INTERRELATIONSHIPS OF POPULATIONS OF THE
PEROMYSCUS BOYLII SPECIES GROUP
(RODENTIA, MURIDAE) IN WESTERN
MEXICO

By MICHAEL D. CARLETON

INTRODUCTION

SINCE OSGOOD (1909) first defined the *Peromyscus boylii* species-group, there has been some uncertainty regarding its composition and the taxonomic level of forms assigned to it. Hooper's (1968) overview of the classification of *Peromyscus* incorporated changes suggested subsequent to Osgood's (*op. cit.*) revision, namely the inclusion of *polius* from the *truei* group and the elevation of *aztecus* and *evides* from subspecies of *boylii* to species rank. As predicted by Hooper (*op. cit.*), the populations named *P. hondurensis* have proved to be only southern representatives of *P. oaxacensis* (Musser, 1969). More recently, two additional species have been shifted to the *boylii* group: *P. stephani* from the subgenus *Haplomylomys* (Lawlor, 1971) and *P. ochraventer* from the *mexicanus* group (Huckaby, 1973). Further, Schmidly (1973) has asserted that *attwateri* is specifically distinct from *P. boylii*. Acceptance of these taxonomic recommendations would bring the number of species in the *boylii* group to ten: *attwateri*, *aztecus*, *boylii*, *evides*, *hylocetes*, *oaxacensis*, *ochraventer*, *pectoralis*, *polius* and *stephani*.

The present study contributes additional distributional and morphological information on populations of *P. boylii*, particularly those known by the subspecific names *simulus* and *spicilegus*. Both of these sets of populations are confined to western Mexico: *simulus* in the coastal lowlands of Sinaloa and Nayarit and *spicilegus* in the Sierra Madre Occidental from southern Chihuahua and Sonora to Jalisco (Osgood, 1909). In evaluating the relationships of these forms, I found it necessary to consider representative samples of several other species

1

assigned to the *boylii* group, namely *aztecus, boylii levipes, b. madrensis, b. rowleyi, evides, hylocetes, oaxacensis* and *pectoralis.*

The other purpose of this paper is to report a new species of *Peromyscus,* described here because it is apparently most closely related to species in the *boylii* group. In fact, my efforts to identify those specimens described below as a new species initially prompted the examination of the *Peromyscus boylii* group in western Mexico reported herein.

Peromyscus winkelmanni, new species
FIGS. 1, 3D

HOLOTYPE.—Adult male, skin, skull and glans penis, UMMZ 110585 (original number John R. Winkelmann 779); collected 25 July 1960 by John R. Winkelmann; one of 12 specimens (UMMZ 110584-91, 110716-9) collected 24-28 July 1960 by John R. Winkelmann and Floyd Downs.

TYPE LOCALITY.—Mexico, Michoacan, 6.3 mi (by road) WSW Dos Aguas, 8000 ft elevation.

GEOGRAPHIC RANGE.—Known only from the type locality and the vicinity of Dos Aguas, Michoacan. Dos Aguas is a small village and adjoining lumber camp located approximately one-half the distance between Aguililla and Coalcoman; Duellman (1965) gives the coordinates as 18° 26′ latitude, 102° 55′ longitude. Eleven additional specimens were taken as follows: 2.5 mi (by road) SE Dos Aguas, 6900 ft, 1; 6.3 mi (by road) WSW Dos Aguas, 8000 ft, 4; 8.4 mi (by road) WSW Dos Aguas, 8000 ft, 6. *Peromyscus winkelmanni* probably inhabits other sections of the coastal sierra in Michoacan.

DIAGNOSIS.—A species of the *boylii* group characterized by large size (greater than *P. hylocetes* or *P. oaxacensis*), "beaded" interorbital region, and elongated glans penis. Further discussion and analysis of the relationships of *P. winkelmanni* are found in following sections of this study.

DESCRIPTION.—Size: External and selected cranial measurements (in mm) of the holotype follow: total length, 263; tail length, 140; hind foot length, 29; ear length, 22; skull length, 33.3; rostrum length, 11.2; braincase width, 14.3; interorbital width, 5.3; molar row length, 5.2; palatal breadth, 3.2. Descriptive statistics of the series of *P. winkelmanni* are given in Appendices II and III.

Color: Pelage coloration of a wet-season specimen is as follows. Dorsum tawny mixed with black. Black hairs predominate on the mid-dorsum, and in two of eight individuals, this concentration gives the impression of a broad, poorly-defined band. The cheeks, sides and
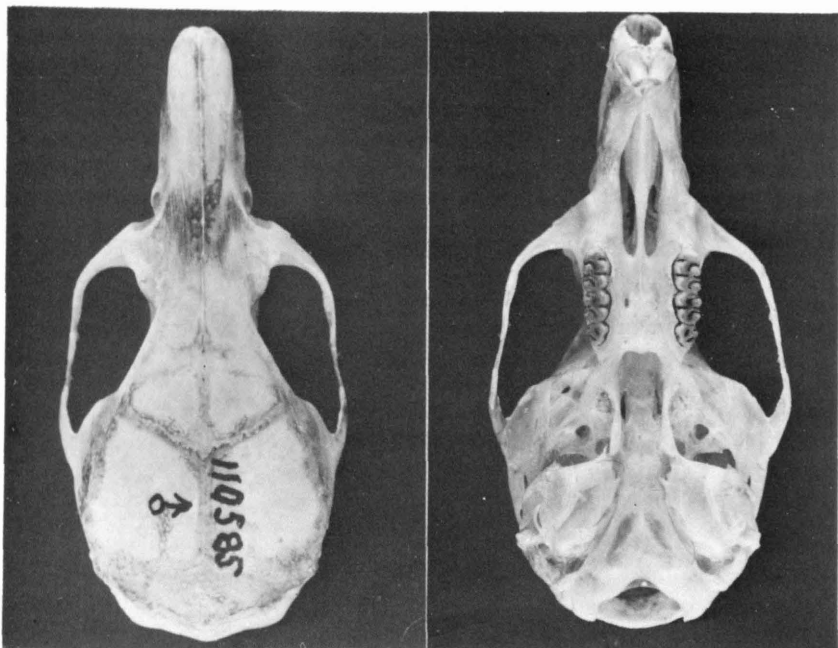
FIG. 1. Dorsal (left) and ventral (right) views of the skull of the holotype (UMMZ 110585) of *Peromyscus winkelmanni.* Total length of skull = 33.3 mm.

flanks are bright tawny, almost cinnamon, and the transition from the dorsal to ventral pelage color is abrupt. Fur of the underparts is dark gray tipped with white; the white tips do not completely obscure the basal gray sections, presenting an overall dusky-white effect. A streak of ochraceous occurs in the pectoral region of the type specimen and four of the seven additional study skins. On the hind foot, dusky fur covers about half of the metatarsal region; the remainder is white. The thinly-haired tail is only slightly darker above than below; transition from the darker dorsal surface of the tail to the lighter underpart is gradual.

Skull: the skull of *winkelmanni* is similar to *P. hylocetes* and *P. oaxacensis* but larger in most mensural characters (Appendix III) and with an interorbital bead or ridge (Fig. 1). This bead is not as strongly pronounced as in *P. banderanus* or *P. megalops* (See Osgood, 1909, pl. 5, p. 274), but is distinct and contrasts with the sharply-angled or shelfed interorbital region of *P. hylocetes* and *P. oaxacensis* (Fig. 8). The dentition is complex: accessory lophs and styles occur in both the upper and lower molars of most of the specimens.

Other traits: Based on examination of fluid-preserved specimens and dried skins, the teat number is six, one pair axillary and two pairs inguinal. The stomach is the discoglandular type in contrast to the pouched stomach found in several species of *Peromyscus* (Carleton, 1973). The glans penis of the holotype is portrayed in Fig. 3D. A more detailed description of it and comparisons will be given in a subsequent section.

HABITAT.—The type specimen was obtained in an area of moderately cutover pine-oak forest with scattered firs. In his field notes, Winkelmann commented that the forest around Dos Aguas was very wet, with moss-covered rocks, downed trees and epiphytes. Additional information on the character of the vegetation near Dos Aguas follows (Duellman, 1965;647):

> "Large oaks, some of which attain heights of 30 meters, are scattered among the pines; in some places the oaks are dominant. The understory consists of various herbs and brushes, principally *Baccharis*, as well as oak and pine seedlings and saplings. The forest ... is on a windward ridge frequently bathed in clouds. Thick mats of mosses and lichens on the trees, and many epiphytes, including large bromeliads and orchids, grow in abundance ... There is a deep layer of mulch on the ground."

MATERIALS AND METHODS

Specimens consisted primarily of conventional study skins and skulls and glandes penes extracted from fluid-preserved specimens, cleared and stained in the manner described by Hooper (1958); a few glandes were removed from museum skins and reconstituted (Hooper, *op. cit.*). I prepared the semi-diagrammatic drawings of the glandes penes using a camera lucida.

Measurements of the skull and glans penis were recorded to the nearest tenth of a millimeter (mm) using a craniometer (Anderson, 1968). Twenty-three characters were quantified. Ten of those are of the skull: (1) greatest length of skull; (2) length of rostrum; (3) greatest zygomatic breadth; (4) breadth of braincase; (5) least interorbital width; (6) length of maxillary tooth row; (7) length of incisive foramen; (8) breadth of palate; (9) greatest width of mesopterygoid fossa; (10) length of auditory bulla. The three external measurements (rounded to the nearest mm) of the skin are those registered by the collector: (11) body length (interpolated from total length and tail); (12) length of tail; and (13) length of hind foot. I excluded ear length because of variation among collectors in method of measuring the ear. Dimensions of the glans penis include (14) length of the glans (measured from the distal tip to attachment of the prepuce); (15) greatest width; (16) length of protractile tip (from the distal tip to ventral lip

of the urinary meatus); and (17) length of the osseous portion of the baculum (excludes the cartilaginous tip). In addition to those 17 morphometric variables, I encoded six qualitative characters (see p. 15), five of the glans penis and one of the skull. The states of development for these six characters are discussed below. Juveniles (in gray juvenal pelage or an early stage of molt to the subadult pelage) were omitted from statistical analyses.

Listed below are the 32 samples (see Fig. 2) utilized in the multivariate analyses. In some instances, specimens from nearby localities were combined to increase sample size. The number in parentheses preceding each locality corresponds to that given in the figures and tables; the number following a locality indicates sample size. Names of species and races follow Hooper (1968) and Baker and Greer (1962) regarding the assignment of Durangan populations to either *Peromyscus boylii rowleyi* or *P. b. spicilegus*. These specific allocations serve to identify the forms considered, but do not necessarily reflect my conclusions concerning their affinities or taxonomic status. More complete locality information and a list of all specimens examined are provided in Appendix I.

Peromyscus aztecus: (1) Metepec, Hidalgo and SW Huauchinango, Puebla, 23.

Peromyscus boylii levipes: (2) San Cristobal de las Casas, Chiapas, 43; (3) Bochil and Pueblo Nuevo, Chiapas, 22; (4) mountains west of Chilpancingo, Guerrero, 29; (5) Uruapan, Michoacan, 54; (6) Dos Aguas, Michoacan, 16; (7) N Ixtlan de Juarez, Oaxaca, 15.

P. b. madrensis: (8) Tres Marias Islands, Nayarit, 11.

P. b. rowleyi: (9) W San Luis, Durango, 24; (10) N Pueblo Nuevo, Durango, 14.

P. b. simulus: (11) N Rosario, Sinaloa, 28; (12) SW Copala, Sinaloa, 10.

P. b. spicilegus: (13) S Pueblo Nuevo, Durango, 11; (14) Santa Lucia, Sinaloa, 11; (15) N Santa Isabel, Nayarit, 52; (16) NNW Magdalena, Jalisco, 18; (17) Sierra de Autlan, Jalisco, 35.

P. evides: (18) E Dos Aguas and Coalcoman, Michoacan, 26; (19) S Uruapan, Michoacan, 15; (20) Los Reyes, Michoacan, 20; (21) mountains west of Chilpancingo, Guerrero, 16; (22) Santa Rosa and Juquila, Oaxaca, 24.

P. hylocetes: (23) Sierra de Autlan, Jalisco, 48; (24) Nevada de Colima, Jalisco, 28; (25) SSE Autlan, Jalisco, 12; (26) NNW San Juan, Michoacan, 26; (27) Cerro San Andreas, Michoacan, 24.

P. oaxacensis: (28) Cerro San Felipe and N Ixtlan de Juarez, Oaxaca, 29; (29) San Cristobal de las Casas, Chiapas, 12; (30) N Pueblo Nuevo, Chiapas, 28.
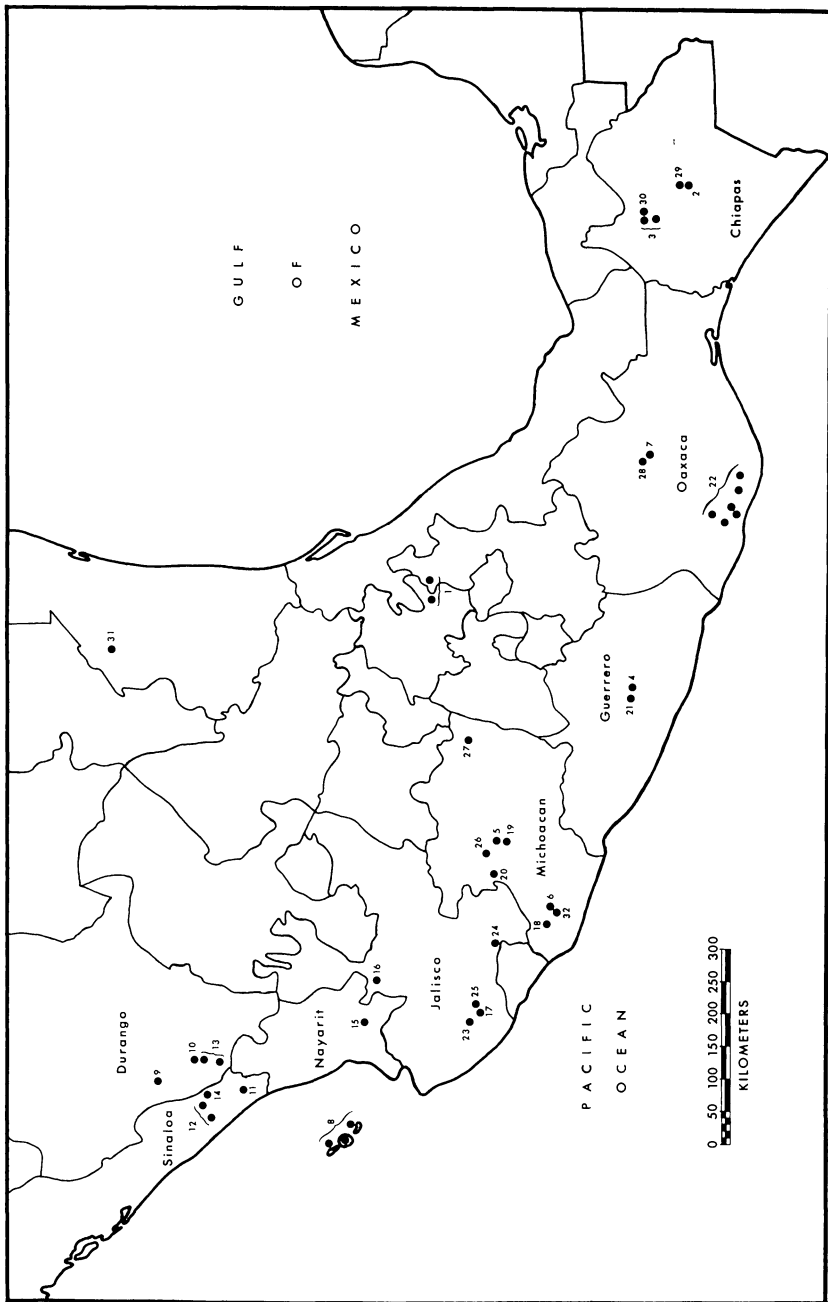
FIG. 2. Map of Mexico indicating location of the 32 samples utilized in the multivariate analyses. Only the principal Mexican states discussed are identified. Locality numbers correspond to those listed in the Materials and Methods.

P. pectoralis: (31) San Carlos Mts., Tamaulipas, 28.
P. winkelmanni: (32) Dos Aguas, Michoacan, 12.

Standard descriptive statistics (mean, standard deviation, standard error of the mean, and range) were derived for the 17 morphometric variables for each of the above 32 samples (operational taxonomic units, OTUs). In three large samples (localities 2, 15 and 23), Student's *t*-tests were performed for each measurement of the skin and skull to detect possible sexual dimorphism. No significant differences (*i.e.*, P≤.05) were discovered for any variable, and therefore, the sexes were pooled in subsequent analyses. Three methods of summarizing phenetic relationships among the samples were employed: a shortest connection network (Prim, 1957), principal component analysis, and cluster analysis. Locality means served as the character states in all three methods. Characters used in the shortest connection network were standardized over all OTUs to have a mean of zero and a standard deviation of one. Principal components were extracted from a correlation matrix in which characters were standardized. Loading of each character on the first three principal components is expressed by a correlation coefficient (Morrison, 1967). To avoid congestion, the projection of OTUs on the components is presented in two-dimensional scatter plots. In the cluster analyses, taxonomic resemblances between OTUs were computed from both correlation and distance matrices using standardized characters. Phenograms were derived from both matrices by the unweighted pair-group method using arithmetic averages (UPGMA) (for discussion, see Sneath and Sokal, 1973), and the coefficient of cophenetic correlation was calculated for each. A linear discriminant function analysis was performed in the manner described by Birney (1973) and Choate (1973) to assist identification of some individuals of unknown identity. Data processing was performed by the Michigan Interactive Data Analysis System (MIDAS), a series of computer programs formulated by the Statistical Research Laboratory at the University of Michigan.

DESCRIPTION AND ANALYSIS OF SAMPLES

GLANS PENIS.—This section amplifies the descriptions of species of the *boylii* group surveyed by Hooper (1958) and Hooper and Musser (1964) and presents information on forms not included in their studies. Anatomical terms utilized are given by Hooper (1958). Number of glandes penes examined and their abbreviated localities, together with mensural data, are enumerated in Appendix II.

Based on the morphology of their phalli, the sampled populations

can be segregated into two groups, one consisting of the forms *aztecus, spicilegus, evides, hylocetes, oaxacensis* and *winkelmanni* and the other of *levipes, madrensis, rowleyi, simulus* and *pectoralis.*

In examples of the first group, the glans penis is broad with a fluted surface and lacks dorsal and ventral lappets (Fig. 3). The baculum is a simple, somewhat slender rod capped with a minute cone of cartilage, usually less than 0.3 mm in length. In all of these forms, the spines are densely packed, the same size on both dorsal and ventral sides of the glans, and are graded in size becoming progressively smaller from the attachment of prepuce toward the tip. Unlike the second group of forms, the boundary between the body and tip of the glans is not marked by dorsal or ventral lappets. Instead there is an irregular scalloped effect at this junction (Fig. 3).

The longitudinal grooves or "fluting" on the body of the glans appears to be a real structural feature and not some artifact of preservation. This trait is not easily verified in poorly preserved specimens or those reconstituted from dry study skins. Nevertheless, longitudinal furrows are demonstrable in well-fixed material. This corrugation of the body of the glans is most pronounced in samples of *aztecus, evides* from Guerrero and Oaxaca, *hylocetes* and *oaxacensis.* The fluting is less conspicuous, but still apparent, in specimens of *evides* from Michoacan and *spicilegus.* No fluting was evident in the four phalli of *winkelmanni.*

Samples of *evides* from Michoacan agree with those of *spicilegus* in proportional aspects of the phallus. Hooper and Musser (1964:4) pointed out that their examples of *evides* differed from those of *hylocetes* and *oaxacensis* in having a proportionately longer protractile tip, less pronounced fluting, and absolutely longer glans and baculum. It should be noted that their specimens of *evides* came from Michoacan, but they did not then have available representatives of *evides* from Guerrero and Oaxaca. My examples of *evides* from those two states are more similar to those of *aztecus, hylocetes* and *oaxacensis* (Figs. 3A-C). In contrast, the populations from Michoacan closely approximate in structure and proportions of the glans penis the samples of *spicilegus* from Durango, Sinaloa, Jalisco and Nayarit. This is clearly demonstrated by the relative size of the baculum (Fig. 4).

In the second complex of taxa (*levipes, madrensis, simulus, rowleyi* and *pectoralis*) there are dorsal lappets, usually a ventral lappet, the body of the glans is not fluted, and the phallus is more slender in conformation. Well-defined dorsal lappets, usually separated by a deep cleft, occur at the distal margin of the body of the glans in all examples of these forms (Fig. 5). The free distal apices of the dorsal
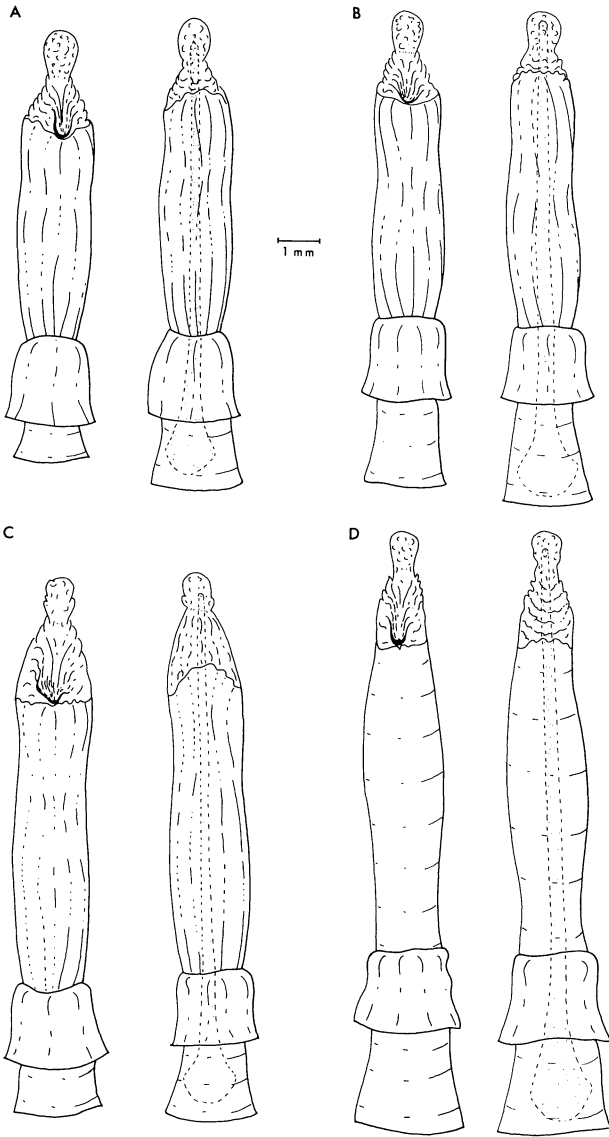
FIG. 3. Ventral (left) and dorsal (right) views of the glans penis in several species of *Peromyscus boylii* group: (A) *P. evides* (UMMZ 117937), W Santa Rosa, Oaxaca; (B) *P. hylocetes* (UMMZ 110597), NW Uruapan, Michoacan; (C) *P. evides* (UMMZ 110616), E Dos Aguas, Michoacan; (D) *P. winkelmanni* (UMMZ 110585, holotype), WSW Dos Aguas, Michoacan. The position of the baculum (dashed lines) is indicated only in the dorsal view. Vertical lines on the body of the glans signify presence of longitudinal furrows.
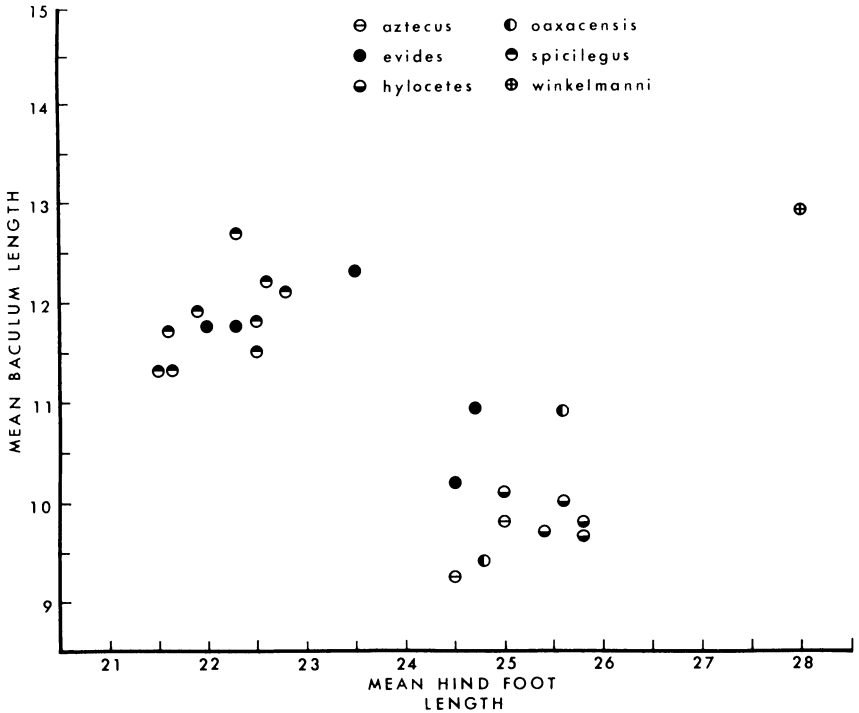
FIG. 4. Size of the baculum relative to hind foot length in several members of the *P. boylii* group. Each point in the scatter diagram represents a sample mean, not measurements of individuals; sample sizes and localities are listed in Appendix II.

lappets partly overlie the delicate tissue of the protractile tip, and spines extend onto both dorsal and ventral lappets.

The ventral lappet is unpaired; it emerges from the ventral border of the urethral orifice and partly covers it. I observed a ventral lappet in examples of *levipes, rowleyi, simulus* and *pectoralis*. In *simulus*, this character is not as strongly pronounced as in *levipes, rowleyi* and *pectoralis,* and in some specimens of *simulus*, there is a slight median cleft at the apex of the ventral lappet. No ventral lappet was distinguishable in the two specimens of *madrensis*. This observation is suspect since my examples were rehydrated from dry study skins. I am more confident, however, of the occurrence of dorsal lappets in those specimens.

The apportionment of spines covering the body of the glans in these forms (except *madrensis*) contrasts with that observed in the previously mentioned assemblage (*aztecus, evides,* etc.). There is an
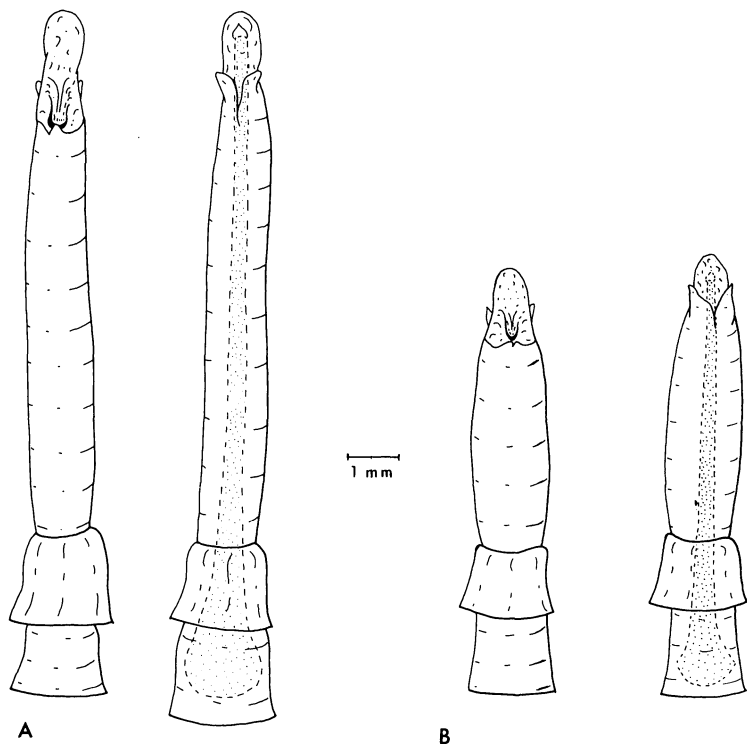
FIG. 5. Ventral (left) and dorsal (right) views of the glans penis in: (A) *P. boylii levipes* (UMMZ 110595), Dos Aguas, Michoacan; and (B) *P. boylii simulus* (UMMZ 101278), N Rosario, Sinaloa. Other information as in Fig. 3.

asymmetry in density and size of spines on the dorsal versus the ventral half of the glans. Near the attachment of the prepuce on the dorsal half of the glans, the spines are noticeably larger and more widely spaced than those on the ventral surface. This asymmetry in distribution of spines was not seen in the examples of *madrensis*.

Absolute and proportional differences in size of the phallus and baculum are evident (Fig. 6). For example, the small absolute size of its phallus readily separates examples of *simulus* from those of *levipes, madrensis, rowleyi* and *pectoralis*. The samples of *levipes* and *rowleyi* are closely similar in anatomy of their phalli with only slight average differences in size.

Only specimens of *pectoralis* have an elongate, lanceolate, cartilaginous cap on the baculum (Clark, 1953; Hooper, 1958).
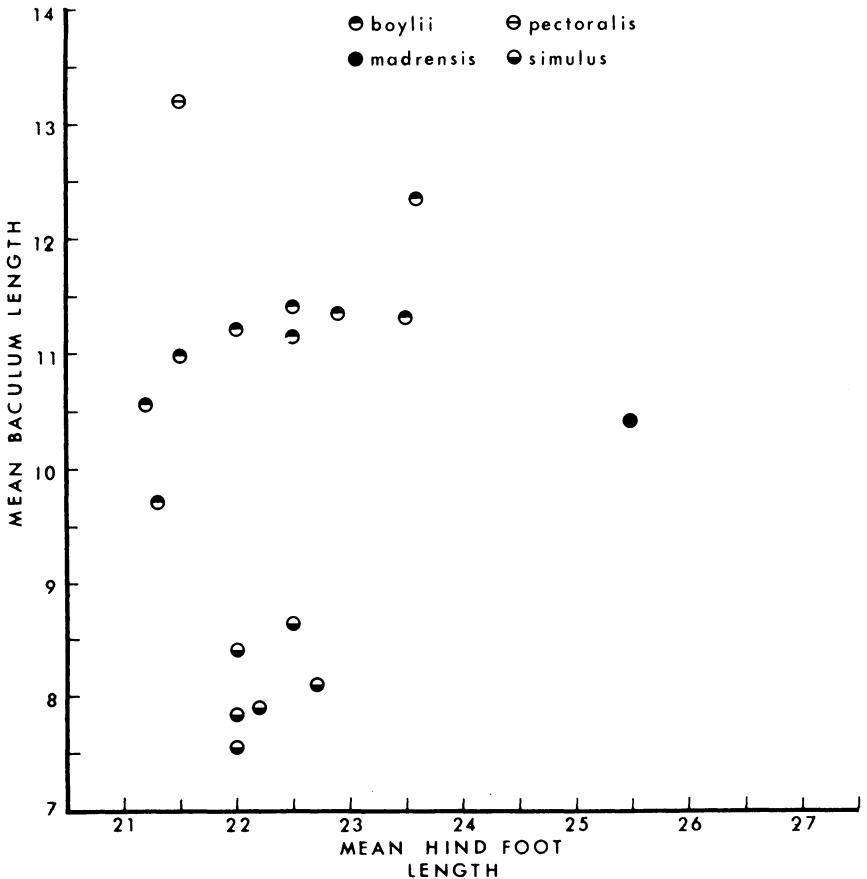
FIG. 6. Size of the baculum relative to hind foot length in several members of the *P. boylii* group. Samples of both *boylii levipes* and *b. rowleyi* are included under the *boylii* symbol. Other information as in Fig. 4.

SKULL.—The interorbital region in samples of *levipes, rowleyi, simulus* and *pectoralis* is hourglass-shaped when viewed dorsally (Fig. 7). In another set of forms, namely *aztecus, evides* (from Guerrero and Oaxaca), *hylocetes* and *oaxacensis*, a distinct shelf occurs at the posterior aspect of the interorbital region (Osgood, 1909). The projection of this shelf disrupts the contour of the interorbital border and imparts a more angled appearance to the interorbital section as viewed from above (Fig. 8). The shelf is not as prominent in examples of *madrensis, spicilegus* and those samples of *evides* from Michoacan. As mentioned above, *winkelmanni* has a weak bead or ridging on its interorbital border (Fig. 8D).
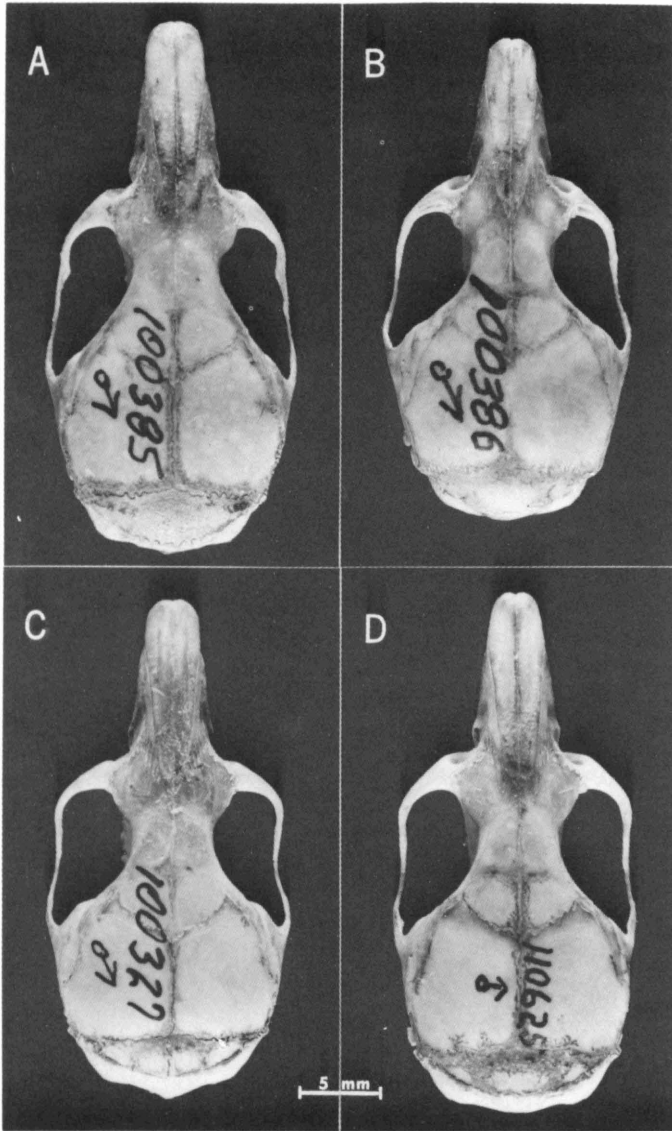
FIG. 7. Dorsal view of skulls of several forms of the *P. boylii* group: (A) *P. boylii spicilegus* (UMMZ 100385), E San Blas, Nayarit; (B) *P. boylii simulus* (UMMZ 100386), E San Blas, Nayarit; (C) *P. boylii rowleyi* (UMMZ 100327), W. San Luis, Durango; (D) *P. boylii levipes* (UMMZ 110625), WSW Dos Aguas, Michoacan. Specimen UMMZ 100385, although assignable to *simulus* on a geographic basis, is an example of *spicilegus*; note its greater size and presence of an interorbital shelf when compared to specimen UMMZ 100386.

FIG. 8. Dorsal views of skulls of (A) *P. evjdes* (UMMZ 117934), Santa Rosa, Oaxaca; (B) *P. oaxacensis* (UMMZ 109591), N Pueblo Nuevo, Chiapas; (C) *P. hylocetes* (UMMZ 95262), WNW Hidalgo, Michoacan; (D) *P. winkelmanni* (UMMZ 110716), WSW Dos Aguas, Michoacan.

Within a population, the shape of the interorbital region is fairly constant among adults, less so in younger animals. Juveniles and subadults of *spicilegus*, for example, 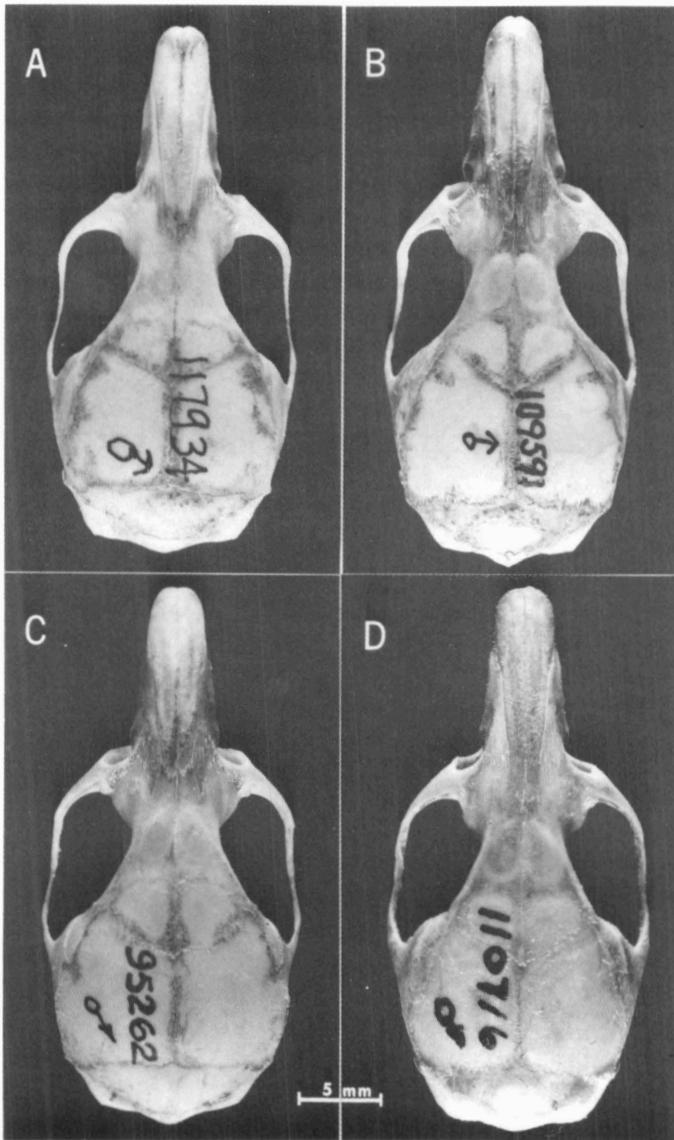may exhibit almost hourglass-shaped interorbital borders, and old adults of *levipes* or *rowleyi* may have a slight shelf. Such ontogenetic variation requries that age of the specimens, as judged by relative wear of the teeth, be considered when comparing series of skulls. Forms with a strongly developed shelf are readily distinguishable from *levipes*.

I found no significant differences in dental characters among the forms other than those indicated by Hooper (1957). Three pair of mammae (one pair axillary and two pairs inguinal) were observed in all samples. In all the taxa for which whole carcasses in fluid were available, *hylocetes* and *madrensis* being the sole exceptions, I observed a discoglandular kind of stomach (see Carleton, 1973).

From this survey of morphological differences in skull and phallus, I coded character states for six qualitative characters as follows (also see Table 1).

(1) Dorsal lappets: absent (0); present (1).
(2) Ventral lappet: absent (0); present, weakly developed (1); present, strongly developed (2).
(3) Occurrence of spines: evenly graded in size and distribution (0); asymmetry in size and distribution (1).
(4) Fluting of glans surface: present (0); absent (1).
(5) Cartilaginous tip: minute cap (0); elongate cone (1).

TABLE I

QUALITATIVE CHARACTERS AND THE APPROPRIATE CHARACTER STATE CODE RECORDED FOR EACH SPECIES OR SUBSPECIES.

Species	Dorsal lappets	Ventral lappet	Occurrence of spines	Fluting	Cartilaginous tip	Inter-orbital region
aztecus	0	0	0	0	0	1
b. levipes	1	2	1	1	0	0
b. madrensis	1	0	0	1	0	1
b. rowleyi	1	2	1	1	0	0
b. simulus	1	1	1	1	0	0
b. spicilegus	0	0	0	0	0	1
evides	0	0	0	0	0	1
hylocetes	0	0	0	0	0	1
oaxacensis	0	0	0	0	0	1
pectoralis	1	2	1	1	1	0
winkelmanni	0	0	0	1	0	2

(6) Interorbital region of skull: hourglass shape (0); shelf (1); weak
     bead (2).

STATISTICAL ANALYSES.—Results of the shortest-connection network,
principal component and cluster analyses disclose three principal asso-
ciations of OTUs (Figs. 9-14).

One consists of samples of *hylocetes* (localities 23-27), *oaxacensis*
(localities 28-30) and *evides* from Guerrero (locality 21) and Oaxaca
(locality 22). The example of *aztecus* (locality 1) is usually located
near this group of OTUs but somewhat at its periphery. Within this
association of OTUs, there is no obvious segregation following the
currently recognized species; this is particularly evident for samples of
hylocetes and *oaxacensis.* Interestingly, OTU No. 28 (*oaxacensis* from
near its type locality) is generally linked with OTU No. 22 (*evides*
from the type locality and its vicinity). Inspection of both the distance
and correlation matrices used to derive the phenograms also indicated
that these two OTUs were more similar to one another than either was
to members of their own taxon.

Representatives of *spicilegus* (localities 13-17) and *evides* from Mich-
oacan (localities 18-20) comprise another set of OTUs that consistently
cluster together. Again, no marked division according to present-day
species alignments is apparent within this grouping. The hiatus between
samples of *evides* from Michoacan and those named *evides* from
Guerrero and Oaxaca reflects overall size differences of skin and skull
as well as proportional ones of the auditory bullae and glans penis.

Examples of *levipes* (localities 2-7) and *rowleyi* (localities 9-10)
form the third major group of OTUs. Dispersion of OTUs within this
cluster partly accords with the subspecific division, samples of *levipes*
averaging larger in size. There is not complete separation, for the
levipes from Uruapan, Michoacan (locality 5) falls among those of
rowleyi from Durango.

The remaining OTUs are variously set apart from the three major
clusters. The outliers include *pectoralis* (locality 31), *winkelmanni*
(locality 32), *madrensis* (locality 8) and *simulus* (localities 11-12). The
position of these OTUs shifts somewhat in the various phenetic analy-
ses with respect to the three main clusters, but the composition of the
principal clusters themselves is not altered appreciably. *P. winkelmanni*
and *pectoralis* are most distinctive. The sample of *winkelmanni* (local-
ity 32) is linked to the complex of OTUs representing *hylocetes,
oaxacensis,* and *evides* from Guerrero and Oaxaca. In the dendrogram
generated from the distance matrix, *winkelmanni* is separated from all
other OTUs at the first bifurcation (Fig. 9). The affinity of *pectoralis*
(locality 31) lies with samples of *levipes* and *rowleyi,* albeit at an
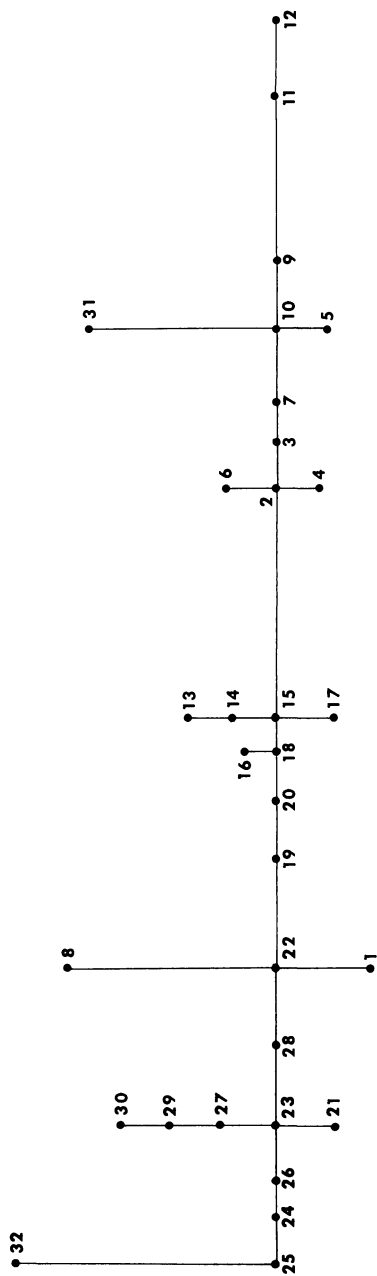
FIG. 9. Shortest connection network of 32 population samples based on 23 standardized characters described in text. The distance between samples is proportional to the amount of dissimilarity over all characters. Taxa represented include: *P. aztecus* (locality 1); *P. boylii levipes* (localities 2-7); *P. b. madrensis* (locality 8); *P. b. rowleyi* (localities 9,10); *P. b. simulus* (localities 11,12); *P. b. spicilegus* (localities 13-17); *P. evides* (localities 18-22); *P. hylocetes* (localities 23-27); *P. oaxacensis* (localities 28-30); *P. pectoralis* (locality 31); *P. winkelmanni* (locality 32).

FIG. 10. Two dimensional projections of the first three principal components using the 32 population samples as cases as described by all characters. Top: Component I versus II. Bottom: Component I versus III. Identification of locality numbers as in Fig. 9 and Materials and Methods section.
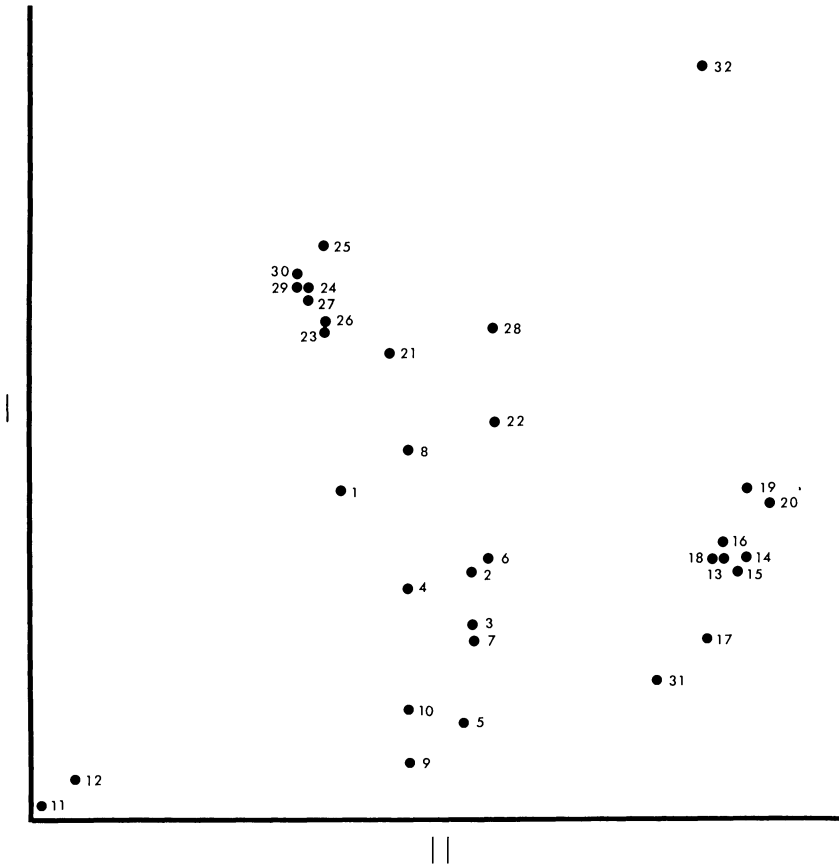
FIG. 11. Scatter plot of Principal Component I versus II using the 32 population samples as cases as described by only the 17 morphometric characters. Identification of locality numbers as in Fig. 9 and Materials and Methods section.
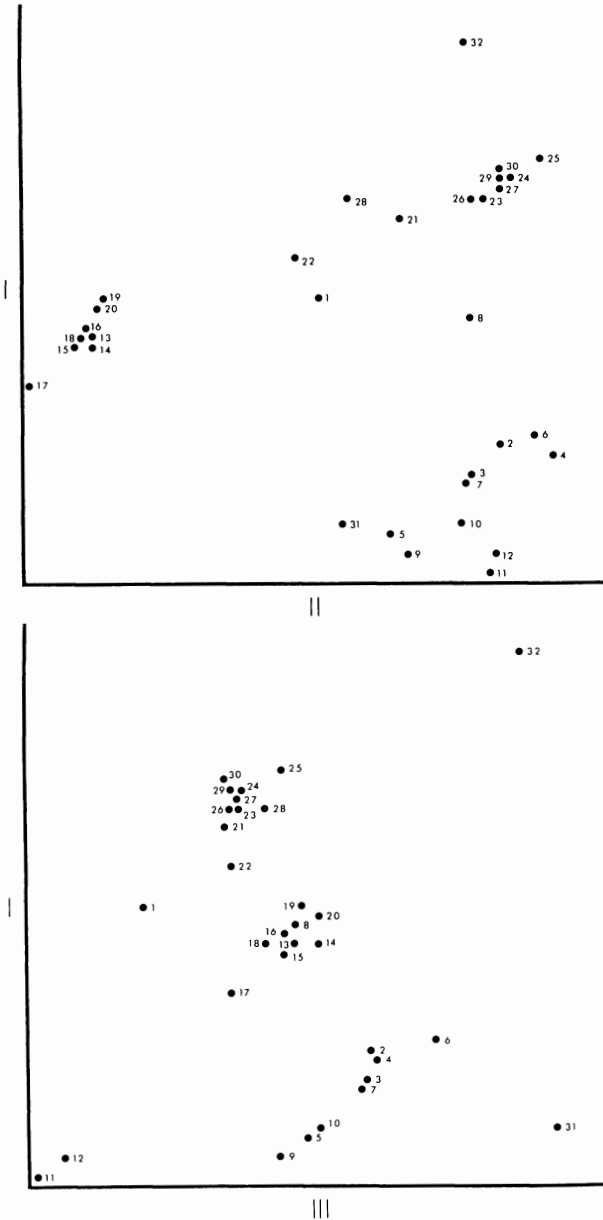
appreciable taxonomic distance. OTUs 11 and 12, representing *simulus*, are also allied with those of *levipes* and *rowleyi*. Nevertheless, there is a definite hiatus between *simulus* and *levipes-rowleyi* in the principal component and cluster analyses (Figs. 7-11). The sample of *madrensis* (locality 8) is not consistently associated with any of the three large clusters of OTUs. In the phenograms, *madrensis* branches from a major stem that also includes representatives of *aztecus, hylocetes, oaxacensis,* and *evides* from Guerrero and Oaxaca. In the projection of principal component I versus III, *madrensis* is interspersed with OTUs of *spicilegus* and *evides* from Michoacan (Fig. 7B).

A general size factor is indicated in the dispersion of OTUs on principal component I (Figs. 10, 11). Similarly, the order of OTUs along

TABLE 2

RESULTS OF PRINCIPAL COMPONENT ANALYSIS USING 17 MORPHOMETRIC
AND 6 QUALITATIVE CHARACTERS FOR ALL 32 SAMPLES (see Fig. 10).

Component	I	II	III
Eigenvalue	13.6	3.6	2.5
% total variance	59.2	74.9	85.8
Independence	1674.8	1473.2	1258.8
df	252	230	209
significance	0.0	0.0	0.0
Length of skull	.96	.21	.11
Length of rostrum	.95	.18	.11
Greatest zygomatic breadth	.96	.16	.10
Breadth of braincase	.94	.16	.20
Least interorbital width	.95	.07	−.05
Length of molar row	.93	.17	.02
Length of incisive foramen	.90	.30	.15
Breadth of palate	.66	.28	.33
Width of mesopterygoid fossa	.88	.06	−.03
Length of auditory bullae	.36	.73	.34
Length of body	.94	.09	.14
Length of tail	.72	.30	.14
Length of hind foot	.84	.38	−.03
Length of glans penis	−.04	−.47	.84
Width of glans penis	.74	−.59	−.11
Length of protractile tip	.19	−.87	.33
Length of baculum	−.04	−.49	.86
Dorsal lappets	−.83	.46	.21
Ventral lappet	−.80	.41	.38
Occurrence of spines	−.86	.43	.20
Fluting of glans surface	−.70	.46	.35
Cartilaginous tip	−.23	−.02	.47
Interorbital region of skull	.87	−.38	−.05

the shortest connection network is strongly influenced by size (Fig. 9), grading from small on the right (samples of *simulus*) to large on the left (the sample of *winkelmanni*). Most qualitative characters also contribute heavily to the first principal component. Characters that exhibit a high correlation with the second principal component include length of the auditory bullae and length of the protractile tip (Table 2). The development of these two variables in *spicilegus* and *evides* from Michoacan primarily accounts for their separation from other OTUs along principal component II (Fig. 10A). In *spicilegus* and *evides*, the bulla are small relative to size of skull and the protractile

FIG. 12. Clusters analysis (UPGMA) of 32 population samples generated from distance matrix using all characters. Coefficient of cophenetic correlation = 0.766. Identification of locality numbers as in Fig. 9 and Materials and Methods section.
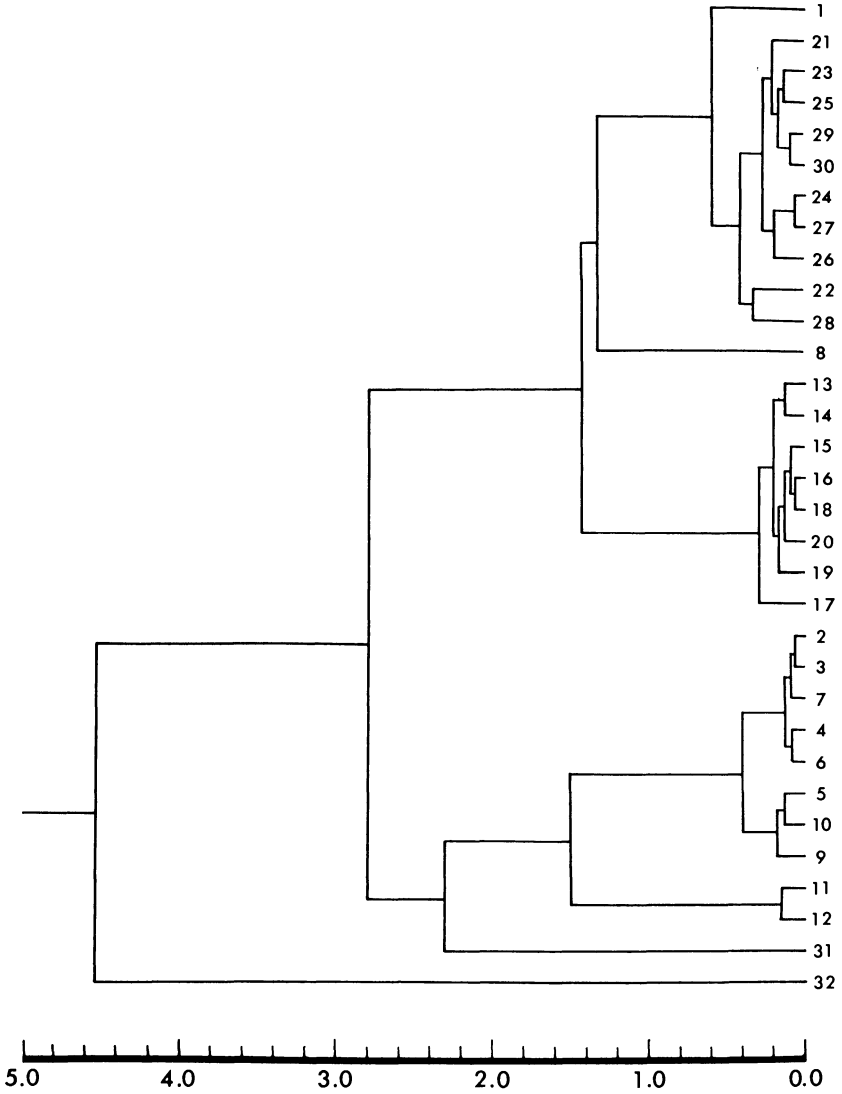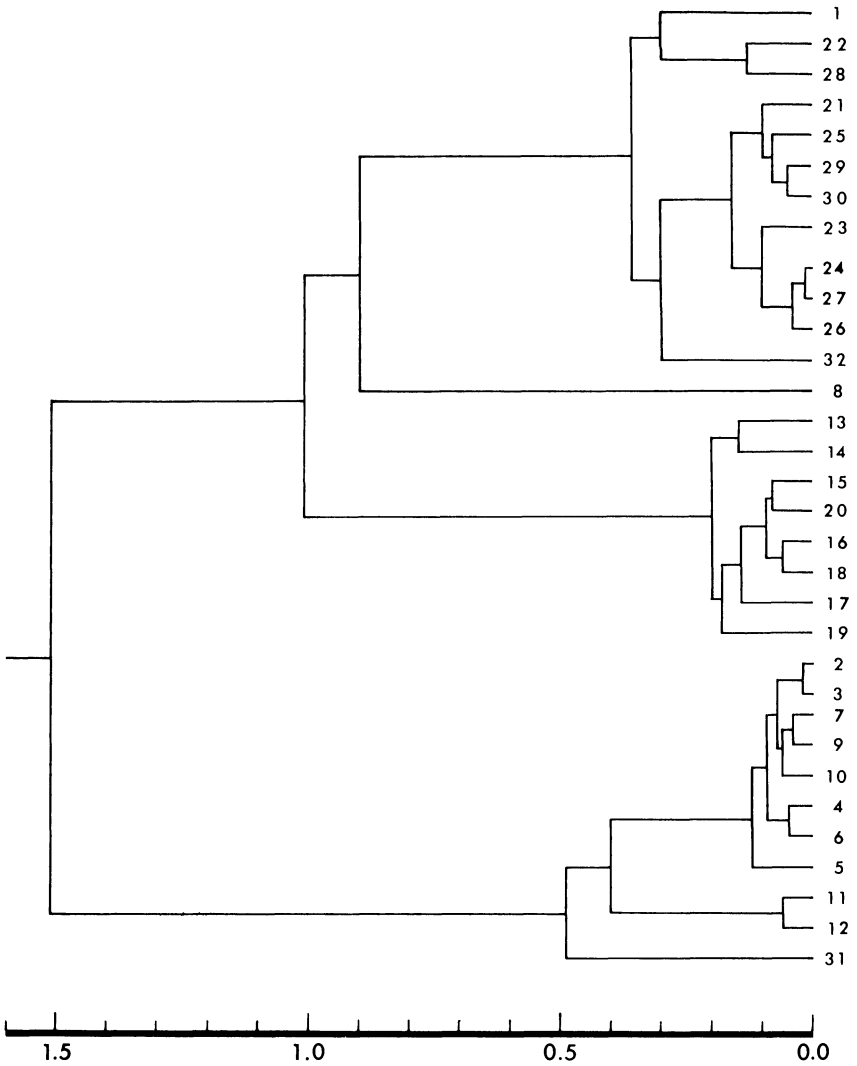
FIG. 13. Cluster analysis (UPGMA) of 32 population samples generated from correlation matrix using all characters. Coefficient of cophenetic correlation = 0.945. Identification of locality numbers as in Fig. 9 and Materials and Methods section.

tip is proportionately long. Length measurements of the glans penis load heavily on principal component III (Table 2).

A higher coefficient of cophenetic correlation was obtained for the phenogram derived from the correlation matrix (.944) than that generated from the distance matrix (.766). The major differences in these two dendrograms involve the branching position of *winkelmanni* (locality 32) and the unification of *aztecus* (locality 1) with *evides* from Oaxaca (locality 24) and OTU No. 28 of *oaxacensis* (compare Fig. 12 to Fig. 13).

Principal component and cluster analyses were first run employing both quantitative and qualitative variables and then using only the quantitative ones for all 32 OTUs. Removal of the six qualitative characters affected some correlations of the remaining variables and components. Dimensions of the skin and skull still contributed largely to principal component I, but length measures of the glans penis were

TABLE 3

RESULTS OF PRINCIPAL COMPONENT ANALYSIS USING 17 MORPHOMETRIC CHARACTERS FOR ALL 32 SAMPLES (see Fig. 11).

Component	I	II	III
Eigenvalue	10.7	2.9	1.4
% total variance	63.2	80.0	88.2
Independence	560.4	400.7	285.0
df	135	119	104
significance	0.0	0.0	0.0
Length of skull	.99	−.01	.00
Length of rostrum	.97	.02	.01
Greatest zygomatic breadth	.98	.03	−.02
Breadth of braincase	.97	.08	.04
Least interorbital width	.94	.00	−.24
Length of molar row	.94	−.01	−.07
Length of incisive foramen	.95	−.04	.13
Breadth of palate	.74	.06	.33
Width of mesopterygoid fossa	.87	.05	−.16
Length of auditory bullae	.53	−.34	.66
Length of body	.95	.08	−.05
Length of tail	.78	−.11	.09
Length of hindfoot	.89	−.23	.02
Length of glans penis	−.04	.88	.44
Width of glans penis	.59	.48	−.54
Length of protractile tip	.04	.92	−.26
Length of baculum	−.04	.90	.40
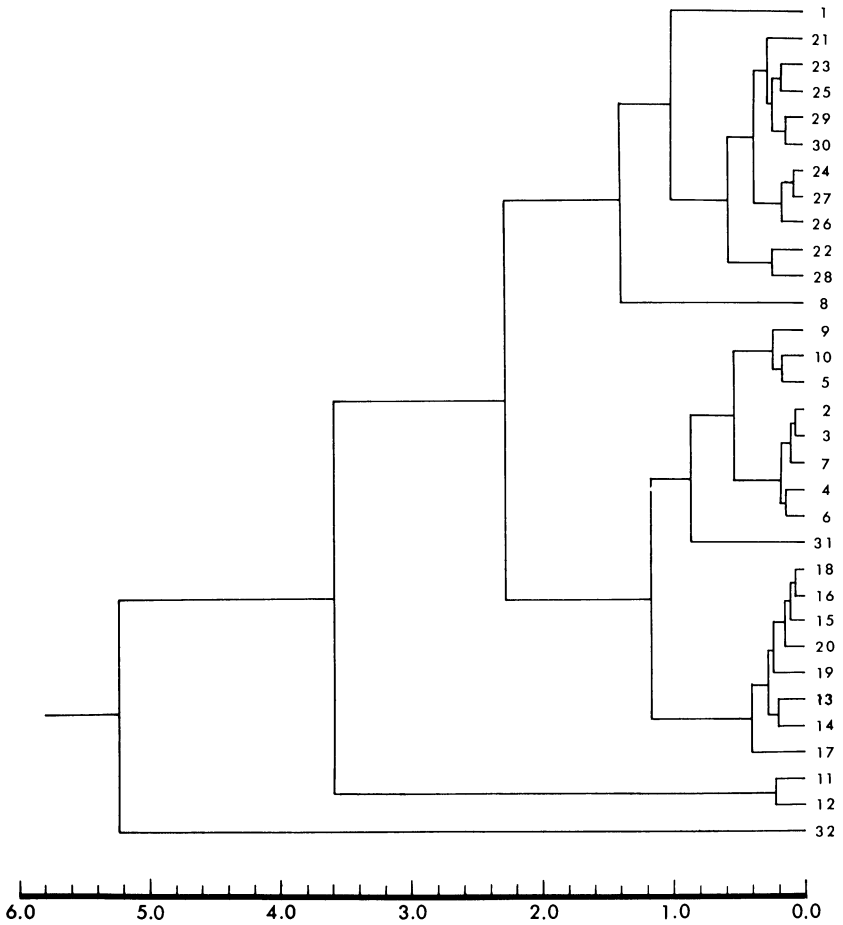
FIG. 14. Cluster analysis (UPGMA) of 32 population samples generated from distance matrix using only the 17 morphometric characters. Coefficient of cophenetic correlation = 0.765. Identification of locality numbers as in Fig. 9 and Materials and Methods section.

weighted heavily on II and length of the auditory bullae and width of glans penis on III (Fig. 10, Table 3). In the cluster analyses, elimination of the qualitative characters somewhat shifted the branching arrangement of OTUs but did not appreciably modify the constitution of the basic clusters. As a result, (1) samples of *simulus* split off from most other OTUs at the second bifurcation instead of forming a pair-group with *levipes* and *rowleyi*, and (2) OTUs of *spicilegus* and *evides* from Michoacan united with those of *levipes-rowleyi* and *pec-*

TABLE 4

DISCRIMINANT MULTIPLIERS DERIVED FOR EACH OF 10 CRANIAL DIMEN-
SIONS THROUGH DISCRIMINANT FUNCTION ANALYSIS OF REFERENCE SAM-
PLES OF *P. BOYLII SIMULUS* (OTU NO. 11) AND *P. BOYLII SPICILEGUS* (OTU
NO. 15).

Greatest length of skull	0.561
Length of rostrum	0.974
Greatest zygomatic breadth	−1.047
Breadth of braincase	1.498
Least interorbital width	0.096
Length of maxillary toothrow	5.489
Length of incisive foramen	−0.455
Breadth of palate	0.845
Greatest width of mesopterygoid fossa	1.822
Length of auditory bulla	−2.858

toralis instead of samples of *hylocetes, oaxacensis,* and *evides* from
Guerrero and Oaxaca (Fig. 14).

Discriminant function analysis was applied to samples of *simulus*
(locality 11) and *spicilegus* (locality 15) using only the ten cranial
measurements. The resultant discriminant multipliers obtained for each
variable (Table 4) were then used to compute a discriminant score for
19 individuals trapped near San Blas, Nayarit, the type locality of
simulus. As indicated by range maps, *simulus* and *spicilegus* pur-
portedly intergrade in the vicinity of San Blas (Osgood, 1909; Hall and
Kelson, 1959). The histogram of discriminant scores of individuals in
the two reference samples has a bimodal distribution with no overlap
(Fig. 15). Furthermore, the 19 unknown specimens are clearly associ-

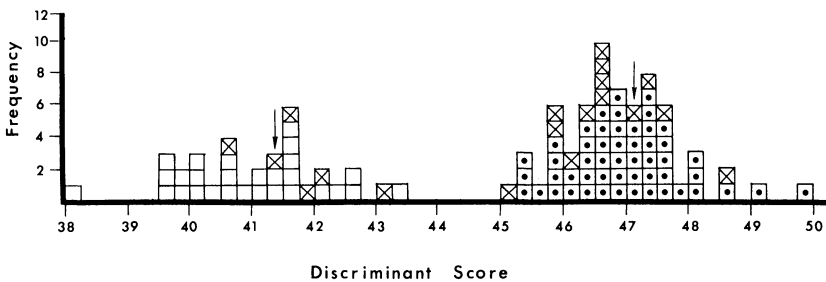FIG. 15. Frequency histogram of discriminant scores of individual specimens as
determined by discriminant function analysis comparing reference samples of *P. boylii
simulus* (locality 11) and *P. b. spicilegus* (locality 15). Open squares = *simulus*; squares
with circle = *spicilegus*; squares with X = unknowns from the vicinity of San Blas,
Nayarit. Arrows indicate two unknowns caught at the same locality.

ated with those of either one or the other reference samples instead of being intermediate. Particularly noteworthy is the placement of two individuals (indicated in Fig. 15) that were trapped at the same locality.

DISCUSSION

In discussing the sympatry of *P. oaxacensis* and *P. boylii levipes,* Osgood (1909:159) remarked that, "Possibly here is another example of two subspecies (*i.e., oaxacensis* and *levipes*) of the same group occurring together, for *levipes* appears to intergrade with *spicilegus, spicilegus* with *evides* and *aztecus,* and quite probably *aztecus* with *oaxacensis.*" Osgood thus first advanced the idea that members of the *Peromyscus boylii* species-group represent some kind of complex rassenkreis with varying levels of fertility and geographic overlap between the several segments. Hooper (1968:53-54) expressed a similar evaluation of the problem, suggesting that ". . . (a) the isolation of eastern and western arms of the range of *boylei*-like forms in Mexico has been removed and (b) the large gap between them has been filled by morphologically different populations from the south and now are incompletely interfertile with those western and eastern series of populations." A review of our current knowledge of this mosaic of forms as it relates to these hypotheses is in order. In view of the many names applied to the populations under study, I have divided the following discussion into several specific taxonomic issues, particularly those which focus on the question of intergradation.

P. boylii spicilegus and *b. simulus*

Allen (1897) named *spicilegus* as a species of *Peromyscus* from Mineral San Sebastian, Jalisco. Later, Osgood (1904) described *simulus* from San Blas, Nayarit, as a subspecies of *P. spicilegus.* He viewed *simulus* as a well-marked form in cranial characters (*e.g.,* short rostrum, anteriorly-squared zygomatic arches and short molar row), but its close similarity to *spicilegus* in pelage color persuaded him to regard *simulus* as a coastal representative of the montane-dwelling *spicilegus.* In his classic revision, Osgood (1909) regarded both *spicilegus* and *simulus* as subspecies of *boylii.* Subsequently, Hooper (1955; 1968) drew attention to the occurrence of two "morphological types" of *P. boylii* in coastal Sinaloa and Nayarit. He reported on a large series of specimens from Chele, Sinaloa, which contrasted with four specimens from near San Blas, Nayarit, in size and development of the supraorbital shelf. On a geographic basis, he assigned all specimens to *P.*

boylii simulus, but remarked that the four specimens from San Blas compare favorably with examples of *spicilegus*. As a result of their transect from Durango into Sinaloa, Baker and Greer (1962) found that some, but not all, characters of *rowleyi* merge into those of *spicilegus* but not those of *spicilegus* into *simulus*.

There is no concrete evidence of integration between *simulus* and the contiguous form *spicilegus*. Instead, the data suggest that those two are specifically distinct. The combination of small size, truncate rostrum, hourglass-shaped interorbital region and anteriorly-squared zygomatic arches distinguishes the skull of *simulus* from that of *spicilegus*. *P. simulus* contrasts sharply with *spicilegus* in characters of the glans penis (e.g., in overall size and presence of dorsal and ventral lappets; compare Figs. 3C and 5B). In the shortest connection network, principal component and clustering analyses, the two samples of *simulus* are far removed from *spicilegus*; they are nearer examples of *rowleyi* and *levipes*, yet with a distinct gap between them.

The fact that *simulus* and *spicilegus* occur sympatrically in the area of San Blas, Nayarit, also argues strongly for their specific status. In the original series of four specimens from east of San Blas reported by Hooper (1955), one individual (UMMZ 100386) is referable to *simulus*. It differs from the other three in lack of a supraorbital shelf, small skull and dentition, and short baculum (8.33 mm). It was caught 3.5 mi E San Blas together with another specimen (UMMZ 100387) that I recognize as *spicilegus*. This is my only record of the two kinds from the same locality; however, both forms have been taken near each other in the vicinity of San Blas (see Appendix I). I have no records of sympatry of *simulus* and *spicilegus* in the northern part of their ranges. Specimens captured near Santa Lucia, Sinaloa, approximately 3000 ft upslope from Copala, fit with *spicilegus*; those from the vicinity of Copala are *simulus*. I have examined the holotype and other specimens used by Osgood in his original description (1904) of *simulus*. There are no examples of *spicilegus* in that lot.

Karyotypic evidence from Schmidly and Schroeter (1974) also suggests that *simulus* and *spicilegus* are specifically distinct. They studied specimens caught near Mazatlan and Concordia, Sinaloa, and San Blas, Nayarit, all of which were referred to *boylii simulus* on a geographic basis. The karyotypes from Sinaloa resembled those obtained for *rowleyi*: three pairs of metacentrics and 20 pairs of acrocentrics to equal a fundamental number of 52. The mice trapped near San Blas, Nayarit, possessed 18 metacentric pairs and only five acrocentric ones, yielding a fundamental number of 82. Skulls and phalli of these latter specimens fit with *spicilegus*, not *simulus*. All, in fact, were utilized in

the discriminant function analysis and were interspersed among known examples of *spicilegus* (Fig. 15). Therefore, the karyotype in Fig. 4 of Schmidly and Schroeter (1974:337) represents *spicilegus*, while only that of the Sinaloan specimens applies to *simulus*.

On the basis of the evidence at hand, it is apparent that the two contiguous "subspecies" of *Peromyscus boylii* in western Mexico do not intergrade in the manner expected if only a single biological species were involved. In an area of probable transition, as near San Blas, Nayarit, the features chacterizing *simulus* and *spicilegus* persist and suggest separate gene pools. The affinities of *simulus* reside closer to *boylii rowleyi* and *b. levipes*. To judge from specimens I studied, *simulus* lives in the arid upper tropical zone within elevations of approximately sea level at San Blas, Nayarit, and Mazatlan, Sinaloa, to 800 ft at Navarette, Nayarit. There is a north-south trend in pelage color. As noted by Osgood (1909:151), specimens from the north (*e.g.*, vincinity of Copala, Sinaloa) are a light tawny, whereas ones from farther south (*e.g.*, San Blas, Nayarit) possess a rich ochraceous pelage converging toward *spicilegus*. This trend probably correlates with moisture. The habitat around Copala consists of arid scrub-thorn forest, while the area near San Blas has thorny brush intermingled with tropical broadleaf forest.

P. boylii levipes, b. rowleyi, and *b. spicilegus*

Although first recognized as a species (Allen, 1897), Osgood (1909) placed *spicilegus* as a subspecies of *P. boylii*. While Allen's description of *spicilegus* was limited to specimens from the type locality (Mineral San Sebastian, Jalisco), Osgood's revision extended its range to include not only the western lowlands of Jalisco and Nayarit, but also the flanks of the Sierra Madre Occidental and the western margin of the central Mexican Plateau. Subsequent authors have questioned both the range of *spicilegus* and its relationship to other populations of *P. boylii*. For example, working with collections from Durango and Jalisco, Hooper (1955:15) doubted that a single species was represented in his samples: "Cranially, the Durangan material fits with *rowleyi* and *boylei*, whereas the Jaliscan samples, *spicilegus* proper, probably belong with *evides* and other subtropical populations." Baker and Greer (1962) restricted the range of *spicilegus* in Durango to the western flanks of the Sierra Madre Occidental and allocated the populations inhabiting the eastern flanks and central area of the Sierra Madre to *rowleyi*. Hooper (1955) recorded the sympatric occurrence of *levipes* and *spicilegus* at a locality west of San Andreas, Jalisco. In addition, he referred specimens from 5500 and 6500 ft in the moun-

tains south of Autlan, Jalisco, to *spicilegus*, but assigned one specimen from 8200 ft to *levipes*. These findings have reduced both the geographic and altitudinal distribution of *b. spicilegus* from that originally outlined by Osgood (1909) and suggest that more than one species is represented in the material from western Mexico that he assigned to *P. boylii.*

The results of the various multivariate analyses support this contention. Examples of *spicilegus* are set apart from those of *levipes* and *rowleyi*. The major traits that account for this separation are qualitative characters of the skull and glans penis; however, length of the auditory bullae and protractile tip, which load heavily on the second component, significantly contribute to this hiatus. In fact, length of auditory bullae is not an adequate measure for conveying the disparity in volume that exists between the bullae of *rowleyi* and especially *levipes* on the one hand and *spicilegus* on the other. The more capacious bullae in *rowleyi* and *levipes* afford a fairly reliable means of separating those forms from *spicilegus*, particularly when used in conjunction with the pronouncement of a supraorbital shelf. Phallic features distinguishing *rowleyi* and *levipes* from *spicilegus* include presence of dorsal and ventral lappets (none in *spicilegus*), proportionately smaller protractile tip, and smaller girth of the penis. This complex of features serves to easily separate adult males of *levipes* and *rowleyi* from those of *spicilegus*. Furthermore, these differences in morphology of the glans penis hold at localities where the subspecies have been said to intergrade.

A case in point is the area around Pueblo Nuevo, Durango, where Baker and Greer (1962) reported on mice collected at three areas: 2 mi N Pueblo Nuevo, 6000 ft; Pueblo Nuevo, 5000 ft; and 6 mi S Pueblo Nuevo, 3000 ft. They commented on the greater length of skull and more pronounced supraorbital shelf in mice obtained 6 mi S Pueblo Nuevo as compared to those trapped 2 mi N. I have examined well-preserved glandes penes from all three localities and have found that characters of the glans penis parallel those of the skull. In those from Pueblo Nuevo and 6 mi S of that city, the glans penis is broad and fluted as in *spicilegus*, while those from 2 mi N have the narrow glans with dorsal and ventral lappets characteristic of *rowleyi*. Two species make contact in the vicinity of Pueblo Nuevo, not two subspecies.

Based on karyotypic and electrophoretic studies, Schmidly and Schroeter (1974) and Kilpatrick and Zimmermann (1975) reached a different conclusion, namely that *rowleyi* and *spicilegus* represent interbreeding populations of one species. The discrepancy is one of

nomenclature, not interpretation of results. I agree that the popula-
tions they (and Lee *et al.*, 1972) examined comprise a single species,
but disagree that the name *spicilegus* properly applies to any of those
sampled populations. Populations that inhabit western Durango and
the highlands of eastern Sinaloa, areas from which their samples were
drawn, constitute western segments of *boylii* proper; whereas,
spicilegus ranges from low to intermediate elevations in those states
(the type locality of *spicilegus* is about 3900 ft). The form *spicilegus*
sensu strictu has been examined karyotypically only by Schmidly and
Schroeter (1974) and, as indicated above, reported under the name
simulus.

I have examined the holotype of *spicilegus*, a series of topotypes,
and much of the same material originally assigned to *spicilegus* by
Osgood (1909:150-151). In my opinion, specimens from approxi-
mately half of those localities are *P. boylii* and conspecific with
populations of *levipes* and *rowleyi*, while the remainder are *P.
spicilegus* (see Appendix I).

In addition to the morphological distinctions enumerated above, *P.
boylii* and *P. spicilegus* may prefer different ecological conditions in
this region of western Mexico. Based on examples at hand, *spicilegus*
ranges from 50 ft around San Blas, Nayarit, to 6500 ft in the wet
montane forests south of Autlan, Jalisco; most localities fall within
3000 to 6000 ft. *Peromyscus boylii* is distributed from 4800 to 9500
ft in western Mexico. Where the two species have taken in nearby
areas, *boylii* occurs at the upslope localities. The two elevational belts
occupied by the two species correspond to broad vegetational zones:
P. spicilegus mainly in the humid upper tropical zone, characterized by
fairly moist cloud forest conditions at intermediate elevations (to 6500
ft), and *P. boylii* in the southern montane woodland zone and in
particular pine-oak habitats (Baker, 1968). In fact, Baker and Greer
(1962) set the boundary of *P. boylii rowleyi* and *spicilegus* in Durango
to coincide with the junction of pine-oak and tropical deciduous
forests. Hooper (1955) contributes other evidence suggesting different
ecological requirements: his samples of *spicilegus* were trapped in a
moist canyon bottom while specimens of *boylii* proper were obtained
on exposed rimrock above the canyon. The contiguous altitudinal
relationship of the two forms may reflect their different ecological
preferences or intimate some sort of competitive displacement.

P. spicilegus and *P. evides*

Osgood (1904) described *evides* as a subspecies of *spicilegus*. The
only specimens then assigned to *evides* consisted of the type series

from Juquila, Oaxaca. In that 1904 paper, Osgood commented on the larger size of the specimens from Juquila compared to *spicilegus* proper, particularly as reflected in the skull and dentition, and mentioned a series from Los Reyes, Michoacan, that appeared intermediate between *spicilegus* and *evides*. In his revision of *Peromyscus*, Osgood (1909) allocated the specimens from Los Reyes to *evides* together with others from Omilteme, Guerrero, and *evides*, like *spicilegus*, was ranked as a subspecies of *boylii*. Later authors (Hall and Villa, 1949; Hall and Kelson, 1959; Hooper, 1961) have followed Osgood in treating these populations from Michoacan, Guerrero and Oaxaca as *P. boylii evides*.

The picture has been complicated by the discovery of sympatry of *levipes* and *evides* in both Michoacan and Guerrero (Hooper, 1961, 1968; Musser, 1964). This has prompted the recognition of *evides* as a distinct species, but curiously, the same sort of evidence (for instance, Hooper, 1955) has not resulted in the elevation of *spicilegus* to specific status. The specific differentiation of *levipes* from *evides* seems clear in view of current knowledge. In addition to instances of sympatry between the two forms, they differ strikingly in morphology of the phallus; other distinguishing traits include the configuration of the interorbital region, shape of the braincase, and size. Excepting the distinction in size, examples of *spicilegus* contrast with those of *levipes* (and *rowleyi*) in exactly the same features. Since the data now suggest that *levipes* is specifically separate from *evides* on the one hand and *spicilegus* on the other, it is appropriate to explore further the relationships of *evides* and *spicilegus*.

The original series of specimens from Los Reyes, Michoacan (Osgood, 1904), is central to the problem. In size and pelage, they resemble examples of *evides* from Guerrero and Oaxaca (particularly the topotypic series from Juquila, Oaxaca), and it was probably for that reason that Osgood (1909) later included the Los Reyes specimens under *evides* rather than *spicilegus*. Current data suggests another interpretation of the affinities of this population and others of the region.

Populations of *evides* from Michoacan, including the series from Los Reyes, are allied closely to *spicilegus*, while those called *evides* from Guerrero and Oaxaca exhibit affinity with representatives of *hylocetes* and *oaxacensis*. Those populations from Michoacan, like other sampled populations of *spicilegus*, possess an absolutely and relatively longer phallus than the *evides* from Guerrero and Oaxaca (Fig. 3). The specimens of *evides* from Guerrero and Oaxaca resemble those of *aztecus*, *hylocetes* and *oaxacensis* in size of baculum and protractile tip. In a

southeasterly transect of samples of *spicilegus* and *evides*, the largest shift in measurements of the skin and skull (Fig. 16; Appendix 3) is observed between Michoacan and Guerrero, not between Jalisco and Michoacan (as one might expect based upon current understanding of distributions — Hall and Kelson, 1959). The various phenetic analyses
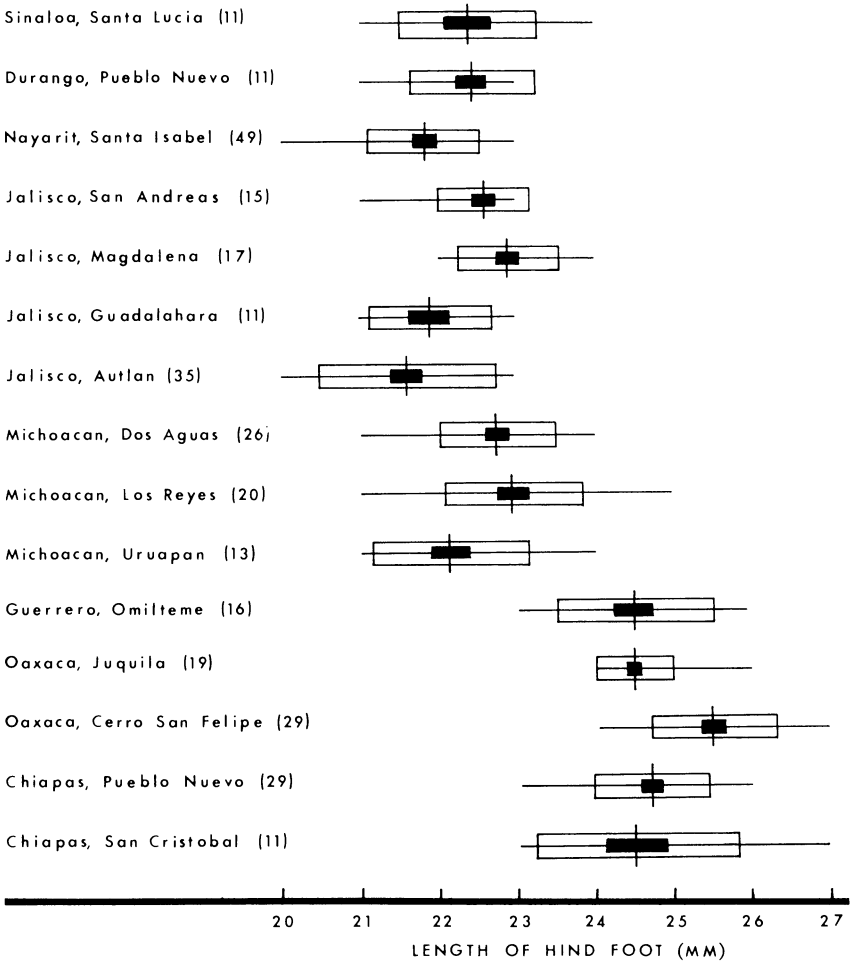
FIG. 16. Dice-Leraas grams of hind foot length of samples from a southeasterly transect through the geographic ranges of *spicilegus* (Sinaloa, Durango, Nayarit and Jalisco), *evides* (Michoacan, Guerrero and Oaxaca, Juquila) and *oaxacensis* (Oaxaca, Cerro San Felipe and Chiapas). Samples from Michoacan, currently considered examples of *evides*, are here allocated to *spicilegus*. Vertical line = the sample mean, horizontal line = range, open rectangle = one standard deviation and closed rectangle = two standard errors of the mean. Sample sizes indicated in parentheses.

reflect this hiatus: the three samples from Michoacan consistently cluster with populations of *spicilegus* from Durango, Sinaloa, Nayarit, and Jalisco. Thus, the Michoacan populations appear to represent a segment of *spicilegus* rather than *evides*. Furthermore, the separation of *spicilegus* from *evides* by the Río Balsas and its arid basin is more persuasive from a zoogeographical standpoint than some barrier between Jalisco and Michoacan.

P. *aztecus,* P. *evides,* P. *hylocetes,* and P. *oaxacensis*

While my study does not focus primarily on this group of forms, they were included to resolve related systematic problems and to ascertain the degree of differentiation of the population herein described as P. *winkelmanni.* Evidence of close relationship of some of those forms was revealed and deserves comment. In the following account, I use *evides* to identify only those populations occurring in Guerrero and Oaxaca.

Peromyscus aztecus, P. evides, P. hylocetes and *P. oaxacensis* are currently treated as distinct species (Hooper, 1968), but *aztecus* and *evides* were formerly considered subspecies of *P. boylii* (Osgood, 1909). Although Osgood (*op. cit.*) hypothesized that the overlap of *levipes* and *oaxacensis* might be an instance of two subspecies occurring together, he nevertheless retained the latter (and *hylocetes*) as a full species. Osgood had clearcut evidence of sympatry of *levipes* with both *hylocetes* and *oaxacensis.* He failed to recognize such documentation for *levipes* with either *aztecus* or *evides,* but suspected that *aztecus* would be found to occur with *levipes.* This prediction has been verified (Alvarez, 1961; Hall and Dalquest, 1963; Musser, 1964). As noted by Hall and Dalquest (1963), both *aztecus* and *levipes* were represented in Osgood's series from Jalapa, Veracruz, and I have found specimens of *aztecus* and *levipes* intermixed in his sample from Huauchinango, Puebla, and both *evides* and *levipes* in the series from the Sierra Madre del Sur west of Chilpancingo, Guerrero.

P. *hylocetes* and *oaxacensis* have been viewed as species since their description (Merriam, 1898b), but Hooper (1968) suggested that they might prove to be conspecific. The results of my study endorse this viewpoint. Although samples of *hylocetes* and *oaxacensis* average larger than *evides* in most morphometric characters, *evides* is similar to those forms in proportional aspects of the glans penis and skull. Of the OTUs representing *evides, hylocetes* and *oaxacensis*, that from the type locality of *evides* (locality 22) is most divergent. Still, that sample often clustered nearest the topotypic series of *oaxacensis* (locality 28). Compared to the holotype of *oaxacensis,* the six specimens con-

stituting the type series of *evides* are distinctive because of their smaller size. To judge from their tooth wear, these specimens are not young, but their general skull conformation suggests immature individuals. Aside from the type series, the other specimens of *evides* examined closely match those of *oaxacensis*.

Nevertheless, Goodwin (1969) listed specimens of *evides* and *oaxacensis* from nearly adjacent sites and even one locality of sympatry (Agua Zarca) in Oaxaca. (Of parenthetic interest, Goodwin, in the same paper, synonomized *P. hylocetes yautepecus* Goodwin under *P. evides*.) At the locality of sympatry, the only appreciable differences between the two individuals he assigned to *evides* and that one called *oaxacensis* are clearly ascribable to age. If the two forms maintain their identities in the mountains of Oaxaca, it is not readily apparent in this lot of specimens. It should be noted that specimens from Nueva Raza, Nopala, and Bocadillo, which Goodwin (1969) reported as *P. evides*, are examples of *P. mexicanus*.

SUMMARY AND TAXONOMIC SUGGESTIONS

In light of the findings presented above, the hypothesis of integradation, at least as originally articulated by Osgood (1909), seems less tenable. For one, *levipes* may be removed from the chain of intergrades, *i.e., levipes-spicilegus-evides-aztecus-oaxacensis* and *hylocetes*. Since Osgood's revision, *levipes* has been shown to occur together with *spicilegus, evides* and *aztecus*. Although the resemblance between *levipes* and these forms, especially *spicilegus*, is sometimes virtually exact in external features, cranial and phallic characteristics suggest its fundamental separation from them. I concur with Schmidly and Schroeter (1974) and Kilpatrick and Zimmermann (1975) that populations of *levipes* intergrade with those of *rowleyi*.

What of interrelationships of the remaining forms? On the one hand, it is doubtful that populations of *spicilegus* (including the Michoacan populations) and *hylocetes* interbreed. *P. hylocetes* is restricted to the highlands of the Cordillera Transvolcanica, where it occurs with the otherwise different form *boylii levipes*; whereas, populations of *spicilegus* are found on the lower slopes of the Cordillera Transvolcanica in Michoacan and Jalisco. Thus, the ranges of the two are stratified altitudinally, but at least one instance of sympatry (20 mi SSE Autlan, Jalisco, 6500 ft) is known (Hooper, 1955).

To the south, the situation is more complex. As suggested by Hooper (1968), P. *oaxacensis* is closely related to and probably conspecific with its northern counterpart, *hylocetes*. In addition, segments of *evides* could be included with *oaxacensis* and *hylocetes*. The three

forms have the aspect of geographic races of a single species. All basically inhabit pine-oak zones in different mountain units: *hylocetes* in the Cordillera Transvolcanica; *evides* in the coastal Sierra Madre del Sur of Guerrero and Oaxaca; and *oaxacensis* in the central mountains of Oaxaca south into Chiapas, Guatemala, El Salvador and Honduras (Musser, 1969).

Still, the distinctiveness of the series of *evides* from the type locality and its vicinity cautions against a quick judgment. At least three explanations deserve consideration. (1) The small size of the type series of *evides* reflects an altitudinal cline, specimens of *evides* representing the smaller end of the size scale and those of *oaxacensis* and *hylocetes* the larger. (2) A separate species inhabits the Sierra Madre del Sur of Guerrero and Oaxaca that bears the same altitudinal relationship to *oaxacensis* as *spicilegus* does to *hylocetes* in the Cordillera Transvolcanica. (3) A rassenkreis exists such that *hylocetes* is interfertile with *oaxacensis* and *evides,* and *evides* with *spicilegus,* but the end members of the circle-species, *i.e., spicilegus* and *hylocetes,* do not interbreed. Assuming a southern origin, for example the mountains in Oaxaca, this last interpretation postulates two northern dispersal routes. The mountains in Puebla and Veracruz that connect the eastern portion of the Cordillera Transvolcanica to the Sierra Madre del Sur of Oaxaca constitute one such corridor. Populations that expanded northward over these highlands differentiated as *hylocetes* in the Cordillera Transvolcanica. Another avenue of dispersal lies between the Sierra Madre del Sur in Guerrero and the coastal Sierra de Coalcoman in Michoacan. Populations that entered via this lower-elevational route gave rise to *spicilegus,* which subsequently spread farther north to the lower slopes of the Cordillera Transvolcanica and along the western flanks of the Sierra Madre Occidental. Although the vegetational zones on these major highland masses are no longer continuous, they undoubtedly were continuous during periods of glacial maxima in the Pleistocene (Martin and Harrell, 1957; Duellman, 1965). Careful collecting along elevational transects in the mountains of Oaxaca, Guerrero, and southern Michoacan would contribute greatly to our understanding of this "species" complex.

The status of *P. aztecus* also requires further study. Certainly, on the basis of qualitative characters of the skin, skull and glans penis, it is closely allied to *hylocetes, oaxacensis* and *evides* (from Guerrero and Oaxaca), but at just what level is not known. In the various phenetic analyses, *aztecus* was consistently set off somewhat at the periphery of those forms. Compared to the *hylocetes-oaxacensis-evides* complex, *aztecus* occurs at slightly lower elevations, principally in the humid

upper tropical zone (Baker, 1968), along the eastern flanks of the Sierra Madre Oriental in Hidalgo, Puebla and Veracruz. Whether southern populations of *aztecus* intergrade with those of *oaxacensis* in the mountains of northern Oaxaca remains to be discovered.

The data now at hand indicate several systematic changes. The two taxa forming the focal point of my study, *simulus* and *spicilegus*, should be accorded specific status. Affinities of *simulus* are with *boylii* and allied species; *simulus* contrasts in many respects with the contiguous form *spicilegus*. Since *simulus* is allopatric to other populations of *boylii*, separated from them by populations of *spicilegus*, this decision solely reflects the amount of morphological divergence as revealed in my analyses. The populations of *spicilegus* correspond only in part to those Osgood (1909) identified as *P. boylii spicilegus*. Many of those samples are here allocated to *P. boylii* (see Appendix I); furthermore, the Michoacan populations currently assigned to *P. evides* are, in my view, referable to *spicilegus*. In addition to details of morphology, documentation of sympatry with *simulus* and *boylii* argues for specific recognition of *P. spicilegus*.

There is no subspecific name available for many specimens of *P. boylii*, such as those from Jalisco, Nayarit and Sinaloa that were formerly assigned to *spicilegus*. In size and especially pelage color, they depart from typical *boylii rowleyi* or *b. levipes*; furthermore, there is evidence that some of these populations are slightly differentiated karyotypically and genetically as well (Schmidly and Schroeter, 1974; Kilpatrick and Zimmermann, 1975). Thus, these populations may represent a new subspecies. To describe them here, without first studying variation over the entire range of *boylii*, would only create additional nomenclatorial problems for some future revisor. Accordingly, I have listed all specimens examined under *P. boylii* instead of subspecies thereof. I have not examined all of Anderson's (1972) series that he allocated to *b. spicilegus;* however, those contained in the U.S. National Museum of Natural History from Chihuahua are examples of true *boylii*, not *spicilegus*.

The status and affinities of *madrensis* require further study, utilizing a larger sample and additional characters. As in the case of many of the currently recognized subspecies of *P. boylii, madrensis* was initially named as a species (Merriam, 1898a). Merriam considered *P. spicilegus* of mainland Mexico as its closest relative. Osgood (1909), like Merriam, allied *madrensis* with *spicilegus,* but treated them both as subspecies of *boylii*. In view of these assertions, I initially suspected that *madrensis* would prove to be only an insular representative of *spicilegus,* but morphological facts argue against this. Specimens of

madrensis exhibit a complex of characters that sets them apart from *spicilegus.* Merriam (1898a) cites the trenchant differences: decidedly larger in most dimensions of the skin and skull (see Appendix 3); ears and maxillary toothrow relatively short; tail indistinctly bicolored, with the terminal 20-30 mm as dark below as above. In addition, the characters and relative size of the glans penis appear appreciably different from that noted in examples of *spicilegus.* The results of my study do not provide sufficient justification for retaining *madrensis* as a subspecies of either *boylii* or *spicilegus*; until new information is assembled, I favor its reinstatement as a species.

The evidence suggests a dichotomy within the *boylii* species group as currently constituted. Based on characteristics of the glans penis and skull, one can discern two assemblages. One consists of *attwateri, boylii* (including the subspecies *ambiguus, baetae, boylii, glasselli, levipes, rowleyi, sacarensis* and *utahensis), pectoralis, simulus* and *stephani.* Perhaps *madrensis, ochraventer* and *polius* belong with this group also. The other assemblage includes *aztecus, spicilegus, winkelmanni* and the *evides-hylocetes-oaxacensis* complex. The first set of species possesses a relatively slender glans penis with dorsal and ventral lappets and an hourglass-shaped interorbital region. In the second group, the glans penis is more robust with a fluted surface and lacks the dorsal and ventral lappets; the interorbital area of the skull exhibits either a shelf or weak bead. Certainly, there is not complete concordance of these traits among all· species of either assemblage. Nevertheless, the two have the aspect of separate groups that can be as practically defined as certain other contemporary species groups listed for the subgenus *Peromyscus*, e.g., the *leucopus* and *maniculatus* species groups. Furthermore, the pattern of distribution of the two sets of species indicates different geographic areas of origin or differentiation. *Peromyscus boylii* and associated species are generally more northern in distribution, possibly originating in the southwestern United States or the Central Mexican Plateau. The center of distribution of *Peromyscus aztecus* and its allies lies farther south in Mexico.

ACKNOWLEDGEMENTS

Wildlife Collections, Texas A & M. Special appreciation is extended to Drs. E. T. Hooper, G. G. Musser, P. Myers and T. Lawlor for their comments and criticisms of various drafts of the manuscript. Field support, allowing collection of some of the specimens reported herein, was provided by the National Science Foundation through NSF GB–5801 to Dr. Emmet T. Hooper, Museum of Zoology, University of Michigan.

LITERATURE CITED

ALLEN, J. A. 1897. Further notes on mammals collected in Mexico by Dr. Audley C. Buller, with descriptions of new species. Bull. Amer. Mus. Nat. Hist., 9:47–58.

ALVAREZ, T. 1961. Taxonomic status of some mice of the *Peromyscus boylii* group in eastern Mexico, with description of a new subspecies. Univ. Kans. Publ. Mus. Nat. Hist., 14:111–120.

ANDERSON, S. 1968. A new craniometer and suggestions for craniometry. *J. Mammal.*, 49:221–228.

_____ 1972. Mammals of Chihuahua Taxonomy and Distribution. Bull. Amer. Mus. Nat. Hist., 148(2):149–410.

BAKER, R. H. 1968. Habitats and Distribution, pp. 98-126. *In:* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publ. Amer. Soc. Mammal., No. 2.

BAKER, R. H. AND J. K. GREER. 1962. Mammals of the Mexican state of Durango. Publ. Mich. St. Univ. Mus., Biol. Ser., 2:25–154.

BIRNEY, E. C. 1973. Systematics of three species of woodrats (Genus *Neotoma*) in central North America. Misc. Publ. Univ. Kans. Mus. Nat. Hist., 58:1–173.

CARLETON, M. D. 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Misc. Publ. Mus. Zool. Univ. Mich., 146:1–43.

CHOATE, J. R. 1973. Identification and recent distribution of white-footed mice (*Peromyscus*) in New England. J. Mammal., 54:41–49.

CLARK, W. K. 1953. The baculum in the taxonomy of *Peromyscus boylii* and *P. pectoralis.* J. Mammal., 34:189–192.

DUELLMAN, W. E. 1965. A biogeographic account of the herpetofauna of Michoacan, Mexico. Univ. Kans. Publ. Mus. Nat. Hist., 15:627–709.

GOODWIN, G. G. 1969. Mammals from the state of Oaxaca, Mexico, in the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist., 141:1–270.

HALL, E. R. AND W. W. DALQUEST. 1963. The mammals of Veracruz. Univ. Kans. Publ. Mus. Nat. Hist., 14:165–362.

HALL, E. R. AND K. R. KELSON. 1959. The mammals of North America. 2 vols. New York, Ronald Press, xxx + 1162 pp.

HALL, E. R. AND B. VILLA. 1949. An annotated checklist of the mammals of Michoacan, Mexico. Univ. Kans. Publ. Mus. Nat. Hist., 1:431–472.

HOOPER, E. T. 1955. Notes on mammals of western Mexico. Occ. Pap. Mus. Zool. Univ. Mich., 565:1–26.

_____ 1957. Dental patterns in mice of the genus *Peromyscus.* Misc. Publ. Mus. Zool. Univ. Mich., 99:1–59.

_____ 1958. The male phallus in mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool. Univ. Mich., 105:1–24.

_____ 1961. Notes on mammals from western and southern Mexico. J. Mammal., 42:120–122.

_____ 1968. Classification, pp. 27-74. *In:* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publ. Amer. Soc. Mammall., No. 2.

HOOPER, E. T. AND G. G. MUSSER. 1964. Notes on classification of the rodent genus *Peromyscus*. Occ. Pap. Mus. Zool. Univ. Mich., 635:1–15.

HUCKABY, D. G. 1973. Biosystematics of the *Peromyscus mexicanus* group (Rodentia). Ph.D. Dissertation, The University of Michigan, ix + 144 pp.

KILPATRICK, C. W. AND E. G. ZIMMERMANN. 1975. Genetic variation and systematics of four species of mice of the *Peromyscus boylii* species group. Syst. Zool., 24:143–162.

LAWLOR, T. E. 1971. Evolution of *Peromyscus* on northern islands in the Gulf of California, Mexico. Trans. San Diego Soc. Nat. Hist., 16:91–124.

LEE, M., D. J. SCHMIDLY AND C. C. HUHEEY. 1972. Chromosomal variation in certain populations of *Peromyscus boylii* and its systematic implications. J. Mammal., 53:697–707.

MARTIN, P. S. AND B. E. HARRELL. 1957. The Pleistocene history of temperate biotas in Mexico and eastern United States. Ecology, 38:468–480.

MERRIAM, C. H. 1898a. Mammals of Tres Marias Islands, off western Mexico. Proc. Biol. Soc. Wash., 12:13–19.

_____ 1898b. Descriptions of twenty new species and a new subgenus of *Peromyscus* from Mexico and Guatemala. Proc. Biol. Soc. Wash., 12:115–125.

MORRISON, D. F. 1967. Multivariate statistical methods. New York, McGraw-Hill Book Co., xiii + 338 pp.

MUSSER, G. G. 1964. Notes on geographic distribution, habitat, and taxonomy of some Mexican mammals. Occ. Pap. Mus. Zool. Univ. Mich., 636:1–22.

_____ 1969. Notes on *Peromyscus* (Muridae) of Mexico and Central America. Amer. Mus. Novit., 2357:1–23.

OSGOOD, W. H. 1904. Thirty new mice of the genus *Peromyscus* from Mexico and Guatemala. Proc. Biol. Soc. Wash., 17:55–77.

_____ 1909. Revision of the mice of the American genus *Peromyscus*. N. Amer. Fauna, 28:1–285.

PRIM, R. C. 1957. Shortest connection networks, and some generalizations. Bell. Syst. Tech. J., 36:1389–1401.

SCHMIDLY, D. J. 1973. Geographic variation and taxonomy of *Peromyscus boylii* from Mexico and the southern United States. J. Mammal., 54:111–130.

SCHMIDLY, D. J. AND G. L. SCHROETER. 1974. Karyotypic variation in *Peromyscus boylii* (Rodentia: Cricetidae) from Mexico and corresponding taxonomic implications. Syst. Zool., 23:333–342.

SNEATH, P. H. A. AND R. R. SOKAL. 1973. Numerical Taxonomy. San Francisco, W. H. Freeman and Co., xv + 573 pp.

APPENDIX I

Specimens Examined

Specimens examined are listed alphabetically by species and state and are contained in the following institutions: American Museum of Natural History (AMNH);

California State University at Long Beach (CSULB); The Museum, Michigan State University (MSU); University of Michigan Museum of Zoology (UMMZ); Texas Co-operative Wildlife Collections (TCWC); U.S. National Museum, Biological Surveys Collection (USNM). The number of specimens follows each locality, and in parentheses following each taxon is the total number of specimens examined.

Peromyscus aztecus (38)—*Hidalgo:* 13 mi NE Metepec, 6600 ft, 9 (UMMZ); *Puebla:* Huauchinango, 4 (USNM); 2 mi SW Huauchinango, 6500 ft, 9 (UMMZ); 5.7 mi SW Huauchinango, 6600 ft, 2 (UMMZ); Pahuatlan, 1100 m, 3 (UMMZ); *Veracruz:* 2.4 mi SW Huatusco, 1 (UMMZ); Jalapa, 5000 ft, 1 (USNM); Mirador, 3800 ft, 8 (USNM); 2 mi N Teocilo, 1000 m, 1 (UMMZ). Topotypes (Veracruz, Mirador) were examined.

Peromyscus boylii (330)—*Chiapas:* Bochil, 1320 m, 17 (UMMZ); 1 mi N Pueblo Nuevo, 5500 ft, 2 (UMMZ); 5 mi N Pueblo Nuevo, 5700 ft, 3 (UMMZ); San Cristobal de las Casas, 2100 m, 23 (UMMZ); 2 mi SE San Cristobal de las Casas, 7200 ft, 1 (UMMZ); 8 mi SE San Cristobal de las Casas, 7800 ft, 8 (UMMZ); 10 mi SE San Cristobal de las Casas, 2330 m, 5 (UMMZ); 8.2 mi E San Cristobal de las Casas, 4 (UMMZ); 4.5 mi W San Cristobal de las Casas, 2 (UMMZ); *Chihuahua:* Sierra Madre, near Guadelupe y Calvo, 7000-9000 ft, 6 (USNM); Sierra Madre, 65 mi E Batopilas, 7000 ft, 12 (USNM); *Durango:* 52 mi SW Ciudad Durango, Hwy 40, 2 (TCWC); 6 mi W La Ciudad, Hwy 40, 2 (TCWC); 22 mi W La Ciudad, Hwy 40, 2 (TCWC); El Salto, 7600-8400 ft, 11 (USNM); La Laguna del Progresso, 8000 ft, 14 (UMMZ); eastern slope Cerro Huehuento, 9500 ft, 9 (UMMZ); 1.5 mi W San Luis, 8000 ft, 24 (UMMZ); 2 mi N Pueblo Nuevo, 14 (MSU); *Guerrero:* 8.6 mi W Chilpancingo, 6400 ft, 4 (UMMZ); Omilteme, 7200 ft, 17 (UMMZ), 3 (USNM); Puerto Chico, 8400 ft, 5 (UMMZ); 12 mi SW Xochipala, 8200 ft, 3 (MSU); *Jalisco:* Volcán de Fuego, 6 (AMNH); Sierra de Autlan, 7000 ft, 2 (UMMZ); 20 mi SE Autlan, 8200 ft, 2 (UMMZ); 2 mi W San Andreas, 5550 ft, 2 (UMMZ); Jacala, 5000 ft, 2 (USNM); La Laguna, 6500 ft, 8 (USNM); Sierra Madre, near Bolanos, 7500-8500 ft, 10 (USNM); Talpa, 2 (USNM); *Michoacan:* Dos Aguas, 7000 ft, 2 (UMMZ); 2 mi W Dos Aguas, 7600 ft, 3 (UMMZ); 6.3 mi WSW Dos Aguas, 8000 ft, 6 (UMMZ); 1 mi NW Dos Aguas, 3 (UMMZ); 3.5 mi N Opopeo, 3 (UMMZ); 11 km W Quiroga, 1 (UMMZ); 1.5 hr (by mule) NE Rancho Baralosa, 8900 ft, 2 (UMMZ); 8.4 mi N Los Reyes, 1 (TCWC); Uruapan, 1 (UMMZ); 2.5 mi E Uruapan, La Presa, 2 (UMMZ); 5 mi S Uruapan, 5000 ft, 7 (UMMZ); 7 mi S Uruapan, 4800 ft, 19 (UMMZ); Parque Nacional Uruapan, 3 (UMMZ); *Nayarit:* Santa Teresa, 6800 ft, 10 (USNM); *Oaxaca:* 12 mi N Ixtlan de Juarez, 9200 ft, 15 (UMMZ): *Sinaloa:* 0.5 mi S Revelcaderos, 6600 ft, 4 (UMMZ); Sierra de Choix, 50 mi NE Choix, 4500-5000 ft, 8 (USNM); *Zacatecas:* Plateado, 2 (USNM); Sierra Madre, 8500 ft, 10 (USNM). Holotypes of *levipes* (Tlaxcala, Mt. Malinche, USNM 53673) and *rowleyi* (Utah, Noland Ranch, AMNH 5070/3950) were examined.

Peromyscus evides (40)—*Guerrero:* Omilteme, 2 (UMMZ); 9 (USNM); 1 mi NW Omilteme, 7260 ft, 6 (USNM); 1 mi SW Omilteme, 7260 ft, 4 (USNM); 6 mi NW Chilpancingo, 5500 ft, 2 (MSU); 12 mi WSW Xochipala, 8200 ft, 2 (MSU); *Oaxaca:* 4 mi S Jalatengo, 5000 ft, 2 (UMMZ); Campemento Río Molino, 7300 ft, 1 (UMMZ); 8 mi SSW Juchatengo, 6300 ft, 1 (MSU); 10 mi N Puerto Escondido, 1 (MSU); Santa Rosa, 1300 m, 3 (UMMZ); 5 mi NW Santa Rosa, 1 (UMMZ); Juquila, 5000 ft, 6 (USNM), 1 (AMNH); Temascaltepec, 5000 ft, 4 (AMNH); Teotepec, 5000 ft, 4

(AMNH); Putla, San Vicente, 4 (AMNH); Yautepec, Santo Tomas Teipan, 6 (AMNH). The holotype (Oaxaca, Juquila, USNM 71426) was examined.

Peromyscus hylocetes (181)—*Jalisco:* Sierra de Autlan, 7600 and 9000 ft, 50 (UMMZ); 20 mi SSE Autlan, 6500 and 8200 ft, 16 (UMMZ); Nevada de Colima, 7500 and 8000 ft, 31 (UMMZ); *Michoacan:* 3 mi E Angahuan, 7200 ft, 2 (UMMZ); 1 mi N Apo, 2700 m, 1 (UMM); 2 mi N Apo, 2700 m, 2 (UMMZ); 3.5 mi E Apo, 3000 m, 3 (UMMZ); 8 mi WNW Hidalgo, 8000 ft, 8 (UMMZ); 9 mi WNW Hidalgo, 8700 ft, 4 (UMMZ); 10 mi NW Hidalgo, Cerro San Andreas, 9400 ft, 17 (UMMZ); Mil Cumbres, 2485 m, 2 (UMMZ); 0.5 mi N Volcán Paricutin, 2 (UMMZ); 3 mi N Volcán Paricutin, 7200 ft, 3 (UMMZ); 6 mi S Patzcuaro, 8000 ft, 7 (UMMZ); 1 mi N San Juan, 2300 m, 1 (UMMZ); 2 mi NNW San Juan, Cerro Cuitzeran, 2350 and 2450 m, 27 (UMMZ); 10 mi NW Uruapan, 7400 ft, 5 (UMMZ). The holotype (Michoacan, Patzcuaro, USNM 50423) was examined.

Peromyscus madrensis (19)—*Nayarit:* Tres Marias Islands, Maria Cleofa, 3 (USNM); Maria Madre, 13 (USNM); Maria Magdalena, 1 (USNM); Isla Júanito, 2 (AMNH). The holotype (Nayarit, Maria Madre Island, USNM 89223) was examined.

Peromyscus oaxacensis (92)—*Chiapas:* 1 mi N Pueblo Nuevo, 5500 ft, 8 (UMMZ); 5 mi N Pueblo Nuevo, 5700 ft, 11 (UMMZ); Pueblo Nuevo, 1700 m, 9 (UMMZ); San Cristobal de las Casas, 2100 m, 7 (UMMZ); 8 mi SE San Cristobal de las Casas, 7800 ft, 2 (UMMZ); 10 mi SE San Cristobal de las Casas, 2330 m, 3 (UMMZ); *Oaxaca:* Cerro San Felipe, 2200, 2300 and 2500 m, 20 (UMMZ); 12 mi N Ixtlan de Juarez, 9200 ft, 9 (UMMZ); Tehuantepec, San Pedro Jilotepec, 3000 ft, 1 (AMNH); Media Loma, 2 (AMNH); Cerro Lachiguiri, 7000 ft, 3 (AMNH); Agua Zarca, 3000 ft, 3 (AMNH); San Isidro, 2 (AMNH); Cerro Baul, Rio Mono Blanco, 2 (AMNH); Sierra Madre N of Zanatepec, 5000 ft, 8 (AMNH); Cerro Atravesado, 4000 ft, 12 (AMNH). The holotype (Oaxaca, Cerro San Felipe, USNM 68426) was examined.

Peromyscus pectoralis (28)—*Tamaulipas:* San Carlos Mts., 20 (UMMZ); 3 mi W El Carrizo, 1500 m, 8 (UMMZ).

Peromyscus simulus (80)—*Nayarit:* Navarette, 800 ft, 3 (USNM); San Blas, 6 (USNM); 1 (CSULB), 1 (UMMZ); 0.5 mi E San Blas, 10 ft, 1 (MSU); 3.5 mi E San Blas, 100 ft, 1 (UMMZ); 2 km E San Blas, 2 (CSULB); 1 mi S San Blas, 4 (CSULB); *Sinaloa:* 5 mi S Copala, 750 ft, 8 (MSU); 4 mi E Concordia, Hwy 40, 7 (TCWC); 15 mi SE Esquinapa, 300 ft, 6 (UMMZ); Mazatlan, 300 ft, 3 (USNM); 2 mi N Mazatlan, 2 (MSU); 5 mi NW Mazatlan, Hwy 15, 1 (TCWC); Rosario, 100 ft, 2 (USNM); 8 mi NNW Rosario, 1 (UMMZ); 15 mi N Rosario, Chele, 300 ft, 31 (UMMZ). The holotype (Nayarit, San Blas, USNM 88088) was examined.

Peromyscus spicilegus (362)—*Colima:* Hacienda San Antonio, 1700 ft, 6 (USNM); *Durango:* Chacala, 3000 ft, 6 (USNM); Juazamota, 1700 ft, 1 (USNM); Pueblo Nuevo, 5000 ft, 3 (MSU); 6 mi S Pueblo Nuevo, 3000 ft, 8 (MSU); *Jalisco:* Ameca, 4000 ft, 17 (USNM); 7 mi W Ameca, 4000 ft, 2 (UMMZ); 10 mi S Ameca, 5800 ft, 3 (UMMZ); 6 mi SSW Autlan, 4500 ft, 4 (UMMZ); 20 mi SSE Autlan, 5000, 5500 and 6500 ft, 31 (UMMZ); Barannca Ibarra, 3000 ft, 6 (USNM); Etzatlan, 3500 ft, 16 (USNM); 12 mi W Guadalajara, 5000 ft, 21 (UMMZ); 2 mi NNW Magdalena, 4500 ft, 18 (UMMZ); Ocotlan, 5000 ft, 1 (USNM); 2 mi W San Andreas, 5000 ft, 15 (UMMZ);

Mineral San Sebastian, 17 (USNM), 4 (AMNH); Estancia, 1 (AMNH); La Laja 3 (AMNH); La Cienaga, 4; Wakenakili Mts., 12 (AMNH); *Michoacan:* 6.5 hrs (by mule) E Coalcoman, 6000 ft, 2 (UMMZ); 6 hrs (by mule) Se Coalcoman, 6000 ft, 8 (UMMZ); 6.4 mi E Dos Aguas, 5900 ft, 6 (UMMZ); 7.5 mi E Do's Aguas, 5600 ft, 10 (UMMZ); Los Reyes, 4800 ft, 33 (USNM); 8.4 mi S Uruapan, 4800 ft, 13 (UMMZ); *Nayarit:* Jalisco, 5000 ft, 1 (USNM); Pedro Pablo, 3500 ft, 1 (USNM); 2 mi E San Blas, 50 ft, 2 (UMMZ); 100 ft, 2 (MSU); 3.5 mi E San Blas, 100 ft, 1 (UMMZ); 4 mi NE San Blas, 100 ft, 2 (UMMZ); 2 mi S San Blas, 7 (TCWC); 4 mi N Santa Isabel, 3800 ft, 52 (UMMZ); 2 mi W Tepic, 2100 ft, 2 (MSU); 20 mi Se Tepic, 3500 ft, 1 (MSU); *Sinaloa:* Santa Lucia, 1 (CSULB); 1 mi E Santa Lucia, 4200 ft, 7 (MSU); 2 mi SW Santa Lucia, 3750 ft, 4 (MSU); Plomosas, 2500-3000 ft, 6 (USNM); *Zacatecas:* Monte Escobedo, 1 (USNM). The holotype (Jalisco, Mineral San Sebastian, AMNH 8373/6657) was examined.

Peromyscus winkelmanni (12)—*Michoacan:* 2.5 mi E Dos Aguas, 1 (UMMZ); 6.3 mi WSW Dos Aguas, 8000 ft, 5 (UMMZ); 8.4 mi WSW Dos Aguas, 8000 ft, 6 (UMMZ).

APPENDIX II

Mean dimensions of glans penis for species covered in this report, with locality data and sample sizes (N).

Species and locality	N	Glans length	Glans width	Protractile tip length	Baculum length
aztecus					
Hidalgo, NE Metepec	2	6.58	1.40	2.14	9.81
Hidalgo, SW Huauchinango	2	6.88	1.58	2.79	9.24
boylii					
Durango, W San Luis	7	8.09	1.25	2.20	10.55
Durango, N Pueblo Nuevo	3	8.46	1.33	1.85	10.96
Durango, Laguna del Progresso	3	7.67	1.14	2.23	9.68
Chiapas, San Cristobal	8	8.40	1.45	2.17	11.16
Guerrero, Omiltemc	8	8.45	1.30	1.92	11.36
Jalisco, La Laguna	1	8.73	1.34	2.19	11.30
Michoacan, Dos Aguas	7	8.98	1.32	2.05	12.35
Michoacan, S Uruapan	5	8.25	1.33	1.99	11.21
Oaxaca, N Ixtlan de Juarez	5	8.62	1.31	2.25	11.40
evides					
Guerrero, Omiltemc	2	7.30	1.65	2.04	10.23
Oaxaca, Santa Rosa	4	7.64	1.67	2.27	10.98

Species and locality	N	Glans length	Glans width	Protrac- tile tip length	Baculum length
hylocetes					
Jalisco, SSE Autlan	11	7.43	1.57	1.78	9.78
Jalisco, Nevada de Colima	9	—	—	—	9.70
Michoacan, NNW San Juan	17	—	—	—	10.13
Michoacan, Cerro San Andreas	10	—	—	—	9.68
Michoacan, NW Uruapan	3	7.33	1.79	2.11	9.96
madrensis					
Nayarit, Tres Marias	2	7.69	1.46	2.37	10.37
oaxacensis					
Chiapas, N Pueblo Nuevo	11	6.58	1.72	2.06	9.43
Oaxaca, N Ixtlan de Juarez	5	7.71	1.76	2.37	10.88
pectoralis					
Tamaulipas, W El Carrizo	6	9.52	1.26	2.38	13.22
simulus					
Nayarit, vicinity San Blas	5	6.00	1.34	1.50	8.64
Sinaloa, SW Copala	4	5.61	1.27	1.42	8.11
Sinaloa, SE Esquinapa	3	5.78	1.31	1.49	7.86
Sinaloa, N Mazatlan	2	5.64	1.40	1.54	7.95
Sinaloa, N Rosario	15	5.25	1.41	1.36	7.89
Sinaloa, E Concordia	2	5.56	1.39	1.56	8.38
spicilegus					
Durango, S Pueblo Nuevo	5	9.17	1.78	2.72	12.12
Jalisco, W Guadalajara	6	8.99	1.58	3.22	12.66
Jalisco, NW Magdalena	5	—	—	—	11.80
Jalisco, SE Autlan	10	—	—	—	11.32
Jalisco, S Ameca	3	—	—	—	11.68
Jalisco, San Sebastian	2	9.20	1.77	2.76	11.50
Michoacan, E Dos Aguas	7	8.46	1.76	2.95	11.75
Michoacan, Los Reyes	2	8.74	1.83	3.18	12.28
Michoacan, S Uruapan	3	8.81	1.74	3.03	11.75
Nayarit, E San Blas	2	8.34	—	3.03	11.75
Nayarit, N Santa Isabel	22	—	—	—	11.88
Sinaloa, Santa Lucia	7	9.36	1.77	2.73	12.19
winkelmanni					
Michoacan, Dos Aguas	4	9.78	1.82	2.63	12.92

APPENDIX III

Selected dimensions of some samples used in the multivariate analyses.

LENGTH OF SKULL

Species and locality number*	N	Mean	1 S.D.	Range
P. aztecus (1)	23	29.3	.74	28.1-31.3
P. boylii (2)	43	28.4	.75	26.2-29.9
P. boylii (4)	29	28.2	.73	26.3-29.6
P. boylii (5)	54	27.2	.54	26.2-28.4
P. boylii (9)	24	26.8	.63	25.7-27.7
P. evides (21)	16	30.4	.73	29.4-31.8
P. evides (22)	24	29.5	.92	28.2-31.4
P. hylocetes (23)	48	30.2	.83	28.1-31.8
P. hylocetes (24)	28	31.0	1.09	29.1-33.3
P. hylocetes (26)	27	31.6	1.15	29.1-33.9
P. madrensis (8)	9	29.2	1.31	27.3-30.9
P. oaxacensis (30)	28	31.2	.74	29.7-32.9
P. oaxacensis (28)	29	30.4	.91	28.5-32.3
P. simulus (11)	28	26.5	.80	24.8-27.9
P. spicilegus (15)	52	28.6	.70	27.2-30.2
P. spicilegus (17)	35	27.9	.83	26.4-29.4
P. spicilegus (18)	26	28.6	.82	27.3-31.0
P. spicilegus (20)	20	28.8	.63	27.4-29.9
P. winkelmanni (32)	12	32.4	.88	31.2-33.9

LENGTH OF ROSTRUM

Species and locality number*	N	Mean	1 S.D.	Range
P. aztecus (1)	23	9.8	.37	9.1-10.9
P. boylii (2)	43	9.4	.41	8.2-10.3
P. boylii (4)	29	9.2	.34	8.4-9.8
P. boylii (5)	54	8.7	.27	8.1-9.2
P. boylii (9)	24	8.8	.37	7.9-9.4
P. evides (21)	16	10.1	.46	9.3-10.8
P. evides (22)	23	9.7	.46	8.9-10.6
P. hylocetes (23)	48	10.1	.39	9.2-11.0
P. hylocetes (24)	28	10.3	.54	9.3-11.2
P. hylocetes (26)	27	10.6	.51	9.4-11.7
P. madrensis (8)	9	9.9	.63	9.0-10.8
P. oaxacensis (30)	28	10.4	.42	9.5-11.1
P. oaxacensis (28)	29	9.9	.48	9.0-10.9
P. simulus (11)	28	8.4	.40	7.4-9.3
P. spicilegus (15)	52	9.3	.38	8.2-10.1
P. spicilegus (17)	35	9.3	.42	8.5-10.2
P. spicilegus (18)	26	9.4	.42	8.6-10.7
P. spicilegus (20)	20	9.5	.40	8.8-10.3
P. winkelmanni (32)	12	10.8	.45	10.1-11.6

*See Materials and Methods

GREATEST ZYGOMATIC BREADTH

Species and locality number*	N	Mean	1 S.D.	Range
P. aztecus (1)	23	14.5	.38	13.8-15.6
P. boylii (2)	43	14.4	.49	13.3-15.6
P. boylii (4)	29	14.3	.42	13.6-15.0
P. boylii (5)	54	13.8	.39	12.9-14.8
P. boylii (9)	24	13.4	.30	12.9-14.0
P. evides (21)	16	15.4	.39	14.9-16.3
P. evides (22)	24	14.8	.64	13.6-15.8
P. hylocetes (23)	48	15.1	.45	14.0-16.0
P. hylocetes (24)	28	15.4	.66	14.3-16.6
P. hylocetes (26)	27	15.7	.61	14.7-16.8
P. madrensis (8)	9	15.0	.75	13.9-15.8
P. oaxacensis (30)	28	15.7	.51	14.7-16.7
P. oaxacensis (28)	29	15.1	.65	13.9-16.4
P. simulus (11)	28	13.4	.44	12.5-14.3
P. spicilegus (15)	52	14.4	.40	13.6-15.2
P. spicilegus (17)	35	14.0	.42	13.2-15.2
P. spicilegus (18)	26	14.5	.43	13.5-15.4
P. spicilegus (20)	20	14.8	.42	14.1-15.6
P. winkelmanni (32)	12	16.2	.56	15.4-17.1

LENGTH OF MAXILLARY TOOTHROW

P. aztecus (1)	23	4.7	.12	4.4-5.0
P. boylii (2)	43	4.3	.10	4.1-4.5
P. boylii (4)	29	4.2	.12	4.0-4.5
P. boylii (5)	54	4.1	.12	3.8-4.3
P. boylii (9)	24	4.1	.13	3.9-4.4
P. evides (21)	16	4.7	.14	4.5-5.0
P. evides (22)	25	4.7	.10	4.5-4.9
P. hylocetes (23)	48	4.8	.14	4.5-5.1
P. hylocetes (24)	28	5.0	.17	4.6-5.2
P. hylocetes (26)	27	5.0	.16	4.6-5.2
P. madrensis (8)	11	4.2	.08	4.1-4.4
P. oaxacensis (30)	28	4.8	.14	4.4-5.0
P. oaxacensis (28)	29	4.9	.14	4.6-5.3
P. simulus (11)	28	3.8	.13	3.6-4.2
P. spicilegus (15)	52	4.4	.15	4.1-4.7
P. spicilegus (17)	35	4.3	.14	4.1-4.6
P. spicilegus (18)	26	4.4	.12	4.2-4.7
P. spicilegus (20)	20	4.5	.14	4.2-4.7
P. winkelmanni (32)	12	5.3	.14	5.1-5.6

TOTAL LENGTH				
Species and locality number*	N	Mean	1 S.D.	Range
P. aztecus (1)	22	205.3	9.8	190-235
P. boylii (2)	31	199.6	11.3	175-231
P. boylii (4)	20	204.8	11.0	184-226
P. boylii (5)	45	191.9	8.3	170-213
P. boylii (9)	23	189.0	6.2	176-201
P. evides (21)	16	221.9	15.6	190-250
P. evides (22)	23	212.7	13.8	193-245
P. hylocetes (23)	45	224.0	11.8	198-250
P. hylocetes (24)	25	220.1	14.5	201-256
P. hylocetes (26)	24	224.3	14.4	198-252
P. madrensis (8)	11	222.6	10.8	210-240
P. oaxacensis (30)	24	231.3	10.1	211-252
P. oaxacensis (28)	28	223.6	14.3	194-260
P. simulus (11)	23	191.6	7.8	179-213
P. spicilegus (15)	49	202.2	10.8	184-238
P. spicilegus (17)	32	199.1	11.9	176-231
P. spicilegus (18)	26	205.0	9.0	184-221
P. spicilegus (20)	20	205.6	14.1	181-230
P. winkelmanni (32)	12	249.2	11.2	235-265

LENGTH OF TAIL				
P. aztecus (1)	22	101.5	7.1	87-116
P. boylii (2)	31	99.3	7.7	85-116
P. boylii (4)	20	103.3	7.7	85-123
P. boylii (5)	45	96.0	5.7	85-114
P. boylii (9)	23	97.0	4.9	88-107
P. evides (21)	16	111.3	8.1	100-130
P. evides (22)	23	107.2	7.8	94-124
P. hylocetes (23)	45	114.2	9.1	99-138
P. hylocetes (24)	25	108.7	8.7	96-130
P. hylocetes (26)	24	111.1	8.0	95-125
P. madrensis (8)	11	119.3	6.6	110-130
P. oaxacensis (30)	24	117.8	7.7	100-134
P. oaxacensis (28)	28	111.1	7.0	97-124
P. simulus (11)	23	97.0	5.2	88-107
P. spicilegus (15)	49	99.0	7.9	84-122
P. spicilegus (17)	32	100.3	8.2	86-124
P. spicilegus (18)	26	100.2	6.5	87-116
P. spicilegus (20)	20	102.4	11.2	81-122
P. winkelmanni (32)	12	129.1	7.9	120-140

LENGTH OF HIND FOOT

Species and locality number*	N	Mean	1 S.D.	Range
P. aztecus (1)	22	23.8	1.1	22-26
P. boylii (2)	35	22.6	1.0	21-25
P. boylii(4)	28	22.7	.53	22-24
P. boylii (5)	50	20.8	.68	20-22
P. boylii (9)	23	21.6	.88	20-23
P. evides (21)	16	24.5	.97	23-26
P. evides (22)	19	24.5	.51	24-26
P. hylocetes (23)	48	25.4	.64	24-27
P. hylocetes (24)	28	25.7	.77	24-27
P. hylocetes (26)	27	25.0	1.0	23-27
P. madrensis (8)	11	26.2	1.2	25-28
P. oaxacensis (30)	27	24.7	.76	23-26
P. oaxacensis (28)	29	25.5	.83	24-27
P. simulus (11)	28	22.2	.84	21-24
P. spicilegus (15)	49	21.8	.71	20-23
P. spicilegus (17)	35	21.6	1.2	20-23
P. spicilegus (18)	26	22.8	.76	21-24
P. spicilegus (20)	20	23.0	.94	21-25
P. winkelmanni (32)	12	27.6	.67	27-29

.