# VARIATION IN THE GLANS PENES AND BACULA AMONG LATIN AMERICAN POPULATIONS OF THE *PEROMYSCUS BOYLII* SPECIES COMPLEX

ROBERT D. BRADLEY, DAVID J. SCHMIDLY, AND ROBERT D. OWEN

*Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843 (RDB and DJS)*
*The Museum, Texas Tech University, Lubbock, TX 79409 (RDO)*
*Present address of RDB: Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409*

ABSTRACT.—Geographic and nongeographic variation was examined in the glans penes and bacula of 34 samples representing five nominate taxa of *Peromyscus boylii*-like forms (*P. boylii rowleyi, P. b. sacarensis, P. beatae, P. levipes levipes,* and *P. l. ambiguus*). Sixteen qualitative and quantitative characters were analyzed by use of cluster and principal-component analyses. Five types of phalli are found among the five taxa examined. One of these types is unique in that epidermal spines are absent from the surface of the glans penis. The other four are described in terms of their differences in size, spine development, furrowing, and length of cartilaginous tip. The pattern of phallic variation among samples of *P. boylii* is not entirely concordant with the pattern depicted by craniometric, biochemical, and chromosomal data. Populations bearing the first, second, and perhaps third phallic types described herein apparently represent undescribed taxa in the *Peromyscus boylii* species complex.

The *Peromyscus boylii* complex is a species-rich group of rodents widely distributed from the western United States throughout the highlands of Mexico and Central America. The most recent investigator of the group (Carleton, 1977; Carleton et al., 1982), drawing upon morphological data, recognized 10 species and aligned them into two distinct assemblages. The most wide-ranging species in the group is the nominate taxon *P. boylii,* which Carleton (1977) regarded as consisting of five subspecies in Latin America (*P. b. ambiguus, P. b. beatae, P. b. levipes, P. b. rowleyi,* and *P. b. sacarensis*).

A variety of character systems recently has been used to investigate systematic relationships among populations of *P. boylii,* and results of these investigations indicate that several of the subspecies recognized by Carleton (1977) actually represent cryptic species. Houseal et al. (1987) surveyed chromosomal variation in Mexican populations of *P. boylii* and recognized five karyotypic groups, which they arranged as three distinct species. These karyotypic groups were designated by fundamental number (FN) and taxon as follows: Group I, FN = 52 (*P. b. rowleyi*); Group II, FN = 48–54 (*P. beatae*); Group III, FN = 56–60 (*P. l. levipes* and *P. l. ambiguus*); Group IV, FN = 65–68, and Group V, FN = 54 (no taxonomic assignments made). Bradley and Ensink (1987) reported that the karyotype of *P. b. sacarensis* (FN = 52 and 54) was similar to *P. beatae,* and T. W. Houseal (pers. comm.) suggests it belongs to karyotype Group II. Biochemical (Rennert and Kilpatrick, 1986, 1987) and craniometric (Castro-Campillo, 1987; Schmidly et al., 1988) data sets thus far have corroborated these taxonomic interpretations.

Although Bradley and Schmidly (1987), Carleton (1977) and Hooper (1958) provided detailed descriptions of the phallus in specimens of *P. boylii,* extensive investigation of intraspecific variation or compared patterns of variation of the phallus with chromosomal, craniometric, and biochemical data has not been conducted. Herein, we report on geographic and nongeographic variation of the glans penes and bacula among the five taxa of the *P. boylii* complex, and we compare and contrast patterns of variation in phalli with those of chromosomal (Houseal et al., 1987), biochemical (Rennert and Kilpatrick, 1986, 1987), and craniometric (Schmidly et al., 1988) data.

## Materials and Methods

Phalli were removed from freshly sacrificed specimens or from fluid-preserved specimens and preserved in a solution of 50 parts ethanol (95%), 40 parts distilled water, 10 parts formalin (39%), and 2 parts glacial acetic acid. Eight qualitative characteristics of each penis were scored from dorsal, ventral, and lateral positions as follows: density of spines on the dorsal surface, density of spines on the ventral surface, size of spines on the dorsal surface, size of spines on the ventral surface, development of dorsal lappets, development of ventral lappets, extent of furrowing, and general shape of the phallus. These were recoded into 21 presence or absence characters for subsequent analysis (Appendix I, Table A).

A single representative of each taxon was examined with the aid of a scanning electron microscope. For this analysis, each phallus was washed in ethanol, critical-point dried, and mounted on a scanning stub with silver-conducting paint. The stubs and phalli then were coated to 200 angstroms with gold and palladium in a Hummer I sputtering unit. Coated specimens were viewed at 15 kiloelectron volts in a JEOL JSM-255 II scanning electron microscope equipped with 190 micron objective aperture. Photomicrographs illustrating various views and structures were made of each penis.

Eight quantitative characters were measured with an ocular micrometer calibrated to the nearest 0.01 mm (Bradley and Schmidly, 1987): length of distal tract, length of glans, length of protractile tip, greatest width of glans, length of baculum, length of cartilaginous tip, width of baculum at base, and greatest width of baculum at the midpoint. The measurements of the baculum and cartilaginous tip required clearing and staining of the phallus (Hamilton, 1946; Hooper, 1958; Lidicker, 1960). Because of the potential loss of epidermal structures, clearing and staining procedures were performed only after a thorough examination of qualitative and quantitative characters of the glans.

Emphasis was placed on using samples with known karyotypic data and including topotypic samples of the five nominate subspecies of *P. boylii*. Where possible, samples derived from single collecting localities served as the Operational Taxonomic Units (samples) for the morphometric analyses. In a few cases, however, adjacent or nearby locality samples were combined to increase sample sizes (Fig. 1, Appendix II) but only if they were karyotypically and morphologically similar. Analysis-of-variance tests and Duncan's multiple-range tests of the Statistical Analysis System (SAS Institute, Inc., 1985) were used to determine if nongeographic variation existed among adult age groups (defined by Schmidly, 1973) or among individuals of polymorphic chromosomal groups (defined by Houseal et al., 1987).

The qualitative characters were used to compute pair-wise similarity values using Jaccard's similarity coefficient (Sneath and Sokal, 1973), which disregards matches based on character-state absences. A phenogram based on the Jaccard coefficient thus depicts similarities among samples based on traditional nonmetric phallic characteristics.

The quantitative characters were standardized to mitigate for the substantial differences among character means in the following analyses. The standardized values then were used to calculate average taxonomic distances (Sneath and Sokal, 1973) between samples. A phenogram based on this measure depicts relationships among samples based on relative size and shape of the various phallic characters. We used the method of unweighted pair-groups using arithmetic averages both for this phenogram and the one based on presence-absence characters.

In addition, we conducted a principal-component analysis based on the character correlation matrix of the standarized quantitative characters. This analysis allowed us to determine which groups of characters behave similarly with respect to these samples, and which characters are useful in differentiating morphometrically among samples. Projection of the sample values onto the first three components and representation in a three-dimensional diagram allowed us to assess the clusters among samples visually. Additional projection of a minimum-spanning tree onto this diagram enabled us to determine the shortest path among samples, and thereby to infer where relationships are not represented accurately by the first three components. Phenograms, principal-component analysis, and the minimum-spanning tree, all were derived by use of the Numerical Taxonomy System of multivariate statistical programs (Rohlf et al., 1979).

## Results

### *Description of Phalli*

The phallus of *P. boylii* compared with those of other species of *Peromyscus* is characterized generally by a medium to large length and width, absence of furrowing on the surface (except *P. b. rowleyi*), one ventral and two dorsal lappets, and triangular-shaped epidermal spines asymmetrical in size and distribution on the dorsal and ventral surfaces (Fig. 2). The baculum is medium in size, rod-shaped with triangular-shaped base, and curved dorsoventrally, with a

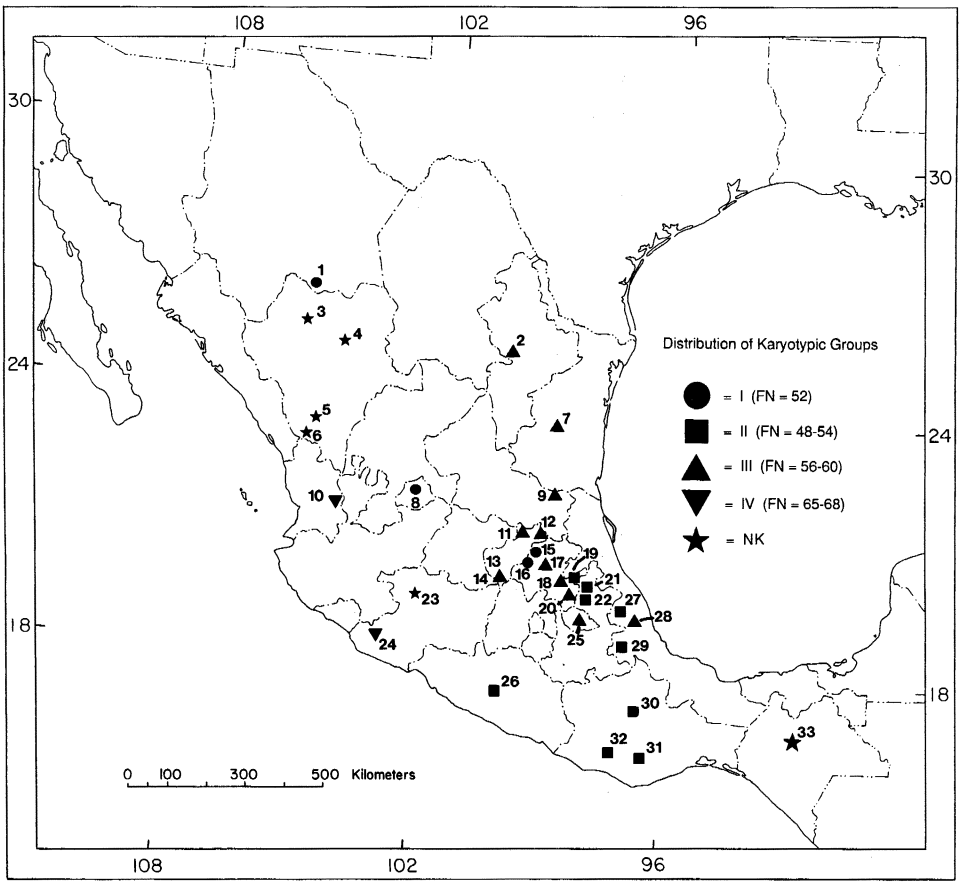


FIG. 1.—Distribution of populations examined. Numbers correpond to samples in Appendix II and symbols correspond to the appropriate karyotypic group (Houseal et al., 1987) or no karyotypic data (NK). Sample 34 from El Hatillo, Honduras, not shown.

minute cartilaginous tip. Bradley and Schmidly (1987) provided more detailed descriptions and scanning electron micrographs of phalli for all nominate taxa in the *P. boylii* species group.

The primary differences between the five taxa of *P. boylii* examined are expressed as gradations in overall size beginning with *rowleyi*, the largest, and grading progressively smaller through *levipes*, *ambiguus*, *beatae*, and *sacarensis*. However, significant variations in epidermal structures among the 34 samples included slight furrowing on the surface of the glans (Fig. 2b) of four samples representative of *P. b. rowleyi* (1, 8, 15, and 16) and samples 3, 5, and 6. This condition, unique among specimens examined, represents an infolding of epidermal tissue similar to that reported in *P. winkelmanni*, but less developed than in *P. aztecus* or *P. spicilegus* (Bradley and Schmidly, 1987). Also, the phalli of specimens of three samples of *P. l. levipes* (12, 13, and 20) lacked spines on the surface of the glans (Figs. 2c and 2d), unique among all *boylii*-like taxa examined.

## *Nongeographic Variation*

*Age variation.*—For the five samples with the largest sample sizes, analysis of variance was used to test whether significant differences in measurements of the phallus existed among three adult age groups. Only specimens from Cola de Caballo, Nuevo León (sample 2) showed significant differences ($P < 0.05$) in phallic size between age groups. A Duncan's multiple-range

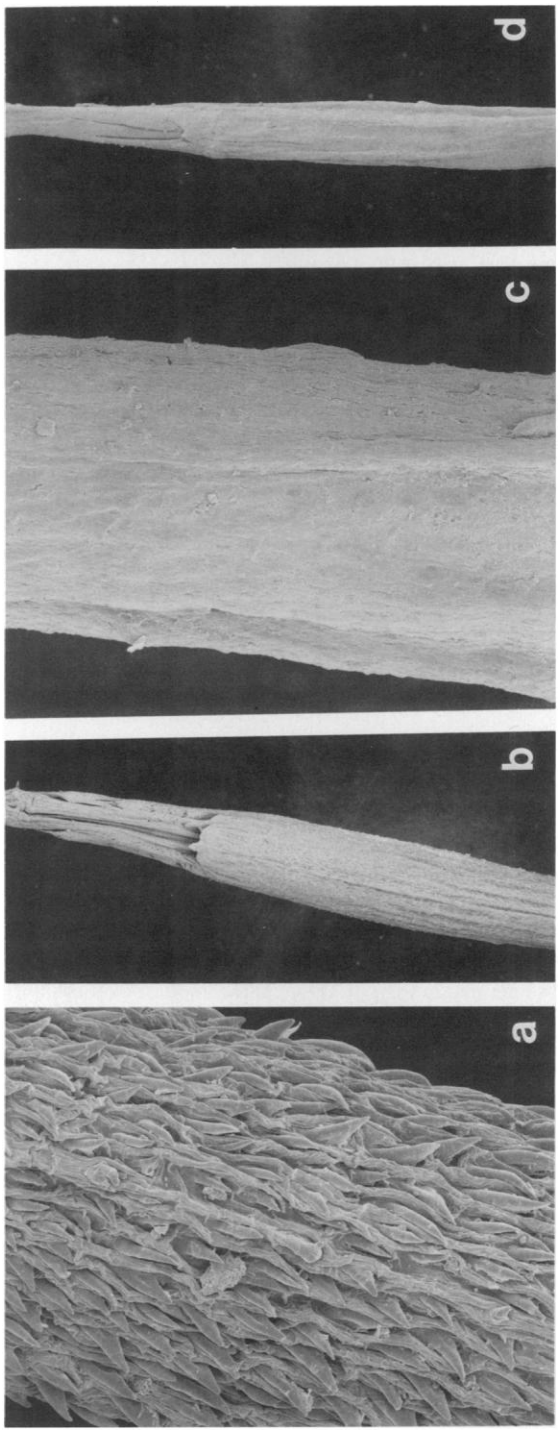


FIG. 2.—Scanning-electron photomicrographs depicting: a, surface of the glans penis of *P. l. ambiguus* (FN = 58) showing the presence of spines and the absence of furrowing (100×); b, surface of the glans penis of *P. b. rowleyi* (FN = 52) showing the presence of spines and furrowing (20×); c, glans penis of *P. l. levipes* (FN = 58) depicting complete absence of spines (100×); d, *P. l. levipes* (same individual) showing additional distal features of the glans (20×).

test revealed that differences among age groups in this sample were attributed to the slightly smaller size in four of the eight characters examined (length of distal tract, length of baculum, width of baculum at base, and greatest width of baculum at the midpoint) for individuals of Schmidly's (1973) age group IV. However, considering the overall low level of age-group variation (one of five samples showed significant variation), age groups IV, V, and VI were combined in subsequent analyses.

*Variation within polymorphic chromosomal groups.*—Analysis of variance also was used to determine if significant differences existed in measurements of the glans penis and baculum among the various karyotypic forms within those samples for which karyotypic polymorphisms existed (karyotypic Groups II, FN = 48–54; and III, FN = 56–60). The sample sizes of two of the other karyotypic Groups (IV, FN = 65–68; and V, FN = 54–56) were too small for statistical analysis. Phalli of 57 individuals from sample 30 (Llano de las Flores, Oaxaca), representing karyotypic Group II (FN = 48–54), showed no significant differences in measurements of phallic characters among individuals representing the range of karyotypic polymorphism in the sample. Therefore, for analyses of geographic variation in phalli, individuals at a locality with fundamental numbers ranging from 48 to 54 were grouped into a single sample.

Because no single sample included the range of possible fundamental numbers represented by karyotypic Group III (FN = 56–60), three samples (2, FN = 56–58; 13 and 14, FN = 58–60; and 17, FN = 58–60) were tested to determine whether the phalli of individuals with different karyotypes from the same locality differed significantly. The phalli of specimens from Cola de Caballo, Nuevo León (sample 2) and Zacualtipán-Molango, Hidalgo (sample 17) showed no significant intrapopulational differences related to differences in fundamental number. However, specimens from Amealco (13 and 14) with FN = 58 showed significant differences in the measurements of all eight phallic characters compared to specimens with FN = 59–60. For this reason, and because sample 13 included FN = 58 spineless forms, the two Amealco samples were arranged as separate samples (Amealco-1 and Amealco-2) in all analyses of geographic variation.

## *Geographic Variation*

The phenogram (Fig. 3) based on Jaccard similarity coefficients of the qualitative characters (Appendix I, Table A) has a cophenetic correlation coefficient of 0.89, indicating relatively little distortion in representation of the similarity matrix. Samples 12, 13, and 20 comprise a well-delineated group different from the remainder, and 8, 7, and 15 are each separated from the other samples by low similarity values. Seven branches occur in which two or more samples are identical in presence-absence characters; of these, three include representatives of more than one of the four karyotypic groups.

The phenogram (Fig. 4) based on average taxonomic distances computed from the quantiative characters (Appendix I, Table B) has a cophenetic correlation coefficient of 0.84, and includes five relatively well-delineated branches. Samples 24 and 6 are both different from the others, and are each alone on a branch. As with the Jaccard phenogram, samples 12, 13, and 20 are similar to each other and are isolated from other samples. Samples 1, 3, 8, 15, and 16 comprise a group, and the remaining 24 samples form the largest of the five primary clusters.

The principal-component analysis (Fig. 5) helps to identify the quantitative characters that define these clusters. The first three components account for 51.2, 16.5, and 13.8% of the variation, respectively. Component I generally is a size factor, having positive loadings for all characters (Table 1). Component II primarily reflects width of the baculum at base, and is correlated negatively with the length of the protractile tip. Component III has a strong correlation with length of the cartilaginous tip. A minimum-spanning tree imposed on the principal-component projections indicates relatively little distortion of relationships among samples by reduction to three axes. Samples 12, 13, and 20 thus are characterized by small overall size and relatively small width of baculum at base, and sample 24 by a relatively long cartilaginous tip (Fig. 5).

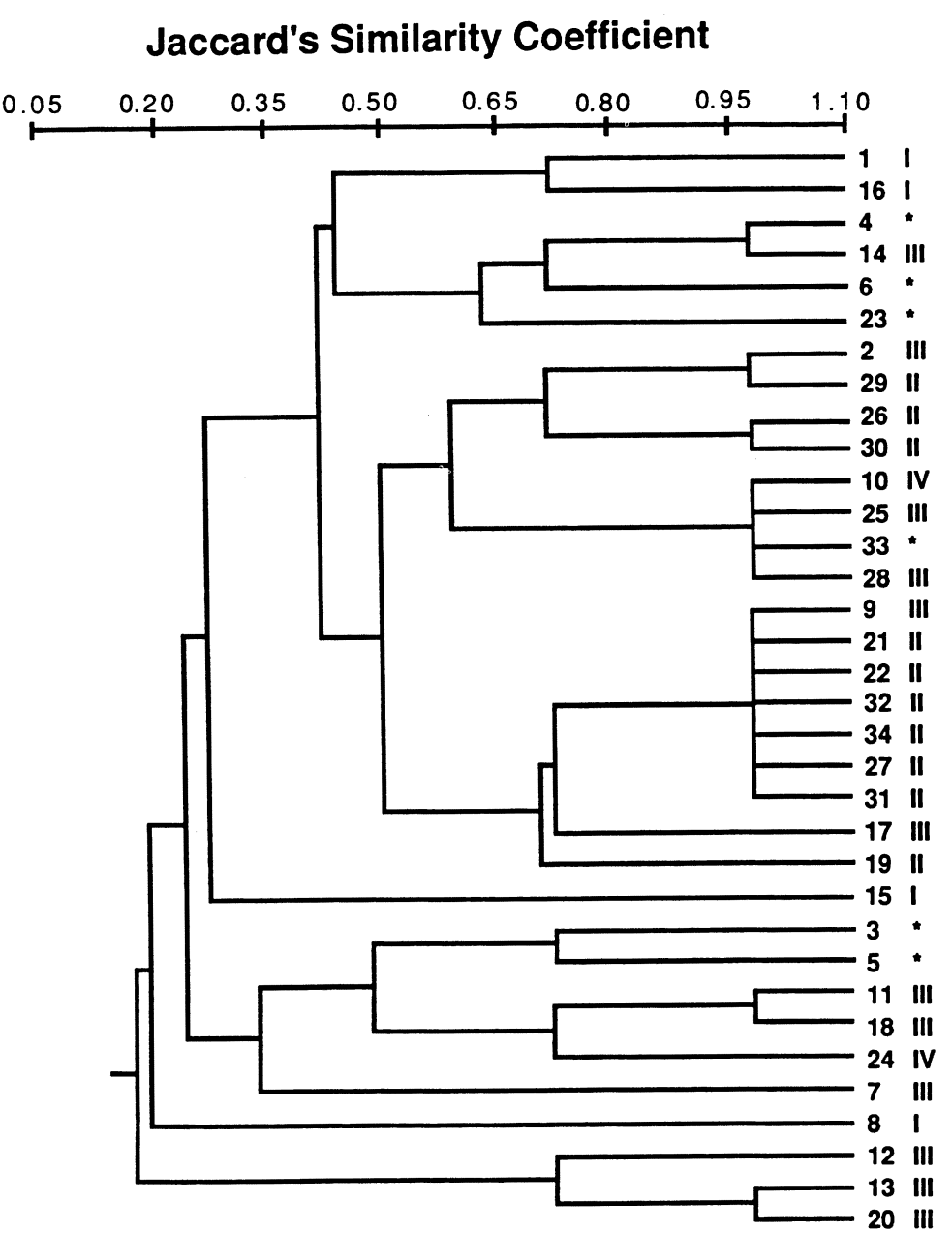


FIG. 3.—Phenogram depicting relationships of the 34 samples (Fig. 1, Appendix II) based on qualitative characters. Phenogram was constructed by use of the unweighted pair-group method using arithmetic averages, based on Jaccard's similarity values between samples. Karyotypic affiliation of each sample follows that of Houseal et al. (1987) and is shown to the right of each sample number: I (FN = 52), II (FN = 48–54), III (FN = 56–60), IV (FN = 65–68), and * (karyotype is unknown). Cophenetic correlation coefficient of the phenogram is 0.89.

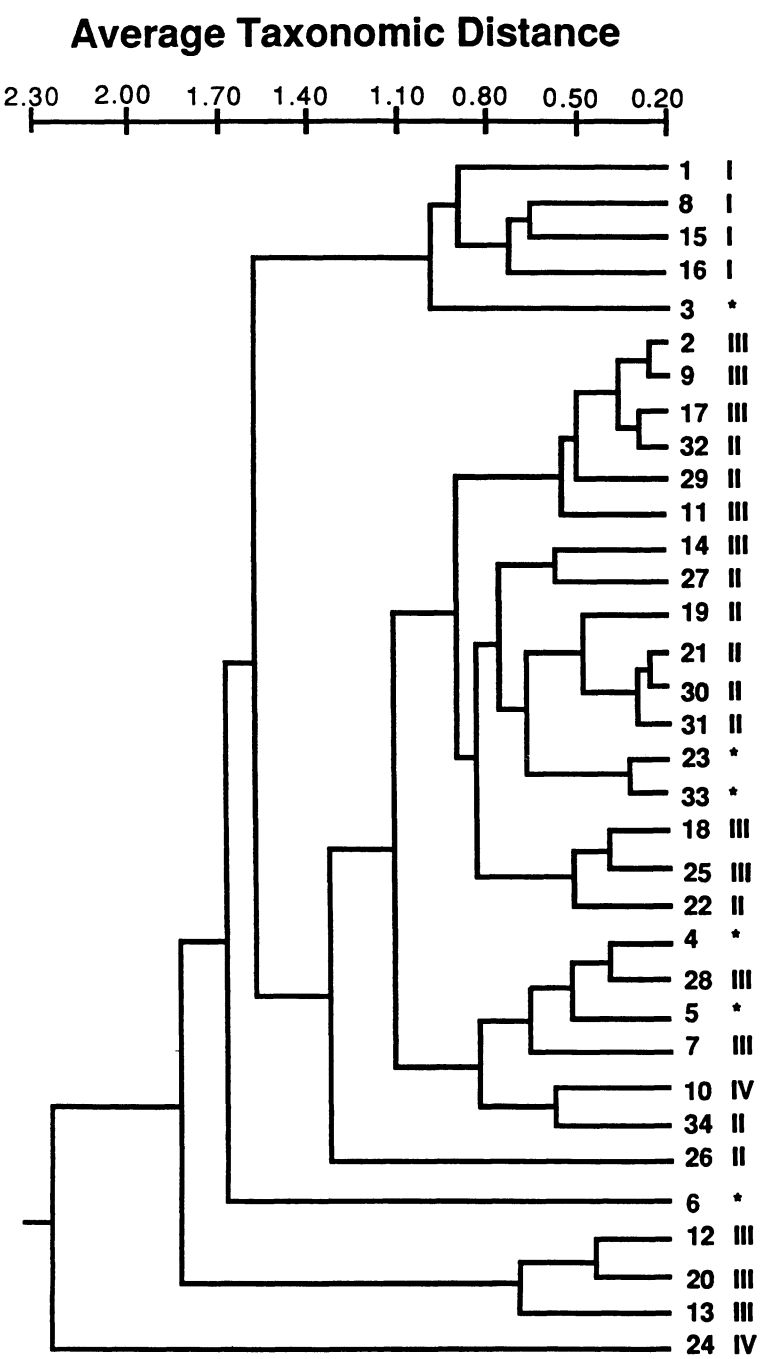


FIG. 4.—Phenogram depicting relationships of the 34 samples (Fig. 1, Appendix II) based on quantitative (continuous) characters. Phenogram was constructed by use of the unweighted pair-group method using arithmetic averages, based on average taxonomic distances between samples. Karyotypic affiliation of each sample follows that of Houseal et al. (1987) and is shown to the right of each sample number: I (FN = 52), II (FN = 48–54), III (FN = 56–60), IV (FN 65–68), and * (karyotype is unknown). Cophenetic correlation coefficient is 0.84.

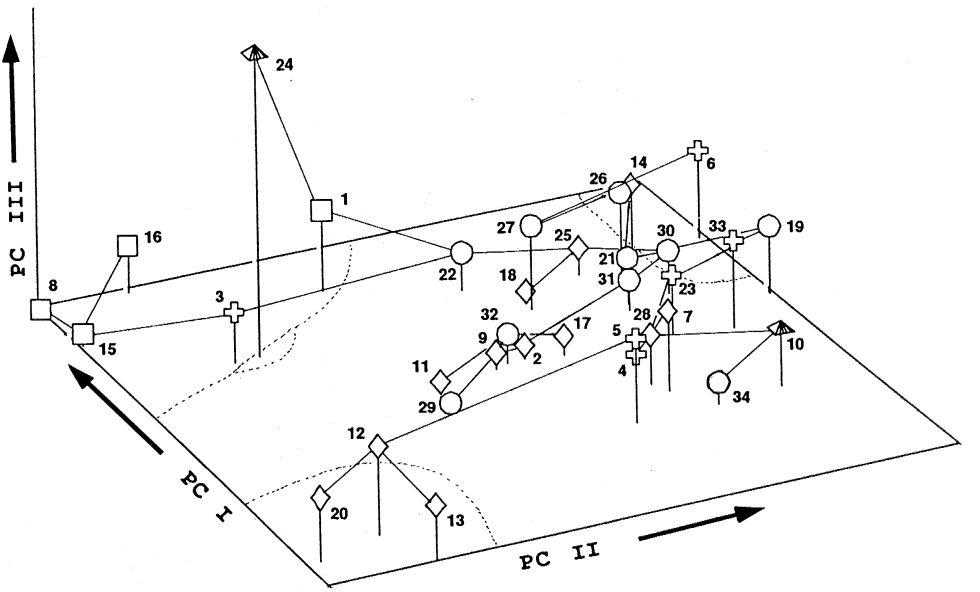


FIG. 5.—Projection of the first three axes from principal-component analysis of quantitative characters. First three components account for 51.2, 16.5, and 13.8% of total variance, respectively. Arrows indicate direction of increasing values on each axis. Samples numbered as in Figs. 3 and 4. Symbols indicate karyotypic group, as follows: squares, I (FN = 52); circles, II (FN = 48–54); diamonds, III (FN = 56–60); pyramids, IV (FN = 65–68); crosses, karyotype unknown. Minimum-spanning tree shows shortest path connecting all samples in unreduced eight-variable space. Dashed lines on base are for visual definition of groups discussed in text.

## DISCUSSION

Based on the presence or absence of qualitative characteristics of the phallus, samples 15 (karyotypic Group I), 7 (III), and 8 (I) are distinct from the others, as is the branch composed of 12, 13, and 20 (the spineless group III samples). No branch on the phenogram (Fig. 3) is associated exclusively with any of the karyotypic groups described by Houseal et al. (1987) and the branches do not reflect exactly the historical or recently refined taxonomy of the species (Schmidly et al., 1988). Also, no branch appears to represent a geographic grouping. Thus, the arrangement based on traditional qualitative characteristics shows little concordance with geographic or karyologic relationships among samples. Because multiple karyotypic forms are found in several groups with identical presence or absence characteristics, we strongly suspect that these characters do not allow us to discriminate accurately among these samples. This is of particular interest because qualitative characters of the glans and baculum traditionally have been considered to be of substantial systematic value, especially among muroid rodents (Hooper, 1958; Lidicker, 1960, 1968). In the present case, however, these data apparently are contradicted by karyotypic (Houseal et al., 1987), cranial (Schmidly et al., 1988), and quantitative penile data (this study). Qualitative penile characters also failed to resolve the trichotomy among topotypic samples of *P. beatae*, *P. l. levipes*, and *P. l. ambiguus* (Bradley and Schmidly, 1987).

The five primary branches of the continuous-character phenogram (Fig. 4) in some cases are related more easily to previously recognized groupings. The most distinct branch consists solely of sample 24, one of two samples from western Mexico belonging to karyotypic Group IV (Fig. 1). This sample is characterized primarily by an extremely long cartilaginous tip (Fig. 5, Table 1). This population historically has been referred to the taxon *levipes* (Carleton, 1977; Hooper, 1961) and was suggested to represent an undescribed taxon on the basis of its unique chromosomal

TABLE 1.—*Character loadings for the first three components of the principal-component analysis using eight quantitative characters.*

| Character | Component | | |
|---|---|---|---|
| | I | II | III |
| Length of distal tract | 0.950 | −0.081 | −0.130 |
| Length of glans | 0.898 | −0.359 | 0.042 |
| Length of protractile tip | 0.690 | −0.571 | −0.329 |
| Greatest width of glans | 0.736 | 0.370 | −0.287 |
| Length of baculum | 0.819 | 0.046 | 0.133 |
| Length of cartilaginous tip | 0.181 | −0.255 | 0.874 |
| Width of baculum at base | 0.525 | 0.790 | 0.104 |
| Greatest width of baculum (midpoint) | 0.632 | 0.181 | 0.318 |

characteristics (Group IV, FN = 65–68—Houseal et al., 1987). However, this sample did not cluster with the other karyotypic Group IV sample (10).

The second most distinct phenetic group comprises samples 12, 20, and 13, the three members of karyotypic Group III that also lack epidermal spines. Morphometrically, this group is characterized by small overall penile size and by small width of baculum at base. This group was the most divergent in the qualitative analyses because of the lack of epidermal spines, whereas the phalli of all other taxa in karyotypic Group III possess spines. The possibility that this "spineless" condition results from an artifact in specimen preparation has been considered. However, the "spineless" forms are from four collecting sites in Queretaro and Hidalgo (samples 12, El Lobo and Santa Inés; 13, Amealco-1; and 20, El Susto), and all specimens from these sites were spineless. The phalli from these specimens were collected and processed simultaneously with others that possessed spines and suffered no loss. In addition, the large sample size (41 specimens) from these localities suggests that loss of spines is not an artifact.

Samples containing the "spineless" specimens are not presently recognized as being taxonomically distinct. Houseal et al. (1987) and Schmidly et al. (1988) arranged them with several other samples from east-central Mexico into the taxon *P. l. levipes*. Chromosomally, the "spineless" specimens are identical to other FN = 58 forms of karyotypic Group III (Houseal et al., 1987), and no biochemical (G. W. Kilpatrick, pers. comm.) or craniometric (Schmidly et al., 1988) distinctions have been found to distinguish them from other samples of *P. levipes*. The three samples with "spineless" phalli are interspersed geographically among other localities of karyotypic Groups I, II, and III in central Mexico (Fig. 1).

Sample 6, from southern Durango, is the third primary branch on the phenogram (Fig. 4). It is distinguished by a combination of characters contributing to all three principal components. Although no karyotypic data are available for these specimens, Schmidly and Schroeter (1974) studied chromosomal variation in specimens of *P. boylii* from Durango, and these specimens demonstrated karyotypic intermediacy (FN = 54–56) between individuals from localities in western Durango and specimens of *P. b. rowleyi* in the eastern part of that state. Carleton (1977) suggested that specimens of *P. boylii* from western Mexico (including Durango) may represent an undescribed subspecies.

Five samples (1, 8, 15, 16, and 3) form a fourth primary branch (Fig. 4). Four of these are the four representatives of karyotypic Group I (*P. boylii rowleyi*) analyzed in this study, and sample 3 (from northern Durango near sample 1) also is recognized in the subspecies, although the karyotype is unknown at present. These five samples are characterized by having a glans penis large in overall size, with relatively long protractile tips, and by the presence of slight furrowing. This phenetic grouping is the only series of samples in this study that corresponds to a formally recognized taxon, namely *P. b. rowleyi*. These samples also were recognized as distinctive on the basis of their monomorphic FN = 52 karyotype (Houseal et al., 1987), fixed differences at the transferrin and salivary amylase loci (Rennert and Kilpatrick, 1986), and small cranial size (Schmidly et al., 1988).

The remaining 24 samples form a large branch containing no member of karyotypic Group I, one of the two members of Group IV, and all members of Groups II and III except the three spineless samples mentioned previously. Within this branch, karyotypic Groups II and III are distributed more or less randomly, suggesting either that these two groups may not reflect true systematic assemblages or, alternatively, that (at least within this restricted section of the *P. boylii* complex) penile morphometric evolution has not paralleled chromosomal changes among samples. This cluster contains samples referable to *P. l. ambiguus*, *P. l. levipes*, *P. beatae*, and *P. boylii sacarensis* according to the most current taxonomy of the *boylii* complex (Houseal et al., 1987; Rennert and Kilpatrick, 1986, 1987; Schmidly et al., 1988).

Additional "qualitative" comparisons of two specimens of karyotypic Group V (one from Los Reyes, Michoacán, and one from Jiquilpan, Michoacán) and two specimens from Los Azufres, Michoacán (karyotypic group undetermined by Houseal et al., 1987) with individuals of the five phallic groups revealed similarities in size and shape to the fifth phallic group. However, this interpretation must be viewed cautiously as the sample size was small for deriving qualitative statistical comparisons.

Although recent investigators of cranial morphology, biochemical, and chromosomal data sets (Houseal et al., 1987; Rennert and Kilpatrick, 1986, 1987; Schmidly et al., 1988) provide taxonomic changes within *P. boylii* (that is, *rowleyi*, *beatae*, and *levipes* [including *ambiguus*] represent distinct species), a qualitative and quantitative evaluation of the glans penis and baculum of specimens of *P. boylii* does not completely support this interpretation. Glans penes and morphology of the baculum is congruent with the biochemical, chromosomal, and cranial data in supporting the distinctiveness of *rowleyi* from other forms of the *boylii* complex. In contrast, the phallic data do not discriminate clearly among recognized taxa of the species *levipes* and *beatae*. However, these data support the suggestion of Houseal et al. (1987) that sample 24 may represent an undescribed taxon; the data also indicate that sample 6 may deserve closer scrutiny using additional data; and these data strongly suggest that samples 12, 13, and 20 may represent a previously undetected species in the *Peromyscus boylii* complex.

## Acknowledgments

We are indebted to T. W. Houseal, S. A. Smith, K. M. Davis, J. Ensink, M. W. Allard, D. Werbitsky, P. D. Rennert, C. W. Kilpatrick, I. F. Greenbaum, and D. W. Hale for their assistance in obtaining specimens. We also are indebted to A. C. Carmichael, The Museum, Michigan State University and P. Myers and L. R. Heaney, University of Michigan Museum of Zoology, for allowing us to borrow specimens. Special thanks to H. Sittertz-Bhatkar for preparing the scanning electron microscope photomicrographs, and to the Texas Agricultural Experiment Station for supporting this aspect of the research. We also thank J. Arroyo-Cabrales, R. A. Van Den Bussche, J. N. Derr, M. J. Hamilton, and L. C. Bradley for comments and assistance during various stages of this manuscript, and J. Logan for typing and word processing. The research was supported by the National Science Foundation through grants DEB 81-17447 (I. F. Greenbaum and D. J. Schmidly) and DEB 81-18966 (C. W. Kilpatrick). We thank the Dirección General de Flora y Fauna Silvestres for granting permission to collect in Mexico, and the numerous faculty and students at Universidad Nacional Autónoma de México who aided our work in Mexico. This paper represents contribution number TA-24946 of the Texas Agricultural Experiment Station.

## Literature Cited

Bradley, R. D., and J. Ensink. 1987. Karyotypes of five cricetid rodents from Honduras. Texas J. Sci., 39:171–175.

Bradley, R. D., and D. J. Schmidly. 1987. The glans penes and bacula in Latin American taxa of the *Peromyscus boylii* species group. J. Mamm., 68:595–616.

Carleton, M. D. 1977. Interrelationships of populations of the *Peromyscus boylii* species group (Rodentia: Muridae) in western Mexico. Occas. Papers Mus. Zool., Univ. Michigan, 675:1–47.

Carleton, M. D., D. E. Wilson, A. L. Gardner, and M. A. Bogan. 1982. Distribution and systematics of *Peromyscus* (Mammalia: Rodentia) of Nayarit, Mexico. Smithsonian Contrib. Zool., 352: 1–46.

Castro-Campillo, A. A. 1987. The systematic status of *Peromyscus boylii ambiguus*. Unpubl. M.S. thesis, Texas A&M Univ., College Station, 50 pp.

Hamilton, W. J., Jr. 1946. A study of the baculum in some North American Microtinae. J. Mamm., 27:378–387.

HOOPER, E. T. 1958. The male phallus in mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool., Univ. Michigan, 105:1–24.

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

HOUSEAL, T. W., I. F. GREENBAUM, D. J. SCHMIDLY, S. A. SMITH, AND K. M. DAVIS. 1987. Karyotypic variation in *Peromyscus boylii* from Mexico. J. Mamm., 68:281–296.

LIDICKER, W. Z., JR. 1960. The baculum of *Dipodomys ornatus* and its implication for superspecific groupings of kangaroo rats. J. Mamm., 41:495–499.

———. 1968. A phylogeny of New Guinea rodent genera based on phallic morphology. J. Mamm., 49:609–643.

RENNERT, P. D., AND C. W. KILPATRICK. 1986. Biochemical systematics of populations of *Peromyscus boylii*. I. Populations from east-central Mexico with low fundamental numbers. J. Mamm., 67:481–488.

———. 1987. Biochemical systematics of populations of *Peromyscus boylii*. II. Chromosomally variable populations from eastern and southern Mexico. J. Mamm., 68:799–811.

ROHLF, F. J., J. KISHPAUGH, AND D. KIRK. 1979. Numerical taxonomy system of multivariate statistical programs. Dept. Ecol. Evol., State Univ. New York, Stony Brook, 112 pp.

SAS INSTITUTE, INC. 1985. User's guide: basics. Version 5 ed. SAS Institute, Inc., Cary, North Carolina, 1,290 pp.

SCHMIDLY, D. J. 1973. Geographic variation and taxonomy of *Peromyscus boylii* from Mexico and southern United States. J. Mamm., 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.

SCHMIDLY, D. J., R. D. BRADLEY, AND P. S. CATO. 1988. Morphometric differentiation and taxonomy of three chromosomally characterized groups of *Peromyscus boylii* from east-central Mexico. J. Mamm., 69:460–480.

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

YATES, T. L., W. R. BARBER, AND D. M. ARMSTRONG. 1987. Survey of North American collections of Recent mammals. J. Mamm. (Suppl.), 68(2):1–76.

*Submitted 2 June 1988. Accepted 28 February 1989.*

## APPENDIX II

### *Specimens Examined*

Sample number and karyotypic group enclosed in parentheses. Population numbers are as shown in Fig. 1, and karyotypic groupings are those of Houseal et al. (1987). All localities are in Mexico, unless otherwise indicated. Museum designations follow Yates et al. (1987).

*Peromyscus beatae.—Sample 19* (Group II): HIDALGO, 7 mi NE Metepec, 2 (TCWC); 12.1 mi NE Metepec, 4 (TCWC); 13 mi NE Metepec, 3 (TCWC); 14.2 mi NE Metepec, 2 (TCWC); 15.8 mi NE Metepec, 1 (TCWC). *Sample 21* (Group II): PUEBLA, 6.9 mi SW Huachinango, 6,600 ft, 27 (TCWC); 7.3 mi SW Huachinango, 6,800 ft, 4 (UMMZ); Honey, 1,900 m, 1 (UMMZ); Huayacocotla, 1 (UMMZ); HIDALGO, 8.3 mi SW Huachinango, 6,800 ft, 13 (TCWC). *Sample 22* (Group II): PUEBLA, 8 mi SE Chignahaupan, 8,600 ft, 4 (TCWC); 9.0 mi SE Chignahaupan, 3 (TCWC); 10 mi SE Chignahaupan, 2 (TCWC); 2 mi NW Zacapoaxtla, 6,600 ft, 2 (UMMZ). *Sample 26* (Group II): GUERRERO, 0.5 mi W Acahuizotla, 3,000 ft, 3 (UMMZ); Agua de Obispo, 2,600 ft, 1 (UMMZ); 53 km SW Casa Verde, 2,500 ft, 1 (UMMZ); 8.6 mi WSW Chilpancingo, 2 (UMMZ), 4 mi SW Filo de Caballo, 7,900 ft, 18 (TCWC); 5.3 mi SW Filo de Caballo, 8,000 ft, 5 (TCWC); 6.4 mi SW Filo de Caballo, 8,400 ft, 7 (TCWC); Omilteme, 11 (UMMZ); 12 mi SW Xochipala, 8,200 ft, 1 (MSU). *Sample 27* (Group II): VERACRUZ, Las Vigas, 10 (UMMZ); 1.9 mi E Las Vigas, 5 (TCWC); 5 mi E Las Vigas, 4 (TCWC). *Sample 29* (Group II): VERACRUZ, Orizaba, 10 (TCWC); 3.1 mi N Tequila, 2 (TCWC); Xometla, 8,200 ft, 17 (TCWC). *Sample 30* (Group II): OAXACA, Ixtlán de Juárez, 1 (UMMZ); 10 mi N Ixtlán de Juárez, 9,300 ft, 1 (MSU); 12 mi N Ixtlán de Juárez, 9,000 ft, 5 (UMMZ), 8 (TCWC); 0.4 mi N Llano de las Flores, 9,200 ft, 7 (TCWC); 0.9 mi N Llano de las Flores, 9,200 ft, 10 (TCWC); 1.5 mi N Llano de las Flores, 9,200 ft, 10 (TCWC); 4 mi S Llano de las Flores, 9,200 ft, 2 (TCWC); Miahuatlán (Campamento Rio Molino), 1 (UMMZ); Cerro San Felipe, 18 (TCWC). *Sample 31* (Group II): OAXACA, 8 mi SSW Juchatengo, 1 (MSU); 2 mi S Suchixtepec, 7,100 ft, 3 (TCWC); 3 mi S Suchixtepec, 7,100 ft, 11 (TCWC). *Sample 32* (Group II): OAXACA, 4 mi E Juquila, 6,000 ft, 3 (TCWC); 6 mi E Juquila, 2 (TCWC). *Sample 33* (no karyotypic data): CHIAPAS, Botchil, 4 (UMMZ); Las Margaritas, 1 (UMMZ); Pueblo Nuevo, 2 (UMMZ); 5 mi N Pueblo Nuevo, 3 (UMMZ); San Cristóbal, 9 (UMMZ); 8 mi SE San Cristóbal, 7,800 ft, 10 (UMMZ); Teopisca, 2 (UMMZ). GUATEMALA, HUEHUETENANGO, La Libertad, 2 (UMMZ); San Marios: Volcán Tajumulsco, 2 (UMMZ).

*Peromyscus levipes ambiguus.—Sample 2* (Group III): NUEVO LEON, Cola de Caballo, 61 (TCWC). *Sample 7* (Group III): TAMAULIPAS, 16 mi SW Ciudad Victoria, 3,600 ft, 2 (UMMZ).

## APPENDIX I

TABLE A.—*Coding scheme and data matrix for qualitative characters.*

| Character and character state | Sample | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 |
| Spines dorsal side | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Absent | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Small | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Medium | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Large | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Very large | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spines ventral side | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Absent | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Sparse and tubercles | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Sparse and medium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dense and tubercles | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dense and very small | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Dense and small | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |
| Dorsal lappets (development) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Poorly | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Moderately | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| Well | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 |
| Ventral lappets (development) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Poorly | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Moderately | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| Well | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| Furrowing | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Absent | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Present | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Overall appearance | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Rod | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Elongate | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

## Appendix I

Table B.—*Character means (in mm, ±1 SE) for samples examined in this study.*

| Sample | Length of distal tract | Length of glans | Length of protractile tip | Greatest width of glans | Length of baculum | Length of cartilaginous tip | Width of baculum at base | Greatest width of baculum (midpoint) |
|---|---|---|---|---|---|---|---|---|
| 1 | 13.07 ± 0.22 | 8.97 ± 0.14 | 2.23 ± 0.07 | 1.82 ± 0.03 | 11.63 ± 0.26 | 0.20 ± 0.02 | 1.39 ± 0.05 | 0.38 ± 0.02 |
| 2 | 12.12 ± 0.16 | 8.08 ± 0.12 | 2.14 ± 0.04 | 1.65 ± 0.03 | 9.92 ± 0.16 | 0.16 ± 0.00 | 1.40 ± 0.03 | 0.33 ± 0.01 |
| 3 | 12.46 ± 0.30 | 8.53 ± 0.21 | 2.35 ± 0.07 | 1.56 ± 0.05 | 10.66 ± 0.16 | 0.17 ± 0.00 | 1.22 ± 0.05 | 0.43 ± 0.03 |
| 4 | 12.01 ± 0.34 | 7.50 ± 0.00 | 1.84 ± 0.17 | 1.42 ± 0.09 | 9.70 ± 0.33 | 0.16 ± 0.01 | 1.31 ± 0.08 | 0.33 ± 0.04 |
| 5 | 11.20 ± 0.33 | 7.78 ± 0.19 | 1.75 ± 0.09 | 1.42 ± 0.04 | 9.35 ± 0.26 | 0.17 ± 0.01 | 1.26 ± 0.04 | 0.35 ± 0.03 |
| 6 | 12.81 ± 0.44 | 8.62 ± 0.45 | 1.86 ± 0.21 | 1.67 ± 0.00 | 10.99 ± 0.70 | 0.15 ± 0.02 | 1.50 ± 0.07 | 0.51 ± 0.06 |
| 7 | 10.76 ± 2.09 | 7.59 ± 1.42 | 1.84 ± 0.17 | 1.50 ± 0.17 | 11.09 ± 0.25 | 0.17 ± 0.00 | 1.33 ± 0.00 | 0.33 ± 0.00 |
| 8 | 14.08 ± 0.44 | 9.64 ± 0.32 | 2.52 ± 0.12 | 1.73 ± 0.06 | 11.89 ± 0.41 | 0.17 ± 0.00 | 1.31 ± 0.07 | 0.35 ± 0.02 |
| 9 | 12.29 ± 0.38 | 8.06 ± 0.25 | 2.09 ± 0.09 | 1.64 ± 0.06 | 10.07 ± 0.39 | 0.16 ± 0.00 | 1.33 ± 0.07 | 0.33 ± 0.00 |
| 10 | 10.84 ± 0.25 | 7.34 ± 0.14 | 1.88 ± 0.08 | 1.52 ± 0.13 | 9.00 ± 0.18 | 0.16 ± 0.00 | 1.42 ± 0.11 | 0.37 ± 0.04 |
| 11 | 12.05 ± 0.91 | 8.39 ± 0.46 | 2.00 ± 0.17 | 1.57 ± 0.01 | 10.70 ± 0.86 | 0.15 ± 0.01 | 1.24 ± 0.11 | 0.31 ± 0.02 |
| 12 | 10.62 ± 0.35 | 7.48 ± 0.29 | 1.96 ± 0.08 | 1.04 ± 0.04 | 9.29 ± 0.31 | 0.17 ± 0.01 | 1.07 ± 0.03 | 0.34 ± 0.01 |
| 13 | 10.59 ± 0.96 | 7.34 ± 0.79 | 1.86 ± 0.10 | 1.05 ± 0.10 | 9.22 ± 1.02 | 0.16 ± 0.00 | 1.06 ± 0.07 | 0.27 ± 0.04 |
| 14 | 12.78 ± 0.22 | 8.56 ± 0.23 | 2.02 ± 0.07 | 1.51 ± 0.04 | 11.44 ± 0.17 | 0.17 ± 0.01 | 1.65 ± 0.05 | 0.39 ± 0.02 |
| 15 | 13.67 ± 0.41 | 9.25 ± 0.29 | 2.36 ± 0.11 | 1.63 ± 0.04 | 11.45 ± 0.48 | 0.16 ± 0.01 | 1.16 ± 0.10 | 0.39 ± 0.05 |
| 16 | 13.50 ± 0.39 | 9.45 ± 0.19 | 2.51 ± 0.09 | 1.63 ± 0.07 | 12.11 ± 0.43 | 0.17 ± 0.01 | 1.37 ± 0.08 | 0.43 ± 0.02 |
| 17 | 12.28 ± 0.22 | 8.19 ± 0.14 | 1.98 ± 0.05 | 1.70 ± 0.04 | 10.09 ± 0.19 | 0.16 ± 0.00 | 1.36 ± 0.04 | 0.32 ± 0.02 |
| 18 | 12.87 ± 0.42 | 8.60 ± 0.27 | 2.14 ± 0.11 | 1.77 ± 0.04 | 10.59 ± 0.58 | 0.16 ± 0.00 | 1.50 ± 0.15 | 0.33 ± 0.00 |
| 19 | 12.01 ± 0.28 | 8.11 ± 0.20 | 1.91 ± 0.09 | 1.65 ± 0.05 | 10.27 ± 0.40 | 0.16 ± 0.00 | 1.59 ± 0.05 | 0.39 ± 0.03 |
| 20 | 10.39 ± 0.78 | 7.84 ± 0.55 | 2.00 ± 0.11 | 1.03 ± 0.08 | 8.42 ± 0.05 | 0.16 ± 0.00 | 1.04 ± 0.08 | 0.33 ± 0.00 |
| 21 | 12.26 ± 0.14 | 8.19 ± 0.09 | 2.08 ± 0.04 | 1.60 ± 0.03 | 10.76 ± 0.13 | 0.16 ± 0.00 | 1.55 ± 0.03 | 0.37 ± 0.01 |
| 22 | 13.10 ± 0.14 | 8.78 ± 0.14 | 2.15 ± 0.12 | 1.68 ± 0.07 | 10.83 ± 0.37 | 0.16 ± 0.01 | 1.45 ± 0.09 | 0.40 ± 0.03 |
| 23 | 12.10 ± 0.16 | 8.00 ± 0.14 | 1.83 ± 0.06 | 1.59 ± 0.03 | 10.79 ± 0.13 | 0.16 ± 0.01 | 1.40 ± 0.05 | 0.36 ± 0.02 |
| 24 | 12.43 ± 0.70 | 8.95 ± 0.37 | 1.95 ± 0.13 | 1.47 ± 0.07 | 10.96 ± 1.41 | 0.31 ± 0.05 | 1.39 ± 0.22 | 0.39 ± 0.04 |
| 25 | 12.85 ± 0.18 | 8.48 ± 0.15 | 2.11 ± 0.05 | 1.79 ± 0.03 | 11.02 ± 0.18 | 0.16 ± 0.00 | 1.52 ± 0.04 | 0.37 ± 0.02 |
| 26 | 12.25 ± 0.23 | 8.00 ± 0.16 | 1.97 ± 0.05 | 1.59 ± 0.04 | 13.40 ± 0.15 | 0.17 ± 0.01 | 1.48 ± 0.03 | 0.38 ± 0.01 |
| 27 | 13.00 ± 0.26 | 8.32 ± 0.20 | 2.04 ± 0.15 | 1.45 ± 0.06 | 10.93 ± 0.22 | 0.17 ± 0.01 | 1.48 ± 0.07 | 0.41 ± 0.02 |
| 28 | 11.52 ± 0.29 | 7.80 ± 0.23 | 1.89 ± 0.08 | 1.49 ± 0.08 | 9.98 ± 0.31 | 0.16 ± 0.00 | 1.38 ± 0.09 | 0.33 ± 0.00 |
| 29 | 12.10 ± 0.26 | 8.04 ± 0.16 | 2.10 ± 0.07 | 1.66 ± 0.04 | 9.33 ± 0.24 | 0.16 ± 0.00 | 1.25 ± 0.07 | 0.31 ± 0.02 |
| 30 | 12.51 ± 0.14 | 8.14 ± 0.09 | 2.03 ± 0.03 | 1.66 ± 0.03 | 10.54 ± 0.12 | 0.16 ± 0.00 | 1.56 ± 0.03 | 0.37 ± 0.01 |
| 31 | 12.48 ± 0.24 | 8.15 ± 0.22 | 2.04 ± 0.06 | 1.66 ± 0.02 | 10.62 ± 0.25 | 0.16 ± 0.00 | 1.52 ± 0.05 | 0.34 ± 0.01 |
| 32 | 12.27 ± 0.52 | 8.27 ± 0.33 | 2.00 ± 0.13 | 1.61 ± 0.08 | 10.45 ± 0.74 | 0.16 ± 0.00 | 1.33 ± 0.10 | 0.33 ± 0.00 |
| 33 | 11.86 ± 0.22 | 8.04 ± 0.18 | 1.80 ± 0.07 | 1.52 ± 0.05 | 10.54 ± 0.16 | 0.17 ± 0.01 | 1.51 ± 0.03 | 0.36 ± 0.02 |
| 34 | 11.12 ± 0.40 | 7.22 ± 0.28 | 1.94 ± 0.06 | 1.67 ± 0.00 | 8.67 ± 0.50 | 0.16 ± 0.00 | 1.33 ± 0.00 | 0.33 ± 0.00 |

*Peromyscus levipes levipes.*—*Sample 9* (Group III): SAN LUIS POTOSI, 0.5 mi W Las Abritas, 3,000 ft, 6 (TCWC); 2 mi W Las Abritaas, 6 (TCWC). *Sample 11* (Group III): QUERETARO, Pinal de Amoles, 1 (UMMZ); 1 mi N Pinal de Amoles, 8,000 ft, 2 (TCWC); 1 mi S Pinal de Amoles, 2 (TCWC); 1 mi W Pinal de Amoles, 1 (TCWC); 3.6 mi SW Pinal de Amoles, 4 (TCWC). *Sample 12* (Group III): QUERETARO, 6.2 mi W El Lobo, 3 (TCWC); 7.6 mi W El Lobo, 7 (TCWC); 1 mi W Santa Inés, 4,500 ft, 22 (TCWC). *Sample 13* (Group III): QUERETARO, 3.6 mi SW Amealco, 1 (TCWC); 3.9 mi SW Amealco, 1 (TCWC); 8.6 mi SE, 1.1 mi E Amealco, 3 (TCWC); 8.6 mi SW, 1.1 mi E Amealco, 1 (TCWC); 11 mi N Amealco, 1 (TCWC). *Sample 14* (Group III): QUERETARO, 3.6 mi SW Amealco, 1 (TCWC); 8.2 mi N, 1.8 mi W Amealco, 5 (TCWC); 8.6 mi SW, 1.1 mi W Amealco, 3 (TCWC); 0.2 mi S Mezquititlán, 5 (TCWC); MEXICO, 2.2 mi S México–Querétaro border, 1 (TCWC). *Sample 17* (Group III): HIDALGO, Zacuáltipan, 2 (UMMZ); 3.1 mi N Zacuáltipan, 6,700 ft, 10 (TCWC); 3.4 mi N Zacuáltipan, 6,400 ft, 9 (TCWC); Molango, 1 (UMMZ); 0.3 mi N Molango, 6 (TCWC). *Sample 18* (Group III): HIDALGO, 2 mi N Mineral del Monte, 8,300 ft, 5 (TCWC). *Sample 20* (Group III): HIDALGO, 3.5 mi W El Susto, 6 (TCWC). *Sample 23* (no karyotypic data): MICHOACAN, Uruapan, 13 (UMMZ); 5 mi S Uruapan (Tzaraque Falls), 5,000 ft, 9 (UMMZ); Tzararacua, 7 (UMMZ). *Sample 25* (Group III): TLAXCALA, 2 mi E Teacalco, 1 (UMMZ); 2 km W Teacalco, 8,400 ft, 5 (TCWC); 8.8 mi E, 0.5 mi S Apizaco, 7,900 ft, 1 (TCWC); 8.8 mi E, 1 mi S Apizaco, 7,900 ft, 17 (TCWC). *Sample 28* (Group III): VERACRUZ, 2 km S Jalapa, 2 (TCWC); 3.6 mi N Jilotepec, 8 (TCWC); Perote, 5 (UMMZ); Jalacingo, 1 (UMMZ); PUEBLA, Teziutlan, 1 (UMMZ).

*Peromyscus boylii rowleyi.*—*Sample 1* (Group I): CHIHUAHUA, 3 mi SW Santa Bárbara, 11 (TCWC); 3.7 mi SW Santa Bárbara, 6 (TCWC). *Sample 8* (group I): AGUASCALIENTES, 0.5 mi W Rincón de Romos, 2 (UMMZ); 6.6 mi W Rincón de Romos, 10 (TCWC). *Sample 15* (Group I): HIDALGO, 1 mi E Jonacapa, 2 (TCWC); 2.3 mi E. Jonacapa, 2 (TCWC); 5.6 mi S Zimapán, 2 (TCWC); 10.9 mi S Zimapán (Hwy 85), 1 (TCWC); 4.4 mi N Trancas, 2 (TCWC). *Sample 16* (Group I): HIDALGO, 5.4 mi SE, 3.2 mi S Ixmiquilpan, 4 (TCWC); 21.3 mi W Ixmiquilpan, 6 (TCWC); 15.4 mi W Ixmiquilpan, 3 (TCWC); 7 mi W Ixmiquilpan, 2 (TCWC).

*Peromyscus boylii sacarensis.*—*Sample 34* (Group II): HONDURAS, FRANCISCO MORAZAN, El Hatillo, 3 (TCWC).

*Peromyscus boylii* ssp.—*Sample 3* (no karyotypic data): DURANGO, 3 mi S Tepehuanes, 5,840 ft, 10 (MSU); 6 mi WNW Chinacostes, 7,100 ft, 2 (MSU). *Sample 4* (no karyotypic data): DURANGO, 1.5 mi W San Luis, 750 ft, 2 (MSU), 12 (UMMZ). *Sample 5* (no karyotypic data): DURANGO, 10 km SSE Llano Grande, 2,650 m, 14 (MSU); Margaritas, 28 mi S, 17 mi W Vicente Guerrero, 2 (MSU); Hacienda Coyotes, 8,120 ft, 3 (MSU); Cerro Huehuento, 2 (UMMZ). *Sample 6* (no karyotypic data): DURANGO, 2 mi N Pueblo Nuevo, 6,000 ft, 2 (MSU); 25 mi NNW El Salto, 1 (UMMZ); ZACATECAS, 15 km SW Valparaíso, 2,250 m, 3 (MSU); 10 km W San Juan Capistrano, 2,900 m, 1 (MSU). *Sample 10* (Group IV): NAYARIT, Ocota (25°51′N, 104°13′W), 4 (TCWC). *Sample 24* (Group IV): MICHOACAN, Dos Aguas, 7,100 ft, 2 (UMMZ); 2 mi W Dos Aguas, 1 (UMMZ); 6.3 mi WSW Dos Aguas, 8,000 ft, 1 (TCWC), 3 (UMMZ); 7.4 mi WSW Dos Aguas, 1 (TCWC).

*Additional specimens examined.*—MICHOACAN, 4.6 mi W Juiquilpan, 1 (TCWC); 9.7 mi S Los Azufres, 2 (TCWC); 8.4 mi N Los Reyes, 2 (TCWC).