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Environments of Pleistocene Beringia: analysis of faunal composition using cenograms

Cenograms are graphs of body size for mammalian faunas. Cenogram analysis is based on correlation between the distribution of body mass in mammalian faunas and two important environmental factors. Aridity is inferred from the slope of medium-sized species and openness of plant formations is correlated with the size gap between medium and small species. Cenogram analysis does not rely on attributes of particular taxa in the community, and thus is relatively free from both taxonomic and taphonomic influences. Cenograms have been used to infer environmental parameters for Paleocene to Oligocene assemblages of mid-latitude North America and Europe, and here are applied to subarctic and arctic faunas. The present-day Yukon boreal forest assemblage produces cenogram statistics that indicate semiarid climate and plant formations about as open as in more southern forests. Taiga and tundra both fall into the arid portion of the moisture gradient, with tundra at an extreme end. These are also extremely open habitats. Cenograms for seven Quaternary faunas of Beringia, ranging from early Pleistocene to latest Wisconsinan, all indicate aridity comparable with taiga conditions and openness similar to tundra. No forest-habitat faunas were detected. Similar arid, open habitats probably appeared in Beringia by the earliest Quaternary and apparently persisted for a major part of the Pleistocene, even at times other than glacial maxima. A late Wisconsinan fauna from Saskatoon, Saskatchewan occupied a semiarid, somewhat open environment comparable to the present-day parkland ecotone. Late Wisconsinan to late Holocene faunas from Charlie Lake Cave, British Columbia show little change through time and lived in an open area of boreal forest, comparable to present-day conditions. Mammalian diversity is very low in Beringia today, and was even more restricted in the Pleistocene among small and medium-sized groups. Pleistocene faunas show the same trends as the present-day mammalian community but express them more strongly. Low diversity in Pleistocene faunas of Beringia is not an artifact of inadequate sampling. Several faunas have been collected carefully enough to indicate actual diversity among small and medium-sized mammals. Interpretation of late Pleistocene Beringian faunas is consistent with weakness of the hydrologic cycle at last glacial maximum; perhaps this condition too was typical of much of the Pleistocene.

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INTRODUCTION

Cenograms are graphs of body size for mammalian faunas. The natural logarithm of body mass in grams is plotted on the Y-axis, with rank (largest to smallest) on the X-axis; the units of measurement and use of natural logarithm are not important except to standardize results. Carnivorans are omitted. Regression lines are plotted for medium-sized mammals (500 grams to 250 kilograms) and small mammals (less than 500 grams); body size in large mammals is not included in this analysis. Steeper slopes in the medium-sized class indicate more arid conditions. Legendre
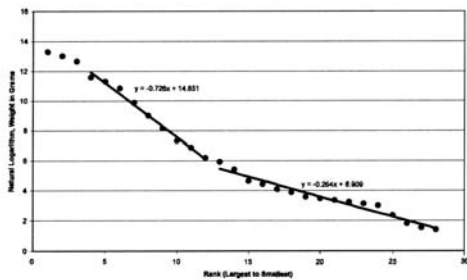
Figure 1   Cenogram, present-day Yukon forest fauna.

(1986) considered that steeper slopes for the small mammal class might indicate lower minimum temperatures. The size gap between small and medium-sized mammals appears to be a measure of relative openness of the environment. This gap is quantified by comparing the logarithms of the smallest mammal above 500 g (in the faunas analyzed here usually the Arctic ground squirrel, *Spermophilus parryi)* and the largest mammal below 500 g.

Legendre (1986; 1987a, b) used cenograms to infer certain environmental parameters and thus paleoenvironmental changes in the great European faunal turnover of the latest Eocene and early Oligocene, the Grande Coupure. Gingerich and others (Gingerich 1989; Severson & Gingerich 1998) have analyzed cenograms for late Paleocene and early Eocene faunas of Wyoming, also to track environmental changes that occurred during an important faunal transition. In both instances, cenograms of modern faunas from Africa, Europe, and North America at latitudes from the Equator to about 40º north and south were used for comparison.

Until now no attempt has been made to use cenogram analysis to understand Pleistocene faunas of Beringia. In this paper I extend the data from lower-latitude environments with cenograms from present-day Yukon forest, taiga, and tundra environments. I use these augmented data to analyze cenograms of seven Pleistocene faunas of Beringia, and confirm some basic attributes of Ice Age Beringian faunas.

CENOGRAMS OF MODERN YUKON FAUNAS

Because cenograms have not previously been used to analyze arctic or subarctic faunas comparative data for the North are lacking. I constructed cenograms for southern Yukon forest, northern Yukon taiga, and northern Yukon tundra faunas using occurrence, habitat, and body mass data given by Banfield (1974) and Youngman (1975) and compared them with cenogram statistics listed by Gingerich (1989: table 31). Figures 1-3 are the new Yukon cenograms. Statistics are summarized in Table 1.

In my analysis I have followed Gingerich (1989: 79) in separating large mammals from medium-sized mammals at 250 kg rather than using Legendre's limit of 8 kg (1986: 193). Each has stated that his chosen limiting number emerges empirically from cenograms for modern faunas. Gingerich's 250 kg limit (ln = 12.4) appears as a natural breakpoint in an earliest Wasatchian (latest Paleocene) forest fauna (1989: fig. 50), but 8 kg (ln = 9.0) corresponds with only an insignificant gap. The same is true of the cenogram for present-day Yukon forest mammals (Fig. 1), where there are a noticeable gap and a change of slope at about 250 kg but there is no appreciable gap at 8 kg, approximately the weight of the American porcupine (*Erethizon dorsatum*). Legendre's 8 kg limit appears as a clear gap in cenograms for more arid and open areas, including the modern Yukon tundra (Fig. 3) and the plains of Rwindi-Rutschuru, Zaire (Legendre 1988: fig. 8). In both these ceno-
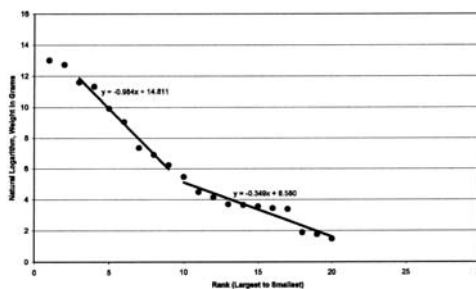

Figure 2   Cenogram, present-day Yukon taiga fauna.

Table 1   Cenogram statistics for modern Yukon mammalian faunas and faunas of lower latitudes.

	Slope small mammals	Slope medium mammals	Break Ln weight in grams
Modern southern Yukon forest	-0.264	-0.726	0.276
Modern north Yukon taiga	-0.349	-0.984	0.787
Modern north Yukon tundra	-0.550	-2.011	1.248

Lower latitude faunas (figures given are means; asterisks indicate parameters that Gingerich (1989: table 31) considered to be consistent with environmental gradients).

	Slope small mammals	Slope medium mammals	Break Ln weight in grams
Vegetation gradient			
Forest	-0.165	-0.292	0.236*
Woodland	-0.167	-0.257	1.367*
Savanna	-0.233	-0.690	1.154*
Moisture gradient			
Humid	-0.157	-0.208*	0.151
Subhumid	-0.172	-0.313*	1.788
Semiarid	-0.244	-0.616*	0.565
Arid	-0.201	-1.058*	1.000

grams 250 kg does not appear as a significant breakpoint, but rather marks a change in slope of the respective regression lines. 250 kg is about the mass of the domestic horse (*Equus caballus*) and cow (*Bos taurus*). In the Yukon tundra (Fig. 3) there are no mammals weighing between 2 and 80 kg, and in the Rwindi-Rutschuru assemblage there are very few between 8 and 30 kg. Presence of a significant gap at eight kg, indicating impoverishment of the middle-sized mammal community, seems to be a characteristic of relatively arid and open environments.

I adopt Gingerich's separation of large and medium-sized mammals at 250 kg both because available cenogram statistics have been calculated on that basis (Gingerich 1989: table 31), and because a 500 to 8000 g range for middle-sized mammals in Beringian faunas would leave little for analysis. At the present state of development of techniques for cenogram analysis the choice seems somewhat arbitrary.

The regression slope for medium-sized mammals of the present-day southern Yukon forest characterizes the climate as semiarid, and indeed most of the southern Yukon receives less that 400 mm of precipitation annual-
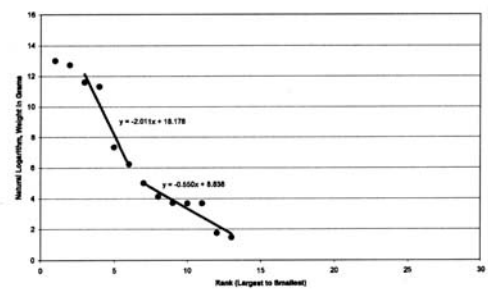

Figure 3   Cenogram, present-day Yukon tundra fauna.

ly while the boreal forest in northern Yukon may get less than half that amount. The break between small and medium-sized mammals (0.276) indicates that this northern forest is about as open as more southern forests. Modern northern Yukon taiga and tundra, by the same criteria, show a trend toward increasing aridity and openness. Statistics from these cenograms supplement those from lower latitudes and provide a greater scope for interpretation.

PLEISTOCENE FAUNAS OF BERINGIA

Having established a baseline for analysis of subarctic and arctic cenograms, I present and analyze some examples from Pleistocene faunas of Beringia. In choosing faunas for cenogram analysis I have tried to avoid assemblages drawn from an excessively large area or stratigraphic range and I have chosen examples where an investigator has made efforts to collect mammals at the lower end of the size range, preferably by using screening or washing techniques.

The Tertiary faunas analyzed by various authors are generally assumed to represent thanatocoenoses, accumulated over a few hundred to some thousands of years and potentially concentrated by depositional agents from an area of unknown size and ecological range. I realize that these Quaternary faunas are also composites to an unknown extent. Although obviously a complex taphonomy including averaging in time and environment may produce erroneous interpreta-

tions, the direction of potential error is predictable: "*aggregating samples from different places or ages necessarily inflates species lists and makes inferred climate appear too wet and vegetation appear too closed*" (Severson & Gingerich 1998). Thus we can infer ancient conditions approximately from cenograms. Refinement in defining faunal assemblages remains a significant challenge, as does the tracking of very short-term environmental changes. It is obvious that the shortest possible time range and the most specific possible stratigraphic context are best. Cenograms are also best regarded as one of many paleoenvironmental indicators to be used in conjunction if possible. On the other hand, cenogram analysis provides an independent tool that does not rely on the often arbitrary and doubtful comparison of modern ecological requirements of mammalian species with the presumed requirements of fossil conspecifics or relatives.

Seven faunas

Seven faunas appeared as good candidates for cenogram analysis:
- Latest Wisconsinan, Bluefish Caves, northern Yukon (Harington 1989; Morlan 1989).
- Late Wisconsinan, Tofty, Alaska (Repenning *et al*. 1964).
- Sangamonian or early Wisconsinan fauna, Old Crow, Yukon Locality CRH 15, between - Disconformity A and the Old Crow Tephra (Morlan 1996).
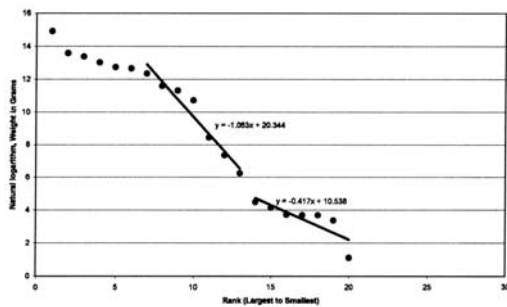- Sangamonian, Old Crow, Yukon Locality
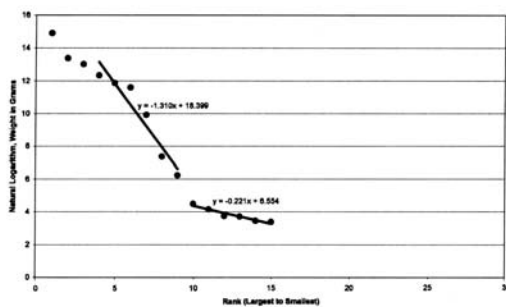

Figure 4 Cenogram, Bluefish Caves fauna.

Figure 5 Cenogram, fauna from Tofty, Alaska.

CRH 44 (faunal list from Pinsof 1996).
- Sangamonian or older, Old Crow, Yukon Locality CRH 15, middle of Unit 2a (Morlan 1996)
- Early and Late Olyorian faunas (early to middle Pleistocene), Siberia (Sher 1986a).

The cenograms follow as Figures 4 to 10; cenogram statistics are summarized in Table 2.

ANALYSIS OF PLEISTOCENE CENOGRAMS

The latest Pleistocene fauna of the Bluefish Caves, northern Yukon (Fig. 4; Table 2), closely resembles a taiga fauna in aridity (medium-sized mammal slope, -1.063) and a tundra fauna in relative openness of plant formations (break in weight at 500 g, 1.766). The very limited diversity of small mammals is comparable to a tundra assemblage. Morlan (1989) hypothesized a range of environments perhaps slightly less open than the range of habitats indicated by cenogram statistics. He placed the fauna within the birch zone of the pollen record and listed microtine rodent species that today prefer both mesic and xeric habitats. This is the only fauna analyzed here that is preserved in an upland situation, perhaps accounting for a strong indication of openness in habitat. Morlan (1989) considered that accumulation from surrounding habi-

tats, including lowlands, was significantly enhanced by both raptors and humans.

A late Wisconsinan fauna from Tofty, Alaska (Fig. 5, Table 2) appears also to represent conditions as arid as modern taiga and as open as tundra. Cenogram interpretation compares favorably with Schweger's (1990: 39) reconstruction of the vegetation of Beringia at last glacial maximum as "treeless and open, displaying both tundra and taiga affinities, with *Salix* (willow) the dominant shrub along streams and flood plains. Shrub *Betula* (birch) and *Populus* (poplar or aspen) may have been present in the most favorable settings." This is a mosaic of habitats from which we could expect a fauna of somewhat mixed affinities to be accumulated and preserved in stream-valley deposits.

Except for the Early Olyorian (Chukochyan) fauna, earliest(?) Pleistocene of Siberia, which shows a medium-sized mammal slope more typical of tundra conditions, the other faunas consistently give the same strong paleoenvironmental signal; they resemble taiga assemblages in apparent aridity and tundra assemblages in openness. None of the faunas analyzed represents a forest environment. The evidence from these faunas indicates that similar conditions prevailed in Beringia for major parts of the Pleistocene back to at least 1.5 million years ago.

Table 2 Cenogram statistics for Pleistocene mammalian faunas of Beringia

	Slope small mammals	Slope medium mammals	Break Ln weight in grams
Bluefish Caves	-0.417	-1.063	1.766
Tofty, Alaska	-0.221	-1.310	1.766
CRH 15, Disconformity A	-0.291	-1.001	1.766
CRH 44	-0.364	-0.871	1.248
CRH 15, Middle 2a	-0.413	-1.120	2.100
Early Olyorian (Chukochyan)	-0.586	-1.652	1.250
Late Olyorian (Akanian)	-0.584	-1.014	1.248

Sher (1986b:187) has anticipated this conclusion: "*It is reasonable to believe that well-established cryoxerophilous communities of tundra-steppe type had already existed in Beringida during Olyorian times as early as about 1.0 million years ago.*" Analysis of cenograms documents this development as probably having occurred somewhat earlier, perhaps by 1.5 million years ago.

Only along the Old Crow River at locality CRH 15 can we track similarly collected and documented assemblages through time. The results are inconclusive: it would appear that both faunas represent arid environments as open as modern tundra. Aridity and openness of vegetational formations may have decreased slightly at some time in the ?Sangamonian, if the slightly smaller medium-mammal slope and break in weight at 500 g for the fauna from Disconformity A are meaningful. Further testing or combination with other measures may allow us to make more confident statements about these first glimpses of the mid-Pleistocene mammal community.

OTHER PLEISTOCENE FAUNAS NORTH OF 50°

Of several Pleistocene faunas from the southern plains of Canada north of 50º N latitude, only one includes a broad enough spectrum of the mammalian fauna for cenogram analysis, with fine screens used in collecting. This is the late Wisconsinan Riddell local fauna from Saskatoon, Saskatchewan, latitude 52º N (SkwaraWoolf 1980; Skwara & Walker

1989). Cenogram statistics (Fig. 11) are: slope small mammals, -0.446; slope medium-sized mammals, -0.878; break in Ln weight, 0.722. These figures indicate an assemblage from a semiarid environment, with habitats perhaps about as open as taiga but more open than boreal forest, considerably more open than mid-latitude forest but less open than woodland savanna. This interpretation fits SkwaraWoolf's (1980) interpretation of conditions much like those of modern Saskatoon, which is in the aspen parkland ecotone.

I have also analyzed the latest Pleistocene and Holocene faunas of Charlie Lake Cave, northeast British Columbia (Driver 1988). The smallest mammals in these assemblages were not collected because of the 3 mm mesh used in the archaeological excavations. Results of cenogram analysis for these faunas are puzzling. Statistics for the late Wisconsinan fauna (Table 3) indicate an environment similar to today's, a relatively open spot in the boreal forest. Intermediate Holocene faunas give very similar results and indicate minimal change from the latest Pleistocene to today, with aridity possibly increasing slightly between 8400 and 4300 years ago, and openness of plant formations possibly increasing at the beginning of the Holocene, then reaching present levels by 4300 years BP.

It is tempting to try to interpret the Sangamonian assemblage from Medicine Hat, Alberta (Russell & Churcher 1972) and the early Pleistocene Wellsch Valley local fauna from Saskatchewan (Stalker & Churcher
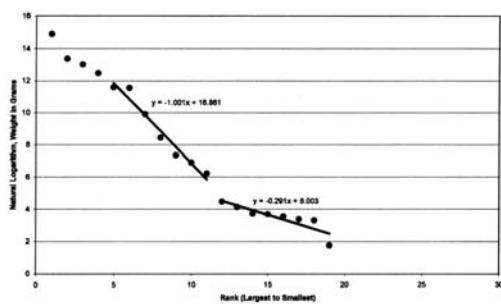

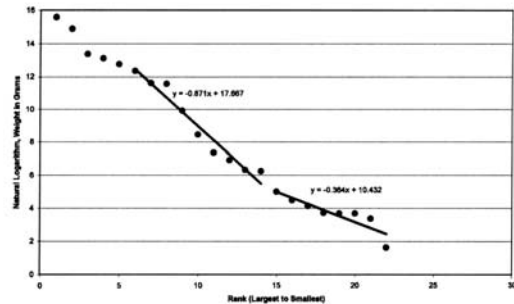Figure 6   Cenogram, fauna of locality CRH 15, Disconformity A.

Figure 7   Cenogram, fauna of locality CRH 44.

Table 3 Cenogram statistics for Charlie Lake Cave, British Columbia.

level	age	Slope small mammals	Slope medium mammals	Break
IIa	10700-10000 BP	-1.129	-0.771	0.709
IIb	9000-10000 BP	-0.722	-0.815	1.162
IIIa-b	7100-8400 BP	-0.545	-0.985	0.709
IIIe	4300 BP	-0.861	-0.985	0.937
IV	4300 BP-Present	-0.399	.0.811	0.937
Present	Present	-0.282	-0.797	0.937

1972) using cenograms, but it appears that both the small and medium-sized portions of the mammalian faunas are underrepresented in collections. A somewhat different problem arises with the mid-Wisconsinan assemblage of January Cave, Alberta (Burns 1991). The small-mammal record is unusually rich and well sampled, and indicates that late Pleistocene diversity among small mammals was high at about latitude 50º N, but the larger medium-sized mammals appear to be too sparsely represented for cenogram analysis.

NORTHERN CLIMATIC FACTORS

Throughout the northern faunas analyzed here, diversity of small and medium-sized mammals is much lower than in faunas from lower latitudes. The comparison with previously analyzed cenograms of modern and ancient faunas from the Equator to about 40º

is striking. Strongly reduced diversity of medium-sized and small mammals in northern Pleistocene faunas is a real indicator of extreme conditions and is not simply an artifact of poor sampling. There are several cases where wet or dry screening has been carried out carefully, with adequate screen sizes and sample volumes (Repenning *et al*. 1964; Guthrie 1968; Morlan 1984, 1996). The results of these studies are consistent and indicate that the small mammals reported from a variety of assemblages represent actual diversity. Thus restricted diversity of small mammals cannot be explained away by invoking poor sampling.

Wilson (1974) found that species abundance among non-volant mammals in North America does not vary much from the tropics to about 50º north latitude, but drops off sharply north of 50º N. At 60º N, diversity of
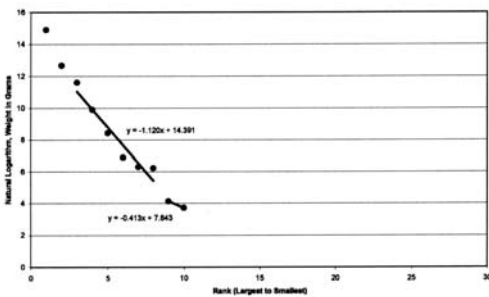

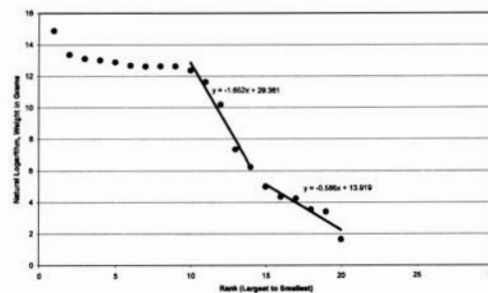Figure 8 Cenogram, fauna of locality CRH 15, middle of Unit 2a.

Figure 9 Cenogram, early Olyorian (Chukochyan) fauna.

quadrupedal mammals is about half that at 45º N. In mid-latitude assemblages Wilson (1974: 131-132) correlated decreased diversity of quadrupeds with less topographic variation and increased evapotranspiration. Although Wilson's negative correlations between diversity of quadrupeds and evapotranspiration were not significant for areas of high evapotranspiration, these factors surely are responsible for greatly reduced diversity in subarctic and arctic areas. Topographic relief alone cannot be responsible for the huge drop-off in northern diversity. Northern north America includes the highest mountains on the continent, but the northern mountains offer fewer additional niches than do their southern counterparts, partly because of increased dryness and lowered treelines and partly because of significant ice cover in the Yukon and Alaska. Thus evapotranspiration is the most likely factor reducing diversity in the North, perhaps coupled with variations in local conditions including glaciation and permafrost.

Some of the environments analyzed here are far more extreme than previously cited ones. The medium-sized mammal slope for tundra is nearly twice as great as the mean for other arid environments (Table 1). At first glance, this comparison seems to indicate a climate that is somehow more arid than arid. At least locally, however, rainfall in the tundra is not much less than in the boreal forest; for example, Shingle Point, on the coast of the Beaufort Sea, has an average annual precipitation of 173 mm while Old Crow, north

of the Arctic Circle but in the boreal forest, averages 192 mm. Clearly this indicator of aridity in the context of extreme, northern environments implies a variety of factors that account for changes in plant formations and differing levels of mammalian diversity. Perhaps the "more arid than arid" effects we are seeing in late Pleistocene faunas reflect the significantly different, weaker hydrologic cycle at the last glacial maximum (Yung et al. 1996). If so, then the consistent signal observed in all these faunas indicates that the same conditions were actually typical of most of the Pleistocene.

Legendre (1986: 203) hypothesized that "*the slope observed for the small-sized species could be an index of minimal temperatures: in more temperate conditions, there are fewer small species than found in tropical conditions.*" If this is the case then the relatively steep small-mammal slopes observed in modern taiga and tundra faunas indicate temperature extremes ranging even below those of the present day. This seems unlikely. On the other hand it is entirely possible that factors that have limited diversity among medium-sized mammals in the subarctic and arctic of Beringia have produced similar effects at both trophic levels. Slopes for small-mammal abundance appear to be consistent with both low extreme temperatures and arid climate.

CONCLUSIONS
Present-day Yukon faunas include a range of arid environments, with extremes apparently far more arid than at lower latitudes. In the
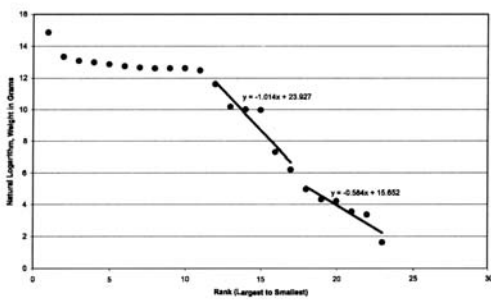

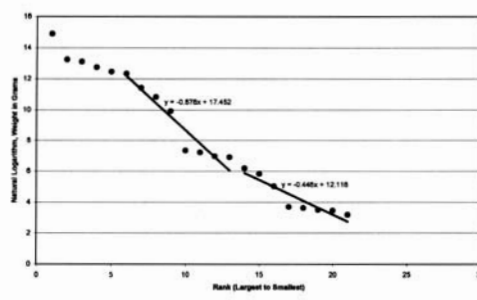Figure 10 Cenogram, late Olyorian (Akanian) fauna.

Figure 11 Cenogram, Riddell fauna, Saskatchewan.

cenograms, regression slopes for medium-sized and small mammals of present-day taiga and tundra are extremely steep, corresponding with the decrease in diversity of quadrupedal mammals north of 50° north latitude, which may in turn be linked to greatly increased evapotranspiration at those latitudes. Northern boreal forest environments are semiarid and vegetational formations are about as open as more southerly forests.

Cenograms of modern Yukon faunas complement and extend data derived by other authors from mid-latitude assemblages. Cenograms of seven Quaternary faunas of Beringia ranging from earliest Pleistocene to late Wisconsinan indicate the persistence of arid conditions and very open environments beginning by the early Pleistocene. These faunas all appear to represent environments as arid as present-day taiga, with a degree of openness of vegetational formations comparable with tundra. No forest-habitat faunas were detected.

Late Wisconsinan faunas of the Bluefish Caves (northern Yukon) and Tofty (interior of Alaska) appear to represent a mosaic of habitats with aridity similar to modern taiga and openness similar to tundra. Low diversity of small and medium-sized mammals in these faunas is consistent with the weaker hydrologic cycle of the last glacial maximum, which might have increased evapotranspiration even further that is the case today. A similar pattern of diversity persisted through major portions of the Pleistocene, according to the data at hand

The Riddell Local Fauna of Saskatoon, Saskatchewan accumulated in a semiarid and somewhat open environment, in agreement with SkwaraWoolf's (1980) assignment to the parkland ecotone according to other criteria. Late Wisconsinan to late Holocene faunas of Charlie Lake Cave, British Columbia also lived in an environment similar to the present-day open boreal forest, with little apparent change through time.

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