MORPHOMETRICS OF THE *PEROMYSCUS LEUCOPUS* SPECIES GROUP (RODENTIA: MURIDAE)

By

Sergio Furtado dos Reis

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1985

ABSTRACT

MORPHOMETRICS OF THE *PEROMYSCUS LEUCOPUS* SPECIES GROUP (RODENTIA: MURIDAE)

By

Sergio Furtado dos Reis

Recent developments in morphometrics include a geometric protocol, the truss network, and the shear analysis that can be used to partition size and shape in the context of principal components analysis. These new developments in morphometrics are evaluated in a study of cranial morphologic differentiation of mice of the *leucopus* species group of *Peromyscus*. The *leucopus* species group of *Peromyscus* comprises two taxa, *P. leucopus* and *P. gossypinus*. The main objectives of this study were (1) to evaluate the ability of the truss networks to discriminate between taxa. (2) To compare the pattern of morphometric differentiaton for *P. leucopus* with that indicated by chromosomal and genic data; and (3) to evaluate the ability of the shear procedure to discriminate populations on the basis of size and shape.

Traditional and truss measurements representing different views of the skull varied in their ability to discriminate among populations, subspecies, and species. Traditional and truss measurements representing the ventral view of the skull generally produced the best

discrimination among taxa. The truss measurement scheme did provide localized information with respect to discrimination not uncovered by the traditional measurement scheme. Allometric coefficients displayed directly on the truss networks reveal a geometric constrast between the orofacial and the cranium in *Peromyscus* that was not clear with the traditional measurements.

The pattern of variation among *P. leucopus* subspecies is complex; different data sets produced different results. Discriminant analysis of dorsal and ventral truss networks showed no geographic trends in morphologic variation, while traditional measurements suggests the existence of discrete clusters of northern and southern subspecies. The results from traditional measurements agree to some extent with chromosomal data which suggest the exitence northeastern and southwestern cytotypes, while results from dorsal and ventral truss networks are comparable with allozyme data for *Peromyscus*. Localized patterns of cranial differenciation observed in *Peromyscus* may be due to high levels of phenotypic plasticity in the skull.

Only minute size effects were removed from principal components 2 and 3 when subject to the shear procedure. Size and shape differentiation is limited within *Peromyscus leucopus*, while *P. leucopus* and *P. gossypinus* show extensive size differentiation.

ACKNOWLEDGEMENTS

I thank my major professor Dr. Donald O. Straney for advice and criticism throughout the development of this project. I also thank the members of my Guidance Committee, Dr. Robert Anstey, Dr. Guy L. Bush, and Dr. Philip Myers for the contributions they provided for the improvement of this work.

I am deeply indebted to Dr. Richard E. Strauss for tutoring me in the use of MIDAS. Dr. Strauss also patiently explained to me several of the recent developments in morphometrics, and provided many computer programs for the analyses presented here. Dr. Marilyn Houck made available her microcomputer for data transfer. I am thankful to Dr. Strauss and Dr. Houck for freely sharing knowledge and ideas with me and above all for their friendship.

I thank Dr. Todd Bierbaum for his friendship and support and for technical help in the initial stages of this work. Bruce C. Jayne shared with me his knowledge of microcomputers.

I am very greatful to the Brazilian Research Council (CNPq) for granting me a scholarship that allowed me to pursue graduate studies.

My wife Mieko helped me in all aspects and phases of this work and ultimately made it possible.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

TITLE PAGE

INTRODUCTION

Most early mammalian taxonomic work, which dealt mainly with descriptions of new taxa, proceeded without the use of measurements of the animals under study. However, with the accumulation of more taxa, it frequently became necessary to use simple measurements to describe effectively the subtle differences apparent to the eye (e.g., Goldman, 1904; Lyon, 1906; Howell, 1910). Morphometrics entered systematics primarily as a tool of communication to speed identification and minimize the need of comparisons for increasingly subtle distinctions among taxa. But measurements were used in a few cases to address the nature of variation in taxonomically important characters within populations of mammals (e.g. Allen, 1894).

By 1900 multiple measurements were commonly taken from samples of individuals for descriptive and revisionary work. For example, Osgood (1904) used four body measurements and over ten skull and dental measurements in his description of new taxa of Peromyscus. Multiple measurements were also used by Osgood (1909) in his classic review to compare and contrast size and shape differences among closely related forms of Peromyscus.

The work of Osgood and others routinely incorporated population samples of individuals from which multiple measurements were taken. This approach characterizes "population systematics", substantially different from the earlier essentialist approach more commonly taken in the early 1900's (Mayr, 1980). The concern with individual variation and the need for the population approach was a consequence of Darwin's earlier assertion that individuals within a population do differ among themselves, thus rendering population samples necessary for the understanding of species variation (Mayr, 1980).

The move away from the essentialist outlook in systematics spurred a large number of studies that called attention to the variability of natural populations (see Mayr and Provine, 1980). Sumner's (1932) work on population variability and genetics of *Peromyscus* is a classic example (Mayr, 1980). In addition to studying the variability of populations, systematists went on to show that characters known to discriminate between species usually varied geographically within a species. (Mayr, 1980). These results lent support to the theory of geographic speciation (Mayr and Provine, 1980) and set the stage for studies of geographic variation, which have played a major role in studies of the nature of species (Gould and Johnston, 1970). Recently the focus of attention on speciation has shifted to the level of population structure (Bush, 1982; Templeton, 1980, 1981 ,1982), while the debate on the relationship between variation within and among populations continues (Charlesworth, Lande, and Slatkin, 1982; Alberch, 1983; Ayala, 1983; Gould, 1983; Maynard Smith et al., 1985).

Despite the population approach and the use of multiple measurements in systematic mammalogy, morphometrics continued in general to play a strictly taxonomic role after the early 1900's (e.g., Goldman, 1917; Nelson and Goldman, 1929; Hall and Davis, 1934). The work of Dice on *Peromycus* is nevertheless an exception. Based upon earlier taxonomic work on *Peromyscus* and following Sumner's pioneering studies on population variation and genetics, Dice set out to study variation at the population level (see Dice 1968; Hooper, 1968). He carried out his work in the best tradition of the Darwinian revolution (Mayr, 1980), by examining the nature of variation within populations to understand the evolution of species differences (Dice, 1932:1). Dice was able to document extensive variation at the population level, and to identify genetic and environmental components contributing to morphometric differentiation in several species of Peromyscus.

Dice analyzed several morphometric traits but treated each character independently without considering the possible implications of covariation among characters. The independent treatment of characters was common practice among evolutionary biologists and systematists during this period (Rensch, 1980). The importance of character covariation had nevertheless been recognized earlier by Darwin (see Provine, 1983:48) in connection with the evolution of maladaptive traits. Sumner (1932) took into account the genetic basis of character covariation in Peromsycus and stressed the importance of character correlations for the understanding of the genetic nature of population differences.

The importance of character covariation was also ignored in other aspects of evolutionary biology. Lande and Arnold (1983) reviewed the literature on selection from the early 1900's up to the present time and found that in most cases only sigle traits were considered. Lande and Arnold extended Pearson's work on multivariate selection and showed that the effects of selection can be statistically partitioned into direct and indirect effects, due to correlation among characters. Lande and Arnold (1983) demonstrated that the measurement of selection on single characters can be misleading because of indirect effects due to correlations with other traits.

The need for the use of multivariate character sets in the study of variation had long been recognized by systematists and evolutionary biologists (Tessier, 1948, 1955; Burt and Banks, 1947; Burma, 1949). Most early efforts to measure variation were nevertheless restricted to very few characters whose intercorrelations were not always adequately assessed (Gould and Johnston, 1972:460). The development of multivariate methods of analysis and, in particular, the widespread availability of statistical packages allowed evolutionary biologists and systematists to address questions of character covariation within and among populations (see Neff and Marcus, 1980). Multivariate morphometrics has today several uses in mammalian systematics. Commonly, discriminant analysis and principal components analysis are used to detect variation and covariation in quantitative traits, and also to assess patterns of phenetic relationships (e.g., Diersing, 1981; Rogers and Schmidly, 1982; Braun and Kennedy, 1984). These studies usually assess morphometric variation within populations and its relationship to variation across populations, and they frequently search for environmental correlates of phenotypic differentiation. In most cases relationships between populations are inferred from the same data used for morphometric analysis, so that no independent assessment of phyletic relationships is possible. Multivariate analyses have also been used to study morphometric differentiation in the context of historical hypotheses (e.g., Straney and Patton, 1980; Smith and Patton, 1982). In these studies morphometrics has a single specific role, that is, to describe the nature of morphologic variation, whose direction of change is then inferred from the phylogenetic relationships of the organisms under study. These studies are less common because they require phylogenetic hypotheses derived from sources other than morphometrics itself. The importance of phylogenetic hypotheses in studies of morphologic evolution cannot be overemphasized since evolutinary inferences on the direction of change can only be made in a phylogenetic context (Fink, 1983; Strauss, 1985; Creighton and Strauss, 1985).

The addition of phylogenetic hypotheses to the study of morphologic evolution is undoubtedly a positive development in morphometrics. However, multivariate morphometrics itself still presents conceptual and analytical shortcomings that may pose limitations to investigation of evolutionary and systematic questions. The main problems faced by morphometrics relate to the generation of variables for analysis and the transformation of these variables into estimates of differences in form among organisms. Measurements should ideally express change in homologous structure across forms, while estimators of form should not confound the contribution of size and shape to the differences among organisms. These analytical and conceptual foundations are necessary before mechanistic attempts to interpret morphological differentiation and divergence are made.

Bookstein and his colleagues (1985) have recently summarized the conceptual and analytical developments made by their group to morphometrics. They approach morphometrics from two different points of view: in the first approach, form change is modelled as deformation by the use of tensor fields, while in the second approach shape differences are estimated by factors representing size and shape. The latter approach is more familiar as it makes use of linear distance measurements on the organisms of study and the algebra of eigenanalysis. There are, however, important innovations in this approach, including models for the choice of measurements and the definition and statistical analysis of size and shape, that have fundamental implications to morphometrics.

Strauss and Bookstein (1982) and Bookstein (1982) notice that morphometrics offers no system for the selection of characters for study, and as a result traditional schemes of measurement often fail at providing adequate coverage of the forms under study. Consequently, if organisms differ due to more localized aspects of the morphology, it is possible that conventional measurements will fail to produce results that reflect the degree of differentiation between organisms. Strauss and Bookstein (1982) argue that measurement schemes should be designed to provide systematic coverage both in terms of area and axes of variation. They developed a method, the truss network, that makes use of homologous anatomical points to generate linear distance measurements that provide even and systematic coverage of the form. Strauss and Bookstein (1982) applied this procedure to a study of discrimination between two species of cottid fishes and found that the truss network provided better discrimination between species than the traditional data set. More importantly, the characters with the highest loadings on the principal components represent localized aspects of the morphlology not sampled by traditional measurement schemes used in fish morphometrics.

Size and shape differences among organisms are also important in addressing fundamental question of population differentiation. The adult form of organisms is the result of complex interactions of rates and timing of expression of traits whose trajectory through ontogeny determines similarity or divergence in size and shape. However, size and shape have to be defined before the relative importance and interaction of these two components can be determined. The definition of size and shape has had a history of conflict and controversy (Neff and Marcus, 1980). Statistical definitions of size inferred from linear distance measurements involve both the univariate and multivariate case. Univariate approaches to the definition of size carry different statistical problems (Strauss, 1985), but they share the assumption that size can be represented by a single measurent (Bookstein, 1982). The multivariate approach, which can be traced to Sewall Wright's factor model (Bookstein, 1982), represents the multivariate model of Jolicoeur (1963; 1984). In this model, size is estimated by the first eigenvector (principal component) of a covariance matrix of log transformed characters. However, the use of principal components analysis in the study of size and shape has also generated conceptual and statistical problems. Several authors have pointed out that labelling components as size and shape may be arbitrary because the independence between components is a consequence of the mathematical derivation of principal components analysis (Neff and Marcus, 1980). Inferences on size and shape thus defined may not have biological significance. The application of principal components analysis to study size and shape variation among groups raises another problem since principal components analysis was designed to analyze correlated variables within a single population (Morrison, 1976; Chatfield and Collins, 1980). Multiple groups may be analysed by principal components analysis, but the method treats the samples as a homogeneous set of observations (Neff and Marcus, 1980).

Bookstein and his group (see Humphries et al., 1980; Bookstein et al., 1985) have recently introduced a modification of principal components, the shear analysis, that addresses the problems of size and shape definition and variation within- and among-group. Humphries et al.'s (1980) model defines discrimination in terms of a two-group system: size, which grows within individuals; and shape, which is the record of differences among groups. In other words, size is a phenomenon occurring at the level of the individual to be modelled as a within group source of variation, whereas shape differences are to be compared among groups. In statistical terms, a size factor, S, which is correlated with group, is obtained by defining within-group size as a component whose loadings are covariances with groups held constant. The shape component, H, is a linear combination of coefficients that are equal to partial covariances with distance measurements controlled for intra-group size. Humphries et al. (1980) used the shear procedure in a study of discrimination at the population and specific level and showed that the shear did improve discrimination among groups. They also observed shape differences inferred from principal component loadings could be interpreted in a geometric context.

The techniques described above represent an improvement over traditional methods of measurement and analysis because they seem to improve discrimination among populations and also allow more meaningful interpretations of the biological basis of morphometric differentiaton. This is an important point, since evolutionary inferences are a function of the resolution of the methods used (Lewontin, 1982). The techniques discussed above represent recent developments and have been applied to studies of fish morphometrics only. The purpose of this study is to assess the usefulness of these morphometric techniques to mammalian cranial morphometrics, and to address specific questions of morphometric variation in selected populations of the *leucopus* group of *Peromyscus* species (Osgood, 1909).

The *leucopus* species group of *Peromyscus* comprises two species, *P. leucopus* and *P. gossypinus*. *Peromyscus leucopus* ranges from the eastern and northern United States to Mexico while *P. gossypinus* is restricted to the southeastern United states (Hall, 1981) (Figure 1). Osgood (1909) recognized 13 subspecies of *P. leucopus* and four subspecies of *P. gossypinus*. In his review of the mammals of North America Hall recognized an additional four subspecies of *P. leucopus* and three of *P. gossypinus*, but retained the essential arrangement proposed by Osgood.

Osgood's subspecific arrangement of the *leucopus* group suggests a pattern of geographically structured variation, and Osgood himself thought that *P. leucopus* as a group could be naturally divided into northeastern and southwestern forms. Recent chromosomal studies of *P. leucopus* by Baker and his coworkers (1983) have indicated a major subdivision within *P. leucopus* between southwestern and northeastern cytotypes. The cytotypes of *P. leucopus* are distinguished by three euchromatic pericentric inversions. Baker et al.'s data on chromosomes thus lend support to Osgood's assessment of a northeastern-southwestern division of *leucopus*, but it shows no concordance with Osgood's formal subspecific arrangement. Recent biochemical work by Robbins et al. (1985) has indicated that the pattern of allozyme variation for *P.*

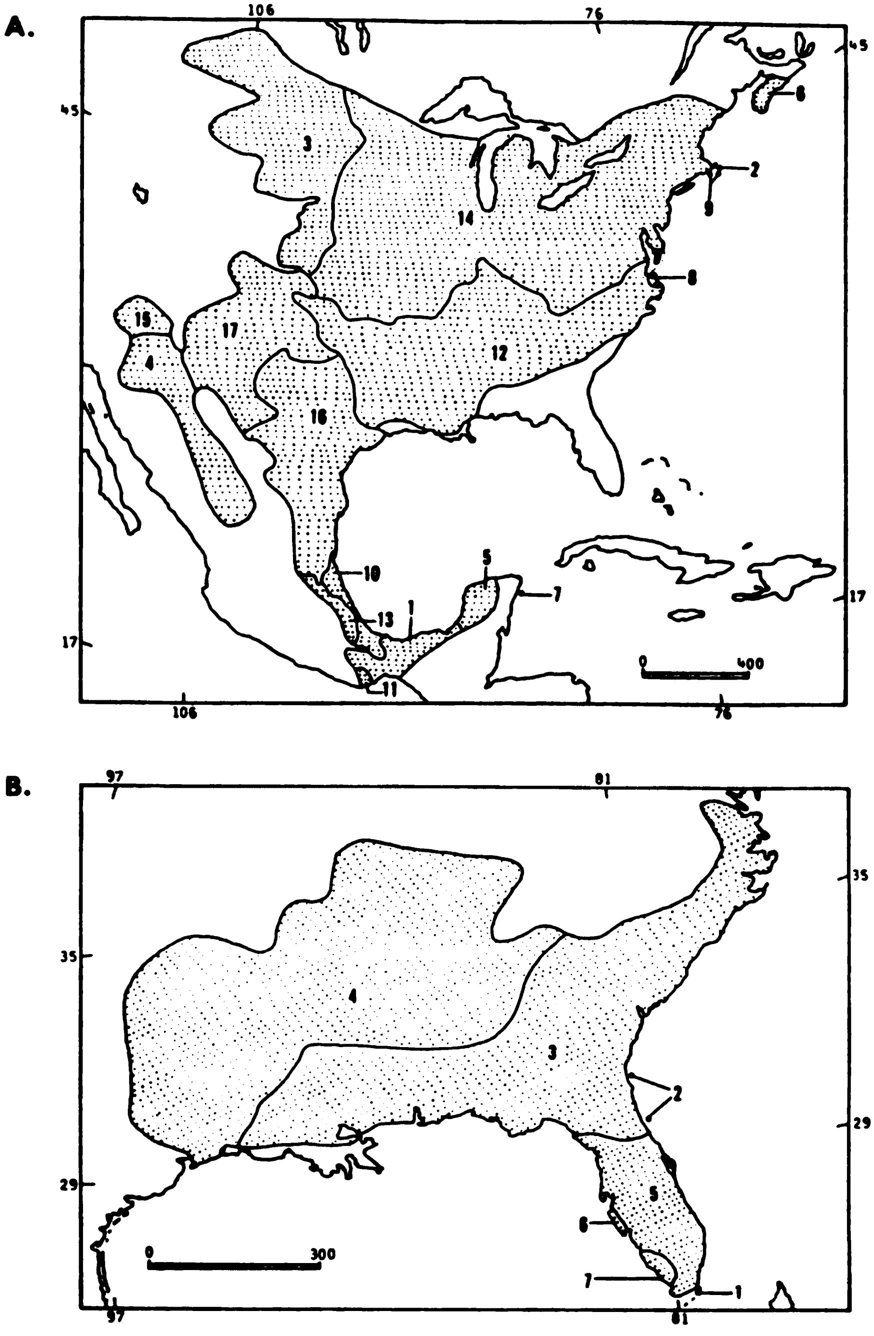

Figure 1. A. Distribution of *Peromyscus leucopus* 1. *affinis* 2. *ammodytes* 3. *aridulus* 4. *arizonae* 5. *castaneus* 6. *caudatus* 7. *cozumelae* 8. *easti* 9. *fusus* 10. *incensus* 11. *lachiguiriensis* 12. *leucopus* 13. *mesomelas* 14. *noveboracensis* 15. *ochraceus* 16. *texanus* 17. *tornillo* B. Distribution of *Peromyscus gossypinus* 1. *allapaticola* 2. *anastasae* 3. *gossypinus* 4. *megacephalus* 5. *palmarius* 6. *restrictus* 7. *telmaphilus*. After Hall, 1981.

leucopus is not congruent with either the currently accepted subspecific boundaries (Osgood, 1909; Hall, 1981) or the chromosomal cytotypes described by Baker et al. (1983). Allozyme variation for polymorphic loci is correlated with geography among *P. leucopus* populations, and is concordant with a model of isolation by distance (Wright, 1943).

The data summarized above suggest that *P. leucopus* has a complex pattern of differentiation. Chromosomal and electrophoretic data do not show congruence between themselves and with the subspecific arrangement of Osgood (1909). The different data sets thus suggest different patterns of differentiation and relationships, but agree to the extent that none can replicate patterns of variation implied by the current subspecific arrangement. *Peromyscus gossypinus* shows similar problems. The biochemical data available for *P. gossypinus* (Robbins et al., 1985) reveals a pattern similar to *P. leucopus* where no congruence is found between genetic relationships and the subspecific boundaries. As in *P. leucopus*, electrophoretic variation in *P. gossypinus* is also correlated with geographic distance.

The morphometric data available for the *leucopus* group is limited. Dice (1937) observed significant amounts of variation in morphometric characters and pelage color in *Peromyscus leucopus noveboracensis* throughout its range. Dice did not find, however, any geographic trend in the pattern of variation of *P. l. noveboracensis*. Dice (1939) also reported differences in skull dimensions and pelage color among *P. leucopus* from several localities in New England and Nova Scotia. Dice (1940) compared *P. leucopus* with *P. gossypinus* from eastern Virginia and found that adults of both species could easily be discriminated on the basis of the larger size of _P. gossypinus_. Engstrom et al. (1982) obtained essentially the same results using discriminant function analysis.

The main objectives of this study are the following: (1) To evaluate the ability of the truss networks to discriminate between populations. Specifically, I want to determine whether discrimination is improved by the truss scheme, and whether localized aspects of the cranial morphology, not sampled by traditional data sets, are important for the discrimination of _P. leucopus_ taxa. The data sets used here provide the most difficult case for evaluation of discrimination performance of different measurement schemes because populations, subspecies, and species of the _leucopus_ group probably show low levels of differentiation. I also want to determine whether the spatial arrangement of the truss networks allow more meaningful geometric explanations of the differences between taxa. (2) To determine whether the pattern of morphometric variation of _P. leucopus_ indicated by canonical variates and cluster analysis is congruent with the current subspecific arrangement or the chromosomal cytotypes, or whether there is a correlation between morphologic distance and geographic distance. I also want to determine if the traits used by Osgood to differentiate between _leucopus_ taxa agree with the results from canonical variates analyses. (3) To evaluate the ability of the shear procedure to discriminate populations on the basis of size and shape and determine whether allometric patterns are similar at the different levels of organization, i.e., among populations and subspecies and between species. Specifically, I want to determine whether _P. gossypinus_ and _P. leucopus_ differ in size alone as previously reported. I also want to determine whether shape differences can be accounted for by the observed differences in allometry. I emphasize that this study is exploratory in nature and is not intended as a revision of the *leucopus* group of *Peromyscus*.

MATERIALS AND METHODS

A total of 289 individuals were examined from 9 subspecies of *Peromyscus leucopus* and 1 subspecies of *P. gossypinus*. For five subspecies, more than one population was represented (*P. l. fusus*: 2; *P. l. noveboracensis*: 4; *P. l. aridulus*: 2; *P. l. leucopus*: 2; *P. l. incensus*: 2). Sample sizes ranged from 11 to 18 (See below, Specimens Examined). In all cases, samples represented individuals collected at one locality or in one localized area, at roughly the same time. All animals used in this study were adults.

Peromyscus skulls were measured with electronic digital calipers (MAX-CAL) interfaced with a TRS Model 100 portable computer (see Marcus, 1983 for a general discussion on electronic acquisition of data in morphometrics). The data were stored on cassette tapes, transferred to an IBM personal computer, and finally sent to the University of Michigan Ahmdal mainframe computer for data analysis. All computations were performed using the Michigan Interactive Data Analysis System (MIDAS), at the University of Michigan.

Measurement schemes

Two measurement schemes were used: the conventional system frequently used in mammalian morphometrics (e.g., Cockrum, 1962; DeBlase and Martin, 1981) and the truss protocol developed by Strauss

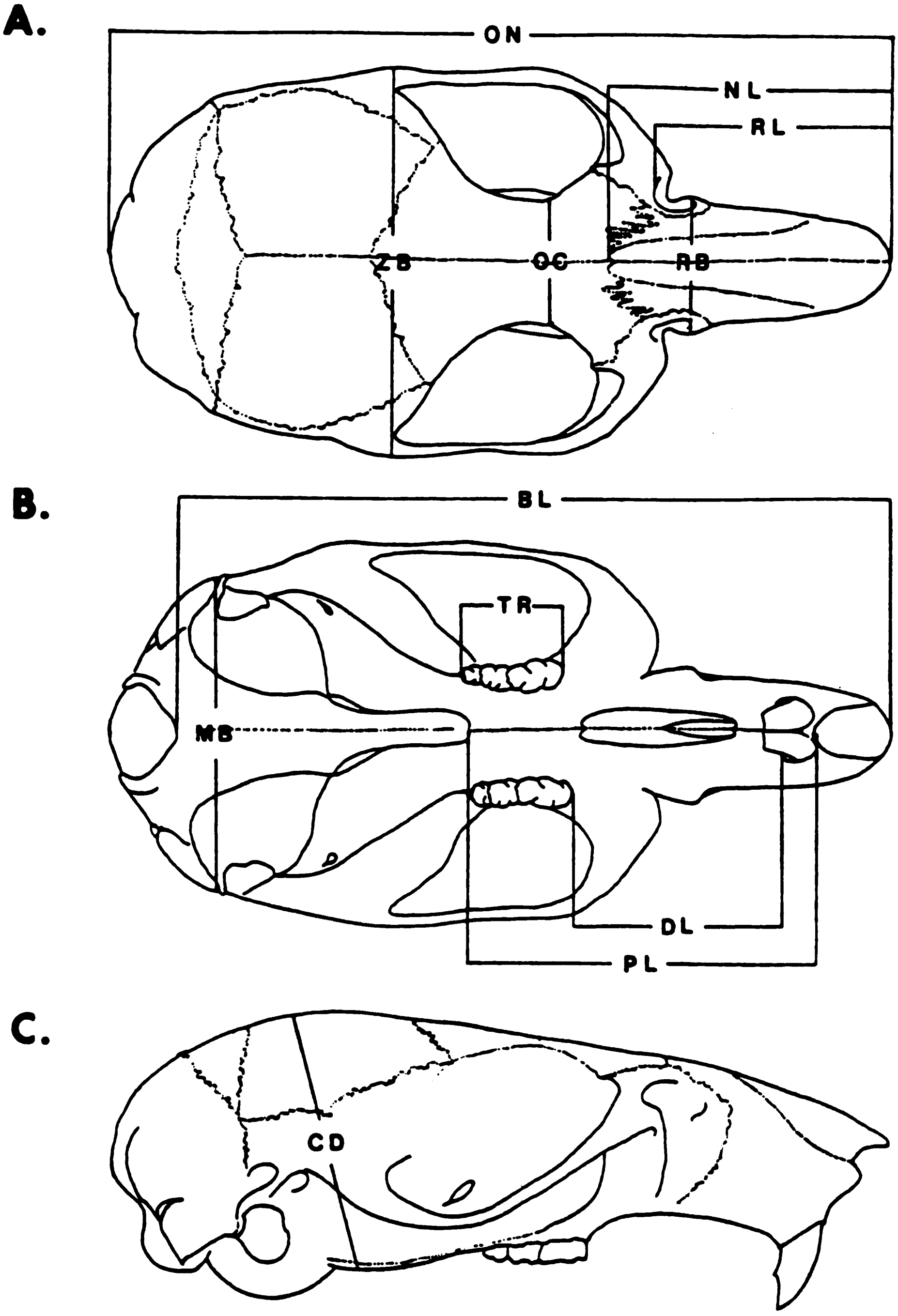

Figure 2. Traditional set of distance measurements.

and Bookstein (1982). Measurements in the conventional system tend to differ with the species studied (Cockrum, 1962:30) but include minimum and maximum distances taken from end points on the cranium that are generally not homologous landmarks. The distances in the conventional scheme can usually be clustered into length, width, and depth measurements. Twelve conventional cranial dimensions were measured on specimens of the leucopus group: occipito-nasal length (ON), rostral length (RL), nasal length (NL), rostral breadth (RB), least interorbital constriction (OC), diastema length (DL), length of upper toothrow (TR), palatal length (PL), basal length (BL), zygomatic breadth (ZB), mastoid breadth (MB), and cranial depth (CD) (Figure 2). Measurements follow Musser (1979).

The truss protocol advanced by Strauss and Bookstein (1982) makes explicit requirements for taking distance measurements on a specimen. The most important element in this protocol are landmarks that are homologous anatomical points from form to form (Strauss and Bookstein, 1982). Pseudolandmarks (Bookstein et al., 1985) are points operationally defined and not necessarily homologous from form to form. Pseudolandmarks are exemplified by the use of minimum and maximum distances in measurements, such as greatest body depth or greatest length of the skull. The terms "anatomical" and "extremal" have also been used for these two types of landmarks (Moyers and Bookstein, 1979). After selection of landmarks, interlandmark distances can be obtained by several schemes of connecting landmarks with measured lines (Strauss and Bookstein, 1982:115). The truss measurement scheme attempts to provide even coverage of measures on a form with relatively few measures. It is neither the most complete nor the minimum-measure scheme, but rather a compromise between these extremes. It requires 5n/2-4 (n=number of landmarks) distances, and is the system used in the present work.

Morphological features in the skull of Peromyscus representing landmarks and pseudolandmarks were defined for the dorsal and ventral surfaces of the skull, as shown in Figure 3. They are defined as follows: DORSAL SIDE: (points 1 and 2) rostral most point of contact of the premaxilla and nasal bones seen seen from the dorsal view, (3-4) point where maxilla, frontal, and nasal bones meet, (5-6) least interorbital constriction, (7-8) point where squamosal, frontal, and parietal bones meet, (9-10) point where the parietal-interparietal suture meets the interparietal-occipital suture, i.e., the end points of the interparietal bone, (11) mid-sagital midpoint of the upper edge of the foramen magnum. VENTRAL SIDE: (12-13) latero-posterior point of incisor-premaxilla interface, (14-15) site of attachment of tendon of M. masseter superficialis (Rinker, 1954), (16-17) rostral most point along midline of the first upper molar (M1), (18-19) caudal most point along midline of the third upper molar (M3), (20-21) paraoccipital process, and point 11, as defined for the dorsal view. Points 5 and 6 are, by definition, the only pseudolandmarks since they are defined in terms of a minimum distance. Points 11, 12, 13, 16, 17, 18, and 19 are not pseudolandmarks by definition, but their determination on the skull is much less precise than the remaining points which represent sutures between bones, sites of muscle attachment, and morphological structures such as the paraoccipital process. It is thus possible that such points might be intermediate between landmarks and pseudolandmarks with respect to homology from form to form.

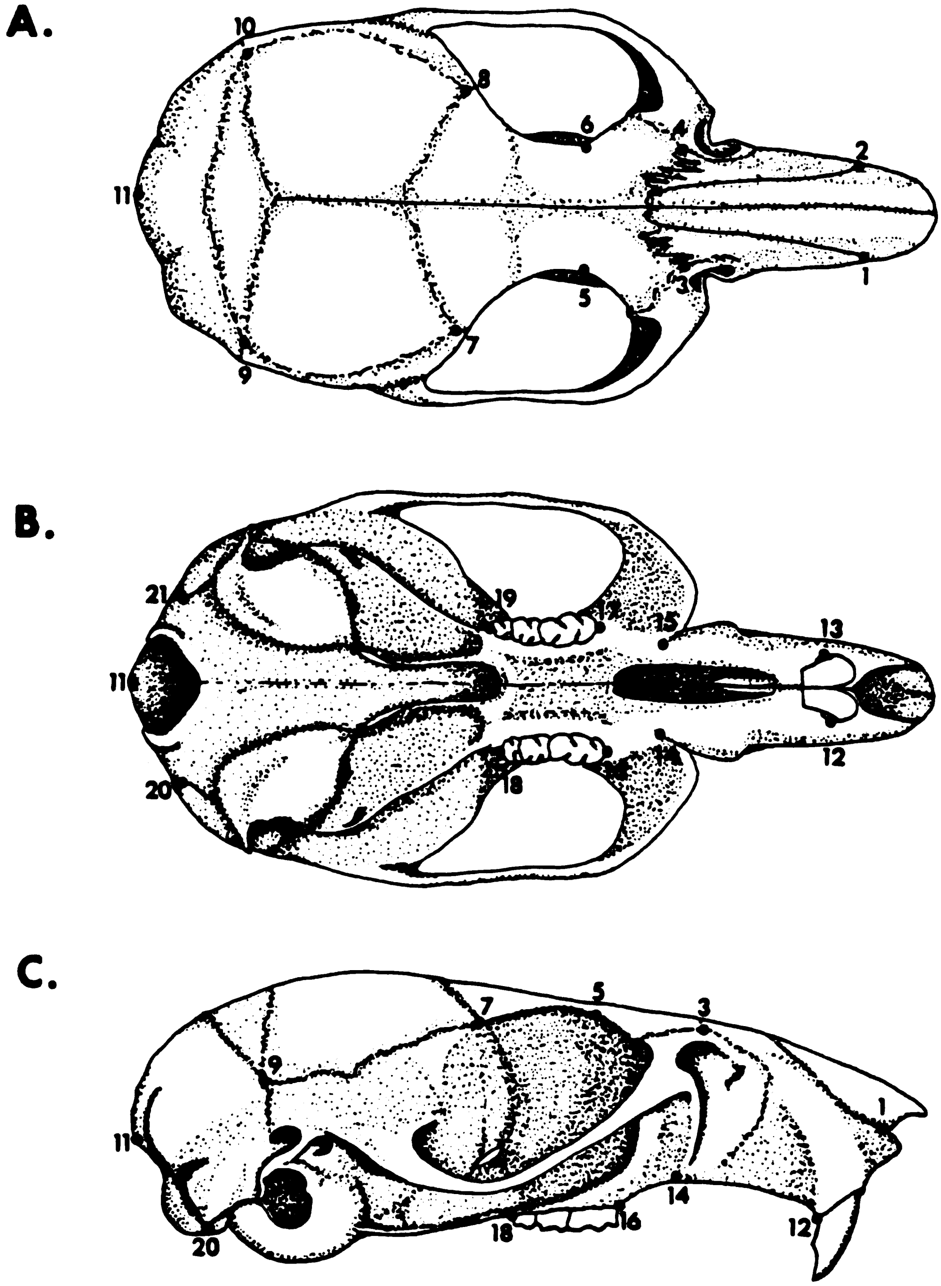

Figure 3. Landmarks used to construct truss networks. A. Dorsal view of the skull. B. Ventral view of the skull. C. Lateral view of the skull.

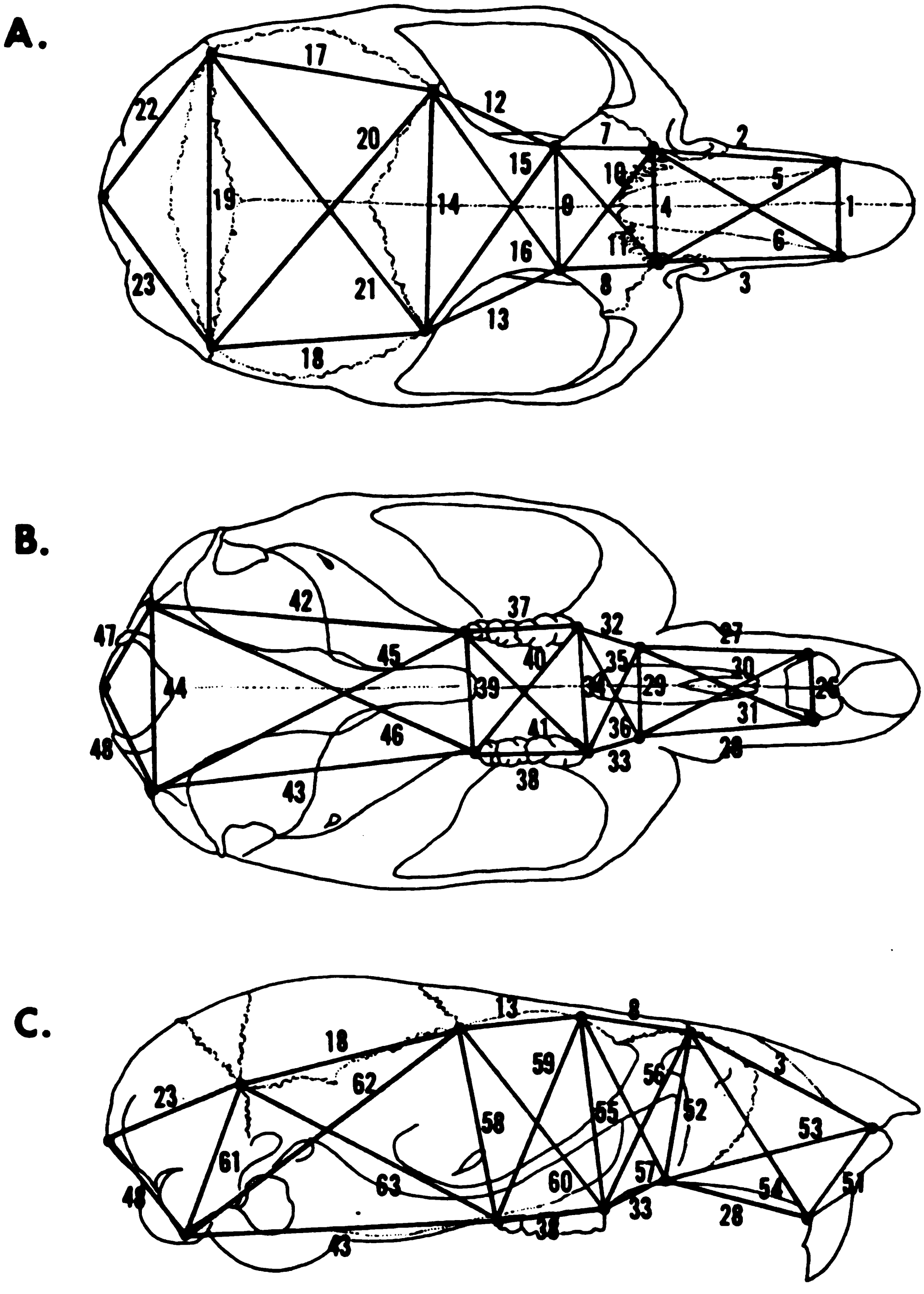

Figure 4. Distance variables used in the truss networks. A. Dorsal view of the skull. B. Ventral view of the skull. C. Lateral view of the skull.

Distance measurements were taken as interlandmark distances for the dorsal and ventral sides of the skull (Fig. 4). Dorsal and ventral landmarks were connected to produce a set of measurements on the lateral view of the skull (Fig. 4). The dorsal, ventral, and lateral surfaces of the skull, when considered separately, generated 23, 23, and 13 distinct interlandmark distances, respectively. All of the landmarks and associated distances produced truss cells (with 6 distances) except for the posteriormost cells of all three data sets of measurements which are triangles (Fig. 4).

The truss measurement schemes were designed as an attempt at detecting shape differences in oblique, horizontal, and vertical directions, thus allowing a systematic coverage of the three separate views of the skull, that is, dorsal, ventral, and lateral. However, the skull is a three-dimensional structure, and biological information on distance measurement can be lost in the process of treating cranial morphometrics based upon separate views. A three-dimensional measurement scheme was also devised using the same landmarks defined for the individual views of the skull except landmarks 3-4 and 14-15, which were excluded (Fig. 5). This data set yielded 28 interlandmark distances, and although it retains the geometric nature of the truss protocol, the diagonal distances were omitted. The three separate views of the skull and the three dimensional measurement scheme yielded, altogether, 63 distinct measurements. The networks for the three views of the skull and the three dimensional measurement scheme are shown in Figure 6. These 63 distance variables were measured on 306 specimens of the leucopus group. Measurement error was evaluated with discriptive statistics (mean, standard deviation, coefficient of

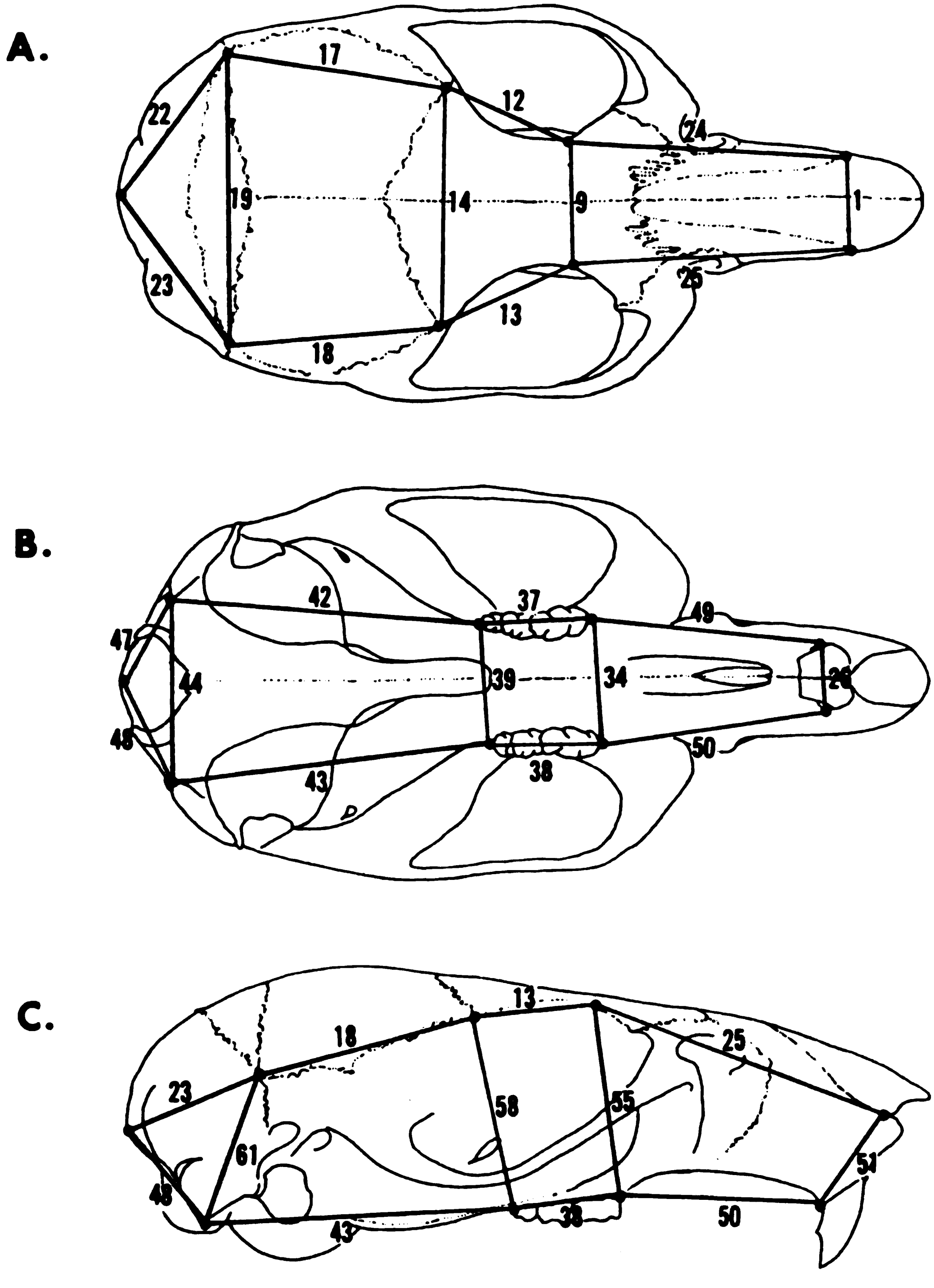

Figure 5. Distance variables used to construct the three dimensional view of the skull. A. Dorsal view of the skull. B. Ventral view of the skull. C. Lateral view of the skull.

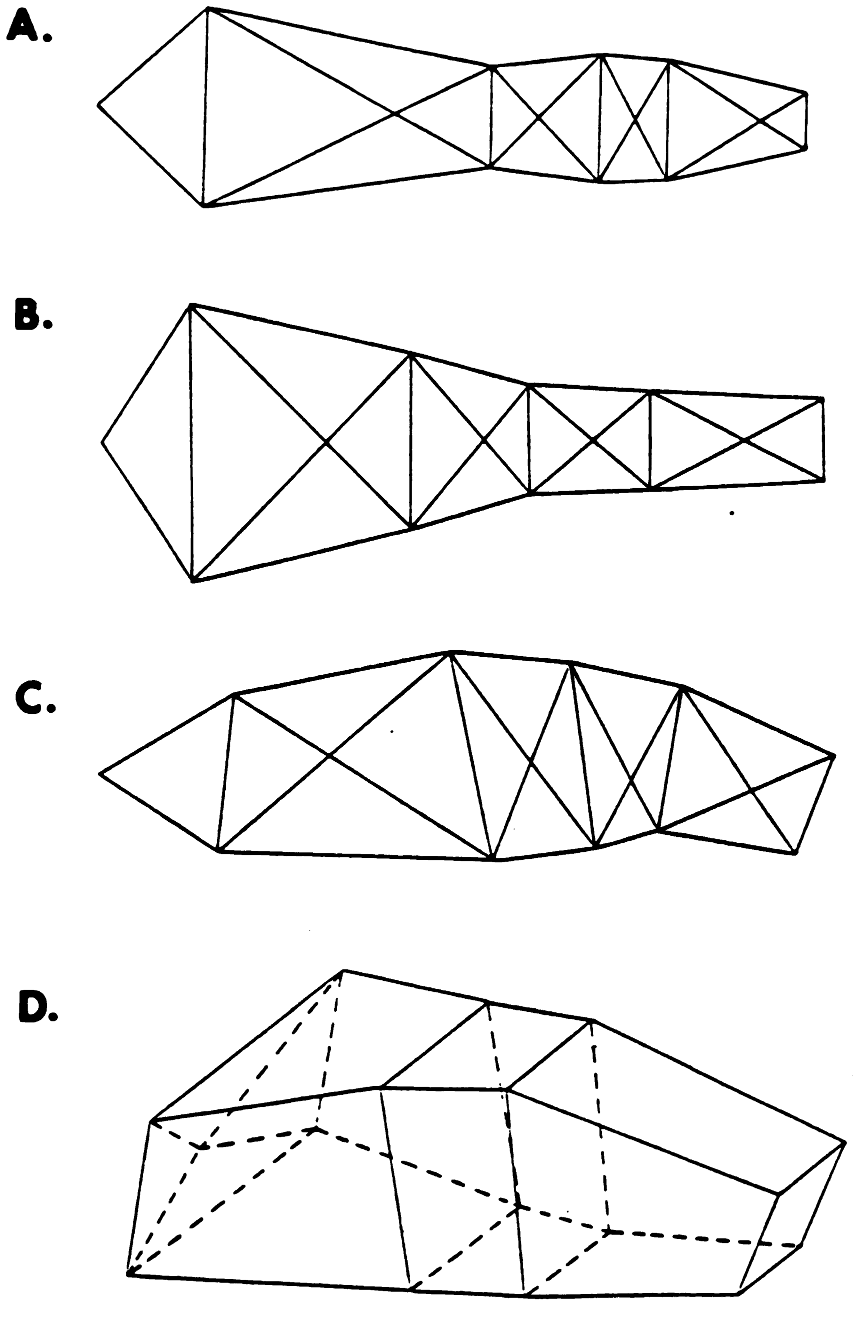

Figure 6. Truss networks (Rostral end to right). A. Dorsal view of the skull. B. Ventral view of the skull. C. Lateral view of the skull (Dorsal to top). D. Three dimensional view of the skull.

variation) for the conventional measurement scheme and the truss networks by measuring one individual ten times on ten different days.

Multivariate analyses

Patterns of discrimination among population samples of *Peromyscus leucopus*, among *leucopus* subspecies, and also between *P. leucopus* and *P. gossypinus* were examined by discriminant function analysis with canonical variates. Separation of *a priori* defined groups is achieved by discriminant analysis through the maximization of a function of the ratio of the among-group to the within-group covariance matrices (Morrison, 1976; Neff and Marcus, 1980). In other words, a ratio of two quadratic forms, the mean square between groups to the within-group mean square, is maximized to yield a linear function with the highest possible F-ratio. Canonical variates were computed and individual scores were plotted in the canonical variate space for all populations in a given analysis. The conventional data set, the 3 truss networks, and the 3-D measurement schemes were analysed by discriminant functions with canonical variates. Phenetic relationships were estimated by clustering taxa with the unweighted pair group method using arithmetic means (UPGMA) (Sneath and Sokal, 1973) based on the Mahalanobis distance between taxa. Minimum spanning trees (Prim, 1957) were constructed using the Mahalanobis D^2 statistics to assess the geographic relationships of the population samples based upon phenotypic resemblance.

Size and shape differences between taxa were evaluated by using the shear procedure developed by Humphries et al. (1980). The shear procedure is a modification of standard principal components analysis. The method is defined as a two-group system in terms of size and shape: size, which grows within individuals, and shape, which represents differences between groups. A size factor, S, is computed from the centered variables across groups. In other words, variables are standardized to zero mean, and the first principal component is extracted from the pooled among-groups covariance matrix. The confounding effects of size are then partialed out of the second principal component through regression analysis. The residual from this regression is used as an estimate of a size-free shape component, H. I computed the shear procedure using a list of commands for MIDAS provided by R. E. Strauss (Museum of Zoology, University of Michigan).

The variables in the conventional, truss networks, and the three dimensional data sets were transformed to logarithms and principal components were calculated from the covariance matrix of distance variables. Individual scores were plotted in the reduced space of the principal components for the same groups studied by discriminant analysis. The percentage overlap between pairs of taxa in the reduced space of both canonical variates and principal components was computed to allow the comparison of the effectiveness of the two techniques to discriminate population samples. Limited jacknifing of the principal components indicate that cöefficients of principal components are stable and do not seem to be affected by sample sizes.

Principal components were also used to study patterns of multivariate static allometry (Jolicoeur, 1963; 1984). Inferences from allometric coefficients are restricted to adult allometry because all the mice used here were adults. The first principal component was used as an estimate of a general size factor if all distance variables of a data set were significantly and positively correlated with the principal component (R. E. Strauss, pers. comm.). When the first principal component can be interpreted as a size factor, the coefficients of the distance variables on the component are proportional to allometric coefficients of the distance variables with respect to size (Jolicoeur, 1963; Strauss, 1985). The loadings of distance variables on the first principal component were rescaled (so that their squares sum to the number of characters) and interpreted as static allometric coefficients on general size (Strauss, 1984; 1985). Values greater than unity describe positive allometry with respect to size whereas those less than unity indicate negative allometry (Jolicoeur, 1963; 1984).

Coefficients of vector correlations (Bryant, 1984; Strauss and Fuiman, 1985) can be used as summary statistics to indicate the degree of similarity between principal components. Coefficients of vector correlations were computed between sheared principal components 2 and 3 and original principal component 2 and 3 to evaluate the whether size effects were removed from original components. Coefficients of vector correlations for pairwise comparisons between principal components were calculated as inner products of distance variable coefficients (Morrison, 1967:44). Statistical and geometric expressions of inner products are, respectively, the sum of cross products and a measure of nonorthogonality (Bryant, 1984). Zero inner products result when vectors are at right angles to each other. Similarly, the inner product of two vectors approaches unity as they approach coincidence (Morrison, 1967). Kendall's rank correlation coefficient (Sokal and Rohlf, 1981) were calculated between allometric coefficients and loadings from principal components 2 and 3 to determine whether shape differences could be accounted for by observed differences in allometry (Bookstein, 1985).

Specimens examined

All of the specimens used in this study are housed in the Division of Mammals of the Museum of Zoology at The University of Michigan. The localities and samples sizes (N) are as follows:

Peromyscus leucopus fusus. Massachusetts: Vineyard Haven (N=20); Martha's Vineyard (N=26).

Peromyscus leucopus noveboracensis. Michigan: Ann Arbor (N=20), Boyne Falls (N=14), Livingston (N=12). Oklahoma: Okesa (N=16).

Peromyscus leucopus aridulus. Nebraska: Cherry Co. (N=11), Dawes Co. (N=17).

Peromyscus l. leucopus. Kentucky: Trigg Co. (N=15). North Carolina: Wake Co. (N=22).

Peromyscus leucopus tornillo. Texas: Brewster Co. (N=12).

Peromyscus leucopus castaneus. Mexico: Campeche (N=13).

Peromyscus leucopus mesomelas. Mexico: Acultzingo (N=12).

Peromyscus leucopus affinis. Mexico: Cuicatlan (N=18).

Peromyscus leucopus incensus. Mexico: Nautla (N=16), Pahuatlan (N=19).

Peromyscus g. gossypinus. Virginia: Cypress Chapel (N=26).

RESULTS

1. Measurement error

Measurement error is very low for traditional measurements. The mean coefficient of variation is 0.33%, with least interorbital constriction showing the largest coefficient of variation (1.02%) and basal length and tooth row length showing the smallest coefficients of variation (0.08%). The mean coefficient of variation for all variables in the truss networks is also low (0.81%), although it is larger than that for traditional measures. Distance variable four (posterior width of nasals) and tooth row length (distance variable 38) have the largest (1.95%) and the smallest (0.00%) coefficients of variation, respectively.

2. Discrimination

2.1 Populations within _Peromyscus_ _leucopus_ subspecies

2.1.1 Discriminant Analysis

Discriminant analysis with canonical variates was used to examine morphological relationships and to assess the degree of divergence at the population level among 2 samples each of _P_. _l_. _fusus_, _P_. _l_.

aridulus, P. l. leucopus, P. l. incensus, and 4 samples of P. l. noveboracensis. Each taxon was analyzed separately. The data set include, for each group of populations, the traditional measurement scheme, the truss networks, and the three dimensional measurement scheme. The lateral and three dimensional data sets could not be analyzed because the within-group covariance matrix was singular.

Traditional measurements

Table 1 summarizes a posteriori probabilities of group assignment for all population samples of P. leucopus examined. All individuals of l. leucopus and incensus are correctly classified to their respectives populations, while the level of misclassification in the remaining populations was low. Only among noveboracensis populations was misclassification appreciable. Twenty five percent of Livingston individuals were misclassified with Boyne Falls individuals, and in the Boyne Falls population 7% were misclassified with Livingston individuals and 14% with Ann Arbor individuals. Other populations had misclassification rates below 15%.

Canonical variates were different for each population. Nasal length contributes a large positive coefficient, while breadth of rostrum and basal length contribute large negative coefficients to the single canonical variate discriminating the Vineyard Haven population from the Martha's Vineyard population of fusus (Table 2). The single canonical variate discriminating the two populations of aridulus separates Cherry Co. individuals with long, narrow skulls from Dawes Co. individuals

Table 1. Percent of individual specimens of a given population sample of *Peromyscus leucopus* subspecies classified to population based on the *a posteriori* classification matrix of a discriminant function analysis. Traditional character set.

	noveboracensis				*fusus*		*aridulus*	
	Livingston	Boyne Falls	Oklahoma	Ann Arbor	Martha's Vineyard	Vineyard Haven	Cherry Co.	Dawes Co.
Livingston	75%	25%	0%	0%				
Boyne Falls	7%	79%	0%	14%				
Oklahoma	0%	0%	88%	12%				
Ann Arbor	5%	0%	0%	95%				
Martha's Vineyard					92%	8%		
Vineyard Haven					5%	95%		
Cherry Co.							91%	9%
Dawes Co.							6%	94%

Table 2. Canonical variate loadings for population samples of *Peromyscus leucopus*. Traditional character set.

	fusus	*aridulus*	*leucopus*	*incensus*	*noveboracensis*		
Character	CVI	CVI	CVI	CVI	CVI	CVII	CVIII
Occipito-nasal length	0.31	1.07	0.70	-2.66	-0.44	0.05	0.38
Nasal length	0.77	-0.06	0.32	-0.37	0.36	-0.25	-0.08
Rostral length	-0.36	-0.50	0.07	0.68	0.12	0.34	0.57
Breadth of rostrum	-0.88	0.25	0.29	0.05	0.06	0.29	0.50
Inteorbital constriction	0.28	0.42	-0.32	-0.61	0.24	-0.37	0.15
Zygomatic breadth	0.34	-1.17	0.90	1.24	0.32	0.39	0.26
Basal length	-0.75	1.09	-2.07	2.64	0.20	-1.42	-0.76
Palatal length	0.01	0.58	0.66	0.53	-1.16	0.65	0.72
Diastema length	-0.56	0.03	0.77	-0.93	1.35	-0.16	-0.41
Tooth row length	0.55	-0.43	0.88	-0.25	0.85	0.28	-0.70
Mastoid breadth	0.11	-1.28	-0.66	-1.38	-0.12	0.17	-0.56
Cranial depth	-0.06	0.11	-0.26	0.25	0.03	0.45	0.60

with short, wider skulls (Table 2). Basal length alone contributes a large negative coefficient to the single canonical variate discriminating the two populations of leucopus (Table 2). This single canonical variate separates the North Carolina population with short skulls from the Kentucky population with longer skulls. Occipito-nasal length has a large negative coefficient, while basal length has a large positive coefficient, on the single canonical variate separating the populations of incensus (Table 2).

The canonical variates analysis of the four noveboracensis populations generates three canonical variates. The first canonical variate accounts for approximately 69% of the variation; the second 27%, and the third accounts for only 4% of the variation. Along canonical variate 1, Livingston individuals have the lowest scores, while those from Oklahoma have the largest (Figure 7). Boyne Falls individuals overlap extensively with Livingston individuals, and slightly with those from Ann Arbor (Figure 7). The population from Ann Arbor occupies an intermediate position between the cluster Livingston-Boyne Falls and the Oklahoma population (Figure 7). Palatal length has a large negative coefficient, while diastema length has a large positive coefficient on this first canonical variate (Table 2). Livingston, Boyne Falls , and Oklahoma populations overlap extensively along canonical variate 2 (Figure 7). The Ann Arbor population is reasonably well separated from the other populations on this variate (Figure 7) and that reflects primarily differences in basal length (Table 2).

The amount of overlap between noveboracensis populations along canonical variate 1 ranges from 0% to 77% (Table 3A). Overlap of

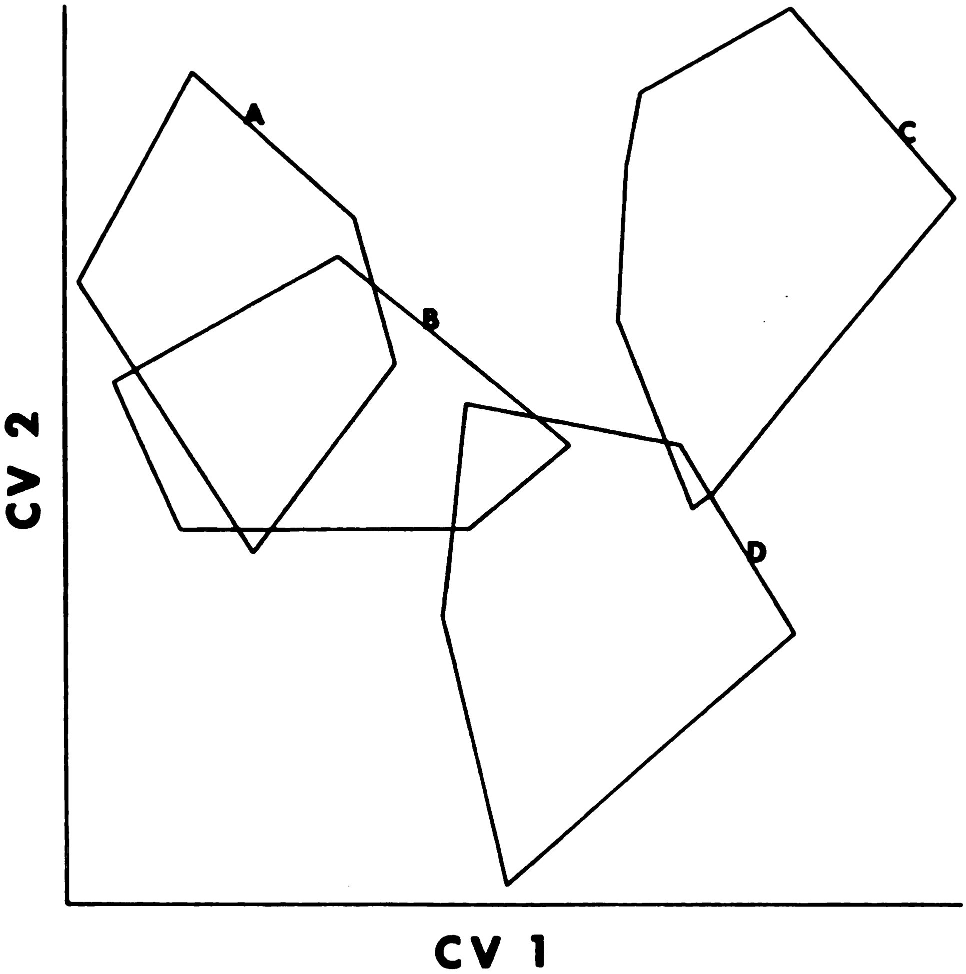

Figure 7. Discriminant analysis of the *noveboracensis* populations of *Peromyscus leucopus*. Traditional character set. A. Livingston, B. Boyne Falls, C. Oklahoma, D. Ann Arbor.

Table 3. Percent overlap between *noveboracensis* populations of *Peromyscus leucopus* along canonical variate 1 (first number) and canonical variate 2 (second number). A. Traditional character set. B. Dorsal truss network. C. Ventral truss network.

A.

	Boyne Falls	Oklahoma	Ann Arbor
Livingston	77%/77%	0%/93%	0%/34%
Boyne Falls		0%/57%	41%/82%
Oklahoma			49%/28%

B.

	Boyne Falls	Oklahoma	Ann Arbor
Livingston	81%/92%	0%/79%	25%/38%
Boyne Falls		0%/37%	3%/59%
Oklahoma			58%/14%

C.

	Boyne Falls	Oklahoma	Ann Arbor
Livingston	81%/21%	0%/0%	69%/0%
Boyne Falls		13%/53%	56%/12%
Oklahoma			0%/78%

populations on the single canonical variate of other subspecies varies from 0% overlap between population samples of *incensus* and *leucopus*, to 17% and 39% overlap between population samples of *fusus* and *aridulus*, respectively. The amount of overlap is substantial between the Ann Arbor and the Boyne Falls and Oklahoma populations of *noveboracensis*; it is even higher between Livingston and Boyne Falls populations (Table 3A). There is no overlap in the remaining pairwise comparisons of *noveboracensis* populations (Table 3A).

The overall amount of overlap among *noveboracensis* populations is larger (28%-93%) along the second canonical variate (Table 3A). The overlap between both Ann Arbor and Livingston populations, and the Oklahoma population is not very extensive (28% and 34%), while in the remaining cases the overlap is at least twice as extensive, ranging from 57% to 93% (Table 3A).

All Mahalanobis distances between populations were significant, except for the D^2 values between the two *aridulus* populations ($D^2=5.43$), and Livingston and Boyne Falls populations of *noveboracensis* from Michigan ($D^2=3.27$). Distances were larger between *fusus* ($D^2=6.79$, $P<.01$), and *leucopus* ($D^2=8.10$, $P<.05$) population samples, and much larger between *incensus* population samples ($D^2=17.02$, $P<.001$). The range of distance values among *noveboracensis* populations (3.27-20.50) is larger than the range within other subspecies (6.79-17.02) (Table 4A).

Truss measurements

Dorsal view. In the dorsal view of the skull the two *aridulus*

Table 4. Mahalanobis D^2 statistic between *noveboracensis* populations of *Peromyscus leucopus*. Unless otherwise indicated, all distances differ significantly from zero (P<.001). A. Traditional character set. B. Dorsal truss network. C. Ventral truss network.

A.

	Boyne Falls	Oklahoma	Ann Arbor
Livingston	3.27ns	20.50	14.32
Boyne Falls		17.05	7.88
Oklahoma			9.19

B.

	Boyne Falls	Oklahoma	Ann Arbor
Livinsgton	3.42ns	13.63	8.90
Boyne Falls		15.50	11.13
Oklahoma			9.50

C.

	Boyne Falls	Oklahoma	Ann Arbor
Livingston	5.89 ns	21.89	13.62
Boyne Falls		14.86	13.19
Oklahoma			23.70

populations were correctly classified by discriminant analysis, although with traditional measures up to 9% of individuals were misclassified. Populations of noveboracensis also exhibit less misclassification in this data set than with traditional measurements (Table 5). The Livingston population, though, continues to be difficult to correctly classify. In the remaining noveboracensis populations, misclassification is smaller than with traditional measures. P. l. leucopus and incensus populations, correctly classified by traditional measures, display up to 14% misclassification using dorsal truss measures (Table 5). Ten percent more Vineyard Haven fusus individuals are misclassified than with traditional measures.

Different distance variables in the dorsal view of the skull contribute large coefficients to the single canonical variate discriminating the populations of fusus, leucopus, and incensus (Table 6). Each of these measurements is contained in different truss cells in the skull, but they all represent measurements of the frontal bone. Among aridulus populations, two measures of the frontal and parietal bones (spanning two separate truss cells) contribute large coefficients to the single canonical variate (Table 6).

Canonical variates analysis of the four populations of noveboracensis generates 3 canonical variates. The first canonical variate accounts for 59% of the variation, the second 32%, and the third accounted for only 6% of the variation. The first canonical variate explains approximately 10% less of the variation in this data set than with traditional measures. The ordination of noveboracensis populations on the canonical variates is identical to that seen for conventional measures, although the Ann Arbor population ovelaps more

Table 5. Percent of individual specimens of a given population sample of *Peromyscus leucopus* subspecies classified to population based on the *a posteriori* classification matrix of a discriminant function analysis. Dorsal truss network.

	noveboracensis				*fusus*		*leucopus*		*incensus*	
	Livingston	Boyne Falls	Oklahoma	Ann Arbor	Martha's Vineyard	Vineyard Haven	KY	NC	Veracruz	Puebla
Livingston	75%	17%	0%	8%						
Boyne Falls	7%	86%	0%	7%						
Oklahoma	0%	0%	94%	6%						
Ann Arbor	0%	0%	0%	100%						
Martha's Vineyard					92%	8%				
Vineyard Haven					15%	85%				
KY							93%	7%		
NC							14%	86%		
Veracruz									94%	6%
Puebla									5%	95%

Table 6. Distance variables with large coefficients on canonical variates for Peromyscus leucopus population samples. Numbers refer to truss cells where variable is located and distance variables (Figure 4). Signs before distance variable number indicate whether the loading is positive or negative.

fusus		aridulus		leucopus		incensus		noveboracensis			
	CVI		CVI		CVI		CVI		CVI		CVII
Cell	Character	Cell	Character	Cell	Character	Cell	Character	Cell	Character	Cell	Character
2	+8 : anterior frontal length	2	-10 : anterior (diagonal) length of frontal	3	-14 : posterior frontal width	3	-5 : diagonal length of nasal	2	+10 : anterior (diagonal) length of frontal	3	-14 : posterior frontal width
		4	+18 : parietal length	3	+15 : posterior (diagonal) length of frontal					4	+20 : diagonal length of parietal

fusus		aridulus		leucopus		incensus		noveboracensis			
	CVI		CVI		CVI		CVI		CVI		CVII
Cell	Character	Cell	Character	Cell	Character	Cell	Character	Cell	Character	Cell	Character
4	-43 : post-palatal length	3	-40 : diagonal distance between M1 and M3	4	-45 : post-palatal (diagonal) length	4	+43 : post-palatal length	3	+38 : tooth row length	1	-30 : diagonal length of rostrum
		4	+45 : post-palatal (diagonal) length			4	-45 : post-palatal (diagonal) length	4	-45 : post-palatal (diagonal) length	4	-45 : post-palatal (diagonal) length

extensively with the Oklahoma population with the present data set (Figure 8A).

The overall amount of overlap along CV1 between the populations (0%-81%) is similar to that in the conventional data set. The populations of fusus (20%), incensus (9%), and leucopus (24%) exhibit more overlap with dorsal truss measures than in the conventional data set, although the reverse is true for the aridulus population (39%). Among noveboracensis populations, the overlap between Livingston and both Boyne Falls and Ann Arbor populations is higher with the dorsal truss measures, while the overlap between Livingston and Oklahoma populations is the same as in the conventional measures (Table 3B). Distance variable 10 (anterior diagonal length of frontal; second truss cell) has a relatively large coefficient on the first canonical variate separating the noveboracensis populations (Table 6; Appendix A1). This variable is a measurement in the same truss cell that separates the fusus populations (Table 6). The overall pattern of loadings on the first canonical variate suggests that the frontal bone is important for the discrimination of most population samples of leucopus (Table 6). Overlap between Boyne Falls and Ann Arbor populations is much smaller in the dorsal view, while the reverse is true for the overlap between Oklahoma and Ann Arbor populations (Table 3B).

The overlap of populations along canonical variate 2 in the dorsal view of the skull has a wider range (14%-92%) than in the conventional data set (Table 3B). Generally, the overlap of noveboracensis populations along canonical variate 2 is smaller in the dorsal truss networks than in the conventional data set (Table 3B). The only exception is the overlap between Livingston and Boyne Falls, and Ann

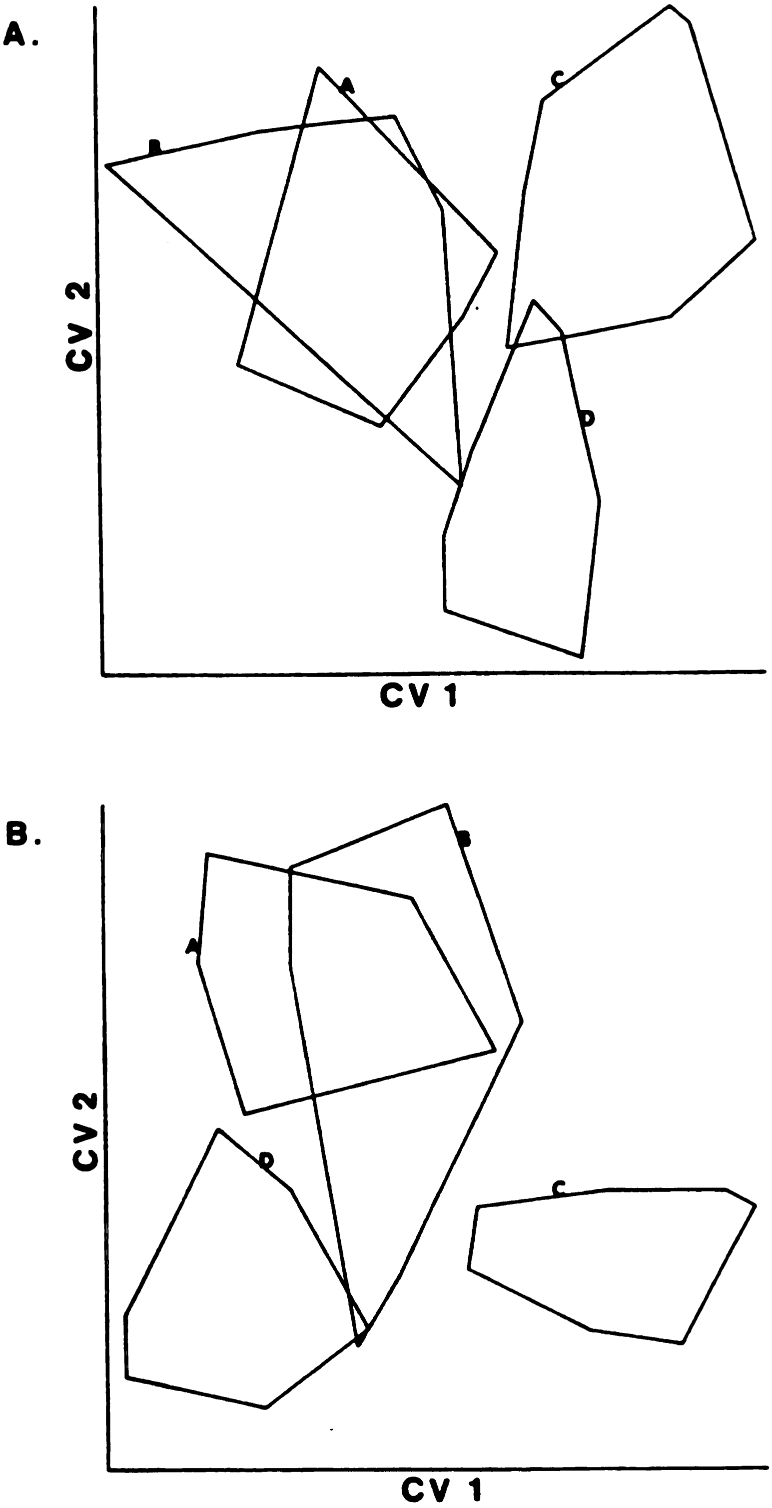

Figure 8. Discriminant analysis of the *noveboracensis* populations of *Peromyscus leucopus*. Truss character set. (A) Dorsal view. (B) Ventral view. A. Livingston, B. Boyne Falls, C. Oklahoma, D. Ann Arbor.

Arbor populations which is slightly larger in the dorsal truss network (Table 3B). Canonical variate 2 separates the noveboracensis populations on the basis of measures with large coefficients in adjacent truss cells spanning the frontal and parietal bones (Table 6).

Mahalanobis distances (Table 4B) between populations are similar to those obtained using traditional measures. P. l. aridulus populations, not significantly differentiated by the traditional scheme are, however, twice as distinct, and significantly so, using dorsal truss measures (D^2=11.91). P. l. fusus and leucopus have D^2 values here (5.56 and 6.37, respectively) similar to those for traditional measures, although the Mahalanobis distance between incensus populations is much smaller here (10.22). The range of D^2 is somewhat less with the dorsal measures (3.42-15.50) than with traditional measures (3.27-20.50) (Table 4B).

Ventral view. P. l. incensus and l.leucopus, which were correctly classified with traditional measures, showed relatively low levels of misclassification here (Table 7). No Vineyard Haven fusus were misclassified nor were Puebla individuals of incensus. Among noveboracensis populations in this data set, only Boyne Falls individuals were more poorly classified than in either dorsal truss or traditional analyses (Table 7). P. l. leucopus individuals were slightly better classified by ventral than by dorsal truss measures. P. l. aridulus individuals were more difficult to classify correctly using ventral rather than dorsal truss measures, though ventral truss measures did as well in classifying these individuals as did traditional measures (Table 7).

Table 7. Percent of individual specimens of a given population sample of *Peromyscus leucopus* subspecies classified to population based on the *a posteriori* classification matrix of a discriminant function analysis. Ventral truss network.

	noveboracensis				*fusus*		*aridulus*		*leucopus*		*incensus*	
	Livingston	Boyne Falls	Oklahoma	Ann Arbor	Martha's Vineyard	Vineyard Haven	Cherry Co.	Dawes Co.	KY	NC	Veracruz	Puebla
Livingston	100%	0%	0%	0%								
Boyne Falls	14%	72%	0%	14%								
Oklahoma	0%	6%	94%	0%								
Ann Arbor	0%	0%	0%	100%								
Martha's Vineyard					92%	8%						
Vineyard Haven					0%	100%						
Cherry Co.							91%	9%				
Dawes Co.							6%	94%				
KY									93%	7%		
NC									95%	5%		
Veracruz											94%	6%
Puebla											0%	100%

The distance variables contributing relatively large coefficients to the canonical variates generally are restricted to the fourth truss cell representing the post-palatal region of the skull (Table 6) for population samples of *fusus*, *leucopus*, and *incensus* (Table 6); in *aridulus* the distance variables contributing relatively large coefficients occur in the third and fourth truss cells (Table 6; Appendix A2).

The three canonical variates discriminating the four *noveboracensis* populations show a similar pattern of variance partitioning to that seen for the dorsal view: the first canonical variate accounts for approximately 58%, the second 33%, and the third only 9%. The ordination of *noveboracensis* populations along the canonical axes is similar to that for both previous data sets, although the axes for the ventral analysis appear rotated counterclockwise about 45^{o} relative to previous analyses (Figure 8B). The distance variables contributing to the discrimination of *noveboracensis* populations along the first canonical variate occur in the third and fourth truss cells. Distance variables represented by the first and fourth truss cells contribute large coefficients to canonical variate 2 discriminating the *noveboracensis* populations (Table 6).

These results differ from those obtained for traditional measures. Measurements contributing large coefficients to the canonical variates in the ventral truss network are mainly restricted to a single truss cell. While basal length contributes a large coefficient to the canonical variates in all populations in the conventional measures, the pattern of distance variables in the ventral truss network indicates which areas are particularly important, with respect to discrimination, over the basal region of the skull.

The percentage overlap range (0%-81%) in the ventral view is similar to previous analyses. The overlap between population samples of fusus is smaller (15%) than in the traditional and dorsal measures, while the overlap between the incensus population samples is equal to the traditional measures and smaller in the dorsal measures. The overlap between the leucopus population samples (8%) is larger in traditional measures and smaller in the dorsal truss network, and the reverse is true for the percentage overlap between aridulus population samples (14%).

The overlap between population samples of noveboracensis is summarized in Table 3C. The overlap between Ann Arbor and the Livingston and Boyne Falls populations is larger in this data set, and the same is true for the Oklahoma and Boyne Falls populations. Overlap between the remaning populations is either smaller or about the same as in the previous analyses (Table 3C).

Mahalanobis distances between populations based on the ventral truss measures were consistently greater than those based on dorsal truss measures (Table 4C). In some cases, there was greater distances between population centroids using this data set than for the traditional data set (fusus (11.37) and leucopus (11.68) populations, and Livingston-Boyne Falls, and Oklahoma-Ann Arbor pairs of noveboracensis). Mahalanobis distances between population samples of aridulus (D^2=7.13) is smaller than for dorsal measures, while the D^2 value between incensus populations is larger than for traditional and dorsal data sets (D^2=19.68). Otherwise, the distances between populations using the ventral truss measures is about the same obtained from traditional measures.

Summary. Ventral truss measures for noveboracensis and fusus produce in general better rates of classification than traditional and dorsal data sets. Dorsal measures produce better results for aridulus populations, while traditional measures produce better classification rates for leucopus. Different measurements contribute large coefficients to the traditional and dorsal data sets, while in the ventral view measurements tend to be restricted to particular areas of the skull. Generally, fusus, aridulus, l. leucopus, and incensus populations show low levels of overlap in the reduced space of the canonical variates in all three data sets. These population samples will be treated separately in the analyses of subspecies differences. Overlap levels were much higher among noveboracensis populations, although there is variation in the amount of overlap between populations across data sets. The Michigan populations of noveboracensis consistently form a cluster which is separated from Oklahoma noveboracensis with varying degrees of overlap. Michigan noveboracensis will thus be combined and treated separately from Oklahoma noveboracensis. Mahalanobis distances between populations in the ventral truss network were consistently larger than those based on dorsal measures, and in some cases larger than traditional measures.

2.1.2 Sheared Principal Components

Principal components analysis was used to examine size and shape differences between the same population samples of P. l. leucopus used in the previous analyses (*P. l. fusus*, *P. l. noveboracensis*, *P. l. aridulus*, *P. l. leucopus*, *P. l. incensus*). I attempted to remove size from the second and third components using the shear procedure (Humphries et al., 1981). However, in all data sets the coefficients of vector correlations between sheared components (H2 and H3) and original components (PC2 and PC3) were very large (average of 0.99 and 0.99, respectively). In other words, the original and sheared components have virtually identical coefficient vectors, indicating that only minute size effects were removed from the original factors. The results reported here are thus based on standard principal components analysis. I also calculated Kendall's rank correlation coefficient (Sokal and Rohlf, 1981; Bookstein et al., 1985) between allometric coefficients computed from the first principal component and loadings from principal components 2 and 3. Significant positive correlations would indicate concordance between allometric coefficients and principal component loadings, suggesting that divergence in cranial form can be accounted for by the observed differences in allometry.

Traditional measurements

The first principal component for *fusus*, *aridulus*, *leucopus*, *incensus*, and *noveboracensis* populations accounts for similar amounts of variation (69%, 67%, 69%, 65%, and 66%, respectively). I interpret the first principal component for all populations as a measure of general size because all coefficients on PC1 were positive and all variables show positive significant correlations with PC1 (Table 8).

Table 8. Principal component loadings for Peromyscus leucopus populations. Unless otherwise indicated, correlation coefficients (r) with the first principal component are significant between P<.05 and P<.01 Traditional character set.

	fusus		aridulus		leucopus		incensus				noveboracensis			
Character	PCI	r	PCI	r	PCI	r	PCI	r	PCII	PCIII	PCI	r	PCII	PCIII
Occipito-nasal length	0.26	0.97	0.28	0.96	0.27	0.99	0.26	0.98	0.04	0.06	0.27	0.97	0.04	-0.10
Nasal length	0.37	0.87	0.48	0.92	0.36	0.93	0.43	0.91	0.07	0.06	0.37	0.89	0.22	0.22
Rostral length	0.40	0.90	0.37	0.86	0.40	0.96	0.38	0.89	0.18	0.35	0.38	0.84	0.43	0.05
Rostral breadth	0.43	0.83	0.32	0.72	0.37	0.90	0.27	0.69	-0.35	0.61	0.35	0.80	-0.36	-0.13
Interorbital constriction	0.11	0.44	0.06	0.27 ns	0.20	0.79	0.11	0.39	-0.39	-0.30	0.15	0.50	-0.17	0.79
Zygomatic breadth	0.23	0.84	0.27	0.88	0.24	0.93	0.25	0.85	-0.02	0.17	0.23	0.80	-0.30	0.10
Basal length	0.33	0.97	0.34	0.95	0.31	0.98	0.32	0.97	0.09	0.03	0.30	0.94	0.12	-0.10
Palatal length	0.27	0.71	0.32	0.92	0.30	0.91	0.33	0.93	0.11	-0.24	0.32	0.92	0.008	-0.24
Diastema length	0.42	0.92	0.34	0.86	0.36	0.94	0.41	0.89	0.19	-0.48	0.41	0.92	0.24	-0.12
Tooth row length	0.01	0.06 ns	0.08	0.32 ns	0.20	0.74	0.13	0.34	-0.72	-0.14	0.21	0.54	-0.58	-0.33
Mastoid breadth	0.15	0.73	0.17	0.64	0.15	0.86	0.24	0.77	-0.18	-0.25	0.19	0.75	-0.23	0.21
Cranial depth	0.11	0.34	0.10	0.40	0.16	0.70	0.09	0.32 ns	0.27	0.002	0.05	0.22 ns	-0.23	0.22

The overlap along PCl between population samples of *fusus*, *aridulus*, *leucopus*, and *incensus* is extensive (Table 9). The population samples of *noveboracensis* show a wider range of variation in the overlap along PCl (Table 9). The Livingston population is totally separated from the Oklahoma population on the basis of size, and it is separated from the Ann Arbor population with only 13% of overlap (Table 9). Boyne Falls also shows some size differentiation from Oklahoma *noveboracensis* and Ann Arbor populations of *P. l. noveboracensis* (Table 9). The ordination of *noveboracensis* populations samples along PCl is very similar to that seen in the different data sets analyzed by canonical variate analysis (Figure 9). Livingston and Boyne Falls populations overlap completely, and are characterized by individuals with small skulls (Figure 9). The Ann Arbor population occupies an intermediate position, and the Oklahoma individuals are characterized by individuals with large skulls (Figure 9).

The second principal component accounts for small amounts of variation within samples (*fusus*, 8%; *aridulus* and *leucopus*, 10%; *incensus*, 13%; and *noveboracensis*, 14%). The overlap along PC2 between population samples of *fusus*, *aridulus*, *leucopus*, and *incensus* is also large (Table 9). Only *P. l. incensus* populations show some differentiation along PC2 and PC3. Overlap levels in the remaining populations involves at least 72% and 92% for PC2 and PC3, respectively (Table 9). The second principal component for *incensus* appears to be a constrast between cranial depth with a positive coefficient and tooth row length with a negative coefficient (Table 8). The third principal component appears to be a constrast between rostral measurements of length and breadth with positive coefficients and diastema length and

Table 9. Percent overlap between *Peromyscus leucopus* populations along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number) Traditional character set.

	noveboracensis			*fusus*	*aridulus*	*leucopus*	*incensus*
	Boyne Falls	**Oklahoma**	**Ann Arbor**				
Livingston	83%/96%/88%	0%/52%/96%	13%/100%/87%				
Boyne Falls		30%/44%/75%	41%/100%/59%				
Oklahoma			77%/26%/88%				
fusus				52%/93%/93%			
aridulus					88%/81%/92%		
leucopus						69%/72%/97%	
incensus							94%/49%/65%

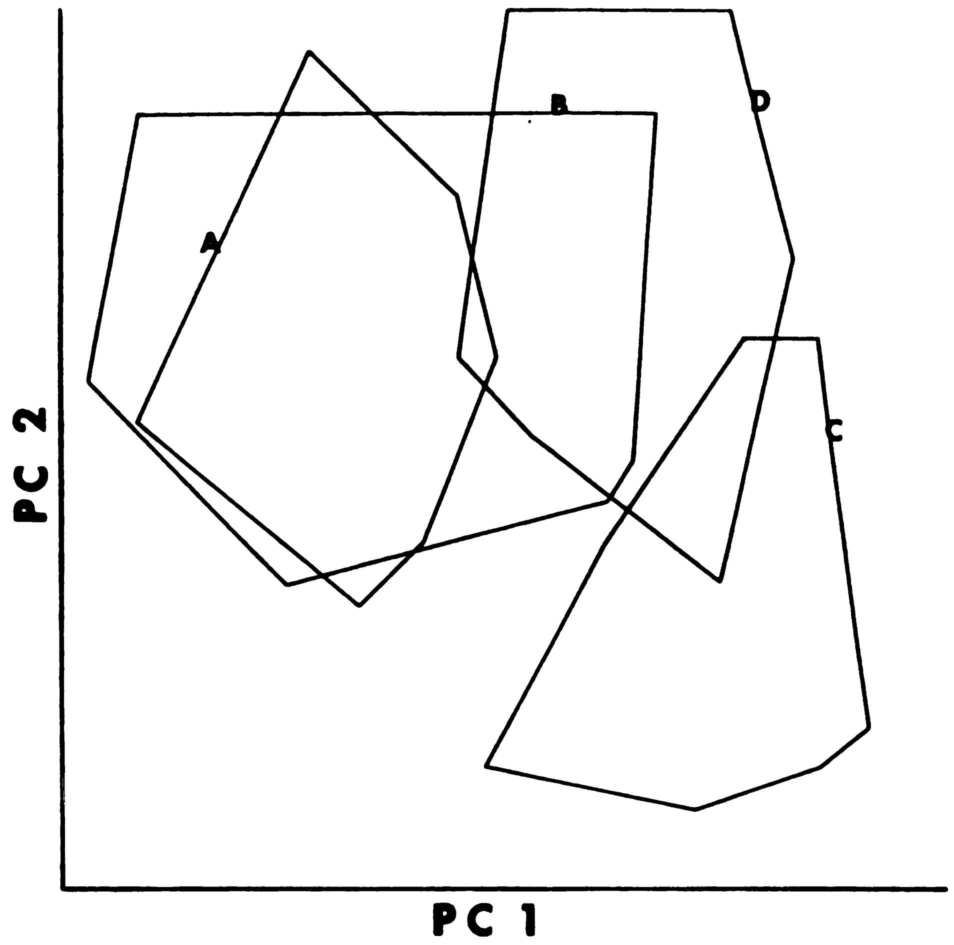

Figure 9. Scatter of noveboracensis populations of Peromyscus leucopus. Traditional character set. A. Livingston, B. Boyne Falls, C. Oklahoma, D. Ann Arbor.

interorbital constriction with negative coefficients (Table 8). Overlap of noveboracensis populations along PC2 is also quite extensive. P. l. noveboracensis from Oklahoma shows some divergence in shape along PC2 from Livingston, Boyne Falls, and Ann Arbor populations of noveboracensis. Ann Arbor noveboracensis show limited differentiation in shape along PC3 from noveboracensis from Boyne Falls (Table 9). Separation along PC2 and PC3 involves at least 96% and 75%, respectively (Table 9). Rostral length has a large positive coefficient, and tooth row length a large negative coefficient on PC2 in noveboracensis (Table 8). Individuals from the Ann Arbor population have longer rostra and shorter tooth rows compared with individuals from Oklahoma. The third principal component is apparently a constrast between interorbital constriction with a positive sign and tooth row length with a negative sign (Table 8).

Despite the generally substantial amounts of overlap between populations samples of leucopus, there seems to be variation in the direction and magnitude of size and size-free shape variation. In other words, some populations differ mainly in size, while others differ both in size and shape; the levels of size and shape differentiation also vary across populations. Close inspection of Table 9 reveals that size and shape relations among populations are not constant. For example, differences between Livingston and other noveboracensis populations are mainly due to size. Differences between Ann Arbor and Livingston populations are also mainly due to size, while Ann Arbor differs from Boyne Falls both in size and shape (along PC3). Differences between Ann Arbor and Oklahoma populations are mainly due to shape along PC2. Populations differences between fusus, aridulus, and leucopus are mainly due to size, while *incensus* populations seem to show some shape differences, specially along PC2.

The pattern of allometry for *noveboracensis* populations inferred from the first principal component is relatively simple. Cranial measurements of length have positive allometric coefficients, except for occipito-nasal length which is isometric with respect to general size (Table 10). Nasal, rostral, and diastema length have strong positive allometric coefficients (1.38, 1.42, and 1.53, respectively), while basal length and palatal length have relatively smaller positive allometries (1.11 and 1.19, respectively). Interorbital constriction, zygomatic breadth, tooth row length, and mastoid breadth have negative allometric coefficients (.55, .87, .76 and .71, respectively). Cranial depth has a very strong negative allometric coefficient (.19). The pattern of allometry thus suggests a relative increase in overall length of the skull, particularly for rostral dimensions, and a relative decrease in dimensions of width in the post-rostrum region with increases in size of the skull. The pattern of allometry for *incensus* populations is similar to that for *noveboracensis* populations.

There is generally concordance between allometric coefficients and loadings on PC2 for *noveboracensis* populations (Kendall's $\tau = .45$; $P<.05$), except for breadth of rostrum which has a negative loading on PC2 and a positive allometric coefficient. On the other hand, there is no concordance between PC3 loadings and allometric coefficients for *noveboracensis* (Kendall's $\tau = .33$, ns). These results suggest that shape differences between *noveboracensis* populations detected along PC2 can be accounted for by observed patterns of allometry, while the same is not true for cranial differences uncovered by PC3. Allometric

Table 10. **Multivariate coefficients of allometry for population samples of *Peromyscus leucopus*. Traditional character set.**

	P. leucopus populations		*P. leucopus* subspecies	*P. leucopus* & *P. gossypinus*
Character	*P. l. incensus*	*P. l. noveboracensis*		
Occipito-nasal length	0.98	1.00	0.97	1.00
Nasal length	1.59	1.38	1.31	1.32
Rostral length	1.42	1.42	1.37	1.45
Rostral breadth	1.00	1.28	1.23	1.18
Interorbital constriction	0.42	0.55	0.56	0.61
Zygomatic breadth	0.92	0.87	0.96	0.90
Basal length	1.19	1.11	1.12	1.12
Palatal length	1.24	1.19	1.18	1.17
Diastema length	1.53	1.53	1.38	1.32
Tooth row length	0.49	0.76	0.75	0.81
Mastoid breadth	0.89	0.71	0.65	0.62
Cranial depth	0.32	0.19	0.54	0.50

coefficients for *incensus* are not concordant with loadings from PC2 and PC3 (Kendall's $\tau = .42$;ns and $\tau = .12$; ns, respectively)

Truss measurements

Dorsal view. The first principal component accounts for about half of the variation within subspecies (*fusus*, 42%; *aridulus*, 50%; *leucoupus*, 44%; *incensus*, 54%; and *noveboracensis*, 46%). In all cases this principal component explains less variation than in the traditional data set. I interpret the first principal component for *fusus* and *noveboracensis* as an estimate of general size since all distances have positive coefficients and positive significant correlations with PC1 (Appendix A3). All variables have positive coefficients and positive significant correlations in *aridulus* and *leucopus* as well, except for variables 4, 14, and 18, which show positive coefficients but do not have significant correlations with PC1 (Appendix A3). Nonetheless, I interpret the first principal component for *aridulus* and *leucopus* as a general size measure. The results for the *incensus* populations were very different since variables 13, 14, and 15 in the third truss cell (the posterior region of the frontal) have significant negative correlations with PC1 (Appendix A3). Therefore, the first principal component for *incensus* cannot be accepted as an estimate of general size. I have not interpreted this component further because it provides very little separation between the two *incensus* populations.

The population samples of *fusus* and *leucopus* show limited separation along PC1, while overlap levels between *aridulus* and

Table 11. Percent overlap between *Peromyscus leucopus* populations along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Dorsal truss network.

	noveboracensis			*fusus*	*aridulus*	*leucopus*	*incensus*
	Boyne Falls	Oklahoma	Ann Arbor				
Livingston	88%/83%/92%	7%/67%/65%	33%/53%/83%				
Boyne Falls		14%/72%/90%	34%/72%/88%				
Oklahoma			51%/97%/94%				
fusus				67%/91%/95%			
aridulus					70%/100%/62%		
leucopus						66%/86%/91%	
incensus							81%/56%/64%

incensus populations involve at least 70% (Table 11). These values are similar to those obtained for the traditional data set. The population samples of *noveboracensis* show a wider range of variation in overlap along PC1 (7%-88%), again similar to the analysis of traditional measures (Table 11). All *noveboracensis* populations show some divergence in size, except for Livingston and Boyne Falls which overlap extensively (88%) along PC1 as in the previous data set (Table 11). Oklahoma *noveboracensis* is the most divergent in size, especially from Livingston and Boyne Falls populations (Table 11). The ordination along PC1 of *noveboracensis* populations is similar in conventional measures (Figure 10A).

The second principal component accounts for about twice as much of the variation in the dorsal view than in the traditional measures in *fusus* and *aridulus* (18%), and approximately the same amount in *leucopus* (13%), *incensus* (17%), and *noveboracensis* (15%). The population samples of *fusus*, *aridulus*, *leucopus*, and *incensus* show overlap levels along PC2 (56%-100%), similar in range to that obtained for the conventional data set (Table 11). *P. l. aridulus* and *incensus* show limited differentiation in shape along PC3 and PC2 and PC3, respectively (Table 11). The second principal component for *aridulus* appears to be a constrast between anterior length of frontal (DV 8; second truss cell) with a negative sign and length of nasals (DV 3; first truss cell) with a positive sign (Appendix A3). The second principal component for *incensus* is a constrast between measurements of nasal bones (DV 3, 4, and 5; first truss cell) with positive coefficients and anterior length of frontal (DV 8; second truss cell) with a negative coefficient. *P. l. noveboracensis* show limited shape

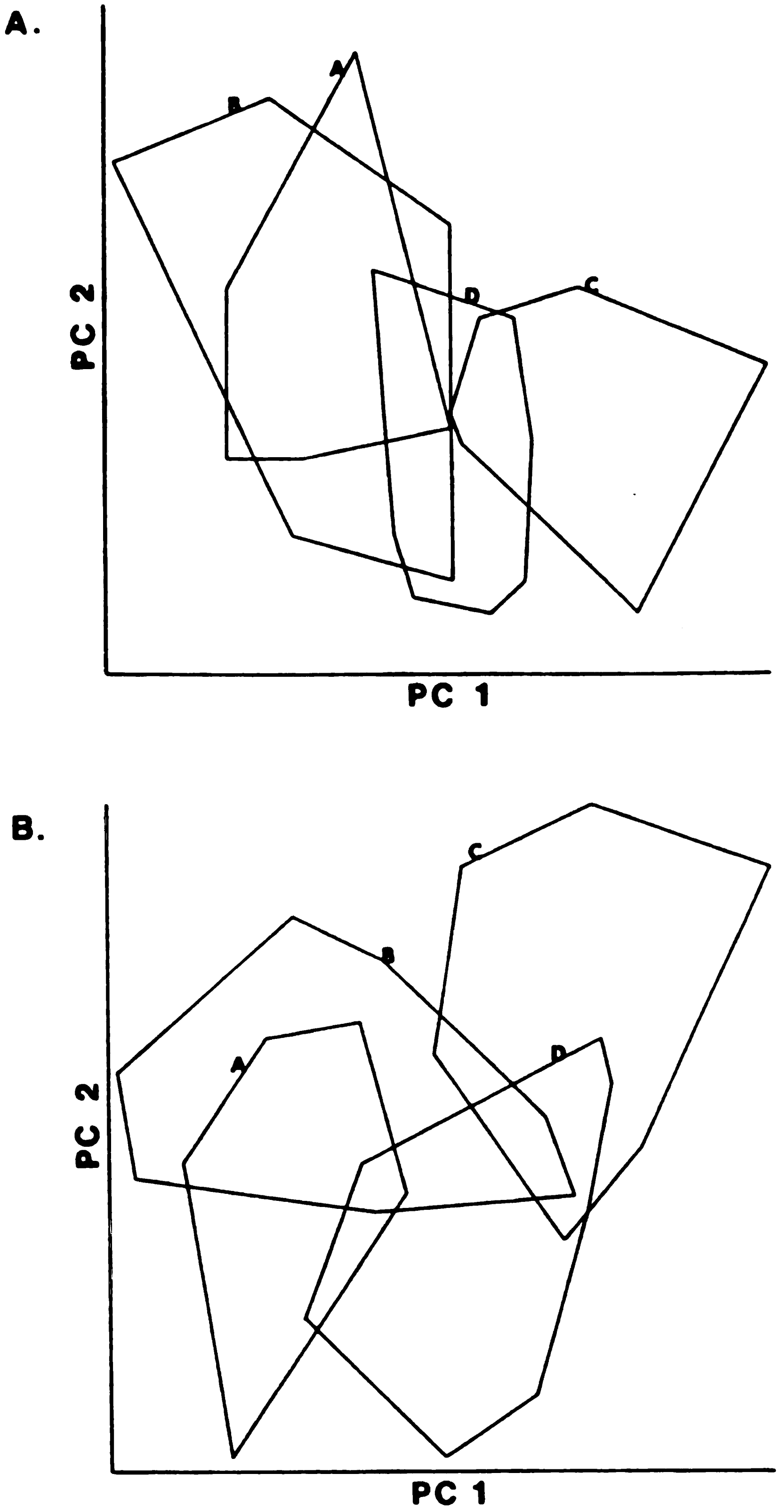

Figure 10. Scatter of noveboracensis populations of Peromyscus leucopus. Truss character set. (A) Dorsal view. (B) Ventral view. A. Livingston, B. Boyne Falls, C. Oklahoma, D. Ann Arbor.

differences in this data set (Table 11). There is limited difference along PC2 and PC3 between Oklahoma and Livingston populations, and between Livingston and Ann Arbor populations along PC2. The second principal component for the *noveboracensis* populations represent a contrast between the anterior length of the frontal (DV 8; second truss cell), which has a negative coefficient, and the several measures on the posterior region of the frontal (DV 13, 14, 15; third truss cell), which have positive coefficients on PC2 (Appendix A3). The third principal component for *noveboracensis* populations appears to be a constrast between the anterior nasal width (DV 1; first truss cell) with a positive sign and nasal length and diagonal nasal length (DV 3 and 5; first truss cell) with negative signs.

As in the previous data set, direction and magnitude of size and shape differences seem to vary across populations. Livingston *noveboracensis* differs from other *noveboracensis* forms in size and shape . Ann Arbor differs from Boyne Falls and Oklahoma populations on the basis of size. Differences between population samples of *fusus*, *aridulus*, and *leucopus*, although limited, are mainly due to size as in the previous data set. *P. l. incensus* populations do show some divergence in shape, especially along the second principal component as in the previous data set.

Skull measurements for *noveboracensis* representing the rostrum and the anterior part of the frontal are positively allometric with respect to general size (range: 1.14-1.55), except for distance variable 4 (posterior nasal width; first truss cell) which has a weak negative allometric coefficient (.93) (Figure 11A). Diagonal, width, and length measurements of the posterior region of the skull are negatively

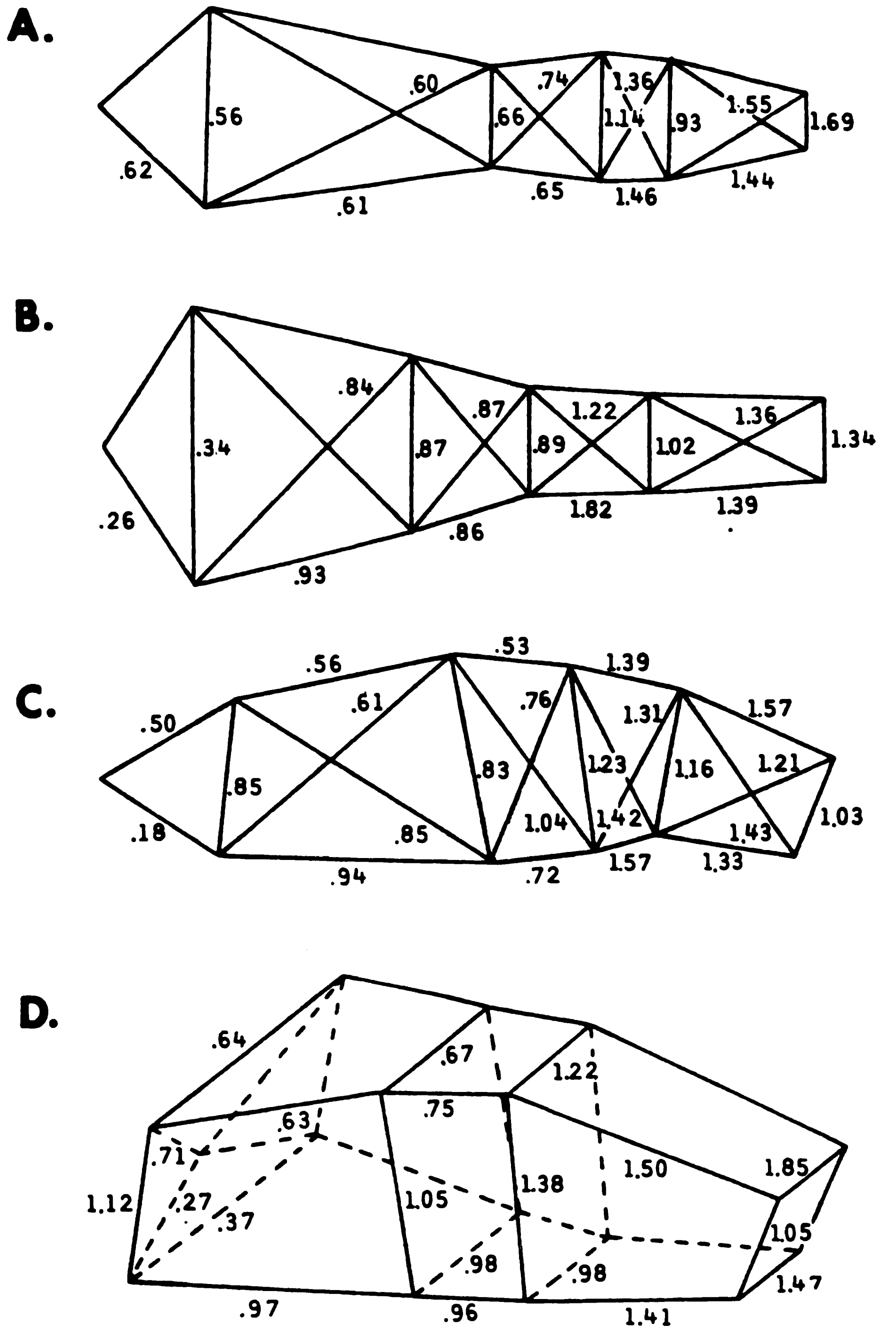

Figure 11. Multivariate allometric coefficients for *Peromyscus leucopus noveboracensis* depicted on the truss networks. A. Dorsal truss network. B. Ventral truss network. Lateral truss network. D. Three dimensional view.

allometric with respect to size (range: .56-.74) (Figure 11A). This pattern of allometry suggests that larger mice will have longer and broader rostra and shorter and narrower posterior crania. These allometric relations are generally similar to those uncovered by the traditional data set. In both cases rostral dimensions are positively allometric.

Allometric coefficients for *noveboracensis* are not concordant with loadings from PC2 and PC3 (Kendall's $\tau=-.45$; $P<.05$ and $\tau=.27$; ns, respectively). The same is true for *aridulus* (Kendall's $\tau=.08$; ns).

Ventral view. The first principal component accounts for about half of the variation within subspecies (*fusus*, 61%; *aridulus*, 48%; *leucopus*, 52%; *incensus*, 61%; *noveboracensis*, 51%). All distance variables have positive coefficients on PC1 for *aridulus*, *leucopus*, *incensus*, and *noveboracensis*, and all correlations with PC1 are positive and significant with very few exceptions (Appendix A4). I therefore interpret these first principal components as an estimate of general size for these populations. Tooth row length has a very small negative coefficient on PC1 for *fusus* (Appendix A4), and a few distance variables are not significantly correlated with PC1 (Appendix A4). Nonetheless, I interpret the first principal component for *fusus* as a general size variable.

The population samples of *fusus*, *aridulus*, *l. leucopus*, and *incensus* show large amounts of overlap along PC1 (Table 12). The values are similar to those obtained for the traditional and dorsal data sets. There is, however, limited size divergence between population samples of *fusus* and *leucopus*, while overlap between population samples of

Table 12. Percent overlap between *Peromyscus leucopus* populations along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Ventral truss network.

	noveboracensis			*fusus*	*aridulus*	*leucopus*	*incensus*
	Boyne Falls	Oklahoma	Ann Arbor				
Livingston	84%/76%/96%	0%/57%/81%	25%/97%/71%				
Boyne Falls		41%/83%/79%	76%/58%/48%				
Oklahoma			78%/53%/53%				
fusus				52%/82%/89%			
aridulus					96%/88%/93%		
leucopus						56%/97%/68%	
incensus							94%/48%/90%

aridulus and *incensus* involves at least 94% (Table 12). The population samples of *noveboracensis* show a wider range of variation in overlap along PC1 as in the previous principal components analyses (Table 12). Livingston and Oklahoma populations of *noveboracensis* here are discriminated on the basis of size without overlap. However, size differences are limited to Livingston and Ann Arbor, and Oklahoma and Boyne Falls in this data set (Table 12). The overall pattern of ordination along PC1 of *noveboracensis* populations is similar to those obtained in the previous analyses (Figure 10B), except that the Oklahoma and Boyne Falls populations show moderate amounts of overlap, as in the traditional data set (Table 12).

The second principal component accounts for a similar amount of variation to that obtained for the traditional view (*fusus*, 9%; *aridulus*, 16%; *leucopus*, 14%; *incensus*, 11%; *noveboracensis*, 15%). The range of overlap along PC2 of population samples of *fusus*, *aridulus*, *leucopus*, and *incensus* is large as in previous analyses (Table 12), and there is only limited shape differences (along PC2) between *incensus* populations as in previous data sets. The second principal component for *incensus* populations appears to be contrast between rostral measurements in the first truss cell (DV 28, 29, and 30) with negative coefficients, and posterior diastema (DV 33; second truss cell), tooth row length (DV 38; third truss cell) and diagonal length of palate (DV 40; third truss cell) with positive coefficients. *P. l. noveboracensis* populations also overlap extensively along PC2 (Table 12; Figure 10B). Ann Arbor *noveboracensis* shows limited differentiation in shape (along PC2 and PC3) from Boyne Falls and Oklahoma populations. Oklahoma and Livingston populations also show some limited shape differences along

PC2. Separation between remaining *noveboracensis* populations along PC2 and PC3 involves at least 76% and 71% overlap, respectively. The second principal component for *noveboracensis* populations is a constrast between post-palatal length (DV 43; fourth truss cell) with a negative sign and tooth row length (DV 38; third truss cell) (Appendix A4). The third principal component appears to be a contrast between rostral measurements (DV 26, 28, and 30; first truss cell) with negative signs and posterior diastema and dental measurements (DV 33 and 38; second truss cell) with positive signs.

Despite relative large levels of overlap along principal components, there seems to be variation in the pattern of size and shape differences across populations is present in this data set. As in the previous data set differences between Livingston and other populations are mainly due to size. Differences between Ann Arbor and other *noveboracensis* populations are mainly due to shape (along PC2 and PC3) as in the conventional data set. Population samples of *fusus* and *leucopus* differ mainly in size, while *incensus* show some shape divergence on PC2 as before.

The pattern of allometry for *noveboracensis* population samples is similar to dorsal measures (Figure 11A, B). Rostral length measurements generally show positive allometry (range: 1.02-1.82), while post-palatal length measurements are negatively allometric with respect to general size (range: .26-.93). A similar pattern of allometry is seen for *incensus* populations (Figure 12B).

There is no concordance between loadings on PC2 and PC3 and allometric coefficients (Kendall's $\tau = .47$; $P<.05$ and $\tau = -.41$; $P<.05$, respectively). The same result is true for *incensus* (Kendall's $\tau =$

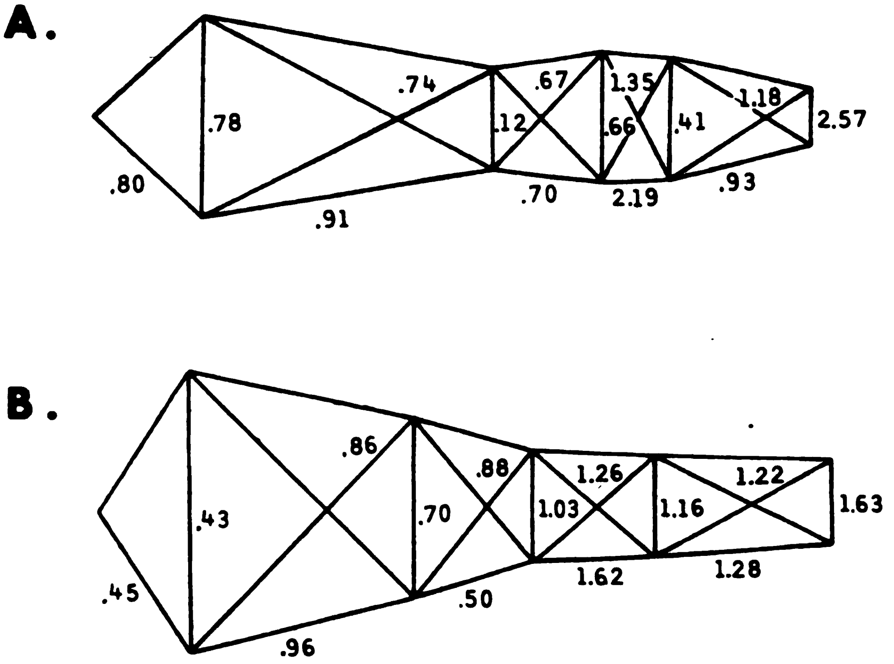

Figure 12. Multivariate allometric coefficients for *Peromyscus leucopus* populations. A. *aridulus* (dorsal truss network). B. *incensus* (ventral truss network).

-.16; ns).

Lateral view. As in the previous analyses of truss networks, the first principal component accounts for about half of the variation within subspecies (fusus, 62%; aridulus, 59%; leucopus, 55%; incensus, 56%; noveboracensis, 58%). I interpret the PC1 for aridulus, leucopus, and noveboracensis as estimates of general size since all distance variables have positive coefficients with PC1 (Appendix A5). All variables have positive significant correlations with PC1 in these populations, except for tooth row length in fusus, distance variables 13 (posterior length of frontal; third truss cell) in incensus, and distance variable 48 in leucopus, which are positive but not significant (Appendix A5). Tooth row length has a small negative coefficient on PC1 for the fusus populations. Nonetheless, I also interpret this component as a general measure of size. The posterior length of the frontal in incensus (distance variable 13; third truss cell) has a negative coefficient on PC1, and a negative significant correlation with PC1 (Appendix A5), and therefore I do not interpret this component as a general measure of size. No further interpretation is attempted because this component does not separate the two populations of incensus.

The overlap along PC1 between population samples of fusus, aridulus, leucopus, and incensus has a wider range of variation in the lateral truss network than in the previous analyses (Table 13), and only the two fusus populations show appreciable discrimination based on size. P. l. noveboracensis populations show divergence in size, except for Livingston and Boyne Falls populations which overlap extensively

Table 13. Percent overlap between *Peromyscus leucopus* populations along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Lateral truss network.

	noveboracensis			*fusus*	*aridulus*	*leucopus*	*incensus*
	Boyne Falls	Oklahoma	Ann Arbor				
Livingston	85%/92%/92%	7%/61%/93%	13%/97%/90%				
Boyne Falls		30%/73%/90%	30%/97%/97%				
Oklahoma			57%/40%/94%				
fusus				14%/98%/84%			
aridulus					89%/74%/100%		
leucopus						76%/97%/97%	
incensus							76%/30%/88%

along PC1 (Table 13). The ordination along PC1 of *noveboracensis* populations is similar to the previous analyses, except that the Livingston and Oklahoma populations overlap by 7%, while in the previous analyses they were separated without overlap (Figure 13A).

P. l. fusus and *aridulus* overlap extensively along PC2 and PC3, but *incensus* show some shape divergence (along PC2) as in previous data sets. The second principal component for *incensus* is a contrast between anterior length of frontal (DV 8; second truss cell) and posterior length of frontal (DV 13; third truss cell) with a positive coefficient (Appendix A5). The second principal component contributes limited separation between population samples of Ann Arbor and Oklahoma *noveboracensis* (Table 13). The second principal component for *noveboracensis* populations appears to be a constrast between posterior length of frontral (DV 13; third truss cell) and tooth row length (DV 38; third truss cell) with a positive sign and distance variable 33 (posterior length of diastema) with a negative sign (Appendix A5).

The pattern of size and shape differences between populations seems to differ from previous data sets. Differences among *noveboracensis* populations are limited to size, except for Oklahoma and Ann Arbor which also show some divergence along PC2.

Again, the general pattern of allometry for *noveboracensis* indicates that rostral measurements of length and width are positively allometric with respect to general size (range: 1.16-1.57), except for anterior depth of rostrum (DV 51; first truss cell) which is isometric. Post-palatal measures show negative allometry (range: .18-.94), except for distance variable 60 (third truss cell) which is isometric (Figure 11C).

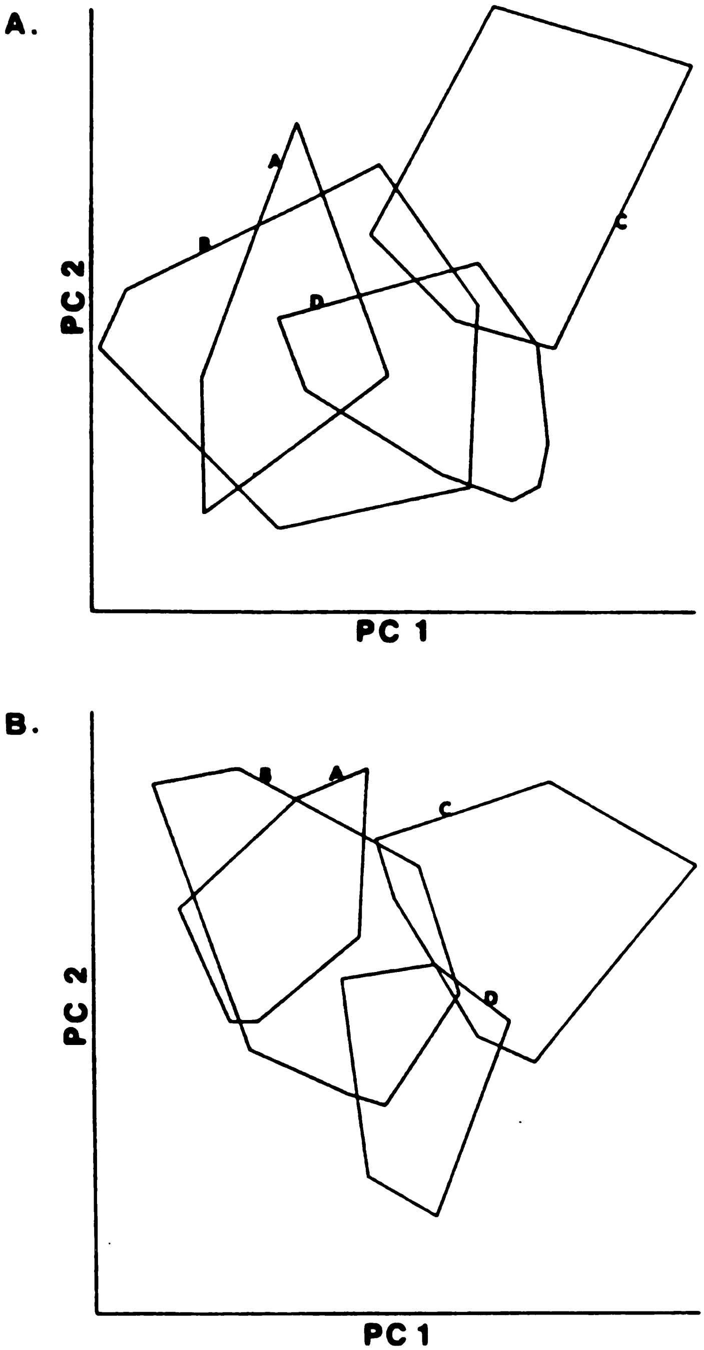

Figure 13. Scatter of noveboracensis populations of Peromyscus leucopus. Truss character set. (A) Lateral truss network. (B) Three dimensional view. A. Livingston, B. Boyne Falls, C. Oklahoma, D. Ann Arbor.

Allometric coefficients and loadings on PC2 and PC3 for *noveboracensis* populations are not concordant (Kendall's $\tau = -.51$; $P < .01$ and $\tau = .04$; ns, respectively). The same result is obtained for *l. leucopus* populations (Kendall's $\tau = -.16$; ns).

Three-dimensional view. The first principal component accounts for about half of the variation within subspecies (*fusus*, 48%; *aridulus*, 55%; *l. leucopus*, 49%; *incensus*, 50%; *noveboracensis*, 48%). Distance variables have positive coefficients on PC1 for all populations, and only in a few cases correlations between variables and PC1 were not significant (Appendix 6). I therefore interpret PC1 as a general size measure for all populations. Population samples of *fusus*, *aridulus*, *l. leucopus*, and *incensus* overlap extensively along PC1 (47%-97%) as in previous analyses, and only *fusus* populations show some divergence in size (Table 14). Again, population samples of *noveboracensis* show a wider range of overlap (0%-67%) (Table 14). All *noveboracensis* populations seem to diverge in size with varying degrees of overlap. Livingston is separated from the Oklahoma and Ann Arbor populations with 0% and 13% overlap, respectively. Size separation between remaining populations involve moderate amounts of overlap (Table 14). The ordination of *noveboracensis* populations along PC1 follows a gradient similar to the traditional, dorsal, and ventral data sets where Livingston and Oklahoma populations are separated with no overlap (Figure 13B). Livingston and Ann Arbor populations show appreciable separation as in the traditional and lateral data set (Figure 13B).

P. l. fusus, *aridulus*, *l. leucopus*, and *incensus* populations do not show any shape differences in this data set (Table 14). *P. l.*

Table 14. Percent overlap between Peromyscus leucopus populations along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Three dimensional view.

	noveboracensis			fusus	aridulus	leucopus	incensus
	Boyne Falls	Oklahoma	Ann Arbor				
Livingston	67%/88%/88%	0%/85%/78%	13%/27%/90%				
Boyne Falls		34%/93%/90%	66%/50%/88%				
Oklahoma			49%/54%/97%				
fusus				47%/100%/100%			
aridulus					84%/96%/100%		
leucopus						76%/94%/88%	
incensus							97%/100%/97%

noveboracensis populations show moderate to extensive amounts of overlap along the second principal component (Table 14; Figure 13B). The Ann Arbor populations shows some shape differentiation (along PC2) from the other *noveboracensis* populations in this data set (Table 14). The second principal component for *noveboracensis* populations is apparently a constrast between positive posterior length and diagonal measurements in the frontal (DV 13 and 14; third truss cell) and depth of rostrum (DV 51; first truss cell) and DV 25 (nasals-interorbital constriction) with negative signs (Appendix A6).

Size and shape relations between *l. leucopus* populations are generally similar to previous data sets (except for the lateral truss network). Livingston *noveboracensis* differs mostly in size from other *noveboracensis* populations, while Ann Arbor shows some divergence in both size and shape. As in previous data sets there is virtually no divergence between *aridulus* populations along principal component axes. *P. l. fusus* shows some divergence in size as before, but *incensus* shows no shape divergence here.

Rostral measurements are positively allometric (range 1.22-1.85) except for anterior depth of rostrum and distance variable 34 (anterior diastema width; second truss cell) which are isometric (1.05 and .98, respectively). Palatal and post-palatal (range: .27-1.05) measurements are either isometric or negatively allometric , except for distance variable 61 which is positively allometric (1.12). Posterior cranial measurements are negatively allometric with respect to general size (Figure 11D). This result is again similar to previous truss networks.

Again, there is no concordance between allometric coefficients and loadings from principal components 2 and 3 (Kendall's $\tau = -.48$; $P<.01$

and γ = .01; ns).

Summary. The first principal component can be used as an estimate of size for all populations in all data sets, except for *incensus* in the dorsal and lateral data sets. Populations seem to vary in the amount of size and shape differences. For example, Livingston *noveboracensis* tends to differ in size from other populations, while Oklahoma and Ann Arbor populations differ in size and shape from other *noveboracensis* populations. Oklahoma *noveboracensis* is consistently separated from other *noveboracensis* populations and will be treated separately in the analyses of subspecies differences. Population samples of *fusus*, *aridulus*, and *l*. *leucopus* show limited differentiation in size, while population samples of *incensus* show some shape differentiation. Levels of overlap among populations of *P*. *leucopus* are, nevertheless, generally high in the reduced space of the principal components, and population samples of *fusus*, *aridulus*, *l*. *leucopus*, and *incensus* will be combined for analyses of subspecies differences. Patterns of allometry are similar for population samples across data sets. The anterior region of the skull is positively allometric with respect with general size, while the posterior region of the skull is negatively allometric.

2.2 *Peromyscus leucopus* subspecies

2.2.1 Discriminant analysis

Discriminant analysis with canonical variates was used to examine morphological relationships at the subspecies level among 14 samples of *Peromyscus leucopus*: *P. l. fusus* (Martha's Vineyard and Vineyard Haven), *P. l. aridulus* (Cherry Co. and Dawes Co.), *P. l. leucopus* (Kentucky and North Carolina), *P. l. noveboracensis* (Michigan and Oklahoma), *P. l. incensus* (Puebla and Veracruz), *P. l. tornillo*, *P. l. affinis*, *P. l. mesomelas*, and *P. l. castaneus*. Lateral and three dimensional data sets were not analyzed because the within-group covariance matrix was singular.

Traditional measurements

The *a posteriori* probabilities of group assignment for *leucopus* subspecies are summarized in Table 15. For no subspecies were all individuals completely and correctly classified, and rates vary from 45% to 88% correct classification. Individuals from most taxa are correctly classified between 70% and 88% of the time. *P. l. incensus* individuals from Veracruz are most correctly classified (88%), and only two individuals are misclassified with *noveboracensis* from Michigan. *P. l. noveboracensis* from Oklahoma, *fusus* from Martha's Vineyard, *aridulus* from Cherry Co., *l. leucopus*, and *tornillo* have low classification rates of about 50%. Individuals from the populations mentioned above are misclassified with five to seven other populations, except for *aridulus* from Cherry Co. (which has individuals misclassified only with *aridulus* from Dawes Co. and *fusus* from Martha's Vineyard.)

Canonical variate 1 for *leucopus* subspecies accounts for about 47% of the total variation in this data set, the second 14%, and the third

Table 15. Percent of individual specimens of *Peromyscus leucopus* subspecies classified to subspecies based on the *a posteriori* classification matrix of a discriminant function analysis. Traditional character set.

	fusus		*noveboracensis*		*aridulus*		*leucopus*		*tornillo*	*incensus*		*mesomelas*	*affinis*	*castaneus*
	MV	VH	MI	OK	CH	DA	KY	NC		PU	VE			
MV	58%	12%	4%	7%	4%	4%				7%			4%	
VH	10%	80%				5%	5%							
MI		2%	70%					12%	4%			4%	4%	4%
OK	6%			50%	6%	13%	6%		6%			13%		
CH	19%				45%	36%								
DA	6%			5%	6%	71%				6%	6%			
KY	7%		6%				60%	7%	6%	7%	7%			
NC			26%				5%	50%			5%		9%	5%
tornillo			17%	9%	8%		8%	8%	50%					
PU	5%		11%						5%	79%				
VE			12%								88%			
mesomelas			17%							8%		75%		
affinis			10%					6%	6%	6%			72%	
castaneus			8%					17%						75%

12%. The pairwise overlap of *leucopus* subspecies along CV1 is often extensive (Table 16; Figure 14A) and varies from 0% to 94%. *P. l. castaneus* is the most distinctive taxon since it is discriminated with no overlap from eight other forms of *leucopus*, while *tornillo* is the least distinct as it can only be discriminated from *aridulus* from Cherry Co. with moderate amounts of overlap (Table 16). *P. l. aridulus* from Cherry Co. is also very distinct and can be discriminated from about twice as many populations as can *aridulus* from Dawes Co. Populations of *l. leucopus* display a similar pattern: *l. leucopus* from North Carolina shows no overlap with five *leucopus* forms, while *l. leucopus* from Kentucky can only be discriminated without overlap from two other forms (Table 16). *P. l. noveboracensis* from Michigan is discriminated without overlap from Vineyard Haven *fusus* and the *aridulus* populations, and from *noveboracensis* from Oklahoma and *fusus* from Martha's Vineyard with low amounts of overlap (6%). In the remaining cases discrimination involves overlap of at least 17% (Table 16).

Canonical variate 1 is a contrast between basal length with a negative sign and diastema length and tooth row length with positive signs. The ordination of subspecies along canonical variates reveals two clusters of nonoverlapping populations (Figure 14B). The first cluster, composed of *castaneus*, *noveboracensis*, and *leucopus* from North Carolina, is represented by individuals with skulls that are relatively short and have relatively long diastema and tooth row, while the second cluster of *fusus* from Vineyard Haven, and *aridulus* populations is characterized by individuals with relatively long skulls and short post incisor diastema (Figure 14B). The remaining populations occupy

Table 16. Percent overlap between *Peromyscus leucopus* subspecies along canonical variate 1 (first number) and canonical variate 2 (second number). Traditional character set.

	fusus(VE)	*noveb*(NE)	*noveb*(OK)	*arid*(CH)	*arid*(DA)	*leucopus*(KY)	*leucopus*(NC)	*tornillo*	*incen*(VE)	*incen*(FU)	*mesomelas*	*affinis*	*castaneus*
fusus(NW)	87/65	6/86	57/88	49/89	86/33	32/76	0/88	66/42	31/90	91/82	21/74	34/93	0/92
fusus(VE)		0/86	86/33	74/42	95/5	17/23	0/43	34/13	15/53	74/31	0/25	21/45	0/63
noveb(NE)			6/82	0/82	0/38	62/49	91/88	78/40	76/81	34/72	62/66	77/92	45/96
noveb(OK)				44/85	79/70	42/81	0/92	68/61	50/78	86/91	21/86	50/94	0/89
arid(CH)					86/64	0/81	0/88	17/39	0/74	40/87	0/88	0/93	0/96
arid(DA)						16/44	0/74	34/93	15/30	56/72	0/69	17/91	0/72
leuco(KY)							35/78	85/63	87/90	79/88	85/81	85/88	0/85
leuco(NC)								65/68	47/74	17/95	32/91	50/95	68/44
tornillo									86/43	87/58	75/63	87/87	38/63
incen(VE)										74/77	75/86	94/76	32/89
incen(FU)											48/90	68/54	0/90
mesomelas												70/93	0/92
affinis													37/93

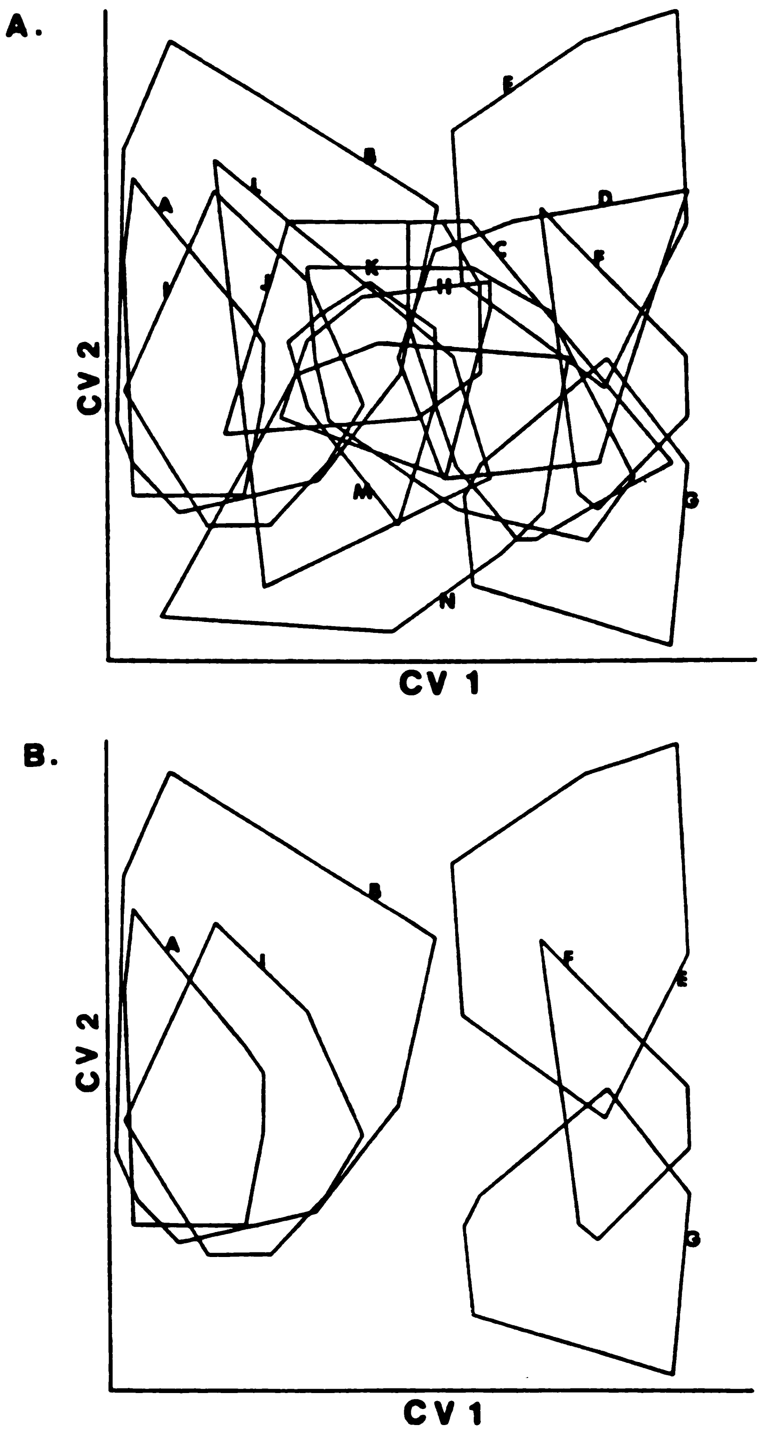

Figure 14. Discriminant analysis of *Peromyscus leucopus* taxa. Traditional character set. (A) All *leucopus* taxa. (B) Non-overlapping clusters. A. *castaneus* B. *noveboracensis* (MI) C. *noveboracensis* (OK) D. *fusus* (Martha's Vineyard) E. *fusus* (Vineyard Haven) F. *aridulus* (Cherry Co.) G. *aridulus* (Dawes Co.) H. *leucopus* (KY) I. *leucopus* (NC) J. *incensus* (Veracruz) K. *incensus* (Puebla) L. *affinis* M. *mesomelas* N. *tornillo*.

intermediate positions with varying levels of overlap between the two major clusters (Figure 14A).

Overlap of populations along CV2 is much larger and no population is discriminated without overlap (Table 16; Figure 14). The only appreciable discrimination occurs between *fusus* from Vineyard Haven and both *aridulus* from Dawes Co. (5%) and *tornillo* (13%). Overlap among the remaining populations varies from 23% to 96%. Canonical variate 2 is a constrast between zygomatic and mastoid breadth with negative coefficients and basal length with a positive coefficient (Table 17).

All Mahalanobis distances between *leucopus* taxa are significantly different from zero (Table 18). *P. l castaneus*, Vineyard Haven *fusus*, and the *aridulus* populations have the largest mean D^2 values (19.87, 17.84, 16.23, and 15.95, respectively), while in the remaining taxa mean D^2 values vary from 8.93 to 13.60. Mahalanobis distances between population samples within *fusus*, *aridulus*, and *leucopus* are small relative to D^2 values between each of these populations and other taxa except in a few cases (Table 18). On the other hand, D^2 values between populations within *noveboracensis* are as larger or larger than most D^2 values between these populations and the other *leucopus* forms. Mahalanobis distances are not correlated with geographic distances separating *leucopus* populations (r=.17) indicating that morphological divergence between taxa is not strictly a function of geographic distance.

The matrix of Mahalanobis distances between taxa was clustered by UPGMA and the result is shown in Figure 15. The distance phenogram reveals two major clusters; one consisting of northern United States populations and the other of largely southern U.S. and Mexican forms.

Table 17. Canonical variate loadings of two different data sets for *Peromyscus leucopus* subspecies (DV=Distance variables).

Traditional character set			Truss character set					
			Dorsal view			Ventral view		
Character	CVI	CVII	Character	CVI	CVII	Character	CVI	CVII
Occipito-nasal length	0.35	-0.54	DV 1	-0.40	-0.24	DV 26	-0.17	0.28
Nasal length	-0.10	-0.28	DV 3	0.82	0.47	DV 28	0.35	0.35
Rostral length	0.53	0.07	DV 4	-0.14	0.32	DV 29	0.08	-0.48
Rostral breadth	0.22	0.79	DV 5	-1.13	-0.07	DV 30	0.24	0.57
Interorbital constriction	0.01	0.38	DV 8	0.54	-0.19	DV 33	0.43	-0.09
Zygomatic breadth	0.45	-0.81	DV 9	0.18	0.04	DV 34	0.21	-0.78
Basal length	-0.99	1.15	DV 10	0.31	0.42	DV 35	0.12	0.17
Palatal length	0.31	0.17	DV 13	0.50	0.36	DV 38	0.63	-0.44
Diastema length	0.64	0.20	DV 14	0.14	-0.36	DV 39	-0.04	0.005
Tooth row length	0.71	-0.27	DV 15	0.15	0.06	DV 40	0.14	0.84
Mastoid breadth	-0.11	-0.64	DV 18	0.80	-0.01	DV 43	-0.43	0.35
Cranial depth	0.21	0.18	DV 19	-0.21	0.002	DV 44	0.19	0.41
			DV 20	-1.07	0.45	DV 45	-0.20	-1.13
			DV 23	0.74	0.06	DV 48	-0.06	-0.31

Table 18. Mahalanobis D^2 statistic between *Peromyscus leucopus* subspecies. Traditional chracter set. Significance levels between P<.005 and P<.0001.

	fusus(VM)	noveb(MI)	noveb(OK)	aridulus(CH)	aridulus(DA)	leucopus(KY)	leucopus(NC)	tornillo	incensus(VE)	incensus(PU)	mesomelas	affinis	castaneus
fusus(NW)	5.79	11.94	3.14	4.05	7.02	7.95	17.02	9.24	10.08	6.63	8.95	10.85	23.09
fusus(VM)		20.62	10.74	11.30	15.58	14.62	27.65	20.74	18.57	14.77	15.42	21.34	34.78
noveb(MI)			11.55	22.93	24.70	5.68	3.16	10.14	9.67	11.49	4.90	9.27	6.50
noveb(OK)				7.50	7.25	8.13	14.36	6.59	17.07	6.45	6.77	12.90	21.02
aridulus(CH)					4.60	15.26	27.23	13.93	19.06	16.56	18.00	20.36	30.16
aridulus(DA)						13.68	24.04	10.70	19.69	13.03	14.25	18.38	34.48
leucopus(KY)							4.32	6.25	6.36	8.28	5.31	6.91	13.40
leucopus(NC)								9.13	10.58	14.96	6.52	10.56	7.25
tornillo									11.88	8.64	6.95	8.22	15.04
incensus(VE)										10.77	11.76	9.16	19.18
incensus(PU)											5.84	10.81	22.39
mesomelas												6.96	12.75
affinis													18.29

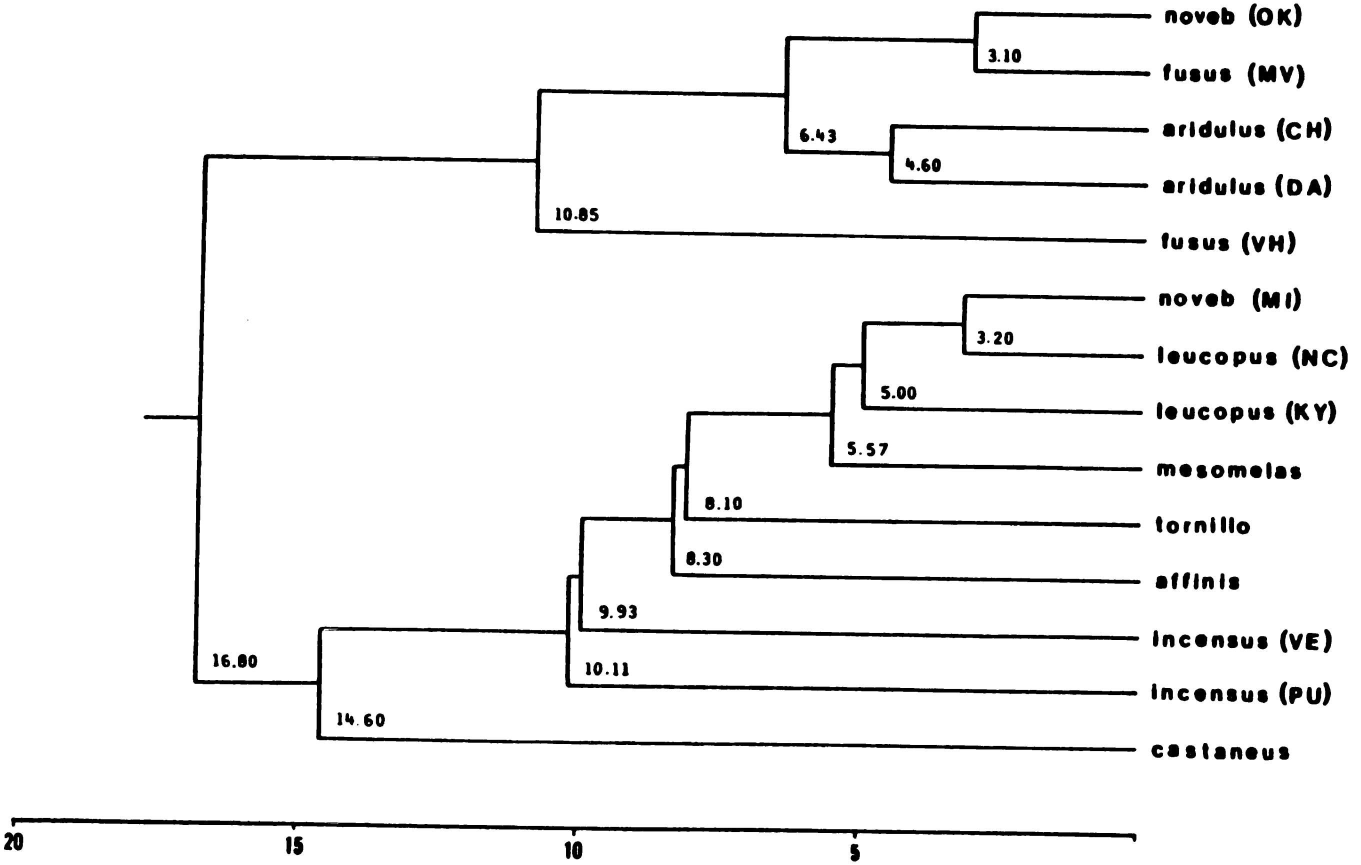

Figure 15. Phenetic relationships among Peromyscus leucopus taxa based on the Mahalanobis D^2 statistic. Traditional character set. Clustering is by the unweighted pair group method using arithmetic means.

Within the latter, U.S. populations form a convex subgroup. P. l. aridulus populations of Cherry Co. and Dawes Co. are the only population samples to be clustered together. For fusus, l. leucopus, incensus, and noveboracensis, one population sample clusters with a different leucopus subspecies before joining its own consubspecific. P. l. noveboracensis populations are most problematic. Oklahoma individuals cluster with other northern U.S. populations, but Michigan individuals cluster well within the southern U.S./Mexico group of populations.

The overall connectedness of localities based on a minimum spanning tree (Prim Network) of the Mahalanobis distances reveals a pattern that is even less geographically meaningful than the UPGMA clustering (Figure 16). Population samples within a subspecies are either not interconnected or join other forms of leucopus before joining their own consubspecifics. Mexican forms are striking for they generally join US forms only. P. l. mesomelas does connect with one Mexican population (Puebla incensus) but it is actually closer to the other population it joins, Michigan noveboracensis.

Dorsal view. Table 19 summarizes the results of a posteriori probabilities of group assignment for l. leucopus subspecies. Overall rates of correct classification are similar to traditional measures (40%-87%), but the present data set yields generally lower rates of correct classification (Table 19). In a few cases percentage classification is either equal in both data sets (Oklahoma noveboracensis and tornillo) or larger for the dorsal measures (Michigan noveboracensis, fusus from Martha's Vineyard, aridulus from

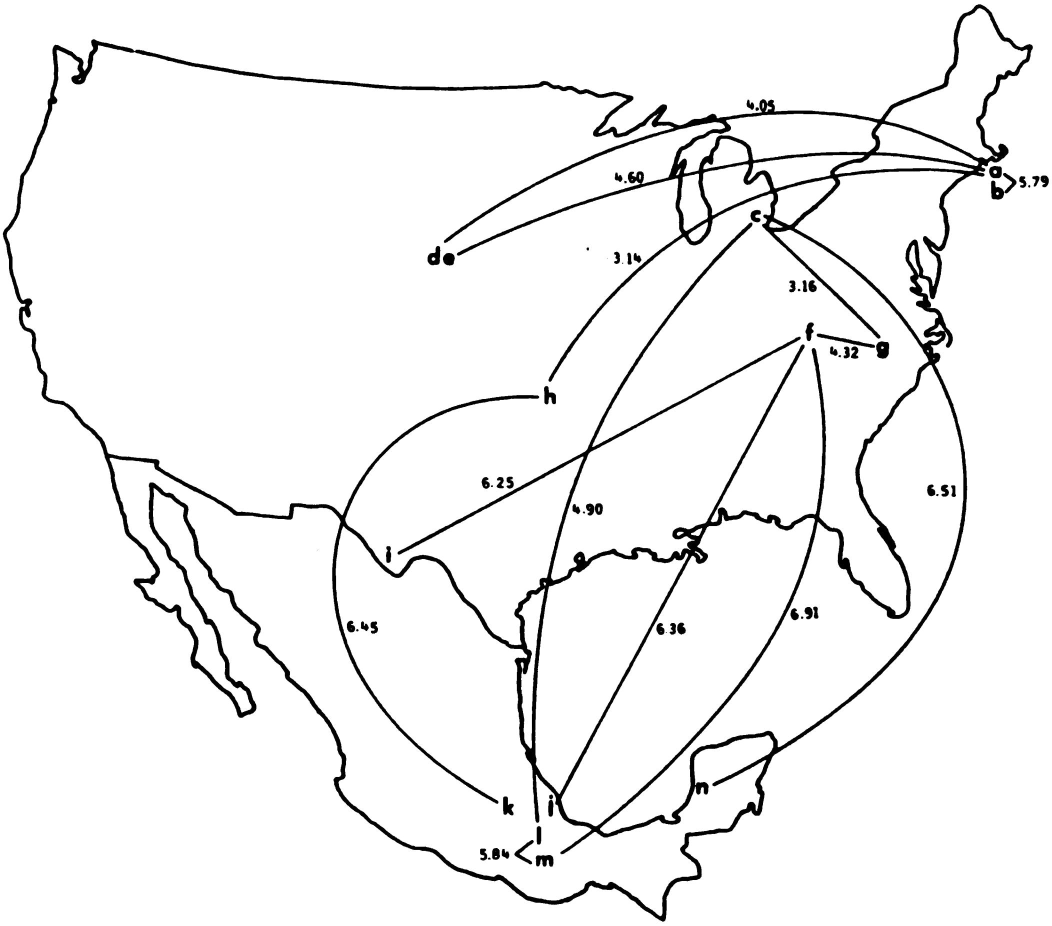

Figure 16. Minimum spanning tree (Prim Network) for samples of *Peromyscus leucopus* taxa based on the Mahalanobis distance. Traditional character set. A. *fusus* (Martha's Vineyard), B. *fusus* (Vineyard Haven), C. *noveboracensis* (Michigan), D. *aridulus* (Cherry Co.), E. *aridulus* (Dawes Co.), F. *leucopus* (Kentucky), G. *leucopus* (North Carolina), H. *noveboracensis* (Oklahoma), I. *tornillo*, J. *incensus* (Veracruz), K. *incensus* (Puebla), L. *mesomelas*, M. *affinis*, N. *castaneus*.

Table 19. Percent of individual specimens of *Peromyscus leucopus* subspecies classified to subspecies based on the *a posteriori* classification matrix of a discriminant function analysis. Dorsal truss network.

	fusus		*noveboracensis*		*aridulus*		*leucopus*		*tornillo*	*incensus*		*mesomelas*	*affinis*	*castaneus*
	MV	VH	MI	OK	CH	DA	KY	NC		PU	VE			
MV	69%	4%	8%	7%		4%		4%	4%					
VH	30%	70%												
MI		2%	87%				4%	2%		5%				
OK	13%		19%	50%	6%			6%	6%					
CH	9%				73%	18%								
DA	6%	6%	6%	11%	12%	47%		6%					6%	
KY			13%			7%	40%	13%			7%	13%	7%	
NC			5%				9%	59%	5%	5%	8%	5%	4%	
tornillo					8%		8%		50%		17%		8%	9%
PU			16%	6%					5%	68%			5%	
VE						13%	6%	19%		5%	44%	13%		
mesomelas				9%			8%				8%	67%	8%	
affinis			6%			5%			6%		10%	6%	67%	
castaneus			31%											69%

Cherry Co., and *l. leucopus* from North Carolina). Individuals from about half of the taxa are correctly classified between 67% and 87% of the time, while individuals from the remaining populations have correct classification rates of about 50%.

Canonical variate 1 for *leucopus* subspecies accounts for 10% less of the total variation (37%) than for conventional measures. However, canonical variate 2 accounts for twice as much of the variation here (30%), while the third canonical variate accounts for a similar small amount of the variance (11%). The range of percentage overlap along CV1 is similar (0%-97%) to the traditional truss measures (Table 20). However, the level of discrimination free of overlap is much lower in the present data set (Table 20). *P. l. fusus* from Vineyard Haven is discriminated from five *leucopus* forms, and is the most distinctive taxon. *P. l. fusus* from Martha's Vineyard is not very distinct, as it can only be discriminated from *incensus* from Veracruz, *mesomelas*, *affinis* and *tornillo* (0%, 8%, 16%, and 16% overlap, respectively). *P. l. castaneus*, the most distinctive taxa in the traditional data set, shows appreciable levels of discrimination here only from *affinis* (6%), *mesomelas* (8%), and *tornillo* (12%). *P. l. aridulus* from Cherry Co. which was discriminated from seven populations in the traditional data set, in this data set can only be separated from Veracruz *incensus* (15%). Discrimination of *aridulus* from other forms involves overlap of at least 39%. Discrimination free of overlap between the remaining taxa is either absent (*noveboracensis*, *aridulus* from Dawes Co., *leucopus* from Kentucky, and *incensus* from Puebla) or very low (*fusus* from Martha's Vineyard, *leucopus* from North Carolina, *affinis*, *mesomelas*, and *tornillo*).

Table 20. Percent overlap between *Peromyscus leucopus* subspecies along canonical variate 1 (first number) and canonical variate 2 (second number). Dorsal truss network.

	fuscus(VB)	noveb(NE)	noveb(OK)	arid(CH)	arid(DA)	leucopus(KY)	leucopus(BC)	tornillo	incen(VZ)	incen(PU)	mesomelas	affinis	castaneus
fuscus(NW)	80/89	89/33	90/76	84/70	86/72	59/63	19/52	16/95	0/81	51/64	8/87	16/86	74/18
fuscus(VB)		87/0	81/44	42/81	46/84	23/34	0/12	0/84	0/28	21/15	0/56	0/66	45/6
noveb(NE)			89/31	72/0	81/8	56/70	21/93	14/66	32/31	46/82	91/31	14/61	61/95
noveb(OK)				81/37	79/91	74/84	34/45	39/82	38/94	69/69	25/93	26/85	79/41
arid(CH)					93/82	85/19	55/0	61/74	15/19	77/7	39/17	45/45	83/0
arid(DA)						88/41	56/21	59/83	18/58	83/36	41/59	43/66	77/20
leuco(KY)							89/78	81/74	68/77	94/88	70/85	70/29	57/68
leuco(BC)								91/71	61/50	90/93	85/50	78/68	26/89
tornillo									79/79	84/74	83/88	77/97	12/64
incen(VZ)										97/69	89/86	50/79	38/59
incen(PU)											84/74	76/81	63/91
mesomelas												83/90	8/52
affinis													6/23

The diagonal length of nasals (distance variable 5; first truss cell) and the diagonal length of parietal (distance variable 20; fourth truss cell) contribute large negative coefficients to CV1 (Table 17). The ordination of leucopus taxa in the space of canonical variates is identical to traditional measures (Figure 17A), although different characters contribute large coefficients to canonical variates in the data sets (Table 17). The first cluster composed of noveboracensis, castaneus, and l. leucopus from North Carolina is characterized by individuals with relatively shorter nasals and parietals, while the second cluster of aridulus from Cherry Co. and fusus from Vineyard Haven is represented by individuals with relatively longer nasals and parietals (Figure 17B). The remaining populations occupy intermediate positions between these two clusters (Figure 17A).

Overlap of populations along CV2 (0%-97%) is similar to that along CV1 and to the overlap along CV2 for conventional measures (5%-96%) (Table 20). However, overlap levels for some subspecies are much lower. P. l. aridulus from Cherry Co. is the most distinctive along CV2 since it is discriminated from castaneus, Michigan noveboracensis, and l. leucopus from North Carolina without overlap, and from incensus from Puebla with low levels of overlap (7%). P. l. castaneus and noveboracensis are also distinctive taxa (Table 20). P. l. castaneus is discriminated without overlap from aridulus (Cherry Co.), and with low levels of overlap from fusus from Vineyard Haven (6%) and affinis (23%). Canonical variate 2 appears to be a constrast between distance variable 13 (posterior length of frontal; third truss cell), distance variables 10 (anterior diagonal length of frontal; second truss cell), and 20 (diagonal length of parietal; fourth truss cell) with positive

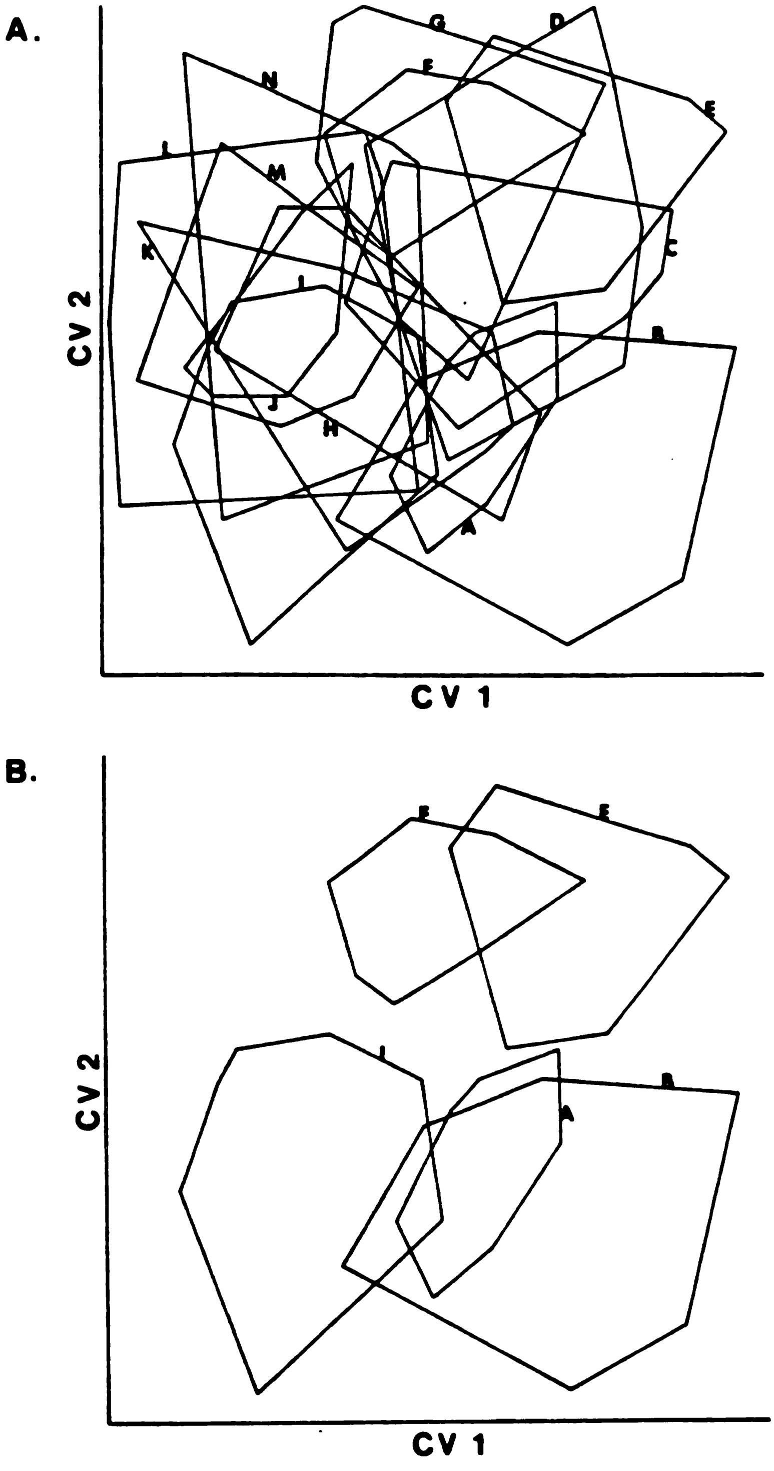

Figure 17. Discriminant analysis of *Peromyscus leucopus* taxa. Truss character set. Dorsal truss network. (A) All *leucopus* taxa. (B) Non-overlapping clusters. A. *castaneus* B. *noveboracensis* (MI) C. *noveboracensis* (OK) D. *fusus* (Martha's Vineyard) E. *fusus* (Vineyard Haven) F. *aridulus* (Cherry Co.) G. *aridulus* (Dawes Co.) H. *leucopus* (KY) I. *leucopus* (NC) J. *incensus* (Veracruz) K. *incensus* (Puebla) L. *affinis* M. *mesomelas* N. *tornillo*.

coefficients, and posterior width of frontal (DV 14; third truss cell) with a negative coefficient (Table 17).

Mahalanobis distances between *leucopus* taxa are significant in all cases (Table 21). Mean D^2 values between taxa are smaller in the dorsal data set than for traditional measures, except for Michigan *noveboracensis* and *mesomelas*. *P. l. fusus* from Vineyard Haven has the largest mean D^2 value (15.69). Mean D^2 values in the remaining taxa vary from 7.42 to 13.56. Mahalanobis distances between population samples within *fusus*, *aridulus*, and *noveboracensis* are generally smaller than D^2 values between each of these populations and other *leucopus* forms. Mahalanobis distance between the two *leucopus* populations, however, is larger than most distances between each of these populations and the other taxa (Table 21). There is a significant correlation ($r=.37$; $P<.05$) between geographic distance and Mahalanobis distances between *leucopus* taxa in this data set. This result indicates that morphological distances, obtained from dorsal truss networks measurements, increase with geographic distance between *leucopus* taxa.

The UPGMA cluster analysis based on the matrix of Mahalanobis distances between taxa is shown in Figure 18. This phenogram reveals a more complex branching pattern than for conventional measures. Each major cluster contains northern and southern U.S. forms and Mexican populations as well. Three major clusters are revealed by the phenogram. The first includes *aridulus* and *l. leucopus* as two distinct convex subgroups, and *noveboracensis* from Oklahoma. The second cluster is composed of equal numbers of Mexican and northern U.S. forms, and a southern U.S. population (*tornillo*). The last cluster includes

Table 21. Mahalanobis D^2 statistic between *Peromyscus leucopus* subspecies. Dorsal truss network. Significance levels between P<.03 and P<.0001.

	fusus(VH)	noveb(MI)	noveb(OK)	aridulus(CH)	aridulus(DA)	leucopus(KY)	leucopus(NC)	tornillo	incensus(VZ)	incensus(PU)	mesomelas	affinis	castaneus
fusus(MV)	2.87	8.99	4.48	7.66	3.68	5.48	13.10	7.04	12.68	10.66	16.96	12.87	9.30
fusus(VH)		15.65	10.80	13.21	9.22	11.73	22.91	15.31	21.77	16.61	24.89	22.35	16.68
noveb(MI)			6.30	20.18	15.78	8.26	10.36	15.52	16.69	10.74	19.78	19.90	7.65
noveb(OK)				5.46	5.51	6.40	10.59	9.08	13.64	11.71	14.29	12.61	12.77
aridulus(CH)					4.08	10.92	16.02	8.71	14.74	17.92	17.35	13.50	20.26
aridulus(DA)						7.05	14.26	5.44	9.33	14.18	13.44	9.34	15.84
leucopus(KY)							13.42	4.10	3.95	5.52	7.41	4.52	7.67
leucopus(NC)								5.90	4.84	7.52	7.89	8.25	9.99
tornillo									4.24	7.23	8.98	5.13	11.38
incensus(VZ)										7.45	6.86	4.42	10.56
incensus(PU)											12.39	8.91	9.92
mesomelas												6.93	19.08
affinis													16.49

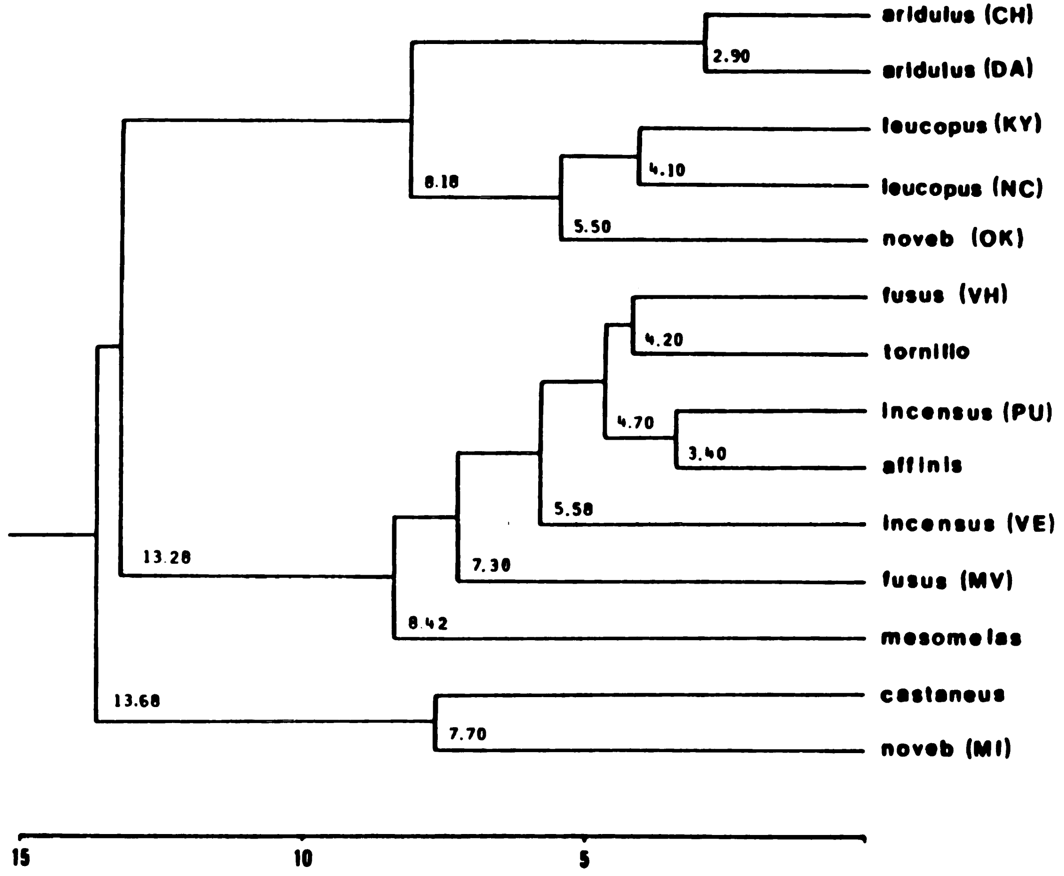

Figure 18. Phenetic relationships among *Peromyscus leucopus* taxa based on the Mahalanobis D^2 statistic. Truss character set. Dorsal truss network. Clustering is by the unweighted pair group method using arithmetic means.

castaneus and Michigan noveboracensis.

Figure 19 shows a minimum spanning tree (Prim Network) connecting geographic localities based on the Mahalanobis distances between taxa. Populations within a subspecies for fusus, noveboracensis, l. leucopus, and aridulus from Cherry Co. are connected to their consubspecifics before they join any other form of leucopus. P. l. aridulus from Dawes Co. is closer to fusus from Martha's Vineyard than Oklahoma noveboracensis and tornillo. The two incensus populations are not linked, but Veracruz incensus is connected with mesomelas and affinis, but it is closer to l. leucopus from Kentucky. The pattern revealed by the Prim Network is difficult to interpret on a geographic basis, since only populations within a subspecies show a pattern of geographic connectedness. This result may explain the (marginally) significant correlation found earlier between geographic and morphologic distance. This correlations is thus considered spurious and will not be taken into consideration in further discussions.

The stable clusters represented in both the UPGMA phenogram and the Prim Networks are the two populations of aridulus, the two populations of leucopus populations, and the cluster of castaneus-noveboracensis (MI).

Ventral view. The results of the a posteriori probabilities of correct classification are presented in Table 22. Rates of correct classification vary from 44% to 95%. Correct classification rates are higher for most subspecies for this data set than in traditional and dorsal data sets (castaneus, noveboracensis, fusus, l. leucopus from North Carolina, affinis, mesomelas, and tornillo; Table 22). In the

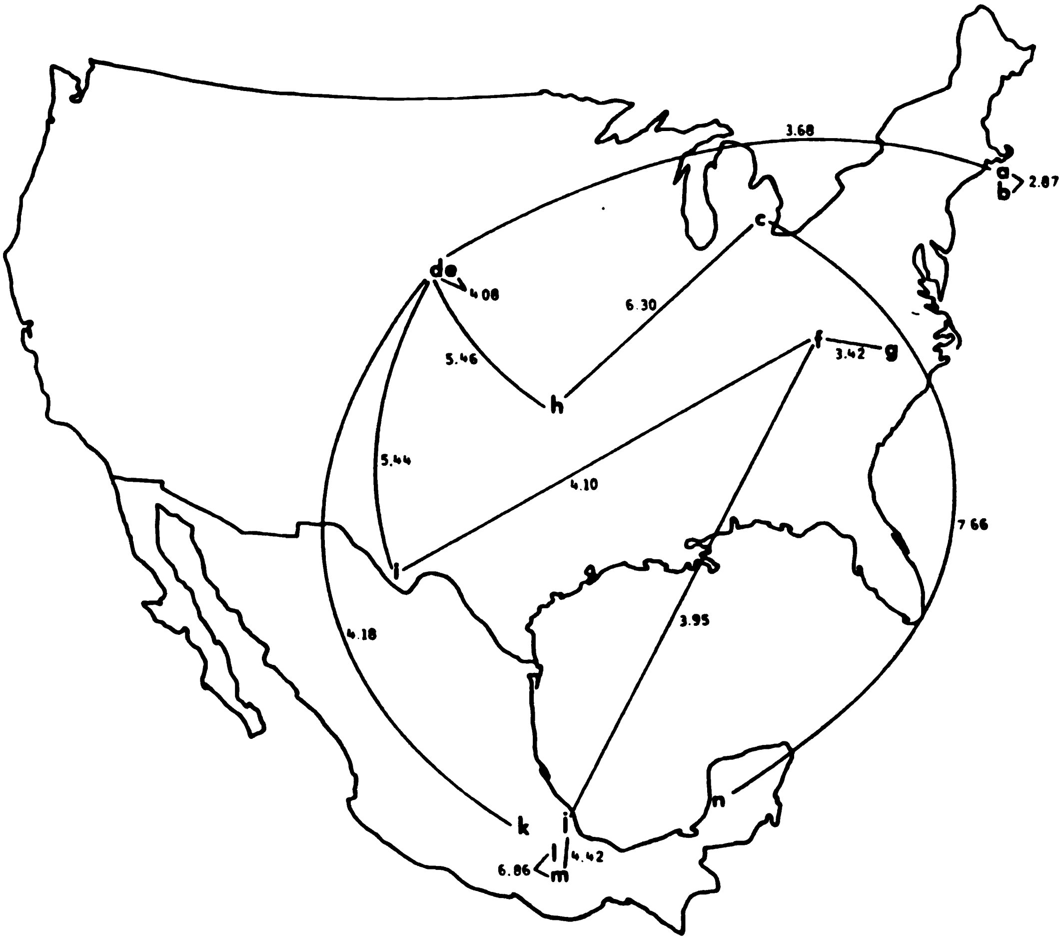

Figure 19. Minimum spanning tree (Prim Network) for samples of _Peromyscus leucopus_ taxa based on the Mahalanobis distance. Truss character set. Dorsal truss network. A. _fusus_ (Martha's Vineyard), B. _fusus_ (Vineyard Haven), C. _noveboracensis_ (Michigan), D. _aridulus_ (Cherry Co.), E. _aridulus_ (Dawes Co.), F. _leucopus_ (Kentucky), G. _leucopus_ (North Carolina), H. _noveboracensis_ (Oklahoma), I. _tornillo_, J. _incensus_ (Veracruz), K. _incensus_ (Puebla), L. _mesomelas_, M. _affinis_, N. _castaneus_.

Table 22. Percent of individual specimens of Peromyscus leucopus subspecies classified to subspecies based on the *a posteriori* classification matrix of a discriminant function analysis. Ventral truss network.

	fusus		noveboracensis		aridulus		leucopus		tornillo	incensus		mesomelas	affinis	castaneus
	MV	VH	MI	OK	CH	DA	KY	NC		PU	VE			
MV	73%	4%	4%	4%		4%				11%				
VH	5%	95%												
MI			89%				9%	2%						
OK	12%		6%	63%		13%				6%				
CH	27%				45%	28%								
DA	12%	6%		17%		59%			6%					
KY			6%				60%	7%	7%		13%		7%	
NC							5%	77%		5%	9%		4%	
tornillo						8%		8%	75%		9%			
PU	16%		5%		5%	5%				63%		6%		
VE	6%		6%				6%	25%		13%	44%			
mesomelas												92%	8%	
affinis			6%				6%	10%					78%	
castaneus			8%											92%

remaining subspecies, percentage of correct classification is either equal to or smaller than traditional or dorsal truss measures. P. l. castaneus, Michigan noveboracensis, fusus from Vineyard Haven, and mesomelas have very high rates of correct classification (92%, 89%, 95%, and 92%, respectively; Table 22). In the remaining subspecies rates of correct classification vary from 44% to 78%.

Canonical variate 1 for leucopus subspecies accounts for approximately 43% of the total variation in the the present data set. This value is close to the traditional measures (47%). The second canonical variate accounts for a proportion of the variance (20%) intermediate between the values for traditional measures and dorsal truss measures, while CV3 accounts for 12%. The range of overlap along CV1 between leucopus subspecies is similar to the previous analyses (0%-95%) (Table 23). However, the level of discrimination free of overlap is higher than for dorsal measures, and is comparable to that for traditional measures. P. l. castaneus and aridulus from Cherry Co. are the most distinctive taxon in the present data set. P. l. castaneus can be discriminated without overlap from about the same number (7) of leucopus populations as in the traditional measures. P. l. aridulus from Cherry Co. here shows levels of discrimination from other leucopus taxa similar to those seen for conventional measures, altough it showed very little differentiation in the dorsal view. P. l. castaneus is also discriminated from Puebla incensus and affinis with little overlap (6% and 10% overlap, respectively). P. l. incensus from Puebla is the least distinctive taxon; it can only be discriminated from castaneus, and from aridulus (Cherry Co.) and l. leucopus (North Carolina) with moderate amounts overlap (23% and 32%,

Table 23. Percent overlap between *Peromyscus leucopus* subspecies along canonical variate 1 (first number) and canonical variate 2 (second number). Ventral truss network.

	fusus(VB)	*noveb*(MI)	*noveb*(OK)	*arid*(CH)	*arid*(DA)	*leucopus*(KY)	*leucopus*(NC)	*tornillo*	*incen*(VE)	*incen*(PU)	*mesomelas*	*affinis*	*castaneus*
fusus(NV)	93/72	18/72	95/93	51/86	88/95	27/95	4/69	50/76	17/93	89/96	45/21	32/57	0/74
fusus(VB)		5/86	94/92	61/48	84/78	11/69	0/24	34/34	6/50	77/74	16/0	13/8	0/94
noveb(MI)			6/90	0/32	0/79	54/43	84/16	93/22	92/39	57/69	34/0	67/5	51/78
noveb(OK)				56/56	85/91	19/74	0/50	50/32	9/66	80/91	43/25	46/29	0/90
arid(CH)					79/75	0/88	0/73	0/61	0/93	23/80	0/30	0/55	0/42
arid(DA)						0/84	0/74	28/69	0/82	64/97	10/34	11/54	0/83
leuco(KY)							30/92	78/89	68/90	65/91	56/37	91/85	0/54
leuco(NC)								77/91	74/76	32/78	6/44	55/85	69/23
tornillo									86/68	84/81	58/79	87/97	44/28
incen(VE)										54/86	46/14	76/56	45/48
incen(PU)											77/35	81/76	6/69
mesomelas												93/73	0/0
affinis													10/6

respectively). *P. l. aridulus* from Dawes Co. is also distinct and can be discriminated without overlap from five other *leucopus* populations. *P. l. leucopus* from Kentucky and North Carolina can be discriminated without overlap from three and four populations, respectively. The remaining populations can be discriminated from between one and three *leucopus* taxa without overlap (Table 23).

Tooth row length (distance variable 38; third truss cell) has a large positive coefficient on CV1 as in the analysis of traditional measures, while distance variable 43 (posterior palatal length; fourth truss cell) has a negative coefficient (Table 17). The ordination of *leucopus* taxa along this canonical variate reveals a pattern similar to the previous analyses (Figure 20A). *P. l. castaneus* and *l. leucopus* from North Carolina form a cluster characterized by individuals with relatively small tooth rows, while *fusus* from Vineyard Haven, *aridulus*, and *noveboracensis* from Oklahoma are represented by individuals with relatively larger tooth rows (Figure 20B). The remaining populations occupy intermediate positions between these two clusters (Figure 20A).

The range of overlap along CV2 (0%-97%) is similar to the first canonical variate (Table 23). *P. l. castaneus*, Michigan *noveboracensis*, and *fusus* from Vineyard Haven are discriminated without overlap from one *leucopus* population each (Figure 20A). This result is intermediate between the traditional measures, where no discrimination free of overlap was obtained, and the dorsal truss measures. The diagonal length of the post-palatal region (distance variable 45; fourth truss cell) has a large negative coefficient on CV2 and distance variable 40 (palatal diagonal length;third truss cell) has a positive coefficient (Table 17).

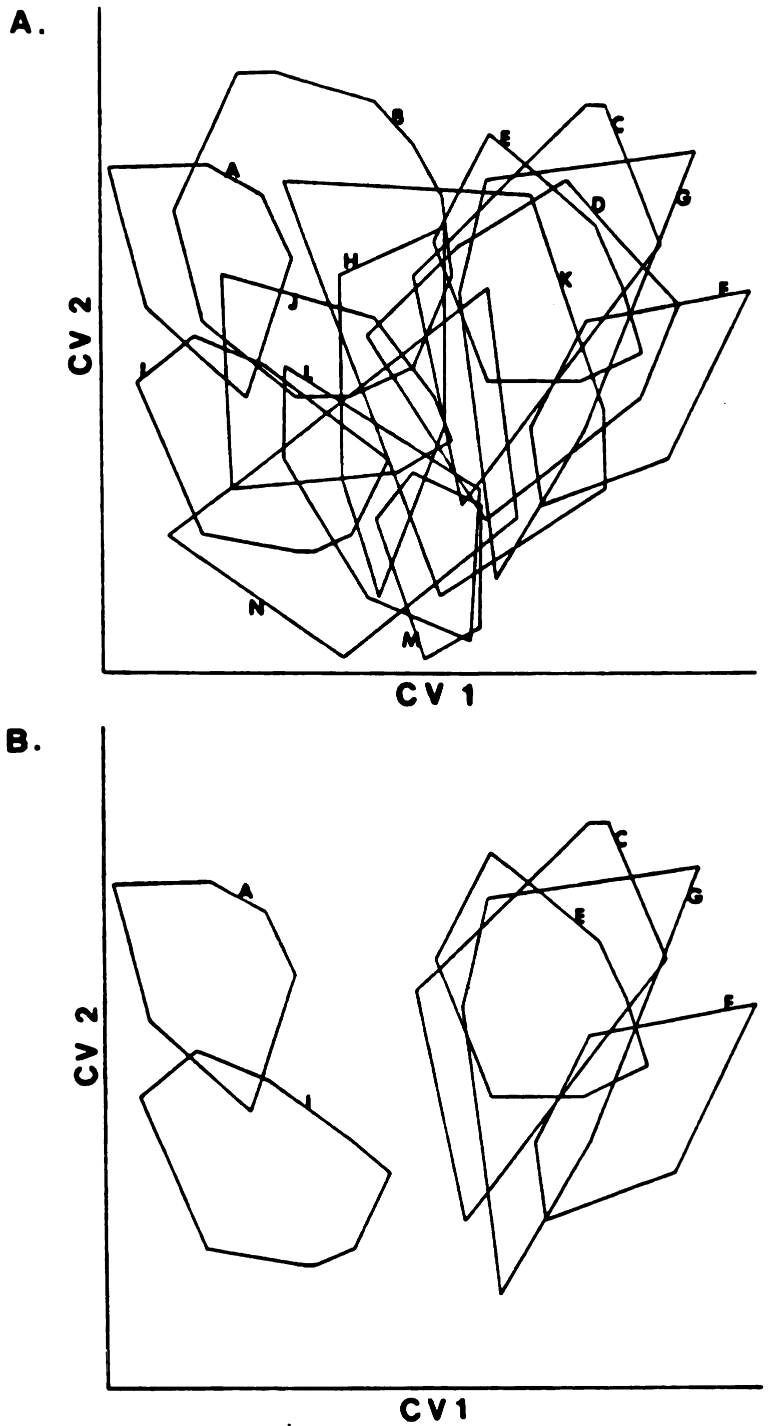

Figure 20. Discriminant analysis of *Peromyscus leucopus* taxa. Truss character set. Ventral truss network. (A) All *leucopus* taxa. (B) Non-overlapping clusters. A. *castaneus*, B. *noveboracensis* (MI), C. *noveboracensis* (OK), D. *fusus* (Martha's Vineyard), E. *fusus* (Vineyard Haven), F. *aridulus* (Cherry Co.), G. *aridulus* (Dawes Co.), H. *leucopus* (KY), I. *leucopus* (NC), J. *incensus* (Veracruz), K. *incensus* (Puebla), L. *affinis*, M. *mesomelas*, N. *tornillo*.

All Mahalanobis distances between leucopus taxa are significant except for the distance between the two aridulus populations and Veracruz incensus and l. leucopus from North Carolina (Table 24). Mean D^2 values are generally high in this data set, and are always larger than mean D^2 values for dorsal measures. Mean D^2 values in the present data set are also larger than mean D^2 values for traditional measures, except for aridulus from Dawes Co., and incensus populations. D^2 values between populations within fusus, aridulus and l. leucopus are generally small compared to D^2 values between these populations and other leucopus taxa. The correlation coefficient between geographic distance and Mahalanobis distances is not significant (r=.14), as in the conventional measures.

The UPGMA cluster analysis based on the matrix of Mahalanobis distances between taxa is shown in Figure 21. The phenogram reveals a pattern of branching of intermediate complexity relative to the previous data sets. There are two major clusters: one formed by southern and northern U.S. forms, and the other consisting of northern U.S., Mexican, and one southern U.S. populations. P. l. leucopus populations form a distinct convex subgroup in the first cluster. They are joined by Oklahoma noveboracensis to form a subcluster of southern U.S. forms. P. l. fusus from Martha's Vineyard and aridulus from Cherry Co. join this major cluster as a northern subcluster. The second major cluster shows a complex pattern of branching with alternating northern U.S. and Mexican taxa.

The minimum spanning tree (Prim Network) based on Mahalanobis distances reveals a complex pattern of geographic connectedness (Figure 22). P. l. aridulus populations are connected at smaller D^2 values

Table 24. Mahalanobis D^2 statistic between *Peromyscus leucopus* subspecies. Ventral truss network. Significance levels between $P<.03$ and $P<.0001$.

	fusus(VM)	noveb(MI)	noveb(OK)	aridulus(CM)	aridulus(DA)	leucopus(KY)	leucopus(NC)	tornillo	incensus(VZ)	incensus(PU)	mesomelas	affinis	castaneus
fusus(NV)	6.41	14.39	6.09	5.26	4.68	9.57	18.92	9.48	11.45	3.49	15.73	13.36	32.88
fusus(VM)		18.84	13.37	11.08	8.79	14.55	27.84	20.27	18.70	11.43	23.94	21.83	37.03
noveb(MI)			13.27	29.20	16.97	7.95	9.18	15.62	7.84	11.34	24.81	15.49	14.24
noveb(OK)				7.57	3.59	12.71	25.23	21.00	19.75	5.85	21.91	18.40	34.46
aridulus(CM)					2.37 ns	16.05	30.69	18.78	22.67	11.32	22.82	17.90	50.47
aridulus(DA)						11.56	24.74	16.11	18.13	8.40	21.64	15.70	39.08
leucopus(KY)							5.52	9.47	5.14	8.37	16.44	6.17	26.15
leucopus(NC)								8.68	2.66 ns	15.44	19.99	9.18	22.87
tornillo									5.67	10.60	13.90	7.21	25.02
incensus(VZ)										10.67	20.60	9.61	19.39
incensus(PU)											11.70	11.41	22.94
mesomelas												9.46	31.13
affinis													23.48

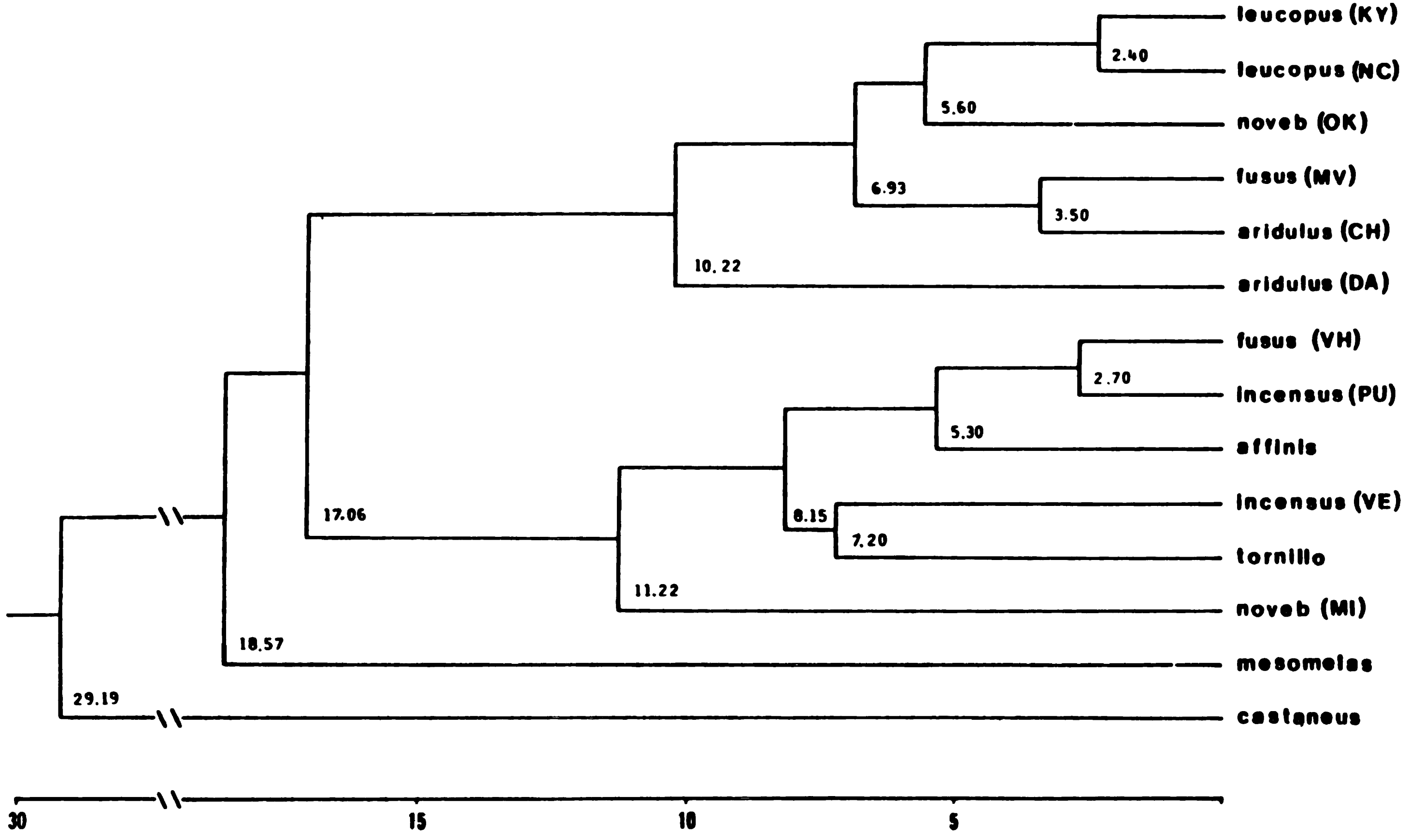

Figure 21. Phenetic relationships among Peromyscus leucopus taxa based on the Mahalanobis D^2 statistic. Truss character set. Ventral truss network. Clustering is by the unweighted pair group method using arithmetic means.

Figure 22. Minimum spanning tree (Prim Network) for samples of *Peromyscus leucopus* taxa based on the Mahalanobis distance. Truss character set. Ventral truss network. A. *fusus* (Martha's Vineyard), B. *fusus* (Vineyard Haven), C. *noveboracensis* (Michigan), D. *aridulus* (Cherry Co.), E. *aridulus* (Dawes Co.), F. *leucopus* (Kentucky), G. *leucopus* (North Carolina), H. *noveboracensis* (Oklahoma), I. *tornillo*, J. *incensus* (Veracruz), K. *incensus* (Puebla), L. *mesomelas*, M. *affinis*, N. *castaneus*.

relative to other *leucopus* taxa they join. *P. l. fusus* populations are also linked but the Martha's Vineyard population is closer to *aridulus* from Dawes Co. and Puebla *incensus*. Populations within *l. leucopus*, *noveboracensis*, and *incensus* are not linked. All Mexican forms connect only with U.S. forms, except *affinis* which is linked to *mesomelas*, although it is closer to *l. leucopus* from Kentucky.

Very few clusters are common to both the UPGMA phenogram and the Prim Network as in the previous data sets. *P. l. fusus* from Martha's Vineyard and *aridulus* from Cherry Co. and *tornillo* and *incensus* from Vera Cruz form clusters in both analyses.

Summary. Rates of correct classification based upon the *a posteriori* classification matrix of a discriminant function analysis were generally better for ventral measures than traditional or dorsal data sets. *Peromyscus leucopus* taxa overlap extensively along canonical variates in all three data sets. The range of percentage overlap between *leucopus* taxa is similar in all three data sets, however the level of discrimination free of overlap is higher for the traditional and ventral measures than for dorsal measures. *P. l. castaneus* is the most distinctive taxon in the traditional and ventral data sets, while *fusus* from Vineyard Haven is the most distinctive taxon in the dorsal data set. Percentage overlap along CV2 is much larger than along CV1. Generally, different traits contribute large coefficients to the canonical variates for each data set.

Mahalanobis distances between taxa were significant in most cases in the three data sets. Mean D^2 values between *leucopus* taxa are generally higher for ventral measures than dorsal and traditional measures. There is no significant correlation between geographic distances and Mahalanobis distances for traditional and ventral measures, while for dorsal measures this correlation coefficient is significant. However, this correlation may be spurious because only population samples within subspecies show a geographic pattern of connectedness. UPGMA cluster analysis and Prim networks of leucopus taxa both generate phenograms that are difficult to interpret on a geographic basis, except for traditional measures. In this case, UPGMA finds two major clusters separating northern US from southern US and Mexican forms.

2.2.2 Sheared principal components

I attempted to remove size from the second and third principal components for leucopus subspecies but the results were similar to those obtained for populations within subspecies. Coefficients of vector correlations between sheared components (H2 and H3) and original components (PC2 and PC3) were near to unity in all data sets (average of.98 and .99, respectively). This result indicates that virtually no size effects were removed from the original components by the shear.

Allometric coefficients computed from the first principal component of pooled samples of P. leucopus taxa are similar to those obtained for noveboracensis populations (Table 10). Traditional cranial measurements of length are positively allometric, except for occipito-nasal length, which is nearly isometric (Table 10). Measurements of width are negatively allometric, except for rostral breadth which is positively allometric. Truss network measurements display a similar pattern of

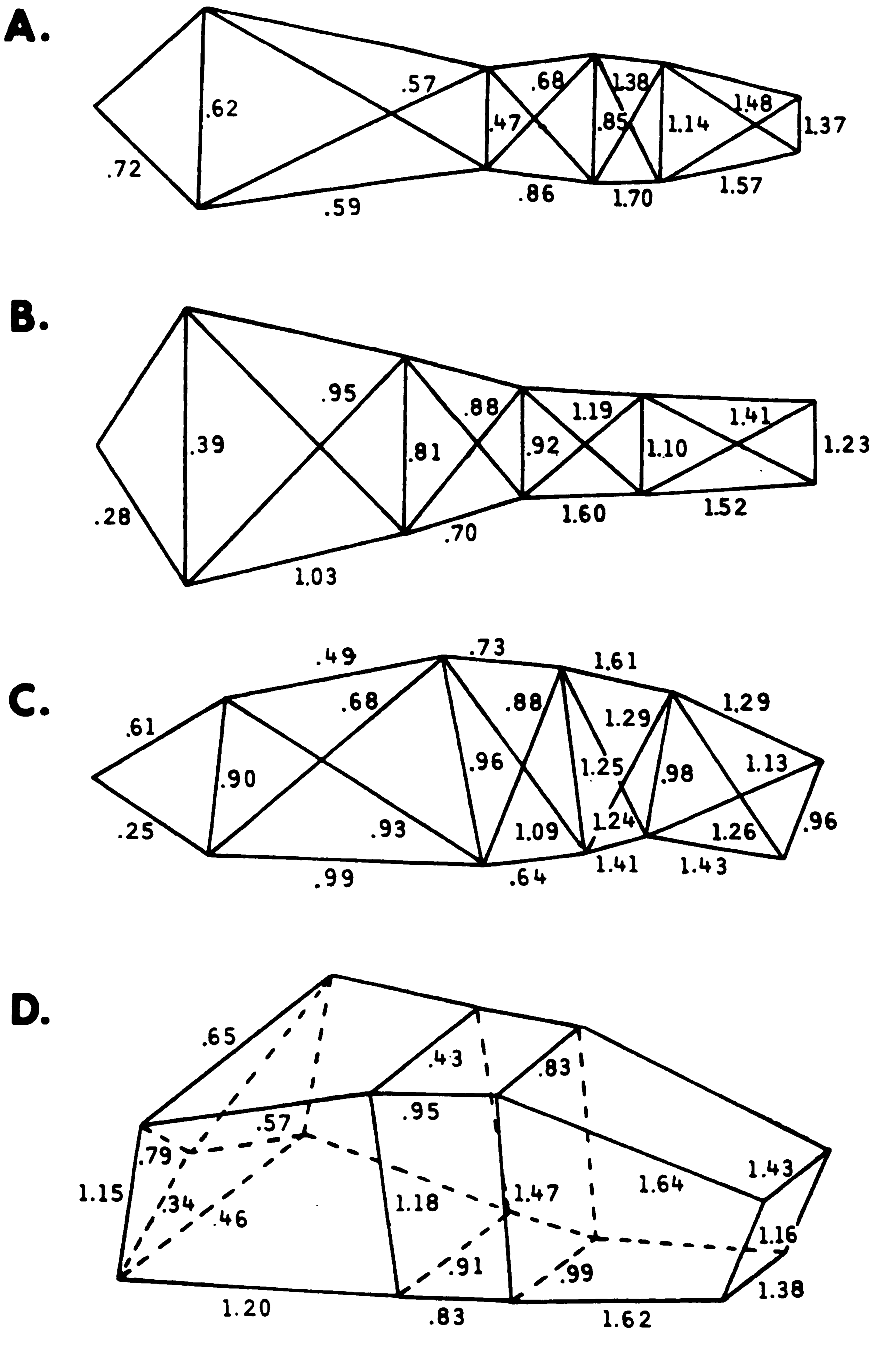

Figure 23. Multivariate allometric coefficients for Peromyscus leucopus subspecies depicted on the truss networks. A. Dorsal truss network. B. Ventral truss network. C. Lateral truss network. D. Three dimensional view.

allometry. Measurements on the rostrum and anterior frontal have positive allometries with respect to general size, while measurements in the posterior region of the skull (representing the cranium and the posterior frontal) are negatively allometric). The truss networks and traditional measures generally indicate similar patterns of allometry. However, it seems that the pattern of truss measurements allows a better allometric constrast between anterior and posterior regions of the skull. Traditional measures render this contrast difficult because the posterior region of the skull is poorly sampled in both length and width dimensions.

There is no concordance between allometric coefficients and principal components loadings on PC2 and PC3 for all five data sets: traditional measures (Kendall's $\tau = -.58$; $P<.01$ and $\tau = -.15$; ns, respectively); dorsal view ($\tau = .03$; ns and $\tau = -.30$; ns); ventral view ($\tau = -.28$; ns and $\tau = -.39$; ns); lateral view ($\tau = -.23$; ns and $\tau = .04$; ns) and three-dimensional view ($\tau = -.55$; $P<.01$ and $\tau = .25$; ns).

Traditional measurements

The first principal component for the pooled samples of *leucopus* subspecies accounts for 75% of the variation, the second 6%, and the third only 4% of the variation. I interpret PC1 as a general size measure because all coefficients are positive, and all characters have positive significant correlations with PC1 (Table 26). The amount of overlap along principal components is generally high (Table 27; Figure 22). *P. leucopus* subspecies tend to differ in size and shape between

Table 25. Principal component loadings for *Peromyscus leucopus* subspecies (DV=Distance variable). *Traditional character* set. All correlations with PC1 are significant (P<.01).

Character	PCI	r	PCII	PCIII
Occipito-nasal length	0.27	0.76	-0.04	0.05
Nasal length	0.36	0.81	-0.28	0.18
Rostral length	0.38	0.66	-0.33	0.35
Rostral breadth	0.34	0.68	0.22	-0.81
Interorbital constriction	0.15	0.85	0.27	0.07
Zygomatic breadth	0.27	0.49	0.14	-0.04
Basal length	0.31	0.36	-0.12	-0.02
Palatal length	0.33	0.57	0.01	0.04
Diastema length	0.38	0.53	-0.24	-0.09
Tooth row length	0.21	0.63	0.72	0.41
Mastoid breadth	0.18	0.69	0.13	0.005
Cranial depth	0.15	0.67	0.25	0.05

Table 26. Percent overlap between *Peromyscus leucopus* subspecies along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Traditional character set.

	noveb (MI)	*noveb* (OK)	*aridulus*	*leucopus*	*tornillo*	*incensus*	*mesomelas*	*affinis*	*castaneus*
fusus	49/59/99	63/98/92	92/97/78	45/49/95	88/79/88	81/83/91	43/47/72	48/84/91	22/26/95
noveb (MI)		51/44/93	59/67/84	96/98/98	96/86/86	91/96/94	54/81/75	89/90/89	75/82/93
noveb (OK)			73/95/57	49/43/91	89/64/75	84/67/76	96/43/79	85/76/85	43/21/96
aridulus				49/66/63	90/73/90	90/86/95	58/50/70	61/83/93	30/20/60
leucopus					92/82/82	89/93/90	51/71/59	87/91/85	88/94/92
tornillo						98/94/98	96/92/88	97/93/93	79/58/71
incensus							96/83/94	94/98/98	60/79/79
mesomelas								87/87/97	63/67/79
affinis									67/83/83

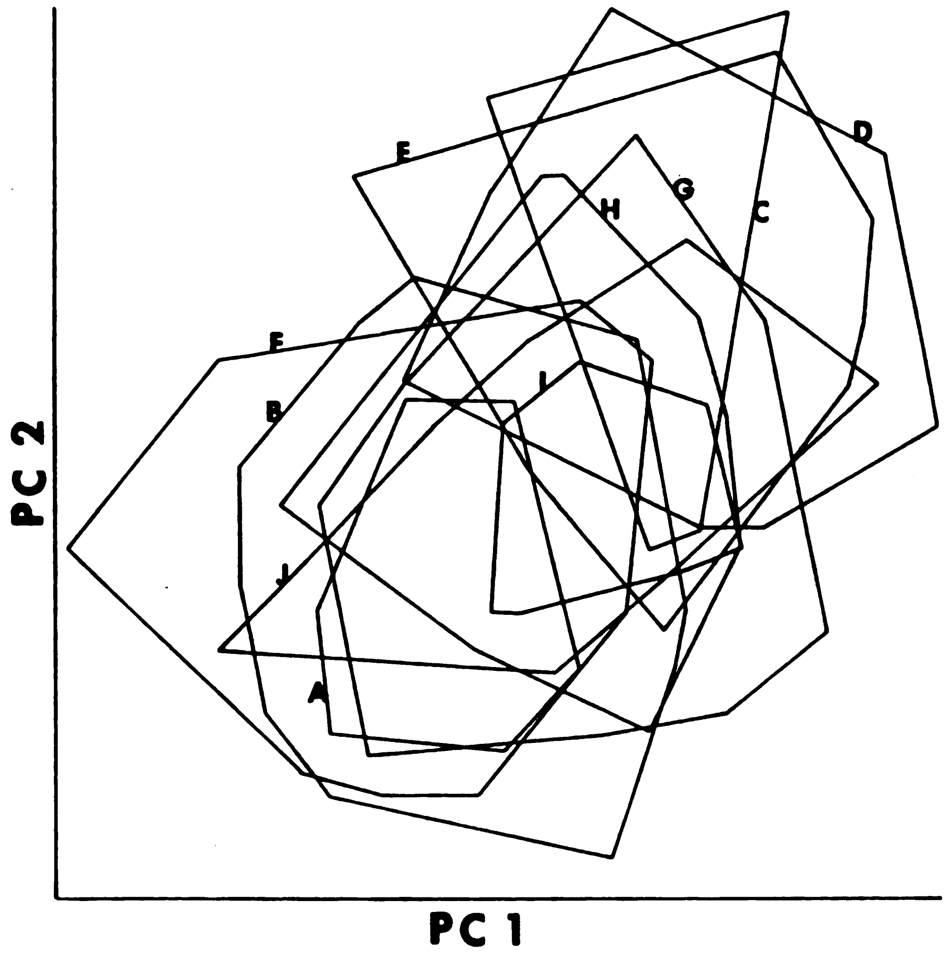

Figure 24. Scatter between *Peromyscus leucopus* taxa. Traditional character set. A. *castaneus*, B. *noveboracensis* (MI), C. *noveboracensis* (OK), D. *fusus*, E. *aridulus*, F. *leucopus*, G. *incensus*, H. *affinis*, I. *mesomelas*, J. *tornillo*.

themselves (Table 27). In other words, subspecies differing from one another in size tend also to differ in shape, except for tornillo which shows limited differences in shape only (along PC2) from Oklahoma noveboracensis and castaneus (Table 27), and affinis which differs from castaneus, aridulus, and fusus in size only. P. l. castaneus is the most differentiated taxon showing relatively low levels of overlap along PC1 with fusus and aridulus. It also shows relatively low levels of overlap along PC2 with fusus, Oklahoma noveboracensis and aridulus. The second principal component shows a contrast between tooth row length with a large positive coefficient and nasal, rostral, and diastema length with negative coefficients (Table 26). The overlap of populations along PC3 is higher than along PC1 and PC2 (57%-99%) (Table 27). PC3 appears to be a contrast between tooth row with a positive sign and rostral length with a negative sign.

Levels of overlap between subspecies are generally high as shown above. However, subspecies seem to differ among themselves in the extent of size and size-free variation. This result parallels findings within P. leucopus populations. For example, castaneus differ both in size and shape from fusus and aridulus, while it differs mainly in shape from noveboracensis from Oklahoma. Differences between fusus, Michigan noveboracensis, aridulus, and the other subspecies, when they exist, tend to be in size and shape as well.

Dorsal view. The partitioning of the variance among leucopus taxa is very different from the analysis of traditional measures. The first principal component explains 30% less of the variation (47%), while the second and third components (18% and 13%, respectively) account for three times more of the variation compared to the traditional data set. I interpret PC1 as a measure of general size since all coefficients are positive, and distance variables have positive significant correlations with PC1 (Appendix A7). Overlap along PC1 is also extensive (25%-100%) (Table 28; Figure 23A). *P. leucopus* subspecies again differ in size and shape as in the previous data set. However, *fusus* here shows little differentiation in size and shape from other subspecies. Results for *tornillo* are also different. *P. l. tornillo* shows some shape differentiation from other subspecies, including relatively low levels of overlap with Michigan *noveboracensis* (along PC2) and *mesomelas* (along PC3). Results for Mexican forms are slighty different here. *P. l. incensus*, *mesomelas*, and *affinis* tend to differ more in shape, mainly along PC3, from other *leucopus* subspecies. *P. l. castaneus* is again the most diverse taxon, differing in size and shape from other forms; shape differences are mainly along PC3. The second principal component appears to be a contrast between nasal measurements (DV 3, 4, and 5; first truss cell) with positive signs and anterior length of frontal (DV 8; third truss cell) with a negative coefficient. The third principal component is a contrast between variables with negative coefficients on the nasal region (distance variables 3, 4, and 5; first truss cell) and variables with positive coefficients on the posterior region of the frontal (distance variables 13, 14, and 15; third truss cell) (Appendix A7).

As in the previous data set, there are differences in magnitude and direction of size and shape between *leucopus* subspecies. For example, *castaneus* differs in size and shape (along PC3) from Oklahoma *noveboracensis* and *aridulus*, but mainly in shape from *mesomelas*. *P. l.*

Table 27. Percent overlap between *Peromyscus leucopus* subspecies along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Dorsal truss network.

	noveb (MI)	*noveb* (OK)	*aridulus*	*leucopus*	*tornillo*	*incensus*	*mesomelas*	*affinis*	*castaneus*
fusus	46/78/100	95/90/84	99/71/97	95/98/92	76/79/66	70/99/98	83/84/90	63/70/100	84/88/75
noveb (MI)		31/82/95	54/15/99	93/87/85	60/30/96	77/85/77	34/19/91	79/25/60	79/89/53
noveb (OK)			95/49/98	51/94/72	86/68/39	73/76/41	93/61/82	85/44/56	24/100/38
aridulus				59/78/92	72/95/44	76/77/69	84/97/79	60/96/67	33/40/58
leucopus					97/63/69	93/99/93	100/77/69	91/82/80	62/97/82
tornillo						96/79/50	100/96/33	97/97/97	74/64/96
incensus							94/85/48	100/81/83	63/77/94
mesomelas								100/97/47	52/56/14
affinis									61/42/97

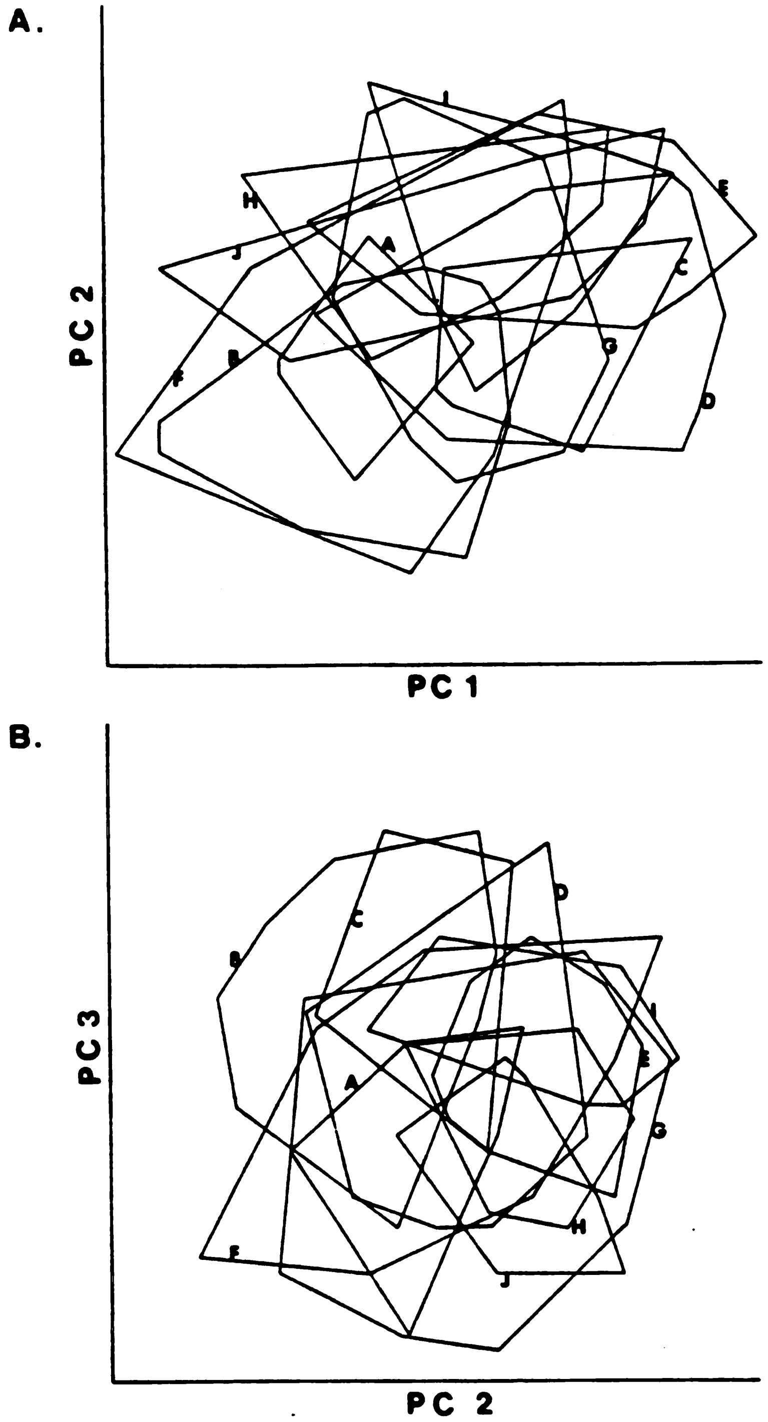

Figure 25. Scatter between *Peromyscus leucopus* taxa. Truss character set. Dorsal truss network. (A) PC2 against PC1. (B) PC3 against PC2. A. *castaneus*, B. *noveboracensis* (MI), C. *noveboracensis* (OK), D. *fusus*, E. *aridulus*, F. *leucopus*, G. *incensus*, H. *affinis*, I. *mesomelas*, J. *tornillo*.

affinis shows some divergence, mainly in shape, from mesomelas and Michigan noveboracensis not seen in the previous data set. P. l. mesomelas differs in size and shape from Michigan noveboracensis, but only in shape from tornillo. P. l. tornillo differs mostly in shape from other leucopus subspecies.

Ventral view. Principal component 1 explains 15% more of the variation among leucopus taxa in this data set than for dorsal measures. However, both PC2 and PC3 explain less variation (10% and 9%, respectively). I interpret PC1 as a size variable since all coefficients are positive, and all distance variables have positive significant correlations with this component (Appendix A8). Levels of overlap along PC1 are as high as in the previous analyses (24%-98%) (Table 29). Results for P. l. leucopus forms in this data set are similar to previous analyses with respect to differentiation in size and shape. In other words, subspecies differing in size from one another, differ in shape as well, except for tornillo. It differs very little from other leucopus taxa here, while it showed shape differentiation for dorsal measures. P. l. fusus here shows levels of differentiation larger than those for dorsal measures, although the reverse is true for Oklahoma noveboracensis. P. l. castaneus is again the most differentiated taxon, showing relatively low levels of overlap along PC1 with fusus, Oklahoma noveboracensis, and mesomelas. P. l. castaneus also differs in shape from fusus (along PC2) and mesomelas (along PC3). Distance variable 33 (posterior length of diastema; second truss cell) has a large negative coefficient on PC2, while tooth row length (DV 38; third truss cell) has a positive coefficient

Table 28. Percent overlap between *Peromyscus leucopus* subspecies along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Ventral truss network.

	noveb (MI)	*noveb* (OK)	*aridulus*	*leucopus*	*tornillo*	*incensus*	*mesomelas*	*affinis*	*castaneus*
fusus	56/75/89	79/90/81	96/99/92	48/42/98	66/93/96	83/86/99	70/60/63	57/57/84	31/24/92
noveb (MI)		55/81/36	57/72/42	98/94/91	98/81/61	89/88/88	40/97/13	86/97/27	80/97/95
noveb (OK)			95/86/91	62/69/60	96/93/93	80/92/75	96/96/78	82/65/97	28/59/62
aridulus				50/55/65	82/87/79	86/84/71	88/60/92	67/59/90	37/59/90
leucopus					94/57/54	80/65/94	58/90/40	78/94/56	90/94/90
tornillo						93/98/89	74/91/73	93/76/83	83/54/71
incensus							72/89/57	94/81/70	67/60/65
mesomelas								77/93/93	24/88/21
affinis									71/90/42

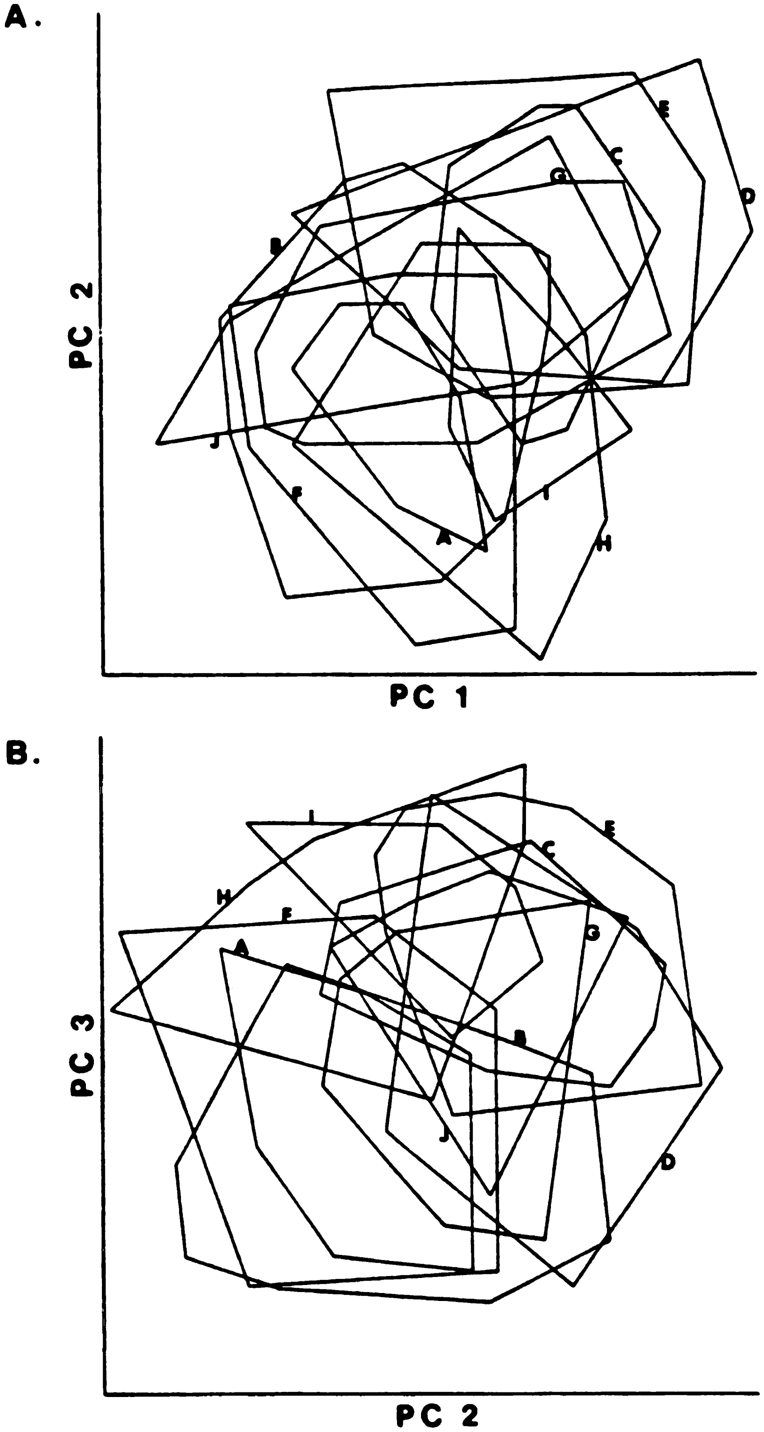

Figure 26. Scatter between *Peromyscus leucopus* taxa. Truss character set. Ventral truss network. (A) PC2 against PC1. (B) PC3 against PC2. A. *castaneus*, B. *noveboracensis* (MI), C. *noveboracensis* (OK), D. *fusus*, E. *aridulus*, F. *leucopus*, G. *incensus*, H. *affinis*, I. *mesomelas*, J. *tornillo*.

(Appendix A8). The third principal component appears to be a constrast between rostral measures with negative coefficients (distance variables 26, 28, and 30; first truss cell) and the width between the first upper molars and tooth row length (distance variables 34 and 38; third truss cell) with positive coefficients (Appendix A8).

Lateral view. The first and second principal components account for amounts of variation similar to that for the ventral truss measures (61% and 9%, respectively); the third component accounts for half as much of the variation (5%) as in ventral truss measures. Again, PC1 appears to be a measure of general size (Appendix A9). Percentage ovelap along PC1 is similar to previous analyses (25%-100%) (Table 30). *P. leucopus* subspecies generally show lower levels of size and shape differentiation in the present data set (Table 30). *P. leucopus* forms generally show lower levels of differentiation in size and shape, except for Michigan *noveboracensis* which shows size differences, though limited, from many *leucopus* taxa in this data set. The same result is true for Mexican forms which differ much less in size in shape here. *P. l. castaneus*, though, still shows relatively large amounts of variation, specially in size, from other *leucopus* taxa. It shows relatively low overlap with *fusus*, Oklahoma *noveboracensis*, and *aridulus* along PC1.

Distance variable 8 (anterior length of frontal; second truss cell) has a large negative coefficient on PC2 and nasal length (DV 3; first truss cell) has a positive coefficient on PC2 (Appendix A9). The third principal component appears to be a constrast between posterior length of diastema (DV 33; second truss cell) with a negative sign and

Table 29. Percent overlap between *Peromyscus leucopus* subspecies along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Lateral truss network.

	noveb (MI)	*noveb* (OK)	*aridulus*	*leucopus*	*tornillo*	*incensus*	*mesomelas*	*affinis*	*castaneus*
fusus	61/76/98	95/100/90	94/68/100	61/95/77	93/60/55	88/96/90	97/71/72	98/53/58	25/97/90
noveb (MI)		52/92/97	68/22/95	94/80/98	98/24/97	100/79/98	59/38/98	90/17/81	66/81/98
noveb (OK)			98/58/93	61/87/83	82/71/96	76/78/100	93/68/71	76/32/68	31/93/90
aridulus				75/75/79	100/95/98	98/81/83	69/97/72	64/96/64	35/53/88
leucopus					94/100/81	96/100/96	69/81/90	94/66/91	71/82/100
tornillo						96/68/89	88/96/100	97/100/97	76/96/92
incensus							98/100/89	98/68/87	71/77/96
mesomelas								100/97/93	60/60/100
affinis									65/39/100

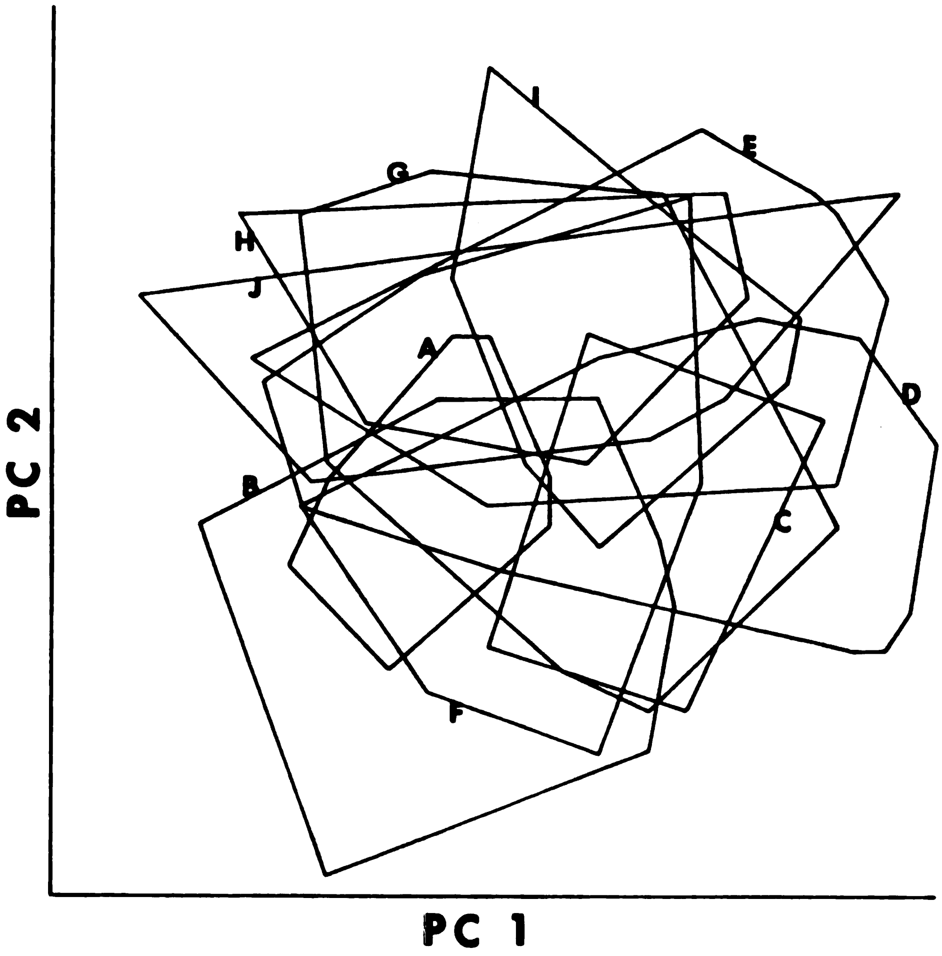

Figure 27. Scatter between *Peromyscus leucopus* taxa. Truss character set. Lateral truss network. A. *castaneus*, B. *noveboracensis* (MI), C. *noveboracensis* (OK), D. *fusus*, E. *aridulus*, F. *leucopus*, G. *incensus*, H. *affinis*, I. *mesomelas*, J. *tornillo*.

distance variable 53 (diagonal length of rostrum; first truss cell) and anterior diastema (DV 28; first truss cell) with positive signs.

Three-dimensional view. The partitioning of the variance is similar to the ventral truss measures. The first principal component accounts for 53% of the variation among *leucopus* taxa, the second 9%, and the third 7%. The first principal component can be interpreted as a general size variable (Appendix A10). Percent overlap levels along PC1 are similar to previous analyses (29%-100%) (Table 30). Subspecies of *P. leucopus* also differ in size and shape in this data set, except for *tornillo* which shows only limited differences in shape along both PC2 and PC3. All Mexican taxa differ more in shape than size, except for *affinis*. *P. l. castaneus* is again the most differentiated taxon, showing relatively low levels of overlap along PC1 with *fusus* and Oklahoma *noveboracensis* (Figure 28). *P. l. castaneus* also shows low levels of overlap along PC2 and PC3 with Oklahoma *noveboracensis*, *aridulus*, and *mesomelas* (Table 30). The second principal component is a contrast between the posterior length of frontal (DV 13; third truss cell) with a positive sign and incisor width (DV 26; first truss cell) with a negative sign (Appendix A10). The third principal component is apparently a constrast between post-frontal length (DV 13; second truss cell) with a positive sign and tooth row length (DV 38; second truss cell) with a negative sign.

Despite relatively large amounts of overlap, *leucopus* subspecies seem to display differences as to the nature of morphologic variation. *P. l. castaneus* differs mainly in size from *fusus*, while it differs mostly in shape from *mesomelas*, Oklahoma *noveboracensis* and *aridulus*

Table 30. Percent overlap between Peromyscus leucopus subspecies along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). Three dimensional view.

	noveb (MI)	noveb (OK)	aridulus	leucopus	tornillo	incensus	mesomelas	affinis	castaneus
fusus	59/92/61	97/74/78	99/99/89	54/93/88	97/90/100	81/81/92	74/62/78	67/88/98	29/47/51
noveb (MI)		43/62/54	62/66/40	91/99/89	98/89/26	90/95/76	56/47/33	83/84/54	93/71/95
noveb (OK)			93/95/84	49/77/74	79/71/82	74/47/90	93/93/93	82/79/88	31/17/31
aridulus				45/71/74	93/80/95	81/54/95	98/95/70	67/80/96	37/7/27
leucopus					93/97/62	90/96/86	53/60/73	85/84/87	80/58/76
tornillo						96/77/83	90/100/79	93/90/90	100/44/20
incensus							77/36/83	98/60/96	100/77/50
mesomelas								80/70/87	60/ 0/32
affinis									68/32/55

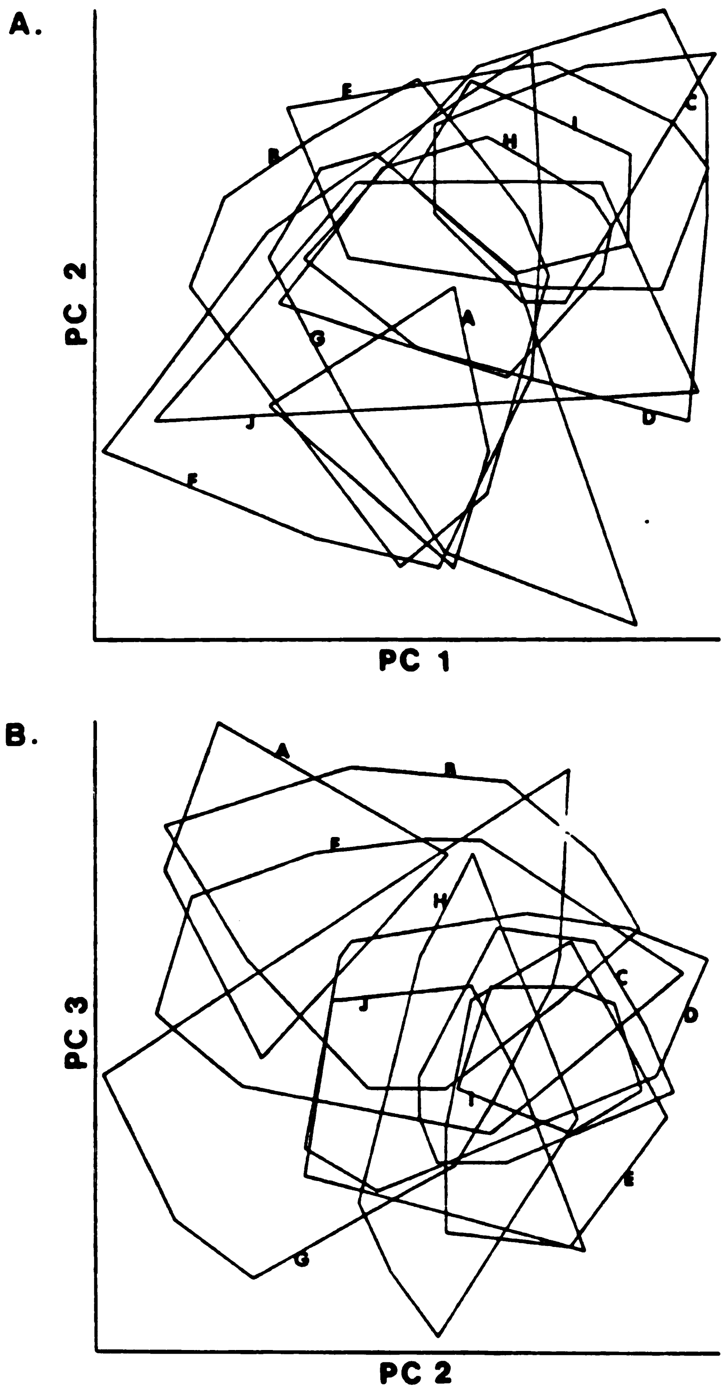

Figure 28. Scatter between *Peromyscus leucopus* taxa. Truss character set. Three dimensional view. (A) PC2 against PC1. (B) PC3 against PC2. A. *castaneus*, B. *noveboracensis* (MI), C. *noveboracensis* (OK), D. *fusus*, E. *aridulus*, F. *leucopus*, G. *incensus*, H. *affinis*, I. *mesomelas*, J. *tornillo*.

with little or no overlap, and from *affinis* and *tornillo* with moderate amounts of overlap. *P. l. castaneus* differs both in size and shape from Oklahoma *noveboracensis* and *aridulus*. *P. l. fusus* tends to differ mostly in size as in previous data sets.

Summary. The first principal component for the pooled samples of *leucopus* taxa can be interpreted as a measure of size in all five data sets. The first principal component for traditional measures accounts for a larger amount of the variation than any of the truss networks. *P. leucopus* taxa overlap extensively in the reduced space of the principal components. In most data sets *castaneus* is separated from a few forms, but always with moderate amounts of overlap. The only exception is the separation between *castaneus* and *mesomelas* without overlap in the three dimensional measurement scheme. Overlap between *leucopus* taxa is generally high along PC2 and PC3. However, there is variation in magnitude and direction of shape differences between subspecies. Allometric coefficients are similar for all data sets. Anterior skull measurements are generally positively allometric with respect to size, while posterior measures show negative allometries. There is no concordance between allometric coefficients and loadings from principal components 2 and 3.

2.3.1 *Peromyscus leucopus* and *P. gossypinus*

2.3.1 Discriminant Analysis

Discriminant analysis with canonical variates was used in this section to examine morphologic relationships between *Peromyscus* gossypinus and P. leucopus taxa. Lateral and three dimensional data sets were not analyzed because the within-group covariance matrix is singular.

Traditional measurements

All gossypinus individuals are correctly classified by the discriminant function of traditional measurements. Canonical variate 1 accounts for 50% of the total variation, the second 14%, and the third 10% of the variation. Overlap along CV1 between gossypinus and leucopus taxa varies from 0% to 87% (Table 31A). P. gossypinus is discriminated without overlap from castaneus, Michigan noveboracensis, l. leucopus from North Carolina, Veracruz incensus, and mesomelas (Figure 29). It is also separated from affinis and l. leucopus from Kentucky with little overlap (5% and 10%, respectively), and from Puebla incensus and tornillo with moderate amounts of overlap (27% and 18% overlap, respectively). Discrimination from the remaining leucopus taxa involves at least 38% overlap (Table 31A). Basal length and tooth row length have large negative and positive coefficients on CV1, respectively (Table 32). P. gossypinus is thus characterized by individuals with relatively larger skulls and tooth rows (Table 32; Figure 29).

Overlap along CV2 between gossypinus and leucopus taxa is much more extensive than in CV1 (Table 31A; Figure 29). The only case of discrimination without overlap occurs between gossypinus and aridulus from Dawes Co. (Table 31A; Figure 29). Discrimination from Kentucky l. leucopus involves only 5% overlap, while separation from tornillo and aridulus from Cherry Co. involves moderate amounts of overlap (26% and

Table 31. Percent overlap between Peromyscus leucopus subspecies and Peromyscus gossypinus along canonical variate 1 (first number) and canonical variate 2 (second number). A. Traditional character set. B. Dorsal truss network. C. Ventral truss network.

		fusus(MV)	fusus(VH)	noveb(MI)	noveb(OK)	aridulus(CH)	aridulus(DA)	leucopus(KY)	leucopus(NC)	tornillo	incensus(VE)	incensus(PU)	mesomelas	affinis	castaneus
A.	gossypinus	71/67	87/83	0/97	38/52	68/22	77/0	10/5	0/48	18/26	0/76	27/64	0/45	5/82	0/89
B.	gossypinus	59/92	96/84	18/21	39/78	58/81	76/95	0/90	0/85	81/95	0/71	0/93	0/81	0/93	5/32
C.	gossypinus	53/96	58/53	0/68	41/80	81/81	60/95	0/93	0/89	8/92	0/85	14/95	0/46	0/81	0/45

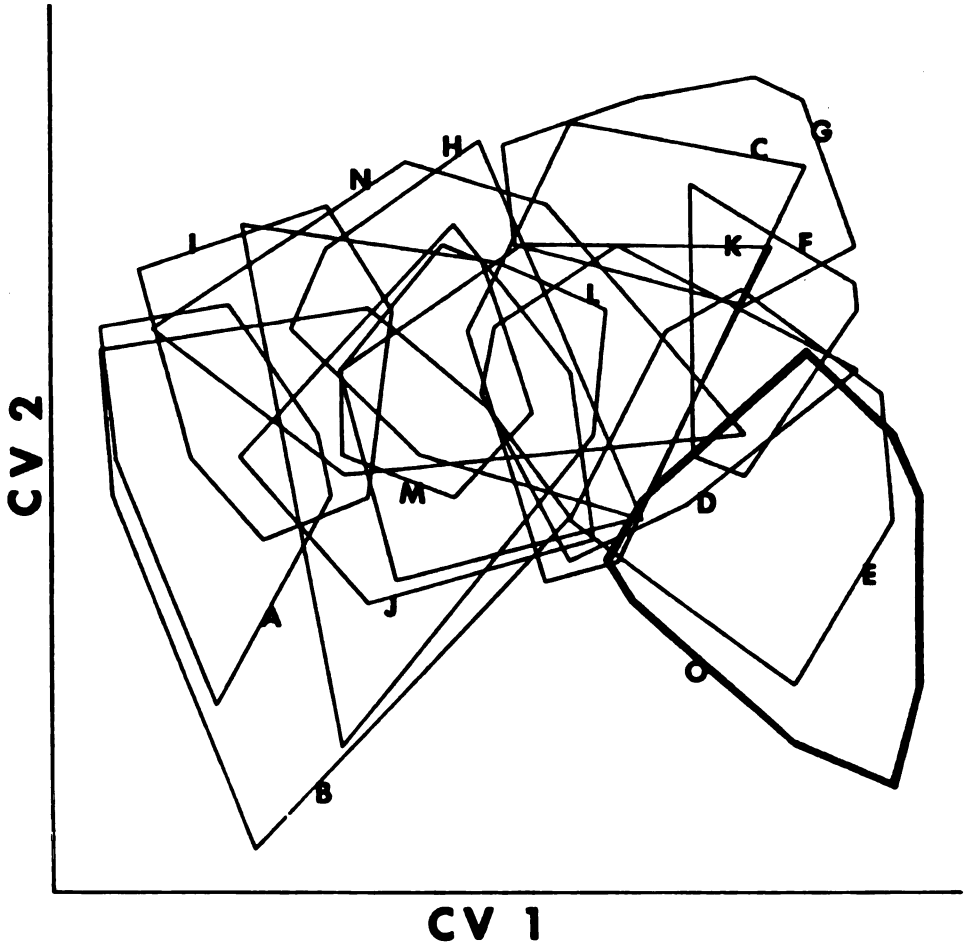

Figure 29. Discriminant analysis of Peromyscus leucopus subspecies and P. gossypinus. Traditional character set. A. castaneus, B. noveboracensis (MI), C. noveboracensis (OK), D. fusus (Martha's Vineyard), E. fusus (Vineyard Haven), F. aridulus (Cherry Co.), G. aridulus (Dawes Co.), H. leucopus (KY), I. leucopus (NC), J. incensus (Veracruz), K. incensus (Puebla), L. affinis, M. mesomelas, N. tornillo, O. gosssypinus.

22%, respectively). Separation between gossypinus and the other forms of leucopus involves at least 45% overlap (Table 31A). Canonical variate 2 is a contrast between zygomatic breadth with a positive sign and basal length with a negative sign (Table 32).

All Mahalanobis distances between gossypinus and leucopus taxa are significant (Table 33A). The mean D^2 value is 18.68. The largest D^2 value is between gossypinus and castaneus (35.79) followed by l. leucopus from North Carolina (34.37), while the smallest value is between gossypinus and fusus from Martha's Vineyard (7.49) followed by Vineyard Haven (8.96). D^2 values between gossypinus and remaining leucopus taxa vary from 10.97 to 23.48 (Table 33A).

The UPGMA cluster analysis based on the matrix of Mahalanobis distances between taxa is shown in Figure 30. The phenogram reveals that gossypinus is phenetically closer to fusus from Vineyard Haven than any other leucopus taxa.

Figure 31 shows a mininum spanning tree (Prim Network) based on Mahalanobis distances between taxa. P. gossypinus is connected to fusus only. However, it is connected to the Martha's Vineyard population and not to the Vinyeard Haven population as in the UPGMA cluster analysis.

Dorsal view. Eighteen individuals (72%) of gossypinus are correctly classified in the present data set. P. gossypinus individuals were misclassified with fusus from Martha's Vineyard (3; 12%) and Vineyard Haven (3; 12%),and aridulus from Dawes Co. (1; 4%).

Canonical variate 1 in this data set accounts for 12% less of the total variation (38%) than for conventional measures. However, CV2

Table 32. Canonical variate loadings of two different data sets for *Peromyscus leucopus* subspecies and *Peromyscus gossypinus* (DV=Distance variable).

Traditional character set			Truss character set					
			Dorsal view			Ventral view		
Character	CVI	CVII	Character	CVI	CVII	Character	CVI	CVII
Occipito-nasal length	0.05	-0.63	DV 1	-0.41	0.14	DV 26	-0.17	0.19
Nasal length	-0.19	0.18	DV 3	1.02	-0.24	DV 28	0.30	0.30
Rostral length	0.49	-0.22	DV 4	0.06	0.30	DV 29	0.004	-0.52
Rostral breadth	0.26	-0.29	DV 5	-0.83	0.74	DV 30	0.28	0.52
Interorbital constriction	0.14	-0.59	DV 8	0.22	-0.47	DV 33	0.15	-0.003
Zygomatic breadth	0.23	0.92	DV 9	-0.09	0.13	DV 34	0.23	-0.78
Basal length	-0.72	-0.92	DV 10	0.54	0.04	DV 35	0.17	0.25
Palatal length	0.27	0.07	DV 13	0.46	-0.21	DV 38	0.53	-0.49
Diastema length	0.42	0.52	DV 14	-0.19	-0.44	DV 39	0.11	-0.12
Tooth row length	0.62	0.38	DV 15	0.16	0.10	DV 40	0.09	1.04
Mastoid breadth	-0.22	0.49	DV 18	0.50	-0.65	DV 43	-0.38	0.33
Cranial depth	0.17	0.12	DV 19	-0.19	0.14	DV 44	0.14	0.37
			DV 20	-0.37	1.14	DV 45	0.009	-1.06
			DV 23	0.57	-0.50	DV 48	0.05	-0.35

Table 33. Mahalanobis D^2 statistic between *Peromyscus leucopus* subspecies and *Peromyscus gossypinus*. A. Traditional character set. B. Dorsal truss network. C. Ventral truss network.

		fusus(MV)	*fusus*(VH)	*noveb*(MI)	*noveb*(OK)	*aridulus*(CH)	*aridulus*(DA)	*leucopus*(KY)	*leucopus*(NC)	*tornillo*	*incensus*(VE)	*incensus*(PU)	*mesomelas*	*affinis*	*castaneus*
A.	*gossypinus*	7.49	8.96	23.48	12.88	10.97	17.16	19.86	34.37	17.30	21.35	13.90	19.33	18.62	35.79
B.	*gossypinus*	3.59	4.67	17.70	8.05	8.97	4.90	11.52	21.93	10.63	17.92	14.69	21.77	16.84	18.79
C.	*gossypinus*	7.95	10.25	30.72	14.92	9.30	11.39	22.99	36.93	19.97	27.42	13.94	21.59	20.81	48.37

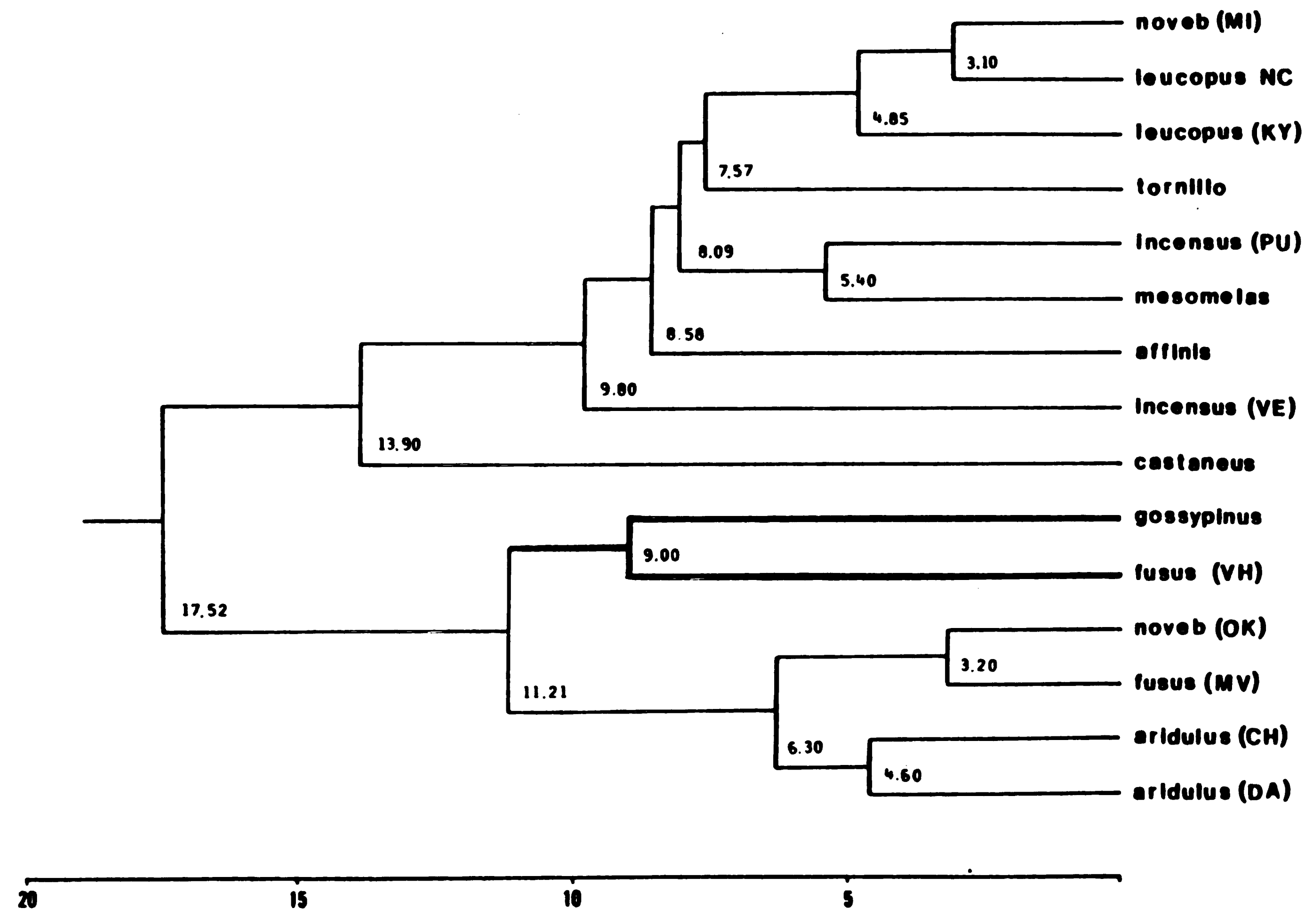

Figure 30. Phenetic relationships between *Peromyscus leucopus* taxa and *P. gossypinus* based on the Mahalanobis D^2 statistic. Traditional character set. Clustering is by the unweighted pair group method using arithmetic means.

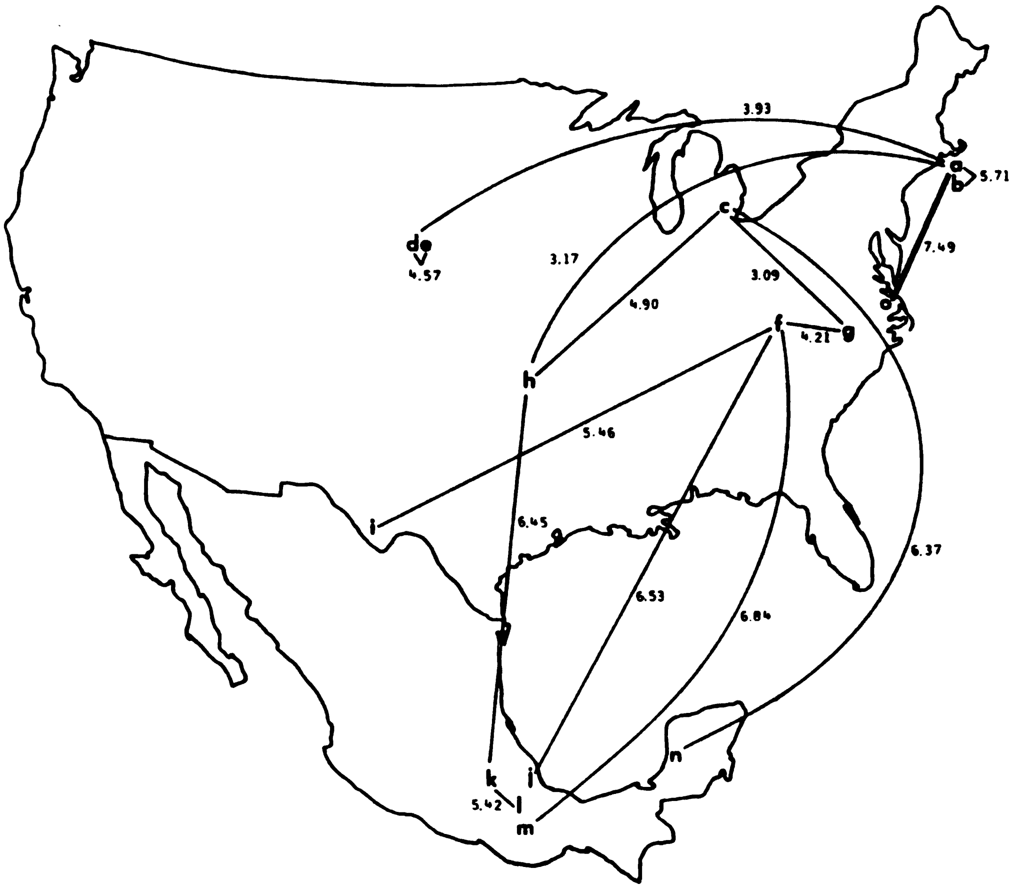

Figure 31. Minimum spanning tree (Prim Network) for samples of Peromyscus leucopus subspecies and P. gossypinus based on the Mahalanobis distance. Traditional character set. A. fusus (Martha's Vineyard), B. fusus (Vineyard Haven), C. noveboracensis (Michigan), D. aridulus (Cherry Co.), E. aridulus (Dawes Co.), F. leucopus (Kentucky), G. leucopus (North Carolina), H. noveboracensis (Oklahoma), I. tornillo, J. incensus (Veracruz), K. incensus (Puebla), L. mesomelas, M. affinis, N. castaneus, O. gossypinus.

accounts for about twice as much the variation (30%) compared to conventional measures. The third canonical variate accounts for the same amount of variation (10%).

As in the previous data set, *gossypinus* is discriminated along CV1 from Veracruz *incensus*, *l. leucopus* from North Carolina, and *mesomelas* without ovelap (Figure 32). It is also discriminated without overlap from Puebla *incensus*, *affinis* and *l. leucopus* from Kentucky (Figure 32; Table 31B), while in the previous data set discrimination between *gossypinus* and these populations involved limited amounts of overlap (Figure 32; Table 31B). Separation between *gossypinus* and *castaneus* and Michigan *noveboracensis* in the dorsal view involves 5% and 18% overlap, respectively, while they are discriminated without overlap in the previous data set. Discrimination between *gossypinus* and the other *leucopus* taxa generally involves similar amounts of overlap relative to traditional measures (Table 31A, B).

Distance variables contributing to CV1 are restricted to nasal bones (Table 32). This result differs from the previous data set where basal length and tooth row length contribute important coefficients to CV1. Canonical variate 1 is a contrast between nasal length (distance variable 3; first truss cell) with a positive sign, and diagonal length of nasals (distance variable 5; first truss cell) with a negative sign. *P. gossypinus* is thus characterized by individuals with relatively longer and narrower nasals compared to the other *leucopus* taxa (Figure 32).

Overlap along CV2 is more extensive, in most cases, in the present data set and varies from 21% to 95% (Table 31B; Figure 32). *P. l. aridulus* from Dawes Co. and *gossypinus* overlap extensively (95%), while

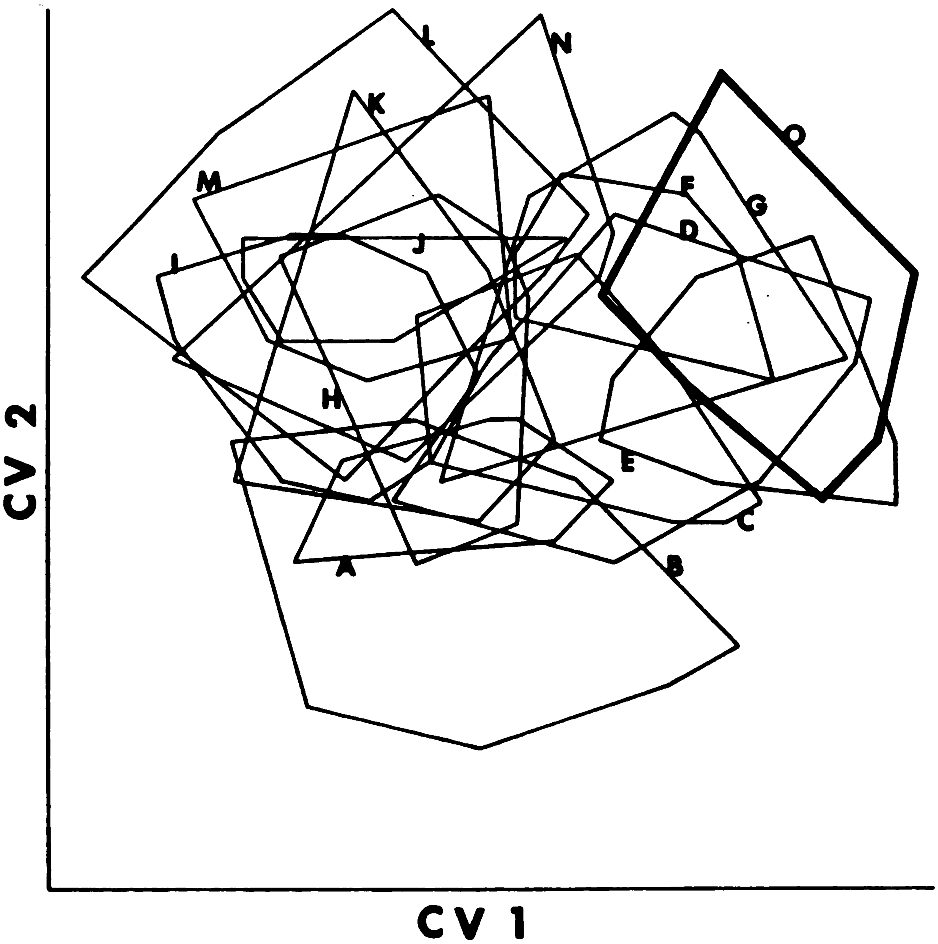

Figure 32. Discriminant analysis of Peromyscus leucopus subspecies and P. gossypinus. Truss character set. Dorsal truss network. A. castaneus, B. noveboracensis (MI), C. noveboracensis (OK), D. fusus (Martha's Vineyard), E. fusus (Vineyard Haven), F. aridulus (Cherry Co.), G. aridulus (Dawes Co.), H. leucopus (KY), I. leucopus (NC), J. incensus (Veracruz), K. incensus (Puebla), L. affinis, M. mesomelas, N. tornillo, O. gosssypinus.

they were discriminated without overlap in the traditional data set. *P. l. castaneus* and Michigan *noveboracensis* are discriminated from *gossypinus* with moderate amounts of overlap (32% and 21%, respectively). In the remaining populations discrimination involves at least 71% overlap (Table 31B; Figure 32). Canonical variate 2 appears to be a constrast between diagonal length of parietal (DV 20; fourth truss cell) with a positive sign and parietal length (DV 18; fourth truss cell) with a negative sign.

Mahalanobis distances between *gossypinus* and *leucopus* forms are significant in all cases (Table 33B). The mean D^2 value between *gossypinus* and *leucopus* taxa is smaller in this data set (13.00). D^2 values in this data set are smaller than for traditional measures, except for D^2 values between *gossypinus* and Puebla *incensus* (14.69) and *mesomelas* (21.77) (Table 33B). The smallest D^2 value is between *gossypinus* and *fusus* from Martha's Vineyard (3.59), while the distance between these two taxa is about twice as large in the previous data set. D^2 between *gossypinus* and the remaining *leucopus* taxa vary from 4.67 to 21.93 (Table 33B).

The UPGMA cluster analysis based on D^2 values between taxa is shown in Figure 33. *P. gossypinus* is phenetically closer to *fusus* as shown in the previous data set. It joins a convex subcluster formed by *fusus* populations.

Figure 34 shows a minimum spanning tree (Prim Networks) connecting geographic localities based on the Mahalanobis distances between taxa. *gossypinus* is connected only to *fusus* from Martha's Vineyard as in the UPGMA phenogram for traditional measures.

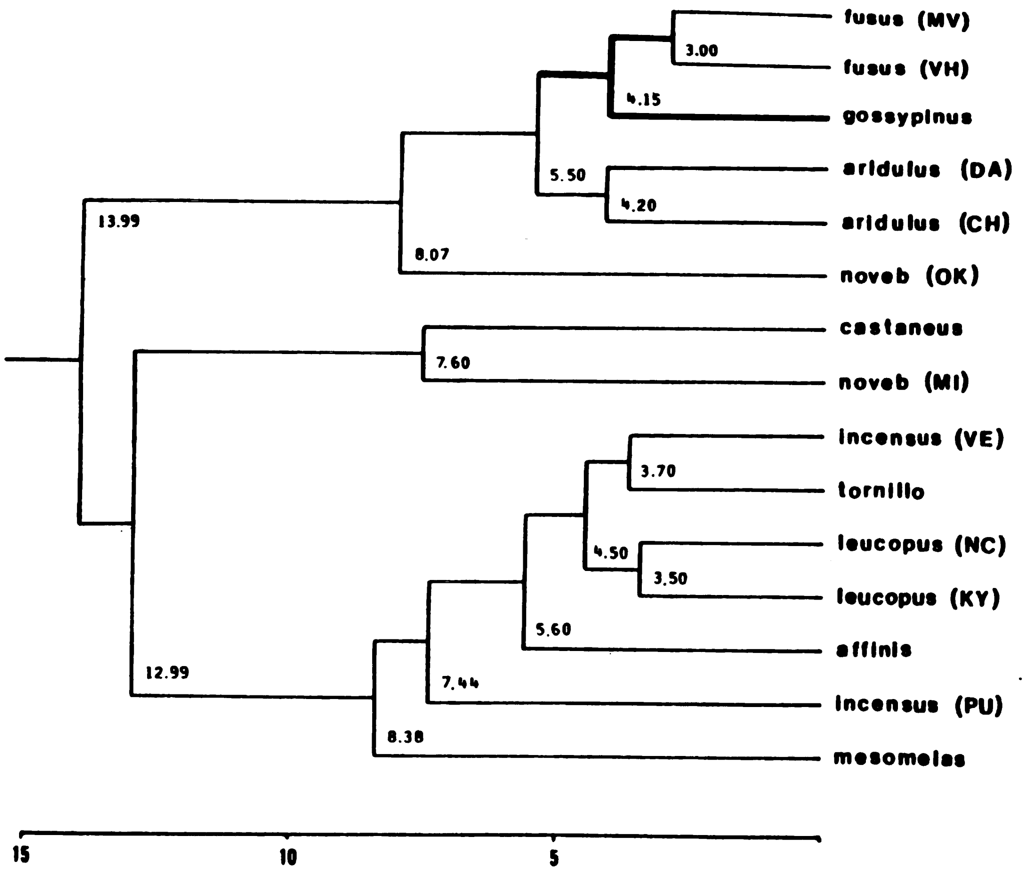

Figure 33. Phenetic relationships between *Peromyscus leucopus* taxa and *P. gossypinus* based on the Mahalanobis D^2 statistic. Truss character set. Dorsal truss network. Clustering is by the unweighted pair group method using arithmetic means.

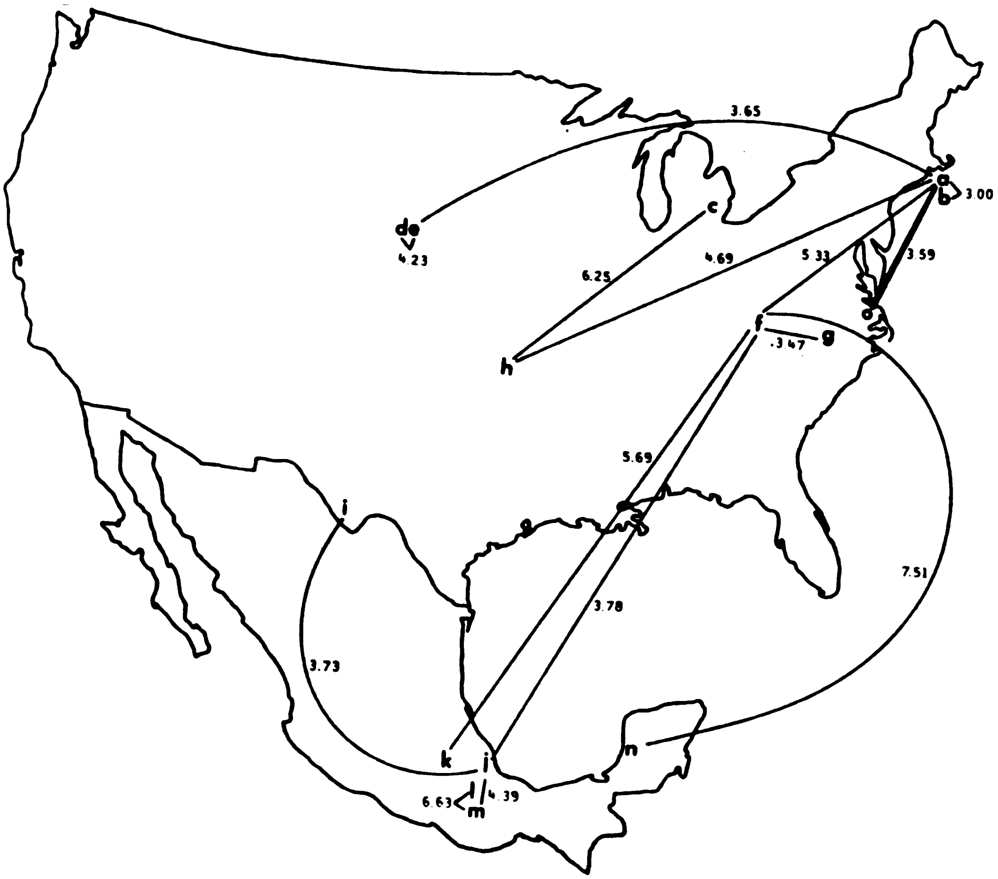

Figure 34. Minimum spanning tree (Prim Network) for samples of Peromyscus leucopus taxa and P. gossypinus based on the Mahalanobis distance. Truss character set. Dorsal truss network. A. fusus (Martha's Vineyard), B. fusus (Vineyard Haven), C. noveboracensis (Michigan), D. aridulus (Cherry Co.), E. aridulus (Dawes Co.), F. leucopus (Kentucky), G. leucopus (North Carolina), H. noveboracensis (Oklahoma), I. tornillo, J. incensus (Veracruz), K. incensus (Puebla), L. mesomelas, M. affinis, N. castaneus, O. gossypinus.

Ventral view. Classification results for this data set are intermediate between traditional and dorsal measurements. Ninety-six percent of *gossypinus* individuals are correctly classified, while the remaining individuals are misclassified with *aridulus* from Cherry Co.

The partitioning of the variance here is similar to the traditional data set. The first canonical variate accounts for 47% of the total variation, the second 18%, and the third 11% of the variation. The overlap along CV1 varies from 0% to 81% (Table 31C). The pattern of discrimination is similar to the previous analyses. *P. gossypinus* is separated from *castaneus*, Michigan *noveboracensis*, *l. leucopus* populations, Veracruz *incensus*, *affinis*, and *mesomelas* without overlap (Figure 35). Puebla *incensus* and *tornillo* are separated from *gossypinus* with relatively low levels of overlap (14% and 8%, respectively). Discrimination in the remaining cases involves at least 41% overlap (Table 31C). Canonical variate 1 in this data set is similar to traditional measures. Tooth row length (DV 38; third truss cell) has a positive coefficient and post-palatal length (distance variable 43; fourth truss cell) has a negative coefficient (Table 32). This result is similar to CV1 for the traditional measures, where tooth row and basal length contribute important coefficients to CV1.

Levels of overlap along CV2 are generally high (Table 31C). There is limited discrimination between *gossypinus* and *castaneus* and *mesomelas*. Canonical variate 2 is apparently a constrast between diagonal palatal length (DV 40; third truss cell) with a positive sign and diagonal post-palatal length (DV 45; fourth truss cell) with a negative sign (Table 32).

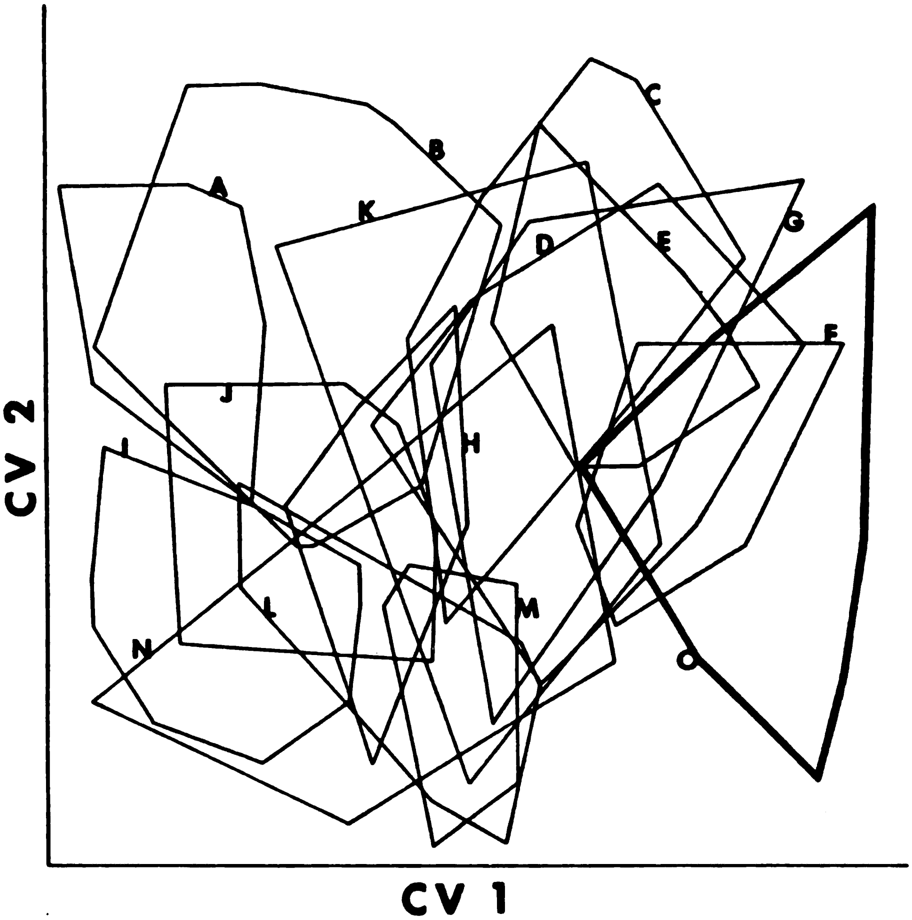

Figure 35. Discriminant analysis of Peromyscus leucopus subspecies and P. gossypinus. Truss character set. Ventral truss network. A. castaneus, B. noveboracensis (MI), C. noveboracensis (OK), D. fusus (Martha's Vineyard), E. fusus (Vineyard Haven), F. aridulus (Cherry Co.), G. aridulus (Dawes Co.), H. leucopus (KY), I. leucopus (NC), J. incensus (Veracruz), K. incensus (Puebla), L. affinis, M. mesomelas, N. tornillo, O. gosssypinus.

The mean D^2 value between *gossypinus* and *leucopus* taxa in the present data set is 21.18. It is larger than the mean D^2 value for traditional measures, and dorsal truss network. All D^2 values for ventral truss measures are larger than for dorsal measures, except for D^2 values between *gossypinus*, Puebla *incensus* (13.94), and *mesomelas* (21.59) (Table 33). D^2 values in the present data set are also larger than D^2 values for traditional measures, except for the distance between *gossypinus* and the Cherry Co. (9.30) and Dawes Co. (11.39) populations of *aridulus* (Table 33). The larger D^2 value is between *gossypinus* and *castaneus* (48.37), while the smallest is between *gossypinus* and *fusus* from Martha's Vineyard (7.95) (Table 34). This latter value is similar to that for traditional measures. D^2 values between *gossypinus* and remaining taxa vary from 10.25 to 36.93 (Table 33C).

The UPGMA phenogram based on Mahalanobis distances between taxa is shown in Figure 36. *P. gossypinus* is phenetically closer to *fusus* from Vineyard Haven as in the traditional data set. It joins a major cluster composed of *fusus* and *aridulus* populations, *noveboracensis* from Oklahoma, and Puebla *incensus*.

The minimum spanning tree (Prim network) shows that *gossypinus* is connected to *fusus* from Martha's Vineyard and not to the Vineyard Haven population as in the UPGMA phenogram (Figure 37).

Summary. All *gossypinus* are correctly classified by the discriminant function of traditional measures only. Some *gossypinus* individuals are misclassified with *fusus* and *aridulus* in the dorsal view, and with *aridulus* in the ventral data set. *P. gossypinus* is

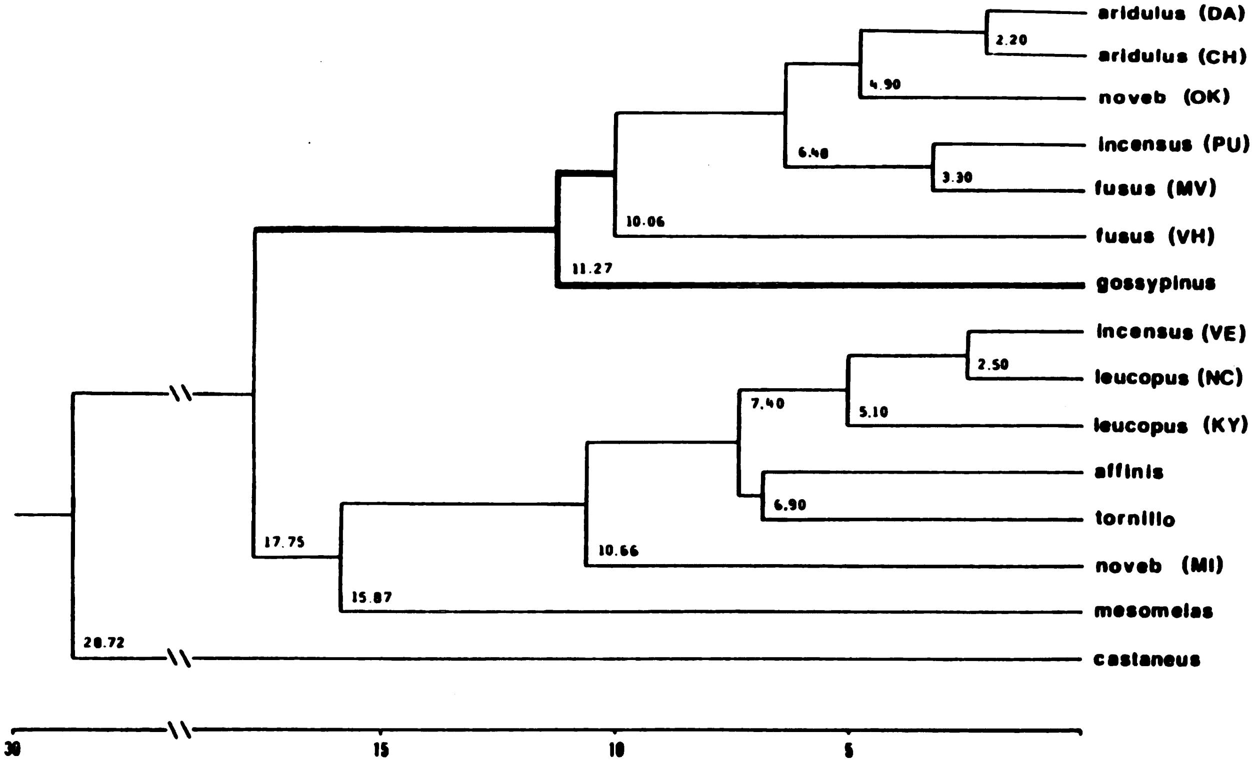

Figure 36. Phenetic relationships between Peromyscus leucopus subspecies and P. gossypinus based on the Mahalanobis D^2 statistic. Truss character set. Ventral truss network. Clustering is by the unweighted pair group method using arithmetic means.

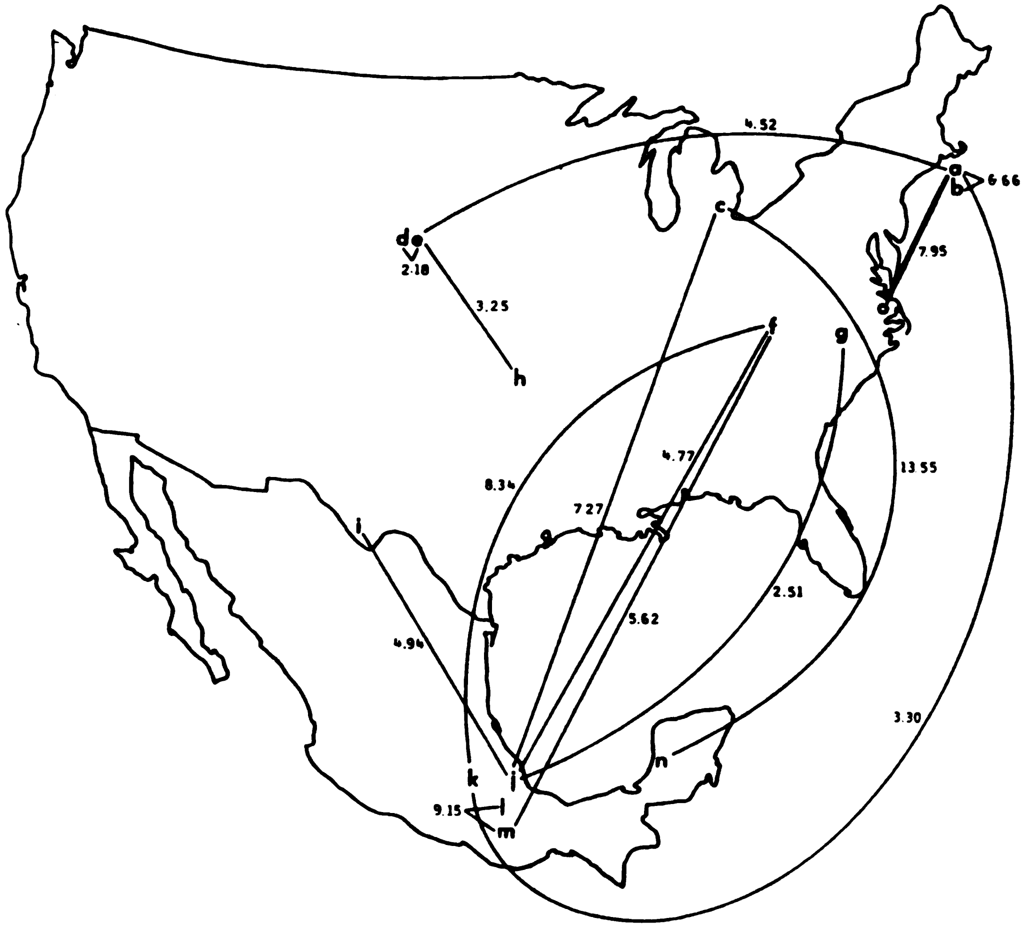

Figure 37. Minimum spanning tree (Prim Network) for samples of *Peromyscus leucopus* taxa and *P. gossypinus* based on the Mahalanobis distance. Truss character set. Ventral truss network. A. *fusus* (Martha's Vineyard), B. *fusus* (Vineyard Haven), C. *noveboracensis* (Michigan), D. *aridulus* (Cherry Co.), E. *aridulus* (Dawes Co.), F. *leucopus* (Kentucky), G. *leucopus* (North Carolina), H. *noveboracensis* (Oklahoma), I. *tornillo*, J. *incensus* (Veracruz), K. *incensus* (Puebla), L. *mesomelas*, M. *affinis*, N. *castaneus*, O. *gossypinus*.

discriminated along CV1 from several leucopus taxa without overlap in all three data sets. Overlap along CV2 is more extensive than along CV1 in the three data sets. Tooth row length and basal length contribute large coefficients to canonical variates in the traditional and ventral views, while measurements of nasal bones contribute large coefficients to dorsal truss measures. Mean D^2 values between gossypinus and leucopus taxa are large for ventral measures and small for dorsal measures, while D^2 values for traditional measures are intermediate in magnitude. P. gossypinus is phenetically closer to fusus populations and it is also connected to fusus in the Prim networks.

2.3.2 Sheared principal components

The results of the shear procedures were similar to that obtained in previous analyses. Coefficients of vector correlations between sheared components (H2 and H3) and original components (PC2 and PC3) were very large (average of .98 and .99, respectively), indicating that only very small size effects were removed from the original components. The results are thus based upon standard principal components analysis.

The first principal component for the pooled samples of Peromyscus leucopus taxa and P. gossypinus can be interpreted as a measure of general size in all five data sets. In all cases principal component coefficients are positive and distance variables have positive significant ($P<.01$) correlations with PC1 (Table 35-37).

Allometric coefficients computed from the first principal component for P. gossypinus and P. leucopus subspecies are generally similar to those for *leucopus* populations and *leucopus* subspecies (Table 10; Figure 38). Anterior skull measurements are positively allometric with respect to general size, while posterior measures have negative allometries.

There is no concordance between allometric coefficients and loadings from PC2 and PC3 in all five data sets: traditional (Kendall's $\tau = -.64$; $P<.01$ and $\tau = .03$; ns, respectively); dorsal view ($\tau = -.01$; ns and $\tau = -0.38$; ns); ventral view ($\tau = -.19$; ns and $\tau = -.34$; ns); lateral view ($\tau = -.23$; ns and $\tau = -.01$; ns); three-dimensional view ($\tau = -.58$; $P<.01$ and $\tau = .29$; ns).

Traditional measurements

The first principal component for the pooled samples of *leucopus* taxa and *gossypinus* accounts for 78% of the variation, the second 5%, and the third only 4%. The amount of overlap along PC1 between *gossypinus* and *leucopus* taxa varies from 0% to 82%. *P. gossypinus* is separated on the basis of size from Michigan *noveboracensis*, *l. leucopus*, *affinis*, and *castaneus* without overlap (Table 34A; Figure 39). *P. l. gossypinus* is also separated from *mesomelas*, *incensus*, and Oklahoma *noveboracensis* with 5%, 15%, and 7% overlap, respectively (Table 34A). *P. gossypinus* individuals have larger skulls compared to most *leucopus* taxa (Figure 39).

Overlap along PC2 is more extensive and varies from 8% to 94%. *P. gossypinus* is separated from *castaneus* with only 8% overlap, and from *mesomelas*, *l. leucopus*, and Michigan *noveboracensis* with relatively low

Table 34. Percent overlap between *Peromyscus leucopus* subspecies and *Peromyscus gossypinus* along principal component 1 (first number), principal component 2 (second number), and principal component 3 (third number). A. Traditional character set. B. Dorsal truss network. C. Ventral truss network. D. Lateral truss network. E. Three dimensional view.

	fusus	*noveb*(MI)	*noveb*(OK)	*aridulus*	*leucopus*	*tornillo*	*incensus*	*mesomelas*	*affinis*	*castaneus*
A. *gossypinus*	82/89/68	0/27/86	7/93/57	60/94/89	0/27/76	45/71/89	15/64/98	5/21/79	0/75/86	0/8/87
B. *gossypinus*	77/96/96	0/82/90	15/88/67	81/85/94	0/95/98	59/78/82	12/85/92	49/78/79	19/79/89	0/92/85
C. *gossypinus*	82/65/97	0/7/57	49/49/95	77/57/94	0/0/74	16/68/92	17/25/85	22/8/89	12/10/90	0/0/38
D. *gossypinus*	76/93/70	0/80/76	32/90/63	71/79/73	0/89/43	62/70/97	25/88/68	76/81/70	0/67/63	0/92/74
E. *gossypinus*	72/96/75	0/97/94	56/73/95	75/79/98	0/93/95	62/97/84	0/88/93	86/68/95	88/98/91	0/58/97

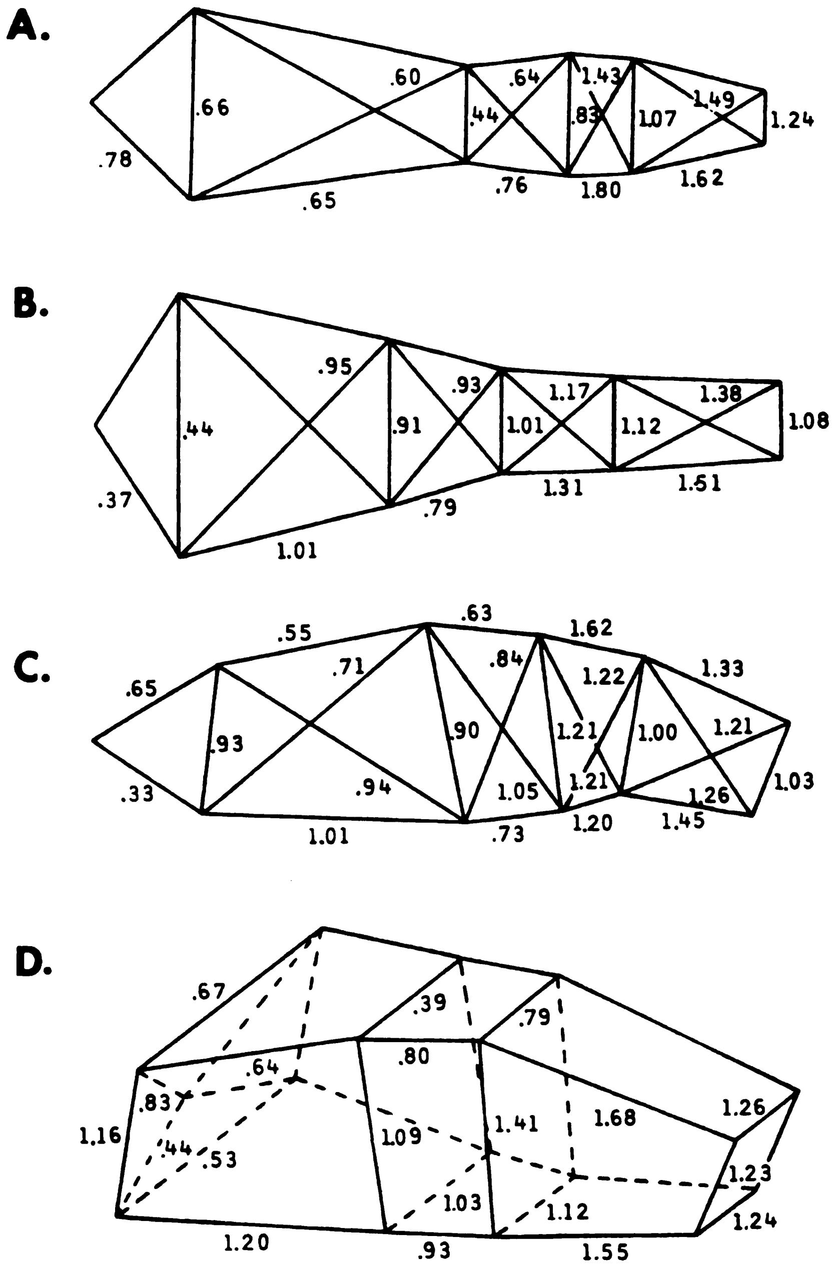

Figure 38. Multivariate allometric coefficients for pooled samples of Peromyscus leucopus subspecies and Peromyscus gossypinus depicted on the truss networks. A. Dorsal truss network. B. Vental truss network. C. Lateral truss network. D. Three dimensional view.

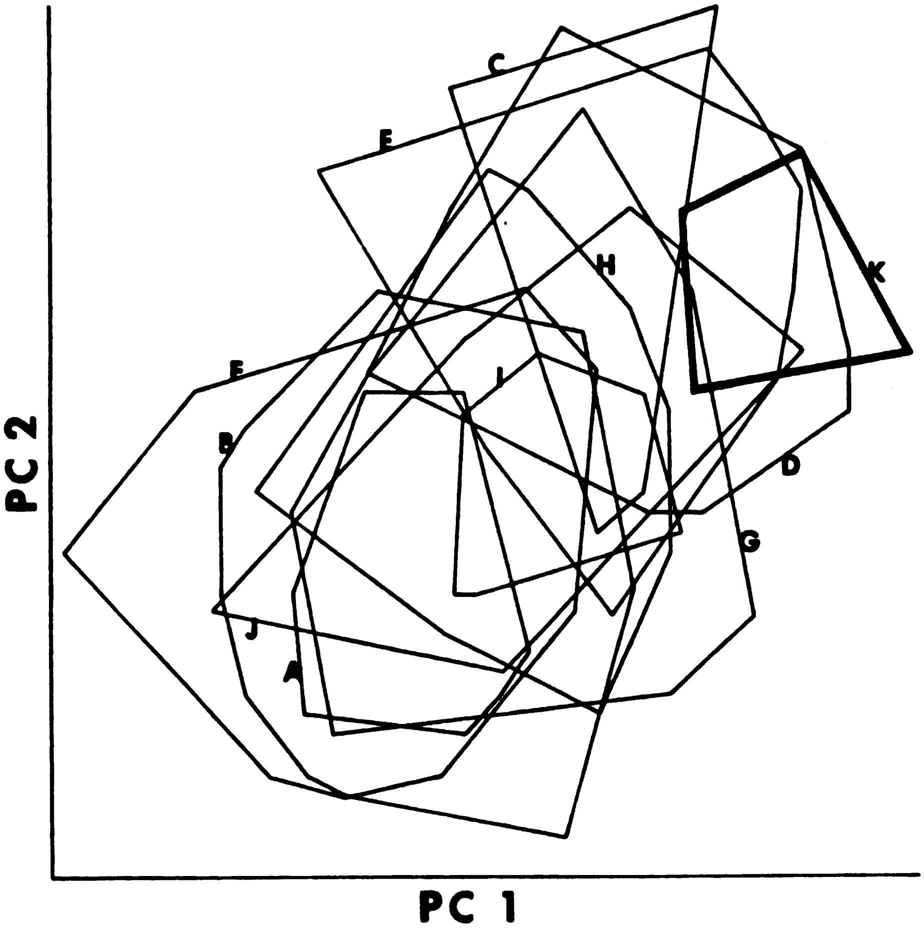

Figure 39. Scatter between *Peromyscus leucopus* taxa and *P. gossypinus*. Traditional character set. A. *castaneus*, B. *noveboracensis* (MI), C. *noveboracensis* (OK), D. *fusus*, E. *aridulus*, F. *leucopus*, G. *incensus*, H. *affinis*, I. *mesomelas*, J. *tornillo*, k. *gossypinus*.

amounts of overlap (21%, 27%, and 27% overlap, respectively). (Table 34A). Nasal length, rostral length, and diastema length have negative coefficients, while tooth row length, interorbital constriction and cranial depth have positive coefficients (Table 35). The second principal component apparently separates gossypinus by its larger tooth row, and also by a constrast between rostral length and cranial depth and interorbital constriction (Table 34A; Figure 39).

Overlap between gossypinus and leucopus taxa along PC3 is very extensive (Table 34A). No interpretation of this component was attempted.

Direction and magnitude of size and shape differences varies between gossypinus and leucopus forms. This result is similar to that found for populations within leucopus and among leucopus subspecies. The main difference between gossypinus and Oklahoma noveboracensis, incensus, and affinis is size, while differences between gossypinus and Michigan noveboracensis, leucopus, mesomelas, and castaneus involves both size and shape.

Dorsal view. The first principal component accounts for about 30% less of the variation in the present data set (50%) relative to the previous analysis. The second and third components account for about three times more of the variation here (17% and 12%, respectively). The range of overlap along PC1 between gossypinus and leucopus taxa is similar here (0%-81%) (Table 34B). P. gossypinus is separated on the basis of size from Michigan noveboracensis, leucopus, and castaneus without overlap as in the previous data set. Separation from affinis involves 19% here (Table 34B; Figure 40A).

Table 35. Principal component loadings for *Peromyscus leucopus* subspecies and *Peromyscus gossypinus* (DV=Distance variable). Traditional character set. All correlation coefficients (r) with the first principal component are significant (P<.01).

Traditional character set

Character	PCI	r	PCII	PCIII
Occipito-nasal lenght	0.28	0.98	-0.04	-0.05
Nasal length	0.37	0.91	-0.25	-0.28
Rostral length	0.40	0.93	-0.31	-0.41
Rostral breadth	0.33	0.85	0.18	0.74
Interorbital constriction	0.17	0.67	0.26	-0.12
Zygomatic breadth	0.25	0.90	0.12	0.13
Basal length	0.31	0.97	-0.12	0.03
Palatal length	0.32	0.94	0.005	0.05
Diastema length	0.36	0.93	-0.26	0.20
Tooth row length	0.22	0.69	0.76	-0.36
Mastoid breadth	0.17	0.81	0.13	0.03
Cranial depth	0.14	0.61	0.23	0.03

Overlap along PC2 and PC3 is very extensive in this data set (Table 34B) and no further interpretation of these components is attempted. Separation of *P. gossypinus* from other *leucopus* taxa in this data set is based in size only, as opposed to traditional measures where both size and shape differences were involved.

Ventral view. The amount of variation explained by the three first components here is intermediate between that obtained in the two previous data sets. The first component accounts for 62% of the variation, the second 10%, and the third 8%. The range of overlap along PC1 is similar to previous data sets (0%-82%). *P. gossypinus* is separated on the basis of size from Michigan *noveboracensis*, *leucopus*, and *castaneus* without overlap, while separation from *affinis* involves some overlap (12%) as in the dorsal view (Table 34C; Figure 40B). Separation from *tornillo*, *incensus*, and *mesomelas* involves moderate amounts of overlap (Table 34C).

The only cases of separation along PC2 without overlap are found in this data set. *P. gossypinus* is totally separated from *leucopus* and *castaneus*, and with little overlap from Michigan *noveboracensis*, *affinis*, and *mesomelas* (Table 34C; Figure 40B). Posterior diastema length (DV 33; second truss cell) has a large negative coefficient and tooth row length (DV 38; third truss cell) has a positive coefficient (Table 36). *P. gossypinus* individuals are thus characterized by larger tooth rows and posterior diastema length relative to *leucopus* taxa (Table 36; Figure 40B). This result is similar to PC2 for traditional measures since tooth row length also contributes a large coefficient to PC2. Diastema length, which is also important for traditional

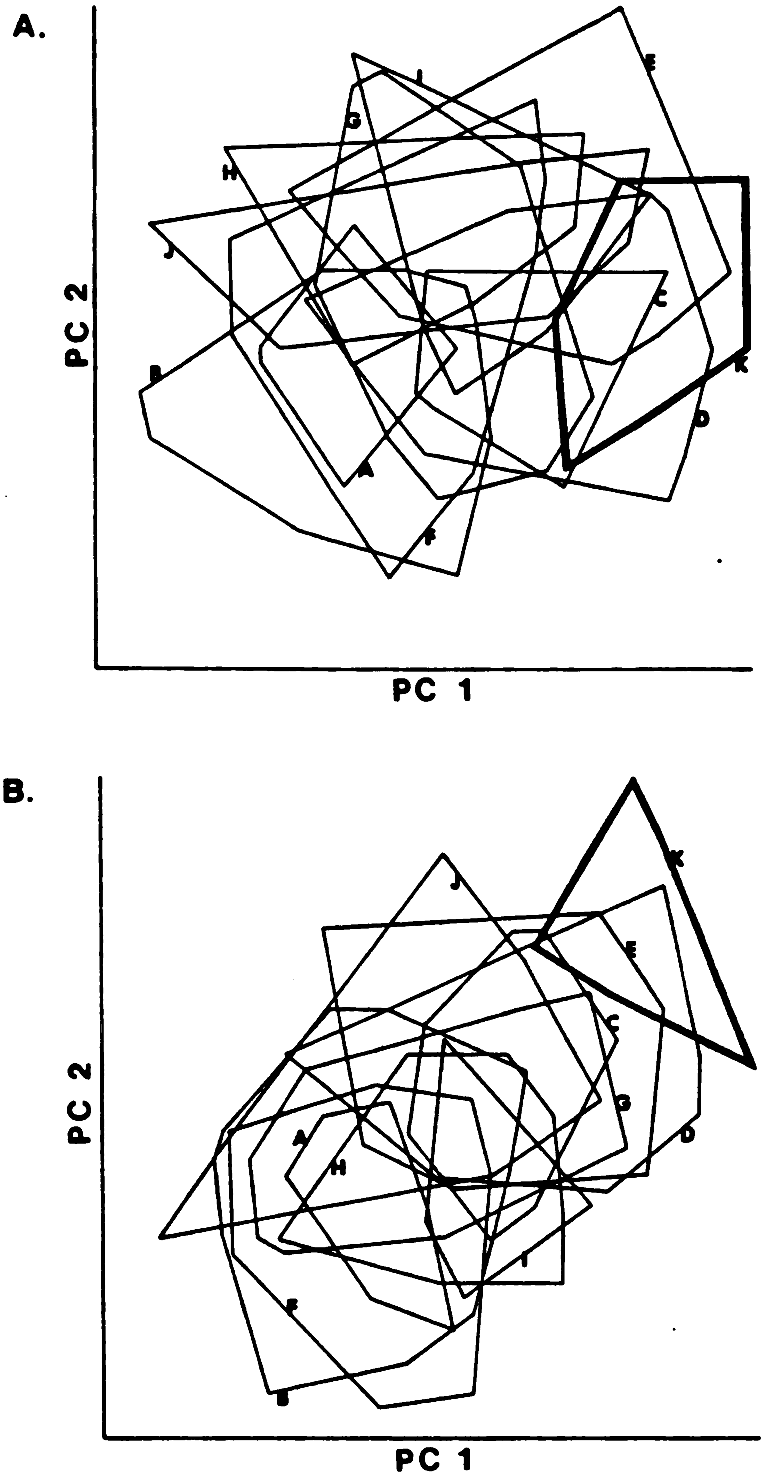

Figure 40. Scatter between *Peromyscus leucopus* taxa and *P. gossypinus*. Truss character set. A. Dorsal truss network. B. Ventral truss network. A. *castaneus*, B. *noveboracensis* (MI), C. *noveboracensis* (OK), D. *fusus*, E. *aridulus*, F. *leucopus*, G. *incensus*, H. *affinis*, I. *mesomelas*, J. *tornillo*, k. *gossypinus*.

measures, is represented here by posterior diastema length (DV 33).

P. gossypinus is thus separated from *leucopus* taxa in both shape and size. In many cases levels of overlap are smaller than both dorsal and traditionall measures. For example, overlap levels along PC2 between *gossypinus* and Michigan *noveboracensis*, *leucopus*, *incensus*, *affinis*, and *castaneus* are much lower here (Table 34C). There is also limited shape separation along PC3 between *gossypinus* and Michigan *noveboracensis* and *castaneus* (Table 34C). The third principal component appears to be a constrast between rostral measures with negative coefficients (DV 26, 28, 30; first truss cell) and posterior diastema (DV 33 and 34; second truss cell) and dental measures (DV 38 and 39; third truss cell) with negative signs (Table 36).

Lateral view. The first three components account for amounts of variation similar to ventral measures. The first principal component accounts for 64% of the variation, the second 8%, and the third 6%. The range of overlap along PC1 is similar to that in previous analyses. *gossypinus* varies in the magnitude of size and shape differences from *leucopus* taxa. *P. gossypinus* is separated on the basis of size from Michigan *noveboracensis*, *leucopus*, and *castaneus* with no overlap as in previous analyses (Table 34D; Figure 41A). *P. gossypinus* is also separated from *affinis* with no overlap.

Overlap levels between *gossypinus* and *leucopus* taxa are generally high. In most cases percentage overlap along PC2 is larger than along PC3. Again, despite the generally high levels of overlap there seems to be variation in the amount of shape variation. For example, *gossypinus* overlaps 97% with *tornillo*, while it overlaps 43% with *leucopus*.

Table 36. Principal component loadings for *Peromyscus leucopus* subspecies and *Peromyscus gossypinus* (DV=Distance variable). Dorsal and ventral truss networks. All correlation coefficients (r) with the first principal component are significant (P<.01).

Dorsal view					Ventral view				
Character	PCI	r	PCII	PCIII	Character	PCI	r	PCII	PCIII
DV 1	0.31	0.73	0.06	-0.07	DV 26	0.27	0.73	-0.17	-0.35
DV 3	0.40	0.83	0.26	-0.20	DV 28	0.39	0.87	0.15	-0.46
DV 4	0.26	0.60	0.33	-0.38	DV 29	0.29	0.80	0.14	0.09
DV 5	0.37	0.85	0.27	-0.21	DV 30	0.35	0.88	0.09	-0.43
DV 8	0.44	0.70	-0.74	0.10	DV 33	0.34	0.69	-0.80	0.29
DV 9	0.20	0.68	0.09	0.02	DV 34	0.26	0.80	0.17	0.33
DV 10	0.35	0.87	-0.26	-0.04	DV 35	0.30	0.93	-0.07	0.17
DV 13	0.19	0.46	0.22	0.61	DV 38	0.20	0.63	0.40	0.27
DV 14	0.11	0.36	0.18	0.45	DV 39	0.23	0.78	0.13	0.24
DV 15	0.16	0.56	0.19	0.39	DV 40	0.24	0.83	0.25	0.20
DV 18	0.16	0.59	-0.04	-0.11	DV 43	0.26	0.85	-0.06	-0.08
DV 19	0.16	0.66	0.05	0.08	DV 44	0.11	0.52	0.07	0.16
DV 20	0.15	0.73	0.05	0.07	DV 45	0.24	0.87	-0.04	-0.03
DV 23	0.19	0.71	-0.02	0.07	DV 48	0.10	0.44	0.06	0.22

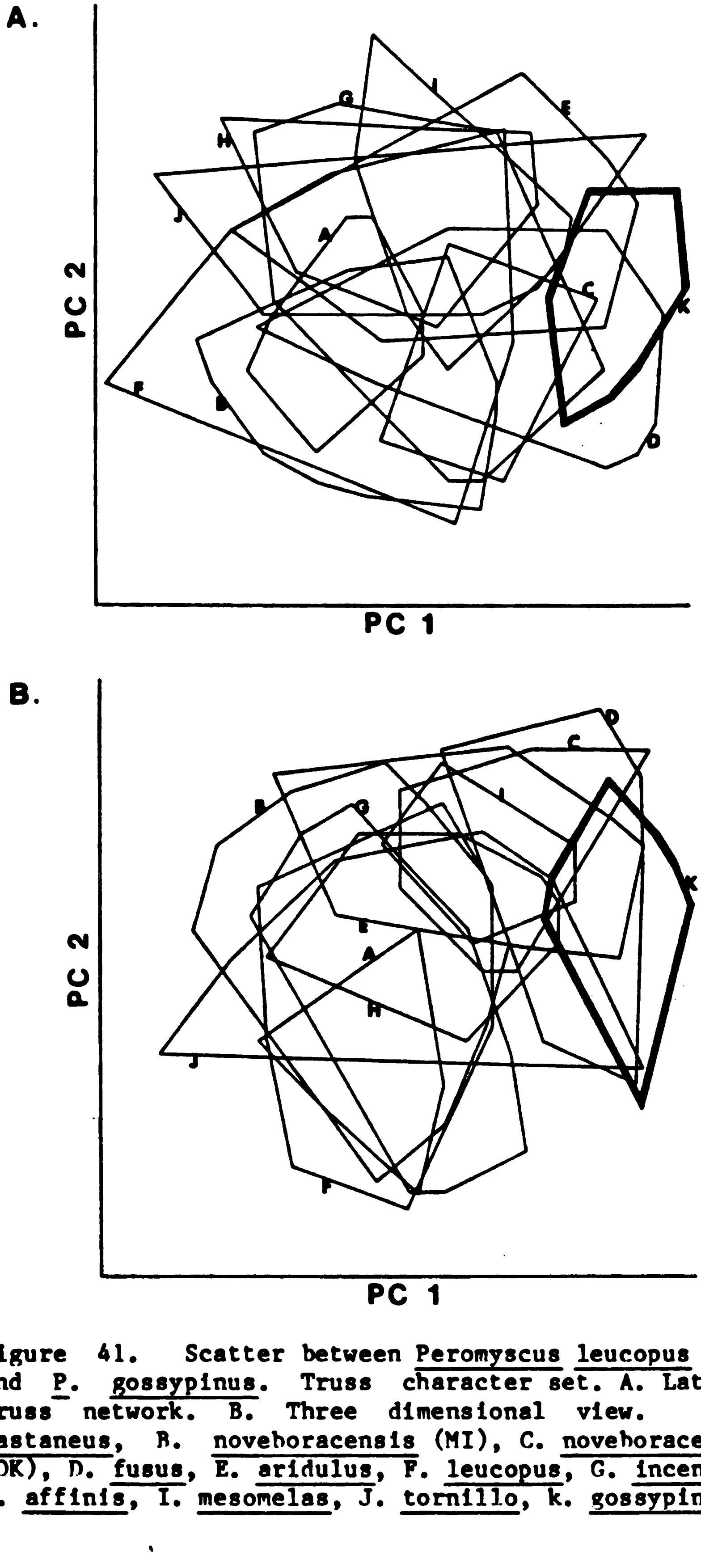

Figure 41. Scatter between _Peromyscus leucopus_ taxa and _P. gossypinus_. Truss character set. A. Lateral truss network. B. Three dimensional view. A. _castaneus_, B. _noveboracensis_ (MI), C. _noveboracensis_ (OK), D. _fusus_, E. _aridulus_, F. _leucopus_, G. _incensus_, H. _affinis_, I. _mesomelas_, J. _tornillo_, k. _gossypinus_.

Principal component 2 seems to be a contrast between nasal length (DV 3; first truss cell) with a positive coefficient and anterior length of frontal (DV 8; second truss cell) with a negative sign (Table 37). Levels of overlap along PC3 are generally smaller than along PC2, but are still high.

Three-dimensional view. The first principal component accounts for 56% of the variation, the second 8%, and the third 7%. These values are similar to ventral and lateral measures. The amount of overlap along PC1 is similar to previous data sets (0%-88%) (Table 34E). Again, gossypinus and leucopus subspecies differ in the magnitude of size differences. P. gossypinus is separated on the basis of size from Michigan noveboracensis, leucopus, and castaneus as in other data sets (Table 34E; Figure 41B). P. gossypinus is also separated from incensus with no overlap, while in the other data sets separation between these two taxa involves variable amounts of overlap. The opposite was observed between P. gossypinus and affinis, where the overlap was very extensive, while in the other data sets separation was complete or involved small amounts of overlap.

Overlap along PC2 is generally extensive, and shape differences are limited to P. gossypinus and P. castaneus. The second principal component appears to be a contrast between posterior length of frontal (DV 13; third truss cell) and posterior width of frontal (DV 14; third truss cell) with positive signs and anterior incisor width (DV 26; first truss cell) with a negative sign (Table 37). Overlap along PC3 is very extensive and involves at least 75%.

Differences between P. gossypinus and P. leucopus taxa are mainly

Table 37. Principal component loadings for *Peromyscus leucopus* subspecies and *Peromyscus gossypinus* (DV=Distance variable). *Lateral* truss network *and three dimensional* view. All correlation coefficients (r) with the first principal component are significant (P<.01).

Lateral view					3-D				
Character	PCI	r	PCII	PCIII	Character	PCI	r	PCII	PCIII
DV 3	0.26	0.81	0.37	0.13	DV 1	0.27	0.73	-0.08	0.14
DV 8	0.32	0.76	-0.77	-0.05	DV 9	0.17	0.65	0.11	-0.15
DV 13	0.16	0.45	0.28	-0.05	DV 13	0.17	0.47	0.67	0.39
DV 18	0.11	0.58	0.01	0.06	DV 14	0.08	0.31	0.57	0.02
DV 23	0.13	0.70	0.01	0.06	DV 18	0.13	0.57	-0.09	-0.27
DV 28	0.29	0.87	-0.12	0.21	DV 19	0.14	0.67	0.13	-0.17
DV 33	0.24	0.66	0.08	-0.87	DV 23	0.18	0.74	0.07	-0.10
DV 38	0.15	0.61	0.06	0.27	DV 25	0.36	0.92	-0.15	-0.02
DV 43	0.20	0.87	0.04	-0.01	DV 26	0.26	0.72	-0.27	0.37
DV 48	0.07	0.41	0.07	-0.004	DV 34	0.24	0.76	0.06	-0.35
DV 51	0.21	0.81	0 004	0.10	DV 38	0.20	0.65	0.09	-0.47
DV 52	0.20	0.84	00.07	0.13	DV 39	0.22	0.76	0.03	-0.24
DV 53	0.24	0.85	-0.13	0.23	DV 43	0.25	0.87	-0.12	0.10
DV 54	0.25	0.89	0.26	0.07	DV 44	0.11	0.53	0.03	-0.16
DV 55	0.24	0.95	-0.05	-0.03	DV 48	0.09	0.46	0.09	-0.23
DV 56	0.24	0.92	-0.10	-0.11	DV 50	0.33	0.91	-0.11	0.12
DV 57	0.24	0.92	0.006	-0.02	DV 51	0.26	0.80	-0.15	0.14
DV 58	0.18	0.88	0.11	-0.03	DV 55	0.30	0.92	-0.07	0.08
DV 59	0.17	0.85	0.12	-0.02	DV 58	0.23	0.88	0.07	0.05
DV 60	0.21	0.91	0.15	0.01	DV 61	0.24	0.76	0.008	0.16
DV 61	0.19	0.73	0.05	0.05					
DV 62	0.14	0.84	0.06	0.04					
DV 63	0.19	0.92	0.06	-0.006					

in size here as in the dorsal and lateral truss networks.

Summary. Results from the shear procedures were similar to previous data sets where only small size effects were removed. The first principal component for pooled samples of *gossypinus* and *leucopus* taxa can be interpreted as a general measure of size for all data sets. *P. gossypinus* is separated on the basis of size from Michigan *noveboracensis*, *leucopus*, and *castaneus* without overlap in all data sets. *P. gossypinus* is larger than most *leucopus* taxa. Shape differences are observed for traditional and ventral measures only. The latter data set produces less overlap between *gossypinus* and *leucopus* taxa than traditional measures. Traits involved in shape differences include rostral measurements, tooth row length, and cranial depth.

DISCUSSION

3.1 Traditional measures and truss networks

Morphometrics has always had at its disposal a large number of statistical techniques to manipulate linear measurements taken from biological forms (see Pimentel, 1979; Neff and Marcus, 1980). The sophisticated nature of multivariate morphometrics is not matched, however, by a comparable methodology for determining how variables are to be selected in the first place. Morphometrics offers no models or guidelines for the selection of characters.

The importance of measurement selection has been acknowledge by several authors. For instance, Olson and Miller (1958) deemed it necessary to dissect mammalian skulls before they selected and interpreted linear measurements. Olson and Miller's aim was to define measurements for the mammalian skull on a functional basis, and in the process they pointed out the difficulty in obtaining such measurements. Cheverud (1982) has recently addressed the question of measurement choice in a study of morphologic integration in the mammalian skull. His measurements were chosen on the basis of theoretical and experimental results of function and development of the mammalian skull. The measurements he sampled represent frontal, orbital, nasal, oral, and masticatory skeletal units. Cheverud also stressed the importance of areal coverage and noted that, ideally, measurement should be restricted to single skeletal units.

These effort have produced only a general sense of what rules might be used for selection of characters for morphometric analyses. Strauss and Bookstein (1982) have recently considered in detail the question of measurement in morphometrics and discussed the problems posed by the lack of procedures for choosing characters for study. Their criticisms can be summarized as follows: (1) distance measurements preferentially sample certain axes of variation, thus resulting in unequal coverage of the forms under study. This sampling bias involves both orientation and areal coverage. (2) Many measurements originate from a single point, often located at the tip of the form. Such points are usually defined in terms of minimum and maximum distances, and their placement may not be homologous from form to form. (3) Measurements usually extend over much of the form, usually spanning several growing units (e.g., bones), and tend to be less informative because they express average covariation.

Strauss and Bookstein (1982) advanced a geometric protocol of measurement, the truss network, whose conceptual and practical implications are very important. Their system of measurement is based upon the _a priori_ selection of anatomical points, the landmarks, and the associated distance measures among them. The landmarks are assumed to be homologous from form to form. The assumption of biological homology raises the standard questions associated with this concept (see Kluge and Strauss, 1985), but obviously does not detract from the conceptual elegance of their model of biological measurement. Secondly, the geometric protocol assumes that the configuration of landmarks can be reconstructed from the measured distances. From these two assumptions there follows the properties of the method, which can be summarized as follows: (1) The truss networks provide an even and systematic coverage of the form with respect to both area and axes of variation. (2) The configuration of landmarks can be archived through the reconstruction of the form from distance measures among landmarks.(3) Accurate estimates of error measurement can be obtained, and these errors can be partitioned by least squares procedures. (4) Average shapes can be constructed from samples of individuals, and loadings from multivariate analyses can be displayed directly on the truss networks to facilitate the interpretation of patterns of differentiation among organisms.

Strauss and Bookstein based their criticisms of standard measurement schemes on those used in fish morphometrics. Their criticisms, however, apply equally well to measurements used in mammalian cranial morphometrics. Measurements used in mammalian cranial morphometrics vary widely in number but are similar in the coverage they provide (e.g., DeBlase and Martin, 1981). Several cranial measurements originate at the tip of the nasal or basioccipital bones and basically sample only the skull midline. Width measurements are limited, and oblique and depth dimensions are virtually unsampled. Measurements generally span several bones, except for measures such as length of nasals. The traditional measurement set used in mammalian cranial morphometrics thus has most of the drawbacks listed by Strauss and Bookstein (1982) for traditional fish measurement schemes.

The truss networks that I used (see Figure 4-6) for Peromyscus leucopus do provide a more even coverage of the skull in terms of area and axes of variation. Some of the truss cells sample single bones, such as nasals and parietals, while in other cases truss measurements divide a single bone into two truss cells, as for example the frontal bone (Figure 4). Truss cells also sample anatomical regions represented by more than one bone, such as the rostral and post-palatal regions of the skull (Figure 4). The measurement error involved with truss networks was larger than that for traditional measurements (Section 1). Truss measurements are defined by anatomical landmarks on the skull which are easily identified. However, the inter-landmark distances of the truss are not as easily obtained with calipers as traditional measurements based on extremal points on the skull. It is thus not surprising that truss measurements gave larger measurement error. Error measurement for truss networks was nevertheless low, averaging less than 1%.

The truss protocol of measurement is a recent development and has been applied so far only to fish morphometrics (Strauss and Bookstein, 1982; Bookstein et al., 1985; Strauss and Fuiman, 1985). The results I obtained for mice of the _Peromyscus_ _leucopus_ group parallel the findings of Strauss and Bookstein with regards to the use of the truss geometric protocol in morphometrics, although they were not as dramatic as those obtained with fishes.

Discriminant _analysis_. _A posteriori_ levels of misclassification were generally low for _P. leucopus_ populations, although rates of correct classification varied between populations across data sets (Table 1, 5, and 7; see Table 38 for summary). Discriminant functions for dorsal and ventral measures produced higher rates of correct

Table 38. Summary of *a posteriori* rates of correct classification for *Peromyscus leucopus* populations. The first number indicates the percentage of individuals correctly classified to population, while the second number indicates the number of populations with which a given population was misclassified.

		Traditional	Dorsal	Ventral
noveb.	Livingston	75%/1	75%/2	100%/0
	Boyne Falls	79%/2	86%/2	72%/2
	Oklahoma	88%/1	94%/1	94%/1
	Ann Arbor	95%/1	100%/0	100%/0
fusus	Martha's Vineyard	92%/1	92%/1	92%/1
	Vineyard Haven	95%/1	85%/1	100%/0
aridulus	Cherry Co.	91%/1	100%/0	91%/1
	Dawes Co.	94%/1	100%/0	94%/1
leuco.	Kentuckey	100%/1	93%/1	93%/1
	North Carolina	100%/0	86%/1	95%/1
incen.	Veracruz	100%/0	94%/1	94%/1
	Puebla	100%/0	95%/1	100%/0

classification for *noveboracensis* populations than for traditional measures. Discriminant functions for traditional measurements yield higher rates of correct classification for *l. leucopus* and *incensus* than for other data sets, while dorsal and ventral truss measures produce higher rates of classification for *aridulus* and *fusus* than for traditional measures. Levels of overlap along canonical variates between population samples of *fusus*, *aridulus*, *leucopus*, *incensus*, and *noveboracensis* were generally lower for ventral truss measures than for traditional and dorsal measures. Traditional and dorsal measures give similar results with respect to discrimination (Section 2.1.1; Table 3). Mahalanobis distances between population samples of *fusus*, *aridulus*, *leucopus*, and *incensus* were generally higher for ventral measures than traditional or ventral measurements (Section 2.1.1). Traditional measures yield higher D^2 distances between population samples than dorsal measures. Similar results were found for the Mahalanobis distances between population samples of *P. l. noveboracensis* (Table 4).

At the subspecific level (Table 15, 19, and 22; see Table 39 for summary), ventral measurements yield higher rates of correct classification than traditional and dorsal measures, while traditional measures give higher rates of correct classification than dorsal measures. The same is not true, however, for the discrimination between *P. gossypinus* and *P. leucopus* taxa. Here, traditional measurements yield higher rates of correct classification than truss network measurements. Overlap along canonical axes 1 and 2 between *P. leucopus* subspecies is generally high for traditional, dorsal, and ventral measures. Traditional and ventral data sets yield better discrimination

Table 39. Summary of *a posteriori* rates of correct classification for *Peromyscus leucopus* subspecies. The first number indicates the percentage of individuals correctly classified to subspecies, while the second number indicates the number of subspecies with which a given subspecies was misclassified.

	Traditional	Dorsal	Ventral
fusus MV	58%/7	69%/6	73%/5
VH	80%/3	70%/1	95%/1
noveb. MI	70%/6	87%/4	89%/2
OK	50%/6	50%/5	63%/4
arid. CH	45%/2	73%/2	45%/2
DA	71%/5	47%/7	59%/4
leuco. KY	60%/6	40%/6	60%/5
NC	50%/5	59%/7	77%/4
tornillo	50%/5	50%/5	75%/3
incen. PU	79%/3	68%/4	63%/5
VE	88%/1	44%/5	44%/5
mesomelas	75%/2	67%/4	92%/1
affinis	72%/4	67%/5	78%/3
castaneus	75%/2	69%/1	92%/1

results than dorsal measures (Table 16, 20, and 23; see table 40 for summary). There are 20 instances of discrimination without overlap along canonical variate 1 and three cases along canonical variate 2 for ventral measures. Traditional measures show 22 cases of discrimiantion free of overlap along canonial variate 1. There are no cases of discrimination without overlap along canonical variate 2. Overlap between P. gossypinus and P. leucopus along canonical variate 1 is relatively similar in the three data sets, although ventral truss measures yield slightly better discrimination results (Table 31). There are five, six, and seven instances of overlap free of discrimination for traditional, dorsal, and ventral data sets, respectively. Ventral measures generally yield larger mean D^2 values between P. leucopus taxa than traditional or dorsal measures, while traditional measures yield D^2 values which are generally larger than dorsal measures (Table 18, 21, 24; Table 41 for summary). The same result is true for the mean D^2 values between P. gossypinus and P. leucopus taxa (Table 33).

The pattern of loadings on canonical variates among P. leucopus subspecies and between P. gossypinus and P. leucopus taxa provide interesting contrast between traditional measurements and truss networks (Table 17, 32). Canonical variate 1 for traditional measures is a contrast between basal length with a negative sign and diastema length and tooth row length with positive signs. In the ventral truss network tooth row length and posterior diastema length have positive coefficients, while post-palatal length has a positive coefficient. Traditional and ventral truss network measurements thus indicate a similar pattern of discrimination between taxa. However, the ventral

Table 40. Summary of percent overlap between *Peromyscus leucopus* subspecies in the canonical variates analysis. First and second numbers under canonical variates 1 and 2 indicate, respectively, the number with which a given subspecies shows no overlap with other subspecies, and the number of subspecies showing levels of overlap up to 30% with other subspecies.

	Traditional		Dorsal		Ventral	
	CV1	CV2	CV1	CV2	CV1	CV2
fusus MV	2/2	0/0	1/3	0/0	1/4	0/1
VH	4/3	0/3	5/2	1/4	2/5	1/2
noveb. MI	3/2	0/0	0/3	2/1	2/3	1/3
OK	2/2	0/0	0/2	0/0	2/2	0/2
arid. CH	7/1	0/0	0/1	3/4	8/1	0/1
DA	4/3	0/2	0/1	0/3	5/3	0/0
leuco. KY	2/2	0/1	0/1	0/2	3/4	0/0
NC	5/1	0/0	1/3	1/2	4/3	0/3
tornillo	0/1	0/1	1/3	0/0	1/1	0/2
incen. VE	1/2	0/1	2/2	0/2	2/3	0/1
PU	1/1	0/0	0/1	0/2	0/2	0/0
mesomelas	4/2	0/1	1/3	0/1	2/3	3/4
affinis	1/2	0/0	1/4	0/2	1/3	0/4
castaneus	8/0	0/0	0/4	1/3	7/2	1/3

Table 41. Summary of mean D^2 values between *Peromyscus leucopus* subspecies for different data sets.

	Traditional	Dorsal	Ventral
fusus MV	9.67	8.91	11.67
VH	17.84	15.69	18.01
noveb. MI	11.73	13.52	15.32
OK	10.27	9.51	15.63
arid. CH	16.23	13.08	18.94
DA	15.95	9.78	14.75
leuco. KY	8.93	7.42	11.51
NC	13.60	11.16	17.00
tornillo	10.57	8.31	13.99
incen. VE	13.37	10.09	13.25
PU	11.59	10.83	11.00
mesomelas	9.57	13.56	19.54
affinis	12.62	11.17	13.78
castaneus	19.87	12.89	29.16

truss network points to measurements that indicate localized aspects of the morphology that are important for discrimination. While traditional measurements indicate that basal length is important, ventral truss measurements partitioned the skull into two more localized areas of importance for discrimination, the post-palatal region of the skull and the posterior region of the diastema. The ventral truss network thus details particular areas of the skull that were only broadly indicated as important by traditional measurements for discrimination between taxa.

This result shows the importance for discrimination of localized aspects of the morphology as emphasized by Strauss and Bookstein (1982), and exemplifies one of the properties of the truss networks. It demonstrates the ability of the truss networks to uncover localized effects in the morphology that are important for discrimination. This is an important property of the truss protocol, which was designed to provide systematic and detailed coverage of the form in terms of area and axes of variation. It may be argued, however, that the localized effects on discrimination may be a consequence of the spatial arrangement of measurements generated by the truss network itself. The results discussed above seem to indicate that this is not the case here. If the whole ventral area of the skull, represented by basal length, were important for discrimination we might expect to find many measurements in ventral truss network having large loadings on canonical variates. However, loadings on canonical variates for ventral measures indicate particular areas of the skull to be of importance for discrimination, suggesting that the pattern of discrimination is not an artifact of the spatial arrangement of the truss measurements.

Principal components analysis. *P. l. noveboracensis* populations show similar levels of overlap along the first principal component in all data sets, although in certain cases lateral and dorsal truss measures yield lower levels of overlap. Overlap along principal components 2 and 3 is also generally large, although traditional and three-dimensional measurement schemes produced slightly lower levels of overlap in some cases. Different data sets produced similar levels of overlap on principal components 1, 2, and 3 for population samples of *fusus*, *aridulus*, *leucopus*, and *incensus* (Table 9, 11, 12, 13, and 14).

Overlap levels among *P. leucopus* subspecies were generally very high, although data sets differ in their ability to discriminate between taxa. Levels of overlap were generally higher for ventral and lateral truss networks. Traditional measurements and the three dimensional measurement scheme generally produced lower levels of overlap between *leucopus* subspecies than other data sets, while dorsal measurements produced intermediate results (Table 26, 27, 28, 29, and 30). Ventral truss measurements generally produced lower levels of overlap between *P. gossypinus* and *P. leucopus* taxa than other measurement schemes (Table 34). Traditional measurements produced lower levels of overlap between *P. gosssypinus* and *P. leucopus* taxa than the remaining truss networks (Table 34).

The results for principal components analysis summarized above indicate that truss networks are an improvement with respect to discrimination in the reduced space of principal components, especially at the subspecific and specific levels. However, as indicated earlier for discriminant analysis, no new axis of variation was uncovered by the truss networks, as was the case with the use of truss networks with fishes (Strauss and Bookstein, 1982). However, the use of truss networks permitted a geometric interpretation of the pattern of allometric coefficients derived from principal components analysis, confirming one of the properties of the truss protocol (Strauss and Bookstein, 1982). Strauss and Bookstein argued that the spatial arrangement of distance measures created by the truss networks should allow interpretations of shape differences in geometric terms. They applied traditional and truss measurement schemes to two species of fishes of the genus Cottus, and showed that the truss networks permitted a geometric interpretation of the loadings from principal component analysis. I obtained a similar result with the allometric coefficients of P. leucopus taxa.

Patterns of allometry for Peromyscus of the leucopus group are similar in all five data sets (Table 10; Figure 11, 12, 23, 38). However, the truss networks indicate a pattern of allometry that is easier to interpret than for traditional measurements. Most measurements in the anterior region of the skull (including rostrum and anterior frontal bone) are positively allometric, while posterior measurements of length, width, and diagonals have negative allometries with respect to the general size vector. This contrast is not altogether clear in the traditional data set because this measurement scheme poorly samples the posterior region of the skull, both in area and axes of variation. The allometric coefficients depicted directly on the truss networks provide an informative geometric constrast between regions of the skull that correspond roughly to the orofacial and neurocranial skull units recognized in cranial functional anatomy (Cheverud, 1982).

The truss protocol proposed by Strauss and Bookstein (1982) is a conceptual and analytical improvement over traditional schemes of measurement. My results discussed in the sections on discriminant analysis and principal components analysis were not as remarkable with respect to discrimination as those obtained by Strauss and Bookstein since no new axis of variation was uncovered by the truss measures. But my results illustrate the potential application of this procedure to mammalian cranial morphometrics. The ventral view of skull seems to be important in the discrimination of Peromyscus taxa and should be taken into account in future morphometric studies of Peromycus. My results also indicate that the traditional measurement scheme currently used in mammalian morphometrics performed well despite the limitations inherent to those kinds of measurements. In many cases, the traditional measurement scheme gave better results with respect to discrimination than the dorsal view of the skull in the discriminant analyses. In the principal components analyses among P. leucopus and between P. leucopus and P. gossypinus, traditional measurements also produced better results with respect to discrimination than some of the truss networks. This is an interesting result because Strauss and Bookstein (1982) demonstrated that traditional measurement schemes used in fish morphometrics failed to detect important axes of variation. Truss networks applied to mammalian cranial morphometrics do reveal localized aspects of the morphology important for discrimination among groups. This localized information is not clearly uncovered by the traditional scheme because measurements do not provide systematic coverage of area and axes of variation. Usually, the localized information provided by the truss networks convey a geometric perspective to the patterns of discrimination and contrast between groups. This is the case with the pattern of loadings on canonical variates and also with the allometric contrast between the anterior and posterior region of the skull.

The results summarized above indicate that different measurement schemes vary in their ability to discriminate between taxa. The different sets of observations (*a posteriori* rates of correct classification, percentage overlap along canonical variates, and Mahalanobis distances between taxa) indicate that in many cases the ventral truss networks produce better discrimination. My results confirm, in part, Strauss and Bookstein's expectations. Strauss and Bookstein (1982) argued that longer measurements are less informative than short ones because they usually span several skeletal units and tend to average variation. On the other hand, short measurement distances contain more localized information than long ones and should improve discrimination. Strauss and Bookstein (1982) demonstrated both assertions with a comparative study of discrimination among fish species of the genus *Cottus*. They showed that the truss network improved discrimination among species over traditional measurement schemes used in fish morphometrics. More importantly, however, they demonstrate that in the *Cottus* species they studied discrimination is based on distance measures with a particular orientation along the fish body. The principal directions of shape differences between species are oriented obliquely to the anterior posterior axis of the fishes

(Strauss and Bookstein, 1982; Bookstein, 1982). This dimension of variation is sampled by the measurements in the truss network, but seldom sampled by traditional schemes of measurement. Similar results were found for fishes of the genus *Atherinella* (Bookstein et al., 1985).

My results indicate that truss networks can behave differently with respect to discrimination, although they all convey localized information. The dorsal view generally yielded poor results when compared to traditional or ventral truss networks. Truss networks can be an improvement over traditional data sets as illustrated by the results that I obtained with the ventral network. But in my case truss networks did not uncover any axis of variation not previously sampled by the traditional data set, as Strauss and Bookstein (1982) found in their application of the truss networks to fish morphometrics. This may explain why the results I obtained here with respect to discrimination were not as dramatic as that found by Strauss and Bookstein (1982) for fishes.

The traditional measurement scheme that I used here did perform well with respect to discrimination. As discussed above, traditional measures generally yield better discrimination compared to the dorsal truss network. This is an interesting result if we consider the relatively poor coverage in area and axes of variation accomplished by the traditional measurement scheme compared to truss networks.

The number of measurements generated by the truss protocol is the only major limitation in this method. The total number of measurements necessary for the construction of truss cells escalates very rapidly with increased number of landmarks. Larger samples may thus be required, especially in the cases where multivariate analyses are sensitive to sample sizes (as is the case with discriminant analysis, Neff and Marcus, 1980). However, the choice of optimal measurements can probably be determined by exploratory studies. Full complements of truss cells might be used at first with a few population samples, to determine which networks should be kept for future analyses. The results that I obtained here with the application of the truss protocol to mammalian cranial morphometrics seem to indicate that the effort to obtain such measurements is worthwhile.

3.2 Size, shape, and static allometry for *leucopus* group of *Peromyscus*

The application of the shear procedure to mice of the *Peromyscus leucopus* species group showed that only negligible size effects were removed from principal component 2 and 3 in all data sets (Section 2.1.2, 2.2.2, and 2.3.2). Coefficients of vector correlations, which measure the similarity of vectors of loadings (Bryant, 1984; Strauss and Fuiman, 1985), were near unity in all cases. Discrimination among populations within, among subspecies of *P. leucopus*, and between *P. leucopus* and *P. gossypinus* was not improved by the use of the shear procedure. This result is at variance with findings by Humphries et al. (1980). They applied the shear procedure to species of *Cyprinodon* and *Rhinichthys* fishes and showed that shape discrimination (along sheared PC2) was much improved over the traditional data set. On the other hand, Strauss and Fuiman (1985) obtained results similar to mine in the application of the shear procedure. Strauss and Fuiman (1985) applied the shear to study body form differences and allometry in larval and adult cottid fishes. They found, however, that vector correlations between sheared and original components were very large (greater than .98), indicating that virtually no size effects were removed. Formal size and shape components, as defined by the shear procedure, are closely approximated by the principal components of a conventional principal components analysis in Strauss and Fuiman's data, and in mine presented here (Humphries et al., 1980). The results presented here for size and shape variation among *P. leucopus* are thus based on standard principal component analysis. These results also indicate that the effectiveness of the shear procedure varies with different data sets, and that this procedure should be used to determine the existence and magnitude of the correlation between shape and size components. In other words, independence between size and shape components has to be empirically determined for a given data set.

Scatter plots of taxa on the principal components of mensural data show extensive overlap among *P. leucopus* (Figure 24-28). Variation in skull morphology is continuous among taxa, with no obvious morphological gaps. *P. leucopus* taxa tend to differ in size and shape among themselves, although this variation is limited. *P. l. tornillo* and *incensus* show little differentiation in size but differ in shape from several other subspecies (Figure 24-28; Tables 26-30).

Levels of differentiation between *Peromyscus gossypinus* and *P. leucopus* are much higher than among *P. leucopus* taxa (Figure 39, 40, 41). *P. gossypinus* shows little differentiation, though, from *P. l. fusus*, *P. l. noveboracensis*, and *P. l. aridulus*. Scatter plots on the principal components show that most differentiation between *P.*

gossypinus and P. leucopus taxa is due to size (Figure 39, 40, 41). P. gossypinus has larger skulls compared to P. leucopus taxa and is characterized by individuals with larger scores than P. leucopus taxa (Table 35-37). This result is in agreement with Osgood's assessment (Osgood, 1906), and also with several studies on the morphologic differences between P. gossypinus and P. leucopus (Dice, 1940; Hooper, 1968; Wolfe and Linzey, 1977) that indicate that size is the main difference between P. gossypinus and P. leucopus taxa. Recently, Engstrom et al. (1982) have conducted multivariate analyses of morphological variation and concluded that the principal distinction between P. gossypinus and P. leucopus is overall size. Nevertheless, my results indicate that P. gossypinus does show shape differentiation from several P. leucopus taxa. The allometric coefficients indicate that P. gossypinus individuals are characterized by longer and broader rostra and narrower cranium relative to P. leucopus.

Patterns of allometric differences observed here for Peromyscus exemplify the properties of the truss protocol of measurement. Strauss and Bookstein (1982) stressed that the spatial arrangement of the truss networks should promote meaningful interpretations of shape differences. Allometric coefficients for Peromyscus mice generally indicate a geometric constrast between anterior and posterior regions of the skull. Similar results were obtained by Bookstein et al. (1985). They applied the truss network in a study of discrimination between Cottus pitensis and C. klamathensis and showed that the pattern of principal component loadings on the truss networks permitted a geometrical interpretation of shape differences between taxa. In their case the pattern of loadings on truss networks indicates a contrast between longer and deeper bodied fishes (Bookstein, 1985).

Patterns of allometry for Peromyscus are similar in all five data sets (Table 10; Figure 11, 12, 23, 38). However, the truss networks indicate a pattern of allometry which is easier to interpret than that for traditional measures. Most measurements in the anterior region of the skull (including rostrum and anterior frontal bone) are positively allometric, while posterior measurements of length, width, and diagonals are negatively allometric with respect to the general size vector. These anatomical regions correspond to the orofacial and neurocranial components of the skull recognized in functional cranial anatomy (Cheverud, 1982; Radinsky, 1985). This contrast is not altogether clear in the traditional data set because this measurement scheme poorly samples the posterior region of the skull, both in area and axes of variation. It is interesting to note that patterns of static allometry are similar at the different levels of organization of Peromyscus. In other words, populations, subspecies and species are characterized by similar static allometric relationships, suggesting that differences among subspecies and between species are extrapolations of those seen at the population level.

There seems to be a trend for allometric coefficients to decrease in magnitude along an anteiror-posterior gradient, with lines of isometry in the Peromyscus skull clearly seen in certain cases. For example, among noveboracensis populations (Figure 11) the posterior region of the rostrum (distance variable 29; first truss cell) and the anterior region of the zygoma (distance variable 60; second truss cell) correspond to isometric lines for ventral and lateral truss networks, respectively. Measurements that are isometric with respect to the size vector can be useful in the study of bivariate allometry. In this case, the single isometric character is used as an estimate of general size (Strauss, 1985). Bivariate allometry is important when the form of the allometric relation between characters is of interest, and also in the study of particular morphological complexes. For example, Strauss (1984) used bivariate allometries to show that extensive morphological variation in the feeding apparatus of haplochromine fishes can be explained by allometry alone.

The results from the principal components analysis indicate that shape differences between Peromyscus of the leucopus group may be complex in nature. Allometric coefficients generally are not concordant with loadings of principal components 2 and 3, except for noveboracensis populations. Here, allometric coefficients for traditional measurements generally agree with the pattern of loadings of other principal components. This is the only case in this work where a large proportion of cranial differences in adults of Peromyscus can be accounted for by the observed allometric differences. In other words, static adult allometry is a reasonable descriptor of shape differences among noveboracensis. Bookstein et al. (1985) found similar results in a study of shape differences between ecophenotypes in the fresh water sculpin Cottus cognatus.

The lack of concordance between allometric coefficients and loadings on subsequent principal components for all other taxa is not, however, unexpected. The two sets of components (the first and the subsequent principal components) represent size and shape estimates in Humphries et al.'s (1980) model, and are obtained by regressing size out components after the first. The independence between size and shape components is thus achieved by a "rotation" (actually, a shear) of the axes and not by the imposition of orthogonality by constrained maximization as in standard principal components analysis (Neff and Marcus, 1980). It is thus remarkable that in some cases these two sets of coefficients agree since they differ conceptully and in statistical derivation. Allometric coefficients give information on size-related shape differences, while subsequent principal components convey information on shape which is not correlated with size (Humphries et al., 1980).

Differences in size and shape of adults for a quantitative trait probably represent the outcome of complex interactions of differences in rates and timing of growth and development (Raff and Kaufman, 1983). Creighton and Strauss (1985) recently described complex relations of rates and timing of growth that determine adult size and shape in cricetine rodents. Creighton and Strauss (1985) used a negative exponential model to estimate growth parameters that were incorporated into Alberch et al.'s (1979) model of heterochronic evolution, and were able to show that, generally, differences in size and shape between cricetine rodents can be accounted for by differences due to pre-natal ontogeny, post-natal growth, and duration of growth. Rates and timing of development were also shown to interact to produce convergent or divergent growth trajectories that account for observed similarities or differences in form among adults. They also found that while absolute duration of growth in quantitative traits is strongly correlated with size, relative timing varies independently of size. Strauss and Fuiman (1985) also showed how shape similarities and differences in adult cottid fishes can be accounted for by variation in larval rates of growth.

These studies show that the importance of timing and rates through ontogeny cannot be overemphasized in the study of mechanisms of size and shape differentiation. Where information on the timing of expression of a trait is not available, analyses are restricted to the components of shape that are determined by changes in relative size, or allometry. Change in relative shape as a function of size in quantitative traits can be expressed as growth allometry (Leamy and Bradley, 1982; Kluge and Strauss, 1985; Strauss, 1984, 1985). Ideally, measurements for quantitative traits should be taken on the individual at several stages of development (Cock, 1968; Leamy and Bradley, 1982), but usually a mixed sample of individuals of different sizes is used. In this case the assumption is made that a composite sample can approximate individual ontongenetic trajectories (Bookstein et al., 1985). The use of cross sectional data sets has given excellent results in the study of the determinants of shape variation in fishes (see Bookstein et al, 1985). This kind of sample is difficult, however, to obtain for animals with "determinate" growth such as mammals, and inferences on size-related shape differences are usually limited to static adult allometry. This is certainly the case with the present study, and even in studies that are designed to include growth allometry, the magnitude of size differences between ages classes tend to be very small. For example, Leamy and Bradley (1982) sampled house mice from 35 days of age up to 5 months, but the range of variation in measurements of skeletal traits is still very small. Data from mammalian species cannot be compared with samples from fish studies, where 4-fold ranges in size differences among individuals are commonly obtained (e.g., Chernoff and Miller, 1982; Barbour and Chernoff, 1984; Strauss, 1984).

Generally, the results here show that the truss networks can improve shape discrimination, but similarly to the discriminant analysis, no radically different axis of variation not covered by the traditional method was found. The results from allometry are nevertheless very interesting. Here the truss networks provide a geometric constrast that cannot be obtained by traditional measures. However, the single most important aspect uncovered by the analysis of size and shape is the potential role played by ontogeny. Determinants of skull size and shape are probably complex and dramatically underscore the need for the sampling of growth stages. The inclusion of data on early stages of ontogeny in studies of form differences among organisms is important for two reasons. First, ontogenetic data can be used to study relative timing of expression of morphologic traits as a function of age (Creighton and Strauss, 1985), and second, to obtain estimates of growth allometry. Information on growth allometry is important because inferences on size-related shape changes cannot be made from adult allometry alone since the two estimates are not necessarily concordant (Cock, 1963; Leamy and Bradley, 1982). Information on allometry and timing can then be combined in trajectory models as exemplified by Kluge and Strauss (1985). The technical difficulties associated with the sampling of mouse skulls are well know (e.g., Leamy and Bradley, 1982). However, the use of cleared and stained skulls from near-term and post-natal specimens, in connection with a digitizing apparatus to collect data, may prove useful to overcome technical problems.

3.3 Phenetic relationships of the *leucopus* group of *Peromyscus*

Canonical variates analyses show extensive variation between population samples of *fusus*, *aridulus*, *l.* *leucopus*, and *incensus* (Section 2.1.1). *P.* *l.* *noveboracensis* populations vary in the extent they differ from one another in the space of canonical variates (Table 3; Figure 8). Oklahoma *noveboracensis* is the most differentiated population of four examined. *P.* *l.* *noveboracensis* populations show a similar pattern of ordination in the reduced space of canonical variates 1 and 2 for traditional and dorsal measures. The ordination of *noveboracensis* along canonical variates 1 and 2 is similar to traditional and dorsal measures if the axes are rotated about 45^{o} counterclockwise. Canonical variates 1 and 2 for ventral measures are similar to traditional measures (Table 6).

Canonical variates analysis indicates that *P.* *leucopus* subspecies overlap extensively, and most variation is continuous along each axis (Figure 14, 17, and 20). Some taxa form discrete non-overlapping clusters, although the clusters predicted by the three data sets are different. Traditional and dorsal measures identify one cluster formed by *castaneus*, Michigan *noveboracensis*, and *l.* *leucopus* from North Carolina. Traditional measures indicate a second discrete cluster that includes *fusus* from Vineyard Haven and the *aridulus* populations, while dorsal measures indicate a cluster formed by *fusus* from Vineyard Haven and *aridulus* from Cherry Co only. Ventral measures also indicate the presence of two non-overlappping clusters: the first with *castaneus*, *l. leucopus* from North Carolina; and the second with the *aridulus* populations, Vineyard Haven *fusus*, and Oklahoma *noveboracensis*. The remaining taxa are distributed along a continuum between the two discrete clusters. The pattern of loadings on canonical variates indicates that different traits contribute for the discrimination of *P. leucopus* taxa in the different data sets (Table 17).

Some of the traits identified as important for discriminating *P. leucopus* taxa in the canonical variates analysis were recognized earlier by Osgood (1909) in his classic treatment of the genus *Peromyscus*. Tooth row length has a large coefficient on the canonical variate separating *aridulus* from *noveboracensis*, and this is one of the traits used by Osgood to distinguish the two forms. Osgood also pointed out that *noveboracensis* and *l. leucopus* skulls were very similar, and these two forms cannot be separated in the canonical variates analysis using traditional measurements (Figure 13). Nevertheless, *l. leucopus* and *noveboracensis* are separated in the canonical variates analysis here by the dorsal and ventral truss networks (Figure 17, 20). Osgood also indicated that *fusus* differed from *noveboracensis* by its longer nasal and rostral region of the skull. His assessment is in agreement with results from dorsal truss measures. Loadings on canonical variate 2 and the ordination of *fusus* with respect to *noveboracensis* indicate that nasal length is indeed important for the discrimination between these two forms.

The morphological relationships revealed by canonical variates analysis raises questions about the current subspecific arrangement of *P. leucopus*. The currently accepted subspecific boundaries for *P.*

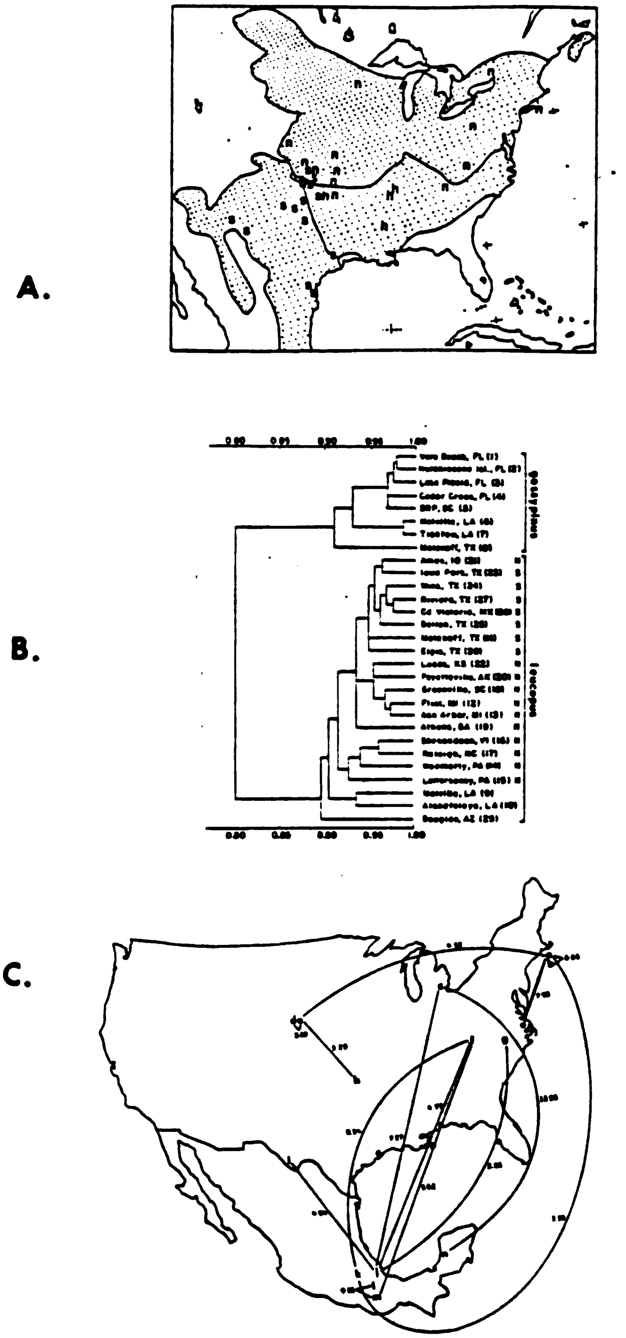

Figure 42. Relationships among mice of the leucopus group of *Peromyscus* based upon different data sets. A. Northeastern and southwestern chromosomal cytotypes (After Baker et al., 1983). B. UPGMA based upon electrophoretic data (After Robbins et al., 1985). C. Prim networks based upon Mahalanobis distances of morphologic data. Present study.

leucopus were established by Osgood (1909), who recognized 13 forms. Osgood himself thought that *P. leucopus* subspecies could naturally be divided into northeastern and southwestern forms, and his overall arrangement of the subspecies shows a decidedly geographic pattern. Hall (1981) added four more subspecies to *P. leucopus* in his recent review of the mammals of North America, but retained the essential arrangement of Osgood.

Baker et al. (1983) have recently produced data from G-banded chromosomes that seem to indicate the existence of two widely distributed chromosomal forms of *P. leucopus* (Figure 42). The two forms of *leucopus* can be distinguished by three euchromatic pericentric inversions, and represent northeastern and southwestern cytotypes. These chromosomal forms have an obvious geographic pattern, but they do not agree with the subspecific boundaries of Osgood (1909) or Hall (1981).

The morphologic relationships indicated by canonical variates analysis carried out here are, nevertheless, difficult to interpret on a geographic basis, except for two northern subspecies, *fusus* and *aridulus*, which tend to be clustered together by the different data sets. There is thus generally no concordance between the pattern of relationships indicated by the chromosomal data of Baker et al. (1983) and the morphometric data presented here, and between these two data sets and the subspecific boundaries of *P. leucopus*.

This lack of congruence between data sets is not, however, restricted to chromosomal or morphological data. Robbins et al. (1985) have recently surveyed allozyme variation in *P. leucopus* and found that the pattern of relationships indicated by genic similarity between leucopus taxa is not concordant with the subspecific arrangement (Figure 42). Their UPGMA phenogram based on Roger's similarity coefficients indicates that populations from similar geographic areas generally cluster together irrespective of their subspecific boundaries. Their cladogram also shows that southwestern populations form a single cluster. This cluster is not, however, clearly differentiated from a larger cluster of northeastern forms, and they concluded that the pattern of relationships indicated by the genic data does not corroborate the major chromosomal division of P. leucopus into southwestern and northeastern cytotypes.

I found a similar north-south pattern of relationships for P. leucopus subspecies. The UPGMA phenogram of D^2 distances derived from traditional measures (Figure 15) reveals two major clusters: one composed of mostly northern U.S. forms, and the other of largely southern U.S. and Mexican forms. This phenogram, however, has a relatively low cophenetic correlation coefficient (r_c=.63), indicating a relatively large amount of distortion between D^2 values and the cophenetic values from the UPGMA phenogram (Sneath and Sokal, 1973). However, a similar pattern of northern and southern forms is confirmed by the Prim networks (Figure 16). This lends some credence to the phenetic relationships displayed by the UPGMA phenogram, because Prim networks are derived by a single-link procedure (Prim, 1958; Chatfield and Collins, 1980), and no statistical manipulation (i.e., averaging) of D^2 values is involved. The phenetic relationships indicated by UPGMA phenogram based upon dorsal and ventral truss networks (Figure 18, 21) point to a complex pattern of differentiation with no apparent geographic trends. The amount of distortion between D^2 values and cophenetic coeffcients is large for dorsal measures (r_c=.54) and even larger for ventral measures (r_c=.10). However, the lack of geographic trends for *P. leucopus* subspecies suggested by UPGMA phenograms for dorsal and ventral data sets is confirmed by Prim networks for the same data sets (Figure 19, 22). These results thus generally indicate a complex pattern of morphological differentiation among *P. leucopus* with no apparent geographic trends.

Robbins et al. (1985) found a significant positive correlation between genetic and geographic distance for *P. leucopus* populations, suggesting a pattern of isolation by distance. I could not find a similar correlation between morphologic distance derived from traditional and ventral measures and geographic distance for *P. leucopus*. The correlation between morphologic distances derived from dorsal measures and geographic distances is, however, significant (section 2.2.1). Close inspection of the Prim Network for dorsal measures (Figure 19) indicates that only populations within *fusus*, *noveboracensis*, and *l. leucopus* are connected with their closest geographic neighbor (i.e., their consubspecifics). The remaining *P. leucopus* forms do not show a pattern of geographic connectedness; they are not linked with their closest geographic neighbor. This result indicates that the pattern of variation for *fusus*, *noveboracensis*, and *l. leucopus* may be concordant with a model of isolation by distance as indicated by the electrophoretic data of Robbins et al. (1985). The same is not true, though, for the remaining *P. leucopus* taxa. In other words, the remining *P. leucopus* taxa show no concordance between morphologic and geographic distance (Figure 16, 19, 22). Prim networks for morphometric data for *P. leucopus* subspecies thus seem to point to localized patterns of differentiation with no apparent geographic trends. Dice (1937, 1939) obtained similar results in studies of variation in *P. leucopus*. He documented extensive variation at the population level in cranial and pelage character but could find no geographic trends in the patterns of variation.

The pattern of geographically localized differentiation and lack of correlation between geographic and morphologic distances among *P. leucopus* forms indicated by the minimum spanning trees may have a biological interpretation. DosReis and Straney (1983) have recently provided evidence for phenotypic plasticity in the morphology of *Peromycus leucopus* skulls. They studied morphologic variation in laboratory-raised populations whose parents were descendants from field-caught specimens of *fusus*, *castaneus*, and *noveboracensis*, and found significant differences in morphometric characters among the laboratory samples, and between laboratory and field populations. More interestingly, each laboratory population responded differently to the controlled environment. These results suggest that (1) differences between natural populations probably have a genetic component since laboratory populations differ significantly among themselves after being exposed to a common environment, (2) environmental effects are important determinants of skull morphology in these populations because laboratory populations differ from field counterparts, and (3) populations are apparently differently plastic in their response to local environmental effects, as indicated by the different response of populations to a common laboratory environment.

The results described above indicate that skull morphology in population samples of fusus, castaneus, and noveboracensis shows significant amounts of phenotypic plasticity. If high levels of phenotypic plasticity are characteristic of P. leucopus, this may facilitate the differentiation of geographically localized cranial morphologies, and explain the lack of geographic pattern in the variation of skull morphology. This situation is apparently similar to the classic ecotypic effects seen in plants (e.g., Clausen, 1951). In fact these results are not altogether surprising since the limited information available indicates that genotype-environment interactions are a relatively common feature in animal populations in nature (Gupta and Lewontin, 1982; Lewontin, 1984; Via, 1984a, b).

A close relationship between P. leucopus and P. gossypinus has long been recognized (Osgood, 1909) and has recently been corroborated by electrophoretic (Avise et al., 1979) and chromosomal data (Stangl and Baker, 1894). The possibility of hybridization between the two has nevertheless been controversial. Dice (1937, 1940, 1968) showed the forms to be interfertile in the laboratory, but field studies have produced no conclusive evidence for hybrydization (McCarley, 1954, 1963). Recent studies of protein variation have shown no evidence of hybridization between P. leucopus and P. gossypinus in areas of sympatry in Arkansas, Tennesse, and Mississipi (Price and Kennedy, 1980) or Georgia (M. H. Smith, pers. comm.). Similar results based on morphometric analyses were obtained by Engstrom et al. (1982). They followed the protocol for hybrid identification suggested by Neff and Smith (1979) and demonstrated that previous reports of hybrids between P. gossypinus and P. leucopus based upon intermediacy of morphologic characters were due to the use of samples of different age classes. P.

gossypinus and P. leucopus individuals of similar age classes were easily separated by multiple discriminant analysis. While this is not disproof of the existence of hybrids (Neff and Smith, 1979), Engstrom et al. (1982) showed that the intermediacy of characters upon which evidence for hybridization is based represent sampling artifacts (Neff and Smith, 1979).

Canonical variates analysis between P. gossypinus and P. leucopus indicates extensive differentiation between the two taxa (Figure 29, 32, 35). Canonical variates show that morphometric differentiation between P. gossypinus and P. leucopus is related to basal length and tooth row length in the traditional measurements, localized measurements in the nasal region for dorsal measurements, and tooth and post-palatal measurements in the ventral truss network (Table 32). In all cases, P. gossypinus is characterized by individuals with larger scores relative to P. leucopus taxa for those measurements. These results also reflect Osgood's general assessment of the relationships between P. gossypinus and P. leucopus. He described the skull of P. gossypinus as rather large and heavy compared to P. leucopus, which is the same relationship seen for all data sets here. Osgood also characterized P. gossypinus teeth as decididely larger, in agreement with findings here for traditional and ventral measurements (Table 32).

Baker et al. (1983) indicated that P. gossypinus is chromosomally closer to the northeastern cytotype of P. leucopus than the southeastern cytotype. The phenetic relationship between P. gossypinus and P. leucoupus based on morphologic traits supports Baker et al.'s assessment. The phenetic relationships between P. gossypinus and P. leucopus indicated by the UPGMA phenograms are much more stable than those for *P. leucopus* subspecies. Phenograms for all data sets show a close phenetic relationship between *P. gossypinus* and *P. l. fusus* (Figure 30, 33, 36). UPGMA phenograms vary, though, in the way they portray the phenetic relationships between *P. gossypinus* and *P. l. fusus* populations. *P. gossypinus* is joined by *P. l. fusus* from Vineyard Haven in a single cluster in the traditional data set, while it is linked to the two *P. l. fusus* populations in the phenogram based on dorsal truss measures. In the ventral view, *P. gossypinus* is closer to Vineyard Haven as in the phenogram for traditional measures, although here the two forms join a larger cluster that includes several other *P. leucopus* taxa. *P. gossypinus* is geographically connected to *P. l. fusus* in all data sets (Figure 31, 34, 37).

The results presented here add to the apparent complex pattern of differentiation of the *leucopus* group of *Peromyscus*. The traditional data set indicates the presence of northern and southern clusters of subspecies, but remaining taxa form a morphological continuum between the two geographic clusters. This pattern of geographic relationships could not be replicated, however, with measurements from the dorsal and ventral views of the skull. These data sets point to localized patterns of differentiation with no apparent geographic trends. This mosaic pattern of differentiation may nevertheless reflect the range of phenotypes produced by high levels of phenotypic plasticity in the skull of *P. leucopus*. The relationship between *P. gossypinus* and *P. leucopus* is stable across data sets, and suggests a close phenetic relationship between *P. gossypinus* and *P. l. fusus*.

APPENDIX

Appendix A1. Canonical variate loadings for *Peromyscus leucopus* populations. Truss character set. Dorsal truss network.

	fusus	*aridulus*	*leucopus*	*incensus*	*noveboracensis*		
Character	CVI	CVI	CVI	CVI	CVI	CVII	CVIII
DV 1	-0.10	0.54	-0.11	-0.06	0.23	-0.24	0.03
DV 3	0.68	-1.93	0.52	0.53	0.06	-0.03	-1.78
DV 4	-0.24	0.83	-0.11	-0.23	-0.18	0.73	-0.21
DV 5	0.00	0.92	0.20	-1.46	0.55	-0.54	1.24
DV 8	1.60	2.19	-0.85	-0.03	-0.29	0.30	0.04
DV 9	0.65	1.15	0.36	0.07	-0.09	-0.23	0.26
DV 10	-0.79	-2.62	1.12	0.62	0.80	-0.57	-0.14
DV 13	0.22	-0.23	-0.44	-0.78	0.07	0.13	0.50
DV 14	0.10	1.01	-1.59	-0.17	-0.66	-0.83	-0.52
DV 15	-0.50	0.31	1.37	0.48	0.40	0.66	0.32
DV 18	-0.30	2.79	-0.12	0.21	-0.16	0.27	0.11
DV 19	-0.57	-0.15	0.33	0.32	0.01	0.20	-0.72
DV 20	-0.47	-2.14	-0.63	-0.40	0.37	0.86	-0.03
DV 23	0.47	-0.80	0.33	0.37	0.00	-0.11	0.84

Appendix A2. Canonical variate loadings for *Peromyscus leucopus* populations. Truss character set. Ventral truss network.

	fusus	*aridulus*	*leucopus*	*incensus*	*noveboracensis*		
Character	CVI	CVI	CVI	CVI	CVI	CVII	CVIII
DV 26	0.80	-0.45	0.63	0.40	-0.10	-0.15	0.18
DV 28	0.42	0.04	0.26	-1.36	-0.60	0.11	0.64
DV 29	0.40	1.42	0.58	-1.23	0.16	0.53	-0.36
DV 30	0.69	-0.20	0.22	1.37	0.34	-0.82	-0.38
DV 33	0.71	-0.77	0.62	0.47	0.46	-0.01	0.71
DV 34	-0.12	0.61	-0.36	0.82	0.65	0.14	0.38
DV 35	-1.27	0.24	-0.16	-0.72	-0.16	-0.32	-0.46
DV 38	-0.41	1.53	0.14	0.21	0.88	-0.06	0.52
DV 39	0.44	1.15	0.02	0.74	-0.13	0.28	0.95
DV 40	0.22	-3.60	0.79	0.87	0.02	-0.27	-0.91
DV 43	-1.79	-0.79	1.17	2.58	0.27	0.13	-0.37
DV 44	0.19	0.43	0.87	0.23	-0.10	0.48	0.33
DV 45	0.89	2.36	-2.52	-3.20	-0.83	-0.71	-0.30
DV 48	-0.26	-0.35	-0.04	0.52	0.56	0.01	-0.68

Appendix A3. Principal component loadings for *Peromyscus leucopus* populations. Truss character set. Dorsal truss network.

	fusus		*aridulus*			*leucopus*		*incensus*				*noveboracensis*			
Character	PCI	r	PCI	r	PCIII	PCI	r	PCI	r	PCII	PCIII	PCI	r	PCII	PCIII
DV 1	0.29	0.66	0.58	0.89	-0.37	0.39	0.77	0.21	0.63	0.19	0.28	0.42	0.81	0.01	0.37
DV 3	0.30	0.71	0.21	0.49	0.05	0.34	0.74	-0.01	-0.03ns	0.57	0.08	0.36	0.73	-0.15	-0.66
DV 4	0.24	0.46	0.10	0.30ns	-0.09	0.20	0.53	-0.006	-0.02ns	0.45	0.03	0.23	0.56	0.05	0.06
DV 5	0.28	0.72	0.27	0.70	0.03	0.31	0.80	-0.005	-0.02ns	0.51	0.22	0.38	0.83	-0.13	-0.47
DV 8	0.61	0.86	0.49	0.78	-0.11	0.29	0.43	0.73	0.96	-0.27	0.34	0.36	0.68	-0.44	0.27
DV 9	0.19	0.58	0.15	0.54	0.37	0.25	0.77	0.06	0.35	0.004	-0.004	0.28	0.72	0.06	0.21
DV 10	0.41	0.91	0.30	0.81	0.15	0.27	0.72	0.36	0.92	0.03	0.18	0.34	0.83	-0.17	0.23
DV 13	0.20	0.42	0.16	0.44	0.42	0.39	0.76	-0.41	-0.81	-0.15	0.66	0.16	0.39	0.55	-0.14
DV 14	0.12	0.30	0.03	0.11ns	0.52	0.29	0.69	-0.23	-0.67	-0.20	0.25	0.16	0.46	0.45	0.10
DV 15	0.14	0.43	0.15	0.64	0.39	0.32	0.79	-0.21	-0.76	-0.10	0.36	0.18	0.58	0.39	-0.008
DV 18	0.11	0.33	0.21	0.67	-0.20	0.06	0.18ns	0.12	0.48	0.15	0.11	0.15	0.51	-0.08	0.03
DV 19	0.10	0.43	0.18	0.72	0.10	0.11	0.44	0.06	0.25ns	0.05	0.20	0.14	0.53	0.21	0.03
DV 20	0.10	0.46	0.17	0.75	0.08	0.11	0.56	0.02	0.11ns	0.06	0.13	0.15	0.68	0.14	0.05
DV 23	0.11	0.40	0.18	0.66	0.17	0.14	0.52	0.10	0.44	0.08	0.12	0.15	0.57	0.11	0.04

Appendix A4. **Principal component loadings for *Peromyscus leucopus* populations. Truss character set. Ventral truss network.**

	fusus		*aridulus*		*leucopus*		*incensus*			*noveboracensis*			
Character	PCI	r	PCI	r	PCI	r	PCI	r	PCII	PCI	r	PCII	PCIII
DV 26	0.34	0.86	0.41	0.73	0.35	0.75	0.41	0.88	-0.19	0.33	0.68	-0.02	-0.32
DV 28	0.42	0.87	0.26	0.68	0.32	0.76	0.32	0.84	-0.32	0.35	0.83	-0.10	-.039
DV 29	0.29	0.75	0.18	0.56	0.21	0.67	0.29	0.71	-0.31	0.25	0.66	0.21	-0.07
DV 30	0.42	0.92	0.32	0.77	0.26	0.69	0.31	0.83	-0.30	0.34	0.86	-0.06	-0.36
DV 33	0.40	0.78	0.57	0.81	0.54	0.80	0.41	0.81	0.39	0.45	0.74	-0.06	0.61
DV 34	0.11	0.49	0.09	0.37ns	0.16	0.54	0.26	0.78	0.24	0.22	0.70	0.25	0.02
DV 35	0.24	0.81	0.25	0.82	0.30	0.88	0.31	0.93	0.18	0.30	0.89	0.01	0.13
DV 38	-0.03	-0.17ns	0.10	0.30ns	0.07	0.23ns	0.14	0.47	0.37	0.21	0.54	0.48	0.31
DV 39	0.15	0.52	0.24	0.61	0.26	0.78	0.18	0.59	0.31	0.22	0.68	0.25	0.05
DV 40	0.11	0.55	0.15	0.57	0.18	0.67	0.22	0.74	0.35	0.22	0.67	0.37	0.12
DV 43	0.31	0.91	0.27	0.78	0.26	0.76	0.24	0.83	-0.22	0.23	0.76	-0.13	-0.18
DV 44	0.05	0.22ns	0.01	0.05ns	0.10	0.40	0.11	0.46	0.05	0.09	0.36	0.15	0.13
DV 45	0.29	0.91	0.23	0.79	0.27	0.83	0.21	0.83	-0.16	0.21	0.80	-0.07	-0.13
DV 48	0.03	0.13ns	0.11	0.43	0.06	0.21ns	0.11	0.49	-0.09	0.06	0.25ns	0.20	0.21

Appendix A5. Principal component loadings for *Peromyscus leucopus* populations. Truss character set. Lateral truss network.

	fusus		aridulus		leucopus			incensus			noveboracensis		
Character	PCI	r	PCI	r	PCI	r	PCII	PCI	r	PCII	PCI	r	PCII
DV 3	0.21	0.77	0.17	0.58	0.25	0.77	0.29	0.03	0.11ns	0.29	0.30	0.85	-0.07
DV 8	0.35	0.79	0.26	0.67	0.28	0.59	-0.78	0.53	0.91	-0.40	0.27	0.70	-0.32
DV 13	0.14	0.46	0.12	0.47	0.20	0.56	0.44	-0.23	-0.59	0.49	0.10	0.34	0.45
DV 18	0.06	0.29ns	0.15	0.72	0.05	0.25ns	0.009	0.10	0.47	0.02	0.11	0.50	0.08
DV 23	0.07	0.38	0.12	0.65	0.10	0.50	-0.007	0.10	0.57	0.03	0.10	0.50	0.16
DV 28	0.30	0.87	0.16	0.63	0.23	0.78	-0.04	0.24	0.78	0.21	0.26	0.87	-0.11
DV 33	0.27	0.73	0.33	0.70	0.30	0.65	0.17	0.30	0.75	-0.13	0.31	0.71	-0.43
DV 38	-0.02	-0.14ns	0.06	0.31ns	0.08	0.37	0.006	0.10	0.48	-0.15	0.14	0.49	0.40
DV 43	0.23	0.91	0.19	0.85	0.19	0.81	0.03	0.20	0.85	0.18	0.18	0.84	-0.06
DV 48	0.04	0.23ns	0.08	0.46	0.04	0.23ns	0.06	0.08	0.37	0.06	0.04	0.19ns	0.19
DV 51	0.18	0.75	0.20	0.82	0.24	0.84	-0.03	0.23	0.74	0.22	0.20	0.75	-0.15
DV 52	0.23	0.86	0.25	0.86	0.24	0.91	-0.05	0.20	0.78	0.18	0.23	0.82	0.20
DV 53	0.25	0.87	0.22	0.77	0.18	0.72	-0.05	0.18	0.70	0.22	0.24	0.81	-0.14
DV 54	0.25	0.88	0.22	0.84	0.27	0.91	0.11	0.13	0.60	0.28	0.28	0.93	-0.09
DV 55	0.24	0.94	0.27	0.96	0.26	0.94	-0.03	0.25	0.91	0.11	0.24	0.95	0.04
DV 56	0.28	0.94	0.28	0.94	0.30	0.96	-0.09	0.27	0.94	-0.0009	0.26	0.94	0.03
DV 57	0.22	0.90	0.26	0.88	0.26	0.93	-0.10	0.27	0.93	0.01	0.28	0.93	0.05
DV 58	0.19	0.86	0.20	0.87	0.18	0.87	0.08	0.11	0.65	0.20	0.16	0.78	0.18
DV 59	0.18	0.87	0.15	0.81	0.16	0.80	0.09	0.10	0.66	0.14	0.15	0.79	0.19
DV 60	0.21	0.90	0.24	0.95	0.20	0.89	0.10	0.08	0.44	0.28	0.20	0.87	0.17
DV 61	0.14	0.55	0.21	0.69	0.17	0.61	0.09	0.18	0.58	-0.08	0.17	0.64	0.23
DV 62	0.11	0.72	0.13	0.78	0.09	0.56	-0.001	0.12	0.76	0.11	0.12	0.75	0.10
DV 63	0.20	0.91	0.22	0.93	0.21	0.88	-0.004	0.14	0.74	0.16	0.17	0.87	0.06

Appendix A6. Principal component loadings for *Peromyscus* *leucopus* populations. Truss character set. Three dimensional view.

Character	fusus		aridulus		leucopus		incensus		noveboracensis		
	PCI	r	PCI	r	PCI	r	PCI	r	PCI	r	PCII
DV 1	0.23	0.60	0.48	0.87	0.35	0.81	0.22	0.70	0.39	0.83	-0.02
DV 9	0.16	0.56	0.12	0.52	0.20	0.69	0.06	0.34	0.25	0.72	-0.001
DV 13	0.22	0.53	0.16	0.53	0.31	0.69	-0.31	-0.64	0.16	0.42	0.53
DV 14	0.11	0.31	0.02	0.08	0.19	0.50	-0.20	-0.62	0.14	0.44	0.41
DV 18	0.07	0.25	0.18	0.69	0.05	0.20	0.11	0.45	0.13	0.49	0.03
DV 19	0.09	0.42	0.16	0.77	0.09	0.39	0.10	0.46	0.13	0.57	0.23
DV 23	0.11	0.44	0.16	0.70	0.13	0.53	0.15	0.64	0.15	0.61	0.10
DV 25	0.36	0.90	0.27	0.88	0.26	0.82	0.29	0.87	0.31	0.81	-0.29
DV 26	0.34	0.84	0.35	0.79	0.28	0.73	0.41	0.88	0.31	0.71	-0.20
DV 34	0.10	0.44	0.05	0.27	0.13	0.52	0.24	0.72	0.20	0.74	0.14
DV 38	-0.03	-0.14	0.11	0.45	0.10	0.40	0.13	0.51	0.20	0.57	0.28
DV 39	0.14	0.49	0.16	0.51	0.19	0.70	0.17	0.57	0.20	0.73	0.14
DV 43	0.33	0.93	0.24	0.86	0.22	0.76	0.24	0.82	0.20	0.75	-0.15
DV 44	0.07	0.30	0.02	0.07	0.06	0.29	0.11	0.46	0.08	0.37	0.07
DV 48	0.06	0.26	0.09	0.42	0.07	0.31	0.11	0.48	0.06	0.24	0.20
DV 50	0.39	0.89	0.27	0.85	0.31	0.86	0.31	0.87	0.29	0.81	-0.24
DV 51	0.25	0.75	0.23	0.77	0.29	0.81	0.26	0.69	0.22	0.66	-0.29
DV 55	0.33	0.93	0.31	0.92	0.31	0.91	0.30	0.87	0.29	0.92	-0.11
DV 58	0.27	0.88	0.23	0.87	0.23	0.91	0.14	0.66	0.22	0.85	0.09
DV 61	0.22	0.60	0.26	0.72	0.22	0.65	0.23	0.58	0.23	0.73	0.07

Appendix A7. Principal component loadings for *Peromyscus leucopus* subspecies. Truss character set. Dorsal truss network.

Character	PCI	r	PCII	PCIII
DV 1	0.34	0.77	0.03	-0.08
DV 3	0.39	0.81	0.25	-0.20
DV 4	0.28	0.61	0.32	-0.39
DV 5	0.37	0.84	0.26	-0.22
DV 8	0.42	0.66	-0.76	0.09
DV 9	0.21	0.69	0.09	0.03
DV 10	0.34	0.85	-0.27	-0.04
DV 13	0.21	0.49	0.21	0.61
DV 14	0.12	0.36	0.18	0.44
DV 15	0.17	0.57	0.18	0.39
DV 18	0.15	0.53	-0.04	-0.10
DV 19	0.15	0.63	0.05	-0.08
DV 20	0.14	0.69	0.05	0.08
DV 23	0.18	0.68	-0.02	0.08

Appendix A8. Principal component loadings for *Peromyscus leucopus* subspecies. Truss character set. Ventral truss network.

Character	PCI	r	PCII	PCIII
DV 26	0.31	0.75	-0.11	-0.33
DV 28	0.38	0.86	0.22	-0.45
DV 29	0.28	0.77	0.18	0.13
DV 30	0.35	0.87	0.14	-0.42
DV 33	0.40	0.77	-0.76	0.25
DV 34	0.23	0.74	0.17	0.32
DV 35	0.30	0.92	-0.05	0.17
DV 38	0.18	0.55	0.43	0.32
DV 39	0.20	0.72	0.12	0.25
DV 40	0.22	0.77	0.28	0.23
DV 43	0.26	0.83	-0.07	-0.09
DV 44	0.10	0.44	0.02	0.17
DV 45	0.24	0.86	-0.06	-0.04
DV 48	0.07	0.33	-0.002	0.23

Appendix A9. Principal component loadings for *Peromyscus leucopus* subspecies. Truss character set. Lateral truss network.

Character	PCI	r	PCII	PCIII
DV 3	0.26	0.78	0.37	0.05
DV 8	0.32	0.73	-0.77	0.04
DV 13	0.15	0.48	0.28	0.25
DV 18	0.10	0.52	0.01	-0.03
DV 23	0.12	0.66	0.02	0.04
DV 28	0.28	0.86	-0.13	0.27
DV 33	0.28	0.72	0.02	-0.84
DV 38	0.13	0.54	0.09	0.20
DV 43	0.20	0.86	0.04	-0.04
DV 48	-0.05	0.32	0.09	-0.08
DV 51	0.19	0.77	-0.008	0.08
DV 52	0.20	0.82	0.08	0.10
DV 53	0.22	0.82	-0.13	0.27
DV 54	0.25	0.87	0.25	0.01
DV 55	0.25	0.95	-0.05	0.001
DV 56	0.26	0.93	-0.11	-0.05
DV 57	0.25	0.91	0.007	-0.07
DV 58	0.19	0.88	0.11	0.01
DV 59	0.18	0.85	0.13	-0.004
DV 60	0.22	0.90	0.15	0.05
DV 61	0.18	0.70	0.05	0.05
DV 62	0.14	0.81	0.06	-0.02
DV 63	0.19	0.91	0.06	-0.03

Appendix A10. Principal component loadings for *Peromyscus leucopus* taxa. Truss character set. Three dimensional view.

Character	PCI	r	PCII	PCIII
DV 1	0.30	0.77	-0.10	-0.12
DV 9	0.17	0.63	0.12	-0.25
DV 13	0.20	0.51	0.65	0.44
DV 14	0.09	0.32	0.55	0.04
DV 18	0.12	0.49	-0.07	-0.30
DV 19	0.14	0.63	0.14	-0.18
DV 23	0.17	0.71	0.07	-0.06
DV25	0.34	0.90	-0.17	0.004
DV 26	0.29	0.74	-0.29	0.28
DV 34	0.21	0.71	0.08	-0.33
DV 38	0.17	0.57	0.14	-0.46
DV 39	0.19	0.70	0.05	-0.20
DV 43	0.25	0.85	-0.13	0.12
DV 44	0.10	0.45	0.05	-0.11
DV 48	0.07	0.36	0.12	-0.20
DV 50	0.34	0.91	-0.12	0.10
DV 51	0.24	0.76	-0.16	0.23
DV 55	0.31	0.91	-0.08	0.05
DV 58	0.25	0.89	0.08	0.007
DV 61	0.24	0.73	0.009	0.20

BIBLIOGRAPHY

BIBLIOGRAPHY

Alberch, P. 1983. Morphological variation in the neotropical salamander genus *Bolitoglossa*. Evolution 37:906-919.

Alberch, P., S.J. Gould, G.F. Oster, and D.B. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296-317.

Allen, J.A. 1894. Cranial variation in *Neotoma micropus* due to growth and individual differentiation. Bull. Am. Mus. Nat. Hist. 6:233-246.

Avise, J.C., M.H. Smith, and R.K. Selander. 1979. Biochemical polymorphism and systematics in the genus *Peromyscus*. VII. Geographic differentiation in members of the *truei* and *maniculatus* species group. J. Mamm. 60:177-192.

Ayala, F. 1983. Microevolution and macroevolution. p.203-227. In: Evolution from Molecules to Man. D.S. Bendall (ed.). Cambridge University Press, Cambridge.

Barbour, C.D. and B. Chernoff. 1984. Comparative morphology and morphometrics of the Pescados Blancos (Genus *Chirostoma*) from Lake Chapala, Mexico. p.111-128. In: Evolution of Fish Speces Flocks. A.A. Echelle and I. Kornfield (eds.). University of Maine at Orono Press, Orono.

Bookstein, F.L. 1982. Foundations of morphometrics. Ann. Rev. Ecol. Syst. 13:451-470.

Bookstein, F.L., B. Chernoff, R. Elder, J. Humphries, G. Smith, and R. Strauss. 1985. Morphometrics in Evolutionary Biology. Special Publication 15. The Academy of Natural Sciences of Philadelphia.

Baker, R.J., L.W. Robbins, F.B. Stangl, Jr., and E.C. Birney. 1983. Chromosomal evidence for a major subdivision in *Peromyscus leucopus*. J. Mamm. 64:356-359.

Bush, G.L. 1982. What do we really know about speciation? p.119-128. In: Perspectives on Evolution. R. Milkman (ed.). Sinauer Ass. Inc., Sunderland.

Bryant, P. 1984. Geometry, statistics, probability: Variations on a common theme. Am. Stat. 38:38-48.

Charlesworth, B., R. Lande, and M. Slatkin. 1982. A neo-Darwinian commentary on macroevolution. Evolution 36:474-498.

Chatfield, C. and A.J. Collins. 1980. Introduction to Multivariate Analysis. Chapman and Hall, London.

Cheverud, J.M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution 36:499-516.

Cock, A.G. 1966. Genetical aspects of metrical growth and form in animals. Quart. Rev. Biol. 41:131-190.

Cockrum, E.L. 1962. Introduction to Mammalogy. The Ronald Press Co., New York.

Creighton, G.K. and R.E. Strauss. 1985. Comparative patterns of growth and development in cricetine rodents and the evolution of ontogeny. Evolution. In press.

DeBlase, A.F. and R.E. Martin. 1981. A Manual of Mammalogy with Keys to Families of the World. 2nd. Ed. Wm. C. Brown Co., Dubuque.

Dice, L.R. 1932. Variation in a geographic race of the deer-mouse, *Peromyscus maniculatus bairdii*. Occ. Papers Mus. Zool., Univ. Mich. 239:1-26.

Dice, L.R. 1937. Variation in the wood-mouse, *Peromyscus leucopus noveboracensis*, in the northeastern United States. Occ. Papers Mus. Zool., Univ. Mich. 352:1-32.

Dice, L.R. 1939. Variation in the wood-mouse, *Peromyscus leucopus*, from several localities in New England and Nova Scotia. Contr. Lab. Vert. Gen. 9:1-16.

Dice, L.R. 1940. Relationships between the wood-mouse and the cotton-mouse in western Virginia. J. Mamm. 21:14-23.

Dice, L.R. 1968. Speciation. p.75-97. In: Biology of *Peromyscus*. J.A. King (ed.). Special Publication no. 2. The American Society of Mammalogists.

Diersing, V.E. 1981. Systematic status of *Sylvilagus brasiliensis* and *S. insonus* from North America. J. Mamm. 62:539-556.

DosReis, S.F. and D.O. Straney. 1983. Morphometrics of *leucopus*-group *Peromyscus*. I. Truss analysis. 63rd Annual Meeting of the American Society of Mammalogists. University of Florida, Gainesville.

Engstrom, M.D., D.J. Schmidly, and P.K. Fox. 1982. Nongeographic variation and discrimination of species within the *Peromyscus leucopus* species group (Mammalia: Cricetinae) in eastern Texas. Texas J. Sci. 34:149-162.

Fink, W.L. 1982. The conceptual relationship between ontogeny and phylogeny. Paleobiology 8:254-264.

Goldman, E.A. 1904. Description of five new mammals from Mexico. Proc. Biol. Soc. Wash. 17:79-82.

Goldman, E.A. 1917. Mammals from Northeastern Middle America. Proc. Biol. Soc. Wash. 30:109-116.

Gould, S.J. and R.F. Johnston. 1972. Geographic variation. Ann. Rev. Ecol. Syst. 3:457-498.

Gupta, A. and R.C. Lewontin. 1982. A study of reaction norms in natural populations of Drosophila pseudoobscura. Evolution 36:934-948.

Hall, E.R. 1981. The Mammals of North America. John Wiley, New York.

Hall, E.R. and W.B. Davis. 1934. Notes on arizona rodents. Proc. Biol. Soc. Wash. 47:51-56.

Hooper, E.T. 1968. Classification. p.27-74. In: Biology of Peromyscus (Rodentia). J.A. King (ed.). Special Publication No. 2. The American Society of Mammalogists.

Howell, A.H. 1910. Notes on mammals of the Middle Mississippi valley, with description of a new wood rat. Proc. Biol. Soc. Wash. 23:23-24.

Humphries, J.M., F.L. Bookstein, B. Chernoff, G.R. Smith, R.L. Elder, and S.G. Poss. 1981. Multivariate discrimination by shape and in relation to size. Syst. Zool. 30:291-308.

Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. Biometrics. 19:497-499.

Kluge, A.G. and R.E. Strauss. 1985. Ontogeny and systematics. Ann. Rev. Ecol. Syst. 16:247-268.

Lande, R. and S.J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210-1226.

Leamy, L. and D. Bradley. 1982. Static and growth allometry of morphometric traits in randombred house mice. Evolution 36:1200-1212.

Lewontin, R.C. 1982. Review of. Perspectives on Evolution. Paleobiology 8:309-313.

Lyon, M.W. 1906. The pigmy squirels of the Nannosciurus melanotis group. Proc. Biol. Soc. Wash. 19:51-56.

Maynard Smith, J., R. Burian, S. Kaufman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert. 1985. Developmental constraints and evolution. Quart. Rev. Biol. 60:265-286.

Mayr, E. 1980. The role of systematics in the evolutionary synthesis. p.123-136. In: The Evolutionary Synthesis. E. Mayr and W.B. Provine (eds.). Harvard University Press, Cambridge.

Mayr, E. and W.B. Provine. 1980. The Evolutionary Synthesis. Harvard University Press, Cambridge.

McCarley, W.H. 1954. Natural hybridization in the Peromyscus leucopus species group of mice. Evolution 8:314-323.

McCarley, W.H. 1963. Distributional relationships of sympatric populations of Peromyscus leucopus and P. gossypinus. Ecology 44: 784-788.

Morrison, D.F. 1976. Multivariate Statistical Methods. McGraw Hill, New York.

Moyers, R.E. and F.L. Bookstein. 1979. The inappropriateness of conventional cephalometrics. Am. J. Orth. 75:599-617.

Neff, N.A. and G.R. Smith. 1979. Multivariate analysis of hybrid fishes. Syst. Zool. 28:176-196.

Neff, N.A. and L.F. Marcus. 1980. A Survey of Multivariate Methods for Systematics. New York:Privately Published.

Nelson, E.W. and E.A. Goldman. 1929. Six new pocket mice from Lower California and notes on the status of some described species. Proc. Biol. Soc. Wash. 42:103-112.

Olson, E.C. and R.L. Miller. 1958. Morphological Integration. University of Chicago Press, Chicago.

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

Osgood, W.H. 1909. Revision of the mice of the American genus Peromyscus. N. Amer. Fauna 28:1-258.

Pimentel, R.A. 1979. Morphometrics. Kendall/Hunt, Dubuque.

Price, P.K. and M.L. Kennedy. 1980. Genic relationships in the white-footed mouse, Peromyscus leucopus, and the cotton-mouse, P. gossypinus. Am. Mid. Nat. 103:73-82.

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

Radinsky, L.B. 1985. Approaches in evolutionary morphology: A search for patterns. Ann. Rev. Ecol. Syst. 16:1-14.

Rogers, D.S. and D.J. Schmidly. 1982. Systematics of spiny pocket mice (Genus Heteromys) of the Desmarestianus species group from Mexico and northern California. J. Mamm. 63:375-386.

Raff, R.A. and T.C. Kaufman. 1983. Embryos, Genes, and Evolution: The Developmental-Genetic Basis of Evolutionary Change. Macmillan, New York.

Rensch, B. 1980. Historical development of the present synthetic Neo-Darwinism in Germany. p.284-302. In: The Evolutionary Systhesis. E. Mayr and W.B. Provine (eds.). Harvard University Press, Massachusetts.

Rinker, G.C. 1954. The comparative myology of the mammalian genera Sigmodon, Oryzomys, Neotoma, and Peromyscus (Cricetinae), with remarks on their intergeneric relationships. Misc. Publ. Mus. Zool. Mus. Zool., 83:1-124.

Robbins, L.W., M.H. Smith, M.C. Wooten, and R.K. Selander. 1985. Biochemical polymorphism and its relationship to chromosomal and morphological variation in Peromyscus leucopus and Peromyscus gossypinus. J. Mamm. 66:498-510.

Sneath, P. and R. Sokal. 1973. Numerical Taxonomy. Freeman, San Francisco.

Sokal, R. and F.J. Rohlf. 1981. Biometry. 2nd. Edition. Freeman, San Francisco.

Stangl, F.B. and R.J. Baker. 1984. A chromosomal subdivision in Peromyscus leucopus: Implications for the subspecies concept as applied to mammals. p.139-145. In: Festschrift for Walter W. Dalquest in Honor of His Sixty-six Birthday. N.V. Horner (ed.). Dept. Biology, Midwestern State University.

Stangl, F.B. and R.J. Baker. 1984. Evolutionary relationships in Peromyscus: Congruence in chromosomal, genic, and classical data sets. J. Mamm. 65:643-654.

Straney, D.O. and J.L. Patton. 1980. Phylogenetic and environmental determinants of geographic variation of the pocket mouse Perognathus golmani Osgood. Evolution 34:888-903.

Strauss, R.E. 1984. Allometry and functional feeding morphology in haplochromine cichlids. p.217-230. In: Evolution of Fish Species Flocks. A.A. Echelle and I. Kornfield (eds.). University of Maine at Orono Press, Orono.

Strauss, R.E. 1985. Static allometry and variation in body form in the South American catfish genus Corydoras (Callichthyidae). Syst. Zool. In Press.

Strauss, R.E. and F.L. Bookstein. 1982. The truss: Body form reconstruction in morphometrics. Syst. Zool. 31:113-135.

Strauss, R.E. and L.A. Fuiman. 1985. Quantitative comparisons of body form and allometry in larval and adult Pacific sculpins (Teleostei: Cottidae). Can. J. Zool. 63:1582-1589.

Sumner, F.B. 1932. Genetic, distributional, and evolutionary studies of the subspecies of deer mice (Peromyscus). Bibliographia Genetica 9:1-106.

Templeton, A.R. 1980. The theory of speciation via the founder principle. Genetics 94: 1011-1038.

Templeton, A.R. 1981. Mechanisms of speciation- a population genetics approach. Ann. Rev. Ecol. Syst. 12:23-48.

Templeton, A.R. 1982. Adaptation and the integration of evolutionary forces. p.15-31. In: Perspectives on Evolution. R. Milkman (ed.). Sinauer, Sunderland.

Via, S. 1984a. The quantitative genetics of polyphagy and insect herbivory. I. Genotype-environment interactions in larval performance on different host plant species. Evolution 38:881-895.

Via, S. 1984b. The quantitative genetics of polyphagy and insect herbivory. II. Genetic correlations in larval performance within and across host plants. Evolution 38:896-905.

Wolfe, J.L. and A.V. Linzey. 1977. Peromyscus gossypinus. Mammalian Species 70:1-5.

Wright, S. 1943. Isolation by distance. Genetics 28:114-138.