

Distribution and Systematics
of *Peromyscus*
(Mammalia: Rodentia)
of Nayarit, Mexico

MICHAEL D. CARLETON, DON E. WILSON,
ALFRED L. GARDNER and MICHAEL A. BOGAN

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ABSTRACT

Carleton, Michael D., Don E. Wilson, Alfred L. Gardner, and Michael A. Bogan. Distribution and Systematics of *Peromyscus* (Mammalia: Rodentia) of Nayarit, Mexico. *Smithsonian Contributions to Zoology*, number 352, 46 pages, 14 figures, 8 tables, 1982.—Distributional patterns, ecological data, and the systematic status of *Peromyscus maniculatus*, *P. boylii*, *P. simulus*, *P. madrensis*, *P. pectoralis*, *P. spicilegus*, and *P. melanophrys* are presented for the state of Nayarit, Mexico. The *Peromyscus boylii* species group is accorded special emphasis because of the uncertainty regarding the relationships and taxonomic level of forms included within it. On the basis of morphometric analyses of external and cranial measurements, examination of chromosomal preparations, and documentation of sympatry, *madrensis*, *simulus*, and *spicilegus* are considered species distinct from *boylii*, instead of subspecies thereof. In Nayarit, *Peromyscus simulus* is confined to the coastal-plain region (sea level to 100 m); *Peromyscus madrensis* occupies the Tres Marias Islands; *Peromyscus spicilegus* inhabits intermediate montane zones (100 to 1600 m) but has been found as high as 2100 m; and *Peromyscus boylii* occurs at high elevations (1900 to 2100 m) in the eastern mountains.

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Distribution and Systematics of *Peromyscus* (Mammalia: Rodentia) of Nayarit, Mexico

*Michael D. Carleton, Don E. Wilson,
Alfred L. Gardner, and Michael A. Bogan*

Introduction

The state of Nayarit, situated along coastal west-central Mexico approximately from 21° to 23° N latitude, encloses an area of striking topographic diversity, including broad expanses of coastal plain near sea level as well as western portions of the Sierra Madre Occidental, where ridges and peaks exceed 2000 meters. In north-eastern Nayarit, the western flanks of the Sierra Madre Occidental rise precipitously above the coastal plains, but in the central sector, south of the Rio Grande de Santiago, mountainous terrain merges more gradually into coastal plain. In the region south of San Blas, foothills closely border the seacoast, pinching off the broad coastal plain that dominates southern Sinaloa and northwestern Nayarit. The Rio Acaponeta, Rio San Pedro, and Rio Grande de Santiago (Figure 1) form the principal drainage of the Sierra Madre Occidental in Nayarit, and their tributaries delimit numerous minor mountain systems. As expected, Nayarit, with its pronounced topographic relief and coastal exposure, harbors a variety of environments and distinctive biotic zones. Following

the classificatory arrangement of life zones by Goldman (1951), Nayarit contains elements of the Lower Tropical, arid and humid subdivisions of the Upper Tropical, Lower Austral, Upper Austral, and Transition zones. Along river valleys, lower-elevational plant communities deeply penetrate the mountainous interior of Nayarit and interdigitate with upper vegetational belts in a complicated pattern. In view of its complex physiography, Nayarit occupies an important position in understanding patterns of mammalian distribution and problems of taxonomy in western Mexico, especially for small mammals of limited vagility.

In this report, we present information on the distribution and specific status of *Peromyscus* in Nayarit, based upon new collections made by staff of the U.S. Fish and Wildlife Service (also see Fisher and Bogan, 1977; Gardner, 1977; Bogan, 1978; and Diersing and Wilson, 1980). Recent studies on the *Peromyscus boylii* species group in western Mexico reflect an uncertainty regarding the relationships and taxonomic level of forms included within it (for example, Hooper, 1968; Lee et al., 1972; Schmidly and Schroeter, 1974; Kilpatrick and Zimmerman, 1975; and Carleton, 1977, 1979). The *boylii* species group realizes some of its greatest diversity along the western coast of

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Mexico, and much of this diversity is demonstrated by populations occurring in the state of Nayarit. The type-localities of *madrensis* Merriam, 1898b (Maria Madre Island), and *simulus* Osgood, 1904 (San Blas), are in Nayarit, and the type-locality of *spicilegus* Allen, 1897 (Mineral San Sebastian), lies in Jalisco just across the southern border of Nayarit. Moreover, populations assignable to either *spicilegus*, *rowleyi*, or *levipes* might be expected to occur in the mountainous regions of eastern Nayarit. All five of these taxa are pertinent to any discussion of the *boylei* complex. Accordingly, our objectives are: (1) to document the species of *Peromyscus* occurring in the state of Nayarit; (2) to review the relationships within the *Peromyscus boylei* species group based on the Nayarit collections housed in the National Museum of Natural History; and (3) to provide additional information on the geographic and ecologic range of each of these species.

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Materials and Methods

All specimens reported herein are housed in the National Museum of Natural History (under the designation USNM for the former United States

National Museum). The majority resulted from recent (1975–1977) surveys of Nayarit conducted by personnel of the Fish and Wildlife Service, but some specimens were collected during the Nelson and Goldman expeditions in Mexico (see Goldman, 1951). Animals generally were processed as conventional study skins and skulls; complete skeletons, whole carcasses preserved in 10% formalin, and karyotypes were also prepared. Fluid-preserved specimens were used to examine male accessory reproductive glands and glandes penes and to determine the number of mammary glands.

In accordance with Carleton's (1980) suggestions, we treat *banderanus* as a species of *Osgoodomys* and omit it from the formal species' accounts. This mouse has been collected at three sites in southwestern Nayarit: Chacala, 30 m, 5; Navarrete, 50 m, 1; Paso de Soquilpa, 100 m, 4. These coastal, lowland localities fit the distributional pattern of *banderanus* as seen in other parts of western Mexico, where it is a coastal-plain species only penetrating the interior along river valleys and inland basins.

The 17 samples included in the numerical analyses are listed below with their locality, sample size, and an identifying abbreviation. Additional specimens examined and complete locality information are provided in the species' accounts (also see Table 1). Specific nomenclature for taxa of the *boylei* species group follows Carleton (1977).

- Peromyscus boylei*: Ocota Airstrip, 37 (= BOYOCO); Santa Teresa, 10; and 13 km SW Santa Teresa, 31 (= BOYSTE).
P. madrensis: Tres Marias Islands, Maria Cleofas, 36 (= MADCLE); Maria Madre, 18 (= MADMAD); Isla San Juanito, 17 (= MADJON).
P. maniculatus: El Refilion, 71 (= MANREF); 2 mi E San Pedro Lagunillas, 55 (= MANLAG).
P. melanophrys: Arroyo de Jiguite, 2 (= MELANO).
P. pectoralis: Arroyo de Jiguite, 4; and 1.8 mi NW Coapan, 3 (= PECTOR).
P. simulus: 1 mi S Cuautla, 59 (= SIMCUA); San Blas and vicinity, 7 (= SIMSAN); Teponahuaxtla, 10 (= SIMTEP).
P. spicilegus: 8 mi S Ahuacatlan, 29 (= SPIAHU); Chacala, 26 (= SPICHA); El Refilion, 37 (= SPIREF); 2 mi E Jalcocotan, 35 (= SPIJAL); Mesa del Nayar, 8; and 2 mi WNW Mesa del Nayar, 5 (= SPINAY).

The occurrence of a mesoloph, mesolophid, and ectolophid was recorded for specimens of the following six population samples.

Peromyscus boylii: Ocota Airstrip, 38; 13 km SW Santa Teresa, 44.

P. madrensis: Tres Marias Islands, 37.

P. simulus: 1 mi S Cuautla, 56.

P. spicilegus: El Refilion, 36; 2 mi E Jalcocotan, 36.

Three states of complexity of these enamel ridges were scored for the first upper and first lower molars of the right side, and their occurrence expressed as a percentage of the total population sample. The states were defined as (0) loph(id)s absent or present only as a small, poorly-defined spur, (1) loph(id)s present and partially extending to the margin of the tooth, (2) loph(id)s present and completely extending to the margin of the tooth, often terminating as a conspicuous style(id).

Twenty-three measurements, four of the skin and 19 of the skull, were recorded to characterize the morphology of the population samples. The total, tail, hind foot, and ear lengths were transcribed from the skin tag and rounded to the nearest 1.0 mm; dimensions of the skull were measured to the nearest 0.01 mm using a craniometer (Anderson, 1968). Specimens exhibiting any trace of gray juvenal pelage were excluded from statistical analyses. The measurements taken (and their definitions where necessary) were (1) total length of skin, (2) length of tail, (3) length of hind foot, (4) length of ear, (5) greatest length of skull, (6) condyloincisive length, (7) length of auditory bulla, (8) postpalatal length (from the anterior margin of the mesopterygoid fossa to the medial and posterior border of the basioccipital), (9) length of mesopterygoid fossa (from the posterior tip of the pterygoid process to the anterior margin of the fossa), (10) palatal length (from the posterior margin of the incisive foramina to the anterior border of the mesopterygoid fossa), (11) length of incisive foramina, (12) alveolar length of maxillary toothrow, (13) greatest zygomatic breadth, (14) mastoidal breadth (distance between the lateral borders of the mastoid processes), (15) greatest breadth across mo-

lars (distance between the labial margins of the second upper molars), (16) postdental palatal breadth (taken at the constriction of the palate behind the molars and in front of the lateral pterygoid fossae), (17) greatest width of mesopterygoid fossa, (18) depth of braincase (taken from the skull in lateral view with the horizontal crosshair aligned on the tip of incisors and ventralmost curvature of the auditory bulla; distance from that level to the dorsalmost contour of the braincase), (19) breadth of braincase (taken behind the squamosal root of the zygomatic arches), (20) least interorbital width, (21) rostral breadth (distance between the lateral projections of the incisive capsules), (22) nasal length, and (23) rostral length.

Preparation of chromosomal material, definition of fundamental number (FN), and descriptive terminology for chromosomal morphology follow Patton (1967). Specimens were karyotyped from the following localities.

Peromyscus boylii: Ocota Airstrip; 2♂, 1♀; 13 km SW Santa Teresa, 1♀.

P. madrensis: Tres Marias Islands, Maria Cleofas, 5♂, 7♀; Maria Madre, 3♀; Isla San Juanito, 7♀.

P. maniculatus: 8 mi S Ahuacatlan, 2♂, 2♀; 1.8 mi NW Coapan, 1♂; 2 mi E Jalcocotan, 2♂; 2 mi E San Pedro Lagunillas, 1♂.

P. melanophrys: Arroyo de Jiguite, Rio Santiago, 4♂, 2♀; Mesa del Nayar, 1♂, 1♀.

P. pectoralis: Arroyo de Jiguite, 1♂, 1♀; 1.8 mi NW Coapan, 3♂, 1♀.

P. simulus: 4 km S Aticama, 1♂; 4 km N Cuautla, 1♀; 1.2 mi S El Casco, Rio Chilte, 2♂, 2♀.

P. spicilegus: Agua Escondida, 2♂, 3♀; 8 mi S Ahuacatlan, 5♂, 4♀; Arroyo de Jiguite, 2♂, 2♀; Arroyo la Taberna, 2 mi WNW Mesa del Nayar, 1♀; Mesa del Nayar, 3♂, 3♀; Chacala, 2♂, 6♀; 1.8 mi NW Coapan, 1♂, 2♀; 10 km N Jala, 2♀; 2 mi E Jalcocotan, 6♂, 5♀; 1 km S La Villita, 4♂, 2♀; 13 km SW Santa Teresa, 1♀; Tempiste, 2♂.

The Biomedical Computer Programs (BMD; Dixon, 1973) and the Numerical Taxonomy System of Multivariate Statistical Programs (NTSYS; Rohlf et al., 1972) were used for statistical analyses. Basic data description (means and variances) was done with BMD01D. Character means of each sample thus obtained were stan-

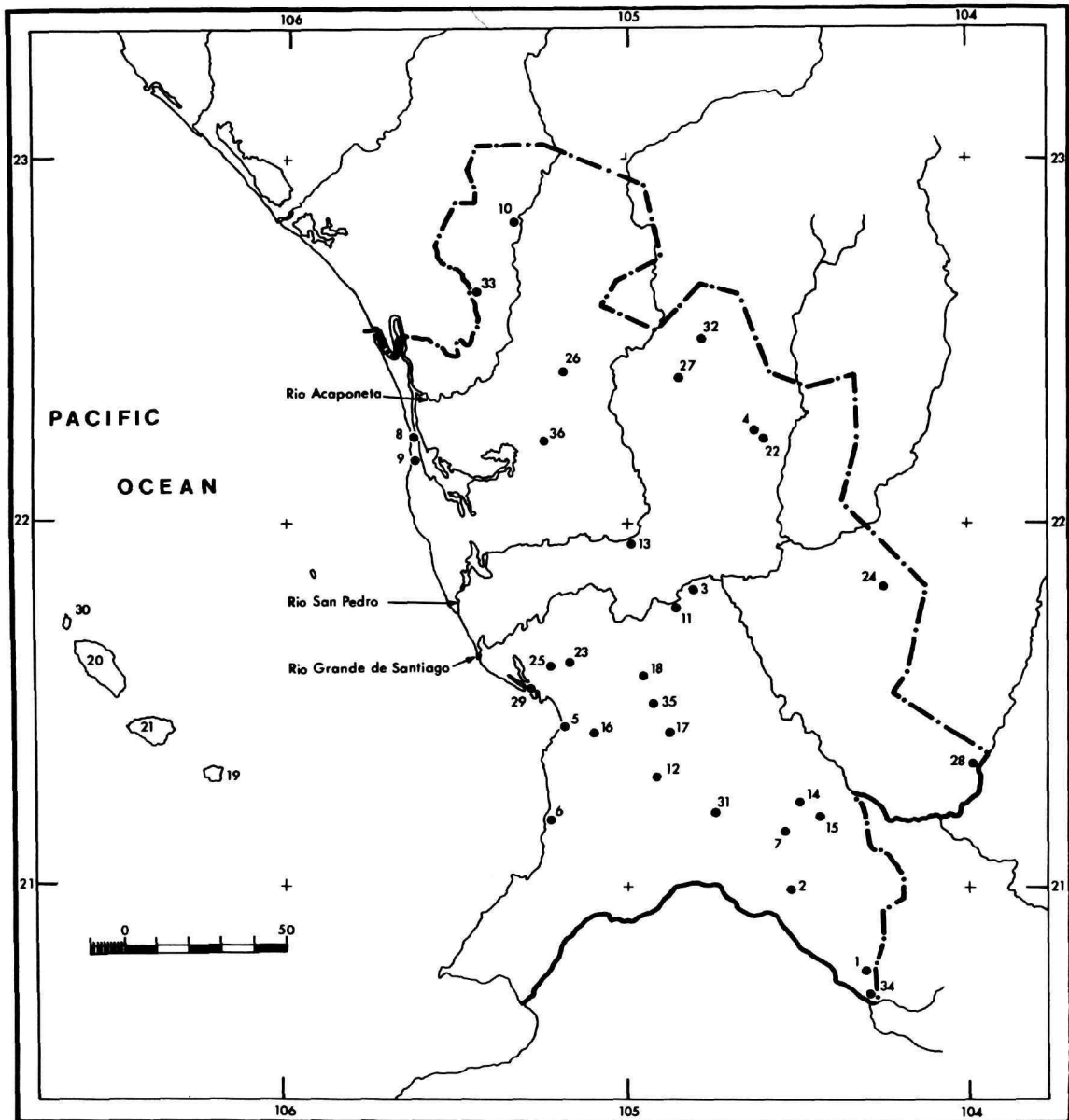


FIGURE 1.—State of Nayarit, Mexico. (Numbers refer to localities given in Table 1.)

standardized (means of zero, standard deviation of one) and used to compute matrices of average distance and correlation coefficients among the samples (or OTU's). The unweighted pair-group

method, using arithmetic averages (UPGMA), was used to cluster the OTU's, and cophenetic correlation coefficients were calculated. Standardized character means also were used to pro-

TABLE 1.—Gazetteer of collecting localities (see Figure 1)

Locality	Coordinates	Elevation (meters)
1. Agua Escondida	20°46'/104°19'	1380
2. Ahuacatlan, 8 mi (by rd) S	20°58'/104°28'	1500
3. Arroyo Jiguite, Rio Grande de Santiago	21°49'/104°48'	100
4. Arroyo Taberna, 2 mi WNW Mesa del Nayar	22°15'/104°40'	1200
5. Aticama, 4 km S	21°27'/105°11'	50
6. Chacala	21°10'/105°13'	30
7. Coapan, 1.8 mi (by rd) NW	21°09'/104°29'	1560
8. Cuautla, 4 km N	22°15'/105°38'	0
9. Cuautla, 1 mi S	22°12'/105°38'	0
10. Cucharas, Rio Acaponeta	22°48'/105°19'	100
11. El Casco, 1.2 mi (by rd) S, Rio Chilte	21°45'/104°51'	60
12. El Refilion	21°18'/104°54'	850
13. El Venado, 3.5 mi (by rd) E	22°57'/104°57'	100
14. Estanzuela	21°16'/104°28'	1380
15. Jala, 10 km N	21°11'/104°25'	1600
16. Jalcocotan, 2 mi E	21°29'/105°04'	500
17. Jalisco	21°26'/104°54'	1000
18. La Villita	21°35'/104°56'	760
19. Maria Cleofas Island	21°18'/106°12'	0-380
20. Maria Madre Island	21°36'/106°34'	0-600
21. Maria Magdalena Island	21°25'/106°24'	0-460
22. Mesa del Nayar	22°12'/104°39'	1300
23. Navarrete	21°38'/105°06'	50
24. Ocota Airstrip	21°50'/104°13'	1900
25. Paso de Soquilpa, 8.8 mi E San Blas	21°36'/105°11'	100
26. Pedro Pablo	22°25'/105°10'	820
27. Rancho Viejo	22°25'/104°51'	2100
28. Rancho Zapotito	21°20'/103°58'	1100
29. San Blas	21°32'/105°17'	0
30. San Juanito Island	21°43'/106°39'	0-40
31. San Pedro Lagunillas, 2 mi E	21°12'/104°43'	1300
32. Santa Teresa	22°29'/104°46'	2100
33. Tacote, 1.4 mi (by rd) N	22°38'/105°27'	15
34. Tempiste, Rio Ameca	20°42'/104°18'	840
35. Tepic	21°30'/104°53'	1000
36. Teponahuxtla	22°13'/105°11'	50

duce a character correlation matrix that was subjected to a principal component analysis. Overall discrimination among the groups was examined by subjecting the raw data for each a priori recognized group to a stepwise discriminant analysis (BMD07M). Plots of the groups onto the two canonical variates were obtained from this analysis. Evaluation of forms occurring in sympatry was made with two-group discriminant analyses (BMD04M). Computer programs were

first applied to all 17 population samples of *Peromyscus* from Nayarit and subsequently to the 13 samples of the *boylii* species group. We have not shown the results of all the analyses because of their redundancy. The computer analyses were done either on the IBM 360/65 at the U.S. Department of Interior's Washington Computer Center or on the Honeywell belonging to the Smithsonian Institution. All statistical methods are discussed in Neff and Marcus (1980).

The *Peromyscus boylii* Species Group in Western Mexico

Since Osgood (1909) first defined the *Peromyscus boylii* group, it has proven to be one of the most difficult complexes in the genus in terms of delimiting the number of biological species. Our comprehension of the relationships and level of differentiation of forms included in it has been hindered by the apparent complexity of their distributions, the subtleness of their morphological differentiation, and a surfeit of available names. During the past 20 years, many contributions have appeared that substantially modified some of Osgood's (1909) subspecific and specific arrangements and that seriously questioned the correctness of others. Because of the confusing array of names involved and their sometimes inconsistent or misleading application in the literature, it is appropriate to provide first a historical review of the systematic treatment of the *boylii* species group and the evidence bearing upon its intrarelationships. Our discussion focuses on taxa whose distribution is localized in western Mexico (namely *madrensis*, *simulus*, and *spicilegus*); however, for purposes of clarity and context, it must also encompass forms (such as *rowleyi*, *levipes*, *evides*, and *aztecus*) whose taxonomy is inextricably linked with the western Mexican populations.

In preparing his taxonomic study of the genus *Peromyscus*, Osgood confronted an imposing number of described forms, 167 alone named after 1885 by his own count (1909). Prior to his revision, *Peromyscus boylii* and its relatives were represented by some 22 taxa, 14 of them described as species. Osgood's delineation of the "*Peromyscus boylii* group" reduced that number to four, with a majority of the former species placed in synonymy under *boylii* (Table 2). Proceeding via a southerly transect through western Mexico, his chain of intergrading subspecies of *boylii* included *rowleyi*, *spicilegus*, *simulus*, *levipes*, and *evides*; a distinctive insular race, *madrensis*, occurred off the coast of Nayarit. Although maintained as separate species, *hylocetes* and *oaxacensis* were viewed by Osgood as somehow part of the same complex,

TABLE 2.—Classifications of the *Peromyscus boylii* species group

OSGOOD, 1909	
<i>boylii</i> (Baird) (incl. <i>attwateri</i> , <i>aztecus</i> , <i>evides</i> , <i>levipes</i> , <i>madrensis</i> , <i>rowleyi</i> , <i>simulus</i> , and <i>spicilegus</i>)	
<i>hylocetes</i> Merriam	
<i>oaxacensis</i> Merriam	
<i>pectoralis</i> Osgood	
HALL AND KELSON, 1959	
<i>boylii</i> (Baird) (incl. <i>attwateri</i> , <i>aztecus</i> , <i>cordillerae</i> , <i>evides</i> , <i>glasselli</i> , <i>levipes</i> , <i>madrensis</i> , <i>rowleyi</i> , <i>sacarensis</i> , <i>simulus</i> , <i>spicilegus</i> , and <i>utahensis</i>)	
<i>hylocetes</i> Merriam	
<i>oaxacensis</i> Merriam	
<i>pectoralis</i> Osgood	
<i>perfulvus</i> Osgood	
<i>polius</i> Osgood	
HOOPER, 1968	
<i>aztecus</i> (Saussure)	
<i>boylii</i> (Baird)	
<i>evides</i> Osgood	
<i>hondurensis</i> Goodwin	
<i>hylocetes</i> Merriam	
<i>oaxacensis</i> Merriam	
<i>pectoralis</i> Osgood	
<i>polius</i> Osgood	
CARLETON, 1977, 1979	
<i>attwateri</i> Allen	
<i>aztecus</i> (Saussure) (incl. <i>cordillerae</i> , <i>evides</i> , <i>hylocetes</i> , and <i>oaxacensis</i>)	
<i>boylii</i> (Baird) (incl. <i>ambiguus</i> , <i>baetae</i> , <i>glasselli</i> , <i>levipes</i> , <i>rowleyi</i> , <i>sacarensis</i> , and <i>utahensis</i>)	
<i>madrensis</i> Merriam	
<i>pectoralis</i> Osgood	
<i>polius</i> Osgood	
<i>simulus</i> Osgood	
<i>spicilegus</i> Allen	
<i>stephani</i> Townsend	
<i>winkelmanni</i> Carleton	
HALL, 1981	
<i>attwateri</i> Allen	
<i>aztecus</i> (Saussure)	
<i>boylii</i> (Baird) (incl. <i>ambiguus</i> , <i>baetae</i> , <i>cordillerae</i> , <i>glasselli</i> , <i>levipes</i> , <i>madrensis</i> , <i>rowleyi</i> , <i>sacarensis</i> , <i>simulus</i> , <i>spicilegus</i> , and <i>utahensis</i>)	
<i>evides</i> Osgood	
<i>hylocetes</i> Merriam	
<i>oaxacensis</i> Merriam	
<i>pectoralis</i> Osgood	
<i>polius</i> Osgood	
<i>stephani</i> Townsend	
<i>winkelmanni</i> Carleton	

fitting into *spicilegus* and the other subspecies through *aztecus* and *evides*.

In reading Osgood's (1909) species accounts, it is readily apparent that he regarded his treatment of the *boylei* complex as inconclusive, a tentative taxonomic framework to be assessed further by additional collections. He suspected that two species were intermixed in some of his samples (e.g., series of *boylei levipes*) and predicted that some of his "races" of *boylei* (e.g., *aztecus* and *levipes*) one day would be discovered sympatrically (a prophesy repeatedly fulfilled after 50 years—Alvarez, 1961; Hall and Dalquest, 1963; Musser, 1964; Carleton, 1977). In view of his skepticism, it is not clear why he rendered certain taxonomic decisions regarding the group, unless one weighs them against the developing evolutionary viewpoints of his period.

Osgood undertook the revision of *Peromyscus* during a time of transition in the species concept, a change from that of the Linnaean species to the polytypic species and an awareness of geographic variation. Indeed, his work on *Peromyscus* heralded the emergence of the polytypic species in the field of systematic mammalogy and still stands as a seminal effort on geographic variation in mammals. Thus, he noted the existence of "intergrades" or of certain samples "approaching" others in morphology and searched for breaks "in the continuous series of definable forms . . ." (Osgood, 1909:157). Osgood found evidence of "breaks" for *levipes* and *hylocetes* and *levipes* and *oaxacensis* by documenting their co-occurrence at certain localities, and accordingly, he retained *hylocetes* and *oaxacensis* as species. Lacking such documentation for the remaining "definable forms," he relegated them to subspecies of *boylei* (actually he failed to recognize instances of sympatry in some of his locality samples, see Hall and Dalquest, 1963; Carleton, 1977). Osgood (1909:159) interpreted variation in the *boylei* group as indicative of varying degrees of reproductive isolation: "Possibly here is another example of two subspecies [in this case, *levipes* and *oaxacensis*] of the same group occurring together, for *levipes* appears to intergrade with *spicilegus*,

spicilegus with *evides* and *aztecus*, and quite probably *aztecus* with *oaxacensis*." Moreover, he seemed to emphasize variation in pelage color as evidence of intergradation. For example, he remarked (1909:146), "Most Mexican specimens of *rowleyi* show slight tendencies toward *spicilegus*, being slightly deeper colored," and again (p. 151), "The type of *simulus*, which was selected with particular reference to its cranial characters, is somewhat darker and nearly the same color as *spicilegus*. It may therefore be regarded as slightly intermediate." Today, however, the suite of cranial traits is now recognized as diagnostic for *simulus* and *spicilegus* and others in the *boylei* group, but coat color in *Peromyscus* is regarded as particularly subject to convergence where two closely related species occupy similar habitat.

Osgood's (1909) arrangement of the *boylei* group remained essentially intact over the next half-century. Hall and Kelson's (1959) classification repeated that of Osgood except for the accommodation of newly described subspecies of *boylei* and a new species (Table 2). In 1945, Osgood named *perfulvus* and provisionally allied it to the *boylei* group, but Hooper (1955) later reassigned *perfulvus* to the *melanophrys* group. Hoffmeister (1951) suggested the transfer of *polius* from the *truei* group, where Osgood (1909) originally placed it, to the *boylei* group.

Information resulting from more recent field collections indicated the need for further reassessment of Osgood's (1909) taxonomic scheme. Alvarez (1961), Hall and Dalquest (1963), and Musser (1964) reported the coexistence of *levipes* and *aztecus* at several localities in eastern Mexico. In western Mexico, *evides* and *levipes* were found in sympatry (Hooper, 1961; Musser, 1964), as were *spicilegus* and *levipes* and *spicilegus* and *hylocetes* (Hooper, 1955). In addition, Hooper (1955) suspected that two forms were confused under the name of *simulus* in the coastal lowlands of Sinaloa and Nayarit, and Baker and Greer (1962) cited the strong differentiation of *simulus* from populations of *boylei* occurring at higher elevations (*spicilegus* and *rowleyi*).

In his synopsis of the genus *Peromyscus*, Hooper

(1968) incorporated some of these findings into a revised classification of the *boylei* species group (Table 2). He recognized *aztecus* and *evides* as species distinct from *boylei* and reiterated Osgood's (1909) notion that the *boylei* complex embraced morphologically different populations having differing levels of interfertility. His disposition of *simulus* and *spicilegus*, forms whose distinctiveness was also supported by distributional and morphological arguments, is not wholly clear, but he did not list them as species.

Hooper's (1968) perceptive overview served to identify problem areas within the *boylei* group and, consequently, to stimulate further research. Musser (1969) corroborated Hooper's (1968) opinion that *hondurensis* was only a geographic variant of *oaxacensis*. Lawlor (1971) allocated *stephani*, a species hitherto classified in the subgenus *Haplomylomys*, to the *boylei* species group, and Schmidly (1973) raised *attwateri* from a subspecies of *boylei* to specific status. A notable development in the past decade is the use of biochemical and karyologic data to analyze relationship in the *boylei* group (Avise et al., 1974; Kilpatrick and Zimmerman, 1975; Lee et al., 1972; Schmidly, 1973; Schmidly and Schroeter, 1974).

Based on evidence from distributional patterns, anatomy of the glans penis, and morphometric analyses, Carleton (1977, 1979) proposed several changes in the composition of the *boylei* group (Table 2). In regard to forms inhabiting parts of Nayarit, he suggested that *madrensis*, *simulus*, and *spicilegus* were species distinct from *boylei* proper. In raising *spicilegus* to species rank, Carleton (1977) redescribed its range to exclude certain populations in Chihuahua, Durango, Sinaloa, and Nayarit, which represented the western extension of true *boylei* (that is, conspecific with *rowleyi* and *levipes*), and to include samples in Michoacan, which had been identified as *evides* (Osgood, 1909; Hall and Kelson, 1959; Hooper, 1968). *Peromyscus simulus*, apparently restricted to the coastal lowlands of Sinaloa and Nayarit, was viewed as sufficiently differentiated to warrant specific segregation from the populations of *boylei* inhabiting the Mexican highlands, although it is

clearly more closely related to *boylei* than to the geographically contiguous species *spicilegus*. The origin of populations on the Tres Marias Islands, *madrensis*, was obscure, but because its distinctiveness exceeded the range of variation observed within samples of either *boylei* or *spicilegus* from the mainland, Carleton (1977) reinstated it as a species pending further study.

Hall's (1981) recent classification (Table 2) basically repeats that of Hooper (1968).

In summary, a markedly different interpretation of propinquity within the *boylei* group has emerged since Osgood's (1909) study. Instead of a circuitously intergrading mosaic of subspecies, Osgood's *Peromyscus boylei* is believed to consist of at least six discrete species: *boylei* (including the subspecies *rowleyi* and *levipes* among others), *attwateri*, *simulus*, *madrensis*, *spicilegus*, and *aztecus* (with the races *cordillerae*, *evides* from Guerrero and Oaxaca, *hylocetes*, and *oaxacensis*). On the basis of their distribution and morphology, these species can be further sorted into two moieties, one consisting of *aztecus*, *spicilegus*, and *winkelmanni*, and the other of *boylei*, *attwateri*, *madrensis*, *simulus*, *stephani*, *pectoralis*, and perhaps *polius*. The morphology and distribution of specimens from Nayarit must be evaluated with regard to these alternative hypotheses.

MORPHOMETRIC ANALYSES.—In the distance phenogram using all 17 samples, examples of *maniculatus* are most dissimilar. The remaining samples are distributed among three clusters, associated primarily on the basis of size (Figure 2). The largest forms, *madrensis* and *melanophrys*, comprise one cluster; the smallest ones, *pectoralis* and *simulus*, form another; and intermediate-sized animals, *boylei* and *spicilegus*, constitute a third. The samples of each of the four *boylei*-group taxa cluster together; however, the heterogeneity of Osgood's (1909) *P. boylei* is demonstrated by the interspersed nature of his "races" of *boylei* among other species of *Peromyscus*.

The cohesiveness of the geographic samples of *boylei*, *simulus*, *madrensis*, and *spicilegus* is reaffirmed in the clustering exercise using only 13 OTU's (Figure 3). The two examples of *boylei* form a pair

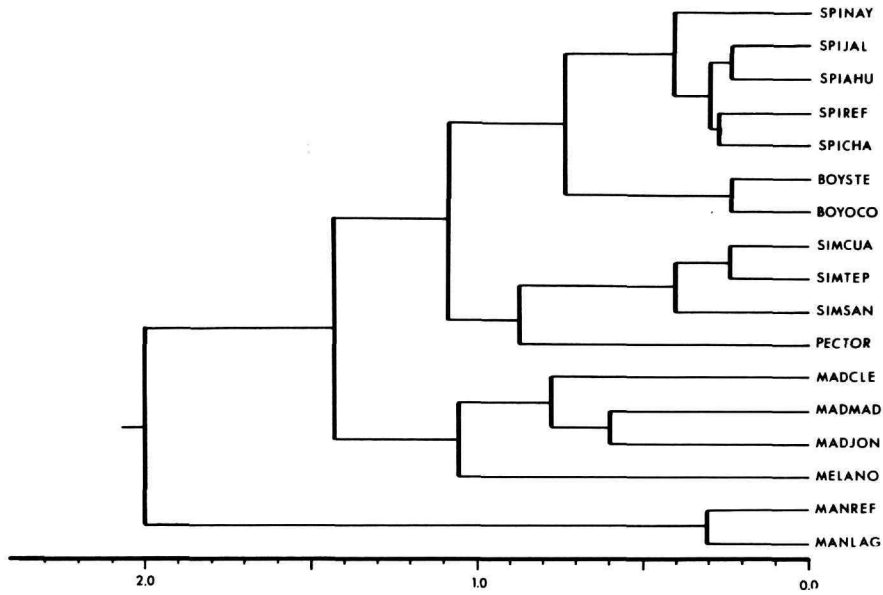


FIGURE 2.—Cluster analysis (UPGMA) of 17 population samples of *Peromyscus* generated from the distance matrix. (Coefficient of cophenetic correlation = 0.786; identification of sample abbreviations given in “Materials and Methods.”)

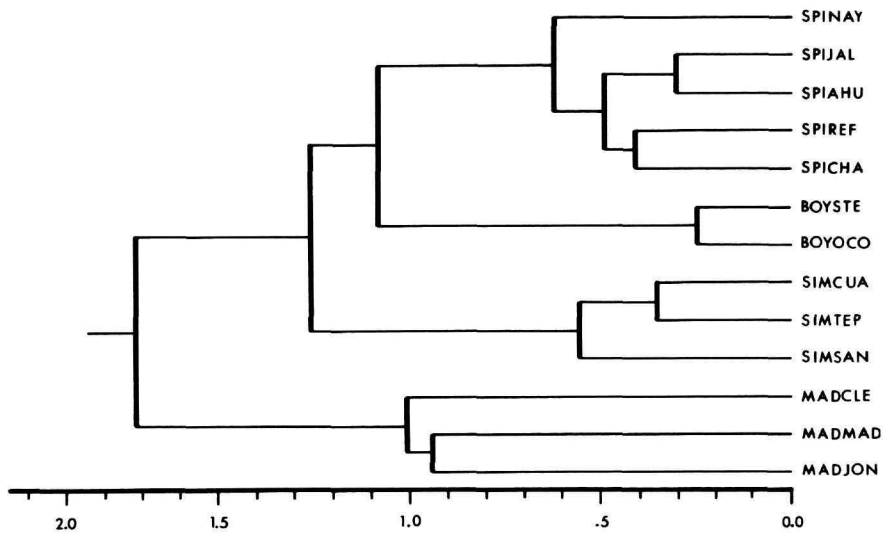


FIGURE 3.—Cluster analysis (UPGMA) of 13 population samples representing *Peromyscus boylii* species group generated from the distance matrix. (Coefficient of cophenetic correlation = 0.870; identification of sample abbreviations given in “Materials and Methods.”)

group with those of *spicilegus*, and *simulus* clusters with this complex at a still lower level of similarity. The three samples of *madrensis* are amalgamated at the lowest level of similarity. In addition, these three OTU's, each from a separate island, exhibit greater distance coefficients with respect to one another compared to those observed for samples of *boyllii*, *simulus*, or *spicilegus*; this result was apparent in every clustering analysis performed.

In the phenogram generated from the correlation matrix, the integrity of certain aggregations is lost. Representatives of *boyllii* again are paired with those of *spicilegus*, but examples of *simulus* and *madrensis* are intermixed in a separate pair group (Figure 4). This finding suggests a fundamental likeness in shape and proportion of the skulls of specimens of *simulus* and *madrensis*, although examples of the two fall at the opposite extremes of size range among *boyllii*-group forms in Nayarit ("Appendix"). The behavior of the

correlation coefficient as a measure of proportion has been noted by Eades (1965) and Minkoff (1965).

The association of OTU's in the principal component analysis resembles the results obtained in the clustering analysis. Four aggregations of population samples, which correspond to *boyllii*, *madrensis*, *simulus*, and *spicilegus*, are readily evident (Figure 5). The discontinuity between any pair of members within an aggregation is generally surpassed by that observed between members from different taxonomic samples. The largest within-group hiatus involves the sample of *madrensis* from Maria Cleofas. The samples are graded along the first principal component from small (examples of *simulus*) to large (those of *madrensis*); predictably, most dimensions are strongly correlated with principal component one (Table 3). The dispersion of samples on principal components two and three reflects conformational differences among the four taxa (Figure 5; Table 3). For example,

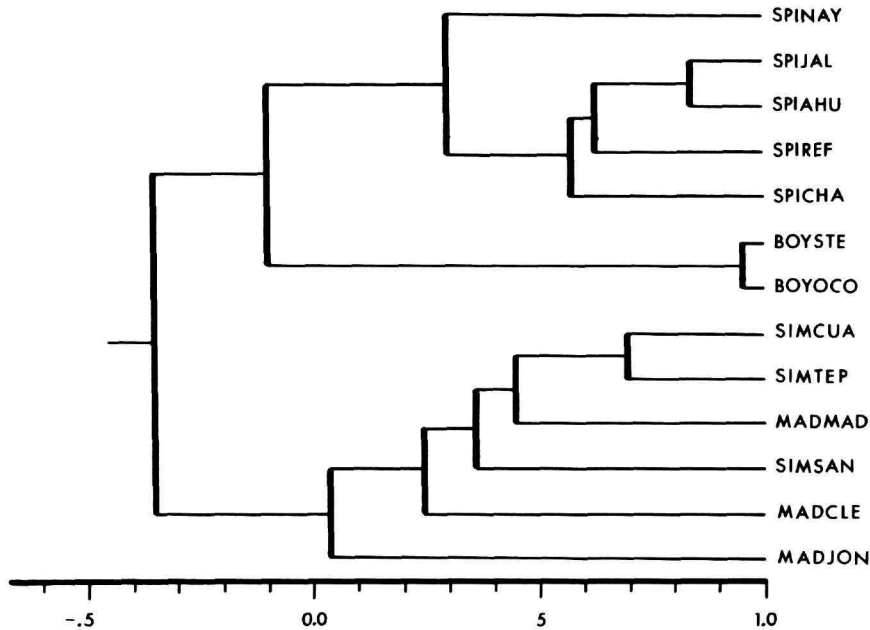


FIGURE 4.—Cluster analysis (UPGMA) of 13 population samples representing the *Peromyscus boyllii* species group generated from the correlation matrix. (Coefficient of cophenetic correlation = 0.899; identification of sample abbreviations given in "Materials and Methods.")

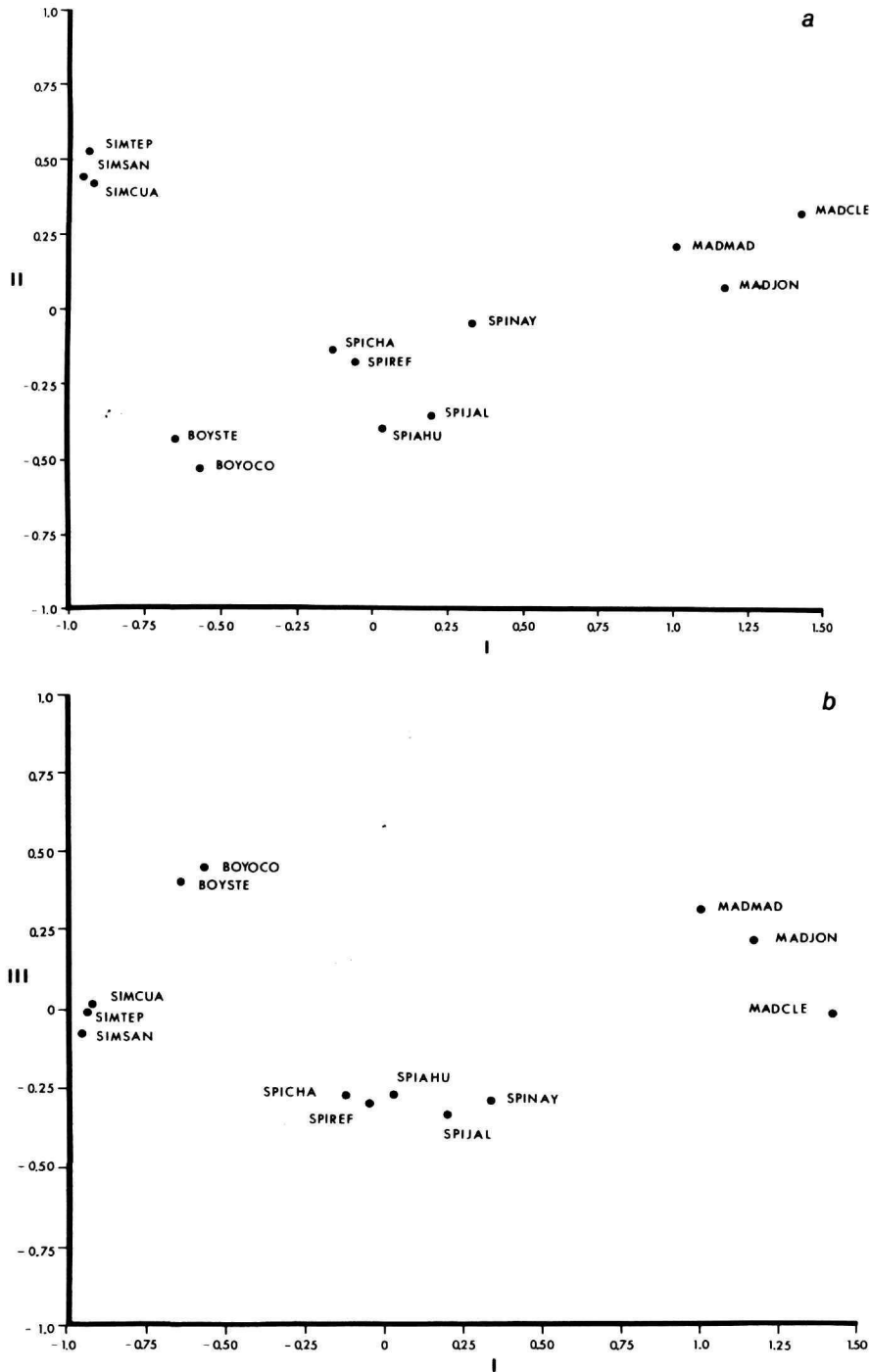


FIGURE 5.—Scatter plots of principal components using 13 population samples representing the *Peromyscus boylii* species group: a, I vs. II; b, I vs. III. (See Table 3; identification of sample abbreviations given in "Materials and Methods.")

TABLE 3.—Results of principal component analysis using samples of the *Peromyscus boylii* species group (see Figure 5)

	I	II	III
Eigenvalue	15.3	3.0	1.9
% total variance	66.6	13.2	8.1
Cumulative % variance	66.6	79.8	87.9
<i>Characters</i>			
Total length of skin	.92	.32	.08
Length of tail	.84	.37	.20
Length of hind foot	.86	.41	.19
Length of ear	-.05	-.38	.80
Greatest length of skull	.99	.06	.01
Condylolincisive length	.99	.07	-.02
Length of auditory bulla	.46	-.64	.53
Postpalatal length	.94	.27	.09
Length of mesopterygoid fossa	.74	.55	-.11
Palatal length	.66	-.43	-.24
Length of incisive foramen	.45	-.11	-.22
Alveolar length of maxillary toothrow	.77	-.51	-.26
Greatest zygomatic breadth	.94	.20	.00
Mastoidal breadth	.94	-.13	.14
Greatest breadth across molars	.96	.15	.07
Postdental palatal breadth	.88	.30	-.06
Breadth of mesopterygoid fossa	.23	-.52	-.72
Depth of braincase	.74	-.56	.19
Breadth of braincase	.81	-.52	-.05
Least interorbital width	.90	-.25	-.06
Rostral breadth	.92	.29	-.20
Nasal length	.94	-.22	-.11
Rostral length	.98	-.11	.12

specimens of *boylii* possess relatively longer pinnae, more inflated auditory bullae, and a broader and deeper braincase. Individuals of *spicilegus* have longer toothrows, absolutely and relatively smaller auditory bullae, and a longer, broader mesopterygoid fossa. Despite their larger size in most dimensions, examples of *madrensis* have relatively smaller pinnae, shorter toothrows, flatter skulls (in profile), and a narrower mesopterygoid fossa. Specimens of *simulus* agree with those of *madrensis* in many proportional features of their skulls.

In order to evaluate further the distinctiveness and integrity of the groups divulged in the cluster and principal component analyses, a stepwise discriminant function analysis was performed, and the first two canonical variates were extracted. We used nine groups (see Table 4),

mainly corresponding to the previously identified population samples, and all 23 variables. We omitted two samples of *simulus* because of inadequate sample sizes and combined the three samples of *madrensis* because many specimens lacked complete data.

The same four groups are clearly delineated (Figure 6). The 95 percent confidence limits of certain samples of *spicilegus* (SPIAHU and SPICHA) and one of *boylii* (BOYSTE) overlap slightly. Nevertheless, their centroids are significantly removed from one another, and the basic pattern of phenetic affinities is unambiguous. Furthermore, the few errors in classification based upon posterior probabilities occurred only between groups within *boylii* or *spicilegus*; no specimens of *simulus* or *madrensis* were misclassified (Table 4). The five variables that contributed most to classification function between groups are: length of hind foot, alveolar length of maxillary toothrow, length of auditory bulla, postdental palatal breadth, and greatest breadth of mesopterygoid fossa. Most of these variables also displayed relatively high correlation coefficients on the second and third principal components and accounted for much of the separation of samples along these axes (see Table 3).

The repeatedly demonstrated integrity of the geographic samples representing *boylii*, *simulus*, *madrensis*, and *spicilegus* intimates some degree of genetic homogeneity within each and raises the question of their level of reproductive isolation. Still, the fact that a battery of multivariate taxonomic programs can consistently distinguish between groups of specimens does not qualify as final, or even strongly persuasive, proof of their reality as biological species. Conceivably, the same results could obtain within a species whose range encompasses abrupt environmental gradients and, therefore, exhibits steep clinal variation. The existence of pronounced vertical relief and sharply defined biotic zones within Nayarit meets this requirement and establishes such a possibility as an explanation for the variation observed within Osgood's (1909) *P. boylii*. A consideration of other lines of evidence is necessarily warranted.

TABLE 4.—Identification of specimens into groups based upon posterior probabilities of classification

Sample	Number of specimens classified into group									
	N	SPIAHU	SPINAY	SPICHA	SPIREF	SPIJAL	SIMCUA	BOYOCO	BOYSTE	MADREN
SPIAHU	29	22	0	4	0	3	0	0	0	0
SPINAY	8	0	5	0	1	2	0	0	0	0
SPICHA	22	2	1	18	0	1	0	0	0	0
SPIREF	28	0	2	1	25	0	0	0	0	0
SPIJAL	35	5	3	1	1	25	0	0	0	0
SIMCUA	50	0	0	0	0	0	50	0	0	0
BOYOCO	37	0	0	0	0	0	0	30	7	0
BOYSTE	31	0	0	0	0	0	0	7	24	0
MADREN	29	0	0	0	0	0	0	0	0	29

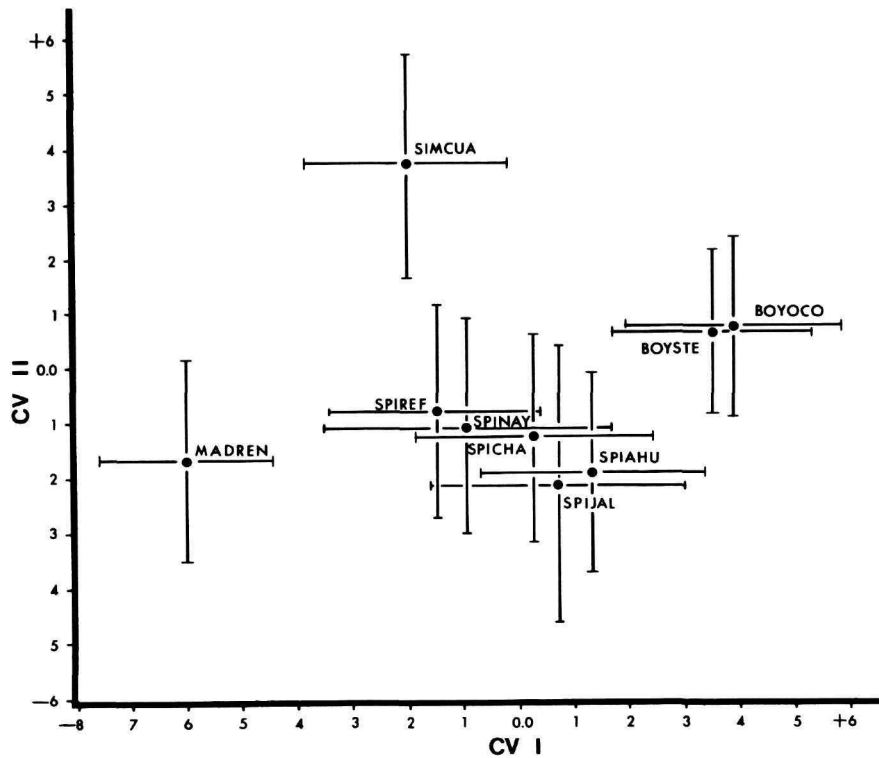


FIGURE 6.—Scatter plot of canonical variates I and II generated from discriminant function analysis of nine population samples representing the *Peromyscus boylii* species group. (Perpendicular lines = 95% confidence intervals of individual canonical variate scores around a group's centroid.)

CRANIAL, EXTERNAL, AND REPRODUCTIVE TRAITS.—In his descriptive and comparative sections, Osgood (1909) frequently enumerated several features of the skull (among them size, inflation of the tympanic bullae, configuration of the interorbital region, and shape of the braincase) to characterize the taxa he included under *P. boylii*. As discovered by subsequent authors (Hooper, 1955, 1961; Alvarez, 1961; Hall and Dalquest, 1963; Musser, 1964; Carleton, 1977), these same features do not exhibit the intergradation suspected by Osgood and still serve adequately to differentiate the various forms. The trenchant cranial traits are summarized here, principally as they apply to the Nayarit populations.

A bony ledge or shelf projects into the postero-medial areas of the orbit in examples of *spicilegus*. As a consequence, the borders of the interorbital region appear more angled or acutely constricted in contrast to the evenly contoured or hourglass-shaped interorbit observed in specimens of *boylii* proper (Figure 7). As noted by Carleton (1977), this distinction seems to vary with age. A pronounced supraorbital shelf occurs in older individuals (as judged by toothwear) of *spicilegus*, whereas it is less obvious in juveniles and subadults, which are more easily confused with *boylii*. Compared to the supraorbital shelf in *aztecus*, *evides*, *hylocetes*, and *oaxacensis*, that in *spicilegus* is weakly developed, a condition Osgood (1909:149) called "incipient." Examples of *aztecus* can be more reliably distinguished from *boylii* based on this character. The interorbital area in specimens of *simulus* and *madrensis* is hourglass-shaped, similar to the condition in *boylii*, but the posteromedial borders of the orbits (i.e., the frontal bones) are more square edged as compared to *boylii*; however, this condition does not match the "shelf" evident in samples of *spicilegus*.

The braincase of *spicilegus* appears more elongate compared to the rounded shape observed in *boylii*, *simulus*, and *madrensis*. Nevertheless, it is not clear whether the cranial cavity of *spicilegus* is actually relatively longer or whether the presence of a supraorbital shelf merely imparts an elongate

appearance. Hall and Dalquest (1963) noted a similar contrast in configuration of the braincase between *aztecus* and *boylii* in Veracruz.

The inflation of the auditory bullae varies markedly among the forms. The bullae in examples of *spicilegus* are diminutive compared to those of *boylii* ("Appendix"; Figure 8), a finding in agreement with Carleton (1977). The distinction is remarkable considering that it is reflected by a single linear measurement, length of the auditory bulla. Undoubtedly, a volumetric index would disclose a greater contrast. The auditory bullae of *simulus* and *madrensis* more closely resemble those in *spicilegus*. Other differences in size and proportions of the skulls are mentioned in the morphometric analyses.

Among the populations surveyed, those of *madrensis* exhibit the simplest dental topography. A mesolophid is absent in the sample of 37 specimens, an ectolophid is infrequently found and, if present, only weakly developed, and the mesoloph is typically incomplete (Table 5). Most specimens of *simulus* possess a conspicuous mesoloph; otherwise, the dentition of *simulus* is comparatively simple like that of *madrensis*. In contrast, representatives of *boylii* and *spicilegus* have relatively complex teeth (Table 5). Both *boylii* and *spicilegus* also differ from *madrensis* and *simulus* with regard to the presence and size of the second primary fold on the lower third molar. In the former two forms, the second primary fold (sensu Hooper, 1957) is usually present as a prominent inflexion, which, after wear, persists as an enamel island. In *madrensis* and *simulus*, the lower third molar lacks a second primary fold, or it exists only as a shallow indentation of the enamel, which often disappears with wear. The general pattern of dental variation within each of the populations supports some of Hooper's (1957) findings. Accessory styles and lophs occur more often on the upper first molar as compared to the lower one, and the ectolophid typically surpasses the mesolophid in frequency of occurrence. Also, populations that inhabit more humid, forested environments (*boylii* and *spicilegus*) display relatively complex enamel configurations, whereas those that

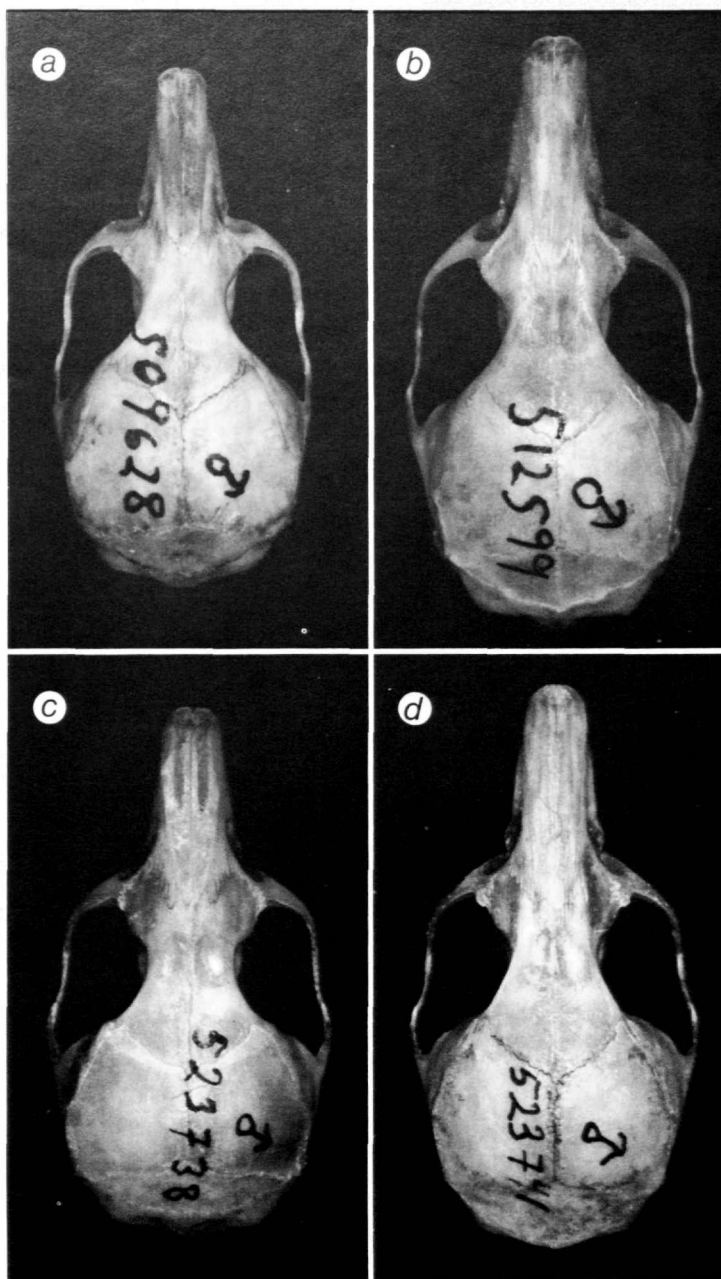


FIGURE 7.—Dorsal view of skulls of several forms of the *Peromyscus boylii* species group: a, *P. simulus* (USNM 509628), Cucharas, Rio Acaponeta; b, *P. madrensis* (USNM 512599), Tres Marias Islands, Maria Cleofas; c, *P. boylii* (USNM 523738), 13 km SW Santa Teresa; d, *P. spicilegus* (USNM 523741), 13 km SW Santa Teresa.



FIGURE 8.—Ventral view of skulls of several forms of the *Peromyscus boylii* species group: *a*, *P. simulus* (USNM 509628), Cucharas, Rio Acaponeta; *b*, *P. madrensis* (USNM 512599), Tres Marias Islands, Maria Cleofas; *c*, *P. boylii* (USNM 523738), 13 km SW Santa Teresa; *d*, *P. spicilegus* (USNM 523741), 13 km SW Santa Teresa.

TABLE 5.—Frequency of occurrence of certain dental traits in species of the *Peromyscus boylii* species group in Nayarit (see text for discussion)

Species and locality	<i>Mesoloph</i>				<i>Mesolophid</i>			<i>Ectolophid</i>		
	<i>N</i>	<i>0</i>	<i>1</i>	<i>2</i>	<i>0</i>	<i>1</i>	<i>2</i>	<i>0</i>	<i>1</i>	<i>2</i>
<i>boylii</i>										
Ocota	38	0	15.8	84.2	50.0	34.2	15.8	42.1	52.6	5.3
Santa Teresa	44	0	9.1	90.9	75.0	20.4	4.6	45.4	45.4	9.2
<i>madrensis</i>										
Tres Marias	37	0	67.6	32.4	100.0	0	0	70.3	29.7	0
<i>simulus</i>										
Cuaautla	56	5.4	21.4	73.2	94.6	5.4	0	75.0	21.4	3.6
<i>spicilegus</i>										
El Refilion	36	0	19.4	80.6	80.6	11.1	8.3	36.1	44.5	19.4
Jalcocotan	36	0	13.9	86.1	75.0	22.2	2.8	33.3	38.9	27.8

occupy arid, open habitats (*madrensis* and *simulus*) have simpler dentitions.

Pelage differences within the *boylii* group are slight, expressed in terms of degree and hence unreliable as diagnostic traits. Osgood's (1909) descriptions of pelage color accurately characterize the *boylii*-group forms occurring in Nayarit. The dorsum of all is basically tawny, differing in the degree of saturation and concentration of dusky hairs; the venter is a shade of grayish white. The dorsal appearance of individuals of *spicilegus* is rich tawny, their flanks, sides, and cheeks bright ochraceous. In *spicilegus*, the expanse of ochraceous color on the cheek, especially below and slightly anterior to the orbit, covers a larger area than in *boylii*, *madrensis*, and *simulus*. As noted by Osgood (1909), examples of *simulus* in Nayarit are practically inseparable from those of *spicilegus* based on pelage characteristics; however, specimens of *simulus* from arid scrub-thorn habitat in Sinaloa are noticeably paler. The dorsal fur of individuals of *boylii* is generally a paler hue and finer in texture as compared to *spicilegus*. The coat color seen in the island populations, *madrensis*, is still paler in tone, closer to buff. An ochraceous pectoral streak occurs in some individuals of each population sample, but its frequency varies. A pectoral streak is uncommon in *spicilegus* (16.4 percent of 152 adult skins) and *simulus* (15.0 percent of 60), common in *boylii* (44.4 percent of 90),

and typical in *madrensis* (93.0 percent of 57). Samples of *boylii* exhibit the most conspicuously bicolored, densely furred tails, but the definition of bicoloration does not approach the condition observed in *leucopus* or *maniculatus*. Bicoloration of the tail is less pronounced in specimens of *spicilegus* as compared to those of *boylii*. Individuals of *simulus* and *madrensis* have an indistinctly bicolored tail, the venter slightly paler than the dorsum and not sharply demarcated; some tails are almost monocolored. Moreover, in specimens of *madrensis*, the tail usually is as dark below as above over the distal one-third to one-half of its length. In *boylii*, the terminal portion of the tail is wholly clothed in white hairs in some individuals from Ocota Airstrip (12 of 48) and Santa Teresa (10 of 44). A terminal white tip is not evident in our samples of *madrensis* and *simulus* and on only three out of approximately 175 *spicilegus*.

Our samples of *boylii*, *madrensis*, *simulus*, and *spicilegus* can be readily separated from one another based on the anatomy of the glans penis. Examination of fluid-preserved and reconstituted material representing all populations listed in "Materials and Methods," as well as others, sustains Carleton's (1977) observations and reaffirms the distinctiveness of the four forms in Nayarit. In males of *boylii*, the glans is long (8–9 mm) and narrow (1.0–1.3 mm) with a short protractile tip (2.0–2.5 mm); the spines on the dorsal surface of

the glans are conspicuously larger and more widely spaced than those on the ventral side; and there are well-defined dorsal and ventral lappets (terminology follows Hooper, 1958). All specimens identified as *spicilegus* lack dorsal and ventral lappets; the body of the glans is marked by longitudinal furrows and covered evenly with small spines; the glans is long (8.5–9.5 mm) but relatively wide (1.5–2.0 mm) and with a long protractile tip (2.7–3.2 mm). Examples of *simulus* agree with those of *boyllii* in the presence of dorsal lappets and the distribution of spines; however, the ventral lappet is weakly developed in *simulus*, and its phallus is appreciably shorter (5.5–6.5 mm), absolutely and relatively wider (1.3–1.5 mm), and has a shorter protractile tip (1.5–1.8 mm). Examples of *boyllii*, *simulus*, and *spicilegus* were figured in Carleton (1977). Because the two specimens of *madrensis* available to Carleton (1977) were rehydrated from dry study skins, his interpretation of their morphology was tentative. The study of six additional glandes from freshly fixed specimens (two each from Maria Madre, Maria Cleofas, and Isla San Juanito) now allows a more accurate description. The glans is moderately long (8.3–9.0 mm) and wide (1.5–1.7 mm) and has a protractile tip (2.0–2.4 mm) as proportionately short as in *boyllii*. Dorsal lappets are present although not as distinct as in *boyllii* and *simulus*; there is no ventral lappet. A dorsal-ventral asymmetry in size and distribution of spines is apparent, but the contrast is less striking than that observed in examples of *boyllii* and *simulus*.

Adult male *boyllii*, *madrensis*, *simulus*, and *spicilegus* have the same basic complement of accessory reproductive glands as reported for the subgenus *Peromyscus* by Linzey and Layne (1969). Preputial glands were not visible macroscopically or detected under a dissecting scope. Six mammary glands (two inguinal pairs, one axillary pair) are evident in all reproductively active females of *boyllii*, *madrensis*, *simulus*, and *spicilegus*.

KARYOLOGY.—Recent investigations have demonstrated notable differences in chromosomal morphology among members of the *boyllii* species group (for example, Lee et al., 1972; Schmidly

and Schroeter, 1974; Kilpatrick and Zimmerman, 1975). Of the *boyllii*-group taxa in Nayarit, karyotypic samples were available for all and usually represented several localities within their distributions (see "Materials and Methods"). Examples of *boyllii*, *madrensis*, *simulus*, and *spicilegus* have a diploid count of 48, as typical of *Peromyscus*, but exhibit considerable diversity in autosomal morphology both within and between taxa.

In specimens of *simulus*, the autosomes consist of one pair of large and one pair of small subtelocentrics, one pair of small submetacentrics, and 20 pairs of evenly graded, large to small acrocentrics to equal a fundamental number of 52 (Figure 9a). The X chromosome is a large subtelocentric, and the Y a small submetacentric or subtelocentric. The only variation detected involved the morphology of the Y chromosome, which is submetacentric in one male from the Rio Chilte but subtelocentric in another male from the same place and the male from near Aticama. The karyotype observed in our samples of *simulus* agrees with that reported for *simulus* from Sinaloa (Schmidly and Schroeter, 1974) and is essentially identical to that found in *b. boyllii*, *b. utahensis*, and *b. rowleyi* (Hsu and Arrighi, 1968; Lee et al., 1972; Schmidly and Schroeter, 1974).

The common fundamental number among samples of *madrensis* is 54: one pair of large and one pair of medium-sized subtelocentrics, two pairs of small submetacentrics, and 19 pairs of acrocentrics sorted from large to small (Figure 9b). A male and female from Maria Cleofas possessed a heteromorphic pair among their acrocentrics, one chromosome having small but distinct short arms (FN=55). The autosomal complement of the other 18 specimens of *madrensis* was uniform. The sex chromosomes consist of a large subtelocentric X and a small subtelocentric Y. Except for the pair of medium-sized subtelocentrics, the chromosomal assortment found in *madrensis* closely resembles that in *simulus*.

Two strikingly different karyotypes are represented in the two samples of *boyllii*, one from Ocota and the other 13 km SW Santa Teresa. The mice from Ocota (three karyotyped) have a high FN,

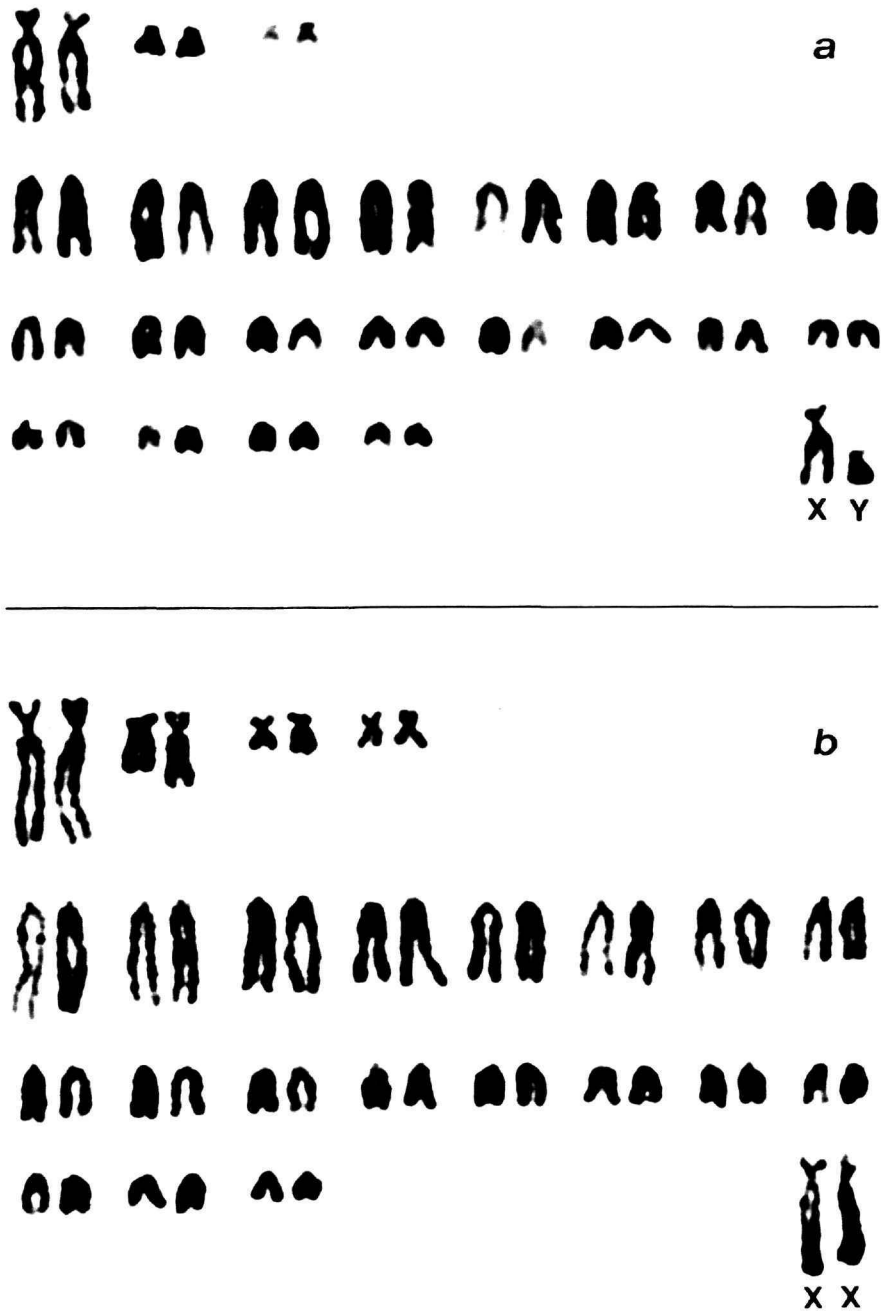


FIGURE 9.—Representative karyotypes: a, *Peromyscus simulus* (USNM 511658), 1.2 km S El Casco, Río Chilte; b, *P. madrensis* (USNM 512574), Tres Marias Islands, Maria Cleofas.

66, consisting of the following autosomes: two pairs of large and five pairs of medium-sized subtelocentrics, one pair of large submetacentrics, one medium and one small pair of metacentrics, and 13 pairs of large to small acrocentrics (Figure 10a). The X chromosome is a large submetacentric, and the Y a small acrocentric in one male and a small acrocentric in the other. Autosomal polymorphism in the size of homologues was noted in a medium-sized pair of subtelocentrics (in one male) and in the medium-sized pair of metacentrics (in the other male and in the female). In each case, the presumptive homologues have the same morphology, but one chromosome is larger than the other.

The single specimen (a female) karyotyped from 13 km SW Santa Teresa has several unpaired autosomes, including a large subtelocentric, a medium submetacentric, and one large and one small acrocentric (Figure 10b). Two pairs of large and one pair of medium-sized subtelocentrics, one pair of medium submetacentrics, one pair of small metacentrics, and 16 pairs of evenly graded, small to large acrocentrics compose the remainder of the autosomal set. With the heteromorphism, the fundamental number is 56. A large pair of subtelocentrics represents the X chromosomes; the Y is unknown. The karyotype of the Santa Teresa female, especially the pres-

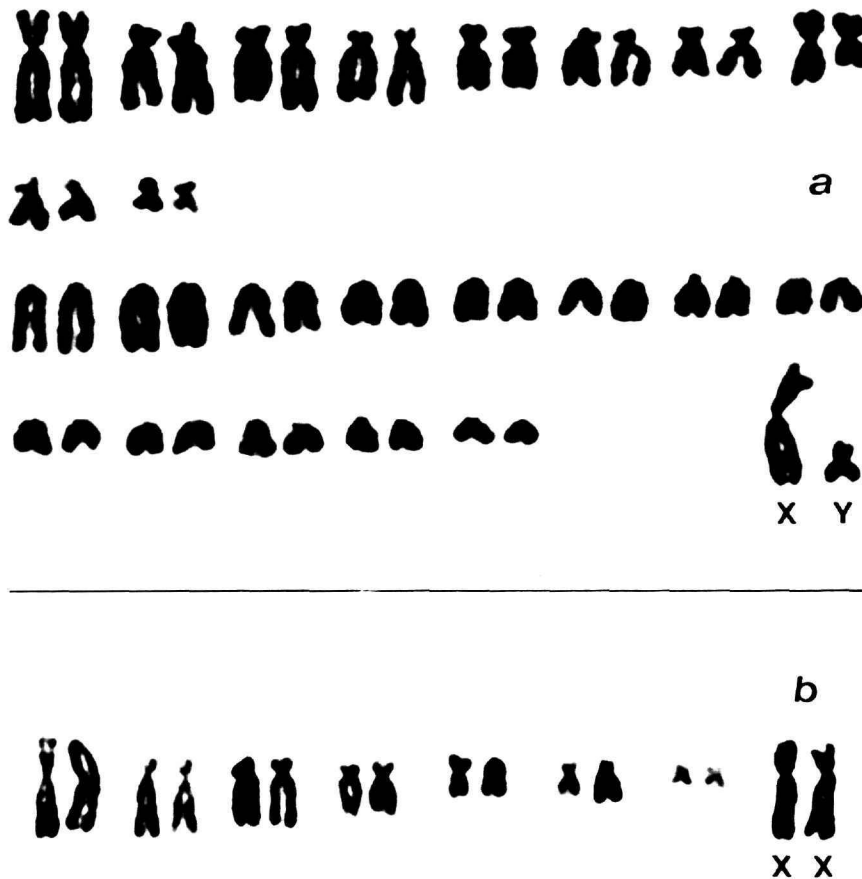


FIGURE 10.—Karyotypes of *Peromyscus boylii*: a, male (USNM 523883) from Ocotá; b, biarmed chromosomes of specimen (USNM 523739) from 13 km SW Santa Teresa.

TABLE 6.—Variation in nonbanded karyotypes of *Peromyscus spicilegus* from Nayarit (no. of acrocentric pairs not including heteromorphic sets; FN = no. of autosomal arms; SM = submetacentric; ST = subtelocentric)

Locality	N		Number of acrocentric pairs			FN						X chromosome morphology				
	♂	♀	4	5	6	79	80	81	82	83	84	♂		♀		
												SM	ST	SM/ST	ST/ST	
Agua Escondida	2	3		3	2		2		3					2		3
Tempiste	2			2					2			1	1			
Chacala	2	6	1	5	2	2			5	1	1	1	1		3	3
Ahuacatlan	5	4	2	4	3	2	1	2	2	1	1	2	3			4
Jala	2			1	1	1			1					2		
Coapan	1	2		1	2	1	1		1			1				2
Jalcocotan	6	5	1	7	3	1	2		7	1			6	1		4
La Villita	4	2		1	5	1	4	1				2	2	1		1
Arroyo Jiguite	2	2		1	3		3		1				2			2
Arroyo Taberna			1	1					1							1
Mesa del Nayar	3	3		6			1	1	4			1	2	1		2
Santa Teresa			1	1					1							1
Totals	29	29	4	33	21	8	14	4	28	2	2	8	21	6		23

ence of a large unique acrocentric, recalls the chromosomal configuration reported for two specimens of *boylly levipes* from Pinal de Amoles, Queretaro (Schmidly and Schroeter, 1974).

The karyotypic formula in *spicilegus* is characterized by a large number of biarmed chromosomes, 17 to 19 pairs, and consequently a high fundamental number, which ranges from 79 to 84 in our sample of 58 specimens from 12 different localities (Table 6). In the typical chromosomal spread, the autosomes consist of a graded series of 15 pairs of large to small subtelocentrics, one pair of medium-sized metacentrics, one pair each of medium and small submetacentrics, and one pair of large and four pairs of medium to small acrocentrics (Figure 11). A large subtelocentric X and small metacentric Y constitute the sex chromosomes.

Considerable diversity exists, however, within and between populations of *spicilegus* (Table 6). Variation is most conspicuous in the ratio of acrocentric to biarmed chromosomes. The distinction between the two most commonly occurring karyotypes, FN=82 and FN=80, usually involves a small pair of chromosomes, which are acrocentrics in some individuals but clearly sub-

telocentrics in others. Such differences, plus some autosomal heteromorphism, result in an FN range of 79 to 84. Variation also is evident in the morphology of the X chromosome, whose alternate form is a large submetacentric (Table 6). Although variable, the karyotype of *spicilegus* is distinctive, and the range and nature of the chromosomal variation we observed does not suggest hybridization between *spicilegus* and any of its congeners.

Schmidly and Schroeter (1974) and Kilpatrick and Zimmerman (1975) interpreted the chromosomal variation in their samples (the latter authors also employed electrophoretic data) as evidence of intergradation between *boylly rowleyi* and *spicilegus*. As noted by Carleton (1977), however, the name *spicilegus* does not properly apply to those populations in Durango and Sinaloa that they and Lee et al. (1972) surveyed as examples of *boylly spicilegus*. The confusion stems from Osgood's (1909) revision, wherein he greatly expanded the range of *spicilegus* to encompass not only the western mountains of Jalisco and Nayarit but also much of the Sierra Madre Occidental and the western reaches of the Mexican Plateau. In doing so, his *boylly spicilegus* became an accre-

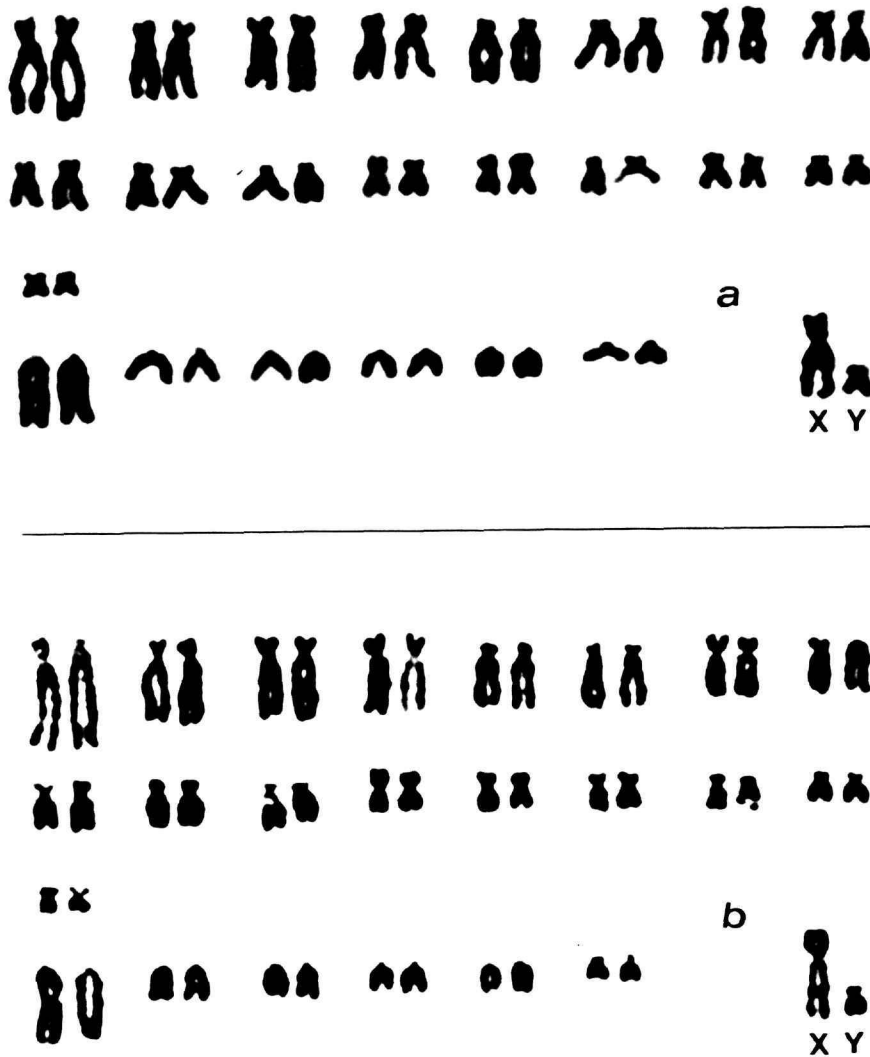


FIGURE 11.—Karyotypes of *Peromyscus spicilegus*: a, common karyotypic configuration as exemplified by a male (USNM 511676) from 10 km N Jala; b, example of autosomal heteromorphism as seen in a male (USNM 511672) from Mesa del Nayar.

tion of *spicilegus*, a species of intermediate elevations and more tropical environments, and the westernmost segments of true *boylii*. The karyotypic information supplied by the above authors confirms the identity of their populations with *rowleyi* and other subspecies of *boylii* but is not evidence of intergradation between *boylii rowleyi* and *spicilegus*. In fact, a marked karyotypic differ-

ence exists between *spicilegus* proper and those mice in Durango and Sinaloa that have been called *boylii spicilegus*. Examples of *spicilegus* consistently display a predominance of biarmed chromosomes and concomitantly high fundamental numbers (79–84) in contrast to specimens of *boylii*, which have a majority of acrocentrics and comparatively low fundamental numbers (52–66).

Schmidly and Schroeter (1974) urged that *simulus* be raised to a species on the basis of its divergent karyotype. We endorse the change in taxonomic status but for reasons other than karyotypic differentiation. The authors had specimens from Sinaloa and from near San Blas, Nayarit, the type-locality of *simulus*. The animals from Sinaloa contained mostly acrocentrics (FN=52), whereas those from near San Blas had a large proportion of metacentrics (FN=82). Unknown to those authors, populations of *spicilegus* range into lower elevations and intermingle with those of *simulus* in the area south and east of San Blas. As first noted by Carleton (1977) and further documented herein, the Nayarit specimens with a high fundamental number represent *spicilegus*. This is the ubiquitous karyotype found in populations inhabiting intermediate montane zones in Nayarit (i.e., *spicilegus*) and is not characteristic of those found on the coastal plain of Nayarit. Mice from the latter region (for example, from near Cuautla and El Casco) possess a low ratio of metacentric to acrocentric chromosomes (FN=52), a karyotype identical to that which Schmidly and Schroeter (1974) reported for *simulus* from Sinaloa. Based upon its karyotype alone, *simulus* is not divergent from populations of *boyllyi*, which also display relatively low fundamental numbers (Table 7).

Much of the karyotypic variation known in *boyllyi* (sensu stricto) resides in those southern Mexican populations known as *levipes* or ones previously misidentified as *spicilegus* (Table 7). On the other hand, populations in the United States and northern Mexico (recognized as the subspecies *boyllyi*, *rowleyi*, and *utahensis*) are chromosomally uniform in having 20 acrocentric pairs and just three biarmed pairs. Our only two localities of *boyllyi* were obtained in the eastern highlands of Nayarit, a region Osgood (1909) placed within the distribution of *boyllyi spicilegus*. The one specimen from Santa Teresa falls within the range of variation described for other *boyllyi*, but the three from Ocota possess three additional pairs of biarmed chromosomes, yielding a higher fundamental number, 66, than previously recorded for

the species. The karyotype of the Ocota specimens resembles that reported for a specimen from Michoacan, which Schmidly and Schroeter (1974) identified as *evides*. Carleton has examined that specimen (Texas Cooperative Wildlife Collection 27265) and considers it an example of *boyllyi levipes*, not *evides*. Thus, in Michoacan as in Nayarit, populations having dissimilar karyotypes but judged to be conspecific on the basis of external, cranial, and penile morphology, live in close geographic proximity. Understanding the nature and pattern of this extraordinary chromosomal variation within *boyllyi* (sensu stricto) requires further investigation.

GEOGRAPHIC DISTRIBUTION AND SYMPATRY.—In the absence of critical genetic information, the sympatric occurrence of two forms and the absence of morphological intermediates at the locality of sympatry constitute the systematist's most persuasive arguments for their "goodness" as biological species. Indeed, it was the accumulation of precisely this sort of information that first altered our perception of relationships in Osgood's *boyllyi* group.

The southern Mexican and Central American populations known as *levipes* played a central role in the development of our present understanding of *boyllyi*-group systematics. Hooper (1955) reported both *levipes* and *spicilegus* from 2 mi W San Andres, Jalisco; examples of the two were segregated ecologically, *spicilegus* in a canyon bottom and *levipes* just upslope on exposed rimrock. Along the eastern slopes of the Sierra Madre Oriental, specimens of *levipes* were trapped together with *aztecus* in Veracruz (Alvarez, 1961) and in Hidalgo (Musser, 1964). The populations that Osgood (1909) arranged under *boyllyi evides* were first recognized as sympatric with *levipes* in Michoacan (Hooper, 1961; but Carleton, 1977, allocated these to *spicilegus*) and then in Guerrero (Musser, 1964). Other instances of sympatry or contiguous allopatry of *levipes* with each of these three forms have been documented (Carleton, 1977). In addition, three specimens of *spicilegus* and one of *simulus* were reported from the same locality east of San Blas, Nayarit (Carleton, 1977).

TABLE 7.—Number of biarmed (BA) and acrocentric (A) chromosomes and fundamental number (FN) in populations of the *Peromyscus boylii* species group (references: 1 = Hsu and Arrighi, 1968; 2 = Lee et al., 1972; 3 = Schmidly and Schroeter, 1974; 4 = Kilpatrick and Zimmerman, 1975; 5 = Carleton, 1977; 6 = Lee and Elder, 1977; 7 = this study)

Taxa and localities	Number of autosomes			Reference
	BA	A	FN	
<i>attwateri</i>	10	36	56	2, 4
Kansas, Oklahoma, Texas				
<i>aztecus hylocetes</i>	26	20	72	6
Jalisco				
<i>aztecus oaxacensis</i>	22	24	68	3
Chiapas				
<i>boylii ambiguus</i>	12, 14	32, 34	58, 60	3, 4
Tamaulipas				
<i>boylii baetae</i>	6, 7	39, 40	52, 53	3
Veracruz				
<i>boylii boylii</i>	6	40	52	2
California				
<i>boylii levipes</i>	6-14	32-40	52-60	2, 3
Chiapas, Hidalgo, Michoacan, Oaxaca, San Luis Potosi, Queretaro				
<i>boylii rowleyi</i>	6	40	52	1, 2, 3, 4
Arizona, New Mexico, Oklahoma, Texas, Utah, Chihuahua, Durango, Sonora				
<i>boylii utahensis</i>	6	40	52	2, 4
Utah				
<i>boylii</i> ssp.				
Durango, Sinaloa	8-10	36-38	54-56	2, 3, 4
Nayarit, Ocota	20	26	66	7
Nayarit, Santa Teresa	12	32	56	7
<i>madrensis</i>	8	38	54	7
Nayarit				
<i>polius</i>	31	15	77	4
Chihuahua				
<i>simulus</i>	6	40	52	3, 7
Nayarit, Sinaloa				
<i>spicilegus</i>	33-38	8-13	79-84	3, 5, 7
Nayarit				

On the basis of skull configuration, two localities of sympatry were suspected among the material recently collected from Nayarit. One site, Cucharas on the Rio Acaponeta, 100 m, involved examples of *simulus* and *spicilegus*; the other, Rancho Viejo, 13 km SW Santa Teresa, *boylii* and *spicilegus*. Two-group discriminant function analyses were performed on reference samples of *simulus* (SIMCUA, N=50) versus *spicilegus* (SPI-

JAL, N=35) and *boylii* (BOYOCO, N=37) versus *spicilegus* (SPIJAL, N=35), using only the 19 cranial variables. The resultant discriminant multipliers were then used to calculate discriminant scores for the unknowns, from Cucharas and near Santa Teresa, and for the reference specimens, and these were plotted in frequency histograms.

In both cases, the discriminant scores of known references are distributed in a bimodal fashion

(Figure 12); however, the ranges of discriminant scores about and even overlap slightly in the *simulus-spicilegus* comparison. Specimens that fall in the zone of overlap or contact are young animals of *spicilegus* or very old individuals of *simulus* and *boyllii*, a reminder that age variation must be considered when comparing skulls. The length of the maxillary tooththrow, zygomatic breadth, breadth of mesopterygoid fossa, and rostral length contribute most to the separation of the *simulus* and *spicilegus* reference samples (Table 8). Length of auditory bulla, length and breadth of mesopterygoid fossa, postdental palatal breadth, and rostral breadth account for much of the distinction between *boyllii* and *spicilegus* (Table 8).

Unknowns from the two localities in question are clearly associated with either one or the other

reference populations (Figure 12), suggesting that there are two species in sympatry at each locality. Examination of the glandes penes of some of the specimens collected at Cucharas and near Santa Teresa disclosed the same distinctive morphologies as described for *simulus*, *boyllii*, and *spicilegus*. The discriminant scores of these particular specimens align them with the reference samples predicted on the basis of their phallic morphology and provide further confirmation that two kinds are present at these places. A karyotype was available for one of the specimens from 13 km SW Santa Teresa. This individual (USNM 523740) possesses a high fundamental number (FN=82), which is typical of *spicilegus*, and was included among *spicilegus* from 2 mi E Jalcoctan in the discriminant function analysis. Regrettably, the one karyotypic example of *boyllii* (FN=56)

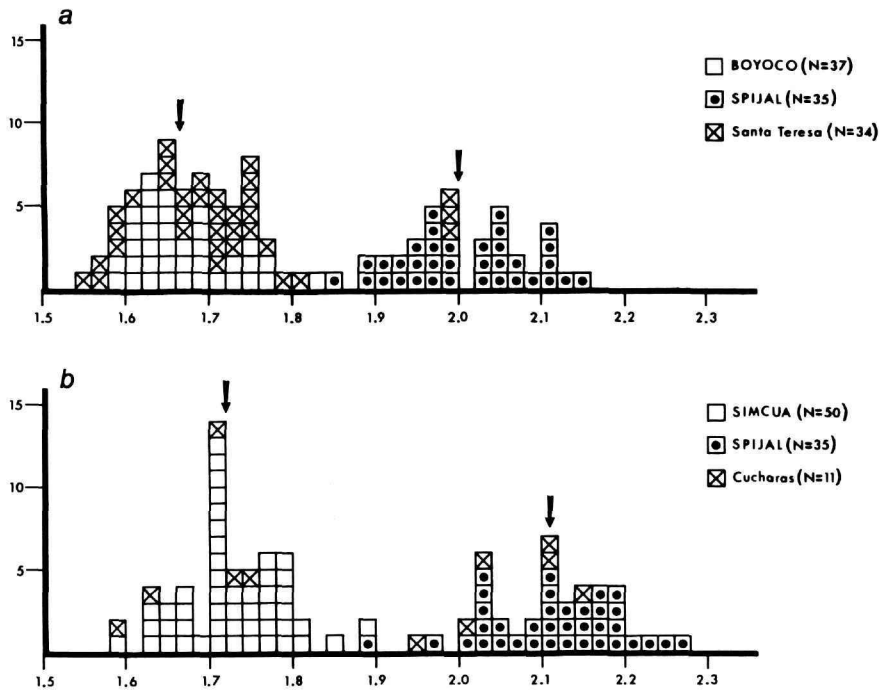


FIGURE 12.—Frequency histograms of discriminant scores determined by two-group discriminant function analyses comparing reference samples: a, *Peromyscus boyllii* (BOYOCO) and *P. spicilegus* (SPIJAL) with unknowns from 13 km SW Santa Teresa; b, *P. simulus* (SIMCUA) and *P. spicilegus* (SPIJAL) with unknowns from Cucharas. (See Table 8; arrows denote mean discriminant scores of four reference samples.)

TABLE 8.—Discriminant multipliers for 19 cranial variables derived from discriminant function analyses of reference samples of *spicilegus* and *boyllii* and *spicilegus* and *simulus*

Character	SPIJAL: BOYOCO	SPIJAL: SIMCUA
Greatest length of skull	.076	-.007
Condylolincisive length	.001	.006
Length of auditory bulla	-.195	.089
Postpalatal length	-.116	-.082
Length of mesopterygoid fossa	.214	-.006
Palatal length	-.022	.095
Length of incisive foramen	-.026	.044
Alveolar length of maxillary toothrow	.068	.221
Greatest zygomatic breadth	-.046	-.123
Mastoidal breadth	-.062	-.058
Greatest breadth across molars	-.003	.061
Postdental palatal breadth	.207	-.104
Breadth of mesopterygoid fossa	.115	.256
Depth of braincase	-.056	.087
Breadth of braincase	.071	.088
Least interorbital width	.059	-.001
Rostral breadth	.169	.006
Nasal length	.025	-.025
Rostral length	-.088	.132

from Santa Teresa is a juvenile, and it was not entered into the discriminant function program. The hypothesis that *boyllii* intergrades with *spicilegus* and that *spicilegus* merges into *simulus* is not substantiated by the pattern of morphological variation observed at these two sites.

Nevertheless, certain geographic samples persuaded Osgood (1909) that these races did in fact merge with one another and with other populations of *boyllii*. These instances can be easily accommodated in retrospect and merit comment for their historical role as purported intermediates. Much of the confusion resulted from the composite nature of populations that Osgood united under the name *boyllii spicilegus*. He thought that Mexican *b. rowleyi* exhibited tendencies toward *spicilegus*, which was partially true in that

his definition of *b. spicilegus* embraced segments of true *boyllii* as well as the lower-elevation species *spicilegus*. Similarly, he viewed his sample of *b. spicilegus* from Santa Teresa as "approaching *simulus*" in morphology. The 10 specimens from Santa Teresa are examples from the westernmost range of *boyllii* proper, not *spicilegus*, and *boyllii* resembles *simulus* in skull conformation. Osgood (1909) listed two localities of *b. spicilegus* that contained specimens "approaching *evides*," one of them Plomosas, Sinaloa, and the other Barranca Ibarra, Jalisco. Specimens from both localities are examples of *spicilegus*. The belief that they represented intergrades toward *evides* may have arisen from their similarity to populations in Michoacan, which Osgood (1909) arranged as *evides*, but which Carleton (1977, 1979) interpreted as the southern representatives of *spicilegus*.

SUMMARY.—Based on the information revealed herein, together with similar lines of evidence regarding these *Peromyscus* in other parts of western Mexico (Hooper, 1955; Carleton, 1977), we treat *madrensis* Merriam, 1898a, *simulus* Osgood, 1904, and *spicilegus* Allen, 1897, as species distinct from *boyllii*. The hypothesis that *madrensis*, *simulus*, and *spicilegus* represent intergrading (or potentially intergrading) races of a single species, *P. boyllii*, finds no support in the patterns of variation we see in the Nayarit collections. Instead, the concordance of several kinds of data—the morphometric analyses, aspects of cranial and reproductive anatomy, chromosomal information, and distributional records—indicates substantial morphological discontinuity between the four sets of populations in Nayarit and, by inference, the occurrence of reproductive incompatibility.

The morphological distinctiveness of *spicilegus* (disembarrassed of some populations that Osgood arranged under *boyllii spicilegus*) and the documentation of its sympatry with *simulus* at lower elevations and *boyllii* at higher elevations compel its recognition as a separate species. *Peromyscus spicilegus* is more closely related to *aztecus* (including the subspecies *evides*, *hylocetes*, and *oaxacensis*), a southern Mexican and Central American species, than to geographically contiguous *boyllii* and *simulus*. *Peromyscus madrensis* and *simulus* are nearer

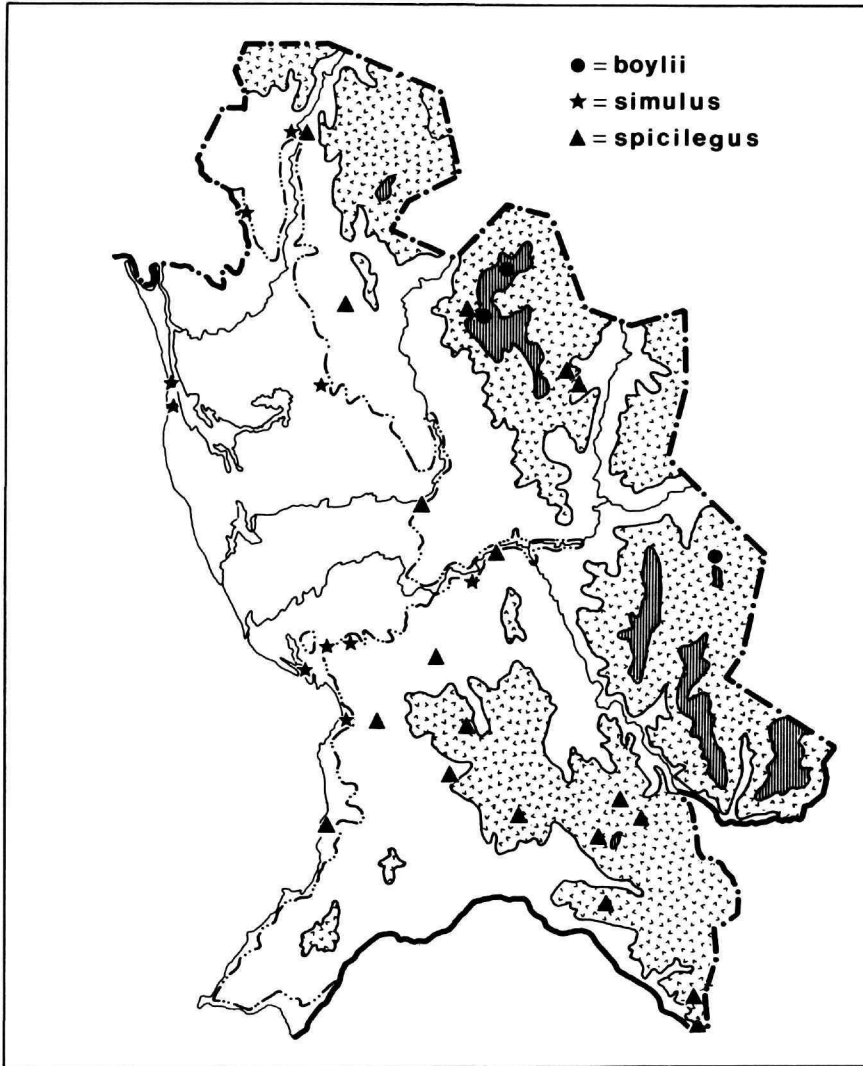


FIGURE 13.—Mainland Nayarit indicating locality records and elevational associations of *Peromyscus boylii* (circles), *P. spicilegus* (triangles), and *P. simulus* (stars). (Dashed/dotted line = 100 m contour; hatched area = elevations between 1000 and 2000 m; vertical lines = elevations at 2000 m and higher.)

in affinity to *boylii* proper. Although not insular in its distribution like *madrensis*, the geographic isolation of *simulus* is equally as effective, being altitudinally separated from *boylii* by approximately 2000 meters of mountainous terrain that is inhabited by intervening populations of *spici-*

legus (Figure 13). Therefore, the test of sympatry in the case of *madrensis* and *simulus* will likely remain irrelevant to their justification as distinct species; however, such recognition is warranted on the basis of their unique combination of traits, which separates them from populations of *boylii*

and which, in degree, matches the differentiation observed between *boylii* and some other species of *Peromyscus*. When divorced of *aztecus*, *evides*, *madrensis*, *simulus*, and *spicilegus*, the residual populations comprising *boylii* form a more morphologically cohesive unit and seemingly represent but a

single species. Yet even after the removal of some of Osgood's (1909) "definable forms," the populations included in *boylii* exhibit substantial variation, especially as revealed in the karyological data, and require further investigation over a broader area of their distribution.

Peromyscus of Nayarit

Key to the Species of *Peromyscus* of Nayarit

1. Tail short (<65 mm), only 60%–70% length of head and body, densely haired and conspicuously bicolored ***P. maniculatus***
Tail long (>75 mm), approximately equal to or longer than head and body, and indistinctly to moderately bicolored 2
2. Tail very long (≥ 130 mm), relatively much longer (about 140%) than head and body; supraorbital shelf well developed; glans penis (13 mm) and baculum (17 mm) relatively long ***P. melanophrys***
Tail moderately long (usually <125 mm), approximately equal to (90%–110%) or only slightly longer than (115%) head and body; supraorbital shelf either moderately developed or absent; glans penis (≤ 11 mm) and baculum (≤ 13.5 mm) relatively short 3
3. Skull with moderately pronounced supraorbital shelf, auditory bullae small, dentition relatively complex; glans penis with longitudinal furrows, dorsal and ventral lappets absent; karyotype with 16–19 pairs of biarmed autosomes (FN=79–84) ***P. spicilegus***
Skull lacking supraorbital shelf; auditory bullae small or moderately inflated, dentition relatively simple or complex; glans penis lacking longitudinal furrows, dorsal lappets present, ventral lappet present or absent; karyotype with 3–10 pairs of biarmed autosomes (FN=52–66) 4
4. Size large (total length usually >210 mm; hind foot usually ≥ 24 mm; skull length usually >28 mm); terminal one-third of tail as dark below as above; dentition relatively simple; ventral lappet absent . ***P. madrensis***
Size small to medium (total length usually <210 mm; hind foot typically ≤ 23 mm; skull length usually <28 mm); tail indistinctly to moderately bicolored along its entire length; dentition simple or complex; ventral lappet on glans present 5
5. Tail relatively long, 115% of length of head and body; hind foot small (usually ≤ 21 mm) and delicate; skull gracile in appearance (rostrum short and narrow, braincase smooth and rounded; tooththrow short) ***P. pectoralis***
Tail approximately equal to length of head and body; hind foot larger (usually >20 mm) and broader; skull more heavily built 6
6. Tail moderately bicolored; tooththrow longer (usually ≥ 4.1 mm); dentition generally more complex; glans penis (>8.0 mm) and baculum (>10.0 mm) absolutely and relatively longer ***P. boylii***

Tail indistinctly bicolored to almost monocolored; toothrow shorter (usually ≤ 4.1 mm); dentition relatively simple; glans penis (< 7.0 mm) and baculum (< 9.00 mm) absolutely and relatively shorter *P. simulus*

***Peromyscus maniculatus labecula* Elliott**

Peromyscus labecula Elliott, 1903:143.

Peromyscus maniculatus labecula.—Osgood, 1909:87.

TYPE-LOCALITY.—Ocotlan, Jalisco.

GENERAL DISTRIBUTION.—West-central Mexico from Durango south through Zacatecas, Guanajuato, Mexico, and Puebla to Morelos in the east and from Nayarit southward through Jalisco to Colima in the west.

DISTRIBUTION IN NAYARIT.—Limited to the southwestern part of the state, south and west of the Rio Grande de Santiago. Most abundant at elevations between 1000 and 1500 meters.

DISTINGUISHING CHARACTERISTICS.—Upper parts grizzled grayish brown with a broad medial strip of darker-colored hairs from top of head to base of tail. Hairs tricolored with dark bases and tips and a paler middle section. Underparts white with dark gray bases of individual hairs showing through. Feet white; ears short with distinct white rims; tail short and sharply bicolored, white below and dark brown above.

The karyotypes in our samples of *P. maniculatus labecula* ($2n=48$; $FN=84$) consist of 19 pairs of banded autosomes arrayed evenly from small to large and four pairs of medium-sized to large unpaired pairs (Figure 14a). The X chromosome is a large submetacentric, and the Y either a medium-sized submetacentric (the male from Coapan) or a small submetacentric (those from near Ahuacatlan and Jalcocotan). This chromosomal formula resembles that found in *P. m. fulvus* and in some populations of *P. m. luteus* and *P. m. rufinus* (Bowers et al., 1973).

The small body size and short, bicolored tail of *Peromyscus maniculatus* readily distinguish it from *pectoralis*, *simulus*, and *spicilegus*, the species with which it is most often collected. Osgood (1909) and Hooper (1955) noted that the smallest examples of *P. maniculatus labecula* occur in the west-

ern lowlands of Nayarit. This observation is borne out by the smaller size of specimens from areas near El Casco and Tepic, localities that represent the lowest elevations recorded for the species in the state. Some specimens are quite similar to *Peromyscus melanotis*, a species as yet unrecorded for the state, but one that may occur in the mountains of eastern Nayarit.

ECOLOGICAL NOTES.—*Peromyscus maniculatus* is not geographically or ecologically widespread in Nayarit. The southwestern part of the state is ruggedly dissected ridge and valley country, with little or no coastal plain. The ridges are covered with tropical deciduous forest grading into oak woodland associations at the upper elevations. Valley bottoms are often sharply cut by small streams, whose meandering patterns have created open grassy or brushy areas. In this type of situation, *maniculatus* often occupies the more open valley bottoms, and *spicilegus* and *pectoralis* the wooded or rocky slopes.

We found *maniculatus* associated with grassy areas at several localities in Nayarit. Just east of Jalcocotan, *maniculatus* commonly occurred in grassy orchards and old field situations in the valley bottom, and *spicilegus* on the rocky slopes and in the deciduous forest on the ridgetops. At El Refilion, *maniculatus* was also concentrated in grassy areas. A trapline that had yielded three *spicilegus* and two *maniculatus* from an ecotonal zone of brushy woodland caught one *spicilegus* and 24 *maniculatus* when moved to the grassy areas in an attempt to collect more *maniculatus*. This species also showed an affinity for wetter areas at this site, where several were taken at the bottom of a small ravine off the river, and others from mesic areas along the road where water seeped out of the bank and flowed to the road. A trapline set among water hyacinth along the edge of the lake near San Pedro Lagunillas also produced

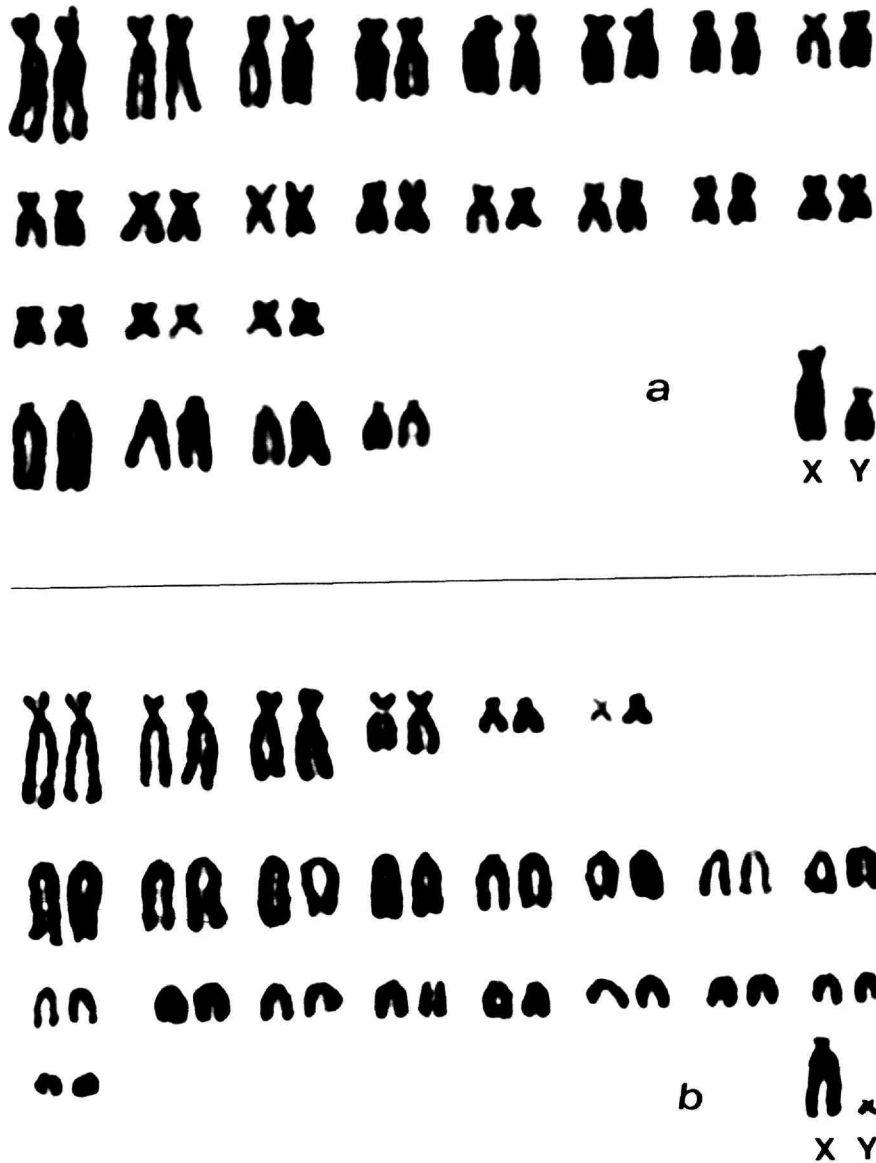


FIGURE 14.—Representative karyotypes: a, *Peromyscus maniculatus labecula* (USNM 511686) from 1.8 mi NW Coapan; b, *P. melanophrys micropus* (USNM 523917) from Arroyo de Jiguite.

numerous *maniculatus*. Hooper (1955) collected this species from an open, grassy plain and from a sparse growth of grass and weeds in pine-oak forest in Jalisco.

The animals from areas near El Casco, at the

confluence of the Rio Chilte and the Rio Grande de Santiago, are the only ones we found at an elevation lower than 700 m. These river valleys are at an elevation of 60 m and are steeply cut through the surrounding, higher terrain. Perhaps

these mice have used the rivers as dispersal corridors from higher elevations to the south.

We collected lactating females in January and males with scrotal testes in March, October, and November. Reproductively inactive individuals were also collected in each of these months, the only times for which data is available.

Other rodents collected at the same localities with *Peromyscus maniculatus* are *P. simulus*, *P. pectoralis*, *P. spicilegus*, *Reithrodontomys fulvescens*, *Neotoma mexicana*, *Baiomys taylori*, *Sigmodon alleni*, *S. arizonae*, *S. hispidus*, *S. mascotensis*, *Oryzomys palustris*, *O. melanotis*, *Rattus rattus*, *Mus musculus*, and *Liomys pictus*.

SPECIMENS EXAMINED.—8 mi (by rd) S Ahuacatlan, 1500 m, 13; 1.8 mi (by rd) NW Coapan, 1560 m, 2; 1.2 mi (by rd) S El Casco, Rio Chilte, 60 m, 2; El Refilion, 850 m, 141; Estanzuela, 1380 m, 1; 2 mi E Jalcocotan, 1500 m, 8; 2 mi E San Pedro Lagunillas, E side lake, 1300 m, 101; Tepic, 1000 m, 3; 1 mi W Tepic, 792 m, 2; 5 mi W Tepic, 792 m, 1.

Peromyscus boylii (Baird)

Hesperomys boylii Baird, 1855:355.

Peromyscus boylii.—Mearns, 1896:139.

TYPE-LOCALITY.—Middle Fork of American River, near Auburn, Eldorado Co., California.

GENERAL DISTRIBUTION.—Southwestern United States southward through the Mexican Plateau and highlands of southern Mexico and Guatemala to El Salvador and Honduras.

DISTRIBUTION IN NAYARIT.—Found only in the mountains (1900–2100 m) in the eastern part of the state.

DIAGNOSIS.—A species of the subgenus *Peromyscus* characterized by a medium-sized skull with rounded braincase and moderately inflated bullae; supraorbital shelf lacking except in very old individuals; teeth relatively complex; bicoloration of tail moderately pronounced; glans penis long and comparatively thin, with a proportionately short protractile tip, and with dorsal and ventral lappets present and typically well defined; karyotype variable with three to 10 pairs of biarmed autosomes ($2n=48$; FN=52–66).

TAXONOMIC REMARKS.—The patterns of variation in *boylii* need to be evaluated over its entire distribution before delimiting formal subspecific limits. Specimens from Nayarit are not easily assigned to either *rowleyi* or *levipes*, the two subspecies having ranges nearest our localities in Nayarit; therefore, we have deliberately not allocated our samples to any of the currently accepted geographic races. Formerly, Osgood's (1909) name combination *boylii spicilegus* would have applied to the populations in eastern Nayarit, but as shown herein and elsewhere (Carleton, 1977), Osgood's perception of the taxon was a composite.

ECOLOGICAL NOTES.—*Peromyscus boylii* is restricted to the pine and pine-oak forests of the higher mountains that form part of the Sierra Madre Occidental in the eastern part of the state. Near Santa Teresa, this species was abundant on rocky hillsides, and its burrows obvious at the base of rocks. When we collected in that area in January, 1977, each burrow entrance was lined with acorns. Burrows were occasionally found at the base of trees. Examples of *spicilegus* came from the rocky bottom of a steep-sided arroyo in the same area. At Ocota in southeastern Nayarit, *boylii* was common throughout mature stands of yellow pine intermixed with several kinds of oak. Entrances to nests were evident at the base of a small cliff overlooking a broad valley and in the banks of small arroyos.

In the January collection of *boylii*, we found most males to be scrotal and most females lactating, and we found numerous juveniles.

The few rodent species co-occurring with *Peromyscus boylii* include *P. spicilegus*, *Reithrodontomys fulvescens*, *Neotoma mexicana*, and *Sigmodon arizonae*.

SPECIMENS EXAMINED.—Ocota Airstrip, 1900 m, 62; Santa Teresa, 2100 m, 10; 13 km SW Santa Teresa, Rancho Viejo, 2100 m, 61.

Peromyscus simulus Osgood

Peromyscus spicilegus simulus Osgood, 1904:64.

Peromyscus boylei simulus.—Osgood, 1909:151.

Peromyscus boylii simulus.—Miller and Kellogg, 1955:495.—

Hall and Kelson, 1959:636.

Peromyscus simulus.—Carleton, 1977:41.

HOLOTYPE.—USNM 88088, adult male, skin and skull from San Blas, Nayarit. Holotype examined.

GENERAL DISTRIBUTION.—Known only from the coastal plain of southern Sinaloa and northwestern Nayarit.

DISTRIBUTION IN NAYARIT.—Limited to the broad coastal plain and associated river valleys in northwestern Nayarit, from sea level to 200 m elevation.

DIAGNOSIS.—A species of the *boylei* species group, subgenus *Peromyscus*, characterized by a small skull with truncate rostrum and short tooth-row (usually less than 4.0 mm); teeth comparatively simple; supraorbital shelf not present; tail indistinctly bicolored or monocolored; glans penis short and broad with dorsal lappets and weakly developed ventral lappet; and karyotype with six biarmed autosomes ($2n=48$; FN=52). Comparisons with other species in the *boylei* group are given above.

ECOLOGICAL NOTES.—Lowland tropical forest of the Arid Upper Tropical Zone is the common habitat of *simulus*. Near Tacote, individuals of *simulus* were commonly found in a small arroyo surrounded by *Cochlospermum*, *Bombax*, *Lysiloma*, *Byrsonima*, *Crescentia*, *Cocoloba*, and *Bursera* but were absent from drier hillsides containing *Agave*, *Acacia*, *Cassia*, and *Sabal* palms. *Peromyscus simulus* was extremely abundant (72% trap success the first night) in a small, coastal palm grove just south of Cuautla. In addition to *Scheelea* palms, the grove contained *Guazuma* and *Bursera*. Large numbers of *simulus* were taken also in thickets of *Acacia*, *Pithecellobium*, and *Asclepias* at the edge of the grove. Further inland from the palm grove, *simulus* occurred in a mangrove (*Conocarpus*) swamp.

Populations of *simulus* penetrate the interior of Nayarit and contact other species of *Peromyscus* where river valleys provide access. Both *simulus* and *spicilegus* were taken at Cucharas, 100 m elevation, on the Rio Acaponeta. Individuals of *simulus* seemed to be localized on the 200-m-wide floodplain of the river, which cuts rather sharply through a series of low hills. Traps set on those

hillsides, which were covered with tropical deciduous forest consisting of *Enterolobium*, *Hymenaea*, *Gliricidium*, *Acacia*, *Hura*, *Bombax*, *Cochlospermum*, and *Luhea*, yielded *spicilegus*. A similar situation obtains near El Casco, 60 m elevation, where the Rio Chilte joins the Rio Grande de Santiago. There, *maniculatus* inhabited the hillsides, and *simulus* occupied the broad valley of the Rio Grande de Santiago.

Pregnant females and males with scrotal testes were taken in February, juveniles in May, and lactating females and males with scrotal testes in September. Nonreproductive animals were also collected in February and May.

Other rodents collected sympatrically with *Peromyscus simulus* include *P. spicilegus*, *P. maniculatus*, *Osgoodomys banderanus*, *Reithrodontomys fulvescens*, *Neotoma mexicana*, *Hodomys alleni*, *Baiomys taylori*, *Sigmodon alleni*, *S. hispidus*, *Oryzomys melanotis*, *O. palustris*, *Rattus rattus*, *Liomys pictus*, and *Perognathus pernix*.

SPECIMENS EXAMINED.—4 km S Aticama, 50 m, 1; 4 km N Cuautla, sea level, 1; 1 mi S Cuautla, sea level, 127; Cucharas, Rio Acaponeta, 100 m, 7; 1.2 mi (by rd) S El Casco, Rio Chilte, 60 m, 4; Navarrete, 50 m, 3; Paso de Soquilpa, 8.8 mi E San Blas, 100 m, 8; San Blas, 6; 1.4 mi N (by rd) Tacote, 15 m, 10; Teponahuaxtla, 50 m, 15.

Peromyscus madrensis Merriam

Peromyscus madrensis Merriam, 1898a:16.—Carleton, 1977:41.

Peromyscus boylei madrensis.—Osgood, 1909:152.

Peromyscus boylei madrensis.—Miller and Kellogg, 1955:495.—Hall and Kelson, 1959:635.

HOLOTYPE.—USNM 89223, adult male, skin and skull from Maria Madre Island, Tres Marias Islands, Nayarit. Holotype examined.

GENERAL DISTRIBUTION.—Confined to the Tres Marias Islands, about 50 miles off the coast of Nayarit.

DISTRIBUTION IN NAYARIT.—Maria Madre Island, Maria Magdalena Island, Maria Cleofas Island, and San Juanito Island.

DIAGNOSIS.—A species of the *Peromyscus boylei*

species group, subgenus *Peromyscus*, distinguished by its large skull and relatively small toothrow and auditory bullae; dentition relatively simple; tail long, indistinctly bicolored, and with terminal one-third as dark below as above; hind feet large (24–28 mm) and pinnae relatively small (17–20 mm); phallus comparatively small with dorsal lappets weakly developed and no ventral lappet; karyotype with four pairs of biarmed autosomes ($2n=48$; FN=54).

TAXONOMIC REMARKS.—The origin of the mammalian fauna of the Tres Marias Islands poses interesting biogeographical questions. In view of the nearness of the Tres Marias Islands to continental Mexico, it might be assumed that the few kinds of mammals living there are only slightly differentiated from mainland forms, at most recognizable as subspecies thereof. Instead, recent studies (Bogan, 1978; Diersing and Wilson, 1980) have affirmed the singular distinctiveness of populations on the Tres Marias with respect to their proximate mainland relatives; so it is with the Tres Marias mouse, *Peromyscus madrensis*.

In naming *madrensis* as a species, Merriam (1898a) expressly considered *spicilegus* its nearest ally. Osgood (1909) echoed this viewpoint but redefined both *madrensis* and *spicilegus* as subspecies of *boylei*; however, Carleton (1977), in raising *spicilegus* to specific level, questioned whether *madrensis* properly belonged as a subspecies of either *spicilegus* or *boylei* and reinstated it as a species based upon its unique traits. The additional specimens of *madrensis* now available support this action and allow a better evaluation of its probable derivation from continental species.

Despite their similarity in size, which probably led Merriam and Osgood to regard them as near relatives, *madrensis* and *spicilegus* differ substantially in a suite of characteristics that suggests a distant phyletic affinity. Trenchant differences involve cranial proportions, development of a supraorbital shelf, dental complexity, morphology of the glans penis, and the number of biarmed chromosomes. With respect to each of these features, *spicilegus* more closely resembles *aztecus* of southern Mexico and Central America, whereas

madrensis agrees with *boylei* and, in particular, with *simulus*.

A prediction of close kinship between *madrensis* and *simulus* appears, at first glance, unexpected, if not wholly improbable. Examples of *madrensis* and *simulus* fall at opposite extremes in the size range of *boylei*-group forms in Nayarit. Nevertheless, the shape and proportions of the skulls of *madrensis* and *simulus* are quite similar, an observation corroborated by the results of the clustering exercise using the correlation coefficient to estimate phenetic resemblance (see Figure 4). Also, the bacular length and length of the glans penis are relatively short in both *madrensis* and *simulus* in contrast to the proportionately long phallus of *boylei* (see Carleton, 1977, fig. 6). Like specimens of *simulus*, those of *madrensis* frequently lack well-developed accessory dental styles and lophes. Karyotypically, *madrensis* differs from *simulus* only in possessing one more pair of biarmed chromosomes, giving a FN of 54 rather than 52. The karyotype of *madrensis* is more like that of *simulus* than any other species of *Peromyscus* in mainland Nayarit. Accordingly, we believe that *madrensis* evolved either from *simulus* or from the ancestral stock that gave rise to *simulus* and *boylei*.

The origin of *madrensis* from *simulus* or a *simulus*-like ancestor is also zoogeographically reasonable. The range of *Peromyscus simulus* occupies the lowland coastal plain in Nayarit, which places it as the geographically most proximate ancestral source in contrast to the montane distributions of *spicilegus* and *boylei*. The geological history of the Tres Marias Islands is poorly known. Hanna (1926) suggested that the area has been above sea level since the Pliocene; the presence of Pliocene reefs on the eastern side of the islands indicates that the area was insular or at least peninsular at that time. The four islands composing the Tres Marias were almost surely united, but a connection with the mainland cannot be established with certainty. A lowering of the sea level by 120 meters, generally accepted as maximal at that latitude during the Pleistocene, would still leave about 30 km of oceanic barrier. The possibility of

rafting at a time when the water gap was narrower is enhanced by the location of the Tres Marias opposite the mouth of the Rio Grande de Santiago. Whether the ancestral *madrensis* became isolated from its coastal progenitor by severance of a land bridge or by rafting cannot be determined at this point.

The morphological distinctiveness of *madrensis* does not necessarily argue for a long time span in isolation. Some features, especially its large body size, may be evolutionarily labile, due either to release from competition with other rodents or to a reduction of predation pressure (see, for example, Heaney, 1978; Wassersug et al., 1979). Interestingly, the taxonomic distances separating our three samples of *madrensis* exceed those recorded between any of the geographic samples of *boylei*, *simulus*, or *spicilegus* (Figure 3), suggesting a higher degree of intraspecific differentiation in connection with their insularity.

ECOLOGICAL NOTES.—On Maria Cleofas, the southernmost island, *Peromyscus madrensis* was abundant in a variety of habitats. Maria Cleofas is the least disturbed of the four islands and harbors an extensive, 30-m-high forest on its eastern part. Specimens of *madrensis* were trapped in this forest as well as in lower, shrubby vegetation near the shore. An arroyo with a fresh-water stream also contained large numbers of these mice.

In 1897, Nelson and Goldman collected *madrensis* on Maria Magdalena (Nelson, 1899), an island 16 km to the northwest of Maria Cleofas. No specimens of *madrensis* were obtained here despite four days of intensive effort to locate them. Their absence now is probably due to the presence of one or more of the introduced species that now abound on Maria Magdalena. *Rattus rattus* occurs throughout Maria Magdalena, even at an elevation of 500 m near its center. This commensal, currently unknown from Maria Cleofas, was unknown from Maria Magdalena at the time of Nelson and Goldman's expedition (Nelson, 1899). Domestic goats and white-tailed deer (*Odocoileus virginiana*), also abundant on the island, have

drastically altered the undergrowth and have left a conspicuous browse line on trees.

Four miles northwest of Maria Magdalena is Maria Madre, the largest of the island complex. This is the only inhabited island, currently serving as a penal colony of approximately 1000 people. *Peromyscus madrensis* was found only in the interior highlands, away from areas where *Rattus rattus* was taken. At one time, the interior was covered by a forest that included abundant Spanish cedar (*Cedrela mexicana*), but extensive logging has left only a few forested patches. Examples of *madrensis* were caught along arroyos and on the surrounding hillsides.

San Juanito, the smallest island, lies three km northwest of Maria Madre. Nelson and Goldman failed to capture *madrensis* in 1897 and attributed their absence to the occurrence of numerous land crabs (Nelson, 1899). Nonetheless, *madrensis* were found to be fairly common on the level, elevated plateau that forms most of the island. The vegetation is low (four to five m in height), spiny, and dense.

Our collections, made in March, contain pregnant, lactating, and nonreproductive females, males with scrotal testes and males with abdominal testes, and juveniles of both sexes.

SPECIMENS EXAMINED.—Tres Marias Islands, Maria Cleofas, 42; Maria Madre, 26; Maria Magdalena, 1; Isla San Juanito, 24.

Peromyscus pectoralis pectoralis Osgood

Peromyscus attwateri pectoralis Osgood, 1904:59.

Peromyscus pectoralis.—Bailey, 1906:57.

TYPE-LOCALITY.—Jalpan, Queretaro.

GENERAL DISTRIBUTION.—Southwestern Coahuila and Durango southward through Zacatecas, San Luis Potosi, Aguascalientes, Nayarit, and Jalisco to Queretaro and Hidalgo in eastern Mexico.

DISTRIBUTION IN NAYARIT.—Previously known only from two localities in the extreme southern part of the state, Ixtlan and near San Jose del Conde (Schmidly, 1972). Probably occurs

throughout most of the southeastern quarter of the state; known elevational range from 100 to 1560 meters.

DISTINGUISHING CHARACTERISTICS.—Of the three species of *Peromyscus* trapped with it, *pectoralis* is most similar in coloration and size to *spicilegus*. Specimens of *pectoralis* can readily be separated by their more diluted pelage color, relatively longer tail, small and delicate hind feet, and slightly built body. The skull of *pectoralis* is more gracile in appearance compared to that of *spicilegus*, especially as reflected in the slender rostrum, smoothly rounded braincase, and short tooththrow. From *melanophrys*, *pectoralis* can be identified by its smaller size and much shorter tail. Examples of *pectoralis* differ from *maniculatus* in having longer and indistinctly bicolored tails. The smoothly globose braincase and the rounded (semicircular) outline of the fronto-parietal suture, which terminates laterally as conspicuous anterior projections of the parietals, distinguish *pectoralis* from all other *Peromyscus* that we have seen from Nayarit.

Our karyotypic samples conform to previous reports for the species (Hsu and Arrighi, 1968; Kilpatrick and Zimmerman, 1975): three pairs of large subtelocentrics; one pair each of medium subtelocentrics, small submetacentrics, and small metacentrics; and 17 pairs of acrocentrics graded evenly in size from small to large (FN=58). A large subtelocentric X and small metacentric Y form the sex chromosomes. One specimen, a male from 1.8 mi NW Coapan, exhibited autosomal heteromorphism in which two pairs of autosomes, both acrocentric in other *pectoralis* karyotyped, each consisted of an acrocentric and a subtelocentric chromosome (FN=60). Kilpatrick and Zimmerman (1975) discovered no chromosomal variation in *pectoralis* they examined, based on many samples throughout its range.

ECOLOGICAL NOTES.—*Peromyscus pectoralis*, like *maniculatus*, is limited to the topographically diverse southern part of the state. Within this area, it occupies habitats generally indistinguishable from those of *spicilegus*. Dry, forested slopes and rocky hillsides often harbor both species. At Ran-

cho Zapotito on the Jalisco border, *pectoralis* was the only *Peromyscus* collected.

Although typically found at higher elevations, *pectoralis* was not uncommon at the place where Arroyo Jiguite joins the Rio Grande de Santiago. This low elevational record (100 m) parallels the situation noted for *maniculatus* at nearby Rio Chilte. Again, a likely explanation for these unexpectedly low elevational records involves the dispersion of populations along the Rio Grande de Santiago, which provides a sharply cut corridor through the highlands extending southward and eastward from the area.

Reproductively inactive animals were collected in January, October, and November. One male taken in November had scrotal testes.

Peromyscus pectoralis occurs sympatrically with *P. melanophrys*, *P. maniculatus*, *P. spicilegus*, *Reithrodontomys fulvescens*, *Neotoma mexicana*, *Baiomys taylori*, *Sigmodon alleni*, *S. arizonae*, *S. mascotensis*, *Oryzomys melanotis*, *O. palustris*, *Rattus rattus*, *Liomys irroratus*, and *L. pictus*.

SPECIMENS EXAMINED.—Arroyo de Jiguite, Rio Grande de Santiago, 100 m, 3; 1.8 mi (by rd) NW Coapan, 1560 m, 7; Rancho Zapotito, 1100 m, 2.

Peromyscus spicilegus Allen

Peromyscus spicilegus Allen, 1897:50.—Carleton, 1977:41.

Peromyscus boylei spicilegus.—Osgood, 1909:149 [part].

Peromyscus boylii spicilegus.—Miller and Kellogg, 1955:495 [part].—Hall and Kelson, 1959:636 [part].

HOLOTYPE.—AMNH 8323/6657, adult male, skin and skull, from Mineral San Sebastian, Mascota, Jalisco. Holotype examined.

GENERAL DISTRIBUTION.—Southern Sinaloa and Durango in the north, through Nayarit, Zacatecas, Jalisco, and Colima, to western and central Michoacan in the south. Known elevational limits from 15 m (2 mi E San Blas, Nayarit) to 2100 m (13 km SW Santa Teresa, Nayarit); most localities lie between 500 and 1600 meters.

DISTRIBUTION IN NAYARIT.—Throughout the southern half of the state and extending northward through the central part along the flanks and foothills of the Sierra Madre Occidental,

generally between 100 and 1600 m elevation. Absent from the coastal plain that dominates the west-central sector of Nayarit.

DIAGNOSIS.—A species of the subgenus *Peromyscus* distinguished by a medium-sized skull with a moderately developed supraorbital shelf and small auditory bullae; teeth relatively complicated, and second primary fold usually prominent on lower third molar; tail weakly bicolored; glans penis long and wide with relatively long protractile tip, body of glans marked with shallow longitudinal furrows, dorsal and ventral lappets absent; and karyotype with 17 to 19 pairs of banded autosomes ($2n=48$; FN=79–84).

TAXONOMIC REMARKS.—Many of the samples that Osgood (1909) arranged under *boylei spicilegus*, primarily those in southern Chihuahua and the highlands of Sinaloa and Durango, have been regarded as *boylei rowleyi* (Hooper, 1955; Baker and Greer, 1962). These reassignments plus the reallocations by Carleton (1977) removed populations of *boylei* that had mistakenly been classified as *spicilegus*. In addition, Carleton (1977) extended the southern distributional limits of *spicilegus* to encompass populations in Michoacan that had been allocated previously to *evides*.

As noted by Osgood (1909) and Hooper (1968), *spicilegus* shares many characteristics with *aztecus*, particularly with the race *a. evides*, and one could argue that *spicilegus* is a subspecies of *aztecus*. Despite the apparent closeness of their affinity, Carleton (1979) pointed out differences and urged retention of *spicilegus* as a species.

If a rassenkreis-like situation exists with respect to the *aztecus* complex, then populations of *spicilegus* and *aztecus hylocetes* represent the noninterbreeding end points of the chain. Thus, examples of *a. hylocetes* intergrade morphologically with those of *a. oaxacensis* of the highlands of central Oaxaca, and the latter with *a. aztecus* on the eastern flanks of the Sierra Madre Oriental and with *a. evides* in the Sierra Madre del Sur of Oaxaca and Guerrero. In the coastal sierras of the latter two states, populations of *a. evides* range lower in elevation, and it is the relatively smaller size and brighter coloration of these specimens

that suggest a relationship to *spicilegus* in Michoacan.

The key to the taxonomic status of *spicilegus* involves understanding the relationships of populations in Michoacan. In his description of *spicilegus evides* (type-locality: Juquila, Oaxaca), Osgood (1904) only mentioned the intermediacy of some specimens from Los Reyes, Michoacan, to those of *spicilegus* in Jalisco and *evides* from its type-locality. The series from Los Reyes was formally allocated to *boylei evides* in Osgood's (1909) revision. This action established the precedent for regarding the Michoacan animals as *boylei evides* (Hall and Villa, 1949; Hall and Kelson, 1959) and later as *Peromyscus evides* (Hooper, 1961, 1968). Carleton (1977), however, drew attention to their strong phenetic resemblance to *spicilegus*. The latter finding constitutes the most persuasive argument for leaving *spicilegus* as a species at this point, for, in Michoacan and Jalisco, populations of *a. hylocetes* occupy the highlands of the Cordillera Transvolcanica and are largely altitudinally segregated from the smaller form *spicilegus*, which inhabits the lower slopes. Hooper (1955) reported a locality of sympatry for *spicilegus* and *a. hylocetes* in western Jalisco.

ECOLOGICAL NOTES.—In many respects, *spicilegus* is the most euryctious species of *Peromyscus* in Nayarit, as it occurs throughout the intermediate montane belt and occupies a broad spectrum of habitats within that zone. At lower and middle elevational localities, arid, rocky hillsides may be the preferred habitat. In such areas, *spicilegus* is usually found on the hillsides, and other species of *Peromyscus* are mostly in arroyo bottoms or broader, grassy valleys. *Peromyscus spicilegus* is common in the pine-oak zone in the southern part of the state. At the highest elevation where *spicilegus* was obtained (Rancho Viejo, 2100 m), they were living on the sides of a steeply cut arroyo that dissected a broad valley in pine forest. In the forest proper, *boylei* was the common species.

Indications of reproduction were noted as follows: males with scrotal testes were caught in January, March, September, and October; lactating females in January, September, and Oc-

tober; and juveniles in February and March. Nonreproductive animals were taken in the same months, as well as in November.

Peromyscus spicilegus was captured together with *P. boylii*, *P. simulus*, *P. pectoralis*, *P. melanophrys*, *P. maniculatus*, *Osgoodomys banderanus*, *Reithrodontomys fulvescens*, *Neotoma mexicana*, *Hodomys alleni*, *Baiomys taylori*, *Oryzomys fulvescens*, *O. melanotis*, *O. palustris*, *Sigmodon alleni*, *S. arizonae*, *S. mascotensis*, *Rattus rattus*, *Mus musculus*, *Liomys irroratus*, and *L. pictus*.

SPECIMENS EXAMINED.—Agua Escondida, 1380 m, 5; 8 mi (by rd) S Ahuacatlan, 1500 m, 46; Arroyo de Jiguite, Rio Grande de Santiago, 100 m, 6; Arroyo Taberna, 2 mi WNW Mesa del Nayar, 1200 m, 5; Chacala, 30 m, 37; 1.8 mi (by rd) NW Coapan, 1560 m, 10; Cucharas, Rio Acaponeta, 100 m, 8; El Refilion, 850 m, 61; 3.5 mi (by rd) E El Venado, 100 m, 1; Estanzuela, 1380 m, 9; 10 km N Jala, 1600 m, 3; 2 mi E Jalcocotan, 500 m, 49; Jalisco, 1000 m, 2; 1 km S La Villita, 760 m, 11; Mesa del Nayar, 1300 m, 9; Pedro Pablo, 820 m, 1; 2 mi E San Pedro Lagunillas, E side lake, 1300 m, 2; Rancho Viejo, 13 km SW Santa Teresa, 2100 m, 6; Tempiste, Rio Ameca, 840 m, 2.

Peromyscus melanophrys micropus Baker

Peromyscus melanophrys micropus Baker, 1952:255.

TYPE-LOCALITY.—3 mi N Guadalajara, Jalisco.

GENERAL DISTRIBUTION.—KNOWN only from extreme southern Durango (Crossin et al., 1973), Nayarit, and Jalisco.

DISTRIBUTION IN NAYARIT.—We have collected specimens only from Mesa del Nayar in the eastern mountains and from Arroyo de Jiguite on the Rio Grande de Santiago in the center of the state. These constitute the first records of this species from the state of Nayarit.

DISTINGUISHING CHARACTERISTICS.—Upper parts buffy or pale reddish with individual hairs gray at bases, paler at tips. Underparts with individual hairs gray at bases and white at tips, giving overall grayish appearance. Tail much longer than head and body, sparsely haired at

base but becoming more densely haired distally and ending with a small tuft. The extremely long tail readily distinguishes *melanophrys* from all other *Peromyscus* in the state.

Chromosomal preparations from animals collected at Mesa del Nayar and Arroyo de Jiguite are uniform. The autosomal complement consists of one small, one medium, and three large subtelocentric pairs, one small metacentric pair, and 17 acrocentric pairs evenly graded, large to small, yielding a fundamental number of 58 (Figure 14b). The X chromosome is a large subtelocentric. The morphology of the Y chromosome is difficult to ascertain because of its minute size, which is decidedly smaller than any of the autosomes. This karyotype contrasts slightly with that reported for Zacatecan *P. melanophrys consobrinus* (Hsu and Arrighi, 1968), which typically possesses one less biarmed pair (FN=56); however, those authors noted some polymorphism in their small sample. The tiny size of the Y chromosome in the Nayarit samples agrees with that documented in the Zacatecan *melanophrys* by Hsu and Arrighi (1968), who reported a minute metacentric in one male but a minute acrocentric in others.

ECOLOGICAL NOTES.—This species inhabits arid rocky areas over most of the central Mexican Plateau (Baker, 1952). Two individuals were collected from a rocky arroyo at Mesa del Nayar, Nayarit, a locality on the western extension of the Sierra Madre Occidental, elevation 1300 m. *Peromyscus melanophrys* probably occurs throughout mountainous eastern Nayarit, as the species is known from similar areas in Durango to the north and Jalisco to the south.

We also collected 10 *melanophrys* from Arroyo de Jiguite on the Rio Grande de Santiago at an elevation of 100 m together with specimens of *pectoralis*, another highland form. Nearby at Rio Chilte, we found *maniculatus*, also more commonly considered a species of higher elevations. We assume that these species are reaching this lowland area along the corridors provided by the Rio Grande de Santiago and the Rio Huayanamota.

It would be interesting to determine the ecological requirements of each of the species that occur in such close proximity within this general area: *maniculatus*, *pectoralis*, *melanophrys*, *simulus*, and *spicilegus*.

The two specimens from Mesa del Nayar are a juvenile female and a male with scrotal testes. The Arroyo Jiguite sample, taken in January, includes males with scrotal testes, others with abdominal testes, and a juvenile. Some females

were lactating, others were not, and one was a juvenile.

Peromyscus melanophrys was recorded sympatrically with *P. pectoralis*, *P. spicilegus*, *Reithrodontomys fulvescens*, *Neotoma mexicana*, *Oryzomys melanotis*, *O. palustris*, *Sigmodon alleni*, *S. mascotensis*, *S. arizonae*, *Rattus rattus*, *Liomys pictus*, and *L. irroratus*.

SPECIMENS EXAMINED.—Arroyo de Jiguite, Rio Grande de Santiago, 100 m, 10; Mesa del Nayar, 1300 m, 2.

Appendix

Measurements (in mm) of Selected Samples of the *Peromyscus boylii* Species Group

<i>Species and sample</i>	<i>N</i>	<i>Mean</i>	<i>Range</i>	<i>1 SD</i>
TOTAL LENGTH				
<i>P. boylii</i> BOYOCO	37	187.0	157–215	14.4
BOYSTE	41	188.4	169–212	10.0
<i>P. madrensis</i> MADCLE	30	225.8	210–250	9.8
MADJON	15	221.9	203–246	11.9
<i>P. simulus</i> SIMCUA	56	189.0	165–238	11.4
<i>P. spicilegus</i> SPIAHU	29	196.9	175–232	13.8
SPIJAL	35	198.9	175–220	10.2
SPIREF	37	192.4	171–232	12.8
LENGTH OF TAIL				
<i>P. boylii</i> BOYOCO	37	93.3	74–114	8.1
BOYSTE	41	91.5	74–113	7.9
<i>P. madrensis</i> MADCLE	30	114.5	103–130	6.6
MADJON	15	110.7	99–126	7.1
<i>P. simulus</i> SIMCUA	56	89.3	78–102	5.6
<i>P. spicilegus</i> SPIAHU	29	97.4	85–115	7.1
SPIJAL	35	95.7	80–108	6.7
SPIREF	37	90.9	79–110	7.3
LENGTH OF HIND FOOT				
<i>P. boylii</i> BOYOCO	37	20.9	19–22	0.8
BOYSTE	41	21.3	18–24	1.3
<i>P. madrensis</i> MADCLE	36	25.6	23–28	1.0
MADJON	17	25.6	25–26	0.5
<i>P. simulus</i> SIMCUA	59	22.4	21–24	0.8
<i>P. spicilegus</i> SPIAHU	29	21.7	20–23	0.7
SPIJAL	35	21.6	20–23	0.9
SPIREF	37	23.2	22–25	0.7
LENGTH OF EAR				
<i>P. boylii</i> BOYOCO	37	19.3	17–22	1.1
BOYSTE	31	18.8	18–21	0.9
<i>P. madrensis</i> MADCLE	33	18.2	17–20	0.7
MADJON	17	18.6	18–20	0.7
<i>P. simulus</i> SIMCUA	59	17.7	16–19	0.8
<i>P. spicilegus</i> SPIAHU	29	18.6	17–21	0.9
SPIJAL	35	17.9	16–20	1.0
SPIREF	37	17.9	17–20	1.0

APPENDIX.—Continued

<i>Species and sample</i>		<i>N</i>	<i>Mean</i>	<i>Range</i>	<i>1 SD</i>
GREATEST LENGTH OF SKULL					
<i>P. boylii</i>	BOYOCO	37	26.94	25.00–28.66	1.02
	BOYSTE	39	26.84	25.34–28.36	0.71
<i>P. madrensis</i>	MADCLE	30	29.84	28.34–31.50	0.91
	MADJON	16	29.77	28.46–31.36	0.82
<i>P. simulus</i>	SIMCUA	58	26.72	24.75–28.69	0.84
<i>P. spicilegus</i>	SPIAHU	29	27.73	25.93–30.18	1.00
	SPIJAL	35	28.26	26.36–30.45	0.98
	SPIREF	34	27.86	25.88–30.75	1.18
CONDYLOINCISIVE LENGTH					
<i>P. boylii</i>	BOYOCO	37	23.76	22.15–25.77	0.91
	BOYSTE	41	23.86	22.47–25.12	0.72
<i>P. madrensis</i>	MADCLE	34	26.52	25.24–28.08	0.77
	MADJON	17	26.28	24.91–27.84	0.82
<i>P. simulus</i>	SIMCUA	57	23.83	22.01–25.12	0.68
<i>P. spicilegus</i>	SPIAHU	29	24.68	23.05–26.87	0.95
	SPIJAL	35	24.94	23.48–27.27	0.90
	SPIREF	37	24.61	22.57–27.34	1.09
LENGTH OF AUDITORY BULLA					
<i>P. boylii</i>	BOYOCO	37	3.94	3.46–4.47	0.21
	BOYSTE	41	3.91	3.48–4.30	0.19
<i>P. madrensis</i>	MADCLE	35	3.83	3.54–4.37	0.16
	MADJON	17	3.81	3.65–4.10	0.14
<i>P. simulus</i>	SIMCUA	59	3.45	3.03–3.80	0.15
<i>P. spicilegus</i>	SPIAHU	29	3.73	3.38–4.05	0.17
	SPIJAL	35	3.63	3.32–4.01	0.17
	SPIREF	37	3.57	3.18–3.87	0.17
POSTPALATAL LENGTH					
<i>P. boylii</i>	BOYOCO	37	9.44	8.49–10.56	0.54
	BOYSTE	41	9.41	8.50–10.62	0.39
<i>P. madrensis</i>	MADCLE	34	10.55	9.70–11.26	0.40
	MADJON	15	10.53	9.91–11.05	0.33
<i>P. simulus</i>	SIMCUA	58	9.54	8.72–10.23	0.38
<i>P. spicilegus</i>	SPIAHU	29	9.69	8.99–11.10	0.49
	SPIJAL	35	9.86	9.24–11.45	0.46
	SPIREF	37	9.57	8.47–10.89	0.57
LENGTH OF MESOPTERYGOID FOSSA					
<i>P. boylii</i>	BOYOCO	37	4.50	3.91–5.00	0.26
	BOYSTE	40	4.54	4.07–5.10	0.26
<i>P. madrensis</i>	MADCLE	25	5.32	4.96–5.68	0.20
	MADJON	14	4.92	4.64–5.25	0.18
<i>P. simulus</i>	SIMCUA	51	4.74	4.22–5.22	0.21
<i>P. spicilegus</i>	SPIAHU	29	4.69	4.23–5.19	0.27
	SPIJAL	35	4.89	4.33–5.35	0.24
	SPIREF	37	4.83	4.38–5.49	0.28

APPENDIX.—Continued

Species and sample		<i>N</i>	Mean	Range	<i>l</i> SD
PALATAL LENGTH					
<i>P. boylii</i>	BOYOCO	37	3.92	3.48-4.45	0.18
	BOYSTE	41	4.04	3.64-4.43	0.21
<i>P. madrensis</i>	MADCLE	36	4.08	3.82-4.45	0.15
	MADJON	17	4.83	4.50-5.27	0.21
<i>P. simulus</i>	SIMCUA	59	3.68	3.32-4.20	0.17
<i>P. spicilegus</i>	SPIAHU	29	4.44	4.02-4.90	0.21
	SPIJAL	35	4.34	3.35-5.24	0.32
	SPIREF	37	4.34	3.92-4.71	0.20
LENGTH OF INCISIVE FORAMEN					
<i>P. boylii</i>	BOYOCO	37	5.64	5.18-6.32	0.27
	BOYSTE	41	5.66	5.21-6.06	0.20
<i>P. madrensis</i>	MADCLE	36	6.18	5.86-6.67	0.20
	MADJON	17	5.41	5.17-5.56	0.13
<i>P. simulus</i>	SIMCUA	59	5.56	4.85-6.12	0.27
<i>P. spicilegus</i>	SPIAHU	29	5.62	5.06-6.25	0.30
	SPIJAL	35	5.71	5.04-6.33	0.34
	SPIREF	36	5.74	4.93-6.61	0.37
ALVEOLAR LENGTH OF MAXILLARY TOOTHROW					
<i>P. boylii</i>	BOYOCO	37	4.32	4.07-4.62	0.13
	BOYSTE	41	4.26	4.02-4.47	0.11
<i>P. madrensis</i>	MADCLE	36	4.46	4.13-4.74	0.14
	MADJON	17	4.48	4.31-4.68	0.09
<i>P. simulus</i>	SIMCUA	59	4.09	3.79-4.52	0.15
<i>P. spicilegus</i>	SPIAHU	29	4.56	4.34-4.86	0.14
	SPIJAL	35	4.54	4.18-4.99	0.18
	SPIREF	37	4.47	4.27-4.92	0.14
GREATEST ZYGOMATIC BREADTH					
<i>P. boylii</i>	BOYOCO	37	13.67	12.59-14.73	0.52
	BOYSTE	40	13.56	12.72-14.82	0.44
<i>P. madrensis</i>	MADCLE	35	15.04	14.44-15.69	0.35
	MADJON	17	14.79	14.10-15.60	0.42
<i>P. simulus</i>	SIMCUA	57	13.95	12.84-14.76	0.44
<i>P. spicilegus</i>	SPIAHU	29	14.01	12.65-15.13	0.54
	SPIJAL	35	14.08	13.14-15.35	0.43
	SPIREF	37	14.13	13.17-16.05	0.62
MASTOIDAL BREADTH					
<i>P. boylii</i>	BOYOCO	37	11.74	11.14-12.23	0.35
	BOYSTE	40	11.63	11.00-12.18	0.30
<i>P. madrensis</i>	MADCLE	35	12.22	11.66-12.68	0.24
	MADJON	17	12.31	11.95-12.66	0.22
<i>P. simulus</i>	SIMCUA	59	11.37	10.67-11.85	0.25
<i>P. spicilegus</i>	SPIAHU	29	11.76	11.01-12.42	0.31
	SPIJAL	35	11.80	11.16-12.42	0.31
	SPIREF	36	11.69	11.02-12.63	0.38

APPENDIX.—Continued

Species and sample		<i>N</i>	Mean	Range	1 <i>SD</i>
GREATEST BREADTH ACROSS MOLARS					
<i>P. boylii</i>	BOYOCO	37	5.35	4.87–5.73	0.20
	BOYSTE	41	5.27	4.79–5.81	0.22
<i>P. madrensis</i>	MADCLE	36	6.14	5.87–6.68	0.18
	MADJON	17	5.83	5.50–6.28	0.22
<i>P. simulus</i>	SIMCUA	59	5.33	4.96–5.80	0.20
<i>P. spicilegus</i>	SPIAHU	29	5.44	5.01–5.89	0.23
	SPIJAL	35	5.50	5.26–5.96	0.16
	SPIREF	37	5.53	5.14–6.22	0.22
POSTDENTAL PALATAL BREADTH					
<i>P. boylii</i>	BOYOCO	37	3.71	3.33–4.09	0.18
	BOYSTE	41	3.75	3.33–4.14	0.16
<i>P. madrensis</i>	MADCLE	36	4.53	4.16–4.90	0.17
	MADJON	17	4.43	4.26–4.61	0.09
<i>P. simulus</i>	SIMCUA	59	3.84	3.49–4.09	0.13
<i>P. spicilegus</i>	SPIAHU	29	4.07	3.69–4.58	0.19
	SPIJAL	35	4.03	3.40–4.35	0.21
	SPIREF	37	4.04	3.64–4.44	0.18
GREATEST WIDTH OF MESOPTERYGOID FOSSA					
<i>P. boylii</i>	BOYOCO	37	1.80	1.51–2.28	0.13
	BOYSTE	41	1.77	1.53–2.14	0.13
<i>P. madrensis</i>	MADCLE	35	1.88	1.66–2.12	0.13
	MADJON	17	1.71	1.56–1.95	0.10
<i>P. simulus</i>	SIMCUA	59	1.70	1.47–2.06	0.11
<i>P. spicilegus</i>	SPIAHU	29	2.03	1.74–2.32	0.17
	SPIJAL	35	2.09	1.77–2.40	0.16
	SPIREF	37	1.96	1.68–2.39	0.16
DEPTH OF BRAINCASE					
<i>P. boylii</i>	BOYOCO	37	9.98	9.41–10.45	0.28
	BOYSTE	41	9.80	9.23–10.41	0.29
<i>P. madrensis</i>	MADCLE	35	9.92	9.45–10.38	0.20
	MADJON	17	10.18	9.80–10.48	0.16
<i>P. simulus</i>	SIMCUA	52	9.39	8.60–9.82	0.25
<i>P. spicilegus</i>	SPIAHU	29	9.93	9.23–10.57	0.35
	SPIJAL	35	10.03	9.42–10.60	0.28
	SPIREF	36	9.72	9.21–10.41	0.28
BREADTH OF BRAINCASE					
<i>P. boylii</i>	BOYOCO	37	12.36	11.79–12.99	0.32
	BOYSTE	41	12.37	11.71–12.92	0.29
<i>P. madrensis</i>	MADCLE	35	12.63	12.16–13.03	0.21
	MADJON	17	12.47	12.08–13.08	0.24
<i>P. simulus</i>	SIMCUA	59	11.96	10.36–12.49	0.35
<i>P. spicilegus</i>	SPIAHU	29	12.50	11.87–13.18	0.36
	SPIJAL	35	12.58	11.88–13.28	0.29
	SPIREF	36	12.41	11.68–13.16	0.40

APPENDIX.—Continued

<i>Species and sample</i>		<i>N</i>	<i>Mean</i>	<i>Range</i>	<i>1 SD</i>
LEAST INTERORBITAL WIDTH					
<i>P. boylii</i>	BOYOCO	37	4.36	4.04–4.65	0.16
	BOYSTE	41	4.34	4.00–4.66	0.15
<i>P. madrensis</i>	MADCLE	36	4.67	4.41–4.90	0.14
	MADJON	17	4.73	4.53–4.99	0.13
<i>P. simulus</i>	SIMCUA	59	4.20	3.66–4.61	0.17
<i>P. spicilegus</i>	SPIAHU	29	4.48	4.27–4.69	0.12
	SPIJAL	35	4.52	4.25–4.82	0.15
	SPIREF	37	4.42	4.09–4.85	0.18
ROSTRAL BREADTH					
<i>P. boylii</i>	BOYOCO	37	4.61	4.25–5.03	0.18
	BOYSTE	38	4.68	4.41–4.96	0.15
<i>P. madrensis</i>	MADCLE	33	5.36	5.02–5.68	0.16
	MADJON	17	5.21	4.86–5.48	0.15
<i>P. simulus</i>	SIMCUA	56	4.85	4.38–5.32	0.22
<i>P. spicilegus</i>	SPIAHU	29	5.00	4.42–5.51	0.25
	SPIJAL	35	4.95	4.61–5.47	0.19
	SPIREF	31	4.93	4.46–5.40	0.20
NASAL LENGTH					
<i>P. boylii</i>	BOYOCO	37	10.53	9.20–11.58	0.55
	BOYSTE	41	10.41	9.18–11.25	0.57
<i>P. madrensis</i>	MADCLE	32	11.64	10.72–12.74	0.45
	MADJON	16	11.09	10.43–12.18	0.46
<i>P. simulus</i>	SIMCUA	59	10.03	9.07–11.13	0.44
<i>P. spicilegus</i>	SPIAHU	29	10.71	9.53–12.09	0.65
	SPIJAL	35	10.89	9.48–12.13	0.60
	SPIREF	34	10.90	9.83–12.19	0.62
ROSTRAL LENGTH					
<i>P. boylii</i>	BOYOCO	37	8.99	7.96–9.93	0.44
	BOYSTE	41	8.92	8.18–9.65	0.38
<i>P. madrensis</i>	MADCLE	32	10.06	9.29–10.88	0.41
	MADJON	16	10.11	9.49–10.94	0.39
<i>P. simulus</i>	SIMCUA	59	8.50	7.70–9.22	0.35
<i>P. spicilegus</i>	SPIAHU	29	9.08	8.25–9.93	0.48
	SPIJAL	35	9.28	8.47–10.18	0.42
	SPIREF	34	9.20	8.32–10.33	0.52

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