SYSTEMATIC STATUS OF *SYLVILAGUS BRASILIENSIS* AND *S. INSONUS* FROM NORTH AMERICA

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ABSTRACT.—Geographic variation in *Sylvilagus brasiliensis* and *S. insonus* from Mexico and Central America was reviewed by univariate and multivariate techniques. Rabbits currently referred to *S. brasiliensis* from the Cordillera de Talamanca of Costa Rica and Panama are referable to a distinct species, *S. dicei* Harris, 1932. *Sylvilagus brasiliensis* occurs in the eastern and southern lowland tropics of Mexico south through Panama and is composed of two well-defined subspecies, *S. b. truei* and *S. b. gabbi*, with a sharp zone of intergradation in southern Chiapas and Guatemala. *Sylvilagus b. consobrinus, S. b. messorius, S. b. tumacus,* and *S. b. incitatus* are all regarded as synonyms of *S. b. gabbi*. Comparisons of the species *S. brasiliensis, S. dicei,* and *S. insonus* indicate that *S. brasiliensis* and *S. dicei* are more closely related than either is to *S. insonus*.

In North America, the forest rabbit, *Sylvilagus brasiliensis,* is known to occur in tropical eastern and southern Mexico southward through Panama. The Omilteme rabbit, *S. insonus,* is known only from the Sierra Madre del Sur of Guerrero, Mexico. At the turn of the century, our taxonomic knowledge of *S. brasiliensis* consisted of only two brief descriptions: that of *Lepus brasiliensis* var. *gabbi* (=*S. brasiliensis gabbi*) from Costa Rica (Allen, 1877); and *Lepus truei* (=*S. brasiliensis truei*) from Veracruz, Mexico (Allen, 1890). Later, Bangs (1901) described *Lepus incitatus* (=*S. brasiliensis incitatus*) from San Miguel Island, Panama, and Allen (1908) described *Lepus gabbi tumacus* (=*S. brasiliensis tumacus*) from Nicaragua. During this time, Nelson (1904) described *Lepus insonus* (=*S. insonus*) from Guerrero, Mexico. Nelson (1909) subsequently reviewed the cottontails of North America and recognized *S. insonus* and *S. brasiliensis* (=*S. gabbi* of Nelson) with three subspecies, *truei, gabbi* (with *tumacus* as a synonym), and *incitatus*. Since that time, two additional subspecies of *S. brasiliensis* have been described, *S. b. messorius* (Goldman, 1912) from Panama, and *S. b. consobrinus* (Anthony, 1917) from Panama. In addition, Harris (1932) described a distinct species, *S. dicei,* from Costa Rica. Hershkovitz (1950) reduced *S. dicei* to a subspecies of *S. brasiliensis,* which now consists of six North American subspecies, *consobrinus, dicei, gabbi, incitatus, messorius,* and *truei*. *Sylvilagus insonus* is monotypic.

This report reexamines the morphology of these taxa using univariate and multivariate techniques. The results of these analyses are compared with current taxonomic findings.

METHODS

Cottontails were aged using the method described by Hoffmeister and Zimmerman (1967). Specimens considered as adults, and from which measurements were taken, were those having the supraoccipital-exoccipital sutures completely fused and obliterated. Females averaged larger than males in all characters, but this difference was slight and not significant (Student's *t*-tests, $P > 0.05$); both sexes were combined to increase sample sizes for statistical analyses.

A total of 166 specimens was examined. In addition, approximately 200 adults of *S. floridanus* and *S. cunicularius* (from Mexico and Central America) were used for comparative purposes. All holotypes of *S. brasiliensis* and *S. insonus* from North America were examined. Total length, tail length, hindfoot length, ear length from the notch, and total weight were taken from each skin tag. Body length was calculated by subtracting total length from tail length. Length of the dry ear, measured from notch to fleshy tip, was taken by me. Twenty-six cranial measurements were taken by me to the nearest 0.05 mm using a dial caliper. These measurements are discussed

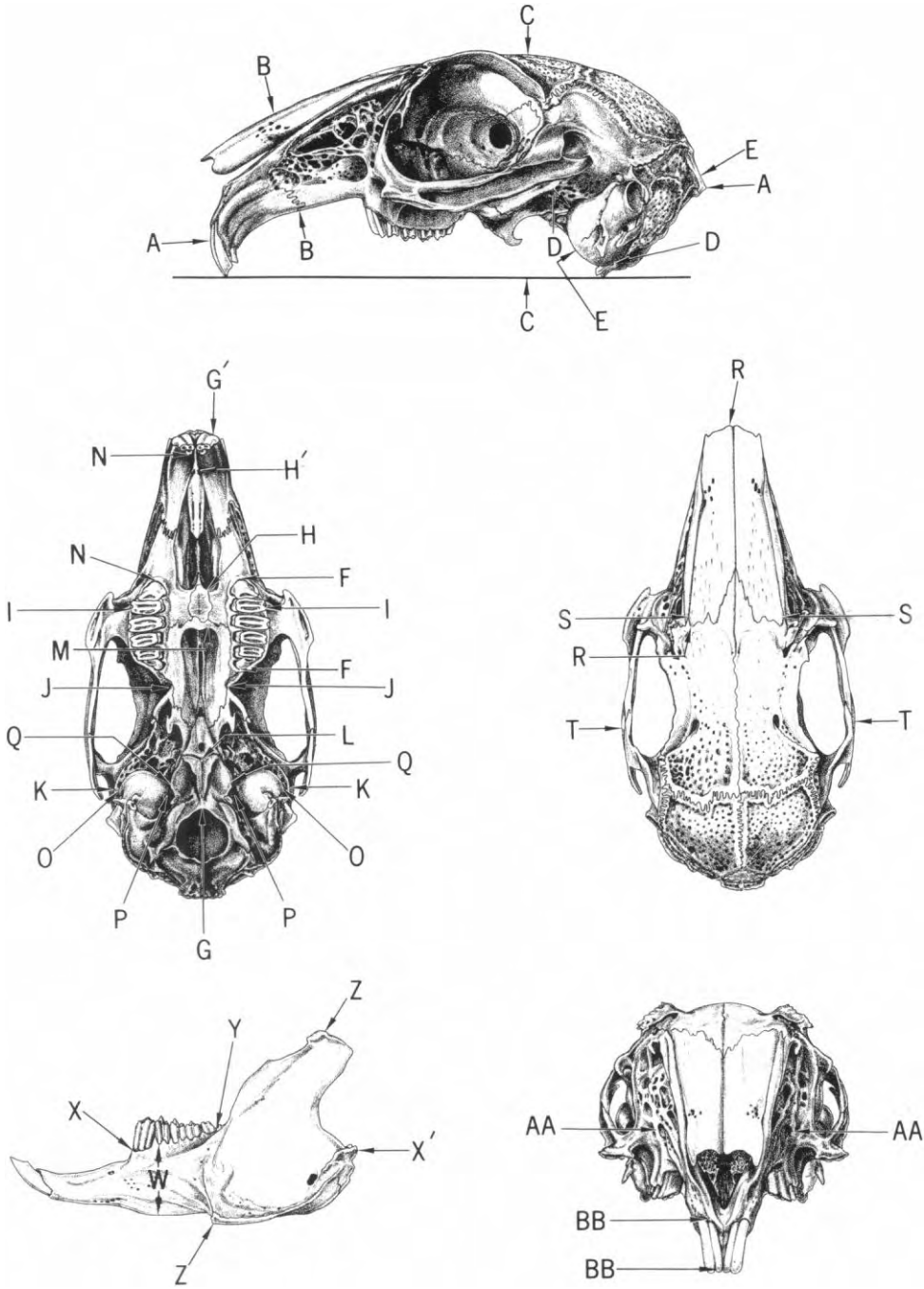

FIG. 1.—Skull of *Sylvilagus floridanus*, UIMNH 49994, from 3 mi W, 5 mi N Groom, Carson Co., Texas, illustrating the 26 cranial measurements taken. Additional details are given in the text.

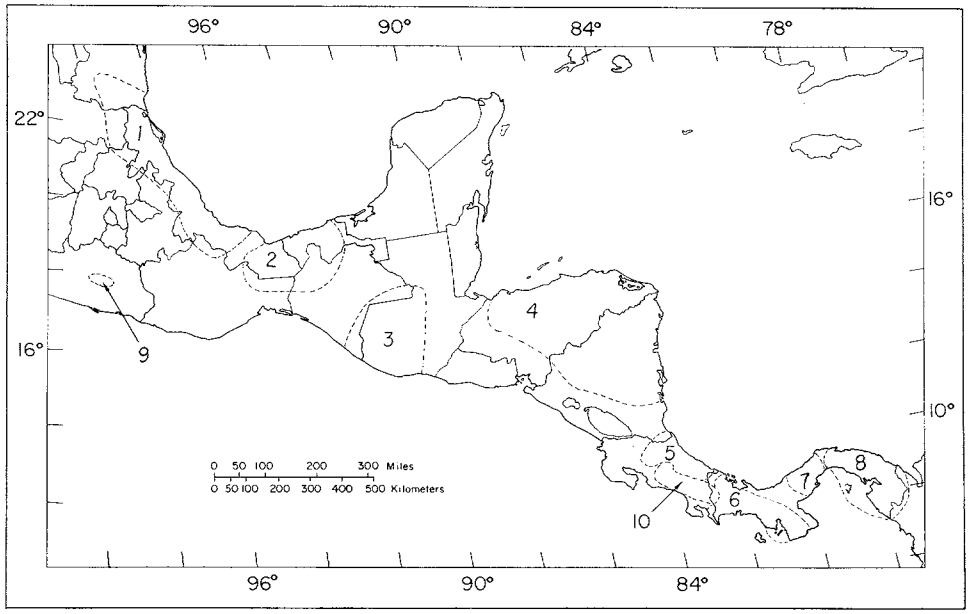

FIG. 2.—A map showing all eight samples of *Sylvilagus brasiliensis* from Mexico and Central America. Also included are sample 9 of *S. insonus* and sample 10 of *S. dicei* (previously considered a subspecies of *S. brasiliensis*). All samples are compared in a principal components analysis in Fig. 3.

by Diersing and Wilson (1980). The measurements (Fig. 1) are: greatest skull length (A–A); rostrum depth (B–B); skull depth (C–C); bulla length (D–D); shield-bullae depth (E–E); maxillary toothrow length (F–F); basal length (G–G′); incisive foramen length (H–H′); breadth across maxillary toothrows (I–I); postdental breadth (J–J); braincase breadth (K–K); basioccipital length (L–G); palate length (M–H); diastema length (N–N); bullae breadth (O–O); carotid foramina breadth (P–P); basioccipital breadth (Q–Q); nasal length (R–R); breadth across nasals (S–S); zygomatic breadth (T–T); ramus height (W); mandible length (X–X′); mandibular toothrow length (Y–X); mandible height (Z–Z); infraorbital canal breadth (AA–AA); and first upper incisor length (BB–BB). Color was qualitatively assessed by visually noting the color of the dorsum, sides, and venter of the body, tops of the hindfeet, and dorsum of the tail.

All localities where specimens were collected were plotted on a map of Mexico and Central America. Localities within 8 km of each other usually were entered as a single dot. For univariate and multivariate analyses of geographic variation, a total of 10 samples was formed (Fig. 2). These samples include nine samples currently referred to *S. brasiliensis* (samples 1–8 and 10) and one to *S. insonus* (sample 9). For each sample, the mean of each character was calculated (Table 1). Utilizing a correlation matrix of the means of the 10 samples, a principal components analysis was used to analyze the major features of geographic variation. The data variables were standardized before computing the scores. Dry ear length and 26 cranial measurements were used for the analysis. Subsequent to the principal components analysis, two bivariate analyses and two discriminant function analyses were used to investigate the phenetic relationships of rabbits in regions of possible intergradation. Each discriminant function analysis consisted of two reference groups and a geographically intermediate test group. All computer techniques were employed on the University of Illinois IBM 360 computer.

Following is a list of abridged localities from which adult specimens were analyzed. These localities are grouped accordingly into the 10 samples. For more detailed locality information, refer to the lists of *Specimens examined*. Localities represented in the samples are: (**1**) Oaxaca (Yetla), Puebla (Metlaltoyuca), San Luis Potosi (Xilitla), and Veracruz (Mirador, Motzorongo,

Otatitlan, Potrero Llano, Tapalapan); (**2**) Chiapas (Ocuilapa), Tabasco (La Venta, Macuspana, Teapa, Villahermosa), and Veracruz (Achotal, Buena Vista, Jaltepec River, Jesus Carranza); (**3**) Chiapas (Huehuetan) and Guatemala (Chinaja, Concepcion del Mar, San Jose); (**4**) Honduras (Ceiba, Danli, Monte Cristo, San Pedro Sula) and Nicaragua (El Recreo, Hacienda Tepayac, Hacienda Teperae, Hacienda la Trampa, San Ramon, Tuma); (**5**) Costa Rica (Estrella Valley, Jimenez, Olivia, Peralta, Rio Sarapiqui, San Carlos, Talamanca); (**6**) Panama (Boquete, Bugaba, Divala, Guanico Arriba, Isla Cebaco, Sibube, Tole); (**7**) Canal Zone (Balboa, Corozal, Fort Sherman, Gatun, Las Cascadas, Lion Hill, Old Panama City, Summit) and Panama (Salud); (**8**) Panama (Armila, Cana, Cerro Azul, Charco del Toro, Jaque, Mandinga, San Miguel Island); (**9**) Guerrero (Omilteme); (**10**) Costa Rica (Cerro Chirripo, Cerro Asuncion, Cervantes, El Copey de Dota, Navarro) and Panama (Cerro Punta).

RESULTS

Geographic Variation

Univariate analyses.—Externally, rabbits from Guerrero, Mexico (sample 9), and those from the Cordillera de Talamanca of Costa Rica and Panama (sample 10) are larger than rabbits of the other eight samples in total length, body length, and hindfoot length (Table 1). Specimens from Mexico and western Guatemala (samples 1–3) are medium in size, and rabbits from the lowlands of Honduras southward through Panama (samples 4–8) average the smallest in these measurements. Rabbits from Panama (samples 6–8) exhibit a slight west to east increase in size. Rabbits in sample 9 are unique in having exceedingly long ears and a long tail. Rabbits from Mexico and western Guatemala (samples 1–3) and those from the Cordillera de Talamanca of Costa Rica and Panama (sample 10) have medium length ears whereas individuals from the lowlands of Central America (samples 4–8) have the shortest ears.

Overall size of the skull, as reflected in greatest skull length, basal length, braincase breadth, and zygomatic breadth, is largest in those rabbits from Guerrero and those from the cordillera of Costa Rica and Panama. Rabbits from Mexico and western Guatemala (samples 1–3) have medium-sized skulls and individuals of all other Central American samples (4–8) have the smallest skulls. In samples 4 through 8, there is a slight increase in skull size from Honduras and Nicaragua to eastern Panama.

In nasal length, rabbits in samples 9 and 10 average the longest. All other samples average smaller with those in samples from Mexico and Guatemala being medium in length, and those from Central America being the shortest. Rabbits in samples 1 through 8 exhibit little geographic variation in postdental breadth, basioccipital breadth, and diastema length. In these same three measurements, individuals from Guerrero are relatively narrow in postdental breadth and basioccipital breadth, and medium-sized in diastema length. Rabbits from the cordillera of Costa Rica and Panama are unusually large in these same measurements.

Inflation of the auditory bullae, as primarily reflected in bulla length and less so in bullae breadth, shield-bullae depth, and skull depth, is greatest among individuals from Mexico (samples 1 and 2). Rabbits from southern Mexico and Guatemala (samples 3 and 9) have medium-sized bullae and rabbits in samples 4 though 8 and 10 have small auditory bullae.

Depth of the mandibular ramus averages smallest in samples 1 through 8, intermediate in sample 10, and largest in sample 9. Length of the maxillary and mandibular toothrows differs little among samples 1 through 8, and is largest in samples 9 and 10. Breadth across the maxillary toothrows follows this same pattern with the exception that sample 9 from Guerrero is relatively narrow and is much like samples 1 through 8, whereas sample 10 is extremely broad.

In general, first upper incisor length, palate length, breadth across the nasals, incisive foramen length, basioccipital length, rostrum depth, carotid foramina breadth, mandible length, mandible height, and infraorbital canal breadth varied in accordance

TABLE 1.—*Mean (±1 SD) for 32 measurements of* Sylvilagus dicei, S. insonus, *and 8 samples of* S. brasiliensis, *all in mm.*

	S. brasiliensis truei			*S. brasiliensis gabbi*					*S. insonus*	*S. dicei*
Characters	Sample 1 n = 10	Sample 2 n = 13	Sample 3 n = 8	Sample 4 n = 18	Sample 5 n = 9	Sample 6 n = 19	Sample 7 n = 13	Sample 8 n = 15	Sample 9 n = 2	Sample 10 n = 11
Total length	388.44 ± 28.6	387.70 ± 30.4	380.83 ± 25.7	361.92 ± 24.6	365.50 ± 15.7	367.89 ± 22.5	365.50 ± 36.8	370.00 ± 24.5	435.00	417.89 ± 27.8
Tail length	22.44 ± 6.39	29.70 ± 13.0	22.60 ± 8.14	17.50 ± 7.17	18.83 ± 11.5	22.06 ± 6.38	21.00 ± 5.66	24.23 ± 5.85	42.50	21.67 ± 7.16
Body length	366.00 ± 29.4	357.91 ± 27.6	355.40 ± 25.8	344.33 ± 22.0	346.67 ± 8.80	345.72 ± 22.9	344.50 ± 34.0	343.46 ± 24.5	392.50	396.22 ± 26.1
Hindfoot length	77.67 ± 7.16	79.90 ± 3.84	79.17 ± 2.04	77.42 ± 6.13	73.33 ± 5.16	75.83 ± 3.67	77.50 ± 3.34	76.57 ± 3.18	92.50	94.00 ± 4.53
Ear length (wet)	58.75 ± 12.6	52.00 ± 2.78	51.50 ± 0.71	46.45 ± 1.92	45.50 ± 0.58	47.17 ± 4.66	46.50 ± 6.02	46.69 ± 2.29	65.00	51.22 ± 2.77
Ear length (dry)	47.36 ± 3.74	44.12 ± 2.27	45.03 ± 1.77	38.66 ± 3.31	38.20 ± 1.31	40.39 ± 1.73	41.21 ± 2.71	41.97 ± 2.32	61.60	44.53 ± 1.62
First upper incisor length	6.83 ± 0.92	6.70 ± 0.30	6.72 ± 0.60	6.22 ± 0.46	5.92 ± 0.44	5.91 ± 0.65	6.05 ± 0.60	6.46 ± 0.32	7.28	7.07 ± 0.53
Palate length	6.07 ± 0.67	6.87 ± 0.48	7.15 ± 0.30	6.95 ± 0.37	7.63 ± 0.50	7.68 ± 0.70	7.16 ± 0.44	7.65 ± 0.73	7.60	6.72 ± 0.50
Greatest skull length	71.92 ± 2.91	72.70 ± 2.64	71.64 ± 2.12	68.86 ± 2.07	69.56 ± 2.03	69.56 ± 2.17	69.86 ± 2.16	70.67 ± 2.24	77.45	75.76 ± 1.91
Basal length	58.41 ± 2.46	59.25 ± 2.49	58.48 ± 1.47	56.62 ± 1.90	56.59 ± 2.02	57.04 ± 2.01	57.05 ± 1.96	58.20 ± 1.81	62.13	61.89 ± 1.94
Zygomatic breadth	34.08 ± 1.44	34.70 ± 0.90	34.20 ± 0.63	32.74 ± 0.76	33.17 ± 0.83	33.00 ± 0.99	33.28 ± 1.39	33.43 ± 1.06	37.50	37.35 ± 1.31
Braincase breadth	25.53 ± 1.69	25.79 ± 0.90	25.34 ± 0.56	24.09 ± 0.89	24.33 ± 0.73	24.07 ± 0.59	23.99 ± 0.73	24.38 ± 0.89	27.88	27.20 ± 0.92
Nasal length	30.05 ± 1.85	31.03 ± 1.48	30.16 ± 1.75	29.79 ± 1.32	29.13 ± 1.37	28.74 ± 1.45	28.79 ± 1.58	28.90 ± 1.45	31.98	32.67 ± 1.15
Breadth across nasals	14.11 ± 0.83	13.59 ± 0.66	14.75 ± 0.61	13.29 ± 0.55	12.71 ± 0.89	12.85 ± 0.77	12.78 ± 0.74	13.17 ± 0.75	14.65	14.64 ± 0.78
Maxillary toothrow length	14.13 ± 0.40	14.69 ± 0.71	14.27 ± 0.26	14.06 ± 0.50	14.29 ± 0.38	13.93 ± 0.57	14.08 ± 0.68	14.52 ± 0.43	15.30	15.23 ± 0.37
Breadth across maxillary toothrows	21.12 ± 0.78	21.44 ± 0.77	20.72 ± 0.70	20.41 ± 0.61	20.61 ± 0.60	20.55 ± 0.71	20.76 ± 1.02	21.35 ± 0.67	21.98	23.08 ± 0.67
Postdental breadth	9.63 ± 0.50	9.93 ± 0.36	9.86 ± 0.54	9.21 ± 0.45	9.72 ± 0.40	9.53 ± 0.52	9.49 ± 0.45	9.68 ± 0.36	9.43	10.77 ± 0.74
Incisive foramen length	18.15 ± 1.33	18.82 ± 1.02	18.33 ± 0.74	17.65 ± 0.75	17.13 ± 0.73	17.51 ± 0.90	17.72 ± 0.63	18.05 ± 0.99	18.75	19.40 ± 0.63
Basioccipital length	8.79 ± 0.55	8.60 ± 0.62	8.29 ± 0.43	7.96 ± 0.46	7.87 ± 0.34	7.91 ± 0.37	7.95 ± 0.34	8.21 ± 0.46	9.23	9.00 ± 0.51
Basioccipital breadth	9.36 ± 0.79	9.19 ± 0.72	9.14 ± 0.41	8.78 ± 0.63	8.97 ± 0.49	9.06 ± 0.82	9.24 ± 0.66	9.52 ± 0.62	8.95	9.95 ± 0.53
Diastema length	20.75 ± 1.56	21.14 ± 0.91	20.88 ± 1.07	20.38 ± 0.74	20.19 ± 0.71	20.34 ± 0.99	21.12 ± 0.85	20.29 ± 1.00	20.75	22.01 ± 0.87
Rostrum depth	13.99 ± 0.69	14.13 ± 0.57	14.36 ± 0.45	13.13 ± 0.43	13.35 ± 0.67	13.19 ± 0.67	13.21 ± 0.50	13.36 ± 0.63	15.65	15.01 ± 0.47
Bulla length	10.18 ± 0.64	10.27 ± 0.29	9.46 ± 0.56	8.79 ± 0.36	8.42 ± 0.35	8.66 ± 0.33	8.82 ± 0.38	8.97 ± 0.40	9.50	8.87 ± 0.44
Bullae breadth	24.33 ± 1.61	23.90 ± 0.85	23.94 ± 0.93	22.02 ± 0.85	22.37 ± 0.95	22.35 ± 0.55	22.91 ± 0.92	22.95 ± 0.68	25.58	24.62 ± 0.79
Shield-bullae depth	20.52 ± 0.56	20.67 ± 0.47	20.23 ± 0.81	18.52 ± 0.68	18.51 ± 0.37	18.71 ± 0.72	18.72 ± 0.46	18.50 ± 0.45	21.15	20.24 ± 0.69
Skull depth	29.82 ± 1.22	29.96 ± 1.01	29.99 ± 1.20	27.97 ± 0.65	28.21 ± 0.93	28.11 ± 0.95	28.15 ± 0.98	28.36 ± 0.73	31.98	30.66 ± 0.65
Carotid foramina breadth	11.17 ± 0.76	10.75 ± 0.61	10.94 ± 0.69	10.44 ± 0.62	11.03 ± 0.70	10.52 ± 0.59	10.84 ± 0.67	10.82 ± 0.60	13.18	12.50 ± 0.36
Infraorbital canal breadth	17.10 ± 0.81	17.30 ± 0.73	17.07 ± 0.97	16.57 ± 0.73	16.59 ± 0.50	16.62 ± 0.83	16.62 ± 0.87	17.48 ± 0.97	18.13	18.84 ± 0.91
Mandible height	34.52 ± 1.69	34.89 ± 1.37	33.37 ± 0.73	33.08 ± 1.51	33.48 ± 1.60	33.89 ± 1.47	34.27 ± 1.25	34.77 ± 1.72	36.08	37.34 ± 1.55
Mandible length	37.38 ± 1.24	37.57 ± 1.40	36.71 ± 1.52	35.38 ± 1.46	35.69 ± 1.01	35.65 ± 1.30	36.22 ± 1.43	36.74 ± 1.36	39.15	39.68 ± 1.45
Ramus height	9.99 ± 0.65	10.05 ± 0.58	9.33 ± 0.41	9.47 ± 0.37	9.07 ± 0.57	9.69 ± 0.67	9.87 ± 0.53	10.15 ± 0.75	10.98	10.49 ± 0.46
Mandibular toothrow length	14.88 ± 0.36	15.46 ± 0.66	14.84 ± 0.43	14.50 ± 0.50	14.76 ± 0.43	14.68 ± 0.55	14.73 ± 0.78	15.28 ± 0.60	16.20	16.09 ± 0.46

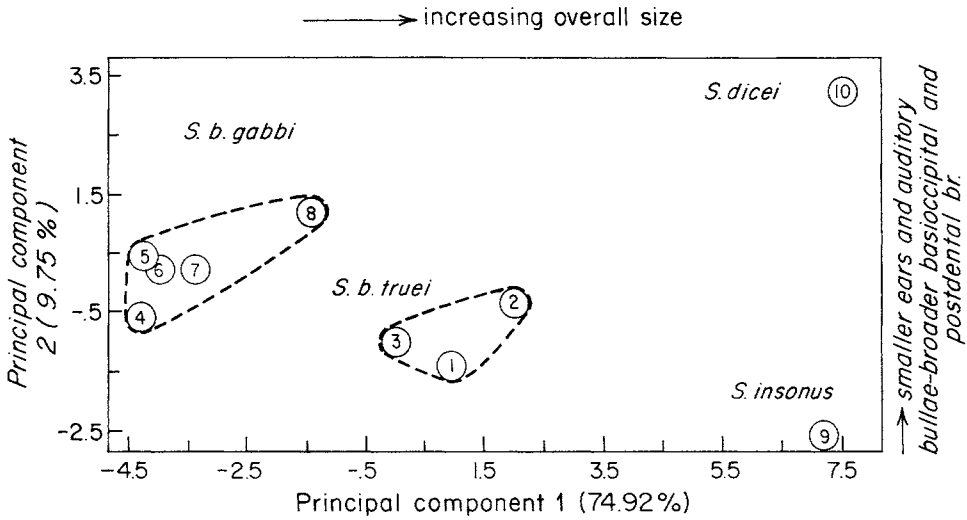

FIG. 3.—A principal components analysis of the 8 samples of *Sylvilagus brasiliensis*, sample 9 of *S. insonus*, and sample 10 of *S. dicei*. Data for the analysis consisted of dry ear length and 26 cranial measurements.

with changes in the overall size of the skull, except that rabbits from the cordillera of Costa Rica and Panama have a short palate and those from Guerrero have short incisive foramina.

Color.—Color variation in the 10 samples is less than that found in such wide ranging species as *S. floridanus*, *S. nuttallii*, or *S. audubonii*. In all samples except 9, the color of the dorsum of the body ranges from a brownish black (more brown than black) in Mexico to western Guatemala to a blackish-brown (more black than brown) in Honduras through Panama. A few specimens from Costa Rica and southern Panama are almost completely black dorsally. The tail is unicolored and is slightly paler than the dorsum. The tops of the hindfeet of rabbits in samples 1 through 8 and 10 are dark brown. Rabbits from Guerrero are unique in having a bicolored tail that is whitish ventrally and blackish with some rufous dorsally. The dorsal pelage is rufous-black and the tops of the hindfeet are whitish.

Multivariate analyses.—The principal components analysis of the 10 samples agreed closely with the univariate analyses. The first principal component explained

TABLE 2.—*List of the 18 cranial characters and their discriminant multipliers used in a discriminant function analysis (Fig. 5) comparing individuals of* Sylvilagus brasiliensis truei *with* S. b. gabbi *from Mexico and Central America. See text for details.*

Character	Discriminant multiplier	Character	Discriminant multiplier
Greatest skull length	−0.177	Incisive foramen length	0.052
Basal length	0.040	Basioccipital length	0.200
Zygomatic breadth	0.105	Basioccipital breadth	−0.233
Braincase breadth	0.090	Diastema length	−0.072
Nasal length	0.051	Rostrum depth	0.142
Breadth across nasals	−0.098	Bulla length	0.642
Maxillary toothrow length	−0.241	Bullae breadth	−0.001
Br. across max. toothrows	−0.050	Shield-bullae depth	0.550
Postdental breadth	0.157	Skull depth	0.115

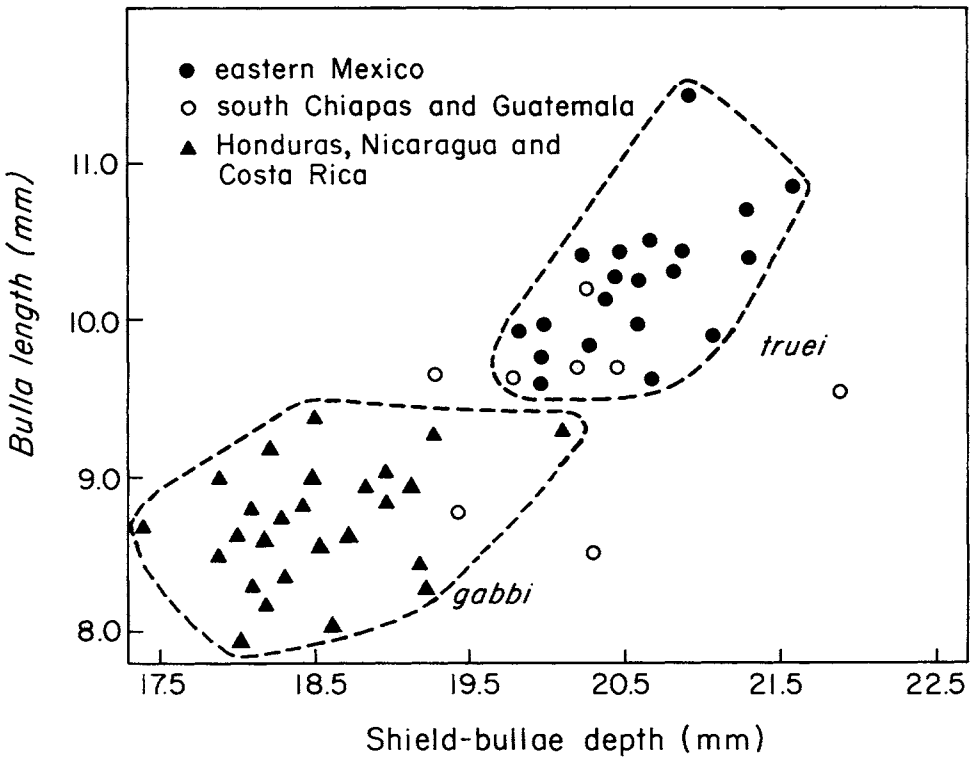

FIG. 4.—A scattergram analysis comparing *Sylvilagus brasiliensis truei* (samples 1–3) from southern Tamaulipas to western Guatemala with *S. b. gabbi* (samples 4–5) from Honduras, Nicaragua, and Costa Rica. Individuals of *S. b. truei* are represented by closed circles (samples 1–2) and open circles (intergrading sample 3) and *S. b. gabbi* by triangles.

74.9% of the total observed variation and separated the 10 samples on overall size differences (Fig. 3). All variables loaded positively on this component, with greatest skull length, basal length, zygomatic breadth, and braincase breadth loading the heaviest. Rabbits from the lowlands of Honduras through Panama are the smallest, those from Mexico and Guatemala are slightly larger, and those from Guerrero and the cordillera of Costa Rica and Panama are the largest.

Principal component 2 explained an additional 9.8% of the total variation and separated samples largely by contrasting dry ear length and length of the auditory bulla against postdental breadth and basioccipital breadth. Rabbits from Guerrero, and to a lesser degree those from Mexico and Guatemala, have the longest ears and largest auditory bullae in combination with the broadest basioccipital and postdental area. Individuals from the cordillera of Costa Rica and Panama, and, to a lesser degree those from Honduras to Panama, exhibit opposite trends in these four characters.

Evidence of Intergradation

Northern and southern samples.—The principal components analysis illustrated that rabbits from Mexico and Guatemala are similar morphologically, but differ considerably from another morphologically coherent group ranging from Honduras to Panama (samples 4–8). Evidence of intergradation in samples 1 through 5 was investigated by a bivariate analysis of shield-bullae depth and bulla length. Individuals from samples 1 and 2 are larger (Fig. 4) in both measurements. Geographically inter-

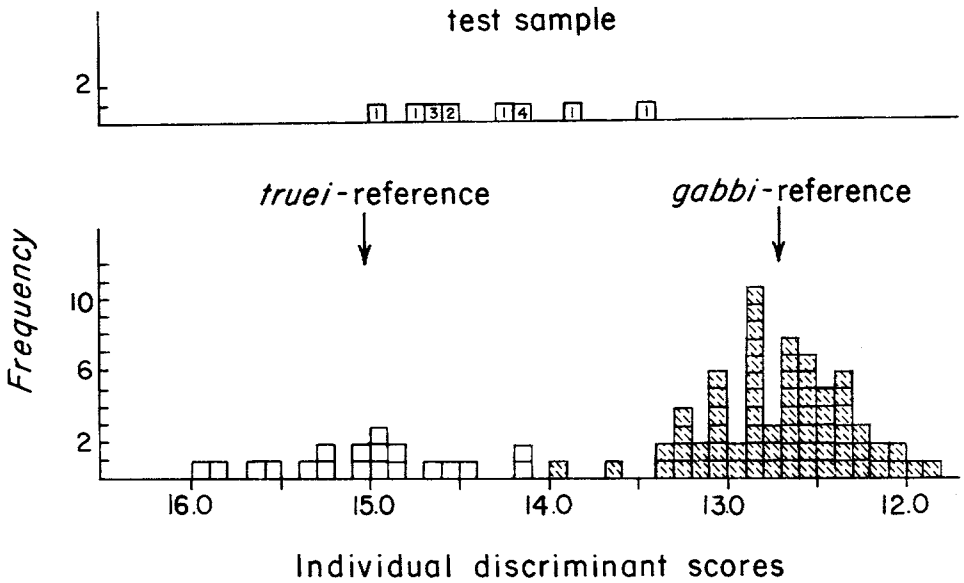

FIG. 5.—A discriminant function analysis comparing individuals of *Sylvilagus brasiliensis truei* with *S. b. gabbi*. The reference sample of *S. b. truei* consists of samples 1 and 2. The reference sample of *S. b. gabbi* consists of samples 4–8. The test sample from southern Chiapas and western Guatemala, which is best referred to *S. b. truei*, is geographically intermediate between samples 2 of *S. b. truei* and 4 of *S. b. gabbi*. For a list of the 18 characters used in the analysis, and their discriminant multipliers, refer to Table 2. Numbers used in the test sample refer to individuals from: 1) Guatemala, Concepcion del Mar; 2) Guatemala, 3 km NW Chinaja; 3) Guatemala, San Jose; and 4) Chiapas, Huehuetan. Arrows mark the mean of each reference group.

mediate individuals from southern Chiapas and Guatemala overlap both groups though most cluster with the northern samples.

A discriminant function analysis was also used to examine the extent of intergradation between the two groups (samples 1–3 and 4–8). Data for the analysis consisted of 18 cranial measurements. These measurements and their discriminant multipliers are given in Table 2. For the analysis, two reference groups were established: 1) samples 1 and 2 from Tamaulipas southward to northern Chiapas (n = 19); and 2) samples 4 through 8 from Honduras through Panama (n = 67). The test group consisted of the geographically intermediate sample 3 (n = 8) from southeastern Chiapas and western Guatemala. In the analysis, those characters that differ the most between the two reference groups, as expressed by *F*-values, are: shield-bullae depth, $F = 208.15$; bulla length, 197.91; braincase breadth, 63.92; and skull depth, 58.37. The reference groups are separable from each other by a discriminant distance of 0.17 (Fig. 5). The geographically intermediate group contains morphologically intermediate individuals having discriminant scores ranging from 13.42 to 14.91. Five adults from one locality (Concepcion del Mar, southern Guatemala) have discriminant scores of 13.42, 13.85, 14.28, 14.79, and 14.91 ($\bar{X} = 14.25$). Three of these five individuals are morphologically most like the northern reference group (*truei*), and the other two are most like the southern group (*gabbi*). Specimens from near Chinaja and San Jose, Guatemala (discriminant scores of 14.50 and 14.69, respectively), and Huehuetan, Chiapas (14.16), are best referred to the northern group, although their morphology approaches that of the southern group.

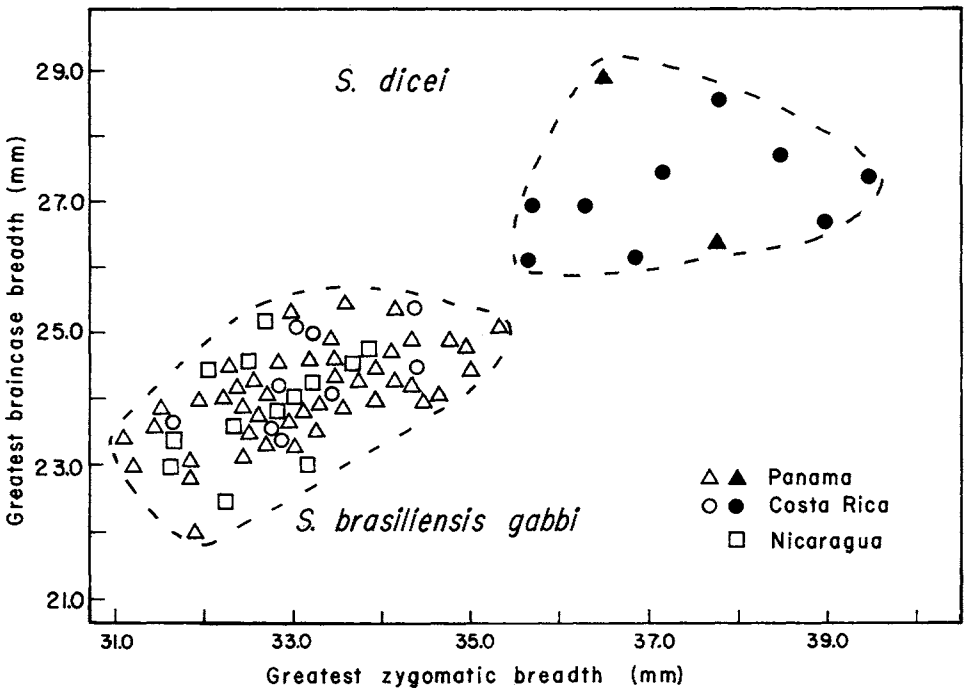

FIG. 6.—A scattergram analysis comparing *Sylvilagus dicei* (sample 10) from central Costa Rica and extreme western Panama with specimens of *S. brasiliensis gabbi* from Nicaragua (southern part of sample 4), Costa Rica, and Panama (samples 5–8). Closed symbols represent specimens of *S. dicei* and open symbols represent individuals of *S. brasiliensis gabbi*.

Highland and lowland samples.—As shown in the principal components analysis, rabbits from the high Cordillera de Talamanca of Costa Rica and western Panama (sample 10) differ markedly (primarily in much larger size) from those of the adjacent lowland tropics of Costa Rica and western Panama (samples 5 and 6). A bivariate analysis of greatest braincase breadth and greatest zygomatic breadth was used to compare individuals from the cordillera with those from the adjacent lowlands of Nicaragua, Costa Rica, and Panama (southern part of sample 4 and samples 5–8). Individuals from the cordillera of Costa Rica and Panama are larger in both measurements than adjacent lowland specimens (Fig. 6).

Discriminant analysis was also used to test for evidence of intergradation between the cordilleran sample and adjacent lowland samples. For the analysis, two reference groups were created: 1) 11 adults (sample 10) from the cordillera of Costa Rica and Panama; and 2) 41 adults from the lowlands of Honduras and Nicaragua (sample 4) and central and eastern Panama (samples 7–8). The test group consisted of 26 adults from the lowlands of Costa Rica and Panama (samples 5 and 6), contiguous with the cordilleran sample. The eight cranial characters used and their discriminant multipliers are: greatest skull length, −0.284; basal length, 0.166; zygomatic breadth, 0.332; braincase breadth, 0.374; breadth across maxillary toothrows, 0.106; rostrum depth, 0.509; skull depth, 0.506; and carotid foramina breadth, 0.339. Those characters that differed the most between the two reference groups, as indicated by *F*-values, were: greatest zygomatic breadth, $F = 125.44$; braincase breadth, 104.11; rostrum depth, 99.35; and skull depth, 97.07. In the analysis, the two reference groups are separated by a discriminant distance of 1.97 (Fig. 7). All individuals of the test group cluster

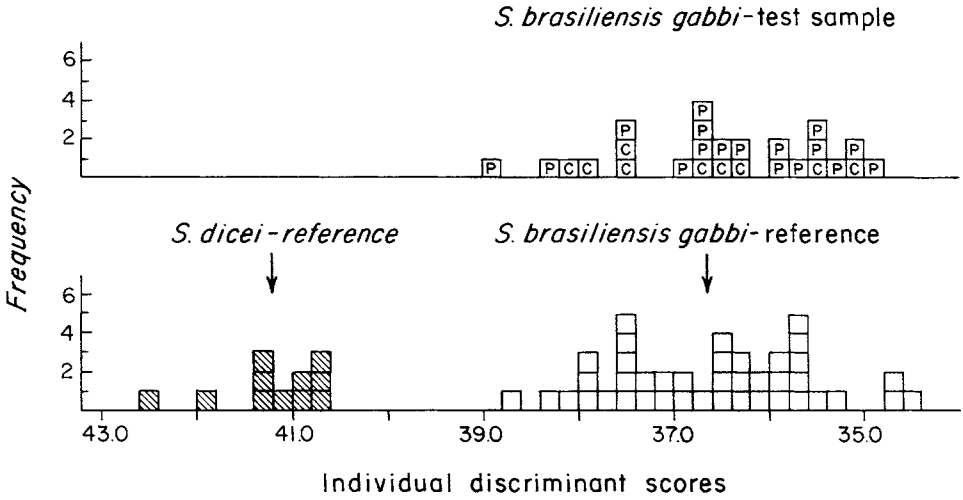

FIG. 7.—A discriminant function analysis comparing *Sylvilagus dicei* with *S. brasiliensis gabbi* from Central America. Two reference samples were used: (1) *S. dicei* (sample 10) from Costa Rica and Panama, and (2) *S. brasiliensis gabbi* from Honduras, Nicaragua, and central and eastern Panama (samples 4 and 7–8). The test sample consisted of individuals of *S. brasiliensis gabbi* from Costa Rica and western Panama (samples 5–6). Test individuals from Costa Rica are represented by squares containing a "C" and those containing a "P" are from Panama. Arrows mark sample means.

with the lowland reference group and all are equally separated from the cordilleran reference group, with the exception of USNM 360257, from Isla Cebaco, Veraguas Prov., Panama. This specimen (discriminant score 38.88) still is well within the morphological range of the lowland rabbits and is far removed geographically from the cordilleran reference group.

DISCUSSION

In North America, *Sylvilagus brasiliensis* (samples 1–8) ranges from Tamaulipas, Mexico, southeastward through Panama. The species is composed of two morphological forms (subspecies): 1) a medium-sized form with large auditory bullae and long ears occurring from Mexico through Guatemala and referable to *S. b. truei*; and 2) a small-sized form with small bullae and short ears occurring from Honduras through Panama and referable to *S. b. gabbi*. A narrow zone of intergradation between these two subspecies is evident in specimens from southern Chiapas and Guatemala. The distribution of the subspecies of *S. brasiliensis* in North America is shown in Fig. 8.

Specimens previously referred to *S. brasiliensis* from the Cordillera de Talamanca (sample 10) of Costa Rica and Panama are markedly larger than contiguous lowland specimens of *S. brasiliensis* (samples 5 and 6). A bivariate analysis and a discriminant function analysis failed to identify any morphological intermediates between cordilleran and lowland forms even though individuals of the two are available at several localities no more than 20 km apart. Because of this lack of observed intergradation, specimens from the cordillera of Costa Rica and Panama are best regarded as a distinct species and are referable to *S. dicei*.

Comparisons of the three species, *S. dicei*, *S. brasiliensis*, and *S. insonus* with each other indicate that *S. brasiliensis* and *S. dicei* are more closely related than either is to *S. insonus*. *S. dicei* differs from *S. brasiliensis* primarily in overall larger external and cranial size, whereas *S. insonus* differs from both *S. brasiliensis* and *S. dicei* in

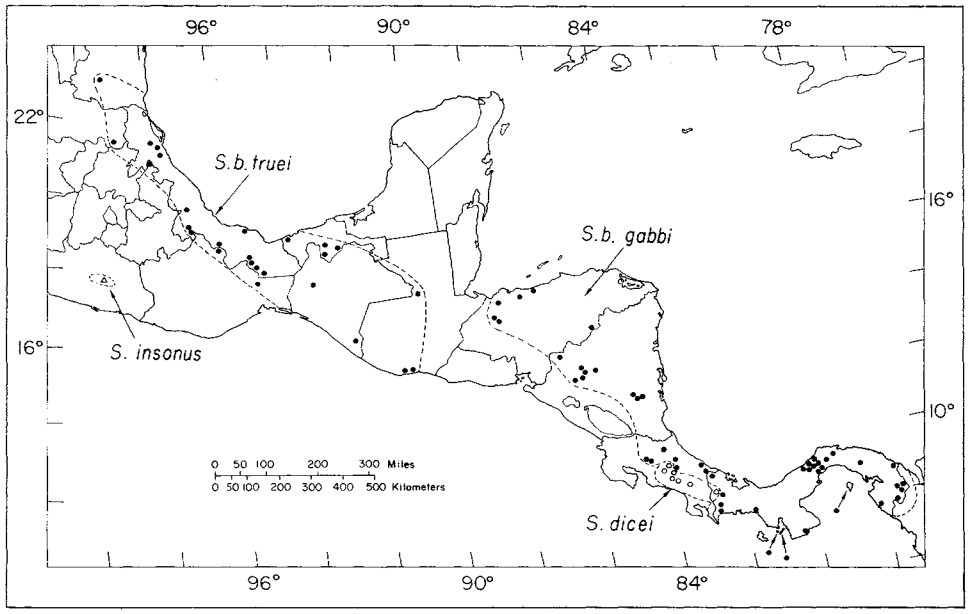

FIG. 8.—Geographic distribution of *Sylvilagus brasiliensis* in Mexico and Central America. Also included are the distributions of *S. insonus* from Guerrero, Mexico, and *S. dicei* from Costa Rica and Panama. Solid circles represent specimens examined of *S. brasiliensis*, open circles *S. dicei*, and triangle *S. insonus*. The dashed lines encircle the general distribution of each designated taxon.

much longer ears, longer bicolored tail (rather than unicolored), narrower basioccipital, narrower postdental breadth, deeper skull, and dorsal extensions of the premaxillaries, which usually extend posterior to the nasals rather than usually shorter than the nasals.

The phylogenetic relationship of *S. insonus* to other species of *Sylvilagus* is unclear. Nelson (1909) believed that *S. brasiliensis* (=*S. gabbi* of Nelson) and *S. insonus* were more closely related to each other than to other species of the genus and placed them in a distinct "*gabbi* group" of the subgenus *Tapeti*. The other two members of the subgenus *Tapeti*, *S. aquaticus* and *S. palustris*, were placed in the "*palustris* group." Hershkovitz (1950) later placed *S. insonus* and *S. aquaticus* in the subgenus *Sylvilagus* (containing most species of the genus), created the monotypic subgenus *Paludilagus* for *S. palustris*, and left *S. brasiliensis* in the then monotypic subgenus *Tapeti*. Based on available material, it seems best to regard *S. brasiliensis* and *S. dicei* as members of the subgenus *Tapeti* and *S. insonus* as a member of the subgenus *Sylvilagus*. Additional specimens of *S. insonus* are needed before a more accurate assessment of its affinities can be made.

TAXONOMY

Sylvilagus brasiliensis (Linnaeus)

Forest rabbit

Distribution.—In North America, along the tropical coastal plain of eastern Mexico (including southern Tamaulipas, eastern San Luis Potosi, Veracruz, eastern Puebla, eastern Oaxaca, and western Tabasco) southward through Chiapas, western Guatemala (unknown from but probably also occurring in the southern part of the Yucatan Peninsula southward to El Salvador), Honduras,

eastern half of Nicaragua, eastern Costa Rica, and Panama. Also found in South America south to southern Brazil and northern Argentina.

Diagnosis.—Body size generally small to medium with small to rudimentary tail, short hindfeet, and extremely short ears. Skull small to medium-sized with shallow mandibular ramus, large maxillary and mandibular toothrows, small rostrum (as measured in diastema length, depth of the rostrum, and breath across the infraorbital canals), markedly small auditory bullae, broad basioccipital, triangular to squared supraoccipital shield, slender posterior section of the supraorbital process (either free from, or attached to, the braincase), supraorbital process raised, dorsal extensions of the premaxillae often extending posteriorly beyond the nasals, flattened skull. Color generally dark brownish-black dorsally (some are grayish and others almost entirely black), sides slightly paler than dorsum, tail unicolored (ventrally and dorsally) and nearly the same color as the dorsum of the body, venter whitish except for a dark brownish throat patch.

Comparisons.—For comparisons of *S. brasiliensis* with *S. dicei* and *S. insonus*, see accounts of those species.

Sylvilagus brasiliensis from eastern and southern Mexico differs from *S. cunicularius* of Mexico in having the dorsum of the body dark brownish-black rather than grayish and dry ear length 51.5 mm or less as compared to 63.5 or more.

Sylvilagus brasiliensis from southern and eastern Mexico south to Costa Rica differs from *S. floridanus* in having a dark dorsal pelage and rudimentary, unicolored tail rather than a reddish-black dorsal pelage and a medium to large-sized, bicolored tail (rufous to reddish-black dorsally and whitish ventrally). Insofar as known, *S. brasiliensis* has three pair of mammae, whereas *S. floridanus* has four pair (Hershkovitz, 1950). The small auditory bullae distinguish the skull of *S. brasiliensis* from that of *S. floridanus*, which has large bullae.

Sylvilagus brasiliensis truei (J. A. Allen)

1890. *Lepus truei* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 3:192.
1909. *Sylvilagus gabbi truei*, Nelson, N. Amer. Fauna, 29:262.
1950. *Sylvilagus brasiliensis truei*, Hershkovitz, Proc. U.S. Natl. Mus., 100:351.

Holotype.—USNM no. 6357/34878, adult, sex unknown, skin and skull, from Mirador, Veracruz, Mexico. Holotype examined.

Distribution.—Dense tropical forests of the coastal plain and lower slopes of the Sierra Madre Oriental of eastern Mexico from Rancho del Cielo in southern Tamaulipas and Xilitla in extreme southeastern San Luis Potosi southeastward through extreme eastern Puebla, Veracruz, extreme northeastern Oaxaca, Tabasco, Chiapas, and the western half of Guatemala (Fig. 8).

Diagnosis.—Large body size with long ears. Skull generally large with extremely large auditory bullae (especially as reflected in bulla length, bullae breadth, shield-bullae depth, and skull depth), broad braincase, widely spreading zygomatic arches, and deep rostrum. Dorsal coloration brownish-black intermixed, sides and tail of nearly the same color as the dorsum only slightly paler, and venter whitish except for a brownish throat patch.

Comparisons.—*Sylvilagus brasiliensis truei* differs from *S. b. gabbi* as follows: larger in total length, body length, and dry ear length; generally larger skull as evident in greatest skull length, braincase breadth, larger auditory bullae (Fig. 4), rostrum depth, and mandible length. No consistent color differences were noted. If specimens of *S. brasiliensis* are eventually collected from the Yucatan Peninsula, eastern Guatemala, or El Salvador, they can be accurately identified as *truei*, *gabbi*, or as intergrades between the two, by the discriminant function analysis (Fig. 5 and Table 2).

Remarks.—Presently, specimens of *S. brasiliensis* are not available from the Yucatan Peninsula. Proper habitat seemingly exists there, and with little doubt, *S. b. truei* will be collected in the southern part of that region in the future. Allen (1906) reported *S. brasiliensis* from Chichen Itza, Yucatan. However, reexamination of the specimen by Jones et al. (1974) revealed it to be *S. floridanus*.

It is not certain why there is a sudden change in the morphology of *S. brasiliensis* in southern Chiapas and Guatemala. There are no apparent major physiographic barriers or extensive biotic changes in this area. However, the range of *S. b. truei* in Mexico and Guatemala overlaps the range of *S. floridanus*, whereas the range of *S. b. gabbi* from Honduras to Costa Rica is complementary to the range of *S. floridanus*. Where their ranges overlap, *S. brasiliensis* and *S. floridanus* converge morphologically in body size and in characters involved with hearing (ear

length and inflation of the auditory bullae). This convergence probably reflects a strong environmental influence.

Specimens examined (43).—CHIAPAS: Huehuetan, 300 ft, 2 (USNM); Ocuilapa, 3,500 ft, 1 (USNM). GUATEMALA: *Alta Verapaz Dept.*: 3 km NW Chinaja, 1 (KU). *Escuintla Dept.*: Concepcion del Mar, 5 (FMNH); San Jose, 1 (USNM). OAXACA: *Juchitan Dist.*: Santo Domingo, 2 (USNM). *Tuxtepec Dist.*: Yetla, 900 ft, 1 (KU). PUEBLA: Metlaltoyuca, 800 ft, 4 (USNM). SAN LUIS POTOSI: Xilitla, 1 (LSUMZ); W of Xilitla, 1 (JDC). TOBASCO: La Venta, 1 (USNM); 5 mi SE Macuspana, 1 (KU); 10 mi N Teapa, 1 (LSUMZ); 5 mi SW Teapa, 1 (KU); 2 mi E Teapa, 1 (KU); 1 mi E Teapa, 1 (LSUMZ); Teapa, 2 (USNM); 8 mi S Villahermosa, 1 (LSUMZ). TAMAULIPAS: Rancho del Cielo, 1 (AMNH). VERACRUZ: Achotal, 2 (FMNH); Buena Vista, 1 (USNM); 8 mi SE Cordoba, city limits of Potrero, 1 (TTU); 30 km SSE Jesus Carranza, 300 ft, 1 (KU); Jaltepec River at Hwy 185, 165 ft, 1 (MVZ); Mirador, 1 (USNM); Motzorongo, 800 ft, 1 (USNM); 2 km N Motzorongo, 1,500 ft, 1 (KU); Otatitlan, 200 ft, 1 (USNM); Potrero Llano, 350 ft, 1 (KU); Tapalapan, Sierra Andreas Tuxtla, 500 ft, 1 (MVZ); 12.5 mi N Tihuatlan, 300 ft, 1 (KU); 35 km NW Tuxpan, 1 (KU).

Sylvilagus brasiliensis gabbi (J. A. Allen)

1877. *Lepus brasiliensis* var. *gabbi* J. A. Allen, *in* Coues and Allen, Monogr. N. Amer. Rodentia, p. 349.
1950. *Sylvilagus brasiliensis gabbi*, Hershkovitz, Proc. U.S. Natl. Mus., 100:351.
1901. *Lepus (Tapeti) incitatus* Bangs, Amer. Nat., 35:633. Type from San Miguel Island, Bay of Panama, Panama. Holotype examined.
1908. *Lepus gabbi tumacus* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 24:649. Type from Tuma, Nicaragua. Holotype examined.
1912. *Sylvilagus gabbi messorius* Goldman, Smiths. Misc. Coll., 60(2):13. Type from Cana, 1,800 ft, mts. of eastern Panama. Holotype examined.
1917. *Sylvilagus gabbi consobrinus* Anthony, Bull. Amer. Mus. Nat. Hist., 35:335. Type from Old Panama City, Panama. Holotype examined.

Lectotype.—As restricted by Nelson (1909:259), USNM no. 11371/37794, adult male, skin and skull, from Talamanca [=Sipurio, Rio Sixaola, near Caribbean Coast], Costa Rica. The lectotype selected by Nelson is one of the three cotypes used by Allen (1877) in the original description. Lectotype examined.

Distribution.—Tropical forests of the northeastern two-thirds of Honduras, southeastward through the eastern half of Nicaragua, northeastern half of Costa Rica, and throughout Panama (Fig. 8).

Diagnosis.—Smallest North American subspecies of *S. brasiliensis*. Small size with especially short ears and hindfeet. Generally small skull with proportionately large maxillary and mandibular toothrows, small auditory bullae, shallow shield-bullae depth, shallow skull depth, narrow braincase, short nasals, and shallow rostrum depth. Color is variable, ranging from near blackish to blackish-brown dorsally, sides and tail only slightly paler than dorsum, and venter whitish except for a dark brownish throat patch.

Comparisons.—For comparisons with *S. b. truei*, see the account of that subspecies.

Remarks.—There is only slight geographic variation in *S. b. gabbi*. Individuals become slightly larger and darker from north (Honduras) to south (Panama). No significant differences were found among *S. b. consobrinus* from Panama, *S. b. incitatus* from Panama, *S. b. messorius* from Panama, *S. b. tumacus* from Nicaragua, and *S. b. gabbi* from Costa Rica. Most of these taxa were described near the turn of the century with only one or two specimens available for descriptive and comparative purposes. With the accumulation of more material, it is now apparent that variation among these taxa is only slightly greater than variation within any one population. These four subspecies are therefore regarded as synonyms of *S. b. gabbi*.

Most of the available specimens of *S. brasiliensis* from Colombia were examined, especially those from northern and north-central Colombia. None of those examined is referable to *S. b. gabbi*. A systematic revision of South American *S. brasiliensis* is needed.

Specimens examined (104).—CANAL ZONE: 6 km W Balboa, 1 (MSU); Corozal, 1 (USNM); 3 mi S Fort Sherman, Mohinga Valley, 1 (USNM); France Field, 1 (USNM); Gatun, 3 (USNM); Las Cascades, 1 (USNM); Lion Hill (=Loma del Leon), 3 (1 UMMZ, 2 MCZ); Old Panama City, 1 (AMNH); Summit, 1 (USNM). COSTA RICA: *Alajuela Prov.*: Cataratos, San Carlos, 1 (AMNH);

Vijagual, San Carlos, 3 (AMNH). *Cartago Prov.*: Santa Teresa Peralta, 5 (AMNH); 2 mi SE Turrialba, Interamerican Institute, 1 (USNM). *Heredia Prov.*: Rio Sarapiqui, 300 ft, 1 (UMMZ). *Limon Prov.*: Jimenez, 600 ft, 2 (UCLA); Olivia, 2 (USNM); Pandora, Estrella Valley, 2 (USNM); Peralta, 2,000–3,000 ft, 1 (UMMZ); Talamanca, 3 (USNM). HONDURAS: *Atlantida Prov.*: 6 mi SW La Ceiba, 250 ft, 1 (TCWC); 4 mi S Monte Cristo, 1 (TCWC). *Colon Prov.*: Rio Coco, 78 mi ENE Danli, 900 ft, 1 (TCWC). *Cortes Prov.*: San Pedro Sula, 5,000 ft, 1 (USNM). *Santa Barbara Prov.*: La Mica, 2,600 ft, 1 (AMNH); San Jose, 3,000 ft, 1 (AMNH). NICARAGUA: *Jinotega Prov.*: Hacienda la Trampa, 2 (1 KU, 1 USNM). *Matagalpa Prov.*: Hacienda Tepayac, 1 (KU); Hacienda Teperae (10.5 km N, 9 km E of Matagalpa), 960 m, 2 (USNM); Matagalpa, 2 (USNM); 3 mi E San Ramon, 1 (KU); Tuma, 1 (USNM). *Nueva Segovia Prov.*: Ocotal, 1 (USNM). *Zelaya Prov.*: no specific locality, 1 (USNM); El Recreo, S side Rio Mico, 25 m, 3 (KU); El Recreo, 71 km ENE Bluefields, 2 (USNM); Escondido River (50 mi from Bluefields), 1 (USNM); N side Rio Mico, El Recreo, 25 m, 1 (KU). PANAMA: *Bocas del Toro Prov.*: Sibube, 7 (USNM). *Chiriqui Prov.*: Bugaba, 1 (MCZ); Boqueron, 5 (AMNH); Boquete, 2 (FMNH); Boquete, 4,000 ft, 1 (UMMZ); Boquete, 3,400–4,500 ft, 1 (MCZ); Divala, 2 (1 UCM, 1 MCZ); Tole, 900 ft, 1 (USNM). *Colon Prov.*: Salud, 1 (USNM). *Darien Prov.*: Boca de Cupe, 3 (AMNH); Cana, 1,800 ft, 1 (USNM); Jaque, jct. Rios Jaque and Imamado, 1 (USNM); Tacarcuna, 1,500–1,950 ft, 2 (AMNH); Tapalisa, 4 (AMNH). *Los Santos Prov.*: Guanico Arriba, 3 (USNM). *Panama Prov.*: Cerro Azul, 2,000 ft, 5 (USNM); Charco del Toro, Rio Maje, 1 (USNM). *San Blas Prov.*: Armila, Rio Armila, 1 (USNM); Mandinga, approx. 300 ft, 2 (USNM). San Miguel Island (=Isla del Rey), 1 (MCZ); San Miguel Island, Pearl Island, 1 (MCZ). *Veraguas Prov.*: Isla Cebaco, 2 (USNM); Isla Gobernadora, 1 (USNM).

Sylvilagus dicei Harris

Dice's cottontail

1932. *Sylvilagus dicei* Harris, Occas. Papers Mus. Zool., Univ. Michigan, 248:1.
1950. *Sylvilagus brasiliensis dicei*, Hershkovitz, Proc. U.S. Natl. Mus., 100:352.

Holotype.—UMMZ no. 64043, adult female, skin and skull, from El Copey de Dota, 6,000 ft, Costa Rica. Holotype examined.

Distribution.—Known only from the Cordillera de Talamanca of Costa Rica and adjacent west-central Panama (Figs. 8 and 9).

Diagnosis.—A large-bodied rabbit with a rudimentary tail, hindfeet of medium length, and short ears. Generally large skull with noticeably short palate, narrow breadth across the nasals, broad across the maxillary toothrows, markedly broad postdental area, broad basioccipital, small auditory bullae, shallow shield-bullae depth, shallow skull depth, broad between carotid foramina, skull flattened, squared to subtriangular supraoccipital shield, slender posterior section of the supraorbital process fused to the braincase, flat supraorbital process. Dorsal pelage a mixture of blacks and browns, sides blackish-gray, tail blackish (if visible), venter whitish except for a brownish throat patch.

Comparisons.—*Sylvilagus dicei* differs from adjacent individuals of *S. brasiliensis* (Honduras to Panama) in having much larger size externally, with an appreciably longer hindfoot; larger skull size, especially in zygomatic breadth (no overlap, Fig. 6), braincase breadth (no overlap), greatest skull length, breadth across the carotid foramina, rostrum depth, skull depth, breadth across the maxillary toothrows, and breadth across the nasals. No consistent color differences were noted.

Sylvilagus dicei differs from *S. insonus* from Guerrero, Mexico, as follows: externally, same general body size with much shorter tail and shorter ears (48.0 or less as compared to 59.7 or more); cranially, same overall size except greater postdental breadth, broader basioccipital (10.90 or more as compared to 8.95 or less), longer diastema, shorter auditory bulla length, and lesser skull depth (29.80 or less as compared to 31.95 or more); and color, dark blackish-brown dorsally rather than pale brownish-black or rufous-black.

Sylvilagus dicei differs from *S. floridanus* from southern Nicaragua and northwestern Costa Rica in having a nearly equal body size with much shorter tail and shorter ears (47.3 or less as compared to 48.3 or more); nearly equal skull size except much broader zygomatic arches, broader braincase, shorter nasals, longer maxillary toothrow (14.80 or more as compared to 14.65 or less), greater breadth across the maxillary toothrows (22.15 or more as compared to 21.65 or less),

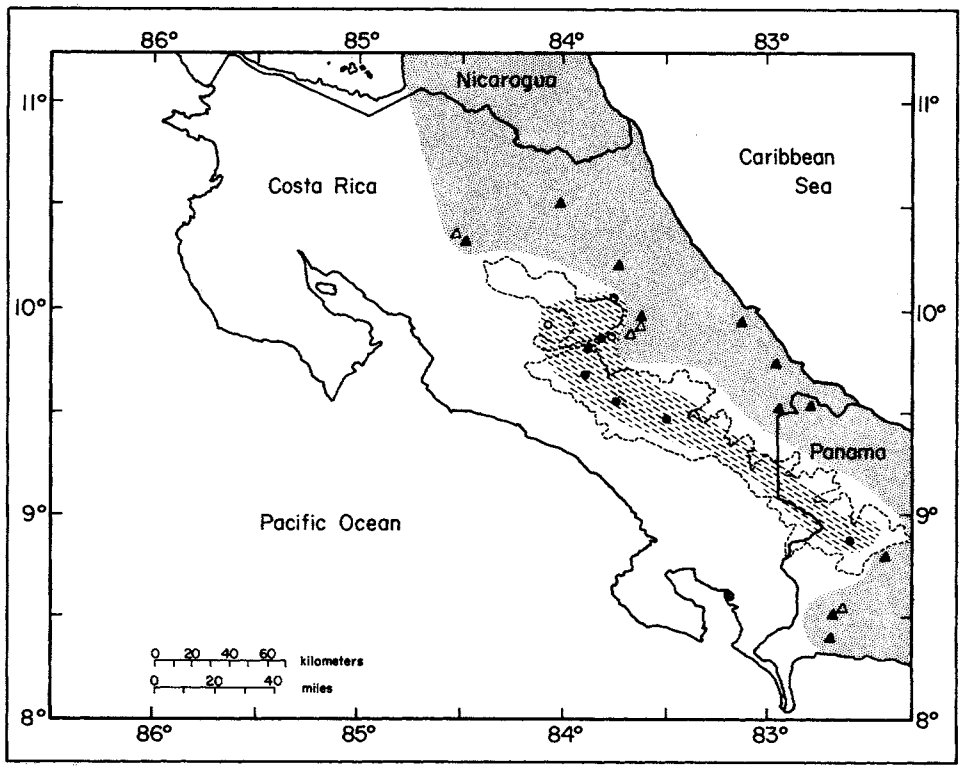

FIG. 9.—The geographic range of *Sylvilagus dicei* in Costa Rica and Panama. Localities represented by adults are shown by solid circles and those represented by open circles are juveniles. In addition, the geographic distribution of *S. brasiliensis gabbi* in Costa Rica and western Panama is given. Localities represented by adults are shown by solid triangles and those represented by open triangles are juveniles. Areas in the dashed lines are over 5,000 ft in elevation. The approximate range of each species is shaded.

greater postdental breadth, longer incisive foramina, longer diastema, shorter auditory bulla length (9.45 or less as compared to 9.65 or more), greater breadth across the carotid foramina (12.05 or more as compared to 11.85 or less), narrower mandibular ramus (11.10 or less as compared to 11.25 or more), and longer mandibular toothrow (15.45 or more as compared to 15.20 or less); and blackish-brown dorsal color rather than chiefly rufous-black.

Remarks.—Harris (1932) described *S. dicei* on the basis of one adult, the holotype. Goodwin (1946) retained *S. dicei* as a distinct species. Later, Hershkovitz (1950:352) considered *S. dicei* a subspecies of *S. brasiliensis* and further suggested that it was "Doubtfully distinct from typical *gabbi* [*S. brasiliensis gabbi*]." Handley (1966:776) noted that "Specimens from Cerro Punta [Panama], 5,300 feet (Chiriqui) may represent an undescribed subspecies [of *S. brasiliensis*]." These specimens are actually referable to *S. dicei*. Additional specimens are needed from the eastern and southern slopes of the cordillera of Costa Rica and Panama to further investigate the taxonomic status of *S. dicei*.

Specimens from Juan Vinas, Rancho de Rio Jimenez, and San Jose in Costa Rica are exceedingly young individuals (probably one or two months old) and are here tentatively assigned, on the basis of geography, to *S. dicei* rather than to *S. brasiliensis*.

The range of *S. dicei* closely approaches the range of *S. brasiliensis* in west-central Panama (Fig. 9). Here, at 5,300 ft, *S. dicei* is known by two specimens from Cerro Punta (discriminant scores of 41.0 and 41.9). Thirteen miles southeast of Cerro Punta at Boquete three adults of *S. brasiliensis* are available from 4,000 ft (discriminant scores of 37.4, 36.7, and 35.4). The two species also occur at nearby localities in Costa Rica. At Cervantes, *S. dicei* is known by a single

specimen (discriminant score of 40.7). *S. brasiliensis* is present 14 miles east of Cervantes, at Peralta (discriminant score of 37.8).

Sylvilagus dicei is a highland species. Adult specimens have been taken as high as 11,600 ft at Cerro Chirripo and no lower than approximately 5,000 ft at Cervantes. In contrast, *S. brasiliensis* occupies the lowlands in Costa Rica and western Panama, mainly on the Caribbean side of the mountains. *S. brasiliensis* does, however, partially encircle the range of *S. dicei*. The former is known from Bugaba (discriminant score of 35.7), Panama, which is south-southwest of the range of *S. dicei* at Cerro Punta, Panama. Also, *S. brasiliensis* is known from San Carlos (discriminant score of 37.4), Costa Rica, which is northwest of the range of *S. dicei* at Cervantes and Navarro.

Specimens examined (16).—COSTA RICA: *Cartago Prov.*: Cerro Asuncion, 11,000 ft, 1 (LSUMZ); Cervantes, 1 (FMNH); El Copey de Dota (about 15 mi S Cartago), in the Cordillera de Talamanca, 6,000 ft, 1 (UMMZ); Juan Vinas, 1 (AMNH); 1 km S Navarro, 2 (KU); Rancho de Rio Jimenez, 3,600 ft, 2 (AMNH). *San Jose Prov.*: headwaters of Rio Talari, Cerro Chirripo, 11,000–11,600 ft, 3 (LSUMZ); Pan American Hwy, at Cerro Asuncion, 1 (MSB); San Jose, 2 (AMNH). PANAMA: *Chiriqui Prov.*: Cerro Punta, Casa Tilley, 5,300 ft, 2 (USNM).

Sylvilagus insonus (Nelson)

Omilteme cottontail

1904. *Lepus insonus* Nelson, Proc. Biol. Soc. Washington, 17:103.
1909. *Sylvilagus insonus*, Lyon and Osgood, Bull. U.S. Natl. Mus., 62:34.

Holotype.—USNM no. 126878, juvenile female, skin and skull, from Omilteme, Guerrero, Mexico. Holotype examined.

Distribution.—Known only from the Sierra Madre del Sur at Omilteme, Guerrero, Mexico (Fig. 8).

Diagnosis.—Large body with short tail, hindfeet of medium length, and ears long. Skull generally large with long palate, broad braincase, narrow breadth across nasals, large maxillary and mandibular toothrows, short incisive foramina, short diastema, narrow basioccipital, medium-sized auditory bullae, extremely broad across the carotid foramina, narrow breadth across the infraorbital canals, shallow shield-bullae depth, shallow skull depth, squared supraoccipital shield, posterior section of the supraorbital process slender and seemingly attached to the braincase, and flat supraorbital processes. Dorsum of the body a mixture of rufous with much black, sides grayish-black, tail reddish-black dorsally, venter whitish except with a brownish throat patch, and hindfeet with much white on top.

Comparisons.—*Sylvilagus insonus* is known only by three specimens and, therefore, comparisons between it and other species cannot be made with the accuracy desired. *S. cunicularius* is the only other species of the genus known from Guerrero. *S. floridanus* is known from areas northwest, north, northeast, and east of Guerrero in Michoacan, Mexico, Morelos, Puebla, and Oaxaca. *S. brasiliensis* is known from about 400 km east of Guerrero in eastern Puebla and eastern Oaxaca. For comparisons of *S. insonus* with *S. dicei* from Costa Rica and Panama see the account of that species.

Sylvilagus insonus differs from *S. cunicularius* from southern Mexico as follows: externally shorter in all measurements especially dry ear length (63.5 or less as compared to 63.6 or more); generally smaller cranially, particularly in upper incisor length (7.45 or less as compared to 8.10 or more), greatest skull length (78.00 or less as compared to 78.35 or more), nasal length (32.10 or less as compared to 32.75 or more), basioccipital breadth (8.95 or less as compared to 9.40 or more), auditory bulla length (9.55 or less as compared to 9.65 or more), shield-bullae depth (21.35 or less as compared to 21.90 or more), skull depth (32.00 or less as compared to 33.50 or more), breadth across the infraorbital canals (18.25 or less as compared to 18.55 or more), mandible height (36.25 or less as compared to 38.30 or more), and mandible ramus depth (11.30 or less as compared to 12.20 or more); color, rufous-black dorsally rather than grayish.

Sylvilagus insonus differs from *S. brasiliensis* (samples 1–3) from eastern Mexico and western Guatemala in being larger in all features, especially dry ear length (59.7 or more as compared to 51.5 or less); generally larger skull, especially in zygomatic breadth (37.50 or more as compared to 36.10 or less), rostrum depth (15.20 or more as compared to 15.10 or less), and breadth across the carotid foramina (12.45 or more as compared to 12.40 or less); color, rufous-black dorsally rather than brownish-black, hindfeet with white and brown hairs rather than entirely brownish.

Sylvilagus insonus differs from montane specimens of *S. floridanus* from central Michoacan, Mexico, Morelos, Puebla, and Oaxaca in its larger body size; larger skull, especially in greatest skull length (76.90 or more as compared to 75.85 or less), maxillary toothrow length (15.20 or more as compared to 14.45 or less), zygomatic breadth (37.50 or more as compared to 35.75 or less), and breadth across the carotid foramina (12.45 or more as compared to 10.90 or less); color, rufous-black dorsally rather than grayish or reddish.

Sylvilagus insonus differs from *S. floridanus macrocorpus* (Diersing and Wilson, 1980) from western Jalisco and western Michoacan as follows: externally, same general size except with longer ears; cranially, same overall size except with smaller auditory bullae (9.55 or less as compared to 10.20 or more), greater breadth between the carotid foramina (12.45 or more as compared to 12.40 or less), and narrower basioccipital (8.95 as compared to 9.00 or more); color, rufous-black dorsally rather than typically reddish.

Remarks.—Nelson (1909) considered the holotype, USNM no. 126878, as an adult. However, the supraoccipital-exoccipital sutures are still open and it is definitely a juvenile rather than an adult.

Specimens examined (3).—GUERREO: Omilteme, 2 (USNM); Omilteme, 7,300 ft, 1 (KU).

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LITERATURE CITED

ALLEN, G. M. 1906. Vertebrates from Yucatan. Mammalia. Bull. Mus. Comp. Zool., 50:101–159.

ALLEN, J. A. 1877. Leporidae. Pp. 265–378, *in* Coues and Allen, Monogr. N. Amer. Rodentia. U.S. Geol. Surv. of the Territories, 11:1–1091.

———. 1890. Notes on collections of mammals made in central and southern Mexico, by Dr. Audley C. Buller, with descriptions of new species of the genera *Vespertilio*, *Sciurus*, and *Lepus*. Bull. Amer. Mus. Nat. Hist., 3:175–194.

———. 1908. Mammals from Nicaragua. Bull. Amer. Mus. Nat. Hist., 24:647–670.

ANTHONY, H. E. 1917. A new rabbit and a new bat from Neotropical regions. Bull. Amer. Mus. Nat. Hist., 37:335–337.

BANGS, O. 1901. The mammals collected in San Miguel Island, Panama, by W. W. Brown, Jr. Amer. Nat., 35:631–644.

CHOATE, J. R., AND H. H. GENOWAYS. 1975.

Collections of Recent mammals in North America. J. Mamm., 56:452–502.

DIERSING, V. E., AND D. E. WILSON. 1980. Distribution and systematics of the rabbits (*Sylvilagus*) of west-central Mexico. Smithsonian Contrib. Zool., 297:1–34.

GOLDMAN, E. A. 1912. New mammals from eastern Panama. Smithsonian Misc. Coll., 60(2):1–18.

GOODWIN, G. G. 1946. Mammals of Costa Rica. Bull. Amer. Mus. Nat. Hist., 87:271–473.

HANDLEY, C. O., JR. 1966. Checklist of the mammals of Panama. Pp. 753–795, *in* Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Mus. Nat. Hist., Chicago, 861 pp.

HARRIS, W. P., JR. 1932. Four new mammals from Costa Rica. Occas. Papers Mus. Zool., Univ. Michigan, 248:1–6.

HERSHKOVITZ, P. 1950. Mammals of northern Colombia. Proc. U.S. Natl. Mus., 100:327–375.

HOFFMEISTER, D. F., AND E. G. ZIMMERMAN. 1967. Growth of the skull in the cottontail (*Sylvilagus floridanus*) and its application to age-determination. Amer. Midland Nat., 78:198–206.

JONES, J. K., JR., H. H. GENOWAYS, AND J. D. SMITH. 1974. Annotated checklist of mammals of the Yucatan Peninsula, Mexico. III. Marsupialia, Insectivora, Primates, Edentata, Lagomorpha. Occas. Papers Mus., Texas Tech Univ., 13:1–31.

NELSON, E. W. 1904. Descriptions of seven new rabbits from Mexico. Proc. Biol. Soc. Washington, 17:103–110.

———. 1909. The rabbits of North America. N. Amer. Fauna, 29:1–314.

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