AN ABSTRACT OF THE THESIS OF

Jennifer K. Frey for the Master of Science Degree
in Biology presented on 13 March 1989

Title: Morphologic Variation in the Mexican Vole (Microtus mexicanus)

Abstract Approved: 

Variation in 19 cranial and four external measurements was assessed for 65 populations of Microtus mexicanus from throughout its range. Discriminant function analysis resulted in the separation of two major groupings of populations. One group included all populations from Mexico, with the exception of the populations from San Antonio de las Alazanas, Coahuila and near Galena, Nuevo Leon. The other group included these exceptions, plus all populations from the United States. These two groups separated on canonical vector I, which was primarily a size factor with all characters, except mastoidal breadth, having negative character loadings. This separation suggested that M. mexicanus is represented by two species; however, principal component analysis failed to separate the two groups.

Multivariate analyses of variance between neighboring populations resulted in the grouping of populations that were not significantly (P > 0.001) from each other. These nonsignificant groupings were often concordant with the distributions of named subspecies. The United States showed
relatively more nonsignificant differences between neighboring populations than populations from Mexico. Populations from the United States were divided into five groups, each representing a subspecies, based upon the nonsignificant groupings derived from the multivariate analyses of variance; this was also supported by a principal component analysis for those populations with small sample sizes from the Music Mountains, Hualapai Mountains, and south of Prescott, Arizona and neighboring populations. Populations from Mexico showed relatively more differentiation as compared to populations from the United States. The multivariate analyses of variance resulted in the separation of 13 groups in Mexico. The greater divergence of Mexican populations is explained by populations from Mexico being relatively old with the United States populations representing a more recent invasion north during the Illinoian glacial period.
MORPHOLOGIC VARIATION IN THE MEXICAN VOLE (*Microtus mexicanus*)

A Thesis
Submitted to
the Division of Biological Sciences
Emporia State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

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May, 1989
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ACKNOWLEDGMENTS

Many thanks to the curators who allowed me to examine specimens and to Elaine Holmes, Thor Holmes, Michael Kennedy, Phyllis Kennedy, Raymond Lee, Robert Timm and Terry Yates who provided accommodations during visits to their respective collections. I also thank Renwick Guyer for his encouragement and support during much of this work and Tanya Timms for her help recording data. Richard Pimentel provided assistance and suggestions with the statistical analysis. Thanks to the members of my committee, Carl Prophet and Dwight Spencer for their guidance and comments concerning the writing of this thesis. Special thanks go to my major advisor, Dwight Moore, who provided advise, hours of help with various aspects of this thesis, direction in my career and academic goals and became an inspiration to me as a biologist.
PREFACE

This thesis has been prepared in a style appropriate for the Journal of Mammalogy to which it will be submitted for publication.
to my parents,

John and Barbara Frey
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIST OF TABLES</td>
<td>ix</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>x</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>METHODS</td>
<td>4</td>
</tr>
<tr>
<td>RESULTS</td>
<td>12</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>43</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>62</td>
</tr>
<tr>
<td>APPENDIX I</td>
<td>68</td>
</tr>
<tr>
<td>APPENDIX II</td>
<td>82</td>
</tr>
<tr>
<td>TABLE</td>
<td>LIST OF TABLES</td>
</tr>
<tr>
<td>-------</td>
<td>----------------</td>
</tr>
<tr>
<td>1.</td>
<td>Nongeographic variation in differences among three age groups of 102 specimens of <em>Microtus mexicanus</em> from Ixtlan de Juarez, Oaxaca.</td>
</tr>
<tr>
<td>2.</td>
<td>Nongeographic variation in differences between sexes of <em>Microtus mexicanus</em> from Willow Creek, New Mexico, and Volcan de Colima, Jalisco.</td>
</tr>
<tr>
<td>3.</td>
<td>Factor loadings on the first three principal component axes for 65 populations of <em>Microtus mexicanus</em>.</td>
</tr>
<tr>
<td>4.</td>
<td>Factor loadings on the first three canonical axes for 65 populations of <em>Microtus mexicanus</em>.</td>
</tr>
<tr>
<td>5.</td>
<td>Factor loadings on the first three principal components for individuals of <em>Microtus mexicanus</em> from populations PR, MU, HU, AF, GV, WI, MR, and SA.</td>
</tr>
</tbody>
</table>
**LIST OF FIGURES**

<table>
<thead>
<tr>
<th>FIGURE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>7</td>
</tr>
<tr>
<td>Locations of pooled populations of <em>Microtus mexicanus</em> from the United States that were included in this study.</td>
<td></td>
</tr>
<tr>
<td>2.</td>
<td>9</td>
</tr>
<tr>
<td>Locations of pooled populations of <em>Microtus mexicanus</em> from Mexico that were included in this study.</td>
<td></td>
</tr>
<tr>
<td>3.</td>
<td>15</td>
</tr>
<tr>
<td>Discriminant function plot of three age groups of <em>Microtus mexicanus</em>.</td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td>19</td>
</tr>
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<td>Plot of 65 populations of <em>Microtus mexicanus</em> on principal components I and II.</td>
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<td>5.</td>
<td>21</td>
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<td>Plot of 65 populations of <em>Microtus mexicanus</em> on principal components I and III.</td>
<td></td>
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<td>6.</td>
<td>25</td>
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<td>Plot of group centroids of 65 populations of <em>Microtus mexicanus</em> on canonical vectors I and II.</td>
<td></td>
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<td>7.</td>
<td>27</td>
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<tr>
<td>Plot of group centroids of 65 populations of <em>Microtus mexicanus</em> on canonical vectors I and III.</td>
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<td>8.</td>
<td>32</td>
</tr>
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<td>Multivariate analyses of variance between populations of <em>Microtus mexicanus</em> from the United States.</td>
<td></td>
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<td>9.</td>
<td>35</td>
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<tr>
<td>Multivariate analyses of variance between populations of <em>Microtus mexicanus</em> from Mexico.</td>
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<td>38</td>
</tr>
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<td>Plot of individuals of <em>Microtus mexicanus</em> from populations PR, MU, HU, AF, GV, MR, and SA on principal components I and II.</td>
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<tr>
<td>11.</td>
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<tr>
<td>Plot of individuals of <em>Microtus mexicanus</em> from populations PR, MU, HU, AF, GV, MR, and SA on principal components I and III.</td>
<td></td>
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</tbody>
</table>
INTRODUCTION

The faunal elements of the mountains of the southwestern United States and Mexico have been the focal points of many systematic and biogeographical investigations (Findley, 1969; Findley and Jones, 1962; Patterson, 1980, 1982, 1984; Sullivan, 1985; Wilhelm, 1982). This region possesses a physical geography and associated habitats that lends itself well to these inquiries. Mountains extend longitudinally through this region, and much of the montane habitat is limited to isolated mountains or disjunct areas of mountainous regions. In addition, vegetational zonation at differing elevations is conspicuous, with desert scrub vegetation occurring at low elevations; this habitat gives way to pinyon-juniper woodland, then to fir or ponderosa pine forest and finally to spruce forest at the highest elevations (Cole, 1982). During Pleistocene glacial fluctuations, montane forests extended into lower elevations providing possible migration routes among populations of montane species. Glacial retreats and associated warming trends then restricted the montane forests to insular patches at high elevation and thus isolated associated faunas (Findley, 1969). These factors result in disjunct islands of boreal vegetation surrounded by low elevation deserts in Recent times. Therefore, mammals associated with the high elevation habitats are separated from other such populations by inhospitable habitat that results in a lack of gene flow among the populations.
One such montane mammal is the Mexican vole (*Microtus mexicanus*). The Mexican vole occurs in montane grassland generally above 2000 m (Wilhelm, 1979) in the ponderosa and mixed coniferous forests (Findley et al., 1975). Its distribution is from southern Utah and Colorado south to southern Oaxaca, Mexico (Hall, 1981). The geographic isolation that results from the habitat requirements of the Mexican vole may result in morphologic differentiation among the disjunct populations via differential selection pressures in different local environments or via genetic drift. Such differentiation of populations is indicated by the division of the species into 12 subspecies throughout its range (Hall, 1981). Subspecies are primarily distinguished by differences in pelage and cranial morphology although no analysis that included specimens from the entire range of the species has been reported.

In addition, karyotypic variation among populations is apparent. Matthey (1957) established the diploid number as 44 with a fundamental number of 54 or 56, as he was unable to identify the sex chromosomes. Wilhelm (1982) also found a diploid number of 44 and fundamental number of 54 from New Mexico and Texas. However, all karyotypes that have been examined from Mexico had a diploid number of 48 and fundamental number of 56, 57 or 58 (Lee and Elder, 1977; Modi, 1987; Moore, unpub. data) except for a population from San Antonio de las Alazanas, Coahuila, which had a diploid
number of 44 and fundamental number of 54. The difference between the cytotypes from the United States and Mexico suggests that *M. mexicanus* may be represented by two species (Modi, 1987). Likewise, genic data have indicated the presence of one group from Mexico, including those from Coahuila, and a separate group of populations from the United States.

Genic and karyotypic data indicate that considerable genetic differentiation exists among populations of *M. mexicanus*. The purposes of this study are therefore to assess the extent of morphologic variation among populations and to determine if differences coincide with subspecific boundaries and described cytotypes, to compare the phylogenies based on morphology with phylogenies based upon genetic data and finally to correlate patterns of morphologic variation with supposed patterns of vicariant events that are associated with Pleistocene glacial periods.
METHODS

Four external characters and 19 cranial characters were recorded from 1775 specimens (Appendix I). Measurements of cranial characters were taken with a dial caliper to the nearest 0.1 mm and were chosen based on their repeatability and utility in describing size and shape of the skull. Measurements of external characters were recorded from specimen tags. These mensural characters were total length (TL), length of tail (LT), length of hind foot (LHF), length of ear (LE), width of nasals (WN), rostral breadth (RB), interorbital constriction (IC), zygomatic breadth (ZB), prelambdoidal breadth (PLB), mastoid breadth (MB), width of foramen magnum (WFM), height of foramen magnum (HFM), width of incisive foramen (WIF), length of incisive foramen (LIF), condylobasilar length (CBL), length of maxillary diastema (LXD), length of rostrum (LR), length of nasal (LN), length of maxillary toothrow (LMT), rostral depth (RD), greatest length of skull (GLS), and length of mandibular diastema (LND). Characters were taken as described by Best (1978), Choate and Williams (1978), DeBlase and Martin (1981), and Hamilton and Heidt (1984) with the following exceptions: rostral breadth, greatest distance across rostrum anterior to zygomatic arches; width of incisive foramen, greatest distance across the incisive foramen; and rostral depth, least height from nasal to premaxillary. Specimens were assigned to one of three age categories; juvenile, subadult, and adult according to the criteria described by Choate and
Williams (1978) and Hoffmeister (1986).

Specimens were divided into 65 populations (Figs. 1 and 2). Populations were defined as those individuals occurring within a 2,134 m contour interval, which is generally the lower elevational limit for *M. mexicanus* throughout its range. Large areas above 2134 m were subdivided such that a population typically occupied an area less than 15 km in diameter.

Analyses of nongeographic and geographic variation were accomplished using BIOSTAT I (Pimentel and Smith, 1986) and BIOSTAT II (Pimentel and Smith, 1986) computer programs. Basic statistics (mean, standard deviation, coefficient of variation, skewness and kurtosis) were calculated for each character for each population using STATS. For the analysis of nongeographic variation, differences among the age groups and between the sexes were tested. The program MDA was used to perform one-way analyses of variance for each character, discriminant function analyses and multivariate analyses of variance. Individuals from Ixtlan de Juarez, Oaxaca (population IX) were tested for differences among the age groups while individuals from Willow Creek in the Mogollon Mountains, New Mexico (population WC) and from Volcan de Colima, Jalisco (population VC) were tested for differences between the sexes. These populations were selected for the analyses because of sufficiently large sample sizes. In addition, one population from the United States and one from
Fig. 1.--Locations of pooled populations of *Microtus mexicanus* from the United States that were included in this study. Solid lines represent 2,134 m contour intervals.
Fig. 2.--Locations of pooled populations of *Microtus mexicanus* from Mexico that were included in this study. Solid lines represent 2,134 m contour intervals.
Mexico were included for the analyses of sexual dimorphism because these populations may represent separate species based upon previous genetic data (Modi, 1987; Moore, unpub. data).

For the analysis of geographic variation, Student-Newman-Keuls multiple range tests were used to determine subsets of populations that were not significantly different from each other for each character utilizing MDA. Principal component analysis (MPCA) was performed on the character means of 65 populations. Principal components were extracted from a 65 X 23 data matrix and scores for each population were derived. Principal component analysis summarizes the variation in the 23 original characters into new variables each of which successively explains some new dimension of the total variation (Neff and Marcus, 1980). In this way, the first two or three components explain a large proportion of the variation in the data set and populations can be plotted along these new variable axes to determine patterns of similarity.

Discriminant function analysis was performed on 65 populations using individuals as operational taxonomic units to maximize differences among the a priori designated populations. This analysis is similar to principal component analysis although it maximizes the amount of among group variation relative to the variation within groups by weighting characters (Neff and Marcus, 1980). The
individuals can then be plotted along the new variable axes with the centroid for an a priori group being a multivariate mean of those individuals. Multivariate analysis of variance was utilized to test the significance between group centroids. A multivariate F-ratio was used to determine the degree of difference among and between populations. A multivariate F-ratio generated from the population means for each character was used to test the difference between the United States and Mexico. In addition multivariate F-ratios were used to test the significance between group centroids of neighboring populations to determine multivariate nonsignificant groupings of populations. The populations from north of Raton, New Mexico (population NR) and west of Raton (population WR) were pooled as were both populations from the Manzano Mountains, New Mexico (populations FJ and RC) to increase sample sizes. Populations that had sample sizes that were too small to be tested in this way (populations HU, MU and PR) were analyzed using principal component analysis. Individuals of these populations were plotted along with individuals from adjacent populations in order to ascertain similarity among populations.
Results

Nongeographic Variation

For differences among the three age groups, 17 of the 23 characters showed a significant difference \( (P \leq 0.05, \text{ Table 1}) \) and the multivariate analysis of variance resulted in a significant difference among the group centroids \( (F = 4.36, \text{ d.f.} = 46, 154, P = 0.00) \). Ninety-five percent confidence ellipses of the three age groups separated primarily along canonical vector I although the adults and subadults showed considerable overlap (Fig. 3). The juveniles were the most distinct showing no overlap with the other two ages. Juveniles were therefore deleted in subsequent analyses while adults and subadults were pooled.

One-way analyses of variance for each character between sexes resulted in significant differences \( (P \leq 0.05) \) for the pre lambdoidal breadth and width of foramen magnum from Willow Creek, New Mexico, and for the width of nasals from Volcan de Colima, Jalisco (Table 2). The multivariate analysis of variance resulted in no significant sexual dimorphism for the Willow Creek population \( (F = 1.86, \text{ d.f.} = 23, 21, P = 0.078) \). Two male individuals were misclassified as females while all females were assigned to their correct a priori group. However, a slight significant difference \( (F = 1.62, \text{ d.f.} = 23, 119, P = 0.049) \) resulted from the test between group centroids for Volcan de Colima, Jalisco. In addition, 26 percent of the males and 28 percent of the females were misclassified. Although these results suggest
Table 1. Nongeographic variation in differences among three age groups of 102 *Microtus mexicanus* from Ixtlan de Juarez, Mexico. Means for each age group and F-ratios resulting from single-classification analysis of variance are presented for each character. Refer to Methods for definitions of characters and to figure 2 for location of the population.

<table>
<thead>
<tr>
<th>Character</th>
<th>Juvenile (N = 9)</th>
<th>Subadult (N = 30)</th>
<th>Adult (N = 63)</th>
<th>F-ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>TL</td>
<td>121.44</td>
<td>139.40</td>
<td>142.57</td>
<td>40.00***</td>
</tr>
<tr>
<td>LT</td>
<td>31.00</td>
<td>32.50</td>
<td>31.78</td>
<td>0.57</td>
</tr>
<tr>
<td>HF</td>
<td>18.00</td>
<td>19.10</td>
<td>19.08</td>
<td>7.57***</td>
</tr>
<tr>
<td>LE</td>
<td>11.89</td>
<td>13.03</td>
<td>13.22</td>
<td>4.06*</td>
</tr>
<tr>
<td>WN</td>
<td>3.14</td>
<td>3.49</td>
<td>3.53</td>
<td>17.92***</td>
</tr>
<tr>
<td>GRB</td>
<td>5.20</td>
<td>5.39</td>
<td>5.36</td>
<td>2.39</td>
</tr>
<tr>
<td>IC</td>
<td>3.76</td>
<td>3.66</td>
<td>3.61</td>
<td>2.54</td>
</tr>
<tr>
<td>ZB</td>
<td>13.46</td>
<td>14.59</td>
<td>14.95</td>
<td>36.81***</td>
</tr>
<tr>
<td>PLB</td>
<td>10.41</td>
<td>10.52</td>
<td>10.62</td>
<td>2.73</td>
</tr>
<tr>
<td>MB</td>
<td>10.42</td>
<td>11.21</td>
<td>11.38</td>
<td>28.94***</td>
</tr>
<tr>
<td>WFM</td>
<td>4.22</td>
<td>4.24</td>
<td>4.30</td>
<td>2.74</td>
</tr>
<tr>
<td>HFM</td>
<td>4.13</td>
<td>4.15</td>
<td>4.06</td>
<td>1.81</td>
</tr>
<tr>
<td>WIF</td>
<td>1.09</td>
<td>1.17</td>
<td>1.25</td>
<td>7.62***</td>
</tr>
<tr>
<td>LIF</td>
<td>3.90</td>
<td>4.36</td>
<td>4.46</td>
<td>12.81***</td>
</tr>
<tr>
<td>CBL</td>
<td>21.37</td>
<td>23.96</td>
<td>24.81</td>
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<tr>
<td>LXD</td>
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<td>8.01</td>
<td>8.44</td>
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</tr>
<tr>
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<td>6.04</td>
<td>6.59</td>
<td>6.83</td>
<td>29.83***</td>
</tr>
<tr>
<td>LN</td>
<td>6.49</td>
<td>7.35</td>
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<tr>
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</tr>
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<td>RD</td>
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<td>4.03</td>
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<tr>
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<td>4.04</td>
<td>4.08</td>
<td>2.27</td>
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* P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001
Fig. 3.—Ninety-five percent confidence ellipses for three age groups of *Microtus mexicanus*. The centroid for the adults is age group 1 (N = 63); subadults, age group 2 (N = 30); and juveniles, age group 3 (N = 9).
Table 2. Nongeographic variation in differences between sexes of *Microtus mexicanus* from Willow Creek, New Mexico, and Volcan de Colima, Jalisco. F-ratios resulting from single-classification analysis of variance are presented for each character. Refer to Methods for definitions of characters and figures 1 and 2 for locations of populations.

<table>
<thead>
<tr>
<th>Character</th>
<th>Willow Creek</th>
<th>Volcan de Colima</th>
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<tbody>
<tr>
<td>TL</td>
<td>0.75</td>
<td>0.26</td>
</tr>
<tr>
<td>LT</td>
<td>0.00</td>
<td>0.13</td>
</tr>
<tr>
<td>HF</td>
<td>1.20</td>
<td>1.48</td>
</tr>
<tr>
<td>LE</td>
<td>0.15</td>
<td>0.48</td>
</tr>
<tr>
<td>WN</td>
<td>0.03</td>
<td>3.87*</td>
</tr>
<tr>
<td>GRB</td>
<td>0.07</td>
<td>0.33</td>
</tr>
<tr>
<td>IC</td>
<td>0.80</td>
<td>0.07</td>
</tr>
<tr>
<td>ZB</td>
<td>0.40</td>
<td>0.41</td>
</tr>
<tr>
<td>PLB</td>
<td>5.57*</td>
<td>0.18</td>
</tr>
<tr>
<td>MB</td>
<td>1.84</td>
<td>0.88</td>
</tr>
<tr>
<td>WFM</td>
<td>8.35**</td>
<td>0.43</td>
</tr>
<tr>
<td>HFM</td>
<td>0.16</td>
<td>0.47</td>
</tr>
<tr>
<td>WIF</td>
<td>1.61</td>
<td>1.42</td>
</tr>
<tr>
<td>LIF</td>
<td>0.18</td>
<td>0.09</td>
</tr>
<tr>
<td>CBL</td>
<td>0.24</td>
<td>0.09</td>
</tr>
<tr>
<td>LXD</td>
<td>0.39</td>
<td>0.05</td>
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<td>LR</td>
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<td>LN</td>
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<td>LMT</td>
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<tr>
<td>RD</td>
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<td>0.08</td>
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<tr>
<td>GSD</td>
<td>1.31</td>
<td>2.46</td>
</tr>
<tr>
<td>GLS</td>
<td>0.04</td>
<td>0.07</td>
</tr>
<tr>
<td>LND</td>
<td>0.64</td>
<td>0.82</td>
</tr>
</tbody>
</table>

* P ≤ 0.05; ** P ≤ 0.01;

b. Population VC, N = 72 males, N = 71 females.
that there is a slight degree of sexual dimorphism in *M. mexicanus*, few individual characters showed a significant difference between the sexes and neither sex was consistently larger in the characters. The sexes were therefore pooled in further analyses to avoid small sample sizes for most populations and to allow for the simultaneous analysis of the populations from the United States and Mexico.

**Geographic Variation**

Population means for each character and range tests are presented in Appendix II. All characters showed significant differences among the 65 populations. No consistent grouping of populations from character to character was seen. Of the 23 characters, only two characters had a nonoverlapping subset. The populations from Hull Tank from the Grand Canyon (population HT) were significantly shorter in the length of hindfoot and the population from the Mimbres Mountains, New Mexico (population MM), was significantly larger for the width of incisive foramen than the other populations.

Results of the principal component analysis of the character means of 65 populations are presented in Figs. 4 and 5. The first principal component accounted for 85.2 percent of the variation; the second, 8.2 percent; and the third, 3.3 percent. Minimum area polygons enclose the two a priori groups postulated by the genic data; that is, one
Fig. 4.—Plot of 65 populations of *Microtus mexicanus* on principal components I and II. Refer to figures 1 and 2 for population locations. Overlaps are indicated by numbers; 1 represents populations WR and PE; 2 represents populations AA, RF, TL, and FJ; 3 represents populations WC and ZU; 4 represents populations EM, SM, and OA; and 5 represents populations MR, TH, and WI.
Fig. 5.--Plot of 65 populations of *Microtus mexicanus* on principal components I and III. Refer to figures 1 and 2 for population locations. Overlaps are indicated by numbers; 1 represents populations EM and MA; 2 represents populations MT and TL; and 3 represents populations CL, PE, and WI.
group from the United States and one group from Mexico. These two groups exhibited considerable overlap on axes I and II, although there was some separation on principal component III. The plot of populations generally followed no particular pattern and many populations such as Alto (population AL), Bonito Lake (population BL), Cloudcroft (population CL) and southern Sacramento (population SS), which all occur within the 2,134 m contour interval of the Sacramento Mountains, New Mexico, were widely separated on the principal component plot. Loadings of the first three principal component axes are presented in Table 3. Principal component I was primarily a size factor with all characters loading negatively except for height of foramen magnum. On principal component II, length of tail loaded high and positive while mastoidal breadth had the highest negative loading. On principal component III, where some separation occurred between the groups, factors loading high and positive were zygomatic breadth and mastoidal breadth while factors loading high and negative were length of ear and length of hindfoot. Therefore, populations from Mexico tended to have larger hindfeet and ears, and smaller mastoidal breadth and zygomatic breadth relative to populations from the United States.

Results of the discriminant function analysis among the 65 populations is presented in Figs. 6 and 7. The multivariate analysis of variance among the populations
Table 3. Factor loadings on the first three principal component axes for 65 populations of *Microtus mexicanus*. Refer to Methods for definitions of characters.

<table>
<thead>
<tr>
<th>Character</th>
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<th>II</th>
<th>III</th>
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<tbody>
<tr>
<td>TL</td>
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<td>-0.400</td>
</tr>
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<td>ZB</td>
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</tr>
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<td>PLB</td>
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<td>-0.184</td>
</tr>
<tr>
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<tr>
<td>WFM</td>
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<tr>
<td>GLS</td>
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<td>0.302</td>
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<tr>
<td>LND</td>
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<td>-0.201</td>
<td>-0.240</td>
</tr>
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</table>
Fig. 6.--Plot of group centroids of 65 populations of *Microtus mexicanus* on canonical vectors I and II. Refer to figures 1 and 2 for population locations. Overlaps are indicated by numbers; 1 represents populations RC and ZU; 2 represents populations AL, FJ and PA; and 3 represents populations MB and MT. In general, populations from Mexico plot to the left of the dashed line, and populations from the United States plot to the right of the dashed line.
Fig. 7.--Plot of group centroids of 65 populations of *Microtus mexicanus* on canonical vectors I and III. Refer to figures 1 and 2 for population locations. Overlaps are indicated by numbers; 1 represents populations GV and WI; 2 represents populations PA and SG; and 3 represents populations CL, MT and RC. In general, populations from Mexico plot to the left of the dashed line, and populations from the United States plot to the right of the dashed line.
resulted in a significant difference ($F = 0.00$, $d.f. = 1472$, 29367, $P = 0.00$). Factor loadings on the first three canonical vectors are presented in Table 4. Canonical vector I was primarily a size factor with all characters except mastoidal breadth loading negatively. Factors loading highest were interorbital constriction and length of maxillary toothrow. Canonical vector II was a size factor. All characters loaded positively with greatest skull depth, width of incisive foramen, mastoidal breadth, prelambdoidal breadth and greatest length of skull loading highest. Canonical vector III was a shape factor. Characters loading high and negative were length of ear and width of incisive foramen while characters loading high and positive were length of rostrum and mastoidal breadth.

Most notably, the discriminant function plot resulted in the separation of two major groupings of populations. One group included Prescott, Arizona (population PR), plus all populations from Mexico with the exception of the populations from San Antonio de las Alazanas, Coahuila (population AS), and near Galena, Nuevo Leon (population GA). The other group included populations AS and GA, plus the remaining populations from the United States. The multivariate analysis of variance between the group centroid for all populations from the United States and those from Mexico resulted in a significant difference ($F = 10.70$, $d.f. = 23, 41, P = 0.000$). These major groups separated along
Table 4. Factor loadings on the first three canonical axes for 65 populations of *Microtus mexicanus*. Refer to Methods for definitions of characters.

<table>
<thead>
<tr>
<th>Character</th>
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<tr>
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<tr>
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<td>LMT</td>
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<td>RD</td>
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<td>LND</td>
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</table>
canonical axis I. Populations from the United States, San Antonio de las Alazanas, Coahuila, and Galena, Nuevo Leon are therefore smaller than the remaining populations from Mexico in all characters except mastoidal breadth.

Within the United States, there was a tendency for populations from the vicinity of the Grand Canyon, Flagstaff and Williams to group together with negative values on canonical vector II and positive values on canonical vector III. In addition, the populations from Prescott, Arizona (population PR), Hualapai Mountains, Arizona (population HU) and north of Raton, New Mexico (population NR), had more negative values than other U.S. populations on canonical vector I. The population from Prescott, Arizona, is situated slightly within the group of Mexican populations. Other populations from the United States showed little distinct pattern and, as in the principal component analysis, many populations from the same mountain range were widely separated on the canonical vector plots. In the vicinity of the Grand Canyon, Flagstaff and Williams, individuals tended to be smaller than other U.S. populations while the populations from Prescott, Arizona, Hualapai Mountains, Arizona, and north of Raton, New Mexico, tended to be larger in all characters except mastoidal breadth than other populations from the United States. Most apparent for Mexican populations was the separation of the populations from San Antonio de las Alazanas, Coahuila and
Galena, Nuevo Leon from other Mexican populations. These populations grouped with those from the United States on canonical vector I. Patzcuaro, Michoacan (population PZ) separated from the other populations with a more positive value on canonical vector II, while the population southeast of Autlan, Jalisco (population AU), and Ixtlan de Juarez, Oaxaca (population IX), separated with more negative values. On canonical vector III, populations from Jalisco, Michoacan, and Oaxaca formed a group of more positive values with respect to other Mexican populations. In Mexico, the population from Patzcuaro, Michoacan tended to be larger for all characters while the populations from Autlan, Jalisco and Ixtlan de Juarez, Oaxaca were smaller for these characters. Populations from southwest Mexico and Oaxaca had smaller ears and width of incisive foramen while the length of rostrum and mastoidal breadth were larger.

Results of the multivariate analyses of variance between neighboring populations are presented in Figs. 8 and 9. Significant differences ($P > 0.001$) between adjacent populations are indicated by dashed lines, nonsignificant differences between populations are indicated by solid lines, and nonsignificant groupings of subspecific status are enclosed by dotted lines. The United States showed relatively more nonsignificant differences ($P > 0.001$) between neighboring populations than populations from Mexico. In the United States, the population from south of
Fig. 8.—Multivariate analyses of variance between populations of *Microtus mexicanus* from the United States. Dashed lines represent a significant difference ($P \leq 0.001$) between populations, while solid lines represent a nonsignificant difference between populations. The dotted lines represent nonsignificant groupings of subspecific status.
Fig. 9.--Multivariate analyses of variance between populations of *Microtus mexicanus* from Mexico. Dashed lines represent a significant difference (\( P \leq 0.001 \)) between populations, while solid lines represent a nonsignificant difference between populations. The dotted lines represent nonsignificant groupings of subspecific status.
Prescott (population PR) and the Hualapai Mountains (population HU) had sample sizes too small to be tested in this analysis. Results of a principal component analysis for these populations plus individuals from the Music Mountains, Arizona (population MU), Grandview Point, Arizona (population GV), Ash Fork, Arizona (population AF), the Mogollon Rim, Arizona (population MR) and Sierra Ancha, Arizona (population SA) are presented in Figs. 10 and 11 and Table 5. The first three principal components accounted for 96.7 percent of the phenetic variation. Individuals from south of Prescott and the Hualapai Mountains clustered loosely together and were separated from the other populations positively on principal component II. The factor loading high and positive on this principal component axis was length of tail, while factors loading high and negative on component II were length of incisive foramen, length of maxillary diastema, and length of nasals. The two individuals from the Music Mountains were the most distinct and separated from the other populations primarily on principal component III. Factors loading high and positive on this axis were width of incisive foramen, length of incisive foramen, and length of hindfoot, while length of ear loaded high and negative on principal component III. Of the remaining populations, individuals showed considerable overlap except for individuals from Sierra Ancha which showed some separation on principal component I. This
Fig. 10.—Plot of individuals from populations PR, MU, HU, AF, GV, MR, and SA on principal components I and II derived for these populations only. Refer to figure 1 for population locations. "O" refers to individuals from GV, "*" refers to individuals from MR, "+" refers to individuals from AF, and "#" refers to individuals from SA.
Fig. 11.—Plot of individuals from populations PR, MU, HU, AF, GV, MR, and SA on principal components I and III derived for these populations only. Refer to figure 1 for population locations. "O" refers to individuals from GV, "*" refers to individuals from MR, "+" refers to individuals from AF, and "#" refers to individuals from SA.
Table 5. Factor loading on the first three principal components for individuals of *Microtus mexicanus* from populations AF, GV, HU, MR, MU, PR, and SA. Refer to Methods for definitions of characters and figure 1 for locations of populations.

<table>
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<th>Character</th>
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<td>LT</td>
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</table>
component axis was primarily a size factor with all
characters loading negatively except for height of foramen
magnum. Characters loading high and negative on principal
component I were total length, zygomatic breadth,
condylobasilar length, and greatest length of skull.
DISCUSSION

The results of the analyses for sexual dimorphism are generally consistent with other studies. Hamilton and Heidt (1984) found no significant sexual dimorphism for 23 cranial characters of *Microtus mexicanus* from Volcan de Colima, Jalisco, and Hoffmeister (1986) found no significant sexual dimorphism in 13 external and cranial characters of *Microtus mexicanus* from the vicinity of Williams, Arizona, and the south rim of the Grand Canyon. However, Hoffmeister (1986) did find females from Escudilla Mt., Arizona (population ES) to be significantly larger in total length, length of hindfoot and length of nasals. Wilhelm (1982) also found that females were always significantly larger in total length from four New Mexico populations, while males were significantly larger in interorbital breadth, depth of skull and length of hindfoot. An exception was females from the San Mateo Mountains (population SM) which were significantly larger in depth of skull and length of hindfoot. In general, studies have reported sexual dimorphism for a few characters from several examined, but have not found one sex to be consistently larger than the other. In addition, the characters showing a significant difference may change from locality to locality. Much of these inconsistencies in univariate statistics may be due to type I errors. For these reasons, it was felt justified to pool the sexes for subsequent analyses.

The results of the discriminant function analysis of 65
populations of Microtus mexicanus resulted in the separation of two major groups; one consisting of populations from the United States, Coahuila and Nuevo Leon and the other consisting of the remaining populations from Mexico, suggesting that M. mexicanus is represented by two species. This division of M. mexicanus into two separate species is supported by karyotypic data. Specimens examined from New Mexico, Texas and Coahuila have a diploid number of 44 and fundamental number of 54 (Judd, 1980; Matthey, 1957; Moore, unpub. data; Wilhelm, 1982). On the other hand, all other populations examined from Mexico have had a diploid number of 48 with a fundamental number of 56, 57 or 58 (Lee and Elder, 1977; Modi, 1987; Moore, unpub. data). Judd (1980) compared the karyotypes of specimens from the United States with those reported from Mexico by Lee and Elder (1977) and concluded that the difference implies two separate evolutionary lineages and may represent distinct species. In addition, Modi (1987) compared a G-banded karyotype from Jalisco to the G-banded karyotypes from the United States presented by Judd (1980) and concluded that they differ by euchromatic rearrangements and heterochromatic differences indicating reproductive isolation by meiotic malassortment in heterozygotes.

Genic data also supports the separation of Microtus mexicanus into two species (Moore, unpub. data). Populations from New Mexico and populations from Mexico
formed two separate clusters in a Wagner tree and UPGMA phenogram and join at a Roger's similarity value of 0.773. Moore (unpub. data) concluded that this similarity value, in comparison with those reported for other Microtus species, indicates that M. mexicanus is represented by two distinct species that are probably sister taxa due to their similarities. These data are supported by the discriminant function analysis of population means from the United States and Mexico which resulted in a significant difference ($F = 10.70$, d.f. = 23, 41, $P = 0.000$).

The association of the population from San Antonio de las Alazanas, Coahuila with other populations is problematic in that the different data sets give conflicting results. In his genic analysis, Moore (unpub. data) found that the population from San Antonio de las Alazanas, Coahuila (population AA) consistently grouped with populations from Mexico. This is in contrast with the discriminant function analysis of 65 populations that placed the population from San Antonio de las Alazanas, Coahuila and the adjacent population from Galena, Nuevo Leon (population GA), in the group from the United States (Figs. 6 and 7). In addition, the San Antonio de las Alazanas population has a diploid number of 44 and fundamental number of 54 (Moore, unpub. data) that is similar to populations from the United States. However, the X chromosome from this location is acrocentric while the X chromosome from all United States populations,
except Mount Taylor, New Mexico (population MT), are metacentric (Moore, unpub data; Wilhelm, 1982); it is unknown whether the remaining autosomes are completely homologous between the populations. Morphologically, the population from San Antonio de las Alazanas clusters with populations from the United States, however, the genic data and the karyotypic data indicate that this population should be considered more similar to the Mexican populations.

Within the United States, the Mexican vole has typically been divided into four subspecies (Hall, 1981; Hoffmann and Koeppel, 1985). The distribution of Microtus mexicanus guadalupensis is considered to be east of the Rio Grande River in New Mexico, Texas and southcentral Colorado (Bailey, 1931; Hall, 1981; Hoffmann and Koeppel, 1985). Anderson (1961), Armstrong (1972), Bailey (1931), Cockrum (1960), and Hall (1981) considered populations west of the Rio Grande in New Mexico, Mesa Verde, Colorado and all populations in Arizona, except for the Hualapai Mountains and the southern portion of Navaho Mountain which extends into Arizona, to be referable to Microtus mexicanus mogollonensis. Hoffmann and Koeppel (1985) departed from this conclusion by excluding from M. m. mogollonensis, populations from Mesa Verde, Colorado, and Mount Taylor and the Zuni Mountains, New Mexico. Hoffmeister (1986) further removed from M. m. mogollonensis those populations from the south rim of the Grand Canyon and from the vicinities of
Williams and Flagstaff, Arizona. *Microtus mexicanus navaho* originally was only referable to specimens from Navaho Mountain in Utah and northern Arizona (Benson, 1935; Hall 1981). Hoffmann and Koeppl (1985), however, included specimens from Mount Taylor and the Zuni Mountains, New Mexico, and Mesa Verde, Colorado, while Hoffmeister (1986) included specimens from the south rim of the Grand Canyon plus those from the vicinities of Williams and Flagstaff, Arizona, in *M. m. navaho*. Finally, *Microtus mexicanus hualpajensis*, was referable only to specimens from the Hualapai Mountains, Arizona (Goldman, 1938; Hall, 1981; Hoffmann and Koeppl, 1985). An exception is Hoffmeister (1986), who also included specimens from Prospect Valley in northwestern Coconino Co., Arizona in this subspecies.

Results of the multivariate analyses of variance indicated that specimens from the Guadalupe Mountains, Texas (population GU) were significantly different from the closest populations east of the Rio Grande in New Mexico (*P* ≤ 0.001, Fig. 8). Populations east of the Rio Grande in New Mexico were not significantly different from populations west of the Rio Grande in New Mexico, nor were they significantly different from population from the Mogollon Rim (population MR), Sierra Ancha (population SA), and White Mountains in Arizona. Thus, populations from the Mogollon Rim, Sierra Ancha, and White Mountains in Arizona, in addition to all populations from New Mexico, are referable
to *M. m. mogollonensis*, while only those individuals from the Guadalupe Mountains, Texas are referable to *M. m. guadalupensis*. These subspecific distributions are supported by Wilhelm (1982) who studied populations from the Guadalupe mountains, Texas (population GU), Sacramento Mountains, New Mexico (vicinity population BL), Manzano Mountains, New Mexico (population FJ), and the San Mateo Mountains, New Mexico (population SM). Based on cranial morphology, he found that the Guadalupe Mountain population was the most distinct of the four populations. In addition, his analyses of cranial and sperm morphology resulted in a close relationship between the Manzano and San Mateo populations suggesting that the Rio Grande is not a boundary between subspecies. Genetic analysis of these four populations found them to be very similar to each other, although the Guadalupe population was the most distinct (Wilhelm 1982). This was also supported by a genetic analysis by Moore (unpub. data) based on Roger's genetic similarity values of three populations on each side of the Rio Grande, although specimens from the Guadalupe Mountains were not included.

Three populations were found to be significantly different (*P < 0.001*) from adjacent populations within *M. m. mogollonensis*. Two of these populations, Black Range, New Mexico (population BR), and Sierra Grande, New Mexico (population SG), had small sample sizes, along with small
sample sizes in adjacent populations, restricting the use of multivariate analysis of variance among the populations. Therefore, these populations were provisionally included within *M. m. mogollonensis*. The population from Escudilla Mountain, Arizona (population EM) was significantly different ($P < 0.001$) from all adjacent populations tested. However, because Escudilla Mountain is surrounded by populations not significantly different from one another ($P > 0.001$) and due to the lack of geographical barriers between it and other populations, specimens from Escudilla Mountain are considered to be included within *M. m. mogollonensis*.

The multivariate analyses of variance found specimens from Navaho Mountain, Utah (population NA), Mesa Verde, Colorado (population MV), south rim of the Grand Canyon, and vicinities of Flagstaff and Williams to be similar, these populations are referred to as *Microtus mexicanus navaho*, which supports the conclusion by Hoffmeister (1986). He found these specimens to be smaller in comparison with the relatively large size of *M. m. mogollonensis* and medium size of specimens from the Hualapai Mountains. He also noted that there was a sharp break in the variation between specimens from the vicinity of Flagstaff and those from near Mormon Lake on the Mogollon Plateau even though there is no apparent geographical barrier. Although specimens from near Mormon Lake were not examined in this study, a significant
difference was found between specimens from the vicinity of Flagstaff and those from the Mogollon Rim. The inclusion of specimens from Mesa Verde, Colorado within *M. m. navaho* is supported by Hoffmann and Koeppl (1985) based on their distributional map.

Specimens from the Hualapai Mountains, Arizona (population HU) and the mountains south of Prescott, Arizona (population PR) are here considered consubspecific as *M. m. hualpaiensis*. This conclusion was based on the results of the principal component analysis of specimens from these populations and adjacent populations. The population from Prescott was situated slightly within the group of Mexican populations on the discriminant function analysis (Figs. 6 and 7), although this is believed to be due to the small sample size and not to any degree of relationship between the Prescott population and those from Mexico. This conclusion contradicts Hoffmiester (1987) who included specimens from the vicinity of the population south of Prescott in *M. m. mogollonensis*. He also suggested that if larger samples were available from the Hualapai Mountains, they might be referable to *M. m. navaho*. Although only two individuals were examined from the Music Mountains, Arizona, these specimens were quite distinct from specimens examined from adjacent populations and likely represent a previously unrecognized subspecies. Hoffmeister (1986) examined two specimens from the lower end of Prospect Valley located
between the Music Mountains population and the populations from the south rim of the Grand Canyon. He included these two specimens within *Microtus mexicanus* hualpaiensis, although he suggested that they also may be referable to *Microtus mexicanus* navaho if larger sample sizes were available. These specimens from Prospect Valley may prove to be related to those from the Music Mountains.

In Mexico, specimens of *Microtus mexicanus* have been divided into eight subspecies (Hall, 1981; Hoffmann and Koepppl, 1985). With few exceptions, the subspecific boundaries have remained virtually unchanged since the subspecies were first described, because no morphologic studies involving many populations from Mexico have been reported. The most northern subspecies is *Microtus mexicanus* madrensis, which occurs in the higher parts of the Sierra Madre Occidental from northwestern Chihuahua south to the canyon of the Rio Mezquital that completely crosses the mountains in southern Durango (Baker and Greer, 1962). Baker and Greer (1962) postulate that there is a gap between this subspecies and *Microtus mexicanus* phaeus which occurs to the south of *Microtus mexicanus* madrensis. Hall (1981) included specimens from the type locality, Sierra Nevado de Colima, Jalisco (population VC), plus specimens from northern Jalisco and northern Queretaro (population JA) in the widely distributed *Microtus mexicanus* phaeus. To the southwest of *Microtus mexicanus* phaeus, Hooper (1955) recognized a subspecies *Microtus mexicanus* neveriae that is known only from the
mountains southeast of Autlan in southern Jalisco (population AU). Likewise, in the mountains of Michoacan, south of the central portion of the range of *M. m. phaeus*, are two subspecies with restricted ranges. The southernmost is *M. m. salvus* known only from Mount Tancitaro (population TA), while the other is *M. m. fundatus* found north of *M. m. salvus* in a band west to the vicinity of Patzcuaro (population PZ; Hall, 1948). *Microtus mexicanus subsimus* occurs along the Sierra Madre Oriental from southern Coahuila and western Nuevo Leon south to southwestern Tamaulipas where it meets the distribution of *M. m. phaeus*. To the east *M. m. phaeus* grades into *M. m. mexicanus* and Bailey (1900) noted that "*mexicanus* and *phaeus* merely show the extremes of differentiation found in one wide ranging and variable form". Hall (1981) included within the range of *M. m. mexicanus* specimens from southern Hidalgo, Volcan de Toluca, Mexico (population VT), west to Las Vigas, Veracruz (population LV) and south to the vicinity of Volcan de Oriziba, Veracruz (population OR). Finally the southernmost subspecies is *M. m. fulviventer*, which occurs in the mountains of Oaxaca south of the range of *mexicanus* (Anderson, 1972).

The multivariate analyses of variance among populations in Mexico resulted in the separation of 13 populations or groups of populations significantly different from other such groups. Several of these groups coincide with, and are
supported by, previous subspecific designations. The populations from El Salto (population ES) and San Luis (population SL) Durango formed a nonsignificant group corresponding to *M. m. madrensis*. In addition, the populations from San Antonio de las Alazanas, Coahuila (population AA) and from near Galena, Nuevo Leon (population GA) also formed a nonsignificant group corresponding to *M. m. subsimus* (Goldman, 1938). Likewise, the populations from southeast of Autlan, Jalisco (population AU), Mount Tancitaro, Michoacan (population TA), and Patzcuaro, Michoacan (population PZ) were each significantly different from all populations tested and are referred to *M. m. neveriae*, *M. m. salvus*, and *M. m. fundatus* respectively (Hall, 1948; Hooper, 1955). The nominal subspecies, *M. m. phaeus*, is represented in this analysis by two populations; one from the type location, Volcan de Colima, Jalisco (population VC), and one from west of Jalpan, Queretaro (population JA). These two populations were significantly different from each other and from adjacent populations indicating that the subspecific designation *M. m. phaeus* refers to the population from Volcan de Colima, as this is the type locality, while the population west of Jalpan, Queretaro represents a distinct population that is probably a separate subspecies.

The multivariate analyses of variance also resulted in the separation of *Microtus mexicanus mexicanus* into three
distinct groups. The type location is from Volcan de Oriziba, Veracruz (population OR), and formed a grouping with the populations from northern Veracruz (populations AL, LV, and PE), the mountain range southeast of Mexico City (population RF and PO) and the District Federal (population DF). The populations from Monte Rio Frio and District Federal are included within *M. m. mexicanus* because the significant difference between Monte Rio Frio and Mount Popocateptle, which occur on the same small mountain range, likely represents a sampling error due to small sample sizes. To the west of this group, the populations from Volcan de Toluca, Mexico (population VT), Villa Victoria, Mexico (VV), and north of Ciudad Hidalgo, Michoacan (population CH), form a separate group significantly different from other groups representing a previously unrecognized subspecies. In addition, to the north of these two groups, the population from near Tulancingo, Puebla (population TU) was significantly different from other populations and is also considered a new subspecies. Finally, the three populations of *M. m. fulviventer* from Oaxaca were significantly different from all populations and from each other. The population from the type locality from the mountain ridge north of Oaxaca City (population OA) is retained as *M. m. fulviventer* while the populations from Tlaxiaco, Oaxaca (population TL) and from north of Ixtlan de Juarez, Oaxaca (population IX) represent previously
unrecognized subspecies. This division is supported by the separation of these populations on the discriminant function and principal component plots.

These subspecific distinctions based on the multivariate analyses of variance and supporting data indicate that populations from Mexico are relatively more distinct from one another as compared with populations from the United States (Figs. 8 and 9). The relatively greater divergence of Mexican populations is also supported by karyotypic data. All specimens examined from New Mexico (vicinities populations AL, CL, MM, MT, SZ, WC, SG, FJ, RC, BL, and SM), Texas (vicinity population GU) and Coahuila (vicinity population AA) have a diploid number of 44 and fundamental number of 54 with one chromosomal polymorphism. (Judd, 1980; Matthey, 1957; Moore, unpub. data; Wilhelm, 1982). The single polymorphism was an acrocentric X chromosome from Mount Taylor, New Mexico (population MT) that is similar to karyotypes from Mexico. On the other hand, all other populations from Mexico have a diploid number of 48 with a fundamental number 56 in Oaxaca (vicinity population IX), 57 or 58 in Michoacan (population PZ), Jalisco (population VC), Durango (population ES), and Mexico (population TO), and 58 in Veracruz (population AL) (Lee and Elder, 1977; Modi, 1987; Moore, unpub. data). In addition, chromosomal polymorphisms have been found in these Mexican populations (Lee and Elder, 1977; Moore, unpub.
data). Genic data also indicates that populations from Mexico are more distinct from one another than are populations from the United States. Moore (unpub. data) found that the mean Rogers' genic similarity value was greater among the United States populations than those from Mexico which show relatively more genetic divergence among themselves. In addition, a cladistic analysis resulted in populations from the United States forming one clade while populations from Mexico formed three clades.

A scenario in which populations from Mexico are relatively old with a more recent invasion north into the United States would account for the divergence of two evolutionary lineages of *Microtus mexicanus* and the dichotomy in the relative divergence of the populations within each region. Karyotypic and genic data support the premise that the Mexican populations are more primitive. Modi (1987) proposed that the primitive karyotype for arvicolids consisted of all acrocentric autosomes and sex chromosomes, with the exception of autosomal pair 27, which is metacentric. Lee and Elder (1977) reported that karyotypes of specimens examined from Mexico consisted of 12 metacentric autosomes, 34 acrocentric autosomes and acrocentric sex chromosomes. Conversely, Judd (1980), Wilhelm (1982), and Moore (unpub. data) reported that the karyotypes of specimens from the United States consist of 12 metacentric autosomes, 30 acrocentric autosomes, an
acrocentric Y chromosome and a metacentric X chromosome (an exception is the population from Mount Taylor, New Mexico, which has an acrocentric X chromosome). The reduction in size or total deletion of two acrocentric chromosomes (Judd, 1980) and the usual presence of a metacentric X chromosome in the karyotypes from the United States specimens indicate that the Mexican populations show a relatively more primitive chromosomal complement compared to those from the United States. Genic data also support this conclusion. Moore (unpub. data) in his electrophoretic analysis of 12 populations of *M. mexicanus* found that the populations from the United States were united, as different from Mexican populations, by four synapomorphic alleles and posses several apomorphic character states indicating that these populations are more derived, while populations from Mexico retained more primitive alleles.

With the cool, stable, moist climate of the Wisconsinan glaciation there was a concommitment downward elevational (approximately 1000 m) and latitudinal shift in vegetational zones in the southwestern United states and Mexico (Clisby and Sears, 1956; Cole, 1982; Dalquest et al., 1969; Harris, 1970; Mead, 1981; Sears and Clisby, 1955; Van Devender et al., 1987; Wells, 1966). Concommitment changes in regional faunas associated with particular vegetational zones occurred and many species, such as the Mexican vole, which now occur in higher vegetational zones, would have been able
to invade new areas by way of temporary corridors formed by the depression of their preferred habitat type. On the other hand, during interglacial periods, vegetational zones would migrate upward isolating boreal faunas on high elevational pockets of habitat. It is hypothesized that *Microtus mexicanus* invaded the United States from Mexico across the relatively lower elevational region between the United States and Mexico during such a depression in vegetational zones. However, populations from Mexico are too genically distinct from those in the United States for voles from Mexico to have migrated north into the United States and speciated from those in Mexico as recently as the Wisconsinan glaciation.

It is unknown when *M. mexicanus* originally appeared in Mexico. Hoffmann and Koeppl (1985) suggest that this species may be a descendant of *Microtus paroperarius* which first appeared in the New World 1.8 millions of years before present (mybp) at the beginning of the Pleistocene (Repenning, 1980). They also concluded that *M. mexicanus* probably diverged via Pleistocene isolation by fragmentation and displacement of taiga biomes during the Illinoian glacial period about 500,000 years ago. Other probable descendants of *M. paroperarius* include *Microtus montanus* (Hoffmann and Koeppl, 1985) and *Microtus pennsylvanicus* which appeared about 475,000 years ago (Guthrie, 1965; Reppening, 1980). Modi (1987) regarded the karyotype of *M.*
mexicanus (2N = 48) primitive relative to other arvicolid karyotypes, and chromosomal comparisons between M. mexicanus and M. pennsylvanicus suggest that M. mexicanus diverged earlier (Hoffmann and Koepppl, 1985), perhaps during the Kansan glacial period. Other data also support the relations of these three species plus the earlier divergence of M. mexicanus. Based on karyotypic data, Modi (1987) concluded that M. mexicanus, M. pennsylvanicus and M. montanus were included in the same clade although M. mexicanus was the most distinct. Likewise, Moore and Janecek (unpub. data) found, based on electrophoretic data, that M. mexicanus, M. pennsylvanicus and M. montanus formed one clade with M. montanus and M. pennsylvanicus being more closely related in a Wagner tree, while a phenogram based on overall similarity places M. mexicanus as being most divergent. Additional support for an earlier divergence of M. mexicanus is provided by the contemporary distributions of these and several other species. Reppening (1980) suggested that more primitive microtines are displaced southward by the appearance of more modern forms during "southward-shifting climate zones that permitted their escape but left them stranded in the mountain tops as the climate again warmed". Four species of primitive Microtus from an even earlier dispersal occur in small isolated areas in southern Mexico and Guatemala mostly south of the current range of M. mexicanus (Hoffmann and Koepppl, 1985; Reppening,
1980) while *M. pennsylvanicus* and *M. montanus* occur mostly north of *M. mexicanus*.

Therefore, *Microtus mexicanus* has possibly been present in Mexico since the Kansan glaciation (1.2 - 0.6 mybp) when it diverged from *Microtus paroperarius*. The Illinoian glacial period following this original appearance of *M. mexicanus* would have provided the climate and associated corridors (probably along the Sierra Madre Oriental and into the United States via the Guadalupe Mountains, Texas) for dispersal into the United States about 500,000 years ago, and separation with speciation during the Sangamon interglacial. This scenario provides an explanation for the morphologic, karyotypic and genic separation of populations in Mexico from those in the United States. In addition, the relatively long occupation of Mexico by *Microtus mexicanus* accounts for the relatively greater degree of genic differentiation, greater karyotypic variation and greater degree of morphological differentiation in Mexico as compared to populations from the United States.
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Specimens examined

Specimens were examined from the following collections:

Museum of Northern Arizona (MNA); University of Arizona (UA); California Academy of Sciences (CAS); Natural History Museum of Los Angeles County (LACM); San Diego Natural History Museum (SDNHM); Museum of Vertebrate Zoology, University of California -Berkeley (MVZ); Field Museum of Natural History (FMNH); Museum of Natural History, University of Illinois (UIMNH); Museum of Natural History, University of Kansas (KU); The Museum, Michigan State University (MSU); Museum of Zoology, University of Michigan (MSUMZ); New Mexico State University (NMSU); Museum of Southwestern Biology, University of New Mexico (MSB); Western New Mexico University (WNMU); American Museum of Natural History (AMNH); Stovall Museum of Science and History, University of Oklahoma (OU); Museum of Zoology, Memphis State University (MSUMZ); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); The Museum, Texas Tech University (TTU); University of Texas at El Paso (UTEP).

MEXICO. CHIHUAHUA: Colima Garcia, 3 (AMNH); Meadow Valley, Sierra Madre, 1 (AMNH); NE side Cerro Mohinora, 3,750 m, 3 (MSU). COAHUILA: 11 mi. E by road San Antonio de las Alazanas, 2 (MSB); 10 mi., E by road San Antonio de las Alazanas, 16 (MSB); 9.2 mi. E by road San Antonio de las Alazanas, 8 (MSB); 14.6 mi. E by road San Antonio de las
Alazanas, 4 (MSB); 11 mi. E San Antonio de las Alazanas, 1 (TCWC); 12 mi. E San Antonio de las Alazanas, 9,000 ft., 25 (KU); 3 mi. S, 13 mi. E San Antonio de las Alazanas, 8,900 ft., 3 (KU); 2 mi. E Mesa de Tablas, 8,500 ft., 6 (KU); 13 mi. E San Antonio de las Alazanas, 9,350 ft., 17 (KU); 13.4 mi. ESE San Antonio, 9,325 ft., 1 (TCWC). COLIMA: Volcan de Fuego, 9,000 ft., 27 (LACM). DISTRICT FEDERAL: 6 mi. SW Villa Alvaro Ohregon, Santa Rosa, 1 (KU); 12 km S, 2 km E Mexico, 2,240 m, 6 (KU); 25 mi. S Mexico, 2,750 m, 2 (KU); 33 km S Mexico, 2,970 m, 5 (KU); 1 mi. Cerro Ocopixco, 2,950 m, 1 (KU); Cienega Chica, 0.75 mi. NNW Xochimilco, 2,220 m, 1 (KU); 2.5 km SW Contreras, 2,850 m, 1 (KU); 2 km E Villa de Guadalupe, Rancho San Pedro el Chico, 13 (UIMNH); Miba Alta, 3,000 m, 1 (AMNH); La Cima, 2,900 m, 2 (AMNH); Col del Valle, 2,400 m, 1 (AMNH); San Bartolome, 2,900 m, 3 (UMMZ); La Cima, 2,900 m, 2 (UMMZ); Xochimilco, 2,400 m, 4 (AMNH), 1 (UMMZ); Milpaalanta, 3,100 m, 1 (AMNH); probably San Matrens, 2 (UMMZ); Contreras, 2,600 m, 6 (UMMZ); Huipulco, 7,600 m, 2 (MVZ). DURANGO: 83 km WSW Durango, 1 (LACM); 6 mi. SW El Salto, 9,000 ft., 4 (LACM); 6 mi. SW El Salto, 6,000 ft., 1 (LACM); San Luis, 2 (AMNH); 3 mi. E Las Adjuntas, 9,950 ft., 2 (KU); 10 mi. SW El Salto, 10,100 ft., 1 (KU); Coyotes, 3 (FMNH); 10 mi. SW El Salto, 8,600 ft., 2 (CAS); 7 mi. NE El Salto, Hacienda Coyotes, 8,200 ft., 1 (CAS); 1.5 mi. W San Luis, 7,550 ft., 4 (MSU); 5 mi. SW El Salto, 8,100 ft., 3 (MSU); 6 mi. SW El Salto, 8,350 ft., 1 (MSU); 6 mi. SW El
Salto, 8,300 ft., 2 (MSU); 18 mi. SSW Tepehuanes, 8,200 ft., 3 (MSU); Hda Coyotes, 8,120 ft., 1 (MSU); 1.5 mi. W San Luis, 7,800 ft., 1 (MSU); 6 mi. SW El Salto, 8,250 ft., 1 (MSU); 6 mi. SSE Los Frailes, 9,650 ft., 1 (MSU); 4 mi. SW Los Frailes, 9,800 ft., 1 (MSU); 7 mi. NE El Salto, Hacienda Coyotes, 8,200 ft., 1 (CAS); 10 mi. SW El Salto, 8,600 ft., 2 (CAS). JALISCO: 2 mi. E Crater Volcan de Colima, 6 (UIMNH); 23.1 mi. W Atenquique, 8,600 ft., (OU); ridge SW Volcan de Fuego, 10,000 ft., 3 (OU); Volcan de Nieve, 8 (AMNH); 23.1 mi. W Atenquique, N slope Volcan de Fuego, 9,500 ft., 1 (MSUMZ); 25.1 mi. W Atenquique, N slope Volcan de Fuego, 9,350 ft., 4 (MSUMZ); 27.3 mi. W Atenquique, N slope Volcan de Fuego, 9,300 ft., 12 (MSUMZ); 24.3 mi. W Atenquique, N slope Volcan de Fuego, 9,075 ft., 8 (MSUMZ), 26 mi. W Atenquique, N slope Volcan de Fuego, 9,300 ft., 59 (MSUMZ); 5.3 mi. W channel 13 T.V. Tower, Nevado de Colima, 9,800 ft., 2 (MSUMZ); 25.1 mi. W channel 13 T.V. Tower, Nevado de Colima, 9,350 ft., 6 (MSUMZ); Volcan de Fuego, 9,800 ft., 16 (KU); Sierra de Autlan, 9,000 ft., 17 (UMMZ); 20 mi. SE Autlan, 8,200 ft., 3 (UMMZ); 8 mi. W Atenquique, 9,100 ft., 9 (MSU); 20 mi. SE Autlan, 9,000 ft., 20 (KU). MEXICO: 1 mi. W Salazar, 9,850 ft., 6 (KU); 10 mi. N, 6 mi. E Valle de Bravo, 7,460 ft., 3 (KU); Nevada de Toluca, NE slope, 13,700 ft., 3 (KU); 1.5 mi. NNW Tenango, 1 (KU); 2 mi. WSW Salazar, 1 (KU); 1 mi. S, 2 mi. W Rio Frio, 10,500 ft., 2 (KU); 10 mi. N, 6 mi. E Valle de Bravo, 7,460 ft., 8
(KU); 45 km ESE Mexico City, Monte Rio Frio, 3,200 m, 2
(KU); 14 mi. NW Toluca, El Rio, San Bernabe, 1 (KU); 17.5 km
S, 7 km W by road Toluca, Nevado de Toluca, 11 (MSB);
between Mexico City and Puebla, 10,300 ft., 5 (AMNH); 23 km
E Mexico City, 7,500 ft., 4 (TCWC); 45 km ESE Mexico City,
Monte Rio Frio, 9,300 ft., 3 (TCWC); 86 km SE Mexico City, N
slope Mt. Popocateptl, 13,500 ft., 5 (TCWC); 6 km E, 3 km S
Amecameca, 2 (UA); 3 mi. W Rio Frio, 10,400 ft., 7 (CAS); 83
km SE Mexico City, N slope Mt. Popecatepotl, 13,500 ft., 1
(TCWC); 45 km ESE Mexico City, Monte Rio Frio, 6 (TCWC); 23
km E Mexico, 7,500 ft., 1 (TCWC); Miahuatlan, San Pedro
Mixtepec, 3 (AMNH); 86 km SE Mexico City, N slope Mt.
Popocatepetl, 13,510 ft., 1 (TCWC); 55 km ESE Mexico City,
10,500 ft., 1 (TCWC); 2 mi. E Salazar, 10,200 ft., 1 (MSU).
MICHOACAN: 2.9 mi. E by road Opopeo, 2 (MSB); 0.3 mi. W
Puerto Garnica, 3 (TCWC); 5 mi. S Patzcuaro, 7,800 ft., 17
(MVZ); 4 mi. S Patzcuaro, 7,800 ft., 13 (MVZ), 1 (CAS); 3.5
mi. S Patzcuaro, 7,900 ft., 7 (MVZ); 9 mi. SE Patzcuaro,
8,000 ft., 9 (MVZ); 6 mi. S Patzcuaro, 8,000 ft., 2 (UMMZ);
10 mi. SE Patzcuaro, 9,200 ft., 10 (UMMZ); 2 mi. E San
Gregorio, 13 (KU); 5 mi. SE Opopeo, 34 (KU); Mt. Tancitaro,
11,400 ft., 3 (FMNH); Sierra Patomba, 9,000 ft., 1 (KU); 12
mi. W Ciudad Hidalgo, 9,150 ft., 13 (KU); Mt. Tancitaro,
10,500 ft., 1 (FMNH); Tancitaro, 1 (FMNH); 10 mi. SE
Patzcuaro, km 52, 9,200 ft., 10 (UMMZ); 10 mi. N Hidalgo,
Cerro San Andres, 9,400 ft., 6 (UMMZ). MORELOS: 45 km S
Mexico City, 9,400 ft., 5 (TCWC); 4 mi. NW Huitzilac, 9,200 ft., 1 (MSU); 4 mi. W Huitzilac, 9,200 ft., 3 (MSU); 1.5 mi. SSW Tres Cumbres, 8,400 ft., 3 (MSU); 4 km N Tres Cumbres, 10,300 ft., 1 (TCWC); Parque Nacional Lagunas, Zempoalas, 9,500 ft., 2 (UMMZ). **NUEVO LEON:** Sierra Potosi, 11,100 ft., 11 (KU); Cerro Potosi, near La Jolla Galeana, 4 (FMNH); 8 mi. WNW Galeana, Cerro del Potosi, 9,250 ft., 4 (MSU); 20 km N Galeana, 7,000 ft., 2 (UMMZ); 14.8 mi. E San Antonio de las Alazanas, by road, 2 (MSB). **OAXACA:** Llano de las Flores, 2,900 m, 34 (KU); Cerro San Felipe, Llano Ingles, 4 (AMNH); Llano de las Flores, Atepec, 9,500 ft., 1 (AMNH); 13.9 mi. N Llano de las Flores, 9,200 ft., 1 (TCWC); 12 mi. N Ixtlan de Juarez, Llano de las Flores, 9,200 ft., 13 (UMMZ); 4 mi. SW Llano de las Flores, 8,200 ft., 1 (UMMZ); N Llano de las Flores, 9,500 ft., 7 (UMMZ); 11 mi. NE Llano de las Flores, 9600 1 (UMMZ); 25.7 mi. NE Guelatao, HW 175, Llano de las Flores, 1 (TTU); km 91, Tlaxiaco-Putla Rd., 7,500 ft., 2 (CAS); 7 mi. N Ixlan de Juarez, 10,000 ft., 4 (CAS); 3 mi. S Llano de las flores = 7 mi. NNW Ixtan de Juarez, 9,900 ft., 4 (CAS); 15 km NE Oaxaca City by airline, Cerro San Felipe, 9,500 ft., 1 (CAS); 10 km N Oaxaca City by airline, Cerro San Felipe, 9,900 ft., 9 (CAS); 11 mi. NE Llano de las Flores, Tuxtepec Rd., 9,600 ft., 1 (UMMZ); 13 mi. NE Llano de las Flores, Tuxtepec Rd., near Cerro Pelon, 9,200 ft., 4 (UMMZ); near Campemento Rio Molino, Hiway 175, 7,300 ft., 2 (UMMZ); 8 mi. W La Cumbre, Tuxtepec Rd., Cerro
San Felipe, 10,000 ft., 1 (UMMZ); 2 km NE San Andres, Chicahuastla, 2,300 m, 3 (UMMZ); km 155 Puerto Angel Rd., 8,375 ft., 1 (CAS); 10 mi. SW Cuquila, 7,800 ft., 3 (MSU); 12 mi. NE Oaxaca., 8,400 ft., 2 (MSU); 15.9 mi. N by road Guelatao de Juarez, 23 (MSB); San Andres, Chicahuaalta, 3 (AMNH); 31.6 km by road S Vista Hermosa, N slope Cerro Pelon, 2,650 m, 13 (KU); 32.3 km by road S Vista Hermosa, S slope Cerro Pelon, 3 (KU). PUEBLA: Honey, 2,000 m, 1 (FMNH); Logo Salido, km 253 E Mexico City, 8,000 ft., 1 (TCWC); 12 km NNE St. Andres, W slope Mt. Orizaba, 10,000 ft., 4 (TCWC); Rancho Ocotal Colorado, 8,800 ft., 2 (UMMZ); 16 km NNE St. Andres, W slope Mt. Orizaba, 11,000 ft., 3 (TCWC); 3 km SSE Acaxochitlan, Curva del Perro, 2,050 m, 10 (KU). QUERETARO: 2 km S Tepozotlan, 2,550 m, 1 (TTU); Amoles, 10 (UMMZ). TLAXCALA: 8 km SW Tiaxcala, 7,500 ft., 4 (TCWC); 3 km S, 11 km W Huamantla, 3,150 m, 1 (TTU). VERACRUZ: Las Vigas, 8,500 ft., 11 (KU); 6 km SSE Altotonga, 9,000 ft., 1 (KU); 1 km W Las Vigas, 8,500 ft., 22 (KU); Las Vigas, 8,000 ft., 28 (KU); 3 km E Las Vigas, 8,000 ft., 3 (KU); 2 km N Perote, 8,000 ft., 3 (KU); Rancho El Capulin, 7 km SW Perote, 2,920 m, 1 (KU); 4 mi. SW Acultxingo, 7,000 ft., 1 (KU); 1.5 mi. S Altotonga, 8 (MSB); 2.1 mi. S Altotonga, Rancho San Emiliano, 4 (MSB); Xuchil, 8 (FMNH); Mt. Orizaba, 2 (FMNH); E slope Mt. Orizaba, 11,100 ft., 1 (CAS); Perote, 3,000 m, 1 (UMMZ), N slope Cofre de Perote, 10,300 ft., 5 (UMMZ).
USA. ARIZONA: APACHE Co.; Escudilla Mt., 41 (UIMNH); 3.5 mi. N Springerville, 3 (UIMNH); 5.5 mi. N, 2 mi. W Springerville, 1 (UIMNH); 1 mi. N Springerville, Becker Lake, 13 (UIMNH); 3.5 mi. N Greer, Hall Creek, 12 (UIMNH); 2.2 mi. S Phelps, Big Lake Rd., 1 (UA); Phelps Botanical Area, White Mts. 9,200 ft., 1 (UA); 11 mi. SE jct. Howley Lake Rd. and HW 73 E, T7N, R24E, 9,000 ft., 1 (UA); Sheeps Crossing, White Mts., 1 (UA); 4.5 mi, E Alpine, SE Luna Lake, T5N, R31E Sec. 18, 7,990 ft., 1 (WMNU); McNary Fish Cultural Station, 1 (MSB); 1.8 mi. E Fort Apache Indian Reservation on Rt. 73, 1 (MSB); 4 mi. S, 16 mi. W Springerville, White Mts., 24 (MSB); 4 mi. S, 16 mi. W Alpine, West Fork campground, T5N, R28E, SW 1/4 Sec. 29, 1 (MSB). COCONINO Co.; Bradshaw City, 3 (AMNH); 18 mi. SE Bly ranger station, Buck Springs guard station = 70 mi. SE Flagstaff, 1 (UA); Grand Canyon Village, athletic field, 4 (UIMNH); 0.75 mi. SW Rowes Well, sewage tanks, Grand Canyon Natl. Park, 5 (UIMNH); Indian Garden, S side Grand Canyon Natl. Park, 2 (UIMNH); Pasture Wash, jct. rd. W9-A and W9, S rim Grand Canyon, ranger station, 4 (UIMNH); Hull Tank, S rim Grand Canyon Natl. Park, 15 (UIMNH); Buggelin Tank, Hance Ranch, Grand Canyon Natl. Park, 14 (UIMNH); Hearst Ranch, Grandview, Grand Canyon Natl. Park, 3 (UIMNH); 0.5 mi. S, 2 mi. W Grandview Pt., Grand Canyon Natl. Park, 1 (UIMNH); 3 mi. N, 0.75 mi. W Flagstaff, 10 (UIMNH); 7 mi. N, 5.5 mi. W Flagstaff, 5 (UIMNH); Coleman Lake, 7 mi. S, 1 mi.
E Williams, 5 (UIMNH): McDougal Flat, 2 mi. S, 6.5 mi. E Williams, 1 (UIMNH): 2.75 mi. N, 0.75 mi. W Flagstaff, 8 (UIMNH); Flagstaff, 3 (UIMNH); Vincent Ranch, 39 mi. S, 16 mi. W Winslow, 4 (UIMNH); Kehl Spring campground, 1 mi. S, 3.5 mi. E Baker Butte Lookout, 3 (UIMNH); Lee Johnson Spring, Baker Butte, 1 (UIMNH); 28 mi. S, 24 mi. W Winslow, 1 (UIMNH); 6 mi. E Flagstaff, 4 (UIMNH); 12.5 mi. N, 5 mi. W Flagstaff, 1 (UIMNH); 12 mi. N, 4.5 mi. W Flagstaff, Little Spring, 1 (UIMNH); 10.5 mi. N, 5 mi. W Flagstaff, 2 (UIMNH); NW slope Agassiz Peak, San Francisco Mts., 9,700 ft., 6 (UIMNH); 6 mi. N, 9.5 mi. W Williams, 10 (UIMNH); 12.75 mi. N, 4.5 mi. W Flagstaff, Little Spring, 14 (UIMNH); Rt. 64, SE boundary Grand Canyon Natl. Park, 4 (UIMNH); 1 mi. S, 1.5 mi. W Williams, 12 (UIMNH); 5 mi. W Flagstaff, 1 (NHMLA); 5 mi. W Flagstaff, 7,200 ft., 2 (UIMNH); San Francisco Mt., 6 (SDNHM); 3 mi. N Flagstaff, Rio de Flag, 7,100 ft., 14 (MNA); 2 mi. N Flagstaff, Museum Northern Arizona, 7,100 ft., 2 (MNA); 3 mi. NW Flagstaff, Chimney Spring Rd., 7,100 ft., 5 (MNA); 8 mi. NW Flagstaff, 1 (UA); Little Spring, San Francisco Mt., 1 (SDMNH); Hart Prairie, San Francisco Mt., 3 (SDMNH); 10 mi. SE Coconino Wash, Grand Canyon, 2 (SDMNH); 1 mi. W Parks, 4 (KU); 12 mi. E Williams, 1 (KU); Little Spring, 8,400 ft., 1 (CAS); San Francisco Mt., 8,500 ft., 4 (CAS); 9 mi. NW Flagstaff, Fort Valley, 1 (TAM); 20 mi. E Flagstaff, Canyon Padre, 6,000 ft., 1 (MNA); 12 mi. W Flagstaff, Navajo army depot, 7,000 ft., 2 (MNA); 3 mi. N,
11 mi. E Blue Ridge ranger station at end of FS 319 E, Wilkins dam site, E Clear Creek, 6,000 ft., 1 (MNA); San Francisco Mt., 4 (CAS); Pivot Rock Spring, 6,950 ft., 1 (MVZ); Long Jim Canyon, S side Grand Canyon Natl. Park, 25 (UINHM); 5 mi. NW Flagstaff, A-1 burn, 1 (MNA); Bakers Butte, 8,000 ft., 12 (MVZ). GILA Co.; Carr's Ranch, Sierra Ancha, 5,410 ft., 9 (MVZ). MOHAVE Co.; Hualapai Mts., 1 mi. W Park, 1 (UIMNH); E slope Hualapai Peak, 7,800 ft., 1 (UIMNH); Music Mtn., T28N, R16W, SE 1/4 Sec. 36, 1 (UA); Music Mtn., T28N, R16W, NW 1/4 Sec. 30, 1 (UA); Hualapai Mts, 1.1 mi. S, 1.8 mi. E Wabayuma Peak, basin in Upper Bull Canyon, T18N, R15W, SE 1/4 of NW 1/4 Sec. 7, 5,840 ft., 2 (UA). YAVAPAI Co.; 7 mi. SE Prescott 1 (UINHM). COLORADO: MONTEZUMA Co.; Park Well, Mesa Verde Natl. Park, 7,450 ft., 4 (KU); Far View Ruins, Mesa Verde Natl. Park, 7,700 ft., 3 (KU); head of East Fork Navajo Canyon, sec. 27, Mesa Verde Natl. Park, 7,900 ft., 1 (KU); 2 mi. NNW Rock Springs, Mesa Verde Natl. Park, 7,900 ft., 1 (KU); Prater Canyon, Mesa Verde Natl. Park, 7,600 ft., 4 (KU); Mesa Verde Park headquarters, 7,000 ft., 4 (KU). NEW MEXICO: BERNALILLO Co.; 3.2 mi. S, 0.5 mi. E Tijeras, Cedro Canyon, T9N, R5E, Sec. 2, 6,760 ft., 1 (MSB); Tree Springs, Sandia Mts., 8,500 ft., 17 (MSB). CATRON Co.; 19 mi. ENE Glenwood, 5 (UIMNH); 4 mi. W Luna, 2 (UIMNH); 10 mi. E Mogollon, Willow Creek, Mogollon Mts., 32 (MSB); 10 mi. N, 5 mi. W Datil, Datil Mts., 8 (MSB); Snow Park, T12S, R17W, Sec. 14, 9,900 ft., 5
(WNMU); White Creek Cabin, T12S, R16W, Sec. 1, 6,850 ft., 7
(WNMU); Gilita Creek near mouth Iron Creek, T10S, R16W, Sec. 
34, 2 (WNMU); McKenny Park airstrip, T12S, R15W, Sec. 19, 4
(WNMU); 15 mi. SW Reserve, Pueblo Park, T8S, R21W, Sec. 24,
6,127 ft., 1 (WNMU); Halfmoon Park, T12S, R17W, Sec. 1, 2
(WNMU); Iron Creek Mesa Lake, T11S, R17W, Sec. 2, 8,300 ft.,
4 (WNMU); 12 mi. E Mogollon, Willow Creek, 1 (WNMU); Middle
Fork Gila River, Trotter Place, T11S, R15W, Sec. 6, 1
(WNMU); Snow Lake, T10S, R16W, Sec. 20, 7,450 ft., 7 (NMSU);
12 mi. E Mogollon, T10S, R17W, Sec. 33, 8,100 ft., 1 (NMSU);
E slope Mache Mt., 9,500 ft., 2 (KU); Apache Creek, 1 (KU);
0.5 mi. W ranger station, Willow Creek, 8,600 ft., 3 (KU);
19 mi. E Alma, 8,200 ft., 1 (TCWC); Gillito Creek, Mogollon
Mts., 1 (MSB); head of Davenport Canyon, Datil Mts., 2
(MSB). CIBOLA Co.; 17.5 mi. E Grants, T12N, R7W, NW 1/4
Sec. 5, 2 (MSB); 6 mi. N, 14 mi. E Grants, T12N, R7W, 5
(MSB). COLFAX Co.; 4 mi. NW Raton, 9 (UIMNH); 4 mi. S, 2 mi.
W Cimarron, 5 (UIMNH); 5 mi. E Raton, 6 (UIMNH); 4 mi. N
Raton, Raton Pass, 4 (UIMNH); 7 mi. E Raton, Malaya Lake, 2
(UIMNH); 4 mi. W Capulin, 1 (UIMNH); 6 mi. W Capulin, 2
(UIMNH). GRANT Co.; 5 mi. N Pinos Altos on NM HW 15, T16S,
R13W, Sec. 9, 7,225 ft., 2 (WNMU); 11.5 mi. NE Pinos Altos
Lake, 4 (WNMU); upper end Lake Roberts, 2 (WNMU); 3.4 mi. N,
0.2 mi. E Pinos Altos, 1 (NMSU); 16 mi. S, 7 mi. N Santa
Rita, Iron Canyon, Black Range, 8 (MSB); 21 mi. S Wall Lake
by road, Black Range, 6 (MSB). LINCOLN Co.; South Fork
Campground, Lincoln Natl. Forest, 1 (TTU); 1 mi. S Monjeau Peak, 8 (UIMNH); 8 mi. SSW Nogal, 1 (UIMNH); 0.1 mi. S, 2.2 mi. E Alto, T10S, R13E, Sec. 32, 9,500 ft., 14 (NMSU); 2.4 mi. N, 4.0 mi. E Sierra Blanca Peak, T10S, R12E, Sec. 25, 8,000 ft., 2 (NMSU); Padilla Point, T8S, R16E, Sec. 18, 9,622 ft., 2 (UTEPE); 1.3 mi. N, 4.9 mi. E Sierra Blanca, Eagle Creek, T10S, R13E, Sec. 31, 8,000 ft., 5 (NMSU); 0.25 mi. N, 2.5 mi. E Ft. Stanton, T9S, R15E, NW 1/4 Sec. 28, 1 (NMSU); 0.1 mi. S, 2.6 mi. E Alto, T10S, R13E, Sec. 31, 7,500 ft., 2 (NMSU); 0.7 mi. S, 2 mi. E Ft. Stanton, T9S, R15E, NW 1/4 Sec. 33, 6,400 ft., 1 (NMSU); 2.0 mi. S, 1.4 mi. E Alto, T11S, R13E, Sec. 11, 7,000 ft., 1 (NMSU); 4 mi. N, 5 mi. W Alto, Bonito Lake, 7,300 ft., 1 (TTU); head of Bonito Reservoir, 8,000 ft., 1 (TTU); 4 mi. W Alto, Eagle Creek, 2 (KU); 5 mi. N, 9 mi. E Capitan, Capitan Mts., 4 (MSB); Monjeau Peak, White Mts., 10,000 ft., 9 (MSB); Capitan Mts., 4 (MSB); Gallinas Mt., 2 (MSB). MCKINLEY Co.; Thoreau, 6,700 ft., 4 (AMNH); 6.5 mi. S Thoreau, Cottonwood Gulch, 2 (AMNH); Upper Nutria, 7,200 ft., 4 (KU); 1 mi. E McGaffey, 8 (MSB). OTERO Co.; 1.75 mi. N, 1 mi. E Cloudcroft, 1 (OU); 0.2 mi. N, 7.7 mi. E Cloudcroft, R14E, T15S, SE 1/4 Sec. 31, 8,400 ft., 1 (NMSU); 0.5 mi. up 16 Springs Canyon E out of Cloudcroft off 82, 4 (UTEPE); 5 mi. S, 2.5 mi. E Cloudcroft, Russian Canyon, Sacramento Mts., 2 (UTEPE); 2 mi. N Musin Cabin, 1 (UTEPE); 0.1 mi. N, 1.8 mi. E Cloudcroft, T16S, R12E, Sec. 4, 8,450 ft., 1 (NMSU); 0.2 mi.
N, 7.7 mi. E Cloudcroft, T15S, R14E SE 1/4 Sec. 31, 8,400 ft., 1 (NMSU); 0.3 mi. N, 1.1 mi. E Cloudcroft, T15S, R15E Sec. 36, 8,550 ft., 1 (NMSU); 11 mi. S, 3 mi. E Cloudcroft, Masterson Springs, Hay Canyon, 8 (TTU); 10 mi. S Cloudcroft, Sacramento Mts., 3 (MSB); 4.5 mi. N, 8.5 mi. E Alamo Peak benchmark, Sleepy Grass picnic area, Lincoln Natl. Forest, 1 (MSB); 4.0 mi. N, 8.5 mi. E Alamo Peak benchmark, 1 (MSB); 2 mi. W Cloudcroft, 1 (MSB); James Canyon campground, 1 (MSB); Lightning Lake, T18S, R12E, Sec. 9, 9,400 ft., 3 (TTU); 22.5 mi. W Pinon by road, Timbersorn Airstrip, 2 (TTU); 0.5 mi. N June, 82-24 N to Ruidoso, 3 (UTEP); 2.4 mi. W Cloudcroft on HW 82, 1 (UTEP). SIERRA Co.; 2 mi. N, 14 mi. W Winston, Taylor Creek, Black Range, 8 (MSB). SOCORRO Co.; 8 mi. S Magdalena, Mill Canyon, 1 (UIMNH); 1 mi. below Bear Trap campground, San Mateo Mts., 1 (UIMNH); 20 mi. S, 19 mi. W Magdalena, Beartrap Canyon, San Mateo Mts., T5S, R7W, Sec. 13, 8,300 ft., 5 (UTEP); head of East Red Canyon, San Mateo Mts., 9,800 ft., 1 (UTEP); 20 mi. S, 19 mi. W Magdalena, Bear Trap Canyon, San Mateo Mts., 6 (MSB); Mt. Withington, San Mateo Mts., 6 (MSB); Mill Canyon, Magdalena Mts., T3S, R4W, Sec. 36, 9 (MSB); head of Water Canyon, Magdalena Mts., 9,300 ft., 4 (MVZ). TORRANCE Co.; 6 mi. W Manzano, Red Canyon campground, 1 (OU); Red Canyon, Manzano Mts., T5N, R5E, NW 1/4 Sec. 34, 3 (UTEP); Fourth of July Canyon, Manzano Mts., T7N, R5E, NE 1/4 Sec. 35, 1 (UTEP); Red River campground, Manzano Mts., 1 (UTEP); Red Canyon, Cibola Natl.
Forest, 3 (TTU); 5.5 mi. W Tajique, 6 (MSB); Fourth of July campground, Cibola Natl. Forest, 2 (TTU); 1.7 mi. S, 4.6 mi. W Manzano, Red Canyon Campground, T5N, R5E, NW 1/4 Sec. 34, 2 (MSB). UNION Co.; 3 mi. S, 3 mi. W Des Moines, Sierra Grande, T29N, R29E, Sec. 30, 7 (MSB). VALENCIA Co.; Ojo Redondo, 1 (AMNH); Ojo Redondo, Mt. Sedgwick, 1 (AMNH); 6.75 mi. N, 11 mi. E Grants, 3 (UIMNH); 0.5 mi. NE La Mosca Peak, Mt. Taylor, 7 (MSB); 4 mi. W McCartys, 8 mi. SE Grants, 2 (WNMU), NW slope Mt. Taylor, 7 (KU); Mirabal Spring, Mt. Taylor, 9,000 ft., 7 (MSB); Agua Fria Creek, Zuni Mts., 5 (MSB); Agua Fria Creek, Zuni Mts., T10N, R12W, line between sec. 21-28, 4 (MSB); 17 mi. NE Grants, La Mosca Tank, 8 (MSB); 16 mi. NE Grants, Lillies Spring, 4 (MSB). TEXAS: CULBERSON Co.; the Bowl, Guadalupe Mts., 9 (UIMNH), 10 (TCWC), 2 (MVZ); Upper Dog Canyon ranger station, Guadalupe Natl. Park, 11 (TTU); Guadalupe Peak campground, Guadalupe Natl. Park, 1 (TTU); Blue Ridge, Guadalupe Mts. Natl. Park, 1 (TTU); the Bowl, Guadalupe Mts., 8,200 ft., 5 (TCWC); Upperdog Canyon, Guadalupe Mts. Natl. Park, 1 (TTU). UTAH: SAN JUAN Co.; Navajo Mt., 8,500 ft., 1 (AMNH); Navajo Mt. near War God Spring, 8,500 ft., 1 (AMNH); War God Spring, Navaho Mt., 8,400 ft., 13 (MVZ); Soldiers Spring, Navaho Mt., 8,800 ft., 3 (MVZ).
APPENDIX II
Table 1. Student-Newman-Keuls multiple range test on total length for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($F > 0.05$) ranges.

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Table 4. Student-Newman-Keuls multiple range test on length of ear for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant (\( P > 0.05 \)) ranges.

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Table 5. Student-Newman-Keuls multiple range test on width of nasals for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($P > 0.05$) ranges.

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Table 7. Student-Newman-Keuls multiple range test on interorbital constriction for 85 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($P > 0.05$) ranges.

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Table 8. Student-Newman-Keuls multiple range test on zygomatic breadth for 65 populations of Microtus mexicanus. Refer to Figure 1 for population locations. Vertical lines represent maximum nonsignificant ($P > 0.05$) ranges.

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Table 9. Student-Newman-Keuls multiple range test on prelabial breadth for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($\pi > 0.05$) ranges.

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Table 9. Student-Newman-Keuls multiple range test on prelambdoidal breadth for 85 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($F > 0.05$) ranges.

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Table 10. Student-Newman-Keuls multiple range test on mastoidal breadth for 85 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($F > 0.05$) ranges.

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Table 11. Student-Newman-Keuls multiple range test on width of foramen magnum for 65 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant (P > 0.05) ranges.

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Table 12. Student-Newman-Keuls multiple range test on height of foramen magnum for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant (P > 0.05) ranges.

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Table 13. Student-Newman-Keuls multiple range test on width of incisive foramen for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($P > 0.05$) ranges.

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Table 14. Student-Newman-Keuls multiple range test on length of incisive foramen for 69 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant (\( P > 0.05 \)) ranges.

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Table 15. Student-Newman-Keuls multiple range test on condylar length for 65 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant (P > 0.05) ranges.

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Table 16. Student-Newman-Keuls multiple range test on length of maxillary diastema for 65 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant (P > 0.05) ranges.

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Table 17. Student-Newman-Keuls multiple range test on length of rostrum for 65 populations of *Microtus mexicanus.* Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($\alpha > 0.05$) ranges.

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Table 18. Student-Newman-Keuls multiple range test on length of nasals for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant (p > 0.05) ranges.

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Table 19. Student-Newman-Keuls multiple range test on length of maxillary toothrow for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($P > 0.05$) ranges.

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Table 20. Student-Newman-Keuls multiple range test on rostral depth for 65 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant (P > 0.05) ranges.

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Table 21. Student-Newman-Keuls multiple range test on greatest skull depth for 65 populations of *Microtus mexicanus*. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($P > 0.05$) ranges.

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Table 22. Student-Newman-Keuls multiple range test on greatest length of skull for 65 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant ($P > 0.05$) ranges.

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Table 23. Student-Newman-Keuls multiple range test on length of mandibular diastema for 65 populations of Microtus mexicanus. Refer to figure 1 for population locations. Vertical lines represent maximum nonsignificant $(P > 0.05)$ ranges.

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Morphologic variation in the Mexican vole
(Microtus mexicanus)

Title of Thesis

Signature of Author

Date

13 March 1989

Signature of Graduate Office Staff Member

Date Received

March 20, 1989