Evolution, Systematics, and Historical Biogeography
of Kangaroo Mice, Genus *Microdipodops*

By

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ABSTRACT

This study examines the evolution, systematics, and historical biogeography of kangaroo mice, genus *Microdipodops* (Rodentia; Heteromyidae) using a synthetic approach. Four levels of evolution are examined in *Microdipodops* including: 1) genotypic expression as determined by protein analysis; 2) gene packaging as assayed by chromosomal analyses; 3) phenotypic expression as assayed by cranial and external morphometrics; and 4) the phenotype as quantified by pelage colorimetrics. In addition, environmental and climatological parameters for *Microdipodops* localities are analyzed and provide one set of constraints under which evolution at the above levels may accur. Patterns of geographic variation within each of these five data sets are elucidated and such information is used to interpret evolutionary events in relation to the historical biogeography of the group. Although each of the above methodologies applied independently has increased our understanding of evolutionary processes, few systematic studies have utilized more than one approach simultaneously. A synthetic or eclectic approach, one utilizing a variety of methodologies to examine different levels of evolution, should, in theory, permit a more complete determination

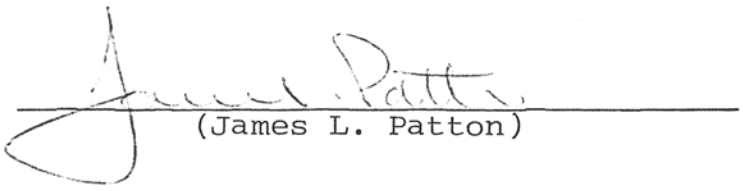
of the phyletic history of the taxa under study, inasmuch as each level of evolution provides inherently different pieces of historical information.

Several nonparametric methods to quantify the patterns of concordance among the data sets are used to assess phylogenetic and environmental determinants of geographic variation. Patterns of chromosomal and morphometric variation are moderately concordant with the phylogenetic inferences based on biochemical analyses. Further, patterns of colorimetric variation were found to be associated with patterns of environmental variation, and moreover, these two data sets were judged to be discordant with those derived from protein, chromosomal, and morphometric analyses.

Two species are recognized within Microdipodops: M. megacephalus and M. pallidus. The time since divergence between these species was estimated to be two million years. Within each species, three megasubspecies are recognized. Megasubspecific differentiations appear to have occurred about one million years ago. In the process of detailing major features of evolution in kangaroo mice, I have recognized two new subspecies (one in each species) and have extended the known geographic distribution of the genus to include the state of Idaho.

Evolutionary biogeographic scenarios are presented to explain patterns of Microdipodops evolution in a temporal and spacial context. Such evolutionary biogeographical

patterns, derived from a synthetic systematic approach, may be used as models for future studies of basin-dwelling animals in the Great Basin.

Approved: 
(James L. Patton)

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INTRODUCTION

With the formulation of modern evolutionary thought and the advent of analytical techniques that permit systematists to approximate the genetic relatedness of populations, mammalian systematists today have the opportunity to test evolutionary concepts and to explore the phylogenetic history of taxa at a depth never before possible. During the past two decades the methodologies that have had increasingly important influence in evolutionary systematics include: 1) electrophoretic analysis of proteins; 2) comparative karyology; and 3) cladistic and phenetic approaches to morphology. Although each of the methodologies, applied independently, has increased our understanding of evolutionary processes, unfortunately very few systematic studies of mammals have utilized more than one approach and only very recently have all three methodologies been employed simultaneously (e.g. Patton et al., 1979; Hafner et al., 1979). Several important studies have indicated a high degree of evolutionary independence of molecular, chromosomal, and morphological evolution (Turner, 1974; Gould et al., 1974; Maxson and Wilson, 1974, 1975; Johnson, 1974, 1975; Avise et al., 1975; King and Wilson, 1975; Kornfield and Koehn, 1975; Johnson et al., 1977; Patton and Yang, 1977), and it appears that the aforementioned methodologies examine and appraise different levels of biological organization or "levels of evolution". A

synthetic approach, one utilizing a variety of methodologies to examine different levels of evolution, should allow for a more complete determination of the phyletic history of the taxa under study, inasmuch as each level of evolution provides inherently different pieces of historical information. Furthermore, a synthetic approach will determine whether molecular, karyotypic, and morphological characters are evolutionarily concordant or discordant and help elucidate instances of mosaic evolution and convergence (Mickevich and Johnson, 1976).

This project is designed to examine the evolution, systematics, and historical biogeography of kangaroo mice, genus Microdipodops (Rodentia; Heteromyidae) using what I term a synthetic or eclectic approach as outlined above. Four levels of evolution are examined within Microdipodops including: 1) genotypic expression as determined by protein analysis; 2) gene packaging as assayed by chromosomal analyses; 3) phenotypic expression as assayed by cranial and external morphometrics; and 4) the phenotype as quantified by pelage colorimetrics. Further, climatological and environmental parameters for Microdipodops localities are analyzed and provide one set of constraints under which evolution at the above four levels may occur. Patterns of geographic variation within each of these five data sets are elucidated and such information is used to interpret effectively evolutionary events in relation to the historical biogeography of the group.

The genus Microdipodops lends itself particularly well to this sort of systematic approach. Surprisingly little information is available concerning the systematics and evolution of the genus, while these topics have been studied extensively in other geomyoid rodents (the families Heteromyidae and Geomyidae), including familiar forms such as kangaroo rats, pocket gophers, and pocket mice. In fact, Microdipodops is one of the most poorly known genera of North American rodents. It follows then, that information that I uncover will not only contribute significantly to our knowledge of evolution in this unique mammalian group, but phylogenetic hypotheses I draw will be constructed from a perspective unbiased relative to previous viewpoints. The group contains two species, M. megacephalus and pallidus, and is restricted in distribution to the Great Basin desert region of North America. Kangaroo mice appear to be a simple, cohesive lineage (as compared to other broadly distributed and taxonomically diverse rodent genera), a fact that should facilitate this study of the systematics of the group. Further, the Great Basin provides an excellent setting upon which the phyletic history of Microdipodops can be viewed. Much is known about the past environments in this region. For example, Blackwelder (1948) presented information about the geologic background; Antevs (1952) discussed climatic change; Morrison (1965) examined lake levels and lacustral intervals; and Chaney (1938, 1940),

Axelrod (1950, 1958), and Tidwell et al. (1972) have analyzed floristic changes throughout the Cenozoic Era. These studies provide an independent time scale, an evolutionary stage, on which the historical biogeography and evolutionary history of kangaroo mice can be interpreted effectively.

Kangaroo Mouse Origins.--Kangaroo mice are regarded as rather bizarre creatures for they manifest a variety of peculiar morphological features including an enormous head (greatest relative inflation of the auditory bullae known among mammals extant or extinct), long, furry hind feet, and a tail that is thickened at midpoint due to fat deposition. Fossil material of Microdipodops is presently unknown and therefore workers addressing the origins of kangaroo mice have had to rely on neontological evidence without the benefit of paleontological insight. An explanation for the absence of kangaroo mice in the fossil record may lie basically in two factors: 1) their small, delicate skeletons (approximately 150 millimeters in total length) may be unable to withstand the rigors of fossilization; or, 2) mammal paleontologists have simply not uncovered the appropriate age deposits in the Great Basin desert or have not examined in adequate detail the material currently housed in museum cases.

Since Merriam's description of the genus Microdipodops nearly a century ago, there has been a considerable amount of speculation and controversy as to the subfamilial affinities

of the group. Does the genus belong to the Perognathinae (pocket mouse lineage) or the Dipodomyinae (kangaroo rat lineage) within the family? Several years ago I pointed out (Hafner, J. C., 1978) that there exists a third alternative that should be considered: the possibility that Microdipodops represents an independent lineage distinct from both pocket mice and kangaroo rats. In that earlier study I directed my attention to resolving this question of the evolutionary relationships of Microdipodops within the family Heteromyidae and performed a detailed phenetic analysis utilizing a broad spectrum of characters. I concluded that Microdipodops was most closely related, phenetically, to the pocket mice and therefore, in the absence of a fossil record and any evidence which would indicate that Microdipodops might represent a separate lineage, kangaroo mice should be considered within the Perognathinae. Recently, however, biochemical data (Hafner, M. S., 1979) would suggest that while Microdipodops is clearly (*) may be marginally closer to Dipodomys than it is to Perognathus. I consider as tentative the biochemical conclusions that the "Proto-Microdipodops" lineage is more closely related to Dipodomys, as tentative, though, due to the inherent errors one realizes when attempting to discriminate among these heteromyid lineages groups such as these that diverged, perhaps simultaneously from one another, so long ago (Miocene). The controversy that surrounds the exact placement of the recently-derived enigmatic genus Microdipodops in the Heteromyidae will certainly rage on, but for present purposes I prefer to retain Microdipodops within the

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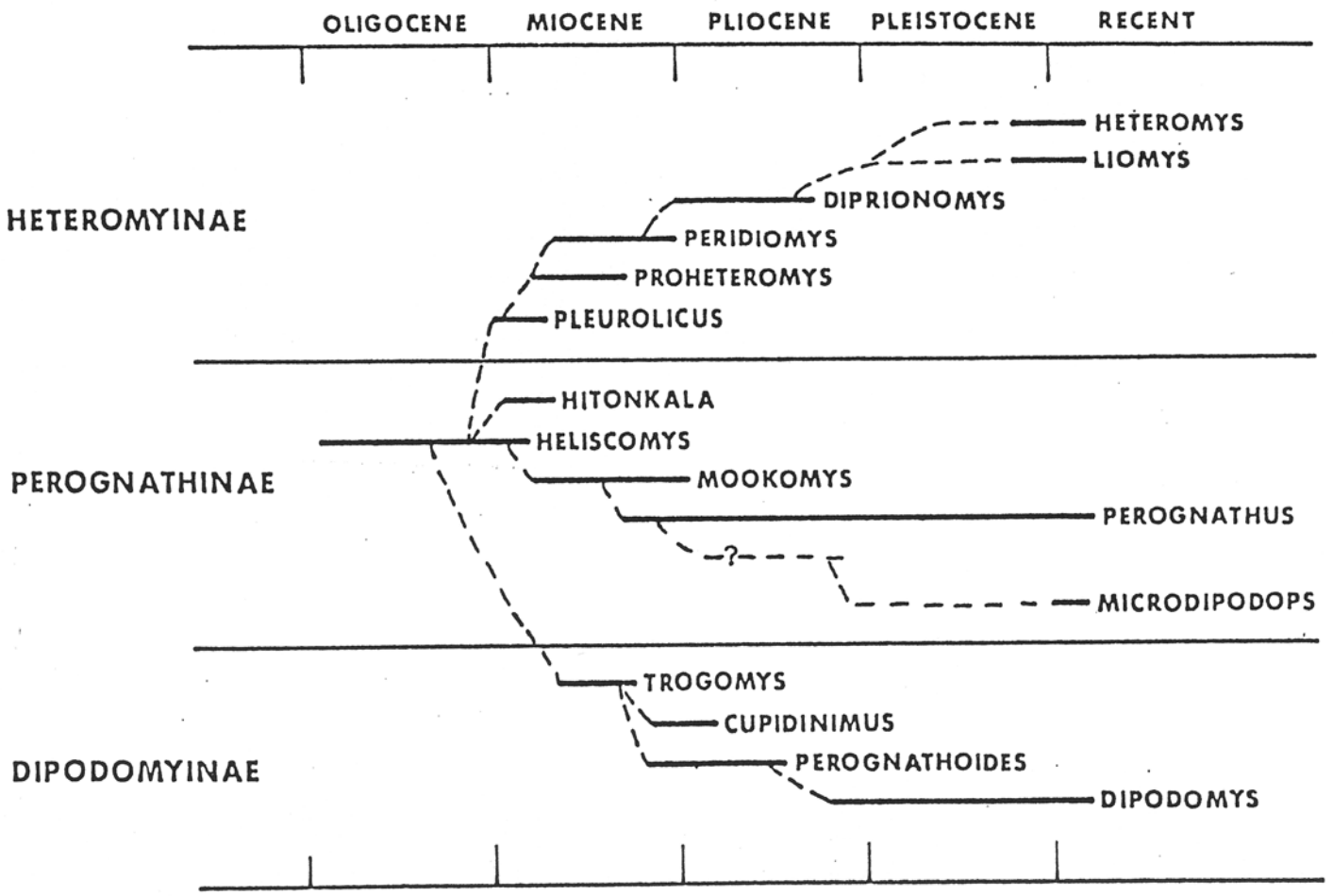
(*) distinct from both Perognathus and Dipodomys, it may represent a sole surviving taxon of a lineage that is

Perognathinae (Fig. 1). Perhaps, we have arrived at an impasse with respect to the Perognathus-Microdipodops-Dipodomys question; given the present limitations of the methodologies at hand we may be unable to resolve this important, yet fuzzy area in heteromyid evolution which may actually be a tricotomous branching event.

Taxonomic History and Prospectus.--Kangaroo mice, less commonly called gnome mice or dwarf kangaroo rats, were described by Merriam in 1891. The genus currently contains two species: M. megacephalus, designated as the type species, and M. pallidus which was described in 1901, also by Merriam. During the ensuing years, several subspecies of Microdipodops were described by various workers (Grinnell, 1914; Goldman, 1926, 1927; Hall and Durrant, 1937, 1941; and Hall, 1941a, 1941b). Hall's (1941b) revision of the genus culminated an era of active interest in the group. Since 1941, not a single publication has appeared which reappraises the patterns of geographic variation and taxonomy of Microdipodops.

The intent of this study is not to deliberate on the exact phylogenetic placement of Microdipodops within the Heteromyidae as was done previously (Hafner, J. C., 1976, 1978), nor to examine the genetics of contact zones between the species M. pallidus and M. megacephalus (Hafner, et al., 1979). This investigation appraises the patterns of character variation within the genus Microdipodops, using a multimethodological or synthetic approach as previously

Figure 1.--Phylogeny of the Heteromyidae showing the position of Microdipodops. Modified from Hafner (1978).


OLIGOCENE
MIOCENE
PLIOCENE
PLEISTOCENE
RECENT
HETEROMYINAE
HETEROMYS
LIOMYS
DIPRIONOMYS
PERIDIOMYS
PROHETEROMYS
PLEUROLICUS
HITONKALA
HELISCOMYS
PEROGNATHINAE
MOOKOMYS
PEROGNATHUS
?
MICRODIPODOPS
TROGOMYS
CUPIDINIMUS
PEROGNATHOIDES
DIPODOMYINAE
DIPODOMYS

discussed, for two primary purposes: 1) to relate our general understanding of processes and principles of evolutionary change to the specific nature of change within a relatively young (several million years) and doubtlessly monophyletic taxonomic group; and 2) to formulate a systematic reappraisal of the genus which, in a rather novel fashion, incorporates information derived from an eclectic set of systematic techniques. The principal questions that will be addressed in this study include: 1) What is the appropriate means for detailing patterns of protein variation in a recently-radiated taxon? 2) To what degree are the five data sets (proteins, chromosomes, morphometrics, colorimetrics, environmental data) concordant with one another? 3) How many species and subspecies are included in Microdipodops and when did these taxa diverge? 4) On what criteria should we recognize species and subspecies? 5) What are the potential advantages of employing my synthetic, multimethodological approach in evolutionary studies?

MATERIALS AND METHODS

Study Area and Fieldwork.--The hydrographic region known as the Great Basin is a roughly triangular region including about 200,000 square miles in the western part of the United States between the Wasatch Mountains and the Sierra Nevada. The majority of the Great Basin is contained within the state of Nevada, but smaller parts include the adjacent states of California, Oregon, Idaho, and Utah. The Great Basin is not, as its name might suggest, a single basin-shaped depression, but is a region that is composed of many subparallel and discontinuous drainage basins.

Within the Great Basin, kangaroo mice are typically found in sandy regions peripheral to basins and playas. Field collecting was directed to maximize capture of kangaroo mice. Collecting activities were conducted at known collecting sites of kangaroo mice (Hall, 1941b) and those additional localities judged to have appropriate Microdipodops habitat. The primary goal was collecting specimens of Microdipodops from widespread localities in the Great Basin. In the process of collecting specimens I accomplished 115 days of fieldword including 18,253 trapnights. Attempt was made to collect specimens at 139 sites (this figure includes several localities visited repeatedly) of which kangaroo mice were captured at less than one-half of the sites visited (47.5 per cent).

The average number of traps (almost exclusively Sherman folding live traps baited with rolled oats and/or birdseed) set per locality was 131.3 traps, with an overall mean success of kangaroo mouse capture of 2.49 per cent. Mean success of capture was elevated to 5.24 per cent when considering only those localities that yielded any kangaroo mice.

Polyacrylamide Gel Protein Electrophoresis.-- Biochemical variability was assayed in 78 individuals using polyacrylamide gel protein electrophoresis. Tissue samples, including blood plasma and homogenate of liver were available for the electrophoretic separation of the plasma proteins and nonspecific esterases, respectively. Protein electrophoretic analysis was performed in three stages: 1) separation of general plasma proteins; 2) separation of selected plasma proteins using diluted plasma samples; and 3) separation of nonspecific esterases.

Plasma samples were prepared for the first stage of electrophoresis with the addition of 50 per cent glycerol (e.g. six drops plasma and three drops 50 per cent glycerol). Diluted plasma samples were prepared for analysis by diluting the above prepared plasma samples 1:30 with tris sulfate glycerol (e.g. 6 drops tris sulfate glycerol and 5 microliters of plasma sample). Samples were prepared for the third phase of the electrophoretic analysis by diluting one volume of liver solution with two volumes of tris

sulfate glycerol (e.g. 3 drops liver homogenate and 6 drops tris sulfate glycerol).

All electrophoretic separations were carried out using vertical slab, polyacrylamide gels (eight per cent concentration) and in discontinuous systems (tris sulfate gels, tris borate electrode buffer). The dimensions of the gels were approximately 150 x 150 millimeters and 0.75 millimeters in thickness. Electrophoresis of general plasma proteins (phase one of the analysis) was performed with the aide of a small, one centimeter wide stacking gel (four per cent acrylamide and tris sulfate buffer) placed above the standard eight per cent separating gel. Separation of the diluted plasma samples and liver samples (phases two and three) were carried out using simply the eight per cent tris sulfate gel. Necessary recipes for acrylamide gel work are tabulated in Appendix A.

Specimen samples were loaded into slots on the top (cathode) side of the gel by use of a Hamilton syringe. A maximum of 13 specimen samples were loaded on a single gel. Five microliters of the plasma and diluted plasma samples (prepared as above) were used, while only 3.5 microliters of the liver samples (prepared as above) were used in the electrophoretic analysis. All electrophoretic separations were carried out in a cold room (approximately 40° F) and were subjected to a maximum of 15 milliamperes and 300 volts of electricity for an average running time of six hours. Once the specimen samples had migrated fully

into the gel during initial phases of electrophoresis (this took approximately 20 minutes at 10 milliamperes), thereafter the current was held at 15 milliamperes and the voltage was observed to increase linearly with the time. When the voltage reached 300 volts (in generally three hours) the electrical power was adjusted to 300 volts constant voltage so as to prevent any possible denaturing of the proteins which might occur with the excessive generation of heat at higher voltages.

Following electrophoretic separation, the gels were treated according to electrophoretic procedures of general staining. General staining for plasma proteins was accomplished by an overnight staining treatment of Coomassie Brilliant Blue (G-250) in perchloric acid solution. Esterase staining required a 30 minute treatment of a stain composed of two substrates (α-NP and α-NA), a coupling agent (Fast Blue RR) and common (low pH monobasic and high pH dibasic) phosphate stain buffers. Gels were then fixed in an eight per cent acetic acid solution (two rinses) following staining. After staining and fixing, the delicate and soft acrylamide gels were transformed into permanent records of electrophoretic analyses by affixing (heat-drying) the acrylamide gels to No. 3 filter paper.

One or two specimen samples were examined biochemically per locality for most localities surveyed in this study. The advantages and rationale for using but a single specimen

in electrophoretic studies (including both the band-counting and locus-by-locus methods) has been discussed and supported by Sarich (1977), Gorman and Renzi (1979), Hafner, M. S. (1979), Cronin et al. (1980), and Ferguson (1980). For several localities, however, larger samples (ten to twelve individuals) were analyzed electrophoretically to determine the extent of intrapopulational protein variability. Such analyses involving these larger population samples were aimed at determining the mean inter-individual protein similarity value, measures of polymorphism and heterozygosity, and to determine the affects (if any) of secondary sexual and seasonal variation on the plasma and nonspecific esterase profiles obtained by polyacrylamide electrophoresis.

Thirty-two protein bands (presumptive loci) were analyzed and scored in the analysis of biochemical variation. In the first phase of the electrophoretic analysis (analysis of general plasma proteins) 22 bands were scored. In the second phase of the analysis (examination of selected plasma proteins using diluted plasma samples) two bands were scored. The idenity of these two bands is known to be transferin and albumin by comparison with zymograms from specific staining procedures. Eight bands were scored in the examination of the nonspecific esterases. Five band attributes aided in the unambiguous identification of each of the 32 bands on the electrophoregrams: 1) color (e.g. blue, black, red, burgundy, pink, yellow, brown);

2) intensity (light to dark); 3) migration distance from origin; 4) band width; and 5) position relative to other bands. Individuals were scored as identical when they shared the same electromorph (presumptive allozyme) and as different when they were homozygous for different electromorphs at a particular band. A value S was used as a measure of genetic similarity and is simply the ratio of bands that have identical mobility to the total number of bands scored (32 bands). All individuals were analyzed and scored for the same 32 bands and similarity values (S) were computed for all pair-wise combinations of individuals. Further detailed discussion of the band-counting method is presented in Sarich (1977) and Ferguson (1980).

Karyology.--Chromosomal data analyzed in the course of this study is based upon 190 karyotyped specimens. Non-preferentially stained chromosome preparations were made using a modification of the in vivo bone-marrow technique described by Patton (1967a). The technique followed in the present study included the use of 0.04 per cent Velban solution (the mitotic inhibitor) and a 0.9 per cent sodium citrate solution (hypotonic reagent). Inasmuch as kangaroo mice are small rodents, it was deemed necessary, at times, to flush bone marrow from both the femurs and the tibias to obtain a sufficient quantity of mitotic material (the tibia yielded the greater amount). A minimum of 10 metaphase cells were inspected for each

animal included in this study and a representative cell was selected and photographed. The diploid number, fundamental number, and chromosome morphology used in the text follow standard methods (Patton, 1967a). Representative karyograms were constructed to facilitate comparisons between populations. The chromosomes were organized into six morphological catagories on the karyograms and within each class, autosomes were arranged in order of decreasing size. Nine characters were used in the analysis of interpopulational chromosomal variability in kangaroo mice. The nine chromosomal characters and the methods of scoring these characters are presented in Appendix B. In addition to the non-preferentially stained karyotypes, C-band analysis (specific staining for constitutive heterochromatin) was performed on selected chromosomal preparations using Patton's (1977) modification of the general C-band technique of Cooper and Hsu (1972).

Morphometric Analyses.--Morphological variability was assayed by examination of a battery of external and cranial morphometric characters. Four external and 16 cranial measurements were taken for each of the 441 specimens analyzed in this phase of the study: total length, tail length, hindfoot length, ear length, greatest length of skull, greatest breadth (across mastoids), basal length, bullar length, maxillary breadth, nasal length, least interorbital breadth, greatest expanse of lateral face

of zygoma (width of zygomatic process of maxilla), least expanse of lateral face of zygoma (taken at the maxillary base of zygoma), greatest length incisive foramina, length incisive foramina at point of greatest breadth (a measure of the posterior foraminal divergence taken from anterior margin of incisive foramina; see Hall, 1941b), greatest breadth incisive foramina, greatest pterygoidal breadth (distance across distal end of one pterygoid), arching of cranial dome (the distance from the dorsal margin of the foramin magnum to a line tangent to nasal-frontal plane), mandibular length, and angular bifurcation (a measure of the expansion of the wings of the angular process of the dentary; see Hafner et al., 1979). The external measurements were read directly from the specimen tag. Cranial measurements were taken with dial calipers and read to the nearest hundredth of a millimeter. Only adult specimens, those showing extensive wear on the permanent fourth upper premolar, were measured and used in the morphometric analyses. Sexes were pooled in all phases of the morphometric analyses as kangaroo mice are known to lack significant secondary sexual dimorphism in general cranial and external characters (Hall, 1941b; Schitoskey, 1968; Hafner, (1976).

Colorimetry.--A total of 686 specimens of kangaroo mice was examined for variation in pelage color using a Bausch and Lomb Spectronic 505 Spectrophotometer. Visible

reflectance of the mid-dorsal pelage was recorded for each specimen through a restricted port (6.5 millimeters in diameter) and recordings were taken at 10 per cent transmittance. All mid-dorsal samples recorded from the specimens were judged to be representative of general adult pelage and areas of excessive wear, active molt, juvenile pelage, and color abnormalities (particularly light or dark spots) were excluded from the analysis. Eight values (characters) were computed from the recordings of reflectance curves for each of the specimens including: relative brightness (= value); dominant wavelength (= hue) excitation purity (= chroma or saturation), trichromatic coefficient x, trichromatic coefficient y, end-point reflectance reading (RX_{10}), mid-point reflectance reading (RY_3), beginning-point reflectance (RZ_1). Colors reported herein were recorded from the chromaticity diagram based upon the Illuminant "C" selected ordinant system.

Environmental Data.--Twenty-eight environmental characters were recorded for the 42 localities tabulated in Table 1. The environmental information was taken from a comprehensive summary of the weather and climate in the Nevadan region over the last half-century (Houghton et al., 1975). The characters used in the study and the methods of scoring these characters are presented in Appendix C. Data for each of the 28 characters were taken directly from figures of isophene contours that appear in the source book by Houghton et al. (1975). Data gathering

Table 1.--Localities and numbers of specimens used in seaprate phases of this study. Traditional species names (designated according to Hall, 1941b) are indicated after each sample name: megacephalus (m), pallidus (p).

Locality Number	Alphabetic Code	Sample Name	Protein Analysis	Chromosome Analysis	Morphometric Analysis	Color Analysis
01	ALKA	Alkali Lake, Oregon (m)	1	1	12	18
02	NARR	Narrows, Oregon (m)	1	2	11	19
03	ALVO	Alvord Lake, Oregon (m)	0	0	11	19
04	RIDD	Riddle, Idaho	1	1	4	5
05	DENI	Denio, Nevada (m)	0	2	0	0
06	CONT	Contact, Nevada (m)	1	2	4	8
07	PAIN	Painted Point, Nevada (m)	0	0	9	13
08	QUIN	Quinn River, Nevada (m)	4	4	13	21
09	JUNG	Jungo, Nevada (m)	1	11	12	20
10	WINN	Winnemucca, Nevada (m)	2	6	12	20
11	SULP	Sulphur, Nevada (m)	2	3	11	19
12	IZEN	Izenhood, Nevada (m)	0	0	12	19
13	SMOK	Smoke Creek, Nevada (m)	1	1	6	10

Table 1 continued (2)

Locality Number	Alphabetic Code	Sample Name	Protein Analysis	Chromosome Analysis	Morphometric Analysis	Color Analysis
14	VERN	Vernon, Nevada (m)	0	2	12	18
15	LOVE	Lovelock, Nevada (p)	0	0	11	11
16	EURE	Eureka, Nevada (m)	1	4	12	19
17	GRAN	Granite Peak, Utah (m)	0	0	16	20
18	CALL	Callao, Utah (m)	1	5	9	12
19	NIXO	Nixon, Nevada	0	1	2	2
20	CHIL	Chilcoot, California (m)	1	4	11	17
21	SPAR	Sparks, Nevada (m)	1	3	4	3
22	WADS	Wadsworth, Nevada (m)	1	5	15	22
23	MTWL	Mountain Well, Nevada (p)	0	0	14	20
24	YERI	Yerington, Nevada (p)	1	5	17	17
25	STEW	Stewart Valley, Nevada (p)	0	0	8	20
26	MONI	Monitor Valley, Nevada (m)	0	0	12	15
27	HOTC	Hot Creek, Nevada (m)	1	4	7	16
28	LOCK	Locks, Nevada (p)	1	3	8	17

Table 1 continued (3)

Locality Number	Alphabetic Code	Sample Name	Protein Analysis	Chromosome Analysis	Morphometric Analysis	Color Analysis
29	SHOS	Shoshone, Nevada (m)	0	0	3	14
30	MILF	Milford, Utah (m)	1	2	11	13
31	FLET	Fletcher, Nevada (m)	34	6	12	20
32	MINA	Mina, Nevada (p)	1	2	7	7
33	TONO	Tonopah, Nevada (p)	2	2	5	16
34	STON	Stone Cabin Valley, Nevada (p)	0	0	12	20
35	BENT	Benton, California (m)	1	1	13	20
36	COAL	Coaldale, Nevada (p)	1	1	12	13
37	SILV	Silver Peak, Nevada (p)	0	0	12	20
38	MUDL	Mud Lake, Nevada (p)	0	0	6	10
39	HIKM	Hiko, Nevada (m)	1	16	11	20
39	HIKP	Hiko, Nevada (p)	1	39	12	19
40	PANA	Panaca, Nevada (m)	1	3	13	17

Table 1 continued (4)

Locality Number	Alphabetic Code	Sample Name	Protein Analysis	Chromosome Analysis	Morphometric Analysis	Color Analysis
41	KAWM	Kawich, Nevada (m)	0	0	10	17
41	KAWP	Kawich, Nevada (p)	13	46	14	20
42	ALAM	Alamo, Nevada (p)	0	3	13	20
Totals			78	190	441	686

was accomplished by placing a transparent locality map overlay on each of the figures and simply recording the environmental data for the 42 localities.

Statistical Procedures.--The scope of this project involves not only the analysis of five separate data sets, but includes a terminal section wherein determinations pertaining to concordance levels among the sets are computed. Therefore, it is necessary, at times, to discuss the different phases of the study separately below. All elaborate statistical procedures were performed on the CDC 6400 computer at the University of California, Berkeley.

For determination of biochemical divergence among populations, cluster analyses were performed on protein similarity (S) and distance (1-S) matrices. The unweighted pair-group method using arithmetic averages (UPGMA) was used in the clustering of the data (Sneath and Sokal, 1973). These procedures were run on the NT-11 (Numerical Taxonomy Package) program of Moss and Bell (1970). In addition to phenetic representation of the genetic divergence among populations, the method of Fitch and Margoliash (1967) was used to construct phylogenetic trees from the protein distance coefficients. Final tree selection from the array of tree topologies was guided by two criteria: 1) the goodness-of-fit criterion (smallest per cent standard deviation) and, 2) the minimization or avoidance of negative branches. Prager and Wilson (1978) have recommended the Fitch and Margoliash method for use with

electrophoretic distance measures. Also, interindividual protein similarity values were subjected to routine statistical analysis (including computation of mean and standard error) to determine one assessment of the extent of intrapopulational genetic variability.

The chromosomal, morphometric, colorimetric, and environmental data sets were subjected to character correlation analyses by employing the PEARSON CORR program of SPSS (Statistical Package for Social Science). Characters highly correlated ($r \approx 0.90$) with others in the matrix were eliminated from further analyses if such characters were judged not to be contributing unique information. Such a practice prevents undue "weighting" of factors through the expression of redundant information in certain statistical routines. It was necessary to eliminate several characters from both the morphometric and colorimetric data sets.

The chromosomal and environmental data sets are each composed of only single values (taken as the mean values) for each of the populations or OTUs (Operational Taxonomic Units) sampled. Hence, because of the inherent qualities of the data sets, there is no intrapopulational variability. UPGMA cluster analyses based upon both correlation (Pearson) and distance (Taxonomic Distance) matrices were used to summarize the interpopulational relationships expressed by the chromosomal and environmental data sets.

General descriptive statistics were computed for the morphometric and colorimetric data sets using the CONDESCRIPTIVE program of the SPSS package. Because of the seeming "plastic" nature of the morphometric and colorimetric characters I was particularly interested in both intrapopulational and interpopulational variability. Therefore, again using the SPSS package, I analyzed these data sets with the DISCRIMINANT program. The DISCRIMINANT program performed a discriminant function analysis among populations of both traditional species and allowed for a single class analysis of variance (ANOVA and F-test) to determine significant differences among character means. Further, this routine calculated generalized distance measures, Mahalanobis D^2, between all population centroids in n-dimensional space and, importantly, provided significance levels for pair-wise combinations of OTUs (F-matrix). Both the morphometric and colorimetric data sets were subjected to a variety of cluster analyses (including both weighted and unweighted methods) and utilized both correlation (Pearson Product-Moment) and distance (Taxonomic Distance) matrices in the construction of phenograms.

The final portions of this study address the concordance among the five data sets with the principal goal to quantify in an objective manner the degree to which one data set is concordant with another. The NONPAR CORR program of SPSS was used here to appraise

to appraise the degree of congruence among the five data sets. The NONPAR CORR program performs Spearman nonparametric (rank) correlations (r_s) and are essentially as powerful in terms of efficiency (91 per cent) as the Pearson r correlations. This nonparametric method was selected because it does not make the numerous assumptions about parameters (see discussion by Siegal, 1956:195) that are made in the parametric case and which may be unrealistic for the five data sets at hand. The most usual means for computing the Spearman r_s is given by,

$$r_s = 1 - \frac{6 \sum_{i=1}^{N} d^2}{N^3 - N}$$

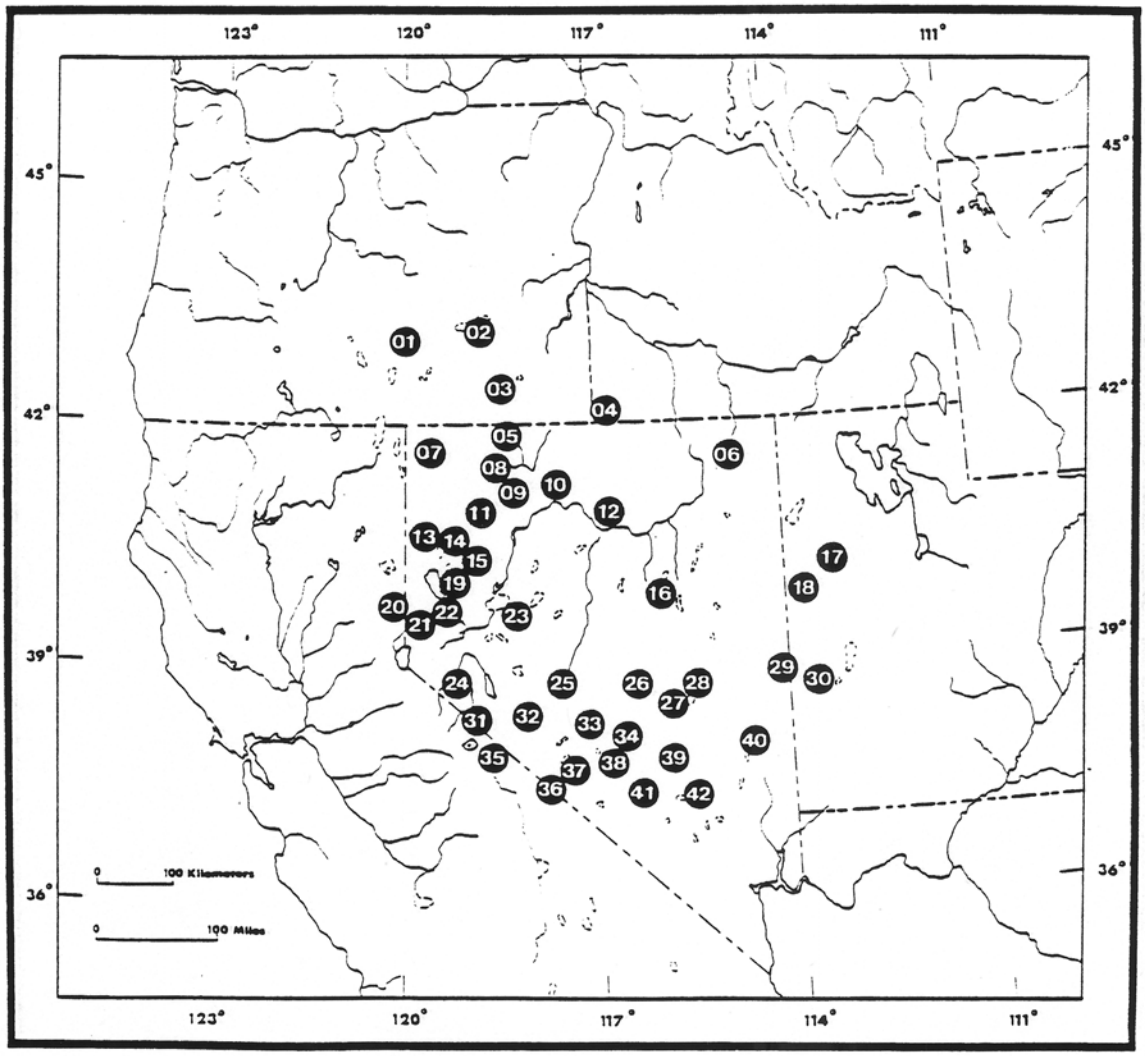
where d_i is the difference between ranks of paired variables. In the present case of determining levels of concordance among the five data sets, N was equivalent for all ten pair-wise combinations. This was accomplished by reducing each of the five data sets to 27 accordant populations for which all data were available. Since the sample size was equivalent between the pair-wise comparisons among the data sets (and hence, the degrees of freedom were equal) the magnitudes of r_s are directly comparable and levels of concordance can be deduced easily without the necessary recourse to significance tables. In addition, coefficients of determination (r^2) were calculated to assess the proportion of variance explained by each of the tests of association.

The Kendall coefficient of concordance, W, (Siegal, 1956; Kendall, 1970) was used to evaluate the null hypothesis that the five data sets are unrelated (independent). The Kendall coefficient of concordance is another nonparametric tool and measures the extent of association among several (k) sets of rankings. W may take values only between 0 and + 1.0 and bears a linear relation to r_s, as follows:

$$r_{s\ (average)} = \frac{kW - 1}{k - 1}$$

Study Specimens and Sampling Localities.--Approximately 2500 specimens of kangaroo mice were handled in the course of the study. For my studies of morphological variability I relied heavily on existing museum specimens. Most unfortunately though, only a small percentage of the total number of available musuem specimens could be utilized in detailing morphometric and colorimetric variability because of restrictive attributes associated with the nature (skull only or skin only), condition (damaged skull or skin), and age (juvenile) of many of the study specimens. Of course, to satisfy my interests in biochemical and karyotypic variability in Microdipodops, it was necessary to collect specimens for tissue and bone marrow samples and to preserve voucher specimens. The final numbers of specimens used in the different phases of this project are tabulated in Table 1. The Locality Numbers listed in Table 1 are used to signal the placement of the localities on the geographical map (Fig. 2). The Alphabetic Codes are used throughout

Figure 2.--Geographic map of western North America indicating the locations of the populations analyzed in this study. Numbers correspond to locality names listed in Table 1.


123°
120°
117°
114°
111°
45°
42°
39°
36°
01
02
03
04
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06
07
08
09
10
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23
24
25
26
27
28
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31
32
33
34
35
36
37
38
39
40
41
42
0 100 Kilometers
0 100 Miles

the text and provide efficient means of conveying the necessarily awkward locality names. The exact specimen localities corresponding to each of the Sample Names of this first table are presented in Appendix D.

Nearly 90 per cent of all available study specimens and holotypic material of kangaroo mice is housed in the mammal collections at the Museum of Vertebrate Zoology, University of California, Berkeley. This single collection was used most extensively in the course of this study and specimens and ancillary material I collected while studying kangaroo mice are deposited here. Other collections of Microdipodops material were also studied, through visit or loan, and include the Museum of Southwestern Biology, University of New Mexico (representative specimens from most areas of the range of the genus); The Museum, Texas Tech University (representative specimens from most areas of the range of the genus); the University of Utah (specimens from two main localities in western Utah: Granite Peak and Milford); and Idaho State University (several specimens in particular from remote southwestern Idaho).

SYNOPSIS OF MICRODIPODOPS NATURAL HISTORY

Kangaroo mice are rather uncommon rodents which are restricted to extremely zeric, sandy habitats in the Great Basin Desert. Not surprising, little published information is presently available concerning the natural history of kangaroo mice. The natural history information summarized below, drawn largely from my field experience, is presented for the purpose of providing background information that will, hopefully, lead to a better appreciation of the patterns of geographic variation and evolution discussed in subsequent sections.

General Habits of Kangaroo Mice.--Kangaroo mice, like other desert-adapted heteromyids are strictly nocturnal and spend the daylight hours within burrows below the surface of the sand. The entrances to their burrows are approximately the size of a quarter dollar (about 25 millimeters in diameter) and the active burrows are routinely plugged, in a rather neat fashion, with a small quantity of sand. The plugging of the entrance to the burrow is an effictive means of protecting the burrow system, with its moist and cool atmosphere, from the hot and desiccating effects of the diurnal desert air. I have excavated many kangaroo mouse burrow systems and, like Hall (1941b) and Bailey (1936), I was unable to find nests within their subterranean chambers.

Bartholomew and MacMillen (1961) note that kangaroo mice are capable of entering torpor at low ambient temperatures

(and hence during inclement weather). To my knowledge they have never been captured during the winter period of mid-November to mid-March. It is not known whether kangaroo mice rely on the adipose tissue, stored conspicuously in the tail, as an energy reserve during these periods of torpor and hibernation. Post-winter above the ground activity seems to begin about late-March with the sex ratio skewed overwhelmingly in favor of the males. The significance of this skewed sex ratio is not clear, but one may speculate that it involves the formation and defense of intraspecific territories by the male during the early phases of the breeding cycle. Alternatively, the early emergence and above ground activity of the males may be intricately associated with recrudescence of the testes and the general physiological changes that occur during spermatogenesis.

The breeding season begins in early spring and young are born in the late spring or early summer depending mainly, of course, on geography (latitude and elevation) and the vicissitudes of the weather. The approximate number of embryos per litter is four, with the young growing to adult size rapidly. By late summer or autumn of their first year the yeanlings have attained adult proportions and even show the degree of tooth wear and development of the auditory bullae that is characteristic of the adult.

Little information is available concerning the food

habits of kangaroo mice save a few anecdotal accounts which detail the cheekpouch contents of several individuals (Hall and Linsdale, 1929; Bailey, 1936; Hall, 1941b). Kangaroo mice are predominantly granivores, though they must certainly have the ability to switch their dietary preferences and capitalize on the sporatic appearances of superabundant quantities of insects in their habitat. Although nothing is known about dietary differences between the species M. megacephalus and M. pallidus, Hafner (1976) and Hafner et al. (1979) pointed out the specific differences in the size and shape of the angular processes, pterygoids, and the incisive foramina suggest that modification of these osseous elements may be associated with divergence in masticatory habits.

The Habitat of Microdipodops megacephalus.--This kangaroo mouse generally occupies the upper elevations of the Upper Sonoran Life-Zone in the Great Basin region and is known to occur from 3900 to 7600 feet. Hall (1941b) noted that edaphic factors control the distribution of this species. Within its geographic distribution M. megacephalus is generally found in and around basins and is restricted to fine sandy soil, or to sandy soil overlaid with fine gravel, that supports only scattered vegetation. It does not inhabit sand dunes per se or gravelly soil, as occasionally has been stated (see, for example, Hall, 1941b, and O'Farrell and Blaustein, 1974a). Wherever this species is found, the preferred soil has several inches of loose

sand that comprises the top soil (whether overlaid with a covering of small gravel or not), which can be easily loosened with the foot and easily records footprints. Hard-packed soil and true gravelly soil are avoided.

The soils favored by M. megacephalus harbor basically one of two particular floral associations depending on elevation and where they occur in the Great Basin. A floral community dominated largely by Artemisia and Chrysothamnus is characteristic of upland kangaroo mouse habitat from central Nevada, and those isolated regions of M. megacephalus distribution about Mono Lake in California, southwestern Idaho, and the dissected areas to the northeast and southwest of Pyramid Lake, Nevada. Elsewhere in the lower reaches of the geographic range of M. megacephalus, including the Bonneville region of eastern Nevada and western Utah, the Oregon plateau region, and the region north and wast of Pyramid Lake, Nevada (Smoke Creek-Black Rock desert), the floral association is dominated by Atriplex, Sarcobatus, and Tetradymia.

I noted in the course of field research that several other rodents were routinely encountered in trap lines in which M. megacephalus was taken. These included: Perognathus longimembris, Perognathus parvus, Dipodomys merriami, Dipodomys ordii, Dipodomys microps, Peromyscus maniculatus, and Onychomys leucogaster. In the western part of the range, Dipodomys panamintinus and infrequently Dipodomys deserti, Eutamius minimus, and Reithrodontomys megalotis

are encountered as members of the rodent community, whereas in the south, Microdipodops pallidus and Onychomys torridus enter the faunal list. Ammospermophilus leucurus is occasionally taken throughout the range of M. megacephalus.

The Habitat of Microdipodops pallidus.--Within the Great Basin, M. pallidus is restricted to the lower portion of the Upper Sonoran Life-Zone and has been found from elevations of 3900 to 6000 feet. These kangaroo mice typically occur on the floor of basins where the soil is quite sandy, with sparce vegetation, and on stabilized dunes peripheral to dry lakes. M. pallidus generally inhabit areas of virtually wind-blown sand that are stabilized by sparce vegetation. Here the soil is always sandy enough that several inches can be displaced with the foot and footprints are left wherever the investigator ventures.

Microdipodops pallidus is extremely specialized and is adapted to one of the most xeric habitats known. These kangaroo mice tolerate little variation in their preferred habitat, a fact that can be appreciated only by field experience. The lower part of the Upper Sonoran Life-Zone supports a flora that forms a zonal position lower than areas supporting Artimisia and is, therefore, floristicly distinct from the adjacent areas inhabited by M. megacephalus. Dominant shrubs characteristic of M. pallidus habitat include Atriplex, Sarcobatus, Grayia, and Eurotia. All four genera are halophytic members of the goosefoot family

(Chenopodiaceae). Excluding Sarcobatus, which is often a couple meters in height, the shrubs are generally less than a meter in height and are widely spaced.

Members of the rodent fauna captured at sites at which M. pallidus also has been taken include: Perognathus longimembris, Perognathus parvus, Dipodomys ordii, Dipodomys merriami, Dipodomys microps, Peromyscus maniculatus, Onychomys leucogaster, and Onychomys torridus. Rather uncommonly, Microdipodops megacephalus, Thomomys talpoides, Ammospermophilus leucurus, Microtus montanus, and Dipodomys deserti also have been encountered in the trap lines with M. pallidus.

RESULTS

Protein Electrophoresis.--Electromorphic variability in 32 bands was assayed by the band-counting technique described earlier. These 32 bands, which perhaps represent a nearly equivalent number of gene loci, encode for plasma proteins and nonspecific esterases which are of the rapidly evolving class (Sarich and Cronin, 1976). Only eight of the 32 bands examined were monomorphic and seemingly fixed for the same electromorph (presumed allele) in all sampled populations. Of the remaining 24 bands, 6 bands were considered as polytypic as they were represented by different (fixed) electromorphs in one or the other species, M. megacephalus and M. pallidus. Electromorph frequencies for the polymorphic bands were not calculated inasmuch as this analysis utilized, largely, the exemplar method (one individual sampled per population) while focusing on the interpopulational genetic divergence (see discussion in Sarich, 1977, and Cronin et al., 1980).

Protein variation was analyzed within four populations representing both species of kangaroo mice for the main purpose of understanding the extent to which the estimates of interpopulational genetic divergence may be affected by individual variation, sex-associated changes (see, for example, Hunter et al., 1964; Furguson, 1980), and variation due to the season in which the sample was taken (for review see Ferguson, 1980). The results of the

intrapopulational analyses are presented in Table 2. The intrapopulational data are presented using both a measure of dispersion of the similarity values (mean $\underline{S}$ within a population) and the more traditional measures of variability used by population geneticists (average number of alleles per locus, heterozygosity, polymorphism).

The Fletcher (FLET) sample was sampled repeatedly to examine any possible seasonal effects (as a result of environmental and physiological changes) on the phenetic expression of the protein bands under study. No seasonal effect was observed in any of the 32 bands scored in this analysis. The three FLET samples and the Kawich (KAWP) sample were available for investigating the possible affects of secondary sexual variation on the expression of the protein bands. Of the 32 bands scored, no differences in electromobility were observed that could be attributed to secondary sexual variation.

The average similarity values (interindividual) within these four populations examined varied from .837 to .895 with a grand mean of .870 (Table 2). This grand mean intrapopulational similarity statistic may be most useful in appraising the overall reliability of the patterns of interpopulational genetic divergence derived by the exemplar method. For example, I would hesitate to attach great importance to patterns of interpopulational genetic divergence above the $\underline{S}$=.870 level. Such relationships (branching sequences and

Table 2. Genic variation within selected popuations of kangaroo mice.

Population	N[a]	S[b]	A[c]	H[d]	P[e]
Microdipodops megacephalus					
FLET (August 1976)	9	.837 (.018)	1.469	.028	.344
FLET (May 1979)	12	.885 (.012)	1.500	.031	.375
FLET (August 1979)	12	.895 (.012)	1.375	.029	.313
Microdipodops pallidus					
KAWP	12	.861 (.014)	1.375	.005	.344

[a]N = Sample size; [b]S = Mean similarity value between individuals with twice standard error in parentheses; [c]A = Mean number of alleles per band (presumptive locus); [d]H = Mean proportion of 32 bands (loci) heterozygous per individual; [e]P = Proportion of 32 bands (loci) polymorphic.

clusters > .87) might be meaningless inasmuch as they are within the expected range of intrapopulational variation.

In addition to the grand mean similarity value discussed above, I utilized a second independent measure to assess the reliability of patterns of interpopulational variability. Four populations, adjacent (four to 10 miles away) to the principal sample localities (Table 1), were selected and analyzed for protein variability. These four additional populations (with the respective and adjacent locality in parentheses) include the following: SWSU (SULP); WWIN (WINN); TODU (TONO); SWKP (KAWP). A fifth additional sample, a chromosomal hybrid (HYQU) from the Quinn River area (QUIN), was also analyzed for degree of biochemical divergence. The amount of genetic divergence between these five pairs of samples (see Table 3 and footnotes) may be used as another conservative measure of the extent of intrapopulational variation, and hence, serve as a yardstick in appraising the meaning of interpopulational patterns. $\underline{S}$ values between these five "test" samples and their respective samples varied from .72 to .91 (Table 3) with a mean value $\underline{S}$ of .832. This average $\underline{S}$, compares favorably with the grand mean $\underline{S}$ (=.870) derived from the population data mentioned above.

Measures of genetic variation within populations of kangaroo mice are summarized in Table 2. These values are generally comparable to estimates obtained for other vertebrates (Nevo, 1978) when assaying admixtures of

Table 3. Protein similarity matrix (above the diagonal) and distance matrix (below the diagonal) for populations of Microdipodops sampled. Five additional samples near to other populations sampled in the study (see footnotes) have been added to provide a conservative means of representing the extent of intrapopulational variability.

	WADS	YERI	MINA	TONO	COAL	KAWP	LOCK	HIKP	ALKA	NARR	RIDD	QUIN	SULP
WADS	----	0.81	0.59	0.75	0.69	0.53	0.69	0.66	0.47	0.41	0.31	0.38	0.34
YERI	0.19	----	0.59	0.72	0.75	0.59	0.63	0.69	0.47	0.44	0.38	0.38	0.34
MINA	0.41	0.41	----	0.63	0.56	0.66	0.56	0.59	0.34	0.38	0.34	0.56	0.53
TONO	0.25	0.28	0.37	----	0.69	0.59	0.75	0.69	0.38	0.41	0.44	0.41	0.41
COAL	0.31	0.25	0.44	0.31	----	0.63	0.63	0.66	0.47	0.44	0.38	0.41	0.38
KAWP	0.47	0.41	0.34	0.41	0.37	----	0.66	0.75	0.44	0.47	0.38	0.44	0.41
LOCK	0.31	0.37	0.44	0.25	0.37	0.34	----	0.91	0.47	0.41	0.31	0.38	0.41
HIKP	0.34	0.31	0.41	0.31	0.34	0.25	0.09	----	0.44	0.41	0.34	0.41	0.38
ALKA	0.53	0.53	0.66	0.62	0.53	0.56	0.53	0.56	----	0.81	0.69	0.63	0.69
NARR	0.59	0.56	0.62	0.59	0.56	0.53	0.59	0.59	0.19	----	0.69	0.63	0.66
RIDD	0.69	0.62	0.66	0.56	0.62	0.62	0.69	0.66	0.31	0.31	----	0.59	0.63
QUIN	0.62	0.62	0.44	0.59	0.59	0.56	0.62	0.59	0.37	0.37	0.41	----	0.88
SULP	0.66	0.66	0.47	0.59	0.62	0.59	0.59	0.62	0.31	0.34	0.37	0.12	----

Table 3 continued (2)

	WADS	YERI	MINA	TONO	COAL	KAWP	LOCK	HIKP	ALKA	NARR	RIDD	QUIN	SULP
JUNG	0.59	0.59	0.47	0.62	0.56	0.53	0.62	0.59	0.37	0.34	0.44	0.06	0.19
WINN	0.59	0.53	0.59	0.56	0.56	0.59	0.56	0.56	0.25	0.19	0.34	0.28	0.31
SMOK	0.62	0.62	0.47	0.59	0.59	0.56	0.62	0.62	0.34	0.34	0.37	0.12	0.03
CHIL	0.53	0.50	0.59	0.53	0.53	0.59	0.53	0.53	0.31	0.22	0.37	0.34	0.31
SPAR	0.53	0.50	0.59	0.59	0.53	0.56	0.56	0.56	0.25	0.22	0.34	0.34	0.31
FLET	0.62	0.62	0.53	0.59	0.56	0.56	0.59	0.59	0.41	0.31	0.44	0.41	0.34
BENT	0.59	0.59	0.53	0.56	0.56	0.56	0.53	0.56	0.41	0.25	0.44	0.37	0.31
CONT	0.59	0.62	0.56	0.59	0.56	0.53	0.59	0.59	0.34	0.22	0.37	0.44	0.41
EURE	0.59	0.59	0.56	0.59	0.53	0.53	0.56	0.56	0.37	0.22	0.44	0.41	0.37
HOTC	0.62	0.62	0.59	0.59	0.56	0.53	0.56	0.56	0.41	0.25	0.44	0.41	0.34
HIKM	0.59	0.62	0.53	0.59	0.56	0.56	0.59	0.59	0.41	0.31	0.47	0.37	0.37
PANA	0.56	0.56	0.56	0.56	0.59	0.62	0.56	0.56	0.41	0.31	0.47	0.41	0.41
MILF	0.59	0.56	0.62	0.62	0.50	0.50	0.53	0.53	0.37	0.23	0.47	0.44	0.44

Table 3 continued (3)

	WADS	YERI	MINA	TONO	COAL	KAWP	LOCK	HIKP	ALKA	NARR	RIDD	QUIN	SULP
CALL	0.59	0.53	0.62	0.62	0.53	0.62	0.59	0.56	0.34	0.34	0.50	0.47	0.47
SWSU[a]	0.62	0.59	0.59	0.59	0.56	0.66	0.59	0.62	0.25	0.34	0.41	0.25	0.16
WWIN[b]	0.56	0.53	0.59	0.56	0.53	0.56	0.56	0.56	0.25	0.12	0.34	0.37	0.37
HYQU[c]	0.59	0.62	0.47	0.62	0.56	0.53	0.62	0.62	0.34	0.37	0.44	0.09	0.19
TODU[d]	0.22	0.28	0.37	0.28	0.22	0.37	0.31	0.31	0.56	0.47	0.62	0.53	0.56
SWKP[e]	0.44	0.47	0.34	0.37	0.34	0.19	0.25	0.28	0.56	0.50	0.59	0.53	0.56

Table 3 continued (4)

	JUNG	WINN	SMOK	CHIL	SPAR	FLET	BENT	CONT	EURE	HOTC	HIKM	PANA	MILF
WADS	0.41	0.41	0.38	0.47	0.47	0.38	0.41	0.41	0.41	0.38	0.41	0.44	0.41
YERI	0.41	0.47	0.38	0.50	0.50	0.38	0.41	0.38	0.41	0.38	0.38	0.44	0.44
MINA	0.53	0.41	0.53	0.41	0.41	0.47	0.47	0.44	0.44	0.41	0.47	0.44	0.38
TONO	0.38	0.44	0.41	0.47	0.41	0.41	0.44	0.41	0.41	0.41	0.41	0.44	0.38
COAL	0.44	0.44	0.41	0.47	0.47	0.44	0.44	0.44	0.47	0.44	0.44	0.41	0.50
KAWP	0.47	0.41	0.44	0.41	0.44	0.44	0.44	0.47	0.47	0.47	0.44	0.38	0.50
LOCK	0.38	0.44	0.38	0.47	0.44	0.41	0.47	0.41	0.44	0.44	0.41	0.44	0.47
HIKP	0.41	0.44	0.38	0.47	0.44	0.41	0.44	0.41	0.44	0.44	0.41	0.44	0.47
ALKA	0.63	0.75	0.66	0.69	0.75	0.59	0.59	0.66	0.63	0.59	0.59	0.59	0.63
NARR	0.66	0.81	0.66	0.78	0.78	0.69	0.75	0.78	0.78	0.75	0.69	0.69	0.72
RIDD	0.56	0.66	0.63	0.63	0.66	0.56	0.56	0.63	0.56	0.56	0.53	0.53	0.53
QUIN	0.94	0.72	0.88	0.66	0.66	0.59	0.63	0.56	0.59	0.59	0.63	0.59	0.56
SULP	0.81	0.69	0.97	0.69	0.69	0.66	0.69	0.59	0.63	0.66	0.63	0.59	0.56

Table 3 continued (5)

	JUNG	WINN	SMOK	CHIL	SPAR	FLET	BENT	CONT	EURE	HOTC	HIKM	PANA	MILF
JUNG	----	0.78	0.84	0.69	0.72	0.56	0.63	0.56	0.63	0.63	0.59	0.56	0.59
WINN	0.22	----	0.72	0.81	0.81	0.63	0.72	0.66	0.72	0.69	0.66	0.69	0.72
SMOK	0.16	0.28	----	0.72	0.69	0.63	0.66	0.59	0.63	0.66	0.66	0.63	0.59
CHIL	0.31	0.19	0.28	----	0.88	0.69	0.78	0.72	0.78	0.75	0.69	0.75	0.75
SPAR	0.28	0.19	0.31	0.12	----	0.63	0.72	0.69	0.75	0.72	0.69	0.69	0.75
FLET	0.44	0.37	0.37	0.31	0.37	----	0.94	0.84	0.88	0.84	0.84	0.81	0.72
BENT	0.37	0.28	0.34	0.22	0.28	0.06	----	0.88	0.97	0.94	0.91	0.88	0.81
CONT	0.44	0.34	0.41	0.28	0.31	0.16	0.12	----	0.91	0.88	0.84	0.78	0.75
EURE	0.37	0.28	0.37	0.22	0.25	0.12	0.03	0.09	----	0.97	0.91	0.84	0.84
HOTC	0.37	0.31	0.34	0.25	0.28	0.16	0.06	0.12	0.03	----	0.88	0.81	0.81
HIKM	0.41	0.34	0.34	0.31	0.31	0.16	0.09	0.16	0.09	0.12	----	0.94	0.84
PANA	0.44	0.31	0.37	0.25	0.31	0.19	0.12	0.22	0.16	0.19	0.06	----	0.84
MILF	0.41	0.28	0.41	0.25	0.25	0.28	0.19	0.25	0.16	0.19	0.16	0.16	----

Table 3 continued (6)

	JUNG	WINN	SMOK	CHIL	SPAR	FLET	BENT	CONT	EURE	HOTC	HIKM	PANA	MILF
CALL	0.44	0.34	0.44	0.28	0.34	0.28	0.22	0.31	0.22	0.25	0.19	0.09	0.19
SWSU[a]	0.34	0.25	0.19	0.31	0.31	0.34	0.37	0.47	0.44	0.47	0.41	0.37	0.41
WWIN[b]	0.31	0.12	0.34	0.25	0.19	0.31	0.25	0.22	0.22	0.25	0.28	0.28	0.28
HYQU[c]	0.06	0.28	0.19	0.37	0.34	0.41	0.44	0.44	0.44	0.44	0.44	0.47	0.47
TODU[d]	0.53	0.44	0.56	0.44	0.44	0.53	0.44	0.47	0.41	0.44	0.47	0.50	0.47
SWKP[e]	0.50	0.56	0.53	0.53	0.53	0.56	0.50	0.47	0.47	0.47	0.50	0.56	0.47

Table 3 continued (7)

	CALL	SWSU[a]	WWIN[b]	HYQU[c]	TODU[d]	SWKP[e]
WADS	0.41	0.38	0.44	0.41	0.78	0.56
YERI	0.47	0.41	0.47	0.38	0.72	0.53
MINA	0.38	0.41	0.41	0.53	0.63	0.66
TONO	0.38	0.41	0.44	0.38	0.72	0.63
COAL	0.47	0.44	0.47	0.44	0.78	0.66
KAWP	0.38	0.34	0.44	0.47	0.63	0.81
LOCK	0.41	0.41	0.44	0.38	0.69	0.75
HIKP	0.44	0.38	0.44	0.38	0.69	0.72
ALKA	0.66	0.75	0.75	0.66	0.44	0.44
NARR	0.66	0.66	0.88	0.63	0.53	0.50
RIDD	0.50	0.59	0.66	0.56	0.38	0.41
QUIN	0.53	0.75	0.63	0.91	0.47	0.47
SULP	0.53	0.84	0.63	0.81	0.44	0.44

Table 3 continued (8)

	CALL	SWSU[a]	WWIN[b]	HYQU[c]	TODU[d]	SWKP[e]
JUNG	0.56	0.66	0.69	0.94	0.47	0.50
WINN	0.66	0.75	0.88	0.72	0.56	0.44
SMOK	0.56	0.81	0.66	0.81	0.44	0.47
CHIL	0.72	0.69	0.75	0.63	0.56	0.47
SPAR	0.66	0.69	0.81	0.66	0.56	0.47
FLET	0.72	0.66	0.69	0.59	0.47	0.44
BENT	0.78	0.63	0.75	0.56	0.56	0.50
CONT	0.69	0.53	0.78	0.56	0.53	0.53
EURE	0.78	0.56	0.78	0.56	0.59	0.53
HOTC	0.75	0.53	0.75	0.56	0.56	0.53
HIKM	0.81	0.59	0.72	0.56	0.53	0.50
PANA	0.91	0.63	0.72	0.53	0.50	0.44
MILF	0.81	0.59	0.72	0.53	0.53	0.53

Table 3 continued (9)

	CALL	SWSU[a]	WWIN[b]	HYQU[c]	TODU[d]	SWKP[e]
CALL	----	0.59	0.69	0.50	0.47	0.41
SWSU[a]	0.41	----	0.69	0.75	0.44	0.34
WWIN[b]	0.31	0.31	----	0.66	0.59	0.47
HYQU[c]	0.50	0.25	0.34	----	0.41	0.47
TODU[d]	0.53	0.56	0.41	0.59	----	0.63
SWKP[e]	0.57	0.66	0.53	0.53	0.37	----

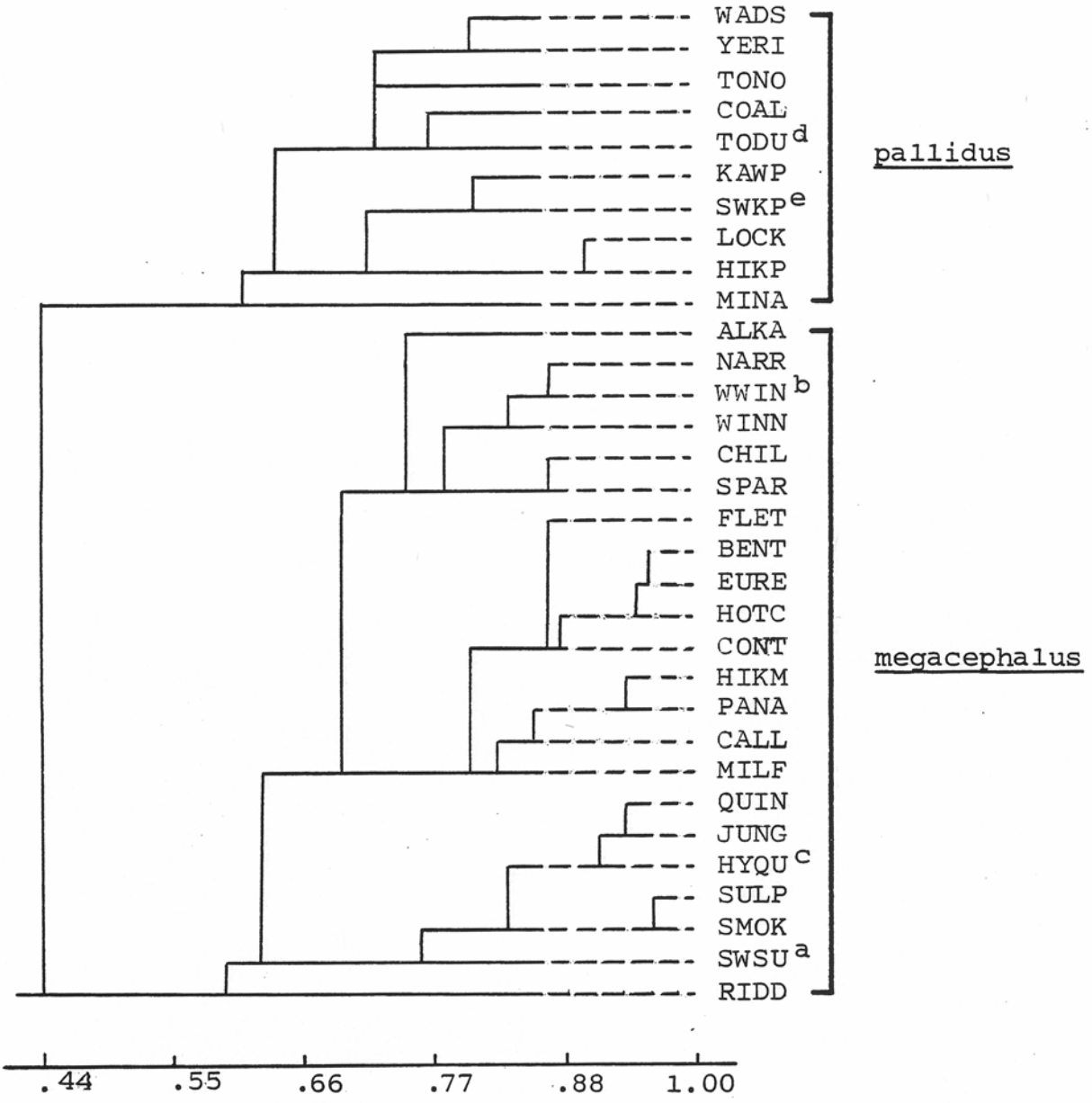
---

[a]SWSU = Addition sample from about three miles southwest SULP sample; [b]WWIN = Additional sample from about five miles east of WINN sample; [c]HYQU = Chromosomal hybrid (40 α/β) individual from QUIN locality; [d]TODU = Additional sample from about five miles south TONO sample; [e]SWKP = Additional sample from about ten miles west of KAWP sample.

slowly evolving and rapidly evolving proteins with starch gel procedures. Hafner et al., (1979) reported values of genic heterozygosity (H=.064) and polymorphism (P=.217) for two other populations of kangaroo mice using the starch gel method and predominantly slowly evolving proteins. Interestingly, the data presented here for heterozygosity average only about one-third of that presented in Hafner et al. (1979), while estimates for polymorphism average about one and one-half times higher than those of Hafner et al. (1979). Whether the differences in genic variation for the populations reported here and between those of our earlier report (Hafner et al., 1979) are due to stochastic events (including temporal changes in population density, bottlenecking, genetic drift, and degree of gene flow), or simply reflects differential attributes inherent in the proteins of separate rate-classes, cannot be answered until more populations have been sampled using the acrylamide approach. Clearly, though, the levels of heterozygosity reported here are rather depressed according to general mammalian standards (Selander and Johnson, 1973; Lewontin, 1974).

Patterns of interpopulational protein variability are expressed in the similarity phenogram (Fig. 3) and the similarity matrix (Table 3) on which it is based. This tree is a phenetic (as opposed to phylogenetic) representation of the protein variation over geography and is used here mainly to illustrate a confidence or reliability level to

Figure 3.--Phenogram (UPGMA) of protein similarity values for 32 samples of Microdipodops (cophenetic correlation coefficient is 0.942). For particulars on the additional five populations (SWSU, WWIN, HYQU, TODU, SWKP) see footnote of Table 1. Region of average intrapopulation similarity (see text) is designated by dashed lines.


WADS
YERI
TONO
COAL
TODU d
KAWP
SWKP e
LOCK
HIKP
MINA
ALKA
NARR
WWIN b
WINN
CHIL
SPAR
FLET
BENT
EURE
HOTC
CONT
HIKM
PANA
CALL
MILF
QUIN
JUNG
HYQU c
SULP
SMOK
SWSU a
RIDD
pallidus
megacephalus
.44
.55
.66
.77
.88
1.00

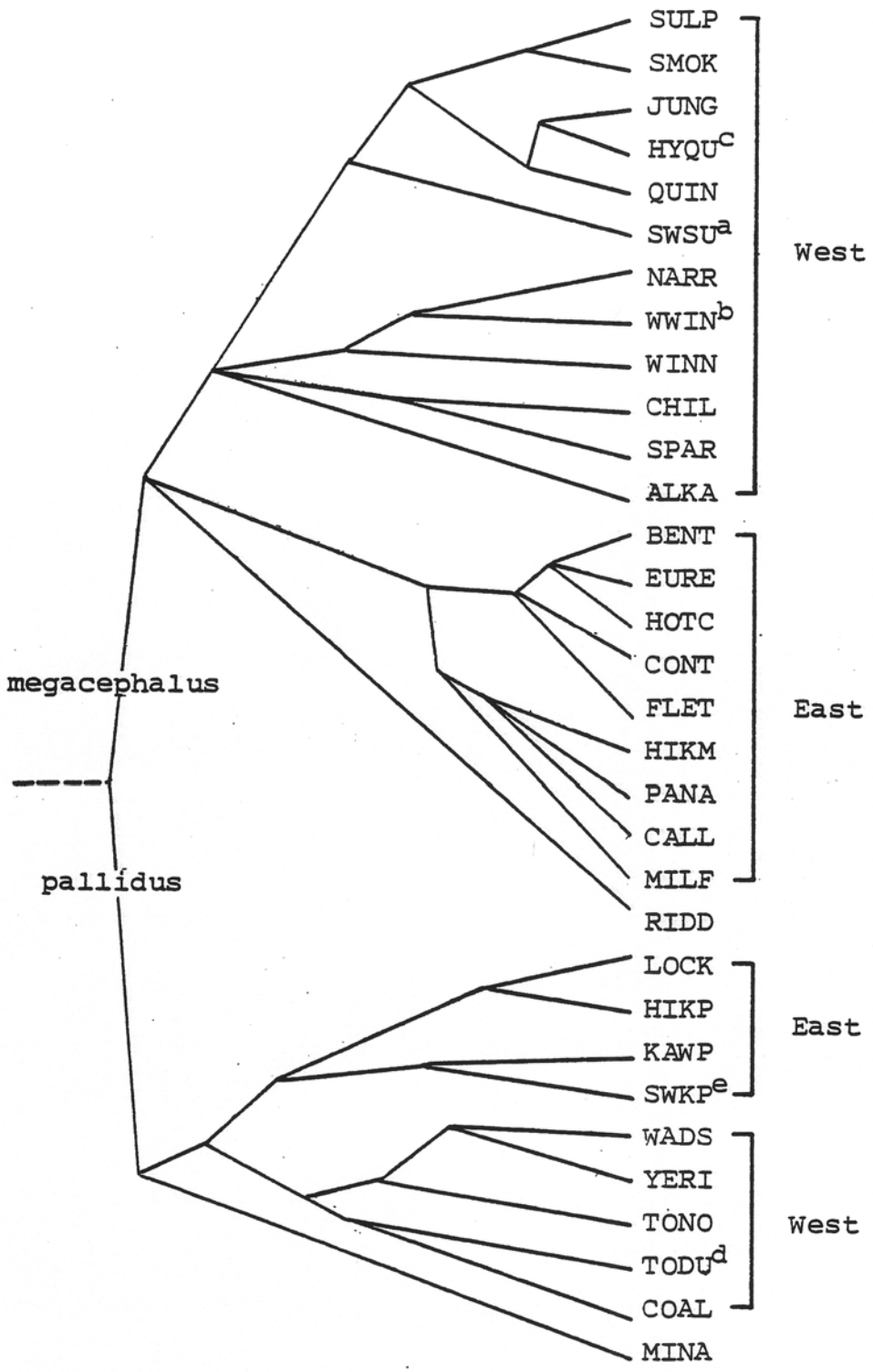
clustered similarity data. That is, extreme caution is advised in deducing relationships among populations which cluster above, say, the .85 similarity levels due to the magnitude of the grand mean intrapopulation similarity value (Fig. 3). Examination of the phenogram clearly indicates the separation of M. pallidus (the upper 10 samples) from M. megacephalus. Within each of these species I am interested mostly in the basic patterns of genetic differentiation. For example, in M. pallidus there are three basic groups: 1) an assemblage distributed in west-central Nevada composed of WADS, YERI, TONO, COAL, and TODU; 2) an east-central group including KAWP, SWKP, LOCK, HIKP; and 3) the distinctive population of MINA. Within M. megacephalus four groups are revealed: 1) a unit distributed in the western Great Basin composed of ALKA, NARR, WWIN, WINN, CHIL, SPAR; 2) another western unit (northwest of Pyramid Lake, Nevada) composed of QUIN, JUNG, HYQU, SULP, SMOK, SWSU; 3) a largely eastern faction containing FLET, BENT, EURE, HOTC, CONT, HIKM, PANA, CALL, MILF; and 4) the isolated RIDD population from southwestern Idaho.

A phylogenetic method (Fitch and Margoliash, 1967) was also used to analyze the genetic divergence among populations of kangaroo mice. This method has been recommended for use in constructing phylogenetic trees from electrophoretic distance measures (Prager and Wilson, 1978) and it allows for the expression of unequal rates of

divergence should they exist. The phylogenetic relationships among the populations of kangaroo mice based on protein distances (D = 1 - S, Table 3) are presented in Figure 4. This phylogenetic tree is in general agreement with the phenogram (Fig. 4) with the exception of relationships within M. megacephalus. The species M. megacephalus and M. pallidus, as before, are clearly separable and the average phyletic distance within each species was calculated to be .297.

The Fitch-Margoliash procedure discriminates three major groups within M. megacephalus: a western and an eastern unit and the distinctive RIDD population from Idaho. The western unit is composed of two subunits including one group distributed about the Smoke Creek-Black Rock desert region north of Pyramid Lake (SULP, SMOK, JUNG, HYQU, QUIN, SWSU) and a second subunit which includes populations in Oregon (NARR and ALKA), southwest of Pyramid Lake (CHIL and SPAR), and the populations about Winnemucca, Nevada (WINN and WWIN). The eastern M. megacephalus unit is composed of one assemblage with central Nevadan populations (EURE, HOTC, and CONT) and the isolated populations about Mono Lake, California (FLET and BENT) and a second subunit including southeastern Great Basin populations distributed on the margins of the Bonneville Basin (HIKM, PANA, CALL, and MILF). Estimates of biochemical divergence indicate a minimal level of heterogeneity of rates across the M. megacephalus geographic

Figure 4.--Phylogenetic relationships of Microdipodops populations based upon genetic distances (1-S) derived from electrophoretic protein comparisons and using the method of Fitch and Margoliash (1967). (Per cent standard deviation is 13.68). See Table 1 for explanation of samples with footnotes.


SULP
SMOK
JUNG
HYQU[c]
QUIN
SWSU[a]
NARR
WWIN[b]
WINN
CHIL
SPAR
ALKA
West
BENT
EURE
HOTC
CONT
FLET
HIKM
PANA
CALL
MILF
East
megacephalus
pallídus
RIDD
LOCK
HIKP
KAWP
SWKP[e]
East
WADS
YERI
TONO
TODU[d]
COAL
West
MINA

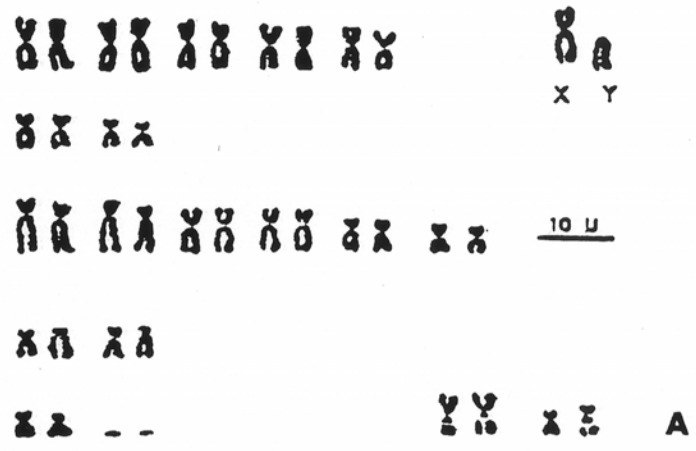
units. For example, the RIDD (Idaho) sample shows a branch length (Fitch-Margoliash mutation distance) of .334 from M. pallidus, whereas the western and eastern units show average legs of .256 and .263 respectively. Further, within the western unit there is heterogeneity in branch length: the Smoke Creek-Black Rock cluster has an average mutation distance of .301, while the other western subunit averages .211.

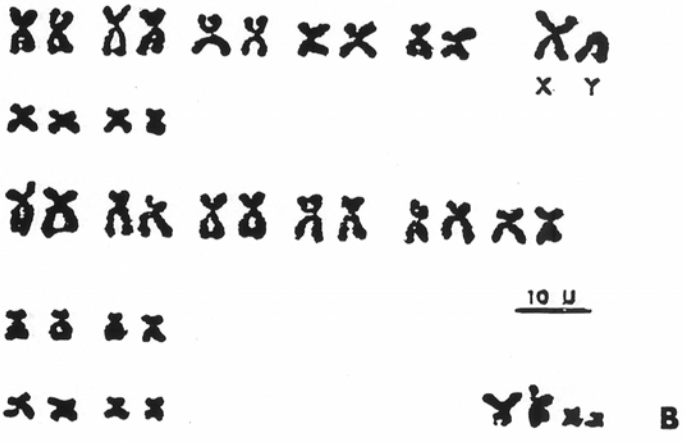
The Fitch-Margoliash method recognizes the same three M. pallidus as delineated by the phenetic clustering routine (Fig. 4). Protein divergence seems to be fairly equivalent among these three units. Average branch lengths for the eastern and western units are .301 and .300 respectively, with Mina's mutation distance being .293.

Chromosomal Analysis.--Karyotypic data collected over the entire geographic range of Microdipodops clearly indicate that kangaroo mice have a diploid number of either 40 or 42. The chromosomal data base presently available consists of 190 karyotyped individuals from 31 main sampling localities for an average of approximately 6 specimens examined per locality. Karyological polytypism was observed in both the 40 and 42 chromosomal forms, but intrapopulational chromosomal variability was not noted in either form.

Microdipodops megacephalus were found to have a diploid compliment of 40 chromosomes (Fig. 5) and were sampled from 21 principal collecting localities. The two chromosomal

Figure 5.--The karyotypes of M. megacephalus. A, M. megacephalus 40-α karyotype; B, M. megacephalus 40-β karyotype. Sex chromosomes are in the upper right and marker autosomes (see text) are in the lower right of each karyotype.


X Y
10 µ
A


X Y
10 µ
B

morphs of M. megacephalus discovered are designated 40-α and 40-β (Greek letter designations follow Patton, 1969) and differ in that there is a small acrocentric pair of chromosomes in the 40-α karyotype (FN = 74) and a small biarmed pair in the 40-β karyotype (FN = 76). The sex chromosomes of M. megacephalus are composed of a large metacentric X chromosome and a medium acrocentric Y chromosome (Fig. 5). O'Farrell and Blaustein (1974a) err in reporting that the X chromosome of this species is a medium acrocentric and the Y chromosome a small subtelocentric.

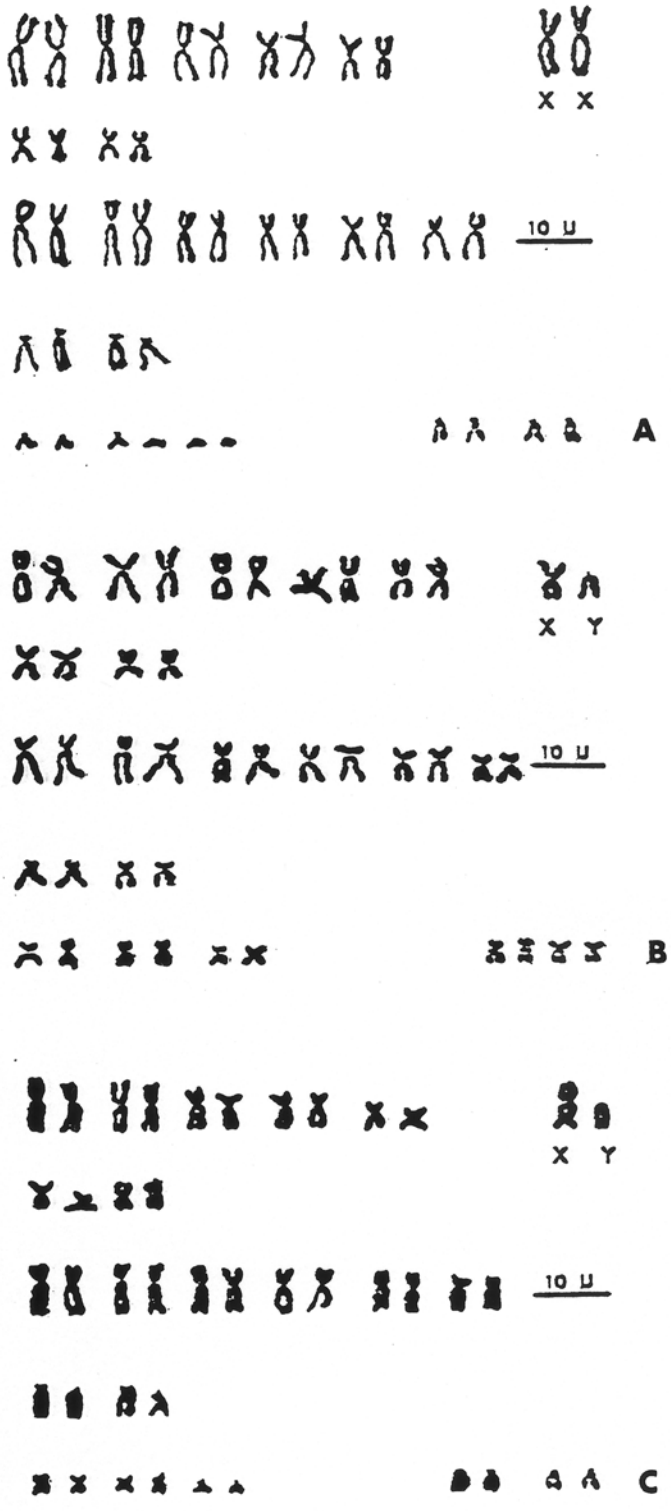
In an attempt to resolve the cytogenetic mechanisms that underlie the relationships between the chromosomal forms of M. megacephalus (40-α and 40-β), C-banding (staining chromosomes preferentially for the presence of constitutive heterochromatin) analysis was performed. C-banding of the M. megacephalus karyotypes revealed that the difference between 40-α and 40-β was due to the presence of heterochromatic arms on the small biarmed pair of chromosomes in the 40-β karyotype. Additionally, it was noted that heterochromatin was mainly centromeric in position in M. megacephalus (and in Microdipodops in general) with a special class of heterochromatin on the Y chromosome.

Microdipodops pallidus karyotypic material was examined from 10 principal localities for chromosomal variability. This species has 42 chromosomes, with three chromosomal races identified and designated 42-α, 42-β, and 42-γ

(Fig. 6). These races differ with respect to the five smallest pairs of chromosomes in each karyotype (the lower row of chromosomes of each karyotype in Fig. 6). M. pallidus 42-α (FN = 70) has three pairs of small acrocentric chromosomes (lower left Fig. 6A) and two pairs of acrocentric marker chromosomes (marker chromosomes are those chromosomes with conspicuous secondary constrictions and are ordered in the lower right of all karyotypes). The karyotype of M. pallidus 42-β (FN = 80) is totally biarmed (Fig. 6B), with the five pairs of chromosomes being metacentric to submetacentric in conformation. The M. pallidus 42-γ karyotype (FN = 80) is similar to the 42-α karyotype, and differs in that the first two small pairs of nonmarker chromosomes are clearly metacentric, while the other three pairs of small chromosomes are judged to be subtelocentric in conformation (compare Fig. 6C with Fig. 6A). The sex chromosomes, like M. megacephalus, are composed of a large metacentric X and a medium acrocentric Y and no deviations from this situation have been found for memebers of the genus (and not as erroneously reported by O'Farrell and Blaustein, 1974b).

The M. megacephalus 40 and the M. pallidus 42 karyotypes were examined rigorously to determine their evolutionary relationships. Close inspection of the karyotypes of Microdipodops reveals that a chromosomal change via a Robertsonian event (Robertson, 1916) is the

Figure 6.--The karyotypes of M. pallidus. A, M. pallidus 42-α karyotype; B, M. pallidus 42-β karyotype; C, M. pallidus 42- karyotype. Sex chromosomes are indicated in the upper right and marker autosomes (see text) in the lower right of each karyotype.


X X
10 μ
A
X Y
10 μ
B
X Y
10 μ
C

only viable hypothesis. In the M. megacephalus 40 karyotype (Fig. 5) there occurs one medium-sized pair of "marker" chromosomes with secondary constrictions and one small pair of marker chromosomes. These constrictions on the marker chromosomes are now known to be nucleolar organizer regions (D. Rogers, personal communication) as evidenced by silver staining techniques (Goodpasture and Bloom, 1975). In the M. pallidus 42 karyotype (Fig. 6) the medium-sized pair of marker chromosomes is conspicuously absent and instead of one, there are two small pairs of marker chromosomes. By invoking either a fusion or fission event involving this peculiar medium-sized pair of marker chromosomes, it is possible to derive either the 40 or 42 chromosomal form (Fig. 7). Further, the array of karyotypic variability in the marker chromosomes of M. pallidus (see Fig. 6), strongly suggests heterochromatic rm addition subsequent to the Robertsonian event (true for either the fusion or fission hypothesis). At present it seems most probable that chromosomal interconversion between the M. megacephalus and M. pallidus karyotypes involves a fission event (see discussion section).

The patterns of interpopulational chromosomal variation in Microdipodops are summarized in the distance matrix (Table 4) and the distance phenogram (Fig. 8A) derived from it. The UPGMA clustering presented here is only one of several clustering algorythms employed, but it was found to be the most reliable (highest cophenetic

Figure 7.--Graphical representation of the Robertsonian change involved in the karyological relationship between the species of kangaroo mice. Secondary constrictions identify the marker chromosomes.

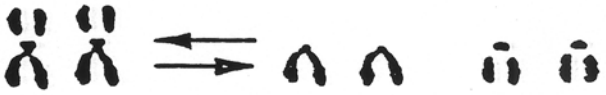


Table 4. Taxonomic Distance matrix based upon nine characters (see Appendix B) comparing 31 populations of kangaroo mice used in the chromosomal study.

	WADS	YERI	MINA	TONO	COAL	KAWP	LOCK	HIKP	ALKA	NARR	RIDD	QUIN	SULP
WADS	-----												
YERI	2.655	-----											
MINA	2.655	0.000	-----										
TONO	2.655	0.000	0.000	-----									
COAL	2.655	0.000	0.000	0.000	-----								
KAWP	2.240	2.353	2.353	2.353	2.353	-----							
LOCK	2.248	2.353	2.353	2.353	2.353	0.000	-----						
HIKP	2.248	2.353	2.353	2.353	2.353	0.000	0.000	-----					
ALKA	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	-----				
NARR	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	-----			
RIDD	2.237	2.051	2.051	2.051	2.051	1.258	1.258	1.258	0.694	0.694	-----		
QUIN	2.237	2.051	2.051	2.051	2.051	1.258	1.258	1.258	0.694	0.694	0.000	-----	
SULP	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	-----

Table 4 continued (2)

	WADS	YERI	MINA	TONO	COAL	KAWP	LOCK	HIKP	ALKA	NARR	RIDD	QUIN	SULP
JUNG	2.237	2.051	2.051	2.051	2.051	1.258	1.258	1.258	0.694	0.694	0.000	0.000	0.694
WINN	2.237	2.051	2.051	2.051	2.051	1.258	1.258	1.258	0.694	0.694	0.000	0.000	0.694
SMOK	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
CHIL	2.237	2.051	2.051	2.041	2.041	1.248	1.248	1.248	0.694	0.694	0.000	0.000	0.694
SPAR	2.237	2.051	2.051	2.051	2.051	1.258	1.258	1.258	0.694	0.694	0.000	0.000	0.694
FLET	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
BENT	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
CONT	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
EURE	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
HOTC	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
HIKM	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
PANA	2.237	2.051	2.051	2.051	2.051	1.258	1.258	1.258	0.694	0.694	0.000	0.000	0.694
MILF	2.237	2.051	2.051	2.051	2.051	1.258	1.258	1.258	0.694	0.694	0.000	0.000	0.694

Table 4 continued (3)

	WADS	YERI	MINA	TONO	COAL	KAWP	LOCK	HIKP	ALKA	NARR	RIDD	QUIN	SULP
CALL	2.237	2.051	2.051	2.051	2.051	1.258	1.258	1.258	0.694	0.694	0.000	0.000	0.694
DENI	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
VERN	2.393	1.661	1.661	1.661	1.661	1.608	1.608	1.608	0.000	0.000	0.694	0.694	0.000
NIXO	0.000	2.655	2.655	2.655	2.655	2.248	2.248	2.248	2.393	2.393	2.237	2.237	2.393
ALAM	2.248	2.353	2.353	2.353	2.353	0.000	0.000	0.000	1.608	1.608	1.258	1.258	1.608

Table 4 continued (4)

	JUNG	WINN	SMOK	CHIL	SPAR	FLET	BENT	CONT	EURE	HOTC	HIKM	PANA	MILF
JUNG	-----												
WINN	0.000	-----											
SMOK	0.694	0.694	-----										
CHIL	0.000	0.000	0.694	-----									
SPAR	0.000	0.000	0.694	0.000	-----								
FLET	0.694	0.694	0.000	0.694	0.694	-----							
BENT	0.694	0.694	0.000	0.694	0.694	0.000	-----						
CONT	0.694	0.694	0.000	0.694	0.694	0.000	0.000	-----					
EURE	0.694	0.694	0.000	0.694	0.694	0.000	0.000	0.000	-----				
HOTC	0.694	0.694	0.000	0.694	0.694	0.000	0.000	0.000	0.000	-----			
HIKM	0.694	0.694	0.000	0.694	0.694	0.000	0.000	0.000	0.000	0.000	-----		
PANA	0.000	0.000	0.694	0.000	0.000	0.694	0.694	0.694	0.694	0.694	0.694	-----	
MILF	0.000	0.000	0.694	0.000	0.000	0.694	0.694	0.694	0.694	0.694	0.694	0.000	-----

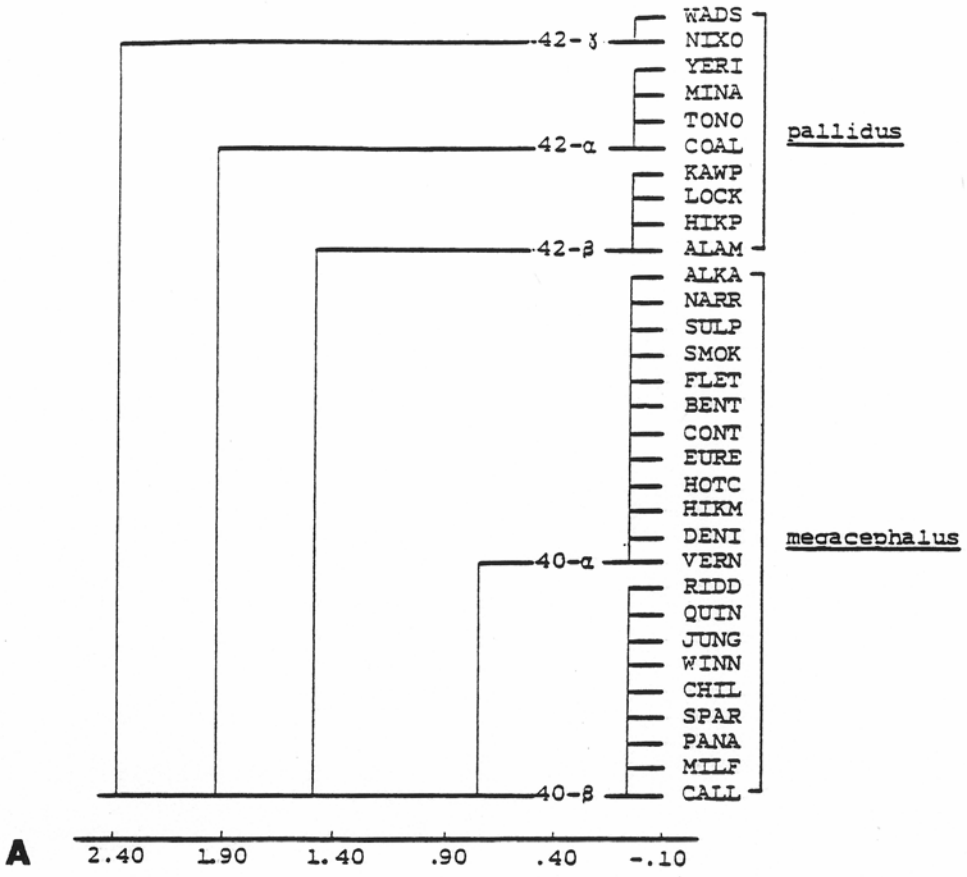
Table 4 continued (5)

	JUNG	WINN	SMOK	CHIL	SPAR	FLET	BENT	CONT	EURE	HOTC	HIKM	PANA	MILF
CALL	0.000	0.000	0.694	0.000	0.000	0.694	0.694	0.694	0.694	0.694	0.694	0.000	0.000
DENI	0.694	0.694	0.000	0.694	0.694	0.000	0.000	0.000	0.000	0.000	0.000	0.694	0.694
VERN	0.694	9.694	0.000	0.694	0.694	0.000	0.000	0.000	0.000	0.000	0.000	0.694	0.694
NIXO	2.237	2.237	2.393	2.237	2.237	2.393	2.393	2.393	2.393	2.393	2.393	2.237	2.237
ALAM	1.258	1.258	1.608	1.258	1.258	1.608	1.608	1.608	1.608	1.608	1.608	1.258	1.258

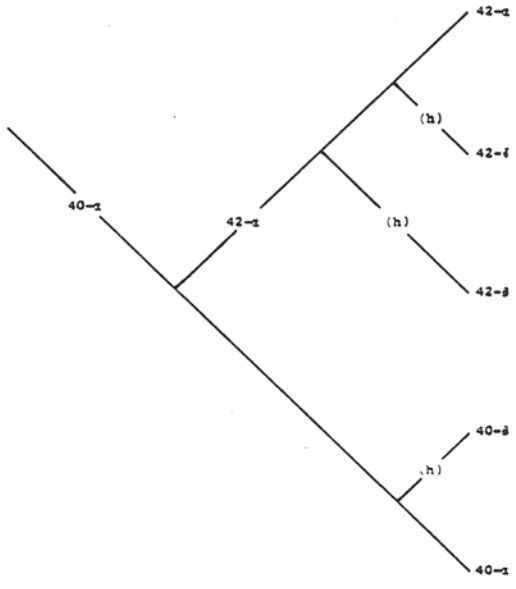
Table 4 continued (6)

	CALL	DENI	VERN	NIXO	ALAM
CALL	-----				
DENI	0.694	-----			
VERN	0.694	0.000	-----		
NIXO	2.237	2.393	2.393	-----	
ALAM	1.258	1.608	1.608	2.248	-----

Figure 8.--Karyotypic relationships in Microdipodops. A, summary (UPGMA distance phenogram) of relationships among the 31 populations analyzed in this study (cophenetic correlation coefficient is 0.984); B, hypothetical scheme of karyotypic evolution assuming a fission event and addition of heterochromatic arms (h).


WADS
NIXO
YERI
MINA
TONO
COAL
KAWP
LOCK
HIKP
ALAM
ALKA
NARR
SULP
SMOK
FLET
BENT
CONT
EURE
HOTC
HIKM
DENI
VERN
RIDD
QUIN
JUNG
WINN
CHIL
SPAR
PANA
MILF
CALL
42-γ
42-α
42-β
40-α
40-β
pallidus
megacephalus
2.40
1.90
1.40
.90
.40
-.10

A

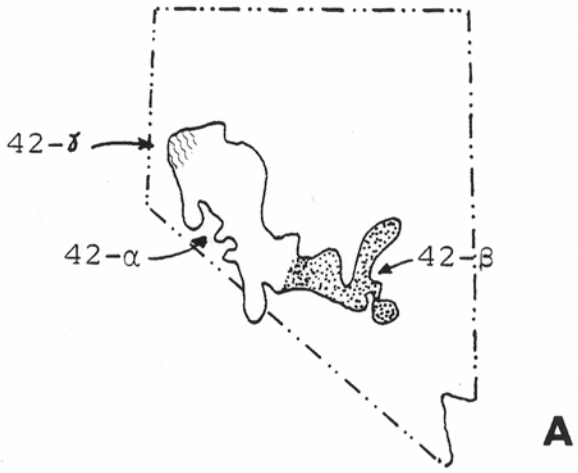

42-α
(h)
42-ε
40-α
42-α
(h)
42-β
40-β
(h)
40-α

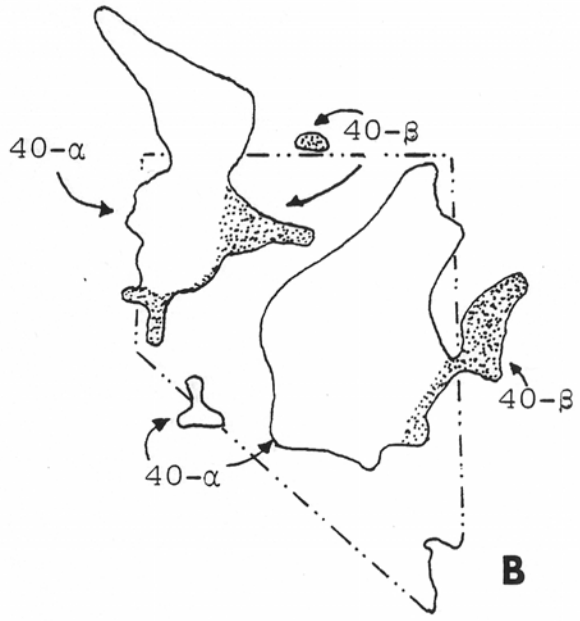
B

correlation coefficient by nearly 10 per cent) in expressing the relationships in the chromosomal data matrix. The relationships depicted in Figure 8A are based on nine characters derived from the nonpreferentially stained karyotypes (see Appendix B) and clearly indicate the separation of the M. pallidus chromosomal races (the top three clusters) from the M. megacephalus chromosomal forms (lower two clusters). The chromosomal phylogeny (Fig. 8B) illustrates the relationships among the karyotypes assuming a fissioning event and addition of heterochromatin. The uppermost cluster (Fig. 8A) unites the two M. pallidus 42-δ populations (WADS and NIXO) from the region about the southern end of Pyramid Lake, Nevada. The second clustering level includes the four 42-α samples (YERI, MINA, TONO, and COAL) which are distributed over the majority of the western range of M. pallidus. The third M. pallidus cluster (42-β) includes four samples (KAWP, LOCK, HIKP, and ALAM) which are distributed about the eastern sector of the M. pallidus range. Figure 9A details the distribution of the M. pallidus chromosomal races over the geographic distribution of this species. The boundary between the karyotypic race 42-α and 42-β (the vicinity southeast of Tonopah, Nevada) coincides nicely with the eastern and western genetic units discussed in the preceeding section.

The two remaining clusters in Figure 8A include the M. megacephalus 40-α and 40-β karyotypic forms. The

Figure 9.--Geographical distribution of the chromosomal forms in Microdipodops. A, distribution of the karyotypes in M. pallidus; B, distribution of the karyotypes in M. megacephalus. The approximate range of each species is indicated and the outline of Nevada is indicated for proper orientation.


42-δ
42-α
42-β
A


40-α
40-β
40-β
40-α
B

40-α karyotype includes 12 samples (ALKA, NARR, SULP, SMOK, FLET, BENT, CONT, EURE, HOTC, HIKM, DENI, and VERN) representing kangaroo mice from such geographically remote areas as Oregon, northwestern Nevada, Mono Lake, California, and central Nevada. The lower cluster on the chromosomal phenogram (Fig. 8A) is composed of nine M. megacephalus 40-β samples (RIDD, QUIN, JUNG, WINN, CHIL, SPAR, PANA, MILF, and CALL). Again, as with the 40-α cluster, this group is an assemblage of populations from fairly disparate geographical areas. The 40-β cluster contains localities from Idaho, northeast and southwest of Pyramid Lake, southeastern Nevada and western Utah. The pattern of the geographic distribution of the chromosomal races of M. megacephalus is very complex, with the polytopic distribution of the karyotypes. One can see from Figure 9B that both chromosomal forms are distributed in a disjunct pattern. This pattern of chromosomal variation in M. megacephalus is quite different from the pattern presented in the previous section (protein variation) and brings to light an important question: Is each M. megacephalus karyotype derived monophyletically, or alternatively, have there been several indipendent derivations of each karyotype within M. megacephalus? After presenting the results from other lines of evidence (morphometrics, colorimetrics, environment) I will return to discuss this question and its pertinent ramifications.

Morphometric Analysis.--As a means by which to assess

the general patterns of phenotypic variability among populations of kangaroo mice I performed the following morphometric analysis which relies largely on multivariate routines. Mickevich and Johnson (1976) aptly note that in certain cases cladistic, rather than phenetic, methods are required for the analysis of morphological character evolution. I do indeed concur with this position, but hasten to add that such methodology is not always applicable, as in the present case. The species of Microdipodops are known to be sibling species morphologically (Hafner et al., 1979) and inasmuch as the species are so similar, a cladistic approach (one requiring the recognition of derived character states) was deemed not feasible. Therefore, the results presented below are based on a phenetic morphological approach.

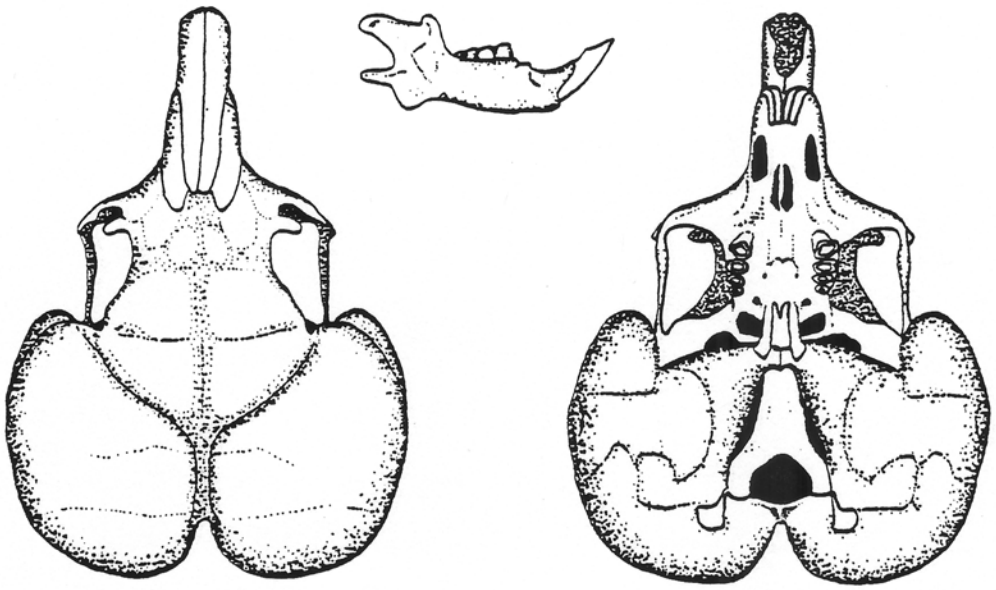
The original 20 variables listed earlier (in the Materials and Methods section) were subjected to a character correlation analysis and of the 20 characters, only a few of the external body measurements (read off museum specimen labels) were found to be highly correlated ($r \approx 0.90$) with one another. For this reason and, more importantly, because the accuracy of all four of the external measurements (total length, tail length, hindfoot length, and ear length) was judged to be extremely unreliable, I opted to omit these four external measurements from the final analysis. The resulting data base is thus pared to 16 cranial variables to examine the phenetic relationships among 43

populations of kangaroo mice. These sixteen characters were selected because of their known ability to discriminate both between and within the species of kangaroo mice. For example, several characters in particular, have been cited (Hall, 1941b; Hafner et al., 1979) as important discriminating characters for Microdipodops: shape of the incisive foramina (diverging posteriorly in M. megacephalus), shape of the pterygoids (distal tip broad in M. pallidus), degree of angualr bifurcation (wings of angular process distinct in M. pallidus), expanse of the lateral face of the zygoma (broad in M. pallidus), and greatest length and breadth of the skull (generally larger in M. pallidus). The degree of differentiation expressed by these characters can be appreciated by examination of skulls of M. pallidus and M. megacephalus (Fig. 10).

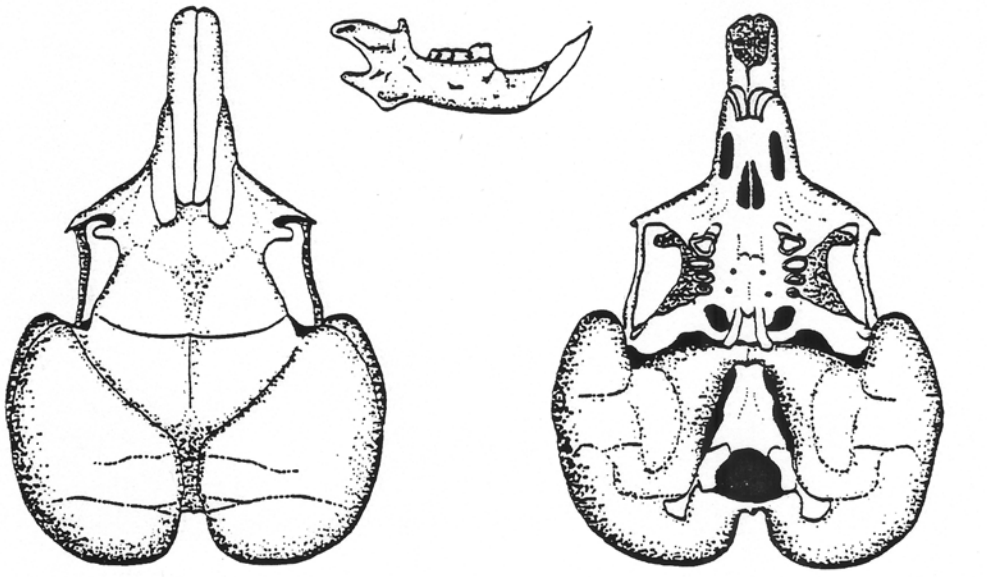
General descriptive statistics for the 43 populations of kangaroo mice are tabulated in Appendix E. It can be seen on inspection of this appendix that, in general, M. pallidus averages larger than M. megacephalus in basic "size" characters (greatest length of skull, greatest breadth of skull, mandibular length) as has been noted previously (Hall, 1941b; Hafner, 1976; Hafner et al., 1979).

Before proceeding with rigorous investigations into patterns of interpopulational relationships, I performed a univariate analysis of variance. Results of the analysis

Figure 10.--Dorsal and ventral views of the skulls and lateral aspect of the dentaries of species of Microdipodops. A, M. pallidus (TTU 24696, 17 mi. S, 5 mi. E Yerington, 5000 ft., Lyon Co., Nevada); B, M. megacephalus (TTU 24662, 2.5 mi. NE Larkin Lake, Alkali Valley, 21.5 mi. S, 10.5 mi. W Hawthorne, 6860 ft., Mineral Co., Nevada). The scale at the bottom is ten millimeters long.



A



B

of variance (Table 5) revealed great heterogeneity among all the sample means for all 16 cranial characters examined with all univariate F-ratios being highly significant ($p < .001$). Traditional character-by-character *a posteriori* test results will not be presented here, for the objective of this study is not to detail patterns of geographic variation in each of the characters at hand, but to deduce the relationships among the populations using an overall phenetic approximation.

Mahalanobis distance values were calculated between all populations of kangaroo mice in discriminant space and were subjected to pair-wise F-test analyses for the purpose of determining whether population centroids were significantly different from one another. This multivariate procedure was deemed necessary before progressing to clustering and ordination methodologies. Of the total pair-wise comparison, only three per cent (30 actual pair-wise distance measures) of the distance values were nonsignificant. None of the 43 populations were omitted from further analyses (clustering and ordination) because the few nonsignificant pair-wise distances were distributed largely in a random manner within the pair-wise F-matrix and such nonsignificance was judged to have arisen from morphological convergence (which is important) or from small sample size effects (when the pair of populations are doubtlessly distinct). In the phenograms that follow I have indicated nonsignificant pair-wise combinations

Table 5. Analysis of Variance summary values (univariate F-ratio for the cranial morphometric variables. Populations of both traditional species (*M. megacephalus* and *M. pallidus*) are included in the analysis. All F values are highly significant ($p < .001$) with 41 and 279 degrees of freedom.

Morphometric variable	F
Greatest Length	7.4247
Greatest Breadth	12.7036
Basal Length	3.8671
Bullar Length	10.7466
Maxillary Breadth	7.9592
Nasal Length	5.6726
Least Interorbital Breadth	5.9445
Greatest Expanse of Lateral Face of Zygoma	4.7384
Least Expanse of Lateral Face of Zygoma	5.6338
Greatest Length Incisive Foramina	5.3776
Length Incisive Foramina at Point of Greatest Breadth	13.5957
Greatest Breadth Incisive Foramina	3.7714
Greatest Pterygoidal Breadth	11.2406
Arching of Cranial Dome	4.9644
Mandibular Length	7.9014
Angular Bifurcation	11.7423

where they occur.

The distance matrix (Table 6) and the distance phenogram (Fig. 11) derived from it (cophenetic correlation coefficient is 0.819) indicate the phenetic relationships among the 43 populations of kangaroo mice. The three M. megacephalus samples of CHIL, SHOS, and GRAN (lower three samples in Fig. 11) are the most distinct of all kangaroo mice samples (being small in most characters, Appendix C) and cluster separately from all other M. megacephalus and M. pallidus samples. Of the remaining samples, the species M. pallidus (upper 16 populations, LOVE to WADS) seems to be phenetically separable from the M. megacephalus samples. The central cluster containing the three samples NIXO, WADS, and SMOK represents a heterogeneous grouping of two M. pallidus samples and one M. megacephalus respectively, and indicates the degree of "fuzziness" in separating the species. Kangaroo mice from the NIXO and WADS samples are small when compared with other M. pallidus samples (see Appendix E) and this explains their separation from other M. pallidus samples. Also, recall that the NIXO and WADS samples were chromosomally distinct (see earlier section) from other M. pallidus samples. In addition to the three distinct M. megacephalus samples (CHIL, SHOS, GRAN), the RIDD sample from Idaho stands out as one of the most disperate M. megacephalus populations (as it did also in the genetic analysis). The lower clustering levels depicted in Figure 11 (basically

Table 6. Product-Moment Correlation matrix (above the diagonal) and Taxonomic Distance matrix (below the diagonal) comparing 43 populations of kangaroo mice used in the analysis of cranial morphometrics.

	LOVE	MTWL	NIXO	WADS	YERI	MINA	STEW	TONO	SILV	COAL	MUDL	STON
LOVE	------	0.532	-0.337	0.171	0.462	0.188	0.465	0.229	0.816	0.466	0.153	0.086
MTWL	0.836	------	0.194	0.761	0.719	0.645	0.810	0.567	0.669	0.684	0.633	0.634
NIXO	1.399	1.299	------	0.633	0.350	0.091	-0.019	0.332	-0.170	-0.126	0.146	0.079
WADS	1.345	1.117	0.909	------	0.580	0.366	0.528	0.685	0.274	0.480	0.545	0.397
YERI	0.957	0.751	1.235	1.281	------	0.251	0.440	0.528	0.452	0.224	0.311	0.420
MINA	0.909	0.794	1.129	1.132	1.137	------	0.468	0.135	0.548	0.394	0.573	0.677
STEW	1.256	0.920	1.856	1.857	1.309	1.379	------	0.320	0.411	0.756	0.637	0.740
TONO	0.867	0.801	1.155	1.293	0.906	0.984	1.153	------	0.332	0.477	0.070	0.104
SILV	0.421	0.731	1.275	1.240	0.966	0.657	1.323	0.821	------	0.542	0.225	0.175
COAL	0.961	0.882	1.582	1.687	1.217	1.124	0.739	0.716	0.963	------	0.314	0.394
MUDL	0.984	0.768	1.212	1.174	1.103	0.650	1.135	1.006	0.925	1.063	------	0.762
STON	1.028	0.760	1.288	1.336	1.013	0.686	0.983	0.964	0.968	0.963	0.561	------

Table 6 continued (2)

	LOVE	MTWL	NIXO	WADS	YERI	MINA	STEW	TONO	SILV	COAL	MUDL	STON
KAWP	0.942	0.681	1.200	1.206	0.901	0.554	1.222	0.803	0.748	1.003	0.809	0.595
LOCK	1.235	0.918	1.224	1.280	1.170	0.820	1.359	0.867	1.066	1.124	0.724	0.855
HIKP	0.872	0.898	1.432	1.576	0.844	1.118	1.193	0.760	0.916	0.940	0.997	1.009
ALAM	1.078	0.800	1.186	1.242	1.212	0.841	1.013	0.875	1.015	1.011	0.653	0.773
ALKA	1.430	1.731	1.496	1.701	1.715	1.521	1.981	1.387	1.505	1.601	1.497	1.546
NARR	1.520	1.684	1.281	1.521	1.739	1.370	2.014	1.396	1.521	1.634	1.398	1.458
ALVO	1.392	1.601	1.319	1.649	1.618	1.375	1.850	1.157	1.382	1.383	1.469	1.397
RIDD	1.218	1.363	1.622	1.450	1.358	1.145	1.880	1.650	1.201	1.830	1.377	1.234
PAIN	0.968	1.242	0.980	1.092	1.344	0.949	1.721	1.080	0.950	1.317	1.129	1.157
QUIN	1.098	1.510	1.292	1.591	1.518	1.165	1.800	1.180	1.135	1.383	1.224	1.272
SULP	0.965	1.497	1.540	1.684	1.636	1.193	1.677	1.235	1.054	1.290	1.253	1.257
JUNG	1.069	1.371	1.226	1.383	1.553	0.943	1.761	1.164	0.979	1.361	1.201	1.172

Table 6 continued (3)

	LOVE	MTWL	NIXO	WADS	YERI	MINA	STEW	TONO	SILV	COAL	MUDL	STON
WINN	1.100	1.319	1.360	1.488	1.506	0.918	1.633	1.150	1.005	1.218	1.120	1.050
IZEN	0.825	1.345	1.402	1.540	1.323	1.024	1.786	1.204	0.804	1.453	1.253	1.248
SMOK	1.638	1.489	1.049	1.042	1.720	1.254	1.915	1.417	1.511	1.687	1.348	1.324
VERN	1.192	1.499	1.519	1.761	1.649	1.179	1.712	1.108	1.129	1.217	1.362	1.268
CHIL	2.243	2.288	1.538	1.522	2.337	1.776	2.912	2.288	2.104	2.660	1.993	2.090
SPAR	1.290	1.471	1.160	1.450	1.448	1.370	1.734	1.198	1.330	1.469	1.433	1.350
FLET	1.400	1.812	1.347	1.649	1.781	1.449	2.196	1.380	1.404	1.691	1.600	1.680
BENT	1.801	2.045	1.318	1.651	1.952	1.715	2.522	1.671	1.727	2.027	1.904	1.967
CONT	1.173	1.536	1.114	1.290	1.508	1.159	1.976	1.366	1.163	1.646	1.369	1.339
EURE	1.011	1.530	1.430	1.490	1.472	1.195	1.976	1.326	1.105	1.587	1.400	1.396
MONI	1.177	1.699	1.433	1.501	1.607	1.327	2.241	1.514	1.203	1.816	1.595	1.640
HOTC	1.228	1.565	1.300	1.498	1.483	1.k87	2.054	1.344	1.135	1.659	1.427	1.376

Table 6 continued (4)

	LOVE	MTWL	NIXO	WADS	YERI	MINA	STEW	TONO	SILV	COAL	MUDL	STON
HIKM	1.071	1.575	1.473	1.682	1.611	1.212	1.890	1.241	1.073	1.401	1.407	1.415
KAWM	1.060	1.554	1.265	1.491	1.501	1.185	1.997	1.264	1.050	1.587	1.432	1.433
PANA	1.181	1.647	1.284	1.447	1.540	1.337	2.084	1.338	1.211	1.668	1.375	1.478
SHOS	2.290	2.600	1.875	1.868	2.542	2.123	3.211	2.532	2.230	2.880	2.235	2.466
MILF	1.407	1.884	1.537	1.491	1.949	1.490	2.388	1.779	1.400	2.019	1.665	1.812
CALL	1.475	1.968	1.670	1.698	1.899	1.510	2.543	1.828	1.408	2.167	1.771	1.899
GRAN	2.030	2.406	1.928	1.812	2.473	1.864	3.039	2.420	1.958	2.711	2.123	2.338

Table 6 continued (5)

	KAWP	LOCK	HIKP	ALAM	ALKA	NARR	ALVO	RIDD	PAIN	QUIN	SULP	JUNG
LOVE	0.212	-0.090	0.575	0.166	-0.424	-0.705	-0.662	0.491	-0.049	-0.373	0.093	-0.277
MTWL	0.717	0.526	0.585	0.635	-0.571	-0.534	-0.620	0.501	-0.114	-0.809	-0.565	-0.418
NIXO	0.146	0.340	0.187	0.363	-0.250	0.057	-0.046	-0.293	0.148	-0.356	-0.699	-0.366
WADS	0.475	0.624	0.521	0.638	-0.417	-0.201	-0.337	-0.062	0.080	-0.745	-0.699	-0.549
YERI	0.553	0.305	0.715	0.245	-0.401	-0.492	-0.487	0.540	-0.203	-0.611	-0.683	-0.711
MINA	0.765	0.633	0.335	0.590	-0.696	-0.452	-0.625	0.417	-0.233	-0.622	-0.440	-0.118
STEW	0.534	0.259	0.230	0.689	-0.352	-0.419	-0.514	0.579	-0.036	-0.585	-0.174	-0.180
TONO	0.456	0.434	0.463	0.417	-0.284	-0.340	-0.193	-0.680	-0.074	-0.617	-0.537	-0.320
SILV	0.491	0.202	0.555	0.261	-0.689	-0.826	-0.723	0.433	-0.201	-0.590	-0.164	-0.175
COAL	0.458	0.171	0.100	0.402	-0.331	-0.423	-0.361	0.229	0.229	-0.587	-0.129	-0.013
MUDL	0.488	0.683	0.412	0.735	-0.390	-0.252	-0.628	0.297	-0.263	-0.460	-0.335	-0.391
STON	0.734	0.526	0.162	0.608	-0.443	-0.313	-0.458	0.641	-0.204	-0.530	-0.308	-0.189

Table 6 continued (6)

	KAWP	LOCK	HIKP	ALAM	ALKA	NARR	ALVO	RIDD	PAIN	QUIN	SULP	JUNG
KAWP	------	0.699	0.474	0.488	-0.770	-0.576	-0.447	0.514	-0.359	-0.864	-0.559	-0.313
LOCK	0.710	------	0.510	0.591	-0.573	-0.250	-0.329	-0.049	-0.379	-0.653	-0.550	-0.362
HIKP	0.964	0.918	------	0.330	-0.546	-0.535	-0.610	0.241	-0.417	-0.615	-0.532	-0.805
ALAM	0.892	0.840	1.055	------	-0.508	-0.373	-0.600	0.183	-0.195	-0.572	-0.310	-0.157
ALKA	1.668	1.740	1.724	1.690	------	0.789	0.653	-0.325	0.288	0.817	0.348	0.251
NARR	1.544	1.549	1.710	1.595	0.607	------	0.798	-0.493	0.380	0.627	0.134	0.219
ALVO	1.376	1.453	1.543	1.576	0.785	0.630	------	-0.492	0.268	0.495	0.237	0.353
RIDD	1.229	1.741	1.759	1.586	1.684	1.716	1.765	------	-0.272	-0.288	-0.073	-0.125
PAIN	1.143	1.354	1.445	1.271	0.946	0.848	0.926	1.261	------	0.225	0.098	0.317
QUIN	1.362	1.457	1.438	1.408	0.583	0.717	01757	1.453	0.715	------	0.630	0.488
SULP	1.340	1.495	1.471	1.368	0.979	1.088	0.959	1.441	0.863	0.576	------	0.640
JUNG	1.159	1.373	1.562	1.276	0.974	0.939	0.890	1.253	0.570	0.614	0.616	------

Table 6 continued (7)

	KAWP	LOCK	HIKP	ALAM	ALKA	NARR	ALVO	RIDD	APIN	QUIN	SULP	JUNG
WINN	1.120	1.356	1.544	1.313	0.923	0.993	0.952	1.274	0.686	0.662	0.748	0.463
IZEN	1.184	1.458	1.357	1.399	1.144	1.275	1.179	1.060	0.913	0.721	0.725	0.703
SMOK	1.333	1.451	1.918	1.359	1.362	1.118	1.209	1.548	0.993	1.332	1.427	1.016
VERN	1.262	1.387	1.531	1.401	1.091	1.168	0.913	1.626	0.931	0.758	0.717	0.597
CHIL	2.020	2.120	2.556	2.171	1.889	1.587	1.908	1.744	1.556	1.801	2.003	1.596
SPAR5	1.338	1.588	1.545	1.407	1.007	0.974	0.828	1.441	0.960	0.961	1.069	0.971
FLET	1.580	1.636	1.648	1.740	0.809	0.728	0.679	1.772	0.900	0.691	0.952	0.913
BENT	1.775	1.866	1.957	2.045	1.267	1.082	1.024	1.984	1.226	1.272	1.533	1.340
CONT	1.320	1.623	1.690	1.499	0.997	1.009	1.038	1.118	0.653	0.784	0.905	0.685
EURE	1.289	1.576	1.496	1.609	1.011	1.050	1.024	1.162	0.732	0.778	0.842	0.817
MONI	1.503	1.785	1.707	1.805	1.093	1.162	1.217	1.226	0.791	0.885	1.045	0.906
HOTC	1.329	1.593	1.678	1.594	1.059	1.198	1.163	1.162	0.855	0.776	0.976	0.686

Table 6 continued (8)

	KAWP	LOCK	HIKP	ALAM	ALKA	NARR	ALVO	RIDD	PAIN	QUIN	SULP	JUNG
HIKM	1.396	1.606	1.561	1.553	0.809	1.051	0.952	1.439	0.774	0.499	0.634	0.603
KAWM	1.334	1.586	1.544	1.535	0.929	1.026	0.936	1.246	0.754	0.606	0.722	0.611
PANA	1.457	1.550	1.551	1.586	0.988	1.116	1.116	1.449	0.896	0.731	0.858	0.900
SHOS	2.366	2.379	2.590	2.490	2.166	1.979	2.228	2.138	1.862	1.983	2.094	1.971
MILF	1.740	1.934	1.991	1.854	1.274	1.288	1.429	1.401	0.975	1.081	1.071	0.978
CALL	1.742	1.026	1.944	1.988	1.505	1.574	1.621	1.445	1.329	1.242	1.321	1.234
GRAN	2.200	2.326	2.502	2.330	2.096	1.947	2.197	1.817	1.651	1.846	1.886	1.698

Table 6 continued (9)

	WINN	IZEN	SMOK	VERN	CHIL	SPAR	FLET	BENT	CONT	EURE	MONI	HOTC
LOVE	-0.278	0.400	-0.587	-0.264	-0.825	-0.307	-0.455	-0.569	-0.189	0.224	0.230	-0.176
MTWL	-0.241	-0.200	0.159	-0.471	-0.215	-0.233	-0.828	-0.578	-0.553	-0.444	-0.513	-0.400
NIXO	-0.478	-0.542	0.442	-0.435	0.568	0.167	-0.115	0.270	-0.017	-0.581	-0.428	-0.221
WADS	-0.490	-0.634	0.422	-0.575	0.126	-0.103	-0.510	-0.166	-0.487	-0.608	-0.626	-0.570
YERI	-0.487	-0.010	-0.148	-0.601	-0.245	-0.075	-0.593	-0.305	-0.255	-0.150	-0.133	-0.082
MINA	0.046	-0.129	0.063	-0.217	0.222	-0.562	-0.686	-0.532	-0.514	-0.428	-0.473	-0.290
STEW	0.012	-0.201	0.317	-0.318	-0.272	0.010	-0.805	-0.679	-0.212	-0.360	-0.582	-0.426
TONO	-0.316	-0.292	0.247	-0.163	-0.220	-0.011	-0.299	-0.085	-0.382	-0.299	-0.294	-0.173
SILV	-0.157	0.352	-0.416	-0.184	-0.583	-0.494	-0.580	-0.521	-0.387	-0.132	-0.001	-0.088
COAL	0.232	-0.309	0.298	-0.044	-0.437	-0.151	-0.554	-0.397	-0.263	-0.255	-0.329	-0.315
MUDL	-0.122	-0.334	0.178	-0.451	0.212	-0.429	-0.705	-0.600	-0.558	-0.522	-0.688	-0.464
STON	0.095	-0.240	0.324	-0.251	0.183	-0.212	-0.827	-0.650	-0.248	-0.392	-0.659	-0.212

Table 6 continued (10)

	WINN	IZEN	SMOK	VERN	CHIL	SPAR	FLET	BENT	CONT	EURE	MONI	HOTC
KAWP	-0.150	-0.203	0.178	-0.262	0.080	-0.260	-0.689	-0.373	-0.450	-0.277	-0.473	-0.257
LOCK	-0.294	-0.419	0.284	-0.259	0.398	-0.436	-0.426	-0.219	-0.742	-0.497	-0.661	-0.412
HIKP	-0.754	-0.009	-0.423	-0.684	-0.227	-0.300	-0.361	-0.223	-0.578	-0.013	-0.036	-0.402
ALAM	-0.240	-0.327	0.390	-0.309	0.176	-0.126	-0.685	-0.580	-0.404	-0.647	-0.792	-0.475
ALKA	0.377	0.024	0.079	0.285	0.014	0.381	0.617	0.370	0.373	0.308	0.350	0.282
NARR	0.199	-0.332	0.350	0.142	0.516	0.385	0.663	0.530	0.196	0.154	0.110	-0.063
ALVO	0.213	-0.171	0.363	0.365	0.312	0.553	0.770	0.724	0.379	0.299	0.222	0.108
RIDD	0.069	0.401	-0.244	-0.192	-0.324	-0.026	-0.689	-0.652	0 004	0.121	-0.029	0.133
PAIN	0.289	-0.335	0.214	0.263	-0.005	0.051	0.188	0.106	0.179	0.175	0.253	-0.048
QUIN	0.429	0.374	-0.215	0.483	0.039	0.165	0.649	0.238	0.442	0.396	0.506	0.487
SULP	0.402	0.485	-0.229	0.574	-0.355	0.088	0.338	-0.121	0.367	0.421	0.322	0.246
JUNG	0.726	0.302	0.227	0.889	0.028	0.082	0.208	-0.080	0.246	0.070	0.076	0.432

Table 6 continued (11)

	WINN	IZEN	SMOK	VERN	CHIL	SPAR	FLET	BENT	CONT	EURE	MONI	HOTC
WINN	------	0.139	0.208	0.746	-0.045	-0.143	0.017	-0.152	0.195	0.038	0.069	0.505
IZEN	0.846	------	-0.689	0.323	-0.517	-0.143	0.030	-0.316	0.221	0.365	0.480	0.552
SMOK	1.115	1.510	------	0.092	0.528	0.428	-0.124	0.160	-0.022	-0.583	-0.722	-0.223
VERN	0.601	0.927	1.384	------	-0.090	-0.083	0.277	-0.020	0.153	0.229	0.227	0.591
CHIL	1.775	1.864	1.308	2.081	------	0.113	0.157	0.348	-0.069	-0.380	-0.427	-0.166
SPAR	1.129	1.147	1.059	1.247	1.801	------	0.306	0.451	0.450	0.101	-0.011	-0.033
FLET	1.071	1.070	1.399	1.082	1.695	1.020	------	0.792	0.343	0.497	0.570	0.088
BENT	1.466	1.540	1.385	1.482	1.553	1.161	0.766	------	0.301	0.183	0.310	0.013
CONT	0.846	0.807	1.077	1.134	1.393	0.886	0.895	1.124	------	0.226	0.301	0.315
EURE	0.935	0.761	1.443	1.069	1.689	1.057	0.799	1.236	0.739	------	0.349	0.128
MONI	1.041	0.813	1.516	1.232	1.563	1.215	0.841	1.164	0.707	0.447	------	0.372
HOTC	0.739	0.682	1.298	0.917	1.599	1.161	1.080	1.352	0.717	0.890	0.791	------

Table 6 continued (12)

	WINN	IZEN	SMOK	VERN	CHIL	SPAR	FLET	BENT	CONT	EURE	MONI	HOTC
HIKM	0.576	0.684	1.445	0.653	1.907	1.138	0.799	1.319	0.782	0.746	0.768	0.680
KAWM	0.840	0.503	1.336	0.927	1.636	0.928	0.695	1.129	0.508	0.599	0.574	0.620
PANA	1.013	0.855	1.392	1.210	1.666	1.130	0.868	1.177	0.769	0.846	0.809	0.697
SHOS	2.165	1.999	2.022	2.394	1.249	2.167	1.782	1.663	1.657	1.823	1.626	1.868
MILF	1.202	1.066	1.402	1.436	1.381	1.292	1.034	1.252	0.799	0.901	0.715	1.027
CALL	1.394	0.947	1.791	1.569	1.571	1.531	1.183	1.427	0.985	1.056	0.839	1.046
GRAN	1.921	1.726	1.972	2.155	1.241	2.118	1.718	1.798	1.505	1.565	1.338	1.703

Table 6 continued (13)

	HIKM	KAWM	PANA	SHOS	MILF	CALL	GRAN
LOVE	-0.054	-0.023	-0.094	-0.205	0.152	0.193	0.149
MTWL	-0.659	-0.690	-0.629	-0.429	-0.573	-0.435	-0.319
NIXO	-0.574	-0.343	-0.175	0.264	-0.438	-0.364	-0.078
WADS	-0.795	-0.767	-0.403	-0.043	-0.550	-0.550	-0.248
YERI	-0.557	-0.351	-0.229	-0.224	-0.596	-0.174	-0.383
MINA	-0.468	-0.598	-0.678	-0.133	-0.533	-0.177	0.177
STEW	-0.476	-0.610	-0.580	-0.545	-0.389	-0.554	-0.432
TONO	-0.365	-0.311	-0.233	-0.364	-0.530	-0.291	-0.448
SILV	-0.153	-0.151	-0.302	-0.216	-0.066	0.211	0.171
COAL	-0.167	-0.528	-0.477	-0.534	-0.181	-0.472	-0.329
MUDL	-0.624	-0.825	-0.355	0.063	-0.412	-0.339	0.043
STON	-0.581	-0.699	-0.503	-0.297	-0.672	-0.506	-0.335

Table 6 continued (14)

	HIKM	KAWM	PANA	SHOS	MILF	CALL	GRAN
KAWP	-0.627	-0.580	-0.595	-0.276	-0.716	-0.311	-0.219
LOCK	-0.708	-0.718	-0.342	0.141	-0.606	-0.252	0.022
HIKP	-0.572	-0.348	-0.109	0.196	-0.256	0.122	0.199
ALAM	-0.627	-0.640	-0.483	-0.149	-0.448	-0.456	-0.064
ALKA	0.561	0.400	0.377	-0.102	0.305	0.043	-0.270
NARR	0.173	0.120	0.091	0.115	0.127	-0.198	-0.100
ALVO	0.295	0.393	0.169	-0.012	0.169	-0.063	-0.270
RIDD	-0.182	-0.108	-0.350	-0.490	-0.335	-0.099	-0.281
PAIN	0.226	-0.058	-0.129	-0.175	0.149	-0.456	-0.028
QUIN	0.738	0.632	0.535	0.135	0.545	0.346	0.143
SULP	0.627	0.326	0.431	0.022	0.732	0.313	0.222
JUNG	0.588	0.400	-0.020	-0.352	0.287	-0.024	-0.027

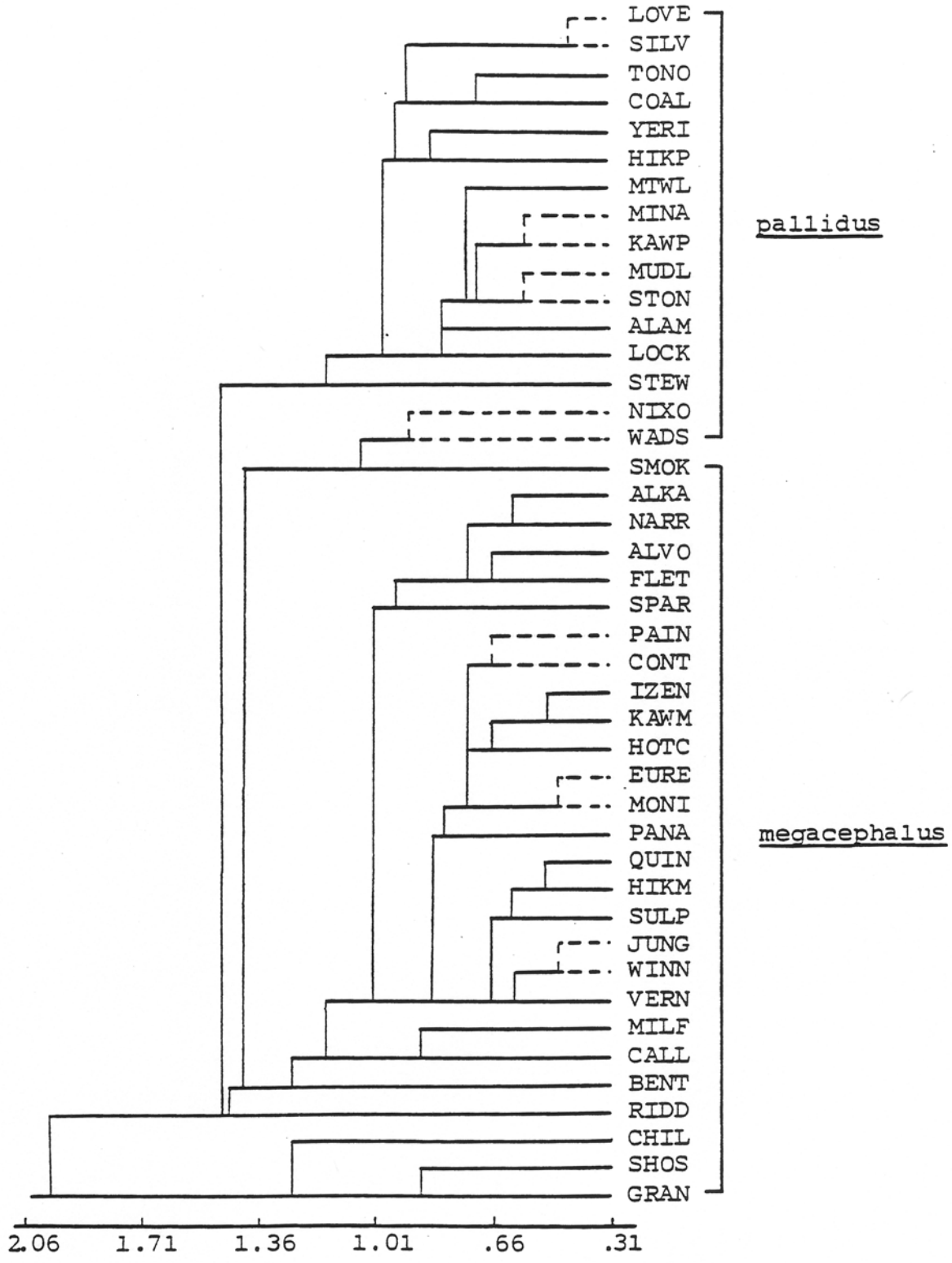
Table 6 continued (15)

	HIKM	KAWM	PANA	SHOS	MILF	CALL	GRAN
WINN	0.642	0.123	-0.048	-0.459	0.075	-0.089	-0.237
IZEN	0.509	0.709	0.247	-0.154	0.303	0.700	0.154
SMOK	-0.361	-0.469	-0.364	-0.272	-0.378	-0.766	-0.550
VERN	0.700	0.433	0.174	-0.335	0.214	0.087	-0 085
CHIL	-0.378	-0.295	-0.201	0.361	-0 337	-0.300	0.111
SPAR	-0.044	0.264	0.024	-0.200	0.139	-0.323	-0.465
FLET	0.514	0.617	0.427	0.359	0.521	0.382	0.259
BENT	0.171	0.330	0.304	0.407	0.270	0.148	0.068
CONT	0.466	0.627	0.266	0.015	0.265	0.240	-0.119
EURE	0.486	0.533	0.238	-0.031	0.395	0.312	0.193
MONI	0.671	0.689	0.395	0.087	0.515	0.525	0.315
HOTC	0.634	0.541	0.512	-0.159	0.104	0.330	-0.193

Table 6 continued (16)

	HIKM	KAWM	PANA	SHOS	MILF	CALL	GRAN
HIKM	------	0.734	0.448	-0.125	0.563	0.496	0.119
KAWM	0.544	------	0.444	0.016	0.494	0.686	0.140
PANA	0.794	0.691	------	0.535	0.574	0.486	0.199
SHOS	2.060	1.792	1.552	------	0.390	0.408	0.716
MILF	1.029	0.842	0.839	1.311	------	0.423	0.516
CALL	1.128	0.845	0.983	1.375	0.878	------	0.514
GRAN	1.813	1.582	1.589	0.887	1.049	1.145	------

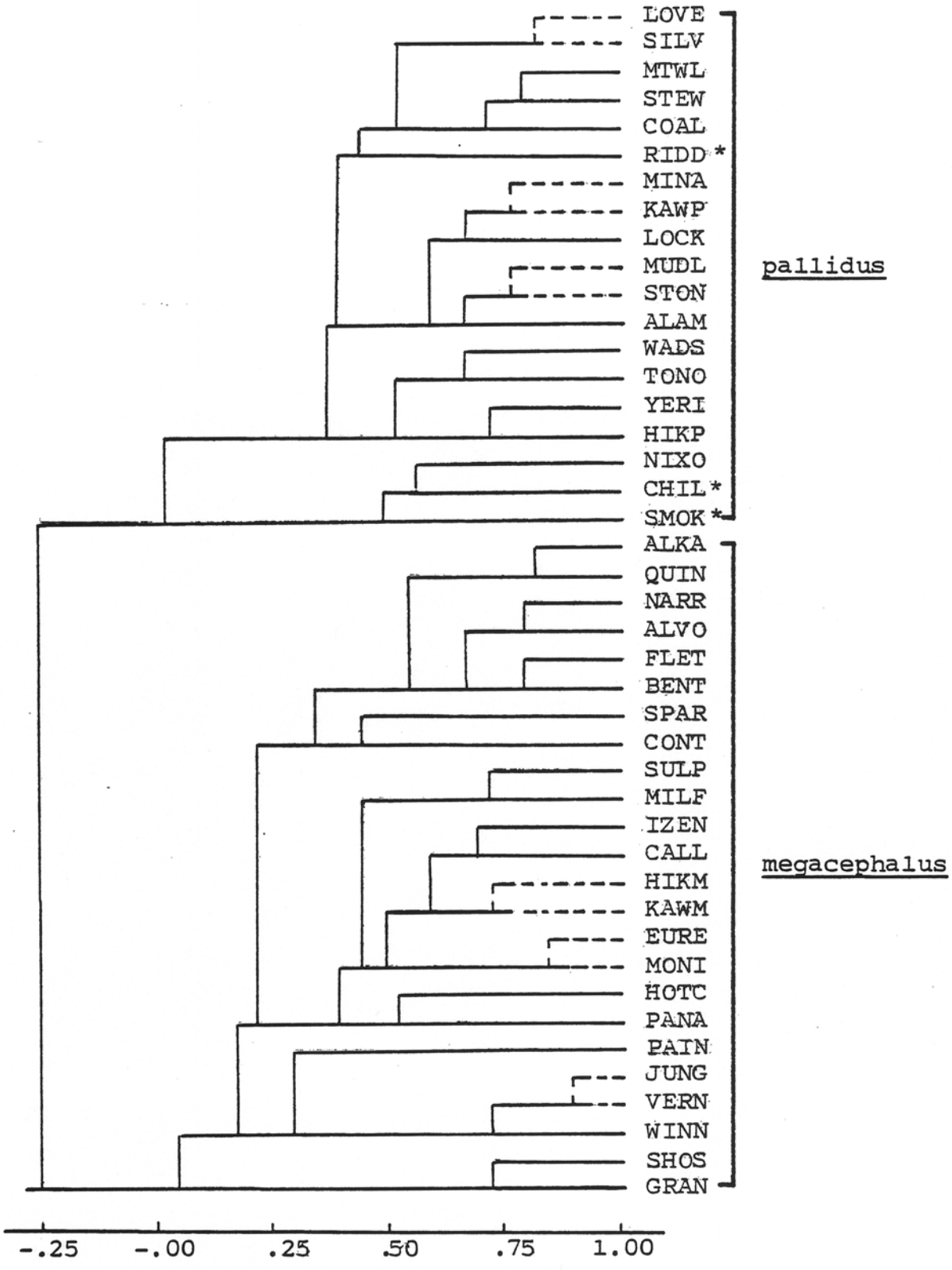
Figure 11.--Distance phenogram (UPGMA) illustrating the morphometric relationships among the 43 populations of kangaroo mice (cophenetic correlation coefficient is 0.819). Nonsignificant clustering levels (assessed by examining the multivariate F ratios, see text) are indicated by the use of dashed lines.


LOVE
SILV
TONO
COAL
YERI
HIKP
MTWL
MINA
KAWP
MUDL
STON
ALAM
LOCK
STEW
NIXO
WADS
SMOK
ALKA
NARR
ALVO
FLET
SPAR
PAIN
CONT
IZEN
KAWM
HOTC
EURE
MONI
PANA
QUIN
HIKM
SULP
JUNG
WINN
VERN
MILF
CALL
BENT
RIDD
CHIL
SHOS
GRAN
pallidus
megacephalus
2.06
1.71
1.36
1.01
.66
.31

those less than 1.0 are difficult to interpret, for, at times, rather remote geographic samples (see Fig. 2) and genetically distant populations (see Fig. 4) are clustered together. These lower levels, thus, are considered to manifest a considerable degree of parallel evolution in morphology. Nevertheless, a rather large degree of the "genetic" information is expressed in these lower clustering levels as seen by the uppermost cluster (LOVE, SILV, TONO, COAL, YERI, and HIKP) which is basically the M. pallidus western genetic unit (see protein analysis) and the second cluster (MTWL, MINA, KAWP, MUDL, STON, ALAM, and LOCK) which is basically the eastern protein unit described earlier.

Examination of the correlation matrix (Table 6) and the correlation phenogram (Fig. 12) based upon it (cophenetic correlation coefficient is 0.810) reveals approximately the same relationships as did the distance matrix and phenogram. Again, populations of M. pallidus (upper large cluster) are easily separable from most M. megacephalus samples (lower main cluster). However, the topology of this dendrogram departs from earlier trees and phenograms in the clustering of the genetically and geographically distinct RIDD population (from Idaho) within the M. pallidus and the SMOK and CHIL populations being grouped together with NIXO (M. pallidus) sample. The geographically remote SHOS and GRAN (M. megacephalus) samples, from southeastern Nevada and western Utah, again

Figure 12.--Correlation phenogram (UPGMA) illustrating the morphometric relationships among the 43 populations of kangaroo mice (cophenetic correlation coefficient is 0.810). Levels of nonsignificance (assessed by examining the multivariate F ratios, see discussion in text) are indicated with dashed lines.


LOVE
SILV
MTWL
STEW
COAL
RIDD *
MINA
KAWP
LOCK
MUDL
STON
ALAM
WADS
TONO
YERI
HIKP
NIXO
CHIL *
SMOK *
ALKA
QUIN
NARR
ALVO
FLET
BENT
SPAR
CONT
SULP
MILF
IZEN
CALL
HIKM
KAWM
EURE
MONI
HOTC
PANA
PAIN
JUNG
VERN
WINN
SHOS
GRAN
pallidus
megacephalus
-.25
-.00
.25
.50
.75
1.00

stand out as being phenetically distinct. Note, also, that the geographically isolated FLET and BENT samples (from the Mono Lake, California area) are clustered together at a high level.

The above phenograms provide an unweighted phenetic assessment of the morphometric relationships among the populations of kangaroo mice. These morphometric phenograms, as well as the phylogenetic tree derived from the protein data (Fig. 4) and the dendrogram from the chromosome data (Fig. 8A), delineate groupings or aggregations of kangaroo mouse populations. As a means by which to determine whether these previously-defined groupings can be discriminated from one another with morphometric criteria, the morphometric data were subjected to discriminant function analysis. Population samples of kangaroo mice (including both traditional species) were treated separately in this analysis without regard to previously-defined aggregations. The standardized canonical coefficients and the discriminant rank for each character used in the analysis are listed in Table 7. The standardized canonical coefficients indicate the relative contributions of each character to each of the discriminant functions, while the discriminant rank is an ordering of the characters (used by the computer in the step-wise procedure) which relates to their general discriminatory power. The first seven discriminant functions accounted for most of the phenetic variation in the analysis (84.9 per cent). Discriminant Function I

Table 7. Standardized canonical variate coefficient and discriminant rank for the 16 cranial morphometric characters.

Morphometric Variable	Discriminant Rank	Discriminant Function I	II	III	IV	V	VI	VII
Greatest Length	10	.4192	- .6008	.7063	.4507	.2191	1.0443	- .5828
Greatest Breadth	9	-.4267	- .6450	.6176	.2643	-.4448	- .0852	- .3079
Basal Length	5	-.1401	.1737	-.1299	-.7710	-.3202	- .5016	.6800
Bullar Length	7	.2919	-1.0076	-.5583	-.6590	.3175	- .7391	.7144
Maxillary Breadth	11	-.3685	.2405	-.7872	-.0408	.0085	.1440	-1.1369
Nasal Length	8	.0500	.4520	.4942	.2149	.6083	.0628	- .2062
Least Interorbital Breadth	1	-.1760	.5468	.0461	.5336	-.2536	- .2760	- .3202
Greatest Expanse of Lateral Face of Zygoma	12	.0208	- .1316	.4985	-.3590	.3688	.1629	.2793
Least Expanse of Lateral Face of Zygoma	15	.1370	.1829	.1498	-.5555	-.9054	.0092	- .5980

Table 7 continued (2)

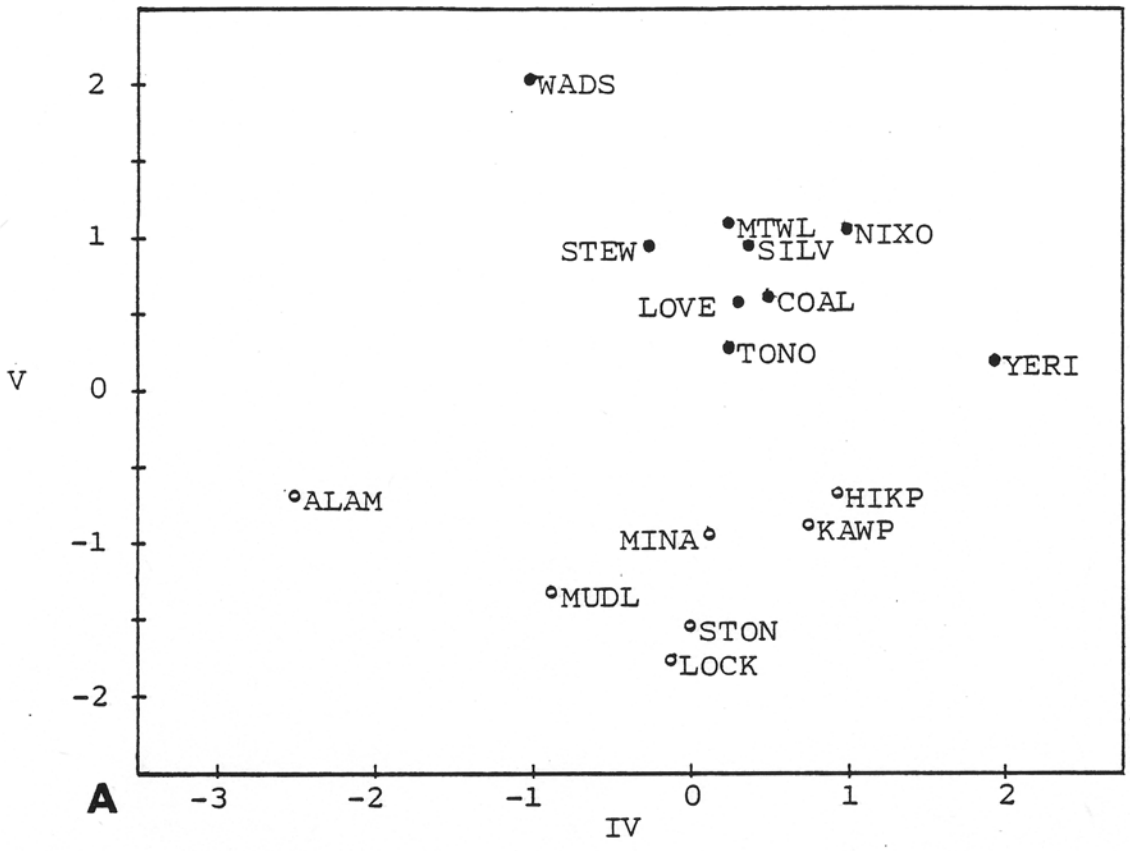
Morphometric Variable	Discriminant Rank	Discriminant Function I	II	III	IV	V	VI	VII
Greatest Length Incisive Foramina	14	-.2433	.2300	.5269	-.2791	.2885	-1.0861	- .0549
Length Incisive Foramina at Point of Greatest Breadth	13	.8364	- .3710	-.2410	.8898	-.8675	.3456	- .2256
Greatest Breadth Incisive Foramina	6	.0789	.1350	.1533	.0965	.1737	- .2414	- .4024
Greatest Pterygoidal Breadth	3	-.6305	- .2175	-.0061	.5282	.3923	.0300	- .2374
Arching of Cranial Dome	16	-.4400	.1978	-.0383	-.5321	-.1094	.0905	- .1772
Mandibular Length	4	-.1840	.5903	.2424	.6541	-.1566	.4506	.6542
Angular Bifurcation	2	-.7899	- .1791	-.0439	.2148	-.6208	- .2896	.1438
Variation Explained (percentage)		38.2	17.3	8.9	6.2	5.6	4.9	3.8

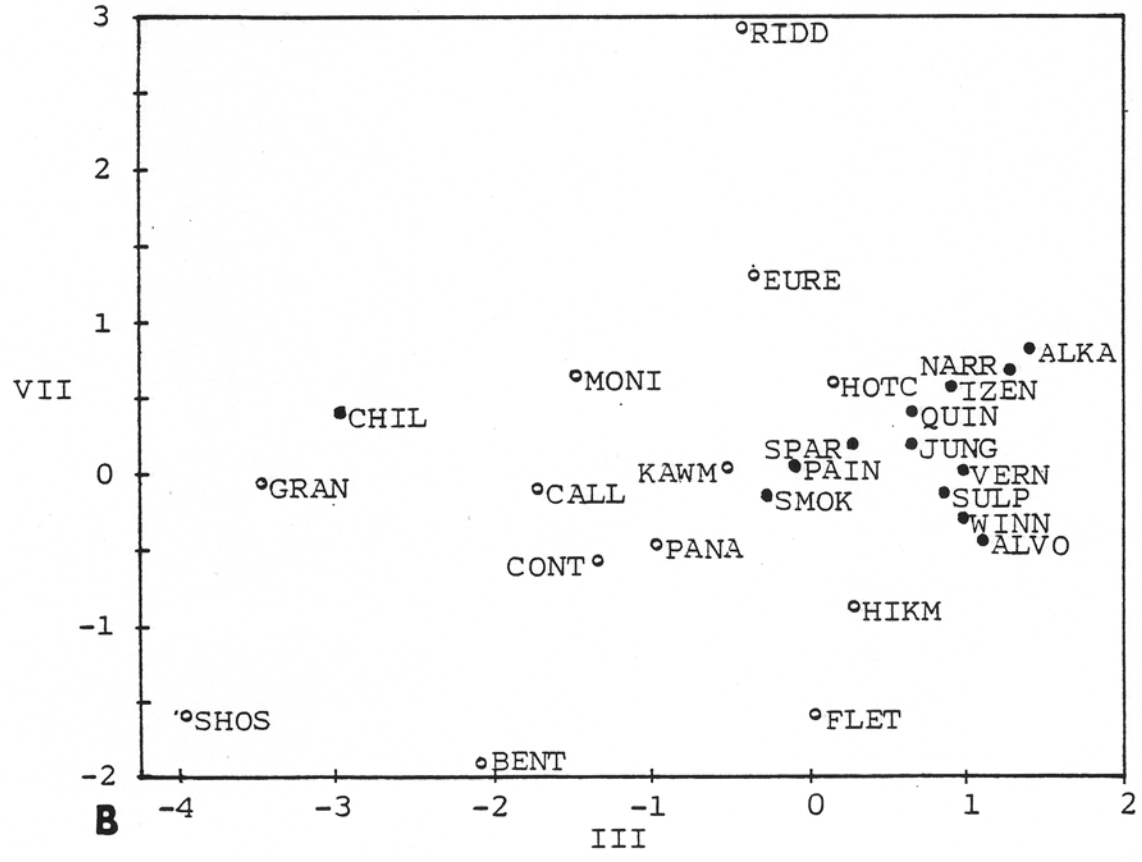
(38.2 per cent of variation) was extremely effective in separating M. pallidus and M. megacephalus, with no overlap among population centroids in discriminant space (not figured). The characters most responsible for separation along this first eigenvector (Table 7) were length of incisive foramina at point of greatest breadth (the incisive foramina of M. megacephalus diverge posteriorly), angular bifurcation (greater in M. pallidus), and greatest pterygoidal breadth (tips of pterygoids broader in M. pallidus).

The remaining eigenvectors (Discriminant Functions II and VII) serve to discriminate among populations within M. pallidus and M. megacephalus. The eastern and western units of M. pallidus, described in the above phenograms and defined earlier by genetic criteria, are best discriminated by the use of Discriminant Functions IV and V (Fig. 13A). Characters most responsible for explaining the separation of these main units of M. pallidus in Figure 13A are least expanse of lateral face of zygoma and nasal length (see Table 7 and Appendix E). The eastern unit of M. pallidus has larger values for the least expanse of lateral face of zygoma measure, and shorter nasals than does the western unit.

The eastern and western units of M. megacephalus defined earlier by genetic criteria were not clearly recognizable by the phenetic clustering methodology (Fig. 11 and 12). Examination of Figure 13B reveals that

Figure 13.--Discriminant function plots illustrating the separation of Microdipodops population centroids based on the morphometric data. A, plot of Discriminant Function IV versus V showing separation of the eastern (circles) and western (dots) units of M. pallidus; B, plot of Discriminant Function III versus VII showing separation of the eastern (circles) and western (dots) units of M. megacephalus.


WADS
MTWL
NIXO
STEW
SILV
LOVE
COAL
TONO
YERI
ALAM
HIKP
KAWP
MINA
MUDL
STON
LOCK
V
IV
A
2
1
0
-1
-2
-3


RIDD
EURE
ALKA
NARR
MONI
HOTC
IZEN
CHIL
QUIN
SPAR
JUNG
KAWM
PAIN
VERN
GRAN
CALL
SMOK
SULP
WINN
ALVO
PANA
CONT
HIKM
SHOS
FLET
BENT
VII
III
B
3
2
1
0
-1
-2
-4
-3
-2
-1
0
1
2

Discriminant Functions III and VII are able to separate the previously defined groups to a modest degree. Characters contributing to the separation of the eastern and western units of M. megacephalus along Discriminant Functions III and VII include: maxillary breadth, greatest length of skull, greatest breadth of skull, bullar length, basal length, and mandibular length (Table 7).

Colorimetric Analysis.--The phenomenon of desert coloration and "substrate races" in mammals has been a subject of great interest to several generations of naturalists (for review, see Harison, 1975). Traditionally, pelage color has played a prominent role in mammalian systematics, particularly at infraspecific taxonomic levels. It seems that for almost any species or subspecies described, one can usually find some reference pertaining to pelage coloration. Most unfortunately, though, such descriptions usually utilize qualitative subjectively based, descriptions. Although detailed colorimetric analyses are routinely employed in systematic treatments of other vartebrate groups (as an example of the use of colorimetry in avian systematics, see Johnson, 1980), colorimetry has been used only rarely in systematic studies of mammals. Where color variation has been rigorously quantified in the context of mammal systematics, the usage was generally restricted to contact zone and transect analyses (e.g. Sands and Findley, 1959; Hendricksen, 1972; Patton et al., 1979), and in fact, we

have very little detailed knowledge of how color quantitatively varies over geography for any mammalian group.

A data base containing 686 individuals from 43 localities was utilized in the present analysis of colorimetric variation in the genus Microdipodops. The principal aim was to detail the main patterns of dorsal pelage color variation among populations of kangaroo mice by using multivariate summary routines. The eight colorimetric variables (listed in the Materials and Methods) were subjected to a character correlation analysis and three characters were eliminated from the analyses as they were highly correlated ($r \geq 0.95$) with others in the matrix and were judged to be contributing only redundant information. The remaining five characters (relative brightness, dominant wavelength, excitation purity, trichromatic coefficient $\underline{x}$, and reflectance RZ_1) were used below to examine patterns of colorimetric variation among the 43 populations. Descriptive statistics for the sampled populations of kangaroo mice are presented in Appendix F. Table 8 details the analysis of variance summary values for the colorimetric variables, and indicates that there is significant heterogeneity among all the sample means (includes both traditional species) for all five of the variables. This univariate a priori test was performed before proceeding with investigations into interpopulational phenetic (colorimetric) relationships.

Table 8. Analysis of Variance summary values (univariate F-ratio) for the colorimetric variables. Populations of both traditional species (*M. megacephalus* and *M. pallidus*) are included in the analysis. All F values are highly significant ($p < .001$) with 42 and 643 degrees of freedom.

Colorimetric Variable	F
Relative Brightness	67.5811
Dominant Wavelength	21.1421
Excitation Purity	49.1288
Trichromatic Coefficient *x*	55.0968
Reflectance RZ_1	43.8200

The colorimetric data set was analyzed multivariately (by means of discriminant function analysis) and Mahalanobis distance values were calculated between all populations of kangaroo mice. To determine whether the populations were significantly different from one another in multivariate space, distance measures between population centroids were subjected to pair-wise F-test analyses. Only 6.8 per cent of the total pair-wise comparisons were found to be nonsignificant. Again, as was the case in the morphometric analysis, none of the sample populations were eliminated because many of the nonsignificant pair-wise distances were judged to be the result of parallelism. Following the statistical conventions used in this study, nonsignificant pair-wise combinations are indicated in the phenogram that follows.

Colorimetric relationships among the 43 populations of kangaroo mice are depicted in the distance phenogram (Fig. 14) and the distance matrix on which it is based (Table 9). Clustering methodologies other than the distance phenogram were examined but yielded less reliable results (i.e., lower cophenetic correlation coefficients) and will not be discussed here. The colorimetric phenogram (cophenetic correlation coefficient is 0.825) shows five northern M. megacephalus populations (ALKA, EURE, ALVO, PAIN, RIDD, and CONT) to be the most divergent of all kangaroo mice. These five populations are extremely dark (least relative brightness) in pelage value and have a yellow hue (dominant

Figure 14.--Distance phenogram illustrating the colorimetric relationships among the 43 populations of kangaroo mice (cophenetic correlation coefficient is 0.825). Levels of pair-wise nonsignificance (assessed by examining the multivariate F ratios, see text) are indicated by the use of the dashed lines. The relative brightness (pale to dark) of each of the main groupings is indicated in parentheses.

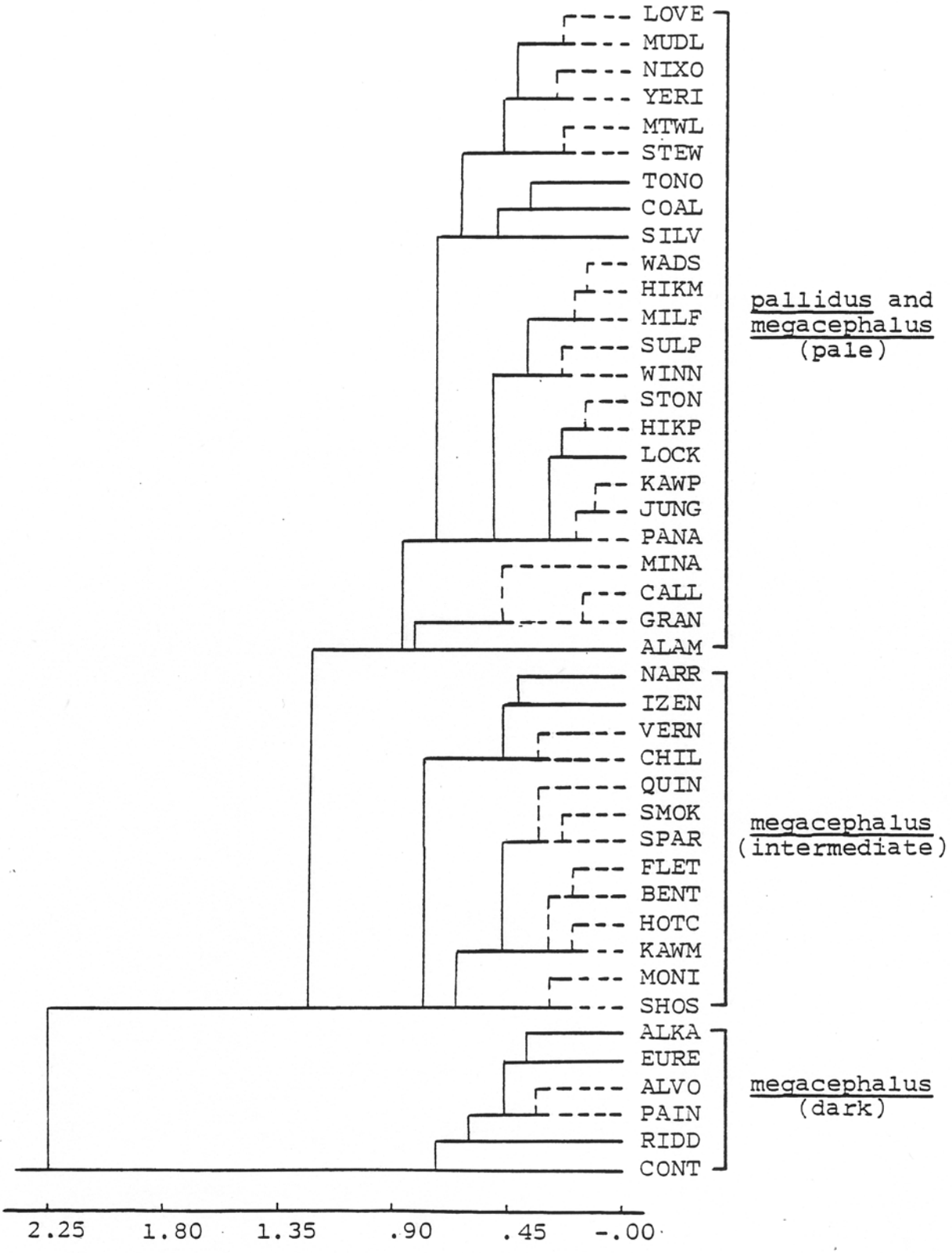

LOVE
MUDL
NIXO
YERI
MTWL
STEW
TONO
COAL
SILV
WADS
HIKM
MILF
SULP
WINN
STON
HIKP
LOCK
KAWP
JUNG
PANA
MINA
CALL
GRAN
ALAM
NARR
IZEN
VERN
CHIL
QUIN
SMOK
SPAR
FLET
BENT
HOTC
KAWM
MONI
SHOS
ALKA
EURE
ALVO
PAIN
RIDD
CONT
pallidus and megacephalus (pale)
megacephalus (intermediate)
megacephalus (dark)
2.25
1.80
1.35
.90
.45
-.00

Table 9. Taxonomic Distance matrix based on five colorimetric characters comparing populations of kangaroo mice.

	LOVE	MTWL	NIXO	WADS	YERI	MINA	STEW	TONO	SILV	COAL	MUDL	STON
LOVE	-----											
MTWL	0.277	-----										
NIXO	0.514	0.453	-----									
WADS	0.529	0.739	0.831	-----								
YERI	0.311	0.383	0.263	0.576	-----							
MINA	0.546	0.782	0.779	0.711	0.611	-----						
STEW	0.489	0.221	0.531	0.885	0.534	1.001	-----					
TONO	0.498	0.481	0.584	1.003	0.586	0.627	0.635	-----				
SILV	0.648	0.575	0.985	1.083	0.907	0.983	0.639	0.611	-----			
COAL	0.623	0.483	0.763	1.145	0.776	0.921	0.540	0.351	0.376	-----		
MUDL	0.226	0.379	0.441	0.658	0.297	0.418	0.592	0.360	0.724	0.603	-----	
STON	0.289	0.540	0.763	0.484	0.519	0.510	0.733	0.706	0.745	0.831	0.421	-----

Table 9 continued (2)

	LOVE	MTWL	NIXO	WADS	YERI	MINA	STEW	TONO	SILV	COAL	MUDL	STON
KAWP	0.350	0.562	0.838	0.604	0.632	0.498	0.761	0.608	0.595	0.710	0.430	0.224
LOCK	0.442	0.709	0.884	0.386	0.633	0.463	0.908	0.812	0.877	0.970	0.526	0.182
HIKP	0.227	0.471	0.668	0.333	0.419	0.543	0.657	0.695	0.771	0.822	0.383	0.120
ALAM	0.809	0.909	1.264	1.087	1.107	0.889	1.053	0.833	0.521	0.785	0.863	0.727
ALKA	2.229	2.405	2.400	1.712	2.256	2.286	2.489	2.707	2.643	2.813	2.365	2.020
NARR	1.526	1.675	1.656	1.017	1.466	1.632	1.749	1.995	2.052	2.131	1.641	1.389
ALVO	2.618	2.781	2.857	2.104	2.640	2.693	2.851	4.101	3.017	3.195	3.760	2.415
RIDD	2.913	3.109	3.196	2.403	2.961	2.903	3.208	3.372	3.291	3.487	3.039	2.678
PAIN	2.658	2.826	2.947	2.160	2.717	2.733	2.901	3.137	3.004	3.214	2.810	2.437
QUIN	0.723	0.875	0.807	0.342	0.609	0.880	0.983	1.156	1.332	1.325	0.804	0.676
SULP	0.440	0.589	0.763	0.222	0.525	0.795	0.704	0.937	0.944	1.019	0.623	0.368
JUNG	0.310	0.520	0.789	0.630	0.593	0.469	0.725	0.538	0.574	0.654	0.374	0.256

Table 9 continued (3)

	LOVE	MTWL	NIXO	WADS	YERI	MINA	STEW	TONO	SILV	COAL	MUDL	STON
WINN	0.612	0.697	0.880	0.366	0.671	0.998	0.758	1.100	1.042	1.140	0.804	0.555
IZEN	1.535	1.644	1.716	1.067	1.525	1.760	1.680	2.028	1.967	2.095	1.695	1.404
SMOK	1.093	1.208	1.115	0.677	0.961	1.259	1.273	1.530	1.675	1.679	1.185	1.043
VERN	1.271	1.371	1.376	0.823	1.204	1.499	1.411	1.747	1.775	1.843	1.410	1.186
CHIL	1.499	1.576	1.501	1.087	1.373	1.714	1.596	1.947	2.033	2.057	1.614	1.453
SPAR	0.994	1.149	1.055	0.552	0.875	1.089	1.248	1.424	1.597	1.601	1.069	0.918
FLET	0.859	1.078	1.119	0.340	0.875	0.898	1.220	1.310	1.396	1.475	0.959	0.672
BENT	0.823	1.067	1.100	0.364	0.852	0.766	1.233	1.237	1.357	1.428	0.893	0.616
CONT	2.013	2.223	2.299	1.502	2.059	1.984	2.342	2.462	2.429	2.598	2.127	1.776
EURE	2.480	2.671	2.763	1.969	2.528	2.495	2.768	2.946	2.868	3.057	2.612	2.252
MONI	1.276	1.485	1.580	0.766	1.333	1.309	1.609	1.737	1.719	1.866	1.400	1.049
HOTC	1.017	1.218	1.250	0.488	1.022	1.078	1.342	1.480	1.541	1.632	1.129	0.836

Table 9 continued (4)

	LOVE	MTWL	NIXO	WADS	YERI	MINA	STEW	TONO	SILV	COAL	MUDL	STON
HIKM	0.509	0.736	0.881	0.125	0.619	0.679	0.893	0.978	1.018	1.109	0.650	0.312
KAWM	0.977	1.187	1.160	0.463	0.939	1.045	1.286	1.430	1.535	1.595	1.073	0.827
PANA	0.410	0.628	0.913	0.512	0.682	0.587	0.811	0.757	0.680	0.838	0.539	0.189
SHOS	1.410	1.638	1.672	0.901	1.433	1.344	1.779	1.841	1.897	2.013	1.498	1.186
MILF	0.670	0.907	1.004	0.210	0.746	0.720	1.068	0.113	1.178	1.270	0.775	0.449
CALL	0.889	1.078	1.143	1.126	1.023	0.470	1.289	0.753	1.043	1.004	0.755	0.842
GRAN	0.788	0.960	1.037	1.077	0.927	0.426	1.167	0.621	0.929	0.872	0.650	0.773

Table 9 continued (5)

	KAWP	LOCK	HIKP	ALAM	ALKA	NARR	ALVO	RIDD	PAIN	QUIN	SULP	JUNG
KAWP	-----											
LOCK	0.297	-----										
HIKP	0.318	0.270	-----									
ALAM	0.520	0.756	0.822	-----								
ALKA	2.194	1.941	2.017	2.500	-----							
NARR	1.502	1.350	1.344	2.034	0.914	-----						
ALVO	2.589	2.343	2.409	2.884	0.410	1.251	-----					
RIDD	2.828	2.575	2.693	3.073	0.765	1.655	0.580	-----				
PAIN	2.593	2.360	2.445	2.835	0.526	1.420	0.323	0.490	-----			
QUIN	0.896	0.693	0.592	1.402	1.685	0.862	2.063	2.404	2.169	-----		
SULP	0.574	0.459	0.287	1.033	0.818	1.121	2.197	2.524	2.246	0.442	-----	
JUNG	0.092	0.335	0.329	0.536	2.249	1.640	2.646	2.888	2.654	0.907	0.595	-----

Table 9 continued (6)

	KAWP	LOCK	HIKP	ALAM	ALKA	NARR	ALVO	RIDD	PAIN	QUIN	SULP	JUNG
WINN	0.747	0.645	0.482	1.164	1.733	1.041	2.096	2.456	2.149	0.490	0.205	0.773
IZEN	1.607	1.398	1.360	1.985	0.926	0.427	1.222	1.687	1.342	0.984	1.097	1.650
SMOK	1.266	1.052	0.962	1.757	1.471	0.572	1.818	2.213	1.968	0.390	0.751	1.284
VERN	1.405	1.197	1.118	1.845	1.228	0.409	1.551	1.991	1.692	0.653	0.857	1.435
CHIL	1.657	1.470	1.372	2.139	1.333	0.501	1.607	2.081	1.801	0.838	1.122	1.697
SPAR	1.138	0.902	0.848	1.634	1.487	0.626	1.856	2.206	1.990	0.276	0.678	1.156
FLET	0.874	0.598	0.654	1.320	1.419	0.763	1.820	2.097	1.887	0.412	0.533	0.910
BENT	0.798	0.509	0.618	1.240	1.525	0.907	1.931	2.170	1.988	0.484	0.580	0.835
CONT	1.932	1.668	1.792	2.223	0.447	0.904	0.814	0.921	0.834	1.520	1.643	1.990
EURE	2.408	2.156	2.263	2.673	0.355	1.242	0.410	0.446	0.369	1.973	2.088	2.466
MONI	1.221	0.958	1.057	1.570	0.986	0.625	1.392	1.641	1.429	0.836	0.906	1.275
HOTC	1.039	0.769	0.813	1.469	1.259	0.593	1.647	1.942	1.724	0.491	0.650	1.078

Table 9 continued (7)

	KAWP	LOCK	HIKP	ALAM	ALKA	NARR	ALVO	RIDD	PAIN	QUIN	SULP	JUNG
HIKM	0.522	0.294	0.297	0.984	1.732	1.090	2.127	2.407	2.165	01465	0.247	0.553
KAWM	1.040	0.780	0.787	1.502	1.341	0.591	1.730	2.044	1.829	0.370	0.623	1.075
PANA	0.162	0.229	0.290	0.576	2.044	1.480	2.437	2.679	2.436	0.832	0.587	0.234
SHOS	1.356	1.072	1.195	1.722	0.977	0.647	1.384	1.580	1.449	0.918	1.080	1.405
MILF	0.643	0.371	0.452	1.089	1.603	0.982	2.044	2.264	2.047	0.461	0.405	0.685
CALL	0.708	0.783	0.915	0.806	2.608	2.046	3.017	3.164	3.022	1.339	1.191	0.683
GRAN	0.629	0.742	0.829	0.745	2.619	2.029	3.027	3.197	3.036	1.289	1.121	0.594

Table 9 continued (8)

	WINN	IZEN	SMOK	VERN	CHIL	SPAR	FLET	BENT	CONT	EURE	MONI	HOTC
WINN	-----											
IZEN	0.995	-----										
SMOK	0.700	0.738	-----									
VERN	0.734	0.389	0.365	----								
CHIL	1.007	0.579	0.459	0.337	-----							
SPAR	0.680	0.837	0.207	0.505	0.647	-----						
FLET	0.591	0.896	0.589	0.701	0.968	0.430	-----					
BENT	0.684	1.063	0.721	0.870	1.123	0.538	0.178	-----				
CONT	1.604	1.015	1.391	1.230	1.396	1.344	1.187	1.251	-----			
EURE	2.016	1.264	1.790	1.563	1.679	1.784	1.669	1.753	0.528	-----		
MONI	0.889	0.714	0.829	0.743	1.023	0.741	0.474	0.564	0.740	1.212	-----	
HOTC	0.655	0.737	0.536	0.578	0.851	0.415	0.182	0.337	1.044	1.511	0.349	-----

Table 9 continued (9)

	WINN	IZEN	SMOK	VERN	CHIL	SPAR	FLET	BENT	CONT	EURE	MONI	HOTC
HIKM	0.404	1.121	0.791	0.909	1.189	0.663	0.382	0.380	1.506	0.975	0.769	0.535
KAWM	0.632	0.769	0.411	0.538	0.777	0.265	0.215	0.350	1.154	1.618	0.495	0.167
PANA	0.646	1.469	1.183	1.290	1.576	1.058	0.763	0.702	1.789	2.258	1.080	0.918
SHOS	1.094	0.877	0.890	0.875	1.092	0.774	0.567	0.607	0.663	1.177	0.287	0.460
MILF	0.522	1.063	0.748	0.869	1.148	0.593	0.235	0.200	1.353	1.839	0.627	0.402
CALL	1.390	2.161	1.716	1.935	2.168	1.541	1.293	1.144	2.266	2.778	1.639	1.471
GRAN	1.319	2.128	1.674	1.893	2.124	1.508	1.275	1.137	2.292	2.801	1.640	1.455

Table 9 continued (10)

	HIKM	KAWM	PANA	SHOS	MILF	CALL	GRAN
HIKM	-----						
KAWM	0.543	-----					
PANA	0.413	0.934	-----				
SHOS	0.917	0.560	1.232	-----			
MILF	0.194	0.420	0.532	0.744	-----		
CALL	1.064	1.462	0.824	1.663	1.099	-----	
GRAN	1.017	1.441	0.761	1.684	1.073	0.134	-----

wavelength) according to colorimetric determination. All other populations of kangaroo mice are yellowish orange in hue (not readily ascertained by eye) and divisible into two main groups: the upper cluster in Figure 14 contains all M. pallidus populations and eight M. megacephalus populations (HIKM, MILF, SULP, WINN, JUNG, PANA, CALL, and GRAN) all of which are pale in pelage value (high relative brightness, see Appendix F). The third major cluster (central group of Fig. 14) contains the remaining M. megacephalus samples and are of intermediate brightness of the three major groupings. The lower clustering levels (those less than 1.0) seem to recognize, to a rather minimal extent, the genetic units within the species defined earlier. This is seen within the upper main cluster which unifies most of the populations of the western genetic unit of M. pallidus (including LOVE, NIXO, YERI, MTWL, STEW, TONO, COAL, and SILV of the first subcluster), and separates these from the other two heterogeneous subclusters including the eastern genetic unit of M. pallidus (STON, HIKP, LOCK, KAWP, and ALAM).

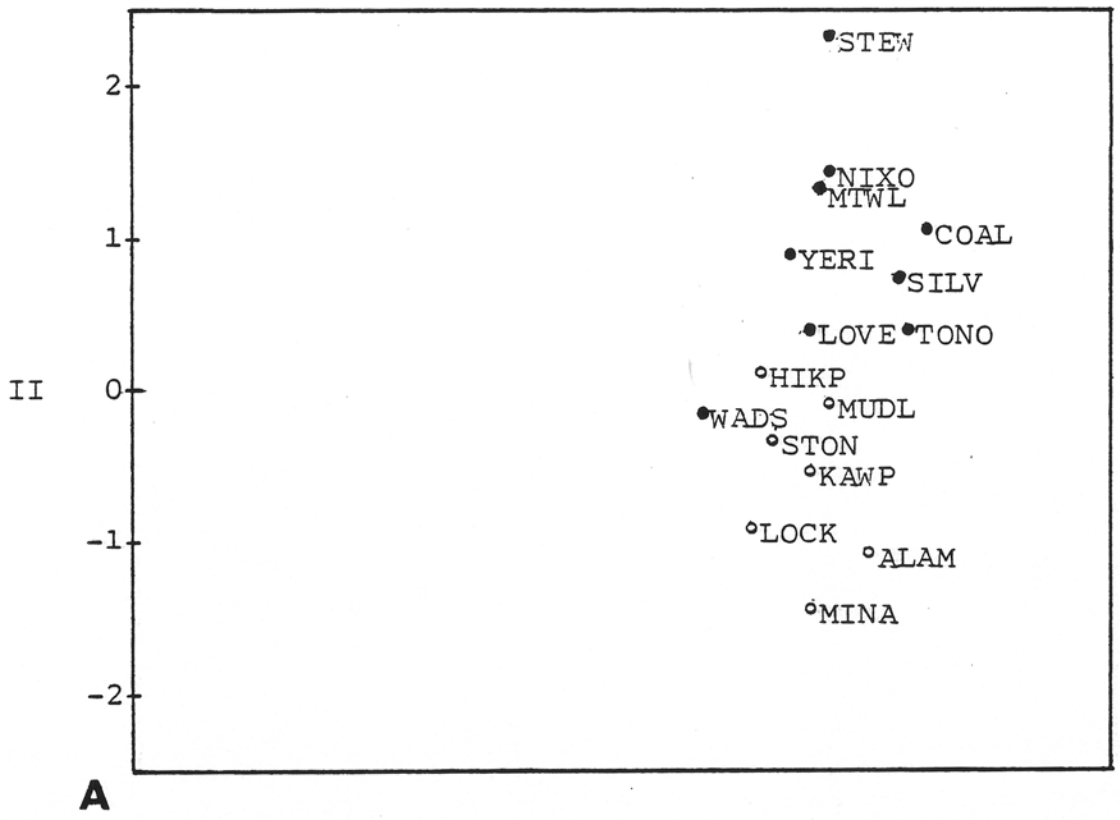
Following the unweighted clustering procedure, the colorimetric data set was subjected to discriminant function analysis to determine whether groups defined in earlier analyses could be discriminated from one another, and moreover, which characters are most important in separating the previously-defined groups. In this analysis, as in the previous case with the morphometric data, population

samples (representing both traditional species) were treated as independent entities (disregarding earlier-delineated aggregations) to ensure objectivity. The standardized canonical coefficients and the discriminant rank for each of the colorimetric characters are listed in Table 10. The first two Discriminant Functions explained 82.9 per cent of the colorimetric variation among the 43 populations of kangaroo mice. Discriminant Function I (Fig. 15) is moderately effective in separating the species M. pallidus and M. megacephalus with the noted exception of the M. megacephalus populations mentioned above that are light in color and appear convergent on the M. pallidus pelage morph. The character contributing most heavily to the separation along this eigenvector is relative brightness (Table 10). Populations of M. pallidus are rather pale, with high relative brightness values (hence the venacular name Pallid Kangaroo Mouse), whereas populations of M. megacephalus are highly variable in brightness (their common name, Dark Kangaroo Mouse, then is not entirely appropriate). Discriminant Function II seems to separate the eastern and western genetic units within both M. pallidus (Fig. 15A) and M. megacephalus (Fig. 15B). The characters most responsible for the separation along this eigenvector are trichromatic coefficient x, reflectance RZ_1, and excitation purity (Table 10 and Appendix F). The western units of both M. megacephalus and M. pallidus, differ from their eastern

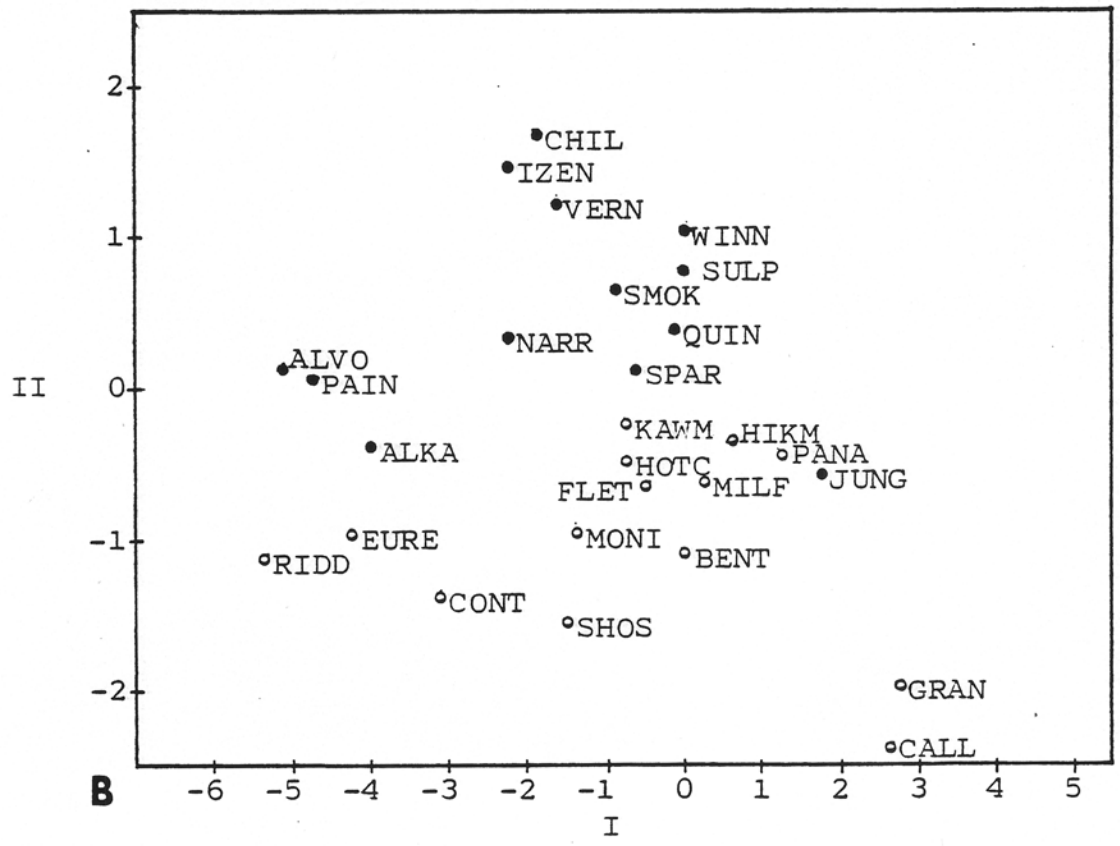
Table 10. Standardized canonical variate coefficients and discriminant rank for the five colorimetric characters.

Colorimetric Variable	Discriminant Rank	Discriminant Function I	Discriminant Function II
Relative Brightness	1	1.0650	- .0543
Dominant Wavelength	5	.3698	- .2498
Excitation Purity	3	.2178	-4.5236
Trichromatic Coefficient $\underline{x}$	2	.6575	6.0109
Reflectance RZ_1	4	.4490	-1.4634
Variation Explained (percentage)		68.6	14.3

Figure 15.--Discriminant function plots illustrating the separation of Microdipodops population centroids based on the colorimetric data. A, plot of Discriminant Function I versus II showing separation of the eastern (circles) and western (dots) units of M. pallidus; B, plot of Discriminant Function I versus II showing separation of the eastern (circles) and western (dots) units of M. megacephalus.


STEW
NIXO
MTWL
COAL
YERI
SILV
LOVE
TONO
HIKP
MUDL
WADS
STON
KAWP
LOCK
ALAM
MINA
2
1
0
-1
-2
II

A


CHIL
IZEN
VERN
WINN
SULP
SMOK
QUIN
NARR
ALVO
PAIN
SPAR
KAWM
HIKM
ALKA
PANA
HOTC
JUNG
FLET
MILF
EURE
MONI
RIDD
BENT
CONT
SHOS
GRAN
CALL
2
1
0
-1
-2
II
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5
I

B

counterparts in having large values for the trichromatic coefficient $\underline{x}$ (indicative of reduced purity), and small reflectance RZ_1 values (beginning-point reflectance readings). Note (Fig. 15A) the position of the MINA is separated from its geographically proximate (western) localities.

Environmental Data.--Systematists, whether studying protein bands on an electrophoretic gel, mensural data gleaned from museum study specimens, or chromosomal photomicrographs, attempt to decipher evolutionary relationships among populations by making inferences which, in the final assessment, are based on phenotypic expressions of genetic loci. Although the environment doubtlessly plays roles of various magnitudes in the phenotypic expression of different types of characters under study, little information is available concerning the relative effect that environmental selective regimes exert on various suites of characters. It is to this end that I undertook a quantification of the environment to which populations of kangaroo mice are presently exposed. The present section describes quantitatively the general environmental regions of the Great Basin and, as such, provides an information base to be used on subsequent sections of this study.

Twenty-eight weather and climatological variables (Appendix C) were examined for 42 kangaroo mouse localities in the Great Basin. The data matrix used in the analysis

of patterns of environmental variability is presented in Appendix G. A character correlation analysis was performed on the data matrix and, as there were no high correlations ($r \geq .90$) among the variables, all characters were considered to be contributing some unique information and were retained in the subsequent analysis.

The distance matrix (Table 11) and the distance phenogram (Fig. 16) with which it corresponds (cophenetic correlation coefficient is 0.722) depict the environmental relationships among the 42 kangaroo mouse localities. From examination of Figure 16, there appear to be four main areas of rough environmental homogeneity (those groups clustering above a distance of 1.25): 1) the northern Great Basin environmental unit; 2) the western Great Basin environmental unit; 3) the south-central Great Basin environmental unit; and 4) the east-central Great Basin environmental unit. I will not discuss all the detailed climatological factors that define each of the four regions (for that specific information see Appendix G), but the following brief summaries will serve the present purposes.

It can be seen (Fig. 16) that the most disparate region is the nothern Great Basin unit which contains the following eight (M. megacephalus) localities: NARR, ALKA, PAIN, ALVO, DENI, RIDD, CONT, and IZEN. This region, (Oregon, Idaho, and northern Nevada) is characterized by having the greatest precipitation and being the coolest of the four environmental units.

Table 11. Taxonomic Distance matrix based on 28 environmental characters comparing localities of kangaroo mice.

	NARR	ALKA	ALVO	RIDD	DENI	CONT	PAIN	QUIN	JUNG	WINN	SULP	IZEN
NARR	-----											
ALKA	0.477	-----										
ALVO	0.603	0.812	-----									
RIDD	0.894	0.978	0.771	-----								
DENI	0.806	1.007	0.365	0.892	-----							
CONT	1.201	1.210	1.073	0.818	1.211	-----						
PAIN	0.800	0.761	0.872	1.207	0.945	1.297	-----					
QUIN	1.340	1.470	0.934	1.282	0.808	1.555	1.356	-----				
JUNG	1.506	1.622	1.126	1.409	0.968	1.679	1.627	0.600	-----			
WINN	1.270	1.394	0.952	1.217	0.812	1.550	1.460	0.748	0.621	-----		
SULP	1.586	1.708	1.231	1.542	1.139	1.738	1.690	0.739	0.578	0.828	-----	
IZEN	1.207	1.271	0.989	1.040	0.894	1.258	1.321	0.976	0.939	0.919	1.096	-----

Table 11 continued (2)

	NARR	ALKA	ALVO	RIDD	DENI	CONT	PAIN	QUIN	JUNG	WINN	SULP	IZEN
SMOK	1.247	1.337	1.024	1.350	1.057	1.611	1.229	0.852	0.967	0.964	0.898	0.975
VERN	1.773	1.866	1.423	1.712	1.301	1.916	1.839	0.945	0.701	0.913	0.424	1.146
LOVE	1.792	1.884	1.446	1.731	1.326	1.940	1.849	0.965	0.729	0.934	0.468	1.152
EURE	1.270	1.253	1.104	1.207	1.204	1.101	1.267	1.372	1.511	1.511	1.571	1.184
GRAN	1.658	1.699	1.366	1.268	1.284	1.324	1.736	1.378	1.317	1.345	1.380	1.094
CALL	1.626	1.625	1.369	1.280	1.330	1.167	1.626	1.540	1.549	1.495	1.625	1.283
NIXO	1.801	1.884	1.501	1.858	1.386	2.089	1.843	1.122	0.956	1.096	0.782	1.234
CHIL	1.128	1.199	0.938	1.144	0.902	1.484	1.244	1.168	1.168	1.069	1.115	1.058
SPAR	1.318	1.379	1.101	1.331	1.031	1.621	1.343	1.060	1.116	1.005	0.968	1.128
WADS	1.780	1.864	1.476	1.838	1.401	2.044	1.823	1.111	1.001	1.136	0.723	1.304
MTWL	1.722	1.809	1.400	1.697	1.276	1.936	1.775	1.097	0.884	0.929	0.692	1.263
YERI	1.398	1.480	1.219	1.467	1.192	1.756	1.437	1.098	1.168	1.146	0.986	1.207

Table 11 continued (3)

	NARR	ALKA	ALVO	RIDD	DENI	CONT	PAIN	QUIN	JUNG	WINN	SULP	IZEN
STEW	1.996	2.088	1.706	1.990	1.620	2.166	2.081	1.374	1.203	1.394	0.846	1.537
MONI	1.619	1.613	1.387	1.605	1.379	1.621	1.420	1.490	1.537	1.582	1.445	1.435
HOTC	1.750	1.816	1.478	1.676	1.442	1.787	1.718	1.295	1.301	1.472	1.210	1.365
LOCK	1.771	1.816	1.503	1.651	1.467	1.744	1.738	1.397	1.359	1.563	1.352	1.431
SHOS	1.647	1.646	1.405	1.476	1.368	1.429	1.629	1.473	1.488	1.470	1.570	1.407
MILF	1.783	1.801	1.526	1.569	1.468	1.611	1.769	1.560	1.535	1.525	1.634	1.516
FLET	1.541	1.606	1.281	1.580	1.255	1.850	1.669	1.305	1.213	1.171	1.077	1.360
MINA	2.164	2.212	1.882	2.146	1.753	2.389	2.279	1.462	1.314	1.442	1.035	1.658
TONO	2.098	2.242	1.824	2.154	1.744	2.322	2.195	1.555	1.420	1.642	1.196	1.699
STON	2.039	2.171	1.760	1.892	1.677	2.123	2.093	1.588	1.559	1.649	1.450	1.632
BENT	1.554	1.538	1.296	1.593	1.270	1.744	1.452	1.378	1.327	1.339	1.204	1.393
COAL	1.660	1.740	1.367	1.673	1.284	1.874	1.621	1.162	1.065	1.220	0.909	1.263

Table 11 continued (4)

	NARR	ALKA	ALVO	RIDD	DENI	CONT	PAIN	QUIN	JUNG	WINN	SULP	IZEN
SILV	1.891	2.025	1.603	1.871	1.534	2.142	1.998	1.272	1.230	1.377	0.991	1.483
MUDL	2.097	2.241	1.854	2.157	1.775	2.433	2.219	1.496	1.448	1.548	1.225	1.695
HIKO	2.083	2.197	1.764	1.902	1.702	2.136	2.214	1.495	1.341	1.561	1.283	1.576
PANA	2.079	2.127	1.740	1.848	1.656	2.093	2.130	1.484	1.333	1.541	1.383	1.572
KAWI	2.333	2.449	2.016	2.173	1.922	2.380	2.405	1.559	1.454	1.648	1.304	1.780
ALAM	2.462	2.573	2.109	2.340	2.020	2.512	2.566	1.776	1.552	1.699	1.435	1.945

Table 11 continued (5)

	SMOK	VERN	LOVE	EURE	GRAN	CALL	NIXO	CHIL	SPAR	WADS	MTWL	YERI
SMOK	-----											
VERN	0.883	-----										
LOVE	0.875	0.115	-----									
EURE	1.318	1.697	1.716	-----								
GRAN	1.344	1.386	1.428	1.205	-----							
CALL	1.487	1.665	1.700	1.064	0.693	-----						
NIXO	0.881	0.611	0.600	1.831	1.667	1.917	-----					
CHIL	0.775	1.136	1.153	1.332	1.251	1.361	1.186	-----				
SPAR	0.635	0.951	0.971	1.463	1.370	1.471	0.942	0.645	-----			
WADS	0.867	0.630	0.620	1.779	1.660	1.881	0.298	1.176	0.929	-----		
MTWL	0.948	0.516	0.549	1.727	1.429	1.580	0.793	1.032	0.849	0.808	-----	
YERI	0.533	0.928	0.935	1.479	1.391	1.589	0.945	0.817	0.641	0.896	0.936	-----

Table 11 continued (6)

	SMOK	VERN	LOVE	EURE	GRAN	CALL	NIXO	CHIL	SPAR	WADS	MTWL	YERI
STEW	1.141	0.747	0.756	1.856	1.571	1.758	1.008	1.335	1.176	0.893	0.797	1.090
MONI	1.270	1.493	1.515	1.256	1.371	1.298	1.626	1.275	1.244	1.583	1.336	1.302
HOTC	1.251	1.269	1.304	1.382	1.317	1.336	1.447	1.420	1.252	1.399	1.154	1.300
LOCK	1.335	1.414	1.455	1.299	1.262	1.225	1.591	1.397	1.332	1.548	1.296	1.394
SHOS	1.416	1.616	1.661	1.026	0.998	0.687	1.800	1.362	1.373	1.761	1.491	1.515
MILF	1.507	1.672	1.715	1.229	1.048	0.834	1.850	1.422	1.447	1.812	1.530	1.608
FLET	0.895	1.002	1.009	1.485	1.456	1.545	1.035	0.957	0.852	1.024	0.853	0.860
MINA	1.255	0.876	0.883	2.056	1.695	1.900	1.122	1.454	1.317	1.075	0.878	1.220
TONO	1.364	1.151	1.179	1.851	1.670	1.835	1.256	1.395	1.368	1.193	1.121	1.287
STON	1.535	1.461	1.492	1.771	1.502	1.555	1.675	1.442	1.404	1.648	1.267	1.535
BENT	0.959	1.149	1.166	1.454	1.406	1.497	1.189	0.922	0.890	1.179	1.021	0.912
COAL	0.820	0.835	0.858	1.458	1.269	1.495	0.937	1.004	0.831	0.924	0.785	0.784

Table 11 continued (7)

	SMOK	VERN	LOVE	EURE	GRAN	CALL	NIXO	CHIL	SPAR	WADS	MTWL	YERI
SILV	1.068	0.905	0.926	1.729	1.408	1.694	1.078	1.227	1.039	1.036	0.834	0.945
MUDL	1.404	1.182	1.209	2.010	1.781	1.939	1.288	1.526	1.360	1.227	1.092	1.322
HIKO	1.507	1.267	1.313	1.660	1.370	1.546	1.554	1.468	1.468	1.525	1.214	1.495
PANA	1.494	1.357	1.400	1.599	1.258	1.397	1.611	1.471	1.492	1.583	1.291	1.525
KAWI	1.579	1.255	1.291	1.945	1.637	1.787	1.549	1.725	1.520	1.499	1.219	1.561
ALAM	1.768	1.356	1.389	2.072	1.859	1.950	1.507	1.794	1.631	1.477	1.257	1.755

Table 11 continued (8)

	STEW	MONI	HOTC	LOCK	SHOS	MILF	FLET	MINA	TONO	STON	BENT	COAL
STEW	-----											
MONI	1.446	-----										
HOTC	1.272	0.965	-----									
LOCK	1.390	0.928	0.410	-----								
SHOS	1.680	1.084	1.087	0.905	-----							
MILF	1.713	1.163	1.102	0.888	0.371	-----						
FLET	1.040	1.208	1.289	1.344	1.442	1.518	-----					
MINA	0.612	1.727	1.413	1.538	1.805	1.800	1.212	-----				
TONO	0.863	1.411	1.287	1.292	1.593	1.389	1.242	0.897	-----			
STON	1.325	1.187	1.016	1.008	1.337	1.252	1.413	1.274	1.002	-----		
BENT	1.237	0.872	1.294	1.289	1.382	1.460	0.670	1.517	1.355	1.473	-----	
COAL	0.941	1.005	0.937	1.019	1.347	1.360	0.801	1.117	0.993	1.151	0.759	-----

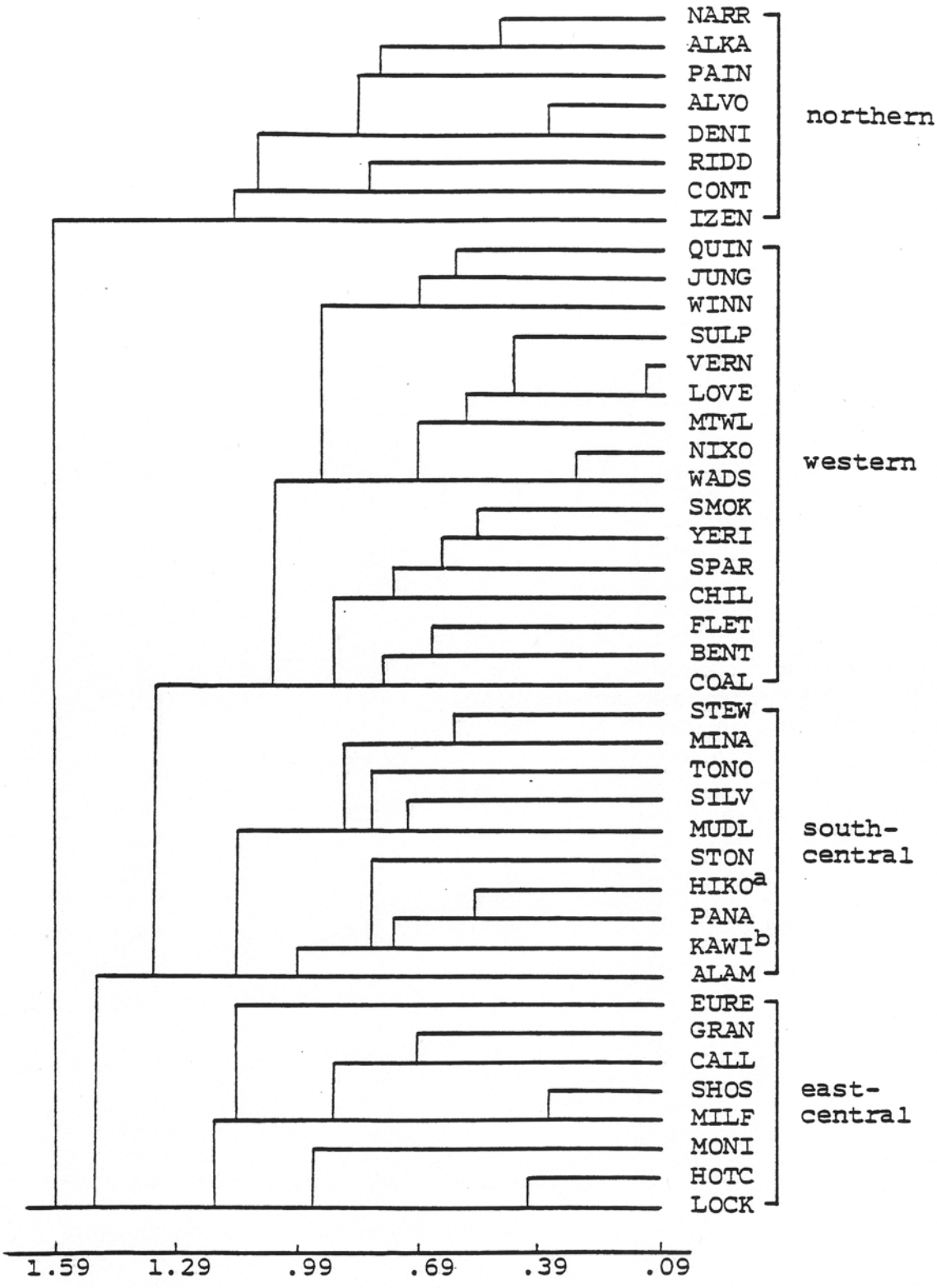
Table 11 continued (9)

	STEW	MONI	HOTC	LOCK	SHOS	MILF	FLET	MINA	TONO	STON	BENT	COAL
SILV	0.802	1.382	1.059	1.197	1.547	1.565	1.000	0.751	0.767	0.982	1.258	0.734
MUDL	1.037	1.650	1.168	1.335	1.708	1.660	1.427	0.867	0.845	1.043	1.651	1.147
HIKO	1.216	1.373	1.011	0.956	1.319	1.251	1.373	1.188	0.923	0.703	1.502	1.084
PANA	1.304	1.283	1.018	0.866	1.131	0.988	1.413	1.350	1.135	0.892	1.455	1.123
KAWI	1.127	1.546	1.099	1.167	1.520	1.461	1.522	1.038	1.003	0.854	1.687	1.199
ALAM	1.282	1.672	1.423	1.431	1.627	1.564	1.481	1.258	1.040	1.144	1.678	1.349

Table 11 continued (10)

	SILV	MUDL	HIKO	PANA	KAWI	ALAM
SILV	-----					
MUDL	0.710	-----				
HIKO	0.903	1.025	-----			
PANA	1.119	1.223	0.551	-----		
KAWI	0.896	0.895	0.629	0.859	-----	
ALAM	1.185	1.177	0.905	1.078	0.787	-----

Figure 16.--Distance phenogram illustrating the environmental relationships of the 42 kangaroo mouse localities (cophenetic correlation coefficient is 0.722). [a]HIKO = locality of sympatry for HIKM and HIKP samples; [b]KAWI = locality of sympatry for KAWM and KAWP samples.


NARR
ALKA
PAIN
ALVO
DENI
RIDD
CONT
IZEN
northern
QUIN
JUNG
WINN
SULP
VERN
LOVE
MTWL
NIXO
WADS
SMOK
YERI
SPAR
CHIL
FLET
BENT
COAL
western
STEW
MINA
TONO
SILV
MUDL
STON
HIKO[a]
PANA
KAWI[b]
ALAM
south-central
EURE
GRAN
CALL
SHOS
MILF
MONI
HOTC
LOCK
east-central
1.59
1.29
.99
.69
.39
.09

The western Great Basin environmental unit (the second major unit on Fig. 16) includes the following 16 localities: QUIN, JUNG, WINN, SULP, VERN, LOVE, MTWL, NIXO, WADS, SMOK, YERI, SPAR, CHIL, FLET, BENT, and COAL. These localities are distributed in western Nevada, in the immediate rain shadow of the Sierra Nevada and include both M. megacephalus and M. pallidus localities. The area stretches from northern Pyramid Lake (Lahonton region) to Fish Lake Valley and is a region of rather complex physiography.

The third environmental region, the south-central Great Basin unit, includes the 10 localities: STEW, MINA, TONO, SILV, MUDL, STON, HIKO, PANA, KAWI, and ALAM. This unit includes only M. pallidus localities, save the possible exceptions of the HIKO and KAWI localities which are localities of sympatry. This area is the lowest in elevation, the hottest, and the driest of the four regions. Additionally, this area has the least physiographic relief of the environmental regions.

The last environmental region, that of the east-central Great Basin, consists of eight localities (the last cluster of Fig. 16): EURE, GRAN, CALL, SHOS, MILF, MONI, HOTC, and LOCK (the sole M. pallidus locality in this group). Several of these localities are distributed in central Nevada (EURE, MONI, HOTC, and LOCK) and are positioned between the different subparallel mountain ranges which characterize central Nevada. The remaining localities (GRAN, CALL, SHOS, AND MILF) from a subcluster (Fig. 16)

and lie on the fringes of the Bonneville Basin in the extremely arid lowland habitats.

DISCUSSION AND CONCLUSIONS

A Molecular Approach to Systematics.--The patterns of molecular variation presented in the foregoing section are based upon polyacrylamide gel electrophoresis of a class of rapidly evolving proteins (plasma proteins and nonspecific esterases) known to accumulate electrophoretically detectable substitutions about 10 times more rapidly than those proteins examined routinely with the starch gel approach (Sarich and Cronin, 1976; Wilson et al., 1977). The relevance of the polyacrylamide technique to the study of rapidly evolving proteins has been recognized only recently by systematic zoologists (e.g., Cronin and Sarich, 1976; Sarich, 1977; Csuti, 1979; Cronin et al., 1980), although the technique was developed over two decades ago (Raymond and Weintraub, 1959). Sarich (1977) and Cronin et al., (1980) have presented detailed discussions of the particular advantages that may be realized when the acrylamide methodology is employed in preference to the now standard, starch gel approach. The technique was used in this study to assay patterns of biochemical variation within Microdipodops for the principal reason that acrylamide electrophoresis of plasma proteins and nonspecific esterases allows for high resolving power in evaluating molecular divergence at low taxonomic levels (temporally close relationships with divergence times of less than three to four million years). The methodology focuses entirely on proteins of the rapidly evolving mode and, as such,

the acrylamide methodology was the appropriate means for examining molecular divergence in Microdipodops.

In an earlier study (Hafner et al., 1979; and unpublished data), we found that although the species M. pallidus and M. megacephalus were distinguishable using standard starch gel allozymic analyses (Nei's D = .23 from that study), this technique was judged not sufficiently sensative to detail biochemical patterns within M. pallidus and M. megacephalus without resorting to the use of prohibitively large sample sizes. Clearly, it would have been "stretching" the range of utility of the starch gel approach to continue in this vein (see discussion by Sarich, 1977; Hafner, 1979) and, moreover, the acquisition of such large samples (N > 20) of kangaroo mice was not feasible (see section on Study Area and Field Work). The acrylamide approach, though provided a means by which to ascertain interpopulational genetic divergence in kangaroo mice by using as few as one individual per sample, while at the same time providing maximal resolution over the time range in question (last 3 million years).

The present study represents the largest protein data set yet examined with the acrylamide method and used for a systematic objective. This study, then seems to confirm the aspirations set forth in Sarich (1977) and Cronin et al. (1980) concerning the potential use and effectiveness of analyses of rapidly evolving proteins in systematic studies. I have described the acrylamide

technique in considerable detail (see Materials and Methods; Appendix A) in hopes of encouraging more widespread acceptance and use of this important methodology for systematic studies treating lower (specific and infraspecific) taxonomic levels.

Evolutionary Concordance.--In the past, systematists relied largely on a single data set (e.g. morphology) to provide for an appraisal of the evolutionary history of a group under study. Quite recently, however, systematists are tending to utilize more than one data set for a concurrent examination of evolutionary relationships. The recent advent of this multimethodological approach in systematic studies stems from several factors, including: 1) the poliferation of new systematic techniques; 2) the use of computers in reducing and summarizing the large data sets; and 3) the realization by systematists that different data sets appraise different levels of biological organization. Once systematists recognized that the different data sets under study could produce unique evolutionary inferences, the subject of evolutionary concordance suddenly came into focus.

Evolutionary concordance is a measure (qualitatively or quantitatively applied) of the degree to which relationships (between populations or taxa) expressed in one data set correspond or are in agreement with the patterns depicted in another data set. Concordance measures may be most useful to systematists in analyzing determinants of

geographic variation. Systematists are, in essence, assessors of the phenotypic variation and any data set under examination (be it biochemical or morphological in nature) manifests to varying degrees both genetically-based and environmentally-produced information. Evolutionary concordance measures, then, may be quite useful to the systematist in understanding which characters are primarily "faithful" genetic indicators and, conversely, which characters are heavily affected by environmental selective pressures. In the present study, for example, proteins are regarded as fairly reliable phylogenetic appraisers (Wilson et al., 1977) of kangaroo mouse evolution and other data sets that might be highly concordant with the protein data would similarly be considered to be expressing mainly phylogenetic information. On the other hand, it would not be surprising if the colorimetric data set was concordant with the environmental data set; pelage color in rodents is doubtlessly responding to environmental selective pressures for crypticity (Benson, 1933; Ingles, 1950; Sands and Findley, 1959; Mayr, 1963; Patton, 1973; Harrison, 1975; Patton et al., 1979). Unfortunately, in most earlier studies of determinants of geographic variation, (for review see Gould and Johnston, 1972) independent phylogenetic data was conspicuously absent from the analysis. With phylogenetic data available in combination with morphological and environmental data, the systematist is afforded the opportunity to judge the

relative weighting of phylogenetic and environmental components inherent in every data set (see Straney and Patton, 1980, for review).

In most previous systematic studies, the concept of evolutionary concordance (or degree of association) among data sets, if mentioned at all, was usually dealt with in a rather casual manner, and often with ill-defined verbal descriptions. In recent years, however, several important attempts have been made to quantify the levels of correspondance among data sets (Crovello, 1969; Adams, 1972; Sneath and Sokal, 1973; Schnell et al., 1978; Mickevich, 1978). Most of the procedures, though, attempt to detail taxonomic congruence among the data sets by comparing either the coefficients of correlation of cophenetic values from phenetic clustering methods (Crovello, 1969; Sneath and Sokal, 1973; Schnell et al., 1978) or the examination of "tree shape" by detailing distortion coefficients and concensus from phylogenetic procedures (Adams, 1972; Mickevich, 1978).

The five data sets (proteins, chromosomes, morphometrics, colorimetrics, and environment) discussed earlier were available for examination of patterns of evolutionary concordance at different levels of Microdipodops evolution. In my study of evolutionary concordance, I did not measure taxonomic congruence among the five data sets because I am principally interested in the degree to which the relationships enumerated within one data matrix correspond

with the others, and less interested in comparing the different tree topologies per se. An alternative means for ascertaining the relationships among the data sets was used in this study. Here I compared the five original distance matrices themselves (not phenograms or trees) by the use of nonparametric measures of association. This procedure utilizes the Spearman correlation coefficient, r_s, in determining concordance among the data sets. The use of phenograms of phylogenetic trees in making comparisons among data sets (taxonomic congruence) was deemed unsatisfactory for two reasons: both phenograms and phylogenetic trees are only general graphic expressions of a data matrix and frequently cannot explain a significant portion of the information contained in a matrix; and quite disparate tree topologies can be produced from a data matrix depending upon the methodology for tree construction. I have avoided these problems by comparing the distance matrices directly.

The analysis of concordance among the five levels of evolution in kangaroo mice are presented in Table 12. For purposes of determining values of evolutionary concordance among the five data sets, each of the data sets (distance matrices) was reduced to include a total of 27 populations (listed in Table 1) for which all data were available. The magnitudes of the concordance coefficients, r_s, then are directly comparable, inasmuch as the sample sizes (N = 351) and degrees of freedom are equal. The five final distance

Table 12. Pair-wise concordance estimates (Spearman correlation coefficient, r_s, given below the diagonal) and proportion of variance explained (coefficient of determination, r^2, above the diagonal) among the five data sets. Coefficients are directly comparable inasmuch as associated degrees of freedom are equal.

	Proteins	Chromosomes	Morphometrics	Colorimetrics	Environment
Proteins	------	.4328	.2454	.0273	.0557
Chromosomes	.6714**	------	.1394	.0000	.0000
Morphometrics	.5094**	.3929**	------	.0331	.0000
Colorimetrics	.1150*	$.0053^{ns}$	.1942**	------	.2246
Environment	.2264**	$.0614^{ns}$	$.0600^{ns}$	.4561**	------

ns = nonsignificant, $p >> .05$; * = $p = .016$; ** = $p < .001$

matrices used in this study of evolutionary concordance are not presented here and are available on request from the author. Examination of Table 12 reveals that seven of the 10 possible pair-wise concordance values were found to be significant ($p < .05$).

Of the seven significant associations (Table 12) the highest concordance level ($r_s = 0.6714$) was found to occur between patterns of protein variation and chromosomal variation. The relationships among the populations of kangaroo mice determined by karyotypic data doubtlessly portray a significant amount of phylogenetic information, but the concordance value is not, perhaps, as high as *a priori* expectations might have been. An estimate of the proportion of the variance in the genetic data explained by the chromosomal data (coefficient of determination, r^2) indicates that the karyotype information is effective in accounting for less than one-half of the total protein variation. This result indicates that while the chromosomal data clearly monitor the phylogenetic distinctiveness of the kangaroo mouse species and the major units in *M. pallidus*, such data do not "recognize" the genetic separation between the eastern and western units of *M. megacephalus*. The obvious conclusion to be drawn is that one karyotypic form within *M. megacephalus* (most probably the 40-β form; see Evolutionary Biogeography) was not derived monophyletically, but there have been one or more independent derivations of this karyotype in each of

the genetic units. The karyotypic forms within M. megacephalus, though, do conform with smaller genetically-defined subunits.

The second highest concordance value occurred between the protein level of evolution and morphometrics (r_s = 0.5094). The patterns expressed by the morphometric data agree in most general respects with the protein data including the separation of the species, the recognition of the eastern and western units within each species, and the distinctiveness of the Idaho (RIDD) sample. It is most interesting to note that the patterns of morphometric variation in kangaroo mice apparently have an appreciably large phylogenetic determinant (assessed by correspondence with protein information). The morphometric patterns were also moderately concordant with the chromosomal patterns (r_s = 0.3929). Hence, the significant component to geographical variation in morphology is a phylogenetic one, and environmental constraints are greatly secondary in importance. This conclusion is in agreement with that from a recent study of pocket mouse (Perognathus goldmani) geographic variation (Straney and Patton, 1980).

The patterns of colorimetric variability in kangaroo mice were found to be moderately concordant (r_s = 0.4561) with the environmental regimens. Colorimetry in kangaroo mice seems to be responding principally to an environmental determinant. This is not unexpected, as the pelage in kangaroo mice, like other terrestrial rodents, is probably

cryptically colored to match the background substrate. Colorimetric variability showed only extremely low levels of correlation with the patterns of protein and morphometric variability (r_s = 0.1150 and 0.1942 respectively), and explained only small portions (less than four per cent) of the variance in either of these two data sets. Interestinly, although pelage colorimetry could not differentiate M. megacephalus from M. pallidus completely, colorimetric analysis could identify certain genetic units within the species (see Fig. 14 and Fig. 15). The general patterns of Figures 14 and 15, though, do indeed seem to reflect predominantly environmental selective pressures. Kangaroo mice from northern (humid) Great Basin localities are extremely dark and, thus, seem to follow Gloger's Rule. Further, several populations of M. megacephalus (HIKM, MILF, SULP, WINN, JUNG, PANA, CALL, and GRAN) seem to occupy particularly arid habitats that are in general aspects similar to M. pallidus habitats and those populations seem to be convergent on M. pallidus pellage characteristics.

Lastly, it can be seen (Table 12) that the pattern expressed in the environmental data set is concordant (r_s = 0.2264) with the pattern of protein variability in kangaroo mice, but the proportion of the variation in the other is minute (about five per cent). The association here is most probably a spurious one in that each data set is concordant with a third independent factor (colorimetrics).

The Kendall coefficient of concordance, W, was utilized

in an effort to determine the overall agreement among the five data sets considered together (Siegal, 1956; Kendall, 1970). The Kendall coefficient of concordance is a nonparametric means of measuring the extent of association among three or more data sets and may be conveniently used in conjunction with the Spearman coefficient (W bears a linear relation to r_s). The null hypothesis that the five data sets used in this study are unrelated was rejected ($W = 0.4154$, $p << .001$).

The patterns of kangaroo mouse variation in three of the five data sets under study here, proteins, chromosomes, and morphometrics, are judged to be driven by phylogenetic determinants of strong to moderate force. Colorimetrics and environment show only extremely low or nonsignificant measures of concordance with the other three sets (Table 12) and are thus considered to be evolutionarily discordant in comparison. When only the protein, chromosomal, and morphometric data sets are examined by use of the Kendall coefficient of concordance, the Kendall W is observed to increase in magnitude ($W = 0.6831$, $p << .001$). The elevated W value reflects the rather good overall congruence among the patterns of variation depicted by the protein, chromosomal, and morphometric data sets.

Both the Spearman coefficient of association (r_s) and the Kendall coefficient of concordance (W) employed here serve as convenient and practical means of evaluating levels of concordance (or discordance) among data sets. Hopefully,

both measures may gain more widespread acceptance in systematic treatments for they seem to provide effective methods of appraising, quantitatively, the degree of association among data sets.

The patterns and levels of concordance presented here, provide an important perspective, a necessary framework, within which I will draw evolutionary conclusions and formulate the taxonomic decisions pertaining to Microdipodops. An analysis of the patterns of evolutionary concordance among the data sets is necessary if one hopes to decipher phylogenetic trends from environmental responses and to be able to recognize parallel evolutionary changes. Moreover, the concordance values provide an unambiguous guide for the selection of taxonomic characters which express primarily phylogenetic information. To summarize, Microdipodops lineage information is best expressed in the protein, chromosome, and morphometric data, whereas the colorimetric data seems to reflect a significant environmental component.

Evolutionary Biogeography.--Throughout the Tertiary there existed a global trend towards a cooler and drier climate (Flint, 1971), which in western North America was marked by the diversification and migration of geofloras (Axelrod, 1950, 1958) and allowed the radiation of desert-adapted lineages in the Heteromyidae (Wood, 1935). Studies of fossil floras indicate that during the Miocene, coniferous forests grew over the Great Basin and that the Sierra Nevada, which stood only 1000 meters above sea level

(the Great Basin being only 300 meters lower), was ineffective in causing a rain shadow and effecting drier climates to its lee (King, 1959; Tidwell et al., 1972; Axelrod, 1976). By the middle Pliocene, precipitation had decreased sufficiently over the Great Basin such that coniferous forests were restricted to the mountains, live oak woodland and oak-juniper woodland characterized the lowlands, and grassland dominated the drier interfluves (Axelrod, 1976). The northern Great Basin region (eastern Oregon and northwestern Nevada) was characterized by a relatively xeric flora by this time as a result of the initial rising of the Cascade Mountains and the northern Sierra Nevada (Chaney, 1944; Wolfe, 1964). The Sierra Nevada diastrophism, which occurred in the Late Pliocene-Pleistocene time (Blackwelder, 1948; Hill, 1975; Axelrod, 1976) created an effective rain shadow over the entire Great Basin region and initiated the present desert conditions (Morrison, 1965). Further, the large sand accumulations, so characteristic of the Great Basin in general and of Microdipodops in particular, were formed during the interpluvial periods of the Pleistocene. Based, in part, on these geological and paleobotanical observations, I postulated that the extremely arid-adapted genus Microdipodops evolved largely in situ in late Pliocene-early Pleistocene time, subsequent to the main Sierra Nevada uplift (see Hafner, 1978, for discussion).

Accepting then a figure of early Pleistocene time

(Blancan age) as a starting point, all infrageneric evolutionary diversification observed today in kangaroo mice must have taken place within this time span (the last three million years). This time framework, hypothesized from information extrinsic to this study, therefore is available for the temporal placement of the M. megacephalus-M. pallidus speciation event, and subsequent infraspecific differentiation over geography.

The Pleistocene Epoch in the Great Basin was dominated by pluvial climatic periods (Morrison, 1965) which were largely synchronous with the appearance of continental glaciers in other regions of North America. These pluvial times were characterized by the occurrence of pluvial lakes which developed in many topographically closed basins in response to paleoclimatic conditions when moisture input exceeded moisture output. Such lakes seem to have been more common in the northern portion of the Great Basin than in the southern region (see Mifflin and Wheat, 1979, for review). Inasmuch as kangaroo mice are basically basin-dwelling rodents, these pluvial lakes, and associated environmental changes, must have exerted a profound effect on Microdipodops evolution. But, precisely what sort of effect the pluvial periods might have had on evolutionary divergence in kangaroo mice is problematic.

Inferences concerning pluvial environmental conditions in the Great Basin have been based on analyses of a broad spectrum of data, including most notably studies of fossil

pollen spectra (e.g. Martin and Mehringer, 1965; Bright, 1966; Mehringer, 1967; Batchelder, 1970; Tidwell et al., 1972), plant macrofossils from the dung of ground sloths (Nothrotherium) and from fossil woodrat (Neotoma) middens (e.g. Harrington, 1933; Laudermilk and Munz, 1934; Wells and Jorgensen, 1964; Wells and Berger, 1967; Mehringer and Ferguson, 1969; Madsen, 1976), lacustral intervals and paleohydrologic analyses (e.g. Morrison, 1965; Mifflin and Wheat, 1979), and fossil animals (e.g. Miller, 1939; Durrant, 1970; Mehringer and Ferguson, 1969). Estimates of pluvial climatic conditions derived from these studies have been both variable, and at times conflicting (see discussion by Axelrod, 1976; Mifflin and Wheat, 1979). For example, estimates of lowering of Life-Zones in the Great Basin range from about 300 meters to 1000 meters depending upon locality. Further, Mehringer and Ferguson (1969) observe the pluvial occurrence of certain rodents and lagomorphs hundreds of kilometers south of their present distributional limits, whereas Durrant (1970) notes the northward range extension of a bat at a different pluvial site. These estimates of simple vertical and latitudinal displacements, though are difficult to interpret and unrealistic as species often responded, not as community units, but independently to climatic changes (see Van Devender and Spaulding, 1979 for discussion).

Notwithstanding the variety of opinion concerning the

exact ecological impact of pluvial climate, there is concensus among regional phytogeographers that the flora of the Great Basin has remained relatively unchanged throughout the Pleistocene (Tidwell et al., 1972; Butler, 1976). With particular regard to the plants that are characteristic of Microdipodops habitats today, it is interesting to observe that pollen from these plant taxa (e.g. Artemisia of the Compositae and memebers of families Chenopodiaceae and Amaranthaceae) were found to be fairly stable components in pollen spectra even during pluvial times (Martin and Mehringer, 1965; Bright, 1966; Batchelder, 1970; Tidwell et al., 1972). According to Tidwell et al. (1972), Pleistocene floras were essentially the same as the floras that occur in the Great Basin today.

The recent quantitative study of pluvial climates by Mifflin and Wheat (1979), using physiographic evidence of paleohydrologic conditions, further supports a conclusion that environmental changes during the Pleistocene were not great. Mifflin and Wheat (1979) determined that only a 5° F mean annual temperature decrease and a corresponding increase in precipitation (average only 68 per cent) relative to modern climates, would be sufficient to account for the pluvial conditions of the Pleistocene. Hence, many basinward environs during pluvial periods would still have existed in arid and semi-arid conditions. That full pluvial climates were not greatly different than modern climates is supported also by early workers

(e.g. Russel, 1896; Jones, 1925; Meinzer, 1922), and it appears that modern climatic conditions of northern Nevada are similar to the pluvial paleoclimate that existed in the southern Great Basin.

Accordingly, the picture that emerges is one describing a moderate, southerly compression of Microdipodops distribution during pluvial times. Fragmentation of kangaroo mouse distributions and geographic isolation of populations probably resulted from these Pleistocene pluvial perturbations. M. megacephalus, which shows a present distribution over that portion of the Great Basin which held the majority of pluvial lakes, most likely sustained great population dissection and isolation. At such times, populations of kangaroo mice may have been restricted to sandy hillsides and strandlines surrounding basins, lakes, and river courses. Conversely, M. pallidus now distributed largely south of that region, may have been disrupted to a lesser degree. Summarizing, it seems that the pluvial sequences probably resulted in a good deal of geographic isolation of populations, allowing for evolutionary divergence.

It seems possible to explain the evolutionary history within Microdipodops with plausible zoogeographic interpretations. Moreover, biogeographical inferences may help in the elucidation of several important evolutionary problems including: 1) the determination of which species of Microdipodops, if either, is primitive

and which is derived; 2) the relationships (cladistic polarity) between the M. megacephalus and among the M. pallidus karyotypes; and 3) the convergent derivation of the karyotypes in M. megacephalus. For example, in respect to the first point, M. pallidus seems to show a variety of derived attributes including: 1) a rather small geographic distribution; 2) extreme ecological specialization (a stenotopic form entirely restricted to sparsely vegetated sand dune habitats; 3) several morphologically derived characters (large overall body size, large auditory bullae, long hind feet for locomotion on a sandy substrate, bifurcation of the angular process of the dentary, broad tip of pterygoid, pale pelage color); and 4) a karyotype, 2n = 42, derived via a fissioning event from a 2n = 40 karyotype (recent evidence indicates that the fission hypothesis is the predominant mammalian chromosomal rearrangement compared to fusion, see Imai and Crozier, 1980). I thus view M. pallidus as being derived in general biology relative to M. megacephalus, but I doubt Hall's (1941b:239) interpretation that M. pallidus is an offspring of M. megacephalus. As the degree of evolutionary diversification in M. pallidus is commensurate to that within M. megacephalus, it appears they represent daughter taxa from an unknown Microdipodops species.

Also, in respect to the primitive or derived states of the karyotypes, it appears that both 40-α and 42-α

karyotypes are the primitive chromosomal types within the species. Within M. megacephalus the 40-α karyotype shows a wider distribution, and therefore, simple commonness would support its primitive status. Further, nearly all populations of M. megacephalus having the 40-β karyotype are distributed in the low basin regions, particularly around dry lakes. During the pluvial periods of the Pleistocene, these areas were under water. Kangaroo mice inhabiting these low basin and drainage regions then, exist in ephemeral environments: these are areas that were first to be covered by the rise of pluvial lakes, and the last to be uncovered during times of recession and desication. This evidence, which includes habitat disruption and the availability of new habitats upon recession of pluvial lakes, supports the hypothesis that the 40-β karyotype is the derived form (through the addition of heterochromatic arms). In M. pallidus, the 42-α karyotype is probably the ancestral for two reasons: 1) the Robertsonian interconversion between the karyotypes of the species requires the addition of heterochromatic arms (in M. pallidus) subsequent to the fission event (see chromosome section); and 2) the 42-α karyotype occurs in two of the three main units in M. pallidus (the commonality argument).

Plausible zoogeographic interpretations, though, must be couched in a temporal framework. As mentioned previously, all diversification within Microdipodops

may have occurred within the last few million years. Importantly, biochemical analyses provide an objective means of testing this geologically-defined time framework. As protein eveolution seems to be proceeding in a primarily divergent and time-dependent manner (Wilson et al., 1977) electrophoretic analyses are useful not only in detailing phylogenetic relationships, but also in approximating the timing of such events.

The formula of Sarich (1977), which is adjusted particularly for rapidly evolving loci ($t = 2.4 \times 10^6 D$) may be used in the present context to detail temporal placements of evolutionary events. Average distance values (D) between phylogenetic units were calculated by the formula $D = -\ln S$ (Sarich, 1977; Cronin et al., 1980). Application of Sarich's (1977) formula yields an average time of divergence estimate between M. megacephalus and M. pallidus of t = 2.00 million years. This estimate fits nicely within the geologically-defined temporal framework. Further, inasmuch as this measure is based upon rapidly evolving proteins, this time estimate is a more accurate resolution of the speciation event than previously published estimates (t = 1.24 to approximately 6 million years) based on starch gel allozymic analyses (Hafner et al., 1979).

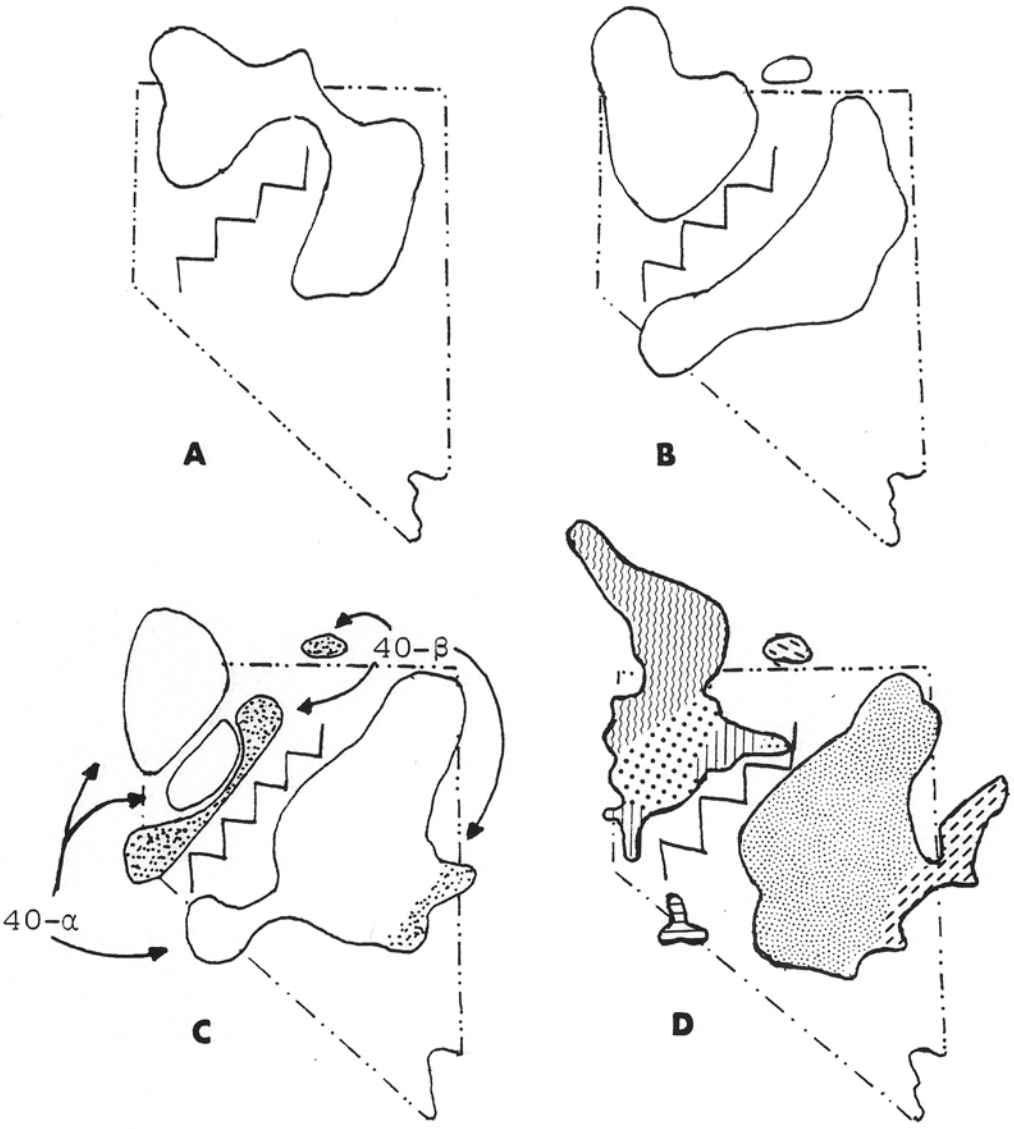
Estimates for divergence times among main infraspecific units within kangaroo mice were also calculated. Infraspecific divergence among the three M. megacephalus units (east, west and the Idaho population) and among the

three M. pallidus units (east, west, and the MINA sample) were found to occur about one million years ago. For example, the average time since divergence between the eastern M. megacephalus phylad and the western unit was found to be about one million years ago (t = 1.05). Similarly, a time since divergence of t = 1.07 was calculated for the western M. pallidus unit and the eastern unit.

With the important evolutionary events in Microdipodops now placed in a temporal context, I will present below a brief summary of the evolutionary biogeography of kangaroo mice. The biogeographical models which follow are inductive; I simply want to portray my knowledge of Microdipodops evolution in a geographical context by the use of chronological sequences. The biogeographical schemes below are based primarily on an allopatric model of evolutionary differentiation.

With respect to the evolution within M. megacephalus the weight of the evidence indicates that there were probably two main groups (an eastern and western unit) that became separated early in the history of the species (Fig. 17A). These units were probably of the 40-α form. Perhaps the Humboldt River and drainage system was influencial in this divergence which quickly resulted in the three principal genetic units of M. megacephalus (Fig. 17B). Based upon time estimates presented above, this fragmentation occurred about one million years ago.

Figure 17.--Zoogeographic scenario for M. megacephalus. Chromosomal forms are indicated in Figure 17C. The angled line in Figure 17B-D represents a potential barrier (Humboldt River and drainage system, see text). See text for description of the sequences A-D. (The outline of the state of Nevada is presented for proper orientation).


A
B
40-β
40-α
C
D

Because of environmental changes during the pluvial history of the area, populations of kangaroo mice became dissected and isolated particularly in several areas including the Humboldt River area (in the west), the Owyhee region of Idaho (in the north), and the Bonneville region (in the east). It may have been in these lowland drainage areas that the 40-β chromosomal forms were independently derived (Fig. 17C). It was also at this stage (Fig. 17C) that kangaroo mice north of Pyramid Lake became isolated from populations to the northwest (Oregon). One obvious factor which could have influenced such isolation (and divergence) was that during the Pleistocene, a large island was created in this area by the pluvial Lake Lahonton (Fig. 18). The geographic placement of this island depicted coincides surprisingly well with the present day range of the distinctive populations about the Smoke Creek and Black Rock Deserts. The close relationship between the kangaroo mice from the Mono region and those animals from central Nevada is also represented in Figure 17C. It is noteworthy to mention that the Mono kangaroo mice are now separated from central Nevadan populations by the low basin-dwelling form, M. pallidus. Figure 17D simply represents, for comparison, the present distribution of M. megacephalus subspecies.

The zoogeographic scenario sufficient to explain the evolution within M. pallidus is presented in Figure 19. The pallidus form probably arose soon after the derivation of

Figure 18.--The Great Basin region showing the pluvial lakes at their maximum height during the Wisconsin period (after Morrison, 1965). The outline of the state of Nevada is used for proper orientation and the scale at lower right equals 100 kilometers.

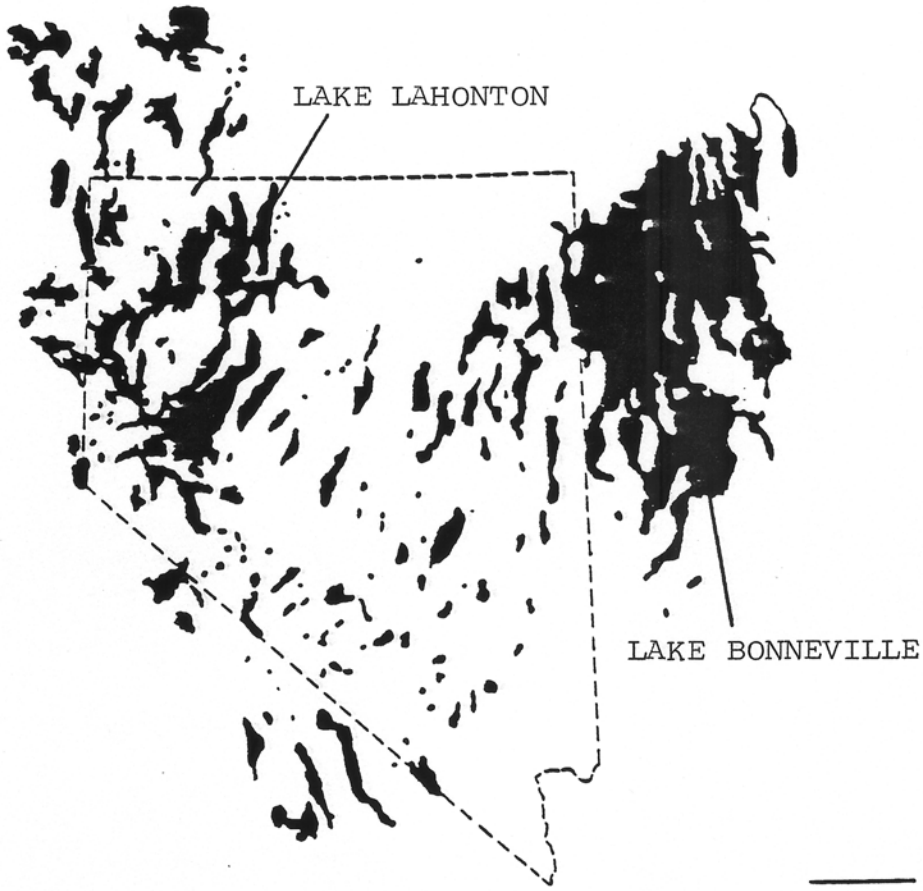
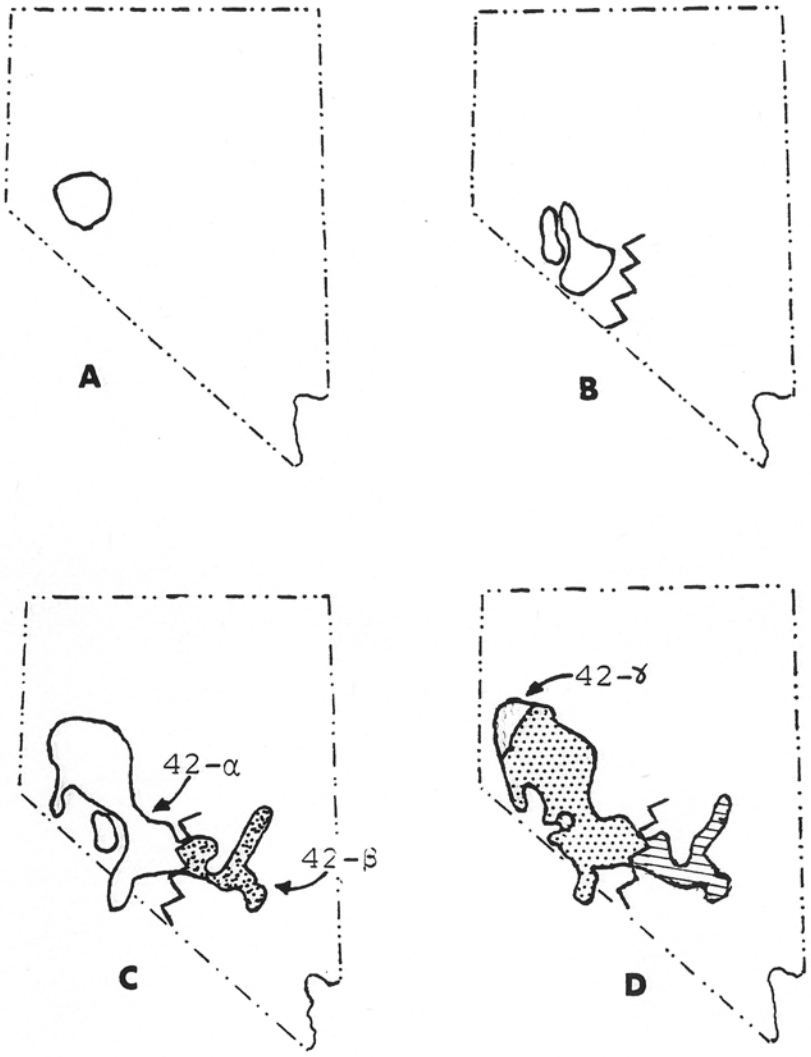

LAKE LAHONTON
LAKE BONNEVILLE

Figure 19.--Zoogeographic sequence for M. pallidus. Chromosomal forms are indicated in Figure 19C and 19D. The angled line in Figure 19B-19D represents a potential barrier (see text). Description of the zoogeographic sequence is presented in the text. (the outline of the state of Nevada is presented for proper orientation).


A
B
42-α
42-β
C
42-δ
D

the genus, and not long after the Sierra Nevada uplift; a likely site for the center of origin of M. pallidus is west-central Nevada where the greatest sand accumulations occur today (Fig. 19A). This early M. pallidus, most likely the 42-α chromosomal form, spread southward in the low basin region of southwestern Nevada and became differentiated into two units: the western unit and the restricted MINA population (Fig. 19B). Further spread of M. pallidus was momentarily prevented due to barriers to dispersal. Four main factors seem to have caused a zoogeographic barrier to south-central Nevada: 1) this region is a transition zone (Dice, 1943; Beatley, 1976) between the Upper Sonoran Life-Zone (characteristic Great Basin environment of Microdipodops) and the Lower Sonoran Life-Zone (Mojave Desert environment); 2) there are a series of mountain ranges in this area, including the low range about Tonopah, Nevada, and the Kawich Mountain range that may have prevented free east-west dispersal and gene flow; 3) this region may have been the north-south corridor by which M. megacephalus was able to disperse westward for the eventual colonization of the Mono region (hence there may have been intense competition between the species here); and 4) one of the few pluvial lakes to exist in this southern region (Mud Lake) occurred at this point (Mifflin and Wheat, 1979). In any event, according to this zoogeographic sequence, a small founder population of M. pallidus (Fig. 19C) eventually skirted around or over

this barrier, and with subsequent isolation, the eastern genetic unit of M. pallidus and the 42-β chromosomal type was formed. I view the sequence depicted in Figure 19B-C to have occurred nearly simultaneously with the three forms diverging about one million years ago. The final scene in M. pallidus evolution, (Fig. 19D) represents the present distribution of M. pallidus subspecies, and includes the rather recent formation (supported by biochemical data) of the 42-γ karyotype in the drainage region south of Pyramid Lake.

These inductive biogeographical scenarios and interpretations presented here may be used as general models for animal evolution in the Great Basin. Future zoogeographic studies of basin-dwelling vertebrates in the Great Basin, moreover, will constitute tests of these hypotheses. Until quite recently, I considered these patterns to be entirely novel. However, a recent study (Loudenslager and Gall, 1980) detailed remarkably similar patterns to the ones outlined here. Loudenslager and Gall (1980), in studying geographic patterns of protein variation in cutthroat trout, Salmo clarki, observed an east-west genetic separation among populations of the subspecies henshawi which is identical to that which I have described for M. megacephalus. Let me point out that the study of Loudenslager and Gall (1980), although detailing patterns of variation for organisms of a different vertebrate class and utilizing a completely different electrophoretic

technique (they used starch gel techniques and large sample sizes in assaying variation in a set of generally slowly evolving proteins), their data yield very similar estimates of time since divergence between these east-west groups. I have calculated time estimates using their data (Loudenslager and Gall, 1980:36-37) and the formula corrected for slowly evolving proteins (Sarich, 1977) and obtain an average time estimate of 1.13 million years since divergence of the eastern and western units of henshawi. This figure compares very well indeed with my results of 1.05 million years obtained when examining the same biogeographical units in the rodent genus Microdipodops. Apparently both the cutthroat trout and the kangaroo mice exhibit similar patterns of evolutionary biogeography. Clearly, this corroboration lends support to the contention that the biogeographical patterns presented here for kangaroo mice may represent generalized biogeographical patterns for basin-dwelling animals in this large region.

Systematic Philosophy.--The recent demonstration that biochemical, karyological, and morphological data sets may exhibit independent rates of evolutionary change (Turner, 1974; Maxon and Wilson, 1974, 1975; Mickevich and Johnson, 1976; Schnell et al., 1978; Larson, 1980) is fundamental to our understanding of general evolutionary processes and impinges directly on modern systematic practices. It now seems that, in many situations, the evolutionary inferences drawn by a systematist will depend

not only on the data base or level of evolution being examined, but sometimes on the methods (usually phenetic or phylogenetic) used to analyze such data. Clearly, inferences of phylogenetic relationships can be formulated most readily and accurately by employing characters that evolve in a primarily divergent and time-dependent manner. Characters which exhibit moderate or even high degrees of parallelism or convergence (e.g. many morphological traits) can be just as useful in constructing phylogenies, but only if one can accurately identify the parallelisms or convergences; this is true whether a phylogenetic method or phenetic clustering is used (see discussion by Mickevich and Johnson, 1976; Schnell et al., 1978; Mickevich, 1978; Larson, 1980). Whereas previous studies indicate that protein evolution frequently progresses in a largely divergent and time-dependent fashion (see Wilson et al., 1977 for review), it follows then that workers who utilize biochemical data will reap the advantage of more precise phylogenetic inference.

Phylogenetic relationships, though, explain only part of the total evolutionary history of a taxonomic group under study. A modern systematic zoologist, striving to formulate a comprehensive determination of evolution within the taxa under study, must analyze several data sets concurrently to detail the different pieces of historical information inherent in the different levels of evolution. For example, in the present study, had one

performed just a chromosomal analysis of this group, I doubt if the parallel derivation of the M. megacephalus (40-β) karyotype would have been detected. One may have simply relied on parsimony and concluded that each chromosomal form in M. megacephalus was monophyletic. This does not mean that chromosomal data are erroneous, but means simply that the chromosomal information in this case is detailing a different piece of M. megacephalus evolutionary history (i.e. history subsequent to the east-west genetic split).

The phylosophy that I have utilized in this systematic treatment of Microdipodops maintains that for a thorough understanding of the evolutionary history of a taxonomic group under study, an eclectic or synthetic approach should be persued as a means to delineate both the phylogenetic and environmental determinants of character variation. Moreover, examination and analysis of one data set can be used to test hypotheses generated by an examination of another. Such a multimethodological avenue of investigation, coupled with quantitative analyses of concordance, allows for the recognition of evolutionary convergence and lays the necessary groundwork for taxonomic decisions.

In this systematic appraisal of kangaroo mice I rely on those character complexes that express predominantly lineage information in making taxonomic decisions. The analyses have shown that the biochemical, chromosomal, and

morphometric data sets are largely free of environmental constraints and that these sets have strong phylogenetic determination. Conversely, the patterns of colorimetric variability expressed in kangaroo mice are relegated to secondary importance inasmuch as the patterns are concordant with the environmental data and therefore likely to reflect a high degree of parallelism. Taxonomic decisions guided by this criterion will thus have a nonarbitrary element and will connote useful historical information to other systematists (see discussion by Simpson, 1961:171-176).

Within species of kangaroo mice, I have chosen to recognize patterns of geographic variation by utilizing both the megasubspecies (Amadon and Short, 1976) and subspecies framework. As a safeguard against a biased, subjective systematic treatment, I have avoided the use of an existing subspecific construct (Hall, 1941b) throughout all phases of the data set analysis. Moreover, the pattern of geographic variation described for each of the data sets was evaluated on its own merits without consideration of past described patterns.

As an evolutionary biologist, I find that megasubspecies and subspecies can be most useful when, and only when, they are used to describe major features of evolution within a species. Conversely, when infraspecific taxa are used to detail chaotic variants, as has been commonly done for a variety of mammalian species, they are

of little value to evolutionary biologists. As a case in point, literally hundreds of subspecies have been described for Thomomys pocket gophers (Hall and Kelson, 1959; and see Simpson, 1961:173) which more often than not, fail to correspond to general evolutionary patterns within the species (for example, see genetic data summarized by Patton and Yang, 1977; personal observation; and unpublished data). The practice of incorporating major features of evolution in an infraspecific taxonomy is consistent with the synthetic approach applied in this systematic study; the features of Microdipodops variability that emerge from this treatment are basically those general and unambiguous phylogenetic patterns that are rooted in several levels of biological organization. The Microdipodops subspecies recognized thusly, will hopefully be, in the words of Johnson (1980:110) "objectively demonstrable" and will connote a "potential evolutionary future".

The megasubspecific epithet, although new to systematics, is used herein to designate taxa within both M. megacephalus and M. pallidus that are approaching species level differentiation (Amadon and Short, 1976). I have adopted the use of megasubspecies in preference to the semispecies descriptor (Mayr, 1963), because of the history of confusion surrounding this latter term (see Johnson, 1980, for discussion). Following the convention outlined in Amadon and Short (1976) megasubspecies are designated by the use of parentheses in the following taxonomic treatment.

By incorporating megasubspecies into a taxonomic framework, I am able to convey a more comprehensive picture of the evolutionary history of Microdipodops than would have been possible with the use of subspecies alone.

Taxonomic Conclusions.--In my examination of the patterns of evolution within kangaroo mice, I have explored biochemical, karyological, morphological (cranial morphometrics and colorimetry), and environmental variation. No regions of hybridization were identified between the traditional species, M. megacephalus and M. pallidus, even though kangaroo mice from several sympatric localities were examined. I agree with Hafner et al. (1979) in affirming the full specific status of these two taxa. All lines of evidence utilized in this study reveal clearly the distinctness of the two species of kangaroo mice and this conclusion is in accord with Hall's (1941b) systematic appraisal of the genus.

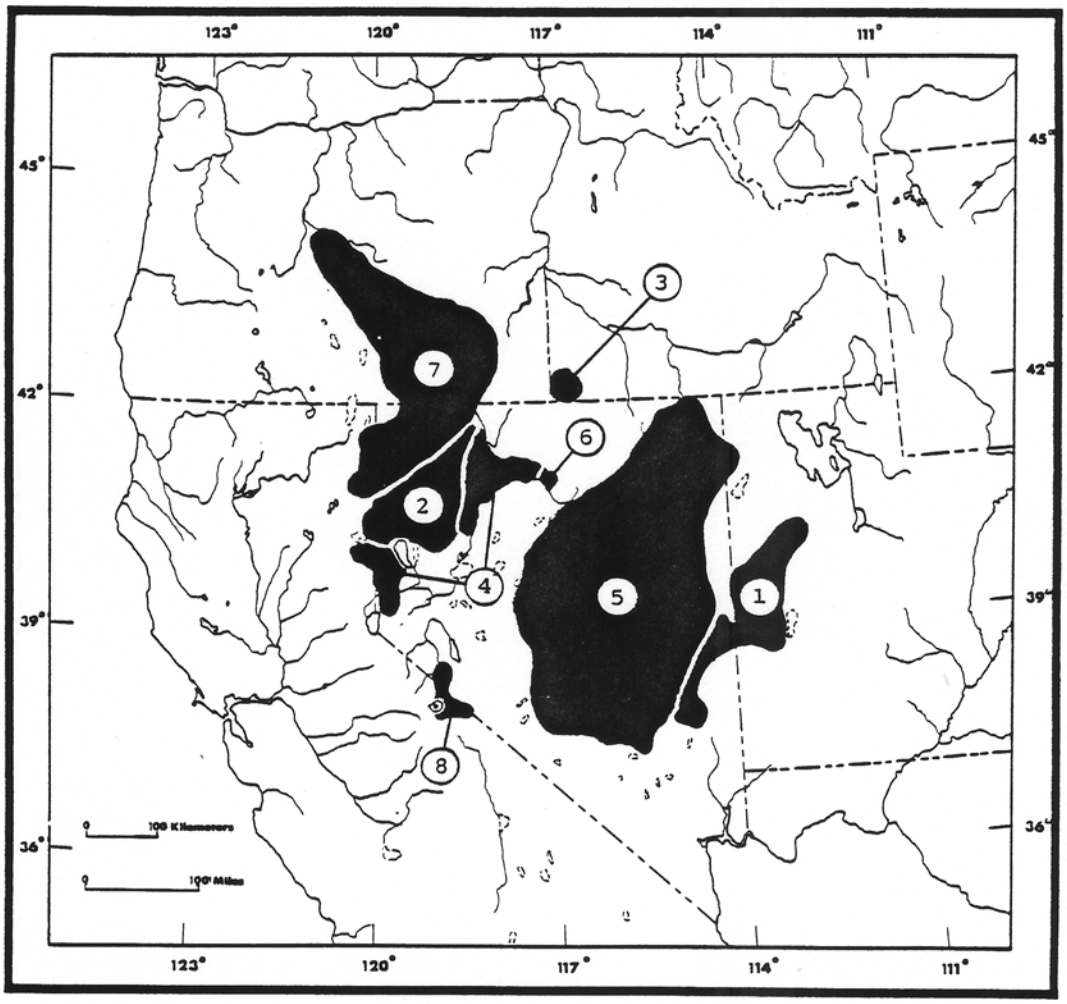
Three principal evolutionary units in M. megacephalus are revealed from this eclectic systematic treatment. These three units, namely the Idaho population (RIDD) and the eastern and western units of M. megacephalus, are biochemically distinct (Fig. 4) and morphologically separable (Fig. 13 and Fig. 15). These groups seem to manifest attributes of both speceis and subspecies, for they are highly distinctive (like species) and are entirely allopatric in distribution (like subspecies). It is for reasons that I have recognized these units at the

megasubspecific level. The Idaho form of kangaroo mouse is new to science and is formally designated M. (megacephalus) atrirelictus (Appendix H). The western megasubspecies is regarded as M. (megacephalus) californicus and the eastern megasubspecis is regarded as M. (megacephalus) megacephalus.

One may question whether or not the three megasubspecies of M. megacephalus are in reality separate biological species. Admittedly, this is a moot point and the solution to this question must ultimately lie in a test of reproductive isolation. As these forms are allopatric in distribution (each unit separated from the other by about one hundred miles of habitat inappropriate for kangaroo mice) a thorough genetic analysis of the natural interaction of the forms in contact, and hence an understanding of the degree to which they have attained reproductive isolation, is not possible. The designation of megasubspecies for these groups is a fair resolution in the present context for I have observed no evidence of any potential reproductive isolating feature in these units (for example a significant chromosomal rearrangement that might lead to meiotic breakdown, an unusual phallic structure, reproductive allochrony, etc.). Therefore, the term species or even allospecies (Amadon, 1966) is deemed less satisfactory.

The geographic distributions of intraspecific taxa recognized for M. megacephalus are indicated in Figure 20.

Figure 20.--The geographic distribution of the eight subspecies of Microdipodops megacephalus. 1, M. m. albiventer; 2. M. m. ambiguus; 3, M. m. atrirelictus; 4, M. m. californicus; 5, M. m. megacephalus; 6, M. m. nexus; 7, M. m. oregonus; 8, M. m. polionotus.


123°
120°
117°
114°
111°
45°
42°
39°
36°
1
2
3
4
5
6
7
8
0 100 Kilometers
0 100 Miles

The northern megasubspecies, M. (megacephalus) atrirelictus is monotypic and is known only from the remote Owyhee region of southwestern Idaho. M. megacephalus atrirelictus, although large in most measurements, has a relatively small maxillary breadth (see Appendix E, Table 7, Fig. 13), and has the darkest pelage (nearly black) of any kangaroo mouse (see Appendix F, Table 10, Fig. 15).

The western megasubspecies, M. (megacephalus) californicus is polytypic and contains four subspecies (Fig. 20): californicus, oregonus, ambiguus, and nexus. M. megacephalus californicus (represented in this study by CHIL, SPAR, and WINN) is distributed immediately southwest of Pyramid Lake and northeast of Pyramid Lake along the Humboldt River. The distribution of californicus then, is polytopic and I consider these units to have become isolated only recently. This subspecies is particularly distinctive in having the 40-β karyotype and having the pure white ventral pelage (a character not quantified in this study). The CHIL sample from near the type locality is quite unusual in morphometric characters (see Fig. 11 and Fig. 13), being more like eastern megacephalus in some features.

The subspecies oregonus (represented by ALKA, NARR, ALVO, and PAIN) is distributed in the northwestern section of the Great Basin (Fig. 18) and is separable from the other forms in this megasubspecies by having the 40-α karyotype and being dark in dorsal pelage color. Importantly, in oregonus the venter is distinctly plumbeous (dark grey)

in color at the base of the hair.

In the center of the western megasubspecies (Fig. 20) is the subspecies ambiguus. Hall's (1941b) choice of this epithet seems most appropriate: populations of kangaroo mice referred to this subspecies in the original description include both karyotypic forms of M. megacephalus and even populations of M. pallidus (from southern Pyramid Lake now designated M. pallidus pallidus). Presently, (in comparison with Hall, 1941b) I consider ambiguus to be distributed basically north of Pyramid Lake, about the Smoke Creek and Black Rock Deserts (including SULP, SMOK, VERN, and QUIN).

The kangaroo mice called ambiguus, though, seem to be a peculiar group even in the present analysis. The subspecies is recognized as being moderately distinctive in the biochemical analysis (Fig. 4), and as having the 40-α karyotype. Significantly, though, this subspecies is intermediate in ventral pelage color between the pure white of californicus and the plumbeous colored hair of orgeonus; the subspecies ambiguus, upon close inspection, has a very light plumbeous color at the base of the belly hair. As such, the range of ambiguus appears as an entire zone of intergradation between the dark northern (oregonus) kangaroo mice and the white-bellied forms to the east and southwest (californicus).

Two rather abrupt "contact" zones were identified: one in the region about Flanigan, Nevada (at the south

end of ambiguus range) and at Quinn River Crossing, Nevada (at the north of ambiguus distribution). At Flanigan, kangaroo mice are highly variable in pelage color: some specimens have buffy dorsal pelage and white ventral pelage like that of californicus, while others have general oregonus qualities including grayish dorsal pelage and gray bases on the hairs of the venter (see also discussion by Hall, 1941b:254-255). The situation is similar at Quinn River Crossing. Yet, more importantly, I detected one chromosomal hybrid (40-α/β) of four specimens examined at Quinn River Crossing. This, then, provides genetic documentation of hybridization between ambiguus (40-α) and californicus (40-β) to the east (unfortunately, no specimens were available for genetic analyses from Flanigan). The other three specimens from Quinn River Crossing had the 40-β karyotype, as did all specimens from the nearby Jungo, Nevada locality (to the southeast). Interestingly though, both Quinn River Crossing and the Jungo (QUIN and JUNG) were found to be most close, biochemically, to the ambiguus (40-α) unit (Fig. 4). Therefore, it seems that both localities effectively delineate a zone of contact between ambiguus and californicus. At present I have no means of distinguishing between hybrid classes on karyotypic criteria alone. But, biochemically, the one chromosomal hybrid (HYQU, Fig. 4) was not intermediate between the Winnemucca samples (WINN and WWIN) and the central ambiguus samples (SMOK and SULP) but clearly shared

greatest allelic similarity with ambiguus. This indicates that the chromosomal hybrid (40-α/β) from QUIN was not an F_1 individual. Although these results are only preliminary I have no reason to suspect that any hybrid class individual would suffer reduced viability or sustain reporductive impairment as a result of hybridization and this would seem to represent a class three (introgressive hybridization) contact zone (see Patton et al., 1979).

The last (fourth) subspecies that I will refer to the western megasubspecies of M. megacephalus is nexus (IZEN in my analyses). This subspecies is known from the vicinity of Izenhood, Nevada (Fig. 20), and seems to be separated from californicus to the west by a low mountain range positioned near Golconda, Nevada. Morphologically, nexus presents several problems. For example, results of the ordination analyses for both morphometric and colorimetrics (Fig. 13 and Fig. 15, respectively) and the colorimetric phenogram (Fig. 14) indicate that nexus is a member of the western megasubspecies, phenetically most similar to oregonus (e.g. NARR or ALKA samples). The morphometric phenograms though (Fig. 11 and Fig. 12), seem to reveal a general phenetic relationship of nexus with the populations of the eastern megasubspecies, M. (megacephalus) megacephalus. Further, unlike californicus, the bases of the hairs on the venter are distinctively plumbeous in nexus and therefore, again, would suggest a similarity to the Oregon kangaroo mice or populations

of the eastern megasubspecies. A third possibility is that nexus is related to the Idaho kangaroo mice, M. megacephalus atrirelictus, which also have the plumbeous color at the base of the belly hairs. Inasmuch as genetic material (proteins or chromosomes) is not presently available for nexus, I must rely on the information presented above, including geographic position, and retain nexus as a separate subspecies. This is conforming with the rule of consistency (see Simpson, 1961:112). Kangaroo mice from just northwest of Golconda are intermediate between californicus and nexus in ventral pelage color (very light plumbeous bases to belly hairs) and this seems to indicate intergradation between these subspecies (see also Hall, 1941b:254).

In the eastern megasubspecies, M. (megacephalus) megacephalus, I recognize three subspecies: M. megacephalus megacephalus, M. megacephalus polionotus, and M. megacephalus albiventer (Fig. 20). These three comprise a relatively "tight" phylogenetic assemblage with two main lineages being detected (Fig. 4). One genetically-defined unit contains the central Nevadan subspecies megacephalus and the subspecies polionotus which is isolated about the Mono Basin and adjoining valley regions of California and western Nevada. This unit is defined both on biochemical data (Fig. 4) and chromosome data (both subspecies megacephalus and polionotus have the 40-α karyotype). The second major genetic group

is represented by albiventer, which ranges from extreme southeastern Nevada to western Utah. Again, populations referred to the subspecies albiventer are grouped on both protein (see Fig. 4) and chromosomal data (albiventer is recognized by having the 40-β karyotype).

The central Nevada subspecies megacephalus has the largest geographic distribution of all Microdipodops subspecies (Fig. 20). It ranges from northeastern to south-central Nevada. My morphometric analyses of megacephalus (including the localities CONT, EURE, MONI, HOTC, HIKM, and KAWM) showed that this form was rather homogeneous (Fig. 11,12, and 13) The colorimetric study reveals that the northern populations (as mentioned previously) were appreciably darker than the more southern populations (see Fig. 15). A qualitative examination of the ventral pelage color, though, revealed that megacephalus is characterized by having the plumbeous color at the basal portion of the hair.

The basic genetic and morphological uniformity of megacephalus over this vast region is striking in comparison with the general trend of great regional differentation in the genus. An explanation of this broad regional similarity in megacephalus may be found in the physiography of central Nevada. Kangaroo mice of megacephalus are distributed in series of north-south aligned basins which are largely separated from other such basins by subparallel mountain ranges. These parallel basins become confluent

both at their northern and southern ends. The geography, therefore, seems to allow relatively free dispersal and gene flow (particularly in a north-south orientation) and as such, may explain the overall patterns of similarity over the range.

The subspecies polionotus, although isolated to the southwest, shows genetic similarity with megacephalus from which it was probably derived. The two subspecies are separated by about 75 miles of lowland habitat which is now occupied by M. pallidus. In contrast to megacephalus, the hair of the venter is pure white to the base in polionotus. The two populations sampled in polionotus (FLET and BENT), although exhibiting a moderate degree of morphometric and colorimetric differentiation (Fig. 13 and Fig. 15), are clustered together at a reasonably high level (see phenogram Fig. 12). The FLET sample (regarded as a separate subspecies by Hall, 1941b) is located in the northern most part of the subspecies range and is slightly larger and darker than the BENT sample to the south. I have analyzed detailed morphological data for several populations between FLET and BENT (unpublished data) and have determined that these populations grade smoothly in characters from the northern FLET population to the southern BENT population. I therefore recognize only one subspecies in this region (polionotus), as the populations are genetically quite similar and there is no abrupt shift in general morphology over the range.

The geographic distribution of the subspecies albiventer (Fig. 20) is restricted to the low-lying basin regions of southeastern Nevada and western Utah. These areas adjoin to the ancestral Bonneville Lake. Populations sampled for albiventer (including PANA, SHOS, MILF, CALL, and GRAN) form a homogeneous unit based on a variety of characters, including: 1) the populations are generally pale in dorsal pelage color (particularly GRAN and CALL, Fig. 15, Appendix F); 2) the hair of the venter is pure white to the base; 3) the skulls are generally small in size, with relatively large maxillary breadths (see Fig. 13 and Appendix E); 4) they are defined chromosomally as having the 40-β karyotype; and 5) they are grouped together in the biochemical analyses (Fig. 4). It's interesting to note that one sampled population of the subspecies megacephalus, HIKM, was found to share great allelic similarity (see Fig. 4) with the albiventer populations. I recognize HIKM, though, as belonging to megacephalus (and not to albiventer) because these mice are darker in dorsal pelage color, have plumbeous bases on venter hair, larger in size, and have the 40-α karyotype. I thus view this HIKM locality (of southeastern Nevada) as being "perched" on the interface between these two distinctive subspecies. Incidentally, it is noteworthy that several populations (not quantified for this study) in the region of White Pine County, Nevada, seem to represent intergrades between the pale albiventer kangaroo mice to the southeast

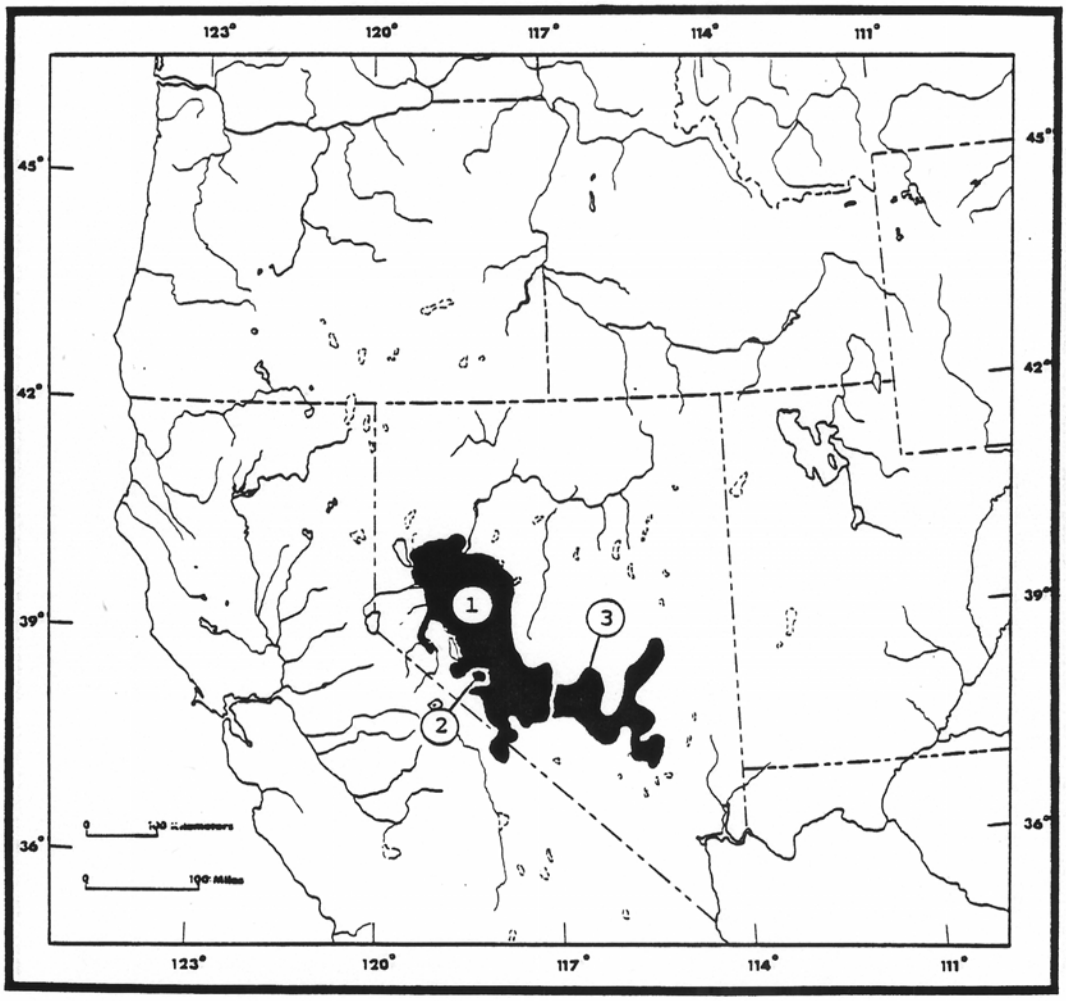
and the darker megacephalus kangaroo mice to the northwest; these kangaroo mice exhibit the light plumbeous bases on the venter hair which is intermediate between the typical megacephalus (dark plumbeous bases) and albiventer (pure white hair) condition.

Within the species M. pallidus there seem to be three main evolutionary units. These units are recognizable both genetically (see Fig. 4 and Fig. 8) and morphologically (see Fig. 13 and Fig. 15) and include: 1) a large unit distributed in the lowland regions of west-central Nevada; 2) an east-central faction; and 3) an isolated population from a single locality located in the midst of the aforementioned large western unit. These three main units of M. pallidus seem to possess traits of both species and subspecies. The forms are doubtless independent evolutionary lineages, but like typical subspecies, the units are entirely allopatric in distribution. On numerous occasions I have searched in vain for kangaroo mice in the regions of potential contact between these units (one potential contact may occur in central Mineral County and another southeast of Tonopah, Nevada). Had I been able to procure specimens from these potential contact areas I would have analyzed the genetic interaction between these forms, and therefore, would have been able to determine whether these units were reproductively isolated from one another. Kangaroo mice are known to have occurred in the vicinity of one of these potential contact areas during the 1930's

(the region southeast of Tonopah, Nevada) but are apparently locally extinct today. Inasmuch as a resolution of this problem rests on genetic documentation of the interaction of the forms in a contact zone, the degree to which these three units may have attained reproductive isolation (and hence specific status) is certainly problematic with no immediate answer. I have, though, decided to recognize these main units within M. pallidus as megasubspecies. These units reflect the similar degree of evolutionary divergence as is seen in the megasubspecies of M. megacephalus, and therefore require equivalence of ranking. The units that are formally recognized include: M. (pallidus) pallidus (the main western form of M. pallidus); M. (pallidus) restrictus (the isolated population in the western range of M. pallidus); and M. (pallidus) ruficollaris (the main eastern unit of M. pallidus.

The megasubspecies M. (pallidus) pallidus is monotypic; the subspecies M. pallidus pallidus includes LOVE, MTWL, YERI, STEW, COAL, TONO, WADS, and NIXO samples. This subspecies is distributed across the majority of the western range of the species and includes the region about the southern end of Pyramid Lake in Washoe County, Nevada (Fig. 21). The samples WADS and NIXO (from the Pyramid Lake area), have diverged slightly in karyotype (42-γ) from other populations of pallidus (42-α. Also, these samples seem to be separated from other

Figure 21.--The geographic distribution of the three subspecies of Microdipodops pallidus. 1, M. p. pallidus; 2, M. p. restrictus; 3, M. p. ruficollaris.


123°
120°
117°
114°
111°
45°
42°
39°
36°
1
2
3
0
100 Kilometers
0
100 Miles

populations of pallidus by being smaller in two characters: least expanse of lateral face of zygoma and length incisive foramina at point of greatest breadth (see Fig. 11 and Fig. 13). With due regard to equivalence of ranking and distinctness, I consider these populations as belonging to the subspecies pallidus, notwithstanding the moderate differences.

The megasubspecies M. (pallidus) restrictus is monotypic and is here regarded as a distinctive evolutionary unit. The form restrictus is isolated about the southern end of Soda Spring Valley in southeastern Mineral County, Nevada (sample MINA). The range of restrictus is surrounded by the subspecies pallidus (Fig. 21), but the forms seem to be separated from one another by alkali-caked regions judged to be uninhabitable for kangaroo mice. Colorimetrically, restrictus is quite divergent: the characters trichromatic coefficient x and purity are particularly discriminating (Fig. 15 and Table 10). Morphometrically, restrictus is clearly separable from all populations of the western subspecies (pallidus), but interestingly, restrictus seems to be convergent on the morphology of the eastern megasubspecies (see Fig. 13).

The eastern megasubspecies, M. (pallidus) ruficollaris contains one subspecies, ruficollaris, and is easily separable from pallidus (the main western megasubspecies) by both genetic and morphological characters (see Fig. 4, Fig. 8, Fig. 13, and Fig. 15). The subspecies ruficollaris

(including the samples MUDL, STON, KAWP, HIKP, LOCK, and ALAM) covers the majority of the eastern range of M. pallidus (Fig. 21).

As a means by which to summarize the taxonomic recommendations detailed in the foregoing accounts, I present below a formal taxonomic list for the genus Microdipodops. In this list the megasubspecific nomen is designated by the use of parentheses (Amadon and Short, 1976). A formal synonymy is presented in Appendix H.

Microdipodops megacephalus

Microdipodops (megacephalus) megacephalus

Microdipodops megacephalus megacephalus

Microdipodops megacephalus polionotus

Microdipodops megacephalus albiventer

Microdipodops (megacephalus) californicus

Microdipodops megacephalus californicus

Microdipodops megacephalus oregonus

Microdipodops megacephalus ambiguus

Microdipodops megacephalus nexus

Microdipodops (megacephalus) atrirelictus

Microdipodops megacephalus atrirelictus

Microdipodops pallidus

Microdipodops (pallidus) pallidus

Microdipodops pallidus pallidus

Microdipodops (pallidus) ruficollaris

Microdipodops pallidus ruficollaris

Microdipodops (pallidus) restrictus

Microdipodops pallidus restrictus

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APPENDIX A

Pertinent recipes for acrylamide gel work.

8% Tris sulfate Gel

10.00 ml Ammonium persulfate (0.2%)

4.50 ml Water

8.00 ml Acrylamide (30%) + 0.8% Bis

7.50 ml Tris sulfate (1.5 M, pH = 9.0)

Reagents are mixed together and 4 drops of Temed are added to initiate polymerization.

4% Tris sulfate Stacking Gel

5.00 ml Ammonium persulfate (0.2%)

2.50 ml Water

1.25 ml Acrylamide (30%) + 0.8% Bis

1.25 ml Tris sulfate (0.5 M, pH = 7.4)

Reagents are mixed together and 2 drops of Temed are added to initiate polymerization.

Tris Borate Electrode Buffer

63 grams Tris (Trizma base)

9 grams Boric acid

Add together and fill to one liter with water.

APPENDIX B

Nine characters used in analyses of chromosomal realtionships and methods of scoring the characters.

1 Diploid number (40 chromosomes, 1; 42 chromosomes, 2).

2 Fundamental number (70, 1; 74, 2; 76, 3; 80, 4).

3 Number of small-sized submetacentric to metacentric non-marker chromosomes (0, 1; 2, 2; 4, 3; 6, 4).

4 Number of acrocentric non-marker chromosomes (0, 1; 2, 2; 6, 3).

5 Number of small-sized subtelocentric non-marker chromosomes (0, 1; 2, 2).

6 Number of medium-sized submetacentric marker chromosomes (0, 1; 2, 2)

7 Number of small-sized submetacentric marker chromosomes (0, 1; 2, 2; 4, 3).

8 Number of small-sized subtelocentric marker chromosomes (0, 1; 4, 2).

9 Number of small-sized acrocentric marker chromosomes (0, 1; 4, 2).

APPENDIX C

Twenty-eight characters used in analyses of environmental variability and methods of scoring the characters.

1 Average number of days each year in which migrating low-pressure centers cross any given area (5 to 10 days, 1; 10 to 15 days, 2; 15 to 20 days, 3).

2 Average number of days each year in which high-pressure centers occur in any given area (5 to 10 days, 1; 10 to 20 days, 2; 20 to 30 days, 3; 30 to 40 days, 4; 40 to 50 days, 5; > 50 days, 6).

3 Average annual percentage of possible sunshine (< 70%, 1; 70 to 75%, 2; 75 to 80%, 3; 80 to 85%, 4; > 85%, 5).

4 Mean annual temperature (< 45°, 1; 45 to 48°, 2; 48 to 50°, 3; 50 to 55°, 4; 55 to 60°, 5; 60 to 65°, 6).

5 Mean January minimum temperature (< 12°, 1; 12 to 20°, 2; 20 to 28°, 3; >28°, 4).

6 Mean July maximum temperature (< 84°, 1; 84 to 92°, 2; 92 to 100°, 3; > 100°, 4).

7 Per cent of total hours in the year in which low-level inversions occur (40 to 45 hours, 1; > 45 hours, 2).

8 Mean annual number of days each year in which maximum temperatures of 90°F or higher are expected (< 20 days, 1; 20 to 30 days, 2; 30 to 60 days, 3; 60 to 90 days, 4; 90 to 120 days, 5).

APPENDIX C (CONTINUED)

9 Mean annual number of days each year in which minimum temperatures of 32°F or lower are expected (120 to 150 days, 1; 150 to 180 days, 2; 180 to 210 days, 3; 210 to 240 days, 4; > 240 days, 5).

10 Highest temperatures expected within a 50 year period (< 100°, 1; 100 to 105°, 2; 105 to 110°, 3; 110 to 115°, 4).

11 Lowest temperatures expected within a 50 year period (0 to 5°, 1; 5 to 10°, 2; 20 to 15°, 3; 15 to 20°, 4; 20 to 25°, 5; 25 to 30°, 6; 30 to 35°, 7; 35 to 40°, 8; > 40°, 9).

12 Average date of first Autumn freeze (earlier than Sept. 1, 1; Sept., 2; Oct., 3; Nov. 1 or later, 4).

13 Average date of last Spring freeze (July 1 or later, 1; June, 2; May, 3; Earlier than May 1, 4).

14 Average growing season based on number of days during which temperatures are always above 32°F (< 100 days, 1; 100 to 120 days, 2; 120 to 140 days, 3; 140 to 160 days, 4; 160 to 180 days, 5).

15 Mean annual growing degree-days with base 86° to 50° (< 1000, 1; 1000 to 2000, 2; 2000 to 3000, 3; 3000 to 4000, 4).

16 Relative heating requirements expressed as mean annual heating degree-days with base 65°F (4000 to 5000, 1; 5000 to 6000, 2; 6000 to 7000, 3; 7000 to 8000, 4; > 8000, 5).

APPENDIX C (CONTINUED)

17 Relative cooling requirements expressed as mean annual cooling degree-days with base 65°F (< 100, 1; 100 to 300, 2; 300 to 500, 3; 500 to 700, 4; 700 to 1000, 5; 1000 to 1500, 6).

18 Average annual precipitation (< 4 inches, 1; 4 to 8 inches, 2; 8 to 16 inches, 3; > 16 inches, 4).

19 Number of days per year with measurable (.01 inch or more) precipitation (30 to 40 days, 1; 40 to 50 days, 2; 50 to 60 days, 3; 60 to 80 days, 4; 80 to 100 days).

20 Percentage of rainy days per year with moderate to heavy (.25 inch or more) precipitation (< 20 days, 1; 20 to 25 days, 2; 25 to 30 days, 3; 30 to 35 days, 4; 35 to 40 days, 5).

21 Per cent probability of no measurable precipitation during the week of 7 to 14 February of any year (< 20%, 1; 20 to 30%, 2; 30 to 40%, 3; 40 to 50%, 4; > 50%, 5).

22 Per cent probability of no measurable precipitation during the week of 9 to 16 August of any year (< 40%, 1; 40 to 50%, 2; 50 to 60%, 3; 60 to 70%, 4; 70 to 80%, 5; 80 to 85%, 6; > 85%, 7).

23 Maximum precipitation to be expected within a 24-hour period on an average of once every 50 years (> 3.0 inches, 1; 2.4 to 3.0 inches, 2; 2.0 to 2.4 inches, 3; < 2.0 inches, 4).

APPENDIX C (CONTINUED)

24 Average frequency (days per year) of thunder storms (< 10 days, 1; 10 to 15 days, 2; 15 to 20 days, 3; 20 to 25 days, 4; 25 to 30 days, 6; > 30 days, 7).

25 Average frequency (days per year) of hailstorms (< 1 day, 1; 1 to 2 days, 2; 2 to 3 days, 3; 3 to 4 days, 4; > 4 days, 5).

26 Mean annual snowfall during the period 1939 to 1968. (< 10 inches, 1; 10 to 40 inches, 2; 40 to 80 inches, 3; > 80 inches, 4).

27 Average number of days each year in which heavy fog (reducing visibility to a quarter mile or less) will occur (< 2 days, 1; 2 to 4 days, 2; 4 to 6 days, 3; 6 to 8 days, 4; > 8 days, 5).

28 Average annual inches of evaporation from surfaces of lakes (< 40 inches, 1; 40 to 42 inches, 2; 42 to 44 inches, 3; 44 to 46 inches, 4; 46 to 48 inches, 5; 48 to 50 inches, 6; 50 to 52 inches, 7; 52 to 54 inches, 8; 54 to 56 inches, 9; 56 to 58 inches, 10; 58 to 60 inches, 11).

APPENDIX D

Exact localities of specimens examined. The Locality Number and Alphabetic Code for each Sample Name are given in parentheses.

Microdipodops megacephalus

ALKALI LAKE, OREGON (01, ALKA)

Lake Co.: 37 mi. N, 14 mi. E Valley Falls; NE edge Alkali Lake, 4200 ft.

NARROWS, OREGON (02, NARR)

Harney Co.: 5 mi. SW Narrows, 4000 ft.

ALVORK LAKE, OREGON (03, ALVO)

Harney Co.: 2 mi. S Borax Spring, S end Lake Alvord, 4300 ft.

RIDDLE, IDAHO (04, RIDD)

Owyhee Co.: 11 mi. S, 44.2 mi. W Riddle, 5000 ft.; 1/2 mi. N Nevada, 2 1/2 mi. E Oregon; Starr Valley, NW 1/4 Section 19, T16S, R5W (B.M.); Near Starr Valley, NW 1/4, NW 1/4 Section 19, T16S, R5W (B.M.).

DENIO, NEVADA (05, DENI)

Humboldt Co.: 0.6 mi. S Denio, 4200 ft.

CONTACT, NEVADA (06, CONT)

Elko Co.: 13 mi. S Contact; 15 mi. S Contact.

PAINTED POINT, NEVADA (07, PAIN)

Washoe Co.: 3 mi. E Painted Point, 5850 ft.; 4 1/2 mi. NE Painted Point, 5800 ft.

APPENDIX D (CONTINUED)

QUINN RIVER, NEVADA (08, QUIN)

Humboldt Co.: 2 mi. S, 0.7 mi. W Quinn River Crossing, 4150 ft.; 1/2 mi. W Quinn River Crossing, 4100 ft.; 2 mi. SW Quinn River Crossing, 4000 ft.; 2 1/2 mi. SW Quinn River Crossing, 4100 ft.; 4 1/2 mi. S Quinn River Crossing, 4000 ft.

JUNGO, NEVADA (09, JUNG)

Humboldt Co.: 13.8 mi. N, 11.2 mi. E Jungo, 4200 ft.; 8 mi. E, 1 mi. N Jungo, 4200 ft.

WINNEMUCCA, NEVADA (10, WINN)

Humboldt Co.: 7 mi. N Winnemucca, 4600 ft.; 7 mi. N Winnemucca, 4400 ft.; 5.5 mi. S, 9.2 mi. W Winnemucca, 4300 ft.; 0.7 mi. S, 10.5 mi. W Winnemucca, 4500 ft.; 0.7 mi. W, 5 mi. W Winnemucca, 4300 ft.

SULPHUR, NEVADA (11, SULP)

Pershing Co.: 2.2 mi. S, 1.2 mi. W Sulphur, 4150 ft.; 1.1 mi. N, 0.4 mi. E Sulphur, 4000 ft.; 1 1/4 mi. N Sulphur, 4050 ft.; 0.9 mi. S, 0.3 mi. E Sulphut, 4100 ft.

IZENHOOD, NEVADA (12, IZEN)

Lander, Co.: 3 mi. S Izenhood.

SMOKE CREEK, NEVADA (13, SMOK)

Washoe Co.: 10.7 mi. S, 25 mi. W Gerlach, 3950 ft.; Smoke Creek, 9 mi. E California Line, 3900 ft.

VERNON, NEVADA (14, VERN)

Pershing Co.: 3 mi. S Vernon, 4250 ft.; 14 mi. N, 26 mi. W Lovelock.

APPENDIX D (CONTINUED)

EUREKA, NEVADA (16, EURE)

Eureka Co.: 22.8 mi. N, 3.6 mi. W Eureka, 5850 ft.; 4 mi. SE Romano, Diamond Valley.

GRANITE PEAK, UTAH (17, GRAN)

Tooele Co.: North base Little Granite Mt., 4700 ft.; North base Little Granite Mtn., 4650 ft.; 7 mi. E North tip Granite Mtn., 4300 ft.; 1 mi. N Horizonal Grid, Dugway Proving Grounds; Horizonal Grid, Dugway Proving Grounds; 2 mi. NW Horizonal Grid, Dugway Proving Grounds; 2 mi. NE Camelback Mtn, 4340 ft.; 200 yd. W Baker - Granite Pk. Road Jct., Dugway Proving Grounds; 3 mi. N Granite Mtn, Dugway Proving Grounds; 8 mi. E, N end Granite Mtn, 4300 ft.

CALLAO, UTAH (18, CALL)

Juab Co.: 7.7 mi. S, 2.7 mi. E Callae, 4500 st.; 5.5 mi. S, 7.8 mi. E Callao, 4400 ft.; 4.2 mi. NE Trout Creek along road, 4590 ft.; 4 mi. SW Trout Creek, 4785 ft.; Near Mayfield Ranch, 4.5 mi. NE Trout Creek, 4590 ft.

CHILCOOT, CALIFORNIA (20, CHIL)

Plumas Co.: 1.6 mi. N Chilcoot (by road), 5120 ft.; 2 mi. N, 1.5 mi. E Chilcoot, T22N, R16E, N edge Section 30, 5400 ft.; 1 mi. N Vinton, 5000 ft.

SPARKS, NEVADA (21, SPAR)

Washoe Co.: 7 mi. N, 3 mi. E Sparks, 4550 ft.

MONITOR VALLEY, NEVADA (26, MONI)

Nye Co.: 10 1/2 mi. E Toquima Mtn., Monitor Valley, 6900 ft.

APPENDIX D (CONTINUED)

HOT CREEK, NEVADA (27, HOTC)

Nye Co.: 3 1/2 mi. E Hot Creek, Hot Creek Valley, 5650 ft.; 19.2 mi. N, 13.4 mi. E Warm Springs, 6000 ft.

SHOSHONE, NEVADA (29, SHOS)

White Pine Co.: 4 mi. S Shoshone, Spring Valley, 5900 ft.

MILFORD, UTAH (30, MILF)

Millard Co.: Pine Valley, 50 mi. W Milford, 5000 ft. Beaver Co.: 12 mi. N, 40 mi. W Milford.

FLETCHER, NEVADA (31, FLET)

Mineral Co.: Fletcher, 6100 ft.; 1/4 mi. N Fletcher, 6100 ft.

BENTON, CALIFORNIA (35, BENT)

Mono,Co.: Taylor Ranch, 2 mi. S Benton Station, 5300 ft.; 1.5 mi. SW River Springs Lakes, Adobe Valley, 6490 ft.

HIKO, NEVADA (39, HIKM)

Lincoln Co.: 6 mi. N, 31 mi. W Hiko, 4800 ft.; 14 mi. NNW Groom Baldy; 17 mi. N Groom Baldy, Penoyer Valley.

PANACA, NEVADA (40, PANA)

Lincoln Co.: 24 mi. W Panaca, 4600 ft.; 21 mi. W Panaca, Desert Valley, 5300 ft.

KAWICH, NEVADA (41, KAWM)

Nye Co.: 5 mi. SE Kawich P.O., 5400 ft.

APPENDIX D (CONTINUED)

Microdipodops pallidus

LOVELOCK, NEVADA (15, LOVE)

Pershing Co.: 21 mi. W, 2 mi. N Lovelock, 4000 ft.

NIXON, NEVADA (19, NIXO)

Washoe Co.: 7.5 mi. N Nixon, 4000 ft.

WADSWORTH, NEVADA (22, WADS)

Washoe Co.: 1.5 mi. N Wadsworth, 4100 ft.; 1 mi. WNW Wadsworth. Lyon Co.: 1/2 mi. SE Wadsworth, 4200 ft.; 1 mi. SE Wadsworth, 4200 ft.

MOUNTAIN WELL, NEVADA (23, MTWL)

Churchill Co.: Mountain Well, 5600 ft.

YERINGTON, NEVADA (24, YERI)

Lyon Co.: 17 mi. S, 5 mi. E Yerington, 5000 ft.

STEWART VALLEY, NEVADA (25, STEW)

Mineral Co.: Fingerrock Wash, Stewart Valley, 5400 ft.

LOCKS, NEVADA (28, LOCK)

Nye Co.: 2 1/2 mi. S Lock's Ranch, Railroad Valley, 5000 ft.; 3 1/4 mi. S Lock's Ranch, Railroad Valley, 5000 ft.; 9 mi. S Lock's Ranch, Railroad Valley, 5000 ft.; Able Spring, 12 1/2 mi. S Lock's Ranch, Railroad Valley, 5000 ft.; 19.2 mi. N, 13.4 mi. E Warm Springs, 6000 ft.

MINA, NEVADA (32, MINA)

Mineral Co.: 8.9 mi. S, 1.2 mi. E Mina, 4400 ft.

TONOPAH, NEVADA (33, TONA)

Esmeralda Co.: 1 1/2 mi. W Miller's Wells, 4800 ft.

APPENDIX D (CONTINUED)

Nye Co.: 5.4 mi. N, 4.9 mi. W Tonopah, 5100 ft.; 11.2 mi. N, 5.5 mi. W Tonopah, 5100 ft.

STONE CABIN VALLEY, NEVADA (34, STON)

Mye Co.: 34 mi. E, 1 mi. N Tonopah, Ralston Valley, 5650 ft.

COALDALE, NEVADA (36, COAL)

Esmeralda Co.: 7 mi. N Arlemont, 5500 ft.; 16.1 mi. S, 11.4 mi. W Coaldale (Jct.), 4900 ft.

SILVER PEAK, NEVADA (37, SILV)

Esmeralda Co.: 8 mi. SE Blair, 4500 ft.

MUD LAKE, NEVADA (38, MUDL)

Mye Co.: N shore Mud Lake, S end Ralston Valley, 5300 ft.

HIKO, NEVADA (39, HIKP)

Lincoln Co.: 6 mi. N, 31 mi. W Hiko, 4800 ft.; 17 mi. N Groom Baldy, Penoyer Valley.

KAWICH, NEVADA (41, KAWP)

Nye Co.: 5 mi. SE Kawich P.O., Kawich Valley, 5400 ft.; 3 mi. S, 4.3 mi. E Gold Reed, 5330 ft.; 2.2 mi. S, 5.6 mi. W Gold Reed, 5080 ft.

ALAMO, NEVADA (42, ALAM)

Lincoln Co.: 4.5 mi. S, 32.5 mi. W Alamo, 4600 ft.; 14 1/2 mi. S Groom Baldy.

APPENDIX E

Summary of cranial variables used in the morphometric analyses for samples of *Microdipodops megacephalus* and *Microdipodops pallidus* (Mean values followed by twice standard error and sample size in parentheses). Measurements are in millimeters.

Alphabetic Code	Greatest Length	Greatest Breadth	Basal Length	Bullar Length
		Microdipodops megacephalus		
ALKA	28.230 (0.180, 12)	18.563 (0.176, 12)	18.585 (0.170, 12)	13.939 (0.166, 12)
NARR	27.859 (0.154, 11)	18.298 (0.180, 10)	18.401 (0.172, 10)	13.621 (0.166, 11)
ALVO	28.257 (0.268, 11)	18.587 (0.328, 11)	18.275 (0.230, 10)	14.103 (0.298, 11)
RIDD	28.535 (1.470, 2)	19.255 (0.190, 2)	18.515 (1.090, 2)	14.515 (0.170, 2)
CONT	28.185 (0.336, 4)	18.513 (0.274, 4)	18.322 (0.476, 4)	14.120 (0.380, 4)
PAIN	28.322 (0.412, 8)	18.434 (0.168, 7)	18.471 (0.254, 8)	14.088 (0.360, 6)
QUIN	28.472 (0.246, 13)	18.873 (0.156, 13)	18.478 (0.154, 13)	14.298 (0.166, 13)
JUNG	28.467 (0.184, 12)	18.868 (0.130, 12)	18.283 (0.104, 12)	14.411 (0.124, 12)
WINN	28.729 (0.290, 12)	18.933 (0.258, 12)	18.441 (0.210, 12)	14.304 (0.182, 12)

APPENDIX E (CONTINUED)

Alphabetic Code	Greatest Length	Greatest Breadth	Basal Length	Bullar Length
SULP	28.864 (0.292, 11)	19.237 (0.280, 11)	18.382 (0.198, 11)	14.845 (0.240, 11)
IZEN	28.750 (0.234, 12)	19.392 (0.172, 12)	18.291 (0.188, 9)	14.827 (0.180, 12)
SMOK	27.923 (0.412, 6)	18.192 (0.388, 5)	18.054 (0.224, 5)	13.507 (0.256, 6)
VERN	28.832 (0.322, 12)	19.066 (0.118, 12)	18.483 (0.232, 12)	14.814 (0.152, 12)
EURE	28.435 (0.342, 12)	18.862 (0.222, 12)	18.444 (0.280, 12)	14.567 (0.188, 12)
GRAN	27.467 (0.364, 13)	18.371 (0.218, 16)	17.611 (0.312, 8)	14.136 (0.184, 16)
CALL	28.066 (0.454, 7)	19.091 (0.390, 8)	17.800 (0.194, 6)	14.619 (0.374, 8)
CHIL	26.971 (0.284, 11)	17.686 (0.172, 11)	17.755 (0.212, 10)	13.099 (0.162, 11)
SPAR	28.280 (0.306, 4)	18.765 (0.268, 4)	18.223 (0.542, 3)	13.960 (0.190, 4)
MONI	28.230 (0.322, 12)	18.768 (0.172, 12)	18.286 (0.256, 12)	14.290 (0.144, 12)
HOTC	28.226 (0.444, 7)	19.004 (0.412, 5)	18.311 (0.174, 7)	14.310 (0.334, 7)
SHOS	26.947 (0.410, 3)	18.047 (0.770, 3)	17.370 (0.488, 3)	13.703 (0.272, 3)
MILF	28.190 (0.318, 3)	18.587 (0.114, 6)	17.810 (0.218, 4)	14.240 (0.150, 5)
FLET	28.147 (0.330, 12)	18.625 (0.214, 12)	18.095 (0.238, 11)	14.063 (0.152, 12)
BENT	27.536 (0.310, 13)	18.122 (0.158, 13)	17.615 (0.342, 4)	13.559 (0.160, 13)

APPENDIX E (CONTINUED)

Alphabetic Code	Greatest Length	Greatest Breadth	Basal Length	Bullar Length
HIKM	28.668 (0.296, 11)	19.014 (0.242, 11)	18.419 (0.142, 11)	14.565 (0.266, 11)
PANA	28.061 (0.298, 13)	18.995 (0.206, 13)	18.152 (0.206, 11)	14.437 (0.218, 13)
KAWM	28.325 (0.534, 8)	18.933 (0.390, 10)	18.232 (0.370, 10)	14.487 (0.364, 10)
		Microdipodops pallidus		
LOVE	28.937 (0.254, 10)	19.621 (0.142, 11)	18.482 (0.314, 8)	15.671 (0.176, 11)
NIXO	27.790 (0.000, 1)	18.230 (0.480, 2)	18.220 (0.540, 2)	13.605 (0.190, 2)
WADS	27.709 (0.184, 15)	18.573 (0.190, 15)	18.107 (0.240, 15)	13.833 (0.196, 15)
MTWL	28.774 (0.354, 14)	19.548 (0.326, 14)	18.428 (0.234, 12)	14.624 (0.250, 14)
YERI	28.683 (0.170, 16)	19.406 (0.188, 17)	18.639 (0.142, 15)	14.478 (0.098, 17)
STEW	29.529 (0.556, 8)	19.767 (0.388, 7)	18.874 (0.374, 5)	14.984 (0.386, 8)
LOCK	28.400 (0.444, 8)	19.452 (0.436, 8)	18.173 (0.306, 7)	14.640 (0.286, 8)
MINA	28.380 (0.332, 7)	19.417 (0.222, 7)	18.289 (0.158, 7)	14.464 (0.208, 7)
TONO	28.512 (0.536, 5)	19.688 (0.288, 5)	18.514 (0.208, 5)	14.566 (0.430, 5)
STON	28.690 (0.222, 11)	19.358 (0.272, 12)	18.695 (0.198, 11)	14.538 (0.202, 12)

APPENDIX E (CONTINUED)

Alphabetic Code	Greatest Length	Greatest Breadth	Basal Length	Bullar Length
COAL	29.227 (0.278, 12)	19.739 (0.202, 12)	18.604 (0.276, 11)	14.797 (0.150, 12)
SILV	28.812 (0.280, 12)	19.690 (0.298, 12)	18.203 (0.272, 11)	14.881 (0.216, 12)
MUDL	28.562 (0.224, 6)	19.207 (0.194, 6)	18.425 (0.282, 6)	14.570 (0.152, 6)
HIKP	28.735 (0.370, 11)	19.937 (0.266, 12)	18.441 (0.152, 10)	14.987 (0.266, 12)
KAWP	28.579 (0.222, 14)	19.605 (0.160, 14)	18.328 (0.190, 13)	14.614 (0.188, 14)
ALAM	28.490 (0.282, 13)	19.533 (0.222, 13)	18.533 (0.186, 13)	14.629 (0.232, 13)

APPENDIX E (CONTINUED)

Alphabetic Code	Maxillary Breadth	Nasal Length	Least Interorbital Breadth	Greatest Expanse of Lateral Face of Zygoma
		Microdipodops megacephalus		
ALKA	11.575 (0.126, 12)	10.267 (0.120, 12)	6.613 (0.062, 12)	1.414 (0.036, 12)
NARR	11.514 (0.138, 11)	10.090 (0.128, 11)	6.760 (0.126, 11)	1.487 (0.040, 11)
ALVO	11.819 (0.154, 11)	10.202 (0.192, 11)	6.866 (0.092, 11)	1.575 (0.054, 11)
RIDD	11.615 (0.010, 2)	9.875 (0.950, 2)	6.625 (0.130, 2)	1.380 (0.120, 2)
CONT	11.913 (0.400, 4)	10.020 (0.248, 4	6.535 (0.168, 4)	1.445 (0.156, 4)
PAIN	11.773 (0.214, 9)	9.993 (0.148, 9)	6.521 (0.180, 9)	1.510 (0.098, 9)
QUIN	11.583 (0.190, 13)	10.057 (0.162, 13)	6.535 (0.120, 13)	1.465 (0.666, 13)
JUNG	11.610 (0.080, 12)	10.075 (0.144, 12)	6.493 (0.126, 12)	1.572 (0.046, 12)
WINN	11.709 (0.208, 12)	10.266 (0.192, 12)	6.513 (0.100, 12)	1.472 (0.072, 12)
SULP	11.616 (0.196, 11)	10.027 (0.146, 11)	6.571 (0.098, 11)	1.517 (0.068, 11)
IZEN	11.524 (0.192, 12)	9.997 (0.134, 12)	6.498 (0.092, 12)	1.464 (0.096, 11)
SMOK	12.050 (0.204, 6)	10.003 (0.204, 6)	6.678 (0.124, 6)	1.628 (0.078, 6)
VERN	11.687 (0.178, 12)	10.150 (0.162, 12)	6.509 (0.106, 12)	1.611 (0.068, 12)

APPENDIX E (CONTINUED)

Alphabetic Code	Maxillary Breadth	Nasal Length	Least Interorbital Breadth	Greatest Expanse of Lateral Face of Zygoma
EURE	11.649 (0.118, 12)	9.788 (0.152, 12)	6.640 (0.072, 12)	1.387 (0.092, 12)
GRAN	11.297 (0.148, 16)	9.307 (0.184, 13)	6.192 (0.100, 16)	1.263 (0.040, 16)
CALL	11.501 (0.230, 7)	9.829 (0.190, 8)	6.373 (0.148, 9)	1.264 (0.084, 8)
CHIL	11.485 (0.124, 11)	9.443 (0.126, 11)	6.511 (0.098, 11)	1.414 (0.054, 10)
SPAR	12.150 (0.410, 4)	10.043 (0.236, 4)	6.762 (0.156, 4)	1.617 (0.116, 4)
MONI	11.564 (0.178, 11)	9.849 (0.226, 12)	6.448 (0.112, 12)	1.352 (0.056, 12)
HOTC	11.647 (0.178, 7)	9.980 (0.246, 7)	6.374 (0.186, 7)	1.456 (0.110, 7)
SHOS	11.627 (0.086, 3)	9.073 (0.360, 3)	6.360 (0.246, 3)	1.207 (0.014, 3)
MILF	11.523 (0.140, 10)	9.776 (0.164, 8)	6.344 (0.096, 11)	1.378 (0.154, 10)
FLET	11.741 (0.180, 12)	9.952 (0.222, 12)	6.632 (0.102, 12)	1.456 (0.058, 12)
BENT	12.173 (0.132, 12)	9.968 (0.176, 13)	6.683 (0.088, 13)	1.438 (0.050, 13)
HIKM	11.731 (0.210, 11)	10.217 (0.142, 11)	6.400 (0.080, 11)	1.431 (0.046, 11)
PANA	11.815 (0.160, 13)	9.722 (0.158, 13)	6.450 (0.118, 13)	1.387 (0.050, 13)
KAWM	11.711 (0.240, 10)	10.013 (0.184, 9)	6.501 (0.208, 10)	1.474 (0.064, 10)

APPENDIX E (CONTINUED)

Alphabetic Code	Maxillary Breadth	Nasal Length	Least Interorbital Breadth	Greatest expanse of Lateral Face of Zygoma
		Microdipodops pallidus		
LOVE	11.955 (0.174, 11)	10.015 (0.132, 10)	6.578 (0.074, 11)	1.467 (0.066, 11)
NIXO	12.340 (0.020, 2)	9.740 (0.000, 1)	6.560 (0.060, 2)	1.600 (0.240, 2)
WADS	12.099 (0.158, 14)	9.732 (0.090, 15)	6.642 (0.078, 15)	1.561 (0.064, 15)
MTWL	12.132 (0.208, 13)	10.117 (0.168, 14)	6.741 (0.106, 14)	1.542 (0.068, 14)
YERI	12.286 (0.168, 17)	9.888 (0.132, 16)	6.782 (0.070, 17)	1.469 (0.078, 17)
STEW	12.470 (0.200, 8)	10.370 (0.290, 8)	6.875 (0.064, 8)	1.614 (0.126, 8)
LOCK	12.155 (0.274, 8)	9.692 (0.118, 8)	6.838 (0.084, 8)	1.538 (0.050, 8)
MINA	11.917 (0.310, 7)	9.991 (0.282, 7)	6.623 (0.134, 7)	1.479 (0.084, 7)
TONO	12.352 (0.344, 5)	10.070 (0.178, 5)	6.702 (0.096, 5)	1.600 (0.058, 5)
STON	12.098 (0.152, 12)	9.979 (0.174, 12)	6.833 (0.082, 12)	1.508 (0.058, 12)
COAL	12.387 (0.144, 12)	10.393 (0.186, 12)	6.738 (0.084, 12)	1.589 (0.074, 12)
SILV	11.946 (0.176, 12)	10.090 (0.182, 12)	6.540 (0.096, 12)	1.495 (0.050, 12)
MUDL	12.000 (0.202, 6)	9.857 (0.120, 6)	6.700 (0.110, 6)	1.433 (0.026, 6)

APPENDIX E (CONTINUED)

Alphabetic Code	Maxillary Breadth	Nasal Length	Least Interorbital Breadth	Greatest Expanse of Lateral Face of Zygoma
HIKP	12.305 (0.212, 12)	9.816 (0.168, 11)	6.786 (0.108, 12)	1.483 (0.062, 12)
KAWP	12.247 (0.124, 13)5	9.898 (0.114, 14)	6.824 (0.100, 14)	1.526 (0.064, 14)
ALAM	12.319 (0.160, 13)	9.868 (0.136, 13)	6.617 (0.082, 13)	1.632 (0.084, 13)

APPENDIX E (CONTINUED)

Alphabetic Code	Least Expanse of Lateral Face of Zygoma	Greatest Length Incisive Foramina	Length Incisive Foramina at Point of Greatest Breadth	Greatest Breadth Incisive Foramina
		Microdipodops megacephalus		
ALKA	1.136 (0.042, 12)	2.634 (0.062, 12)	1.840 (0.132, 12)	1.048 (0.066, 12)
NARR	1.155 (0.042, 11)	2.538 (0.052, 11)	1.881 (0.062, 11)	1.064 (0.054, 11)
ALVO	1.135 (0.064, 11)	2.531 (0.058, 11)	2.035 (0.086, 11)	1.098 (0.066, 11)
RIDD	0.940 (0.000, 2)	2.230 (0.080, 2)	1.630 (0.220, 2)	0.775 (0.090, 2)
CONT	1.027 (0.118, 4)	2.420 (0.164, 4)	1.015 (0.042, 4)	0.925 (0.134, 4)
PAIN	1.051 (0.066, 9)	2.406 (0.060, 9)	1.701 (0.092, 9)	1.006 (0.054, 9)
QUIN	1.134 (0.092, 13)	2.538 (0.066, 13)	2.079 (0.070, 13)	1.025 (0.068, 13)
JUNG	1.130 (0.048, 12)	2.381 (0.046, 12)	1.829 (0.066, 12)	0.988 (0.074, 12)
WINN	1.185 (0.078, 12)	2.359 (0.052, 12)	1.822 (0.080, 12)	0.990 (0.036, 12)
SULP	1.135 (0.066, 11)	2.515 (0.094, 11)	2.040 (0.072, 11)	0.980 (0.078, 11)
IZEN	1.023 (0.074, 12)	2.434 (0.072, 12)	1.950 (0.064, 12)	0.960 (0.042, 12)
SMOK	1.182 (0.098, 6)	2.363 (0.120, 6)	1.297 (0.434, 6)	0.903 (0.084, 6)
VERN	1.209 (0.058, 12)	2.408 (0.068, 12)	1.952 (0.062, 12)	1.076 (0.052, 12)

APPENDIX E (CONTINUED)

Alphabetic Code	Least Expanse of Lateral Face of Zygoma	Greatest Length Incisive Foramina	Length Incisive Foramina at Point of Greatest Breadth	Greatest Breadth Incisive Foramina
EURE	0.981 (0.086, 12)	2.412 (0.078, 12)	1.915 (0.096, 12)	1.050 (0.068, 12)
GRAN	0.969 (0.064, 16)	2.262 (0.040, 15)	1.787 (0.068, 15)	0.960 (0.066, 15)
CALL	0.988 (0.068, 8)	2.414 (0.068, 8)	1.919 (0.178, 8)	0.986 (0.060, 8)
CHIL	1.105 (0.046, 11)	2.233 (0.078, 11)	1.570 (0.192, 11)	0.896 (0.026, 11)
SPAR	1.015 (0.018, 4)	2.550 (0.038, 4)	1.900 (0.100, 4)	0.948 (0.074, 4)
MONI	0.938 (0.083, 12)	2.408 (0.062, 12)	1.948 (0.104, 12)	1.047 (0.066, 12)
HOTC	1.087 (0.116, 7)	2.403 (0.056, 7)	1.994 (0.086, 7)	0.951 (0.140, 7)
SHOS	1.033 (0.148, 3)	2.423 (0.018, 3)	1.997 (0.066, 3)	0.913 (0.036, 3)
MILF	0.999 (0.066, 10)	2.463 (0.102, 10)	1.834 (0.122, 10)	0.948 (0.054, 10)
FLET	1.074 (0.088, 12)	2.546 (0.058, 12)	2.071 (0.058, 12)	1.146 (0.062, 12)
BENT	1.028 (0.054, 13)	2.504 (0.140, 13)	2.110 (0.100, 13)	1.132 (0.050, 13)
HIKM	1.104 (0.060, 11)	2.464 (0.106, 11)	2.025 (0.118, 11)	1.057 (0.090, 11)
PANA	1.095 (0.062, 13)	2.569 (0.068, 13)	2.000 (0.080, 13)	0.968 (0.066, 13)
KAWM	1.014 (0.062, 10)	2.463 (0.104, 10)	2.004 (0.114, 10)	1.011 (0.104, 10)

APPENDIX E (CONTINUED)

Alphabetic Code	Least Expanse of Lateral Face of Zygoma	Greatest Length Incisive Foramina	Length Incisive Foramina at Point of Greatest Breadth	Greatest Expanse Incisive Foramina
		Microdipodops pallidus		
LOVE	0.973 (0.066, 11)	2.445 (0.052, 11)	1.608 (0.288, 11)	0.967 (0.078, 11)
NIXO	1.060 (0.160, 2)	2.425 (0.110, 2)	1.645 (0.330, 2)	0.960 (0.160, 2)
WADS	1.015 (0.034, 15)	2.373 (0.062, 15)	0.865 (0.128, 15)	0.901 (0.030, 15)
MTWL	1.044 (0.048, 14)	2.353 (0.072, 14)	1.156 (0.214, 14)	0.918 (0.036, 14)
YERI	0.950 (0.036, 17)	2.434 (0.060, 17)	1.472 (0.156, 17)	0.925 (0.066, 17)
STEW	1.149 (0.066, 8)	2.445 (0.078, 8)	1.348 (0.216, 8)	0.881 (0.060, 8)
LOCK	1.234 (0.034, 8)	2.354 (0.072, 8)	1.371 (0.122, 8)	1.023 (0.060, 8)
MINA	1.126 (0.058, 7)	2.239 (0.098, 7)	1.584 (0.220, 7)	0.954 (0.044, 7)
TONO	1.096 (0.080, 5)	2.478 (0.224, 5)	1.430 (0.254, 5)	1.058 (0.056, 5)
STON	1.185 (0.052, 12)	2.319 (0.070, 12)	1.620 (0.108, 12)	0.870 (0.058, 12)
COAL	1.148 (0.048, 12)	2.446 (0.074, 12)	1.620 (0.172, 12)	1.027 (0.056, 12)
SILV	1.012 (0.054, 12)	2.357 (0.086, 12)	1.595 (0.252, 12)	0.974 (0.080, 12)
MUDL	1.202 (0.094, 6)	2.397 (0.094, 6)	1.428 (0.106, 6)	0.900 (0.038, 6)

APPENDIX E (CONTINUED)

Alphabetic Code	Least Expanse of Lateral Face of Zygoma	Greatest Length Incisive Foramina	Length Incisive Foramina at Point of Greatest Breadth	Greatest Breadth Incisive Foramina
HIKP	1.044 (0.064, 12)	2.501 (0.066, 12)	1.670 (0.064, 12)	1.051 (0.054, 12)
KAWP	1.101 (0.044, 14)	2.246 (0.060, 14)	1.544 (0.084, 14)	0.959 (0.034, 14)
ALAM	1.184 (0.050, 13)	2.408 (0.052, 13)	1.285 (0.230, 13)	0.909 (0.054, 13)

APPENDIX E (CONTINUED)

Alphabetic Code	Greatest Pterygoidal Breadth	Arching of Cranial Dome	Mandibular Length	Angular Bifurcation
		Microdipodops megacephalus		
ALKA	0.675 (0.060, 12)	6.426 (0.148, 12)	10.530 (0.122, 12)	0.329 (0.036, 11)
NARR	0.708 (0.034, 11)	6.699 (0.172, 11)	10.470 (0.098, 11)	0.340 (0.020, 10)
ALVO	0.757 (0.040, 10)	6.433 (0.222, 11)	10.440 (0.066, 11)	0.329 (0.022, 11)
RIDD	0.695 (0.170, 2)	6.429 (0.140, 2)	10.595 (0.510, 2)	0.395 (0.070, 2)
CONT	0.705 (0.034, 4)	6.418 (0.426, 4)	10.157 (0.076, 4)	0.327 (0.048, 4)
PAIN	0.839 (0.046, 9)	6.699 (0.216, 9)	10.428 (0.182, 9)	0.304 (0.064, 9)
QUIN	0.734 (0.074, 12)	6.584 (0.208, 13)	10.420 (0.070, 13)	0.372 (0.032, 11)
JUNG	0.731 (0.046, 10)	6.523 (0.196, 12)	10.361 (0.054, 12)	0.318 (0.038, 12)
WINN	0.772 (0.062, 12)	6.474 (0.144, 12)	10.512 (0.124, 12)	0.321 (0.050, 12)
SULP	0.737 (0.070, 10)	6.688 (0.212, 11)	10.292 (0.106, 11)	0.267 (0.040, 11)
IZEN	0.745 (0.080, 8)	6.419 (0.166, 12)	10.317 (0.126, 12)	0.436 (0.032, 12)
SMOK	0.732 (0.078, 5)	6.510 (0.246, 6)	10.465 (0.176, 6)	0.298 (0.054, 6)
VERN	0.790 (0.040, 11)	6.347 (0.180, 12)	10.462 (0.114, 12)	0.325 (0.036, 12)

APPENDIX E (CONTINUED)

Alphabetic Code	Greatest Pterygoidal Breadth	Arching of Cranial Dome	Mandibular Length	Angular Bifurcation
EURE	0.705 (0.044, 11)	6.482 (0.208, 12)	10.409 (0.102, 12)	0.286 (0.026, 12)
GRAN	0.676 (0.060, 11)	6.895 (0.268, 15)	9.865 (0.106, 16)	0.275 (0.046, 13)
CALL	0.701 (0.100, 8)	6.297 (0.274, 7)	9.880 (0.188, 9)	0.411 (0.068, 8)
CHIL	0.615 (0.038, 6)	6.454 (0.250, 11)	10.149 (0.098, 10)	0.356 (0.028, 11)
SPAR	0.625 (0.076, 4)	6.510 (0.278, 4)	10.605 (0.166, 4)	0.333 (0.072, 4)
MONI	0.733 (0.062, 12)	6.382 (0.208, 12)	10.332 (0.112, 12)	0.299 (0.040, 11)
HOTC	0.789 (0.060, 7)	6.030 (0.212, 7)	10.459 (0.178, 7)5	0.377 (0.048, 7)
SHOS	0.793 (0.108, 3)	6.723 (0.232, 3)	9.806 (0.130, 3)	0.300 (0.084, 3)
MILF	0.683 (0.088, 4)	6.598 (0.394, 6)	10.207 (0.134, 8)	0.280 (0.058, 6)
FLET	0.698 (0.048, 12)	6.522 (0.242, 12)	10.224 (0.136, 12)	0.322 (0.046, 11)
BENT	0.733 (0.050, 12)	6.346 (0.252, 11)	10.324 (0.112, 13)	0.312 (0.046, 12)
HIKM	0.733 (0.086, 11)	6.395 (0.252, 11)	10.362 (0.144, 11)	0.318 (0.040, 10)
PANA	0.832 (0.090, 10)	6.312 (0.138, 13)	10.323 (0.100, 12)	0.315 (0.038, 13)
KAWM	0.691 (0.100, 9)	6.345 (0.416, 8)	10.213 (0.148, 10)	0.372 (0.052, 9)

APPENDIX E (CONTINUED)

Alphabetic Code	Greatest Pterygoidal Breadth	Arching of Cranial Dome	Mandibular Length	Angular Bifurcation
		Microdipodops pallidus		
LOVE	0.903 (0.066, 10)	6.888 (0.256, 11)	10.492 (0.138, 11)	0.391 (0.042, 11)
NIXO	0.905 (0.230, 2)	6.740 (0.300, 2)	10.395 (0.010, 2)	0.520 (0.040, 2)
WADS	0.949 (0.046, 14)	6.797 (0.167, 15)	10.405 (0.100, 15)	0.403 (0.035, 15)
MTWL	0.974 (0.044, 12)	6.971 (0.200, 14)	10.761 (0.126, 14)	0.494 (0.032, 14)
YERI	1.013 (0.050, 15)	6.558 (0.166, 17)	10.774 (0.114, 17)	0.578 (0.042, 17)
STEW	0.916 (0.056, 7)	7.241 (0.210, 8)	10.861 (0.158, 8)	0.454 (0.052, 7)
LOCK	0.979 (0.056, 8)	6.905 (0.188, 8)	10.586 (0.242, 8)	0.534 (0.054, 8)
MINA	0.856 (0.040, 7)	6.960 (0.272, 7)	10.509 (0.146, 7)	0.469 (0.070, 7)
TONO	0.930 (0.060, 2)	6.648 (0.270, 5)	10.588 (0.168, 5)	0.458 (0.132, 5)
STON	0.885 (0.050, 12)	6.850 (0.240, 11)	10.655 (0.112, 12)	0.456 (0.044, 12)
COAL	0.974 (0.064, 12)	7.017 (0.206, 12)	10.735 (0.132, 12)	0.387 (0.064, 12)
SILV	0.930 (0.044, 12)	6.819 (0.208, 12)	10.483 (0.134, 12)	0.437 (0.048, 12)
MUDL	0.888 (0.048, 6)	7.137 (0.388, 6)	10.643 (0.170, 6)	0.482 (0.062, 6)

APPENDIX E (CONTINUED)

Alphabetic Code	Greatest Pterygoidal Breadth	Arching of Cranial Dome	Mandibular Length	Angular Bifurcation
HIKP	0.977 (0.038, 12)	7.047 (0.232, 12)	10.725 (0.124, 12)	0.559 (0.050, 12)
KAWP	0.900 (0.032, 13)	6.695 (0.170, 14)	10.609 (0.134, 13)	0.464 (0.024, 14)
ALAM	0.822 (0.032, 13)	7.186 (0.184, 13)	10.543 (0.100, 13)	0.497 (0.040, 13)

APPENDIX F

Summary of colorimetric variables of samples of Microdipodops megacephalus and Microdipodops pallidus (Mean value followed by twice standard error in parentheses). Relative brightness, excitation purity, and reflectance are given in per cent and dominant wavelength is in millimicrons.

Alphabetic Code	N	Relative Brightness	Dominant Wavelength	Excitation Purity	Trichromatic Coefficient x	Reflectance RZ_1
			Microdipodops megacephalus			
ALKA	18	61.141 (1.190)	578.167 (0.566)	.057 (.004)	.321 (.000)	.530 (.008)
NARR	19	64.091 (1.318)	580.421 (0.414)	.071 (.006)	.325 (.002)	.542 (.006)
ALVO	19	58.387 (0.802)	577.737 (0.730)	.049 (.004)	.319 (.000)	.512 (.004)
RIDD	5	58.984 (0.806)	576.600 (1.624)	.037 (.006)	.317 (.002)	.530 (.008)
CONT	8	64.472 (1.672)	578.125 (1.162)	.057 (.010)	.321 (.002)	.555 (.006)
PAIN	13	59.515 (1.464)	576.846 (1.128)	.053 (.008)	.320 (.002)	.515 (.008)
QUIN	21	69.993 (1.142)	581.333 (0.318)	.090 (.004)	.329 (.000)	.570 (.008)
JUNG	20	76.954 (1.388)	580.300 (0.412)	.112 (.008)	.333 (.002)	.599 (.006)

APPENDIX F (CONTINUED)

Alphabetic Code	N	Relative Brightness	Dominant Wavelength	Excitation Purity	Trichromatic Coefficient $\underline{x}$	Reflectance RZ_1
WINN	20	71.165 (1.308)	580.500 (0.308)	.104 (.004)	.332 (.002)	.557 (.008)
SULP	19	72.122 (1.668)	580.579 (0.232)	.104 (.004)	.331 (.000)	.570 (.010)
IZEN	19	64.054 (0.892)	579.842 (0.382)	.082 (.004)	.327 (.000)	.525 (.006)
SMOK	10	66.722 (1.124)	581.500 (0.448)	.083 (.004)	.328 (.002)	.554 (.008)
VERN	18	65.108 (0.922)	580.778 (0.346)	.085 (.004)	.328 (.002)	.537 (.006)
EURE	19	60.327 (2.894)	577.316 (1.082)	.050 (.006)	.319 (.002)	.536 (.006)
GRAN	20	80.701 (1.364)	580.650 (0.300)	.107 (.004)	.332 (.000)	.632 (.008)
CALL	12	80.929 (2.228)	580.500 (0.390)	.103 (.006)	.331 (.002)	.637 (.012)
CHIL	17	63.022 (1.312)	581.529 (0.424)	.079 (.008)	.327 (.002)	.529 (.010)
SPAR	3	68.010 (3.610)	581.333 (0.666)	.082 (.010)	.327 (.002)	.565 (.022)
MONI	15	68.084 (1.516)	579.200 (0.592)	.078 (.008)	.325 (.002)	.565 (.008)
HOTC	16	68.464 (1.446)	580.125 (0.404)	.083 (.010)	.327 (.002)	.569 (.008)
SHOS	14	67.916 (1.190)	579.429 (0.456)	.069 (.006)	.324 (.002)	.574 (.006)
MILF	13	72.263 (1.274)	580.154 (0.674)	.092 (.006)	.329 (.002)	.581 (.010)

APPENDIX F (CONTINUED)

Alphabetic Code	N	Relative Brightness	Dominant Wavelength	Excitation Purity	Trichromatic Coefficient x	Reflectance RZ_1
FLET	20	69.930 (1.048)	580.250 (0.408)	.086 (.008)	.328 (.002)	.576 (.006)
BENT	20	71.557 (1.426)	580.250 (0.320)	.085 (.004)	.327 (.002)	.585 (.008)
HIKM	20	72.146 (1.510)	580.250 (0.380)	.099 (.008)	.330 (.002)	.581 (.008)
PANA	17	76.336 (2.116)	579.882 (0.512)	.108 (.006)	.332 (.002)	.590 (.014)
KAWM	17	69.176 (1.314)	580.588 (0.616)	.082 (.006)	.327 (.002)	.567 (.008)
			Microdipodops pallidus			
LOVE	11	75.249 (1.758)	581.000 (0.000)	.111 (.006)	.333 (.002)	.589 (.008)
NIXO	2	74.639 (5.160)	582.500 (1.000)	.110 (.012)	.334 (.004)	.587 (.024)
WADS	22	71.737 (1.386)	580.545 (0.388)	.097 (.006)	.330 (.002)	.577 (.008)
MTWL	20	75.709 (1.456)	581.350 (0.218)	.119 (.004)	.335 (.000)	.581 (.008)
YERI	17	73.974 (1.684)	581.824 (0.462)	.106 (.010)	.333 (.002)	.587 (.008)
STEW	20	75.288 (1.382)	581.550 (0.270)	.124 (.004)	.336 (.000)	.571 (.008)
LOCK	17	74.901 (1.282)	580.118 (0.890)	.101 (.004)	.331 (.002)	.595 (.012)

APPENDIX F (CONTINUED)

Alphabetic Code	N	Relative Brightness	Dominant Wavelength	Excitation Purity	Trichromatic Coefficient $\underline{x}$	Reflectance RZ_1
MINA	7	76.877 (1.808)	581.000 (0.618)	.099 (.008)	.331 (.002)	.616 (.012)
TONO	16	79.135 (1.688)	581.563 (0.256)	.119 (.002)	.335 (.000)	.608 (.012)
STON	20	75.425 (1.504)	580.350 (0.418)	.105 (.006)	.332 (.002)	.588 (.006)
COAL	13	79.974 (1.534)	581.231 (0.332)	.130 (.006)	.337 (.002)	.597 (.006)
SILV	20	80.150 (1.184)	580.200 (0.372)	.131 (.006)	.337 (.002)	.588 (.012)
MUDL	10	76.584 (1.858)	581.400 (0.326)	.110 (.004)	.333 (.000)	.598 (.012)
HIKP	19	74.704 (1.234)	580.684 (0.434)	.105 (.004)	.332 (.002)	.585 (.006)
KAWP	20	77.404 (1.910)	580.150 (0.418)	.110 (.006)	.332 (.000)	.596 (.010)
ALAM	20	80.976 (1.350)	579.150 (0.364)	.122 (.010)	.334 (.002)	.605 (.006)

APPENDIX G

Matrix of characters used in the analyses of environmental relationships. Alphabetic codes are in accord with those presented in Table 1. Character numbers follow Appendix C.

Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
NARR	1	5	1	1	2	2	1	2	3	2	8	2	2	1	1	5	2	3	5	2	1	4	3	1	2	2	4	4
ALKA	1	4	1	1	2	2	1	2	3	2	8	2	2	1	1	5	1	3	5	2	1	4	3	2	3	3	4	4
ALVO	2	5	1	2	2	2	1	2	3	3	6	2	2	1	2	4	3	3	5	2	1	4	3	1	2	2	4	4
RIDD	2	6	1	2	1	2	2	2	2	3	8	2	2	1	2	4	2	3	5	3	1	4	3	2	3	2	5	2
DENI	2	5	1	2	2	2	1	3	3	3	6	2	2	1	2	3	4	3	5	2	1	4	3	1	2	2	4	4
CONT	3	6	1	2	1	2	2	1	3	3	9	1	2	1	2	4	2	3	4	1	1	3	2	4	4	2	4	2
PAIN	1	4	1	1	2	1	1	2	4	2	6	1	2	1	1	4	3	3	4	2	1	5	3	1	3	3	4	5
QUIN	2	5	1	2	2	2	1	3	3	4	5	2	3	2	3	2	4	2	4	2	2	5	4	1	2	2	3	5
JUNG	2	5	1	3	2	3	1	4	2	4	5	2	3	2	3	2	4	2	4	2	2	5	3	1	2	2	2	6
WINN	2	5	1	3	2	3	1	4	2	4	6	2	3	2	2	3	4	3	4	2	2	5	4	2	2	2	3	5
SULP	2	4	2	3	2	3	1	3	2	4	5	2	3	3	3	2	4	2	2	1	3	5	3	1	1	2	3	7
IZEN	2	5	1	3	2	2	2	4	2	3	7	2	2	2	2	3	3	2	3	1	1	6	3	3	3	2	3	4
SMOK	1	2	3	3	2	2	1	3	3	3	5	1	3	2	2	3	4	2	3	2	2	7	3	2	2	2	4	4

APPENDIX G (CONTINUED)

Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
VERN	2	3	3	4	2	3	1	4	2	4	4	2	3	3	3	2	4	2	2	1	3	6	3	2	1	2	3	7
LOVE	2	3	3	4	2	3	1	4	2	4	4	2	3	3	3	2	4	2	2	1	3	7	3	2	1	2	3	7
EURE	3	4	2	2	2	2	2	1	4	3	5	2	2	2	1	3	2	2	4	3	1	4	2	4	4	2	2	5
GRAN	3	4	2	4	1	2	2	3	2	3	6	2	2	2	2	2	4	2	4	3	2	2	2	7	2	2	3	4
CALL	3	4	2	4	1	2	2	2	3	2	6	2	2	2	2	2	4	3	4	3	2	2	2	7	4	2	2	4
NIXO	1	2	3	4	3	3	1	4	2	4	4	2	3	2	3	2	4	2	1	1	2	7	3	2	1	2	4	6
CHIL	1	2	3	3	2	2	1	3	2	3	6	2	2	3	2	3	3	3	4	3	2	5	2	2	2	2	5	4
SPAR	1	2	4	3	2	2	1	3	2	3	5	2	3	2	2	2	3	3	2	2	2	5	3	2	2	2	5	5
WADS	1	2	3	4	3	3	1	3	2	4	4	2	3	2	3	2	4	2	1	1	3	7	3	2	1	2	4	6
MTWL	2	2	3	4	2	3	1	4	2	3	4	2	3	3	3	2	4	3	2	2	3	6	3	2	1	2	3	9
YERI	1	2	4	4	2	2	1	3	3	3	6	2	3	2	2	3	3	2	2	3	3	6	3	2	1	2	5	6
STEW	2	2	4	4	2	3	1	3	2	3	4	3	3	3	3	2	5	2	1	1	5	6	2	2	1	2	3	9
MONI	3	2	3	3	2	1	2	2	3	2	4	2	3	2	2	3	4	3	1	3	2	4	1	2	2	3	2	9
HOTC	3	2	3	3	2	2	2	2	2	1	3	2	3	2	3	2	4	2	1	3	2	3	3	2	2	2	1	9
LOCK	3	2	3	3	2	2	2	2	2	1	3	2	3	2	3	2	4	2	2	4	2	2	2	2	3	2	1	8

APPENDIX G (CONTINUED)

Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
SHOS	3	3	3	3	2	2	2	2	3	2	5	2	3	2	2	2	4	3	4	4	2	1	2	6	4	2	1	5
MILF	3	3	3	3	2	2	2	2	2	2	4	2	3	2	2	2	5	3	4	5	2	1	2	6	4	2	1	5
FLET	2	1	3	4	2	3	1	3	3	3	3	3	3	2	2	3	3	3	1	3	2	6	2	2	1	2	4	5
MINA	2	1	4	4	2	3	1	4	2	3	4	3	3	4	3	2	6	2	1	2	5	6	3	2	1	1	3	8
TONO	2	2	4	4	3	2	1	3	2	3	4	3	3	4	3	2	5	2	1	3	4	4	1	2	1	1	2	10
STON	3	2	3	3	2	1	2	3	1	2	3	3	3	4	3	2	5	3	1	4	3	3	2	2	2	1	2	10
BENT	2	1	3	4	2	2	1	3	3	3	3	2	3	2	2	3	3	3	1	3	2	5	1	2	1	3	4	5
COAL	2	1	3	4	2	2	1	3	2	3	3	2	3	2	2	2	4	2	1	3	2	5	2	2	1	2	3	9
SILV	2	1	4	4	2	2	1	3	2	3	4	3	3	3	3	2	4	2	1	3	3	5	3	2	1	1	3	11
MUDL	2	2	4	4	3	2	1	3	1	2	4	3	3	4	3	2	5	2	1	3	4	4	4	2	1	1	2	11
HIKM	3	2	3	4	2	2	2	3	1	3	2	3	3	4	3	2	4	2	3	4	3	2	2	2	2	1	1	10
HIKP	3	2	3	4	2	2	2	3	1	3	2	3	3	4	3	2	4	2	3	4	3	2	2	2	2	1	1	10
PANA	3	2	3	4	2	2	2	3	1	3	2	3	3	3	3	2	5	2	4	5	3	2	2	3	3	2	1	9
KAWM	3	2	4	4	2	2	2	3	1	3	2	3	4	4	3	1	5	2	2	3	4	3	3	2	2	1	1	11
KAWP	3	2	4	4	2	2	2	3	1	3	2	3	4	4	3	1	5	2	2	3	4	3	3	2	2	1	1	11

APPENDIX G (CONTINUED)

Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
ALAM	3	2	4	5	3	3	2	3	1	4	1	3	4	4	3	1	5	3	2	3	3	3	2	2	2	1	1	11

APPENDIX H

Synonymy of named forms with comments on type specimens and descriptions of geographic distributions of subspecies.

GENUS MICRODIPODOPS

1891. Microdipodops Merriam, N. Amer. Fauna, 5:115-117; (type species, Microdipodops megacephalus Merriam).

Microdipodops megacephalus

1891. Microdipodops megacephalus Merriam, N. Amer. Fauna, 5:115-117, original description.

1901. Microdipodops californicus Merriam, Proc. Biol. Soc. Washington, 14:127-128.

1914. Microdipodops polionotus Grinnell, Univ. California Publ. Zool., 12:301-304.

Microdipodops (megacephalus) megacephalus

Microdipodops megacephalus megacephalus Merriam

1891. Microdipodops megacephalus Merriam, N. Amer. Fauna, 5:115-117, original description.

1941. Microdipodops megacephalus megacephalus, Hall, Field Mus. Nat. Hist., Zool. Ser., 27:258-260.

1941. Microdipodops megacephalus sabulonis Hall, Proc. Biol. Soc. Washington, 54:59.

Holotype.--Adult male (skin with skull), United States

APPENDIX H (CONTINUED)

National Museum of Natural History, 24417/31823. Collected by Vernon Bailey on 23 October 1890; original no. 2005.

Type Locality.--Halleck, Elko Co., Nevada.

Distribution.--Central portion of the Great Basin including Elko, Lander, Eureka, White Pine, Nye, Esmeralda, and Lincoln counties of Nevada (Fig. 20).

Diagnosis.--Kangaroo mice of this subspecies are the most generalized in morphology in the entire genus (see Fig. 13 and Appendix E). Body size is medium to large and the incisive foramina are divergent posteriorly and sharply pointed anteriorly. Auditory bullae are only moderately inflated. Dorsal pelage color is variable, but specimens are medium to dark in coloration (Fig. 15, Appendix F). Chromosomally, this subspecies has the 40-α karyotype (see Fig. 5). Ventral pelage color is plumbeous basally and white distally; distal tips sometimes with a light buffy wash.

Comparisons.--These kangaroo mice are separated from other subspecies of the eastern megasubspecific unit, (megacephalus), most easily by pelage color and karyotypic characters. From albiventer (to the east), megacephalus is readily differentiated by the 40-α karyotype (and not the 40-β karyotype) and having plumbeous bases to the ventral hairs (albiventer) has pure white belly hairs). Further, megacephalus differs from albiventer by large overall body size and

APPENDIX H (CONTINUED)

darker dorsal pelage. This subspecies differs from polionotus (from the Mono Basin region of California and Nevada) in having plumbeous bases to the ventral hairs, instead of pure white hairs of the venter. From the western subspecies (including nexus, californicus, ambiguus, and oregonus), megacephalus is separated by protein analyses (see Fig. 4) and by colorimetric characters (lowered values for trichromatic coefficient x and larger values for reflectance RZ_1, see Fig. 15). From atrirelictus, this subspecies differs by smaller body and cranial proportions, the 40-α karyotype, and lighter pelage color.

Comments.--Specimens from the northern section of the range (particularly Elko County) are extremely scarce in collections. The explanation of the scarcity of the northern specimens probably lies in the fact that the habitat and climate is only marginally appropriate (approaching rather gravelly soil and cool climate) for kangaroo mice. Kangaroo mice of this subspecies seem most similar morphologically, to the oregonus populations (both have the 40-α karyotype, rather dark dorsal pelage, and plumbeous bases on the hairs of the venter). Importantly, though, oregonus belongs to the western genetic unit (see Fig. 4) and thus seems to represent an instance of parallelism.

APPENDIX H (CONTINUED)

Microdipodops megacephalus polionotus Grinnell

1914. Microdipodops polionotus Grinnell, Univ. California Publ. Zool., 12:302, original description.

1941. Microdipodops megacephalus polionotus, Hall, Field Mus. Nat. Hist., Zool. Ser., 27:251-252.

1941. Microdipodops megacephalus nasutus Hall, Field Mus. Nat. Hist., Zool. Ser., 27:251.

Holotype.--Adult male (skin with skull), Museum of Vertebrate Zoology, 17031. Collected by C. D. Holliger on 10 July 1912; original No. 184.

Type Locality.--McKeever's Ranch, 2 mi. S Benton Station, 5200 ft., Mono Co., California.

Distribution.--Mono Lake and adjoining valley regions of California and Nevada. Ranges from Fletcher, Nevada to the north, to extreme head of Owens Valley to the south (Fig. 20).

Diagnosis.--Kangaroo mice of the subspecies polionotus have the 40-α karyotype. Dorsal pelage color is gray and variable in brightness (Fig. 15 and Appendix F); hairs of the venter are pure white to base. In cranial measurements, these animals are large in maxillary breadth, and small in basal length, bullar length and mandibular length (Fig. 13, Appendix E).

Comparisons.--Comparisons with megacephalus are made in the account of that form. From californicus, this race

APPENDIX H (CONTINUED)

differs in having the 40-α instead of the 40-β karyotype and have grayish rather than buffy dorsal pelage. Further, polionotus is separated from californicus and other subspecies to the north (those forms of the western megasubspecies) by protein analyses (see Fig. 4).

Comments.--This subspecies is variable in size and color: the kangaroo mice are largest and darkest to the north and grade smoothly in characters to lighter colored and smaller kangaroo mice in the south. Genetic data indicate that this subspecies seems to be most closely related to populations of the megacephalus to the east (Fig. 4 and Fig. 8).

Microdipodops megacephalus albiventer Hall and Durrant

1937. Microdipodops pallidus albiventer Hall and Durrant, J. Mamm., 18:357, original description.

1941. Microdipodops megacephalus albiventer, Hall, Field Mus. Nat. Hist., Zool. Ser., 27:263-264.

1941. Microdipodops megacephalus paululus Hall and Durrant, The Murrelet, 22:5.

1941. Microdipodops meagcephalus leucotis Hall and Durrant, The Murrelet, 22:6.

1941. Microdipodops megacephalus megacephalus, Hall, Field Mus. Nat. Hist., Zool. Ser., 27:258-260 (in part).

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Holotype.--Adult male (skin with skull). Museum of Vertebrate Zoology, 52803. Collected by Ward C. Russell on 30 May 1932; original No. 2188.

Type Locality.--Desert Valley, 21 mi. W Panace, 5300 ft., Lincoln Co., Nevada.

Distribution.--Southeastern Nevada (Lincoln and White Pine counties) and western Utah (Tooele, Juab, and Millard counties). See Figure 20.

Diagnosis.--This subspecies is small in most cranial measurements (Fig. 13 and Appendix E) and is buffy to very pale in dorsal pelage color (Fig. 15 and Appendix F). This form is characterized by the 40-β karyotype and has pure white hairs of the venter.

Comparisons.--Comparisons between albiventer and megacephalus are made in the account of that subspecies.

Comments.--The area of geographic distribution of albiventer represents the western margins of the Bonneville Lake region. Kangaroo mouse habitat is this low basin region which are distinctly more arid (low, sparsely vegetated habitats) than those characterizing megacephalus in central Nevada. Specimens from southern White Pine County, Nevada are referred to albiventer largely because of the pure shite hairs of the venter. Specimens from northern and central White Pine County (Steptoe Valley region) seem to represent intergrades (judging by the coloration of the ventral pelage) between albiventer and

APPENDIX H (CONTINUED)

megacephalus.

Microdipodops (megacephalus) californicus

Microdipodops megacephalus californicus Merriam

1901. Microdipodops californicus Merriam, Proc. Biol. Soc. Washington, 14:128, original description.

1941. Microdipodops megacephalus californicus, Hall, Field Mus. Nat. Hist., Zool. Ser., 27:250-251.

1941. Microdipodops megacephalus ambiguus Hall, Field Mus. Nat. Hist., Zool. Ser., 27:252-256 (in part).

Holotype.--Subadult male (skin with skull). United States National Museum of Natural History, 101227. Collected by Walter K. Fisher on 7 August 1900; original No. 1596.

Type Locality.--Sierra Valley, near Vinton, Plumas Co., California.

Distribution.--Southwest of Pyramid Lake (eastern Plumas County, California, and southern Washoe and Ormsby counties, Nevada) and the environs west of the Humboldt River (southeastern Humboldt County and north-central Pershing County, Nevada) in western Great Basin (see Fig. 20).

Diagnosis.--Kangaroo mice of this subspecies share the following derived characters: buffy dorsal pelage color; pure white (to base) hairs of the venter; the 40-β karyotype.

APPENDIX H (CONTINUED)

Comparisons.--The subspecies californicus differs from all adjacent taxa (megacephalus, polionotus, ambiguus, and oregonus) by having the 40-β karyotype (versus the 40-α karyotype). From ambiguus and nexus, this subspecies differs in having pure white hair on the venter, whereas ambiguus shows a slight plumbeous color and nexus shows a distinct plumbeous color at the bases of the belly hairs.

Comments.--Specimens of this subspecies appear rather intermediate in body size and cranial proportions, save the population from near the vicinity of the type locality (Chilcoot, California). These Californian specimens are quite small in most cranial measurements (see Fig. 13 and Appendix E), though agree with other californicus populations in genetic (protein and chromosome) criteria (Fig. 4 and Fig. 8) and colorimetric characters (Fig. 15). The subspecies californicus is polytopic, and positioned on both the northeastern and southwestern flanks of the geographic range of ambiguus (Fig. 20). In the vicinity of southeastern Humboldt County, californicus extends as far west as Jungo and Quinn River. The two subspecies are largely separated from one another here by the Jackson Mountains. In southern Washoe County the subspecies californicus seems to be moderately separated from ambiguus by the hills (Sand Pass) immediately south of the Smoke Creek Desert. Both of these areas seem to be zones of contact between californicus and ambiguus (see discussion

APPENDIX H (CONTINUED)

in text).

Microdipodops megacephalus oregonus Merriam

1901. Microdipodops megacephalus oregonus Merriam, Proc. Biol. Soc. Washington, 14:127, original description.

Holotype.--Subadult male (skin with skull). United States National Museum of Natural History, 80128. Collected by Clark P. Streator on 18 August 1896; original No. 5430.

Type Locality.--Wild Horse Creek, 4 mi. NW Alvord Lake, Harney Co., Oregon. .

Distribution.--Southeastern Oregon (Crook, Lake, Harney and Malheur counties), northwestern Nevada (Washoe and Humboldt counties), and northeastern California (Modoc and Lassen counties). See Figure 20.

Diagnosis.--This subspecies is large in overall body size and cranial measurements (Fig. 13 and Appendix E). Chromosomally, oregonus is characterized by the 40-α karyotype. The dorsal pelage of oregonus is dark (Fig. 15 and Appendix F) and the hair of the venter has distinct plumbeous bases.

Comparisons.--From ambiguus this subspecies differs most notably in having darker dorsal pelage and dark gray bases (instead of light gray bases) of the ventral hair. Comparisons between oregonus and atrirelictus are given in the account of that form.

APPENDIX H (CONTINUED)

Comments.--Populations of oregonus are distributed to the north of ambiguus. Populations of this subspecies may be locally extinct now in Crook County, Oregon due to the adverse effect of human activity including ranching and farming practices.

Microdipodops megacephalus ambiguus Hall

1941. Microdipodops megacephalus ambiguus Hall, Field Mus. Nat. Hist., Zool. Ser., 27:252-256, original description.

1941. Microdipodops megacephalus medius Hall, Field Mus. Nat. Hist., Zool. Ser., 27:256-257.

Holotype.--Adult male (skin with skull), Musuem of Vertebrate Zoology, 73840. Collected by E. Raymond Hall on 25 July 1936; original No. 5285.

Type Locality.--1 1/4 mi. N Sulphur, 4050 ft., Humboldt Co., Nevada.

Distribution.--Western Humboldt, western Pershing, and central Washoe countied in Nevada and eastern Lassen County, California. This distribution is about the Smoke Creek and Black Rock Deserts (Fig. 20).

Diagnosis.--Kangaroo mice of the subspecies ambiguus are pale in dorsal pelage color (Fig. 15, Appendix F) and have a faint plumbeous color at the base of the ventral hairs. This subspecies has the 40-α karyotype.

Comparisons.--Comparisons between californicus and

APPENDIX H (CONTINUED)

oregonus are made in accounts of those subspecies.

Comments.--This subspecies is intermediate in most respects between oregonus to the north and californicus to the east and south. Zones of contact between californicus (at Quinn River Crossing and near Flanigan) have been identified (see discussion in text).

Microdipodops megacephalus nexus Hall

1941. Microdipodops megacephalus nexus Hall, Field Mus. Nat. Hist., Zool. Ser., 27:257, original description.

Holotype.--Adult male (skin with skull) Museum of Vertebrate Zoology, 70917. Collected by Ward C. Russell on 22 May 1936; original No. 4466.

Type Locality.--3 mi. S Izenhood, Lander Co., Nevada.

Distribution.--Extreme northern Lander County and southeastern Humboldt County (Fig. 20).

Diagnosis.--Kangaroo mice of this subspecies are intermediate in general body size and cranial characters (Fig. 13, Appendix E). The dorsal pelage is characterized by large values for tricoefficient x, and small values for reflectance RZ_1 (Fig. 15, Appendix F). The hair of the ventral pelage has plumbeous bases.

Comparisons.--From californicus, this taxon differs in having plumbeous bases on the hair of the venter..

APPENDIX H (CONTINUED)

Comments.--This subspecies is restricted to a small geographic region in the vicinity of Izenhood and Golconda. Specimens from the vicinity east of Golconda seem to indicate intergradation with californicus (see discussion in text). Field reconnaissance of the area about the type locality (Izenhood) indicated that kangaroo mice may be locally extinct.

Microdipodops (megacephalus) atrirelictus

Microdipodops megacephalus atrirelictus new subspecies

Holotype.--Adult female (skin plus skull, frozen tissue, karyotype, skeleton), Museum of Vertebrate Zoology (not yet catalogued). Collected by John C. Hafner on 8 October 1978; original No. 1428.

Type Locality.--11 mi. S, 44.2 mi. W Riddle, 5000 ft., Owyhee Co., Idaho.

Distribution.--Extreme southwestern Owyhee County, Idaho. Known only from the vicintiy of the type locality (see Fig. 20).

Diagnosis.--These kangaroo mice are large in body proportions and cranial measurements (Fig. 13 and Appendix E). This subspecies is distinct from all other kangaroo mice based on protein analyses (Fig. 4). Chromosomally, atrirelictus has the 40-β karyotype. The dorsal pelage of atrirelictus is the darkest of all

kangaroo mice (Fig. 15 and Appendix F).

Comparisons.--From ambiguus, megacephalus, and oregonus this subspecies differs in having the 40-β karyotype, larger overall body size, greater cranial measurements, and darker dorsal pelage color. From californicus, this form differs in having darker dorsal pelage, larger body size and cranial measurements, and plumbeous bases on the hairs of the venter.

Comments.--This subspecies is a highly distinctive form which is isolated along the East Fork of the Little Owyhee River. The form is not common locally and is known from only five specimens.

Microdipodops pallidus

1901. Microdipodops pallidus Merriam, Proc. Biol. Soc. Washington, 14:127, original description.

1926. Microdipodops megacephalus lucidus Goldman, Proc. Biol. Soc. Washington, 39:127.

1927. Microdipodops megacephalus dickeyi Goldman, Proc. Biol. Soc. Washington, 40:115.

1941. Microdipodops megacephalus ambiguus Hall, Field Mus. Nat. Hist., Zool. Ser., 27:252-256 (in part).

Microdipodops (pallidus) pallidus

Microdipodops pallidus pallidus Merriam

1901. Microdipodops pallidus Merriam, Proc. Biol. Soc.

APPENDIX H (CONTINUED)

Washington, 14:127, original description.

1941. Microdipodops pallidus pallidus, Hall, Field Mus. Nat. Hist., Zool. Ser., 27:269-271.

1941. Microdipodops megacephalus ambiguus Hall, Field Mus. Nat. Hist., Zool. Ser., 27:252-256 (in part).

1926. Microdipodops megacephalus lucidus Goldman, Proc. Biol. Soc. Washington, 39:127.

1927. Microdipodops megacephalus dickeyi Goldman, Proc. Biol. Soc. Washington, 40:115.

Holotype.--Adult female (skin with skull), United States National Museum of Natural History, 93520. Collected by Harvy C. Oberholser on 11 May 1898; original No. 101.

Type Locality.--Mountain Well, Churchill Co., Nevada.

Distribution.--Southwestern Pershing County and southeastern Washoe County southward through Esmeralda County, Nevada and into Oasis, Mono County and Deep Spring Valley, Inyo County, California (see Fig. 21).

Diagnosis.--Kangaroo mice of this subspecies have small values for the least expanse of lateral face of zygoma measure, and long nasals (Fig. 13, Appendix E). Dorsal pelage color of this subspecies is characterized by large values for the trichromatic coefficient x, and small values for reflectance RZ_1 (Fig. 15, Appendix F). Chromosomally, pallidus has predominantly the 42-α karyotype; the 42-γ karyotype of pallidus is restricted to

APPENDIX H (CONTINUED)

the small region about the southern end of Pyramid Lake.

Comparisons.--From ruficollaris and restrictus, this subspecies differs in: longer nasals; smaller measurements for the least expanse of lateral face of zygoma; larger values for trichromatic coefficient x (indication of reduced purity in pelage color); and smaller values for pelage reflectance RZ_1 readings. Further, from ruficollaris, pallidus differs in having the 42-α or 42-ϒ karyotypes rather than the 42-β karyotype. Also, pallidus differs from both ruficollaris and restrictus in patterns of protein variability (Fig. 4).

Comments.--This subspecies occupies the largest range of M. pallidus and occurs in the low basin region of western Nevada.

Microdipodops (pallidus) ruficollaris

Microdipodops pallidus ruficollaris Hall

1941. Microdipodos [sic] pallidus ruficollaris Hall, Proc. Biol. Soc. Washington, 54:60, original description.

1941. Microdipodops pallidus ruficollaris (corrected spelling) Hall, Field Mus. Nat. Hist., Zool. Ser., 27:272-273.

1941. Microdipodops pallidus ammophilus Hall, Field Mus.

APPENDIX H (CONTINUED)

Nat. Hist., Zool. Ser., 27:273.

1941. Microdipodops pallidus purus Hall, Field Mus. Nat. Hist., Zool. Ser., 27:273-274.

Diagnosis.--This subspecies of M. pallidus has large values for the least expanse of lateral face of zygoma measurement and short nasals (see Fig. 13 and Appendix E). Dorsal pelage color is characterized by large values of reflectance RZ_1 and small values for the trichromatic coefficient x (Fig. 15 and Appendix F). Chromosomally, ruficollaris possesses the 42-β karyotype (Fig. 6).

Comparisons.--From restrictus, ruficollaris differs in having the 42-β karyotype instead of the 42-α karyotype. Further, protein analyses readily differentiate ruficollaris from restrictus (Fig. 4). Comparison with pallidus are given in the account of that form.

Comments.--The subspecies ruficollaris inhabits the eastern section of the range of M. pallidus. This subspecies abuts the eastern subspecies, pallidus, in the area southeast of Tonopah, Nevada. Kangaroo mice seem to be locally extinct today in this region of potential contact, although they have been captured in this area in the past.

Microdipodops (pallidus) restrictus

Microdipodops pallidus restrictus new subspecies

APPENDIX H (CONTINUED)

Holotype.--Adult male (skin plus skull, frozen tissue, karyotype, skeleton), Museum of Vertebrate Zoology (not yet catalogued). Collected by John C. Hafner on 2 August 1979, original No. 1463.

Type Locality.--8.9 mi. S, 1.2 mi. E Mina, 4400 ft., Mineral Co., Nevada.

Distribution.--Known only from type locality. This population seems to be isolated to a distribution in Soda Spring Valley at the southern end of Rhodes Salt Marsh, and separated from populations of pallidus in Mineral County (Fig. 21).

Diagnosis.--Kangaroo mice of this subspecies have large values for the least expanse of lateral face of zygoma measurement, and short nasals (Fig. 13, Appendix E). Moreover, these kangaroo mice are small in overall cranial measurements, including: greatest length of skull, bullar length, maxillary breadth, and greatest length incisive foramina. With respect to colorimetric characters, restrictus has high values for reflectance RZ_1 and small values for trichromatic coefficient x and purity (see Fig. 15 and Appendix F). This subspecies has the 42-α karyotype.

Comparisons.--Comparisons between restrictus and the other two subspecies of M. pallidus are made in those accounts.

APPENDIX H (CONTINUED)

Comments.--As this subspecies is known from only one seemingly isolated population in southeastern Mineral County, much more collecting is needed to document the extent of its range and potential genetic interactions with pallidus (the neighboring subspecies) should the forms come into contact. Chromosomally, restrictus is similar to pallidus, but biochemically and morphologically it is quite divergent (indeed convergent on the ruficollaris morphology; see Results).