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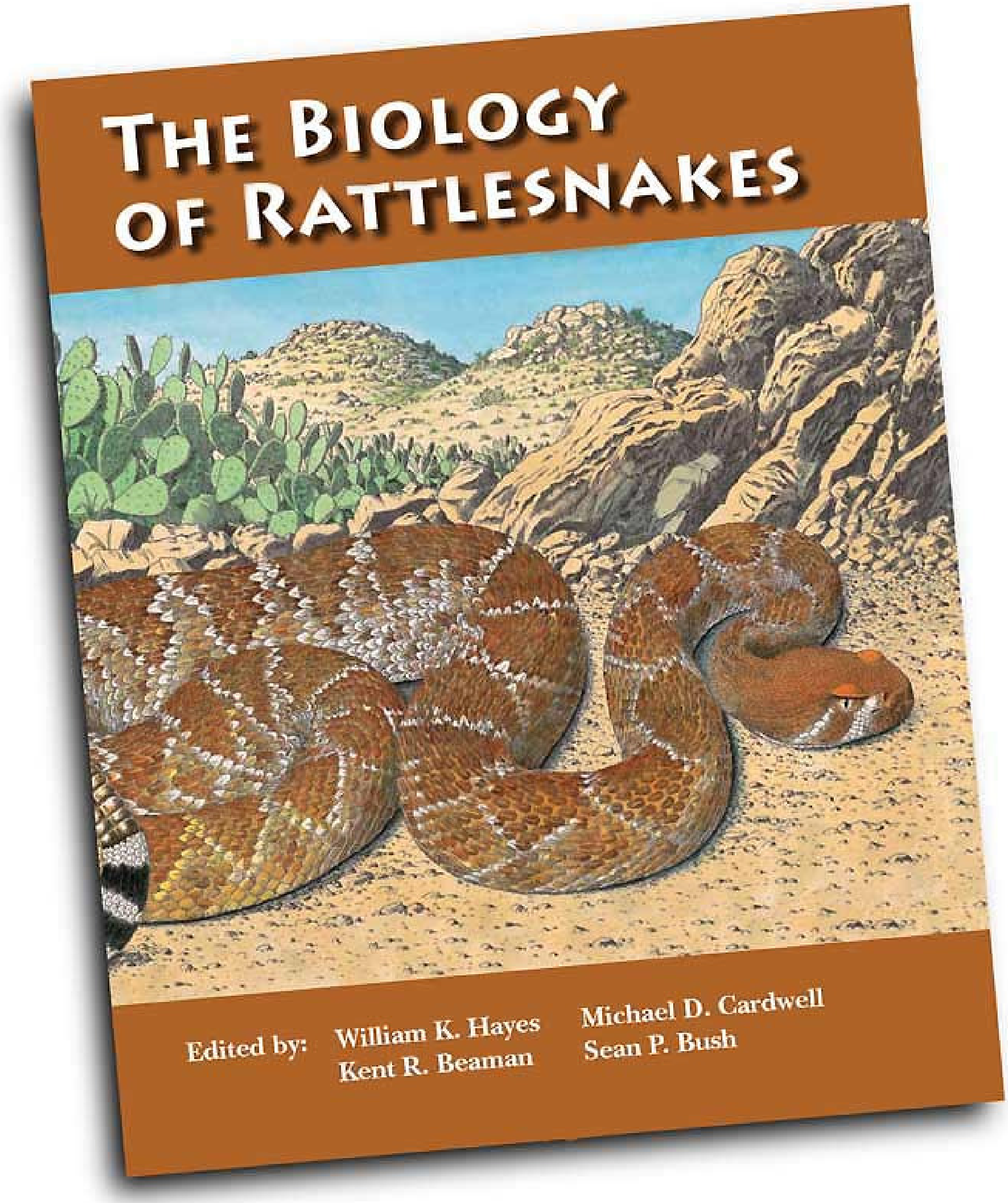

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Geographic Variation in Western Diamond-Backed Rattlesnake (*Crotalus atrox*) Morphology

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Abstract.—The Western Diamond-backed Rattlesnake (*Crotalus atrox*) is one of the most widespread rattlesnakes in North America, yet no previous study has examined geographic variation in morphology across the range of this species. I examined 673 museum adult specimens from throughout the geographic range of *C. atrox* for 37 morphological traits, including scale counts (meristics), morphometrics (body size measurements), and color pattern. Data were analyzed using multivariate principal component analyses and univariate regressions. Some scale counts exhibited clinal variation from east to west, including the number of ventral scales (higher numbers in the west for both sexes), the number of head scales before the supraoculars (higher numbers in the east for adult females), color (darker animals in the east for both sexes), and number of body blotches (increasing number eastward in males). Body size varied with latitude, resulting in larger (measured by SVL) snakes northward. The presence of larger snakes in northern latitudes follows Bergmann's rule, which is consistent with some recent studies of squamates. Overall, there was no clear separation of populations into biogeographic regions or previously described genetic groups. In contrast to many vertebrate taxa that occur in North American deserts and show marked population divisions or species breaks across this same area, *C. atrox* appears to represent one continuously distributed population with clinal variation in morphology throughout its range.

Introduction

Studies of geographic variation within species provide the foundation for a broader understanding of evolution, biogeography, ecology, conservation, biodiversity, and speciation (e.g., Gould and Johnston, 1972; Endler, 1977; Zink and Remsen, 1986; Coyne, 1994; Cicero, 1996; Wake and Jockusch, 2000). Widespread species are particularly interesting to study because they generally inhabit numerous distinctive biogeographic, ecological, and environmental zones, making them good candidates for studies of speciation (e.g, Endler, 1977; Zink and Remsen, 1986; Coyne, 1994; Allsteadt, et al., 2006).

The Western Diamond-backed Rattlesnake (*Crotalus atrox*) has a widespread distribution in North America (Campbell and Lamar, 2004; Castoe et al., 2007) and is an interesting taxon for examining geographic and clinal variation across a large range. *Crotalus atrox* has one of the largest distributions of any rattlesnake, and probably has the largest range of any North American rattlesnake except *C. oreganus*/*C. viridis* (Pook et al., 2000; Ashton and de Queiroz, 2001; Douglas et al., 2002). Currently, *C. atrox* is monotypic, although the species was previously composed of three or more subspecies (e.g., *C. atrox atrox, C. atrox sonoranensis, C. atrox lucasensis*). These subspecies were synonymized or assigned to different species by Klauber (1930).

I used morphological characters to investigate variation across the range of *C. atrox*. Only a few other studies have examined morphological variation across a single species of rattlesnake (Murphy et al., 1994; Ashton, 2001b; Boback, 2003; Allsteadt et al., 2006). Geographic variation in the morphology and color pattern of *C. atrox* has been previously documented. Klauber (1930) and Boyer (1953) conducted the most extensive analyses to date on *C. atrox* morphology; Klauber (1930) compared 192 specimens from three different regions in North America (Oklahoma-Texas, Arizona, Sonora), and Boyer (1953) analyzed 228 specimens from Oklahoma. Klauber (1930) found variation in coloration and scale counts, with higher numbers of ventral scales in Arizona specimens and darker individuals in Texas and Oklahoma compared to western specimens. He hypothesized that additional differences may remain to be discovered between more southerly (Mexican) and northerly forms, although he did not think any populations warranted subspecific status.

Boyer (1953) conducted a more in-depth treatise of *C. atrox* in the Wichita Mountain Wildlife Refuge, Comanche County, Oklahoma. He compared his results to Klauber's (1930) study, and found populations in Oklahoma were most similar to Mexican specimens for various scale counts. From these comparisons, Boyer (1953) concluded that there was an east-to-west trend in scale counts in *C. atrox*, with increasing counts of dorsal, ventral, caudal, and infralabial scale rows in the west, along with greater variability of these traits in western populations. A few traits, such as number of intersupraocular scales, displayed an increasing trend from south to north.

Castoe and colleagues (2007) examined the phylogeography and population structure of *C. atrox* using mitochondrial DNA (ND4–the fourth subunit of NADH dehydrogenase; Figure 1). Genetic structure was observed

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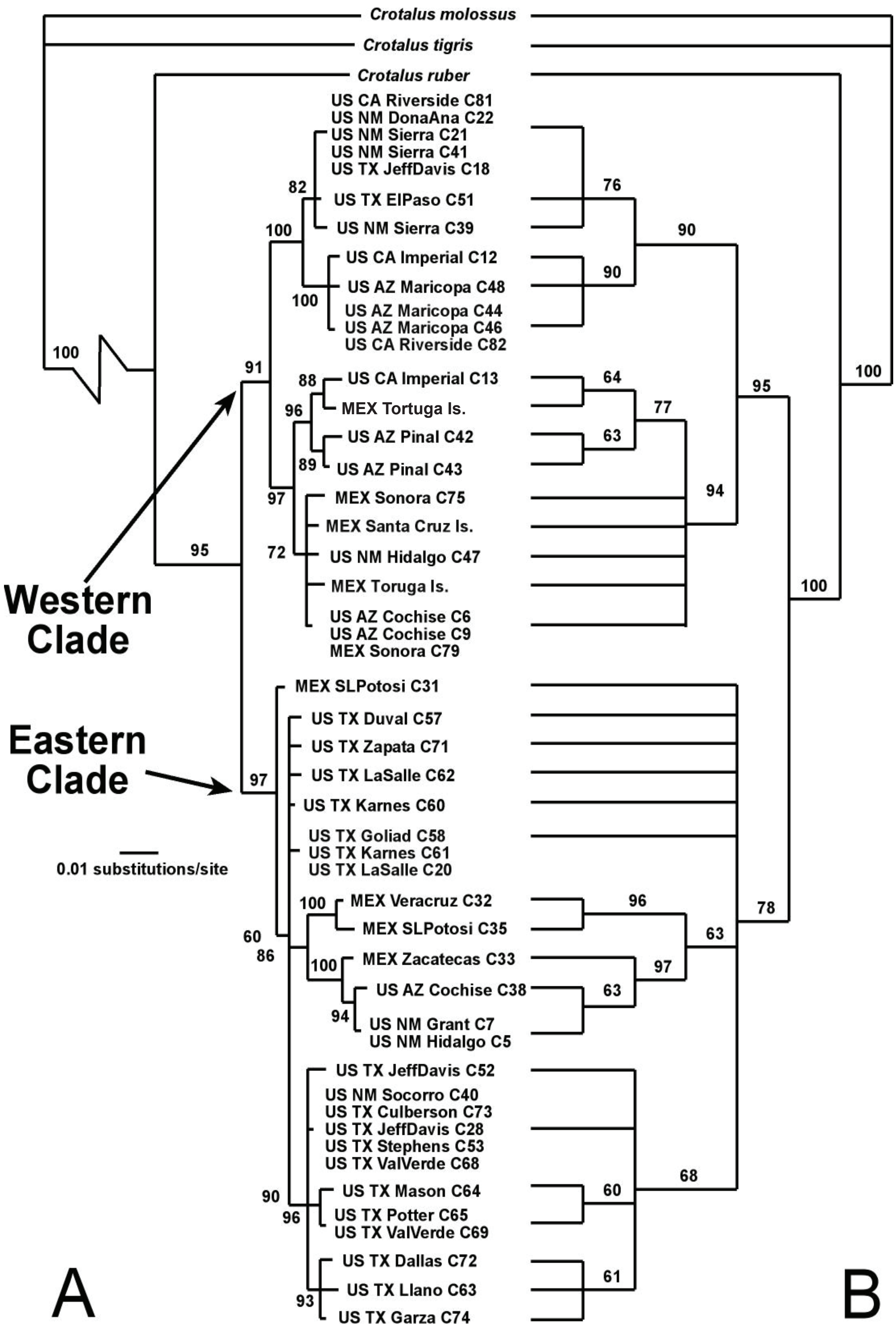

Figure 1. Alternative hypotheses of intraspecific relationships within the Western Diamond-backed Rattlesnake (*Crotalus atrox*) using mitochondrial gene ND4, with outgroups included. (**A**) Fifty percent majority rule consensus phylogram estimated using Bayesian phylogenetic methods. Numbers next to nodes represent posterior probability values. (**B**) Strict consensus of 12 equally-parsimonious trees from maximum parsimony analysis. Numbers next to nodes represent bootstrap support values. From Castoe et al. (2007).

among geographic regions, including the Chihuahuan Desert, Sonoran Desert, Southern Plains, and Tamaulipan Plains. Although these populations were probably once isolated in multiple Pleistocene refugia on either side of the continental divide, subsequent range expansions and post-glacial population growth, especially in eastern populations (east of the continental divide), explains the present gene flow and contact between these haplotype lineages, with evidence for recent flow from a west-to-east direction (Castoe et al., 2007).

Many ecological and evolutionary rules (e.g., Bergmann's rule, Gloger's rule, Cope's rule) may be relevant to explaining and elucidating clinal and geographic patterns of variation within and amongst species (Ashton, 2001a, b, 2002; Ashton and Feldman, 2003; Burtt and Ichida, 2004). Bergmann's rule may be particularly relevant in explaining patterns of geographic variation in *C. atrox*, and is defined as a trend within species, usually in endothermic vertebrates, towards large size in cooler environments (Ashton, 2001a). We can test the hypothesis that Bergmann's rule applies to *C. atrox* by comparing average temperatures with body size or using latitude as a proxy for temperature. Recent studies have found that some reptiles (*C. viridis*, turtles) follow this trend, but others don't (*C. oreganus*, other lizards and snakes; Ashton, 2001b; Ashton and Feldman, 2003).

The purposes of this study are to: 1) quantify geographic variation in *C. atrox*; 2) determine if morphological variation is structured by geographic/biogeographic regions or genetic groups (Castoe et al., 2007); 3) determine if patterns of variation are clinal or stepped/discrete; and 4) consider trends across longitude and latitude, specifically whether these patterns follow Bergmann's rule and how they compare to other studies of Bergmann's rule and clinal patterns in reptiles (e.g., Ashton, 2001a; Ashton and Feldman, 2003).

Materials and Methods

I examined 922 specimens from throughout the range of *C. atrox* from ten museums (AMNH, CAS, CM, KU, LACM, MVZ, SDNHM, UMMZ, USNM, UTA; museum symbolic codes follow Leviton et al., 1985) and from the personal collection of Travis J. LaDuc (TJL) of the University of Texas, Austin (Appendix I). Whenever possible, internal reproductive organs of all specimens were examined, or, when not possible, small mid-ventral sagittal incisions (1-2 cm) were made in the tails to determine gender of animals, as the retracted hemipenes appear as tendon-like structures in males (Klauber, 1972). Adults are defined as animals that have evidence of previous reproduction (females have opaque oviducts, enlarged follicles, or ovulation scars (corpus lutea), and males have tightly coiled and opaque efferent ducts, indicating the presence of sperm).

Samples were examined from throughout the range of *C. atrox* (Fig. 2), including the following regions: Sonoran Desert (422 specimens); Chihuahuan Desert/Trans Pecos area (234); the Southern Plains/Ozarks area in Texas, Oklahoma, and Arkansas (121); and the coastal plains of Texas and Mexico (141; See Appendix I). Of these 922 specimens, 659 were from the USA and 263 from Mexico; 444 were adult males, 229 were adult females, and 241 were juveniles (both males and females). Specimens also were categorized into three groups based on a molecular phylogeography (derived from the mitochondrial gene ND4) by Castoe et al. (2007; Fig. 1): Western ($N = 514$), Eastern ($N = 351$) and Central ($N = 55$; Fig. 2). Overall, the Western and Eastern groups match apparent clades from the phylogenies (Fig. 1), while the Central group is comprised of specimens from southeastern Arizona and southwestern New Mexico. This latter area has haplotypes from both Eastern and Western clades of *C. atrox* (Castoe et al., 2007). Specifically, the Western group consists of specimens in the western United States, including California; Arizona west of Cochise County; New Mexico west of and including Dona Ana County (except Hidalgo and Grant counties); western Texas (El Paso); and western Mexico (west of longitude 106º W), including the states of Durango, Chihuahua, Sinaloa, western Sonora, and islands in the Gulf of California (San Pedro Martir, Santa Cruz, Santa Maria, and Turner islands). An

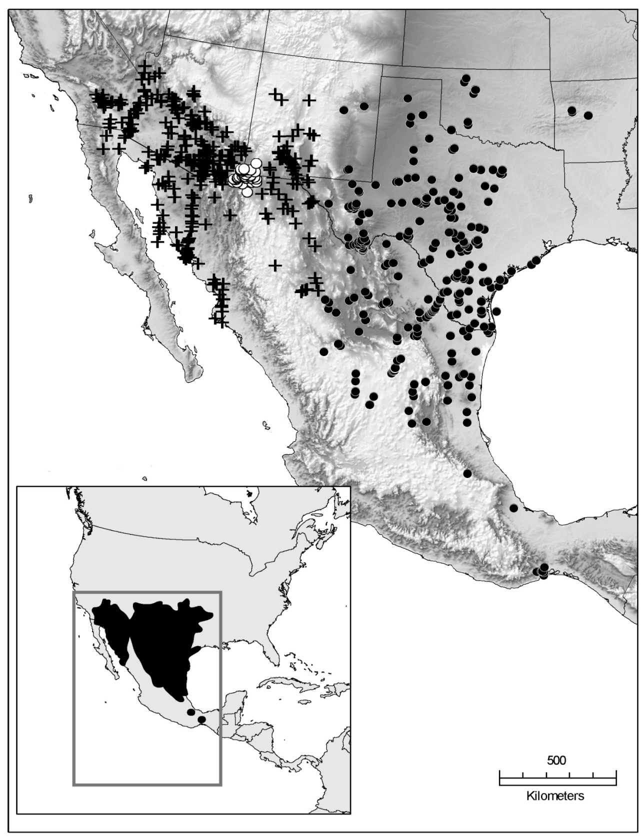

Figure 2. Location of 915 georeferenced specimens of *Crotalus atrox* used in this study. Black crosses represent the Western group, white circles represent the Central group and black circles represent the Eastern group. Inset shows North America with the geographic range of *C. atrox*, including two isolated populations in Tehuantepec (Oaxaca) and Veracruz, Mexico (from Castoe et al., 2007; Campbell and Lamar, 2004).

Table 1. Results of the first three component loadings for adult male Western Diamond-backed Rattlesnakes (*Crotalus atrox*) for all data, shown with the proportions of variance for each principal component. Large component loadings are bold and italicized. These three components account for 24% of the variation in the data.

Variable	PC1	PC2	PC3
Percentage of Total Variance	10.491	7.515	6.030
Eigenvalue	3.462	2.480	1.990
ROSTWIDTH	***0.488***	-0.368	0.248
ROSTHEIGHT	***0.585***	-0.295	0.119
HEADWD	***0.690***	-0.203	-0.383
HEADHT	***0.690***	-0.203	-0.383
HEADLENGTH	***0.639***	-0.297	0.127
TAILLENGTH	0.253	-0.381	-0.046
BASLRATLENG	***0.544***	-0.087	0.064
ROSTNO	-0.030	0.190	0.000
INTERCAN	0.269	0.166	0.155
BEFSUPRAOC	0.281	***0.534***	0.267
INTERSUPRA	0.277	0.349	0.214
INTERNASL	0.290	0.155	0.044
LOREALS	0.243	0.326	0.269
PREFOVEALS	0.267	***0.480***	-0.075
POSTFOVLS	0.200	0.353	0.116
SUBOCULARS	0.019	0.263	0.367
POSTOC	0.111	-0.086	0.316
INTEROCULAB	0.157	***0.542***	-0.214
INTERRICT	0.361	0.348	-0.223
POSTOCSTRIPE	0.253	-0.044	0.127
SUPRALAB	0.131	0.261	-0.235
INFRALAB	0.100	0.276	***-0.419***
DORSANT	0.137	0.237	0.085
DORSPOST	0.183	0.165	-0.320
PREVENT	0.049	0.202	***-0.397***
VENTRALS	-0.239	0.175	***-0.432***
RATFRING	0.372	0.041	0.022
CAUDALS	0.036	-0.036	-0.280
BODYBLOTCH	0.184	0.003	-0.277
PRENSLCONT	-0.143	-0.212	-0.039
POSTNSLCONT	0.200	0.353	0.116
INFRALABDIV	0.133	-0.285	-0.136
COLOR	0.281	0.131	0.291

Eastern Group consists of specimens from areas of Texas east of El Paso (east of longitude 106º W); New Mexico east of and including Otero County; all of Oklahoma and Arkansas; and the following states in Mexico: Coahuila, Hidalgo, Nuevo León, Querétero, Oaxaca, San Luis Potosí, Tamaulipas, Veracruz, and Zacatecas (Fig. 2). The Central group consists of specimens from Cochise County, Arizona, and Hidalgo and Grant counties, New Mexico.

All specimens were georeferenced (latitude and longitude determined) based on locality information from museum records or using a Garmin GPS 12 unit in the field (for UTA specimens collected by the author). Quadrat maps at 1:250,000 scale of Mexico (1979), DeLorme Atlas and Gazetteers of the United States (Arkansas, Arizona, California, New Mexico, Oklahoma, and Texas; 1999), and the Alexandria Digital Library Gazetteer Server (May 2003) were used to obtain latitude and longitude of collecting localities as listed in museum records. These sources all use a WGS84 (World Geodetic System 1984) datum.

Originally, 68 morphological characters, including meristic, mensural, and categorical (ordered state, dichotomous, and nominal scale) were taken for each specimen. Appendix II contains descriptions of characters and their abbreviations. These traits were reduced to 37 characters, as many were repetitive (right and left sides were counted on all meristic characters) and some showed no variation across specimens (numbers of canthal [CANTHAL], nasal [NASALS], supraocular [SUPRAOC], and preocular [PREOC] scales). In meristic traits with scales counts for right and left sides, all left counts were removed from analyses, except where no right counts were made, in which case left counts were used in place of right counts. The 37 characters used in all further analyses consisted of seven mensural traits, 26 meristic traits, and four categorical traits.

All specimens were analyzed in two separate groups: adult males ($N = 444$) and adult females ($N = 229$). Adults of *C. atrox* are known to be strongly sexually dimorphic (Boyer, 1957; Klauber, 1972; Beaupre et al., 1998), so males and females were analyzed separately. Juvenile measurements were not analyzed for this study, as juvenile mensural characters are often highly variable (Burbrink, 2001), and allometry of the snakes' measurements can change drastically from youth to adulthood (Beaupre et al., 1998). All analyses were performed in SYSTAT 8.0. All mensural (measurement) data were $\log_{10}$ transformed to linearize the data and reduce individual variation in size and its effect on the analysis (Thorpe and Leamy, 1983; Burbrink, 2001; Herrel et al., 2001). The transformed mensural data were then regressed against body size (represented by SVL) to account for differences in size among individuals and the residuals from the regressions were used in place of the original measurements in further analyses (Campbell and Smith, 2000; Burbrink, 2001; Herrel et al., 2001). I was investigating whether populations were different in the shape of various traits; therefore, using residuals allowed differences among mensural characters to refer only to relative size and shape and not to overall body size (Thorpe and Leamy, 1983; Sokal and Rohlf, 1995; Burbrink, 2001; Herrel et al., 2001). Reist (1985, 1986) found that a "univariate computation of residuals provides the best estimate of shape of characters in ectothermic vertebrates with continuous growth" (as quoted from Burbrink, 2001). Using residuals for the mensural traits also standardized them against a mean so they could be compared to other types of traits in the analyses, such as meristic and ordered-state characters.

Snout-vent length was removed from all further principal component analyses, as no residuals existed for SVL. Body size (as represented by SVL) was compared as a univariate variable among groups. All outliers from regressions were checked with original data to determine if they were incorrectly entered. All incorrectly entered data were rectified and any questionable data were removed. All data (categorical, meristic and mensural) were then standardized so they could be compared.

Principal components analysis (PCA) was chosen for analyzing the data because it can be used to reduce a large amount of data into a smaller set of composite variables which can then be used as a generalized phenotype in further analyses (McGarigal et al., 2000). Because PCA is an unconstrained ordination method, it could find the essential factors responsible for patterns without taking the group membership of the data into account. There were no independent or dependent variables; the analysis simple tries to determine the "gradients of maximum variation in the data set" (McGarigal et al., 2000).

Principal component analyses were originally performed on all data as three non-mutually exclusive partitions of traits for adult males and females separately. The first set of data consisted of all mensural, categorical, and meristic data. The second set consisted of all mensural and categorical data, and the third set consisted of meristic data alone. This followed closely the methodology of Burbrink (2001) and allowed individuals that were missing data in some traits to be included in some of the analyses examining regional differences. Results from PCA were similar for all three data partitions; therefore, only results from first data set using all character types will be presented hereafter.

The analysis for both adult males and females was run with the following 37 traits: number of rostral scales (ROSTNO); number of intercanthal scales (INTERCANTH); number of scales on the head before the supraoculars (BEFSUPRAOC); number of intersupraocular scales (INTERSUPRAOC); number of internasal scales (INTERNSLS); number of loreal scales (LOREALS); number of prefoveal scales (PREFOV); number of postfoveal scales (POSTFOV); number of lacunal scales (LACUNAL); number of subocular scales (SUBOC); number of postocular scales (POSTOC); number of interoculabials (INTEROCULAB); number of interrictals (INTERRICT); number of supralabial scales anterior to the rictus where postocular light stripe ends (POSTOCUSTRIPE); number of supralabial scales (SUPRALAB); number of infralabial scales (INFRALAB); number of gular scales (GULAR); number of mid-dorsal scales (DORSMID); number of anterior dorsal scales (DORSANT); number of posterior dorsal scales (DORSPOST); number of preventral scales (PREVEN); number of ventrals (VENTRALS); number of rattle fringe scales (RATFRINGE); number of caudal scales (CAUDALS); number of body blotches (BODYBLOTCH); number of dark tail rings (TAILRINGS); contact between the prenasal scale and the first supralabial scale (PRENASLCONT); contact between the postnasal scale and the upper preocular scale (POSTNASLCONT); number of infralabials divided (INFRALABDIV); overall color (COLOR); height of the rostral scale (ROSTHT); width of the rostral scale (ROSTWIDTH); length of the head (HEADLENGTH); height of the head (HEADHT); width of the head (HEADWD); length of the tail (TAILLENGTH); and length of the basal rattle (BASLRATLENGTH; Appendix II).

Table 2. Results of the first three component loadings for adult female *Crotalus atrox* for all data, shown with the proportions of variance for each principal component. Large component loadings are italicized. These three components account for 27% of the variation in the data.

Variable	PC1	PC2	PC3
Percentage of Total Variance	11.189	8.523	7.043
Eigenvalue	3.580	2.727	2.254
ROSTWIDTH	0.266	0.304	0.297
ROSTHEIGHT	0.303	0.343	***0.524***
HEADWD	0.249	0.322	***0.531***
HEADHT	0.037	0.094	***0.416***
HEADLENGTH	***0.382***	***0.485***	***0.437***
TAILLENGTH	-0.126	***0.449***	0.157
BASLRATLENG	0.164	0.283	0.262
INTERCAN	0.326	0.195	-0.354
BEFSUPRAOC	***0.690***	0.162	-0.432
INTERSUPRA	***0.566***	0.230	-0.391
INTERNASL	0.111	0.196	-0.072
LOREALS	***0.608***	0.148	-0.108
PREFOVEALS	***0.492***	-0.053	-0.012
POSTFOVLS	0.324	-0.120	-0.070
SUBOCULARS	0.170	0.031	-0.172
POSTOC	0.379	0.107	-0.123
INTEROCULAB	***0.417***	-0.336	0.046
INTERRICT	***0.470***	-0.354	0.230
POSTOCSTRIPE	0.222	0.133	-0.212
SUPRALAB	***0.421***	-0.184	-0.051
INFRALAB	0.289	***-0.511***	0.138
DORSMID	0.236	***-0.446***	***0.382***
DORSANT	0.300	-0.378	0.179
DORSPOST	0.197	-0.288	0.316
PREVENT	0.188	-0.208	-0.060
VENTRALS	0.068	***-0.641***	0.111
CAUDAL	-0.092	0.271	0.051
BODYBLOTCH	-0.086	-0.258	-0.188
TAILRINGS	0.284	0.013	-0.104
POSTNSLCONT	***0.568***	-0.028	-0.026
INFRALABDIV	-0.015	0.105	0.263
COLOR	0.115	0.315	-0.318

After running these analyses for males and females with all variables and examining the component loadings, all traits with principal component (PC) loading scores for PC 1-3 between 0.185 and –0.185 were removed from both analyses. This cut-off was chosen because all traits with component loadings in this range contributed very little to the analyses and showed no variability among groups. All traits with component loadings in this range were causing more noise in the data and taking away variance from traits with higher component loading scores, which were contributing to differences in phenotypic variance. Traits that do not load significantly on any components may be eliminated from a study if they do not contribute to the objectives of the study (Hair et al., 1977; McGarigal et al., 2000). Since the objectives of my study were to compare variability of traits among regions to see if there is clinal separation, those with low variability were not useful in my analyses and were, therefore, removed. For all further analyses, LACUNAL, GULAR, DORSMID, and TAILRINGS were removed for males and ROSTNO, LACUNAL, PRENASLCONT, GULAR, and RATFRINGE were removed for females.

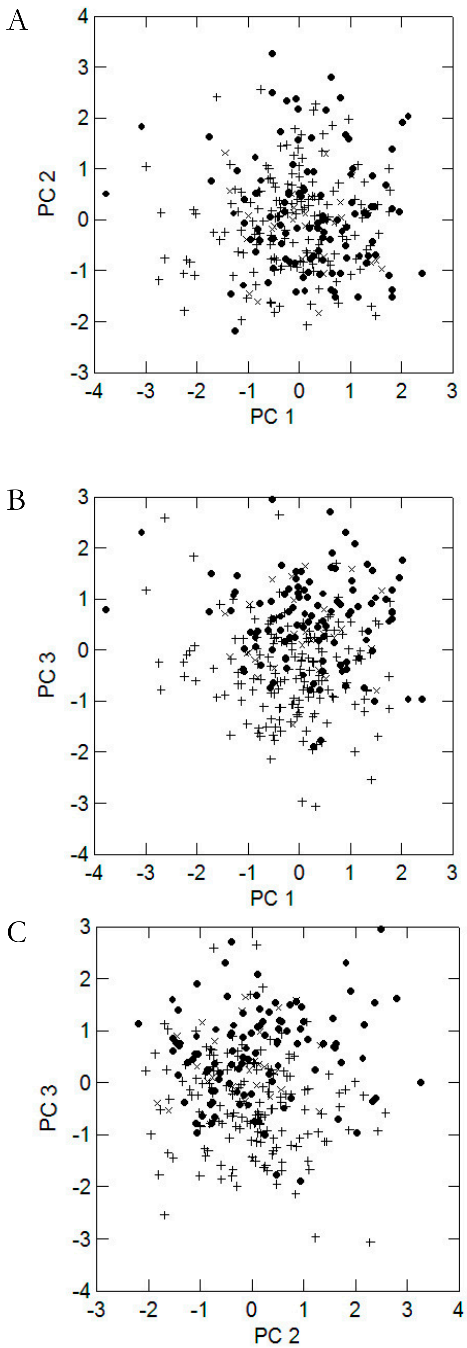

Figure 3. Multivariate plots of adult male data showing first three principal component axes. Specimens are shown by geographic location: Western group (+), Central group (X), and Eastern group (•). (**A**) Plot of first two principal component (PC) scores separated by group. (**B**) Plot of PC 3 and PC 1 scores separated by group. (**C**) Plot of PC 3 and PC 2 scores separated by group.

All PC factor scores with overall eigen values >1 were saved for all individuals, and these were plotted for examination, using group (Western, Eastern, Central) as a categorical variable. Principal component factor scores of all individuals were regressed against latitude and longitude, separately. Some univariate measurements (VENTRALS, Log (SVL), BEFSUPRAOC, BODYBOTCH, COLOR, TAILRINGS) were also regressed against latitude, longitude, and/or Log (SVL), to examine whether north-south or east-west clinal variation or correlations with body size exist.

Results

The first three component loading scores for all data from males (Table 1) and females (Table 2) are shown. Tables 3 and 4 provide average measurements, body size, and scale counts for adult males and females, respectively, for all three groups.

Principal component and regression analyses for adult males.—For males, the first three principal components accounted for 24 % of the variation in the data (Table 1). The traits with the largest component loadings in PC 1 for males were primarily mensural characters (Fig. 3A-B). This is very common in morphological analyses using ordination where differences in size have been accounted for, as much of the variance is often contained in these continuous measurements of size (Lestrel, 2000; Burbrink, 2001). Large loadings on PC 1 included BSLRATLENGTH, HEADHT, HEADWD, ROSTHT, ROSTWIDTH, and RATFRINGE, which are all positively correlated with each other and with PC 1. Principal component 2 had a number of large loading scores and most of these were scale counts, such as BEFSUPROC, INTEROCULAB, and PREFOV (Table 1). These were all positively correlated with each other and PC 2, whereas some mensural traits, such as TAILLENGTH, ROSTWIDTH, and ROSTHT, were negatively correlated with PC 2. Thus, as PC 2 gets larger, numbers of scales on the dorsal and lateral surfaces of the head increase and some mensural traits decrease. Plots of PC 1 and PC 2 (Fig. 3A) and PC 1 and PC 3 (Fig. 3B) did not show any clear separation of the three groups. The Eastern group appeared to be more spread out on the PC 1 axis and all of the variation of the Western and Central groups was contained within the dispersal of the Eastern group.

When comparing the plot of PC 2 and PC 3 (Fig. 3C) to the plots of PC 1 and PC 3 (Fig. 3B) and PC 1 and PC 2 (Fig. 3A), more differentiation between groups was obvious along the PC 3 axis. Principal component 3 separated the Eastern and Western groups more (Fig. 3B-C) than PC 1 or PC 2. The primary traits that contributed to PC 3 were VEN-

TRALS, INFRALAB, DORSPOST, BODYBLOTCH, and PREVEN (Table 1), which were negatively correlated with PC 3. Traits ROSTWIDTH, POSTOC, and SUBOC had the largest component loadings that were positively correlated with PC 3. When PC 3 was regressed against latitude and longitude, some clinal variation was apparent (Fig. 4A-B). The PC 3 factor scores decreased with increasing latitude northward (Fig. 4A; $R^2 = 0.082$, $F_{1,293} = 26.19$, $P < 0.0001$), and there was a correlation of higher PC 3 factor scores with decreasing longitude (Fig. 4B; $R^2 = 0.234$, $F_{1,293} = 89.47$, $P < 0.0001$). VENTRALS had the highest component loading score for PC 3 (Table 1). When numbers of ventral scales were regressed against longitude (Fig. 4C; $R^2 = 0.099$, $F_{1,430} = 47.15$, $P < 0.0001$), the number of ventral scales decreased from west to east. In contrast, snout-vent length for males seemed to show no clinal pattern with longitude, with a slope that was not significantly different from zero (figure not shown; $R^2 = 0.004$, $F_{1,431} = 1.78$, $P = 0.183$.). When log (SVL) was regressed against latitude for adult males, there was a positive correlation, with body size increasing northward (Fig. 4D; $R^2 = 0.041$, $F_{1,431} = 18.486$, $P < 0.0001$).

Principal component and regression analyses for adult females.—The PCAs for adult females were slightly different than those for adult males (Fig. 5), as there appeared to be much more variation in meristic traits contributing to variation of PC 1 (Table 2). One common feature between males and females was that the amount of variation in the Eastern group encompassed the variation in the other two groups in the PC plots (Fig. 5A-C).

The traits with the highest loadings for PC 1 were BEFSUPRAOC (number of scales before supraoculars, equivalent to the number of scales on the dorsal surface of the head), INTERSUPRAOC, LOREALS, PREFOV, INTERRICT, and SUPRALAB. Therefore, numbers of scales on the top and sides of the head are important and variable across individual adult females. CAUDALS, BODYBLOTCH, and INFRALABDIV (a dichotomous categorical variable designating whether first infralabials are divided) were negatively correlated with PC 1.

The plots of PC 1 and PC 2 (Fig. 5A), PC 1 and PC 3 (Fig. 5B), and PC 2 and PC 3 (Fig. 5C) for adult females suggested that PC 2 was the separating factor across Eastern, Western, and Central groups. For PC 1, the largest component loading scores were traits that determined dorsal and lateral head scale counts. For PC 2, the traits with the largest component loading scores were numbers of body scales (VENTRALS, INFRALAB, and DORSMID; Table 2). These three traits were negatively correlated with PC 2 and other mensural factors, such as ROSTHT, ROSTWIDTH, HEADLENGTH, and TAILLENGTH, which were positively correlated with PC 2. Thus, numbers of ventral scales in females were negatively correlated with body size factors (tail length, head length, etc.)

When number of ventral scales (VENTRALS; Fig. 6A; $R^2 = 0.102$, $F_{1,222} = 23.35$, $P < 0.0001$) and number of scales before supraoculars (BEFSUPRAOC; Fig. 6B; $R^2 = 0.124$,

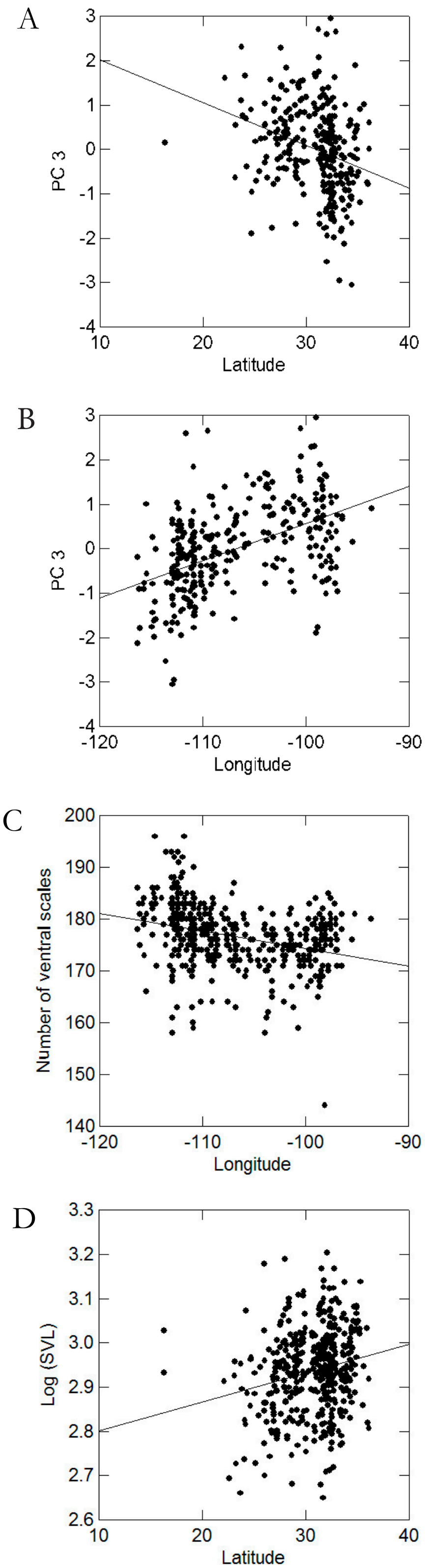

Figure 4. Relationship between various factors and latitude and longitude for adult males. (**A**) Regression of PC 3 scores vs. latitude: $R^2 = 0.082$, $F_{1,293} = 26.19$, $P < 0.0001$. (**B**) Regression of PC 3 scores vs. longitude: $R^2 = 0.234$, $F_{1,293} = 89.47$, $P < 0.0001$. (**C**) Regression of numbers of ventral scales vs. longitude: $R^2 = 0.099$, $F_{1,430} = 47.15$, $P < 0.0001$. (**D**) Regression of log (snout-vent length) vs. latitude: $R^2 = 0.041$, $F_{1,431} = 18.49$, $P < 0.0001$.

Table 3. Average scale counts, body size, and measurements for adult male *Crotalus atrox* from Western, Central, and Eastern groups (see Methods for group localities). Number of specimens (*N*), mean ± 1 SD of each character, and range of character values are reported for each group.

Variable	Western	Central	Eastern
ROSTWIDTH *N*	240	49	137
Mean ± SD	4.26 ± 0.67	4.40 ± 0.76	4.57 ± 0.94
Range	2.40-6.90	3.30-6.96	2.60-8.30
ROSTHEIGHT *N*	240	49	137
Mean ± SD	4.88 ± 0.81	4.96 ± 0.88	5.03 ± 1.03
Range	2.35-7.30	3.40-7.40	3.15-8.60
HEADWD *N*	220	45	132
Mean ± SD	27.62 ± 5.62	27.24 ± 6.29	28.95 ± 7.19
Range	16.10-45.50	18.70-45.65	14.95-54.40
HEADHT *N*	211	46	123
Mean ± SD	13.22 ± 2.74	13.50 ± 3.25	13.63 ± 3.60
Range	7.80-24.50	8.45-22.25	7.20-24.20
HEADLENGTH *N*	232	47	136
Mean ± SD	38.72 ± 6.22	39.19 ± 7.38	40.89 ± 9.03
Range	24.65-59.95	25.80-55.95	22.15-67.40
TAILLENGTH *N*	244	49	140
Mean ± SD	70.57 ± 15.19	71.32 ± 15.58	73.50 ± 20.66
Range	33-128	40.00-102.50	32.00-143.00
BASLRATLENG *N*	235	46	133
Mean ± SD	13.81 ± 2.07	13.55 ± 2.36	14.15 ± 2.70
Range	7.65-20.10	9.40-19.80	7.45-21.60
SVL *N*	244	50	143
Mean ± SD	879.95 ± 171.93	881.38 ± 203.66	904.10 ± 229.41
Range	446.00-1474.00	511.00-1380.00	457.00-1601.00
ROSTNO *N*	245	49	141
Mean ± SD	1.01 ± 0.09	1.00 ± 0	1.01 ± 0.08
Range	1-2	1	1-2
CANTHAL *N*	245	49	141
Mean ± SD	2.00 ± 0	2.00 ± 0	2.00 ± 0
Range	2	2	2
INTERCAN *N*	245	49	140
Mean ± SD	2.55 ± 0.74	2.71 ± 0.74	2.59 ± 0.94
Range	1-5	2-4	1-9
SUPRAOC *N*	245	49	141
Mean ± SD	1.00 ± 0	1.00 ± 0	1.00 ± 0
Range	1	1	1
BEFSUPRAOC *N*	243	48	140
Mean ± SD	17.23 ± 4.10	17.94 ± 3.94	18.87 ± 4.39
Range	7-32	9-28	8-31
INTERSUPRA *N*	244	48	140
Mean ± SD	4.81 ± 1.03	4.69 ± 0.88	5.014 ± 1.13
Range	3-7	3-6	2-8
NASALS *N*	245	49	141
Mean ± SD	2.00 ± 0	2.02 ± 0.143	2.01 ± 0.08
Range	2	2-3	2-3
INTERNASL *N*	245	49	141
Mean ± SD	0.96 ± 0.22	1.00 ± 0	1.00 ± 0
Range	0-2	1	1
LOREALS *N*	243	48	140
Mean ± SD	1.09 ± 0.42	1.23 ± 0.43	1.26 ± 0.51
Range	0-2	1-2	0-3
PREFOVEALS *N*	242	47	140
Mean ± SD	7.04 ± 1.75	7.34 ± 1.46	6.79 ± 1.66
Range	2-13	4-10	3-11
POSTFOVLS *N*	240	47	140
Mean ± SD	4.26 ± 0.88	4.55 ± 1.00	4.31 ± 0.88
Range	2-8	2-7	3-8
LACUNALS *N*	240	47	140
Mean ± SD	2.01 ± 0.14	2.02 ± 0.15	2.02 ± 0.15
Range	1-3	2-3	2-3
PREOCULARS *N*	241	48	141
Mean ± SD	2.00 ± 0.06	2.02 ± 0.14	2.00 ± 0
Range	2-3	2-3	2

SUBOCULARS *N*	241	49	141
Mean ± SD	3.17 ± 0.46	3.31 ± 0.65	3.44 ± 0.59
Range	2-4	2-5	2-5
POSTOC *N*	242	48	140
Mean ± SD	2.42 ± 0.57	2.56 ± 0.65	2.63 ± 0.57
Range	1-4	2-5	2-4
INTEROCULAB *N*	242	48	140
Mean ± SD	2.34 ± 0.50	2.23 ± 0.47	2.44 ± 0.58
Range	1-4	1-3	1-4
INTERRICT *N*	232	44	133
Mean ± SD	29.72 ± 2.46	28.77 ± 1.83	29.57 ± 2.07
Range	22-40	23-32	23-36
POSTOCSTRIPE *N*	205	41	130
Mean ± SD	1.12 ± 0.52	1.32 ± 0.61	1.57 ± 0.68
Range	0-4	0-2	0-3
SUPRALAB *N*	238	49	143
Mean ± SD	15.19 ± 1.00	15.37 ± 0.81	15.36 ± 1.07
Range	13-18	14-18	13-19
INFRALAB *N*	239	48	141
Mean ± SD	16.66 ± 1.11	16.33 ± 1.04	1.23 ± 0.43
Range	11-19	13-18	1-2
GULARS *N*	243	49	141
Mean ± SD	6.72 ± 1.14	6.55 ± 0.96	6.60 ± 1.04
Range	4-13	4-10	4-9
DORSMID *N*	245	49	142
Mean ± SD	25.31 ± 1.22	24.80 ± 1.19	25.06 ± 1.20
Range	21-32	22-28	21-29
DORSANT *N*	246	49	141
Mean ± SD	28.41 ± 2.80	27.92 ± 2.61	29.50 ± 3.25
Range	22-41	23-35	21-41
DORSPOST *N*	246	49	142
Mean ± SD	20.69 ± 1.53	20.33 ± 1.30	20.50 ± 1.83
Range	15-30	17-23	15-31
PREVENT *N*	248	49	141
Mean ± SD	3.69 ± 1.03	3.31 ± 0.92	3.44 ± 0.90
Range	1-8	1-5	1-6
VENTRALS *N*	245	49	142
Mean ± SD	178.36 ± 6.31	175.04 ± 3.90	174.84 ± 5.76
Range	158-196	164-184	144-195
RATFRING *N*	239	48	138
Mean ± SD	12.63 ± 1.41	12.71 ± 1.18	12.62 ± 1.35
Range	10-18	11-16	10-17
CAUDALS *N*	247	48	140
Mean ± SD	24.22 ± 2.43	24.17 ± 1.71	24.35 ± 2.20
Range	10-29	21-29	16-29
BODYBLOTCH *N*	244	45	139
Mean ± SD	34.55 ± 3.16	33.93 ± 3.37	33.78 ± 2.60
Range	16-43	25-43	25-40
TAILRINGS *N*	247	49	140
Mean ± SD	4.74 ± 0.84	4.45 ± 0.87	4.91 ± 0.98
Range	3-7	2-6	3-7
RATTLENO *N*	244	46	135
Mean ± SD	7.05 ± 3.13	6.30 ± 2.96	6.87 ± 2.37
Range	0-28	1-13	2-13
PRENSLCONT *N*	242	48	141
Mean ± SD	1.87 ± 0.34	1.90 ± 0.31	1.91 ± 0.84
Range	1-2	1-2	1-2
POSTNSLCONT *N*	242	48	140
Mean ± SD	1.26 ± 0.68	1.34 ± 0.64	1.55 ± 0.84
Range	1-5	1-4	1-5
INFRALABDIV *N*	241	48	141
Mean ± SD	1.39 ± 0.49	1.38 ± 0.49	1.23 ± 0.43
Range	1-2	1-2	1-2
COLOR *N*	244	49	142
Mean ± SD	2.01 ± 0.60	1.94 ± 0.63	2.39 ± 0.66
Range	1-3	1-3	1-3
BUTPRES *N*	245	47	136
Mean ± SD	1.25 ± 0.44	1.36 ± 1.07	1.40 ± 0.49
Range	1-2	1-2	1-2

$F_{1,219}$ = 30.94, P < 0.0001) were regressed against longitude, an interesting clinal pattern was apparent for females. Number of ventral scales in females (Fig. 6A) decreased eastward, as in males (Fig. 4C), whereas number of scales before supraoculars (a possible analog to head size if scale size is fixed) increased eastward (Fig. 6B). These two traits (VENTRALS, BEFSUPRAOC) appeared to be negatively correlated with each other (Table 2).

Body size (log (SVL)) did not significantly correlate with longitude (Fig. 6C; R^2 = 0.004, $F_{1,224}$ = 0.91, P = 0.341). But, as seen in males, there was a significant regression of female body size (log (SVL)) against latitude, with a slight increase in body size northward (R2 = 0.022, $F_{1,223}$ = 4.95, P = 0.027). Finally, the largest component loading score for PC 1 was BEFSUPRAOC, and PC 1 increased eastward (Fig. 6D; R^2 = 0.108, $F_{1,175}$ = 21.18, P < 0.001), just as BEFSUPRAOC did (Fig. 6B).

Principal component 2, which was negatively correlated with number of ventral scales, increased eastward (Fig. 7A; R^2 = 0.180, $F_{1,175}$ = 38.29, P < 0.0001). Plots of PC 1 (Fig. 6D) and PC 2 (Fig. 7A) accounted for more variation (11% and 18%, respectively) regressed against longitude than the univariate traits alone (VENTRALS, SVL, and BEFSUPRAOC; Fig. 6A-C).

Principal component 2 decreased with increasing latitude (Fig. 7B; R^2 = 0.083, $F_{1,175}$ = 15.90, P < 0.0001). Thus, PC 2, which was negatively correlated with number of ventral scales and positively correlated with many mensural traits, decreased northward for adult females. This slope of the regression for PC 2 vs. latitude accounted for only 8% of the variation in values, whereas the slope of PC 2 vs. longitude accounted for 18%. Therefore, longitude accounts for more variation in these traits.

Color pattern trends for males and females.—Color pattern (in terms of COLOR, BODYBLOTCH, and TAILRINGS) showed some variation across males and females (Tables 3-4). In males, COLOR (from light to medium to dark) increased significantly with body size (log (SVL); R^2 = 0.020, $F_{1,427}$ = 8.56, P = 0.0036). Thus, males were darker with larger body sizes (Table 3). Body size slightly increased northward in males (Fig. 4D; R^2 = 0.041, $F_{1,431}$ = 18.49, P < 0.0001), but COLOR did not significantly increase with latitude (R^2 = 0.0041, $F_{1,427}$ = 1.78, P = 0.183) in males. Instead, COLOR in males was significantly correlated with longitude (R^2 = 0.087, $F_{1,427}$ = 40.88, P < 0.0001).

Females showed a similar color pattern variation to males, with COLOR positively correlated with body size (so females are darker in color when they are larger; R^2 = 0.049, $F_{1,221}$ = 11.36, P = 0.0009). Body size in females also significantly increased northward (R^2 = 0.022, $F_{1,223}$ = 4.95, P = 0.0272). COLOR did not significantly correlate with latitude (R^2 = 0.003, $F_{1,221}$ = 0.68, P = 0.412), but significantly increased eastward, as in males (R^2 = 0.112, $F_{1,221}$ = 27.99, P < 0.0001).

Number of body blotches in males decreased significantly eastward (as longitude increased; R^2 = 0.015, $F_{1,420}$ = 6.30, P = 0.0125), but this relationship was not significant in females (R^2 = 0.010, $F_{1,221}$ = 3.37, P = 0.0675). Likewise, there was not a significant relationship between male number of body blotches or female number of body blotches and latitude (male: R^2 = 0.009, $F_{1,420}$ = 3.67, P = 0.057; female: R^2 = 0.007, $F_{1,221}$ = 1.59, P = 0.209).

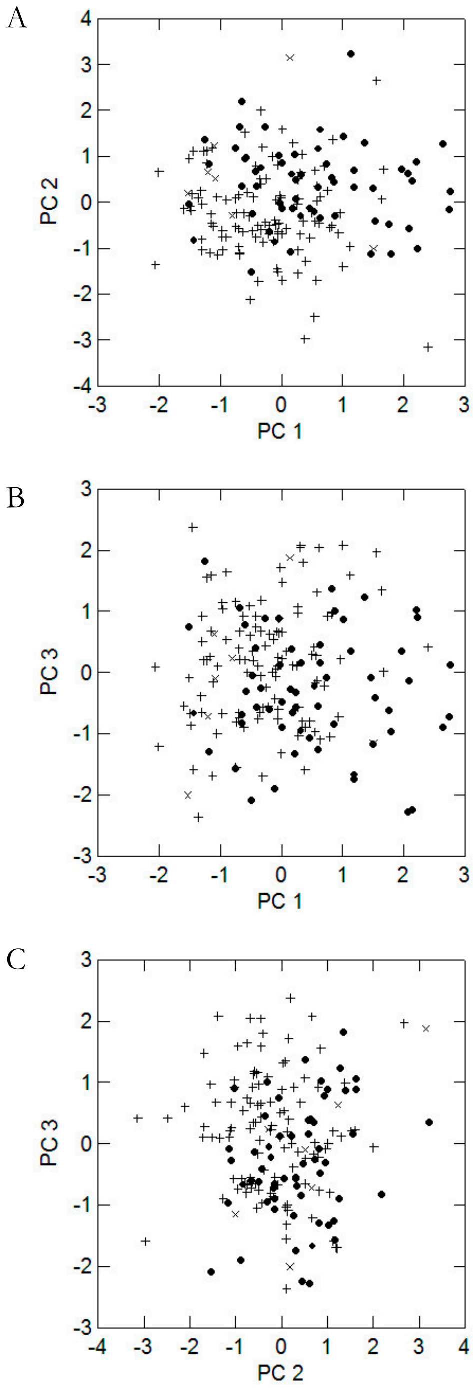

Figure 5. Multivariate plots of adult female data showing first three principal component axes. Specimens are shown by geographic location: Western group (+), Central group (X), and Eastern group (•). (**A**) Plot of first two principal component (PC) scores separated by group. (**B**) Plot of PC 3 and PC 1 scores separated by group. (**C**) Plot of PC 3 and PC 2 scores separated by group.

Previously, number of tail rings were removed from the analysis after the first PC was run for males, as this trait exhibited very little variation among individuals. Following this pattern, number of tail rings had no significant correlation with longitude in males ($R^2 = 0.008$, $F_{1,428} = 3.24$, $P = 0.072$) or females ($R^2 = 0.013$, $F_{1,221} = 2.83$, $P = 0.094$), and this trait showed little geographic variation, with ranges for males from 3-7 (average 4.45-4.91) and females from 2-9 (average 3.57-4.00) throughout their range (Table 3-4).

Discussion

Clinal patterns in meristic characters.—Many vertebrates in North America exhibit splits in their distribution patterns, resulting in distinct eastern and western populations or sister species, such as Cyprinodon fishes (Minckley et al., 1986), the Yellow Mud Turtle (*Kinosternon flavescens*; Serb et al., 2001), horned lizards (*Phrynosoma* spp.; Reeder and Montanucci, 2001), many colubrid snake species (Stebbins, 1985), the Lyre Snake (*Trimorphodon biscutatus*; LaDuc and Johnson, 2003), the Western Rattlesnake (*C. oreganus*/*C. viridis*; Ashton and de Queiroz, 2001), the scaled quail complex (*Callipepla* spp.; Zink and Blackwell, 1998), and pocket mice (*Perognathus* and *Chaetodipus* spp.; Riddle, 1995). In the western part of North America, east and west regions are separated by the Continental Divide, and this geological feature may represent a substantial barrier to gene flow (Morafka, 1977).

Morafka's vicariant model of North American deserts (1977) states that eastern and western populations of many herpetofaunal species should form two groups, with separation between Chihuahuan and Sonoran Desert. *Crotalus atrox* displays this pattern in its intraspecific molecular phylogeny (Castoe et al. 2007), although this is less clear in morphological differences among groups.

Crotalus atrox exhibits clinal geographic variation in some scale counts along an east/west continuum. Pfrender et al. (1998) stated that reptiles with large ranges, especially snakes and turtles, often show an east-to-west orientation, instead of north-to-south. They hypothesized that the duration of winter may be the limiting factor in keeping taxa with large ranges from dispersing northward (Pfrender et al., 1998). As *C. atrox* is a species with a very large range that shows east-to-west variation, temperature and length of winter may be limiting its range size also.

Factors that are important in separating out clinal variation in *C. atrox* are meristic values, especially number of ventral scales or segmental counts. Western *C. atrox* have higher ventral and caudal counts for males than eastern snakes. This conclusion fits the original observation by Klauber (1930) that *C. atrox* in Arizona had the highest numbers of ventral scales compared to Oklahoma, Texas, and Sonora, Mexico populations. Boyer (1953) also concluded that there was an east-to-west trend in scale number variation, with greater ventral, dorsal, caudal, and infralabial scale numbers in the west when comparing his Oklahoma snakes to Klauber's 1930 results.

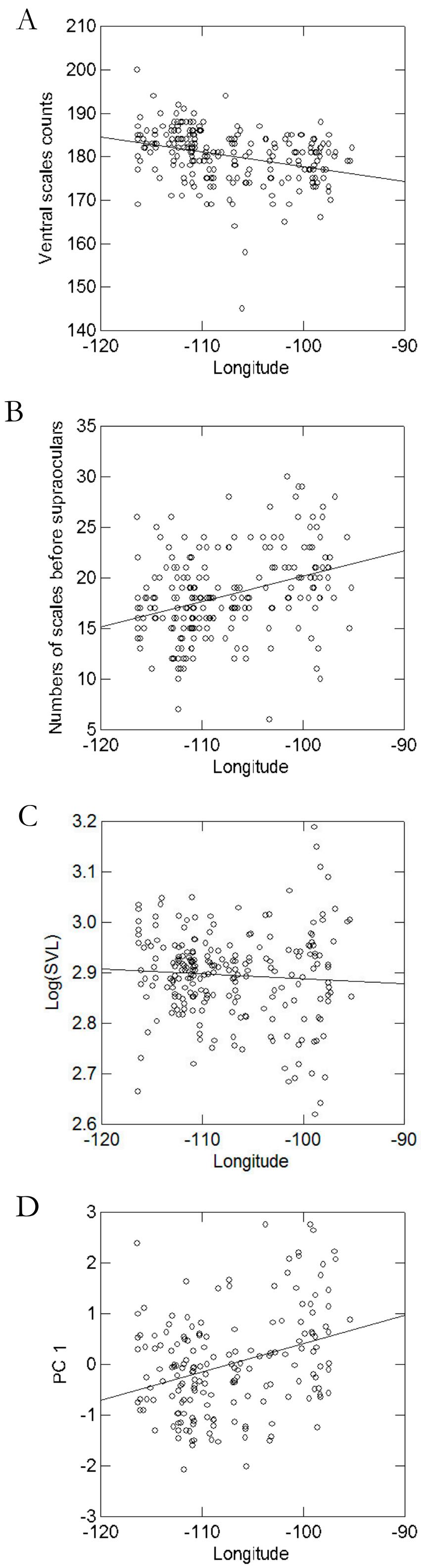

Figure 6. Relationship between various factors and longitude for adult females. (**A**) Regression of number of ventral scales vs. longitude: $R^2 = 0.102$, $F_{1,222} = 23.35$, $P < 0.0001$. (**B**) Regression of BEFSUPRAOC (Scales before supraoculars) vs. longitude: $R^2 = 0.124$, $F_{1,219} = 30.94$, $P < 0.0001$. (**C**) Plot of log 10 (SVL) vs. longitude: $R^2 = 0.004$, $F_{1,224} = 0.91$, $P = 0.341$. (**D**) Regression of PC 1 vs. longitude: $R^2 = 0.108$, $F_{1,175} = 21.18$, $P < 0.001$.

Table 4. Average scale counts, body size, and measurements for adult female *Crotalus atrox* from Western, Central, and Eastern groups (see Methods for group localities). Number of specimens (*N*), mean ± 1 SD of each character, and range of character values are reported for each group.

Variable	Western	Central	Eastern
ROSTWIDTH *N*	140	9	69
Mean ± SD	3.98 ± 0.53	4.02 ± 0.74	4.07 ± 0.76
Range	2.90-5.40	3.10-5.60	2.65-6.80
ROSTHEIGHT *N*	140	9	69
Mean ± SD	4.40 ± 0.60	4.58 ± 0.67	4.52 ± 0.93
Range	2.90-6.30	4.00-6.20	2.75-7.00
HEADWD *N*	134	9	67
Mean ± SD	24.92 ± 4.30	26.15 ± 6.10	25.89 ± 6.68
Range	16.20-37.50	19.25-35.65	16.10-45.80
HEADHT *N*	129	8	67
Mean ± SD	12.11 ± 2.17	12.59 ± 1.91	11.93 ± 3.43
Range	7.40-18.80	9.10-15.30	6.35-21.20
HEADLENGTH *N*	136	9	68
Mean ± SD	34.91 ± 4.51	37.84 ± 5.48	36.85 ± 8.27
Range	22.40-47.60	28.00-47.70	22.50-62.20
TAILLENGTH *N*	143	10	72
Mean ± SD	49.94 ± 8.49	53.30 ± 11.14	48.74 ± 11.27
Range	28-82	41-76	27-84
BASLRATLENG *N*	138	9	71
Mean ± SD	12.58 ± 1.71	13.38 ± 1.25	12.69 ± 2.51
Range	6.55-16.75	11.40-15.80	6.80-19.70
SVL *N*	142	11	74
Mean ± SD	797.58 ± 124.17	845.36 ± 125.87	801.58 ± 217.06
Range	462.00-1120.00	583.00-1028.00	416.00-1546.00
ROSTNO *N*	143	9	72
Mean ± SD	1.00 ± 0	1.11 ± 0.33	1.00 ± 0
Range	1	1-2	1
CANTHAL *N*	143	9	72
Mean ± SD	2.00 ± 0	2.00 ± 0	2.00 ± 0
Range	2	2	2
INTERCAN *N*	143	9	71
Mean ± SD	2.47 ± 0.75	2.57 ± 0.53	2.87 ± 0.89
Range	1-6	2-3	1-5
SUPRAOC *N*	143	9	71
Mean ± SD	1.00 ± 0	1.00 ± 0	1.00 ± 0
Range	0	0	1
BEFSUPRAOC *N*	142	9	71
Mean ± SD	17.22 ± 3.64	18.00 ± 2.18	20.61 ± 4.52
Range	7-28	16-23	6-30
INTERSUPRA *N*	141	9	71
Mean ± SD	4.33 ± 1.01	4.33 ± 0.87	5.06 ± 1.03
Range	0-7	3-6	3-7
NASALS *N*	142	9	70
Mean ± SD	2.01 ± 0.08	2.00 ± 0	2.00 ± 0
Range	2-3	2	2
INTERNASL *N*	142	9	71
Mean ± SD	0.95 ± 0.22	1.00 ± 0	2.00 ± 0
Range	0-1	1	2
LOREALS *N*	139	9	71
Mean ± SD	1.27 ± 0.51	1.11 ± 0.78	1.47 ± 0.63
Range	0-3	0-2	0-3
PREFOVEALS *N*	139	9	71
Mean ± SD	7.07 ± 1.71	7.33 ± 1.94	7.31 ± 1.58
Range	1-13	5-11	4-12
POSTFOVLS *N*	138	9	70
Mean ± SD	4.51 ± 0.92	5.11 ± 1.97	4.14 ± 1.03
Range	2-8	4-10	3-9
LACUNALS *N*	138	9	70
Mean ± SD	2.03 ± 0.21	2.00 ± 0	2.00 ± 0.17
Range	2-4	2	1-3
PREOCULARS *N*	138	9	70
Mean ± SD	2.00 ± 0	2.00 ± 0	2.00 ± 0
Range	2	2	2

SUBOCULARS *N*	138	9	70
Mean ± SD	3.16 ± 0.50	3.33 ± 0.71	3.39 ± 0.60
Range	2-4	2-4	2-5
POSTOC *N*	138	9	70
Mean ± SD	2.38 ± 0.53	2.11 ± 0.33	2.77 ± 0.66
Range	1-3	2-3	2-6
INTEROCULAB *N*	138	9	70
Mean ± SD	2.37 ± 0.53	2.33 ± 0.50	2.57 ± 0.55
Range	1-4	2-3	2-4
INTERRICT *N*	135	9	69
Mean ± SD	28.61 ± 2.33	27.22 ± 1.72	29.33 ± 2.27
Range	20-35	24-30	25-34
POSTOCSTRIPE *N*	126	9	65
Mean ± SD	1.20 ± 0.62	1.22 ± 0.67	1.62 ± 0.63
Range	0-3	0-2	0-3
SUPRALAB *N*	140	9	70
Mean ± SD	15.25 ± 0.85	15.44 ± 0.73	15.53 ± 1.11
Range	13-17	14-16	13-19
INFRALAB *N*	140	9	70
Mean ± SD	16.54 ± 1.16	16.00 ± 1.12	16.30 ± 1.05
Range	14-20	14-18	13-19
GULARS *N*	141	9	71
Mean ± SD	6.79 ± 1.11	7.11 ± 0.93	6.58 ± 0.94
Range	3-10	6-9	4-8
DORSMID *N*	144	9	73
Mean ± SD	24.88 ± 1.29	23.78 ± 0.97	24.75 ± 0.93
Range	21-28	23-25	23-27
DORSANT *N*	144	9	73
Mean ± SD	28.19 ± 2.89	27.11 ± 1.17	28.50 ± 2.90
Range	20-38	25-29	23-36
DORSPOST *N*	144	9	72
Mean ± SD	20.56 ± 1.27	19.67 ± 1.23	20.19 ± 1.47
Range	17-24	18-21	16-24
PREVENT *N*	144	9	73
Mean ± SD	3.61 ± 0.95	3.33 ± 0.71	3.58 ± 0.90
Range	1-6	2-4	2-6
VENTRALS *N*	143	9	73
Mean ± SD	181.24 ± 6.86	177.44 ± 3.25	178.77 ± 4.88
Range	145-200	173-181	165-188
RATFRING *N*	139	8	71
Mean ± SD	12.76 ± 1.87	12.25 ± 0.89	12.56 ± 1.53
Range	10-22	11-13	10-21
CAUDALS *N*	143	9	72
Mean ± SD	19.15 ± 1.85	19.00 ± 2.60	12.56 ± 1.53
Range	12-27	17-25	14-26
BODYBLOTCH *N*	142	9	73
Mean ± SD	34.09 ± 3.14	34.22 ± 2.77	33.88 ± 2.68
Range	23-46	28-37	29-43
TAILRINGS *N*	143	9	72
Mean ± SD	3.75 ± 0.76	3.57 ± 0.88	4.00 ± 1.09
Range	2-6	2-5	2-9
RATTLENO *N*	144	9	72
Mean ± SD	6.72 ± 2.69	7.22 ± 2.22	6.38 ± 2.42
Range	1-13	3-10	1-13
PRENSLCONT *N*	139	9	69
Mean ± SD	1.76 ± 0.43	1.78 ± 0.44	1.84 ± 0.37
Range	1-2	1-2	1-2
POSTNSLCONT *N*	139	9	70
Mean ± SD	1.39 ± 0.65	1.22 ± 0.67	1.54 ± 0.65
Range	1-4	0-2	1-4
INFRALABDIV *N*	138	9	71
Mean ± SD	1.38 ± 0.49	1.33 ± 0.50	1.21 ± 0.41
Range	1-2	1-2	1-2
COLOR *N*	143	9	73
Mean ± SD	2.04 ± 0.60	1.89 ± 0.33	2.47 ± 0.65
Range	1-3	1-2	1-3
BUTPRES *N*	144	9	72
Mean ± SD	1.31 ± 0.47	1.00 ± 0	1.49 ± 0.50
Range	1-2	1	1-2

Klauber (1941) found a similar east-west pattern of ventral scale variation in 11 species of southern California snakes, as did Cross (1979). These species included *Arizona elegans, Chionactis occipitalis, Crotalus ruber, Hypsiglena ochrorhynchus, Lampropeltis getula, Leptotyphlops humilis, Pituophis catenifer, Salvadora grahamiae, Rhinocheilus lecontei, Tantilla eiseni,* and *Trimorphodon vandenburghi*. These snakes inhabited both coastal and desert zones, and numbers of ventral scales (which correspond to vertebral number) were significantly higher in all desert populations, which are east of the coastal areas. Both authors thought that higher numbers of ventral scales were correlated with a snake's ability to move on sand.

Crotalus atrox in southeastern California, southwestern Nevada, and northwestern Arizona has higher numbers of ventral scales compared to other regions, with the highest being 200 scales (see average values in Tables 3 and 4). This is the driest and hottest part of the range of *C. atrox*, where it intersects with the western shore of the Colorado River and into Joshua Tree National Park. Substrate and temperatures could affect the ventral counts, as it appears to have done in the other aforementioned snakes (Klauber, 1941; Cross, 1979).

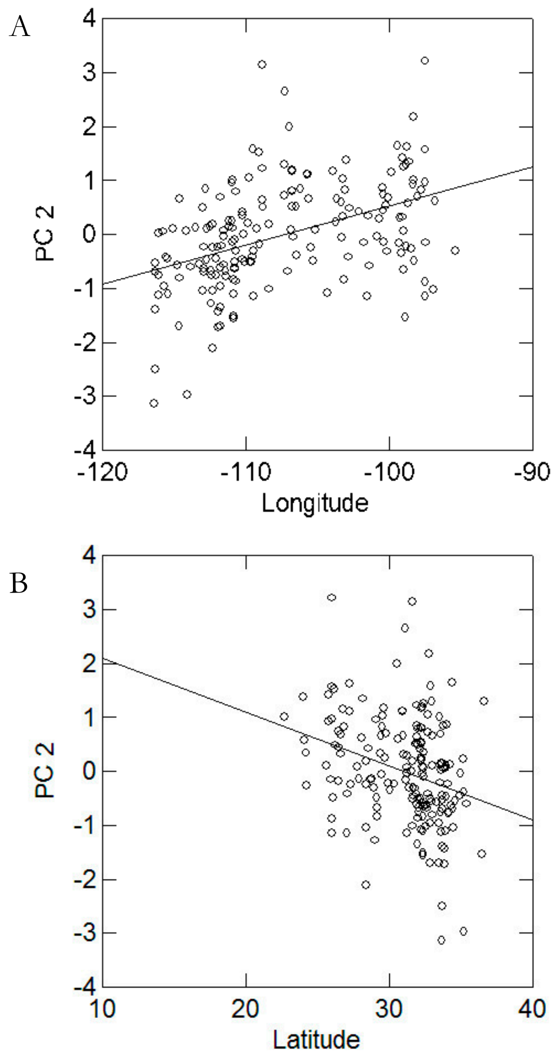

Figure 7. Regression of PC 2 with latitude and longitude for adult females. (**A**) Regression of PC 2 vs. longitude: $R^2 = 0.180$, $F_{1,175} = 38.29$, $P < 0.0001$. (**B**) Regression of PC 2 vs. latitude: $R^2 = 0.083$, $F_{1,175} = 15.90$, $P < 0.0001$.

Higher vertebral numbers (corresponding to number of ventral scales) in the western part of the range of *C. atrox* may be related to selection on movement over sandy soil compared to the rocky or vegetation-covered soil of their more eastern counterparts. Shine (2000) proposed a number of selection advantages to having higher vertebral numbers, including natural selection resulting in increased crawling speed, selection in females for larger size to allow higher fecundity, and sexual selection acting on males to have large trunk sizes. Kelley et al. (1997) found that *Thamnophis elegans* coastal populations had lower vertebral numbers vs. inland populations and that those with lower body vertebral numbers moved faster in habitats with more vegetation or rocks (call "push-points" in their study). They also found that snakes with more vertebrae are more flexible and could achieve greater lateral bending than snakes with fewer vertebrae (Kelley et al., 1997), which supports the idea that higher vertebral numbers in *C. atrox* may benefit moving on sandy soil with fewer "push-points."

Among group versus within group variation of trait.—A common feature throughout the analyses is that the amount of variation in the Eastern group seems to encompasses the variation in the other two groups, as seen in the principal components analyses (Figs. 3 and 5). Allsteadt et al. (2006) found similar variation in *Crotalus horridus*, which previously had been split into a number of subspecies. All groups (southern, northern and western) exhibited extensive overlap in patterns of coloration and in the canonical analysis of meristic data. Thus, Allsteadt et al. (2006) concluded that the intergradation and variation seen were so great, with strong clinal variation, that *C. horridus* must represent a single widespread species. *Crotalus atrox* displays similar clinal variation with overlapping variation among groups, and is also considered a single, widespread species. Castoe et al.'s (2007) results suggest that there has been recent expansion from west to east, which could explain the overlap of the Eastern group of *C. atrox* with the Western and Central groups. Thus, the eastern population could contain a large amount of recent influx of variation from the western populations.

Morphometrics, body size variation, and Bergmann's rule.—In general, mensural characters (or shape of mensural characters) for adult males or females do not distinguish the three regional groups (Eastern, Central and Western), but there does seem to be clinal variation in some morphometric traits, such as body size along a latitudinal gradient. This is apparent when examining the regressions of body size (SVL) vs. latitude for males (Fig. 4D) and body size (SVL) vs. latitude for females. Moreover, there is a significant trend for body size to increase northward in adult males (Fig. 4D, $R^2 = 0.041$, $P < 0.0001$) and adult females ($R^2 = 0.022$, $P = 0.027$).

Ashton and colleagues investigated body size variation along a latitudinal gradient in a number of different vertebrates (Ashton et al., 2000; Ashton, 2001; Ashton and Feldman, 2003). Although Bergmann's rule (larger animals in colder climates) was originally applied only to endotherms, a number of recent studies have examined this ecogeographic rule in ectotherms (e.g., preceding references; Van Voorhies, 1996; Partridge and Coyne, 1997; Arnett and Gotelli, 1999). In their studies of tetrapods, Ashton and Feldman (2003) found that some North American tetrapods follow Bergmann's rule (mammals, turtles) while others reverse it (snakes, lizards), all following a north/south trend in body size variation. Plausible reasons for this phenomenon have included colder temperature increasing growth (Van Voorhies, 1996; Atkinson and Sibly, 1997) and, conversely, lower resource availability decreasing growth (Arnett and Gotelli, 1999).

In *C. atrox*, adult males and females have larger body sizes in higher latitudes (Fig. 4D), following Bergmann's rule. Ashton (2001) found that *C. viridis* follows Bergmann's rule and was larger at higher latitudes, but *C. oreganus* does not follow Bergmann's rule and is smaller in northern areas. He attributed these differences between closely related taxa to differences in duration of hibernation. *Crotalus viridis* occurs in colder environments and hibernates longer, whereas *C. oreganus* occurs in warmer environments and hibernates for less time.

Color pattern variation.—Body color of both male and female *C. atrox* specimens becomes darker with larger body size. Although body size tends to increase in the northern part of the range, color does not significantly increase with increasing latitude. However, adults of both sexes become darker eastward. This pattern may follow Gloger's rule, which states that endotherms (most notably birds) are darker in more humid environments (Zink and Remsen, 1986; Burtt and Ichida, 2004). For birds and mammals, this pattern expresses itself as darker animals in the tropics, near the southern parts of their range for North American species (Burtt and Ichida, 2004). But for *C. atrox*, the eastern parts of the range encompass the Ozarks of Arkansas and the Southern and Tamaulipan Plains of eastern Mexico, central and eastern Texas, and Oklahoma. These areas are much more humid than the dryer, western parts of the range, in the Chihuahuan and Sonoran Deserts of west Texas, Arizona, southeastern California, and Mexico. Eastern areas also have a very different kind of habitat, with mixed woodland and outcrops, compared to desert scrub and desert grasslands in the west. Thus, habitat type could also be affecting the darker colors found in the eastern part of the range. Klauber (1930) also saw darker individuals in his eastern populations, with Texas and Oklahoma snakes being darker compared to western populations in Sonora and Arizona. In the present study, *C. atrox* males had increasing numbers of blotches eastward, but females did not.

Sexual dimorphism was found in tail ring patterns of *C. atrox* from Oklahoma for other studies (Boyer, 1957; Quinn, 1979), and was seen here with males having higher numbers of tail rings than females (Table 3). Otherwise, this character showed no significant geographic variation throughout its range, varying so little that it was removed from the principal component analysis for males.

The literature reports a number of rare color patterns in *C. atrox*, including exceptionally dark individuals from Pedro Armendariz lava fields in Socorro and Sierra Counties, New Mexico (Best and James, 1984), and other aberrant individuals from central Texas (Gloyd, 1958; Yancey et al., 1997), including some with extremely pale coloration and few blotches, or blotches that have transformed into longitudinal stripes (Yancey et al., 1997). These seem to be accounts of variation within populations without any clear clinal variation, although in the case of the *C. atrox* from lava fields, this is clearly substrate matching. Similar variation is known from many other squamates, including extremely pale lizards in White Sands, New Mexico, and melanistic *Sceloporus undulatus* in the Carrizozo lava fields of New Mexico (Rosenblum et al., 2004).

Conclusions and further questions.—*Crotalus atrox* may truly be considered a widespread species with a large geographic range. It does not seem to vary in any discernible pattern for most morphometric, meristic, and categorical traits across its range. Most differences are seen across an east-to-west continuum, except body size, which varied along a north/south transect. Yet, even with the moderate amounts of phenotypic variation seen across groups in *C. atrox*, there is more variation within these groups. This is in contrast to a number of studies on various vertebrate taxa, which show hidden patterns of vicariance and cryptic species across this same continuum, including horned lizards (Reeder and Montanucci, 2001), Lyre Snakes (LaDuc and Johnson, 2003), and pocket mice (Riddle, 1995), among others. Morafka (1977) hypothesized that the region around the continental divide at the border of Arizona and New Mexico, near the Animas, Peloncillos, and Chiricahua Ranges, is a barrier (termed the "Cochise Filter Barrier") to mixing between populations on either side of these mountain ranges. However, *C. atrox* shows intergradation of their mitochondrial genes (Castoe et al., 2007), with a mix of haplotypes from both the Eastern and Western groups in this exact region.

What drives geographic variation in morphology and color pattern in *C. atrox* on such a large geographic scale? Predictive modeling in a GIS (geographical information systems) framework may provide insights into the relationships between morphology (e.g., numbers of ventral scales, number of head scales before the supraoculars, body size, color) and important environmental variables (e.g., humidity, temperature, precipitation, seasonality, and elevation). In addition, contrasting or exploring the ecological niches in present vs. past climates will help predict areas where populations of *C. atrox* were during the last glacial maxima and why they show introgression in some areas today. Integrating molecular (Castoe et al., 2007) and morphological variation in *C. atrox* with GIS will help elucidate the factors causing these biogeographic patterns that we see today.

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Appendix I
Specimens of *Crotalus atrox* Examined

MEXICO: Baja California Norte: (MVZ 10728-29 adult males, SDNHM 17051 juvenile female, USNM 53064 adult male, USNM 53065 adult female). **Chihuahua**: (AMNH 85264 adult male, AMNH 138251 juvenile male, AMNH 138252 adult male, CM 59816 juvenile male, CM 59817 adult female, CM 59818 adult male, CM 59819 juvenile male, CM 59820 adult female, CM 59821 juvenile male, CM 59822 adult female, CM 59825 adult female, CM 59826 adult male, CM 59827 adult female, CM 59828-29 adult males, CM 59847-48 adult males, CM 59853 adult male, CM 59854 adult female, CM 61788 adult male, CM S-6369 adult female, KU 47336 adult male, MVZ 24391 juvenile male, MVZ 46688 adult female, MVZ 56321 juvenile male, MVZ 56979 adult male, MVZ 71309 adult female, USNM 263 adult male, USNM 46475 adult male, USNM 104614 adult male, USNM 106419-20 adult females, USNM 104622-23 adult males, USNM 104624-25 adult females, USNM 238307 adult female, USNM 257938 adult male). **Coahuila**: (AMNH 67036 adult female, AMNH 88821 adult male, AMNH 93668 juvenile female, AMNH 150123 adult female, AMNH 150124-25 adult males, AMNH 150126 juvenile male, CAS 91815 adult male, CM 42843 adult male, CM 42844 adult male, CM 48159-61 juvenile males, CM 48263 juvenile female, CM 51198 adult male, CM 51263 juvenile male, CM 59832 juvenile female, KU 28150 adult male, KU 28151 juvenile female, KU 338583 adult male, KU 33851 adult male, KU 38332 adult female, KU 38333 juvenile male, KU 39570 juvenile female, SDNHM 6572 adult male, SDNHM 60473 juvenile male, USNM 241537-38 adult males, USNM 241539 juvenile male). **Durango**: (AMNH 68343 juvenile female, CM 59823 juvenile, CM 59824 adult male, CM 59839 adult male). **Hidalgo**: (UTA 12566). **Nuevo León**: (AMNH 150128 adult female, AMNH 150129-30 adult males, AMNH 150131-32 adult females, AMNM 62277 juvenile male, AMNH 63819 adult male, AMNH 74539 adult male, AMNH 86005 adult female, CM 53966 juvenile, CM 53967 juvenile female, CM 59851 adult male, KU 128807 male juvenile, KU 128808 juvenile female, KU 128809 adult female, LACM 66943 juvenile male, MVZ 36741-42 adult males, UMMZ 75864 adult male, UTA 8810 adult male, UTA 8811 juvenile male). **Oaxaca**: (AMNH 65887 juvenile female, AMNH 88825 juvenile male, UMMZ 82747 juvenile female, UMMZ 82748 adult female, UMMZ 82749 juvenile male, UMMZ 82750 juvenile female, UMMZ 82751 adult, UMMZ 82752 adult male, UMMZ 114590 juvenile male). **San Luis Potosí**: (AMNH 10737 juvenile male, AMNH 87998 adult male, CM 59850 adult male, KU 67737 juvenile female, UMMZ 122124 juvenile male, UMMZ 126182 adult male). **Sinaloa**: (CAS-SUR 24092 adult female, KU 67738 adult male, KU 69938 adult female, KU 83417 juvenile male, KU 83418 female juvenile). **Sonora**: (AMNH 69669 adult female, AMNH 73781 adult male, CAS 14364 adult female, CAS 19354 adult female, CAS 53241-43 adult males, CAS 103468 adult female, CAS-SUR 10034 adult male, CAS-SUR 14029 adult female, CAS-SUR 14362 juvenile male, CAS-SUR 14363 adult male, CAS-SUR 14365 adult female, CAS-SUR 14366 adult male, CM 25225 adult male, KU 23771 adult male, KU 43565-66 adult males, KU 45335 adult male, KU 45336 adult female, KU 45337 juvenile female, KU 45338 adult male, KU 78962 adult male, LACM 7194 adult male, LACM 7195 juvenile female, LACM 7196 juvenile male, LACM 9163 adult male, LACM 9164, LACM 9165 juvenile male, LACM 9166 adult male, LACM 25177 juvenile male, LACM 104422 adult male, LACM 104423 adult female, LACM 104424 adult male, LACM 104425 juvenile female, LACM 104426 adult male, LACM 104427 juvenile male, LACM 104428 adult male, LACM 104429 adult female, LACM 104430 adult male, LACM 104431 adult male, LACM 104432 juvenile female, LACM 104433 adult male, LACM 104434 adult female, LACM 104435 juvenile female, LACM 104436 juvenile male, LACM 104437 adult female, LACM 104438 juvenile female, LACM 104439 adult female, LACM 104440-42 adult males, LACM 104443 juvenile male, LACM 104444 juvenile female, LACM 104445 adult female, LACM 104446 juvenile male, LACM 135477 adult male, MVZ 10171-72 adult males, MVZ 21033-34 adult males, MVZ 26167 juvenile male, MVZ 37803 adult male, MVZ 50843 adult male, MVZ 50844 adult female, MVZ 76403-04 adult males, MVZ 80030 adult male, SDNHM 2328-29 adult females, SDNHM 2330 adult male, SDNHM 2770 adult female, SDNHM 3176 adult male, SDNHM 21957 adult male, SDNHM 35911 adult male, SDNHM 42800 adult male, SDNHM 44344-46 adult males, SDNHM 44347 adult female, SDNHM 44348-49 adult males, SDNHM 46091 adult male, SDNHM 48021-22 adult females, SDNHM 48024 adult female, SDNHM 49646 adult female, UMMZ 78447 adult female, UMMZ 78448 adult male, UMMZ 113047 adult male, UMMZ 114119 adult male, UMMZ 128005 adult female, USNM 21045-46 adult males, USNM 21824 adult male, USNM 222065 adult female, USNM 222066-67 adult males, USNM 222068 adult female, USNM 222069-70 adult males, USNM 238289-90 juvenile males, USNM 240695 adult female, USNM 248158-59 adult males, USNM 248219 male juvenile, UTA 17829 adult male). **Tamaulipas**: (AMNH 73588 adult male, AMNH 93436 adult male, AMNH 150120 adult male, AMNH 150121 adult female, CAS 141898 juvenile, KU 61296 adult female, KU 61297 adult male, KU 61298 adult female, KU 68119 adult male, MVZ 36743 adult female, MVZ 36744 adult male, SDNHM 6574 adult female, UMMZ 101269 adult male, UMMZ 119434 adult male, UMMZ 124753 adult male, USNM 37577, USNM 110607-09 adult males, UTA 8812). **Veracruz**: (KU 24129 juvenile female, USNM 46474 adult female). **Zacatecas**: (AMNH 98850 adult female, AMNH 98854 adult female, AMNH 98855 female juvenile, AMNH 98856 juvenile male, AMNH 118069 adult male, AMNH 118070 juvenile female, AMNH 118550 juvenile male, AMNH 150122 adult male, CAS 59833 adult male, CAS 59849 adult male, CAS 59855 adult female, CAS 89769 juvenile, MVZ 143534 adult female).

USA: Arkansas: Perry Co.: (USNM 118513 juvenile male). Polk Co.: (KU 84389 adult male). Yell Co.: (KU 69434 juvenile male). **Arizona**: Cochise Co.: (AMNH 75473 adult male, AMNH 91627 adult female, AMNH 107532 adult male, AMNH 115625 juvenile male, CAS 12705 adult male, CAS 81462 adult female, CAS 12715 adult male, CAS 100131 juvenile female, CAS 141800 juvenile male, CAS 170450 juvenile female, CAS 192777 male juvenile, CAS 129779 male juvenile, CAS 192778 juvenile female, CAS 192781 adult male, CAS 195857 juvenile male, CAS 195858 adult male, CM 40180 adult female, CM 40420 adult female, CM 48519 adult male, CM 66067 juvenile male, CM 67032-33 adult males, CM 69867 female juvenile, CM 69871 juvenile, CM 70640-41 adult males, CM 83664 juvenile male, MVZ 209122 male, MVZ 226241, MVZ 229780, MVZ 229781 adult, MVZ 229782 adult female, MVZ 229785 adult male, SDNHM 2771 juvenile female, SDNHM 34452 juvenile female, SDNHM 40895 juvenile male, UMMZ 69738 adult female, UMMZ 69739 adult male, UMMZ 71330-31 adult males, UMMZ 114096 adult male, USNM 14742-43 adult males, USNM 218682 adult female, USNM 226659 adult female, USNM 246584 adult female, USNM 246585 adult male, USNM 246586 juvenile male, UTA 17316 juvenile male, UTA 26526 juvenile male). Gila Co.: (CAS 192785 adult female, CM 51549 juvenile, CM 51550 juvenile male, CM 51829 adult female, CM 51910 juvenile female, CM 51911 adult female, SDNHM 9919 adult male, UMMZ 64901 adult male, UMMZ 64902-03 adult females, UMMZ 64904 adult males, UMMZ 68464 adult males). Graham Co.: (CAS 87412 juvenile female, CM 48678 juvenile male, CM 48743 adult male, CM 70669 adult female, CM 71203 adult female, CM 71204 adult male, CM 71255 adult female, CM 71362 adult female, CM 71370 adult male, CM 71375 adult male, SDNHM 34451 adult male, USNM 51757-58 adult males, USNM 51759 juvenile male). Greenlee Co.: (CAS 192792 juvenile male, CAS 192793 adult male, CM 71233 adult male, CM 71631 adult male). La Paz Co.: (CAS 91625 adult female, USNM 253064 adult female). Maricopa Co.: (AMNH 99318 adult female, CAS 17532-33 adult female, CAS 17534 adult male, CAS 17537 juvenile female, CAS 17538 adult male, CAS 20813 juvenile female, CAS 65086 adult male, CAS 65698 adult male, CAS 80673 adult male, CM 19827 juvenile, CM 53735 juvenile female, CM 54015 adult female, CM 68471 adult male, SDNHM 2706 adult male, SDNHM 2769 adult female, SDNHM 2777 juvenile male, SDNHM 3235 adult male, SDNHM 3295 adult male, SDNHM 9344-45 adult males, SDNHM 17627 adult female, SDNHM 20883 adult female, SDNHM 22409 adult male, SDNHM 23062-63 adult female, SDNHM 23939 adult male, SDNHM 23940-41 adult females, UMMZ 224274-5 adult males, UMMZ 70342 adult female, UMMZ 70346 adult male, UMMZ 79309 adult male, USNM 129422 adult male, USNM 246587-88 juvenile males, USNM 246589 juvenile female, USNM 246594 adult male, USNM 246597 adult male). Mojave Co.: (CAS 62980 adult female, UMMZ 59835 adult female, UTA 50692 juvenile male). Pima Co.: (AMNH 26028-29 adult females, AMNH 26030-31,33 adult males, AMNH 26043 adult male, AMNH 26045 adult female, AMNH 26048-49 adult males, AMNH 26050 adult female, AMNH 26053 adult female, AMNH 26054 adult female, AMNH 26062 adult male, AMNH 26066 adult female, AMNM 26067 adult male, AMNH 62736 adult male, AMNH 64345 juvenile female, AMNM 67248 adult female, AMNH 127858 adult male, CAS 34265 adult male, CAS 34266 adult female, CAS 34267-69 adult males, CAS 34270 adult female, CAS 34271 adult male, CAS 34272-73 adult males, CAS 35297 adult male, CAS 80734 juvenile female, CAS 80735 juvenile male, CAS 92463 adult male, CAS 100129 adult male, CAS 152532-34 adult males, CAS 192786 adult female, CAS 192787-88 juvenile male, CAS 192789 female adult, CAS-SUR 1708, CAS-SUR 1712, CAS-SUR 10342 adult male, CM 19284 adult female, CM 21319 adult female, CM 47771 adult male, CM 53817 adult female, CM 53858 juvenile male, CM 67018 juvenile male, CM 67023 adult male, CM 67035 adult male, CM S-4444 adult male, LACM 145646 juvenile female, MVZ 6723 adult female, MVZ 7959 adult male, MVZ 10744 adult male, MVZ 22409 adult male, MVZ 74284 adult male, MVZ 74285-86 adult females, MVZ 76669 adult male, MVZ 78059 juvenile male, MVZ 78060 adult male, MVZ 180260 juvenile male, MVZ 196871 adult male, MVZ 206949 adult male, MVZ 206950 adult female, MVZ 206951 adult male, MVZ 209123 adult male, MVZ 229872, UMMZ 69740, UMMZ 224276 juvenile male, USNM 56687 male juvenile, USNM 167731 adult male, USNM 246602 adult female, USNM 246919 adult male, UTA 14461 juvenile female, UTA 19408 adult male, UTA 32350 juvenile female). Pinal Co.: (AMNH 26046 adult female, USNM 246590 juvenile male, USNM 246591 juvenile female, USNM 246592 female juvenile, USNM 246593 male juvenile, USNM 246603 adult male, USNM 246604 male juvenile, UTA 32351 adult male). Santa Cruz Co.: (CAS 192790-91 adult male, UMMZ 75801 adult male, UMMZ 224277 adult female, USNM 474 adult male, USNM 4713 adult female). Yavapai Co.: (AMNH 68472 adult male, AMNH 70866 adult female, AMNH 70867 adult male, CAS 63879-80 adult males, CAS 63889-92 adult males, CAS 65085 adult male, CAS 65091-92 adult males, CAS 65112 adult male, CAS 65113 adult female, CAS 65114 adult male, CAS 65696-97 adult males, CAS 65969-72 adult males, CAS 65973 adult female, CAS 156188 adult male, CM 67020-21 adult males, CM 67024 adult female, CM 67025-27 adult males, CM 67028-30 adult males, CM 67034 adult female, CM 67036 adult female, CM 67037 adult male, CM 67038 juvenile male, CM 67039 juvenile, CM 67040 adult female, CM 67041 female juvenile, CM 69444 female juvenile, SDNHM 2136 adult male, USNM 253063 juvenile male). Yuma Co.: (AMNH 64346 juvenile male, CAS 33656 adult male, CM 67022 adult male, UMMZ 152749 adult male, USNM 467 adult male, USNM 469 juvenile male, USNM 21825 adult male). Unknown locality in AZ: (CM 71898 adult female). **California**: Imperial Co.: (CAS 208531 adult male, CAS-SUR 7233 adult female, KU 55637 adult male, LACM 27976 adult male, LACM 36613 adult female, LACM 37838 adult female, LACM 36614 adult female, LACM 116539 male juvenile, MVZ 1004 adult male, MVZ 1005 adult female, MVZ 1830 juvenile male, USNM 0476-77 juvenile males-Paratypes, USNM 22046 adult female, USNM 44302 adult male, USNM 56282 adult male, USNM 222785 adult female). Riverside Co.: (AMNH 58979 adult female, AMNH 60549 adult female, AMNH 63817 adult female, AMNH 63818 adult female, CAS 43244 juvenile female, CAS 63939 juvenile male, CAS 71345-46 adult females, KU 84557-58 adult females, LACM 3015 adult male, LACM 3016 male, LACM 20180 juvenile male, LACM 20181 adult male, LACM 20182 juvenile female, LACM 20183 adult female, LACM 20184 juvenile female, LACM 27977 juvenile male, LACM 104380 adult female, LACM 104381 juvenile female, LACM 104388 juvenile male, LACM 104389-90 adult males, LACM 104391 adult female, LACM 104392 adult male, LACM 104393 adult female, LACM 104394-95 juvenile female, LACM 104396 adult male, LACM 104397-98 juvenile female, LACM 104400 adult male, MVZ 405 adult male, MVZ 407 adult female, MVZ 443 juvenile male, MVZ 1835 adult female, MVZ 40916 juvenile male, MVZ 44689 juvenile female, MVZ 61011 adult female, UMMZ 96877 adult). San Bernardino Co.: (LACM 104399 adult male, MVZ 180355 male juvenile). **Nevada**: Clark Co. :(CAS 19917 adult male, MVZ 16692 adult male, MVZ 16693 juvenile male, MVZ 36148 adult female). **New Mexico**: Bernalillo Co.: (adult female). Cibola Co.: (UMMZ 86633 adult male). Doña Ana Co.: (CAS 100130 juvenile female, CM 18324 adult male, CM 58975 adult male, CM 60568 adult male, CM 65921 juvenile female, CM 65964 adult female, CM 65966 adult male, CM 65967 juvenile female, CM 67217 adult female, CM 58979 adult male, CM 60567 adult male, CM 65943 adult male, CM 65948 juvenile male, CM 67013 adult male, LACM 134011 adult female, LACM 134012-14 adult males, LACM 134015-16 adult females, LACM 134017 adult male, LACM 134018 adult female, LACM 134019 adult male, LACM 134020 male juvenile, LACM 134021 adult female, LACM 134022-24 adult males, LACM 134025 adult female, MVZ 134124 adult male, USNM 102265 adult female, UTA 25110 adult male). Eddy Co.: (UMMZ 122979 adult male, UMMZ 122980 adult female, USNM 307979 juvenile female). Grant Co.: (AMNH 81793 adult male, AMNH 99855 adult male, AMNH 131297 juvenile female). Guadalupe Co.: (USNM 32731 juvenile male). Hidalgo: (AMNH 57464 adult female, AMNH 67244 juvenile male, AMNH 74871 adult male, AMNH 75257 adult female, AMNH 77612 adult male, AMNH 76222 adult, AMNH 80038 adult male, AMNH 80158 adult male, AMNH 81792 adult male, AMNH 90405 adult male, AMNH 99319 adult female, AMNH 123913 adult male, CM 18341 adult female, CM 18342 adult male, CM 69863 adult female, CM 70633 adult male, CM 18338 adult male, LACM 134852 adult female, MVZ 70344 adult male, MVZ 209131 adult male, MVZ 225562 adult male, MVZ 229786 adult male, MVZ 229787 adult female, USNM 320316 adult male). Lincoln Co.: (MVZ 16417 adult male). Luna Co.: (CM 107292 adult male, UMMZ 74127 adult male, USNM 80076 juvenile male, USNM 320315 adult male). Otero Co.: (AMNH 4119 adult male, CAS 204102 adult male). Quay Co.: (UMMZ 68465 adult female). Sierra Co.: (CM 31354 adult male, CM 48826 adult female, CM 51355 juvenile male, CM 51356 adult female, CM 58967 adult male, MVZ 24852 female juvenile, USNM 320317 adult male). Socorro Co.: (CM 67031 adult female, MVZ 180336 juvenile male, MVZ 180337 adult female, UTA 25656 adult male). Valencia Co.: (MVZ 20566 adult male). **Oklahoma**: Blaine Co.: (CM 44630 adult male, CM 91667 adult male, KU 19484 adult male). Comanche Co.: (UMMZ 77128 adult male, UMMZ 77565 adult female, USNM 313384 adult male). Jackson Co.: (UMMZ 86543 adult female). Major Co.: (UMMZ 81337 adult female). Woods Co.: (UMMZ 95620 adult female). **Texas**: Aransas Co.: (UMMZ 69732-34 adult males, UMMZ 116277 adult male, UTA 5146 juvenile female). Armstrong Co.: (CAS-SUR 10396 adult female). Atascosa Co.: (UTA 22348 juvenile male). Baylor Co.: (UTA 10304 juvenile male, UTA 36739 juvenile female). Bell Co.: (KU 72934 adult male). Bexar Co.: (AMNH 7421 adult, AMNH 14153 juvenile female, AMNH 17082 juvenile female, AMNH 17800 juvenile male, CAS 31113 adult male, KU 84411-13 juvenile males, UMMZ 79306 adult male, USNM 4224 juvenile, USNM 56686 juvenile female, USNM 79288a juvenile female, USNM 798288b male juvenile, USNM 157312 adult male, USNM 160859 juvenile female, USNM 163629 adult male, USNM 313386 adult male). Bosque Co.: (KU 175575 adult male). Brazoria Co.: (UMMZ 116251 adult female). Brewster Co.: (AMNH 62985 adult female, AMNH 73559-60 adult males, AMNH 101372 adult female, AMNH

112245 male juvenile, CAS 192794 juvenile male, CM 67014 adult male, CM 67015 adult female, KU 206359 juvenile male, MVZ 147989 adult male, UMMZ 66042 adult male, UMMZ 66043 juvenile female, UMMZ 66925-27 adult males, UMMZ 69741 adult male, UMMZ 72093 juvenile female, UMMZ 72094 adult female, UMMZ 92763 adult male, UMMZ 92766 adult male, UMMZ 96874 adult male, UMMZ 114347 adult female, UMMZ 114348 adult male, UMMZ 114349 adult female, USNM 218938 juvenile male). Briscoe Co.: (UTA 15632 adult male). Brooks Co.: (CM 13618). Brown Co.: (AMNH 66077 adult male, AMNH 66650 juvenile female). Calhoun Co.: (USNM 255 adult male-Paratype, USNM 7760 adult male-Paratype, USNM 7761 adult male-Holotype). Cameron Co.: (AMNH 17032 adult female, AMNH 17033 adult male, AMNH 17036 adult female, AMNH 17037 adult male, AMNH 17038 adult female, AMNH 17040-41 adult females, CAS 13171 adult male, CAS 13173 adult male, UMMZ 54017a-b juvenile males, UMMZ 54017c-f juvenile females, USNM 52282-3 juvenile males, USNM 56684 juvenile female, USNM 56685 juvenile male, USNM 238855 juvenile male, USNM 238856 juvenile female, UTA 36743 adult female, CM R-388 adult female). Coke Co.: (KU 84403 adult female). Comal Co.: (AMNH 64797 juvenile female, UMMZ 71328 adult male, UMMZ 71329 adult female, UMMZ 72541-42 adult males, UMMZ 72543 adult female, USNM 313385 adult male, USNM 100632 juvenile female). Concho Co.: (KU 84395 juvenile female, UMMZ 55313 juvenile male). Cottle Co.: (CAS-SUR 10418 adult female). Crosby Co.: (UTA 33704 juvenile female). Dallas Co.: (UTA 57 juvenile female, UTA 1030 adult male, UTA 17060 adult male, UTA 28777 adult male, UTA 28779 adult female, UTA 28780 adult male). Eastland Co.: (KU 1671-72 adult males, KU 1673 adult female, KU 1679 adult female, KU 1680 adult male, KU 1681 adult female, KU 216077 adult male). El Paso Co.: (CM 57849 adult male, CM 57852 adult female, CM S-6374 adult female). Garza Co.: (CLS 576 adult female). Hidalgo Co.: (LACM 136373, USNM 82295 adult female). Hill Co.: (UTA 36740 adult female). Howard Co.: (CAS-SUR 9892 adult female). Hudspeth Co.: (USNM 147899 juvenile female, UTA 2882 juvenile male). Hutchinson Co.: (CM 67019 adult male). Irion Co.: (KU 84405 adult female, TJL 876 adult female). Jeff Davis Co.: (CM 57854 juvenile male, CM 57855 adult male, UMMZ 49958 juvenile female, UMMZ 49960 adult male). Jim Hogg Co.: (CAS 13933 juvenile female, UMMZ 69735 adult female). Kendall Co.: (USNM 27058 juvenile female). Kenedy Co.: (AMNH 98857 adult female, AMNH 98858 female, AMNH 117972 adult male, MVZ 68468 adult male). Kerr Co.: (MVZ 33947 adult male, USNM 157313 juvenile male, USNM 26379 adult female). LaSalle Co.: (UTA 16700 adult male). Martin Co.: (KU 84397 juvenile female, USNM 19792 adult male). Mason Co.: (UMMZ 70347 adult male). Matagorda Co.: (UMMZ 103262 adult female, UMMZ 116276 adult female). Maverick Co.: (AMNH 93376 adult female, MVZ 128168 adult male, USNM 1301 juvenile, USNM 32728 adult male). McCulloch Co.: (KU 84396 adult male, UTA 1328 adult female, UTA 2051 adult female, UTA 36744 female juvenile). McMullen Co.: (CM 67017 adult female, KU 145978 juvenile female, TJL 948 adult male, UTA 16616 adult male, UTA 17188 adult male, UTA 17205 adult female, UTA 18515 juvenile female). Medina Co.: (MVZ 52386 adult female). Mitchell Co.: (UTA 526 juvenile male). Motley Co.: (CAS-SUR 10417 adult female). Nolan Co.: (CM 144745 adult female). Nueces Co.: (AMNH 4115 adult male, USNM 32734-36 juvenile males). Palo Pinto Co.: (AMNH 64123 adult male, CM 24966 adult female, KU 84391 adult male, KU 84393 adult male, KU 84408 adult male, UTA 30725 adult male). Pecos Co.: (CAS-SUR 9780 adult female). Presidio Co.: (CM 67016 adult male, KU 189228 adult male). Reeves Co.: (CM 49016 adult male, CM 49020 adult male, KU 74706 adult female, KU 74707 adult male, UMMZ 79305 adult male, UMMZ 92764 juvenile female, UMMZ 96875 juvenile female). Runnels Co.: (KU 84404 juvenile female). San Patricio Co.: (SDNHM 9432 adult male, USNM 307980 adult male, UTA 5145 adult male). Starr Co.: (KU 222560 adult male, UTA 18516 adult female). Sutton Co.: (KU 84407 juvenile male). Tarrant Co.: (CM S-8665 juvenile male). Tom Green Co.: (KU 84394 juvenile male, KU 84398 juvenile male, KU 84399 juvenile female, KU 84400-01 juvenile males, KU 84402 juvenile female, KU 84406 juvenile female, KU 84409 adult male, KU 84414 adult female, MVZ 38217 adult male, KU 206360-61 adult males). Travis Co.: (MVZ 128106 juvenile male, MVZ 128107 juvenile female). Upton Co.: (AMNH 88409 adult male). Uvalde Co.: (USNM 32730 adult male, USNM 32737 juvenile male, UTA 32342 juvenile male). Val Verde Co.: (CM 115819 juvenile male, KU 174960 adult male, KU 206358 juvenile male, USNM 32733 adult male, MVZ 139392 juvenile male, USNM 32736-37 adult males, USNM 218939 adult male). Webb Co.: (AMNH 9334 juvenile female, KU 145979 adult male, KU 84390 adult male, KU 84415 adult male, MVZ 129361 juvenile female, USNM 321531-32 juvenile females, USNM 321541 adult male, UTA 17123 juvenile male). Winkler Co.: (UTA 36738 adult female). Unknown locality in Texas: (CM R-1396 adult male, CM S-6185 juvenile male, SDNHM 21582 adult male, SDNHM 21584 adult male).

Appendix II
Characters of *Crotalus atrox* Examined

All measurements were taken in mm with Vernier calipers. If both right and left sides were measured/counted, this is stated below.

Mensural Characters

ROSTHT–height of rostral scale. Measured from the rostral contact with the internasal median suture to the ventral most extension of the rostral scale (Burbrink, 2001).

ROSTWIDTH–width of rostral scale. Measured from the widest point of the scale, where it contacts the right and left supralabials (Klauber, 1972).

HEADLENGTH–length of head, from rostral tip to the posterior apex of the retroarticular process of the compound bone (Burbrink, 2001). Both right and left.

HEADHT–height of head, taken at the rictus. Both right and left.

HEADWD–width of head, taken across the top of the head at the rictus

TAILLENGTH–tail length, measured from the posterior edge of the anal plate to the posterior edge of the rattle fringe, at the basal rattle segment.

BASLRATLENGTH–basal rattle length, measured basal rattle segment height when standing dorsal to ventral (see Klauber, 1972; same as basal rattle width in his text).

SVL–snout-vent length, measured from anterior rostral tip to posterior margin of anal plate.

Meristic Characters

ROSTNO–number of rostral scales.

CANTHAL–number of canthal scales (Klauber, 1972), both right and left.

INTERCANTH–number of intercanthal scales, minimum distance between canthals, not including canthals.

SUPRAOC–number of supraocular scales, both right and left.

BEFSUPRAOC–number of scales before supraoculars on anterior head dorsum, includes internasals, canthals, all intercanthals, up to and not including the first intersupraoculars (Klauber 1930).

INTERSUPRAOC–number of scales between supraoculars, taken at minimum distance between supraoculars.

NASALS–number of nasal scales, both right and left.

INTERNSLS–number of internasal scales, both right and left.

LOREALS–number of loreal scales, both right and left.

PREFOV–number of prefoveal scales (Klauber, 1972), both right and left.

POSTFOV–number of postfoveal scales (Klauber, 1972), both right and left.

LACUNAL–number of lacunal scales (Klauber, 1972), both right and left.

PREOC–number of preocular scales, both right and left.

SUBOC–number of subocular scales (Klauber, 1972), both right and left.

POSTOC–number of postocular scales (Klauber, 1972), both right and left.

INTEROCULAB–number of interoculabial scales, minimum distance between eye and labial scales, not including labials or suboculars. Both right and left.

INTERRICT–number of interrictal scales in a straight line between the corners (rictus) of the mouth, not including labial scales (Klauber, 1972).

POSTOCUSTRIPE–number of supralabial scales anterior to the rictus where postocular light stripe ends. States: at rictus (0), 1 scale anterior to rictus (1), 2 scales anterior to rictus (2), 3 scales anterior to rictus (3), 4 scales anterior to rictus (4). Both right and left.

SUPRALAB–number of supralabial scales, from first scale posterior to the rostral scale to the last scale at the rictus. Both right and left.

INFRALAB–number of labial scales, from the first scale posterior to the anterior genial scale, to the last scale at the rictus. Both right and left.

GULAR–number of gular scales, single count in a line from chin shield (genial) to the first pre-ventral, both right and left.

DORSMID–numbers of dorsal scales taken around the body, starting at the midbody.

DORSANT–number of dorsal scales taken around the body, about one head length posterior to the head.

DORSPOST–number of dorsal scales taken around the body, 5 scales anterior to the tail.

PREVEN–number of preventral scales, starting at the first anterior ventral scale that is wider than high (where gulars end), to the first ventral scale that contacts the first dorsal scale.

VENTRALS–total number of ventral scales beginning with the first scale row that contacts the first dorsal scale on both sides of the venter, and not including the anal plate (Dowling, 1951; Burbrink, 2001).

RATFRINGE–rattle fringe scales, total number of scales contacting the basal (proximal) rattle segment.

CAUDALS–number of caudal scales, first scale posterior to the anal plate to the last scale anterior to the proximal rattle, on the ventral surface (Klauber, 1972).

BODYBLOTCH–number of body blotches or diamonds that are present starting at the nuchal region, stopping anterior to the tail.

TAILRINGS–total number of dark (black) rings around the tail.

RATTLENO–number of rattle segments (not used in analyses).

Categorical Characters

PRENASLCONT–contact between the prenasal scale and the first supralabial scale, both right and left. States are no (1) or yes (2) (Klauber, 1930).

POSTNASLCONT–contact between the postnasal scale and the upper preocular scale, both left and right. States are: upper preocular scale in contact with the postnasal (1), contact prevented by loreal (2), contact prevented by canthal (3), contact prevented by loreal and canthal (4), or contact indeterminate (5) (Klauber, 1972).

INFRALABDIV–First infralabial divided, both right and left (Klauber, 1930). States are no (1) or yes (2).

COLOR–overall body coloration, states: light (1), medium (2), or dark (3).

BUTTPRES–button (apical segment of rattle) present, states are no (1) or yes (2), not used in analyses.

AGE–adult or juvenile, based on whether snake is reproductive (see methods).

SEX–male or female, determined by examining reproductive organs directly in abdominal cavity or by incision in tail to examine presence of retracted hemipenes.