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Morphological variation in the lancehead pitviper *Bothrops asper* (Garman) (Serpentes: Viperidae) from Middle America

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Abstract: Variation of morphological characters in the pitviper *Bothrops asper* (Garman) was studied in terms of scutellation, color patterns, and landmark measures for 374 Middle American specimens. Gender, ontogeny, and geographic effects were examined for each character. In this species, females are larger than males and have more ventral and dorsal rows, and can be distinguished by some landmark variables. Males have a higher number of subcaudals and usually are more heavily pigmented in the supralabial region. Age does not affect scutellation, although it does influence pigmentation patterns. Geographic differences were evident in several traits. The seven Middle American populations included in these analyses can be clustered in two major groups: those from Mexico and Nuclear Central America and those from Isthmian Central America. Distinction between these groups is possible in terms of univariate statistics and differences are explained in terms of population fragmentation due to the dynamics of rainforest during Quaternary or by isolation by distance among populations within each region.

Key words: *Bothrops asper*, scutellation, pit-viper, Costa Rica, Middle America.

The genus *Bothrops* is composed by 31 species of pitvipers commonly referred as lanceheads (Campbell and Lamar 1992) that are widely distributed in the Neotropics. Owing to their size and abundance in cultivated and suburban areas, several species included in this genus are the most important causes of human envenomation in the region (Bolaños 1984). However, the taxonomy of several common members of *Bothrops* is still far from being resolved, and the identity of several forms remains unclear. This is particularly true in distinguishing among the species of the *B. atrox* complex, which includes the widespread *B. atrox, B. asper*, and *B. moojeni* and other closely related forms (*e.g. B. lanceolatus, B. marajoensis, B. venezuelensis*) (Campbell and Lamar 1989, Wüster *et al.* 1996). The *atrox* complex includes large species distributed from the lowlands of the Amazon Basin northward to Central America, that are "superficially quite similar to one another in appearance"(Campbell and Lamar 1989, p. 180). In general, these snakes have concealing coloration that contributes to their resemblance, but also exhibit extended overlap of scale counts. *Bothrops asper* is the only species of the complex that reaches Middle America (for distribution details see Campbell and Lamar 1989) but its taxonomic identity is still under considerable debate. Some authors (Wilson and Meyer 1985, Villa *et al.* 1988, Schätti and Kramer 1991) consider *B. asper* as conspecific with *B. atrox*, whereas others (Peters and Orejas-Miranda 1970, Campbell and Lamar 1992) regard these two taxa as distinct species.

Working in a suspected sympatric zone in western Venezuela, Markezich and Taphorn (1993) were unable to distinguish between *B. asper* and *B. atrox*, and their morphological data indicated the presence of only one taxon in the region. They proposed that taxonomic

confusion involving these two species is related to high intraspecific variation of the meristic characters typically used in their taxonomy, and suggested that a comprehensive analysis of the intrapopulational variation along the geographic areas that they inhabit would help resolve the *atrox-asper* problem. In this paper, I followed their suggestion and, as a first step toward taxonomic clarification, I investigated the morphological variation in *B. asper* from Middle America. My goal was to describe the extent of variation in morphological characters in this species and to evaluate the effects of geographic, sexual, and ontogenetic factors on such variation. I will show that these factors do affect characters used in the taxonomy of this species.

MATERIALS AND METHODS

Specimens examined and morphological characters: I examined 374 specimens of *B. asper* preserved in several museums (see Material examined), and additional samples from the live collection at the Instituto Clodomiro Picado, Universidad de Costa Rica.

Fig. 1. Collecting localities in Middle America of *Bothrops asper* analyzed in this study. Specimens were pooled in seven localities: 1) San Luis de Potosí, 2) Gulf, 3) Southern Mexico, 4) Eastern Guatemala, 5) Southern Guatemala, 6) Caribbean CA, 7) Pacific ICA. Note that localities 1–5 occur in Mexico and Nuclear Central America; whereas localities 6–7 occur in Isthmian Central America.

Twenty-eight morphological characters, including scale counts, head shape, and color pattern commonly used in taxonomic work in the genus *Bothrops* were recorded. Measurements and scale counts follow Peters (1964): 1) head length; 2) head width; 3) snout length; 4) interorbital length; 5) supralabial scales; 6) infralabial scales; 7) preocular scales; 8) postocular scales; 9) interocular scales; 10) canthal scales; 11) intercanthal scales; 12) prefoveals; 13) subfoveals; 14) postfoveals; 15) internasals; 16) ventrals (Dowling 1951a); 17) preventrals; 18) subcaudals; 19) dorsal scale rows; 20) loreals; 21) interrictals; 22) supralabial band: number of posterior supralabial scales edged by dark postorbital band; 23) relative length of keels on midbody dorsal scales (Markezich and Taphorn 1993). Color pattern characters were evaluated *a posteriori* by the creation of ranked codes for various states: 24) supralabial spots: degree of supralabial pigmentation: from 0 (immaculate supralabials) to 3 (supralabials highly pigmented); 25) canthal spotting: scored as presence/absence of dark coloration in canthal area; 26) degree of ventral mottling: from 1 (almost no pigmentation) to 4 (heavily pigmented); 27) midbody lateral blotch shape: six distinct patterns were scored in terms of the relative size and shape of the lateral design; 28) blotch number: counted from the neck to the vent, on the left side of the specimen.

Life stage, geographic and sexual variation: Gender was determined by examining the tail and by observing the hemipenis in male specimens, but because of the state of preserved specimens the gender was determined in only 341 specimens. Geographic variation was assessed comparing measures of individuals from seven biogeographical regions (Fig. 1): 1) Potosí: individuals from San Luis de Potosí, Mexico; 2) Gulf: including specimens from lowlands along the Gulf of Mexico and the Yucatán Peninsula; 3) Southern Mexico: including specimens from moderate elevations of Oaxaca and Chiapas; 4) Eastern Guatemala: including specimens from the Caribbean slope of Guatemala, Belize, and Honduras; 5) Southern Guatemala: including samples from the Pacific

slope of Guatemala (Escuintla, Quetzaltenango), 6) Caribbean Isthmian Central America: including samples from the Caribbean slope of Isthmian Central America: Nicaragua (Zelaya), Costa Rica, and Panamá; 7) Pacific Isthmian Central America: including samples from the Pacific slope of Costa Rica and Panamá.

Life stage was estimated as a function of total body size. Specimens were grouped into three categories: 1) adults: individuals exceeding 110 cm and 98 cm total length in females and males, respectively (following Solórzano and Cerdas 1989); 2) juveniles: specimens ranging from 60-98 cm if male, or 60-110 cm if female, total length; 3) young-of-the-year: individuals with a total length of less than 60 cm.

Statistical analyses: The effect of gender, region, and life stage —as well as their interactions— on mean differences in scale counts were examined under a 3-way Anova. Normality was tested using the Shapiro-Wilk statistic (Gnanadesikan 1977) and non-normal distributed variables were transformed using the function $v = x^{1/2} + (x+1)^{1/2}$ (Sokal and Rohlf 1981). Levene's test (Winer *et al.* 1991) was used to test the assumption of homogeneity of variance. Specific differences in particular parts of the analysis of variance were assessed using Tukey-Kramer tests after sequential Bonferroni correction of the significance level (Rice 1989). Because there were unequal numbers of observations and missing values for some of the subclasses, I used type IV Sums of Squares to test the estimable portions of effects on the observed variation (Milliken and Johnson 1992). Log-linear analyses were performed in the examination of color pattern characters. For head and body measurements, patterns of sexual dimorphism were examined with multivariate discriminant function analysis at each life stage. All statistical analyses were performed

TABLE 1

Means (SD) of scutellation characters and dorsal blotch number by locality in females of Bothrops asper *from Middle America. Locality numbers are as follows: 1) Potosí, 2) Gulf of Mexico, 3) Southern Mexico, 4) Eastern Guatemala, 5) Southern Guatemala, 6) Caribbean ICA, 7) Pacific ICA*

Locality (N)	Subcaudal	Ventral scales	Mid-body dorsals	Interrictal scales	Inter-oculars	Blotch number
1	61.50	210.00	27.00	30.00	11.75	20.00
(4)	(1.29)	(1.41)	(0.00)	(1.00)	(2.75)	(1.41)
2	62.37	211.00	26.80	27.24	10.68	22.45
(33)	(3.53)	(6.50)	(1.06)	(1.80)	(1.69)	(2.01)
3	62.85	210.71	26.71	28.45	10.36	22.35
(11)	(2.85)	(5.19)	(0.99)	(2.16)	(1.49)	(1.59)
4	66.36	206.34	27.12	27.40	9.96	23.95
(20)	(4.35)	(14.3)	(0.97)	(1.42)	(1.37)	(1.91)
5	62.54	208.18	27.27	26.90	10.63	22.27
(11)	(2.73)	(4.57)	(0.47)	(1.22)	(1.38)	(2.72)
6	64.51	197.37	26.50	26.02	8.60	19.24
(81)	(3.10)	(8.79)	(1.24)	(1.60)	(1.78)	(2.76)
7	65.01	196.00	26.00	27.75	9.00	17.00
(33)	(1.41)	(4.24)	(3.46)	(2.21)	(0.81)	(1.41)
193	62.13	205.67	26.77	27.68	10.14	21.04
	(2.66)	(6.42)	(1.17)	(1.63)	(1.61)	(1.97)

TABLE 2
Means (SD) of scutellation characters and dorsal blotch number by locality in males of Bothrops asper *from Middle America. Locality numbers are as in Table 1*

Locality (N)	Subcaudal	Ventral scales	Mid-body dorsals	Interrictal scales	Inter-oculars	Blotch number
1	64.25	203.00	26.00	29.25	12.00	20.50
(4)	(1.70)	(5.35)	(1.00)	(2.62)	(0.81)	(0.47)
2	67.47	209.26	25.40	26.62	9.41	22.76
(27)	(4.15)	(7.41)	(0.91)	(1.52)	(1.45)	(2.04)
3	69.66	210.33	25.80	28.00	9.50	22.33
(4)	(1.36)	(4.16)	(1.09)	(1.15)	(1.73)	(1.15)
4	71.13	209.71	25.60	26.47	8.86	24.47
(21)	(2.78)	(4.26)	(0.89)	(1.20)	(1.80)	(2.22)
5	68.18	208.90	26.45	27.63	9.90	22.81
(11)	(1.66)	(2.21)	(0.93)	(2.24)	(1.37)	(1.47)
6	69.47	196.54	25.04	25.27	8.86	19.00
(44)	(3.50)	(6.15)	(0.85)	(1.66)	(1.69)	(2.08)
7	67.55	185.83	25.24	25.50	8.33	19.66
(9)	(6.41)	(21.30)	(1.16)	(0.53)	(1.22)	(1.50)
120	68.24	203.28	25.72	26.96	9.51	21.64
	(2.18)	(9.17)	(0.58)	(1.43)	(1.07)	(1.90)

using the CSS statistical package (Statsoft Inc. Oklahoma 1993).

RESULTS

Variation in scale counts: Low variation in the scale counts was observed for several head scales (range, mode): supralabials (7-9, 7), infralabials (7-8, 7), preoculars (1-3, 2), postoculars (0-3, 2), canthals (1-3, 1), prefoveals (0-5, 2), posfoveals (0-3, 0), internasals (1-3, 2), loreal (1-3, 1). Length of keels on dorsal scales was relatively large: in all specimens the keel extended to the posterior apex of colinear scale.

Statistical parameters in morphological characters in each physiographic region are shown in Tables 1 and 2. The number of ventral scales ranged from 187 to 255 in females and 147 to 229 in males. Significant gender ($F_{1,6} = 9.48$, $P < 0.05$) and geographical effect ($F_{6,274} = 21.40$, $P < 0.0001$) accounted for this variation. For each sex, regions located in Mexico and Nuclear Central America (from here on MNCA, regions 1-5 on Fig. 1) and those included in Isthmian Central America (from here on ICA, regions 6-7) showed notable differences in the number of ventral scales (Tukey-Kramer tests, $P < 0.05$ in each case). Specimens from ICA populations have the lowest means for ventral scales in both sexes (Tables 1 and 2). No effect of stage or any of the interactions were significant for ventral scale variation.

Subcaudals ranged between 50-73 pairs in females and 53-78 in males. The number of subcaudals exhibited sexual dimorphism ($F_{1,275} = 60.1$, $P < 0.001$) but no geographic or life stage variation. Overall, males tended to have a higher number of subcaudals than females (Tables 1 and 2).

Number of dorsal row scales varied between 21 and 29 rows. Females of *B. asper* had, on average, significantly more dorsal rows at

TABLE 3
Means (SD) of landmark measures of adults of Bothrops asper *from Middle America*

Sex	Head* length (mm)	Head width (mm)	Snout length (mm)	Interocular width (mm)	SVL** (cm)	Tail* length (cm)
Female (n = 65)	57.92 (11.20)	40.37 (9.81)	16.10 (2.99)	20.36 (3.41)	127.65 (22.20)	18.82 (2.92)
Male (n = 41)	44.25 (7.39)	28.22 (6.06)	13.07 (2.33)	16.31 (2.83)	105.82 (19.75)	17.35 (2.58)
Total (n = 109)	52.78 (9.32)	35.80 (7.97)	14.96 (3.13)	18.83 (3.76)	119.44 (23.75)	18.27 (2.88)

* Significant test ($F_{1,120} = 7.70$, $P < 0.006$)
** Significant test ($F_{1,120} = 4.28$, $P < 0.05$)

mid-body than males ($F_{1,271} = 38.31$, $P < 0.0001$). For dorsal scales, the effect of locality was also significant ($F_{6,271} = 3.47$, $P = 0.004$), and *post hoc* comparisons indicated that males from ICA differed in mean dorsal rows ($F_{6,175} = 3.76$, $P < 0.01$). However, the absence of a sex-locality interaction, make the locality effect suspect. Furthermore, the coefficients of variation for dorsal rows in each sex were roughly similar (4.52 in females, and 3.89 in males). Thus, I attributed the observed locality effect in dorsal rows to the confounding effect of sexual dimorphism. There was no significant effect of life stage or any of the interactions for dorsal scale rows. Dorsal row reduction (*sensu* Dowling 1951b), estimated as number of dorsal scales reduced at a level one head length from the vent, also differed between sexes ($F_{1,269} = 14.12$, $P < 0.0003$). Scale counts at this level are usually 19 in males and 21 in females. No local or stage related factors accounted for differences in the observed values of this reduction.

Interrictal scales ranged between 22-33 scales. The only significant differences found for interrictal scales were among localities ($F_{6,243} = 9.307$, $P < 0.00001$). *Post hoc* comparisons indicated that ICA samples had the lowest means. Identical results were obtained for the number of interocular scales ($F_{6,268} = 8.39$, $P < 0.001$).

In summary, geographic differences between samples grouped as MNCA and ICA were detected in counts of several characters, whereas stage generated no significant effect on the variation of any meristic characters. The interactions do not play a role in accounting for sexual or geographic effects in scutellation in *B. asper*.

Variables describing head shape and body size were highly correlated (r^2 ranged between 0.73 and 0.91). In adult specimens, significant sexual dimorphism was found in head length, SVL, and tail length (Table 3). In adults, only one canonical function discriminated between morphological measures of males and females (Mahalanobi's $D = 3.63$, $F_{6,108} = 14.28$, $P < 0.0001$). This discriminant function is comprised mainly of head length and width (Table 4). Identified redundant variables were interocular width and snout length, both exhibiting the highest correlation with other variables. A classification function constructed *a posteriori* correctly classified 91% of the females and 75% of the males included in the analysis. Though variance-covariance matrices differed between sexes ($X^2 = 90.17$, df = 21, $P < 0.0001$), this analysis supported sexual dimorphism by landmark measurements among adults.

Sexual dimorphism also was determined at other age classes, but interpretation of discriminant function is harder at those life stages. In

TABLE 4
Factor structure coefficients (factor loadings) of seven morphological measures in Bothrops asper. *At each life stage, a single discriminant function was obtained. Life stages are as follow: adults (I), juveniles (II), and young-of-the-year (III)*

	Life stage		
Character	I	II	III
Head length	-0.718	-0.340	-0.182
Head width	-0.736	-0.238	-0.188
Snout length	-0.572	-0.311	-0.176
Interocular length	-0.660	-0.305	-0.184
Snout-vent length	-0.532	-0.072	-0.462
Tail length	-0.264	-0.138	-0.186
Eigenvalue	0.840	0.564	0.603

specimens of age class II (60-98 cm, Table 4) the discrimination function seems to be based also on head dimensions, but factor loadings are low (< 0.340). In contrast, in specimens less than one year old, the discriminant function seems to be based primarily on body size (factor loading = 0.46, all others < 0.188, Table 4). Covariance matrices for each sex were homogeneous in both cases (Box-M test = 35.16, X^2 = 33.31, df = 21, P < 0.05). Therefore, I concluded that *B. asper* exhibits sexual dimorphism in landmark characters, a dimorphism that is consistent in any age category. From the discriminant analysis, in neonates and specimens of less than one year old, the discrimination is mainly due to body length. As age increases, head dimensions acquire more importance for gender discrimination. No effect of locality in landmark measures was noticed in adults of *B. asper* ($F_{24,203}$ = 0.586, P = 0.109).

Color pattern variation: Various degrees of pigmentation were observed among the studied specimens. Several snakes had melanistic supralabials, with the pigment completely diffused in these scales. Spots are not distributed homogeneously along the supralabial scales, but rather along the upper edge and sutures between scales. Overall, supralabial spotting is bimodal, with most specimens being low (36.4%) or heavily (25%) pigmented. In neonates and young males such distribution of pigment gave the impression of labial stripes. There is a negative correlation between degree of pigmentation and life stage (Spearman r = -0.512, df = 299, P < 0.0001) and young individuals tend to have more melanistic supralabials. Sexual differences in the degree of supralabial pigmentation is also clear and males usually are more heavily pigmented than females (X^2 = 189.63, df = 17, P < 0.0001).

In *B. asper* the dark supralabial (= postorbital) band, when present, is 1-1.5 scales in width. From my analysis, life stage is related to supralabial band (Spearman r = 0.545, df = 260, P < 0.0001), whereas no locality or gender effect were significant. Supralabial mottling was related to supralabial band (Spearman r = 0.521, df = 262, P < 0.0001).

The degree of ventral pigmentation also varies among individuals. The belly usually had a series of spots that were distributed every two scales at the lateral margin of some ventrals. Degree of ventral mottling shows a Poisson-like distribution, strongly skewed toward low degree of pigmentation. In my sample, only seven individuals have a diffuse pigmentation that covers almost all the ventral scales. The frequency distribution of ventral mottling indicates that males tend to be more pigmented than females (X^2 = 61.76, df = 19, P < 0.0004). A marginal correlation of ventral mottling with life stage (Spearman r = -0.1318, df = 175, P = 0.049) was observed only in females, making the relationship between these factors unclear.

The number of dorsal blotches ranged between 14 and 28 in *B. asper*. Differences in this character by region ($F_{6,267}$ = 30.94,

TABLE 5

Sexual, ontogenetic, region, and elevation effects on character variation in Middle American populations of Bothrops asper. *The significant presence (+) or absence (-) of an effect in each morphological variable is indicated. Only variable characters are presented. An asterix indicates departures from Markezich and Taphorn (1993) results*

Character	Sex	Ontogeny	Region	Elevation
Tail length	+	-	-	-
Interoculars	-	-	+	-
Ventrals*	+	-	+	-
Subcaudals	+	-	-	-
Dorsal rows*	+	-	-	-
Interrictals	-	-	+	-
SL spots*	+	+	-	-
Ventral mottling*	-	+	-	-
Blotch shape	+	-	+	-
Blotch number*	-	-	+	-
SL band	-	+	-	-

$P < 0.00001$) correspond to differences between samples from ICA and those from MNCA. Isthmian localities had lower mean values of blotch number for males and females (Tables 1 and 2). The number of dorsal blotches were only correlated with ventrals (Spearman $r = 0.678$, df = 302, $P < 0.00001$) and interrictal scales (Spearman $r = 0.256$, df = 273, $P < 0.0001$). Life stage was negatively correlated to blotch number (Spearman $r = -0.212$, df = 304, $P < 0.0001$), with smaller individuals having fewer blotches. This relationship may result from a confounding effect of locality, as indicated by the non-significant correlation in some populations when corrected by locality.

Dorsal blotches were categorized into six shape patterns that ranged from the A-shaped pattern characteristic of *B. asper* (86%) to the rectangular blotches typical of *B. atrox* (less than 3% of specimens). The A-shaped blotches can be bordered (33%) or not (67%) by a white marginal line. Canthal spotting is present in a large proportion (72%) of individuals and is not affected by any of the factors considered.

Finally, elevation was not significantly correlated with any of the color pattern variables studied here.

DISCUSSION

Table 5 summarizes geographic, sexual and ontogenetic effects on variation in morphological characters studied here. With the exception of elevation, all other factors contribute to some extent to the morphological variation observed among individuals of *B. asper*.

Life stage changes affect pigmentation patterns exclusively, and does not account for changes in scutellation. This is not surprising because scale development occurs late in embryogenesis (Madeson 1985), and after hatching the only process occurring is scale regeneration. However, it is interesting that characters

affected by stage also are influenced by sex; thus hormonal influence might play a role in their diversity.

As with other species of the genus (Janeiro-Cinquini *et al.* 1991, 1992), *B. asper* exhibits conspicuous sexual dimorphism; body size is the most useful character for distinguishing between sexes at any comparable age. Sexual size differences in neonates of this species have been reported previously (Solórzano and Cerdas 1988) but parental investment in body mass for each sex is similar. Discriminant analysis suggests the value of head dimensions in gender distinction in *B. asper*. Head dimorphism has been found in newborn offspring of several other taxa (Shine 1991, Solórzano 1990) and is not the result of sex differences in prey types or feeding rates. In *Thamnophis sirtalis*, for example, this dimorphism is attributed to gonadal hormones (Shine and Crews 1988). It is unknown whether this is the case for the morphological dimorphism observed in *B. asper*, but the discriminatory contribution of head dimensions increases with age, implying a possible relationship with changes in hormonal control.

Sexual variation in the observed scale counts might be related to size dimorphism *in B. asper*. Longer tails in males result from an increase in the number of caudal vertebrae, a feature that is reflected in the number of subcaudal scales in this and other snake species (Voris 1975). Higher body measures of females are influenced by the relatively higher proportion of body vertebrae, which in turn relates to a higher number of ventral scales. *Bothrops asper* females also exhibit a higher number of dorsal scale rows, a condition that is likely to occur in other species of the genus. Klauber (1943) reported dorsal row dimorphism in six species of *Crotalus*, with females having more dorsal rows than males; however, observed differences between sexes were less than 1%, and he concluded that the sexual difference in the number of rows among these species is negligible (Klauber 1972). The increase in the number of ventral scales and dorsal rows might reflect an adaptative advantage that favored an expansion of the maternal abdominal volume achieved by an increase in number of abdominal vertebrae.

Geographic variation: Differences among populations of *B. asper* were evident for blotch shape and number, ventral, interrictal, and interocular scales. Intraspecific geographical variation in scale counts in snakes have been attributed to the effects of temperature (Fox 1948, Osgood 1978). Osgood (1978) induced changes in newborn ventral scales by placing gravid *Natrix fasciata* at different temperatures. However, Arnold (1988) argued against the possibility of such temperature effect, pointing out that geographic variation is larger in magnitude than any temperature effect on snake scales ever produced in laboratory conditions. In my *B. asper* sample, geographic differences in mean ventrals were 2-4 standard deviations among ICA and MNCA samples. Thus, the observed geographic variation was higher than the one standard deviation obtained experimentally by Osgood (1978). Obviously, this comparison is valid only if the temperature-induced shift in *B. asper* is similar to the one reported for *N. fasciata*, an assumption that I did not test. Nevertheless, fluctuations of mean temperatures in the tropical lowlands of Caribbean Central America are slight, making a temperature influence unlikely. Therefore, environmental heterogeneity does not seem to account for the observed scale counts variation between ICA and MNCA samples.

Morphological variation found in samples from different localities can result from isolation by distance. Assuming uniform rates of migration throughout the region, it can be expected that near populations would show greater genetic (and phenotypic) similarity than those situated farther apart. If this is the case, a positive correlation between morphological divergence and geographic distance should be expected. A significant association of divergence in meristic characters with the distances among localities was observed (Fig. 2), thus supporting this hypothesis. In general, populations in Isthmian Central America have lower

Fig. 2. Correlation between Mahalanobis distance in morphological characters and geographic distance among sampled localities of *Bothrops asper*. Meristic (solid dots, black line) and color pattern characters (open squares, dashed line) were analyzed. The distance between any two populations was estimated as a linear measure; one unit in the abscisa represents 120 km. The slope of meristic characters regression is significant (r^2 = 0.42, P < 0.0003), while no significant correlation was found for the color pattern characters (r^2 = 0.06, P > 0.24).

means for all meristic characters. Differences among populations in color characters, however, were not correlated with geographic distances (Fig. 2).

Historical events in the dynamics of populations might play a role in the observed geographic variation. Based on the observed variation, populations of *B. asper* are divisible into at least two groups: populations occurring in Nuclear Central America and Mexico and those occurring in Isthmian Central America. Given the distribution of *B. asper* and related species within the *atrox* complex, the ancestor of *B. asper* might have occurred in northern South America, and —subsequently— invaded Middle America from the south, soon after the reconnection of Nuclear Central America by the isthmian link during the Pliocene (Savage 1966). The alternative hypothesis that the differentiation occurred in Nuclear Central America is less convincing because only one species of *Bothrops* currently exists in the region. Fragmentation of the population might have occurred during the synthesis and complex dynamics of rain forests in the region, an event that was strongly influenced by glacial fluctuations during the Pleistocene (Morley 2000). Since current rain forests in the region are as young as 10 000 years old (Leyden 1984), fragmentation of populations of the inhabitants of mesic forest such as *B. asper* might be extremely recent, thus precluding further morphological differentiation.

My data indicate no effect of elevation on variation in morphological characters. Elevation variation has been reported for a series of characters in snakes, especially pigmentation patterns and the adaptive value of melanistic forms at high elevations has been proposed (Williams 1988). Markezich and Taphorn (1993) found variation in interocular scales, ventral mottling and blotch shape in *B. atrox* from different elevations. In their analyses, specimens were grouped in two categories (piedmont and llanos) and this elevational effect could be confounded by strictly locality differences. Elevation divisions in my study were set arbitrarily at 600 m, and very few individuals examined came from elevations above 1000 m. Therefore the elevational distribution of characters examined here deserve further investigation, but most populations of *B. asper* are restricted to low elevations and only in a few areas does this species range above 1000 m.

Taxonomic remarks: From the assessment of factors influencing morphological variation in *B. asper* several conclusions may be drawn. First, despite the extensive variation observed, only one species of *Bothrops* occurs in Central America and Mexico. The taxonomic value of some characters commonly employed in *B. atrox-asper* keys (Peters and Orejas-Miranda 1970, Campbell and Lamar 1992) must be regarded with caution, especially because several of the traits greatly overlap between species or are influenced by gender, locality, or life stage. Color characters may be particularly misleading, due to the ontogenetic influence on them. However, I believe that some useful information can still be obtained from color traits. In particular, Markezich and Taphorn (1993) regarded blotch shape from *B. atrox* as a continuous character, coded as a transition from rectangular blotches to triangles.

Almost 60% of their specimens show rectangular/trapezoidal blotches, whereas only 14% of specimens from Middle America can be grouped into this category. Therefore, using blotch shape it is possible to distinguish between snakes from these two taxa most of the time. I have analyzed specimens of *B. atrox* from Colombia and Venezuela (Appendix) and arrived at the conclusion that blotch shape is a useful taxonomic character in the *B. atrox-B. asper* problem.

The analysis presented here is only a first step in resolving the taxonomy of some of the species on the *B. atrox* complex. Recently, Wüster *et al.* (1996) analyzed the systematics *of B. atrox, B. moojeni* and *B. marajoensis* using morphological characters. They were able to differentiate between populations of the first two species, but the status of *B. marajoensis* remains uncertain due to the great heterogeneity of morphological traits observed among populations. Multivariate analyses of morphological characters like these, using large sample sizes and accounting for different environmental effects acting on the characters, are likely to reveal the patterns of variation and clarify the status of problematic populations of cryptic lanceheads. Finally, further analysis, including use of molecular characters should be conducted to investigate the variational patterns revealed in this study, in particular the differentiation between Nuclear and Isthmian populations.

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RESUMEN

La variación morfológica de *Bothrops asper* fue estudiada en 374 especímenes mesoamericanos en términos de escamación, patrones de coloración y medidas corporales. El efecto de sexo, ontogenia y geografía fue examinado para cada carácter. Se observó dimorfismo sexual en varios caracteres: las hembras son más largas y poseen más filas de escamas dorsales y ventrales, pudiéndoseles distinguir además a partir de otras medidas corporales. Los machos poseen un mayor número de subcaudales y están más fuertemente pigmentados en la región supralabial. El patrón de escamación no es afectado por la edad, aunque esta sí influye en los patrones de pigmentación. Basado en las diferencias observadas en caracteres morfológicos, las siete poblaciones de *B. asper* incluídas en este análisis pueden ser agrupadas en dos regiones: aquellas provenientes de México y Centroamérica Nuclear y las incluídas en Centroámerica Istmica. La distinción entre estos grupos es posible mediante análisis univariable y son explicadas en términos de fragmentación de población debido al desarrollo de los bosques lluviosos en la región o al aislamiento por distancia entre poblaciones incluídas en cada región.

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APPENDIX
MATERIAL EXAMINED

Institutional abbreviations are as listed in Leviton *et al.* (1985).

Bothrops asper. **Belize**: Manatee Rd. (FMNH 3480, 4197); Cayo: Privason Creek, Mountain Pine Ridge (AMNH126449, 126450; FMNH 3480; 0.4 mi S Belmopan on Hummingbird Hwy (KU 157657); Toledo: Blue Creek Village (UTA R-11072); **Colombia**: Chocó (UTA R-6770); Putumayo: Puerto de Bombeo Guamez (KU 140417); **Costa Rica**: Alajuela: Santa Clara (AMNH12770); Ciudad Quesada (LACM 114147-48); Cartago: Turrialba (AMNH 69720; KU 30963, 30999, 31008, 34007, 56004); Moravia de Turrialba: (KU 63197); Pavones (UTA R-12921-27, 12931-38, 14507-10); Guanacaste: Tenorio: Finca Las Flores (KU 34008-10); Heredia: Paso Azul (AMNH 17337, 17386), Puerto Viejo (KU 103908, MVZ 206329), La Virgen (KU 63915); Limón: Limón (AMNH 17380, 17382, UTA R-34157), Guápiles (AMNH 64448), Tortuguero (AMNH 89163-65, LACM 131113), Penshurt (AMNH 99681), El Diamante (KU 25677), Linda Vista de Siquirres (UTA R-12996); Puntarenas: Pto. Jimenez (AMNH 17278), 4.5 km Rincón de Osa (KU 102537, LACM 114149), 14 km NW Buenos Aires (KU 63916), Golfito (LACM 59196), Río Peñas Blancas (UTA R-32494); San José: no other locality (AMNH 17384); **Guatemala**: Alta Verapaz: Sierra de Las Minas, Pueblo Viejo (UTA R-26636, 26638, 26640), 1 km S (air) Finca Tinajas (UTA R-26637); Escuintla: S Slope Volcán de Agua, Finca Rosario Vista Hermosa (UTA R-21877-78, 21882, 21885, 21886-91, 21893-4, 21898-901, 21906, 21908, 28618-19); Izabal, Los Amates, Sierra del Espíritu Santo (KU 191151-52, UTA R-28620), Montañas del Mico,WSW Puerto Santo Tomás, Las Escobas (KU 191154-58, 191503, UTA R-14531, 21905, 23062-63, 33127-28); Las Dantas, El Estor (MVZ 160504-05, UTA R-8834, 15651, 21872), Mariscos (UTA R-21873), Canoas (UTA R-21907), Sierra de Santa Cruz, Finca Semuc, 1 km rd S headquarters (UTA R-26643-44), Morales, Sierra de Caral, Aldea Negro Norte (UTA R-37430); Petén: 25 km Flores (AMNH 110664-65), Sojío, 12 km S of La Libertad (AMNH 69972), 8 mi S Uaxactún (KU 157658), Tikal (UTA R-22226, 35017), 15 km NW Chinajá (KU 55704), Sayaxché (KU 57138), Quiriguá (AMNH 122764); Quetzantenango: Finca El Carmen, km 197 on CA-2 (UTA R-21904); **Honduras**: Atlántida: Quebrada de Oro (KU 200507); Copán: Quebrada Grande (KU 200621); Cortez: Agua Azul (AMNH 26151); Lancetilla (AMNH 46952); Olancho: Sierra de Agalta (FMNH 236415); Toro: 6 km S El Progreso (MVZ 171546), no other locality (AMNH 29965, 32573); **Mexico**: Chiapas: Mal Paso (TCWC 21546), La Esperanza (AMNH 66455, USNM 110433), Ocozocoautla (LACM 59198), Ruinas de Palenque (KU 94137, USNM 110430, LACM 20236), Javarinero (USNM 110431), Chicharras (USNM 46602), Sabana de San Quintín (KU 94138); Oaxaca: Temescal (LACM 28261, 48462-43, MVZ 78100), 10 mi S Oaxaca (MVZ 150506), Río Valle Nacional, San Cristóbal (FMNH 28463), Santo Domingo (USNM 47931-32), 12.7 km Valle Nacional Bridge (UTA R-14529), Sierra Juárez, Metates (UTA R-14530, 25850); Puebla: Hueytamalco (AMNH 123919); San Diego (AMNH 58225), Vegas de Suchi (AMNH 58231), Necaxa, Río Necaxa (AMNH 76433); Quintana Roo: Xkanha, boundary of Campeche and Quintana Roo (AMNH 7860), 9 km W Puerto Juárez (KU 70908), 12 km N of Tulum (CAS 150329-30, UTA R-17095), Pueblo Nuevo X-Can (KU 70906-07), 17.9 mi NE Felipe Carrillo (KU 157659-60, 171742), 8.1 mi SW Vicente Guerrero (KU 157661), 22 km N Kantunil Kin (KU 171758), Caobas, 86 km W Chetumal (KU 75003), Cancún Airport (MVZ 160199), between Tulum and Coba at km 14 (UTA R-17031); San Luis Potosí: Antigua Morelos,

Salto de Agua (TCWC 6974, AMNH 110389, KU 24033), Chapulhuaco, Hidalgo (AMNH 67315), 2 mi W Tamuin (AMNH 93434), 10 mi W Ebano (KU 24032), Xilitla region (KU 24080), El Naranjo (LACM 128458); Tabasco: Zapato Junction (CAS 114091),14 mi NE Maculteped (KU 157662), Teapa (USNM 46406), no other data (USNM 46595); Tamaulipas: no other data (CAS 71773), Río Sabinas (LACM 20229-31); Veracruz: Río Quetzalpan (TCWC 19157), 2 mi E Tabarca. Lago Catemaco (TCWC 21394, MVZ 76142), 2 km NW Sontecomapan (TCWC 21395), Los Tuxtlas (TCWC 21396, 21912), 21 mi E Las Chaspas (TCWC 21397), Palmilla, Tlacopayan (AMNH 4290-91), Veracruz (AMNH 79034), Tezonapa (CAS 74396), SW Jesus Carranza (KU 23915, 23995-97, 27008), 20 km ENE Jesus Carranza (KU 27009-11, 27565-67), Paso del Macho (KU 26473), 10 mi S Alvarado (LACM 20228), Mirador (USNM 25047-48, 25212), Orizaba (USNM 30220), San Rafael (USNM 32149), 7 km NW Sontecomapan (UTA R-2748, 2920, 3021, 3063, 9444, 9460, 22580), W slope Santa Marta (UTA R-3010),12 mi NW Tuxpan (AMNH 93435), Mirador (USNM 25046); Yucatan: Kikil, 6 km N Tizimin (KU 157663), 12 mi S Río Lagartos (KU 75004); Campeche: Encarnación (FMNH 105314-17), 8 km N Xpujil (KU 75001); no other data: (USNM 30243, 30244); **Nicaragua**: Zelaya: El Recreo (LACM 20232-34, KU 112957-58, 125013), Cukra trail to Kanawa (AMNH 12705), Kanawa (AMNH 12708), Bluefields (AMNH 12707-09), Cupitna Camp (AMNH 12711-13), Río Huahuasban (AMNH 70244), Río Cama (AMNH 70256, 7413), Kyras, Río Coco (LACM 74145); Musawas Waspues River (AMNH 75221); Chontales: Villa Somoga (LACM 20235); **Panama**: Bocas del Toro: Río Changuinola, Queb. Guabo, 16 km W Almirante (AMNH 119093-95, KU 107849), Almirante (KU 80246), Río Chico (AMNH-64447), Península Valiente (KU 96986); Chiriquí: no further data (MCZ 26882-94), 16 mi W Potrerillos (MVZ 35563-67), Panamerican Highway, 27 mi NW David (MVZ 78768); Cristóbal (AMNH 36189); Darién: Río Subcutí (AMNH 36209), Turia Valley (CAS 71738-42), Río Tuira at Río Mono (KU 97031,107853-56), El Real (KU 107857-58, 80603), Río Chucunaque, 7 km above Río Mortí (KU-107859-62), Santa Fe, Río Sabana (KU 112571), Yaviza (MVZ 83439-40); Panamá: Altos de Maja (AMNH 109640), Barro Colorado Island (AMNH 63409, 85616, MVZ 78076), Canal Zone, Ft. Clayton (AMNH 81974, 130934, FMNH 31743-46, KU 107850-52, 112572), Canal Zone, Curundu (KU 75765, 80276-81), Midbasin Chagres and mouth of Piquini River (MCZ 37086-88),Tocumen Airport, Panamá (MVZ 78769); San Blas: Camp Sasardi (KU 112569), Camp Summit (KU 112570); Veraguas: Río Concepción (KU 112567); no other data (FMNH 68049); **Trinidad**: Arima: St. George , 7 km N Arima, Smila Research Station (UTA R-22345), Aripo River (UTA R-17862); **Venezuela**: Aragua: 34.2 km Maracay-Ocumare de la Costa Rd. (KU 182732), Maracay, El Limón (KU-182733).

Bothrops atrox: **Colombia**: Meta: Serranía de la Macarena, Caño Sardinita (UTA R-3377), 34.7 km E Puerto Gaitán (UTA R-3378), Lomalinda (UTA R-3590, 3610, 3771-72, 3848, 3850, 3862); **Venezuela**: Amazonas: Puerto Ayacucho (UTA R-30826).