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SYSTEMATICS AND POPULATION ECOLOGY OF LATE PLEISTOCENE BIGHORN SHEEP (*OVIS CANADENSIS*) OF NATURAL TRAP CAVE, WYOMING

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Large numbers of Late Pleistocene bighorn sheep (total counts of identifiable elements: 4,497) *Ovis canadensis,* are described from the Natural Trap Cave, northern Wyoming. The specimens consist of nearly-intact skulls and enough post-cranial materials to assemble several complete sheep skeletons. Most of the fossils yield radiocarbon dates from 12,000 to 21,000 BP, while the oldest are more than 110,000 years old as dated by the fission-track method on the volcanic ash. The specimens resemble modern bighorn sheep (*Ovis canadensis*) in having shallow lachrymal fossae and relatively wide rostra, in contrast to the Asian argali (*Ovis ammon*), which exhibit deep fossae and narrow rostra. The sheep also have a proportionally large body size. A direct ancestor-descendent relationship between modern and the fossil sheep in North America seems probable. Reduction of body size seems likely to have occurred at the end of Pleistocene or the beginning of Holocene time. Young males predominated among the fossil sheep found in the Natural Trap Cave.

† † †

INTRODUCTION

Natural Trap Cave, south of the Wyoming-Montana border and Crow Indian Reservation, NW ¼, SE ¼, SEC. 28, T58N, R94W, Big Horn County, Wyoming, is a 26 m deep karst-sinkhole on the west side of the Big Horn Mountains in north central Wyoming (Fig. 1). The cave entrance, 4.6 m in diameter, is on the top of a gentle slope hidden from view until animals reached its edge, and therefore acted as a trap (for general environment, faunal list, and stratigraphy, see Gilbert, 1978; Martin and Gilbert, 1978a, 1978b; Wang, 1984; Chomko and Gilbert, 1987; Walker, 1987).

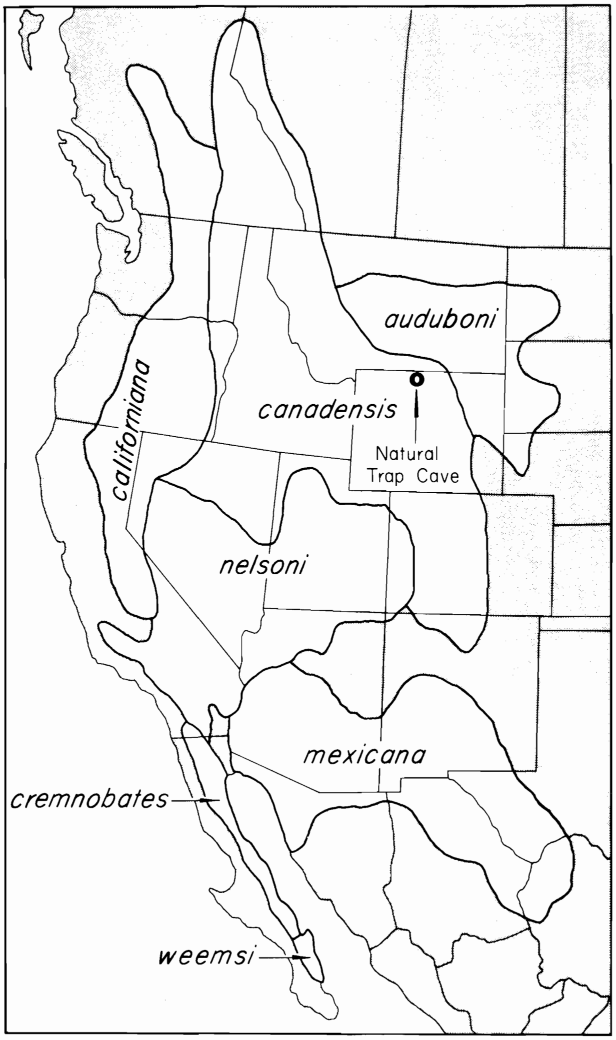

FIGURE 1. Modern bighorn sheep (subspecies) distribution (adapted from Monson and Sumner, 1980), with the Natural Trap Cave locality marked in circle.

Since 1974, 30,935 specimens were excavated and curated in the Museum of Natural History of the University of Kansas; 4,497 of these have been identified as bighorn sheep (*Ovis canadensis*), representing a minimum of 47 individuals (by counts of left astragali). Three nearly complete and eight partial skulls were excavated.

Radiocarbon dates from the majority of fossil materials found so far in Natural Trap Cave range from around 21,000 to 12,000 years old. Three lenses of volcanic ash were found in the 1980 excavation; approximately 3 dm beneath the ashes, a partial sheep skull and a tibia were excavated. The uppermost layer of the ash has been fission-track dated at 110,000 BP (Gilbert et al., 1980). The most recent expedition (summer 1985) found yet another cave under the ash, in which a complete horse skull was found. Screen-washing of the lower cave deposits yielded a microfauna characteristic of a Sangamon interglacial deposit.

Two North American wild sheep species are currently recognized: *Ovis canadensis* and *Ovis dalli* (thin-horned sheep or Dall sheep). The geographic subspecies *Ovis canadensis canadensis* now occupies the general area where the fossils were found (Fig. 1). *Ovis canadensis auduboni* of the northwestern Great Plains recently became extinct. *Ovis nivicola* from eastern Siberia west of Beringia, is probably the sister-group of North American wild sheep.

Severtzov (see Sushkin, 1925), a Russian naturalist, first considered the problem of bighorn zoogeography. He believed that *Ovis nivicola* was derived from North American *O. canadensis*, and that *O. canadensis* was intermediate between the Central Asian argali *O. ammon* and the snow sheep *O. nivicola*. The scenario of migration built on this hypothesis was later known as "reverse" or "double" migration theory, which was later supported by another Russian scientist N. Nasonov (Sushkin, 1925).

Alternatively, Cowan (1940) recognized the possibility that the sheep remained in the north on both sides of Beringia and suggested that "the reduced size of the rostral portions of the skull of [*O.*] *nivicola* together with the small rump patch seem to me to be undoubted primitive characters." He hypothesized that *O. canadensis* was isolated from the stocks ancestral to *O. nivicola* and *O. dalli* by the transcontinental ice sheet in North America, and became adapted to the more southerly environment, and never migrated back across Beringia to Asia.

Hoffmann (1976) advanced a "double gate" hypothesis concerning the migration routes between North America and Central Asia during the Pleistocene. Nadler, Hoffmann, and Woolf (1973) and Nadler, Korobitsina, Hoffmann, and Vorontsov (1973) postulated the following scenario of pachycerine (primarily North American) sheep evolution: *1.* Riss (Illinoian) glacial period: pachycerine sheep formed in the ice-free Beringian glacial refugium; *2.* Sangamon interglacial period: pachycerine sheep migrated south into the western United States through the ice-free corridor; *3.* Eemian (Sangamon)-Holocene?: differentiation of *O. nivicola* from *O. dalli; 4.* Würm (Wisconsin) glaciation: isolation of *O. canadensis* from other pachycerine sheep.

The bighorn sheep were some of the latest immigrants to North America. An understanding of bighorn natural history will lend insight into the latest history of the Ice Age.

The main purpose of this paper is to present morphological (largely cranial) studies of bighorn sheep from Natural Trap Cave, and to tackle the problems of systematics, evolution, and population variation of North American bighorns.

MATERIALS AND METHODS

All of the Natural Trap Cave sheep materials are housed in the Division of Paleontology, Museum of Natural History, University of Kansas, as is a cast of the fossil specimen published by Stovall (1946). Two excellent argali skulls from Central Asia were borrowed from the Zoological Museum, University of Montana, Missoula. Measurements on modern specimens of *Ovis canadensis canadensis* were made from collections of the University of Montana and the University of Wyoming, Laramie, by Dr. B. M. Gilbert, and from specimens of *O. c. californiana, O. c. nelsoni, O. c. mexicana, O. dalli dalli,* and *O. d. stonei* in the Division of Mammalogy, Museum of Natural History, University of Kansas.

Sectioning and polishing of teeth followed the procedure of Bourque et al. (1978). All measurements were based on the standard of von den Driesch (1976).

Abbreviations for institutions: UMZM — Zoological Museum, University of Montana, Missoula; UWA — Department of Anthropology, University of Wyoming, Laramie; KUMA — Division of Mammalogy, University of Kansas, Lawrence; KUVP — Division of Vertebrate Paleontology, University of Kansas, Lawrence.

TAXONOMIC DESCRIPTION OF NATURAL TRAP CAVE SHEEP

Lachrymal fossa

Gromova (see Korobitsina et al., 1974) placed *Ovis nivicola, O. dalli,* and *O. canadensis* in the subgenus *Pachyceros,* which represents a distinct lineage from the rest of the Old World sheep. The subgenus was characterized (Ellerman and Morrison-Scott, 1951) by the relatively broad skull (short facial region) and shallow lachrymal fossa (pit), in contrast to the narrow skull and deep lachrymal fossa of the Old World subgenus *Ovis,* which included *O. ammon,* Central Asian argali, probably the sister-group of *Pachyceros.* The preorbital gland occupies the lachrymal fossa, which is situated in front of the orbit (Fig. 2). Associated with this is a difference in external morphology of the preorbital gland (Geist, 1971a): in subgenus *Ovis,* the gland appears externally as a horizontal slit, but in North American bighorn (*O. canadensis* and *O. dalli*) it is a vertical, half-moon-shaped skinfold projecting beyond the facial hair.

Assuming the Asian argali to be the outgroup of pachycerine sheep, it follows that argali's deep fossa is primitive and the shallow fossa in modern North American bighorn would be derived. All three skulls (KUVP 31421, 35033, 35035 [Fig. 2]) from Natural Trap Cave that preserve the structure have very shallow lachrymal fossae (Figs. 2, 3). Three argali skulls (one *Ovis ammon poli,* KUMA 138997, from Tadzhikistan, USSR; one *O. a. ammon,* KUMA 12333, from the Altai Mountains; one *O. a. poli,* KUMA 26679, from the Pamir Mountains) in the collections of Museum of Natural History, University of Kansas, show much deeper fossae than Natural Trap Cave sheep and the two species of modern North American sheep (Fig. 2).

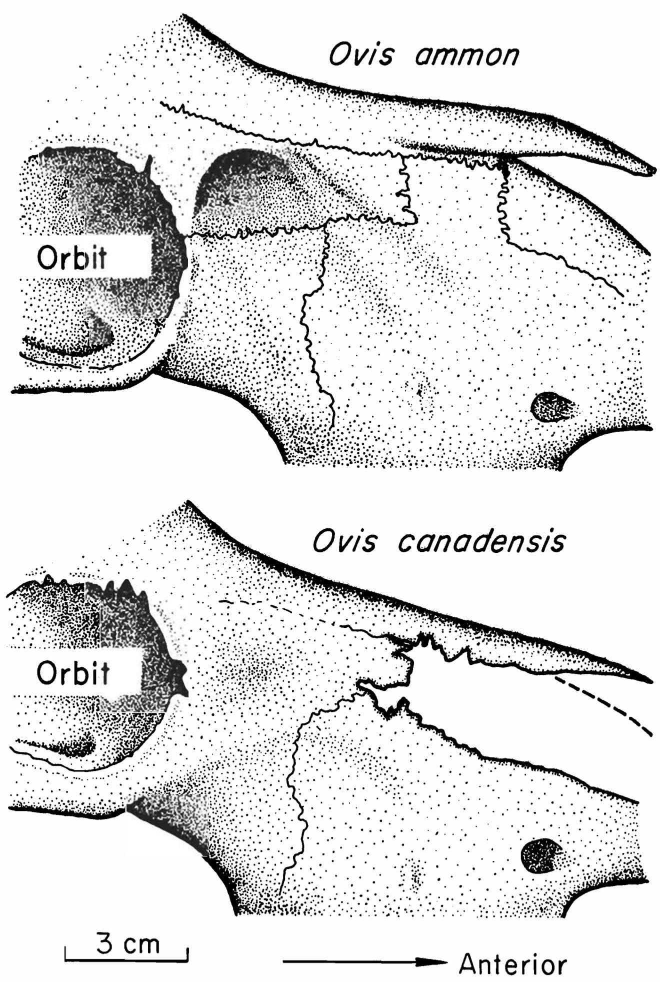

FIGURE 2. Illustration of lateral view of skull of North American bighorns (KUVP 35035) (lower) and Asian argali (KUMA 138998) (upper), showing the characteristic differences in lacrymal fossae.

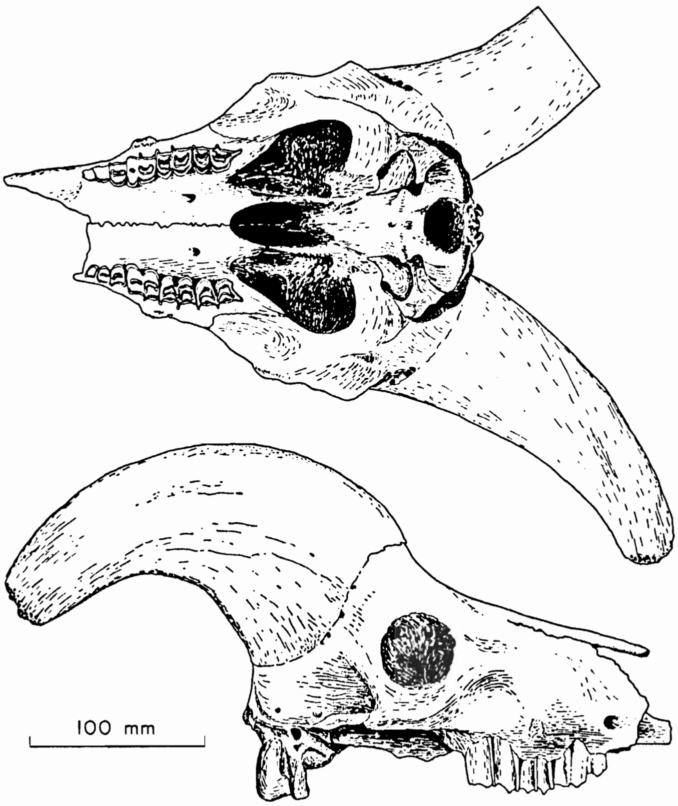

FIGURE 3. Illustrations of specimen KUVP 35035. Upper: ventral view; Lower: lateral view.

Stock and Stokes (1969) observed that two of the Great Basin fossil specimens that have the lachrymal and rostral regions partially intact showed that "the lachrymal pits (fossae) are weakly defined." Furthermore, in Late Pleistocene fossil argali (*O. ammon shantungensis*), from eastern China, "the lachrymal fossae are fairly large and conspicuous" (Matsumoto, 1926), supporting the view that reduced depth of the lachrymal fossae is a valid synapomorphy for *Pachyceros.*

Relative width of rostrum

This is thought to be another character that distinguishes *Ovis (Pachyceros)* from *O. (Ovis)* (Fig. 3) (Eiterman and Morrison-Scott, 1951). Unfortunately, in none of the Natural Trap Cave specimens was the delicate anterior premaxillary preserved, making direct measurements of this structure impossible. In this study, an alternative index of relative rostral width is devised for this comparison. Table I presents the ratio of the facial breadth over least breadth between the orbits (as defined by von den Driesch, 1976, *Fig. 9A),* It measures how fast the rostrum tapers toward the anterior end (the smaller the number, the narrower the rostrum). The small sample size does not permit a definite answer, but it appears that argali sheep can be readily separated from pachycerine sheep in this character, and in terms of rostral proportion, Natural Trap Cave sheep also group with the latter sheep.

TABLE I.

Species	Specimen Number	Relative Snout Width
O. ammon ammon	UMZM 12333	0.758
O. ammon poli	UMZM 26679	0.736
O. ammon	KUMA 138998	0.759
N.T.C. sheep	KUVP 31421	0.780(?)
N.T.C. sheep	KUVP 35033	0.843
N.T.C. sheep	KUVP 35035	0.922
O. canadensis californiana	KUMA 1771	0.798
O. canadensis mexicana	KUMA 54861	0.843

TABLE I. Relative width of the rostra of different species. Determined by dividing measurement of facial breath (across facial tuberosities) by measurement of least width between orbits, see von den Driesch, 1976: fig. 9a). Question mark indicates an estimate of the measurement.

Sections of horns and skulls

The outline of the cross-sections of the horn core base has attracted much emphasis from early workers, who were impressed by the great diversity of sheep-horn shape. However, the outlines of sheep horns (e.g., *Ovis ammon, O. canadensis,*) vary with age and geography, rendering it difficult to use.

Geist (1966, 1968a, 1968b, 1971a, 1971b, and in manuscript) argued that sheep-horn morphology is directly correlated with the behavior, or the way the horns clash with each other, during fighting for dominance. He suggested a trend wherein more advanced sheep have bigger, heavier horns. Accordingly, *Ovis canadensis* should have relatively the most massive horns among New World sheep. This was also substantiated by him through showing that there were highly-developed frontal sinuses or pneumations above the brain and extremely thick skull bones. Schaffer and Reed (1972), in their study on sheep and goat behavior and its related cranial morphology, cut sections of the horns and skulls of many sheep and goats. The results showed that *O. canadensis* has distinctly better-developed horn-core and frontal sinuses (as a result of selection for reduction of brain damage during combats) than does *O. ammon.* One of the skulls of the Natural Trap Cave sheep was sectioned and shows the well-developed sinuses characteristic of *O. canadensis* (Fig. 4). Several other broken skulls also exhibit highly-developed sinuses. Additional information was obtained by sectioning one horn-core of each of the *O. canadensis* and *O. dalli* specimens. There is clearly a transformation series of progressively better-developed pneumation from *O. ammon,* through *O. dalli* to *O. canadensis.*

Growth position of horns

The frontal in *Ovis ammon* is very wide between the two horns, whereas in Natural Trap Cave sheep and modern North

American sheep this is relatively narrow. This is probably due to the fact that the horns of North American sheep, including Natural Trap Cave specimens, are more erect in front view, reducing the space between the two horns to a valley, in contrast to the laterally-projecting horns of the argali, leaving a wide space between them.

Other skull morphology

The occipital condyles of the Trap Cave sheep are unusually low (Fig. 3) and well below the palatine plane, whereas the condyle of most modern North American sheep and Asian argali are not. This could have been associated with horn-clashing behavior, during which impact on the cervical vertebrae must have been tremendous. Further study is needed to determine how thew condyle morphology correlates with the way sheep clash.

DISCUSSION: SYSTEMATICS

This analysis would have been more complete had the skulls of Siberian snow sheep, *Ovis nivicola,* the presumed third allospecies of pachycerine sheep, been available. However, should my conclusions concerning pachycerine sheep skull characters be correct, the snow sheep can be predicted to have he advanced pachycerine characters of well-developed frontal and horn core sinuses, etc., as well as the characters that have been demonstrated above to be exclusively pachycerine (e.g., shallow lachrymal fossa and broad rostrum).

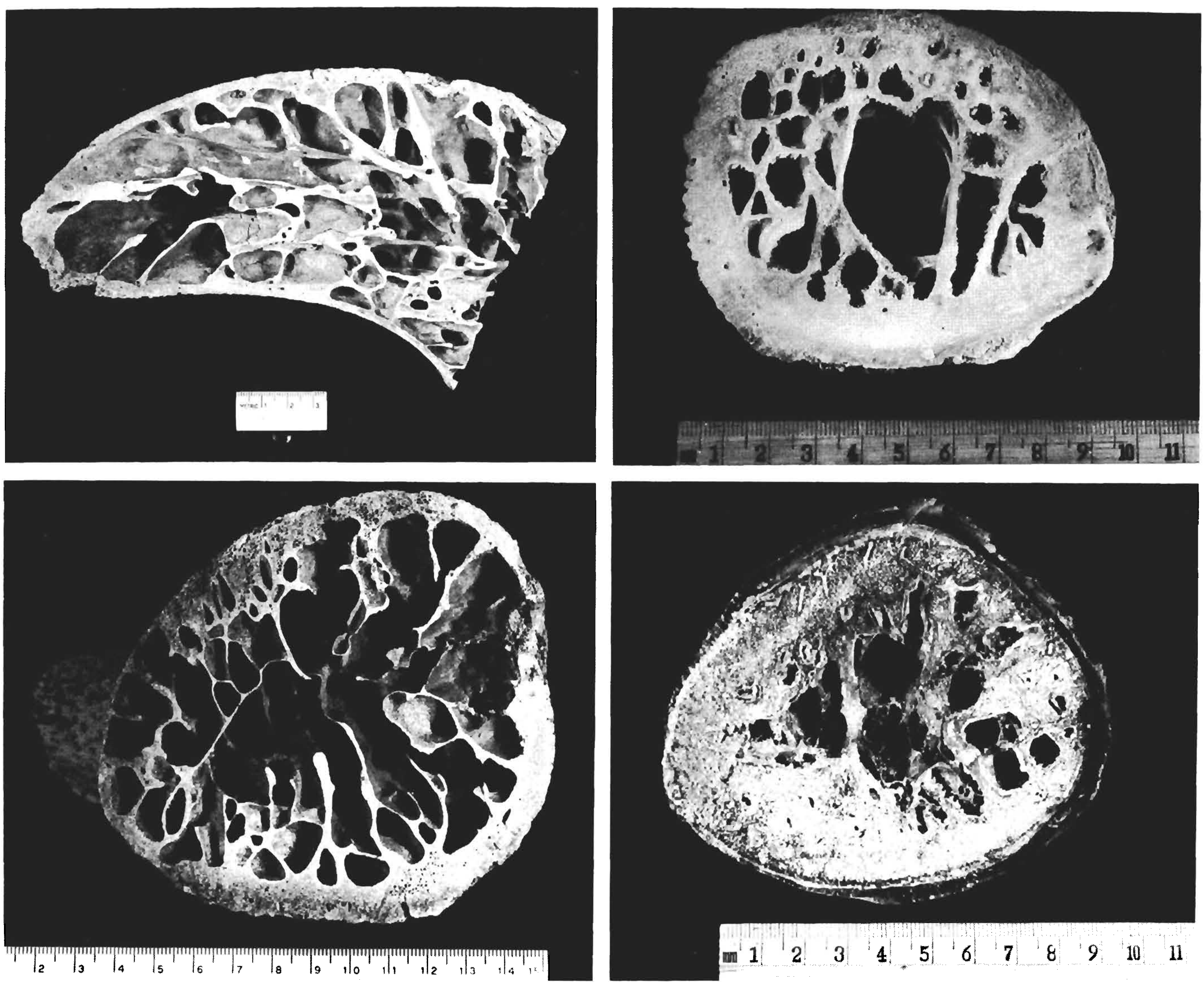

FIGURE 4. **(A)** Longitudinal and **(B)** cross sections at the base of the horn-core of a Natural Trap Cave sheep, showing the horn-core sinuses. Same cross sections of horn-core of **(C)** *O. canadensis* and **(D)** *O. dalli*. For comparison with that of *O. ammon, see* Schaffer and Reed (1972).

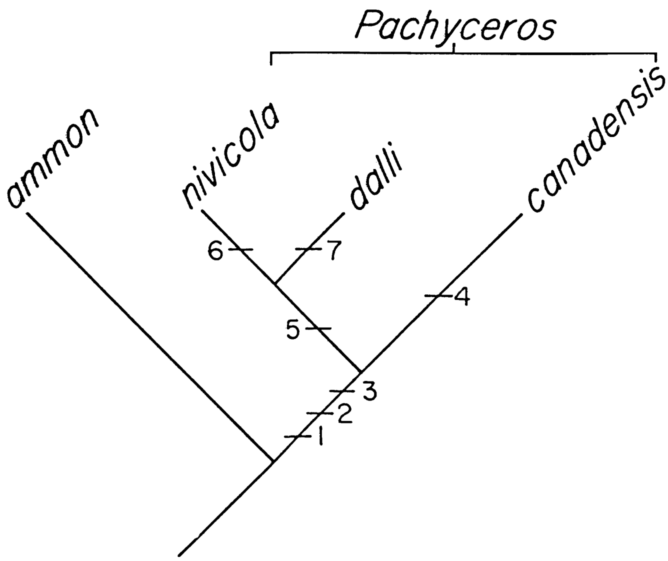

FIGURE 5. Proposed phylogeny of pachycerine sheep. Natural Trap Cave sheep are here included in *O. canadensis*.
Synapomorphies: 1. shallow lacrymal fossae; 2. broad rostrum; 3. well-developed horn core sinuses; 4. full development of frontal pneumation; 5. shorter horn-core (Geist, 1971a); 6. chromosomes 2n = 52; 7. coat color white.

The phylogeny of North American wild sheep is shown in Fig. 5, in which *Pachyceros* is defined by four synapomorphies. *Ovis ammon* (2n = 56) is used as the outgroup of *Pachyceros*. However, the mouflon sheep *O. musimon* of western Europe and the Near East has a chromosome number, 2n = 54, identical with that of *O. canadensis* and *O. dalli*, raising a problem for future study.

Even though most people accept *Ovis canadensis* and *O. dalli* as two distinct species, the only morphological characters proposed to distingish the two species are coat color, body size, and horn form (Cowan, 1940; Geist, 1971a). This poses problems concerning the relationship between Natural Trap Cave and other North American sheep. The Cave sheep do not seem to have osteological characters distinguishing them from either *O. canadensis* or *O. dalli*. However, it is widely accepted that continental and cordilleran ice caps acted as a barrier during the Wisconsinan to initiate the divergence between *O. canadensis* and *O. dalli*. Therefore, geographical distribution should be an aid to taxonomy. The Cave sheep, located south of the glacial ice and isolated from the Beringian sheep population, diverged along an evolutionary pathway toward modern *O. canadensis*.

Comparisons with other fossil North American sheep

Ovis catclawensis. Hibbard and Wright (1956) described a partial lower jaw of a bighorn sheep from Catclaw Cave in Mohave County, Arizona. The specimen was named as a new fossil species, *Ovis catclawensis*, and was said to differ from *O. canadensis* in "its larger size and wider lower premolars and molars." Measurements of the same tooth dimensions of Natural Trap Cave sheep (Table II) demonstrate that *O. catclawensis* falls within the ranges of Natural Trap Cave sheep, except for width of the M/3.

TABLE II.

	Natural Trap Cave				Cat Claw Cave*
	N	Mean	*SD*	Range	N = 1
Alveolar length (P/2-M/3)	11	103.81	2.35	100.8-108.0	101.0
Transverse Width of P/2	9	7.90	0.36	7.5-8.5	8.5
Transverse Width of P/3	11	9.40	0.31	8.9-9.9	9.8
Transverse Width of M/1	11	10.92	0.48	10.2-11.4	11.0
Transverse Width of M/2	11	11.96	0.54	11.0-12.5	12.5
Transverse Width of M/3	11	11.48	0.66	10.1-12.3	12.8

TABLE II. Measurements (in mm) of lower teeth from Natural Trap Cave compared with that from Cat Claw Cave.
*Measurements from Hibbard and Wright (1956).

TABLE III.

	Locality	*N*	Mean	Range	*SD*
Maximum core circumference	NTC	11	350.7	322-378	16.6
	LB	12	363	330-385	14.1
Maximum diameter horn core	NTC	10	122.6	112-133	5.9
	LB	12	118	101-127	6.7
Mastoid width	NTC	6	113.3	107-120	5.2
	LB	5	110	100-115	6.1
Minimum basioccipital width	NTC	8	32.06	28.8-34.5	2.21
	LB	6	32	29-33	1.65
Orbital width	NTC	7	183.5	174-194	7.1
	LB	5	172	165-180	12.5

TABLE III. Cranial measurements (in mm) of Natural Trap Cave (NTC) and Lake Bonneville* (LB) specimens.
*Measurements from Stokes and Condie (1961).

In addition, Hibbard and Wright (1956) mentioned the separation between anterior and median lobes at the base of M/3 in *O. catclawensis*. There is, however, no separation in juvenile sheep (tooth not fully erupted) of specimens from Natural Trap Cave, whereas some degree of separation is present in adult sheep. This indicates that the Catclaw Cave specimen was probably an adult. Therefore, *O. catclawensis* is here regarded as conspecific with the Natural Trap Cave sheep.

Great Basin specimens. Stokes and Condie (1961) examined 15 partial bighorn skulls from Pleistocene lake deposits at Lake Bonneville near Salt Lake City, Utah, and concluded that their material was similar to Central Asian argali. They assigned the fossils to *Ovis catclawensis* because their analysis was almost exclusively based on size. However, in the light of new data, the above senior author re-evaluated the Pleistocene Great Basin material and concluded that their specimens had shallow lachrymal fossae and wide rostra, and that the fossils actually resembled *O. canadensis* more closely than *O. ammon*. Hence, *O. catclawensis* was regarded by them as a restricted temporal population of *O. canadensis* (Stock and Stokes, 1969). The measurements published by Stokes and Condie are similar to those from Natural Trap Cave (Table III). The two sets of measurements overlap almost completely.

Since they have the same cranial dimensions, share the same diagnostic characters, and are almost contemporaneous (Lake Bonneville sheep are dated 15,000–12,000 BP), Natural Trap Cave and Lake Bonneville sheep are here referred to the same species.

Other fossil sheep. A single fossil skull from Bloomfield, San Juan River, New Mexico, was described by Stovall (1946); a cast of this was available for the present study. Stovall observed that "it agrees in almost every detail with a Recent specimen of *O. canadensis*..." The measurements of the specimen fall within the range for Natural Trap Cave sheep, although several are close to the lower limit. The horn core is more like those of Natural Trap Cave than modern bighorns in that it tapers more gradually than for the modern form. One feature of the San Juan River specimen that does seem to differ from the specimens examined in the collections of the University of Kansas is that there is a rather large concavity on the frontal and parietal bones above the occipital.

Corner (1977) described a sample of "at least seven individuals" of bighorn sheep from several Late Pleistocene gravel pits along the Republican River, Red Willow County, Nebraska. He assigned the sheep to *Ovis catclawensis,* again due to their comparable size. Most of the specimens are horn-cores and are similar to the Natural Trap Cave sheep. Measurements of all of the adult male specimens (4) are very close to that of the mean from Natural Trap Cave sheep. Therefore, the Nebraska specimens probably represent the easternmost distribution of Late Pleistocene bighorn sheep except one doubtful record from Ohio — *Ovis mammularis* Hildreth. It is more interesting, however, to note that the Red Willow sheep population is the only known Pleistocene bighorn that lived in the High Plains and was "driven onto the Great Plains from their normal ranges by cold associated with advancing alpine and continental glaciations." (Corner, 1977).

Furthermore, sheep collections in the Museum of Arid Land Biology from New Mexico, radiocarbon dated 15,030 ± 210 BP, also "compare favorably" with measurements of the Lake Bonneville specimen (Harris and Mundel, 1973); they are, therefore, the same size as the Natural Trap Cave sheep.

Finally, a partial right horn core of a large sized *O. canadensis* was described from the Late Pleistocene of Arapahoe County, Colorado (Wang and Neas, 1987). The specimen is the largest Pleistocene sheep in record, and is otherwise quite similar to sheep from Natural Trap Cave.

Conclusions. Figure 5 shows the inferred phylogency of New World wild sheep. Based on current information, the following three points can be inferred about the Pleistocene fossil bighorns:

a. The fossils exhibit the characteristics of North American pachycerine sheep, and therefore they had already diverged from the Palaearctic subgenus *Ovis;*

b. In terms of cranial morphology, the sheep were quite uniform all over western United States in the late Wisconsinan (21,000-10,000 BP);

c. Bighorns have not changed very much morphologically in the last 100,000 years, except for body size.

POPULATION ECOLOGY OF NATURAL TRAP CAVE SHEEP

Body size

Table IV gives some dimensions of Natural Trap Cave sheep compared to modern bighorns. Natural Trap Cave sheep average 6.3 percent larger than modern male *Ovis canadensis canadensis* from the collection of the University of Montana, whereas the latter average 8.4 percent larger than the same subspecies (male only) from the collection of the University of Wyoming. The larger difference in size among modern populations suggests that bighorns probably have the genetic potential to reach the size of Natural Trap Cave sheep.

Geist (1968b, 1971a), using mountain sheep-horn morphology, rump-patch size, and behavior, claims that the present distribution of North American bighorns is the result of retreat of ice of the Wisconsinan glaciation followed by subsequent reinvasion of the uninhabited areas by sheep from southern refugia (California and Nevada) at the end of the Pleistocene. Under the optimal environmental conditions of the "empty" habitat, the sheep grew to their maximum phenotypic size through neotenization. This process is supposed to be proportional to the dispersal of the sheep — the more distant from the southern refugia, the longer the sheep had undergone neotenization and therefore attained larger size. The model also includes a phase of stagnation when the new population saturated the environment, the quality of the population declined, and populations of smaller body size were selected.

TABLE IV.

		N	Mean	*SD*	Range
Humerus	NTC	15	246.6	8.44	239-269
	UM	10	241.7	7.33	232-252
	UW	5	225.8	5.12	218-232
Radius	NTC	28	257.6	12.7	235-293
	UM	10	256.1	6.89	248-270
	UW	5	232.6	5.73	225-240
Metacarpal	NTC	30	206.5	8.47	187-229
	UM	10	199.7	5.76	192-208
	UW	5	189.8	4.38	186-195
Femur	NTC	15	299.6	12.1	280-314
	UM	10	293.2	8.47	282-308
	UW	6	272.7	8.80	257-281
Tibia	NTC	17	350.2	16.0	324-373
	UM	10	344.0	7.80	334-360
	UW	6	323.2	5.31	313-327
Metatarsal	NTC	33	231.3	10.7	212-243
	UM	10	222.5	5.21	215-231
	UW	6	209.2	3.60	205-213

TABLE IV. Comparison between the greatest length (in mm) of limb bones among three collections of fossil and modern *Ovis canadensis*. NTC: Natural Trap Cave; UM: *O. c. canadensis* from University of Montana. UW: *O. c. canadensis* from University of Wyoming. All measurements of modern specimens are from male only.

TABLE V.

	Humerus vs. Metacarpal	Radius vs. Metacarpal	Femur vs. Metatarsal	Tibia vs. Metatarsal
Natural Trap Cave sheep	1.20	1.24	1.30	1.51
O. c. canadensis	1.21	1.28	1.32	1.55
American Pronghorn	0.92	0.99	1.04	1.21

TABLE V. Mean ratio of greatest length (von den Driesch 1976) between upper and lower limb bones. Number of specimens for each element: Natural Trap Cave, 15–33; *O. c. canadensis,* 13; American Pronghorn (from Natural Trap Cave), 6–16.

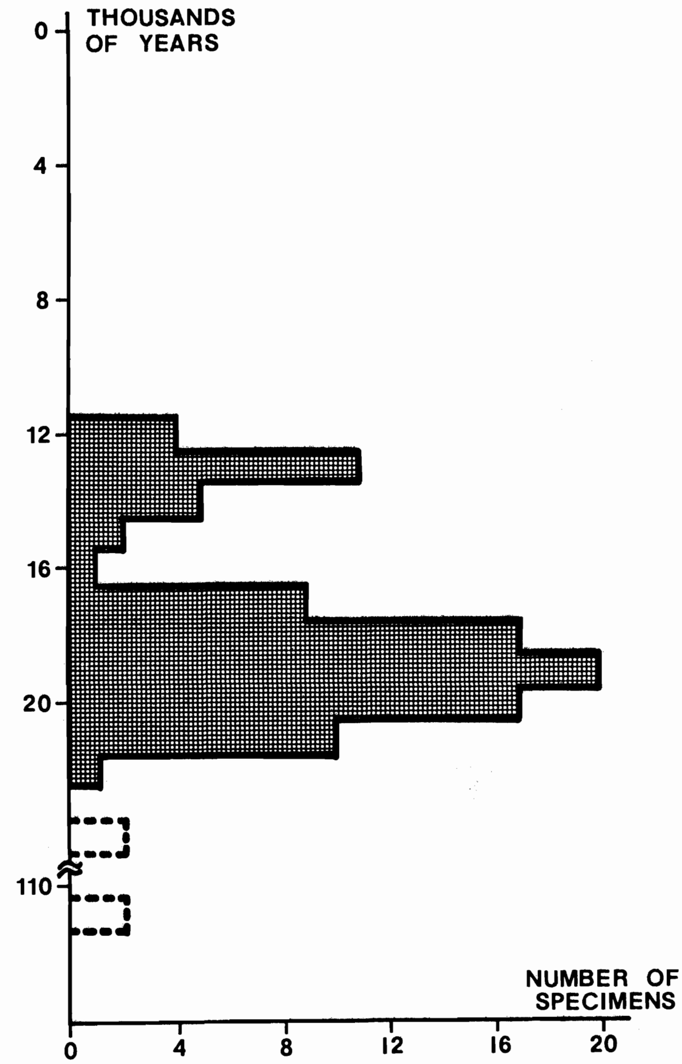

FIGURE 6. Histogram showing the frequencies of occurrence of Natural Trap Cave sheep based on individual metapodials. The broken lines indicate uncertainty of exact ages.

Harris and Mundel (1973) explored the possibility of size reduction in bighorn sheep at the close of the Pleistocene. To quote their conclusion: "In view of the fossil record, ...much of the specific character of *O. canadensis* was set by mid-Wisconsin time, that populations with relatively large-sized males were widespread in western United States and northern Mexico throughout the latter half of the Wisconsin, and that as a result of environmental deterioration, there was a general selection for smaller size at the close of the Pleistocene." They estimated that the transitional period from large to small was less than 2,000 years.

Both models postulate size reduction, but as Harris and Mundel pointed out, Geist's glaciation hypothesis requires a "post-mid-Wisconsin extinction of all bighorns outside a California-Nevada refugium."

Evidence from Natural Trap Cave seems to be consistent with the proposal by Harris and Mundel. Figure 6 is a histogram showing the chronological occurrence of Natural Trap Cave bighorns based on metapodials, which are preserved in larger numbers than other elements. The increase in numbers after 21,000 BP is probably due to sampling (the volume of matrix dug from above the 21,000 BP layer is about five times more than that excavated below it). It seems that large bighorns were living in the northern Rocky Mountains continuously throughout the Wisconsinan, even as far back as the Sangamon, perhaps interrupted by fluctuations of population density. However, a major decline after 12,000 BP at Natural Trap Cave appears to be real, which can be accounted for by the rapid climatic change between the Pleistocene and Holocene (e.g., Mörner, 1973). Preliminary pollen analysis of the deposits at Natural Trap Cave does not show a marked vegetational change during that period of time except for some increase in pines (unpublished data by William Johnson, Department of Geography, University of Kansas). Bighorn sheep continue to exist at higher elevations in the Big Horn Mountains at the present time.

At present, size reduction seems to be the most probable explanation for the difference in size and between the Ice-Age and modern sheep, unless a major extinction can be shown to have occurred at the end of Pleistocene that wiped out all large mountain sheep populations of Pleistocene North America. The size reduction seems to have taken place after 12,000 BP, i.e., at or after the transitional period between Pleistocene and Holocene.

Relative length of limb bones

Based on the cursorial nature of the majority of the large mammal fauna, Martin and Gilbert (1978b) reasoned that the immediate environment around the Natural Trap Cave had been open country as it is now. Forest dwellers such as *Martes* were explained as "occasional visitors."

Consequently, Martin and Gilbert (1978a, 1978b) speculated that Natural Trap Cave sheep had relatively long legs adapted to open country and steppes for fast running to escape natural enemies such as the American cheetah-like cat, *Miracinonyx trumani*, and the American lion, *Panthera atrox*. The ratio of limb-bone length to metapodial-length was calculated for Natural Trap Cave sheep, modern Rocky Mountain sheep *(Ovis canadensis canadensis)*, and typical cursorial American pronghorn *(Antilocapra americana americana)*, (Table V). (The smaller the ratio, the longer the metapodials relative to other limb bones). These data show that the relative length of the legs of Natural Trap Cave sheep is slightly longer than that for their modern relatives, and therefore more capable of running than their modern relatives. But it is not quite comparable to that of *Antilocapra*.

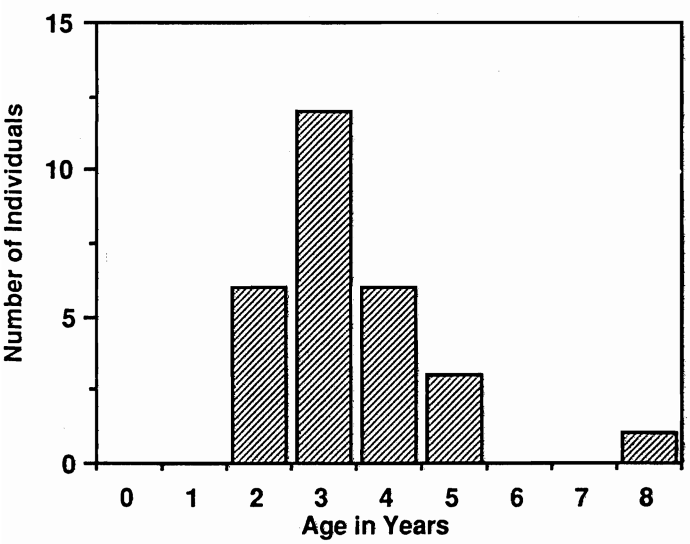

FIGURE 7. Age distribution of Natural Trap Cave bighorn sheep. Derived from cemental annulation of left incisors (see text). Sample size of incisors: 28.

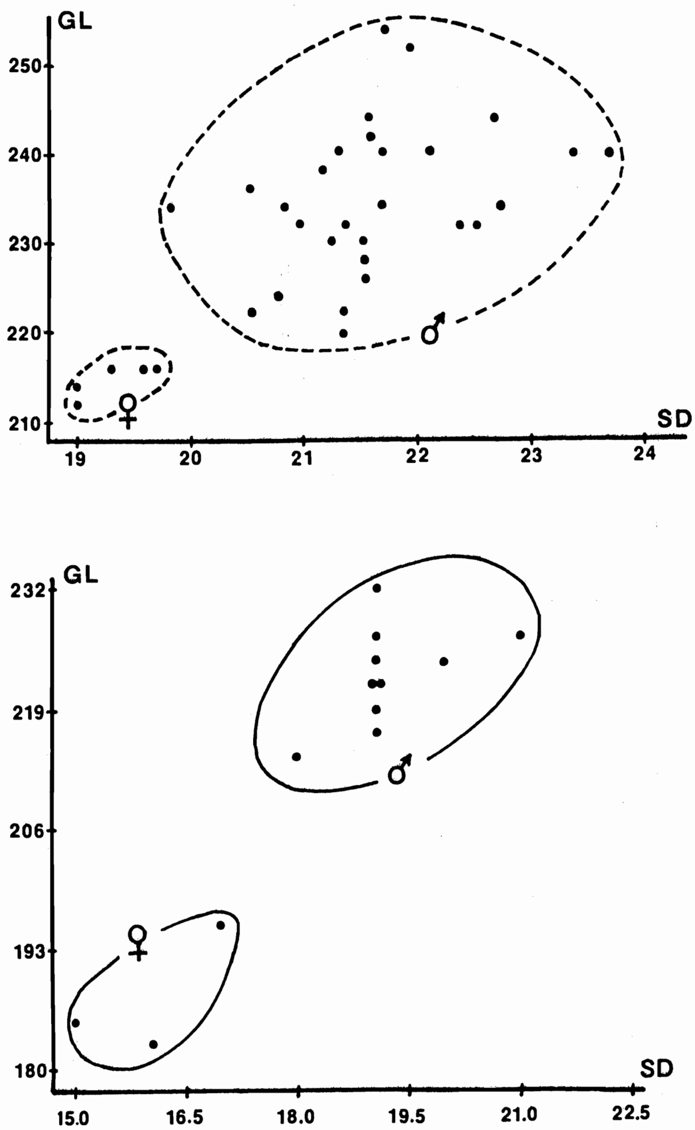

FIGURE 8. Plots of measurements of greatest length (GL) over smallest breadth of diaphysis (SD) of metatarsals, showing sexual dimorphism. Upper: Natural Trap Cave sheep. Lower: modern *O. c. canadensis* (measurements of University of Montana sample).

Population composition of bighorn sheep

Cemental annulation has been shown to be one of the best methods to determine individual ages of bighorn sheep (Turner, 1977). The sectioning technique of Bourque et al. (1978), with certain modifications, is applied to the first left incisors of Natural Trap Cave sheep (28 in total) (Fig. 7). The presumed age of death by counts of cemental annulation is generally quite young: 18 of them were under 4 years of age. (Modern bighorns have an average life expectancy of 6.7–10.1 years [Geist, 1971a].) This age distribution is generally supported by fusion sequence of different elements of bones. Examples of complete fusion of the epiphysis with the diaphysis (stage 4 of Walker [ms]), representing ages from 3.3 years in cervical vertebrae to 1.5 years in phalanges, are relatively rare in the Natural Trap Cave sample. Only 17% of all third-through-seventh-cervical vertebrae are completely fused, indicating an age of 3.3 years or older. Likewise, 17% of metacarpals are entirely fused (2.3 years or older); and 80% of phalanges (1.5 years or older). This age distribution could become even younger if preservational bias is taken into consideration, which tends to favor larger adults (to be published in separate paper on taphonomy).

Sexual dimorphism is highly conspicuous in all species of modern wild sheep except males under two years of age. One of the most obvious characteristics is the size of the horns. This is also true of horn cores: those of males are several times larger than those of females. In addition, body size is also a good indicator of sex: adult rams often weigh twice as much as adult ewes (Cowan, 1940).

Of the 11 partial skulls in the collection from Natural Trap Cave, none is from female. Thirty-three adult metatarsals (the epiphysis is completely fused with the diaphysis) were measured, and the greatest length (GL) and smallest breadth of the diaphysis (SD) (von den Driesch, 1976) were plotted and compared with modern *Ovis canadensis canadensis* (Fig. 8). Only five of the 33 metatarsals (15%) show clear separation from the remainder; these probably represent females.

The 15 skulls of the Lake Bonneville specimens are males "as evidenced by the massive horn cores and large teeth," according to Stokes and Condie (1961). They speculated that "perhaps the spot [where the sheep were found] was frequented by solitary old males no longer associated with the herds in their normal ranges." On the other hand, there was the possibility of sample bias by wave action.

An important advantage of the Natural Trap Cave sample is that all animals died *in situ*. Thus, the uneven sex ratio must be due to some behavioral characteristics of the sheep. Young males were apparently more vulnerable to falling into the cave. Modern bighorn populations showed apparent segregation during most times of the year except rutting seasons (around November and December), and inexperienced young adults sometimes went alone to unfamiliar areas (Geist, 1971a). The trapping of bighorns in the cave might have favored the more adventurous young males. In fact, 15 out of the 28 sectioned incisors (for age determination, see above) have indications of winter death. However, caution should be exercised because it is sometimes difficult to make a clear judgment about the outer most layers of the cement.

CONCLUSIONS

The fact that all of the Pleistocene North American fossil sheep are pachycerine-like generally supports Nadler's et al. (1973) hypothesis that they have migrated into the western United States dring the Sangamon interglacial period. *Ovis canadensis* was subsequently isolated from other pachycerine sheep during the Wisconsinan period. The Wisconsinan glaciation made it nearly impossible for the sheep south of the glacial front to go back through Beringia to give rise to *O. nivicola*.

The Natural Trap Cave sheep are very similar morphologically to modern bighorn sheep. The larger size is probably within the range of genetic potential in the modern bighorns. Considering the fact that Rocky Mountain bighorns currently reside in the Natural Trap Cave area, and that they probably occupied the area continuously as far back as the Sangamon, it is logical to assign the Natural Trap Cave sheep to *O. canadensis*. *Ovis catclawensis,* which is morphologically indistinguishable from both Pleistocene and Recent *O. canadensis,* is here synonymized with *O. canadensis.*

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REFERENCES

Bourque, B. J., K. Morris, and A. Spiess. 1978. Determining the season of death of mammal teeth from archaeological sites: a new sectioning technique. *Science,* 199(3): 530–531

Chomko, S. A., and B. M. Gilbert. 1987. The Late Pleistocene/Holocene faunal record in the northern Bighorn Mountains, Wyoming. *In* R. W. Graham, H. A. Semken, Jr., and M. A. Graham (eds.), *Late Quaternary mammalian biogeography and environments of the Great Plains and Prairies.* Illinois State Musem Scientific Papers, 22: 394–408.

Corner, R. G. 1977. A Late Pleistocene-Holocene vertebrate fauna from Red Willow County, Nebraska. *Transactions of the Nebraska Academy of Sciences,* 4: 77–93.

Cowan, I. M. 1940. Distribution and variation in the native sheep of North America. *American Midland Naturalist,* 24(3): 505–580.

Ellerman, J. R., and T. C. S. Morrison-Scott. 1951. *Checklist of Palaearctic and Indian mammals, 1758–1946.* London, British Museum (Natural History): 810p.

Geist, V. 1966. The evolutionary significance of mountain sheep horns. *Evolution,* 20: 558–566.

__________ . 1968a. On the interrelation of external appearance, social structure of mountain sheep. *Zeitschrift für Tierpsychologie,* 25: 199–215.

__________ . 1968b. On delayed social and physical maturation in mountain sheep. *Canadian Journal of Zoology,* 46: 899–904.

__________ . 1971a. *Mountain sheep, A study on behavior and evolution.* Chicago and London, The University of Chicago Press: 383p.

__________ . 1971b. On the relationship of ecology and behaviour in the evolution of ungulates: theoretical considerations. *In* International Symposium on the Behavior of Ungulates and its Relation to Management, *University of Calgary, Alberta, Paper No. 10:* 235–246.

__________ . On the Pleistocene history of bighorns and some problems of adaptation. [Manuscript.]

Gilbert, B. M. 1978. Natural Trap Cave. *Wyoming Wildlife,* 42(1): 10–13.

__________, D. Pearsall, and J. Boellstorff. 1980. Post-Sangamon record of volcanism and climatic change at Natural Trap Cave, Wyoming. *American Quaternary Association, Sixth Biennial Meeting, Abstracts and Program.*

Harris, A. H., and P. Mundel. 1973. Size reduction in bighorn sheep *(Ovis canadensis)* at the close of the Pleistocene. *Journal of Mammalogy,* 55(3): 678–680.

Hibbard, C. W., and B. Wright. 1956. A new Pleistocene bighorn sheep from Arizona. *Journal of Mammalogy,* 37(1): 105–107.

Hoffmann, R. S. 1976. An ecological and zoogeographical analysis of the Quaternary period. *In* V. L. Kontrimarichus (ed.), *Beringia in Cenozoic,* Acad. Sci. USSR., Far-Eastern Scientific Centre.

Korobitsina, K. V., C. F. Nadler, N. N. Vorontsov, and R. S. Hoffmann. 1974. Chromosomes of the Siberian snow sheep, *Ovis nivicola,* and implications concerning the origin of Amphiberingian wild sheep (subgenus *Pachyceros). Quaternary Research,* 4: 235–245.

Martin, L. D., and B. M. Gilbert. 1978a. An American lion, *Panthera atrox,* from Natural Trap Cave, north central Wyoming. *Contributions to Geology, University of Wyoming,* 16(2): 95–101.

__________, and __________. 1978b. Excavations at Natural Trap Cave. *Transactions of the Nebraska Academy of Sciences,* 6: 107–116.

Matsumoto, H. 1926. On a new fossil race of bighorn sheep. *Science Reports of Tohoku Imperial University Sendai (Japan),* 10: 28–39.

Monson, G., and L. Sumner, eds. 1980. *The desert bighorn, its life history, ecology and management.* Tucson, The University of Arizona Press: 370p.

Mörner, N.-A. 1973. Climatic changes during the last 35,000 years as indicated by land, sea and air data. *Boreas,* 2: 33–54.

Nadler, C. F., R. S. Hoffmann, and A. Woolf. 1973. G-band patterns as chromosomal markers, and the interpretation of chromosomal evolution in wild sheep *(Ovis). Experientia,* 29(1): 117–119.

__________, K. V. Korobitsina, R. S. Hoffmann, and N. N. Vorontsov. 1973. Cytogenetic differentiation, geographic distribution, and domestication in Palearctic sheep *(Ovis). Sonderdruck aus Zeitschrift für Säugetierkunde,* 38: 109–125.

Schaffer, W. M., and C. A. Reed. 1972. The co-evolution of social behavior and cranial morphology in sheep and goats. *Fieldiana Zoology,* 61(1): 1–88.

Stock, A. D., and W. L. Stokes. 1969. A re-evaluation of Pleistocene bighorn sheep from the Great Basin and their relationship to living members of the genus *Ovis. Journal of Mammalogy,* 50(4): 805–807.

Stokes, W. L., and K. C. Condie. 1961. Pleistocene bighorn sheep from the Great Basin. *Journal of Paleontology,* 35(3): 598–609.

Stovall, J. W. 1946. A Pleistocene *Ovis canadensis* from New Mexico. *Journal of Paleontology,* 20(3): 259–260.

Sushkin, P. P. 1925. The wild sheep of the Old World and their distribution. *Journal of Mammalogy,* 6(3): 145–157.

Turner, J. C., 1977. Cemental annulations as an age criterion in North American sheep. *Journal of Wildlife Management,* 41(2): 211–217.

von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletins,* Harvard University, 1: 1–137.

Walker, D. N. 1987. Late Pleistocene/Holocene environmental changes in Wyoming: the mammalian record. *In* R. W. Graham, H. A. Semken, Jr., and M. A. Graham (eds.), *Late Quaternary mammalian biogeography and environments of the Great Plains and Prairies.* Illinois State Museum Scientific Papers, 22: 334–392.

__________ . (ms). The sequence of epiphyseal fusion in the Rocky Mountain bighorn sheep. [To be published.]

Wang, X. 1984. *Late Pleistocene bighorn sheep (Ovis canadensis) of Natural Trap Cave, Wyoming.* Master's thesis, University of Kansas: 65p.

__________, and J. F. Neas. 1987. A large bighorn sheep, *Ovis canadensis* (Artiodactyla: Bovidae), from the Late Pleistocene of Colorado. *The Southwestern Naturalist,* 32: 281–283.