

Comparison of Temporal and Geographical Skull Variation  
among Nearctic Modern, Holocene and Late Pleistocene Gray  
Wolves (*Canis lupus*) (and selected *Canis*)

by

Gloria D. Goulet

A thesis  
presented to the University of Manitoba  
in fulfilment of the  
thesis requirement for the degree of  
Master of Science  
in  
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Winnipeg, Manitoba  
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COMPARISON OF TEMPORAL AND GEOGRAPHICAL SKULL VARIATION  
AMONG NEARCTIC MODERN, HOLOCENE AND LATE PLEISTOCENE GRAY  
WOLVES (Canis lupus) (and selected Canis)

BY

GLORIA D. GOULET

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba  
in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

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Gloria Goulet

For my children Sara Danielle and L. Christian Goulet, in  
recognition of their unwavering encouragement and support.

"The world needs an embodiment of the frontier mythology, the sense of horizons unexplored, the mystery of uninhabited miles. It needs a place where wolves stalk the strand lines in the dark, because a land that can produce a wolf is a healthy, robust and perfect land."

-Robert B. Weeden

## ABSTRACT

The hypothesis that current gray wolf geographic populations differ as a result of adaptation to varying ecological requirements in different habitats was tested. The relationship between variation in skull characteristics among temporal (late Pleistocene and Holocene) and modern geographical populations and prevailing environmental conditions was investigated in an attempt to determine the cause of variation (genetic divergence or physiological response).

Results indicated that size variation among modern gray wolf geographical populations was due to physiological adaptation to environmental conditions, while skull shape variation among temporally separated North American canid populations may be due to genetic divergence. Based on the results I suggest that wolf-like canids evolved allopatrically in both the Nearctic and Palearctic. Further, the modern Nearctic gray wolves included here were descendants of Eurasian wolves that spread to North America across the Beringian land bridge during intermittent Pleistocene glaciation events.

Evidence suggests that the great plains subspecies (*C. l. nubilus*) evolved with the prairie habitat that developed in mid-latitude North America at the end of the latest glaciation. Despite the lack of evidence for heritability of distinctive traits, subspecies designation should be

retained because of evidence indicating that the plains gray wolf was ecologically distinct from gray wolves inhabiting adjacent regions. I suggest that ecological preferences communicated from parent to offspring likely contributed to the temporal maintenance of size variation among post-Pleistocene gray wolf populations.

Similarities in skull shape characteristics between Rancholabrean dire wolves (*C. dirus*) and gray wolves of Eurasian ancestry suggest that the two species were closely related. Based on the results I suggest that the dire wolf was a "hypermorphic" form (Geist, 1987) of the gray wolf, that evolved in response to abundant resources, more equable climatic conditions and possible interspecific competition with contemporaneous late Pleistocene predators.



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My children Sara and Christian encouraged and supported me through all stages of my education and I dedicate this thesis to them. My former spouse Lorne was equally supportive.

A number of museum staff made my visit to institutions with collections pleasant as well as productive. Dr. Bill Akersten (ISUM), Dr. Larry Martin and Bill Chorn (KUVVP), the mammal collections staff at the University of Kansas Museum of Natural History, Dr. Dick Cannings (UBC), Linda Gordon (USNM), David Campbell (CMN) and David Baron (SMNH). I am indebted to Chris Shaw (LACM) for providing me with extensive information as well as specimen measurements and to Dr. Carron Meaney (DMNH) for personally transporting valuable specimens. Ross Lilly and Dr. Jim Clayton (DFO) and Jack Dubois (MMN) provided helpful information. Lorne Gould, Jane Rawluk and many members of the Speleological Society of Manitoba provided volunteer assistance and/or guidance through Manitoba's karst formations. G. Dyck very kindly translated portions of Bibikov's (1985) text.

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## LIST OF ABBREVIATIONS

mya - million years ago  
y.B.P.- years before present

### Institutions

CMN - Canadian Museum of Nature  
DMNH - Denver Museum of Natural History  
ISUM - Idaho State University Museum  
KU - University of Kansas Museum of Natural History  
KUP - University of Kansas, Vertebrate Paleontology  
MMN - Manitoba Museum of Man and Nature  
SMNH - Saskatchewan Museum of Natural History  
UBC - University of British Columbia Zoology Museum  
UCM - University of Colorado Museum  
UM - University of Manitoba (Mammalogy)  
USNM - U.S. National Museum of Natural History  
LACM - George C. Page Museum

### Locality Codes

#### Canadian Provinces

AB - Alberta  
BC - British Columbia  
MB - Manitoba  
NT - Northwest Territories  
SK - Saskatchewan  
YK - Yukon

#### American States

AK - Alaska  
AZ - Arizona  
CA - California  
CO - Colorado  
ID - Idaho  
KS - Kansas  
KY - Kentucky  
MD - Maryland  
MT - Montana  
NB - Nebraska  
ND - North Dakota  
NM - New Mexico  
OK - Oklahoma  
SD - South Dakota  
WY - Wyoming

#### Countries

MX - Mexico  
RU - Russia

## INTRODUCTION

Patterns of geographic variation among extant populations of a species are of interest to investigations of systematics and evolution. Darwin and Wallace were the first to recognize the value of evident population differentiation to studies of evolutionary change (Futuyma, 1986). Populations that vary among different geographical regions are defined as *subspecies* (*i.e.* "a set of populations of a species that share one or more distinctive features and occupy a different geographical area from other subspecies", Futuyma, 1986, p. 555).

Since subspecies are identified from evidence of the heritability of observed trait variation (Mayr et al., 1953), it is important, although frequently problematic, to determine whether the differentiation is due to genetic divergence or phenotypic (non-heritable) response to ecological conditions. While genetic divergence is expected to occur among geographically isolated populations of a species, as a result of genetic drift, mutation and natural selection (Mayr et al., 1953), Eldridge (1985) proposed that genetic alteration can also appear in response to selective pressure in the absence of isolation. Conversely, phenotypic variation among geographic populations may occur where no genetic alteration is evident (*i.e.* phenotypic expression of a genotype varies with prevailing conditions that regulate the rate of biochemical reactions) (Futuyma,

1986).

In a recent investigation into the causative factors of morphological variation in a widely-distributed mustelid (*Mustela erminea*), Eger (1990) determined that population variation in skull size was due to environmental conditions, while skull shape variation resulted from previous isolation in glacial refugia. In contrast, Thorpe (1991) found that morphological differentiation among, within-island Tenerife gecko (*Tarentola delalandii*) populations resulted solely from response to varying ecological conditions. In addition, Geist (1992) recently proposed that the extant North American bison (*Bison bison*) has no subspecies, since the modern forms currently recognized as wood bison (*B. b. athabasca*) and plains bison (*B. b. bison*) were primarily distinguished by coat characteristics that are alterable within one year following a change in diet.

Previous investigations of geographical variation among modern North American gray wolves (*Canis lupus*) resulted in the recognition of 24 subspecies (Hall, 1981), based largely on the work of Goldman (1944), who observed character differences in body size, color of the pelage, dentition and skull shape among populations inhabiting various geographical regions. The validity of Goldman's subspecific designations were subsequently questioned because he did not apply modern taxonomic and statistical methods, and included small sample sizes from some geographical regions (Rausch,



1953; Jolicoeur, 1959; Kelsall, 1968; Skeel and Carbyn, 1977; Pedersen, 1982; Nowak, 1983).

Subsequent investigators have attributed differentiation among gray wolf populations to; 1) adaptation to environmental conditions (Skeel and Carbyn, 1977) and isolation in glacial refugia (Jolicoeur, 1959; Nowak, 1983); 2) latitudinal effects and prey size (Alaskan wolves) (Pedersen, 1982); 3) correlation of body size to size of prey (Schmitz and Kolenosky, 1985); and 4) hybridization with coyotes (*C. latrans*) (Kolenosky and Standfield, 1975; Lehman et al., 1991). Recent genetic evidence of coyote mtDNA genotypes in wolf phenotypes from eastern and southern regions of North America (Lehman et al., 1991; Wayne and Jenks, 1991) was interpreted by Lehman et al. (1991) as confirmation that hybridization between the three extant North American *Canis* species (i.e. *C. lupus*, *C. latrans* and *C. rufus*) occurred both recently and in the distant past.

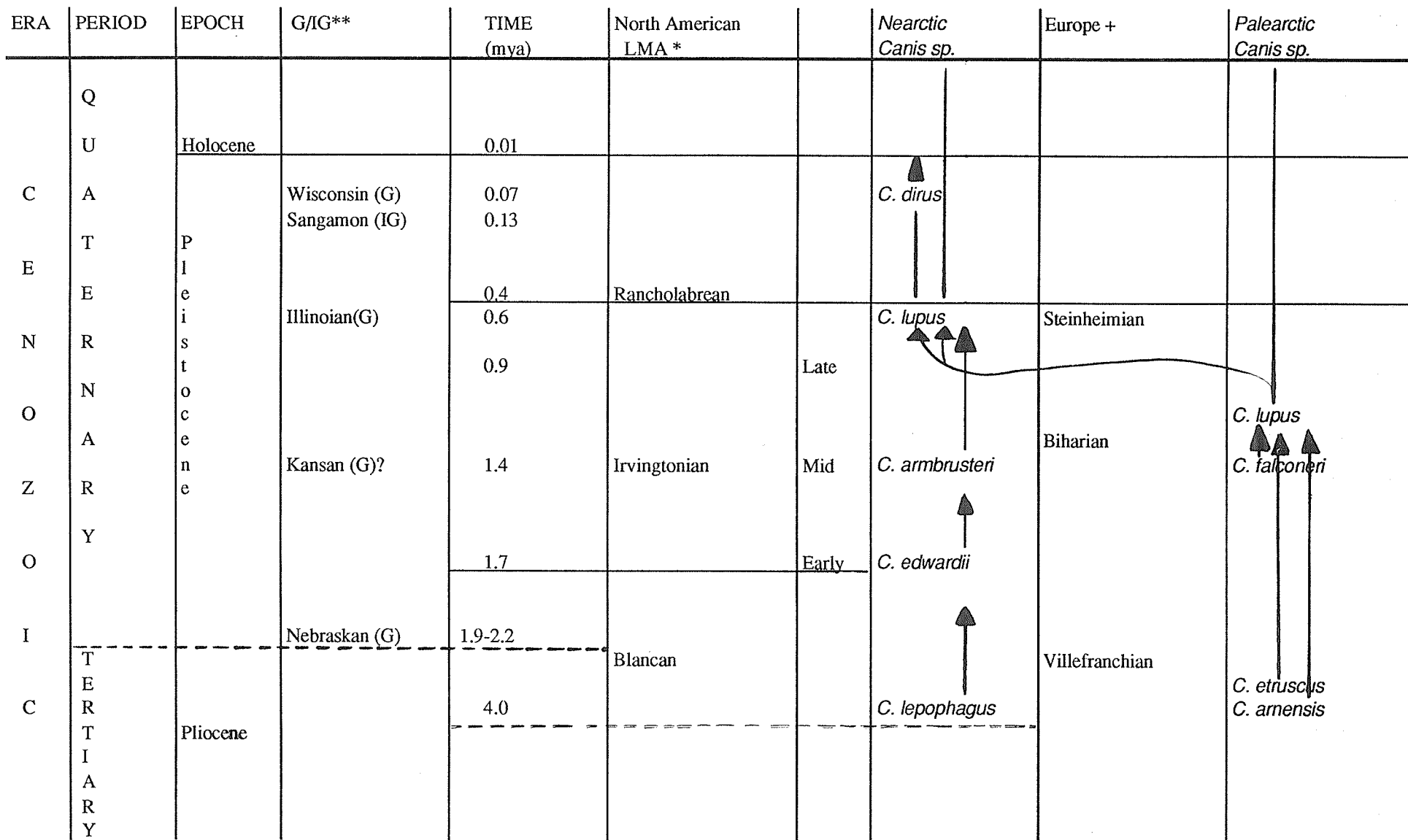
The fossil record indicates that canids arose in North America during the early Oligocene (approximately 35 mya), from a small, digitigrade, fox-like animal (*Hesperocyon*) (Martin, 1989) that subsequently spread to the Old World during a period when the continents were joined by a land bridge (Carroll, 1988).

North American fossil faunas have been utilized to define geological time intervals known as Cenozoic Land

Mammal Ages (Savage and Russell, 1983), that are generally correlative with Old World deposits. Land Mammal Ages are defined by the first and last appearance of new taxa in the fossil record and characterized by the interval's faunal composition (Woodburne, 1987). The fossil record for both Eurasian and North American *Canis* has been generally interpreted in the sequence shown in Figure 1. A late Pliocene coyote-like canid, with a holarctic distribution is the apparent ancestral form that gave rise to both the wolf and coyote lineages (Nowak, 1979; Kurtén and Anderson, 1980). Although virtually indistinguishable, the ancestral *Canis* contains two distinct species; Palearctic *C. arnensis* and Nearctic *C. lepophagus* (Kurtén and Anderson, 1980) (Figure 1).

Old World *C. arnensis* gave rise to the small late Villefranchian wolf, *C. etruscus* (Kurtén and Anderson, 1980), while *C. lepophagus* was ancestral to North American coyotes and to the early Irvingtonian wolf-like *C. edwardii* (Kurtén and Anderson, 1980). *C. edwardii* closely resembled the Late Villefranchian *C. etruscus* (Kurtén and Anderson, 1980), generally accepted as the progenitor of *C. lupus* (Nowak, 1979). *C. edwardii* gave rise to the mid-Irvingtonian *C. armbrusteri*, that was morphologically similar to the Palearctic *C. falconeri* (Kurtén 1968). The resemblance between the latter two species led Kurtén and

Figure 1. The approximate geological age and range of selected Nearctic and Palearctic wolf-like *Canis*. Arrows indicate disappearance from the fossil record. Dashed line (---) indicates equivocal boundary between intervals; LMA = North American Land Mammal Age; G/IG\*\* = glacial/interglacial, after Lundelius et al., 1987 and Kurtén and Anderson, 1980; ? = dating of interval is indefinite; \* = after Woodburne, 1987; + = after Savage and Russell, 1983; fossil record of *Canis sp.* = after Kurtén, 1968; Nowak, 1979; Kurtén and Anderson, 1980; Bibikov, 1985.



Anderson (1980) to suggest they may be conspecific. The fossil record of *Canis* from the late Pliocene through the Pleistocene suggests that temporally separated bi-directional faunal movement across the Bering Land Bridge (reviewed by Lundelius et al., 1987) may have greatly influenced the evolution of canids, resulting in the current taxonomic confusion surrounding extant North American canids (i.e. *C. lupus*, *C. rufus* and *C. latrans*).

Gray wolves that morphologically resembled modern forms, first appeared in Old World faunal assemblages about one million years ago (Kurtén, 1968) and later in North American fossil faunas, suggesting that the gray wolf spread to this continent across the Bering Land Bridge during a period of glaciation (identified as the Illinoian) approximately 600,000 y.B.P. (Nowak, 1979). Although recent evidence suggests that there were far more Pleistocene glacial intervals than the four previously recognized (Nebraskan, Kansan, Illinoian and Wisconsin), the above nomenclature was retained here for the purpose of clarification because the time intervals they refer to are widely known and understood.

*C. lupus* was widely distributed but relatively rare on this continent during the following interglacial (Sangamon, approximately 130,000-80,000 y.B.P., Hodgson, 1991). Dyke and Prest (1987) suggest that the fauna inhabiting ice-free regions of North America during the succeeding glaciation

(Wisconsin), which began (approximately) 80,000 y.B.P. in northern latitudes (Hodgson, 1991) and 70,000 y.B.P. in mid-latitude North America (Lundelius et al., 1987), may have been isolated for approximately 11,000 years. Conversely, other findings indicated that gene flow between the two regions was relatively unrestricted throughout the Wisconsin (Lundelius et al., 1987).

The site of origin of the Rancholabrean dire wolf (*C. dirus*) has not been satisfactorily explained to date due to the relatively instantaneous appearance of this species in mid- and southern latitude Rancholabrean deposits (from south of 51° N. latitude to Talara, Peru in South America) (Churcher, 1959; Martin, 1974; Nowak, 1979; Kurtén and Anderson, 1980). The lack of dire wolf fossils from Eurasia and northern North American latitudes suggests that *C. dirus* arose and evolved in the New World from either North American (e.g. *C. armbrusteri*, Nowak, 1979), Eurasian immigrant (e.g. *C. lupus*, Martin, 1974), or South American (e.g. *C. nehringi*, Churcher, 1959) canid stock. However, Churcher (1959) observed that the large fossil wolves recovered from Talara, Peru were more similar to dire wolf specimens from Rancho La Brea, California, than to *C. nehringi*, suggesting that the two South American species were only distantly related. Although the origin of the dire wolf is problematic, the large number of recoveries from Rancholabrean sites (Nowak, 1979) suggests that this

form was the dominant North American wolf during the late Pleistocene.

Paleoclimatic evidence indicates that the northwestern refugium was an extension of an open habitat, referred to as the "mammoth steppe" by Guthrie (1984), that dominated Europe and Eurasia during the late Pleistocene (Guthrie, 1984), while semi-open vegetation interspersed with woodland areas prevailed south of the glaciers (Sims, 1988). In North America, the mammoth steppe was gradually replaced by forests during the late Wisconsin (Guthrie, 1990). As well, a shift towards an open grassland habitat occurred in the Great Plains region of mid-latitude North America, due to an increase in aridity and ambient temperature which resulted in drought and recurrent fires across the relatively level plains (Sims, 1988).

Recently reported evidence of genetic divergence among widespread North American gray wolf populations indicates that at least four mitochondrial DNA (mtDNA) genotypes can be traced to a common ancestor, likely in the Palearctic (Lehman et al., 1991). Mitochondrial DNA is useful for studies of species divergence due to a relatively high average substitution rate and clonal, maternal inheritance in nearly all cases, in mammals (Wilson et al., 1985). The rate of sequence divergence for a number of groups has been determined from correlation with fossil evidence to be approximately 2% per million years (Wilson et al., 1985).

The rate of intraspecific sequence divergence in canids is problematic, however, due to the possible retention of primitive genotypes and an increase in the rate of mutation during periods of rapid climatic change (Wayne et al., 1990). This suggests that mtDNA phylogenies may not always reflect species phylogenies in canids (Wayne et al., 1990). The four North American genotypes, as well as a fifth genotype that occurs in gray wolves from Iraq, can be traced to a common ancestor (Lehman et al., 1991), suggesting that: a) gray wolves may retain primitive mtDNA, as there is no evidence of subsequent divergence among the four genotypes; or, b) the diverged forms of those genotypes (as well as additional genotypes) have disappeared due to extensive gray wolf extirpation (Young, 1946) in North America. The lack of confirmation of a constant rate of intraspecific mtDNA divergence in canids suggests that evidence of a correlation between morphological divergence and climatic change may be useful for determining the chronology of variation in modern gray wolf populations.

I tested the hypothesis that modern gray wolf geographic populations differ in skull characteristics in relation to prevailing environmental conditions, as a result of physiological response to varying ecological requirements in different regions. I expected that temporally separated gray wolf populations would differ in skull traits that were correlative with prevailing conditions. Finally, I compared



skull characteristics among modern and fossil gray wolves and selected fossil *Canis* to examine evolutionary trends among the various groups.

## MATERIALS AND METHODS

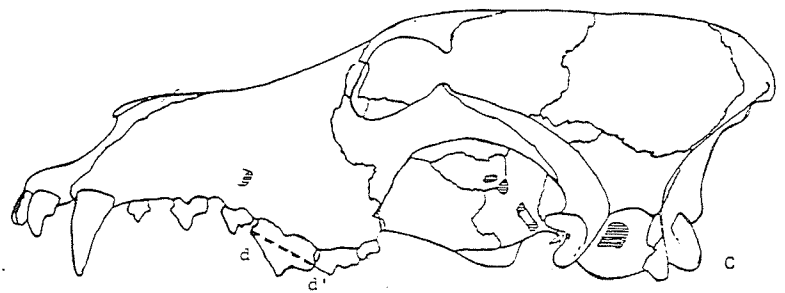
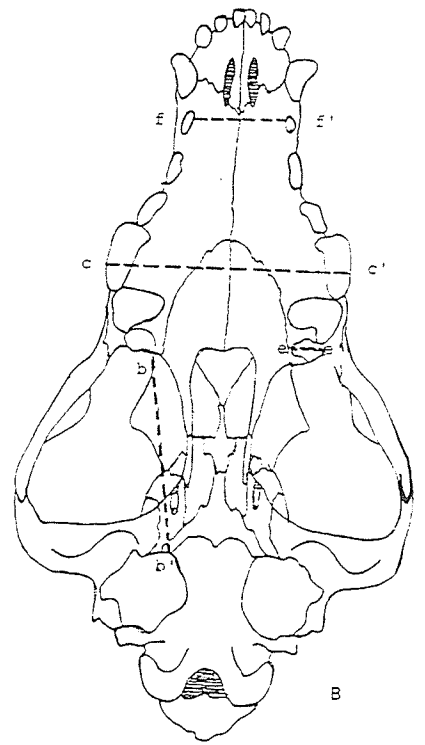
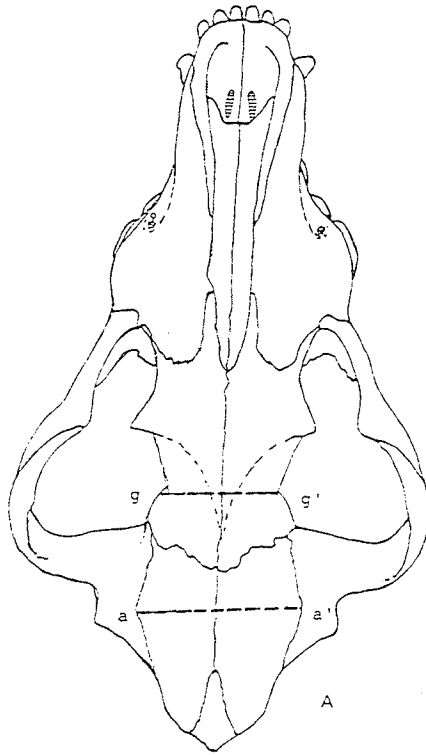
### Specimens and Measurements

North American institutions that maintain natural history collections were canvassed by mail to assess the number of available fossil and modern gray wolf specimens (The Official Museum Directory, 1990, The American Assoc. of Museums, National Register Publishing Co.; and, The Official Directory of Canadian Museums and Related Institutions, 1990, published by Canadian Museums Association).

Measurements were obtained from 246 gray wolf, *C. lupus*, skulls, 234 mandibles, and one dire wolf, *C. dirus*, skull. Lower jaw elements were subsequently deleted from the analyses due to a relatively high incidence of missing, broken, worn or chewed processes and difficulty in obtaining accurate measurements on some curved surfaces. A number of fossil and modern specimens with missing elements were also eliminated from the analyses.

Dial callipers were used to obtain measurements (to the nearest 0.1 mm) of seven skull characters from adult specimens only (Figure 2) (See Appendix 1 for specimen collection information and dimensions). Skull element measurements for the two hundred and nineteen specimens ultimately included in the analyses were acquired by: 1) original data obtained by author; 2) previously published data (Nowak, 1979); and, 3) data obtained from staff at the George C. Page Museum, California, Appendix I).

Figure 2. *Canis* skull elements included in the analyses.  
A = dorsal view; B = ventral view; C = lateral view. a-a' = BRNCS; b-b' = M<sup>2</sup>BL; c-c' = MAXTH; d-d' = P<sup>4</sup>CLN; e-e' = M<sup>2</sup>CWT; f-f' = PALP<sup>1</sup>; g-g' = POCNS. See Material and Methods for description of measurements.



The measurements used were; (1) braincase width (BRNCS) - maximum width of braincase across the level of parietotemporal sutures; (2) length from  $M^2$  to auditory bullae (M2BL) - minimum distance from posterior edge of alveolus of  $M^2$  to depression in front of auditory bullae at base of muscular process; (3) maximum crown width across upper cheek teeth (MAXTH) - greatest breadth between labial surfaces of most widely separated upper cheek teeth ( $P^4$  or  $M^1$ ); (4) crown length of  $P^4$  (P4CLN) - maximum anteroposterior length of crown measured from labial aspect; (5) crown width of  $M^2$  (M2CWT) - maximum crown width of  $M^2$ ; (6) palatal width at  $P^1$  (PALP1) - minimum width between alveoli of first upper premolars; and, (7) postorbital constriction (POCNS) - least width across frontals at constriction behind postorbital processes.

Adult gray wolves (of both sexes) were identified by full closure of the basioccipital-basisphenoid suture and fully erupted canines, criteria previously found to be approximately 90% accurate for determining the age of red foxes (*Vulpes fulva*) (Gilbert, 1973). Mech (1970) observed that gray wolf pups are morphologically indistinguishable in size from older pack members by October of the year in which they are whelped. Canines are fully erupted and skulls have reached maximum dimensions by the time gray wolves are 15 months old (Nowak, 1979). In order to examine the variation

between juvenile and adult specimens shown by the characters, I used a series of 43 gray wolves of various ages collected during 1949-1955 from Manitoba locations (UBC, Appendix 1).

Gray wolves are sexually dimorphic (Jolicoeur, 1959; Skeel and Carbyn, 1977). Males are generally larger than females, although Goldman (1944) found that sexual size dimorphism was less evident in some geographic populations (e.g. the prairie wolf, *C. l. nubilus*). As this present study was concerned with variation among temporal and spatial populations, differences in size between the sexes was considered to be a component of the population variation, since the sex of all fossil and some modern specimens was not available, and sexual size dimorphism in ancient populations should not be assumed.

The possibility that Holocene and modern specimens may represent dogs (*C. familiaris*) could not be ignored (Walker and Frison, 1982). Although unequivocal identification of a specimen as a gray wolf is problematic, due to the close relationship between the two species (Olsen, 1985), evidence of intentional dental modification (truncation of the canines, presumably to prevent injury to handlers and other dogs), as well as overcrowding and extensive tooth decay will often be apparent in adult subfossil domestic dogs (Walker and Frison, 1982). For this reason specimens from native archaeological sites were not utilized. Skulls from

fur-trading forts (e.g. Fort Union, Montana, and Fort Carlton, Saskatchewan) were closely examined and utilized if dentition was relatively robust and there was no evidence of deliberate tooth modification or extensive decay. A large number of gray wolf specimens currently housed in the U.S. National Museum that were collected from Fort Union during 1856 and 1857 were included in the analyses after personal examination, despite previous contention that they may be domestic dogs (Walker and Frison, 1982). The specimens were relatively small, compared to wolves from northern regions, which may have contributed to the problem in identification. I am confident however that the Fort Union specimens (n=17) I examined and included in the following analyses represent gray wolves as: 1) they exhibit no dental decay or modification; 2) it is unlikely that such a large number of dogs would have been identified as gray wolves by experienced Biological Survey collectors (Lt. G.K. Warren and Dr. V. Hayden), and 3) it is unlikely that so many dog skulls would have been brought to the fort for trading, when gray wolves were apparently highly visible and plentiful on the open plains (Young, 1946; Dary, 1974). The canid skulls from Fort Carlton (stored in SMNH) appeared to represent both dog and gray wolf. Historical documentation shows that cattle kept outside the fort were frequently attacked by wolves (Carbyn, 1984), suggesting that the canids collected from that site may represent animals killed by the fort's

inhabitants for livestock protection. Two of the Fort Carlton specimens that I examined were included in the analyses.

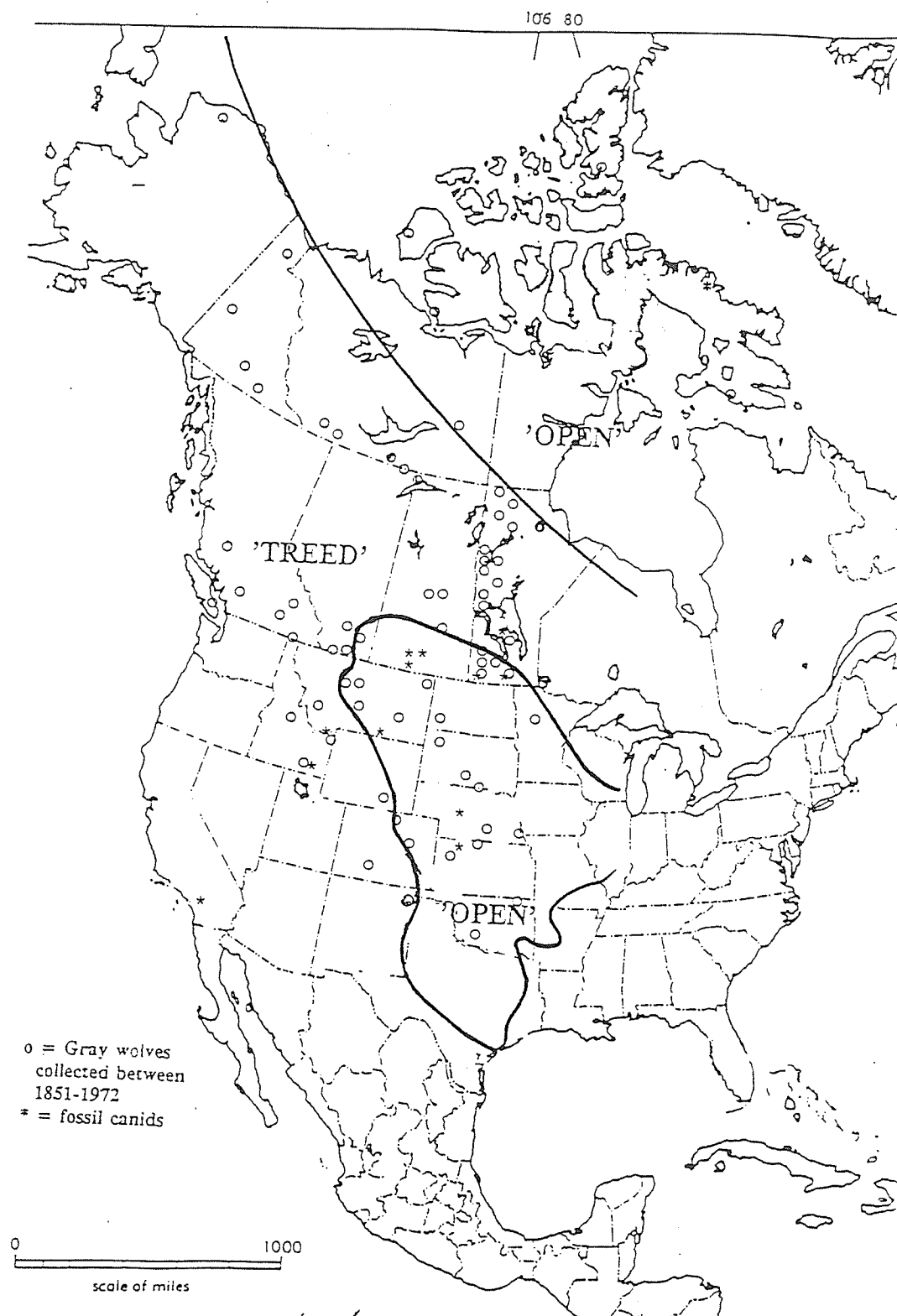
Previously published cranial and dental measurements (see Nowak, 1979) of late Pleistocene gray wolf, dire wolf (*C. dirus*), coyote (*C. latrans*) and Irvingtonian Armbruster's wolf (*C. armbrusterii*) were included in the analyses to increase the sample size of fossil specimens.

### **Specimen categorization**

Geographical and temporal variation was examined by grouping specimens into units, based on collection location, collection date (for living wolves), geological age (for fossil and subfossil wolves), and major vegetation zones inhabited (modern populations). Modern specimens were assigned to 'north' (collected north of 50° N.Lat.) or 'south' (collected south of 50° N.Lat.); 'open' (collected from grassland and/or arctic tundra habitats) or 'treed' (collected from intermontane and forest habitats) (Barbour and Billings, 1988); and 'early' (collected from 1851 to 1920) or 'late' (collected between 1921 and 1972) groups in order to assess latitudinal effects (north and south), major habitat zones (open and treed), and the effects of human disturbance (early and late) on skull variation (Figure 3 and Appendix I). Wolves collected from 1851-1920 were expected to represent adequately the North American (pre-European contact) gray wolf geographical populations since they



Figure 3. Localities of *C. lupus* collected to the north and south of 50° N. latitude from 'open' and 'treed' habitats. Because of the scale of the map, the marker represents more than one specimen from some sites. Open circles (o) indicate localities where gray wolves were collected between 1851 and 1972; asterisks (\*) indicate sites where canid fossils were recovered.



comprise specimens collected during government initiated wolf removal programs (Young, 1946).

Nowak (1983) previously found that larger gray wolves were generally collected to the north of the 49th parallel. However, as the grassland habitat currently extends north of the Canadian-American border into Manitoba, Saskatchewan and Alberta (and likely extended even farther north during the Holocene, Ritchie and Yarranton, 1978), I designated the 50th parallel as the division between 'north' and 'south' units in order to include more of the prairie habitat within the 'south' group.

Fossil gray wolf specimens were assigned to a Holocene ( <10,000 y.B.P. to 1851) or late Pleistocene ( <41,000 to >10,000 y.B.P.) group on the basis of data accompanying the specimen (Appendix I).

### **Statistical Analysis**

Multivariate analysis was utilized to describe the relative statistical positions of defined temporal and spatial groups. Principal Components Analysis reduces a large number of correlated variables to a few uncorrelated factors that account for most of the observed variation in the data. The indices are ordered so that principal component one (Prin1) explains the largest amount of variation, principal component two (Prin2) the second largest amount, and so on. Lawrence and Bossert (1967) previously suggested that 20 individuals were required to

account for 'within' gray wolf population variation. Due to the descriptive nature of the statistical program (SASPC PrinComp), and the relatively small sample sizes of some units, the significance of the results was not tested.

While the small sample sizes of some fossil groups preclude drawing conclusions based on the results, they are, however, useful for indicating trends in population variation.

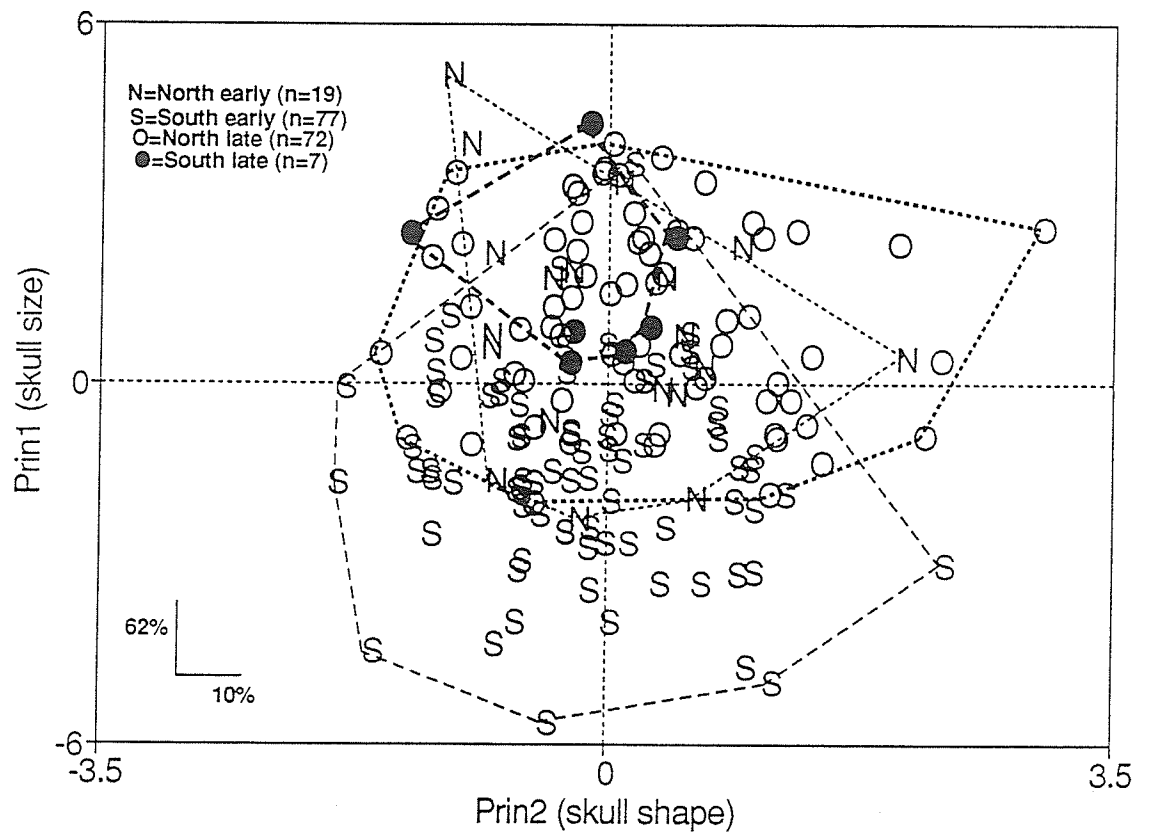
## RESULTS

The (approximately) equal positive eigenvector loadings obtained on Prin1 in the following analyses indicates that the first principal component is an index of overall size variation. Prin2 explains a specified proportion of the remaining variation between individuals, which is due to differences in skull shape. The eigenvector loadings on Prin2 are weighted to indicate which of the highly correlated variables provide the greatest contribution to the observed variation in each of the following analyses (Appendix II). Positive and negative values indicate how they are correlated.

### **Geographical Variation in Modern Gray Wolf Skulls (1851-1972) (n=175)**

Sixty-two percent of the total variation among individuals was due to differences in overall size (Prin1). The remaining variation was due to skull shape variation (Prin2). Ten percent of that difference was accounted for by a negative correlation between cranial and rostral width (and the relative size of the upper carnassial) (P4CL) (Appendix II, Table A). Gray wolves with a wide cranial region, narrow nose and small P<sup>4</sup> scored highest on Prin2 (Figure 4). Gray wolves collected from north of 50° North latitude were generally larger than 'south' specimens obtained prior to 1921 (Prin1) (Figure 4). 'Late' 'south' gray wolves were also larger than 'early' 'south' specimens

Figure 4. Plot of first and second principal components scores from a multivariate analysis of seven skull characters for 175 *C. lupus* assigned to four descriptive units (collected north (N) and south (S) of 50° N. lat., from 1851 to 1921; and north (O) and south (●) of 50° N. lat., from 1921 to 1972). Polygons enclose scores for all individuals within a descriptive group. Sixty-two percent of the variance was explained by Prin1 and 10% of the remaining variation was accounted for on Prin2. The eigenvector values of individual variables is indicated in Appendix II, Table A.



(Figure 4).

Skull shape was randomly distributed among the four units in this analysis (Figure 4).

**Modern Gray Wolf Skulls (1851-1920) (n=96)**

The ninety-six observations were subjected to three separate analyses; 1) sexual size dimorphism; 2) variation between 'north' and 'south' descriptive units; and 3) correlation of variation with broad habitat types; *i.e.* 'open'- specimens collected from tundra and grassland regions, and 'treed' - gray wolves taken in intermontane and forested regions.

Sexual size dimorphism, previously recorded by Jolicoeur (1959), and Skeel and Carbyn (1977), was assessed to verify the validity of this data set. Males were found to be larger than females (Prin1)(Figure 5). The extensive overlap in skull shape variation between both sexes indicated that shape was not sex related (Prin2)(Figure 5).

The first principal component (Prin1) explains 60% of the total variation (an index of size), and the second component (Prin2) accounts for 11% of the remaining variation which is due to skull shape differences. The largest skulls scored higher on Prin1, and high scores on Prin2 represented specimens with wide crania, and small cheek teeth (Figures 6 and 7) (Appendix II, Table B).

Specimens collected from 'south' areas were more variable in skull shape than those from the 'north'



Figure 5. Plot of first and second principal components scores from a multivariate analysis of seven skull characters for 24 male (V) and 17 female (O) *C. lupus* collected from 1851 to 1920 in the western half of North America. Polygons enclose scores for all individuals within a descriptive group. Sixty percent of the variance was explained by Prin1 and 11% of the remaining variation was accounted for on Prin2. The eigenvector values of individual variables is indicated in Appendix II, Table B.

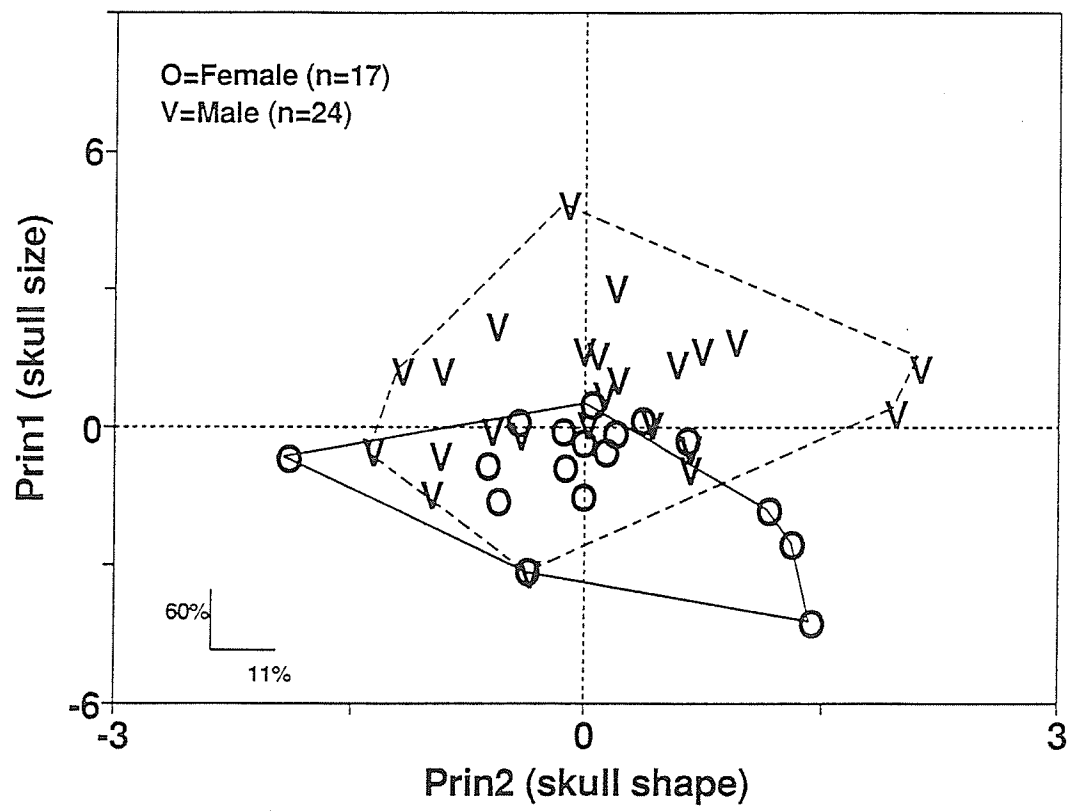


Figure 6. Plot of first and second principal components scores from a multivariate analysis of seven skull characters for *C. lupus* collected from 1851 to 1920, to the north (●) and south (○) of 50° N. latitude. Polygons enclose scores for individuals within a descriptive group, excluding the anomalous points that are indicated by arrows (the large south skulls that are located within the 'north' polygon are from southern Alberta and Montana; the small north skulls that are observed in the 'south' grouping represent specimens from Ft. Carlton, Saskatchewan, and Arctic tundra localities). Sixty percent of the variance was explained by Prin1 and 11% of the remaining variation was accounted for on Prin2. The eigenvector values of individual variables is indicated in Appendix II, Table B.

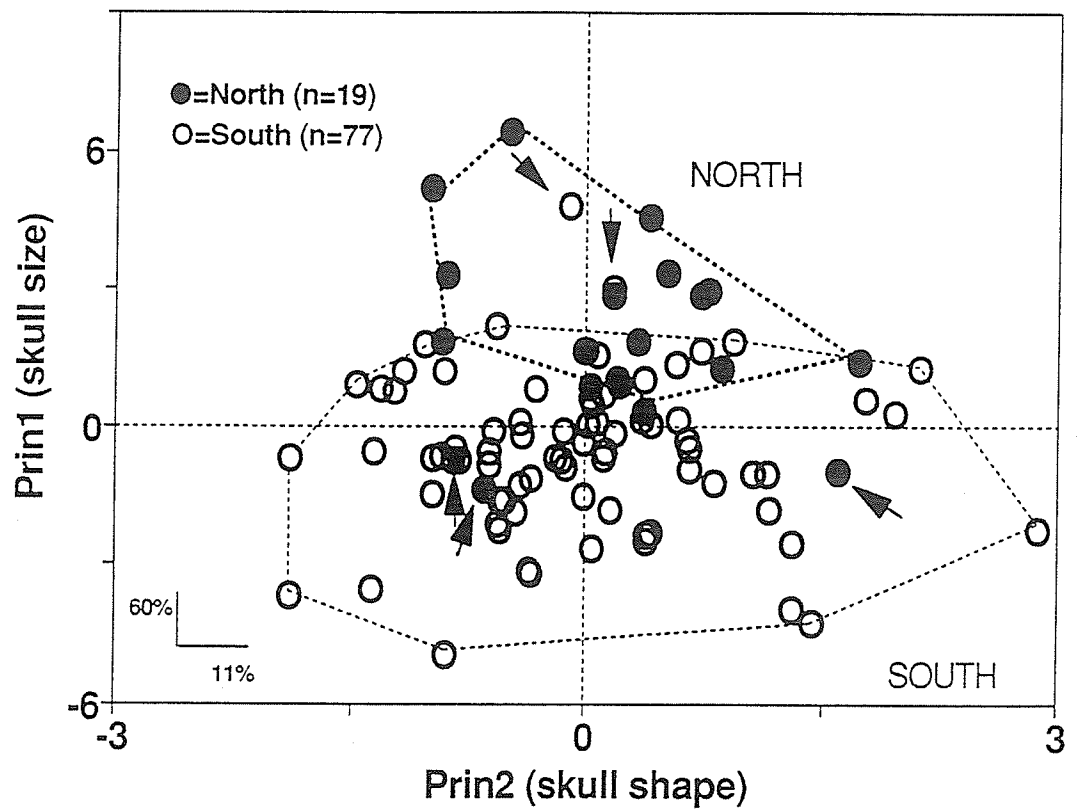
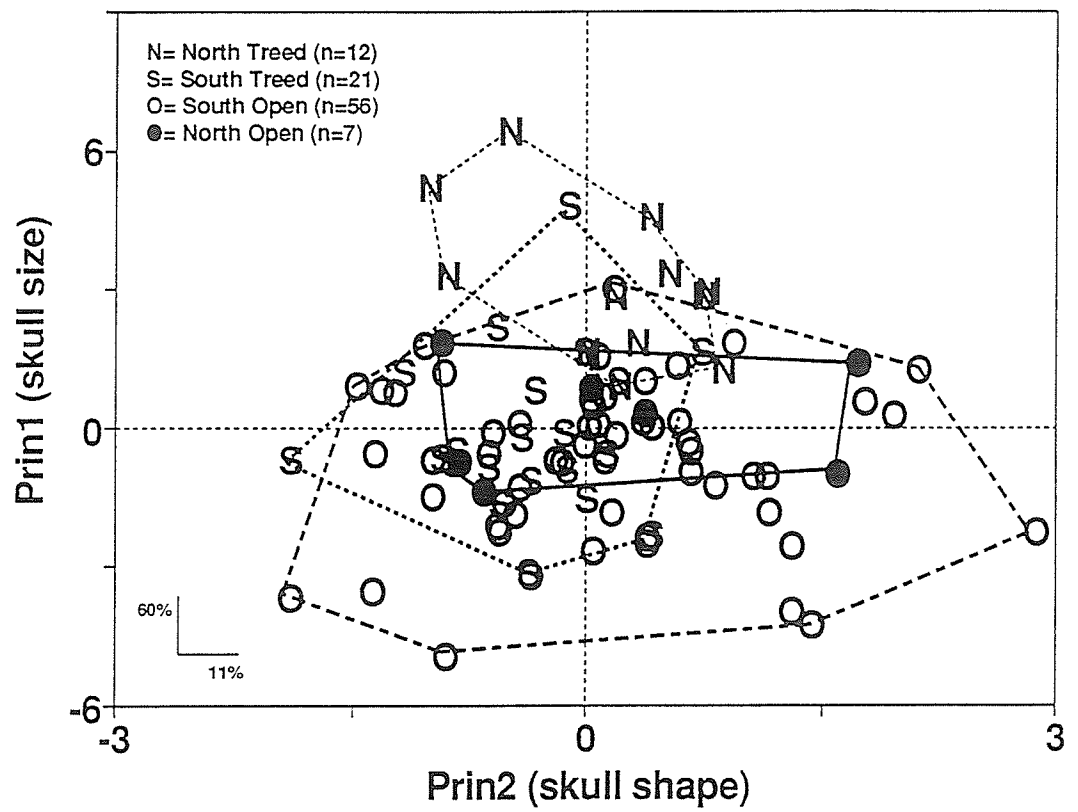


Figure 7. Plot of first and second principal components scores from a multivariate analysis of seven skull characters for *C. lupus* collected from 1851 to 1920 from habitats that are (predominately) open (●,O) and treed (N,S). Polygons enclose scores for all individuals within a descriptive group. Sixty percent of the variance was explained by Prin1 and 11% of the remaining variation was accounted for on Prin2. The eigenvector values of individual variables is indicated in Appendix II, Table B.



(Figure 6). Specimens from forest and intermontane regions were less variable in skull shape than those from open habitats (Figure 7).

Anomalies included two large 'south' specimens from southern Alberta and Montana (collected in 1896 and 1906, respectively), that were more similar to 'north' gray wolves; and three relatively small 'north' skulls collected from prairie and tundra localities that resembled the majority of 'south' gray wolves in size (Figure 6).

The largest gray wolves were collected from forested regions in the Northwest Territories, Yukon, Manitoba, Alberta and Montana; and the smallest from habitats with open vegetation in Montana, Oklahoma, Nebraska and Colorado.

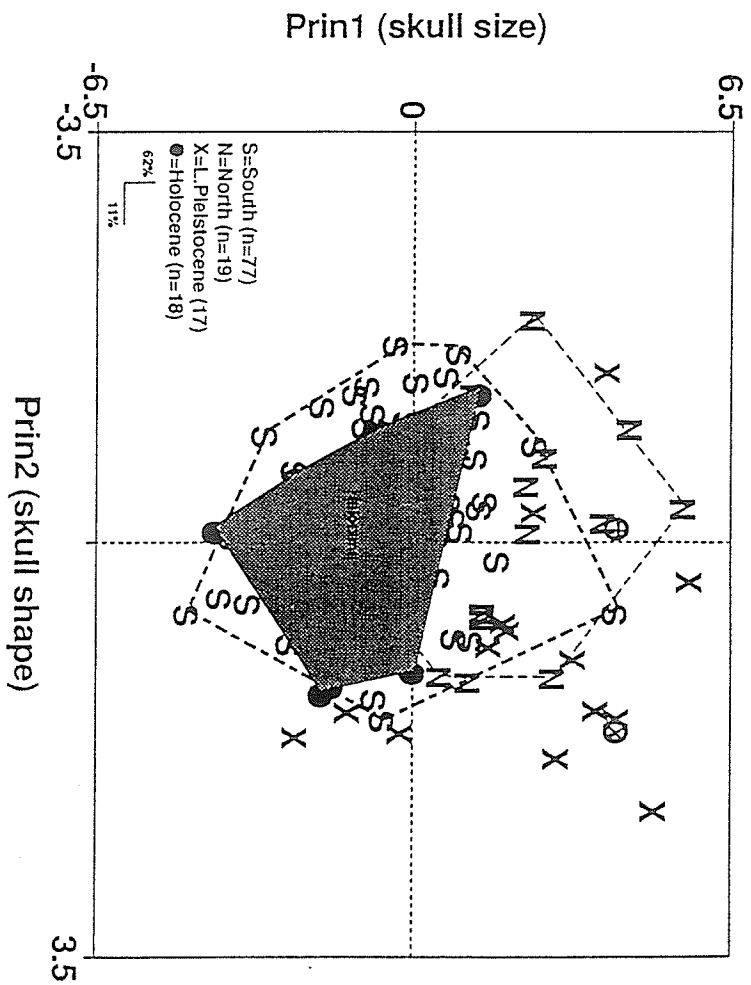
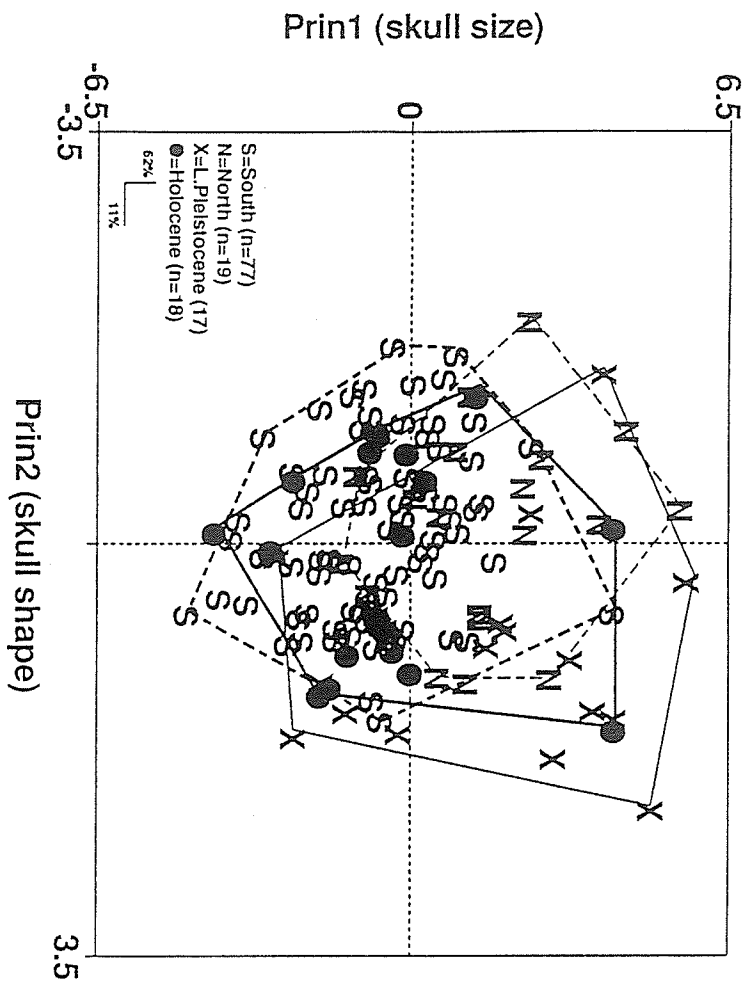
**Temporal variation among Gray Wolf Skulls (n=131)**

Prin1 accounted for 62% of the total variation (size index) among fossil and recent gray wolf skulls. Prin2 explained 11% of the remaining variation (due to skull shape difference) among the specimens. The largest specimens had the highest scores on Prin1, while gray wolves with a wide, short cranium, relatively large cheek teeth and a narrow rostrum scored highest on Prin2 (Figure 8, a and b) (Appendix II, Table C).

There was extensive overlap in size between the four descriptive units, although late Pleistocene and 'north' units were generally larger than Holocene and 'south' descriptive groups (Figure 8a). Skull shape traits among

Figure 8. Plot of first and second principal components scores from a multivariate analysis of seven skull characters for 131 *C. lupus* assigned to four descriptive units (modern specimens collected from north (N) and south (S) of 50° N.lat., between 1851 and 1920; fossil specimens from Holocene deposits between approximately, 10,000 y.B.P. and 1850 (●); and fossils from late Pleistocene deposits between 40,000 to 10,000 y.B.P. (approximately) (X); a, polygons enclose scores for all individuals within a descriptive group; b, a filled polygon encloses scores for all Holocene specimens, excluding probable anomalies: ⊕ = collected from a cave in Manitoba's interlake region (MMM N V2237) that is more similar to modern 'north' specimens; and, ⊗ = collected from Moonshiner Cave, Idaho, that is more similar to late Pleistocene gray wolf specimens. Sixty-two percent of the variance was explained by Prin1 and 11% of the remaining variation was accounted for on Prin2. The eigenvector values of individual variables is indicated in Appendix II, Table C.





late Pleistocene gray wolves were relatively analogous, with the exception of one individual from Rancho La Brea, California (LACM 2300-56) that was more similar in shape to recent gray wolves from western forested regions in the Yukon and Northwest Territories, than to other late Pleistocene gray wolves (Figure 8). Body size within the late Pleistocene group was variable. The largest gray wolves were collected from Natural Trap Cave (NTC), Wyoming and Rancho La Brea (RLB), California sites; the smallest from late Pleistocene sites in Wyoming, Mexico, Kansas and Rancho La Brea, California. There was an increase in skull shape variation from the wide, relatively short cranium, large teeth and narrow nose observed in late Pleistocene gray wolves to the narrower, relatively long cranium with smaller teeth and wider nose observed in a number of Holocene specimens and a majority of recent gray wolves (Figure 8).

#### **Fossil and Modern Canids (n=219)**

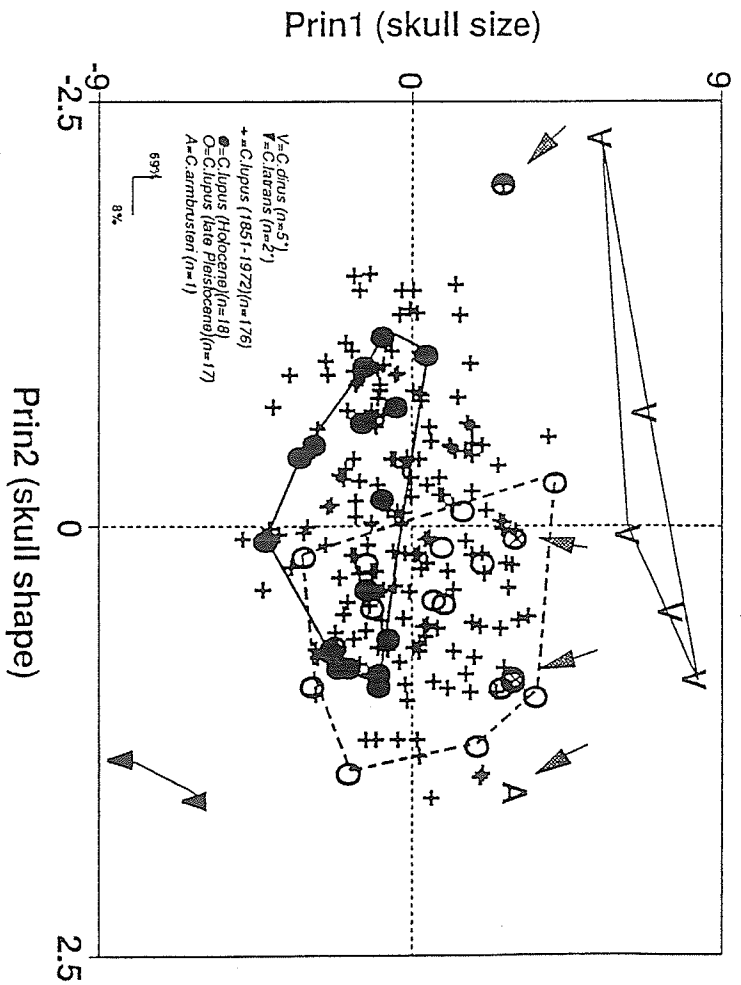
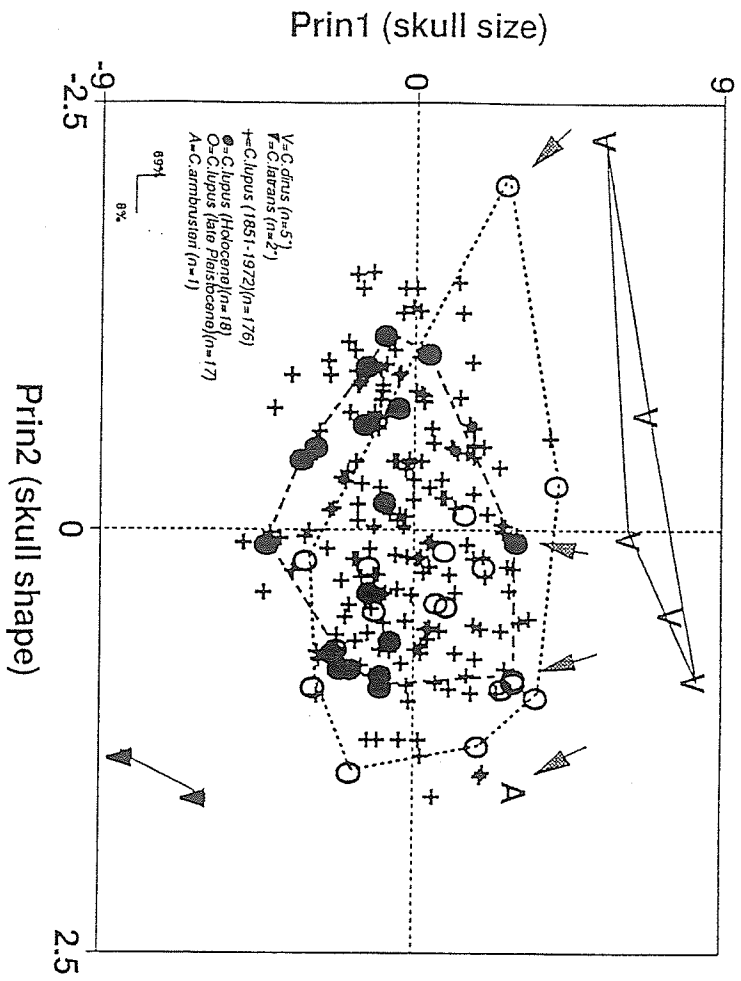
A number of closely related fossil canids were included with (fossil and modern) *C. lupus* specimens to assess whether temporally separated gray wolf populations can be distinguished from other fossil canid species (i.e. Irvingtonian *C. armbrusteri*; Rancholabrean *C. dirus* and *C. latrans*), for the seven characters included in the analysis.

The first principal component (Prin1) explained 69% of the total variation among the specimens, and was an index of

overall size. The second principal component (Prin2) accounted for 8% of the rest of the total variation that was due to differences in skull shape characteristics. The largest skulls scored highest on Prin1 (Figure 9). Skulls that displayed a relatively wide braincase, large terminal upper molar and narrow nose, had the highest scores on Prin2, while individuals with a relatively small  $M^2$ , narrow cranium and wide nose, scored lowest (Figure 9). The relatively equivalent (positive and negative) weights on Prin2 eigenvectors (Appendix II, Table D) indicates that all seven variables contributed equally to skull shape variation.

Three distinct size groups were distinguished on the vertical axis (Prin1)(Figure 9). The largest and smallest individuals are the Rancholabrean dire wolves and coyotes, respectively. Although Rancholabrean coyotes were larger than they are at present (Nowak, 1979), there is no apparent overlap in size with any gray wolf temporal unit (Figure 9). The two coyote points represent one individual from Arizona and the mean of approximately 39 specimens from Rancho La Brea, CA (data from Nowak, 1979). The dire wolves represent temporally (approximately 100,000 to 10,000 y.B.P.) and spatially (Idaho, California, Kentucky and Mexico) separated individuals, and one data point that is the mean of 62 individuals from Rancho La Brea, California (data from Nowak, 1979). Late Pleistocene gray wolves were generally

Figure 9. Plot of first and second principal components scores from a multivariate analysis of seven skull characters for 219 *Canis* spp. assigned to four descriptive units; modern *C. lupus* (+); fossil *C. lupus* (Holocene = ●, late Pleistocene = ○); fossil *C. latrans* (▼), *C. dirus* (V) and *C. armbrusteri* (A). \* = one data point represents an average value from more than one specimen. Polygons enclose a, scores for all individuals within a descriptive group; and, b, scores for all individuals within a descriptive group, excluding: group extremes (⊕), and probable anomalies (⊗) that are indicated by arrows. Sixty-nine percent of the variance was explained by Prin1 and 8% of the remaining variation was accounted for on Prin2. The eigenvector values of individual variables is indicated in Appendix II, Table D.



larger than Holocene specimens from the same mid-latitude regions (Figure 9). The one specimen of Irvingtonian *C. armbrusteri* (data from Nowak, 1979) included in the analysis was similar in size to Late Pleistocene gray wolves. The majority of Late Pleistocene gray wolves from widely-distributed locations (California, Wyoming, Kansas, Mexico, Colorado) had a relatively wide cranium, large  $M^2$  and narrow nose, skull shape characteristics also observed in the one Irvingtonian wolf, some of the Late Pleistocene dire wolves, all late Pleistocene coyotes, and a modern gray wolf specimen from Russia (Figure 9). The one exception was a skull recovered from Rancho La Brea, California that was more similar in shape to a Sangamon (75,000 to 100,000 y.B.P.) *C. dirus* from American Falls, Idaho (ISUM 6377-52, my measurements) (Figure 9).

There was extensive variation in skull shape among the dire wolf specimens from widely-distributed fossil localities (California, Idaho, Mexico and Kentucky) (Figure 9). A trend toward an increase in skull shape variability was evident among Holocene and modern wolf groups (Figure 9). Holocene gray wolf skulls were more variable in shape, when compared to late Pleistocene gray wolf specimens, and modern gray wolves also display considerable skull shape variation (Figure 9).

The one *C. armbrusteri* individual included in this analysis differs in size from the fossil coyotes, although

similarity in skull shape is evident between the two groups (wide braincase and relatively narrow rostrum) (Figure 9).

**North American Fossil Wolves from the mid-Irvingtonian to late Pleistocene interval (n=22)**

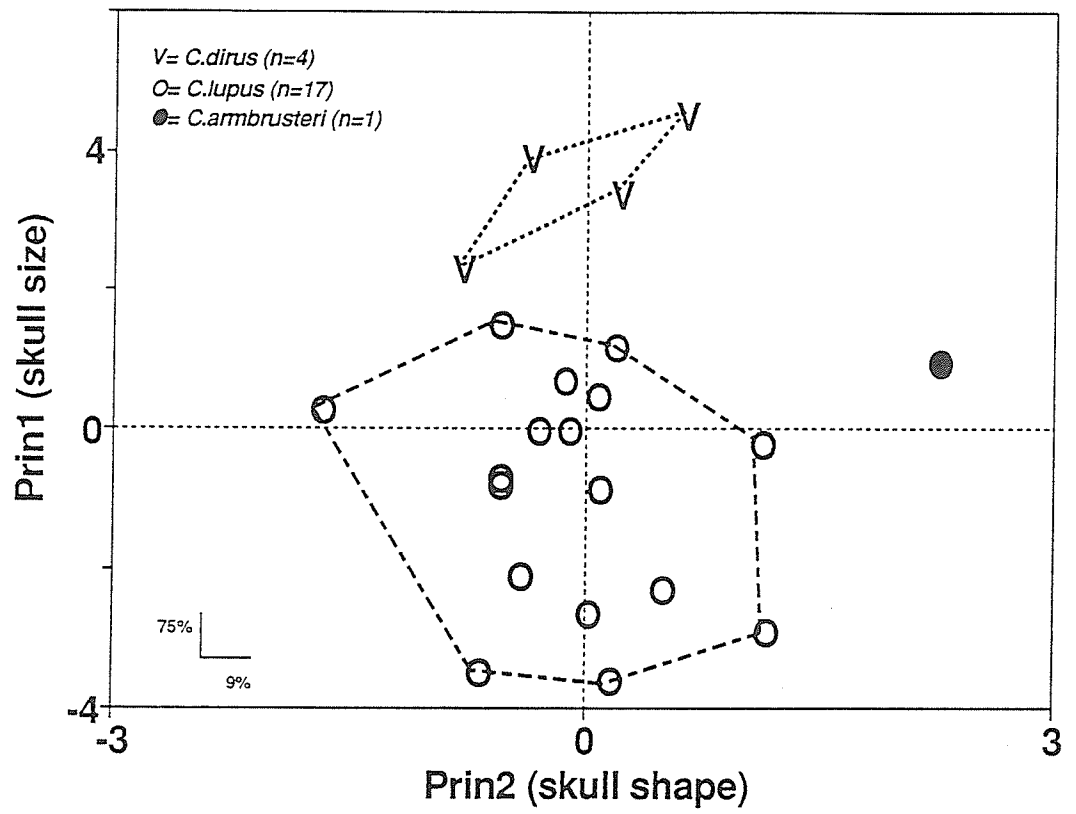
In the following analysis, four late Pleistocene dire wolf specimens from California, Idaho, Mexico and Kentucky were included with seventeen gray wolves from California, Mexico, Wyoming, Colorado and Kansas to assess the similarity between potentially contemporaneous individuals. One fossil wolf from the earlier Irvingtonian interval (approximately 1.9 - 0.4 mya) (Cumberland Cave, Maryland - data from Nowak, 1979) was included to investigate evidence of morphological variation among temporally separated populations.

The first principal component accounted for 75% of the total variation among the individuals. The approximately equal eigenvector loadings on Prin1 indicate it was an index of skull size. Prin2 explained nine percent of the rest of the total variation, that was due to differences in skull shape. In this analysis the relative width of the upper terminal molar ( $M^2$ ) was the most substantial contributor to the observed variation (Appendix II, Table E).

The dire wolves had larger skulls than wolves in other fossil groups (gray and Armbruster's) (Figure 10). There was greater size variation within the gray wolf group than within the dire wolf unit (Prin1) (Figure 10), although the

Figure 10. Plot of first and second principal components scores from a multivariate analysis of seven skull characters for 17 late Pleistocene gray (*C. lupus*) (O) and 4 dire (*C. dirus*) wolf (V) specimens and one Irvingtonian wolf (*C. armbrusteri*) (●). Polygons enclose scores for all individuals within a descriptive group. Seventy-five percent of the variance was explained by Prin1 and 9% of the remaining variation was accounted for on Prin2. The eigenvector values of individual variables is indicated in Appendix II, Table E.





smaller number of dire wolf specimens ( $n=4$ ), in comparison to gray wolves ( $n=17$ ), may not provide a true picture of *C. dirus* size variation. There is greater size variation between gray wolf specimens from Rancho La Brea, California, than between the dire and gray wolves from that site (Figure 10). The one Armbruster's wolf falls within the size range of the gray wolf specimens (Figure 10). The relative size of the upper terminal molar in fossil *C. dirus* and *C. lupus* was similar and invariably smaller than that observed in the one specimen of Irvingtonian *C. armbrusteri* (Figure 10). One fossil from the Rancho La Brea tar pits that is catalogued as a gray wolf, has an extremely small upper terminal molar (LACM 2300-56) (Figure 10).

## DISCUSSION

### Geographic Variation in Modern Gray Wolf Skulls (1851-1972)

While measuring a series of gray wolf skulls collected in Manitoba during the early 1950's (currently stored in UBC), I noted that juvenile animals (collected in the winter of their first year of life) were readily distinguishable from older individuals, on the basis of incomplete suture fusing for some elements and general skull fragility. I am confident, therefore, that the specimens included here represent adult gray wolves.

A number of the smaller 'early' and 'late' 'north' gray wolves were from open habitats (prairie and tundra regions), indicating that size was correlated with environmental conditions. The resemblance in size between 'early' 'north' and 'late' 'south' gray wolves suggests that the latter group likely represent individuals that dispersed south from more northerly latitudes in response to habitat alteration and persecution. Irrigation practices associated with farming and ranching pursuits modified the relatively arid pre-(European)contact prairie grasslands (Sims, 1988). Gray wolves from northern treed regions likely dispersed to the modified region in response to the effects of human disturbance (e.g. an increase in the availability of easily obtained food at town-site garbage dumps and farms with domestic livestock). Mech (1987) observed that a wolf pack utilizing a dump-site in northeastern Minnesota was

relatively more successful over a 16-year period, than wolf packs in adjacent territories that primarily hunted ungulate prey. In addition, gray wolves in northern regions were also being disturbed and destroyed as a result of wolf-removal programs (see Carbyn, 1983), factors which would likely disrupt their normal dispersal patterns.

An increase in skull shape variation among a number of 'late' 'north' Manitoba wolves may be due to the location of the province, which is situated between the eastern deciduous forest, southern great plains and northern boreal forest. The dispersal of gray wolves north from the plains, south from the tundra, and west from the eastern forest likely all contributed to the extensive skull shape variation observed in specimens collected from Manitoba during the early 1950's. The relative rarity and larger size of post-1920 'south' gray wolf skulls suggests that the great plains subspecies *C. l. nubilus* was extinct by 1921 due to extirpation and habitat loss.

#### **Recent Gray Wolf Skulls (1851-1920)**

Gray wolf skulls that were collected from 1851 to 1920 (likely) represent the geographical races that inhabited western North America prior to contact with Europeans (Young, 1946).

Size variation was correlated with habitat. Larger gray wolves generally inhabited forested regions where average precipitation levels are higher than in areas of

open vegetation (tundra and grassland), where smaller gray wolves were collected. McNab (1971) found that animals inhabiting arid regions are generally smaller than those from areas with higher precipitation levels, due to a requirement for a lower basal metabolic rate in mammals living in dry habitats. Mendelssohn (1982) also observed that gray wolves inhabiting arid regions in Israel are smaller than the wolves in adjacent locations where the precipitation level is higher.

Bergmann's rule, which states that body size should increase with a decrease in temperature, is frequently invoked to explain geographical differentiation (Bibikov, 1985; Pedersen, 1982). This hypothesis has been refuted by Geist (1987a), however, on the grounds that it does not consider other physiological factors of great importance to cold-adapted endotherms (e.g. heat dissipation, Scholander, 1955), and is frequently violated. For example, Thurber and Peterson (1991) found that the larger body size of coyotes inhabiting eastern mid-latitude regions (in comparison to coyotes from northwestern North America) was correlated with an enhanced food supply. Size discontinuities that have previously been described for gray wolf populations (Jolicoeur, 1959; Skeel and Carbyn, 1977) suggest that current variation cannot be explained solely as a result of latitude and altitude effects.

A correlation between gray wolf body size and the size

of major ungulate prey was also previously proposed to explain current geographic variation (Skeel and Carbyn, 1977; Pedersen, 1982), i.e. larger wolves are associated with larger prey. That relationship was contradicted, however, by the medium-sized great plains wolf (*C. l. nubilus*) that hunted the largest North American ungulate, *B. bison* (Young, 1946; Dary, 1974). One explanation for the latter discrepancy between predator body size and prey size involves habitat type. Gittleman (1989) found that group size was larger among predatory carnivores that hunted large prey (100-400 kg.) in habitats with 'open' vegetation, suggesting that the size of the prey is not the only factor influencing predator body size. It may be that the relatively smaller body size of the bison-hunting plains wolf was offset by an increase in pack size. Historical accounts of large packs of gray wolves (12-15 individuals, Young, 1946) associated with bison herds on the great plains (Dary, 1974), indicates that they may have hunted in larger groups, compared to those inhabiting 'treed' regions (7 or less individuals in more than 70% of total observations, Mech, 1970). In addition sexual dimorphism was not as noticeable among the great plains subspecies (Goldman, 1944).

#### **Temporal Variation among Gray Wolf Skulls**

The extensive overlap in the size and shape of the skull among the groups was expected, due to low taxonomic

rank (subspecies) and sexual size dimorphism (evident in modern populations). Although the small sample size of gray wolves from some regions precludes drawing conclusions based on these results, some trends are noteworthy; a) there is an apparent shift in skull shape from a wide, relatively short cranium, large cheek teeth and narrow nose, in late Pleistocene specimens, to a relatively long, narrow cranium, with a wide nose and more gracile dentition in specimens collected from Holocene and recent populations; b) Holocene specimens were generally smaller in size than the majority of late Pleistocene specimens; and c) some recent tundra wolves had skull shape characteristics similar to the majority of late Pleistocene gray wolves. The smaller size of gray wolves from mid-latitude regions at the end of the latest glaciation was apparently maintained throughout the duration of the Holocene (the last 10,000 years).

The variation in size among Rancho La Brea (RLB) individuals was also apparent in three individuals from Natural Trap Cave (NTC). Stratigraphic evidence from both sites (RLB, Marcus and Berger, 1984; NTC, Gilbert and Martin, 1984) indicated that specimens were likely deposited over a 25,000 (RLB) or 40,000 (NTC) year interval, during which time morphological variation would be expected. Conversely, the observed size variation may be due to sexual size dimorphism but that suggestion cannot be tested with fossil and sub-fossil material. Some of the skulls that

were assigned to the late Pleistocene interval, may, in fact, have been deposited during the last 10,000 years. The smallest late Pleistocene specimen was from a cave near NTC (ISUM BLM{A}) for which no deposition or associated faunal information was available. This specimen was included in the late Pleistocene descriptive unit due to the proximity of the recovery site to NTC. It was more similar, however, in size and shape to a Holocene fossil from Idaho (USNM 243578) and a modern specimen collected in 1893, from Colorado (USNM 52059).

There is extensive evidence for an increase in aridity at the Pleistocene-Holocene boundary that culminated in the Hypsithermal Interval between seven and four thousand y.B.P. (Ritchie and Yarranton, 1978; Meyer et al., 1992). Fossil evidence from a number of mid-Holocene locations indicates that the prairie grassland was more extensive during that interval than at present (Bayrock, 1964; Ritchie and Yarranton, 1978). For example, Holocene gray wolf fossils ( $4870 \pm 90$  y.B.P., BGS 1213 Brock Univ.) collected from a gypsum quarry in Manitoba ( $51^{\circ} 47'$  N. Lat.) were recovered with faunal components suggesting that a grassland habitat dominated the region during that period (white-tailed jackrabbit, *Lepus townsendi* and thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*), although the area is at present transitional boreal forest (Goulet and Lammers, in prep.).



Size similarity between modern 'north' gray wolves and their late Pleistocene counterparts from that geographical region (Nowak, 1979), suggests that 'north' populations did not undergo size reduction at the end of the Wisconsin.

The notable decrease in size between the late Pleistocene and mid-Holocene fossils is correlative with evidence of rapid environmental change that occurred west and south of the glaciers approximately 10,000 y.B.P. in North America (Broecker, Ewling and Heezen, 1960; Anderson, Mathewes and Schweger, 1989; Dohrenwend et al., 1991; Smiley et al, 1991; Meyer et al., 1992). A post-glacial decrease in body size was previously described for a number of extant species that survived the late Pleistocene extinctions; bighorn sheep, *Ovis canadensis* (Wang, 1988), pronghorn, *Antilocapra americana* (Chorn, Frase and Frailey, 1988), bison, *Bison bison* (Wilson, 1980), moose, *Alces alces*, caribou, *Rangifer tarandus*, muskox, *Ovibos moschatus* (Guthrie, 1984), wolverine, *Gulo gulo*, wolf, *C. lupus* (Gilbert and Martin, 1984), coyote, *C. latrans* (Nowak, 1979), and marten, *Martes americana* (Youngman and Schuler, 1991). A reduction in the size of social organs (antlers and horns) and general form was evident in Holocene ungulates recovered from the northwestern refugium, when compared to their late Pleistocene progenitors (Guthrie, 1984). Kurtén (1968) described analogous dwarfing among certain European species that survived extinction at the end

of the latest glaciation.

A lack of evidence for extensive extinction or size reduction in pre-Wisconsin interglacial faunal assemblages (Gilbert and Martin, 1984) suggests that the climatic change defining the late Pleistocene-Holocene boundary was unique (Guthrie, 1990).

Skull shape variation is evident in modern gray wolves from major geographical regions of North America. Eastern gray wolves (*C. l. lycaon*) have a narrow rostrum in comparison to specimens collected from central and western North America (Schmitz and Kolenosky, 1985). There is evidence that morphological diversity in skull shape may be limited in canids due to ontogenetic scaling (Wayne, 1986), suggesting that observed trends in skull shape traits may be heritable.

#### **Fossil and Recent Canids**

The modern gray wolf, *C. lupus*, first appeared in the late Pleistocene of Eurasia (Kurtén, 1968). In North America, the gray wolf was recognized from late Irvingtonian and early Rancholabrean locations (Nowak, 1979; Kurtén and Anderson, 1980), indicating that *C. lupus* spread from Eurasia to North America across the Bering land bridge. Recent evidence indicates that there were likely more Pleistocene glacial intervals than the four at present recognized (Nebraskan, Kansan, Illinoian and Wisconsin) (Martin and Martin, 1987), suggesting that bi-directional

faunal movements were not limited to four distinct chronological intervals. Nowak (1979) indicated that wolf-like canids were lacking from the fossil record of Beringia prior to the Illinoian glaciation and pre-Illinoian wolves were recovered exclusively from mid-latitude locations. However, a specimen identified as *C. cf. etruscus* was recovered from Medicine Hat, Alberta, with a mammalian fauna representative of the Blancan-Irvingtonian boundary (Harington, 1978), approximately 1.9-1.8 mya (Figure 1). The lack of pre-Illinoian wolves in the fossil record of Beringia may also be due to deposition bias. In addition, fossils are frequently recovered from placer mines and gravels and silts that are difficult to age due to the lack of stratigraphy associated with those deposits (Harington, 1978; Olsen, 1985).

Palearctic *C. lupus* was large during the mid-Pleistocene, but relatively smaller and more abundant during the Late Pleistocene (Bibikov, 1985), in contrast to the situation in mid-latitude North America, during the Wisconsin glaciation, where small numbers of relatively large gray wolves were recovered (the results obtained here were in agreement with Nowak, 1979).

Nowak (1979) previously found that gray and dire wolves were more similar in skull shape to each other, than either was to the Irvingtonian wolf (*C. armbrusteri*). The former two species share additional distinctive skull traits;

relatively small, moderately inflated tympanic bullae and small  $M^2$  (Nowak, 1979). Conversely, *C. armbrusteri*, *C. latrans* (and some modern red wolves) exhibit relatively large  $M^2$ , and large, well-inflated tympanic bullae (Nowak, 1979).

The relative size of the upper terminal molar is related to function and therefore quite variable within the Canidae (Wayne, 1986). However, variation in the phenotypic expression of traits that are highly correlated with functional morphology provide clues to behavioral and physiological differences between closely related groups.

Although the one Armbruster's wolf individual and small sample of dire wolves included here precludes drawing conclusions, the results were in agreement with previously described character differences among Nearctic wolf species (Martin, 1974; Nowak, 1979; Kurtén and Anderson, 1980).

There is an indication that skull shape characteristics of fossil Nearctic wolves may reflect their lineage. Wolf species that arose in the New World display a trend toward skull shape traits similar to that found in coyotes, in contrast to (possible) descendants of Eurasian immigrants (*i.e.* modern *C. lupus* from roughly west of 100° W. longitude and *C. dirus*).

#### **North American Fossil Wolves from the mid-Irvingtonian to late Pleistocene Interval**

The distinguishing characteristics that separate *C.*

*dirus* from other wolf-like canids include; a) relatively larger size; b) well-developed inion that extends posteriorly and downwards (Webster's dictionary defines INION as "the external occipital protuberance of the skull"); and, c) robust dentition and an incomplete anterolingual cingulum on  $M^1$  that frequently ends at the protocone in *C. dirus* specimens (Nowak, 1979). Kurtén (1984) recognized two geographic races of dire wolves. *C. d. dirus*, collected from sites located east of the Rocky Mountains, differs from the western subspecies, *C. d. guilday*, that is generally larger in overall size with relatively longer distal limb bones and a shorter  $P^2$ .

With the exception of the very robust carnassials, none of the three previously described characteristics are unique to the dire wolf. The very large extant wolves of the western arctic regions of North America approach or exceed the size of some of the late Pleistocene dire wolves (Nowak, 1979; Kurtén and Anderson, 1980). The extensive projection of the inion has also been observed in a number of closely related modern and fossil wolves; e.g. the recent great plains subspecies, *C. l. nubilus* (Goldman, 1944); fossil Irvingtonian wolves from the Coleman IIA site (Martin, 1974); a specimen from a Holocene deposit in Gypsumville, Manitoba (Goulet and Lammers, in prep.); and a late Pleistocene gray wolf from Alaska (Olsen, 1985). The inion

extension is related to function, implying that the dire wolves (and other wolves displaying that characteristic) required increased musculature for stronger jaws, as a result of dietary demands. With respect to the incomplete anterolingual cingulum on  $M^1$ , this condition also occurs in four out of 75 modern gray wolf specimens collected from northwestern regions of the continent and in 20% of a random sample of specimens that includes modern gray wolves from mid-latitude regions (Martin, 1974). This characteristic was also evident in one mid-Irvingtonian wolf, described as *C. armbrusteri*, from Coleman IIA, Florida (Martin, 1974). The preceding discussion on the anterolingual cingulum signifies that this trait is ineffectual for defining a species.

There is no well-supported evidence of *C. dirus* in the fossil record of North America prior to the last interglacial (Nowak, 1979) (Sangamon, which began approximately 130,000 y.B.P., Lambeck and Nakado, 1992), where specimens were recovered from widely-distributed mid-latitude locations, including Alberta, Idaho and Florida (Nowak, 1979).

The similarity in dire and gray wolf skull shape characteristics and extensive variation in shape displayed by both of the former species, leads me to conclude that *C. dirus* evolved in North America, from gray wolves that originated in Eurasia.

Geist's (1987b) "dispersal theory" suggests that peripheral populations may give rise to giant morphs that are not necessarily genetically diverged from the parent form, during intervals when material resources are abundant. This theory was proposed to explain the large size of body and social organs (horns and antlers) observed in late Pleistocene ungulates, compared to their Holocene and recent counterparts (Geist, 1987b). The latter were described by Geist (1987b) as "maintenance types" that reflect adaptation of the "hypermorphic" form to periods when resources are limited. Geist's (1987b) theory may account for the sudden appearance of *C. dirus* in the fossil record as a successful "hypermorph" of a gray wolf progenitor, in response to prevailing late Pleistocene conditions that included abundant resource availability, large size of prey, and possible interspecific competition with other large carnivores (e.g. sabre-toothed cat, *Smilodon floridanus* and american lion, *Panthera atrox*). Fossil evidence suggests that a canid similar in dental and skull shape characteristics to the modern *C. lupus*, was a contemporary of *C. dirus* during the late Pleistocene (Nowak, 1979). It is apparent however that a lack of chronostratigraphic intervals in (many) late Pleistocene fossil locations and problems in identifying wolf-like canid remains require care be taken when drawing conclusions concerning the possible coexistence of fossil wolves based on the deposition

information (Table 1). The lack of unequivocal chronostratigraphic intervals in most fossil recovery sites was due, in part, to the nature of bone deposition and burial. Most late Pleistocene carnivore remains are from "natural trap" sites from which animals were unable to escape after falling in (e.g. Natural Trap Cave, Wyoming, Martin and Gilbert, 1978), or becoming mired in sediments (Rancho La Brea, California, Marcus and Berger, 1984). The above sites were either continually (NTC, Martin and Gilbert, 1978), or intermittently (RLB, Marcus and Berger, 1984) active as traps. Late Pleistocene deposits that lacked sedimentary stratigraphy were frequently aged (geologically) on the basis of the faunal assemblage correlated with inferred position of the leading edge of the glacier. For example, if a deposit contained both boreal and grassland species, it was suggested deposition occurred over a time interval that included sequential cold (during glaciations) and warm (interglacial/interstadial) stages (Parmalee, Munson and Guilday, 1978). There is evidence, however that the late Pleistocene climate in mid-latitude North America was more seasonally equable, in comparison to current conditions, resulting in the occurrence of complex community structures that have no modern analogs (Martin and Martin, 1989).

Late Pleistocene *C. lupus* specimens are relatively rare in the fossil record of North America. This was previously



Table 1. Selected sites where *C. dirus* and *C. lupus* fossil remains were recovered (RS = chronostratigraphic deposit; RLB = Rancho La Brea, California)

- Notes:
- 1 - resembles modern northern wolves
  - 2 - identification as *C. lupus* not confirmed
  - 3 - pit active for relatively short period
  - 4 - identified as *C. rufus*
  - 5 - identification problematic due to lack of complete skull and limb elements
  6. may be one individual, represented by post-cranial material (W/ pers.comm.)
  7. resembles RLB *C. dirus*
  8. very small *C. lupus*

(p=probable; P&O/72 = Parmalee and Oesch, 1972; W/74 = Webb, 1974; PMB/78 = Parmalee, Munson and Guilday, 1978; N/79 = Nowak, 1979; M&B/84 = Marcus and Berger, 1984; W/92 = Walker, pers. comm., 1992)

SITE	REF.	RS	C.dirus	C.lupus
Ventana Cave-AZ	N/79	no	x	x
Samwell Cave-CA	N/79	no	x	x <sup>1</sup>
Kittrick-CA	N/79	no	x	x <sup>2</sup>
Maricopa Brea-CA	N/79	no	x	x
Rancho La Brea-CA ++	M&B/84			
Pit 61 & 67		no	x	n=2
Pit 77		p	x	n=1 <sub>3</sub> <sup>p<sup>4</sup></sup>
Pit 13		p	x	n=6
Pit 3		yes	x	n=7
Pit 10		yes	x	n=1
Pond Dump		no	x	n=2
(pits 3,4,61 + 67)				
Pit 91		yes	p	n=1
Pit 81		p	x	n=1
Pit 4		no	x	n=1
Pit 2		-	x	n=1
Pit 51		-	x	n=1
No data				n=5
Melbourne-FL	W/74	-	x	x <sup>4</sup>
	N/79			
Vero-FL	W/74	-	x	x <sup>4</sup>
	N/79			
Devil's Den-FL	W/74	-	x	x <sup>4</sup>
	N/79			
Jaguar Cave-ID	N/79	no	(cf)	x
Harrodsburg Crevice	PMG/78	yes	(cf -- Indet. --)	<sup>5</sup>
-IN				
Brynjulfson Caves-MO	P&O/72	no	x	x
Hermit's Cave-NM	N/79	yes	x	x
Natural Trap	W/92	yes	x <sup>6</sup>	n=35
Cave-WY				
San Josecito-	N/79	-	x <sup>7</sup>	x <sup>8</sup>
Nuevo Leon				

attributed to ecological differences between the gray and dire wolves (Stock, 1942), or greater intelligence of gray wolves (Kurtén and Anderson, 1980), implying that the latter species was less likely to get trapped. Conversely, Hemmer (1978a,b) determined that dire wolves were highly social ("characteristic of the animals with highly developed intellectual activity") as a result of the cephalization index (*c.i.*) score that he calculated for that species (*c.i.*=15.5), in comparison to highly social modern gray wolves (Mech, 1970) (*c.i.*=13.5). In addition, Bibikov (1985) found that most late Pleistocene gray wolves from the former U.S.S.R. were recovered from asphalt traps that were analogous to those that functioned at Rancho La Brea, California, suggesting that *C. lupus* was not intentionally avoiding the trap sites in California, but rather, did not occur there continually throughout the 25,000 year (Shaw and Quinn, 1986) period of entrapment history.

Extinct bison (*B. antiquus*) and horse (*Equus occidentalis*) remains represent the largest number of trapped herbivores. It has been estimated that entrapment of one large fossil herbivore every 10 years, over the 25,000 year period of fossil fauna accumulation, would adequately account for all the large mammal and bird fossils collected by the museum to date (Shaw and Quinn, 1986).

The very large numbers of dire wolves collected at each fossil recovery site at RLB suggests that entire wolf packs

may have perished in each entrapment incident. The trap sites were likely analogous to modern "poison bait" stations used by "wolfers" to kill wolves, that continued to attract and poison non-target animals (e.g. avian and terrestrial scavengers) after the wolves were dead.

In addition, current behavioral research suggests that gray wolves would be represented in larger numbers, due to their hunting and scavenging habits, if they were continual residents at Rancho La Brea during the 25,000 year entrapment history.

Most of the late Pleistocene fossil locations where *C. dirus* and *C. lupus* were recovered together can be disregarded as evidence of sympatry due to confusion over specimen identification (Table I). There are a few chronostratigraphic deposits, however, from which both of the above species were recovered (e.g., Rancho La Brea, C. Shaw, pers. comm., 1992), suggesting that they may have been intermittently sympatric. The ages of the various sites at the Rancho La Brea location have been detailed by Marcus and Berger (1984). It seems significant that the Rancho La Brea wolves exhibit temporal size variation. Dire and gray wolves from the most recent RLB pit sites are generally smaller than those from older deposits (dire wolf, Marcus and Berger, 1989; gray wolf, results of this research).

Although there is no clear indication of gray and dire wolf sympatry during the late Pleistocene at Rancho La Brea,

CA, I suggest that the two species were likely ecologically separated, due to gray wolf preference for the climate and habitat of more northerly latitudes.

Pit #3 at RLB has two distinct stratigraphic units. The upper 15 feet (approximately) was radio-carbon dated from 12,000 to 15,000 y.B.P., while those specimens collected at  $\geq 22$  feet are more than 19,000 years old (Marcus and Berger, 1984).

Marcus and Berger (1984) noted a deposition hiatus at Rancho La Brea, of approximately 3600 years (from  $\sim 15,700$  to  $\sim 19,300$  y.B.P.). The interval correlates with the late Wisconsin glacial maximum which may have affected the ambient temperature at that location (Marcus and Berger, 1984). Cooler weather would have resulted in congealed asphalt. Marcus and Berger (1984) concluded that there is only a 5% probability that the deposition hiatus is due to chance. Of the seven gray wolf specimens collected from pit #3, five were from 8.5 - 19 feet below datum, and two were from a caved-in section (Shaw, pers. comm., 1992). A number of radio-carbon dates from this location indicate that this trap was active for two relatively short time periods (from 12,000 to 15,000 and  $\sim 19,000$  to 21,000 y.B.P.). (Marcus and Berger, 1984).

Pit #10 has two distinct intervals. One is about the same age as the younger part of pit #3, and the other is much younger, containing *Homo* and *Ursus arctos* remains. The

one gray wolf from this pit may have been associated with either unit. Pit #91 is an older deposit (from about 28,000 to 40,000 y.B.P.) with two distinct bone units apparent (Marcus and Berger, 1984).

Some pits where gray and dire wolves have been recovered in association were apparently active as traps for relatively short time periods, suggesting that the two species were sympatric. Pit #13 was active for a short period between 12,000 to 15,000 y.B.P., while pits #61-67 - have the shortest deposition history (<3000 years) and are the youngest of known RLB sites (Marcus and Berger, 1984). It may be significant that the two gray wolf specimens collected from Pits #61-67 were relatively small, in comparison to gray wolves from other pits, although this may just reflect sexual size dimorphism (Jolicoeur, 1959). Pit #77 was represented by one P<sup>4</sup>, not considered here to be adequate evidence for the presence of the gray wolf in that deposit. The Pond Dump comprises specimens from Pits 3, 4, 61 and 67. The two skulls recovered were described as late Wisconsin gray wolves (Shaw, pers. comm., 1992) (refer to Table 1 for number of gray wolf specimens recovered at each site).

The other major difficulty in determining whether dire and gray wolves coexisted resulted from ambiguous taxonomic identification of fossil wolf specimens. Therefore, where chronostratigraphy is evident, identification of specimens

is problematic; e.g. the Sangamon Harrodsburg Crevice, Indiana site where the lack of complete skull and limb elements impedes positive identification. Measurements indicate that the canids are approximately the same size as modern northern wolves (Parmalee et al., 1978). In the Hermit's Cave, New Mexico site the specimen identified as a gray wolf was associated with a man-made hearth, while dire wolf remains were collected from a different stratigraphic interval (Nowak, 1979). The Natural Trap Cave, Wyoming site has yielded about 35 gray wolf individuals and one possible dire wolf (Walker, pers. comm., 1992), that was identified from post-cranial material only.

Florida fossil localities list the occurrence of late Pleistocene and early Holocene dire wolves in association with red wolves (*C. rufus*) (Webb, 1974) (Table 1). Wolves collected from pre-Sangamon Florida deposits were more similar to *C. armbrusteri* (Nowak, 1979) or *C. lupus* (Martin, 1974).

The evidence concerning dire and gray wolf sympatry is inconclusive. It may be that late Pleistocene *C. dirus* and *C. lupus* represent ecological variants of the same species. This problem may be resolved when radio-carbon dates are obtained for both species from the same deposition levels at Rancho La Brea. The relatively rare gray wolf recoveries from the Rancho La Brea site suggests that they may have occurred infrequently at that site, due, likely, to an

adaptation to the generally colder climatic conditions that occurred closer to the leading edge of the glacier. This view is supported by evidence of a (relatively) large number of gray wolves (and possibly one dire wolf) collected from the Natural Trap Cave, Wyoming site (Walker, pers. comm., 1992), which was a continuation of the steppe-tundra habitat that dominated Beringia during the late Pleistocene (Martin and Martin, 1987).

Eldridge and Gould (1985) postulated that new species arise rapidly from "peripheral isolates" that appear instantaneously in the fossil record. The descendant and ancestral forms are expected to display the greatest morphological differences when the descendant first appears in the range of the ancestral form. The relatively instantaneous appearance of *C. dirus* in the fossil record of widely distributed early Sangamon localities suggests to me that the dire wolf represents a successful example of rapid speciation and range expansion.

#### **Ecological vs. genetic adaptation**

Palynological evidence suggests that late Pleistocene Holarctic climatic conditions were relatively equable, with an increase in seasonality evident toward the end of that epoch (Vereshchagin and Baryshnikov, 1984; Guilday, 1984; Lundelius et al., 1987; Wells and Stewart, 1987). A taiga-like biome that was periodically ravaged by fire, dominated the ice-free region south of the glacier (Wells and Stewart,



1987) and a vast "mammoth steppe" covered most of Europe, Eurasia, the Bering Land Bridge and the northwestern refugium (Guthrie, 1984; Vereshchagin and Baryshnikov, 1984).

Evidence for equable climatic conditions comes from widely distributed Wisconsin fossil faunal assemblages, composed of taxa that have no modern analogues (Kurtén and Anderson, 1980; Guthrie, 1984; Martin and Martin, 1987). The combination of post-fire succession of the vegetation and relatively equable seasonality in the southern refugium contributed to the coexistence of a number of species that are currently ecologically segregated (Wells and Stewart, 1987; Anderson et al, 1989).

An abrupt change in climatic conditions and vegetation patterns marked the end of the latest glaciation (Broecker et al., 1960; Guthrie, 1984; Barnosky et al., 1987; Anderson et al., 1989; Smiley et al., 1991). In Eurasia, numerous short-lived advance and retreat ice-oscillations (between 12,000 to 10,000 y.B.P.) preceded the change from a "mammoth steppe" to a forest-dominated habitat in Siberia, the northern Urals, the Russian plains and in the Far East (Vereshchagin and Baryshnikov, 1984). In North America, a warm, moist trend developed in the northwest (Anderson et al., 1989; Guthrie, 1984) and grasslands replaced the central forested plains (Stewart, 1987; Anderson et al., 1989; Smiley et al, 1991). Intense eolian activity in the

Mojave desert (Dohrenwend et al., 1991), and fire-related alluvial sedimentation in Yellowstone National Park, approximately 10,000 y.B.P. (Meyer et al., 1992), indicate that drought-like conditions dominated mid-latitude North America at the end of the late Pleistocene. The post-glacial increase in seasonality, temperature and aridity apparently limited the range of some organisms that were unable to cope with climatic extremes (Pruitt, 1959), resulting in contemporary communities that are defined by the occurrence of unique species composition.

Relict populations of boreal plants and animals that are at present found at higher altitudes and latitudes than their late Pleistocene counterparts underwent range contraction as a result of the climatic change (Wells and Stewart, 1987). For example caribou (*Rangifer tarandus*) and badger (*Taxidea taxus*) were contemporaneous in widely distributed late Pleistocene locations, although they are at present confined to forest and tundra (caribou) and grassland (badger) habitats (Harrington, 1978; Kurtén and Anderson, 1980; Guthrie, 1990). Guthrie (1990) proposed that complex habitat factors contributed to the greater diversity of late Pleistocene faunas, suggesting that full glacial temperatures in Alaska and Siberia were seasonal, with warm summers and cold, windy winters. As endothermic mammals are more sensitive to food resources than to fluctuations in temperature, the present distribution of

herbivorous animals was apparently influenced by a shift from a heterogeneous pattern of vegetation in the late Pleistocene, to the strongly zonal features currently evident (Barnosky, Grimm and Wright, 1987; Guthrie, 1990).

Results of recent molecular studies were unable to elucidate the genetic relationships among current geographical races of gray wolves, although four gray wolf mtDNA genotypes were identified (Lehman et al., 1991). Two of the four genotypes are widespread, one genotype may be limited to locations in Alaska, Northwest Territories, Yukon and Montana, while the fourth mtDNA genotype was unique to Riding Mountain National Park, Manitoba (although the small sample size of two may be misleading). Interestingly, some gray wolves from Minnesota and northwestern Ontario (exclusively) display a coyote-like mtDNA genotype not found in extant coyotes. Lehman et al. (1991) interpreted this observation as confirmation of coyote-gray wolf hybridization in the distant past.

I suggest that an alternate explanation may be that one, or both of these 'coyote-like' genotypes reflect divergence between coyotes and wolf-like canids in North America. This conclusion is based on genetic evidence suggesting that Nearctic coyotes split into two clades approximately one million years ago (Lehman et al, 1991), assuming a constant mtDNA substitution rate of 2% per million years. Coyote mtDNA genotypes from one widely

distributed clade did not occur in any gray wolf phenotypes, while coyote mtDNA genotypes from the second clade were frequently evident in individuals identified as gray wolves (Lehman et al., 1991).

In addition, early North American wolves (e.g. Irvingtonian *C. armbrusteri*) and modern red wolves more closely resembled coyotes than gray and dire wolves in skull shape characteristics (relative cranial and rostral width), size and inflation of the tympanic bullae and relative size of  $M^2$  (Nowak, 1979). Wayne (1986) suggested, however, that the size of the terminal upper molar ( $M^2$ ) reflects the intensity of selection for functional dentition in canid taxa, indicating that trait may not be useful for determining phylogenetic relationships. It may, however, indicate ecological differences among species.

Although it is not possible at present to establish conclusively whether the size variation among current geographic populations of gray wolves is a result of genetic divergence or "ecological expression" (phenotypic adaptation) it is apparent that a decrease in the size of the skull among mid-latitude populations at the end of the Wisconsin was strongly correlated with rapid environmental change. The lack of evidence for genetic divergence among extant Nearctic gray wolves (Lehman et al., 1991) and evidence of a decrease in size that was strongly correlated with changing climatic conditions suggests that observed

size variation among recent populations may be a result of ecological adaptation.

Skull shape variation may, however, be due to genetic divergence. Although the results obtained here are of exploratory value only, due to small sample sizes (in some cases), temporal separation of groups, and use of an average value representing some individual specimens (*i.e.* *C. latrans* and *C. dirus*), certain trends are evident that may be interpreted in evolutionary terms. Despite the extensive variation evident in the temporally and geographically separated gray wolf populations, skull shape characteristics among the majority of late Pleistocene gray wolf specimens were generally similar. While this could be due to deposition bias, as a result of the relatively small sample of fossils that may not reflect the total population variation, it probably does reflect actual taxonomic relationships.

Paleontological samples are relatively scarce in comparison to contemporary specimens, and may not account for all the variation evident in a natural population. As a result of this an assumption is made in paleontology that most of the specimens represent the population average (Lammers, pers. comm., 1992). Conversely it may be argued that the fossil specimen represents a population variant that perished as a direct result of being different (Lammers, pers. comm., 1992). The factors contributing to

the deposition, burial and subsequent retrieval of fossils are so capricious, however, that it is unlikely that only population variants are being recovered. As well, a number of fossil specimens included here were of advanced age at death. The fact that they survived to old age implies that either they were not radically different from other members of their population, or conversely, were more "fit" to survive as a result of the differences.

Two possible interpretations are presented to explain the extensive skull shape variation observed in recent North American gray wolf populations. First, modern North American gray wolves may be descendants of two wolf lineages that arose allopatrically in North America and Eurasia, from a common ancestor with a holarctic distribution (i.e. *C. arnensis*=Old World and *C. lepophagus*=New World) (Figure 1). Recently reported evidence of genetic divergence between coyotes and gray wolves places the split between the two species at approximately 2.4 to 1.2 mya (Lehman et al., 1991), in agreement with geological evidence indicating that the late Blancan/early Irvingtonian was a period of extensive intercontinental migration associated with climatic change (Lundelius et al., 1987).

The fossil record indicates that the modern *C. lupus* (conspecific with the Old World gray wolf) did not arrive in North America until the late Irvingtonian (600,000 to 400,000 y.B.P.), although Palearctic gray wolves were

evident in Europe approximately one million years ago (Kurtén, 1968).

Specific identification of Nearctic wolf-like canids prior to the late Irvingtonian was frequently problematic, however, due to a dearth of complete skulls from some sites (Nowak, 1979) and an observed skull shape similarity between closely related canid specimens, possibly resulting from morphological shape constraints that characterize canids (Wayne, 1986). Nowak (1979) adeptly synthesized the available information on fossil and modern canid specimens in "North American Quaternary *Canis*" and concluded that modern North American gray and red wolves were descendants of wolf lines that arose in Eurasia and North America, respectively.

Second, the North American ancestral canid (*C. lepophagus*) gave rise to coyote-type canids exclusively. All wolf-like canids originated in the Old World, and subsequently spread to North America, during temporally separated intermittent Pleistocene glacial intervals, when a land bridge joined the two continents. Fossil evidence indicates that while canids originated in the New World, the major radiation of the group occurred in the Palearctic (Martin, 1989).

Although previously observed morphological similarity between some temporally synchronous and temporally separated Palearctic and Nearctic wolf-like canids (Figure 1) (Kurtén,

1968; Nowak, 1979) may result from morphological constraint on skull characteristics (Wayne, 1986) that limit shape variation, the groups may also represent widely-distributed conspecifics. The potential of large mobile mammals to disperse long distances over short time intervals (Matthew, 1930), and evidence of bi-directional faunal movement across the Bering land bridge throughout the Pleistocene Epoch (Lundelius et al., 1987) lend credibility to the latter hypothesis. The late Villefranchian *C. etruscus* closely resembled the early Irvingtonian *C. edwardii* (Kurten and Anderson, 1980) (Figure 1), while Kurtén (1968) viewed the contemporaneous Nearctic *C. armbrusteri* and Palearctic *C. falconeri*, conspecific.

Sequence divergence of mtDNA among recent gray wolf populations from North America and Iraq indicate that modern Nearctic wolves split from a common ancestral form approximately 300,000 y.B.P., based on a standard rate of mtDNA evolution (Lehman et al., 1992). Although there are apparent problems in determining rates of intraspecific mtDNA divergence among canids (Wilson et al., 1985; Wayne et al., 1990), the evidence that at least four distinct mtDNA wolf genotypes occur in North America could be interpreted as representing temporally separated gray wolf movements from the Old World to North America. There is no evidence of subsequent divergence within the four North American gray wolf genotypes, suggesting that gray wolves may retain



primitive mtDNA (Wayne et al., 1990). Retention of primitive mtDNA was previously proposed to explain a lack of sequence divergence among some jackal groups as well (Wayne et al., 1990).

Given the propensity of bone and dentition to undergo change over relatively short time periods, in response to selective pressure (Geist, 1987b), evidence of the temporal maintenance of traits that are correlated with function suggests that they would be useful for distinguishing evolutionary relationships. The relatively large size of the Armbruster's wolf  $M^2$ , in comparison to that observed in gray and dire wolf specimens, implies that the diet of that wolf likely resembled modern coyotes which also have a relatively large  $M^2$ .

In addition, the above events were not likely mutually exclusive, suggesting that both episodal movements of wolf-like canids from Eurasia and divergence among North American canids contribute to the morphological variation observed in modern North American wolf populations. Fossil evidence indicates that endemic Nearctic canids were relatively restricted to mid-latitude locations (Nowak, 1979). The only canid remains of North American origin that have been recovered from north of approximately  $54^{\circ}$  N. latitude, were a small number of Wisconsin coyotes from Cripple Creek, Alaska (0.1% of total individuals) (Guthrie, 1968). Habitat and prey preferences may have contributed to partitioning of

wolf groups during intervals when resources and climatic conditions were relatively stable (e.g. during the late Pleistocene, Martin and Martin, 1987). The rapid climatic changes and extinction of the late Wisconsin megafauna that mark the end of that period, likely resulted in a restructuring of the wolf population. The extensive increase in skull shape characteristics that appeared during the Holocene agrees with this conclusion, and likely reflects the spread of late Pleistocene gray wolf populations from the northwestern refugium to mid-latitude North American locations.

#### **Temporal maintenance of geographical populations**

An interesting aspect concerning the social behaviour of gray wolves needs to be addressed. How was the notable size difference between recent 'north' and 'south' populations maintained over time, in a highly mobile predator, where both sexes may disperse long distances from natal territories when sexually mature (Mech, 1987)? Factors that may contribute to restricting gene flow between adjacent populations may include habitat and prey preference (Skeel and Carbyn, 1977) and variable dispersal strategies (Mech, 1987). Gray wolf pups spend up to 20% of their lifespan learning from older pack members how to catch what they eat (Mech, 1970). In addition, there is evidence that wolves may be adverse to switching from one large prey species to another, possibly as a result of their cultural

learning. During a period of rapid decline in the white-tailed deer population in northeastern Minnesota, during the late 1960's, only one gray wolf pack was observed to switch their primary prey, from deer to moose (Mech, pers.comm., 1990), although the latter were apparently continually available as an alternate food resource (Nelson and Mech, 1981). In another occurrence, gray wolves did not prey on a bison herd in the Mackenzie Bison Sanctuary, located on the western end of Great Slave Lake, Northwest Territories, for a period of twenty years following bison introduction into that region (Carbyn, 1987). The above information supports the suggestion that prey preference may influence the direction of gray wolf dispersal and distance travelled - within habitats that contain familiar prey species.

How do the above findings affect the taxonomic status of gray wolf geographic populations? Futuyma (1986) contends that it is inaccurate to say that a characteristic is either environmentally or genetically based, since phenotypic expression is a result of the interaction between the genotype and its milieu (including both intrinsic and extrinsic factors). In addition, Mayr et al. (1953, p. 32) argues "that there is no geographical race that is not also an ecological race, nor an ecological race that is not also a geographical race".

Although it is not within the scope of this thesis to attempt restructuring North American gray wolf

classification, I propose that evidence of temporal maintenance of certain traits (such as size) indicating that a geographical population has diverged ecologically from adjacent populations, merits *subspecies* designation, despite a lack of evidence for genetic divergence.

## SUMMARY and CONCLUSIONS

1. Current variation in skull size among north and south gray wolf populations was a result of ecological adaptation to environmental conditions.
2. Trends in skull shape variation indicated that Nearctic wolf populations descended from wolf-like canids that originated in both North America and Eurasia.
3. Nearctic gray wolves were descendants of Eurasian ancestors.
4. The temporal maintenance of size variation among 'north' and 'south' gray wolf populations during the last 10,000 years suggested that ecological preferences were communicated from parent to offspring, likely influencing the distance and direction of dispersal from a natal territory.
5. The great plains wolf should retain the subspecies designation *C. l. nubilus*, based on evidence of temporal maintenance of skull characteristics that reflect ecological adaptation to the prairie habitat.
6. Rancholabrean dire wolves were closely related to ancestral gray wolves that originated in the Old World. Large size and robust carnassial specialization suggest "hypermorphic" development of traits that are associated with function, as a result of resource abundance and possible interspecific competition with other large carnivores (e.g. sabre-tooth cat, *S. floridanus*; american lion, *P. atrox*).

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**APPENDIX 1.** This appendix provides data on *Canis lupus* specimens unless indicated otherwise, that are included in the analyses. ('OBS'=observation number: +=*C.dirus*, #=*C.latrans*, \*=*C.armbrusteri*; 'SPEC'=institution; 'NUM.'=specimen number: PRUITT=mammal lab, Dept. of Zoology, University of Manitoba - FT.CRLTN=Archaeology collection, SMNH - BLM(A)=on loan to ISUM from Bureau of Land Management - ARCHEO.A=Archaeology Dept. ISUM - BOX 65=uncatalogued skull at UBC, Dept. of Zoology Museum - NOWAK, 1979=data from Nowak, 1979, Appendix B; 'HAB': O=open, T=treed; 'LAT./LONG.'=geographical coordinates; 'AGE': S=south, N=north, H=Holocene, LPL=late Pleistocene, LPL/H=late Pleistocene OR Holocene; 'SEX': M=male, F=female, U=unknown; 'COLLO'=collection location - refer to list of ABBREVIATIONS, x=62 =data from Nowak, 1979 - average values determined from 62 individual skulls; 'DT/DEP'=date and deposition information - i.e. 1943=collection date, CAVE=fossil recovery site, K = one thousand years; ~5K\*=radio-carbon dated at 5000 y.B.P., NTC=Natural Trap Cave, WY site, SNBO=sand blow-out, SEDEP=sediment deposit, LATU=lava tube, RLB=Rancho La Brea, CA site, mIRV=mid-Irvingtonian. BRNCS, M2BL, MAXTH, P4CLN, M2CWT, PALP1, POCNS =variables included in the analyses, refer to Materials and Methods for measurement descriptions.

OBS	SPEC	NUM.	HAB	LAT.	LONG.	AGE	SEX	COLLO	DT/DEP	BRNCS	M2BL	MAXTH	P4CLN	M2CWT	PALP1	POCNS
01	MMMN	372	O	49 21 N	97 22 W	S	M	MB	1943	70.8	72.5	86.0	28.5	15.5	35.1	45.0
02	MMMN	2996	O	50 50 N	100 00 W	N	M	MB	1972	65.1	70.7	81.5	25.4	14.0	32.3	37.9
03	MMMN	V2236	T	51 52 N	98 32 W	H	U	MB	CAVE	65.6	62.3	78.2	26.1	14.3	28.3	38.2
04	MMMN	V2237	T	51 23 N	97 29 W	H	U	MB	CAVE	70.8	74.4	84.6	27.2	14.1	35.3	46.8
05	UM	533RRR	O	79 30 N	76 00 W	N	M	NT	>21	63.9	65.4	79.0	26.2	13.8	31.7	41.5
06	UM	CM11	O	68 06 N	135 30 W	N	F	NT	>21	65.0	72.2	83.5	25.7	14.2	32.1	43.8
07	UM	PRUTT	T	60 00 N	114 00 W	N	U	AB	>21	63.4	61.6	80.4	26.3	13.2	34.3	39.6
08	UM	PRUTT	T	60 00 N	114 00 W	N	U	AB	>21	68.8	63.1	78.7	25.4	13.2	32.2	44.7
09	MMMN	V2230	O	51 47 N	98 35 W	H	U	MB	~5K*	66.9	68.2	85.0	25.1	11.9	33.1	43.8
10	MMMN	V2231	O	51 47 N	98 35 W	H	U	MB	~5K*	64.0	63.1	79.4	23.7	12.0	30.7	41.2
12	UCM	10588	T	40 - N	107 - W	S	F	CO	1906	59.9	60.2	79.5	25.4	12.0	28.4	38.6
13	UCM	10587	T	40 - N	107 - W	S	M	CO	1907	68.0	70.9	83.2	25.1	13.0	32.0	39.4
14	UCM	10589	T	38 00 N~	108 00 W	S	M	CO	1907	63.6	65.9	76.9	24.8	13.4	29.7	40.2
15	UCM	10590	T	38 00 N~	108 00 W	S	F	CO	1908	66.1	63.0	80.2	23.7	13.8	29.5	38.5
16	DMNH	1630	T	41 00 N~	102 00 W	LPL/H	U	CO	CAVE	66.5	70.8	84.1	24.9	15.0	34.1	42.5
17	DMNH	6837	T	40 00 N~	108 00 W	S	F	CO	1918	65.0	58.4	75.0	24.3	13.1	27.9	38.5
18	DMNH	1861	T	39 00 N	108 30 W	S	F	CO	1921	66.4	68.0	82.6	23.8	14.0	33.4	40.5
19	DMNH	6656	T	45 00 N~	110 00 W	S	U	MT	1918	62.5	65.0	79.0	25.3	12.8	30.7	36.4
20	DMNH	1844	T	45 00 N~	110 00 W	S	U	MT	1920	65.3	60.5	73.0	23.2	13.0	25.5	38.3
21	KU	2142	T	49 00 N	118 12 W	S	F	BC	1890	67.0	57.9	76.0	24.4	13.8	28.7	40.5
22	KU	2143	T	49 00 N	118 12 W	S	M	BC	1881	66.4	63.7	84.4	28.0	13.4	32.5	40.1
24	KU	7575	O	38 51 N	100 10 W	S	U	KS	1920	65.8	63.2	80.7	24.1	13.3	30.8	38.5
26	KU	138996	E	U.S.S.R.		-	M	RU	1983	67.8	64.4	82.2	26.7	14.1	31.5	46.1
27	KU	2141	O	No Man's Land		S	M	OK	1888	62.0	60.5	74.1	24.3	13.7	27.9	39.7
28	KU	2138	O	No Man's Land		S	M	OK	1888	66.9	59.9	78.7	23.9	13.2	29.0	40.1
29	KU	2139	O	No Man's Land		S	F	OK	1888	65.1	53.6	70.8	22.5	11.3	25.6	35.5
30	KUVP	51276	O	44 50 N	108 23 W	LPL	U	WY	NTC	73.3	66.3	94.2	28.3	13.9	38.6	47.7
32	KUVP	57910	O	44 50 N	108 23 W	LPL	U	WY	NTC	69.8	60.1	82.0	26.7	13.0	34.4	43.2
40	KUVP	51306	O	44 50 N	108 23 W	LPL	U	WY	NTC	68.0	62.0	84.8	26.2	13.2	32.4	46.6
47	SMNH/M107	14035	O	49 40 N	106 50 W	H	U	SK	SNBO	64.7	60.2	77.2	23.6	13.8	30.0	43.5
48	SMNH/M113	14040	O	50 56 N	106 09 W	H	U	SK	SEDEP	63.4	53.7	74.0	24.3	13.5	28.9	38.4
51	SMNH	FT.CRLTN	O	52 52 N	106 32 W	N	U	SK	1860	66.4	63.2	81.2	25.8	12.5	30.9	38.0
52	SMNH	FT.CRLTN	O	52 52 N	106 32 W	N	U	SK	1860	65.0	58.3	79.8	23.7	11.5	31.5	40.4
55	SMNH	P1033	O	50 27 N	105 49 W	H	U	SK	SNBO	63.7	62.6	83.2	25.1	13.1	31.9	36.6
56	ISUM	BLM(A)	O	44 50 N~	108 23 W	LPL/H	U	WY	CAVE	64.3	59.8	72.6	22.9	12.5	26.8	35.8
57	ISUM	19835	T	43 25 N~	112 00 W	H	U	ID	~5K	62.9	63.8	78.5	24.9	13.6	30.9	40.5
58	ISUM	19838	T	43 25 N~	112 00 W	H	U	ID	~5K	67.8	62.7	87.4	27.7	15.7	36.1	47.7
59	ISUM	19836	T	43 25 N~	112 00 W	H	U	ID	~5K	64.1	58.9	73.1	22.1	12.5	30.8	35.4
60	ISUM	19837	T	43 25 N~	112 00 W	H	U	ID	~5K	67.6	54.7	74.6	24.3	12.5	28.2	38.6
61+	ISUM	6377.52	-	43 00 N	113 00 W	LPL	U	ID	>75K	71.2	80.5	99.3	30.4	13.7	40.0	44.8



OBS	SPEC	NUM	HAB	LAT.	LONG.	AGE	SEX	COLLO	DT/DEP	BRNCS	M2BL	MAXTH	P4CLN	M2CWT	PALP1	POCNS
63	ISUM	38241	T	43 30 N	114 00 W	H	U	ID	LATU	60.7	57.8	70.7	22.1	11.9	25.4	37.0
65	ISUM	32329	T	43 30 N	114 00 W	H	U	ID	LATU	65.5	60.2	77.8	25.3	12.8	28.6	40.5
66	ISUM	24717	T	43 25 N~	112 00 W	H	U	ID	~5K	65.0	65.8	79.2	25.2	13.7	32.5	36.9
67	ISUM	23920	T	43 25 N~	112 00 W	H	U	ID	~5K	64.6	63.7	78.8	24.7	12.0	31.2	38.7
68	ISUM	ARCHEO.A	T	43 25 N~	112 00 W	H	U	ID	LATU	63.7	58.6	78.9	23.4	13.7	27.1	40.3
70	UBC	6151	T	50 19 N	122 48 W	N	M	BC	1945	71.3	72.5	82.5	24.3	14.0	32.4	51.7
71	UBC	6148	T	50 19 N	122 48 W	N	M	BC	1936	65.5	69.4	77.9	24.4	14.1	30.0	42.9
72	UBC	6146	T	49 19 N	124 54 W	S	M	BC	1932	67.5	67.5	80.3	26.5	15.3	27.7	42.7
73	UBC	1494	T	49 03 N	113 54 W	S	M	AB	1945	64.7	69.8	81.7	26.9	14.2	28.7	44.2
74	UBC	2398	T	51 47 N	119 19 W	N	F	BC	1947	68.3	74.1	85.0	25.0	13.5	36.0	47.2
75	UBC	BOX65	T	59 03 N	100 00 W	N	F	MB	1953	67.2	61.7	76.5	25.7	13.5	29.6	44.8
76	UBC	3101	T	54 47 N	99 47 W	N	U	MB	1950	71.0	69.6	84.6	25.7	13.5	33.9	40.1
77	UBC	4244	T	54 47 N	99 47 W	N	M	MB	1949	68.9	70.2	85.0	28.2	15.2	33.2	46.4
78	UBC	874	T	52 30 N	125 20 W	N	M	BC	1943	66.8	70.4	78.5	25.9	13.9	30.7	41.0
79	UBC	6746	T	54 47 N	99 47 W	N	F	MB	1954	66.1	65.5	76.6	25.0	14.6	29.7	36.3
80	UBC	6742	T	53 54 N	99 21 W	N	F	MB	1954	67.4	64.2	72.0	23.9	13.3	30.2	41.6
82	UBC	6743	T	55 44 N	101 20 W	N	F	MB	1954	64.8	63.4	76.1	24.7	14.3	29.5	41.5
83	UBC	6747	T	55 44 N	101 20 W	N	M	MB	1953	69.1	69.2	82.7	27.5	14.7	34.8	42.9
84	UBC	6728	T	55 44 N	101 20 W	N	M	MB	1954	65.4	72.3	88.6	26.8	13.6	33.7	41.5
85	UBC	6737	T	57 45 N	99 42 W	N	F	MB	1954	66.7	64.0	78.0	25.3	13.5	30.3	45.2
86	UBC	6734	T	57 45 N	99 42 W	N	F	MB	1954	69.7	65.3	82.4	25.8	14.2	30.2	42.3
87	UBC	6739	T	53 33 N	100 20 W	N	M	MB	1954	70.2	70.5	86.5	27.3	14.4	35.9	42.4
88	UBC	6729	T	57 53 N	101 40 W	N	F	MB	1953	68.5	67.1	79.3	25.3	14.4	30.3	40.6
89	UBC	6732	T	59 03 N	100 00 W	N	M	MB	1953	63.1	70.6	82.0	26.6	14.4	32.6	43.4
90	UBC	6740	T	57 00 N	97 50 W	N	M	MB	1954	69.8	70.3	85.2	26.6	13.0	34.8	44.6
91	UBC	6785	T	57 45 N	99 42 W	N	F	MB	1954	68.0	63.1	78.7	26.4	14.2	30.8	40.3
92	UBC	6795	T	57 45 N	99 42 W	N	F	MB	1954	65.3	61.3	75.1	25.9	14.1	28.0	41.5
93	UBC	6804	T	57 47 N	98 33 W	N	M	MB	1954	64.0	70.3	83.9	25.7	13.6	33.0	37.4
94	UBC	6784	T	55 44 N	101 20 W	N	M	MB	1954	65.0	68.7	80.6	24.6	12.7	29.1	38.4
95	UBC	6805	T	57 08 N	100 14 W	N	M	MB	1954	71.8	65.6	85.8	26.9	14.7	34.9	41.2
96	UBC	6806	T	59 34 N	101 10 W	N	F	MB	1954	66.1	60.9	77.9	23.6	12.2	29.1	41.0
97	UBC	6786	T	57 47 N	98 33 W	N	F	MB	1954	63.9	61.4	80.3	25.5	13.8	31.5	35.7
98	UBC	6787	T	56 54 N	95 14 W	N	F	MB	1954	67.8	64.9	81.1	22.4	14.3	31.1	47.2
99	UBC	6791	T	58 50 N	100 00 W	N	F	MB	1954	67.7	62.9	75.7	24.2	13.3	31.1	42.5
100	UBC	6788	T	59 03 N	100 00 W	N	M	MB	1953	66.4	66.1	78.2	24.0	12.8	32.4	43.5
101	UBC	6793	T	57 53 N	101 40 W	N	F	MB	1954	67.6	62.6	78.2	26.1	13.9	29.8	42.6
102	UBC	6828	T	59 34 N	101 10 W	N	F	MB	1954	66.4	61.9	82.1	25.3	13.1	30.1	34.3
103	UBC	6872	T	55 44 N	101 20 W	N	M	MB	1954	65.5	72.1	85.3	27.4	14.2	33.7	42.9
105	UBC	6832	T	57 08 N	100 14 W	N	F	MB	1954	68.7	65.1	77.9	25.4	13.8	31.8	38.2
106	UBC	6815	T	58 50 N	100 00 W	N	F	MB	1954	67.6	62.9	75.0	24.0	13.1	31.7	41.0

OBS	SPEC	NUM.	HAB	LAT.	LONG.	AGE	SEX	COLLO	DT/DEP	BRNCS	M2BL	MAXTH	P4CLN	M2CWT	PALP1	POCNS
107	UBC	6816	T	59 16 N	101 29 W	N	M	MB	1954	67.4	63.8	85.4	26.4	15.0	33.0	45.6
108	UBC	6834	T	57 45 N	99 42 W	N	M	MB	1954	69.3	67.2	84.4	27.1	14.4	33.6	41.5
109	UBC	6836	T	55 44 N	101 20 W	N	M	MB	1954	70.3	72.1	82.9	26.0	14.8	33.6	41.1
110	UBC	6837	T	57 45 N	99 42 W	N	F	MB	1954	66.2	62.5	78.8	26.0	14.0	30.5	39.1
112	UBC	6943	T	54 55 N	98 38 W	N	M	MB	1951	71.7	70.2	83.2	25.3	13.4	33.5	47.2
113	UBC	6951	T	54 47 N	99 47 W	N	F	MB	1954	67.8	63.9	80.7	24.9	14.1	32.4	43.0
114	UBC	6941	T	56 38 N	100 40 W	N	M	MB	1951	69.0	69.5	87.0	26.5	14.9	34.5	47.6
115	UBC	6954	T	54 22 N	101 00 W	N	F	MB	1954	64.5	67.4	78.1	24.6	12.3	32.0	40.7
116	UBC	6940	T	59 03 N	100 00 W	N	M	MB	1954	69.6	69.4	86.7	26.6	15.1	36.9	46.2
117	UBC	6966	T	54 06 N	101 22 W	N	M	MB	1954	69.7	63.6	86.0	27.0	13.6	36.0	43.8
118	UBC	6958	T	59 03 N	100 00 W	N	F	MB	1953	67.4	63.0	81.9	26.5	13.3	31.8	37.7
119	UBC	6909	T	Northern		N	M	MB	1955	67.0	64.8	83.5	25.5	13.7	36.6	43.6
120	UBC	6953	T	54 04 N	101 18 W	N	M	MB	1954	69.4	70.2	80.6	27.0	14.7	34.2	44.7
121	UBC	6964	T	57 53 N	101 40 W	N	M	MB	1953	68.7	71.3	89.1	27.1	14.6	34.4	45.6
122	CMN	94	O	63 00 N	71 30 W	N	M	NT	1885	68.8	62.1	79.7	24.8	13.3	30.9	47.2
123	CMN	1875	O	36 27 N	103 10 W	S	M	NM	1893	67.0	63.2	82.2	25.2	14.1	31.0	43.2
124	CMN	2789	O	68 00 N	115 00 W	N	M	NT	1916	65.5	63.7	82.8	27.3	14.0	31.3	41.2
125	CMN	2790	O	68 00 N	115 00 W	N	F	NT	1915	66.4	60.9	76.9	25.7	13.4	28.9	34.0
126	CMN	2791	O	68 00 N	115 00 W	N	M	NT	1915	67.1	60.5	79.4	25.7	13.8	30.4	41.8
127	CMN	3506	O	71 59 N	126 00 W	N	U	NT	1915	64.1	65.4	75.3	24.2	13.5	26.5	36.8
128	CMN	3726	O	36 27 N	103 10 W	S	F	NM	1893	65.4	60.7	72.2	23.2	11.5	29.3	36.3
129	CMN	4899	O	68 00 N	75 00 W	N	U	NT	1923	68.8	61.4	77.6	22.4	13.2	31.1	43.1
130	CMN	5550	O	68 00 N	75 00 W	N	F	NT	1923	63.2	63.4	75.9	24.6	13.0	29.4	37.4
131	CMN	6003	O	63 09 N	107 52 W	N	U	NT	1924	68.6	58.8	84.3	27.7	14.1	34.3	42.8
132	CMN	6006	O	63 09 N	107 52 W	N	M	NT	1924	67.6	66.6	87.4	27.2	15.9	33.2	45.6
133	CMN	6005	O	63 09 N	107 52 W	N	M	NT	1924	67.5	69.8	82.8	24.7	14.3	30.0	40.4
134	CMN	6004	O	63 09 N	107 52 W	N	F	NT	1924	67.5	68.3	83.9	23.7	14.7	34.5	37.4
135	CMN	8745	T	59 15 N	113 15 W	N	U	AB	1927	66.7	69.4	83.5	25.9	14.2	32.2	41.1
136	CMN	8744	T	59 15 N	113 15 W	N	U	AB	1927	68.2	73.9	87.2	27.0	15.1	34.0	46.0
138	CMN	8746	T	59 15 N	113 15 W	N	U	AB	1927	68.5	69.2	81.8	26.7	14.2	31.7	41.6
139	CMN	17282	O	50 50 N	100 00 W	N	M	MB	1943	65.0	73.2	80.1	25.7	14.6	30.1	41.9
141	CMN	19177	O	50 50 N	100 00 W	N	F	MB	1946	64.8	65.3	77.6	22.7	13.8	30.8	43.5
142	CMN	17530	O	71 17 N	156 47 W	N	U	AK	1936	68.9	65.7	85.0	26.1	14.3	33.7	47.5
143	CMN	21569	T	50 50 N	100 00 W	N	U	MB	1907	68.4	75.2	84.6	28.3	13.9	33.6	47.1
144	CMN	21567	O	49 52 N	99 22 W	S	M	MB	1946	68.3	72.3	86.2	25.7	13.6	34.4	45.1
145	CMN	16869	T	52 50 N	118 08 W	N	U	AB	1939	63.9	73.8	82.6	25.2	14.9	29.9	41.8
146	CMN	14106	T	63 30 N	139 44 W	N	U	YK	1935	68.6	73.8	86.1	27.6	15.5	34.4	47.0
147	CMN	14919	O	63 04 N	107 57 W	N	U	NT	1936	67.9	67.1	81.7	24.2	14.5	32.8	43.9
148	CMN	18254	T	61 51 N	121 18 W	N	M	NT	1944	71.2	73.1	81.0	25.9	15.4	31.1	45.0
149	CMN	16943	T	54 00 N	106 25 W	N	M	SK	1940	67.1	77.1	83.7	27.7	15.5	32.5	41.0

OBS	SPEC	NUM.	HAB	LAT.	LONG.	AGE	SEX	COLLO	DT/DEP	BRNCS	M2BL	MAXTH	P4CLN	M2CWT	PALP1	POCNS
150	CMN	16942	T	54 00 N	106 25 W	N	M	SK	1940	66.6	75.7	88.6	25.7	13.7	33.4	43.3
151	CMN	18338	T	59 31 N	111 28 W	N	U	AB	1945	67.5	67.7	89.1	27.5	15.7	35.4	42.8
152	CMN	18342	T	59 31 N	111 28 W	N	U	AB	1945	67.7	66.8	84.3	25.7	14.9	31.7	43.7
156	USNM	3002	O	48 00 N~	104 00 W	S	U	MT	1857	66.7	57.4	74.1	23.4	11.0	26.8	43.4
159	USNM	3007	O	48 00 N~	104 00 W	S	U	MT	1857	62.4	59.7	72.5	24.4	12.9	29.2	38.6
160	USNM	3009	O	48 00 N~	104 00 W	S	U	MT	1857	59.7	54.5	73.2	23.3	13.0	28.7	31.2
162	USNM	2972	O	48 00 N~	104 00 W	S	U	MT	1857	64.8	63.6	84.1	26.2	13.9	33.9	39.2
164	USNM	2975	O	48 00 N~	104 00 W	S	U	MT	1857	65.1	58.9	75.4	23.6	13.3	29.9	34.4
165	USNM	2984	O	48 00 N~	104 00 W	S	U	MT	1857	63.3	62.9	80.6	23.6	11.6	30.5	39.5
166	USNM	2976	O	48 00 N~	104 00 W	S	U	MT	1857	68.3	64.4	82.2	24.9	12.0	30.6	40.7
167	USNM	2996	O	48 00 N~	104 00 W	S	U	MT	1857	67.5	60.4	76.4	24.8	12.3	27.6	38.9
168	USNM	2994	O	48 00 N~	104 00 W	S	U	MT	1856	64.9	58.6	77.0	26.6	12.5	29.4	37.8
169	USNM	2946	O	48 00 N~	104 00 W	S	U	MT	1857	64.7	49.4	76.0	24.2	12.3	29.2	35.0
171	USNM	2944	O	48 00 N~	104 00 W	S	U	MT	1856	67.0	64.5	80.3	24.4	13.4	33.5	40.0
172	USNM	2943	O	48 00 N~	104 00 W	S	U	MT	1857	63.8	65.9	77.9	23.6	12.7	31.2	37.8
176	USNM	2950	O	48 00 N~	104 00 W	S	U	MT	1857	63.2	55.2	71.9	22.2	11.3	26.9	37.3
177	USNM	2948	O	48 00 N~	104 00 W	S	U	MT	1857	64.5	57.0	76.3	25.2	14.0	29.2	39.0
178	USNM	271657	O	46 48 N	95 50 W	S	M	MN	1941	66.2	70.3	77.7	25.4	14.5	31.2	39.6
180	USNM	2953	O	48 00 N~	104 00 W	S	U	MT	1857	64.1	54.6	76.7	23.7	12.6	30.6	42.8
182	USNM	2968	O	48 00 N~	104 00 W	S	U	MT	1857	65.3	67.1	79.7	25.6	13.3	29.0	41.4
183	USNM	2966	O	48 00 N~	104 00 W	S	U	MT	1857	64.3	58.8	74.0	22.8	12.9	26.8	38.8
184	USNM	148560	T	51 35 N	101 00 W	N	U	MB	1906	65.1	69.8	81.1	24.1	13.1	32.1	44.4
185	USNM	148561	T	51 35 N	101 00 W	N	U	MB	1906	64.1	67.7	85.0	25.5	12.9	33.7	41.1
187	USNM	11592	O	39 00 N~	98 00 W	S	U	KS	1871	63.2	56.4	77.6	25.9	13.2	30.2	40.6
188	USNM	139156	O	39 00 N~	98 00 W	S	U	KS	1872	65.5	63.5	79.6	25.7	12.2	31.5	39.3
189	USNM	85421	O	38 14 N	104 36 W	S	M	CO	1898	64.7	63.7	80.1	26.1	12.5	30.0	38.7
191	USNM	52059	O	38 00 N~	103 00 W	S	M	CO	1893	62.0	60.6	72.3	23.1	12.7	25.6	36.3
193	USNM	51863	O	38 00 N~	103 00 W	S	U	CO	1893	61.1	63.0	77.0	24.6	12.7	28.6	40.1
194	USNM	51434	O	38 00 N~	103 00 W	S	M	CO	1893	68.2	67.1	82.4	25.1	13.2	33.0	42.1
195	USNM	187972	O	48 22 N	111 50 W	S	F	MT	1883	64.1	62.5	76.9	23.5	11.4	29.8	37.4
196	USNM	8005	O	48 00 N~	105 00 W	S	U	MT	1868	61.1	49.6	69.1	22.4	12.5	27.2	32.0
198	USNM	211143	O	46 24 N	105 50 W	S	M	MT	1916	64.1	63.8	84.1	24.9	12.7	32.4	39.8
199	USNM	223691	O	Mispah		S	F	MT	1917	66.2	55.3	78.1	23.4	13.3	32.7	41.5
200	USNM	224441	O	46 24 N	105 50 W	S	M	MT	1916	64.9	61.9	79.8	24.6	13.3	28.6	43.5
201	USNM	224442	O	46 24 N	105 50 W	S	F	MT	1916	65.8	59.3	77.3	24.8	13.2	31.0	38.8
202	USNM	224443	O	46 24 N	105 50 W	S	F	MT	1917	64.6	60.4	82.9	24.6	13.3	31.3	41.5
203	USNM	228133	O	46 24 N	105 50 W	S	M	MT	1917	62.6	69.5	80.2	24.9	12.7	31.1	36.5
205	USNM	884	O	41 00 N~	99 00 W	S	U	NB	1851	64.0	64.2	82.3	25.9	13.7	33.7	35.6
206	USNM	1312	O	41 00 N~	99 00 W	S	M	NB	1853	64.8	61.1	80.4	25.8	14.3	32.1	41.9
207	USNM	887	O	41 00 N~	99 00 W	S	U	NB	1851	63.1	64.0	81.7	26.3	13.7	30.9	39.6

OBS	SPEC	NUM.	HAB	LAT.	LONG.	AGE	SEX	COLLO	DT/DEP	BRNCS	M2BL	MAXTH	P4CLN	M2CWT	PALP1	POCNS
208	USNM	147703	O	34 30 N	98 30 W	S	M	OK	1906	64.7	59.4	79.2	25.5	13.7	29.9	34.4
209	USNM	196943	O	36 41 N	94 58 W	S	U	OK	1902	65.4	64.0	78.7	24.5	12.4	32.0	32.9
210	USNM	196944	O	36 41 N	94 58 W	S	U	OK	1902	62.3	60.3	74.2	24.1	12.6	28.7	35.6
211	USNM	69486	O	46 55 N	103 31 W	S	M	ND	1894	66.1	63.3	83.6	24.9	13.2	32.4	42.8
212	USNM	69487	O	46 55 N	103 31 W	S	M	ND	1894	65.4	58.9	76.4	22.7	13.3	30.3	41.5
213	USNM	118692	T	Gallo Canyon		S	M	NM	1902	63.1	64.0	84.6	24.8	13.3	34.9	44.2
214	USNM	3521	O	41 03 N	95 52 W	S	U	NB	1859	64.0	58.9	73.0	24.8	12.3	29.5	37.7
215	USNM	2568	O	41 03 N	95 52 W	S	M	NB	1856	68.0	68.4	78.5	24.2	11.7	32.3	39.5
216	USNM	1315	O	41 00 N~	99 00 W	S	U	NB	1853	62.2	61.3	80.5	25.6	14.1	32.6	41.9
217	USNM	3343	O	41 00 N~	99 00 W	S	U	NB	1857	60.2	53.8	71.5	23.6	13.0	27.8	34.8
218	USNM	223729	O	Folsom		S	M	SD	1916	68.6	68.5	83.1	24.5	11.7	33.7	40.3
219	USNM	227682	O	45 01 N	102 02 W	S	F	SD	1917	61.7	64.9	79.4	24.1	13.1	33.3	40.8
220	USNM	271617	O	45 30 N	103 30 W	S	M	SD	1925	66.6	66.1	85.3	27.9	14.6	36.1	41.0
221	USNM	12906	O	43 00 N	97 00 W	S	U	SD	1872	61.0	58.9	76.9	23.3	12.7	29.7	37.2
222	USNM	12907	O	43 03 N	98 33 W	S	U	SD	1873	63.0	55.6	75.9	23.0	12.3	28.6	38.2
223	USNM	210683	O	43 43 N	102 23 W	S	F	SD	1915	66.6	62.7	77.3	25.2	12.6	33.4	37.3
224	USNM	9002	T	61 51 N	121 20 W	N	U	NT	1868	67.5	71.1	86.5	26.8	13.5	31.6	42.0
225	USNM	221852	O	43 31 N	104 02 W	S	F	SD	1916	66.9	57.9	79.3	26.0	12.9	29.5	38.6
226	USNM	242907	T	53 33 N	113 28 W	N	M	AB	1907	70.9	67.2	82.3	27.0	14.4	32.3	44.6
227	USNM	177370	T	Smith Landing		N	M	AB	1911	66.9	74.4	87.4	24.9	13.1	34.8	41.9
228	USNM	9000	T	61 51 N	121 20 W	N	U	NT	1869	66.8	67.0	82.4	26.2	13.7	29.4	44.5
229	USNM	9001	T	61 51 N	121 20 W	N	U	NT	1869	71.0	77.9	90.6	30.1	14.7	34.8	43.5
230	USNM	78120	O	49 42 N	112 49 W	S	M	AB	1896	69.1	72.4	85.9	26.0	13.8	33.1	39.6
231	USNM	215247	T	43 12 N	112 00 W	S	F	ID	1916	61.4	63.4	79.1	25.2	13.6	30.3	34.9
232	USNM	216405	T	44 38 N	111 14 W	S	M	ID	1916	68.1	68.1	83.2	24.6	13.0	33.2	34.4
233	USNM	215803	T	44 40 N	113 21 W	S	U	ID	1916	64.9	68.7	83.2	24.8	13.3	31.0	38.0
234	USNM	227084	T	Argora		S	M	ID	1917	65.2	68.0	83.3	26.2	14.0	29.6	37.5
235	USNM	159367	T	43 48 N	115 07 W	S	M	ID	1909	61.8	61.8	78.9	25.3	12.9	30.9	37.7
236	USNM	214893	T	44 38 N	111 14 W	S	F	ID	1916	62.5	62.0	78.8	24.0	12.5	32.0	38.0
237	USNM	214478	T	62 04 N	130 17 W	N	M	YK	1916	65.8	73.7	87.3	26.9	15.0	39.2	45.5
238	USNM	214477	T	62 04 N	130 17 W	N	M	YK	1916	68.7	67.7	83.4	26.3	13.5	33.9	43.6
239	USNM	134496	T	63 00 N	132 00 W	N	U	YK	1904	65.6	76.0	83.6	26.7	14.5	32.7	42.7
240	USNM	134497	T	63 00 N	132 00 W	N	U	YK	1904	64.9	65.8	81.5	24.0	13.6	31.6	42.7
241	USNM	4415	T	49 00 N	114 03 W	S	U	MT	1861	64.8	58.8	75.5	25.5	13.5	30.1	37.0
242	USNM	243578	T	42 45 N	113 29 W	H	U	ID	LATU	65.7	54.4	73.2	24.0	11.7	28.8	33.0
243	USNM	13949	T	48 56 N	113 40 W	S	U	MT	1874	62.7	58.0	78.2	25.3	12.6	29.6	38.8
244	USNM	228351	T	44 40 N	113 21 W	S	F	MT	1918	65.3	64.0	77.5	24.2	13.4	29.6	34.6
245	USNM	234700	T	42 39 N	111 36 W	S	F	ID	1920	59.7	58.6	75.1	22.6	12.1	29.1	36.1
246	USNM	156824	T	47 45 N	110 40 W	S	M	MT	1908	71.1	70.0	85.5	27.5	15.0	35.4	44.0
247	MMMN	V91	O	49 22 N	99 07 W	H	U	MB	SNBO	66.0	60.6	77.2	25.5	12.9	28.7	40.6

OBS	SPEC	NUM	HAB	LAT.	LONG.	AGE	SEX	COLLO	DT/DEP	BRNCS	M2BL	MAXTH	P4CLN	M2CWT	PALP1	POCNS
248	LACMHC	2600-3	T	34 00 N	118 00 W	LPL	U	CA	RLB	63.6	60.9	74.9	25.5	13.8	30.1	38.3
249	LACMHC	2600-6	T	34 00 N	118 00 W	LPL	U	CA	RLB	70.1	61.3	84.7	27.6	13.9	32.2	48.4
250	LACMHC	607	T	34 00 N	118 00 W	LPL	U	CA	RLB	71.2	65.8	87.8	29.2	14.0	32.7	48.3
251	LACMHC	615	T	34 00 N	118 00 W	LPL	U	CA	RLB	69.8	66.1	86.2	28.7	14.2	32.4	48.1
252	LACMHC	2600-5	T	34 00 N	118 00 W	LPL	U	CA	RLB	64.9	55.8	78.6	26.9	13.1	28.6	42.6
253	LACMHC	2600-7	T	34 00 N	118 00 W	LPL	U	CA	RLB	73.4	60.8	87.3	30.7	14.7	35.8	46.0
254	LACMHC	2300-56	T	34 00 N	118 00 W	LPL	U	CA	RLB	66.4	69.0	94.2	28.9	12.6	37.0	43.9
255	LACMHC	2600-4	T	34 00 N	118 00 W	LPL	U	CA	RLB	68.0	58.4	74.9	24.0	12.6	26.2	42.1
256	LACMHC	2300-44	T	34 00 N	118 00 W	LPL	U	CA	RLB	63.9	62.8	79.7	27.1	14.2	33.0	45.4
257	LACMRLP	R37093	T	34 00 N	118 00 W	LPL	U	CA	RLB	67.8	63.5	92.4	28.7	14.0	31.1	44.9
258+	NOWAK	1979	-	N/A		LPL	U	MX	CAVE	76.0	74.0	103.0	33.7	15.0	37.2	54.2
259+	NOWAK	1979	-	N/A		LPL	U	CA(x=62)	RLB	74.7	72.4	96.2	31.8	15.2	39.3	49.3
260#	NOWAK	1979	-	N/A		LPL	U	AZ	CAVE	56.9	43.1	57.1	19.6	11.3	20.2	32.9
261+	NOWAK	1979	-	N/A		LPL	U	KY	~13k	78.0	82.0	100.7	30.5	15.7	39.0	57.3
262+	NOWAK	1979	-	N/A		LPL	U	CA	~40K	72.5	75.5	99.0	33.0	15.6	40.0	47.8
263	NOWAK	1979	T	39 20 N	101 42 W	LPL	U	KS	-	67.0	54.5	73.0	23.1	14.0	30.0	34.0
264*	NOWAK	1979	-	N/A		LPL	U	MD	mIRV	75.0	77.0	80.0	27.9	15.5	30.7	43.0
265#	NOWAK	1979	-	N/A		LPL	U	CA(x=~39)	RLB	60.5	48.2	61.2	21.1	11.8	22.2	36.7
266	NOWAK	1979	T	N/A		LPL	U	MX	CAVE	63.0	50.5	75.0	25.0	12.4	26.5	40.5

## APPENDIX II.

Table A. Correlations of characters with the first two principal components extracted from the correlation matrix for seven measurements on 175 *C. lupus* specimens collected between 1851 and 1972.

Variable	Eigenvector	
	Prin1	Prin2
BRNCS	0.347751	0.565788
M2BL	0.390191	-0.110056
MAXTH	0.428539	-0.237860
P4CLN	0.375507	-0.427358
M2CWT	0.360975	-0.122328
PALP1	0.389026	-0.162608
POCNS	0.347168	0.622217
Eigenvalue	4.342	0.734
Proportion (%)	62	10

Table B. Correlations of characters with the first two principal components extracted from the correlation matrix for seven measurements on 96 *C. lupus* specimens collected between 1851 and 1920.

Variable	Eigenvector	
	Prin1	Prin2
BRNCS	0.324936	0.564452
M2BL	0.405553	0.038502
MAXTH	0.450270	-0.000853
P4CLN	0.395591	-0.318263
M2CWT	0.319295	-0.634031
PALP1	0.396464	-0.026243
POCNS	0.334029	0.419447
Eigenvalue	4.198	0.795
Proportion (%)	60	11

Table C. Correlations of characters with the first two principal components extracted from the correlation matrix for seven measurements on 131 fossil and recent *C. lupus* specimens. (Late Pleistocene - approximately 40,000 to 10,000 y.B.P.; Holocene - approximately 10,000 y.B.P. to 1850; modern - 1851-1920).

Variable	Eigenvector	
	Prin1	Prin2
BRNCS	0.349309	0.295932
M2BL	0.354150	-0.608627
MAXTH	0.442702	-0.221710
P4CLN	0.406572	0.233272
M2CWT	0.311820	0.437718
PALP1	0.399261	-0.363677
POCNS	0.366925	-0.323733
Eigenvalue	4.351	0.743
Proportion (%)	62	11

Table D. Correlations of characters with the first two principal components extracted from the correlation matrix for seven measurements on 219 fossil (*C. lupus*, *C. latrans*, *C. dirus*, *C. armbrusteri*) and modern (*C. lupus*) specimens.

Variable	Eigenvector	
	Prin1	Prin2
BRNCS	0.369588	0.357985
M2BL	0.368105	-0.334188
MAXTH	0.420257	-0.337191
P4CLN	0.391427	-0.033536
M2CWT	0.338832	0.444053
PALP1	0.391356	-0.460449
POCNS	0.360703	0.485949
Eigenvalue	4.823	0.561
Proportion (%)	69	8

Table E. Correlations of characters with the first two principal components extracted from the correlation matrix for seven measurements on 22 fossil wolf (*C. lupus*, *C. dirus*, *C. armbrusteri*) specimens.

Variable	Eigenvector	
	Prin1	Prin2
BRNCS	0.377440	0.262538
M2BL	0.376381	0.228285
MAXTH	0.406188	-0.383662
P4CLN	0.397417	-0.250627
M2CWT	0.325272	0.750609
PALP1	0.384302	-0.246981
POCNS	0.373440	-0.211036
Eigenvalue	5.217	0.662
Proportion (%)	75	9