Ann. Zool. Fennici 28:175–186
Helsinki 19 February 1992

ISSN 0003-455X

New paleoecological and paleoethological information on the extinct helmeted muskoxen from Alaska

R. Dale Guthrie

Guthrie, R. D., Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99709

Received 25 March 1990, accepted 3 September 1990

A newly discovered horn sheath is described for the extinct helmeted muskox, *Bootherium*. This is the first complete female horn sheath described for that species. The sheath was fitted to a *Bootherium* skull, revealing a very different form than exhibited by those of living muskox, *Ovibos*, and suggests a different behavioral emphasis in its use. Also, plant remains from ingested food and from possible faecal samples were examined histologically to reconstruct diet of *Bootherium*. These suggest a slightly different diet than that of *Ovibos*.

1. Introduction

In addition to the familiar muskox (*Ovibos moschatus*), a second muskox species, called the helmeted or woodland muskoxen (*Bootherium bombifrons*) also occurs in late Pleistocene deposits in North America. Helmeted muskoxen remains are found in unglaciated regions of Canada and the Southwestern United States: from California, Louisiana and Texas in the south, Pennsylvania in the east, and north to Alaska and the Yukon Territory. Although helmeted muskox fossils are common, very little information exists about their ecology and ethology. What was their preferred habitat and diet? Did they compete with *Ovibos*? How did they defend themselves against predators? Evidence presented here provides insight into these questions, but first I must address their taxonomic status.

There has been little agreement on the generic or specific name of this species. Confusion is due primarily to failure in distinguishing male and female skulls, as reviewed by Harington (1977) and Kurtén & Anderson (1980). Clearly female specimens have been referred to as the genus *Bootherium* and males as *Symbos*. Recent publications have argued that *Bootherium* specimens are indeed females, but that the name

Fig. 1. Both the horny sheath and the horn cores of helmeted muskox are quite different from those of *Ovibos*. Male helmeted muskoxen have horn sheaths which fuse along the mid-line creating an apparent single horn (a). These sheaths are supported by relatively short simple horn cores which are only slightly flattened in male helmeted muskoxen (b). The horn cores of *Ovibos* (c) bend more rapidly downward and the bases spread out to form plates over the frontals which support the dorsally thickened and flattened horn sheath. The above illustrations are fossils from the Fairbanks area, redrawn from photographs.

Bootherium takes precedence over *Symbos* (McDonald & Ray 1987, 1989) uniting female and male skulls within the species *Bootherium bombifrons*. However, Nelson (1987) proposed that although *Bootherium sargenti* is the female of *Symbos cavifrons*, fossils designated as *Bootherium bombifrons* are a valid specific taxon different from *Symbos*. I will follow McDonald & Ray (1989) and include all *Bootherium* and *Symbos* under the genus *Bootherium*.

I have used the common name "helmeted muskoxen". Kurtén & Anderson (1980), following some earlier authors (e.g., Semken et al. 1964), used the common name "woodland muskoxen," but there are two reasons not to use this name. Local groups within species of living ungulates are sometimes known by their habitats, for instance woodland caribou. Thus the term woodland muskoxen can suggest (nonexistent) woodland populations of living muskoxen. Secondly, helmeted muskox were not limited to woodland habitats; they lived in central Alaska during the peak of the last glaciation, marine isotope stage 2, (Harington 1977, McDonald 1984) when there were no woodlands in Alaska. Within the limits of this paper "helmeted muskoxen" should be a clear enough reference. In Alaska during the late Pleistocene there seem to have been only 2 species of muskoxen; *Ovibos* and the now extinct helmeted species — the latter is the subject of this paper.

The general build of helmeted muskoxen was different than *Ovibos*: its legs were longer, the body less elongated and hair shorter and darker (Harington 1977, McDonald 1984). There are other differences as well, and I will discuss some of these in the context of ethological and ecological characteristics. The most obvious and striking feature of helmeted muskox fossils is their unusual horns. Helmeted muskoxen have a characteristic sexual dimorphism in their horns, at least as great as living muskoxen (*Ovibos*), but in a different pattern.

2. Horn shape and use

Male helmeted muskoxen had very large heavy horns which formed an expanded platform on the frontals somewhat similar to *Ovibos*. In mature bulls, however, medial borders of the horns fused into an expanded "helmet" (Fig. 1). We know these details because at least two specimens from frozen sediments in interior Alaska have been found with complete horn sheaths attached to the skull: F:AM A-651-3600 from Dome Creek collected in 1952, and F:AM A-235-1002 from Upper Cleary Creek collected in 1939, both by Otto Geist and now in the American Museum of Natural History, New York (McDonald & Ray 1989).

In some aspects, the shape of the bony, distal, horn cores of female helmeted muskox differ

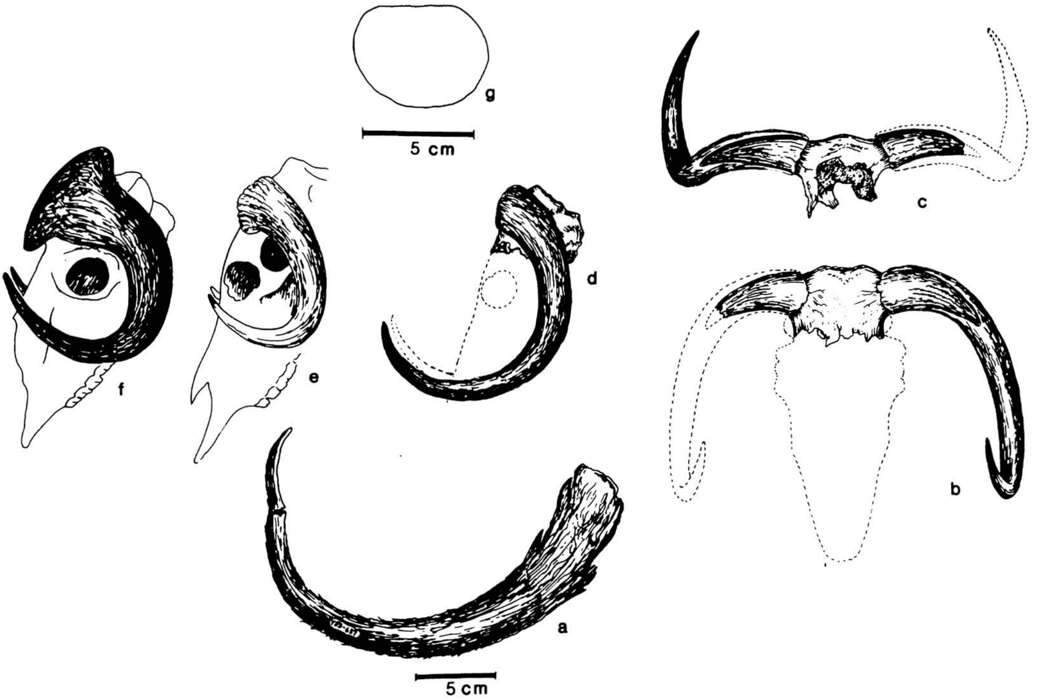

Fig. 2. The unique features of a female helmeted muskox horn (a) can best be seen when it is reconstructed on a real horn core, here seen in frontal view (b) and occipital view (c), and in lateral view (d) compared with a profile of a female *Ovibos* (e). The horn tip of the helmeted muskox protrudes well out in front of the facial line, illustrating, that unlike males (f), female horns were not well suited for clashing. This long forward protrusion would, however, have been quite usable in predator defense. In cross-section the bony horn core at its base is rounded, with a slightly flattened anterior face (g).

little from those of males, other than the abovementioned fusion of the latter along the midline (The distal horn cores of male and female *Ovibos* are also similar to one another in general shape). The horn cores of male and female helmeted muskoxen do differ considerably in size and robustness, particularly in the proximal parts which form the base where clashing occurs. Female helmeted muskox skulls are distinguished by the absence of pitting on the frontals where medial fusion of horn sheaths occurs in males. This dramatic difference in the base of male and female horn cores led systematists to describe two genera from the male and female horn cores. This confusion occurred before the more complete, sexually quite dimorphic, skulls with horn sheaths had been found in Alaska. In fact, the horn sheath described in this paper further clarifies that issue of sexual dimorphism and its interaction with anatomy and behavior.

Horns of female helmeted muskoxen did not fuse medially but retained a wide space between the medial portions of the bases (Fig. 2), almost like *Bos* and most bovids. Horn patterns of female helmeted muskoxen have been reconstructed from the bony horn cores (a number of these are present in museum collections). Horn sheaths from adult females with complete distal tips have not been described, and to my knowledge, have not been found until now.

McDonald & Ray (1989) describe a female *Bootherium*, F:AM-30508, from Fairbanks, Alaska which had one incomplete horn without tip. McDonald (1984) has also described, in a progress report, a partial mummy of a female helmeted muskoxen (F:AM A-293-5268) collected from Fairbanks Creek, Alaska in 1940, which presumably still has horn sheaths. However, this specimen is a sub-adult female (2 years old). From this McDonald (1984) showed that helmeted muskoxen were taller and not as elongated from head-to-tail as comparable specimens of *Ovibos*. He also concluded based on examination of hair remaining on the specimen that helmeted muskoxen were generally of darker color than living muskoxen.

In this paper I shall describe a single, rather complete specimen of a left horn sheath belonging to a female helmeted muskoxen. The sheath is the wrong shape to fit the horncores of either males or females of *Ovibos*, *Praeovibos*, or *Soergelia*, but does logically fit cores of female *Bootherium*. Because this isolated find cannot be contextually associated with a female *Bootherium*, the identification has to be based on most reasonable fit, both in shape of horn core cavity and in overall sheath pattern. The thin base would eliminate the possibility of it belonging to a male *Bootherium*. It was obtained during placer mining operations and collected on Lilian Creek, Alaska (65°30′N and 148°30′W) during a Bureau of Land Management project to salvage Quaternary fossils, supervised by John Cook. Because horn shape can be an important indicator of agonistic behavior and in some cases anti-predator defense (Geist 1966), this horn-sheath from a female helmeted muskox not only clarifies the appearance of adult females, it also offers new insights into aspects of their behavior. The keratin was dated at greater than 40 000 yr. B. P. (PITT-0218).

The horn sheath measures 60.9 cm along its dorsal border. At half its length it is 12 cm in circumference. The cavity into which the bony core fits is 21.5 cm deep along the dorsal curve. It is not possible to measure the base circumference because portions are missing and this portion has split apart in drying. The horny base which covers the anterior surface of the bony core averages about 0.5 cm in thickness — relatively thin. The general texture and composition of the horn is ovibovine in character: rather fibrous, like a weathered horn of *Ovibos* and very unlike horn of bison or mountain sheep. The stringy fibers are arranged linearly and do not show marked annuli as do horns of mountain sheep (*Ovis dalli*). Only on the proximal end can suggestions of annulae be seen. The color of the entire horn is quite dark, more like bison horn than the translucent yellowish color characteristic of *Ovibos* (Fig. 2). The yellowish horns of *Ovibos* are tipped with a contrasting black pigment. The reverse pattern of dark horns with yellowish-white tips as seen in kudu, *Tragelaphus strepsiceros*, apparently did not occur in either sex of helmeted muskoxen.

Aside from quite different bases, the shape of this female horn sheath is somewhat similar to he male's, but more slender (Fig. 1 and 2) and, most importantly, it arcs in a more forward facing position (Fig. 2). The horn sheath looks almost as long as those of mature males. Small sexual differences in horn length are not unique to helmeted muskoxen. Female horns of Rocky Mountain goat (*Oreamnos americanus*) and Oryx (*Oryx oryx*) are as long or longer than male horns, for example. Also it is common for female bovid horns to be similar to but not conform exactly to the shape of the more robust male horns.

Packer (1983) has argued that female bovid horns have an important role in predator defense, which accounts for their slightly different shape. Females do not regularly use their horns in intraspecific combat so their horns do not have to be as thick as male horns. Males clashing into each other experience twice the force as a female hitting a fixed predator (Packer 1983). Geist (1966) has proposed that the flattened frontal horn boses of muskox serve as an intraspecific clashing device while the sharp hook tip functions mainly in predator defense. Muskox (*Ovibos*) are not fast runners and they lack endurance, so they must stand and defend themselves and their young. Against social predators, such as wolves, they form a tight cluster or line; the powerful upward thrust of their sharp-hooked horns is an effective weapon.

The shape of male and female helmeted muskoxen horns suggests a similar use against predators. In fact, the more forward position and slender contours of the longer female helmeted muskox horns seem even better suited than those of males as a defense against predation. The distal parts of the male horns arc more laterally,

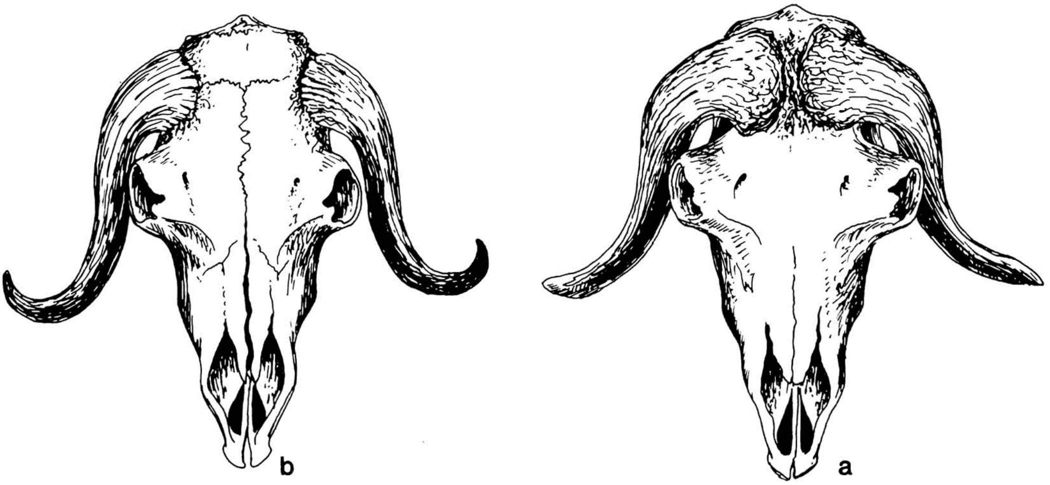

Fig. 3. Female adult *Ovibos* have horns which almost abut against each other along the medial line (a). However, in young females (b), the horn cores are of a rather primitive pattern, emerging laterally from the frontals, and not meeting medially. In this one trait, young *Ovibos* are similar to adult female helmeted muskoxen. As a functional weapon, this is an emphasis on the horn tip and not on the horn base.

away from the heavy bos used for frontal clashing, but the horn tips of females swept forward, hooking in front. This form would have precluded violent clashes between females, but would not have prevented head-to-head contact on the anterior-dorsal surfaces of the horn bases, as in agonistic pushing. In fact, this frontal surface was slightly flattened along just such a plane in females (Fig. 2). The thinness (0.5 cm) of the horn sheath over the flattened horn base, in contrast to the very thick male base, also indicates that clashing among helmeted muskox females was not a regular phenomenon. This is notable because older *Ovibos* females have thicker horn bases that do almost meet along the medial line and are thus quite capable of absorbing blows from mild frontal clashes (Fig. 3).

The peculiar shape of all muskoxen horns, the flattened proximal portion extending horizontally downward, seems to be due to the functional separation of a broad clashing plane and the sharply hooked distal end. Impact of intraspecific clashes is taken on the bases where the horn is backed by a bony core. The bony horn core of both helmeted muskox and *Ovibos* are very short and stubby. Most of the horn sheaths are thus solid keratin. This allows the solid keratin to be long, slender, and sharp. In addition to its anti-predator role, it should be stated that male *Ovibos* also use this sharp tip intraspecifically to dig the ground in display and to dig into the opponent's rear as the latter run from a fight (Gray 1984).

Compared with *Ovibos*, the horns of female helmeted muskoxen are more primitive and not so clearly shaped into parts for different uses. Horn cores of female helmeted muskox look more akin to those of *Soergelia*, the middle Pleistocene muskoxen which ranged across Eurasia and North America and which was possibly ancestral to the helmeted muskox. The open, V-shaped contours of *Soergelia* horn cores would have served to catch an opponent in a clash, not unlike the V-shaped pattern of mountain sheep horns which serve that same function. Except that, to judge from the horn core shape of *Soergelia*, the clash was taken, not in a sheep's downward blow, or the upward thrust of bison, but head-on. *Soergelia* thus represents an intermediate step in the evolutionary process from upright V-pattern horns to the fully bent horns of helmeted muskoxen (Fig. 4). In this process the contact zone of the clash moved from the open-V to the bases, which became flattened. The horn portion expanded to cover most of the bos and the entire blow was taken on the frontals themselves and not on the bony horn cores — as seen in male *Ovibos* and male helmeted muskoxen. In their widely-spaced, slightly flattened bases, female helmeted muskox thus retain a more primitive male horn pattern (Fig. 4) and one similar to a young female *Ovibos* (Fig. 3).

The female helmeted muskoxen skull cap onto which I fitted the newly found horn sheath to reconstruct its position (Fig. 2) is also a recently found specimen, in the private collection of Walter Roman, the miner. During the summer of 1986, while Walter Roman was mining north of Fairbanks in Pearl Creek (65°02′N, 147°05′W), he uncovered a skull cap with horn cores, which I would like to describe. The occiput, basicranium, and face anterior to the braincase are missing. Both horn cores are present, but the very distal portion of the right is absent. The relatively closed

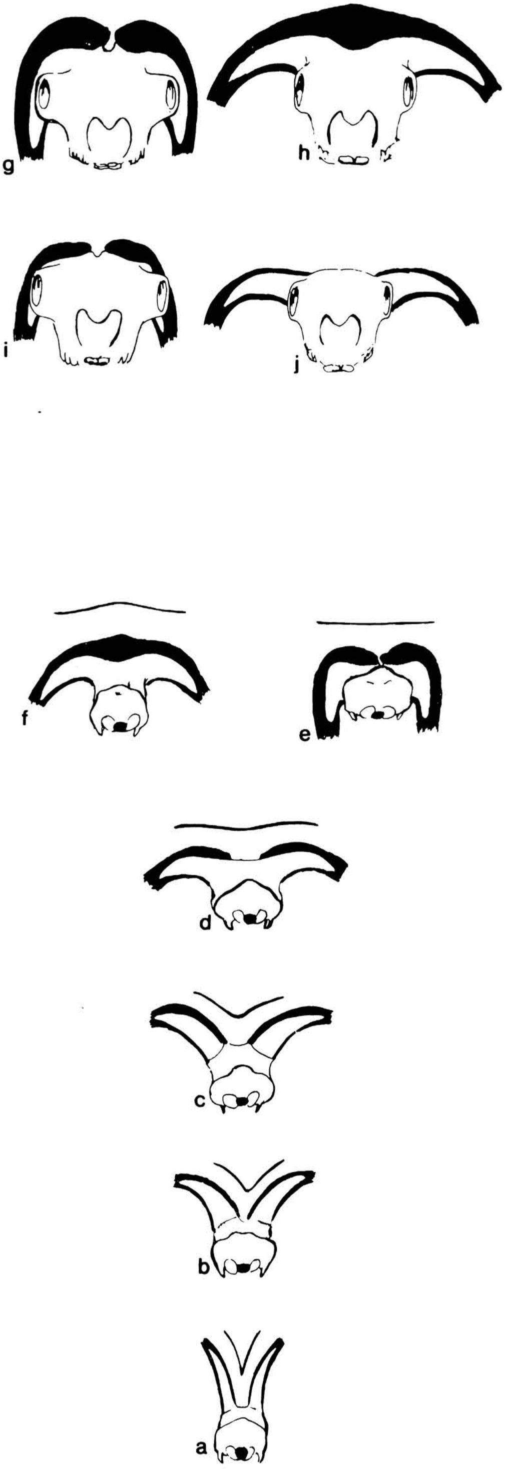

Fig. 4. Below (a–e) is a diagramatic portrayal of the concept that ovibovine horns came from a more typical bovid horn shape. Only the proximal portion of the horny sheath is illustrated, in order to separate its evolution from that of the distal end (the horn tip). The earliest ovibovines had mainly sharp-tipped offensive horns with only a thin sheath around the horn base (a), much like the Rocky Mountain goats (*Oreamnos*). In some groups, horn bases assume a defensive role, that of catching the opponent's horns with their own, much like extant sheep (*Ovis*). As a result the anterior and medial portion of the horny base is thickened (b). Some of the mid-Pleistocene muskox (*Soergalia*) had horns shaped with an "open-V" arrangement (c), as do male blue sheep (*Pseudois*). To get from an open-V stage to the late Pleistocene muskox, they necessarily had to pass through a laterally-placed horn stage (d) as seen to some degree in the extant Takin (*Budorcas*), and of course female helmeted muskoxen as portrayed in this paper. Extant muskox have carried this trend of horn flattening to its most extreme by having shifted the combat to the very base of the horns and bent horn core ventrally (e). Male helmeted muskox have shifted the clash point medially, but, unlike *Ovibos*, still retain the laterally-extended horn core (f). — Above (g–j) is a diagramatic comparison of *Ovibos* and helmeted muskoxen horn bases, showing both males and females: (g) male *Ovibos*, (h) male helmeted muskoxen, (i) female *Ovibos*, (j) female helmeted muskoxen.

nature of the skull sutures show this specimen is a mature adult and not a sub-adult. The transverse diameter of the bony horn-core base is 64 mm; vertical diameter is 58 mm; circumference at horn core burr is 197 mm; the least distance between core bases on the anterior face is 90 mm; and the length of the horn core along its dorsal surface is 212 mm. These measurements are almost identical to those listed by Harington (1977) on another Alaskan specimen USNM 2324 from Eschscholtz Bay, and slightly less than those he lists for specimens from the Old Crow region in the Yukon Territory, and from Michigan.

3. Ethological comparisons between *Ovibos* and helmeted muskoxen

One must first stress the similarities between these ovibovines. Sexual dimorphism in body size and in weaponry is similar. This similarity lets us say with some confidence that, like *Ovibos* (Gray 1984), helmeted muskox were polygynous. Dominant males associated with females mainly during the breeding season; they were not in mixed groups year around. As for intraspecific clashes, the horn helmet of males is constructed as a fused unit. This is slightly divergent from *Ovibos*. The bos of the latter is formed from discrete, separately-flattened horn bases, however one base is usually dominant, forming a convex arc into the other's concave mediate margin. Horns of helmeted male muskoxen are thickest along the midline where the bases fuse (Fig. 4). Males of both species have skull-horn construction which can/could withstand enormous clash impact. Like *Ovibos*, male helmeted muskox probably established dominance during rut by running clashes, colliding with full force, bounding back and displaying. Unlike bison which absorb much of the blow on specially structured frontal bone bumpers, thick scalp dermis and a springy bonnet of hair, the skull of helmeted muskox is not structured with bony sinuses to absorb such shock. This role is assumed by fibrous horny boses. Fibers are wrinkled in an "Ovibos-like" pattern unlike mountain sheep or bison.

Dominance displays of male helmeted muskox may have been different than *Ovibos*. The lateral display of *Ovibos* is accented by their long bodies and draping tresses. The mane on the dorsal part of shoulders and neck forms a high crest, likewise a crest is present to a lesser degree over the sacrum. These mounds of hair are exaggerated by contrasting color; a white "saddle" makes the humps appear even higher (personal observation). Helmeted muskox anatomy, the horn exaggeration, taller lankier body and shorter pelage all suggest a more "cephalized," frontal or angular body presentation — as in bison or moose (Geist 1966).

Unlike sheep, the nasal area of male helmeted muskoxen is rather fragile, indicating the clash was confined to the horn bos. The long sharp tips of male horns arc laterally away from the clashing plane (Fig. 1), suggesting that anti-predator uses were secondary when it came to selection pressure and horn shape. The main role of male horns was in intraspecific clashing. Judging from the shape of the female's horns which arc frontally, they did not experience these intense selection pressures for intraspecific clashing. Females used their horns primarily in anti-predator defense.

As with *Ovibos*, the horns of helmeted females suggest that defense against social predators was a group defense, hence females were probably social for much of the year. Such long, thin, sharply hooked horns are effective only if social predators can be kept at the forward end of the body (Kruuk 1972). That is possible only with a group defense. Jingfors (1984) has shown that, unlike many bovids, *Ovibos* does not leave the female group during parturition, a behavior in this case probably related to social defense of the young.

In virtually all cases where female bovids are horned, young are born in the open, their development is precocious and they do not experience a "hider" phase (Guthrie in prep.). These weeks after birth are critical for open-ground ungulates. Predators too small to threaten an adult female can sometimes overpower and kill a neonate, unless the baby is defended by the mother. The female helmeted muskoxen could have defended "follower" young, as do *Ovibos*, without a trace of the hider phase.

On the whole, *Ovibos* are not very mobile, they normally live in a comparatively restricted region throughout the year. Short, powerful legs allow them to negotiate steep slopes but are unsuited to longer seasonal movements or to deep snow (Klein et al. 1987). Helmeted muskoxen, on the other hand, had considerably longer legs, especially metapodials, which allowed energetically more efficient travel than *Ovibos*. This greater potential, and probably actual, mobility would have meant different kinds of social interactions. When associates in an area are not known individually and new individuals are encountered each season and rutting period, ungulates usually wear more elaborate, rank-specific social ornamentation (Geist 1966, Estes 1974, Guthrie 1980). The larger horns of male helmeted muskox may be a part of this relationship.

For these social reasons I suspect the pelage pattern of mature male helmeted muskox was striking in color and form. The broadly ranging American bison (*Bison bison*) and Alaskan moose (*Alces alces*) males, for example, are more striking in appearance than European counterparts living in restricted home ranges. Unfortunately the only mummy of helmeted muskox from Alaska is a juvenile female, so we have no way to know if male helmeted muskox were more elaborately adorned with social paraphernalia than male *Ovibos*.

The shorter pelage of helmeted muskox may also be related to greater mobility: less volume of pelt to carry, less to wet, and a tendency to move to more protected landscapes in severe weather. The long tresses and stubby legs of *Ovibos* are part of the more sedentary life-history strategy which allow muskox to remain sedentary in the winter conserving energy rather than seeking new and distant sources of food.

4. Diet of helmeted muskoxen in Alaska

In addition to behavioral implications gleaned from this recently excavated horn sheath, I have some new information about Alaskan helmeted muskox diets. I was able to extract identifiable plant remains from infundibula of cheek teeth of six different fossil skulls of this species. The skulls were found in interior Alaska, where permafrost had prevented decomposition of the plants. Although it had been decades since most of the fossil skulls were collected, and these had since been washed, dried, and kept in museum storage; because the plant bolus is packed so tightly within the narrow infundibulum it remains relatively intact and well preserved even during extreme curatorial preparation. (I have worked with recent skulls that were boiled, degreased, and bleached and yet tooth contents seem comparable to samples taken from freshly killed animals.) Plant samples from the teeth of other Alaskan Pleistocene species were also taken; these will be reported elsewhere.

Paleontologists normally deal with cusp patterns of teeth and not the negative spaces between them. For that and other reasons very little work has been done on infundibulum contents. Artiodactyl teeth have especially large and deep infundibula, unlike equids and mammoths which have most of their intercusp spaces filled with cementum. As cheekteeth erupt above the alveolar surface, infundibula fill with plant material being eaten at that time. Acidic conditions in the mouth and the lack of cellulase enzymes result in relatively good preservation of plant materials, comparable to a miniature peat bog. This material is compressed into a tough bolus that can be teased out with dental picks.

Epidermal fragments in the bolus are moderately well preserved and sufficiently characteristic to identify to general plant groups.

Epidermal analysis of faecal samples is widely-used management technique to assess ungulate diets (Hansen 1976). At present two full-time commercial laboratories process such samples. This technique has been used on fossil faecal samples to study paleodiets of ground sloths (Hansen 1978); but because plant epidermal tissues preserve well only in special conditions, paleontological applications of this technique are limited to unique depositional environments, among them the frozen ground of Alaska.

Epidermal identifications for this study were made by Terry Foppe at the Composition Analysis Department, Colorado State University. Six male helmeted muskox skulls with teeth containing identifiable plant fragments are listed in Table 1, as well as a seventh sample taken from fossil faeces. Grass cuticles were identified as related to three groups of cool-season grasses: *Agropyron*-like, *Bromus*-like, and *Poa*-like. No sedges were recognized in these teeth, although one specimen consisted of grass cuticles from an unidentified species. Two specimens had been eating considerable portions of woody plants, as revealed by bark which was not identified to taxa. Half of the tooth contents of one animal were from *Vaccinium*, an ericad shrub genus. Two other individual helmeted muskoxen skulls had identifiable cuticles solely of *Vaccinium*. This plant genus is found primarily in woodlands, heaths, and bogs. Judging from pollen, ericads were probably common during interstades (marine isotope stage 3) and interglacials, and uncommon to absent during the last full glacial, Duvany Yar or marine isotope stage 2 (see Hopkins et al. 1982). These three *Vaccinium*-eating specimens may date from the former warm/wet episodes; however, *Vaccinium* is an insect-pollinated genus and may not be a reliable part of the fossil pollen spectrum. Taken at face value, these samples of helmeted muskox diet characterize the species as an eclectic feeder, capable of feeding in woodlands but also able to use the more xeric end of grassland vegetation. The skulls from which these plant samples were taken are still undated. It is possible that the specimens containing *Vaccinium* date from interglacial and/or interstadial times while those with teeth containing predominantly glass cuticles date from nearer full glacial times.

Table 1. Epidermal analysis from plants (%) from helmeted muskoxen teeth. Samples from individual animals are numbered 1–8. Percentages for each specimen of different plant groups on left are listed in the table. To the far right is a total compilation percentage for all 8 specimen.

Specimen:	1	2	3	4	5	6	7	8	Tot.
Woody plant bark			35						13
Vaccinium				100	50		100		31
Salix								100	13
Grass									
Agropyron-like	30								4
Bromus-like			65			100			12
Poa-like					50				6
Unidentified	70	100							13

Specimen identifications: 1 = A-201-4200 Little Eldorado Creek, 2 = 30502-543 Cleary Creek, 3 = 6037 Engineer Creek, 4 = 2167 Cripple Creek, = A-254-4209 Little Eldorado Creek, 5 = A-254-4209 Little Eldorado Creek, 6 = A-254-4215 Little Eldorado Creek, 7 = 4032 BX-290 Little Eldorado Creek, 8 = 204-4254 Little Eldorado Creek.

In 1939 Otto Geist collected a skeleton of helmeted muskox (F:AM 2044254) and with it a cluster of faeces labeled *Symbos*, and apparently associated with a partial mummy of helmeted muskox. These were C14 dated (SI-291) at greater than 40 000 yr. B.P. The Composition Analysis Department at Colorado State University identified plant fragments in a small sample of the faeces to consist totally of willow. I have listed all specimens and infundibular plant contents in Table 1 (infundibular Nos. 1–7 plus the No. 8 faecal sample). The possible helmeted muskox faeces are in pelletized winter form (Fig. 5). They fit a pattern of hard winter pellets characteristic of all northern cervids and most bovids, but are distinguishable in shape from those of *Ovibos*.

Pelletizing in the small intestine has been assumed to be a water conservation strategy. It allows animals to subsist without eating much snow (an energetically costly way to obtain water). Pelletizers form pellets in the small intestine and bunch them into large aggregates in the colon. Bison and horse are not pelletizers, instead their winter faeces occur in flattened plates (Fig. 5); equids having less flattened plates than bison. Bison and horse dehydrate the faeces in the colon and hence have colon diameter plates. Bison and equids (and mammoths) were adapted to consuming coarser grass stems and to passing larger plant fragments through their gut, than the pelletizers listed above. It may be that this coarser material does not pelletize well into small "bon-bon" forms. Or, it may be that the more rapid gut-transit time of large species which feed on low nutrient forage precludes pelletizing. Bison and equids lose more moisture with defecation than pelletizing species. For example, caribou (*Rangifer*) on a winter diet of lichen and moose (*Alces*) eating willow stems, both have a faecal moisture content of almost exactly 50% (Staaland et al. 1986, R. G. White pers. comm.). On the other hand I found winter horse faeces to have moisture content of around 77%. This latter value, however, was obtained from horses with access to free water. Judging from the possible faeces of helmeted muskoxen, they pelletized their faeces like *Ovibos* as a means of water conservation.

5. Comparisons of *Ovibos* and helmeted muskox niches

Late Pleistocene fossils of *Ovibos* and helmeted muskoxen are found in unglaciated Alaska and the Yukon Territory as well as south of the continental ice in mid-continent North America (Kurtén & Anderson 1980). The coexistence of these related genera immediately raises the question of competition; however, differences in body conformation as well as the plants found in Alaskan helmeted muskox teeth indicate these species were not identical in their habitat uses.

Klein et al. (1987) showed that leg-length in caribou is associated with degree of mobility and substrate; long-legged populations have a history of annual migrations. They compared *Rangifer* and *Ovibos* and proposed that *Ovibos* is anatomically and behaviorally a more sedentary species. The same argument could be used in a comparison of the long-legged helmeted muskox and short-legged *Ovibos*. The conformation of helmeted muskox was more suitable for efficient long distance travel and deeper snow.

Field studies of existing muskox populations show they eat primarily sedges or willows, or both. This is rather curious, as most ungulates can be divided into graminoid feeders or browsers, especially during winter. Plants from the teeth of helmeted muskox show that they, like *Ovibos* were also rather opportunistic, eating both graminoids and woody plants. However, unlike living *Ovibos* which prefers mesic habitats and eats sedges and willow, plants from helmeted muskox teeth were more xeric, mainly upland grasses and woody plants. In a study of competition between *Rangifer* and *Ovibos* on Melville Island, Thomas & Edmonds (1984) found caribou tended to select exposed upland sites while muskoxen occupied more mesic habitats. Musk-

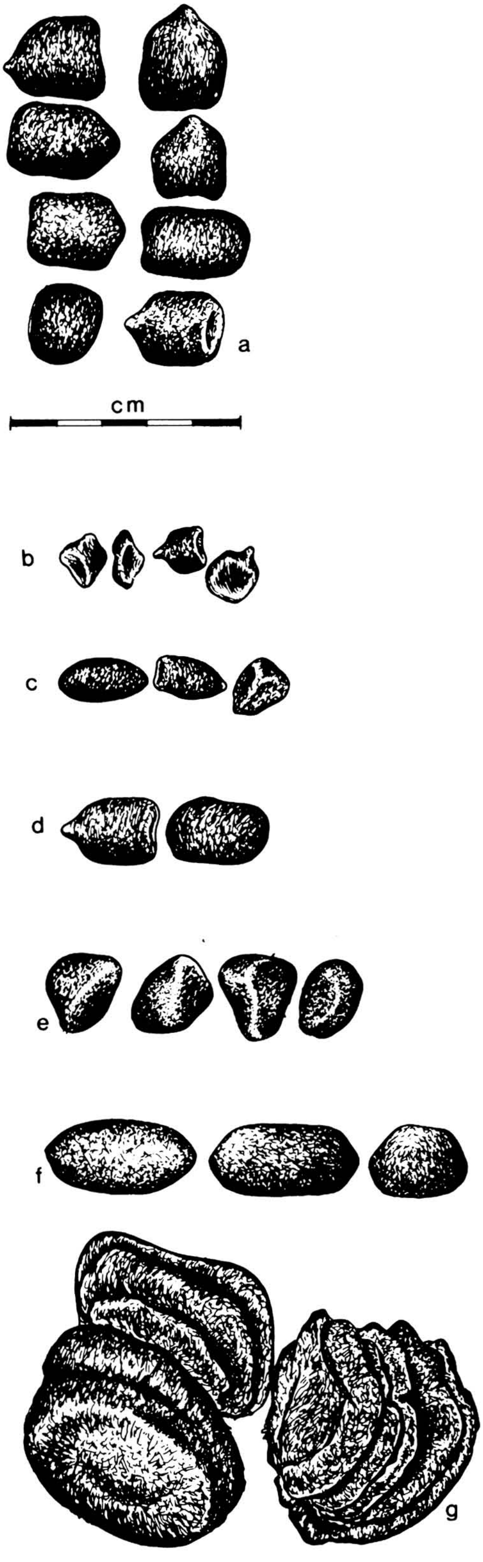

Fig. 5. Winter faeces of Pleistocene age from (a) possible helmeted muskoxen compared with winter faeces of (b) caribou (*Rangifer tarandus*), (c) dall sheep (*Ovis dalli*), (d) wapiti (*Cervus canadensis*), (e) muskox (*Ovibos moschatus*), (f) moose (*Alces alces*), (g) bison (*Bison bison*). These are representative specimens, although faeces shape is quite variable depending on diet, season, age, and sex. Scale is in centimeters.

ox, in their studies, although highly selective, were not as selective as caribou. Muskoxen chose coarser more fibrous forage.

We cannot assume that the *Rangifer–Ovibos* comparison above is completely analogous to helmeted muskox and *Ovibos* relations but plant material found in the teeth of helmeted muskox do point to a niche separation. I think helmeted muskox selected slightly more xeric vegetation and preferred more arid habitats in general.

6. Extinction of helmeted muskox and survival of *Ovibos*

There are few radiocarbon dates on helmeted muskoxen, possibly because helmeted muskox are not as spectacular as mammoth and their remains have never been found associated with human artifacts. It's therefore difficult to evaluate time of extinction. However, one late date of 11 100 ± 400 yr B.P. (Semken et al. 1964) is similar to dates of other Pleistocene megafauna which suffered late Pleistocene extinctions (Kurtén & Anderson 1980). The obvious question is why helmeted muskox became extinct while *Ovibos* survived.

At this point we should note that *Ovibos* did become extinct throughout much of its range. During the last full glacial (marine isotope stage 2) *Ovibos* existed in Spain, across Eurasia and Alaska, and in midcontinent North America. By the late Holocene, at least, *Ovibos* was completely extinct in Eurasia and only spotty populations survived north of the Arctic circle in North America. *Ovibos* appears to have been confined to this High Arctic habitat in North America not so much by human hunting pressure as by competition with other ungulates and scarcity of habitats with appropriate vegetation and limited snow. (Most regions where *Ovibos* is found today have little precipitation, usually less than 20 cm.) *Ovibos* became extinct early in this century on the North Slope of the Brooks Range in Alaska well after the introduction of firearms. *Ovibos* are being successfully returned to norther habitats both in Alaska, Scandinavia and the USSR (Lent 1989). But it is difficult to imagine fitting helmeted muskox into modern arctic and subarctic habitats. Caribou (*Rangifer*), moose (*Alces*), and muskox (*Ovibos*) seem to thoroughly exploit the edible forage on nonmountainous winter ranges in northern landscapes. In fact, there are areas, such as Svalbard, where caribou have existed without muskox and as a consequence have extended their dietary preferences to include former muskox specialities and in fact became somewhat muskox-like morphologically. On Svalbard, introduced muskox were outcompeted by these indigenous caribou (Klein & Staaland 1984). I think competition for more limited resources was the proximate factor in the extinction of helmeted muskox as well as the regional extinction of *Ovibos*.

In the far north where helmeted muskox and *Ovibos* once coexisted, utilizing more and less xeric ends of the Mammoth Steppe environment, less xeric habitats expanded and helmeted muskox habitat was eliminated altogether. Or, in refuges of remaining habitats, i.e., snow blow river bottoms emerging from mountain passes, helmeted muskox were in direct competition with grazing specialists like bison. The expanding Holocene mesic boreal forest was also occupied by an efficient competitor. Moose (*Alces alces*) arrived in Alaska from Asia about this time. Unlike ovibovines, with their conservative life-history adaptations to climax vegetation, moose are adapted to early succession vegetation occurring after forest fires or along riparian corridors. Moose succeeded as the willow (*Salix*) eater extraordinaire; able to convert tall willows into twin, sometimes triplet, moose calve each spring. Moose had other adaptations to these more mesic Holocene habitats, such as specialized structures for aquatic feeding. Long legs and special hooves allow moose to flourish in deep winter snows and boggy summer landscapes where few other ungulates survive.

Vaccinium and other shrubs do exist in many areas of Alaska, but snow is frequently too deep or too wind-packed to allow winter access. Additionally, many slow-growing shrubs are heavily defended against herbivory by secondary compounds (Bryant & Kuropat 1980). Likewise, although a dense cover of sedge blankets many muskegs and wet tundras of Alaska, these sedges are difficult to reach through deep or packed snow, and the standing dead winter vegetation is very low in nutrients, and hence digestibility (Batzli 1980, Bliss et al. 1981).

The present debate about late Pleistocene extinctions has polarized into arguments for human overkill *vs.* changes in climate and vegetation. I have argued the case for climatic-vegetational change (Guthrie 1982, 1984a, 1984b, 1985) and still contend it best accounts for the demise of such species, allowing bison to dominate an area previously shared by many large bodied grazing species. The more homogeneous Holocene habitats finally reached the point that the dietarily unspecialized muskoxen (both species) were unable to compete for appropriate habitats at midlatitudes. I would propose that this ecological shift at the Pleistocene-Holocene boundary caught *Bootherium* without suitable range and left *Ovibos* clinging to the bare outer margins of its former range.

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