GEOGRAPHIC VARIATION IN THE SOUTH AMERICAN CRICETINE RODENT *BOLOMYS LASIURUS*

REGINA H. MACÊDO AND MICHAEL A. MARES

Department of Zoology and Oklahoma Museum of Natural History, University of Oklahoma, Norman, OK 73019

ABSTRACT.—Variation in cranial morphology of *Bolomys lasiurus* was examined using univariate and multivariate statistical procedures to evaluate approximately 1,000 specimens grouped into seven samples. Sexual dimorphism was found for 20 of the 24 characters analyzed, and the extent of dimorphism is similar throughout the range of the species. Principal components and cluster analyses indicated the presence of two distinct groups: (1) the northernmost Amazonian specimens and (2) significantly smaller specimens from other parts of the species' range.

There are approximately 214 species and 46 genera (Honacki et al., 1982) of South American muroid rodents. In diversity of species and number of individuals, these mice surpass all other mammals of the Neotropical Region (Hershkovitz, 1972), and have been partitioned into eight tribes. One of these, the Akodontini, encompasses a group of closely allied, short-tailed, vole-like genera distributed throughout the grassy regions of South America (Hershkovitz, 1972); most are broadly omnivorous, with some species specialized for an insectivorous diet (Meserve, 1981; Pearson, 1983). Past and present difficulties in establishing boundaries for genera and species groupings have led to disagreement on the composition of this tribe.

Lack of detailed study has prevented the construction of a stable taxonomy for South American muroids. Their fairly recent invasion of South America via the Panamanian land bridge (Mares, 1985; Patterson and Pascual, 1972; but see Hershkovitz [1972] and Reig [1984] for an alternative viewpoint) may have been followed by rapid phyletic differentiation and an explosive diversification of species (Bianchi et al., 1971). These events may be largely responsible for present-day difficulties in the recognition of akodont species.

In this study, we examine the akodont, *Bolomys lasiurus*, a small rodent having a tail much shorter than the total head and body length and a generally dark brown color (Avila-Pires, 1958). The ears are short and covered with hair the same color as the body (see Taxonomic History for detailed discussion of other characteristics).

Bolomys lasiurus occurs in many habitats south of the Amazon (Hershkovitz, 1962), but is mainly found in the *cerrado* and the *caatinga* of central and northeastern Brazil. The *cerrado* is an endemic savanna complex that covers approximately 1.5 million km^2 of central Brazil. The occurrence of a predictable dry season characterizes the region (Eiten, 1972; Joly, 1975). The semiarid *caatinga* of northeastern Brazil is characterized by drought-deciduous forests and dry plant formations, interspersed with thorn woodlands and thorn scrub (Sarmiento, 1975). Although widely distributed in the *cerrado* and *caatinga* of central and northeastern Brazil (Alho, 1982; Mares et al., 1981), *B. lasiurus* also occurs in a variety of other areas, such as the Amazon and Atlantic Forest regions (Mares et al., 1985), as well as in the *chaco* and the *pantanal*. The *chaco* is a deciduous xerophytic forest covered with formations of palms, savannas, and saline steppes (Alho, 1982); in contrast, the *pantanal* of southwestern Brazil is a seasonal marsh, dotted with cerrado-covered hummocks (Eiten, 1982).

Geographic variation in *B. lasiurus* has not been examined. The objectives of this study are to define the nature and extent of geographic variation in *B. lasiurus* using a morphometric analysis, as well as to examine sexual dimorphism and individual variation among the populations.

TAXONOMIC HISTORY

Bolomys lasiurus at various times has been considered to be a member of *Akodon* (Ellerman, 1941), *Zygodontomys* (included by Hershkovitz, 1962, in the phyllotines), and *Bolomys* (Reig, 1978).

Thomas (1910) listed *lasiurus* Lund under *Zygodontomys*. Osgood (1912, p. 52 as cited in Tate, 1932) wrote of *Zygodontomys:* "Although formerly associated with *Oryzomys* the species of this genus seem to

have much in common with *Akodon* ...." This opinion was shared by Thomas (1916) who assigned *Zygodontomys* to the akodont group, thus removing it from the oryzomyine assemblage. He also subdivided the *Akodon* group into seven genera: *Zygodontomys*, *Akodon*, *Abrothrix*, *Thalpomys*, *Thaptomys*, *Bolomys*, and *Chroeomys*. The skull of the newly erected genus, *Bolomys*, was detailed as being "stout and strongly built, with broad square-edged interorbital region. Zygomatic plate projected forward. Palatal foramina narrowed behind, continued well between the molars. Bullae very large. First molar apparently without anterior notch" (Thomas, 1916:339). Distinction between *Zygodontomys*, *Akodon*, and *Bolomys* rested mainly upon claw size, bullar size, external characteristics (tail length; eye size), cranial characteristics (supraorbital edges squared or beaded; width of interorbital region), and upon dental morphology (M^1 with or without notch on anterior surface).

Tate (1932) followed Thomas (1910) in considering *lasiurus* a *Zygodontomys*. Five clusters of species within *Zygodontomys* were recognized by Tate (1932), the first three inhabiting the Neotropics north of the Amazon River and the other two groups occurring south of that river. In the latter two groups he included the following species: *lasiurus*, *arviculoides*, *tapirapoanus*, *orobinus*, and *brachyurus*.

Ellerman (1941) criticized Thomas' (1916) division of *Akodon* into seven genera, and subsequently included in *Akodon* the following genera: *Thalpomys*, *Thaptomys*, *Bolomys*, *Chroeomys*, *Deltamys*, *Hypsimys*, and *Abrothrix* Waterhouse. As for *lasiurus*, Ellerman (1941, p. 410) regarded it as "probably a member of the genus *Akodon*."

Cabrera (1961) followed Ellerman (1941) in including within *Akodon* various genera named by Thomas. Cabrera accepted *Zygodontomys* as a valid genus, although he pointed out its close similarity to *Akodon*, especially when considering the Brazilian forms. He reduced the 12 South-American species recognized by Ellerman (1941) to only four: *brevicauda*, *lasiurus* (containing *fuscinus* and *pixuna*), *microtinus*, and *punctulatus*. In addition, Cabrera indicated that *Hesperomys brachyurus* Wagner was a possible synonym for *lasiurus*. *Zygodontomys* continued to be controversial as to its taxonomic position within the different tribes of the Sigmodontinae. Hershkovitz (1962) suggested that *Zygodontomys* was an annectant form between phyllotine and akodont rodents, but he nonetheless placed *Zygodontomys* in the phyllotine group. He also separated the genus into two distinctive geographic branches: a northern group typified by *Z. brevicauda*, ranging north of the Amazon River and into Central America; and a southern group, occupying habitats south of the Amazon, throughout Brazil.

Hooper and Musser (1964) provided extensive data on phallic morphology for *Zygodontomys*. They included *lasiurus* as a species of *Zygodontomys*, in spite of the fact that bacular mounds, the urethral process, and the baculum in *lasiurus* approach conditions observed in *Akodon*.

A new genus, *Cabreramys*, was erected by Massoia and Fornes (1967). It comprised a distinct group of akodont species: *amoenus*, *obscurus*, and *lasiurus*. In comparing *Cabreramys* with *Akodon*, the authors stressed several morphological differences. *Akodon*, for instance, has wider nasals and opisthodont incisors; also, the molars are more complex. *Cabreramys* was also contrasted with *Zygodontomys*, the latter having a proportionately larger and narrower cranium, and wider nasals.

Thomas' (1916) subdivision of *Akodon* into several new genera was partly supported by Bianchi et al. (1971) who suggested, on the basis of karyology, the following forms as deserving full generic status: *Abrothrix*, *Akodon*, *Blarinomys*, *Bolomys*, *Chroeomys*, *Hypsimys*, *Lenoxus*, *Microxus*, *Notiomys*, *Oxymycterus*, *Podoxymus*, *Thalpomys*, and *Thaptomys*. This classification was followed by Gardner and Patton (1976). They excluded *Zygodontomys* from the phyllotine group due to its high diploid number (Pearson and Patton, 1976), and suggested that its affinities might lie closer to the akodonts. Karyotypically, *lasiurus* was found to be sharply distinct from other *Zygodontomys*, and was thus included in *Akodon*.

A classification along the same lines as that proposed by Massoia and Fornes (1967) was presented by Reig (1978); however, he considered that *Bolomys* was a distinct genus and had priority over *Cabreramys*. In *Bolomys*, he included *lasiurus* (comprising *brachyurus*, *arviculoides*, *fuscinus*, and *pixuna*), as well as: *obscurus* (including *benefactus*), *amoenus*, *lactens* (including *orbus*, *negrito*, and *leucolimnaeus*), and *lenguarum* (including *tapirapoanus*).

The classification established by Corbet and Hill (1980) was similar to that of Bianchi et al. (1971). In *Bolomys* they placed *albiventer*, *amoenus*, *berlepschii*, and *lactens*. They recognized *Cabreramys*, which comprises *benefactus*, *lenguarum*, and *obscurus*. Finally, they placed *lasiurus* in *Zygodontomys*.

The karyology of *lasiurus* was reviewed by Maia and Langguth (1981), who, like Pearson and Patton (1976), suggested that this species does not belong in the genus *Zygodontomys*. Karyotypes of $2n = 34$ and 33, and FN = 34 confirm the diploid number already described by Yonenaga (1973) for this species. Maia and Langguth (1981) emphasized the great difference between the karyotypes of *lasiurus* and of *Z. microtinus*, $2n = 88$ and $2n = 84$ (Gardner and Patton, 1976; Kiblisky et al., 1970). Accordingly, due to morphological and cytogenetic evidence, Maia and Langguth (1981) maintained that *lasiurus* should be placed in *Bolomys*.

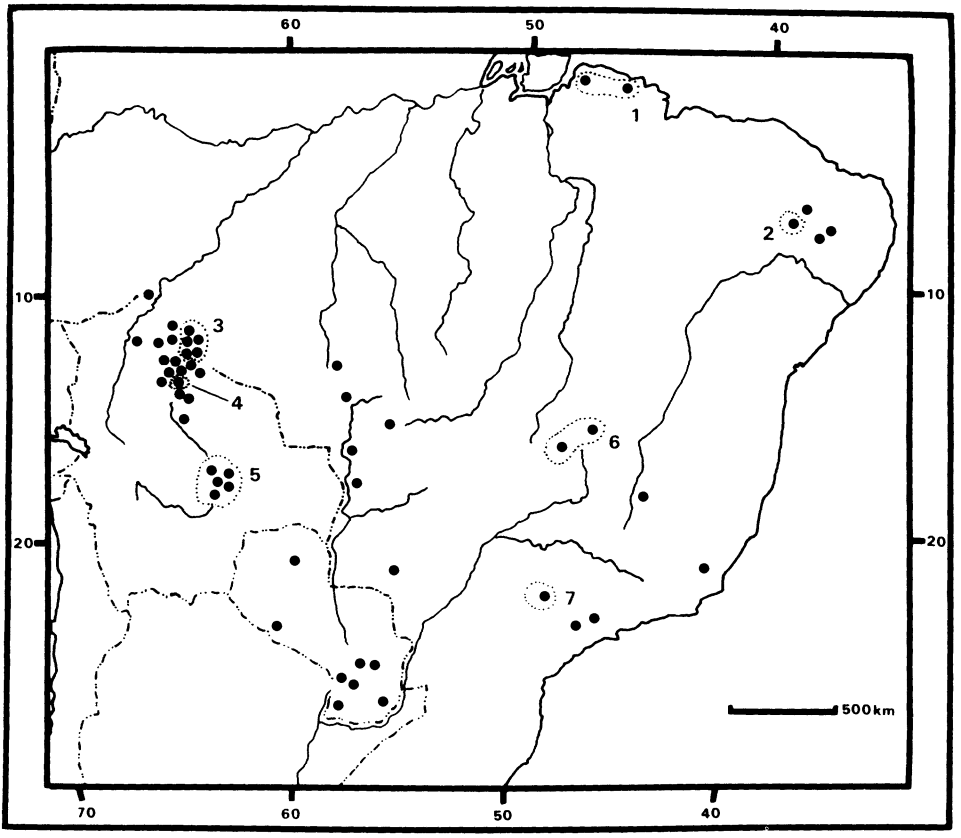

FIG. 1.—Map of geographic groups of *Bolomys lasiurus*. Each dot represents a location from which specimens were examined. Dots enclosed and numbered represent groups included in the statistical analyses. Habitats of the samples: 1 = lowland rain forest; 2 = *caatinga*; 3 and 4 = upland rain forest; 5 = *chaco*; 6 = *cerrado*; 7 = upland deciduous forest.

The taxonomic status of *lasiurus* was also examined by Voss and Linzey (1981), who followed Gardner and Patton (1976) in referring *lasiurus* to *Akodon*. They suggested that the name *Zygodontomys* be restricted to the *brevicauda*-like rodents occurring north of the Amazon Basin. They based their opinion on ventral prostate morphology as well as dental and chromosomal evidence. In this report, we follow Reig (1978) in assigning *lasiurus* to the genus *Bolomys*.

MATERIALS AND METHODS

A total of 1,007 specimens was examined in the following museums: American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM); Field Museum of Natural History (FMNH); National Museum of Natural History (USNM); Oklahoma Museum of Natural History, University of Oklahoma (OU); University of Michigan Museum of Zoology (UMMZ); and Museum of Vertebrate Zoology, University of California (MVZ). Of the total number of specimens examined (see Appendix I), 763 (414 males and 349 females) actually were used in the analyses.

The following cranial and mandibular measurements were taken with dial calipers: (1) cranial depth, (2) greatest length of skull, (3) condylobasal length, (4) nasal length, (5) zygomatic breadth, (6) breadth of braincase, (7) rostral breadth, (8) nasal width, (9) least interorbital breadth, (10) palatilar length, (11) basioccipital length, (12) palatal width at M^1, (13) palatal width at M^3, (14) length of maxillary tooth row, (15) diastema length, (16) incisive foramina length, (17) tympanic bullae width, (18) tympanic bullae length, (19) mandibular length, (20) distance between mental formen and mandibular condyle, (21) distance between tips of coronoid and ventral angular processes, (22) distance between tips of coronoid and dorsal angular

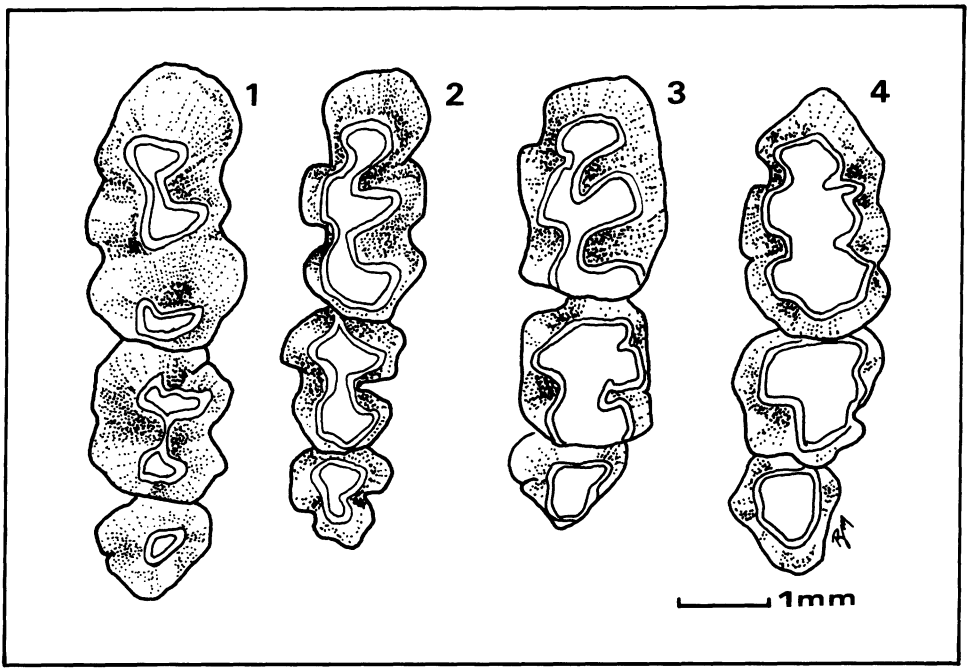

FIG. 2.—Molar tooth wear in *B. lasiurus*. Upper right molars 1, 2, and 3 are shown from anterior to posterior for each of the four age classes (1–4), with 1 being the youngest and 4 the oldest.

processes, (23) distance between mandibular foramen and mandibular condyle, (24) and length of mandibular tooth row.

Specimens were assembled into geographic groups by pooling geographically adjacent collections. The objective was to obtain statistically meaningful samples from geophysically and phytogeographically homogeneous areas (Fig. 1).

A total of seven groups of localities (OTUs—operational taxonomic units) was analyzed in detail. Specimens were assigned to four age categories on the basis of tooth wear (Fig. 2). Juveniles (6.5% of total) were assigned to category 1; subadults (24.8% of total), adults (66.8% of total), and old adults (1.9% of total) to categories 2, 3, and 4, respectively. Age categories corresponded to the amount of wear shown by the molar cusps.

All specimens in age category 1 were excluded from analyses, thus substantially reducing variation due to age. Analysis of variance was used to verify significant differences among specimens assigned to age categories 2, 3, and 4; very highly significant differences ($P < 0.001$, $d.f. = 3$) were found for all characters. These three age classes are clearly morphologically distinct, and a correction for age was deemed necessary before subsequent analyses could be carried out (see Table 1 for sample sizes by age, sex, and locality). Age

TABLE 1.—*Sample sizes for each locality by age class and sex. M = male, F = female.*

		Age class						
		Subadult		Adult		Old adult		
Sample	n =	M (104)	F (90)	M (303)	F (251)	M (7)	F (8)	Total (763)
1			2	26	13			41
2		48	38	38	50	1		175
3		1	7	40	42	2	3	95
4		17	12	30	25			84
5			3	23	13	1		40
6		14	12	37	21	3	5	92
7		24	16	109	87			236

category 3 (see Fig. 2) was used as representative of the average adult specimen. Individuals in age categories 2 and 4 were corrected to this standard through the addition or subtraction of differences existing between means for all characters, when compared to the means of age category 3. The correction for age should provide a good approximation, as it was not a strictly linear correction (i.e., the amount corrected for each character from age category 2 to 3 was not the same amount as that from category 4 to 3). The mean percent correction over all characters for age categories 2 (subadult) and 4 (old adult) was 5.6 and 3.2% , respectively. Thus, growth changes were assumed to occur at a more rapid rate during younger age categories than among older animals. This assumption has been borne out in many studies (e.g., Mello, 1978*a*, 1978*b*; Villafañe, 1981*a*, 1981*b*).

Extensively damaged specimens yielding fewer than 17 of the measurements also were excluded from the analyses. For missing values on other specimens (which comprised approximately 5% of our total measurements) linear regression on characters that explained the greatest amount of variance was utilized to estimate missing data ("Missing Data Estimator" program, Dennis M. Power). Thus, 53% of all specimens had all measurements available. Most specimens with missing characters usually lacked only one or two values (32%); only 6 specimens lacked 7 measurements.

All analyses were carried out on the IBM-3081 computer of the University of Oklahoma. Subroutines from the Statistical Analysis System (SAS; Barr et al., 1976) yielded standard statistics for male and female specimens. A two-way analysis of variance (ANOVA) was employed to indicate differences between males and females in each locality, and among geographic areas. The percentage difference between males and females was obtained by computing the difference between sexes for each character over all localities (males minus females), multiplying the difference by 100, and dividing the resulting value by the average of the male and female means. A similar computation for percentage differences was employed by Schnell et al. (1985) in a study of sexual dimorphism in spotted dolphins (*Sturnella attenuata*). A Duncan's Multiple Range test (Duncan test, PROC GLM from SAS) was used to indicate maximally nonsignificant subsets among geographic localities. NT-SYS programs developed by Rohlf et al. (1982) were used on standardized data (i.e., character means = 0, character variances = 1) to generate a matrix of average taxonomic distance coefficients. The UPGMA (unweighted pair-group method using arithmetic averages) clustering method was employed to construct dendrograms of phenetic distance. These phenograms were then compared to the original matrices to compute the coefficient of cophenetic correlation, which reflects the accuracy of the similarity values in the phenogram in relation to those in the original similarity matrix (Sneath and Sokal, 1973). The first three principal components were extracted from the correlation matrix among characters, and projections (based on standardized data) of the OTUs (population means) onto the principal component axes were plotted.

Multivariate analyses indicated the presence of three partially separated groups composed of the seven originally designated samples. A stepwise discriminant function analysis (Program P7M of BMDP-83; Dixon, 1983) was employed to differentiate among these three reference samples. The F-value to enter was specified at 4.0 ($P < 0.001$). Results showed much overlap among the samples, and suggested the existence of only two major groups. Discriminant function analysis was employed to discriminate maximally between these two groups. This procedure indicates those characters that give the maximum discrimination between samples. Individual specimens can be projected onto the discriminant axis to visualize the separation between groups. The probability of correct classification of specimens in the a priori designated reference samples also can be calculated.

Results

Intrapopulation Variation

Secondary sexual variation.—Sexual dimorphism was found for 20 of the 24 characters (Table 2); of these, 18 were dimorphic at a very highly significant level ($P < 0.001$, $d.f. = 1$). The distance from the mandibular foramen to the articular condyle was highly significant ($P < 0.01$, $d.f. = 1$), bullar width was significantly dimorphic ($P < 0.05$, $d.f. = 1$), and four characters were nonsignificant: nasal width, palatal width at M^3, toothrow length, and mandibular toothrow length. The percent difference between males and females is also given in Table 2. Males were consistently larger than females in all samples, and the pattern of sexual dimorphism remained uniform for all localities; interactive effects between locality and sex factors were not statistically significant for any of the characters.

Individual variation.—Coefficients of variation were evaluated within sexes for all characters. There were no intralocality differences in variation between the sexes. Over all localities, coef-

TABLE 2.—*Variation in means of 24 cranial characters in* B. lasiurus. *Percentage differences between sexes*[a] *and significance levels for secondary sexual dimorphism shown in parentheses:* *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. *Lines below OTU numbers and ranked means denote nonsignificant subsets.*

Character	Means and nonsignificant subsets													
	Males							Females						
Cranial depth (1.12; ***)	6	7	3	4	5	1	2	6	7	1	5	3	4	2
	11.07	11.00	10.80	10.76	10.76	10.67	10.64	10.84	10.82	10.77	10.64	10.60	10.59	10.57
Skull length (2.00; ***)	5	1	2	3	7	4	6	5	1	2	7	4	6	3
	29.35	29.23	28.83	28.54	28.48	28.44	28.38	28.66	28.64	28.19	28.07	27.94	27.92	27.87
Condylobasal length (1.86; ***)	5	1	2	7	3	6	4	1	5	7	2	6	3	4
	28.16	28.10	27.80	27.51	27.31	27.28	27.25	27.85	27.62	27.16	27.10	26.77	26.70	26.66
Nasal length (1.75; ***)	2	5	3	4	6	7	1	2	5	1	6	7	3	4
	9.95	9.95	9.83	9.79	9.67	9.64	9.60	9.79	9.75	9.71	9.58	9.54	9.48	9.41
Zygomatic breadth (1.84; ***)	5	1	7	6	2	3	4	1	5	7	2	6	3	4
	15.58	15.58	15.39	15.34	15.29	15.19	15.13	15.60	15.19	15.18	15.08	14.91	14.86	14.76
Breadth of braincase (0.68; ***)	5	6	7	1	4	3	2	5	1	7	6	3	4	2
	13.71	13.40	13.36	13.31	13.26	13.20	13.06	13.64	13.39	13.34	13.21	13.14	13.05	12.92
Rostral breadth (3.66; ***)	6	2	5	4	3	1	7	6	2	5	1	7	4	3
	5.34	5.34	5.31	5.27	5.25	5.24	5.21	5.17	5.13	5.12	5.10	5.09	5.00	4.99
Nasal width (1.12; NS)	2	6	1	3	7	5	4	2	1	6	3	7	5	4
	3.72	3.67	3.65	3.64	3.52	3.50	3.50	3.67	3.61	3.57	3.56	3.55	3.52	3.44
Interorbital constriction (2.00; ***)	5	6	3	1	7	4	2	5	1	6	3	7	4	2
	5.15	5.13	5.05	5.03	5.00	5.00	4.98	5.05	5.00	5.00	4.92	4.92	4.91	4.87

TABLE 2.—*Continued.*

Character	Means and nonsignificant subsets													
	Males							Females						
Palatilar length (1.85; ***)	1 13.28	4 13.27	3 13.21	5 13.15	7 13.09	2 13.00	6 12.88	1 13.15	7 12.97	5 12.96	3 12.93	4 12.89	2 12.77	6 12.54
Basioccipital length (2.74; ***)	1 4.76	2 4.50	5 4.49	4 4.35	7 4.34	3 4.33	6 4.28	1 4.60	5 4.42	2 4.36	7 4.31	3 4.21	4 4.18	6 4.15
Palatal width at M1 (1.71; ***)	1 3.76	5 3.69	7 3.60	2 3.57	6 3.53	3 3.43	4 3.23	1 3.80	5 3.55	7 3.55	6 3.49	2 3.45	3 3.39	4 3.16
Palatal width at M3 (0.00; NS)	1 3.37	6 3.13	7 3.03	5 2.98	3 2.96	2 2.94	4 2.88	1 3.31	6 3.21	5 3.06	7 3.04	3 2.89	2 2.89	4 2.85
Toothrow length (0.43; NS)	5 4.77	1 4.73	4 4.68	7 4.67	3 4.67	2 4.60	6 4.56	1 4.80	5 4.76	7 4.68	3 4.68	4 4.58	2 4.57	6 4.46
Diastema length (1.61; ***)	7 8.27	1 8.21	6 8.19	5 8.13	2 8.12	3 8.00	4 7.97	1 8.16	7 8.12	6 8.07	5 8.00	2 7.95	4 7.86	3 7.83
Incisive foramina length (1.25; ***)	1 6.86	7 6.58	6 6.41	2 6.33	5 6.29	3 6.23	4 6.22	1 6.74	7 6.46	6 6.34	5 6.28	4 6.24	2 6.17	3 6.16
Bullar width (0.86; *)	2 4.74	5 4.73	6 4.72	7 4.67	3 4.63	1 4.62	4 4.62	2 4.71	6 4.68	7 4.66	1 4.64	5 4.63	3 4.61	4 4.55

TABLE 2.—*Continued.*

Character	Means and nonsignificant subsets													
	Males							Females						
Bullar length (2.46; ***)	4 5.82	2 5.81	7 5.78	3 5.78	1 5.75	6 5.74	5 5.67	2 5.67	4 5.65	7 5.64	1 5.64	3 5.64	5 5.56	6 5.55
Mandibular length (1.74; ***)	5 16.98	7 16.95	1 16.89	4 16.78	2 16.70	3 16.70	6 16.51	1 17.01	7 16.80	3 16.48	2 16.40	5 16.30	4 16.30	6 16.19
Mental foramen to articular condyle (1.20; ***)	1 13.55	7 13.46	4 13.46	5 13.42	3 13.38	2 13.31	6 13.25	1 13.62	7 13.30	5 13.19	3 13.18	2 13.15	4 13.14	6 13.07
Coronoid to ventral angular process (2.55; ***)	2 8.52	1 8.51	5 8.39	4 8.32	3 8.25	7 8.21	6 8.19	1 8.39	2 8.25	5 8.12	7 8.10	6 8.04	4 8.00	3 7.99
Coronoid to dorsal angular process (3.08; ***)	1 7.80	2 7.79	4 7.60	5 7.53	7 7.49	6 7.44	3 7.44	1 7.69	2 7.55	7 7.37	6 7.26	3 7.20	5 7.18	4 7.17
Mandibular foramen to articular condyle (1.01; **)	1 4.31	5 4.02	7 3.99	2 3.96	3 3.92	6 3.91	4 3.88	1 4.37	5 4.03	7 3.95	2 3.89	6 3.84	4 3.83	3 3.80
Mandibular toothrow length (0.42; NS)	1 4.96	5 4.81	4 4.77	7 4.77	3 4.74	6 4.73	2 4.66	1 4.90	5 4.81	3 4.78	7 4.78	4 4.73	2 4.66	6 4.63

[a] The difference between sexes (males minus females) multiplied by 100, with the resulting product divided by the average of the male and female means.

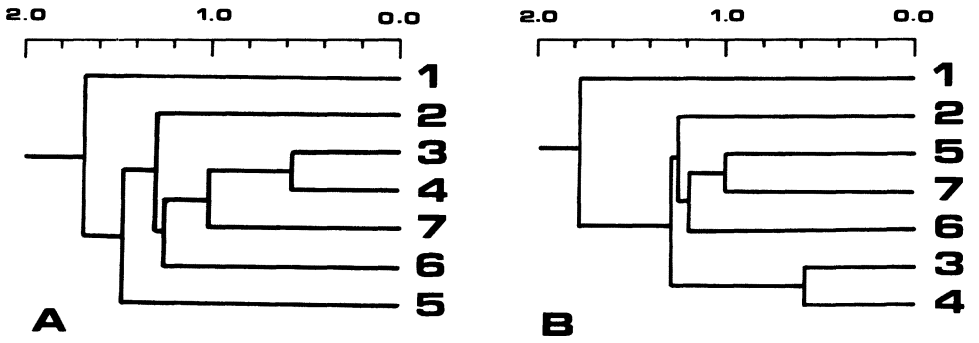

FIG. 3.—Distance phenograms of numbered samples (coded as in Fig. 1) of (A) male and (B) female *Bolomys lasiurus* and clustered by unweighted pair-group method using arithmetic averages.

ficients of variation ranged from 2.28 (bullar width, females) to 11.94 (distance between coronoid and dorsal angular process, males). Considering all characters over all samples, the average *CV* for males was 5.23, and for females, 5.18. The following measurements exhibited high *CVs*: Distance between mandibular foramen and articular condyle, palatal width at M^1, distance between coronoid and dorsal angular process, and rostral breadth. The highest intralocality *CV* values were almost totally restricted to specimens of locality 5. Females from this locality (central Bolivia) exhibited *CVs* exceeding 10 for the following measurements: basioccipital length, mandibular length, distance between mandibular foramen and articular condyle, and between coronoid and dorsal angular process. Males of this same sample displayed substantial variability only in the last character. The only other character found to be highly variable was palatal width at M^1, with a *CV* of 10.04 for females of sample 6.

Geographic Variation

Univariate analyses.—Results of Duncan's Multiple Range test for each of the 24 characters are shown in Table 2. OTUs 1 and 5 are frequently among the largest samples, with OTU 1 being the largest for nine characters in both male and female samples. OTUs 4 and 6 are generally smaller for most of the characters. No significant differences for character means among localities were found for male rostral breadth, and for bullar length in both sexes. Nonoverlapping subsets were found for several characters, most frequently in the case of OTU 1. Both sexes from locality 1 were significantly larger in basioccipital length, incisive foramina length, distance between mandibular foramen and articular condyle, and mandibular toothrow length. Females of locality 1 had values significantly larger than those of the remaining OTUs for the following characters: zygomatic breadth, palatal width at M^1, and distance between mental foramen and articular condyle. Males from this sample had significantly larger palatal width at M^3. Cranial depth is significantly larger in male specimens from central and southern Brazil (OTUs 6 and 7, respectively), as is skull breadth in males and females from OTU 5 (central Bolivia). Females of localities 1 and 6, and males of locality 1, exhibited larger palatal width at M^3. The remaining characters showed from one to four overlapping subsets, but no distinctive groupings.

Multivariate analyses.—Distance phenograms summarizing multivariate trends for males and females are shown in Fig. 3. Male samples (Fig. 3A) are sharply divided: The first division contains OTU 1, from the Amazonian region; the second grouping comprises OTUs 2, 3, 4, 7, and 6; locality 5, from central Bolivia, is the sole sample in the third division of the phenogram. For females (Fig. 3B), the pattern of isolation of locality 1 found for the males is repeated. In both phenograms, sample 2, from the xeric *caatinga*, is also somewhat distinctive. In the female phenogram this locality stands out to a greater degree than does sample 5 from central Bolivia.

The loadings of characters on the first three principal component axes are presented in Table 3. Component I has high correlations with most characters for both sexes. In the males, the first

TABLE 3.—*Character loadings on the first three principal components involving character means from seven geographic localities.*

Character	Males			Females		
	I	II	III	I	II	III
Cranial depth	−0.451	0.426	−0.662	0.426	−0.472	0.338
Skull length	0.850	0.234	0.269	0.842	0.047	0.154
Condylobasal length	0.865	0.281	0.304	0.946	0.035	0.078
Nasal length	−0.236	0.147	0.512	0.623	−0.426	−0.271
Zygomatic breadth	0.851	0.512	−0.083	0.995	0.007	−0.089
Breadth of braincase	0.352	0.593	−0.560	0.602	0.027	0.730
Rostral breadth	−0.337	0.611	0.596	0.409	−0.887	0.020
Nasal width	−0.102	0.157	0.700	0.424	−0.467	−0.687
Interorbital constriction	0.059	0.785	−0.320	0.495	−0.235	0.785
Palatilar length	0.483	−0.737	−0.213	0.622	0.772	0.005
Basioccipital length	0.904	−0.117	0.392	0.936	0.165	−0.159
Palatal width at M^1	0.771	0.520	0.106	0.938	−0.237	0.013
Palatal width at M^3	0.689	0.155	−0.069	0.758	−0.403	0.326
Toothrow length	0.725	−0.195	−0.315	0.715	0.591	0.151
Diastema length	0.449	0.496	−0.162	0.791	−0.410	0.122
Incisive foramina length	0.741	−0.019	−0.099	0.855	0.040	0.120
Bullar width	−0.178	0.825	0.393	0.298	−0.786	−0.440
Bullar length	−0.466	−0.744	0.291	−0.031	0.563	−0.800
Mandibular length	0.701	−0.175	−0.309	0.763	0.375	−0.257
Mental foramen to articular condyle	0.732	−0.575	−0.335	0.885	0.359	−0.111
Coronoid to ventral angular process	0.615	−0.151	0.749	0.862	−0.074	−0.435
Coronoid to dorsal angular process	0.548	−0.306	0.721	0.733	−0.110	−0.635
Mandibular foramen to articular condyle	0.946	−0.052	0.075	0.966	0.144	0.027
Mandibular toothrow length	0.864	0.168	−0.326	0.716	0.645	0.221

component explains 40.4% of the variation among population means. Components II and III account for 20.2% and 17.2% of the variation, respectively. For the females, the first component accounts for 53.7% of the variation; the second and third components explain 18.7% and 15.0%, respectively.

A three-dimensional plot of the first three principal components for males (Fig. 4A) indicates that there is an increase in size of most cranial characters from left to right along component I. Component II places OTUs with wide rostrums and bullae to the front of the model, and those with narrow rostrums and long bullae to the back. The third component is represented by the heights of the stalks in the three-dimensional plot. OTUs with wide and shallow crania are positioned closest to the plane depicted in the figure. OTUs 4, 3, 2, and 7 are characterized by smaller cranial characters in general but, more specifically, by narrower rostrums and bullae. OTUs 1, 5, and 6 are outliers. Specimens from locality 1 are distinctively larger in most characters, with longer and narrower bullae. OTU 5, by contrast, contains individuals with very short and wide bullae. Male *B. lasiurus* from the *cerrado* of central Brazil (OTU 6) are distinctively smaller in most cranial characters.

A three-dimensional plot for the first three components extracted from the female correlation matrix is presented in Fig. 4B. Female specimens comprising OTU 6 reflect the trend found for males: They are smaller in most cranial characters, but have relatively broad rostrums and bullae. OTU 1 is positioned at the far right of the plot, indicating that specimens from this sample have large values for size-related characters highly associated with Principal Component I.

Principal components analysis suggested two, and possibly three, groups involved in the seven original samples: (1) the Amazonian populations; (2) the central Bolivian sample; (3) and a third group composed of all remaining OTUs, including sample 2 (from the *caatinga*), which is also somewhat distinct. A stepwise discriminant function analysis was used to identify those characters that best distinguished these three reference samples. Significant overlap among these samples

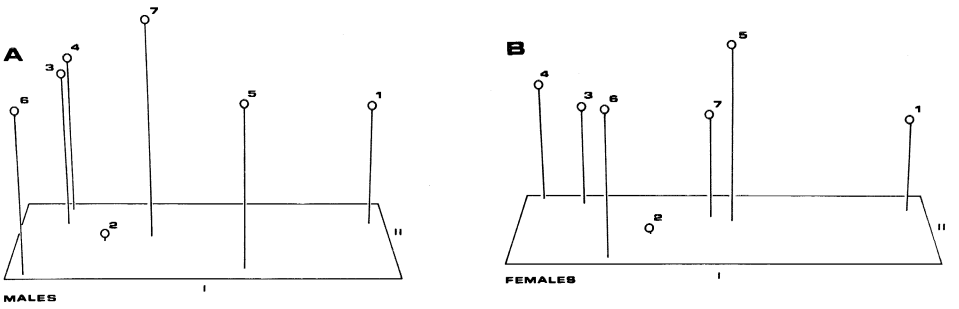

FIG. 4.—Three-dimensional projections of (A) male and (B) female sampled localities of *Bolomys lasiurus* onto the first three principal components based on character correlation matrices. Samples are coded as in Fig. 1.

was apparent in the results. The central Bolivian specimens were completely separated from the Amazonian ones, but overlapped greatly with all other remaining specimens. Thus, two well differentiated groups were defined: an Amazonian cluster; and a large division containing the remaining populations. A second stepwise discriminant function analysis (Fig. 5) was then used to discriminate maximally between these two groups: (1) the Amazonian cluster; (2) and all remaining samples, including those from central Bolivia and the *caatinga*. The resulting function for the males included 11 characters (Table 4). The most useful character for differentiating between the Amazonian and the other specimens was palatal width at M^3. A group of seven variables, taken in combination, was found to discriminate well between these two groups for the females. Of these, distance between the mandibular foramen and the articular condyle was the most useful character.

Coefficients for the functions of both males and females are given in Table 4. Standardized coefficients indicate the relative importance of individual characters in placing specimens on the axis. Additional specimens can be projected onto the axis by using the unstandardized discriminant coefficients. The classification functions indicated that the probability of correct classification for specimens in the first (Amazonian) and second (Others) groups was 84.6% and 95.6%, respectively, for males, and 100% and 87.7% for females.

DISCUSSION

Nongeographic variation.—Individual variation, as shown by the coefficients of variation, was small and in most cases within the expected range—from 2 to 8—that is typical for morphological features of mammals (Long, 1969; Simpson, 1953). Sexual dimorphism was found for 83% of the 24 measurements used. The percentage difference between sexes was computed for each character (see Methods) to test whether such highly significant sexual dimorphism was a function of the large sample size. Indeed, much of the sexual dimorphism involves small percentage differences (Table 2); the largest difference was 3.66% for rostral breadth. In no characters were females larger than males.

There are few references in the literature concerning sexual dimorphism in South American cricetine rodents. Barquez et al. (1980) found no significant difference between sexes in an assemblage of akodontine species from northwestern Argentina. Avila-Pires (1958) published morphometric measurements for a number of South American species, enabling us to compute the percentage differences between sexes for some characters of *B. lasiurus arviculoides*, although he had few specimens available. As a result, although sexual dimorphism patterns are suggested, they are not statistically demonstrated. The percentage differences for external measurements, based on Avila-Pires' (1958) data, ranged from approximately 2 for tail length to 8 for hindfoot length. These values were substantially larger than those for cranial characters. The percentage differences in cranial characters ranged from −4.5 for rostrum length (suggesting that the rostrum

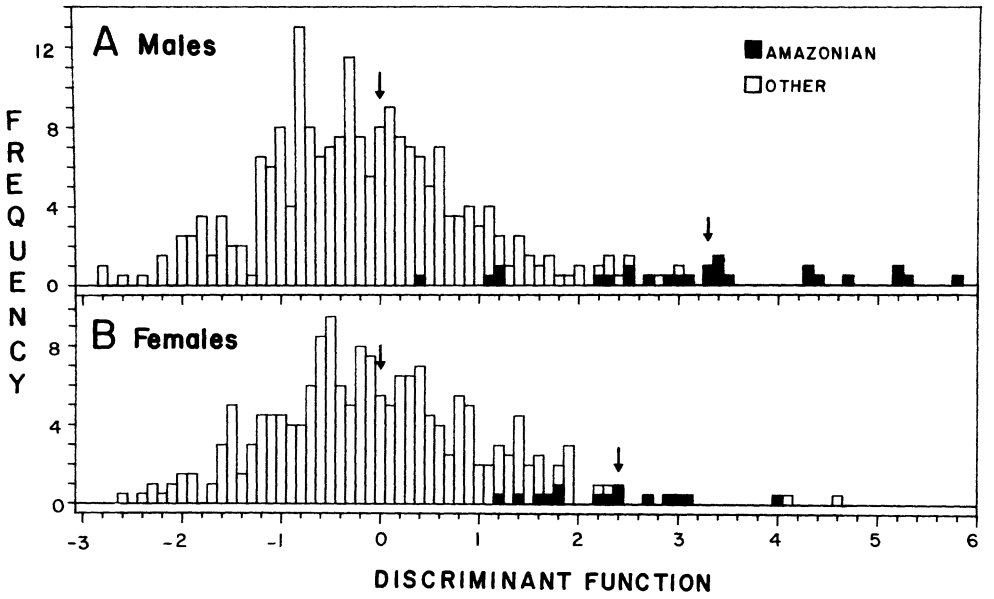

FIG. 5.—Projections of *B. lasiurus* (A) males and (B) females onto the discriminant function axis generated by stepwise discriminant function analysis. Mean projection values for each group are indicated by arrows.

is elongate in females relative to males) to 4.1 for palatal foramina. Males in Avila-Pires' (1958) study were larger in 85% of the 13 characters reported. It is likely that his report of females being larger in 15% of the characters is simply due to small sample sizes; our study indicates that females are never on the average larger than males in skull measures.

Percentage differences computed from morphometric measurements reported for a related species, *Akodon azarae* (Massoia, 1971), revealed similar patterns of sexual dimorphism. Percentage differences were minor in almost all characters, ranging from −2.9 for hindfoot length to 9.6 for interparietal length; the latter value was exceptionally high and is undoubtedly due to the limited sample size and/or measurement error. Males were larger than females in 88% of the 17 characters measured.

Geographic variation.—Virtually every known animal species having an extensive distribution has been shown to vary geographically; such variation is often correlated with environmental heterogeneity (Mayr, 1970). Subspecific taxonomic designations should reflect geographic patterns of genetic variation.

Four subspecies have been included in *B. lasiurus* (Honacki et al., 1982; Reig, 1978): *B. l. brachyurus* Wagner, type locality, Itararé, São Paulo, Brazil; *B. l. fuscinus* Thomas, type locality, Ilha de Marajó, mouth of the Amazon, Brazil; *B. l. pixuna* Moojen, type locality, Crato, Ceará, Brazil; and *B. l. arviculoides* Wagner, type locality, Brazil, no specific locality indicated. The present system of subspecific nomenclature reflects the species' occurrence in different habitats: *B. l. fuscinus* from the lowland rain forests of northern Brazil; *B. l. pixuna* from the *caatinga* of northeastern Brazil; *B. l. brachyurus* from what was originally an area of upland deciduous forest, but which is now mostly farmland; and *B. l. arviculoides*, from a general area extending from the northeastern *caatinga* to the *cerrado* of Mato Grosso (Brazil) and the northern *chaco*. These subspecific designations were made without the support of statistically based studies of morphological, karyological, or other types of data. Our study has elucidated geographic and sexual patterns of variation for *B. lasiurus*, and indicated that there are marked morphological differences between animals of two groups. One group is from a single habitat, while the second group, containing individuals with morphometrically uniform skulls, occurs in several distinct habitats.

TABLE 4.—*Statistics for stepwise discriminant analysis of male and female* Bolomys lasiurus.

Character	*F*-value to enter	Order of entry	Coefficients[a] Unstandardized	Coefficients[a] Standardized	Classification functions[b] Amazonian	Classification functions[b] Other
Males						
1. Cranial depth	27.16	2	−1.3812	−0.4883	61.711	66.512
2. Skull length	4.56	10	0.4081	0.1443	23.799	22.381
4. Nasal length	28.10	5	−1.0430	−0.3687	−6.930	−3.305
11. Basioccipital length	31.70	6	1.6737	0.5918	−5.941	−11.758
13. Palatal width at M^3	53.39	1	2.1066	0.7448	5.545	−1.776
15. Diastema length	9.17	7	−0.9086	−0.3212	−32.773	−29.615
16. Incisive foramina length	20.87	4	1.3250	0.4685	6.496	1.891
17. Bullar width	5.83	9	−1.2206	−0.4315	117.894	122.137
19. Mandibular length	6.91	11	−0.4641	−0.1641	−6.914	−5.301
23. Mandibular foramen to articular condyle	9.08	8	1.0054	0.3555	−11.627	−15.121
24. Mandibular toothrow length	31.82	3	1.7471	0.6177	87.446	81.374
Constant			−0.1357		−933.344	−927.591
Females						
7. Rostral breadth	5.90	7	−1.1285	−0.3617	12.791	15.479
11. Basioccipital length	9.23	4	1.4720	0.4718	26.069	22.562
13. Palatal width at M^3	9.27	2	1.8685	0.5988	19.429	14.978
15. Diastema length	8.03	3	−1.5487	−0.4963	9.913	13.602
16. Incisive foramina length	7.65	5	1.0299	0.3301	9.769	7.315
23. Mandibular foramen to articular condyle	29.91	1	1.6897	0.5415	−1.181	−5.206
24. Mandibular toothrow length	4.50	6	1.7108	0.5483	119.649	115.573
Constant			−14.9879		−489.205	−450.910

[a] For canonical variable, which in the two-group case is equivalent to the discriminant function.
[b] Used with original measurements. Add products of measurements and function values to constant; classify as Amazonian or Other depending on which results in the highest value for its classification function.

The Amazonian group (sample 1) examined in this study is clearly distinct morphometrically from the remaining samples. The phenograms for both sexes (Fig. 3) reveal that the Amazonian group is notably different morphologically from the other samples. The three-dimensional plots (Fig. 4) suggest that males of central Bolivia (sample 5) are larger than average in several cranial features. They often are among the largest samples for several characters, as are the females from this central Bolivian area (Table 2). In breadth of braincase, both sexes are significantly larger than individuals from other localities, and are placed in a separate subset. Both males and females from this central area of Bolivia exhibit intermediate morphometric characters in relation to those shown by the Amazonian specimens and the remaining samples, but are in general closer to the latter. Because these specimens were collected in the central Bolivian *chaco*, they fall within the geographic range of *B. lenguarum* (Reig, 1978). However, although morphometrically distinct in several cranial characters, the quantitative differences are very small, and they are clearly *B. lasiurus*.

The third principal component, represented by the vertical axis, summarizes the differences between sample 2 and the other groups. It reflects a relatively small proportion (i.e., 17.2% for males and 15% for females) of the total variance among means. Thus, animals from the *caatinga* (sample 2) differ from other groups only in having somewhat wider and shallower crania.

The three-dimensional plots of the principal components (Fig. 4) also suggest that the Amazonian specimens can be separated from all others by their overall larger size in most cranial characters. The variation in means of the cranial characters (Table 2) reveals that they are significantly larger in five characters for males, and in seven for females. The Amazonian animals of both sexes are significantly larger in basioccipital lengths, incisive foramina lengths, mandibular foramen to articular condyle distances, and mandibular toothrow lengths. In comparison with

other localities, Amazonian males have a larger palatal width at M^3, whereas Amazonian females have wider zygomata, larger palatal widths at M^1, and greater distances from mental foramen to articular condyle.

The discriminant function analysis for both sexes (Fig. 5) uses discriminant scores, calculated from a linear function of characters within each group, to emphasize differences between the two groups. In spite of the fact that discriminant scores overlap for Amazonian versus other samples, the discriminant characters used for both males and females provide considerable distinction between the groups. Future research may show that the Amazonian population is specifically distinct. Our data do not warrant such recognition at this time; however, in view of the data presented, we conclude that there are at least two morphometrically distinct groups of rodents included in *B. lasiurus*. Our results suggest that there may be no more than two, however. These include an Amazonian group, and a second one that comprises the remaining localities from the rest of the species' range. The subspecific name, *Bolomys lasiurus fuscinus*, originally used by Thomas (1897), should be applied to northern populations in the proximity of the Ilha de Marajó and near the mouth of the Amazon River. The subspecific name *Bolomys lasiurus lasiurus* Lund, 1841 should be employed for the remaining populations. These two subspecific designations thus reflect cranial morphometric differences between a group of larger *B. lasiurus* restricted to the lowland rain forests south of the Amazon River, and remaining animals of smaller proportions from throughout the species' range. Our results indicate that the non-Amazonian samples are uniform regarding cranial morphology. Further research, however, using pelage, post-cranial morphology, karyology, etc., could bring to light differences unrelated to cranial morphology.

The cranial differentiation between these two forms may be the result of one or more factors. With respect to environmental selective agents of possible importance, locality 1 is the sole sample from the humid region of the lowland rain forest. All remaining populations are from drier habitats, ranging from the semiarid *caatinga* of northeastern Brazil to the centrally located savannas of the *chaco*. The possibility of cranial morphology being the result of selection for some adaptive trait cannot be discarded. However, as several authors have pointed out (Mayr, 1963; Rohlf and Schnell, 1971), isolation by distance, especially in the case of peripherally located populations, will often produce geographic variation as a result of reduced gene flow. Chance patterns brought about by stochastic factors might persist if the population, as is the case of the Amazonian group, is on the edge of the species' range. Further research is required to distinguish between these two possibilities.

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APPENDIX I

Specimens Examined

Sample locality numbers (coded as in Fig. 1) of specimens actually used in the statistical analyses are indicated in brackets. BOLIVIA. Beni (total 283): Baures River Mouth, 26 (AMNH) [3]; Camino Vilches, 3 (FMNH); opposite Cascajal, 1 (AMNH); opposite Costa Marques, 44 (AMNH) [3]; 1 km above Costa Marques, 3 (AMNH) [3]; 2 km above Costa Marques, Brazil, 4 (AMNH) [3]; below Costa Marques on Itenez River, 2 (AMNH) [3]; 1.5 km below Costa Marques, 2 (AMNH) [3]; 1.5 km NW Guayaramarin on Mamoré River, 16 (AMNH); 15 km above Horquilla on Machupo River, 14 (AMNH) [3]; Itenez Province, Fortaleza, approx. 75 km S Santa Ana, 1 (USNM); Itenez Province, Magdalena, 1 (USNM); confluence of Itenez and Curicha rivers, 6 (AMNH); 12 km NNW Limoquije on Mamoré River, 8 (AMNH); 15 km S Limoquije on Mamoré River, 1 (AMNH); Mamoré River at 13°35′ lat. S, 3 (AMNH); Pampa de Meio on Itenez River, 12 (AMNH) [3]; opposite Príncipe da Beira, 6 (AMNH) [3]; Puerto Caballo on Mamoré River, 89 (AMNH) [4]; Puerto More on Itenez River, 3 (AMNH) Remanso on Itenez River, 1 (AMNH); 23 km W San Javier on Mamoré River, 4 (AMNH); San Joaquin, 15 (FMNH); San Marco, 2 (FMNH); 10 km W San Pedro, 7 (AMNH); 4 km S Santa Ana at 11°41′ lat. S on Mamoré River, 1 (AMNH); Yacuma River, 2 km from mouth, 1 (AMNH); Yacuma Province, Ecuador, 1 (USNM); Yacuma Province, Fortaleza, 4 (USNM); Yacuma Province, Palácio Ranch approx. 90 km S Santa Ana, 2 (USNM). Santa Cruz (total 47): Ayacucho, 4 (USNM) [5]; Ibañez, 12 (USNM) [5]; Palmar, 4 (USNM) [5]; Santa Cruz, 4 (USNM) [5]; Sara Province, 7 km N Santa Rosa Ducia, 1 (AMNH); Vermejo, 3500 ft, 7 (AMNH) [5]; Warnes, 15 (USNM) [5]. BRAZIL. Ceará (total 2): Crato, 1 (USNM); Crato, Floresta Nacional Acaripe, 1 (CM). D.F. (total 72): 20 km S Brasília, 65 (OU) [6]; 25 km S Brasília, 7 (OU) [6]. Goiás (total 8): Anápolis, 1000 m, 8 (AMNH) [6]. Mato Grosso (total 18): Corumbá city airport, 1 (USNM); Corumbá, Santa Theresa, 1 (USNM); Cuiabá, 2 (USNM); Descalvados, 4 (FMNH); Fazenda

Acurizal, 1 (USNM); Maracajú, 500 m, 1 (AMNH); Tapirapoan on Siputuba River, 3 (AMNH); Urucum, 1 (FMNH); Urucum, 400 ft, 1 (AMNH); Urucum de Corumbá, 2 (FMNH); Utiarity on Papagaio River, 1 (AMNH). Minas Gerais (total 7): Três Marias, Ilha das Marias, 5 (OU); 6 km S Viçosa, Mata da Prefeitura, 2 (USNM). Pará (total 48): Belém, 5 (USNM) [1]; Belém Virus Lab, 8 (AMNH) [1]; Belém, Utinga, 8 (USNM) [1]; Belém, Utinga, Área Experimental, 1 (USNM) [1]; Belém, Utinga, Bacia Água Preta, 4 (USNM) [1]; Bragança, 1 (USNM) [1]; Bragança, Jandiaí, Caratatena, 20 (USNM) [1]; Santarém, Mojuí dos Campos, 1 (USNM). Pernambuco (total 219): Municipality of Exú, Exú, 189 (CM) [2]; 1 km S Exú, 5 (CM) [2]; 1.5 km SW Exú, 6 (CM) [2]; Escola Agrícola de Exú, 3 (CM) [2]; Exú, Fazenda Pinheira, 7 (CM) [2]; São Lourenço da Mata, Estação Ecológica do Tapacurá, 1 (CM); Serra Talhada, Fazenda Saco, 1 (CM); Municipality of Serra Talhada, Triunfo, 7 (CM). Piauí (total 3): Arara, 3 (FMNH). São Paulo (total 251): Casa Grande, 2 (USNM); Itapetininga, 248 (USNM) [7]; Varjão, 1 (USNM). PARAGUAY. Boqueron (total 5): 419 km, by road, NW Villa Hayes, 2 (UMMZ); Rio Verde, NW Villa Hayes by road, 3 (MVZ); Caaguazú (total 2): Caaguazú, 2 (AMNH). Chaco (total 6): 50 km WNW Fortín Madrejón, 1 (AMNH); 50 km WNW Fortín Madrejón, Cerro León, 1 (UMMZ); 50 km WNW Madrejón, Misión Nuevo Tribo, 4 (UMMZ). Cordillera (total 2): 1.6 km, by road, S Tobatí, 1 (UMMZ); 1 mi S Tobatí, 1 (MVZ). Itapua (total 1): 20 km NNE Encarnación, by road, El Tirol, 1 (UMMZ). Misiones (total 13): 2.7 km N San Antonio, by road, 11 (UMMZ); San Ignácio, 2 (USNM). Paraguarí (total 13): Parque Nacional Ibycuí, 13 (UMMZ). Presidente Hayes (total 7): 24 km NW Villa Hayes, 2 (UMMZ); Chaco Experimental Station, 295 km NW Villa Hayes, by road, 2 (MVZ); 213 km NW Villa Hayes, by road, 2 (MVZ); 295 km NW Villa Hayes on Trans Chaco Hwy, 1 (MVZ).