

# TAXONOMIC STATUS AND RELATIONSHIPS OF *PEROMYSCUS BOYLI* FROM EL SALVADOR

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**ABSTRACT.**—The status and affinities of *Peromyscus boylii cordillerae* and *P. b. sacarensis*, both described from El Salvador, are evaluated using principal components analysis. Representative examples of *P. aztecus*, *P. boylii levipes*, *P. evides*, *P. hylocetes*, *P. oaxacensis*, and *P. spicilegus* are included for comparative purposes. It is concluded that *sacarensis* is a subspecies of *P. boylii*, while *cordillerae* is related to *aztecus*, *evides*, *hylocetes*, and *oaxacensis*. Because many traits that separate the latter five taxa vary significantly with elevation, it is hypothesized that they represent segments of a once continuous montane species.

In 1928, Donald R. Dickey reported on a series of *Peromyscus* collected by Ruben A. Stirton in the mountains of El Salvador. Dickey described two subspecies of *Peromyscus boylii* in that paper: *cordillerae* from the slopes of Mt. Cacaguatique (1,067 to 1,555 m), a mountain isolated from the major cordilleras in Central America, and *sacarensis* from San José del Sacare, a place in the foothills (1,097 m) of the main highland mass in eastern El Salvador. A related form, *Peromyscus oaxacensis*, was taken in cloud forest at higher elevations (2,195 to 2,438 m) at Los Esesmiles, located on a spur of mountains continuous with the main highland masses near the Honduran border. In his descriptions, Dickey drew attention to the similarities in size and pelage color between *cordillerae* and *boylii aztecus* and compared *sacarensis* to *b. levipes* and *b. simulus*. Later authors have followed Dickey's taxonomy for *Peromyscus boylii* in El Salvador (Burt and Stirton, 1961; Hall and Kelson, 1959; Ondrias, 1960).

Dickey's concept of the species *P. boylii* was obviously influenced by Osgood's (1909) revision of the genus *Peromyscus* in which *aztecus*, *evides*, *spicilegus*, and *levipes* were all treated as subspecies of *P. boylii*. Subsequent evidence, derived from new records of sympatry and additional morphological data, has suggested that *aztecus*, *evides*, and *spicilegus* are specifically distinct from "true" *boylii*, as represented in southern Mexico and Central America by the subspecies *levipes* (Alvarez, 1961; Carleton, 1977; Hooper, 1955, 1961, 1968; Musser, 1964, 1969). As a result, the composition of *P. boylii* has been substantially altered and its morphological limits have been redefined since Dickey (1928) described these two subspecies.

During an investigation of some forms of *boylii* in western Mexico (Carleton, 1977), I recognized that one of Dickey's subspecies, *cordillerae*, is allied with the *aztecus-evides-oaxacensis* complex and, therefore, incorrectly classified as a subspecies of *boylii*. The purposes of this study are, first, to substantiate this finding and, second, to assess the level of taxonomic differentiation of *cordillerae* with respect to *aztecus* and related forms.

## MATERIALS AND METHODS

Specimens used in this study were primarily skins and skulls. In addition, I examined the glandes penes, which were either extracted from fluid-preserved whole carcasses or reconstituted from dry museum skins (Hooper, 1958). Ten dimensions of the skull and four of the phallus were recorded to 0.1 mm using a craniometer (Anderson, 1968); three measurements of the skin, rounded to the nearest 1.0 mm, were taken from the collector's field tag. These measurements were described by Carleton (1977). Juveniles, judged on the basis of pelage and dental features, were excluded from statistical analyses.

This study focuses on the status and affinities of *P. boylii cordillerae* and *b. sacarensis*. Representatives of other species in the *Peromyscus boylii* species-group are included as standards for comparison. Twenty-four samples (number of sample in parentheses) representing the

six species treated herein are listed below, together with abbreviated localities and the number of specimens examined. Complete locality data for specimens examined are provided in the taxonomic revision section and in Carleton, 1977: Appendix I. The specimens are contained in the American Museum of Natural History (AMNH); Museum of Vertebrate Zoology, Berkeley (MVZ); The Museum, Michigan State University (MSU); The University of Michigan Museum of Zoology (UMMZ); and National Museum of Natural History, Biological Surveys Collection (USNM).

*Peromyscus aztecus*.—MEXICO. (1) Hidalgo: Metepec, and Pueblo, SW Huauchinango, 23.

*P. boylii cordillerae*.—EL SALVADOR. (2) Deptos. Morazan and San Miguel: Mt. Cacaguatique, 61.

*P. b. levipes*.—MEXICO. Chiapas: (3) San Cristobal de las Casas, 43; (4) Bochil, 22.

*P. b. sacarensis*.—EL SALVADOR. (5) Depto. Chalatenango: San José del Sacare, 18.

*P. evides*.—MEXICO. (6) Guerrero: mountains W Chilpancingo, 16. (7) Oaxaca: Juquila and Santa Rosa, 24.

*P. hyllocetes*.—MEXICO. Jalisco: (8) Sierra de Autlan, 48; (9) Nevado de Colima, 28; (10) SSE Autlan, 12. Michoacan: (11) NNW San Juan, 26; (12) Cerro San Andreas, 24.

*P. oaxacensis*.—MEXICO. Oaxaca: (13) Cerro San Felipe, 29. Chiapas: (14) San Cristobal de las Casas, 12; (15) N Pueblo Nuevo, 28. EL SALVADOR. (16) Depto. Chalatenango: Los Esesmiles, 31.

*P. spicilegus*.—MEXICO. (17) Durango: S Pueblo Nuevo, 11. Jalisco: (18) NNW Magdalena, 18; (19) Sierra de Autlan, 35. Michoacan: (20) E Dos Aguas and Coalcoman, 26; (21) S Uruapan, 15; (22) Los Reyes, 20. (23) Nayarit: N Santa Isabel, 52. (24) Sinaloa: Santa Lucia, 11.

The localities and numbers of specimens examined of bacula and glandes penes are:

*Peromyscus aztecus*.—MEXICO. Hidalgo: 13 mi NE Metepec, 2. Puebla: 2 mi SW Huauchinango, 2. Veracruz: 0.5 mi NE Las Minas, 2.

*P. boylii cordillerae*.—EL SALVADOR. Depto. San Miguel: Mt. Cacaguatique, 6.

*P. b. levipes*.—MEXICO. Chiapas: 1 mi N Pueblo Nuevo, 7; 5 mi N Pueblo Nuevo, 2.

*P. b. sacarensis*.—EL SALVADOR. Depto. Chalatenango: San José del Sacare, 1.

*P. evides*.—MEXICO. Guerrero: Omilteme, 2. Oaxaca: 4 mi S Jalatengo, 1; Campamento Rio Molino, 1; Santa Rosa, 2; 8 mi SSW Juchatengo, 1.

*P. hyllocetes*.—MEXICO. Jalisco: Sierra de Autlan, 10; Nevado de Colima, 9. Michoacan: Cerro Cuitzeran, 17; Cerro San Andreas, 10; 10 mi NW Uruapan, 3.

*P. oaxacensis*.—EL SALVADOR. Depto. Chalatenango: Los Esesmiles, 6. MEXICO. Chiapas: 1 mi N Pueblo Nuevo, 7; 5 mi N Pueblo Nuevo, 3. Oaxaca: 12 mi N Ixtlan de Juarez, 5.

*P. spicilegus*.—MEXICO. Durango: 6 mi S Pueblo Nuevo, 5. Jalisco: 12 mi W Guadalajara, 6; 2 mi NNW Magdalena, 5; 20 mi SSW Autlan, 10; 10 mi S Ameca, 3. Michoacan: 6.4 mi E Dos Aguas, 6; 8.4 mi S Uruapan, 3; Los Reyes, 4. Nayarit: 4 mi N Santa Isabel, 22. Sinaloa: 1 mi E Santa Lucia, 6.

The mean, SD, SE and range of the 13 measurements of the skin and skull were calculated for each of the 24 samples. Correlations and linear regressions of the morphometric variables against elevation were performed for some of the samples. Phenetic relationships among the samples were described by principal components analysis. In this analysis, sample means for the 13 variables of the skin and skull were employed as character states. The principal components were extracted from a correlation matrix in which all characters were standardized; the contribution of each variable to the first three principal components is expressed as a correlation. Statistical computations were carried out by the Michigan Interactive Data Analysis System (MIDAS), a series of computer programs developed by the Statistical Research Laboratory of the University of Michigan.

## RESULTS

*Cranial and external features*.—The skulls of *cordillerae* and *sacarensis* differ in most mensural characters (Table 1). This disparity is particularly evident in the greatest length of skull and breadth across the zygomatic arches. In overall size, *cordillerae* more nearly resembles *oaxacensis* than its supposed conspecific, *sacarensis*.

In addition to size, specimens of *cordillerae* and *sacarensis* can also be distinguished on the basis of certain proportional features of the skull. Individuals of *cor-*

TABLE 1.—Selected cranial and external measurements (mm) of *Peromyscus boylii*-group forms from El Salvador. Means, ranges, and SDs are given.

Dimension	<i>Peromyscus b. sacarensis</i> San Jose del Sacare N = 15	<i>Peromyscus cordillerae</i> Mt. Cacaguatique N = 32	<i>Peromyscus oaxacensis</i> Los Esesmiles N = 26
Length of skull	27.7 25.4–28.6 0.83	29.7 28.1–31.3 0.83	30.4 28.8–32.6 0.89
Length of rostrum	9.1 8.0–9.8 0.46	10.0 9.3–10.8 0.40	10.3 9.4–11.4 0.50
Greatest zygomatic breadth	14.0 13.4–14.5 0.34	14.7 14.0–16.3 0.48	14.8 13.9–16.1 0.44
Least interorbital width	4.3 4.1–4.7 0.16	4.7 4.4–5.1 0.15	4.8 4.4–5.1 0.17
Length of maxillary toothrow	4.2 4.0–4.4 0.15	4.6 4.3–5.0 0.17	4.9 4.4–5.1 0.14
Length of incisive foramen	5.7 5.1–6.2 0.32	6.3 5.9–7.0 0.26	6.3 5.6–6.7 0.30
Length of auditory bulla	3.8 3.6–4.1 0.17	3.8 2.8–4.2 0.23	4.0 3.7–4.3 0.17
Total length	198.2 177–215 13.1	220.0 195–266 16.0	236.3 204–263 14.3
Length of tail	99.0 80–107 8.3	113.9 97–130 7.61	125.6 109–136 7.62
Length of hind foot	22.3 21–23 0.50	24.4 23–26 0.73	26.7 26–29 0.80

*dillerae* possess a supraorbital shelf or ledge; heavier, more robust molars; and a more elongate braincase. The supraorbital borders of *sacarensis* are smooth or hourglass-shaped when viewed dorsally, and the braincase is more rounded (compare, Figs. 7C and 8A in Carleton, 1977). Although their auditory bullae average the same length (Table 1), those of *sacarensis* are relatively more inflated on their ventromedial aspect. Finally, the zygomatic arches of *sacarensis* are squared anteriorly, while they are more gently convergent in *cordillerae*. This suite of characters is virtually the same as has been used previously to separate *boylii levipes* from either *aztecus* (Alvarez, 1961; Hall and Dalquest, 1963), *evides* (Hooper, 1961; Musser, 1964) or *spicilegus* (Hooper, 1955; Carleton, 1977).

Pelage coloration of species of *Peromyscus* exhibits extreme evolutionary convergence, perhaps as a result of differences in local temperature and humidity regimens, and provides few reliable diagnostic traits. The rich, deep russet in specimens of *cordillerae*, particularly along the flanks, resembles the pelage color of *aztecus* or some populations of *evides* (such as those inhabiting the coastal Sierra Madre del Sur in Oaxaca). The pelage of *cordillerae* contrasts with the muted ochraceous tones in *oaxacensis* from Los Esesmiles. The color of the upperparts in *sacarensis* is much

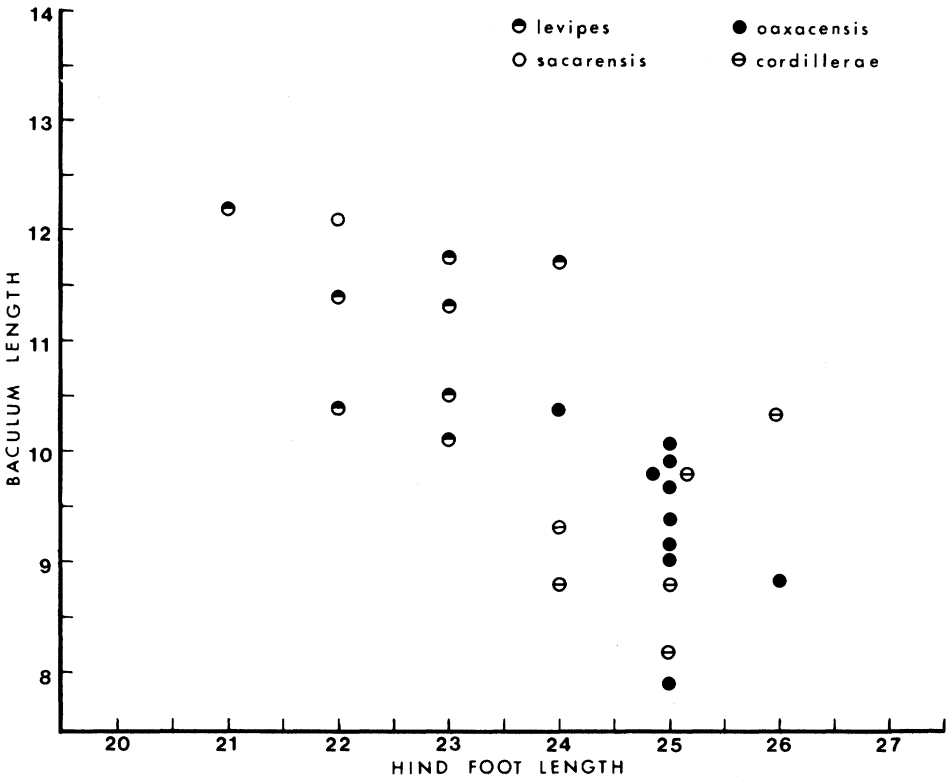


FIG. 1.—Bivariate scatter plot of length of baculum (mm) versus length of hind foot (mm) for specimens of *P. boylii levipes* (Chiapas: San Cristobal de las Casas), *P. b. sacarensis* (El Salvador: San José del Sacare), *P. b. cordillerae* (El Salvador: Mt. Cacaguatique) and *P. oaxacensis* (Chiapas: N Pueblo Nuevo).

less saturated than in *cordillerae*. The pale tawny effect resembles that of *P. simulus* from Sinaloa (Osgood, 1909) and departs from the grayish-buff coloration of typical *boylii levipes* from the highlands of Guatemala and southern Mexico. The *boylii sacarensis* from San José del Sacare were collected in dry ravines among oaks and scattered pines (Dickey, 1928), a locality assigned to the Arid Upper Tropical zone by Burt and Stirton (1961), and the dilute tawny color of *sacarensis* may be a response to the more arid climate. Certainly, this area strongly differs climatically from the cooler, humid, pine-oak zones occupied by *boylii levipes*.

As noted by Dickey (1928), the hind feet of both *cordillerae* and *sacarensis* are almost wholly white from the tarsus to the digits. In contrast, *aztecus*, *evides*, and *oaxacensis* generally have a streak of dusky extending from the tarsus onto the metatarsus. This trait offers a moderately reliable means of differentiating *aztecus*, *evides*, and *oaxacensis* from *boylii levipes*.

The tail of *sacarensis* is more densely furred than that of *cordillerae* and is faintly bicolored. This bicoloredness is not, however, as pronounced as that observed in most individuals of *boylii levipes*.

*Baculum and glans penis*.—Quantitative and qualitative features of the phalli suggest an association of *cordillerae* with *oaxacensis* and related forms, instead of with *boylii*.

The length of the baculum in *cordillerae* is both absolutely and relatively shorter than that of *boylii*, but matches that of *oaxacensis* (Fig. 1).

TABLE 2.—Results of first principal component analysis and correlations of the characters with the first three principal components extracted.

Variable	Principal component		
	I	II	III
Eigenvalue	9.8	0.8	0.8
Cumulative percent			
total variation	75.0	81.6	87.9
Degrees freedom	77	65	54
Significance	0.0	0.0	0.0
Length of skull	0.99	0.03	0.04
Length of rostrum	0.96	0.01	-0.02
Greatest zygomatic breadth	0.92	0.18	0.03
Breadth of braincase	0.93	-0.01	0.20
Least interorbital width	0.88	-0.20	0.20
Length of molar row	0.94	-0.17	0.21
Length of incisive foramen	0.95	0.13	0.12
Breadth of palate	0.60	0.53	-0.56
Width of mesopterygoid fossa	0.73	-0.43	-0.34
Length of auditory bulla	0.72	0.39	0.34
Length of body	0.82	0.11	-0.10
Length of tail	0.80	-0.26	-0.34
Length of hindfoot	0.92	-0.18	-0.01

Trenchant dissimilarities between the glandes of *cordillerae* and *sacarensis* may be summarized as follows. The circumference of the body of the glans penis in *cordillerae* substantially exceeds that of *sacarensis*. In specimens of *cordillerae*, longitudinal grooves or furrows mark the body of the glans; these are absent in the one specimen of *sacarensis*. Large, widely-spaced spines occur at the base of the glans in *sacarensis*; in *cordillerae*, these spines are evenly graded in size and more densely packed. Finally, dorsal and ventral lappets are present in *sacarensis* but absent in *cordillerae* (compare Figs. 3A and 5A in Carleton, 1977, for illustration of these differences in related forms). For each of these traits, *cordillerae* resembles examples of *aztecus*, *evides*, *hylocetes*, and *oaxacensis*, while *sacarensis* agrees with those of *boylei rowleyi* and *b. levipes* (Carleton, 1977; Hooper, 1958; Hooper and Musser, 1964).

*Principal components analysis.*—Only the 10 skull and three external measurements were used in the principal components program. As expected, most dimensions loaded heavily on the first principal component, and the dispersion of OTUs suggests an overall size factor for this component (Fig. 2 and Table 2). Breadth of palate, width of mesopterygoid fossa, and length of auditory bullae contribute significantly to the second principal component.

There is a hiatus separating the two samples from El Salvador. *Peromyscus boylei cordillerae* (sample no. 2) is interspersed among an elliptical scatter of OTUs representing *P. aztecus*, (no. 1), *evides* (nos. 6, 7), *hylocetes* (nos. 8–12), and *oaxacensis* (nos. 13–16); *boylei sacarensis* (no. 5) is positioned near the two examples of *boylei levipes* (nos. 3, 4) from Chiapas (Fig. 2). No distinct separation of OTUs of *P. spicilegus* (nos. 17–24) from *boylei* (as represented by *levipes* and *sacarensis*) is apparent. This was anticipated because most characters distinguishing the two involve proportional and qualitative features of the skull and glans penis (Carleton, 1977), data not included in the principal components analysis. On size alone, specimens of *P. spicilegus* are largely inseparable from those of *boylei rowleyi*, *b. levipes*, or *b. sacarensis*.

Inspection of the somewhat linear scatter of OTUs of *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis* (Fig. 2) suggests that a common factor, other than general

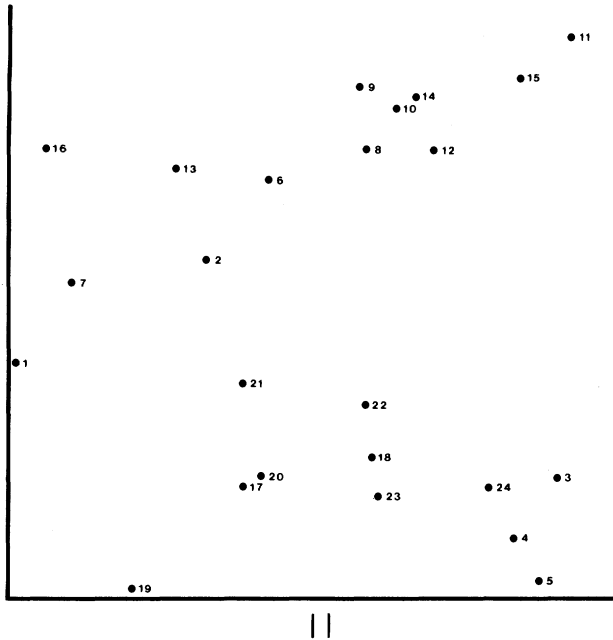


FIG. 2.—Scatter plot of Principal Component I versus II using the 24 population samples as cases as described by the 13 morphometric variables (also see Table 2). Taxa represented include: *P. aztecus* (sample no. 1), *P. boylii cordillerae* (no. 2); *P. b. levipes* (nos. 3, 4); *P. b. sacarensis* (no. 5); *P. evides* (nos. 6, 7); *P. hylocetes* (nos. 8–12); *P. oaxacensis* (nos. 13–16); and *P. spicilegus* (nos. 17–24). See Materials and Methods for locality information.

size, is affecting the characters that load on principal components I and II. In particular, the dispersion of the two samples of *evides* implicates elevational effects: the *evides* sample from Oaxaca came from 1,525 m in altitude; whereas, individuals of *evides* from Guerrero were trapped at approximately 2,200 m. Also noteworthy is the placement of *aztecus* and *cordillerae*, taxa generally inhabiting elevations lower than those occupied by *oaxacensis* and *hylocetes*. In the first principal components analysis, individuals trapped at different elevations on the same mountain were included in a single OTU; for example, the *oaxacensis* from Cerro San Felipe were collected at 2,400 and 2,800 m, and the *hylocetes* from NNW San Juan were trapped at 2,350 and 2,450 m on Cerro Cuitzeran.

The principal components analysis was repeated, this time dividing the OTUs according to collecting elevations where appropriate. Hence, OTUs representing the five taxa, *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis*, were increased from 13 to 20. Again, sample means of the 13 skull and external variables served as the character states in this analysis. The general conformation of OTUs remained the same in the second analysis (Fig. 3). There is an elongate constellation of points representing *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis*; the two samples of *cordillerae* are set far apart from *sacarensis*, which still clusters near examples of *b. levipes*; and OTUs of *spicilegus* fall near those of *b. levipes* and *b. sacarensis* but are distinctly separated from the former five taxa. In addition, the correlations of the various characters with the principal components stayed largely the same (Table 3).

The relationship of eight pairs of OTUs from the slopes of a single mountain or within a mountain system (for instance, the two samples of *evides* are from different

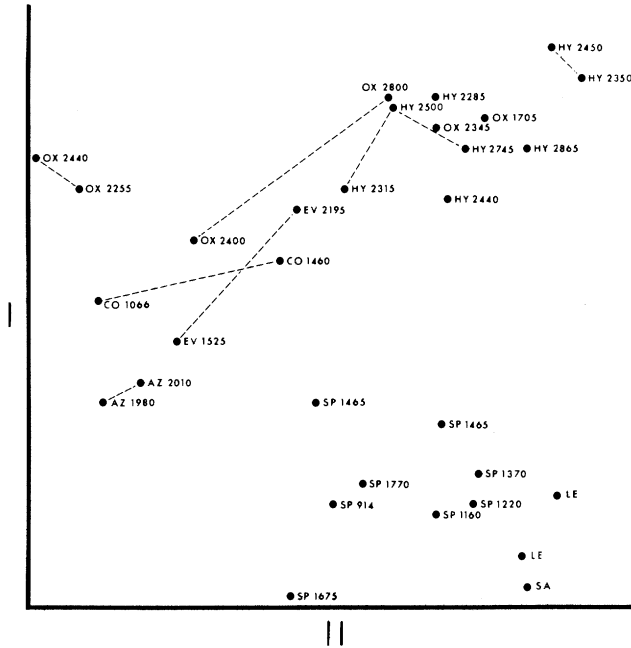


FIG. 3.—Scatter plot of Principal Component I versus II using 31 population samples as cases as described by the 13 morphometric variables (also see Table 3). Taxa are indicated by two-letter abbreviations followed by their elevation of collection in meters. Dashed lines connect samples from the slopes of same mountain or within a single montane system.

TABLE 3.—Results of second principal component analysis and correlations of the characters with the first three principal components extracted.

Variable	Principal component		
	I	II	III
Eigenvalue	9.6	1.0	0.9
Cumulative percent total variation	74.0	81.5	88.4
Degrees freedom	77	65	54
Significance	0.0	0.0	0.0
Length of skull	0.99	0.05	0.06
Length of rostrum	0.96	-0.04	0.24
Greatest zygomatic breadth	0.92	0.24	-0.08
Breadth of braincase	0.93	0.08	0.12
Least interorbital width	0.89	-0.09	0.20
Length of molar row	0.92	-0.17	0.29
Length of incisive foramen	0.94	0.19	0.14
Breadth of palate	0.57	0.44	-0.66
Width of mesopterygoid fossa	0.71	-0.52	-0.23
Length of auditory bullae	0.75	0.40	0.29
Length of body	0.84	0.10	-0.17
Length of tail	0.77	-0.37	-0.34
Length of hindfoot	0.90	-0.26	0.05

Mexican states but inhabit the same mountainous unit, the Sierra Madre del Sur) is especially interesting. An increase in elevation accompanies an increase in principal component (PC) score in seven out of eight cases along the first principal component, and in five out of eight possibilities along the second principal component (Fig. 3). Increase in elevation, therefore, seems to account for much of the linear scatter of these OTUs on PC I versus PC II. The correlations of PC I and PC II scores of these 20 OTUs against elevation are highly significant, as are most regressions of the 20 sample means for each morphometric variable on elevation (Table 4; Figs. 4, 5).

#### DISCUSSION

The morphological evidence, as presented in the numerical analysis, argues for removal of *cordillerae* Dickey (1928) as a subspecies of *Peromyscus boylii*. The other geographic race of *boylii* that Dickey described from El Salvador, *sacarensis*, properly belongs with *rowleyi* and *levipes* as subspecies of *boylii*. The taxonomic disposition of *cordillerae*, whether to reassign it as a subspecies of another form or to elevate it to full species rank, is less obvious and compels an evaluation of the status of such related forms as *aztecus*, *evides*, *hylocetes*, and *oaxacensis*. One could, as another alternative, place *cordillerae* in complete synonymy with another species, but this option raises the same questions as does reallocation at the subspecific level.

The first alternative, reassignment of *cordillerae* as a subspecies of another species, prompts the attendant question: a subspecies of which other species? As noted by Dickey (1928), *cordillerae* closely resembles *aztecus* in many respects, particularly in overall size and pelage color. This resemblance is indicated by the results of the principal components analyses, but these results also suggest the lack of any clear distinction between samples of *cordillerae* and *evides*, *hylocetes*, or *oaxacensis*. To call *cordillerae* a subspecies of *aztecus*, assuming one can defend this allocation on the basis of morphological differentiation, would create a peculiar distributional pattern, one unlike that of other small mammals inhabiting the Central American highlands. *Peromyscus aztecus* is distributed along the Atlantic-facing slopes of the Sierra Madre Oriental, and separated from *cordillerae* (on the Pacific side of Central America) by *P. oaxacensis*, whose range covers the mountains of southern Mexico and Guatemala to Honduras and El Salvador. Such a patchy distribution is zoogeographically improbable.

A more plausible zoogeographic explanation involves derivation of *cordillerae* from populations occupying the neighboring highlands in Honduras and eastern El Salvador, those which currently bear the name *oaxacensis*. Due to the position of Mt. Cacaguatique as an outlier of the main cordillera in El Salvador, it is doubtful that the humid pine-oak vegetation inhabited by *cordillerae* is connected with pine-oak habitats in the main highlands. Nevertheless, such a connection could easily have existed during the Pleistocene at times of glacial maxima (Duellman, 1965). A depression of vegetation zones by only 500 m would provide continuous pine-oak forest from Mt. Cacaguatique along a ridge of low hills to the Sierra de Guajiquiro in Honduras, and allow dispersal of populations that subsequently became isolated and differentiated as *cordillerae*. In their study of the effects of glaciation on the biotas of Mexico, Martin and Harrell (1957) suggested a vertical displacement of vegetation zones by as much as 1,000 m. Thus, one might consider *cordillerae* a geographic variant of *oaxacensis*. Certainly, the two forms possess many basic similarities, especially in the structure and proportions of the glans penis, conformation of the skull, and dentition.

If one accepts the inclusion of *cordillerae* as a subspecies of *oaxacensis* as the most parsimonious taxonomic treatment, then the specific distinctness of *aztecus* and *evides* must be questioned. Such a consideration is unavoidable because the traits that distinguish *cordillerae* from *oaxacensis* are the same sort that separate *evides* from *oa-*



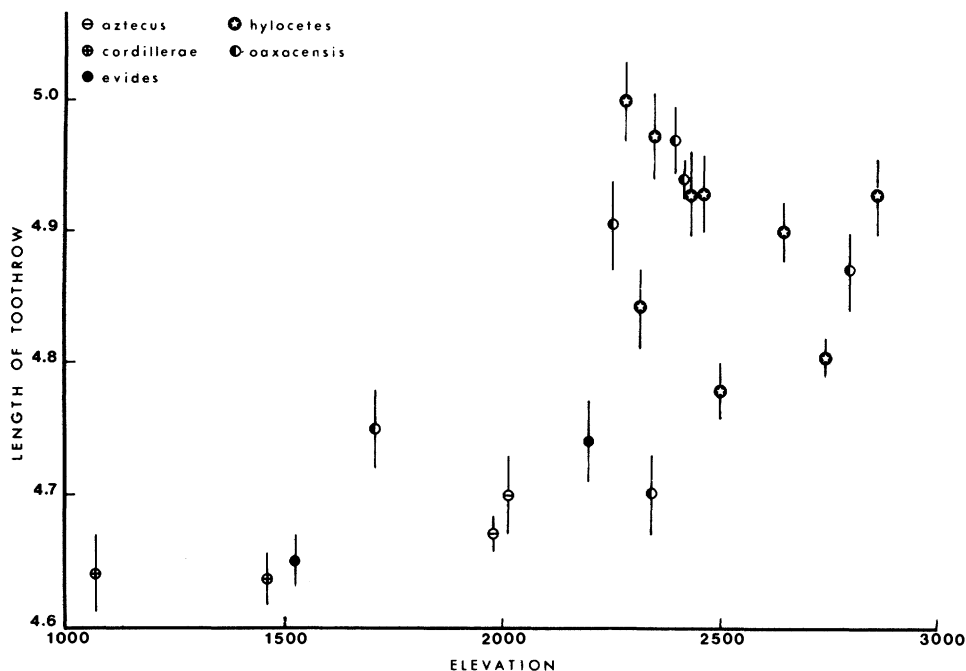


FIG. 4.—Regression of length of maxillary tooththrow (mm) on collecting elevation (m) for samples of *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis* (also see Table 4). Solid lines correspond to two SDs above and below the sample mean.

TABLE 4.—Least squares regression equations of morphometric variables and principal component scores against elevation, for all OTUs ( $N = 20$ ) representing *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis*.

Variable	F	Level of significance	$r$	$r^2$	$Y = aX + b$
Length of skull	7.0	0.016	0.53	0.28	$Y = 0.00087X + 28.6$
Length of rostrum	2.9	0.104	0.37	0.14	NS
Greatest zygomatic breadth	4.7	0.043	0.46	0.21	$Y = 0.00043X + 14.2$
Breadth of braincase	14.4	0.001	0.67	0.44	$Y = 0.00045X + 12.6$
Least interorbital width	9.4	0.007	0.58	0.34	$Y = 0.00014X + 4.5$
Length of maxillary tooththrow	16.6	0.001	0.69	0.48	$Y = 0.00020X + 4.4$
Length of incisive foramen	5.3	0.032	0.48	0.23	$Y = 0.00024X + 5.9$
Breadth of palate	0.5	0.487	0.16	0.03	NS
Width of mesopterygoid fossa	7.9	0.012	-0.55	0.30	$Y = -0.009X + 2.4$
Length of auditory bulla	8.7	0.008	0.57	0.33	$Y = 0.00025X + 3.5$
Length of body	12.1	0.003	0.63	0.40	$Y = 0.00561X + 98.6$
Length of tail	0.1	0.787	0.06	0.004	NS
Length of hindfoot	6.2	0.023	0.51	0.26	$Y = 0.00090X + 23.1$
PC I Score	9.7	0.006	0.59	0.35	$Y = 0.00231X - 1.1$
PC II Score	5.0	0.038	0.47	0.22	$Y = 0.00110X + 0.3$

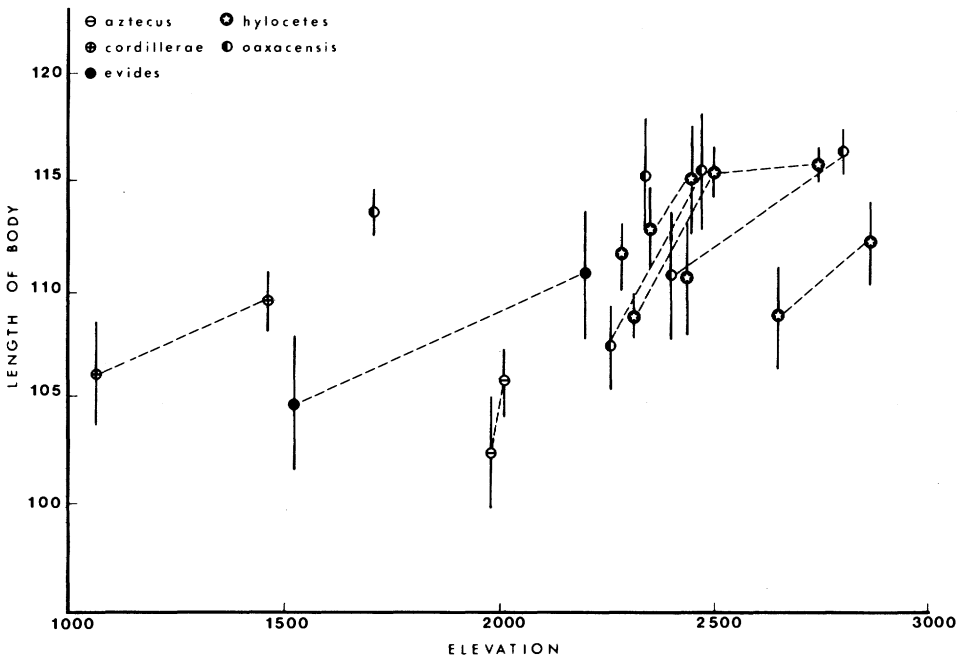


FIG. 5.—Regression of length of body (mm) on collection elevation (m) for samples of *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis* (also see Table 4). Dashed lines connect samples obtained on the slopes of the same mountain or within a single montane system. Solid lines correspond to one SE of the sample mean.

*xacensis*, or *aztecus* from *oaxacensis*, namely a generally richer pelage color and smaller size. *Peromyscus hylocetes* of the Cordillera Transvolcanica of Mexico also should be included within this complex; its propinquity to *oaxacensis* has been suggested previously (Hooper, 1968; Carleton, 1977). Applying a degree-of-morphological-differentiation criterion to this complex of forms in a consistent manner (and in the absence of other evidence indicating either hybridization or genetic discontinuities), one faces the choice of either considering these five taxa as a subspecies of one widely ranging species—*P. aztecus* (de Saussure, 1860) has priority—or retaining each, including *cordillerae*, as a distinct species. Hooper (1968:33) aptly characterized a classification as the “systematist’s best summary estimate of relationships among the organisms with which he is concerned . . .” For the reasons enumerated below, I favor adoption of the first alternative as the “best summary estimate” for these five named forms.

1.—In range of morphological divergence, samples of *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis* exhibit patterns of divergence usually seen between subspecies. For example, extremes of size and pelage color between *evides* and *oaxacensis* correspond to those seen between smaller- (such as *rowleyi*) and larger-bodied (*levipes* or *baetae*) populations of *boylei* in Mexico. Variability in length of baculum among samples of these five taxa (Fig. 6) closely mimics that recorded for many samples of a single species, as for example, within *P. boylei* or *P. spicilegus*. Moreover, the general shape of the skull—particularly the development of a supraorbital shelf and possession of an elongate braincase—is basically alike in these five forms. As noted by Hooper and Musser (1964) and Carleton (1977), the glandes penes of *aztecus*, *evides*, *hylocetes*, and *oaxacensis* conform to one general plan: they are comparatively short and broad; their surface is covered by finely graded spines and marked by

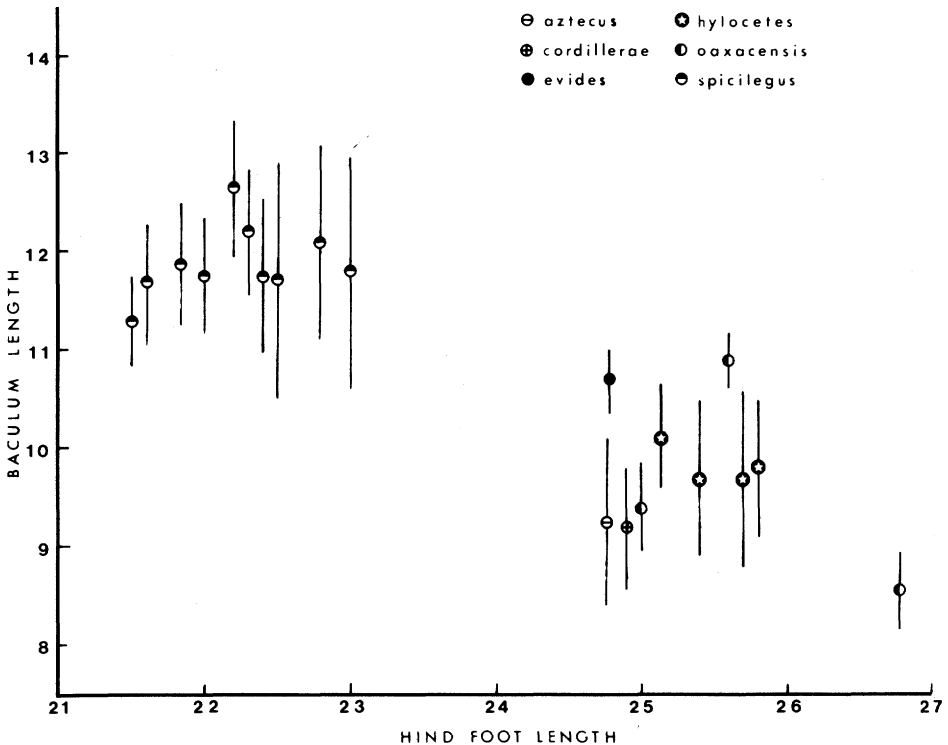


FIG. 6.—Scatter plot of length of baculum (mm) versus length of hind foot (mm) for samples of *aztecus*, *cordillerae*, *evides*, *hylocetes*, *oaxacensis*, and *spicilegus*. Solid lines correspond to two SE above and below the sample mean.

longitudinal furrows; all lack dorsal and ventral lappets; and their bacula are straight, relatively slender, and tipped with a minute cap of cartilage. The glans penis of *cordillerae* also fits this structural plan.

2.—The morphological features used to distinguish these nominative species seem to be subject to elevational effects. When one reviews Osgood's (1909) descriptive and comparative sections for *aztecus*, *evides*, *hylocetes*, and *oaxacensis* (the former two he listed as subspecies of *boyllii*), the diagnostic traits most often repeated are ones of overall size (principally as evidenced by external measurements, size of skull, and length of toothrow), richness of pelage color, density of fur on the tail, and size or inflation of the auditory bullae. Individuals of *hylocetes* average largest in size, and possess more inflated bullae, duller pelage, and a densely-haired, bicolored tail. At the other extreme, specimens of *evides* are definitely smaller with less-inflated bullae, exhibit a richer tawny pelage color, and have sparsely-haired, indistinctly-bicolored tails. Examples of *aztecus* more nearly resemble those of *evides*, while specimens of *oaxacensis* are intermediate with regard to these characters.

Specimens of *aztecus* and *evides* (especially samples then available to Osgood, 1909) have been collected at lower elevations (usually 1,000–2,000 m) than those of either *oaxacensis* (1,500–2,500 m) or *hylocetes* (generally above 2,300 m). As demonstrated above, most means of the 13 morphometric variables are significantly correlated with elevation for the 20 samples representing *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis* (Figs. 3–5; Table 4). I believe this correlation accounts for the elongated scatter of these 20 OTUs in the plot of PC I versus PC II. Moreover, when one examines samples collected on slopes of the same mountain or mountain

system but at different elevations, the general trend is one of increase in size (Figs. 3 and 5). The magnitude of size differences observed between some of these nominative species (compare *aztecus* and *hylocetes*, Fig. 4) is sometimes duplicated by samples collected at different elevations within species (for example, the divergence of samples of *oaxacensis*, Fig. 4). This is not always the case, for reversals with increased altitude sometimes occur for certain pairs of samples depending on the specific variable in question. The general relationship, however, is apparent.

Actually, the degree of correlation between elevation and any of these morphometric variables is higher than might be expected, when one considers the variety of climatic and biotic factors that probably change with elevation. Conceivably a direct measure of one of these environmental variables would show stronger correlations than simply elevation. Whatever the causal factors involved, taxonomists have recognized as separate species isolated segments of a once continuous montane species, particularly those moieties that now inhabit different elevational zones.

The population that Dickey (1928) named *cordillerae* may be viewed as a natural evolutionary test of this hypothesis. The insular nature of Mt. Cacaguatique, segregated from the major cordilleras in that part of Central America, permits a reasonable zoogeographic reconstruction of events resulting in the isolation of populations found there today (see above). Because Mt. Cacaguatique only rises to 1,651 m, populations so restricted could not simply follow the retreat of temperate pine-oak forests up the mountain when the climate ameliorated during interglacial periods. Such populations either became extinct or adapted to a more humid tropical situation. The complex of characters exhibited by specimens of *cordillerae*—a rich cinnamon-colored pelage, indistinctly bicolored tail, overall smaller size of skull and body, and less inflated bullae—perhaps reflects some of the changes that accompanied this adaptation. This suite of characters appears in populations that today inhabit lower elevations along the Sierra Madre Oriental (*aztecus*) and the Sierra Madre del Sur (*evides*). The past zoogeographic history of these populations cannot be as clearly interpreted, because the mountain systems they occupy are not wholly isolated like Mt. Cacaguatique. The Sierra Madre del Sur merges with the central Oaxacan highlands (inhabited by *oaxacensis*), and the southern portion of the Sierra Madre Oriental adjoins these same highlands in Oaxaca as well as the eastern reaches of the Cordillera Transvolcanica. Therefore, patterns of population dispersion, isolation, and secondary contact have probably been much more complex.

3.—Circumstantial evidence for considering the five taxa as a single species derives from distributional data for other Central American small mammals dwelling in similar elevational belts and ecological situations. For instance, the combined range of *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis* is nearly congruent with that of *Reithrodontomys sumichrasti*, a harvest mouse that occupies a similar elevational range and vegetational type (Hooper, 1952:66, map 3). The montane shrews of the *Cryptotis mexicana* species group fit this distributional pattern as well (Choate, 1970). Although Choate (1970:243) derived populations that inhabit the Cordillera Transvolcanica (*C. goldmani alticola*) by dispersal across the Rio Balsas from Guerrero, I believe a more likely corridor for the migration of a *hylocetes* predecessor existed from the highlands of Oaxaca, through Puebla, to the eastern limb of the Cordillera Transvolcanica. Populations then spread to the westernmost reaches (in Jalisco and Michoacan) of this high, volcanically-active ridge of mountains.

One might argue that *P. spicilegus* should also be included as a subspecies of *aztecus*. Morphological features of *spicilegus* clearly indicate its near relationship to this complex. Furthermore, that *spicilegus* resides at even lower elevations (generally 800–1,800 m), plus its smaller size and the apparent association of size and elevation, strongly bolsters this viewpoint. However, this action is not warranted at the present time for the following reasons.

First, in all the phenetic analyses (data presented here and in Carleton, 1977), samples of *spicilegus* are consistently set apart from those representing *aztecus*, *cordillerae*, *evides*, *hylocetes*, and *oaxacensis*. This hiatus is as large as that separating *boyllii* (*rowleyi*, *levipes*, and *sacarensis*) from that group of five taxa, and *Peromyscus boyllii* is unquestionably specifically distinct from them (Alvarez, 1961; Carleton, 1977; Hooper, 1968; Musser, 1964). Although the general conformation of the skull of *spicilegus* resembles that of *aztecus* and its subspecies (*cordillerae*, *evides*, *hylocetes*, and *oaxacensis*), the dissimilarity in phenetic dispersion in the principal components analyses suggests a basically different correlation of parts.

Second, the glans penis and baculum of *spicilegus* are both absolutely and proportionately longer than in *aztecus* (Fig. 6). In addition, the protractile tip of *spicilegus* exceeds that of *aztecus*, and the body of the glans lacks the pronounced furrows typical of the other five taxa studied (Carleton, 1977).

Third, populations of *spicilegus* generally range into more humid, tropical vegetation zones at lower elevations than is usually true of the *aztecus* complex.

Fourth, Hooper (1955) recorded the sympatric occurrence of *spicilegus* and *hylocetes* (herein treated as a subspecies of *aztecus*) in the mountains southeast of Autlan, Jalisco. Based on specimens examined, the range of *spicilegus* includes intermediate elevations on the Cordillera Transvolcanica in Colima, Jalisco, and Michoacan; portions of the Sierra de Coalcoman in Michoacan; and the western flanks of the Sierra Madre Occidental in Jalisco, Zacatecas, Nayarit, Sinaloa, and Durango (Fig 7).

The classification proposed here rests primarily on external and cranial features, anatomy of the glans penis, and distributional records. As such, it needs to be tested and corroborated by other data, such as those from karyotypic and electrophoretic studies. The karyotypic information currently available, although limited, does not contradict this taxonomic scheme. The karyotypes of both *oaxacensis* and *hylocetes* exhibit an intermediate number of banded chromosomes; the fundamental number of *oaxacensis* is 68 (Schmidly and Schroeter, 1974), while that of *hylocetes* is 72 (Lee and Elder, 1977). This difference in number of autosomal arms is less than that recorded for populations of *P. boyllii*, which possess fundamental numbers ranging from 52 to 60 (Schmidly and Schroeter, 1974; Kilpatrick and Zimmerman, 1975). The chromosomal complement displayed by *P. spicilegus*, in contrast, consists of a large proportion of metacentrics; the fundamental number is 82 (Schmidly and Schroeter, 1974, as modified by Carleton, 1977). Chromosomal investigations of *aztecus*, *evides*, *cordillerae*, and the populations of *spicilegus* in Michoacan are clearly desirable, as well as further study of *P. boyllii* populations. Additional collecting and range documentation are needed, too. In particular, the mountains in Puebla and Oaxaca require surveys to ascertain the distribution of *oaxacensis* with respect to *aztecus*, *hylocetes*, and *evides*. The mountains east and west of the Rio Balsas (the Sierra Madre del Sur in Guerrero and the Sierra de Coalcoman in Michoacan) are poorly known faunistically. Collections made there could help resolve the status of *spicilegus* with respect to *evides*. Finally, more detailed elevational transects should be performed.

In summary, five named forms have the aspect of geographic races of a single species that inhabit different mountain units: *aztecus* in the southern portion of the Sierra Madre Oriental; *cordillerae* on Mt. Cacaguatique; *evides* in the Sierra Madre del Sur; *hylocetes* in the Cordillera Transvolcanica; and *oaxacensis* (the most widely distributed) in the Mexican highlands of Oaxaca, Chiapas, Guatemala, Honduras, and in El Salvador (Fig. 7). Because these taxa, as currently understood, are entirely allopatric, the occurrence of reproductive isolation cannot be used to measure their specific distinctiveness. Rather one must infer the existence of reproductive incompatibility on the basis of degree of morphological difference (*sensu* Mayr, 1969: 196–197). In my judgement, that divergence, as revealed here, does not warrant separate species recognition.

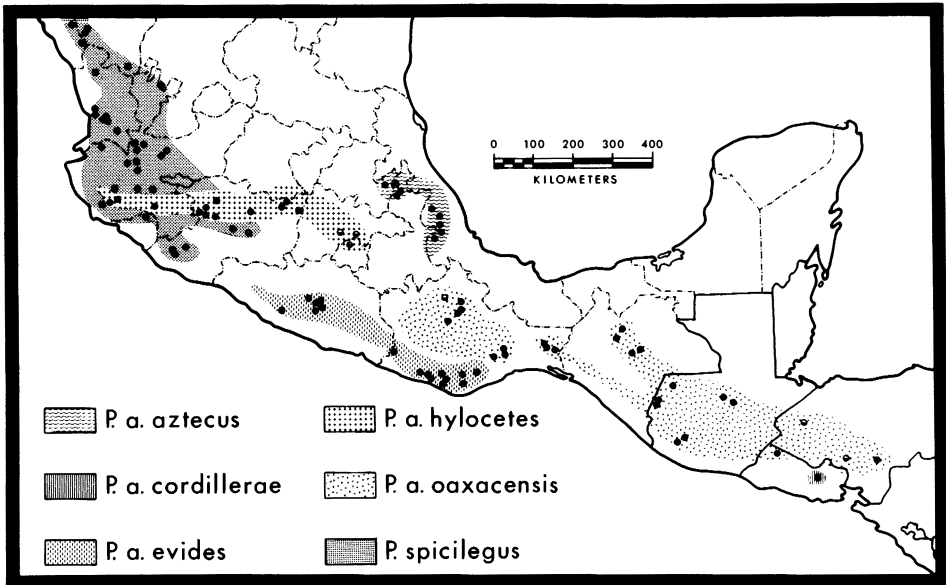


FIG. 7.—Map showing the distribution of *Peromyscus spicilegus* and the five subspecies of *P. aztecus*. Closed circles signify specimens examined by me; half-closed circles indicate literature records.

***Peromyscus aztecus***  
(synonomies under subspecies)

*Peromyscus aztecus aztecus* (Saussure)

*H[esperomys] aztecus* Saussure, 1860:105, Plate 9, fig. 4.

*P[eromyscus] aztecus*, Thomas, 1894:365.

*Peromyscus boylei aztecus*, Osgood, 1909:156.

*Peromyscus boylii aztecus*, Hall and Kelson, 1959:633.

*Peromyscus aztecus*, Alvarez, 1961:113; Hall and Dalquest, 1963:305; Musser, 1964:9; Hooper and Musser, 1964:12; Hooper, 1968:38.

*Lectotype*.—Designated by Osgood (1909:157) as the mounted specimen with skull in the Geneva Museum, Switzerland; one of the three specimens used by Saussure in his original description.

*Type locality*.—MEXICO: Veracruz—vicinity of Mirador, about 3,800 ft elevation.

*Distribution*.—Known from the eastern slopes (1,000–2,010 m) of the Sierra Madre Oriental in Hidalgo, Puebla, and Veracruz; pine-oak vegetation in Humid Upper Tropical zone (sensu Baker, 1968).

*Specimens examined*.—46 as follows. MEXICO: Hidalgo—13 mi NE Metepec, 6,600 ft, 9 (UMMZ); Puebla—Huachinango, 4 (USNM); 2 mi SW Huachinango, 6,500 ft, 9 (UMMZ); 5.7 mi SW Huachinango, 6,600 ft, 2 (UMMZ); Pahuatlan, 1,100 m, 3 (UMMZ); Veracruz—2.4 mi SW Huatusco, 1 (UMMZ); Jalapa, 5,000 ft, 1 (USNM); 1.5 mi NE Las Minas, 5 (USNM); Mirador, 3,800 ft, 8 (USNM); 2 mi N Teocelo, 1,000 m, 1 (UMMZ); 0.5 mi NE Las Minas, 3 (USNM). Topotypes were examined.

*Peromyscus aztecus cordillerae* Dickey

*Peromyscus boylii cordillerae* Dickey, 1928:2; Hall and Kelson, 1959:635.

*Peromyscus boylei cordillerae*, Burt and Stirton, 1961:56.

*Holotype*.—Skin and skull of old adult female, Dickey Collection, University of California, Los Angeles no. 10716; collected 24 November 1925 by Ruben A. Stirton.

*Type locality*.—EL SALVADOR: Departamento San Miguel—Mt. Cacaguatique, 3,500 ft elevation.

*Distribution*.—Known only from the slopes (1,066–1,555 m) of Mt. Cacaguatique, Deptos. San Miguel and Morazan, El Salvador; oaks with scattered pine in Humid Upper Tropical zone.

*Specimens examined*.—61 as follows. EL SALVADOR: Depto. Morazan—Mt. Cacaguatique, 4,500 ft, 1 (MVZ); 4,800 ft, 16 (MVZ); 5,000 ft, 4 (MVZ); 5,100 ft, 4 (MVZ); Depto. San Miguel—Mt. Cacaguatique, 3,500 ft, 28 (MVZ), 4 (UMMZ); 4,000 ft, 2 (MVZ), 2 (UMMZ). Topotypes were examined.

### *Peromyscus aztecus evides* Osgood

*Peromyscus spicilegus evides* Osgood, 1904:64.

*Peromyscus boylei evides* Osgood, 1909:152.

*Peromyscus hylocetes yautepecus* Goodwin, 1955:4.

*Peromyscus boylii evides*, Hall and Kelson, 1959:635.

*Peromyscus evides*, Musser, 1964:9; Hooper and Musser, 1964:12; Hooper, 1968:38 (part); Goodwin, 1969:175 (part).

*Holotype*.—Skin and skull of young adult male, National Museum of Natural History, Biological Survey Collection (USNM) no. 71426; collected 28 February 1895 by E. W. Nelson and E. A. Goldman.

*Type locality*.—MEXICO: Oaxaca—Juquila, 5,000 ft elevation.

*Distribution*.—Pine-oak vegetation of the Humid Upper Tropical and Southern Montane Woodland zones in the Sierra Madre del Sur (800–2,500 m) of Guerrero and Oaxaca; specimens in Michoacan, formerly called *evides*, were referred to *P. spicilegus* by Carleton, 1977.

*Remarks*.—Goodwin (1955) described *yautepecus* from the Sierra Madre del Sur in Oaxaca as a subspecies of *P. hylocetes*, but later (1969) allocated *yautepecus* to *P. evides*. As noted by Goodwin (1955), the type series of *yautepecus* averages slightly larger than the topotypic series of *evides* from Juquila, Oaxaca. Specimens of *yautepecus* were collected at a slightly higher elevation (Santo Thomas Teipan, 7,500 ft) than the *evides* from Juquila (5,000 ft) but closely resemble in size and coloration other examples of *evides*, such as those from Guerrero, from similar elevations. Consequently, I have placed *yautepecus* in synonymy under *P. aztecus evides*.

*Specimens examined*.—61 as follows. MEXICO: Guerrero—Omiteme, 2 (UMMZ); 9 (USNM); 1 mi NW Omiteme, 7,260 ft, 6 (USNM); 1 mi SW Omiteme, 7,260 ft, 4 (USNM); 6 mi NW Chilpancingo, 5,500 ft, 2 (MSU); 12 mi WSW Xochipala, 8,200 ft, 2 (MSU); 43 km (by road) N Tecpan de Galeano, 800 m, 3; Oaxaca—4 mi S Jalatengo, 5,000 ft, 2 (UMMZ); Campamento Rio Molino, 7,300 ft, 1 (UMMZ); 8 mi SSW Juchatengo, 6,300 ft, 1 (MSU); 10 mi N Puerto Escondido, 1 (MSU); Santa Rosa, 1,300 m, 3 (UMMZ); Juquila, 5,000 ft, 6 (USNM); 1 (AMNH); Temascaltepec, 5,000 ft, 4 (AMNH); Teotepec 5,000 ft, 4 (AMNH); Putla, San Vicente, 4 (AMNH); Yau-tepec, Santo Thomas Teipan, 6 (AMNH). The holotype was examined.

### *Peromyscus aztecus hylocetes* Merriam

*Peromyscus hylocetes* Merriam, 1898:124; Osgood, 1909:159; Hall and Villa, 1949:462; Hooper, 1955:16; Hall and Kelson, 1959:637; Hooper and Musser, 1964:12; Hooper, 1968:38.

*Holotype*.—Skin and skull of adult male, National Museum of Natural History, Biological Survey Collection no. 50423; collected 27 July 1892 by E. W. Nelson and E. A. Goldman.

*Type locality*.—MEXICO: Michoacan—Patzcuaro, 7,000 ft elevation.

*Distribution*.—Pine-oak and fir forests of the southern Montane Woodland zone of the Cordillera Transvolcanica (1,980–3,085 m) in the states of Jalisco, Colima, Michoacan, Estado de Mexico, Morelos, and the Distrito Federal.

*Specimens examined*.—196 as follows. MEXICO: Jalisco—Sierra de Autlan, 7,600 and 9,000 ft, 50 (UMMZ); 20 mi SSE Autlan, 6,500 and 8,200 ft, 31 (UMMZ); Michoacan—3 mi E Angahuan, 7,200 ft, 2 (UMMZ); 1 mi N Apo, 2,700 m, 1 (UMMZ); 2 mi N Apo, 2 (UMMZ); 3.5 mi E Apo, 3,000 m, 3 (UMMZ); 8 mi WNW Hidalgo, 8,000 ft, 8 (UMMZ); 9 mi WNW Hidalgo, 8,700 ft, 4 (UMMZ); 10 mi NW Hidalgo, Cerro San Andreas, 9,400 ft, 17 (UMMZ); Mil Cumbres, 2,485 m, 2 (UMMZ); 0.5 mi N Volcan Paricutin, 2 (UMMZ); 3 mi N Volcan Paricutin, 7,200 ft, 3 (UMMZ); 6 mi S Patzcuaro, 8,000 ft, 7 (UMMZ); 1 mi N San Juan, 2,300 m, 1 (UMMZ); 3 mi NNW San

Juan, Cerro Cuitzeran, 2,350 and 2,450 m, 27 (UMMZ); 10 mi NW Uruapan, 7,400 ft, 5 (UMMZ); Patamban, 31 (USNM). The holotype was examined.

*Peromyscus aztecus oaxacensis* Merriam

*Peromyscus oaxacensis* Merriam, 1898:122; Osgood, 1909:158; Hall and Kelson, 1959:636; Hooper and Musser, 1964:12; Hooper, 1968:38; Goodwin, 1969:175 (part).

*Peromyscus hondurensis*, Goodwin, 1941:1.

*Holotype*.—Skin and skull of adult male; National Museum of Natural History, Biological Survey Collection (USNM) no. 68426; collected 1 September 1894 by E. W. Nelson and E. A. Goldman.

*Type locality*.—MEXICO: Oaxaca—Cerro San Felipe, 10,300 ft elevation.

*Distribution*.—Sistema Montañosa in Oaxaca, highlands of Chiapas south into Guatemala, Honduras, and El Salvador; generally pine-oak habitats and lower edge of boreal fir forests of the Southern Montane Woodland zone; known elevational range 980 to 3,140 m.

*Remarks*.—In his description, Goodwin (1941) allied *P. hondurensis* with *P. lophurus*, but subsequently Musser (1969) identified *hondurensis* as simply a variant of *P. oaxacensis*. Accordingly, I here consider *hondurensis* as a synonym of *P. aztecus oaxacensis*.

*Specimens examined*.—192 as follows. GUATEMALA: Alta Verapaz—3 km E Tactic, 4 (UMMZ); Finca Concepcion, 1 (UMMZ); Esquintla—Volcan de Agua, Finca El Rosario, 3 (UMMZ); Huehuetenango—4 km NW Santa Eulalia, 2,980 m, 1 (UMMZ); Hacienda El Injerto, 1,600 m, 1 (UMMZ); 3.6 mi W Hacienda El Injerto, 4 (UMMZ); Suchitepequez—Finca San Rafael, 7,000 ft, 4 (UMMZ); Solola—0.5 m E Panajachel, 1,800 m, 4 (UMMZ). EL SALVADOR: Chalatenango—Los Esesmites, 7,200 ft, 2 (MVZ), 7,250 ft, 7 (MVZ), 7,400 ft, 4 (MVZ); 7,800 ft, 3 (MVZ), 8,000 ft, 13 (MVZ), 2 (UMMZ). HONDURAS: Morazan—Cerro Yyuca, 6,100 ft, 2 (UMMZ). MEXICO: Chiapas—1 mi N Pueblo Nuevo, 5,500 ft, 25 (UMMZ); 5 mi N Pueblo Nuevo, 5,700 ft, 11 (UMMZ); Pueblo Nuevo, 1,700 m, 9 (UMMZ); San Cristobal de las Casas, 2,100 m, 7 (UMMZ); 8 mi SE San Cristobal de las Casas, 7,800 ft, 8 (UMMZ); 10 mi SE San Cristobal de las Casas, 2,330 m, 3 (UMMZ); Oaxaca—Cerro San Felipe, 2,200, 2,300 and 2,500 m, 20 (UMMZ); 12 mi N Ixtlan de Juarez, 9,200 ft, 19 (UMMZ); Cerro Pelon, 13 mi NE Llano de las Flores, 2,700 m, 2 (UMMZ); Tehuantepec, San Pedro Jilotepec, 3,000 ft, 1 (AMNH); Media Loma, 2 (AMNH); Cerro Lachiguiri, 7,000 ft, 3 (AMNH); Agua Zarca, 3,000 ft, 3 (AMNH); San Isidro, 2 (AMNH); Cerro Baul, Rio Mono Blanco, 2 (AMNH); Sierra Madre N of Zanatepec, 5,000 ft, 8 (AMNH); Cerro Atravesado, 4,000 ft, 12 (AMNH). The holotype was examined.

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