

Paleoecological Significance of Mummified Remains of Pleistocene Horses from the North Slope of the Brooks Range, Alaska

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ABSTRACT. Radiocarbon dates from horse fossils found on the North Slope of Alaska show that horses did live there during the last peak glacial (Duvanny Yar Interval, Marine Isotope Stage 2). Some previous paleoecological studies have assumed the region's climate was too extreme for large mammals during the Duvanny Yar. Hoof structure suggests the Pleistocene horses survived on winter range characterized by low snowfall and/or snow removal by wind. Hoof growth rate suggests a substantial dietary volume of exposed dead grass during winter; hoof wear pattern indicates the horses were able to remain relatively sedentary, requiring neither long-distance winter migration nor constant digging through snow for food. Bones with mummified soft tissue may have been buried and preserved by wind-drifted eolian silt.

Key words: horse, Pleistocene, paleoecology, Alaska, paleontology

RÉSUMÉ. Un datage au radiocarbone de fossiles de chevaux découverts sur la pente nord de l'Alaska montre que des chevaux ont effectivement vécu à cet endroit au cours de la dernière période glaciaire (intervalle Duvanny Yar, isotope marin étape n° 2). Des études paléocéologiques antérieures ont émis l'hypothèse que le climat de la région était trop froid pour les grands mammifères durant l'intervalle Duvanny Yar. La structure des sabots donne à penser que les chevaux du pléistocène survivaient à l'hiver en paissant dans des endroits caractérisés par de faibles chutes de neige ou bien où la neige était déblayée par le vent. Le taux de croissance des sabots laisse supposer que durant l'hiver, le régime des chevaux se composait en grande partie d'herbe sèche exposée à l'air. Le régime d'usure des sabots indique que les chevaux étaient capables de rester relativement sédentaires, n'ayant besoin ni d'émigrer à de longues distances pour l'hiver, ni de creuser constamment la neige pour trouver leur nourriture. Les os qui contiennent des tissus momifiés ont pu être enterrés et conservés dans du limon éolien apporté par le vent.

Mots clés: cheval, pléistocène, paléocéologie, Alaska, paléontologie

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INTRODUCTION

During the summer of 1983, a complete forefoot (including hoof), skull (with considerable connective tissue), and radius (with attached tendons and dehydrated muscle fibers) were found freshly thawed from a deposit of frozen Pleistocene silt in northern Alaska. These horse remains were found on the Titaluk River, at 69°35' N, 156°35' W (Fig. 1), a tributary of the Ikpiukuk River. The three parts were collected separately, eroded out of a loess exposure. A C14 sample of the hoof keratin produced a date of 17 190 ± 240 (DIC-2418).

These remains of horses that lived on the unglaciated North Slope of the Brooks Range during the peak of the last major glacial advance are of interest for several reasons. For one, some researchers have proposed Alaska was not inhabited by large grazers during peak glacial episodes (Colinvaux and West, 1984). Full glacial Beringia has been portrayed as a bleak "polar desert" by several palynologists (Ritchie and Cwynar, 1982; Ritchie, 1984; Cwynar, 1982), and the North Slope, specifically, has been pictured by Quaternary geologists as a cold, windy desert, hostile to large mammals (Carter, 1981a,b; Carter *et al.*, 1984; Nelson, 1986).

Unlike mustangs in the high-plains states, feral populations of domestic horses have not survived in northern Alaska. Horses need human assistance to overwinter in the far North because there is generally little they can eat, and what there is, is deeply buried by snow. Though low temperatures can be stressful, they are not the critical problem. When provided with adequate food and water, horses in Alaska can survive and reproduce with little or no shelter from the weather (Dalton, 1989). Horses seem to require windswept landscapes where grasses are exposed. There are two places in the Alaskan interior where domestic horses have overwintered without

supplemental food: on the White River, in the southern Wrangell Mountains, and at Healy, in one of the major passes of the Alaska Range. These are uniquely windy localities. Horses overwintering on free-range in these special areas exist at well below maintenance levels, with high mortality, low fecundity, and low recruitment. No comparable overwintering areas occur today on the North Slope of the Brooks Range.

The documented presence of wild horses on the North Slope at the peak of the last glaciation indicates winter conditions were more amenable to large grazers than they are today. All northern wild, large mammals prefer snow to liquid water in winter and have evolved a water-conserving physiology that requires modest snow intake. We can assume that northern Pleistocene equids developed similar abilities and that, while stressful, they were able to endure winter months without free water. Thus, the critical variable may be neither low temperatures nor free water, but rather the presence of adequate winter forage.

Hundreds of Pleistocene horse bones have been found on the North Slope, and it is our impression from collecting there and from examination of other people's North Slope fossil collections that horses were the most common large mammal (for example, of the 21 metapodials the senior author has collected, 15 are horse and 6 are bison). In interior Alaska, bison metapodials are more common than those of horses by a ratio of about 5:3 (Guthrie, 1968). However, few of the Pleistocene bones collected from the North Slope have been dated. Prior to dating Titaluk River horse bones presented in this paper, we dated some horse bones from farther downstream on the Ikpiukuk River (Valley of the Willows). These bones had washed from sandy sediments and were not *in situ*. They were well preserved; most of the collagen remained in the bones, and some dehydrated marrow was present. These

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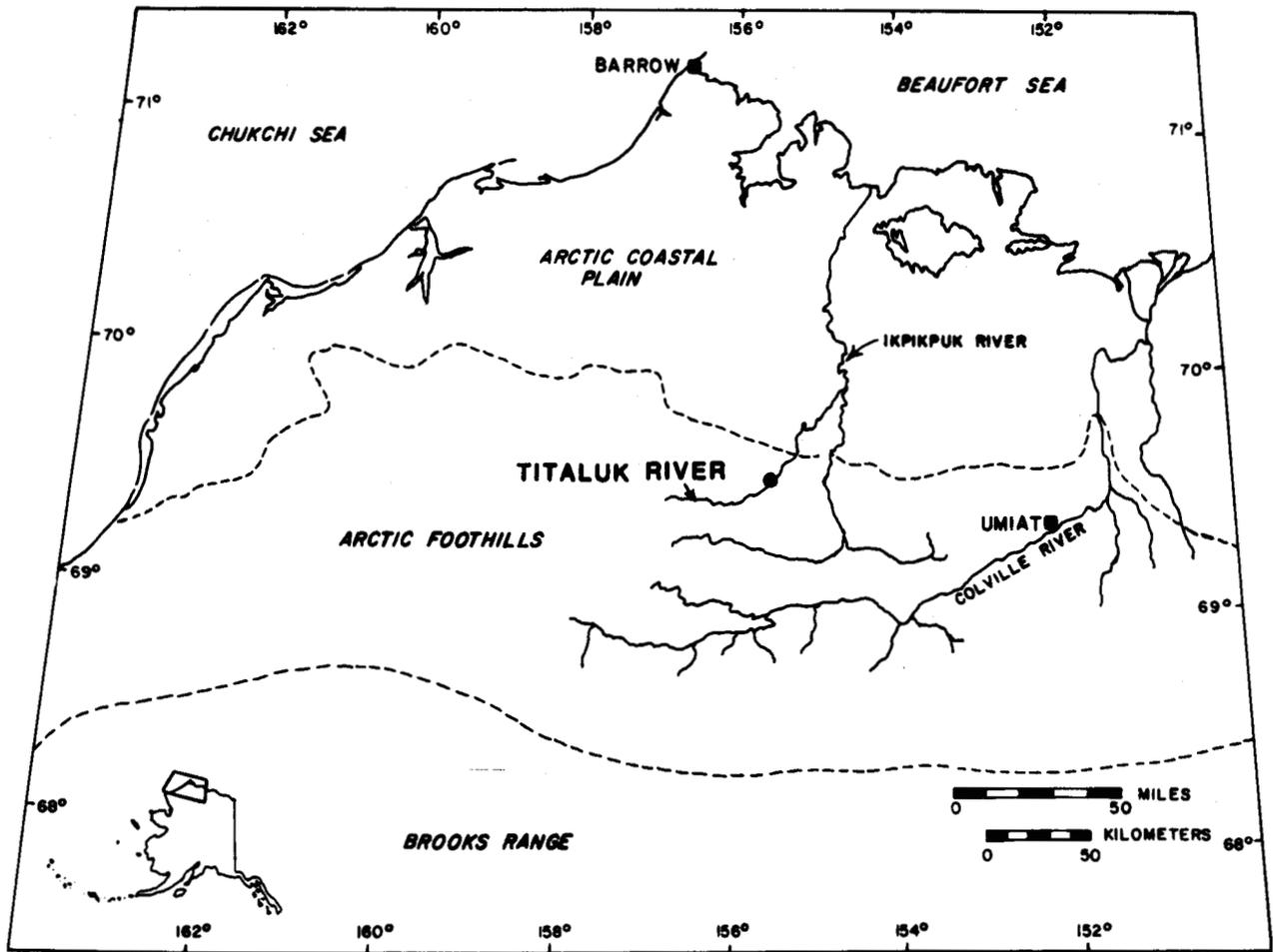


FIG. 1. The North Slope of the Brooks Range. The fossil horse site on the Titaluk River is located at the margin of the Arctic Foothills and is shown by the large black dot. The river meanders along the wide valley floor and occasionally contacts the valley margins, creating a bluff exposure. The site is one of these exposures. Most, if not all, of the horse fossils seem to have been derived from the loess portion, which seems to represent a deposit of Duvanny Yar age. The large sand sea of fossil dunes lies on the Arctic Coastal Plain near the Beaufort Sea between the Ikiqpuq and the Colville rivers; the loess was probably derived from this sand sea (Carter, 1981a). (Map modified from Nelson *et al.* 1988.)

collagen dates are: $>40\ 000$ (I-9320); $>40\ 000$ (I-9319); $32\ 270 \pm 1500$ (I-9275); $23\ 910 \pm 470$ (I-9318); $20\ 810 \pm 410$ (I-9274); and $19\ 250 \pm 360$ (I-9371).

The Titaluk sections studied by Nelson (1982) were mainly Interstadial (Boutellier Interval, 28 ka to beyond the C14 range) in age. However, the C14 dates of three of the six metapodials we dated from the Valley of the Willows were from the last glacial phase (Duvanny Yar Interval, or Marine Isotope Stage 2), roughly 28-14 ka. Some researchers have questioned radiocarbon dates from Alaskan megafauna of Duvanny Yar age (Colinvaux and West, 1984), mainly on theoretical grounds. Others are skeptical of the reliability of such bone dates because once most of the collagen is decomposed, such bones are easily contaminated (Hassan and Hare, 1978). Fortunately, most of the original collagen is present in Alaskan Pleistocene bones. We shall illustrate that fossil specimens from the Titaluk River are, indeed, of Duvanny Yar age, and the conclusions derived from the dates add further to our understanding of Alaskan paleoecology during Duvanny Yar times.

PALEOECOLOGY IN A HOOF

In addition to securing a date for the presence of horses on the North Slope during the last full glacial, the Titaluk

horse hoof also provides clues to Duvanny Yar environmental conditions and the species identity of the horse. The identity of the common Pleistocene horses that occurred in Beringia is a matter of long-standing controversy. Savage (1951) argued from Hay's (1917) description that the fossil Alaskan horse, *Equus lambei*, was a caballid, a group conspecific with or closely related to domestic horses. Quinn (1957) and Harington and Clulow (1973) have argued that the Beringian horse is a wild ass or hemionid. Part of this problem is that horse fossils seldom occur in complete skeletal associations in Alaska; usually they are isolated bones. Individual elements of hemionid-like equids are, indeed, found rather commonly. This has been recently confirmed by Hans-Peter Uerpmann (pers. comm. 1983) in his work with postcranial bones in the collections at the University of Alaska Museum. However, most fossil dentition and skulls are definitely of caballid character (Eisenmann, 1980, 1981; Forsten, 1986).

Thus, there seem to be at least two kinds of equids in late Pleistocene Alaska: hemionids and caballids. The presence of caballids has been confirmed by the frozen Selerikan mummy of a mare from the Indigirka River basin in eastern Siberia, dating at 37 ka. This region was contiguous with Alaska during the last glaciation, at which time the Bering-Chukchi Platform was exposed. The Selerikan horse had

broad hooves characteristic of caballids (Vereshchagin and Lazarev, 1977). The small- to modest-sized late-Pleistocene caballid species, which occurred across the Mammoth Steppe (Guthrie, 1982), seems to be one species or species complex with chronological and local geographic variants, but probably no more variable than, say, monospecific reindeer (*Rangifer tarandus*), which had a comparable distribution. This caballid pony has been given several names: *Equus lenensis*, *Equus przewalskii*, *Equus ferus*, *Equus lambei* and *Equus caballus*. As with most equid taxonomy, these northern horses are in a nomenclatural mudmire, but the most recent discussion by Groves (1986) proposes that *Equus ferus* Boddaert (1785) has priority.

The Titaluk River specimen fits descriptions presented by others of the Beringian variant of this widely distributed caballid species or species complex. The dentition and skull are characteristic of the common Beringian horse, with wide protolophes on the upper molars, and the skull is relatively broad for its short length. The well-preserved forefoot hoof is broad, like a true caballid, and not cupped, like an ass-like equid.

To imagine the incongruity of horses living on the Alaskan North Slope today, one has only to walk away from ridges and stream beds, heading cross-country through endless boggy tussocks, flooded polygonal ground and thaw lakes, to realize that it is no place for horses. It is quite difficult terrain for a human hiker, and we have far less weight per foot surface than horses. Winter access to ungulate rangelands is severely restricted by wind-packed snow. And, once through the snow, North Slope grasses and sedges supply only marginal winter forage. Early explorers and guides on the North Slope either let their horses die of starvation or killed them for food. The margin between what horses require and what is available in the winter is so great that guides currently working on the North Slope do not consider overwintering their horses there.

The Titaluk hoof is darkly pigmented in cross-section, characteristic of all wild equids, although the surface is a frosted mahogany color. The most interesting feature of the hoof is its wear pattern (Fig. 2a,b); it shows two distinct features with regard to the worn outer margin. The first is a very slow rate of wear on the lateral hoof wall. This differential wear rate is so great that local veterinarians have, at first glance, mentioned the possibility of laminitis or founder, a hoof pathology that comes from infection along the germinal growth line of the hoof. It results in deformed hooves due to the differential growth between medial and lateral margins. But closer examination of the fine growth lines arching around the hoof confirm that this is a wear phenomenon, not a shape produced by pathologically differential growth.

Differential growth can occur on wet substrates, but this produces the opposite hoof deformity — a pinching in of the "heels," or posterior edges of the hoof wall (Hanauer, 1977). Rather, all the characteristics of the Titaluk specimen suggest a usual growth rate, but a reduced rate of lateral wear on a hard, smooth substrate.

The flare and excess growth on the Titaluk hoof indicates that it is a late winter hoof. One finds such extremes in accumulated hoof growth during late winter, when horses are less active and when non-abrasive snow covers the ground. The wide overgrowth wings seen on the Titaluk hoof can sometimes be seen on domestic Alaskan horses with hooves untrimmed from summer to spring.

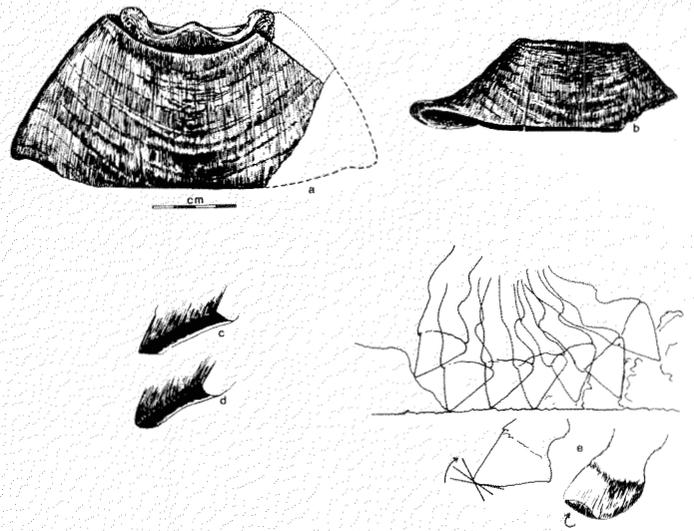


FIG. 2. The Titaluk hoof. The dorsal view is shown in (a) and the anterior view in (b). The third phalanx can be seen protruding from the upper side of (a). The lateral hoof overgrowth can be compared with the normal wear on the medial axis. The wear margin of this medial axis has a flat, sharply defined, edge (c), as opposed to the more usual rounded "roll-over" conformation (d). This roll-over shape is a product of normal walking gait in soft but abrasive material; however, it can become exaggerated when the front hoof is used in digging (e).

Overgrowth due to lack of wear on the Titaluk River fossil is so extreme that it suggests both inactivity and a winter diet with ample protein for hoof growth. This phenomenon of growth rates exceeding wear is exaggerated when animals are eating excellent forage. Observations of domestic horses and wild sheep kept by the first author suggest that hoof growth rates, especially in winter, seem to be associated with protein intake. Extreme protein deficiencies result in arrested or slowed hoof growth rates, at least in winter.

An exact measurement of the amount of winter hoof growth is difficult. According to local horse veterinarians and farriers, a growth rate of about 6-8 mm per month for all domestic horses is normal. The total length of the lateral hoof edge on the fossil hoof was 126 mm, while the medial wear had reduced the hoof to only 91 mm. If about one-half the length of the lateral hoof edge was removed, the hoof would be back to a summer contour. For purposes of calculation, we will assume one-half the growth of the lateral edges was produced during winter. Thus, 63 mm of growth for the winter would produce a growth rate of 8 mm for an 8 month winter or 7 mm for a 9 month winter, similar to that of domestic horses.

The excess accumulation of hoof on this Titaluk specimen would also suggest, then, that winter conditions were such that it was not forced to continually move great distances in search of food. The low wear rate indicates a more sedentary life, overwintering on local range for most of the long winter.

The lateral wall hoof overgrowth is so great on this specimen that one might be tempted to propose that it was from an injured or diseased leg favored by the animal as it walked, if it were not for the existence of wear on the forward or anterior edge (Hanauer, 1977). Yet, on the anterior edge the hoof has a normal rate of wear, and the amount of hoof present there does not overextend the subunguis (sole, in horseman parlance) or ventral hoof by any great amount.

The normal length of hoof in this anterior medial edge shows that the hoof was not favored by limping, nor was its shape due to some disease. Thus, it would appear that the unworn lateral hoof wings were the result of a relatively hard, smooth, non-abrasive substrate where most of the weight was placed on the forward part of the hoof (Trapani, 1983).

There are some other improbabilities to weigh in the disease argument. The increased predation susceptibility of an injured leg would not likely have allowed the animal to limp the many months required to produce a hoof overgrowth. The likelihood that the only fossil horse hoof found in Alaska would be from a diseased leg is likewise low. Late winter is a stressful period for northern ungulates and a time of peak mortality — an animal that died in late winter, like this one, would be most common in the fossil record, as should be fossil parts that represent late winter conditions.

According to the interior Alaskan veterinarians and farriers with whom we discussed the hoof, this lateral overgrowth would normally fracture off during the spring, when activity and wear occurred on rough substrates. At this time the hoof would again resume its normal contour. And, in fact, one side shows a raw fracture surface where excess growth has already broken away, leaving an irregular, and still relatively unworn, edge.

Horses normally wear their hoof edges in a rounded fashion (Fig. 2d). This wear, called roll-over by horsemen, is created by the "breakover" in a normal walk as the leg swings posteriorly beyond the center of gravity. The phalanges, or "pastern joint," reaches its maximum degree of forward flexure, and the point of the hoof rolls on the ground as it is lifted antero-dorsally. Roll-over is considered a natural wear pattern, but it is greatly exaggerated by soft, abrasive substrates or by digging. Caribou normally use their hooves in digging snow craters to uncover lichen. Horses are also adept at using their forefeet to uncover grasses, but a hoof used for such digging shows a very characteristic roll-over wear pattern; the anterior margin is rounded from the hoof (Fig. 2e), describing an arc as it is rotated posteriorly in a scraping motion. The wear margin on the Titaluk horse's hoof shows no trace of roll-over but runs in a sharp, straight line (Fig. 2c), intersecting the normal arc of the hoof's margin, indicating it was not used for digging. A marked roll-over wear pattern is observed today in Alaskan horses that dig in the snow to expose grass or to loosen it before eating the snow for moisture.

We presume that the absence of wear indicative of digging in this fossil horse hoof means that the Titaluk horse ate grass that was exposed above the snow. This would mean discontinuous or very shallow snow cover, because it is unlikely that the sward was very high in an arid landscape. Since the degree of roll-over is greater with longer strides, it is also likely that this horse did little long-distance travel or running. The acute angle of wear on the hoof (with the wide, flaring lateral walls) meant a more vertical lift of the foot with each step (Emery *et al.*, 1977), as if it was walking slowly on frozen silt or packed snow.

IMPLICATIONS FOR WINTER RANGE QUALITY

At this point two obvious questions demand some explanation. First of all, why are equid bones apparently the most common Quaternary large mammal fossil on the North Slope, in contrast to the Alaska interior, where bison remains are

most common? Secondly, how can one account for the low rate of hoof wear and moderately good rate of hoof growth during the Duvanny Yar?

Why should horses outnumber bison on the North Slope, when they do not anywhere else on the Mammoth Steppe? Horses and bison seem to occur together as a grazing team throughout the Mammoth Steppe (Guthrie, 1982). Though there is competitive overlap in their grazing adaptations, in many respects bison and caballid horses are quite complementary grazers. As a monogastric-caecalid, horses utilize both ends of the food quality spectrum. Horses process energy-rich foodstuffs, such as small grass seeds, in their simple stomach, and nutrients are absorbed in the small intestine. The finer fractions of very fibrous foods, such as grass stems, can be processed in the caecum, while coarsest fractions are bypassed directly to the colon. This bypass arrangement allows for quick transit time through the gut. A horse's caecal size-fraction selectivity and the ability to greatly increase gut transit time mean that horses can subsist on extremely low protein grasses by compensating for poor quality with increased quantity. They can, more or less, eat around the clock. This fundamental difference between caecalids and ruminants makes for different and complementary grazing strategies (Janis, 1976; Guthrie, 1984a) on a varied rangeland. The mammoth figured into this rangeland partitioning as a caecalid capable of tolerating even more fiber than horses, if a sufficient volume of food was available. Thus a triad of large grazers, mammoth, horse and bison dominated the Mammoth Steppe for nearly a million years.

Ruminants, such as bison, are especially effective winter grazers when quality is modest and volume is limiting, because the rumen can thoroughly process low-quality food by recycling urea. However, with increasing volumes of relatively undigestible fiber, ruminants decrease gut transit time (see Guthrie, 1984a, for a review). Thus, on a sparse winter range of modest quality, a large grazing ruminant would be expected to have a slight edge over a caecalid. However, on a poorer quality but relatively abundant winter range, a large caecalid grazer would be expected to excel.

Thus, the dominance of late Pleistocene horse fossils on the North Slope suggests that winter range was more appropriate for equid adaptations than for bison adaptations. This is consistent with Carter's (1981a) and Nelson's (1986) reconstructions of extreme winter aridity. Standing dead plant tissue exposed to weather, as opposed to being anchored in at least a modest snow cover, could be expected to lose a significant portion of its nutrients throughout the winter. Horses could operate better than bison under these conditions. It must be remembered that these comparisons between the North Slope and Alaska's interior are a matter of different bison-horse ratios, not a matter of reciprocal exclusivity. Like horse bones, mammoth fossils are also common on the North Slope, but because of their quite different size and preservability, it is difficult to make a fair assessment of their relative abundance, and very few are dated or associated with any stratigraphic control.

SIZE OF THE TITALUK FOREFOOT COMPARED TO OTHER ALASKAN FOSSILS AND OTHER EQUIDS

Hoof size is a rough indicator of environmental adaptations. Hoof size relates to bearing surface area and hence is informative about substrate. Hoof size can be adjusted

for body weight, since long bone width correlates with weight. Large hooves should thus have a wide third phalanx in relation to their articular width. Figure 3 plots the width of forehoof, as judged by the width of the third phalanx (coffin bone) of the foreleg (Fig. 3, GB), in comparison to long bone width, as judged by articular surface (Fig. 3, AB). The Titaluk specimen is moderately wide in comparison to other Alaskan equids, but not extremely so. Eisenmann (1984) made this same width comparison among the living equids, and although she did not give absolute measurements but used an index (maximal width x 100/articular width), we can use this same index for the Titaluk specimen, which has an index of 153. She found the *E. przewalskii*, *E. kiang* and *E. grevyi* were all broad hoofed, with respective mean indices of 157, 158 and 159 (all wider than the Titaluk third phalanx). She argued that the former two species live in snow for a considerable part of the year, even though their summer substrates are dry. I would add that *Equus grevyi* is a species that exists in more sandy, loose soils of Ethiopia. The other equids, *E. hemionus*, *E. burchelli*, *E. zebra* and *E. africanus*, all have narrower hooves than the Titaluk specimen, with respective forefoot mean indices of 141, 143, 136 and 142.

In comparison to other specimens from Alaska (Fig. 3), one can see that the Titaluk specimen falls well within the core of the forefoot third phalanx measurements. Unknown to the first author at the time these measurements were taken, individual hindfoot and forefoot third phalanges are separable not by quantitative dimensions, but qualitatively by general shape. The cluster plots are not discontinuous — that is, there is some overlap between forefoot and hindfoot in most measurements from the Alaskan sample. Unfortunately, these were collected over a long period of time from a variety of sources, some of which are no longer accessible, so hind and forefeet are combined in these graphs. However, when lengths are plotted against widths (Fig. 4), the Titaluk third phalanx is more on the margin of the scatter, although there are other specimens that are even more peripheral. In angle of slope (Fig. 5), the Titaluk third phalanx is also at the extreme margins of the distribution, with an angle of 41°.

The heterogeneous scatter of points in these plots can be accounted for by the fact that the other Alaskan fossil

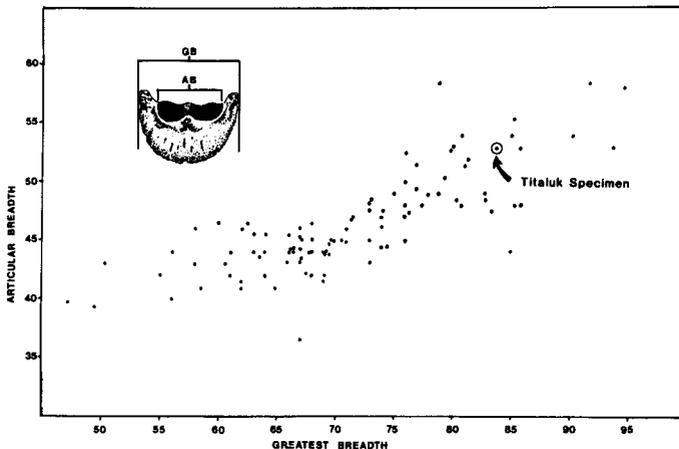


FIG. 3. The greatest breadth of the third phalanx plotted against the greatest articular breadth from Pleistocene Alaskan equids. The Titaluk specimen falls within the middle part of the upper scatter. Both fore and hind third phalanges are included in this plot; the right portion of the scatter represents the wider fore hoof. Although the Titaluk hoof is not absolutely broad, it is a fairly broad forefoot (84 mm) in comparison to other Alaskan fossils. (Measurements in mm.)

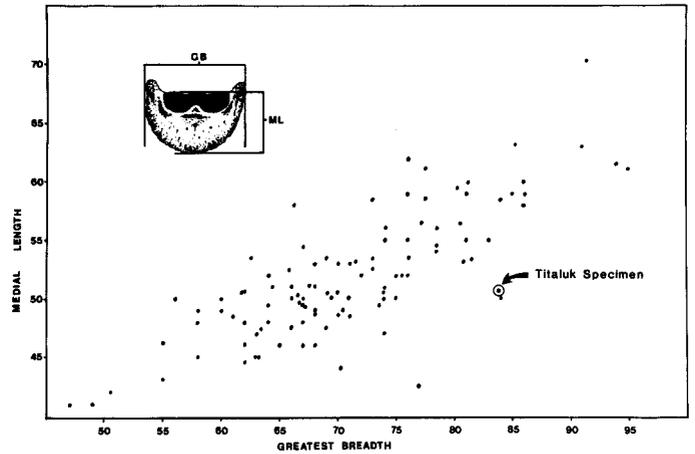


FIG. 4. The greatest breadth of the third phalanx plotted against the greatest medial length from Pleistocene Alaskan equids. The Titaluk specimen falls at the margin of the scatter. The cluster of points in the upper right represents the broad phalanges of Titaluk specimen. It is not only broad in comparison to the absolute widths of the other Alaskan specimens, it is proportionally one of the broader hooves when compared to its length. (Measurements in mm.)

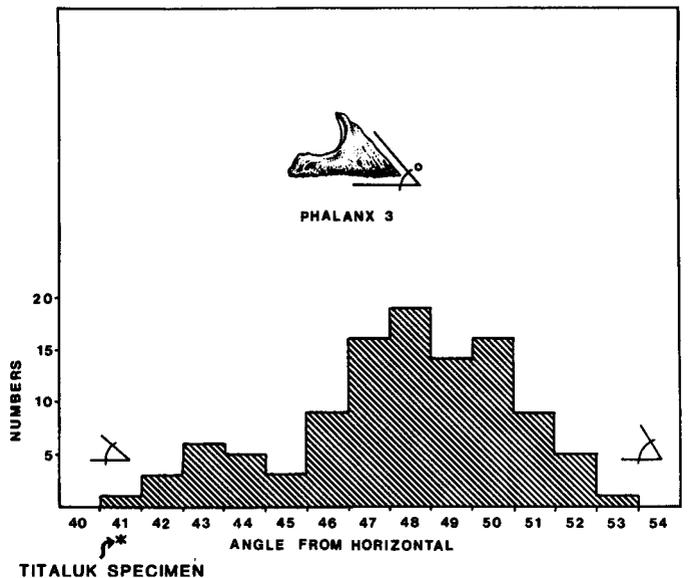


FIG. 5. A comparison of the hoof angle using the third phalanx of Pleistocene Alaskan equids. The angle of the Titaluk specimen is at the most extreme of the distribution, with a quite shallow angle.

specimens were collected over a long period of time from throughout the state in a variety of Pleistocene (and possibly late Pliocene) deposits by a variety of collectors. It must be remembered that these plots include both sexes and virtually all age groups of specimens from at least two quite divergent lines (hemionid and caballid) and from a variety of habitats, and they represent a considerable time period during which evolution probably occurred in both lines. Despite the wide context, we feel it is informative to record the Titaluk specimen within the known variations.

SIGNIFICANCE OF THESE PALEOECOLOGICAL INTERPRETATIONS FOR THE NORTH SLOPE

Compared to other periglacial areas in North America, the vast North Slope plain has received relatively little attention from Quaternary geologists. The very informative

work by Nelson (1982, 1986) and Carter (1981a,b, 1983; Carter *et al.*, 1984) are exceptions to this. The general tenor of their conclusions, while not necessarily in disagreement with our findings, emphasize (1) the absence of full glacial sediments containing megafaunal records and imply (2) that the fauna are primarily of interstadial age (Boutellier Interval), because conditions were too harsh for large mammals to exist during full glacial times (Duvanny Yar). We argue that their conclusions are, indeed, not exclusive to our findings, because either they have inadvertently concentrated on exposures where the loesses of Duvanny Yar age are absent (Nelson's sites farther downriver), or perhaps some of the Duvanny Yar sediments may have been misidentified due to contamination from reworked, earlier, Boutellier-aged organic material.

In a recent paper these authors (Nelson *et al.*, 1988) identified Boutellier-aged contamination in Holocene deposits on the Ikpikpuk. Therefore, it seems possible that some of the Duvanny Yar alluvial sediments also contain organic material originating from Boutellier-aged deposits. Presumably, most of the pre-Holocene fossil organic material is from Boutellier-aged alluvial deposits on the Ikpikpuk and Titaluk rivers. Increased moisture during that interstade would have produced a higher standing plant biomass than in the following, drier Duvanny Yar. Thus, the most likely source of organic remains in the Duvanny Yar alluvium would be reworked detritus of Boutellier age. Hence, radiocarbon dates from plant material in Duvanny Yar sediments may occasionally date to Boutellier times. Mammal bones can undoubtedly be reworked as well, but our interests lie specifically in dating fauna, not sediments or plant material. Bones with tendons and marrow are not only excellent material to date; the presence of this soft tissue makes it less likely that they are reworked from older deposits.

The Duvanny Yar dates on Ikpikpuk River horses listed earlier in this paper (from bones collected in the river sand among what appeared to be Boutellier-aged, richly organic alluvial deposits) and the 17 ka horse hoof from the Titaluk suggest that the megafauna was possibly as abundant during the Duvanny Yar as during the Boutellier.

We are in agreement with Carter *et al.*'s (1984) identification of the widespread Duvanny Yar sediments (in their 36-13.5 ka zone) as eolian deposits. They proposed these were created as a downwind dispersal (toward the Arctic Foothills) of sand and silt from the vast sand sea located west of the Colville River. Stoker (the second author of this paper) collected the 17 ka horse hoof in colluvium at the base of a loess section, so we assumed an association. However, upon reading Carter's and Nelson's works, we were in doubt about our association. Thus, we returned in August 1987 to the Titaluk site where the hoof fossil was collected (Fig. 6). While there, we examined the section and took *in situ* samples from underlying crossbedded sandy sediments, which contained considerable plant detritus (we assumed this to be of Boutellier age). But we were not able to find any large mammals *in situ* in these lower deposits. We were able to collect a large assemblage of mammal fossils, which we proposed would be Duvanny Yar in age, as many still had loess from the thick, overlying sediments attached or were collected directly from the loess. Horse bones were most common, but bison (*Bison priscus*), mammoth (*Mammuthus primigenius*) and caribou (*Rangifer tarandus*) were also abundant.

The C14 sample from the uppermost margin of the lower

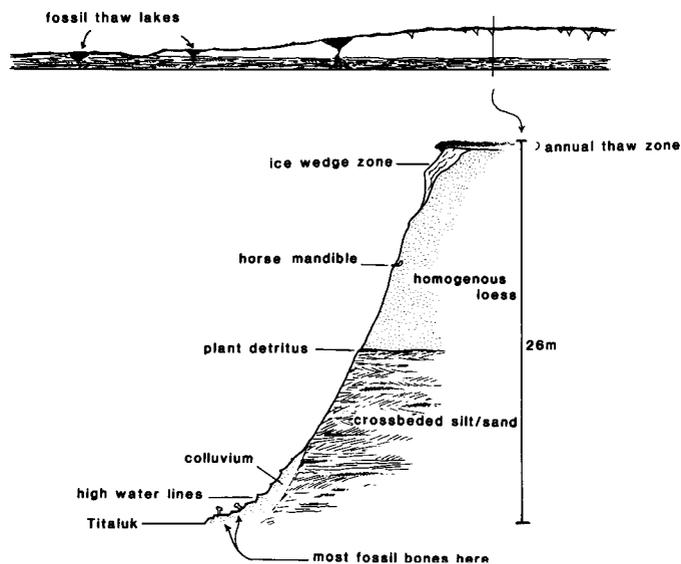


FIG. 6. A sectional profile on the Titaluk River where the horse fossils were found. The upper face view of the exposure covers about 1 km of river section. Most of the bones were found in the colluvium at the foot of the slope, but the horse mandible was found in the upper portion, which consisted of eolian silt. This loess represents the Duvanny Yar Interval, whereas the underlying crossbedded material represents the Boutellier Interval. Plant detritus from the top of the crossbedded portion was dated at $31\,990 \pm 920$ (GX-13940).

sandy alluvial deposit (Fig. 6) was dated at $31\,990 \pm 920$ (GX-13940). This corresponds closely to late Boutellier age. Bone collagen from a horse mandible (Fig. 7c) (AK-109-V-1) protruding from the loess about halfway up in that section dated to $21\,220 \pm 800$ (GX-13939). Bone marrow from a radius with mummified tendons (Fig. 7a) from the colluvium at the base of the section (Fig. 6) dated to $21\,420 \pm 440$ (GX-13941).

Bone dates recorded by Carter *et al.* (1984) have prompted incorrect conclusions as to the presence of large mammals on the North Slope during Duvanny Yar times. Carter *et al.* (1984:21) observed (discussing cool, dry summers of the late Boutellier Interval):

In spite of these severe conditions, radiocarbon dating of fossil bones shows that large herbivores such as mammoth, horse, and bison were present in the Arctic Foothills at this time.

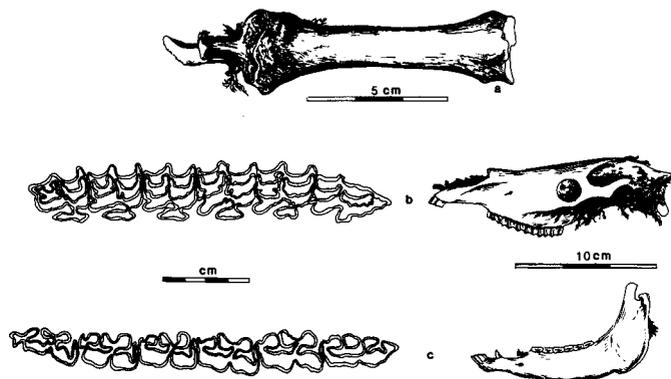


FIG. 7. Three of the horse bones, which have soft tissue attached, from the same locality where the hoof was found: (a) radius-ulna (AK-109-V-2) dated to $21\,200 \pm 440$ (GX-13941), (b) skull (AK-V71-3) undated, (c) mandible (AK-109-V-1) dated to $21\,200 \pm 800$ (GX-13939).

However, none of the dates on those large mammals is younger than 28 ka. Aridity may have become even more pronounced and summer temperatures more depressed after 28 ka, coincident with the expansion of glaciers in the Brooks range.

The loess from which we collected the horse bones had no obvious plant inclusions and in appearance was undistinguishable from Fairbanks loess. The horse mandible was quite fresh in appearance, as were the other fossils. Presumably most had thawed from frozen sediments that summer. This particular part of the section seemed to have a relatively high concentration of bones in the loess. A bison skeleton was found in one 3 m stretch of the same loess colluvium; presumably, it was almost complete before being transported downslope. The mummified tissue (keratin from the hoof and white marrow inside the radius) from these fossil horse bones should give one of the most reliable dates of any material used for C14 dating. It would be very unlikely that they could be contaminated to any significant extent.

Nelson (1986), discussing the unlikely possibility of people living on the North Slope during mid-Wisconsin times, has argued that the large mammal biomass, now living in a well-watered landscape, would have been even more depauperate during arid Boutellier times, and by implication even more reduced during the Duvanny Yar. But it is, in fact, excess moisture that today limits large mammal biomass and diversity in the Arctic. Water-logged soils restrict nutrient turnover and limit plant productivity throughout the North. Lack of drainage, in effect, favors conservative, unpalatable plant species that are well defended against herbivory by secondary plant compounds (see Guthrie, 1982, 1984a,b, 1985, 1990, for a review of these implications for the Pleistocene-Holocene transition). The requisites of a productive habitat for large mammals, in the Arctic especially, are not a simple matter of moisture availability.

Another important factor regulating ungulate numbers, alluded to indirectly by Carter *et al.* (1984), is extreme winter aridity, as indicated by sand wedges. Access to winter forage is the main factor limiting ungulate abundance in the far North (Klein, 1970). Both packed snow and deep powder snow limit ungulate access to forage. Winter mortality for grazing ungulates can be reduced by less snow and/or snow removal by wind. While the Titaluk horse hoof supports the conclusion of extreme winter aridity proposed by Carter *et al.* (1984), it also illustrates that megafauna could live on the North Slope during the most arid extreme at the peak of the Duvanny Yar.

Carter *et al.* (1984) referred to Duvanny Yar loess along the Arctic Foothills, but this loess seems not to have been examined in a detailed stratigraphic study. Judging from the exposed sections on the Titaluk, the broad tableland that forms the termination of the foothills overlooking the Arctic Coastal Plain seems to consist mainly of loess. Preservation of the horse fossils with attached mummified tissue in this dry loess may not have been by the same processes that account for large mammal mummy preservation throughout the rest of Beringia (Guthrie, 1990). Most Beringian mummies seem to have been covered by downslope redeposition of water-saturated soil. It is possible that on these flat tablelands dry loess was seasonally reworked into drifts by wind. The cold, dry climate may have slowed decomposition of mammalian remains. Some bones may have been maintained in this state until buried beneath the active thaw zone. The processes that preserved these partial horse mummies remain unclear.

It is tempting to imagine that this loess steppe in the Arctic Foothills was some kind of an ungulate refuge from the arid sand sea on the Arctic Coastal Plain. However, most large sand dune regions of the earth do support a modest diversity and biomass of large mammals. Carter (1981a) mentions finding a bison metapodial in dune sand of the sand sea. It is quite likely that interstices of vegetation within the dunes and along intersecting rivers allowed large mammals to use the entire North Slope, as well as the now submerged continental shelf, during the Duvanny Yar.

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