

GEOGRAPHICAL VARIATION IN WOLVES (Canis lupus L.)  
OF NORTHWESTERN NORTH AMERICA

by

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## ABSTRACT

Five hundred wolf specimens were studied. They represent populations from Alaska to Keewatin and from Vancouver Island to Manitoba. Pelage color varies nearly from black to white. There are no discrete color phases. Pale wolves are more numerous and dark wolves less numerous toward the tundra (northeastward) between Great Slave Lake and Great Bear Lake. Judging from color variation, wolf populations intermingle by associating with caribou at migration. Male wolves are larger than females (approximately 4% in linear skull dimensions). Northeastern individuals have a shorter and relatively broader skull than southwestern ones. Multivariate divergence in twelve skull dimensions is approximately proportional to geographical separation. This may express genetic differentiation by incomplete isolation. But the pronounced northeastward zonation of the environment may have direct influences upon growth processes. Interpretations in terms of genetic affinities are hypothetical and taxonomic conclusions are postponed. Simultaneous analysis of biometrical data appears indispensable to disclose major trends of geographic variation.

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## INTRODUCTION

The last comprehensive taxonomic study of North American wolves (Canis lupus L.) was that of Goldman (Young and Goldman, 1944). It consisted largely of qualitative skull and pelage descriptions and such procedures failed to show clearly geographic variation in the species as a whole.

Large collections of wolves have been made during recent control operations in northwestern Canada by the Canadian Wildlife Service and the Manitoba Game Department. This material has been deposited in the Museum of Zoology of the University of British Columbia. It forms the main object of the present study. Comparisons were made with British Columbia, Alaska and High Arctic material, some of which was borrowed from the British Columbia Provincial Museum, the National Museum of Canada and Dr. R. Rausch, Anchorage, Alaska.

Much of the limitations of previous studies appears to be due to inefficient methods of analysis. Finding optimum biometrical techniques has therefore been a major aim of this investigation.

The author worked under the guidance of Dr. I. McT. Cowan, Department of Zoology, University of British Columbia. Field aspects of the problem were discussed with several members of the Canadian Wildlife Service. Dr. S. W. Nash, Department of Mathematics, gave numerous explanations on multivariate analysis. Help in mathematics was received from Marcel Banville, Dept. of Physics, W. R. Knight and Bomshik Chang, Dept. of Mathematics and many others. Most calculations were done at the Computing Centre,

with much assistance from the personnel. The author is indebted to Dr. I. McT. Cowan for a critical reading of the manuscript and to other members of the Department of Zoology for advice on illustrations. Discussions with fellow graduate students lead to clarification of several ideas. Financial support came from the Wildlife Conservation Fund of the Canadian Industries Limited. All of this is gratefully acknowledged.

## MATERIAL and DATA

Specimens were grouped by localities of origin (fig. 1). The number of specimens at hand and their most obvious characteristics were considered in delimiting the groups. Sample size and sex composition were taken into account throughout the analysis (table 1). There was only half a dozen juvenile specimens (estimated younger than six months) and they were excluded.

Only four areas are represented by large samples : British Columbia (group K), Manitoba ( I ), and the Northwest Territories between Great Slave Lake and Great Bear Lake ( groups D, E and G). Two arrows have been lined up on these large samples in the map (fig. 1) and in some subsequent graphs. They point approximately northeastward and northwestward and help to refer biometrical differences to their geographical context.

Skulls were available for most specimens while there were pelage and body data for only part of the collection. The analysis of geographic variation was therefore based primarily on skull dimensions. Photographic transparencies of the carcasses were available for four samples of the Northwest Territories and the frequencies of types of pelage coloration were compared.

Twelve skull dimensions were measured. They were chosen for their descriptive value and for the ease with which they could be measured consistently. They are referred to by coded designations ( Li, Wi, Ci and Ti ) and defined as follows :

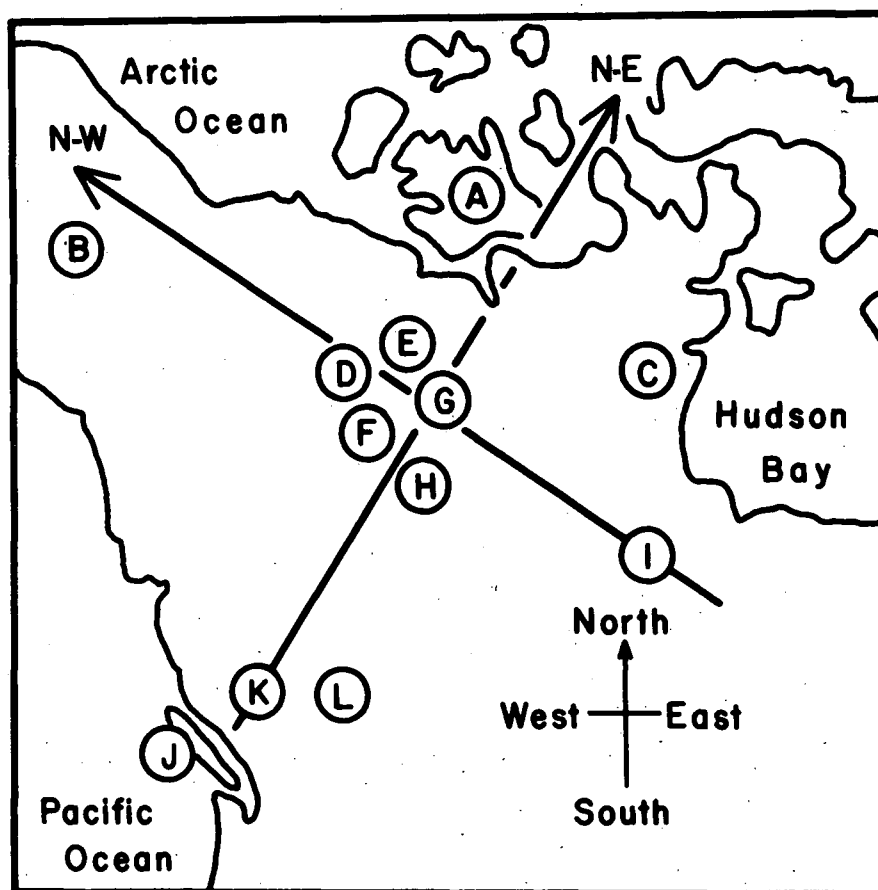


Figure 1 : Geographical origin of the samples.

Table 1 : Sample sizes and sex-compositions.

Locality	group	males	females	undetermined	total
High Arctic	A	11	8	-	19
Alaska	B	3	3	3	9
Keewatin	C	5	3	6	14
	D	41	39	-	80
Northwest Territories	E	41	40	-	81
	F	12	8	-	20
	G	33	33	-	66
	H	-	-	9	9
Manitoba	I	73	64	-	137
Vancouver Island	J	5	5	-	10
Interior B. C.	K	15	12	18	45
Rocky Mountains	L	6	3	-	9
					<u>499</u>



( L 1 ) : MEASUREMENTS OF LENGTH

- ( L 1 ) : Condylbasal length : Distance from the anterior tip of the premaxillae to the plane of the posterior border of the occipital condyles.
- ( L 2 ) : Palatal length : Distance from the alveolus of the median upper incisor on one side to the notch of the posterior edge of the palatal shelf on the same side.
- ( L 3 ) : Post-palatal length : Distance from the notch of the posterior edge of the palatal shelf on one side to the posterior face of the ventral lip of the foramen magnum on the median line.

( W 1 ) : MEASUREMENTS OF WIDTH

- ( W 1 ) : Zygomatic width : Greatest distance across the zygomatic arches.
- ( W 2 ) : Palatal width at M 1 : Greatest distance between the outer edges of the alveoli of the first upper molars.
- ( W 3 ) : Palatal width at Pm 2 : Least distance between the inner edges of the alveoli of the second upper premolars.
- ( W 4 ) : Interglenoid width : Least distance between the postglenoid foramina.
- ( W 5 ) : Interorbital width : Least distance across the frontal bones between the orbits.

( C i ) : MEASUREMENTS EXPRESSING BRAINCASE DEVELOPMENT

( C 1 ) : Least width of the cranium : Least distance across the frontal bones behind the postorbital processes.

( C 2 ) : Interbullar breadth : Distance between the auditory bullae where they angle with the basioccipital bone.

( T i ) : TOOTH MEASUREMENTS

( T 1 ) : Length of the upper carnassial : Distance from the anterior surface of the upper carnassial to its posterior surface at the level of emergence from the alveolus.

( T 2 ) : Length of the first upper molar : Greatest distance from the anterior surface of the first upper molar to its posterior surface at the level of the crown and in the axis of the two outer cusps.

These twelve skull measurements are illustrated in figure number two.

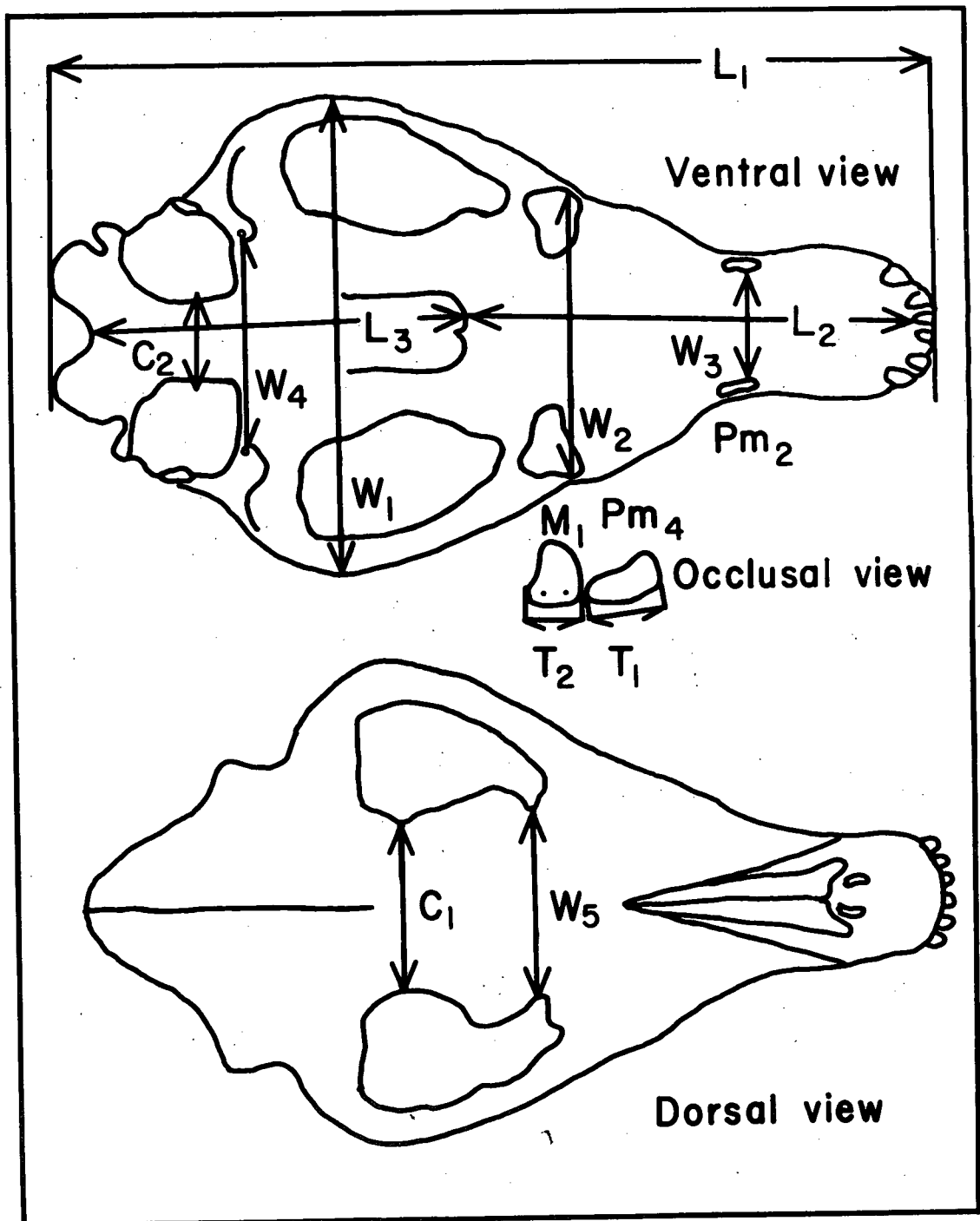


Figure 2 : Skull dimensions measured and coded designations.

## TECHNIQUES OF ANALYSIS

In the physico-chemical sciences variation arises mostly from errors of measurements. Biological variation on the other hand results largely from objective factors. In biological statistics therefore, describing variation concisely is more important than assessing the probability that sets of observations fit a single hypothesis.

Associating biometrical data between themselves and/or with age data is generally necessary to bring out their full meaning. In the analysis of animal form large use has been made of arbitrary age estimates and of ratios of dimensions. Age estimates of wild mammals are generally far less precise than bone measurements except for a few species exhibiting "growth-rings" or other definite criteria of age. Ratios express a proportion by a single figure but they dissociate form from size and they are inefficient for more than two dimensions.

Bivariate scatter diagrams or their multivariate version (Anderson, 1954) are the best simple analytical tool. However multiassociated data usually yield more information through multivariate analysis (Hotelling, 1954; Quenouille, 1952; Yates, 1950). The latter takes into account all intercorrelations of the variables. Animal form can thus be analysed without age estimates save for a broad preliminary classification of the material. Multivariate techniques permit the analyst to express information with maximum conciseness. Most recent applications have unfortunately featured too abstract

a presentation. Expressing the results of a study in terms of the original variables is preferable in practise. Multivariate analysis is now within the reach of biologists thanks to Murdoch's excellent introduction (1957) to linear algebra and analytic geometry.

## VARIATION IN PELAGE COLORATION

Pelage coloration of wolves is highly variable in intensity, in hue and in pattern. There are no obviously discrete color phases as in some polymorphic species.

Detailed verbal descriptions are clearly unsuitable for large samples. The photographic transparencies examined for pelage coloration were classified into four arbitrary types according to the general darkness of pigmentation : dark, darkish, whitish and white. Such arbitrary types do not correspond in the wolf to actually discrete color phases. Such a classification is also only approximate and fits adequately only the present material. It does disclose however a gradual change in color-type frequencies analogous to the clines in color-phase frequencies of the red fox and the black bear (Cowan, 1938).

The relative frequency of pale wolves increases in a northeastward direction (toward the tundra) between Great Slave Lake and Great Bear Lake in the Northwest Territories (fig. 3). There are gradually more white and whitish and fewer dark and darkish individuals in samples F, D, E, and G successively. Samples D and E differ little from each other but differ significantly from the two extreme samples (95% chi squared).

Recent barren-ground caribou studies (Banfield, 1954; Kelsall, 1957) have shown caribou to migrate more through areas D and E than through areas F and G. Differences of pelage coloration between wolf populations appear therefore to be inversely proportional to the local importance of caribou migrations. But wolves are often observed

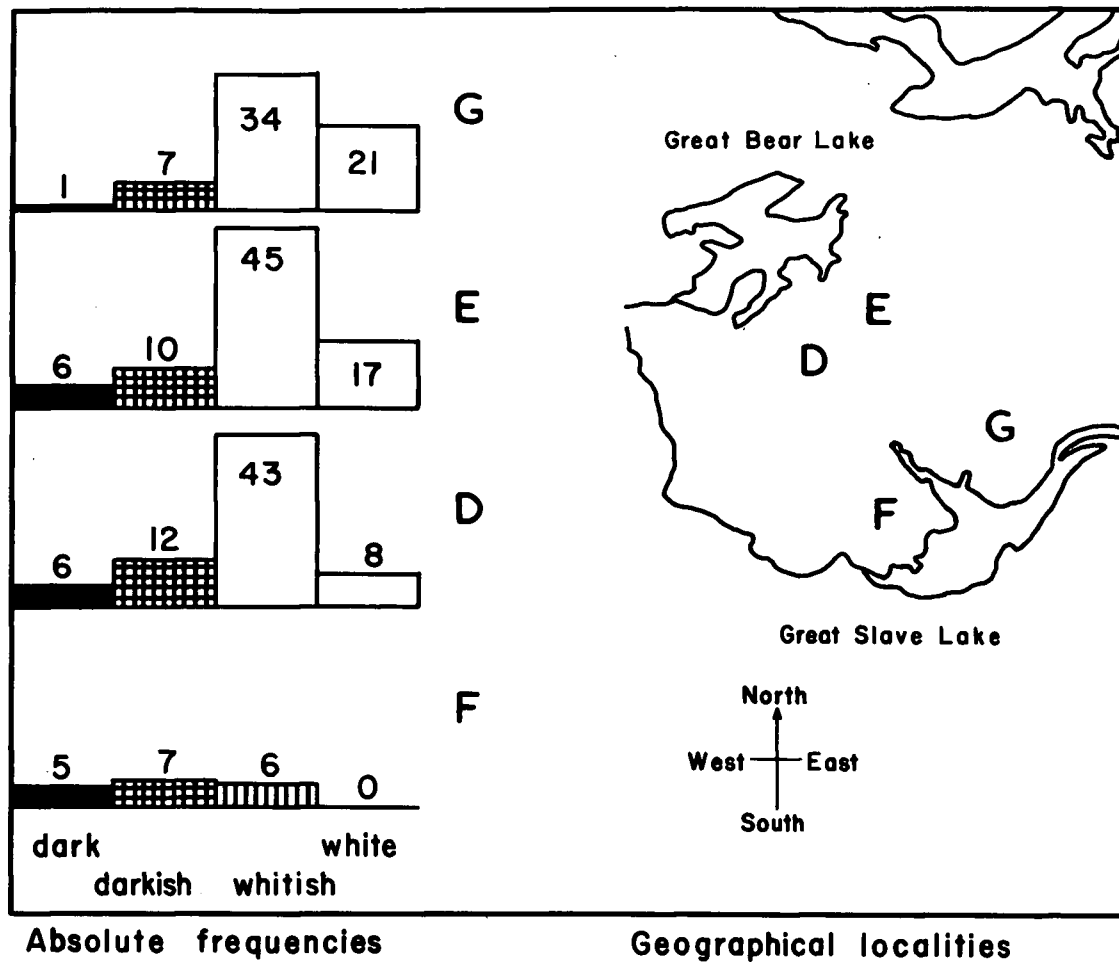


Figure 3 : Northeastward increase in the relative frequency of pale wolves between Great Slave Lake and Great Bear Lake ( toward the tundra ) .

with caribou herds (Banfield, 1951). This suggests that wolf populations intermingle by associating with caribou at migration.

A relatively higher frequency of dark individuals has been reported for the Rocky Mountains (Cowan, 1947). The short-distance cline exhibited by the present material may therefore be part of a long-distance cline going at least from the Rockies to the Northwest Territories. More data on the pelage coloration of wolves may eventually show analogy with the pattern of geographical variation of color-phase frequencies of the red fox and the black bear (Cowan, 1938; Butler, 1947).



## VARIATION IN SKULL SIZE AND FORM : BIVARIATE ANALYSIS

Overall skull size can be satisfactorily described by condylobasal length (L 1) and zygomatic width (W 1). Bivariate dot diagrams of these two dimensions were made and 95% equal-frequency ellipses were calculated following the procedure discussed by Defrise-Gussenhoven (1955).

Figure 4 summarizes the most important information : males reach a skull size approximately 4% greater than females (in linear dimensions). This agrees with Hildebrand's (1952) conclusions regarding the body size of Canidae. Other facts brought out are the lesser maximum skull size (they are closer to the left lower corner of the graph) and the greater relative breadth (they are closer to the left upper corner of the graph) of northeastern wolves. Groups L, I, D + E + G, and A are successively closer to the left side of the graph. This ordering of samples according to skull size and relative breadth is strikingly similar to the ordering of the localities of geographical origin projected upon a line of northeastward direction. Such gradual geographic variation was termed "clines" by Huxley (1938).

The same shortness and greater relative breadth of skull of northeastern wolves shows in a scatter diagram (figure 5) of interglenoid width (W 4) on post-palatal length (L 3). The skulls of wolves from the Northwest Territories ( G ) are shorter and broader than those of wolves from British Columbia ( K ) with respect to these two dimensions. But here the difference of proportion increases with size. This is a difference of relative growth rate.

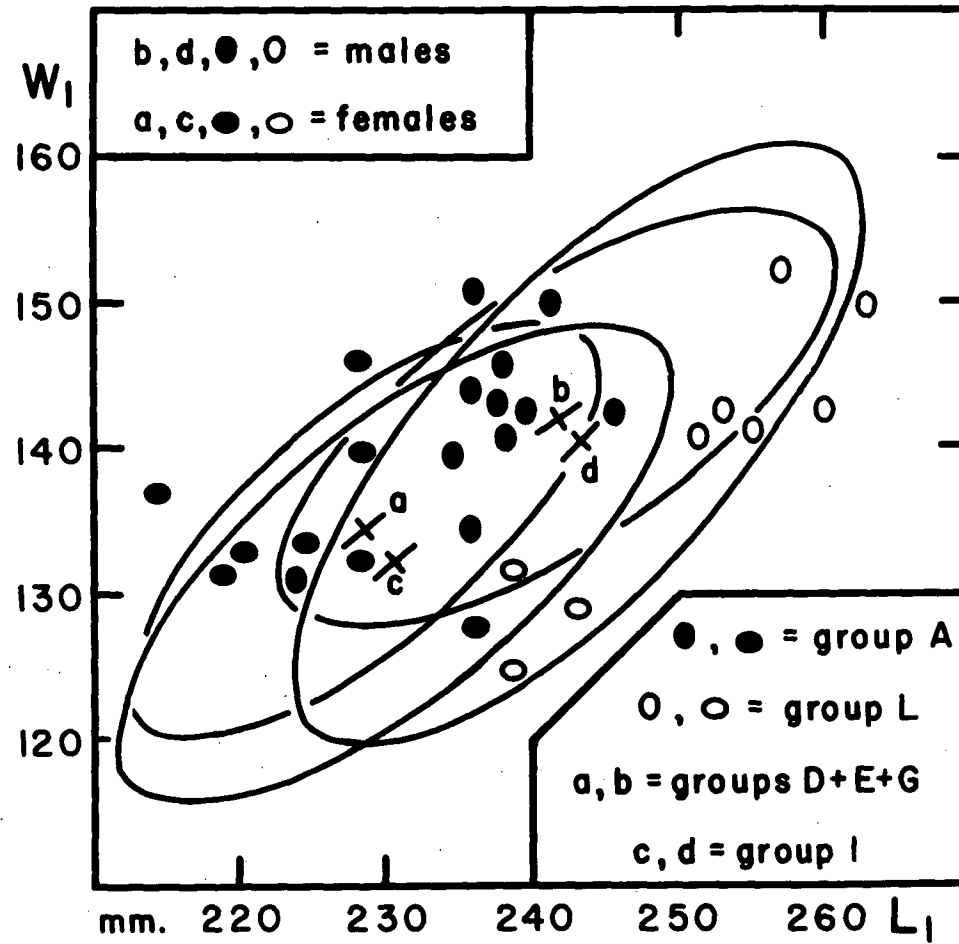


Figure 4 : Sexual and geographic variation in overall skull size and proportions as illustrated by condylbasal length (L<sub>1</sub>) and zygomatic width (W<sub>1</sub>).

Equal-frequency ellipses fit the data satisfactorily; there is no obvious trend curvature and no need for a logarithmic transformation. Rates of relative growth are of considerable biological interest (Huxley, 1932) and a multivariate analysis of growth in wolf skulls is planned for the near future.

A third bivariate association shows geographical variation (figure 6) : interbullar breadth ( C 2 ) against carnassial length ( T 1 ). The wolves from Manitoba ( I ) and the Northwest Territories ( D + E ) are at the center of this graph and constitute the average. The wolves from British Columbia ( K ) have a shorter carnassial than the average and those from Vancouver Island ( J ) a narrower interbullar space. Simple examination of the skulls confirms what the graphical analysis summarizes. Distinct spaces show in between the small teeth of British Columbia wolves and the ten Vancouver Island specimens have markedly "inflated" bullae with a narrow interval. Surprisingly in this graph the Vancouver Island wolves differ the most from those to which they are the closest geographically. Further discussion of this will follow the joint multivariate analysis of all twelve skull dimensions.

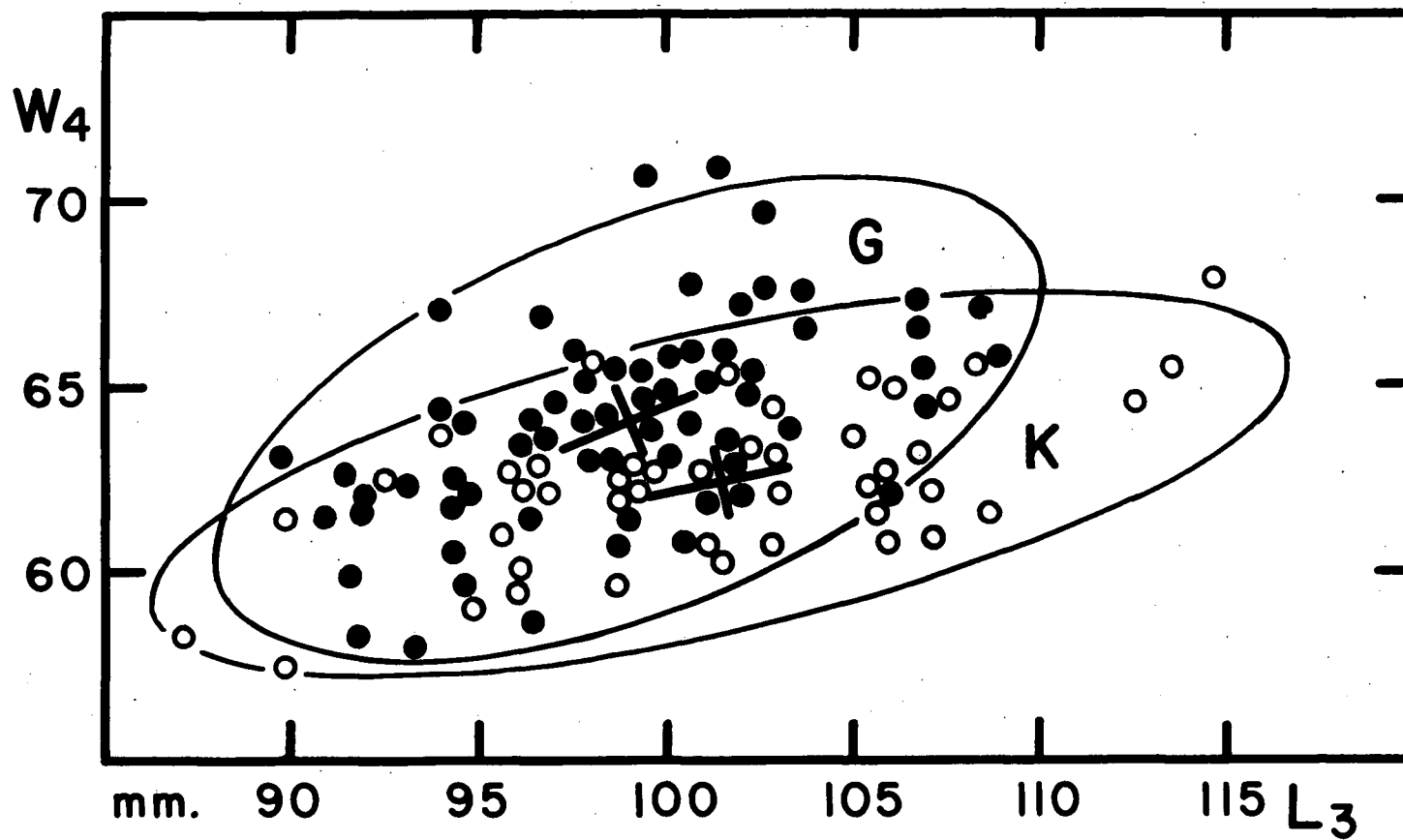


Figure 5 : Geographical variation in a relative growth rate. Interglenoid width ( $W_4$ ) against post-palatal length ( $L_3$ ).

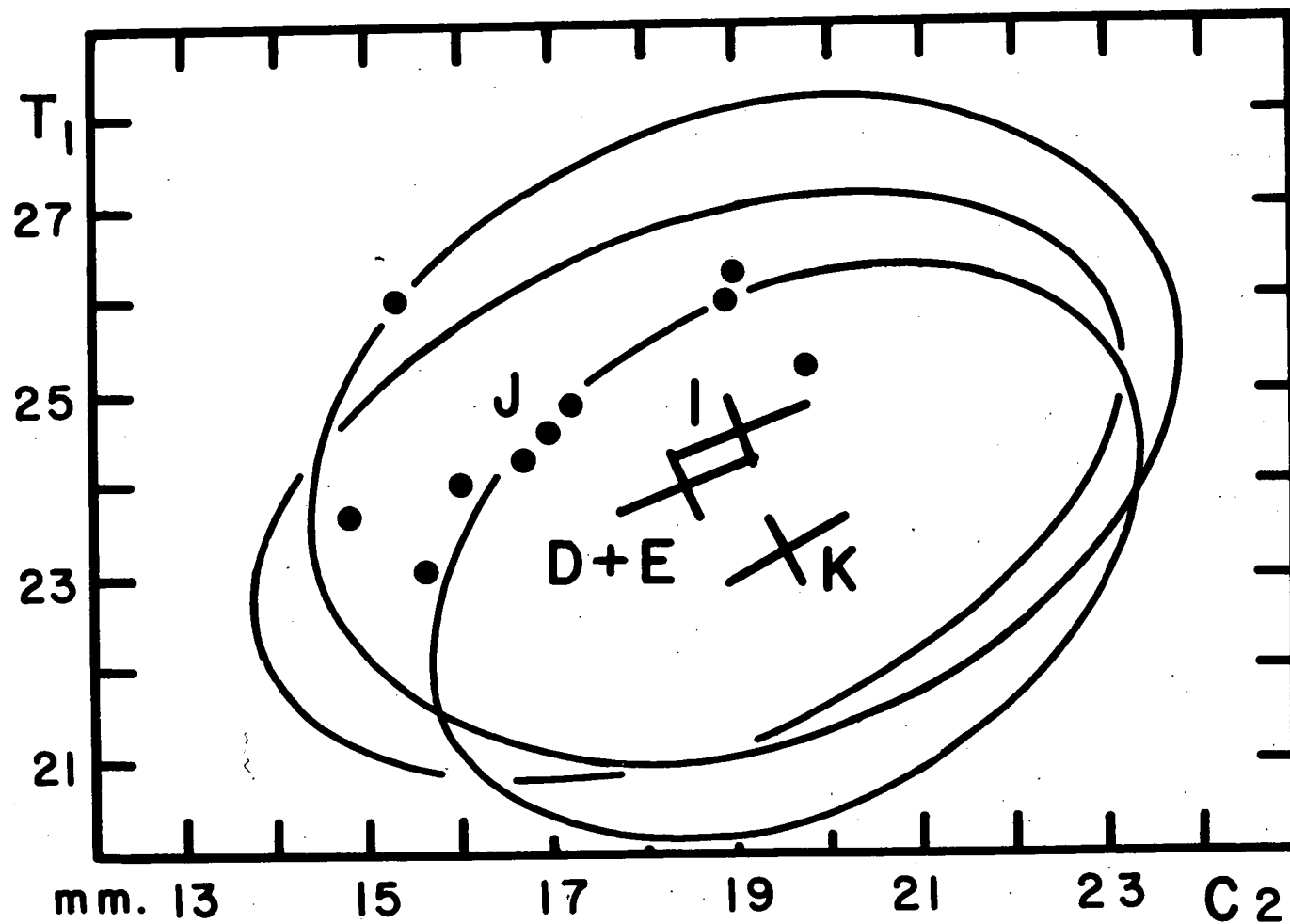


Figure 6 : Geographical variation in interbullar breadth (C 2) and upper carnassial length (T 1).

## VARIATION IN SKULL DIMENSIONS : MULTIVARIATE ANALYSIS

Several multivariate techniques are available for joint biometrical variation. Some lead to overall estimates of between-sample differences ("distance functions"); others lead to combinations of measurements revealing the pattern of divergence or "configuration" of groups ("discriminant functions"). Distance functions express variation as a whole. Discriminant functions disclose the principal components of variation underlying the intercorrelations of the variables.

Discriminant analysis was carried on here following Rao's (1952 :370-378) procedure. Sexual skull differences having shown to be mostly size differences (fig. 4), sexes were kept together to emphasize geographical variation in skull proportions. The within-group product matrix W, generated by the individuals around their group means, came from the 409 specimens of the four largest samples (K, G, D + E, and I ). The between-group product matrix B, generated by the group means around the grand mean came from eleven geographical groups totalling 499 specimens. The B and W matrices were therefore divided by 499 and 409 respectively before calculation of the discriminant functions.

Inspecting the means of the twelve skull dimensions in the eleven geographical groups (table 3) permits a rapid check upon the reality of the trends of joint variation disclosed by discriminant functions. Tabulating other statistics or the original data would consume too much space without making anything explicit.

Discriminant functions K (also called characteristic,

canonical, latent or eigen-vectors) and their variance components  $D$  (characteristic roots or eigen-values) are defined by the following matrix equation :  $KB = DKW$  . They were calculated on an electronic digital computer by matrix operations (Murdoch, 1957 :165-166) corresponding to the transformations suggested by Rao (1952 :357,367). Matrices were diagonalized following Jacobi's method. The within-group variances and covariances of the discriminant functions checked ( $KWK' = I$ ) to two or three significant digits, which is acceptable.

All of these mathematical manipulations correspond to the analysis of between-group variation taking within-group variation as a unit of measurement. This standardization should minimize the effects of differences in age-composition of the samples.

All components of standardized between-group variation add up to 1.5464 . The first five add up to 1.4533 and account for 94% of the total. To each of these five components correspond twelve coefficients for the original variables in the discriminant functions (table 2). The statistical significance of these variance components was tested as prescribed by Rao (1952 :372) for large samples taking 409 as total number of observations. The probability of such large components under a null hypothesis is less than 1% for the first four and less than 5% for the fifth.

The configuration of groups in the two first discriminant functions (figure 7) is recognizably similar to the disposition of the localities of origin on a geographical map. Northern samples congregate in the left upper corner of the graph, eastern samples in the

Table 2 : Discriminant functions. Variance components and coefficients of the skull dimensions.

Function		K 1	K 2	K 3	K 4	K 5
Variance component		.8048	.2761	.1846	.1221	.0657
% of total variance		52%	18%	12%	8%	4%
Coefficients of the skull dimensions	L 1	-.1557	.0645	.2345	.0728	-.1623
	L 2	-.0198	-.1640	-.3480	-.0302	.3744
	L 3	-.0097	.0755	-.2077	-.1402	.1204
	W 1	.0538	-.0498	-.0786	-.0137	-.1650
	W 2	.0172	-.0442	-.1125	-.0182	-.0332
	W 3	-.0080	-.0080	.6301	.3135	.0472
	W 4	.2271	.0993	.0428	-.1227	.1459
	W 5	.1712	-.1420	.0910	-.1803	.1783
	C 1	-.1261	.0044	-.0952	.1221	-.0366
	C 2	-.1970	.1324	.0908	-.2741	-.1258
	T 1	.5036	.7033	-.2729	.4297	.2522
	T 2	.1784	-.3466	.3857	-.4070	.1848



Table 3 : Group means of the skull dimensions in discriminant analysis.

GROUP	N	L 1	L 2	L 3	W 1	W 2	W 3	W 4	W 5	C 1	C 2	T 1	T 2
A	19	231.63	113.84	98.84	139.37	80.32	32.90	65.84	45.44	40.08	19.20	25.77	17.54
B	9	245.67	123.11	102.22	140.45	81.33	35.36	65.65	46.86	43.06	19.46	24.40	17.70
C	14	234.14	116.79	98.50	135.29	78.72	33.67	64.01	45.71	40.52	18.70	24.50	17.33
D+E	161	234.73	117.30	98.49	138.56	78.37	33.58	63.78	46.37	41.28	18.45	23.99	17.28
F	20	242.15	119.55	103.15	140.75	79.63	33.79	65.07	45.64	41.64	19.67	25.13	17.42
G	66	235.98	118.35	99.00	137.76	78.13	33.18	64.05	46.08	41.03	18.59	24.42	17.36
H	9	243.33	120.89	102.89	140.22	79.59	34.39	64.34	46.27	40.49	20.54	23.91	17.19
I	137	237.20	117.75	99.88	136.52	78.63	34.01	63.82	45.11	41.15	19.03	24.61	17.34
J	10	236.30	119.60	98.30	136.70	77.73	31.85	61.15	44.13	41.94	17.03	24.82	16.70
K	45	240.18	119.36	101.40	135.27	76.92	32.97	62.49	44.07	42.16	19.50	23.28	16.80
L	9	251.00	123.45	106.33	139.67	79.91	32.73	66.10	47.51	42.61	22.23	25.23	17.76

right upper corner and inversely for southern and western samples.

The two arrows of northeastward and northwestward directions correspond to those of the map (fig. 1) and help to evaluate the similarity of the pattern of biometrical divergence with the pattern of geographical origin. Discrepancies come mostly from small samples. The major one is the respective position of Alaska ( B ) and Vancouver Island ( J ) wolves.

But the group configuration of the third and fourth discriminant functions (figure 9) compensates largely that discrepancy : Vancouver Island wolves contrast sharply with all others and Alaska wolves are further from the southern ones than all other northern ones.

The first component of multivariate variance (  $D 1 = 52\%$  of total ) corresponds very closely to a northeastward direction and is markedly greater than the next largest one (  $D 2 = 18\%$  of total ) .

Sets of vectors ("arrows") bearing the coded designations of the skull dimensions indicate their contributions to the discriminant functions. Each vector shows the change in the discriminant plane that the corresponding dimension would generate if it varied independently (by 1 standard deviation in fig. 9 and by 2 in fig. 7). Such is not the case of course and these vectors must be considered jointly rather than separately.

Northeastern wolves differ generally from southwestern ones (fig. 7) by a decrease in skull length (  $L 1$  and  $L 3$  ) and in braincase development (  $C 1$  and  $C 2$  ) opposed to an increase in skull breadth (  $W 1$ ,  $W 4$ , and  $W 5$  ). Eastern wolves have a longer upper

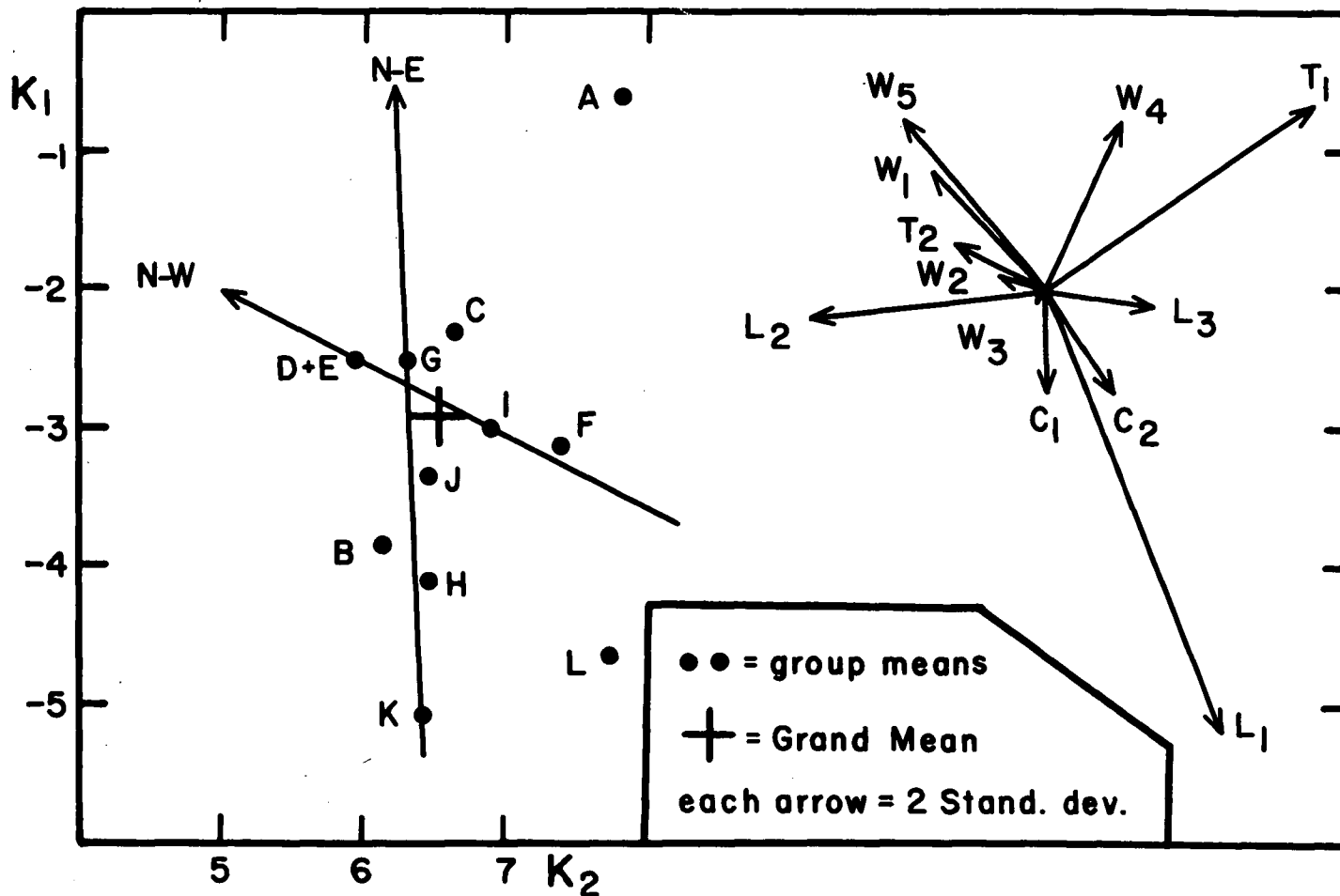


Figure 7 : Group configuration (left) in the first two discriminant functions (  $K_1$  and  $K_2$  ) and variation of the skull dimensions (right); N-W and N-E arrows correspond to those of the map (fig. 1); see text for explanations.

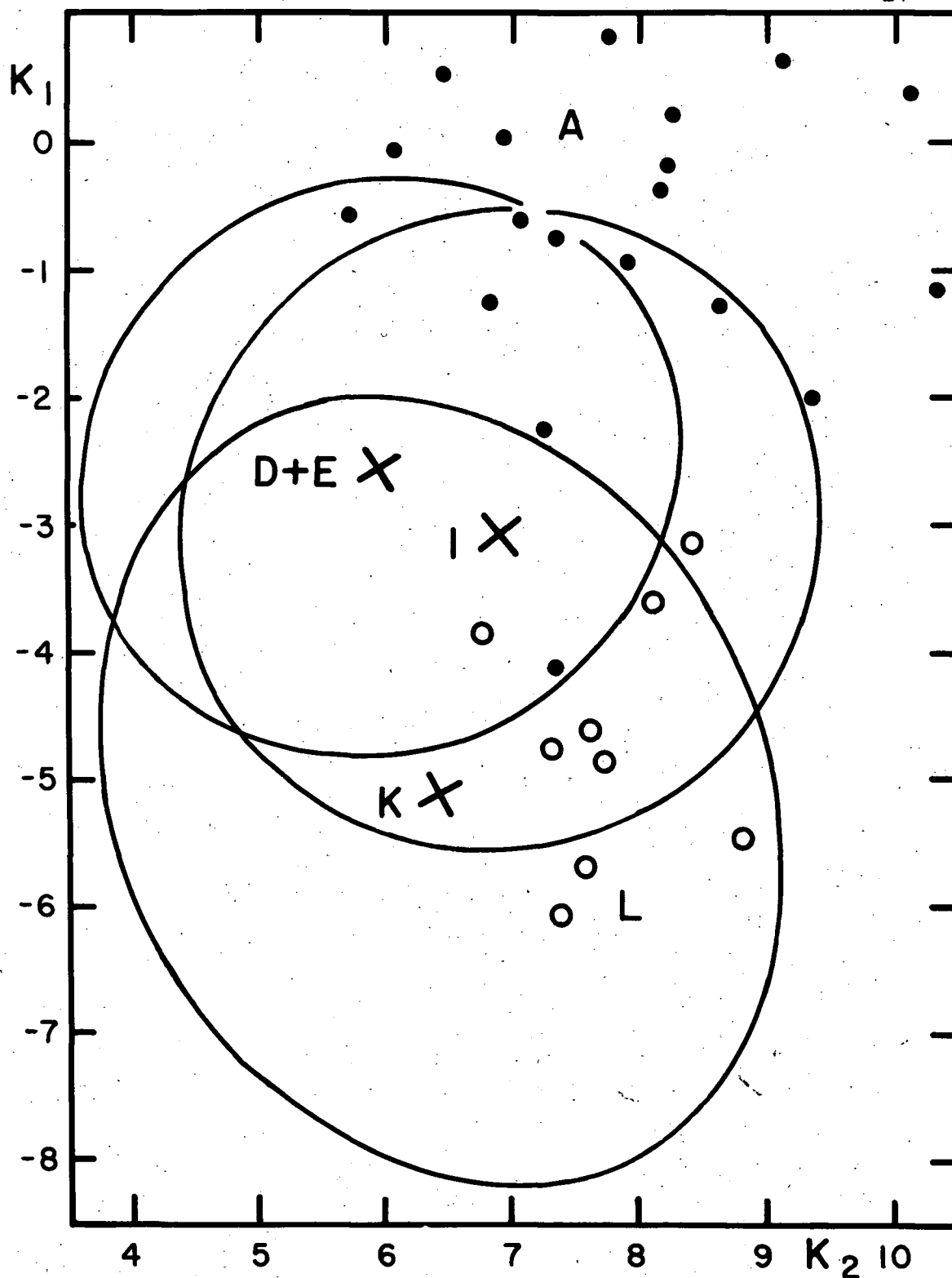


Figure 8 : Biometrical overlapping in discriminant functions  $K_1$  and  $K_2$  illustrated by 95% equal-frequency ellipses; crosses and dots represent group means and individuals respectively; letters refer to closest symbols.

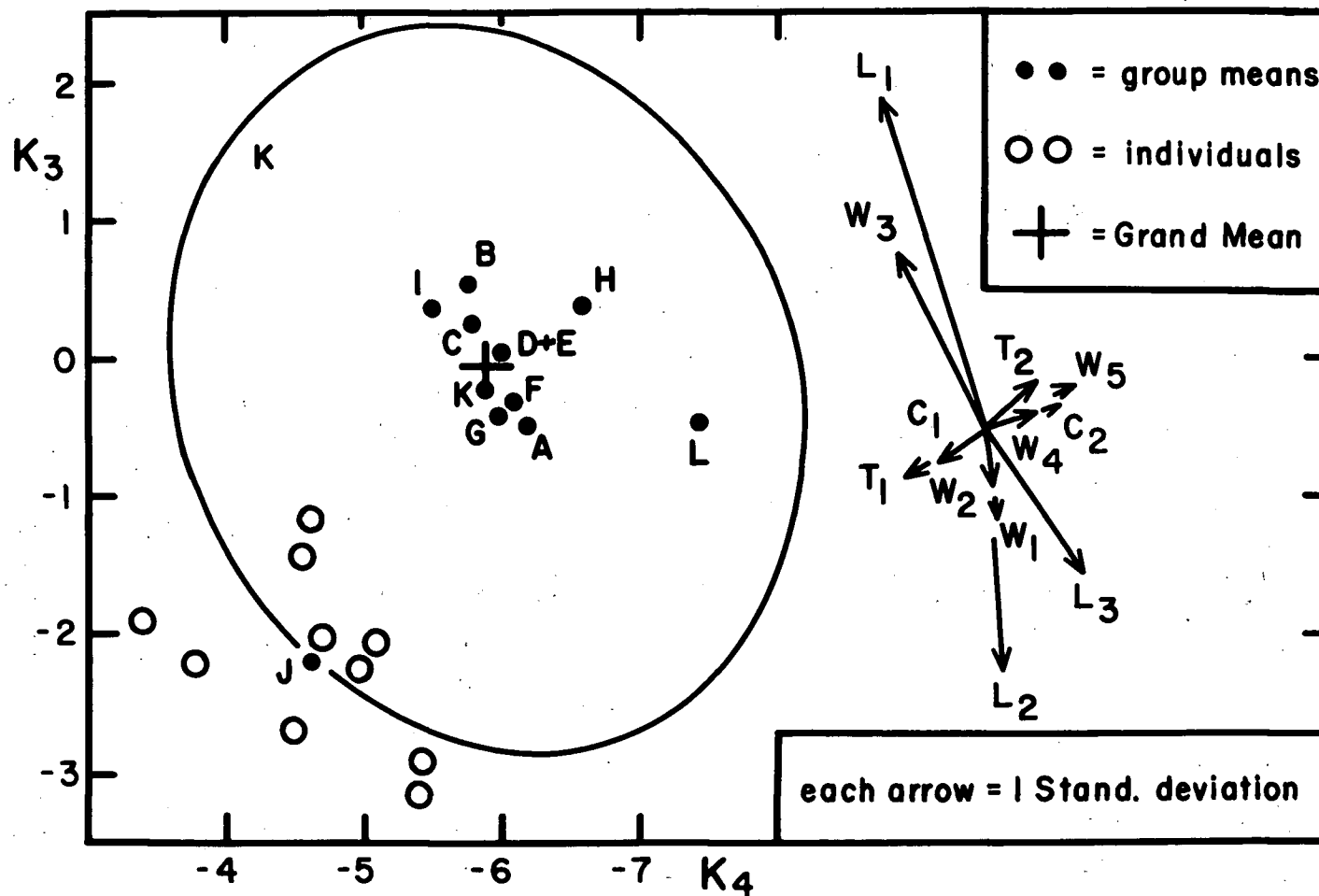


Figure 9 : Group configuration (left) in discriminant functions  $K_3$  and  $K_4$  and variation of the skull dimensions (right); 95% equal-frequency ellipse of group K ; see text for explanations.

carnassial ( T 1 ) and a shorter palate ( L 2 ) than western ones. Such East-West variation had not shown up with simpler analytical techniques.

Vancouver Island wolves ( J ) differ very much from others (figure 9) by six skull dimensions (greater T 1, C 1; lesser T 2, C 2, W 4 and W 5) and very little with respect to the six others. The role of these two groups of dimensions is contrasted not only by the directions but also by the lengths of their vectors. Vancouver Island wolves are much further from the grand mean than the arrows ( 1 standard deviation each ) of their discriminators are long.

The amount of biometrical overlapping can be shown satisfactorily by the individual observations of small samples and by 95% equal-frequency ellipses of large samples. British Columbia wolves ( K ) overlap by approximately 50% (figure 8) with Manitoba ( I ) and Northwest Territories wolves ( D + E ). The wolves from the Rocky Mountains ( L ) are intermediary and overlap largely both with those from British Columbia and those from Manitoba. High Arctic wolves ( A ) overlap by approximately 50% with those from the mainland. The lowermost point of sample A represents a subadult female from Coronation Gulf which should have been grouped with mainland specimens and is relatively narrow-skulled. Save for this exception, High Arctic wolves do not overlap with those from the Rockies. Larger samples would probably do to some extent however. Vancouver Island wolves overlap (fig. 9) by approximately 50% with others.

To sum up, this material shows northeastern wolves to have generally shorter and relatively broader skulls than southwestern

ones and eastern wolves to have a shorter palate and a longer carnassial tooth than western ones. Such a generalization is approximate however : the correspondence between the patterns of biometrical divergence and of geographical separation is imperfect and the first two discriminant functions account for only 70% of total variance. More variance is associated with a northeastward direction than with any other one. Vancouver Island wolves differ markedly from others by six skull dimensions but very little with respect to the six others. The amount of biometrical divergence and overlapping between all groups is approximately proportional to the degree of geographical separation by distance, insularity, etc.

## INTERPRETATIONS AND CONCLUSIONS

The proportionality of biometrical divergence to geographical separation could readily be interpreted in terms of population genetics. Genetic differentiation within an incompletely panmictic population should theoretically be proportional to geographical distance and other factors of isolation (Malécot, 1948; Wright, 1951). The high mobility of wolves would compensate for the extent of their area of distribution and tend to erase the amount of differentiation probably induced by isolation during recent glaciations. Between-group variation is most pronounced northeastward. Sampling has perhaps much to do with the predominance of northeastward variation in this study. But genetical differentiation may be actually greater in that direction.

The genetical interpretation of geographical variation is not the only one available however. The marked northeastward zonation of the environment may have direct influences upon the growth processes involved in skull development. The peripheral dimensions of length and breadth of the skull of Canidae reach full development at a later age than the posterior central region (Huxley, 1880). This appears to be indeed a general pattern of mammalian skull development (Baer, 1954). Particular growth processes could be especially affected if they were in progress during temporary physiological disturbances. Juvenile sheep with thyroid deficiencies grow skulls with normal braincase and teeth but with underdeveloped facial region (Tbodd and Wharton, 1934). Their descriptions would fit



surprisingly well the skulls of northeastern wolves with large teeth cramped in a short palate. Stockard and others ( 1941 ) found pituitary and thyroid abnormalities more frequently in domestic dog breeds with short-broad skulls than in those with long-narrow skulls. The facial development of arctic wolves may therefore possibly be hindered by a low activity of the pituitary and thyroid glands.

Seasonal periodicity of the environment (light, temperature, food, etc.) may have effects upon growth just as on other physiological activities. Molts and coat-color changes of weasels were controlled photoperiodically by Bissonnette and Bailey ( 1944 ); the pituitary gland was considered to be involved. Seasonal periodicity is also known to act through endocrine glands and metabolic factors upon bird migrations, on the reproductive cycles of various vertebrates, etc. Large mammals should be especially affected by seasonal periodicity in prairies and tundra where climatic and ecological conditions are so homogeneous. The northward increase in seasonal periodicity of the environment may therefore have something to do with the skull dimensions reached by wolves. Studies of seasonal variations in wolf behavior may give valuable clues on the effect of arctic winters on the endocrine balance and the metabolism of young wolves. Such studies should also lead to a more integrated view of wolf and dog behavior than either Scott ( 1950 ) or Stockard ( 1941 ) have reached.

Inasmuch as geographical variation expresses genetic differentiation, this analysis may improve our knowledge of genetic affinities. Manitoba wolves are quite closely similar to the ones of

the Northwest Territories from which Alaska wolves also show little difference. Vancouver Island wolves have features of their own but in other respects they resemble northern wolves more than those presently inhabiting the Interior of British Columbia. It is perhaps with northern populations that Vancouver Island had its last free biotic contact. As for the High Arctic wolves, their biometrical characteristics are in good accordance with their geographical position and they give no clear indications of unsuspected genetic affinities.

Taxonomical interpretations of geographical variation can only be accepted when the latter is known to express mostly genetic differentiation. More research is necessary to evaluate direct environmental effects in the present problem. The wolves of Vancouver Island and those of the Interior of British Columbia exhibit pronounced characteristics. Such characteristics fit quite well into the general pattern of variation however and there seems to be no point in thinking of subspecific units unless further studies show variation between populations to be somewhat abrupt. Ascertaining the relationships of western wolves requires more material from Vancouver Island, Alaska, Alberta and the regions in between. On the other hand, the analysis of variation should be extended to the species as a whole or at least to all its North American representatives. There are quite certainly too many subspecific designations in use (Miller and Kellog, 1955).

Goldman's (Young and Goldman, 1944) failure to detect the major trends of geographical variation seems largely due to his

approach. He compared specimens in detail only with those from neighbouring localities. Gradual variation cannot show up clearly unless all samples are compared simultaneously.

Joint trends of variation constitute a "multidimensional field" of variation rather than just "clines" (Huxley, 1938). Multivariate analysis is optimum for multiassociated biometrical data. It should eventually bring out relationships of growth phenomena and geographic variation with physiology and population genetics.

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