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SYSTEMATIC REVISION OF THE GENUS *LACHESIS* DAUDIN, 1803 (SERPENTES, VIPERIDAE)

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Abstract: The genus *Lachesis* Daudin, 1803 was partitioned into six geographic groups to evaluate the taxonomic status and phylogenetic relationships among these groups. Characters of external morphology and hemipenial anatomy were evaluated. Results obtained through the phylogenetic and statistical analyses support recognition of the Central American species *L. melanocephala* and *L. stenophrys* as distinct species, whereas the South American *L. muta* is recognized as monotypic, without further differentiation in subspecies. These results provide further evidence of the independence of the Central American and South American lineages and are congruent with other studies based on molecular data.

Key words: Biogeography; *Lachesis*; Phylogeny; Systematics; Taxonomy; Viperidae

The genus *Lachesis* Daudin, 1803 as currently recognized (Zamudio and Greene, 1997) includes: *Lachesis muta* (Linnaeus, 1766), *Lachesis stenophrys* Cope, 1876, and *Lachesis melanocephala* Solórzano and Cerdas, 1986. *Lachesis muta* includes two subspecies: *L. m. muta* (Linnaeus, 1766) and *L. m.*

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rhombeata Wied-Neuwied, 1824. The nominal subspecies is distributed among the equatorial forests of Brazil, Guyana, Venezuela, Trinidad and Tobago, Bolivia, Peru, and Pacific slopes of Ecuador and Colombia (Campbell and Lamar, 1989). *Lachesis m. rhombeata* occurs in the Atlantic Forest, from the Brazilian state of Ceará (Borges-Nojosa and Lima-Verde, 1999) to the state of Rio de Janeiro. *Lachesis stenophrys* is found on the Atlantic versant of Costa Rica, Panama, and southern Nicaragua, while *L. melanocephala* is distributed along the Pacific coast of southeastern Costa Rica (Campbell and Lamar, 1989). The diagnostic external morphological features of the genus include tuberculate, almost pyramidal dorsal scales and the twice-divided distal subcaudal scales (Campbell and Lamar, 1989; Hoge and Romano, 1973). Despite uncertainty of its relationship among New World crotalines, the monophyly of *Lachesis* has been supported by many studies (Gutberlet and Harvey, 2002; Parkinson, 1999; Vidal et al. 1999; Werman, 1992).

Zamudio and Greene (1997) conducted a comprehensive study to estimate phylogenetic relationships within *Lachesis* using mitochondrial DNA. Their results suggest the independence of Central and South American lineages and show that specimens from Mato Grosso, Brazil (*L. m. muta*) are more closely related to the Atlantic Forest specimens (*L. m. rhombeata*) than to individuals from Surinam and Ecuador (*L. m. muta*), suggesting that the current taxonomy needs to be revised.

In this paper, we evaluate the validity of the currently recognized taxa of *Lachesis* using characters related to external morphology and hemipenes, investigate the phylogenetic relationships among some geographic groups, and redefine the geographical distribution of valid taxa.

Materials and Methods
Character Description

Morphological data related to squamation, hemipenes, and color pattern were collected from 265 alcohol-preserved specimens (Appendix I). Museum acronyms follow Leviton et al. (1985), with the addition of Universidade Federal do Ceará, Fortaleza (UFC); Instituto

Vital Brazil, Niterói (IVB); and Instituto Clodomiro Picado, San Jose, Costa Rica (ICP). Terminology follows Gutberlet (1998) for morphological features, Klauber (1972) for squamation, and Dowling and Savage (1960) and Myers and Campbell (1981) for hemipenes. The characters were selected from those used by Campbell and Solórzano (1992), Gutberlet (1998), Werman (1992), and Zamudio and Greene (1997). Character descriptions are given as follows.

1. Number of anterior dorsal scale rows (AD), counted at a position one head length posterior of the quadrate-mandibular articulation
2. Number of middorsal scale rows (MD), counted at midbody
3. Number of posterior dorsal scale rows (PD), counted at a position one head length anterior of the medial portion of cloaca
4. Number of ventrals (VE), counted following the method of Dowling (1951)
5. Number of subcaudals (SC), counted following the method of Peters (1964) and including those that are twice-divided
6. Number of supralabials (SL), counted following Gutberlet (1998)
7. Number of infralabials (IL), positioned between the mental scale and the posterior corner of the mouth (rictal region)
8. Prelacunal and second supralabial scale (PS), not fused (a) or fused (y)
9. Number of subfoveal rows (SF), defined according to Klauber (1972)
10. Number of intersupraoculars (IS), counted in a straight line from one supraocular to the other (supraoculars not included)
11. Number of suboculars (SO), scales below the eyes that contact the orbit
12. Number of interoculolabials (IO), counted according to Klauber (1972), including one supralabial and one subocular
13. Number of prefoveals (PF), bordered by the supralabials, nasals, loreals, lacunals, and subfoveal scales (if present)
14. Number of canthals (CA), counted according to Gutberlet (1998)
15. Number of interrictals (IR), counted according to Gutberlet (1998)

16. Loreal scale (LO), entire (0) or fragmented (1); positioned between the superior preocular scale and the postnasal scale
17. Rostral scale (RO), higher than broad (0) or broader than high (1); positioned between the first pair of supralabials
18. Number of preoculars (PO), one (0) or two (1); positioned in front of the ocular orbit
19. Preocular/supralacunal scales (PO/SUL), fused (0) or separated (1)
20. Parietals (PA), keeled (0) or tuberculate (1)
21. Internasals (IN), larger than the adjacent scales (0) or not distinct (1)
22. Prenasals (PNA), small (0) or large (1)
23. Postnasal (PON), contacts first supralabial (0) or no contact (1)
24. Sublacunal (SLC), entire (0) or divided (1); positioned posterior to the prelacunal scale (anteriormost scale inside the loreal pit)
25. Chinshields (CS), counted including the first pair of infralabials
26. Chinshields-infralabials (CS-IL), the lowest number of gular scales rows between the first scale after chinshields and the infralabial scales, examining both sides
27. Number of gulars between the chinshields and the first ventral (GV), the fewest scales between the first gular after chinshields and the first ventral scale (for this character the first ventral was considered to be the first one that was wider than long)
28. Width of the postocular stripe (WP), number of scale rows contained by the stripe at it broadest portion
29. Basal and lateral spines (HS), less than 15 spines per lobe (0); 25 to 50 spines per lobe (1); more than 70 spines per lobe (2)
30. Calyces on lateral surfaces of hemipenial lobes, restricted to distal portion (0); extending proximally to level of crotch (1)
31. Dorsal color of head, head with well defined dark blotches (0); head with inconspicuous dark blotches (1); head with practically no pigment, only some sparse dark punctations (2); head completely dark (3)
32. Color pattern of dorsal blotches along the body, dorsal blotches forming vertical bars laterally (0); not forming vertical bars laterally (1)

Statistical Analysis

For purposes of this analysis, the genus *Lachesis* was partitioned into six geographic groups, corresponding to specimens located on the Atlantic ($n = 29$) and Pacific ($n = 7$) versants of Central America, north ($n = 37$) and south of the Amazon River ($n = 68$), in Mato Grosso (Brazil) ($n = 56$), and within the Atlantic Forest of Brazil ($n = 68$). The Central American groups were defined based on current taxonomy and on a particular natural barrier (cordillera of Talamanca) that exerts influence on their distribution (Zamudio and Greene, 1997). Specimens from the Atlantic Forest and Amazonian region correspond to the currently recognized subspecies of South American *Lachesis* (Campbell and Lamar, 1989; Zamudio and Greene, 1997). Based on the results of Zamudio and Greene (1997), we consider specimens from Mato Grosso as a distinct group. We defined groups from north and south of the Amazon River to evaluate whether this natural barrier has played any role in the diversification of *Lachesis*.

In this study, analysis of specimens from northwestern South America, on the Pacific coast of Ecuador and Colombia (the Chocó region), was not possible. A single specimen from the province of Darien, Panama, was examined and shows features similar to *L. muta*. The results of Zamudio and Greene (1997) concerning specimens from the Chocó region are inconclusive. Nevertheless, Campbell and Lamar (2004) recognize the groups from northwestern South America as a distinct species, *L. acrochorda* (García, 1896), and suggest that this fourth species may be closely related to *L. muta*.

Principal components analysis (PCA; Manly, 2000) was performed to evaluate the distribution of the specimens in multivariate space without a priori definition of the groups, whereas multivariate analysis of variance (MANOVA; Zar, 1999) and discriminant analysis (Manly, 2000) were employed to study the variation between and within each previously defined group. Orthogonal comparisons (Sokal and Rohlf, 1995) among some groups were performed. The MANOVA was further used to verify the existence of sexual dimorphism within each group. Characters

that showed insufficient variation to justify the assumption of normality were not included in the statistical analysis. The following 13 characters were employed: number of anterior, middorsal, and posterior dorsal scale rows (three counts); ventral scales; subcaudals (including those that are twice-divided); supralabials; infralabials; intersupraoculars; interrictals; chinshields; chinshields-infralabials; gulars between the chinshields and the first ventral; and width of postocular stripe. In a later analysis, the South American specimens were classified, independent of their origin, based only on dorsal color of the head (character 31), and the new groups were subjected to discriminant analysis. This criterion was used because South American subspecies are diagnosed according to this feature (Campbell and Lamar, 1989; Hoge, 1966). Specimens from Mato Grosso were identified on the discriminant graph to compare their distribution in discriminant space to the currently recognized subspecies. In all analyses, assumptions of univariate normality and homoscedasticity were evaluated with the Kolmogorov-Smirnov's test and Levene's test, respectively (Zar, 1999). To test the robustness of the results obtained, we used the bootstrap method (Manly, 1991) with 1000 pseudoreplications using MatLab 4.2c1 for Windows (Mathworks, 1994). All statistical tests were performed with a significance level of 0.05, except the orthogonal comparisons (significance level of 0.01) in which a conservative position was adopted (following Sokal and Rohlf, 1995). The 95% confidence limits of the statistically significant variables in the multivariate variance analysis were compared among the different geographic groups to evaluate the level of overlap. Variables were considered taxonomically informative when the confidence limits did not overlap.

Phylogenetic Analysis

A phylogenetic matrix containing 26 morphological characters selected from the list above was analyzed. The tree was rooted with the outgroup method (Nixon and Carpenter, 1993). Outgroup taxa were *Bothriechis lateralis*, *B. nigroviridis*, and *Atropoides nummifer*. These taxa were chosen based on the analyses of Werman (1992), Zamudio and Greene (1997), and especially Parkinson (1999). Characters that showed no variation in both ingroup and outgroup (17–19; 23–24) were not used. Overlapping meristic characters (1–7; 9–15; 25–28) and qualitative polymorphic characters (8) were coded by the generalized frequency coding (GFC) method (Smith and Gutberlet, 2001), using the program Code This! (Gutberlet et al., 2000). The method incorporates features of the frequency bins (Wiens, 1995) and gap weighting (Thiele, 1993) methods. The GFC method divides polymorphic characters into subcharacters, which allows coding of the entire frequency distribution and, consequently, incorporates more information in the analysis compared to previous methods (Smith and Gutberlet, 2001). We used the USW (unequal subcharacter weighting) option of Code This! to weight the subcharacters. Subcharacter weights were adjusted according to Smith and Gutberlet (2001) so that equal weights were assigned to conventionally coded and generalized frequency coded characters. Binary and multistate (non-meristic) characters were treated as unordered. Characters coded by the GFC method were treated as ordered. A GFC matrix included a total of 284 characters (7 conventional and 277 subcharacters), of which 95 were uninformative and, thus, excluded from analysis. The GFC matrix is not presented due to space considerations, but can be obtained from the authors. In a second analysis, the polymorphic characters were coded by the gap weighting method (Thiele, 1993) using the median of each character (Table 1) for each taxon to avoid the effect of outliers in the analysis. The resulting matrix (Table 2) included the original 26 morphological characters, although Character 25 (chinshields) was not infomative. A third analysis combined our morphological data with mtDNA sequence data from Zamudio and Greene (1997). The combined analysis matrix contained 812 characters, of which 254 were parsimony-informative.

We performed parsimony analyses (Farris and Kluge, 1986; Kluge and Farris, 1969) using PAUP* 4.0b8a for Macintosh (Swofford, 2001) to infer a hypothesis of phylogenetic relationships for the genus *Lachesis*. The six geographic groups defined in the statistical analyses were treated as terminal taxa. The

TABLE 1.—Medians of the overlapping meristic characters used in the phylogenetic analysis using gap weighting coding method. MT = Mato Grosso; SA = south Amazon River; AF = Atlantic Forest; NA = north Amazon River; ACA = Atlantic coast Central America; PCA = Pacific coast Central America; MAX = maximum value; MIN = minimum value; BL = *Bothriechis lateralis*; BN = *Bothriechis nigroviridis*; AN = *Atropoides nummifer*. Numbers of the characters are described in the Materials and Methods section.

	MT	SA	AF	NA	ACA	PCA	BL	BN	AN	MAX	MIN
1	3,64	3,64	3,61	3,61	3,61	3,64	3,18	3,14	3,26	3,64	3,14
2	3,58	3,58	3,53	3,56	3,58	3,64	3,14	3,04	3,26	3,64	3,04
3	3,26	3,26	3,26	3,26	3,26	3,26	2,97	2,77	2,94	3,26	2,77
4	5,42	5,43	5,39	5,42	5,30	5,35	5,09	5,06	4,79	5,43	4,79
5	3,61	3,58	3,56	3,64	3,69	3,69	4,22	4,0	3,62	4,22	3,58
7	2,40	2,30	2,40	2,40	2,30	2,30	2,44	2,40	2,40	2,30	2,40
8	2,77	2,77	2,77	2,77	2,71	2,76	2,56	2,40	2,56	2,77	2,40
10	0,69	0,69	0,69	0	0	0	0	0	1,10	1,10	0
11	2,64	2,64	2,64	2,56	2,56	2,56	2,08	1,95	2,24	2,64	1,95
12	0,69	1,10	0,69	1,10	1,10	1,10	1,39	1,10	1,10	1,39	0,69
13	1,79	1,95	1,79	1,79	1,95	1,95	1,39	1,61	1,87	1,95	1,39
14	1,10	1,39	1,10	1,10	1,24	0,69	1,35	1,61	1,87	1,87	0,69
15	1,61	1,61	1,39	1,61	1,61	1,61	1,39	1,39	1,50	1,61	1,39
16	3,43	3,43	3,47	3,40	3,40	3,37	3,28	3,22	3,30	3,47	3,22
26	2,40	2,40	2,40	2,40	2,40	2,44	2,40	2,40	2,20	2,44	2,20
27	2,20	2,20	2,20	2,20	2,30	2,30	2,08	1,79	1,95	2,30	1,79
28	2,20	2,08	1,79	2,08	1,87	1,95	1,70	1,60	1,49	2,20	1,49
29	1,25	1,10	1,25	0,92	1,10	—	—	—	1,08	1,25	0,92

combined analysis used the mtDNA sequences from Zamudio and Greene (1997), which correspond to the geographic groups of our study. These sequences are available in the GenBank/EMBL database under accession numbers U96016–20, U96022–24, U96026–29, and U96033–34. We assumed equal weights for every codon position based on the results of Zamudio and Greene (1997). The branch-and-bound option was used to search for the most-parsimonious trees (Hendy and Penny, 1982). The bootstrap method (Felsenstein, 1985) using 1000 pseudoreplications was performed to estimate the robustness of the obtained branches.

RESULTS

Statistical Analysis

Multivariate variance analysis showed sexual dimorphism in all analyzed groups; therefore, males and females were analyzed separately. Because our sample from the Pacific coast of Central America had few specimens, we assumed this sample to be sexually dimorphic based on the results of other groups.

TABLE 2.—Matrix of character states coded by gap weighting method used in maximum parsimony analysis. Numbers of the characters are described in the Materials and Methods section.

	Characters																							
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	19	20	21	24	25	26	27	28	29	31	32
B. lateralis	c	g	k	m	z	z	l	y	a	f	z	a	o	a	g	0	0	1	1	v	o	h	?	0	?	?
B. nigroviridis	a	a	a	l	r	s	a	y	a	a	p	k	u	a	a	0	0	1	1	v	a	e	?	0	?	?
A. nummifer	g	j	j	a	b	s	l	a	z	l	p	v	z	n	i	l	0	1	0	a	i	a	m	1	?	?
L. muta (MT)	z	x	z	z	c	s	z	b	q	z	a	s	j	z	v	1	1	0	0	v	u	z	z	2	0	1
L. muta (SA)	z	x	z	z	b	a	z	b	q	z	p	z	p	z	v	1	1	0	0	v	u	v	o	2	1	1
L. muta (AF)	y	u	z	x	a	s	z	a	q	z	a	s	j	a	z	1	1	0	0	v	u	l	z	2	0	1
L. muta (NA)	y	w	z	z	d	s	z	r	a	w	p	s	j	z	s	1	1	0	0	v	u	v	a	2	1	1
L. stenophrys	y	x	z	u	f	a	v	t	a	w	p	z	m	z	s	1	1	1	0	v	z	n	o	2	2	0
L. melanocephala	z	z	z	w	f	a	l	b	a	w	p	z	a	z	p	1	1	1	0	z	z	q	?	2	3	0

The MANOVA between all groups was significant for females ($F = 12.4026$; $P < 0.01$; $n = 110$) and males ($F = 14.2202$; $P < 0.01$; $n = 155$). An orthogonal comparison between south and north Amazon River specimens was not significant for females ($F = 2.4582$; $P = 0.05$; $n = 38$), but the difference was significant for males ($F = 4.2598$; $P < 0.01$; $n = 67$). The group from Mato Grosso was significantly different from the sample formed by specimens from north and south of the Amazon River for females ($F = 8.2261$; $P < 0.01$; $n = 58$) and males ($F = 12.0246$; $P < 0.01$; $n = 103$). The Atlantic Forest group was significantly different from the sample formed by specimens from north and south of the Amazon River for females ($F = 18.7199$; $P < 0.01$; $n = 73$) and males ($F = 20.8826$; $P < 0.01$; $n = 100$). The specimens from Mato Grosso and from the Atlantic Forest were significantly different for females ($F = 8.4516$; $P < 0.01$; $n = 55$) and males ($F = 14.4941$; $P < 0.01$; $n = 69$).

The results of the PCA were similar to the discriminant analysis and, therefore, are not shown. Discriminant analysis differentiated the groups of females and males through the first two discriminant functions, which corresponded to 89% of the entire variation. The combination of the third discriminant function, with the first or second functions, showed no satisfactory discrimination in either sex. To visualize the level of differentiation among groups, the obtained scores were plotted, and both graphs show a clear differentiation between South and Central American groups (Fig. 1). Groups from Amazonia and Atlantic Forest are differentiated from each other, but specimens to the north and south of the Amazon River are poorly distinguished, supporting the results of the MANOVA. Specimens from Mato Grosso occupy a position between Amazonian and Atlantic Forest groups.

In the third analysis, based on the dorsal color of the head, the canonical plot graphs show discrimination between the two existing patterns in both sexes (Fig. 2). The first two discriminant functions represented 95% of the variation in females and 98% in males. Nevertheless, specimens from Mato Grosso are scattered along both axes, not forming an intermediate group as in the previous discriminant analyses (Fig. 1). Furthermore, there is no congruence between the localities of the specimens from Mato Grosso and the position they occupy in the graph, i.e., geographically close localities are not necessarily proximal in the graph. Because specimens from Mato Grosso do not show any correlation between head-color pattern and geographical distribution in the discriminant space (Fig. 2), it is not possible to diagnose these two putative subspecies based on head coloration.

Phylogenetic Analysis

The GFC analysis yielded a single most-parsimonious tree with 1,144,536 weighted steps, consistency index of 0.744, and rescaled retention index of 0.563 (Fig. 3). The gap weighting analysis generated a single most-parsimonious tree with 820 weighted steps, consistency index of 0.789, and rescaled retention index of 0.624, showing a topology identical to the tree recovered by GFC (Fig. 3). The combined data analysis recovered five most-parsimonious trees with 3,034,042 weighted steps, consistency index of 0.817, and rescaled retention index of 0.612. The strict consensus of these trees is similar to the trees recovered by the other analyses, the ambiguities being restricted to relationships among the outgroups (Fig. 3). The following synapomorphies are relative to morphological data supported under both GFC and gap weighting coding methods, under ACCTRAN and DELTRAN optimization criteria. The clade formed by the genus *Lachesis* is supported by three unambiguous synapomorphies relative to the outgroup selected: number of intersupraoculars, tuberculate parietals, and more than 70 spines per lobe on the hemipenis. The clade formed by the South American groups of *Lachesis* is supported by two unambiguous synapomorphies: internasals distinct from adjacent scales, and dorsal blotches not forming vertical bars laterally. The clade formed by the Central American groups is supported by one unambiguous synapomorphy under the ACCTRAN criterion of optimization: dorsal blotches forming vertical bars laterally. Atlantic Forest, Mato Grosso, and south Amazon River groups form a clade supported by one unambiguous synapomorphy: number of intersupraoculars.
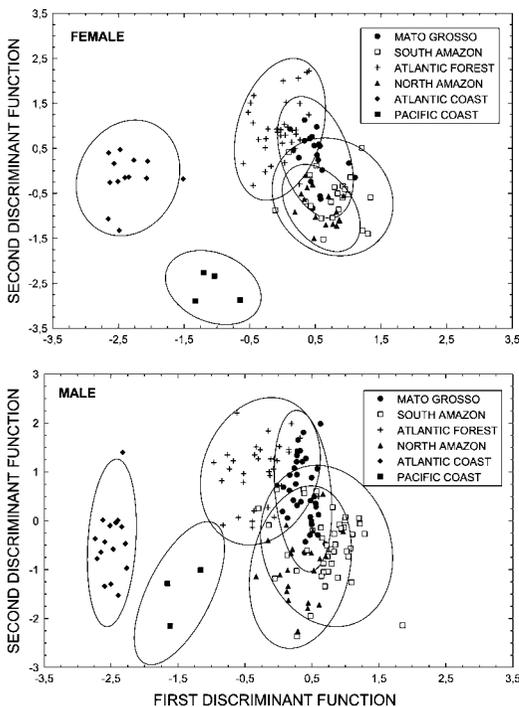
FIG. 1.—Canonical analysis of the six female and male geographic groups of *Lachesis* with the respective 95% confidence limits ellipse for each group.
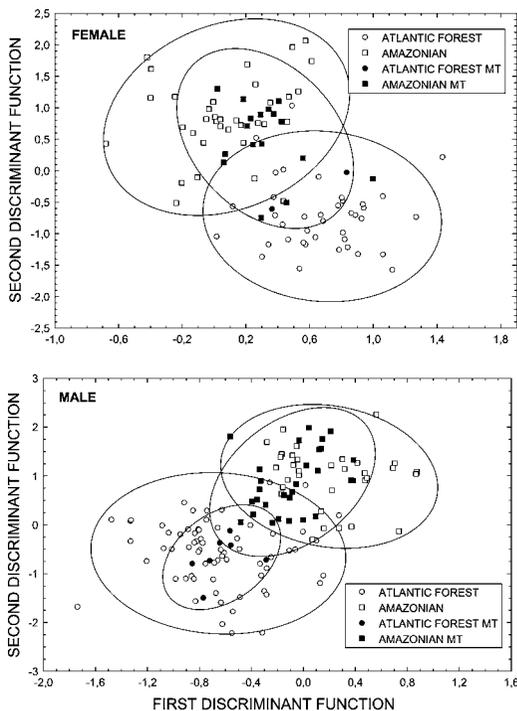
FIG. 2.—Canonical analysis of the female and male geographic groups of *Lachesis* based on the dorsal color pattern of the head. Atlantic Forest and Amazonian patterns correspond to states 0 and 1 of Character 31, respectively. Atlantic Forest MT and Amazonian MT correspond to specimens from Mato Grosso, Brazil, with states 0 and 1 of Character 31, respectively.

The clade formed by the Mato Grosso and Atlantic Forest groups is supported by one unambiguous synapomorphy: head generally with well defined dark blotches. None of the South American geographic groups have autapomorphies. The group from the Pacific coast of Central America, *L. melanocephala*, is supported by one autapomorphy: head completely dark. The group from the Atlantic coast of Central America, *L. stenophrys*, is supported by one autapomorphy under the DELTRAN optimization criterion: head with practically no pigment, showing only some sparse dark punctation.

Geographic Variation in Lachesis

The general morphological features that distinguish the groups of *Lachesis* are readily apparent. The Atlantic Forest group has slightly fewer ventral scales than the Amazonian and Mato Grosso groups. Specimens from the Atlantic Forest have a wider postocular stripe. The prelacunal and second supralabial scales are not fused in the Atlantic Forest group, and this character is variable in other groups. The north Amazon group possesses a slightly narrower postocular stripe compared to other groups. Specimens from Mato Grosso have a wider postocular stripe than Amazonian groups. Central American groups have fewer ventral scales than South American groups. However, with the exception of ventral scales, these features are not completely fixed in these groups and show a high degree of overlap (Table 3). Another relevant feature, though variable, is that members of the Atlantic Forest and Mato Grosso groups have more conspicuous blotches on the dorsum of the head than do Amazonian groups. Central American specimens can be easily diagnosed by the color pattern of the head. The Atlantic Coast group possesses a head that almost completely lacks black pigmentation, while specimens from the Pacific Coast have a completely black head.

DISCUSSION

The statistical analysis distinguished both Central and South American groups of *Lachesis*. South American subspecies are distinct according to some characters (Table 3), but specimens from Mato Grosso are intermediate. The Mato Grosso group is phylogenetically more closely related to the Atlantic Forest group (Fig. 3). However, in the discriminant analysis, data points from Mato Grosso are distributed among Amazonian and Atlantic Forest groups, precluding an unambiguous diagnosis. The characters Color of the Dorsum of the Head and Width of Postocular Stripe, commonly used to distinguish the South American subspecies according to Wied-Neuwied (1824) or Hoge (1966) and Hoge and Romano (1978), are variable in all geographic groups.

Most of the characters we used in the phylogenetic analysis are of the type usually avoided due to the variation that they exhibit in the terminal taxa (Thiele, 1993). These characters (quantitative and polymorphic) are normally excluded from phylogenetic analysis for a variety of reasons, e.g., they show intraspecific variation (Gensel, 1992), are arbitrarily defined (Cox and Urbatsch, 1990), or are highly homoplastic (Campbell and Frost, 1993; Wiens, 1995). Nevertheless, these types of characters are common and are occasionally used in studies, such as ours, that aim to examine inter-intraspecific variation (Campbell and Frost, 1993; Gutberlet, 1998; Wiens, 1999, 2000). Moreover, the ideal character concept varies according to the author, and the criteria for choosing and excluding characters are generally unclear (Poe and Wiens, 2000). Although some criticism of this type of character may be valid (Crother, 1990; Farris, 1966; Mayr, 1969), recent studies corroborate that these characters do have phylogenetic information and should be considered (Gutberlet, 1998; Gutberlet and Harvey, 2002; Smith and Gutberlet, 2001; Wiens, 1995, 1998). The criticism of arbitrary coding of quantitative character states is a problem that may also influence qualitative characters; furthermore, most morphological characters describe quantitative variation, regardless of whether they are coded
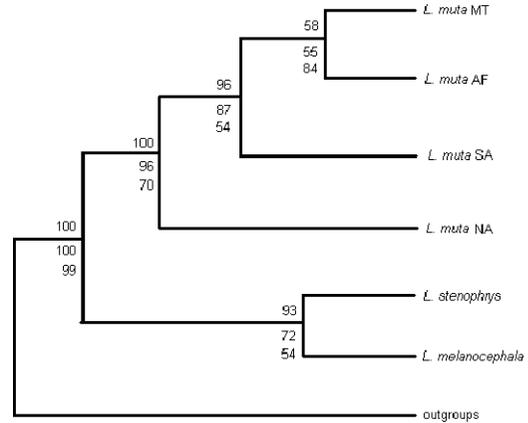
FIG. 3.—Most-parsimonious tree recovered for the geographic groups of *Lachesis*. Numbers along the branches represent bootstrap values from the three analyses performed. Bootstrap values were estimated from 1000 pseudoreplicates and are listed (from top to bottom) for combined data, GFC method, and gap weighting method. MT = Mato Grosso; SA = south Amazon River; AF = Atlantic Forest; NA = north Amazon River.

qualitatively or quantitatively (Poe and Wiens, 2000; Wiens, 2001). The GFC method simply translates the frequency distributions of the characters into a set of discrete states, avoiding the use of central tendency measures that could be labeled arbitrary (Smith and Gutberlet, 2001). The GFC method seems to be the most appropriate for treating this problem. Another relevant consideration is whether or not to order the multistate characters (Hauser and Presch, 1991; Kluge, 1991). Gap weighting (Thiele, 1993) and frequency bins (Wiens, 1995) demand that characters be ordered, which may not be a problem if, as Slowinski (1993) argues, the ordering of characters rarely causes changes in the tree topology. The GFC method allows the use of ordered or unordered characters (Smith and Gutberlet, 2001).

The three phylogenetic analyses yielded trees with similar topology (Fig. 3). In general, the bootstrap proportions in the analysis that used GFC are greater than in gap weighting (Fig. 3). Also, the number of clades supported with bootstrap proportions of 70% or greater means, according to Hillis and Bull (1993), great probability of accuracy. These results are similar to a previous study comparing some parsimony coding methods (Smith and Gutberlet, 2001) and provide additional evidence

TABLE 3.—Variation in the taxonomically informative variables used to differentiate the geographic groups of *Lachesis*. Data from males and females are grouped. Amazonian groups are analyzed together. VE = number of ventral scales; WP = width of the postocular stripe.

| Variables | Mato Grosso (*n* = 56) | | Amazonian (*n* = 105) | | Atlantic Forest (*n* = 68) | |
	95% confidence limits	Amplitude of variation	95% confidence limits	Amplitude of variation	95% confidence limits	Amplitude of variation
VE	224–227	220–232	226–228	219–236	218–222	213–231
WP	2.5–3	1.5–3.5	1.5–2	1–2.5	2.5–3	1.5–4

that GFC can be used to accurately reconstruct phylogeny. Concerning the combined data, bootstrap proportions are generally greater than in the first two analyses, indicating compatibility between morphological and molecular data. The tree topology obtained in our study is congruent with the results of Zamudio and Greene (1997), based on molecular data, and supports the use of quantitative and polymorphic characters in phylogenetic analysis. In our study, these characters were phylogenetically informative and corroborated previous hypotheses derived from independent sources of data.

The results of the phylogenetic analysis combined with statistical data suggest independence between the South and Central America clades, as suggested by Zamudio and Greene (1997). Although the Central American clade is supported by just one unambiguous synapomorphy under ACCTRAN optimization, the South American clade is supported by two unambiguous synapomorphies under both optimization criteria. The taxonomic status of the two currently recognized Central American species is supported by our study.

The results for South American *Lachesis* suggest that the groups from Mato Grosso and the Atlantic Forest are more closely related to each other than to the Amazonian groups. Zamudio and Greene (1997) also obtained this result, corroborating our conclusion. The north Amazon group seems to have been the first to diverge, being the sister group of the remaining South American groups. These conclusions have relevant implications for currently recognized South American taxa. *Lachesis m. muta* is distributed throughout the Amazon basin, including Mato Grosso. *Lachesis m. rhombeata* is restricted to the Atlantic Forest. According to the cladogram

(Fig. 3), *L. m. muta* is paraphyletic, because specimens from Mato Grosso are more closely related to *L. m. rhombeata* than to *L. m. muta*. Considering the specimens from Mato Grosso as *L. m. rhombeata* would not solve this problem, as *L. m. muta* remains paraphyletic, because the Amazonian groups are not monophyletic according to this analysis. The alternative for making the two taxa monophyletic is to restrict the distribution of *L. m. muta* to latitudes north of the Amazon River and extend the distribution of *L. m. rhombeata* from the Atlantic Forest to south of the Amazon basin. Nevertheless, the north Amazon group has no features that unambiguously distinguish it from the others. Statistical analysis reveals that this group is very similar to the south Amazon group and to specimens from Mato Grosso. In the phylogenetic analysis, this group has no unambiguous autapomorphies. Although the postocular stripe is generally thinner compared to other groups, the degree of overlap is large and a diagnosis of this taxon becomes difficult. The same reasoning prevents the recognition of other South American groups as distinct species.

A hypothesis that may explain the results obtained in our study for South American groups of *Lachesis* is that, during the Pleistocene, the Neotropical region had alternations of moist/hot and dry/cool eras (Haffer, 1969; Van der Hammen, 1972, 1974). These events caused successive expansions and retractions of the forest (Ab'Saber, 1977*a*; Van der Hammen and Asby, 1994). Bigarella and Andrade-Lima (1982) proposed, based on the morphoclimatic domains of Ab'Saber (1977*b*), that the Amazonian Forest and the Atlantic Forest were in contact during some period in the Quaternary through the region currently occupied by the "Caatinga." De Vivo (1997)

postulated that this connection between Amazonian and Atlantic forests was capable of sheltering arboreal species of mammals that are typical of tropical forests. The same connection probably allowed some species, which at present have disjunct distributions in the Amazonian and Atlantic forests, to have contiguous populations during the Quaternary, thus curtailing allopatric speciation (De Vivo, 1997). Costa (2003) argued that Central Brazilian forests are fundamental to explanations of the distribution patterns of some lowland small mammals. Nevertheless, there are no fossil records of *Lachesis* from the "Caatinga" domain. All that can be suggested is that the Amazonian and Atlantic Forest groups of *Lachesis* somehow maintained gene flow that prevented a total differentiation between them and that this connection probably occured through the region now known as Mato Grosso.

Based on these results, we can state that the examined South American groups have morphological differences among them; however, these differences are not sufficiently fixed (Davis and Nixon, 1992) to distinguish two or more independent lineages in the genus *Lachesis* in South America. The taxonomic status of the two currently recognized subspecies is herein altered in order to work solely with monophyletic taxa. Thus, the subspecies *Lachesis muta rhombeata* Wied-Neuwied, 1824 is placed in the synonymy of *Lachesis muta* (Linnaeus, 1766).

TAXONOMY

Taxonomic History

Linnaeus (1766) described *Crotalus mutus* with the type locality as Surinam. Daudin (1803) described the genus *Lachesis* to accomodate the species *C. mutus* Linnaeus, 1766. Wied-Neuwied (1824) described *Lachesis rhombeata* and designated Brazil as the type locality. Cope (1876) described *Lachesis stenophrys* from the type locality of Sipúrio, Costa Rica. Boulenger (1896) placed *L. rhombeata* and *L. stenophrys* in the synonymy of *L. muta*. Taylor (1951) recognized the validity of *Lachesis muta stenophrys* Cope, 1876 and, by fiat, of *L. m. muta* (Linnaeus, 1766) as the nominal subspecies. Hoge (1966) described *Lachesis m. noctivaga*, with the type

locality as the city of Vitória, state of Espírito Santo, Brazil. Hoge and Romano (1978) placed *L. m. noctivaga* in the synonymy of *L. muta rhombeata* and restricted the type locality of the latter taxon to Vitória, Espírito Santo. Solórzano and Cerdas (1986) described *Lachesis m. melanocephala* with the type locality of southeastern Costa Rica. Zamudio and Greene (1997) elevated *L. m. stenophrys* and *L. m. melanocephala* to species level, while maintaining the taxonomic status of South American taxa.

Taxonomic Account

Lachesis Daudin, 1803

1803 *Lachesis* Daudin, Bull. Sci. Soc. Philomath. Paris (2)3:188. Type-species: *Crotalus mutus* Linnaeus, 1766

1811 *Trigonocephalus* Oppel, 1811 [dated 1810], Ann. Mus. Hist. Nat., Paris 16:388. Latreille, 1801. Type-species: *Scytale ammodytes* Latreille, 1801

1815 *Trigalus* Rafinesque, Analyse Nat. (Herpetol. section):77. [Replacement name for *Trigonocephalus* Oppel]

1820 *Cophias* Merrem, Tent. Syst. Amph., 191:154. Type-species: *Cophias crotalinus* Gmelin, 1788

Diagnosis.—The only oviparous New World crotaline genus. Dorsal scales verrucate, parietals tuberculate, hemipenes with more than 70 spines per lobe, and twice-divided distal subcaudals.

Description.—Large snakes reaching approximately 3 m total length (TL). Head distinct from body. Body in cross section triangular or round. Head scales granular. Rostral triangular, broader than high; nasals divided; prenasals large, postnasals usually not touching first supralabial, internasals distinct or not; usually three small canthal scales; single, elongate postocular; 10–18 intersupraoculars usually not keeled; tuberculate parietals; 26–35 interrictals; 8–11 supralabials, third larger; 12–16 infralabials, first pair in contact behind the mental; first two pairs of infralabials usually touch first pair of chinshields; 0–6 prefoveals; 0–1 subfoveal row; sublacunal entire; lacunolabial present or absent; loreal undivided, approximately as high as broad and contacting anterior margin of upper preocular;

two preoculars, longer than high, and bordering the loreal pit; inferior preocular fused to supralacunal; upper preocular contributing to canthus rostralis and larger than inferior preocular; 5–6 interoculolabials; eye relatively small, distance between tangent to ocular globe and tangent to rostral 3–3.5 times eye diameter; vertical pupil; dorsal scale formula 30–42/29–41/22–28 rows; dorsals longer than wide at midbody, becoming almost as long as wide on distal portion of body; dorsals without apical pits and scales from vertebral region strongly keeled, verrucate; this feature less conspicuous in paraventral region where dorsal scales may lack keels; 197–236 ventrals; cloacal scale undivided; 41–56 subcaudals; initial pairs may be entire, most are divided whereas distally the subcaudals are twice-divided.

Color in preservative.—Dorsum of head creamish yellow or brown with black or dark brown blotches with different levels of fragmentation. Black postocular stripe varying from 1–4 rows wide. Body creamish yellow with a brighter distal portion. Dorsal, dark brown to black rhomboidal blotches along the body (18–35), sometimes blotches acquiring a triangular or zig zag aspect. Laterally these blotches may grow narrower, forming vertical bars or maintaining the rhomboidal aspect. Eventually these blotches extend to the ventral scales. Ventrally the head and body are ivory white without blotches.

Geographic distribution.—South American Amazonian forests and Atlantic Forest in Brazil. Central America, in southern Nicaragua, Costa Rica, and Panama (Campbell and Lamar, 2004; Fig. 4). Usually inhabits primary forests; sometimes found in secondary forests.

Lachesis muta (*Linnaeus, 1766*)

1766 [*Crotalus*] *mutus* Linnaeus, Systema Naturae, Ed. 12:373. Type-locality: Surinam

1789 *Coluber crotalinus* Gmelin, Systema Naturae, Ed. 13(1):1094. Type-locality: not given

1801 *Scytale catenatus* Latreille, *In* Sonnini and Latreille, Hist. Nat. Rept. 3:162. Type-locality: Surinam

1802 *Scytale ammodytes* Latreille, *In* Sonnini and Latreille, Hist. Nat. Rept. 3:165. Type-locality: Ceylon [In error]

1802 *Coluber alecto* Shaw, Gen. Zoology, Amphibians, 3(2):405. Type-locality: Ceylon [In error]

1803 *Lachesis mutus*; Daudin, Hist. Nat. Rept. 5:351

1803 *Lachesis ater* Daudin, Hist. Nat. Rept. 5:354. Type-locality: Surinam

1811 *Trigonocephalus ammodytes*; Oppel, Ann. Mus. Hist. Nat., Paris 16:390

1820 [*Cophias*] *crotalinus*; Merrem, Tent. Syst. Amph., 191:144

1822 *Trigonoceph*[*alus*] *crotalinus*; Schinz, Das Thierreich Grund. Naturgesch. Ver. Anat. 2:144

1822 *Lachesis muta*; Schinz, Das Thierreich Grund. Naturgesch. Ver. Anat. 2:144

1822 *Lachesis atra*; Schinz, Das Thierreich Grund. Naturgesch. Ver. Anat. 2:144

1822 *Scytale catenata*; Schinz, Das Thierreich Grund. Naturgesch. Ver. Anat. 2:144

1824 *Bothrops surucucu* Wagler, in Spix, Spec. Nov. Serp. Brazil:59, pl. 23. Type-locality: Brazil

1824 *Lachesis rhombeata* Wied-Neuwied, Abbild. Nat. Brazil, Lief. 5:pls. 5, 5a. Type-locality: Brazil

1825 *C*[*rasedocephalus*] *crotalinus*; Gray, Ann. Philos. (2)10:205

1854 *Lachesis mutus*; A.-M.-C. Duméril, Bibron, and A.-H.-A. Duméril, Erp. Gén. 7(2):1486

1872 *Trigonocephalus* (*Lachoesis*) *brasiliensis* Liais, Clim. Géol., Faune Géogr. Brésil: 306–307. Type-locality: not given, probably Rio Doce, MG, Brazil (Hoge and Romano, 1978)

1872 *Trigonocephalus rhumbeatus*; Liais, Clim. Géol., Faune Géogr. Brésil:306

1872 *Lachoesis rhumbeata*; Liais, Clim. Géol. Faune Géogr. Brésil:306

1896 *Lachesis mutus*; Boulenger, Cat. Sn. Brit. Mus. 3:534

1898 *Lachesis muta*; Boettger, Kat. Rept. Samml. Mus. Senckenb. Naturforsch. Ges. 2:137

1951 *Lachesis muta muta*; Taylor, Univ. Kansas Sci. Bull. 34:184. Type-locality: Surinam

1966 *Lachesis muta noctivaga* Hoge, Mem. Inst. Butantan, 32:162, pl. 20 (1965). Type-locality: Vitória, ES, Brazil

1978 *Lachesis muta rhombeata*; Hoge and Romano, Mem Inst. Butantan, 40/41:54
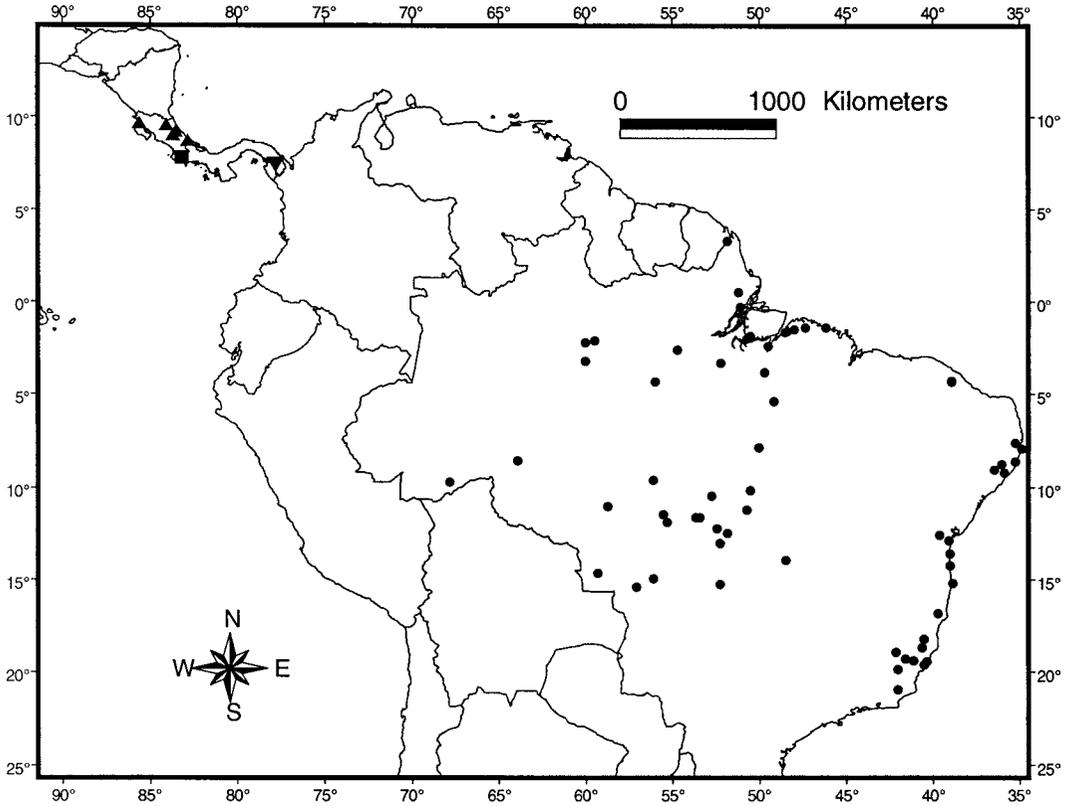
FIG. 4.—Localities of specimens examined of the genus *Lachesis*. Key: *Lachesis muta* ●; *Lachesis melanocephala* ■; *Lachesis stenophrys* ▲; *Lachesis* from Darien, Panamá ▼.

(1976/77). Type-locality: Restrict to Vitória, ES, Brazil, in this work

Diagnosis.—Distinguished from *L. steno-phrys* and *L. melanocephala* by having more ventral scales (215–234 in females and 213–236 in males), compared to 197–211 in females and 198–204 in males of *L. stenophrys* and 211–214 in females and 209–214 in males of *L. melanocephala*. Additionally, the head of *L. muta* is not uniformly black as in *L. melano-cephala*, but has dark blotches over much of its surface; the head of *L. stenophrys* is nearly immaculate. The dorsal blotches in *Lachesis muta* do not form vertical bars laterally as in *L. stenophrys* and *L. melanocephala*.

Description.—Largest specimen a male 2510 mm SVL and 216 mm TL; body round in cross section; postnasals usually not touch-ing first supralabial; internasals distinct; 3–5 canthals; 11–15 intersupraoculars in females and 10–18 in males; 26–35 interrictals in both

sexes; 9–11 supralabials in females and 8–11 in males; 13–16 infralabials in both sexes; 1–6 prefoveals in females and 1–5 in males; 0–1 row of subfoveals; lacunolabial present or absent; 8–14 chinshields in females and 6–14 in males; chinshields separated from infra-labials by 5–10 scales in females and 5–11 in males; 3–13 gulars between chinshields and first ventral in females, 4–13 in males; dorsal scale formula 33–41/31–41/23–28 and 30–40/ 29–38/22–27 in females and males, respective-ly; 215–234 ventrals in females and 213–236 in males; 41–53 subcaudals in females and 44–56 in males; 9–20 rows of twice-divided subcau-dals in females and 9–22 in males.

Color in preservative.—Dorsum of head creamish yellow or brown, with dark brown or black blotches with different levels of frag-mentation, varying from dark dots along the head forming small blotches or lines mainly on the posterior portion of the head, enhancing the granular appearance of the dorsum of

head, or head with conspicuous blotches forming markings that contrast greatly with ground color. Black postocular stripe varying from 1–4 rows in width in females and 1–3.5 in males. Dark brown or black rhomboidal dorsal blotches varying from 24–35 in females ($n = 45$) and 18–33 in males ($n = 74$), not forming vertical bars laterally and usually extending to the second or third dorsal scale row; blotches sometimes reaching ventral scales.

Hemipenis.—Usually extending 8–10 subcaudals; bilobed, lobes larger than the hemipenial body that laterally has two basal depressions; sulcus spermaticus divides approximately at midlength, between the bottom of hemipenial body and the point of bifurcation of the lobes and is centrolineal; hemipenis naked proximally; region above the sulcus spermaticus bifurcation is densely spinose (approximately 95–108 spines; $n = 12$); internal surface of lobes has a larger number of spines compared to external surface, which also has larger spines; apical region calyculate, calyces of medial surface of each lobe extend more distally compared to calyces of lateral surface; on hemipenial asulcate side, adjacent to the bifurcation of lobes, tiny spines present.

Geographic distribution.—Occurs in tropical forests of Brazil, Guyanas, Venezuela, Trinidad, Bolivia, Peru, Ecuador, and Colombia. Pacific slopes of Ecuador, Colombia, and province of Darien, Panama. Atlantic Forest in Brazil from the state of Ceará to the state of Rio de Janeiro. Moreover, occurs in the states of Amazonas, Pará, Amapá, Roraima, Rondônia, Acre, Mato Grosso, and Goiás (Campbell and Lamar, 2004; Fig. 4).

Lachesis stenophrys *Cope, 1876*

1876 *Lachesis stenophrys* Cope, Journ. Acad. Nat. Sci. Phila. 8(2) (1875):152. Type-locality: Sipúrio, Costa Rica
1896 *Bothrops achrocordus* Garcia, Ofídios Venen. Cauca:22, pl. 4. (but see discussion)
1951 *Lachesis muta stenophrys*; Taylor, Univ. Kansas Sci. Bull. 34:184
1997 *Lachesis stenophrys*; Zamudio and Greene, Biol. J. Linn. Soc. 62:436

Diagnosis.—Distinguished from *L. melanocephala* by having head that is predominantely unpigmented dorsally. Furthermore, *L. stenophrys* has fewer ventral scales (197–211 in females; 215–234 in males) than *L. muta.*

Description.—Largest specimen a male 2050 mm SVL and 198 mm TL; body somewhat triangular in cross section; postnasals not touching first supralabial; internasals distinct or not; 3–5 canthals; 10–12 intersupraoculars in females and 10–13 in males; 26–31 interrictals in females and 27–31 in males; 8–9 supralabials in females and 8–10 in males; 12–15 infralabials in females and 13–15 in males; 1–3 prefoveals; 0–1 subfoveal rows; lacunolabial present or absent; 9–14 chinshields in females and 8–13 in males; chinshields separated from infralabials by 7–10 scales in females and 7–9 in males; 4–6 gulars between chinshields and first ventral in both sexes; dorsal scale formula 35–39/33–37/24–26 and 34–38/31–37/24–25 in females and males, respectively; 197–211 ventrals in females and 198–204 in males; 46–53 subcaudals in both sexes; 8–17 rows of twice-divided subcaudals in females and 11–16 in males.

Color in preservative.—Dorsum of head creamish yellow or brown, with some sparse dark brown or black punctations. Black postocular stripe varying from 1.5–2.5 scale rows in width in both sexes. Dark brown or black rhomboidal dorsal blotches varying from 23–37 in males ($n = 10$) and 24–36 in females ($n = 8$). Blotches usually becoming narrower laterally, forming vertical bars. However, even when vertical bars are absent blotches are narrower laterally compared to *L. muta.*

Hemipenis.—General structure similar to *L. muta*; 81–98 spines in each lobe ($n = 3$).

Geographic distribution.—Atlantic slopes of Costa Rica, Panama, and southern Nicaragua (Campbell and Lamar, 2004; Fig. 4).

Lachesis melanocephala *Solórzano and Cerdas, 1986*

1986 *Lachesis muta melanocephala* Solórzano and Cerdas, J. Herpetol. 20:463–466
1997 *Lachesis melanocephala*; Zamudio and Greene, Biol. J. Linn. Soc. 62:436

Diagnosis.—Distinguished from other species of *Lachesis* by having the dorsum of the head completely black.

Description.—Largest specimen a female 1800 mm SVL and 197 mm TL; body somewhat triangular in cross section; postnasals may contact first supralabial; internasals not distinct; four canthals; 11–12 intersupraoculars in both sexes; 29–31 interrictals in females and 28–29 in males; 8–9 supralabials

in both sexes; 13–14 infralabials in females and 12–13 in males; 0–2 prefoveals; 0 subfoveal scale rows; lacunolabial present or absent; 5–11 chinshields in females and 10–11 in males; chinshields separated from infralabials by 8–9 scales in females and 7–9 in males; 5–10 gulars between chinshields and first ventral in females, and 5–6 in males; dorsal scale formula 40–42/39–40/25 and 36–40/34–39/25–26 in females and males, respectively; 211–214 ventrals in females and 209–214 in males; 35–38 subcaudals in females and 39–40 in males; 13–15 rows of twice-divided subcaudals in females and 12–14 in males.

Color in preservative.—Dorsum of head completely black. Postocular stripe fused with the black dorsum of the head. Dark brown or black rhomboidal dorsal blotches vary from 24–35 in males (*n* = 3) and 26–37 in females (*n* = 4). Blotches similar to *L. stenophrys*.

Hemipenis.—General structure similar to *L. muta* and *L. stenophrys*; 91–96 spines on each lobe (*n* = 4).

Geographic distribution.—Restricted to Pacific coast of southeastern Costa Rica, especially at Osa Peninsula (Campbell and Lamar, 2004; Fig. 4).

RESUMO

O gênero *Lachesis* Daudin, 1803 foi dividido em seis grupos geográficos para se avaliar a posição taxonômica e as relações filogenéticas entre estes grupos. Foram usados caracteres relativos à morfologia externa e hemipênis. Resultados obtidos através das análises filogenética e estatística suportam o reconhecimento das espécies centro-americanas *L. melanocephala* e *L. stenophrys* como espécies distintas, enquanto a espécie sul-americana *L. muta* é reconhecida como monotípica, sem a divisão em subespécies. Tais resultados confirmam uma independência das linhagens da América Central em relação à América do Sul e são congruentes com outros estudos que utilizaram dados moleculares.

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APPENDIX I

Specimens Examined

Atropoides nummifer (*n* = 4).—Costa Rica: *Cartago:* Turrialba, Buena Vista: MZUCR 1502; *San Jose:* Tarrazu, San Marcos: MZUCR 112; *Puntarenas:* Coto Brus, Alturas de Coton: MZUCR 10877–78.

Bothriechis lateralis (*n* = 3).—Costa Rica: *Heredia*: Barva, P. N. Braulio Carrillo: MZUCR 9445; San Raphael, El Tirol: MZUCR 13257; *Alajuela*: Palmares, Palmares: MZUCR 12727.

Bothriechis nigroviridis (*n* = 2).—Costa Rica: *San Jose*: Dota, San Gerardo: MZUCR 11151; *Heredia*: Barva, P. N. Braulio Carrillo: MZUCR 9441.

Lachesis muta (*n* = 229).—Brazil: *Acre*: Rio Branco: MCPRS 2710; *Amapá*: Ferreira Gomes: IB 25404; Oiapoque: IB 24830; IB 13876; Rio Tracajuba: IB 25406; *Amazonas*: Presidente Figueiredo: MPEG 18845; MPEG 17589; MPEG 17554; MPEG 17763; MPEG 17522; IB 52391–93; IB 52406–11; IB 52924–26; IB 53440–41; IB 53542; IB 53423; IB 52707–09; Manaus: IB 52923; IB 43218; IB 45997; IB 43615; IB 40929; IB 43156; IB 41406; *Pará*: Altamira: IB 43149; Ananindeua: MPEG 16822; IB 46586; IB 48080; Apeú: MPEG 1203; Belém: MPEG 6359; IB 46558; IB 41296; IB 42952; IB 42656; IB 46123; Breves: IB 41521; Cametá: IB 2551; Colônia Nova (near Rio Gurupi-BR-316): MPEG 15058; Itaituba: IB 55687; Marabá: MPEG 10162; MPEG 16523; MPEG 16509;

MPEG 13424; MPEG 17232; MPEG 16786; MPEG 18484; MPEG 12807–08; MPEG 17163; MPEG 16514; MPEG 15530; MPEG 16773; IB 54648; Melgaço: MPEG 19144; Peixe-Boi: MPEG 17861; Porto Jarbas Passarinho (Rio Araguaia): MPEG 12744; Redenção: IB 40905; Santarém: IB 51542; Taciateua: MPEG 507; Tucuruí: IB 49544–49; IB 49927; IB 46169; IB 46988–90; IB 48081–82; IB 48085; IB 49918–22; IB 47780; IB 46657; IB 47701; IB 46670; IB 48078; IB 51543; IB 49915–16; IB 48230; IB 46642; IB 46664; Viseu: MPEG 10161; *Rondônia*: Porto Velho: IB 50978; IB 33715; MPEG 17760; *Mato Grosso*: Alta Floresta: IB 44586; IB 53012; IB 42231; IB 42114; IB 49030; IB 52953; IB 41526; IB 41523; IB 47001; Jacaré (Alto Xingu): IB 41324; Barra do Garça: IB 54352; IB 32226; IB 32920; IB 40866; IB 41294; IB 41325; IB 40736; IB 45965; IB 41428; IB 41457; Cumbica air base: IB 43834; Cáceres: IB 37512; IB 37295; IB 40087; Canarana: IB 50076; IB 54350; Cuiabá: IB 50117; IB 50974; Juína: MNRJ 4753; Lagoa Augusta: IB 22287; Pontes e Lacerda: IB 55684; Reserva Gorotoré: IB 37514; Ribeirão Cascalheira: IB 55688; IB 54352; IB 56342; IB 54646–47; IB 55015; IB 56481; IB 55683; IB 55685–86; Santa Terezinha: IB 50116; São Félix do Araguaia: IB 54953; IB 55060; IB 54838; IB 55681–82; São José do Xingu: IB 46793; Sinop: IB 50976; IB 50992; MNRJ 3544; Vera: IB 43845; *Goiás*: Niquelândia: MNRJ 8028; *Alagoas*: Quebrângulo: IVB 2909; IVB 2993; IVB 2975–76; IVB 2985; Rio Largo: IB 25122; São José da Laje: IB 54916; IB 54224; IB 54351; Utinga: IB 1140; IB 1154; *Ceará*: Guaramiranga: IB 56222; Pacoti: UFC 2064–65; *Pernambuco*: no proc.: IB 7162; no proc.: IB 1023; no proc.: IB 1000; no proc.: IB 3189; no proc.: DMB 418; Barreiras: IB 8697; IB 8698; IB 8699; Nazaré da Mata: IB 10; Recife: IB 44555; IB 2734; IB 4548; IB 46792; IB 34442; Socorro do Jaboatão: IB 42424; *Paraíba*: no proc.: IB 51283; *Bahia*: no proc: IB 3220; Amargoza: IB 4549; Ilhéus: IB 16923; IB 16118; MNRJ 3039; Valença: MNRJ 4760; Maraú: IB 3057; Teixeira de Freitas: IB 52945; Belmonte: IB 51492; *Minas Gerais*: Carangola: IB 8439; IB 8429; Lajinha: IB 29283; Cachoeirinha: IB 8683; IB 9320; IB 9308; IB 9309; IB 9310; Caratinga: IB 00009; *Espírito Santo*: Calçado: IB 7631; Colatina: IB 30602; IB 32294; IB 31433; IB 43916; Guandu: IB 8685; IB 8684; IB 8605; IB 8649; IB8499; Vitória: IB 17957 (holotype of *L. m. noctivaga*); São Domingos: IB 30926; IB 25123; São Gabriel da Palha: IB 52042; IB 50975; IB 50578; IB 51282; IB 51228; IB 53013; IB 50487; *Rio de Janeiro*: Santa Maria Madalena: IVB 001; Panamá: *Província de Darién*: UCR 8061.

Lachesis stenophrys (*n* = 29)*.—Costa Rica: *Alajuela*: São Miguel, Guapilito: MZUCR 12644; *Cartago*: Turrialba, Pavones: MZUCR 7146; *Heredia*: Sarapiqui, Porto Viejo (E. B. La Selva): MZUCR 3126; MZUCR 5804; *Limon*: Siquirres, Alto Guayacán: MZUCR 14079–80; MZUCR 13710; *Limon*: Talamanca: MZUCR 7412.

Lachesis melanocephala (*n* = 7)*.—Costa Rica: *Puntarenas*: Golfito, Pl. Blanca: MZUCR 1589.

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* The specimens of *L. stenophrys* and *L. melanocephala* examined at Instituto Clodomiro Picado, San Jose, Costa Rica, have no collection numbers and, consequently, are not presented in the above list.