditary ones, little affected by environment. I stress here differences in kind, not in degree (as does quantitative taxonomy) and dismiss subspecies based on comparative morphometrics, as this method is incapable of differentiating genetic, epistatic, environmental and true statistical variation. Experimental, but not comparative, morphometrics may give taxonomically valid results.

In 1989 Agriculture Canada, in concert with federal, provincial and territorial wildlife agencies, proposed to exter-

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minate the bison (*Bison bison* Linnaeus 1758) in Wood Buffalo National Park (WBNP) and replace these, allegedly "worthless hybrids" (*Bison bison bison* x *athabascae*; see van Zyll de Jong, 1986) and carriers of bovine tuberculosis and brucellosis, with so-called "wood bison" (*B. b. athabascae* Rhoads 1897) free of the diseases. The Bison Disease Task Force was struck to deal with matters of information and a panel formed by the Federal Environmental Assessment Review Office (FEARO) held public hearings on the plan 15-26 January 1990; the panel upheld Agriculture Canada's position (Connelly *et al.*, 1990). The purpose of this paper is to reassess bison taxonomy.

WOOD BISON TAXONOMY REVIEWED

In his major review of *Bison*, Allen (1876) considered the contradictory reports about wood and plains bison and chose not to formalize the distinction; neither did Hornaday (1887). However, Rhoads (1897) formally recognized wood bison as the subspecies *Bison bison athabascae* Rhoads 1897 but relied on second-hand descriptions of *one* specimen, which he did not examine. He admitted that the reports about differences between wood and plains bison were imprecise and contradictory (Rhoads, 1897; Roe, 1970:43-57). Rhoads used J. Macoun's description of wood bison: "Size larger, colors darker, horns slender, much longer and more incurved and hair more dense and silky than in *B. bison*." What taxonomic criteria are valid or not was not considered, but as van Zyll de Jong (1986) points out, criteria for subspecies distinction remain obscure and unsettled even now.

As determined by the careful and critical Roe (1970:43-57), there is little doubt that in historic times bison existed in at least two forms, a dark, large, shy, non-migratory wood bison in the north, and a smaller, lighter, aggressive, migratory plains bison in the south. There may have also been populations of mountain bison (Meagher, 1973), possibly analogous to the small mountain wisent (*B. bonasus caucasicus*) of Europe (Heptner *et al.*, 1961), as well as some regional differences that native people recognized (Seton, 1929:709). Roe (1970) was not concerned if these differences were taxonomically relevant, that is, of *genetic* origin, or if they were ecotypic, that is, a product of environmental circumstances; he was concerned if the differences reported had some foundation in reality. He concluded they had.

Roe (1970), in his evaluation of the historical literature, unfortunately did not take into account the notable seasonal and age-related differences in the characteristics of bison coats, nor, excepting colour, did he address within-population variability of pelage features in bison. Macoun's account of the wood bison specimen's pelage published in Rhoads (1897) would also fit a plains bison. Also, bulls may shed their long display hair in fall (Lott, 1979). Since bison push abrasive snow with their head during feeding, there may be wear on the head hair during winter.

One finds among plains and wood bison old bulls with fairly uniformly coloured hair on the body and with poorly developed chaps and display robes (see Figs. 1b, 3b). (Figures 1-11 are arranged in a sequence suitable for comparison.) The "Radford bull" described by Seton (1929) could have been an example of these. These old bulls may have regressed testes (analogous to what happens in old bulls of African buffalo *Syncerus caffer*; Sinclair, 1977). These bulls suggest that old age may bring about changes to the display hair.

No good illustrations of wood bison made prior to 1925 appeared to exist. The exception, Rowan's (1929) popular article containing one sketch and one photo of wood bison, escaped attention, as did his archives. Hewitt (1921:Plate 12) published a fuzzy photo of a distant wood bison bull obscured by vegetation. Garretson (1938:12) shows the photo of a mounted wood bison head with a short, erect frontal hair mop and a thin, pointed beard, no different from a plains bison. The best description is by Seton (1929) of a large bull shot on 1 December 1909 by Harry V. Radford 120 km southwest of Fort Smith and exhibited in Calgary in 1914; the mount has proven untraceable. It is surprising that Seton (1911), who habitually made high-quality sketches of plants and animals, would leave sketches of plains bison (Seton, 1909) but not of wood bison. Two photos of wood bison taken in the field (Seton, 1929:Plate CIV) show tiny, indistinct images, not only obscured by vegetation, but apparently retouched as well. I was unable to trace the original photos in the archives. The upper photo of Plate CIII in Seton (1929) shows two bison in captivity, one of which has "wood bison" characteristics, but Seton fails to comment. Were there no differences for him to notice?

William Rowan, of the University of Alberta, a zoologist with exceptional artistic abilities who was well acquainted with plains bison from Bison National Park and who observed and collected original wood bison in 1925, apparently saw no differences between them. He wrote: "They [the wood bison] are generally considered to be an offshoot from the plains race, but on what evidence I am unaware" (Rowan, 1929:360).

McDonald (1978), in a comprehensive taxonomic review of *Bison*, used size and horn core characteristics as taxonomic criteria. He upheld the subspecies *B. b. athabascae* but considered the differences from *B. b. bison* slight and not applicable to all individuals. While horn core differences are controversial taxonomic criteria interspecifically (Guthrie, 1966), they are doubtful taxonomic criteria intraspecifically due to allometric changes associated with body size. McDonald's (1978:463) assumption that *athabascae* is genetically larger than *bison* proved unfounded.

In the late 19th century the bison population in what is now WBNP went through a "bottleneck" of possibly 300-500 individuals (Seton, 1911:320); it increased to about 1500 in the 1920s. Some 6673 plains bison, mainly yearlings and two-year-olds, were introduced to WBNP from what was once Buffalo National Park near Wainwright, Alberta, commencing 25 June 1925. Many did not survive the relocation (Van Camp, 1989). The plains bison were carriers of bovine tuberculosis and brucellosis (Honess and Winter, 1956; McHugh, 1972; Broughton, 1987). Subsequently, plains bison bred with wood bison and infected them with the diseases.

However, due to N.S. Novakowski, of the Canadian Wildlife Service, bison that appeared to have escaped hybridization were discovered along the Nyarling River (NR) in WBNP in 1957. Two herds were salvaged from this stock, one in 1963 to the Mackenzie Bison Sanctuary (MBS) and one in 1965 to Elk Island National Park (EINP). The NR bison in the MBS originate from 6 males and 12 females, the herd in EINP from 4 males and 17 females. Both herds of wood bison are thus based on small samples of the wood bison gene pool. The claim that 37 (actually 39) wood bison, which formed the founding stock for the MBS and EINP herds, captured a "significant part" of the genetic diversity of wood bison (p. 57 of

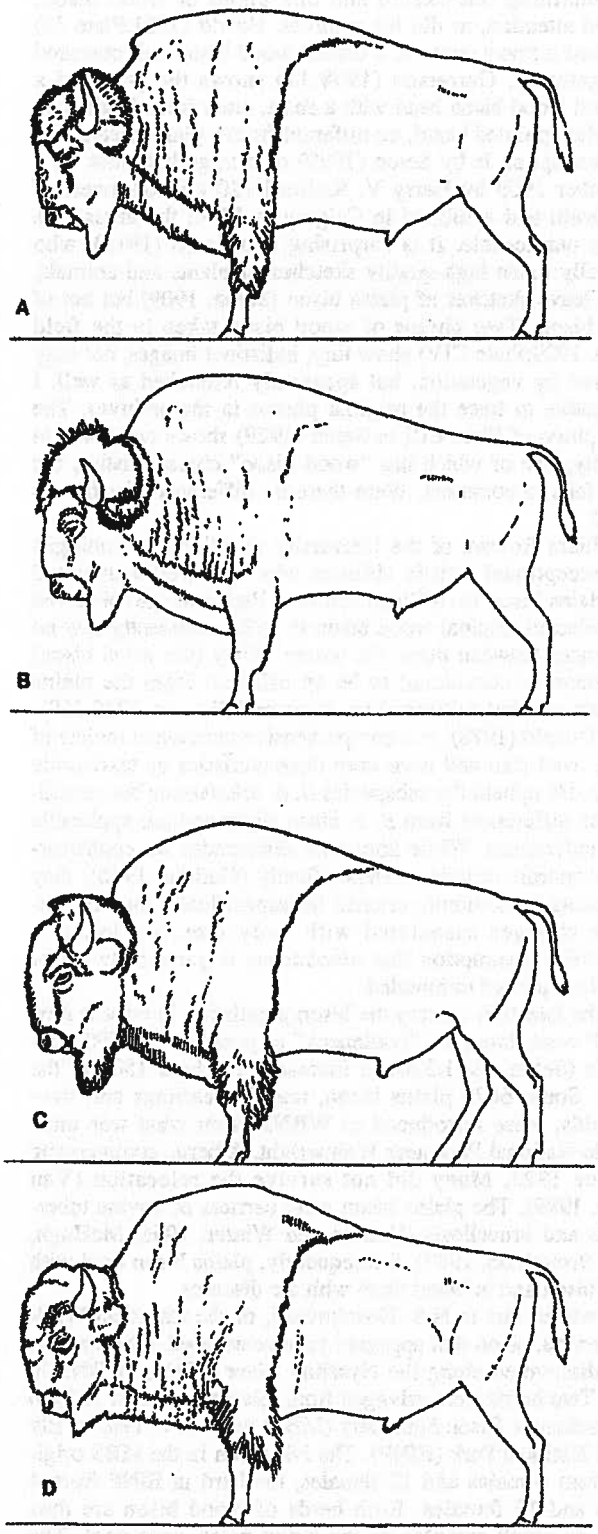

FIG. 1. Some variation in the coat and humps of bison bulls arranged and sketched for comparability: a) A Montana bull in late-winter coat with an unusual hump morphology (McHugh, 1972:198-199). b) A very old white Montana bison bull, called Old Medicine, in late winter coat. Note the absence of chaps or distinct long-haired cape (McHugh, 1972:198-199). c) Mature plains bison bull Black Dog in late-summer pelage (Garretson, 1938:5). d) Mature plains bison bull from Elk Island National Park (EINP) in mid-summer during mating season.

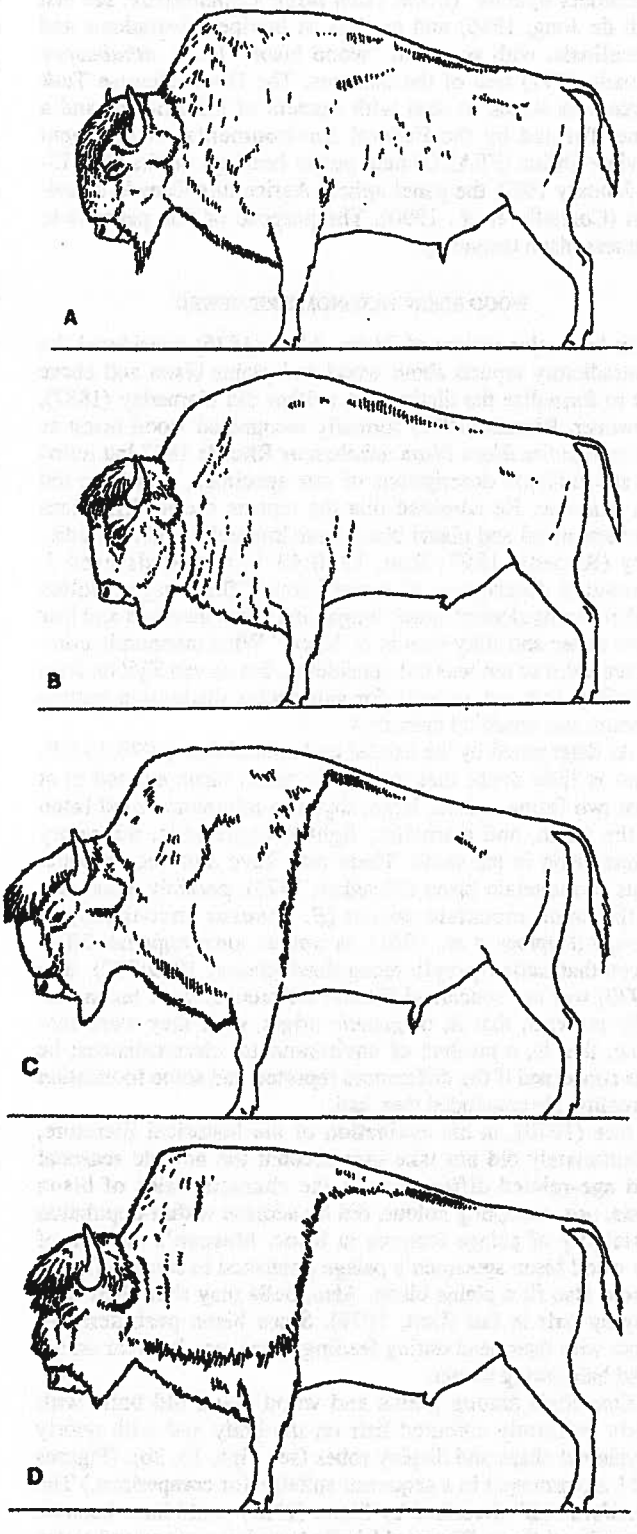

FIG. 2. Archetypal wood bison bulls of Nyarling River (NR) origin in Elk Island National Park (EINP), and southern plains bison bull. a) Old NR bull in summer coat (28 July 1980) without visible sign of a cape and short display hair on head and front legs (van Zyll de Jong, 1986:42, Fig. 1). b) Old southern plains bison bull during hair shedding in early summer, held in Hamburg zoo in 1923 (Krumbiegel, 1980:154, Fig. 5). c) Younger NR bull in August 1977 (van Zyll de Jong, 1986:42, Fig. 3). d) NR bull in mid-winter 1979.

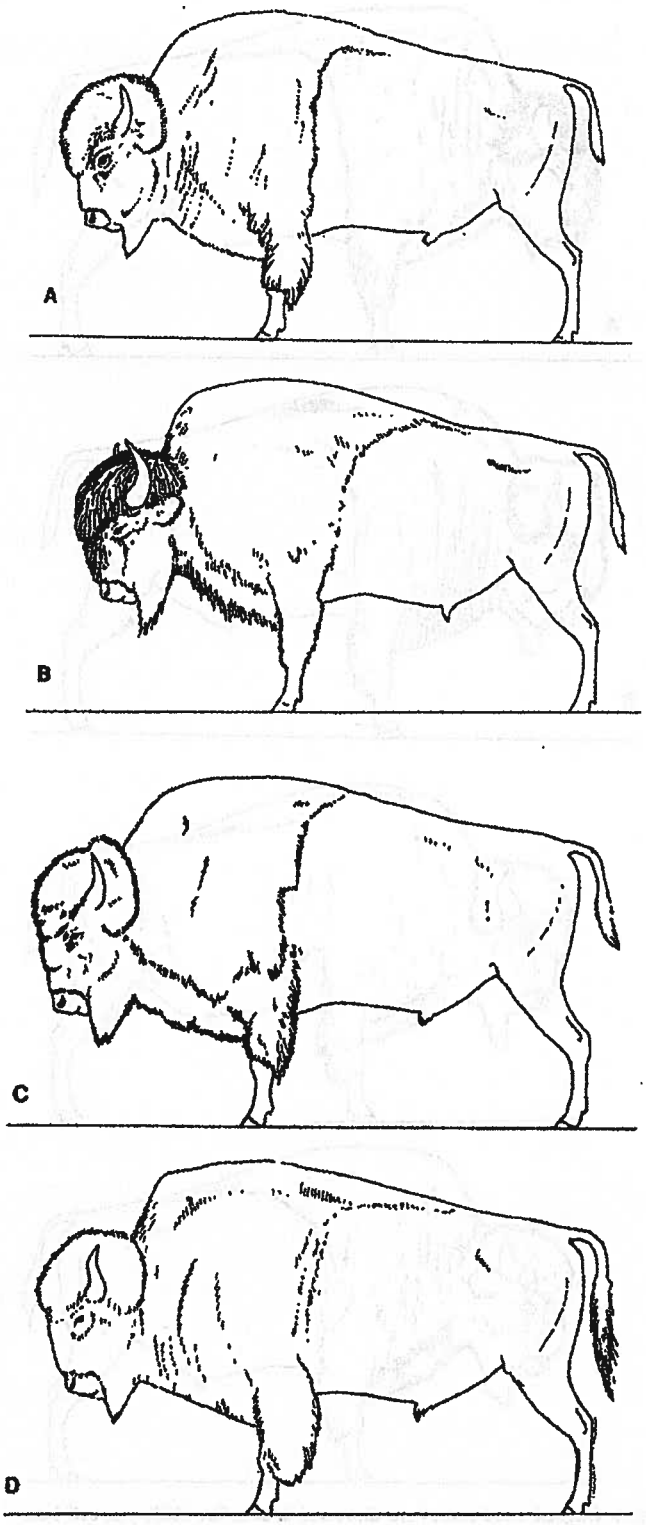

FIG. 3. More southern plains and NR bison: a) Fairly young bull from the Texas Goodnight herd, after archival photos. b) "Old Tex," very old bull originating from Texas bison in winter hair, renowned for his long record horns, held in captivity in Yellowstone National Park in 1926 (Maegher, 1973, Fig. 23). Note reduced chaps and long bonnet hair. c) NR bull from EINP in mid-winter (1979) with well-developed display coat. d) Young NR bull held captive in Calgary Zoo till 1991 in early summer coat.

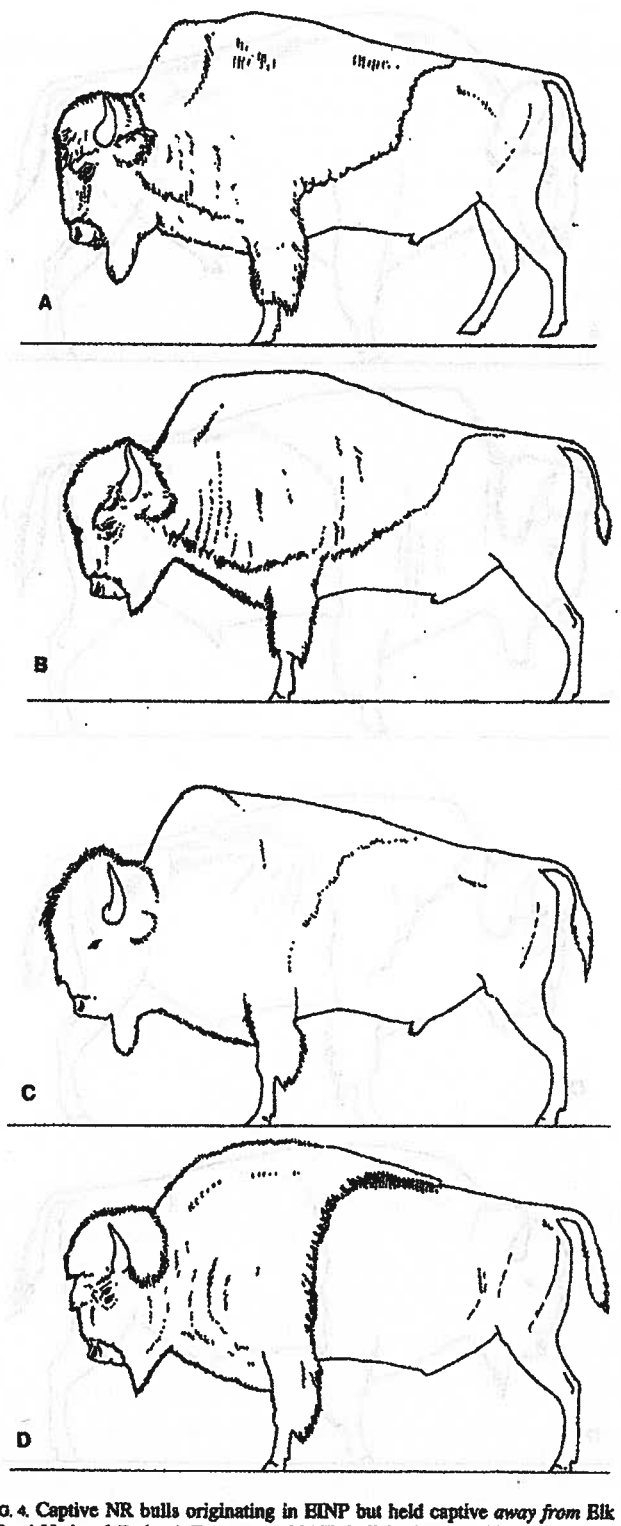

FIG. 4. Captive NR bulls originating in EINP but held captive *away from* Elk Island National Park. a) Four-year-old NR bull in August 1980 held on the Wildlife Reserve of western Canada, near Cochrane, Alberta. The display hair is well developed. This bull features the long cape. b) A three-year-old NR bull transferred to a paddock in the central Yukon, where natural forage was supplemented with hay. The bull shows a well-developed display coat one year after leaving EINP. c) Mature wood bison bull in Moose Jaw Wild Animal Park, with long-haired display coat (17 June 1983). d) Four-year-old NR bull held captive in display paddock in Banff National Park in February 1991. The display hair is long everywhere.

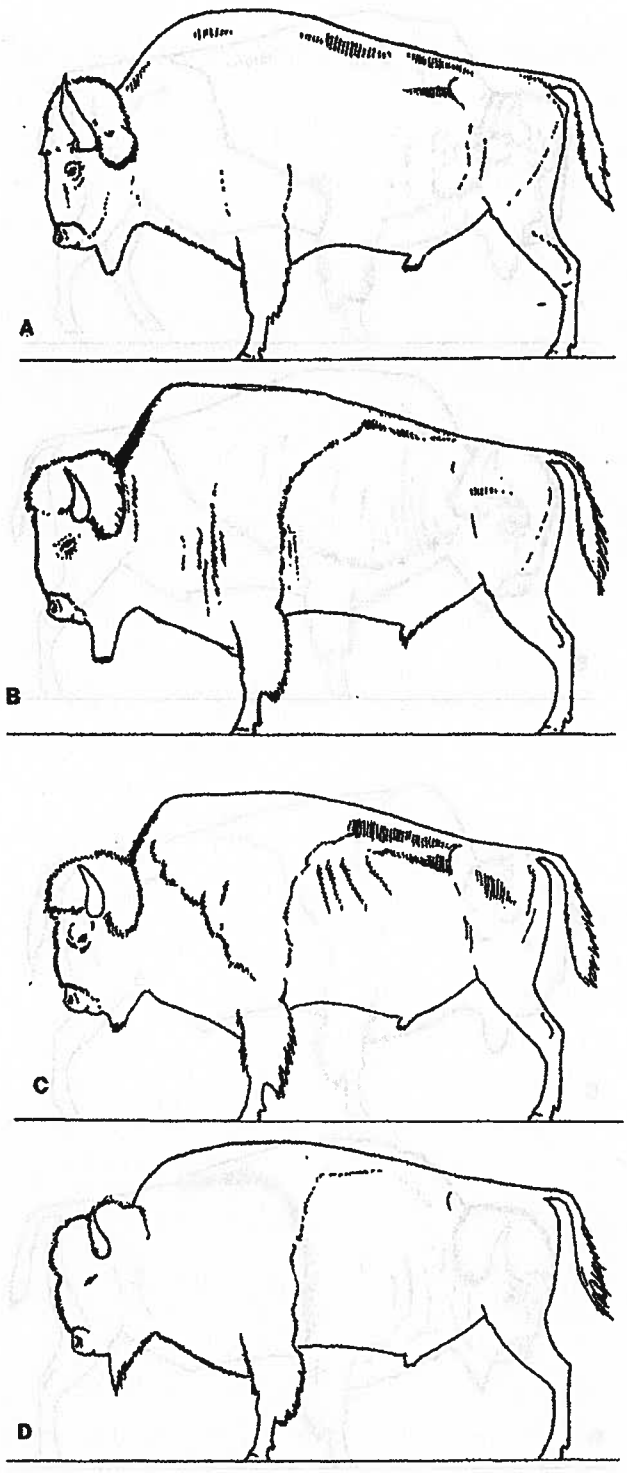

FIG. 5. NR bison in the Mackenzie Bison Sanctuary in May 1990. a) An old, emaciated bull well into shedding, with short chaps but long bonnet hair between the horns, a full beard and a tall hump that is not elevated anteriorly. b) Mature bull beginning to shed with long-haired display coat and anteriorly elevated hump. c) Mature bull with long display hair and elevated anterior hump. d) Young bull with low hump, depressed anterior and mid-length display hair and scraggly beard.

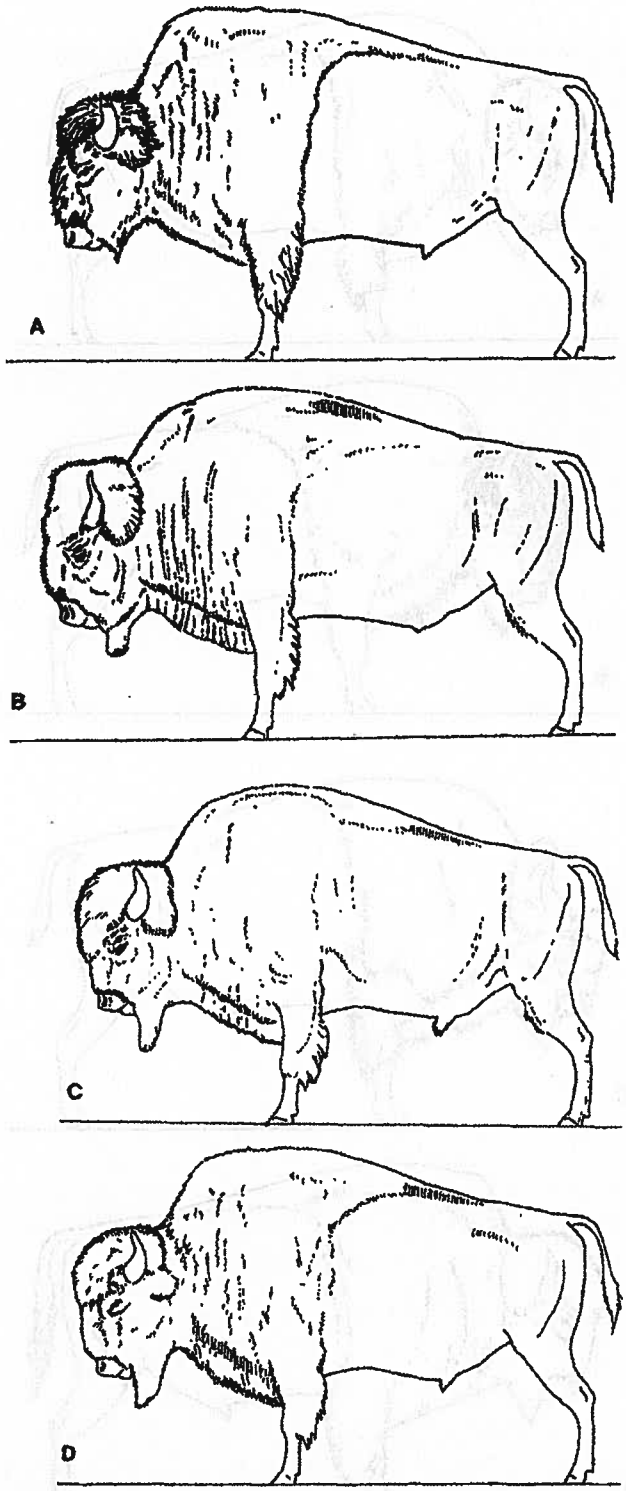

FIG. 6. Original wood bison bulls illustrated in or before 1925, plus bull from captivity. a) An old wood bison bull taken in early September 1925 and sketched from two sketches and one photograph left by William Rowan in the archives of the University of Alberta. Note short-haired display hair, patterned much as in plains bison. The hump shape is conjectural. b) Old bull in early fall with long-haired display hair, but still without a cape. From photo by Rowan. c) Mature bull with long-haired display hair but still without cape in late summer. From photo by Rowan. d) NR bull from EINP in captive herd in Toronto Metro Zoo, 3 September 1984 (van Zyll de Jong, 1986:43, Fig. 6).

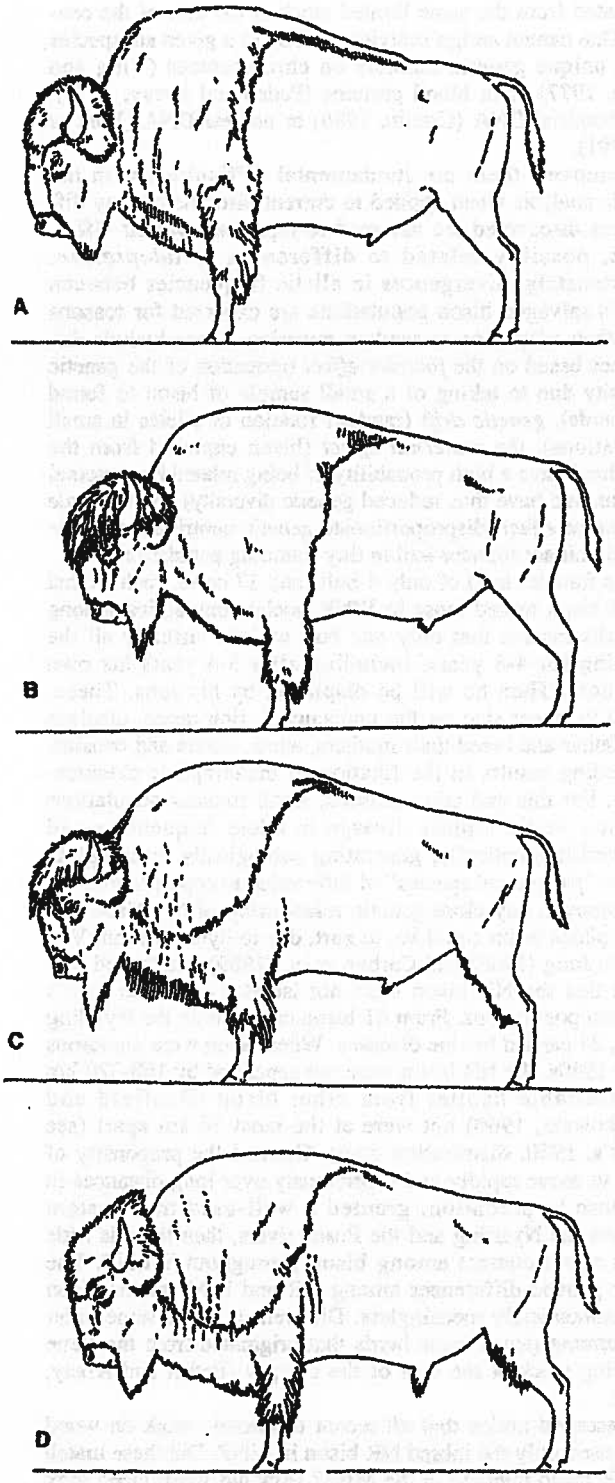

FIG. 7. Northern and southern plains bison bulls. a) A bull from Yellowstone National Park showing the high hump found in this bison population (Meagher, 1973). b) Captive southern plains bison bull with long, procumbent frontal hair (after Heck, 1936). c) A bull from the Wichita Mountain Reserve in summer, with features reminiscent of the southern plains bison as described by Krumbiegel (1980). Note the long frontal hair and thin, though long, display hair. d) Other bulls from the Wichita Mountain Reserve featured typical "plains bison" features (the display hair on this bison's head is blown back by wind).

the Compendium of Government Agencies Submissions) is unacceptable. It confounds absolute population size with effective population size and ignores the subsequent loss of genetic information through genetic drift, maternal relatedness and, especially, the male-dominance effect (see below).

The next authors to provide descriptions and illustrations of wood bison were Geist and Karsten (1977). They made detailed comparisons of NR bison and plains bison held separately in EINP. Their "wood bison" agreed with the partial description by Seton (1929) of the Radford Bull and was confirmed by van Zyll de Jong (1986), who used the same groups of plains and "wood bison" in EINP. Van Camp (1989) published a photo of a bull from Hook Lake, east of the Nyarling River, with classical "wood bison" features. The image of wood bison by Geist and Karsten (1977) became the archetye of the "wood bison phenotype," at which conservation efforts were henceforth directed.

However, following the publication of Geist and Karsten (1977), directors of zoos pointed out that captive wood bison did not conform to the published descriptions but had hair coats similar to northern plains bison. A herd of "wood bison" held captive near Edmonton and examined by Geist and Karsten on 24 October 1975 also had northern plains bison features. These bison, strikingly different from the wood bison in nearby EINP, were dismissed as potential hybrids. Peter Karsten, then a member of the committee for the rehabilitation of wood bison, notified the committee and voiced concerns about the "wood bison" phenotype. He made arrangements for two herds of NR bison to be established in or near Calgary to observe their development.

Krumbiegel (1980) proposed that plains bison be segregated into two subspecies, a "southern plains bison," the nominal subspecies (*Bison bison bison* Linnaeus 1758) and a "northern plains bison" (*B. b. montanae* Krumbiegel 1980). He followed here an earlier lead by Heck (1936), who drew attention to the differences between the bison German zoos acquired before the 1870s and those just before and after World War I. Krumbiegel's (1980) description of southern plains bison pelage is close to that of Geist's and Karsten's (1977) for wood bison (Fig. 2b); the same pelage appeared to grow on two purported subspecies, *B. b. bison* and *B. b. athabascae*. Krumbiegel (1980) published in German, but subsequently his views appeared in English (Krumbiegel and Sehm, 1989).

Van Zyll de Jong (1986) dismissed Krumbiegel's (1980) research of historic sources on the basis of inadequate sampling and because van Zyll de Jong's (1986) morphometric analysis failed to distinguish southern from northern plains bison. Unfortunately, craniometry distinguishes differences related to *size*, not necessarily differences related to genetics, and van Zyll de Jong's (1986) data shows that all plains bison had skulls of similar size. This is illustrated, for instance, by the findings of Bohlken (1967) that *B. bonasus* (wisent) is craniometrically closer to *B. b. bison* than the latter is to *B. b. athabscae*, even though *B. bonasus* is biologicaly quite different from *B. bison*. For instance, post-cranially, wisent are quite different from bison (Bohlken, 1967; Guthrie, 1989), much less adapted to cursorial life and, compared to the latter, notoriously difficult to keep in captivity, in part due to the wisent's adaptations to browsing (Heck, 1936). Wisent have much less-differentiated display hair and a different shedding pattern from bison, and the calves do not have the light neonatal coat.

Van Zyll de Jong (1986) accepted multiple photographic images for pelage analysis of wood bison from the inbred herd of NR bison in EINP. Relying for data on an inbred herd, no matter how well sampled, describes with increasing precision at best a small range of the natural variation. At the worst, it accepts phenodeviants as normal. Krumbiegel's (1980; Krumbiegel and Sehm, 1989) historic sources on bison covered a wide span in geography and time, which gives some credence to his conclusions. His claim that southern and northern plains bison are taxonomically distinct rests on pelage differences virtually identical to those accepted as valid taxonomically by van Zyll de Jong (1986). He published photos of captive EINP wood bison that had pelages typical of northern plains bison (Figs. 4c, 6d) but appeared unaware that captive wood bison assumed plains bison features.

Concurrent with conventional means of defining wood and plains bison taxonomically, attempts were made to analyze genetic differences among bison populations. The results were ambiguous. Peden and Kraay (1979) found that plains bison populations differed in blood-typing reagents and carbonic anhydrase alleles as much as did the NR bison from plains bison in EINP, even though different herds of plains bison originated from the same limited stock at the turn of the century. One cannot assign individual bison to a given subspecies using unique genetic markers on chromosomes (Ying and Peden, 1977) or in blood proteins (Peden and Kraay, 1979), mitochondrial DNA (Cronin, 1986) or nuclear DNA (Bork *et al.*, 1991).

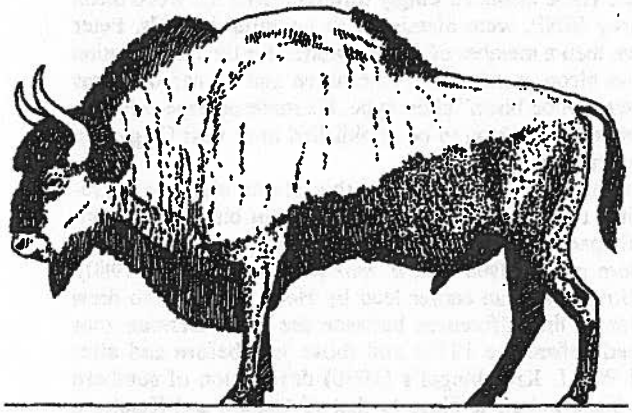

FIG. 10. External features of the extinct long-horned Eurasian-Alaskan steppe bison, *B. priscus*, regarded as an ancestor of *B. bison*, after Geist (1971) and Guthrie (1989).

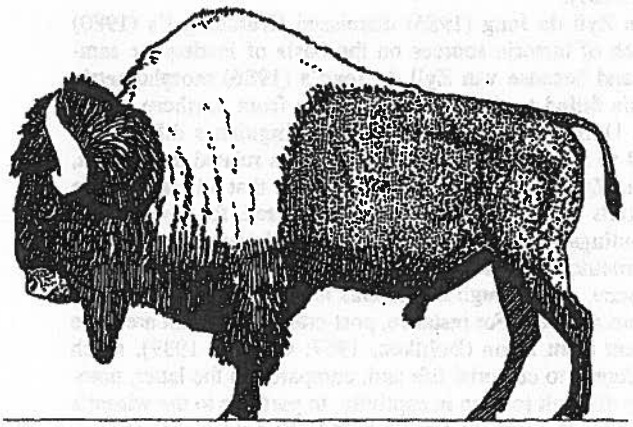

FIG. 11. Reconstruction of the extinct North American late Pleistocene thick-horned bison *B. antiquus*, regarded as an ancestor of *B. bison*.

Moreover, there are fundamental difficulties with the genetic analysis when applied to current bison herds: any differences discovered are assumed to represent *evolved* differences, possibly related to differences in *adaptation*. Unfortunately, divergences in allelic frequencies between today's salvaged bison populations are expected for reasons other than adaptation or random mutation. These include differences based on the *founder effect* (reduction of the genetic diversity due to taking of a small sample of bison to found new herds), *genetic drift* (random fixation of alleles in small populations), the *maternal effect* (bison captured from the same herd have a high probability of being related by maternal descent, and have thus reduced genetic diversity) and the *male dominance effect* (disproportionate genetic contribution of the most dominant founder bull in tiny founding populations).

In a founder herd of only 4 bulls and 17 cows, such as that of NR bison turned loose in EINP, social competition among the bulls insures that only *one* bull will do virtually all the breeding for 4-6 years, including after 3-4 years his own daughters. Then he will be displaced by his sons. These, grown to larger size on the unoccupied, rich range, displace their father and breed their mothers, aunts, sisters and cousins. Inbreeding results in the fixation of meaningless phenodeviants. For this and other reasons, small founder populations of bison would rapidly diverge in allele frequencies and impoverish genetically, generating zoologically meaningless genetic "pseudo-subspecies" of little value to conservation.

Moreover, any close genetic relationship of NR bison and EINP plains bison could be, in part, due to hybridization. Van Zyll de Jong (1986) and Carbyn *et al.* (1989) marshalled evidence that the NR bison were not isolated from the park's southern populations. From 61 bison captured on the Nyarling River, 24 carried bovine diseases. When bison were numerous in the 1940s, the NR bison were not separated by 160-320 km of unsuitable habitat from other bison (Banfield and Novakowski, 1960) but were at the most 16 km apart (see Fuller's, 1950, distribution map). Granted the propensity of bison to move rapidly and capriciously over long distances in response to predation, granted a well-used trail system between the Nyarling and the Peace rivers, then there is little doubt about contact among bison throughout WBNP. The minor genetic differences among NR and EINP plains bison are taxonomically meaningless. Differences of the same order exist among plains bison herds that originated from the same founding stock at the turn of the century (Peden and Kraay, 1979).

It escaped notice that *all* recent taxonomic work on wood bison used only the inbred NR bison in EINP. Did these match the NR bison released in the MBS? How did wood bison look prior to 1925, before mixing with plains bison in WBNP? How did EINP wood bison change in captivity? How did they resemble "southern plains bison," and were such still extant?

Beninde (1937), in a study of transplanted red deer, found that different genotypes transplanted to the same environment converge on the resident phenotype. This was subsequently experimentally confirmed using passerine birds by James

(1983). This implies that plains bison transplanted into wood bison habitat and given time to overcome the tenacious phenotypic lag-effect to changes in environment, the maternal effect transmitted non-genetically over several generations (Vogt, 1948; Chandra, 1975; Denenberg *et al.*, 1962; Denenberg and Rosenberg, 1967; Beach *et al.*, 1982), will assume the wood bison phenotype. Do current "hybrids" in WBNP look like wood bison?

ARCHETYPAL WOOD BISON

The most distinct differences between the archetypal "plains" and "wood" bison from EINP (Figs. 1,2) are 1) the absence of long-haired, dense "chaps" in wood bison of both sexes; 2) the absence of a long-haired, usually light cape that terminates sharply behind the front legs; 3) the procumbent, long, thin frontal display hair, in contrast to the "Afro" hairrole of the plains bison; 4) the thin, short beard of the wood bison, compared to the full beard of the plains bison; 5) the short-haired ventral neck mane of the wood bison, compared to the long-haired neck mane of the plains bison; 6) a taller, more pronounced anterior hump in the wood bison, while plains bison (normally) had a lower hump with the anterior part of the hump lower than the main hump (Geist and Karsten, 1977; van Zyll de Jong, 1986). However, this is not a consistent characteristic, as plains bulls with wood bison humps are found, and vice versa.

In principle, the NR bison of EINP differ from northern plains bison by short display hair on the head, neck, cape and front legs. The display hair grows more slowly during spring, summer and fall than in plains bison. Thus in early fall the cape may be only outlined, but in winter the display hair has grown in place and is then reminiscent of plains bison, but shorter in length. In summer, after shedding the winter hair, big EINP wood bison may appear virtually "naked." Young bulls show more of a procumbent hair mop than do old bulls.

Southern plains bison bulls, as described and illustrated by Heck (1936), Krumbiegel (1980) and Krumbiegel and Sehm (1989), had a procumbent frontal hair mop of long hair; some had a short-haired display robe terminating behind the shoulders; some had full- and some had thin-haired chaps or no chaps at all (Figs. 2b,3b) and a short ventral neck mane. These claims are supported, in part, by two photos of southern bulls in captivity in Germany (one a very old bull — Fig. 2b) and by early 19th-century sketches of northern and southern plains bison. (In these sketches, both subspecies of plains bison have an elevated anterior hump, a feature considered diagnostic of wood bison [van Zyll de Jong, 1986], but not absent in plains bison. This identity may be due to artistic licence.)

These are the sources of southern plains bison I examined: 1) Wolfgang Frey kindly sent me photos of southern plains bison bulls from the Goodnight Herd, which he had found in the archives at the Historical Panhandle Plains Museum in Canyon, Texas, and in the Antonius Collection in Berlin. The remnants of the Goodnight Herd are the only unadulterated plains bison, derived entirely from stock captured in the Panhandle of Texas by Charles Goodnight, beginning in 1878 (Garretson, 1938). Three young bulls feature somewhat short, erect display hair on the head, while the fourth bull, a large mature male, has a long-haired "Afro," a full beard and long neck hair. All had robes cut off behind the shoulders and good chaps. None features a long-haired, procumbent hair mop. The hump line was typical for plains bison. 2) In Seton (1929), Plate CIII has three photos of captive plains bison; the upper one shows two bison, one of which matches Krumbiegel's (1980; Krumbiegel and Sehm, 1989) description of southern plains bison. 3) Thomas and Toweill (1982:513) show a photo of a bison bull confronting a hunting party in Kansas in 1867. The bull, partially obscured, has a small hair mop on his head with procumbent frontal display hair, a diffuse cape and a low hump typical of plains bison. It appears to have chaps. 4) "Old Tex," a bull originating from Texas bison and held many years in Yellowstone National Park (Maegher, 1973; see Fig. 3b), fits Krumbiegel's description. 5) The southern plains bison phenotype can be identified today only with difficulty in photos of the Wichita Mountain herd. Seven of eight bulls are close to northern plains bison; one bull only approaches the phenotype of southern plains bison (Fig. 7b).

Van Zyll de Jong (1986), in addition to examining pelage characteristics, applied morphometrics to populations of plains and wood bison. He concluded that the NR bison were more similar to the original wood bison than to plains bison. Not unmindful of the pitfalls inherent in morphometrics as a tool to analyze taxa, van Zyll de Jong (1986) felt that his case was strengthened by what he thought were three relevant facts: 1) That bison collected before 1925 from the original wood bison range conformed closely to the EINP and MBS wood bison, while individuals from all three populations differed noticeably from the plains bison in EINP and from old plains bison samples. 2) That in EINP wood and plains buffalo were distinct, although they lived in the same environment. 3) That in captivity neither wood nor plains bison changed their respective appearances.

It turns out that all three contentions are invalid (see below); cranial similarities to original wood bisons by NR bison from EINP and MBS are based on size, an unacceptable taxonomic criterion; comparative morphometry distinguishes populations, not taxa. EINP wood and plains bison live under different forage regimes, while the "wood bison" phenotype changes in captivity or in transplants to a "northern plains bison" phenotype.

CAPTIVE AND TRANSPLANTED WOOD BISON

Captive or transplanted wood bison from EINP look much like northern plains bison. In addition to the plains-bison-like wood bison bulls in captivity in Toronto and Moose Jaw (van Zyll de Jong, 1986:43), NR bisons from EINP in four captive herds assumed a northern plains bison exterior (long-haired and dense chaps, long-haired and sharply bordered display coats, "Afro" hair mops, full beards and long ventral manes; some bulls have a high anterior hump, some do not; Figs. 4, 6d).

1) The EINP wood bison bull on Smeeton's game farm near Cochrane, four years old (Fig. 4a), had a hump reminiscent of NR bison in EINP (as did the large bull held captive in Moose Jaw, Fig. 4c), but had an upright hair mop, a large, broad beard, long nape hair and dense chaps. His cape, sharply set off from the short, dark body hair, however, was unusual; it was a "long cape," reminiscent of the extinct *Bison priscus* (Fig. 9). The two cows had regular northern plains bison features.

2) Four adult EINP bison of NR origin held in the display paddock of Banff National Park show classic plains bison features (Fig. 4d). The four-year-old bull has an exceptionally tall "Afro" hair style, a very light, long-haired cape distinctly set off just behind the front legs and a long beard, chaps and nape.

3) All four EINP wood bison held until early 1991 in the Calgary Zoo had northern plains bison features (see Fig. 3d).

4) Thirty-four EINP wood bison were released in a large enclosure in the central Yukon Territory on 6 March 1986. Photos from winter 1986/87 to fall 1987 were available. Three full-grown bulls appeared in their 1987 pelage as follows: one had plains bison features, except for a high first hump; one had "wood bison" features, except for a light, well-delineated cape and moderately long chaps; one had plains bison features, including the first hump lower than the second, but the display hair was short everywhere (Fig. 4b). From six adult cows only one had an elevated first hump; one had a high hump, but the first hump was not taller than the second. All had chaps and well-delineated capes, except the cow with the tall first hump. Her chaps were long but thin, and the cape, though well developed, blended into the body hair gradually.

5) In examining captive plains bison from EINP, the bison herd held in 1963 in the buffalo paddock of Banff National Park and bison from Waterton National Park, as well as pictures of wood bison in EINP in different seasons, one notices certain variations: since the cape grows out fully in late summer, plains bison in early summer may have little cape and feature no distinct delineation of the cape. The plains bison held in 1963 in Banff had very tall humps in which the height of the anterior hump varied with the posture, often exceeding the second hump. Body colour varied with the wetness of the fur. Plains bison in summer with wet fur are as dark as wood bison under the same condition. EINP wood bison in the Yukon holding enclosure looked a lot more like "wood bison" during the spring moult than at other times of the year; some had long, thin procumbent hair, a thin beard, virtually no ventral mane and short, thin chaps. Observations in the Leipzig Zoo suggest that the long hair in the chaps of wood bison can be pulled out readily (letter from W. Frey to S.N. Stuart, IUCN, 1987). The long display hair of plains bison bulls drops out before winter (Lott, 1979).

Van Zyll de Jong's (1986) assumption that wood and plains bison retain their phenotypic characteristics in captivity is not tenable.

NYARLING RIVER EINP AND MBS SPECIMEN COMPARED

I examined colour photos of nine male and four female bison from the Mackenzie Bison Sanctuary taken in May 1990. These descended from bison captured at the Nyarling River, as are the wood bison held in EINP (Fig. 5).

1) A bull, apparently three to four years old, has an erect hair mop between the horns, a short beard, good chaps, full tail; no noticeable cape development, but light (brown) hair slants down from tail-root to elbow. A short, black, mid-dorsal streak leads to the hump. The tall hump peaks anteriorly, as in EINP wood bison.

2) The remaining bulls were all older or very old animals in various stages of shedding. All had an erect, well-developed hair mop between the horns, as well as long-haired, thick chaps on the front legs. Three had massive beards, three did not; one was grazing and his beard was hidden. One had the long cape, four had a cape cut off behind the front legs and three were too advanced in shedding to tell. In five bulls the hump peaked anteriorly; in three it did not.

3) The bison cows were in a nursery herd. They were all tall-humped, with flat hump lines, peaking in front in two cows but peaking over the shoulders in two other cows. All had erect hair mops and long, dense chaps.

These bison from the MBS, although of the same origin as the EINP wood bison, showed little similarity to the EINP animals.

NYARLING RIVER BISON AND WBNP BISON COMPARED

In a colour photo of WBNP bison, the animals are fully shed out with the capes growing in; the season is mid-summer. All twelve old, mature bulls have tall humps; in eleven the anterior is higher. In a second photo six of eight large bulls have the hump elevated anteriorly. Of fourteen unobstructed capes, only one is a long cape, seven are short capes and in seven others the colour extends back to the hip, but only over the shoulders is the cape hair long. Procumbent hair mops can be seen only in young bulls. The black dorsal neck stripe is well exposed because the cape hair is still short. All cows have capes of the extended type. In another photo three bulls have cut-off capes and big, erect hair mops on the head; the chaps are invisible in deep grass. All three have humps that peak anteriorly, possibly because they hold their heads high in the deep sedges. In another photo all five bulls have short capes, big chaps, erect hair mops and anteriorly elevated humps.

In a selection of slides taken in early fall in WBNP one sees bulls with long capes, short capes and barely distinct capes ranging in colour from straw-blond to reddish dark brown. All big bulls but one have big erect hair mops and chaps. One bull, however, has no chaps, a long cape and short head hair; he also resembles in colouration and hump shape a *Bison priscus* (Fig. 9). The bison bulls and cows of WBNP are not discernibly different from those in the MBS, and they share with EINP bison from the NR the high, anteriorly elevated hump. They look much like captive EINP wood bison or large plains bison. However, a few individuals resemble the "archetypical wood bison," except for having a long, light cape, and have humps reminiscent of those of *B. priscus* (Geist, 1971:Fig. 7; Guthrie, 1989:Fig. 5.13). Different hair styles segregating out in the same population suggest a strong hereditary polymorphic component for the hair patterns.

NYARLING RIVER AND ORIGINAL WOOD BISON COMPARED

In November 1990, W. Fuller, University of Alberta, mentioned a portrait sketch of wood bison made by the late William Rowan. John Foster kindly checked the Rowan Archives, where he found photos and sketches of wood bison, as well as an original of Rowan's (1929) article.

One is a portrait sketch of an old wood bison bull shot in early September 1925 and published in Rowan (1929). The bull has rather short but erect display hair all around; there is no procumbent hair mop between the horns (Fig. 6a). A poorly exposed photograph of apparently the same downed bull confirms the shortness of the hair between the horns. The head resembles a mature NR bull in van Zyll de Jong (1986:45 Fig. 6) that van Zyll de Jong considers to be similar to the "plains bison" phenotype.

Rowan, in a second sketch of a wood bison bull, attached said portrait to a plains bison bull body. This was not a technical sketch, but a Christmas card. The photo of the downed bull shows a darkish cape with hair only slightly longer than the body hair, with a light streak right behind the front leg. It

appears to be a classical short cape, as it extends on the back along the spine, but not over the ribs; I cannot discern a dark mid-dorsal stripe on the neck. The upper front legs are short haired, with sparse strands of long hair; the rear margins of the leg, where long chap hair is expected to grow, is not visible. Rowan's "Christmas card bull" does have big chaps.

The photo Rowan (1929) published of a wood bison herd at Graham's Ford in 1925 was augmented by a second one of the same herd, the negative of which was discovered by Ian MacLaren. Both show a distant herd and the images are small and somewhat obscured. There are bulls with large humps, but I see only one hump elevated anteriorly. They sport big, erect frontal display hair, but some have short-haired and procumbent hair mops; the cows have short beards and frontal hair. One can decipher several light, apparently short-haired capes, distinctly set off right behind the shoulders. The front legs are largely obscured by shrubs, but the few visible are noticeably thicker than the hind legs, indicating at least modest chaps.

Rowan's 1925 diary held additional sketches and loose photos, among them three photos of bison bulls (Fig. 6), of which only one resembles bulls from the NR herd in EINP. The bulls have not yet grown the display capes. Their heads resemble those of plains bison; the hump is tall, but not dissimilar to that of plains bison, and they have well-developed chaps on the rear margins of the front legs, and even some elongation of hair on the hind legs. Another photo of a herd of wood bison shows animals with light capes sharply cut off behind the shoulders and large, erect mops of hair on the heads. Unfortunately, these photos are not labeled, and only their presence in the 1925 diary suggests that they are photos of wood bison. These and the *bona fide* photos and sketches of wood bison suggest that, excepting possibly one bull at Graham's Ford, the phenotype of wood bison in 1925 in WBNP was not that of NR "archetypal wood bison" in EINP. The pre-1925 wood bison resemble present WBNP, MBS and EINP wood bison in captivity, or plains bison. Therefore the NR bison in EINP stand apart in their external appearance, excepting the lone Hook Lake bull whose photo was published by Van Camp (1989) and an occasional bull in WBNP (Fig. 9). Before explaining the "archtypal wood bison phenotype," we must turn to a discussion of taxonomic criteria commonly employed.

MORPHOMETRY NOT TAXONOMICALLY RELEVANT

A review of taxonomic papers on large mammals shows that while taxonomists have increasingly refined methods of detecting differences among populations, they have lagged behind in analyzing the nature of these differences (Geist, 1989, 1991a). Much faith is placed in skeletal measurements and the analysis thereof by means of sophisticated multivariate statistical methods, as exemplified in the taxonomy of American bison by van Zyll de Jong (1986).

The use of morphometry to detect genetic differences, however, is like using a rubber band to measure distance. While morphometry is a good tool to segregate *populations* (where factors of individual variation such as genetic relatedness, resource abundance, behavioural traditions, climatic effects, etc., vary in the *same* direction), it is an inadequate tool to segregate *taxa*. Comparative morphometry confounds genetic, epistatic, environmental and statistical variation, and thus confuses phenotype with genotype and homology with analogy. Morphometrics applied to phenotypes cannot, in principle, isolate the hereditary differences among populations. That can be done only with characteristics whose expression depends on high penetrance of genes, and that can only be identified experimentally.

Body size and shape are not independent, and both are much affected by environment; body size changes with net nutrition, while shape changes with size (allometry) and with muscular forces (Ingebrigtsen, 1923; Vogt, 1936, 1948; Beninde, 1937; Iljin, 1941; Slijper, 1942; Du Brul and Laskin, 1961; Wood *et al.*, 1962; Klein, 1964; Gottschlich, 1965; Zeuner, 1967; Risenfeld, 1969; Meunier, 1977; Ellenberg, 1978; Klein *et al.*, 1987).

This old and well-demonstrated knowledge, which is the essence of the discipline of animal science and its "theory of centripetal growth" (Wilson, 1952, 1958; Palsson and Verges, 1952; Hammond, 1971) and of the practice of and research pertaining to orthodontics, has not been included in the practice or theory of taxonomy. Phenotype plasticity has been widely ignored in biology (Geist, 1978:116-144, 1989, 1991a), although this may be changing, as in 1989 a whole issue of *Bio Science* (Vol. 39, No. 7) was devoted to phenotype plasticity. Phenotype plasticity is reflected in adaptive phenotype extremes (ecotypic morphs), which were independently proposed by many authors. Stimulated by the early work of animal scientists, Geist (1971, 1978, 1989), Hutton (1972), Shackleton (1973), Horejsi (1976) and Bunnell (1978) identified high-quality (later "dispersal") and low-quality (later "maintenance") phenotypes. Other examples are: Fruehentwickler and Spaetentwickler (Ellenberg, 1978); paedomorphs and paramorphs (Albrecht, 1979, in Balon, 1985); dispersers and biders (Packard and Mech, 1983:166). Similar conclusions were reached by ornithologists (Watson and Moss, 1972), entomologists (Wellington, 1960; Harrison, 1980), limnologists (Calow, 1980; Calow and Townsend, 1980), hesitantly approached by students of small mammals (Lidicker, 1975; Gaines and McClenaghan, 1980), but well accepted and incorporated into life history theory by ichthyologists (Balon, 1981, 1984, 1985; Noakes and Balon, 1982; see also Bruton, 1989). There are epigenetic studies dealing with this phenomenon (Waddington, 1957; Lovtrup, 1974). Models of mammalian ecotypic plasticity may be applicable to humans (Geist, 1978, 1989).

Rhoad's designation *athabascae* became accepted because free-living wood bison are larger than plains bison in size (Roe, 1970; van Zyll de Jong, 1986). However, body size and size-related (allometric) differences in body proportions are poor taxonomic criteria. Thus wood bison may have been larger because they lived at higher latitudes (a phenomenon usually ascribed to the invalid Bergmann's Rule; Geist, 1987a). Plains bison may have been small because of the high cost of migration, analogous to small-bodied migratory reindeer (Reimers, 1972). Plains bison in zoos grow very large (Dathe, 1984), and under the same captivity regime plains and wood bison bulls grow to the same size (Renecker *et al.*, 1989). A 10% difference in linear dimensions (equivalent to a 33% difference in mass) between free-living wood and plains bison is taxonomically meaningless.

Consequently, bison may differ in size and shape due to differences in local ecology rather than differences in heredity, and the segregation of wood and plains bison on morphometric grounds (van Zyll de Jong, 1986) is taxonomically without

meaning. The differences in skull size between wood and plains bison samples are substantial. If so, then the shape of the skull and post-cranial skeletons will be affected by allometric growth; the sensitive multivariate analysis cannot but show a statistically significant difference here. This difference has biological, but not taxonomic, significance.

A quick check on whether conspecifics differ genetically in size is to check the length of tooth rows. Teeth are tissues of "high growth priority" that tend to be fully developed almost irrespective of the environment (Beninde, 1937). Table 3 in van Zyll de Jong (1986) indicates that tooth-row length is virtually identical for all bison populations he studied. This suggests that wood and plains bison are genetically of the same size, a conclusion upheld by Renecker *et al.* (1989) in an experimental study: bulls of both forms grew under the same conditions to the same body size. However, female wood bison grew larger than female plains bison. Even if this experimental difference is genetic, it may be due to an accidental selection effect, since van Zyll de Jong (1986) found no significant differences in sexual size dimorphism between wood and plains bison.

Van Zyll de Jong (1986) suggested that because the original wood bison and NR bison in the MBS and EINP were similar morphometrically and distinct from current and historical plains bison, the difference reflects genetic differences. That conclusion is unacceptable on ecological grounds: all samples of wood bison, current and historic, came from low-density (expanding), non-migratory populations. All wood bison not only had access to more resources for growth and development, but did not need to spend these resources in costly migration.

Moreover, wood and plains bisons in EINP do not live in the same environment as van Zyll de Jong (1986) assumed. The plains bison live in a dense population and are competing for resources not only with one another, but also with a dense population of elk. Wood bison in EINP, however, then lived at low density without competition from elk. Differences in resource availability are critical to growth and development, not identity of climate, land form and regional plant communities.

ARE PELAGE CHARACTERISTICS TAXONOMIC CRITERIA?

Social organs, in particular the nuptial pelage, have been used historically in ungulate taxonomy (e.g., Lydekker, 1915; Haltenorth, 1963; Geist, 1991a). They include manes, tassels, colour patterns on the face and rump patch, tail characteristics, the presence and size of skin glands and the presence, size and shape of horn-like organs. "Horns" may vary noticeably in size and complexity with environment, but pelage and gland characteristics have been assumed to be good taxonomic criteria, shaped by hereditary factors with a high penetrance — that is, pelage features were assumed to express themselves signature-like in individuals irrespective of environment and "breed true." Whether raised in the wild or in captivity, the races of ungulates can often be recognize by their pelage and "horns" — by their "uniform."

Also, the social markings of both parents are expressed in hybrids of the F_1 generation, as shown by many examples in Krumbiegel (1954), including F_1 hybrids of wisent and bison. Consequently, one can recognize not only parents, but F_1 hybrids of most species pairs. While the number of hair follicles and the characteristics of hair are influenced by nutrition (Ryder, 1983), nuptial pelages appeared resistant to nutrition. Taxonomic confusion has arisen when account was not taken of the age- and sex-related differences and the seasonal pelage changes due to rapid hair growth, wear and shedding (see Geist, 1991a).

While nuptial pelage features were the best available taxonomic criteria, there were troubling observations, in addition to the instability in the pelage of wood bison. Lion males (*Panthera leo*) show different amount of mane development depending on the size of prides they dominate, which in turn is a function of predator density (Guthrie, 1989). Thus large manes (a hindrance in hunting, but apparently a protection in fighting) are typical of male lions holding big prides, while short manes are found where lion prides are small and the population densities are low. There is considerable variation in the size of manes among males, even where prides are large.

IS BODY SHAPE DIAGNOSTIC OF BISON SUBSPECIES?

Much attention has been paid to the shape of the hump. "Wood bison" purportedly have a taller hump than plains bison, with the fore-hump often more pronounced and elevated (van Zyll de Jong, 1986). But Maegher (1977:132) points out that in Yellowstone National Park bison have higher humps compared to other plains bison (Fig. 7a). Unfortunately, van Zyll de Jong (1986: Figs. 29, 30) plots the absolute, not relative, lengths of neural spines, and wood bison, larger than plains bison, have longer neural spines.

Since wood bison exceed plains bison by about 10% in cranial dimensions (van Zyll de Jong, 1986:Table 3), a 10% increase in the length of neural spines in plains bison (van Zyll de Jong, 1986:Table 12) brings them to within one standard deviation of the same lengths as those of wood bison. Since hump size increases rapidly during ontogeny, it suggests that neural spines elongate with positive allometry. If so, then the height of the hump in large bison should be relatively greater than in small bison.

Guthrie (1989), in a study of humps in extinct and extant bison, showed that in a wood bison bull shot prior to 1925 the hump must have been *longer* than in plains bison due to the great length of neural spines on T3-T7. The old plains bison bull used in comparison had rather short spines, and the EINP wood bison was intermediate. Unfortunately, this pattern is not reflected in the data published by van Zyll de Jong (1986).

The apparent height and size of the forward hump may vary with how a bison holds its head (Mohr, 1952; Guthrie, 1989). With the head raised, the splenius and rhomboideus muscles contract and bulge, enlarging the anterior hump and making it rise; with the head lowered, so is the relative height of the anterior hump. Bison that habitually have to scan for predators with an elevated head (ancestral steppe bison of Eurasia; wood bison) or who feed with their heads elevated on tall vegetation (wood bison, wisent) are expected to have a larger front hump than bison that feed almost continually on short sward (American plains bison). One expects that wood and plains bison held under the same conditions will converge in hump shape.

Furthermore, the hump appears more accentuated in the EINP wood bison because the anterior hump line, unlike that of plains bison, is not obscured by long hair radiating from the head. A plains bison with an "Afro" appears to have "less"

hump than a wood bison, even though the distance from horn base to hump peak may be the same. Clearly, the hump as a taxonomic characteristic is in need of further study.

BRIEF REVIEW OF BISON HISTORY

Two discoveries made during this investigation (the "long cape" in some EINP and WBNP bison, and the segregation into short- and long-haired display coats in WBNP bulls) necessitate a brief review of American bison evolution prior to explaining the "wood bison phenotype" of the NR bison in EINP. These differences, linked to Guthrie's (1989) data on extended neural spine lengths on T3-T7 in an original wood bison bull, point to isolated *B. priscus* characteristics in WBNP bison.

Two hypotheses describe the origin of *Bison bison*: the first contends that it is derived solely from the late glacial Siberian immigrant *B. occidentalis* (Geist and Karsten, 1977; Flerov, 1977), which was part of an east Siberian fauna that spread south into America with the extinction of the Rancholabrean megafauna. Here the large, long-horned Siberian bison dwarfed into the small, short-horned *B. bison* of today (Wilson, 1980).

Guthrie (1989) attributed the dwarfing to a change in predator fauna: the long-horned bisons confronted large cats (lions, tigers, homeothers, saber-tooth cats) and the large, cursorial, predacious short-faced bears (*Arctodus*); the extant bison, shy and less fleet-footed (Smiley 1978), contended primarily with wolves. Fossil evidence suggests a replacement of indigenous *B. antiquus* by Siberian bison about 10 000 B.P. (Wilson and Churcher, 1984), shortly after the severe cold pulse known in Europe as the Younger Dryas Stadial (Nilsson, 1983).

The second hypothesis maintains that *B. bison* is indigenous in origin, derived from *B. antiquus*, whose two subspecies *occidentalis* (northern) and *antiquus* (southern) hybridized into *B. bison* after the Altithermal warm phase (McDonald, 1978). Earlier, Skinner and Kaisen (1947) suggested that *B. bison* is derived from hybrids of Siberian *B. occidentalis* and indigenous *B. antiquus*; this is considered likely by Guthrie (1989). The late Pleistocene/early Holocene expansion of *B. antiquus* postulated by McDonald (1978) finds a parallel in *Ovis canadansis* (Geist, 1985): a big-horned southern sheep, very large in the late Pleistocene, radiated northward towards a thin-horned sheep (*O. dalli*) entering from Beringia (Geist, 1985). In the case of *Bison*, but not *Ovis*, the two forms may have met and hybridized.

The absence of Siberian bison in North America, as postulated by McDonald's hypothesis (1978), is unlikely, granted that the large mammals from eastern Siberia are nearly identical to those in North America. Thus Altai and American wapiti (*Cervus elaphus canadensis*) appear indistinguishable and represent the same subspecies (Flerov, 1952). The large east Siberian *Rangifer tarandus phylarchus* has the dark withers and belly typical of primitive caribou, not Eurasian reindeer (Flerov, 1952; Heptner *et al.*, 1961). The moose *Alces alces gigas* is found on both sides of the Bering Strait, and according to Flerov (1977), so was the wood bison. The pachycerine sheep (*Ovis nivicola/dalli*) are remarkably similar, as are brown bears (*Ursus arctos*), wolves (*Canis lupus*), small mammals and the people. It is unlikely for elk, caribou, moose and thin-horned sheep to enter, but not Siberian bison. Under either scenario, *B. bison* is a recent evolutionary product, only some 4000-5000 years old (McDonald, 1978; Wilson, 1980).

In opposition to the hybridization hypothesis are the differences in hair coats of the late Pleistocene *B. priscus* (Fig. 10) and *B. bison* and the shape of the hump, which in *B. bison* resembles that of *B. antiquus* (Guthrie, 1989:196-199). Bison in Pleistocene Alaska had a distribution of neural spine lengths similar to that of European steppe bison (*B. priscus*) and still retained by the European wisent (*B. bonasus*), despite shorter neural spines. The pattern of neural spine lengths in *B. bison* is similar to that of *B. antiquus*. It is here where the occasional *priscus*-like characteristics of bison in WBNP become significant.

The fossil record indicates that the distribution and abundance of bison varied greatly in the Holocene. Wood bison may have been left behind on patches of relict prairie and riparian meadows as boreal forests closed in about 4500 B.P., after the Altithermal period. Another southern shift in bison distribution correlated with cool climates about 700 B.P. (McDonald, 1978). The segregation was not complete even in recent historic times, as plains and wood bison did meet. This happened along the Peace River, where an old plains bison bull was shot in 1866. Roe (1970:51, 54) examined this incident, which had been reported to Ernest Thompson Seton by Elzear Mignault, and considered Mignault a reliable witness. Note that this meeting of southern and northern bison took place at a date well after bison had been severely depleted in Alberta (Hewitt, 1921). Moreover, our notion of continuous forests segregating plains from wood bison is based on a false landscape image: burning by natives maintained open grassland where today, untouched by fire or buffalo grazing, continuous aspen and conifer forests cover the land (Lewis, 1977; McCormack, 1990).

ON THE ORIGIN OF CANADIAN PLAINS BISON

While Seton (1929), Garretson (1938) and the June 1948 issue of The Beaver shed light on the origins of the Canadian plains bison in the former Bison National Park (BNP) at Wainwright, Alberta, the most detailed account is by G.D. Coder (1975) in an unpublished Ph.D. dissertation. All plains bison originate from six primary captures of wild bison calves between 1873 and 1889; at least five of these contributed to the Canadian herd assembled in BNP by 1914: "Buffalo" Charles J. Jones captured 56 calves in northern Texas and added 10 other bison bought from owners in Kansas and Nebraska; (Sam) Walking Coyote's 4 calves, captured probably in northern Montana, started the Pablo-Allard herd; the Alloway brothers captured 5 calves, and Samuel Bedson captured 3 calves in Saskatchewan; Charles Goodnight started his herd with 5 calves and 2 adult Texas bison; Fredric Dupree's herd originated probably from 5 calves that were caught along the Yellowstone River.

The BNP herd began in 1873 from 4 calves caught by (Sam) Walking Coyote from the Pend d'Oreille Tribe near the Milk River, close to Buffalo, Montana, according to Garretson (1938:215), but in southern Alberta, according to The Beaver. They were brought to the Flathead Reservation in Montana, where they multiplied. In 1883, 12 of the bison were bought by C.A. Allard and M. Pablo. In 1893, 26 bison were added to their herd from the herd of C.J. (Buffalo) Jones; an additional 18 cattle × bison hybrids were isolated on Wild Horse Island in Flathead Lake. Buffalo Jones's herd originated mainly from

Texas bison caught in the wild, but in 1889 he bought 58 Saskatchewan bison and 8 catello from Samuel Bedson of Stony Mountain, Manitoba. The remainder of Bedson's herd went to Sir Donald A. Smith (later Lord Strathcona), who donated 13 of these bison to Banff National Park. Three of Goodnight's Texas bison had been brought to Banff in 1887. Bedson's bison came from the McKay-Alloway herd based on 5 calves captured in Saskatchewan in 1873 and 1874; Bedson secured 3 additional calves. Between 1 June 1907 and 6 June 1912, M. Pablo delivered 716 bison, of which 631 went to BNP and the others to EINP. On 31 October 1909, 77 bison were added to BNP from the Banff herd, and 10 more on 31 March 1914; in 1910 and 1911 another 30 bison were added from the Conrad herd (based on bison from Allard's estate) near Kalispell, Montana. Only the Dupree herd appears not to have contributed to the plains bison in BNP. It is this mixture of southern and northern plains bison that was in turn mixed with wood bison in WBNP beginning in 1925. If the Canadian plains bison are hybrids of two subspecies, then the formal designation should be *B. b. bison* x *montanae*, and the current subspecific designation *B. b. bison* is invalid.

THE "WOOD BISON" PHENOTYPE EXPLAINED

The display coat of *Bison* acts analogous to antlers in elk. Keeping all factors equal, the display hair increases in length with nutrition — the richer the forage in nutrients essential for hair growth, the longer and denser the hair in the cape, beard, nape and the hair mops on the head. The coat of bison thus acts as a luxury organ that reflects the owner's competence at foraging. Consequently, the short-haired display robe of the "archetypal EINP wood bison" is ecotypic. Placing these bison on better food changes them into long-haired "plains bison"; one expects that the richer the food in summer in hair-building amino acids, such as supplied by plants growing on sulfur-rich prairie soils, the better the growth of display hair. Also, analogous to antlers, the growth of the display coat is likely to be retarded in young and in old bulls.

In EINP the wood bison mimic what happens to bull elk and moose. A sample of 26 bull elk 4.5 years of age and older shot 2-12 December 1980, when the bulls had little fat, gave an average body weight of 379 (SD=30) kg (Table 1). This makes bull elk in EINP the largest-bodied recorded in North America, much heavier than the 330 kg (Flook, 1970) for a comparable sample of bull elk in Banff National Park (BaNP). Yet the antler length of the EINP bull elk was only 109.6 cm (n=17, SD=6.2 cm); the largest antlers weighed only 7.2 kg. Bull elk in BaNP averaged a (low) 10 kg in antler mass, while the antlers averaged 119 cm (n=54, SD=10.1 cm) in length and weighed maximally 13.3 kg. The antlers of EINP bulls were short, short-tined, straight-beamed and narrow in spread — that is, they were juvenile-like or paedomorphic in form. Moreover, big antlers, cut off and put in water to measure the specific gravity, usually floated; they were spongy and of low specific gravity. Therefore, the large bull elk from EINP had a much lower antler mass than the smaller-bodied bulls from Banff.

A sample of 30 bull moose from EINP 3.5 years of age and older, taken at the same time as the elk, averaged a respectable lean whole weight of 456 kg (SD=44.0). The antlers averaged only 7.8 tines (n=12, SD=1.7) and 99.1 cm in spread (n=10, SD=13.0); the largest antlers had only 119.5 cm spread and 9 tines. The largest three sets of antlers weighed 6.1, 5.7 and 5.1 kg respectively (Table 1). For big bulls one expects 14-18 kg of antler mass and at least 18 tines. Thus the big bull moose and elk from EINP grew rather poor antlers, a parallel to the big-bodied wood bison bulls, which grew a short-haired display coat.

The following hypothesis explains the anomaly in body size and size of display organs in elk, moose and bison in EINP: the bulls are subject in spring to an intense flush of nutritious young foliage, forbs, sedges and grasses, because of productive soils; EINP is fairly even in elevation. This flush allows a rapid intake of a high-protein diet, which permits rapid skeletal growth. However, the phenology progresses rapidly, and the forage turns not only fibrous, but also toxic under the browsing pressure of many ungulates in EINP. Consequently, the ungulates soon experience a shortage of nutrients essential for hair and antler growth. They cannot satisfy the demand by moving to sites with better nutrition (e.g., riparian communities fertilized annually by alluvium, or by following the phenology pulse in elevation, as is possible for ungulates living in mountains), because all movements are cut short by tall fences. Therefore, in summer antlers of EINP elk and moose and the display hair of wood bison grow at reduced rates. Large-bodied males are expected to be more affected than small-bodied males, as the growth and maintenance needs of the former exceed those of the latter.

TABLE 1. Body (whole, $(kg)^{1.35}$lean), antler (kg) and relative antler masses (grams per wt $(kg)^{1.35}$) in bull elk and moose

	n	x_1(wt)kg body	n	x_2(wt)kg antler	g(wt·kg)$^{1.35}$	
1. moose	29	479	35	18.2	4.39	Maine, U.S.A.
2. moose	—	565	145	22.9	4.40	Alaska
3. moose	—	500	—	20.0	4.50	Eastern Siberia
4. moose	1	450	1	14.5	3.80	British Columbia
5. moose	1	492	1	14.0	3.25	Ontario
6. moose	1	542	1	24.0	4.90	Alberta
7. moose	1	455	1	6.1	1.57	Elk Island N. P.
EINP	1	405	1	5.8	1.74	Elk Island N. P.
	1	466	1	5.1	1.27	Elk Island N. P.
8. elk	1	479	1	15.3	3.74	Manitoba
	1	326	1	11.5	4.66	Manitoba
9. elk	—	333	8	10.0	3.98	Banff N. P.
10. elk	—	350		13.8-15.5	5.1-5.7	New Mexico
11. elk	—	350		9.1-14.5	3.3-5.3	Alberta
12. elk	—	300		14.0	5.1	Mongolia
13. elk	25	379		7.2	2.4	Elk Island N. P.

1. A sample of trophy bulls from Maine, courtesy R. Arsenault, Gorham, Maine.
2. Alaska bulls.
3. East Siberian moose.
4. A big bull from southern British Columbia.
5. A large, but not trophy-sized, Ontario bull.
6. A large trophy bull from Alberta.
7. Three bull moose from EINP.
8. Two large bull elk from Riding Mountain National Park.
9. Averages reported for old bulls from Banff National Park.
10. Trophy antler weights from New Mexico.
11. Antler weights of mature bulls from Alberta.
12. Siberian wapiti from Altai Mountains, Mongolia.
13. EINP bull elk and the heaviest set of antlers weighed. (No. 2-6, 8-13 from Geist, 1987b.)

The long procumbent display hair arises from lack of annual shedding, normal in vigorous bulls (Lott, 1979), and from a reduced growth of under wool in summer; the "Afro" arises when the display hair is lifted by a vigorous growth of under wool.

Bison phenotypes with reduced display pelage (wood bison) are thus expected to arise where nutrition limits hair growth after the shedding of winter hair. This could happen to some northern "bog-bison," as well as to "desert bison" in southern states on marginal habitat or to old bulls in captivity. In short, Heck (1936), Krumbiegel (1980) and Krumbiegel and Sehm (1989) probably reported something real about southern bison, just as did Geist and Karsten (1977) and van Zyll de Jong (1986) about "wood bison" held in EINP. However, as they reported, it appears on ecotypic differences only. Still, a few bulls in WBNP may be short-haired in display coats for genetic reasons, making such a hair pattern (Fig. 9) a *polymorphism*. I suggest that the species *Bison bison* is void of subspecies. The foregoing has implications to an understanding of both the evolution of bison and their conservation.

EVOLUTION

Some bison of WBNP appear to share characteristics with *B. priscus* (Fig. 10), whose appearance is fairly well known (Geist, 1971; Guthrie, 1989). This suggests that *B. bison* is a hybrid of *B. antiquus* and Siberian steppe bison; it allows one to identify the luxurious plains bison pelage as similar to what *B. antiquus* probably carried (Fig. 11). This bison lived in southern latitudes and was exposed to a high heat load from the sun in summer, when the bulls were maximally active during the rut. That would explain both the blondness of the cape as a reflector of solar radiation and the near "naked" condition of American bison after the loss of winter hair in early summer. With dense display hair on the forequarters, there is a great need to shed heat when running on hot days. European wisent do not show a comparable nakedness, but grow a hair coat simultaneously with the moult.

Male bison have relatively and absolutely larger humps than cows, suggesting that the hump's musculature is crucial in combat (Guthrie, 1989). Since increased body size is associated with increased social competition (see adaptive ecotypic morphs), one would expect relatively larger humps and more sturdy skulls in large-bodied bison. The skeleton of *B. antiquus*, such as the specimen in the Los Angeles County Museum, shows an exceedingly tall hump, with T3 as the longest neural spine, as compared to T1 and T2 in *B. bison* and T5 in *B. priscus*. The skull of *B. antiquus* was massive and thick horned, suggesting forceful combat.

According to Guthrie (1989), the hump permits a high suspension of the front legs, increasing stride length and speed. *B. antiquus* must have had a very long stride length and high speed. This was also concluded by Smiley (1978), who showed that these bison had muscle insertion patterns on their front legs favouring speed over power. This is plausible granted big, long-legged Rancholabrean predators. Severe culling predation would select, in addition, for large horns and for display hair that functions antler-like as a luxury organ (Geist, 1987b, 1991b). It would have augmented the horn display in *B. antiquus* and made it a fronto-lateral display, as opposed to a broadside display in *B. priscus* (Guthrie, 1989). That would have made a large tail significant in *priscus*, but not in *antiquus*. With increasingly cursorial adaptations one expects an elaborate courtship display with luxury organs that reflect a male's success in foraging and saving nutrients from maintenance and growth towards luxury. Running from predators in open plains selects for mothers able to bear large, highly developed young at birth that can soon run as fast and long as their mothers. Such young, fed on rich milk, rapidly outgrow the dangerous neonatal period. Their mothers would enhance the fitness of daughters by selecting as fathers superior foragers, those who have the big luxury organs to prove it. The bull's display hair functions analogously to antlers for it is shed after the mating season (Lott, 1979).

CONSERVATION AND HYBRIDIZATION

Lack of attention to phenotype plasticity in bison taxonomy has created peculiarities. The assumption that pelage features are fixed would, following Krumbiegel (1980), make *B. b. athabascae* Rhoads 1897 a *nomem nudum*, as *B. b. bison* Linnaeus 1758 has priority — that is, *B. b. bison* = *B. b. athabascae*. However, "wood bison" bulls from EINP placed on superior food would, by growing a *normal* coat, become "northern plains bison" — that is, *B. b. athabascae* = *B. b. montanae*. They would now lose their legal protection under the Alberta Wildlife Act, because not even experts might distinguish them from plains bison. The view that WBNP bison be killed off and replaced by genetically impoverished "wood bison" from EINP would destroy the largest continuous, well-tested gene pool of the species *B. bison* and give priority to the impoverished gene pool of an inbred phantom subspecies. Even if the bison of WBNP were hybrids of valid subspecies, which they are not, I agree with O'Brian and Mayr (1991) that such hybridization is not a biological tragedy, and is absurd in view of the evolution of bison, or of other mammals.

The American *B. bison* emerges as a dwarfed hybrid of indigenous southern big-horned *B. antiquus* and thin-horned northern Siberian *B. occidentalis*. It fluctuated greatly in abundance and range in the Holocene. Its prairie populations penetrated virtually to the edge of its northern distribution, insuring continuing mixing of populations, thereby minimizing geographic differentiation and excluding from this process probably not even the dispersed populations of wood bison.

Wood and plains bison were in contact in historic times, particularly if forests were periodically removed by native-set fires. There was probably gene flow between southern and northern bison. Our surviving plains bison are hybrids of northern and southern plains bison, and the salvaged NR bison are hybrids of wood bison and hybrid plains bison. Hybridization between closely related subspecies is, in nature, common enough in North America:

1) White Dall's sheep (*Ovis dalli dalli*) met grayish-black Stone's sheep (*O. d. stoni*) and left a mass of gray integrates, the "fannin sheep," across northern British Columbia and the Yukon Territory; we classify all "fannins" as Stone's sheep.

2) Mule deer (*Odocoileus hemionus hemionus*) hybridize extensively with black-tailed deer (*O. h. columbianus*) in British Columbia on the heights of the Costal Ranges (Cowan, 1936; M.A. Cronin, Yale Univ., pers. comm. 1989), as do the subspecies *sitkensis* and *columbianus* in coastal British Columbia (Cowan, 1936). The subspecies *injoensis* may be a hybrid of *hemionus* × *californicus* (Wallmo, 1981).

3) Consider the mule deer: its mitochondrial DNA show it to be a hybrid of white-tailed deer mothers (*O. virginianus*) and black-tailed deer fathers (*O. hemionus*); it arose from such a cross repeatedly (Cronin, 1986; Carr *et al.*, 1986; Stubblefield *et al.*, 1986). Currently, the two ethological barriers that segregate breeding between white-tailed and mule deer are breaking down due to human action (Lingle, 1989). Are we to conclude that mule deer, because they originated as hybrids, are a worthless life form?

4) Hybridization among white-tailed deer subspecies is a subject beyond resolution, because white-tailed deer recolonized this continent, alone or with human help, after their near demise at the turn of the century (Seton, 1906; Bersing, 1956). It is impossible to determine what met and mixed or from where various releases of white-tailed deer originated.

5) The Columbian white-tailed deer (*O. v. leuccurus*) appears to have done some hybridizing with Columbian black-tailed deer (Gavin, 1985). Does that warrant abandoning its protected status?

6) Note the "hybridization" of elk (*C. e. canadensis*): it is a late Siberian immigrant to North America, identical in external appearance and social signals to elk in northern Mongolia. Today elk across North America are largely derived from reintroduced Yellowstone elk, plus an admixture of local elk that survived the commercial slaughter at the turn of the century (Robbins *et al.*, 1981).

Hybridization is genetic pollution and a biological tragedy when it destroys a population's ability to survive under extreme environmental conditions, such as severe predation or weather, narrow seasonal windows or resource shortages. For instance, reintroduced Alpine ibex (*Capra ibex*) mixed with either Nubian ibex (*C. nubiana*; Turcek, 1951) or domestic goats (*C. hircus*; Grodinski and Stuwe, 1987) became extinct because births were spread over much of the year, including winter, instead of being concentrated within a narrow period in spring. The young born in winter died of exposure; those born in summer failed to reach survivable size before winter and also died of exposure. Crosses of Siberian roe bucks (*Capreolus pygargus*) and European roe deer females (*C. capreolus*) led to birth complications due to larger than normal foetuses (Turcek, 1951; Stubbe and Passarge, 1979). European wild boar (*Sus scrofa*) appear to have various admixtures of domestic pig, recognizable by the presence of spotted individuals. Spotting is associated with decreased survival, lower oxygen-binding capacity in the blood, decreased thermoregulatory ability and poorer development of the under wool (Briedermann, 1986:94). Huge antlers, a common goal of so-called "improvement" through hybridization of deer, were found to be detrimental to their bearers because stags with large, complex, unwieldy antlers were prone to be killed by smaller-antlered stags in fighting; in the Rominten Heath, where red deer were managed for large trophy antlers, this was a painful concern since stags with outstanding antlers might be killed in fighting, instead of by dignitaries hunting there as guests (Frevert, 1977). Hybridization of mule and white-tailed deer results in offspring that have neither parent's anti-predator behaviour (Lingle, 1989).

The test of the effects of hybridization is survival under severe environmental conditions. Using this criterion, then the "predator pit" within which WBNP bison are currently found (Carbyn *et al.*, 1989) should eliminate whatever detriments hybridization might have had. Considering the foregoing, the 1925-28 mixing of plains and wood bison in WBNP, while culturally tragic, because it was avoidable, is not a biological tragedy. There is no evidence for subspecies in *B. bison*, and no taxonomic justification for destroying the bison of WBNP.

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PHENOTYPIC VARIATION IN REMNANT POPULATIONS OF NORTH AMERICAN BISON

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Eight external characters distinguishing plains bison (*Bos bison bison*) and wood bison (*B. b. athabascae*) were analyzed in six extant populations of plains bison and five populations of animals with ancestry of wood bison to test whether panmixis occurred in Wood Buffalo National Park following the introduction of plains bison and to test whether the variation is ecophenotypic. Character states were polarized from wood to plains bison and scored numerically. Frequencies of individual scores and indices were analyzed by a series of tests, and populations were ranked according to phenotype. Analysis of overall phenotypic variation based on all eight characters revealed three significantly different groups: plains bison; the subpopulation from Pine Lake; the other subpopulations from Wood Buffalo National Park. Results indicate that panmixis has not occurred since the 1925–1928 introduction of plains bison to the Park and that the characters studied are genetically based.

Key words: *Bos bison*, phenotypic variation, conservation

A central goal in conservation biology is to maintain or restore biological diversity for its intrinsic values, to sustain the health of ecological systems, and to meet human needs (Salwasser, 1990). The bison (*Bos bison*), once an important biotic element of North American grasslands, contributed substantially to the material and cultural well-being of the aboriginal human population and, in part, supported the early colonization of the interior of the continent by Europeans. During the past century, the species was reduced to a few remnant populations ranging in size from a few to several hundred individuals, together comprising <900 bison (Roe, 1970). Conservation and recovery of bison have gained in popularity in recent years because of the cultural, biological, and commercial value of this large herbivore. Consequently, there is a need to document the range of phenotypic and genotypic variation within and among historical and contemporary populations to provide a basis for conserving existing diversity within the species.

The near extermination of bison precluded comprehensive study of historical geographic variation. Analysis of skeletal, largely cranial, material preserved in museum collections (McDonald, 1981; van Zyll de Jong, 1986) has cast some light on the extent and nature of past geographic variation, but the geographic variation of external characters in historical populations will remain largely a matter of conjecture. Extant populations of plains bison (*B. b. bison*) are descended from small founding populations comprising animals from north-

ern and southern regions of the historical range. The exact proportion of each in the founding herds and their genetic contribution to extant herds can only be approximated. At the turn of the century, the largest remnant population of bison, the northern wood bison (*B. b. athabascae*), resided in and around the area that is now Wood Buffalo National Park. Under protection, this population increased to ca. 2,000 by the early 1920s (Soper, 1941). Despite genetic introgression resulting from the introduction of >6,000 plains bison from southern Canada into central Wood Buffalo National Park in 1925–1928, bison from one subpopulation near the Nyarling River showed closer morphological resemblance to the indigenous wood bison than to the introduced plains bison (Banfield and Novakowski, 1960).

External phenotypic variation in wood bison from the Nyarling River and plains bison from Elk Island National Park was first analyzed subjectively by Geist and Karsten (1977) and later by van Zyll de Jong (1986), who used a quantitative approach. The external phenotypic variation of the other subpopulations in Wood Buffalo National Park has not yet been studied. Efforts to re-establish wood bison in other areas of its historical range have focused solely on bison captured in the area of Needle Lake and the Nyarling River in 1963 and 1965. The number of founding animals was limited to 18 for the Mackenzie Bison Sanctuary and 23 for Elk Island National Park. The taxonomic status of remaining herds living in the area of Wood Buffalo National Park is of interest with regard to the possibility of conserving additional genetic variation within contemporary wood bison.

Here we present results of a quantitative analysis of external phenotypic variation in a number of remnant populations including those from the area of Wood Buffalo National Park, which were not studied previously. We discuss the results in relation to historical geographic variation of bison in North America, infraspecific taxonomy, and conservation of biological diversity within the species. The study received its impetus from the Wood Bison Recovery Team and emphasizes bison from the area of Wood Buffalo National Park, the core of the historical range of the wood bison (Soper, 1941; van Zyll de Jong, 1986).

We postulated that hybridization of wood and plains bison, following the latter's introduction to Wood Buffalo National Park, was not the pervasive event it was assumed to be and did not result in a phenotypically homogeneous population (see Van Camp, 1989). We speculated that hybridization occurred primarily where the plains bison were released and in adjacent, easily accessible areas. More remote and less accessible indigenous populations were less affected. In the absence of unrestricted, random mating, these differential effects should still be measurable today. The hypothesis we test is that there was restricted mating, i.e., no free interchange of genes, among subpopulations in Wood Buffalo National Park. The alternative hypothesis is that panmixis occurred, resulting in phenotypically uniform subpopulations. To test our hypothesis, we predict that subpopulations in the area of Wood Buffalo National Park will show significant phenotypic differences. Those in areas nearest the introduction site, or easily accessible from it, will have the highest frequencies of traits characteristic of plains bison; those in areas farthest away, or least accessible, will have lower ones.

A second hypothesis we test dates to Hornaday (1889) and recently was revived by Geist (1991). It claims that phenotypic differences between wood and plains bison are ecophenotypic in nature (sensu Mayr, 1969), i.e., the phenotypes are induced by environmental factors and are nongenetic. In other words, there is no genetically based discontinuity in geographic variation in North American bison consistent with subspecies. To test this hypothesis, we predict that bison of the *B. b. athabascae* phenotype moved to the habitat of *B. b. bison* (or

vice versa) will assume the phenotype of the latter in the first succeeding and subsequent generations.

MATERIALS AND METHODS

Populations sampled.—Populations of bison sampled are grouped into three categories: 1) plains bison; 2) wood bison from the Nyarling River area; 3) taxonomically undetermined subpopulations in the area of Wood Buffalo National Park. Six populations of plains bison were sampled from: Custer State Park, South Dakota; Delta Junction, Alaska; Fort Niobrara National Wildlife Refuge, Nebraska; Elk Island National Park, Alberta, Canada; National Bison Range, Montana; Yellowstone National Park, Wyoming (animals from Grand Teton National Park were included in this sample). Wood bison from the Nyarling River area are represented by samples from Elk Island National Park, Alberta, Canada, and the Mackenzie Bison Sanctuary, Northwest Territories, Canada. The taxonomically undetermined category includes three subpopulations from the area of Wood Buffalo National Park: Pine Lake; Sweetgrass; Slave River Lowlands. Designations of subpopulations of bison in Wood Buffalo National Park follow those of Wilson and Milne (1992), except for the subpopulation from the area of the Little Buffalo that we combined with the one from Hook Lake to maximize the size of the sample and designated as Slave River Lowlands. Of the four subpopulations residing strictly in the park, only those from Pine Lake and Sweetgrass are represented in our study. No photographs were obtained from the areas of the Garden and Nyarling rivers. However, the latter is represented by animals from Mackenzie Bison Sanctuary and Elk Island National Park, descendants of animals caught near the Nyarling River in 1963 and 1965, respectively. Populations listed under categories 2 and 3, all from the area of greater Wood Buffalo National Park, are referred to collectively as such in the text. For reasons of economy and convenience, all populations, subpopulations, and samples are referred to in the text by the geographic name of the area of origin.

Data for external phenotypic variation were obtained from photographs and video recordings that show animals in profile. Photographic records used in this study are cataloged and deposited at the Canadian Museum of Nature, Ottawa, Ontario, Canada.

Nongeographic variation.—To prevent genetically controlled, nongeographic, intraspecific variation from confusing geographic variation (Thorpe, 1976), variation attributable to sexual dimorphism was isolated by analyzing each sex separately. Ontogenetic variation was eliminated by analyzing adults only. The effect of seasonal variation was neutralized by using photographs taken in July and August (i.e., during the breeding season).

The development and characteristics of the horns in males and females (Fuller, 1959; Hornaday, 1889) were the criteria used to assign individuals to the appropriate age class and to determine inclusion in the sample. The validity of criteria used to determine age classes for populations of bison in northern Canada (Fuller, 1959) was confirmed for both subspecies at Elk Island National Park where a large number of known-age bison were present. Mature males (≥7 years old) comprise two age classes defined as follows: B3 or adult, characterized by horns with tips curved in, but smooth; B4 or prime, characterized by similar curvature of the horn, but with a "step" a short distance from the tip or with moderate brooming. Individuals with heavily broomed horns were excluded. Mature females (≥3 years old) are characterized by horn tips commonly curved strongly over the head (in adult males the tips point inward, but do not curve over the frontal area).

Direct environmental induction.—To detect environmentally induced variation in the characters studied, genetically related populations from localities with widely different environmental conditions were included in the analysis. For example, we compared a population of plains bison introduced to Alaska in 1928 from Montana (Burris and McKnight, 1973), living under boreal conditions in the prehistoric range of the wood bison, with its sister population on the National Bison Range. Conversely, we compared descendants of wood bison transplanted from the area of the Nyarling River to Elk Island National Park, part of the historical range of the plains bison, with bison of the same stock moved to the Mackenzie Bison Sanctuary in the historical range of wood bison.

Characters examined and methods of scoring.—Eight external features, three describing the hump and five describing the pelage, were examined and scored. Variation in each character was divided into a number of states (Fig. 1),

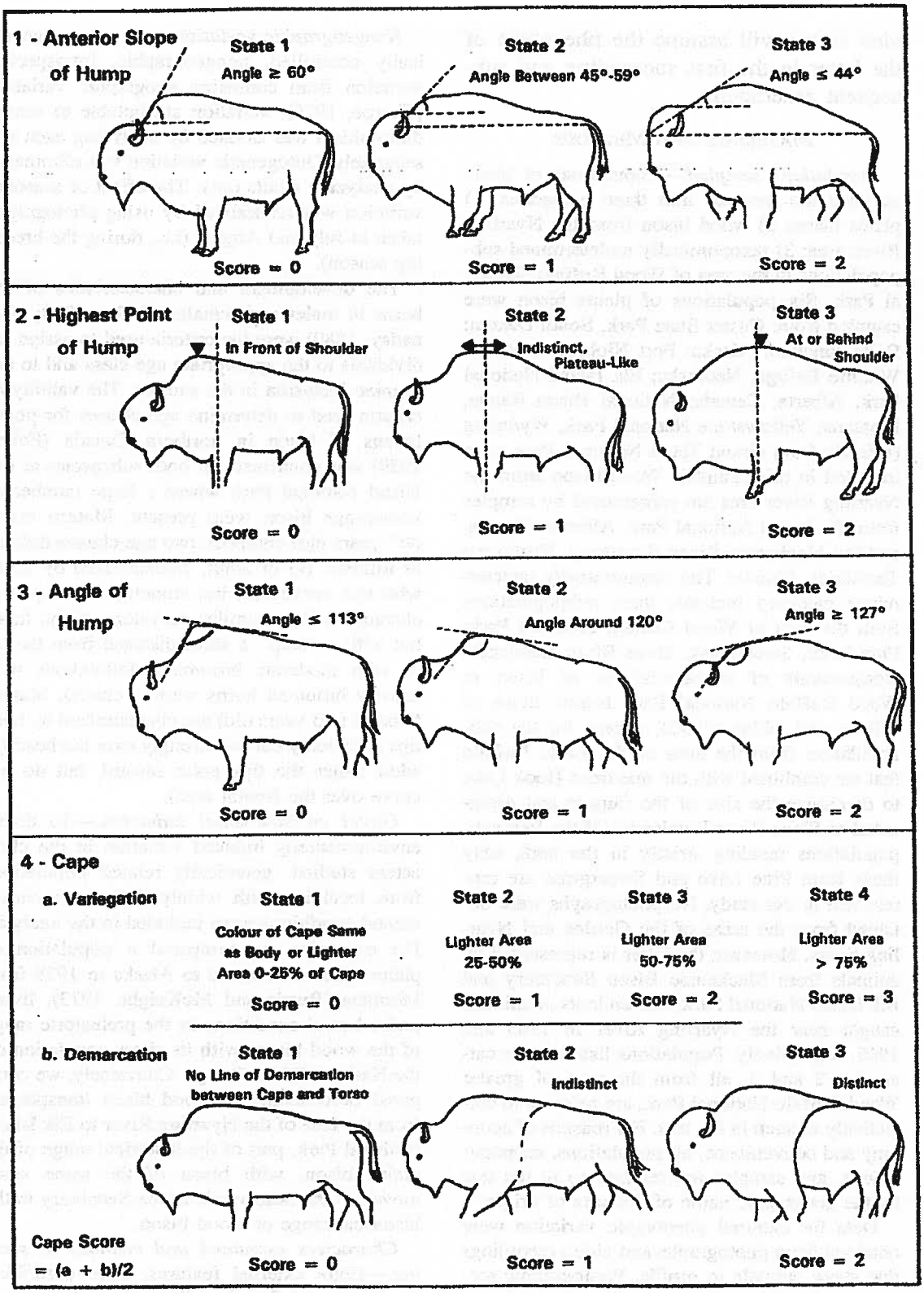
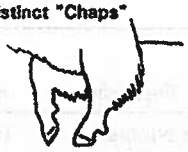


FIG. 1.—Character gradients, character scores and the calculation of the character index (sum of eight character scores) for adult male bison. Character states of *Bos bison athabascae* on the left, and those of *B. b. bison* on the right.

5 - Hair on Upper Front Leg

State 1	State 2	State 3
Short, Not Much Longer Than Nearby Areas of the Body	Longer Than in 1, But Not Forming Distinct "Chaps"	Long and Dense Forming Distinct "Chaps"
		
Score = 0	Score = 1	Score = 2

6 - Frontal Display Hair



State 1	State 2	State 3	State 4
Ratio #1/#2 = 0.20-0.40	Ratio #1/#2 = 0.41-0.60	Ratio #1/#2 = 0.61-0.80	Ratio #1-#2 > 0.80
Score = 0	Score = 1	Score = 2	Score = 3

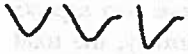
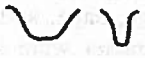
7 - Ventral Neck Mane



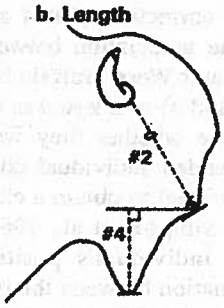
State 1	State 2	State 3	State 4
Ratio #3/#2 = 1.20-1.40	Ratio #3/#2 = 1.41-1.60	Ratio #3/#2 = 1.61-1.80	Ratio #3/#2 > 1.80
Score = 0	Score = 1	Score = 2	Score = 3

8 - Beard

a. Shape

State 1	State 2	State 3
 Pointed	 Rounded	 Blunt
Score = 1	Score = 2	Score = 3

b. Length



State 1	State 2	State 3
Ratio #4/#2 = 0.20-0.40	Ratio #4/#2 = 0.41-0.60	Ratio #4/#2 > 0.60
Score = 0	Score = 1	Score = 2

Beard Score = (a + b)/2

FIG. 1.—Continued.

TABLE 1.—*Frequencies of character scores for six characters in 11 populations of bison. The populations are ranked according to similarity, and those followed by the same letter are not significantly different.*

Hump										Cape								
		Score										Score						
Population	*n*	0	1	2	3	4	5	6		Population	*n*	0.0	0.5	1.0	1.5	2.0	2.5	
Fort Niobrara	10	0	0	0	0	2	2	6		Custer State	19	0	0	1	0	2	16	a
National Bison Range	35	0	0	0	0	5	23	7	a	Fort Niobrara	10	0	0	0	2	2	6	a
Delta Junction	18	0	0	0	3	3	10	2	ab	Elk Island National Park Plains	36	0	3	13	5	5	10	
Elk Island National Park Plains	38	0	0	0	7	17	12	2	b	Delta Junction	16	0	1	1	5	7	2	
Custer State	23	0	0	1	2	4	12	4	b	National Bison Range	34	0	0	3	3	9	19	b
Yellowstone National Park	43	0	0	1	4	13	23	2	b	Yellowstone National Park	40	2	2	5	3	16	12	bc
Pine Lake	21	0	3	3	7	6	2	0	c	Elk Island National Park Wood	28	1	5	3	5	8	6	c
Slave River Lowlands	6	1	0	1	2	2	0	0	c	Slave River Lowlands	6	2	0	1	1	0	2	c
Elk Island National Park Wood	28	8	2	9	6	3	0	0	c	Pine Lake	21	1	0	1	4	15	0	
Mackenzie Bison Sanctuary	32	1	9	13	4	5	0	0	c	Mackenzie Bison Sanctuary	31	13	5	1	11	1	0	d
Sweetgrass	16	8	2	5	1	0	0	0	c	Sweetgrass	15	8	5	1	1	0	0	d

forming a gradient. These states were assigned a numerical value, using a system of additive scoring (Sneath and Sokal, 1973). The lowest value represents the most extreme state in wood bison, and the highest represents the most extreme state in plains bison. Each character was weighted equally. Thus, in the two characters of the pelage, cape, and beard, where two aspects of a character were scored separately, the total was divided by two to obtain the final score (Fig. 1). Scoring was done in one of two ways. One involves comparing a character on the photograph to the standard characters in Fig. 1 and assigning it the corresponding value. The other involved measuring distances or angles on the photograph. Measurements were transformed to size-independent ratios by dividing them by a standard measurement. Angles and ratios were assigned scores based on their numerical value. Details are given in Fig. 1. Characters and methods used here are those described by van Zyll de Jong (1986), modified to increase objectivity and precision as described.

Scoring was done from photographs of profiles of mature animals with the head in a normal position. Normal position of the head was defined by the angle between a line from the eye to the base of the tail and the horizontal axis of the body (Fig. 1) being ca. 4 + 2°. To reduce bias and inconsistency further, scoring was done by one observer on randomly selected photographs without information as to geographic origin.

Data analysis.—Frequency distributions of scores and indices in populations were examined in several ways. For each character, we tested the hypothesis that the distribution of its states did not differ in each pair of populations using the *G*-test and Williams' correction (Sokal and Rohlf, 1981). Second, the association between different characters in greater Wood Buffalo National Park (categories 2 and 3) was tested in the same manner to determine whether they were independent. Third, we added individual character scores for each individual to obtain a character index (Mayr, 1969; Simpson et al., 1960), which characterizes an individual's position along an axis of discrimination between the two forms compared. The character index, therefore, determines an individual's degree of phenotypic

TABLE 1.—*Extended.*

Chaps						Frontal display hair						
		Score						Score				
Population	*n*	0	1	2		Population	*n*	0	1	2	3	
Custer State	20	0	0	20	a	Custer State	20	0	1	12	7	a
National Bison Range	34	0	0	34	a	Delta Junction	17	0	0	13	4	a
Fort Niobrara	12	0	0	12	a	Fort Niobrara	12	0	1	10	1	a
Yellowstone National Park	43	0	0	43	a	National Bison Range	44	0	2	31	11	a
Delta Junction	14	0	0	14	a	Elk Island National Park Plains	38	0	13	20	5	b
Elk Island National Park Plains	38	0	6	32	b	Yellowstone National Park	43	0	14	22	7	b
Pine Lake	21	2	5	14	b	Pine Lake	21	1	6	10	4	b
Slave River Lowlands	4	0	2	2	bc	Mackenzie Bison Sanctuary	31	0	13	16	2	b
Mackenzie Bison Sanctuary	31	7	17	7	c	Elk Island National Park Wood	27	0	12	13	2	b
Sweetgrass	8	4	2	2	c	Slave River Lowlands	6	0	6	0	0	c
Elk Island National Park Wood	28	13	10	5	c	Sweetgrass	16	5	8	3	0	c

resemblance to either subspecies and can be used in a quantitative analysis of phenotypic variation within and among populations. We employed a *G*-test using Williams' correction (Sokal and Rohlf, 1981) to examine the independence of phenotypic variation and populations. Finally, we used correspondence analysis (Greenacre, 1984) to determine the relative positions of the sampling units to one or more axes and to each other to maximize information about phenotypic similarities. Correspondence analysis allows one to compare frequencies of rows or columns in a two-way table by mathematically decomposing the chi-square into components similar to that of principal-components analysis. Unlike principal-components analysis, correspondence analysis uses frequencies or discrete data rather than continuous measurements. In correspondence analysis, chi-square distances can be computed and used to describe phenotypic relationships among populations quantitatively. Chi-square distance also was used to rank populations on the basis of frequency of character states. Calculations for *G*-test and correspondence analysis were performed using BIOM-pc and NTSYS-pc software (Rohlf, 1988, 1990).

RESULTS

There was essentially no difference in external phenotypic characters between males and females (van Zyll de Jong, 1986). Therefore, we report only results obtained from adult males.

Variation in individual characters.—The scores for the three characters describing the shape of the hump were added and analyzed as one. All six populations of plains bison are more similar to one another with respect to shape of the hump than to any of the subpopulations from the area of greater Wood Buffalo National Park (Table 1). The population from Fort Niobrara is significantly different from other populations of plains bison (comparison with the most similar population; National Bison Range, $G = 6.48$, $d.f. = 2$, $P < 0.05$) and had the highest modal score (6). All other populations of plains bison form two overlapping nonsignificant subsets. The modal score characteristic of most of these populations is 5, except for Elk Island National Park where it is 4. All subpopulations from the area of greater Wood Buffalo National Park form a nonsignificant subset that differs significantly from all populations of plains bison ($G = 201.5$, $d.f. = 6$, $P < 0.005$). The modal scores from the area of greater Wood

TABLE 1.—*Extended.*

Ventral neck mane							Beard					
		Scores							Score			
Population	*n*	0	1	2	3		Population	*n*	0–0.5	1–1.5	2	
Custer State	20	0	1	9	10		Delta Junction	14	2	9	3	a
National Bison Range	33	2	6	21	4	a	Custer State	20	4	14	2	a
Fort Niobrara	11	0	3	6	2	a	National Bison Range	32	7	25	0	a
Delta Junction	18	0	7	7	4	a	Fort Niobrara	10	5	5	0	ab
Yellowstone National Park	43	2	11	20	10	a	Yellowstone National Park	43	15	26	3	ab
Elk Island National Park Plains	35	1	15	11	8	b	Elk Island National Park Plains	38	13	23	2	ab
Pine Lake	21	4	9	7	1	bc	Elk Island National Park Wood	28	14	14	0	bc
Elk Island National Park Wood	27	1	16	9	1	bc	Mackenzie Bison Sanctuary	31	16	15	0	bc
Slave River Lowlands	6	2	4	0	0	c	Pine Lake	21	12	9	0	bc
Mackenzie Bison Sanctuary	30	8	16	6	0	c	Slave River Lowlands	6	4	2	0	bc
Sweetgrass	16	7	6	3	0	c	Sweetgrass	16	13	3	0	c

Buffalo National Park show a wider range of variation, with the highest in Pine Lake (3) and lowest in Sweetgrass (0). Nyarling wood bison from Elk Island National Park and the Mackenzie Bison Sanctuary have the same modal score (2).

A pattern of separation between plains bison and populations from the area of greater Wood Buffalo National Park also is evident in the cape, but is not as clear as it is in the hump (Table 1). The subsets National Bison Range-Yellowstone National Park and Yellowstone National Park-Slave River Lowlands overlap, evincing a less distinct separation between the plains bison and subpopulations from the area of greater Wood Buffalo National Park. Modal scores vary widely and are not concordant with the plains-greater Wood Buffalo National Park division.

Frequencies of the states of chaps show a clear division between most populations of plains bison and the subset Elk Island plains-Slave River Lowlands and overlapping subset Slave River Lowlands-Nyarling wood bison from Elk Island (Table 1). The modal score for all plains populations is 2. The modal score for subpopulations from greater Wood Buffalo National Park varies widely from 2 in Pine Lake and 1 in Mackenzie Bison Sanctuary to 0 in Sweetgrass and Nyarling wood bison from Elk Island.

Frontal display hair shows a pattern of three non-overlapping subsets (National Bison Range versus plains bison from Elk Island, $G = 8.1$, $d.f. = 3$, $0.05 > P > 0.025$; Nyarling wood bison from Elk Island versus Slave River Lowlands, $G = 6.5$, $d.f. = 2$, $0.025 < P < 0.05$). The subset in the middle comprises plains bison and samples from greater Wood Buffalo National Park. Modal scores, similarly, show a relatively uniform pattern, being 2 for all populations except Slave River Lowlands and Sweetgrass.

A separation into plains bison and bison from greater Wood Buffalo National Park is discernible in the ranking of the groups on the basis of ventral neck mane, but they are linked by broadly overlapping nonsignificant subsets (Table 1). Custer State differs significantly from National Bison Range ($G = 9.81$, $d.f. = 3$, $0.025 < P < 0.05$). In most plains populations, the modal score is 2 or higher, except for plains bison from Elk Island where it is 1. In samples from

TABLE 2.—*Frequencies of character indices in 11 populations of bison. The phenotypic gradient from left to right indicates increasing characteristics of plains bison. Populations followed by the same letter are not significantly different.*

Population	*n*	Character index								
		2–3.5	4–5.5	6–7.5	8–9.5	10–11.5	12–13.5	14–15.5	16–17.5	
Custer State	21	0	0	0	0	2	2	11	6	a
Fort Niobrara	9	0	0	0	0	0	2	5	2	a
National Bison Range	37	0	0	0	0	1	8	23	5	a
Delta Junction	12	0	0	0	0	2	2	6	2	ab
Elk Island National Park Plains	37	0	0	0	3	12	11	9	2	b
Yellowstone National Park	43	0	0	0	3	10	13	14	3	b
Pine Lake	22	0	0	5	2	8	6	1	0	c
Elk Island National Park Wood	27	2	6	4	9	4	2	0	0	c
Mackenzie Bison Sanctuary	31	2	7	11	6	4	1	0	0	
Slave River Lowlands	4	1	1	1	0	1	0	0	0	cd
Sweetgrass	8	4	3	1	0	0	0	0	0	d

greater Wood Buffalo National Park the modal score is 1, except for Sweetgrass, where it is 0.

The pattern of frequency distributions for the beard is similar to that of the ventral neck mane. There is a definite ranking of plains bison and bison from greater Wood Buffalo National Park into two groups, which also is evident from the distribution of the modal scores (Table 1). However, overlap between non-significant subsets is even broader than for ventral neck mane.

In subpopulations of greater Wood Buffalo National Park significant association exists between cape and chaps ($G = 13.2$, $d.f. = 4$, $P = 0.01$), cape and frontal display hair ($G = 11.3$, $d.f. = 2$, $P < 0.005$), and frontal display hair and ventral neck mane ($G = 19.7$, $d.f. = 2$, $P < 0.005$). The hump and beard are not significantly associated with any of the other characters.

Overall phenotypic variation.—Comparison of overall phenotypic variation in the samples (Table 2) evinced a clear division into three groups. The first group comprises all samples of plains bison within which two overlapping nonsignificant subsets occur. The second group contains only Pine Lake, and the third, all other samples from greater Wood Buffalo National Park, which form two overlapping nonsignificant subsets. Pine Lake is phenotypically clearly intermediate and differs significantly from the most similar plains sample ($G = 25.9$, $d.f. = 5$, $P < 0.005$) as well as from the most similar samples from greater Wood Buffalo National Park ($G = 22.1$, $d.f. = 5$, $P < 0.005$).

The extent to which subpopulations in greater Wood Buffalo National Park have been affected by past interbreeding with plains bison can be judged from the amount their character indices overlap those of populations of plains bison. To this end, we calculated the percentage and its 95% confidence limits of individuals in each sample having indices equal to or higher than the lowest observed index for plains bison (class 8.0–9.5). Of the subpopulations in greater Wood Buffalo National Park, Pine Lake overlapped most extensively with the populations of plains bison, 77%. Nyarling wood bison, represented by samples from Elk Island National Park and the Mackenzie Bison Sanctuary, overlapped less (45%, *CI* of 32–58). No overlap was observed between Sweetgrass and plains bison, but the Sweetgrass sample was small ($n = 8$) and the confidence limits correspondingly wide (*CI* of 0–33). In the even smaller sample from Slave River Lowlands ($n = 4$), the observed overlap was 25%.

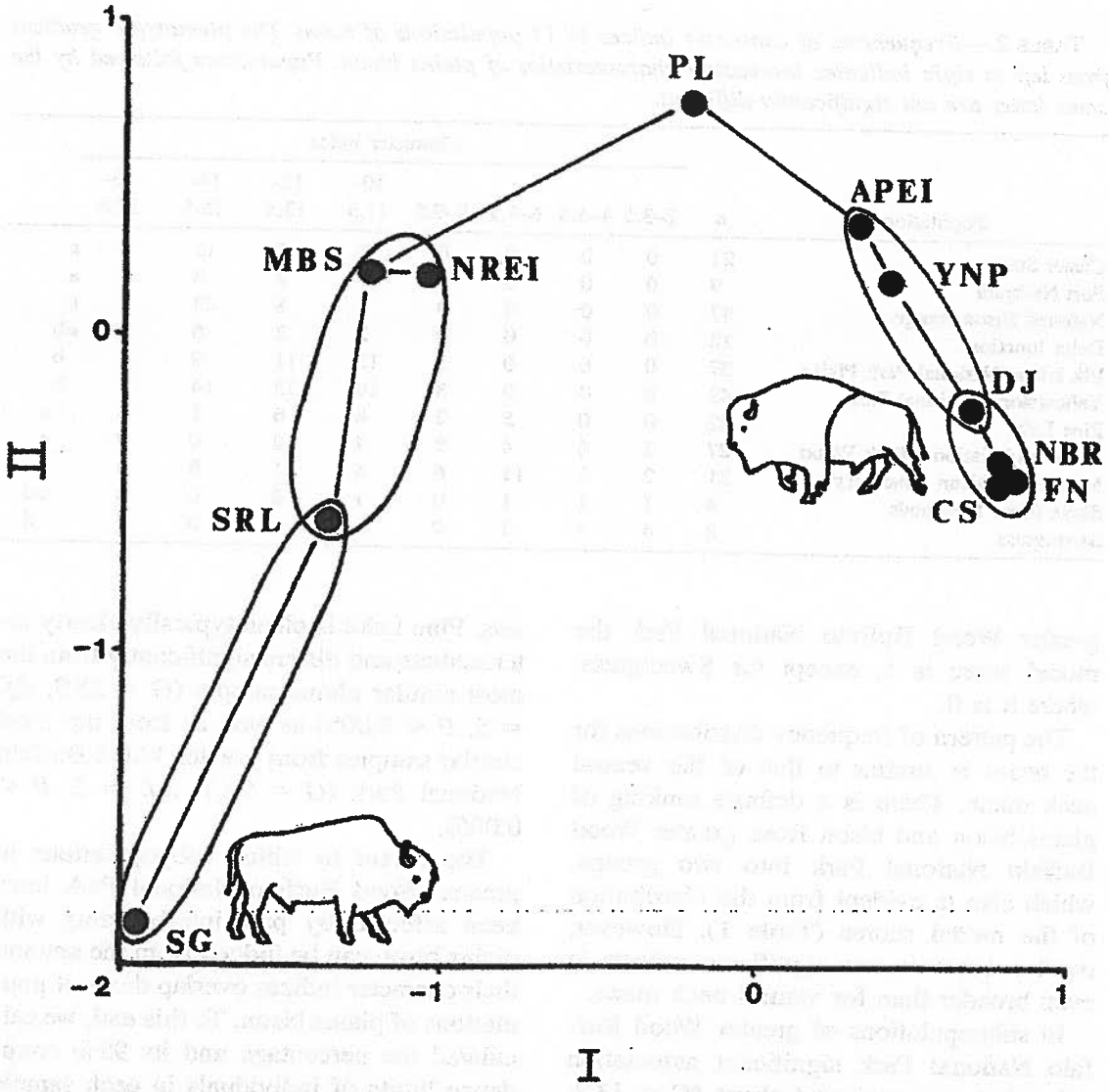


FIG. 2.—Results of correspondence analysis of external phenotypic variation in 11 populations of bison. A plot of row factors for the frequency data of Table 2 shows the ordination of the populations. A minimum-spanning tree connects nearest neighbors. Ellipses indicate nonsignificant subsets. Populations are from left to right: SG, Sweetgrass; SRL, Slave River Lowlands; MBS, Mackenzie Bison Sanctuary; NREI, Elk Island National Park wood bison; PL, Pine Lake; APEI, Elk Island National Park plains bison; YNP, Yellowstone National Park; DJ, Delta Junction; NBR, National Bison Range; CS, Custer State; and FN, Fort Niobrara.

Results of the correspondence analysis depict the ordination of populations based on phenotype (Fig. 2). The first axis represents most of the phenotypic variation. Phenotypes characteristic for wood bison are on the left; those characteristic for plains bison on the right of the graph. Populations of plains bison are well separated from the majority of subpopulations from greater Wood Buffalo National Park except Pine Lake, which is intermediate. Distances indicated by the minimum-spanning tree may not accurately reflect the phenotypic inter-relationships between samples that did

not differ significantly in the previous analysis. Pine Lake, which differs significantly from either of its closest neighbors, is considerably closer to plains bison from Elk Island National Park than to Nyarling wood bison from the same park. Chi-square distances among all pairs of groups are listed in Table 3. Sweetgrass and Slave River Lowlands are most remote from plains bison from Elk Island, followed by Nyarling wood bison from the Mackenzie Bison Sanctuary and Elk Island National Park.

TABLE 3.—*Chi-square distances between pairs of 11 populations of bison (males).*

Population	Population										
	1	2	3	4	5	6	7	8	9	10	11
1. Custer State	0.000										
2. National Bison Range	0.650	0.000									
3. Fort Niobrara	0.437	0.339	0.000								
4. Yellowstone National Park	1.056	0.840	0.937	0.000							
5. Delta Junction	0.485	0.436	0.473	0.637	0.000						
6. Elk Island National Park Plains	1.243	1.101	1.187	0.278	0.839	0.000					
7. Sweetgrass	3.362	3.327	3.345	3.238	3.279	3.253	0.000				
8. Pine Lake	1.780	1.682	1.752	1.057	1.447	0.923	3.233	0.000			
9. Slave River Lowlands	2.359	2.351	2.391	2.087	2.192	2.048	1.581	1.795	0.000		
10. Elk Island National Park Wood	2.103	2.052	2.090	1.637	1.921	1.595	2.609	1.566	1.530	0.000	
11. Mackenzie Bison Sanctuary	2.183	2.142	2.178	1.834	2.020	1.811	2.593	1.405	1.266	0.849	0.000

DISCUSSION

Impact of hybridization.—Our analyses reveal that subpopulations in greater Wood Buffalo National Park are phenotypically heterogeneous, with Pine Lake having the highest frequency of traits characterizing plains bison. The release of plains bison in 1925–1928 occurred at several points along the eastern boundary of the park below the confluence of the Peace and Slave rivers, i.e., in the area of the present subpopulation at Pine Lake (Fig. 3). Our observations are, thus, in general agreement with the predictions of the first hypothesis that there was no free exchange of genes. The finding that bison from Sweetgrass are phenotypically most remote from plains bison from Elk Island National Park was unexpected in view of their relative proximity to the release sites. The remoteness suggests that there has been relatively little reproductive contact between subpopulations at Sweetgrass and Pine Lake. Bison from Slave River Lowlands are represented by a small sample in this study. However, data indicate that bison in this area are phenotypically at least as distinct from those in the area of Pine Lake as those of the other subpopulations (Sweetgrass; Nyarling wood bison from Elk Island National Park and the Mackenzie Bison Sanctuary). The evidence supports the absence of panmixis since the introductions >60 years ago. The reasons for this are not clear. Information on movements of bison and on the stability of subpopulations in greater Wood Buffalo Na-

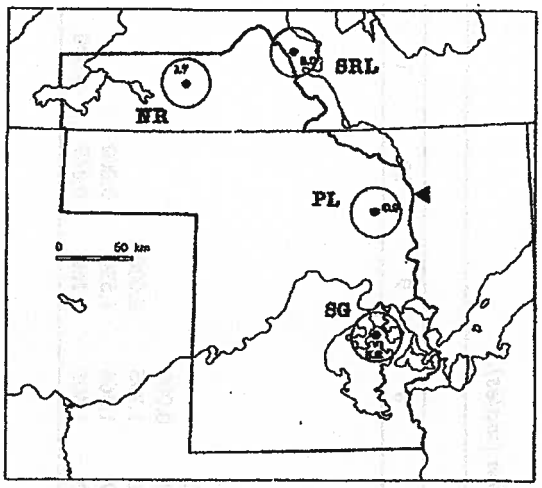


FIG. 3.—Approximate centers of distribution of subpopulations of bison in Wood Buffalo National Park in relation to the area where the release of plains bison took place in the period 1925–1928 (indicated by the black triangle). Chi-square distances of the subpopulations from the parental stock of plains bison (Allard-Pablo), shown in the circles, indicate the extent to which interbreeding has affected the external phenotype of present subpopulations. The subpopulations shown are: NR, Nyarling River; PL, Pine Lake; SRL, Slave River Lowlands; and SG, Sweetgrass.

tional Park in the past is lacking. Recent studies (Wilson and Milne, 1992) have yielded information that supports the existence of relatively discrete subpopulations (absence of significant seasonal movements and limited exchange between areas), which may constitute demes. This continuing study of movements of bison will provide further insight in the dynamics of subpopulations in greater Wood Buffalo National Park.

Concordance of genealogy and phenotype.—Results of our analysis strongly support a genetic basis for the phenotypic characters studied. This conclusion is based on the observation that the known genealogical (i.e., genetic) relationships of the populations studied are highly concordant with the phenotypic relationships. The "sibling" populations, those derived from the same "parent" population, show remarkable agreement between genealogy and phenotypic similarity. Populations of plains bison from Delta Junction and the National Bison Range, descendants from the same stock, are neighbors in phenotypic space (Fig. 2). They do not differ significantly with respect to phenotype after >60 years apart in widely differing environments. Bison at Delta Junction are free-roaming and live in boreal forest. Bison on the National Bison Range, conversely, are fenced, live in temperate grassland-open forest and are managed quite intensively. Similarly, the two populations of wood bison from the Mackenzie Bison Sanctuary and Elk Island National Park were derived from the same subpopulation in Wood Buffalo National Park. They do not differ significantly in the morphological characters studied, after living separately under different environmental conditions since 1963. In the Mackenzie Bison Sanctuary, the animals live in boreal and subarctic woodlands, interspersed by marshes, where they lead a natural existence subject to predation and the environment. In contrast, their relatives in Elk Island National Park live in a fenced, temperate, aspen parkland, where they lead a semi-natural existence and are not subject to predation. Evidence provided by these sibling populations falsifies the hypothesis that phenotypic differences between plains and wood bison are environmentally induced.

The other populations, whose genealogies are more uncertain, show the same general concordance between phenotype and kinship. The populations in the nonsignificant subset Custer State-Fort Niobrara-National Bison Range-Delta Junction (Fig. 2) stem from founding stock containing northern plains bison with admixtures of southern (Texas) strains (Coder, 1975; N. S. Novakowski, in litt.). Custer State was established in 1914 with animals from Wyoming. Fort Niobrara originated in 1913 from six animals from Nebraska and two from the Allard estate (via Yellowstone National Park). The National Bison Range

dates from 1909, and its founding stock comprised Allard-Pablo (36) and Texas (10) stock. Delta Junction, as we have already seen, derives directly from the herd at the National Bison Range. Plains bison from Yellowstone National Park and Elk Island National Park, which form the other nonsignificant subset, differ from other plains bison to a greater degree. Yellowstone National Park's founding stock consisted of northern (Allard-Pablo) and southern (Texas) plains bison and a significant proportion (30–40%) of indigenous Yellowstone bison (Meagher, 1973). Plains bison in Elk Island National Park were derived from northern plains bison with an unknown admixture of Texas stock.

The results of our analyses support a genetic basis for the phenotypic characters that distinguish plains bison from bison in greater Wood Buffalo National Park. Our study indicates that the shape of the hump and the pelage characters are independent. Four of the five pelage characters, conversely, showed significant associations, which suggests that they may be genetically linked.

Relevance to infraspecific taxonomy.—The phenotypic variation in present remnant populations can only be partially interpreted in terms of the past geographic variation, because the exact composition of the founding herds is not known. However, results of our study agree with those based on cranial data from historical populations (van Zyll de Jong, 1986). Both show variation within plains populations to be much less than that between plains and wood (or present greater Wood Buffalo National Park) bison. It is probable that external phenotypic differences observed in modern populations reflect a past morphological discontinuity between plains and wood bison.

In the recent past, North American bison occupied a vast range, but they were most numerous on the central plains. The geographic variation in historical populations appears to have been largely clinal in a south-north direction, but there was a morphological discontinuity in the northwestern part of the species' range in the area of the boreal forest-grassland transition (van Zyll de Jong, 1986, 1993). The distinctness of wood and plains bison probably was maintained by a combination of behavioral and ecological factors. Most important among these were seasonal movements of plains bison (Gordon, 1979; Moodie and Ray, 1976; Morgan, 1980), which ensured separation of the two forms during the rut. The subspecific status of the historical populations of wood and plains bison is well founded and fits the definition given by Avise and Ball (1990). As to the taxonomic status of present subpopulations in greater Wood Buffalo National Park, the situation is less straightforward. All could, strictly speaking, be designated as intergrades (*B. b. bison* × *B. b. athabascae*) because even the most remote of the subpopulations appear to have been affected to some degree by the introduction of plains bison. To combine all subpopulations in the same category would obscure detection of significant differences and that some subpopulations are closer to the original wood bison than others. It would be more useful and informative to designate the clearly intermediate subpopulation (Pine Lake) as an intergrading population (*B. b. bison* × *B. b. athabascae*) and the others (Sweet Grass, Nyarling, Slave River Lowlands), being considerably more distant from plains bison and closest to the original wood bison, as *B. b. athabascae*.

Conservation policy.—In Canada, present conservation policy encompasses infraspecific groups based on geographic distinctiveness. Any group below the species level may be designated by the Committee on Species of Endangered Wildlife in Canada (COSEWIC) as endangered or threatened, if it is geographically distinct based on discontinuity in gene flow, geographical barriers, breaks in breeding distribution, ecotypic variation, taxonomic differentiation, genetic analysis, or other compelling

evidence and the population represents a significant proportion of the historical range of the species in Canada. Based on our findings, we recognize that existing subpopulations in greater Wood Buffalo National Park and those populations derived from them represent the closest living relatives of the original wood bison. Despite hybridization, some subpopulations retain a high proportion of animals resembling indigenous wood bison. Consistent with the Committee's criteria, these subpopulations should be added to those already on the list (Nyarling wood bison in the Mackenzie Bison Sanctuary, Elk Island National Park, and populations derived from these).

While data now available, in our view, warrant formal recognition of contemporary plains and wood bison as subspecies, the debate on whether this recognition is valid should in no way affect their conservation as separate entities. The important issue is the conservation of genetically-based geographic variation in North American bison that reflects a pattern of evolutionary divergence and geographic discontinuity that has developed within the past 10,000 years. After their devastating impact on the species in the past, humans continue to control the evolutionary destiny of bison. There is thus an implicit responsibility to preserve as much of the intraspecific diversity as possible, to allow for continued adaptation and evolution as well as for utilitarian purposes. Geographic variation should be preserved in populations where natural processes and factors operate most freely. Accidental crossbreeding of northern and southern forms of bison resulting from escapes of privately-owned, commercial bison or the willful introduction of one form into the range occupied by the other will lead to further loss of intraspecific diversity and conflicts with one of the central objectives of conservation biology. Phylogeny is a time-dependent process, in part, resulting from accumulated genetic differences in the absence of gene flow. The possibility that geographic variants possess unique adaptations and have the potential to evolve into new species are compelling reasons for conserving them (O'Brien and Mayr, 1991).

Managers of public and private herds of bison cannot afford to be complacent about conservation of geographic variability. Erosion of genetic variability tends to advance rapidly under domestication. Domestication places the species in a state of total dependence where natural selection is replaced largely by artificial selection based on economic and husbandry considerations. Experience with several traditional domestic animals indicates that recovery of original genetic diversity is difficult or impossible once domestication has progressed to a stage where existing breeds are highly selected for specific purposes and primitive breeds and wild stocks have become extinct (Crawford, 1984). Artificial selection and hybridization to obtain certain traits dictated by economic and animal husbandry considerations make good business sense, but rapidly diminish the genetic resource. Wild stocks, therefore, serve as a genetic bank that can be drawn upon to improve domestic breeds when the need arises.

It takes little reflection to conclude that the responsibility for conserving intraspecific diversity rests primarily with public agencies and not private interests. Only public agencies can provide the continuity and long-term protection of intact ecosystems large enough for all natural forces to act on a large-sized species such as bison. A conservative approach to the conservation of intraspecific diversity in bison would be to manage geographic variants separately in large, viable populations under conditions as close as possible to those of primeval times. Aldo Leopold implored "to keep every cog and wheel is the first precaution of intelligent tinkering" (Noss, 1989). We would be wise to bear this analogy in mind as we forge plans for the conservation of remnant populations of bison for present and future generations.

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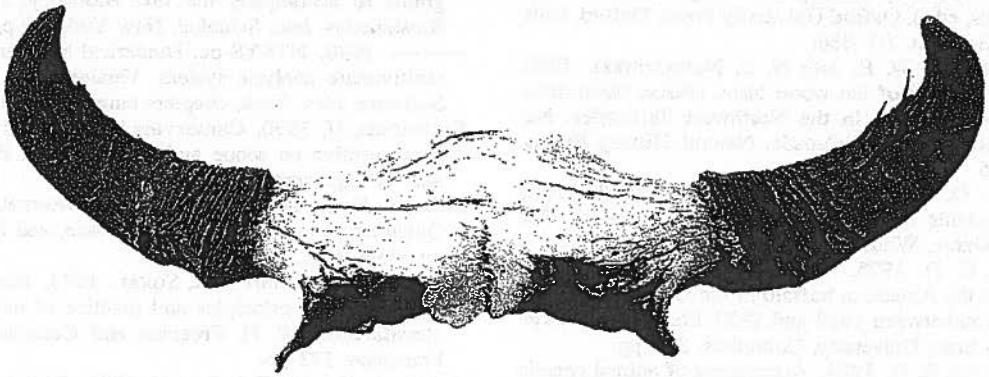
THE ANALYSIS OF A LATE HOLOCENE BISON SKULL FROM THE ASHLEY NATIONAL FOREST, UTAH



National Park Service - Midwest Archeological Center

THE ANALYSIS OF A LATE HOLOCENE BISON SKULL FROM THE ASHLEY NATIONAL FOREST, UTAH

By

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National Park Service
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Introduction

"I doubt the bison had much respect for altitude, and I believe they went as high as they choose" (Warren 1927:61).

Documenting the range of mammalian species was an important aspect of biologists working in the late 19th and early 20th century, especially with respect to shrinking habitat from expanding settlement in the intermountain west. This was particularly true of the North American bison (*Bison bison*, Linnaeus 1758) which was reduced to a few hundred individuals at the beginning of the 20th century with their long-term preservation uncertain (Shell 2002:viii).

Altitudinal range, as well as latitudinal and longitudinal, were often reported in scientific journals. Fryxell (1926) reported on a number of bison specimens in the Medicine Bow Mountains of Wyoming at altitudes ranging from 2895 to 3658 m (9500 to 12,000 ft). In a later article Frxyell (1928) reports on high altitude bison records from Colorado, Wyoming, and Montana. High altitude bison citings in southern and northern Colorado are also reported by Cook (1930), Warren (1927), and Beidleman (1955). More recently, Wilson (1974) reported on bison remains from above timberline in the Bighorn Mountains of northern Wyoming. With possible climate-driven ice/snow-field melting in high altitude and latitude region, a new source of bison remains has been established (Lee et al. 2004).

Unfortunately, few high altitude records of bison have been reported in Utah. Madsen (2000) reports that 30 genera of late Quaternary fauna have been found in alpine settings. However, only two high altitude sites, Mastodon Sinkhole (3232 m [10,604 ft]) in Sanpete County (Gillette and Madsen 1993 citing W. Miller personal communication) and Huntington Canyon (2740 m [2743 ft]) near the crest of the Wasatch Plateau (Gillette and Madsen 1993; Madsen 2000), produced bison. The paucity of high altitude bison remains from Utah is therefore noteworthy (Table 1). While the Gilbert Peak bison represents a single individual, it does contribute significantly to our knowledge of high elevation fauna.

This study takes its queue from Fryxell (1928:139), a statement which may be more imperative today:

> *It is now out of the question to turn bison loose on the plains. The only portions, if any, of the former range of the bison that could now possibly be restocked are certain uninhabited tracts in or adjacent to the mountains—within the national forests and national parks. Hence, obviously, the importance of preserving such scraps of information as can be obtained at this late period concerning the former range and life habits of the bison in our western mountains.*

Therefore, it is the purpose of this study to provide some of these *scraps of information* using contemporary research techniques (e.g., Cannon 1997). These include radiometric dating, metric analysis of the specimen and its relationship to other intermountain and high altitude specimens, and stable isotope analyses. Stable carbon and nitrogen isotope analyses have the potential to yield information on the diet and ecology of an individual. Cool (C_3) and warm (C_4) season grasses have been demonstrated to have distinct ratios of ^{13}C to atmospheric CO_2 due to their particular photosynthetic pathways. Another stable isotope that is linked to trophic level and potentially important for investigating diet and herbivore migration is $\delta^{15}N$. Nitrogen is an important component of life with its primary source from atmospheric nitrogen (N_2). Results of these techniques will provide a more complete understanding of the age and ecology of this particular individual, and how it compares with other late Quaternary bison.

As Walker (1992) explains there are still temporal and spatial gaps in the Holocene

record of bison and isolated skulls can help fill them. He goes on to further argue that isolated bison skulls can provide specific information for understanding the paleoecology and evolution of the species. Information derived from detailed study of isolated bison skulls can have implications for a number of social and ecological issues (Van Vuren 1987:65), such as the management and restoration of ecosystems (Lyman 1996; Lyman and Cannon 2004), zoogeography (Lyman and Livingstone 1983), and ethnography (Bamforth 1988; Reeves and Peacock 2001).

While this study focuses on the results of various analyses conducted on the Gilbert Peak bison, the context of the study is regional in scope. This study, along with an earlier one (Cannon 1997), provide the initiation of a larger study to understand the biogeography of bison in the intermountain west within the context of long term climate change (Cannon 2001; Lyman 2004).

Table 1. High elevation fauna sites from Utah.

SITE	ELEVATION	COUNTY	AGES (yrs BP)	FAUNA	REFERENCE
Silver Creek	1950 m	Summit	> 40 ka	25 mammalian and non-mammalian species	Miller 1976
Mastodon Sinkhole	3232 m	Sanpete	7590 ± 100 7650 ± 100 <10,000*	*Mammut americanum*	Miller 1987
Blonquist Rockshelter	2125 m	Summit	5640 ± 260 7985 ± 480 9665 ± 550	Numerous small mammal species	Nelson 1988; Nelson et al. 1989
Huntington Canyon	2981 m	Sanpete	8430 ± 110 to 12,340 ± 85	*Arctodus simus*, *Mammuthus columbi*, *Equus* sp., *Bison* sp., *Camelops* sp.	Gillette and Madsen 1992, 1993; Madsen 2000

*Age determined by racemization analysis.

Environmental Context

Introduction

Rising from the Wyoming and Uinta basins to the north and south, respectively, the Uinta Mountains form a distinct topographic unit in northeastern Utah that parallels the southern border of Wyoming. The Ashley National Forest (ANF) is generally coextensive with the Uinta Mountains. The Uinta Mountains have been further defined into three distinct subsections (Stokes 1986).

The Gilbert Peak skull was recovered in the area defined as the High Uintas Subsection which forms the crestal portion of the Uinta Mountains (Figure 1). The subsection includes the western half of the mountains and extends from approximately Mirror Lake in the west to Fox Lake in the east. The Uinta High Wilderness is generally coextensive with this geologic area (Stokes 1986).

The High Uintas include Utah's highest peak, Kings Peak (4123 m [13,528 ft]), as well as the headwaters of the Provo, Weber, Duschesne, Uinta, and Bear Rivers. Glaciation has produced gently sloping, semicircular, flat-bottomed cirque valleys that are separated by steep-walled arêtes. The area is also known for the hundreds of rock-rimmed lakes that have been left by the glaciers. Modern timberline is 3505 m (Stokes 1986:245-246).

The growing season in this high elevation region is short with temperatures in the summer seldom above 26° C (80° F). Precipitation falls mostly as snow, totaling about 1016 mm (40 in). Climatic information from the Ashley National Forest web page (www.fs.fed.us/r4/ashley/).

Modern Environment

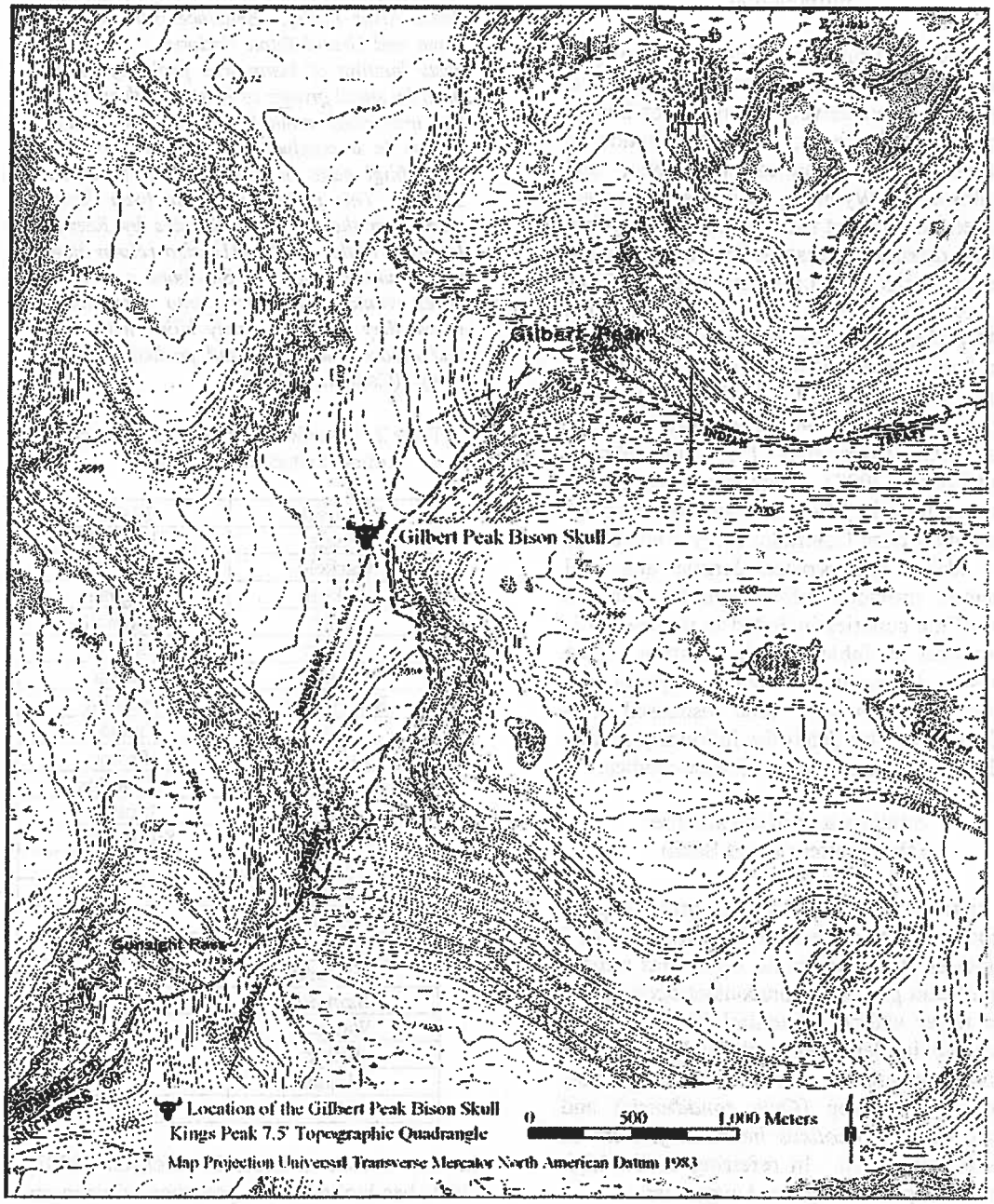
The Gilbert Peak bison skull was recovered from a ridge southwest of Gilbert Peak at an elevation of 3840 m (12,600 ft) AMSL in Summit County along the boundary between the Ashley and Wasatch National Forests (Figure 2). Gunsight Pass between Gilbert Peak and Kings Peak is to the southwest (Figure 3). The area consists of alpine vegetation with surface cobbles common. Soils are shallow and well-drained. Tundra vegetation is present in the immediate area. Common species include perennial herbs (*Geum rossi*, *Silen acaulis*, *Paronychia pulvinata*, *Arenaria obtusiloba*, *Trifolium nanum*, *Kobresia myouroides*, *Polygonum bistoroides*, *Eriophorum chamissonis*), perennial grasses (*Deschampsia caespotosa*, *Festuca ovina*, *Koeleria cristata*, *Trisetum spicatum*), sedges (*Carex* sp.), and willow (*Salix* sp.). Vegetation information is based upon Utah vegetation codes and cover types as defined by Edwards et al. (1995).

To the east the landscape slopes dramatically into a boggy area with an unnamed lake that is drained by Gilbert Creek. This area is part of the headwaters of the Uinta River. Engelmann spruce (*Picea engelmannii*) are present along the edge of the boggy area. The wet meadow vegetation consists mostly of grasses, forbs, sedges, and rushes (Figure 4).

Dietary studies of bison in the Henry Mountains of southeastern Utah (Van Vuren 1982: Table 1) and Yellowstone National Park (Meagher 1973: Table 17) indicate that grasses and sedges are highly preferred forage.

The skull was recovered from the steep gravel and boulder-covered slope on the southwest slope of Gilbert Peak (Figure 5). The find location is about 1900 m west of the headwaters of Gilbert Creek (see Figure 4).

Figure 2. Find location of the Gilbert Peak bison skull as modified Kings Peak, Utah 7.5 minute topographic quadrangle.



Regional Evidence of Bison

Introduction

The record of bison remains from late Quaternary sites in the region is fairly extensive, and almost exclusively the result of human predation (Figure 6). The distribution in northern Utah, southeastern Idaho, and southwestern Wyoming indicates bison were present throughout the Holocene with population density fluctuating in relation to climate patterns (e.g., Lupo and Schmitt 1997). In compiling data on bison in the region the FAUNMAP database was initially consulted, but was supplemented by the regional literature. These include La Point (1987), Janetski and Madsen (1990), Thompson and Pastor (1995), Bruder et al. (1999), and Johnson and Loosle (2002). State site records were also reviewed. Mary Sullivan provided information from Colorado; Mary Anne Davis for Idaho; and Kristen Jensen and Joel Janetski provided information for Utah. A list of the counties included in the review is presented in Table 2 with a listing of the sites in Appendix A. While regional evidence of bison have been discussed elsewhere in greater detail the following section will present an overview of these studies.

Southeastern Idaho and the Northeastern Great Basin

In a review of bison-bearing archeological deposits from eastern and central Idaho, I indicated that reliance on bison was a more significant part of the precontact economy in the wider valleys of central Idaho with an increase in dependence through time. In more mountainous regions other ungulates, particularly sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*), were of more importance. In referring to the high mountain plateau regions I suggested:

> *Bison populations in the mountains are probably of lower density and more dispersed. This pattern may have facilitated a different hunting strategy than the massive drives and traps that appear on the plains, and presumably in the wider valleys (e.g., the Snake River Plain). Evidence from Yellowstone and Grand Teton National Parks suggests hunting of bison was probably practiced by small groups of hunters either stalking individual animals or trapping small groups in a conducive topographic setting (e.g., bluff edge or marshy area [Cannon 1991]). This pattern has also been documented in the Northern Rockies by Reeves (1978). Butler (1978:111) also relates how small hunting bands of Shoshone on snowshoes would chase bison into deep snow where they could be easily killed with bow and arrow, butchered, and packed back to camp*" (Cannon 1997:20).

Table 2. Counties reviewed for evidence of precontact bison remains.

Colorado	Idaho
Eagle	Bannock
Garfield	Bear Lake
Jackson	Bingham
Lake	Bonneville
Moffat	Caribou
Pitkin	Cassia
Rio Blanco	Franklin
Rout	Oneida
Summit	Power
Utah	**Wyoming**
Cache	Lincoln
Daggett	Sweetwater
Davis	Uinta
Duchesne	
Morgan	
Rich	
Salt Lake	
Summit	
Wasatch	
Weber	
Uintah	
Utah	

In two recent articles, Henrickson (2003, 2004) has looked at the presence of bison on the Snake River Plain of Idaho and its relative importance in the regional precontact diet. Using a prey choice model to orient her investigation, she concludes that "bison were probably always taken when encountered" (Henrickson 2003:283), but that the

sagebrush steppe environment of the Snake River Plain would have supported a much reduced population in comparison to the short-grass prairies of the Great Plains (Henrickson 2004:914).

Henrickson's analysis further supports Lupo and Schmitt (1997) who assert that bison populations were climatically limited, but when they were available, as during Fremont times (after AD 1300), were an important resource. The inability of the sagebrush-steppe of the Intermountain West to support large herds of bison has also been argued by Mack and Thompson (1982) and Daubenmire (1985).

High altitude bison remains in Utah are rare, as are high altitude local faunas in general (Gillette and Madsen 1993). Madsen (2000) has suggested a seasonal use of high altitude valleys in the Wasatch Plateau during post-glacial times by mammoth, mastodon, horse, camel, and bison. These patterns are similar to modern migrations of ungulates through multiple floristic zones, for example the seasonal migration of bison in the Henry Mountains of southeastern Utah (e.g., Van Vuren 1982). Meagher (1973) in her study of Yellowstone bison indicates that seasonal movements between elevation zones include seasonal changes in the vegetation, the rut, and biting insects.

Southwestern Wyoming

Lubinski (2000) examined 93 radiocarbon-dated faunal assemblages from 58 sites in the Wyoming Basin of southwestern Wyoming. In this study Lubinsksi found, through a variety of measures, bison were found to be a dominant genera along with *Antilocapra*, *Spermophilus*, *Sylvilagus*, and *Lepus*. In examining the dietary selection of bison and antelope (bison prefer grasses while antelope browse primarily on sagebrush), climatic conditions may influence the relative availability of these two species. For example, during moist phases grasses will be more common and support relatively more bison, while during more xeric times antelope will be more prevalent due to an increase in sagebrush.

Lubinski's (2000:184) analysis, based upon climatic reconstruction by Eckerle and Obey (1995), indicates bison were more prevalent during the moist earliest Holocene (10,000-9000 yrs BP), the moist middle Neoglacial (3500-1800 yrs BP), and the moist Little Ice Age (500-150 yrs BP). Although Lubinski (2000:184) indicates that understanding subsistence and climate in the Wyoming Basin is still in "its infancy" his work does provide an initial step in bringing together a large dataset in the resolution of this issue.

Colorado

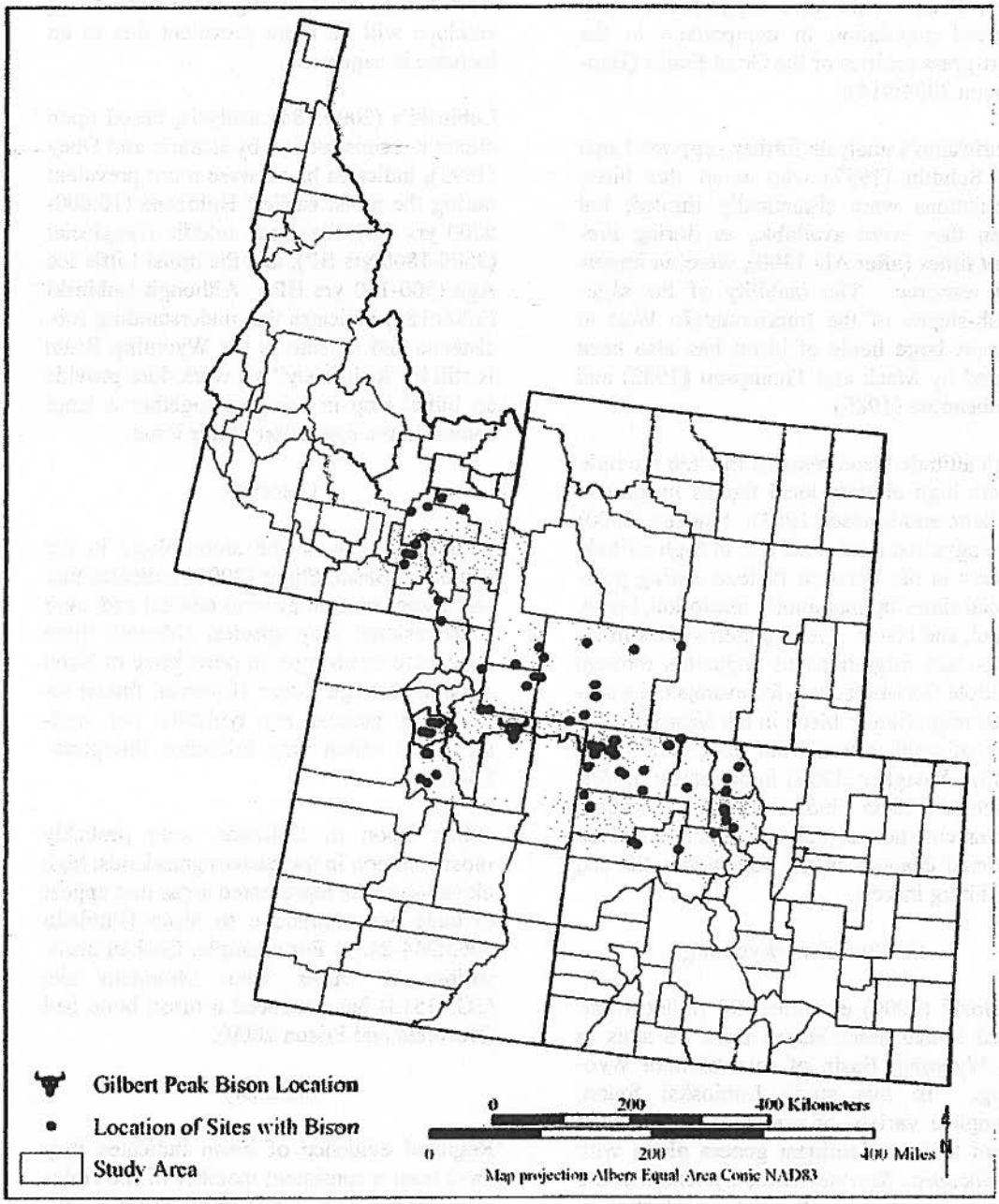
In an overview of the archaeology in the Gunnison Basin, Stiger (2001) indicates that bison were present prior to contact and were an occasional prey species, although there appears to be changes in prevalence of bison remains through time. However, faunal remains in general are typically not well-preserved which may influence interpretations.

While bison in Colorado were probably most common in the eastern grasslands, high elevation parks represented areas that appear to have been attractive to bison (Pitblado 2003:244-245). For example, Goshen occupations at Upper Twin Mountain site (5GA1513) has produced a bison bone bed (Kornfeld and Frison 2000).

Summary

Regional evidence of bison indicates they have been a consistent member of the Holocene mammalian community, although climate may have influenced herd numbers and the availability of bison as a human prey item.

Figure 6. Regional map illustrating location of precontact sites with bison remains.



Description and Examination of the Skull

Description

The Gilbert Peak bison skull is represented by the proximal portion of the cranium including the horn cores with preserved horn sheaths. A portion of the frontal bone is also preserved, while the occipital region is eroded with only the occipital condyles and the area around the foreman magnum present (Figure 7). Colonies of the lichen *Xanthoria elegens* are present on the horn sheaths and in the interior of the skull (Figure 8). This species of lichen is common on calcium-rich rocks, old bones, and old wood in alpine regions of the Rocky Mountains (Kershaw et al. 1998:344).

The incomplete nature of the specimen limits the number of measurements. All available skull measurements follow those defined by McDonald (1981a:43-47) which are based upon those originally defined by Skinner and Kaisen (1947). Measurements for the Gilbert Peak skull are presented in Table 3.

Sexing of the Gilbert Peak bison was based upon relative robustness of the skull and horn core morphology. Female skulls are typically smaller in size, and some features, such as horn cores and eye orbits, are less massive. Male horn cores have a distinct burr or rim at the dorsal base, while females typically do not have a distinct burr, and the horn core often blends with the neck and frontals (McDonald 1981a:44). The Gilbert Peak skull has distinct burrs at the base of the horn cores, suggesting it is a bull.

A less subjective means of assessing gender is the metric comparison of the Gilbert Peak skull with other skulls of known gender. Utilizing McDonald's (1981b) data for other western United States bison, the dorso-ventral diameter of the horn core was plotted against spread of the horn cores. The plot indicates that the Gilbert Peak bison skull is a large male (Figure 9).

Assessing age at death of archeological bison is typically conducted through wear patterns of mandible teeth (e.g., Frison and Reher 1970). Unfortunately, the teeth are not preserved in this specimen. Suture closure is another means of assessing relative age. McDonald (1981a:44) considered a skull mature:

> *If the sagittal frontal suture was completely fused posteriorly from about midway between the planes of the orbits and bases of the horn cores, and if the frontal-parietal sutures were completely fused from the sagittal origin laterally and ventrally to below the level of the ventral horn core bases.*

McHugh (1958) and Fuller (1959) suggest that the size and shape of the horn can be used to determine age. While this can be used as a relative means for assessing age in populations, it is not of particular value.

Counting the number of growth rings on the horn sheath was also suggested by McHugh (1958:31) as a means of estimating age. However, he cautions that the determination should be increased by three years to allow for the juvenile period when no obvious rings are formed. Reynolds, et al. (1982) discount the counting of rings as a reliable estimate of age.

For the Gilbert Peak skull, the sagittal frontal suture appears to be almost completely fused (Figure 7a), suggesting an adult. In his master's thesis Wilson (1975: Figure 7 and 8) presented a preliminary study of age based upon allometric growth. Plotting two skull measurements against known ages he illustrated logarithmic curves for estimating age. Walker (1992) applied this technique in his study of isolated bison skull from the Seminoe Reservoir, Carbon County, Wyoming. For the Gilbert Peak bison skull only one skull measurement was available for study, least width of frontals.

Superimposing the Gilbert Peak measurement onto Walker's graph (1992: Figure 7 lower), an estimated age at death for the Gilbert Peak bison is 12 years (Figure 10).

Figure 7. Gilbert Peak bison skull views: (a) dorsal view; (b) nuchal view; and (c) basal view.

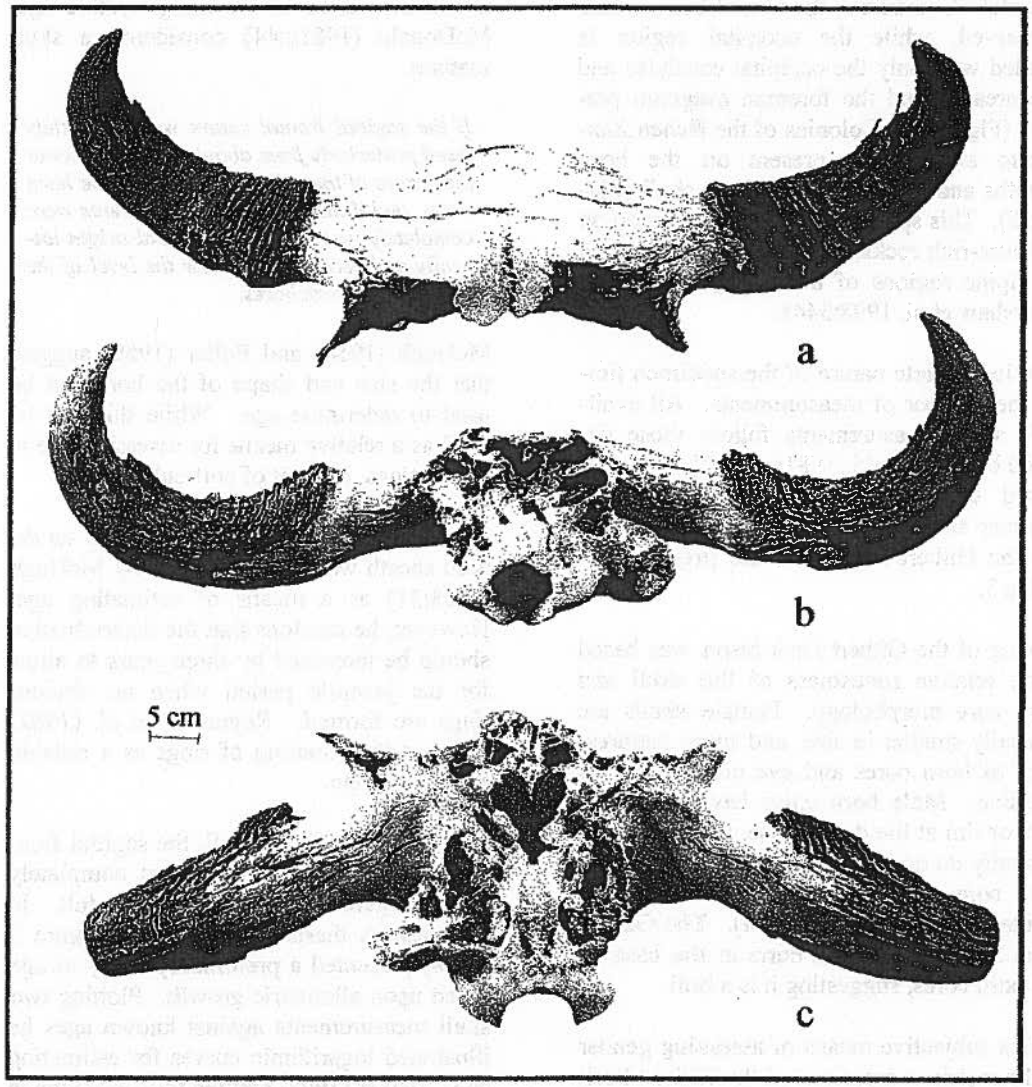


Table 3. Skull measurements following McDonald (1981a). All measurements are presented in millimeters. Data on *Bison occidentals* are from McDonald (1981a:Table 25), *Bison bison athabascae* from McDonald (1981a:Table 34), *Bison bison bison* from McDonald (1981a:Table 29), and high altitude bison are from McDonald (1981b:550-553) and Wilson (1974: Table III). All specimens used in analysis are males.

Measurement*	Gilbert Peak	*Bison antiquus occidentalis*				*Bison bison athabascae*				*Bison bison bison*				High Altitude Bison			
		N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
Spread of horn core, tip to tip (SHTT).	657	77	779.3	626-1055	76.9	9	681.2	542-848	92.0	128	603.9	510-778	44.7	17	602.4	508-719	55.7
Horn core length, tip to burr (CLUC).	295	86	277.8	186-392	39.1	9	1235.1	165-323	43.9	134	190.7	124-270	24.7	19	185.5	140-225	23.7
Straight line distance, tip to burr, dorsal horn core (TB).	210	81	248.1	175-350	31.8	9	207.0	154-277	34.4	132	172.4	120-243	21.4	19	171.8	127-216	22.7
Dorso-ventral diameter, horn core base (VD).	105	85	94.6	70-114	8.4	9	91.5	81-106	8.7	139	81.9	69-99	6.4	23	84.2	69-99	8.6
Minimum circumference, horn core base (CHC).	266	89	300.3	237-355	27.7	9	289.1	254-322	22.9	142	255.4	199-324	19.5	22	260.8	228-305	21.5
Width of occipital at auditory openings (GWA).	281.2	61	262.0	238-294	13.2	10	273.6	243-298	15.3	120	243.9	220-270	9.7	17	249.3	228-276	12.6
Width of occipital condyles (CW).	110	71	135.0	111-151	7.7	11	130.1	118-139	6.4	122	126.6	111-140	5.7	18	123.1	106-138	8.7
Depth, nuchal line to dorsal margin of foramen magnum (DEF).	-	57	104.0	89-120	7.0	10	99.6	92-114	6.6	112	98.7	81-115	6.2	-	-	-	-
Antero-posterior diameter, horn core base (TD).	90.8	91	98.8	77-120	10.1	9	97.2	83-109	9.5	142	83.4	67-103	6.3	25	84.9	74-97	7.2
Least width of frontals, between horn cores and orbits (WHCO).	280	74	296.6	261-348	16.8	10	293.4	273-313	10.5	135	271.1	237-318	12.6	22	271.1	248-294	11.9

Measurement*	Gilbert Peak	*Bison antiquus occidentalis*				*Bison bison athabascae*				*Bison bison bison*				High Altitude Bison			
Greatest width of frontals at orbits (GPW).	-	64	348.0	311-394	16.7	10	354.0	326-384	14.8	117	324.6	289-356	12.9	19	232.1	280-356	18.1
M1-M3, inclusive of alveolar length.	-	3	97.3	90-102	6.4	1	91.7	-	-	22	90.6	81.8-97.9	4.4	-	-	-	-
M3, maximum width, anterior cusp.	-	2	28.4	27.8	29.1	1	27.9	-	-	22	27.7	22.3-31.4	1.6	-	-	-	-
Distance, nuchal line to tip of premaxillae (OP).	-	25	564.3	511-606	24.8	7	578.6	562-604	15.2	56	535.2	500-583	17.0	-	-	-	-
Distance, nuchal line of nasal-frontal suture (ON).	-	57	259.8	233-287	12.3	9	256.0	240-276	13.4	106	245.7	214-279	12.2	14	241.6	206-279	22.4
Angle of divergence of horn cores, forward from sagittal (AHC).	70°	62	72.1°	63°-83°	5.2°	6	71.0°	63°-77°	5.0°	124	67.7°	58°-79°	4.4°	-	-	-	-
Angle between foramenmagnum and occipital planes (OF).	-	57	129.6°	110°-142°	7.3°	9	129.4°	119°-144°	8.8°	115	133.8°	118°-159°	7.6°	-	-	-	-
Angle between foramen magnum and basioccipital planes (BF).		56	113.4°	98°-126°	5.6°	9	113.8°	106°-125°	6.6°	115	110.5°	100°-129°	5.0°	-	-	-	-

*Abbreviations are those used in Figure 13.

Figure 8. Close-up of left horn sheath (nuchal view) illustrating colony of *Xanthoria elegens* and individual horn sheath cones sampled for stable isotope analysis.

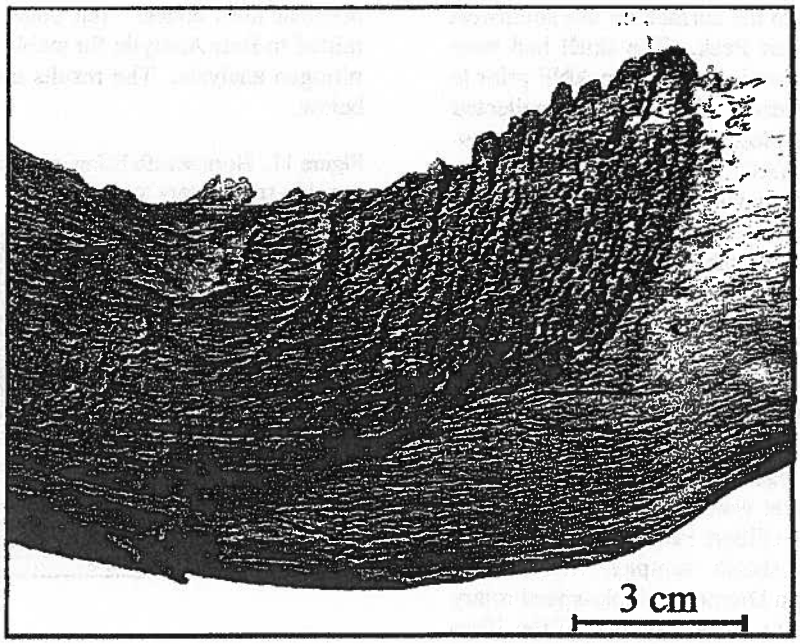
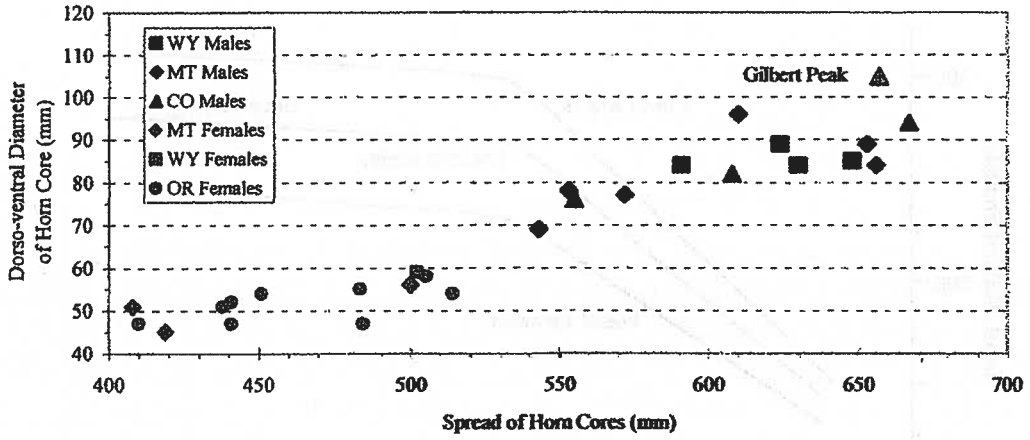


Figure 9. Plot of Gilbert Peak bison skull in relation to male bison skulls from western United States specimens. Data presented in Appendix C.



Preparation

As previously noted, the bison skull was recovered from the surface on the southwest slope of Gilbert Peak. The skull had been known for several years on the ANF prior to it being recovered. The skull was collected by ANF archeologist Brian Storm and transported to MWAC. No formal stabilization of the specimen was conducted, except for the removal of adhering sediments with a soft brush. A sample from the skull was cut from the basal portion of the occipital bone for radiocarbon assay (see below).

The horn sheath is a keratinized epidermis that covers the horn and consists of many periodically developed horn cones which tightly cling together (Bubenik 1990:5). It is these cones that were sampled for an annual record of the Gilbert Peak bison. Removal of the horn sheath samples was accomplished using a Dremel variable-speed rotary tool (Figure 11). After removal of the 10-x-4-cm section of the right horn sheath, it was placed in distilled water for approximately eight hours (Figure 12). Rehydration of the sheath allowed for the separation of the individual horn cones. Ten cones were submitted to Beta Analytic for stable carbon and nitrogen analysis. The results are presented below.

Figure 11. Horn sheath being cut using Dremel variable-speed rotary tool.

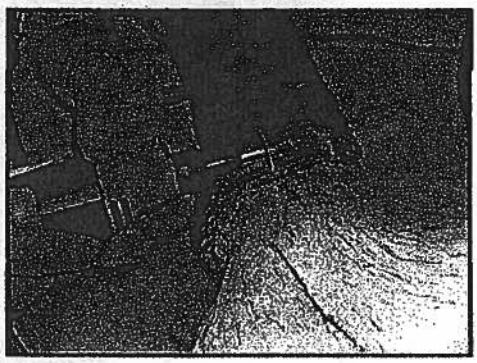


Figure 10. Semi-log plot of least width of frontals to individual age in late Pleistocene and modern bison skulls (adapted from Walker 1992: Figure 7).

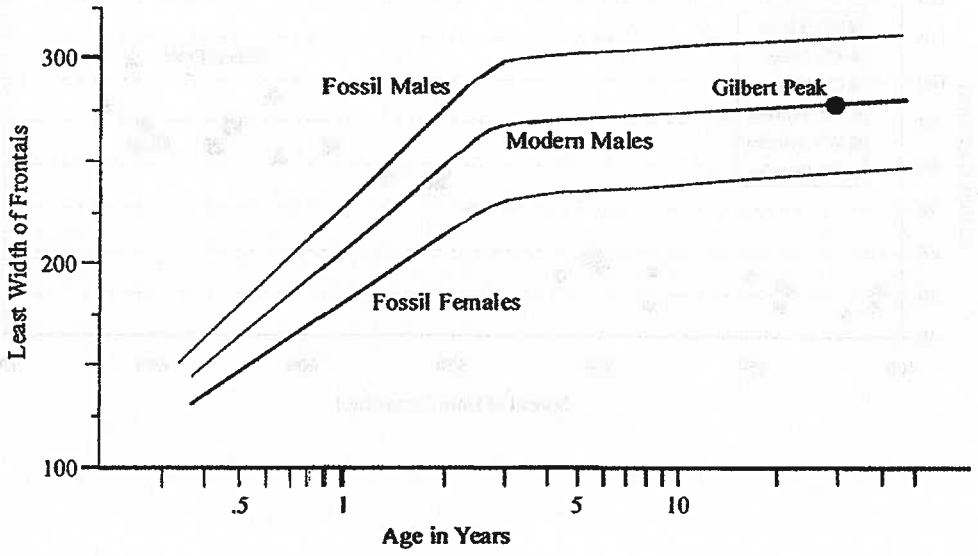
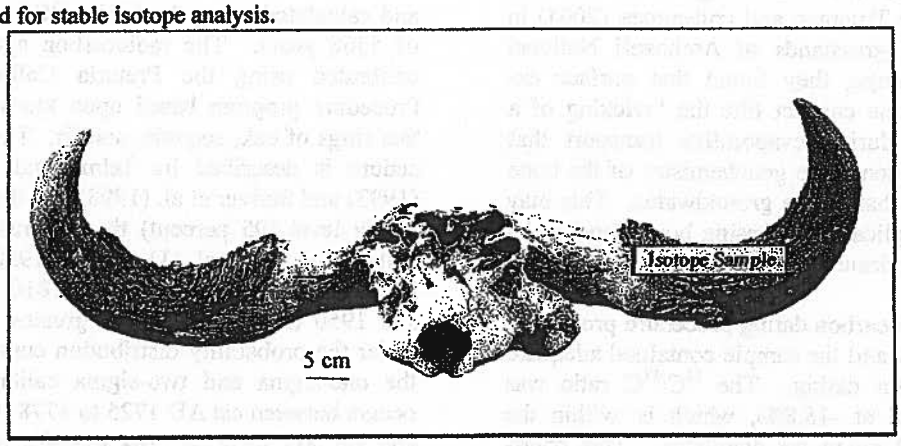


Figure 12. Dorsal view of Gilbert Peak bison skull. Hatched area illustrates portion of horn sheath removed for stable isotope analysis.



Radiocarbon Dating Results

In order to accurately place the specimen within a historical context, a 11.79-gram sample was collected from the skull and submitted to Beta Analytic for radiocarbon assay. The sample was removed from the basal portion of the occipital bone.

The sample was processed by Beta Analytic using the accelerator mass spectrometry (AMS) technique. Standard procedures for bone dating included collagen extraction with alkali. The protocol for collagen extraction specimens involved the initial assessment of the material for friability or softness. Specimens of very soft bone usually do not provide reliable ages. If a bone is judged to have sufficient collagen fraction, >5 percent original collagen remaining (Hedges and van Kliken 1992), it is washed in deionized water and gently crushed. Next, dilute, cold HCl acid is repeatedly applied and replenished until the mineral fraction (bone apatite) is eliminated. The collagen is then dissected and inspected for rootlets. If rootlets are found, they are also removed when replenishing the acid solutions. If a sufficient quantity of collagen is present (as was with this sample), NaOH is applied to ensure the absence of secondary organic acids (Hood 2004a). Hedges and van Kliken (1992) review the treatment of bone for AMS dating. In their opinion, " the methods that date carefully extracted and purified [collagen] gelatin, and can demonstrate analytically that the material dated corresponds to the composition expected for gelatin, are adequate for the great majority of bones that have lost up to 95 percent of indigeneous protein" (Hedges and van Kliken 1992:290). Beta Analytic adheres to these standards.

Hedges and van Kliken (1992) warn that contamination must always be suspected for poor or intermediate preservation, and if the specimen lacks evidence of a recognizable collagen signature, there is no longer any support for believing that the extracted organic material is indigenous. Contamination can come from a number of sources depending upon the particular environment. However any, and probably all buried bone is liable to have incorporated exogenous soluble and insoluble organic materials, such as rootlets, soil humics, or other molecules mobilized in groundwater. Bone is particularly susceptible to absorption of these contaminants due to its high surface area (10 m^2g^{-1}). Fortunately, the "humic" fraction is nearly always extractable from bone with alkali pretreatment (NaOH), and generally provides an accurate or younger date (Hedges and van Kliken 1992:284). With

surface materials, such as the Gilbert skull, weathering and leeching are most critical in the preservation of collegen. In a recent study by Trueman and colleagues (2004) in the arid grasslands of Amboselli National Park, Kenya, they found that surface exposed bone can act like the "wicking of a candle" during evaporative transport that may influence the geochemistry of the bone towards that of the groundwater. This may have implications of using bone geochemistry as environmental proxies.

The radiocarbon dating procedure proceeded normally and the sample contained adequate carbon for dating. The $^{13}C/^{12}C$ ratio was measured at -18.8‰, which is within the expected range for ungulates. This measurement indicates that sufficient collagen was present for an accurate radiocarbon age. The $^{15}N/^{14}N$ ratio was also measured for this specimen which produced a value of 7.3‰ (Hood 2004a). Published $\delta^{15}N$ values for bison range from 2.9‰ to 6.9‰ (Cannon 1997; Table 4; Figure 13).

The radiocarbon age obtained is 150 ± 40 yr BP (Beta-192144). The radiocarbon years before present are referenced to AD 1950 and calculated using the Libby ^{14}C half life of 5568 years. The radiocarbon age was calibrated using the Pretoria Calibration Procedure program based upon known-age tree rings of oak, sequoia, and fir. The procedure is described by Talma and Vogel (1993) and Stuiver et al. (1998). At the two-sigma level (95 percent) the calibrated results range from cal AD 1660 to 1950 with intercepts at cal AD 1680, 1740, 1810, 1930, and 1950 (Figure 14). The greatest areas under the probability distribution curves for the one-sigma and two-sigma calibrations occurs between cal AD 1725 to 1778 (0.362) and cal AD 1665 to 1784 (0.480), respectively (Table 5), and implies that the age of the bison's death is statistically more likely to be of this age rather than the other calibrated ages. Based upon this information it is most likely that this bison died during the early to mid-eighteenth century.

Table 4. Results of stable isotope analysis of modern North American bison specimens. Alaska data from Bocherens et al. (1994:Table 4), Konza, Niobrara, Wood Buffalo, and Yellowstone data from Tieszen et al. (1996), Wind Cave data from Tieszen (1994:Table 5),and Fawn Creek data from Cannon (1997:Table 6).

Specimen	Collagen Rank	Percent Yield	Percent Nitrogen	Percent Carbon	C/N	$\delta^{13}C$	$\delta^{15}N$	Appatite $\delta^{13}C$
Gilbert Peak	-	-	-	-	-	-18.8	+7.3	-
Fawn Creek	3	25.9	14.8	41.5	3.3	-19.6	+6.5	-10.8
Alaska	-	-	-	-	-	-20.5	+4.4	
Konza, KS	-	-	-	-	-	-13.8	+5.5	
Niobrara, NE	-	-	-	-	-	-15.9	+2.9	
Wind Cave, SD	-	*6.5*	-	-	*3.22*	*-18.7±0.2*	*+6.4±0.23*	
Wood Buffalo, NWT	-	-	-	-	-	-23.9	+6.6	
Yellowstone, WY	-	-	-	-	-	-23.4	+6.9	

Table 5. Results of calibration using CALIB 4.4.

Percent Area Enclosed	cal AD Age Ranges	Relative Area Under Probability Distribution
68.3 (1 sigma)	1672-1695	0.150
	1725-1778	**0.362**
	1799-1813	0.097
	1839-1876	0.199
	1917-1949	0.192
95.4 (2 sigma)	**1665-1784**	**0.480**
	1790-1890	0.346
	1909-1950	0.174

Figure 13. Plot of $\delta^{15}N$ against $\delta^{13}C$ values for modern North American bison specimens from high altitude, high latitude, and central Great Plains. Data from Bocherens et al, (1994), Tieszen (1994), Tieszen et al. (1996), and Cannon (1997).

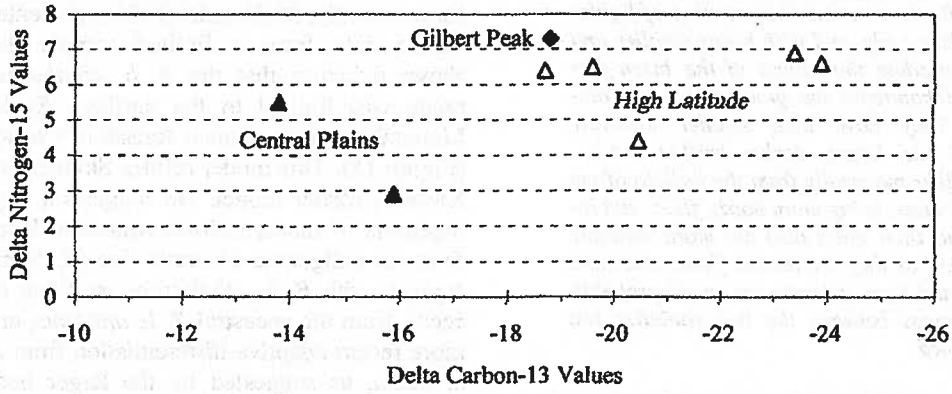
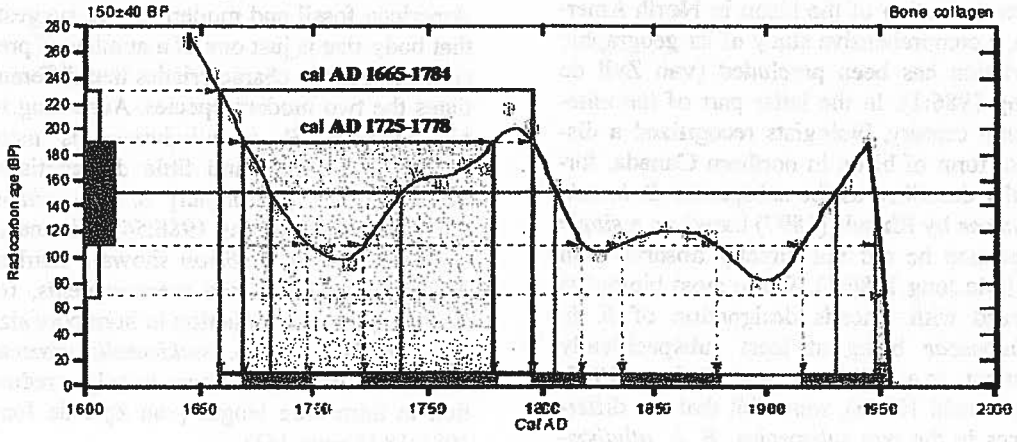


Figure 14. Results of calibration of radiocarbon age to calendar years. The calibration range presented in red represents the 2-sigma range and the area in blue represents the 1-sigma range.



Bison Taxonomy

Since the nineteenth century, when trappers, explorers, and zoologists first ventured into the Rocky Mountains, there has been controversy surrounding the species of bison occupying these regions. The earliest accounts are ripe with descriptions of the exploits of the "Woodland or Mountain Bison" (e.g., Christman 1971). Various historical accounts of the "mountain" bison indicate they "were more hardy, fleet, and wary, and had darker finer, curlier hair" than the Plains bison (Meagher 1973:14-15). Superintendent Norris (1880) describes the bison of Yellowstone National Park in the Superintendent's Annual Report:

> *Bison or Mountain Buffalo...Bison, so called, in the Park, are somewhat smaller, of lighter color, less curly, and with horns smaller and less spreading than those of the bison formerly inhabitated the great parks of Colorado. They have also smaller shoulder humps, and larger, darker brisket wattles. They differ materially from the buffalo of the Great Plains, being more hardy, fleet, and intelligent; their hides also are more valuable for robes, as they are darker, finer, and more curly; and these animals are, in all probability, a cross between the two varieties just mentioned.*

In fact, considering the geographic range of bison in North America, some authors have suggested there may have been several distinct geographic forms. However, with the near extinction of the bison in North America, a comprehensive study of its geographic variation has been precluded (van Zyll de Jong 1986:1). In the latter part of the nineteenth century, biologists recognized a distinct form of bison in northern Canada, formally described as the subspecies *B. b. athabascae* by Rhoads (1897) based on a single specimen he did not directly observe (van Zyll de Jong 1986:1). While most biologists agreed with Rhoads designation of *B. b. athabascae* being at least subspecifically distinct (e.g., Skinner and Kaisen 1947; McDonald 1981a), some felt that the differences in the two subspecies, *B. b. athabascae* and *B. b. bison*, were of little consequence (van Zyll de Jong 1986:1).

According to van Zyll de Jong (1986:1), the decimation of the bison herds prior to firsthand study and the small number of specimens available for study contributed to the diversity of opinions. In one of the first quantitative studies of museum specimens—primarily crania—Skinner and Kaisen (1947) argued for an overlap in distribution of the two subspecies—*B. b. athabascae* and *B. b. bison*—along the eastern slopes of the Rocky Mountains. However, their argument was unconvincing due to the lack of cranial and postcranial specimens for comparison.

More recently, McDonald (1981a) presented metric data from a limited sample that shows evidence that the *B. b. athabascae* range was limited to the northern Rocky Mountains and the boreal forests of Canada (Figure 15). This model refutes Skinner and Kaisen's earlier model. He suggests a phylogenesis of modern North American bison from an indigenous Nearctic line (*B. b. antiquus)*, with *B. b. athabascae* evolving directly from the ancestral *B. b. antiquus*, or a more recent adaptive differentiation from *B. b. bison*, as suggested by the larger body size of *B. b. athabascae*. However, van Zyll de Jong (1986), studying presumed pure *B. b. athabascae* specimens from northwestern Canada and comparing them to other North American fossil and modern bison, suggests that body size is just one of a number of presumably genetic characteristics that differentiates the two modern species. According to his analyses, *B. b. athabascae* is more probably "a direct and little differentiated descendant of [Beringian] *B. b. occidentalis"* (van Zyll de Jong 1986:54). His analysis found that *B. b. bison* shows a marked difference in horn core measurements, reflecting a general reduction in horn core size in comparison to *B. b. occidentalis*, whereas with *B. b. athabascae* there is only a reduction in horn core length (van Zyll de Jong 1986:18 [Figure 16]).

Arguing for genetic variation, as opposed to ecophenotypic, van Zyll de Jong (1986:54-55) illustrates how the interaction of ecological and behavioral factors, gene flow, and natural selection can account for the maintenance of the distinctiveness of the two modern species. Specifically, the boreal forest ecotone acted as a natural barrier to contact with *B. b. bison* in the grasslands to the south. Interbreeding was also minimized due to the limited seasonal movement of the two populations within their respective home ranges. The diverse habitats occupied by the two populations may also have promoted "differential directional selection" of a specific allele frequency or phenotype that provided them with a greater degree of fitness for surviving in their respective environments.

In a preliminary a molecular study of DNA from several populations of wood and plains bison in Canada and the United States Strobeck attempted to determine the status of the two subspecies. Based on this study, Strobeck concluded that wood and plains bison "do not form distinct phylogenetic groups and are not genetically distinct subspecies" (Strobeck 1992:15). With the similarity in mtDNA types from both "wood" and "plains," the possibility that they may have been distinct subspecies in the past is also refuted, Strobeck asserts.

Geographic isolation of populations may have the effect of creating different genotype frequencies in different herds. Strobeck (1992:15-16) contends from his study that "each population represents a geographical genetic isolate of a once vast population of bison." This genetic isolation may provide some clues to the morphological variability we see in bison populations. This observation is similar to what van Zyll de Jong (1986:55) found in his morphometric analysis. He goes on to suggest that similar mechanisms are still in operation among ungulates (e.g., caribou) today and can be studied.

In a more inclusive study Wilson and Strobeck (1999) surveyed 11 microsatellite loci of 11 bison populations in order to calculate the genetic variation and genetic distances of wood and plains bison. Their expectation being that large genetic distance should exist between wood and plains bison.

One result of their study was that all the sampled bison populations are genetically distinct from one another. According to the authors this was not unexpected and probably a result of the founder effect and genetic drift which resulted "from the small number of transfers between herds that have occurred, are probably responsible for the uniqueness of these populations" (Wilson and Strobeck 1999:493). Of particular interest to this study is that the genetic distance between the Yellowstone bison is not as large as expected if these bison were a distinct population (i.e., mountain bison). The authors indicate indigenous Yellowstone bison were "driven to the area by hunters" (Wilson and Strobeck 1999:493), and, therefore, represent mountain-dwelling plains bison.

Understanding the taxonomy of the Gilbert peak bison may not be adequately addressed without genetic analysis, but morphological differences in adult skulls has been commonly used to determine how individual animals, or populations, compare. In differentiating between *B. b.* athabascae and *B. b. bison*, McDonald (1981a) used horn core morphology as key characteristics both in size and shape.

Using a ratio diagram (Simpson 1941) we can explore how the Gilbert Peak bison compares to other populations. The ratio diagram was applied by van Zyll de Jong (1986) in trying to establish an evolutionary history between modern bison species and the extinct *Bison antiquus occidentalis*. The ratio diagram is a univariate technique in which measurements can be compared to a standard. To replicate van Zyll de Jong's study (1986: Figure 16), as well as that of Walker (1992: Figure 6), *B. antiquus occi-*

dentalis is used as the standard. The technique is a plot of the difference between the log of a measurement from a comparative specimen or the mean of a population (e.g., high altitude bison) and the log of the measurement of a conspecific specimen. The comparative specimen is set to zero with dimensions with negative values indicating the specimen is smaller with a positive value indicating a larger specimen (Lyman 2004).

The results of this comparison are interesting and suggest the Gilbert Peak bison is larger in some dimensions and smaller in others than the standard (Figure 16). Specifically, a comparison of select horn core measurements indicates that the Gilbert Peak bison skull is within the range of each of these groups (Figure 17).

The Gilbert Peak skull horn core morphology is more similar to *B. bison athabascae* being larger than either the high altitude or the *B. bison bison* populations. The large size of the Gilbert Peak skull and its incompleteness may influence the results of the comparison. Another possibility exists that genetic isolation of populations may be expressed in the phenotype (see Wilson and Strobeck 1999). Wilson (1974b) illustrates a similar situation from the Casper site in which phenotypic characteristics of two populations may have contributed to the single herd. However, he suggests gene flow between the two populations. Genetic isolation of intermountain populations in the west may be expressed phenotypically, as discussed by van Zyll de Jong (1986:54-55). More interestingly, the Gilbert Peak bison is larger than all populations, including the standard (*B. antiquus occidentalis*) in several horn core dimensions (Figure 16). A more definitive understanding of the genetic relatedness of intermountain populations will have to wait for genetic analysis, such as mtDNA.

Figure 14. Range of modern bison species based upon distribution map of Reynolds et al. (1982: Figure 49.1).

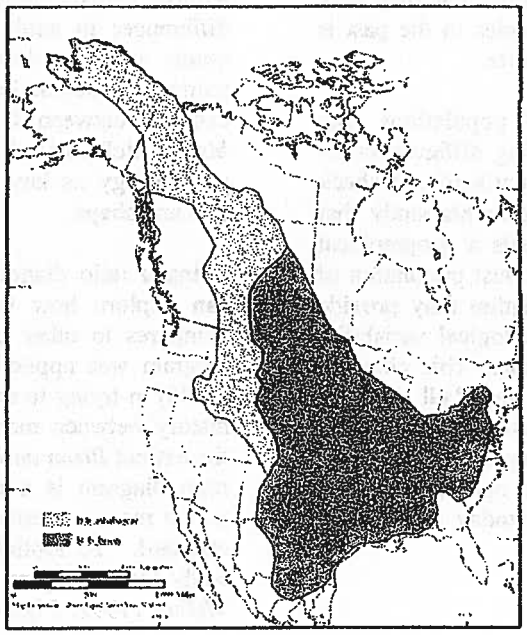


Figure 16. Ratio diagram comparing 10 skull dimensions of the Gilbert Peak specimen in comparison with *Bison bison bison, Bison bison athabascae*, and *Bison antiquus occidentalis*, with the latter serving as a standard. All measurements included in analysis are from male skulls. (*B. antiquus occidentalis* (N=31) data from van Zyll de Jong 1986: Table 1; *B. b. athabascae* and *B. b. bison* from McDonald 1981a: Table 29 and 34, respectively). McDonald's data used in analysis is only from males. Only those measurements that were available from the Gilbert Peak bison skull were used in this analysis.

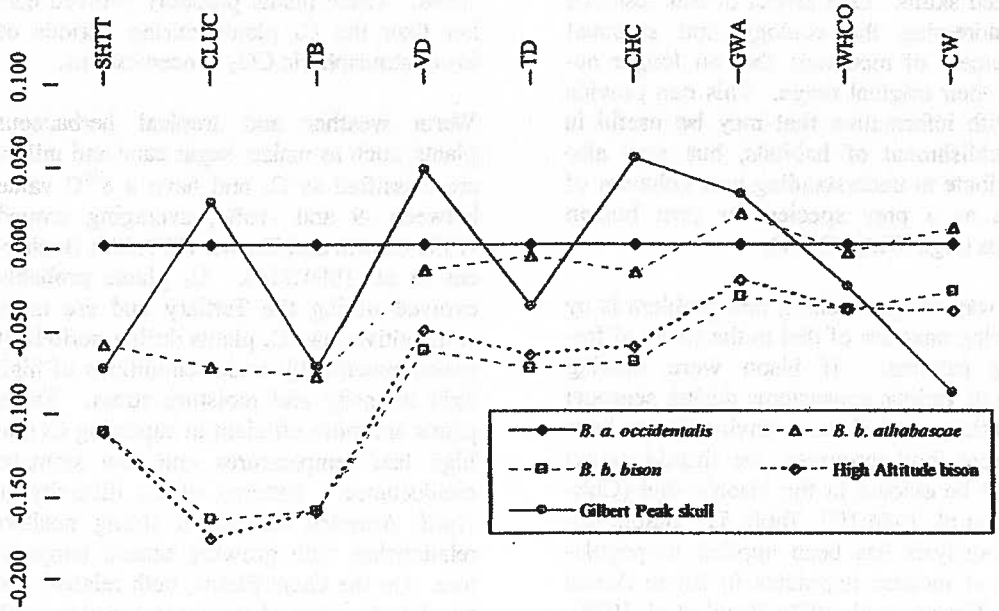
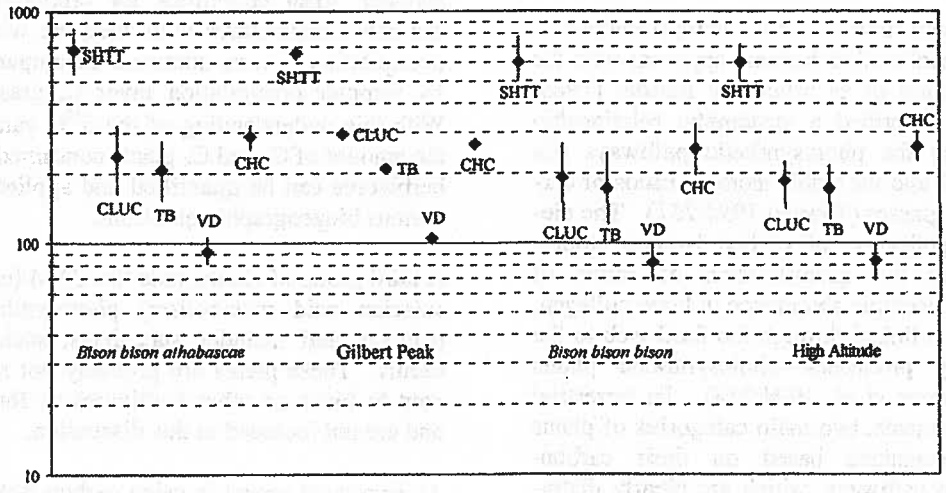


Figure 17. Comparison of select horn core measurements of Gilbert Peak bison skull with other taxonomic and regional groups to illustrate amount of overlap in range of measurements. See Table 3 for measurement abbreviations.



Results of Stable-Isotope Analyses

Introduction

As was mentioned in the introduction, there are several reasons for the investigation of isolated skulls. One aspect of this research is addressing the ecology and seasonal movement of mammals that no longer occupy their original range. This can provide us with information that may be useful in reestablishment of habitats, but may also contribute to understanding past behavior of bison as a prey species for past human groups (e.g., Widga 2004).

One way of approaching this problem is by applying analyses of diet to the study of foraging patterns. If bison were moving through various ecosystems during seasonal migrations, and if these environments have different food resources, we should expect this to be evident in the bison's diet (Chisholm et al. 1986:193; Table 5). Stable isotope analysis has been applied to populations of modern ungulates in South Africa (e.g., Tieszen et al. 1979; Vogel et al. 1978), as well as to other fossil vertebrates (e.g., Bocherens et al. 1994; Heaton 1995) in order to understand their dietary selection.

Stable Carbon Isotope Analysis

The application of carbon isotope analysis to ecological studies became apparent with the publication of an article by Bender (1968) which described a systematic relationship between the photosynthetic pathways (C_3 and C_4) and the stable isotopic ratios of carbon in grasses (Tieszen 1994:261). The dietary application of carbon isotope studies involves the quantification of ratios of $^{13}C/^{12}C$ isotopic abundance in bone collagen, which is linked through the food web to the primary producers—photosynthetic plants (Bocherens et al. 1994:214). In terrestrial environments, two main categories of plants are recognized based on their carbon-fixation pathways, which are clearly distinguished by their stable carbon isotope ratios (Figure 18). The C_3 plants represent about 90% of all plants and include all trees and herbaceous plants from cold and temperate climates. Their $\delta^{13}C$ values range between -23‰ and -32‰ with an average of about -26‰. These plants probably evolved earlier than the C_4 plants during periods of lower atmospheric CO_2 concentrations.

Warm weather and tropical herbaceous plants, such as maize, sugar cane and millet, are classified as C_4 and have a $\delta^{13}C$ value between -9 and -16‰, averaging around -13‰ (Smith and Brown 1973:505; Bocherens et al. 1994:214). C_4 plants probably evolved during the Tertiary and are more competitive than C_3 plants during periods of stress, specifically under conditions of high light intensity and moisture stress. These plants are more efficient in capturing CO_2 at high leaf temperatures and low stomatal conductance. Patterns of C_4 diversity in North America indicate a strong positive relationship with growing season temperature. On the Great Plains, both relative and absolute C_4 grass abundances correlate with mean annual temperature (MAT) and mean annual precipitation (MAP). In contrast, C_3 grass abundance decreases with MAT and summer precipitation. Since C_3 plants do most of their growing in the spring and early summer, ideal conditions for productivity are cool temperatures with adequate winter precipitation. Warm summers accompanied by summer precipitation favor C_4 grasses. With this understanding of the $\delta^{13}C$ values, the amount of C_3 and C_4 plants consumed by herbivores can be quantified and applied to various biogeographic questions.

A third group of plants, uses the CAM (crassulacian acid metabolism) photosynthetic pathway and includes succulents, such as cactus. These plants are probably not relevant to bison or other herbivores as forage and are not included in this discussion.

An important aspect in using carbon isotope analysis in reconstructing diets is that varia-

tions in atmospheric values of $\delta^{13}C$ have varied in predictable ways through time, and under different environmental conditions. In systems where the respiratory release of CO_2 does not mix freely with the atmosphere, such as in closed canopy forests, the ambient CO_2 can become depleted resulting in higher negative values for both C_3 and C_4 plants (Tieszen 1994:264). An example from the Amazonian forests measured $\delta^{13}C$ values being as negative as -37‰. In comparison, open habitats of C_3 grasses average about -26.5‰ (van der Merwe and Medina 1991:250). This depletion is transferred to other trophic levels and must be taken into account when considering diet for forest-dwelling herbivores, as well as humans (Tieszen 1994:264).

The anthropogenic addition of CO_2 to the atmosphere over the past two centuries through the burning of fossil fuels has depleted atmospheric CO_2 of $\delta^{13}C$. This input has also enhanced decomposition associated with agriculture and deforestation. Preindustrial $\delta^{13}C$ values of -6.45‰ have been measured from Antarctica ice cores, compared with modern conservative estimates at -8.0‰. Based on this knowledge significant adjustments must be made in the reconstruction of past diets and paleoecological interpretations. Therefore, an adjustment of about 1.5‰ must be made to Holocene samples dating to before A.D. 1800 in comparison to modern values (Tieszen 1994:264). The presence and distribution of C_3 and C_4 plants in the environment is not random but related to environmental factors, specifically temperature. C_3 and C_4 plant abundance can be predicted from surface energy and moisture balance characteristics of the soil. With increasing latitude and longitude a corresponding increase in C_3 species is expected (Figure 19). An example from Kenya illustrates this point—within low altitude, open savannas all grasses are C_4 and nearly all trees and shrubs are C_3; above 1800 m, C_4 grasses begin to be replaced by C_3 grasses and at 3000 m nearly all grasses are C_3 (Tieszen 1994:265).

In a study from southeast Wyoming, Boutton et al. (1980) demonstrated that the percentage of C_3 biomass increased with elevation (Figure 20). Regressions of relative biomass abundance of C_3 and C_4 plants on climatic variables illustrated that both mean annual temperature and mean annual precipitation were equally reliable predictors. Temperature was also a factor the authors felt strongly influenced the ratios.

On the Great Plains, increases in C_3 grasses is correlated with increasing latitude. In south and southwest Texas C_4 grasses are represented at 68 and 82 percent, respectively, decreasing to 35 percent in South Dakota. Browse species, such as the sedges, do not show as clear a temperature dependent distribution as grasses. *Carex*, a common genus of sedge in the mountains, is C_3 (Tieszen 1994:265). Grass composition for Idaho estimates about 18 percent C_4 species (Teeri and Stowe 1976:Table 2).

It is therefore expected that generalist consumers of grass biomass should have a modern isotopic signal that reflects the mixture of C_3 and C_4 species in the utilized environment (Table 6). However, since climatic changes have been demonstrated for various *periods during the course of the Holocene*, vegetation values should be expected to reflect these climatic shifts (Whitlock 1993). This temporal variable is another complicating factor involved in the interpretation of isotopic signals from paleosamples (Tieszen *1994:166*).

In a paper by Connin and colleagues (1998), they sought to apply stable isotope ratios extracted from herbivore teeth to test the current model of LGM climate and vegetation for the southwestern United States. Community Climate Model (CCM) simulations and plant macrofossil data, primarily from packrat middens, indicate a pattern of cooler temperatures and winter-dominated precipitation. This climatic regime would favor communities dominated by C_3 plants. Their sample consisted of five genera of

megaherbivores dating from 40 to 10 ka and recovered from various contexts in Arizona, California, Nevada, and New Mexico. The taxa represented include *Mammuthus* sp., *Bison* spp., *Equus* spp., *Camelops* spp., and Antilocaprids. They argue that this suite of herbivores provides a better sampling of the regional vegetation because of their physiology and behavior, particularly their seasonal migration. For example, bison and mammoth are preferential, but not obligate grazers and subsist on the most abundant plant species; camels and horses are browsers, as well as antelope. These species provide a much more rigorous assessment of vegetation communities than do packrats, which tend to sample only local, rocky upland environments.The results of their study indicate a substantial eastward increase in C_4 plant consumption by the herbivores, with some local patterns of C_4-dominated grazing. Connin and colleagues (1998) argue that this data implies a pattern of significant availability of C_4 plants, and a pattern of significant summer rainfall in parts of southern Arizona and New Mexico throughout the last glaciation.

Figure 18. $\delta^{13}C$ values in parts per million for common graminoid plants and forb species of the Niobrara Valley Preserve, Nebraska (from data in Steuter et al. 1995).

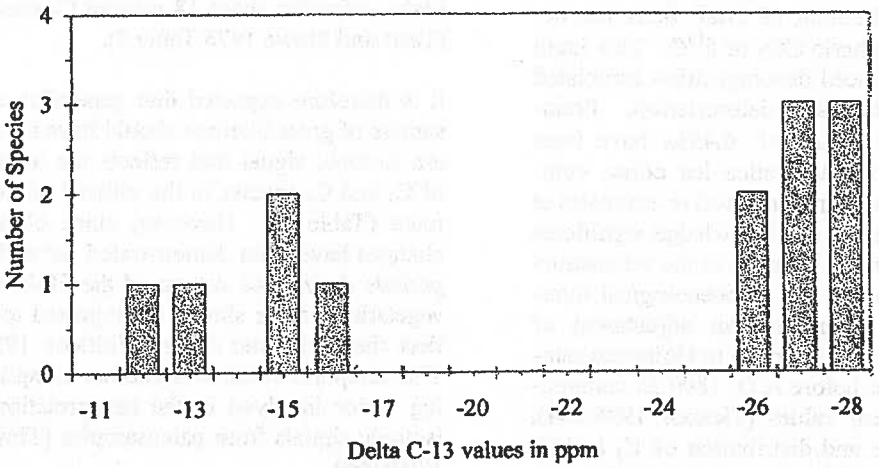


Table 6. List of plants identified in diet of bison from Yellowstone National Park (Meagher 1973:Table 17), Henry Mountains, Utah (Van Vuren 1984:Table 1), shortgrass plains of northeastern Colorado (Peden 1976:Table 1), and northern mixed prairie of Badlands National Park, South Dakota (Plumb and Dodd 1993:Table 2) and their photosynthetic pathway. Pathway data provided by Brooks (1995: Table 3.3) and Larry Tieszen (1997: personal communication).

Species	Common Name	Pathway
Yellowstone National Park, Wyoming		
Carex sp.	Sedge	C_3
Juncus	Wire rush	C_3
Carex	Spike-sedge	C_3
Phlox sp.	Phlox	C_3
Potentilla	Northwest cinquefoil	C_3
Eriogonum umbellatum	Sulfur eriogoum (buckwheat)	C_3
Taraxacum sp.	Dandelion	C_3
Antennaria sp.	Pussytoes	C_3
Potentilla fruticosa	Shrubby cinquefoil	C_3
Trifolium sp.	Clover (introduced)	C_3
Allium sp.	Onion	C_3
Collinsia sp.	*Blue-eyed Mary*	C_3
Artemisia tridentate	Big sagebrush	C_3
Cornus stolonifera	Red dogwood	C_3
Rubus sp.	Raspberry	C_3
Vaccinium caespitosum	Dwarf huckleberry	C_3
*Amelanchier*sp.	Serviceberry	C_3
Artemisia frigida	Fringed sagebrush	C_3
Pinus contorta	Lodgepole pine	C_3
Equisetum sp.	Horsetail	C_3
Cassiope sp.	Moss	C_3
	Lichen	C_3
Festuca idahoensis	Idaho fescue	C_3
Agropyron spicatum	Wheatgrass	C_3
Henry Mountains, Utah		
Agropyron spp.	Crested wheatgrass	C_3
Bromus ciliatus	Bromegrass	C_3
Carex spp.	Sedge	C_3
Festuca spp.	Fescue	C_3
Koeleria cristata	Junegrass	C_3
Oryzopsis humneoides	Indian ricegrass	C_3
Poa spp.	Blue grass	C_3
Sitanion hystrix	Squirreltail	C_3
Stipa spp.	Needlegrass	C_3
Astragalus spp.	Milk vetch	C_3
Oxytropis spp.	Locoweed	C_3
Artemisia spp.	Sagebrush	C_3
Symphoricarpos spp.	Snowberry	C_3
Northeastern Colorado		
Agropyron smithii	Crested wheatgrass	C_3
Aristida longeseta	Red threeawn	C_3
Artemisia frigida	Sagebrush	C_3
Bouteloua gracilis	Blue grama	C_4
Carex heliophila	Sedge	C_3
Eriogonum sp.	Buckwheat	C_3
Festuca octoflora	*Sheep fescue*	C_3

Species	Common Name	Pathway
Sphaeralcea crytandrus	Sand Dropseed	
Stipa commauma	Needlegrass	C_3
Badlands National Park, South Dakota		
Agropyron cristata	Crested wheatgrass	C_3
Agropyron repens	Couch grass	C_3
Agropyron smithii	Western wheatgrass	C_3
Bromus inermus	Smooth brome	C_3
Bromus tectorum	Cheatgrass	C_3
Carex lanuginose	Sedge	C_3
Carex filifolia/eleocharis	Needleleaf sedge	C_3
Hordeum jubatum	Foxtail barley	C_3
Poa pratensis	Kentucky bluegrass	C_3
Spartina pectinata	*Prairie cordgrass*	C_3
Stipa comata	Needle-and-thread grass	C_3
Stipa spartea	Needlegrass	C_3
Stipa viridula	Needlegrass	C_3
Andropogon geradii	Big bluestem	C_4
Bouteloua curtipendula	Sideoats grama	C_4
Buchloe dactyloides	Buffalo grass	C_4
Calamovilfa longifolia	Prairie sandreed	C_4
Muhlenbergia cuspidate	Stonyhills muhly	C_4
Panicum virgatum	Switchgrass	C_4
Schizachyrium scoparium	Little bluestem	C_3
Sorghastrum nutans	Indiangrass	C_3
Ambrosia psilostachya	Cuman ragweed	C_4
Astragalus crassicarpus	Milkvetch	C_4
Mellilotus officianalis	Yellow sweetclover	C_4
Medicago sativa	Alfalfa	C_4
Psoralea argophylla	Silverleaf scurf pea	C_4
Solidago canadensis	Goldenrod	C_4
Sphaeralcea coccinea	Scarlet globemallow	C_4
Tragopogon dubius	Goatsbeard	C_4
Amorpha canescens	Lead plant	C_3
Glychyrhizza lepidota	American licorice	C_4

Figure 19. Map of the United States illustrating approximate percentage of C_4 plants (after Teeri and Stowe 1976).

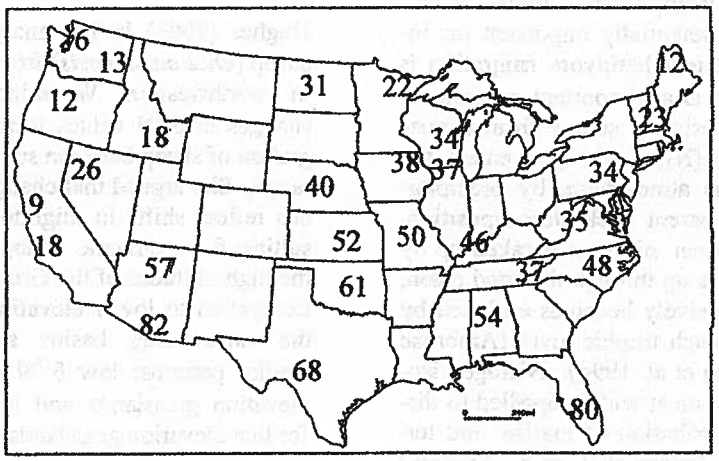
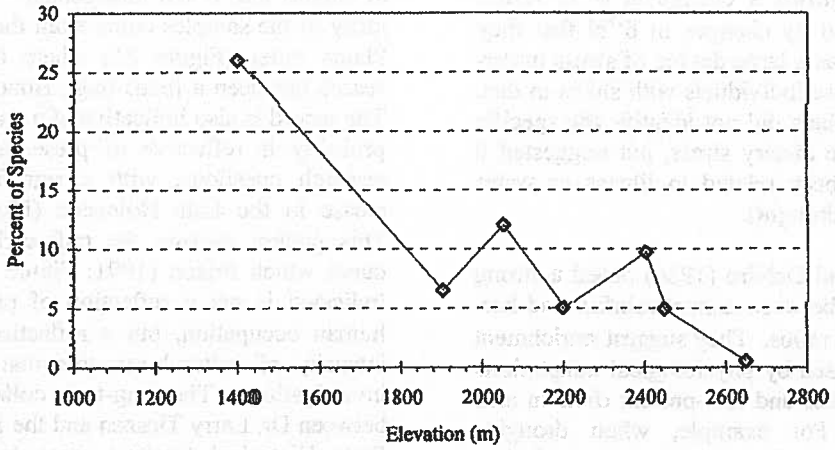


Figure 20. Percent of species with C_4 pathway along an altitudinal transect in southeast Wyoming (after Boutton et al. 1980).



Stable Nitrogen Isotope Analysis

Another stable isotope that is linked to trophic level and potentially important for investigating diet and herbivore migration is $\delta^{15}N$. Nitrogen is an important component of life with its primary source from atmospheric nitrogen (N_2). Nitrogen enters the soil through the atmosphere, by precipitation, or from parent rock decomposition. Once in the system, nitrogen is taken up by plants and moves up through the food chain, where it progressively becomes enriched by 2-5‰ through each trophic level (Ambrose 1991; Bocherens et al. 1994). Nitrogen isotopes have been most widely applied to discerning the contribution of marine and terrestrial foods in human diets (e.g., Ambrose 1991).

The potential of dietary stress can also be assessed by examining $\delta^{15}N$ values. In examining horn sheath annuli of bison from the Central Plains, Tieszen and colleagues (1996) identified a change in $\delta^{13}C$ values accompanied by changes in $\delta^{15}N$ that they interpreted as a large degree of stress undergone by these individuals with shifts in diet. The researchers did not identify the specific cause of the dietary stress, but suggested it may have been related to illness or water stress (i.e., drought).

Ambrose and DeNiro (1986) noted a strong correlation between annual rainfall and herbivore $\delta^{15}N$ ratios. They suggest enrichment may be caused by physiological adaptations to water stress and low-protein diets in arid habitats. For example, when drought-tolerant mammals are water stressed they will concentrate ^{15}N in their tissues and eliminate ^{14}N in urea, producing greater isotopic variability and more tolerant values than obligate drinkers. In arid, or saline environments (<400 mm of precipitation), these herbivores are more depleted than browsers living in the same environment (Ambrose and DeNiro 1986; Heaton et al. 1986).

Hughes (2003) in her analysis of bighorn sheep (*Ovis canadensis*) from Mummy Cave in northwestern Wyoming argued that changes in $\delta^{15}N$ values were related to migration of sheep between summer and winter range. She argued that changes in these values reflect shifts in migratory behavior resulting from climatic change. Bison from the high altitudes of the Greater Yellowstone Ecosystem to lower elevation grasslands of the surrounding basins should illustrate similar patterns: low $\delta^{15}N$ values for high elevation grasslands and high $\delta^{15}N$ values for low elevation grasslands.

The Western North American Isotopic Record

A review of the stable carbon isotopic record of bison in western North America (data base compiled by author) indicates a pattern of studies that is not unexpected. The majority of the samples come from the Central Plains states (Figure 21) where bison research has been a focus (e.g., Bozell 1995). The record is also indicative of a pattern that probably is reflective of preservation and research questions, with a significant increase in the Late Holocene (Figure 22). This pattern mirrors the radiocarbon date curve which Frison (1991: Figure 2.5) has indicated is not a reflection of prehistoric human occupation, but a reflection of the intensity of cultural resource management investigations. The long-term collaboration between Dr. Larry Tieszen and the Nebraska State Historical Society accounts for the large number of Nebraska and South Dakota samples (J.R. Bozell, personal communication 1997; see also Bozell et al. 1997). More focused case studies, such as Gadbury et al. (2000), are also included in the data set and reflect specific research topics.

Figure 21. Stable carbon isotope samples (n=412) by state and Canadian Province.

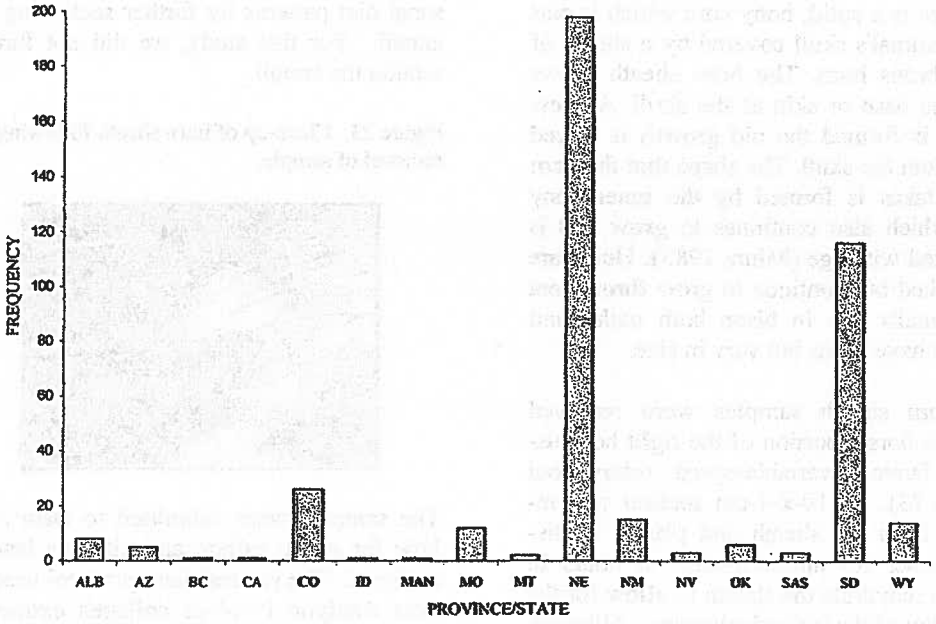
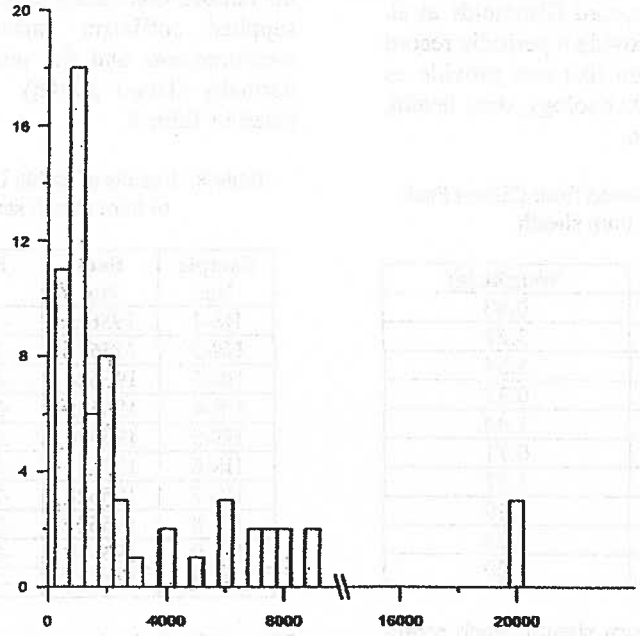


Figure 22. Stable isotope samples for western North America by years before present.



Results

The horn is a solid, bony core which is part of the animal's skull covered by a sheath of hard fibrous horn. The horn sheath grows from the base or skin at the skull. As new growth is formed the old growth is forced away from the skull. The shape that the horn sheath takes is formed by the inner bony core, which also continues to grow and is correlated with age (Miura 1985). Horns are never shed but continue to grow throughout the animal's life. In bison both males and females have horns but vary in size.

The horn sheath samples were removed from the dorsal portion of the right horn using a Dremel variable-speed rotary tool (Figure 23). A 10-x-4-cm section was removed from the sheath and placed in distilled water for approximately 8 hours in order to rehydrate the sheath to allow for the separation of the individual cones. Although the growth rings or cones do not necessarily represent an annual record (Reynolds et al. 1982:997), they do provide a periodic record of the individual bison that can provide us with information on its ecology, diet, health, and possible migration.

Table 7. Samples removed from Gilbert Peak bison skull horn sheath.

Sample No.	Weight (g)
HS-1	0.43
HS-2	3.28
HS-3	5.54
HS-4	0.33
HS-5	1.44
HS-6	0.71
HS-7	1.57
HS-8	2.39
HS-9	3.25
HS-10	2.29

Ten samples of the horn sheath, each representing a single horn cone, were submitted to Beta Analytic for stable carbon and nitrogen isotopic analysis (Table 7). The samples were numbered consecutively from the oldest (HS-1) to most recent (HS-10). In a similar study, Tieszen et al. (1996) used the horn sheath in determining annual and seasonal diet patterns by further sectioning the annuli. For this study, we did not further section the annuli.

Figure 23. Close-up of horn sheath following removal of sample.



The samples were submitted to Beta Analytic for stable carbon and nitrogen isotope analyses. The pretreatment protocol used by Beta Analytic involves collagen extraction with alkali, which is discussed in detail in the radiocarbon dating section. Each sample supplied sufficient carbon for accurate measurements and the analyses proceeded normally (Hood 2004b). The results are listed in Table 8.

Table 8. Results of stable isotopic analyses of horn sheath samples.

Sample No.	Beta No.	$\delta^{13}C$	$\delta^{15}N$
HS-1	195622	-21.9	+6.9
HS-2	*195623*	*-21.7*	*+7.4*
HS-3	195624	-20.7	+7.4
HS-4	195625	-20.3	+8.1
HS-5	195626	-22.0	+6.5
HS-6	195627	-20.7	+8.6
HS-7	195628	-22.1	+9.4
HS-8	195629	-22.1	+6.4
HS-9	195630	-21.6	+8.3
HS-10	195631	-22.0	+5.2

The analyses indicate that the horn sheaths provide a record of stable carbon and nitrogen isotope signatures of assimilated foods as was demonstrated in an earlier study by Tieszen et al. (1996). The values indicate

variability in $\delta^{13}C$ values that range between -20.3‰ and -22.1‰ with a mean of -22.51‰ that indicates a diet that is highly oriented towards C_3 vegetation (Figure 24). This is not unexpected and represents a diet that is similar to modern bison in the Henry Mountains (Van Vuren 1984; Table 6).

The results of the $\delta^{13}C$ values show little variation which may suggest that C_4 vegetation was not available to this bison (Figure 25). Tieszen et al. (1996) saw similar patterns in high elevation (i.e., Yellowstone) and high latitude (i.e., Wood Buffalo) bison. In areas, such as at Konza and Niobrara, bison have access to a more variable plant community and this is indicated by their $\delta^{13}C$ values.

In comparing the $\delta^{15}N$ values with respect to $\delta^{13}C$ values, Tieszen et al. (1996) found that shifts in values were correlated in the Konza and Niobrara specimens and suggest a shift in diet may have been accompanied by a large degree of stress. However, the circumstances surrounding the diet changes is unknown and may have involved the individuals being moved to its respective preserve which may also account for the stress.

The pattern of changes in $\delta^{15}N$ values of the Gilbert Peak bison tend to follow that of $\delta^{13}C$ values (Figure 24). In general, as $\delta^{15}N$ values increase the $\delta^{13}C$ values become less negative. Hughes (2003) noted a similar pattern with bighorn sheep and suggested higher $\delta^{15}N$ values were an indication of use of lower elevation range. The Gilbert Peak values may reflect a similar migratory pattern of bison using various habitats over the course of its life.

Another possible explanation involves nitrogen waste through urine. Steele and Daniel (1978) have found that in herbivorous mammals, urea is the main form of nitrogen waste and the ^{15}N isotopic composition in urine is lower than the ^{15}N isotopic composition of the vegetation they subsist on. With the elimination of urea collagen $\delta^{15}N$ values are elevated. As Fizet et al. (1995) relate protein quality also has an effect of lower $\delta^{15}N$ values in herbivores due to less urea in the urine. Ambrose and DeNiro (1986) demonstrated that modern East African herbivorous mammals living in arid areas have increasingly higher $\delta^{15}N$ values. These higher levels are related to the excretion of urine highly concentrated in urea, a strategy for water conservation.

Based upon this information, Fizet et al. (1995) argue that higher $\delta^{15}N$ values of mammal collagen from the French Pleistocene Marillac cave layer #7 was related to an episode of aridity between 45,000 and 40,000 years BP. Other paleoclimatic proxy data support this interpretation. The elevated levels of $\delta^{15}N$ values for the Gilbert Peak bison may reflect periods of increased aridity at periods during its life and may provide evidence of short-term climate shifts.

The period from approximately AD 1450 to 1800 has been labeled the Little Ice Age (Fagan 2000) and characterized by reduced temperatures and increased effective moisture, as indicated by a final high stand of the Great Salt Lake (Currey 1990). Glacial advances have also been suggested for this period in the Wind River Range (Richmond 1986), the Colorado Front Range (Benedict 1973), and the Teton Range (Richmond 1986). Mesic indicator small mammal species reappear in deposits from Lamar Cave in Yellowstone National Park (Hadly 1996) and bison are reported as being at their highest Holocene levels (Butler 1978; Frison and Reher 1980). Using historic and modern photographic evidence from the northern Uinta Mountains, Munroe (2003) provides evidence of growing season depression prior to AD 1870. While uniform cooler temperatures and increased effective moisture have traditionally been suggested for the Little Ice Age, more recent research is suggesting more variability (e.g., Jacoby D'Arrigo 1989; Kaplan et al. 2002)

While the Gilbert Peak bison skull alone does not provide definitive evidence for un-

derstanding past climatic conditions, it does provide us with a beginning towards this end. Because herbivores were so abundant in the past they provide important climate proxy. Comparison with modern bison of known ecology and migration patterns, suggest as those from the Henry Mountains, would provide a more meaningful comparison.

Figure 24. Percent C_4 vegetation is individual bison diet based upon $\delta^{13}C$ values as computed by Brooks (1995:77). Samples are arranged from south (left) to north (right).

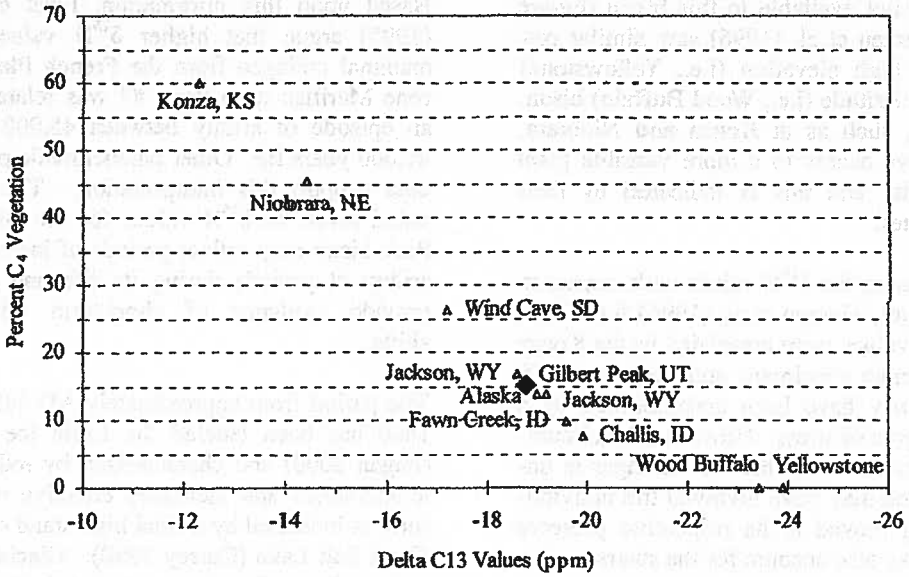
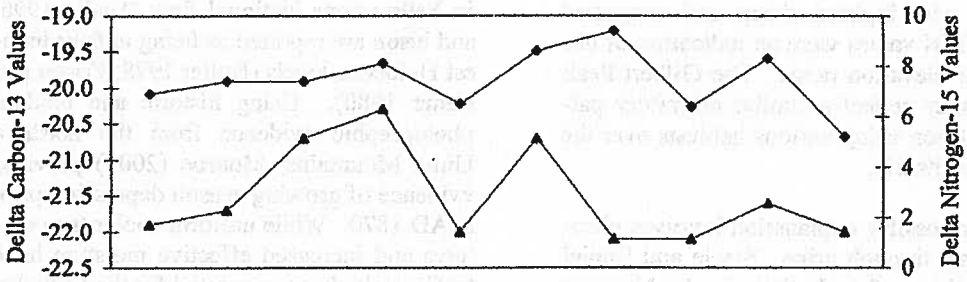


Figure 25. Results of stable carbon and nitrogen analyses preformed on horn sheath cones. Results are oriented from oldest (HS-1) on the left to youngest (HS-10) on the right. Upper line is $\delta^{15}N$ values.



Conclusions

By the time Mormon pioneers began settling in Utah bison were probably largely extinct from its western range, all but eliminating the opportunity for biologists to study the animal. Bison today are limited to two small reintroduced herds in the state—the Antelope Island herd in the Great Salt Lake and the Henry Mountains herd in southeastern Utah (Durrant 1952).

A partial bison skull was recovered from the vicinity of Gilbert Peak in the high Uinta Mountains of northeastern Utah at an elevation of 3840 m. Vegetation in the immediate area is generally alpine, but to the east of the find location is the headwaters of Gilbert Creek, a boggy area surrounded by Engelmann spruce. Although bison remains have been discussed in the zoological and archeological literature these reports tend to be descriptive. This study is unique because it combines traditional craniometric analyses to understand the sex, species, and age at death of the individual, but also uses contemporary chemical analyses to date the age of the specimen and to understand its ecology and potential migration patterns.

Metric analysis of the skull suggests the animal was a mature male, possibly over 10 years of age. The individual was very large and in several measurements of the horn cores is larger than either *B. b. bison* or *B. b. athabascae*, considered to be the largest of the modern bison (McDonald 1981a:108). However, the taxonomic classification of the individual is probably not possible without DNA analysis (e.g., Richards et al. 1993).

Radiometric assay of the skull produced an age of 150 ± 40 yrs BP which calibrates to between cal AD 1665 to 1784. The age of this bison is significant because it falls within a climatic episode known as the Little Ice Age. This climatic period is characterized as a time when temperatures were colder than previous centuries and alpine glaciers around the world were advancing.

The results of the stable carbon and nitrogen isotope analyses suggest this individual was subsisting almost exclusively on C_3 vegetation. The isotopic values from the ten horn sheath samples indicates variability in the $\delta^{15}N$ values that may either reflect annual use of high and lower elevation areas, or possibly periods in the bison's life when water conservation was important. Higher $\delta^{15}N$ values have been linked to higher concentrations of urea in urine either due to water stress or lower quality food protein. This signal may have a climatic component and provide clues to more variability in climate patterns during the Little Ice Age. Larger samples of bison and comparison with modern bison with known ecologies will help to sort out these issues.

Over the past decade a relatively new application of geochemical techniques have provided another group of data to bear upon the problem of paleoecological reconstruction—the analysis of stable isotope signatures of herbivore bone and teeth (McFadden and Cerling 1996). Herbivores are particularly relevant to the study of paleoecological reconstruction for a number of physiological and ecological reasons:

1. *Herbivores, particularly bison (Bison sp.), are widespread worldwide and are a common component of fossil and subfossil assemblages (Guthrie 1990).*

2. *Bison were a major component of the Great Plains post-glacial ecosystem and a major prey species of native groups prior to European contact (e.g., Frison 1991; Fisher and Roll 1998).*

3. *Depending upon their particular dietary requirements, herbivore grazing will reflect the relative abundance of vegetation in a particular ecosystem (Tieszen 1991). For example, bison are relatively unselective grazers due to their requirement of large volumes of forage. This requirement limits their ability to be selective (Peden 1976). In contrast, an-*

telope are highly selective herbivores, subsisting almost exclusively on sagebrush (Schwartz and Ellis 1981).

4. *Stable carbon isotope analysis is an effective tool in determining photosynthetic pathways (Bender 1968). It has also been applied to the tissue of primary consumers in determining their diet (DeNiro and Epstein 1981). As Chisholm et al. (1986) noted in their initial study, if bison (as well as other migratory animals) are moving through various ecosystems during their annual migrations, and if these environments have different food resources, it should be evident in the bison's diet, as expressed by stable carbon isotope signatures.*

5. *As tissues develop, they incorporate carbon and the isotopic value of these tissues reflects the relative amounts of the ingested carbon. Bone, which is commonly preserved in fossil and subfossil contexts, is a likely candidate for analysis, but because bone is constantly in a state of growth and modification the isotopic values reflect an aggregate or averaged record of the individual's diet over an extended period of time (Larson et al. 2001). Studies by Chisholm (1989) and Tieszen (1994) indicate that complete bone replacement occurs over a period of about 10 years.*

6. *Teeth, in contrast to bone, preserve a detailed record of an individual's foraging history through the incremental growth of the tooth enamel. By sampling a tooth, particularly the third molar, a geochemical record reflecting the individuals foraging history can be extracted at the resolution of subannual (Gadbury et al. 2000; Larson et al. 2001).*

Understanding bison ecology and migration patterns through the study of sub-fossil bison is one of the few methods we can reconstruct past conditions. Bison today are confined to small, isolated herds that are typically not allowed to range freely within their historic ranges. If we are to truly manage the few surviving intact public areas in a meaningful way, we must be willing to expend the effort to study how ecosystems have developed through time (e.g., Lyman and Cannon 2004; Cannon and Cannon 2004). Today ungulate management is a very politically charged issue, and much of the information used to make the management decisions is based on modern studies of herds under confined situations (e.g., Berger and Cunningham 1994). Few, if any, studies incorporate long-term data such as that available from paleostudies (CUMYNP 2002). Studies, such as stable-isotope analysis, provide a means to decipher paleoenvironmental conditions to model future changes and the restoration of habitats. As this study has demonstrated, and previously articulated by Walker (1992), isolated bison skulls can provide significant information that can be used to fill gaps in our understanding of bison.

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State	Site Number	State	Site Number
CO	5EA799	ID	10BK26
CO	5GA639	ID	10BM56
CO	5GA1119	ID	10BV30
CO	5GA1155	ID	10BV93
CO	5GA1513	ID	10OA2
CO	5GA1847	ID	ISUM52002
CO	5GA2414	ID	ISUM72003
CO	5JA239	ID	American Falls
CO	5JA344	ID	Rainbow Beach
CO	5JA712	ID	Weston Rockshelter
CO	5MF3	ID	Moonshiner
CO	5MF9	ID	Middle Butte
CO	5MF309	UT	42RI1
CO	5MF398	UT	42UT104
CO	5MF605	UT	42UT150
CO	5MF625	UT	42UT591
CO	5MF630	UT	42UT592
CO	5MF638	UT	42UT636
CO	5MF969	WY	48LN74
CO	5MF1215	WY	48LN317
CO	5MF2631	WY	48LN1468
CO	5MF2747	WY	48SW5
CO	5MF2775	WY	48SW101
CO	5MF2877	WY	48SW998
CO	5MF2912	WY	48SW2302
CO	5MF2913	WY	48SW2385
CO	5MF3450	WY	48SW2590
CO	5RB716	WY	48SW2981
CO	5RB729	WY	48SW5057
CO	5RB2435	WY	48SW5222
CO	5RB2727	WY	48UT199
CO	5RT487	WY	48UT390
CO	5RT971	WY	48UT1186
CO	5RT973		

Appendix B:
Provenience Information of Comparative Bison Specimens Used In Analyses from Western North America

Provenience of comparative high altitude bison specimens from western North American.

Specimen Number[1]	Provenience	Elevation (meters)[2]	Reference
Male Specimens			
AMNH M1399937	Sheep Mountain, Wyoming	2921	McDonald 1981b:550-553
CoMNH 1846	Near Pagoda, Colorado	2004	McDonald 1981b:550-553
UCy A(K)	Crowsnest Pass (DjPp-8), Alberta		McDonald 1981b:550-553
UCy A(L)	Crowsnest Pass (DjPp-8), Alberta		McDonald 1981b:550-553
UCM G:S29G	15 mi SE from Walden, Colorado	2469	McDonald 1981:550-553b
UCM G:S66	Mt. Audubon, Colorado	3438	McDonald 1981b:550-553
UCM G:4278	Near Leadville, Colorado	3094	McDonald 1981b:550-553
UCM G(A)	Near Ward, Colorado	2792	McDonald 1981b:550-553
UM Z5461	Yogo Peak, Montana	2683	McDonald 1981b:550-553
UM Z5462	Beartooth Plateau, Wyoming-Montana	3042	McDonald 1981b:550-553
UM Z13251	Beartoooth Plateau, Wyoming	3042	McDonald 1981b:550-553
USGS (A)	Barger Gulch, Colorado	2225	McDonald 1981b:550-553
USNM M168816	Big Horn Mountains, Wyoming		McDonald 1981b:550-553
UWy (B)	Union Pass, Wyoming	2807	McDonald 1981b:550-553
UWy (C)	Big Horn Mountains, Wyoming	-	McDonald 1981b:550-553
UWy (D)	Wind River Mountains, Wyoming	-	McDonald 1981b:550-553
FC-1	Fawn Creek, Salmon River Mountains, Idaho	2256	Cannon 1997:Table 3
BH-1	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-2	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III 4
BH-3	Bighorn Mountains, Wyoming	-	Wilson 197:Table III 4
BH-4	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-5	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-6	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-7	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-8	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-9	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-10	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
Female Specimens			
AMNH M16322	Montana	-	McDonald 1981b:562-565
USNM M122672	Big Dry Creek, Montana	-	McDonald 1981b:562-565
USNM M122685	Big Dry Creek, Montana	-	McDonald 1981b:562-565
UWy C3071	Buffalo Creek, Wyoming	-	McDonald 1981b:562-565
UWy C30	Glenrock, Wyoming	-	McDonald 1981:550-553b
USNM M248950	Malheur Lake, Oregon	-	McDonald 1981b:566-569
USNM M249844	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M249847	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M249848	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M249849	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M250089	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M250090	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M250091	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M250095	Malheur Lake, Oregon	-	McDonald 1981b: 566-569

1. Specimen number abbreviations: AMNH=American Museum of Natural History; CoMNH= Denver Museum of Nature and Science (formerly Colorado Museum of Natural Museum); UCy= University of Calgary; UCM= University of Colorado Museum; UM= University of Montana; USGS= United States Geological Survey; USNM= United States National Museum; UWy=University of Wyoming.
2. Elevation was obtained through the USGS Place Name database (http://geonames.usgs.gov/) and should be considered approximate.

Appendix C:
Craniometric Data For High Altitude And Western Bison
Used In Comparative Study

Specimen	Sex	SHTT	CLUC	TB	VD	CHC	TD	WHCO	GPW	ON	OP	GWA	CW	DEP	AHC	BP	OF
AMNH M1399937	M	630	192	178	84	269	88	279	331	239	530	253	134	94	62	112	145
CoMNH 1846	M	667	205	193	94	287	97	281	330	248	-	235	138	106	63	110	140
UCy A(K)	M	645	185	174	77	240	76	-	-	-	-	-	-	-	68	-	-
UCy A(L)	M	-	-	-	83	258	81	-	-	-	-	-	-	-	-	-	-
UCM G:S29Q	M	608	180	172	82	258	82	265	-	222	-	243	120	88	72	109	133
UCM G:S66	M	555	179	169	76	244	82	254	-	-	-	-	-	-	-	104	143
UCM G:4278	M	-	-	-	-	-	79	258	314	-	-	249	111	-	-	102	135
UCM G(A)	M	-	221	209	99	297	97	286	327	262	-	-	-	-	71	-	-
UM Z5461	M	543	154	139	69	237	78	262	326	-	-	-	-	-	64	-	-
UM Z5462	M	589	166	148	-	-	-	-	-	-	-	-	125	98	79	-	-
UM Z13251	M	591	214	184	84	255	82	273	321	235	-	-	-	-	64	-	-
USGS (A)	M	667	200	183	92	288	94	287	343	279	-	251	120	109	62	112	135
USNM M168816	M	648	175	166	85	264	87	294	351	251	568	257	138	104	67	109	128
UWy (B)	M	-	-	-	77	232	74	260	-	-	-	245	124	90	71	107	153
UWy (C)	M	-	-	-	-	-	-	272	326	-	-	249	131	101	69	113	133
UWy (D)	M	624	198	187	89	257	81	262	313	-	-	233	114	97	64	110	136
BH-1	M	576	186	167	89	254	83	270	324	-	429	264	121	105	-	-	-
BH-2	M	-	-	-	-	286	86	272	330	-	466	250	106	92	-	-	-
BH-3	M	-	190	162	86	248	92	-	-	-	-	-	-	-	-	-	-
BH-4	M	541	143	140	71	235	76	266	298	210	-	228	121	102	-	-	-
BH-5	M	-	-	-	76	-	83	267	280	206	-	-	-	105	-	-	-
BH-6	M	-	-	-	92	273	94	292	356	267	445	276	124	102	-	-	-
BH-7	M	-	-	-	-	-	78	-	-	-	-	248	124	-	-	-	-
BH-8	M	508	140	127	70	228	79	248	296	218	397	234	114	89	-	-	-
BH-9	M	576	197	181	92	265	95	270	319	232	403	264	128	92	-	-	-
BH-10	M	719	225	216	98	305	95	276	324	248	438	260	128	121	-	-	-
FC-1	M	554	175	170	82.4	257	85.5	270	330	265	-	-	-	-	64	-	-
AMNH M16322	F	408	125	113	51	161	48	218	272	214	431	202	120	88	66	106	138
USNM M122672	F	500	122	122	56	165	51	218	264	216	484	197	114	83	70	114	115

Specimen	Sex	SHTT	CLUC	TB	VD	CHC	TD	WHCO	GPW	ON	OP	GWA	CW	DEP	AHC	BF	OF
USNM M122685	F	419	129	121	45	146	47	225	262	211	574	205	123	81	62	107	142
UWy C3071	F	502	129	128	59	191	61	227	272	199	-	205	113	76	70	101	144
UWy C30	F	-	-	-	53	168	54	224	272	203	479	206	115	84	68	118	118
USNM M248950	F	483	145	139	55	171	53	221	267	219	506	205	123	89	-	113	134
USNM M249844	F	438	123	117	51	157	51	213	268	216	491	199	112	78	-	107	131
USNM M249847	F	441	134	122	47	154	49	208	265	213	483	187	111	80	64	107	133
USNM M249848	F	484	135	129	47	153	51	224	276	221	494	202	115	95	69	109	131
USNM M249849	F	451	164	146	54	173	54	218	268	225	516	205	115	86	59	119	123
USNM M250089	F	514	134	134	54	163	51	214	272	216	479	206	115	89	69	110	141
USNM M250090	F	505	177	161	58	182	60	229	281	218	508	219	129	98	-	118	127
USNM M250091	F	441	135	124	52	163	52	218	287	210	486	203	114	88	65	103	135
USNM M250095	F	410	120	111	47	144	45	199	256	211	478	192	111	85	65	111	137

Addendum II

BIOCHEMICAL STUDIES

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Niche variability in late Holocene bison: a perspective from Big Bone Lick, KY

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Abstract

The Big Bone Lick (Boone County, Kentucky) bison fauna offer a glimpse into the population dynamics and behavioral characteristics of eastern *Bison bison* during the late Holocene. Examination of the Big Bone Lick dentitions suggests a single kill event that took place during winter or spring. Furthermore, osteometric comparisons of crania and metacarpals between the Big Bone Lick (BBL) bison and western Bison samples suggest that this species adapted to environmental conditions in the eastern US by adjusting developmental timing rather than through overt morphological change. Finally, isotopic ($\delta^{13}C$, $\delta^{18}O$) analyses of bison tooth enamel hydroxylapatite and a unique progression of tooth wear in older age groups indicate these bison were obligate browsers that exhibited substantial differences in inter-annual land-use patterns. The BBL bison assemblage represents a healthy, in situ bison population that successfully occupied a different ecological niche than bison on the Great Plains. Subsistence models that incorporate these animals should consider these important differences.
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Keywords: Bison; Ohio River valley; Paleoecology; Late Holocene; Stable isotopes; Dentition

1. Introduction

Bison bison is a keystone species in Great Plains ecosystems [36] and a prominent part of Great Plains archaeological assemblages. As such, considerable effort has been expended in understanding the grazing habits, social structure and ecological relationships of this species (e.g., [17,18,25,28,49,58]). In general, these studies have been regionally focused on modern grasslands and their borders, despite the widespread presence of bison in the Holocene fossil record and in ethnohistoric accounts throughout much of North America (e.g., [1,8,10,47,53,54,60,61,63,64]). This species thrived throughout a large part of the continent and their range encompassed an incredible amount of ecological variability.

While bison are a persistent part of the archaeological record over a large area, it has been difficult to insert this important subsistence resource into foraging models because there are many aspects of bison land-use and behavior that remain unknown. If bison were consistently available, or displayed relatively predictable movement patterns that would make them seasonally available to human hunters, it would be expected that they would be a highly ranked resource, especially if human populations were familiar with hunting techniques capable of procuring many animals simultaneously [16]. Unfortunately, historic accounts of bison provide confusing and often conflicting accounts of availability and predictability within a particular region, and it will always be unclear how these recent accounts apply to animal populations in the more distant past. As such, it is important to address the ecology of this resource through archaeological materials directly, rather than relying on inappropriate links between scant historic documentation and the archaeological record. This study provides a first step in understanding intra-specific paleoecological relationships in eastern bison populations during the late Holocene.

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1.1. Environmental and historical background

The Big Bone Lick (BBL) locality has been known to paleontologists and natural historians for over 250 years. Located approximately 30 km southwest of Cincinnati, Ohio in the Bluegrass region of northern Kentucky, the BBL locality was characterized by deciduous forest with oak/hickory as the dominant vegetation prior to European settlement in the 1700s. The BBL locality is located along Big Bone Creek, a first order tributary of the Ohio River, at its confluence with Gum branch (Fig. 1). The Big Bone creek valley is separated from the Ohio River by the remnant of a high Pleistocene terrace. However, land sediment assemblages spanning the late Pleistocene and Holocene are present in the Big Bone Creek valley [72]. For more background on the Big Bone Lick locality, the reader is directed to Tankersley [72–74], Schultz et al. [66,67], and Jillson [32].

Between 1962 and 1966, excavations sponsored by the University of Nebraska State Museum and the National Science Foundation focused on the Big Bone Creek valley [66,67]. Unclear stratigraphic associations of the BBL deposits and the absence of chronometric dates for the faunal assemblages prompted this work. A specific goal of these investigations was to clarify the possible association of Pleistocene and Holocene forms of bison and other fauna for which BBL was the type locality [65]. Over the course of five field seasons, a large number of 10 × 10-foot units were excavated into the alluvial fill of the Big Bone Creek valley in three different localities. Locality 1 was located on the T-0 (lower terrace of Late-Wisconsin/Holocene age) north of Big Bone Creek and east of the mouth of Gum Creek. Three primary bone-bearing strata were identified in locality 1 (Fig. 2; Table 1). Zone A (2.1–2.6 m BS) contained domesticated animals (dog, cow, pig, horse), modern bison, whitetail deer, historic crockery, bricks and worked building stone. Zone B (2.6–3.5 m BS) yielded modern bison, elk, and deer remains. These fauna were associated with chipped stone debitage and tools; however, there is no mention of cultural features such as hearths. Occasionally, reworked Pleistocene faunal remains were present at the base of this zone. Tankersley [73] has suggested this zone dates to 530 ± 105 BP (UGa-4291; 2 sigma calibrated, 680–310 cal BP). Finally, the primary Pleistocene deposit in this locality was designated Zone C (3–4.5 m BS). This zone contained the remains of giant ground sloth (*Mylodon* sp.), mastodon (*Mammut americanum*), large bison (*Bison antiquus*), musk ox (*Bootherium* sp.), giant moose-like deer (*Cervalces scotti*), caribou (*Rangifer* sp.), and horse (*Equus* cf. *complicatus*). Radiocarbon dates from this zone indicate an age of 10,600 ± 250 BP (W-1358; 2 sigma calibrated, 13,150–11,550 cal BP).

This study is primarily concerned with the late Holocene bison fauna represented in the UNSM collection from locality 1, Zone B. During the winters of 2002 and 2003, collections-based research undertaken at the UNSM focused on four main issues in understanding the BBL *Bison bison* fauna. First, eruption and wear patterns of bison dentitions from BBL were examined in order to estimate age-at-death. Second, selected skeletal elements (calcanei, metacarpals, and crania)

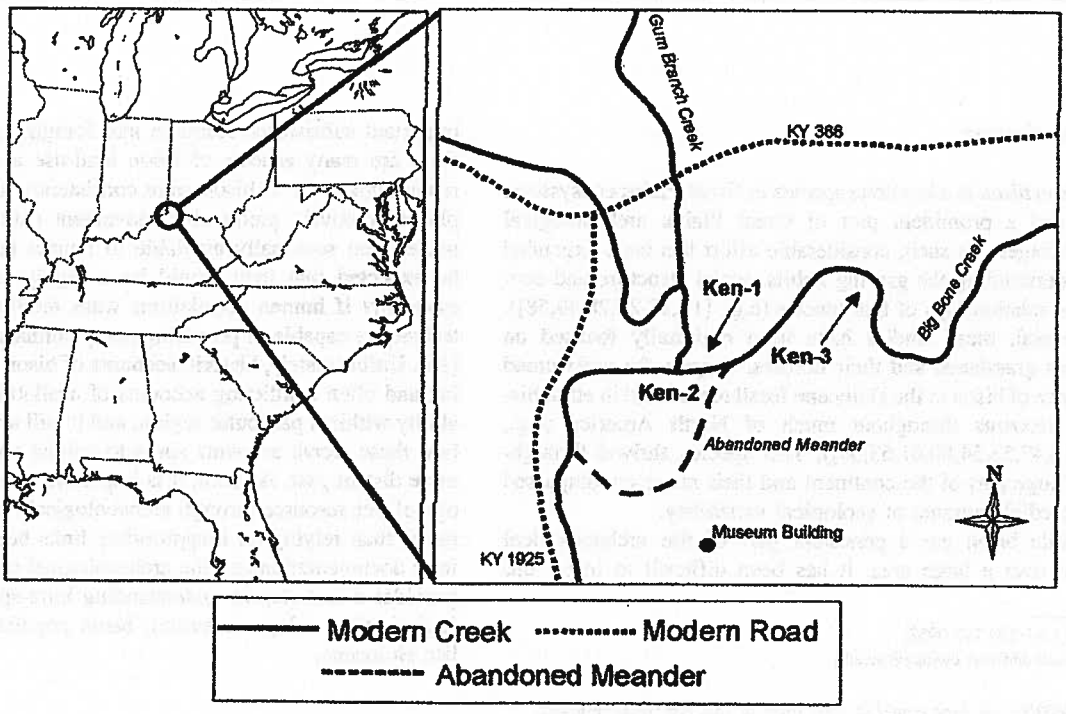

Fig. 1. Map showing location Big Bone Lick locality, Boone County, KY.

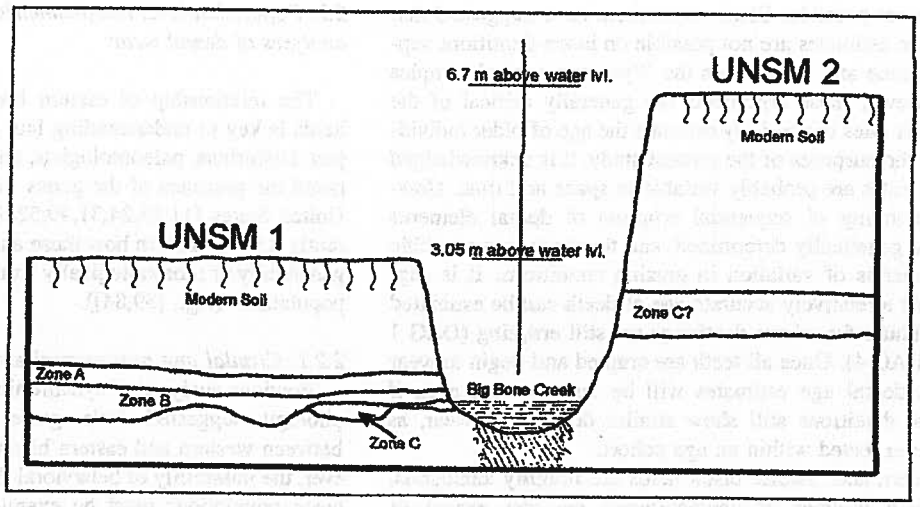

Fig. 2. General stratigraphic section of Big Bone Lick, localities 1 and 2. Adapted from Schultz et al. [66].

were measured to complement the dental estimates of age and to construct the sex ratio of what was thought to be a single bison herd. Additionally, the morphological and developmental characteristics of this population were compared to western samples in order to examine variability in late Holocene bison biogeography. Finally, isotopic analyses ($\delta^{13}C$, $\delta^{18}O$) of bison enamel carbonate and additional analyses of tooth wear in older age groups provide independent estimates of paleodietary preferences.

At least 54 modern bison are represented in the UNSM collection from Locality 1, Zone B. While there may have been some mixing in the lower levels of this zone, Pleistocene and modern bison could be distinguished from each other on the basis of element size and the presence of surface damage due to reworking in the gravelly matrix.

2. Methods

2.1. Herd demography and seasonality

Over the last several decades, numerous researchers have developed methods for documenting the demographic characteristics of mammalian skeletal remains. In the case of bison, Skinner and Kaisen [69] provided a useful scheme for aging fragmentary crania, particularly since they are organized according to increasing degrees of suture fusion (Table 2). However, this scenario does not accommodate the more precise estimates of age that are possible through the close examination of dental (maxillary or mandibular) remains. Modern bison experience a birth pulse in late spring, with most calves being born in April through early May [6]. This characteristic of bison reproductive behavior produces distinct clusters of dental eruption and wear within a herd according to age-cohort. The eruption and wear sequence originally proposed by Frison and Reher [19] for a late Prehistoric bison kill in northern Wyoming has been refined as more known age-at-death individuals are added to the database and researchers better understand spatial and temporal variability in wear patterns [59,77]. Through the sub-annual precision of rapidly erupting juvenile dentitions, season-specific age-at-death

Table 1
Summary of materials recovered by the UNSM from BBL locality 1

Faunal zone	Depth (m BS)	Chronology	Materials
A	2.1–2.6	Historic (early 1800s)	Domesticated animals (cow, dog, horse), bison, deer, crockery, china, bricks, reworked Pleistocene fauna
B	2.6–3.4	Late Prehistoric (530 ± 105 BP)	Bison, elk, deer, chipped stone, reworked Pleistocene fauna
C	3.0–4.6	Late Pleistocene (10,600 ± 250 BP)	Giant Ground Sloth, Mastodon, large bison, musk ox, Pleistocene deer, caribou, horse

Table 2
Criteria for aging bison cranial remains

Dental age[a] (years)	Cranial age[b]	Demographic group[c]	Description
0.1–2.5	I-S, A-S	1 (Immature)	Immature and adolescent; M_1 and M_2 in full wear, M_3 still erupting, frontal, lacrimal, nasal, and supra-occipital sutures unfused
2.5–4.0	S-1, S-2	2 (Young adult)	Young adult; all molars in full wear, frontal, lacrimal, nasal and supra-occipital sutures unfused, but skull has reached adult size
>4.0	S-3, S-4	3 (Fully mature)	Fully mature; all molars are worn to well-worn, all sutures fuse, skull is adult size

[a] Dental age is from Reher and Frison [59]: 65.
[b] Cranial age is from Skinner and Kaisen [69]: 146–147.
[c] The simplified scheme utilized in this study.

estimates are possible. Some researchers have suggested that precise age estimates are not possible on bison dentitions separated in time and space from the Wyoming control samples [81]; however, these arguments are generally critical of the use of wear rates to precisely estimate the age of older individuals. For the purposes of the present study, it is acknowledged that wear rates are probably variable in space and time. However, the timing of sequential eruption of dental elements should be genetically determined, and thus is less susceptible to the vagaries of variation in grazing conditions. It is suggested that a relatively accurate age-at-death can be estimated for individuals for whom dentitions are still erupting (DAG 1 through DAG 4). Once all teeth are erupted and begin to wear however, dental age estimates will be less precise, even if groups of dentitions still show similar degrees of wear, as would be expected within an age cohort.

If modern and historic bison herds are roughly analogous, there are a number of characteristics we can expect of prehistoric bison herds. First, different demographic groups utilize the landscape differently from each other. Cow/calf herds are somewhat more sedentary than bull groups and are attracted to open meadows or prairies during the warm season. These groups would be made up of adult females and juveniles of both sexes. They may also include very low numbers of adult males [6,45,51]. Adult males, on the other hand, are loosely organized into groups of young bulls but may also be found as isolated individuals. In the Great Plains, these groups utilized topographically rugged areas and breaks more often than cow/calf herds. Modern ecological studies suggest that these different demographic groups rarely shared seasonal patterns in land-use, with the exception of the rut period in the late summer [17,18,45]. From these patterns we can establish some expectations for the BBL assemblage. If the demographic signature of the BBL population is similar to known patterns in natural aggregations of bison, then there is the possibility that the late Holocene component of BBL represents a catastrophic, multi-animal, kill event (whether naturally or culturally occurring). If, however, the BBL assemblage shows some bias towards particular age or sex groups, then there may be certain taphonomic or cultural filters affecting the assemblage, and we cannot make any assumptions that the BBL assemblage was a single-event accumulation.

Individuals can also be sexed through the quantitative examination of both cranial and post-cranial remains. Male bison are significantly larger than female animals of the same age, both in body size and in the size of display organs (i.e., horns). As such, many weight-bearing post-cranial elements (e.g., calcanei, metacarpals) or parts of the crania that can be linked to horn-size are relatively reliable indicators of individual sex. When standardized measurements are compared in a scatterplot, adult males and females constitute separate clusters. Young males are often difficult to separate from adult females, thus female counts may be slightly elevated. However, by choosing adult specimens (i.e., using elements that fuse at a particular age), then this problem can be partly alleviated.

2.2. Population-level morphometric comparisons and analyses of dental wear

The relationship of eastern bison populations to western herds is key to understanding late Holocene bison biogeography. Historians, paleontologists, and archaeologists alike have noted the presence of the genus *Bison* throughout the eastern United States [11,23,24,31,49,52,53,63,66,67,73,75], but currently it is not known how these animals differed behaviorally, genetically or morphologically from well-documented western populations (e.g., [59,84]).

2.2.1. Cranial and post-cranial elements

Previous analyses of synchronic differences in cranial morphology suggested little gross morphological difference between western and eastern bison populations [49,79]. However, the possibility of behavioral divergence between regional bison populations must be examined in order to assess the effectiveness of modeled human procurement tactics and to address larger patterns in bison behavioral ecology.

This study utilizes detailed morphometric characterizations of two bison skeletal elements to characterize bison populations: crania (Fig. 3) and metacarpals (Fig. 4). Our current understanding of bison evolution relies heavily on morphological differences in bison crania. Comprehensive studies by Skinner and Kaisen [69], Wilson [83–85] and McDonald [48,49] were strongly oriented towards defining and refining temporal and spatial patterning in bison cranial remains. While these studies also included post-cranial specimens to a certain extent, it was generally accepted that post-cranial elements did not possess the taxonomic distinctiveness of crania [49,69,70]. The goals of these studies were concerned primarily with understanding broad morphological differences between different chrono-species or sub-species.

However, I have included bison post-cranial remains in the current study of synchronic variability in bison populations because they are sensitive to broad nutritional and behavioral limitations on animal body-size and growth patterns. Through the analysis of post-cranial remains we can examine highly plastic adaptive mechanisms at work in bison populations. While morphology and/or size has been used to delineate different bison populations in the past (e.g., [22,49,79]), researchers have had little success in understanding the causal factors underlying this variability, particularly given what has traditionally been seen as very minor morphological/metric differences between co-eval bison populations. Instead, I suggest that less visible characteristics of bison populations may be the focus of evolutionary processes. These characteristics may include, but are not limited to, variables such as growth-rate, developmental timing, life-history variables, or animal behavior.

In order to illustrate the relationship of the BBL bison sample to populations from the Great Plains, a number of late Holocene archaeological and paleontological sites were used as a basis for comparison (Fig. 5, Table 3). There are 164 crania from 10 dated localities, and 153 metacarpals from 18 dated localities used for comparison. These data were subsequently

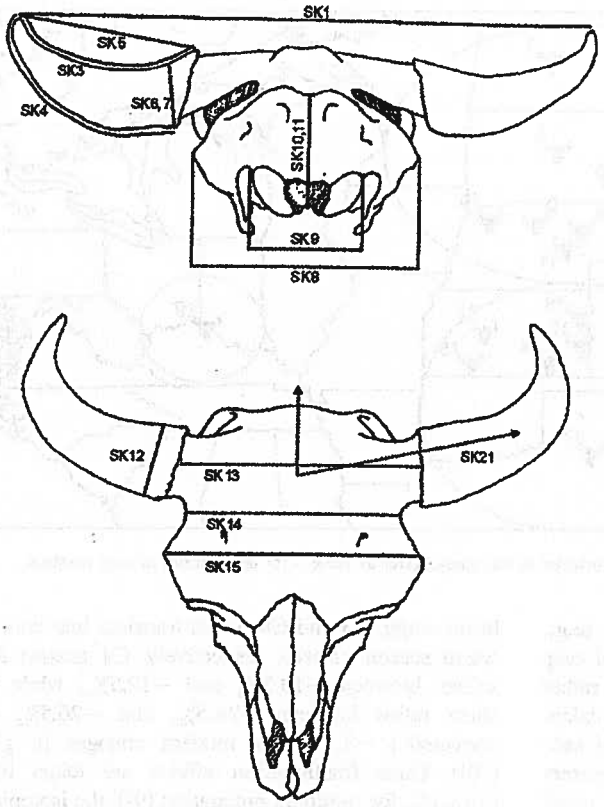

Fig. 3. Measurements taken on bison crania. (SK1) Spread of horn cores, tip to tip, (SK3) Core length on upper curve, tip to burr, (SK4) length of core on lower curve, tip to burr, (SK5) length, tip of core to upper base, at burr, (SK6) Vertical diameter of core, (SK7) Circumference of core at base, (SK8) Greatest width at auditory openings, (SK9) Width of occipital condyles, (SK10) Depth of skull, occipital crest to top of Foramen Magnum, (SK11) Depth of skull, occipital crest to bottom of Foramen Magnum, (SK12) Transverse diameter of core, (SK13) Width of skull between bases of horn cores, (SK14) Width of skull between horn cores and orbits, (SK15) Greatest post-orbital width, (SK21) Angle posteriorad divergence of horn core (degrees). (SK22) Angle of proximal horn core depression (degrees, not shown, see Skinner and Kaisen [69]: 144), angBF/angOF (degrees, not shown, see McDonald [49]: 45). Figure adapted from van Zyll de Jong [79].

lumped into regional samples representing late Holocene bison in the Northern Plains, Southern Plains and Great Basin. The central Platte River valley provides the dividing line between the first two regions, approximating Hornaday's [30] division of the Northern and Southern bison herds.

2.2.2. *Paleodietary inferences from dental wear patterns*

The progression of dental wear can also distinguish between animals occupying different dietary niches. While the wear rates of older age groups are not very helpful for examining precise age-at-death, taken as a whole, these data provide a multi-year diachronic perspective on the influence of dietary choices on tooth wear and dental longevity. Tooth mesowear studies have been used to broadly reconstruct herbivore diets at mid-range temporal scales [14] and are certainly relevant to understanding bison paleodiets in the eastern US.

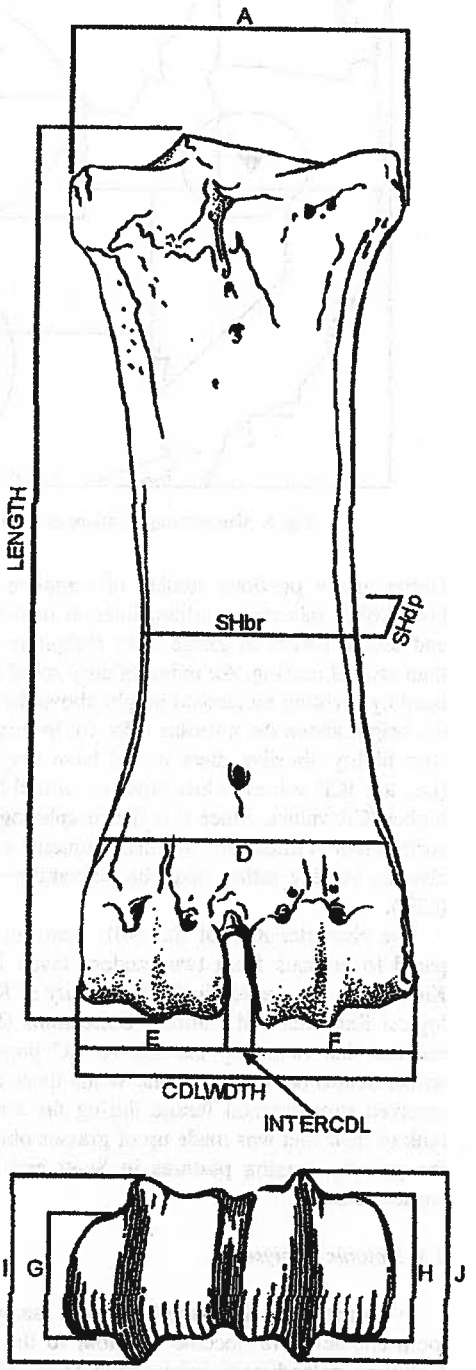

Fig. 4. Measurements taken on bison metacarpals. LENGTH) maximum length, (SHbr) minimum shaft breadth, (SHdp) minimum shaft depth, measured at a right angle to SHbr, (CDLWDTH) maximum width of distal articular surface, (INTERCDL) width of opening between medial and lateral condyles, (A) Proximal breadth, (B) Proximal depth (not shown), (D) Distal breadth, above condyle, (E) breadth, medial condyle, (F) breadth, lateral condyle, (G) depth, medial trochlea, (H) depth, lateral trochlea, (I) depth, medial sagittal ridge, (J) depth, lateral sagittal ridge.

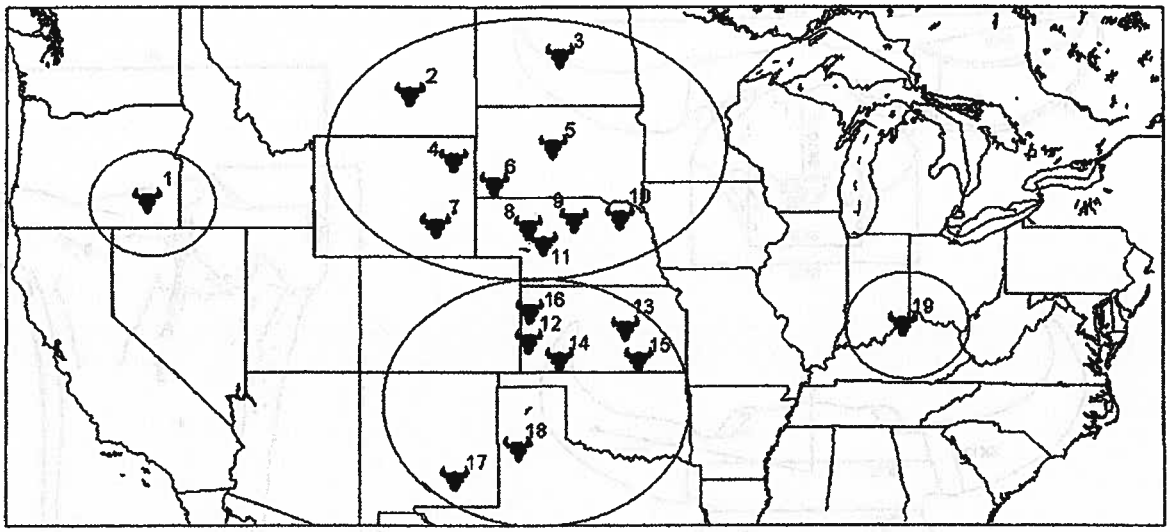

Fig. 5. Map showing locations of *B. bison* samples included in this study. Refer to Table 3 for descriptions of map numbers.

Unlike many previous studies of ungulate mesowear (e.g., [14,34,68]), this study utilizes interval measurements of cusp and saddle height to gauge cusp sharpness and relief rather than ordinal scoring. An index of cusp relief (ICR) was calculated by dividing metaconid height above the alveolus by saddle height above the alveolus (Fig. 6). In this scheme, grazers with highly abrasive diets would have very low cusp relief (i.e., low ICR values) while browsers would have significantly higher ICR values. Since it is the morphology of the occlusal surface that is important, all measurements are taken from the alveolar surface rather than the cementum–enamel junction (CEJ).

The characteristics of the BBL dentitions are then compared to animals from two modern bison herds in western Kansas that are curated in the University of Kansas Anthropological Research and Cultural Collections (KU-ARCC). The animals that make up the KU-ARCC population represent winter deaths or culling events. While these animals probably received supplemental forage during the winter months, the bulk of their diet was made up of grasses obtained throughout the year by grazing pastures in Scott and Finney counties, western Kansas.

2.3. Isotopic analyses

In recent years intra-tooth isotopic analyses of ungulate tooth enamel have become essential to the interpretation of herbivore paleodietary information (e.g., [21,26,56]). These studies provide an alternative perspective on the niche structure of the BBL animals that is independent of tooth morphology and regional paleoclimate constructions.

The carbon isotope composition ($\delta^{13}C$) of herbivore tissues translates into relative contributions of C3 and C4 plants to the diet [2,46]. The $\delta^{13}C$ values of enamel carbonate in bison have been primarily used to reconstruct past vegetation conditions. In most North American grasslands, the core of the bison range, C3 and C4 plants translate into cool season and warm season grasses, respectively. C4 grasses exhibit $\delta^{13}C$ values between −10.5‰ and −12.5‰, while C3 grasses show ratios between −24.5‰ and −26.5‰ (values are corrected + ~1.5‰ for modern changes in global $\delta^{13}C$; [76]). Once fractionation effects are taken into account (+14.1‰ for ruminant bioapatite; [9]), the isotopic separation of plants with these different photosynthetic pathways (and the environmental conditions associated with them) allows $\delta^{13}C$ in the carbonate portion of bison enamel bioapatite to be used as a quantitative proxy for prehistoric vegetative conditions [13,55,44]. In the eastern US, the interpretation $\delta^{13}C$ values in bison dentitions is complicated by the incorporation of woody C3 browse in to the diet. For this reason, strongly negative $\delta^{13}C$ values may indicate a diet of cool season grasses, woody vegetation, or a mixed diet consisting of both woody browse and cool season grasses. In these areas additional lines of evidence are needed to address paleodietary issues in prehistoric herbivores.

The oxygen isotope composition ($\delta^{18}O$) of biological materials is usually understood to track the paleotemperature of meteoric water [37,41–43]. However, larger rivers, springs, or groundwater-augmented lakes will often exhibit different $\delta^{18}O$ values than the meteoric average due to snowmelt runoff, differential evaporation, and the incorporation of aquifer waters [12,35]. In bison bioapatite, the $\delta^{18}O$ value reflects body-water $\delta^{18}O$ values during tooth formation [21,26]. Unlike small ungulates that have made physiological adjustments to arid landscapes (e.g., *Antilocapra americana*), the isotopic composition of body-water in bison should closely track the isotopic value of water intake, not leaf moisture [7,42].

Recent emphasis on the $\delta^{18}O$ values of serially sampled herbivore teeth has highlighted the potential of incremental growth structures for understanding prehistoric seasonality patterns [15,26,21]. It remains unclear how the isotopic

Table 3
Comparative samples of Late Holocene age. (a) *B. bison* crania and (b) *B. bison* metacarpals

Region	Locality (map #)	Date (cal AD)	Sex	Age	Crania MNI	Reference
(a) *B. bison* crania						
Eastern US	Big Bone Lick, KY (19)	1270–1640	Female	Young adult	7	This study
				Fully mature	8	
			Male	Fully mature	5	
Northern Great Plains	Big Dry Creek, MT (2)	Historic	Female	Fully mature	2	[48]
			Male	Fully mature	10	
	Big Hill Springs, AB (not shown on map)	Late Holocene	Male	Fully mature	6	[48]
	Humbug Creek, NE (10)	Late Holocene	Female	Immature	2	This study
				Young adult	2	
				Fully mature	3	
			Male	Young adult	3	
				Fully mature	25	
	Vore, WY, Lower kills (4)	1400–1800	Female	Young adult	27	This study
				Fully mature	1	
			Male	Young adult	5	
				Fully mature	17	
	Wardell, WY (7)	350–950	Female	Immature	2	[84]
			Male	Fully mature	3	
				Immature	1	
	White River, SD (6)	Historic	Female	Fully mature	5	[48]
			Male	Fully mature	5	
Southern Great Plains	Garnsey, NM (17)	1450–1500	Female	Fully mature	6	[85]
	Lubbock Lake, TX (18)	Late Holocene	Male	Fully mature	7	[48]
Great Basin	Malheur Lake, OR (1)	Late Holocene	Female	Fully mature	9	[48]
			Male	Fully mature	3	

Region	Locality (map #)	Date (cal AD)	Sex	Metacarpal MNI
(b) B. bison metacarpals[a]				
Eastern US	Big Bone Lick, KY (18)	1270–1640	Female	32
			Male	5
Northern Great Plains	25KH68, NE (11)	~1000	Male	2
	Dinehart Village, SD (5)	1000–1300	Male	1
	Double Ditch, ND (3)	1500–1781	Female	1
	Humbug Creek, NE (10)	Late Holocene	Female	2
			Male	7
	McIntosh, NE (8)	1283–1440	Female	6
			Male	2
	Shultz Site, NE (9)	1–600	Female	13
			Male	9
	Spain Site, SD (5)	1450–1650	Female	1
			Male	2
	Talking Crow, SD (5)	1300–1450	Female	2
			Male	1
	Two Teeth, SD (5)	1675–1850	Female	2
			Male	1
	Vore—lower kills, WY (4)	1400–1800	Female	9
			Male	8
Southern Great Plains	Arkansas City Sites, KS (15) (14CO3, 14CO332)	1550–1700	Male	3
			Female	2
	Lundeen Site, KS	1250–1350	Female	4
			Male	1
	Sharp's Creek, KS (13)	1550–1700	Female	1
	Buresh Site, KS (16)	1000–1500	Female	1
			Male	12
	14SR305, KS (16)	1000–1500	Female	2
			Male	6
	Duff Modern Herd, KS (12)	Modern	Female	4
			Male	1
	Garnsey, NM (17)	1450–1500	Female	6
			Male	4

[a] All measurements by the author with the exception of Garnsey (Speth, 1983).

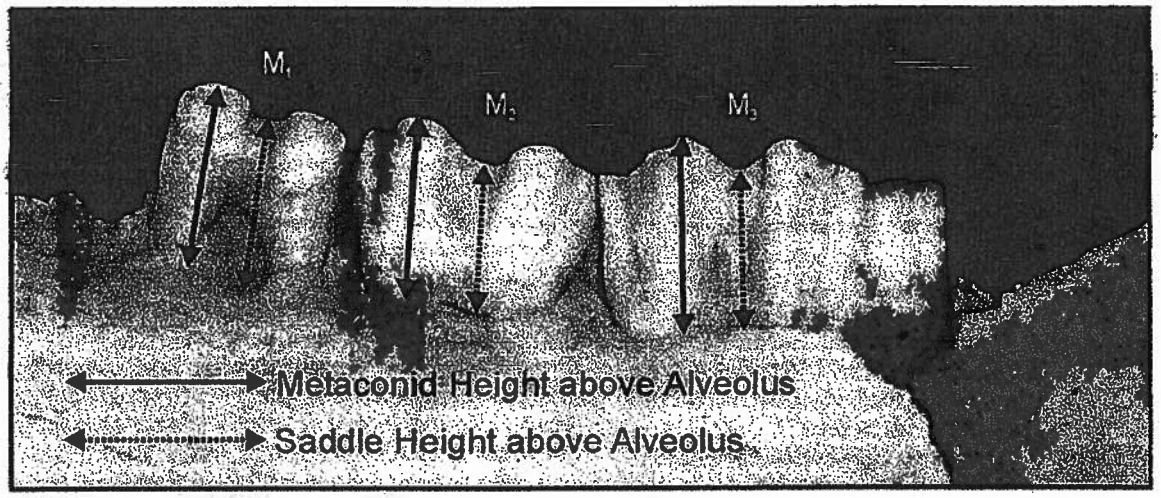

Fig. 6. Measurements on bison dentitions.

signature preserved in tooth enamel carbonate actually relates to "real-time" isotopic changes in body-water or dietary input [40,86]. However, within the age-cohort structure of a single bison herd, all teeth should show similar seasonal timing in eruption and mineralization rates. Furthermore, the starting point of each chronology should begin in late April or May, so we can appropriately compare $\delta^{18}O$ or $\delta^{13}C$ sequences between different age cohorts. In other words, while it may be difficult to associate a particular portion of a tooth (e.g., 1 cm above the CEJ) with a particular time of year (e.g., April), that particular portion of the tooth should represent a similar time of year in all members of the herd. This is an important distinction to make. It allows for comparison of ecologically important variables between different animals (1) without assuming constant mineralization rates [86], (2) by bypassing potential seasonal damping effects [26,29], and (3) preventing errors in interpretation related to delays between input signals and enamel mineralization [3,40].

In the case of the BBL bison, down-tooth isotopic sequences from consecutive age groups provide a snapshot of the waters ingested ($\delta^{18}O$) or dietary intake ($\delta^{13}C$) during the formation of the tooth. If the herd undertook seasonal

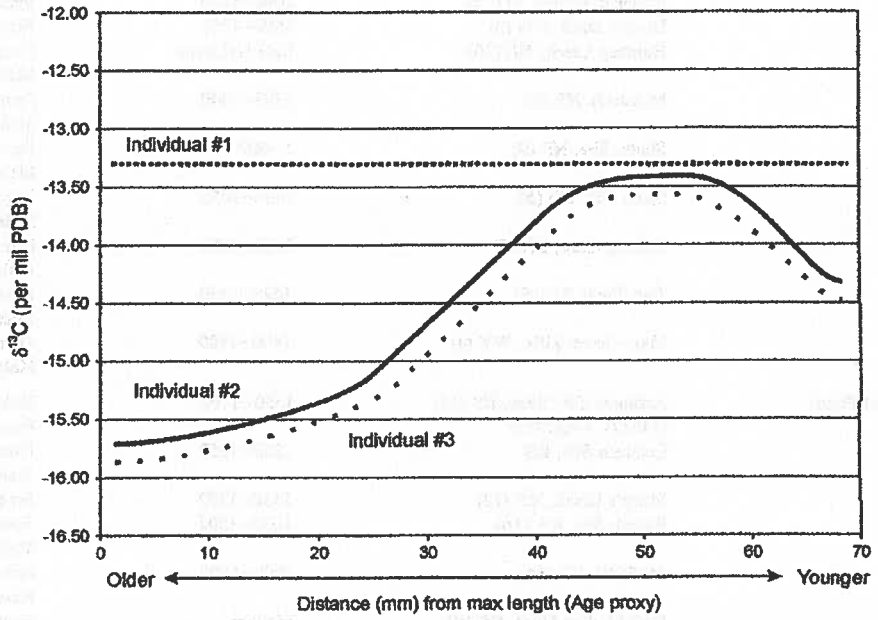

Fig. 7. Expectations of the model. Individuals 2 and 3 show parallel sequences of isotopic values throughout the tooth. These animals represent a hypothetical herd where the home range is very similar each year with respect to the proportion of C3/C4 grasses ingested. Individual 1 would have grazed areas with more C4 plant material during the early part of tooth formation and may or may not have shared a range with individuals 2 and 3 during the later part of tooth formation.

migrations, as has been proposed by Jakle [33] and Webb [80] on the basis of historic records, we would expect the timing of use of certain surface waters or pastures to be consistent between age groups (Fig. 7). If however, herd movements were less seasonally predictable, or based on super-annual cycles, then we would expect differences in the down-tooth sequence of isotopic values of tooth enamel carbonate. In this way, analyses of $\delta^{18}O$ or $\delta^{13}C$ can be used to highlight differences or similarities in land-use patterns for different age-cohorts of the BBL sample.

Two lower M_3s were selected from Dental Age Groups (DAG) 4 and A. These teeth were sampled longitudinally along the metaconid at approximately 7–10 mm intervals with a Dremel. Five milligrams of each sample were pretreated in a 2% NaOCl solution to remove organic contaminants and a 0.1N acetic acid leach to remove secondary carbonates (following [38]). The purified samples were then submitted to the University of Michigan Stable Isotope Laboratory where they were processed in a Finnegan MAT 251 triple collector isotope ratio mass spectrometer coupled to a Finnigan Kiel automated preparation device. Both $\delta^{13}C$ and $\delta^{18}O$ values are expressed as per mil (‰) relative to the standard, PDB (PeeDee Belemnite).

3. Results

3.1. Population structure and seasonality of the BBL Bison bison fauna

Dentitions from a minimum of seven animals (11 mandibles) from the first three age-cohorts were suitable for estimating seasonality. At least two individuals are present in DAG 1. Three additional individuals are present in DAG 2 and five animals in DAG 3 (Table 4, Fig. 8). Relatively tight age-at-death estimates within these age groups suggest that the Late Holocene deposits at BBL are from a single episode, multi-animal kill. While it is unclear at this time whether these animals died through the course of human subsistence pursuits or some other natural catastrophe, field documentation of chipped

Table 4
Characteristics of the BBL bison lower dentitions

Age group	Element	Age est.	Left	Right	MNI	Description
1	dP_4	0.5–0.6	2	2	2	dP_4 is in full wear, rear ectostylid is worn and connected to the occlusal surface. M_1 shows light to moderate wear on all facets but VII and VIII. M_2 visible in crypt
	M_1		1	2	2	
	M_2		0	1	1	
2	dP_4	1.5–1.7	2	4	4	Anterior and posterior ectostylids of dP_4 are in wear, but anterior is not yet connected to main wear surface. M_1 is in full wear, but ectostylid not yet worn. M_2 is almost erupted to level of other teeth. Wear is variable (facets I–II, I–V, or I–VII)
	M_1		2	2	2	
	M_2		3	2	3	
	M_3		0	1	1	
3	dP_4	2.6–2.9	1	5	5	dP_4s are in heavy wear. M_1 and M_2 are in full wear. Ectostylid of M_1 is in wear and may or may not by connected to the main occlusal surface. M_3 is still erupting. The first cusp exhibits variable light wear (facets I–IV)
	M_1		1	2	2	
	M_2		1	2	2	
	M_3		1	2	2	
4	P4	3.5–3.9	1	2	2	Light wear on P_3 and P_4. M_1 is in full wear with the ectostylid worn and connected to the main occlusal surface. Ectostylid of M_2 is 2–5 mm from occlusal surface. M_3 is in full wear with the ectostylid ~1 cm from main wear surface
	M_1		1	2	2	
	M_2		1	2	2	
	M_3		1	1	1	
A	M_1	NA	1	1	1	M_1 in full wear. M_2 also in full wear. Ectostylid is a ring of enamel, still unconnected from occlusal surface. M_3 in full wear, but ectostylid still unworn
	M_2		2	1	2	
	M_3		2	1	2	
B	M_1	NA	1	1	1	M_1 and M_2 in full wear, but ectostylid of M_2 is still unconnected from occlusal surface. M_3 in full wear, but ectostylid is still unworn
	M_2		2	1	2	
	M_3		2	1	2	
C	M_1	NA	1	3	3	M_1 and M_2 in full wear, but ectostylid of M_2 is still unconnected from occlusal surface. M_3 in full wear, but ectostylid is still unworn. Distinguished from DAG B by crown height of M_3
	M_2		1	2	2	
	M_3		1	1	1	
D	M_1	NA	1	1	1	All teeth in wear. M_2 ectostylid in wear and connected to main occlusal surface. Ectostylid of M_3 is worn, but unconnected
	M_2		1	0	1	
	M_3		1	0	1	
E	M_1	NA	1	0	1	All teeth in full wear. M_2 ectostylid in wear and connected to main occlusal surface. Ectostylid of M_3 is worn, but unconnected. Distinguished from DAG D by crown height of posterior molars
	M_2		3	0	3	
	M_3		5	3	5	
F	M_1	NA	1	1	1	All teeth in heavy wear. M_3 ectostylid worn and connected to main occlusal surface
	M_2		1	1	1	
	M_3		4	2	4	

Age estimates for the first three age groups and terminology are taken from Todd et al. 1996 and the references cited therein.

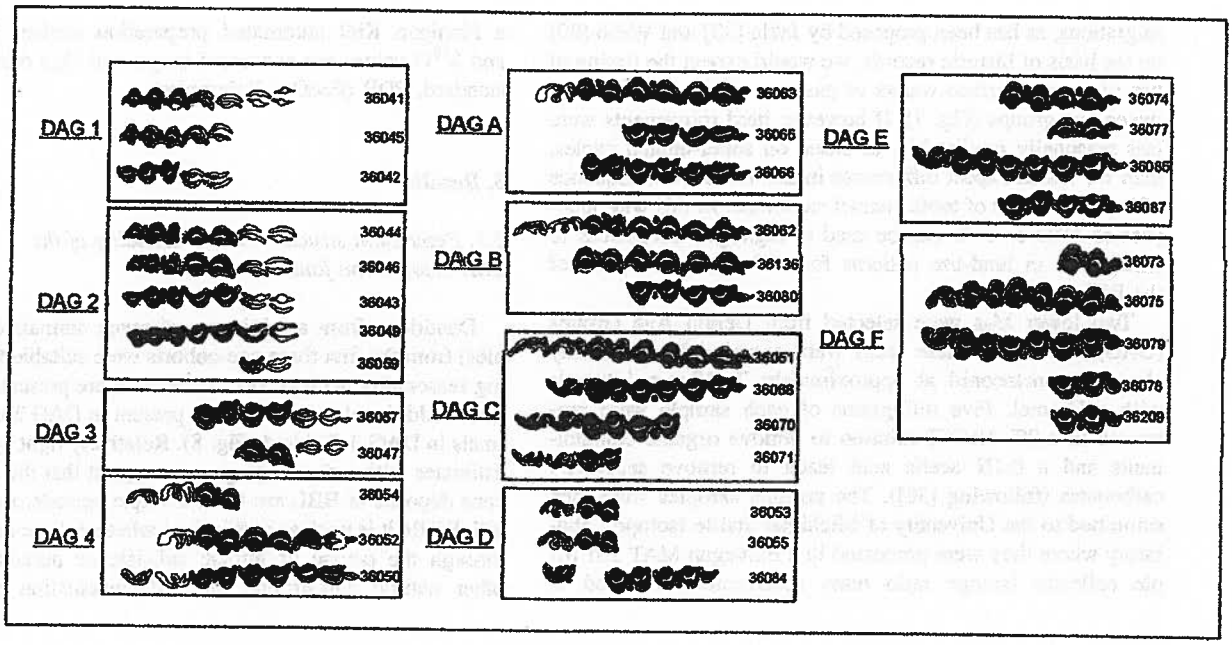

Fig. 8. Schematic drawings of eruption and wear patterns in the BBL bison lower dentitions.

stone debitage and tools within the Late Holocene bonebed strongly suggest the former [67].

If the timing of bison reproductive synchrony in the eastern US is similar to that of prehistoric bison on the Great Plains, the eruption and wear patterns of the younger BBL dentitions can offer a fine-grained, age-at-death estimate at a seasonal resolution. These estimates range from $y + 0.5$ to $y + 0.9$ (winter or spring). Interestingly, animals of the same age show consistent seasonality estimates, but this consistency is not always evident between age groups. For instance, the age-at-death for DAG 1 is 0.5–0.6 years. However, DAG 2 age estimates are slightly later (1.5–1.7 years) and DAG 3 age estimates (2.6–2.9 years) are even later than DAG 2. These discrepancies are probably a function of a relatively unique molar wear progression that becomes more pronounced in older age groups at BBL (see below).

In order to determine whether there was a cultural or natural bias in the makeup of the BBL death assemblage, sex ratios were calculated from measurements of two sexually dimorphic post-cranial element classes (calcanei and metacarpals) representing 54 animals (Table 5).

Forty-one individuals are represented by left calcanei. Of these, there are three specimens that represent adult males, 20 that are from adult females, 11 that are unfused but are large enough to be young male animals, and seven specimens from juveniles. In modern bison, calcanei fuse during the fifth (males) and sixth (females) years of life [27]. If this pattern also applies to the BBL bison, there are probably 14 males, 20 females (≥6 years old) and seven individuals whose sex is indeterminate (Fig. 9).

Table 5
Sex representation of selected cranial and post-cranial elements

Skeletal element	*MNE*	*No. of males (%)*	*No. of females (%)*	*No. of juveniles (%)*
Calcanei	41	3 (6.2)	20 (41.7)	18 (37.5)
Metacarpals	38	8 (21.1)	27 (71.1)	12 (31.5)
Crania	22	5 (22.7)	8 (36.4)	7 (31.8)

Metacarpals do not include adult males of indeterminate sex (MNE = 3).

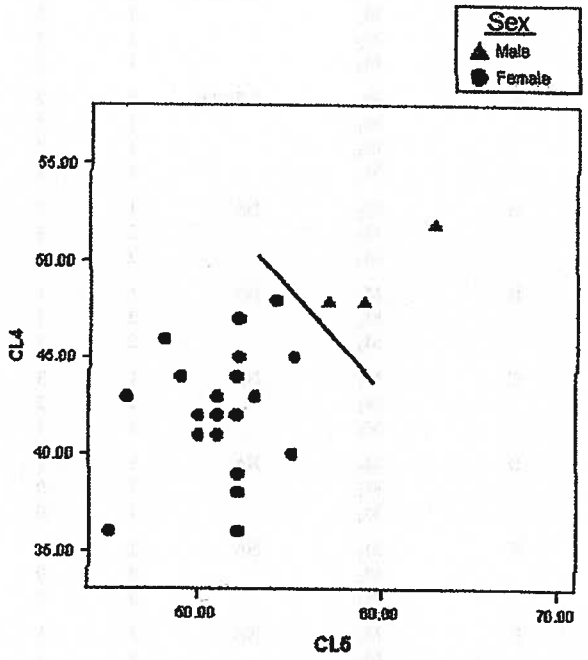

Fig. 9. Bivariate plot of adult calcanei measurements. Measurements after Hill [27].

Metacarpals fuse slightly earlier than calcanei, at ~4 years of age [5,39]. A minimum of 38 adults, (8 males, 27 females and 3 adult individuals of indeterminate sex) are represented by left metacarpals. An additional 12 juvenile animals are present (<4 years old), including four young males. Interestingly, the juvenile specimens show internal clustering that may represent specific age-cohorts (Fig. 10).

Likewise, crania are strongly sexually dimorphic in horn core characteristics, as well as overall size. The sex ratio of the BBL crania roughly parallels the post-cranial data, suggesting the presence of five adult males, eight adult females and seven sub-adult females (Fig. 11).

In all, the ratio of male to female adult animals is roughly 1:3, similar to cow/calf herds in western bison populations [18,62]. However, it is also interesting to note that the number of adolescent males (unfused but already the size of adult female specimens) exceeds the number of adult males. These young males may be a non-reproductive demographic class of a cow-calf herd. If modern and historic bison herds are any indication of prehistoric herd dynamics, then there does not seem to be any obvious natural or cultural selection bias in the BBL assemblage based on age or sex.

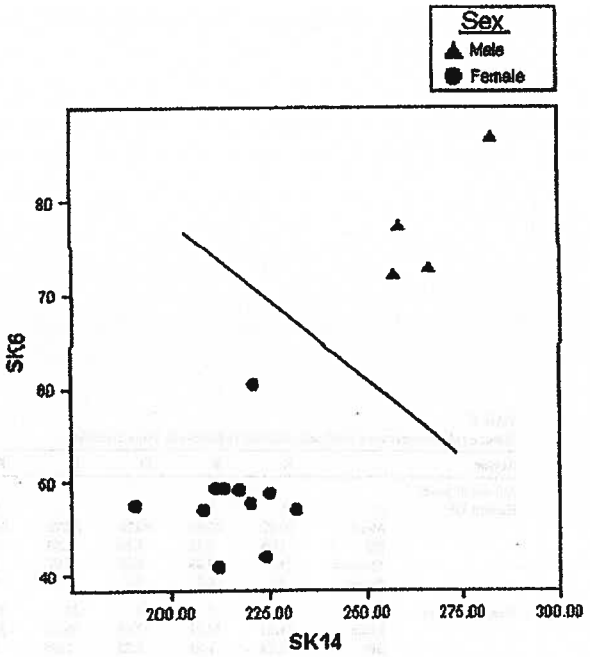

Fig. 11. Bivariate plot of adult cranial measurements. See Fig. 3.

3.2. Population level morphometric comparisons

Numerous researchers have examined Holocene changes in the size of bison post-cranial elements (e.g., [4,27,28,57,70]). Rarely however, have these studies included large population samples that are located outside of the Great Plains (but see [47,49,79] for exceptions). The BBL Late Holocene bison fauna has the potential to offer insights into the morphological variability of this species throughout its range.

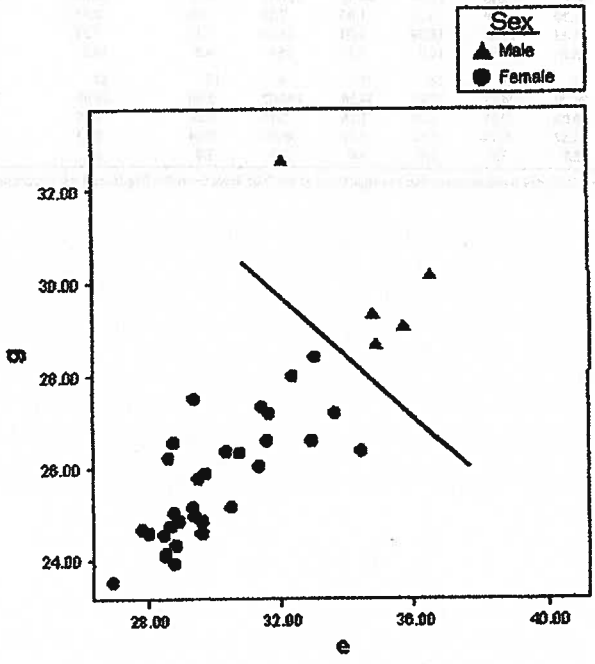

Fig. 10. Bivariate plot of adult metacarpal measurements. See Fig. 4.

3.2.1. Metacarpals

Two population samples of late Holocene metacarpals were compared to the BBL sample (i.e., Northern Great Plains, Southern Great Plains). Most breadth measurements of distal metacarpals are significantly smaller in BBL males and females than those of Plains populations (Table 6). Furthermore, BBL females show more significant departures from their Great Plains counterparts than male animals. A bivariate plot of these measurements shows that BBL female metacarpals fuse when the element is smaller than those of Great Plains females, but as the animals grow, the bone continues to remodel and increase in breadth, reflecting increased body-weight (Fig. 12). Since metacarpals fuse at about four years of age, the pattern present in the BBL females could represent two scenarios. First, long bone fusion could progress faster in these animals than in other populations, in which case the increased breadth indicates growth and bone remodeling after fusion. Alternatively, the BBL animals may not have completed growth by four years of age and continued to significantly increase body-size into their fifth and sixth years. Unlike breadth, metacarpal length and depth dimensions in female animals are generally indistinguishable from Great Plains populations. If the latter scenario were correct, then we would expect some BBL females to be much larger than the Plains mean in depth/length dimensions as well as in breadth. However, we do not see this pattern, suggesting that metacarpal fusion occurred earlier in BBL females.

Table 6
Metacarpal measurements from selected late Holocene *B. bison* localities

Region		A	B	D	E	F	G	H	I	J	Length	INTERCDL	CDLWDTH	SHbr	SHdp
(A) Adult males															
Eastern US	*N*	5	5	5	5	4	5	5	3	3	4	4	5	5	5
	Mean	70.30	40.60	**70.78**	**34.75**	33.69	30.00	27.59	39.81	**38.06**	210.75	4.94	**72.98**	**44.41**	28.54
	SD	1.95	2.45	**1.66**	**1.70**	1.33	1.60	1.74	0.72	**0.03**	16.92	0.27	**2.16**	**2.11**	1.39
	Variance	3.79	5.98	**2.75**	**2.87**	1.78	2.55	3.03	0.52	**0.00**	286.25	0.07	**4.65**	**4.44**	1.93
	Range	4.9	6.7	**3.7**	**4.5**	3.2	4.0	4.3	1.3	**0.1**	36.0	0.6	**5.3**	**5.6**	3.8
Northern Plains	*N*	7	7	30	32	32	31	32	30	30	17	21	21	16	16
	Mean	71.61	42.21	**73.55**	**36.82**	35.09	30.55	27.44	40.27	**38.42**	206.29	4.81	**75.33**	**46.71**	29.50
	SD	2.72	1.21	**3.23**	**1.88**	2.34	1.06	1.05	1.39	**1.27**	4.12	0.87	**2.86**	**4.71**	1.92
	Variance	7.39	1.47	**10.44**	**3.54**	5.49	1.13	1.11	1.93	**1.62**	16.97	0.76	**8.18**	**22.16**	3.67
	Range	7.7	3.6	**12.1**	**7.6**	10.9	4.3	4.2	5.5	**5.1**	15.0	3.8	**9.9**	**18.4**	5.7
Southern Plains	*N*	0	0	23	22	22	23	23	19	21	11	23	21	12	12
	Mean			**74.51**	**37.66**	35.67	30.66	27.74	40.87	**38.95**	207.36	5.38	**77.25**	**47.90**	29.76
	SD			**3.70**	**1.57**	1.48	1.06	1.13	1.35	**1.31**	7.28	0.67	**2.52**	**2.41**	1.28
	Variance			**13.65**	**2.45**	2.18	1.13	1.28	1.83	**1.72**	53.05	0.45	**6.35**	**5.79**	1.65
	Range			**14.1**	**6.4**	6.8	5.0	4.7	5.1	**4.4**	22.0	2.6	**10.5**	**8.9**	3.5
(B) Adult females															
Eastern US	*N*	32	32	32	32	32	32	32	26	25	22	32	32	32	32
	Mean	61.12	34.84	**60.65**	**29.92**	**27.75**	**25.67**	23.39	34.59	33.24	196.32	4.90	**62.20**	**35.86**	24.34
	SD	3.76	3.17	**3.51**	**1.82**	**1.89**	**1.27**	1.29	1.86	1.84	7.21	0.78	**3.44**	**2.35**	1.53
	Variance	14.12	10.02	**12.29**	**3.33**	**3.56**	**1.62**	1.65	3.44	3.37	51.94	0.61	**11.84**	**5.53**	2.33
	Range	15.3	16.4	**15.8**	**7.5**	**9.9**	**4.8**	4.9	7.5	8.0	34.0	4.0	**15.4**	**10.0**	5.8
Northern Plains	*N*	9	9	22	21	21	23	22	22	21	11	16	15	11	11
	Mean	61.13	35.56	**62.66**	**31.39**	**30.10**	**26.97**	23.66	34.64	34.49	197.91	4.53	**64.20**	**36.81**	24.82
	SD	3.16	1.83	**2.95**	**1.28**	**1.12**	**1.20**	4.44	3.88	1.43	7.16	1.06	**2.74**	**1.85**	1.18
	Variance	9.96	3.35	**8.71**	**1.64**	**1.24**	**1.43**	19.68	15.09	2.04	51.29	1.12	**7.51**	**3.41**	1.39
	Range	11.1	5.5	**11.1**	**5.7**	**3.7**	**5.0**	21.8	14.3	6.7	26.0	4.5	**10.2**	**6.8**	4.0
Southern Plains	*N*	0	0	14	14	13	14	14	14	14	6	13	13	6	6
	Mean			**64.76**	**31.56**	**30.17**	**26.98**	24.27	35.86	34.34	199.67	5.20	**66.08**	**37.91**	27.31
	SD			**2.41**	**1.34**	**1.03**	**0.93**	0.85	1.24	1.18	5.16	0.66	**1.85**	**1.33**	4.07
	Variance			**5.83**	**1.79**	**1.07**	**0.87**	0.73	1.54	1.39	26.67	0.44	**3.43**	**1.77**	16.53
	Range			**9.1**	**5.1**	**3.4**	**3.7**	2.8	5.4	4.0	13.0	2.8	**6.2**	**3.7**	10.9

Measurements A through J follow Speth [71], see Fig. 4 for other measurements. Boldface type indicates measurements that are significant at the 0.05 level from the Big Bone Lick population (using ANOVA function of SPSS 12.0 for Windows, equal variances not assumed).

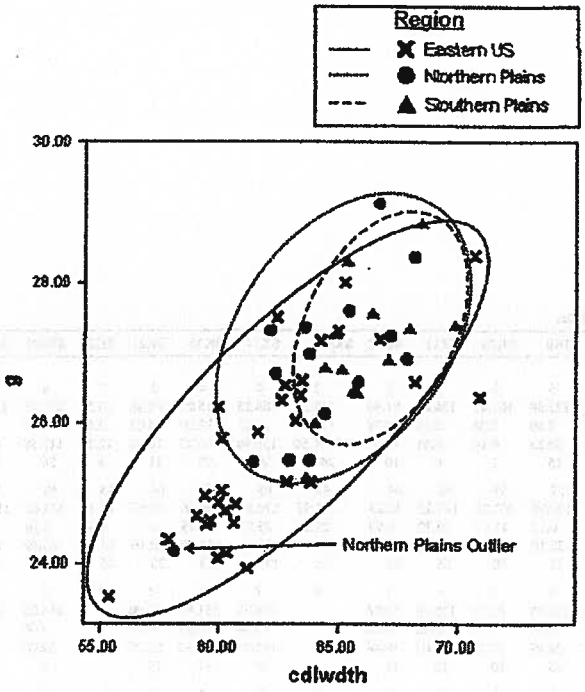

Fig. 12. Bivariate plot of late Holocene female bison metacarpals.

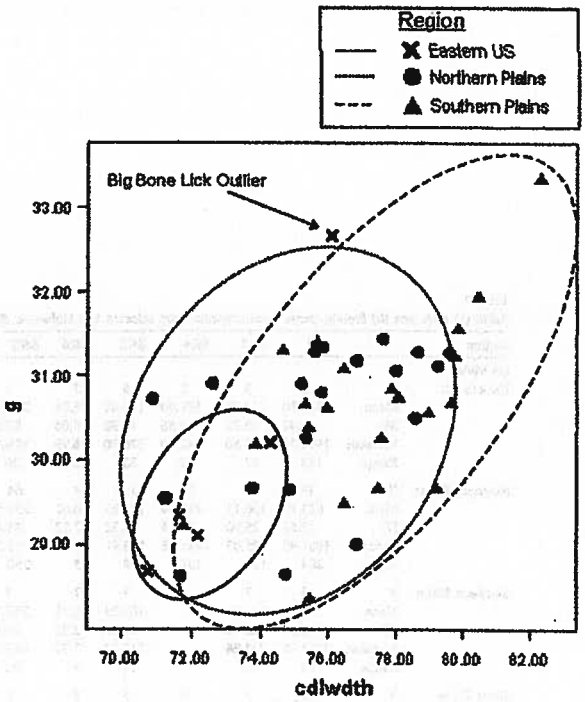

Fig. 13. Bivariate plot of late Holocene male bison metacarpals.

Male metacarpals also show breadth dimensions that are significantly smaller than Great Plains males (Table 6; Fig. 13). However, due to the small sample size of the BBL males ($N = 5$), it is more difficult to generalize about animal developmental patterns.

3.2.2. Crania

Extant scenarios of bison evolution are driven by morphological patterns in cranial shape and size (e.g., [25,49,69,84]). The same morphological plasticity that makes these elements ideal for diachronic studies of population-level evolutionary change also makes them well-suited to examining morphological variability in widely separated but relatively synchronic bison populations during the late Holocene.

BBL cranial measurements were compared to other peripheral populations (e.g., Malheur Lake, OR), as well as to a large baseline sample from the Great Plains (Table 7). In general, all crania showed similar values, indicating no obvious differences between the BBL population and other regional populations. BBL males show significant differences from the Northern Plains sample in maximum skull width (SK8); however, the Northern Plains mean for skull width is also significantly different from the Southern Plains mean. This difference may simply be a function of the small male sample size in the BBL and Southern Plains bison population data. Other measurements reflecting skull width (e.g., SK14, SK15) do not show significant differences between these populations. BBL females show significant differences in skull height (SK11) with female bison from the Southern Plains and Great Basin. However, as with the male sample, these significant differences are not duplicated in other measurements of the height dimension (e.g., SK10) and similarly may be the result of the small female sample size in the adult age group.

3.3. Niche structure of the BBL bison: dental and isotopic perspectives

The above morphometric studies suggest that the eastern *B. bison* sample at BBL differs from Great Plains populations primarily in developmental timing and diet. This latter difference was further explored through the examination of carbon and oxygen stable isotopes ($\delta^{13}C$, $\delta^{18}O$) in bison enamel carbonate and the progressive wear patterns of bison dentitions.

A comparison of cusp relief between the BBL and Great Plains bison samples is informative (Table 8, Fig. 14). The modern bison from western Kansas show smaller index values throughout the life of the M_2 than BBL animals of roughly the same age. These data show significant flattening of the occlusal wear surface in Plains bison by DAG 6. In contrast, BBL dentitions do not progress to flat occlusal surfaces. While there is some flattening of M_2s with age, these values never approach those of similar aged animals from the Great Plains. These differences suggest distinct dietary preferences in these bison populations. The Great Plains animals have a diet consisting of abrasive forage such as shortgrasses, combined with high levels of grit in their diets. Alternatively, the BBL animals exhibit wear that is much more like browsing animals such as deer or elk.

Table 7
Adult (a) male and (b) female crania measurements from selected late Holocene *B. bison* localities

Region		SK1	SK3	SK4	SK5	SK6	SK7	SK8	SK9	SK10	SK11	SK12	SK13	SK14	SK15	SK21	SK22	SKON	ANGBF	ANGOF
(a) Male[a]																				
Eastern US	*N*	5	5	2	5	5	5	5	5	3	3	5	2	4	4	5	2	4	3	3
	Mean	586.80	172.00	191.00	158.40	76.74	283.80	239.60	122.58	101.43	136.47	81.30	148.50	266.25	315.25	68.20	16.50	251.75	113.00	134.00
	SD	44.47	18.75	15.56	17.90	6.06	17.91	11.55	5.50	0.38	3.10	3.79	171.83	11.81	12.09	4.02	3.54	10.84	7.94	13.89
	Variance	1977.70	351.50	242.00	320.30	36.73	320.70	133.30	30.23	0.14	9.61	14.37	29524.50	139.58	146.25	16.20	12.50	117.58	63.00	193.00
	Range	113	47	22	33	15	39	26	15	1	6	10	243	26	28	11	5	26	15	25
Northern Plains	*N*	59	57	38	57	64	64	57	57	49	48	64	43	63	53	64	43	46	15	46
	Mean	623.19	196.12	232.84	179.35	80.61	251.53	255.37	125.88	107.22	147.13	82.83	261.95	270.52	326.66	68.67	14.12	243.63	111.67	136.54
	SD	43.61	25.00	35.24	23.32	7.82	35.40	12.97	6.17	17.37	16.30	6.99	25.59	23.03	11.75	4.71	4.94	8.16	4.79	23.81
	Variance	1901.95	625.07	1241.65	543.91	61.21	1253.30	168.31	38.10	301.84	265.60	48.88	655.05	530.48	138.00	22.16	24.44	66.59	22.95	566.74
	Range	204	115	158	124	35	250	52	31	58	55	29	115	179	53	23	25	35	15	126
Southern Plains	*N*	6	7	0	7	7	7	4	4	4	4	7	0	7	5	4	0	2	3	3
	Mean	583.00	178.71		164.29	76.71	256.71	237.00	126.25	98.25	138.00	82.86		278.71	331.60	67.00		244.00	104.33	142.33
	SD	34.80	27.08		22.63	2.75	10.83	1.41	6.24	5.50	6.00	4.30		13.84	16.65	4.69		5.66	2.89	7.51
	Variance	1211.20	733.24		512.24	7.57	117.24	2.00	38.92	30.25	36.00	18.48		191.57	277.30	22.00		32.00	8.33	56.33
	Range	82	79		70	8	32	3	15	10	12	11		38	41	10		8	5	15
Great Basin	*N*	3	3	0	3	3	3	3	3	3	3	3	0	3	3	3	0	3	3	3
	Mean	619.67	206.00		189.33	84.67	271.33	247.33	126.67	101.00	139.67	87.67		267.00	317.67	64.00		240.33	109.00	135.67
	SD	32.04	23.58		21.46	6.81	22.85	2.08	3.21	6.00	6.81	6.11		9.85	19.63	2.00		7.37	2.00	3.51
	Variance	1026.33	556.00		460.33	46.33	522.33	4.33	10.33	36.00	46.33	37.33		97.00	385.33	4.00		54.33	4.00	12.33
	Range	62	46		39	13	41	4	6	12	13	12		19	34	4		14	4	7

Region		SK1	SK3	SK4	SK5	SK6	SK7	SK8	SK9	SK10	SK11	SK12	SK13	SK14	SK15	SK21	SK22	SKOP	SKON	ANGBF	ANGOF
(b) Female																					
Eastern US	*N*	7	8	4	8	8	8	6	7	6	6	8	4	4	0	7	4	0	0	6	5
	Mean	470.57	127.50	157.25	122.75	51.19	158.38	202.33	112.90	84.08	121.82	49.50	227.50	209.25		69.57	13.25			102.00	139.60
	SD	43.54	18.72	24.70	17.12	4.80	9.58	7.61	2.96	6.31	4.11	4.59	12.58	13.33		5.16	1.71			14.41	1.67
	Variance	1895.62	350.57	610.25	293.07	23.08	91.70	57.87	8.79	39.79	16.91	21.11	158.33	177.58		26.62	2.92			207.60	2.80
	Range	104.00	53.00	57.00	46.00	13.30	21.00	18.00	7.60	17.00	11.00	14.00	30.00	30.00		16.00	4.00			42.00	4.00
Northern Plains	*N*	10	10	3	10	10	10	11	11	11	11	10	4	10	9	6	4	6	9	7	11
	Mean	454.80	125.60	141.67	120.30	50.60	160.70	206.82	116.18	85.82	119.27	51.40	212.50	215.60	263.33	66.50	10.00	475.83	216.67	109.57	132.64
	SD	32.35	16.64	16.07	14.35	3.81	9.93	13.12	4.92	13.19	8.51	3.34	10.50	7.50	8.65	3.73	6.16	8.33	12.23	4.93	8.67
	Variance	1046.62	276.93	258.33	205.79	14.49	98.68	172.16	24.16	173.96	72.42	11.16	110.33	56.27	74.75	13.90	38.00	69.37	149.50	24.29	75.25
	Range	94.00	62.00	30.00	53.00	11.00	30.00	39.00	14.00	50.00	32.00	9.00	22.00	22.00	30.00	9.00	14.00	19.00	37.00	15.00	27.00
Southern Plains	*N*	4	5	5	5	6	6	5	5	4	4	6	4	4	3	4	3	3	3	0	0
	Mean	425.75	120.60	144.40	114.40	52.67	159.83	202.00	111.60	72.75	110.50	52.33	172.00	216.50	262.67	65.75	14.00	469.33	201.33		
	SD	52.65	29.77	42.65	26.78	5.43	15.38	4.12	10.33	3.20	1.73	4.46	12.03	9.00	18.56	6.24	6.56	6.11	1.15		
	Variance	2771.58	886.30	1819.30	717.30	29.47	236.57	17.00	106.80	10.25	3.00	19.87	144.67	81.00	344.33	38.92	43.00	37.33	1.33		
	Range	112.00	72.00	109.00	63.00	14.00	41.00	10.00	26.00	7.00	3.00	12.00	29.00	20.00	37.00	14.00	13.00	12.00	2.00		
Great Basin	*N*	9	9	0	9	9	9	9	9	9	9	9	0	9	9	6	0	9	9	9	9
	Mean	463.00	140.78		131.44	51.67	162.22	202.00	116.11	87.56	123.56	51.78		216.00	271.11	65.17		493.44	216.56	110.78	132.44
	SD	34.91	18.63		15.52	4.00	11.71	9.07	6.03	6.39	5.15	4.02		8.89	9.20	3.71		13.68	4.82	5.21	5.32
	Variance	1219.00	346.94		240.78	16.00	137.19	82.25	36.36	40.78	26.53	16.19		79.00	84.61	13.77		187.03	23.28	27.19	28.28
	Range	104.00	57.00		50.00	11.00	38.00	32.00	18.00	20.00	17.00	15.00		30.00	31.00	10.00		38.00	15.00	16.00	18.00

See Fig. 4 for the location of measurements. Boldface indicates measurements that are significant at the 0.05 level from the Big Bone Lick population (using ANOVA function of SPSS 12.0 for Windows, equal variances not assumed).

[a] All measurements from Skinner and Kaisen [69] or McDonald [49].

Table 8
Selected measurements on bison M_2s

Locality	DAG	MNE	Mean metaconid height (SD)	Mean entoconid height (SD)	Mean saddle height (SD)	Mean index of cusp relief (SD)
Big Bone Lick	4	1	25	24.5 (4.5)	16.05 (1.6)	1.68
	5 (A)	2	28	27.0 (1.4)	15.33 (0.6)	1.81 (0.08)
	6 (B)	3	27 (3.1)	27.0 (4.2)	17.33 (1.5)	1.58 (0.17)
	7 (C)	3	28 (2.6)	28	16 (3.6)	1.78 (0.27)
	8 (D)	1	30	29	22	1.36
	9 (E)	3	24 (2.08)	24.33 (2.5)	17.33 (1.5)	1.42 (0.22)
	10 (F)	1	25	26	19.5 (2.12)	1.39
KU-ARCC	3	4	27 (2.31)	22.66 (4.6)	19.5 (2.38)	1.39 (0.06)
	5	2	27 (2.83)	25.5 (2.12)	22.0 (4.24)	1.24 (0.11)
	6	3	29 (3.51)	28.0 (2.65)	24.67 (2.08)	1.16 (0.06)
	7	1	33	29	26	1.27
	8	1	31		26	1.19

All measurements taken from the alveolar surface. For the purposes of visualization, BBL age groups A through F are recoded as age groups 5 through 10.

Stable isotope analyses provide another line of evidence in examining bison paleodietary preferences. Two lower M_3s from BBL DAG 4 and DAG A were sampled longitudinally along the metaconid at 7–10 mm intervals. The results are presented in Figs. 15 and 16, and Table 9. When compared to published $\delta^{13}C$ values for bison teeth (e.g., [21]: 82–83; [26,44]), it is clear that the BBL animals had a diet higher in C3 plants than their Great Plains counterparts (the range of $\delta^{13}C$ values on bison enamel carbonate from modern bison in Wyoming is −11.5‰ to −9.5‰; [21]). Additionally, tooth 4210-65 shows ~3‰ oscillation in the $\delta^{18}O$ values that may be indicative of seasonal changes in temperature, particularly between ~26 mm, which is the lowest $\delta^{18}O$ value, and ~47 mm which is the highest. Tooth 4320-65 shows less pronounced changes in $\delta^{18}O$ (~1.2‰), although we also see a jump in values at roughly 40 mm. Tooth 4210-65 changes rather abruptly between a more C4 and more C3 diet. In contrast, tooth 4320-65 shows gradually increasing $\delta^{13}C$ values throughout the length of the metaconid. The less significant change throughout the formation of the molar suggests that this animal grazed pastures with more C3 plants during the formation of the tooth as compared to 4210-65.

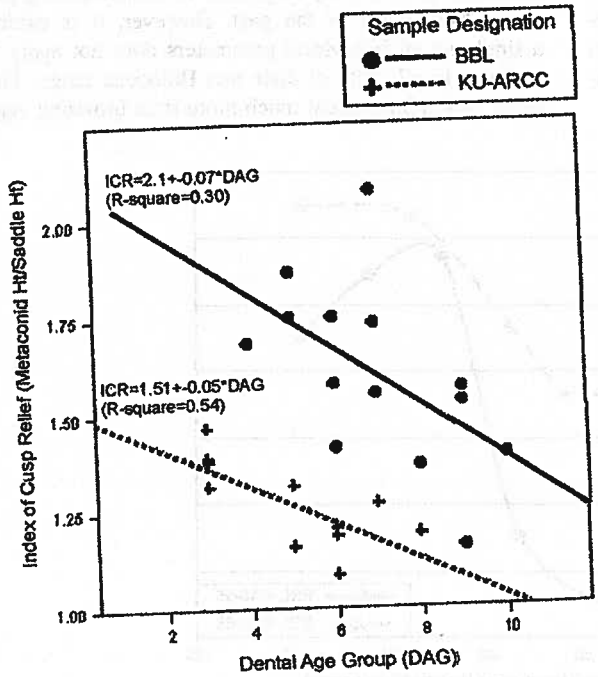

Fig. 14. Comparison of cusp relief in the BBL and Modern bison samples.

While this small pilot project is limited by sample size, the results of these isotopic analyses indicate paleodietary differences between Great Plains populations and eastern bison. They also suggest that differences between age groups within bison herds may be more nuanced than previously thought. $\delta^{13}C$ analyses and trends in dental wear support the inference of a browsing diet for the BBL bison; however, there were even substantial differences in isotopic trends between the BBL individuals themselves. It has been suggested that Great Plains bison herds exhibited significant herd cohesiveness both historically and prehistorically (e.g., [20,58]; but see [50,78] for alternative views) and that this behavior would translate into a relatively tight range of isotopic values on bone for individual herds [82]. These BBL data however, indicate that the averaging effects of bone remodeling and remineralization may mask significant annual differences in landscape use and grazing/browsing behavior.

4. Summary and conclusions

The large sample of *B. bison* at BBL has provided a benchmark for understanding the ecological parameters of eastern bison during the late Holocene. Analyses of dentitions indicate that the late Holocene component of BBL is a biologically cohesive population, consistent with the interpretation that the bison present in this sample were part of a single herd. Furthermore, emption patterns indicate a winter or spring (y + 0.5 to y + 0.9) seasonality event, although an unusual succession of molar wear diminishes the precision of this estimate.

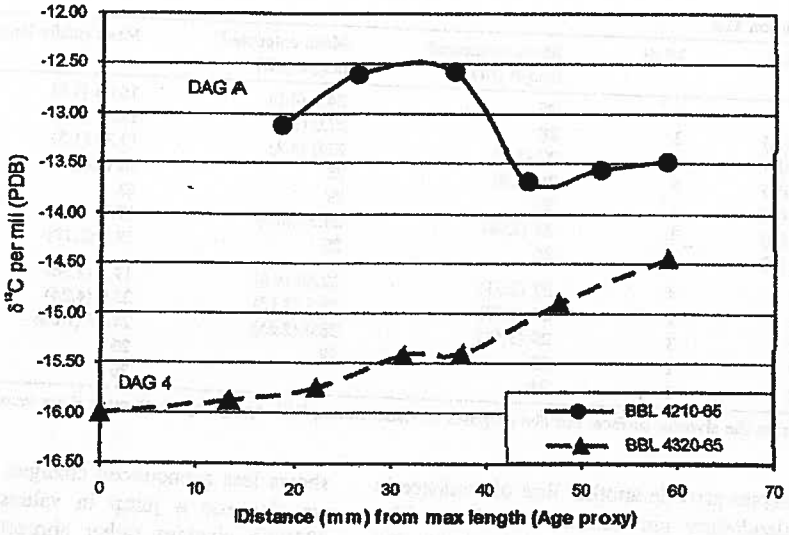

Fig. 15. $\delta^{13}C$ values of down-tooth samples of BBL lower M_3s.

While the relatively unique wear succession in BBL lower molars precludes the identification of older age groups and, thus, a precise estimate of the demographic characteristics of the BBL bison, the examination of sexually dimorphic post-cranial elements such as calcanei and metacarpals indicates a sex ratio of roughly 1 male to 3 females. The BBL assemblage is dominated by adult females and calves, with the occasional young bull, and is consistent with a cow/calf herd.

Morphologically, the BBL bison are very similar to their Great Plains counterparts. Comparative analyses of the BBL metacarpals and crania suggest that overall BBL males and females are slightly smaller than Great Plains animals. BBL females also show differences in developmental timing, with metacarpals continuing to increase breadth after the distal condyles fuse.

Finally, molar cusp relief and isotopic analyses of enamel carbonate suggest dietary differences between eastern and western bison populations. Woody browse made up a significant part of the BBL bison diet. These animals were not simply occupying a "grassland" niche along river valleys and in abandoned fields, they successfully utilized forested areas and did not exhibit predictable inter-annual movement patterns that would have made them susceptible to intercept hunting techniques.

Reconstructing general paleoecological trends in prehistoric taxa is extremely important to understanding predator/prey relationships in the past. However, it is evident that a single set of behavioral parameters does not apply equally to bison in all parts of their late Holocene range. The BBL bison would have spent much more time browsing vegetation

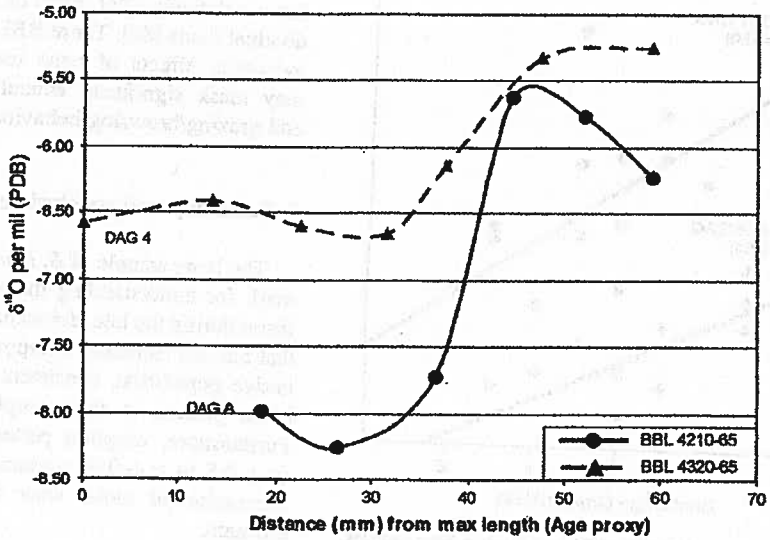

Fig. 16. $\delta^{18}O$ values of down-tooth samples of BBL lower M_3s.

Table 9
Isotopic values for BBL M_3s

Catalog No.	Sample ID	mm above CEJ	mm from Max length	$\delta^{13}C$	$\delta^{18}O$
BBL 4320-65	2LI	1	59	−14.45	−5.26
(DAG 4)	4LI	12.5	47.5	−14.89	−5.32
	5LI	22.5	37.5	−15.40	−6.14
	6LI	28.5	31.5	−15.41	−6.65
	7LI	37.5	22.5	−15.74	−6.60
	9LI	46.5	13.5	−15.88	−6.41
	11LI	60	0	−16.00	−6.58
BBL 4210-65	8LI	1	59	−13.48	−6.23
(DAG A)	7LI	8	52	−13.57	−5.77
	6LI	15.5	44.5	−13.68	−5.62
	5LI	23.5	36.5	−12.58	−7.73
	4LI	33.5	26.5	−12.61	−8.25
	3LI	41.5	18.5	−13.11	−7.98

Since we are interested in comparing seasonal events measured from the inception of tooth, the distance from CEJ must be converted into a measure of age, *in this case, the distance from the maximum length* (i.e., oldest part of the tooth). This value is calculated by subtracting "mm above CEJ" from the length of an unworn metaconid (i.e., 60 mm above the CEJ). $\delta^{13}C$ and $\delta^{18}O$ are expressed in per mil PDB.

in forested areas with concomitant effects on herd size, social structure and nutrition ([49]: 196–203). This study has highlighted some areas where eastern bison differ from Great Plains populations; however, future work must focus on how these animals were utilized within regional subsistence systems.

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"They Went as High as They Choose:" What an Isolated Skull Can Tell Us about the Biogeography of High-altitude Bison

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Abstract

In 2003 a partial bison skull was recovered by Ashley National Forest archaeologists from an elevation of 3840 m (12,600 ft) above mean sea level on Gilbert Peak in the Uinta Mountains of Utah. The skull consists of a portion of the frontal, occipital region, and horn cores including horn sheaths. Through the analysis of the individual cones of the horn sheath, a record of the animal's dietary and migration patterns were obtained. While high-altitude bison remains have been discussed in the scientific literature periodically, they have not gone beyond the descriptive. In addition to descriptive and metric analysis of the skull, radiometric assay and stable isotope analyses were applied. The radiocarbon age of the specimen is 150 ± 40 yr BP (cal. A.D. 1725–1778). Metric analysis of the skull indicates it was an older adult male, which compares well with *Bison bison athabascae* (wood bison) in size and is larger than either *Bison bison bison* (plains bison) specimens or other high-altitude bison. However, it is probable this individual represents a member of the species *Bison bison bison*, but phenotypic characteristics (e.g., large horn size) may be the result of gene flow. More definitive taxonomic placement of the Gilbert Peak bison may not be resolved without genetic analysis.

Introduction

I doubt the bison had much respect for altitude, and I believe they went as high as they choose (Warren, 1927: p. 61).

Documenting the range of mammalian species was an important focus for biologists working in the late 19th and early 20th centuries, especially with respect to shrinking habitat from expanding settlement in the Intermountain West of the United States. This was particularly true of the North American bison (*Bison bison* Linnaeus 1758); it had been reduced to a few hundred individuals at the beginning of the 20th century, and its long-term preservation was uncertain (Shell, 2002: p. viii).

Altitudinal range, as well as latitudinal and longitudinal, were often reported in scientific journals. Fryxell (1926) reported on bison specimens in the Medicine Bow Mountains of Wyoming at altitudes ranging from 2895 to 3658 m (9500 to 12,000 ft), followed by a report on high-altitude bison records from Colorado, Wyoming, and Montana (Fryxell, 1928). High-altitude bison sightings in southern and northern Colorado are also reported by Cook (1930), Warren (1927), and Beidleman (1955). More recently, Wilson (1974a) reported on bison remains from above timberline in the Bighorn Mountains of northern Wyoming. With climate-driven ice/snowfield melting in high-altitude and high-latitude regions, a new source of bison remains has been uncovered (Lee et al., 2006).

Unfortunately, few high-altitude records of bison have been reported in Utah. Madsen (2000) reports that 30 genera of late Quaternary fauna have been found in alpine settings. However, only two high-altitude sites, Mastodon Sinkhole (3232 m [10,604 ft]) in Sanpete County (Gillette and Madsen, 1993, citing W. Miller, personal communication) and Huntington Canyon (2981 m [9780 ft]) near the crest of the Wasatch Plateau (Gillette and Madsen, 1993; Madsen, 2000), produced bison. The paucity of high-altitude bison remains from Utah is therefore noteworthy. While the Gilbert Peak bison represents a single individual, it does contribute significantly to our knowledge of high-elevation fauna.

This study takes its cue from Fryxell (1928: p. 139), a statement which may be more imperative today:

> *It is now out of the question to turn bison loose on the plains. The only portions, if any, of the former range of the bison that could now possibly be restocked are certain uninhabited tracts in or adjacent to the mountains—within the national forests and national parks. Hence, obviously, the importance of preserving such scraps of information as can be obtained at this late period concerning the former range and life habits of the bison in our western mountains.*

Therefore, it is the purpose of this study to provide some of these *scraps of information* using contemporary research techniques (e.g., Cannon, 1997; Cannon, 2001). These include radiometric dating, metric analysis of the specimen and its relationship to other intermountain and high-altitude specimens, and stable isotope analyses. Stable carbon and nitrogen isotope analyses have the potential to yield information on the diet and ecology of an individual. As Walker (1992) explained, there are still temporal and spatial gaps in the Holocene record of bison, and isolated skulls can help fill them. Isolated bison skulls can provide specific information for understanding the paleoecology and evolution of the species. Information derived from detailed study of isolated bison skulls can have implications for a number of social and ecological issues (Van Vuren, 1987: p. 65), such as the management and restoration of ecosystems (Lyman, 1996; Lyman and Cannon, 2004), zoogeography (Lyman and Livingstone, 1983), and ethnography (Bamforth, 1988; Reeves and Peacock, 2001).

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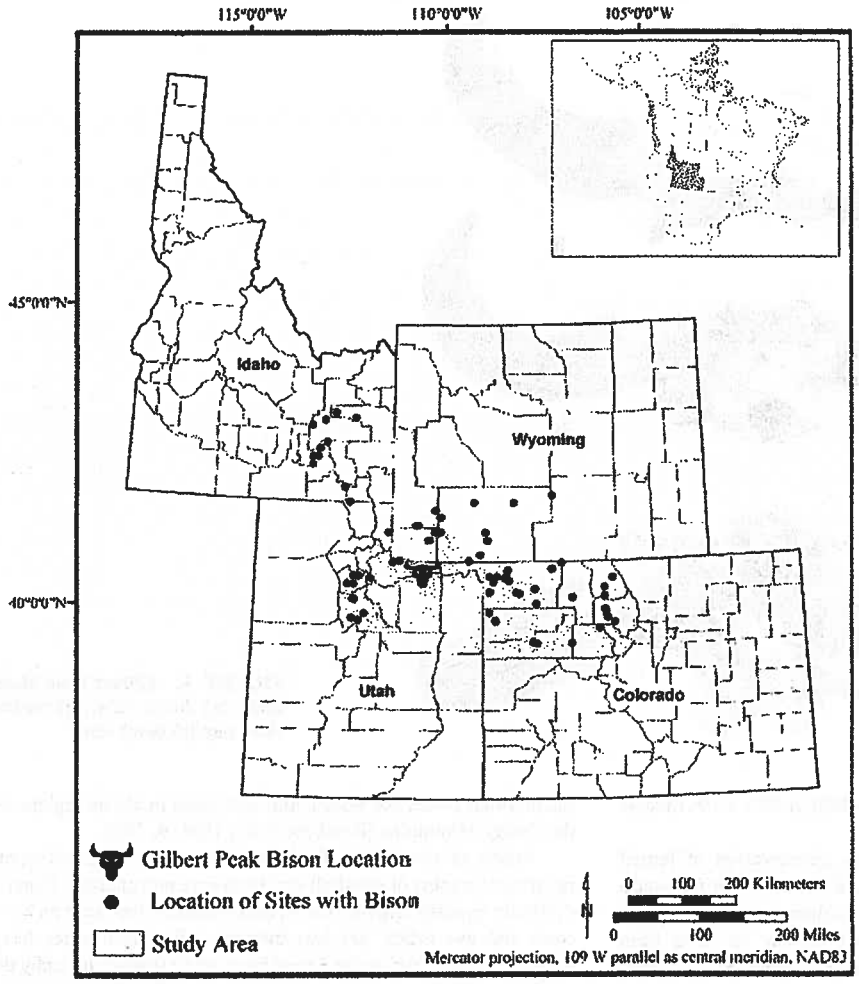

FIGURE 1. Regional map illustrating location of precontact sites with bison remains in relation to Gilbert Peak bison find location.

While this study focuses on the results of various analyses conducted on the Gilbert Peak bison, the context of the study is regional in scope. This study, along with an earlier one (Cannon, 1997), provide the initiation of a larger research goal to understand the biogeography of bison in the Intermountain West within the context of long-term climate change (Cannon, 2001; Lyman, 2004).

Environmental Context

U.S. Forest Service archaeologists recovered the Gilbert Peak bison skull from a steep gravel- and boulder-covered ridge southwest of Gilbert Peak at an elevation of 3840 m (12,600 ft) above mean sea level (AMSL) in Summit County along the boundary between the Ashley and Wasatch National Forests (Fig. 1). The area consists of alpine vegetation with surface cobbles common. Soils are shallow and well-drained. Tundra vegetation is present in the immediate area. As defined by Edwards et al. (1995), common species include perennial herbs (*Geum rossi, Silen acaulis, Paronychia pulvinata, Arenaria obtusiloba, Trifolium nanum, Kobresia myouroides, Polygonum bistoroides, Eriophorum chamissonis*), perennial grasses (*Deschampsia caespotosa, Festuca ovina, Koeleria cristata, Trisetum spicatum*), sedges (*Carex* sp.), and willow (*Salix* sp.).

To the east, the landscape slopes dramatically into a boggy area with an unnamed lake that is drained by Gilbert Creek, near the headwaters of the Uinta River. Engelmann spruce (*Picea engelmannii*) are present along the edge of the boggy area. The wet meadow vegetation consists mostly of grasses, forbs, sedges, and rushes.

Regional Evidence of Bison

The record of bison remains from late Quaternary sites in the region is extensive, and almost exclusively the result of human predation (Cannon, 2004; Fig. 2). The distribution in northern Utah (Lupo and Schmitt, 1997), southeastern Idaho (Butler, 1978; Cannon, 1997; Plew and Sundell, 2000), and southwestern Wyoming (Lubinski, 2000) indicates bison were present throughout the Holocene with population density possibly fluctuating in relation to climate patterns. However, several authors have argued that the sagebrush-steppe never supported large herds of bison (Mack and Thompson, 1982; Daubenmire, 1985), therefore making for an inconsistent resource (Henrikson, 2003, 2004).

Lubinski's (2000) research in southwestern Wyoming focused on the dietary selection of antelope and bison within the context of shifting climatic regimes (Eckerle and Hobey, 1995). His results indicate that archeological bison were more prevalent during

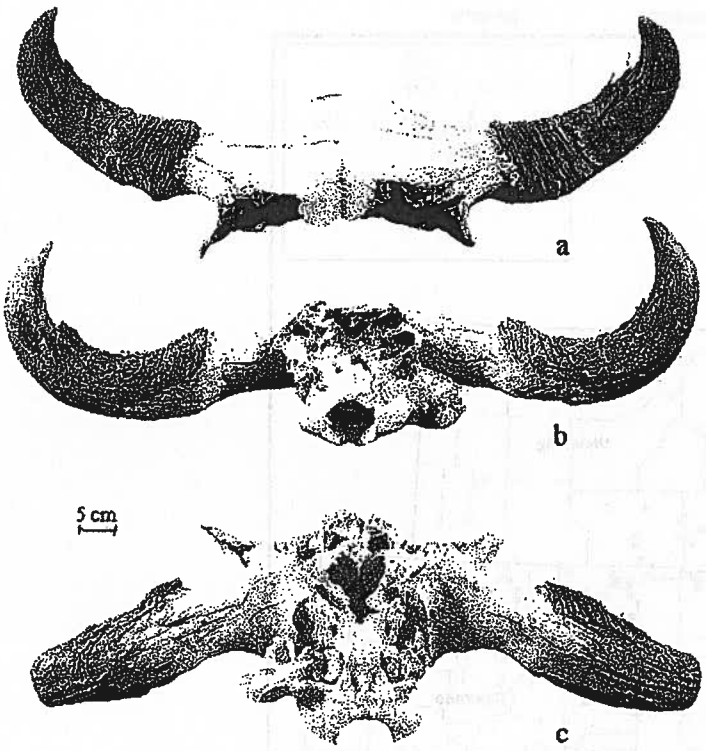

FIGURE 2: Gilbert Peak bison skull: (a) dorsal view, (b) nuchal view, and (c) basal view.

moist periods of the Holocene (10,000–9000 yr BP; 3500–1800 yr BP; 500–150 yr BP).

In the southern Rocky Mountains, preservation of faunal remains may influence interpretations. While bison in Colorado were probably most common in the eastern grasslands, high-elevation parks represented areas that appear to have been attractive to bison (Kornfeld and Frison, 2000; Stiger, 2001; Pitblado, 2003).

High-altitude bison remains in Utah are rare, as are high-altitude local faunas in general (Gillette and Madsen, 1993). Madsen (2000) has suggested a seasonal use of high-altitude valleys in the Wasatch Plateau during post-glacial times by mammoth (*Mammuthus* sp.), mastodon (*Mammut* sp.), horse (*Equus* sp.), camel (*Camelops* sp.), and bison (*Bison* sp.). These patterns are similar to modern migrations of ungulates through multiple floristic zones, for example the seasonal migration of bison in the Henry Mountains of southeastern Utah (e.g., Van Vuren, 1982) and Yellowstone National Park (Meagher, 1973).

Regional evidence indicates bison have been a consistent member of the Holocene mammalian community, although climate may have influenced herd numbers and the availability of bison as a human prey item.

Description and Examination of the Skull

DESCRIPTION

The Gilbert Peak bison skull is represented by the proximal portion of the cranium including the horn cores with preserved horn sheaths. A portion of the frontal bone is also preserved, while the occipital region is eroded with only the occipital condyles and the area around the foramen magnum present (Fig. 2). Colonies of the lichen *Xanthoria elegens* are present on the horn sheaths and in the interior of the skull. This species of lichen is common on calcium-rich rocks, old bones, and old wood in alpine regions of the Rocky Mountains (Kershaw et al., 1998: p. 344).

Sexing of the Gilbert Peak bison was initially based upon relative robustness of the skull and horn core morphology. Female skulls are typically smaller in size, and some features, such as horn cores and eye orbits, are less massive. Male horn cores have a distinct burr or rim at the dorsal base, while females typically do not have a distinct burr, and the horn core often blends with the neck and frontals (McDonald, 1981a: p. 44). The Gilbert Peak skull has distinct burrs at the base of the horn cores, suggesting it is a bull.

A less subjective means of assessing gender is the metric comparison of the Gilbert Peak skull with other skulls of known gender. All available skull measurements follow those defined by McDonald (1981a: pp. 43–47) as modified from Skinner and Kaisen (1947) and are presented in Table 1. Utilizing McDonald's (1981b) data for other western United States bison, the dorso-ventral diameter of the horn core was plotted against spread of the horn cores. The plot indicates that the Gilbert Peak bison skull is a large male (Fig. 3; Table 2).

Assessing age at death of archaeological bison is typically conducted through wear patterns of mandible teeth (e.g., Frison and Reher, 1970). Unfortunately, the teeth are not preserved in this specimen. McHugh (1958) and Fuller (1959) suggested that the size and shape of the horn can be used to determine age. While this can be used as a relative means for assessing age in populations, it is not of particular value for individuals. Counting the number of growth rings on the horn sheath was also suggested by McHugh (1958) as a means of estimating age. However, Reynolds et al. (1982) disregarded the counting of rings as a reliable estimate of age.

Suture closure is another means of assessing relative age (McDonald, 1981a). For the Gilbert Peak skull, the sagittal frontal suture is almost completely fused (Fig. 2a), suggesting an adult.

TABLE 1

Skull measurements following McDonald (1981a). All measurements are presented in millimeters except for those marked in degrees. Data on *Bison antiquus occidentalis* are from McDonald (1981a:Table 25), *Bison bison athabascae* from McDonald (1981a: Table 34), *Bison bison bison* from McDonald (1981a: Table 29), and high altitude bison from McDonald (1981b: 550–553) and Wilson (1974: Table III). All specimens used in analysis are males.

Measurement	Gilbert Peak	*Bison antiquus occidentalis*				*Bison bison athabascae*				*Bison bison bison*				High-altitude bison			
		N	Mean	Range	σ	*N*	Mean	Range	σ	*N*	Mean	Range	σ	*N*	Mean	Range	σ
Spread of horn core, tip to tip (SHTT)	657	77	779.3	626–1055	76.9	9	681.2	542–848	92.0	128	603.9	510–778	44.7	17	602.4	508–719	55.7
Horn core length, tip to burr (CLUC)	295	86	277.8	186–392	39.1	9	1235.1	165–323	43.9	134	190.7	124–270	24.7	19	185.5	140–225	23.7
Straight line distance, tip to burr, dorsal horn core (TB)	210	81	248.1	175–350	31.8	9	207.0	154–277	34.4	132	172.4	120–243	21.4	19	171.8	127–216	22.7
Dorsoventral diameter, horn core base (VD)	105	85	94.6	70–114	8.4	9	91.5	81–106	8.7	139	81.9	69–99	6.4	23	84.2	69–99	8.6
Minimum circumference, horn core base (CHC)	266	89	300.3	237–355	27.7	9	289.1	254–322	22.9	142	255.4	199–324	19.5	22	260.8	228–305	21.5
Width of occipital at auditory openings (GWA)	281.2	61	262.0	238–294	13.2	10	273.6	243–298	15.3	120	243.9	220–270	9.7	17	249.3	228–276	12.6
Width of occipital condyles (CW)	110	71	135.0	111–151	7.7	11	130.1	118–139	6.4	122	126.6	111–140	5.7	18	123.1	106–138	8.7
Depth, nuchal line to dorsal margin of foramen magnum (DEP)	—	57	104.0	89–120	7.0	10	99.6	92–114	6.6	112	98.7	81–115	6.2	—	—	—	—
Antero-posterior diameter, horn core base (TD)	90.8	91	98.8	77–120	10.1	9	97.2	83–109	9.5	142	83.4	67–103	6.3	25	84.9	74–97	7.2
Least width of frontals, between horn cores and orbits (WHCO)	280	74	296.6	261–348	16.8	10	293.4	273–313	10.5	135	271.1	237–318	12.6	22	271.1	248–294	11.9
Greatest width of frontals at orbits (GPW)	—	64	348.0	311–394	16.7	10	354.0	326–384	14.8	117	324.6	289–356	12.9	19	232.1	280–356	18.1
M1–M3, inclusive of alveolar length	—	3	97.3	90–102	6.4	1	91.7	—	—	22	90.6	81.8–97.9	4.4	—	—	—	—
M3, maximum width, anterior cusp	—	2	28.4	27.8	29.1	1	27.9	—	—	22	27.7	22.3–31.4	1.6	—	—	—	—
Distance, nuchal line to tip of premaxillae (OP)	—	25	564.3	511–606	24.8	7	578.6	562–604	15.2	56	535.2	500–583	17.0	—	—	—	—
Distance, nuchal lint to nasal-frontal suture (ON)	—	57	259.8	233–287	12.3	9	256.0	240–276	13.4	106	245.7	214–279	12.2	14	241.6	206–279	22.4
Angle of divergence of horn cores, forward from sagittal (AHC)	70°	62	72.1°	63–83°	5.2°	6	71.0°	63–77°	5.0°	124	67.7°	58–79°	4.4°	—	—	—	—
Angle between foramen magnum and occipital planes (OF)	—	57	129.6°	110–142°	7.3°	9	129.4°	119–144°	8.8°	115	133.8°	118–159°	7.6°	—	—	—	—
Angle between foramen magnum and basioccipital planes (BF)	—	56	113.4°	98–126°	5.6°	9	113.8°	106–125°	6.6°	115	110.5°	100–129°	5.0°	—	—	—	—

Wilson (1975: Figs. 7 and 8) presented a preliminary study of age based upon allometric growth. Plotting two skull measurements against known ages, he illustrated logarithmic curves for estimating age. Walker (1992) applied this technique in his study of an isolated bison skull from the Seminoe Reservoir, Carbon County, Wyoming. For the Gilbert Peak bison skull, only one skull measurement was available for study: least width of frontals. Superimposing the Gilbert Peak measurement onto Walker's graph (1992: Fig. 7 lower), an estimated age at death for the Gilbert Peak bison is 12 years (Fig. 4).

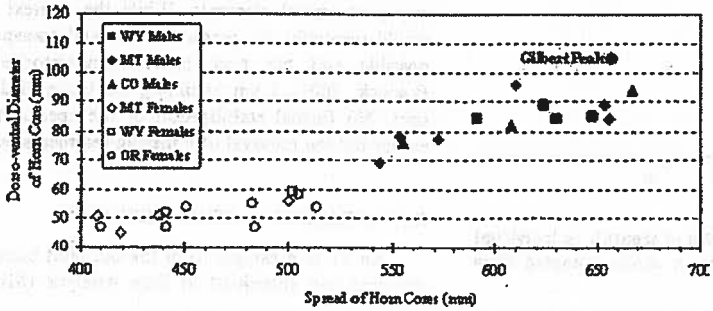

FIGURE 3. Plot of Gilbert Peak bison skull in relation to male bison skulls from western United States specimens. Data presented in Table 2. WY = Wyoming, MT = Montana, CO = Colorado, and OR = Oregon.

TABLE 2

Craniometric data for high altitude and western bison used in comparative study. Measurement abbreviations are presented in Table 1. All measurements are presented in millimeters except for those marked in degrees. AMNH = American Museum of Natural History, CoMNH = Colorado Museum of Natural History, UCy = University of Calgary, UCM = University of Colorado Museum, UM = University of Montana, USGS = U.S. Geological Survey, USNM = University of Nebraska State Museum, UWy = University of Wyoming, BH = Bighorn Mountains, Wyoming, specimen, FC = Fawn Creek, Idaho, specimen.

Specimen	Sex	SHTT	CLUC	TB	VD	CHC	TD	WHCO	GPW	ON	OP	GWA	CW	DEP	AHC (°)	BF (°)	OF (°)
AMNH M1399937	M	630	192	178	84	269	88	279	331	239	530	253	134	94	62	112	145
CoMNH 1846	M	667	205	193	94	287	97	281	330	248	—	235	138	106	63	110	140
UCy A(K)	M	645	185	174	77	240	76	—	—	—	—	—	—	—	68	—	—
UCy A(L)	M	—	—	—	83	258	81	—	—	—	—	—	—	—	—	—	—
UCM G:S29G	M	608	180	172	82	258	82	265	—	222	—	243	120	88	72	109	133
UCM G:S66	M	555	179	169	76	244	82	254	—	—	—	—	—	—	—	104	143
UCM G:4278	M	—	—	—	—	—	79	258	314	—	—	249	111	—	—	102	135
UCM G(A)	M	—	221	209	99	297	97	286	327	262	—	—	—	—	71	—	—
UM Z5461	M	543	154	139	69	237	78	262	326	—	—	—	—	—	64	—	—
UM Z5462	M	589	166	148	—	—	—	—	—	—	—	—	125	98	79	—	—
UM Z13251	M	591	214	184	84	255	82	273	321	235	—	—	—	—	64	—	—
USGS (A)	M	667	200	183	92	288	94	287	343	279	—	251	120	109	62	112	135
USNM M168816	M	648	175	166	85	264	87	294	351	251	568	257	138	104	67	109	128
UWy (B)	M	—	—	—	77	232	74	260	—	—	—	245	124	90	71	107	153
UWy (C)	M	—	—	—	—	—	—	272	326	—	—	249	131	101	69	113	133
UWy (D)	M	624	198	187	89	257	81	262	313	—	—	233	114	97	64	110	136
BH-1	M	576	186	167	89	254	83	270	324	—	429	264	121	105	—	—	—
BH-2	M	—	—	—	—	286	86	272	330	—	466	250	106	92	—	—	—
BH-3	M	—	190	162	86	248	92	—	—	—	—	—	—	—	—	—	—
BH-4	M	541	143	140	71	235	76	266	298	210	—	228	121	102	—	—	—
BH-5	M	—	—	—	76	—	83	267	280	206	—	—	—	105	—	—	—
BH-6	M	—	—	—	92	273	94	292	356	267	445	276	124	102	—	—	—
BH-7	M	—	—	—	—	—	78	—	—	—	—	248	124	—	—	—	—
BH-8	M	508	140	127	70	228	79	248	296	218	397	234	114	89	—	—	—
BH-9	M	576	197	181	92	265	95	270	319	232	403	264	128	92	—	—	—
BH-10	M	719	225	216	98	305	95	276	324	248	438	260	128	121	—	—	—
FC-1	M	554	175	170	82.4	257	85.5	270	330	265	—	—	—	—	64	—	—
AMNH M16322	F	408	125	113	51	161	48	218	272	214	431	202	120	88	66	106	138
USNM M122672	F	500	122	122	56	165	51	218	264	216	484	197	114	83	70	114	115
USNM M122685	F	419	129	121	45	146	47	225	262	211	574	205	123	81	62	107	142
UWy C3071	F	502	129	128	59	191	61	227	272	199	—	205	113	76	70	101	144
UWy C30	F	—	—	—	53	168	54	224	272	203	479	206	115	84	68	118	118
USNM M248950	F	483	145	139	55	171	53	221	267	219	506	205	123	89	—	113	134
USNM M249844	F	438	123	117	51	157	51	213	268	216	491	199	112	78	—	107	131
USNM M249847	F	441	134	122	47	154	49	208	265	213	483	187	111	80	64	107	133
USNM M249848	F	484	135	129	47	153	51	224	276	221	494	202	115	95	69	109	131
USNM M249849	F	451	164	146	54	173	54	218	268	225	516	205	115	86	59	119	123
USNM M250089	F	514	134	134	54	163	51	214	272	216	479	206	115	89	69	110	141
USNM M250090	F	505	177	161	58	182	60	229	281	218	508	219	129	98	—	118	127
USNM M250091	F	441	135	124	52	163	52	218	287	210	486	203	114	88	65	103	135
USNM M250095	F	410	120	111	47	144	45	199	256	211	478	192	111	85	65	111	137

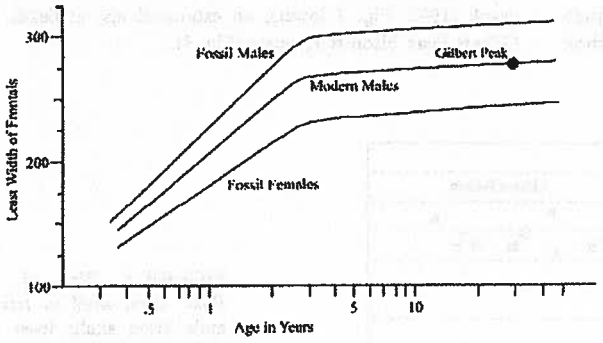

FIGURE 4. Semi-log plot of least width of frontals to individual age in late Pleistocene and modern bison skulls (adapted from Walker, 1992: Fig. 7).

PREPARATION

The bison skull was recovered from the surface on the southwest slope of Gilbert Peak. The skull had been known for several years in the Ashely National Forest prior to it being recovered. A cursory survey of the immediate area did not produce any post-cranial elements. While the context of the substrate would normally not preserve bone, and transport by humans is possible and has been noted ethnohistorically (Reeves and Peacock, 2001), I am assuming the bison died close to its find spot. No formal stabilization of the specimen was conducted, except for the removal of adhering sediments with a soft brush.

RADIOCARBON DATING RESULTS

An 11.79 g sample from the occipital bone of the skull was removed and submitted to Beta Analytic (Miami, Florida) for

TABLE 3

Results of stable isotope analysis of modern North American bison specimens. Alaska data from Bocherens et al. (1994: Table 4); Konza, Kansas; Niobrara, Nebraska; Wood Buffalo, Northwest Territories; and Yellowstone, Wyoming, data from Tieszen et al. (1996); Wind Cave, South Dakota, data from Tieszen (1994: Table 5); and Fawn Creek, Idaho, data from Cannon (1997: Table 6). $\delta^{13}C$ values presented for the pre-1800 specimens, Gilbert Peak and Fawn Creek are those measured and uncorrected. The values in parentheses are adjusted by 1.5‰ as suggested by Tieszen et al. (1996) when comparing Holocene samples prior to A.D. 1800 with modern samples.

Specimen	Collagen rank	Yield (%)	Nitrogen (%)	Carbon (%)	C/N	$\delta^{13}C$	$\delta^{15}N$	Apatite $\delta^{13}C$
Gilbert Peak	—	—	—	—	—	−18.8 (−20.3)	+7.3	—
Fawn Creek, ID	3	25.9	14.8	41.5	3.3	−19.6 (−21.1)	+6.5	−10.8
Alaska	—	—	—	—	—	−20.5	+4.4	—
Konza, KS	—	—	—	—	—	−13.8	+5.5	—
Niobrara, NE	—	—	—	—	—	−15.9	+2.9	—
Wind Cave, SD	—	6.5	—	—	3.22	−18.7±0.2	+6.4±0.23	—
Wood Buffalo, NWT	—	—	—	—	—	−23.9	+6.6	—
Yellowstone, WY	—	—	—	—	—	−23.4	+6.9	—

radiocarbon assay using the accelerator mass spectrometry (AMS) technique. The radiocarbon dating procedure proceeded normally, and the sample contained adequate carbon for dating. The $^{13}C/^{12}C$ ratio was measured at −18.8‰, which is within the expected range for ungulates. This measurement indicates that sufficient collagen was present for an accurate radiocarbon age. The $^{15}N/^{14}N$ ratio was also measured for this specimen, which produced a value of 7.3‰ (Hood, 2004a). Published $\delta^{15}N$ values for bison range from 2.9‰ to 6.9‰ (Cannon, 1997; Table 3; Fig. 5).

The radiocarbon age obtained is 150 ± 40 yr BP (Beta-192144). At the 2σ level (95%), the calibrated results range from cal. A.D. 1660 to 1950 with intercepts at cal A.D. 1680, 1740, 1810, 1930, and 1950 (Talma and Vogel, 1993; Stuiver et al., 1998; Table 4). Statistically, this bison likely died during the early to mid-18th century.

Bison Taxonomy

Since the 19th century, there has been controversy surrounding the species of bison occupying the Rocky Mountains. The earliest accounts are rife with descriptions of the exploits of the "Woodland or Mountain Bison" (e.g., Christman, 1971). Various historical accounts (e.g., Norris, 1880) of the "mountain" bison indicate they "were more hardy, fleet, and wary, and had darker finer, curlier hair" than the plains bison (Meagher, 1973: pp. 14–15).

In fact, considering the geographic range of bison in North America, some authors have suggested there may have been several distinct geographic forms. However, with the near extinction of the bison in North America, a comprehensive study of its geographic variation has been precluded (van Zyll de Jong,

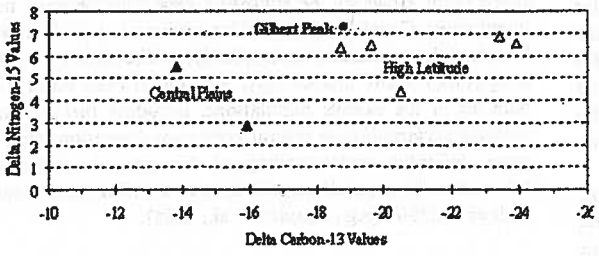

FIGURE 5. Plot of $\delta^{15}N$ against $\delta^{13}C$ values for modern North American bison specimens from high altitude, high latitude, and central Great Plains. Data from Bocherens et al. (1994), Tieszen (1994), Tieszen et al. (1996), and Cannon (1997).

1986: p. 1). In the latter part of the 19th century, biologists recognized a distinct form of bison in northern Canada, formally described as the subspecies *B. b. athabascae* by Rhoads (1897), based on a single specimen he did not directly observe (van Zyll de Jong, 1986: p. 1). While most biologists agreed with Rhoads's designation of *B. b. athabascae* being at least subspecifically distinct (e.g., Skinner and Kaisen, 1947; McDonald, 1981a), some felt that the differences in the two subspecies, *B. b. athabascae* and *B. b. bison*, were of little consequence (van Zyll de Jong, 1986: p. 1).

The decimation of the bison herds prior to firsthand study and the small number of specimens available for study contributed to the diversity of opinions (van Zyll de Jong, 1986). In one of the first quantitative studies of museum specimens—primarily crania—Skinner and Kaisen (1947) argued for an overlap in distribution of the two subspecies—*B. b. athabascae* and *B. b. bison*—along the eastern slopes of the Rocky Mountains. However, their argument was unconvincing due to the lack of cranial and postcranial specimens for comparison.

In response to Skinner and Kaisen, McDonald (1981a) presented metric data from a limited sample that shows evidence that the *B. b. athabascae* range was limited to the northern Rocky Mountains and the boreal forests of Canada. He suggested a phylogenesis of modern North American bison from an indigenous Nearctic line (*B. b. antiquus*), with *B. b. athabascae* evolving directly from the ancestral *B. b. antiquus*, or a more recent adaptive differentiation from *B. b. bison*, as suggested by the larger body size of *B. b. athabascae*. However, van Zyll de Jong (1986) suggested that body size is just one of a number of presumably genetic characteristics that differentiates the two modern species. According to his analyses, *B. b. athabascae* is more probably "a direct and little differentiated descendant of

TABLE 4

Results of calibration using CALIB 4.4.

Percent area enclosed	cal. A.D. age ranges	Relative area under probability distribution
68.3 (1σ)	1672–1695	0.150
	1725–1778	0.362
	1799–1813	0.097
	1839–1876	0.199
	1917–1949	0.192
95.4 (2σ)	1665–1784	0.480
	1790–1890	0.346
	1909–1950	0.174

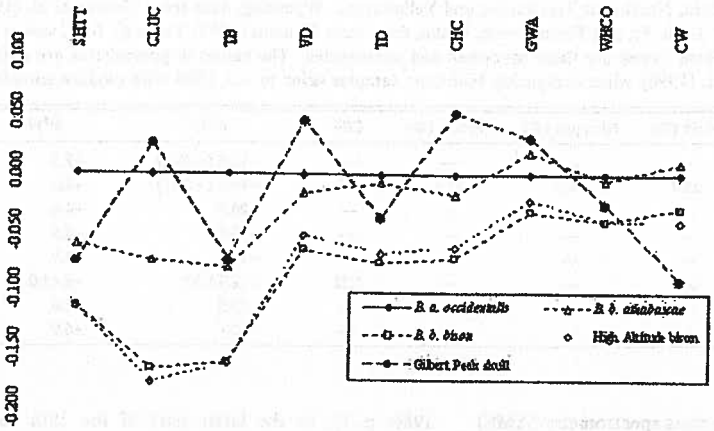

FIGURE 6. Ratio diagram comparing 10 skull dimensions of the Gilbert Peak specimen in comparison with *Bison bison bison*, *Bison bison athabascae*, and *Bison antiquus occidentalis*, with the latter serving as a standard. All measurements included in analysis are from male skulls. (*B. antiquus occidentalis* [*N* = 31] data from van Zyll de Jong, 1986: Table 1; *B. b. athabascae* and *B. b. bison* from McDonald, 1981a: Tables 29 and 34, respectively). McDonald's data used in analysis is only from males. Only those measurements that were available from the Gilbert Peak bison skull were used in this analysis. See Table 1 for measurement abbreviations.

[Beringian] *B. b. occidentalis*" (van Zyll de Jong, 1986: p. 54). His analysis found that *B. b. bison* shows a marked difference in horn core measurements, reflecting a general reduction in horn core size in comparison to *B. b. occidentalis*, whereas with *B. b. athabascae* there is only a reduction in horn core length (van Zyll de Jong, 1986: p. 18; Fig. 6).

The interaction of ecological and behavioral factors, gene flow, and natural selection can account for the maintenance of the distinctiveness of the two modern species according to van Zyll de Jong (1986: pp. 54–55). Specifically, the boreal forest ecotone acted as a natural barrier to contact with *B. b. bison* in the grasslands to the south minimizing interbreeding and potentially promoting "differential directional selection" of a specific allele frequency or phenotype that provided them with a greater degree of fitness for surviving in their respective environments.

In a genetic study, Wilson and Stroebeck (1999) surveyed 11 microsatellite loci of 11 bison populations in order to calculate the genetic variation and genetic distances of wood and plains bison; their expectation was that large genetic distance should exist between wood and plains bison. Stroebeck's (1992) results from an earlier study led him to conclude that the genetic isolation of bison populations produced the morphological variability apparent in these populations.

One result of their study was that all the sampled bison populations are genetically distinct from one another. According to the authors, this was not unexpected and was probably a result of the founder effect and genetic drift which resulted "from the small number of transfers between herds that have occurred, [which] are probably responsible for the uniqueness of these populations" (Wilson and Stroebeck, 1999: p. 493). Of particular interest to this study is that the genetic distance between the Yellowstone bison is not as large as expected if these bison were a distinct population (i.e., mountain bison). The authors indicated indigenous Yellowstone bison were "driven to the area by hunters" (Wilson and Stroebeck, 1999: p. 493) and, therefore, represent *mountain-dwelling plains bison* (emphasis mine).

Understanding the taxonomy of the Gilbert peak bison may not be adequately addressed without genetic analysis, but morphological differences in adult skulls has been commonly used to determine how individual animals, or populations, compare. In differentiating between *B. b. athabascae* and *B. b. bison*, McDonald (1981a) used horn core morphology as key characteristics both in size and shape.

Using a ratio diagram (Simpson, 1941) we can explore how the Gilbert Peak bison compares to other populations. The ratio diagram was applied by van Zyll de Jong (1986) in trying to establish an evolutionary history between modern bison species and the extinct *Bison antiquus occidentalis*. The ratio diagram is a univariate technique in which measurements can be compared to a standard. To replicate van Zyll de Jong's study (1986: Fig. 16), as well as that of Walker (1992: Fig. 6), *B. antiquus occidentalis* is used as the standard. The technique is a plot of the difference between the log of a measurement from a comparative specimen or the mean of a population (e.g., high-altitude bison) and the log of the measurement of a conspecific specimen. The comparative specimen is set to zero with dimensions with negative values indicating the characteristic is smaller with a positive value indicating a larger attribute (Lyman, 2004).

The results of this comparison are interesting and suggest the Gilbert Peak bison is larger in some dimensions and smaller in others than the standard (Fig. 6). Specifically, a comparison of select horn core measurements indicates that the Gilbert Peak bison skull is within the range of each of these groups (Fig. 7).

The Gilbert Peak skull horn core morphology is more similar to *B. bison athabascae*, being larger than either the high-altitude or the *B. bison bison* populations. The large size of the Gilbert Peak skull and its incompleteness may influence the results of the comparison. Another possibility is that genetic isolation of populations may be expressed in the phenotype (see Wilson and Stroebeck, 1999). Wilson (1974b) illustrated a similar situation from the 10,000-year-old Casper site in which phenotypic characteristics of two populations may have contributed to the single herd. However, he suggested gene flow between the two populations. Genetic isolation of intermountain populations in the West may be expressed phenotypically, as discussed by van Zyll de Jong (1986). More interestingly, the Gilbert Peak bison is larger than all of the sample populations, including the standard (*B. antiquus occidentalis*) in several horn core dimensions (Fig. 6). A more definitive understanding of the genetic relatedness of intermountain populations will have to wait for genetic analysis, such as mtDNA (e.g., Shapiro et al., 2004).

Results of Stable Isotope Analyses

One aspect of this research is addressing the ecology and seasonal movement of mammals that no longer occupy their

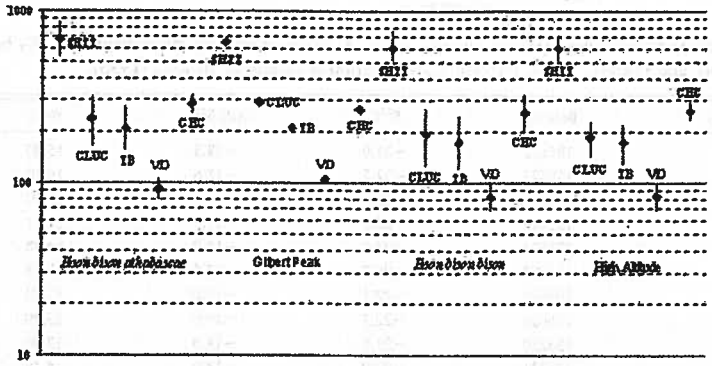

FIGURE 7. Comparison of select horn core measurements of Gilbert Peak bison skull with other taxonomic and regional groups to illustrate amount of overlap in range of measurements. See Table 1 for measurement abbreviations.

original range. This can provide us with information that may be useful in reestablishment of habitats and other conservation biology issues (e.g., Lyman and Cannon, 2004), but may also contribute to understanding past behavior of bison as a prey species for past human groups (e.g., Widga, 2004).

One way of approaching this predicament is by applying analyses of diet to the study of foraging patterns. If bison were moving through various ecosystems during seasonal migrations, and if these environments had different food resources, we should expect this to be evident in the bison's diet (Chisholm et al., 1986: p. 193; Table 3). Stable isotope analysis has been applied to modern ungulates (e.g., Tieszen et al., 1979; Vogel et al., 1978) as well as to fossil vertebrates (e.g., Bocherens et al., 1994; Heaton, 1995) in order to understand their dietary selection.

STABLE CARBON ISOTOPE ANALYSIS

The application of carbon isotope analysis to ecological studies became apparent with the publication of an article by Bender (1968), which described a systematic relationship between the photosynthetic pathways (C_3 and C_4) and the stable isotopic ratios of carbon in grasses (Tieszen, 1994). The dietary application of carbon isotope studies involves the quantification of ratios of $^{13}C/^{12}C$ isotopic abundance in bone collagen, which is linked through the food web to the primary producers—photosynthetic plants (Bocherens et al., 1994). In terrestrial environments, two main categories of plants are recognized based on their carbon-fixation pathways, which are clearly distinguished by their stable carbon isotope ratios. The C_3 plants represent about 90% of all plants and include all trees and herbaceous plants from cold and temperate climates. Their $\delta^{13}C$ values range between −23‰ and −32‰ with an average of about −26‰.

Warm weather and tropical herbaceous plants, such as blue grama (*Bouteloua gracilis*), big bluestem (*Andropogon gerardi*), and buffalo grass (*Buchloe dactylides*), are classified as C_4 and have a $\delta^{13}C$ value between −9 and −16‰ with an average around −13‰ (Smith and Brown, 1973; Bocherens et al., 1994). Patterns of C_4 diversity in North America indicate a strong positive relationship with growing season temperature. On the Great Plains, both relative and absolute C_4 grass abundances correlate with mean annual temperature (MAT) and mean annual precipitation (MAP). In contrast, C_3 grass abundance decreases with MAT and summer precipitation. Since C_3 plants do most of their growing in the spring and early summer, ideal conditions for productivity are cool temperatures with adequate winter precipitation. Warm summers accompanied by summer precipitation favor C_4 grasses. With this understanding of the $\delta^{13}C$ values, the amount of C_3 and C_4 plants consumed by herbivores can be quantified and applied to various biogeographic questions.

A third group of plants uses the CAM (crassulacian acid metabolism) photosynthetic pathway and includes succulents, such as cactus. These plants are probably not relevant to bison or other herbivores as forage and are not included in this discussion.

The presence and distribution of C_3 and C_4 plants in the environment is not random but related to environmental factors, specifically temperature. C_3 and C_4 plant abundance can be predicted from surface energy and moisture balance characteristics of the soil. With increasing latitude and altitude, a corresponding increase in C_3 species is expected (Boutton et al., 1980; Tieszen, 1994).

On the Great Plains, an increase in C_3 grasses is correlated with increasing latitude. In south and southwest Texas, C_4 grasses are represented at 68 and 82%, respectively, decreasing to 35% in South Dakota. Browse species, such as the sedges, do not show as clear a temperature dependent distribution as grasses. *Carex*, a common genus of sedge in the mountains, is C_3 (Tieszen, 1994).

It is therefore expected that generalist consumers of grass biomass should have a modern isotopic signal that reflects the mixture of C_3 and C_4 species in the utilized environment. However, since climatic changes have been demonstrated for various periods during the course of the Holocene, vegetation values should be expected to reflect these climatic shifts (e.g., Thompson et al., 1993). This temporal variable is another complicating factor involved in the interpretation of isotopic signals from paleosamples (Tieszen, 1994). A number of recent studies have demonstrated the value of herbivore isotopic signatures for discerning changes in vegetation communities (e.g., Connin et al., 1998) within herd variability (e.g., Gadbury et al., 2000) and behavior (e.g., Larson et al., 2001).

STABLE NITROGEN ISOTOPE ANALYSIS

Another stable isotope that is linked to trophic level and potentially important for investigating diet and herbivore migration is $\delta^{15}N$. Nitrogen (N_2) enters the soil through the atmosphere, by precipitation, or from parent rock decomposition. Once in the system, nitrogen is taken up by plants and moves up through the food chain, where it progressively becomes enriched by 2–5‰ through each trophic level (Ambrose, 1991; Bocherens et al., 1994). Nitrogen isotopes have been most widely applied to discerning the contribution of marine and terrestrial foods in human diets (e.g., Ambrose, 1991).

The potential of dietary stress can also be assessed by examining $\delta^{15}N$ values. In examining horn sheath annuli of bison from the Central Plains, Tieszen (1994) identified a change in $\delta^{13}C$ values accompanied by changes in $\delta^{15}N$ that he interpreted as a large degree of stress undergone by these individuals with shifts in diet. The researcher did not identify the specific cause of the

TABLE 5

Results of stable isotopic analyses of horn sheath samples (Hood, 2004b). Adj $\delta^{13}C$ values illustrate enrichment of 3.1‰ between keratin and diet (Cerling and Harris, 1999). Percent C_4 vegetation is following Brooks (1995).

Sample no.	Weight (g)	Beta no.	$\delta^{13}C$	Adj $\delta^{13}C$	$\%C_4$	$\delta^{15}N$
HS-1	0.43	195622	−21.9	−18.8	15.20	+6.9
HS-2	3.28	195623	−21.7	−18.6	16.50	+7.4
HS-3	5.54	195624	−20.7	−17.6	23.40	+7.4
HS-4	0.33	195625	−20.3	−17.2	26.21	+8.1
HS-5	1.44	195626	−22.0	−18.9	14.48	+6.5
HS-6	0.71	195627	−20.7	−17.6	23.45	+8.6
HS-7	1.57	195628	−22.1	−19.0	13.79	+9.4
HS-8	2.39	195629	−22.1	−19.0	13.79	+6.4
HS-9	3.25	195630	−21.6	−18.5	17.24	+8.3
HS-10	2.29	195631	−22.0	−18.9	14.48	+5.2

dietary stress but suggested it may have been related to illness or water stress (i.e., drought).

Ambrose and DeNiro (1986) noted a strong correlation between annual rainfall and herbivore $\delta^{15}N$ ratios. They suggested enrichment may be caused by physiological adaptations to water stress and low-protein diets in arid habitats. For example, when drought-tolerant mammals are water stressed they will concentrate ^{15}N in their tissues and eliminate ^{14}N in urea, producing greater isotopic variability and more tolerant values than obligate drinkers. In arid or saline environments (<400 mm yr^{-1} of precipitation), these herbivores are more depleted than browsers living in the same environment (Ambrose and DeNiro, 1986; Heaton et al., 1986).

Hughes (2003), in her analysis of Holocene bighorn sheep (*Ovis canadensis*) from Mummy Cave in northwestern Wyoming, argued that changes in $\delta^{15}N$ values were related to migration of sheep between summer and winter range. She argued that changes in these values reflect shifts in migratory behavior resulting from climate change. Bison from the high altitudes moving into lower elevation grasslands of the surrounding basins should illustrate similar patterns: low $\delta^{15}N$ values for high-elevation grasslands and high $\delta^{15}N$ values for low-elevation grasslands.

RESULTS

The horn is a solid, bony core which is part of the animal's skull and is covered by a sheath of hard fibrous horn. The shape that the horn sheath takes is formed by the inner bony core, both of which continue to grow and are correlated with age (Miura, 1985).

Horn sheath samples were removed from the dorsal portion of the right horn using a Dremel variable-speed rotary tool. A 10- × 4-cm section was removed from the sheath and placed in distilled water for approximately 8 h in order to rehydrate the sheath to allow for the separation of the individual cones. Although the growth rings or cones do not necessarily represent an annual record (Reynolds et al., 1982), they do provide a periodic record of the individual bison that can provide us with information on its ecology, diet, health, and possible migration.

Ten samples of the horn sheath, each representing a single horn cone, were submitted to Beta Analytic for stable carbon and nitrogen isotopic analysis. The samples were numbered consecutively from the oldest (HS-1) to most recent (HS-10). The pretreatment protocol used by Beta Analytic involves collagen extraction with alkali. Each sample supplied sufficient carbon and nitrogen for accurate measurements, and the analyses proceeded normally (Table 5).

The analyses indicate that the horn sheaths provide a record of stable carbon and nitrogen isotope signatures of assimilated foods as was demonstrated in an earlier study by Tieszen (1994). The values, adjusted by 3.1‰ for enrichment between keratin and diet (Cerling and Harris, 1999), indicate variability in $\delta^{13}C$ values that range between −17.2‰ and −19.0‰, with a mean of −22.51‰, which indicates a diet that is oriented toward C_3 vegetation (Fig. 8). This is not unexpected and represents a diet that is similar to modern bison in the Henry Mountains (Van Vuren, 1984). However, the large percentage of C_4 vegetation in the diet is unusual for a bison living in high-altitude environments. The C_4 vegetation may result from seasonal migrations to low elevations, but may also represent a climatic signal of drought conditions during the 18th century.

The pattern of changes in $\delta^{15}N$ values of the Gilbert Peak bison tend to follow that of $\delta^{13}C$ values (Fig. 9). In general, as $\delta^{15}N$ values increase, the $\delta^{13}C$ values become less negative. The Gilbert Peak values may reflect a similar migratory pattern of this bison using various habitats over the course of its life.

Another possible explanation involves nitrogen waste through urine. Steele and Daniel (1978) have found that in herbivorous mammals, urea is the main form of nitrogen waste, and the ^{15}N isotopic composition in urine is lower than the ^{15}N isotopic composition of the vegetation they consume. With the elimination of urea collagen, $\delta^{15}N$ values are elevated. As Fizet et al. (1995) related, protein quality also has an effect of lower $\delta^{15}N$ values in herbivores due to less urea in the urine. Ambrose and DeNiro (1986) demonstrated that modern East African herbivorous mammals living in arid areas have increasingly higher $\delta^{15}N$ values. These higher levels are related to the excretion of urine highly concentrated in urea, a strategy for water conservation.

Based upon this information, Fizet et al. (1995) argued that higher $\delta^{15}N$ values of mammal collagen from the French Pleistocene Marillac Cave layer #7 was related to an episode of aridity between 45,000 and 40,000 yr BP. Other paleoclimatic proxy data support this interpretation. The elevated levels of $\delta^{15}N$ values for the Gilbert Peak bison may reflect periods of increased aridity at periods during its life and may provide evidence of short-term climate shifts.

The period from approximately A.D. 1450 to 1800 has been labeled the Little Ice Age (Fagan, 2000) and was characterized by reduced temperatures and increased effective moisture, as indicated by a final high stand of the Great Salt Lake (Currey, 1990). An increase in sagebrush pollen and higher water levels at Ruby Marsh during the last 500 years indicates "the coolest and/or moistest conditions since the early Holocene," presumably a Little Ice Age signal (Thompson, 1992). Glacial advances have also been suggested for this period in the Wind River Range

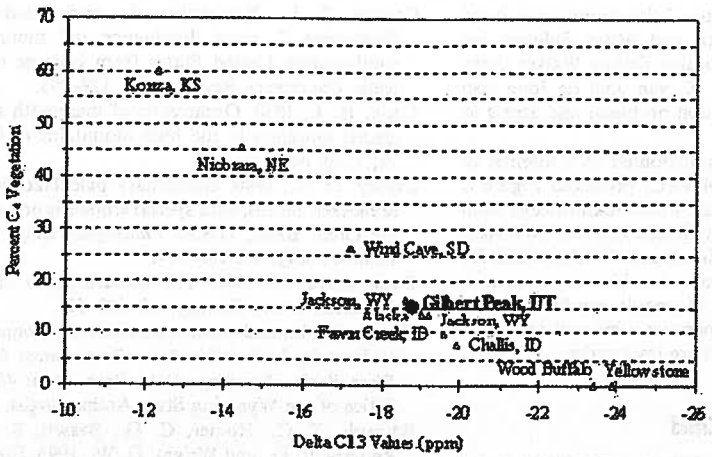

FIGURE 8. Percent C_4 vegetation is individual bison diet based upon $\delta^{13}C$ values as computed by Brooks (1995: p. 77). Samples are arranged from south (left) to north (right). KS = Kansas, NE = Nebraska, SD = South Dakota, WY = Wyoming, ID = Idaho, and UT = Utah.

(Richmond, 1986), the Colorado Front Range (Benedict, 1973), and the Teton Range (Richmond, 1986). Mesic indicator small mammal species reappear in deposits from Lamar Cave in Yellowstone National Park (Hadly, 1996), and bison are reported as being at their highest Holocene levels (Butler, 1978; Frison and Reher, 1980). Using historic and modern photographic evidence from the northern Uinta Mountains, Munroe (2003) provided evidence of growing season depression prior to A.D. 1870. While uniform cooler temperatures and increased effective moisture have traditionally been suggested for the Little Ice Age, recent research is suggesting more variability (e.g., Jacoby and D'Arrigo, 1989; Kaplan et al., 2002).

Local tree-ring records from the Uinta Basin Watershed indicate "the most intense dry regime in the proxy record [A.D. 1226–2000] occurred during the late 18th century from 1772 through 1786." While this was not an exceptionally long drought, it did encompass four of the driest years (1773, 1774, 1780, and 1786) in the entire record (Gray et al., 2004: p. 953). Earlier in the 18th century, decade-long droughts are also present. These periods of drought overlap with the radiocarbon date obtained from the Gilbert Peak bison and may provide an explanation for elevated $\delta^{15}N$ values and the small C_4 vegetation component derived from the $\delta^{13}C$ value obtained from the skull (−18.8‰ or 15.17%). Another possibility is that the bison lived a majority of its life at lower alpine elevations, and the skull was transported to the high country by humans.

Conclusions

In 2003 a partial bison skull was recovered by Ashley National Forest archaeologists from an elevation of 3840 m (12,600 ft) AMSL in the Uinta Mountains. The skull consists of a portion of the frontal, occipital region, and horn cores including horn sheaths. While high-altitude bison remains have been discussed in the scientific literature periodically, they have not gone beyond the descriptive. The radiocarbon age of the specimen is 150 ± 40 yr BP (cal A.D. 1725–1778). Metric analysis of the skull indicates it was an older adult male, which compares well with *Bison bison athabascae* (wood bison) in size and is larger than either *Bison bison bison* (plains bison) specimens or other high-altitude bison. However, it is probable this individual represents a member of the species *Bison bison bison*, but phenotypic characteristics (e.g., large horn size) may be the result of gene flow. More definitive taxonomic placement of the Gilbert Peak bison may not be resolved without genetic analysis. Stable carbon and nitrogen isotopic signatures were obtained from 10 individual cones from the preserved horn sheath. The results suggest a diet oriented toward cool season C_3 vegetation but with a significant contribution from warm season C_4 vegetation. The more positive $\delta^{13}C$ values and higher $\delta^{15}N$ values may be a climate signal of warmer or more arid conditions, a record preserved in the local Uinta Basin tree-ring record. As this study has demonstrated, and previously articulated by Walker (1992), isolated bison skulls can provide significant information that can be used to fill gaps in our understanding of bison paleoecology.

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A number of individuals have assisted me over the years in understanding the application of stable isotope analysis to mammal ecology. These individuals include Sheri Fritz, Susan

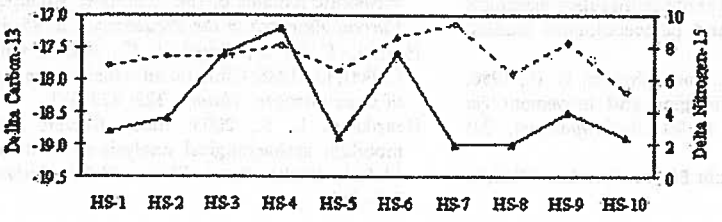

FIGURE 9. Results of stable carbon and nitrogen analyses preformed on horn sheath cones of the Gilbert Peak bison. Results are oriented from oldest (HS-1) on the left to youngest (HS-10) on the right. Upper dotted line is $\delta^{15}N$ values. $\delta^{13}C$ values (solid line) have been adjusted for keratin enrichment of 3.1‰.

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BLOOD GROUPS AND THE TAXONOMIC STATUS OF AMERICAN BUFFALO AND DOMESTIC CATTLE

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The generally accepted taxonomic position of the American buffalo (*Bison bison*) and domestic cattle (specifically, *Bos taurus*) is that of separate genera in the subfamily Bovinae. That the two species might very well occupy positions in the same genus is suggested by one of several alternative taxonomic designations for the American buffalo, notably, *Bos americanus* (see Roe, 1951). The two species are apparently fully cross-fertile, but only the females among the F_1 hybrids seem to be fertile (Deakin et al., 1942). Attempts to differentiate the two species by means of the classical precipitin technique have not been uniformly successful (Wolfe, 1939) and even when turbidimetric methods of measuring precipitates are used, the two species always stand closely side by side (Boyden et al., 1951). In this connection the question arises whether more extreme differences in precipitin values might be found between and perhaps even within breeds of domestic cattle. Likewise, attempts to demonstrate a clearly definitive difference between the two species by means of cross-absorbing antisera produced in rabbits against both bison and cattle red cells yielded equivocal results (Owen et al., 1958). In the case of each antiserum, absorption with a pool of red cells from the heterologous species succeeded in removing the greater portion and sometimes all of the antibodies directed against the red cells of the homologous species. Such observations suggest that the antigenic structure of the red cells of bison and domestic cattle must be very similar, and this was borne out to a considerable degree by blood typing bison with a rather large battery of blood-typing antibodies (reagents) which had been developed specifically for the purpose of exploring individual differences in cattle. For example, Owen et al. observed antigenic factors in bison blood which appeared to be indistinguishable from the bovine blood factors named **A**, **C**, **J**, **S**, **W**, **X**, and **Z**. Nevertheless, some rather marked differences were noted between the blood types of the two species, and those differences appeared to be significantly greater than any of the between-breed differences encountered in blood typing domestic cattle. For example, it appeared that the complex B locus of cattle is either not represented in bison or, if present, is occupied solely by alleles whose products (phenogroups) are essentially non-reactive with any of the 21 B system reagents used in that study.

The data reported by Owen et al. (1958) were actually collected during the years 1945–47. Since then, we have had the opportunity to develop in this laboratory an entirely new battery of cattle blood-typing reagents which derive from antisera independent of those used as sources of reagents by Owen et al. or by Miller and Stone (1955) in a further study of bison blood types. In connection with another study (Stormont and Suzuki, 1958), we had the opportunity to type three bison with our reagents. The results of those tests provided evidence which tended to narrow the magnitude of the blood-type differences between the two species. Further inquiry was therefore prompted and through the courtesy of Mr. Julian A. Howard, Refuge Manager of the Wichita Mountains Wild Life Refuge, Cache, Oklahoma, and Dr. D. C. Bostwick, we received 56 samples of citrated bison blood on October 29, 1959. (This was the same herd from which Owen et al. obtained 44 of the 69 samples used in their study, and it was also the same herd from which

TABLE 1. *The 41 classified "facsimile" reagents used in typing the 56 bison blood samples*[1]
(Information is given on the number of replicas of each reagent, as shown within parentheses; the letters a, b, c, ... etc. ... m indicate the sources of the antisera from which the reagents were obtained, and the decode for these letters is given as follows: a = cattle isoimmune serum; b = rabbit anti-cattle serum; c = sheep isoimmune serum; d = rabbit anti-bison serum; e = rabbit anti-bactrian camel serum; f = goat anti-cattle serum; g = sheep anti-cattle serum; h = rabbit anti-human A serum; i = cattle anti-human A serum; j = normal cattle serum; k = normal sheep serum; l = normal pronghorn antelope serum; m = cattle anti-bison serum.)

Reagents by systems	Sources and replicas	Reagents by systems	Sources and replicas	Reagents by systems	Sources and replicas
A system		*B system*		*F–V system*	
A_1	a (1)	A′	a (1)	F	b (2); d (1); e (1); f (1); k (1); l (2)
A_2	b (1)	D′	a (1)	V	a (3); b (1); g (1); m (1)
H	a (2)	E_1'	a (1); b (1)		
B system		E_2'	a (1)	*J system*	
B	a (1)	E_3'	a (1); c (1)	J	h (3); i (1); j (2)
G	a (5)	I′	a (2)	*L system*	
I	a (1); c (1)	J′	a (2)	L	a (1)
K	a (2)	K′	a (3)	*S system*	
O_1	a (1)	*C system*		S	a (2)
O_2	a (1)	C_1	a (2)	U_1	a (1); b (1)
P	a (1)	C_2	a (1)	U_2	a (1)
Q	a (1)	R	a (3); c (1)	U′	a (1)
T_1	a (1)	W	a (2)	H′	a (2)
T_2	a (1)	X_1	a (1); d (1)	*Z system*	
Y_1	a (1)	X_2	a (1)	Z	a (2); b (1)
Y_2	a (2)	L′	a (6)	*Z′ system*	
				Z′	a (1)

[1] Facsimile reagents are simply reagents which in blood typing cattle are known to be replicas or near-replicas of cattle reagents which have been previously described in the literature.

Miller and Stone obtained 193 samples for their study.) The present report is concerned with the results of blood typing those 56 samples. Data are also presented on the occurrence of certain natural antibodies and soluble blood group substances in the plasma of the bison blood samples.

MATERIALS AND METHODS

Hemolytic techniques, as described in previous reports cited by Owen et al. (1958), were used in this as well as the two previous studies. The only deviation in technique of the present study concerned sources of complement. Heretofore, fresh frozen rabbit sera has been used exclusively as complement in cattle and bison blood typing. We have observed, however, that a few of our reagents, particularly our anti-J reagents prepared from rabbit antisera engendered by immunizing with human red cells of type A (Stormont and Suzuki, 1960), have little or no lytic activity when complemented with fresh rabbit sera but do promote specific hemolysis when activated by fresh guinea pig sera used diluted in a range of 1:15 to 1:20.

In table 1 we have listed 41 cattle blood-typing reagents used in the present study which are known to be facsimiles or near-facsimiles in tests of cattle of the vast majority of the reagents used in the two previous studies. We also have noted in table 1 the source of each antiserum from which the various reagents were derived and the number of replicas of each reagent.

In table 2 are listed the new reagents, a total of 25, whose reactions with bison red cells have not previously been described. As in table 1, we have indicated in table 2 the sources of antisera from which the new reagents were derived and also the number of replicas of each reagent.

TABLE 2. *The 25 classified "new" reagents used in typing the 56 bison bloods*

(The number of replicas of each reagent is shown within parentheses. The decode of the sources of antisera is as follows: a = cattle isoimmune serum; b = rabbit anti-cattle serum; c = sheep isoimmune serum; d = normal cattle serum.)

Reagents by systems	Sources and replicas
A system	
D	b (7)
B system	
B_2	a (1)
I_2	a (2)
O_x	a (1)
P_x	a (1)
A_2'	a (1)
B′ or NF6	a (2)
E_x'	a (4)
F′	a (1)
G′	a (2)
O′ or NF8	a (1)
Y′ or NF4	a (1)
NF7	a (1)
S2	c (1)
S5	c (1)
S26	c (1)
S27	c (1)
S34	c (1)
C system	
E	a (2)
NF12	a (1)
J system	
Oc	d (1)
M system	
M_1	a (1)
M_2	a (1)
S system	
S + H′	a (2)
U_1 + H′	a (1); b(1)

All the reagents listed in tables 1 and 2 are classified reagents. That is, they have been classified with respect to the known genetic systems of blood groups in cattle in which they react (see Stormont, 1958). Attention is called to the reclassification of H′ reagent, which in the two previous studies had been regarded as being reactive in a system (the H′ system) independent of the 10 systems listed in tables 1 and 2. We have shown that H′ reagent reacts in the S system of bovine blood groups. Likewise, attention is called to a reclassification of the new D reagent (table 2) which was previously believed (Stormont and Suzuki, 1956) to be reactive in a new system (the D system) independent of the others. As pointed out in a brief note published elsewhere (Stormont et al., 1960), it was the results of typing the present sample of 56 bison bloods which provided the first clue (see table 3) relating the reactions of D antibodies to the A system of cattle.

RESULTS

Bona fide or true cross reactions, as determined by appropriate absorptions, were obtained in typing bison red cells with the facsimile reagents A_1, A_2, C_1, C_2, F, J, L, S, V, W, X_1, X_2, Z, and E_3' of table 1 and also with the new reagents D, M_2, P_x, S + H′, one of the two U_1 + H′, E_x' and NF (new factor) 12 of table 2. All the remaining reagents (27 in table 1 and 18 in table 2) produced no bona fide cross reactions with the red cells of bison. In this connection, however, we should mention that one of the five replicated G reagents (table 1) produced lysis of all 56 bison bloods but that the reactions, as readily demonstrated by absorbing the particular reagent with both bison red cells and with G-positive cattle cells, could not be attributed to the specific G antibodies in the reagent. Rather, they were due to certain heterophile antibodies which were probably present in the normal serum of the cow which produced the antiserum. At any rate, absorption of this particular G reagent with G-positive cattle red cells provided us with a testing fluid which could be used to distinguish bison red cells from those obtained from domestic cattle.

Summarized in table 3 are the reactions of the 15 reagents which distinguished individual differences in the 56 bison bloods. By means of appropriate symbols (see table 3), we have attempted to differentiate partial or incomplete cross reactions from complete cross reactions believed to be fully equivalent to the reactions obtained with the particular reagents in typing animals of the homologous species. Likewise, dosage reactions (indicative of two doses of a given blood factor) are differentiated

the reactions. The phenogroup A_1D cross reacted with A_1, A_2, and D antibodies whereas the "–" alternative was non-reactive with all of the A system reagents presently available. Estimates of the frequencies of the two alleles which control these phenogroups in the Oklahoma or Wichita population of bison are given in table 4.

The question arises whether the phenogroups A_1D and "–" of bison have their equivalents in domestic cattle. At the time these data were collected we could not be certain, since, as already noted, it was the present results which first called our attention to the fact that reagent D must be reacting not only in the A system of bison but also in the A system of cattle. Reanalysis of the A system of cattle has indicated (Stormont et al., 1960) that a minimum of seven phenogroups is required to explain the reactions of reagents A_1, A_2, D, and H with cattle bloods. Since all seven of these phenogroups exhibit positive reactions with one or more of the A system reagents, there is as yet no evidence for a phenogroup equivalent to the "–" alternative in bison. We have, however, observed an A system phenogroup in cattle which exhibits the same reactions as A_1D of bison. We have not had the opportunity to compare it with bison A_1D in absorptions with D reagent. As indicated in table 3, the D reactions of bison blood were not fully equivalent to those of cattle blood. When bison red cells of phenotype A_1D were used to absorb D reagents not all of the D antibodies for cattle were exhausted. However, in those tests there were no cattle which possessed phenogroup A_1D to the exclusion of other D-positive phenogroups. Further study is therefore required in order to decide whether A_1D of bison is equivalent to A_1D of cattle in the extent to which it will absorb D antibodies.

The B System in Bison

As indicated by the large number of B system reagents (tables 1 and 2) used in typing cattle, the B system of cattle is extremely complex. This is further indicated by the fact that we presently recognize, in our laboratory alone, 251 B phenogroups and their controlling alleles. A list of some of the B phenogroups of cattle and estimates of the frequencies of their alleles in several breeds of cattle are given elsewhere (Stormont, 1958).

Only three of the 37 B system reagents (tables 1 and 2) cross reacted with bison red cells. These were the reagents E_3' (facsimiles of the E_3' reagent used in two previous bison studies), P_x and E_x'. All three of these reagents are known to produce related patterns of cross reactions with cattle red cells. Each of the three reagents distinguished individual differences in bison, but, as shown in table 3, they produced the same reactions in the parallel tests.

As in the A system of bison, these results can be explained by postulating a single pair of bison phenogroups which we designate as E_x' and "–". Phenogroup E_x', as indicated by the results summarized in table 3, shows partial cross reactions with P_x and E_3' reagents but exhibits essentially complete cross reaction with the E_x' fraction of antibodies in the serologically complex E_x' subtyping reagents. As indicated in table 4, the "–" alternative in the bison B system has its homologue in domestic cattle, and that homologue occurs rather frequently in certain breeds such as Herefords and Shorthorns (see Stormont, 1958). There is no evidence so far for a B phenogroup in cattle which is equivalent to E_x' of bison. The closest resemblance to it is probably O_xE_3' of cattle. This phenogroup differs from E_x' of bison primarily by the fact that it cross reacts with O_x antibodies and also reacts more completely with E_3' and P_x antibodies than does phenogroup E_x' of bison. Estimates of the frequencies of the alleles which control phenogroups E_x' and "–" in the Oklahoma population of bison are given in table 4.

The C System in Bison

The C system is the second most complex system of blood groups recognized in cattle. Over 30 C phenogroups and their controlling alleles are presently known.

All the C system reagents (table 1 and table 2) except R, L′, and E produced bona-fide cross reactions with bison red cells. The two facsimile reagents X_1 and X_2, and the new reagent designated NF12 (table 2) cross reacted intensely with all 56 bison bloods. The cross reaction of NF12 antibodies with all 56 bison bloods was fully expected in view of the fact that NF12 reacts with all C phenogroups in cattle which are characterized by either or both blood factors **R** and **X**.

The reactions of the three C system reagents, notably C_1, C_2, and W, which distinguished individual differences in bison are summarized in table 3.

The present results with C system reagents, we believe, can be attributed to a minimum of three bison phenogroups designated X_1, WX_1, and C_2WX_1. A fourth C phenogroup, designated C_1WX_1, might be indicated by the weak or partial cross reactions obtained with our two C_1 reagents in tests of the red cells of bison numbered 47 and 65 in table 3. We have, however, for the purpose of the present report, taken the position that bison 47 and 65 were probably homozygous for phenogroup C_2WX_1 and that the weak reactions of their red cells with C_1 reagents resulted from a double dose of blood factor $\mathbf{C_2}$.

Estimates of the frequencies of the three alleles controlling phenogroups X_1, WX_1, and C_2WX_1 in the Oklahoma population of bison are given in table 4. Also, as noted in table 4, we have indicated that phenogroups X_1 and WX_1 have known homologues in domestic cattle but that, so far, there is no known homologue of C_2WX_1.

The F-V System in Bison

The F-V system in domestic cattle is typified by a single pair of phenogroups F and V which are controlled by a pair of alleles such that three phenotypes F (or F/F), FV (or F/V), and V (or V/V) are recognized. Recent observations in our laboratory suggest that the regular V phenogroup of cattle is divisible into two subgroups. Atypical variants of blood factor **V** have also been noted in this and other laboratories in typing *Bos indicus*, and there is suggestive evidence that variants of **F** also exist. In the present study, however, the reactions of bison red cells with F and V reagents were compared only with the regular F and V phenogroups of *Bos taurus*.

Partial cross reactions of all bison bloods of the present study were obtained with all of our F and V reagents (table 1) except in the case of the one F reagent obtained from a rabbit antiserum against the red cells of bison and the one V reagent obtained from a cattle antiserum against bison red cells. The reactions of the latter reagents were, of course, fully equivalent to those obtained with cattle red cells since, in these instances, bison rather than cattle represented the homologous species. However, two of the F reagents and three of the V reagents failed to produce visible hemolysis with bison red cells at the dilutions at which these reagents are ordinarily used in typing cattle. Nevertheless, absorption of these reagents as well as the other "partially" cross-reactive F and V reagents had a pronounced effect on the antibody populations. In each instance, the titer and degree of reactivity with cattle red cells were considerably reduced.

We propose that these results can be attributed to a single phenogroup in the F-V system of bison. We have designated this phenogroup as FV_b and note in table 4 that it does not presently have a known homologue in domestic cattle. Comparison of F-V variants in cattle with phenogroup FV_b of bison is a subject for further study.

That phenogroup FV_b of bison can be used to engender both F and V antibodies which will distinguish the three phenotypes F, FV, and V of domestic cattle is indicated by the sources of one of the F and one of the V reagents (table 1) used in the present study.

The J System in Bison

In the study of Owen et al., only one J reagent, a normal serum obtained from cow 17Z, was used. Nevertheless, it was possible, as in typing cattle, to distinguish

different degrees of reactivity with J-positive bison red cells. In the present study we employed three J reagents obtained by immunizing J-negative rabbits with human red cells of type A, one J reagent obtained by immunizing a J-negative cow with human red cells of type A, and two normal cattle serums which contained rather strong J isolysins (see table 1). With these reagents, as explained in the note to table 3 and as indicated by appropriate symbols in table 3, we were able to distinguish four main categories of J reactions which were typical of the four main categories of J reactions distinguished by these reagents in typing cattle bloods.

Although we propose that a minimum of four J alleles, with homologues in cattle, are required to explain these four categories, we made no attempt to distinguish between these alleles in estimating the gene frequencies given in table 4.

The blood plasmas of each of the 56 bison were examined for the presence of natural isolysins and heterolysins, in particular any heterolysins which might serve to distinguish cattle from bison. No antibodies of the latter specificity were observed.

All J-negative bison (table 3) possessed natural isolysins for J of bison and these also reacted with J of cattle. The activity of these natural J antibodies, as in J-negative cattle, varied from extremely weak to very strong from individual to individual.

In addition to the occurrence of natural anti-J, some of the bison (nos. 48, 59, and 57 in table 3) possessed natural lysins for cattle bloods of subtype U_1. Such antibodies are occasionally encountered in the normal serum of cattle (Stone and Miller, 1961).

The bison plasmas were also examined for the presence of heterolysins for the red cells of domestic sheep (*Ovis aries*) and for lysins which might distinguish group R from group O sheep. Ten of the J-negative bison and six of the J-positive bison possessed heterolysins for the red cells of all sheep. None of the bison possessed lysins specific for the red cells of group O sheep but all J-negative bison, as expected, possessed lysins specific for the red cells of group R sheep. (The R population of antibodies always includes anti-J, and both the J and R fractions are readily absorbed by sheep red cells of group R as well as by human red cells of groups A and AB.) The results were typical of those we have obtained in screening normal cattle serums or plasmas for anti-J, anti-R, anti-sheep O, and anti-human A, except in bison sera that we encountered no antibodies specific for the red cells of group O sheep. However, as pointed out by Sprague (1958b), natural antibodies specific for the red cells of group O sheep have so far been found only in one breed of cattle, the Hereford.

Some of the bison plasmas were examined not only for soluble J substance but also for the recently discovered soluble Oc substance (Sprague, 1958a). Three J-Oc phenotypes indistinguishable from three of the four types described by Sprague (1959a) in studies of cattle were encountered. These were the types J (soluble J but no Oc), JOc (soluble J and Oc), and Oc (soluble Oc but no J). None of the plasmas that were examined lacked both J and Oc activity. As in the case of JOc-positive and Oc-positive cattle, the red cells of JOc-positive and Oc-postive bison were not lysed by Oc antibody (specifically, natural bovine anti-sheep O).

The L System in Bison

The L system in domestic cattle is presently characterized by two phenogroups: L and its negative alternative "–", distinguished by tests with L reagent.

In the present and previous studies, all bison bloods were L-positive and the reactions were fully equivalent to those obtained in typing domestic cattle, thereby indicating, as shown in table 4, that the allele for L must be at or near fixation in the Oklahoma population of bison. However, as noted in the study of Owen et al., the red cells of one of 9 F_1 hybrids (cattalo) were L-negative thereby indicating

TABLE 4. *Phenogroups in the A, B, C, F–V, J, L, M, S, Z, and Z′ systems of bison blood groups and estimates of their gene frequencies in the Oklahoma population*

Genetic systems	Phenogroups	Gene frequencies	Known homologues in cattle	Known blood factors associated with each phenogroup
A	A_1D	0.22	Yes?[1]	A_1, A_2 and D[2]
	"–"	0.78	No	None
B	E_x'	0.25	No	P_x,[2] E_x'[2] and E_x'
	"–"	0.75	Yes	None
C	X_1	0.64	Yes	X_1, X_2 and NF12
	WX_1	0.22	Yes	W, X_1, X_2 and NF12
	C_2WX_1	0.14	No	C_2, W, X_1, X_2 and NF12
F–V	FV_b	1.00	No	F^2 and V^2
J	J	0.55	Yes	J
	"–"	0.45	Yes	None
L	L	1.00	Yes	L
M	M_2	0.05	Yes	M_2
	"–"	0.95	Yes	None
S	S_b	0.21	No	S
	"–"	0.79	Yes	None
Z	Z	0.63	Yes	Z
	"–"	0.37	Yes	None
Z′	"–"	1.00	Yes	None (see Addendum)

[1] Homologues have not been compared in absorption tests.
[2] "Partial" cross reactions only with the respective cattle reagents.

that the allele for the negative alternative occurs in some bison.

The M System in Bison

As shown in table 3, five bison bloods cross reacted with antibodies in the M_2 reagent and the reactions were fully equivalent to those obtained in testing the bloods of domestic cattle of subtype M_2. As in cattle, the M_2 reactions of bison red cells (table 3) appeared to be independent of those obtained in the systems A, B, C, J, S, and Z.

It is concluded, therefore, that two alleles which control the phenogroups M_2 and the "–" alternative can account for the results obtained in typing these 56 bison with cattle M reagents. Estimates of the frequencies of the two alleles in the Oklahoma population are given in table 4.

The S System in Bison

The five reagents, S, U_1, U_2, U′, and H′ are presently used in typing the S system of domestic cattle and with these five reagents it has been possible to distinguish five phenogroups SH′, U_1H′, U_2, H′ and a negative alternative designated "–". As may be noted by the symbolism used in designating these cattle phenogroups, the S-positive phenogroup (SH′) and the U_1-positive phenogroup (U_1H′) are characterized in part by the fact that they both react with H′ antibodies. That is to say, we have yet to find in typing domestic cattle any S-positive or U_1-positive or SU_1-positive bloods which are negative with H′ antibodies.

In view of the association of blood factors **S** and $\mathbf{U_1}$ with blood factor **H′** in domestic cattle, we were particularly anxious to re-examine S-positive bison bloods with all available H′ reagents, since in the two previous studies there was no indication of an **H′** or **H′**-like blood factor in bison. For this reason, we used not only our pure H′ reagents but also incorporated

S + H′ and U_1 + H′ reagents (table 2) in the present study. The latter reagents can be converted to pure S and pure U_1 reagents by absorbing with cattle bloods of type H′ but cannot at present be converted to pure H′ reagents, by absorbing with cattle red cells, for reasons already indicated.

The results of the present study, as summarized in table 3, reaffirm the presence of an S blood factor in bison which seems to be fully equivalent to S of cattle. Nevertheless, there was no indication that bison red cells of any type will cross react with cattle H′ antibodies. The results are compatible with the interpretation that there are but two S phenogroups indicated in the Oklahoma population of bison: one designated S_b, which produces complete cross reactions with cattle S antibodies and also exhibits weak, partial cross reactions with one of our two U_1 + H′ reagents (see table 3), and the other designated "–", which like its homologue in cattle is non-reactive with any of the reagents presently used in typing the S system.

Estimates of the frequencies of the two alleles which control the S phenogroups of bison are given in table 4.

As a result of these studies, it is perhaps of some practical interest to point out that antisera or reagents which contain both S and H′ antibodies can be converted to H′ reagents by utilizing S-positive bison bloods in the absorptions.

The Z System in Bison

Two Z phenogroups, indistinguishable from their homologues in cattle, were previously recognized by Owen et al. (1958). The present data merely reaffirm those observations. The reactions obtained with Z reagents, including dosage reagents, are as summarized in table 3, and estimates of the frequencies of the two Z alleles in the Oklahoma population are given in table 4.

The Z′ System in Bison

The Z′ system in cattle is presently characterized by two phenogroups Z′ and its negative alternative "–". Phenogroup Z′ has proved to be either absent or rare in all breeds of *Bos taurus* so far studied.

As in the two previous studies, all bison of the present study were Z′-negative. Assuming that the Z′ locus is represented in bison, the only conclusion which can presently be drawn is that it is occupied solely by an allele whose product is non-reactive with Z′ antibodies. This allele has its homologue in cattle (see Addendum).

Discussion

In retrospect we have seen that some of the main points of difference in the blood-type comparisons of bison and cattle have either vanished or have considerably diminished. The first and perhaps foremost point, as set forth by Owen et al. (1958), was the virtually complete non-reactivity of bison bloods with 21 different reagents known to be reactive in the B system of cattle, an observation which indicated that the B locus is either absent in bison or is occupied solely by alleles whose products (phenogroups), like that of the allele designated *b* in cattle, were essentially non-reactive with the B reagents used in that study. We now know that neither of those indications was correct. The B locus is definitely represented in bison by at least two alleles, and the product of one of those alleles cross reacts not only with our facsimile E_3' reagents but also with two new B system reagents, namely, P_x and E_x'. Furthermore, one of those two alleles has what would presently appear to be its precise homologue in the allele *b* of cattle. The fact that we presently do not recognize a B phenogroup in cattle which is fully equivalent to E_x' of bison is not critical since the same situation occurs when breeds of cattle are compared. For example, phenogroup $BO_2Y_1A'E_3'G'$, whose controlling allele has a frequency of 0.42 in Milking Shorthorns and 0.03 in Holstein-Friesians, has so far not been encountered in our studies of Herefords (see Stormont, 1958).

The second point made by Owen et al. was the complete non-reactivity of bison bloods with H′ antibodies, in contrast to

the regular appearance of this blood factor with high frequency in equivalent samples of various breeds of cattle. Although this observation was reaffirmed by the data of Stone and Miller (1955) and by the present data, the significance of the point has been considerably reduced following recent observations made in this laboratory which have shown that **H′** is a member of the S system of cattle rather than a separate system by itself. It is certain that the S locus is represented in bison, in spite of the fact that there is no evidence in that species for blood factors related to $\mathbf{U_1}$, $\mathbf{U_2}$, **U′**, and **H′** of cattle. Even though no phenogroup equivalent to S_b of bison has as yet been detected in cattle, the fact that such a phenogroup occurs in bison makes us hopeful that its homologue may eventually be found in cattle.

The third point made by Owen et al. was the observation that all phenogroups in the C system of bison cross reacted strongly with reagents X_1 and X_2, while in cattle there are numerous C phenogroups which do not cross react with these reagents. The present data in no way detract from this salient feature; rather they add to it by the inclusion of still another reagent, namely, NF12, which cross reacted with all bison C phenogroups. However, in contrast with the two previous studies which reported positive reactions of all bison bloods with L′ reagent, none of six replicated L′ reagents of the present study produced reactions with bison red cells. The present results substantiate the opinion of Owen et al. that the previous L′ reactions were not of the nature of true cross reactions.

The fourth and final point made by Owen et al. was the indication of an allele F^{V_2}, controlling a phenogroup designated V_2, which would appear to be fixed in bison but has so far not been recognized in domestic cattle. We now know that the phenogroup produced by the bison F-V allele is partially cross reactive not only with V antibodies but also with F antibodies of various origin. Furthermore, we have been able to show that this particular bison phenogroup, designated FV_b in the present study, is capable of engendering antibodies which parallel the reactions of both F and V reagents in the cattle blood-typing tests. These differences between the F-V phenogroups in bison and cattle still stand as perhaps the most definitive differences between the two species. The question is, however, just how much longer will they stand? As already intimated elsewhere in this report, there is evidence for more than two alleles at the F-V locus of cattle and the product of one of the additional alleles might possibly turn out to be serologically indistinguishable from FV_b.

Actually, one of the most striking differences between the two species is probably not so much the allelic divergence at the various blood-group loci but rather the lack of heterogeneity in blood group alleles in bison, particularly at the B locus, as contrasted with the great heterogeneity in cattle. Several explanations could be advanced to account not only for the lack of diversity in bison but also to account for the extensive diversity in cattle but only one needs to be emphasized here, namely, the fact that our present populations of American buffalo have all been developed in modern times from foundation stocks of only a few animals (see discussion by Owen et al., 1958). We can never know precisely what the picture of bison blood groups was when literally millions of buffalo roamed the plains of North America, but better estimates can be made when we have more information not only on other herds of bison but also on blood-group heterogeneity in other wild species as contrasted with domestic forms that have arisen from them or have been closely associated with them in derivation. Hence, there is need to pursue much further the studies of blood groups in the subfamilies Bovinae, Caprinae, and Ovinae which are so richly represented by both wild and domestic species. Reed (1959) has expressed the opinion that comprehensive studies of blood groups in both wild and domestic

sheep would undoubtedly help clarify the taxonomic situation.

In their discussion of the reactions of bison red cells with cattle blood-typing antibodies, Owen et al. (1958) pointed out that there are no formal criteria whereby blood-typing antibodies developed for the purpose of differentiating individuals within one species, as cattle, may be used in differentiating species of the same or a different genus. We know, for example, that most of the bovine blood factors have significantly different frequencies in the various breeds of *Bos taurus*; and often of greater magnitude are the differences between breeds in the frequencies of alleles at each of the blood-group loci. This is particularly true for the complex B and C loci. We might expect, as mentioned by Owen et al., that there would be more extreme differences between species than between breeds or races within a species. We might also expect that some alleles, perhaps many or even all at any given locus, would have no precise homologues in related species of different genera but that their products would nevertheless exhibit some serological cross reactions. But, as the species under examination become even more distantly related it might be expected that the products of alleles at homologous loci would share fewer or no cross reactions. The key to certain of these events can be predicted merely by examining what has already been learned about allelic differentiation at such loci as B and C in cattle. Many pairs of contrasting B phenogroups or contrasting C phenogroups can be picked which do not share cross reactions with any of the presently known blood-typing reagents. If this can happen within a species, it must surely happen between species. The X-Z system of sheep (Rasmusen, 1958) is superficially homologous in many respects to the F-V system of cattle. Nevertheless, there is as yet no evidence for cross reactions between these two systems. This, however, does not exclude the possibility that homologous loci are involved.

The most desirable approach for comparing blood-group relationships of related species is that of using antibody-reagents which have been developed for the purpose of exploring individual differences in each of the species to be compared. In the bison-cattle comparisons we have not had available a battery of reagents developed specifically for bison even though a few of the reagents in the present study were derived from antisera directed against bison red cells. Therefore, one can only conjecture to what extent isoimmunization of bison would provide blood-typing antibodies which would distinguish further individual differences in bison and which might not cross react at all with cattle red cells. Some undoubtedly would cross react with cattle red cells and many of those that would can be predicted from what is already known about bison blood groups. On the other hand, if the present assay of blood groups in bison, as accomplished solely with cattle reagents, reflects most of the inherent blood-group variation in that species (and we are inclined to believe that it might), we could make some accurate predictions regarding the number of reagents that could be developed by the use of bison blood alone. We could also predict certain reagents now known to cross react with bison red cells which could not be developed, namely, X_1, X_2, NF12, F, L, and V simply for the reason that the genes for these blood factors seem to be fixed in bison. Bison isoimmune antiserum directed against such phenogroups as A_1D in the A system and E_x' in the B system would behave as monospecific reagents in the bison tests but should prove to be fractionable on absorption with appropriately selected cattle bloods. Indeed, if the present picture is a close approximation of the actual, the curious circumstance arises whereby reagents developed specifically for exploring blood groups in cattle would be just as useful as bison reagents in demonstrating individual differences in bison and at the same time would provide considerably more information on systems of bison blood groups as well as more information

on the serologic complexity of the phenogroups.

The question has arisen whether bison might possess one or more blood group systems not detectable by cattle reagents. All we can say at present is that there is little indication of such systems from the results of using cattle red cells in cross-absorbing both rabbit and cattle antisera against bison red cells. The antibodies in the rather low-titered "bison specific" reagents which have been developed from rabbit anti-bison serum can, for example, be attributed to phenogroup FV_b.

We believe that the answers to some of these questions will be forthcoming. In the meantime, it is established that at least 9 of the 10 blood group systems now recognized in domestic cattle are represented in bison. This observation, in conjunction with the observation that most of the blood-group alleles in bison (table 4) seem to have close homologues if not precise homologues in cattle, suggests that the two species are very closely related in evolutionary derivation, indeed, close enough in our opinion to justify their inclusion in the same genus.

In connection with another study (Stormont and Suzuki, 1958), we had the opportunity to test our cattle reagents with the red cells of one or more representatives of some other species (*Bubalus bubalis*, *Syncerus caffer*, *Anoa depressicornis*, *Boselaphus tragocamelis*, and *Taurotragus oryx*) in the subfamily Bovinae. However, in no instance was there any indication that any of these species stand near bison in the degree of blood-group relationship to cattle.

The only extensive comparisons of blood groups in cattle with those in a species other than bison, we believe, are the comparisons being made in this laboratory between the blood groups in domestic sheep (*Ovis aries*) and cattle. Serologic relationships have been established between the complex B and C systems of the two species and between the S system of cattle and the M system of sheep (Rasmusen et al., 1958; Rasmusen, 1960; Rasmusen et al., 1960; and certain unpublished data), and these relationships are in addition to the earlier known relationship between the J system of cattle and the R-O system of sheep (see Sorensen et al., 1954). But, in contrast with the bison-cattle comparisons, the sheep-cattle relationships extend only to the loci and not to the alleles. All the known phenogroups of the B, C, M, and R-O systems in sheep are clearly distinguishable from those of the equivalent systems in cattle. This also applies to the blood factors of the two species even though, for example, reagents which are identical in specificity in the cattle tests to such reagents as I, R, E_3', and NF6 (or B') have been prepared from sheep isoimmune antisera. Another blood-type distinction, which has some taxonomic significance in artiodactyls (see Stormont and Suzuki, 1958), is that sheep are Forssman-positive whereas bison and cattle are Forssman-negative.

Summary

Data are presented on the results of blood typing 56 American buffalo (*Bison bison*) with 66 different cattle blood-typing reagents.

Evidence is presented which indicates that at least nine genetic systems of blood groups now recognized in cattle have their homologues in bison. These are the systems A, B, C, F-V, J, L, M, S, and Z. Comparisons are drawn between blood factors common to bison and cattle, and between the phenogroups in each of the systems of the two species. It is shown that most of the bison phenogroups and, by implication, their controlling alleles have closely similar or precise homologues in cattle. It is also shown that bison have soluble blood group substances serologically indistinguishable from the J and Oc properties of cattle. The same is true for the isohemolysins anti-J and anti-U_1 and certain heterohemolysins which occur naturally in the two species.

Certain differences between the two species, notably those encountered in typing the F-V and C systems, still persist and those differences are probably more ex-

treme than any so far encountered in comparing various breeds of domestic cattle. Furthermore, there is a marked reduction of heterogeneity in bison blood groups as contrasted with cattle. This is particularly true in the B system. Nevertheless, there are many striking resemblances that outweigh the few differences.

The over-all results indicate close taxonomic affinity of the two species. On the basis of the evidence on blood groups and on other observations mentioned in the introductory remarks of this report, further consideration should be given to the proposition that the American buffalo and domestic cattle deserve to be recognized as members of the same genus.

ADDENDUM

Since the manuscript was submitted, it has been observed in this laboratory that the rare bovine blood factor named Z′ actually belongs to the A system of bovine blood groups. This observation obviates the need to consider Z′ as representing a separate blood-group locus as was done in this paper. The blood-group loci which should be considered are A, B, C, F-V, J, L, M, S, and Z. On this basis it is clear that each of the 9 blood-group systems presently recognized in *Bos taurus* has a known homologue in American buffalo, thereby narrowing somewhat more the differences between the two species.

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Chromosomal homology of wood bison and plains bison

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YING, K. L., and D. G. PEDEN. 1977. Chromosomal homology of wood bison and plains bison. Can. J. Zool. 55: 1759–1762.

Karyotypes of wood bison (*Bison bison athabascae*) and plains bison (*Bison bison bison*) were studied. Both subspecies were characterized by the same number of chromosomes ($2n = 60$), acrocentric autosomes, submetacentric X chromosomes, and an acrocentric Y chromosome. G-banding patterns suggest that when comparing wood bison and plains bison, 20 pair plus the sex chromosomes are homologous. Whether or not the remaining nine pair of chromosomes are homologous remains unknown.

YING, K. L., et D. G. PEDEN. 1977. Chromosomal homology of wood bison and plains bison. Can. J. Zool. 55: 1759–1762.

On a étudié les caryotypes des bisons *Bison bison athabascae* et *Bison bison bison*. Les deux sous-espèces comportent le même nombre de chromosomes ($2n = 60$), des autosomes acrocentriques, des chromosomes X sub-métacentriques et un chromosome Y acrocentrique. Les bandes G permettent de constater qu'il y a homologie de 20 paires de chromosomes et des chromosomes sexuels chez les deux sous-espèces. Le cas des neuf autres paires de chromosomes reste encore à élucider.

[Traduit par le journal]

Introduction

The genus Bison exists in three forms; the wood bison (*Bison bison athabascae*), the plains bison (*Bison bison bison*), and the European bison or wisent (*Bison bonasus bonasus*).

The wood bison is the largest form of the genus. Two hundred years ago the animal roamed the north of Saskatchewan, Alberta, and southern ranges of the North West Territory. Records also show that the wood bison inhabited the east slopes of the Rocky mountains south to Colorado. Aspen parkland and coniferous forests have been the main habitat. The plains bison was the most common form in North America. It roamed freely over most of the great plains from Mexico into Canada.

The wood bison (Anonymous 1975) stands taller in the hind extremities, and has a proportionately higher hump. It measures 1.95 m at the shoulder. A mature bull weighs up to 1000 kg. Its fur appears darker and thicker than that of plains bison. The latter has a shoulder height of 1.9 m, and a maximum of 950 kg. There is heavy fur covering on the upper front legs on the plains bison, but it is absent on the wood bison. The European bison (Wisent) reaches 1.8 m at the shoulder with adult bulls weighing 770 kg. The Wisent carries its head higher, and has the least prominent shoulder hump of the three forms of bison.

At one time wood bison ranged throughout the forest of western Canada by the tens of thousands. Slaughtered by commercial hunters during the last century and decimated more recently by disease and hybridization with their close cousins, the plains bison, the subspecies was thought to be extinct. In 1957, a remnant herd (Banfield and Novakowski 1960) of about 200 head was discovered in Wood Buffalo National Park, Northwest Territories. From this herd animals were moved to the Mackenzie Bison Sanctuary in the Northwest Territories and to Elk Island National Park near Edmonton, Alta. The present population consists of about 300 animals at the former site and 100 at the latter.

Recently the Canada Wildlife Act of 1973 became effective to protect this and other endangered species and attempts are being made to establish wood bison herds in selected areas of their original habitat.

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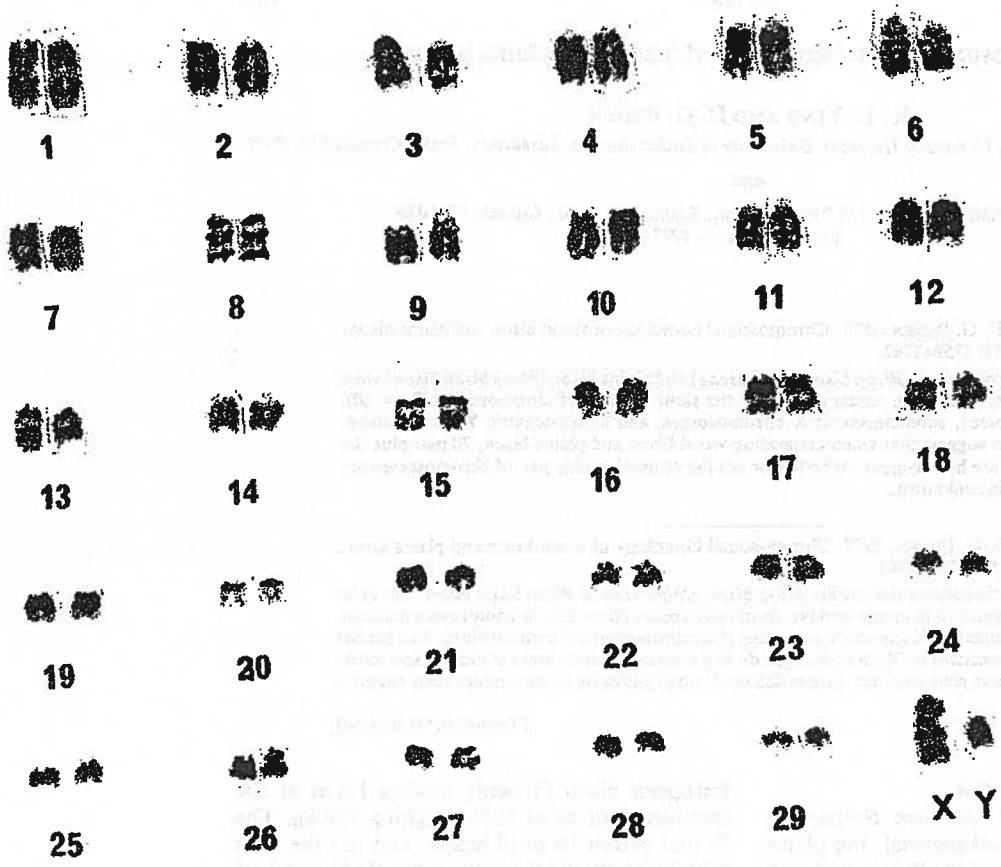

FIG. 1. A G-banded male karyotype of wood bison (*Bison bison athabascae*).

The purpose of this study was to karyotype the wood bison and plains bison in an attempt to test the chromosomal homology between these two species. If any nonhomology exists between the two species it would then be possible to distinguish between the hybrid and pure wood bison by studying their chromosomes. This would be of great value in the conservation of such endangered species.

Materials and Method

Blood samples were obtained from two female and one male plains bisons and from one male wood bison. Nine drops of heparinized whole blood were mixed in each tube with 5 ml culture medium made up from 4 ml TC 199 synthetic nutrient solution and 1 ml fetal calf serum. To this, gentamicin and phytohaemagglutinin *P* were further added and pH adjusted before being incubated in a chamber of 37°C for 3 days. Colcemid was added during the last 3 h of culture. At the end of 72 h, cells were harvested by removing the supernatant culture medium after centrifugation. Cells were then treated with KCl hypotonic solution and fixed in methanol–acetic acid mixture. Fresh fixatives were replaced two more times before making chromosome preparations. On one occasion, skin from the ventral side of the tail and scrotum was biopsied from a male wood bison and the method of culture and harvesting was according to that described by Ying and Butler (1971). Chromosome preparations were stained in giemsa with or without trypsin treatment. Trypsin–giemsa technique used to produce G bands followed the method of Wang and Federoff (1972). Chromosomes were first counted under microscope from 50 metaphase spreads of each sample studied, and well-spread ones with chromosomes showing distinct G-banding patterns were photographed for karyotyping.

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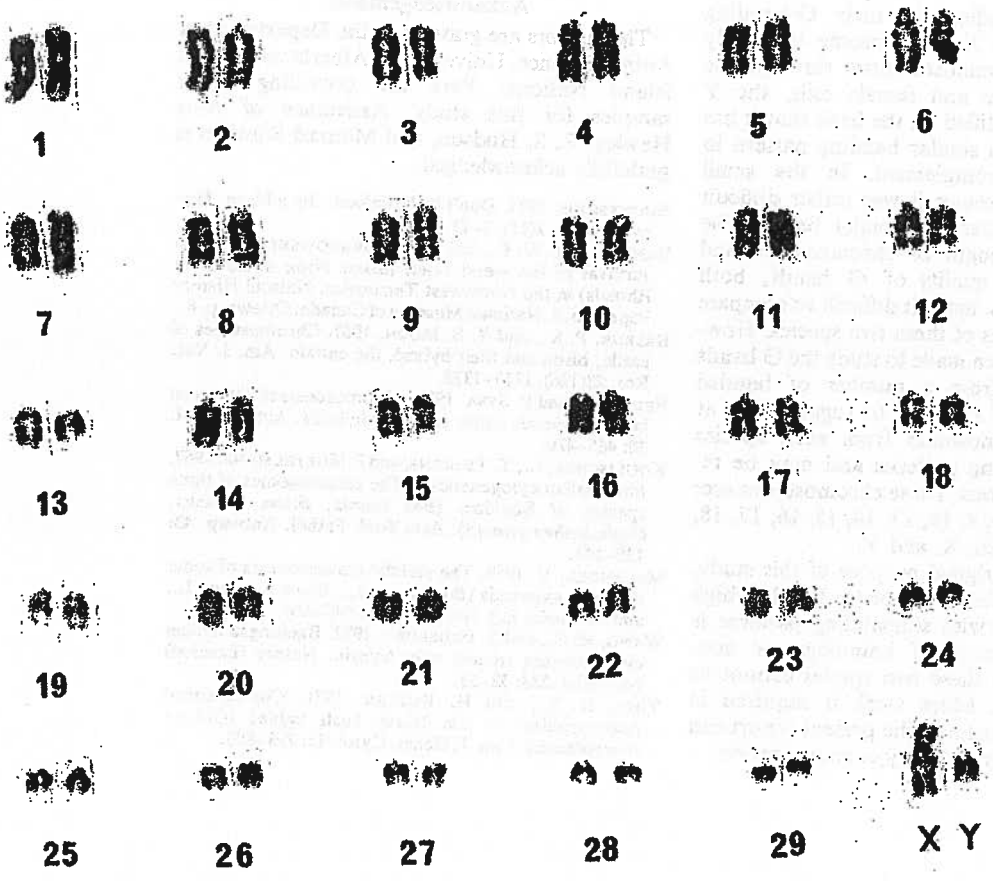

FIG. 2. A G-banded male karyotype of plains bison (*Bison bison bison*).

Results and Discussion

Wood bison and plains bison possess a diploid number of 60 chromosomes. The 58 autosomes are all acrocentrics, the X chromosome is submetacentric, and the Y chromosome is a small acrocentric. However, the short arm of the Y in both species sometimes is rather prominent and could be recognized as a small submetacentric in some cells. Before the advent of the banding techniques, other investigators reported that the Y chromosome in the American bison (referred to in this paper as plains bison) was a small acrocentric (Basrur and Moon 1967) while that of the European bison was a small submetacentric (Melander 1959; Koulischer *et al.* 1967; Fedyk and Sysa 1971). According to these studies, the diploid number in the plains and European bisons is the same ($2n = 60$), with morphologically identical autosomes (acrocentric) and X chromosome (submetacentric). To include our own observations, it can be concluded that the three species all have the same chromosome number, acrocentric autosomes, and submetacentric X chromosome, but the Y chromosome may be variable.

From our present study, the male karyotypes of wood and plains bisons are illustrated in Figs. 1 and 2. In each karyotype the homologues

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are matched according to their G-banding patterns. While the X chromosome is readily recognized as the submetacentric through the study of both male and female cells, the Y chromosome is identified on the basis that it has no counterpart with similar banding pattern in the chromosome complement. In the small acrocentric chromosomes it was rather difficult to obtain bands other than major bands. The variation in the length of chromosomes and the unsatisfactory quality of G bands, both technical drawbacks, made it difficult to compare all the chromosomes of these two species. However, efforts have been made to study the G bands of chromosomes from a number of banded karyotypes and we are able to suggest that at least certain chromosomes from each species have similar banding patterns and may be regarded as homologous. These chromosomes are: Nos. 1, 2, 3, 4, 5, 6, 8, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 26, X, and Y.

In view of our original purpose of this study, such work is far from complete. Until a high quality of G band with subbanding patterns is achieved the question of homology or non-homology between these two species cannot be solved completely. More work is required in achieving such a goal and the present report can be regarded as a preliminary communication.

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Brood size manipulations in herring gulls

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Herring gull broods were artificially increased to four and five chicks while others were reduced to one chick. The growth rates of chicks and chick weights at fledging were similar among all control and experimental broods. The experimentally increased brood sizes had a slightly higher fledging success than control broods, and the fledging success of one-chick experimental broods was higher than that of one-chick control broods. Thus, chick survival was not reduced in larger brood sizes and the number of young fledged per pair of adults increased with brood size. Further, chicks in large broods were at no weight (or viability) disadvantage despite the presence of a larger number of brood mates. We conclude that food was not limiting either the growth rate or fledging success of chicks from broods larger than the modal clutch size, and suggest that parents used local, abundant, artificial food sources in addition to their natural food supply.

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Comparison of blood characteristics in plains bison, wood bison, and their hybrids

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Two hundred and eight blood samples were collected from four plains bison herds, one wood bison herd, and one herd that is assumed to be a hybrid between wood and plains bison. Haemolytic tests were made using 13 cattle blood typing reagents. Red cell carbonic anhydrase alleles were checked using electrophoresis. The frequencies of each blood trait within each of the six herds were determined. Comparisons of all possible pairs of herds for each trait were made and at least two significant differences ($P < 0.05$) were found in every case. Ten blood characteristics were used to discriminate among the six herds. Bison from Santa Catalina Island, California, were similar to those from the National Bison Range, Montana, and they jointly differed from the herd from Oklahoma and the three from Canada. The Canadian herds, which included wood bison, hybrid bison, and plains bison, were relatively similar to each other. Differences among the plains bison herds were at least as great as those among the two subspecies and their hybrids. These findings are discussed in relation to herd histories and to the variability among North American bison populations.

PEDEN, D. G., et G. J. KRAAY. 1979. Comparison of blood characteristics in plains bison, wood bison, and their hybrids. Can. J. Zool. 57: 1778–1784.

Deux cent huit échantillons de sang ont été prélevés chez quatre troupeaux de bisons des plaines, un troupeau de bisons des bois et chez un troupeau présumé hybride des deux sous-espèces. Treize réactifs ont été utilisés lors d'épreuves hémolytiques destinées à établir les types de sang. Les allèles de l'anhydrase carbonique des érythrocytes ont été déterminés par électrophorèse. La fréquence de chacune des caractéristiques sanguines a été évaluée pour chacun des troupeaux. La comparaison entre toutes les paires possibles de troupeaux, pour chaque caractéristique, a révélé, dans chaque cas, l'existence d'au moins deux différences significatives ($P < 0.05$). Dix caractéristiques sanguines ont servi de critères de distinction entre les six troupeaux. Les bisons de l'Île Santa Catalina en Californie sont semblables à ceux du National Bison Range du Montana et les bisons de ces deux troupeaux diffèrent du troupeau d'Oklahoma et des trois troupeaux canadiens. Les troupeaux du Canada, qui comptent des bisons des bois, des bisons hybrides et des bisons des plaines, sont relativement semblables les uns aux autres. Les différences entre les troupeaux de bisons des plaines sont au moins aussi importantes que les différences entre les deux sous-espèces et leurs hybrides. Ces résultats sont examinés à la lumière de l'histoire de ces troupeaux et de la variabilité au sein des populations nord-américaines de bisons.

[Traduit par le journal]

Introduction

The taxonomic status of wood bison (*Bison bison athabascae* Rhoads) is not clear. Although wood bison are usually distinguished from plains bison (*Bison bison bison* L.) by large size, large horncores, dark woolly pelage, and a relatively small amount of hair on their upper forelegs and in their beard, contradictory observations are abundant.

Wood bison were recorded as being larger than plains bison by Hearne, Thompson, Henry, Butler, Nelson, and Seton (Roe 1970). Other reports (Graham 1922; Anonymous 1922) confirm this view. In contrast, Roe cites the observations of Harmon and Buffalo Jones and records of the Hudson's Bay Company, which state that wood bison are smaller. Although data are lacking for wood bison, body size is highly variable in plains bison, with the average weight for a mature bull being 727 kg (National Buffalo Association, personal communication). At more than twice this weight, the largest known individual of either subspecies

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was a plains bull of 1518 kg (Anonymous 1972). Measurements of attributes of horn-cores and skulls appear to be sufficiently variable within populations that meaningful comparisons among populations of bison have not yet been made (Allen 1974; Skinner and Kaisen 1947; Shackleton *et al.* 1975). Although Roe (1970) and Allen (1974) cite numerous records that state that wood bison have a darker pelage, Geist and Karsten (1977) note that "in the wood bison bull, the long hair on the head, face, and beard appears to be less dark in colour than that of the prairie bison."

Two herds are recognized by the Government of Canada as being wood bison. These are located in Elk Island National Park (EINP), Alberta, and the Mackenzie Bison Sanctuary, Northwest Territories. Both of these herds were founded with individuals that were identified as wood bison on the basis of large body sizes, skull measurements, and dark woolly pelage (Banfield and Novakovski 1960).

It has been shown that several blood typing reagents detecting antigenic factors of the red blood cells of cattle (*Bos taurus*) also react with the red blood cells of the American bison (Miller and Stone 1955; Owen *et al.* 1958; Stormont *et al.* 1961). Sartore *et al.* (1969) and Morris *et al.* (1977) described a polymorphism of the red cell carbonic anhydrase of bison, consisting of six phenotypes, controlled by three alleles.

Because of the controversy about the taxonomic status of wood bison, this study was purposed to compare wood bison, plains bison, and their hybrids in terms of their reactions with cattle blood typing reagents and of their frequencies of carbonic anhydrase alleles.

Materials and Methods

Two hundred and eight blood samples were collected from six bison herds during a 9 month period beginning September, 1976. Thirty-two came from plains bison and 32 from wood bison at EINP. Forty-seven came from plains bison at the National Bison Range (NBR), Montana; 48 from the Wichita Mountains Wildlife Refuge (WMWR), Oklahoma; 23 from plains bison at the Santa Catalina Island Conservancy (SCIC), California; and 26 from the bison at Wood Buffalo National Park (WBNP), which are assumed to be hybrids between wood bison and plains bison.

Using the historical accounts of Dary (1974) and Mrs. Carl Sherwin and A. D. Propst (personal communication), we traced the ancestries of the hybrid and plains herds. The EINP, NBR, and SCIC plains bison can be traced to stock obtained in varying proportions from Saskatchewan, the Texas panhandle, and the Alberta–Montana border. The WMWR herd was founded with stock supplied by the New York Zoological Society. These plains bison were descendents of individuals captured in the Texas panhandle and in Kansas. The WBNP hybrid bison resulted from a mixing of 1500 wood bison from WBNP with 6700 plains bison having the same ancestry as the EINP plains herd. The wood bison herd at EINP was founded with animals that Banfield and Novakovski (1960) discovered in WBNP and identified as pure wood bison. As accurate herd histories and records of the numbers of each age–sex class from each source herd were not kept it is not possible to precisely describe the relative importance of the genetic contribution of each source to the six herds studied.

Blood samples were taken from either the jugular vein or the tail vein and collected in vacutainer tubes containing either heparin or EDTA as anticoagulant. The samples were shipped as soon as possible to the blood typing laboratory in Ottawa by air-express. The average transit time between drawing and arrival was 3 days.

The blood samples were tested with a set of cattle blood typing reagents that was known from previous tests in this laboratory to react with bison red cells. The hemolytic test used was essentially the same as described by Ferguson (1941). The reagents used were: anti-O_1, anti-O_3, anti-A′, anti-E′$_2$, anti-E′$_3$, anti-Q′, anti-F_1, anti-F_2, anti-V, anti-Z, anti-S, anti-A_1, anti-A_2, anti-D, anti-Z′, and anti-L. The reagent anti-L was used on samples from four herds only. Two replicas of the reagents anti-O_1, anti-O_3, and anti-V and three replicas of the reagents anti-A′ and anti-E′$_2$ were used.

The reagents were obtained from cattle isoimmune sera with the exception of three. Anti-F_2 was prepared from a sheep anticattle serum and anti-D and anti-Z′ from the pooled sera of rabbits immunized with cattle red blood cells. All the reagents were prepared in the Canadian cattle blood typing laboratory except anti-Q′, which was provided by Dr. H. C. Hines of the Ohio State University.

The factors O_1, O_3, A′, E′$_2$, E′$_3$ and Q′ belong to the B system of cattle. F_1, F_2, and V to the F system, and A_1, A_2, D, and Z′ to the A system. The factors Z, S, and L belong to separate systems (Stormont 1962).

Red cell hemolysates, obtained by freezing and thawing washed red blood cells, were tested for hemoglobin polymorphism using the method described by Braend *et al.* (1962) and for carbonic anhydrase polymorphism using the method of Sartore *et al.* (1969). Plasma samples were subjected to starch gel electrophoresis using methods that detect polymorphism in cattle transferrins (Kristjansson and Hickman 1965) and in cattle amylase and albumin (Gasparski and Stevens 1968).

As the history of the six herds was not accurately known and since we have not yet determined whether the cattle blood typing reagents detected specific alleles in bison, we have emphasized the phenotypic differences among the six herds. Chi-square tests (and exact binomial tests, whenever a characteristic was totally absent from a herd) were used to compare the frequencies of each blood type and each carbonic anhydrase allele among the six herds.

A step-wise discriminate analysis was used to test for differences among the six herds in terms of 12 blood characteristics (A′, E′$_2$(197), E′$_2$(179), Q′, F_1, F_2, V, Z, S, A, D, Z′) and three alleles of carbonic anhydrase. This procedure was also used to indicate (*a*) which blood characteristics most readily distinguish differences among the herds and (*b*) the fidelity with respect to these blood characteristics of individual members of each herd.

The R_0 index (index of overlap, Horn 1966), which is derived from information theory, was used to compare the overall similarity among bison herds. The degree of similarity is proportional to R_0 and may range from zero to one. The most similar pair of herds was first pooled to form one group. New values of R_0 were then calculated comparing all possible pairs among the new group and the remaining three original herds. In this man-

TABLE 1. Frequencies (%) of positive reactions of cattle blood typing reagents with bison red cells

Reagent for factor	Herd					
	NBR plains	SCIC plains	WMWR plains	EINP plains	EINP wood	WBNP hybrids
A′	0	0	0	21.9 (7.3)	0	0
E'_2(197)	2.2 (2.0)	0	6.3 (3.5)	3.1 (3.1)	0	15.4 (7.1)
E'_2(179)	0	13.0 (7.0)	58.3 (7.1)	3.1 (3.1)	0	3.9 (3.2)
Q′	100	95.7 (4.2)	89.6 (4.4)	90.6 (5.2)	96.9 (3.1)	92.3 (5.2)
F_1	61.7 (7.1)	43.5 (10.3)	18.8 (5.6)	87.9 (5.9)	84.4 (6.4)	46.2 (9.7)
F_2	100	100	89.6 (4.4)	96.9 (3.1)	100	88.5 (6.3)
V	83.0 (5.5)	82.6 (7.9)	6.2 (3.5)	9.4 (5.2)	3.1 (3.1)	23.1 (8.3)
Z	95.7 (2.9)	69.6 (9.6)	93.8 (3.5)	84.4 (6.4)	40.6 (8.7)	92.3 (5.2)
S	57.4 (7.2)	21.7 (8.6)	27.1 (6.4)	21.9 (7.3)	6.2 (4.3)	19.2 (7.7)
A_1–A_2	21.3 (6.0)	4.3 (4.2)	27.1 (6.4)	28.1 (7.9)	28.1 (7.9)	26.9 (8.0)
D	74.5 (7.3)	43.4 (4.2)	41.7 (7.1)	34.3 (8.4)	31.2 (8.2)	38.5 (9.5)
Z′	89.4 (4.5)	65.2 (9.9)	0	0	0	0
L	nt	nt	100	100	100	92.3 (5.2)
Sample size	47	23	48	32	32	26
Approximate herd size	400	400	600	400	7000	100

NOTE: The standard deviation of the frequencies is given in parentheses under the frequency. nt indicates not tested.

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ner, a dendrogram was prepared by the sequential pooling of most similar groups until all five had been included and only one group remained.

Results

The results of the hemolytic tests are summarized in Table 1 in the form of frequencies of positive reactions with the cattle blood typing reagents.

The bison cells reacted with none of the four reagents for the cattle O factors and neither with the E'_3 reagent and one of the V reagents. Bison cells always reacted strongly with the reagents for the cattle red cell antigenic factors A′, Q′, F_2, Z, S, A_1, A_2, and L. The reaction patterns of anti-A_1 and anti-A_2 were identical.

Two of the reagents for E'_2 showed a few weak reactions with the same cells. The results obtained with the more strongly reacting one, anti-E'_2(197) are reported. Another E'_2 reagent, anti-E'_2(179), showed reactions that varied from rather weak to moderately strong, but reacted with more blood samples than did anti-E'_2(197).

The reagents anti-D and anti-Z′ also showed reactions that varied in strength. Anti-D reacted with all cells that reacted with the A_1 and A_2 reagents and with some other cells.

The F_1 reagent usually gave weak reactions with the plains bison cells, but much stronger reactions with the cells of the wood bison and the crossbreds. The F_2 reagent reacted with many more animals than the F_1 reagent. In two herds (WMWR and WBNP) a few animals did not react with any of the F and V reagents (5 and 3 respectively).

Six phenotypes of carbonic anhydrase were observed. The distribution of the six phenotypes in the six herds is shown in Table 2. Assuming that

TABLE 2. Distribution of the six carbonic anhydrase phenotypes in six herds of bison, and the calculated gene frequencies

Carbonic anhydrase phenotype	Observed and expected numbers in each of the herds													
	NBR plains		SCIC plains		WMWR plains		EINP plains		EINP wood		WBNP hybrids		Total	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
1	0	1.5	1	3.1	14	15.1	0	1.2	1	0.5	2	1.9	18	23.3
1–2	16	12.4	15	9.2	13	11.8	11	8.5	6	6.5	10	9.7	71	60.1
1–3	1	1.5	0	1.5	13	11.8	1	1.3	0	0.2	0	0.6	15	16.9
2	23	25.0	3	6.7	3	2.3	14	15.7	24	23.7	12	12.4	79	85.8
2–3	7	6.2	4	2.2	2	4.6	6	4.9	1	1.1	2	1.4	22	20.4
3	0	0.4	0	0.2	3	2.3	0	0.4	0	0	0	0	3	3.3

Gene	Gene frequencies					
	NBR plains	SCIC plains	WMWR plains	EINP plains	EINP wood	WBNP hybrids
1	0.18	0.37	0.56	0.19	0.12	0.27
2	0.73	0.54	0.22	0.70	0.86	0.69
3	0.09	0.09	0.22	0.11	0.02	0.04

NOTE: Obs., observed; Exp., experimental. The expected numbers are calculated using the gene frequencies and assuming that the herds are in genetic equilibrium.

TABLE 3. Blood characteristics for which significant differences ($P < 0.05$) in pair-wise comparison of six bison herds were found using chi-square tests

	Wood bison, EINP	Hybrid bison, WBNP	Plains bison			
			EINP	NBR	SCIC	WMWR
Wood bison						
EINP	—					
Hybrid bison						
WBNP	F_1, Z	—				
Plains bison						
EINP	A′, Z	A′, F_1				
NBR	V, Z, S, D, Z′	E'_2(197), V, S, D, Z′, CA-1, CA-2, CA-3	A′, F_1, V, S, D, Z′	—		
SCIC	F_1, V, Z′	V, Z′	A′, F_1, V, Z′	Z, S, P, Z′	—	
WMWR	E'_2(179), F_1, Z, S, CA-1, CA-2, CA-3	E'_2(179), F_1	A′, E'_2(179), F_2, CA-2, CA-3	E'_2(179), F_1, V, S, D, Z′, CA-2, CA-3, Q′	E'_2(179), V, Z, Z′, CA-2, CA-3	—

each of the three bands is controlled by one allele, gene frequencies in each herd were calculated and shown in the bottom part of Table 2. Using these gene frequencies, the expected number of animals of each phenotype was calculated assuming that the herds are in genetic equilibrium. A chi-square test on the total numbers expected and observed of each type gave a value of 3.9, indicating agreement between observed and expected numbers.

No variation was detected in hemoglobin, transferrin, albumins, and amylase when using the methods that detect polymorphism in these proteins in cattle.

Significant ($P < 0.05$) differences in the frequencies of at least two characteristics were found in every pair-wise comparison of the six bison herds (Table 3). The only blood characteristics that did not show a significant difference on the basis of chi-square tests were E'_2(197), F_2, A, and L. Five characteristics were selected by the step-wise discriminate analysis for jointly accounting for 99% of the dispersion of the blood samples among the six herds of bison. In step one, the NBR and SCIC herds were separated from each other and from the other four herds on the basis of blood group factor Z′. In step two, the WMWR herd was distinguished from the three Canadian herds on the basis of Z′ and E'_2(179). In step three, the inclusion of blood

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TABLE 4. Number of blood samples (percentage in parentheses) drawn from each source herd that were classified and misclassified by discriminate analysis

	Herds into which blood samples were classified					
			Plains bison			
Source herd	Wood bison, EINP	Hybrid bison, WBNP	EINP	NBR	SCIC	WMWR
Wood bison EINP	25 (78)	1 (3)	6 (19)	0 (0)	0 (0)	0 (0)
Hybrid bison WNBP	3 (12)	13 (50)	4 (15)	0 (0)	3 (12)	3 (12)
Plains bison						
EINP	9 (28)	3 (9)	17 (53)	1 (3)	0 (0)	2 (6)
NBR	0 (0)	2 (4)	0 (0)	40 (85)	5 (11)	0 (0)
SCIC	1 (4)	3 (13)	0 (0)	2 (9)	17 (74)	0 (0)
WMWR	2 (4)	6 (13)	2 (4)	1 (2)	1 (2)	36 (75)

group factor V refined the differences described on the basis of Z′ and E'_2(179) but did not reveal any additional significant differences. In step four, blood group factor Z combined with Z′, E'_2(179), and V to characterize the differences between wood bison and plains bison from EINP, and between wood bison from EINP and hybrid bison from WBNP. In step five, factor F was included in the discriminate function to characterize a difference between hybrid bison from WBNP and plains bison from EINP. In additional steps, another five blood characteristics (A′, CA-1, CA-2, CA-3, D) refined the descriptions of the differences among the herds, whereas five more (A_1, E'_2(197), S, F_2, Q) did not contribute significantly to the differences as determined by discriminate analysis.

Results of the discriminate analysis of the blood traits tested indicated that at least a few blood samples drawn from any particular herd can be expected to be misclassified into one of the other five herds (Table 4). For example, 78% of the wood bison blood samples were characterized as belonging to the wood bison population, while 19% and 3%, respectively, more closely resembled individuals from the EINP plains bison and the hybrid bison herds. Of the EINP plains animals, 53% were correctly classified as members of that herd, whereas 28, 3, 6 and 9%, respectively, were misclassified as EINP wood bison, NBR and WMWR plains bison, and as WBNP hybrid bison. Similarly, 85% of NBR animals, 74% of SCIC bison, 75% of WMWR bison, and 50% of WBNP hybrid bison were correctly classified. Misclassification was most frequent in the EINP and hybrid bison herds.

The R_0 dendrograms separated the six herds into three major groups, with the SCIC and the NBR plains herds in one, the WMWR herd in the second, and the WBNP and the two EINP herds in the third (Fig. 1). Like the discriminate analysis, the R_0 dendrogram also indicated that the EINP and hybrid herds were the most similar pair among the three Canadian herds.

Discussion

To accept the subspecific status of wood bison according to Mayr (1963, p. 348) the following definition must hold true: "that a subspecies is an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species." Whether or not living wood bison can be uniquely distinguished from all plains bison on the basis of skulls, horn-cores, skeletons, and pelage is not known. Not until studies of several herds, with adequate sample sizes from each, are completed, can such conclusions be reached.

It was, therefore, decided to study some bison populations using cattle blood typing reagents. These reagents were prepared specifically for detecting antigens on the red blood cells of cattle. The specificity of most of these reagents has been

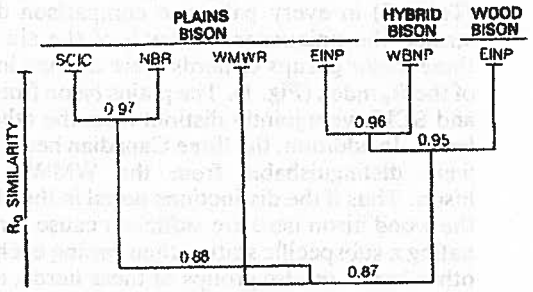

FIG. 1. Dendrogram indicating overall similarity of six bison herds. The most similar groups of herds in the tree are indicated by branches having the highest R_0 values.

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confirmed in at least one comparison test organized by the International Society for Animal Blood Group Research. Their reactions with bison red cells can be explained in three ways: (*a*) the antigens of bison are identical to those in cattle; (*b*) the antigens in bison are similar to those in cattle and give cross reactions; (*c*) the cattle reagents could contain heterologous antibodies reacting with bison cells, but not with cattle cells.

Stormont *et al.* (1961) concluded that the nine blood group systems they studied are homologous in bison and cattle; some antigens in bison are identical to those in cattle, whereas others give strong or partial cross reactions with the cattle reagents. Owen *et al.* (1958), studying the NBR herd, reported that their Z′ reagent did not react with bison cells. Stormont *et al.* (1961), studying the WMWR herd, found that their D reagent reacted only with A-positive bison cells. In this study reactions were obtained with the Z′ reagent and cells from bison in two herds, including the NBR herd. Also, in every herd studied, bison were found that reacted with the D reagent but not with the A reagents. These reactions of our Z′ and D reagents could be caused by heterologous antibodies. As the aim of this study was to determine whether there are differences between bison populations, no efforts were made to determine the exact relation between the bison and the cattle red cell antigens.

On the basis of the blood characteristics that were analyzed in this study, 78% of the wood bison were found to be more similar to the average type for this herd than they were to any of the other five herds from which samples were taken. Therefore, it can be concluded that, on the basis of blood characteristics, the wood bison at EINP differed from the other five populations.

Not only did the wood bison herd differ from the plains bison, but each of the other herds was also found to be unique in terms of the blood characteristics. Even though significant differences (Table 3) in every pair-wise comparison demonstrated the uniqueness of each of the six herds, three major groups of herds were defined in terms of the R_o index (Fig. 1). The plains bison from NBR and SCIC were jointly distinct from the other four herds. In addition, the three Canadian herds jointly were distinguishable from the WMWR plains bison. Thus if the distinctions noted in the blood of the wood bison herd are sufficient cause for designating a subspecific status, then raising each of the other herds, or else groups of these herds, such as the two from the NBR and the SCIC, to individual subspecies can be justified.

The ancestry of the four plains bison herds considered in this study can be traced to the mixing of animals from four common geographic sources and yet these herds still manifest considerable variability among themselves. Differences as great as those between the two plains herds from WMWR and NBR (Table 3) were observed despite the fact that both are in part descendants of founding stock captured in the Texas panhandle. This difference between the WMWR and NBR herds was greater than all of those between the wood bison herd and any individual plains herd. Thus, with respect to the blood characteristics considered in this study, the difference between the wood bison and plains bison was not any more significant than those observed among plains bison having similar sources as part of their recent ancestry.

As the three Canadian herds were relatively similar to each other, the assumption of isolation of wood bison from the hybrid bison in WBNP must be questioned. Banfield and Novakovski (1960) stated that, at WBNP, because tuberculosis was absent in the newly discovered wood bison herd, but was present in neighbouring hybrid bison, and because inhospitable terrain separated these two groups of bison, mixing of wood bison with animals having plains bison ancestry did not occur. In this study, the EINP plains bison, the hybrid bison, and the wood bison, as a group, were relatively similar to each other and distinctly distinguishable from the other three plains bison herds (Fig. 1).

The similarity of the hybrid and EINP plains bison is not surprising since 6700 head of an estimated 8200 animals in the founding stock of the hybrid herd came from the same source as the founding stock of the EINP plains bison. Whether or not the wood bison actually crossed with plains bison to form a hybrid is not known. Rather, hybridization has been assumed. If they did hybridize, the degree to which each source contributed to the hybrid gene pool is not known. If the original wood bison were very similar, in terms of blood characteristics, to the original founding stock of the EINP plains bison herd, then hybrid animals would also likely be similar. However, unless by chance the original wood bison were similar to the EINP plains herd, our data indicated that the three Canadian herds may have a common ancestry.

Blood samples from wood bison of the Mackenzie Bison Sanctuary have not been, but should be, tested. If this herd is found to be relatively similar to the three Canadian herds examined in this study, then the foregoing interpretations of our data are supported. If it differs, the variability of blood traits within the presently recognized subspecies renders these attributes useless for distinguishing between

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them. Thus, our results indicate that, with respect to the blood characteristics considered in this study, the taxonomic status of wood bison and plains bison can be questioned.

Development and use of more tests for red cell antigens and blood enzymes and tests to demonstrate the genotype or phenotypic character of red cell response of bison are needed. These tests, along with measurements of morphological and skeletal traits, need to be applied to adequate numbers of individuals in both wood bison herds, in the hybrid bison herd, and in several plains bison herds in order to clarify the taxonomic status of the living subspecies of *Bison bison*.

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Addendum III

GENETIC STUDIES