

GEOGRAPHIC VARIATION AND TAXONOMIC STATUS OF THE SOUTHERNMOST POPULATIONS OF *LIOPHIS MILIARIS* (LINNAEUS, 1758) (SERPENTES: COLUBRIDAE)

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We analyzed geographic variation in southern populations of *Liophis miliaris* and tested the hypothesis that *L. m. semiaureus* is a valid species. We examined 222 specimens from Argentina and Paraguay, including those from the areas of overlap of *L. m. semiaureus* and *L. m. orinus*, and compared these data with previous taxonomic revisions. We performed univariate statistical tests comparing *L. m. semiaureus* and *L. m. orinus*, and a discriminant function analysis using three morphological variables to compare four subpopulations, including two of *L. m. semiaureus* and two of *L. m. orinus*. We examined coloration in life in 152 specimens. These data and analyses support the hypothesis of *L. semiaureus* as a valid species: univariate analyses show significant differences in ventral and subcaudal numbers, and snout-vent length/tail length ratio between the two putative subspecies. *L. m. semiaureus* has significant more ventrals and subcaudals than *L. m. orinus*. Discriminant analysis separated two defined populations corresponding to *L. m. orinus* and *L. m. semiaureus*. Populations of *L. m. semiaureus* that are in contact with *L. m. orinus* populations show the highest ventral values of all of the *L. m. semiaureus* populations examined by us. We recorded differences in coloration among the juveniles of both subspecies, including specimens from neighbouring localities. The distributions are parapatric and have different ecological and historical settings. We discuss the validity of some diagnostic characters that have been used to distinguish *L. m. semiaureus*.

Key words: geographic variation, *Liophis miliaris semiaureus*, snake, taxonomy

INTRODUCTION

The colubrid snake *Liophis miliaris* (Linnaeus, 1758) has had a complex taxonomic history that has been summarized by Gans (1964) and Dixon (1983). Gans (1964) reviewed the morphological variation within the species, and although he discovered at least four “groupings”, he refrained from naming subspecies, preferring to interpret the “groupings” as “samplings from the range of a single polymorphic species” (Gans 1964). However, because of the “peculiar interdigitation of ventral-count records along the northeastern edge of the high-count plateau” (i.e., southern Brazil, north-eastern Argentina, and southeastern Paraguay), Gans (1964) unsuccessfully attempted to find concordant characters that coincided with the high ventral counts of the southern population which might indicate that two replacing species were involved.

Dixon (1983) discussed the history of the holotype of *L. m. miliaris* and restricted it to Surinam, in northern South America, correcting Gans’ (1964) assignation to Santos, São Paulo, Brazil. Additionally, Dixon (1983, 1989) included *L. amazonicus* (Dunn, 1922), *L. chrysostomus* (Cope, 1868) and *L. mossoroensis* Hoge & Lima-Verde 1972 as subspecies of *L. miliaris*. Furthermore, he proposed subspecies status for the four

“groupings” discovered by Gans (1964), for a total of seven subspecies: *Liophis miliaris miliaris* Linnaeus, 1758, *L. miliaris chrysostomus* (Cope, 1868), *L. miliaris amazonicus* (Dunn, 1922), *L. miliaris mossoroensis* Hoge & Lima-Verde, 1972, *L. miliaris merremii* (Wied, 1821), *L. miliaris orinus* (Griffin, 1916), and *L. m. semiaureus* (Cope, 1862).

The subspecies of *Liophis miliaris* defined by Dixon (1983) have allopatric and parapatric distributions in distinct hydrological basins or subsectors in the greater South American basin (Dixon, 1983, 1989). In southern South America, *L. m. semiaureus* (type locality: “Paraguay”, without more data, probably from the mouth of the Paraguay River according to Gans, 1964) shows remarkable morphological differences from the other forms, mainly in the number of ventrals and color pattern (Gans, 1964; Dixon, 1983). Dixon (1983) analyzed these differences, but supported the inclusion of these populations as subspecies of *L. miliaris*.

In this paper, we test the hypothesis that the populations of *L. m. semiaureus* (Cope, 1862) constitute a valid species separate from *L. miliaris*. We add new data, and discuss the diagnoses of Gans (1964) and Dixon (1983) for this taxon.

MATERIALS AND METHODS

We examined 222 specimens of *Liophis miliaris* from Argentina and Paraguay (see Appendix 1; Fig. 1). Standard methods for the study of snake taxonomy

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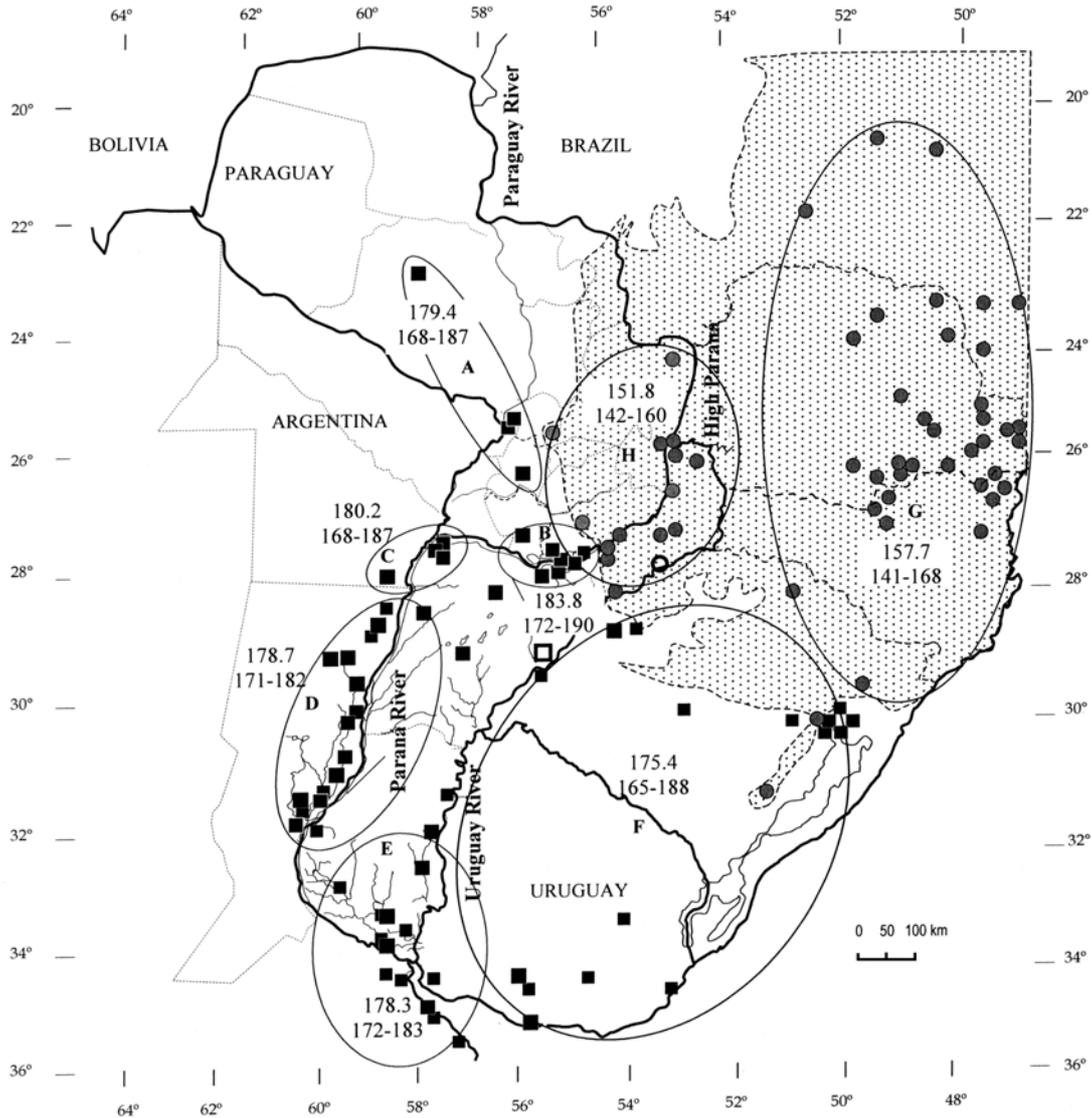


FIG. 1. Distribution of specimens of *Liophis m. semiaureus* (squares) and *L. m. orinus* (circles). Shaded area shows the Atlantic Forest Phytogeographic province (according to Galindo Leal & Camara 2003). The ventral number (mean above and range below) of *L. m. semiaureus* populations (A, B, C, D, E and F) and *L. m. orinus* populations (G and H) are indicated. The subpopulations of *L. m. semiaureus* from Argentina-Paraguay (A to E) and Uruguay-South of Brazil (F), and the subpopulations of *L. m. orinus* from Argentina-Paraguay (G) and Brazil (H) were used in discriminate function analysis (see methodology). The white circle and square show the localities of hatchlings specimens illustrated in Fig. 3.

were used. Ventral counts were made from the first scute wider than long, up to but not including the anal, following Gans (1964). Caudal counts were of pairs of segments, from the pair immediately anterior to the terminal spine, up to the last precloacal pair (Gans, 1964). Terminal spines were not included in subcaudal counts. Morphometric measurements were recorded using a ruler to the nearest millimetre for body and tail lengths. Snout-vent length (SVL) was measured from the tip of the snout to the posterior edge of the anal plate and tail length (TL) from the posterior edge of the anal plate to the tip of the tail. We used TL/SVL ratio given as percentage. We determined sex on specimens by making an incision posterior to the vent, and looking for with a dissecting scope the presence or absence of hemipenes. We examined living coloration in 152 adults and juve-

niles, and coloration in preservative in additional 70 specimens.

The univariate normality assumptions of numerical characters were verified using Shapiro-Wilks test, while homogeneity of variance was verified with the *F*-test. We performed parametric (Student *t*) and non-parametric (Mann-Whitney) univariate statistical tests (depending on the normality and homogeneity of the variables) to compare sexual dimorphism and population differences among *Liophis miliaris* examined by us.

We performed a simple linear correlation on ventral number against latitude for all *Liophis miliaris* examined by us and for each subspecies to determine whether clinal variation exists. The expected cline of ventral variation is that the northern populations have the low-

est ventral numbers (*L. m. orinus*) and the southernmost populations have the highest ventral numbers (*L. m. semiaureus*).

Additionally, we performed a discriminant function analysis comparing four subpopulations, including two of *L. m. semiaureus* (Paraguay-Argentina and Uruguay-South Rio Grande do Sul state, Brazil) and two of *L. m. orinus* (Paraguay-Argentina and north Rio Grande do Sul to Minas Gerais, Brazil; Fig. 1), using ventral and subcaudal numbers, and TL/SVL ratio. Other measurements were excluded to avoid covariant characters. We used the Gans' (1964, Table 1) data for subpopulations of *L. m. semiaureus* from Uruguay and south of Rio

Grande do Sul state in Brazil ($n=62$) and *L. m. orinus* from north of Rio Grande do Sul, Santa Catarina, Paraná, São Paulo and Minas Gerais states in Brazil ($n=291$), following Dixon's (1983) subspecific assignment and distribution.

All statistical analyses were performed using Infostat (2002) version 1.6 with significance level of 0.05.

RESULTS

SCALATION AND MEASUREMENT CHARACTERS

Although all comparisons yielded the normal colubrid pattern wherein males average fewer ventrals

TABLE 1. Variation and sexual dimorphism of some characters in *Liophis miliaris* southern populations examined by us. Abbreviations: F, female; M, male; n , sample size; SD, standard deviation; range: minimum and maximum values; U , Mann-Whitney statistic value.

Characters	Subspecies	Sex	n	Mean	SD	Range	Statistical comparison
Ventrals	<i>orinus</i>	F	16	152.2	4.89	143 160	$U=213$
		M	14	151.3	4.91	142 158	$P=0.4401$
	<i>semiaureus</i>	F	118	182.2	4.25	171 190	$U=6886$
		M	74	181.4	4.62	168 190	$P=0.32$
Subcaudals	<i>orinus</i>	F	15	52.9	3.26	47 61	$U=244$
		M	14	55.2	4.58	50 67	$P=0.1348$
	<i>semiaureus</i>	F	103	57.8	3.71	43 65	$U=5856.5$
		M	66	58.5	3.19	50 68	$P=0.4244$
Total length (TOL)	<i>orinus</i>	F	15	514.9	284.41	175 906	$U=204.00$
		M	14	432.5	215.69	208 798	$P=0.3708$
	<i>semiaureus</i>	F	101	764.8	266.57	234 1457	$U=4379.50$
		M	66	619.5	151.52	199 967	$P<0.0001$
Tail length (TL)	<i>orinus</i>	F	15	94.4	48.65	33 164	$U=204.50$
		M	14	85.4	41.89	38.7 154	$P=0.3824$
	<i>semiaureus</i>	F	101	127.72	41.6	35 220	$U=4374.5$
		M	68	107.8	27.33	35 164	$P<0.0003$
Snout-vent length (SVL)	<i>orinus</i>	F	17	445.9	242.23	142 804	$U=206.5$
		M	14	347.1	175.24	168 644	$P=0.1647$
	<i>semiaureus</i>	F	117	660.9	232.02	198 1259	$U=5305.5$
		M	73	517.8	125.96	164 803	$P<0.0001$
TL/SVL	<i>orinus</i>	F	15	22.7	1.83	20 26	$U=258.5$
		M	14	24.8	3.40	20 35	$P=0.0314$
	<i>semiaureus</i>	F	100	20.3	1.86	16 25	$U=6530$
		M	65	21.4	1.61	17 26	$P=0.0001$

TABLE 2. Univariate analysis comparing *L. m. orinus* and *L. m. semiaureus* subspecies. Abbreviations: n , sample size; SD, standard deviation; U , Mann-Whitney statistic.

Characters	<i>L. m. orinus</i>			<i>L. m. semiaureus</i>			Statistical comparison	
	n	Mean	SD	n	Mean	SD	U value	P value
Ventrals	31	151.81	4.76	193	181.89	4.41	496	<0.0001
Subcaudals	30	54.03	3.98	170	58.05	3.52	1379.5	<0.0001
Total length	30	486.5	255.92	170	702.81	240.31	1885.5	0.0001
Tail length	30	91.89	45.27	169	119.08	37.93	2148.5	0.0043
Snout-vent length	32	409.76	218.8	193	604.28	213.09	2217.5	0.0001
TL/SVL	30	23.67	2.82	168	20.93	5.09	4627.5	<0.0001

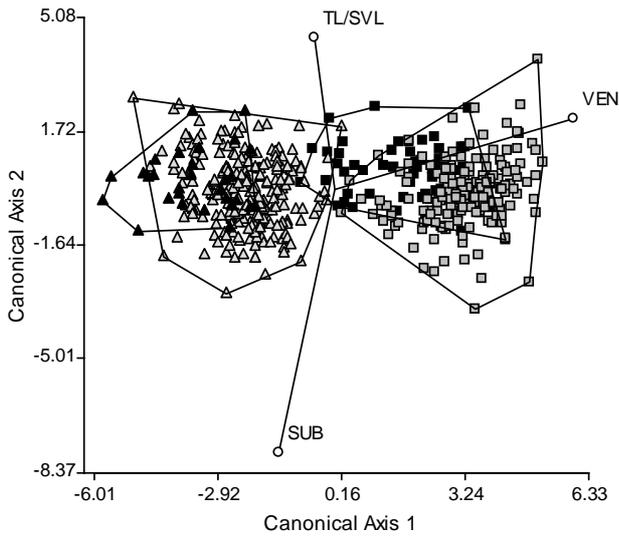


FIG. 2. Biplot of discriminant analysis among morphological variables (VE: Ventrals, SUB: Subcaudals, TL/SVL: Tail length/Snout-vent length ratio) of *L. m. orinus* (Argentina-Paraguayan populations black triangles and Brazilian populations shaded triangles) and *L. m. semiaureus* (Argentina-Paraguayan populations shaded squares and Uruguayan-Brazilian populations black squares (see Fig. 1).

and more subcaudals than females, none of the differences were significant. All measurements showed significant sexual dimorphism in *L. m. semiaureus* but not in *L. m. orinus*, with exception of TL/SVL, in which males had relatively longer tails in both taxa (Table 1). Females of *L. m. semiaureus* averaged significantly longer than males in all measurements (Table 1).

The univariate analyses showed significant differences in all characters examined between the two subspecies (Table 2). Ventral numbers did not overlap between the subspecies in specimens examined by us, with a very significantly higher number of ventrals in *L. m. semiaureus*. The ventrals ($U=114682.5, P<0.0001$), subcaudals ($U=64287, P<0.0001$) and TL/SVL ratio ($U=32599.5, P<0.0001$) showed significant differences between the two subspecies when combining our data with Gans' data. The numbers of ventral for all these sample is 141 to 168 (mean 157.1) for *L. m. orinus* ($n=322$), and 165 to 190 (mean 180.3), for *L. m. semiaureus* ($n=255$).

The discriminant analyses showed that *L. m. orinus* subpopulations are separated from the *L. m. semiaureus* subpopulations with a small degree of overlap (Fig. 2). The subpopulations of *L. m. orinus* from Paraguay-Argentina (our data) and Brazil (Gans' data) were grouped

TABLE 3. Results of discriminant analysis of three morphological variables and four subpopulations two of *L. m. orinus* and two *L. m. semiaureus* (see Fig. 1).

	Canonical axis 1	Canonical axis 2
Ventrals	1.05	0.37
Subcaudals	-0.25	-1.36
TL/SVL	-0.09	0.79



FIG. 3. Hatchlings specimens of *L. miliaris orinus* (206 mm TOL) (a) and *L. miliaris semiaureus* (244 mm TOL) (b), both with umbilical scars, caught between 30 and 28 January of 2000, respectively, from two localities separated by 170 km airline (see Fig. 1). Photos by A. Giraud.

among them. *L. m. semiaureus* subpopulations from Paraguay-Argentina (our data) and Uruguay-South Brazil (Gans' data) were also grouped (Fig. 2). Most of the variation of canonical discriminant axis 1 is explained by number of ventral scales while most of the variation of axis 2 is explained by number of subcaudal scales (Table 3).

The correlation between ventral numbers and latitude for *Liophis miliaris* examined by us was not significant (Spearman correlation, $r=-0.05591, n=219, P=0.4104$), and *L. m. semiaureus* populations showed a lower negative significant correlation between ventral numbers and latitude (Spearman correlation, $r_s=-0.45, n=194, P<0.0001$). Populations of *L. m. semiaureus* that are in contact with *L. m. orinus* populations show the highest ventral values of all of the *L. m. semiaureus* populations examined by us (Fig. 1).

COLORATION

The two subspecies show differences in coloration and pattern. Both have a pattern called "salt and pepper" by Peters & Orejas Miranda (1970), with dorsal scales having light bases and dark free margins, giving

TABLE 4. Summary of characters of *Liophis miliaris* subspecies. Modified from Dixon (1983), with addition of our data marked in bold.

Subspecies	Ventrals			Subcaudals			TL/TOL		
	<i>N</i>	Mean	Range	<i>N</i>	Mean	Range	<i>N</i>	Mean	Range
<i>L. miliaris amazonicus</i>	6	155.2	148-159	2	75.5	75-76	No data		
<i>L. miliaris chrysostomus</i>	63	159.4	153-172	49	59.5	53-64	31	19.35	16.8-21
<i>L. miliaris merremii</i>	126	146.5	135-156	112	49.5	40-56	65	18.5	15-22.2
<i>L. miliaris miliaris</i>	19	156	142-163	15	57	51-64	10	18.9	17.6-20
<i>L. miliaris mossoroensis</i>	23	158.7	148-166	23	50.8	45-56	23	17	15.3-18.5
<i>L. miliaris orinus</i>	302	158.4	147-169	246	56.2	47-69	203	19.06	15-22.4
<i>L. miliaris orinus</i>	31	151.81	142-160	30	40.3	47-67	30	19.17	17-26
<i>L. miliaris semiaureus</i>	100	176.2	163-190	84	56.7	50-68	79	17.915	7-20.5
<i>L. miliaris semiaureus</i>	193	181.89	168-190	170	58.05	43-68	168	17.24	13-21

the overall appearance of an olive-green snake. In *L. m. semiaureus* the general coloration is lighter because the dark line that borders the distal scale edge is narrower than in *L. m. orinus*. In *L. m. orinus* the dark colour extend to the center scale (Giraudo, 2001: Plate 14). In *L. m. semiaureus*, the midbody and posterior ventral plates have a continuous dark line along the entire distal scale border. In *L. m. orinus*, this dark line is narrower and generally discontinuous or very faded in the central and posterior portion of the belly. The general adult colour pattern is more regular and has less variation in *L. m. semiaureus* than in *L. m. orinus*.

The coloration of the hatchlings of *L. m. orinus* coincides with the description and figures shown by Gans (1964), and is characterized by a thin light nuchal V-shaped collar (white in fixed and yellow in live specimens) that is one or two dorsal scales wide, bordered by a parallel anterior V-shaped dark parietal-occipital band and by a parallel posterior wider V-shaped dark band (black in fixed and live specimens) occupying three to four dorsal scales. This black-light-black nuchal collar is followed by a well-defined series of dark dorsal and lateral blotches, more developed in the anterior part of the body. These have a tendency to coalescence towards the tail (Fig. 3a), forming a lateral black caudal stripe. In contrast, in hatchlings of *L. m. semiaureus*, the black-light-black nuchal collars are very narrow and poorly defined, and the dark lateral and dorsal blotches are poorly developed, consisting of a series of small spots that are very reduced posteriorly (Fig. 3).

DISCUSSION AND CONCLUSIONS

Gans (1964) described the body coloration of juveniles from the southern, high-ventral count population as being relatively uniform, not showing the alternating dark and light zones found in more northern populations. Additionally, these juveniles had smaller and more subdued dark markings. However, later in the same paper, Gans (1964) also described and illustrated the striking retention of juvenile blotches in several adult specimens from near Montevideo and Buenos Aires.

We cannot corroborate Gans' (1964) statement (followed by Dixon 1983) that *L. m. semiaureus* retains a juvenile blotched pattern in the populations of Argentina and Paraguay. Several specimens of *L. m. semiaureus* between 257 and 449 mm of total length (TOL) and all larger specimens have the adult coloration pattern. On the contrary, the *L. m. orinus* examined retained the juvenile colour pattern in older specimens including several adults, such as FML 975 (647 mm TOL), which retained vestiges of a light nuchal collar and dark lateral blotches on the anterior body.

Dixon (1983), probably following Gans (1964), indicated in the diagnosis of *L. m. semiaureus* "pronounced retention of dorsal blotch patterns in adults". We have not found adults of *L. m. semiaureus* with retained juvenile blotch patterns in a large sample from Argentina and Paraguay ($n=193$), including several specimens collected in the surroundings of Buenos Aires (in the MACN and MLP collections). We consider that the retention of juvenile is atypical within *L. m. semiaureus* in the populations of Argentina and Paraguay (the type locality being in the latter country), and therefore this coloration is not a diagnostic character for the taxon. However, according to Gans (1964) and Achaval and Olmos (2003), we observed the retention of juvenile patterns in 10 of 21 specimens of *L. m. semiaureus* (48%) from Uruguay populations.

Dixon (1983) indicated in the diagnosis of *L. m. semiaureus* a range of 163 to 190 ventrals with a mean of 176.2 ($n=100$). We found a similar range (168 to 190) but our mean (181.9, $n=193$) and the minimum value are slightly higher than Dixon's. We consider that these minimal differences probably are due to that Dixon (1983) included in his material of *L. m. semiaureus* two specimens from Montecarlo, near Iguazú Falls (province of Misiones), which were not examined by us but we suspect to be *L. m. orinus* as all material examined by us from the area of Montecarlo corresponds to *orinus*, and this locality is in the Interior Atlantic Forest of Argentina (Giraudo 2001), well off the range of *L. m. semiaureus*.

In the total sample of 255 specimens of *L. m. semiaureus* (range 165 to 190, mean of 180.3 including

our data and Gans' data) only 14 overlap slightly with the maximum values of ventrals of *L. m. orinus* (one from Argentina, one from Paraguay, six from Uruguay and six from Rio Grande do Sul Brazil), with values between 165 to 168 ventrals. These specimens could be considered intermediates between the two subspecies, although another possible explanation lies in the large number of snakes that are rafted down the Paraguay-Paraná and the Uruguay river systems in floating mats of water hyacinths (Achaval *et al.* 1979). For this reason, these snakes could be also considered *L. m. orinus* that have come down from the upper parts of the river system. On the other hand, in the total sample of 322 specimens of *L. m. orinus* (141 to 168 ventrals, mean of 157.1) only 19 overlap slightly with the minimum values of ventrals of *L. m. semiaureus* (165 to 168), but notably all they are of areas relatively far from the subspecies contact zone (14 of São Paulo state, two of Santa Catarina state and two of Paraná state in Brazil). We considered that probably these are extreme values of ventrals included in the variation of the *L. m. orinus* subspecies.

The following data and analyses support that *Liophis m. semiaureus* is a valid species:

(1) Specimens of *L. m. semiaureus* have higher number of ventrals than any *Liophis miliaris* (Table 4), without significant overlap, and this difference is very significant with respect to the contiguous populations of *L. m. orinus*. Other characters show the same pattern, according to both univariate and multivariate analyses (see results and Table 1).

(2) There is no clinal variation in the number of ventrals, supported by an insignificant correlation between ventrals and latitude in all examined specimens, and by a significant negative correlation in *L. m. semiaureus*.

(3) The closest population of *L. m. semiaureus* to *L. m. orinus* show the highest ventral scale counts of all the *L. m. semiaureus* populations examined by us (see population B in Fig. 1). These populations of both subspecies are separated by only 40 km along the same river and they are connected by the Paraná River. A large number of snakes are swept down in seasonal floodings of this river in floating mats of water hyacinths called "camalotales" (e.g. Achaval *et al.* 1979). In spite of this, we did not record any intermediate specimens in this area. This is indirect evidence of null or low genetic exchange between these populations. Gans (1964) observed the same pattern as he included a line in the map of his Figs. 8 and 10 representing the region where an abrupt jump takes place in the number of ventrals of *Liophis miliaris*. Gans (1964) stated that "It is interesting to note that the low-count plateau seems to send a finger south into Rio Grande do Sul, as the single specimen from Cerrito a low count in contrast to the high count of specimens in the adjacent localities in Pelotas and Rio Grande do Sul". Cerrito is located in southeastern hills of Rio Grande do Sul, Brazil, considered one of the most southern areas of Atlantic biogeographical in-

fluence (Galindo & Câmara, 2003; Lema, 1994), while Pelotas is in adjacent lowlands that have a Pampean biogeographical influence (Lema, 1994).

(4) We recorded differences in coloration among the juvenile of both subspecies, including specimens of nearby localities (170 airline-km) (see results and Fig. 3).

(5) The subspecies *L. m. orinus* inhabit the Atlantic biogeographical province in hills, plateaus and mountains of eastern Paraguay, northeastern Argentina and southeastern Brazil (Fig. 1). This area is dominated by Atlantic rainforest, and the main aquatic habitats are streams and rivers characterized by basaltic channel with rapid stream and a narrow flood valley. The subspecies *L. m. semiaureus* inhabit lowlands of Chaco-Pampean plain in great floodplain rivers with extensive alluvial valleys forming several lentic aquatic habitats such as marshes and lagoons. Their distributions are parapatric in areas with different ecological and historical settings.

We conclude that *L. semiaureus* is a well defined taxon. The possible existence of a few intermediates specimens in ventral counts did not invalidate our conclusions. We follow the evolutionary species concept postulated by Wiley (1978) and discussed by Frost & Hillis (1990), Frost *et al.* (1992) and Giraudo (1997), frequently used in herpetology (e.g., Collins, 1991; Reichling, 1995). In light of this concept *Liophis semiaureus* is undoubtedly a valid species.

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APPENDIX 1

SPECIMENS EXAMINED

Museum abbreviations are: CENAI: Centro nacional de Investigaciones Iológicas collection, actually deposited in MACN, Buenos Aires; CCP: Colección privada Caa Porá, Iguazú, Misiones; CIES: Centro de Investigaciones Ecológicas Subtropicales, Parque Nacional Iguazú, Misiones; CUNAM: Universidad Nacional de Misiones, Posadas, Misiones; FML: Fundación Miguel Lillo, Tucumán; MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; MLP: Museo de La Plata, La Plata, Buenos Aires; MNHNP: Museo Nacional de Historia Natural del Paraguay, San Lorenzo; UNNEC: Universidad Nacional del Nordeste, Corrientes.

Liophis miliaris orinus. ARGENTINA: Misiones Province: Caingúas Department: 2 de Mayo CENAI 314, 3319, Balneario Arroyo Cuña Piru CFA 801; Candelaria Department: Santa Ana CENAI 3349; Gral. M. Belgrano Department: Deseado, Arroyo Bruaca CCP 30- 31; Arroyo San Jorge MACN 34627; Eldorado Department: Eldorado MACN 28008-28009; Iguazú Department: Parque Nacional Iguazú, Barrio de Guardaparques CIES 10, 54; Parque Nacional Iguazú CIES 21, 25, 68, 206, 222; Parque Nacional Iguazú, acceso a Puerto Canoas CIES 43; Puerto Iguazú INALI 1203- FML 205; 25 de Mayo Department: 25 de Mayo INALI 1053; El Bonito FML 676-1- 676-2; San Ignacio Department: Gobernador Roca CFA 58; Arroyo El Rosario, 25 Km de San Pedro FML 975; PARAGUAY: Cordillera Department: Itacurubí de la Cordillera MNHNP 2607; Canindeyu Department: 11 Km S de Katuete MNHNP 3777-3835; Itapúa Department: Itapúa, Arroyo Tingazú, 52 km NW of Pirapó MNHNP 8863; Paraguay without precise localities MNHNP 8787 MNHNP 9497

Liophis miliaris semiaureus. ARGENTINA: Buenos Aires Province: Capital Federal: Reserva Costanera Sur MACN 34559; Ensenada Department: Punta Lara MACN 31979, 31980, 31981, 31982; Punta Lara CENAI 2945; Magdalena Department: Magdalena CENAI 3199, 3200; Luján Department: Dique Luján MACN 34644; San Pedro Department: Vuelta de Obligado MACN 36080; Isla Giovannini, Río Barca Grande, Delta bonaerense MACN 29956; Delta Bonaerense MACN 25071; Quilmes Department: Quilmes MACN 864; Corrientes Province: Capital Department: Laguna Pampín, Barrio Las Lomas CFA 111, 195, 214, 222, 243, 247, 257, 292, 567, 756, 788, 789; Laguna Soto CFA 30; Corrientes, Barrio Santa Rita CFA 146; Granja Yatay CFA 741, 742; CAPRIM, San Cayetano CFA 790; 10 km S of Loreto, nacional route 12 CFA 326; Mercedes Department: Mercedes CENAI 3443; Ituzaingó Department: Isla Oculto UNNEC 470; 23 km S of Santo Tomé, nacional route 14 INALI 1047; national route 12 INALI 44; Entre Ríos Province: Concordia Department: Concordia, 12 km W of Colonia Roca INALI 1104; Colón Department: Arroyo Barú MACN 30694; Victoria Department: 1 km S of Rincón de Nogoya, provincial route 11 INALI 1517; Islas del Ibicuy

Department: 2 km N of Médanos, provincial route 12 INALI 1489; 11 km NW of Médanos, provincial route 12 INALI 1512; Villa Paranacito INALI 1550; 37 km E of Puerto Ibicuy INALI 1559, 1560; 40 km E of Puerto Ibicuy INALI 1562; 3 km al NE of Villa Paranacito INALI 1551. Misiones Province: Capital Department: Posadas, Puente internacional CUNAM 179; Nemesio Parma CUNAM 309; Posadas, Arroyo El Zaimán CUNAM 316; Posadas CUNAM 340, 341; Santa Fe Province: Garay Department: 12 km N of Santa Rosa, provincial route 1 (31° 21' S - 60° 15' O) INALI 187; 11 km N of Santa Rosa, provincial route 1 (31° 22' S - 60° 17' O) INALI 193; 4 km N of Colonia San Joaquín, provincial route 1 INALI 504; 4 km N of Helvecia, provincial route 1 INALI 610; Saladero Cabal, provincial route 1 INALI 614; 13 km S of Cayastá, provincial route 1 INALI 738; Vuelta del Dorado, Cayastá INALI 835; 8 km S of Santa Rosa de Calchines, provincial route 1 INALI 1293; 5 km S of Cayastá, provincial route 1 INALI 1383; 8 km S of Cayastá, provincial route 1 INALI 1627; 8 km S of Santa Rosa, provincial route 1 INALI 1630; 2 km S of Santa Rosa, provincial route 1 INALI 999; General Obligado Department: Arroyo Ceibal, nacional route 11 INALI 217, 223; El Rabón INALI 688; La Capital Department: 8 km S of Laguna Paiva, provincial route 2 INALI 989; Santo Tomé INALI 1079; Arroyo Potrero INALI 1292; 3 km N Ascochinga, provincial route 2 INALI 1597; 5 km N of Rincón INALI 1611; 4 km N of Arroyo Leyes INALI 1612; Santa Fe INALI 1632; San Javier Department: 16 km N of San Javier, provincial route

1 INALI 966; 40 km N of Alejandra, provincial route 1 INALI 978; 36 km N of San Javier, provincial route 1 INALI 1275; 19 km N of Alejandra provincial route 1 INALI 1525; Vera Department: 4 km E of Vera, provincial route 98 INALI 639; 14 km E of Vera, provincial route 98 INALI 645; BRAZIL: Rio Grande do Sul state: Estación Ecológica TAIM, Brasil, Nelson Perez CFA 434; PARAGUAY: Central Department: Areguá MNHNP 6573, 6574, San Lorenzo MNHNP 2527; Itapúa Department: Isla Cururú MNHNP 4605, 4606, 4607, 4608, 4613, 4614, 4615, 4616, 4617, 4618, 4619, 4620, 4666, 4667, 4668, 4669, 4670, 4671, 4672, 4673, 4674, 4675, 4676, 4677, 4678, 4680, 4681, 4683, 4684, 4685, 4686, 4687, 4688, 4689, 4690, 4691, 4692, 4693, 4695, 4696, 4697, 4698, 4699, 4700, 4701, 4702, 4703, 4704, 4705, 4706, 4707, 4708, 4709, 4710, 4711, 4712, 4713, 4714, 4715, 4716, 4717, 4719, 4720, 4751, 4752, 4753, 4754; Isla Guasú'i MNHNP 4811, 4812, 4837, 8350; Isla Modesto MNHNP 4750, 4939; Isla Paloma MNHNP 6591, 8338, 8365 Isla Talavera MNHNP 4609, 4610, 4611, 4612, 4744, 4745, 4746, 4747, 4748, 4749, Isla Yacyreta MNHNP 4810, 4839, 4861, 4862, 4863, 4864, 4865, 4961, 6705, 6710, 6712, 6713, 7947, 8356, 8357, 8360, 8364, 9164; Isla Yacyreta, José Cué MNHNP 4838; Misiones Department: Ruta San Ignacio-Yabebyry Km 70 MNHNP 9145; Paraguari Department: 26°06'27"S; 56°56'38"O MNHNP 6749; Presidente Hayes Department: Estancia Salazar, km 340 route "Trans Chaco" MNHNP 6638.