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## Are Amazonia Rivers Biogeographic Barriers for Lizards? A Study on the Geographic Variation of the Spectacled Lizard *Leposoma oswaldoi* Avila-Pires (Squamata, Gymnophthalmidae)

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**ABSTRACT.**—With improvements in taxonomic resolution in recent years, the Amazon basin is increasingly recognized as containing restricted-range taxa and areas of endemism. For many of these taxa, rivers delimit their geographic distributions and separate sister species. Among most lizards the geographic pattern is not clear. We attempt to determine the existence of cryptic diversity in the Spectacled Lizard *Leposoma oswaldoi* by analyzing the geographic variation in its morphology. We specifically tested whether the Rio Madeira, Rio Purus, Rio Aripuanã, and Rio Roosevelt delimit differentiated lizard forms. Using multivariate analysis, we detected that males of *L. oswaldoi* have larger heads than females but females have longer bodies. Large rivers, such as the Rio Purus and Rio Madeira, do not play a significant role in the geographic variation of *L. oswaldoi*. However, specimens from two localities on opposite banks of the upper Rio Aripuanã occupy the lower and upper ranges of variation in *L. oswaldoi* and are distinct from all other specimens analyzed. This unusual pattern differs from one of the main river hypothesis predictions, which is that similarity between individuals on opposite river banks should increase with decreasing barrier strength. We hypothesize that the differences in river dynamics between the lower and upper Rio Aripuanã during mid-Miocene through the Pleistocene could explain our results, although phylogeographic evidence is lacking to support such a hypothesis. The elucidation of recent and ancient processes that shaped diversity in *Leposoma* could provide important clues to understand the formation of the megadiversity of Amazonia.

The Amazon basin, long known for its stupendous species richness (Mittermeier et al., 1997), is increasingly recognized as containing taxa with restricted ranges and areas of endemism within the vast expanse of rainforest (Cracraft, 1985; Patton et al., 2000; Roosmalen et al., 2002; Geurgas and Rodrigues, 2010). For birds and primates, the major Amazonian tributaries delimit the geographic ranges of many species, including species complexes with allopatric distributions on opposite banks of these rivers (Sick, 1967; Ayres and Clutton-Brock, 1992; Roosmalen et al., 2002; Cohn-Haft et al., 2007). In most other groups of animals, however, the patterns of geographic distribution are not so clear, either for lack of data or because rivers do not serve as barriers (da Silva and Patton, 1998; Patton et al., 2000; Avila-Pires et al., 2009; Geurgas and Rodrigues, 2010). Furthermore, the recognition of cryptic taxa in formerly widespread species calls attention to unnoticed patterns of geographic variation (e.g., Fouquet et al., 2007; Simões et al., 2008; Geurgas and Rodrigues, 2010; Pellegrino et al., 2011).

Lizards are one group for which a well-defined pattern of geographic distribution has yet to be detected. Generally, a distinction has been made between eastern and western Amazonia, including replacement of sister-species, but without identification of an exact border or concordant distributions among numerous taxa (Avila-Pires, 1995; Avila-Pires et al., 2009). Part of this vagueness could be due to imprecise taxonomic understanding and cryptic diversity, as evidenced by a recent molecular analysis of the tiny Amazonian leaf-litter gekkonid, *Chatogekko amazonicus* Andersson 1918 (Amazon Gecko), found to be a complex of at least five allopatrically distributed phylogenetic species not distinguishable by external morphology (Geurgas and Rodrigues, 2010). Other small, terrestrial, upland forest lizard species are candidates for similar cryptic diversity, and potentially congruent patterns of geo-

graphic variation, such as has been found for some small terrestrial frogs (Fouquet et al., 2007; Simões et al., 2008) and as has long been recognized in understory birds (Cracraft, 1985; Cohn-Haft et al., 2007).

Lizards of the genus *Leposoma* appear to be good candidates for showing comparable patterns of cryptic diversity. Like *Chatogekko*, they are very small leaf-litter inhabitants of upland forest. Additionally, *Leposoma* is one of the most species-rich genera in the Gymnophthalmidae and is second only to *Anolis* as the richest genus of Brazilian Amazonian lizards (Avila-Pires, 1995; Bérnils, 2012). Yet despite this relatively high diversity, usually only two species are found at any given site, one of which is the widespread *Leposoma percarinatum* Müller 1923 (Müller's Tegu) (e.g., Gardner et al., 2007; Vogt et al., 2007; Vitt et al., 2008; Mendes-Pinto and Souza, 2011). The second species, usually poorly sampled, appears to have smaller distributions and to replace one another geographically. Recent taxonomic revisions and collecting in previously unsampled sites led to the description of three new species of *Leposoma* from central Amazonia alone (Avila-Pires, 1995; Rodrigues and Avila-Pires, 2005), suggesting that the true diversity and distribution of this group is still poorly known.

We examine geographic variation in morphology of one of these recently described species, the Spectacled Lizard *Leposoma oswaldoi*, and attempt to assess cryptic diversity. This study could provide clues about the recent processes responsible for the diversification within *Leposoma*. In particular, we examine whether external morphology shows clinal variation as a function of distance or whether distinct groupings exist. As this species occurs primarily in the Rio Madeira basin, where the Madeira itself and its tributaries (the Rio Aripuanã, Rio Roosevelt, and Rio Abacaxis) are known to be barriers for birds and primates, we tested specifically whether these rivers delimit differentiated forms of *Leposoma* (Cracraft and Prum, 1988; Ayres and Clutton-Brock, 1992; Roosmalen et al., 2002; Cohn-Haft et al., 2007).

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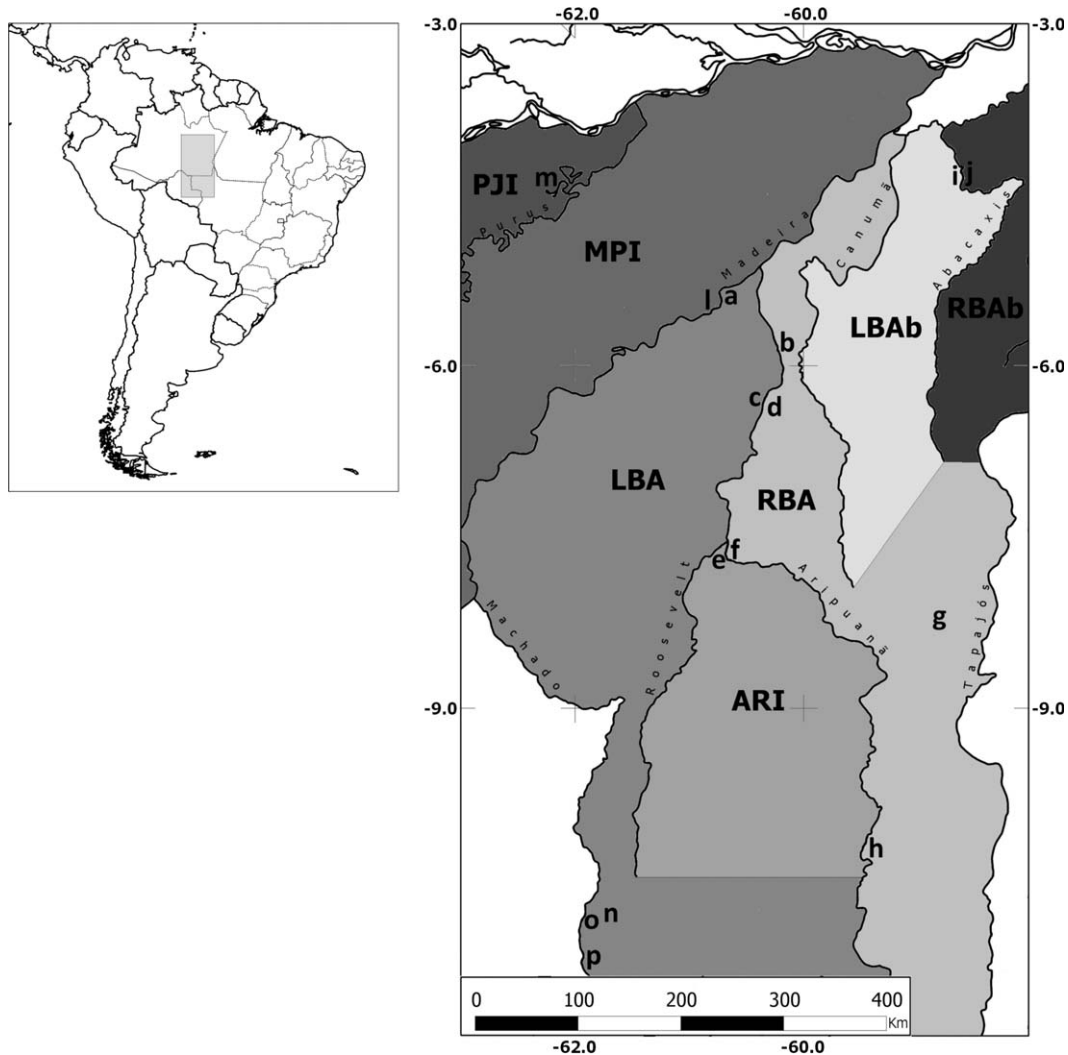


FIG. 1. Localities included in the analysis (small caps) and hypothesized groups based on main rivers (all caps). Gray scale refers to geographic extension of groups. RBA = right bank of Rio Aripuanã; LBA = left bank of Rio Aripuanã; ARI = Aripuanã - Roosevelt interfluvium; RBAb = right bank of Rio Abacaxis; LBAb = left bank of Rio Abacaxis; MPI = Madeira - Purus interfluvium; PJI = Purus-Juruá interfluvium. Localities: (a) Itapinima; (b) Lago Cipotuba; (c) Arauazinho; (d) Igarapé Extrema; (e) Projó Left; (f) Projó Right; (g) PAREST Sucundurí; (h) Aripuanã; (i) São Sebastião; (j) Igarapé Açú; (l) Cachoeirinha; (m) Lago Ayapuá; (n) Nova Colina; (o) Cachoeira do Nazaré; (p) Ministro Andreazza - Nova Brasília.

#### MATERIALS AND METHODS

**Study Species.**—Two purported clades (species complexes) are presently recognized for the genus *Leposoma*: the *Leposoma parietale* species group and the *Leposoma scincoides* species group (Ruibal, 1952; Rodrigues, 1997; Pellegrino et al., 2011). The species of the *L. scincoides* group are all associated with Brazilian Atlantic Rainforest, with their distribution restricted to eastern South America (Rodrigues, 1997; Rodrigues and Borges, 1997; Rodrigues et al., 2002). The species of the *L. parietale* group are distributed throughout the western portion of South and Central America, ranging from Amazonia to Costa Rica (Ruibal, 1952; Avila-Pires, 1995; Rodrigues and Avila-Pires, 2005). In the region of our study, the forests south of the Rio Solimões, Central Amazonia, records of *Leposoma* are scattered but two species are known to be present: *Leposoma sneathlageae* Avila-Pires 1995 (also known as Spectacled Lizard) and *L. osvaldoi* (Avila-Pires, 1995). Avila-Pires (1995) recognized and named *L. osvaldoi* and *L. sneathlageae* from the sparse material available at the time. Historically, both species had been confused with *Leposoma parietale* Cope 1885 (Common Root Lizard), whose distribution is

now understood to be restricted to north of the Rio Solimões. *Leposoma osvaldoi* was described based on six specimens collected from near the BR-364 road in the states of Rondônia and Mato Grosso, Brazil (Nascimento et al., 1988; Avila-Pires, 1995). Its distribution was subsequently expanded northward to the municipality of Borba in the state of Amazonas (Pinto, 1999), and eastward to Espigão do Oeste in the state of Rondônia (Macedo et al., 2008), along with several localities in the state of Mato Grosso (Kawashita-Ribeiro et al., 2011; Pellegrino et al., 2011).

**Study Specimens.**—We collected specimens of *L. osvaldoi* during several field expeditions to the southern Amazonia since 2005; they are deposited in the Collection of Amphibians and Reptiles at the Instituto Nacional de Pesquisas da Amazônia (INPA). In addition we examined all relevant material at the Museu de Zoologia da Universidade de São Paulo (MZUSP) of *L. osvaldoi* from 15 localities (66 adult individuals [44 males and 22 females], Fig. 1; Table 1).

**Morphological Measurements.**—We took standardized digital photographs of all individuals using a camera connected to a stereomicroscope. Scale and body measurements were made

TABLE 1. Summary of localities of *Leposoma osvaldoi* used in analysis of morphological variation.<sup>a</sup>

Locality	Code	Group	<i>n</i> males	<i>n</i> females	State	Latitude (WGS 84)	Longitude (WGS 84)
Itapinima	a	LBA	2	1	AM	-5.41060	-60.72720
Lago Cipotuba	b	RBA	-	2	AM	-5.80139	-60.22111
Arauazinho	c	LBA	2	1	AM	-6.29017	-60.37143
Igarapé Extrema	d	RBA	3	-	AM	-6.32060	-60.34743
Projó Left	e	ARI	3	1	AM	-7.63818	-60.66912
Projó Right	f	RBA	2	-	AM	-7.62049	-60.66989
Parque Estadual (PAREST) Sucunduri	g	RBA	-	1	AM	-8.22284	-58.81219
Aripuanã	h	RBA	15	-	MT	-10.17556	-59.45139
São Sebastião	i	LBAb	2	1	AM	-4.30889	-58.63639
Igarapé Açú	j	RBAb	10	6	AM	-4.34417	-58.63500
Cachoeirinha	l	MPI	4	6	AM	-5.48940	-60.83440
Lago Ayapuá	m	PJI	1	-	AM	-4.44110	-62.15060
Nova Colina	n	LBA	-	1	RO	-10.79206	-61.69266
Cachoeira do Nazaré	o	LBA	-	1	RO	-10.80993	-61.90481
Ministro Andreazza – Nova Brasília	p	LBA	-	1	RO	-11.19755	-61.51667
Total			44	22			

<sup>a</sup> WGS = World Geodetic System; RBA = right bank of Rio Aripuanã; LBA = left bank of Rio Aripuanã; ARI = Aripuanã-Roosevelt interfluvium; RBAb = right bank of Rio Abacaxis; LBAb = left bank of Rio Abacaxis; MPI = Madeira-Purus interfluvium; PJI = Purus-Juruá interfluvium; AM = Amazonas; MT = Mato Grosso; RO = Rondônia.

using Adobe Photoshop CS3 Extended 10.0®. We used photographs of millimeter-ruled paper taken at the same magnification to convert measurements to millimeters. Following Uzzel and Barry (1971), we took 20 measurements from all specimens (Fig. 2): snout-vent length (SVL) = length from the snout to the cloacal aperture; interparietal length (INTL) = greatest length of interparietal scale; anterior width of interparietal (INTAW) = greatest width in the anterior portion of interparietal scale; posterior width of interparietal (INTPW) = greatest width in the posterior portion of interparietal scale; parietal length (PARL) = greatest length of right parietal scale; frontoparietal length (FRPL) = greatest length of right frontoparietal scale; frontoparietal width (FRPW) = greatest width of right frontoparietal scale; frontal length (FROL) = greatest length of frontal scale; anterior width of frontal (FROAW) = greatest width in the anterior portion of frontal scale; posterior width of frontal (FROPW) = greatest width in the posterior portion of frontal scale; length of first supraocular (1SUPL) = length of the suture between first right supraocular and frontal; length of second supraocular (2SUPL) = length of the suture between second right supraocular and frontal; length of third supraocular (3SUPL) = length of the suture between third right supraocular, frontal and frontoparietal; contact between frontoparietals (FROPCO) = length of the medial suture between frontoparietals; contact between prefrontals (PRECO) = length of the medial suture between prefrontals; length of cephalic scales (CEFL) = length from the snout to posterior margin of interparietal; head width (HEAW) = greatest width of head; head length (HEAL) = length from snout to the anterior margin of ear opening; head height (HEPROF) = greatest height of head, usually from posterior portion of chin to parietal; and trunk length (TRUNKL) = length from posterior margin of ear opening to the cloacal aperture.

*Analysis of Geographic Variation.*—The size of individuals (here expressed by SVL) is recognized as a factor that makes it difficult to compare samples directly, especially when one wishes to compare shape differences between species, genera, or higher taxonomic levels (Sokal and Rohlf, 1995). The size effect is smaller in intraspecific analysis, as in our study, but it still exists and must be taken into account. Another important factor to consider is morphometric sexual dimorphism, a very common trait in lizards (Preest, 1994; Herrel et al., 1996; Herrel et al., 1999; Cox et

al., 2007), although there are no records of morphometric dimorphism in *Leposoma*. The only known difference between the sexes in *Leposoma* is in body color. Males of *Leposoma* show a bright red ventral coloration at reproductive maturity, which is absent in females.

To correct for morphometric variation of size and sex, we used a multivariate regression approach. The function general linear models (GLM) of the statistical package Statistica® (Statistica 7.0, StatSoft) allowed the geographical component of morphometric variation to be analyzed independent of size and sex. We built a GLM whereby the only predictor variables used were size (SVL) and sex, and we used the residuals in a standardized principal component analysis (PCA) to determine whether specimens were grouped in multivariable space and by which variables. We then classified specimens into seven groups according to their geographic locations relative to the main rivers (Fig. 1): right bank of Rio Aripuanã (RBA), left bank of Rio Aripuanã (LBA), Aripuanã-Roosevelt interfluvium (ARI), right bank of Rio Abacaxis (RBAb), left bank of Rio Abacaxis (LBAb), Madeira-Purus interfluvium (MPI), and Purus-Juruá interfluvium (PJI). The side of river bank (right or left) was defined as one looked downstream. Additionally, we performed two separate PCAs using the same residuals for localities in Rio Aripuanã and the Rio Abacaxis watersheds (Fig. 3). All PCAs were performed on PAST software (Hammer et al., 2001).

The scores of the first principal component (PC1) from the first PCA were used as a synthetic variable of morphological variation in *L. osvaldoi*. This allowed two approaches to further analysis. First, we computed means and standard deviations of scores from PC1 for every locality with more than three specimens (Table 1) to analyze whether the positions of different localities overlapped in PC1, thus giving us an idea about dissimilarity between populations. Second, we compared the relationship between geographic distances of localities and the difference between means of PC1 scores from all locality pairs (i.e., “morphological distance” between populations) through a linear regression. This analysis was performed to detect the relative importance of geographic distance in explaining the morphological variation in *L. osvaldoi* and, thus, to assess possible clinal structure in our dataset.

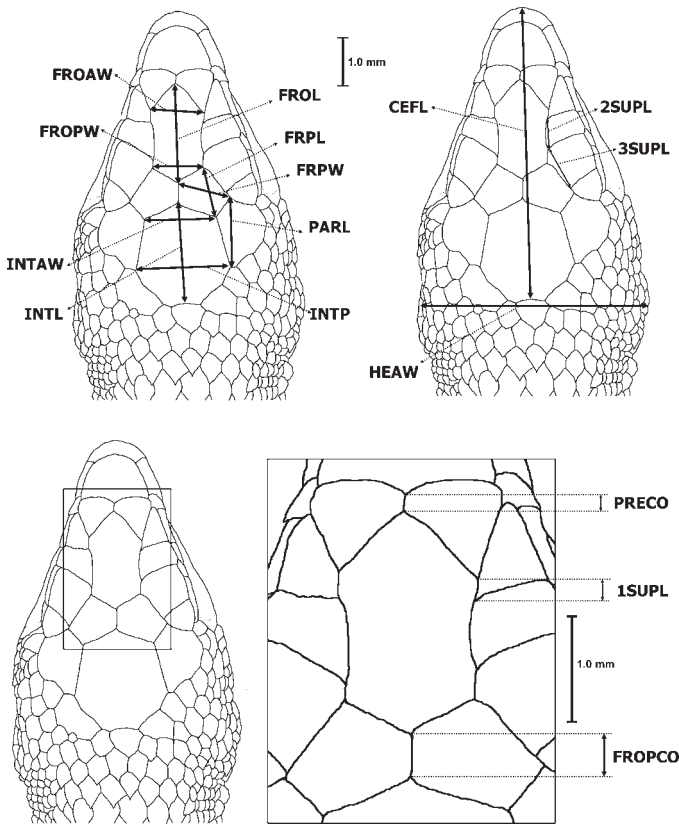


FIG. 2. Measurements made on specimens of *Leposoma osvaldoi*, represented by specimen INPA 17707. INTL = interparietal length; INTAW = anterior width of interparietal; INTPW = posterior width of interparietal; PARL = parietal length; FRPL = frontoparietal length; FRPW = frontoparietal width; FROL = frontal length; FROAW = anterior width of frontal; FROPW = posterior width of frontal; 1SUPL = length of first supraocular; 2SUPL = length of second supraocular; 3SUPL = length of third supraocular; FROPCO = contact between frontoparietals; PRECO = contact between prefrontals; CEFL = length of cephalic scales; HEAW = head width.

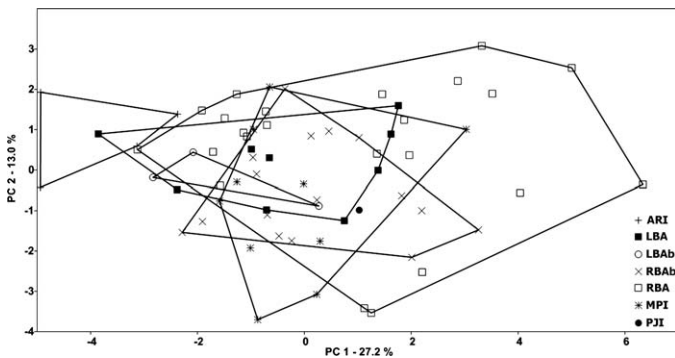


FIG. 3. Scatter plot of the first two principal components of PCA performed with GLM residuals from all individuals analyzed. Points in the graphic are connected according to the biogeographic groups proposed as follows (localities that belong to each group are in parentheses): RBA = right bank of Rio Aripuanã (Lago Cipotuba, Igarapé Extrema, Projó Right, PAREST Sucundurí, Aripuanã); LBA = left bank of Rio Aripuanã (Itapinima, Arauazinho, Nova Colina, Cachoeira do Nazaré, Ministro Andreazza/Nova Brasília); ARI = Aripuanã-Roosevelt interfluvium (Projó Left); RBAb = right bank of Rio Abacaxis (Igarapé Açú); LBAb = left bank of Rio Abacaxis (São Sebastião); MPI: Madeira-Purus interfluvium (Cachoeirinha); PJI = Purus-Juruá interfluvium (Lago Ayapuá).

TABLE 2. Univariate results of the general linear model. Asterisks indicate that values are significant at  $P < 0.05$ .

Variable <sup>a</sup>	SVL		Sex	
	F	P	F	P
INTL	10.057*	0.002*	6.797*	0.011*
INTAW	1.781	0.187	2.113	0.151
INTPW	4.417*	0.040*	1.156	0.286
PARL	24.109*	0.000*	16.612*	0.000*
FRPL	2.025	0.160	10.766*	0.002*
FRPW	4.880*	0.031*	10.875*	0.002*
FROL	1.783	0.187	0.934	0.338
FROAW	15.590*	0.000*	14.014*	0.000*
FROPW	3.927	0.052	12.587*	0.001*
1SUPL	0.030	0.863	1.906	0.172
2SUPL	6.432*	0.014*	6.737*	0.012*
3SUPL	6.155*	0.016*	2.698	0.105
FROPCO	6.172*	0.016*	3.256	0.076
PRECO	1.962	0.166	3.711	0.059
CEFL	21.428*	0.000*	9.729*	0.003*
HEAW	27.729*	0.000*	48.169*	0.000*
HEAL	21.171*	0.000*	1.847	0.179
HEPROF	3.142	0.081	6.102*	0.016*
TRUNKL	—	—	8.921*	0.004*

<sup>a</sup> INTL = interparietal length; INTAW = anterior width of interparietal; INTPW = posterior width of interparietal; PARL = parietal length; FRPL = frontoparietal length; FRPW = frontoparietal width; FROL = frontal length; FROAW = anterior width of frontal; FROPW = posterior width of frontal; 1SUPL = length of first supraocular; 2SUPL = length of second supraocular; 3SUPL = length of third supraocular; FROPCO = contact between frontoparietals; PRECO = contact between prefrontals; CEFL = length of cephalic scales; HEAW = head width; HEAL = head length; HEPROF = head height; TRUNKL = trunk length.

RESULTS

*Size and Sexual Variation.*— Of the 20 variables analyzed, 11 were significantly correlated with size (Table 2). Eleven variables showed strong sexual dimorphism in *L. osvaldoi*, all exhibiting higher values in males except for TRUNKL, for which females presented higher values (Table 2; Fig. 4). Sexual dimorphism was strongest in HEAW with males having significantly broader heads than in females, independent of size and geography.

*Geographic Variation.*—In the first PCA (Table 3; Fig. 3), it was clear that the majority of specimens grouped together regardless

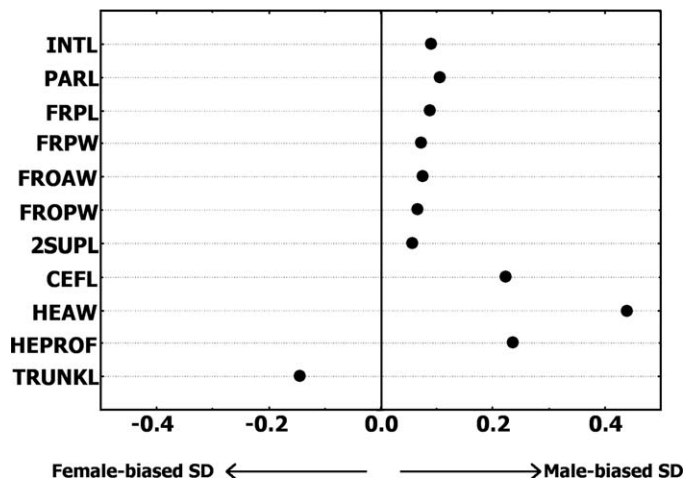


FIG. 4. Measurements showing significant sexual dimorphism (SD) in *Leposoma osvaldoi*. Points on the graph represent the difference between average partial residuals obtained in GLM. Positive values: male-biased SD. Negative values: female-biased SD. Variables are explained in Fig. 2.

TABLE 3. Summary of first PCA results. Loadings are ordered by largest scores on PC1.

PC	Eigenvalue	% variance	Variable <sup>a</sup>	Loadings				
				PC1	PC2	PC3	PC4	PC5
1	5.164	27.178	FRPW	0.813	-0.095	0.284	-0.254	0.099
2	2.456	12.928	INTAW	0.758	0.102	-0.007	-0.331	0.058
3	1.866	9.822	HEAW	0.757	-0.179	-0.168	-0.106	-0.041
4	1.717	9.039	FRPL	0.713	-0.210	0.500	-0.221	0.023
5	1.432	7.535	INTL	0.625	0.547	0.043	0.093	-0.082
6	1.208	6.359	INTPW	0.617	0.019	-0.219	-0.368	0.212
7	1.117	5.880	FROAW	0.596	0.277	0.110	0.223	-0.244
8	0.832	4.376	HEPROF	0.570	-0.179	-0.400	-0.085	0.097
9	0.670	3.526	HEAL	0.565	-0.433	-0.398	0.377	-0.225
10	0.509	2.681	FROPW	0.532	0.183	-0.246	0.290	0.340
11	0.466	2.451	CEFL	0.410	0.434	0.455	0.363	0.168
12	0.372	1.957	2SUPL	0.322	0.593	0.191	0.000	-0.572
13	0.350	1.843	FROPPO	0.304	-0.538	0.417	-0.143	-0.074
14	0.295	1.554	3SUPL	0.255	-0.091	-0.020	0.032	0.489
15	0.217	1.144	FROL	0.139	0.782	-0.287	0.121	0.281
16	0.170	0.893	PRECO	0.109	-0.256	0.628	0.374	0.139
17	0.084	0.441	PARL	0.045	-0.168	0.105	0.776	0.065
18	0.075	0.395	1SUPL	-0.114	-0.051	0.055	0.066	0.613
19	0.000	0.000	TRUNKL	-0.565	0.433	0.398	-0.377	0.225

<sup>a</sup> See Table 2 for an explanation of the variables.

of the river category to which they belong; those specimens occupied the middle portion of PC1 (Fig. 3). Individuals of RBA showed the greatest range of variation in morphology. Specimens from the ARI represented the opposite extreme of PC1 (negative values), being represented by only one locality, Projó Left (Figs. 1, 3). Variables that weighed more heavily on PC1 were the three dimensions of the interparietal scale (INTL, INTAW, INTPW), the two dimensions of the right frontoparietal (FRPL, FRPW), and the HEAW (Table 3). Thus, PC1 mainly represented variation in the dimensions of the interparietal, frontoparietal, and head width.

The PCAs performed for Rio Aripuanã and Rio Abacaxis watersheds (Fig. 5) demonstrated that there is no distinction between individuals from the left and right banks of the lower Rio Aripuanã (localities a, b, c, and d on Fig. 5). In the upper Rio Aripuanã, however, the two localities with larger sample size, Aripuanã (locality h;  $n = 15$ ) and Projó Left (locality e;  $n = 4$ ), did not overlap on PC1. The greatest morphological variation of the RBA group was from Aripuanã, with the majority of specimens from this locality isolated on the positive extreme of the graph (Fig. 5). Additionally, there seemed to be a weak distinction between individuals from opposite banks of Rio Abacaxis; however, the low sample size of locality i (São Sebastião) did not allow firm conclusions.

We applied a multivariate analysis of variance (MANOVA) to test if scores on PC1, PC2, PC3, and PC4 (together accounting for 59% of the morphological variance) were significantly different between localities with more than two individuals (Aripuanã, Projó Left, Igarapé Extrema, Arauazinho, Cachoeirinha, Itapinima, Igarapé Açú, São Sebastião). Only the scores on PC1 differed significantly between the localities ( $F = 6.36$ ;  $P = 0.00002$ , Fig. 6). Then we performed an a posteriori test (Tukey HSD for unequal  $n$ ) on PC1 scores to determine where differences between localities were significant. Projó Left differed significantly from Aripuanã ( $P = 0.00014$ ), Igarapé Açú ( $P = 0.00431$ ), and Cachoeirinha ( $P = 0.02992$ ). Aripuanã also differed significantly from Igarapé Extrema ( $P = 0.02786$ ) (Fig. 6).

The mean and standard deviation of geographic distances between localities was  $371.9 \pm 214.8$  km. The maximum

distance between two localities was 830.0 km and the minimum was 2.0 km. The linear regression between geographic and morphological distances between localities was marginally significant ( $P = 0.06$ ); however, the geographic distance between localities seems to explain a small portion of morphological variation ( $r^2 = 0.032$ ) (Fig. 7). For instance, Projó Left and Aripuanã, the two most-different populations of *L. osvaldoi*, were 312.6 km distant.

## DISCUSSION

*Sexual Dimorphism.*—This is the first time that sexual head size dimorphism (SHSD) has been documented for *Leposoma*. SHSD is a widespread trait in lizards (Anderson and Vitt, 1990; Bull and Pamula, 1996; Herrel et al., 1999; Vitt et al., 2003) including three other genera of the Gymnophthalmidae, *Neusticurus*, *Cercosaura*, and *Vanzosaura* (Pianka and Vitt, 2003). Reference to three selective forces is usually made to explain the evolution of larger heads in male lizards: 1) intrasexual interactions, expressed by aggressive behavior (combat) between males (Anderson and Vitt, 1990; Bull and Pamula, 1996); 2) intersexual interactions, expressed by copulatory bites (Herrel et al., 1996; Herrel et al., 1999); and 3) reduction of food niche overlap between males and females (e.g., males are able to eat larger prey than are females) (Schoener, 1967; Stamps, 1977; Preest, 1994).

Female-biased sexual dimorphism in trunk length is also common in lizards and is referred to in the literature as sexual size dimorphism (SSD). SSD is also recorded here for the first time in *Leposoma*, and *L. osvaldoi* follows the general pattern of female-biased SSD found in other species of the Gymnophthalmidae (Cox et al., 2007). The SSD can appear because of fecundity selection, whereby larger females are selected by an increase in number of offspring and thus leave more descendants (Cox et al., 2007). This does not seem to be the case for *L. osvaldoi* because gymnophthalmids, including *L. osvaldoi* (S. M. Souza, pers. obs.), usually have a fixed clutch size of two eggs (Pianka and Vitt, 2003). Cox et al. (2003:1666) suggested another possibility: "In species with low population densities, females may be widely dispersed and male-male agonistic encounters are presumably less common. Under these conditions, intra-

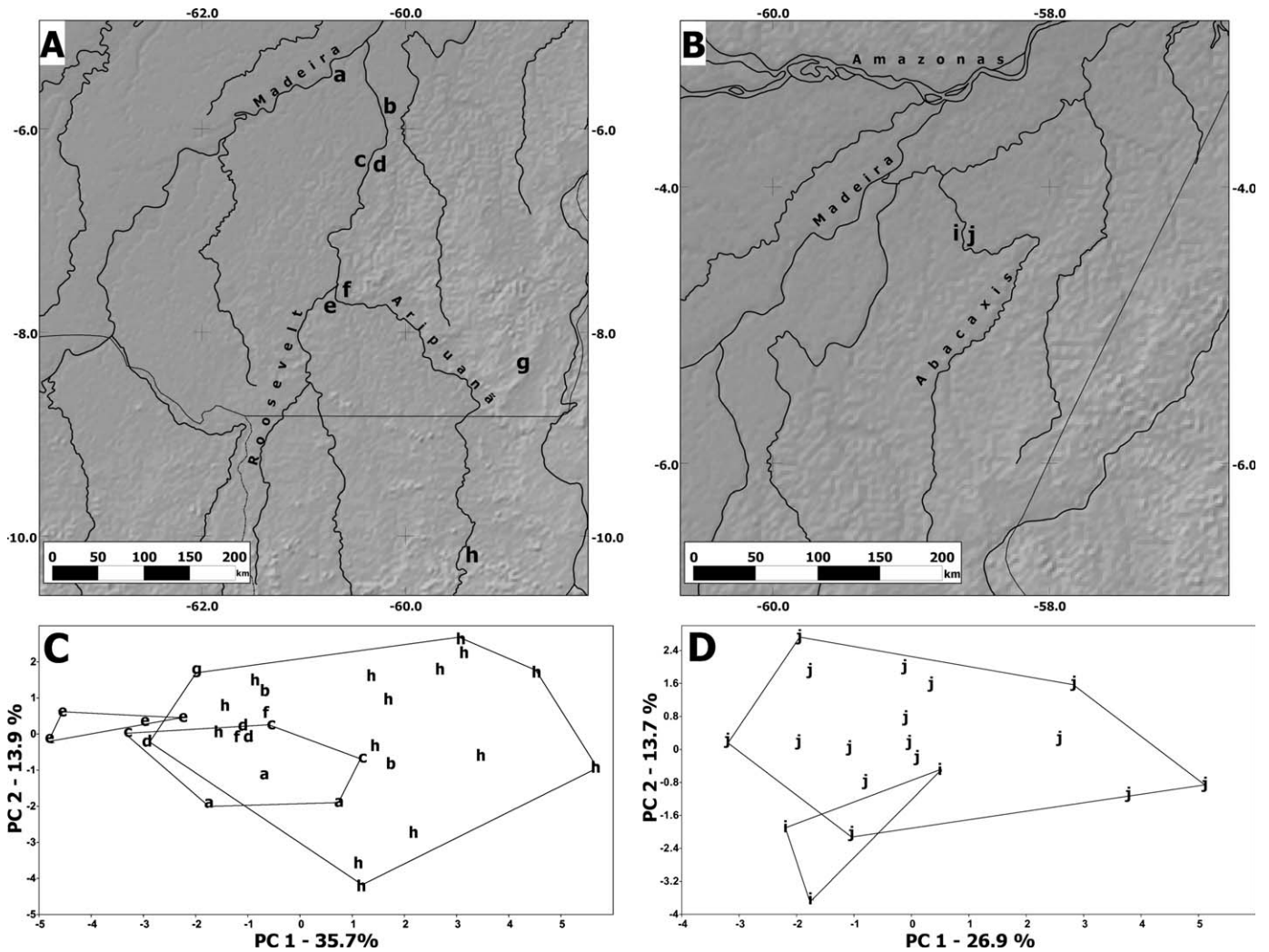


FIG. 5. (A) Localities used in PCA performed specifically at Rio Aripuanã watershed; (B) localities used in PCA performed specifically at Rio Abacaxis watershed; (C) scatter plot of first two principal components of PCA performed with GLM residuals only from individuals of Rio Aripuanã watershed; (D) scatter plot of first two principal components of PCA performed with GLM residuals only from individuals of Rio Abacaxis watershed. Localities: (a) Itapinima; (b) Lago Cipotuba; (c) Arauzinho; (d) Igarapé Extrema; (e) Projó Left; (f) Projó Right; (g) Parque Estadual Sucundurí; (h) Aripuanã; (i) São Sebastião; (j) Igarapé Açú.

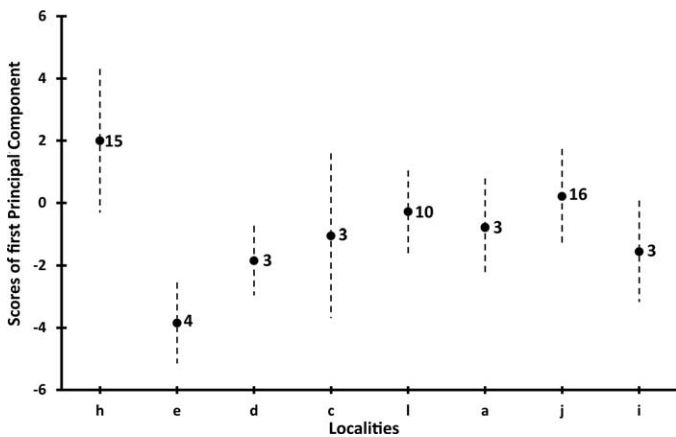


FIG. 6. Mean and standard deviation of scores obtained from first principal component (PC1) of eight localities that had a sample size greater than three. Numbers next to mean dots represent the sample size of each locality. Localities are arranged in crescent latitudinal order: (h) Aripuanã; (e) Projó Left; (d) Igarapé Extrema; (c) Arauzinho; (l) Cachoerinha; (a) Itapinima; (j) Igarapé Açú; (i) São Sebastião.

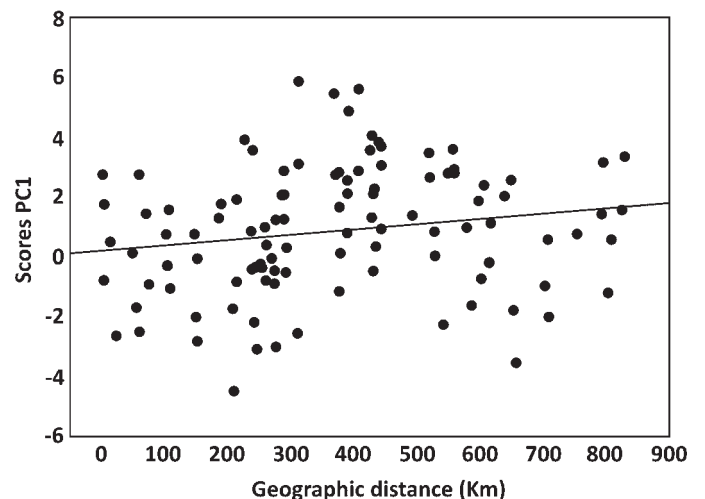


FIG. 7. Scatter plot of pairwise geographic distances and the differences between means of PC1 scores between 15 localities included in this study.

sexual selection acting on males should favor the evolution of early reproduction, high mobility, and time and energy budgets allowing for substantial mate searching, thus selecting for small males." This possibility does not appear to be applicable in *Leposoma* because they are the most abundant gymnophthalmids in several Amazonia herpetofaunal surveys (e.g., Vogt et al., 2007; Avila-Pires et al., 2010; S. M. Souza, pers. obs.). Currently the lack of data, including information on intrasexual and intersexual relationships and reproductive strategies of both males and females, hampers our ability to reach definitive conclusions about the appearance of SHSD and SSD in *L. osvaldoi*.

*Geographic Variation.*—*Leposoma osvaldoi* exhibits significant geographic variation in morphology, related mainly to dimensions of the interparietal and frontoparietal scales. These results agree with previous studies that used the shape and size of the interparietal, in addition to other characters, as a diagnostic characteristic among species of the *L. parietale* group (Uzzel and Barry, 1971; Avila-Pires, 1995).

Geographic distance between localities does not appear to influence the morphological variation of *L. osvaldoi* in a significant way. Our results suggest that geographic distance and morphological distance (given by the difference between means of PC1 scores from all locality pairs) are not strongly related and other factors may be influencing morphological variation. This also indicates that there is no clinal variation in the morphology of *L. osvaldoi*. In fact, we present evidence that morphological variation is relatively constant between populations, with few exceptions (see below).

Our results indicate that the large rivers running across the study area have little influence on morphological variation in *L. osvaldoi*. Specimens from both sides of the Rio Madeira, a well-established faunal divisor in Amazonia (Ayres and Clutton-Brock, 1992; Haffer, 1992; Roosmalen et al., 2002; Cohn-Haft et al., 2007), do not form distinct groups in relation to the set of morphometric characters analyzed. The only individual analyzed from the PJI is grouped with other specimens from the PMI and Madeira-Tapajós interfluvium, (which corresponds to the sum of the areas of LBA, ARI, RBA, LBA<sub>b</sub>, and RBA<sub>b</sub>). Likewise, the Rio Abacaxis does not appear to delimit distinguishable forms.

On the other hand the upper Rio Aripuanã is home to two sites where specimens were remarkably different from the others. In Projó, left bank of Rio Aripuanã, specimens showed small values of interparietal and frontoparietal scale dimensions. In contrast, specimens from Aripuanã, located south of Projó and on the right bank of Rio Aripuanã, occupied the opposite extreme of morphological variation, with greater values of interparietal and frontoparietal scale dimensions. All other specimens analyzed fall between these two morphological extremes. One of the main predictions of the riverine hypothesis, as broadly proposed, is that similarity between individuals at opposite riverbanks should increase with decreasing barrier strength (i.e., gene flow in headwaters is expected to be higher than at a river's mouth) (Gascon et al., 2000). We found the opposite pattern, with specimens from opposite banks of lower Rio Aripuanã being indistinguishable, which was not true for the upper Rio Aripuanã.

The geological history of the Rio Aripuanã may provide a possible hypothesis for the pattern of geographic variation we describe. The landscape of the lower Rio Aripuanã during the mid-Miocene through the Pleistocene (ca. 13 million years ago [Mya] until 1.8 Mya) was dominated by a phenomenon that

produced megafans (Latrubesse, 2002; Wilkinson et al., 2010). Megafans are formed when a fast-flowing river reaches a flat terrain, slowing and spreading its course into a cone-shaped area that can exceed hundreds of kilometers in length. The Rio Aripuanã megafan extended through a large area, with its apex situated a few kilometers north of Rio Roosevelt's mouth flowing into Rio Madeira, approximately from Novo Aripuanã to Manicoré (Wilkinson et al., 2010). This means that the lower Rio Aripuanã was a very dynamic system for a long period of time, changing the location of its main river channel several times during this period. This would have certainly allowed an increase in gene flow between organisms at opposite banks. Meanwhile, in the upper Rio Aripuanã the river appears to have been a much-less dynamic system, as it runs through the stable pre-Cambrian Brazilian Shield. This stability over time could have led to differentiation among *L. osvaldoi* populations from Projó and Aripuanã, assuming that the river prevented gene flow between populations on opposite banks. Rio Roosevelt may have also acted as a barrier preventing gene flow between northern and southern (i.e., Projó) populations. Of course, this hypothesis lacks confirmation from other sources, and evolutionary processes are only testable under a phylogenetic framework, an endeavor beyond the scope of our analysis. Such phylogeographic studies of *L. osvaldoi* are necessary to verify the existence of distinct evolutionary units under the name *L. osvaldoi*, their geographic distribution, and what processes led to their origin.

The role of the rivers in the Amazon Basin in the diversification and distribution of *Leposoma* is not yet fully understood, although our current knowledge of the evolutionary history of the *L. parietale* group prevents one from discarding rivers as important biogeographical barriers for *Leposoma*. A recently proposed phylogeny for *Leposoma* based on 1,830 base pairs from regions of three mitochondrial genes and one nuclear gene places the divergence between the *L. parietale* and *L. scincoides* groups in the early Miocene, 22.15 Mya. The beginning of the diversification of the *L. parietale* group in Amazonia occurred approximately during the mid-Miocene, 13.48 Mya (Pellegrino et al., 2011). This time frame coincides approximately with the establishment of the Amazon Basin as it is known today (10 Mya, Hoorn et al., 2011). However, the present-day distribution of nominal species does not appear to be river-created, with sister species being separated by the course of the main rivers of the Amazon Basin. This is true at least for *L. osvaldoi* (occurring on both sides of Rios Purus, Madeira, and Tapajós) and *Leposoma guianense* (Spectacled Lizard), a primarily Guianan species that also occur on both sides of the lower Rio Amazonas (Avila-Pires et al., 2012). This distribution pattern could indicate either the lack of a river effect in *Leposoma* diversification or an evolutionary history marked by distribution expansion and colonization events. However, questions remain: If large rivers (such as the Rio Madeira) do not appear to influence the distribution of *L. osvaldoi* (or other species), then what were the main factors that led to the diversification within the genus? In addition, why are the distribution patterns in lizards so different from those in birds and primates? Whatever the case, it is clear that *Leposoma* has a complex evolutionary history in Amazonia. Knowing the details of this history can provide important clues that may elucidate the formation of the megadiverse Amazonian biota.

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#### APPENDIX 1. Material examined

##### *Leposoma osvaldoi*

**BRAZIL.** AMAZONAS. Cachoeirinha, INPA 12155, 12157–12165, 12168–12169, leg. M.T. Rodrigues and C. Carrara; Comunidade Projó, left bank Rio Aripuanã, upper mouth of Rio Roosevelt, INPA 17708–17710, 17713, leg. S.M. Souza; Comunidade Projó, right bank Rio Aripuanã, upper mouth of Rio Roosevelt, INPA 17707, 17711, leg. S.M. Souza; Igarapé Açú, right bank Rio Abacaxis, MTR 12735–12736, 12764–12765, 12769, 12807, 12816, 12874, 12882, 12888, 12894–12895, 12915, 12989, 12993–12995 leg. M.T. Rodrigues, J. Cassimiro, J.M.B. Ghellere, S.M. Souza; Igarapé Arauazinho, left bank Rio Aripuanã, INPA 12894, 12896, 12899, leg. V.T. Carvalho; Igarapé Extrema, right bank Rio Aripuanã, INPA 12895, 12897–12898, 12900, 12902–12903, leg. V.T. Carvalho; Itapinima, right bank Rio Madeira, INPA 12166–12167, 12156, leg M.T. Rodrigues, C. Carrara; RDS Piagaçú-Purus, Lago Ayapua, left bank Rio Purus, INPA 14129, leg. F. Waldez; Lago Cipotuba, right bank Rio Aripuanã, MZUSP 91388–91390, leg. M.T. Rodrigues; Comunidade São Sebastião, left bank Rio Abacaxis, MTR 12822, 12858, 12864, 13026 13266, leg. M.T. Rodrigues, J. Cassimiro, J.M.B. Ghellere, S.M. Souza. RONDÔNIA. Cachoeira do Nazaré, Rio Machado (synonymous: Rio Ji-Paraná), MZUSP 66339, leg. A.L. Gardner. Ministro Andreazza (synonymous: Nova Brasília), MZUSP 62330, leg. P.E. Vanzolini; Nova Colina, MZUSP 62168, leg. P.E. Vanzolini. MATO GROSSO. Aripuanã, right bank Rio Aripuanã, MZUSP 82703–82706, 82709, 82712–82716, 82722, 82724, 82730, 82732, 82734, leg. M.T. Rodrigues.