

# THE LARGE FRUIT BATS (GENUS *ARTIBEUS*) OF MIDDLE AMERICA, WITH A REVIEW OF THE *ARTIBEUS JAMAICENSIS* COMPLEX

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ABSTRACT.—Useful characters for identification of Middle American representatives of *Artibeus inopinatus*, *Artibeus hirsutus*, *Artibeus jamaicensis*, and *Artibeus lituratus* are discussed and a synoptic key to the four species is presented.

Geographic variation and differentiation in Middle American *Artibeus jamaicensis* are discussed. The study is based on examination of nearly 1600 specimens, 1300 of which are in the Texas Cooperative Wildlife Collection. Four areas of differentiation are recognized.

(1) The humid tropical and subtropical areas of the Atlantic versant from northern Chiapas southeastward to eastern Panamá. In this area the bats are large, dark in color, and have 2/3 (two upper and three lower) molars. A suitable name for this population is *Artibeus jamaicensis richardsoni* J. A. Allen.

(2) The comparatively drier coastal plains and offshore islands from Tamaulipas, México, southeastward to the Yucatán Peninsula, British Honduras and the Bay Islands of Honduras. Bats in this area are small in size, have 2/3 molars and are dark in color except in the northern part of the region where they tend to become wood brown. A suitable name for this population is *Artibeus jamaicensis yucatanicus* J. A. Allen.

(3) The relatively dry Pacific slopes of México from Oaxaca north to Sinaloa. There the bats are small in size, wood brown in color, and more than 95 per cent of the population has 3/3 molars in contrast to the 2/3 usually found elsewhere in Middle America. A suitable name for this population is *Artibeus jamaicensis triomylus* Handley.

(4) The drier interior and Pacific slopes from eastern Oaxaca southeastward to the Guanacaste region of Costa Rica. There the bats are small in size, wood brown in color, and more than 95 per cent of the population has 2/3 molars. The smallest of all Middle American *A. jamaicensis* are found in this population and a new name for it is proposed.

Four species of large fruit bats of the genus *Artibeus* occur in Middle America. Arranged in ascending order of size, they are *Artibeus inopinatus* Davis and Carter, *Artibeus hirsutus* Andersen, *Artibeus jamaicensis* Leach, and *Artibeus lituratus* Olfers. Although this report is concerned primarily with *A. jamaicensis*, it seems advisable to discuss briefly the other three species because of the difficulty some workers have in making satisfactory determinations. All measurements are in millimeters.

*Artibeus inopinatus* is by far the smallest of the group and can readily be identified in the field by its pale gray coloration, short forearm (48–53), and the slight fringe of hair on the edge of the uropatagium near the midline. This fringe is less conspicuous than it is in *A. hirsutus*, but is clearly discernible. Small size alone, however, will not separate *inopinatus* from a local population of *A. jamaicensis* in the coastal region of El Salvador where some individuals have a forearm as short as 50. One must then rely on other characters, such as

coloration, number of molars (3/3 in *inopinatus*; usually 2/3 in *jamaicensis* from this region) and the presence or absence of the uropatagial fringe.

*Artibeus hirsutus* can readily be identified in the field by the presence of a conspicuous fringe of hairs on the edge of the uropatagium; molars are 3/3. It occurs sympatrically in western México with *Artibeus jamaicensis triomylus* Handley, which resembles *hirsutus* in size, color, and number of molars, but lacks the uropatagial fringe.

Because of the substantial geographic variation present in *Artibeus jamaicensis* in Middle America and the fact that it occurs sympatrically with each of the other three species treated here, the identification of individual specimens is by no means a simple task for the uninitiated. This is especially true when one is dealing with specimens of *jamaicensis* and *lituratus*, the two largest species of *Artibeus* in the region. However, there are a number of morphological features which, when used in combination, readily separate the two.

Most useful in the field are (1) the "frosted" appearance of the underparts of *jamaicensis* as contrasted with the nearly uniform "chocolate" coloring of *lituratus*, (2) obscure facial stripes in *jamaicensis* (prominent, in *lituratus*), and (3) the degree of adherence of the skin to the pectoral muscles. In the more than 100 *lituratus* I have personally prepared as study specimens, the skin was so firmly attached to the breast muscles that I had considerable difficulty in removing it. After skinning eight to 10 specimens, the base of my thumb nail was painfully sore from the continuous pressure exerted on it in the skinning process. In *jamaicensis* the skin is loosely attached to the pectoral muscles and can easily be separated from them. I believe a blindfolded person could identify with complete accuracy all specimens of these two species on the basis of this morphological difference alone.

In the laboratory, cleaned skulls provide several cranial differences that are useful in separating them. These are included in the diagnostic key presented below. A simple "mechanical separator" is a skull vial with an inside diameter of 18.5 mm. Skulls of more than 90 per cent of the several hundred adult *jamaicensis* examined from Middle America fit easily in this size vial. The reverse is true for *lituratus*; less than 10 per cent of the several hundred skulls examined will fit in that size vial.

Length of forearm is not a completely reliable indication of identity of all Middle American representatives of these two species although the forearm is normally longer (63–75) in *lituratus* than it is in *jamaicensis* (50–66). In most of Middle America the two can be separated in the field by forearm length alone, but in the Atlantic versant from Chiapas to Panamá, where the largest representatives of *jamaicensis* in Middle America occur, mean length of the forearm usually exceeds 60, frequently exceeds 64, and reaches 66 in some individuals. Pirlot (1968) also found that in Venezuela, length of forearm alone was of only fair reliability in separating the two species in the field.

Greatest length of skull likewise is not a completely reliable measurement for separating the two species in Middle America. In *lituratus* this measure-

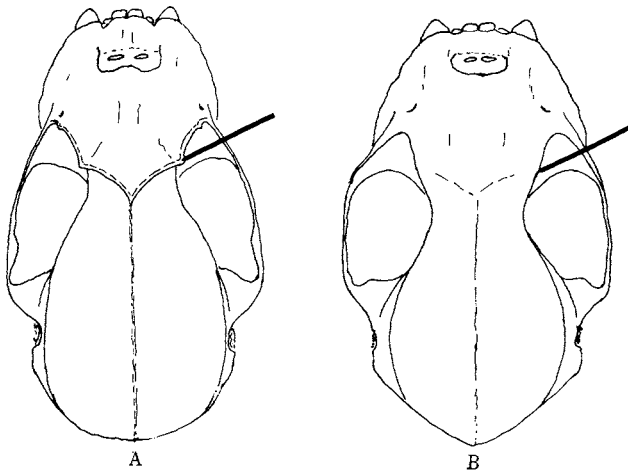


FIG. 1.—Outline drawings, dorsal view, of the skulls of *Artibeus lituratus* (A) and *Artibeus jamaicensis* (B). Note the prominent pre- and postorbital processes and the distinct beading converging to meet the sagittal crest in *lituratus*. These features normally are absent in *jamaicensis*.

ment usually exceeds 30; in most specimens of *jamaicensis* it is less than 29, but in the population of *jamaicensis* inhabiting the Atlantic versant, particularly from Nicaragua to Panamá, the skulls of many individuals exceed 30 and the largest examined measures 32.1. Consequently, in final analyses one must rely on other than mensural characters to be sure of identification. The following diagnostic key enumerates characters which, when taken in combination, I have found useful in making determinations of these four species.

#### DIAGNOSTIC KEY TO THE LARGER MIDDLE AMERICAN FRUIT BATS, GENUS *ARTIBEUS*

1. Edge of uropatagium with a noticeable fringe of hairs, particularly in the postanal region; greatest length of skull usually less than 27; molars 3/3. .... 2
- Edge of uropatagium naked or nearly so; greatest length of skull usually more than 27; number of molars normally 2/3, except in *A. j. triomylus* in which it is normally 3/3. .... 3
2. Smaller, forearm near 52 (48–53); greatest length of skull near 25.5 (25–26); maxillary tooththrow less than 9.5 (8.8–9.2); apparently confined to the Pacific lowlands of El Salvador, Honduras and Nicaragua. .... *Artibeus inopinatus*
- Larger, forearm near 56 (51–59); greatest length of skull near 27 (26.0–27.5); maxillary tooththrow near 10 (9.8–10.0); restricted to western México from Guerrero and Morelos north to Sonora. .... *Artibeus hirsutus*
3. Underparts usually seal brown without “frosting”; facial stripes prominent; size large, forearm near 68 (63–75); skull large, the greatest length usually more than 30, and with prominent postorbital and preorbital processes, these united with a beading that traverses the frontal region obliquely and meets the prominent sagittal crest (see Fig. 1); molars normally 2/3 (one exception in 201 specimens examined); skin so firmly attached to flesh in pectoral region that it is quite difficult to remove. .... *Artibeus lituratus*

Undeparts variable in color geographically but always "frosted"; facial stripes obscure, skull usually lacks prominent preorbital and postorbital processes, but old individuals may have them weakly developed; number of molars variable geographically (3/3 in western México, normally 2/3 in other parts of Middle America); forearm usually less than 62 (50-66); skin in pectoral region not firmly attached to flesh. -----

----- *Artibeus jamaicensis*

### **Artibeus jamaicensis**

Because of the large number of *A. jamaicensis* that have become available in the Texas Cooperative Wildlife Collections as one result of a five-year research program we have conducted on the bats of Middle America, it became necessary to determine their identity and to evaluate the considerable variation that was evident in the assemblage. Handley's review (1965) adequately treated the *triomylus* segment, but his referral of all other middle American *jamaicensis* to the subspecies *yucatanicus* cannot be reconciled with the geographic variation present in our material.

### MATERIALS

The present study is based on examination of 1599 specimens of *A. jamaicensis*, 26 from the island of Jamaica and the balance from Middle America. Of this total, 1300 are deposited in the Texas Cooperative Wildlife Collections, Department of Wildlife Science, Texas A & M University. They are listed as "*specimens examined*" under each subspecies account without designation. Specimens deposited in other collections are designated as follows: AMNH, American Museum of Natural History, New York; BJH, Private collection of Bruce J. Hayward, Silver City, New Mexico; KU, University of Kansas Museum of Natural History, Lawrence; LACM, Los Angeles County Museum of Natural History; LSU, Louisiana State University Museum of Zoology, Baton Rouge; UA, University of Arizona Department of Zoology, Tucson; UO, University of Oklahoma Stovall Museum, Norman.

The sample of 26 specimens from the island of Jamaica are deposited in the American Museum of Natural History, New York; Department of Biology, Colgate University, Hamilton, N. Y.; and the University of Florida State Museum, Gainesville. To the individuals in charge of the several collections from which I examined specimens, I express my appreciation for their cooperation and assistance.

No attempt was made to examine all of the Middle American specimens of *jamaicensis* available in American collections because I felt that most of them would merely duplicate material already examined.

### VARIATIONS

*Sexual variation.*—I have been unable to detect significant sexual differences in measurements or coloration in any of the available samples. Consequently, data relating to both sexes have been combined in the statistical analyses.

*Age variation.*—Obviously young individuals in which the cartilaginous epiphyses of the finger joints are readily discernible are consistently smaller in all measurements than adults. But those juveniles in which the finger joints are merely swollen and in which the epiphyses and diaphyses appear to be united are as large as adults in all mensural features. Apparently juveniles attain adult proportions within 3 to 4 months after birth. Therefore, in this species only those individuals in which the epiphyses are distinctly separated from the diaphyses need to be segregated for statistical treatment.



FIG. 2.—Dorsal view of the skulls of two adult males of *Artibeus jamaicensis* to illustrate extremes in size in specimens from Middle America. No. 19636, from El Castillo, Nicaragua, is referable to the population herein designated as *A. j. richardsoni*; no. 7408, from near La Libertad, El Salvador, is from the population herein named as a new subspecies.

*Seasonal variation.*—At the few localities from which specimens are available from more than one season of the year, no seasonal variation in color or in length of pelage is discernible.

*Individual variation.*—Within samples, variation in cranial measurements, based on five samples, selected at random, of 20 individuals each, is usually less than 10 per cent of the minimum value of each variate tested. Among six cranial variates, length of skull varied least (mean variation of 7.1 per cent and extremes of 6.0 and 8.5 per cent) followed by: zygomatic breadth, 7.6 (4.8–10.6); length of maxillary toothrow, 8.1 (6.7–9.4); length of mandibular toothrow, 8.3 (4.8–9.6); length of palate, 9.7 (8.8–11.0) and width across second upper molars, 10.1 (7.9–13.2). Wing measurements are more variable. Among these, length of forearm is least variable with a mean variation in the five samples of 11.0 (8.7–15.7) per cent, followed by length of metacarpal III, 12.6 (10.5–19.2); length of phalanx 2, d III, 15.3 (9.4–18.6) and length of phalanx 1, d III, 15.6 (12.5–17.9).

*Geographic variation.*—Variations in color and mensural values are moderate within samples, but, depending on geographic position, they are much more extreme between samples than I had anticipated. Extent of variation in size

of skull between samples is best illustrated in Fig. 2, in which two adult males are compared. The one on the left (19636) is from El Castillo on the Río San Juan in the Atlantic versant of Nicaragua; that on the right (7408), from near La Libertad on the Pacific coast of El Salvador. The largest skull in the sample of 20 from El Castillo is 31.6 in length (mean length of sample, 30.07); the smallest skull in the sample of 20 from near La Libertad, 26.2 (mean length of sample, 27.27). Thus, the difference between the longest and shortest skulls in the two samples is 5.4 or 20.6 per cent of the lesser value. This percentage is more than twice as great as the maximum (8.5) found within samples. Difference between the means of these two samples (10.1 per cent) is also greater than the variation within them (8.5 and 7.6 per cent, respectively).

Further evidence of variation between samples is depicted in Fig. 3, in which length of forearm in 17 samples is compared. Furthermore, samples from the mesic Atlantic versant of Middle America are noticeably darker, more blackish, than those from the xeric Pacific segment.

The number of molars in *jamaicensis* varies geographically. In those bats that occupy the Pacific versant of México (from southwestern Oaxaca northward) the normal complement is 3/3 (70 of 71 specimens for which data are available). Throughout the remainder of Middle America the normal complement is 2/3. In 725 specimens from other sections of Middle America for which data are available, 691 or 95.3 per cent have 2/3 molars; in 10 specimens (1.4 per cent) the number is 2/2; in seven individuals (1.0 per cent) the number is 2/2 on one side and 2/3 on the other; in nine individuals (1.2 per cent) the number is 2/3 on one side and 3/3 on the other, and in only eight individuals (1.1 per cent) is a full complement of 3/3 present. Thus, despite variability in the number of molars, the high degree of constancy of a particular combination (3/3 or 2/3) geographically merits recognition as a useful character in systematic studies of this species of *Artibeus*.

Because geographic patterns of variability are discernible in this species, one must conclude that individual subpopulations are more or less sedentary and that isolating barriers prevent free gene flow throughout the entire population in Middle America. At any rate, differences associated with geographic position have developed. This is well illustrated when one compares the small *jamaicensis* occupying the Islas de la Bahía, situated 20 to 30 miles off the north shore of Honduras, with the much larger bats on the adjacent mainland.

Because *jamaicensis* occupies an altitudinal range in Middle America from sea level to about 6000 feet, no topographical barrier separates the bats occupying the Atlantic lowlands from those of the Pacific except in regions where the mountains exceed elevations of 6000 to 7000 feet. Consequently, one might expect free gene flow between populations occupying the Atlantic and Pacific versants in such places as Honduras and El Salvador where the mountains of the interior highlands are relative low. But such is not the case. Bats occupying the Atlantic lowlands in this region are considerably larger and darker than those occupying the Pacific lowlands of El Salvador. However, there is a more

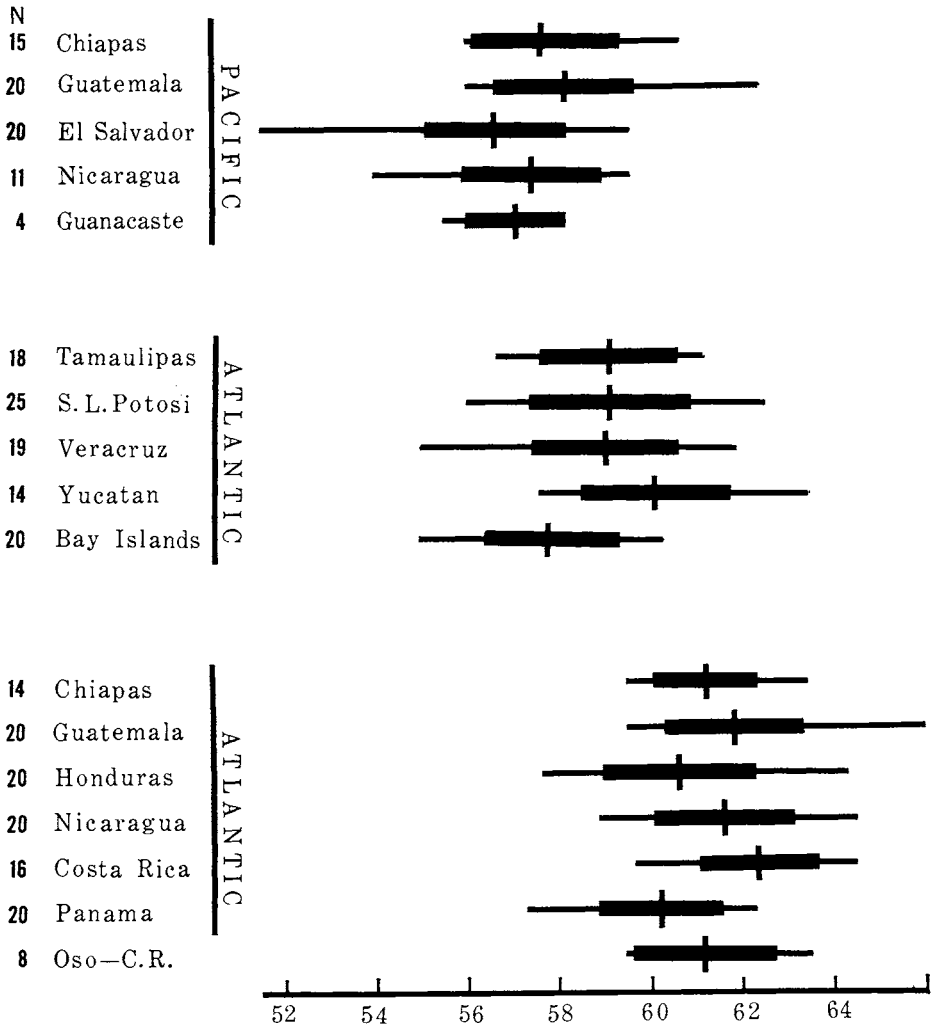


FIG. 3.—Geographic and individual variation in length of forearm in 17 samples of Middle American *Artibeus jamaicensis*. The wide black bar represents one standard deviation above and below the mean (cross bar) of the sample; range of individual variation within samples is indicated by the narrow line.

or less gradual change from one to the other, which I interpret as intergradation. This is well illustrated in Fig. 4 in which length of skull is plotted against zygomatic breadth in four samples taken in a north-south transect from the Atlantic lowlands of Honduras and Guatemala to the Pacific lowlands of El Salvador. Parameters outlined by the "box" in the figure are a skull length of 28.45 (vertical) and a zygomatic breadth of 17.05 (horizontal). Note that along the Atlantic coast (A) 46 (88.5 per cent) of the 52 bats in the sample have a

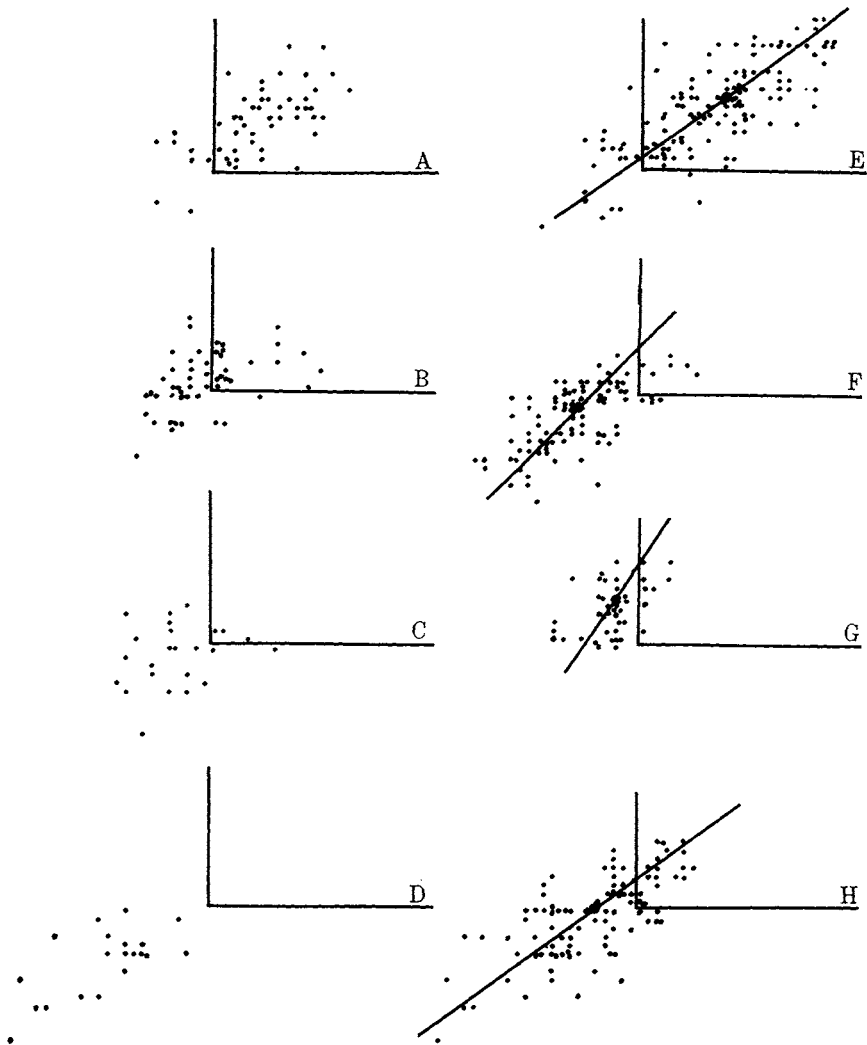


FIG. 4.—Length of skull plotted against zygomatic breadth in samples of Middle American *Artibeus jamaicensis*. Vertical line of the “box” represents a skull length of 28.45; horizontal line, a zygomatic breadth of 17.05. A to D represent four samples from a belt transect from north (top) to south across Middle America. A is a sample of 52 individuals from the north coast of Guatemala and Honduras; B, a sample of 52 from Santa Barbara, Copán, and Comayagua, Honduras, north of the continental divide; C, a sample of 24 from Nueva Ocotepeque, La Esperanza, and Marcala, south of the continental divide in Honduras; D, a sample of 20 from near La Libertad in the Pacific lowlands of El Salvador.

The right hand figures (E–H) represent combined samples from belts paralleling the two coast lines. E is a sample of 127 individuals from the humid tropical forest area of the Atlantic versant from Chiapas to Costa Rica. Notes that most of the individuals fall above the parameters of the “box.” F is a sample of 93 individuals from the drier parts of the Atlantic versant from Tamaulipas, México, to British Honduras. G is a sample of



skull length exceeding 28.45 combined with a zygomatic breadth exceeding 17.05. In the coastal region of El Salvador (D), however, all of the sample of 20 adults are below the outlined parameters. In the sample of 24 plotted in (C) from Nueva Ocotepeque, La Esperanza, and Marcala, all of which are on the Pacific side of the continental divide in Honduras, only three individuals (12.5 per cent) exceed those parameters, whereas of the 52 specimens from Santa Barbara, Copán, and Comayagua on the Atlantic side of the continental divide in central Honduras, 18 (34.6 per cent) exceed those parameters.

When one plots the same data for samples from transects paralleling the two coast lines, definite geographic patterns develop in which the bats within each transect are more or less alike, yet different from those in the other transects. This is clearly evident in Fig. 4 and Tables 1 to 3. Note that in the top section (E) of the chart, based on a sample of 127 adults from northern Chiapas (Mal Paso) southeastward along the coast from Guatemala to Costa Rica, 107 (84.3 per cent) of them exceed the parameters of 28.45 and 17.05. This pattern probably occurs also throughout Panamá, but I have seen specimens from too few localities to verify this assumption. In a sample of 24 adults from the Pacific side of the Department of Veraguas, 20 (83.3 per cent) of them exceed those parameters; in a sample of 21 from Chepó, east of the Panamá Canal, 76.2 per cent of them exceed the parameters. The same relationship is found in the bats of southeastern Costa Rica from the Panamanian border as far westward as the vicinity of Puntarenas. In addition to large size, bats falling into this pattern are dark in color, often nearly black. An acceptable name for this population is *Artibeus jamaicensis richardsoni* J. A. Allen.

A second pattern is found in the Gulf coastal region from British Honduras and Yucatán northward to Tamaulipas. In a sample of 93 specimens from this transect (see Fig. 4, F) only six (6.5 per cent) exceed the parameters mentioned above. In this group those bats from the southern half of the area involved are dark in color like those in the first-mentioned pattern, but from San Luis Protosí northward they become paler. Bats from the islands of Roatan and Guanajo off the northern coast of Honduras fit into this pattern. In a sample of 40 adults from these islands only one of them exceeded the parameters here used. A suitable name for this population is *Artibeus jamaicensis yucatanicus* J. A. Allen.

A third pattern is found in the Pacific versant of México (from Guerrero northward) in which 98 per cent of the bats have 3/3 molars as opposed to the 2/3 condition usually found elsewhere in Middle America. In addition, these bats are relatively small and pale in color. Handley (1966) recognized this

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43 individuals from the Pacific lowlands of Nayarit and Guerrero, México. Note that none of this sample has a zygomatic breadth less than 17.0. H is a sample of 94 individuals from the relatively dry interior and Pacific slopes from Chiapas southeastward to the Guanacaste region of Costa Rica. Samples E and H are from opposite coastal areas.

population as distinct and named it *triomylus* in allusion to the full complement of molars.

A fourth pattern (Fig. 4, H) is found in the Pacific lowlands from Chiapas to the Guanacaste region of Costa Rica. In a sample of 94 from this region 18 (19.1 per cent) exceed the parameters, but of those from the coastal region of El Salvador none exceeds them. In fact, the smallest individuals of *jamaicensis* handled in this study are from the Pacific coastal region of Guatemala and El Salvador. In addition to generally small size, bats from this region are pale in color. This population appears to be without a name and is described and named beyond.

*Artibeus jamaicensis richardsoni* J. A. Allen

*Holotype*.—Adult male, skin and skull, no. 28335 American Museum of Natural History, collected on 3 January 1906, at Matagalpa, Nicaragua, by W. B. Richardson.

*Distribution*.—In general, the Atlantic versant of Middle America, exclusive of the Yucatán Peninsula, from northern Chiapas, México, southeastward into Panamá, thence westward along the Pacific coast to the vicinity of Puntarenas, Costa Rica (see Fig. 5).

*Diagnosis*.—Largest (see Tables 1–3) and darkest of the Middle American *jamaicensis*. Greatest length of skull near 29, length of palate (to front of incisors) usually 14 or more, mean length of forearm (including carpals) near 61.

*Remarks*.—The skull of the holotype of *richardsoni* is larger in many respects than the average of 13 topotypes, but the wing elements are shorter. This is evident in the following measurements in which those of the type are given first, followed by the means and extremes (in parentheses) of the topotypes: greatest length of skull, 29.4, 29.04 (28.0–30.2); zygomatic breadth, 17.0, 17.62 (16.9–18.8); maxillary toothrow, 10.7, 10.35 (9.9–10.7); width across M2–M2, 12.6, 12.88 (12.1–13.5); length of palate (to front of incisors), 14.8, 14.15 (13.6–15.0); mandibular toothrow, 11.7, 11.38 (10.8–11.8); length of mandible, 20.3, 19.81 (19.0–20.4); forearm, 53.9, 59.41 (55.6–62.1); metacarpal III, 49.5, 55.8 (52.3–57.8); phalanx 1, d III, 14.6, 17.28 (16.0–18.2); phalanx 2, d III, 27.2, 28.80 (27.0–30.8). Since I measured both the type and the series of topotypes, measurements are comparable. The type has 2/2 molars on one side; 2/3 on the other. All topotypes except one have 2/3 molars on both sides; the exception has a molar formula of 2/3–3/3.

In applying the name *richardsoni* to this population of *jamaicensis*, it should be pointed out that bats from Matagalpa, as well as from Yalaguina and Dario, are paler than individuals from the Caribbean coastal area of Nicaragua. This difference appears to be associated with environmental conditions that result from differences in rainfall. The coastal region has a much heavier rainfall than the Matagalpa region even though the latter is situated north of the continental divide in the Atlantic versant.

Andersen (1908), first reviewer of the genus, divided the large Middle American *Artibeus*, exclusive of *A. hirsutus* Andersen, into two species on the basis of the number of molars. He assigned those bats with 3/3 molars to *Artibeus planirostris* Spix and those with 2/3 molars to *Artibeus jamaicensis* Leach. In so doing, he placed *Artibeus lituratus* Olfers as a subspecies of *jamaicensis*. Hershkovitz (1949) recognized this error, pointed out that the presence or absence of the small M3 is not constant throughout the range of any one of these bats and concluded that this "character" has no value as a criterion on which to separate species of these bats. In essence, he placed the larger of these bats in one species (*A. lituratus*) and the smaller ones in a second species (*A. jamaicensis*). He considered *A. planirostris* a subspecies of the latter. I concur with this arrangement.

At the same time, Hershkovitz (*op. cit.*) placed *Artibeus jamaicensis richardsoni* as a synonym of *Artibeus jamaicensis jamaicensis* Leach from the island of Jamaica, but he recognized *Artibeus yucatanicus* J. A. Allen as a valid subspecies of *A. jamaicensis*. In so doing,

TABLE 1.—Mean measurements in millimeters of nine samples of *Artibeus jamaicensis richardsoni* from Middle America.

Variable	Chiapas (near Mal Paso)	Guatemala (Alta Verapaz)	Guatemala (Puerto Barrios)	Honduras (Coastal)	Topotypes of <i>richardsoni</i>	Nicaragua (Castillo)	Costa Rica (Coastal)	Panamá (Veraguas)	Panamá (Chepó)
Sample size	14	12	20	20	13	20	16	20	21
Greatest length of skull	28.94	28.77	29.03	28.99	29.04	30.07	29.96	29.20	28.83
Zygomatic breadth	17.54	17.62	17.64	17.64	17.62	18.23	18.30	17.88	17.42
Postorbital constriction	7.22	7.28	7.24	7.36	7.18	7.38	7.44	7.31	7.14
Maxillary toothrow	10.18	10.20	10.35	10.32	10.35	10.70	10.81	10.49	10.46
Width across M2–M2	12.79	12.74	12.97	12.81	12.88	13.34	13.50	13.06	13.03
Length of palate	14.17	14.16	14.16	14.15	14.15	14.76	14.82	14.51	14.20
Length of mandible	19.88	19.61	19.84	19.72	19.81	20.60	20.64	20.38	19.87
Mandibular toothrow	11.17	11.16	11.35	11.28	11.38	11.77	11.86	11.56	11.42
Forearm	61.25	62.42	61.85	60.61	59.41	61.61	62.39	60.21	60.42
Metacarpal III	57.43	58.25	57.74	57.12	55.88	57.92	58.46	56.88	56.43
Phalanx 1, d III	17.91	18.53	18.10	17.97	17.28	18.30	18.56	17.80	17.66
Phalanx 2, d III	29.46	30.52	30.31	30.18	28.80	30.38	30.77	29.59	30.13

he ascribed to *A. j. jamaicensis* a distribution that includes not only the island of Jamaica, but also the major portion of Middle America. Although several authors have followed Hershkovitz in this regard, I cannot accept this arrangement for several reasons. In the first place, Jamaica is more than 400 miles from the closest part of Middle America and, because of the comparatively sedentary habits of these bats, there is little possibility at present of gene flow between the bats on Jamaica and those in Middle America. Furthermore, the populations of *jamaicensis* currently occupying the Gulf and Caribbean coastal areas of Middle America (*yucatanicus* and *richardsoni*) are readily distinguished from Jamaican specimens on the basis of darker, more blackish, coloration and a lesser width across the postorbital processes.

Gravid females of *richardsoni* have been taken in the months of February, March, April, May, July, August, and December. In all instances save one a single embryo was present; the exception involved twins.

*Specimens examined* (total number of 641).—MEXICO. *Chiapas*: 10 mi. W Mal Paso, 400 ft, 2 ♂♂, 7 ♀♀; 6 km NE Mal Paso, 400 ft, 1 ♂ (alc. plus skull), 2 ♀♀, 5 km ESE Pichucalco, 200 ft, 1 ♂, 2 ♀♀ (1 alc.); 21 km WSW Teapa (Tabasco), 200 ft, 1 ♂; 3 mi. SSE Soyalo, 3000 ft, 1 ♂, 2 ♀♀; Florida, 50 km E Altamirano, 1700 ft, 4 ♂♂, 5 ♀♀; Yaxoquintela, 37 km NE Altamirano, 1900 ft, 1 ♀; La Soledad, 16 mi. NE Las Margaritas, 3600 ft, 1 ♂, 1 ♀ (UA); 8 km S Solosuchiapa, 400 ft, 4 ♂♂, 1 ♀ (UA). *Tabasco*: 1–3 mi. E Teapa, 49 ♂♂, 25 ♀♀ (LSU). GUATEMALA. *Alta Verapaz*: Chinaja, 550 ft, 2 ♂♂, 5 ♀♀ (KU); Languin Cave [= Languin], 1022 ft, 2 ♂♂, 6 ♀♀ (KU); 1 km W Coban, ca. 3500 ft, 1 ♀ (alc., KU); Finca Los Alpes (ca. 20 km S Languin), 3250 ft, 1 ♂ (alc., KU); Río San Simon, 6 km NE Raxrujá, 450 ft, 3 ♂♂, 9 ♀♀; 10 mi. N Sebol, 900 ft, 3 ♂♂, 1 ♀. *Izabal*: 25 km SSW Puerto Barrios, 300 ft, 9 ♂♂, 21 ♀♀. HONDURAS. *Cortes*: 8 mi. SW San Pedro Sula, 500 ft, 1 ♀. *Santa Barbara*: 7 km N Santa Barbara, 400 ft, 9 ♂♂ (4 alc.), 16 ♀♀ (8 alc.). *Copán*: Copán, 2145 ft, 16 ♂♂ (5 alc.), 14 ♀♀ (6 alc., 1 skel.); 5 km E Santa Rita, 2440 ft, 1 ♀. *Intibucá*: 5 km NE Jesus de Otoro, 2100 ft, 1 ♂. *Atlantida*: 1 mi. W Tela, sea level, 3 ♂♂ (2 alc.), 1 ♀ (alc.); Lancetilla, 100 ft, 3 ♂♂, 2 ♀♀; 17 mi. W La Ceiba, 50 ft, 1 ♂, 1 ♀; 9 mi. W La Ceiba, 25 ft, 13

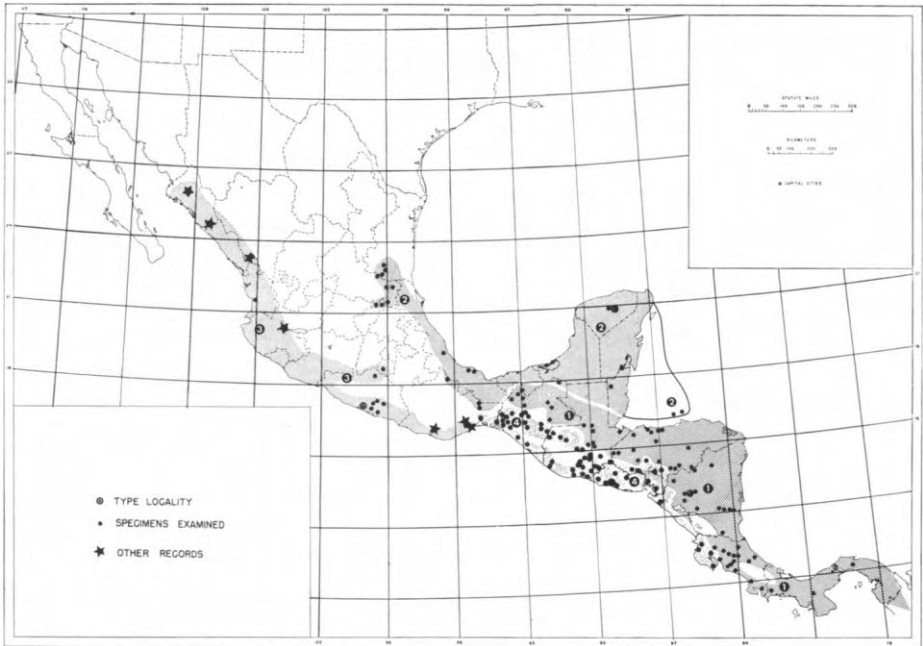


FIG. 5. Map of Middle America showing the distribution of the four recognized subspecies of *Artibeus jamaicensis*: 1, *Artibeus jamaicensis richardsoni*; 2, *Artibeus jamaicensis yucatanicus*; 3, *Artibeus jamaicensis triomylus*; 4, *Artibeus jamaicensis paulus*.

♂♂, 4 ♀♀. Yoro: 8 km W Yoro, 2210 ft, 2 ♂♂, 1 ♀; 3 km W Yoro, 2275 ft, 3 ♂♂, 2 ♀♀. *Francisco Morazan*: 10 mi. NE Talanga, 3400 ft, 1 ♂, 1 ♀. *Olancho*: 40 km E Catacamas, 1625 ft, 33 ♂♂ (19 alc.), 46 ♀♀ (23 alc.); Río Coco, 78 mi. ENE Danlí, 900 ft, 1 ♂, 6 ♀♀. *El Paraiso*: 6–7 km E Danlí, 2210 ft, 7 ♂♂, 12 ♀♀; 21 km E Danlí, 1500 ft, 3 ♂♂, 4 ♀♀; Chichicaste, 1560 ft, 16 ♂♂ (8 alc.), 22 ♀♀ (7 alc.). NICARAGUA. *Zelaya*: 10 km W Rama, 130 ft, 4 ♂♂ (2 alc.); Rama, 50 ft, 1 ♀; Cacao, 22 km W Muelle de las Bueyes, 400 ft, 1 ♂, 2 ♀♀; Bonanza, 850 ft, 6 ♂♂, 2 ♀♀ (KU). *Jinotega*: Río Coco, 87 mi. NNE Jinotega, 900 ft, 2 ♀♀. *Madriz*: Yalaguina, 2300 ft, 2 ♂♂ (1 alc.), 8 ♀♀ (1 alc.). *Matagalpa*: Finca Tepeyac, 10½ km N, 9 km E Matagalpa, 3 ♂♂, 2 ♀♀ (KU); 1–3 mi. W Matagalpa, 2300 ft, 9 ♂♂, 4 ♀♀; 2 mi. SE Dario, 1500 ft, 4 ♂♂, 2 ♀♀. *Boaca*: San Francisco, at K 92, 400 ft, 1 ♂. *Chontales*: 1 km NW La Gatiada [= 25 km ENE Villa Somoza], 1300 ft, 1 ♂, 2 ♀♀. *Río San Juan*: El Castillo, 130 ft, 19 ♂♂ (6 alc.), 21 ♀♀ (4 alc.); 1 km S El Castillo, 425 ft, 1 ♂, 4 ♀♀. COSTA RICA. *Alajuela*: 2 mi. W Alajuela, 3000 ft, 1 ♂, 1 ♀; 18 mi. NE Naranjo, 2900 ft, 2 ♂♂; Santa Clara de San Carlos, 1 ♂ (LSU). *Heredia*: 6 mi. SSE Puerto Viejo, 3 ♂♂ (2 alc.), 1 ♀ (skel.); ½ mi. W Puerto Viejo, 1 ♀ (LSU); 3 mi. N Heredia, 5600 ft, 2 ♂♂. *Guanacaste*: 5 mi. E Tilaran, 2300 ft, 1 ♂, 2 ♀♀ (LSU). *Limón*: Finca La Lola [= 38 km WNW Puerto Limón], 160 ft, 4 ♂♂, 6 ♀♀ (LSU). *Cartago*: Pacure [= Jicotea, 15 km E Turrialba, ca. 2800 ft], 1 ♂ (LSU). *San José*: vicinity Santa Ana, ca. 3600 ft, 4 ♂♂, 2 ♀♀ (LSU); Colorado, 1 ♂, 2 ♀♀ (LSU) (not plotted); Caspirola, 2 ♂♂, 2 ♀♀ (LSU) (not plotted); Cangrejal, 2800 ft, 7 ♂♂, 2 ♀♀ (LSU); 2 km ESE Bajos de Jorco, ca. 3000 ft, 1 ♀ (LSU). *Puntarenas*: 6½ mi. N, 2 mi. W Puntarenas, 100 ft, 3 ♂♂ (alc.), 6 ♀♀ (alc.); 9 mi. ENE Puerto Golfito, 100 ft, 1 ♂, 1 ♀; 1–4 mi. NE Palmar, 300 ft, 2 ♂♂, 3 ♀♀; Julieta, near

TABLE 2.—Mean measurements in millimeters of seven samples of *Artibeus jamaicensis yucatanicus* and one of *A. j. triomylus*.

Variable	Tamaulipas	San Luis Potosí	Veracruz	Campeche and Yucatan	Topotypes	British Honduras	Bay Islands, Honduras	<i>A. j. triomylus</i> (Guerrero)
Sample size	18	25	19	14	8	4	20	20
Greatest length of skull	28.06	27.48	28.18	27.57	27.30	27.65	27.69	28.18
Zygomatic breadth	16.95	16.70	16.97	16.89	16.46	16.80	16.77	17.55
Postorbital constriction	7.20	7.06	7.09	7.19	7.11	7.08	7.06	6.89
Maxillary toothrow	10.02	9.79	9.97	9.70	9.59	9.73	9.80	10.12
Width across M2–M2	12.49	12.36	12.49	12.05	11.81	12.28	12.25	12.71
Length of palate	13.76	13.36	13.76	—	13.10	13.40	13.28	13.66
Length of mandible	19.00	18.82	19.19	18.64	18.16	18.58	18.70	19.12
Mandibular toothrow	10.91	10.77	10.87	10.68	10.40	10.55	10.80	10.89
Forearm	59.10	59.10	59.04	60.11	57.88	59.80	57.85	59.02
Metacarpal III	55.12	55.46	55.31	56.21	53.67	55.78	54.25	54.76
Phalanx 1, d III	17.17	17.00	16.98	17.32	16.57	17.50	16.64	16.51
Phalanx 2, d III	28.64	28.04	27.98	28.78	27.66	28.65	27.00	27.97

sea level, 1 ♂ (LSU). PANAMA. *Chiriquí*: 11 mi. W Concepción, 200 ft, 1 ♀. *Veraguas*: 2 mi. S San Francisco, 200 ft, 9 ♂ ♂, 12 ♀ ♀; 2 mi. W Soná, 200 ft, 2 ♂ ♂, 2 ♀ ♀. *Panamá*: 18 km WSW Chepó, 200 ft, 12 ♂ ♂ (3 alc.), 17 ♀ ♀ (7 alc.).

#### *Artibeus jamaicensis yucatanicus* J. A. Allen

*Holotype*.—Adult male, skin and skull, no. 12038/10469 American Museum of Natural History, collected on 17 March 1896, at Chichén-Itzá, Yucatán, México, by Frank M. Chapman.

*Distribution*.—The Atlantic versant of México from Tamaulipas southward through the Yucatán Peninsula into British Honduras and the Bay Islands of Honduras (see Fig. 5).

*Diagnosis*.—A relatively small (see Tables 1 to 3), dark-colored representative of *A. jamaicensis*. Mean length of skull varying from 27.30 to 28.18 in seven samples (Table 2); mean length of forearm in the same samples varying from 57.85 to 60.11; maxillary toothrow normally less than 10.0; more than 90 per cent of the individuals have a skull length of less than 28.45 combined with a zygomatic breadth of less than 17.05 (Fig. 4 F).

*Remarks*.—Compared with *richardsoni*, *yucatanicus* is smaller in most mensural variates, but is indistinguishable in color except in San Luis Potosí and Tamaulipas where the bats are somewhat paler. The holotype of *yucatanicus* is slightly larger than the average of eight topotypes, measurements of which follow (type first, followed by mean value of the topotypes and extremes in parentheses): greatest length of skull, 28.0, 27.30 (26.7–28.1); zygomatic breadth, 17.2, 16.46 (16.0–17.3); maxillary toothrow, 9.9, 9.59 (9.3–10.0); width across M2–M2, 12.2, 11.81 (11.0–12.4); length of palate, 13.8, 13.10 (12.5–13.9); length of mandible, 18.9, 18.16 (17.5–18.9); mandibular toothrow, 10.8, 10.40 (10.0–11.0); forearm, 58.0, 57.88 (56.0–61.1); metacarpal III, 57.5, 53.67 (51.2–56.5); phalanx 1, d III, 17.0, 16.5 (16.1–17.0); phalanx 2, d III, 29.5, 27.66 (26.2–29.8). The type has 2/3 molars as do all the topotypes except one, which has 2/2.

My first acquaintance with this bat was near Plan del Río, Veracruz, in 1942 when shortly after nightfall I observed in the headlights of my car a narrow stream of bats emerging

from a brushy ravine, rising a few inches above a 30-inch-high "guard rail" on the canyon side of the highway, dropping almost immediately to a height of about a foot above the pavement, crossing the highway, and then disappearing up the slope of the brush-covered hill. The flight lasted about 10 minutes and must have involved several hundred bats. Their flight pattern reminded me of a string of pelicans using the "follow-the-leader" technique in flying over an uneven substrate. It did not vary despite my efforts to knock some of them out of the air with the branch of a bush, and at no time did I see an individual more than 2 feet above the irregular terrain. I later found a colony of several hundred individuals occupying a shallow cave near a waterfall in the ravine about 400 yards from the site where the above observation was made.

I have records of gravid females of this subspecies for the months of March, June, July, and August.

*Specimens examined* (total number of 206).—MEXICO. *Tamaulipas*: Cueva del Abra, 2 mi. W El Abra, 1000 ft, 1 ♂; 30 mi. NNW El Mante, 975 ft, 2 ♀♀; Río Sabinas, Pano Ayuctle (near Gomez Farias), 5 ♂♂, 3 ♀♀ (UO); 4 mi. N Antigua Morelos (near Pachón), 5 ♂♂, 6 ♀♀ (UO). *San Luis Potosí*: 12 km NE Valles, 250 ft, 6 ♂♂, 15 ♀♀ (LSU); El Salto, 2000 ft, 4 ♂♂, 1 ♀ (LSU); Taninul, 650 ft, 1 ♂ (LSU); 3½ mi. NW Xilitla, 2200 ft, 1 ♀. *Queretaro*: Jalpan, 2550 ft, 2 ♂♂; 11 mi. W Jalpan, 2500 ft, 1 ♀. *Veracruz*: Plan del Río, 1 ♂; San Andres Tuxtla, 1200 ft, 1 ♂; 2 mi. E Lago Catemaco, 2 ♂♂, 18 ♀♀. *Oaxaca*: 25 mi. S Tuxtepec, 2 ♀♀ (skin only, LACM); 12–24 mi. N Matias Romero, 1 ♂, 1 ♀, 1 skeleton (LACM); Montebello, 1 (skel., LACM) (not plotted). *Tabasco*: ½ mi. S Balancan, 1 ♂ (LSU). *Campeche*: Ciudad del Carmen, Isla del Carmen, 4 ♀♀ (KU); 1 km SW Puerto Real, 10 ft, Isla del Carmen, 5 ♀♀ (KU). *Yucatán*: Chichén-Itzá, 6 ♂♂, 1 ♀ (alc. plus skull) (AMNH); Oxkintok, 1 ♂ (alc. plus skull) (AMNH) (not plotted); Pisté, 5 ♂♂, 8 ♀♀ (KU), 2 ♂♂. BRITISH HONDURAS. Gallon Jug, 400 ft, 2 ♀♀ (LSU); ¾ mi. E Corazal, 3 ♂♂ (2 skins only), 4 ♀♀ (3 skins only) (LSU). HONDURAS. *Islas de la Bahía*: Roatan Island, 24 ♂♂ (17 alc.), 14 ♀♀ (all alc.); Guanaja Island, 29 ♂♂ (4 alc.), 16 ♀♀ (5 alc.).

#### *Artibeus jamaicensis triomylus* Handley

*Holotype*.—Adult female, skin and skull, no. 126554 U. S. National Museum, collected on 17 April 1903 at Papayo, 25 ft, Guerrero, México, by E. W. Nelson and E. A. Goldman.

*Distribution*.—Endemic to the Pacific versant of México from Oaxaca and Morelos northward to southwestern Durango and northern Sinaloa (see Fig. 5).

*Diagnosis*.—A small, wood brown representative of *jamaicensis* with 3/3 molars; zygomatic breadth seldom less than 17.0.

*Remarks*.—Bats of this subspecies are about the same size as those of *yucatanicus*, but they are paler (less blackish) and more than 95 per cent of the specimens examined have three upper molars in contrast to the two normally found in other Middle American *jamaicensis*. Measurements of the holotype (from Handley, 1966) are toward the lower limits of variation in the sample I have measured. Following are measurements of the type, followed first by the mean values of a sample of 20 individuals from near the type locality and then the extremes in parentheses: greatest length of skull, 27.6, 28.18 (27.5–28.8); zygomatic breadth, 17.1, 17.55 (17.0–18.0); maxillary tooththrow, 9.9, 10.12 (9.8–10.4); width across M2–M2, 12.3, 12.71 (12.2–13.2); forearm, 59.4, 59.02 (56.5–61.2). Handley (*op. cit.*) recorded lower minimum values in the specimens he examined. For mean values of other variates in my sample see Table 2.

The lowlands of western México are inhabited by several other endemic species and subspecies of bats, among which are *Mormoops megalophylla rufescens* Davis and Carter, *Musonycteris harrisoni* Schaldach and McLaughlin, *Chiroderma salvini scopaeum* Handley, *Artibeus hirsutus* Andersen, *Artibeus phaeotis nanus* Andersen and *Natalus stramineus mexicanus* Miller. Consequently, that region appears to be a well-marked ecologic unit that is effectively isolated from that portion of the Pacific versant of Middle America southeast of

the Isthmus of Tehuantepec. This conclusion receives support from the fact that such bats as *Saccopteryx leptura* (Schreber), *Uroderma bilobatum* Peters and *Uroderma magnirostrum* Davis reach the northernmost limits of their known distribution in the Pacific lowlands of Middle America at the Isthmus of Tehuantepec. None of them has been recorded north of the Isthmus.

The only record of gravid *triomylus* females I have is for the month of December. Anderson (1960) reported gravid females taken in Sinaloa in June.

*Specimens examined* (total number of 55).—MEXICO. *Nayarit*: Tepic, 3120 ft, 1 ♀. *Guerrero*: Acahuizotla, 2800 ft, 14 ♂♂, 9 ♀♀; Agua del Obispo, 3300 ft, 6 ♂♂, 4 ♀♀; 3 mi. N Colotlipa, 2700 ft, 1 ♂, 1 ♀; 17 km S Taxco, 4000 ft, 1 ♂; Tres Palos (25 km E Acapulco), 10 ft, 3 ♂♂, 9 ♀♀; Xaltianguis, 1600 ft, 1 ♂, 2 ♀♀. *Morelos*: Alpuyecá, 3500 ft, 3 ♂♂.

*Additional records*.—Handley (1966) listed several localities for this subspecies in Nayarit, Jalisco, Colima, Michoacán, Morelos, and Guerrero. Anderson (1960) recorded specimens from 32 mi. SSE Culiacan and ½ mi. E Piaxtla in Sinaloa. Baker and Greer (1962) reported two specimens from near Pueblo Nuevo, Durango. Villa (1966) reported one specimen from Sinaloa de Leyva, Sinaloa (the northernmost record) and several others from Nayarit, Jalisco, Michoacán, Morelos, and Guerrero, and Genoways and Jones (1968) listed specimens from southernmost Zacatecas. Goodwin (1969) recorded 51 specimens from Oaxaca: all of those from western Oaxaca (25) had 3/3 molars, but only 68 per cent of those from near the city of Tehuantepec had 3/3 molars (the remainder had 2/3). Thus, the vicinity of Tehuantepec is an area of intergradation of *triomylus* with adjacent subspecies.

#### *Artibeus jamaicensis paulus*, new subspecies

*Holotype*.—Adult female, skin and skull, no. 21953 Texas Cooperative Wildlife Collection, collected on 23 June 1967, 7½ km WNW La Libertad, elevation ca. 500 feet, Department of La Libertad, El Salvador, by Richard K. LaVal, original number 1540.

*Distribution*.—The dry tropical and subtropical sections of Middle America from Chiapas, México, southeastward to the Guanacaste region of Costa Rica (see Fig. 5).

*Diagnosis*.—A small, wood brown representative of *A. jamaicensis* resembling *A. j. triomylus* in size and color, but normally with only two upper molars. Measurements of the holotype: greatest length of skull, 28.1; zygomatic breadth, 16.9; postorbital constriction, 7.0; maxillary tooththrow, 9.9; width across M2–M2, 12.2; length of palate, 13.2; mandibular length, 18.8; mandibular tooththrow (C–m3), 10.8; forearm, 58.1; metacarpal III, 55.0; phalanx 1, d III, 16.4; phalanx 2, d III, 28.2. For comparison with mean values of a sample of 20 individuals from (and near) the type locality see Table 2.

*Remarks*.—Characters of this subspecies are best developed in those bats occupying the Pacific lowlands of Guatemala and El Salvador. They are smaller than those in Oaxaca and Chiapas to the northwest and in Costa Rica to the southeast, and they are substantially smaller and paler than those occupying the Atlantic lowlands (see Figs. 2 and 4). The name *paulus* alludes to the small size of the new subspecies.

Although individuals from the dry Pacific slopes of Oaxaca, the dry Grijalva River basin of Chiapas, the dry tropical and subtropical sections of Guatemala, and the dry Comayagua Valley of Honduras north of the continental divide are somewhat larger than those from El Salvador, they are smaller and paler than those that inhabit the humid tropical areas of the Atlantic lowlands. Because of this I deem it best to refer them to *paulus*. In most of Nicaragua and Honduras the continental divide is a convenient line of demarcation between *paulus* and *richardsoni*.

Thirteen specimens from near Tapanatepec and La Ventosa, Oaxaca, in the Isthmus of Tehuantepec, appear to be intergrades of *richardsoni*, *yucatanicus* and *paulus*. They are like *richardsoni* in having a palatal length of 14.0 or more in nine of the 13 individuals and a mean zygomatic breadth of 17.36. They are like *yucatanicus* in having a mean forearm

TABLE 3.—Mean measurements in millimeters of seven samples of *Artibeus jamaicensis paulus* from the Pacific versant of Middle America.

Variable	Chiapas (below 1000 ft)	Guatemala	El Salvador	Honduras (Nueva Ocotepeque)	Honduras (Pacific Lowlands)	Nicaragua (San Antonio)	Costa Rica (Guacacaste Lowlands)
Sample size	15	20	20	20	6	11	4
Greatest length of skull	28.24	28.12	27.27	28.13	28.45	27.99	28.53
Zygomatic breadth	17.30	16.92	16.42	16.93	17.15	17.07	17.20
Postorbital constriction	7.05	7.06	6.93	7.12	7.10	7.00	7.15
Maxillary toothrow	10.10	10.05	9.82	9.92	9.97	9.93	10.15
Width across M2–M2	12.66	12.50	12.17	12.30	12.33	12.21	12.55
Length of palate	13.84	13.83	13.21	13.57	13.80	13.60	13.95
Length of mandible	19.23	19.15	18.45	18.90	19.32	19.04	19.40
Mandibular toothrow	11.12	11.04	10.71	10.85	10.93	10.93	11.10
Forearm	57.76	58.17	56.43	57.72	59.78	57.48	57.10
Metacarpal III	54.23	54.35	52.76	54.21	56.50	53.39	54.65
Phalanx 1, d III	16.27	16.88	15.81	16.77	17.47	16.84	16.48
Phalanx 2, d III	27.52	27.66	26.73	27.77	29.08	26.72	27.75

length of 59.4; they resemble *paulus* in color and in mean length of skull (28.5). They are here referred to *paulus* on the basis of geographic position.

Intergradation between *paulus* and *richardsoni* occurs commonly along the borders of their respective ranges from Guatemala to Costa Rica. Consequently, the allocation of single specimens from the zone of intergradation has to be subjective and more or less arbitrary.

The number of molars in *paulus* is normally 2/3 (95 per cent of a sample of 270 individuals). Only one of the sample had a full complement of 3/3 molars and five individuals lacked the third molar completely, thus with a 2/2 molar formula. Eight others had a combination of 2/2–2/3 or 2/3–3/3.

This bat normally roosts in caves, abandoned mines, or hollow trees, but near Progreso, Guatemala, I shot two females from a structure resembling a squirrel nest located near the top of a pine tree. Pregnancy records for females of *paulus* are for the months of February, March, April, and July.

*Specimens examined* (total number of 671).—MEXICO. *Oaxaca*: 4 mi. E Tapanatepec, 800 ft, 9 ♂♂ (2 alc.), 5 ♀♀ (1 alc.); La Ventosa, 1 skel. (LACM). *Chiapas*: 5–6 mi. N Arriaga, 600–800 ft, 31 ♂♂ (17 alc. plus skull), 23 ♀♀ (21 alc. plus skull); 8 mi. N Arriaga, 2500 ft, 11 ♂♂ (6 alc.), 19 ♀♀ (14 alc.); Río Gallina, 12 mi. E Ortiz Rubio on Villa Flores road, 2 ♂♂ (BJH); 3 mi. E Cintalapa, 1700 ft, 2 ♀♀; 7 mi. NW Cintalapa, 2600 ft, 3 ♂♂; 7 mi. WSW Ocozocautla, 2500 ft, 1 ♂, 2 ♀♀; 2 mi. SE Tuxtla Gutierrez, 2600 ft, 5 ♂♂, 8 ♀♀; 35 mi. SSE Tuxtla Gutierrez, 2200 ft, 2 ♂♂, 13 ♀♀ (3 alc. plus skull); 38 mi. SSE Tuxtla Gutierrez, 1800 ft, 1 ♂, 2 ♀♀; Río Dorado, 40 mi. SSE Tuxtla Gutierrez, 1800 ft, 1 ♂; 4 mi. NE Chiapa de Corzo, 2000 ft, 4 ♂♂, 2 ♀♀; 4 mi. N Chiapa de Corzo, K 1110, 3000 ft, 4 ♂♂, 7 ♀♀ (5 alc. plus skull); 4 km SSE Chiapa de Corzo, 1300 ft, 1 ♂; 1.3 mi. SE Zapaluta [= La Trinitaria], 5700 ft, 12 ♂♂ (2 alc.), 25 ♀♀ (12 alc., 2 skel.); 10 mi. S Zapaluta, 3000 ft, 4 ♂♂, 1 ♀; 18 mi. S La Trinitaria, 2800 ft, 3 ♂♂, 3 ♀♀; 4 km ENE San Lucas [= ca. 35 km SSE La Trinitaria], 3300 ft, 3 ♂♂, 2 ♀♀;



8 mi. SE Tonalá, 100 ft, 1 ♂, 4 ♀♀ (UA); 15 km SE Tonalá, 100 ft, 1 ♀; 5 km SE Pijijapan, 100 ft, 1 ♂, 1 ♀; 2 km N Sesecapa, 100 ft, 1 ♀. GUATEMALA. *Huehuetenango*: La Democracia, 3300 ft, 1 ♀; 2 km E Aguacatán, 5265 ft, 2 ♂♂, 5 ♀♀ (4 alc.); 4 km WSW San Miguel Acatán, 5850 ft, 2 ♂♂ (alc. plus skull). *Quiché*: 1 km WNW Sacapulas, 3900 ft, 15 ♂♂ (12 alc.), 13 ♀♀ (10 alc.). *Baja Verapaz*: San Miguel Chicaj, 3100 ft, 15 ♂♂ (5 alc.), 18 ♀♀ (5 alc.); 2 km SE Salamá, 3100 ft, 10 ♂♂ (1 alc.), 18 ♀♀ (8 alc.). *El Progreso*: Agua Caliente, at K 29, 2800 ft, 1 ♂, 1 ♀; K 36, near San Antonio La Paz, 3400 ft, 2 ♀♀; K 72, ca. 5 km W El Progreso, 1600 ft, 2 ♀♀. *Chiquimula*: 20 km SSE Chiquimula, 1800 ft, 10 ♂♂ (1 alc.), 16 ♀♀ (4 alc.). *Jutiapa*: 5 km NE Jutiapa, 3000 ft, 1 ♂, 1 ♀; 6 mi. S Asunción Mita, 2000 ft, 3 ♂♂; 1 mi. SE Monogoy, 3 ♀♀ (KU). *Retalhuleu*: 2 mi. SE Champerico, sea level, 1 ♂ (KU); 3 km Retalhuleu, 1000 ft, 1 ♀. *Escuintla*: 8 km NW Puerto de San José, 50 ft, 3 ♂♂, 1 ♀; 4 mi. W Escuintla, 880 ft, 1 ♀ (KU); 2 mi. E Palín, 4000 ft, 4 ♂♂, 9 ♀♀. *Guatemala*: 5 mi. S Guatemala City, 4950 ft, 1 ♀ (KU); Villalobos, 13 km S Guatemala City, 4200 ft, 1 ♂; Amatitlán, 3800 ft, 1 ♂, 5 ♀♀. *Santa Rosa*: Astillero, 25 ft, 2 ♂♂, 1 ♀ (KU); 2 km E Taxisco, 700 ft, 1 ♀. EL SALVADOR. *Sonsonate*: 13.5 mi. S, 9 mi. E Sonsonate, 1 ♂ (alc.). *La Libertad*: 3–7 km E La Libertad, 50 ft, 20 ♂♂ (16 alc.), 11 ♀♀ (9 alc.); 7½ km WNW La Libertad, 500 ft, 3 ♂♂, 2 ♀♀; 1–4 km W La Libertad, 30 ft, 4 ♂♂ (3 alc.), 16 ♀♀ (4 alc.); 13 km W La Libertad, 50 ft, 3 ♂♂ (2 alc.), 11 ♀♀ (10 alc.); 20 km W La Libertad, 800 ft, 7 ♂♂ (3 alc.), 10 ♀♀ (4 alc.); 10 mi. W La Libertad, 7 ♂♂ (5 alc.), 7 ♀♀ (5 alc.); 20 mi. W La Libertad, 10 ft, 1 ♂. *Cuscatlán*: 14 km NW Suchitoto, 815 ft, 1 ♂ (alc.), 1 ♀ (alc.). *Chaletenango*: 20 km W Chaletenango, 815 ft, 11 ♂♂ (7 alc.), 6 ♀♀ (4 alc.). HONDURAS. *Ocotepeque*: 1 km W Nueva Ocotepeque, 2730 ft, 4 ♂♂, 17 ♀♀. *Intibucá*: La Esperanza, 5200 ft, 3 ♂♂, 4 ♀♀. *La Paz*: Marcala, 3900 ft, 1 ♀. *Valle*: 6 km E Amatillo, 200 ft, 2 ♂♂, 1 ♀; 10 km E San Lorenzo, 25 ft, 2 ♂♂, 1 ♀. *Distrito Central*: 1 mi. S Comayagua, 3250 ft, 1 ♂, 1 ♀; 10 mi. SE Tegucigalpa, 5135 ft, 5 ♂♂, 3 ♀♀. *Comayagua*: Comayagua, 1890 ft, 23 ♂♂ (15 alc.), 33 ♀♀ (20 alc.); 3 km W Comayagua, 1890 ft, 3 ♂♂, 4 ♀♀ (2 alc.); 12.7 km S Comayagua, 1890 ft, 5 ♂♂, 7 ♀♀ (3 alc.); 17 km S Comayagua, 1890 ft, 2 ♂♂, 10 ♀♀. NICARAGUA. *Chinandega*: San Antonio, 50 ft, 6 ♂♂, 5 ♀♀ (KU). COSTA RICA. *Guanacaste*: Playa del Coco, sea level, 2 ♀♀ (LSU); 4½ mi. N, 4 mi. W Liberia, 900 ft, 1 ♀ (alc.); 3 mi. S, 10 mi. W Las Cañas, 10 ft, 2 ♂♂ (alc.), 8 ♀♀ (6 alc.). *Puntarenas*: 3 km N Tambor, sea level, 1 ♂ (LSU).

#### ACKNOWLEDGMENTS

This contribution (no. TA-7919 of the Texas Agricultural Experiment Station, Texas A & M University) results from Project 1556, which was supported in part by National Science Foundation grant GB3201.

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