GEOLOGICAL SURVEY OF CANADA
COMMISSION GEOLOGIQUE DU CANADA

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BERINGIA DURING THE LATE PLEISTOCENE: ARCTIC-STEPPE OR DISCONTINUOUS HERB-TUNDRA? A REVIEW OF THE PALEONTOLOGICAL EVIDENCE

J.V. MATTHEWS, JR.

Geological Survey of Canada (Calgary)
3303 - 33 Street N.W.
Calgary, Alberta T2L 2A7

October 1979

Preprint prepared for discussion at Burg Wartenstein Symposium No. 81:

PALEOECOLOGY OF THE ARCTIC-STEPPE MAMMOTH BIOME

8-17 June 1979

Sponsored by the Wenner-Gren Foundation, New York

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A REVIEW OF THE PALEONTOLOGICAL EVIDENCE*

John V. Matthews, Jr.
Geological Survey of Canada
601 Booth Street
Ottawa, Ont. K1A 0E8

*A revised version of this paper, shortened and taking account of comments offered at the symposium, is being prepared for publication in a forthcoming book. That book will include all of the papers discussed at the symposium plus introductory and synthesis sections by the four editors (D.M. Hopkins, C.E. Schweger, S. Young and J.V. Matthews, Jr.).

INTRODUCTION

When Eric Hultén first used the term "Beringia" in 1937 it was as a designation for the now flooded land bridge which he belived must have existed between Alaska and Siberia in order to explain the distribution of certain groups of plant species (Hultén, 1968). Subsequent authors, e.g. Yurtsev (1976), have tended to view Beringia in a larger context, including as I do when I use the term below, all of the area between the Kolyma River in east Siberia and the Mackenzie River in the Canadian Northwest Territories, plus the intervening continental shelf areas shallower than about 200 m.

In large measure this Wenner-Gren conference is about Beringia, particularly the unique environmental conditions which apparently prevailed there during the late Pleistocene when Paleolithic man was a member of the Beringian fauna.

Beringia and its environmental history have been the subject of several international conferences and subsequent books (Hopkins, 1967; Kontrimavichus, 1976), the most recent of these being the 1976 AMQUA conference on "Hot and Cold Deserts during the last glaciation" in Tempe, Arizonia (American Quaternary Association, 1976). The Tempe meeting was not by any means the most exhaustive treatment of the subject, but it was the conception site for this Wenner-Gren workshop since it was there that it became clear to the organizers (we all took part in the Tempe meeting) that the question of late Pleistocene environments in Alaska, the Yukon and east Siberia actually transcends Beringia. For example, I suggested at Tempe (Matthews, 1976a), following the lead set by Guthrie (1968a) and others, that the late Pleistocene had witnessed the existence of an arctic-steppe biome stretching from Europe and the Ukraine all the way to the Laurentide glacial limit in northwestern North America. Beringia would have constituted only part of this region. Moreover, the questions which arose following the steppe-tundra session at Tempe showed as well that a better knowledge of this biome would best be served by involvement of some specialists whose interests have nothing to do with Beringia or any other aspect of the Quaternary research milieu. Consequently the guest list for this meeting is more catholic than others which have dealt with Beringia. It nevertheless includes an ample number of paleontologists since the data on which the environmental reconstructions are based are ultimately paleontological and geological.

My contribution to the 1976 AMQUA meeting was an extended abstract reviewing the paleontological evidence available at that time. Some of the same facts mentioned in the abstract were presented in more detail, with proper attribution, in a subsequent manuscript (Matthews, In Press), but because it has not yet been published (and is now out of date), and the original abstract is being cited by some authors as a comprehensive review, there still exists a need for a detailed account of the available paleontological evidence. Furthermore it seems appropriate that this be done within the context of the two most disparate interpretations of the character of late Pleistocene tundra in Beringia: (1) that it was a discontinuous tundra similar physiognomically to present polar desert or (2) that it was a type of northern grassland--arctic steppe.[1]

PALYNOLOGY

Paleoecological studies in Alaska and the Yukon Territory (see papers in this series by Schweger, Ager, and Ritchie) provide the data for a general summary of late Pleistocene vegetational change in eastern Beringia. The sequence of events outlined below, derived mainly from palynological efforts, is intended as a framework within which certain aspects of the fossil evidence can be discussed.

SYNOPSIS OF PLEISTOCENE VEGETATION CHANGE

The environment of the last interglacial in east Beringia is portrayed by data from sites in Western Alaska (Colinvaux, 1967; Matthews, 1974a) the Northern Yukon (Lichti-Federovich, 1974; Morlan and Matthews, 1978) and several localities on the Northern Yukon coast (Rampton, In Press). They show that during the Sangamon, just as today, large regions of east Beringia were forested. In both western Alaska and the Northern Yukon spruce treeline appears to have stood well beyond its existing limit (Matthews, 1974a; Rampton, In Press; D.M. Hopkins, Cape Espenberg data - pers. comm., 1975), and pine probably grew near the Old Crow region, also north of its present boundary (Lichti-Federovich, 1974). *Larix* and other plant species not common there today extended their range to the northern part of the Old Crow basin (Matthews, unpublished). All these facts suggest that climate in east Beringia was warmer than at present.

Early and middle Wisconsinan environments are poorly documented at most Alaskan sites, but there is an accumulating body of evidence from the Old Crow region (Northern Yukon) for an early Wisconsinan interstadial during which spruce forests were more closed than they are at present and contained shrub species that do not grow there today. Climate was apparently warm enough to cause degradation of permafrost (note existence of ice wedge pseudomorphs in the Old Crow and Bluefish portions of Fig. 1), and may for a time have been even warmer than at present. The unconformity (or the Eva Formation), separating the Goldstream Formation and Gold Hill Loess at Fairbanks exposures (Fig. 1), may represent the same early Wisconsinan interval instead of the Sangamon interglacial as suggested by Péwé (1975a).[2] If so, the climate of interior Alaska during the early Wisconsinan (upper Gold Hill Fm.) must have been cold enough for formation of permafrost and ice wedges (Péwé, 1975a). This was the case in the Old Crow area where pollen evidence (Lichti-Federovich, 1974), combined with recent stratigraphic observations, implies shrub tundra conditions. Pollen and macrofossils from both areas show that the early Wisconsinan interstadial was followed by a return to cold, tundra conditions, implying a marked reduction of forest cover over all of east Beringia (Lichti-Federovich, 1974; Matthews, 1970, and unpublished information).

According to pollen sequences from the southern Yukon and central Alaska (Rampton, 1971; Matthews, 1974b) spruce forest once again existed in the central part of east Beringia 25-30 thousand years ago, but it was apparently more open than that of the present, and treeline was probably lower compared to its existing elevation. Significantly some of the plant species growing in the Fairbanks area at the time have contemporary northern limits far to the south, but this does not necessarily mean climate then was warmer than today (Matthews, 1974b). Pollen spectra from several western Alaskan sites indicate existence of birch-dominated shrub tundra at around 30000 B.P. (Colinvaux, 1967; Colbaugh, 1970; Hopkins, et al., 1976; Schweger, 1976). To date no record of a correlative climatic event has been recognized in the

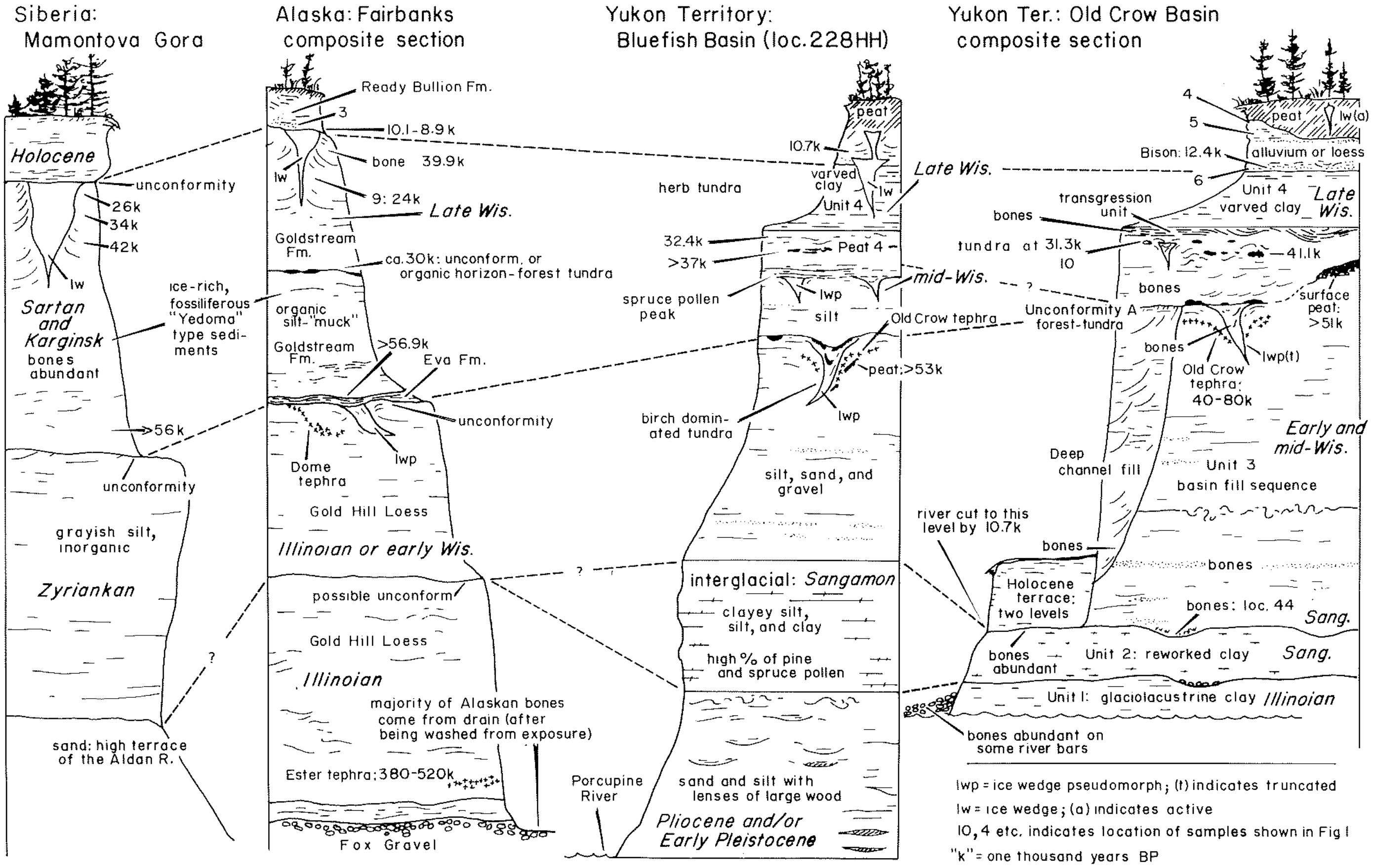

FIGURE 1. Stratigraphy at several different sites in Beringia. Yukon Territory data from studies currently in progress as well as Hughes, 1972 and Morlan and Matthews, 1978; Fairbanks section modified from Péwé, 1975a, 1975b; Mamontova Gora section based in part on Péwé et al., 1977. Note that correlation and suggested age of some units differs from those suggested originally: The Eva Formation and associated unconformity (Goldstream/Gold Hill Loess) are judged to have formed approximately 50-80 thousand years ago during the same climatic oscillation that caused deep thawing, reforestation and erosion (Unconformity A) at Old Crow and Bluefish sections (Dome tephra has yet to be dated and despite its similar position is probably not equivalent to the Old Crow Tephra — J.A. Westgate, pers. comm., 1979). The mid-section unconformity at Mamontova Gora is provisionally assigned to this same interstadial rather than the last interglacial (see Péwé et al., 1977). Suggested interglacial age of lower clayey silt unit at Loc. 228 HH is based on pollen evidence (Lichti-Federovich, 1974) and differs

FIGURE 1 CONT'D

from the glaciolacustrine interpretation given in Hughes, 1972. The suggested Sangamon (Sang.) interglacial age of Unit 2 and lower Unit 3 on the Old Crow composite section is based on occurrence of insect and plant macrofossils indicative of a warmer climate than at present (Morlan and Matthews, 1978 and Matthews, unpublished). Note the various sources of bone at the Fairbanks and Old Crow sections.

Northern Yukon Territory (except possibly for some subtle and still poorly understood features of lacustrine pollen sequences — J.C. Ritchie and L. Cwynar, pers. comm., 1978), but that region is well north of western Alaska, Fairbanks and the southern Yukon sites mentioned above; and consequently, may not have witnessed as drastic a vegetional change.[3]

Except for persistence of small groves of spruce and possibly tree birch (Matthews, unpublished) east Beringia lacked forests between 25000 and about 10000 years ago. During the last few thousand years of this period, before the rise in spruce percentages that marks reforestation of inland areas, tundra at many east Beringian sites was apparently characterized by presence of a significant cover of shrub birch (Ager, 1975; Ritchie, 1977). Prior to that most east Beringian sites, whether lakes from which cores have been raised or alluvial sections, yield pollen spectra largely lacking spruce, birch, and alder and dominated by grass and/or sedge, relatively high percentages of Artemisia as well as Salix, and pollen of a variety of herbs, among them species of Cruciferae, Chenopodiaceae, and Compositae. Fossil spectra with somewhat similar characteristics are found in early Pleistocene sediments at Cape Deceit (Matthews, 1974a) and in sediments of probable Illinoian age at Fairbanks (Matthews, 1970). Such "herb-zone" assemblages are not duplicated by the pollen rain of contemporary tundra regions (Ritchie, 1977; Birks, 1977), and most workers concede that they represent a tundra environment qualitatively different from that of any present tundra region. But beyond this general conclusion there exist important differences of opinion.

HERB-ZONE OPTIONS

It has been suggested that the high percentages of *Artemisia* and grass pollen in herb-zone type spectra indicate steppe-tundra (Colinvaux, 1967; Colbaugh, 1968; Matthews, 1970, 1974a, 1974b; Ager, 1975; Schweger, 1976) in which soils were warm, dry and less acidic than on present tundra and seasonal thawing deeper (Matthews, 1976a; Yurtsev, 1976). Ritchie (1976, 1977) argues instead that the relative abundance of grass and *Artemisia* pollen in herb-zone spectra, even the fact that their influx values at some sites are higher in the herb-zone than in others (Ritchie, 1977; Ager, 1975), does not necessarily imply a particular type of vegetation since both taxa contain species that grow in a variety of habitats, and to date it has not been possible to distinguish grass or *Artemisia* species on the basis of their pollen. His point is well taken. Some pollen spectra of the herb-zone type probably do not even represent tundra (Maher, 1972), and grasses do grow in a variety of tundra biotopes. But most species of *Artemisia* in the north occur at dry, well drained localities where the active layer is thick, or permafrost absent, and mosses and acidophilous plants such as heaths are rare (Hanson, 1951; Corns, 1974). Thus while high percentages of grass pollen could represent poorly drained tundra dominated by *Dupontia*, *Arctophila*, and other semi-aquatic grasses (*see* Colinvaux, 1967, p. 214 *for an example*), when *Artemisia* percentages are also high we may assume better drainage than is typical of most existing tundra sites. This conclusion is supported by the low bryophyte percentages in most herb-zone spectra.

The pollen rain at a site (influx of pollen grains/cm^2/yr.) often reflects existing vegetation better than does the relative abundance of the various pollen types, and consequently is a valuable parameter in interpreting vegetational significance of fossil pollen sequences (Davis *et al.*, 1972). Fossil influx values have been computed at two Beringian sites (Ager, 1975; Ritchie, 1977) and additional data of that type will soon be available from other parts of east Beringia (Cwynar, 1978; Ritchie, pers. comm.). Ritchie states (1977) that because herb-zone spectra are associated with low influx values, similar to the 150-800 gr/cm^2/yr range of modern tundra sites, the environment represented can hardly have been a grassland or steppe. Instead he suspects the tundra which existed during the height of the late Wisconsinan was more similar physiognomically to polar desert than to either grassland or typical low arctic tundra (Ritchie, 1977; In Press). Polar desert is not the climatic analogue of herb-zone tundra since Artemisia is not a high arctic species (Porsild, 1973) and neither are many of the plants whose macrofossils are associated with herb-zone spectra (see below; Matthews, 1974a, 1974b). Nevertheless, the physiognomic comparison may be valid, at least for some areas, and merits close examination.

Non-palynological evidence (Foscolos, et al., 1977) indicates that the Yukon Territory, where some herb-zone influx values are as low as 50 gr/cm^2/yr. (Cwynar, 1978), did have a very arid, cold climate during the height of the late Wisconsinan, but I doubt that all sites from that region will yield influx values as low.[4] Furthermore, there is reason to be cautious in assuming that low influx of pollen means low plant cover. The diagram relating influx to tundra type in Birks (1973) is persuasive, but as Ritchie states (1977) it is based on only short-term observations (Ritchie and Lichti-Federovich, 1967). The pollen rain at a site may vary greatly from year to year (Ritchie, 1977), and hence several years of data are required for a reliable estimate of influx. Moreover there have been few attempts to relate pollen influx at a site to local vegetation (see Ritchie, 1977), but where this has been done it is obvious that site related factors (other than short term climatic anomalies) may also greatly influence pollen influx values (e.g., Maher, 1972; Hyvärinen, 1977).[4] As well, some fossil studies (Heusser, 1973; Andrews et al., 1979) show spectacular down-core changes of influx values that are unlikely to be correlated with similar magnitude changes of former plant cover. At polar desert sites low plant cover is obviously one important cause of low influx values (Ritchie and Lichti-Federovich, 1967), but the tendency for all tundra areas to exhibit low pollen production (150-800 gr/cm^2/yr) may be due in part to the well known propensity for asexual or intermittent reproduction among high latitude plants (Mosquin, 1966; Billings, 1974).

Thus, I do not believe that the low influx values in the herb-zones at M Lake (Ritchie, 1977) and Birch Lake (Ager, 1975) preclude the existence of steppe-like conditions. There is very little available information on absolute pollen rain of present grassland areas, especially perenially frozen steppelands, but judging from fossil evidence outside Beringia the pollen rain of some former grassland sites approached that of tundra (Ritchie, 1969). Conceivably a change of climate could cause pollen production in a grassland to fall to tundra levels with very little change in cover values or flora.[5]

What I am suggesting is that herb-zone spectra may represent steppe-tundra in which the pollen influx was low becuase of intermittent flowering of anemophilous (wind pollinated) plants such as grasses. A slightly different explanation for low herb-zone influx values (Ritchie, 1977) is that they mark environments dominated by "palynologically silent" plants such as lichens, many mosses and entomophilous spermatophytes. That this option also applies is confirmed in many samples by the low percentage of bryophytes (macro-remains as well as spores) and abundance of seeds and fruits of *Potentilla* and various species of Cruciferae and Caryophyllaceae.

Such macrofossils provide valuable alternative evidence of past vegetation. In one case (Matthews, 1974a) abundant caryopses of *Poa* suggest that the high percentage of grass pollen in a late Pleistocene sample reflect mesic to xeric substrates rather than typical wet tundra grassland. Macrofossil evidence also shows that *Scutellaria galericulata*, a plant of damp areas of the present boreal and grassland zones and not found beyond treeline,was nevertheless growing in the herb-rich tundra of late Wisconsinan interior Alaska (Matthews, 1974b). Other plants not typical of existing tundra, e.g. *Ranunculus cymbalaria*, *Glyceria grandis*, *Corispermum hyssopifolium* are also represented in a 16000 year old assemblage from the northern Yukon (Matthews, unpublished). And finally, many macrofossil assemblages associated with herb-zone pollen spectra contain remains of *Androsace*, *Stellaria*, *Papaver* and other plants typical of upland, herb rich fell-field sites; yet, in most cases the sediments in which such fossils occur accumulated in lowland areas which at present support an entirely different suite of plants.

MACROFOSSILS

It should be obvious from what has been stated above that plant macrofossils such as seeds and fruits provide important evidence for interpreting palynological data. In recent years fossils, chiefly those of beetles, have also begun to serve as paleoenvironmental indicies (Coope, 1970, *for a review*).

A large body of macrofossil evidence is now available for Beringia. Both plant and insect fossils have been studied at a number of sites in east Beringia (Matthews, 1968, 1974a, 1974b, 1975), and a multitude of unpublished data exists for the Northern Yukon. However few macrofossil assemblages have been treated quantitatively partly because of difficulties inherent in different methods of sample preparation or the lack of adequate numbers of fossils in many samples. Nevertheless there are a few samples which are suitable for quantitative comparison. Figure 2 is an attempt to compare them. To facilitate this I have grouped the fossils into complexes. Mostly these represent clearly defined aspects of the former environment and could be appropriately designated (e.g., aquatic complex, riparian complex, etc.), but I have purposely refrained from doing this because the paleoecological significance of some complexes is not clear. Instead, they are named according to their taxonomic content.

Before the results presented in Figure 2 can be discussed, some of the characteristics of the macrofossil complexes need explanation.

PLANT MACROFOSSIL COMPLEXES

Potentilla - Cruciferae Complex

This assemblage type has already been mentioned in conjunction with the discussion of the herb-zone pollen spectra. As Figure 2 shows it characterizes many of the assemblages associated with pollen spectra dominated by grass, sedge or *Artemisia*. Some of the highest percentages of *Potentilla* achenes occur in early Pleistocene samples that contain significant amounts of birch pollen. The species of *Potentilla* comprising the P-C complex is unknown, but it is probably not *P. fruticosa*, which is relatively common today in some upland, mesic, or edaphic forest-tundra sites (Ritchie, 1977; Douglas, 1974). In addition, all species with sculptured achenes, as well as *P. palustris* and *P. anserina* are ruled out.

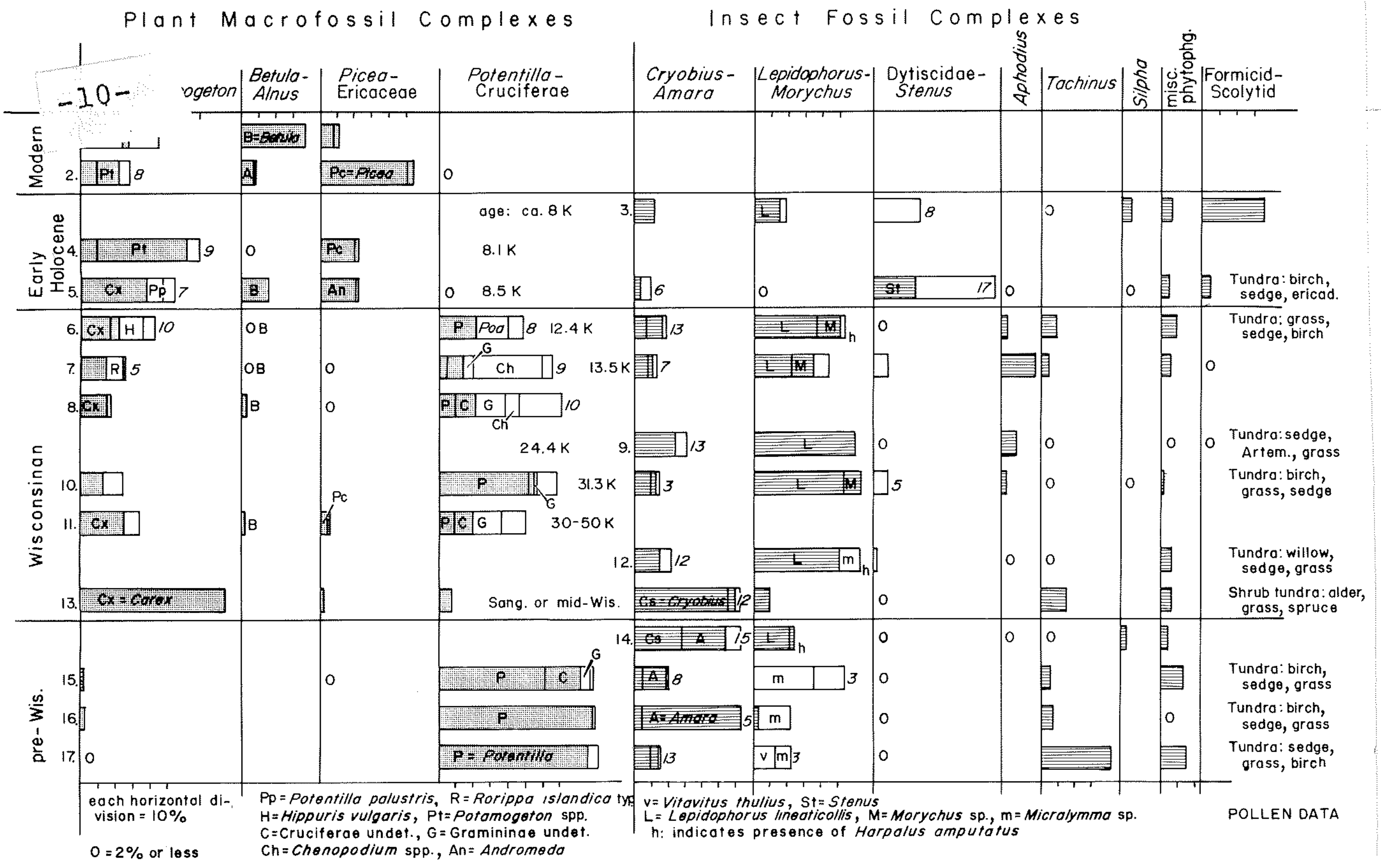

FIGURE 2. Relative abundance of plant and insect macrofossils from east Beringian sites. See text for definition of complexes. Italicized number following some bars indicates the taxonomic diversity of the complex. Pollen data from Matthews (1970, 1974a) and unpublished reports by C.E. Schweger (three most common pollen types are listed).

SITES: (1) Loc.11, Old Crow Flats, Y.T (GSC-2389: 170±50); (2) Loc.11, Old Crow Flats, MRA 7-23-78-8: modern river alluvium; (3) Ready Bullion Fm., Fairbanks, Alaska; (4) Loc.32, Old Crow Flats (GSC-1243: 8100±160); (5) Loc.44, Old Crow Flats (GSC-2605: 8460±120; (6) Deering Fm., Cape Deceit, Alaska, S-6 (I-4781: 1240±180) (Matthews, 1974a); (7) HH 75-9, Bell Basin, Y.T. (GSC-2553: 13500±310); (8) Loc.11, Old Crow Flats, MRA 7-23-78-17 (12-13 thousand years, immediately above Unit 4, Fig. 1); (9) Eva Creek, Goldstream Fm., Fairbanks District, 3-3C, (I-2116: 24400±650) (Matthews, 1968, 1970); (10) Loc.32, Old Crow Flats (GSC-1191: 31300±640); (11) Loc.11, Old Crow Flats, MRA 7-23-77-1 (immediately below Unit 4, Fig. 1); (12) Eva Creek, Goldstream Fm., Fairbanks District, 3-3B, (Matthews, 1968, 1970); (13) Deering Fm., Cape Deceit, Alas., S-5 (early Wisconsinan or Sangamon) (Matthews, 1974a); (14) "Dawson Cut mammoth", Goldstream Fm., Fairbanks District (Matthews and Guthrie,

FIGURE 2 CONT'D.

in prep.); (15) Deering Fm., Cape Deceit, Alas., S-1 (Matthews, 1974a); (16) Inmachuk Fm., Cape Deceit, Alas., S-12 (Matthews, 1974a); (17) Cape Deceit Fm., Cape Deceit, Alas., S 13-67 (plant macrofossils), S 10-67 (insect fossils) (early Pleistocene — Matthews, 1974a).

Note that Chenopodium and Gramineae account for a large percentage of the fossils in some examples of the P-C complex.

Carex - Potamageton Complex

This complex includes macrofossils of many plants that grow in or around the margins of small ponds and lakes. Sometimes the complex is relatively well represented in alluvial sediments, but this probably results from flushing of flood plain ponds during periods of high water.

INSECT COMPLEXES

Unlike plant macrofossil assemblages, which are made up of reproductive disseminules and are thus likely to be biased by differential production of fruits and seeds, the insect percentages in Figure 2 represent the actual relative abundance of individual beetles, based on the minimum number represented by identified fragments.

Cryobius - Amara Complex

Many of the closely related and morphologically similar species of the subgenus Cryobius (Pterostichus: Carabidae) are obligate or facultative tundra inhabitants. They are often the most abundant groundbeetles at mesic tundra sites and their fossils dominate Beringian assemblages (Matthews, 1974a; Sher et al., 1977; S. Kieslyov, pers. comm., 1979). Amara alpina, a common tundra beetle, and the ground beetle occuring furthest north (Blake and Matthews, 1979), is also well represented in some samples and when its fossils are numerous (sample 16, Figure 2) implies more xeric tundra than those assemblages in which Cryobius is abundant. High percentages of A. alpina also suggest scant vegetation cover. Thus the Cryobius complex represents tundra conditions. The species in it occur mostly in present tundra areas, but some wet tundra sites yield assemblages that have only a meagre representation of Cryobius (5 in Fig. 2). Sediments with significant quantities of wood and other fossils indicative of woodland environments (Formicid - Scolytid complex) seldom contain many fossils of the Cryobius complex.

Lepidophorus - Morychus Complex

This group represents very dry substrates and/or scattered vegetation. It lacks analogues in present day Beringia partly because the pill beetle Morychus is so rare (or rarely collected) there. In contrast to Morychus the weevil Lepidophorus lineaticollis is one of the most common species of terricolous beetles in east Beringia. It lives at dry, sandy sites along river floodplains, fell-field sites, grassy meadows, as well as beneath leaf litter in Populus tremuloides and P. balsamifera stands.

The Morychus - Lepidophorus complex dominates a late Wisconsinan assemblage from Cape Deceit Alaska (Fig. 2) and numerous other Wisconsinan age assemblages from the Old Crow region (Matthews, 1974a and unpublished).

Morychus fossils are also numerous in some east Siberian assemblages (S. Kieslyov, pers. comm., 1979; Sher et al., 1977), but not Lepidophorus which apparently doesn't live there today. The small weevil Vitavitus thulius does occur in Siberian fossil assemblages and in some cases replaces Lepidophorus in east Beringian samples. Like Morychus it also is a rare or rarely collected beetle, but it probably lives in sandy floodplain areas because its fossils are most abundant in Holocene and Pleistocene alluvium.

Another common member of the L-M complex that does not occur in Siberian samples is "Micralymma". Much has been made of the occurrence of fossils of this tiny beetle at inland sites of Alaska (Matthews, 1974a), but these arguments are now compromised because an undescribed species very similar to Micralymma -- so much so that its fossils could be mistaken for it -- has recently been collected at very dry sites beneath Alnus bushes along the Old Crow and Porcupine rivers. The fossils occur in many of the samples from that same area, including modern river detritus. Though my original interpretation of the paleoenvironmental significance of Micralymma is probably wrong, its fossils or those of the similar new species do signify xeric local conditions.

Tachinus, Aphodius, and Silpha Complexes

The paleoenvironmental meaning of dominance of any of these complexes is not clear. Most fossils in the Tachinus complex are from either T. apterus or T. brevipennis (see comments concerning the identity of these two species in Matthews, 1974a and Hopkins et al., 1976). Both seemingly occur in areas of rich tundra vegetation, most often near marine coastlines.

Many species of Aphodius are dung feeders, and Coope (1970) has interpreted abundance of Aphodius fossils at a site in England as indicating the presence of large mammals. The case is not so clear in Alaska because most of the Aphodius fossils cannot be identified to species and some of the Alaskan Aphodius currently live in ground-squirrel nests. What is clear is that in general specimens of Aphodius are very rare in contemporary tundra biotopes. Apparently this was not the case in the past.

Sample 14 in Figure 2 is an assemblage of insect fossils found in association with the bones of a single old mammoth at Fairbanks Alaska (Matthews and Guthrie in prep.). Carcass fly puparia were common. Fossils of the carrion beetle, Silpha coloradensis, were much rarer but still more abundant than in many other assemblage. Together the fossils of these two types of insects show that the bones represent a death assemblage. S. coloradensis is presently a very rare, alpine beetle leaving another species, S. lapponica, to fill the carrion niche on contemporary lowland and alpine tundra. Silpha lapponica, on the other hand, was apparently rare in late Pleistocene tundra (Matthews, 1975). Carrion assemblages similar to sample 14 have been found in association with mammoth bones at several sites in east Siberia (Medvedev and Voronova, 1977). Like sample 14, the Siberian fossils show that the woolly mammoth was capable of surviving in a tundra environment.

Misc. Phytophagous Complex

Included here are several species of weevils and leaf beetles. In Siberia middle Pleistocene equivalents of the phytophagous complex contain fossils of a weevil (Stephanocleonus cf. eruditis) which presently lives in steppe and mountain-steppe areas of Asia (Sher et al., 1977). Except for rare fragments of the ground bettle, Harpalus amputatus, now found at some open grassy sites in interior Alaska and the southern Yukon and a common member of the North American grassland fauna, obligate steppe species do not occur in any of east Beringian insect complexes. H. amputatus has never been collected at tundra sites, yet as Fig. 2 shows, its fossils are associated with "tundra" assemblages.

PALEOENVIRONMENTAL IMPLICATIONS

A common theme of many of the tundra samples shown in Figure 2 is shared dominance by the Cryobius and Lepidophorus - Morychus complexes. Some of these also contain significant percentages of Aphodius and/or Tachinus, and by this combination of characteristics they differ from assemblages representing existing tundra conditions. Sample 5 is analogous to a modern tundra site; its poorly drained character is well illustrated by dominance of the Dytiscidae - Stenus and Carex - Potamogeton complexes.

As indicated above some features of the Lepidophorus - Morychus complex can be duplicated at existing riparian sites in Alaska and the Yukon. The few living specimens of Morychus that have been collected in the north come from such areas and Lepidophorus is a common floodplain beetle. Nevertheless, it is unlikely that the L-M complex implies river side habitat since many of the other beetles which typically occur there, in both tundra and taiga areas, are missing as fossils. Furthermore the L-M complex also occurs in upland samples such as those from Fairbanks exposures (assemblages 9 and 12 in Fig. 2) and even in the basal sediments at Bluefish Cave near Old Crow (Cinq-Mars, 1978, 1979 ms.). The L-M complex probably signifies arid substrates. Many of the plants of the Potentilla - Cruciferae complex, which appears to fluctuate in phase with the L-M and Cryobius - Amara complexes, are also typical of xeric sites.

These several lines of macrofossil evidence support the conclusion drawn on the basis of the herb-zone pollen spectra, that the late Pleistocene environment of Beringia, though treeless and cold, was actually quite unlike present tundra. The macrofossils also suggest that plant cover may not have been as high as it presently is in most zone 4 tundra regions, but neither was it as discontinuous in the lowlands as that of present polar desert and polar semi-desert. Furthermore the abundance of beetle fossils, especially the diversity of ground-beetles, shows that regional climate was not much colder than it is today in the southern part of tundra zone 3 (Young, 1971). Macrofossil evidence also indicates that despite low percentages of Picea pollen, some small grooves of spruce may have persisted in east Beringia during the late Wisconsinan phase of maximum climatic severity. On the other hand, existence of larger tracts of riparian forest - the presumed refugia of subarctic plants (Hultén, 1963) - seems to be ruled out.

VERTEBRATE FOSSILS

Most evidence discussed above comes from localities in east Beringia and the conclusions drawn relate primarily to that region. Nevertheless, similar pollen and macrofossil data from sites in Asia and eastern Europe show that those areas were also characterized by treeless, periglacial environments during portions of the Pleistocene. The Bering Land bridge was in existence for part of that time, and during the coldest periods, the forest corridor that presently separates tundra and steppe in Asia, disappeared. Consequently, cold treeless (tundra?) conditions prevailed across all of Beringia and the unglaciated areas of western Siberia east to the Ukraine (Frenzel, 1968; Grichuk, 1971; Veličko, 1975, Alekseev et al., 1973, Klein, 1973; Kraev, 1975; Tomirdiaro, 1975, 1977; Giterman 1976 and In Press). Indeed a treeless environment, though possibly not a periglacial climate, existed well west of the Ukraine though the Mediterranean to southwestern Europe (van der Hammen, et al., 1971), while unglaciated areas of Europe north of the Alps were polar desert (van der Hammen et al., 1971).

The mammalian fauna of this Pleistocene biome displays a high degree of uniformity. Local faunas from Europe, the Ukraine, Siberia, Beringia and even south central Asia consistently contain fossils of woolly mammoth, horse, large horned bison, and caribou — the so-called mammoth complex (Pidoplichko, 1956; Kurtén, 1968; Guthrie, 1968a; Kalke, 1976; Sher, 1974; Harington, 1977, 1978). Regional distinctions existed (e.g., woolly rhinoceros restricted to Asia; *Camelops* to Alaska; and typical steppe mammals in faunas of southern Siberia-Vangengejm, 1975, Kvasov, 1977). But some steppe forms, such as *Lagurus* and *Saiga*, extended their ranges tremendously during the coldest phases of the Pleistocene (Vangengejm, 1975; Sher, 1968; Sutcliffe and Kowalski, 1976; Kurten, 1968; Anderson, 1977). *Saiga tatarica* fossils of which are considered to be evidence that late Pleistocene tundra was fundamentally different from that of today (Sher, 1968; Matthews, 1976a) even entered Alaska and Canada during the late Pleistocene.

The ungulate fauna of Beringia was taxonomically more diverse during the Pleistocene than at present, and this plus the fact that most of the large ungulates of the mammoth complex were grazers rather than browsers is considered *prima facie* evidence that late Pleistocene tundra was similar to cold grassland (Guthrie, 1968a). In other words it has been concluded, on the strength of mammalian fossil evidence that the decline of forest communities in east Beringia during the height of the Wisconsinan involved more of a change than simple expansion and intermingling of alpine and lowland tundra. What is presumed to have formed instead was an entirely different type of treeless environment, one capable of supporting a complex ungulate fauna (Matthews, 1976a). Note, however, that such conclusions are based on the assumption that assemblages of large mammal bones from individual sites (local faunas) actually represent living ungulate communities or biocoenoses. Some workers doubt that this is the case (Schweger and Habgood, 1976); consequently an examination of the validity of the assumption is an essential first step in the interpretation of the vertebrate evidence.

BIOCOENOSES OR MIXED ASSEMBLAGES

Local Faunas

Table 1 is a first attempt to compile a complete list of mammals found at late Pleistocene sites in Beringia, Siberia and the Ukraine. No one would suggest that the entire list represents a single biocoenosis. Even the mammalian assemblage from well delimited regions such as the Old Crow basin in the Yukon contains taxa which are obviously of different age or represent different environments. Even considering such blatant discrepancies, the list in Table 1 does little to reveal which mammals were members of living communities. In fact it could be argued that there is no basis for assuming that the four typical members of the mammoth complex were living associates in any one area.

One way to define the taxonomic composition of the Pleistocene large mammal community of a region is to determine the frequency of association of the various taxa occurring as fossils. This is only feasible where a number of local faunas have been studied. The Ukraine is such a region and Figure 3 summarizes the degree of association of taxa in 139 Ukrainian local faunas (Pidoplichko, 1956). It shows that there is a strong association between mammoth, horse, bison and caribou - the four members of the mammoth complex and the same four that dominate several fossil assemblages from Alaskan localities (Guthrie, 1968a). In the Ukraine the woolly rhinoceros, *Coelodonta*, was a fifth member of the group, but even though it did occur in far eastern Siberia during the late Pleistocene, it apparently never entered east Beringia. Figure 3B suggests that the relative abundance of the various members common to the mammoth complex in Alaska and the Ukraine varied, but this could be due to the very small size of the Alaskan samples or to the fact that some of the Ukrainian local faunas are probably archaeological and thus biased for certain mammals, e.g. mammoth.

Interregional distinctions of the type implied by Fig. 3b are to be expected since variation in terrain and range conditions is bound to favour different members of the mammoth complex in different areas. There is some indication that the relative abundance of bison and horse was not the same in interior Alaska as in the Yukon Territory, but again the best evidence of such regional faunal distinctions comes from the Ukraine and Siberia (Klein, 1973; Kvasov, 1977).

While Figure 3 shows that the members of the mammoth complex were living associates over an entire region, it is desirable to know whether this was also the case at particular sites. The content of mammalian local faunas is often cited as verification of this fact (eg. Guthrie, 1968a, Vereshchagin, 1974). In reality because of the way most fossils have been collected and the type of sediments in which they occur, the majority of such assemblages constitute very poor

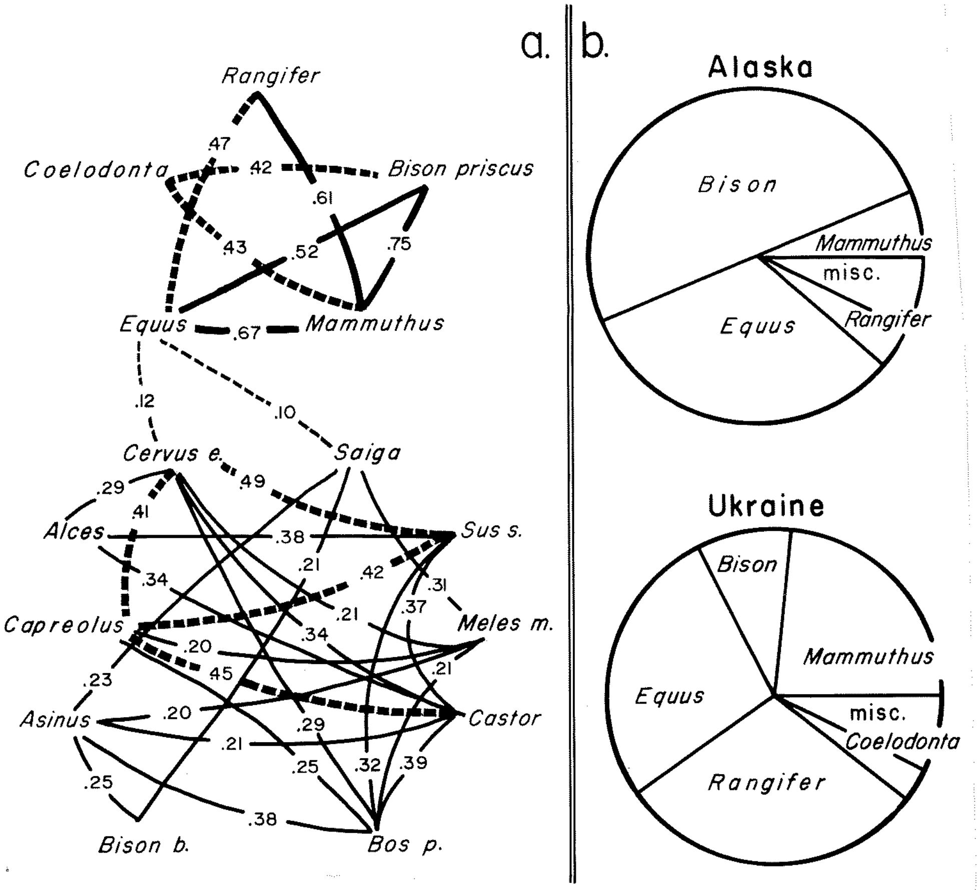

FIGURE 3. (a) Degree of association (Jaccard's coefficient) of some mammalian taxa in Ukrainian fossil assemblages. Heavy line: 0.6-1.0; heavy dashed line: 0.4-0.6; light solid line: 0.2-0.4; and light dashed line (shown only for Equus, Cervus, and Saiga): less than 0.2. Note that the taxa fall into two clusters which are only weakly associated. Fossils of domestic mammals are often associated with taxa in the lower cluster. The diagram is based on a matrix constructed using data from 139 Ukrainian local faunas listed in Pidoplichko, 1956.

(b) Comparison of relative individual abundance of large mammals from late Pleistocene sites in interior Alaska and various sites in the Ukraine. Alaskan diagram portrays pooled percentages of faunal elements from the four local faunas listed in Guthrie 1968a. The Ukrainian diagram portrays relative abundance of total ungulate individuals in 23 local faunas containing Mammuthus, Bison, and Equus (from Pidoplichko, 1956).

evidence for such a conclusion (Schweger and Habgood, 1976). Local faunas from east Beringia illustrate the problem.

Three areas of east Beringia are famous as sources of Pleistocene mammal fossils. Two of them — Dawson placer mining district and the Old Crow Basin — are in the Yukon Territory; the other is the Fairbanks mining district and the source of the data analyzed by Guthrie (1968a). He dealt with assemblages from four different placer mines near Fairbanks. The original collections were made in the 1930's when mining activity was at a peak,and most of the fossils were collected at the base of the exposure, in the "drains", where they accumulated during hydraulic removal of the frozen, organic silts that overlie gold-bearing gravels (Fig. 1). The frenzy of mining activity in the 1930's made "bone collecting" a full-time activity. Little attention was paid to in situ occurrences or stratigraphy, and it is unlikely that such observations would have been of much value since the exposures were changing daily and the climatic implications of subtle differences in silt stratigraphy were not recognized until many years later (Péwé, 1975a). The silts yielding most of the bones are highly organic, fetid, and usually ice-rich, much like the ice-rich and highly fossiliferous "yedoma" sediments which blanket much of the interfluvial areas of Siberia (Péwé, 1975a; Tomirdiaro, 1975, 1977; Péwé, et al., 1977). In central Alaska and the Dawson district of the Yukon Territory as in Siberia the ultimate origin of the silts is as loess derived from exposed portions of the continental shelf or large outwash streams, but the fossiliferous sediments are a colluvial facies and consequently stratigraphic inversions are common and difficult to recognize (Repenning et al., 1964; Péwé et al., 1977). Fossil bone is especially likely to be rebedded with younger sediments (Hopkins, 1974), and since many of the Fairbanks and Dawson fossils have undergone at least two cycles of redeposition, the assemblages can hardly be called biocoenoses. For example, according to Figure 1 fossils collected in the drains at Fairbanks exposures may range in age from pre-Illinoian to Holocene, and represent both forested and tundra environments. Bones collected exclusively from the Gold Stream Fm. do not offer more evidence of contemporaneity because they could potentially represent nearly all of Wisconsinan time. Similar problems attend the interpretation of local faunas from the Dawson district. In the absence of supporting evidence, such as ^{14}C dates, these assemblages must be considered as very poor indicies of contemporaneous life associations. The same dismal prognosis appears to apply to most local faunas from the yedoma type sediments in Siberia (Vereshchagin, 1974, 1977).

Bones from the Old Crow Basin occur in an alluvial context (Harington, 1977, 1978; Morlan and Matthews, 1978; Morlan, 1978a). Those discovered on the river bars in the Old Crow Basin potentially span the entirety of Wisconsinan and Sangamon time (i.e., more than 120 000 years), but in reality the time interval is probably even longer since the identity and stage of evolution of some of the fossils indicates they are derived from older units than those presently exposed in the basin (Harington, 1977). Many of the bones from the Old Crow region occur "in situ" at an unconformity between Holocene sediments and the clays of Unit 2 (Fig. 1), but these too may represent all of Wisconsinan time and several different types of environments, ranging from forest to forest-tundra and tundra. Local faunas from two Old Crow sites (locality 44 and locality 15 - see Table 1) have more restricted temporal ranges, but not enough so to rule out the possibility that they as well are mixtures of two different mammalian communities.[6] Thus the mammalian assemblages from the Old Crow region like those from Fairbanks and Dawson, provide no unequivocal evidence for existence of particular ungulate biocoenoses (Schweger and Habgood, 1976). The most that can be assumed is that the four members of the mammoth complex were probably associates in east Beringia during the late Pleistocene. Other lines of evidence are needed in order to further delimit the composition of Pleistocene ungulate communities.

Archaeological Information

All of the local faunas from the Old Crow Basin are found on unconformities. An archaeological site is an unconformity, but its temporal hiatus is negligible compared to that represented by most mammalian local faunas; consequently, mammalian faunas from archaeological sites are valid approximations of biocoenoses.

Unfortunately adequately dated late Pleistocene archaeological sites containing identified faunal material are rare in east Beringia. Only three have a bearing on the composition of former ungulate communities. Bison (and perhaps mammoth) were living near the Dry Creek site in central Alaska about 11000 years ago (Thorson and Hamilton, 1977). Bison and horse bones have also been found at the Trail Creek sites in western Alaska (Larsen, 1968) although there the actual bones are dated (see Fig. 4) and there is no assurance that both taxa were residents of the area when the cave was occupied by man. Another important cave site — Bluefish Cave in the Yukon Territory — is now under study and significantly its lowest level, dated on the basis of preliminary pollen evidence as late Pleistocene, contains a diverse mammal fauna including several ungulate species (horse, elk, caribou) (Cinq-Mars, 1978; 1979 ms.). The best archaeological evidence of a mammoth complex biocoenosis comes from sites in eastern Siberia (Klein, 1971; Mochanov, 1978a, 1978b) which show that the common associates of the mammoth complex (Rangifer, Bison, Mammoth and Equus) lived at the same time and in the same regions during the late Wisconsinan-Sartan (30000-10000 years BP). A careful review of the primary Siberian archaeological literature and ^{14}C dates is required, but for the time being it is significant that archaeological sites in that region show positively what is only suggested by undated Ukrainian, Siberian and Alaska-Yukon local faunas, i.e., that the members of the mammoth complex were associates within a living ungulate community.[7]

Radiocarbon Dated Bones

Radiocarbon dates on identified bone provide another means of assessing the diversity of the Pleistocene ungulate community. Figure 4 contains published and unpublished dates on fossils collected in the Yukon and Alaska, some ^{14}C dates on Siberian carcasses, and a few archaeological dates. According to the figure, Bison, Mammoth, Equus, Rangifer and Alces were co-inhabitants of east Beringia between 30 and 34 thousand years ago. Dates for Bison, Mammoth and Equus also overlap at around 15000 years BP. Between 23 and 27 thousand years ago at least seven species of large ungulates apparently lived in east Beringia, considerably more than occur on present tundra, but less than has been assumed on the basis of composition of local faunas (Guthrie, 1968a; Péwé, 1975a; Harington, 1977, 1978). Five of the dated taxa occurring during this time interval come from Fairbanks sites, this being the best evidence from any Beringian locality for existence of a diverse local ungulate biocoenosis. The environment of Fairbanks 23-27 thousand years ago was tundra (Matthews, 1974b), but climate was probably not as severe as during the peak of the late Wisconsinan at 18-20 thousand years BP. Only Bison and Symbos occur in that interval; however, since so few dates are available such negative evidence has little significance. Certainly there is no cause to assume from Fig. 4 that the absence of ^{14}C dates on mammoth in the 22-16 thousand range indicates they migrated south to warmer areas at that time (Heintz and Garutt, 1965). On the other hand the absence of dates younger than ten thousand years for most taxa is significant since it marks an event — the last appearance of many lineages — which is well illustrated by other evidence. As yet there are too few dates to indicate whether all species disappeared in one short time period, but some archaeological data (Mochanor 1978b) suggest there may have been marked regional differences in time of extinction of mammoth.

INDICATOR SPECIES

A few of the mammals recorded as fossils in east Beringia have been accorded special paleoenvironmental significance: specifically that they indicate the presence of cold steppe conditions with well drained substrates and deep seasonal thawing (Matthews, 1976a). In most cases it is also assumed that they were members of the mammoth complex. The validity of these assumptions requires scrutiny.

Saiga tatarica

This diminutive antelope is poorly adapted for life in terrain like that of modern tundra, yet its fossils have been found in northeastern Siberia, Alaska, and the Northwest Territories of Canada (Sher, 1968; Harington, 1978). Presumably they occupied this region during the

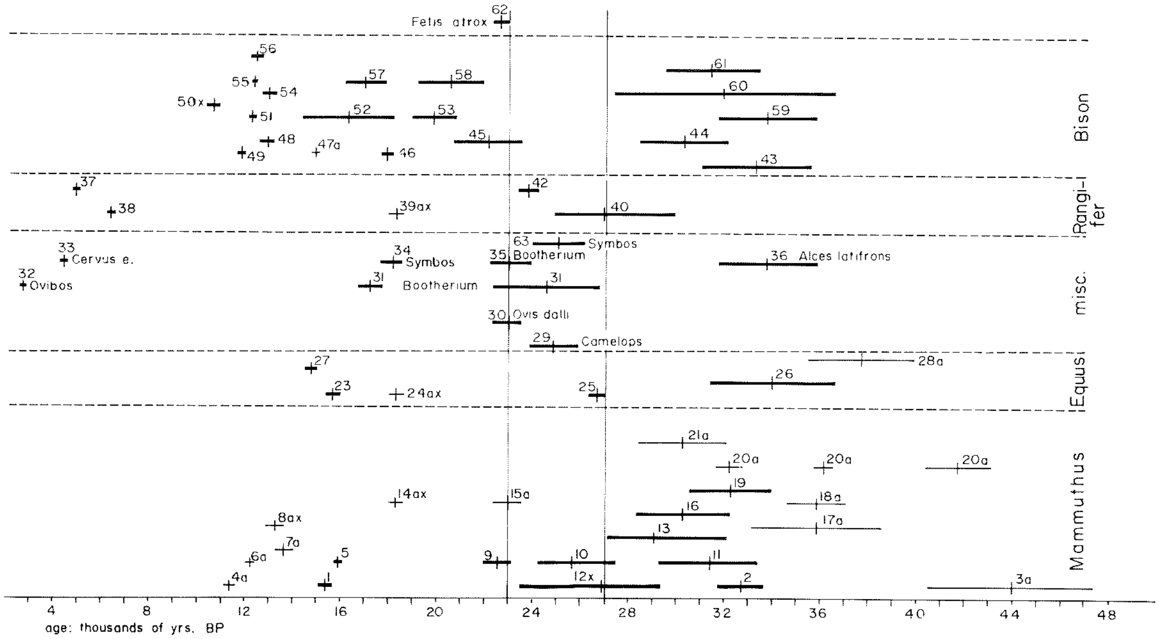

FIGURE 4. Finite Radiocarbon dates for Beringian and Asian large mammals. "x" after number indicates indirect date (most archaeological dates). Heavy bars — east Beringia; light bars and "a" after number — Siberia and Ukraine.
<u>ALASKA</u>: (unless noted see Péwé, 1975a): (1) SI-453; (2) ST-1632; (11) ST-1721; (12x) AU-90 (Hopkins <u>et al</u>., 1976);
(23) Trail Creek Cave, K-1210 (Larsen, 1968); (25) SI-355; (31) SI-454 and SI-455 on same specimen (identified as <u>Ovibos</u> in Péwé, 1975a; <u>Bootherium</u> in Harington, 1977); (34) SI-851; (35) SI-292; (43) SI-842; (46) SI-841; (48) SI-290; (50x) Dry Creek Site (Thorson and Hamilton, 1977); (52) M-38; (53) SI-837; (54) Trail Creek Cave, K-1327 (Larsen, 1968); (55) SI-1633; (57) SI-838; (58) SI-839; (60) SI-843; (61) SI-1721; (62) SI-456; (63) SI-850.
<u>YUKON TERRITORY</u> (unless noted see Harington, 1977): (5) GSC-1893; (9) I-3573; (10) GX-1568 (bone apatite); (13) GX-1567 (bone apatite); (16) I-3576; (19) I-4226; (26) I-4222; (27) I-3569; (29) I-2117; (30) I-4225; (32) I-3568; (33) I-4255; (36) I-4229; (37) I-8642; (38) I-4221; (40) GX-1640 (bone apatite); (42) I-8580; (44) I-3571; (45) I-3570; (49) I-7765; (51) I-7764; (56) I-3574; (59) I-4224.
<u>SIBERIA AND UKRAINE</u>: (3a) T-299, "Berezovka mammoth", oldest of two determinations (other: 31750±2500) Heintz and Garutt, 1965); (4a) T-297, "Taimyr mammoth" (Heintz and Garrut, 1965); (6a) Berelekh (Harington, 1978);

FIGURE 4 CONT'D.

(7a) Berelekh (Lozhkin, 1977); (8ax) Ukraine, Molodova V, horizon 3 (Klein, 1973); (14ax) Pechora R., Byzovaja Site (Klein, 1971); (15a) "Dima mammoth" (H.E. Gove, pers. comm., 1979); (17a) T-169, should be considered as minimum date (Heintz and Garutt, 1965); (18a) T-171, Delta of Lena R., should be considered as minimum date (Heintz and Garutt, 1965); (20a) "Shadrin mammoth", three dates on some carcass (Solonevich _et al_., 1977); (21a) T-298, Gyda R., two other dates on same tissue: 33500±1000 (Heintz and Garutt, 1965); (24ax) Pechora R., Byzovaja Site (Klein, 1973); (28a) T-461, Indigirka district (Heintz, 1966); (39ax) Pechora R., Byzovaja Site (Klein, 1973); (47a) T-489, Bnolkalaach R., N.E. Siberia (Heintz, 1966).

latest Pleistocene, but I am not aware of any ^{14}C dates on _Saiga_ bone to support this contention and some of the Alaskan fossils come from deposits which almost certainly predate the last glaciation (Péwé, 1975a). _Saiga_ fossils are not often encountered in archaeological sites, but of such occurrences none are known from sites east of the Yenisei River (Klein, 1971). Also, even though the Ukraine is near the present range of _Saiga_, fossils of that animal are rather rare in Ukrainian local faunas, and when they do occur it is usually in association with Holocene and domestic vertebrates, not the typical members of the mammoth complex (Pidoplichko, 1956; Vereshchagin, 1967; Fig. 3). Saiga antelopes were abundant in southwestern France during a late phase of the last glaciation (as well as during the penultimate glaciation) (Delpech and Heintz, 1976), and apparently they also occurred at that time north of the Alps in western Europe (Kurtén, 1968). I have suggested that _Saiga_ _tatarica_ was a member of the mammoth complex in east Beringia (Matthews, 1976a _and_ In Press), but in view of the Ukrainian evidence, this may have been the case for only short periods of time when climate was most arid. One high priority for future research should be attempts to ^{14}C date some of the _Saiga_ fossils from Alaska and east Siberia.

Mustelidae

Bones of the North American badger, _Taxidea_ _taxus_, are the most common mustelid fossils in Fairbanks local faunas (Anderson, 1977), but since none have been dated or found in more chronologically discrete assemblages, the question of whether the badger was a member of the mammoth complex remains unresolved. Taxidea fossils have been considered to be evidence of steppe-tundra (Matthews, 1976a; Harington, 1977; Anderson, 1977), but it is strange, if this is so, that the species did not move into eastern Asia. The land bridge might have acted as a filter to the westward migration of both Taxidea and Camelops just as it apparently did to eastward movement of the steppe adapted woolly rhinoceros. However, if this were the case one might expect the old world badger, Meles meles, to have filled the vacant badger niche in eastern Siberia during the Pleistocene. Apparently this did not occur. The easternmost Meles fossils in archaeological sites are from the Ob basin (Table 1) and in the Ukraine, Meles meles, like the Saiga, is primarily a member of the mammalian group which includes Holocene and domestic mammals (Fig. 3). One wonders, therefore, if Taxidea actually did occupy east Beringia during the cold phases of the Pleistocene.

Remains of the Asian steppe ferret, Mustela eversmanni, occur in local faunas from Fairbanks and Old Crow regions (Anderson, 1977; Harington, 1977) None have been ^{14}C dated nor have they been found in narrowly dated assemblages, hence ferrets might not have been associated with the full glacial mammoth complex (e.g., Anderson, 1977). Mustela eversmanni may be conspecific with the North American black-footed ferret, Mustela nigripes, so the fossils do not necessarily imply trans-Beringian movement as in the case of the Saiga antelope. Instead the ferret, like the badger, could have invaded east Beringia from the south. In the Ukraine Mustela eversmanii fossils are rare, but the few local faunas in which they do occur contain Meles, Saiga and the steppe fox (Vulpes corsac) instead of the typical members of the mammoth complex (Pidoplichko, 1956).

Woolly Mammoth

The woolly mammoth, Mammuthus primigenius, has been the subject of more comment and speculation than any of the other members of the late Pleistocene large mammal community. Much of this attention undoubtedly results from the frozen carcasses found in Siberia (Tikhomirov, 1958; Farrand, 1961; Garutt, 1964), the most recent find, the infant "Dima mammoth", being at once the best preserved and most unusual specimen of them all.[8]

One author (Krause, 1978) has attempted to revive the old argument that the woolly mammoth was actually a warm climate herbivore, but the frozen carcasses from Siberia reveal a whole suite of soft tissue characters that are those expected of any mammal adapted to arctic conditions. Even without such evidence, the conclusion would be the same, since ^{14}C dates (a line of evidence not discussed by Krause, 1968) and associated floral and faunal remains (Farrand, 1961; Medvedev and Voronova, 1977; Solonevich et al., 1977; and Fig. 2, sample 14) show conclusively that the woolly mammoth was capable of surviving in a periglacial environment. According to evidence discussed above and samples 1 and 5 in Figure 5, Mammuthus primigenius lived in central Alaska and the central Yukon about 15 to 16 thousand years ago when both regions possessed herb-rich tundra vegetation and at a time when the climate of the latter area was probably extremely arid as well as cold (Foscolos, et al., 1977). However, the woolly mammoth was not restricted to such severe environments. One specimen from western Alaska and the Taimyr mammoth apparently lived in a shrub tundra environment (Hopkins, et al., 1976; Tikhomirov, 1958). The mammoth from Locality 44 in the Old Crow Flats lived in forest-tundra environment with climate similar to or even warmer than that of the present. Likewise, the stomach contents of the Siberian "Shadrin mammoth" strongly imply that it died in an open Larix woodland (Solonevich et al., 1977). Finally, some of the east Beringian mammoth dates in Fig. 5 fall within a time period when parts of Alaska and the Yukon were experiencing a phase of forest expansion and regional thawing (see above). Thus even though it can be shown that the woolly mammoth lived in Beringia when the climate was severe and the entire region was treeless, it may also have been capable of surviving on tundra similar to that of the present or even in taiga.[9] In other words it is probably wrong to consider woolly mammoth fossils alone as indicies of a special type of treeless environment.

Stomach contents of several of the Siberian mammoth carcasses strongly imply that the woolly mammoth was a grazer (Tikhomirov, 1958; Solonevich et al., 1977). This seems to be the obvious implication of its complex teeth since its molar shearing index (an indication of grazing efficiency?) is 80% higher than in the Asian elephant which itself feeds primarily on grasses (Maglio, 1973; McKay, 1973). Stomach content analyses may also lead to some erroneous conclusions if too much reliance is placed on occurrence of rare fossils or the peculiar conditions that may prevail during the death of a mired animal are not carefully considered.[10]

The two living elephant species differ in many features, yet their respective systems of social organization are similar. Was the social structure of woolly mammoth populations at all like that of modern elephants? The question has obvious archaeological implications, and has already been suggested (Saunders, 1977). Careful comparison of age characteristics in natural collections of mammoth bones, e.g., those from the Berelekh "mammoth cemetary" (Vereshchagin, 1974, 1977) and the Hot Springs mammoth site, (Agenbroad, 1978) with archaeological assemblages such as those in the Ukraine (Pidoplichko, 1969) and North America may tell us much about social organization of _M. primigenius_ and related species.

The woolly mammoth like the modern elephant was undoubtedly highly "K" selected, tending to maintain a large standing crop at the expense of slow growth rates and low reproduction (Petrides and Swank, 1965), and they probably faced some of the same survivial problems encountered by other long lived species (Miller, 1976). The precarious status of the African elephant in many areas of its range and the way they have responded to hunting and cropping (Laws, 1974) offers some facinating prospects for comparison with the effect of Paleolithic hunting on woolly mammoth. On the other hand it could be argued that the two surviving elephant species are so different from the mammoth as to make such comparisons meaningless. The issue merits further consideration.

Caribou

One implication of Figure 3 is that the Caribou, _Rangifer tarandus_, was an important member of the mammoth complex. Caribou occur in almost all late Pleistocene local faunas and as well they constitute a component of many late Paleolithic archaeological assemblages (Klein, 1971, 1973; Mochanov, 1978a). Thus caribou seem to have been a prime food resource of paleolithic man; yet of the four dominant members of the mammoth complex, it was the only one to survive to the present. The significance of this fact to models suggesting man as the main cause of large mammal extinction in North America is obvious.

Except for an occasional moose, caribou and muskox are the only large ungulates occupying present day tundra. Both are extensive rather than intensive feeders, which means they utilize a wide spectrum of intermittently grazed forage (Klein, 1970; Bliss, 1975a). This type of feeding behaviour is likely one of the factors contributing to the success of caribou and muskox in Holocene tundra, but it seems inimical to their existence within the more complex late Pleistocene ungulate community. Why, if the caribou thrives in the absence of competitors today, was it apparently also successful in an environment where its range was shared with 3-7 other ungulates? Perhaps the answer is that caribou are more adaptable than their present specialized behaviour indicates. On the Chukchi Peninsula the Khargin reindeer phenotype represents relatively rapid adaptation to range depleted of lichens (Kryuchkov, 1976). Accordingly Pleistocene caribou may have been different in terms of feeding behaviour and response to competition than their Holocene counterparts.

DISCUSSION

This Wenner-Gren workshop comes at a time when the tempo of paleoenvironment research in east Beringia is at an all time high. J.C. Ritchie and his associates have embarked on an extensive palynological study of lake cores from the Yukon Territory where Hanging Lake, in the northern part, promises to become the standard for the region (Cwynar, 1978), just as Birch Lake is now for interior Alaska (Ager, 1975) and Imuruk Lake for western Alaska (Colinvaux, 1964). These plus Ager's ongoing pollen studies in southwestern Alaska, Giterman's unpublished work (in conjunction with D.M. Hopkins) from the Bristol Bay area and pollen from several promising cores recently raised at sites in northern Alaska (D.M. Hopkins, pers. comm.) should help to define the zonal features of late Wisconsinan vegetation in east Beringia. Alluvial exposures in the Northern Yukon and Alaska are also under study. Sediments from such sections have limitations for pollen analysis, but they offer the unique opportunity for close comparison of several types of paleoenvironmental evidence, and alluvial sections often span greater periods of time than lacustrine sequences.

These new data are undoubtedly discussed in the accompanying papers of this series, and as a result some of the conclusions drawn above may have to be modified. But I believe that the evidence reviewed here is sufficient to indicate the following first approximation of late Wisconsinan-Sartan environments in Beringia:

1. Alaskan snowline was lower and active ice wedges occurred in the interior portion of the state (Péwé, 1975a), both facts which indicate colder climate and existence of permafrost. Sand wedges in the central Yukon Territory attest to extreme aridity as well as cold (Foscolos _et al_., 1977).
2. A common feature of mammalian communities from Europe to the Northern Yukon was presence of mammoth, horse, bison and caribou - the mammoth complex. Additional species indicative of tundra climates occurred as far south as the Ukraine and certain steppe species invaded east Beringia from both southern North America and Asia. The mammalian biocoenoses of east Beringia were not as diverse as has been suggested on the basis of local faunas but they almost certainly included more large grazing ungulate species than occur in contemporary tundra environments.
3. Forests virtually disappeared from east Beringia. Pollen evidence also shows that shrub birch and alder, both common in contemporary hypoarctic regimes,were also rare. Cold climate has been suggested as the cause (Matthews, 1970), but other factors, some of them non-climatic, may have contributed to this pattern. Macrofossils of plants and insects suggest the climate was no colder than on southern Banks Island today (Young's Zone 2). Grasses and _Artemisia_ were probably more important components of the regional vegetation than is currently the case, but by itself this fact indicates no particular type of tundra environment. However, when considered with the available macrofossil evidence, the two lines of evidence suggest a tundra drier and more steppe-like than that of the present, i.e., with a greater representation of upland grasses, sedges and herbs. In the Yukon Territory where nearly all lowland habitat was flooded by meltwater lakes, tundra may have been discontinuous and physiognomically similar to polar desert yet

if so it must have had a level of primary productivity high enough to support several species of large ungulates. In contrast existing polar desert and polar semi-desert areas support an exceptionally low ungulate standing crop,[11] probably because the discontinuous nature of the vegetation strains even the capabilities of extensive grazers like caribou and muskox.

4. Plant macrofossils from a few east Beringian sites imply alkaline substrates but the best evidence of this and development of xeric steppe-like biotopes comes from sites in Siberia (Sher *et al.*, 1977; Giterman, In Press).
5. Finally, loess deposition was widespread in Beringia and Ukraine. Most of the large mammal fossils from Siberia and Alaska come from ice-rich "yedoma" type silts which are the partly reworked facies of primary loess. Because loess and its redeposited facies are richer in soluble cations than contemporary tundra soils (Péwé, 1975a, Tomirdiaro, 1977), areas where significant thicknesses accumulated are likely to have been characterized by edaphic plant communities (Yurtsev, 1976).

Most workers agree that Beringian tundra of the late Wisconsinan was different qualitatively and perhaps quantitatively from present tundra. Some envision an environment most similar physiognomically to present day polar desert, but in my opinion this analogy, though based on strict interpretation of the lacustrine pollen evidence, falls short of accounting for some of the vertebrate and macrofossil evidence. The same applies to the argument that upland and interfluvial regions were essentially like modern tundra with only the wide floodplains being steppe-like (Péwé, 1975a). Certainly this was not the prevailing situation in Siberia (Tomirdiaro, 1977).

I believe that the paleontological evidence implies tundra conditions which were more steppe-like in uplands as well as lowlands, over large areas of Beringia . Vegetation zones would have existed, especially in maritime regions and despite the large size of the land bridge this zonality probably caused it to be a narrow constriction or filter to dispersal of steppe species (Sergin and Shcheglova, 1976; Yurtsev, 1976). Compared to east Beringia, Siberian steppe-tundra was much better developed and more prevalent because there a cold and extremely continental climate prevailed, facilitating the expansion of true steppe species (Yurtsev, 1972; Vangengejm, 1975; Tomirdiaro, 1977; Giterman, In Press). Cold treeless steppe-like environments occurred well beyond the limits of Beringia and constituted part of what I have termed an "arctic-steppe" biome stretching in its many forms from the eastern Yukon as far west as the Ukraine. Others have referred to this biome as tundra-steppe, periglacial-steppe and mammoth-steppe. Both modern polar desert and mid-continental grassland differ in fundamental ways from arctic-steppe. Possibly the closest existing analogue is the periglacial steppe occupying the wide valleys of the Pamir region in the Soviet Union and Afghanistan (Agakhanyantz and Lopatin, 1978; Petocz, 1978).

PRODUCTIVITY

Measurement and interpretation of primary and secondary productivity in ecosystems is a science in its own right and a subject beyond the scope of this paper. Nevertheless there are several conclusions, drawn on the basis of paleontological evidence, that require a more detailed airing than they have received in the past. One of these is that the diversity of the late Pleistocene ungulate fauna implies a greater biomass of ungulates and a higher level of primary productivity than modern tundra (Guthrie, 1968a; Klein, 1970; Bliss, 1975a; Matthews, 1976a).

The ungulate standing crop of modern tundra is low but is this due only to low levels of primary above ground productivity? A positive answer presupposes that the several large ungulates which existed in late Pleistocene treeless environments had no more feedback effect on their environment, than do caribou and muskox. But grazing, trampling and manuring do increase productivity and nutrient cycling in modern tundra (Bliss, 1975b; Bunnell _et al._, 1975), and these feedback loops must have been enhanced when the ungulate community contained 2-3 times more species than now. Thus the character of modern tundra — its moss-dominated, poorly drained substrates and abundance of heaths as well as its apparent low ungulate carrying capacity — may be partly due to the absence of certain key ungulate species.

Above-ground primary productivity in contemporary tundra is constrained by temperature and photoperiod (Miller and Tieszen, 1972), neither of which were significantly different during the Pleistocene. Hence tundra of that period could not have had markedly higher levels of primary productivity. Warmer soils, feedback loops associated with large ungulates, and possibly differences in chemistry of soils developed in loess may have had some effect on productivity and nutrient cycling (Haag, 1974), but the most important factor for large ungulates was likely a change in the relative abundance of certain types of plants. Today mosses constitute a large share of primary production in tundra yet they are not utilized by large herbivores (except as ballast). Furthermore extensive bryophyte cover is positively correlated with poor drainage and shallow permafrost table (cold soils), and in some areas mosses act as a sink for nutrients leached from standing vascular plants (Bunnell _et_ _al_., 1975). According to pollen and macrofossils, bryophytes were not as abundant during the Pleistocene. Sedges, grasses and other herbs seem to have comprised more of the regional vegetation cover and may have been adequate to support a greater diversity of ungulates even at times of lower total plant cover.

Finally, the assumption that ungulate diversity indicates greater ungulate carrying capacity needs qualification. Figure 5 is an attempt to test this relationship, and although it is flawed by inadequate information for central North America, the different methods used to census large mammals and estimate their total biomass, and certain assumptions I have had to make, it does suggest that there is no simple relationship between carrying capacity and ungulate diversity. The range for tundra sites overlaps the one for the North American mid-continent, and some African grassland-savannah sites, with many more ungulates than exist anywhere in North America, support a biomass of ungulates which is no greater than that of North American sites. The most that can be stated from the figure is that the higher diversity of ungulates in late Pleistocene treeless environments may imply a carrying capacity an order of magnitude higher than at present.[12] Comparison of arctic-steppe with African sites (Matthews, 1976a) definitely seems to be unfounded.[13]

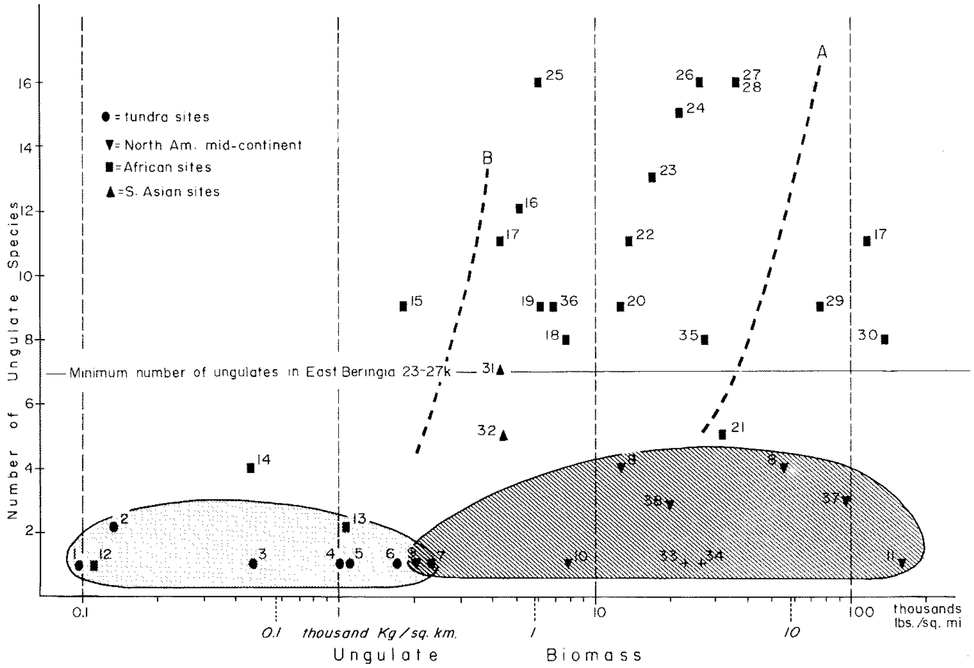

FIGURE 5. Comparison of ungulate carrying capacity and taxonomic diversity. Line "A" separates African forest-savannah from grassland, steppe, and savannah sites; "B" the latter from very arid steppe and desert. Stippled: range of tundra sites; Cross-hatched: range of mid-continental North American sites.

TUNDRA: (1) Alaskan and Canadian tundra (Klein, 1970); (2) Banks Is., NWT, maximum caribou estimate — Miller, 1978. Muskox — Hickey and Steele, ms 1978; (3) Agapa, west Taimyr Peninsula, USSR (Vassiljevskaja et al., 1975); (4) Northeast Devon Island, NWT (Muskox — Scotter and Telfer, 1975); (5) Skoog's estimate for Alaskan caribou (Davis, 1978); (6) Nelchina Basin, Alaska (Guthrie, 1968a); (7) Kevo, Finland (Kallio, 1975) and Hardangervidda, Norway (Østbye, 1975).

NORTH AMERICAN MID-CONTINENT: (8) Elk Island Natl. Park, Alberta (max. and min. — Telfer and Scotter, 1975); (9) Oklahoma prairie (Telfer and Scotter, 1975); (10) Wood Buffalo Natl. Park (Bison only — Scotter and Telfer, 1975); (11) Bison on tall grass prairie (cattle stocking estimates — McHugh, 1972); (37) Missouri River Breaks, Montana (estimated maximum — Mackie, 1970); (38) Prairie (west USA, DeVos, 1969).

AFRICAN SITES: (unless noted see Child, 1968, Table 28). (13) Sahara, arid; (14) Tchad, subdesert to steppe; (15) Kenya, subdesert, grass and bush;

FIGURE 5 CONT'D.

(16) Kenya, desert-grass-bush; (17) Congo, savannah-forest ecotone (high and low values) (Child, 1968, Telfer and Scotter - 1975); (18) Rhodesia, mopane veld; (19) Kenya, Acacia-Themeda grassland; (20) Kenya, Nairobi Natl. Park, Acacia-Themeda grassland; (21) Congo, forest-savannah mosaic; (22) Kenya, steppe to desert grass bush; (23) Kenya, Acacia-Themeda grassland; (24) Tanganyika (Serengeti), grassland and Acacia savannah; (25) Tanganyika (Tarangine Game Res.), Acacia savannah; (26) Rhodesia (Hendersons), "open mopane woodland"; (27) Tanganyika, grassland; (28) Tanganyika (Tarangiri Game Res.); (29) Uganda (Queen Elizabeth Natl. Park), ecotone forest-savannah; (35) Tanganyika/Kenya, steppe and savannah; (36) Kenya (Leroghi), highland grassland and forest; (33) Tsavo, elephants, (Laws, 1974); (34) Uganda, elephants, (Telfer and Scotter, 1975).
SOUTH ASIA: (31) Wilpattu Natl. Park, Sri Lanka (McKay, 1973); (32) Gal Oya, Sri Lanka (McKay, 1973).

CLIMATE

The cold, dry climate proposed for the arctic-steppe biome is in accord with the pattern predicted for the entire Northern Hemisphere at the height of the Late Wisconsinan-Sartan glaciation (Gates, 1976). Existence at this time of the Bering Land bridge plus exposure of large areas of the continental shelf north of Alaska and Siberia probably enhanced this trend by causing the climate of interior parts of east and west Beringia to become even more continental than they are now. For example, existence of the land bridge would have tended to reduce winter snowfall in interior Alaska (Bilello, 1974) and Streten's (1974) work suggests that it also may have caused summers to be both drier and warmer than now.

This seems to be a contradiction since interior Alaska and the Yukon were treeless at the time and the absence of trees in the north is normally attributed to cool summer temperatures. Cool summers, maritime locations, and existence of tundra are all highly correlated at present (Young, 1978), and thus any movement toward greater climatic continentality during the Pleistocene would seem to call for an expansion rather than decline of forests. The following example shows that this may not have been true.

Omyakon in northeastern Yakutia is considered by some to be both

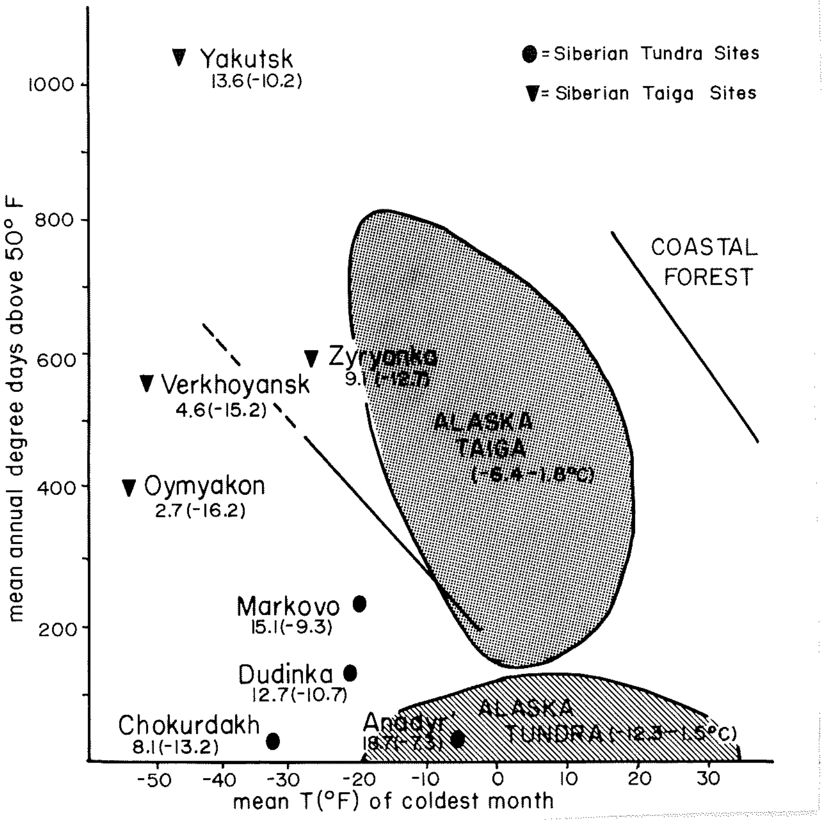

Figure 6. Comparison of climate at sites in Alaska and Siberia. Number next to site name indicates mean annual temperature (centigrade in parentheses)

the cold pole and pole of continentality in the Northern Hemisphere (Yurtsev _et al_., 1975). Winters are very cold; summers, short but warm. Winter temperatures and low snow cover account for existence of active ice wedges. Other types of periglacial structures occur on nearby slopes, which receive more snow than the valleys. Omyakon is forested but is outside of the range of spruce (Yurtsev, _et al_., 1975) and the tree species which do grow there do not inhabit east Beringia[14]. Plotted on Hopkins' (1959) diagram relating distribution of Alaskan taiga and tundra to temperature parameters (Figure 6), Omyakon falls well outside the field for Alaskan taiga sites. In other words, the climate of east Beringia during the late Wisconsinan need not have differed much from the cold, dry climate of northeastern Yakutia to account for treeless conditions which prevailed in Alaska and the Yukon. Maritime tundra undoubtedly existed in Beringia, but nearly all such sites are presently flooded.

The Omyakon scenario is only one of several that may be constructed for late Pleistocene interior Alaska. Other workers have suggested that summer climate was cooler than today (Péwé, 1975a) or that absence of trees was the result of aridity (Ager, 1975; Young, 1976). The significance of the Omyakon example is that it shows once again we must not look only to modern tundra and modern tundra climates in the search for analogues to condtions which prevailed in Beringia during the Pleistocene.

DEVELOPMENT OF ARCTIC-STEPPE

Most of the discussion to this point has centered on the environmental conditions of the Late Wisconsinan or Sartan because that is the interval of time for which exist the most data. There are only a few sites in east Siberia, Alaska and the Canadian Northwest Territories which provide information on the existence of steppe-like tundra at earlier time periods.

Lowland tundra existed in the northern hemisphere as early as the late Tertiary (Matthews, 1976b; Giterman and Kartashova, 1976; Sher *et al.*, 1977), and even at that time differed from present tundra in terms of its flora and fauna. But these distinctions involve presence of relict species or phylogenetic antecedents to members of the present tundra biota and are not indicative of a tundra environment as markedly different from present tundra as was arctic-steppe.

Fossil localities in the lower Kolyma basin in eastern Siberia and the Cape Deceit site in western Alaska have yielded evidence of early and middle Pleistocene tundra environments (Sher, 1974; Sher *et al.*, 1977; Matthews, 1974a). The mammalian faunas at such sites are similar. The mammoth complex is not represented but its antecedents are in the form of primitive horses, caribou and,a primitive species of mammoth (Sher, 1974; Guthrie and Matthews, 1971). In Siberia primitive muskox are also present, while Cape Deceit contains remains of *Cervus*.

In terms of insects and plant fossils these early and middle Pleistocene sites contain definite evidence of xeric tundra. Previously I suggested (Matthews, 1976 and in press) that this was a characteristic of only late Pleistocene tundra. It still may be so in western Alaska since at Cape Deceit the greatest development of the Lepidophorus - Morychus complex and highest percentages of Artemisia and grass pollen occur in latest Wisconsinan sediments (Matthews, 1974a). But in east Siberia the early Pleistocene Olyer sediments are dominated by the L-M complex (though without Lepidophorus which apparently doesn't occur there) including species of steppe insects (Sher et al., 1977; S. Kieslyov, pers. comm., 1979); and pollen spectra show high percentages of Artemisia and grass (Giterman, in press; Sher et al., 1977). In one Siberian section, however, high percentages of Artemisia are associated with significant amounts of shrub pine pollen and taiga insects, - a testimony to the correctness of Ritchie's admonition that Artemisia alone does not signify steppe-tundra.

If existence of the Bering Land bridge enhanced the climatic continentality of Beringia, then the development of steppe conditions at sites in east Siberia and Alaska probably fluctuated according to the degree of emergence of the land bridge. In the Bering Sea region tectonism has acted to modulate the effect of eustatic fluctuations; consequently the area of the land bridge was not the same at each phase of cold climate. During the Illinoian (Hopkins, 1973) it was narrower; for a large part of the early Pleistocene it may not have existed at all (Hopkins, et al., 1974).

The land bridge was almost certainly breached during interglacials and at such times tundra environments in east Siberia and Alaska seem to have been similar to those of the present (Sher et al., 1977; Matthews, 1974a). A major difference was that interglacial tundra undoubtedly supported, in addition to caribou and muskox, some of the other ungulates of the mammoth complex. Also, in Siberia, a few steppe insects occur in assemblages which on other grounds appear to be of interstadial or interglacial age (Sher, et al., 1977).

EXTINCTION

What I have attempted to present here is a view of Pleistocene tundra environments in east Beringia using all of the evidence at hand. From the standpoint of paleontology this encompasses the primary producers (pollen and plant macrofossils) and the primary and secondary consumers (fossil insects and large mammals). Of all the taxa discussed only a few - members of the large mammal fauna - are extinct, but I believe that they constituted such an important element of the biota that their demise actually represents the extinction of the whole system. Even those who reject the arctic-steppe concept must admit that future full-glacial tundra environments in Beringia will differ from those of the past by the absence of woolly rhinoceros, mammoths, Bison priscus, Symbos and some of their associated carnivores.

The mammoth complex undoubtedly constituted an important element of the Beringian biota during the penultimate glaciation. The ensuing Sangamon interglaciation reinstated tundra similar to that of the present and forest cover, but it did not result in the wave of large mammal extinctions which characterized the start of the Holocene interglacial. Man was one of the members of the late Wisconsinan fauna, and it is most probable that his presence was a key factor in late Pleistocene extinction (Martin, 1967). But in Beringia the effect of man was probably indirect since extinction seems to have occurred there at a time of drastically changing environments. We obviously need much more information on the sequence of extinction, but at present it appears that many of the Beringian large mammals disappeared at about the time that climate warmed, large areas changed from herb tundra to mesic and poorly drained shrub tundra, loess deposition ceased (due to flooding of the continental shelf and glacier retreat), and large areas began to be reforested. One need not assume that mammoths and other members of the mammoth complex could not reside in forested areas and wet contemporary tundra in order to suggest that such changes would have been highly detrimental to this grazing community (Kvasov, 1977; Tomirdiaro, 1977). What does seem strange, however, is that the maximum period of thawing and increase of forest cover — i.e., the most unsuitable period for steppe adapted ungulates in Beringia — occurred later in the Holocene; whereas the large ungulates all seem to have been extinct some 2000 years earlier. Should we expect to eventually obtain early Holocene dates for mammoth and other extinct ungulates; or was the change in environment which caused their extinction less directly associated with world climatic change and more closely related to the decline of continentality brought on by disappearance of the land bridge and emergent shelf areas? The answer is not in, but I suspect it will be the latter.

Extinction of the mammoth complex and its associates may not be as closely associated with the arrival of man as has been indicated. Paleolithic hunters of mammoth and other ungulates, lived in eastern Siberia well before the end of Pleistocene (Mochanov, 1978a). Caribou was hunted but did not become extinct. Bison priscus did disappear but not in the same sense as mammoth, especially if it is an adaptive stage in a single lineage which still survives (Guthrie, 1978). The horse became extinct in North America and west Beringia but not in steppe areas of Asia, where Saiga and until recently close analogues to some of the large Beringian predators also survived. Elk are now extinct in east Beringia but did not disappear until well after the appearance of man there. And finally, there is accumulating evidence (Morlan, 1978a; Morlan and Matthews, 1978) which strongly suggests that man was an inhabitant of the Northern Yukon as early as the start of the late Wisconsinan, meaning that he was an associate of the mammoth complex long before the start of late Pleistocene climatic and environmental disruptions.[15]

In view of these facts I believe the argument that man had a sudden, catastophic influence on the mammalian fauna of Beringia is unrealistic. The possibility that new hunting techniques or technological breaththroughs occurred near the end of the late Pleistocene cannot be ruled out, and apparently was an important factor in extinction elsewhere (Klein, 1978), but a more likely scenario for Beringia is that the demise of the large ungulate community and the arctic-steppe environment occurred during a period of climatic and environmental stress as a result of over-hunting and poor game management by an extremely opportunistic and culturally fortified predator.

A vivid example of how complex this process may have been is given in a study of the effects of isolation on ungulates and other mammals trapped on the islands formed by the filling of Lake Kariba (Child, 1968). Some of the findings run counter to commonly espoused theories and observations on the relation of social structure and crowding. For example, social interaction and activity declined. With the baboons hierarchial troop structure broke down and large adult males dispersed to forage on their own, but the remnants formed a cohesive potentially fecund nucleus. Sex ratios changed dramatically in some gregarious ungulate species (Impala), hardly at all in others (Zebra); and a few large mammals, such as elephants and some carnivors, benefited from the flush of vegetation and the availability of concentrated prey. Many of the recorded responses at Lake Kariba are those which allow certain ungulates to survive in a "boom or bust" arid environment, but they also cause certain species to be highly susceptible to mismanagement and/or human hunting pressure (Child, 1978).

The decline of arctic-steppe conditions in Beringia, followed by reforestation and establishment of the modern type tundra, probably also resulted in formation of isolated enclaves where range was optimal and biomass temporarily high.[15] In geological and evolutionary terms these events, lasting several thousands of years, were extremely rapid, but I do not pretend that they are comparable with the instant refugia at Lake Kariba. What the Kariba example does show is that: (1) Each of the species within an integrated mammalian community may react differently to range restrictions and climatic change, and (2) At such times over hunting (mismanagement) of one or a couple of species of ungulates may cause the decline of the entire ungulate community. This seems to me the most plausible explanation for extinction of arctic-steppe mammals.

FOOTNOTES

[1] Several definitions are required. In this paper "tundra" is used for lowland areas where climate precludes the survival of all but isolated stands of trees and is cold enough to promote the development of permafrost. Normally this implies a mean annual temperature slightly below 0°C, but since most tundra areas in east Beringia possess active ice wedges, mean annual temperature values are typically lower than -6°C (Péwé, 1966).

Tundra has been divided into zones on the basis of vegetation (Bliss, 1975) and floristics (Young, 1971). The latter system is easily calibrated with regional climatic parameters and is the one of greatest paleontological value because the distributions of many insect species also coincide with Young's zones (Matthews, 1974a; Blake and Matthews, 1979; K. Philip, unpub. ms.).

In polar desert and polar semi-desert regions plant cover is very low (5-20%) and consists mostly of lichens and mosses (Bliss, 1975). The soils are distinctive (Tedrow, 1977) and climate very severe. Polar desert is the dominant type of tundra within Young's zones 1 and 2, and although wet lowland areas with nearly 100% plant cover (excellent areas for large herbivores) do occur within those zones, they form but a fraction of the total area (Bliss, 1975). Plant cover is higher in Zone 3 and nearly 100% at all sites in tundra Zone 4 which borders forest and forest-tundra regions.

"Steppe" as used in this paper indicates dry grassland (as opposed to wet semi-aquatic grassland) with significantly higher plant cover than in polar desert and polar semi-desert areas.

[2] See Fig. 1. Péwé (1975a) correlated the Eva Fm. and the associated unconformity between the Goldstream Fm. and the Gold Hill Loess with the Sangamon because they represent a time >56900 years ago when spruce existed in the Fairbanks area and degredation of permafrost was occurring. We now can document a similar episode of deep thawing and reforestation in the Old Crow area of the Northern Yukon (Morland and Matthews, 1978), only there the event is known, from fission track dates on the Old Crow tephra and radiocarbon dates, to have occurred 50-80 thousand years ago during the Wisconsinan. At Fairbanks sections this same interstadial is probably represented by the Goldstream-Gold Hill unconformity and Eva Formation forest bed. This conclusion is supported to some degree by recent mapping and dating efforts in the Alaska Range (Hamilton, 1974). The lower part of the Gold Hill Loess unit must be of Illinoian age, as suggested by Péwé (1975a), because the Ester tephra (Fig. 1) is clearly pre-Wisconsinan (Briggs and Westgate, 1978). I suspect that the Sangamon interglacial is represented in Fairbanks exposures by a subtle unconformity (and possibly a geochemical fluctuation — see Péwé, 1975a, p. 45) within the Gold Hill Loess.

[3] All lowland areas of the Yukon, except the north coast, were occupied by large meltwater lakes between approximatley 30000 and 13000 years ago. The transgressive phase of lake formation in the Old Crow basin may have obliterated all evidence of the 30000 year old climatic fluctuation seen elsewhere ("transgressive unit" in Fig. 1). However, it should also be noted that autochthonous peats from the Old Crow basin suggest that climate was as cold or colder than at present 31000 years ago (sample 10. Fig. 2).

4 The exceptionally low influx value (50 gr/cm^2/yr) in the herb-zone at the base of the Hanging Lake sequence (Cwynar, 1978) may be due partly to the fact that the site was near a very large meltwater lake during late Wisconsinan time. The lake, because of its size, probably diluted regional pollen rain. Furthermore, since it undoubtedly maintained an ice cover well into the growing season, local pollen production, particularly by early flowering plants, may also have been inhibted. If so late season plants such as Artemisia and some grasses would have been favored.

Hanging Lake, like other northern Yukon lakes now understudy, is located in the uplands of east Beringia. In view of present vegetation differences between upland and lowland tundra sites, it is to be expected that its influx of fossil pollen will differ from that at lower elevation sites.

5 At Winnipeg, Manitoba the herb component of the pollen rain deviated significantly in two successive years of monitoring (Ritchie and Lichti-Federovich, 1963). During one of the years herb pollen influx fell as low as 300 gr/cm^2/yr, a figure similar to that at some modern tundra sites. Whatever the cause, this decline in herb pollen production was probably not matched by a change of similar magnitude in plant cover.

6 The local fauna from Unit 2 and basal Unit 3 at Locality 44 represents one such assemblage (see "bones loc. 44" in Old Crow composite, Fig. 1). The fauna includes Equus cf. verae, Rangifer, and Mammuthus. The species of mammoth is unknown, and Bison is absent. A camel fossil, mentioned in Harington (1978) and Mammut fossils have been found in the underlying clay (Harington's Unit 1). Plant and insect fossils suggest that the climate was warmer than at present during deposition of the basal sands of Unit 3 (Matthews, 1975 and unpublished), a conclusion supported by the fossils of the spotted skunk, Spilogale (Table 1.) On the other hand the mammalian assemblage also includes, as does the insect fauna, indicators of cold climate, and since the sediments were probably deposited at the end of the Sangamon interglacial, we cannot rule out the possibility that the Loc. 44 local fauna contains a mixture of late interglacial and early glacial elements.

Many vertebrate fossils have been found along Unconformity A at the locality 15 section in the Old Crow Basin (Morlan, 1978a, 1978b) (see Fig. 1 and Table 1), but even though that hiatus represents no more than 40000 years (and probably much less), the mammalian assemblage may be mixed because the unconformity marks thawing and erosion which occurred during an early Wisconsinan interstadial. In other words there is a possibility that the Loc. 15 local fauna includes mammals adapted to the warmer conditions prevailing at the time of thawing (when spruce existed in the area) and reworked fossils from sediments which accumulated in a colder, probably treeless, environment. Note in Table 1 that remains of giant beaver Castoroides and Dicrostonyx occur in the OC(15) local fauna.

7 The members of the mammoth complex occur along with other ungulates in late Paleolithic sites in the Ukraine. According to Klein (1973) and Veličko (1975) many of these sites were occupied during periods of cold periglacial climate, but apparently this conclusion is not universally accepted (Vereshchagin and Kuzmina, 1977). For example, some workers believe the principal cultural and bone bearing horizons at the Kostyenki sites correspond with times when broad leaf forests and milder, more moist climates existed in the Ukraine.

8 Caution must be used in interpreting the environmental significance of thse fossils since it is often difficult to determine accurately if the enclosing sedments refer to the environment in which the mammal lived. Some carcasses or fragments thereof were redeposited before final burial (Vereshchagin, 1977) and the carcasses of those animals that died as a result of becoming mired definitely intrude older sediments. Harington (1978, p. 71) cites a case in which the carcass of a recently mired reindeer would bear little or no relationship to either the pollen or macrofossils found in the host sediments.

9 Note, however, that this conclusion is based on the common assumption that all proboscidian bones found at northern sites refer to *Mammuthus primigenius*. In many cases the diagnostic teeth are missing and Harington (1977) indicates that fossils (some probably rebedded) of several other types of mammoth as well as mastodon have been found in late Pleistocene sediments in east Beringia. Thus the supposed interglacial forest-tundra mammoth from Locality 44 may not be *M. primigenius*, and the fossils referred to mammoth at the western Alaska site, discussed in Hopkins *et al.*, (1976), were actually only identified as proboscidian.

10 King (1977) shows that palynofloras from feces are poor indicies of regional environments, and the same conclusion should be true of stomach contents. For example, the stomach from a *Bison priscus* carcass in the Kolyma Lowland was dominated by grass and *Artemisia* pollen, but did not contain any birch pollen, which was abundant in the host sediments (Sher, 1974).

Some of the carcasses represent animals that were mired for some time before death. The contents of their stomachs may represent vegetation at the site of entrapment rather than the normal food preference. Perhaps this explains the abundance of moss spores and diversity of moss macroremains in the stomach of the Shadrin mammoth (Solonevich *et al.*, 1977).

Some authors have drawn detailed conclusions on the basis of palynomorphs which represent only a fraction of a per cent of the entire stomach assemblage (Tikhomirov, 1958). In any other pollen diagram these elements would be considered only as allochthonous "noise".

11 The present standing crop of Peary Caribou on Melville Island is so low (22 lbs/mi.^{2}) as to fall outside the arbitrary range for tundra sites shown in Figure 5. Even the higher 1961 estimate for the Melville Island population represents a low standing crop compared to other tundra sites (Miller, 1978).

12 If each species of Pleistocene ungulate was represented by small populations or herds, a diverse community would not necessarily imply a high standing crop. Guthrie (1978) suggests, for example, that it is incorrect to assume that *Bison priscus* was as abundant on its range in Alaska as *Bison bison* was in the great plains,and the same may be true of other large mammal species (Martin and Neuner, 1978). However, there is a minimum number below which a particular species is no longer stable with extinction a virtual certainty (Miller and Botkin, 1974), and this threshold may be relatively high for certain long lived species like the elephant (Miller, 1976).

13 Although the African environment changed in response to Quaternary climatic fluctuations, some type of forest-savannah environment (the most productive type according to Fig. 5) has probably existed somewhere on that continent since the mid-Tertiary. Over this long span of time a complex ungulate community with a fine-tuned grazing succession developed (Bell, 1971). Ungulate communities as complex as those of African forest savannah probably disappeared from North America during the late Tertiary. Since then the extent of grasslands in the mid-continent has fluctuated greatly in response to Quaternary climatic oscillations. Consequently, I doubt that Pleistocene ungulate biocoenoses in Beringia were ever as effectively integrated and as taxonomically complex as those of Africa today.

14 June, July, and August temperatures of 9.5°C, 13°C, 10°C and 11°C, 14°C, 11°C are the minimum required for introduction and reliable reproduction respectively of black spruce near its limit (Black, 1977). Comparable degree day thresholds are 1200 and 1330. Temperatures for the three critical months at Omyakon are 11.6°, 14.7°, and 10.8° (Wernstedt, 1972), and I estimate a total of about 1160 degree days. Thus black spruce would probably not grow and reproduce at Omyakon.

Photoperiod seems to be the critical factor for breaking vegetative and reproductive dormancy in white spruce, but after that event temperature becomes the dominent developmental parameter (Owens *et al.*, 1977; Owens and Molder, 1979). Omyakon currently has only ca. 600 degree days above the critical 5°C threshold, whereas some spruce populations are known to require at least 700 degree days to complete all seasonal developmental stages (Owens *et al.*, 1972). Apparently white spruce would not survive at Omyakon either.

15 As indicated earlier many of the bones thought to have been modified by man occur at the base of exposures or along unconformities which represent most of Wisconsinan time. Some of the dated bone artifacts obviously represent human popultions living in the area before the basin was flooded by a glacial meltwater lake; but it is wrong to assume that all of the fossils, particularly the human mandible (Irving *et al.*, 1977), are mid-Wisconsinan, since the alluvium or loess which caps the lake sediments (Unit 4) at many exposures also contain fossils of extinct mammals (*Bison crassicornis* at Loc. 11). These sediments probably represent the short period of time immediately following rapid drainage of Glacial Lake Old Crow. A large unfrozen clay and silt plain would have existed for a thousand or so years and might have constituted optimal ungulate habitat

at the very time (12000-13000 B.P.) when regional environments were becoming less suiteable for large mammal grazers. If man were a resident of the area, he too would probably have lived on the lake plain; hence some of the undated bone artifacts found at the base of exposures may actually be of latest Wisconsinan rather than mid-Wisconsinan age.

TABLE 1

Late Pleistocene Mammals From Beringia, Siberia, And The Ukraine[1]

LARGE HERBIVORES

Mammuthus sp. — OC(15,44)[2]
Mammuthus primigenius (woolly mammoth) — Ur; S(w,e,fe); Al; OC; D
M. armeniacus (= *M. trogontherii* — steppe mammoth) — OC
M. meridionalis — Ur; OC*
Mammut americanum (American mastodon) — Al; OC; D
Bison priscus (= *B. alaskensis* and *B. crassicornis*) — Ur; S(w,e,fe); OC; D
B. bonasus — Ur
B. bison — Al; D
Bison sp. — OC(15)
Bos sp. (= *Poephagus*, yak) — S(w); Al?
Bos primigenius (auroch) — Ur; S(e)
Ovibus moschatus — Ur; S(fe); Al; OC; D
Praeovibos priscus — OC*
Praeovibos sp. — Al
Symbos cavifrons — Al; OC; D
Boötherium sargenti (♀ of *Symbos*?) — Al; OC: D?
Soergelia cf *elisabethae* — OC*
Capra sibirica (ibex) — S(e)
Ovis dalli (= *O. nivicola*) — S(e); Al; D
O. ammon (argali sheep) — S(w,e)
Camelops sp. — Al; D
Paracamelus sp. — OC?
Sus scrofa — Ur; S(e)
Saiga tatarica (= *S. ricei*) — Ur; S(e,fe); Al
Spiroceros kjaktensis (spiral horned antelope) — S(e)
Gazella gutturosa (mongolian gazelle) — S(e)
Alces alces — Ur; NS; Al; OC; D
A. latifrons — OC; D; Al
Alces sp. — OC(15)
Megaloceros (= *Megoceros*) — Ur; S(e)
Cervus elaphus (= *C canadensis*) — Ur; S(w,e,fe); Al; OC; D
Capreolus capreolus (roevdeer) — Ur; S(w,e)
Rangifer tarandus — Ur; S(e,fe); Al; OC(15,44); D

Equus cf. *scotti* — OC; D

E. caballus (small form = to *A. hemionus*, Harington 1977) — Ur; S(fe)

E. (*Asinus*) *lambei* (= *A. hemionus*?) — Ur; S(w,e,fe); Al; OC; D

E. (*Asinus*) *kiang* — Al; OC; D

E. tarpan (= *E. przewalskii*) — Ur; S(w,e,fe)

E. cf. *(Plesippus) verae* — OC(44)*; D

Equus sp. — Al; OC(15)

Coelodonta antiquitatis (woolly rhinoceros) — Ur; S(w,e,fe)

Megalonyx jeffersoni (Jefferson's ground sloth) — Al; OC

LARGE CARNIVORES

Ursus spelaeus (cave bear) — Ur

U. arctos — Ur, S(w,e,fe), Al; OC; D

U. americanus (black bear) — OC

Ursus sp. — OC(15)

Arctodus simus yukonensis (Yukon short face bear) — Al; OC; D

Smilodon sp. (saber tooth cat) — Al?

Homotherium (scimitar cat) — Al?; OC; D

Felis leo atrox (= *Macrofelis spelaea*, *F. spelaea*) — Ur; S(e,fe); Al; OC(15); D

F. pardus — Ur

F. cf. *concolor* — OC

Crocuta crocuta (cave hyena) — Ur; S(w)

Canis lupus — Ur; S(w,e,fe); Al; OC; D

C. dirus — Al?

C. familiaris — OC

C. latrans — Al

Cuon sp. (dhole) — OC

SMALL CARNIVORES

Lynx canadensis — Al; OC(15)

L. lynx — Ur

Felis sylvestris — Ur

Vulpes vulpes — Ur; S(w,e,fe); Al; OC

V. corsac (steppe fox) — Ur

Alopex lagopus (arctic fox) — Ur; S(e,fe); Al; OC(15,44); D

Taxidea taxus (North American badger) — Al; D

Meles meles (Old World badger) — Ur; S(w)

Gulo gulo — Ur; S(e,fe); Al; OC(44)

Mustela putorius (pole cat) — Ur

M. vison (mink) — Al

M. nivalis (weasel) — Ur

M. sarmatica — Ur

M. eversmanni (steppe ferret, = *M. nigripes*?) — Ur; Al; OC

M. erminea — S(w); OC(15)

Mustela sp. — OC(44)

Spilogale sp. (spotted skunk) — OC(44)

Martes nobilis — OC

M. pennanti (Fisher) — OC

M. martes — Ur

Lontra (= *Lutra*, otter), OC

MEDIUM AND SMALL HERBIVORES AND INSECTIVORES

Erethizon (porcupine) — Al

Castor canadensis — Al; OC(15,44); D

C. fiber — Ur; S(e,fe)

Castoroides ohioensis (giant beaver) — OC(15)

Sciurus vulgaris — S(e)

Marmota monax (woodchuk) — OC(15)

M. bobak (steppe marmot) — Ur; S(w,e)

Spermophilus parryi (= *Citellus undulatus*, ground squirrel) — S(w,e); Al; OC(15,44); D

S. suslicus — Ur

Microtus gregalis (= *M. miurus*, meadow vole) — Ur; S(e,fe); Al; OC(15)

M. oeconomus — S(w,e,fe); Al; OC(15)

M. arvalis — Ur

M. pennsylvanicus — OC(15)

M. xanthognathus — Al; OC(15); OC(44)

Lemmus sibiricus (= *L. obensis*) — Ur; S(fe); Al; OC(15,44)

Dicrostonyx torquatus (collared lemming) — Ur; S(fe); Al; OC(15); OC(44)

D. cf. *henseli* — Al; OC(15)

Clethrionomys rutilus — S(fe); OC(15); OC(44) cf.

Clethrionomys sp. — Al

Phenacomys intermedius — OC(15

Synaptomys sp. — Al?

Lagurus lagurus (steppe vole) — Ur; S(e)

L. luteus — Ur

Ondatra zibethicus (muskrat) — Al; OC(15,44)

Ochotona princeps (pika) — OC(44); Al

O. hyperborea — S(fe)

O. pusilla — S(e)

O. cf. *whartoni* (giant pika) — Al?; OC*

Ochotona sp. — Ur

Lepus americanus (snow shoe hare) — OC(15)

L. timidus — S(e,fe)

Lepus tolai — S(w)

L. arcticus (Arctic hare) — OC(15,44)

Lepus sp. — Al

Sorex cf. *arcticus* — Al

S. cf. *obscurus* — OC(15)

Planisorex cf. *dixonensis* — OC*

PRIMATES

Homo sp. — Ur; S(w,e,fe); Al; OC

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*Indicates taxa that are probably older than oldest exposed sediments in Old Crow basin.

[1] Based on Pidoplichko, 1956; Guthrie, 1968a, 1968b; Klein, 1971; Guthrie and Matthews, 1971; Sher, 1968, 1974; Vangengejm, 1975; Anderson, 1977; Harington, 1977, 1978; Harington and Clulow, 1973; and R.E. Morlan, 1978b

[2] Regional abbreviations: Ur = Ukraine; S = Siberia, w(west Siberia — Ob Basin), e (east Siberia — Yenisei to trans Baikal area), fe (far eastern Siberia — Lena-Aldan to Chukotka); Al = Alaska; OC = Old Crow, Northern Yukon, 15 = Locality 15 — Unconformity A (see Fig. 1), 44 = Locality 44 — Unit 3 at base (see Fig. 1); D - Dawson area, Yukon Territory.

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TO / À: Dr. J. Fyles
Chief Geologist

FROM / DE: Dr. N.C. Ollerenshaw

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OUR FILE — N / RÉFÉRENCE: 203.2.25

YOUR FILE — V / RÉFÉRENCE:

DATE: November 13, 1984

SUBJECT / OBJET: O.F. 1116

Permission is requested to release the following open file material:

O.F. 1116: FACIES AND RESERVOIR ANALYSIS, KEE SCARP FORMATION, NORMAN WELLS AREA, NORTHWEST TERRITORIES

by N.R. Fischbuch

This unedited Open File, which consists of 50 pages of text, 3 cross-sections, and 1 isopach map, describes the lithofacies of the Kee Scarp reef complex and uses data gathered from that reef complex to predict the presence of oil-bearing reef complexes in adjacent regions. Core was examined from 17 wells in and adjacent to the Norman Wells oil field, comprising 1458 metres of reefal material. Lithological units were correlated using gamma density and gamma sonic mechanical logs. Porosity values from the core analyses are plotted on the cross-sections.

This Open File material is available for viewing at all Geological Survey libraries, at the Resident Geologist's office in Whitehorse, Yukon, and the Mining Recorder's Office in Yellowknife, N.W.T. Copies may be obtained at the user's expense from Riley's Datashare International Limited, P.O. Box 6730, Station D, Calgary, Alberta T2P 2V8, and from the Mining Recorder's Office, Department of Indian and Northern Affairs, 4th Floor, Bellanca Building, P.O. Box 1500, Yellowknife, N.W.T. X1A 2R3.

N.C. Ollerenshaw
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