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REVIEW OF THE GENUS *URODERMA* (CHIROPTERA)

WILLIAM B. DAVIS

ABSTRACT.—The genus *Uroderma* (order Chiroptera, family Phyllostomatidae) is reviewed. Two species are recognized, both occupying a range from Bolivia and Brazil northward to the Isthmus of Tehuantepec in México. *Uroderma bilobatum* Peters, described in 1866, is divided into five geographic races as follows: *U. b. bilobatum* Peters in eastern Bolivia, Brazil, the Guianas, and most of Venezuela; *U. b. thomasi* Andersen in western Bolivia, Perú, and Ecuador; *U. b. trinitatum*, described as new, from the island of Trinidad; *U. b. convexum* Lyon in western Venezuela, Colombia, most of Panamá, and the Pacific versant of Middle America to Oaxaca; *U. b. molaris*, described as new, in the Atlantic versant of Middle America from western Panamá to Veracruz, México. The second species of *Uroderma*, which is described as new, occurs sympatrically with *U. bilobatum*. It differs in having a deep, heavy rostrum, a broad, shield-shaped mesethmoid, facial stripes faint or completely lacking, and in lacking an edging of white on the ears.

At the turn of the century when Dr. Knud Andersen (1908) reviewed the genus *Uroderma* only 26 specimens were available to him, 13 from all of South America, 12 from Panamá, and one from Costa Rica. On the basis of that material he recognized two species—*Uroderma thomasi*, which he described in 1906 from two specimens in alcohol from two localities in western Bolivia, and *Uroderma bilobatum* Peters (type locality, São Paulo, Brazil) to which he ascribed a range extending from southern Brazil and Perú northward in South America to Trinidad, Venezuela, and Colombia, and into Central America as far as Miravalles, Costa Rica. To the latter he assigned as a junior synonym *Uroderma convexum* Lyon (1902), described on the basis of two young specimens in alcohol from Colon, Panamá, with the following comment: "*U. convexum* is in every respect indistinguishable from *U. bilobatum* from Brazil, Peru, Ecuador, Colombia, Venezuela and Trinidad."

In the present study I have examined and measured 736 specimens of *Uroderma*, mostly skins with skulls, including the type and/or paratype of each of the four trivial names that have been proposed in this genus. One name, *Uroderma validum* Elliot, was originally proposed for a large member of the genus *Artibeus* and is now placed as a synonym of *Artibeus lituratus*, so it is excluded from further discussions of the nomenclature of the genus *Uroderma*.

The data were stratified initially by sex and age classes, but sexual differences in those features judged to be useful taxonomically are not significant in the material at hand. One must be more discerning, however, regarding age differences. Except for those of the molars, measurements taken from obviously young specimens (*i.e.*, with cartilaginous finger joints) fall in the lower part of the range of variation for most variates measured. In this report all measure-

ments are given in millimeters, all weights are in grams, and measurements of forearm and metacarpal include the wrist.

I am indebted to the following institutions and their respective curators for the privilege of examining specimens in their custody. Abbreviations are those that appear in the text to identify sources of material used: AMNH (American Museum of Natural History, New York); BJH (private collection of Bruce J. Hayward, Silver City, New Mexico); BMNH (British Museum (Natural History), London); BZM (Institut für Spezielle Zoologie und Zoologisches Museum, Berlin); FM (Field Museum of Natural History, Chicago); KU (University of Kansas Museum of Natural History, Lawrence); LACM (Los Angeles County Museum, Los Angeles, California); LSU (Louisiana State University Museum of Zoology, Baton Rouge); MCZ (Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts); MNH (Museo de Historia Natural La Salle, Caracas, Venezuela); MSU (Michigan State University Museum, East Lansing); MVZ (Museum of Vertebrate Zoology, University of California, Berkeley); ROM (Royal Ontario Museum, Toronto); TCWC (Texas Cooperative Wildlife Collections, Texas A&M University, College Station); UA (University of Arizona Department of Zoology, Tucson); UCV (Universidad Central de Venezuela, Caracas); UF (University of Florida State Museum, Gainesville); UMMZ (University of Michigan Museum of Zoology, Ann Arbor); USNM (United States National Museum, Washington, D. C.).

The available specimens segregate into two distinct, nearly sympatric groups. One is characterized by (1) a heavy, deep rostrum, (2) dorsal profile of skull from crown to tip of snout a gradual, nearly straight slope (Fig. 1), (3) mesethmoid markedly expanded laterally so as to form a shieldlike structure as seen in frontal view (Fig. 2), (4) facial stripes poorly developed or even absent, (5) conch of ear concolor (no white or yellowish edging, at least in museum specimens), (6) general body color variable but tending toward the yellows. This group occurs throughout tropical South America and along the Pacific versant in Middle America as far north as Oaxaca. It seems to be absent on the Atlantic versant.

The second group occurs sympatrically with the first throughout the former's range and, in addition, it occupies the Atlantic versant of Middle America. Most records are from elevations below 2000 feet, but in Middle America specimens have been taken at an elevation of 5000 feet. The highest altitudinal record for South America is 6000 feet at Guayabamba, Perú. This group is characterized by (1) a depressed rostrum, (2) dorsal profile of skull from crown to tip of snout usually markedly depressed in the frontal region (Fig. 1), (3) mesethmoid narrow and strap-shaped (Fig. 2), (4) facial stripes bold and sharply contrasting with the dark color of the head, (5) conch of ear edged with yellowish white (in museum specimens, but usually bright yellow in life), (6) general body color variable but the browns are predominant. It is to this group that all the previously proposed names apply and since Peters' *Uroderma bilobatum* is the oldest name in the genus it has priority. As pointed

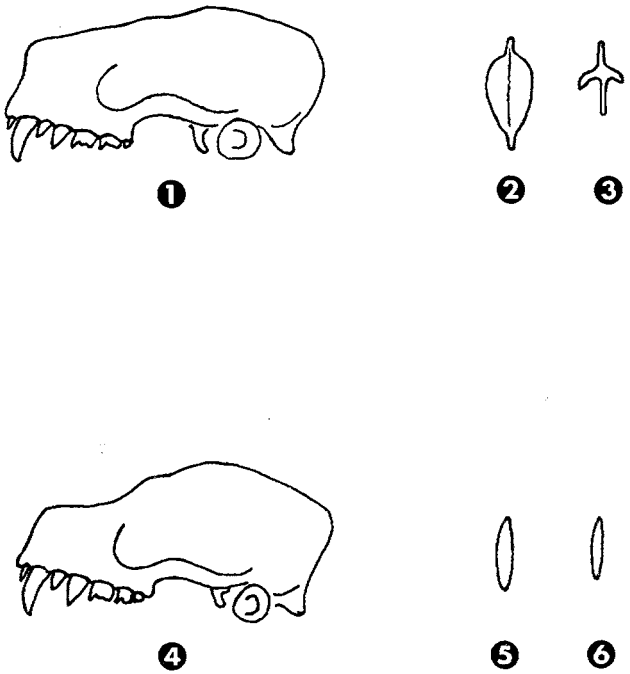

FIG. 1.—Outline drawings to illustrate the dorsal profile of the skull (1 and 4), general appearance of the mesethmoid as viewed under magnification through the anterior nasal opening (2 and 5), and a cross-section view of the mesethmoid (3 and 6). Nos. 1, 2, and 3 are of *Uroderma magnirostrum*; 4, 5, and 6, of *Uroderma bilobatum*.

out below, *Uroderma convexum* Lyon and *Uroderma thomasi* Andersen have validity as names for two of the five geographic races (subspecies) of *Uroderma bilobatum* recognized in this study.

DEEP-ROSTRUM GROUP

The first group is specifically distinct from the second and without a name. Although the first specimen of this new species was collected in 1893 at Valencia, Venezuela, a total of only seven had been preserved in the available collections until the advent of the present decade when mist nets became popular devices for capturing bats. I first encountered this bat in the field in October 1966, on the Pacific coastal plains of Honduras. All specimens to date have come from localities less than 1000 feet in elevation. These facts strongly suggest basic differences in the habits of the two species and that those bats with a deep rostrum are not "tent-makers" as are members of the species *Uroderma bilobatum*. That this new species is not rare in nature, at least in some areas, is attested to by the fact that 60% of the *Uroderma* taken on recent expeditions to Bolivia by personnel of the American Museum of Natural History are referable to it. In Middle America, however, it rarely has been taken by collectors and then only in small numbers at any given locality.

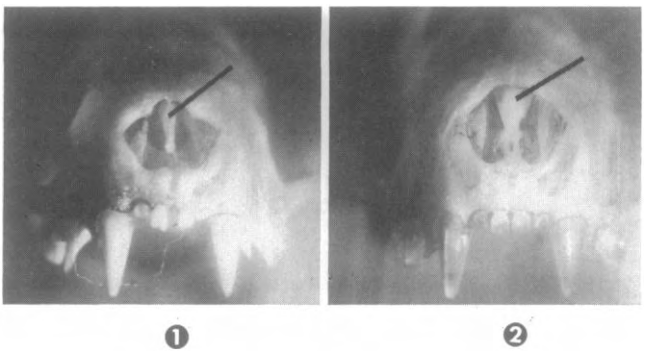

FIG. 2.—Photographs of the anterior narial area of (1) *Uroderma bilobatum* and (2) *Uroderma magnirostrum*. Compare the size and shape of the mesethmoids.

I have examined and measured 82 specimens of the first group, 23 from Middle America and 59 from South America, but I have found little evidence of geographic variation. The largest sample available is comprised of 36 specimens from five localities along the eastern edge of the Departamento de Beni, Bolivia. In this sample the range of individual variation of each variate measured is nearly identical with the range of that variate in the entire population sample. If one excludes the Bolivian sample, two geographic areas of differentiation are discernible—one includes Perú and northeastern Brazil, and the other includes Venezuela, Colombia and Middle America. Mean values of several measurements, for example, length of maxillary toothrow, width across molars, and greatest length of skull, are larger in the samples from Perú and Brazil. But because the observed differences may be merely an expression of small sample size from all areas other than Bolivia, and because the range of variation of each variate in the Bolivian sample nearly encompasses the range of the same variate in each of the other samples, I believe it best to defer further consideration of geographic variation in this group until adequate material is available for meaningful statistical treatment.

For this group of bats I propose the name

Uroderma magnirostrum, new species

Type.—Adult male, skin and skull, no. 17189 Texas Cooperative Wildlife Collections, collected 18 November 1966, by William B. Davis 10 km E San Lorenzo, 25 ft, Departmento de Valle, Honduras; original no. 7366.

Diagnosis.—Skull with deep rostrum, the dorsal profile from crown to tip of snout a gradual, nearly straight-line slope; mesethmoid greatly expanded laterally to produce a shieldlike structure in anterior aspect and roughly cross-shaped in cross-section (Figs. 1 and 2); facial stripes with reduced intensity of color or lacking; ear conch concolor, without whitish edging; dorsal surface of uropatagium hairy to a line beyond the knees. Dorsal body stripe and body color similar to those in *U. bilobatum*, but body color tends to be paler, more yellowish.

Measurements.—See Table 1.

Comparisons.—Needs to be compared only with *Uroderma bilobatum* (see beyond). Ex-

FIG. 3.—Map showing the distribution of *Uroderma magnirostrum* based on locality records of specimens examined.

ternally, some of the specimens resemble *Chiroderma*, but the two are readily separated by cranial characters.

Remarks.—No information is available on the roosting and feeding habits of this species. All but seven of the available specimens were captured in "mist" nets. All specimens I have taken personally were caught in nets set across shallow, slow-moving streams in an arid tropical habitat. A female captured June 20 in El Salvador contained a single fetus 21 in crown–rump length; another captured alive July 23 in Nicaragua gave birth (aborted?) to one youngster that measured 28 (crown–rump) and weighed 3.3. Ten of the 17 females captured in Bolivia in September were gravid, each with a single embryo (5 to 19 in crown–rump length).

Specimens examined.—A total of 82, as follows: MEXICO. *Oaxaca*: 20 mi NW La Ventosa, 2 ♀ ♀ (AMNH); Tepanatepec, 1 ♂ (AMNH). *Chiapas*: 21 km SE Tonalá, 100 ft, 1 ♀ (LACM); 15 km SE Tonalá, 100 ft, 1 ♂ (TCWC). EL SALVADOR. *Chalatenango*: 20 km W Chalatenango, 250 m, 1 ♀ (TCWC). *La Libertad*: 13 km W La Libertad, 15 m, 2 ♀ ♀ (TCWC). HONDURAS. *Valle*: 6 km E Amatillo, 60 m, 3 ♀ ♀ (TCWC); 10 km E San Lorenzo, 25 ft, 3 ♂ ♂ (TCWC). NICARAGUA. *Rivas*: 3 km N, 4 km W Sapoá, 40 m, 1 ♀ (KU). PANAMA. *Cocle*: 2 mi E Río Hato, 3 ♀ ♀, 2 ♂ ♂ (USNM). *Veraguas*: Isla Cébaco, 2 ♀ ♀, 1 ♂ (USNM). COLOMBIA. *Cundinamarca*: Villeta, 1 ♀ (alc., skull) (AMNH). PERU. *Loreto*: Balta, Río Curanja, 2 ♀ ♀, 2 ♂ ♂ (LSU); mouth of Río Mazán, 1 (sex unknown), 2 ♀ ♀ (AMNH); Sarayacu, Río Ucayali, 1 ♀ (AMNH). BOLIVIA. *Beni*: Guayaramerin, 2 ♀ ♀, 2 ♂ ♂ (AMNH); 4 km above Costa Marquez, 1 ♀ (skeleton) (AMNH); Pampa de Meio, 1 ♀ (skeleton) (AMNH); Río Iténez, opposite Costa Marquez, 11 ♀ ♀, 6 ♂ ♂ (AMNH); Boca del Río Baures, 7 ♀ ♀ (2 alc., skulls; 1 skull only), 6 ♂ ♂ (2 alc., skulls; 1 skeleton) (AMNH). VENEZUELA. *Carabobo*: Valencia, 1 (sex unknown) (BMNH). *Trujillo*: 46 km WNW Valera, 39 m, 1 ♂ (USNM). *Bolivar*: Al Orinoco, Palya del Medio,

TABLE 1.—*Selected measurements of* Uroderma magnirostrum, *with means followed by extremes in parentheses.*

	Type	Females	*N*	Males	*N*
Forearm	41.2	43.3 (41.0–46.6)	36	42.1 (36.0–43.8)	22
Third metacarpal	41.2	42.8 (40.5–45.5)	39	41.9 (35.0–43.7)	21
Greatest length of skull	22.5	23.2 (21.9–24.9)	51	23.1 (22.0–24.1)	25
Zygomatic breadth	12.5	12.7 (12.1–13.2)	50	12.7 (12.0–13.5)	24
Breadth of cranium	9.7	9.8 (9.4–10.3)	50	9.7 (9.0–10.0)	25
Maxillary toothrow	7.7	8.0 (7.5–8.5)	50	8.0 (7.7–8.3)	25
Width across molars	8.6	9.0 (8.4–9.5)	50	8.9 (8.5–9.3)	26
Mandibular toothrow	8.2	8.6 (8.0–9.1)	47	8.6 (8.2–9.1)	25

Isla de Cuba (= 50 km NE Puerto Páez), 7 ♀ ♀ (UCV). BRAZIL. *Pará*: 1 ♀ (alc., skull) (BMNH). Belem, 1 ♂ (USNM); Boim, Río Tapajós, 3 ♀ ♀ (1 alc., skull) (MCZ).

SHALLOW-ROSTRUM GROUP

Of the numerous characters examined, including color, pelage, sex, weight, 10 cranial measurements, and four of the wing, only total length of skull, zygomatic breadth, length of maxillary toothrow, width across the molar series and size (length and width of occlusal surface) of the second lower molar were found to be useful in the study of geographic variation in this species.

Based on greatest length of skull (Fig. 4) the specimens segregate into three geographic groups: (1) those from South America (except Colombia), in which the means of this measurement normally exceed 22.9; (2) those from Colombia, most of Panamá, and the Pacific versant from Costa Rica to Oaxaca, in which the means are less than 22.8; and (3) those from the Bocas del Toro region of Panamá to Veracruz, México, on the Atlantic versant of Middle America, in which the means again exceed 22.9. In South America, excluding Colombia, the specimens from Perú and Trinidad are largest, those from Venezuela and Brazil, smallest.

Analyses of data on length of maxillary toothrow and width across the upper molars (M2–M2) reveal the same general pattern: a population in South America (excluding Colombia) in which the mean length of the maxillary toothrow ranges from 8.0 to 8.3; a population of smaller individuals in Colombia and the Pacific versant of Middle America in which the mean length of the maxillary toothrow ranges from 7.68 in Colombia to 7.95 along the Pacific versant of Middle America; and a third group occupying the Atlantic versant of Middle America from Bocas del Toro, Panamá, to Veracruz, México, in which the mean length is 8.2.

Ratios of mean length of maxillary toothrow/mean width across the molars clearly indicate two areas of differentiation. In one, comprising all of South America, with the exception of Colombia, this ratio is 88.82 in the sample (48) from eastern Brazil, 88.20 in the sample (17) from Trinidad, 88.46 in the 34 from Perú and Ecuador, and 89.89 in 19 from Bolivia. The second area comprises Colombia and Middle America. This ratio is 86.58 in the sample from

TABLE 2.—*Comparisons of certain measurements, percentages and ratios of* Uroderma bilobatum.

Sample area	Maxillary toothrow		Width across molars				
	Mean length	Per cent greater than 8.2	Mean	Per cent greater than 9.2	Per cent combined*	Ratio**	*N*
Eastern Bolivia, Brazil, the Guianas, and Venezuela	8.04	16.4	9.06	22.4	10.4	88.85	67
Trinidad	8.3	58.8	9.4	70.6	47.0	88.29	17
Western Bolivia, Perú, and Ecuador	8.3	52.9	9.36	76.4	47.0	88.67	34
Colombia, Panamá, and Pacific versant of Middle America	7.86	4.7	9.13	32.8	3.8	86.09	213
Atlantic versant of Middle America	8.2	36.9	9.53	95.4	37.0	86.04	65

* Percentage of individuals in the sample that have a maxillary toothrow exceeding 8.2 *combined* with a width across the molars exceeding 9.2.

** Ratio of mean length of maxillary toothrow to mean width across M2–M2.

Colombia (46), 86.31 in that (167) from Panamá (exclusive of the Bocas del Toro region) and the Pacific versant of Middle America, and 86.04 in the sample of 65 from the Atlantic versant. Thus, in the samples from Colombia and Middle America the width across the molars is relatively greater, compared with length of maxillary toothrow, than it is in the population from South America exclusive of Colombia.

The close agreement of this ratio among all samples from South America, exclusive of Colombia, suggests that all are from the same population even though the linear measurements of the individuals from (1) Perú and Ecuador and (2) Trinidad deviate noticeably from those of individuals from eastern Bolivia, Brazil, the Guianas and Venezuela. This is evident in Table 2. For example, in the samples from Brazil and Bolivia to Venezuela the mean length of the maxillary toothrow is 8.04 and in only 10.4% of the sample of 67 does it exceed 8.2, whereas in the Trinidad sample of 17 the mean is 8.3 and 58.8% exceed 8.2; in the sample of 34 from Perú and Ecuador the mean is also 8.3 and 52.9% exceed 8.2. These data clearly reveal that the specimens from Trinidad and Perú–Ecuador have longer maxillary toothrow in general than the rest of the South American population.

In the samples from Colombia and Middle America there appear to be two populations. One occupies Colombia, Panamá (except the Bocas del Toro region), and the Pacific versant as far north as Oaxaca. The other occupies the Atlantic versant from Bocas del Toro, Panamá, north to Veracruz. In the sample of 211 from the first population the mean length of the maxillary toothrow is less than 8.0 and in only 10 (4.7%) individuals does it exceed 8.2. In the

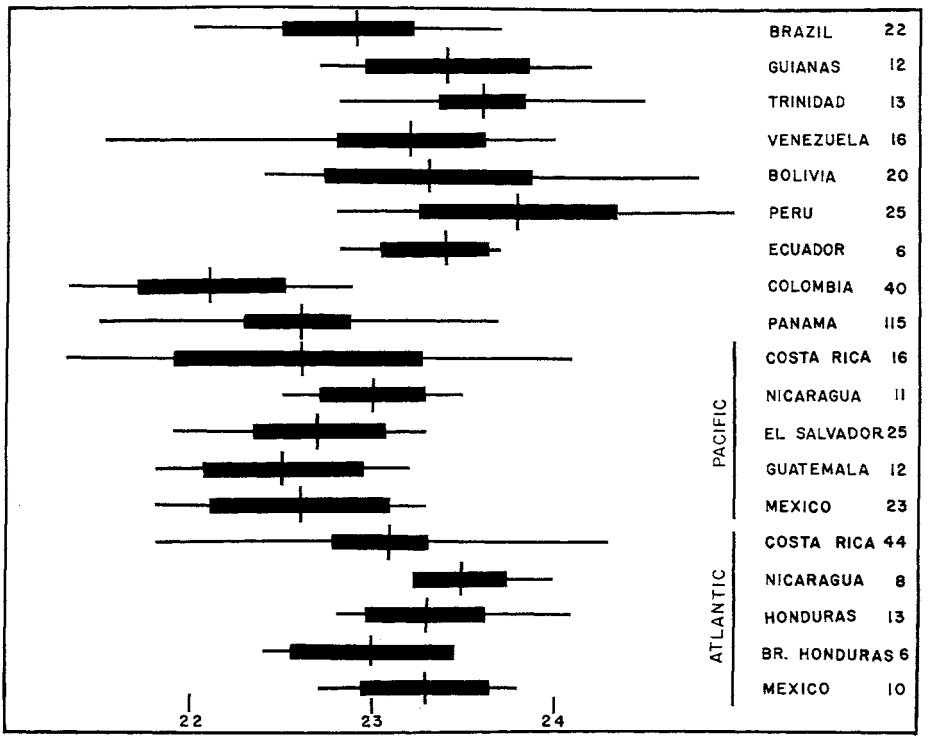

FIG. 4.—Means and extremes of skull length in samples of *Uroderma bilobatum*. The broad bars represent one standard deviation above and below the means. Sample size is given at extreme right.

second population (Atlantic versant) the mean length of the toothrow is 8.2 and in 36.9% of the individuals it exceeds 8.2. A major difference between these two Middle American populations is found in the width across the molars. In the sample from the Atlantic versant the mean width is 9.53 and in 95.4% of the individuals it exceeds 9.2. In the Colombian sample the mean width is 8.9 and in only 6.5% does it exceed 9.2; in that from Panamá and the Pacific versant the mean is 9.2 and 40% of the sample exceeds 9.2. This high percentage is due, at least in part, to the lack of any physical barrier to the mingling of populations from the Pacific and Atlantic versants in western Costa Rica and the Nicaraguan lowlands.

In an effort to measure differences in the size of teeth in these bats, I selected m2 because it is relatively easy to measure under magnification and it reflects geographic variation. To facilitate handling these data I used an "index" derived by multiplying occlusal length by occlusal width and dropping the decimal point. Fig. 5 presents these data graphically. Five populations are revealed by this index, one occurring in eastern Bolivia, Brazil, the Guianas, and Venezuela, one in Perú and Ecuador, one in Trinidad, one in the region

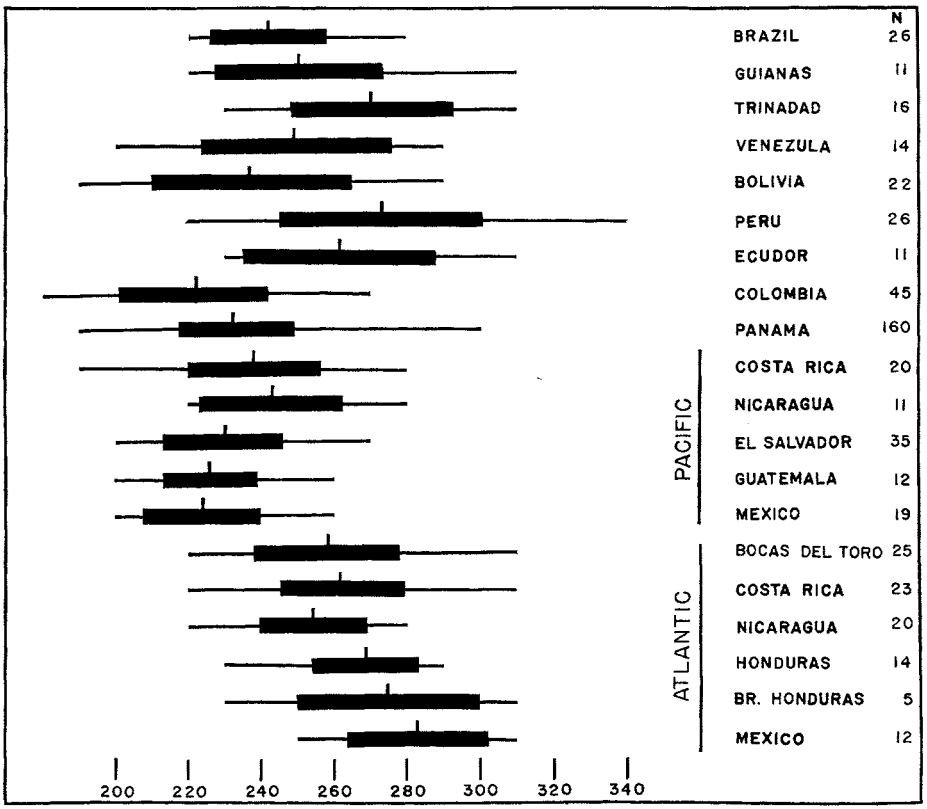

FIG. 5.—Means and extremes of the m2 index in samples of *Uroderma bilobatum*. The broad bars represent one standard deviation above and below the means. Sample size is given at extreme right.

from Colombia through Panamá and along the Pacific versant to México, and the fifth along the Atlantic versant from Bocas del Toro, Panamá, to Veracruz, México.

The abrupt decrease in the size of m2, as reflected by the index, in the Colombian sample and in those from the Pacific versant of Middle America is clearly evident in Fig. 5. Also, one can observe the rather abrupt increase in size of this tooth in the samples from the Atlantic versant. In fact, the largest m2 is found in those bats from eastern México. The marked contrast in size of this tooth in bats from the Atlantic and Pacific versants of México is evident in the figure. On the Atlantic side the mean index value is 283; on the Pacific it is 224, with little overlap in the values.

When length of maxillary toothrow is plotted against width across the molars in scatter diagrams for the same samples, significant group differences are also revealed (Table 2 and Fig. 6). In the sample from western Bolivia, Perú, and Ecuador and the one from Trinidad the mean value of both measure-

TABLE 3.—*Means and extremes of zygomatic breadth and greatest length of skull in* Uroderma bilobatum *and the percentage of each sample in which both measurements in combination exceed 13.0 and 23.0, respectively.*

Sample area	*N*	Percentage of Individuals*	Zygomatic breadth	Length of skull
Eastern Bolivia, Brazil, Guianas, and Venezuela	64	18.7	12.81 (12.0–13.5)	23.16 (21.5–24.0)
Trinidad	8	75.0	13.21 (12.6–13.8)	23.74 (22.8–24.5)
Ecuador, Perú, and western Bolivia	27	62.0	13.28 (12.8–13.9)	23.78 (22.8–25.0)
Colombia, Panamá, and Pacific versant of Central America	255	9.4	12.84 (12.0–13.8)	22.56 (21.1–24.1)
Atlantic versant of Central America	88	59.0	13.27 (12.5–14.3)	23.24 (21.8–24.5)

* Percentage of individuals in which the zygomatic breadth exceeds 13.0 *combined* with length of skull in excess of 23.0.

ments falls in the "box" outlining intersects of values above 8.25 and 9.25. In the samples from the Atlantic versant of Middle America the mean values intersect below the 8.25 line but considerably beyond a projection of the 9.25 line. In the other two sample areas the mean values intersect at points substantially short of both the 8.25 and the 9.25 lines outlining the "box." Thus, in the last two areas—(1) eastern Bolivia, Brazil, the Guianas, and Venezuela, and (2) the region from Colombia along the Pacific versant of Middle America to Oaxaca—less than 12% of the individuals in each area has a maxillary toothrow greater than 8.2 *combined* with a width across the molars in excess of 9.2. On the other hand, in the Trinidad sample, the percentage is 47; in that from western Bolivia to Ecuador it is also 47 and in that from the Atlantic versant of Middle America, 37.

When zygomatic breadth is plotted against greatest length of skull in scatter diagrams, for each of the five geographic groups mentioned above, rather marked differences can be seen. These are shown in the tabulation (Table 3) of the percentage of individuals in each area in which the zygomatic breadth and the length of the skull exceed 13.0 and 23.0, respectively. These data are presented graphically in Fig. 7.

In summary, on the basis of available data five areas of geographic differentiation in the species *Uroderma bilobatum* can be recognized, as follows:

(1) Eastern Bolivia, Brazil, the Guianas, and most of Venezuela. For the bats in this region Peters' name *bilobatum* is appropriate. These are medium in size for the species with the greatest length of the skull averaging 23.16 and the zygomatic breadth averaging 12.81, and less than 20% of the individuals

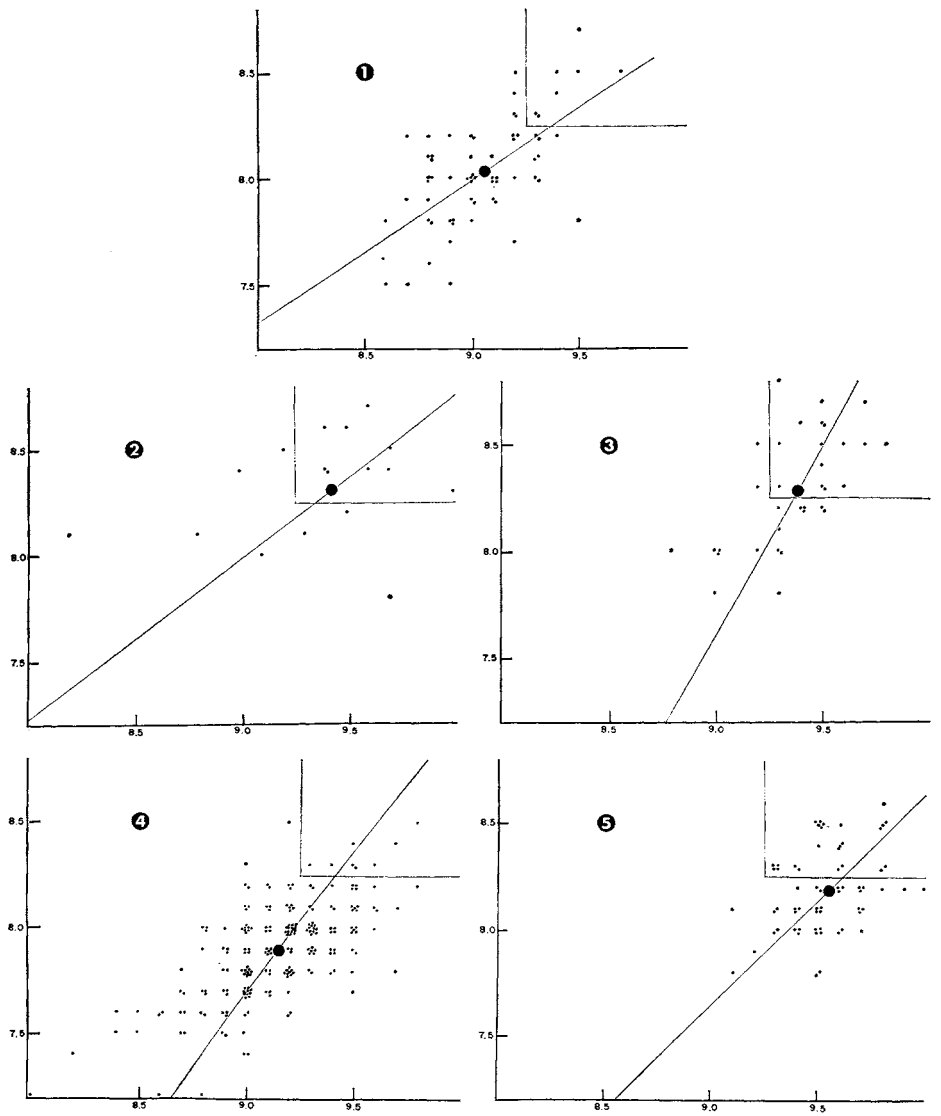

FIG. 6.—Scatter diagrams correlating length of maxillary toothrow (vertical axis) with width across M2–M2. Means are indicated by the large dots. Box at the upper right in each graph delineates values above 8.2 and 9.2. (1) Sample from eastern Bolivia, Brazil, the Guianas, and Venezuela, (2) sample from Trinidad, (3) sample from western Bolivia, Perú, and Ecuador, (4) sample from Colombia, Panamá (except Bocas del Toro area), and the Pacific versant of Middle America, (5) sample from the Atlantic versant of Middle America.

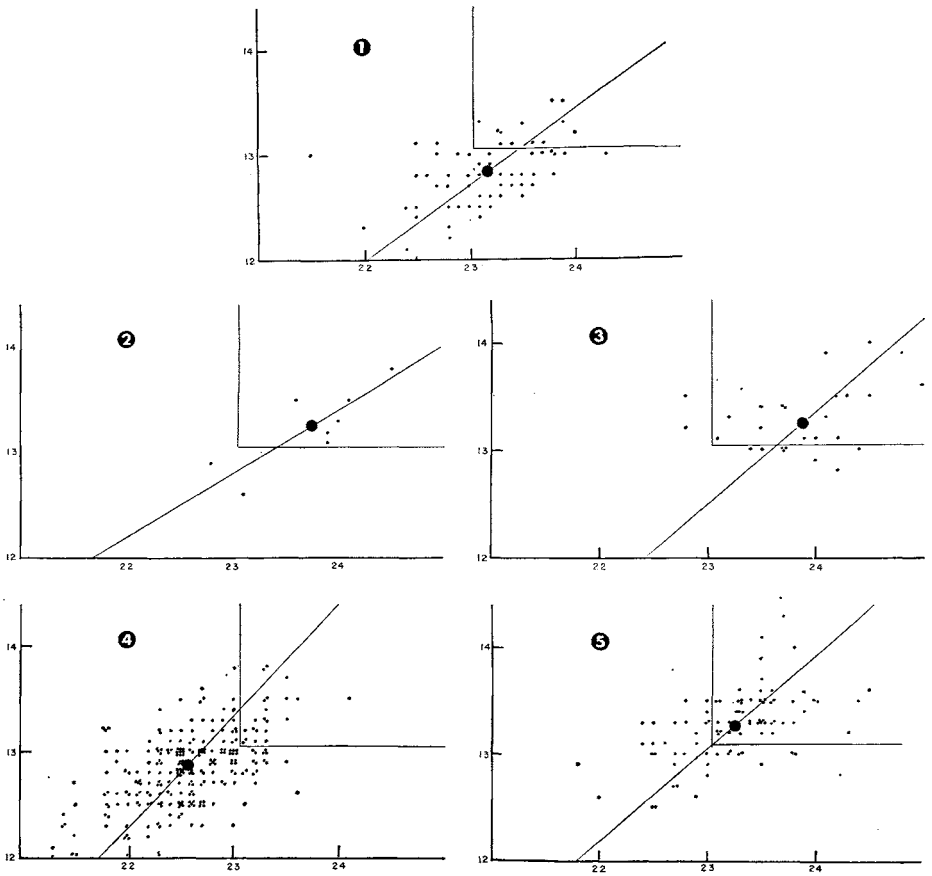

FIG. 7.—Scatter diagrams correlating zygomatic breadth (vertical axis) with greatest length of skull. Means are indicated by the large dots. Box at the upper right in each graph delineates values above 13.0 and 23.0. Samples numbered as in Fig. 6.

in the sample have a zygomatic breadth exceeding 13.0 *combined* with a skull length exceeding 23.0; mean length of maxillary toothrow is 8.04 with less than 17% of the sample exceeding 8.2; mean width across M2-M2 is 9.06, with less than 25% of the measurements exceeding 9.2; m2 index averages 250 and seldom exceeds 270.

(2) Trinidad. Individuals in the admittedly small sample from the island of Trinidad are noticeably larger than their mainland counterparts. Greatest length of skull averages 23.74 and zygomatic breadth averages 13.21, and in 75% of the specimens the former exceeds 23.0 and the latter, 13.0. Length of maxillary toothrow averages 8.3 with nearly 59% of the sample exceeding 8.2; width across M2-M2 averages 9.4 with 70% of the measurements falling above 9.2; the mean m2 index is 270 with 67% of the sample of 16 falling between 248 and 293. This population is without a name.

(3) Perú, Ecuador and western Bolivia. For the bats in this region Andersen's name *thomasi* is available and appropriate. Individuals in this group are large. Mean length of skull is 23.78 and mean zygomatic breadth is 13.28, and in 62% of the sample the skull length exceeds 23.0 *combined* with a zygomatic breadth in excess of 13.0. Mean length of the maxillary toothrow is 8.3 with this measurement exceeding 8.2 in 53% of the sample; mean width across M2-M2 is 9.36 with this measurement exceeding 9.2 in 76% of the sample; the mean m2 index is about 270.

I can find no quantitative or qualitative differences between this population of bats and the one on the island of Trinidad. But I feel compelled to treat them as different populations and, therefore, different taxa because of geographic position. The two populations are separated by a distance of nearly 2000 miles and the intervening area is occupied by the smaller *bilobatum* of Peters.

(4) Western Venezuela, Colombia, Panamá exclusive of the Bocas del Toro region, and the Pacific versant of Middle America northwestward as far as Oaxaca, México. This population is comprised of the smallest individuals in the species. Mean length of the skull is 22.56 and mean zygomatic breadth is 12.84, and in less than 10% of the sample of 255 is the skull length more than 23.0 *combined* with a zygomatic breadth of more than 13.0; mean length of the maxillary toothrow is 7.96 with less than 5% of the measurements exceeding 8.2; mean width across M2-M2 is 9.13 with about one-third of the sample exceeding 9.2; the mean m2 index is about 230 with fully 80% of the sample falling below 260. Lyon's name *convexum* is available and appropriate for this population.

(5) Atlantic versant of Middle America from Bocas del Toro, Panamá, northwestward to Veracruz, México. This population is characterized by moderate size for the species, relatively broad facial region and a high m2 index. Mean length of the skull is 23.24 and mean zygomatic breadth is 13.27, and in 59% of the sample of 88 the skull length exceeds 23.0 in *combination* with a zygomatic breadth in excess of 13.0; mean length of the maxillary toothrow is 8.2 with only 37% of the sample exceeding 8.2; mean width across M2–M2 is 9.53, greatest of all the groups, and in 95% of the sample it exceeds 9.2; the mean m2 index is about 270, but this index gradually increases from a mean of 258 in the Bocas del Toro region of Panamá to one of 283 in Veracruz (see Fig. 5). No name is available for this population.

Uroderma bilobatum bilobatum Peters

1865. *Phyllostoma personatum* Peters, Monatsb. preuss. Akad. Wiss., p. 587 (not Wagner).
1866. *Uroderma bilobatum* Peters, Monatsb. preuss. Akad. Wiss., p. 394.
1878. *Artibeus bilobatus*, Dobson, Catalogue of the Chiroptera in the British Museum, p. 518.
1908. *Uroderma bilobatum* Andersen, Proc. Zool. Soc. London, p. 217.
1908. *Uroderma convexum*, Andersen, Proc. Zool. Soc. London, p. 218. Colon, Panamá.
1957. *Uroderma bilobatum bilobatum*, Cabrera, Catalogo de los mamíferos de America del Sur, 1: 79.

TABLE 4.—*Selected measurements of* Uroderma bilobatum bilobatum, *with means followed by extremes in parentheses.*

	Type	Females	*N*	Males	*N*
Forearm	42.5	42.1 (39.3–44.6)	29	42.3 (40.0–43.6)	14
Third metacarpal	41.0	41.1 (38.3–43.3)	30	41.8 (39.5–43.3)	17
Greatest length of skull	22.8+	23.0 (21.5–24.0)	29	23.3 (23.0–23.8)	17
Zygomatic breadth	—	12.8 (12.0–13.3)	26	12.9 (12.4–13.5)	17
Breadth of cranium	10.0	9.9 (9.6–10.2)	28	9.8 (9.4–10.3)	18
Maxillary toothrow	8.5	8.0 (7.5–8.5)	28	8.1 (7.5–8.7)	17
Width across molars	9.2	9.1 (8.8–9.5)	27	9.1 (8.7–9.7)	18
Mandibular toothrow	9.0	8.6 (8.1–9.0)	29	8.8 (8.3–9.3)	18

Type.—Juvenile, sex not recorded, bearing the following notation on the label: "B.Z.M. /red asterisk/ Uroderma bilobatum Ptrs /411/ Sao Paulo/Sello."

The name *Uroderma bilobatum* Peters was based on four specimens, a juvenile (collected by Sello) from São Paulo, Brazil, which Andersen (1908), first reviewer of the genus, designated as "the type," two specimens from Cayenne, French Guiana, and one from an unknown locality. I have examined the type (BZM 411) and one (adult male, BZM 410) of the two specimens from Cayenne. Both are mounted specimens with expanded wings and in good condition. The skulls, formerly inside the mounts, were removed for study. The basal part of each cranium is missing (presumably removed by the taxidermist who prepared the mounts), but the critical parts, including rostrum and teeth, have been preserved.

The type, BZM 411, is a juvenile with cartilaginous epiphyses in the wing elements; skull with "shallow" rostrum and narrow mesethmoid; basal part of cranium, left zygoma and proximal half of left mandible missing; facial stripes distinct and contrasting with adjacent dark color of head; dorsal stripe distinct; ears faintly edged with whitish; general body color above and below sooty brown. The adult male from Cayenne is essentially like the type, but the skull is longer (24.2 +) and the middorsal stripe is evident only on the rump.

Diagnosis.—A medium-sized member of the *bilobatum* group with depressed rostrum, narrow mesethmoid, conspicuous facial stripes, and light-edged ears. Greatest length of skull averages 23.16 (21.5–24.3) and mean zygomatic breadth is 12.81 (12.0–13.5), with less than 20% of the individuals having skulls that exceed 23.0 *combined* with a zygomatic breadth in excess of 13.0; mean length of maxillary toothrow 8.04 (7.5–8.7), with less than 15% of the individuals exceeding 8.2 (the type, 8.5); mean width across M2-M2 9.06 (8.7–9.7), with less than 30% exceeding 9.2 (the type, 9.2), and with less than 11% of the individuals having a toothrow in excess of 8.2 *combined* with a width across M2-M2 exceeding 9.2, whereas 20% of the sample falls below the combination of 8.0 and 9.0 for these two measurements; mean ratio of toothrow to width across molars 88.82; m2 index averaging 250 and rarely exceeding 270.

Measurements.—See Table 4.

Distribution.—Known from eastern Bolivia, eastern Brazil, the Guianas, and Venezuela (see map, Fig. 8).

Comparisons.—See accounts of the other subspecies.

Specimens examined.—Total of 75, as follows: BRAZIL. *São Paulo*: São Paulo (type of *bilobatum* Peters) (BZM). *Pará*: Belem, 5♀♀, 4♂♂ (alc.) (USNM), 2♀♀ (FM); Boim, Río Tapajóz, 1♂ (MCZ); Ilho do Taiuma, Río Tocantins, 1♀, 3♂♂ (AMNH); Limõatuba, Río Tapajóz, 8♀♀, 1♂ (AMNH). BOLIVIA. *Beni*: 2 Boca del Baures, 2♀♀ (AMNH); Río Iténez, opposite Costa Marquez, Brazil, 8♀♀, 5♂♂ (AMNH); Guayaramarin, 1♂ (AMNH); Río Mamoré, 5 km S Guayaramarin, 1♀, 1♂ (AMNH); opposite Pto. Acre (= Ustares), 1♀ (AMNH). FRENCH GUIANA. Cayenne, 1♂ (Peter's syntype of *bilobatum*) (BZM). BRITISH GUIANA. Weri More, 1♀, 1♂ (ROM); Nappi Cr.,

TABLE 5.—*Selected measurements of* Uroderma bilobatum trinitatum, *with means followed by extremes in parentheses.*

	Type	Females	N	Males	N
Forearm	42.0	43.1 (41.4–44.2)	3	41.5 (40.0–42.7)	5
Third metacarpal	42.0	41.5 (39.4–43.2)	4	41.3 (39.5–42.5)	6
Greatest length of skull	23.9	23.7 (22.8–24.5)	5	23.8 (23.1–23.9)	8
Zygomatic breadth	13.1	13.4 (12.9–13.8)	4	13.0 (12.6–13.3)	4
Breadth of cranium	10.0	9.9 (9.6–10.1)	4	9.9 (9.6–10.1)	6
Maxillary toothrow	8.4	8.3 (7.8–8.6)	5	8.4 (8.1–8.7)	8
Width across molars	9.4	9.5 (9.1–10.0)	5	9.3 (8.2–9.7)	8
Mandibular toothrow	9.0	9.1 (8.6–9.5)	5	9.0 (8.8–9.2)	8

Kanuku Mts., 1 ♂ (ROM); Central Farm, Cayo District, 1 ♂ (ROM); Wau Wau, Rupununi District, 1 ♀ (ROM); Kanashen, Rupununi District, 2 ♂ ♂ (ROM); near Marurawaunowa, Rupununi District, 1 ♀ (ROM); Ishi Wau, E of Marurawa, Rupununi District, 2 ♀ ♀, 1 ♂ (ROM). VENEZUELA. *Sucre*: Calocar, 1 ♀ (USNM). *Bolivar*: Ciudad Bolivar, 1 ♂ (AMNH), Suapure, 1 ♀ (AMNH). *Anzoategui*: San Miguel, 960 m, 4 ♀ ♀ (AMNH). *Carabobo*: San Esteban, 1 ♂ (AMNH), 3 ♂ ♂ (BMNH); El Trompillo, 3 ♀ ♀ (BMNH). *Federal District*: Caracas, 950 m, 1 ♀ (MNH). *Barinas*: Res. Forestal de Ticoporo, 230 m, 1 ♀ (MNH). *Tachira*: Carretera Panamericana, 1 ♂ (MNH). *State unknown*: Central Zone of Venezuela, 1 ♀ (MNH).

Uroderma bilobatum trinitatum, new subspecies

1897. *Artibeus bilobatus,* J. A. Allen and Chapman, Bull. Amer. Mus. Nat. Hist., 9: 15. Trinidad, W. I.

1957. *Uroderma bilobatum bilobatum,* Cabrera, Catalogo de los Mamíferos de America del Sur, 1: 79. La isla Trinidad.

1961. *Uroderma bilobatum bilobatum,* Goodwin and Greenhall, Bull. Amer. Mus. Nat. Hist., 122: 254. Trinidad.

Type.—Adult male, skull and alcoholic carcass, no. 7483 American Museum of Natural History, collected on 25 March 1894, at Caparo 150 ft, Caroni County, Trinidad, by F. M. Chapman; original no. 764.

Diagnosis.—A large representative of the species *U. bilobatum.* Greatest length of skull 23.7; zygomatic breadth 13.1; maxillary toothrow 8.4; m2 index 285.

Measurements.—See Table 5.

Distribution.—The island of Trinidad.

Comparisons.—When compared with the mainland population of *bilobatum, trinitatum* is noticeably larger. Greatest length of skull averages 23.74 and zygomatic breadth averages 13.21, and 75% (less than 20% in *bilobatum*) of the sample have a skull length in excess of 23.0 *combined* with a zygomatic breadth in excess of 13.0; mean length of maxillary toothrow 8.3, with nearly 59% (less than 15% in *bilobatum*) of the measurements in excess of 8.2; mean width across M2-M2 9.4, with 70% (less than 30% in *bilobatum*) of the sample exceeding 9.2, and with 47% (less than 11% in *bilobatum*) of the sample having a toothrow exceeding 8.2 *combined* with a width across M2-M2 exceeding 9.2; mean m2 index 270 as compared with 250 in *bilobatum.*

Remarks.—I have been reluctant to name the population on the island of Trinidad because I can find no characters that separate it from the similarly large *U. bilobatum thomasi* in Ecuador, Perú, and western Bolivia. If one recognizes *thomasi* as a valid subspecies, then it becomes necessary to recognize *trinitatum* for the same reasons. The

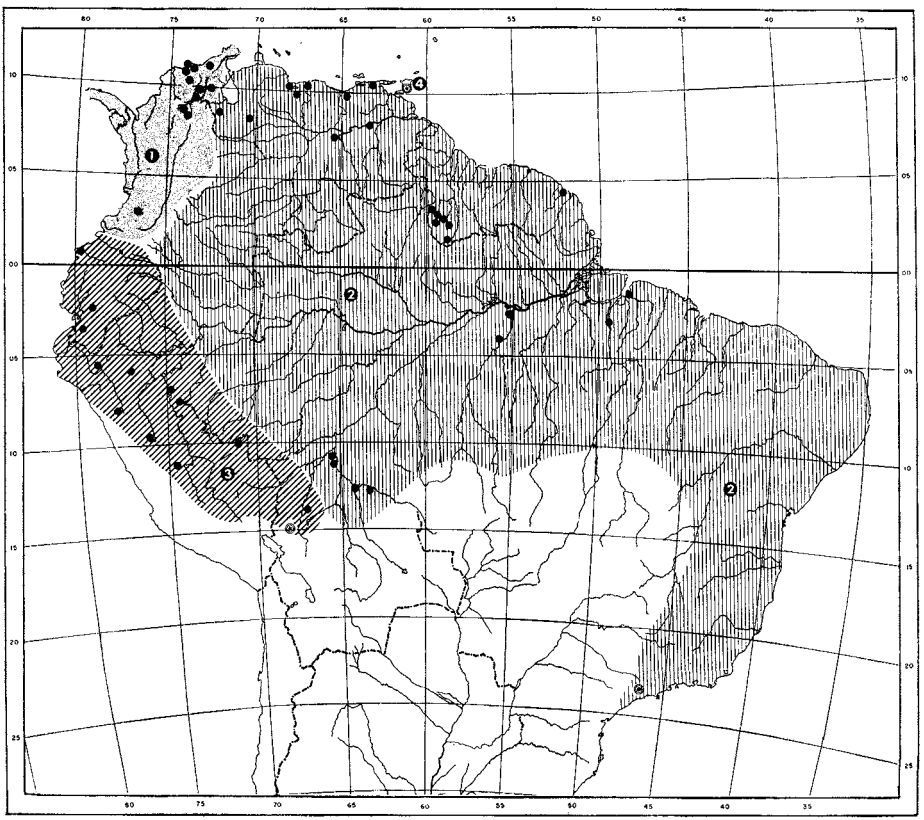

FIG. 8.—Map showing the distribution of *Uroderma bilobatum* in South America. (1) *U. b. convexum*, (2) *U. b. bilobatum*, (3) *U. b. thomasi*, (4) *U. b. trinitatum*.

alternative is to recognize neither and to consider all South American *U. bilobatum*, except those from Colombia, as referable to one subspecies.

Specimens examined.—Total of 19, as follows: TRINIDAD. Caparo, 150 ft, 3♀♀, 3♂♂ (AMNH); Aripo Heights, 1♂ (AMNH); Diego Martín, 1♂ (AMNH); Granville, 1♀, 1♂ (USNM); Guayac-Uayare, Río Claro, 1♀ (AMNH), 1♀, 1♂ (USNM); Arima Valley, 1♀ (juv.), 2♂♂ (UF); Pt. Coco, 1♀ (USNM).

Uroderma bilobatum thomasi Andersen

1880. *Artibeus* (*Uroderma*) *bilobatus*, Thomas, Proc. Zool. Soc. London, p. 396. Sarayacu, Ecuador.

1906. *Uroderma thomasi* Andersen, Ann. Mag. Nat. Hist., ser. 7, 18: 419. Bolivia.

1949. *Uroderma bilobatum thomasi*, Sanborn, J. Mamm., 30: 281. Perú.

Type.—Adult male, skin and skull, no. 1.2.1.37 British Museum (Natural History), collected on 11 October 1900, at Bellavista, 1400 ft, Departamento de Beni, Bolivia (15°S, 68°W), by Perry O. Simons; original no. 1259.

Uroderma thomasi Andersen was based on two adult males from Bolivia, the type from Bellavista and the paratype, from Reyes, both in Departamento de Beni. I have examined

TABLE 6.—*Selected measurements of* Uroderma bilobatum thomasi, *with means followed by extremes in parentheses.*

	Paratype	Females	*N*	Males	*N*
Forearm	43.5	42.2 (40.7–44.5)	9	42.2 (40.5–43.9)	16
Third metacarpal	43.5	41.5 (40.0–44.0)	14	41.8 (39.0–43.5)	21
Greatest length of skull	24.8	23.8 (22.8–25.0)	12	23.7 (22.8–24.8)	20
Zygomatic breadth	13.9	13.2 (12.8–13.6)	9	13.3 (12.9–13.9)	16
Breadth of cranium	10.6	10.0 (9.7–10.0)	11	9.9 (9.6–10.6)	20
Maxillary toothrow	8.5	8.3 (7.8–8.7)	14	8.3 (7.8–8.8)	21
Width across molars	9.8	9.4 (9.0–9.6)	14	9.3 (8.8–9.8)	21
Mandibular toothrow	9.3	8.9 (8.5–9.2)	14	9.0 (8.5–9.6)	20

the paratype (BMNH no. 0.8.3.19) collected by Viaggio di L. Balzan in 1892 and preserved in alcohol. The skull has been removed, cleaned and is intact. This specimen, although large, has the shallow rostrum, narrow mesethmoid, distinct facial stripes, and light-rimmed ears characteristic of *U. bilobatum* Peters. Consequently, *U. thomasi* Andersen is here considered to be conspecific with *U. bilobatum* Peters, a relationship first recognized by Sanborn (1949).

Diagnosis.—A large representative of *Uroderma bilobatum.* Greatest length of skull averages 23.78 (24.7 in the type and 24.8 in the paratype) and mean zygomatic breadth is 13.28 (13.9 in the paratype), with 62% of the sample having a skull length exceeding 23.0 *combined* with a zygomatic breadth exceeding 13.0; mean length of maxillary toothrow 8.3, with 53% of the sample exceeding 8.2; mean width across M2-M2 9.36, with 70% of the sample exceeding 9.2 and 47% of the sample having a toothrow exceeding 8.2 *combined* with a width across M2-M2 exceeding 9.2; mean m2 index about 270, *i.e.* the m2 measures about 1.8×1.5.

Measurements.—See Table 6.

Distribution.—Ecuador, Perú and western Bolivia (see map, Fig. 8).

Comparisons.—When compared with *U. b. bilobatum*, *U. b. thomasi* is noticeably larger (see Tables 2 and 3). Mean length of skull, 23.78 as opposed to 23.16 in *bilobatum* and mean zygomatic breadth is 13.28 as opposed to 12.81, and 62% (rather than less than 20%) of the sample have a skull length greater than 23.0 *combined* with a zygomatic breadth greater than 13.0; mean length of maxillary toothrow 8.3; mean width across M2-M2 9.36, with 47% (as opposed to less than 11%) of the sample with a toothrow exceeding 8.2 *combined* with a width across M2-M2 exceeding 9.2; mean m2 index about 270 as opposed to 250.

Compared with *U. b. convexum* from Colombia and Central America, *thomasi* is considerably larger (see Tables 2 and 3). Mean length of skull is 23.78 as opposed to 22.56, mean zygomatic breadth 13.28 as opposed to 12.84, mean length of maxillary toothrow 8.3 as opposed to 7.86, and mean m2 index about 270 as opposed to about 230.

Remarks.—The only specimen I have seen from Bolivia (from which country both the type and the paratype of *thomasi* came) that is referable to *thomasi* is the paratype from Reyes. All the others are noticeably smaller and are more like *U. b. bilobatum* from eastern Brazil, the Guianas, and Venezuela. The difference in size is particularly noticeable when one compares charts correlating length of maxillary toothrow with width across M2-M2. None of the specimens from eastern Bolivia has a toothrow exceeding 8.2 combined with a width across M2-M2 exceeding 9.2, whereas in the material from Ecuador, Perú, and western Bolivia 47% of the sample exceed these combination limits. Also, in the material from eastern Bolivia only four of the 19 specimens have a skull length exceeding 23.0 *combined* with a zygomatic breadth exceeding 13.0. In the specimens here referred to *thomasi* the percentage of the sample exceeding these limits in combination is 62. In other

words, there seems to be a rather abrupt break in the measurements of *thomasi* and *bilobatum* where their ranges meet in Bolivia. The sharpest break in the data, however, occurs between *thomasi* and the population of *convexum* occurring in Colombia (see Tables 2 and 3 and Figs. 4 and 5).

It should be pointed out that the type and paratype of *thomasi* (both males) are large individuals for this subspecies and their measurements fall near or at the upper limits of the range of variation for each variate measured. The largest individual in the sample is an adult female from the Río Chinchao, Huánaco, Perú, whose skull is 25.0 in length.

I had anticipated that the population of *U. bilobatum* inhabiting the coastal area of Ecuador would be comprised of small individuals like those occurring in Colombia, but this is not the case. In the specimens from coastal Ecuador for which skull measurements are available, mean length of the skull is 23.4 (22.8–23.7), mean zygomatic breadth is 13.2 (12.0–13.5), mean length of maxillary toothrow is 8.2 (7.8–8.7), mean width across the molars is 9.3 (8.8–9.7), and the mean m2 index is 263 (234–300). Means for the same measurements in the sample from Colombia are 22.2, 12.7, 7.7, 8.9 and 221; those for the Peruvian sample, 23.9, 13.3, 8.3, 9.3, and 270. On the basis of these sets of measurements, it is evident that the Ecuadoran bats are much closer in size to those from Perú than to those from Colombia.

It appears that in the equatorial region of South America the Andes are not as effective a barrier to the dispersal of *Uroderma* as are the mountains in Middle America. The highest elevation in the Andes from which specimens are available is 6000 feet, but I suspect that more intensive field work in Ecuador and northern Perú will reveal that *Uroderma* occurs in some of the lower passes (9000 feet) where suitable climatic and vegetative conditions are found. See Macbride (1936:14) for comments on the vegetation of northern Perú.

Specimens examined.—Total of 38, as follows: ECUADOR. *Esmeraldas*: Esmeraldas, sea level, 3♀♀ (juv.), 3♂♂ (AMNH). *Oriente*: Ovila, 1♂ (LACM) (not plotted). *Guayas*: St. Juan, 15 mi. W Huigra, 870 ft, 1♀, 2♂♂ (BMNH); near Manglar Alto, 1 (skin only) (UMMZ). *El Oro*: 9 mi. S Zaruma, 2000 ft, 2♂♂ (TCWC). PERU. *Cajamarca*: Pomará, 1♀, 1♂ (AMNH). *San Martín*: Yuracayacu, 2500 ft, 1♀ (MCZ), 3♀♀ (BMNH). *Huánuco*: Río Chinchao, San Antonio, 1♀ (USNM), 1♀ (MCZ). *La Libertad*: Guayabamba, 6000 ft, 3♀♀, 2♂♂ (AMNH). *Loreto*: 61 mi SE Pucallpa, 300 ft, 2♂♂ (TCWC); Yarinachoa, *ca.* 250 ft, 1♀, 4♂♂ (LSU); Puerto Indiana, Río Amazonas, 1♂ (AMNH); Balta, Río Curanga, 2♀♀, 2♂♂ (LSU). *Junín*: Chanchomayo, 1500 m, 1♂ (BMNH). BOLIVIA. *Beni*: Reyes, 1♂ (paratype of *thomasi*) (BMNH).

Uroderma bilobatum convexum Lyon

1902. *Uroderma convexum* Lyon, Proc. Biol. Soc. Washington, 15: 83.
1908. *Uroderma bilobatum*, Andersen, Proc. Zool. Soc. London, p. 217. Several localities in Panamá; Costa Rica.
1920. *Uroderma bilobatum*, Goldman, Smiths. Misc. Coll., 69(5): 198. Panamá.
1949. *Uroderma bilobatum*, Hershkovitz, Proc. U. S. Nat. Mus., 99: 442. Colombia.
1959. *Uroderma bilobatum bilobatum*, Hall and Kelson, The mammals of North America, 1: 131, part. México, Costa Rica, Panamá.
1966. *Uroderma bilobatum bilobatum*, Villa, Los Murciélagos de México, p. 278, part. Chiapas.
1966. *Uroderma bilobatum bilobatum*, Jones, Univ. Kansas Publ., Mus. Nat. Hist., 16: 457. Guatemala.

Type.—Young female in alcohol (skull removed and cleaned), no. 111722 U.S. National Museum; collected on 28 May 1901, at Colon, Panamá, by J. W. Humphreys.

The name *Uroderma convexum* Lyon was based on two specimens in alcohol, with skulls removed, from Colon, Panamá. I have examined both the type (USNM 111722) and the

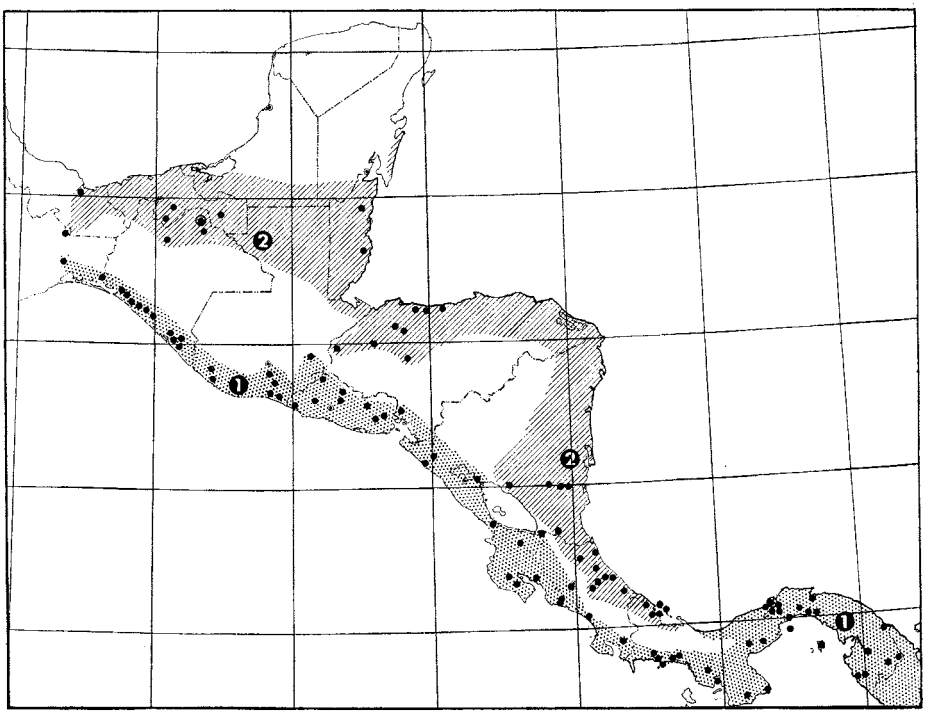

FIG. 9.—Map showing distribution of *Uroderma bilobatum* in Middle America. (1) *U. b. convexum*, (2) *U. b. molaris*.

paratype (USNM 111721) and each has the shallow rostrum, narrow mesethmoid, distinct facial stripes, and light-rimmed ears that are diagnostic of the species *U. bilobatum* Peters.

Diagnosis.—Smallest of the *U. bilobatum* complex. Mean length of skull, 22.56 (22.4 in the type) and mean zygomatic breadth 12.84 (12.5 in the type) and less than 10 percent of the population has a skull length greater than 23.0 *combined* with a zygomatic breadth greater than 13.0; mean length of maxillary toothrow 7.86 (7.8 in the type); mean width across M2–M2 9.13 (9.2 in the type) and with less than 5% of the population with a toothrow exceeding 8.2 *combined* with a width across M2–M2 exceeding 9.2; mean m2 index about 230 with fully 80% of the sample falling below 260.

Measurements.—See Table 7.

Distribution.—Western Venezuela, Colombia, Panamá (exclusive of the Bocas del Toro region) and the Pacific versant of Middle America as far as Oaxaca, México (see map, Fig. 9).

Comparison.—Compared with *U. b. bilobatum*, *U. b. convexum* is smaller in almost all variates measured. Mean length of skull 22.56, as opposed to 23.16; mean length of maxillary toothrow 7.86, as opposed to 8.04; mean m2 index 230, as opposed to 250. In zygomatic breadth and width across M2–M2 *convexum* and *bilobatum* are nearly identical with means of 12.84 versus 12.81 and 9.13 versus 9.06, respectively. As a result, the ratio of length of maxillary toothrow to width across M2–M2 (based on mean values) is lower (86) in *convexum* than it is (88) in *bilobatum*. For comparisons with other adjacent subspecies see accounts of same.

Remarks.—Of 11 pregnancies recorded among 58 females examined of this subspecies, three are in January (21 and 24), five in February (13 and 15), one in May (29), one in

TABLE 7.—*Selected measurements of* Uroderma bilobatum convexum, *with means followed by extremes in parentheses.*

	Type	Females	*N*	Males	*N*
Forearm	43.8	41.9 (39.5–44.5)	88	41.4 (38.9–44.2)	53
Third metacarpal	43.0	40.8 (37.7–44.2)	92	40.4 (37.6–44.2)	59
Greatest length of skull	22.4	22.5 (21.1–24.1)	93	22.7 (21.8–23.5)	60
Zygomatic breadth	12.5	12.8 (12.0–13.8)	81	12.9 (12.2–13.5)	55
Breadth of cranium	10.0	9.7 (9.2–10.4)	89	9.8 (9.3–10.5)	55
Maxillary toothrow	7.8	7.9 (7.2–8.4)	123	8.0 (7.2–8.5)	77
Width across molars	9.2	9.1 (8.2–9.8)	124	9.1 (8.5–9.6)	72
Mandibular toothrow	8.5	8.5 (7.8–9.1)	124	8.6 (8.0–9.1)	74

July (24) and one in November (13). Seemingly this group of bats does not have a restricted breeding season.

Site of capture as indicated on specimen labels, other than mist nets, includes "in hollow tree" (20), "under leaf of banana tree" (15), "under palm leaf" (1), "under cocoanut palm" (3), "under eave of house" (1). Numbers in parentheses indicate occurrences. These data suggest that hollow trees and banana groves are favored roosting sites for these bats, at least in Middle America.

Specimens examined.—Total of 390, as follows: MEXICO. *Oaxaca*: Tapanatepec, 1 ♂ (AMNH); 20 mi. NW La Ventosa, 2 ♀♀ (AMNH). *Chiapas*: Finca Ocuilapa, 8 mi. S Tonalá, 1 ♀, 1 ♂ (BJH), 1 ♀, 1 ♂ (UA), 1 ♀, 1 ♂ (LACM); 10 km SE Tonalá, 2 ♀♀, 1 ♂ (UA), 7 ♂♂ (LACM); 12½ km SE Tonalá, 1 ♀, 6 ♂♂ (LACM); 15 mi. ESE Tonalá, 2 ♂♂ (LACM); 11 km NW Escuintla, 100 ft, 2 ♀♀ (UA), 1 ♀, 2 ♂♂ (LACM); 2 km SE Huixtla, 100 ft, 2 ♀♀ (TCWC); 16 mi. NW Huixtla, 3 (sex unknown) (UA); 38 km N Huixtla, 2 ♀♀, 5 ♂♂ (LACM); 20 km SE Pijijiapan, 2 ♀♀, 3 ♂♂ (LACM); 23 km WNW Pijijiapan, 4 (sex unknown) (UA); 12 mi. SW Pijijiapan, sea level, 1 ♀ (skull only) (UMMZ). GUATEMALA. *Santa Rosa*: Astillero, 25 ft, 1 ♀ (KU); *Guatemala*: Amatitlán, 3800 ft, 1 ♂ (TCWC). *Escuintla*: 8 km NW Puerto San José, 50 ft, 1 ♀, 1 ♂ (TCWC); 2 mi. E Palín, 4000 ft, 1 ♀, 5 ♂♂ (TCWC). *Retalhuleu*: 20 km NW Retalhuleu, 2000 ft, 2 ♀♀ (TCWC). *Chiquimula*: 20 km SSE Chiquimula, 550 m, 2 ♂♂ (TCWC). EL SALVADOR. *Cuscatlán*: Colima, 1000 ft, 6 ♀♀, 2 ♂♂ (MVZ); 14 km NW Suchitote, 250 m, 6 ♀♀, 1 ♂ (TCWC). *Chalatenango*: 20 km W Chalatenango, 1 ♀, 2 ♂♂ (TCWC). *Ahuachapán*: Barra de Santiago, sea level, 3 ♂♂ (MVZ). *Santa Ana*: Lake Guija, El Talón, 1450 ft, 1 ♀ (MVZ). *Sonsonate*: Chilata, 2000 ft, 3 ♂♂ (MVZ). *Morazan*: 1 mi. N Divisadero, 800 ft, 2 ♀♀, 3 ♂♂ (MVZ); 4½ mi. W Divisadero, 650 ft, 4 ♀♀, 2 ♂♂ (MVZ). HONDURAS. *Valle*: 6 km E Amatilla, 60 m, 1 ♂ (TCWC). NICARAGUA. *Chinandega*: 10 km S Chinandega, 10 m, 1 ♀ (KU); San Antonio, 15 m, 1 ♂ (KU). *Managua*: 3 km N, 4 km E Sabana Grande, 4 ♀♀ (KU). *Rivas*: 12.5 km S, 13 km E Rivas, 125 ft, 2 ♀♀ (TCWC); 11 km S, 3 km E Rivas, 50 m, 2 ♀♀, 1 ♂ (KU). COSTA RICA. *Alajuela*: Los Chiles, 1 ♂ (juv.) (LACM). *Guanacaste*: Los Huecos (= Las Huacas, *ca.* 15 mi. SE Nicoya) 100 ft, 2 ♀♀, 1 ♂ (UMMZ); 8 mi. S Santa Cruz, 1200 ft, 1 ♀ (UMMZ); Miravalles, 15 mi. E Liberia, 1 ♂ (BMNH). *Puntarenas*: 9 mi. ENE Golfito, 100 ft, 4 ♀♀ (TCWC); Dominical, sea level, 2 ♀♀ (UMMZ); 6.5 mi. N, 2 mi. W Puntarenas, 100 ft, 2 ♀♀, 3 ♂♂ (TCWC). *San José*: Santa Ana, *ca.* 4000 ft, 1 ♀ (LSU); Jabillo, (*ca.* 10 km N Parrita), 1 ♀, 1 ♂ (FM); San Geronimo (Río Pirris), 1 ♂ (USNM). PANAMA. *Chiriquí*: Bogaba, 1 ♀, 5 ♂♂ (MCZ); Brava Island, 1 ♀ (BMNH); Cuesta de Piedra, 3000 ft, 1 ♀, 1 ♂ (USNM); 3 mi. W David, 150 ft, 2 ♀♀, 1 ♂ (USNM); Guabalá, 50 ft, 5 ♀♀, 2 ♂♂ (USNM); Pedregal, 10 ft, 1 ♀, 1 ♂ (USNM); San Vicente, 1600–1800 ft, 8 ♀♀ (one skull only) (USNM); Tolé, 800 ft, 5 ♀♀, 5 ♂♂ (USNM). *Veraguas*: 2 mi. W Soná, 200 ft, 1 ♂ (TCWC); 3 mi. E Soná, 100 ft, 1 ♂ (USNM); Gobernador

TABLE 8.—*Selected measurements of* Uroderma bilobatum molaris, *with means followed by extremes in parentheses.*

	Type	Females	N	Males	N
Forearm	44.0	43.7 (41.6–45.7)	43	43.4 (41.2–45.0)	26
Third metacarpal	42.0	42.7 (39.9–45.0)	46	42.3 (39.5–44.4)	26
Greatest length of skull	23.5	23.2 (21.8–24.1)	56	23.4 (22.5–24.5)	36
Zygomatic breadth	13.6	13.3 (12.5–14.3)	54	13.2 (12.5–13.6)	36
Breadth of cranium	10.0	9.9 (9.5–10.4)	44	10.0 (9.5–10.4)	26
Maxillary toothrow	8.6	8.2 (7.6–8.5)	58	8.3 (7.8–8.6)	36
Width across molars	9.8	9.5 (9.1–9.9)	46	9.6 (9.3–10.0)	26
Mandibular toothrow	9.4	8.9 (8.5–9.2)	47	9.0 (8.5–9.4)	26

Island, 1 ♂ (BMNH). *Los Santos*: Las Palmitas, 1 ♀, 2 ♂♂ (USNM); Guanico Arriba, 2 ♂♂ (SNM); Punta Mala, 1 ♀, 1 ♂ (USNM). *Cocle*: El Copé 425 m, 1 ♀ (USNM); El Potrero, 1 ♀, 2 ♂♂ (USNM); Olá, 500 ft, 1 ♀, 1 ♂ (USNM); 2 mi. E Río Hato, 100 ft, 2 ♀♀, 1 ♂ (USNM). *Panamá*: Panamá Viejo, 2 ♂♂ (USNM); Betarria (suburb of Panama City), 1 ♂ (USNM); Panama City, 3 ♀♀, 2 ♂♂ (UMMZ); Cerro Azul, 1 ♀, 1 ♂ (USNM); Pacora, 1 ♂, 1 sex not given (USNM); Ancon (near Panama City), 1 ♂ (USNM); San Miguel Island (= Isla del Rey), 1 ♀ (MCZ); Taboga Island, 1 ♀, 1 ♂ (USNM); 18 km WSW Chepo, 200 ft, 7 ♀♀, 6 ♂♂ (TCWC). *Canal Zone*: Fort Sherman, 1 ♀, 1 ♂ (UA); Río Indio, near Gatun, 12 ♀♀ (USNM); Colon (type and paratype, USNM); 1 mi. E, 4 mi. S Colon, 3 ♀♀, 1 ♂ (MVZ); 5 mi. NE Gamboa, 2 ♀♀ (MVZ); Summit Experimental Garden, 5 ♀♀, 4 ♂♂ (MVZ), 2 ♀♀ (KU), 39 ♀♀, 1 ♂ (USNM). *Darien*: Pta. Pina (near Jaqué), 1 ♂ (USNM), 1 ♂ (UA); Boca de Cupe, 7 ♀♀, 14 ♂♂ (USNM); El Real (near Boca de Cupe), 1 ♂ (USNM); mouth of Río Paya, 5 ♀♀, 5 ♂♂ (USNM); Tacarcuna Village, 1 ♂ (USNM). *San Blas*: Armila (Quebrado Venado), 1 ♀, 4 ♂♂ (USNM); Mandinga, 3 ♀♀ (USNM). VENEZUELA. *Zulia*: Sierra de Perija, 1 ♀ (USNM). COLOMBIA. *Guajira*: Barbacoas, 1 ♂ (AMNH). *Magdalena*: Onaca, near Santa Marta, 2200 ft, 1 ♀ (BMNH) (not plotted); Cacaogualito (near Santa Marta), 1 ♂ (AMNH); Bonda, 8 ♀♀, 4 ♂♂ (AMNH); Colonia Agricola de Caracolicito, 2 ♀♀ (USNM); Santa Marta (in mountains near) 400 m, 5 ♀♀, 1 ♂ (USNM); Río Guamiral, near Valledupar, 6 ♀♀, 6 ♂♂ (USNM); Sierra Negra, near Valledupar, 3 ♀♀, 1 ♂ (USNM) (not plotted). *Bolivar*: Río San Pedro, 2 ♀♀ (alc.) (USNM); Norosi, Río San Pedro, 1 ♀, 1 ♂ (USNM). *Norte de Santander*: Guamalito El Carmen, 3 ♀♀ (USNM). *Vallé*: Cali, 3300 ft, 1 ♀ (BMNH). *Department unknown*: Colonia Agriquanicito, 2 ♀♀ (USNM) (not plotted).

Uroderma bilobatum molaris, new subspecies

1946. *Uroderma bilobatum*, Goodwin, Bull. Amer. Mus. Nat. Hist., 87: 318. Costa Rica.
1959. *Uroderma bilobatum bilobatum*, Hall and Kelson, The mammals of North America, 1: 131, part. Tabasco.
1966. *Uroderma bilobatum bilobatum*, Villa, Los Murciélagos de México, p. 278, part. Tabasco.

Type.—Adult male, skin and skull, no. 16603 Texas Cooperative Wildlife Collections, collected 16 mi. NW Palenque, 100 ft, Chiapas, México, by Dilford C. Carter on 20 February 1965; original no. 5599.

Diagnosis.—A member of the *Uroderma bilobatum* complex. Molars relatively large with a mean m2 index of 270 and seldom falling below 250; mean length of skull 23.24, with 75% of the sample (88) 23.0 or more; mean zygomatic breadth 13.27, with 87% of the sample 13.0 or more; mean length of maxillary toothrow 8.2, with 94% of the sample 8.0 or more.

Measurements.—See Table 8.

Distribution.—The Atlantic versant of Middle America from the Bocas del Toro region of Panamá northwestward to southern Veracruz, México (see map, Fig. 9).

Comparisons.—For comparisons with the other subspecies of *Uroderma bilobatum* consult the summary on geographic variation, preceding the accounts of subspecies.

Remarks.—North and west of Panamá, *Uroderma bilobatum* occupies the lowlands (up to an elevation of 5000 feet) of both coastal regions in an elongated H-pattern, the cross-bar of which occurs in the Nicaraguan lowlands. In most of Costa Rica and in the region northwest of the Nicaraguan isthmus the population on the Atlantic versant is separated from that on the Pacific by high mountains that appear to serve as barriers to these bats and hence to free gene flow. This barrier effect is most pronounced at the western end of the H in the Chiapan region of southern México. Specimens from the Atlantic lowlands of southern Veracruz, Tabasco and Chiapas are so different from those of the Pacific lowlands of Chiapas and Oaxaca that one has no difficulty in separating them. Those from the Atlantic versant are darker in color, have longer forearms, larger skulls, and larger cheek teeth. As one progresses eastward to Panamá the differences become obliterated. This can perhaps be best illustrated with data on the size of m2.

The mean m2 index of 12 specimens from Veracruz, Tabasco, and northern Chiapas is 283, with extremes of 250 and 310. On the Pacific versant the mean m2 index of 20 specimens from Chiapas is 224, with extremes of 200 and 260. This difference can best be appreciated by inspection of Fig. 5. As one progresses eastward along the Atlantic lowlands from Veracruz to Panamá, the m2 index gradually gets smaller. In British Honduras the mean index is 275, in Honduras, 268, in Nicaragua, 254, in Costa Rica, 262, in the Bocas del Toro region of Panamá, 256, and in the rest of Panamá, 227.

On the Pacific versant the mean m2 index is low in Chiapas (224), Guatemala (226), and El Salvador (230). It increases to 243 in Nicaragua where no effective mountain barrier separates the two coasts, then decreases to 238 in Costa Rica and to 227 in Panamá. Along the entire Pacific versant from Oaxaca to Panamá the mean m2 index is about 231; it reaches or exceeds 260 in only nine of the 254 specimens measured (one in El Salvador, two in Nicaragua, one in Costa Rica and five in Panamá exclusive of the Bocas del Toro region). Along the Atlantic versant from Veracruz to the Nicaraguan isthmus in only six instances is the index less than 260 in a sample of 30, and in only two instances is it as low as 230. From Nicaragua eastward to Panamá the index of samples from the Atlantic versant becomes smaller, but it is still larger than that from samples on the Pacific versant at the same latitude.

The only breeding data available for this subspecies are the records of eight gravid females captured at Almirante, Bocas del Toro, Panamá, January 16 to 20, each of which contained one small embryo 6 to 8 in crown–rump length.

Specimens examined.—A total of 133, as follows: MEXICO. *Veracruz*: 1 mi. E Jaltipan 50 ft, 2 ♀♀ (TCWC). *Tabasco*: ¾ mi. S Balancán, 1 ♂, 2 ♀♀ (LSU); 1 mi. E Teapa, 1 ♀ (LSU); 10 mi. E, 19 mi. N Macuspana, 1 ♂ (KU). *Oaxaca*: near Matias Romero, 1 ♀ (MSU). *Chiapas*: Palenque, 300 m, 1 ♂ (KU); 16 mi. NW Palenque, 100 ft, 1 ♂ (TCWC); 4 mi. SE Solusuchiapa, 700 ft, 1 ♀ (KU); 8 km S Solusuchiapa, 400 ft, 1 ♀, 2 ♂♂ (LACM). BRITISH HONDURAS. Rockstone Pond, *ca.* 35 km NNW Belice, 1 ♂, 3 ♀♀ (ROM); Regalia, Stann Creek District, 1 ♂ (LSU). HONDURAS. *Cortés*: La Lima, 2 ♂♂, 1 ♀ (TCWC); 12 mi. N San Pedro Sula, 200 ft, 4 ♀♀ (TCWC); 1 mi. NW Jaral, 2300 ft, 1 ♂ (LSU). *Copán*: Copán, 660 m, 1 ♂ (TCWC). *Santa Barbara*: 7 km N Santa Barbara, 1 ♂ (TCWC). *Atlantida*: Lancetilla, 1 ♀ (TCWC); 9 mi. W La Ceiba, 25 ft, 2 ♀♀ (TCWC); 1 mi. W Tela, 1 ♀ (TCWC). NICARAGUA. *Zelaya*: 10 km W Rama, 40 m, 5 ♀♀, 4 ♂♂ (TCWC); Cacao, 400 ft, 3 ♀♀, 2 ♂♂ (TCWC). *Chontales*: La Gatiada, 1300 ft, 1 ♀ (TCWC). *Boaco*: 14 km S Boaco, 220 m, 1 ♀ (KU); San Francisco, K 92, 400 ft, 1 ♂ (TCWC). *Río San Juan*: El Castillo, 40 m, 2 ♀♀, 1 ♂ (TCWC). COSTA RICA. *Heredia*: Río Sarapiquí, Puerto Viejo, 300 ft, 1 ♂ (UMMZ); La Selva Station, 4 km S Puerto Viejo, 2 ♂♂ (LACM). *Limón*: Tortuguero, 1 ♀ (LACM);

Pandora, 30 km SSE Limón, 17 m, 2 ♀♀, 1 ♂ (LACM); La Lola, 10 ♀♀ (LACM), 1 ♀ (USNM); Río Madre de Dios, on RR, 1 ♀ (LACM); Cariari (NE of Guapiles), 3 ♂♂ (LSU). *Cartago*: Peralta, 1150 ft, 2 ♀♀ (AMNH). PANAMA. *Bocas del Toro*: Bocas del Toro, 1 ♂ (USNM); Almirante, 26 ♀♀, 25 ♂♂ (USNM); 7 km SSW Changuinola, 1 ♂ (USNM); Boca del Drago (near Almirante), 1 ♀ (USNM); Isla Bastimentos, 1 ♀ (USNM); Sibube (near Almirante), 1 ♀ (USNM).

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Literature Cited

Andersen, K. 1908. A monograph of the chiropteran genera *Uroderma, Enchisthenes,* and *Artibeus*. Proc. Zool. Soc. London, pp. 204–319.

Lyon, M. W., Jr. 1902. Description of a new phyllostome bat from the Isthmus of Panama. Proc. Biol. Soc. Washington, 15: 83–84.

Macbride, J. F. 1936. Flora of Peru, part 1. Field Mus. Nat. Hist., Bot. Ser., 13: 3–320.

Sanborn, C. C. 1949. Mammals from the Rio Ucayali, Peru. J. Mamm., 30: 277–288.

Department of Wildlife Science, Texas A&M University, College Station. *Accepted 4 June 1968.*