REVIEW OF THE EPTESICUS BRASILIENSIS COMPLEX IN MIDDLE AMERICA WITH THE DESCRIPTION OF A NEW SUBSPECIES FROM COSTA RICA

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ABSTRACT: Study of the types of Vesperus propinquus Peters and Vesperus (Marsipolaemus) albigularis Peters, both of which are allegedly from Central America and currently referred to the genus Eptesicus, reveals that both are representatives of previously named Old World species. V. propinquus is a synonym of Eptesicus nilssonii, and V. albigularis is a synonym of Vespertilio murinus. Eptesicus gaumeri (J. A. Allen) is considered the valid name for the lowlands population of small short-haired Eptesicus in Middle America. A population of somewhat larger short-haired Eptesicus in Costa Rica and western Panamá is described as new. The small long-haired Eptesicus occupying the highlands of Middle America, described and named Eptesicus chirquinus by Thomas, appears to be identical with Eptesicus andinus J. A. Allen from the highlands of Colombia. A synoptic key to New World Eptesicus is presented.

Nearly a century ago Peters (1872) described two species of bats on the basis of three untagged alcoholic specimens which purportedly came from Middle America. To one specimen (no. 4233 Berlin Museum) "aus Mexico" he gave the name Vesperus (Marsipolaemus) albigularis. To the other two (no. 2704 Berlin Museum) "aus Ysabel de Guatemala" he gave the name Vesperus propinquus. Both species are currently assigned by American workers to the genus Eptesicus, although Miller (1907, p. 210), who examined the type in Berlin, pointed out that one of them, Vesperugo (Marsipolaemus) albigularis, is "merely a specimen of Vespertilio murinus." Through the courtesy of Dr. K. Zimmermann of the Museum der Humboldt-Universität, I have been privileged to examine Peters' types.

The type of albigularis is poorly preserved but its unique characters are clearly discernible. The most striking external features are (1) the clear white throat and (2) the voluminous ear with its club-shaped tragus (Fig. 1). The conch of the ear has nearly twice the area of that in Eptesicus "brasiliensis"; its lower attachment is near the angle of the mouth, where it joins a shallow, forward-opening pouch, devoid of hair on the inside and possibly glandular in nature, on the side of the lower jaw. A rather wide flap is attached to the posterior rim of the conch; the anterior portion of the ear extends a considerable distance anteriorly beyond the eye, and the tragus is rather short, wide and truncate at the tip. Alston's (1879–1882) figure (pl. 3, no. 1) is accurate in essential details.

The inner upper incisor is unlike that of any other *Eptesicus* I have seen. It is *triangular* in cross section and has three distinct cusps. The one at the posterior angle is shortest; that at the anteromedial angle is longest. All these are features of *Vespertilio murinus* Linnaeus.

None of the above features is found in any of the more than 200 other specimens of *Eptesicus* I have examined except for the young individual

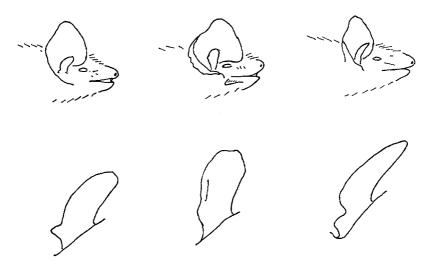


Fig. 1.—Comparative size, shape and position of the ear (upper series) and the tragus (lower series) of *Eptesicus propinquus* Peters (left), *Marsipolaemus albigularis* Peters (center) and *Eptesicus gaumeri* of the "brasiliensis" complex (right).

which is a cotype of *Vesperus propinquus* Peters. This young specimen differs from the type of *albigularis* only in smaller size and in the absence of the white throat patch. None of the three specimens Peters used in describing *albigularis* and *propinquus* bears a label, which fact gave ample opportunity for the mixup that must have occurred.

The description of Vesperus propinquus was based on the larger of the two specimens that Peters referred to this species. Consequently, it alone should be designated as the lectotype of propinquus, and the young specimen should be referred to Vespertilio murinus. The lectotype is in a good state of preservation and it, too, is unique among American representatives of the genus Eptesicus. It has a relatively large ear, the anterior rim of which reaches to the middle of the eye; the tragus is short, curved and blunt. The most striking feature is found in the upper incisors. The inner tooth is sharp-pointed, but bifid; the outer one is long and reaches nearly to the tip of the inner tooth (Fig. 2), as it does in Eptesicus nilssonii of the Old World. In all other American Eptesicus the outer upper incisor barely extends beyond the cingulum of its larger mate (in all age classes which have attained permanent incisors).

Because the types of both albigularis and propinquus are unique insofar as American Eptesicus are concerned, because both of them can readily be aligned with Eurasian species, and because there obviously was a mixup of the unlabeled specimens Peters had at hand when he described them, both trivial names, albigularis and propinquus, properly apply to Old World bats, the former as a synonym of Vespertilio murinus Linnaeus, the latter as a synonym of Eptesicus nilssonii Keyserling and Blasius.





Fig. 2.—Comparative size and shape of the left upper incisors of Eptesicus propinquus (left) and Eptesicus gaumeri of the "brasiliensis" complex (right).

A third species of small Eptesicus from Middle America was described and named Adelonycteris gaumeri by J. A. Allen (1897) on the basis of a single specimen from Izamal, Yucatán. Later, Osgood (1941) received a specimen from Achotal, Veracruz, which he compared with Peters' description of propinquus and with the holotype of Allen's gaumeri. Osgood concluded that the Achotal specimens showed "no specific or subspecific differences" from gaumeri and that "gaumeri is a synonym" of propinquus. I have not been able to examine the type of gaumeri, but I have compared the Achotal specimen with the type of propinquus. The two are strikingly different. The specimen from Achotal has upper incisors, ears and tragus like those figured for "brasiliensis" (Figs. 1 and 2). In addition the feet are much smaller and the tibia shorter. Assuming Osgood's conclusion (that the Achotal specimen does not differ materially from the type of gaumeri) is valid, then I must conclude that gaumeri and propinquus are not conspecific. The name gaumeri, therefore, becomes available.

Exclusive of albigularis and propinquus, three other recognizable forms of small Eptesicus occur in Middle America. One of them, characterized by (1) long, lax pelage, (2) blackish upperparts, (3) long forearm (42.3–48.0 mm) and (4) large cheek teeth (M^2 measures ca. 2.0×1.7 mm), was described by Thomas (1920) and given the binomial designation Eptesicus chiriquinus. The other two have (1) relatively short pelage, the upperparts varying from rufous through brown to black, and (2) small cheek teeth (M^2 measures ca. 1.7×1.5).

Members of the "brasiliensis" complex that I have examined segregate into two groups on the basis of size of the cheek teeth. Those with large teeth (M² measuring ca. 2.0 mm in width and 1.7 mm in crown length) include E. andinus J. A. Allen, E. brasiliensis (Desmarest), E. argentinus Thomas, E. chiriquinus Thomas, and probably E. montosus Thomas and E. inca Thomas. Those with small cheek teeth include E. innoxius (Gervais), E. punicus Thomas, E. furinalis (D'Obrigny), E. chiralensis H. E. Anthony, E. melanopterus

(Jentink), E. fidelis Thomas, probably E. diminutus Osgood, and the two forms in Middle America.

Those with large cheek teeth can be divided into two groups on the basis of pelage. One, the brasiliensis group comprising argentinus and brasiliensis, has short pelage, and the two appear to be conspecific, yet recognizable as subspecies. This supports Cabrera's (1957) arrangement of these two as subspecies of Eptesicus brasiliensis (Desmarest). A second group with long, soft pelage and long forearm (43–48 mm) includes E. andinus, E. chiriquinus, E. montosus and E. inca, hereafter referred to as the andinus group. These four may be conspecific. I have compared two of Allen's paratypes of andinus with virtual topotypes of chiriquinus from Panamá and can find no significant differences. Both groups are dark-colored (seal brown), have long forearms, large cheek teeth, and long, lax dorsal pelage. I concur with Hershkovitz (1949) and Cabrera (1957) in aligning chiriquinus as a synonym of andinus, but I do not agree with them in placing andinus as a subspecies of the short-haired E. brasiliensis.

Those taxa with small cheek teeth that I have examined, namely E. punicus, E. innoxius, E. furinalis, E. melanopterus, E. chiralensis, E. fidelis and the two populations from Middle America, segregate into two groups on the basis of size. One of these (the innoxius group) is diminutive and includes E. innoxius of western Ecuador and Peru (greatest length of skull, 14.5–15.8; zygomatic breadth 9.3–10.0; maxillary tooth row, 5.3–6.0; forearm 37.0–38.7) and E. punicus also from the coastal area of Ecuador and Peru (greatest length of skull, 14.1–14.8; zygomatic breadth, 8.9–9.0; maxillary tooth row, 4.9–5.3; forearm, 35). In both of these species the skull has only faint indications of sagittal and lambdoidal crests. E. diminutus of the Bahia region of Brazil (greatest length of skull, 14.3; maxillary tooth row, 5.1; forearm ca. 36) and E. fidelis from Argentina (greatest length of skull, 13.9; maxillary tooth row, 5.0; forearm, 34) also appear to be referable to this group, although I have not seen specimens of the former.

The second group with small cheek teeth is comprised of medium-sized individuals (greatest length of skull, 15.2–17.1; zygomatic breadth, 10.0–11.5; maxillary tooth row, 5.4–6.3; forearm, 37–43.5) and includes *E. furinalis* from northeastern Argentina, *E. melanopterus* from the Caribbean coast of South America, *E. chiralensis* from the mid-altitudes of western Ecuador and the two forms from Middle America. Since *furinalis* is the oldest name available, I shall use it without prejudice as a designation for this group, the members of which may or may not constitute a single allopatric species.

One of the two representatives of the *furinalis* group in Middle America is comprised of small individuals for which the name *E. gaumeri* J. A. Allen is available. The other population, composed of larger individuals, which appears to intergrade with *gaumeri*, is without a name. I propose that it be known as

Eptesicus gaumeri carteri subsp. nov.

Type.—Adult female, skin and skull, no. 10,099 Texas Cooperative Wildlife Collections; Turrialba, 2,600 ft, Prov. de Cartago, Costa Rica; collected by Dilford C. Carter, 21 March, 1963; original no. 4762.

Diagnosis.—A medium-sized member of the furinalis group of Eptesicus with the forearm averaging about 41 mm (range 38.6–43.5); pelage short (6–7 mm) as compared with andinus (about 10 mm); upperparts reddish brown to blackish brown; underparts paler, washed with buff or whitish buff; greatest length of skull 16–17 mm, averaging 16.6 in males, 16.7 in females; cheek teeth relatively small, crown of M² measuring about 1.65 in width and 1.5 in length.

Distribution.—Currently known from Costa Rica and Panamá.

Measurements.-See Tables 1 and 2.

Comparisons.—Differs from andinus in having shorter dorsal fur (6–7 mm as opposed to 9–10); shorter foot (8.5–9 as opposed to 9–10); tibia shorter, usually less, rather than usually more, than 16; skull smaller, averaging 16.7 (range 16.0–17.1 rather than averaging 17 (range 16.2–18.1); cheek teeth noticeably smaller, M^2 measuring about 1.7×1.5 rather than 1.9×1.7 .

Differs from gaumeri in being larger in most measurements; greatest length of skull averaging 16.6 rather than 15.8; zygomatic breadth averaging 11.0 as opposed to about 10.5; forearm usually more, rather than less, than 40 (Fig. 3).

Specimens examined.—Total number, 75, as follows: Costa Rica: La Iberia, 300-1,000 ft, Limón, 1 &, 2 & (DRD); Sta. Teresa Peralta, Cartago, 2 & &, 6 & (AMNH); Turrialba, 2,600 ft, Cartago, 7 & &, 36 & (TCWC); 3 mi. SE Turrialba, Cartago, 1 & (UM); 18 mi. NE Naranjo, 2,900 ft, Alajuela, 13 & (TCWC); Villa Quesada, 4,100 ft, Alajuela, 1 & (skin only) (CNHM). Panamá: Sibube, Bocas del Toro, 4 & & (USNM); 7 km SSW Changuinola, Bocas del Toro, 2 & Q, 1 & (USNM).

Eptesicus gaumeri gaumeri J. A. Allen

Type.—Adult female, no. $\frac{12753}{11040}$, American Museum of Natural History, collected by George F. Gaumer at Izamal, Yucatán, México.

Diagnosis.—Smallest of the furinalis group of Eptesicus in Middle America. Forearm usually less than 40 mm; greatest length of skull seldom exceeding 16 and averaging about 15.5; zygomatic breadth seldom exceeding 10.6. Two color phases: (1) upperparts blackish or blackish brown with underparts washed with buff or white, (2) upperparts russet with underparts cinnamon or golden.

Distribution.—From Panamá northward into México as far as the states of Jalisco, Morelos and San Luis Potosí.

Measurements.—See Tables 1 and 2.

Comparisons.—See accounts of carteri and andinus.

Remarks.—This subspecies appears to be an inhabitant of the lowlands of Middle America. Most of the specimens examined are from localities below an elevation of 1,000 ft.

Several obvious errors of measurement crept into Allen's description of gaumeri. For example, he gave the length of the ear as 21; the tragus, 11; the tibia, 70; greatest length of skull, 18. Dr. Karl Koopman kindly remeasured the skull and the elements of the wing of the type and provided me with new data (Tables 1 and 2). These measurements fall within the range of variation of the population of small *Eptesicus* occupying the lowlands of Middle America.

The specimen (no. 123334 AMNH) which Goodwin (1942a) referred to

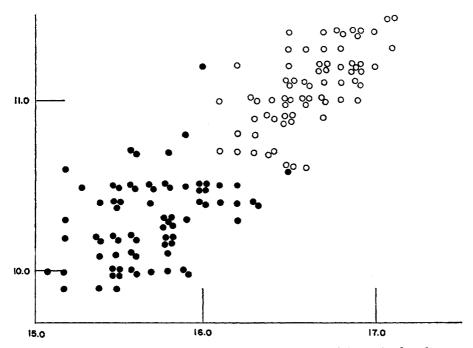


Fig. 3.—Scatter diagram of length of skull in millimeters (abscissa) plotted against zygomatic breadth (ordinate) in two populations of *Eptesicus gaumeri* in Middle America. Solid circles = E. g. gaumeri; open circles, E. g. carteri.

E. propinquus and later (1942b) to E. albigularis proves, on comparison with Peters' types of these two species, to be referable to neither. Rather, it is a color variant of E. g. gaumeri. It differs from other members of this subspecies only in that the underparts are more heavily washed with white and the upperparts are somewhat paler.

Specimens examined.—Total number, 104, as follows: Panamá: Tapia, Panamá, 13 (alc) (MCZ); San Pablo, Canal Zone, 299 (USNM); Tocumen, Panamá, 19 (USNM); San Lorenzo, 200 ft, Chiriquí, 1º (USNM). Nicaragua: 3 mi. NNW Diriamba, Carazo, 1 & (KU); 1 mi. SE Yalaguina, 2,600 ft, Madriz, 1 9 (TCWC). Honduras: Comayaguela, Tegucigalpa, 1 ♂ (AMNH); Ruinas de Copán, Copán, 2 ♂ ♂, 3 ♀ ♀ (TCWC); 2 mi. W San Pedro Sula, Cortez, 2 & &, 1 9 (TCWC); Lancetilla, 3 mi. S Tela, Cortez, 2 & & (alc) (CNHM). Guatemala: 2 km E Taxisco, 700 ft, Santa Rosa, 1 & (TCWC). México: Pueblo Nuevo X-Can, 10 m, Quintana Roo, 1 & (KU); Yucatán (no specific locality), 2 (1 skull only) (ANSP); Piste, 10 m, Yucatán, 1 & (KU); Balchacaj, Laguna de Terminos, Campeche, 1 9 (alc) (CNHM); ½ mi. W Miramar, Tabasco, 499 (LSU); Rancho El Tumbo, 4 km E El Zapote, Macuspana, Tabasco, 19, 28 & (alc) (IB); Finca Ocuilapa, 8 mi. S Tonalá, Chiapas, 2 & &, 4 \ \ \ (BJH), 2 & &, 4 \ \ \ (UA), 8 \ \ \, 2 & & (IB); Río Escondido, 19 km N Tonalá, 100 m, Chiapas, 299, 288 (IB); 12 km SSE Tonalá, 100 m, Chiapas, 1499 (IB); Tolocita (= Tolosa), Oaxaca, 19 (MSU); Achotal, Veracruz, 19 (CNHM); 1 mi. E Jáltipan, 50 ft, Veracruz, 1 9 (TCWC); 25 mi. W Santiago Tuxtla, Veracruz, 1 9 (TCWC); Río Blanco, 20 km W Piedras Negras, 400 ft, Veracruz, 13, 12 (KU); 2 km N Motzorango, 1,500 ft, Veracruz, 1 & (KU); 5-7 km W Potrero, 1,700 ft, Veracruz, 2 & & , 2 ♀ ♀ (KU); 12½ mi. N Tihuitlán, 300 ft, Veracruz, 19 (KU); Tuxpan, Veracruz, 299 (KU); 4 km

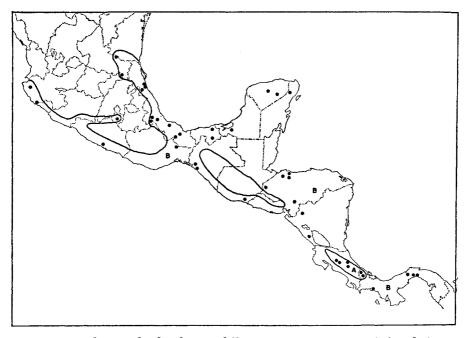


Fig. 4.—Map showing the distribution of *Eptesicus gaumeri gaumeri* (B) and *Eptesicus gaumeri carteri* (A) in Middle America. Circles represent localities from which specimens were examined.

NE Tuxpan, Veracruz, 599 (KU); 3 mi. ENE Tlacotalpan, 13 (IB); 1 km W Huichihuayán, San Luis Potosí, 13 (LSU); El Salto, ca. 2,000 ft, San Luis Potosí, 13 (LSU); Cueva del Salitre, Morelos, 1099, 13 (alc) (IB); Supongo, 1 km N Coyuca, Guerrero, 13 (IB); 15 km NW Cihuatlán, Jalisco, 13 (KU); Sierra de Cuale, 4,100 ft, Jalisco, 13 (KU).

Eptesicus andinus J. A. Allen

Type.—Adult male, no. 33807, American Museum of Natural History, collected 26 March 1912, by J. A. Allen and Leo E. Miller at Valle de las Papas, 10,000 ft, Huila, Colombia.

Diagnosts.—Dorsal pelage long (9–10 mm) and fluffy; forearm 42 to 48 mm; membranes black; upperparts blackish (seal brown) to black; underparts blackish, washed with buff or umber; hind foot large (9–10, dry; skull with distinct "helmet" at juncture of sagittal and occipital crests; teeth relatively large (M^2 1.9 \times 1.7 mm).

Distribution.—Chiapan Highlands southward to the highlands of Colombia and Ecuador. Measurements.—See Tables 1 and 2.

Comparisons.—Differs from all other small Middle American Eptesicus as follows: foot 10 to 12% larger; pelage long (9-10 mm) and silky; teeth noticeably larger, crown of M^2 averaging 1.9 in width and 1.7 in length on lateral face (as opposed to 1.7×1.5 or less).

Remarks.—This species has been collected mainly in highland areas. The type of andinus came from 10,000 ft in the Central Andes; the type of chiriquinus (here considered a synonym of andinus) came from the slopes of Cerro Chiriquí in Panamá. Two females from Cerro Hoya, Los Santos, are smaller than most of the Panamanian specimens of andinus, but since the

Table 1.—External measurements of Middle American Eptesicus (exclusive of E. fuscus) in millimeters—averages followed by extremes in parentheses

					-		
Number	Forearm	Metacarpal III	Digit III Phalanx 1	Digit III Phalanx 2	Tibia	Foot (dry)	Remarks
				andinus			
	46.6	42.5	16.6	13.9	17.0 (one)	10.0	2 paratypes of andinus
(46.5		16.5	1	ł	1	Type of chiriquinus
o+ o+ ∞	46.0		16.7	14.6	17.0	9.4	From Panamá
	(44.9 - 48.0)	(40.0-44.0)	(15.6-18.0)	(13.1-16.0)	(15.8-17.7)	(8.7-10.4)	
11 & &	44.5		15.5	13.2	16.8	6.3	=
	(42.4-46.5)	(39.0-43.0)	(15.0-16.5)	(12.5-14.1)	(16.2-18.0)	(9.0-9.5)	
				carteri			
Type	41.5		15.3	13.2	15.3	8.3	
36 9 9	41.5	39.0	15.6	12.9	15.4	8.3	
	(38.6 - 43.5)		(14.6-16.4)	(12.1-14.7)	(14.7-16.0)	(7.8-9.1)	All from Turrialba. Costa Rica
633	40.5	37.6	14.9	12.1	15.4	8.3	
	(39.6-42.5)	(36.7-38.8)	(14.3-15.6)	(11.3-12.9)	(15.1-15.6)	(8.0-9.0)	
				gaumeri			
Type	38.0		15.0	11.0	14.0	8.0	Measured by Karl Koopman
13 9 9	38.9		13.9	11.4	14.5	8.3	From Nicaragua, Honduras,
	(37.4 - 41.3)	(35.0-37.5)	(13.0-14.8)	(10.5-12.1)	(13.4-15.6)	(7.5-8.8)	Guatemala and México
13 & &	38.9		14.2	11.5	14.3	8.0	From Nicaragua, Honduras.
	(37.9-40.0)	(35.0-37.2)	(13.3-14.6)	(11.0-12.1)	(13.6-14.9)	(7.5-8.9)	Guatemala and México

TABLE 2.—Selected cranial measurements, in millimeters, of Middle American Eptesicus (exclusive of E. fuscus)—averages followed by extremes in parentheses

Number	Greatest length of skull	Zygomatic breadth	Breadth of cranium	Length of maxillary tooth row C-M*	Width across Ma-Ms	Length of palate	Width X length of crown of M ²	Remarks
					andinus	Si		
	16.9	10.9	7.9	6.2	7.0	6.7	1.9×1.65	2 paratypes of andinus
	16.2	11.1	7.8	6.3	1	7.0	1.9×1.75	Ms of type of chiriquinus mea-
								sured by J. E. Hill. Other mea-
o+ o+ 8	17.5	11.7			7.3	7.3	1.98×1.70	strements face anomas.
	(16.7-18.1)		(7.8-8.2)	9	(7.1-7.5)	(7.1-7.5) (7.0-7.6)	$(1.8 \times 1.65 - 2.1 \times 1.7)$	From Panamá
11 8 3	16.9	11.1			7.0	7.2	1.86×1.69	
	(16.2-17.4)	(10.7-11.4)	(7.2-7.9)	(6.1-6.7)	(8.8-7.3) (7.0-7.5)	(7.0-7.5)	$(1.7 \times 1.65 - 1.9 \times 1.8)$:
					carteri	***		
Type	17.1	11.3	7.7	6.0	8.8	6.9	1.7×1.6	
36 9 9	16.7	11.1		0.9	6.9	6.7	1.7 imes 1.5	From Turrialba, Costa Rica
	(16.3-17.1)	(10.7-11.5)	(7.3-8.0)	(5.8-6.3)	(6.6-7.2)	(6.6-7.2) $(6.4-7.0)$	$(1.6 \times 1.5 - 1.8 \times 1.6)$	
633	16.6	11.1		0.9	6.7	6.7	1.7 imes 1.5	From Turrialba, Costa Rica
	(16.2-17.0)	(10.9-11.4)	(7.6-7.8)	(5.9-6.1)	(6.6-6.8) (6.5-7.0)	(6.5-7.0)	$(1.6 \times 1.6 - 1.7 \times 1.5)$	
					gaumeri	r		
Type	15.2	10.6	8.8	5.4	6.1	6.1	i	Measured by Karl Koopman
21 9 9	15.8	10.3		5.6	6.4	6.2	1.6×1.5	From Nicaragua, Honduras,
	(15.5-16.5)	(10.1-10.7)		(7.0-7.6) (5.4-6.0) (6.2-6.7) (5.8-6.4)	(6.2-6.7)	(5.8-6.4)	$(1.6 \times 1.4 - 1.7 \times 1.5)$	Guatemala, and México
16 3 3	15.6	10.4		5.6	6.4	0.9	1.6 imes 1.5	From Nicaragua, Honduras,
	(15.4-16.1)	(10.0-11.2)	(7.0-7.7)	(7.0-7.7) (5.5-5.8) (6.1-6.7) (5.5-6.5)	(6.1-6.7)	(5.5-6.5)	$(1.6 \times 1.4 - 1.7 \times 1.4)$	Guatemala, and México



Fig. 5.—Map showing the distribution of *Eptesicus andinus* (including *montosus*) in Middle and South America. Solid circles indicate localities from which specimens were examined.

dorsal pelage is long (approx. 10 mm) and lax, the second upper molar measures 1.9×1.7 , 2.0×1.7 , and the length of the forearm falls within the range of variation found in specimens from Chiriquí, they are referred to *andinus*.

The specimen from Chiapas differs from the Panamanian and Colombian specimens in having darker (more blackish) upperparts and underparts, slightly smaller ear and more slender tragus, shorter forearm (42.3) and shorter tibia (15.8 as opposed to 17.0). Even so, it is referable to the species *E. andinus* on the basis of its large teeth and long, silky dorsal pelage. Additional specimens, however, may reveal that the population in the Chiapan area is sufficiently different to warrant subspecific status.

(7)

(8)

SYNOPTIC KEY TO AMERICAN REPRESENTATIVES OF THE GENUS EPTESICUS

- 1. M^2 2.5 \times 1.9 or more; forearm 46 or more, usually near 50; greatest length of skull 17.4 or more, usually about 20. Range extends from southern Canada south to Venezuela—Eptesicus fuscus
- 1¹ Combination of measurements less than above; occurs from México south to Argentina
- Argentina (2) 2. Upper cheek teeth large (M^2 about 2.0×1.7) (3)
- 2¹ Upper cheek teeth small (M² about 1.7×1.5 or less) (6)
- 3. Pelage short, about 7 mm or less on back (E. brasiliensis group) (4)
- 3¹ Pelage long, 9-10 mm on back; upperparts blackish or Prout's brown (E. andinus group) (5)
- 4. Forearm 43-46; length of skull ca. 17; upperparts pale, wood brown; northeastern Argentina and Paraguay. E. brasiliensis argentinus
- 4¹ Forearm usually less than 42 (37-42.5); upperparts reddish brown to blackish; lowlands of Brazil and Colombia. E. brasiliensis brasiliensis
- Greatest length of skull more than 16.5 (16.2-18.1); forearm about 46 (42.5-48); highlands of Ecuador and Venezuela north to Chiapas, México. E. andinus andinus
- 5¹ Greatest length of skull less than 16.5 (15.6–16.2); forearm 43–46; highlands of Brazil, Bolivia and Peru. E. andinus montosus (E. inca Thomas considered a synonym)
- 6. Zygomatic breadth usually less than 10.0 (9.3-10.0); greatest length of skull less than 16 (averaging 15.3); sagittal crest absent or only slightly developed; forearm usually less than 38; maxillary tooth row 5.7 or less (E. innoxius group)
- 6¹ Zygomatic breadth usually more than 10.0 (10.0-11.5); greatest length of skull more than 15 (15.2-17.1); sagittal crest present but weakly developed; forearm more than 37 (37.4-43.5); maxillary tooth row 5.3-6.3 (E. furinalis group)
- Maxillary tooth row, 5.3-6.0; forearm 37-38; western Ecuador and Peru. E. innoxius (E. punicus considered a synonym)
- 71 Maxillary tooth row, 4.9-5.3; forearm, 34-36. Includes two forms in eastern Brazil and Argentina which are probably conspecific if not identical. E. diminutus (includes E. fidelis)
- 8. Greatest length of skull averaging 16.6 (16.2–17.1); forearm averaging 41 (39.6–43.5); maxillary tooth row 6 (5.8–6.3); middle altitudes of Costa Rica, and Panamá. E. gaumeri carteri
- 8¹ Measurements less (9)
- 9. Upperparts fulvous (11)
- 9¹ Upperparts mostly blackish brown or bister (10)
- Zygomatic breadth more than 11; width across M^s-M^s, 6.8; maxillary tooth row
 5.5; northern Brazil, the Guianas and Venezuela. E. melanopterus
- 10¹ Zygomatic breadth usually less than 11, averaging 10.4; width across M³-M³ 6.4 (6.1-6.7); maxillary tooth row 5.6 (5.4-6.0); lowlands of Middle America. E. gaumeri gaumeri
- 11. Underparts ochraceous; forearm, 38-41; greatest length of skull, 15.6-16; maxillary tooth row, 5.8-5.9; western Ecuador. E. chiralensis
- 11¹ Underparts buffy; forearm, 34-38; greatest length of skull, 15.0-16.3; maxillary tooth row, 5.3-5.6, northeastern Argentina and Paraguay. E. furinalis

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