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#### REVIEW OF THE LARGE FRUIT-EATING BATS OF THE ARTIBEUS "LITURATUS" COMPLEX (CHIROPTERA: PHYLLOSTOMIDAE) IN MIDDLE AMERICA

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The realization that two size-classes of *Artibeus* "*lituratus*" occur sympatrically at Santa Barbara, Honduras, prompted this study. At a site seven kilometers north of that town, a field party from the Department of Wildlife and Fisheries Sciences, Texas A&M University, collected 17 males and 24 females in the period from 25 March to 1 April 1969. Among adult females, 15 are large, with the greatest length of the skull (GLS) ranging from 30.7 to 32.0 millimeters (mm.), coupled with a forearm length (FA) varying from 66.5 to 73.7. Nine are small, with the GLS values ranging from 28.2 to 29.0; the FA values, from 62.4 to 68.2. Among adult males, eight are small, with the GLS values ranging from 28.3 to 30.8, coupled with FA values of 63.3 to 68.0. Nine are large, with GLS values varying from 31.0 to 32.0, coupled with FA values of 68.0 to 70.5. A similar situation was found in a sample of 32 individuals from the vicinity of Brus Laguna on the Caribbean coast of Honduras. Of 15 adult females, 11 are large, with GLS values ranging from 30.5 to 32.6, coupled with FA values varying from 67.5 to 74.5. Four are small, with GLS values varying from 29.0 to 30.5, coupled with FA values ranging from 64.3 to 67.8. Of 17 adult males, six are large, with GLS values varying from 31.0 to 32.1, coupled with FA values ranging from 69.4 to 74.0; 11 are small, with GLS values

of 28.0 to 30.0, couples with FA values of 61.0 to 67.5. In an effort to determine the extent of this situation in the Central American Core, that region between the Isthmus of Tehuantepec and the Isthmus of Nicaragua, I examined the 775 specimens in the Texas Cooperative Wildlife Collections (TCWC), as well as 148 from collections at The Museum, Texas Tech University (TTU); University of Arizona (UA); Louisiana State University Museum of Zoology (LSU); University of Michigan Museum of Zoology (UMMZ), and the American Museum of Natural History (AMNH).

Specimens were first separated by sex into three age classes: 1) obvious juveniles with cartilaginous epiphyses and wide spaces separating the phalangeal bones of the fingers, coupled with an overall small size; 2) subadults, those individuals of adult or nearly adult size with the phalanges of the fingers in close contact and their ends swollen for some distance from the joints; and 3) adults, with the phalanges of the fingers completely ossified and their joints knoblike in external appearance. After eliminating juveniles and most of the subadults, as well as those fluid-preserved specimens from which the skulls had not been removed and cleaned, 594 adults (255 males and 339 females) were available for study. Measurements selected for statistical treatment were taken by me to the nearest 0.1 millimeter with dial calipers as follows: GLS, greatest length of the skull, including the upper incisors; ZYG, breadth of the skull across the zygomatic arches; MB, width of the skull across the mastoids; POC, least width of the skull at the postorbital constriction; MXT, length of the maxillary toothrow, (C-M2); M-M, width across the upper toothrows at M2-M2; LM, greatest length of the mandible; MDT, length of the mandibular toothrow, (c-m3) excluding the incisors; FA, length of the forearm, including the carpals, with the wing closed. Weights are those taken in grams by the collector and recorded on the labels.

Initial separation into small and large size-classes was based on visual inspection of the raw data. Those individuals of both sexes with GLS values of 30.0 or more were considered large; the others, small. The GLS and FA values of the small group clustered around 27 and 66, respectively; those of the large group, around 31 and 72. Examination of the data in Table 1 suggested that the upper limit (considered as the mean plus 2 sd) of the GLS values of the small size-class females is close to 30.2 and that the lower limit (considered to be the mean minus 2 sd) of the

TABLE 1.—Comparison of selected measurements of a sample of large-size females (*Artibeus lituratus palmarum*) from Tela on the humid tropical northern coast of Honduras with a sample of small-size females (*Artibeus intermedius*) from the xeric interior Valley of Comayagua about 160 kilometers south of Tela. Note that practically no overlap occurs in the two samples.

	GLS	MXT	M—M	MDT	FA	INDEX	WT
<b>Large Size-Class (N=10)</b>							
	32.4	11.5	-14.8	12.8	73.8	83.7	90.7
	31.6	11.3	14.4	11.9	68.3	78.4	86.9
	32.5	11.5	14.1	12.5	72.0	82.0	87.1
	32.5	11.3	14.2	12.4	71.0	81.1	64.5
	30.4	11.1	13.5	12.1	69.2	78.5	53.5
	31.4	11.7	13.9	12.8	71.2	80.9	75.5
	31.8	11.2	14.0	12.3	74.8	84.1	67.6
	33.0	11.5	13.9	12.9	75.0	84.9	76.6
	31.8	11.1	13.9	12.4	71.0	80.8	70.2
	31.1	11.1	13.7	12.1	72.3	81.5	74.6
$\bar{x}$	31.85	11.33	14.04	12.42	71.86	81.59	74.72
SD	0.53	0.20	0.44	0.34	2.21	2.18	10.96
<b>Small Size Class (N=9)</b>							
	29.0	10.5	13.3	11.7	66.2	75.1	49.1
	29.6	10.7	13.2	11.7	66.4	75.6	59.4
	29.7	10.7	13.4	11.9	65.8	75.1	
	29.9	10.3	13.1	11.3	67.0	76.1	56.7
	29.6	10.4	12.7	11.7	66.8	75.6	57.1
	29.0	10.3	12.7	11.3	63.7	72.8	48.5
	29.1	10.4	12.6	11.3	66.5	75.3	45.6
	28.4	10.5	13.2	11.6	62.2	71.4	52.2
	29.1	10.3	13.2	11.1	67.3	76.0	52.9
$\bar{x}$	29.27	10.46	13.04	11.51	65.77	74.78	52.69
SD	0.47	0.16	0.30	0.29	1.72	1.6	4.8

large size-class females is about 30.8. In making a revised division into the two groups shown in Table 2, all individuals with a GLS value of 30.5 or less, save for nine females classed as large because of their long forearms, were placed in the small size-class; those above 30.5, in the large size-class.

A *t*-test of a sample of 20 females and 12 males from near Teapa in the Mexican state of Tabasco revealed that females were significantly larger than males in GLS, MXT, and LM values. Because of this, and also because more females than males were available, further statistical treatment was confined mainly to the females.

TABLE 2.—Frequency distribution at 0.4 mm. intervals of the GLS values of 333 adult females and 254 adult males of the *Artibeus lituratus*-like complex in Middle America. Note that two nearly normal, slightly overlapping distribution curves exist in the data for each sex.

GLS values	Small		Large	
	♀	♂	♀	♂
27.0-27.3	0	1		
27.4-27.7	1	6		
27.8-28.1	6	8		
28.2-28.5	21	22		
28.6-28.9	23	24		
29.0-29.3	60	39		
29.4-29.7	33	27		0
29.8-30.1	29	15	0	11
30.2-30.5	11	0	9	10
30.6-30.9	0		8	11
31.0-31.3			35	41
31.4-31.7			37	22
31.8-32.1			30	9
32.2-32.5			24	6
32.6-32.9			4	2
33.0-33.3			2	1
33.4-33.7			0	0

To test the validity of my observation that two size-classes existed in the material at hand, I prepared a frequency distribution tabulation (Table 2) of the GLS values of 333 females and 255 males. Results demonstrate that the GLS values of each sex do indeed produce two nearly exclusive and approximately normal distribution curves. Among females, only 20 (six per cent of the sample) fall in the area of overlap, which for that sex is the interval 30.2-30.5. Among males, 26 (10.1 per cent of the sample) fall in the zone of overlap, which is the interval 29.8-30.1.

Although GLS or other values alone were useful in separating 90 per cent or more of the individuals into small and large size-classes, it became obvious that additional criteria were required to make satisfactory allocations of doubtful individuals. I therefore selected five easily measured features and devised a size index based on summing the squares of the FA and four cranial measurements; namely, MXT, GLS, M-M and MDT and then extracting the square root. This computations was made for each specimen. Although not incorporated as an element in the index because it was not available for many of the specimens, weight is also a helpful criterion in making determinations of size-class. Mean weight of eight small size-class, nongravid females from the

vicinity of Comayagua, Honduras, is 52.7 (45.6-59.4) grams; that of 11 males from the same area, 47.3 (43.9-58.7) grams. Comparable values for 10 nongravid females and eight males of the large size-class from the vicinity of Tela, Honduras, are 78.4 (64.5-90.7) and 63.3 (55.2-68.9), respectively.

Usefulness of the computed index is perhaps best illustrated by considering the 41 specimens from near Santa Barbara, Honduras. By combining the index with GLS and FA values, I found it possible to separate all but one female and one male of the Santa Barbara sample into large and small size-classes. Individuals with a GLS of 30.5 or less combined with an FA value of 68.0 or less and an index value of 78 or less were considered small; those with higher values, large. Results of using these criteria in combination are presented in Table 3. Note that determination of one female (19517) and one male (19458) (about 5 per cent of the sample) is still doubtful. In each instance, low FA and index values are combined with a high GLS value. In instances of this sort, the preponderance of evidence provided by the actual measurements of each individual support classifying it as a possible hybrid assignable to the small size-class, although the original designations, based on GLS values alone, placed them in the large size-class. Better results were obtained in making the final determinations of the 32 individuals from the vicinity of Brus Laguna (Table 4). Each specimen fell within the parameters mentioned above.

North of the Isthmus of Tehuantepec, small size-class individuals predominate, but there are a few large size-class individuals (all females) in my sample, as follows: *Tamaulipas*: 30 mi. NNW Mante, 25687♀ (GLS, 31.0; FA, 68.4; index, 78.1). *Queretaro*: 2 mi. S Conca, 27708♀ (30.6; 70.0; 79.5). *Veracruz*: 2 km. NW Alazan, 25309♀ (31.0; 71.6; 80.9); Balzaporte, 31290♀ (32.5; 72.0; 81.3), 31293♀ (31.7; 69.0; 79.1). *Guerrero*: Acahuzotla, 5152♀ (30.1; 72.0; 80.6). All of the 82 other specimens from north of the Isthmus fall within the parameters listed above for the small size-class. I strongly suspect that examination of a much larger sample (for example, 300 to 400 specimens) than I had from north of the Isthmus, would increase substantially the ratio of large to small bats (6.8 per cent reported here).

South of the Isthmus of Tehuantepec there are many more instances of sympatry of the two size-classes. In general, the two sizes are clear cut and readily apparent, but occasional hybridization probably occurs. For example, two females from El Salvador

TABLE 3.—Comparative GLS, FA, and Index values of 41 adult *Artibeus "lituratus"* from a single locality seven kilometers north of Santa Barbara, Honduras. Each specimen is here placed in its final category based on consideration of the three criteria.

Large size-class				Small size-class			
TCWC No.	GLS	FA	Index	TCWC No.	GLS	FA	Index
19473♀	31.0	70.5	80.0	19474♀	29.6	68.2	77.3
19477♀	30.7	68.8	78.2	19475♀	28.2	65.0	73.6
19479♀	31.5	71.2	80.9	19476♀	29.0	65.0	73.9
19480♀	31.9	70.5	80.5	19478♀	28.8	66.5	75.2
19481♀	31.8	70.0	79.9	19488♀	28.3	64.5	73.3
19482♀	31.6	71.0	80.7	19489♀	28.7	66.0	74.7
19483♀	31.0	70.0	79.4	19515♀	28.2	62.4	71.1
19484♀	32.0	73.7	83.1	19516♀	28.4	62.5	71.2
19485♀	32.0	71.5	81.4				
19487♀	31.3	69.6	79.3				
19513♀	32.0	70.0	80.1	19458♂	30.8	66.6	75.3
19514♀	31.8	72.5	82.2	19466♂	30.1	66.0	74.5
19517♀	31.6	66.5	76.5	19467♂	30.5	66.3	75.0
19573♀	32.0	70.0	80.1	19468♂	30.2	68.0	76.4
				19469♂	29.5	65.5	74.4
19574♂	31.8	72.5	82.2	19470♂	29.2	66.6	75.4
19457♂	32.0	69.3	79.3	19471♂	28.3	63.5	72.2
19459♂	31.1	70.5	79.1	19472♂	28.5	63.3	72.1
19460♂	31.3	69.0	77.9				
19461♂	31.0	69.5	78.2				
19462♂	31.0	69.8	78.3				
19463♂	31.2	69.0	77.7				
19464♂	31.2	68.2	76.8				
19465♂	31.0	68.0	76.8				
19472♂	31.2	69.8	78.5				

(TTU 28219 and 28240) have diagnostic values as follows: GLS, 29.5 and 29.9; FA, 70.3 and 70.0; index, 78.9 and 78.8, respectively. I have considered them as probable hybrids because the relationship of their GLS, FA, and index values are abnormal. Their GLS values are those of normal small size-class individuals whereas their FA and index values are normal for large size-class individuals, to which class I have assigned them. A probable hybrid (19533♀) from Copán, Honduras has the reverse arrangement with a GLS of 31.0 coupled with FA and index values of 66.0 and 75.8, respectively. I have assigned this individual to the small size-class because most of its measurements are within the normal range of small individuals.

The data presented above convince me that two populations of *lituratus*-like *Artibeus* occur in Middle America and that each

TABLE 4.—Comparative GLS, FA, and Index values of 32 adult *Artibeus "lituratus"* from three localities within four miles of Brus Laguna, Honduras. Each specimen is placed in its final designated category based on consideration of the three criteria.

Large size-class				Small size-class			
TCWC No.	GLS	FA	Index	TCWC No.	GLS	FA	Index
24545♀	31.2	71.0	80.5	24549♀	30.2	64.3	74.0
24548♀	31.8	73.8	83.3	24553♀	30.5	67.8	76.9
24552♀	31.8	67.5	77.9	24567♀	29.4	66.5	75.4
24554♀	31.0	70.0	79.4	24572♀	29.0	65.0	74.0
22555♀	31.5	70.4	79.9				
24556♀	31.0	70.2	79.5	24542♂	29.0	67.5	76.0
24557♀	32.6	74.5	84.2	24547♂	29.3	63.0	71.4
24558♀	31.2	71.0	80.5	24551♂	30.0	67.0	75.2
24560♀	32.5	72.6	81.6	24564♂	28.2	62.5	71.3
24561♀	30.5	68.9	78.3	24565♂	28.5	63.5	72.3
24563♀	31.0	70.5	80.0	24566♂	29.5	64.8	74.0
				24568♂	29.0	66.5	75.1
24543♂	31.5	72.2	80.8	24569♂	28.0	62.4	71.1
24544♂	31.0	69.4	78.0	24570♂	28.8	63.4	72.4
14546♂	31.8	74.0	82.5	24571♂	29.2	66.5	75.3
24550♂	31.7	69.5	78.4	24573♂	28.5	61.0	70.1
24559♂	31.4	70.2	79.0				
24562♂	32.1	69.5	78.5				

merits taxonomic recognition. Because the two occur sympatrically at several localities, each would seem to merit specific status. The relationship of the two is reminiscent of that between *Carollia subrufa* and *Carollia perspicillata* in the same geographic area. Currently the name *Artibeus lituratus intermedius* is being applied to all Middle American representatives of the *Artibeus "lituratus"* complex (Goodwin, 1969; Jones and Carter, 1976; Hall, 1981). J. A. Allen described *intermedius* in 1897 on the basis of two adults and five nearly full-grown young from San José and Limón, Costa Rica, respectively. He stated that *intermedius* is "rather smaller than *A. palmarum* [which he and Frank Chapman had described a month earlier on the basis of specimens from Trinidad] and much darker, with the head stripes narrower and much less distinct, and the cheek stripes obsolete." Andersen (1908), in his review of the genus *Artibeus*, treated *A. palmarum* as a subspecies of *Artibeus jamaicensis* with *A. intermedius* as a junior synonym. Sixty years later, Goodwin (1969), in his treatise on Oaxacan mammals, stated that "a comparison of Oaxacan and Trinidadian specimens shows that the Oaxacan specimens are larger [italics mine], darker in color,

and different in some cranial details. *Artibeus intermedius* J. A. Allen is reinstated here, as a subspecies of *lituratus*, and is applied to Oaxacan and other Middle American specimens of the species. The name *Artibeus lituratus palmarum* should be used only for specimens from Trinidad (the type locality) and vicinity." His action not only changed the name of the Middle American bats, but it also removed *Artibeus femurvillosum* Bangs (1899), from the Santa Marta region of northeastern Colombia, from the synonymy of *A. palmarum* where J. A. Allen (1900) had placed it. Consequently, *A. femurvillosum* was reinstated as the name for the bats of the *Artibeus lituratus* complex in northern South America and possibly for one of the two size-classes found in Middle America.

Direct comparison of the holotypes of *A. intermedius* and *A. femurvillosum* has not been possible. The former is an adult male for which Allen (1897) gave the following measurements: GLS, 29; M-M, 12; FA, 65. The means of five adult females available to me from near the type locality are: GLS, 29.3; MXT, 10.2; M-M, 12.7; MDT, 11.3; FA, 66.4. Comparable measurements taken by D. C. Carter of the holotype of *femurvillosum*, a male, are: 29.9, 10.8, 11.2, 12.1. The forearms are damaged and could not be measured. On the basis of those data and the measurements of Trinidadian specimens recorded in Table 5, I regard both of those type specimens as representatives of the small size-class. Because Allen's *intermedius* has two years of priority over Bangs' *femurvillosum*, it is the valid name for the small "lituratus-like" *Artibeus* in Middle America and northern South America, with *A. femurvillosum* as a junior synonym.

Data presented in Table 5 leave little doubt that the large Middle American bats of this complex should be assigned to the species *Artibeus lituratus*. The only remaining question involves a name for them. Goodwin's (1969) assertion that Oaxacan specimens are larger than those from Trinidad appears to be a *lapsus*. The mean measurements that he gave for four Oaxacan females (pp. 82-83, table 10) are: GLS, 29.7; MXT, 10.78; M-M, 12.95; FA 68.58. Those of eight females from Tapanatepec, Oaxaca, that I measured are: GLS, 29.41; MXT, 10.48; M-M, 12.96; FA, 66.59. Means for six females from Trinidad are, respectively, 31.23, 10.93, 13.48, 69.83. Goodwin's conclusion that the name *palmarum* is not applicable to the Oaxacan specimens for which he gave measurements is, I believe, justified, but his restriction of that name to bats from Trinidad (type locality) and



TABLE 5.—Comparative measurements of large size-class females of *Artibeus lituratus* from Middle America with those of *A. l. lituratus* from near Rio de Janeiro, Brasil, and eastern Perú, and *A. l. palmarum* from Trinidad.

TCWC No.	GLS	ZBR	MXT	M-M	MDL	MDT	FA	Index
<b>Brus Laguna, Honduras</b>								
24554	31.3	19.0	10.3	13.5	21.5	12.0	70.0	79.4
24555	31.5	18.8	10.7	13.2	21.6	11.8	70.4	79.9
24556	31.0	19.2	10.7	13.3	21.5	11.7	70.2	79.5
24558	31.2	20.0	11.1	13.7	21.5	12.4	71.0	80.5
24560	32.5	20.2	11.2	14.1	22.4	12.6	72.6	82.5
24561	30.5	18.8	11.0	13.6	20.5	12.0	69.0	78.4
$\bar{x}$	31.3	19.3	10.8	13.6	21.5	12.1	70.5	80.0
<b>Depto. de Loreto, Perú</b>								
27426	32.7	19.4	11.5	14.5	22.5	12.3	72.0	82.2
27425	31.9	18.9	11.2	13.6	22.2	12.4	76.0	85.0
27428	31.0	19.0	11.5	14.0	21.7	12.4	72.0	81.4
29585	30.3	18.3	11.0	13.3	21.5	12.2	70.8	79.9
29587	31.1	19.0	11.0	14.0	21.6	12.0	67.5	77.4
12322	31.0	19.5	10.7	13.4	22.0	12.0	71.7	81.9
$\bar{x}$	31.3	19.0	11.2	13.8	21.9	12.3	71.9	81.3
<b>Near Rio de Janeiro, Brasil</b>								
22823	32.2	19.3	11.6	14.0	22.1	12.5	71.0	81.0
28662	31.5	18.6	11.5	13.7	22.2	12.5	73.0	82.4
28663	31.3	18.9	11.5	14.0	22.0	12.5	70.2	80.0
28664	32.1	19.5	11.6	14.0	22.2	13.0	72.6	82.5
28665	32.5	19.8	11.5	14.4	22.5	12.6	71.8	81.9
28666	32.5	19.4	11.6	14.0	22.6	12.5	74.0	83.8
$\bar{x}$	32.0	19.3	11.6	14.0	22.3	12.6	72.1	81.9
<b>Trinidad</b>								
6308	30.1	18.4	10.7	13.0	21.1	11.7	71.4	79.3
3561 LSU	32.5	19.6	11.5	14.2	22.4	12.6	68.7	79.2
3564 LSU	31.0	18.8	11.0	13.5	21.5	12.0	71.0	80.3
3566 LSU	31.2	18.9	10.6	13.3	21.7	11.8	66.7	76.5
3572 LSU	30.8	18.5	10.7	13.5	20.5	11.7	68.5	77.9
3574 LSU	31.8	19.4	11.1	13.4	21.5	12.2	70.4	79.3
$\bar{x}$	31.2	18.9	10.9	13.5	21.5	12.0	69.8	79.2

vicinity is not. Examination of the data in Table 5 reveals no significant differences in the measurements of bats from Trinidad and those from the northern coastal area of Honduras. Consequently, use of the name *Artibeus lituratus palmarum* Allen and

Chapman for the large bats of the *A. lituratus* complex in Middle America seems appropriate.

Restoration of *Artibeus intermedius* J. A. Allen to specific status, which I here propose, and the transfer of *Artibeus fallax* Peters and *Artibeus hercules* Rehn to the species *Artibeus planirostris* (Spix) (see Patten, 1971; Koopman, 1978) leaves the species *Artibeus lituratus* (Olfers), as visualized by Jones and Carter (1976), with only two subspecies; namely, *Artibeus lituratus lituratus* and *Artibeus lituratus palmarum*. I visualize *A. l. lituratus* as occupying the the tropical and subtropical regions of South America south of the Orinoco Basin and east of the Andes, and *A. l. palmarum* as occupying northern South America, including Trinidad, and Middle America, mainly on the Gulf-Caribbean versant, commonly to the Ishtmus of Tehuantepec, thence in diminishing numbers to Nayarit and Tamaulipas in western and eastern México, respectively.

### *Artibeus intermedius* J. A. Allen

#### Allen's Fruit-eating Bat

1891. *Artibeus carpolegus*, J. A. Allen, Bull. Amer. Mus. Nat. Hist., 3:205.  
 1897. *Artibeus intermedius* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 9:33.  
 1908. *Artibeus planirostris planirostris*, Andersen, Proc. Zool. Soc. London, 1908:237 (part).  
 1908. *Artibeus jamaicensis palmarum*, Andersen, Proc. Zool. Soc. London, 1908:278 (part).  
 1949. *Artibeus lituratus palmarum*, Hershkovitz, Proc. U.S. Nat. Mus, 99:447.  
 1969. *Artibeus lituratus intermedius*, Goodwin, Bull. Amer. Mus. Nat. Hist., 141:87.

*Type locality*.—San José, Department of San José, Costa Rica. Elevation ca. 3500 feet.

*Diagnosis*.—A relatively large (forearm, 61-68; weight 43-59), brownish, leaf-nosed bat with two distinct, whitish supraorbital stripes extending from the snout onto the forehead; malar stripes obscure or missing; no mid-dorsal stripe; underparts normally darker than upperparts and not frosted (individual hairs lack the whitish tips found in the similar-sized *Artibeus jamaicensis*); uropatagium narrow and deeply excised; no tail; number of molars normally 2/3, but the third lower molar is missing on one or both sides in about 2 per cent of the population. This species is most closely related to *Artibeus lituratus*, but smaller (see Tables 1-4).

*Distribution*.—Recorded from the Mexican states of Sinaloa and Tamaulipas southward through Middle America, mainly in

the drier tropical and subtropical vegetation zones, into the northern part of South America. Observed elevational range in the Central American Core varies from near sea level to 5700 ft. in the highlands of Chiapas.

*Habitat.*—In Middle America this species is associated with Tropical Thorn Forest, Tropical Deciduous Forest, and Pine-oak vegetation zones. All the specimens that I examined from the Central American Core had been captured in mist nets sets across streams or near banana groves and fruit-bearing trees. Those taken in the Mexican state of Guerrero with firearms were found hanging singly or in small groups in the exposed entrances of caves where no artificial light was needed to shoot them (Lukens and Davis, 1957). In the Mexican state of San Luis Potosí, Dalquest (1953) found single individuals just within the mouths of large caves, where it was quite light, or hanging from the shaded roofs of small niches in cliffs. I have seen no evidence that they utilize foliage roosts such as those used by the closely related *Artibeus lituratus*.

*Specimens examined.*—Unless indicated otherwise, specimens are deposited in the Texas Cooperative Wildlife Collections at Texas A&M University. MEXICO: *Tamaulipas*: 67 km. S Ciudad Victoria, 1 ♀ (TTU 13004); 30 mi. NNW Mante, 300 m., 3 ♀♀ (25688; 25691-92), 2 ♂♂ (25689-90); Río Sabinas at Hwy. 85, 25 mi. NNW Mante, 300 ft., 1 ♀ (25348). *San Luis Potosí*: El Salto Falls, 1300 ft., 1 ♀ (28679), 3 ♂♂ (28676-78); 3.5 mi. NW Xilitla, 2800 ft., 1 ♀ (24359), 1 ♂ (24358). *Querétaro*: Hda. X-Conca, 2 mi. S X-Conca, 2200 ft., 5 ♀♀ (27703-07), 2 ♂♂ (27709; 27920); 11 mi. NW Jalpan, 2500 ft., 1 ♀ (24360); Hda. Sharpton, 16 mi. NNW Jalpan, 2000 ft., 2 ♀♀ (25349; 25351), 1 ♂ (25350). *Puebla*: 2 mi. W Villa Avila Comacho, 250 m., 1 ♂ (25310). *Veracruz*: 2 km. NW Alazan, 20 m., 1 ♂ (25308); 1 mi. E Jaltipan, 50 ft., 1 ♀ (8221), 1 ♂ (8222); Río Queltapan, 2 mi. E Lago Catemaco, 2 ♀♀ (11170; 11172); 5 ♂♂ (11171; 11173-11176); 5 km. NNW San Juan Diaz Covarrubia, 520 ft., 1 ♂ (21185). *Nayarit*: 2 mi. W Tecualá, 1 ♀ (TTU 5838). *Guerrero*: Acahuizotla, 2800 ft., 10 ♀♀ (5139; 5146-49; 5347; 5838; 5841; 6488-89), 5 ♂♂ (4992; 5344; 5839-40; 6490); Agua de Obispo, 3300 ft., 2 ♂♂ (6491-92); 1 mi. SSE Almolonga, 1 ♀ (7382), 1 ♂ (35106); Colotlipa, 2700 ft., 1 ♂ (5153); Palos Blancos, 1 ♂ (7384); El Papayo, 25 ft., 1 ♀ (5670), 3 ♂♂ (5668-69; 5671); Tres Palos, 10 ft., 1 ♀ (6380), 2 ♂♂ (6379; 6381). *Oaxaca*: 9.5 mi. S Matias Romero, 1 ♀ (TTU 10876); 6.5 mi. NE Tapanatepec, 1 ♀ (TTU 11012); 4 mi. E Tapanatepec, ca. 800 ft., 7 ♀♀ (16685-91), 5 ♂♂ (16811-15). *Tabasco*: ½ mi. S Balancan, 1 ♀ (LSU 8281), 2 ♂♂ (LSU 8280, 8282); 1 mi. E Teapa, 200 ft., 1 ♂ (LSU 7513); 13.6 mi. W Villahermosa, 1 ♀ (TTU 10834), 5 ♂♂ (TTU 10832-34; 10721; 11016). *Chiapas*: 5 mi. N Arriaga, 800 ft., 2 ♀♀ (17024; 17027), 2 ♂♂ (17025-26); 4 mi. NE Chiapa de Corzo, 2200 ft., 1 ♂ (8455); Florida, 50 km. E Altamirano, 590 m., 1 ♀ (9300), 4 ♂♂ (9297-98; 9301; 9306); 23.6 mi. NW Huixtla, 400 ft., 1 ♀ (35095); 7 mi. S Ixtapa, 3500 ft., 2 ♂♂ (20997-98); 7 mi. W Mal Paso, 500 ft., 1 ♂ (16709); 5 km. E Puerto Arista, 25 ft., 1 ♀ (35105), 6 ♂♂ (35100-01; 35103-04; 25077-78); La Soledad 16 mi. NW Las Margaritas, 3600 ft., 1 ♂ (UA 9418); 12 mi. E Ortiz Rubio on Villa

Flores rd. 1 ♀ (UA 10796); Rancho San Miguel, 32 mi. SW Cintalapa, 2 ♀♀ (TTU 11245; 11248), 3 ♂♂ (TTU 11244; 11246-47); 3 mi. SSE Soyalo, 3000 ft., 1 ♂ (8456); 3.8 mi. SW Tapachula, ca. 200 ft., 5 ♀♀ (TTU 11138-39; 11366-68), 7 ♂♂ (TTU 11137; 11140; 11363-65; 11370-71); 6.8 mi. N Tapachula, 2 ♂♂ (TTU 11212-13); 2 km. WSW Teapa, 200 ft., 2 ♀♀ (16701; 16705); 15 km. SE Tonalá, 100 ft., 1 ♀ (21186), 1 ♂ (14438); 11.9 mi. SE Tres Picos, Puente Mosquito, 1 ♀ (TTU 11215), 2 ♂♂ (TTU 11216-17); 18 mi. S Trinitaria, 2800 ft., 5 ♀♀ (8214-15; 8217-19), 2 ♂♂ (8216; 8220); 35 mi. SSE Tuxtla Gutierrez, 2200 ft., 4 ♀♀ (16799-802), 1 ♂ (16798); 38 mi. SEE Tuxtla Gutierrez, 1800 ft., 6 ♀♀ (16805-810), 2 ♂♂ (16703-04); Yaxoquintela, 37 km. NE Altamirano, 590 m., 1 ♀ (9295), 1 ♂ (9294); 2 mi. S Zapaluta, 5700 ft., 2 ♀♀ (8457; 8459), 2 ♂♂ (8458; 8460); 10 mi. S Zapaluta, 3000 ft., 2 ♀♀ (8463; 8466), 4 ♂♂ (8461-62; 8464-65); 13.8 mi. S Zapaluta, 2700 ft., 1 ♂ (9297). GUATEMALA: *Chimaltenango*: 2 mi. S Chimaltenango, 5700 ft., 3 ♀♀ (14442; 14449-50), 3 ♂♂ (14439-41). *Chiquimula*: 20 km. SEE Chiquimula, 550 m., 3 ♀♀ (17708-09; 17711), 1 ♂ (17710). *Alta Verapaz*: San Cristóbal Verapaz, 1380 m., 8 ♀♀ (17719-24; 17726; 17728), 3 ♂♂ (17725; 17727; 17729). *Baja Verapaz*: 2 km. SE Salamá, 950 m., 2 ♀♀ (17700; 17702), 2 ♂♂ (17701; 17703); San Miguel Chinaj, 950 m., 1 ♀ (17699). *El Progreso*: Agua Caliente at k 29 on hwy. to Puerto Barrios, 2800 ft., 3 ♂♂ (8660-62). *Escuintla*: 2 mi. E Palín, 4000 ft., 1 ♀ (14451), 1 ♂ (14452). *Guatemala*: Amatitlán, 3800 ft., 3 ♀♀ (14448; 18446; 18448), 4 ♂♂ (18444-45; 18447; 18452); *Jutiapa*: 15 km. NE Jutiapa, 300 ft., 2 ♀♀ (18449-50), 1 ♂ (18451). *Quiché*: 1 km. WSW Sacapulas, 1200 m., 3 ♂♂ (17704-06). *Retalhuleu*: 3 km. N Retalhuleu, 1000 ft., 3 ♀♀ (14445-47), 2 ♂♂ (14443-44). *San Marcos*: El Carmen, 1600 ft., 5 ♀♀ (21187-91), 6 ♂♂ (21192-97). BELIZE: ¾ mi. E Corozal, 7 ♀♀ (LSU 8612-14; 8616-17; 8620; 8622), 1 ♂ (LSU 8615). EL SALVADOR: *Chilatenango*: 20 km. W Chilatenango, 280 m., 2 ♀♀ (19455-56). *La Libertad*: 8.4 mi. NW Colón, 1 ♀ (TTU 13012). vic. La Libertad, 10-15 m., 6 ♀♀ (22029; 22031-33; 22035-36); 20 km. W La Libertad, 250 m., 2 ♀♀ (22039-40); 20 mi. W La Libertad, 10 ft., 1 ♀ (8663). *La Paz*: 3 mi. NW La Herradura, 1 ♂ (TTU 16910).. *San Miguel*: 3 mi. W San Miguel, 1 ♀ (TTU 16917), 1 ♂ (TTU 16923). *San Salvador*: 1 mi. W Ilopongo Airport, 1 ♀ (TTU 28226), 5 ♂♂ (TTU 13014-15; 28225; 28117-28). *Usulután*: 2 mi. E Usulután, 11 ♀♀ (TTU 16269; 28229-34; 28236-39), 3 ♂♂ (TTU 16927-28; 28235). HONDURAS: *Atlántida*: 9 mi. W La Ceiba, 25 ft., 2 ♀♀ (14752; 14760); 1 mi. W Tela, sea level, 1 ♂ (14734). *Choluteca*: 36 km. SE Choluteca, 600 m., 2 ♀♀ (24018; 24021), 3 ♂♂ (24017; 24019-20). *Comayagua*: Comayagua, 580 m., 6 ♀♀ (22003-08), 6 ♂♂ (21997-22002); 3 km. W Comayagua, 580 m., 3 ♀♀ (22014-16), 5 ♂♂ (22009-22013). *Copán*: Copán, 660 m., 1 ♀ (19533). *Cortes*: La Lima, 40 m., 2 ♂♂ (10938-39). *Distrito Central*: 1 mi. S Comayagua, 1000 m., 2 ♂♂ (18453-54); 10 mi. SE Tegucigalpa, 1580 m., 2 ♀♀ (18455-56). *Gracias A Dios*: Brus Laguna, 10 ft., 4 ♀♀ (24549; 24533; 24567; 24572), 1 ♂ (24566); 4 mi. N Brus Laguna, sea level, 8 ♂♂ (24542; 24547; 24551; 24568-71; 24573); Uta Almuk, nr. Brus Laguna, 50 ft., 2 ♂♂ (24564-65). *Intibucá*: La Esperanza, 1660 m., 3 ♀♀ (21986-88), 5 ♂♂ (21981-85); 5 km. NE Jesús de Otero, 640 m., 5 ♀♀ (21989-93). *La Paz*: Marcala, 1200 m., 1 ♀ (21996), 2 ♂♂ (21994-95). *Ocatepeque*: 4 km. N Nueva Ocatepeque, 840 m., 2 ♀♀ (17686; 17688), 1 ♂ (17687); 1 km. W Nueva Ocatepeque, 840 m., 6 ♀♀ (17692-96; 17698), 4 ♂♂ (17689-91; 17697). *Santa Barbara*: 7 km. N Santa Barbara, 120 m., 9 ♀♀ (19474-76; 19478; 19488-89; 19515-17), 8 ♂♂ (19458; 19466-71; 19577); 12 km. N Santa Barbara, 100 m., 1 ♀ (TTU 13001). *Valle*: 6 km. E Amatillo, 600 m., 3 ♀♀ (18443; 18462-63), 7 ♂♂ (18439-42; 18460-61; 18464); 10 km. E San Lorenzo, 25 ft., 2 ♀♀ (18457-58), 1 ♂ (18459). NICARAGUA: *Carazo*:

Ponchmil, 3 km. SE Masachapa, 25 ft., 3 ♀♀ (35108; 35110; 35112), 4 ♂♂ (35109; 35111; 35113-14). *Madriz*: Yalaguina, 2200 ft., 1 ♀ (21211), 12 ♂♂ (21198-202; 21204-10). *Matagalpa*: 2 mi. S Dario, 1500 ft., 1 ♂ (9641); 1 mi. W Matagalpa, 2300 ft., 1 ♂ (21213). 3 mi. W Matagalpa, 2300 ft., 1 ♀ (21212), 1 ♂ (21214); 4 mi. E Matagalpa, 2600 ft., 1 ♀ (21213), 4 ♂♂ (21216-19). *COSTA RICA*: *Guanacaste*: Finca La Pacifica, 1 ♀ (UMMZ 125175, skull only). Los Huecos, 100 ft., 1 ♀ (UMMZ 65082). 3 mi. S, 10 mi. W Las Cañas, 1 ♀ (8097). *San José*: San Pedro, 3800 ft., 1 ♀ (LSU 8951); vic. San José, 3000 ft., 5 ♀♀ (AMNH 131810; 131813-14; 131816-17), 1 ♀ (UMMZ 116672). *PANAMA*: *Veragues*: 2 mi. S San Francisco, 200 ft., 6 ♀♀ (9654-56; 9658-59; 9661), 1 ♂ (9651); 2 mi. S Soná, 200 ft., 1 ♂ (9662).

*Artibeus lituratus palmarum* J. A. Allen and Chapman

Large Brown-bellied Fruit-eating Bat

1878. *Artibeus perspicillatus*, Dobson, Catalogue of the chiroptera in the collection of the British Museum, p. 579.
1897. *Artibeus palmarum* J. A. Allen and Chapman, Bull. Amer. Mus. Nat. Hist., 9:16.
1908. *Artibeus jamaicensis palmarum*, Andersen, Proc. Zool. Soc. London, 1908:278.
1949. *Artibeus lituratus palmarum*, Hershkovitz, Proc. U.S. Nat. Mus., 99:447.
1969. *Artibeus lituratus intermedius*, Goodwin, Bull. Amer. Mus. Nat. Hist., 141:87 (part).

*Type locality*.—Botanical Gardens at Port of Spain, Trinidad.

*Diagnosis*.—Largest member of the genus *Artibeus* (forearm, 69-75; mean weight of males, 63 grams, that of females, 76); two pairs of prominent facial stripes, the supraorbital pair most conspicuous; underparts dark brown, often chocolate color, and not frosted with white-tipped hairs as in *Artibeus jamaicensis*; skin in the pectoral region firmly attached to the underlying muscles and thus making the animal difficult to skin. This species is most closely related to Allen's fruit-eating bat, *Artibeus intermedius*, but larger (compare measurement in Tables 1-4). Molars normally 2/3, rarely 2/2 (1 of 150 individuals examined).

*Distribution*.—From the Isthmus of Tehuantepec southward, mainly on the Gulf-Caribbean versant of the Central American Core, into South America. Altitudinal range from near sea level to approximately 3600 feet.

*Habitat*.—Most common in the Tropical Rain Forest vegetational zone, but also occurs sparingly in Tropical Deciduous Forests. It appears to be essentially a canopy bat in that it roosts there, and in the subcanopy, under broken or crossed palm fronds, in vine-tangled crowns of subcanopy trees, and in dark, cavelike recesses on the undersides of the crowns of canopy-height trees (Morrison, 1980). On the island of Trinidad, it has also been

found roosting in hollow silk-cotton trees (*Ceiba*) (Goodwin and Greenhall, 1961).

*Specimens examined* 332.—Unless indicated otherwise, specimens are deposited in the Texas Cooperative Wildlife Collections. MEXICO: *Tamaulipas*: 30 mi. NNW Mante, 300 m., 1 ♀ (25687). *Queretaro*: Hda. X-Conca, 2 mi. S Conca, 2200 ft., 1 ♀ (27908). *Veracruz*: 2 km. NW Alazan, 20 mi., 1 ♀ (25309); 1.3 km. NE Balzaporte, 2 ♀♀ (31292-93). *Guerrero*: Acahuizotla, 2800 ft., 1 ♀ (5152). *Tabasco*: 1 mi. E Teapa, [ca. 200 ft.], 19 ♀♀ (LSU 7514; 8207-09; 8288-89; 8291-95; 8297-99; 8301-04; 8312-13), 12 ♂♂ (LSU 7513; 8285-87; 8290; 8296; 8300; 8305-06; 8310-11; 8314); 5.4 mi. N Teapa [ca. 200 ft.], 3 ♂♂ (TTU 11122-24); 13.6 mi. W Villahermosa [ca. 100 ft.], 2 ♀♀ (TTU 10828-29), 4 ♂♂ (TTU 10718; 10722; 10823; 10835). *Chiapas*: Florida, 50 km. E Altamirana, 525 m., 2 ♀♀ (9302; 9304), 6 ♂♂ (9301; 9303; 9305-06; 9298-9); La Soledad, 16 mi. NW Las Margaritas, 3600 ft., 1 ♀ (UA 9419); 18 mi. S La Trinitaria, 2800 ft., 1 ♂ (8213); 6 km. NE Mal Paso, 400 ft., 5 ♀♀ (16706-08; 17014-15); 7 km. WNW Mal Paso, 500 ft., 2 ♂♂ (16709-10); 10 mi. W Mal Paso, 400 ft., 3 ♀♀ (16713-15); 2 ♂♂ (16711-12); 5 km. ESE Pichucalco, 200 ft., 1 ♀ (16704); 3.8 mi. SW Tapachula [ca. 300 ft.], 2 ♀♀ (TTU 11369; 11372); 21 km. WSW Teapa, 200 ft., 6 ♀♀ (16692-94; 16696; 16699-700), 4 ♂♂ (16695; 16697-98; 16703); 15 km. SE Tonalá, 100 ft., 1 ♂ (14437); Yaxoquintela, 27 km. NE Altamirano, 590 m., 1 ♂ (9296). GUATEMALA: *Alta Verapaz*: Río San Simón, 6 km. NE Roxrujá, 140 m., 1 ♂ (17707). *Izabal*: 25 km. SSW Puerto Barrios, 300 ft., 2 ♀♀ (17714; 17718), 5 ♂♂ (17712-13; 17715-17). EL SALVADOR: *Cuscutlán*: 1.2 mi. W Suchitoto, 390 m., 1 ♀ (TTU 12994). *La Libertad*: La Libertad, 25 ft., 1 ♀ (TTU 28219); *Usulután*: Usulután [ca. 500 ft.], 1 ♀ (TTU 28240). HONDURAS: *Atlántida*: 7 mi. E La Ceiba, 100 ft., 1 ♀ (14765), 1 ♂ (14766); 9 mi. W La Ceiba, 25 ft., 10 ♀♀ (14761; 14753-57; 14759; 14761; 14763-64), 2 ♂♂ (14758; 14766); Lancetilla, 40 m., 5 ♂♂ (24022-26); 1 mi. W Tela, sea level, 2 ♀♀ (14730; 14732); 3 ♂♂ (14731-32; 14735); 3 mi. E Tela, sea level, 1 ♂ (14750); 4 mi. SW Tela, 25 ft., 10 ♀♀ (14738-46; 14749), 3 ♂♂ (14737; 14747-48); 8 mi. W Tela, 25 ft., 1 ♂ (14736). *Copán*: Copán, 660 m., 11 ♀♀ (19528-32; 19534-38; 19976, skel. only), 10 ♂♂ (19518-27); Ruinas de Copán, 900 m., 2 ♀♀ (10932; 10934), 1 ♂ (10933). *Cortes*: 1 mi. N Jaral, 2000 ft., 2 ♀♀ (LSU 9018-19), 1 ♂ (LSU 9020); 2 mi. W San Pedro Sula, 100 ft., 2 ♀♀ (10935; 10937), 1 ♂ (10936); 12 mi. W San Pedro Sula, 1 ♀ (14767). *Gracias A Dios*: vic. Brus Laguna, 25 ft., 11 ♀♀ (24545; 24548; 24552; 24554-58; 24560-61; 24563), 6 ♂♂ (24543-44; 24546; 24550; 24559; 24562). *Olancho*: 6 mi. SE Catacamas [ca. 1000 ft.], 2 ♀♀ (TTU 28242; 28245), 6 ♂♂ (28241; 28243-47); 40 km. E Catacamas, 500 m., 3 ♂♂ (19539-41). Río Coco, 78 mi. ENEE Danlí, 900 ft., 11 ♀♀ (9674-84), 9 ♂♂ (9668-73; 9724-26). *El Paraíso*: Chichicaste, 480 m., 2 ♀♀ (22026-27), 1 ♂ (22025); 7 km. E Danlí, 620 mi., 3 ♂♂ (22022-24); 21 mi. E Danlí, 460 m., 3 ♀♀ (22019-21), 2 ♂♂ (22017-18). *Santa Barbara*: 7 km. N Santa Barbara, 120 m., 15 ♀♀ (19473; 19477; 19479-85; 19487; 19513-14; 19517; 19573-74), 9 ♂♂ (19457; 19459-65; 19472); 12 km. N Santa Barbara, 100 m., 2 ♀♀ (TTU 13002-03). NICARAGUA: *Boaco*: San Francisco, at K 92 on Rama Road, 400 ft., 1 ♀ (8655). *Estelí*: 2 mi. S. Estelí, 3300 ft., 1 ♀ (8654), 1 ♂ (8653). *Madriz*: Yalaguina, 2300 ft., 3 ♀♀ (8651-52; 21203), 4 ♂♂ (8649-50; 21209-10). *Río San Juan*: El Castillo, 40 m., 10 ♀♀ (19494-95; 19498-505), 4 ♂♂ (19490-93); 1 km. S El Castillo, 150 m., 2 ♀♀ (19496-97). *Zelaya*: Cacao, 22 km. W Muelle de los Bueyes, 400 ft., 3 ♀♀ (8656-68); 1 ♂ (8659); 4.5 km. NW Rama, 100 m., 1 ♀ (35107), 2 ♂♂ (TTU 12995-96); 7.3 mi. W Rama, 4 ♂♂ (12997-13000); 10 km. W Rama, 50 m., 5 ♀♀

(19545-49), 3 ♂♂ (19542-44). COSTA RICA: *Cartago*: Moronia, 1116 m., 1 ♀ (UMMZ 112018). *Puntarenas*: Dominical, nr. sea level, 1 ♀ (UMMZ 112021); 4 mi. NE Palmar, 100 ft., 1 ♂ (9667); 9 mi. ENE Puerto Gullfó, 100 ft., 8 (7 skull only) ♀♀ (9666, 9713a-9713h), 3 ♂♂ (9663-9665). *San José*: Colorado, 1 ♀ (LSU 11480). PANAMA: *Veragues*: 2 mi. S San Francisco, 200 ft., 3 ♀♀ (9653; 9657; 9660), 1 ♂ (9652). *Canal Zone*: Corozal, 1 ♂ (UMMZ 105859). COLOMBIA: *Cauca*: Popayán, 6400 ft., 3 ♀♀ (12317-19), 2 ♂♂ (12135-16). VENEZUELA: *Miranda*: 27 km. N Altagracia de Orituca, 2200 ft., 3 ♀♀ (10277-78; 10288), 2 ♂♂ (10287; 10289). TRINIDAD: LaBrae, 1 ♀ (6308). Manzanillo, 1 ♂ (LSU 13635). Port of Spain, 5 ♀♀ (LSU 3561; 3564; 3566; 3572; 3574), 3 ♂♂ (LSU 3557; 3567-68).

*Specimens examined and referred to Artibeus lituratus lituratus.*—BRASIL: *Rio de Janeiro*: Univ. Rural, Municipio do Itaguaí, 6 ♀♀ (22823; 22662-66), 3 ♂♂ (22824-26). PERU: *Loreto*: Centro Unión, 10 km. SE Iquitos, 2 ♀♀ (27425-26); Mishana, 34 km. WNW Iquitos, 3 ♀♀ (27428; 29585; 29587), 4 ♂♂ (27427; 29586; 29589-80); Pucallpa, 500 ft., 1 ♂ (12320); 27 mi. ESE Pucallpa, 500 ft., 1 ♀ (12322), 2 ♂ (12321).

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