VARIATION IN SKULL MORPHOLOGY OF BROWN BEARS (*URSUS ARCTOS*) FROM CAUCASUS

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There has been debate over the taxonomic status of brown bears (*Ursus arctos*) from Caucasus, for almost 150 years. At the end of the last century, different forms of Caucasian bears living in the same area were described. Subsequently, researchers recognized from one to four subspecies of brown bears from Caucasus. We collected measurements on skulls of bears, conducted electrophoretic analysis of variation in blood proteins, and conducted 7 years of field surveys in Caucasus. Multivariate analysis of cranial variables revealed the existence of three groups, or ecomorphs, apparent in both male and female Caucasian bears, which supported previous work that showed diversity in this group. The existence of these groups was not due to age, geographic variation, or temporal changes in populations. Different distributions between morphs was documented in both crania and field observations. The most likely explanation of these differences was a Mendelian inheritance of the whole complex of differences. Differences in territorial behavior during the mating season among males of various ecomorphs suggest selective breeding. Despite the discovery of three polymorphic proteins, no firm conclusions could be made because the diversity in these proteins did not relate to results from the cranial analysis.

Key words: *Ursus arctos,* brown bear, genetic diversity, Caucasus

The history of brown bears (*Ursus arctos*) in Caucasus, is complex. According to Vereshchagin (1959), there were three to four species of *Ursus* in Caucasus during the Pleistocene. Although some of these forms may have belonged to the same species, there is a long history of heterogeneity of Caucasian bears. The first description of Caucasian bears was made by Middendorf (1851), who distinguished a new subspecies, *U. a. meridionalis.* He used this name for all bears of the European mountains, Transcaucasus, and Middle Asia. Dinnik (1897, 1914) reported on two forms of brown bears in Caucasus, *U. a. meridionalis* and *U. a. typicus.* Apart from morphological differences, he mentioned ecological differences between the subspecies (e.g., use of different habitats).

Based on the study of skulls and skins, Satunin (1915) claimed that three subspecies of brown bears existed in Caucasus. Two of these coincided with those de-scribed by Dinnik (1914), but he renamed *U. a. typicus* as *U. a. caucasicus* because of differences between the latter and European bears. The third subspecies, *U. a. lasistanicus,* was considered close to *U. a. syriacus* from the Middle East. Smirnov (1916, 1919) divided Caucasian bears into two varieties and five races. These varieties corresponded to the subspecies of Dinnik (1897), and one of the races corresponded to *U. a. lasistanicus;* the rest were new. He also offered the first quantitative measure—the ratio of postorbital constriction to condylobasal or facial length—to differentiate taxa.

Ognev (1924) simply referred to all the races described by Smirnov as subspecies, but Adlerberg (1935), although noting the extreme diversity of Caucasian bears, reduced the number of subspecies to one, *U. a. syriacus,* and included them with bears from the Middle East. Geptner et al. (1967) referred to two subspecies, *U. a. meridio-*

nalis and *U. a. syriacus.* Kudaktin (1983) distinguished four phenotypes of Caucasian bears during his long-term field study. Three of these concurred with the subspecies of Satunin (1915), but one was previously unknown. Tikhonov (1987, in litt.) agreed with Geptner et al. (1967) and assumed that two subspecies of brown bears occurred in Caucasus.

We reviewed the taxonomy of Caucasian brown bears using statistical analysis of craniometric variables, electophoresis of blood proteins, and field observations. We tested if the existence of ecological forms (=ecomorphs) and visually distinguished characteristics of skulls could be supported by comprehensive statistical analysis and if mechanisms to maintain polymorphism (e.g., age or geographic variability) could be identified.

MATERIALS AND METHODS

Craniometric data.—We measured 39 craniometric variables (Fig. 1) to the nearest 1.0 mm. Moreover, variability of 11 phenetic parameters was examined, including shape of both front and back sides of nasals, shape of the upper part of the forehead, shape of the back side of palatinae, the presence or absence of PM^{1-3} and PM_{1-3}, and the location of the location of the beginning of sagittal crest. Because none of these provided significant results, we have not included a more detailed description. We located 245 skulls of Caucasian brown bears in 17 public and 4 private collections.

Because of concerns over differentiating Caucasian bears from immature skulls, we used only skulls from adult bears (*n* = 88) in our taxonomic analysis. Adult bears were identified from the total sample based on tooth development and wear (V. G. Voronov, in litt.) and closure of the basioccipitale-basisphenoideum suture, which closes around 6–8 years of age (Rausch, 1963). Skulls of old bears had no traces of sutures, except for the squamosum-jugale suture, which is related to continued enlargement of the zygomatic width (Fig. 1).

Sex of 50 of the 88 skulls was determined from the museum label or by asking the hunters that killed the bear. Sex of the remaining 38 skulls was determined according to external features, such as size, relative width of the skull, and development of sagittal crest (in general, all larger in males). Other external features given by B. P. Zavatzkiy (in litt.) for determination of sex in bears (e.g., shape of nasalae, development of the gutters on palatinae) appeared to be lacking in Caucasian bears when applied to the skulls with known sex. Fifty-eight skulls were from males, and 30 were from females.

When measuring skulls in collections, males of the same age class seemed to be represented by two morphs that differed in size, structure (robust or gracile), and development of crests. Skulls of one of the morphs resembled skulls of females, but sex of all "dwarf" males was known from museum records. More detailed description of these visual differences was given by Lobachev et al. (1991). The morph affiliation of each male skull was recorded for further comparison with the results of statistical analysis. No apparent morphs could be visually determined among female skulls.

Statistical analysis.—Distributions of all 39 variables were examined separately for both sexes. With the exception of teeth measurements, histograms were polymodal especially for males. Preliminary examination of homogeneous groups based on skull characteristics was accomplished by cluster analysis. We tried to overcome the known disadvantages of this method by using several compositions of variables created from the initial one according to the skull blocks distinguished by Muzhchinkin (1987). In his opinion, based on the thorough study of ontogenesis of the skulls in seals and terrestrial carnivores, skulls of Fissipedia can be provisionally divided into six blocks (Fig. 1), with evolutionary changes occurring relatively independently. Variables describing the first five blocks formed five compositions of variables for clustering; the sixth set included measurements of the mouth; and the seventh set included only tooth measurements.

Euclidean distance was the only metric that we used for clustering. Some investigators (McBee et al., 1985) considered the choice of linkage as the crucial point for successful and reliable classification. Aldenderfer and Blashfield (1985) proposed that for data such as ours average and far neighbor (complete) linkages were most suitable; thus, we tried both of these methods. The number of clusters was not defined in advance.
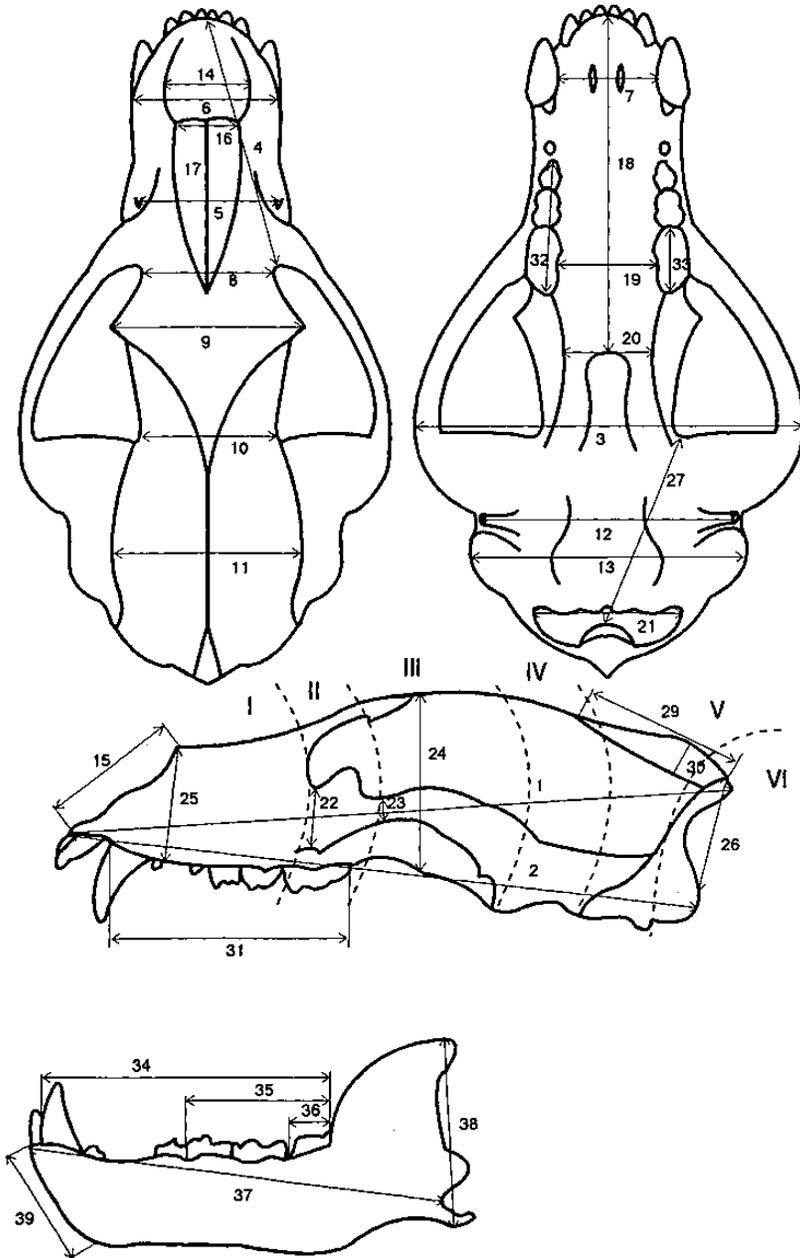
FIG. 1.—Measurements of the skulls of brown bears from Caucasus that were used in discriminant function analyses; Roman numericals correspond to blocks delimited by Muzhchinkin (1987).

We addressed two problems by using discriminant function analysis. First, we verified stability and reliability of classes in both sexes. Second, we created a key for determination of sex and morph of Caucasian bears using cranial measurements. For the first purpose, analysis was conducted separately for males and females; samples were combined for the second. Groups obtained by clustering were corrected with discriminant analysis until 100% correspondence of initial and predicted groups was achieved. Second, we examined stability of the groups by

weighting different observations. For instance, all observations with of one or more factor overlapped with observations from other groups received a zero weight, but the weight of those outside the overlapping zones equaled one. The same procedure was performed with all skulls where sex was not definitely known.

Some of the measurements were missing because of defects of the skulls. Therefore, a calculation of missing measurements was needed for including those skulls in the analyses. We chose variables that were most closely correlated with missing variables and estimated values for missing measurements.

We conducted cluster and discriminant-function analysis on ratios and volumetric measurements; e.g., ratios of all measurements of the skulls to maximum length and zygomatic width, ratios of squared variables to multiplied products of maximum length and zygomatic width, volume of brain case, and volume of nasal cavity. Separation of the sample with ratios of postorbital constriction divided by maximum or facial lengths (Smirnov, 1916, 1919) was given particular attention. All distributions of derivative variables were unimodal and did not suggest that groups occurred in our sample. Thus, there were no differences among groups that could have derived from allometric growth and consequently different proportions of the skulls. Variation in phenetic values also was so low that no division was possible according to the outcome from our analysis.

Statistical analyses were done with SYSTAT 3.0 (Wilkinson, 1990), but SAS (1988) was used to compare covariance matrices of groups. Analogous algorithms of analysis for biological classification were used (Nevo et al., 1988; Sneath and Sokal, 1973; Zeida and Voskar, 1987).

Electrophoretic analysis.—Ten blood samples from different bears were collected in 1988–1989. Seven bears were killed in the vicinity of the Shakhe River in eastern Caucasus by local game officers, and we joined their team to collect blood from hearts. Three bears were immobilized in zoos at Yerevan ($n = 1$), Armenia and Tbilisi ($n = 2$), Georgia, with Sernylan (dose = 1.2–1.5 mg/kg). After immobilization, we collected samples from the femoral vein. Samples were put immediately into an insulated container with salted ice at ca. −3°C. In the laboratory, blood was stored at −20°C for 2–18 months.

We used the electrophoretic methods of Harris and Hopkinson (1976) with slight variations in buffer contents. The following proteins were examined: albumin (A), hemoglobin (H), transferrin (T), esterase (E), sorbitol-dehydrogenase (SDG), 6-phospho-gluconat-dehydrogenase (6-PGD), lactate-dehydrogenase (LDG), glucose-6-phosphate-dehydrogenase (G-6-PDG), tetrasolium oxidase (TO), and alkaline phosphatase (AP). Analysis of malate-dehydrogenase was unsuccessful due to the low fermentive activity.

Field investigations.—Field expeditions were conducted from May to September 1983–1989 mainly in the Caucasian State Biospheric Nature Reserve and bordering Golovinskiy Reserve. The study area was ca. 750 km². Urushten Valley (45.7 km²) was studied with particular care. Our primary methods were tracking and visual observations of bears. Individual bears were identified by size of their tracks by adapting the method of Klein (1959) to a mountainous terrain (Kudaktin and Chestin, 1987) and recognition of individual bears by differences in body build and color. We spent 561 days in the field, walked 4,650 km of foot trails, and observed 232 bears.

RESULTS

Craniometric variables.—The heterogeneity of skulls of Caucasian bears that could be noticed visually in collections was confirmed by the analysis of histograms and two- and three-dimensional plots of variables (Fig. 2a, b). We used cluster analysis to further examine distributions of cranial characteristics. According to dendrograms obtained by clustering, there were three classes of both males and females, although those groupings were more explicit in males. Composition of clusters differed slightly, but the same skulls typically occurred in the same cluster for both sexes. The most distinct class was *lasistanicus* (we marked morphs with historic subspecies names to avoid confusion with terminology), which had smallest and most gracile skulls.

Variables for discriminant analysis were selected according to their correlation with the grouping variable and their contribution to the formation of canonical factors. Linear discriminant analysis divided sample of
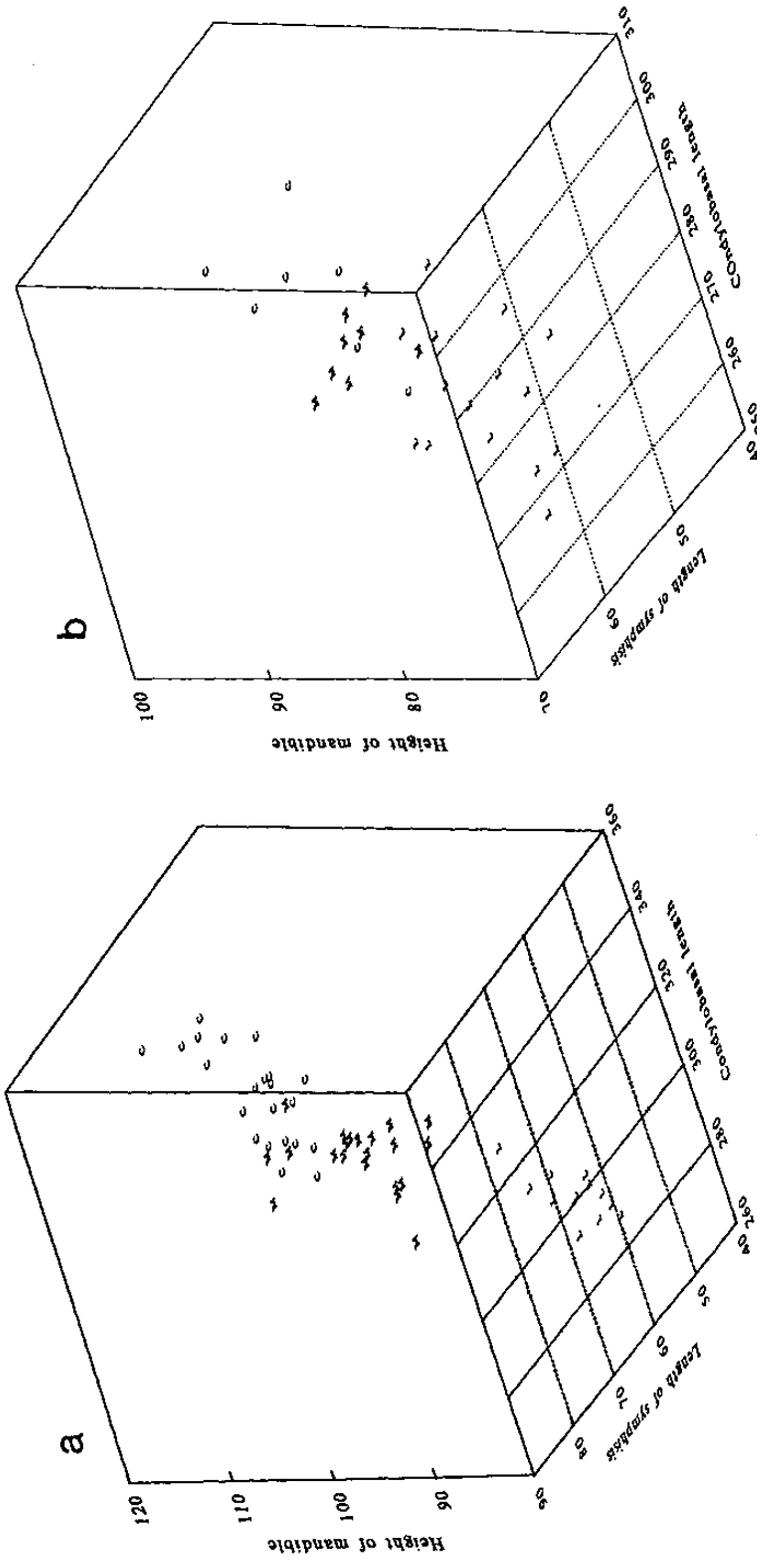
FIG. 2.—Three-dimensional plots of the skull measurements of a) male and b) female Caucasian brown bears (c = *caucasicus*, m = *meridionalis*, and l = *lasistanicus*).
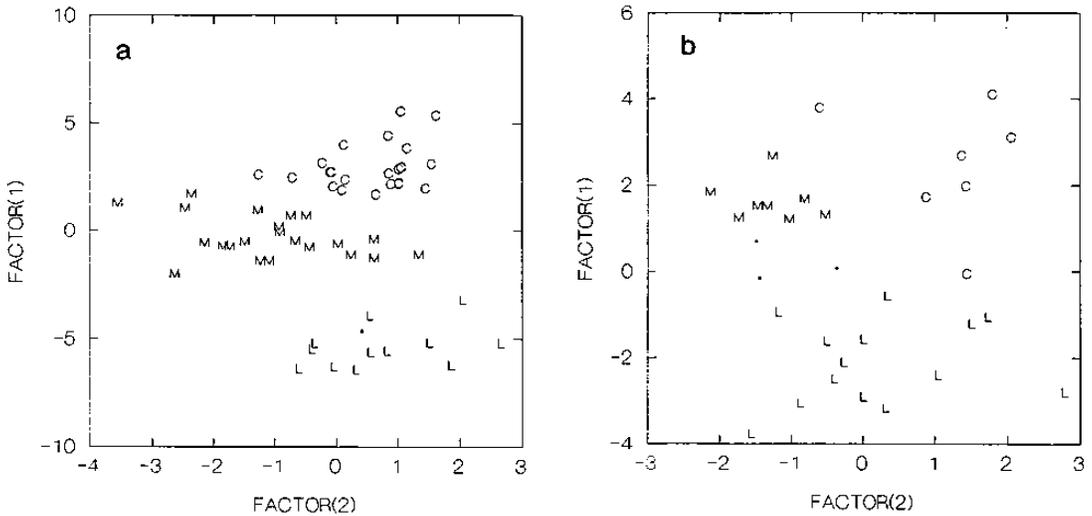
FIG. 3.—Distribution of canonical variables from skull measurements of a) male and b) female Caucasian brown bears in the space of canonical variables created from skull measurements (C = *caucasicus*, M = *meridionalis*, and L = *lasistanicus*).

males into three groups with 100% correspondence between initial and predicted classes and included skull variables 1, 13, 37, 38, 39 (Fig. 1). The minimum probability of correct determination was 0.8 (Fig. 3). Because male *lasistanicus* could be distinguished visually from three-dimensional plots (Fig. 2a) without multivariate techniques, the remaining question was the reliability of the distinction between male *caucasicus* and *meridionalis*. We used discriminant-function analysis to examine the grouping of male *caucasicus* and *meridionalis*; the set included variables 1, 37, and 38 (Fig. 1). Linear-discriminant analysis resulted in 100% correspondence of initial and predicted groups, with the canonical correlation of 0.85. Centroids of male *caucasicus* and *meridionalis* were different (*P* < 0.001). We also attempted to distinguish between male *caucasicus* and *meridionalis* with the same variables that we used for the entire male sample (variables 1, 13, and 37–39); the canonical correlation was 0.89.

Grouping of females was less stable because of the smaller sample size and required more variables than for males. Only quadratic discriminant analysis appeared to

be an adequate because of inequality of covariance matrices. The outcome from this analysis was similar to that for the males (Fig. 3b), with the final set formed by variables 1, 13, 26, 37, and 38 (Fig. 1). The initial and predicted classes corresponded to each other, and the lowest probability of proper determination equaled 0.9.

We discovered that the height from the lowest edge of foramen occipitale magnum to the upper point of lambdoid suture (variable 26, Fig. 1) was the likely cause of inequality of covariance matrices among female groups. Inclusion of that variable in the set for males resulted in the same phenomenon. Perhaps, different correlations occurred among the groups, but disparity of covariances may occur either because of true different correlations or because of too diverse dispersions of variables. Unfortunately, sample sizes for each particular morph were too small for comparison of correlations.

We failed to separate the entire sample according to sex because male *lasistanicus* were always classified as females. Our attempt to divide the whole sample into six groups (male *lasistanicus, meridionalis*,

TABLE 1.—*Frequencies of skull morphs among age groups of Caucasian brown bears collected in 1830–1990.*

Age class	Females			Males		
	lasistanicus	*meridionalis*	*caucasicus*	*lasistanicus*	*meridionalis*	*caucasicus*
Adults	9	5	5	8	14	6
Seniors	6	3	2	4	8	18
Total	15	8	7	12	22	24

caucasicus; female *lasistanicus, meridionalis,* and *caucasicus*) also was unsuccessful. Thus, we combined female *meridionalis* and *caucasicus* and male *lasistanicus* and performed the division into four groups (I—male *caucasicus,* II—male *meridionalis,* III—female *meridionalis* and *caucasicus* and male *lasistanicus,* and IV—female *lasistanicus*) with skull variables 1, 6, 12, 13, 26, 37, 38 and 39 (Fig. 1) in quadratic discriminant function analysis. The division again appeared to have 100% correspondence with the lowest probability of correct determination of 0.67. The second step consisted of dividing group III into original female *meridionalis* and *caucasicus* and male *lasistanicus.* The set for quadratic discriminant analysis was formed by variables 1, 12, 13, 26, 30, and 38 (Fig. 1). All the observations were properly classified with the lowest probability equaling 0.8. To obtain 100% correspondence, however, it was necessary to include height of sagittal crest (variable 30), which likely is able to grow after closure of sutures.

Our entire sample of 88 skulls could not be divided either by sex or morph in one step, but the two-stage separation using similar sets of variables provided good results. This was explained by the absolute metric range of differences between female *meridionalis* and *caucasicus* and male *lasistanicus,* which was less than that between male *caucasicus* and *meridionalis* and female *lasistanicus.* Therefore, differences between male *meridionalis* and *caucasicus* and female *lasistanicus* determined the scale of factors that could not discriminate

differences between female *meridionalis* and *caucasicus* and male *lasistanicus.*

After completing the analysis of our initial data, we located four skulls of bears from the Caucasus and Middle East at the British Natural History Museum (one male from Turkey and three females, one from Syria and two from Caucasus). Because there is no (and never was a) gap between ranges of bears from Caucasus and the Middle East, they can be regarded in the same taxonomic group. The inclusion of these skulls in our sample did not affect results for males or females. The three new females were classified as *meridionalis* and the male as *lasistanicus* (stars in Fig. 3).

The most important variables for all divisions involved three dimensions: length, width, and height. Our entire sample was characterized, according to *t*-criteria, by reliable differences in the height of mandible (variable 38, Fig. 1), maximum length (1), and length and height of sagittal crest (29–30) for all 6 groups (three in each sex). We noted that 29 of 39 variables provided significant and reliable differences between female *lasistanicus* and *meridionalis,* 10 of 39 between female *meridionalis* and *caucasicus,* 34 of 39 for male *lasistanicus* and *meridionalis,* and 30 of 39 for males *meridionalis* and *caucasicus.* Our contention that the influence of age was excluded by using skulls with closed basioccipitale-basisphenoideum suture was supported by a lack of correlation ($r_s = 0.53$, $P > 0.05$) between morph and age; only the oldest males had more individuals in the largest morph (Table 1). We also examined the

TABLE 2.—*Frequencies of skull morphs in Caucasian brown bears collected during various periods (excluding observations with unknown date of collection).*

Collecting period	Females			Males		
	lasistanicus	*meridionalis*	*caucasicus*	*lasistanicus*	*meridionalis*	*caucasicus*
1830–1870		1		1		
1871–1900		2	1	2	7	3
1901–1930	3	4	5	4	3	14
1931–1960	3				3	1
1961–1990	7	1		5	8	5

possibility of temporal changes (i.e., steady reduction or increase in size during this century, which would be recorded in changing ratios of morphs) in Caucasian bears in mammal collections. This hypothesis was not supported by the correlation between morphs' abundance and period of collection ($r_s = 0.23$, Table 2).

Known locations where bears were killed or found were plotted (Fig. 4), but tests to evaluate allopatric or sympatric distribution of various morphs were difficult. This evaluation also was complicated because we lacked data on habitat use of killed bears during the breeding season in late spring-early summer. Most bears were killed by hunters in autumn, thereby making examination of allopatry during the breeding season impossible. In western Caucasus, however, skulls of different morphs of bears were obtained in all seasons. Because half of our sample (50%) came from there, we
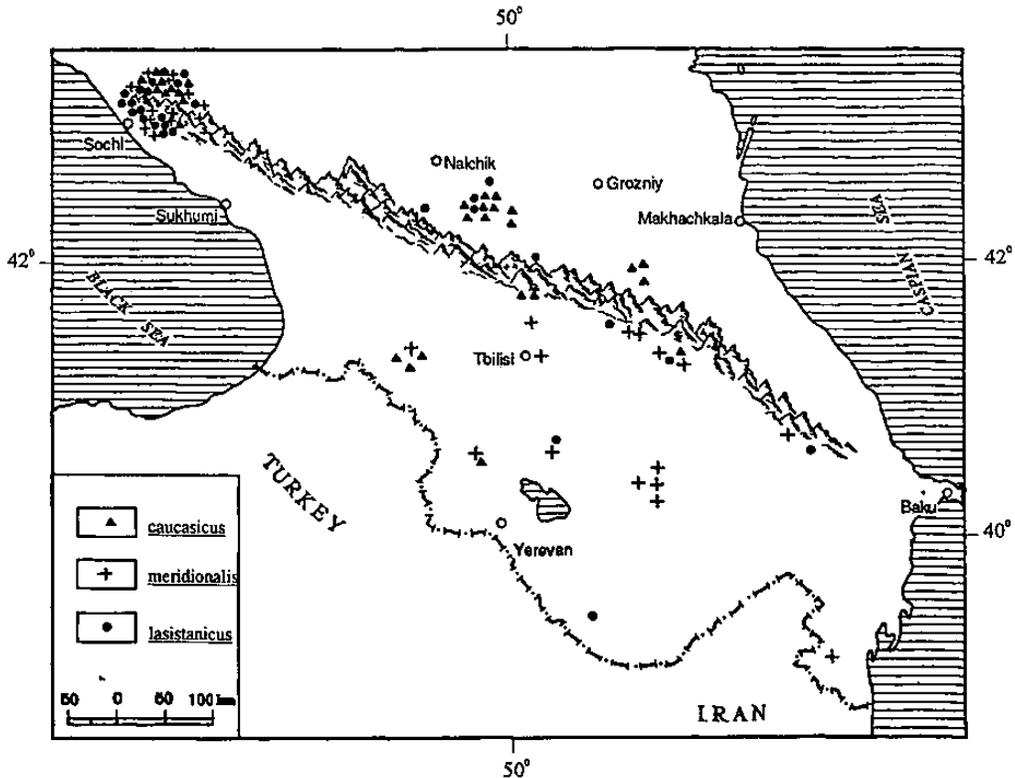

FIG. 4.—Locations of where Caucasian brown bear skulls were collected.

TABLE 3.—*Percentage of morphs in Caucasian brown bears according to field and collection data.*

Morph	Females		Males	
	Field	Collection	Field	Collection
lasistanicus	39	50	24	21
meridionalis		27		38
caucasicus		23		41
meridionalis/caucasicus	61		76	

assumed sympatric distribution of the morphs in the entire region. The ratio of morphs differed between sexes: *lasistanicus*: *meridionalis*: *caucasicus* = 1:2:2 in males and 2:1:1 in females (Table 3). Nevertheless, we concluded that three discrete morphs of bears existed in relation to skull size in both sexes in Caucasus.

Electrophoretic analysis.—There were no differences in A, H, E, SDG, G-6-PDG, TO, and AP, but 6-PDG, LDG and T appeared to be polymorphic. Polymorphism of these proteins was not related with groupings from the cranial analysis; two individuals of *meridionalis* had different alleles for T, 6-PDG, and LDG between themselves and from the other eight individuals. One of the *meridionalis* was heterozygous both in T and LDG, but the other nine individuals were identically homozygous for T. A female *meridionalis* had the common alleles for all proteins, but its offspring had unique alleles for T, 6-PDG, and LDG.

Field investigations.—From the beginning of field work, we visually could distinguish two morphs of Caucasian bears (Lobachev et al., 1988). Samples from hunters were *meridionalis* and *caucasicus*, which we could not separate in the field, and a small *lasistanicus*. Differences were in size, fur color (the hair of *lasistanicus* had grayish ends, causing individuals look silvery and iridescent while moving), and body build (the small morph was more gracile). Short hair of *lasistanicus* gave the

impression of longer extremities (ears, tail, and limbs).

We observed distinct and nonoverlapping home ranges only in male *caucasicus* and *meridionalis* during the breeding season (late May–June). After breeding females appeared on the territory of a male, they stayed there until the end of mating. Our 11 observations of mating bears included eight homogeneous couples (seven *caucasicus* or *meridionalis* and one *lasistanicus*) and three heterogeneous couples of male *caucasicus* or *meridionalis* and female *lasistanicus*. No couples formed by male *lasistanicus* and female *caucasicus* or *meridionalis* were observed or reported by staff it the reserve. We observed individual *caucasicus* and *meridionalis* in coniferous forest, but *lasistanicus* occurred mostly in beech (*Fagus orientalis*) forests at low elevations, or the alpine zone. Female *lasistanicus* were most common morph, but in males *lasistanicus* were the least common morph based on both visual observations and collections (Table 3).

DISCUSSION

The dissimilarity of male *caucasicus* and *meridionalis* in our discriminant analysis (Fig. 4), and the lack of visual distinction between them in the field make their distinction doubtful. However, the division using only three variables was justification for three rather than two groups, because Wake and Kronmal (1977) showed that results of discriminant analysis were highly reliable if four or less variables form factors and no more than two groups each contain ≥25 observations. Those criteria were met for male *caucasicus* and *meridionalis*.

The comparison of primary statistics of various groups using *t*-tests showed that measurements of teeth did not differ between female *lasistanicus* and *meridionalis* and male *lasistanicus* and *meridionalis*, but they varied significantly between *meridionalis* and *caucasicus* in both sexes. This mirroring of intermorph distinctions between sexes provide some evidence to the

correspondence of size morphs in males and females.

Male Caucasian bears demonstrated greater variability in cranial measurments than females, similar to reports for the mole rat (*Spalax*—Nevo et al. 1988, Peshev, 1989) and the European otter (*Lutra lutra*—Zeida and Voskar, 1987). Some common features of Caucasian bears with other species were observed in correlation patterns of skull measurements. Manning (1971) found a low correlations of measurements of teeth and postorbital width with other skull variables in polar bears (*U. maritimus*). Nevo et al. (1988) mentioned low correlations of measurements of teeth with skull size in mole rats. We also noted low correlations of postorbital width and other skull variables which explains why Smirnov (1916, 1919) divided Caucasian bears according to the index of postorbital width to maximum or facial lengths. Indeed, low variability and relative independence of postorbital width allow treating this variable as a constant, making Smirnov's index a constant divided by changeable lengths, which are themselves useful for distinguishing different morphs. Therefore, Smirnov's (1916, 1919) indices more likely reflect variability of maximum and facial skull lengths rather than particular importance of postorbital width for classification of morphs.

Comparison of our results with those of Ognev (1924) was difficult because he provided data for only three of five groups. Nonetheless, the crucial point from Ognev's (1924) data was that there was practically no overlap between values of maximum and condylobasal lengths of different groups. According to our study, only the smallest morph, *lasistanicus,* can be clearly distinguished from the remaining sample by these variables.

Variablès in the discriminant function analysis in our study were similar to those obtained by other researchers. Yoneda and Abe (1976) studied sexual dimorphism in brown bears of Japan and reported signifi-

cant differences between sexes in size of canines, condylobasal length, mastoid width, height of mandible, height of occiput, length of palate, and rostral width. We used four of these measurements to distinguish morphs in Caucasian bears. Moreover, we could substitute maximum skull length with condylobasal length without changing our groupings but with slight deterioration of probabilities of correct classification.

A similar list of variables for discriminant analysis was reported by Nevo et al. (1988), who studied craniometric variation in four chromosomally different species of mole rats. Four of eight variables that they used were the same as ours (e.g., height of mandible, height of occiput, width between meatus acusticus extermus, and rostral width). Species of mole rats were distributed allopatrically in areas with different climatic conditions. Regression analysis showed that 75% of morphological variation was related to temperature and humidity gradients (Nevo et al., 1988). Mole rats spend most of their time under the ground and therefore do not move long distances. Bears in Caucasus demonstrated the opposite behavior; they moved over a wide range, occupied different habitats depending on season, and sometimes concentrated in particular places (Lobachev et al., 1988). Because of this, it was not possible to explain the existence of three morphs of Caucasian bears by climatic variation, especially assuming sympatry, which also was reported by Adlerberg (1935) based on fewer data.

We did not find any unique·electrophoretic markers in blood proteins for the three morphs of Caucasian bears that paralleled skull variability, but we could not compare frequencies of alleles because of the small sample. Because of this, we cannot draw conclusions about reproductive relations between morphs. Allendorf et al. (1979) examined 13 proteins of polar bears and reported complete homogeneity of 52 samples. Wolfe (1983) succeeded in searching

for differences between *U. americanus* and *U. arctos* (*n* = 93) using variation in the activity of glucose-6-phosphate-isomerase. Two esterases, haemoglobins, LDG, and phosphoglukomutase-1 appear to be polymorphous in *U. americanus* (Wathen et al. 1985).

Variability of protein activity in Caucasian bears, although not related with craniometric groupings, seemed to be high compared with other investigations; three of 10 proteins were polymorphous and four of 10 samples differed from the others by one or two enzymes. This level of variability was similar to those described by Goldman et al. (1989) in a comparison of seven ursids, the raccoon (*Procyon lotor*), and the giant panda (*Ailuropoda melanoleuca*) by one-dimensional (18 polymorphic alleles of 44) and two-dimensional electrophoresis (106 of 289). Genetic heterogeneity in Caucasian bears appeared to be higher than in North American black bears (5 polymorphic proteins of 23; Wathen et al., 1985) and polar bears (zero polymorphic proteins of 13; Allendorf et al., 1979).

As was demonstrated in field experiments and observations by Pazhetnov (1979), occupation of individual ranges by male brown bear in Central Russia in advance of breeding may be crucial for their reproductive success. Because we did not observe individual ranges in male *lasistanicus* during breeding (Lobachev et al. 1988), they may have lower reproductive success than male *meridionalis* and *caucasicus*.

It would be possible to recognize the three morphs as distinct species, because the range of variation corresponded to that reported for other species (Mayr, 1963). We documented, however, mating of different morphs during field investigations (Lobachev et al. 1988), and electrophoretic analysis suggested interbreeding populations. Additionally, subspecific status for each morph does not seem justified. The International Code of Zoological Nomenclature (1985) allows distinguishing subspecies if a taxon is characteristic not only of a particular geographic area but also to a certain environment. We believe, however, that in referring to subspecific status, it is important to note mechanisms of isolation from other subspecies. In our study, we found no evidence of isolating mechanisms and thus do not support numerous attempts to divide Caucasian brown bears into several subspecies. Consequently, we regard Caucasian brown bears as a single subspecies that is the same as bears in the Middle East, *U. a. syriacus.* Middendorf (1851), who described *U. a. meridionalis,* presumably either did not know about the former description or had no opportunity to compare his own material with those from the Middle East.

There is evidence for a balanced polymorphism in. the literature when discrete morphs coexist in one population while each of them receives a certain advantage in terms of natural selection either in different seasons (Timofeev-Resovskiy et al., 1977) or in various phases of population dynamics. For example, color morphs of voles (*Microtus*) in northern Siberia occurred in different proportions depending on the population density in particular year (Krivosheev et al., 1983). Nevertheless, in all these instances, studies dealt with r-selected species, usually breeding several times a year, whereas bears are typical K-strategists with long life cycles and low fertility. If we assume that the three morphs in Caucasian bears developed from similar young because of some environmental factors, we would expect extremely high mortality of young due to natural selection eliminating the intermediates. This is not supported by the long-term monitoring of population demography (Kudaktin and Chestin, 1993).

We cannot explain the existence of morphs of Caucasian bears either by age, individual variations, or polymorphism (Krivosheev et al., 1983; Kudaktin and Chestin, 1993; Timofeev-Resovskiy et al., 1977). We suggest that the observed phenomenon is related to genetics and Men-

delian inheritance of intermorph differences because of discreteness of morphs in Caucasian bears with no intermediates. Metric variables in organisms usually are characterised by polygenic inheritance with partial rather than full dominance of alleles. This outcome explains normal and therefore unimodal distributions of size (Ayala, 1983; Lobashev, 1969; Yablokov, 1966). Our conclusions do not support this idea, but we do not know what particular genetic mechanism underlies size polymorphism in Caucasian bears.

We propose using the term "ecomorph" to describe groups in Caucasian bears. We suggest using historic subspecies names to distinguish among ecomorphs without mentioning genus and species; i.e., *lasistanicus, meridionalis,* and *caucasicus.*

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