Another Look at Wolf Taxonomy

■ Ronald M. Nowak

Multivariate analyses, using 10 measurements from each of 580 skulls of modern male wolves, indicate the presence of five subspecies of ***Canis lupus*** *in North America:* ***arctos****, a large-toothed arctic wolf;* ***occidentalis****, a large animal of Alaska and western Canada;* ***nubilus****, a moderate-sized wolf, originally found from Oregon to Newfoundland and from Hudson Bay to Texas;* ***baileyi****, a usually smaller wolf of the southwest; and* ***lycaon****, a small subspecies now restricted to southeastern Canada. Individuals taken in the northwestern conterminous United States since 1940 represent occidentalis. Eurasian subspecies include an arctic wolf (****albus****), a large north-central form (****communis****), and a widespread animal of moderate size (****lupus****), which resemble their North American counterparts more than they resemble one another. A small, but broad-skulled, subspecies (****cubanensis****) occurs in the Caucasus. Small, narrow-skulled wolves, showing little statistical overlap with one another or with any other populations, are present in southwestern Asia (****pallipes****) and southeastern North America (****rufus****).*

Introduction

Hall (1981), based largely on the morphological studies of Goldman (1937, 1944), recognized 24 subspecies of gray wolf (*Canis lupus*) in North America (Fig. 1). Sokolov and Rossolimo (1985) recognized nine additional subspecies of *Canis lupus* in Eurasia (Fig. 2), but reduced the accepted number in the New World to seven. Other authorities, relying mainly on morphometric techniques, also have indicated that some of the subspecies listed by Hall may be invalid (Rausch 1953, Jolicoeur 1959, Skeel and Carbyn 1977, Pedersen 1982, Walker and Frison 1982, Bogan and Mehlhop 1983, Nowak 1983, Friis 1985, Hoffmeister 1986). In contrast, there have been suggestions that the subspecies *C. l. lycaon* of the Great Lakes region, as mapped by Hall (1981), is divisible between two, three, or even four taxonomic units (Kolenosky and Standfield 1975, Schmitz and Kolenosky 1985a, Standfield 1970, Van Ballenberghe 1977). However, these suggestions might be based partly on consideration of hybrids of the gray wolf and coyote (*C. latrans*), that have appeared in the eastern Great Lakes region (Nowak 1979).

Analyses of mitochondrial DNA have indicated to some authorities that interbreeding between *C. lupus* and *C. latrans* has also taken place in the western Great Lakes region — Minnesota and adjacent parts of Ontario — and that a substantial "hybrid zone" has formed there (Lehman et al. 1991). Similar studies have suggested that the red wolf (*C. rufus*) of the southeastern United States may have resulted entirely from interbreeding of *C. lupus* and *C. latrans*, and that its historic range (Fig. 1) represents a "hybrid zone" (Wayne and Jenks 1991). Such studies have been questioned (Dowling et al. 1992). Elsewhere in this volume (Nowak et al. this volume) evidence is presented that *C. rufus* is a primitive, distinctive kind of wolf, not a hybrid, and that interbreeding of *C. lupus* and *C. latrans*, if it has occurred at all in the western Great Lakes region, has resulted in no lasting phenotypic effects. Questions of hybridization thus are not emphasized in this paper, but the issue of whether the red wolf is a species, as regarded by most authorities, or a subspecies, as suggested by Lawrence and Bossert (1967, 1975), is of concern. In order to deal with that issue, as well as with the most meaningful systematic division of the gray wolf, this paper covers, for the first time, substantial data on morphometric variation in wolves on a worldwide basis.

Materials and Methods

This study is limited to 580 skulls of full grown male wolves taken in historical time. Previous work (Nowak 1979) showed that while the sexes are significantly different in most measurements, and preferably should not be combined in one sample, analyses using either sex produce much the same results. Skulls of animals under 12 months old, and of some large wolves under 24 months old, have not attained full size in all dimensions and thus are not usable. The number of specimens in each series, and representative of each taxon, is given in Table 1. I measured all North American and some Eurasian specimens, but most of the latter were measured by others (see "Acknowledgments") following my diagrams and descriptions. I was not selective, but used all data available from skulls known or judged to be those of full grown males and that yielded all desired measurements, though a few specimens were eliminated because of damage, incomplete collection information, or suspected influence from hybridization with domestic dogs (*C. familiaris*).

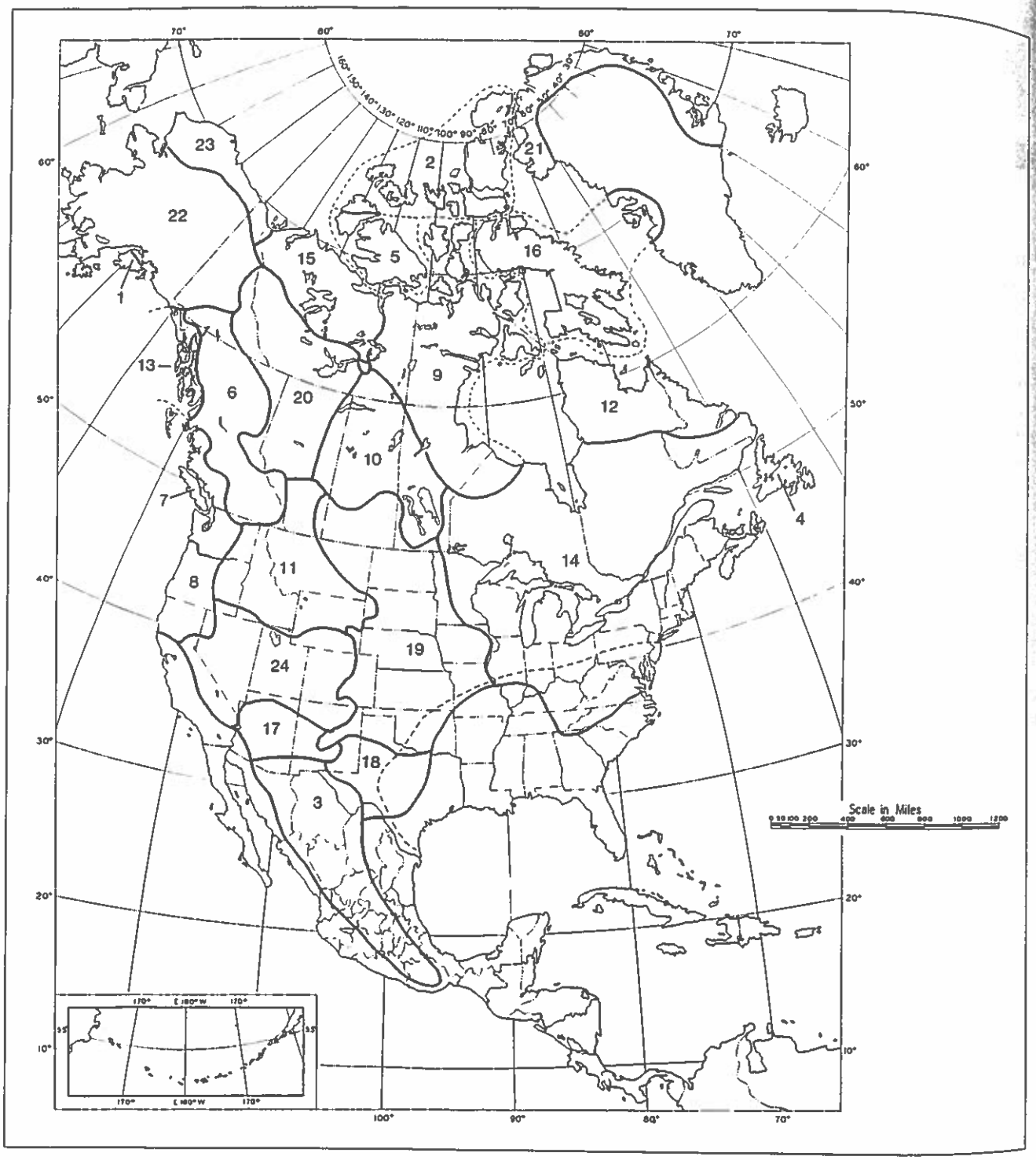
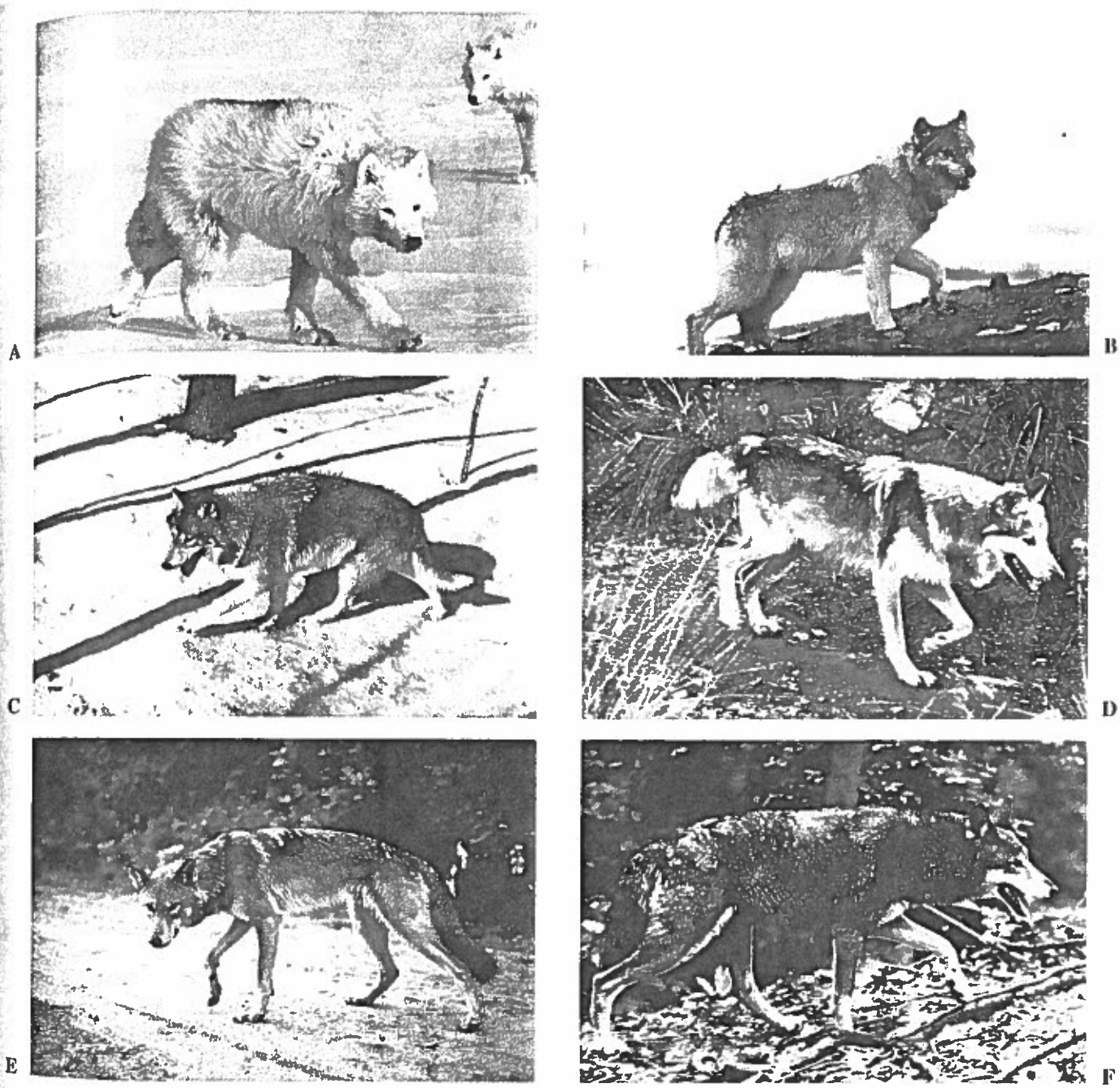


Fig. 1. *Original geographical distribution of wolves in North America. The 24 subspecies of gray wolf (**Canis lupus**) recognized by Hall (1981) are:*

*1. **alces***	*7. **crassodon***	*13. **ligoni***	*19. **nubilus***
*2. **arctos***	*8. **fuscus***	*14. **lycaon***	*20. **occidentalis***
*3. **baileyi***	*9. **griseoalbus***	*15. **mackenzii***	*21. **orion***
*4. **beothucus***	*10. **hudsonicus***	*16. **manningi***	*22. **pambasileus***
*5. **bernardi***	*11. **irremotus***	*17. **mogollonensis***	*23. **tundrarum***
*6. **columbianus***	*12. **labradorius***	*18. **monstrabilis***	*24. **youngi***

*The red wolf (**Canis rufus**) occupied the southeastern quarter of the continent, the approximate northern and western limits of its range being marked by the dashed line on the mainland.*



*The six kinds of North American wolves, as suggested by this study: a) Arctic Island wolf (**Canis lupus arctos**), photo: L.D. Mech; b) Alaskan wolf (**Canis lupus occidentalis**), photo: L.D. Mech; c) Minnesota wolf (**Canis lupus nubilus**), photo: L.D. Mech; d) Mexican wolf (**Canis lupus baileyi**), photo: D.R. Parsons; e) Algonquin park wolf (**Canis lupus lycaon**), photo: G. Forbes; f) red wolf (**Canis rufus**), photo: W. Muñoz.*

The following 10 measurements (Fig. 3) were used for analysis: 1) greatest length of skull (length from anterior tip of premaxillae to posterior point of union); 2) zygomatic width (greatest distance across zygomata); 3) alveolar length of maxillary toothrow (distance from anterior edge of alveolus of P1 to posterior edge of alveolus of M2); 4) maximum width across upper cheek teeth (greatest breadth of skull measured between outer sides of crowns of P4); 5) palatal width at first premolars (minimum width between inner margins of alveoli of P1); 6) width of frontal shield (maximum breadth across postorbital processes of frontals); 7) height from toothrow to orbit (minimum distance from outer alveolar margin of M1 to most ventral point of orbit); 8) depth of jugal (minimum depth of jugal anterior to postor-

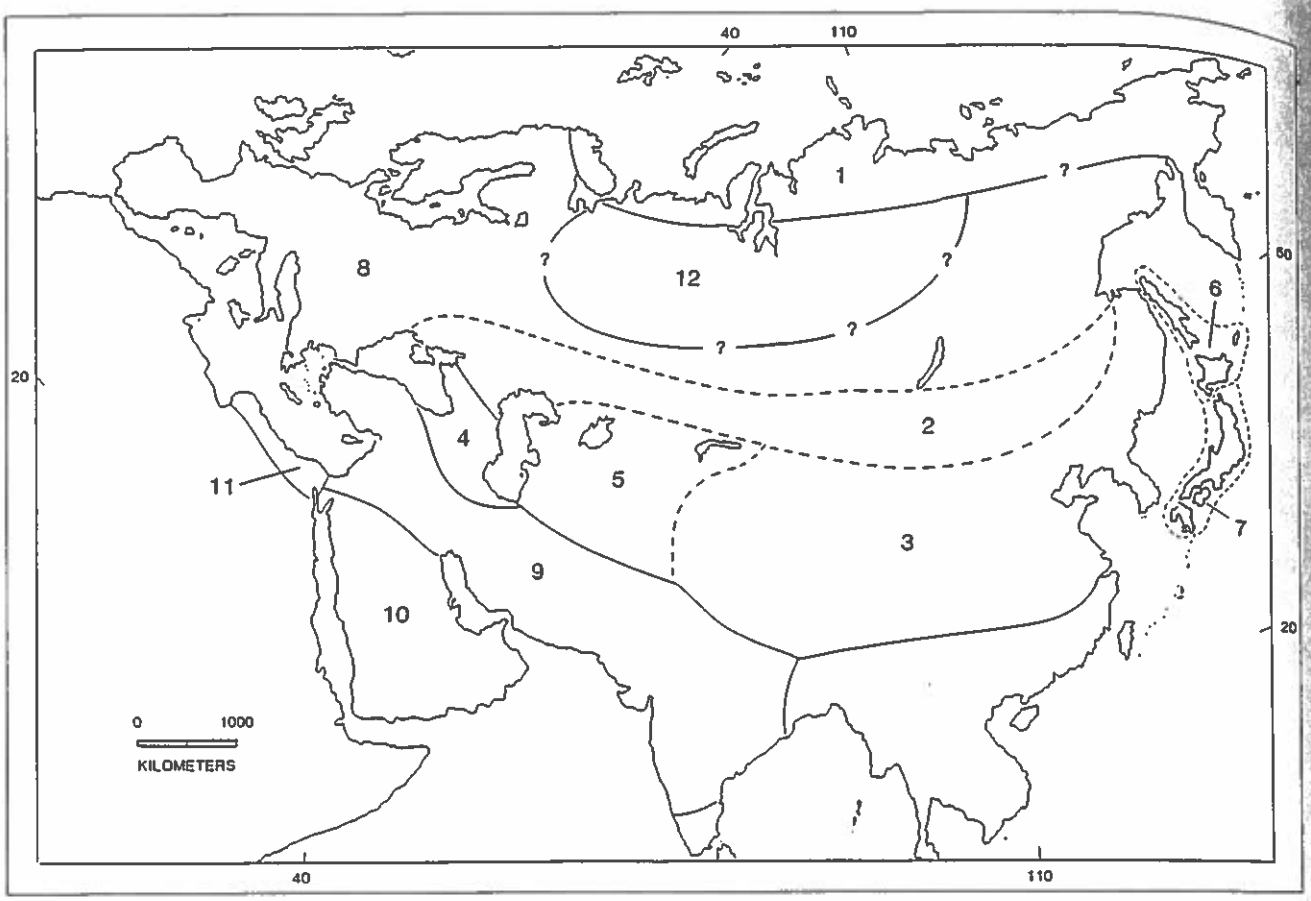


Fig. 2. *Original geographical distribution of gray wolf (**Canis lupus**) in the Old World. Sokolov and Rossolimo (1985) recognized the following subspecies: 1) **albus**, 2) **campestris**, 3) **chanco**, 4) **cubanensis**, 5) **desertorum**, 6) **hattai** (= **rex**), 7) **hodophilax**, 8) **lupus**, 9) **pallipes**. The subspecies 10) **arabs**, regarded as a synonym of **pallipes** by Sokolov and Rossolimo (1985), sometimes is considered valid, and the subspecies 11) **lupaster** sometimes is assigned to **C. lupus** rather than to **C. aureus**. This study supports combining **campestris**, **chanco**, and **desertorum** with the subspecies **lupus**, but distinguishing the subspecies 12) **communis**. As indicated by the question marks (?), the extent of the range of **communis** is problematical, and there also is uncertainty as to whether northeastern Siberia is occupied by **communis**, **albus**, or **lupus**.*

bital process, at right angle to its anteroposterior axis); 9) crown length of upper carnassial (maximum anteroposterior length of crown of P4 measured on outer side); and 10) crown width of second upper molar (maximum transverse diameter of M2 measured from outermost point to innermost point of crown). Means for all series are listed in Table 1.

These measurements are thought to express major adaptive features of the skull: overall size, grasping power, cranial protection, and cutting and crushing capacity. They are among 15 used in previous work (Nowak 1979); the others — braincase width, width of rostrum at C1, postorbital constriction, length from toothrow to bulla, and diameter of C1 — are considered redundant, less precise, and/or useful mainly to distinguish domestic dogs from wild canids, rather than to separate different kinds of wolves.

Expression of the results of this study depends entirely on computer-based, multivariate analysis of these 10 measurements. Other measurements, nonmeasurable characters of the skull, and features of the pelage and postcranial skeleton are given little or no consideration. Previous experience (Nowak 1979) indicates that such an approach is acceptable for a review of recent wolves and that evaluation of the other characters would not affect or would reinforce conclusions. However, I do recognize that utilization of a larger set of measurements or assessment of regularity in nonmeasurable characters could, in certain cases, lead some workers to distinguish additional taxonomic groupings. The measurements that I used are probably among those that best reflect what a person actually sees in a skull. Their combination and comparison through multivariate analysis is not considered a solution to classification problems, but rather a means of efficiently and objectively presenting conclusions that a person might make after examining many specimens or reviewing many individual measurements.

All measurements were subjected to canonical discriminant analysis using the Statistical Analysis System (SAS

Table 1. Means of measurements (numbered as in Fig. 3 and text) for wolf groups analyzed (listed approximately in order discussed in text).

Group	*n*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*
columbianus	8	275.8	147.0	89.53	83.89	32.34	64.61	43.36	20.09	25.78	14.18
griseoalbus	10	271.5	144.8	89.26	84.51	34.23	66.82	44.38	20.32	27.18	14.47
occidentalis	50	276.2	148.2	90.74	85.13	33.29	68.37	43.99	21.11	26.81	14.46
pambasileus	24	275.3	148.4	91.15	85.86	33.70	68.65	44.40	20.78	27.25	14.66
tundrarum	13	273.8	146.1	90.95	84.72	32.47	68.88	43.36	20.51	27.38	15.00
main northern group (above 5 combined)	105	275.2	146.6	90.63	85.09	33.30	68.07	44.00	20.80	26.94	14.55
fuscus	10	257.4	138.7	85.82	81.71	31.33	69.29	40.67	20.72	25.52	13.47
irremotus	14	253.9	139.7	86.41	83.14	31.13	62.74	38.98	18.99	25.52	13.47
lycaon (Minnesota)	28	256.3	139.3	86.27	81.13	31.77	64.34	39.31	19.61	24.99	14.12
mogollonensis	17	253.5	140.4	84.34	81.11	31.06	66.65	39.81	19.26	25.37	13.65
monstrabilis	7	257.4	138.3	84.40	79.51	31.63	65.06	40.27	18.84	25.56	13.16
nubilus	15	256.7	137.5	84.93	80.55	31.95	65.57	39.87	19.77	25.39	13.19
youngi	28	257.5	140.0	86.25	83.18	32.79	66.55	39.45	19.89	25.65	13.81
main southern group (above 7 combined)	119	256.1	139.3	85.69	81.72	31.81	65.62	39.62	19.62	25.39	13.67
ligoni	26	263.0	144.3	86.75	82.88	33.29	67.99	41.93	20.15	25.60	14.15
crassodon	6	258.5	141.7	86.78	81.27	31.60	68.02	40.12	19.30	26.25	14.30
baileyi	21	243.9	136.3	81.78	77.40	29.98	60.62	38.95	18.79	24.49	12.59
arctos	22	256.5	142.4	86.81	84.45	32.31	65.48	41.73	19.35	27.45	13.98
hudsonicus	14	258.7	139.8	85.89	82.06	32.02	63.51	41.16	18.99	26.07	14.11
lycaon (west Ont.)	14	255.6	138.9	84.92	80.81	30.97	65.29	39.26	19.14	25.11	13.99
lycaon (Algonquin)	13	250.2	134.6	83.87	78.13	28.85	63.75	37.98	17.82	24.90	14.69
rufus	33	236.5	121.3	79.48	69.74	26.18	54.80	33.58	16.03	23.35	13.71
campestris	34	251.3	137.2	84.81	79.23	31.05	64.80	39.73	19.09	25.96	14.29
chanco	23	248.0	134.9	84.43	77.20	29.71	61.33	37.83	18.33	25.08	13.91
desertorum	20	252.3	134.1	87.57	78.25	29.58	63.04	38.73	17.99	25.72	14.00
lupus (above 3 combined)	77	250.6	135.7	85.41	78.37	30.27	63.30	38.90	18.58	25.63	14.10
albus	20	263.0	147.1	88.30	84.65	33.03	70.11	41.48	19.08	26.65	14.95
communis	20	270.2	150.9	87.70	86.08	34.19	74.48	43.01	21.40	26.83	13.89
pallipes	30	221.4	118.0	76.53	68.98	26.75	56.44	33.98	15.30	22.99	12.20
cubanensis	14	237.5	136.5	80.58	76.74	29.26	63.34	37.80	-.-	23.36	12.82

Institute 1987). This method is similar to that employed in my previous work on *Canis* (Nowak 1979) and is the same as used in various recent taxonomic studies of mammals (e.g., those by Goodyear 1991 and Jones et al. 1991). Essentially, the various measurements, weighted by their ability to best distinguish the particular groups being analyzed, assign each specimen a total numerical value referred to as the first canonical variable. The next best distinguishing combination, uncorrelated with the first, provides a second canonical variable, and so on.

Commonly, a single graphical position is plotted based on the first two canonical variables arranged as perpendicular axes. The result looks much like a bivariate scatter diagram, but the numerical positions are abstracts, and the overall mean of all the positions is standardized to zero. High positive values may actually express small size, and vice versa. Characters given greatest weight change with the set of groups being compared, and so the statistical distribution of a given group may change as it is compared to various others. The legend for each of the following graphs (Figs. 4, 6, 7, 8, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19) lists the three

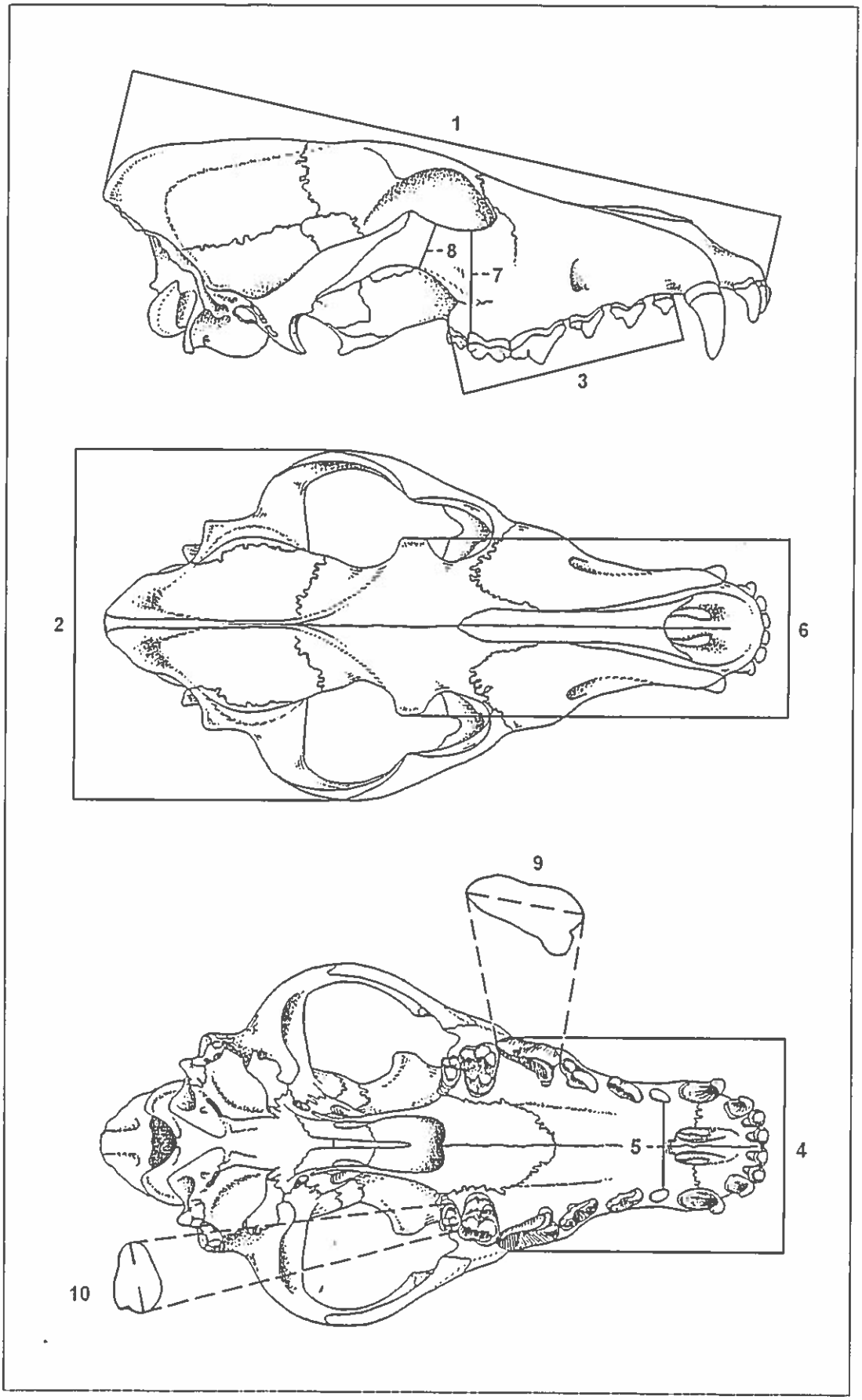


Fig. 3. *Three views of a skull of* ***Canis lupus****, showing the 10 characters used in statistical analyses (see text for descriptions). The drawings were made by Irene Brady, based on originals in Hall (1981).*

Table 2. Statistical distance, D^2, between nominal subspecies of *Canis lupus* in western North America.

Distance from group	*tundrarum*	*pambasileus*	*occidentalis*	*columbianus*	*griseoalbus*	*fuscus*	*irremotus*	*youngi*	*mogollonensis*	*nubilus*	*monstrabilis*	*lycaon*
tundrarum		1.15	1.50	5.17	2.97	12.15	12.25	9.47	10.79	11.67	10.27	10.23
pambasileus	1.15		0.68	4.18	1.58	14.34	13.09	10.75	12.68	12.81	11.07	12.15
occidentalis	1.50	0.68		2.36	.83	12.33	12.08	9.58	11.55	10.88	9.82	10.22
columbianus	5.17	4.18	2.36		6.69	15.95	12.16	12.30	13.01	12.93	10.88	11.12
griseoalbus	2.97	1.58	2.83	6.69		14.16	14.34	10.37	12.88	10.93	8.84	12.51
fuscus	12.15	14.34	12.33	15.95	14.16		5.95	2.84	2.99	1.91	4.94	3.96
irremotus	12.25	13.09	12.08	12.16	14.34	5.95		3.08	3.00	4.89	6.24	3.79
youngi	9.47	10.75	9.58	12.30	10.37	2.84	3.08		2.78	1.84	4.23	1.78
mogollonensis	10.79	12.68	11.55	13.01	12.88	2.99	3.00	2.78		2.92	3.00	2.70
nubilus	11.67	12.81	10.88	12.93	10.93	1.91	4.89	1.84	2.92		1.47	3.19
monstrabilis	10.27	11.07	9.82	10.88	8.84	4.94	6.24	4.23	3.00	1.47		5.26
lycaon	10.23	12.15	10.22	11.12	12.51	3.96	3.79	1.78	2.70	3.19	5.26	

characters that contributed most to each canonical variable. Individual specimens can be assigned positions in relation to established groups. The mean position of each group also can be plotted and the statistical distances between the means (this distance being known as the D^2 of Mahalanobis) can be calculated to assess affinity.

Results and Discussion

The North-South Division in Western North America

Past investigations (Skeel and Carbyn 1977, Nowak 1983, Friis 1985) suggested that there might be a major systematic division of North American *C. lupus* along a line extending from the Pacific to the western Great Lakes, roughly following the border between Canada and the United States. Seven named subspecies meet along this line: *columbianus*, *occidentalis*, and *griseoalbus* to the north, and *fuscus*, *irremotus*, *nubilus*, and *lycaon* to the south. I decided to compare these populations, and also several neighboring subspecies farther to the north (*tundrarum*, *pambasileus*) and south (*youngi*, *mogollonensis*, *monstrabilis*), to evaluate the idea that the statistical break along the aforementioned line might be substantially more pronounced than that separating populations falling entirely on one side of the line. The subspecies *hudsonicus*, found just to the northeast, is treated separately below. In order to allow comparison between the most geographically proximal populations of the gray wolf and red wolf in subsequent analyses, the sample of *lycaon* is limited to Minnesota (23 specimens) and Isle Royale (five specimens) and that of *monstrabilis* is limited to Texas (seven specimens). For purposes of helping to evaluate the question of whether western Great Lakes wolves may be changing through recent hybridization with the coyote, the sample of *lycaon* is also limited to individuals taken since 1960. Otherwise, all specimens from the western conterminous United States were taken prior to 1940 (except for one skull of *monstrabilis* collected in 1942).

Plotting the means of the first two canonical variables of each named subspecies indicates a division based mainly on large size in wolves to the north and smaller size in those to the south (Fig. 4). Only the means are shown, because there was such extensive overlap between the five northern subspecies, on the one hand, and between the seven southern subspecies, on the other, that plotting all of the statistical boundaries of the groups would have made the figure too confusing. Table 2 gives the statistical distances between all subspecies, while Figure 5 maps the distances between neighboring subspecies. The statistical distance between neighbors across the Pacific-Great Lakes line is in all cases much greater than the distance between any two subspecies, whether neighbors or not, on one side of the line. Therefore, more is involved than simply a north-south cline in size. The northern series and the southern series evidently represent two main systematic groupings of *C. lupus*, which may in turn serve as standards with which other populations and individuals may be compared.

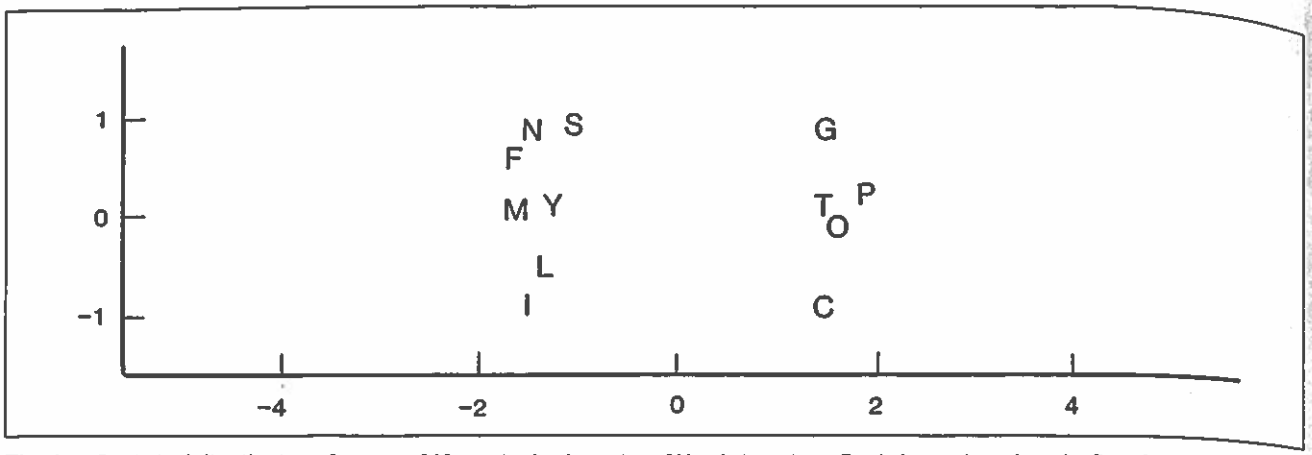
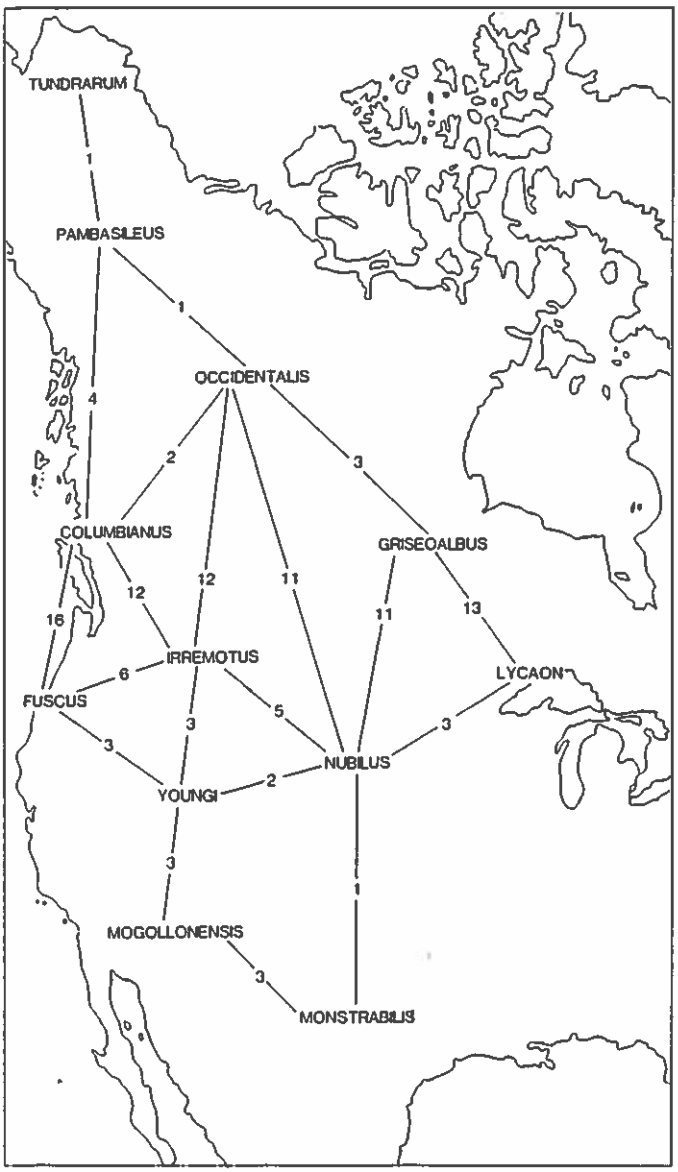


Fig. 4. *Statistical distribution of means of 12 nominal subspecies of North American* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Letters indicate mean positions of groups: C —* ***columbianus****; F —* ***fuscus****; G —* ***griseoalbus****; I —* ***irremotus****; L —* ***lycaon****; M —* ***mogollonensis****; N —* ***nubilus****; O —* ***occidentalis****; P —* ***pambasileus****; S —* ***monstrabilis****; T —* ***tundrarum****; Y —* ***youngi****. Characters (see Fig. 3) contributing most to high positive values are: first canonical variable, large 1, large 7, large 9; second canonical variable, small 2, small 7, large 4.*



Other Subspecies of Western North America

Based on recent studies (Pedersen 1982, Bogan and Mehlhop 1983, Friis 1985) three additional nominal subspecies of western North America may be associated with the main southern group: *ligoni* of the southeastern Alaska panhandle, *crassodon* of Vancouver Island, and *baileyi* of Mexico and adjacent border parts of the southwestern United States. Friis (1985) found statistical affinity between *ligoni*, *crassodon*, and *fuscus*, but indicated that each warranted subspecific status. She also suggested that populations of coastal and south-central British Columbia were referable to *ligoni*, rather than to *fuscus*. Sokolov and Rossolimo (1985) combined *ligoni*, *crassodon*, and *fuscus* into a single subspecies. In my own analysis (Fig. 6), *fuscus* and *crassodon* are completely separable, but a series of 26 *ligoni* (as compared to 11 used by Friis) overlaps slightly with *fuscus* and substantially with *crassodon*. Moreover, when *fuscus*, *ligoni*, and *crassodon* are compared to all western populations (see below), their recognition as full subspecies becomes questionable.

Figure 7 shows an analysis in which my single main northern group, comprising the combined samples of *columbianus*, *griseoalbus*, *occidentalis*, *pambasileus*, and *tundrarum*, is compared to a single main southern group, comprising the combined samples of *fuscus*, *irremotus*, *lycaon*, *mogollonensis*, *monstrabilis*, *nubi-*

Fig. 5. *Statistical distances (rounded to whole numbers) between those 12 nominal subspecies of North American* ***Canis lupus*** *shown in Figure 4.*

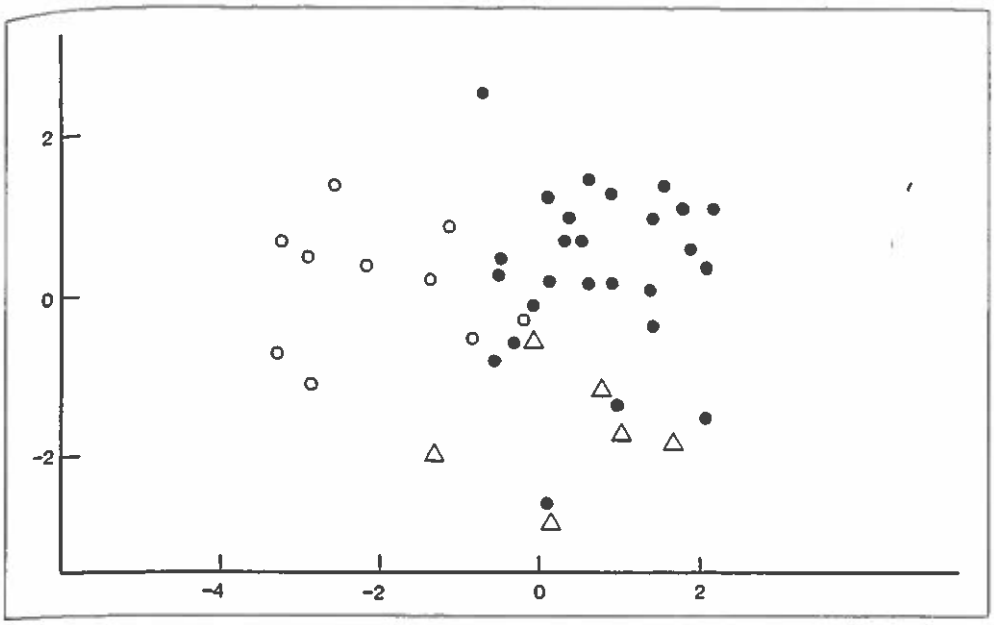


Fig. 6. *Statistical distribution of three nominal subspecies of North American* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Dots,* ***ligoni****; open circles,* ***fuscus****; triangles,* ***crassodon****. Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 2, small 4, large 5; second canonical variable, small 9, large 1, large 4.*

lus, and *youngi*. Also considered as groups in this analysis are the nominal subspecies *ligoni*, *crassodon*, and *baileyi*.

The subspecies *ligoni* occurs in the same latitudinal range as the members of my main northern group, but is partly isolated by mountains, glaciers, and waterways. While in the analysis (Fig. 7) it is partly encompassed by the statistical limits of the main northern systematic group of *C. lupus*, as developed above, *ligoni* falls mostly within the limits of the main southern group. It is also statistically closer to the southern group ($D^2 = 2.7$) than to the northern group ($D^2 = 4.6$), though it probably has been influenced extensively through intergradation with the latter. Using methodology similar to mine, but somewhat larger samples, Pedersen (1982) regarded *ligoni* as subspecifically distinct from *pambasileus*, a component of my northern group.

The positions (Fig. 7) of several individuals from near the Pacific coast of British Columbia, within the range of *C. l. fuscus*, as mapped by Hall (1981), are indicative of affinity with *ligoni* and thus supportive of findings by Friis (1985). However, *crassodon* of Vancouver Island falls entirely

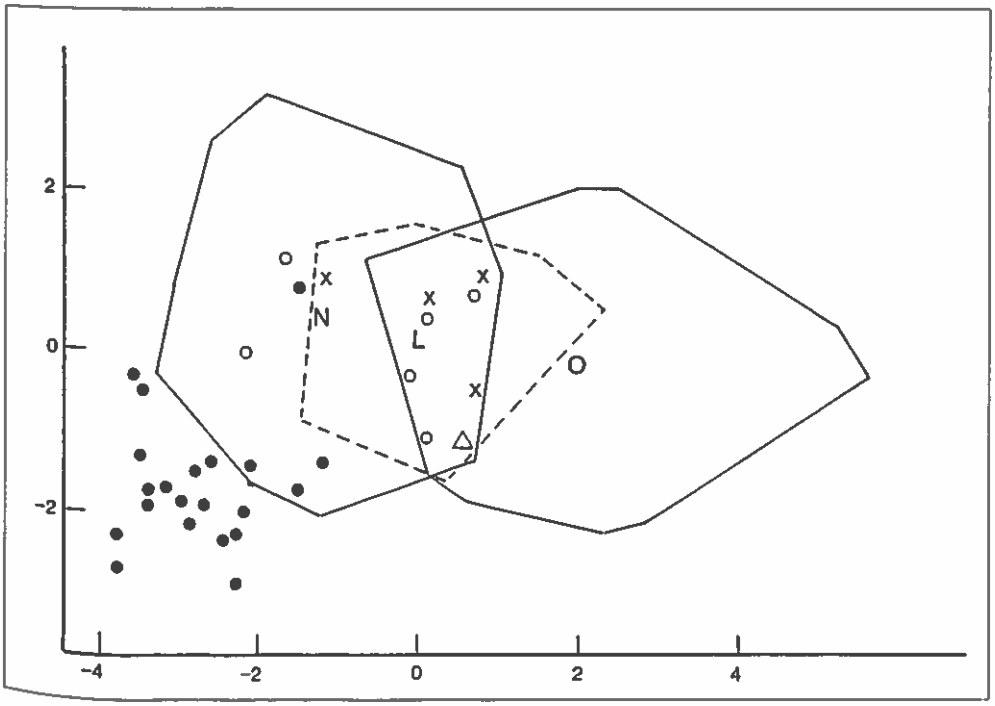


Fig. 7. *Statistical distribution of five groups and various individuals of North American* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of main northern group (letter O shows mean position) and main southern group (letter N shows mean); dashed lines, limits of* ***ligoni*** *(letter L shows mean); dots,* ***baileyi****; open circles,* ***crassodon****; x's, individuals from coastal British Columbia; triangle, one individual* ***labradorius****. Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 1, large 7, large 9; second canonical variable, small 2, small 7, large 1.*

within the overall statistical range of my main southern group. *Crassodon* originally was distinguished partly on the basis of nonmeasurable characters, especially in that the anterior margin of P4 is directed inward and backward. I found this feature of P4 to be pronounced in most of the 19 skulls of *crassodon* that I examined, though only in two of the six adult males used in my statistical analysis. While there is a reasonable case for giving subspecific status to *crassodon*, based on nonmeasurable characters and statistical separation from *fuscus*, its statistical position in relation to North American wolves in general, and to *ligoni* in particular, suggests inclusion within my main southern group of *C. lupus*.

Quite different is the situation of *baileyi*, which lies almost entirely outside the range of variation of the other groups. A single specimen from New Mexico, geographically well within the range of *baileyi*, is statistically close to the mean of my southern group. This individual is close to other *baileyi* in greatest length and zygomatic width, but is larger in width across upper cheek teeth, palatal width at P1, and diameter of M2. Otherwise, my findings with respect to *baileyi* correspond with those of Hoffmeister (1986), who continued to recognize *baileyi* as a subspecies with generally the same content assigned by Goldman (1944), and who placed *mogollonensis*, the nominal subspecies immediately to the north, in the synonymy of *youngi*, which in turn is here considered part of the main southern group. My findings do not correspond with those of Bogan and Mehlhop (1983), who regarded *mogollonensis* and *monstrabilis* as part of *baileyi*, with the resulting entity subspecifically distinct from *nubilus* and *youngi*.

One additional named subspecies found in western North America and south of the arctic is *alces* of the Kenai Peninsula in Alaska. The wolf evidently was eliminated from the Kenai by humans by about 1915, though a population was reestablished through migration from the north in the 1960's and 1970's (Peterson and Woolington 1982). Based on five specimens collected in 1904–1905, Goldman (1944) regarded the original population as a distinct subspecies, being perhaps the largest of North American wolves. Rausch (1953) and Pedersen (1982) questioned this designation. The original specimens consist of two adult females and three males that are not full grown and thus not suitable for inclusion in my analyses. The females are large, but are matched in this regard by several females of *occidentalis* that I have examined. All five skulls have carnassial teeth that are smaller than those of many other specimens in my main northern group. *Alces* hence appears to be a component of that group.

Adjustments to Subspecific Ranges

Most of the specimens used in my sample of *baileyi* and in the standard samples of my main northern (*columbianus*, *griseoalbus*, *occidentalis*, *pambasileus*, *tundrarum*) and southern (*fuscus*, *irremotus*, *lycaon*, *mogollonensis*, *monstrabilis*, *nubilus*, *youngi*) groups were assigned to nominal subspecies based on the ranges indicated by Goldman (1944) and Hall (1981). However, one individual from Duck Mountain in west-central Manitoba, classified as nubilus by those authorities, was included in my sample of *griseoalbus*. Several other specimens also suggest that the range of my main northern group originally extended farther to the south than usually thought, and that this range has moved still farther south in recent decades. These specimens were not included in the above standard samples, but are considered below.

Figure 8 compares my main northern and southern groups, and *baileyi*, and shows the relative positions of certain other individuals. Skulls from southern Alberta and the Little Belt Mountains of central Montana, which had been assigned by Goldman (1944) and Hall (1981) to *irremotus*, are statistically nearer to the main northern group. Admittedly, the Montana specimen could be considered part of an intergrading population, an unusually large member of the southern group (such as do occur elsewhere), or a wandering individual. Wolves are known to make extensive movements, even well across supposed subspecific lines. Fritts (1983) reported one that covered a straight-line distance of 886 km, moving from northeastern Minnesota to Saskatchewan. A specimen taken in 1925 in extreme northwestern South Dakota also falls well within the northern group and may represent a wolf that wandered southward after native populations had been extirpated.

Human persecution nearly eliminated the gray wolf from the conterminous United States. By the late 1920's the only substantive resident populations occurred in the northern Great Lakes region (Nowak 1983). The region from which wolves had disappeared corresponded largely with the range of the southern group of *C. lupus*, as designated above. Later occurrences to the west of the Great Lakes region apparently represent wandering individuals or range extensions from the north. All 11 specimens of males from the northwestern quarter of the conterminous United States, collected since 1940, fall beyond the range of variation of the southern group of *C. lupus* (Fig. 8), and probably represent a recent southward expansion of the northern group. These specimens were taken in the following states: Idaho, 1; Montana, 5; Oregon, 1; South Dakota, 2; and Washington, 2. They include three specimens collected in northwestern Montana in 1988–1989, which are the largest skulls of *C. lupus* ever taken in the conterminous United States; they approach the size of several taken in 1966–1974 in Alberta, which are the largest ever recorded for the species (Gunson and Nowak 1979). Four other specimens of males collected 1989–1991 in the Dakotas are statistically like the southern group and most likely moved westward from the existing Minnesota population.

In compiling my series of *baileyi*, I followed Hoffmeister (1986) in including a specimen from the Galiuro Mountains, Graham County, Arizona, which had been assigned to *mogollonensis* by Bogan and Mehlhop (1983), Goldman

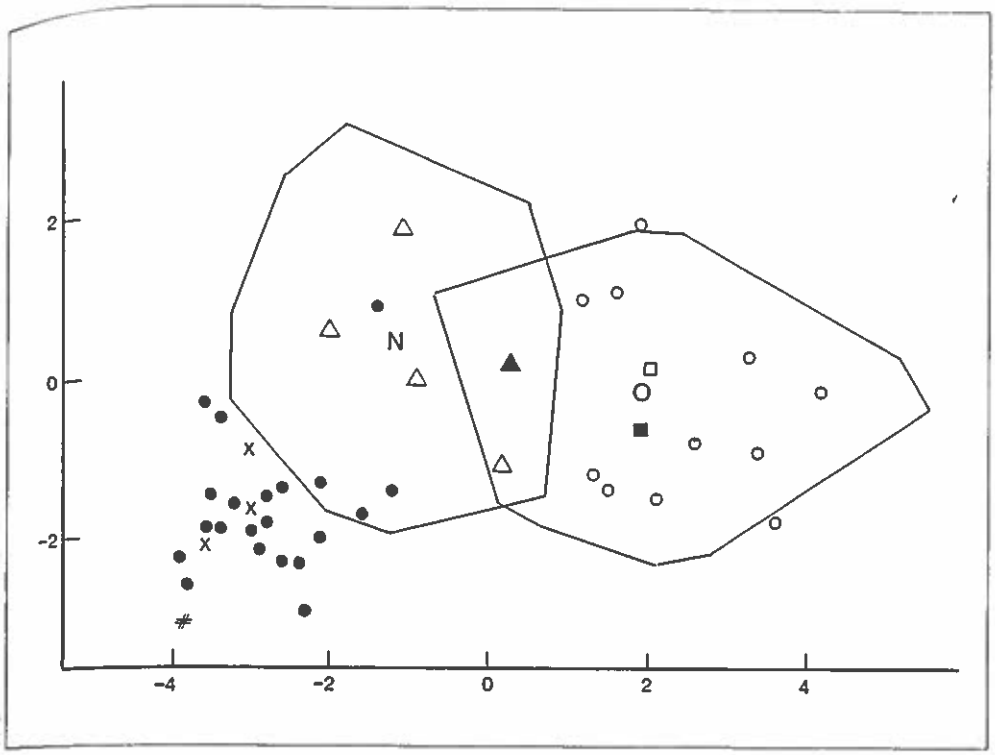


Fig. 8. *Statistical distribution of three groups and various individuals of North American* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of main northern group (letter O shows mean) and main southern group (letter N shows mean); dots,* ***baileyi****; open circles, individuals taken in the northwestern quarter of the conterminous United States since 1940; open triangles, individuals collected 1989-1991 in the Dakotas; solid triangle, individual from Alberta originally assigned to* ***irremotus****; open square, individual from Little Belt Mountains of Montana; solid square, individual taken in northwestern South Dakota in 1925; x's, individuals of* ***baileyi*** *collected recently in Arizona and Texas; crosshatch, individual from Gila National Forest originally assigned to* ***mogollonensis****. Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 1, large 7, large 9; second canonical variable, small 2, small 7, large 4.*

(1944), and Hall (1981). This allocation, together with others by Hoffmeister, suggests that the natural range of *baileyi* extends just to the north of the Gila River. This distribution, in turn, brings into question the status of a series of specimens taken on the Gila National Forest of New Mexico, which is bisected by the Gila River. These specimens were assigned to *mogollonensis* by Goldman. However, one seemed to me to be unusually small for that subspecies and was withheld for comparison at this point. Its position, most proximal to the statistical bounds of *baileyi*, is shown in Figure 8.

It is likely that individuals from the geographic range of *baileyi* regularly dispersed into the range of populations to the north and vice versa. After these more northerly populations were eliminated by people during the 20th century, the occurrence of wolves within their ranges would be attributable to *baileyi* dispersing from Mexico, where the subspecies evidently still survives (Ginsberg and MacDonald 1990). Such occurrence is indicated by the statistical positions (Fig. 8) of a male taken in 1957 near Concho, Apache County, Arizona, well within the original range of *mogollonensis*, and of two males collected in 1970 in Brewster County, Trans-Pecos Texas, which were reported by Scudday (1972).

Arctic Wolves

Four subspecies of *C. lupus* have been described from the arctic islands off North America, mostly on the basis of only a few specimens. A group of skulls, from the range assigned by Hall (1981) to the subspecies *arctos* and *bernardi*, is largely distinguishable from both the main northern and main southern groups of *C. lupus* (Fig. 9). Individual skulls from the range assigned by Hall (1981) to the subspecies *mackenzii*, on the mainland nearest to the western arctic islands, are statistically encompassed by the limits of the main northern group, though are shifted in the direction of the island wolves. In contrast, the position of a specimen of *C. l. manningi* from Baffin Island is well beyond the statistical range of the other island wolves and indicative of affinity with the main southern group.

Manning and MacPherson (1958) concluded that *bernardi* of Banks Island (based on material collected in 1914–1916) had been replaced by another population (material taken in 1953–1955) that they assigned to *arctos*, but that I (Nowak 1979) thought differed both from *bernardi* and *arctos*. In reassessing this situation, it seems unlikely that the more recent specimens from Banks Island, apparently having originated from within the range of *arctos* and having been collected over a brief period, could represent anything more than a subpopulation of *arctos*, albeit one showing rather extreme characters. I also question whether the original population of *bernardi* was more than another subpopulation of *arctos* showing only modest development of the characters of the subspecies. As Jolicoeur (1959) suggested, the severe environment of the arctic might influence ontogenetic cranial development of the skull; such effect could vary from time to time, thereby increasing the impression of differences between populations.

In any event, examination of *arctos*, including the newer Banks Island material, and a review of the measurements of

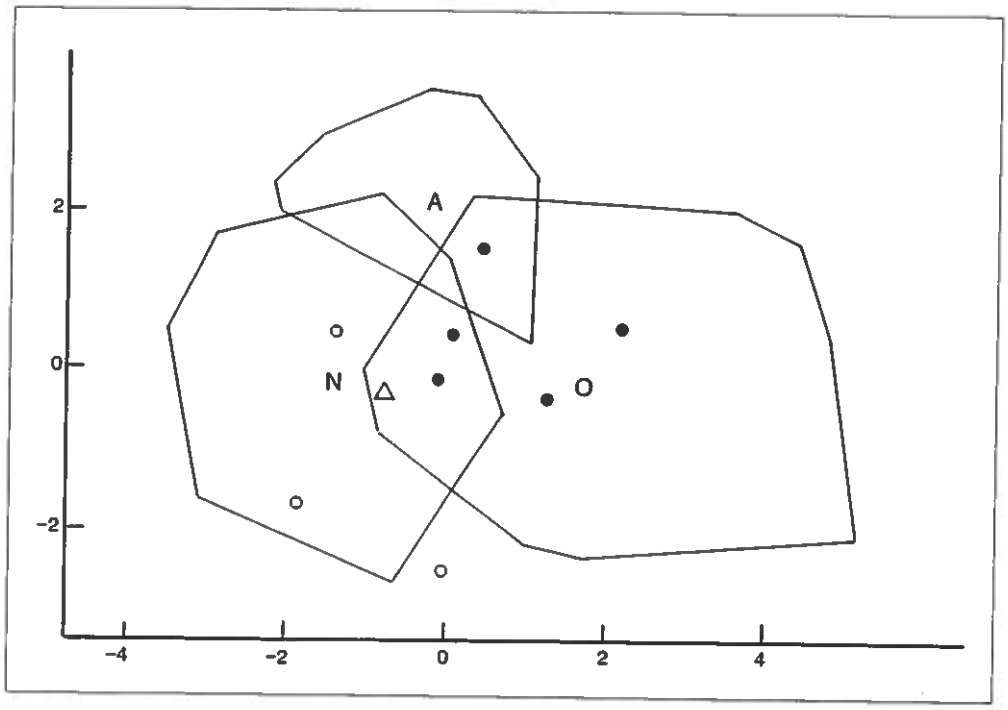


Fig. 9. *Statistical distribution of three groups and various individuals of North American* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of main northern group (letter O shows mean), main southern group (letter N shows mean), and* ***arctos*** *(letter A shows mean); dots, individuals of nominal subspecies* ***mackenzii****; open circles, individuals of* ***beothucus****; triangle, one individual* ***manningi****. Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 1, large 7, large 2; second canonical variable, small 1, large 9, large 7.*

the five known adults of original *bernardi*, as published by Goldman (1944), indicate that all of the involved populations share the most consistent distinguishing character of *arctos*, which is relatively large carnassial teeth. That condition, together with the results of canonical analysis of available material, suggest that the name *arctos* is appropriate for the subspecies occupying the region from Ellesmere to Banks and Victoria islands, and Greenland (Marquhard-Peterson this volume).

I have examined only two specimens of the Greenland wolf, *C. l. orion*, and both are probably females. I see no substantive basis for separating them from *arctos*. Goldman (1944), who saw only a single skull, also suggested affinity to *arctos*. Moreover, Dawes et al. (1986) pointed out that wolves moved freely across the ice between Ellesmere Island and Greenland, and recommended referring the animals in northern and eastern Greenland to *arctos*.

Wolves of Northeastern Canada

The nominal subspecies *C. l. hudsonicus*, which was assigned a large range to the west of Hudson Bay (Hall 1981), falls almost entirely within the range of variation of the southern group (Fig. 10). Goldman (1944) observed that the skull of *hudsonicus* is "decidedly smaller" than that of *occidentalis*, occurring just to the west, and Kolenosky and Standfield (1975) hinted at affinity between *hudsonicus*, *nubilus* (as delineated by Hall), and the western Ontario population of *lycaon*.

Skeel and Carbyn (1977) came to a different conclusion regarding *hudsonicus*. Although their preliminary multivariate analyses suggested that *hudsonicus* might be more closely related to populations of my southern group than to those of the northern group, cluster analysis and multidimensional scaling techniques showed male *hudsonicus* to fall close to males from Wood Buffalo National Park (Alberta and Mackenzie District of Northwest Territories), within the range of *occidentalis*. A separate cluster was formed by males from Jasper (Alberta) and Prince Albert (Saskatchewan) national parks, also within the range of my northern group. This incongruity may be explainable through consideration of an unusual sex ratio in Skeel and Carbyn's sample from Wood Buffalo National Park: 24 males and five females. Although experience indicates that males frequently do outnumber females in a given series of canid specimens, a near five to one ratio is totally unexpected and is unlike that in any of the other seven samples used by Skeel and Carbyn. They reported that of the 29 specimens from Wood Buffalo Park, 20 actually were unknown as to sex and that 18 of those were classified as males by statistical probability using a stepwise discriminant analysis. I suggest that something went amiss in this operation, that females were included in the male sample, and that had these females not been used the group of males from Wood Buffalo Park would have fallen statistically nearer to the other samples of *occidentalis* than to *hudsonicus*. My own sample of *hudsonicus* consists of eight specimens known to be males and six that I judged to be males, but the latter are limited to skulls that exceed the average of the known males in greatest length.

Kelsall (1968) expressed doubt that *hudsonicus* is distinguishable from *occidentalis*, just to the west, noting that wolves from the former's range annually invade the latter's

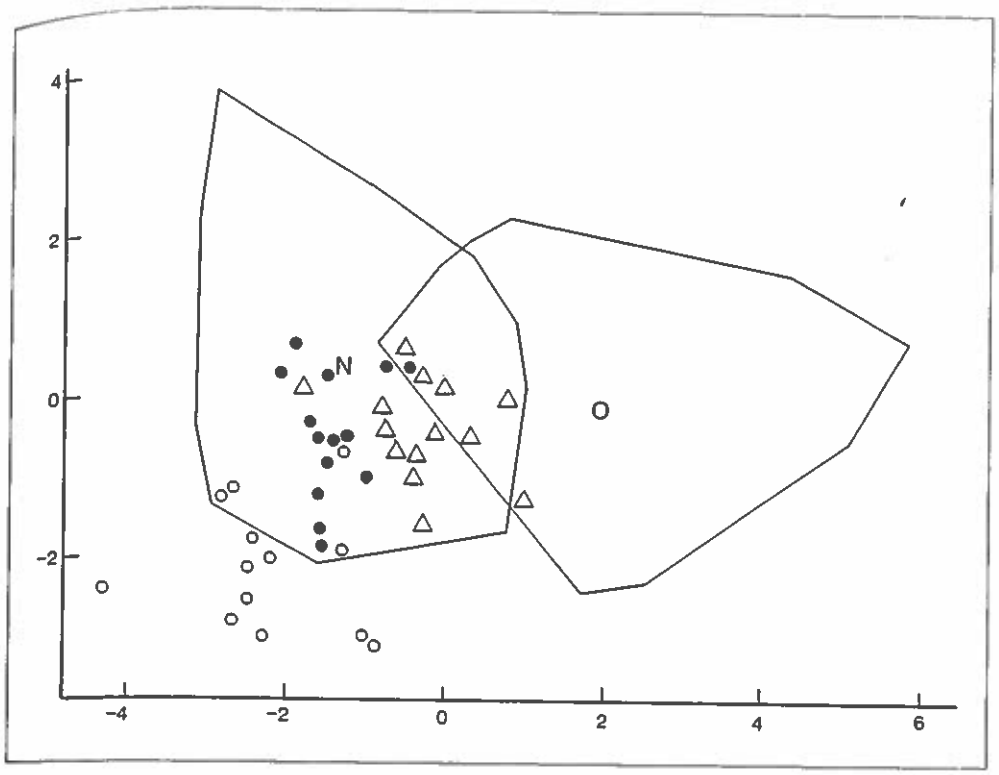


Fig. 10. *Statistical distribution of five groups of North American* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of main northern group (letter O shows mean) and main southern group (letter N shows mean); dots, western Ontario* ***lycaon****; open circles, Algonquin* ***lycaon****; triangles,* ***hudsonicus****. Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 1, large 7, large 2; second canonical variable, small 10, large 5, large 8.*

range, following caribou herds for hundreds of kilometres. However, he also stated that biologists, game officers, hunters, and trappers have long used gross morphological features to separate the wolves of the tundra, the main habitat of *hudsonicus*, from the wolves of the taiga, the main habitat of *occidentalis*. The presence of a component of the southern group of wolves in this far northern region could be associated with the failure of the main northern group of wolves to expand into a relatively unproductive habitat, in which it would have to depend almost entirely on the rather small barren-ground caribou.

Its assignment to the main southern systematic group of *C. lupus* makes *hudsonicus* a key to the classification of other northeastern populations. The statistical position of my one specimen of *manningi* (Fig. 9), being much closer to the southern group than to *arctos*, is now reasonable, because the range of *hudsonicus* extends to immediately south of Baffin Island (Fig. 1). Measurements listed by Goldman (1944) also show that *manningi* does not share the most definitive character of *arctos*, the relatively large carnassial teeth. Indeed, *manningi* originally was distinguished from *arctos* on the basis of its much smaller teeth and more slender proportions. Dawes et al. (1986) noted that wolves appearing on the west-central coast of Greenland probably originate on Baffin Island, and thus in a population here considered associated with my main southern group.

The vast range of the nominal subspecies *labradorius*, to the east of Hudson Bay, is represented only by a single specimen in my analyses. It is a large individual with closest statistical affinity to the northern group, though it also lies just within the limits of the southern group and of *ligoni* (Fig. 7). I have seen two skulls of immature *labradorius*, unknown as to sex, and one of an adult, probably female. That examination, together with review of the measurements of three adult males listed by Goldman (1944), indicates that *labradorius* falls closest to my main southern group. Goldman suggested affinity between *labradorius* and the Newfoundland island subspecies *beothucus*, and noted that both contrast markedly with populations of *lycaon* in southeastern Canada. My own analysis of three specimens (Fig. 9) indicates that *beothucus* has affinity with my main southern group and not with *arctos*, with which it was synonymized by Sokolov and Rossolimo (1985).

Lycaon

Although Goldman (1944) considered the range of the subspecies *C. lupus lycaon* to extend westward to Minnesota, he noted that specimens from the Great Lakes region grade toward *nubilus* of the Great Plains. More recently there has been a growing consensus that the western populations of *lycaon*, at least those of Minnesota, actually are more closely related to *nubilus* than to populations of *lycaon* in Quebec and southeastern Ontario (Mech and Frenzel 1971b, Kolenosky and Standfield 1975, Skeel and Carbyn 1977, Van Ballenberghe 1977, Schmitz and Kolenosky 1985a). Evidence presented above (Figs. 4 and 5, Table 2) indicates that post-1960 Minnesota *lycaon* have affinity to pre-1940 populations of the western conterminous United States and

should be combined with my main southern group of *C. lupus*. There is no suggestion that Minnesota *lycaon* has hybridized with *C. latrans* or any other species.

A series of *lycaon* from southwestern Ontario, the area north of the Minnesota border and Lake Superior, falls near the center of variation of my main southern group (Fig. 10). However, a series from southeastern Ontario is mostly beyond the range of the others. To minimize the chance of using specimens affected by hybridization between *C. lupus* and *C. latrans* (see below), I restricted my sample of southeast Ontario *lycaon* to Algonquin Provincial Park and its immediate vicinity, where there is a relatively dense and well-protected wolf population on an extensive tract of natural habitat.

My analyses support combining both Minnesota and west Ontario *lycaon* with my main southern group, but recognizing southeast Ontario *lycaon* as representative of another subspecies. The case for a remarkable division between two kinds of wolves in Ontario, a larger animal to the west and a smaller one to the southeast, was announced by Standfield (1970) and developed by Kolenosky and Standfield (1975). The latter authorities practically suggested specific separation, stating (p. 71): "the ranges of the two types overlap throughout a broad band across east-central Ontario, but there is no conclusive evidence of their interbreeding." Nonetheless, Kolenosky and Standfield's multivariate analyses of cranial measurements do show the two kinds to have about the same degree of statistical overlap that I found (Fig. 10). They also reported a third and still smaller kind of wolf, occurring in extreme southern Ontario, but suggested that it represented hybridization between *C. lupus* and *C. latrans*. My own previous work (Nowak 1979) reported the presence of such hybrids in southern Ontario and Quebec and suggested that they were contributing to the introgression of wolf genes into the coyote population now expanding through the northeastern United States.

Schmitz and Kolenosky (1985a) presented a modified interpretation of the status of *lycaon*. Based on multivariate analyses of both body and skull measurements, they concluded that the three previously identified kinds of wolves in Ontario are all clinal variants of *lycaon*, that the west Ontario population is more closely related to the southeast Ontario population than to the Minnesota population, and that the small animal of extreme southern Ontario is not a coyote-wolf hybrid, but a form of *lycaon* that arose within the last 75 years. They also recognized three morphologically distinct kinds of *C. latrans* in Ontario, noting that two of those kinds may have resulted from coyote-wolf hybridization.

In designating six distinctive kinds of wild *Canis* in Ontario (not including still others in Minnesota), Schmitz and Kolenosky may not have fully appreciated both the individual variability of the genus and the extent to which hybridization may have affected the situation. The graphical portrayals of their analyses plot only centroids and do not allow visualization of statistical approach and overlap of the different groups. Some of their results seem incongruous; for example, that wolves exhibit clinal variation, but are divisible into morphologically distinct groups, and that wolves have not been influenced by hybridization with coyotes, but that some coyote populations may be descended from coyote-wolf hybrids. Their Table 2 suggests that, for males at least, the skull of the small "wolf" of extreme southern Ontario is more like the skull of coyotes than like the skull of other wolves. Some of their cranial measurements (including five on just the mandibular and occipital condyles) may express traits that have become randomly and temporarily established in populations, rather than long-term adaptive characters. Their description of overall differences between the skulls of Minnesota and west Ontario wolves seems incorrect. The measurements for my own series of Minnesota *lycaon* and west Ontario *lycaon* are closer than those for any other two series that I examined (see Table 1).

In short, I do not accept the conclusions of Schmitz and Kolenosky (1985a), at least with respect to the relationships of west Ontario wolves and to the (nonhybrid) origin of populations in extreme southern Ontario. My analyses do strongly support the suggestions of Kolenosky and Standfield (1975) that west Ontario wolves are closely related to populations in Minnesota (and in the western conterminous United States) and that they are separated by a subspecific line from populations in southeastern Ontario.

Because the type locality of *lycaon* is Quebec City, that name would be retained, considering the above analysis, for the subspecies of wolf in southern Quebec and southeastern Ontario. Populations of western Ontario, Minnesota, and other parts of the western Great Lakes region would now be covered by the subspecific name appropriate for my entire southern group. On the basis of nomenclatural priority, that name would be *C. l. nubilus* Say, 1823. Likewise, the appropriate name for the entire northern group would be *C. l. occidentalis* Richardson, 1829. In the following discussions, however, it is sometimes more convenient to continue using the names recognized by Hall (1981).

The Red Wolf

For purposes of this study, it was decided to use only geographic/temporal samples of *C. rufus* that previous work (Nowak 1979) indicated were not affected by hybridization with *C. latrans*. One such series was taken in southern Missouri prior to 1930. Available material from that area and time shows that the red wolf and coyote were sympatric, but completely distinguishable from one another; no intermediate specimens are known. Another series comprises specimens that lived in modern time, but prior to 1940 in Florida, Alabama, Mississippi, Louisiana, and the Big Thicket area of extreme southeastern Texas. These specimens are the only usable male wild *Canis* from that region and time; no *C. latrans*, hybrids, or *C. lupus* were present. Fortuitously, these two samples are the two substantive series of *C. rufus* that are most geographically removed from one another, and

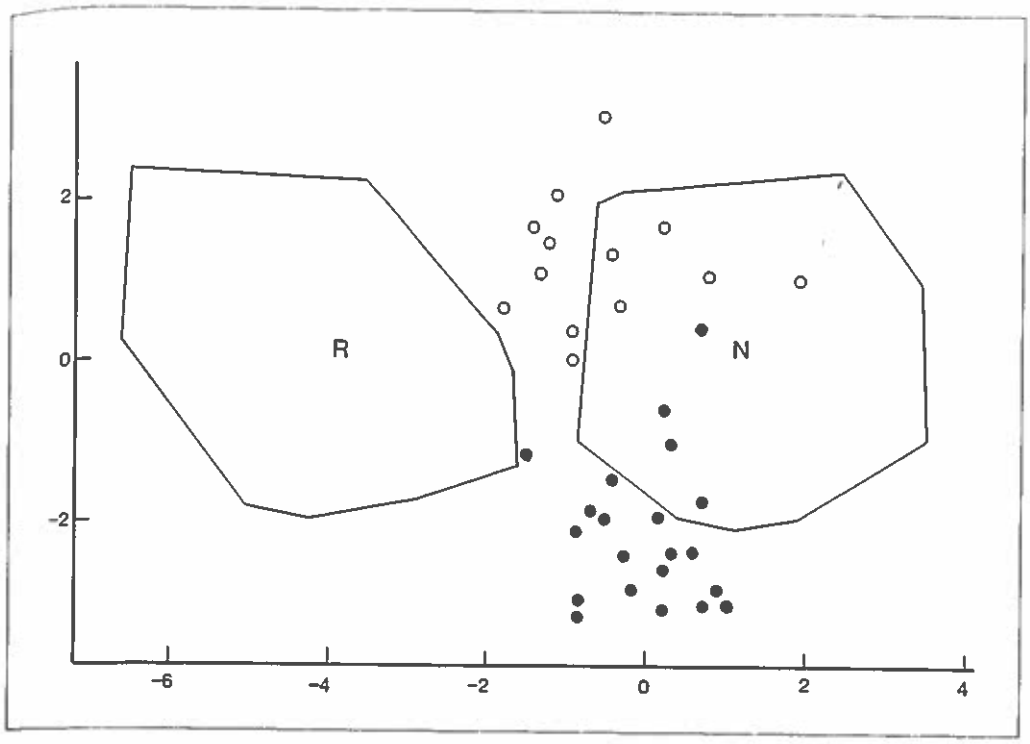


Fig. 11. *Statistical distribution of four groups of North American wolves, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of main southern group of* **Canis lupus** *(letter N shows mean) and of* **Canis rufus** *(letter R shows mean); dots,* **Canis lupus baileyi***; open circles, Algonquin* **Canis lupus lycaon***. Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 4, large 7, large 2; second canonical variable, large 1, small 2, large 10.*

so are most advantageous for assessing geographic variation. Moreover, they also represent the populations of *C. rufus* that are nearest to the most proximal populations of *C. lupus* that are represented by substantive series of specimens; as mapped by Hall (1981), those are *nubilus* and Minnesota *lycaon* in the case of Missouri *C. rufus*, and Texas *monstrabilis* in the case of the southern *C. rufus*. The two red wolf samples are thus advantageously placed with regard to assessing whether the statistical difference between *C. lupus* and *C. rufus* is greater than that separating populations within each species.

Figure 11 shows a canonical analysis comparing the combined series of *C. rufus* with the main southern group of North American *C. lupus*, and with the series of the two smallest kinds of North American gray wolf, *baileyi* and Algonquin *lycaon*. *C. rufus* does not statistically overlap any of the series of *C. lupus*, though its bounds are approached closely by a single specimen each of *lycaon* and *baileyi*. This analysis is primarily a comparison of the red wolf with the gray. Therefore, *lycaon* and *baileyi* are more extensively overlapped by other *C. lupus* than is the case in analyses comparing only groups of *C. lupus*. *Lycaon* and *baileyi* are shown to be fully distinguishable from one another, but *C. rufus* is the only North American wolf that falls completely outside the statistical range of the main northern and southern groups of *C. lupus* (the separation from the northern group is assumed based on the statistical location of *rufus* relative to the southern group).

Figure 12, based on a canonical analysis, shows the statistical distances between the two separate samples of *C. rufus*, between those samples and the nearest neighboring nominal subspecies of *C. lupus*, and between the latter subspecies and their nearest neighboring subspecies of *C. lupus*. The statistical distances between the two red wolf samples and between the various gray wolf samples are relatively small, while the distances separating the red wolf samples from the gray wolf samples are relatively great. This distinction and indeed lack of any clinal approach, in the region where the southeastern range of *C. lupus* met the western edge of the range of *C. rufus*, is perhaps the best argument for maintaining each as a full species. Although there are no specimens to show that the gray wolf actually was sympatric with unmodified populations of the red wolf, extensive material from central Texas demonstrates that *C. lupus* occurred in the immediate vicinity of a large population of *C. rufus* x *C. latrans* and was not involved in the hybridization process (Nowak 1979, Nowak et al. this volume).

In contrast to the above, populations of *C. lupus* in southeastern Canada apparently do show a morphological approach toward *C. rufus*. Unfortunately, available specimens from the eastern United States are too scarce and too fragmentary to allow determination of whether the red and gray wolves intergraded in that region (Nowak 1979). Also, while some specimens of *C. lupus lycaon* of southeastern Ontario fall very near the statistical limits of *C. rufus* (Fig. 11), there is the possibility that those specimens have been affected by hybridization involving *C. latrans* (see above). It is tempting to speculate that Kolenosky and Standfield's (1975) finding of a trenchant division between a large wolf

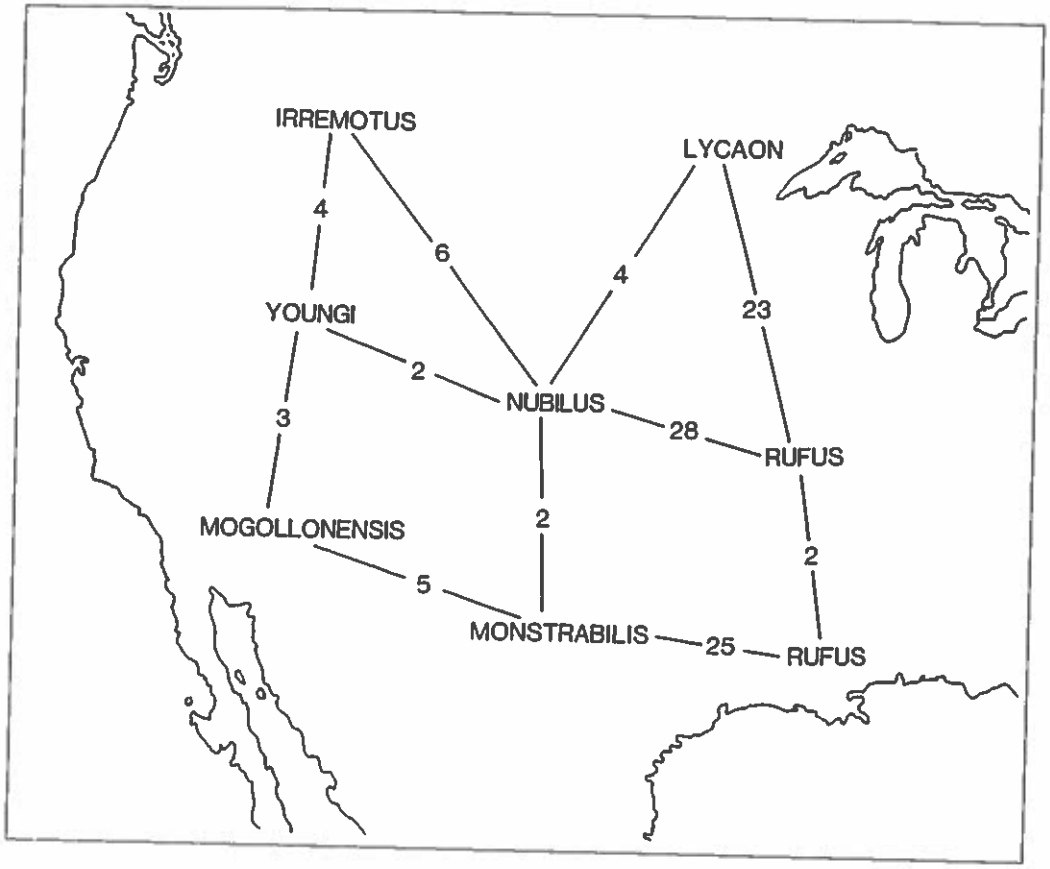


Fig. 12. *Statistical distances (rounded to whole numbers) between* ***Canis rufus*** *and neighboring subspecies of* ***Canis lupus****.*

and a small wolf in southeastern Ontario was actually the discovery of the long-sought line where the gray wolf met the red. For the moment, however, the question remains open.

Eurasian Wolves

Figure 13 shows a canonical analysis comparing series corresponding to five of the subspecies of *C. lupus* that Sokolov and Rossolimo (1985) recognized as occurring in China and the former Soviet Union. My samples are distributed as follows: *albus*, northwestern Siberia; *campestris*, southeastern European Russia and southern Siberia; *chanco*, China, the Himalayas, and extreme southeastern Siberia; *desertorum*, Kazakhstan; and *lupus* (as explained below, the involved population is reassigned to the subspecies *communis*), the Perm region in the central Urals. There is considerable overlap between the samples of *campestris*, *chanco*, and *desertorum*, but *albus* and, especially, *lupus* are more distinct. This division is reinforced when the samples of *campestris*, *chanco*, and *desertorum* are combined into a single series that is compared with the others (Fig. 14).

Few specimens and no substantial series from Europe west of Russia were available for this study. However, as shown in Figure 14, two individuals from Sweden fall well within the overall statistical limits of *campestris*, *chanco*, and *desertorum*. Sweden is the type locality of the subspecies *C. lupus lupus* Linnaeus, 1758. It therefore may be that *campestris*, *chanco*, and *desertorum* are synonyms of *C. lupus lupus* and that the combined entity has a vast range extending from at least northwestern Europe to China. It then would also become necessary to apply a different name to the distinctive population of north-central Russia, which Sokolov and Rossolimo (1985) had considered part of *lupus*. According to those authorities the chronologically next available name for a Russian wolf is *C. lupus communis* Dwigubski, 1804.

Further analyses (Figs. 15 and 16) suggest that subspecies of *C. lupus* in northern Eurasia are comparable to those of North America. *C. lupus lupus*, a widely distributed wolf of moderate size, is statistically closer to the main southern group of North American *C. lupus* than to its nearest geographical neighbors. Likewise, *communis*, a large subspecies, has more affinity to the main northern group of North American *C. lupus* than to other Eurasian wolves, and *albus* shows affinity to North American arctic wolves.

The parallel situation on the two continents may extend even further. Figure 17 shows full statistical separation between *C. lupus lupus* (now comprising the combined sample of *campestris*, *chanco*, and *desertorum*) and a series of the nominal subspecies *pallipes* from Israel, including the Golan Heights, and India. This remarkable distinction of *pallipes* is comparable to the position of *rufus* of southeastern North America; both have relatively small and narrowly

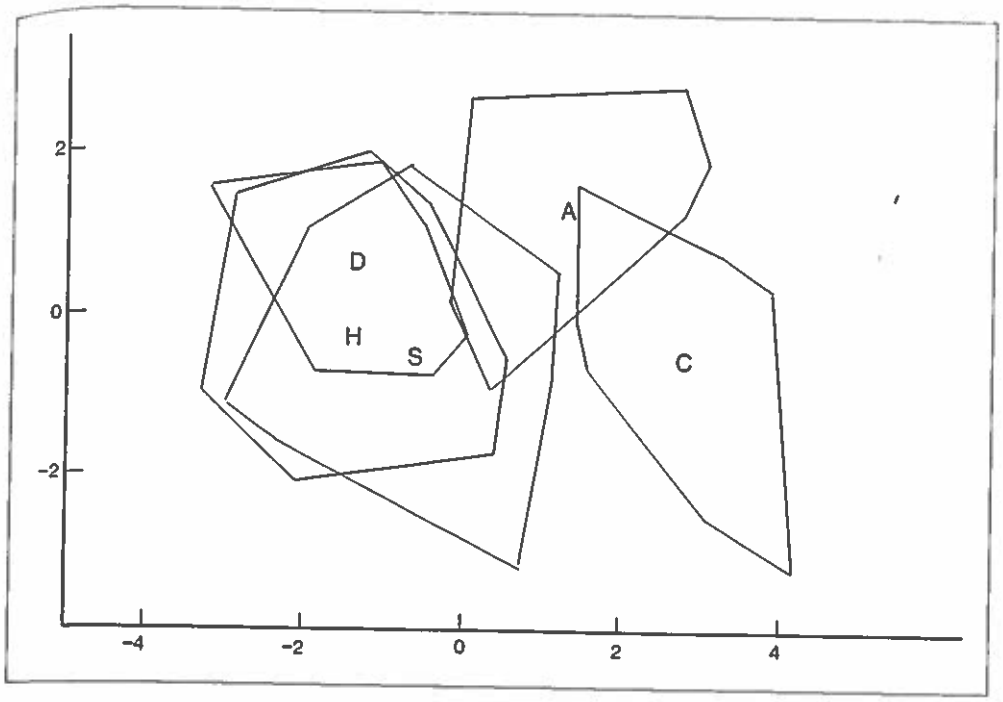


Fig. 13. *Statistical distribution of five nominal subspecies of Old World* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of* ***albus*** *(letter A shows mean),* ***campestris*** *(letter S shows mean),* ***chanco*** *(letter H shows mean),* ***communis*** *(letter C shows mean), and* ***desertorum*** *(letter D shows mean). Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 2, large 4, large 1; second canonical variable, small 8, large 3, large 2.*

proportioned skulls. An analysis (Fig. 18) of all three of the small southern wolves — *rufus, pallipes, baileyi* — demonstrates near total statistical separation, but very slight overlap between *rufus* and *pallipes*. That a small wolf, statistically comparable to *C. rufus*, exists far beyond the range where it could be influenced by hybridization with *C. latrans*, is further evidence against Wayne and Jenks' (1991) suggestion that the red wolf originated as a gray wolf-coyote hybrid.

Late in this study, I received measurements of a series of the sixth subspecies of *C. lupus* that Sokolov and Rossolimo (1985) recognized in the former Soviet Union, *C. l. cubanensis* of the Caucasus. Unfortunately, measurement number 8, depth of jugal, seems to have been taken incorrectly. Also received were data on a small series of wolves from eastern Uzbekistan. Because both of these series are geographically intermediate to *C. l. lupus* and *pallipes*, there was need to determine whether they might

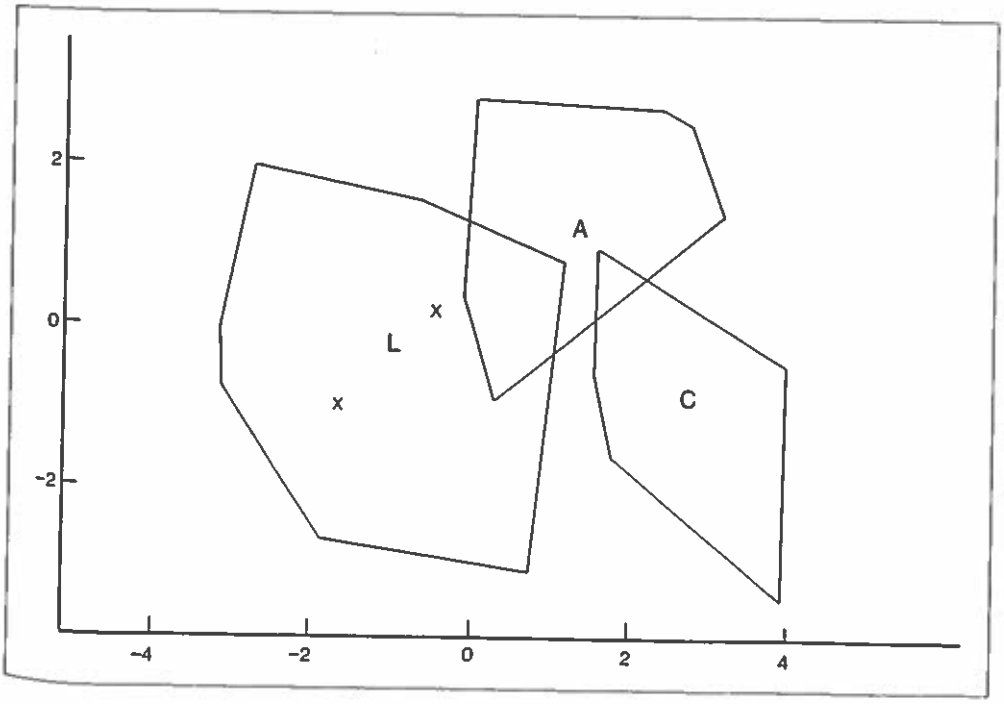


Fig. 14. *Statistical distribution of three subspecies and two individuals of Old World* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of* ***albus*** *(letter A shows mean),* ***lupus*** *(incorporating* ***campestris****,* ***chanco****, and* ***desertorum****; letter L shows mean), and* ***communis*** *(letter C shows mean); x's, two individuals of C.* ***lupus lupus*** *from Sweden. Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 2, large 4, large 1; second canonical variable, small 8, large 2, small 1.*

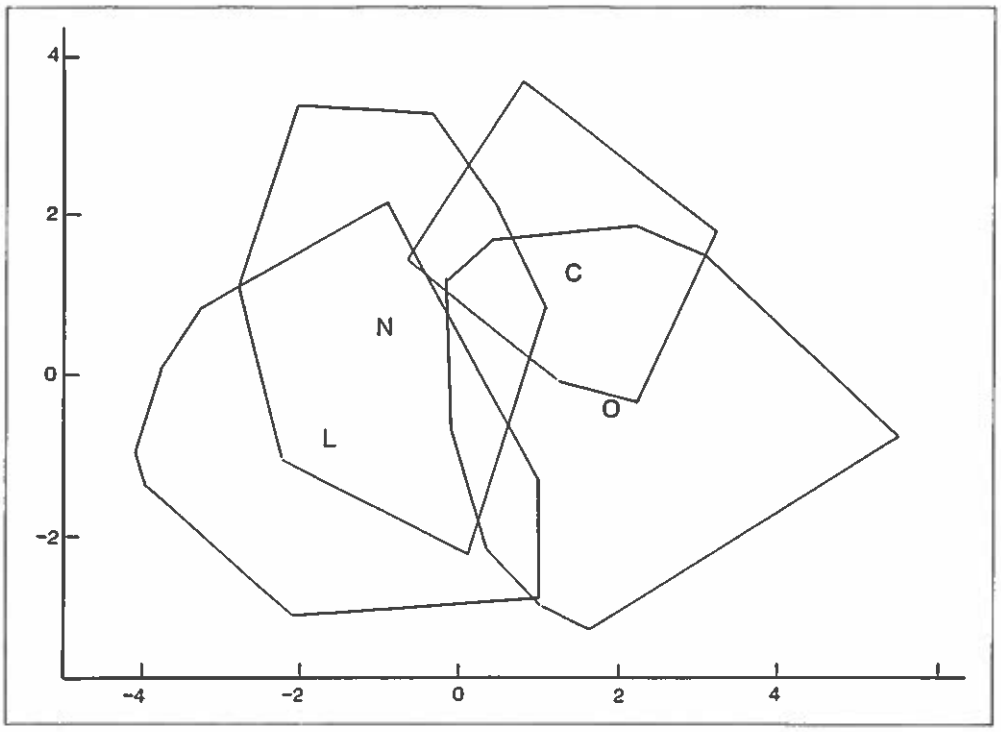


Fig. 15. *Statistical distribution of four groups of* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of the Eurasian subspecies* **communis** *(letter C shows mean), the Eurasian subspecies* **lupus** *(letter L shows mean), the North American main northern group (letter O shows mean), and the North American main southern group (letter N shows mean). Characters (Fig. 3) contributing most to high positive values are: first canonical variable, large 1, large 2, large 9; second canonical variable, large 4, small 7, small 10.*

represent intergrading populations, and thus a new canonical analysis (Fig. 19) was done comparing *lupus*, *pallipes*, *cubanensis*, and the Uzbek individuals, but using only nine measurements. The Uzbek specimens fall predominantly within the statistical bounds of *lupus*, though there is a close approach to *pallipes*. *Cubanensis* apparently is a valid subspecies in its own right, overlapping only slightly with *lupus* and very slightly with *pallipes*. This latter statistical connection, however, suggests that *pallipes* also be regarded as a subspecies of gray wolf. It evidently has affinity to the red wolf as well, but the geographic and temporal separation of *pallipes* and *rufus* is so great (see below), and the

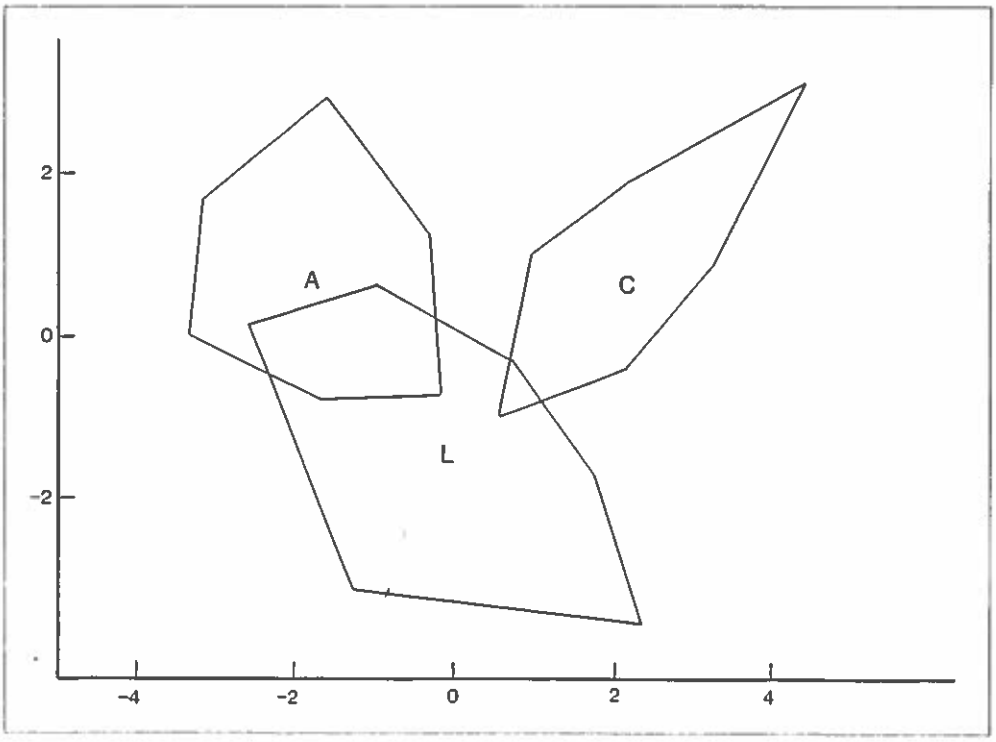


Fig. 16. *Statistical distribution of three subspecies of* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of North American* **arctos** *(letter A shows mean), Eurasian* **albus** *(letter L shows mean), and Eurasian* **communis** *(letter C shows mean). Characters (see Fig. 3) contributing most to high positive values are: first canonical variable, large 1, small 7, large 8; second canonical variable, small 10, small 2, large 8.*

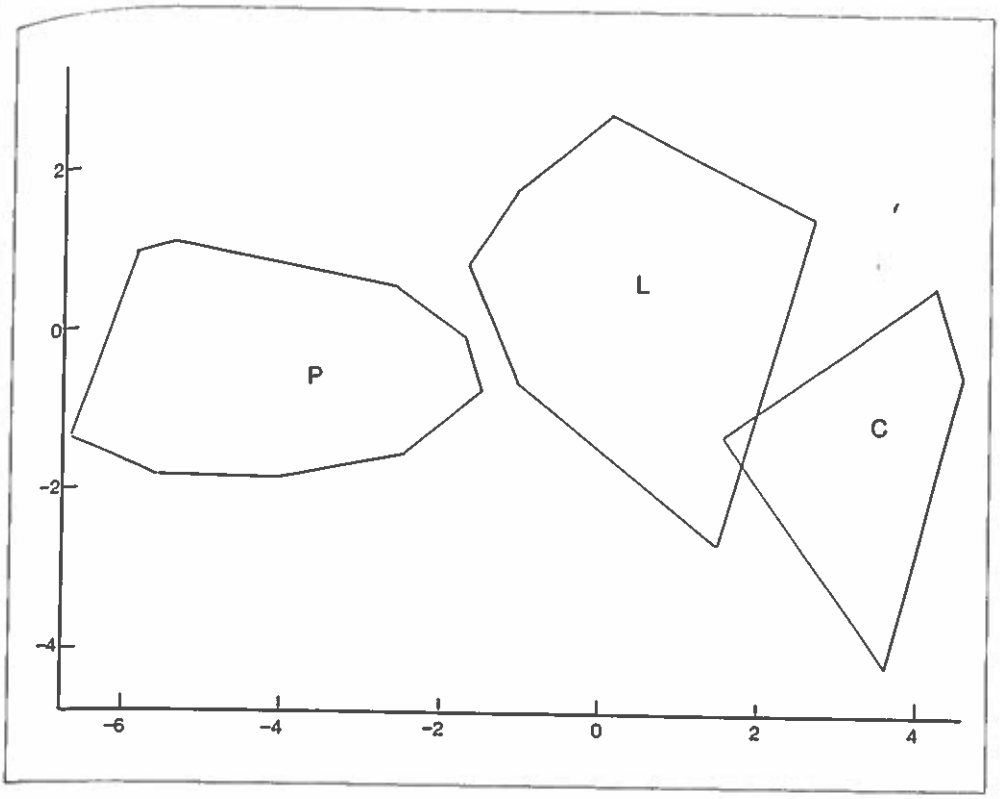


Fig. 17. *Statistical distribution of three subspecies of Old World* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of* ***communis*** *(letter C shows mean),* ***lupus*** *(letter L shows mean), and* ***pallipes*** *(letter P shows mean). Characters (see Fig. 3) contributing most to high positive values are: first canonical variable, large 1, large 4, large 8; second canonical variable, large 10, large 3, small 6.*

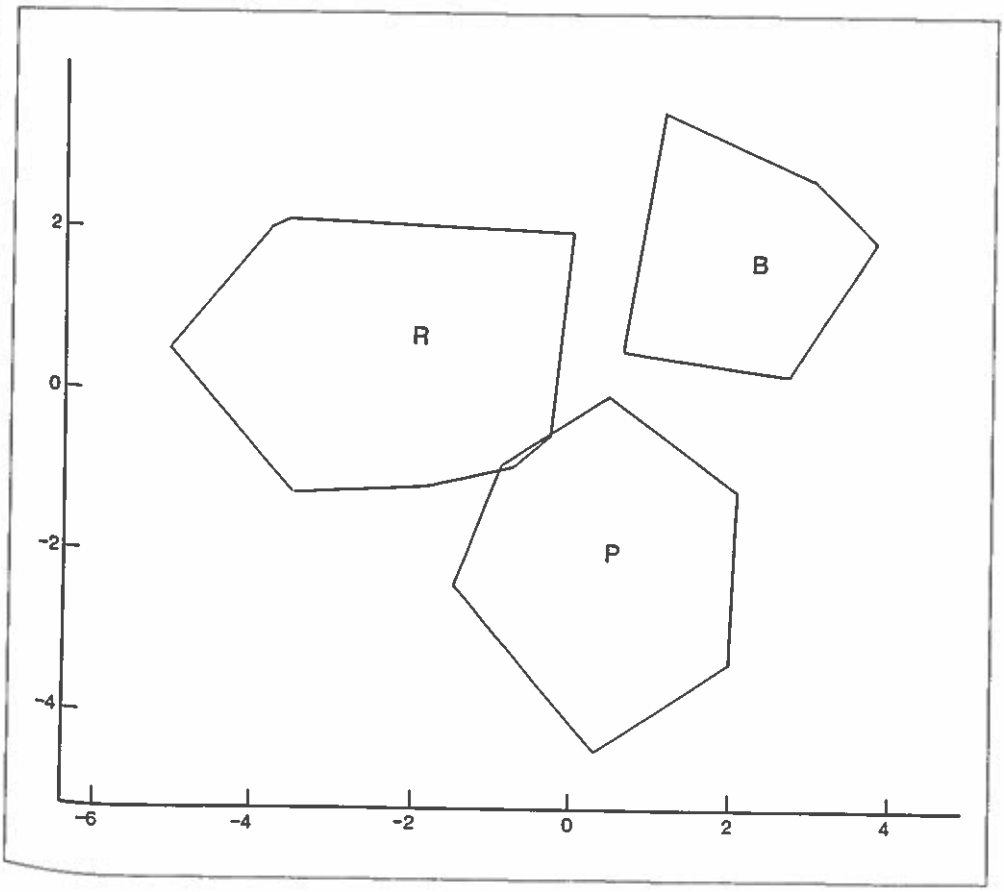


Fig. 18. *Statistical distribution of three groups of wolves, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of North American* ***Canis rufus*** *(letter R shows mean), North American* ***Canis lupus baileyi*** *(letter B shows mean), and Eurasian* ***pallipes*** *(letter P shows mean). Characters (Fig. 3) contributing most to high positive values are: first canonical variable, small 1, large 4, large 7; second canonical variable, large 1, large 2, large 8.*

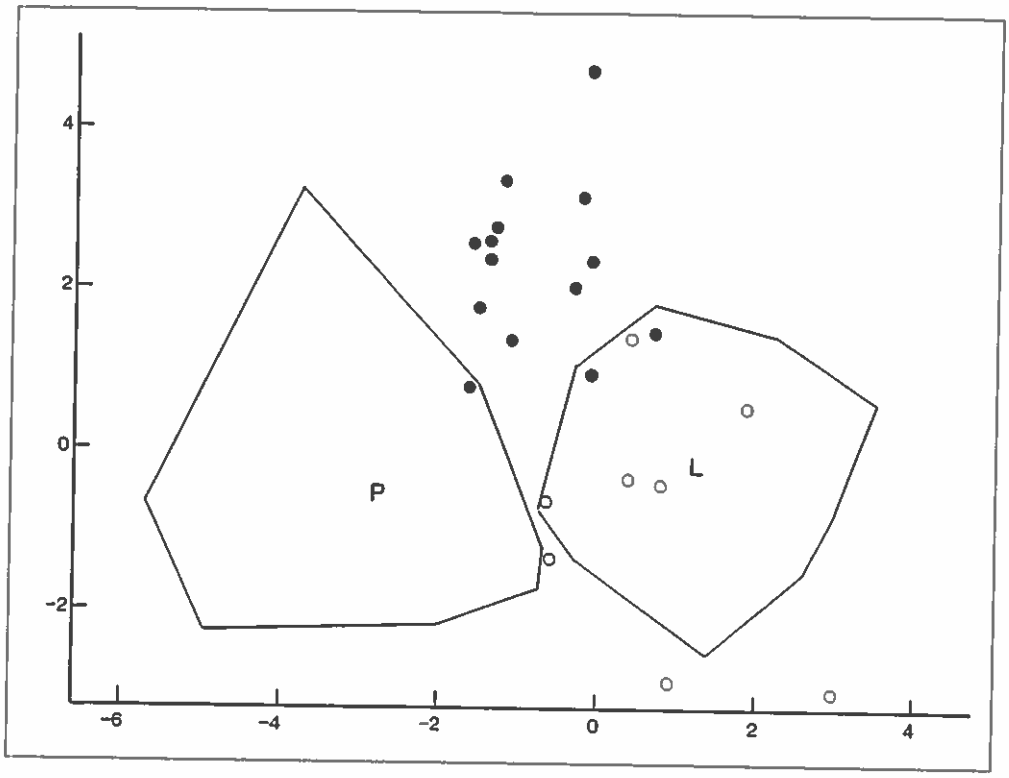


Fig. 19. *Statistical distribution of three subspecies and certain individuals of Old World* ***Canis lupus****, based on the first (horizontal axis) and second (vertical axis) canonical variables. Solid lines, limits of* ***lupus*** *(letter L shows mean) and* ***pallipes*** *(letter P shows mean); dots,* ***cubanensis****; open circles, individuals from eastern Uzbekistan. Characters (see Fig. 3) contributing most to high positive values are: first canonical variable, large 1, large 4, small 7; second canonical variable, large 2, small 1, small 9.*

morphological overlap so slight, that *rufus* is here considered to represent a full species.

Sokolov and Rossolimo (1985) recognized two other Eurasian subspecies, *hattai* (= *rex*) on Hokkaido and *hodophilax* on the other Japanese islands. Both are long extinct and are known by only a few specimens. I have measurements on one of each. Those of *hodophilax* are far below those of my other series and of little use for comparison. Those of *hattai* indicate a large animal comparable to my main northern group of North American *C. lupus*.

Sokolov and Rossolimo placed *arabs* of the Arabian Peninsula in the synonymy of *pallipes*, though Harrison (1968) and Mendelssohn (1982) had regarded *arabs* as distinct. The geographic boundary of *pallipes* and *arabs* is not well defined. Mendelssohn thought that *arabs* occurred in extreme southeastern Israel and that the rest of the country was occupied by several distinctive populations of *pallipes*. I could see no meaningful place to draw morphological lines between Israeli wolves and included all in my sample of *pallipes*. I had measurements on only two other possible specimens of *arabs* and on only a few of *lupaster* from Egypt, which Ferguson (1981) had considered a small *C. lupus* rather than a large *C. aureus* (golden jackal), as it is usually classified. These measurements are below the size limits of those of all my other series and were not subjected to comparative analysis.

Systematic Implications

Questions about species definition seem to be increasing, though complete lack of morphological intergradation, where two populations approach without physical barriers, argues for specific distinction. There is less consensus on what constitutes a subspecies. Certain characters may become established in a local, partly isolated population, and some authorities may, perhaps properly, use such characters as the basis of subspecific recognition. My investigation largely disregarded such questions and concentrated on general trends in measurable size and proportion that could be evaluated on a continent-wide or worldwide basis. Substantive statistical breaks in such trends, as discussed above, were taken as evidence of taxonomic division. A combination of my statistical analyses and other investigations (Jolicoeur 1959, Kolenosky and Standfield 1975, Skeel and Carbyn 1977, Nowak 1979, 1983, Ferguson 1981, Pedersen 1982, Friis 1985, Dawes et al. 1986, Hoffmeister 1986, Nowak et al. this volume), the nomenclatural matters discussed above, and the literature cited suggests recognition of the following species and subspecies of modern wolves, with original geographic distributions as shown (names in parentheses are additional subspecies recognized by Hall (1981) and Sokolov and Rossolimo (1985) and that would be regarded as synonyms under this classification; question marks (?) indicate subspecies that I did not subject to statistical analysis):

Canis rufus Audubon and Bachman, 1851, southeastern Kansas and central Texas to Pennsylvania and Florida (now

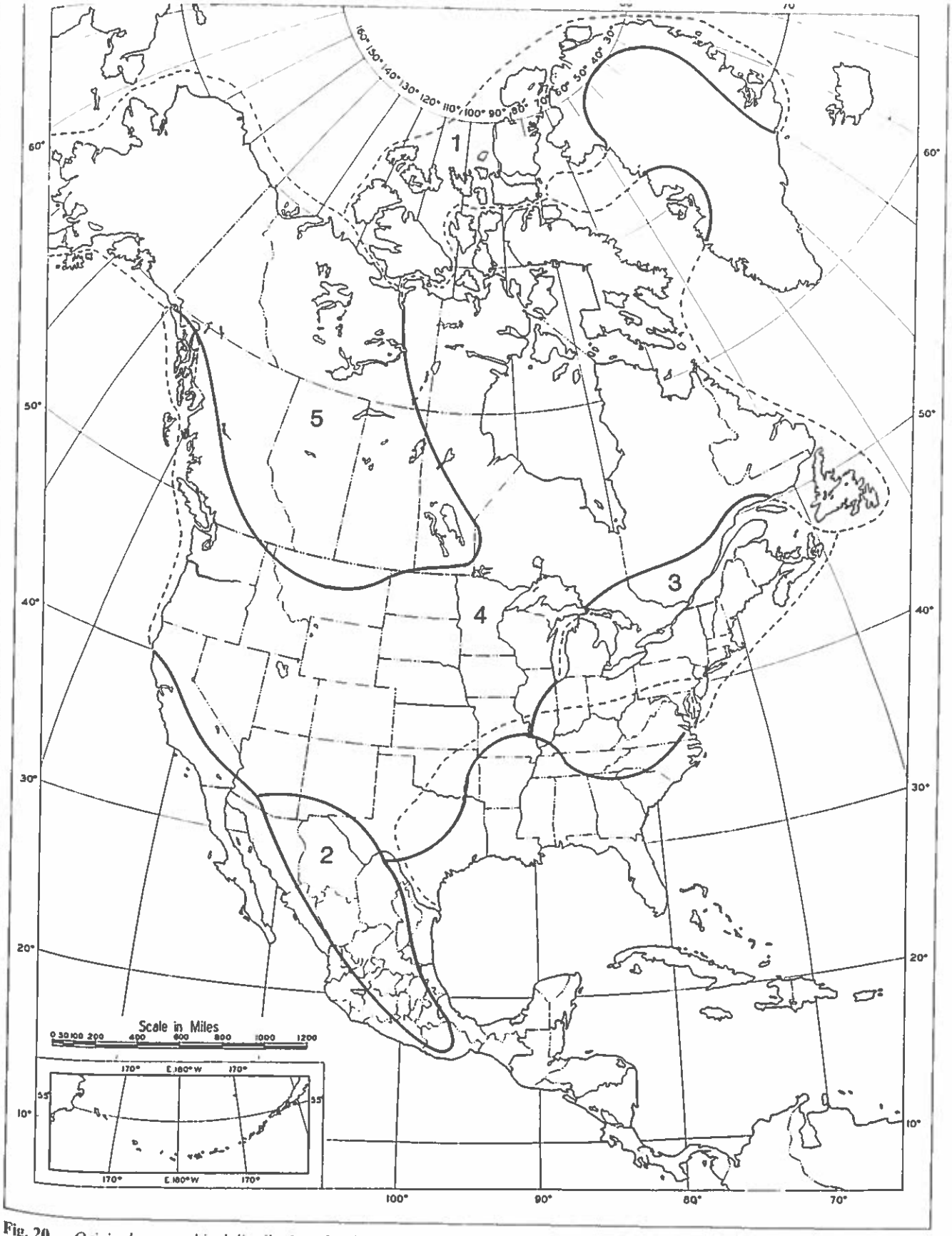


Fig. 20. *Original geographical distribution of wolves in North America, showing the five subspecies of* ***Canis lupus*** *recognized by this study: 1)* ***arctos****, 2)* ***baileyi****, 3)* ***lycaon****, 4)* ***nubilus****, 5)* ***occidentalis****. The red wolf (****Canis rufus****) occupied the southeastern quarter of the continent, the approximate northern and western limits of its range being marked by the dashed line on the mainland.*

evidently extirpated from the wild except for a reintroduced population in eastern North Carolina and a few individuals released at other sites);

Canis lupus pallipes Sykes, 1831, Israel to India;

(?) *Canis lupus arabs* Pocock, 1934, Arabian Peninsula;

(?) *Canis lupus lupaster* Hemprich and Ehrenberg, 1832, Egypt, Libya;

(?) *Canis lupus hodophilax* Temminck, 1839, Japan except Hokkaido (extinct);

Canis lupus lycaon Schreber, 1775, southeastern Ontario, southern Quebec, formerly south to an undetermined point in the eastern United States;

Canis lupus baileyi Nelson and Goldman, 1929, southern Arizona, southwestern New Mexico, extreme southwestern Texas, highlands of Mexico south to Oaxaca (now extirpated from the wild except for a few possible survivors in northwestern Mexico);

Canis lupus cubanensis Ognev, 1923, Caucasus and adjacent parts of Turkey and Iran;

Canis lupus lupus Linnaeus, 1758 (*campestris, chanco, desertorum*), Europe east to an undetermined point in Russia, central Asia, southern Siberia, China, Mongolia, Korea, Himalayan region (now greatly reduced in distribution, especially in western Europe);

Canis lupus nubilus Say, 1823 (*beothucus, crassodon, fuscus, hudsonicus, irremotus, labradorius, ligoni, manningi, mogollonensis, monstrabilis, youngi*), southeastern Alaska, southern British Columbia, conterminous United States from Pacific to western Great Lakes region and Texas, Ontario except southeast, northern and central Quebec, Newfoundland, northern Manitoba, Keewatin, eastern Mackenzie, Baffin Island, occasionally west-central Greenland (now evidently extirpated in the western conterminous United States);

Canis lupus arctos Pocock, 1935 (*bernardi, orion*), northern and eastern Greenland, Queen Elizabeth Islands (Ellesmere, Prince Patrick, Devon, etc.), Banks and Victoria Islands;

Canis lupus albus Kerr, 1798, extreme northern Eurasia;

Canis lupus communis Dwigubski, 1804, known with certainty only from the Ural Mountain region of north-central Russia, but probably occurring over much of eastern Europe and Siberia;

(?) *Canis lupus hattai* Kishida, 1931 (= *C. l. rex* Pocock, 1935), Sakhalin, Hokkaido (extinct);

Canis lupus occidentalis Richardson, 1829 (*alces, columbianus, griseoalbus, mackenzii, pambasileus, tundrarum*), Alaska, Yukon, Mackenzie, British Columbia, Alberta, Saskatchewan, southern Manitoba, northern Montana (now evidently expanding range into northwestern conterminous United States).

The revised historical distribution of *C. lupus* in North America is shown in Figure 20; that in Eurasia was indicated in Figure 2. The above list attempts to follow systematic order to the extent allowed by linear arrangement. Taxa considered more primitive are placed first and those considered closely related are grouped together. In this regard, the list reflects my view that the resemblance of certain North American to certain Eurasian taxa is based less on convergence than on actual phylogenetic affinity.

Fossil evidence (Nowak 1979, Kurtén and Anderson 1980) indicates that the wolf group separated from the coyote line in the early Pleistocene (perhaps about one million years ago). By the Irvingtonian, primitive small wolves, perhaps identical with modern *C. rufus*, were widespread in southern North America. A branch of this group probably entered the Old World, where it gave rise to *C. lupus*. This background, together with the above statistical analyses, suggest that *pallipes* represents a segment of the original American invading stock that underwent only modest development of the characters of *C. lupus*. Like *C. rufus* in the New World, its retention of primitive features may be associated with its relatively warm environment. Other remnants of a primitive stock of small, warmth-adapted wolves might be represented by *arabs, lupaster*, and *hodophilax*, and possibly *deitanus* of Spain (see Nowak 1979: 95), though the association of all of these taxa with *C. aureus* (golden jackal) requires investigation.

Farther north in Eurasia, *C. lupus* became larger, and apparently by the end of the Illinoian glaciation (300,000 years ago) it moved into North America (Nowak 1979). This stage in the evolution of the species is expressed today in the widespread groups of moderate-sized and generalized wolves that I have referred to *C. lupus lupus* in Eurasia and *C. lupus nubilus* in North America. Glacial movements and other environmental changes in the late Pleistocene may have resulted in splitting off of segments that gave rise to other subspecies, as suggested in previous work (Nowak 1983). *Baileyi* seems to have been isolated by desert barriers; a small gray wolf skull from San Josecito Cave, Nuevo Leon, indicates that the Mexican wolf was established by the Wisconsinan glaciation. Certain remains from Rancho La Brea (southern California) and Yukon (Nowak 1979), together with the current distribution of *arctos* and *albus*, suggest former widespread occurrence for a group of wolves represented by some of today's arctic populations.

The development of the largest gray wolves, *occidentalis* in the New World, and *communis* in the Old, may have occurred in the late Pleistocene, perhaps in connection with the disappearance of the dire wolf, lion, and several other large cursorial carnivores. During the Wisconsinan glaciation, the forebears of *occidentalis* may have been isolated in eastern Beringia, an ice-free refugium including most of Alaska. The modern distribution of *occidentalis* suggests a recent outward expansion from the northwest, perhaps involving the takeover of the range of other kinds of wolves. Remarkably, this process appears to be continuing to this day.

Conservation Implications

Reducing subspecific names to synonyms carries the danger that the affected populations will be given less attention for conservation purposes. In the case of most of the subspecies so reduced in this study, the question is largely academic, because they apparently are already extinct (*alces, beothucus, bernardi, crassodon, fuscus, irremotus, mogollonensis, monstrabilis, orion, youngi*). Of the others so reduced, none are thought to be in imminent danger of extinction (Ginsberg and Macdonald 1990), though the entire species *C. lupus* is appropriately classified as vulnerable by the World Conservation Union (IUCN). Moreover, the United States Endangered Species Act requires classification and protection, not only of endangered and threatened biological species and subspecies, but also of distinct vertebrate population segments. This provision has been interpreted broadly over the years, having been applied to morphologically or genetically distinct groups, to island populations, and frequently, to segments separated from others simply by a geopolitical line.

The conservation significance of some gray wolf subspecies is enhanced by their continued recognition as distinctive taxa, even after the above statistical analyses. *C. lupus baileyi* is represented by fewer than 10 individuals in the wild and by a small captive population (Ginsberg and Macdonald 1990). *C. l. arctos*, though widespread, occurs at low densities in a harsh, but fragile, environment (Miller this volume). *C. l. lycaon* is now known to be restricted to a small range, where it is in close proximity to human activity and is subject to genetic swamping through hybridization with *C. latrans*. *C. l. pallipes* and *C. l. arabs* have been greatly reduced in numbers and probably no longer occur in a natural ecological or behavioral context. *C. l. communis*, a newly distinguished taxon, is little known with regard to status and distribution, but could be vulnerable to consequences of political and economic upheaval.

Reintroduction of wolves to Yellowstone National Park and other areas is now under consideration, and there are questions as to the source of the animals for such projects. The above analyses indicate that the extirpated wolf population of the Yellowstone region is closely related to the living population of Minnesota, both regarded here as part of the subspecies *C. l. nubilus*. However, the subspecies *C. l. occidentalis* may have occurred originally as far south as central Montana, a short distance from Yellowstone, and may have been expanding its range southward even before human intervention. There is no reason to think that *occidentalis*, which has now reoccupied northwestern Montana, would be an inappropriate component of the Yellowstone ecosystem.

The red wolf has already been reintroduced successfully to coastal North Carolina. However, recent questions about its systematic status have led to widespread criticism of efforts being made for its conservation. My study supports recognition of the red wolf as a valid taxon and has provided further evidence against the idea that it originated as a hybrid of *C. lupus* and *C. latrans*. If the latter view were correct, we would expect the red wolf to blend morphologically into its parental species, and the striking statistical break that actually separates *C. rufus* from adjacent populations of *C. lupus* would not be possible. That a wolf population may approach *C. rufus* morphologically, without hybridization with *C. latrans*, is now demonstrated by the statistical position of the Old World *pallipes*. However, except for the slight overlap between samples of *pallipes* and *rufus*, the red wolf is statistically separate from all series of *C. lupus*, including neighboring populations. Whether *C. rufus* is considered a full species or a subspecies, it is the most distinctive kind of wolf in the world.

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