# A NEW RECORD OF GIANT SHORT-FACED BEAR, *ARCTODUS SIMUS*, FROM WESTERN NORTH AMERICA WITH A RE-EVALUATION OF ITS PALEOBIOLOGY

## Steven D. Emslie[1] and Nicholas J. Czaplewski[2]

ABSTRACT. Remains of the extinct giant short-faced bear, *Arctodus simus,* from Labor-of-Love Cave in Nevada constitute the first record of this species in eastern Nevada. The skeleton was found in association with black bear remains, *Ursus americanus,* eroding from a gravel lens in silt sediments along the banks of a stream flowing through the cave. The deposits are probably late Pleistocene in age. The *Arctodus* remains are from a small adult and represent one of the most complete skeletons recovered of this species. Association of cranial with postcranial bones allowed us to determine proportions and ratios of limb elements in a single individual. The hypothesis that *A. simus* was a highly predaceous cursorial carnivore is examined. We prefer to believe that this animal was largely herbivorous, based upon comparative studies of the skull and functional morphology of the jaw in living *Tremarctos ornatus,* and upon the noncursorial features in the limbs of *A. simus.*

## INTRODUCTION

The recovery of a partial skeleton of the giant short-faced bear, *Arctodus simus,* and the black bear, *Ursus americanus,* from a cave in east-central Nevada, represent the first records of these bears from eastern Nevada; *U. americanus* currently occurs in western Nevada (Hall, 1946). The cave and the bear remains were originally discovered by members of a local speleological society in Ely, Nevada, who named the cave "Labor-of-Love Cave." Other mammals represented at this cave include *Ursus* cf. *arctos* and *Ovis canadensis.*

The cave is located at the base of a limestone cliff on the east side of the Schell Creek Range, White Pine County, Nevada. The east-facing entrance is at an elevation of 2050 m. The cave extends over 137 m into the mountain along a fault plane and consists of one main passage. Currently, a small stream flows the entire length of the cave and emerges at the base of a talus slope 30 m below the cave entrance. Air and water temperatures in the cave remain constant year-round at 10°C.

Postcranial material from Labor-of-Love Cave includes the first associated limb elements of *A. simus* on which relative proportions can be determined. This analysis, together with earlier studies on the living spectacled bear, *Tremarctos*

*ornatus,* an animal similar in structure to *A. simus,* allows a re-evaluation of the paleobiology of the latter species.

We conclude that *A. simus* was not necessarily adapted for a cursorial, predaceous life-style, nor could it have attained its large size by strict carnivory. Based on skull and jaw architecture, tooth morphology and wear, and limb structure, *A. simus* was probably largely herbivorous, but retained bone-crushing capabilities and may have been an opportunistic predator and scavenger.

## SITE LOCATION

Two concentrated bone deposits (BC-1, BC-2) were found in two pools of water along the stream edge, and located approximately 10 m apart at the rear of the cave (Fig. 1a). Diversion of stream flow through fissures in the limestone bedrock maintains these pools as quiet backwater areas.

In summer 1982, under an emergency permit from the U.S. Forest Service, one of us (SDE) collected and preserved bones from the two pools before they were washed away by fluctuations in stream flow or stolen by vandals. The permit was authorized under the aegis of the Natural History Museum of Los Angeles County (LACM) where the specimens are now housed. Bones in the cave were photographed, mapped, and collected over a period of three days. Spatial orientation of bones was mapped (Figs. 1b, 2) by triangulation, using two or three large aluminum nails, placed in the substrate at each bone concentration. Each bone was then carefully removed, wrapped in aluminum foil to avoid contamination, assigned a field number, and packed in a labeled box prior to removal from the cave. Excavations in cave strata were not initiated, and are planned for future investigations. Consequently, no detailed analyses of cave sediments have been completed. The material was transported

1. Department of Zoology, University of Florida, Gainesville, Florida 32611.

2. Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011.
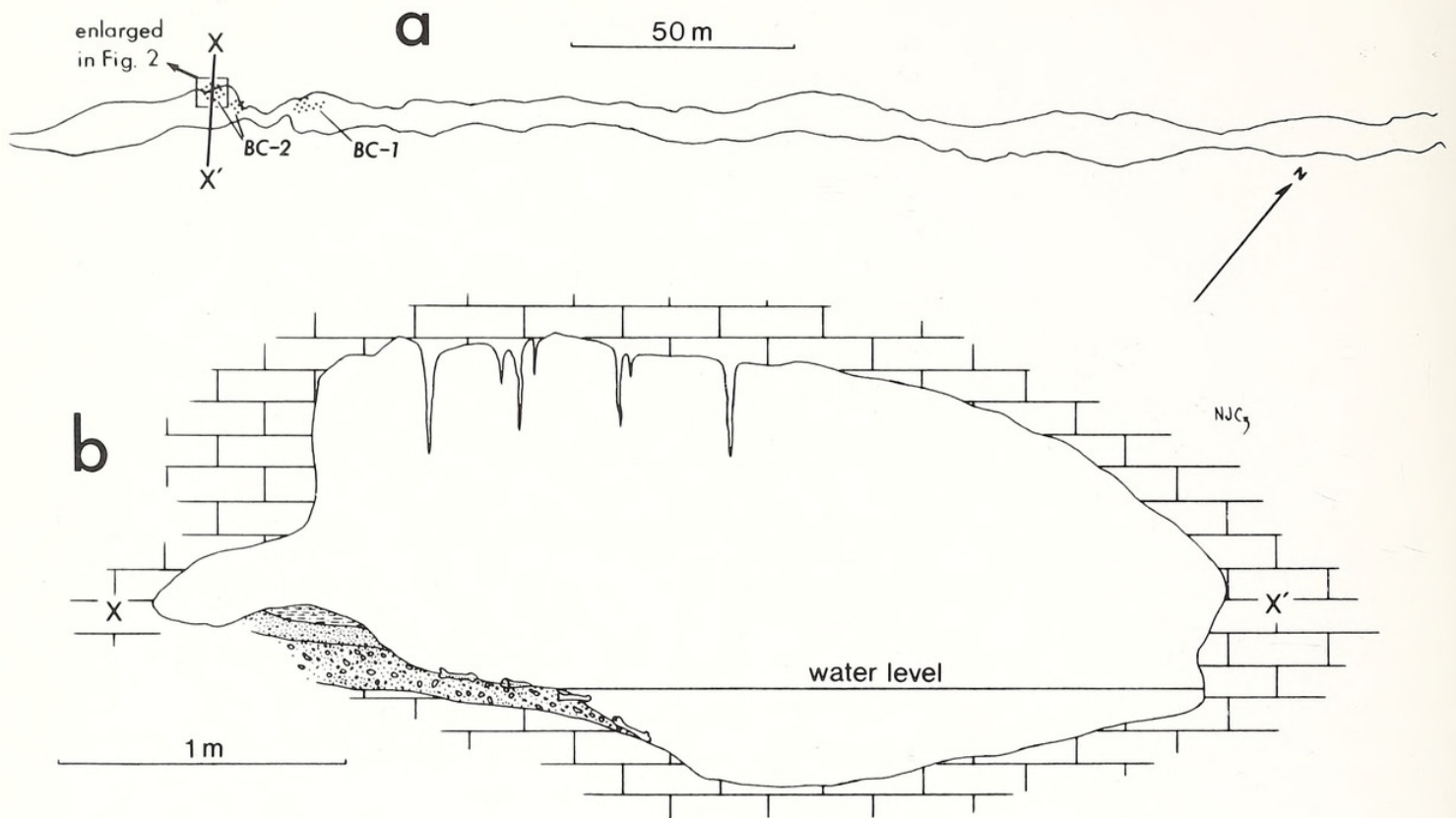
**Figure 1.** Plan view (a) and cross section (b) of Labor-of-Love Cave showing the locations of Bone Concentrations (BC) #1 and #2 and the gravel lens from which the bones at BC-2 were eroding.

to the George C. Page Museum of LACM for curation and transferred to LACM for permanent storage. The bones were identified using comparative collections of Pleistocene and Recent mammals in the museum. Other fossil remains of *A. simus* at the American Museum of Natural History, New York, and Recent remains of *Ursus arctos* and *U. americanus* at the U.S. National Museum, Washington, D.C., were also examined.

All vertebrate fossils recovered from the cave are identified below, but only the remains of *A. simus* are discussed in detail in this paper.

### SYSTEMATIC PALEONTOLOGY

#### Order Carnivora

#### Family Ursidae

#### Genus *Ursus* Linnaeus, 1758

#### *Ursus americanus* Pallas, 1780
(Black Bear)

**REFERRED MATERIAL.** LACM 122435, several skull fragments including maxillae and premaxillae, both lower jaws, atlas, axis, one thoracic and three other vertebral frag-

ments, both scapulae, humeri, ulnae, radii, a right tibia, metacarpal II (right and left), III (right), IV (right and left), and V (right and left), metatarsal III (right) and IV (right), and ten rib fragments; LACM 123780, left tibia; LACM 123783, diaphyses of right and left humeri; LACM 123786, right $M_1$.

**DISCUSSION.** LACM 122435 was recovered from BC-1 and represents an immature individual, approximately 3–4 years old at times of death based on epiphyseal fusion of long bones. LACM 123780 was also found in BC-1 but represents another individual. LACM 123783 and 123786 were found eroding from the gravel lens at BC-2, in direct association with bones of *A. simus* (Fig. 2b, c). A minimum of three *U. americanus* individuals are represented.

#### *Ursus* cf. *U. arctos* Linnaeus, 1758
(Grizzly Bear)

**REFERRED MATERIAL.** LACM 123782, diaphysis of left tibia.

**DISCUSSION.** This tibia, found at BC-1, compares well in size and morphology to that of a modern Kodiak bear (Fig. 3). It is more robust, with a shaft flared at both proximal and distal ends, and has a more sharply ridged shaft than in other bear species. These characters are lacking in late Pleis-

**Table 1. Measurements of the right mandible (LACM 122434) of *Arctodus simus* from Labor-of-Love Cave, Nevada.**

| | |
|---|---|
| Length, anterior base of $C_1$ to condylar process | 253.0 mm |
| Depth of mandible at $P_3$ | 56.5 mm |
| Depth of mandible at coronoid process | ca. 112–113 mm |
| Alveolus length, $C_1$–$M_3$ | 154.0 mm |
| Alveolus length, $P_1$–$M_3$ | 120.5 mm |
| Alveolus length, $P_2$–$M_3$ | 111.0 mm |
| Alveolus length, $P_3$–$M_3$ | 98.2 mm |
| Alveolus length, $P_4$–$M_3$ | 87.0 mm |
| Alveolus length, $M_1$–$M_3$ | 74.5 mm |
| Alveolus length, $M_2$–$M_3$ | 44.2 mm |
| $C_1$, anterior–posterior length | 28.0 mm |
| greatest width | 19.7 mm |
| $M_1$, anterior–posterior length | 30.2 mm |
| trigonid length | 19.8 mm |
| trigonid width | 12.8 mm |
| talonid width | 17.2 mm |
| $M_2$, anterior–posterior length | 28.0 mm |
| trigonid width | 20.1 mm |
| talonid width | 18.3 mm |
| $M_3$, anterior–posterior length | 18.7 mm |
| greatest width | 14.5 mm |

**Table 2. Measurements of teeth (right maxilla) of *Arctodus simus* (LACM 122434) from Labor-of-Love Cave, Nevada.**

| | |
|---|---|
| Alveolus length, $C^1$–$M^2$ | 137.6 mm |
| Alveolus length, $P^1$–$M^2$ | 100.1 mm |
| Alveolus length, $P^2$–$M^2$ | 93.0 mm |
| Alveolus length, $P^3$–$M^2$ | 87.3 mm |
| Alveolus length, $P^4$–$M^2$ | 78.7 mm |
| Alveolus length, $M^1$–$M^2$ | 56.3 mm |
| $C^1$, anterior–posterior length | 27.9 mm |
| greatest width | 17.9 mm |
| $P^4$, anterior–posterior length | 20.8 mm |
| greatest width | 14.7 mm |
| $M^1$, anterior–posterior length | 24.1 mm |
| greatest width | 23.8 mm |
| $M^2$, anterior–posterior length | 35.0 mm |
| greatest width | 21.7 mm |

tocene remains of *A. simus* and *U. americanus* from Labor-of-Love Cave and Rancho La Brea, and from modern *U. americanus*.

## Genus *Arctodus* Leidy, 1854

### *Arctodus simus* (Cope) 1879
(Giant Short-faced Bear)

**REFERRED MATERIAL.** LACM 123781, proximal left femur; LACM 122434, numerous skull fragments including premaxillae and maxillae, both lower jaws (see Tables 1, 2; Figs. 4, 5), humeri, radii, ulnae, femora, and tibiae, atlas, right metacarpal III, right metatarsal V, fibula fragment, phalanx, and one rib fragment.

**DISCUSSION.** LACM 123781 was recovered from BC-1 and is from an immature individual as it lacks the proximal epiphysis. LACM 122434 was recovered from BC-2 and represents one adult individual. A minimum of two *A. simus* individuals are represented.

## Order Artiodactyla

**REFERRED MATERIAL.** LACM 123784, fragmented humerus.

**DISCUSSION.** This specimen, recovered from BC-2, is too fragmented for positive identification beyond order, but is from a deer-sized animal. Its position in the pool at time of discovery is shown in Figure 2a.

### Family Bovidae

### Genus *Ovis* Linnaeus, 1758

### *Ovis canadensis* Shaw, 1804
(Bighorn Sheep)

**REFERRED MATERIAL.** LACM 123785, left $M^3$.
**DISCUSSION.** Recovered from BC-1.

## GEOLOGIC HISTORY AND TAPHONOMY

Exact geologic age of the fossils is not known; two bones, an ulna of *U. americanus* from BC-1 and a humerus of *A. simus* from BC-2, were submitted to Beta Analytic, Coral Gables, Florida, for radiocarbon dating. Dates on collagen of 4160 ± 180 years B.P. were obtained for the ulna of *U. americanus* and 5320 ± 120 years B.P. for the humerus of *A. simus* (Murray Tamers, pers. comm.). The unusually young date for *A. simus* is inconsistent with other fossil records of this species. Error in the dates may be due to low amounts of carbon obtained from the bone or to contaminants in the water within the cave. All previous finds of *A. simus* are older than 12,650 ± 350 years B.P. (Kurtén and Anderson, 1980) and are associated with faunas characteristic of the Pleistocene (Irvingtonian and Rancholabrean Land Mammal Ages). Based on the number and diversity of complete speleothems we believe that Labor-of-Love Cave has been sealed since at least the close of the Pleistocene, or approximately 12,000 years B.P., and that the above C14 ages do not reflect the true ages of this material.
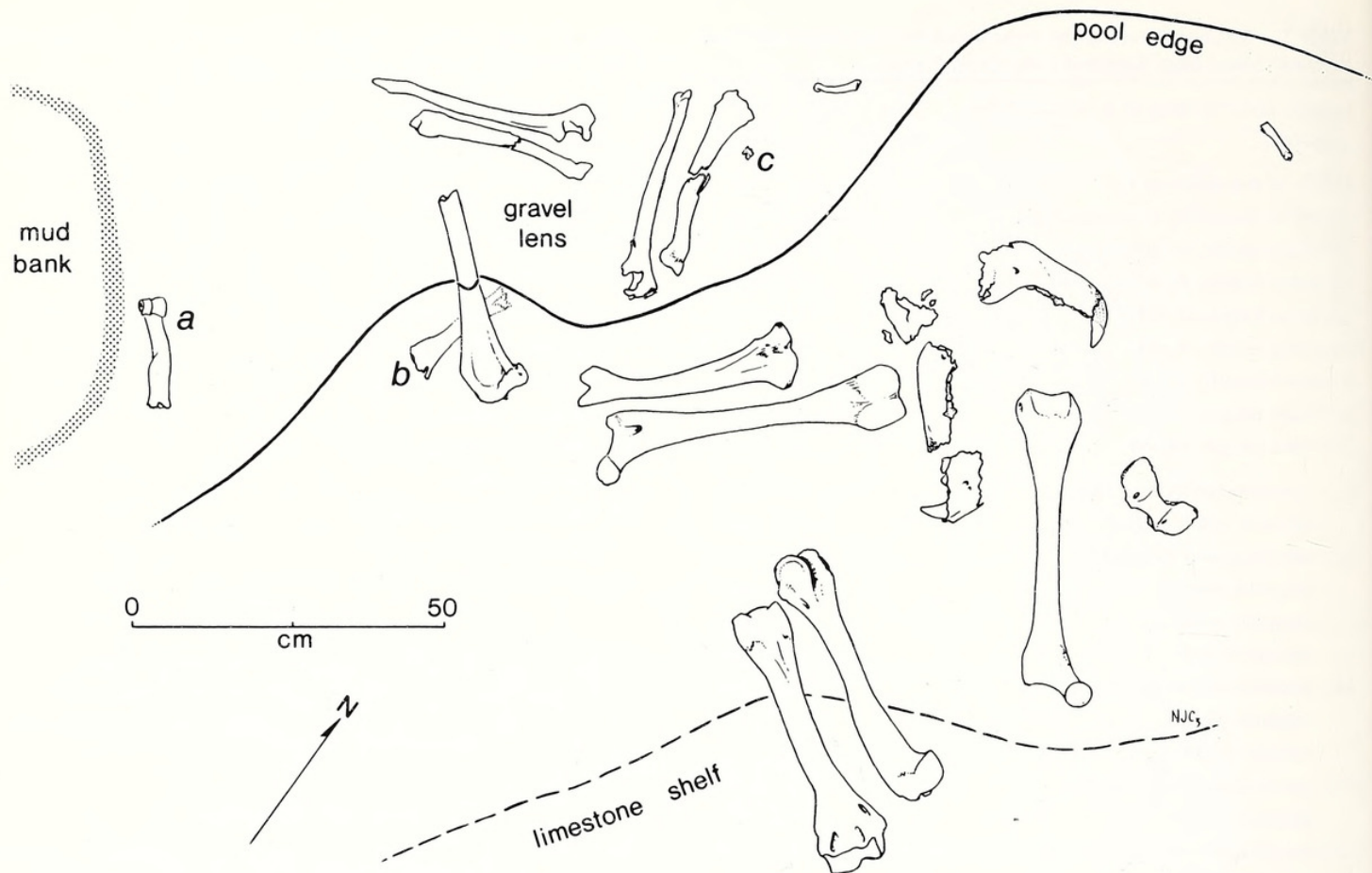
**Figure 2.** Plan view of the bones at BC-2. All bones shown are from one skeleton of *Arctodus simus* except (a) Artiodactyla humerus, (b) *Ursus americanus* humerus, and (c) *U. americanus* right $M_1$.

Labor-of-Love Cave developed within mountains formed primarily of uplifted Dunderberg Shale and limestone of middle to late Cambrian age (Hose and Blake, 1976). The cave follows a fault plane through the limestone. Examination of speleothems, flowstone, and stratified silt deposits indicates the cave has undergone alternate periods of filling from perhaps several entrances, erosion of these sediments, and pronounced changes in cave environment. Hanging flowstone shelves were observed throughout the cave at heights where water and/or sediments once existed, between 0.5 and 1.5 m above current levels. Several stalagmites undercut by erosion are now tilted, and clay sediments still cling to the walls of the cave near the roof.

All bones at BC-1 were lying submerged at the bottom of the pool or partially buried in silt in the bottom. Bones at BC-2 were lying at the bottom of the pool, and on the surface of a gravel lens at the pool edge (Fig. 2). Undisturbed deposits nearby show this gravel lens is overlain by a 20-cm-thick layer of sandy silt, followed by a 25–30-cm-thick layer of fine silt (Fig. 1b). Bones exposed on the gravel lens included nearly articulated pairs of radii and ulnae and a partially

buried tibia of *A. simus* (Fig. 6b), and the molar and a left humerus of *U. americanus*. The close association and articulation of the remains of *A. simus* suggest the gravel lens is the site of primary deposition of these bones (Fig. 2).

Fine, densely packed laminar cross-bedded deposits are still present in the rear of the cave (Fig. 6c) indicating that deposition and erosion of sediments has been occurring over a long period of time. We believe that the bear skeletons have eroded from the deposits relatively recently, based on their completeness and close association at each bone concentration. Some bones were found where originally deposited, in the gravel lens at BC-2. Those bones which were eroded from these sediments probably were transported only a short distance (<5 m) before being redeposited as found. Both bear skeletons had fragmented skulls (possibly caused by the pressure of overlying sediments) and corresponding skeletal elements preserved at each pool. Possible carnivore tooth marks on the bone suggest the bear carcasses had been scavenged prior to burial. The absence of pelves or complete scapulae may support this conclusion as these elements are usually the first to be destroyed during carnivore feeding (Hill, 1980;

Binford, 1981). Most of the ribs, vertebrae, and phalanges from these skeletons were not recovered, presumably having been washed downstream or redeposited in gravel bars. These elements were found by Voorhies (1969) to be most susceptible to fluvial transportation in experiments with Recent mammal carcasses.

The relative completeness of the black bear skeleton from BC-1 and the short-faced bear skeleton from BC-2 suggests that these animals died in the cave, perhaps during a period of winter hibernation. Bones of other animals found in the cave also display breakage and tooth marks, and may represent food items transported to the cave by carnivores.

## PALEOECOLOGY

Detailed information on the paleoecology of eastern Nevada during the late Pleistocene is available from recent studies in Smith Creek Canyon, Snake Range, which is located 75 km northeast of Labor-of-Love Cave. The elevation of the entrance to this canyon is 1710 m and the area is similar in topography and environment to the area of Labor-of-Love Cave. Studies of the paleoecology at Smith Creek Canyon can, therefore, be useful in reconstructing the habitat available to *A. simus* in eastern Nevada during the late Pleistocene.

Analysis of packrat middens from three caves in Smith Creek Canyon provided Thompson (1979) with specific information on the vegetation of this area during the late Wisconsinan and early Holocene. His results indicated that many plants occurred in the canyon during the Pleistocene that are found only at higher elevations today. These plants included bristlecone pine (*Pinus longaeva*), fern-bush (*Chamaebatiaria millefolium*), gooseberry currant (*Ribes montigenum*), cliff-bush (*Jamesia americana*), and bush oceanspray (*Holodiscus microphyllus*). Spruce (*Picea*) and fir (*Abies*) were absent from the samples. Thompson (1979) postulated that the period 12–13,000 years B.P. was characterized by greater effective moisture than today with conditions changing to those of the present by 10,500 years B.P.

Thompson (1979), Thompson and Mead (1982), and Mead et al. (1982) have shown that much of the Great Basin during the late Pleistocene consisted of pluvial lakes. Above lake level, valleys were dominated by sagebrush (*Artemisia tridentata*) cover, similar to the area today. Alpine glaciers extended down to 2800 m in elevation in the Snake Range, 75 km northeast of Labor-of-Love Cave. Vertebrates recovered from the Snake Range, Smith Creek Cave (dated at ≥12,000 years B.P.) and packrat middens from Smith Creek Canyon, include species now restricted to higher elevations or higher latitudes. These include *Ochotona princeps, Spermophilus richardsonii, Thomomys talpoides, Phenacomys intermedius,* and *Mustela vison.* One undescribed bone identified as *Ursus* sp. from Smith Creek Cave is a questionable identification (Miller, 1979).

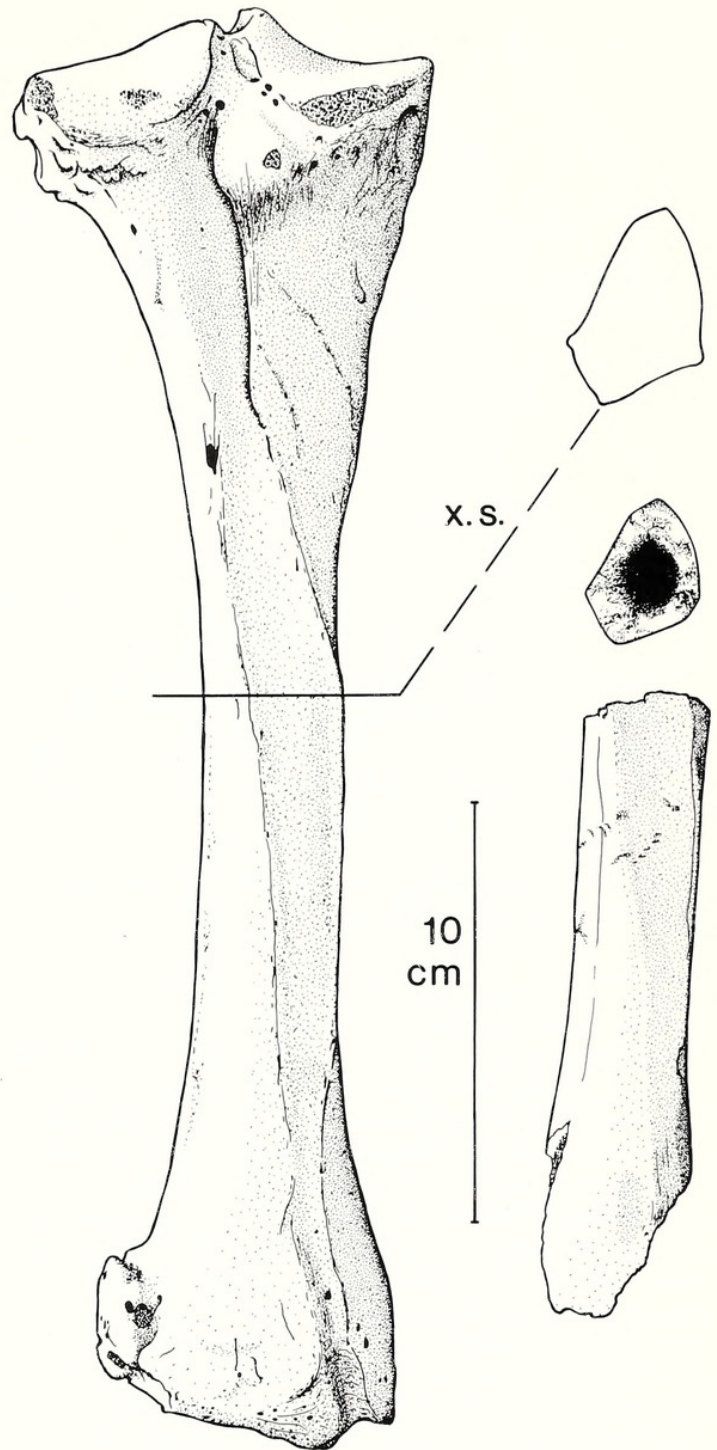In summary, the late Pleistocene habitat of eastern Nevada



**Figure 3.** The partial left tibia (LACM 123782) of *Ursus* cf. *arctos* found at BC-1 compared to a tibia of Recent *U. arctos middendorfi.* Note the characteristic flaring of the shaft at the proximal and distal ends, and the distinct ridges in *U. arctos* and the fossil specimen.

probably consisted of pluvial lakes and open, sagebrush-covered flats in the valley bottoms. Mountain ranges surrounding the valleys bore alpine glaciers above 2800 m with subalpine to alpine faunal and floral elements in the canyons and valley
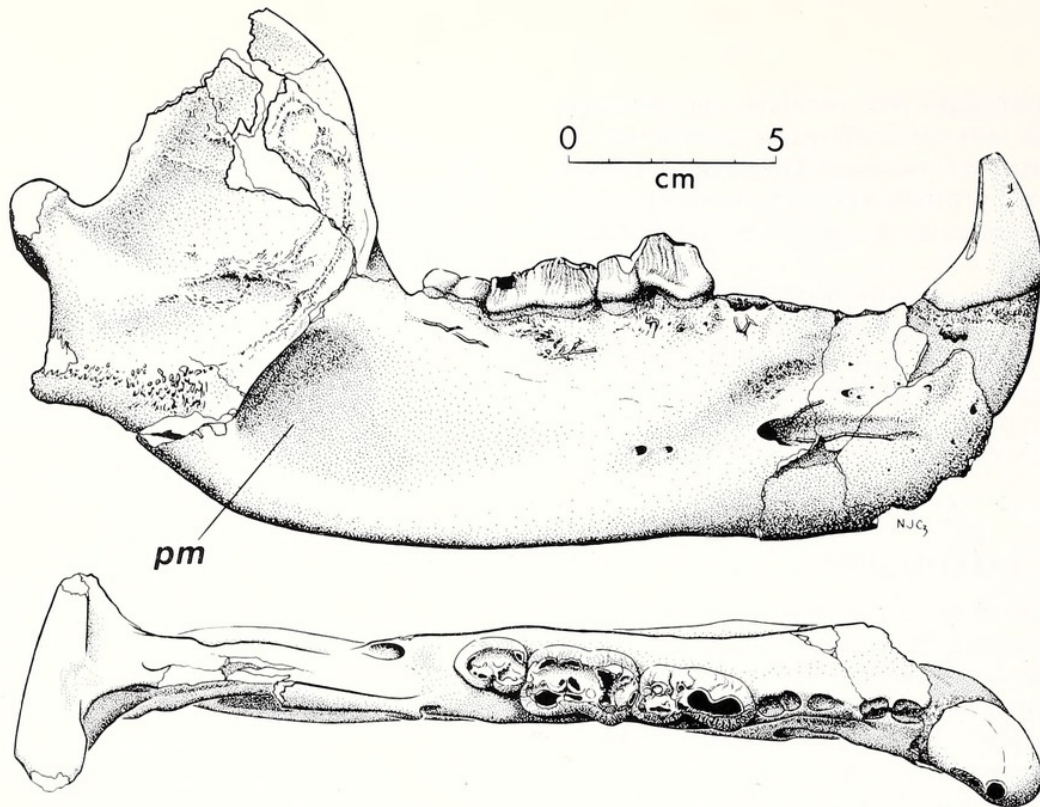
**Figure 4.** The right mandible (LACM 122434) of *Arctodus simus* from Labor-of-Love Cave showing the premasseteric fossa (pm) characteristic of the subfamily Tremarctinae. The position of this specimen in the pool at time of discovery is shown in Figure 2.

edges. Open forests of bristlecone pine and other conifers extended to the valley edge.

## DISCUSSION

*Arctodus simus* remains have been reported from fossil localities throughout North America, particularly western North America (Kurtén and Anderson, 1980). Other Pleistocene records not reported by Kurtén and Anderson include several elements of a large *A. simus* from northern Utah (Nelson and Madsen, 1983), a fragmentary partial skeleton from Duck Flat, Washoe County, Nevada (D.R. Tuohy, in litt.), numerous cranial and postcranial elements from Natural Trap Cave, Big Horn County, Wyoming (L.D. Martin, pers. comm.), an isolated tooth from Adair County, Oklahoma (Puckette, 1976), a cranium, five vertebrae, and partial pelvis from Hot Springs Mammoth Site, Fall River County, South Dakota (L. Agenbroad, pers. comm.), and a skull, femur, and ten vertebrae from Cueva Quebrada, Val Verde County, Texas (Lundelius, 1984). Isolated material from Rancho La Brea has permitted a composite construction of the complete skeleton of *A. simus*. An unpublished record of this species from American Falls, Idaho, consists also of a relatively complete skeleton, but the postcranial elements are fragmented and incomplete (Jon Becker, pers. comm.) and are not useful for proportional analyses. A nearly complete skeleton from Fulton County, Indiana, is currently under analysis by William Turnbull and associates (pers. comm.). Consequently, the material from Labor-of-Love Cave constitutes one of the most complete skeletons from one individual recovered in North America. This provides more accurate proportional data on limbs, with which to evaluate the paleobiology of *A. simus*.

## PALEOBIOLOGY

Kurtén (1967), in his singular monograph on *Arctodus* bears, stated that *A. simus* had cursorial adaptations, and was probably a highly predaceous carnivore. His conclusion was based primarily on the long limbs, slender leg elements, and "felid-like" characters of the skull of *A. simus* when compared to other ursids. However, we contend that this species may have been largely herbivorous based upon characteristics in the skull, limbs, and body size. In addition, anatomic and functional morphologic comparisons with the living spectacled bear, *Tremarctos ornatus,* add support to our argument. Finally, sympatric records of Pleistocene bears suggest that *Arctodus* and *Ursus* species used different feeding strategies.

## SKULL

Kurtén (1967) described the skull of *A. simus* as having several felid-like characteristics such as a shortened face, large rostral breadth, high vaulted calvarium, and similar orientation of the zygomatic arches, and he used these convergent features to advance his hypothesis that *A. simus* was an active carnivore. However, these skull features may be related to large body size and reduction of premolars in bears, and a

comparison to felids is inappropriate. In addition, the same features are present in the skull of *Tremarctos ornatus,* the only living relative of *Arctodus* (Davis, 1955). The South American spectacled bear (*T. ornatus*) is primarily herbivorous, feeding on bromeliads, leaves, tree bark and fruits, berries, and cactus fruits and pulp, and only occasionally eats carrion; reports of these bears killing prey are uncertain (Peyton, 1980).

One important similarity in the jaw of *Tremarctos* and *Arctodus* is the presence of a premasseteric fossa (Fig. 4). In a detailed examination of the structure of the dentary and related muscles in *T. ornatus,* Davis (1955) concluded this fossa has one of two functions: it is either a depression accommodating a small cheek pouch formed in the oral vestibule (as in the mandrill, *Papio maimon*), or it reflects modeling in jaw architecture to allow a larger zygomaticomandibularis muscle. This muscle, which is important in allowing lateral grinding motions of the jaw and aids in elevating the mandible, is large in herbivorous animals and small in carnivorous animals (Davis, 1964). Since the size of the premasseteric fossa is far too small to be a useful cheek pouch for the size and food requirements of *T. ornatus,* it is probably related more to the jaw mechanics to accommodate a large zygomaticomandibularis muscle (Davis, 1955). Davis (1955:43) also points out that "a functional pouch occurs elsewhere only in social animals that compete for food (primates), or in animals that forage for food and retreat to a safe place to masticate it (rodents). Bears fall into neither of these categories." In regards to the fossa itself, Davis (p. 44) states that it does not interfere with the trajectory systems of the skull and "is situated in tissue that contributes little or nothing to the internal support of the mandible." A similar function for the premasseteric fossa can be projected for *A. simus,* because its jaw architecture is very similar to the closely related *T. ornatus.* Although morphologic associations between fossil and living animals should be made with caution, we believe the close affinities of these two bears permit reliable comparisons.

The teeth of *A. simus* also suggest a largely herbivorous diet. Kurtén (1967) suggested that *A. simus* was predaceous based primarily on the high-crowned nature of the first lower molar, and the relatively large size of the canines. He noted that the protoconid and paraconid in the first molar form a carnassial shear with the paracone and metacone of the upper fourth premolar. He additionally referred to the trenchant shape of the first lower molar. Such a carnassial shape is characteristic of many carnivorous fissipeds, but we believe it is not developed in *A. simus.* Instead, with moderate wear, the protoconid and paraconid apices of the first molar are worn to a relatively flat, blunt loph. While the $M_1$ of *Arctodus* is high-crowned, it is no more trenchant than that of other bears and, like *U. arctos,* it wears flat. Moreover, the only apparent shear facet is worn into the labial surface of the tooth in the indentation between the talonid and trigonid where the paracone of $M^1$ occludes, not along the labial sides of the paraconid and protoconid (Fig. 4). This small shear facet would be relatively inefficient for slicing flesh. The trigonid of $M_1$ is tall and conical, somewhat reminiscent of the
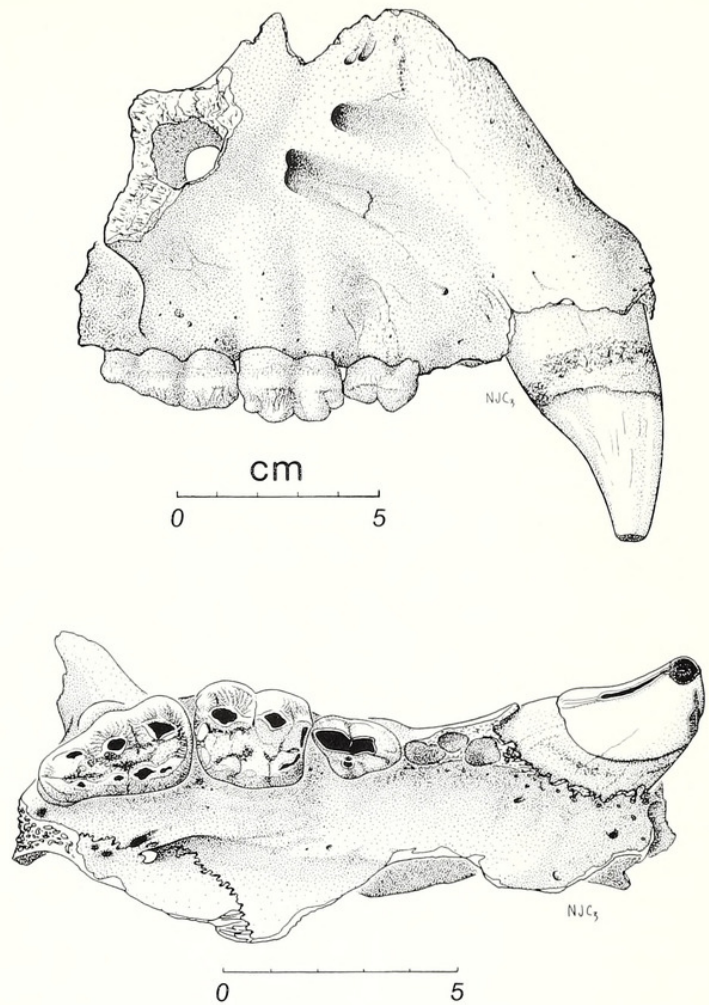


**Figure 5.** The right maxilla (LACM 122434) of *Arctodus simus* from BC-2. Its position in the pool at time of discovery is shown in Figure 2.

bone-crushing posterior premolars of hyaenas. The talonid forms an offset, small crushing platform that is confluent with those of the posterior molars. Perhaps the offset nature of this tooth functions in crushing plants and bone. The $M_2$ is extremely broad relative to its length (Table 1) and forms, with the third molar, a large crushing platform as in omnivorous bears. Although cusps of canids and felids can wear flat, particularly in aged animals, the general trend in most highly predaceous carnivores is to maintain a sharp, shearing blade on the carnassials. Except in very young specimens, all of the material of *A. simus* that we have observed (including that at the Los Angeles County Museum of Natural History and the American Museum of Natural History) have flattened cusps. In summary, these characters of the teeth indicate to us that *A. simus* may have been omnivorous or primarily herbivorous, but had bone-crushing capabilities.

*Tremarctos ornatus,* like *A. simus,* has shorter dentaries and an overall shorter face when compared to *Ursus arctos* (Davis, 1955) and is rarely predaceous, as already noted. Although the polar bear, an obligate carnivore, has carnassials that are no more sectorial than those of other living

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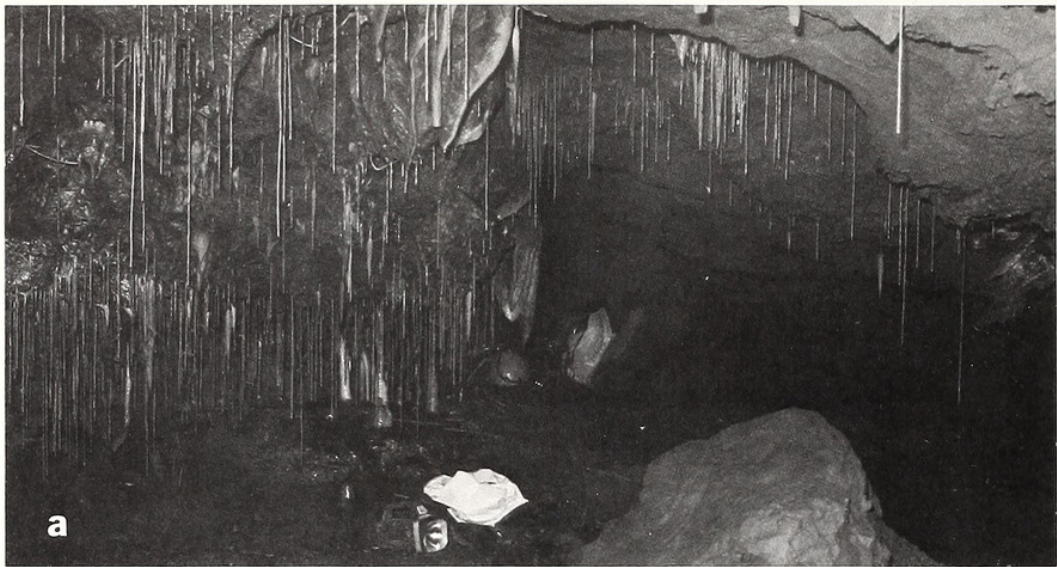
bears, they do have tall, pointed cusps in the unworn condition, and the teeth show a trend towards homodonty (DeMaster and Stirling, 1981), indicating possible convergence with carnivorous pinnipeds. Additionally, the lack of sectorial teeth in the polar bear may simply reflect its relatively late (mid-Pleistocene) derivation from bunodont *U. arctos* (Kurtén, 1964). Moreover, while no one would argue that felids are not highly predaceous with teeth adapted to a carnivorous diet, such dental morphology does not necessarily mandate carnivory; *Felis planiceps* of southeast Asia seems to prefer fruit (Goodwin, 1954). Consequently, Kurtén's suggestion that *A. simus* was highly predaceous based on skull structure and teeth cannot be substantiated.

## LIMB PROPORTIONS

The major value of the *A. simus* postcranial material from Labor-of-Love Cave is that it provides an opportunity to examine relative limb proportions from a single individual. Table 3 provides measurements of the limb elements of the partial skeleton of *A. simus* from BC-2. Length proportions of limb elements are compared to similar proportions for several species of *Tremarctos, Arctodus,* and *Ursus* (Table 4). Kurtén's proportions for the fore- and hindlimb elements were determined using composite material from several fossil specimens. He found little variation in limb proportions within *A. simus,* though considerable size variation within the taxon was noted. Our calculations (Table 4) indicate that the limb proportions of *A. simus* are lower than those given by Kurtén (1967) but still evince considerable divergence from other bear taxa; forelimb proportions do not overlap with Recent bears or fossil *Tremarctos,* and hindlimb proportions overlap only slightly with *U. arctos.* This divergence can be attributed, as Kurtén concluded, to the relatively longer limbs of *A. simus* compared to other bears.

The strongest evidence for cursorial adaptation in *A. simus* offered by Kurtén (1967) was its relatively long slender legs. The humerus and femur are longer than the radius and tibia, respectively. Hildebrand (1982) discusses skeletal and other adaptations which increase speed in cursorial animals, including an increase in limb length. However, the lengthening of limbs in cursorial animals usually takes place in the distal limb segments, not the proximal as in *A. simus.* Longer proximal limb elements are a feature of digging animals, such as the badger, and of mediportal and graviportal animals, such as bears (Davis, 1964). *A. simus,* however, lacks other characteristics of a digging life-style such as a long olecranon on the ulna and long claws. Other non-cursorial characteristics of bears include plantigrade feet (which is noted for *A. simus* by Kurtén) and a stride with no or scarcely any unsupported intervals (Hildebrand, 1982).
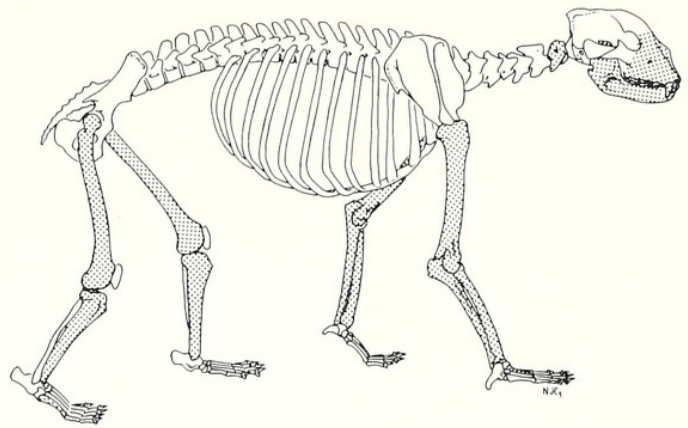


Figure 7. Skeleton of *A. simus* with shaded bones indicating elements recovered from the adult individual represented at BC-2.

If *A. simus* was largely herbivorous and not a highly predaceous, cursorial carnivore, another explanation for its long limbs is needed. An interesting comparison can be made with the maned wolf, *Chrysocyon brachyurus,* of South America. This fox inhabits open, tall-grass prairies (Nowak and Paradiso, 1983), has extremely long and slender limbs relative to body size (as in *A. simus*), is not especially swift nor does it take swift prey (Hildebrand, 1954), and runs with a loping gait (John Eisenberg, pers. comm.). The long limbs may be an adaptation for increased vision over tall ground cover in an open habitat (Nowak and Paradiso, 1983). A similar interpretation may be applied to *A. simus* in the Great Basin, where its former habitat is known, but the habitat for this species throughout its range in the Pleistocene of North America is largely unknown. It is equally possible that the longer limbs of *A. simus* were used in tearing and pulling down vegetation, including shrubs and small trees, in order to feed on leaves, fruits or bark.

## BODY SIZE

The body size attained by *A. simus* may also be an indication of herbivory. Body size is limited by many factors, including specialization to specific habitats and diet (Eisenberg, 1981). In terrestrial mammals, herbivores usually have a larger biomass and greater numerical density than carnivores. This trend is caused by a more restricted energy base available to carnivores according to Eisenberg (1981) who also discusses the average size of recent mammalian genera (using head and body length) in relation to niche specialization. Table 5 summarizes these data in comparison to *A. simus.* This table indicates that Recent terrestrial carnivores are limited to a maximum size by their diet, and that omnivory has allowed

Figure 6. The gravel and silt deposits at BC-2. (a) The gravel lens containing the remains of *A. simus* (LACM 122434) extends from the mound of sediments in the right foreground to the kneeling figure. The stream and pool containing bones are to the right; water is flowing in the direction of the figure, toward the cave entrance. (b) An articulated radius and ulna, and a partly buried tibia of *A. simus* eroding from the gravel lens as shown in Figure 2. (c) Finely laminated and cross-bedded sediments just upstream of BC-2 are all that remain of deposits that once nearly filled the cave.

**Table 3.** Measurements (in mm) of limb bones of *Arctodus simus* (LACM 122434) from Labor-of-Love Cave. Breadth reflects the greatest lateral-medial breadth, and depth reflects the greatest anterior-posterior depth at each point of measurement.

| Element | Total length | Proximal breadth | Proximal depth | Transverse diameter prox. head | Least breadth shaft | Least depth shaft | Distal breadth | Distal depth |
|---|---|---|---|---|---|---|---|---|
| Left ulna | 375 | 28.8 | 65.2 | — | — | — | — | — |
| Left radius | 355 | — | 37.9 | — | 26.2 | 17.1 | — | 26.0 |
| Right humerus | 454 | 79.5 | — | 97.7 | 35.3 | 33.9 | — | 62.8 |
| Right femur | 490 | 124.0 | 58.0 | 62.7 | 39.6 | 30.4 | 99.0 | 56.2 |
| Right tibia | 352 | 90.0 | 81.7 | — | 31.2 | 34.0 | 63.6 | 40.5 |
| Right V metatarsal | 85 | 22.5 | 23.3 | — | 11.7 | 10.5 | 18.3 | 15.3 |
| Right III metacarpal | — | 17.5 | 31.1 | — | 13.5 | 13.1 | — | — |

bears to attain larger average sizes. The largest living bear is the Kodiak Bear, *U. a. middendorfi,* with a mean biomass of approximately 300 kg (Eisenberg, 1981: Appendix 2), although individual bears may be as large as 700 kg (Novak and Paradiso, 1983). It should be pointed out that the giant panda (*Ailuropoda melanoleuca*), a herbivore, reaches a biomass of approximately 182 kg and a head and body length of 1200–1300 mm, indicating an herbivorous diet does not necessarily result in a large body size.

In comparing measurements of *A. simus* (as estimated by Kurtén, 1967), to Eisenberg's data (Table 5) and our own, it is apparent that this species exceeded the modern limitations for a terrestrial carnivore. Only two Recent skeletons of *U. arctos* (USNM 216206 and USNM 199252, Alaskan males)

equal or exceed the size of *A. simus* from Labor-of-Love Cave, which we believe to be a small adult, perhaps a female, compared to other finds. A recent record of *A. simus* from Utah, representing the largest known individual of this species, was estimated by Nelson and Madsen (1983) to have been 25–30% larger than all previous records, and to have weighed between 620–660 kg. This estimate is over four times the average size of the largest terrestrial carnivore (*Panthera*) today. These measurements place *A. simus* well within the size range of modern (and Pleistocene) terrestrial frugivore/omnivores and herbivore/grazers as presented by Eisenberg. If we accept Kurtén's interpretation of *A. simus* as having been primarily carnivorous, then this animal was atypical in size. It is more logical to assume that *A. simus* reached its

**Table 4.** Comparison of relative proportions of limb segments of *Arctodus simus, Tremarctos floridanus, T. ornatus, Ursus arctos,* and *U. americanus* using greatest length for each element, in mm.

| | *Arctodus simus* | | | | *T. floridanus*[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Male[1] | Female[1] | Hay Springs[1] | Labor-of-Love Cave | Male | Female | *T. ornatus*[2] | *U. arctos* | *U. americanus* |
| $\dfrac{\text{Radius}}{\text{Humerus}} \times 100$ | | | | | | | | | |
| N | 1/2 | 5/6 | — | 1/1 | 3/3 | 2/3 | 4/4 | 9/9 | 5/5 |
| x̄ | 87.6 | 85.6 | — | 78.2 | 83.0 | 83.8 | 84.3 | 88.4 | 90.3 |
| Range | — | — | — | — | — | — | 82.8–86.0 | 83.0–95.0 | 85.5–97.9 |
| $\dfrac{\text{Tibia}}{\text{Femur}} \times 100$ | | | | | | | | | |
| N | — | 7/7 | 1/1 | 1/1 | 3/3 | 7/7 | 4/4 | 9/9 | 5/5 |
| x̄ | — | 74.5 | 74.8 | 71.4 | 73.4 | 74.0 | 79.5 | 73.5 | 77.0 |
| Range | — | — | — | — | — | — | 74.8–81.7 | 70.4–75.1 | 74.8–78.4 |

[1] Data from Kurtén (1967); we were unable to repeat his calculation of the male R/H ratio from his Table 27 and have changed this value according to data he provides in Tables 10 and 11. However, because these ratios are based on non-associated elements from different localities, their accuracy is questionable.
[2] Data from Kurtén (1966).

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great size by being primarily omnivorous or herbivorous. We have demonstrated here that the hypothesis for herbivory is equally plausible to one of carnivory, but neither hypothesis can be rejected with an analysis of functional morphology. We prefer to believe that *A. simus* was primarily herbivorous, as *T. ornatus,* but also may have been an opportunistic predator and scavenger with bone-crushing capabilities.

## SYMPATRY OF PLEISTOCENE BEARS

The remains at BC-2 indicate a co-occurrence of *A. simus* and *U. americanus* in this area of Nevada. Sympatric records of these two bears are not unusual and have been documented at several Pleistocene localities including Rancho La Brea and McKittrick (Merriam and Stock, 1925; Schultz, 1938). However, associations of *A. simus* and *U. arctos* are rare and have occurred only at Little Box Elder Cave in Wyoming and Fairbanks II in Alaska (Kurtén and Anderson, 1974, 1980). Kurtén and Anderson (1980) speculate that invading *U. arctos* in the late Wisconsinan may have played a role in the extinction of *A. simus* through competition. However, this scenario is at odds with Kurtén's earlier suggestions that *A. simus* was a highly predaceous carnivore. If we accept Kurtén's interpretations it seems unlikely that the larger and more powerful *A. simus* could be out-competed by the smaller and less powerful *U. arctos.* Finally, apparent sympatry of *U. americanus* and *A. simus* during the late Pleistocene is more likely if the former species was omnivorous, as it is today, and the latter species was largely herbivorous. In this situation, the invasion of a third species, *U. arctos,* which can be primarily carnivorous in parts of its range today (Nowak and Paradiso, 1983), may have allowed a sympatric relationship between these three species. If further investigations in Labor-of-Love Cave provide more positive evidence for an association of *A. simus* and *U. arctos* there, valuable insights on the interspecific relationship of these species may be gained.

## ACKNOWLEDGMENTS

**Table 5. Comparisons of the macroniche, average length, and weight of Recent mammalian genera (after Eisenberg, 1981) to the proposed niche, length (estimated by Kurtén, 1967) and weight (estimated by Kurtén, 1967 and Nelson and Madsen, 1983) of *Arctodus simus.***

| Taxon | Niche | [1]Average head and body length (mm) | [2]Range of average weights (kg) |
|---|---|---|---|
| *Equus* | Terrestrial herbivore/ grazer | 1508 | 166–260 |
| *A. simus* | Terrestrial herbivore/ omnivore | 1432 | 270–660 |
| *Ursus* | Terrestrial frugivore/ omnivore | 817 | 77–300 |
| *Panthera* | Terrestrial carnivore | 718 | 39–151 |

[1] Average head and body length for Recent mammalian genera was derived by Eisenberg (1981, Table 43, p. 265) by summing the mean values for the two extreme size-classes in a genus.
[2] Range of weights for Recent mammalian genera was taken from weights of all species within a genus as presented by Eisenberg (1981, Appendix 2).

## LITERATURE CITED

Binford, L. 1981. *Bones: Ancient men and modern myths.* New York: Academic Press.

Davis, D.D. 1955. Masticatory apparatus in the Spectacled Bear. *Fieldiana—Zoology, Chicago Museum of Natural History* 37:25–46.

———. 1964. The Giant Panda a morphological study of evolutionary mechanisms. *Fieldiana—Zoology Memoirs, Chicago Natural History Museum* 3:1–339.

DeMaster, D.P., and I. Stirling. 1981. *Ursus maritimus.* Mammalian Species 145:1–7.

Eisenberg, J.F. 1981. *The mammalian radiations.* Chicago: University of Chicago Press.

Goodwin, G.G. 1954. Mammals of the air, land, and waters of the world. In *The animal kingdom,* Book 1, ed. F. Drimmer, 570. Garden City: Doubleday.

Hall, E.R. 1946. *Mammals of Nevada.* Berkeley, University of California Press.

Hildebrand, M. 1954. Comparative morphology of the body skeleton in Recent Canidae. University of California Publications in Zoology 52:399–470.

———. 1982. *Analysis of vertebrate structure,* 2nd ed. New York: Wiley.

Hill, A. 1980. Early postmortem damage to the remains of some contemporary east African mammals. In *Fossils in the making: Vertebrate taphonomy and paleoecology,* ed. A.K. Behrensmeyer and A.P. Hill, 131–155. Chicago: University of Chicago Press.

Hose, R.K., and M.C. Blake, Jr. 1976. *Geology and mineral resources of White Pine County, Nevada. Part I: Geology.* Nevada Bureau of Mines and Geology Bulletin 85, 32 pp. University of Nevada, Reno.

Kurtén, B. 1964. The evolution of the polar bear, *Ursus maritimus* Phipps. Acta Zoologica Fennica 108:1–26.

———. 1966. Pleistocene bears of North America. 1. Genus *Tremarctos,* spectacled bears. Acta Zoologica Fennica 115.

———. 1967. Pleistocene bears of North America. 2. Genus *Arctodus,* short-faced bears. Acta Zoologica Fennica 117.

Kurtén, B., and E. Anderson. 1974. Association of *Ursus arctos* and *Arctodus simus* (Mammalia: Ursidae) in the late Pleistocene of Wyoming. *Breviora* 426:1–6.

———. 1980. *Pleistocene mammals of North America.* New York: Columbia University Press.

Lundelius, E.L., Jr. 1984. A late Pleistocene mammalian fauna from Cueva Quebrada, Val Verde County, Texas. Special Publication Number 8 Carnegie Museum of Natural History, 456–481. Contributions in Quaternary Vertebrate Paleontology: A volume in Memorial to John E. Guilday, ed. H.H. Genoways and M.R. Dawson. Pittsburgh.

Mead, J.I., R.S. Thompson, and T.R. Van Devender. 1982. Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake Range, Nevada. Transactions San Diego Society Natural History 20(1):1–26.

Merriam, J.C., and C. Stock. 1925. Relationships and structure of the short-faced bear, *Arctotherium,* from the Pleistocene of California. Carnegie Institute Publication No. 347.

Miller, S.J. 1979. *The archaeological fauna of four sites in Smith Creek Canyon.* Nevada State Museum Anthropology Papers Number 17, 272–331. The Archaeology of Smith Creek Canyon, Eastern Nevada, ed. D.R. Tuohy and D.L. Randell. Carson City.

Nelson, M.E., and J.H. Madsen, Jr. 1983. A giant short-faced bear (*Arctodus simus*) from the Pleistocene of northern Utah. Transactions Kansas Academy Sciences 86:1–9.

Nowak, R.M., and J.L. Paradiso. 1983. *Walker's mammals of the World,* 4th ed. Baltimore: Johns Hopkins University Press.

Peyton, B. 1980. Ecology, distribution, and food habits of spectacled bears, *Tremarctos ornatus,* in Peru. Journal of Mammalogy 61:639–652.

Puckette, W. 1976. Notes on the occurrence of the short-faced bear (*Arctodus*) in Oklahoma. Proceedings of the Oklahoma Academy of Science 56:67–68.

Schultz, J.R. 1938. A late Quaternary mammal fauna from the tar pits of McKittrick, California. Carnegie Institute Publication No. 487:111–215.

Thompson, R.S. 1979. *Late Pleistocene and Holocene packrat middens from Smith Creek Canyon, White Pine County, Nevada.* Nevada State Museum Anthropology Papers Number 17, 362–368. The Archaeology of Smith Creek Canyon, Eastern Nevada, ed. D.R. Tuohy and D.L. Randell. Carson City.

Thompson, R.S., and J.I. Mead. 1982. Late Quaternary environments and biogeography in the Great Basin. Quaternary Research 17:39–55.

Voorhies, M.R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. University of Wyoming, Contributions to Geology, Special Paper 1:1–69.