

SYSTEMATICS OF THE *BOTHROPS ATROX* COMPLEX (REPTILIA: SERPENTES: VIPERIDAE) IN BRAZIL: A MULTIVARIATE ANALYSIS

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ABSTRACT: We analyze the systematics of pitviper populations normally assigned to the species *Bothrops atrox*, *B. moojeni*, and *B. marajoensis* using multivariate analysis of morphological characters. Most populations of *B. moojeni* are clearly distinct from *B. atrox*, but there are phenotypically intermediate populations where the ranges of the two forms meet, suggesting the existence of a hybrid zone. The status of the populations currently assigned to *B. marajoensis* remains uncertain, as the populations assigned to this species are heterogeneous and poorly differentiated from *B. atrox*. This study confirms the results of previous workers, who found low levels of divergence within the *B. atrox* species complex.

Key words: Reptilia; Viperidae; Snakes; *Bothrops*; Systematics; Hybrid zones; Geographic variation; Multivariate analysis; South America

BOTHROPS ATROX and the species allied to it constitute a complex and taxonomically controversial group. A number of species and subspecies have been described in recent years (Hoge, 1965; Sandner Montilla, 1979, 1981, 1990), and there has been considerable debate about the affinities of some of the populations involved (Campbell and Lamar, 1989, 1992; Johnson and Dixon, 1984; Markezich and Taphorn, 1993; Sandner Montilla, 1990; Schätti and Kramer, 1993). Sadly, a considerable part of this debate has been carried out in an unnecessarily antagonistic manner. Points of contention include the status of the taxa *B. xanthogrammus*, *B. asper*, *B. moojeni*, *B. marajoensis*, *B. isabelae*, *B. pradoi*, and *B. leucurus* and the relationships between various South and Central American populations and the Caribbean taxa *B. caribbaeus* and *B. lanceolatus*. The *B. atrox* complex is one of the principal causes of venomous snakebite in much of Latin America (Bolaños, 1984; Cardoso, 1992; Otero et al., 1992). A sound taxo-

nomic framework for this group is therefore important for venom research and antivenom treatment of snakebite victims.

The various studies carried out so far, which have failed to yield a well substantiated classification for the *B. atrox* group, were based on conventional taxonomic techniques, using a character-by-character approach. In view of the levels of ontogenetic variation, sexual dimorphism, and superficially striking microgeographic variation in this complex, the failure of this approach is unsurprising. Dixon (*in* Golay et al., 1993) emphasized the importance of an approach based on the use of all available material and a broad set of characters in the investigation of the population systematics of these animals. Multivariate analysis of morphological characters can reveal patterns of variation that may be obscured by incongruent variation in superficially conspicuous characters, and it has been proved useful in other studies of complex groups of venomous snakes, such as Asiatic cobras and Russell's viper (Wüster and Thorpe, 1987, 1989, 1990, 1991, 1992; Wüster et al., 1992a,b).

In this paper, we present preliminary results on the status and interrelationships of the species *Bothrops atrox*, *B. moojeni*,

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and *B. marajoensis* obtained through the use of multivariate morphometrics. Both *B. moojeni* and *B. marajoensis* were described by Hoge (1965), but their status as species distinct from *B. atrox* has been questioned, especially in the case of *B. marajoensis* (Campbell and Lamar, 1989; Cunha and Nascimento, 1993). It should be noted that the distribution of *B. moojeni* extends much further north and west into the state of Mato Grosso than previously recognised (compare Fig. 1 with Campbell and Lamar, 1989, and Puerto, 1992). Its presence in the Pantanal was reported by Wüster et al. (1994).

MATERIALS AND METHODS

Approximately 250 preserved specimens of *Bothrops* from a number of collections in the United States, Brazil and Europe were examined by the first author. A total of 87 morphological characters relating to head, body and tail scalation, pattern, internal anatomy, and head and body proportions were recorded from each specimen.

The ventral and subcaudal scales were numbered using the method of Dowling (1951). The position of a character along the body was recorded as the number of the ventral or subcaudal scale opposite which it was situated. In order to compensate for variation in the number of ventral and subcaudal scales, this was then transformed to percent ventral scale (% VS) or percent caudal scale (% CS) position (Thorpe, 1975). The encroachment of color pattern features onto the body was measured as the number of dorsal scale rows involved. This was then expressed as a percentage of the total number of dorsal scale rows at the level (% DS). The snout-vent length (SVL) and the tail length were measured to the nearest 1 mm with a string; other linear dimensions were measured to the nearest 0.01 mm with digital callipers.

For canonical variate analysis, specimens were grouped by locality into Operational Taxonomic Units (OTUs). In order to avoid within-OTU geographic variation, and the formation of OTUs with two sympatric species, each proposed OTU was checked for these considerations by use of

principal components analysis (PCA). OTUs used in this study are listed in Table 1. All characters were checked for among-OTU variation by means of analysis of variance. Only characters showing significant among-OTU variation were selected for further analysis. These are listed in Table 2. The pooled within-OTU regression coefficient of each linear character against the SVL was obtained by analysis of covariance, and all linear measurements were regressed a standard SVL of 1000 mm before further analysis.

We used canonical variate analysis (CVA) for the investigation of patterns of geographic variation in this complex. This technique maximizes the separation between groups relative to the within-group variance, taking into account the within-group correlation between characters, and it is a standard technique for the multivariate analysis of geographic variation. See Thorpe (1976, 1980) for a discussion of this technique. Characters that clearly violate the statistical assumptions of this technique by being invariable within many OTUs and variable in some others were not included in the analyses. CVA 1 was run on the OTUs with male specimens and CVA 2 on the OTUs with female specimens listed in Table 1, using the relevant characters listed in Table 2. The result of each CVA was verified by running a PCA on the character means of each OTU. The resulting ordination plots were functionally identical to the CVA plots in all cases, showing that the statistical assumptions of CVA had not been materially violated.

RESULTS

The analysis for males (Fig. 2) shows clear separation along the first canonical variate between most of the populations conventionally assigned to *Bothrops moojeni*, from the Brazilian states of Paraná, São Paulo, Mato Grosso, Mato Grosso do Sul, and Goiás, and the populations normally assigned to *B. atrox* and *B. marajoensis*. However, some populations from southern and southwestern Pará [Conceição do Araguaia—OTU 400; Cachimbo—OTU 401], Tocantins (Natividade—OTU 402), and from southwestern Piauí (Uru-

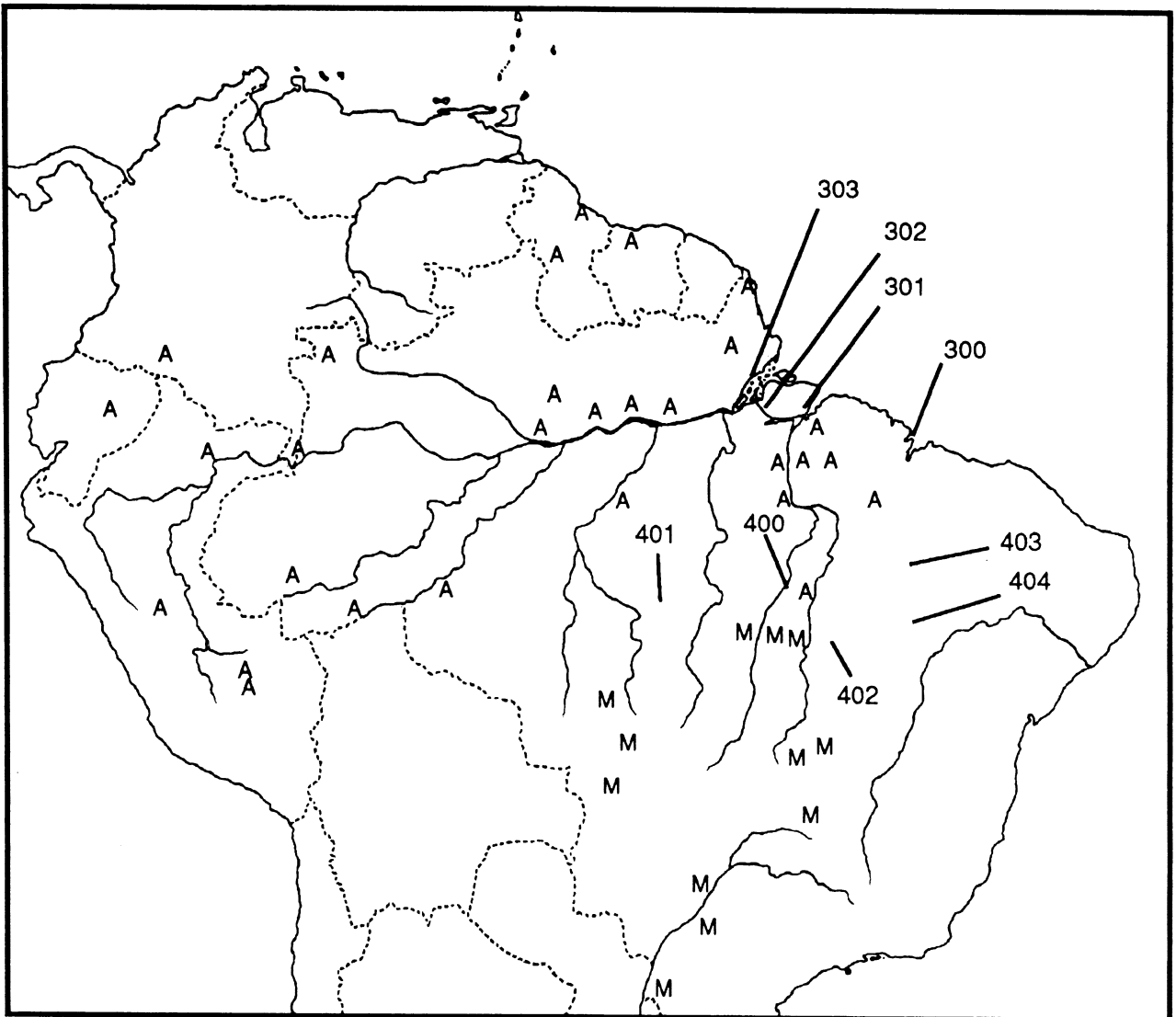


FIG. 1.—Geographic location of specimens of *Bothrops atrox* (indicated by the letter A), *Bothrops moojeni* (indicated by the letter M), and those OTUs specifically mentioned in the text (indicated by their number—cf. Table 1).

quí—OTU 403) appear to be morphologically intermediate between “typical” *B. moojeni* and the two other species. Specimens from the eastern portion of Ilha de Marajó (type locality for *B. marajoensis*—OTU 301) and coastal areas of Maranhão (OTU 300) are somewhat separated from the remaining samples of *B. atrox* along the first canonical variate, being partially intermediate between *B. atrox* and *B. moojeni*. Specimens from the western part of Ilha de Marajó (OTU 302) and the Macapá area, Amapá (OTU 303) group together with the remaining specimens of *B. atrox*. See the map in Fig. 1 for the locality of origin of the specifically discussed OTUs.

In females, this pattern of geographic

variation is less clearly defined. The populations normally assigned to *Bothrops moojeni* are phenotypically distinct from those usually assigned to *B. atrox*. Phenotypically intermediate populations include those from Conceição do Araguaia (Pará—OTU 400) and southwestern Piauí (Avelino Lopes—OTU 404), whereas female specimens of OTUs 402 and 403 do not exhibit an intermediate phenotype, unlike the corresponding males. OTU 300 (coastal Maranhão) appears phenotypically close to *B. moojeni*, whereas the populations from eastern and western Marajó Island (OTUs 301–302) do not appear to be strongly differentiated from each other or from “typical” *B. atrox*.

TABLE 1.—List of OTUs used in this study and sample size for each sex. Species designations follow mostly Campbell and Lamar (1989), with modifications according to phenotype: OTUs 100–199 would be classified as *B. atrox*, OTUs 200–299 as *B. moojeni*, OTUs 300–399 as *B. marajoensis*, and OTUs 400–499 are populations shown to be phenotypically intermediate between *Bothrops moojeni* and *Bothrops atrox* in this paper in either or both sexes. The usage of these specific epithets in the analyses is primarily designed to help the reader, and should not be taken as confirming the validity of these species.

OTU	Locality	Sample size	
		Males	Females
100.	Surinam	1	0
110.	Guyana	2	2
120.	Northern Peru and neighbouring Colombia	6	6
121.	Departamento de Cuzco, Perú	1	0
122.	Manú National Park, Departamento Madre de Dios, Perú	2	1
123.	Panguana, Rio Lullapichis, Rio Pachitea, Huánuco, Perú	2	1
130.	Pastaza Province, Ecuador	3	3
150.	Balbina Dam, Pres. Figueiredo, Amazonas, Brazil	8	8
151.	Itacoatiara, Amazonas, Brazil	5	6
152.	Manaus Area, Amazonas, Brazil	2	1
153.	Iauarête, Amazonas, Brazil	0	1
154.	Porto Velho Region, Rondônia, Brazil	1	3
155.	Acre State, Brazil	1	2
156.	Belém area, Pará, Brazil	6	10
157.	Tome-Açu, Pará, Brazil	2	0
158.	Left side of Rio Tocantins, Tucuruí, Pará, Brazil	8	4
159.	Right side of Rio Tocantins, Tucuruí, Pará, Brazil	0	8
160.	Marabá, Pará, Brazil	0	1
161.	Itaituba, Pará, Brazil	0	3
162.	Curral Grande, Monte Alegre, Santarém, Pará, Brazil	11	6
163.	Mouth of Rio Trombetas, Pará, Brazil	0	1
164.	Barra do Corda region, Maranhão, Brazil	3	0
165.	Oiapoque, Amapá, Brazil	1	0
166.	Serra do Navio, Amapá, Brazil	0	1
167.	Guaraí, Tocantins, Brazil	0	1
200.	Southern Goiás and Brasília region, Brazil	7	6
201.	Presidente Prudente region, São Paulo, Brazil	3	4
202.	Itaipú Dam, Foz do Iguaçu, Paraná, Brazil	6	5
203.	Ilha Solteira Dam, Mato Grosso do Sul, Brazil	8	7
204.	Eastern and northeastern Mato Grosso, Brazil	4	2
205.	Ilha do Bananal, Tocantins, Brazil	0	1
206.	Formoso do Araguaia, Tocantins, Brazil	0	1
300.	São Bento, coastal Maranhão, Brazil	9	8
301.	Eastern part of Marajó Island, Pará, Brazil	3	2
302.	Breves, western part of Marajó, Pará, Brazil	2	3
303.	Macapá area, Amapá, Brazil	1	0
400.	Conceição do Araguaia, Pará, Brazil	3	1
401.	Cachimbo, Pará, Brazil	1	0
402.	Almas, Natividade, Tocantins	2	1
403.	Uruçui, Piauí, Brazil	1	1
404.	Avelino Lopes, Piauí, Brazil	0	1

DISCUSSION

The results of this study show a relatively weak level of morphological differentiation between the nominal species in this group, with the existence of phenotypically intermediate populations, and some incongruence between the patterns

of geographic variation exhibited by males and females.

While the populations of *B. moojeni* from the greater part of that species' range are clearly distinct from Amazonian *B. atrox*, some populations from the areas where the ranges of the two species approach each other show intermediate phe-

TABLE 2.—Characters used for multivariate analysis of the *Bothrops atrox* complex. Characters are numbered as originally recorded and to facilitate maintaining continuity with future publications using different characters. Characters tagged “m” were used in analyses of males, characters tagged “f” in analyses of female specimens. Differences in character usage between the sexes are due to differential character availability in crucial specimens, and the fact that some characters showing significant between-OTU variation in one sex do not necessarily do so in the other.

1. No. of ventral scales	mf
2. No. of subcaudal scales	mf
5. Dorsals at 10% VS length	mf
6. Dorsals at 20% VS length	mf
7. Dorsals at 40% VS length	mf
8. Dorsals at 50% VS length	mf
9. Dorsals at 60% VS length	f
11. Dorsals at 100% VS length	mf
13. %CS position of reduction from 14 to 13 tail scale rows	mf
14. %CS position of reduction from 13 to 12 tail scale rows	f
15. %CS position of reduction from 12 to 11 tail scale rows	mf
16. %CS position of reduction from 11 to 10 tail scale rows	mf
17. %CS position of reduction from 10 to 9 tail scale rows	mf
18. %CS position of reduction from 9 to 8 tail scale rows	mf
19. %CS position of reduction from 8 to 7 tail scale rows	mf
20. %CS position of reduction from 7 to 6 tail scale rows	mf
25. No. in intersupraocular scales	mf
26. No. of scales around eye.	f
27. No. of scales contacting supraoculars	f
28. No. of scales contacting 3rd-last supralabials	m
29. No. of scales separating lacunolabial from nasal	f
33. No. of scales between second pair of canthals	mf
39. No. of supralabials encroached on by postorbital stripe	mf
40. No. of scales encroached on by postorbital stripe	m
41. % of last supralabial covered by dark pigment from postorbital stripe	mf
44. No. of half-bands on body	mf
45. Mean width of 3 half-bands at 50% VS length at 2nd paravertebral scale row	mf
46. Mean maximum width of 3 half-bands around 50% VS length	mf
47. Lowest scale row involved 3 half-bands around 50% VS length	mf
49. %DS separation of lower and upper parts of 3 half-bands around 50% VS length	mf
50. %VS width of lower sections of 3 half-bands around 50% VS length	mf
51. %VS distance between 3 half-bands around 50% VS length	mf
56. Percentage of middle 5 ventrals covered in dark pigment	mf
58. Tail length	m
59. Head length (snout to end of mandible)	f
60. Head width across supraoculars	m
63. Length of supraoculars	f
64. Width of supraoculars	m
65. Height of rostral	f
66. Separation between supraoculars	m
67. Separation between eye and pit	m
68. Distance eye to nostril	m
69. Distance from eye to tip of snout	mf
73. Maximum length of pit	m
74. %VS position of anterior edge of thyroid	mf
75. %VS position of posterior tip of heart	m
76. %VS position of anterior tip of liver	m
77. %VS position of posterior end of anterior lobe of liver	mf
78. %VS position of posterior end of posterior lobe of liver	mf
79. %VS position of anterior end of right testis	m
80. %VS position of posterior end of right testis	m
81. %VS position of anterior end of left testis	m
82. %VS position of posterior end of left testis	m
84. %VS position of posterior end of right kidney	m

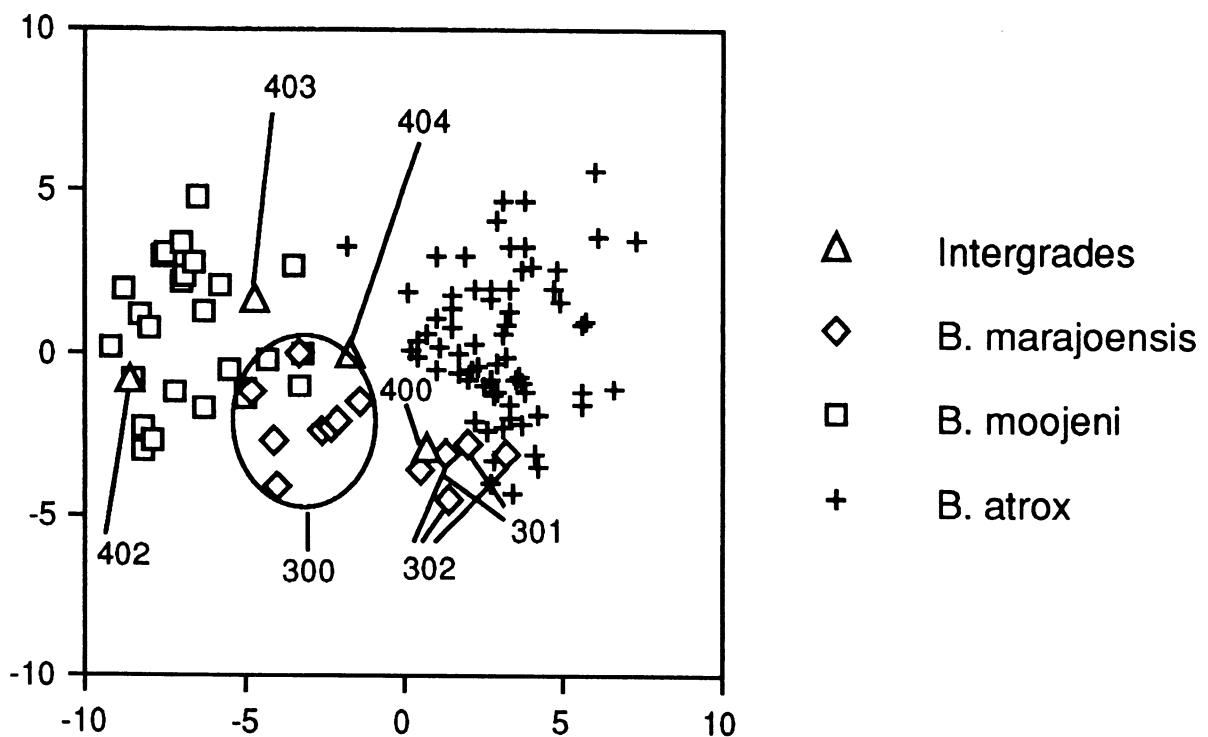
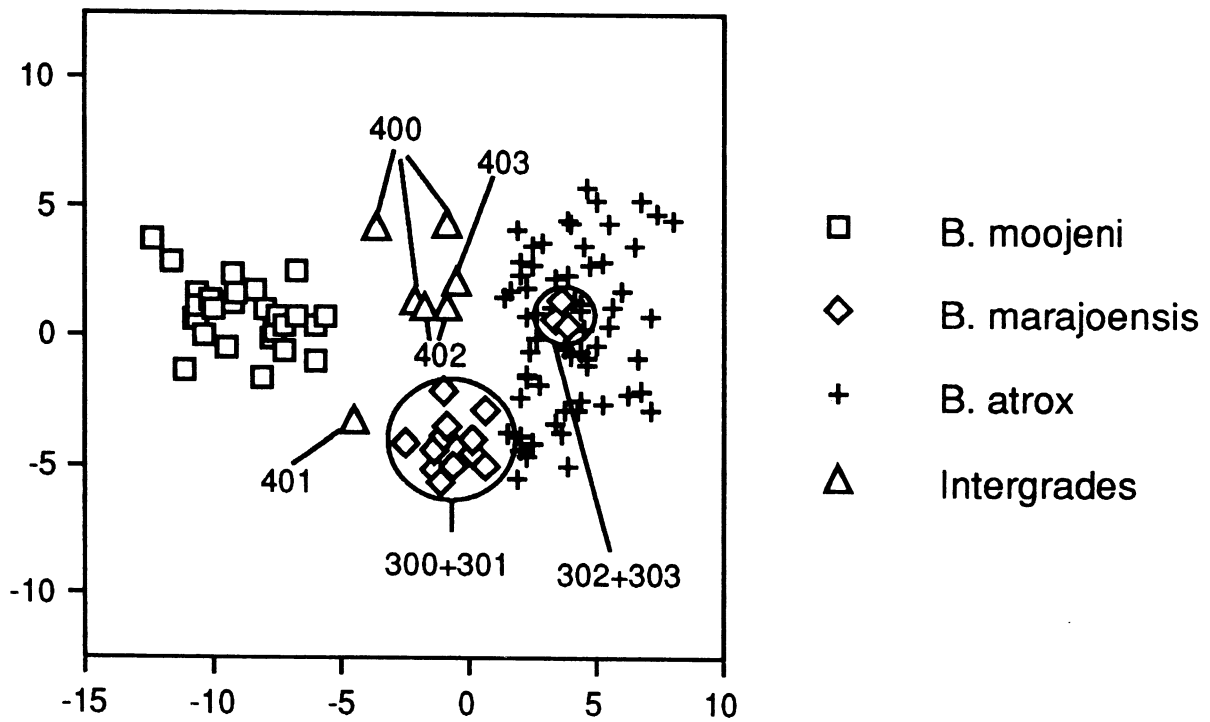


FIG. 2.—Ordination of specimens of *Bothrops* along the first two canonical variates of CVA 1 (top = males) and CVA 2 (bottom = females). Numbers used to indicate specimens indicate the numbers of OTUs mentioned in the text (cf. Table 1): 300 = São Bento, Maranhão; 301 = eastern Ilha de Marajó, Pará; 302 = western Ilha de Marajó, Pará; 303 = Macapá area, Amapá; 400 = Conceição do Araguaia, Pará; 401 = Cachimbo, Pará; 402 = Natividade, Tocantins; 403 = Uruçuí, Piauí; 404 = Avelino Lopes, Piauí.

notypic profiles, suggesting the existence of a hybrid zone. There is some incongruence between the sexes concerning the affinities of some populations: the males of OTUs 402 and 403 (Natividade and Uruçui) are phenotypically intermediate between *B. atrox* and typical *B. moojeni*, whereas females of the same OTUs group with "typical" *B. moojeni*.

Bothrops moojeni and *B. atrox*, as currently understood, occupy different habitats (dry cerrado vegetation and rainforest, respectively). Several potential causes could account for the observed pattern of geographic variation and the apparent hybrid zone: (1) *B. moojeni* as conventionally understood, may constitute a group of phenotypically distinct southern populations of *B. atrox*, differentiated due to selection for different environmental conditions; (2) the two forms may be different species, with converging adaptation for more similar environmental conditions where their distributions meet; or (3) the morphologically intermediate specimens may represent a secondary hybrid zone between not yet fully reproductively isolated species.

These causal hypotheses can be tested through the phylogenetic analysis of selectively neutral mitochondrial DNA sequences, which can test whether each nominal species does in fact consist of a monophyletic group of populations, and through the use of statistical hypothesis-testing packages such as partial Mantel tests, which can separate the effects of phylogeny and current selection in the causation of the observed geographic variation in morphology (Thorpe et al., 1994).

The case of *Bothrops marajoensis* is also complex. CVAs 1 and 2 show incongruent geographic variation in males and females. In the case of male specimens, the populations from western Marajó Island [which were assigned to *B. atrox* by Campbell and Lamar (1989)], the Macapá area and northeastern Pará [tentatively assigned to *B. marajoensis* by Campbell and Lamar (1989)] group with populations conventionally classified as *B. atrox*, whereas populations from the eastern part of Marajó Island (type locality of *B. marajoensis*) and

coastal Maranhão show some differentiation from *B. atrox*, and are phenotypically somewhat intermediate between *B. atrox* and *B. moojeni*. These differentiated OTUs from eastern Marajó and coastal Maranhão originate from relatively open and frequently inundated zones, whereas the populations of *B. atrox* as well as the specimens from the western part of Marajó Island originate from forest areas. In the case of the females, the populations from both eastern and western Marajó Island are little distinct from populations of *B. atrox*, whereas the OTU from Maranhão shows some phenotypic similarity to *B. moojeni*.

Due to the incongruence of the pattern of geographic variation between the sexes, the status of *Bothrops marajoensis* cannot be finally resolved on the basis of these results. However, it is obvious that the level of divergence between this species and *B. atrox* is very weak, and the status of this form as a separate species must be regarded as open to doubt. If *B. marajoensis* is a valid species, then its range appears to be restricted to a few isolated distribution pockets on the eastern part of Marajó Island and the mangroves of northern Maranhão. All specimens from Amapá examined by the authors were assignable to *B. atrox*, as was all material from northeastern Pará.

In conclusion, this study has elucidated the pattern of geographic variation in morphology exhibited by these populations of *Bothrops*. The species of the *B. atrox* group show low levels of phenotypic differentiation, with some incongruence between the sexes. The low levels of differentiation between the nominal species of the *B. atrox* complex parallel the results of Werman (1992), who found low levels of allozyme divergence in South American *Bothrops*, and our own mtDNA sequence data, which show low levels of divergence within this complex (unpublished data). The geographic variation in the phenotype of these snakes appear to be related to ecological differences. The possibility that the observed variation is the result of ecogenetic adaptation rather than a reflection of population phylogeny cannot be rejected on the basis of our data, and requires testing

by other methods. The ecology of these animals (relatively low vagility, ambush predation, reliance on camouflage) makes it likely that ecological factors, in particular those related to camouflage, would result in intense selection for adaptation to local conditions. This could explain much of the extensive and complex geographic variation found in this group.

RESUMO

Analisamos a sistemática das populações de crotalíneos normalmente classificadas como *Bothrops atrox*, *B. moojeni* e *B. marajoensis*, utilizando métodos de análise de multivariância de características morfológicas. A maioria das populações de *B. moojeni* são claramente distintas de *B. atrox*, mas existem populações com fenótipo intermediário na zona de contacto entre as duas formas, o que sugere a existência de uma zona de hibridização. O status das populações atualmente classificadas como *B. marajoensis* permanece incerto, pois estas populações são heterogêneas e pouco distintas de *B. atrox*. Estes resultados confirmam os resultados de outros autores, que encontraram baixos níveis de divergência dentro do complexo *B. atrox*.

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