Journal of Mammalogy, 82(3):760–774, 2001

TAXONOMIC STATUS OF *MOLOSSUS BONDAE* J. A. ALLEN, 1904 (CHIROPTERA: MOLOSSIDAE), WITH DESCRIPTION OF A NEW SUBSPECIES

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We document the known distribution of *Molossus bondae* as far south as northern Argentina. Argentine specimens include the type series of *M. obscurus currentium* Thomas, 1901, a name with priority over *M. bondae.* Analysis of morphometric variation across the species' geographic range revealed the presence of 3 distinct populations of *M. bondae.* We reassessed taxonomic and nomenclatural status of populations previously included under the name *M. bondae* and concluded that the valid name for this taxon is *Molossus currentium* Thomas. Based on 12 cranial and 2 external characters we recognize 3 subspecies for this species, 1 of which we formally describe as new.

Key words: Chiroptera, geographic variation, Molossidae, *Molossus bondae, Molossus currentium,* sexual dimorphism, South America

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Bats of the genus *Molossus* inhabit Neotropical America from northern Mexico to southern Argentina. In a review of the genus, Miller (1913) recognized 19 species based on specimens deposited at the United States National Museum. Subsequent work (Allen 1916; Goodwin 1956, 1959) added yet more species. However, several names were synonymized as the extent of intra- and interspecific variation became better understood (Cabrera 1958; Husson 1962). In more recent accounts, numbers of recognized species vary from 5 to 8 (Dolan 1989; Freeman 1981; Koopman 1993). Disagreements have arisen because species of *Molossus* are morphologically similar, differing mostly in size. The addition of genetic characters to distinguish among species has clarified taxonomy of this group by providing a higher degree of resolution for Central American and northern South American populations (Dolan 1989), but little is known about southern populations. To date, only 2 species (*M. ater* and *M. molossus*) are recognized as occurring south of Colombia, Ecuador, and Venezuela.

As part of a survey of small mammals in Paraguay (Willig et al. 2000), a sample of 27 individuals of a 3rd species of *Molossus* was collected near Bahía Negra, Alto Paraguay. After comparison with museum specimens, we assigned these individuals to *M. bondae.* The nearest published record for *M. bondae* was >2,500 km N of Bahía Negra (3 km NE Vinces, Ecuador). Further research revealed additional specimens from Paraguay, Argentina, and Brazil, including 12 collected in Goya, Corrientes Province, Argentina, 11 of which constituted the series used to describe *M. obscurus currentium* Thomas, 1901. The name *M. obscurus currentium* predates *M. bondae* Allen by 3 years, thus a reevaluation of the

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epithet *bondae* was in order. Our objectives were to redefine the known geographic range of *M. bondae,* to describe and compare qualitative and quantitative morphologic variation across its geographic range, and to reevaluate the nomenclatural status of populations of *M. bondae.*

MATERIALS AND METHODS

Specimens examined.—We examined 168 specimens of *M. bondae* from Central and South America (Appendix I). Specimens are deposited at the American Museum of Natural History, New York (AMNH); British Museum (Natural History), London, United Kingdom (BMNH); Field Museum of Natural History, Chicago, Illinois (FMNH); Museo Nacional de Historia Natural del Paraguay, San Lorenzo (MNHNP); Muséum d'Histoire Naturelle, Geneva, Switzerland (MHNG); Museum of Texas Tech University, Lubbock (TTU); Texas Cooperative Wildlife Collection, Texas A&M University, College Station (TCWC); and National Museum of Natural History, Washington, D.C. (USNM). Some specimens remain uncatalogued, but have a field number (TK) associated with any extant material. Standard museum preparations of skins and skulls, specimens in alcohol with skull removed, and complete skeletons were examined. We recorded age and fur coloration from museum skins. We also took 2 external and 12 cranial measurements on dry skins and skulls, respectively, to the nearest 0.01 mm using a digital caliper. Measurements and their acronyms were: greatest length of the skull, including incisors (GLS); condylocanine length (CCL); condylobasal length, including incisors (CBL); mastoid breadth (MAB); zygomatic breadth (ZYG); breadth across upper canines (BAC); breadth across upper molars (BAM); length of rostrum (perpendicular distance between the posterior tangent at the level of the last molars and the anterior tangent across the upper incisors; LNR); length of maxillary toothrow (MAX); length of upper molariform toothrow (UML); length of mandibular toothrow (MTR); length of lower molariform toothrow (LML); total length (TL); length of tail (TAIL); length of hind foot (HF); length of ear (EAR); weight (WT); forearm length (FAR); and length of 3rd metacarpal (MCIII).

Quantitative analysis.—All morphometric analyses were based on 154 adult specimens (phalangeal epiphyses and basisphenoid suture completely ossified). External measurements from tags were not used in quantitative analyses because of potential interpreparator differences. For all subsequent analyses, observations were log-transformed, and missing data were estimated using the estimation-maximization algorithm of Little and Rubin (1987). Exploratory principal component analysis was performed using all variables to assess morphometric variation across the species' geographic range. Because molossids are sexually dimorphic, males and females were analyzed separately.

For each principal component analysis, we calculated structure coefficients or vector correlations (Pearson's correlation between a variable and each principal component [PC]). Vector correlations are a measure of how closely a variable and a principal component are related and therefore reflect relative importance of a variable on the corresponding axis (Bryant 1984; Kleka 1980). The principal component analysis allowed us to propose a hypothesis of differentiation across the range of the species. To test this hypothesis, we used a 2-way multivariate analysis of variance, based on the same set of characters, to evaluate significance of morphometric divergence between populations while controlling for effects of secondary sexual variation. Wilks' lambda was used as the test statistic in multivariate analysis of variance. We also conducted 2-way analysis of variance region-by-sex on all characters, to evaluate the importance of each in distinguishing among geographic regions while accounting for secondary sexual dimorphism. To avoid overestimating significance of particular characters in multiple univariate comparisons, we applied a sequential Bonferroni test to the set of comparisons before ascribing statistical significance (Rice 1989). Tukey's multiple comparisons tests were performed for each character to determine differences among geographic regions. The level of significance for all statistical tests was set at $\alpha = 0.05$. Statistical analyses were performed using the SAS statistical software (SAS Institute Inc. 1995) and Matlab for Windows, version 4.2c (The MathWorks 1994).

RESULTS

Quantitative morphologic variation.—Patterns of morphometric variation across

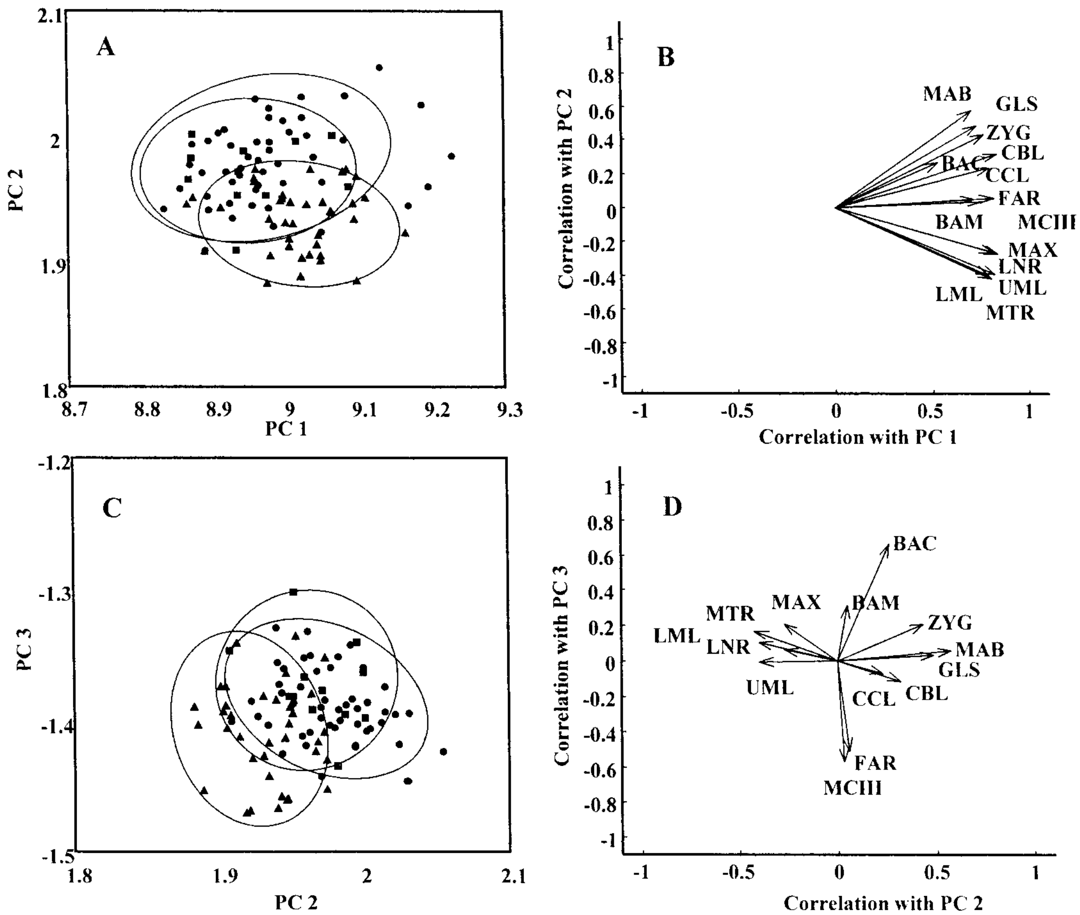

FIG. 1.—A and C) Position of female *Molossus currentium* in principal components space as defined by 12 cranial and 2 external characters; circles = Central America, squares = northern South America, triangles = southern South America; the 95% confidence ellipses for each region are superimposed on scores of principal components. B and D) Vector correlations of characters with principal component axes; lengths of arrows are proportional to importance of characters in defining principal components; abbreviations of characters as in text.

Neotropical America, as summarized by principal component analysis, were alike for males and females (Figs. 1 and 2) and differed in magnitude of differentiation. For females, principal component 1 (PC1) accounted for 59% of the total variation in the sample (Table 1). Distribution of individuals along PC1 indicated that the size range was similar across populations examined, except for 3 specimens from Brus Laguna, Honduras. Those were unusually large individuals but still were ascribable to *M. bondae* (Dolan and Carter 1979; Fig. 1). PC2 and PC3 each account for <13% of the total variation in the sample (Table 1). Specimens from southern South America tended to have low scores on PC2 and PC3. Forearm length and length of the 3rd metacarpal had high, negative correlations with PC3, whereas breadth across upper canines was correlated positively with this axis. Mastoid breadth had a relatively high, positive correlation with PC2. Therefore, individuals from southern South America tended to have large bodies, proportionally small skulls, and narrow braincases.

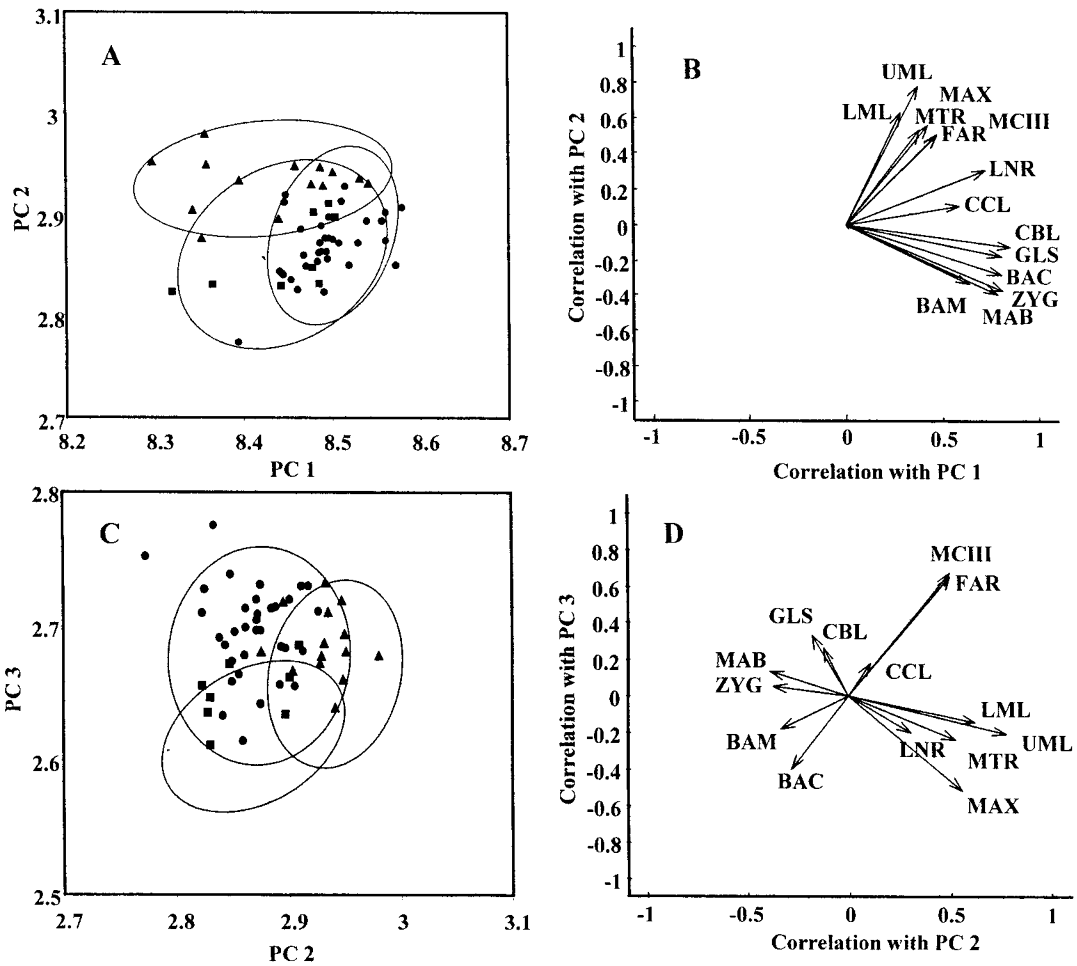

FIG. 2.—A and C) Position of male *Molossus currentium* in principal components space as defined by 12 cranial and 2 external characters; circles = Central America, squares = northern South America, triangles = southern South America; the 95% confidence ellipses for each region are superimposed on scores of principal components. B and D) Vector correlations of characters with principal component axes; lengths of arrows are proportional to importance of characters in defining principal components; abbreviations of characters as in text.

For males, PC1 accounted for 42% of the total variation in the sample (Table 1). On average, individuals from Central America had higher scores on PC1 (Fig. 2). In contrast, clinal variation occurred along PC2; southern South American specimens had high scores on PC2, whereas Costa Rican individuals had the lowest scores on that axis. That trend was more evident in the plot of PC2 versus PC3 (Fig. 2). PC2 and PC3 accounted for 19% and 12.8% of the total variation in the sample, respectively. Specimens from Central America and northern South America had low scores on PC2, whereas specimens from Paraguay and Argentina had high scores. Along PC3, northern South American specimens had low scores, whereas southern South American and Central American individuals scored high on PC3. Forearm length and length of 3rd metacarpal had high, positive vector correlations with PC3. PC2 was cor-

TABLE 1.—Results of principal component analysis of 12 cranial and 2 external characters of *Molossus currentium,* by sex; 1st row for each sex is the percentage of variance explained by each component; acronyms as defined in text. PC, principal component.

Sex	Character[a]	PC1	PC2	PC3
Females	% Explained	59.04	11.44	9.91
	GLS	0.72	0.49	0.03
	CCL	0.79	0.24	−0.08
	CBL	0.83	0.32	−0.12
	MAB	0.69	0.58	0.04
	ZYG	0.76	0.44	0.19
	BAC	0.52	0.28	0.65
	BAM	0.71	0.06	0.31
	LNR	0.82	−0.27	0.07
	MAX	0.83	−0.26	0.21
	UML	0.82	−0.39	0.00
	MTR	0.81	−0.41	0.18
	LML	0.78	−0.39	0.11
	FAR	0.81	0.040	−0.51
	MCIII	0.75	0.014	−0.57
Males	% Explained	41.86	18.83	12.78
	GLS	0.80	−0.18	0.33
	CCL	0.58	0.11	0.18
	CBL	0.84	−0.12	0.26
	MAB	0.78	−0.38	0.14
	ZYG	0.81	−0.37	0.04
	BAC	0.80	−0.28	−0.40
	BAM	0.63	−0.33	−0.18
	LNR	0.71	0.31	−0.20
	MAX	0.42	0.56	−0.52
	UML	0.37	0.78	−0.21
	MTR	0.38	0.53	−0.24
	LML	0.28	0.62	−0.14
	FAR	0.47	0.50	0.65
	MCIII	0.47	0.50	0.67

[a] GLS, greatest length of skull; CCL, condylocanine length; CBL, condylobasal length; MAB, mastoid breadth; ZYG, zygomatic breadth; BAC, breadth across upper canines; BAM, breadth across upper molars; LNR, length of rostrum; MAX, length of maxillary toothrow; UML, length of upper molariform toothrow; MTR, length of mandibular toothrow; LML, length of lower molariform toothrow; FAR, forearm length; MCIII, length of 3rd metacarpal.

related positively with variables that described length of the toothrows but was correlated negatively with variables that described skull width. In general, specimens available could be divided into 3 major groups corresponding to 3 geographic regions: bats with large bodies, long toothrows, and narrow braincase (Paraguay, Argentina); individuals with large bodies, short toothrows, and wide braincase (Costa Rica, Honduras, Nicaragua); and individuals with small bodies, wide braincase, and short toothrows (Colombia, Ecuador, Panama, Venezuela). Those 3 regions were identified as southern South America, Central America, and northern South America, respectively. We tested the null hypothesis that no difference existed among regions. Significance of the region-by-sex interaction term in the multivariate analysis of variance (Table 2) reflected differences in the expression of geographic variation between males and females. Multivariate differences between sexes also were highly significant. In particular, the magnitude, but not direction, of sexual dimorphism was dependent on region. Males were always larger than females, with the Central American population exhibiting the highest sexual dimorphism and the southern South American population the lowest. From a univariate perspective, all characters showed significant differences between sexes (Table 2), although the interaction term was significant only for zygomatic breadth.

Significant differences between regions were found for 10 of 14 characters (Table 2). Central American specimens had significantly longer and wider skulls than those from the remaining regions. Southern South American bats were significantly larger in measurements related to the length of the toothrows (length of upper molariform toothrow, length of mandibular toothrow, and length of lower molariform toothrow). Specimens from northern South America were smaller in forearm length and length of 3rd metacarpal, indicating a comparatively smaller body size. Consistent with univariate results, the multivariate analysis of variance was highly significant for the effect of region (Table 2).

Qualitative morphologic variation.—Pelage coloration was examined in all available skins. Pelage was darker on the dorsum and paler on the venter in all specimens. Individual hairs were darker on the

TABLE 2.—Significance of a univariate analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA) comparisons, region-by-sex, for 3 populations of *Molossus currentium*: 1, Central America; 2, northern South America; 3, southern South America. Regions above a common line in the multiple range test were not significantly different from each other. Those above different lines were significantly different from each other.

Variable[a]	Region[b]	Sex[b]	Region by sex[b]	Multiple range test (region)[c]
MANOVA	<0.001*	<0.001*	0.012*	
ANOVA				
GLS	<0.001*	<0.001*	0.069	1 2 3
CCL	0.003	<0.001*	0.182	1 3 2
CBL	0.001*	<0.001*	0.013	1 2 3
MAB	<0.001*	<0.001*	0.038	1 2 3
ZYG	<0.001*	<0.001*	0.003*	1 2 3
BAC	<0.001*	<0.001*	0.018	1 2 3
BAM	0.010	<0.001*	0.015	1 2 3
LNR	0.294	<0.001*	0.039	3 1 2
MAX	0.101	<0.001*	0.192	3 2 1
UML	<0.001*	<0.001*	0.323	3 1 2
MTR	<0.001*	<0.001*	0.664	3 1 2
LML	<0.001*	<0.001*	0.335	3 1 2
FAR	<0.001*	0.001*	0.422	3 1 2
MCIII	<0.001*	<0.001*	0.431	3 1 2

[a] GLS, greatest length of skull; CCL, condylocanine length; CBL, condylobasal length; MAB, mastoid breadth; ZYG, zygomatic breadth; BAC, breadth across upper canines; BAM, breadth across upper molars; LNR, length of rostrum; MAX, length of maxillary toothrow; UML, length of upper molariform toothrow; MTR, length of mandibular toothrow; LML, length of lower molariform toothrow; FAR, forearm length; MCIII, length of 3rd metacarpal.

[b] Asterisks denote significant values after sequential Bonferroni adjustment ($\alpha = 0.05$, multivariate test statistic, Wilks' lambda).

[c] Means arranged from large to small.

tips and became paler toward the base. Dorsal coloration varied from a lustrous black to orange-red or blond. Many individuals had an intermediate coloration, being dull brown on the dorsum with a pale brown venter. Individual hairs varied from black tips and brown bases, to reddish or yellow tips with yellowish or white bases. Variation in color did not follow any discernible geographic pattern, and all shades may have occurred within a single population (Dolan 1989).

DISCUSSION

Nomenclatural implications.—Recognition of a 3rd, morphologically distinct population of *M. bondae* for southern South America and the fact that this population includes a specimen that is the name-bearing type of a formerly described taxon, calls for a reassessment of the nomenclatural status of these populations.

The name *Molossus bondae* was based on a series of specimens from Bonda, 7 mi E Santa Marta, Magdalena Province, Colombia. Allen (1904) designated a type (AMNH 23661) and referred to 3 ''topotypes,'' 2 of which remain at the AMNH (Dolan 1989). One of us (C. López-González) examined and measured the holotype (Table 3), which is within the range of variation for *M. bondae* as defined by Dolan (1989).

Thomas (1901) described *M. obscurus currentium* as subspecies of *M. obscurus* Geoffroy, 1805, from a series collected in Goya, Corrientes, Argentina. The description of Thomas (1901) gives enough information to recognize the type specimen of *M. obscurus currentium* as conspecific with *M. bondae.* J. Arroyo-Cabrales kindly examined and measured the type series of *M. obscurus currentium* deposited at the BMNH. Those measurements (Table 3) also place the Argentine specimens within the range of variation for *M. bondae.*

Sanborn (1932) synonymized *M. currentium* and *M. obscurus*, but analysis of more recent data indicates that the epithet *obscurus* originally was applied to a specimen of *M. molossus* as currently understood (Carter and Dolan 1978). Further revisions of the family Molossidae (Freeman 1981) and the genus *Molossus* (Dolan 1989) place the name *obscurus* as a synonym of *M. molossus.* Dolan (1989) regarded *M. obscurus currentium* as a junior synonym of *M. molossus.* The name *currentium* is available

TABLE 3.—Basic statistics for 14 selected morphometric measurements of *Molossus currentium*, by region and sex. Measurements of the holotypes of *Molossus obscurus currentium* Thomas, *Molossus bondae* Allen, a specimen from Brazil, and a *Molossus* sp. from Mexico also are included.[a]

	GLS	CCL	CBL	MAB	ZYG	BAC	BAM	LNR	MAX	UML	MTR	LML	FAR	MCIII
Central America (Honduras, Nicaragua, Costa Rica)														
Females (n = 37)														
$\bar{X}$	19.1	16.3	16.8	11.4	11.7	4.8	8.4	6.7	6.5	5.3	7.2	6.2	40.6	42.3
SD	0.49	0.45	0.43	0.42	0.32	0.14	0.26	0.19	0.22	0.15	0.19	0.17	1.34	1.34
Minimum	18.1	15.4	16.1	10.7	11.3	4.6	7.8	6.4	6.0	5.0	7.0	6.0	38.1	39.9
Maximum	20.1	17.4	17.8	12.2	12.4	5.2	9.0	7.3	7.0	5.6	7.8	6.7	44.2	45.8
Males (n = 27)														
$\bar{X}$	20.4	17.2	17.8	12.1	12.4	5.2	8.7	7.0	6.7	5.3	7.6	6.4	41.7	43.5
SD	0.32	0.23	0.24	0.2	0.19	0.15	0.16	0.16	0.22	0.12	0.16	0.12	0.65	0.68
Minimum	19.9	16.9	17.4	11.8	12.1	4.9	8.5	6.6	6.1	5.0	7.2	6.2	40.5	42.2
Maximum	21.2	17.6	18.2	12.5	12.8	5.5	9.0	7.3	7.1	5.5	7.9	6.7	42.6	44.9
Northern South America (Colombia, Ecuador, Panama, Venezuela)														
Females (n = 24)														
$\bar{X}$	18.6	16.0	16.6	11.2	11.6	4.8	8.3	6.6	6.5	5.2	7.2	6.1	39.4	41.0
SD	0.32	0.3	0.3	0.27	0.24	0.13	0.2	0.16	0.16	0.15	0.17	0.18	0.94	0.9
Minimum	18.1	15.4	16.0	10.8	11.3	4.6	8.0	6.4	6.2	4.9	7.0	5.8	37.4	39.2
Maximum	19.4	16.8	17.5	11.7	12.2	5.1	8.7	7.0	6.7	5.5	7.6	6.5	41.1	43.0
Males (n = 15)														
$\bar{X}$	19.8	17.0	17.6	11.9	12.3	5.2	8.6	7.0	6.8	5.3	7.6	6.4	40.7	42.2
SD	0.38	0.3	0.31	0.24	0.16	0.16	0.2	0.15	0.13	0.09	0.17	0.18	1.2	1.15
Minimum	19.0	16.3	17.0	11.4	12.0	4.8	8.4	6.6	6.5	5.1	7.1	6.1	38.3	40.4
Maximum	20.4	17.3	18.1	12.2	12.6	5.4	9.0	7.3	7.0	5.4	7.8	6.8	42.2	44.1
Southern South America (Paraguay, Argentina)														
Females (n = 37)														
$\bar{X}$	18.6	16.3	16.8	11.2	11.7	4.8	8.4	6.8	6.6	5.4	7.4	6.3	41.0	42.7
SD	0.34	0.46	0.37	0.29	0.27	0.13	0.23	0.17	0.18	0.15	0.2	0.18	1.03	1.16
Minimum	18.0	15.5	15.9	10.6	11.2	4.5	7.8	6.4	6.3	5.0	7.0	6.0	39.0	40.0
Maximum	19.29	17.5	17.6	11.9	12.2	5.1	8.9	7.2	7.0	5.8	7.8	6.7	42.9	45.0
Males (n = 14)														
$\bar{X}$	19.6	17.0	17.4	11.6	12.0	5.0	8.4	7.0	6.8	5.4	7.7	6.5	41.7	43.5
SD	0.46	0.49	0.44	0.52	0.35	0.17	0.23	0.27	0.14	0.13	0.17	0.18	1.09	1.00
Minimum	18.7	16.3	16.7	10.5	11.4	4.7	8.0	6.4	6.5	5.2	7.4	6.3	40.1	41.6
Maximum	20.3	17.8	18.0	12.3	12.5	5.2	8.8	7.3	7.0	5.6	8.0	6.9	43.6	44.7

TABLE 3.—Continued.

	GLS	CCL	CBL	MAB	ZYG	BAC	BAM	LNR	MAX	UML	MTR	LML	FAR	MCIII
Argentina, Corrientes, Goya (holotype of *M. obscurus currentium* Thomas, female, adult)														
	19.8	17.4	17.3	10.5		4.9	8.3	6.3	6.7		7.6		41.8	42.4
Brazil, Amazonia, Manaos (female, juvenile)														
	17.7	15.3	15.7	10.2		4.9	8.0	6.8	6.6	5.2	7.3	6.4		
Colombia, Santa Marta, Bonda (holotype of *M. bondae*, female)														
	18.4	16.0	16.5	11.1		4.7	8.2	6.7	6.6	5.2			40.1	41.3
Mexico, Quintana Roo, 6 km NE San Miguel, Cozumel (female, adult)														
	17.6	15.5	15.6				7.8		6.3	5.1	6.9	6.0	41.5	43.5

[a] GLS, greatest length of skull; CCL, condylocanine length; CBL, condylobasal length; MAB, mastoid breadth; ZYG, zygomatic breadth; BAC, breadth across upper canines; BAM, breadth across upper molars; LNR, length of rostrum; MAX, length of maxillary toothrow; UML, length of upper molariform toothrow; MTR, length of mandibular toothrow; LML, length of lower molariform toothrow; FAR, forearm length; MCIII, length of 3rd metacarpal.

and has priority over *bondae*; thus, the valid name for the species formerly known as *M. bondae* is *Molossus currentium* Thomas, 1901: *M. bondae* Allen 1904 is a junior synonym. Although differences exist in some cranial proportions and external size, southern South American, northern South American, and Central American populations are sufficiently similar that we consider them to be conspecific based on morphometric data. To our knowledge, no karyotypic or molecular information is available regarding the degree of interpopulational variation of *M. bondae* across its geographic range. Dolan (1989) compared allozymes of 2 populations in Central America and found intraspecific variation in allelic frequency for 1 locus in 1 allele out of 15 examined, but no other data are available on phenotypic variation other than morphologic data.

Geographic distribution.—The northern distribution of *M. currentium* extends as far as Quintana Roo, Mexico, based on 1 record, a female collected near Cozumel (Alvarez and Ramírez-Pulido 1972). The specimen was tentatively ascribed to *M. currentium* based on measurements reported (Alvarez and Ramírez-Pulido 1972; Goodwin 1942). However, upon detailed examination, LaVal (1977) concluded that Goodwin's (1942) specimens were not ascribable to *M. currentium,* and Dolan (1989) considered it a dubious record. We examined and measured the specimen from Cozumel, a young adult female with a partially broken skull (IBUNAM 9883, Instituto de Biología, Universidad Nacional Autonoma de México, Mexico City, Mexico). Measurements of this specimen (Table 3) closely agree with those from specimens reported by Goodwin (1942) as *M. currentium* from Honduras. The specimen from Cozumel and those from Honduras are too small to be *M. currentium* and correspond more closely to *M. aztecus* (Dolan 1989). Therefore, the northernmost record for *M. currentium* is from Brus Laguna, Gracias a Dios, Honduras (Dolan 1989).

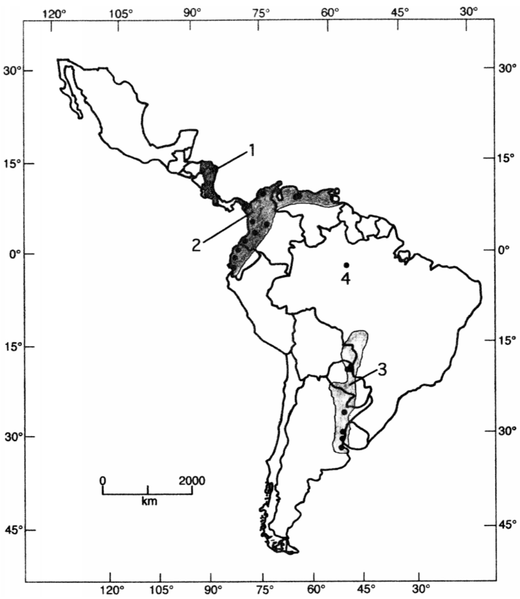

FIG. 3.—Geographic distribution of *Molossus currentium*: 1) *M. currentium robustus* n. subsp., 2) *M. c. bondae*, 3) *M. c. currentium*, and 4) specimen from Manaos, Brazil (see text); circles represent specimens examined and literature records.

Further records for *M. currentium* are documented along the Caribbean slope of Central America from northeastern Honduras to Panama. In northern South America, records are available from western Ecuador, Colombia, and Venezuela (Albuja V. 1982; Dolan 1989; Eisenberg 1989; Koopman 1994; Reid 1997; Timm et al. 1989). No records for localities farther south are available in the literature, except for 1 sample of *Molossus* from Manu Biosphere Reserve, Peru. This record contains a footnote that reads ''may include *M. bondae*'' (Pacheco et al. 1993). The specimens were later ascribed to *M. molossus* (S. Solari, pers. comm.). Dolan (1989) suggested that the distribution of *M. currentium* could be restricted to Colombia, but Handley (1976) and Koopman (1993, 1994) extended distributional limits to Venezuela and Ecuador. We document the occurrence of this taxon as far south as Argentina, Brazil, and Paraguay (Fig. 3), as follows.

ARGENTINA: Buenos Aires: Capital Federal (TTU 32630), female, skin and skull, collected on 29 September 1961. Tigre (TTU 32706), female, skin and skull, collected in January 1971. Entre Ríos: Gualeguachú, Islas del Ibicui (TTU 32705), female, collected on 4 March 1967. These specimens belong to the Abel Fornes collection. Corrientes: Goya (12, BMNH 98.3.4.23–33, USNM 141530), skins and skulls, collected between 1895 and 1896 by R. Perrens (Thomas 1901). BMNH 98.3.4.28 is the type specimen of *Molossus obscurus currentium* Thomas, 1901. The complete series from the BMNH was assigned to that taxon by Thomas in the original description of *M. obscurus currentium*. These specimens were reported as *M. molossus* by Barquez et al. (1999).

BRAZIL: Amazonas: Manaos (USNM 123828), skin and skull, collected in 1899 (exact date not specified) by H. von Ihering. The specimen is a juvenile female, with phalanges not fused and 3 deciduous teeth remaining. It bears a tag from the Museu Paulista, numbered ''N. 504.a'' that also reads ''*Molossus manausinus obscurus* E. Geoff.'' with collection locality ''E. S. Paulo,'' scratched out, and then ''Manaos'' underlined. Given this information, and the apparent habitat preferences of this species in southern South America, it is possible that the specimen had been collected in the state of São Paulo rather than in the Amazon Basin.

PARAGUAY: Alto Paraguay: Bahía Negra, Estancia Doña Julia, 5 km N Ciudad, 20 m from Río Paraguay (9, MNHNP 0384–86, 0389–93, 0397), collected on 3 October 1984 by I. Gamarra de Fox. Estancia Doña Julia, 20°10.98′S, 58°4.42′W, 60 m (27, TK 61004–13, 61016–18, 61020–31, 61056, 61149), collected between 13 and 20 February 1996 by C. López-González, S. J. Presley, F. Pintos, and F. Hoffmann. Fuerte Olimpo (5, FMNH 145296, 145274, 145290, MHNHP 1956, 1960) collected between 15 and 17 October 1991 by R. D. Owen, D. D. Gettinger, and C. Shuster. Laguna General Díaz (2, MHNG 1744.82, 1744.83), collected on 19 November 1987 by personnel of the Geneva Museum of Natural History. The sample includes skins, skulls, and specimens in alcohol with the skull extracted. López-González (1998) and Willig et al. (2000) reported some of these records previously as *M. bondae*. Individuals from Estancia Doña Julia, Alto Paraguay, were collected in mist nets as they emerged from the roof of a wooden house. *Eumops patagonicus* (sensu Barquez et al. 1999), *Myotis albescens*, and *M. nigricans* also were collected with *M. currentium*. All Paraguayan localities are associated closely with the Paraguay River and the Paraguayan portion of the Pantanal. Anually flooded palm-savannas constitute the dominant plant association. Specimens from Argentina were collected in Goya and Buenos Aires on the Paraná–La Plata River; and in Gualeguaychú (= Gualeguachú), on the Uruguay River bank; areas historically covered by palm-savannas alternating with forests dominated by species of the genus *Prosopis* (Bucher 1980).

Taxonomic implications.—The pattern of univariate and multivariate variation in *M. currentium* across its range identifies 3 distinct forms. Although the pattern of variation is the same for both sexes, the degree to which differences are expressed is sex-dependent, as reflected in the multivariate analysis of variance results. For females, differences in cranial length and width are minimal (Table 3; Fig. 1), and considerable overlap exists among populations.

Central American *M. currentium* are relatively large, both cranially and externally, with a large and broad braincase, well-developed sagittal and lambdoidal crests, and short toothrows. Specimens from northern South America are smaller than those from Central America both cranially and externally, but they are similar in cranial shape, having a stout, short-muzzled appearance. Specimens from southern South America are comparable in overall cranial size to those from northern South America, but they have relatively narrow skulls and longer toothrows, which impart a delicate, elongated appearance in contrast to northern individuals. However, externally, they are as large or larger than Central American specimens.

No subspecies have been designated previously for *M. currentium*. We recognize Central American, northern South American, and southern South American populations as taxa distinct at the subspecific level (Fig. 3). Populations from southern South America belong to the nominate subspecies; northern South American populations represent *M. currentium bondae*, and Central American populations comprise an unnamed taxon that we designate as follows.

Molossus currentium robustus, new subspecies

Holotype.—Adult female, skin and skull, TTU 29548 deposited at the Museum of Texas Tech University, Lubbock. Collected 29 July 1977 from Rama, Zelaya, Nicaragua, 25 m, by P. G. Dolan (collector number 803; Fig. 4). Karyotype reference number TK 12399.

Diagnosis.—*Molossus c. robustus* is the largest subspecies of *M. currentium* in overall cranial size (Table 3). In addition to size, its robust skull and relatively short and broad rostrum differentiate *M. c. robustus* from all other known geographic races of the species.

Distribution.—Central America from northern Honduras (Brus Laguna, Gracias a Dios is the northernmost available record) to Costa Rica (Fig. 3). In this area, the species has been collected in the moist lowlands of the Caribbean versant at elevations $<$3,500 ft (1,067 m—Dolan 1989).

Description of holotype.—The type specimen has dark-brown, almost black dorsal pelage. Individual hairs are darker on tips with paler brown bases. Ventral pelage is slightly paler than that of dorsum and contains some gray hairs giving a salt-and-pep-

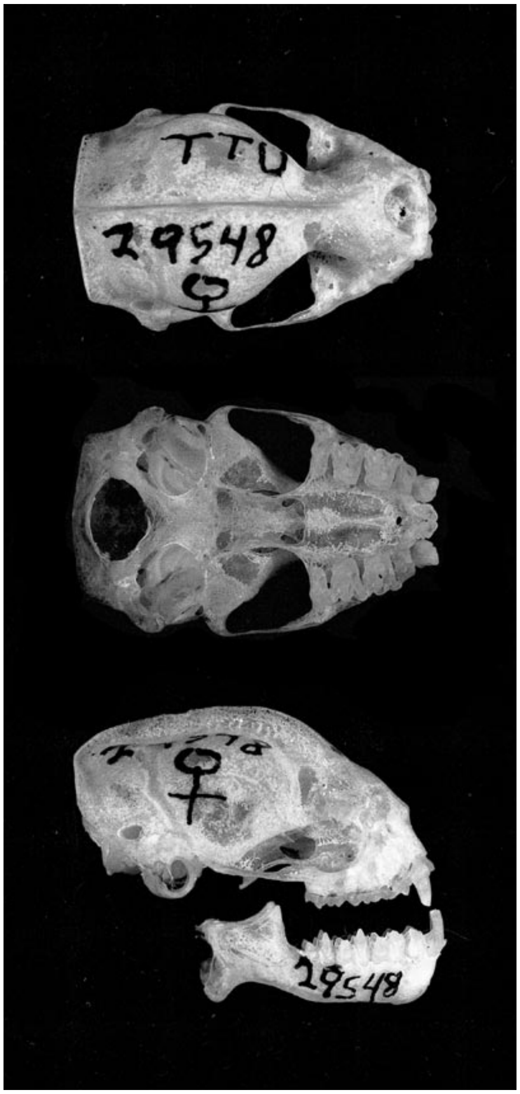

FIG. 4.—Dorsal (top), ventral (middle), and lateral (bottom) views of the holotype of *Molossus currentium robustus* n. subsp. (TTU 29548, adult female). Photograph by W. Mueller, Museum of Texas Tech University.

per appearance. Individual hairs are distally dark brown, fading to whitish bases, with hairs shorter on abdomen (1–2 mm) than on throat and chest (2–3 mm). Membranes are uniformly dark brown. The distal portion of the right wing membrane is slightly torn. Skull of holotype is stout and has well-developed sagittal and lambdoidal crests (Fig. 4). The skull is in good condition except for a broken left pterygoid. External measurements (mm) of holotype are: TL, 109; TAIL, 38; HF, 10; EAR 14; FAR (dry), 41.2; MCIII, 42.1; WT, 21.0 g. Cranial measurements (mm) are: GLS, 19.1; CCL, 16.1; CBL, 16.7; MAB 11.5; ZYG 11.8; BAC 4.7; BAM, 8.4; LNR, 6.6; MAX, 6.4; UML, 5.3; MTR, 7.0; LML, 6.2.

Comparisons.—*Molossus c. robustus* is similar in skull shape to *M. c. bondae.* Both subspecies include individuals with robust, wide braincases, and short toothrows. Nonetheless, *M. c. robustus* is larger than *M. c. bondae* in overall cranial size and external measurements. Compared to *M. c. robustus,* skulls of *M. c. currentium* are significantly larger and have a relatively narrow braincase and long toothrows, resulting in a slender, more delicate appearance.

Remarks.—The epithet *robustus* is from the Latin word meaning ''stout'' and refers to the distinctively large robust appearance of this subspecies. The type specimen was pregnant with a 25-mm embryo in the right horn of uterus.

Literature records.—COSTA RICA: Limón: Cariari, Río Tortuguero (Gardner et al. 1970). Heredia: Puerto Viejo (near La Selva—LaVal 1977). NICARAGUA: Greytown (= San Juan del Norte—Miller 1913).

Molossus currentium bondae J. A. Allen

1904. *Molossus bondae* J. A. Allen, Bulletin of the American Museum of Natural History 20:228. Type locality ''Bonda, Santa Marta, Colombia.''

Holotype.—Adult female, AMNH 23661, skin and skull, collected on 10 February 1900 in Bonda, Rio Manzanares (7 mi E Santa Marta), Magdalena, Colombia (Dolan 1989), by H. H. Smith (original number 1235). According to Allen (1904) the name was ''represented by the type and three topotypes (in alcohol), collected by M. Francis C. Nicholas.'' The type and 2 of the topotypes (paratypes) are extant at the AMNH

(Dolan 1989). Measurements of type are given in Table 3.

Distribution.—*Molossus c. bondae* is known from the lowlands of Colombia, Panama, Venezuela, and Ecuador (Dolan 1989; Handley 1976). A northwest–southeast cline of geographic variation may exist in Central America and northern South America. However, no specimens are available yet to close the gap in distribution represented by western Panama (Fig. 3). If the juvenile specimen from Manaos, Brazil, reported above, belongs to this subspecies, its distribution would extend to the forested areas of northern Brazil.

Description.—Allen (1904) described the holotype of *M. bondae* as ''reddish brown, clouded with darker; below paler, light reddish brown, slightly mottled with darker.'' Topotypes were described as ''dark brown, showing that the species is dichromatic.'' Some specimens from Venezuela are yellow-brown with bases of hairs yellowish. *M. c. bondae* has well-developed sagittal and lambdoidal crests, and a relatively wide, short-muzzled skull, characteristics that give the skull of this subspecies a robust appearance. Externally, it is the smallest subspecies. Measurements of the type specimen and a series of *M. c. bondae* are given in Table 3.

Comparisons.—Smaller external measurements, wide and short rostrum, and a robust cranium (as opposed to long and narrow) separate *M. c. bondae* from *M. c. currentium. M. c. bondae* is similar in skull shape to *M. c. robustus,* but smaller external measurements and overall cranial size in the former make the 2 morphologies distinct.

Remarks.—The southernmost limits of this subspecies are uncertain. Dolan (1989) considered *M. currentium* (as *M. bondae*) as a ''forest'' *Molossus* based on its known distribution in Central America. However, South American records indicate that *M. currentium* also occurs in more open habitats, such as grasslands, savannas, and palm forests. If South America was once covered by continuous savanna (Prance 1982), then *M. c. bondae* and *M. c. currentium* may represent relict populations from a formerly continuous distribution. Amazonia may effectively isolate these 2 populations from each other, facilitating the incipient differentiation of the southern South American subspecies, *M. c. currentium,* morphologically the most divergent. Presence of *M. currentium* in Amazonia is documented by a single specimen of dubious origin. Even if correctly assigned to Manaos, it may represent an incidental record.

Literature records.—COLOMBIA: Choco: Nóvita, 150 ft (J. A. Allen 1916). Cundinamarca: región de Bogotá, 2,750–3,750 m (Aellen 1970). Nariño: Barbacoas, 75 ft (J. A. Allen 1916). Valle del Cauca: Cali, 1,060 m (Aellen 1970). ECUADOR: Guayas: Isla Silva (Albuja V. 1982).

Molossus currentium currentium Thomas, 1901

1901. *Molossus obscurus currentium* Thomas, Annals and Magazine of Natural History, Series 7 8:438. Type locality ''Goya, Corrientes,'' Argentina.

1913. *Molossus currentium* Miller, Proceedings of the United States National Museum 46:89. Name combination.

Type material.—Adult female, BMNH 98.3.4.28, skin and skull, collected on 1 October 1896 in Goya, Corrientes Province, Argentina, by R. Perrens (original number 124). A series of 10 paratypes, skin and skull (BMNH 98.3.4.23–27, BMNH 98.3.4.29–33) is at the British Museum of Natural History (J. Arroyo-Cabrales, pers. comm.).

Distribution.—From northern Argentina and Paraguay along the margin of the Paraguay–Paraná River system, and on the Uruguay River, at elevations $<$150 m (Fig. 3). This bat probably occurs across the Paraguay–Paraná and Uruguay rivers, from the Brazilian Pantanal of Mato Grosso and eastern Bolivia, south to northern Argentina, inhabiting seasonally flooded palm-savannas.

Description.—The holotype is dark, chocolate brown on dorsum, with a grayish brown venter. Bases of individual hairs are light brown on dorsum and almost white on ventral side; membranes are dark brown (J. Arroyo-Cabrales, pers. comm.). Of 23 skins examined, 21 had paler, dull brown coloration on the dorsum with grayish-brown underparts. No specimens are reddish or blond. This subspecies has a relatively long, slender skull that is particularly distinctive in females. Sagittal and lambdoidal crests are well developed in both sexes; the degree of crest development seems to be a function of age, rather than a sexually dimorphic trait. External and cranial measurements of the holotype are given in Table 3.

Comparisons.—See previous accounts for comparisons.

Literature records.—None.

Resumen

Se documenta la distribución de *Molossus bondae* hasta el norte de Argentina. Los ejemplares argentinos incluyen la serie típica de *M. obscurus currentium* Thomas, nombre que tiene prioridad sobre *M. bondae.* El análisis de la variación morfométrica de poblaciones provenientes de localidades que incluyen toda el área de distribución de la especie, indica que existen 3 formas discernibles de *M. bondae.* Se reevaluó el estado taxonómico y nomenclatural de dichas poblaciones, concluyéndose que el nombre válido para este taxón es *Molossus currentium* Thomas. Con base en 12 caracteres craneales y dos externos, se reconocen tres subespecies, para esta especie, una de las cuales se describe como nueva.

Acknowledgments

For museum research and data processing, each author was supported by Grants-in-Aid of Research from the American Society of Mammalogists and by Summer Research awards from the Department of Biological Sciences, Texas Tech University. A Summer Research Award from the Graduate School, Texas Tech University, provided additional support for S. J. Presley. Collection of Paraguayan specimens was supported by grants from the National Science Foundation to R. D. Owen and M. R. Willig (DEB-9400926, DEB-9741543, and DEB-9741134). The Office of the Vice President for Research and Graduate Studies and Office of Research Services at Texas Tech University (D. J. Schmidly and R. Sweazy) also provided substantial financial support to that project. Numerous Paraguayans and institutions lent help and hospitality, among them the Ministerio de Agricultura y Ganaderia del Paraguay (C. Fox), the Museo Nacional de Historia Natural del Paraguay (I. Gamarra de Fox), and especially the office of the Convention for International Trade of Endangered Species (A. L. Aquino). For their efforts and dedication in the field, we are grateful to I. Mora and F. Pintos. For assistance in the field or with logistic arrangements, we thank P. Gorresen, R. Stevens, H. Amarilla, G. Terol, S. Frutos, S. Mezik, R. Fariña, J. Pintos, M. Mieres, and A. Candia. We also thank N. Simmons (AMNH); R. J. Baker and R. R. Monk (TTU); F. Baud (MHNG); F. A. Cervantes (IBUNAM); I. Gamarra de Fox (MNHNP); C. O. Handley, Jr., and L. K. Gordon (USNM); P. Jenkins (BMNH); and B. D. Patterson (FMNH) for granting access to information and specimens under their care. C. Sánchez-Hernández and J. Arroyo-Cabrales kindly examined or facilitated examination of material from Europe and México. J. Arroyo-Cabrales, A. L. Gardner, O. J. Polaco, and 2 anonymous reviewers provided helpful comments on earlier versions of this manuscript. Permission to use photographs of holotype was kindly granted by the Museum of Texas Tech University.

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Submitted 29 November 1999. Accepted 20 December 2000.

Associate Editor was Joseph A. Cook.

APPENDIX I

Specimens examined.—Museum and field-number acronyms are listed in text.

Molossus currentium robustus (68).—COSTA RICA: Cartago: Colorada, 1 mi N Turrialba, 3,100 ft (24, TCWC 10152–75); 2.5 mi E Turrialba, 500 m (3, TCWC 14168, 14170, 14619); Turrialba (20, TTU 29514–33). HONDURAS: Gracias a Dios: Brus Laguna (4, TCWC 24584–87). Olancho: Río Coco, 78 mi ENEE Darli, 900 ft (1, TCWC 10176). NICARAGUA: Zelaya: Rama, 25 m (16, TTU 29534–49).

Molossus currentium bondae (43).—COLOMBIA: Magdalena: Finca Veracruz, Bonda (5, USNM 507212–15, 507218); 7 mi (11.2 km) E Santa Marta, Bonda (AMNH 23661, type of *M. bondae*). ECUADOR: Esmeraldas: 3 km W Majua, 640 ft (1, USNM 513509). Los Ríos: Puerto Nuevo, 3 km NE Vinces (1, USNM 513510). Morona de Santiago: Sucua (1, TTU 40649). PANAMA, Darién: Tacaracuna Village Camp, 3,200 ft (20, USNM 310279–98). VENEZUELA: Carabobo: Montalbán, 1,091 m (1, USNM 441960); 10 km NW Urama, Río Yaracuy, 25 m (12, USNM 374189, 374192, 374194–95, 374197–99, 374201–03, 374205–06). Yaracuy: SE Camp, 25 m (1, USNM 387786).

Molossus currentium currentium (56).—ARGENTINA: Buenos Aires: Capital Federal (1, TTU 32630); Tigre (1, TTU 32706). Entre Ríos: Gualeguachú, Islas del Ibicui (1, TTU 32705). Corrientes: Goya (12, BMNH 98.3.4.23–33, USNM 141530). PARAGUAY: Alto Paraguay: Bahía Negra, Estancia Doña Julia, 5 km N ciudad, 20 m Río Paraguay (9, MNHNP 0384–86, 0389–93, 0397; Estancia Doña Julia, 20°10.98′S, 58°04.42′W, 60 m (26, TK 61004–14, 61016–18, 61020–31, 61056, 61149); Fuerte Olimpo (4, FMNH 145274, 145290, 145296, MNHNP 1956); Laguna General Díaz (2, MHNG 1744.82, 1744.83).

Molossus currentium ssp. (1).—BRAZIL: Amazonas: Manaus (USNM 123828).