GEOGRAPHIC VARIATION IN THE FISHING BAT, *NOCTILIO LEPORINUS*

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ABSTRACT.—Based on study of 388 specimens of *Noctilio leporinus* from throughout the range of the species, three geographic areas of differentiation can be recognized. One is the rim of the Caribbean Basin where the bats are large in size and, although variable in color, usually have a distinct but pale middorsal stripe. The appropriate name for these bats is *Noctilio leporinus mastivus* (Vahl). The second area includes the Guianas and the Amazon Basin where the bats are small in size, dark in color, and often without a pale middorsal stripe. For these bats the earliest name appears to be *Noctilio leporinus leporinus* (Linnaeus). The third area includes eastern Bolivia and the drainage basin of the Río Paraná south of the Brazilian Highlands and north of latitude 30° S where individuals tend to be the largest and palest of the species. The earliest name for these bats appears to be *Noctilio leporinus rufescens* Olfers.

Bats of the family Noctilionidae are restricted to the lowlands of Middle and South America and the West Indies and can be separated into two groups on the basis of size. Those adults with a foot shorter than 20 millimeters, a combined length of tibia and foot shorter than 40 millimeters, a forearm usually shorter than 70 millimeters, and a weight less than 40 grams constitute the species *Noctilio labialis* (Kerr). The second group is a species comprised of larger and heavier bats with a foot longer than 25 millimeters, a combined length of tibia and foot longer than 50, a forearm longer than 75, and a weight more than 50 grams. These larger bats, *Noctilio leporinus* (Linnaeus), are the subject of this report.

The current practice of recognizing four subspecies of *Noctilio leporinus*, namely *N. l. mexicanus* Goldman, *N. l. mastivus* (Vahl), *N. l. leporinus* (Linnaeus) and *N. l. rufipes* D'Orbigny, is based largely on conclusions reached by Cabrera (1938) in his effort to determine the valid scientific name for the Argentinian population of this species. His study is helpful insofar as the disposition of the dozen or so names proposed for segments of the species is concerned, but it reveals little information on the extent and nature of geographic variation. He was aware that in 1883 Pelzen used the name *Noctilio rufescens* for the southern segment of the large fishing bat, but he was unaware that Olfers had used that name in 1818 for Paraguayan *Noctilio*. Consequently, Cabrera believed that D'Orbigny's use of *Noctilio rufipes* in 1835 gave that name priority over *rufescens*. Cabrera (1938) ascribed a range to *N. l. leporinus* that included all of Central America and the northern part of South America, southeastward in Brazil at least as far as Bahia. He regarded *N. l. mexicanus* as "una forma de pequeño tamaño" restricted to the Guerreran region of México, and *N. l. mastivus* as a larger form restricted to the "Antillas." He assigned to *N. l. rufipes* a range comprised of Bolivia,

Paraguay, and northeastern Argentina. Hall and Kelson (1959:87) restricted *mastivus* to the Greater Antilles, assigned all of the Middle American populations of the species to *mexicanus*, and all of those from the Lesser Antilles to the nominate race, *leporinus*. Koopman (1968) referred the specimens from Trinidad and the Lesser Antilles to *mastivus* on the basis of size.

In an attempt to stabilize the taxonomy and nomenclature of *Noctilio leporinus*, particularly in Middle America, I have assembled 388 specimens from throughout its range to obtain an estimate of individual, sexual, and geographic variation in the species.

Listed below are the institutions from which I examined specimens, together with their respective designations used in the lists of specimens examined and the names of individuals who provided me with specimens or data. To these individuals I express my sincere appreciation for their assistance and cooperation. AMNH—American Museum of Natural History, New York City (K. F. Koopman); CM—Carnegie Museum, Pittsburgh, Pennsylvania (C. A. Heppenstall); FM—Field Museum of Natural History, Chicago, Illinois (J. C. Moore); FORNES—Private collection of the late Abel Fornes, Salta, Argentina; IB—Instituto de Biología, Universidad Nacional Autonoma de México, México City (J. Ramírez-Pulido); KU—University of Kansas Museum of Natural History, Lawrence (J. K. Jones, Jr.); LASALLE—Museo de Historia Natural La Salle, Caracas, Venezuela (C. J. Joly T.); LACM—Los Angeles County Museum of Natural History, Los Angeles (D. R. Patten); LSU—Louisiana State University Museum of Zoology, Baton Rouge (G. H. Lowery, Jr.); MCZ—Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts (C. W. Mack); MG—Museum D'Histoire Naturelle, Geneva, Switzerland (V. Aellen); MSU—Michigan State University Museum, East Lansing (R. H. Baker); MVZ—Museum of Vertebrate Zoology, University of California, Berkeley (W. Z. Lidicker); PSMNH—Puget Sound Museum of Natural History, Tacoma, Washington (M. L. Johnson); RNH—Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (A. M. Husson); ROM—Royal Ontario Museum, Toronto, Canada (R. L. Peterson); SNM—"Senckenberg" Natur Museum und Forschungs Institut, Frankfurt, Germany (H. Felten); TORRE—Private collection of Luis de la Torre, Chicago, Illinois; TCWC—Texas Cooperative Wildlife Collections, Texas A&M University, College Station; TTU—Texas Tech University, Lubbock (R. J. Baker); UA—University of Arizona, Tucson (E. L. Cockrum); UCLA—University of California at Los Angeles (T. R. Howell); UI—University of Illinois Museum of Natural History, Urbana (D. F. Hoffmeister); UMMZ—University of Michigan Museum of Zoology, Ann Arbor (W. H. Burt); USNM—United States National Museum, Washington, D.C. (C. O. Handley, Jr., and R. H. Pine); UZM—Universitetets Zoologiske Museum, Kobenhavn, Danmark (F. W. Braestrup).

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Nongeographic Variation

The largest sample available from a restricted geographic area, hence presumably from a single, freely interbreeding population, is that from the coastal region of Chiapas, México. I selected this sample, mainly from the vicinity of Tonalá, for study of nongeographic variation, segregated the specimens by sex and then by age into juvenile (with cartilaginous epiphyses) males,

TABLE 1.—*Selected measurements of adult* Noctilio leporinus *from the Pacific versant of Chiapas, México, presented to show the extent of individual and sexual variation in this geographically restricted population.*

Measurement	Males ($N = 17$)				Females ($N = 17$)			
	Mean	SD	Extremes	CV	Mean	SD	Extremes	CV
Condylobasal length	25.24	0.43	24.7–25.9	1.70	24.17	0.62	23.5–25.8	2.56
Zygomatic breadth	20.00	0.35	19.3–20.5	1.75	18.81	0.45	17.8–19.6	2.39
Cranial breadth	14.69	0.27	14.2–15.2	1.84	14.19	0.79	13.7–14.7	5.57
Maxillary toothrow	10.68	0.15	10.5–10.9	1.40	10.34	0.19	10.1–10.5	1.84
Width across M3-M3	13.36	0.23	13.0–13.9	1.72	12.89	0.19	12.5–13.2	1.47
Mandibular length	19.14	0.39	18.2–19.9	2.04	18.34	0.42	17.6–18.8	2.29
Lower toothrow c-m3	11.59	0.27	10.7–11.9	2.33	11.09	0.18	10.8–11.5	1.62
Forearm	85.09	1.89	81.6–88.1	2.22	84.48	1.91	81.2–87.3	2.26
Metacarpal III	80.92	1.84	77.5–84.6	2.27	79.26	1.32	77.1–81.2	1.66

juvenile females, adult males, adult females and used only measurements of adults in the analyses.

Except for the single, whitish, middorsal stripe, there is considerable variation in dorsal color in the sample. In a series from near Pijijiapan, for example, upper parts of the three females taken on 9 March are orange; of the eight males taken on the same day four are dark orange, two are reddish orange, one is orange brown and one is orange. Five males captured in March, July, and August near Tonalá are brown; the remainder, taken in November and December, are orange as are all females taken in March, July, August, and October. Inasmuch as I have examined brown specimens captured in the months of March, July, August, October, and December at various localities in Middle America, it seems unlikely to me that brown color represents a stage in the molt sequence as some of my associates suggest. The paler shades of orange, however, do appear to be the result of wear or bleaching or both. Thus, in the entire sample from Chiapas, the color of males is more variable than that of females, but this relationship does not hold throughout the range of the species. Overall, the color of females appears to me to be as variable as that of males. For additional comments on this subject see Villa-R. (1966).

Adult males average larger than adult females in all dimensions measured, but there is overlap in the values of most measurements (Table 1). There is little difference between sexes in the Coefficient of Variation (CV) of each variate in the sample which suggests that either sex can be used in a study of geographic variation. The most striking cranial difference between males and females is the presence in adult males of a high, thin sagittal crest. This structure is poorly developed in juvenile males and in females of all ages. Correlated with the degree of development of the sagittal crest, which serves as an area of attachment for the temporal muscle, is an increase in the size of the *M. temporalis*. This muscle is better developed in adult males than in adult females. Thus, the head of an adult male in the flesh is larger than that

of an adult female with similar external measurements. Also, the mandibular ramus is 30 per cent deeper in males than in females (3.5 as opposed to 2.5).

Of all the variates measured, the least variable in both sexes is length of maxillary toothrow, followed by width across the third upper molars (M3-M3) (Table 1). The spread between the shortest and the longest maxillary toothrow in the sample of 17 adult females is only 0.4 (10.1 to 10.5). Theoretically, if all the adult females in the Pacific versant of Chiapas could be measured, the length of the maxillary toothrow of 99 per cent of them would fall within the parameters of 9.96 and 10.72, a spread of only 0.76.

Geographic Variation

Although the CV values in Table 1 indicate that data from either sex can be used to measure geographic variation in this species, I arbitrarily selected females because they vary less with age in development of the sagittal crest, the other cranial ridges, and the mastoidal processes. To simplify the handling of data I pooled the samples from each of 10 geographic areas selected because specimens were available and, more importantly, because previous studies (Davis, 1966, 1968, 1970) revealed that most of them are areas of geographic differentiation in several other species of bats. In other instances, areas 7, 8, and 10 for example, the presence of unusually small individuals in the vicinity of Faro and Obidos (lower Amazon) made it desirable to compare that sample with samples from the Middle Amazon (area 7, Fig. 2), the Upper Amazon (area 10), and the Guianas (area 9). Based on data presented in Table 2 and Fig. 1, I was able to recognize three major areas of differentiation.

There is a northern area embracing all of northern South America (west of Guyana), Trinidad, the West Indies, and Middle America in which individuals of *Noctilio leporinus* attain near maximum size for the genus. Uniformity of the populations in this region is evident from comparisons of the means of each variate tested in sample areas 1 through 6. This conclusion is reinforced graphically in Fig. 1 where two of the least variable cranial features (length of maxillary toothrow and width across M3-M3) are correlated. In this figure, data from each of 10 sample areas are plotted against a standard set of parameters developed for area 3 (West Indies), based on data from 13 females from the Dominican Republic and eight from other Antillean islands. Bats in areas 3, 5 and 6 (the Caribbean complex) are alike in the two variates correlated and comprise an assemblage of homogeneous populations (Fig. 1). Bats from areas 1 (Pacific versant of México north of Oaxaca), 2 (Atlantic versant from Veracruz through Honduras) and 4 (Pacific versant of Middle America from Oaxaca through Nicaragua) differ slightly from the Caribbean samples (areas 3, 5 and 6) in that the mean width across the molar series is consistently greater in relation to length of maxillary toothrow. Even so, the nearly complete overlap of numerical values precludes recognition of two

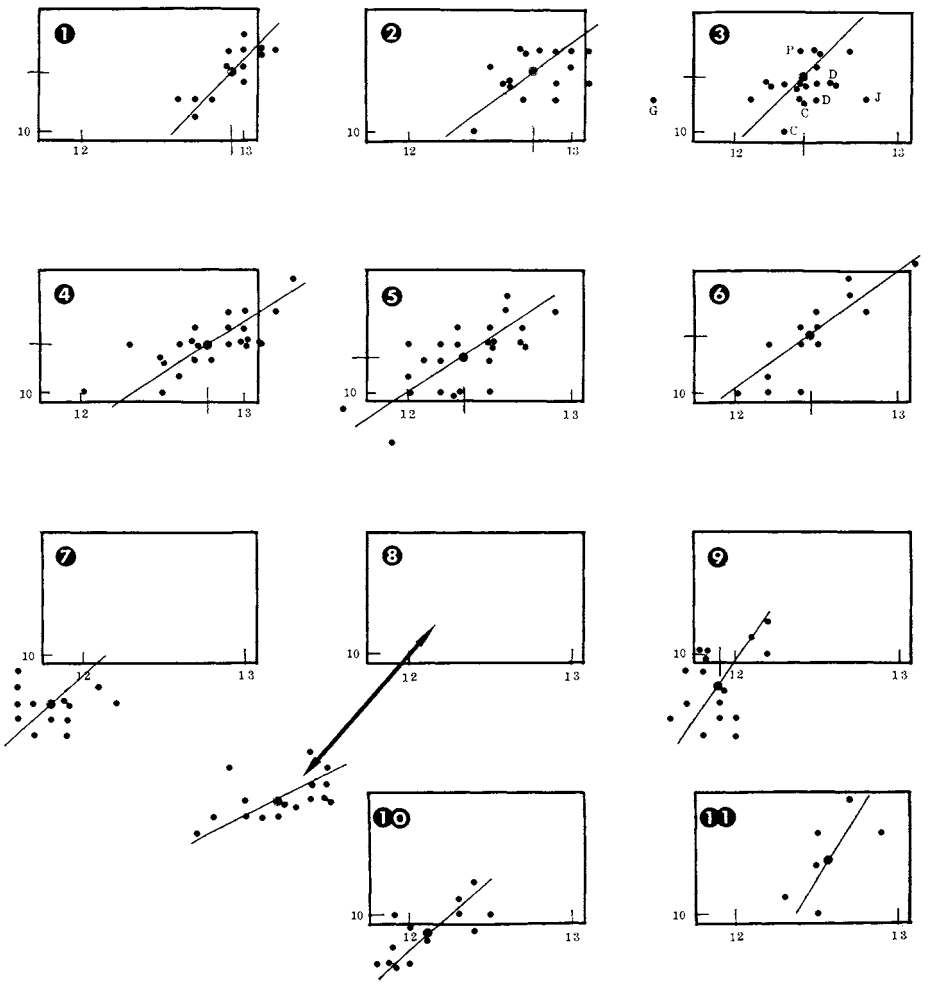

FIG. 1.—Scatter diagrams correlating length of maxillary toothrow (vertical axis) with width across the third upper molars (M3-M3) (horizontal axis) in samples of adult female *Noctilio leporinus* from 11 sample areas. Parameters of the horizontal lines represent two standard deviations (SD, 0.30) above and below the mean width across M3-M3 (12.38) in the sample from the Caribbean area (sample area 3); those of the vertical lines, two standard deviations (SD, 0.13) above and below the mean length of the maxillary toothrow (10.30) in the same sample. Regression lines were not calculated, but rather were simply drawn through points of intersect of the first and third quartiles of the two variates. Means are represented by the large dots. Values from all other samples are plotted against parameters established for the Caribbean sample. See Fig. 2 for location of the sample areas.

taxa in this assemblage. *Noctilio leporinus mastivus* (Vahl) appears to be the valid name for the bats in these six sample areas.

A second area of differentiation includes Guyana, Surinam, Cayenne (herein collectively termed the Guianas) and the Amazon Basin (sample

TABLE 2.—*Comparative measurements of five selected variates in pooled samples of adult female* Noctilio leporinus *from 10 geographic regions. Given for each variate are the mean, the extremes, and one standard deviation of the mean.*

Area	Condylo-basal length	Zygomatic breadth	Maxillary toothrow	Width across M3-M3	Length of forearm	*N*
1. Guerrero north to Sinaloa	24.30 (23.8–24.7) ±0.38	18.95 (18.5–19.3) ±0.28	10.32 (10.1–10.6) ±0.17	12.92 (12.6–13.2) ±0.18	86.65 (82.3–91.6) ±2.40	15
2. Veracruz southward to Honduras	24.10 (23.5–24.7) ±0.35	18.91 (18.0–19.2) ±0.38	10.35 (10.0–10.5) ±0.14	12.78 (12.4–13.1) ±0.21	86.38 (84.0–88.8) ±1.77	17
3. West Indies	23.97 (22.8–24.5) ±0.39	19.03 (18.0–19.5) ±0.44	10.30 (10.0–10.5) ±0.13	12.38 (12.1–12.8) ±0.30	85.21 (81.4–87.7) ±1.55	21
4. Pacific versant, Oaxaca to Nicaragua	24.12 (23.1–25.6) ±0.58	18.86 (17.8–19.6) ±0.45	10.31 (10.1–10.7) ±0.20	12.79 (12.3–13.3) ±0.29	84.37 (81.2–89.0) ±2.33	25
5. Costa Rica, Panamá, Colombia, Venezuela	23.72 (22.9–24.5) ±0.55	18.59 (18.0–19.7) ±0.43	10.22 (9.7–10.6) ±0.22	12.33 (11.6–12.9) ±0.30	84.71 (78.0–91.8) ±3.28	23
6. Trinidad	23.93 (23.5–24.8) ±0.47	18.69 (17.8–19.2) ±0.39	10.36 (10.0–10.8) ±0.25	12.46 (12.0–13.1) ±0.29	85.12 (82.0–89.5) ±2.31	13
7. Upper Amazon Basin	23.21 (22.6–23.7) ±0.35	18.45 (17.6–19.2) ±0.39	9.90 (9.5–10.2) ±0.17	12.13 (11.7–12.4) ±0.29	82.57 (82.0–84.0) ±1.05	9
8. Lower Amazon Basin (near Obidos, Pará)	21.36 (21.1–21.8) ±0.25	17.11 (16.3–17.7) ±0.35	9.07 (8.9–9.3) ±0.11	11.13 (10.7–11.5) ±0.28	76.35 (75.2–78.0) ±1.01	10
9. Guyana, Surinam, and Cayenne	22.44 (21.9–23.2) ±0.39	17.78 (16.8–18.3) ±0.43	9.83 (9.5–10.2) ±0.22	11.91 (11.6–12.2) ±0.17	79.09 (73.0–85.5) ±2.78	11
10. Bolivia and Argentina	23.81 (23.0–25.0) ±0.92	19.28 (18.5–19.8) ±0.46	10.33 (10.0–10.7) ±0.25	12.57 (12.3–12.9) ±0.21	88.23 (87.0–90.0) ±1.57	7

areas 7, 8, and 9 in Table 2 and 7 through 10 in Fig. 1). There the bats are smaller, with a high percentage of the individuals in the samples falling below the parameters set by the West Indian sample (area 3). Note in Fig. 1 that only four of 58 individuals in the samples had a maxillary toothrow longer than 10 millimeters and in only 11 individuals was the width across the third upper molars greater than 12. Also, the means, represented by the large dot in each diagram, are well below the parameters set for the sample in area 3. The smallest individuals in all samples are from area 8 (Faro and Obidos, lower Amazon); individuals from areas 7 (middle Amazon), 9 (the

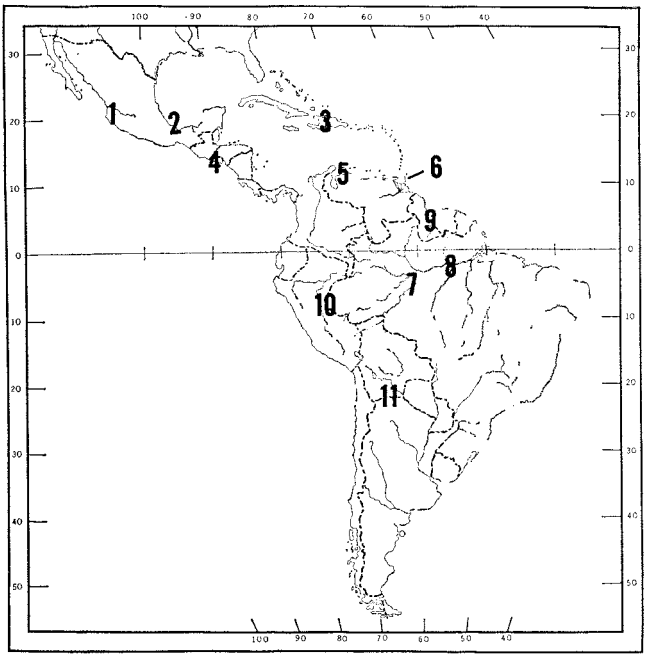

FIG. 2.—Map showing the areas from which data were pooled to provide information on which the scatter diagrams in Fig. 1 are based. Sample area 1 comprises the Pacific versant of México from Guerrero northward to Sinaloa; area 2, lowlands bordering the Gulf of México from Veracruz southeastward to Honduras; area 3, West Indies—undesignated individuals are from the Dominican Republic, C from Cuba, D from Dominica, G from Grenada, J from Jamaica, and P from Puerto Rico; area 4, Pacific versant of Middle America from Oaxaca to the Isthmus of Nicaragua; area 5, Costa Rica, Panamá, northern and western Colombia, and northern Venezuela; area 6, Trinidad; area 7, middle Amazon Basin (region around the confluence of the Río Madeira with the Amazon); area 8, lower Amazon Basin (vicinity of Faro and Obidos); area 9, Guyana, Surinam, and Cayenne (collectively termed Guianas in the text); area 10, upper Amazon Basin in Perú; area 11, eastern Bolivia and northwestern Argentina.

Guianas), and 10 (eastern Perú) are all about the same size and larger than individuals in the Faro-Obidos sample. The appropriate name for bats from areas 7 through 10 is *Noctilio leporinus leporinus* (Linnaeus).

The third area encompasses eastern Bolivia and the drainage basin of the Río Paraná in Paraguay, northern Argentina and southern Brazil (Table 2, sample area 10; Fig. 1, sample area 11). There the bats are larger than those in the Amazon Basin and the Guianas and, especially in Argentina and Paraguay, paler. Specimens from eastern Bolivia are large like those from Argentina and Paraguay, but are dark in color like specimens from along the Amazon River. Consequently, I consider the Bolivian specimens as intergrades, but, because of large size, have referred them to the southern population. I have not been able to find morphological features other than slightly

longer forearm and paler coloration that will separate the southern (Argentina–Paraguay) and northern (Middle America) populations with any degree of reliance, but, because the two assemblages appear to be effectively separated from each other by the Amazon Basin in which the bats are noticeably smaller in size and darker in color, I regard the two as subspecifically distinct and probably derived independently from the small *N. l. leporinus*. The name for the southern population, as pointed out by Hershkovitz (1959), is *Noctilio leporinus rufescens* Olfers.

Accounts of Subspecies

Noctilio leporinus mastivus (Vahl)

1797. *Vespertilio mastivus* Vahl, Skrifter af Naturhistorie-Selskabet Kjobenhavn, 4:132, pl. 7.
1884. *Noctilio leporinus mastivus*, True, Proc. U.S. Nat. Mus., 7:603.
1915. *Noctilio leporinus mexicanus* Goldman, Proc. Biol. Soc. Washington, 28:136.

Holotype.—None appears to be extant. The name is based on material from St. Croix, U.S. Virgin Islands, West Indies.

Diagnosis.—Large for the species and usually with a distinct whitish middorsal stripe; dorsal color variable, ranging from bright orange to grayish brown. Length of the forearm in females averages 85.2, with extremes of 81.4 and 87.7; condylobasal length, 23.97 (22.8 to 24.5); maxillary toothrow usually more than 10. For other measurements see Table 2.

Distribution.—The West Indies, northern South America, and Middle America as far north in the lowlands of México as Sinaloa and Veracruz; southward on the Pacific coast of South America to Esmeraldas, Ecuador (Fig. 3).

Remarks.—Vahl's description and figure of *mastivus* were based on a single specimen collected prior to 1793 by John Ryan on St. Croix Island, one of the three U.S. Virgin Islands (then a Danish possession). According to Dr. F. W. Braestrup (personal correspondence), Zoological Museum of the University, Copenhagen, "there is no specimen here with these data, and I have found no indication that it has been in this collection [Zoological Museum]," although Vahl (1797:130) clearly stated that the specimen was given to the collection of the Society.

Examination of values presented in Fig. 1 and Table 2 indicates that individuals in the samples from areas 1 through 6 (the Caribbean borders) are similar in size and considerably larger than individuals from the Guianas and the Amazon Basin. Consequently, I believe that the assemblage constitutes a group of populations in which gene flow is relatively unrestricted. These bats are strong fliers, frequently forage over salt water (Güdger, 1945), and have been reported some distance from land (Huey, 1932, reported that one flew aboard a ship anchored about a mile offshore in Panamá Bay). I further believe that they have had little difficulty in island-hopping in the West Indian assemblage of islands.

Contrary to Goldman's (1915) statement that individuals of *leporinus* from the west coast of México (Guerrero) are smaller than those from the West Indies, data presented here in Fig. 1 and Table 2 indicate the reverse, although the differences are slight. In my opinion *Noctilio leporinus mastivus* (Vahl) is the proper name for all of the large *Noctilio* in areas surrounding the Caribbean Basin and that *Noctilio leporinus mexicanus* Goldman is a junior synonym.

The occurrence of *N. leporinus* in the vicinity of Esmeraldas, Ecuador is based on Tomes' (1860) report of the capture of several individuals of that species there by a Mr. Fraser in 1859. I have examined no specimens from western Colombia or western Ecuador

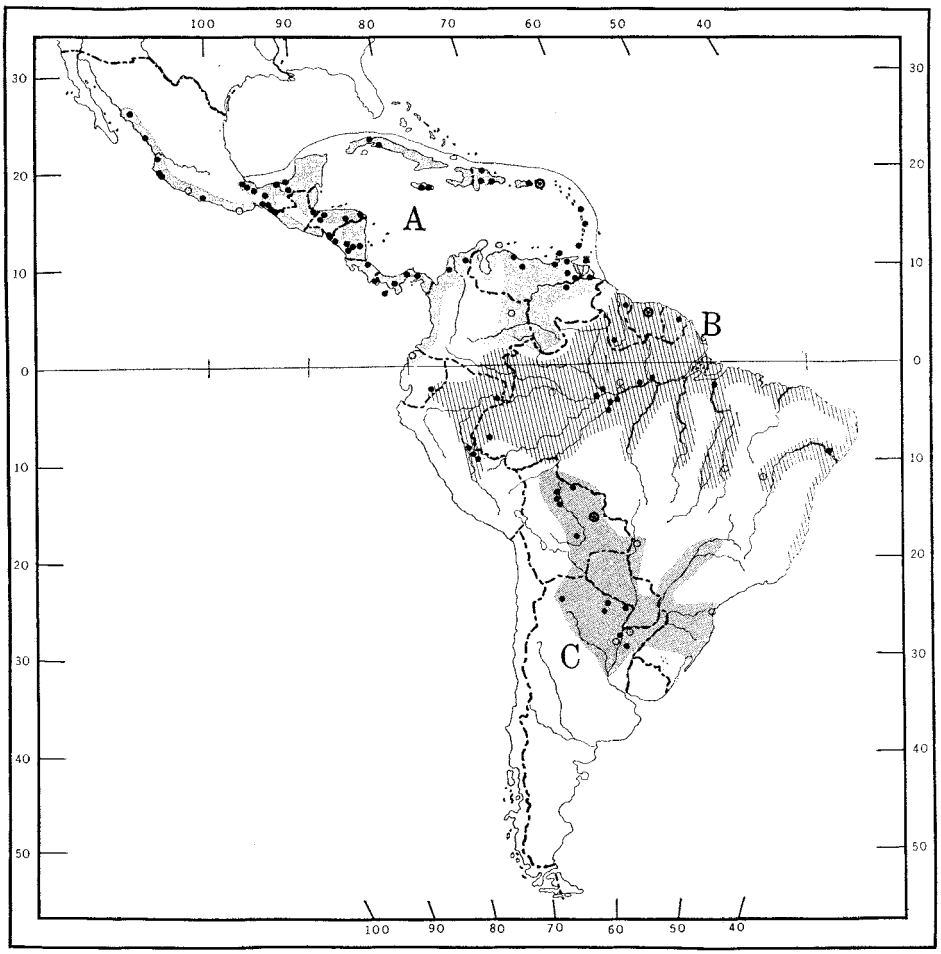

FIG. 3.—Map showing the distribution of the three subspecies of *Noctilio leporinus* herein recognized: A, *N. l. mastivus* (Vahl); B, *N. l. leporinus* (Linnaeus); C, *N. l. rufescens* Olfers. Solid circles indicate localities from which specimens were examined; open circles represent published records from the literature. A star within a circle indicates the type locality.

so I have referred the population in that region of South America to *mastivus* on geographic grounds alone.

Specimens examined (total number, 265).—MÉXICO. *Campeche*: 1 km. SW Puerto Real, Isla del Carmen, 1♂, 2♀♀ (KU). *Chiapas*: 11 km. NW Escuintla, 100 ft., 1♀ (skel. only, UA), 1♀ (LACM); 5 km. SE Pijijiapan, 100 ft., 2♂♂, 1♀ (TCWC); 20 km. SE Pijijiapan, 1♂, 1♀ (UA), 8♂♂, 3♀♀ (LACM); Puente Mosquito, 23 km. WNW Pijijiapan, 100 ft., 7♂♂ (1 skel. only, 3 skins only, UA); 6 km. NE Mal Paso, 400 ft., 1♂ (TCWC); Río Ocuilapa, 12 km. SSE Tonalá, 100 m., 7♂♂, 6♀♀ (IB), 1♀ (TCWC); 10 km. SE Tonalá, 4♂♂, 2♀♀ (LACM); 14–15 km. SE Tonalá, 100 ft., 5♂♂ (IB), 6♂♂, 1♀ (TCWC), 1♂ (LACM). *Guerrero*: Papayo, 25 ft., 3♂♂ (including type of

mexicanus), 3♀♀ (USNM), 1♀ (KU). *Jalisco*: Cuitzamala, 25 ft., 2♂♂, 1♀ (KU); 2 mi. N Tenacatita, 25 ft., 2♂♂, 2♀♀ (KU). *Nayarit*: San Blas, 1♀ (LACM). *Oaxaca*: Tapanatepec [*ca.* 100 ft.], 1♂, 5♀♀ (AMNH); 4 mi. E Tapanatepec, 800 ft., 1♂, 1♀ (TCWC). *Sinaloa*: Isla Palmita de la Virgen, 25 ft., 3♂♂, 7♀♀ (KU); San Benito, 400 ft., 1♂ (KU). *Tabasco*: 12½ mi. N Balancán, 2♂♂, 2♀♀ (LSU); ½ mi. W Miramar, 3♂♂, 1♀ (LSU). *Veracruz*: 1 mi. E Jaltipan, 50 ft., 1♂, 2♀♀ (TCWC); Río San Juan, 21 mi. W Santiago Tuxtla, 1♂, 1♀ (TCWC); 28 mi. S Santiago Tuxtla, 1♀ (TCWC). GUATEMALA. *Izabal*: 25 km. SSW Puerto Barrios, 300 ft., 1♀ (TCWC). HONDURAS. *Cortes*: 2 mi. W San Pedro Sula, 1♀ (TCWC); 7 mi. NW San Pedro Sula, 100 ft., 8♂♂ (TCWC), 1♂ (MSU). *Gracias A Dios*: Brus Laguna, 25 ft., 2♀♀ (TCWC). *Olancho*: 40 km. E Catacamas, *ca.* 1625 ft., 2♀♀ (TCWC). *Santa Barbara*: 7 mi. N Santa Barbara, 325 ft., 1♀ (TCWC). *Valle*: 10 km. E San Lorenzo, 25 ft., 1♂ (TCWC). NICARAGUA. *Chinandega*: Potosí, 5 m., 1♀ (KU). *Chontales*: Hato Grande, 60 m., 3♂♂, 1♀ (KU). *Managua*: 12 km. E Managua, 150 ft., 2♀♀ (UCLA). *Rivas*: 4 km. S, 1½ km. E Alta Gracia, Isla de Ometepe, 40 m., 4♂♂, 1♀ (KU). *Zelaya*: Cacao, 22 km. W Muelle de las Bueyes, 400 ft., 1♂ (TCWC). COSTA RICA. *Limón*: Tortuguero, 1♀ (TCWC). *Puntarenas*: 9 mi. ENE Golfito, 100 ft., 1♂ (TCWC). PANAMÁ. *Canal Zone*: Juan Mina, 5 mi. NE Gamboa, 1♂, 1♀ (MVZ). *Panamá*: 18 km. WSW Chepó, 200 ft., 6♂♂, 2♀♀ (TCWC). *Veraguas*: Coiba Island, Hermosa Bay, 1♂ (LACM); 2 mi. S San Francisco, 200 ft., 3♂♂, 3♀♀ (TCWC). COLOMBIA. *Bolívar*: El Boquerón, San Onofre, 1♂ (MG—measured by V. Aellen). *Magdalena*: Río Guaimaral, Valledupar, 1♂ (FM). VENEZUELA. *Amacuro*: San Francisco de Guayo, 3♂♂, 2♀♀ (LaSalle); Uinikina, 10 m., 2♂♂ (LaSalle). *Bolívar*: Río Candelaria, 60 m., 1♀ (LaSalle). *Guarico*: Zaraza, 1♂, 1♀ (LaSalle). *Miranda*: Tacarigua de la Laguna, 1♂ (UI). *Monogas*: 6 mi. SW Barrancas, 3♂♂, 7♀♀ (UI); Los Aceites, 1♂, 2♀♀ (LaSalle). *Nueva Esparta*: San Francisco de Macanao, 1♀ (KU). *Sucre*: Cumana, 10 m., 1♂, 2♀♀ (KU); Playa Colorada, 1♂ (LaSalle); 1½ km. NW El Pilar, 2♀♀ (KU). TRINIDAD. Blanchisseuse, 1♂ (TTU); Ceral, 4♀♀ (LACM); Fuzabad, 2♂♂, 6♀♀ (TCWC); Las Cuevas, 1♂, 1♀ (TTU); North Manzanilla, 1♀ (TCWC); Port of Spain, 4♂♂ (LSU); Trinidad, 1♂, 2♀♀ (USNM), 1♂, 1♀ (FM). BRITISH WEST INDIES. Antigua Island, 1♂ (FM); Grenada Island, 1♀ (skull only) (USNM); Dominica, St. Joseph Parish, Clark Hall Estate, 100 ft., 1♀ (KU), mouth of Layou River, 2♀♀ (KU). U.S. VIRGIN ISLANDS. St. John Island, Lameshur, 1♂ (KU); St. Croix Island, 1♂ (UZM); St. Thomas Island, 2♂♂, 3♀♀ (UZM). PUERTO RICO. Loisa Vieja (= Old Loisa), 2♀♀ (USNM), 1♂ (UM); no exact locality given, 2♂♂, 1♀ (UZM). DOMINICAN REPUBLIC. *Duarte*: El Limón, Yuna River, 2♂♂, 1♀ (PSMNH). *LaVega*: Boca del Río Maimon, 7♂♂, 10♀♀ (PSMNH); Hda. Nigua, 10 km. SW San Cristóbal, 4♂♂, 2♀♀ (PSMNH). CUBA. *Habana*: Habana, 1♂, 1♀ (TCWC); Los Almacigos, Isle of Pines, 1♀ (FM). JAMAICA. Kingston, 1♂ (USNM); Spanish Town, 1♀ (USNM).

Noctilio leporinus leporinus (Linnaeus)

1758. [*Vespertilio*] *leporinus* Linnaeus, Syst. Nat., ed. 10, 1:32.
1776. *Noctilio americanus* Linnaeus, Syst. Nat., ed. 12, p. 88.
1823. *Noctilio rufus* Spix, Sim. et Vespert. Brasil, pl. XXXV, p. 57, fig. 1.
1826. *Noctilio unicolor* Wied, Beitr. Naturg. Brasil, p. 223.
1938. *Noctilio leporinus leporinus*, Cabrera, Notas Mus. La Plata, 3:14.

Holotype.—None designated. Linnaeus based the name *leporinus* on Seba's description and plate of Vespertilio, Cato similis, Americanus published in 1734. Seba's description and plate are reproduced by Husson (1962); the figure is that of a female. Thomas (1911:131) restricted the type locality to Surinam.

Diagnosis.—Smallest of the *N. leporinus* complex. Forearm of adult females averages less than 80; length of maxillary toothrow averages less than 10; mean width across M3-M3

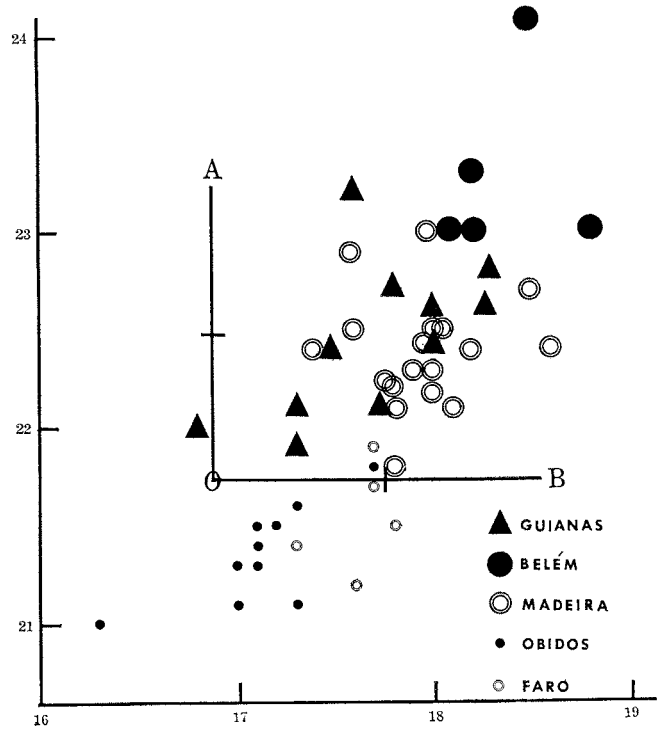

FIG. 4.—Scatter diagram correlating condylobasal length (A–O axis) with zygomatic breadth (B–O axis) in five samples of adult female *Noctilio leporinus* from the Guianas and the Amazon Basin of Brazil: triangles = 11 near topotypes of *N. l. leporinus* (Linnaeus) from Guyana, Surinam, and Cayenne; large solid circles = five from the Rio Tocantins area near Belém, Pará; small solid circles = 10 from near Obidos, Pará; small open circles = five from near Faro, Amazonas; large open circles = 19 from the lower reaches of the Río Madeira and the Río Negro, Amazonas. Line A–O equals two standard deviations above and below the mean condylobasal length (22.44 ± 0.78) of the near topotypes of *N. l. leporinus*; line B–O, two standard deviations above and below the mean zygomatic breadth (17.68 ± 0.86) of the same sample. The other four samples are thus compared with the parameters of the two tested variates established for near topotypes of *N. l. leporinus*.

less than 12; dorsal stripe obscure or lacking in most specimens. Additional measurements are given in Table 2.

Distribution.—The Guianas and the Amazon Basin of Brazil, Ecuador and Perú (Fig. 3).

Remarks.—The small size of bats assigned to *N. l. leporinus* is best seen in the samples from near Obidos and Faro, Brazil (sample 8, Figs. 1 and 2). Note in Fig. 1 that all individuals in this sample fall far outside the parameters set for the sample from area 3 (the Antilles). In sample 9 from the Guianas, including measurements of individuals from Surinam, the type locality, recorded by Husson (1962), the mean length of the maxillary toothrow and that of width across the molars also fall outside the parameters, but the values are larger than those in sample 8. I interpret this as indicating that the population occupying the Guianas is composed of intergrades between the small bats of the Amazon Basin and the large bats of the Caribbean region and, thus, are not truly representative of the nominate subspecies.

Because the values depicted in samples 9 (Guianas), 7 (Río Madeira region), and 10 (eastern Perú) (see Fig. 1) are similar, one might logically conclude, on the other hand, that these are the true values of *leporinus* and that the unusually small size of individuals in sample 8 represents an anomalous condition. I have considered the possibility that sample 8 represents a taxon distinct from *leporinus*, but have rejected it because I can detect no morphological differences other than size, and no apparent ecologic or geographic barrier separates the Obidos-Faro area from other parts of the Amazon Basin. Even so, some unexplained phenomenon is exerting an influence, because as one proceeds up the Amazon River from near Belém where the bats are larger than those from the Guianas, a sharp break in size, based on condylobasal length plotted against zygomatic breadth, occurs in the Obidos-Faro region (compare values of samples in Fig. 4). Some 400 kilometers farther west, at the confluence of the Río Madeira with the Amazon, the bats are larger than those from the Obidos-Faro area. And still farther west, in eastern Perú, they are as large as those from the Guianas and approach the size of those from sample area 11 (Bolivia and Argentina). In spite of the observed cline, the bats from sample areas 7, 8, 9, and 10, based on data presented in Fig. 1, are smaller than those in all other samples and, except for sample 8, they appear to represent a homogeneous assemblage.

Specimens examined (total number, 109).—GUYANA. 25 mi. NE Dadanawa, 8♂♂, 9♀♀ (ROM); Tauraculli [= Taurakuli], 65 mi. up Abary River, 3♂♂ (ROM). CAYENNE. Cayenne, 1♂, 4♀♀—2 skins only (FM). SURINAM. Paramaribo, 1♀ (RNH). BRAZIL. *Acre*: Cruzeiro do Sul, 1♀ (LACM). *Amazonas*: Lago do Arara, Solimoes, 2♂♂, 2♀♀ (SNM); Rio Madeira, Borba, 4♀♀ (AMNH); Rio Madeira, Igarape Auara, 5♀♀ (AMNH); Rio Madeira, Rosarinho, 4♀♀ (AMNH); Rio Negro, near Manaos, 5♀♀ (AMNH); Villa Bella Imperatriz, Santa Clara, 5♀♀ (AMNH). *Pará*: Boca do Igarape Piaba, Rio Amazonas [= 12 mi. W Obidos on north bank], 9♂♂, 11♀♀ (MCZ); Faro, N bank Amazon River, 5♀♀ (AMNH); Ilhado Taiuna, Rio Tocantins, 5♀♀ (AMNH). *Pernambuco*: Acude, 1♂ (Torre). PERÚ. *Loreto*: 11 mi. SE Pucallpa, 300 ft., 2♂♂, 4♀♀ (TCWC); 38 mi. SE Pucallpa, 300 ft., 1♂, 2♀♀ (TCWC); 61 mi. SE Pucallpa, 300 ft., 5♂♂, 4♀♀ (TCWC); Puerto Indiana, Río Amazon [= near Iquitos], 5♀♀ (AMNH). ECUADOR. *Napo Pastaza*: Río Bobonaza, Montalvo, 1♂ (FM).

Noctilio leporinus rufescens Olfers

1818. *N[octilio] rufescens* Olfers, *in* Eschwege, Journal von Brasilien, p. 225.
1835. *Noctilio rufipes* D'Orbigny, Voyage dans l'Amérique Méridionale, Atlas Zool., Mammiferas, lamina 9, figs. 1–4.
1883. *Noctilio rufescens*, Pelzen, Brasilische Saugthiere, p. 38.
1938. *Noctilio leporinus rufipes*, Cabrera, Notas Mus. La Plata, 3:14.
1959. *Noctilio leporinus rufescens*, Hershkovitz, J. Mamm., 40:340.

Holotype.—None appears to be extant. The name *rufescens* is based on the *chauve-souris rougeâtre* of Azara; type locality, Paraguay.

Diagnosis.—Largest and palest subspecies of the species. Much larger than *leporinus* from the Amazon Basin. Mean length of the forearm in females 88.2, with extremes of 87.0 and 90.0 in the sample available; condylobasal length, 23.8; length of maxillary toothrow 10 or more. Other measurements are given in Table 2.

Distribution.—Eastern Bolivia and the upper parts of the drainage basin of the Río Paraná system in Argentina, Paraguay, and southern Brazil, mainly north of 30° S latitude (Fig. 3).

Remarks.—Cabrera (1938) reviewed the nomenclature of this southern population of *N. leporinus* and concluded that *Noctilio rufipes* D'Orbigny was the earliest available name. He rejected the name *rufescens* with the following comments (p. 13): "De los nombres publicados después de *rufipes*, el único que podria corresponder a la misma subspecie es *rufescens*, que parece tener como base el "roxizo" de Azara; pero tanto esta

denominación como *macropus* y *longipes*, además de ser posteriores en muchos años a la aplicada por D'Orbigny, fueron simplemente incluídas por Pelzen [Brasilische Saugethiere, 1883:38] en la sinonimia de *Noctilio leporinus* como nombres usados por Natterer en el catálogo manuscrito de sus colecciones." Hershkovitz (1959), however, pointed out that: "The name *rufescens* Olfers based on the Paraguayan *chauve-souris rougeâtre* of Azara (1801, 2:280) takes priority over *Noctilio rufipes* D'Orbigny, 1836 (Voy. Amérique Mérid., Mamm., pl. 9, figs. 1–4) from Río San Miguel, Guarayo, Bolivia."

Specimens examined (total number, 14).—BOLIVIA. *Beni*: Apere River, 5 km. from mouth, 1 ♀ (AMNH); mouth Baures River, 1 ♀ (AMNH); mouth Ibare River, 1 ♀ (AMNH); Puerto Siles, 1 ♂ (AMNH). *Santa Cruz*: Santa Cruz de la Sierra, 1 ♀ (CM). ARGENTINA. *Corrientes*: Corrientes, 1 ♂ (Fornes); Mercedes, 1 ♂ (Fornes). *Formosa*: Clorinda, 1 ♂, 2 ♀ ♀ (TCWC); E del Campo, 1 ♂ (Fornes); Pozo del Tigre, 1 ♂, 1 ♀ (Fornes). *Jujuy*: Yuto, 1 ♂ (skull only, AMNH).

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