Journal of Mammalogy, 104(3):562–577, 2023
https://doi.org/10.1093/jmammal/gyad012
Published online March 23, 2023

Morphological relationships among populations support a single taxonomic unit for the North American Gray Wolf

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The Gray Wolf (*Canis lupus*) is viewed as one of the most diverse mammal species. In North America, the diversity of its forms is debated, with views conflicting on subspecies designation. The present study aimed to reinvestigate the skull morphometric variation among North American populations while attempting to unveil underlying causal factors. A large sample of vouchered museum skulls, collected from 12 ecogeographical populations spanning the North American range of the species, was examined and 21 craniodental characters were measured. Skull shape showed within-population variations but provided evidence for a high morphological affinity among populations. Allometric analyses also pointed to similar evolutionary paths among populations. However, significant size-related differentiation was revealed within and among populations. Skull size could be related to three insulin-like growth factor-1 gene (*IGF-1*) alleles. Ecological conditions that should determine prey type and availability accounted for most of the skull size variation. In contrast, no evidence of geographical isolation of populations was detected. The results support the existence of a single morphological pool of North American gray wolf populations that could be equated with one taxonomic unit. This study raises again the question of the diversity of forms in this species in North America and calls into question the validity of previously recognized species and subspecies based on genetics and morphology.

Key words: *Canis lupus*, craniometry, gray wolf, North America, shape, size, skull morphology, subspecies, taxonomy

The Gray Wolf (*Canis lupus*) diverged from *Canis etruscus* about 800,000 years ago in Asia, then extended its range to different parts of Asia and Africa (Kurtén and Anderson 1980; Paquet and Carbyn 2003; Wang and Tedford 2008). Over time, from at least the Late Pleistocene (Kurtén and Anderson 1980), the species evolved toward hypercarnivory and increased in size to specialize in killing and feeding upon large ungulates and became the largest member of the extant family Canidae (Mech 1974; Van Valkenburgh and Koepfli 1993; Brooke et al. 2014; Mallory et al. 2019). Such a correlated increase in hypercarnivory and body size acts like an evolutionary ratchet–after a lineage evolves toward specialization on larger prey, a larger body size evolves over time, and size reaches an upper limit with no reverting possible (Stanley 1979; Van Valkenburgh et al. 2004; Van Valkenburgh 2007).

During the Wisconsin glaciation, gray wolves in high Arctic latitudes were genetically isolated from their Asian congeners and diversified further, but the rate of diversification would then have slowed, and the species would have reached a final stage where it was assumed that it could no longer be a potential ancestor for new taxa (Stanley 1979; Van Valkenburgh and Koepfli 1993; Van Valkenburgh 1999; Van Valkenburgh et al. 2004).

Major glacial retreats after the post-Würm glaciation era (in the past 30,000 years) allowed the species to expand its range into North America, following large ungulate prey that also entered the continent (Wang and Tedford 2008; Chambers et al. 2012; Koblmüller et al. 2016; Loog et al. 2020). Several invasions introduced one or more morphs (subspecies), one of which would possibly displace its predecessor while admixing genetically with it (Chambers et al. 2012; Koblmüller et al. 2016; Loog et al. 2020). Dispersal and convergence of populations during these postglacial episodes would have contributed to genetic diversity and phenotypic variation in the species.

Much attention has been paid to morphological and genetic variation in the species, but studies have provided equivocal results (Chambers et al. 2012). Genetic structure of populations, gene flow, and morphology in the species were reported to be affected by isolation by distance and by biogeographical barriers imposed by topography and strong environmental and climate gradients (Roy et al. 1994; Carmichael et al. 2001; Geffen et al. 2004; Muñoz-Fuentes et al. 2009; O'Keefe et al. 2013; Leonard 2014; Schweizer et al. 2015). Geographical variation would have yielded distinct ecomorphs and given rise to a variety of subspecies. However, owing to lower population densities, high dispersal ability of individuals, and a connectivity among populations of the species (Wabakken et al. 2007; Jimenez et al. 2017; Joly et al. 2019)–albeit biased toward dispersal within natal habitats (Sanz-Pérez et al. 2018)–high gene flow could have occurred among populations (Roy et al. 1994; Wayne et al. 1995; Carmichael et al. 2001; Weckworth et al. 2011; Cronin et al. 2015; Gopalakrishnan et al. 2018; Sinding et al. 2018). Possible natural hybridization with other canid species complicates even more the issue that was termed "*Canis* soup" (Wilson et al. 2009:S80) that postulates that all historical wolves were a product of hybridization (Wilson and Reeder 2005).

Varying numbers of subspecies based primarily on descriptions of skull and pelage characters have been delineated throughout North America (Goldman 1944; Hall 1981; Nowak 1995; Wilson and Reeder 2005; Chambers et al. 2012). Although several authors have agreed on the necessity to reduce the profusion of gray wolf subspecies across North America (Jolicoeur 1959; Lawrence and Bossert 1967; Skeel and Carbyn 1977; Kennedy et al. 1991; Brewster and Fritts 1995; Nowak 1995; Wayne et al. 1995; Carmichael et al. 2001, 2007, 2008; von-Holdt et al. 2011), a consensus has not been reached.

The primary objectives of this study were two-fold: (1) to (re)assess morphological differences and affinities of gray wolf populations across North America; and (2) to unveil any possible genetic and ecological processes that might better explain morphological variation within the species. Following the recommendations of Chambers et al. (2012), I reassessed variation in skull morphology and structuring among populations based on geographically comprehensive morphometric analyses by use of large skull samples spanning most of the North American range of the species, including those from previously undersampled areas. North–south and west–east sampling transects were employed to assess morphological differences in a geographic context. Additionally, size and shape attributes were analyzed because many aspects of the biology of a species such as metabolism, diet, and mobility are directly related to size (Kleiber 1932; Gillooly et al. 2001; Speakman 2005)–and shape can reflect a different array of similarities or differences (Humphries et al. 1981; Reist 1985; Jungers et al. 1995).

Materials and Methods

Sample collection.—Gray Wolf vouchered skulls used in this study (Appendix I) were collected from 12 ecogeographical areas encompassing most of the North American range of the species (southern United States excluded). These areas were distributed along north–south and west–east sampling transects–(High Arctic [Ellesmere Island and adjacent islands], Baffin Island, West Barren Ground [Arctic Alaskan, north of the Endicott Mountains, and Mackenzie area], East Barren Ground [Kivalliq area], Ungava Peninsula, West [taiga] Boreal, Montane [Rocky Mountains], East [taiga] Boreal, Alexander Archipelago, Vancouver Island, Great Lakes, and Mixed Wood; Fig. 1). The range covered by the samples encompassed geographical and biological barriers, including islands, the Rocky Mountains, large rivers, and a diversity of biomes. This sampling strategy was designed to avoid potential misleading conclusions that might come from reliance on a few local populations to represent the North American range of the species.

Skull measurements.—Twenty-one characters were examined and measured, 15 cranial (skull and mandible) and six dental (Fig. 2). In damaged skulls, measurements of missing characters were estimated by stepwise multiple linear regression equations from specimens within the same population (Sokal and Rohlf 1995). Thus, skulls having no more than two missing character from 264 females and 274 males were used (Fig. 1). Sampling was designed to include nearly the same number of specimens per population, that is, ca. 30–50 (about half females, and half males) for each of the 12 populations. Measurements were recorded to the nearest 0.01 mm with digital callipers connected to a computer for immediate recording and avoiding potential errors due to manual data capture. To minimize the effect of variation due to age and growth (ontogenetic allometry), only fully grown adults were measured. The age of the specimens was either known from museum records, and reconfirmed, or assessed from full eruption of teeth, tooth wear, and complete cranial suture closure. Measurements were validated via reexamination and rerecorded in the instance of outliers or odd values.

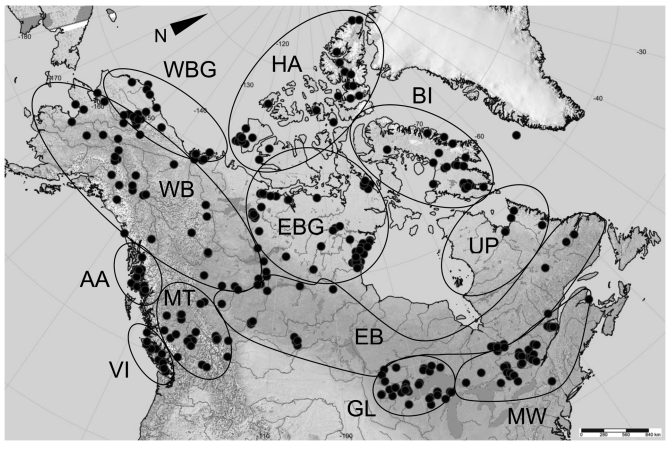

Fig. 1.—Locations (Canada, United States) of the 538 Gray Wolf (*Canis lupus*) specimens from Canada and the United States examined in the present study. HA: High Arctic; BI: Baffin Island; WBG: West Barren Ground; EBG: East Barren Ground; UP: Ungava Peninsula; WB: West Boreal; MT: Montane; EB: East Boreal; AA: Alexander Archipelago; VI: Vancouver Island; GL: Great Lakes; and MW: Mixed Wood.

Statistical analyses.—One-way analysis of variance (ANOVA) was conducted to test intersex differences between the mean values of each character. Two-way multivariate analysis of variance (MANOVA) was used to assess the effects of sex and populations simultaneously and test the interaction between the two factors (Populations × Sex) to reveal any effect of one factor on the other. The differences in means between groups of individuals with respect to the 21 craniodental characters were tested by MANOVA with a Wilks' λ. *F*-values were calculated to assess variability of distance between points within the same group versus the variability in distance among points. Variance components were partitioned to evaluate proportion of within- and among-group variation. The within-group component might reflect environmental variation whereas the among-group component might reflect genetic variation (Sokal and Rohlf 1995).

Normality of the data was tested by the Kolmogorov–Smirnov statistic with a Lilliefors significance level. Homogeneity of variances was tested by the Levene's test; equality of covariance matrices was tested by the Box's *M* test; multivariate normality was tested by the Mardia's test; and correlation matrices were examined for multicollinearity among variables.

Principal components analysis (PCA) was performed on the covariance matrix derived from the morphometric data sets to reveal structure in the relationships among characters and detect distinct groups of individuals or populations. Identification of groups was achieved by exploratory hierarchical clustering analysis (HCA) using the Ward's algorithm and Euclidian distances. The Ward method maximizes the between-group sum of squares, while minimizing the sums of squares within groups (Ward 1963). Root-mean-square standard deviation (RMSSTD), pseudo *F*-ratio (CHF), and pseudo *T*-square (PTS) tests were used to validate the number of groups of individuals or populations. Kruskal–Wallis nonparametric ANOVA (NPANOVA) by ranks was used to test differences among PC scores of groups of individuals or populations. Tukey tests for pairwise multiple comparisons also were performed as post hoc tests to these analyses. Linear discriminant function analysis (DFA) stepwise procedure was performed to assess the statistical robustness of groups identified after PCAs and to determine which of the craniodental characters best describe each of the groups, and the degree of difference between groups (Sokal and Rohlf 1995; Brown and Wicker 2000). The jackknifed classification method was performed to measure classification error. Squared Mahalanobis distances (D^2) were calculated to assess morphological affinities and relationships (phenetic distance) among groups (De Maesschalck et al. 2000). *F*-statistics computed from D^2 verified the degree of differentiation of pairwise distances between groups. Correlation matrices were screened to avoid using redundant characters.

Hedges' *g* (small modification of Cohen's *d* as a pooled sample standard deviation, instead of the population standard deviation, was used in the denominator) was calculated to assess standard effect size (point estimate and 95% confidence interval). This statistic assesses the amplitude of observed effects independently from the sample size used, allowing for

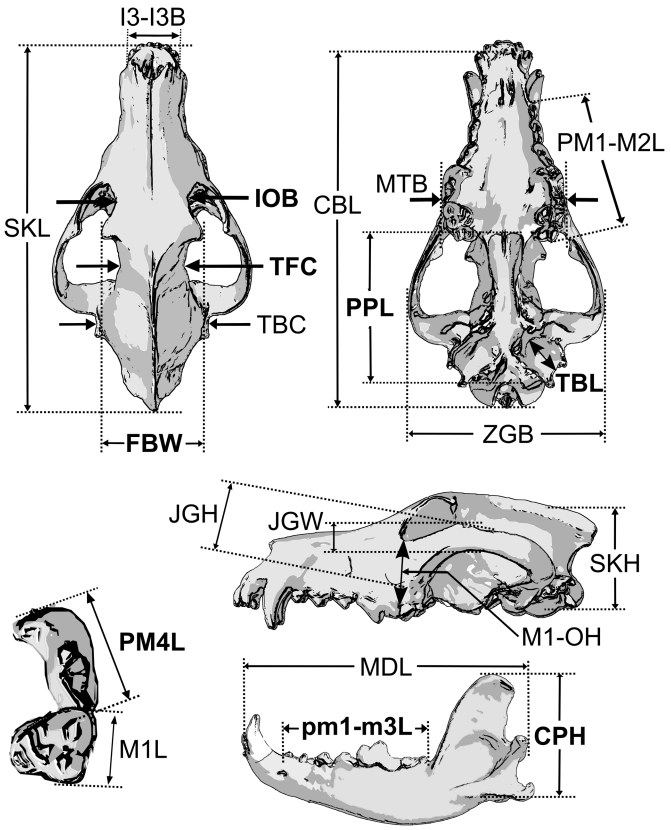

Fig. 2.—Views of the skull and mandible of a Gray Wolf (*Canis lupus*: CMNMA 8802, housed at the Canadian Museum of Nature, Ottawa, Ontario, Canada) illustrating the 21 craniodental characters examined and measured in the present study. Variables that most distinguish the main groups of ecogeographical populations as per linear discriminant function analyses are indicated with bold fonts. SKL–skull length, greatest length from the anterior edge of the premaxillae to the protuberance of the sagittal crest; CBL–condylobasal length, length from the anterior edge of the premaxillae to the posteriormost projections of the occipital condyles; SKH–skull height, height from the sagittal crest (top of the interparietal bone) to the lower edge of the foramen magnum; PPL–postpalatal length; ZGB–zygomatic breadth, maximum breadth across zygomatic arches; FBW–frontal bone width, maximum width across the postorbital processes; IOB–interorbital breadth; TFC–temporal fossa constriction, minimum cranial width at the rear edge of the postorbital processes; TBC–temporal bone constriction, minimum width at the squamous part of the bone; M1–OH–M1 to orbit height, height from the edge of the alveolus of the upper molar 1 (between PM4 and M1) to the lowermost edge of the orbit; JGH–jugal height, height from the lowermost edge to the uppermost edge of the jugal; JGW–jugal width; MDL–mandible length, length from the upper edge of the symphysis to the articular condyle; CPH–coronoid process height, height from lower edge of the angular process to top of coronoid process; TBL–tympanic bulla length; I3–I3B–upper incisors 3 breadth, width across incisors at alveoli edge; MTB–maxillary tooth breadth, maximum crown breadth across upper PM4/M1; PM1–M2L–upper premolars and molar row length, length at teeth crown; PM4L–upper premolar 4 length, at the crown; M1L–upper molar 1 length, at the crown; and pm1–m3L–lower premolar 1 to molar 3 length, at the edge of the alveoli edge.

better interpretation of the effects (Cohen 1988; Nakagawa and Cuthill 2007; Fritz et al. 2012).

Size-adjusted data in the form of shape ratios were used to investigate size-free shape differences among groups. The raw measurements of craniodental characters were divided each by the geometric mean (GM) to obtain size-adjusted variables (the DM-RAW in Jungers et al. 1995). GM was computed as the *n*th root of the product of craniodental characters that reflected size in the skulls. Such shape variables allowed for identification of individuals of the same shape in studies of Primates and tigers (Jungers et al. 1995; Mazák 2010).

Furthermore, relationships between craniodental characters and an indicator of skull size were investigated to reveal any allometric patterns. The simple allometric equation $\log(Y) = \alpha\log(X) + \log(b)$ (the linear logarithmic model of $Y = bX^{\alpha}$), in which α is the allometric slope, b the intercept, X an indicator of skull size, and Y a craniodental character (X and Y were raw data), models allometries (White and Gould 1965; Gould 1971). The two allometric parameters, α and b, were obtained by ordinary least-squares regressions (Pélabon et al. 2014). Visual inspection of residual plots was conducted, and Durbin–Watson's and Breusch–Pagan's statistics were calculated to test for normality, linearity, homoscedasticity, and independence of residuals. Variables that distinguish between groups effectively for both sexes, as revealed by PCA and stepwise DFA, were retained for this investigation. A general linear model (SYSTAT's GLM) was performed to test for differences between allometric slopes among groups (Tabachnick and Fidell 1996).

The statistical programs SYSTAT 13, Statgraphics Centurion XVI, and PAST 3 were used to conduct analyses.

Results

Sexual dimorphism.—Sexual dimorphism differences were detected between sexes in 100% of the data set. Males exhibited larger average values than those of females in all 21 craniodental characters (ANOVA, $P < 0.001$). A variance partition analysis showed that relatively more variation occurred within sex than among sexes, 70.5% vs. 29.5%, respectively. Two-way MANOVA revealed effects for sex (Wilks' $\lambda = 0.664$, $F_{10,502} = 25.4$, $P < 0.001$), and for ecogeographical populations ($\lambda = 0.149$, $F_{110,3769} = 9.92$, $P < 0.001$), with interaction between populations and sex ($\lambda = 0.742$, $F_{110,3769} = 1.39$, $P < 0.01$). In testing for differences for each character among the 12 ecogeographical populations, and using the whole set of female and male specimens combined, differences were detected in all 21 characters (ANOVA, $P < 0.001$). Relatively more variation occurred within than among the 12 populations, 78.8% vs. 21.2%, respectively. Consequently, to avoid that part of variation due to sexual dimorphism, sexes were analyzed separately in subsequent analyses. With sexes analyzed separately, the results of the ANOVA were significant for all 21 characters in females and males ($P < 0.05$).

Assessment of skull size variation.—The first two principal components, PC1 and PC2, accounted for a combined 85% and 84% of the total variation among female and male specimens, respectively (Table 1), whereas PC3 accounted for <4% of variation in males.

PC1 accounted for nearly 74% and 76%, in females and males, respectively (Fig. 3). The highest loadings were observed with condylobasal length (CBL) and mandible length (MDL), and secondarily zygomatic width (ZGW) in both sexes (Table 2), suggesting that PC1 primarily reflected a size component. To test for this relationship, PC1 scores were regressed to skull length (SKL). The correlation was very high ($r = 0.96$) and significant ($P < 0.001$) in both sexes. This component showed a size gradient with large-sized skulls congregating on the positive side and small-sized skulls on the negative side of PC1 (Fig. 3).

In both sexes, three distinct size classes (small, medium, and large) were identified based on PC1 scores, and as inferred from Hedges' *g* nonoverlap between any two size class comparisons was uniformly high (percentage varied from 85.4% between medium-sized and large-sized skulls in males to 98% between small-sized and large-sized skulls in females and males). In all instances, probability of superiority, i.e., the percentage of occasions when a randomly sampled member of the distribution with the higher mean will have a higher score than a randomly sampled member of the other distribution (Fritz et al. 2012), was >95%. DFA confirmed that this segregation was robust with a 100% discrimination rate among the three size classes in both sexes (Table 3, Supplementary Data SD1).

In females, small-sized skulls (SKL = 229.7 mm ± 7.9, $n = 54$) were 13.5% smaller than large-sized skulls (SKL = 260.8 mm ± 7.3, $n = 67$); medium-sized skulls (SKL = 244.8 mm ± 6.2, $n = 143$) were intermediate in their mean length value. The same size difference ranges were observed among males, with small-sized skulls (SKL = 242.9 mm ± 7.5, $n = 57$) being 13% smaller than large-sized skulls (SKL = 273.6 mm ± 6.8, $n = 74$), and medium-sized skulls (SKL = 258.4 mm ± 5.8, $n = 140$) being intermediate. SKL was significantly different among these three classes (ANOVA, $P < 0.001$ in both sexes). These size classes were widespread across the 12 ecogeographical populations (Fig. 4).

Discrimination of and relationships among groups of populations.—Twenty craniodental characters were used in the covariance matrix. SKL, which was highly correlated to CBL, was set aside for additional exploration of the data. The 12 populations overlapped extensively on the PC1–PC2 plane, and no apparent partitioning of the craniodental characters into distinct populations or groups of populations could be clearly observed in either sex (Fig. 3). The skulls from each population occupied a large space of the PC1–PC2 plane, thus suggesting high within-population variation. Likewise, a variance partition (by use of linear dimensions of the 21 characters) showed that relatively more variation occurred within rather than among the 12 populations–69.45% vs. 30.55% in females, and 77.66% vs. 22.34% in males.

Table 1.—Eigenvalues of the first principal components (PC1 and PC2) and percent of variance accounted for (%), and results of nonparametric ANOVA (NPANOVA) for the significance of differences between group means of the principal components for 20 craniodental characters in female and male gray wolves (*Canis lupus*) from Canada and the United States. AT: Arctic Tundra; BF: Boreal Forest; and TF: Temperate Forest. Tukey test was performed post hoc in pairwise comparisons: ns: not significant; ***$P < 0.001$; **$P < 0.01$; and *$P < 0.05$.

Principal component	Females					Males				
	Eigenvalue	%	NPANOVA *H*-value	*P*	Tukey test	Principal component	Eigenvalue	%	NPANOVA *H*-value	*P*	Tukey test
Raw data											
1	342.26	74.40	83.06	0.000	BF > AT > TF***	1	375.39	76.27	96.48	0.000	BF > AT > TF***
2	47.93	10.42	34.36	0.000	AT > BF*** AT > TF** BF vs. TF, ns	2	36.90	7.50	10.62	0.005	AT > BF** TF > BF* AT vs. TF, ns
Size-adjusted data											
1	0.002	38.28	27.44	0.000	BF > AT*** TF > AT*** BF vs. TF, ns	1	0.001	30.38	6.55	0.038	BF > AT* AT vs. TF, ns BF vs. TF, ns
2	0.001	13.15	4.89	ns	ns	2	0.001	15.95	9.86	0.007	TF > BF** TF > AT* BF vs. AT, ns

However, nonparametric tests revealed some significant differences in PC1 scores among populations. In females, West Boreal and Montane showed significant differences in their distributions in 91% instances in the pairwise comparisons ($P < 0.05$) even though they were statistically similar to each other; East Boreal and Great Lakes showed significant differences in 64% instances; and Mixed Wood showed significant differences in 91% instances. Among other populations, Alexander Archipelago showed significant differences in a maximum of 45% instances, thus indicating a much larger overlap between populations. In males, West Boreal and Montane were significantly different from the remaining populations in 82% and 73% instances; East Boreal, Alexander Archipelago, and West Barren Ground showed significant distribution differences in 82% (including Montane and West Boreal), 73%, and 64% instances; the remainder of the populations had equal significant differences in 45% instances.

Finer comparisons were performed by Mahalanobis distances (D^2) calculated with key PCA and DFA variables (Table 4). In females, high morphological affinities (D^2 = 1.53–2.88) were observed between: (1) West Boreal, Montane, and East Boreal; (2) Great Lakes and Mixed Wood; and (3) High Arctic, Baffin Island, West Barren Ground, and East Barren Ground. Alexander Archipelago, Vancouver Island, and Ungava Peninsula were outliers in this regard, although the Vancouver Island wolves showed some close affinity with those from Baffin Island (D^2 = 3.57) and Alexander Archipelago (D^2 = 4.23), Alexander Archipelago with Great Lakes (D^2 = 4.03), and Ungava Peninsula with Baffin Island (D^2 = 4.06). In males, high affinities (D^2 = 0.77–3.43) were observed between: (1) West Boreal, Montane, East Boreal, and West Barren Ground; (2) Great Lakes and Mixed Wood; and (3) High Arctic, Baffin Island, East Barren Ground, and Ungava Peninsula. Vancouver Island showed some affinity with Great Lakes (D^2 = 3.77), and Alexander Archipelago stood alone with no great affinity with any other population.

Further ecomorphological and geographical differences and relationships were explored by HCA. Two validation tests, PTS and CHF in females and RMSSTD and CHF in males, supported three groups of populations (Fig. 5, Supplementary Data SD2). A few populations were reassigned to obtain the most ecogeographically meaningful partition and with the highest percentage of nonoverlap among groups, as inferred from Hedges' *g*. Populations were clustered in accordance with their respective biomes, Arctic Tundra (AT), Boreal Forest (BF), and Temperate Forest (TF). Alexander Archipelago could have been grouped with Vancouver Island (Pacific coastal temperate rainforest) in TF, which also included Great Lakes and Mixed Wood, but the highest percentages of nonoverlap on PC1 were obtained when it was grouped with BF populations instead.

In both sexes, the highest percentage of nonoverlap was observed between BF and the other two groups (in females and males, respectively: BF vs. TF = ~73% and 76%; BF vs. AT = ~63% and 65%)–the smallest was between AT and TF (~31% in both sexes; Fig. 6). With DFA, an average of 77% (jackknifed = 76%) and 72% (jackknifed = 71%) of

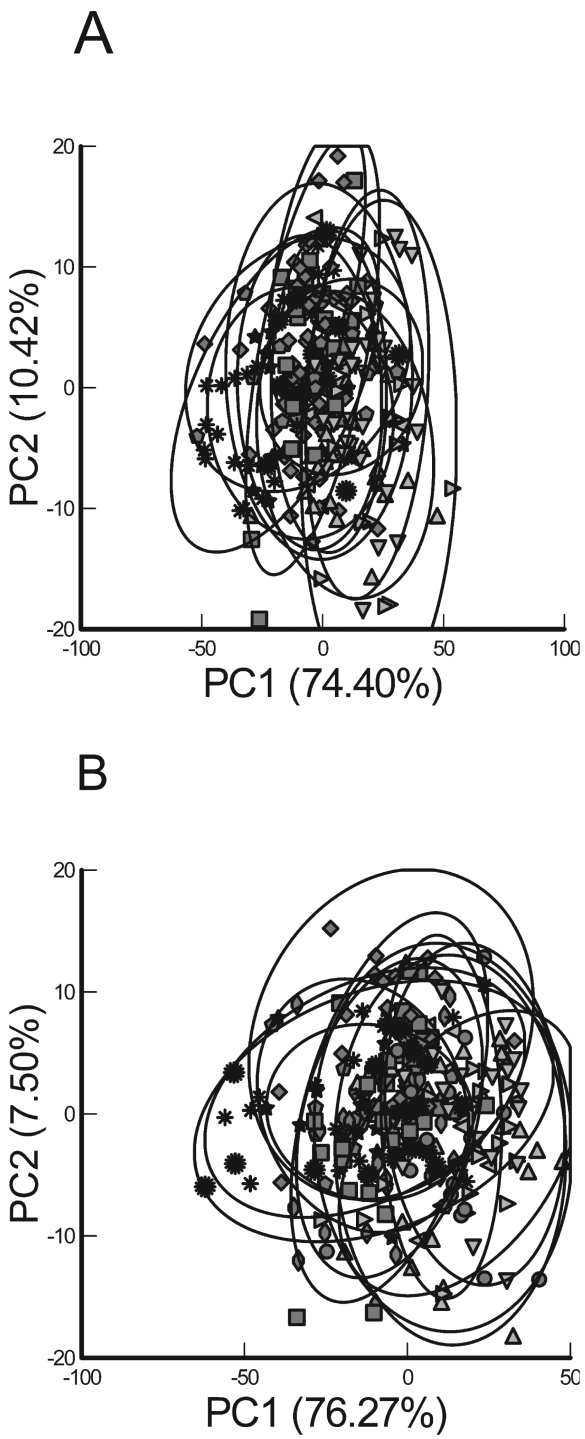

Fig. 3.—Plots of the raw data scores on the PC1–PC2 plan showing the 12 Gray Wolf (*Canis lupus*) ecogeographical populations (delineated with a 90% ellipse) from Canada and the United States. A: females; B: males. Symbols represent each population.

the specimens were correctly assigned with seven and six nonredundant craniodental characters in females and males, respectively (Table 5, Supplementary Data SD3). Significant differences among the three group centroids were observed in females (Fig. 7A; $\lambda = 0.38$, $F_{14,510} = 22.35$, $P < 0.001$) and

Table 2.—Factor loadings of principal component analysis (RD: raw data; SAD: size-adjusted data) for 20 craniodental characters in female and male gray wolves (*Canis lupus*) from Canada and the United States. See full description of craniodental characters in Fig. 2 for acronyms. Bold values indicate variables with high loadings.

Craniodental characters	Females			Males		
	PC1 RD	PC1 SAD	PC2 SAD	PC1 RD	PC1 SAD	PC2 SAD
CBL	**10.29**	**0.019**	0.005	**11.11**	**0.016**	0.005
ZGW	**6.07**	**–0.018**	–0.005	**6.22**	**–0.016**	–0.007
SKH	3.29	–0.001	–0.001	3.38	–0.002	–0.002
PPL	4.46	0.006	0.001	4.88	0.006	0.002
FBW	3.49	**–0.022**	**0.010**	2.91	**–0.017**	**0.017**
IOC	2.59	–0.011	0.006	2.42	–0.007	0.007
TFC	1.47	–0.006	**0.013**	0.91	–0.002	**0.010**
TBC	2.58	0.001	0.004	2.89	0.001	0.000
MDL	**8.73**	0.010	0.003	**9.18**	0.009	0.005
CPH	3.94	0.001	–0.000	3.87	0.001	–0.003
JGH	2.26	–0.005	–0.002	2.48	–0.004	–0.001
JGW	1.29	–0.005	–0.002	1.28	–0.004	–0.001
M1–OH	2.68	–0.003	–0.001	2.64	–0.001	0.000
TBL	0.39	0.001	0.003	0.52	0.000	0.001
PM1–M2L	3.35	0.007	0.007	3.48	0.009	0.005
MTB	2.93	–0.001	0.006	3.16	0.001	0.001
I3–I3B	1.42	0.001	0.002	1.45	0.001	0.001
PM4L	0.74	0.001	0.003	0.68	0.001	0.001
M1L	0.40	0.001	0.002	0.36	0.001	0.000
pm1–m3L	3.51	0.008	0.009	3.84	0.009	0.006

males (Fig. 7B; $\lambda = 0.41$, $F_{12,526} = 24.72$, $P < 0.001$). *F*-statistics showed that AT and TF were the most similar ($F_{7,255} = 14.54$ and $F_{6,263} = 16.91$, in females and males, respectively); the most distant groups were BF and AT ($F_{7,255} = 27.86$) in females, and BF and TF ($F_{6,263} = 32.12$) in males.

These affinity values, combined with the percentage of nonoverlap on PC1 between AT and TF, suggested the relevance of two groups of populations; BF (Group 1), and AT and TF combined (Group 2; Fig. 5), as also supported by RMSSTD in females and PTS in males (Supplementary Data SD2). DFA yielded the highest discrimination rate and corroborated the robustness of this partition. An average of 84% (jackknifed = 82%) and 83% (jackknifed = 82%) of the specimens were correctly assigned with seven key variables in females and males, respectively (Supplementary Data SD4 and SD5). Significant differences between the two group centroids were observed in females ($\lambda = 0.56$, $F_{7,256} = 28.33$, $P < 0.001$) and males ($\lambda = 0.55$, $F_{7,263} = 30.22$, $P < 0.001$). In females, function 1 (DF1) primarily described a pattern of increasing lower premolar 1 to molar 3 length (pm1–m3L) and coronoid process (CPH) (associated with Group 1) and decreasing interorbital breadth (IOB; associated with Group 2). In males, DF1 primarily described a pattern of decreasing postpalatal length (PPL) that split Group 1 (associated with PPL) from Group 2.

Shape analysis.—PC2 on untransformed data demonstrated shape- and size-related morphological variation. To control for this size effect, a PCA was conducted on size-adjusted data. The three characters CBL, MDL, and ZGW were retained for calculation of the GM as, combined, they reflected overall

skull size. The first three principal components accounted for a combined 61% and 57% of total variation in females and males, respectively (Table 1). In both sexes, PC1 described a pattern that contrasted CBL to ZGW and width of the frontal bone (FBW), i.e., the longer skulls become relatively narrower, which suggested the presence of some allometric relationship; PC2 described a pattern of increasing FBW and temporal fossa constriction (TFC), which related to the involvement of the frontal area of the skull in shape patterns; PC3 (9.59% and 10.41%, in females and males, respectively) described a pattern of increasing maxillary tooth breadth (MTB).

The 12 populations overlapped so extensively that none could be easily distinguished on the PC1–PC2 plane (51.43% and 46.33% of total variation, in females and males, respectively). On PC1, significant differences were detected between Ungava Peninsula and the 11 other populations in females and males (100% instances in the pairwise comparisons, $P < 0.05$). For other populations, the only significant differences were between East Boreal and High Arctic and the other populations (in 64% and 45% instances, respectively) in females, and only between Montane and Mixed Wood and other populations in males. On PC2, in females, only Ungava Peninsula differed significantly and the most frequently from the other 11 populations, that is, in 55% instances; in males, Vancouver Island and East Boreal most often showed significant differences from other populations, that is, in 73% and 64% instances, respectively—other significant differences were detected much less frequently, that is, in 36% instances for High Arctic and once (9%) with regards to Ungava Peninsula.

Considering the three groups of populations, in females, significant differences were detected on PC1 between AT and BF ($P < 0.001$) and AT and TF ($P < 0.01$), and on PC2 between AT and BF ($P < 0.05$) and BF and TF ($P < 0.01$); in males, no significant differences were observed on PC1 and on PC2 there was only one between BF and TF ($P < 0.05$). However, extensive overlap in skull shapes were observed among the three groups (Fig. 8), which pointed to their great similarities. On PC1, the percentage of nonoverlap ranged from ~8% (BF and TF) to ~41% (BF and AT) in females, and ~5% (AT and TF) and ~28% (BF and AT) in males. On PC2, the nonoverlap ranged from 0% (AT and TF) to ~21% (BF and TF) in females, and ~8% (BF and AT) to ~28% (BF and TF) in males.

Allometric relationships.—Allometric analysis statistics for the 12 populations were calculated for 10

Table 3.—Function loadings and percentage of variance accounted for by each function of stepwise discriminant function analysis for comparing the three size classes in female and male gray wolves (*Canis lupus*) from Canada and the United States. See full description of craniodental characters in Fig. 2 for acronyms. Bold values indicate variables with high loadings. Hyphen indicates variables not retained in the stepwise process.

Craniodental characters	Females		Males	
	Function 1	Function 2	Function 1	Function 2
	% of variance		% of variance	
	98.7	1.3	98.5	1.5
CBL	**0.91**	**–0.63**	**0.94**	0.53
ZGB	0.58	**0.88**	–	–
FBW	–	–	0.25	**–0.74**
TBC	–	–	0.20	–0.40
PM4L	**–0.83**	0.20	–0.21	–0.48
M1L	**0.85**	–0.07	–	–

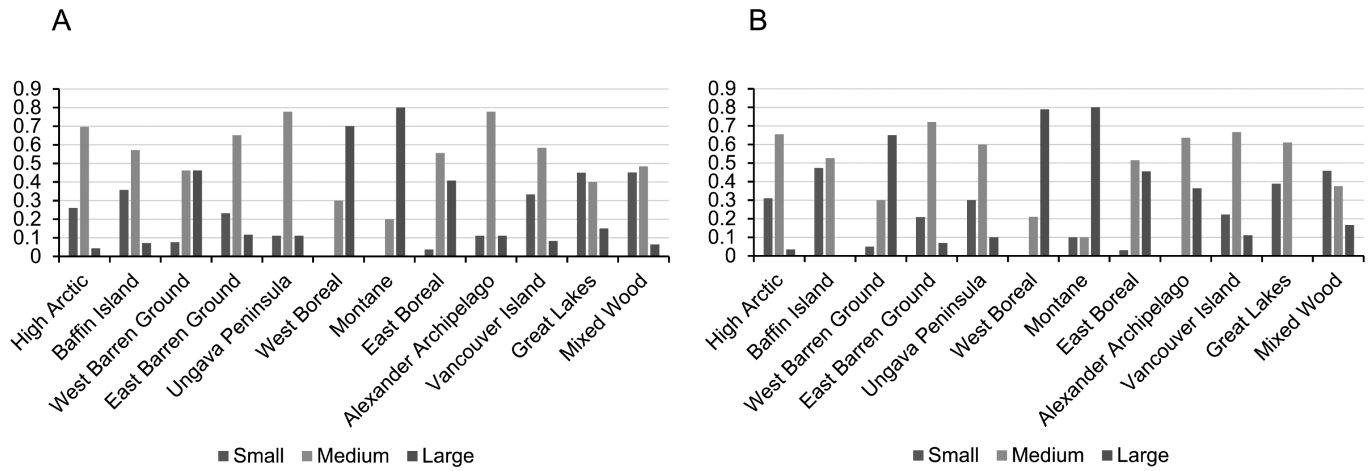

Fig. 4.—Distribution of the frequencies of the three size classes among the 12 Gray Wolf (*Canis lupus*) ecogeographical populations from Canada and the United States. A: females; B: males.

Table 4.—Mahalanobis distances (D^2) for the assessment of the affinities between the 12 ecogeographical populations in the female (bottom left) and male (top right) gray wolves (*Canis lupus*) from Canada and the United States by use of 10 key craniodental characters in principal component analyses and linear discriminant function analyses. Bold values indicate high morphological affinities between groups. HA: High Arctic; BI: Baffin Island; WBG: West Barren Ground; EBG: East Barren Ground; UP: Ungava Peninsula; WB: West Boreal; MT: Montane; EB: East Boreal; AA: Alexander Archipelago; VI: Vancouver Island; GL: Great Lakes; and MW: Mixed Wood.

	HA	BI	WBG	EBG	UP	WB	MT	EB	AA	VI	GL	MW
HA		**2.87**	6.67	**2.61**	**3.16**	12.79	11.10	7.33	14.03	10.78	10.17	8.18
BI	**2.25**		6.12	**0.90**	**3.10**	9.88	8.69	6.32	13.60	8.71	6.56	5.48
WBG	**1.53**	**2.71**		4.35	5.71	**1.85**	**1.20**	**0.77**	11.27	7.32	6.19	5.29
EBG	**2.48**	**1.85**	**1.85**		**3.43**	7.23	7.31	4.39	16.68	9.33	7.84	6.46
UP	4.82	4.06	4.55	6.17		9.06	8.84	6.09	10.72	6.65	4.84	3.66
WB	7.73	7.12	**2.88**	5.06	7.15		**1.31**	**2.03**	17.65	10.41	8.40	8.39
MT	11.51	11.88	5.50	9.62	12.52	**2.77**		**1.14**	13.01	7.87	5.83	7.13
EB	5.80	5.53	**2.12**	**2.67**	8.56	**1.71**	**2.46**		13.80	6.85	5.70	6.480
AA	6.93	6.21	5.37	8.23	5.45	7.97	6.85	6.12		10.09	11.01	11.07
VI	5.46	3.57	5.19	7.84	6.24	9.18	9.64	7.89	4.23		3.77	8.01
GL	6.73	4.72	6.62	5.28	6.70	7.92	10.65	5.63	4.03	6.85		**2.50**
MW	4.59	5.45	7.16	6.02	6.36	11.65	15.14	8.76	6.10	8.85	**2.21**	

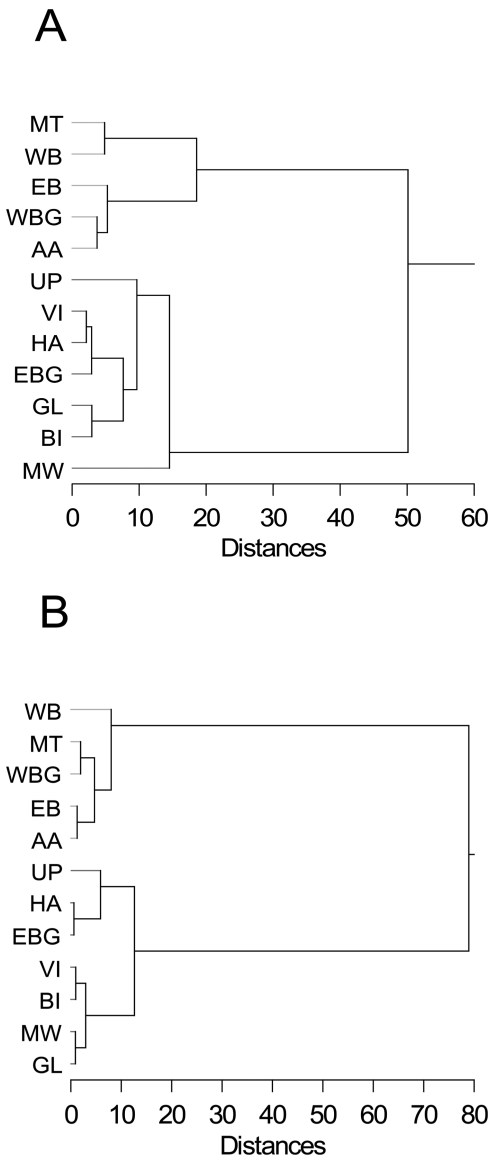

Fig. 5.—Cluster dendrograms (Ward's algorithm and Euclidian distances using populations centroid on PC1 and PC2) illustrating the relationships among the 12 Gray Wolf (*Canis lupus*) ecogeographical populations from Canada and the United States. Validation tests for the number of groups are given in Supplementary Data SD4 for each dendrogram. A: females; B: males. HA: High Arctic; BI: Baffin Island; WBG: West Barren Ground; EBG: East Barren Ground; UP: Ungava Peninsula; WB: West Boreal; MT: Montane; EB: East Boreal; AA: Alexander Archipelago; VI: Vancouver Island; GL: Great Lakes; and MW: Mixed Wood.

craniodental characters that where key to identifying (PCA) and discriminating (DFA) among populations (Supplementary Data SD6). Scaling relationships observed in females were very comparable to those in males. TFC and SKL, however, showed two different patterns in their relationship in the two sexes–TFC grew relatively faster in females than in males (allometric slopes $\alpha = 0.64$ in females and 0.38 in males).

A wide range of relationships was observed in both sexes, with most of the craniodental characters scaling allometrically

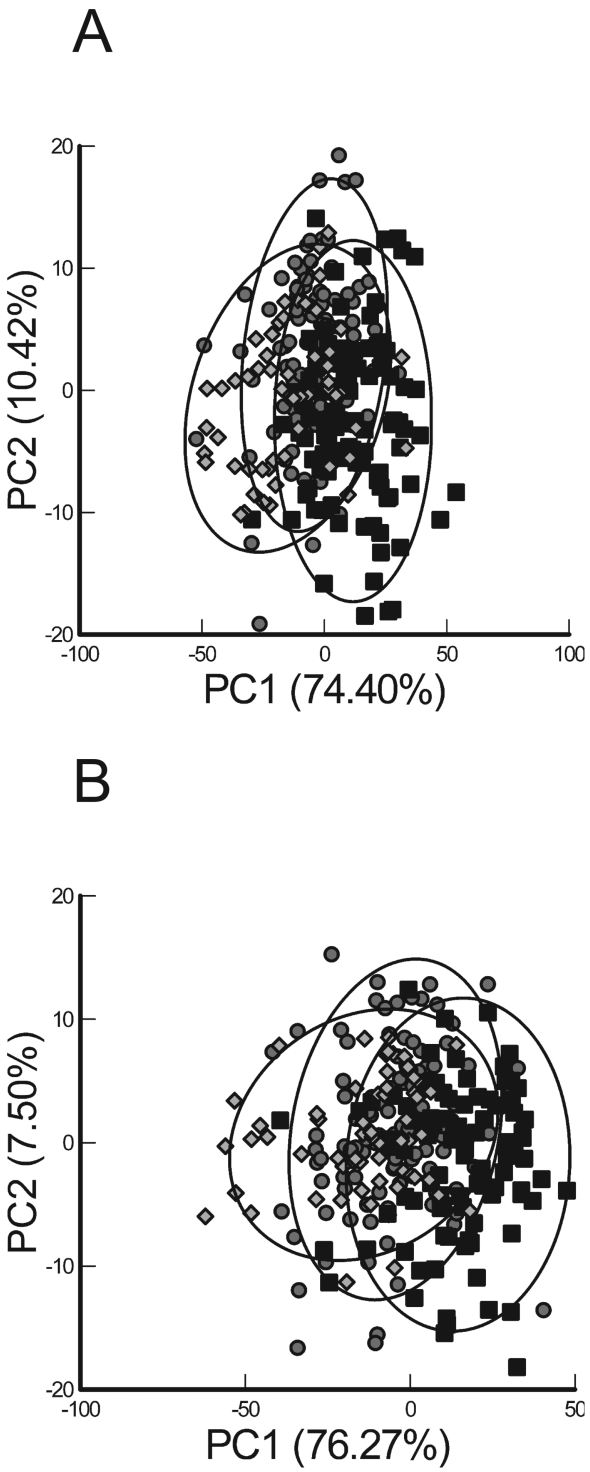

Fig. 6.—Plots of the raw data scores on the PC1–PC2 plan showing the three main groups of ecogeographical populations in the Gray Wolf (*Canis lupus*; delineated with a 90% ellipse) from Canada and the United States. A: females; B: males. Circles: Arctic Tundra; squares: Boreal Forest; and diamonds: Temperate Forest.

to SKL. Two characters regarding the width of the frontal area of the skull, FBW (in females) and IOB (in both sexes), and CPH (in both sexes) scaled isometrically to SKL. Negative allometry was observed in the other craniodental characters. Differential increase rates were observed in these instances. The growth of TBL was by far the slowest; upper premolar 4 length (PM4L) was second to TBL in slow growth; characters of the skull base (CBL and PPL) and the mandible (MDL) grew at a relatively slower pace than the longest axis of the skull, although approaching to isometry.

Considering the three groups of populations, the allometric slopes all were statistically equal, except for TFC ($P < 0.05$) in females due to this character displaying a higher slope value and scaling isometrically rather than allometrically to SKL in TF. Neither the allometric slopes nor the intercepts varied greatly among the three groups, although some differences could be seen in the intercepts (Supplementary Data SD7).

Discussion

Using comparative morphological approaches, this study argues for a single pool of North American Gray Wolf populations. In particular, the skull shape patterns are similar and widespread across the 12 ecogeographical populations surveyed and none characterizes any population as unique. They support substantial within-population morphological diversity indicating a possible strong environmental effect (likely prey species) on skull morphology, and a significant skull shape-related affinity among the populations. However, the data do not support the subspecies reported for North American gray wolves, including the eastern wolf that was previously recognized as a different species (Rutledge et al. 2010, 2015; Heppenheimer et al. 2018). The equality in the allometric slopes among the three ecogeographical groups of populations investigated supports such an among-populations similarity and furthermore suggests a single evolutionary path across the North American range of the species. The parallels observed between the intercepts of each group of populations also point to comparable and similar evolutionary paths. A signal of a unique evolutionary process for the southern latitudes areas was detected in females with a significant difference in the TFC slopes. However, the analyses on males did not confirm such an assumption.

In Canidae, skull shape is largely under the control of genetic components (Schoenebeck and Ostrander 2013). The 12 populations, therefore, should display significant genetic similarities (functional genes). Future genetic analyses should test the hypothesis that North American gray wolves can be treated as a single pool of populations, which was previously suggested by mitochondrial DNA restriction-site analyses (Wayne et al. 1995). If supported, this hypothesis would be consistent with the hypothesis that North American gray wolves derive from a single Pleistocene ancestral population. Following dispersal across a Beringian land bridge about 25,000 years ago, expansion of modern gray wolves would have replaced indigenous, earlier Pleistocene wolf populations and thence southward into North America following retreat of the ice sheets about 16,000 years ago (Koblmüller et al. 2016; Loog et al. 2020).

However, some regional site fidelity–perhaps associated with ecological preferences–could maintain a recognizable level of genetic uniqueness despite high gene flow occurring among the populations. In support of this pattern, several populations surveyed herein were previously shown to display some genetic uniqueness (e.g., Carmichael et al. 2007). For example, the TF group includes populations from the Great Lakes, which were genetically determined as an ecotype of the gray wolf (vonHoldt and Aardema 2020). Some genetic distinctiveness has also been observed in the Mixed Wood area distributed in the eastern region (Chambers et al. 2012; vonHoldt and Aardema 2020), and on Vancouver Island (Muñoz-Fuentes et al. 2009)–these populations had previously been considered as different subspecies (Hall 1981; Wilson and Reeder 2005). Among-group shape differences are detected in my analyses, yet their standard effect size is small (percentage of nonoverlap most often ≤28%) and visually subtle. As such, they likely do not play a role in biological function variation (Nakagawa and Cuthill 2007) because 33% (medium effect size) has been suggested as a threshold for size differences between groups resulting in functional differences (Cohen 1988), although these benchmarks have been debated. Here, any genetic differences are not reflected in skull shape and might be limited to neutral mutations.

Herein, size is shown to account for most of the variation. In all instances, the partitions have no strong geographical foundation sensu stricto (latitudinal gradient, islands, physical barriers such as high mountains, large rivers, and lakes, distances, etc.). None of the three size-related morphotypes is exclusive to any specific population or geographically proximate groups of populations. Eastern wolves were reported to be small-bodied and to possess small-sized skulls (Nowak 1995)–here, although a large proportion possess a small-sized skull, an almost equal proportion display a medium-sized skull (47% in females, 38% in males), whereas a lesser proportion is characterized by a large-sized skull (6% in females, 17% in males). Group 1, which is generally associated with large-sized skulls, includes neighboring boreal and montane forests populations. Group 2, generally associated with medium- and small-sized skulls, is an amalgamation of geographically and ecologically disjunct populations, i.e., the arctic biome at the northern end of the range of the species, and the temperate biome at the southern end. Hypothetically, size may reflect a latitudinal gradient (Bergmann's rule; Meiri and Dayan 2003; Plassais et al. 2022), although linear measurements do not perfectly reflect this gradient (Meiri and Dayan 2003). Skull size does not support Bergmann's rule (i.e., a trend of increasing body size as latitude increases)–skulls of Arctic wolves in northern latitudes do not average larger than those of BF wolves in lower latitudes. Notwithstanding significant differences detected herein in the size of skulls, wolves from TFs overlap extensively with the Arctic wolves (percentage of nonoverlap = ~31%; i.e., small effect size). Bergmann's rule therefore appears to reverse in northern latitudes, which corroborates previous results (Geist 1987).

Size in gray wolves is a complex trait that could be related to variation in allelic frequencies of several quantitative trait loci, including the insulin-like growth factor-1 gene (*IGF-1*), which encodes a growth factor. In domestic dogs, size was found to be strongly associated with three major alleles of this gene (Sutter et al. 2007; Boyko et al. 2010; Gray et al. 2010; Hoopes et al. 2012; Plassais et al. 2019, 2022). Specifically, the 207-bp allele is associated with large size, and the 211-bp allele is associated with small size in dogs (Gray et al. 2010). *IGF-1* alleles found in the gray wolf worldwide spanned the entire range observed in dogs, with possible additional variation (Gray et al. 2010). Both the small allele, which would represent the ancestral state, and the large allele existed in Pleistocene wolves, with the small allele being less frequent (Plassais et al. 2022). In modern wolves, the intermediate 209-bp allele is highest in frequency (41%; Gray et al. 2010). In this study, medium-sized wolf skulls are most frequent: 54% in females, and 51% in males; thus, the underlying explanation of size differences among the 12 populations and the two groups of populations may reside in differences in *IGF-1* allele frequencies, which could be under selection and vary according to ecological attributes.

Prey size has been reported to influence gray wolf size (Schmitz and Kolenosky 1985; Kyle et al. 2006; Wiwchar and

Table 5.—Function loadings and percentage of variance accounted for by each function of stepwise discriminant function analysis for comparing the three main groups of Gray Wolf (*Canis lupus*) populations from Canada and the United States. See full description of craniodental characters in Fig. 2 for acronyms. Bold values indicate variables with high loadings. Hyphen indicates variables from this set not retained in the stepwise process.

Craniodental characters	Females		Males	
	Function 1	Function 2	Function 1	Function 2
	% of variance (eigenvalue)		% of variance (eigenvalue)	
	68.4 (0.86)	31.6 (0.34)	66.7 (0.77)	33.3 (0.38)
FBW	–	–	0.23	0.21
IOB	**0.54**	**0.59**	–	–
TFC	–0.22	–0.42	–	–
PPL	–0.48	**–0.87**	**–0.68**	**0.65**
CPH	**–0.64**	**0.56**	–0.36	**–0.58**
TBL	0.39	0.28	0.42	–0.09
PM4L	0.34	**0.68**	0.48	**–0.85**
pm1–m3L	–0.44	0.04	–0.49	–0.16

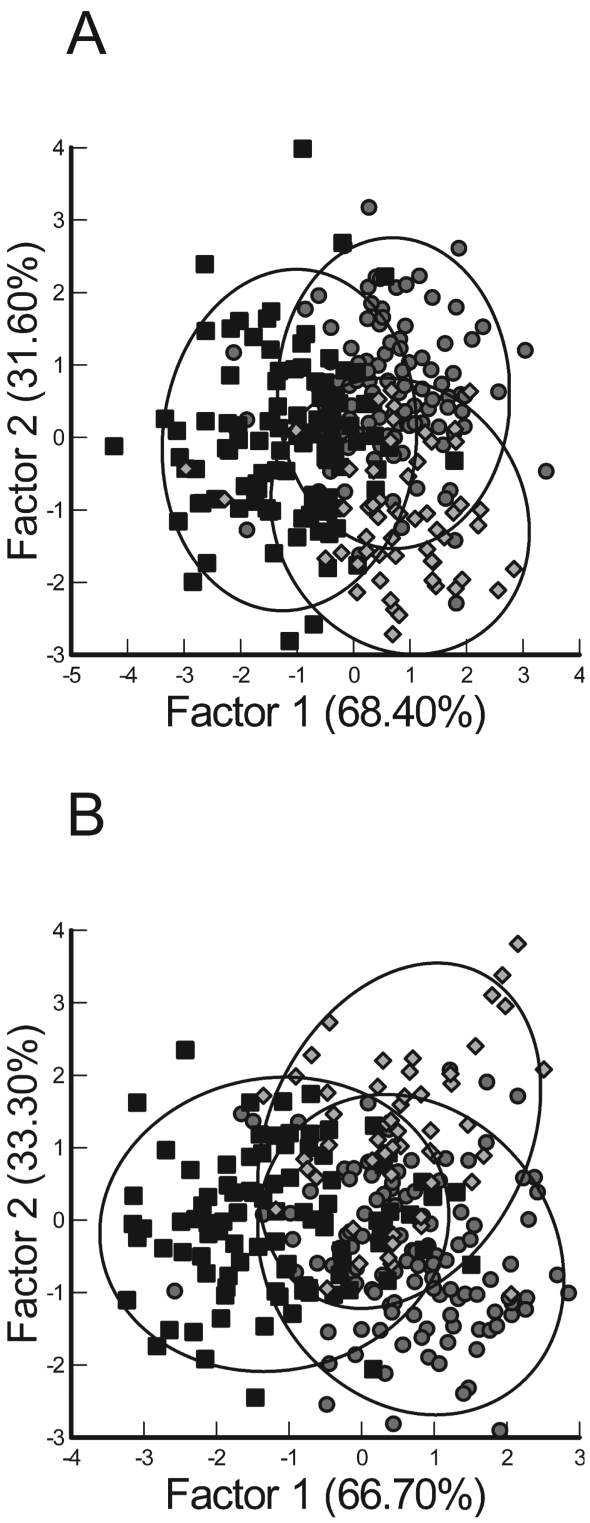

Fig. 7.—Plots of DF1 and DF2 scores from linear discriminant function analysis showing the three main groups of ecogeographical populations in the Gray Wolf (*Canis lupus*; delineated with a 90% ellipse) from Canada and the United States. A: females; B: males. Circles: Arctic Tundra; squares: Boreal Forest; and diamonds: Temperate Forest.

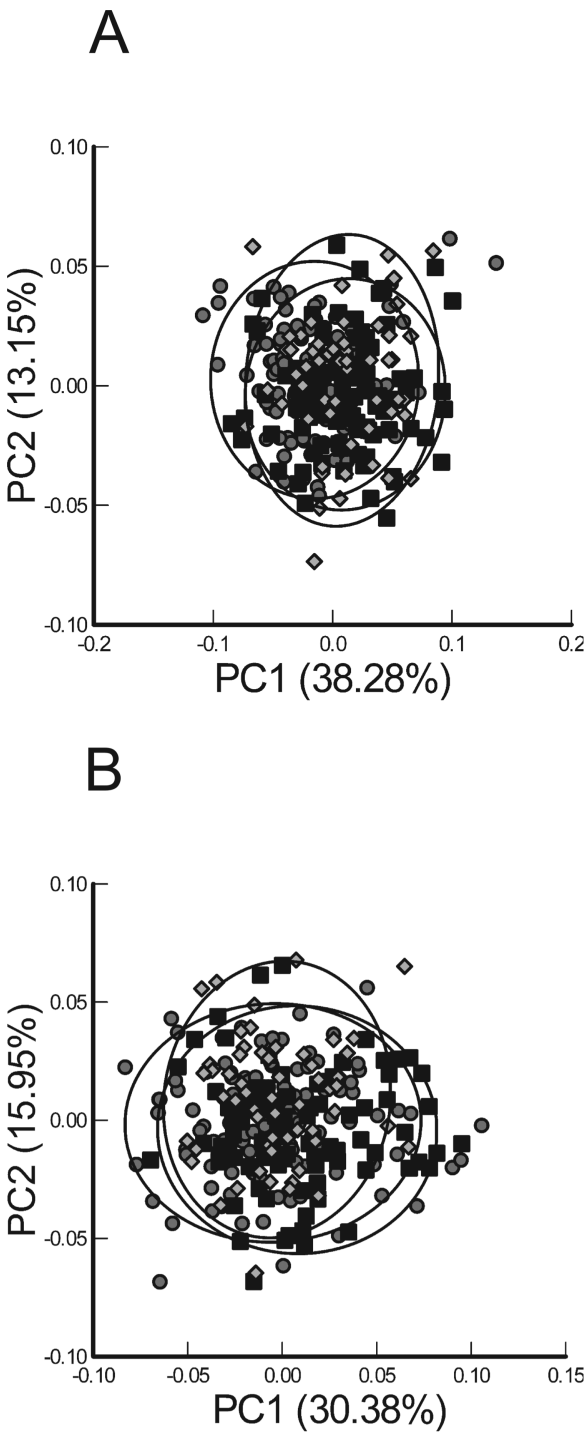

Fig. 8.—Plots of the size-adjusted data scores on the PC1–PC2 plan showing the three main groups of ecogeographical populations in the Gray Wolf (*Canis lupus*; delineated with a 90% ellipse) from Canada and the United States. A: females; B: males. Circles: Arctic Tundra; squares: Boreal Forest; and diamonds: Temperate Forest.

Mallory 2012; Mallory et al. 2019). In this study, large-sized skulls are more frequent where large ungulates (bison, moose, and elk) abound, in boreal and montane forests; medium-sized and small-sized skulls prevail in habitats with higher frequencies of smaller ungulates, in AT (caribou and muskox), and TF

(mule deer, black-tailed deer, and white-tailed deer; Naughton 2012). Wolves from the coastal temperate rainforest, including the Alexander Archipelago and the British Columbia Pacific islands, feed primarily upon black-tailed deer (Holleman and Stephenson 1981; Szepanski et al. 1999; Darimont et al. 2004), and may occasionally feed upon larger prey (elk and moose), with moose perhaps being more often consumed than previously thought (Holleman and Stephenson 1981; Person et al. 1996; Szepanski et al. 1999; Lafferty et al. 2014). Salmon also represents a substantial part of the seasonal diet of Alexander Archipelago wolves (Szepanski et al. 1999). Access to this high-quality food source should increase body size beyond predictions based on geographical origins and genetic characteristics (Weckworth et al. 2011).

The substantial within-population variation in skull shape also suggests an interplay between diet and skull morphology. Two shape-related morphotypes were revealed (PC1 with size-adjusted data); longer and narrower skulls, and shorter and relatively wider skulls. Considering the allometric analyses, three craniodental characters, frontal bone width (FBW), IOB, and CPH, scale isometrically to the length of the skull (SKL), indicating that these traits maintain a constant shape as skull size increases. However, allometric scaling is common, indicating a change in the general shape of the skull with size. The width (ZGW) scales allometrically to SKL, pointing to the same relationship revealed by PC1. Characters extending along the base of the skull, CBL for instance, grow in this same way. This finding suggests that while most parts of the skull decelerate in growth rate during development, the sagittal and the nuchal crests continue to grow into later stages of development; such prolonged enlargement of the sagittal and nuchal crests provides more surface for the attachment of temporalis muscles and subsequently more powerful bite and teeth clenching forces useful during prey hunting (Tseng and Wang 2010). This is corroborated by the development pattern of CPH, which scales isometrically to SKL in both sexes. CPH equates with the size of the surface for the attachment of the masseteric muscle. By growing concomitantly with the skull, it shapes a larger masseteric fossa for a bulkier masseter. Likewise, TFC scales allometrically to SKL, but this character grows more slowly in males than in females (smaller allometric slope), which should result in a relatively wider temporal fossa space in males. The bulkiness of the masticatory muscles is associated with the size of this space. Furthermore, much of the stress during a carnassial bite is distributed in the temporal fossa area (Slater et al. 2009; Tseng and Wang 2010), pointing to a more powerful bite in males. These observations likely reflect differences in bite force and ecological (behavioral ecology) roles of wolves in the ecosystem.

This study also clarifies several taxonomic issues and possibly provides new insights by reconsidering the taxonomic value of morphological variation in North American gray wolves. Coat color in its diversity of hues and patterns has been used to infer intraspecific taxonomy in the Gray Wolf (Goldman 1944; Jolicoeur 1959; Mech 1970). Coat coloration pattern is a complex mechanism affected by genetic and ecological factors in this species (Sponenberg and Rothschild 2001; Apollonio et al. 2004; Anderson et al. 2009; Hedrick 2009; Schweizer et al. 2018), reflecting both a latitudinal gradient (Gloger's rule; Jolicoeur 1959) and hybridization with dogs (Khosravi et al. 2015; Schweizer et al. 2018). Coat color also reflects climatic, physiological, and behavioral determinants in vertebrates (Ducrest et al. 2008; Roulin 2014). Thus, the taxonomic value of coat coloration must be debatable with regards to subspecies of wolves. Gray wolf subspecies have been recognized based on size-related skull differences, sometimes in combination with coat color attributes (Goldman 1944; Nowak 1995). Rather, results from this study suggest that size in North American gray wolves better reflect food type and availability rather than geographical determinants and phylogenetic relationships, and therefore taxonomic recognition of separate subspecies. Size also may reflect hybridization with other canids (Clutton-Brock et al. 1994; Kyle et al. 2006; Nowak 2009). Overall fluctuating changes occurred in the size of the skulls and shape of some skull features of Arctic wolves in the period of 1930–1950, possibly due to hybridization with dogs (Clutton-Brock et al. 1994). Results reported here support the prediction that environmental factors are more significant than geographical characteristics in determining genetic and morphometric variation in North American gray wolves (Geffen et al. 2004; Carmichael et al. 2007; Musiani et al. 2007).

In examining skull size and shape of populations north of 45° latitude (excluding the southern *C. l. baileyi*) and assessing the amplitude of differences (degree of significance combined with standard effect size), this study demonstrated an overall morphological similarity among North American gray wolf populations. More morphological variation occurs within than among populations. The substantial within-population component would reflect a combination of processes, including unequal access to quality food and possible differential developmental processes, dispersal history, genetic characteristics (functional genes, e.g., *IGF-1* alleles), and possible hybridization with other canids. The among-population component observed in skull size could be due to natural selection acting most likely through geographic variation in prey type (ungulates of different body masses, catchability, and risk) and availability (densities and differential biogeographical distributions) to favor one of three *IGF-1* alleles over another. Based on skull morphological variation, this study argues for a single taxonomic unit for North American gray wolf populations.

Acknowledgments

This research was supported and funded by the Canadian Museum of Nature (Beaty Center for Species Discovery). I am truly indebted to the following curators and collections managers who eagerly allowed me to use the collections they manage and set me up to carry out my work in the best conditions possible: Link Olson (UAM), Don McAlpine and Mary Sollows (NBM), Marie-Ève Gingras (LUBD), Judith Eger and Suzanne Woodward (ROM), Gavin Hanke and Lesley Kennes (RBCM),

Rebecca Banasiak and Lawrence Heaney (FMNH), and Charles Potter (USNM). Veronica Chevasco and Danielle Fraser (CMN) reviewed a first draft. Leslie Carraway and Frank Mallory made useful comments and suggestions that improved this manuscript.

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Classification matrix for comparing size classes.

Supplementary Data SD2.—Cluster analysis validation tests.

Supplementary Data SD3.—Classification matrix for comparing three groups of populations.

Supplementary Data SD4.—Classification matrix for comparing two groups of populations.

Supplementary Data SD5.—Discriminant function loadings and percentage of variance for comparing two groups of populations.

Supplementary Data SD6.—Allometric analysis statistics for pooled populations.

Supplementary Data SD7.—Allometric analysis statistics for groups of populations.

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Submitted 7 April 2022. Accepted 23 December 2022.

Associate Editor was Leslie Carraway.

APPENDIX I

Museum catalog number of the 538 vouchered Gray Wolf (*Canis lupus*) specimens used for the present study. AMNH–American Museum of Natural History, United States; CMNMA–Mammal collection of the Canadian Museum of Nature, Canada; FMNH–Field Museum of Natural History, United States; LUBD–Laval University Biology Department, Canada; NBM–New Brunswick Museum, Canada; RBCM–Royal British Columbia Museum, Canada; ROM–Royal Ontario Museum, Canada; UAM–University of Alaska Museum, United States; and USNM–National Museum of Natural History, United States. Localities for the specimens listed are available at the Global Biodiversity Information Facility portal (https://www.gbif.org/).

Institution	Catalog number
AMNH (5)	169525, 169526, 169527, 169528, 169529
CMNMA (299)	2790, 2792, 2794, 2795, 2796, 3339, 3504, 3506, 4868, 5572, 5575, 5576, 5741, 6048, 8802, 8803, 8804, 12566, 16869, 16942, 17011, 17098, 17099, 17148, 17158, 17236, 17310, 17312, 17575, 17576, 17578, 17591, 18254, 19176, 19565, 19566, 19568, 19569, 19580, 19582, 19584, 19585, 19808, 19811, 19812, 19815, 20314, 20316, 20317, 20320, 20679, 21100, 21454, 21456, 21457, 21458, 21464, 21465, 21466, 21471, 21472, 21519, 21520, 21521, 21522, 21523, 21530, 21539, 21540, 21541, 21542, 21543, 21544, 21566, 21604, 21733, 22024, 22025, 22026, 25836, 25840, 25841, 25844, 26316, 26317, 26318, 29074, 29075, 29186, 29202, 29203, 29204, 29206, 29207, 30045, 30053, 30923, 30925, 31758, 31792, 31793, 31794, 31797, 33629, 33630, 33631, 34690, 34691, 35165, 35217, 36162, 46736, 46737, 51132, 51136, 51137, 51138, 51175, 51176, 51177, 51178, 52713, 52756, 52758, 52764, 52765, 52793, 52794, 52796, 52797, 52798, 53985, 53989, 53992, 53993, 53994, 53996, 53998, 53999, 54002, 54004, 54005, 54009, 54021, 54022, 54023, 54025, 54104, 54105, 54106, 54232, 54233, 54234, 54239, 54240, 54248, 54249, 54252, 54253, 54254, 54255, 54256, 54258, 54259, 54260, 54261, 54263, 54266, 54267, 54270, 54271, 54272, 54280, 54284, 54285, 54287, 54289, 54290, 54292, 54294, 54324, 54325, 54341, 54343, 54380, 54443, 54449, 54451, 54452, 54457, 54555, 54557, 54559, 54607, 54609, 54611, 54612, 54613, 54621, 54622, 54624, 54625, 54627, 54628, 54629, 54645, 54646, 54647, 54648, 54649, 54650, 54651, 54655, 54659, 54665, 54670, 54671, 54672, 54673, 54674, 54675, 54676, 54679, 54683, 54685, 54686, 54692, 54694, 54705, 54718, 54727, 54731, 54744, 54748, 54749, 54753, 54755, 54768, 54769, 54771, 54772, 54774, 54775, 54776, 54777, 54787, 54794, 54795, 54798, 54799, 54800, 54802, 54803, 54812, 54814, 54815, 54816, 54822, 54827, 54829, 54830, 54833, 54836, 54845, 54846, 54890, 54894, 54974, 54975, 54976, 54978, 54980, 54989, 54999, 55003, 55006, 55010, 55038, 55039, 55040, 55042, 55043, 55185, 55186, 55188, 55191, 55200, 55201, 55205, 55206, 55207, 55211, 55219, 55220, 55222, 75561, A20673, A23136
FMNH (11)	21207, 43964, 72961, 72962, 138773, 138774, 138779, 138780, 138781, 138782, 138791
LUBD (31)	214, 351, 357, 371, 375, 378, 379, 387, 397, 753, 757, 1337, 1351, 3032, 3033, 3034, 3039, 3040, 3042, 3044, 3045, 3046, 3048, 3063, 3065, 3074, 3076, 3094, 3098, 3099, 3100
NBM (29)	4453, 4465, 4466, 4468, 4481, 4482, 4488, 4489, 4490, 4493, 4494, 4495, 4498, 4500, 4503, 4508, 4509, 4510, 4511, 4512, 4516, 4517, 4518, 4523, 4524, 4525, 4526, 4528, 11985
RBCM (43)	1350, 1352, 1441, 1862, 1863, 1864, 1966, 3339, 3559, 4262, 4263, 4264, 4656, 4698, 4700, 4728, 5304, 5544, 5550, 5647, 5648, 5659, 5660, 6965, 7394, 7634, 7998, 8580, 9724, 10244, 10245, 10246, 11442, 13918, 13934, 13937, 13948, 13949, 13956, 13961, 15329, 15332, 2418X
ROM (25)	11281, 11282, 16890, 18653, 18746, 18778, 19532, 19536, 19540, 20121, 20305, 23405, 23406, 30407, 281261, 312162, 333241, 339202, 339204, 339206, 339208, 3112291, 3112294, 3210164, 3210165
UAM (58)	10339, 10916, 10922, 16623, 16624, 16653, 16671, 16675, 16676, 16684, 16686, 16694, 16696, 16703, 16708, 16739, 16743, 16744, 16745, 16765, 16810, 17003, 17097, 17101, 17106, 17109, 17235, 17237, 17301, 17410, 17553, 17559, 17611, 17657, 18016, 18018, 18080, 18111, 18112, 18126, 18170, 18171, 18185, 18199, 18402, 18426, 21338, 21340, 21342, 21375, 21376, 21377, 21378, 21380, 21385, 37050, 37051, 37052
USNM (37)	150421, 168820, 170692, 178452, 180281, 242289, 242290, 243323, 243395, 265071, 289933, 289995, 347915, 347917, 347921, 347922, 347926, 347927, 512005, 512019, 512020, 512022, 512025, 513676, 513677, 513680, 514917, 514918, 514919, 514920, 529879, 530430, 530431, 530432, 530434, 530437, 530438