SPECIFIC AND EVOLUTIONARY RELATIONSHIPS OF KANGAROO MICE, GENUS MICRODIPODOPS

by

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A THESIS

IN

ZOOLOGY

Submitted to the Graduate Faculty
of Texas Tech University in
Partial Fulfillment of
the Requirements for
the Degree of

MASTER OF SCIENCE

Approved

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December, 1976

ACKNOWLEDGMENTS

Appreciation is gratefully extended to Drs. J. Knox Jones, Jr., and Hugh H. Genoways for advice during this study and for critical evaluation of the manuscript. Valuable criticism and advice in all phases of the study was provided by Mark S. Hafner, David J. Hafner, and John W. Bickham. I am grateful to Mark S. Hafner, David J. Hafner, and Patti M. Hafner who offered valuable assistance in the field work associated with this study. Dr. Robert J. Baker kindly made his laboratory facilities and field equipment available to me throughout the study. John W. Bickham and Dr. Baker offered their advice and technical help with chromosomal preparations and interpretations. I am indebted to the following individuals who provided identifications and information concerning ectoparasites: Dr. James E. Keirans (ticks), Dr. John M. Kinsella (fleas), Dr. K. C. Emerson (lice). Technical assistance with the preparation of the glans penis and spermatozoa was provided by Stephen L. Williams. Drs. Genoways and William R. Atchley provided guidance in the statistical analyses in the dissertation. Patti M. Hafner kindly performed all clerical tasks. Partial financial support was provided from the Graduate School, Texas Tech University.

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I. INTRODUCTION

Kangaroo mice, less commonly called gnome mice or dwarf kangaroo rats, constitute the rodent genus Microdipodops and are members of the family Heteromyidae. The genus, containing but two species, inhabits the sandy Upper Sonoran desert regions in the Great Basin region of North America. C. Hart Merriam described the genus Microdipodops in 1891 and designated M. megacephalus as the type species. The second species, M. pallidus was described in 1901, also by Merriam. During the ensuing years, several subspecies of Microdipodops were described by various workers (Grinnel, 1914; Goldman, 1926, 1927; Hall and Durrant, 1937, 1941; and Hall 1941a, 1941b). Hall's (1941b) comprehensive revision of the genus culminated an era of active interest in the group. Since 1941, there has been no attempt to reappraise the taxonomy of Microdipodops and only one paper (Schitoskey, 1968) has contributed new information to the systematics of the genus. In fact, little is known of the general life history of these interesting mammals.

One aim of my study was to investigate the specific relationships of the species of Microdipodops. A wide spectrum of techniques were employed including morphometrics, karyology, and study of the glans penis, spermatozoa, baculum, and ectoparasites. Unfortunately, measurements reported in Hall's 1941 revision were generally based on small sample sizes. With adaquate sample sizes, Schitoskey (1968) demonstrated that the variation within one race of M. megacephalus

was considerably greater than indicated by Hall's data, and his findings cast serious doubt on the validity of Hall's entire systematic arrangement. The extent of nongeographical variation must be documented before decisions at the subspecific level can be formulated. With this in mind, a correlary purpose of this study was to document the extent of populational variation in a subspecies representing each species of Microdipodops. Besides documenting such variation, comparisons of characters at the specific level should be useful for further systematic studies.

There remains to date a considerable amount of controversy over the subfamilial affinity of the genus. Is Microdipodops actually more closely related to kangaroo rats, Dipodomys (Dipodomyinae), or to the pocket mice, Perognathus (Perognathinae)? Merriam (1891) in the description of the genus noted: "In external appearance it looks like a heavy, thickset pocket mouse of the Perognathus olivaceus [= parvus] type, with a hydrocephalic head and abnormally large, furry hind feet." Wood (1935) in his treatise on the evolutionary relationships of heteromyids likewise thought Microdipodops was most closely related to Perognathus, particularly the silky pocket mice (subgenus Perognathus). Simpson (1945) followed Wood in his classification of mammals, but Setzer (1949) was disinclined to place Microdipodops with any of the then recognized subfamilies. Reeder (1956), based on an extensive review of both fossil and recent heteromyids, placed Microdipodops in the subfamily Dipodomyinae. Many paleontologists today follow Reeder (for example, Lindsay, 1972) in his interpretation of the phyletic placement of kangaroo mice.

II. METHODS AND PROCEDURES

SPECIMENS

In this study nine species representing three genera of the family Heteromyidae were examined and compared. Species examined include Microdipodops megacephalus, Microdipodops pallidus, Perognathus flavus, Perognathus longimembris, Perognathus intermedius, Perognathus hispidus, Dipodomys merriami, Dipodomys ordii, Dipodomys panamintinus.

The majority of the specimens used were collected by the author using Sherman folding live-traps, although some specimens were collected by other individuals. Specimens of Microdipodops used, as well as specimens of other heteromyids used for comparative purposes, were largely preserved as standard museum skins and skulls. The specimens are deposited at the following institutions: The Museum, Texas Tech University (TTU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum of Southwestern Biology, University of New Mexico (MSB); and the personal collection of Mark S. Hafner (MSH). The abbreviations following each collection are used to identify that collection in the following text. In the course of the study, eight of the 12 holotypes representing the nominal taxa within Microdipodops megacephalus were examined; those not seen included M. m. californicus, M. m. leucotis, M. m. megacephalus, and M. m. oregonus. All holotypes of races of Microdipodops pallidus were examined excepting that of M. p. pallidus.

EXTERNAL AND CRANIAL MEASUREMENTS

All specimens used in this study from which external and cranial mensural data were taken were adults. External measurements used in the morphometric analysis were total length, length of tail, and length of hind foot. Seven cranial measurements were taken on each skull: greatest length, basal length, greatest breadth, nasal length, maxillary breadth, least interorbital breadth, and mandibular length. All cranial measurements follow Lidicker (1960) except that of the mandibular length, which follows Schitoskey (1968). All cranial measurements were taken with dial calipers and were read to the nearest 0.01 millimeter.

GLANS PENES AND BACULA

Glandes used in this study were taken exclusively from freshly killed animals and were preserved immediately in 10 per cent formalin. After approximately two days, the glandes were transferred to 70 per cent ethanol. Only phalli from adult specimens were used because those from sub-adults were found to be underdeveloped and lacking in adult traits such as spines. Detailed drawings of the external morphology of the glandes were made by means of a camera lucida and measurements were taken directly from drawings using dial calipers. All measurements used in the study are in millimeters. Measurements and terminology of the glans penis follow that of Hooper (1958) and Genoways (1973).

To discern the relative placement and morphology of the baculum,

glandes were withdrawn from ethanol and cleared. They were placed in a 2 per cent solution of potassium hydroxide for five days by which time the bacula had become faintly visible. The glandes were then stained in a saturated solution of Alizarine Red for two days. Finally, the glandes were passed through four stages of increasing concentration of glycerine and eventually stored in pure glycerine. Drawings of bacula with respect to the glandes were again made by means of the camera lucida. The entire above sequence of handling and clearing of the glandes follow the precedures outlined by Davis and Gore (1936), Hooper (1958), and Genoways (1973).

SPERMATOZOA

Spermatozoa were obtained by removing a piece of the cauda epididymus from freshly killed specimens. All animals were mature and sexually active with the exception of specimens of Microdipodops megacephalus, which were seasonally inactive and necessitated the administration of gonadotropins (see below) to produce sperm. A small quantity of the epididymal fluid (containing mature spermatozoa) was suspended in 0.9 per cent solution of sodium citrate. Several drops of this solution was then spread on a microscope slide and the slides were air dried, after which they were fixed by dipping them briefly into a solution of one part acetic acid and four parts absolute methenol. The spermatozoa were then stained using the hematoxylin and eosin procedure and cover slips were affixed using Permount.

Spermatozoa were photographed and measurements of the tail

(including neck and midpiece) were taken by means of a curvimeter directly from negatives (4 by 5 inches) where each 1.25 mm equals one micron. Measurements of the length and width of the head were taken by means of dial calipers from enlarged camera lucida drawings. All measurements were converted to microns. Measurements and terminology follow Forman (1968) and Genoways (1973), except for the tail as mentioned above.

Adult Microdipodops megacephalus from which sperm was recovered were sexually inactive (October and November) and were given 0.1 milliliter injections (intraperitoneally) of a follicle-stimulating hormone (FSH) and human chorionic gonadotropin (HCG) solution (200 I U FSH and 100 I U HCG per 0.1 milliliter). One specimen, which eventually produced much sperm, was given eight such injections and was sacrificed 42 days after the initial injection. During the administration of the gonadotropins, a light regime of 14 to 16 hours was maintained and the animals were housed at room temperature.

CHROMOSOME PREPARATIONS

Chromosome preparations from dividing bone marrow cells were made using an in vivo Velban and hypotonic citrate sequence modified from Patton (1967a) and Baker (1970). Inasmuch as Microdipodops is a small rodent, it was at times deemed necessary to flush bone marrow from both the femurs and the tibias to obtain a sufficient quantity of material (the tibia yielded the greater amount). Preparations were stained with Giemsa and cover slips were affixed

with Permount. A mounted slide was then scanned under the microscope and a representative cell was selected and photographed. A minimum of 10 metaphase cells were inspected for each animal included in the study. The diploid number, fundamental number, and chromosome morphology used in the text follow standard methods (Patton, 1967a).

ECTOPARASITES

Microdipodops used in the ectoparasite study were live trapped using Sherman folding traps. Traps were routinely set before dusk and checked at dawn the following morning. Immediately, or as soon as was possible after checking the traps, specimens of Microdipodops were carefully inspected for ectoparasites, often employing the aid of a hand lens of binocular dissecting microscope. Any ectoparasites found were placed in a 70% solution of ethanol and determinations were made by the authorities identified in the acknowlegements section. Specimens of ectoparasites found on Microdipodops are deposited at the Rocky Mountain Laboratory, Hamilton, Montana (RML).

STATISTICAL ANALYSIS

Descriptive statistics were computed using a general program termed SIMPLE. The program was developed by Charles T. Gaskins of Texas Tech University and computes the mean, standard deviation, standard error, coefficient of variation, range, and parameters of skewness and kurtosis. In the analysis only adult specimens were used and sexes were treated separately to ascertain the amount of sexual dimorphism. When two group means were compared (males in

comparison with females), the BMD 01V program was employed. This program employs a single class analysis of variance or ANOVA (F-test) to determine significant differences between means (Sokal and Rohlf, 1969). The significance was set at .05 throughout the study.

Canonical variate analysis was employed to determine the degree of multivariate morphometric divergence between species of Microdipodops. This analysis was performed on the 10 variables listed in the previous section using the BMD-07M stepwise discriminant analysis program. The discriminant analysis program also provided a means by which the discriminatory value of a character could be assessed and thereby ranked according to its discriminatory "ability". Results of the canonical variate analysis are presented graphically using a frequency histogram of the first canonical variable. The BMD-04M two group discriminant analysis program was used to obtain the generalized distance statistic, Mahalanobis D^2. For a discussion of this analysis, see Baker et al. (1972) and Patton (1973).

The 1974 version of the NTSYS program was used to perform the multivariate analysis in the section of evolutionary relationships where the phenetic relationships of the species are discussed. This program was developed by F. J. Rohlf, J. Kishpaush, and D. Kirk at the State University of New York at Stony Brook. In the analysis, OTU's were different species of heteromyids and the characters were mean measurements of coded attributes (see appendices I and II). All characters were standardized. Cluster analysis was based upon both correlation and distance matrices and the principal components analysis were performed using the NTSYS program.

As part of the NTSYS, a character correlation matrix was generated and characters highly correlated with others in the matrix (those usually of a size factor) were eliminated. The final matrix contained 45 characters (Appendix I). Cluster analyses, using UPGMA (unweighted pair-group method using arithmetic averages), were performed on the correlation and distance matrices producing correlation and distance phenograms. The matrix of correlation among character was again employed to extract the first three principal components. A three-dimensional projection of the OTU's (species) onto the first three principal components was drawn using isometric graph paper. Discussions of the mechanics and theory of these tests were given by Sneath and Sokal (1973). These analyses have been used in a similar fashion by Choate (1970) and Genoways (1973) among others.

All univariate and multivariate statistical analyses were executed on the IBM 370-145 computer at Texas Tech University.

III. TAXONOMY

GENUS *MICRODIPODOPS*

1891. *Microdipodops* Merriam, N. Amer. Fauna, 5:115-117, 30 July; type species, *Microdipodops megacephalus* Merriam.

Diagnosis.--Order Rodentia, suborder Myomorpha, family Heteromyidae, subfamily Perognathinae; small heteromyid (adults 130 to 180 mm. in total length); eyes relatively small; pelage silky; ventrad type molt pattern; dorsal skin gland absent; tail slightly longer than body; tail with greater width in middle than at base or tip and with no crest; no median ventral foramina in caudal vertebrae; manus long and slender; pes large, densely haired and with five toes; cuboid-astragalas contact and ectocueiform of hour-glass shape present in tarsus; dental formula 1/1, 0/0, 1/1, 3/3; upper incisor sulcate; cheekteeth hypsodont but not ever-growing; cheekteeth with more than one root except third molars; cusps on cheekteeth soon worn away, leaving a ring of enamel surrounding a lake of dentine; lower premolar (p_4) with X-pattern; H-pattern on lower molars; upper and lower third molars much reduced; skull with relatively most highly inflated auditory bullae of any heteromyid; hamular process of lacrimal projecting free of maxilla; zygomatic process of maxilla reduced; locomotion quadrupedal, quadrupedal saltating, and ricochetal; restricted to the Upper Sonoran Life-zone on areas of vegetated sand in the Great Basin of North America.

Etymology.--The generic name is a combination of *micro-* (small)

di- (two), podo- (foot), and ops (appearance)--all from Greek. The name was appropriately given to describe the appearance of this small mouse with large hind feet.

Comparisons.--The genera Perognathus and Microdipodops comprise the subfamily Perognathinae. Perognathus is separable into two distinctive subgenera, Perognathus and Chaetodipus, and these will be compared separately with Microdipodops. From Perognathus sensu stricto, Microdipodops can be distinguished as follows: cheekteeth higher crowned; H-pattern always present on unworn lower molars; bullae much more highly inflated, so much so as to completely obscure the interparietal; tail having greatest width at midpoint; pes greatly elongated and more densely haired; tendancy towards ricochetal locomotion. In addition to the above discriminating characters, Microdipodops further differs from Chaetodipus as follows: bullae even proportionately larger; pelage silky; tail not crested-penicillate; vertices of sperm head broadly rounded; glans penis long in respect to the length of the baculum (approximately 70 per cent); glans penis with urethral lappets.

Microdipodops differs from the genus Dipodomys in smaller body size and in the following aspects, among others: cheekteeth rooted; occlusal surface of worn molariform teeth showing enamel rings; lower premolar with five or six cusps; upper incisor always sulcate; no pit on mandible behind third molar; bullae more highly inflated; zygomatic region of maxilla reduced; lacrimals projecting free; dorsal skin gland absent; cervical vertebrae usually not fused;

tail wider at midpoint; tail not crested-penicillate; no median ventral foramina in caudal vertebrae; tail without white longitudinal stripes; manus long and slender; halux only slightly reduced, never absent; cuboid-astragalas contact and ectocuneiform of hour-glass shape present in tarsus; white flank stripes absent; diploid number of chromosomes never greater than 42; tip of baculum not strongly upturned; head length of spermatozoa greatly exceeding head width; eyes relatively small.

Comparisons between Microdipodops and the mostly Neotropical heteromyine species are not discussed here and may be found elsewhere (Wood, 1935).

KEY TO SPECIES OF MICRODIPODOPS

1. Occurring in Nevada and marginally in adjacent regions of California, Oregon, Idaho, and Utah (Fig. 1); pterygoids slender (Fig. 7B); incisive foramina divergent posteriorly (Fig. 5); angular process without bifurcation (Fig. 5); 40 chromosomes (Fig. 15); parasitized by Dermacentor parumapertus, Ixodes kingi, Meringis hubbardi, and Ischyropoda furmani; pelage brownish to grayish black; distal portion of tail usually darkened.....Microdipodops megacephalus.

1[1]. Occurring mainly in Nevada and only marginally in California (Fig. 2); pterygoids with broad wings (Fig. 7A); incisive foramina parallel-sided (Fig. 6); angular process modestly bifurcated (Fig. 6); 42 chromosomes (Fig. 16); known to be parasitized only by Dermacentor parumapertus; dorsal pelage pallid buff; distal portion of tail never

darkened.....*Microdipodops pallidus*.

SPECIES ACCOUNTS

Microdipodops megacephalus

Dark Kangaroo Mouse

1891. *Microdipodops megacephalus* Merriam, N. Amer. Fauna, 5:115-117, 30 July.

1901. *Microdipodops californicus* Merriam, Proc. Biol. Soc. Washington, 14:127-128, 19 July.

1914. *Microdipodops polionotus* Grinnell, Univ. California Publ. Zool., 12:301-304, 15 April.

Holotype.--Adult male (skin with skull), United States National Museum (NMNH), 24417/31723, taken on 23 October 1890 by Vernon Bailey, original number 2005.

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

Diagnosis.--Dorsal pellage pale brownish to grayish black; distal portion of tail usually darkened; pterygoids slender; incisive foramina diverging posteriorly; angular process without bifurcation; 40 chromosomes; parasitized by *Dermacentor parumapertus*, *Ixodes kingi*, *Meringis hubbardi*, and *Ischyropoda furmani*; occurs in the upper part of the Upper Sonoran Life-zone of the Great Basin; habitat characterized by the shrubs *Artemesia tridentata* and *Chrysothamnus* sp.

Etymology.--The specific name is a combination of the Greek words *mega*, large, and *cephala*, head. *Microdipodops megacephalus*, the type

species, has, in actuality, a smaller head than the later recognized species Microdipodops pallidus. The large head, though is a generic trait.

Comparisons.--M. megacephalus is the smaller and darker colored of the two species within the genus. In general, all mensural characters of M. megacephalus, both cranial and external (including glans penis), are smaller than those of M. pallidus. Results of the descriminant function analysis comparing the two species showed that mandibular length and hind foot length were the most highly weighted cranial and external characters, respectively. Dorsal pelage varies from pale brownish to grayish black, but generally exhibits, to some extent, a grayish hue. M. pallidus, in contrast, is pallid buff dorsally, lacking any trace of gray. This pelage color difference is of invaluable aid, because it serves as the only character by which the two species can be separated readily in the field. Even at localities of sympatry, pelage color is quite reliable as a diagnostic character.

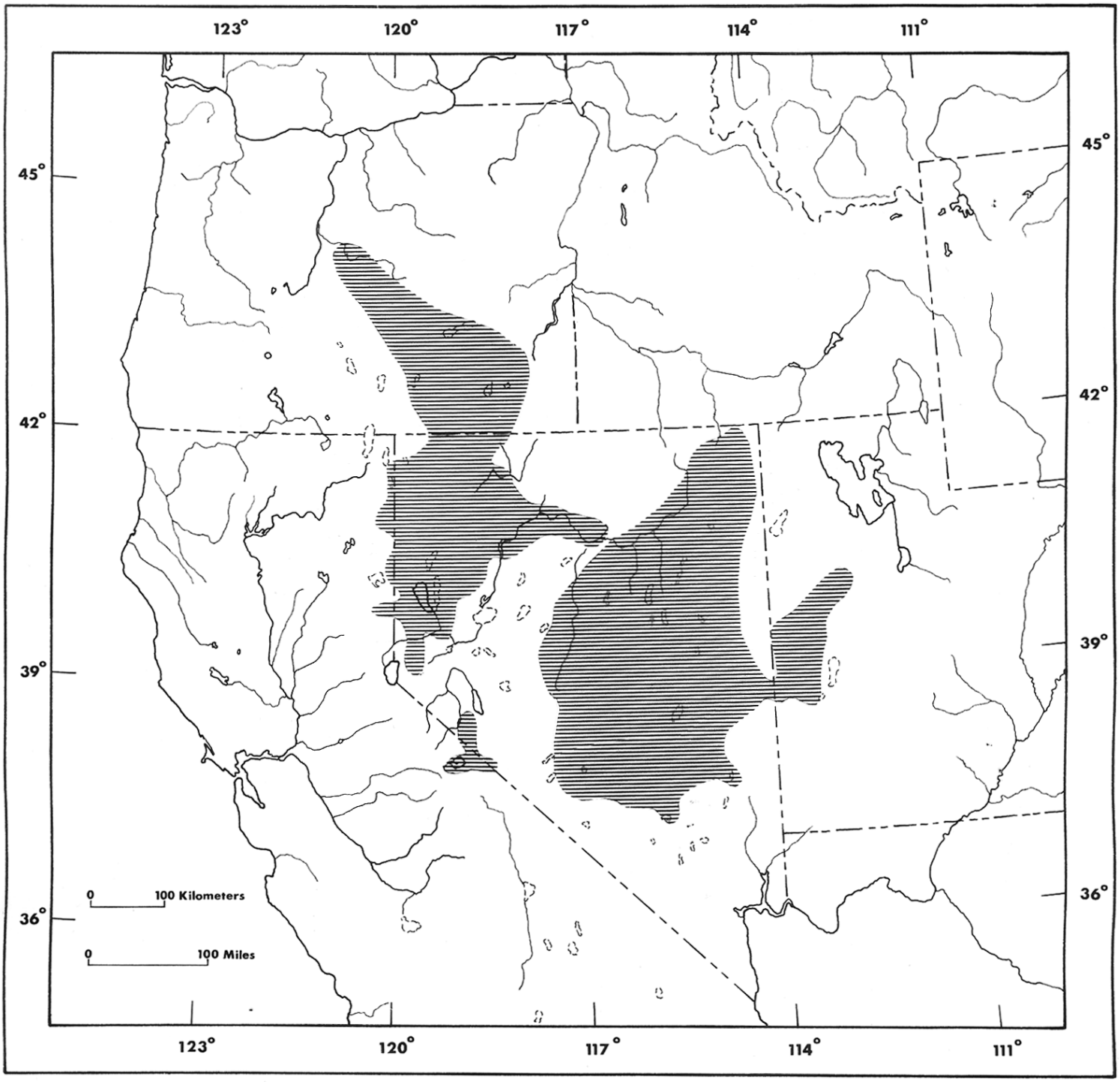
In addition to the overall darker pelage, M. megacephalus usually has the distal sixth to half of the tail decidely darkened. M. pallidus never has this terminal darkening of the tail. Characteristics of the pterygoids, the incisive foramina, and the angular processes, when considered together serve as good cranial characters to distinguish the species. In contrast to the slender pterygoids of M. megacephalus, M. pallidus has broad pterygoid wings. The incisive foramina of M. megacephalus are divergent as compared to the parallel-sided condition in M. pallidus, and the angular process is not split.

Karyotypically, M. megacephalus has 40 chromosomes, whereas M. pallidus has 42. Dermacentor parumapertus, one of four species of ectoparasites known to occur on M. megacephalus, also occurs on M. pallidus, but is the only known ectoparasite of that species. The head of the spermatozoa is considerably larger in M. megacephalus than in M. pallidus, although the shape is similar. M. megacephalus occurs generally in habitat that supports Artemesia tridentata and Chrysothamnus, whereas M. pallidus prefers lower areas featuring an entirely different floristic association.

Geographic Distribution.--Microdipodops megacephalus inhabits a large part of the Great Basin, occurring mainly in Nevada, and marginally in adjacent states of California, Oregon, Idaho, and Utah. The geographic range of the species is shown in Fig. 1. M. megacephalus shows preference for the upper part of the Upper Sonoran Life-zone and is known to occur at elevations up to 7600 feet.

Geographic Variation.--Within the upper part of the Upper Sonoran Life-zone, Microdipodops megacephalus is restricted to xeric, sandy areas about basins. Edaphic conditions favorable to the species are distributed in a discontinuous manner; consequently the species does not occur ubiquitously throughout its geographic range. Rather, it occurs in many disjunct populations that are to varying degrees genetically restricted from one another. Hall (1941b) assessed the amount of geographic variation within M. megacephalus and concluded that 12 subspecies existed. Since that time, there has been no systematic reappraisal of intraspecific variation in this species. Schitoskey (1968),

Fig. 1.--The geographic distribution of the Dark Kangaroo Mouse, *Microdipodops megacephalus* (after Hall, 1941b).


123°
120°
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although, did study nongeographic variation in one subspecies, M. m. megacephalus. He determined that variation was so great in that one race, that it emcompassed variables that supposedly characterize several other described races and that a systematic revision was in order. I concer with Schitoskey that a revision is needed and, in fact, have several manuscripts in preparation that treat intraspecific variation in M. megacephalus. The 12 subspecies, as recognized by Hall (1941b) are as follows:

M. m. albiventer Hall and Durrant, 1937:357; type locality, Desert Valley 21 mi. W Panaca, 5300 ft., Lincoln Co., Nevada.

M. m. ambiguus Hall, 1941b:252; type locality, 1¼ mi. S Sulfur, 4050 ft., Humboldt Co., Nevada.

M. m. californicus Merriam, 1901:128; type locality, Sierra Valley, near Vinton, Plumas Co., California.

M. m. leucotis Hall and Durrant, 1941:6; type locality, 18 mi. SW Orr's Ranch, 4400 ft., Tooele Co., Utah.

M. m. medius Hall, 1941b:256; type locality, 3 mi. S Vernon, 4250 ft., Pershing Co., Nevada.

M. m. megacephalus Merriam, 1891:115; type locality, Halleck, Elko Co., Nevada.

M. m. nasutus Hall, 1941b:251; type locality, Fletcher, 6098 ft., Mineral Co., Nevada.

M. m. nexus Hall, 1941b:257; type locality, 3 mi. S Izenhood, Lander Co., Nevada.

M. m. oregonus Merriam, 1901:127; type locality, Wild Horse Creek, 4 mi. NW Alvord Lake, Harney Co., Oregon.

M. m. paululus Hall and Durrant, 1941:5; type locality, Pine Valley, ½ mi. E headquarters building of Desert Range Exp. Station, U.S. Forest Service, sec. 33, T 25 S., R. 17 W; Salt Lake B. M., Millard Co., Utah.

M. m. polionotus Grinnell, 1914:302; type locality, McKeever's Ranch, 2 mi. S Benton Station, 5200 ft., Mono Co., California.

M. m. sabulonis Hall, 1941a:59; type locality, 5 mi. SE Kawich P.O., 5400 ft., Kawich Valley, Nye Co., Nevada.

Ecology.--Microdipodops megacephalus 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 found in and around basins and is restricted to fine sandy soil, or to sandy soil overlaid with fine gravel that supports 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 a particular floral association. Two composits, basin sagebrush, Artemesia tridentata, and rabbit-brush, Chrysothamnus sp., are the two dominant plants,

and usually one or both occur wherever M. megacephalus is found. Only in marginal areas where megacephalus occurs near the bottom of its altitudinal range do other shrubs assume dominancy. Additionally, it was noted that the bushes are usually one meter or less in height, the spacing between bushes is often two meters or more, and there is a general dearth of annual grasses.

I noted in the course of field work 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, Onychomys leucogaster. In the western part of the range, Dipodomys panamintinus and infrequently Eutamius minimus and Reithrodontomys magalotis are encountered as members of the rodent community, whereas in the south Microdipodops pallidus and Onychomys torridus enter in the faunal list. Ammospermophilus leucurus is occasionally taken throughout the range of M. megacephalus.

Potential predators of Microdipodops megacephalus seen at collecting sites include the coyote, Canis latrans, and the burrowing owl, Speotyto cunnicularia.

Microdipodops pallidus

Pallid Kangaroo Mouse

1901. Microdipodops pallidus Merriam, Proc. Biol. Soc. Washington, 14:127-128, 19 July.

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

Museum (NMNH) 93520, taken on 11 May 1898 by Harry C. Oberholser, original number 101.

Type locality.--10 mi. E Stillwater, near Sink of the Humboldt and Carson (according to Vernon Bailey, the locality is Mountain Well, Hall, 1941b), Churchill Co., Nevada.

Diagnosis.--Dorsal pelage pallid buff; venter always white to base of hairs; tail never darkened distally; wings of the pterygoids broad; incisive foramina parallel-sided; angular process with bifurcation; 42 chromosomes; ectoparasites uncommon, Dermacentur parumapertus the only species known; occurs zonally below areas that support Artemesia tridentata in the lower part of the Upper Sonoran Life-zone of the Great Basin; characteristic shrubs include Grayia spinosa, Eurotia lanata, Atriplex sp. and Sarcobatus sp.

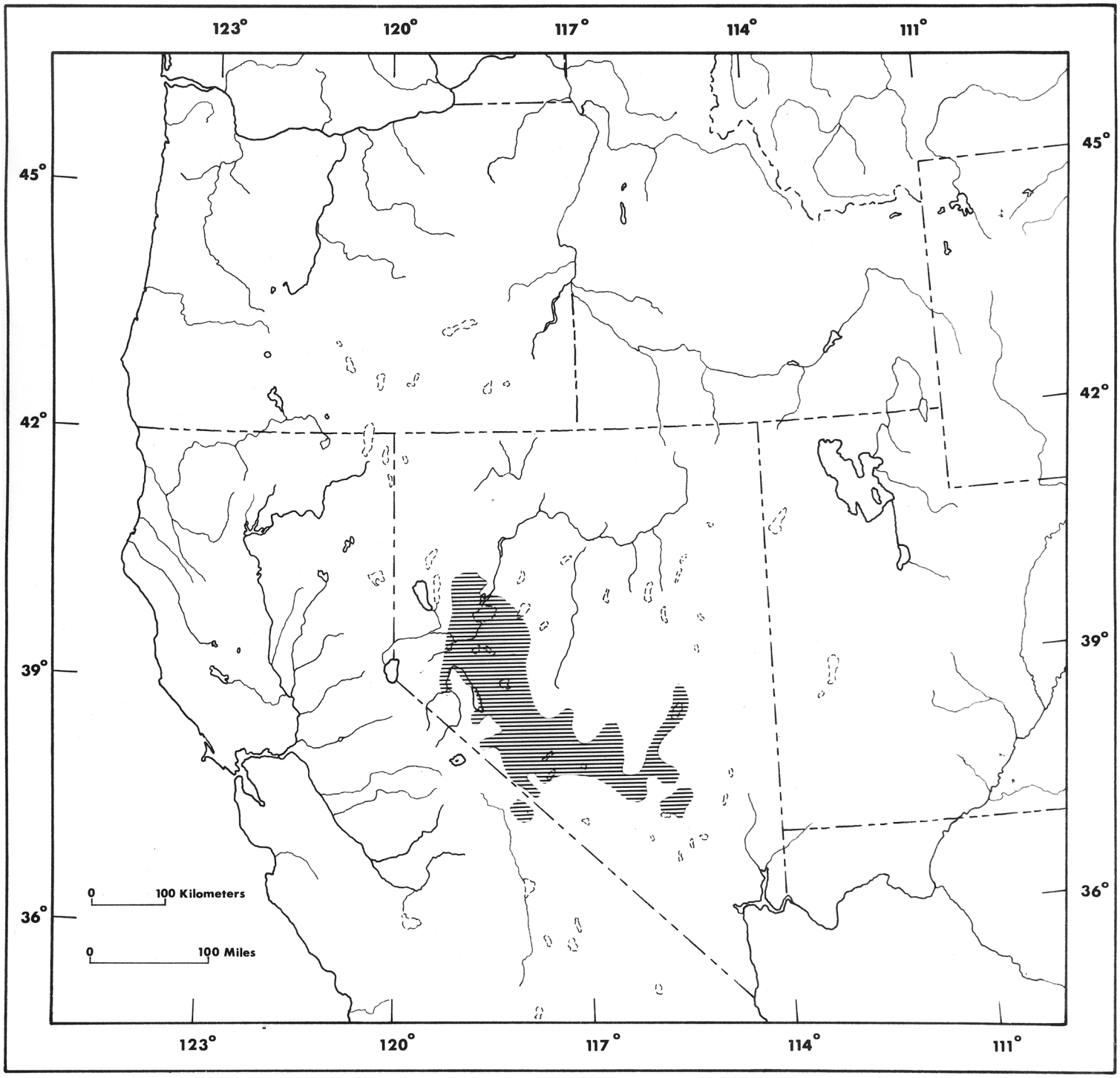
Etymology.-- The specific name pallidus, in reference to the pale color of the pelage, is of Latin origin.

Comparisons.--For comparisons with Microdipodops megacephalus see account of that species.

Geographic Distribution.--The geographic distribution of Microdipodops pallidus is shown in Fig. 2. This species occurs in the lower portion of the Upper Sonoran Life-zone in Nevada and only marginally in California. M. pallidus is recorded occurring as low as 3900 feet (Hall, 1941b) and I have taken the species up to 6000 feet in elevation.

Geographic Variation.--The geographic distribution of Microdipodops

Fig. 2.--The geographic distribution of the Pallid Kangaroo Mouse, Microdipodops pallidus (after Hall, 1941b).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0 100 Kilometers
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pallidus is quite discontinuous over the known range of the species, although the geographic range is about one-third that of M. megacephalus. Interestingly, only a third the number of geographic races have been described for M. pallidus as for M. megacephalus. The four subspecies recognized by Hall (1941b) are as follows:

M. p. ammophilus Hall, 1941b:273; type locality, Able Spring, 12½ mi. S Lock's Ranch, Railroad Valley, 5000 ft., Nye Co., Nevada.

M. p. pallidus Merriam, 1901:127; type locality, 10 mi. E Stillwater, near Sink of the Humboldt and Carson, (Mountain Well according to Vernon Bailey -- Hall, 1941b), Churchill Co., Nevada.

M. p. purus Hall, 1941b:273; type locality, 14½ mi. S Groom Baldy, Lincoln Co., Nevada.

M. p. ruficollaris Hall, 1941a:60; type localtiy, 5 mi. SE Kawich P.O., 5400 ft., Kawich Valley, Nye Co., Nevada.

Ecology.--Within the Great Basin, Microdipodops pallidus is restricted to the lower part of the Upper Sonoran Life-zone and has been found from elevations of from 3900 to 6000 feet. The 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. The mice, generally, inhabit areas of virtually wind-blown sand, that are stabilized by sparce vegetation. At localities where Microdipodops pallidus is sympatric with Microdipodops megacephalus, the mice are known to occur on an overall firmer soil of sand mixed with gravel, away from the basin bottoms. In any event, 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 in North America. These mice do not tolerate appreciable variation in their preferred habitat, a fact that can be appreciated only by field experience. The lower part of the Upper Sonoran Life-zone (where M. pallidus occurs) supports a flora that forms a zonal position lower than areas supporting Artemesia tridentata and is, therefore, floristicly distinct from most areas inhabited by M. megacephalus. Only at localities of sympatry does M. pallidus occur with Artemesia. Dominant shrubs characteristic of Microdipodops pallidus habitat include Grayia spinosa, Eurotia lanata, Atriplex sp., and Sarcobatus sp. All four genera are members of the goosefoot family (Chenopodiaceae) and are halophytes. Excluding Sarcobatus, the shrubs are generally less that a meter in height and are widely spaced. Often over the entire area, the vegetation is no more than a third of a meter in height. The habitat is also nearly devoid of annual grasses and certainly lacks any grass covering.

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

that could potentially prey upon pallid kangaroo mice are the coyote, the kit fox (Vulpes macrotis), the burrowing owl, the great horned owl (Bubo virginiana), and the gopher snake (Pituophis melanoleucus).

IV. SPECIFIC RELATIONSHIPS

MORPHOMETRICS

Since the pioneering study by Hall (1941b) only one paper has appeared in which the morphometric analysis of Microdipodops has been treated. Schitoskey (1968) described the intrapopulation variation in M. m. megacephalus and employed standard descriptive statistics. Unfortunately, mensural data were given only minimal statistical consideration in Hall's (1941b) revision and his sample sizes were quite small. Schitoskey's work revealed that the variation found in the one race he investigated encompassed the range of variation of several other subspecies as detailed by Hall (1941b) and, therefore, cast serious doubt on the entire systematic scheme employed by Hall.

Before taxonomic decisions concerning geographic variation of a species can be made, the extent of nongeographic variation must be delimited. Nongeographic variation is composed of the variation due to age, secondary sexual features, and differences among individuals. A sample representing each species of Microdipodops was collected for this part of the study--M. m. nasatus and M. p. pallidus (the subspecies pallidus, aside from being the nominate subspecies, has the largest geographic range of any race in the species). The intent of the investigations in this section is: 1) to estimate parametric values for 10 morphological characters within a sample of each species of Microdipodops; 2) to determine characters that show least individual

variation and, therefore, are most useful for taxonomic decisions in a systematic study of the genus; and 3) to gain insight into the morphological relationships between the two species.

Specimens were assigned to age classes following primarily Lidicker (1960) and Schitoskey (1968). Each individual was placed in one of three age catagories according to the following scheme: "juvenile," with permanent dentition absent (third molar not erupted) or incomplete (presence of a deciduous fourth premolar); "subadult," having complete permanent dentition, cheekteeth showing only slight wear and auditory bullae tending to be opaque; "adults," with occlusal surface of each cheektooth worn to the extent that a ring of enamel surrounded a lake of dentine and auditory bullae translucent. An analysis of morphological variation due to age could not be made because only a few subadult and juvenile kangaroo mice were collected at each locality. Therefore, the kangaroo mice used in this study were exclusively adults.

Univariate Analysis

Measurements and descriptive statistics for Microdipodops megacephalus nasutus and Microdipodops pallidus pallidus are presented in Tables 1 and 2. It can be seen upon inspection of these tables that Microdipodops megacephalus nasutus averages smaller than does Microdipodops pallidus pallidus in all external and cranial measurements except nasal length.

Taxonomic decisions based upon meager sample sizes are often

Table 1.--External and cranial measurements and descriptive statistics for Microdipodops megacephalus nasutus. Means for males and females that are not significantly different at $P < .05$ are marked NS.

Measurements and sex	N	Mean ± 2 SE	Range	CV	F_s F
Total Length					
Male	24	155.33 ± 1.98	(148.00-170.00)	3.12	0.26 NS
Female	17	154.51 ± 3.32	(140.00-164.00)	4.43	4.09
Tail Length					
Male	24	84.46 ± 1.40	(78.00-90.00)	4.07	0.03 NS
Female	17	84.71 ± 2.97	(74.00-96.00)	7.23	4.09
Hind Foot Length					
Male	24	24.63 ± 0.35	(23.00-26.50)	3.50	0.99 NS
Female	17	24.35 ± 0.42	(23.00-26.00)	3.54	4.09
Greatest Skull Length					
Male	24	28.08 ± 0.24	(26.38-29.29)	2.13	0.01 NS
Female	17	28.06 ± 0.32	(26.95-29.31)	2.33	4.09
Basal Length					
Male	24	18.20 ± 0.13	(17.75-18.78)	1.96	0.90 NS
Female	17	18.31 ± 0.22	(17.51-19.19)	2.45	4.09
Greatest Skull Breadth					
Male	24	18.61 ± 0.20	(17.27-19.62)	2.64	0.65 NS
Female	17	18.50 ± 0.18	(17.96-19.33)	1.97	4.09
Nasal Length					
Male	24	9.94 ± 0.10	(9.36-10.42)	2.55	0.92 NS
Female	17	10.04 ± 0.20	(9.22-10.70)	4.19	4.09

Table 1.--Continued.

Measurements and sex	N	Mean ± 2 SE	Range	CV	F_s F
Maxillary Breadth					
Male	24	11.70 ± 0.15	(10.78-12.41)	3.23	1.37 NS
Female	17	11.84 ± 0.17	(11.42-12.68)	2.92	4.09
Least Interorbital Breadth					
Male	24	6.51 ± 0.06	(6.19-6.76)	2.30	1.06 NS
Female	17	6.58 ± 0.13	(6.12-7.17)	3.94	4.09
Mandibular Length					
Male	24	10.13 ± 0.08	(9.73-10.47)	2.03	0.29 NS
Female	17	10.17 ± 0.12	(9.72-10.71)	2.33	4.09

Table 2.--External and cranial measurements and descriptive statistics for Microdipodops pallidus pallidus. Means for males and females that are not significantly different at $P < .05$ are marked NS.

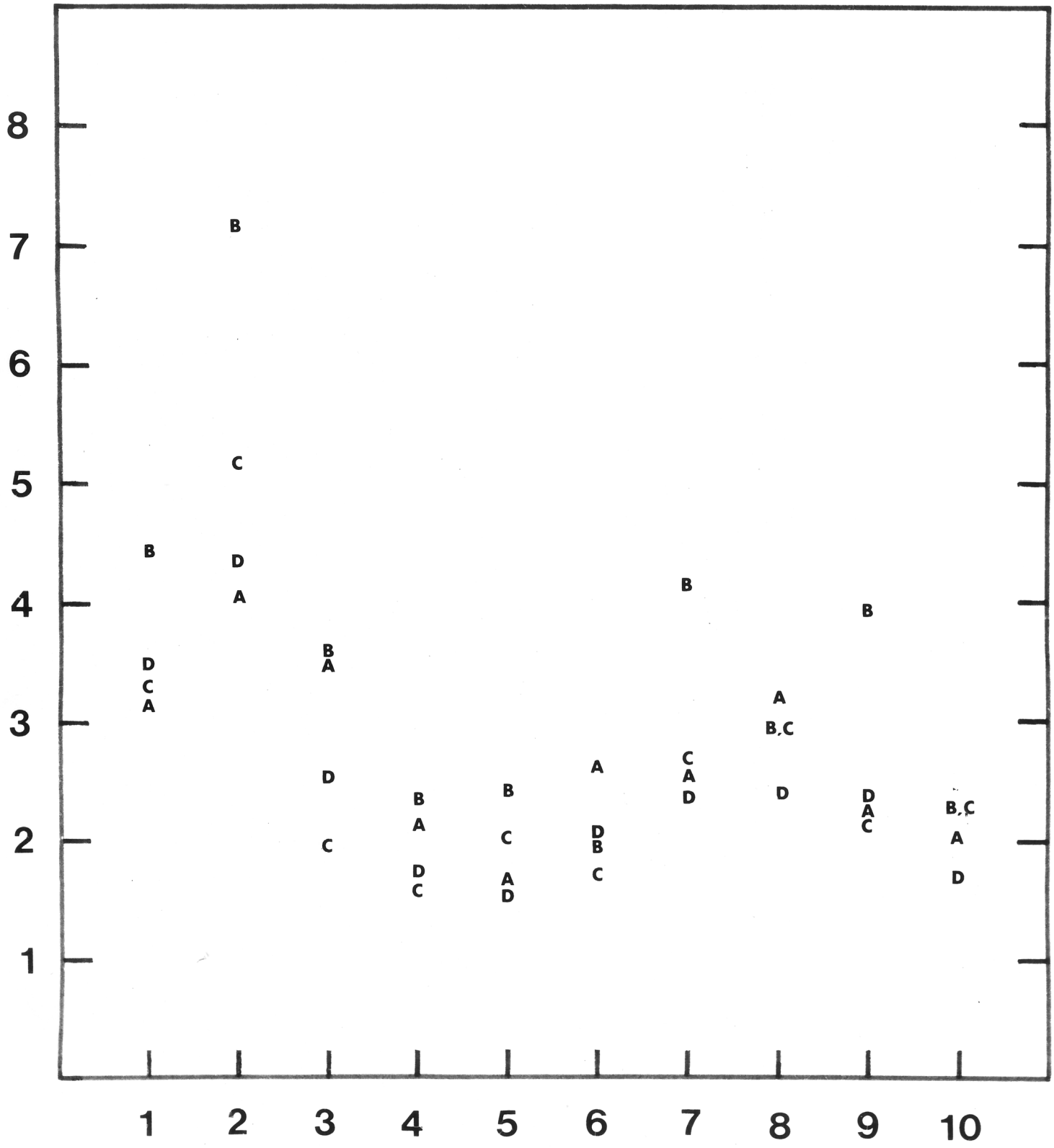
Measurements and sex	N	Mean ± 2 SE	Range	CV	F_s F
Total Length					
Male	15	156.00 ± 2.63	(146.00-162.00)	3.27	0.53 NS
Female	14	157.43 ± 2.90	(145.00-166.00)	3.45	4.21
Tail Length					
Male	15	86.40 ± 2.33	(79.00-93.00)	5.23	0.00 NS
Female	14	86.43 ± 2.00	(79.00-91.00)	4.32	4.21
Hind Foot Length					
Male	16	25.69 ± 0.26	(25.00-26.50)	1.99	0.93 NS
Female	14	25.89 ± 0.35	(24.50-26.50)	2.53	4.20
Greatest Skull Length					
Male	16	28.72 ± 0.23	(28.06-29.42)	1.60	0.42 NS
Female	14	28.61 ± 0.27	(27.21-29.36)	1.74	4.20
Basal Length					
Male	16	18.54 ± 0.19	(18.06-19.23)	2.04	0.59 NS
Female	14	18.64 ± 0.15	(17.91-19.14)	1.53	4.20
Greatest Skull Breadth					
Male	16	19.32 ± 0.17	(18.63-19.82)	1.73	0.19 NS
Female	14	19.38 ± 0.21	(18.78-20.23)	2.06	4.20
Nasal Length					
Male	16	9.92 ± 0.13	(9.31-10.34)	2.71	0.04 NS
Female	14	9.90 ± 0.13	(9.26-10.24)	2.40	4.20

tenuous and this appears to be the case with several subspecies of Microdipodops. For example, a diagnostic character of Microdipodops megacephalus nasutus is reportedly its long hind foot, which has been recorded as averaging 25.3 mm. (Hall, 1941b). Using adequate sample sizes (Hall's data was based on only four individuals), a hind foot length of nearly one millimeter less is here shown to be the case (Table 1), and should prove a better estimate of the parametric mean. The taxonomic status of this particular race will be treated in another paper (in preparation). The original statistical data presented for Microdipodops pallidus pallidus (Hall, 1941b) is somewhat reliable as a sample size of 20 individuals was used.

Cockrum (1954) in his study of Peromyscus leucopus stated that measurements yielding a low coefficient of variation (CV averaging less than 3.10) might prove most useful for studies of geographic variation. Measurements with a low CV do not necessarily vary geographically; yet, should geographic variation exist in these characters, such differences could be readily documented statistically.

Individual variation in Microdipodops megacephalus nasutus.--For the three external measurements used (Table 1) the range of coefficients of variation were from 3.12 (total length for males) to 7.23 (tail length for females). In all three measurements, values for females were higher than those for males. Values for the seven cranial measurements range from 1.69 (basal length for males) to 4.19 (nasal length for females). Females were less variable than males

Fig. 3.--Coefficients of variation (along the ordinate) of external and cranial measurements used in this study. The measurements along the abscissa are as follows: 1, total length; 2, tail length; 3, hind foot length; 4, greatest skull length; 5, basal length; 6, greatest skull breadth; 7, nasal length; 8, maxillary breadth; 9, least interorbital breadth; 10, mandibular length. The plotted letters refer to the taxa as follows: A, Microdipodops megacephalus (males); B, Microdipodops megacephalus (females); C, Microdipodops pallidus (males); D, Microdipodops pallidus (females).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presented in Fig. 3 are well within the range of those found in rodents in general (Long, 1968, 1969, 1970) and in heteromyids in particular (Lidicker, 1960; Schitoskey, 1968; Schmidly, 1971; Genoways, 1973). In the two species of Microdipodops studied, external measurements varied more than did cranial measurements, undoubtedly resulting from the fact that external measurements are inherently the more variable, and they cannot be taken as accurately as cranial measurements or with the precision. Most values for cranial measurements of Microdipodops megacephalus nasutus are less than 3.00. These seven cranial measurements, therefore, should prove most useful in studies of geographic variation as they vary only slightly. For Microdipodops pallidus pallidus, all coefficients of variation for the seven cranial measurements and for length of hind foot are less than 3.00; similarly, these measurements should be of value in studies of geographic variation. Microdipodops pallidus is generally less variable than Microdipodops megacephalus in all measurements studied (Fig. 3). Interestingly, Hafner and Hafner (1975) found M. pallidus also to be behaviorally less variable than Microdipodops megacephalus. Lastly, there is in Microdipodops pallidus, in contrast to Microdipodops megacephalus, little sexual difference in the magnitudes of the coefficients of variation.

Secondary sexual variation.--To ascertain whether the sexes of each species were significantly different in size, mean values for adult males were tested against those for adult females using the single classification ANOVA. Results of these tests are presented in Talbes 1 and 2. The

mean values for males of Microdipodops megacephalus nasutus were slightly larger than those for females in two external and two cranial measurements and smaller in one external and five cranial measurements. For Microdipodops pallidus pallidus the males were larger in only four cranial measurements and smaller in three external and three cranial measurements. In both taxa studied, though, the sexes were not significantly different in any of the measurements used. Schitoskey (1968), in his study of nongeographic variation of Microdipodops megacephalus megacephalus found significant sexual dimorphism in only one measurement, zygomatic breadth, of 25 studied. Zygomatic breadth was not employed in the present study. In light of the absence of significant sexual dimorphism, it is concluded that sexes should be combined and treated together in future systematic studies employing the measurements herein used.

Significant sexual variation in size is not commonly known in heteromyid rodents although few species have been thoroughly studied. Instances of sexual dimorphism have been documented statistically for Liomys (Genoways, 1973) and Dipodomys (Lidicker, 1960; Genoways and Jones, 1971; Schmidly, 1971). Apparently, Perognathus has only slight sexual variation in size (Hall, 1946) and in this respect seems to agree with the genus Microdipodops.

Multivariate Analysis

To ascertain the morphological relationship between the two species of Microdipodops, a two-group discriminant analysis (BMD-04M) and

a stepwise discriminant function analysis (BMD-07M program) were employed. These programs determine the extent of multivariate morphological difference between the species, employing two interrelated tests--discriminant function and canonical variate analyses. The sexes were treated together in the analysis.

Most important to this study of the specific relationships of Microdipodops is a determination of the relative value of the 10 mensural characters in discriminating between the two species. The stepwise discriminant analysis program permits an ordering of the variables by their discriminatory ability. Characters that provide minimal within-sample variance, yet maximal between-sample variance are good discriminators and have high taxonomic weight. The ranked order of measurements according to their discriminatory power in decreasing order is as follows: 1) mandibular length; 2) basal length; 3) least interorbital breadth; 4) nasal length; 5) hind foot length; 6) total length; 7) greatest skull breadth; 8) greatest skull length; 9) tail length; 10) maxillary breadth.

The canonical variate analysis often is used in solving systematic problems at areas of sympatry. Such analysis, for example, has been used to compare possible hybrids to either reference sample (Patton, 1973) and to separate closely related taxa (Baker et al., 1972). In the present study, the analysis was performed on samples of Microdipodops megacephalus nasutus and M. p. pallidus taken from areas of allopatry. These allopatric samples were chosen so that the extent of morphologic divergence between them could be ascertained

and the results could serve as a basis for future studies at sympatric areas where character divergence may be involved.

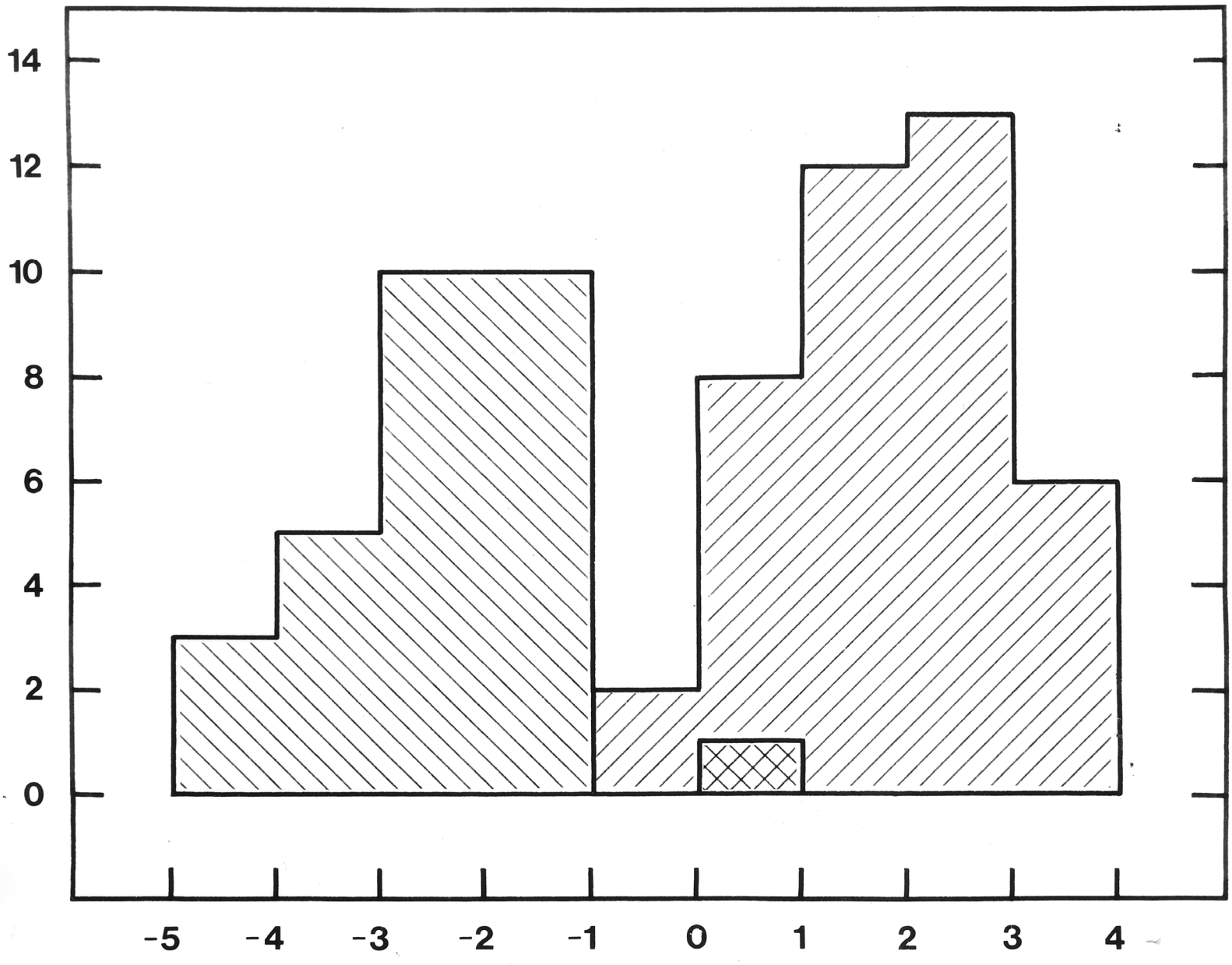
In the analysis one discriminant function achieves separation of the two groups. Standardized coefficients for the first eigenvector are given in Table 3. These standardized values indicate the relative contribution of each measurement to the vector (Baker et al., 1972). In the first canonical variate, the standardized coefficients indicate that mandibular length and basal length are overwhelmingly responsible for the variation along this vector. These results agree with the stepwise analysis.

A histogram of the first canonical variate is presented in Fig. 4 and illustrates the phenetic relationship between the two species. The square root of the Mahalanobis generalized distance statistic (D^2) was found to be 4.17. The null hypothesis ($D^2=0$) of no morphometric divergence among the species of Microdipodops was rejected at $P < .001$ ($F=25.648$, degrees of freedom = 10 and 59). The multivariate morphological divergence between the two centroids appears slight, and most of the difference between them appears to be in size (Tables 1, 2, and 3). Posterior probalilities were used to construct an identification matrix which determines the amount of phenetic overlap between the species based on the 10 characters. The classification matrix indicates that the taxa are separable and that only two of the 70 individuals (2.86 per cent) were "misclassified" in the analysis. Only the two best discriminating characters, mandibular length and basal length were needed to achieve this high level of identification. Mandibular length alone was able to correctly identify all but five

Table 3.--Standardized canonical variate coefficients for the first eigenvector.

Measurement	I
Total Length	0.3510
Tail Length	-0.1551
Hind Foot Length	-0.2493
Greatest Skull Length	0.2326
Basal Length	0.6996
Greatest Skull Breadth	-0.3692
Nasal Length	0.3792
Maxillary Breadth	0.0368
Least Interorbital Breadth	-0.3404
Mandibular Length	-1.1983

Fig. 4.--Histogram of the first canonical variate (abscissa). Frequency of individuals is along the ordinate. Microdipodops pallidus is distributed to the left, and Microdipodops megacephalus to the right.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individuals (7.14 per cent).

Conclusions.--Clearly mandibular length and basal length are characters of high taxonomic weight, as they are good discriminators between the "homeomorphic" species of Microdipodops. The phenetic divergence between the species seems slight; overlap was only 2.86 per cent. One hundred per cent accuracy in classification using standard cranial and external morphometrics is not assumed; unlike morphometric characters, certain other characteristics, for example chromosomes, are irrefutable classificatory agents. Additionally, inasmuch as the two species of Microdipodops closely resemble each other morphologically, it may be difficult in future studies to identify supposed hybrids (see Hall, 1941b) on purely morphometric grounds using the canonical variate analysis. However, in sympatric situations, the degree of similarity perhaps would not be so great as shown here.

Specimens of Microdipodops used in this morphometric study are as follows: M. megacephalus, Fletcher, 6098 ft., Mineral Co., Nevada, 34 (MVZ) and ¼ mi. N Fletcher, 6100 ft., Mineral Co., Nevada, 7 (MVZ); M. pallidus, 17 mi. S, 5 mi. E Yerington, 5000 ft., Lyon Co., Nevada, 30 (TTU).

QUALITATIVE CRANIAL CHARACTERS

Qualitative cranial characters of interest here are those characters that help to discriminate between the species. Probably no single character can satisfactorily separate the taxa over the entire geographic range of the genus, but when characters are considered

together discrimination is achieved.

Hall (1941b:244) stated that the two races M. m. megacephalus and M. m. sabulonis, in comparison with all subspecies of M. pallidus, differed, among other characters, in having the "...nasals extending posteriorly quite or almost as far as do premaxillae rather than extending posteriorly to a point considerably short of that reached by premaxillae." He further indicated that the character does not hold everywhere for the other 10 subspecies of M. megacephalus. Yet, the nasals-premaxillae relationship was used as a diagnostic character of M. megacephalus in the key to species of the genus in Hall and Kelson (1959:508). Furthermore, and to complicate matters, the M. megacephalus skull (MVZ 70942) from Winzell, Nevada, given to illustrate the species in Hall (1941b), Hall (1946), Hall and Kelson (1959), and O'Farrell and Blaustein (1974a) is in fact atypical in the nasals-premaxillae relationship, even when compared to other specimens in the series from Winzell. Admittedly, there may exist in some races of M. megacephalus the tendancy for the nasals to project back near the posterior end of the premaxillae, but the relationship appears to serve only as a weak diagnostic character of the species. Ingles (1965) however, quantified the nasals-premaxillae relationship, (premaxillae extending less than a millimeter beyond the nasals in M. megacephalus and well beyond them in M. pallidus), and used it as a diagnostic character for kangaroo mice in eastern California and Oregon.

Several other characters including the incisive foramina, the

pterygoids, and the angular process seem to be conservative and reliable diagnostic features over the entire range of the genus. The specific difference in the shape of the incisive foramina was first mentioned by Hall (1941b). From Figs. 5 and 6 it can be seen that the sides of the incisive foramina are divergent posteriorly in M. megacephalus, whereas they are parallel-sided in M. pallidus. The shape of the pterygoid bones also is quite diagnostic as can be seen in Fig. 7. The wings of the pterygoids are slender in M. megacephalus and quite expanded in M. pallidus. And lastly, the angular process of the dentary is bifurcated in M. pallidus, but this condition is mostly absent in M. megacephalus (Figs. 5 and 6).

The three diagnostic characters mentioned above (incisive foramina, pterygoids, angular process) are related to, or are components of, the masticatory apparatus and it appears that the functional significance of such noted differences between the species is explained by differential food habits. The incisive foramina for instance, is known to be a passageway connecting the mouth with the vomeronasal organ (Jacobson's organ), and serves in a "mouth-smelling" function. The observed differences in the incisive foramina between the species could indicate a differential ability to discriminate among food items. The pterygoid bones and the angular process serve as anchorage points for the important adductor muscles of the jaw, the pterygoideus and the masseter muscles. Modification of these osseous elements signals divergence in masticatory habits. Although the dentition of Microdipodops was given only cursory attention in the present study, dental differences between the species appear to be absent, except that

Fig. 5.--Dorsal and ventral views of the skull and lateral aspect of the dentary of Microdipodops megacephalus (TTU 24663, 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 lower right is ten millimeters long.

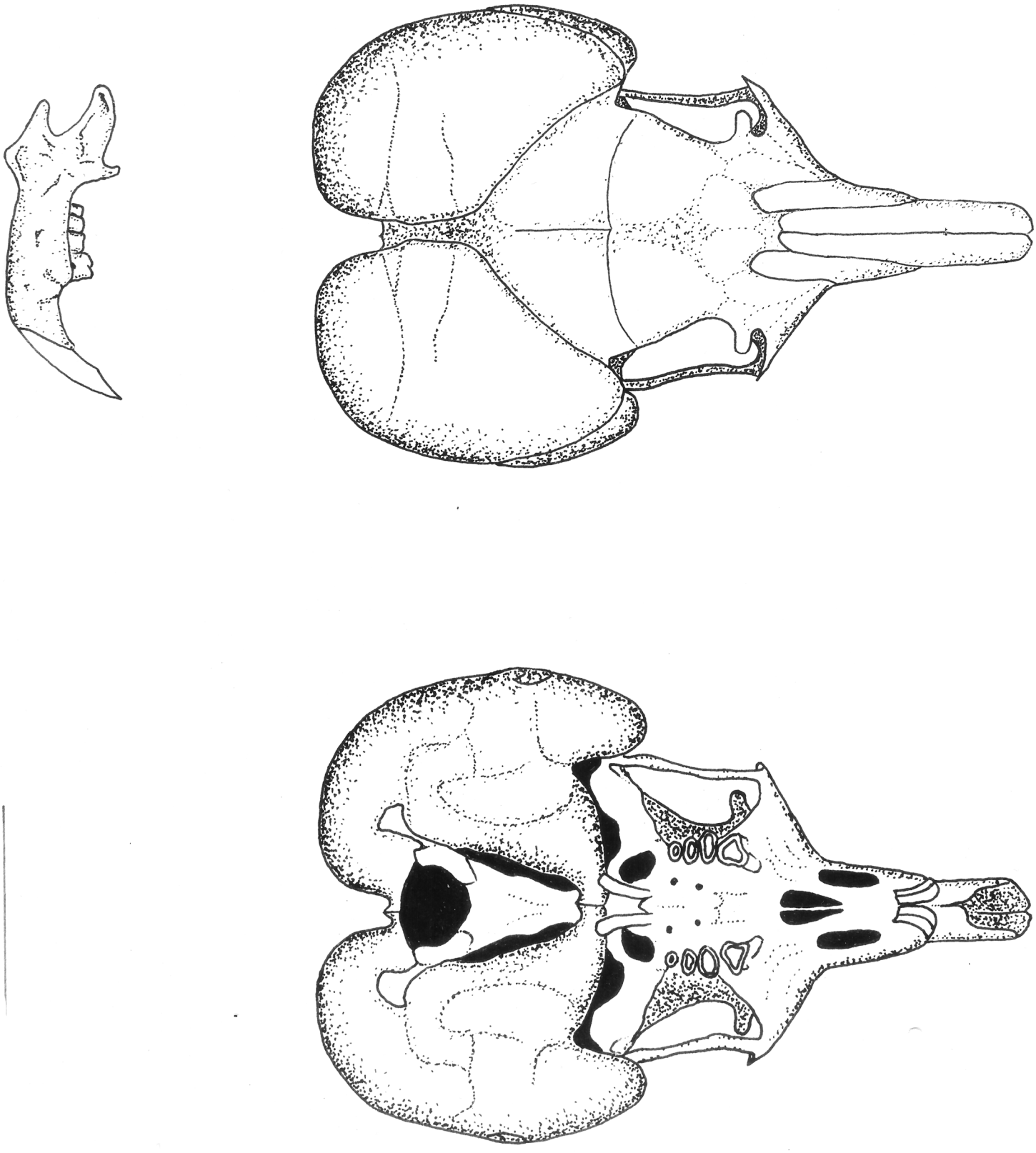


Fig. 6.--Dorsal and ventral views of the skull and lateral aspect of the dentary of Microdipodops pallidus (TTU 24696, 17 mi. S, 5 mi. E Yerington, 5000 ft., Lyon Co., Nevada). The scale at the lower right is ten millimeters long.

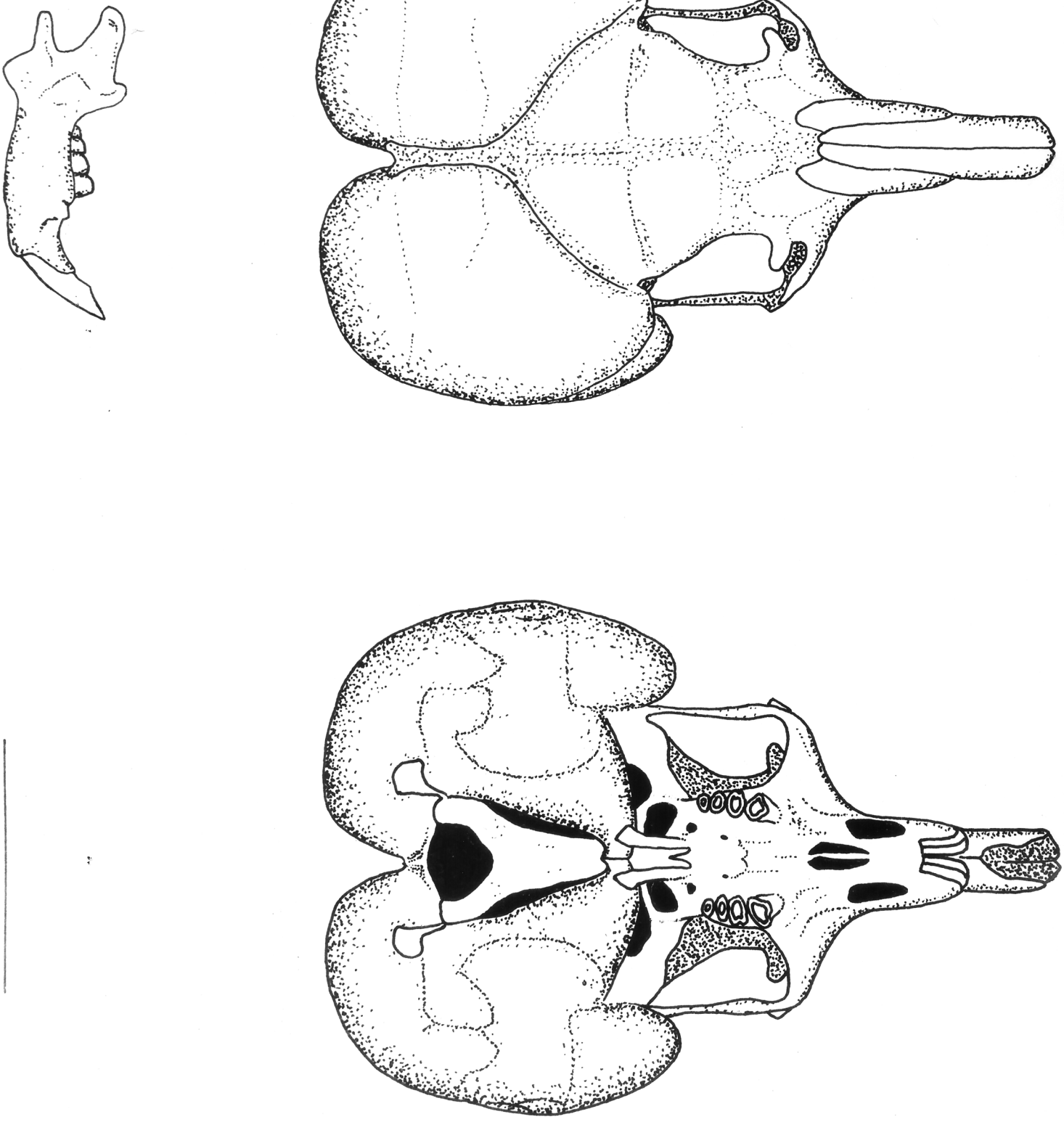
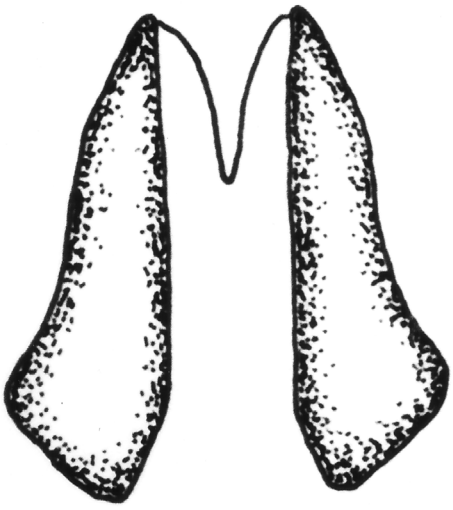
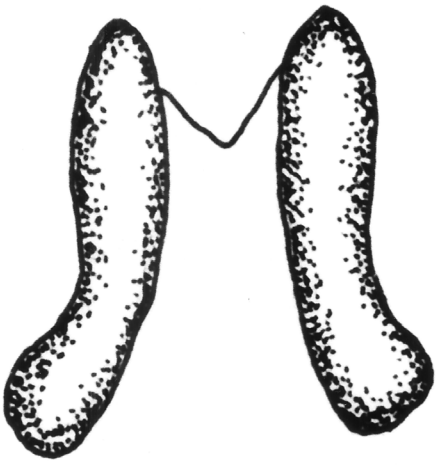


Fig. 7.--Expansion of the wings of the pterygoids in Microdipodops. A, M. pallidus (TTU 24702, 17 mi. S, 5 mi. E Yerington, 5000 ft., Lyon Co., Nevada); B, M. megacephalus (TTU 24654, 2.5 mi. NE Larkin Lake, Alkali Valley, 21.5 mi. S, 10.5 mi. W Hawthorne, 6860 ft., Mineral Co., Nevada). The scale at the right is two millimeters long.



A



B

M. pallidus may have slightly larger molars.

The diet of kangaroo mice has not been thoroughly studied. Only brief statements detailing the cheekpouch contents of several individuals of each species are in the literature (Hall and Linsdale, 1929; Bailey, 1936; Hall, 1941b; Hall, 1946). The osteological evidence is clear and inasmuch as the species do favor different floral associations, it appears quite reasonable that the mice may have dissimilar diets.

Conclusions.--Three qualitative characters, incisive foramina, pterygoid bones, and the angular process, were found to be quite reliable in specific determinations between the two species over the entire geographic range of the genus. Conversely, the relationship between the nasals and the premaxillary bone appears to be a relatively unreliable diagnostic trait. It should be stressed that determinations be made with consideration of all three diagnostic characters, and whenever possible, the utilization of pelage characters and ansillary data. All three characters, coincidentally, do indicate differential food habits between the species.

MORPHOLOGY OF THE GLANS PENIS

The glans penis has been shown to be a valuable tool in systematic studies of rodents (Hooper, 1958, 1959, 1960, 1961, 1962; Hershkovitz, 1966; Lidicker, 1968; and others) but the glandes of heteromyids have received little attention. The one exception being the comparative study of the structure in heteromyine mice by Genoways (1973). In the

present study, the phalli of both species of Microdipodops, four species of Perognathus, and three species of Dipodomys are examined and compared.

Microdipodops (Fig. 8).--The species of Microdipodops have quite similar phalli that seem to differ only in proportion (Table 4). M. pallidus possesses the longer and thicker phallus. When the species were compared using the single classification ANOVA, two of the measurements in Table 4, total length of glans and length of tip, were found to be significantly different. The glans penis in both species of Microdipodops is rather slender, cylindrical, and is covered with spines. The structures are nearly equal in width and height. The widest point occurs at or near the base. Along the dorsum there is a single conspicuous groove, also seen in Perognathus flavus. Interestingly, a similar groove was noted in Heteromys lepturus (Genoways, 1973:283), but not in any species of Liomys. Within the terminal crater and ventral to the baculum are the paired urethral lappets. An individual lappet appears simple and unilobed, but there is a small folded lobe towards the proximal end, deep within the terminal crater. The rim of the terminal crater is notched a deep V-shape both dorsally and ventrally.

Perognathus flavus (Fig. 9A).--This phallus is largely cylindrical but the width slightly exceeds the height (Table 5). The dorsal groove is present in this species as it is in Microdipodops. The urethral lappets appear bilobed, although the proximal lobe is only weakly

Fig. 8.--The glans penis of Microdipodops. A, M. megacephalus (TTU 24688); B, M. pallidus (TTU 24708). The scale at the bottom is three millimeters long. From top to bottom the dorsal, lateral and ventral views are shown.

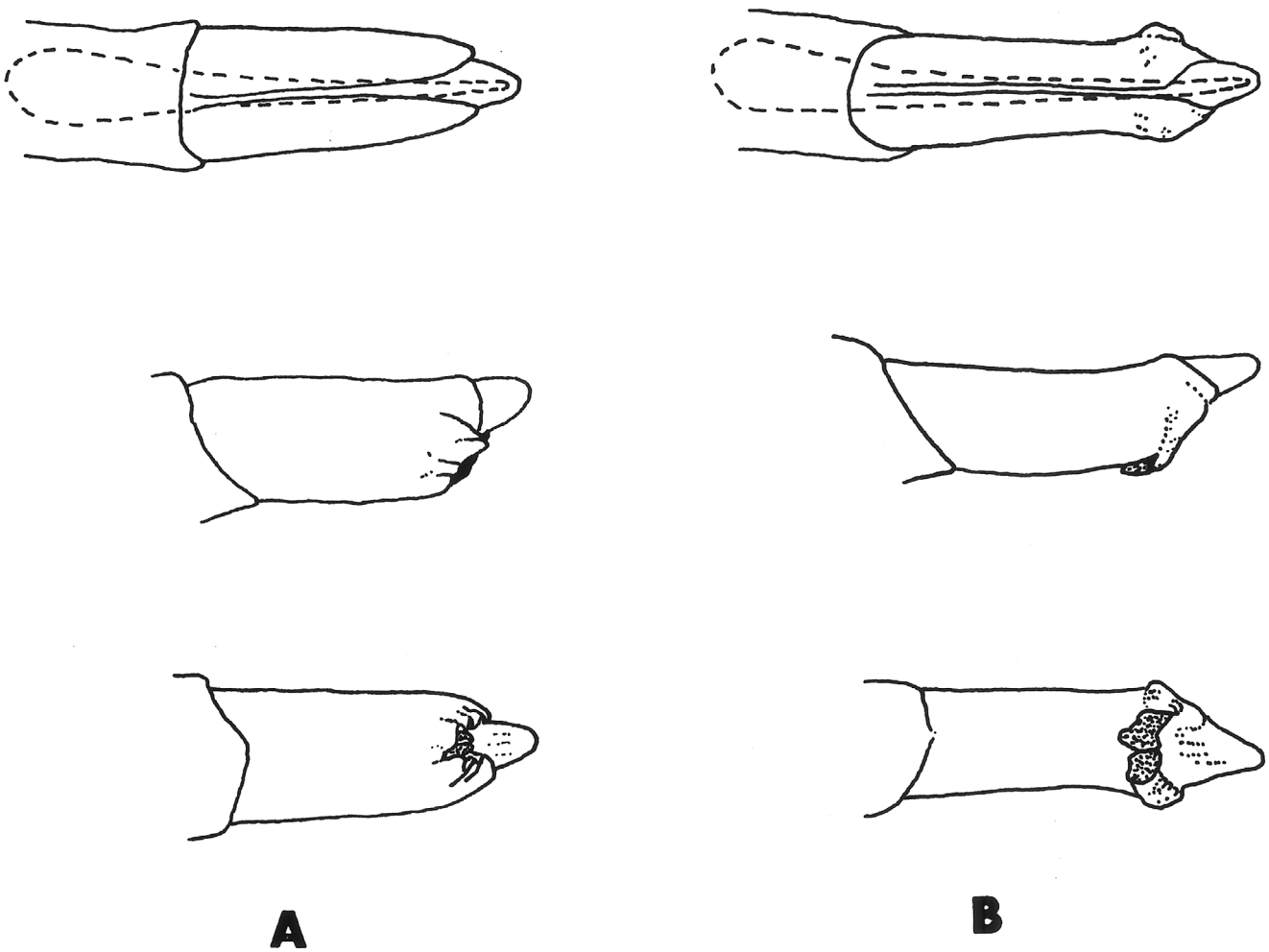

A
B

Table 4.--Measurements and statistics of the glans penes of Microdipodops. Means that are significnatly different at $P < .05$ are marked with an asterisk; those that are not significantly different are marked NS.

Measurements and species	N	Mean ± 2 SE	Range	CV	F_s F
Length of Glans					
M. megacephalus	10	3.93 ± 0.19	3.33-4.21	7.46	33.33*
M. pallidus	10	4.93 ± 0.29	4.18-5.51	9.44	4.41
Tip Length					
M. megacephalus	10	0.47 ± 0.05	0.34-0.58	17.03	4.63*
M. pallidus	10	0.59 ± 0.10	0.41-0.83	26.03	4.41
Width of Glans					
M. megacephalus	10	1.45 ± 0.11	1.22-1.79	12.36	0.15 NS
M. pallidus	10	1.48 ± 0.14	1.11-1.83	14.95	4.41
Height of Glans					
M. megacephalus	10	1.43 ± 0.08	1.21-1.57	9.33	0.15 NS
M. pallidus	10	1.46 ± 0.13	1.23-1.82	13.52	4.41

Fig. 9.--The glans penis of the silky pocket mice (subgenus Perognathus). A, Perognathus flavus (TTU 24864); B, Perognathus longimembris (TTU 24868). From top to bottom the dorsal, lateral and ventral views are shown. The scale at the bottom is three millimeters long.

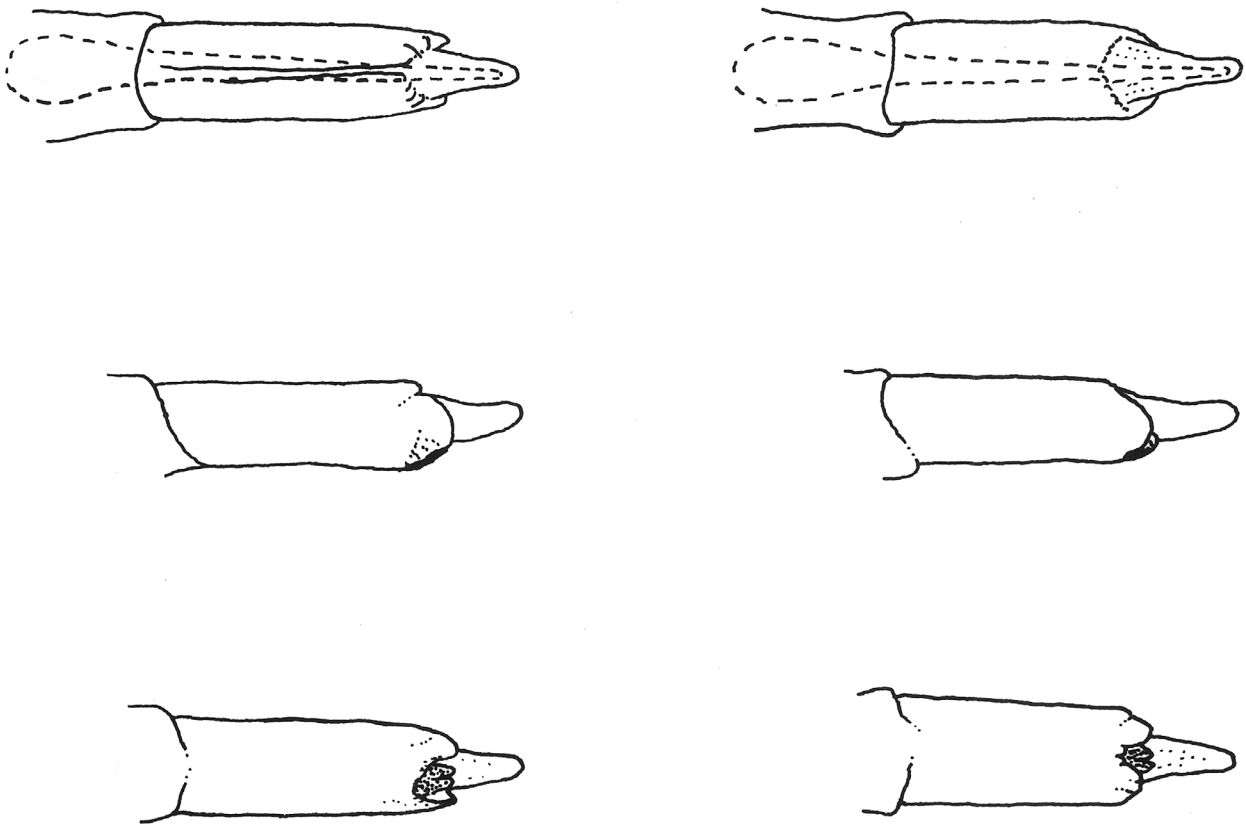

A
B

Table 5.--Measurements of the glans penes in selected species of *Perognathus* and *Dipodomys*.

Species and number	Length of glans	Tip Length	Width of glans	Height of glans
Perognathus intermedius (TTU 24866)	6.41	1.16	1.50	1.29
Perognathus hispidus (TTU 24865)	8.43	1.79	2.01	1.80
Perognathus longimembris (TTU 24868)	4.24	1.01	1.23	1.11
Perognathus flavus (TTU 24864)	4.73	0.87	1.23	1.09
Dipodomys merriami (TTU 24887)	6.96	1.71	1.44	1.87
Dipodomys ordii (TTU 24913)	5.54	0.98	2.01	1.91
Dipodomys panamintinus (MSH 294)	5.77	1.06	2.19	2.34

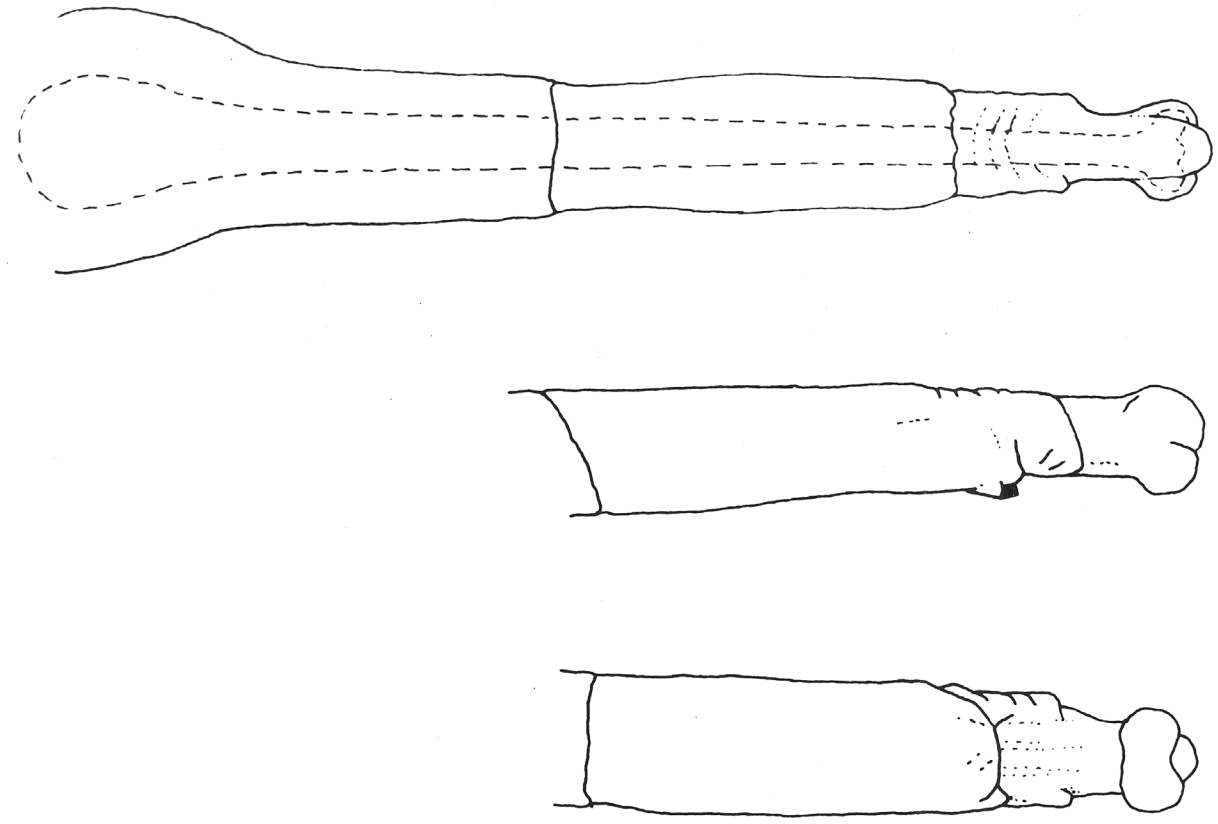
developed. The rim of the terminal crater is without a notch dorsally, but with a V-shaped notch on the ventral side, as in P. longimembris.

Perognathus longimembris (Fig. 9B).--The glans penis of P. longimembris is spinous (as were the glandes of all the other species used in this study) and cylindrical. The width of the glans slightly exceeds its height (Table 5). The tip is long and comprises nearly one-quarter of the total length of the glans. As can be seen in the firgure; the glans penis is rather simple and lacks the dorsal groove. Additionally, the urethral lappets appear to be unilobed and lacking of folds or excessory lobes. The rim of the terminal crater is notched ventrally, whereas no such notch is present dorsally. The general features of this phallis agree with that of P. flavus, except that the latter possesses the dorsal groove.

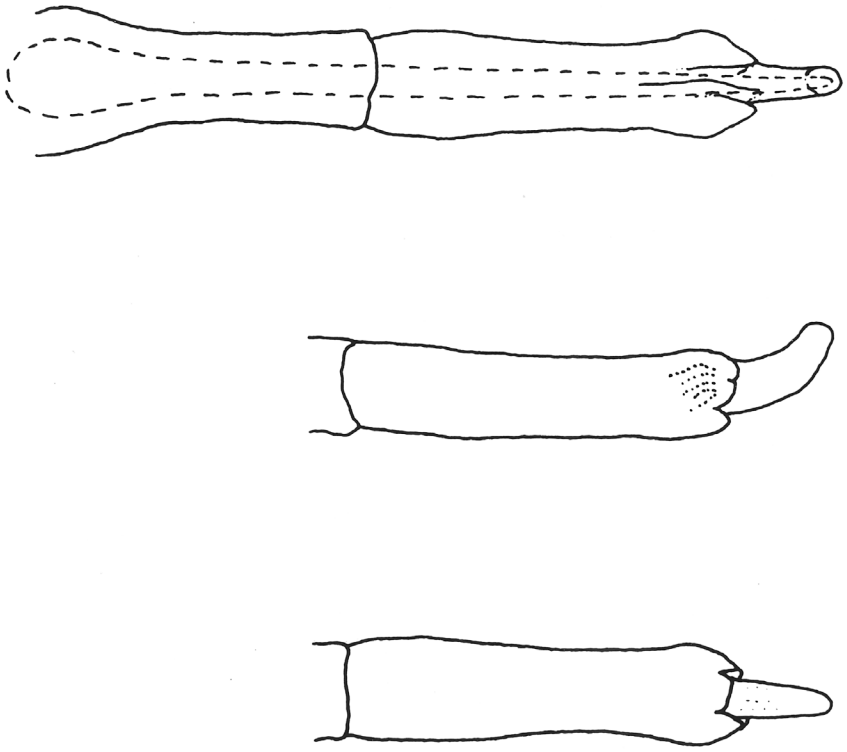
Perognathus intermedius (Fig. 10B).--The glans penis in this pocket mouse is extremely long and slender (Table 5). The rim of the terminal crater appears notched in a deep V-shape dorsally, and has shallow dual notches ventrally. Within the terminal crater and ventral to the baculum, the urethral opening is void of urethral lappets. Length of the glans and absence of the urethral lappets are aspects of P. intermedius that agree with those of P. hispidus. A partial and weakly developed dorsal groove is apparent in this species.

Perognathus hispidus (Fig. 10A).--In general, the glans of P. hispidus is unlike any other heteromyid. This is apparently due

Fig. 10.--Dorsal, lateral and ventral views of the glans penis of the subgenus Chaetodipus. A, Perognathus hispidus (TTU 24865); B, Perognathus intermedius (TTU 24866). The scale at the lower left is three millimeters long.



A



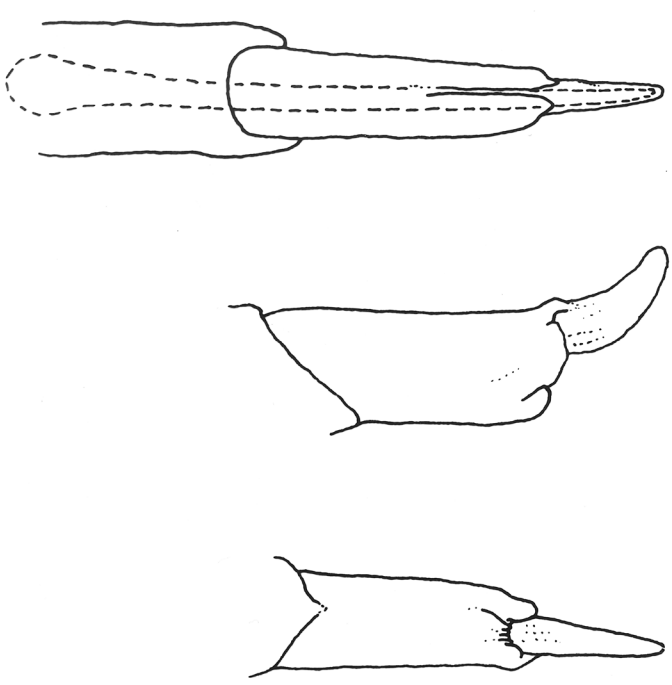
B

to the ornate trifid tip of the baculum. The glans penis of P. hispidus is the longest of the nine species included in this study (Table 5). As in that of P. intermedius, the glans of P. hispidus is both long and cylindrical, and lacks the urethral lappets. The glans is lacking the dorsal groove. The rim of the terminal crater is without a notch on the dorsum and ventrally the rim is modified into a urethral vent, in some ways similar to the glans of P. intermedius.

Dipodomys merriami (Fig. 11A).--The glans penis of this kangaroo rat is both the longest and the narrowest of the glandes of the three kangaroo rats studied. (Table 5). It is considerably higher than wide and has the longest tip of the three species of Dipodomys. The rim of the terminal crater forms a deep V-shaped notch dorsally and extends proximally to create a dorsal groove. This groove extends only partially the length of the glans. Ventrally, the rim of the terminal crater also forms a V-shape. The urethral lappets are long in comparison to those of kangaroo mice and pocket mice, and are bilobed. The second lobe is much reduced and folded back onto the primary lobe.

Dipodomys ordii (Fig. 11B).--The glans penis of D. ordii is the shortest among the three species of Dipodomys under study (Table 5) and, in contrast to the glans of D. merriami, is nearly cylindrical in shape. The rim of the terminal crater forms V-shaped notches both dorsally and ventrally. On the dorsum there occur two partial grooves, separated from each other by a ridge. The tip extends only slightly

Fig. 11.--Dorsal, lateral and ventral views of the glans penis of *Dipodomys*. A, *D. merriami* (TTU 24887); B, *D. ordii* (TTU 24913); C, *D. panamintinus* (MSH 294). The scale at the lower right is three millimeters long.



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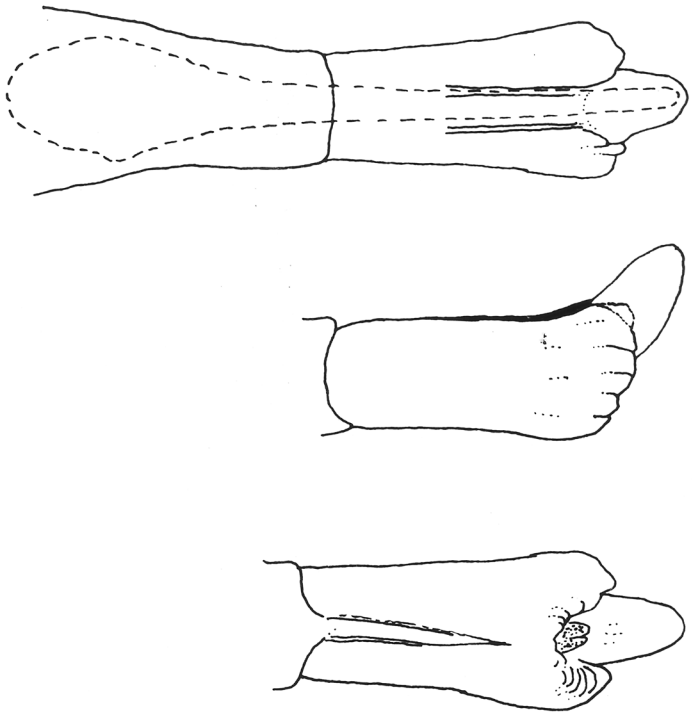

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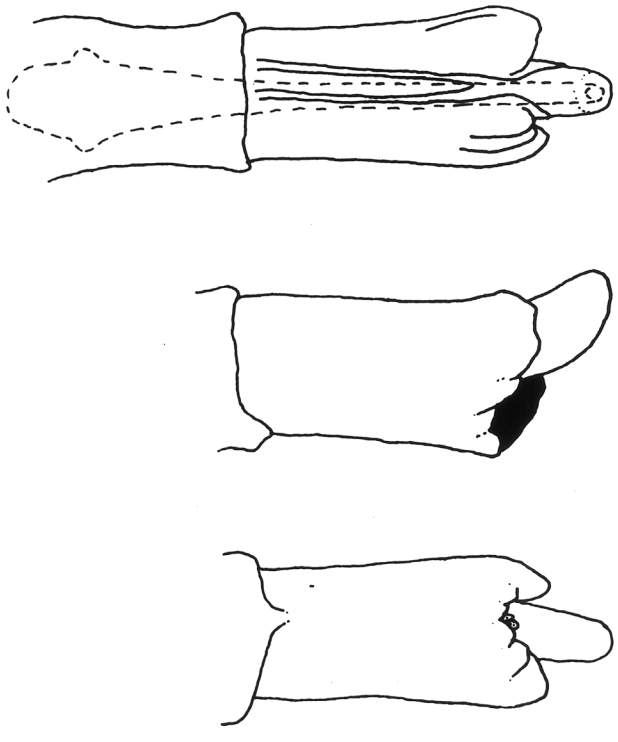


C

as compared to the other species. The urethral lappets are weakly bilobed and similar to those of the other species of Dipodomys.

Dipodomys panamintinus (Fig. 11C).--The glans penis of D. panamintinus is slightly higher than wide and is intermediate in length when compared to the other species of Dipodomys (Table 5). On the dorsum there occur two grooves, somewhat similar to the condition found in D. ordii. The rim of the terminal crater is V-shaped both in dorsal and ventral aspects. The urethral lappets are long and exhibit a weakly developed secondary lobe, which is folded over at the proximal end as in the other species of Dipodomys.

Conclusions.--The glans penis of the nine heteromyid species studied were found to be spinous and have simple urethral lappets or lack them entirely. Interestingly, Genoways (1973) found the glans penis of heteromyines to be nonspinous and have rather ornate urethral lappets. Any possible explaination of the significance of this difference must wait a time when more species have been thoroughly studied.

There appear to be three morphological types among the nine species examined. the first group is composed of Microdipodops and the silky pocket mice, Perognathus flavus and Perognathus longimembris. Members of this group have cylindrical phalli, possess a single dorsal groove (excepting P. longimembris), and small unilobed to weakly bilobed urethral lappets. The second type, includes the pocket mice of the subgenus Chaetodipus (P. hispidus and P. intermedius). This morphological group is characterized by

a long and slender glans penis, lacking urethral lappets and dorsal grooves, and with the rim of the terminal crater forming a vent-like urethral opening. The last group containing the kangaroo rats, has a rather high and narrow glans (excepting D. ordii), with partial single or double dorsal grooves, long urethral lappets, and strongly upturned tips.

Glandes used in this study were taken from specimens (all adults) as follows: Microdipodops megacephalus, 2.5 mi. NE Larkin Lake, Alkali Valley, 21.5 mi. S, 10.5 mi. W Hawthorne, 6860 ft., Mineral Co., Nevada, 7 (TTU 24652, 24654, 24658, 24662, 24671, 24677, 24680), and 0.5 mi. SE Alkali Lake, Aurora Valley, 17.5 mi. S, 6.5 mi. W Hawthorne, 7040 ft., Mineral Co., Nevada, 3 (TTU 24686-24688); Microdipodops pallidus, 17 mi. S, 5 mi. E Yerington, 5000 ft., Lyon Co., Nevada, 10 (TTU 24694, 24695, 24698, 24645, 24706, 24707, 24708, 24710, 24833, 24834); Perognathus flavus, 4.5 mi. S, 12 mi. E Lubbock, 3200 ft., Lubbock Co., Texas 1 (TTU 24864); Perognathus longimembris, 6 mi. N, 31 mi. W Hiko, 4800 ft., Lincoln Co., Nevada, 2 (TTU 24867, 24868); Perognathus hispidus, 3.5 mi. S, 12 mi. E Lubbock, 3200 ft., Lubbock Co., Texas 1 (TTU 24865); Perognathus intermedius, 5 mi. N, 2 mi. W, Socorro, 4800 ft., Socorro Co., New Mexico, 1 (TTU 24866); Dipodomys merriami, 17 mi. S, 5 mi. E Yerington, 5000 ft., Lyon Co., Nevada, 1 (TTU 24887); Dipodomys ordii, 15 mi. S, 11 mi. W Dugway, 4550 ft., Tooele Co., Utah, 2 (TTU 24913, 24917); Dipodomys panamintinus, 0.15 mi. E Walker Pass Summit, 11.0 mi. W Inyokern, 5100 ft., Kern Co., California, 1 (MSH 294).

BACULAR MORPHOLOGY

Bacular morphology has been widely used in systematic studies of North American rodents during the last 40 years. Pioneering studies by Burt (1936), Wade and Gilbert (1940), Burt and Barkalow (1942), and Hamilton (1946) manifest the importance of the baculum as a taxonomic tool. Heteromyids, in particular, have received considerable attention including the studies by Burt (1936) and Burt (1960) on Perognathus, Burt (1936) and Best and Schnell (1974) on Dipodomys, Burt (1960) and Schitoskey (1968) on Microdipodops, Burt (1960) and Genoways (1973) on Liomys, and Genoways (1973) on Heteromys. In the present study, the bacula of nine species of heteromyids, all of which have been previously described, are compared and a new interpretation of the relationships among the taxa is presented.

The bacula of both species of Microdipodops, four species of Perognathus, and three species of Dipodomys are illustrated in lateral aspect in Fig. 12. Lateral aspect was chosen because most of the variation among the bacula is within the sagittal plane, as opposed to the transverse or frontal planes. In the illustration, proportional relationships among the bacula have been ignored for the sake of clarity, and the proximal termination of the glans penis is indicated in each case.

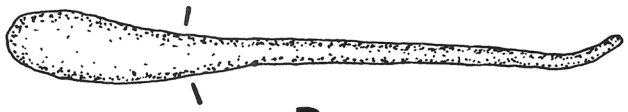
Microdipodops megacephalus (Fig. 12A).--The baculum of the Dark Kargaroo Mouse was first described by Schitoskey (1968) and the

Fig. 12.--Bacula of nine species of heteromyids. Bacula are drawn to the same size, regardless of scale and shown in lateral aspect. A, Microdipodops megacephalus (TTU 24688); B, Microdipodops pallidus (TTU 24708); C, Perognathus flavus (TTU 24864); D, Perognathus longimembris (TTU 24868); E, Perognathus intermedius (TTU 24866); F, Perognathus hispidus (TTU 24865); G, Dipodomys panamintinus (MSH 294); H, Dipodomys merriami (TTU 24887); I, Dipodomys ordii (TTU 24913).

A

B

C



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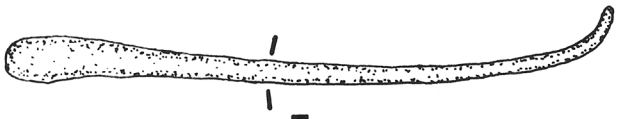

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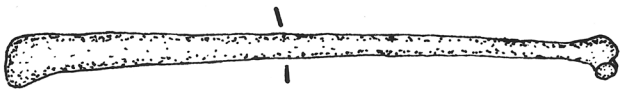

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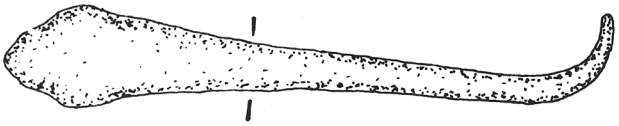

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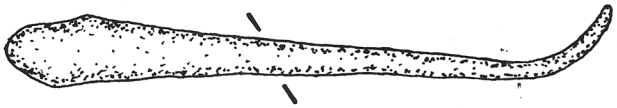

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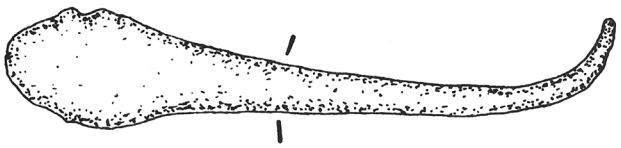

I

illustration of the baculum of M. megacephalus in Fig. 12A agrees with his. The baculum has a gentle upturned tip that begins its ascent in the distal one-third section. The base is not strongly bulbous, as in M. pallidus and some species of Dipodomys, but only moderately inflated. The glans penis is moderately long with respect to length of the baculum, (67 per cent the length).

Microdipodops pallidus (Fig. 12B).--This species has a baculum similar to that of M. megacephalus, but differing in the presence of a more massive, bulbous base. The baculum of M. pallidus illustrated in Fig. 12B agrees well with that figured by Burt (1960). Burt (1960) indicated that the tip is strongly upturned in M. pallidus. It is my interpretation that, in comparison to other heteromyids, the tip has only a gentle curve, which ascends from a point one-third back on the bone. The glans penis of M. pallidus is 66 per cent the length of the baculum.

Perognathus flavus (Fig. 12C).--The baculum of this mouse is thin and slightly arched in the mid-section. The base is only moderately bulbous and the tip is mildly upturned in the distal one-eighth. The glans penis is 72 percent the length of the baculum in the individual in Fig. 12C. This baculum in all respects is similar to that of P. longimembris.

Perognathus longimembris (Fig. 12D).--The baculum of this silky pocket mouse is similar to that of P. flavus. It differs from P. flavus though, in having the slender shaft less arched. The base is

moderately bulbous, and the tip is gradually upturned in the distal one-eighth of the bone. The glans penis, in length, is 71 per cent that of the baculum, and again agrees with P. flavus in this respect.

Perognathus intermedius (Fig. 12E).--This baculum shows the sharply upturned tip and the general sigmoid profile characteristic of the subgenus Chaetodipus (Burt, 1936, 1960). The shaft is quite long and the base is moderately bulbous. The length of the glans penis is 57 per cent that of the baculum and in this respect agrees with P. hispidus.

Perognathus hispidus (Fig. 12F).--The baculum of this mouse is quite different; the tip is modified into three prongs, which in end view give a trifid appearance. No other heteromyid is known to have a baculum with this tip ornamentation. The baculum is quite long in proportion to the glans (the glans is 54 per cent the length of the baculum) and is slightly arched. The base is only slightly enlarged. The baculum is similar to that of P. intermedius in the relationship between the length of the glans penis and the length of the baculum.

Dipodomys panamintinus (Fig. 12G).--This baculum is quite similar in shape to the other two species in this study. The tip is sharply upturned and the base is bulbous. The shaft gradually tapers to the tip, and is fairly straight. The length of the glans penis is 59 per cent that of the baculum.

Dipodomys merriami (Fig. 12H).--The baculum of D. merriami is slenderer and less bulbous at the base than in the other two species of Dipodomys examined in this study. In other aspects, including the gradual taper of the shaft and the sharp upturn of the tip, this baculum is similar to that of other Dipodomys. The glans penis is 56 per cent the length of the baculum.

Dipodomys ordii (Fig. 12I).--The baculum of this species has the greatest basal inflation in any of the three species of Dipodomys examined. As in the other members of the genus, the shaft is relatively straight and the tip is sharply upturned. The baculum is also characteristically long (or the glans penis is short) because the glans measures only 54 per cent the length of the baculum.

Conclusions.--The bacula used in this study were taken from adult specimens and all illustrations presented are in agreement with those in the literature. Among the nine species examined, four bacular "morphs" are apparent: those of Dipodomys, subgenus Chaetodipus, subgenus Perognathus, and Microdipodops. The bacula of Dipodomys have bulbous bases, strongly upturned tips, and a short glans penis with respect to the baculum (glans less than 60 per cent the length of the latter). P. intermedius and P. hispidus, both presently considered members of the subgenus Chaetodipus, are quite dissimilar in structure of the bacular tip. They do, however, agree in the relationship of the length of the baculum to that of the glans and are grouped together here only on that basis. P. flavus and P. longimembris belong in the subgenus Perognathus and agree well

in bacular morphology. Bacula of both have moderately upturned tips, slender shafts, and a relatively long glans penis (more than 70 per cent the length of the baculum). The species of Microdipodops are quite similar in bacular morphology, differing only in degree of inflation of the basal end. Burt (1960) stated the baculum of Microdipodops "...is definitely intermediate between those of the silky pocket mice and the kangaroo rats." I cannot concur completely, because Microdipodops lacks the sharply upturned tip and long baculum (relative to the glans penis) as is the case in the species of Dipodomys examined. Microdipodops does, however, appear quite similar in these two aspects to the silky pocket mice (subgenus Perognathus). It was noted in the previous section that the glans penis of Heteromys lepturus had a dorsal groove as does Microdipodops. Interestingly, the baculum of Heteromys as well as a few species of Liomys more closely resembles that of Microdipodops than does the baculum of any species considered in the present study.

Specimens used in this study of the bacular morphology are identified in the previous section on the morphology of the glans penis.

MORPHOLOGY OF SPERMATOZOA

The use of spermatozoan morphology in mammalian systematics is a relatively new innovation. Sperm from a relatively few species of mammals have been examined and used in assessing systematic relationships; the few instances were reviewed by Forman (1968). Genoways (1973)

presented a rather detailed study of the sperm of Liomys and, additionally, made a brief statement as to the relative shape of the sperm head in Perognathus pernix. This information is all that is available in the literature on the sperm from heteromyids. In the present study, sperm from nine species (the same nine compared in the other sections) were examined and compared in the hopes that the study may help to elucidate the specific and evolutionary relationships of the genus Microdipodops.

In this study of the morphology of spermatozoa, a distinct midpiece was not identified in any of the nine species of heteromyids. The neck appeared highly variable in length and, therefore, simply a presence or absence of this trait was recorded.

Microdipodops megacephalus (Fig. 13A).--The sperm of M. megacephalus is the largest of the nine species examined. Note (Table 6) that in both greatest head length and greatest head width the sperm of this species is significantly larger than that of M. pallidus. The head is elongated and the vertices are smoothly rounded. The head is similar in shape to that of M. pallidus, as well as the species of the subgenus Perognathus (P. flavus and P. longimembris). A neck is apparent, although the midpiece was not discernable (as was the case with all other species in the study). An acrosomal tip was noted in several sperm, but in others it seems to have been lost in preparation. The acrosomal tip is similar to that shown in Fig. 13C for M. pallidus. The tail appears to be of medium length and not significantly different from that of M. pallidus (Table 6).

Fig. 13.--Sperm heads of nine species of heteromyids in lateral aspect. A, Microdipodops megacephalus; B, Microdipodops pallidus; C, Microdipodops pallidus showing acrosomal tip; D, Perognathus longimembris; E, Perognathus flavus; F, Perognathus hispidus; G, Perognathus intermedius; H, Dipodomys merriami; I, Dipodomys panamintinus; J, Dipodomys ordii. The scale to the left is one micron long.

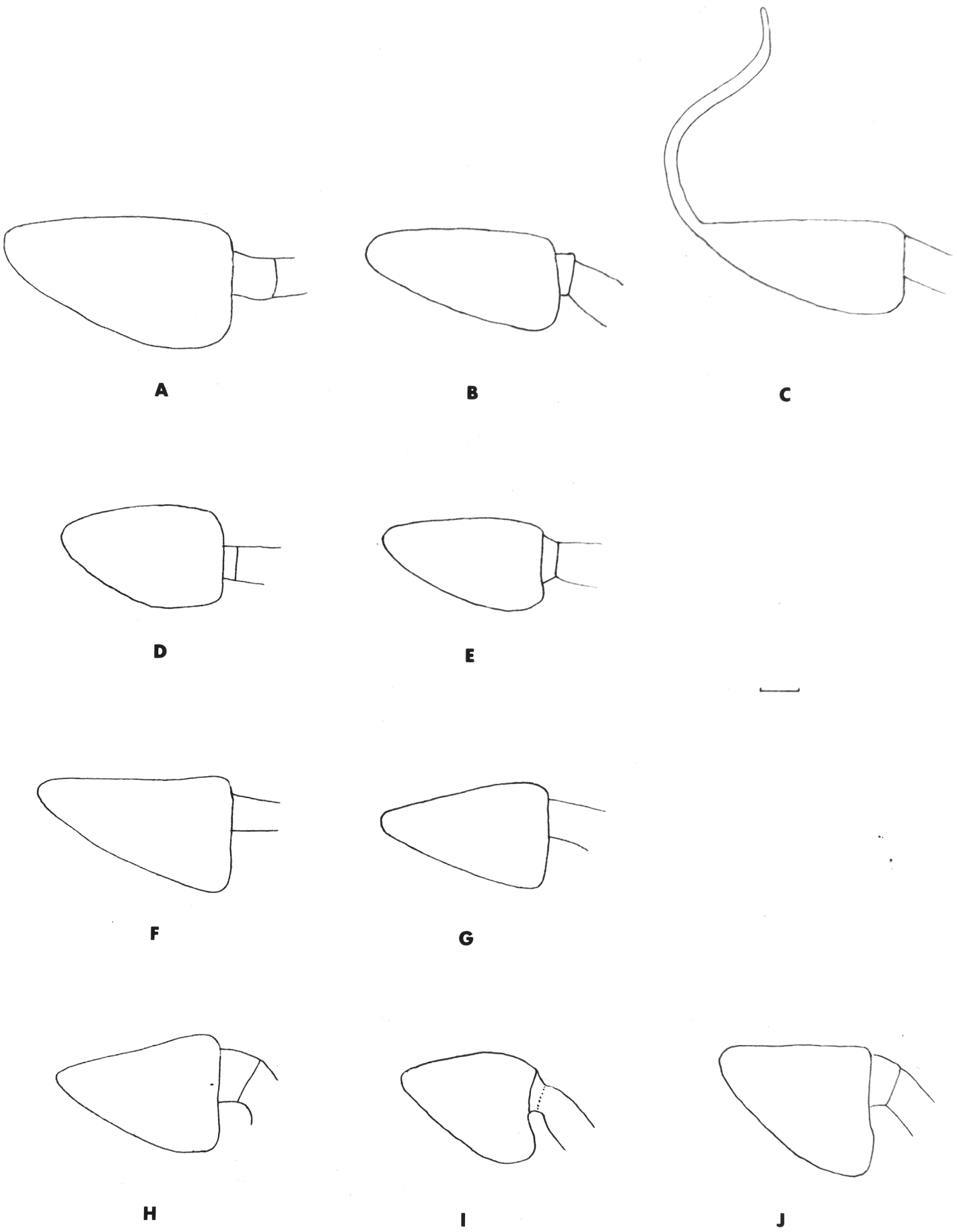
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Table 6.--Measurements (in microns) and statistics of the head and tail of the spermatozoa of nine species of heteromyids. Means between species of Microdipodops that are significantly different at $P < .05$ are marked with an asterisk; those that are not significantly different are marked NS.

Species	N	Mean	± 2SE	Range	CV	F_s F
			Greatest head length			
M. megacephalus	6	6.16	0.43	(5.58-7.00	8.46	23.35*
M. pallidus	10	5.17	0.19	(4.72-5.72)	5.94	4.60
P. intermedius	2	4.37		(4.32-4.42)		
P. hispidus	2	5.45		(5.27-5.63)		
P. flavus	2	4.73		(4.53-4.93)		
P. longimembris	2	4.50		(4.43-4.56)		
D. merriami	2	4.70		(4.64-4.75)		
D. ordii	2	4.84		(4.76-4.92)		
D. panamintinus	2	4.01		(4.00-4.02)		
			Greatest head width			
M. megacephalus	6	3.34	0.30	(2.88-3.76)	11.09	55.36*
M. pallidus	10	2.41	0.08	(2.15-2.53)	5.06	4.60
P. intermedius	2	2.60		(2.57-2.62)		
P. hispidus	2	3.02		(2.96-3.08)		
P. flavus	2	2.30		(2.22-2.37)		
P. longimembris	2	2.75		(2.75)		
D. merriami	2	3.14		(3.04-3.24)		

Table 6.--Continued

Species	N	Mean	± 2SE	Range	CV	F_s F
D. ordii	2	3.35		(3.30-3.40)		
D. panamintinus	2	2.81		(2.75-2.87)		
		Tail length				
M. megacephalus	5	134.88	3.26	(129.60-138.40)	2.71	0.56 NS
M. pallidus	5	133.28	2.75	(129.60-136.00)	2.31	5.32
P. intermedius	2	129.20		(128.00-.30.40)		
P. hispidus	2	154.00		(153.60-154.40)		
P. flavus	2	96.80		(95.20-98.40)		
P. longimembris	2	116.40		(113.60-119.20)		
D. merriami	2	171.60		(170.40-172.80)		
D. ordii	2	146.40		(144.00-148.80)		
D. panamintinus	2	137.20		(135.20-139.20)		

Microdipodops pallidus (Fig. 13B).--The sperm of M. pallidus seems to be similar to that of M. megacephalus in all aspects excepting size of head. From Table 6 it can be seen that M. pallidus has lower coefficients of variation for sperm measurements than does M. megacephalus. The neck appeared to be quite variable in size, as was the case in the other species that possessed this structure.

Perognathus longimembris (Fig. 13D).--The spermatozoa of P. longimembris are small in head size and have relatively short tails. Only the sperm of P. flavus possesses a tail shorter than that of P. longimembris (Table 6). The head appears less triangular in shape as its sides are rounded when compared to the other species examined and has smoothly rounded vertices. The neck region was observed in this species. The sperm is quite similar to that of P. flavus in all characters, except the rounding of the long sides of the head.

Perognathus flavus (Fig. 13E).--The sperm of this species is remarkably similar to that of Microdipodops, although considerably smaller (Table 6). The head is elongated and with rounded vertices. A neck region is present. The tail was found to be the shortest among all species examined. In general characters, the sperm most closely resembles that of P. longimembris, except that the head seems less inflated in P. flavus.

Perognathus hispidus (Fig. 13F).--The sperm head of this species is shaped like an elongated isosceles triangle and the vertices

form rather sharp angles. A neck region was not observed in this species. The general shape of the head resembles that of P. intermedius, but the tail is considerably longer and the head is larger.

Perognathus intermedius (Fig. 13G).--The sperm of P. intermedius most closely resembles that of P. hispidus in that both have the head shaped like an elongated isosceles triangle. The vertices are sharply pointed as in P. hispidus, but the head is smaller and the tail is shorter. An ill-defined neck region was observed in some specimens.

Dipodomys merriami (Fig. 13H).--The sperm head of this species resembles an equilateral triangle in shape. The vertices of such a triangle (head) are acute. The head is of medium size, but the tail (see Table 6) is extremely long. A neck piece is evident in this species. The general morphology of the spermatozoa is similar to the other two species of Dipodomys examined.

Dipodomys panamintinus (Fig. 13I).--The sperm head is shaped like that of D. merriami and D. ordii, yet it differs in the possession of a basal notch. Of the three species of Dipodomys examined, D. panamintinus had the smallest sperm (Table 6). The neck region is only weakly defined in this species.

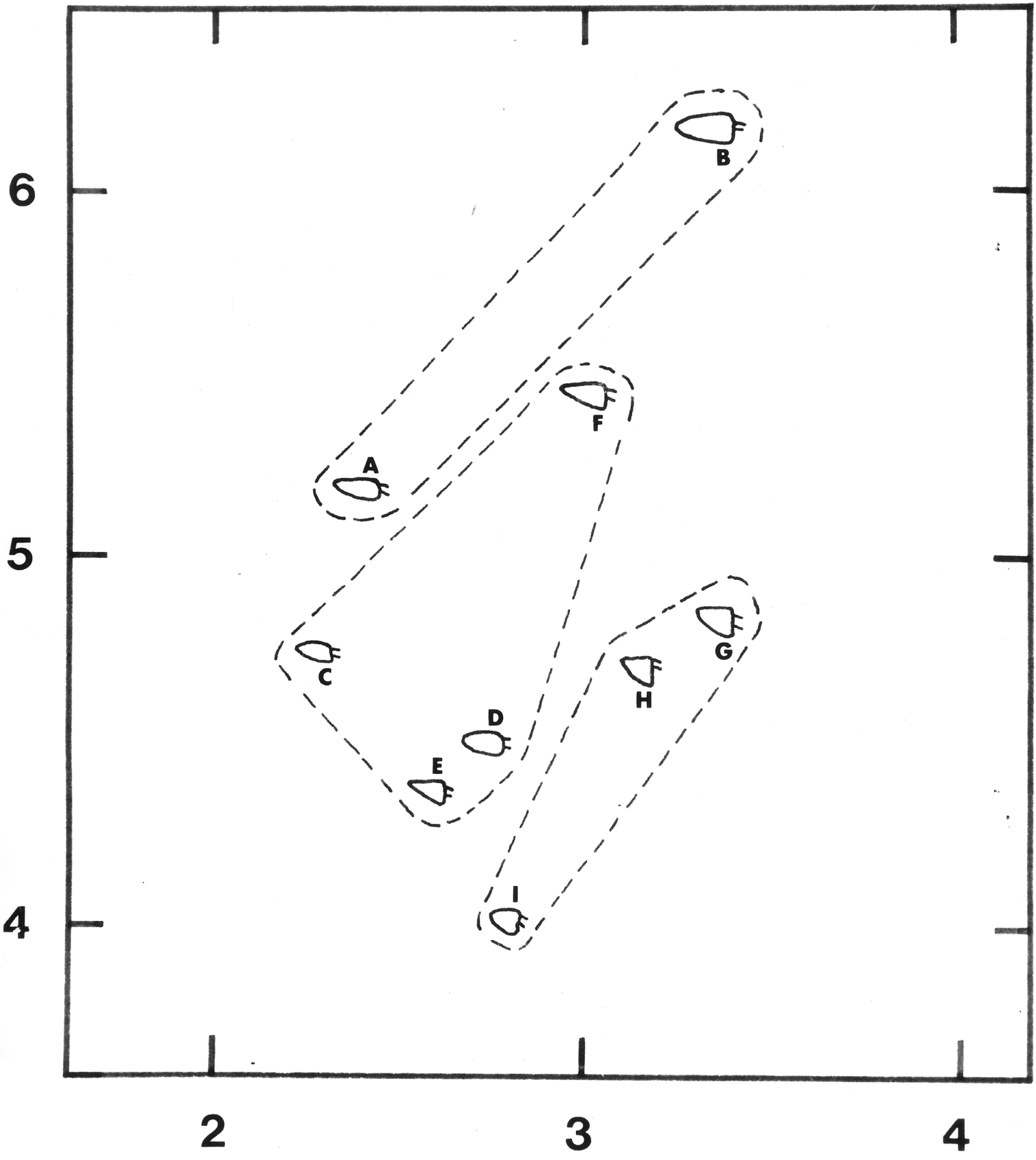
Dipodomys ordii (Fig. 13J).--The sperm head in this species shows the typical equilateral triangle shape found in the other species of Dipodomys. The head is shaped much like that of D. merriami, although the apex is less acute. The head is about the size of D. merriami,

but the tail is considerably shorter (Table 6). D. panamintinus, in comparison, is smaller. The neck region is distinct in this species.

Conclusions.--Four types of spermatozoa were evident among the nine species of heteromyids examined (Fig. 13). Spermatozoa of the first group, the species of Microdipodops, have especially long heads. The head is roughly triangular in shape with rounded vertices. The tail is of medium length. The second group is represented by the species P. flavus and P. longimembris (of the subgenus Perognathus). Sperm of this group are similar to those of Microdipodops, but the head is smaller and the tail is short. The sperm of the chaetodipine species, P. intermedius and P. hispidus, form the third group. Here the sperm head resembles an elongated isosceles triangle in shape, with acute vertices. P. hispidus is peculiar in some respects, because the tail is quite long and a neck was not discernable. The last group contains D. merriami, D. panamintinus, and D. ordii. The head of Dipodomys sperm approximates an equilateral triangle, with the apex fairly acute, and has a rather long tail.

Judging from Fig. 13 and the measurements in Table 6, the sperm of silky pocket mice (P. flavus and P. longimembris) clearly resemble those of Microdipodops. The sperm of chaetodipine pocket mice and kangaroo rats form distinctive groups, each quite dissimilar and each clearly separable from the Microdipodops sperm. In Fig. 14 a bivariate plot of sperm head width as opposed to sperm head length is presented and illustrates the phenotypic divergence in head proportion between the three heteromyid genera. Proportionately, the sperm head

Fig. 14.--Bivariate plot of sperm head width (abscissa) versus sperm head length (ordinate) in nine species of heteromyids. Dashed lines indicate taxonomic groupings. Taxa are as follows: A, Microdipodops pallidus; B, Microdipodops megacephalus; C, Perognathus flavus; D, Perognathus longimembris; E, Perognathus intermedius; F, Perognathus hispidus; G, Dipodomys ordii; H, Dipodomys merriami; I, Dipodomys panamintinus.


6
5
4
2
3
4
A
B
C
D
E
F
G
H
I

of Microdipodops is definately similar in general structure to the head in the genus Perognathus. Microdipodops, however, has a longer head, whereas Dipodomys possesses a shorter head than in the species of Perognathus studied.

Specimens used in the study of sperm morphology were taken from: Microdipodops megacephalus, 0.5 mi. SE Alkali Lake, Aurora Valley, 17.5 mi. S, 6.5 mi. W Hawthorne, 7040 ft., Mineral Co., Nevada, (TTU 24688); Microdipodops pallidus, 17 mi. S 5 mi. E Yerington, 5000 ft., Lyon Co., Nevada, (TTU 24834); Perognathus intermedius, 5 mi. N, 2 mi. W Socorro, 4800 ft., Socorro Co., New Mexico, (TTU 24866); Perognathus hispidus, 3.5 mi. S, 12 mi. E Lubbock, 3200 ft., Lubbock Co., Texas, (TTU 24865); Perognathus flavus, 3.5 mi. S, 12 mi. E Lubbock, 3200 ft., Lubbock Co., Texas, (JCH 846); Perognathus longimembris, 6 mi. N, 31 mi. W Hiko, 4800 ft., Lincoln Co., Nevada, (TTU 24868); Dipodomys merriami 6 mi. S, 2.5 mi. W Sutcliffe, 4200 ft., Washoe Co., Nevada, (JCH 838); Dipodomys ordii, 15 mi. S, 11 mi. W Dugway, 4550 ft., Tooele Co., Utah, (TTU 24917); Dipodomys panamintinus, 2 mi. E Searles Station, 9 mi. NNE Johannesburg, 3200 ft., San Bernardino Co., California, (MSH 354).

COMPARATIVE KARYOLOGY

In the past decade or so, a considerable amount of chromosomal information on heteromyids has appeared in the literature. Most species of the family have been karyotyped and it is therefore surprising that little karyotypic information is available for the genus Microdipodops.

It is the intent of the present study to compare the karyotypes of both species of Microdipodops and to ascertain their evolutionary affinities within the family Heteromyidae. In the course of my study of the chromosomes of this genus, intraspecific chromosomal variation has been identified in both species. Inasmuch as intraspecific karyotypic variation is not within the scope of this section, the details will be presented elsewhere.

Microdipodops megacephalus polionotus (Fig. 15 and Table 7).--The diploid number of chromosomes in the species M. megacephalus is 40, regardless of intraspecific chromosomal variation. In the race polionotus there appear to be three pairs of metacentrics, 15 pairs of submetacentrics to subtelocentrics, and a small pair of acrocentric chromosomes that comprise the autosomal compliment. O'Farrell and Blaustein (1974a) reported that the X chromosome of this species is a medium acrocentric and the Y chromosome a small subtelocentric. I have personnally examined the chromosomal preparations from which their information was derived, (as well as karyotypes of approximately 100 kangaroo mice from throughout the geographic range of the genus) and conclude that the sex chromosomes, doubtless, are comprised of a large metacentric X chromosome and a medium acrocentric Y chromosome. The fundamental number is 74 in M. megacephalus polionotus.

Microdipodops pallidus pallidus (Fig. 16 and Table 7).--The pallid kangaroo mouse has 42 chromosomes. The morphology of the autosomes in M. p. pallidus were: three pairs of metacentrics, 16 pairs of submetacentric

Fig. 15.--Karyotype of Microdipodops megacephalus polionotus, 2N=40 (JCH 396).

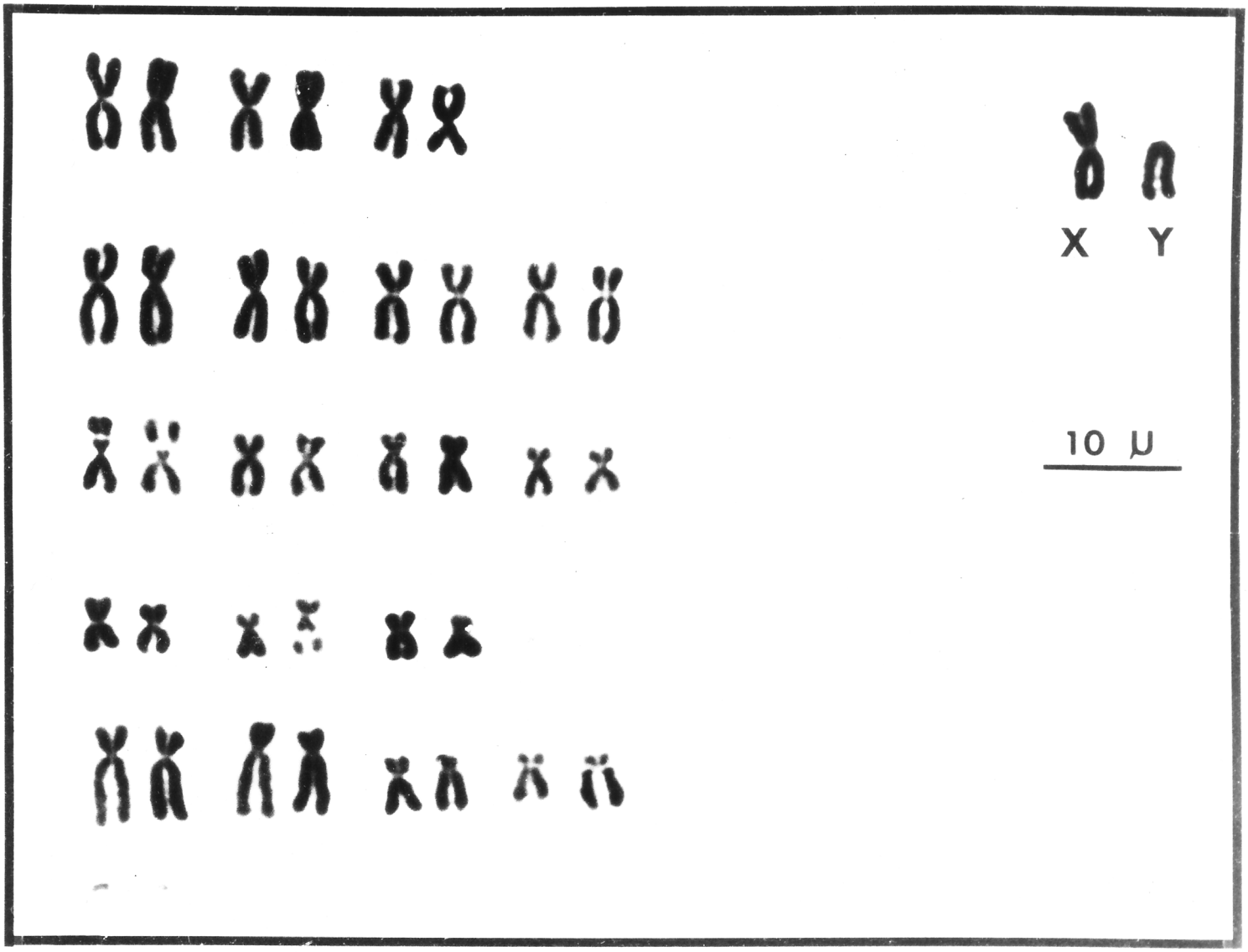
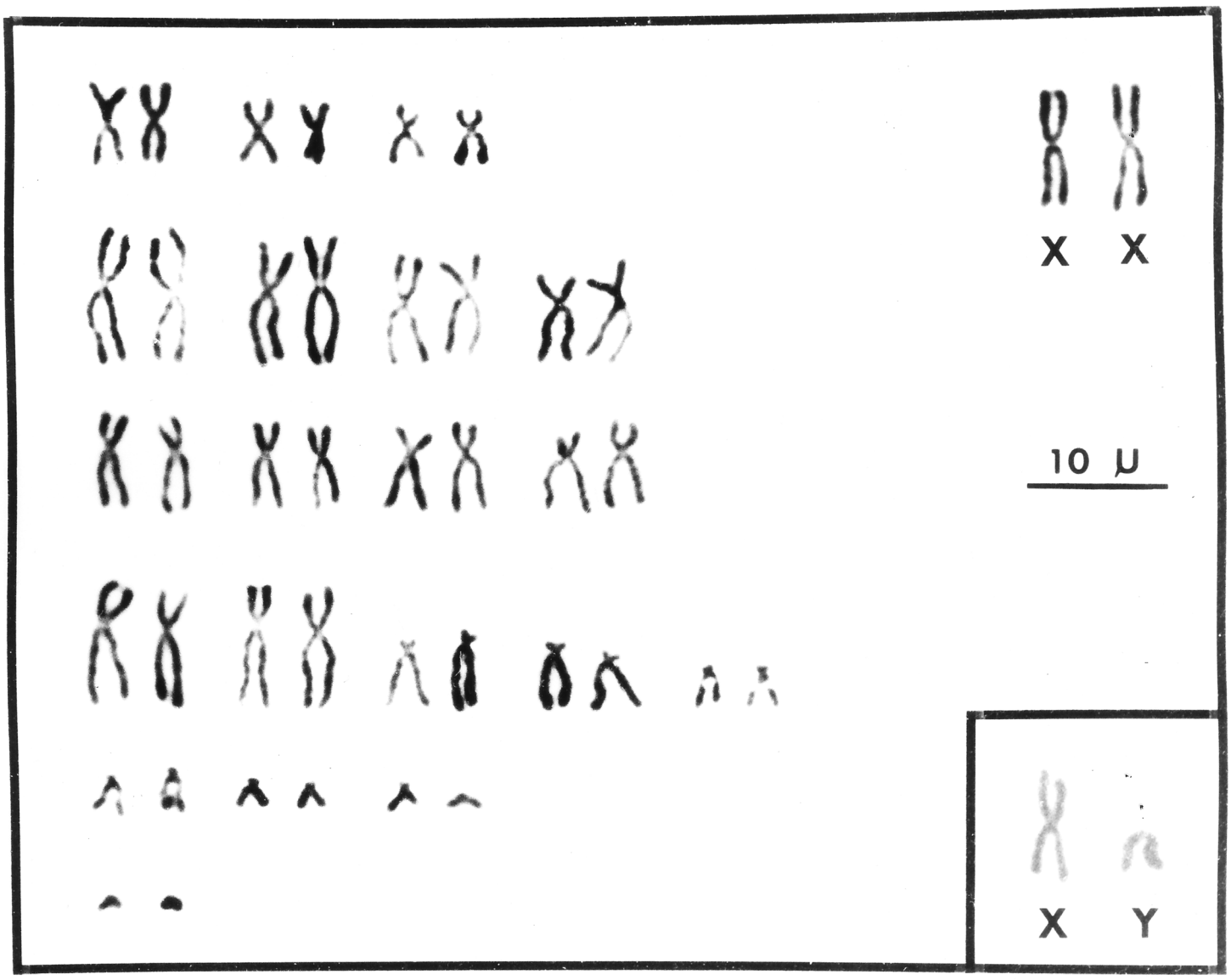

X
Y
10 μ

Table 7.--Somatic chromosome numbers and morphological types in two species of the genus Microdipodops. Autosome numbers refer to number of homologous pairs. M = metacentric, SM = submetacentric, ST = subtelocentric, A = acrocentric, FN = fundamental number.

			Autosomes				
Species	2N	FN	M	SM-ST	A	X	Y
M. megacephalus polionotus	40	74	3	15	1	M	A
M. pallidus pallidus	42	78	3	16	1	M	A

Fig. 16.--Karyotype of Microdipodops pallidus pallidus, 2N=42 (JCH 388). Male sex chromosomes are from JCH 389.


X X
10 µ
X Y

to subtelocentrics, and one pair of acrocentric chromosomes. The sex chromosomes are composed of a large metacentric X and a medium acrocentric Y, and no deviations from this situation have been found for members of this genus. O'Farrell and Blaustein (1974b) erroneously reported a medium acrocentric X and a small subtelocentric Y. The fundamental number in the karyotypes examined is 78.

Conclusions.--The diploid number of chromosomes in M. megacephalus and M. pallidus were 40 and 42, respectively. In each species there is a large metacentric X chromosome and a medium acrocentric Y chromosome. Additionally, from Figs. 15 and 16 it can be seen that each cytotype has three pairs of metacentrics, 8 pairs of submetacentrics, two pairs of large subtelocentrics, two pairs of medium subtelocentrics, and one pair of acrocentrics that appear homologous with those found in M. megacephalus.

In ascertaining the specific relationship between the two species, it seems that, chromosomally, we have a question in accounting for the difference in diploid number as to whether a Robertsonian fusion or fission occurred. Chromosomal evolution in mammals generally progresses from a high chromosomal number to a lower number, with centric fusion being the main mechanism (Hsu and Mead, 1969; Matthey, 1958; Nadler, 1966, 1969). A narrow classical interpretation would suggest, then, that the primitive karyotype of the genus in that represented by M. pallidus (2N=42), and that two pairs of chromosomes (probably the two small pairs of subtelocentrics) fused, forming the

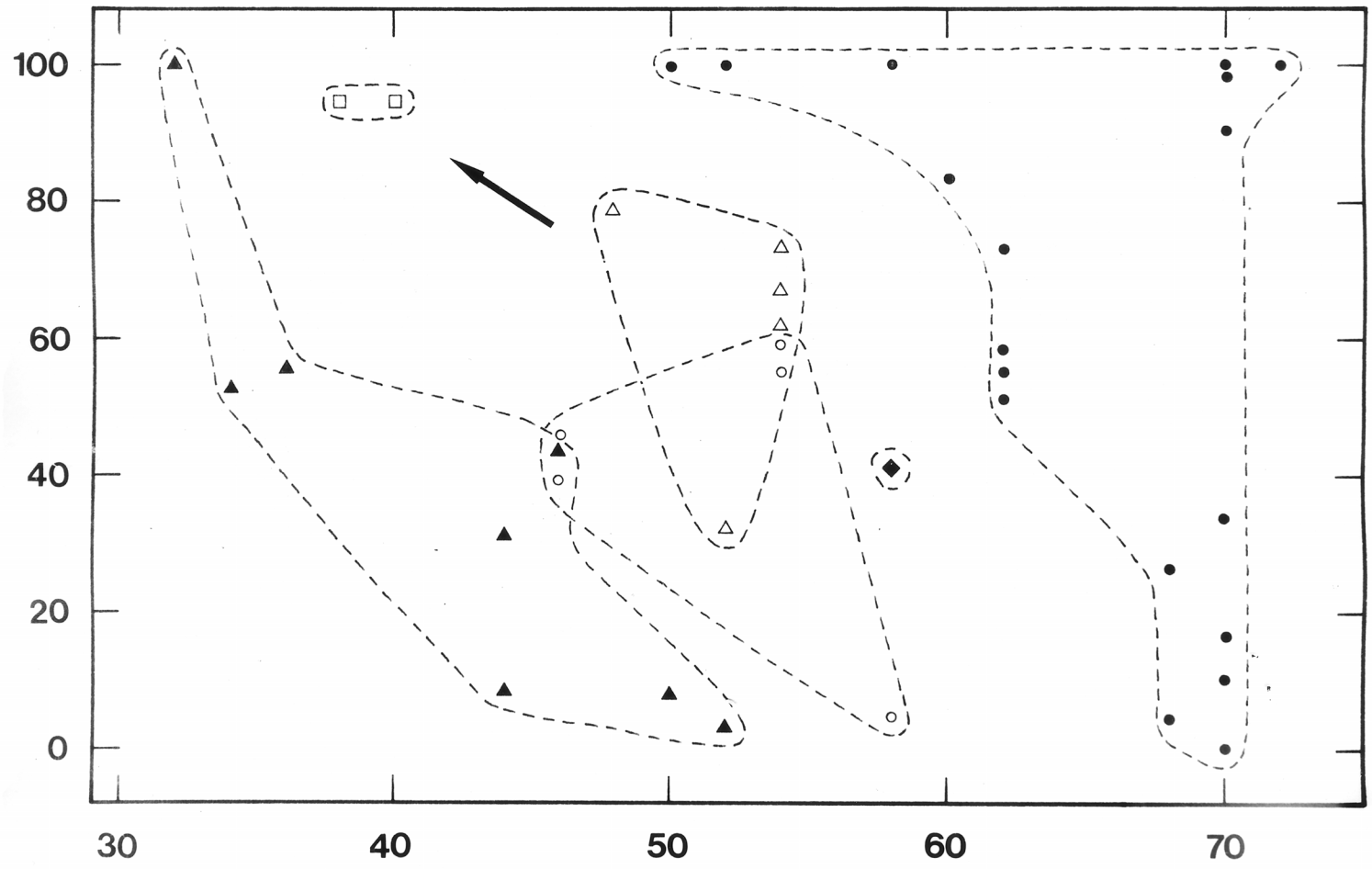
40 chromosomal "morph." This classical interpretation may be unacceptable as a scheme for chromosomal evolution in Microdipodops, because it would completely ignore pertainent ecological, geographical, and morphological differences between the species.

M. megacephalus occurs at higher elevations than does M. pallidus and on soils that were first exposed by the recession of Pleistocene pluvial lakes. M. megacephalus, then, probably has the older geographic range of the two species. The geographic distribution of M. megacephalus is three times greater than that of M. pallidus and coincidently, three times as many races have been described in megacephalus than in the latter. Again, phenetic diversity indicates that more time has been available to this species for genetic divergence. Lastly, M. megacephalus appears to be the less specialized, morphologically, of the two (Hall, 1941b). The above factors indicate to me that M. megacephalus is the more primitive of the two species. Therefore, although instances of chromosomal fission are rare in mammals (Hoffmann and Nadler, 1968; Pizzimenti, 1976), it seems logical to at least suggest that chromosomal fission has occurred in Microdipodops. If this in fact is the case, then one small pair of submetacentrics in M. megacephalus gave rise to the two pairs of small subtelocentrics in M. pallidus by centric fission and subsequent pericentric inversions. The karyotype of M. megacephalus differs further from that of M. pallidus in having two pericentric inversions.

Karyotypic information from 39 species of heteromyids was sequestered in an attempt to discern the phyletic affinity of Microdipodops.

Chromosomal data for the heteromyids is presented graphically in Fig. 17. Data for Dipodomys was obtained from Stock (1974), that for Perognathus was obtained from Patton (1967a, 1967b), and the Liomys and Heteromys data is from Genoways (1973). Fig. 17 is a bivariate plot of per cent biarmed autosomal chromosomes ((FN/AN)-1x100) versus the autosomal number. Six taxonomic groups are indicated: Microdipodops, Liomys, Heteromys, Dipodomys, and the subgenera Chaetodipus and Perognathus. Within each group (excluding the small Microdipodops and Heteromys group) we see a negative correlation between per cent of biarms and autosomal number. Species with a high per cent of biarmed chromosomes are basically the specialized taxa such as P. hispidus, P. flavus, Microdipodops, D. merriami, D. microps, and D. deserti. Conversely, those with a low per cent of biarmed chromosomes and high autosomal number are mostly the generalized (primitive) species such as P. penicillatus, and L. irroratus. D. ordii appears enigmatic inasmuch as it is morphologically generalized yet possesses a reorganized karyotype (see Stock, 1974). Karyotypically, Microdipodops clearly most closely resembles members of the genus Peroganthus (Fig. 17). In consideration of the mechanism of chromosomal evolution within the family, it appears that the Microdipodops karyotype could have been easily derived from taxa in the subgenus Perognathus by centric fusion. Viewed alone, the similarity between the karyotypes of Microdipodops and those of the subgenus Perognathus serves as perhaps a weak argument as to the phyletic affinities of Microdipodops. The relationship though, cannot be dismissed as

Fig. 17.--Chromosomal trends in the family Heteromyidae: a bivariate plot of per cent biarmed autosomal chromosomes (ordinate) versus the autosomal number (abscissa). Six taxonomic groups are indicated as follows: closed triangles, subgenus Chaetodipus; open triangles, subgenus Perognathus; open squares, Microdipodops; closed diamond, Heteromys; open circles, Liomys; closed circles, Dipodomys. The arrow indicates the possible derivation of Microdipodops from the silky pocket mice (subgenus Perognathus).


100
80
60
40
20
0
30
40
50
60
70

meaningless, inasmuch as the conclusion drawn from chromosomal data is in concord with the results from studies of external and cranial morphology, spermatozoa, and the glans penis.

Karyotypes used in this study were taken from: M. megacephalus polionotus, 1.5 mi. SW River Spring Lakes, Adobe Valley, 6490 ft., Mono Co., California; M. pallidus pallidus, 17 mi. S, 5 mi. E. Yerington, 5000 ft., Lyon Co., Nevada.

ECTOPARASITES

The discussion of ectoparasites of Microdipodops presented in this section is based upon all records appearing in the literature and from ectoparasites obtained in the field and identified by experts (listed in the acknowlegments). A list of ectoparasites for species of Microdipodops is presented in Table 8.

Microdipodops megacephalus.--Of the two species of Microdipodops, M. megacephalus possesses a greater diversity of ectoparasites, although the fauna is comparatively meager when rodents in general are considered. Two species of ixodid ticks (Dermacentor parumapertus and Ixodes kingi) have been recorded, as well as one mite (Ischyropoda furmani) and one flea (Meringis hubbardi). Ectoparasites appear to be uncommon on this species, and in my field work I was able to collect only several fleas from M. megacephalus. Johnson (1966) noted that only 8.3 per cent of the individuals of M. megacephalus examined were infested by the tick, Dermacentor parumapertus.

Table 8.--Ectoparasites from species of Microdipodops.

Ectoparasite species	Host Source
	Microdipodops megacephalus
Dermacentor parumapertus	Johnson (1966)
Ixodes kingi	Johnson (1966)
Ischropoda furmani	Whitaker and Wilson (1974)
Meringis hubbardi	Hubbard (1947); personal observation
	Microdipodops pallidus
Dermacentor parumapertus	(this paper)

Microdipodops pallidus.--There are no records of ectoparasites from M. pallidus in the literature. During this study, a single larval tick, Dermacentor parumapertus (RML 64860) was collected and constitutes a first record of an ectoparasite found on this species. This tick is also found on M. megacephalus, Perognathus, Dipodomys and other mammals.

The dearth of ectoparasites on Microdipodops, as compared to other rodents was first observed by Hall and Linsdale (1929) who found only one tick (not identified). Later studies by Hubbard (1947), Johnson (1966), and my work have corroborated their early observation. Undoubtedly, the xeric and dusty environment to which Microdipodops is adapted does not generally favor most ectoparasites. Although both species of Microdipodops inhabit dry sandy regions in the Upper Sonoran Life-zone, it is noteworthy that M. megacephalus occurs at the higher elevations, in more coarse soils, and under more mesic conditions. Inasmuch as M. megacephalus evidently possesses a more diverse ectoparasite fauna than does M. pallidus, it is reasoned that this is a consequence of the less harsh somewhat more mesic environment of megacephalus, which is generally favorable to ectoparasites.

It was the aim of this study on ectoparasites to gather not only ecological information, but evolutionary information concerning Microdipodops. Unfortunately, none of the ectoparasites found on Microdipodops is specific to it, or even restricted to the genus. All ectoparasites (ticks, mites, and fleas) of Microdipodops happened to be common desert-adapted species. It is, therefore,

impossible to make any evolutionary statement based on the ectoparasites thus far collected. If lice should be found on Microdipodops, the situation may be markedly different. The anoplurun lice of the genus Fahrenholzia are restricted to heteromyid rodents and are highly host specific. Lice from Microdipodops could produce important evidence on phylogenetic relationships of their hosts.

V. EVOLUTIONARY RELATIONSHIPS

Since Merriam's description of the genus Microdipodops in 1891 there has been a considerable amount of speculation as to the subfamilial affinities of the group. Does the genus belong to the Perognthinae (the pocket mouse lineage) or the Dipodomyinae (kangaroo rat lineage)? Here is where the comparison should be made and not with the mostly neotropical Heteromyinae with which Microdipodops shares only a few characters. Liomys and Heteromys are clearly evolutionarily independent of the genera Perognathus and Dipodomys (Wood, 1935; Genoways, 1973). Wood (1935) employing both dental and osteological characters in his study, concluded that Microdipodops was most closely related to the genus Perognathus. Conversely, Reeder (1956) determined that Microdipodops was a member of the Dipodomyinae on the basis of dental features alone. These paleontological studies (Wood, 1935; Reeder, 1956), presumably hampered by the lack of fossil material of Microdipodops, have not settled the issue.

In an attempt to objectively discern the phyletic affinities of Microdipodops, cluster analyses based upon both correlation and distance matrices and a principal components analysis were employed. Taxa used in the analyses are the same nine used in the previous section of specific relationships (Perognathus intermedius and Perognathus hispidus of the subgenus Chaetodipus, Perognathus flavus and Perognathus longimembris of the subgenus Perognathus,

Microdipodops megacephalus, Microdipodops pallidus, Dipodomys merriami, Dipodomys ordii, and Dipodomys panamintinus). Other specimens used in addition to those cited previously are listed in Appendix A. Characters used in the analyses, methods of scoring characters, and the data matrix are presented in Appendices B and C. Forty characters, mainly those discussed in previous sections, were contained in the data matrix and used to determine the phenetic relationships of the taxa.

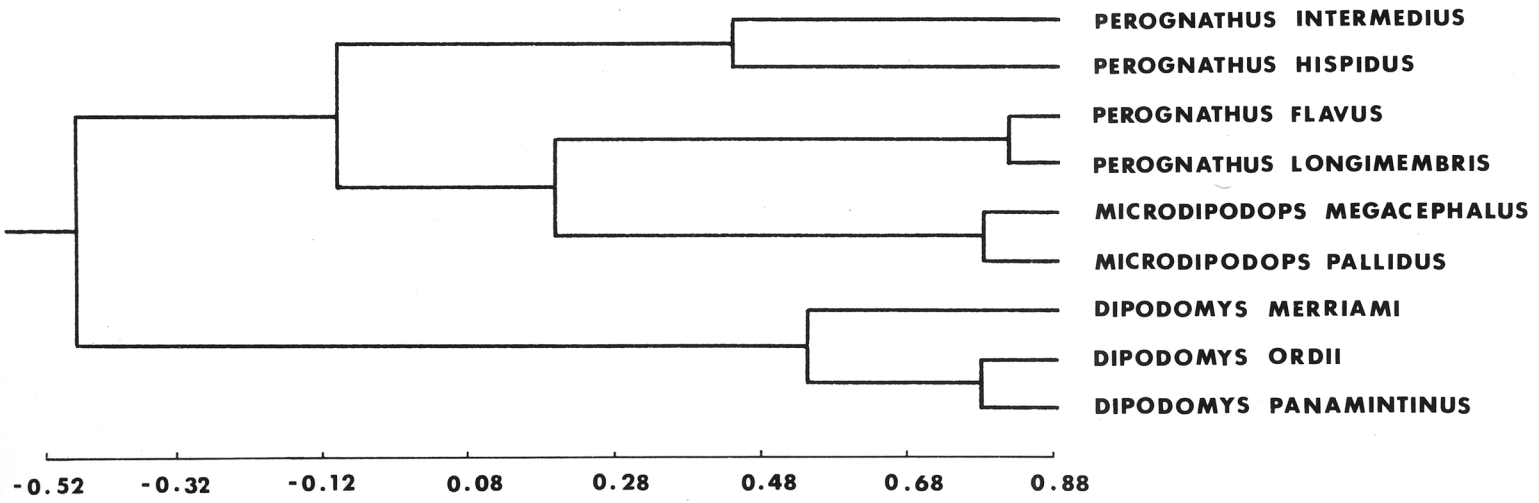
In this section phyletic relationships are inferred on the basis of phenetic similarity and dissimilarity. The heteromyid taxa analyzed doubtlessly are closely related (in fact, the two subfamilies were considered one by Ellerman, 1940) and some degree of convergence is surely present. To account for convergence I incorporated many diverse characters so that, hopefully, many different suites of genes would be involved. Phenetic comparisons and evolutionary inferences thus were based on an overall genotypic representation and not, say, on strictly ectomorphological characters.

The correlation matrix (Table 9) and the correlation phenogram (Fig. 18) derived from it (cophenetic correlation coefficient is 0.976) clearly indicate that the species of Microdipodops are not closely related to Dipodomys, but rather to the silky pocket mice of the subfamily Perognathinae. The three species of Dipodomys show little correlation with the species of Perognathus and Microdipodops (all correlation coefficients greater than -0.317). The silky pocket mice (P. flavus and P. longimembris) proved to be the most

Table 9.--Correlation matrix based upon 40 characters comparing nine species of heteromyids.

	P. intermedius	P. hispidus	P. flavus	P. longimembris	M. megacephalus	M. pallidus	D. merriami	D. ordii	D. panamintinus
P. intermedius	1.000								
P. hispidus	0.445	1.000							
P. flavus	0.096	-0.021	1.000						
P. longimembris	0.036	-0.018	0.823	1.000					
M. megacephalus	-0.285	-0.121	0.152	0.203	1.000				
M. pallidus	-0.218	-0.205	0.245	0.218	0.783	1.000			
D. merriami	-0.317	-0.344	-0.605	-0.523	-0.417	-0.450	1.000		
D. ordii	-0.365	-0.466	-0.542	-0.599	-0.373	-0.465	0.568	1.000	
D. panamintinus	-0.328	-0427	-0.589	-0.605	-0.464	-0.344	0.530	0.781	1.000

Fig. 18.--Correlation phenogram based upon the matrix of correlation among 40 characters, illustrating the phenetic relationships among the nine taxa of heteromyids.


PEROGNATHUS INTERMEDIUS
PEROGNATHUS HISPIDUS
PEROGNATHUS FLAVUS
PEROGNATHUS LONGIMEMBRIS
MICRODIPODOPS MEGACEPHALUS
MICRODIPODOPS PALLIDUS
DIPODOMYS MERRIAMI
DIPODOMYS ORDII
DIPODOMYS PANAMINTINUS
-0.52
-0.32
-0.12
0.08
0.28
0.48
0.68
0.88

highly correlated species (0.823), whereas, the species of Microdipodops were the next most highly correlated pair (0.783).

Examination of the distance matrix (Table 10) and the distance phenogram (Fig. 19) based upon it (cophenetic correlation coefficient 0.961) reveal the same relationships as did the correlation matrix and phenogram. Again, Microdipodops is most closely associated with the species of the subgenus Perognathus. Microdipodops and the species of Perognathus are distantly related to the species of Dipodomys (with all distance coefficients being greater than 1.501).

In the principal components analysis, the first eight components explained 100 per cent of the phenetic variation based upon the matrix of correlation of 40 characters. The first three principal components, alone, explained 83.72 per cent of the variation. It is evident from examination of this three-dimensional plot of the first three principal components (Fig. 20), that component I effectively separates the species of Dipodomys from the other six taxa (Microdipodops and Perognathus). Hence, component I descriminates between the subfamilies and, in so doing, accounts for 55.76 per cent of the total variation. Characters that contributed significently to the separation of the groups along this component (Table 11) were: 1, greatest skull length (positive value); 2, greatest skull breadth (positive); 3, condition of lacremals (negative); 4, molars rooted or non-rooted (negative); 15, presence or absence of a mid-dorsal gland (positive); 18, presence or absence of flank stripes (positive); 21, locomotion (positive); 27, total length (positive); 28, width of maxillary arm (positive);

Table 10.--Distance matrix based upon 40 characters comparing nine species of heteromyids.

	P. intermedius	*P. hispidus*	*P. flavus*	*P. longimembris*	*M. megacephalus*	*M. pallidus*	*D. merriami*	*D. ordii*	*D. panamintinus*
P. intermedius	0.000								
P. hispidus	1.023	0.000							
P. flavus	1.009	1.374	0.000						
P. longimembris	1.012	1.337	0.447	0.000					
M. megacephalus	1.223	1.441	1.042	0.970	0.000				
M. pallidus	1.087	1.374	0.907	0.876	0.483	0.000			
D. merriami	1.635	1.844	1.843	1.842	1.645	1.574	0.000		
D. ordii	1.637	1.858	1.804	1.747	1.575	1.534	0.946	0.000	
D. panamintinus	1.633	1.850	1.832	1.761	1.627	1.501	0.989	0.593	0.000

Fig. 19.--Distance phenogram derived from the distance matrix illustrating the phenetic relationships among the nine taxa of heteromyids.

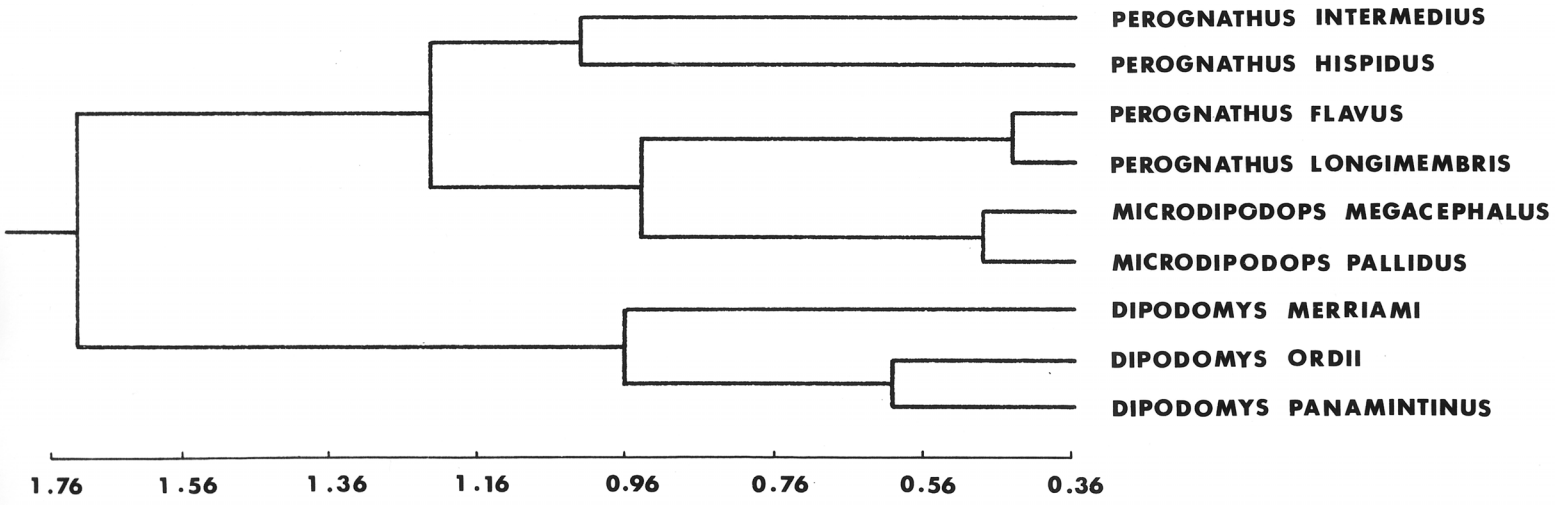

PEROGNATHUS INTERMEDIUS
PEROGNATHUS HISPIDUS
PEROGNATHUS FLAVUS
PEROGNATHUS LONGIMEMBRIS
MICRODIPODOPS MEGACEPHALUS
MICRODIPODOPS PALLIDUS
DIPODOMYS MERRIAMI
DIPODOMYS ORDII
DIPODOMYS PANAMINTINUS
1.76
1.56
1.36
1.16
0.96
0.76
0.56
0.36

Fig. 20.--Three-dimensional projection of nine heteromyid taxa onto the first three principal components. Taxa are as follows: A, Perognathus intermedius; B, Perognathus hispidus; C, Perognathus flavus; D, Perognathus longimembris; E, Microdipodops megacephalus; F, Microdipodops pallidus; G, Dipodomys panamintinus; H, Dipodomys ordii; I, Dipodomys merriami.

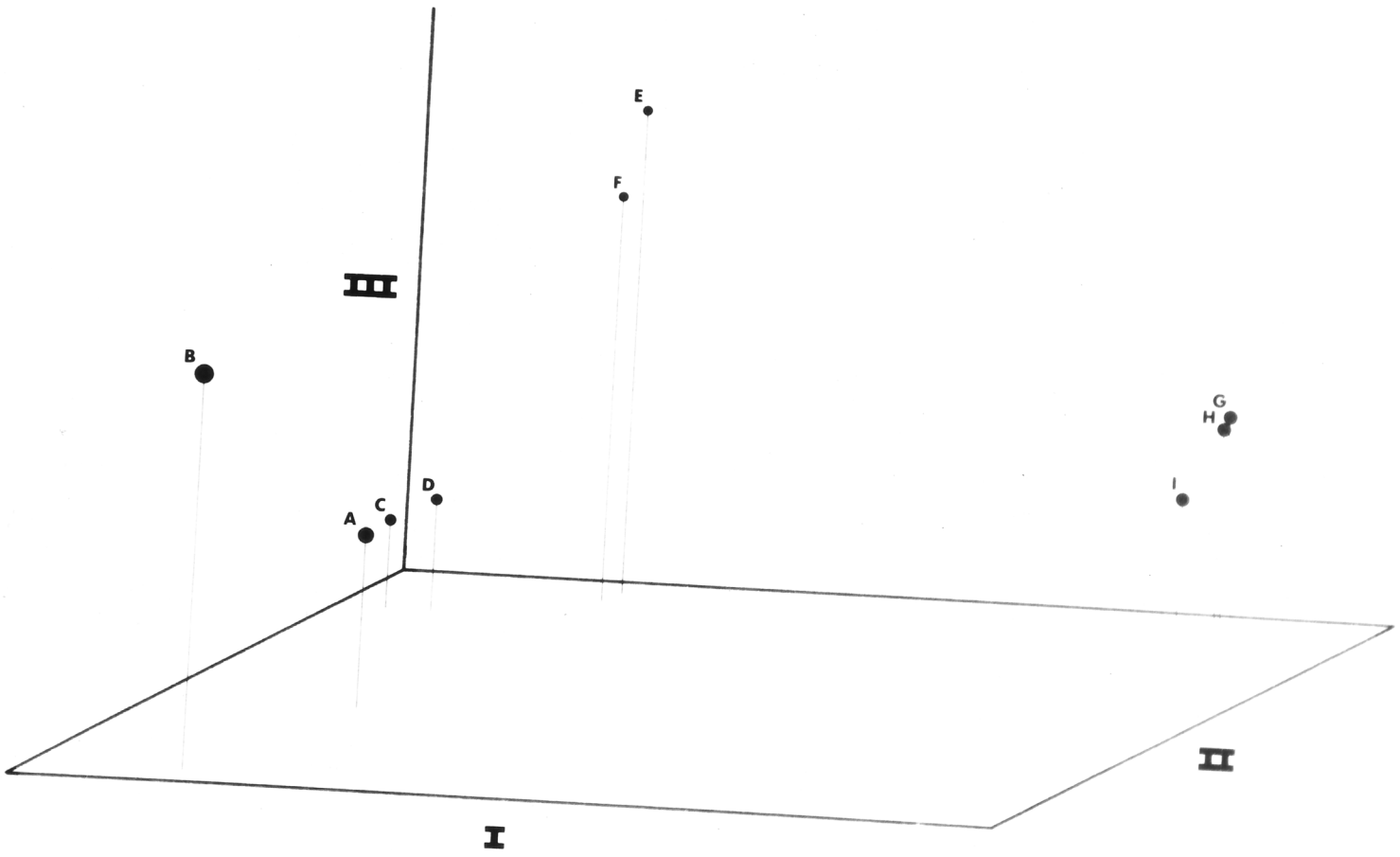

E
F
III
B
G
H
D
I
C
A
II
I

Table 11.--Factor matrix from correlation among 40 characters of nine species of heteromyids.

Character	Component I	Component II	Component III
1	0.921	-0.189	0.325
2	0.909	0.090	0.395
3	-0.987	0.003	0.125
4	-0.987	0.003	0.125
5	0.701	0.271	-0.458
6	0.732	0.309	-0.203
7	-0.506	0.330	-.673
8	0.227	-0.925	0.055
9	0.347	0.876	-0.070
10	0.742	0.295	0.036
11	0.314	-0.920	0.153
12	0.720	0.194	-0.370
13	0.347	0.876	-0.070
14	0.627	-0.429	0.399
15	0.987	-0.003	-0.125
16	0.611	9.724	0.271
17	0.806	-0.238	-0.278
18	0.987	-0.003	-0.125
19	0.749	0.313	0.043
20	0.755	0.526	0.177

Table 11.--Continued

Character	Component I	Component II	Component III
21	0.937	0.258	0.219
22	0.595	-0.478	0.368
23	0.251	-0.821	-0.240
24	0.845	-0.294	0.314
25	-0.362	0.112	0.759
26	0.512	-0.125	0.423
27	0.917	-0.320	0.163
28	0.983	-0.101	-0.056
29	-0.389	-0.854	-0.250
30	0.886	-0.309	0.289
31	0.987	-0.003	-0.125
32	-0.625	-0.281	0.039
33	0.987	-0.003	-0.125
34	-0.267	0.550	0.744
35	0.987	-0.003	-0.125
36	-0.987	0.003	0.125
37	0.855	-0.319	-0.344
38	-0.474	0.058	0.192
39	0.081	-0.012	0.504
40	0.987	-0.003	-0.125

31, presence or absence of tail stripes (positive); 33, wear patterns of molars (positive); 35, condition of vertebrae (positive); 36, presence or absence of astragalus-cuboid contact (negative); and 40, presence or absence of a white ring at the base of the tail (positive).

Component II, which explains 18.33 per cent of the total phenetic variation, serves to distinguish between the three groups within the Perognathinae (that is, Microdipodops and the subgenera Chaetodipus and Perognathus). From examination of Fig. 20, it can be seen that Microdipodops is clearly nearest the silky pocket mice (P. flavus and P. longimembris). Characters mostly responsible for separation along this axis (Table 11) were: 8, length of glans penis (negative); 9, presence or absence of urethral lappets (positive); 11, length of baculum (negative); 13, condition of pelage (positive); 23, length of tip of glans penis (negative); and 29, greatest interparietal width (negative).

The third component serves to separate the congeneric species. Component III explains 9.64 per cent of the total phenetic variability. The characters with high weighting in this component were: 7, morphology of the Y chromosome (negative); 25, length of sperm head (positive); and 34, presence or absence of tail with greatest diameter in middle (positive).

The results of the principal components analysis are in accord with the correlation and distance phenograms and clearly indicate that Microdipodops belongs to the Perognathinae and is most closely related to the silky pocket mice as represented by P. flavus and P. longimembris.

Following a cursory and superficial examination of skins and skulls of Microdipodops, Dipodomys, and Perognathus, one may conclude (erroneously) that, on the basis of two very obvious characters (size of hind foot and inflation of the bullae) Microdipodops is morphologically quite similar to Dipodomys. Results of the present study, however, indicate that the above mentioned characters are simply convergent in nature and, indeed, they are virtually the only characteristics shared between the genera.

Elongation of the pes in heteromyids is a consequence of adaptation to sandy desert soil and the ricochetal mode of locomotion. The long hind foot in Microdipodops and Dipodomys is an example of convergence. Structurally, the pes is quite different in each genus. In Dipodomys there exists the marked tendency for atrophication of the halux (see character 39, halux-heel measurement). In several species of Dipodomys the halux is lost completely, leaving only four toes. But in Perognathinae (including Microdipodops) there exists a different trend in that all five toes are retained and in no species is the halux markedly reduced (as in Dipodomys) or absent. Additionally, the tarsal elements are entirely different (character 36, tarsal elements). Bullae inflation appears to reflect the ecological affinities of the species. Arid-adapted heteromyid species generally have larger bullae than do the more mesic- and tropical-adapted taxa. The fact that Microdipodops and Dipodomys have greatly inflated bullae is, in itself, of no phyletic significance, because bullar inflation is known to be quite variable in the genus Perognathus.

Certainly some characters, such as bullar inflation and length of hindfoot, are more plastic than others and, therefore, less reliable in determining phyletic relationships. Characters dealing with reproduction would seem to be rather conservative, for example. Examination and analysis of such characters (glans penis, spermatozoa, and baculum) clearly indicate the close relationship between silky pocket mice (subgenus Perognathus) and kangaroo mice. The karyotype, too, seems conservative and, again Microdipodops seems to be allied to the Perognathus based on karyotypic data. A detailed description of the differences between Dipodomys and Microdipodops are presented elsewhere (see section on diagnosis and comparisons of the genus Microdipodops).

Microdipodops is most closely related to the silky pocket mice and was probably derived from the pocket mouse lineage, or it may represent a lineage distinct from either Perognathus or Dipodomys. In either event, the question remains as to when, where, and under what circumstances might such a specialized genus have evolved. From the work of Axelrod (1950) it is known that there was a continual trend toward increasing aridity throughout the Tertiary in southwestern North America. Doubtlessly, this warming trend was intimately associated with the general evolutionary events of the family Heteromyidae (Wood, 1935). The oldest known fossils of Perognathus date from Miocene. During that period, the Great Basin and much of southwestern North America was subhumid to semiarid in climate. Climatic conditions at that time are deemed inappropriate for selection of an extremely arid-adapted group such as Microdipodops

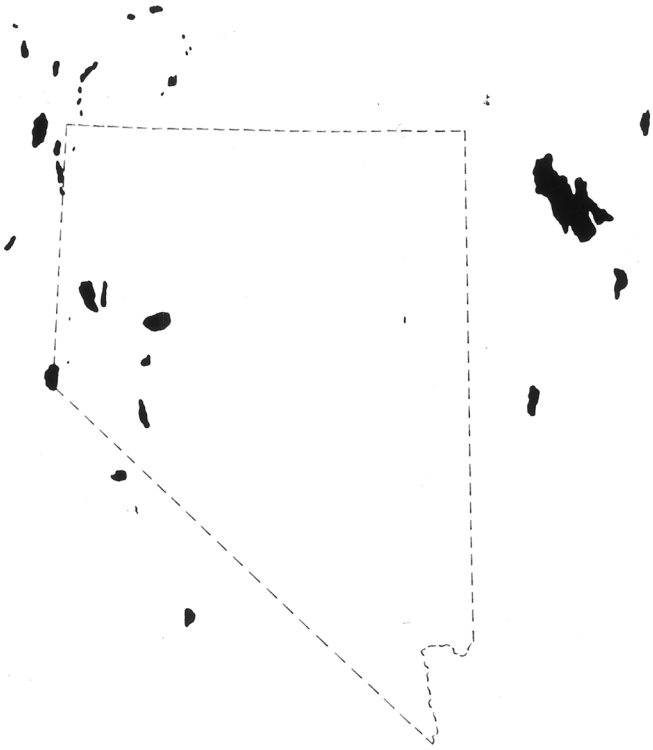
and it is postulated that the genus evolved largely *in situ* in early Pleistocene time, subsequent to the Sierra Nevada diastrophism.

Following the Sierra Nevada diastrophism of late Pliocene-Pleistocene age (Blackwelder, 1948), the Great Basin was positioned in a rain shadow and the present desert climate was initiated (Morrison, 1965). The Sierra Nevada, and to a lesser extent the discontinuous subparallel ranges within the Great Basin created during the crustal unrest of late Pliocene-Pleistocene times, effectively removes moisture from the generally eastward-moving air from the Pacific Ocean and allows little precipitation to reach the floor of the basins. Additionally, it was during the interpluvial periods of the Pleistocene that the large sand accumulations in the Great Basin were formed.

The perognathine ancestor to *Microdipodops* was presumably adapted to semiarid grassland or subhumid scrub habitat, or both. The Sierra Nevada diastrophism, which formed the Great Basin desert provided the impetus for the evolution of a rodent (*Microdipodops*) that could adapt to the newly available and extremely xeric sandy habitat. Although the origin of *Microdipodops* in early Pleistocene time (Blancan age) may seem quite recent (most genera of rodents arose during the Tertiary), it must be remembered that the genus is narrowly adapted and suitable environmental conditions did not exist prior to that time. Moreover, the shift from the ancestral semiarid grassland adaptive zone to the xeric, sandy habitat (new adaptive zone) probably was accomplished by rather rapid "quantum" evolution. Downs (1956), McLaren (1960), and Simpson (1953) have associated tachytelic rates

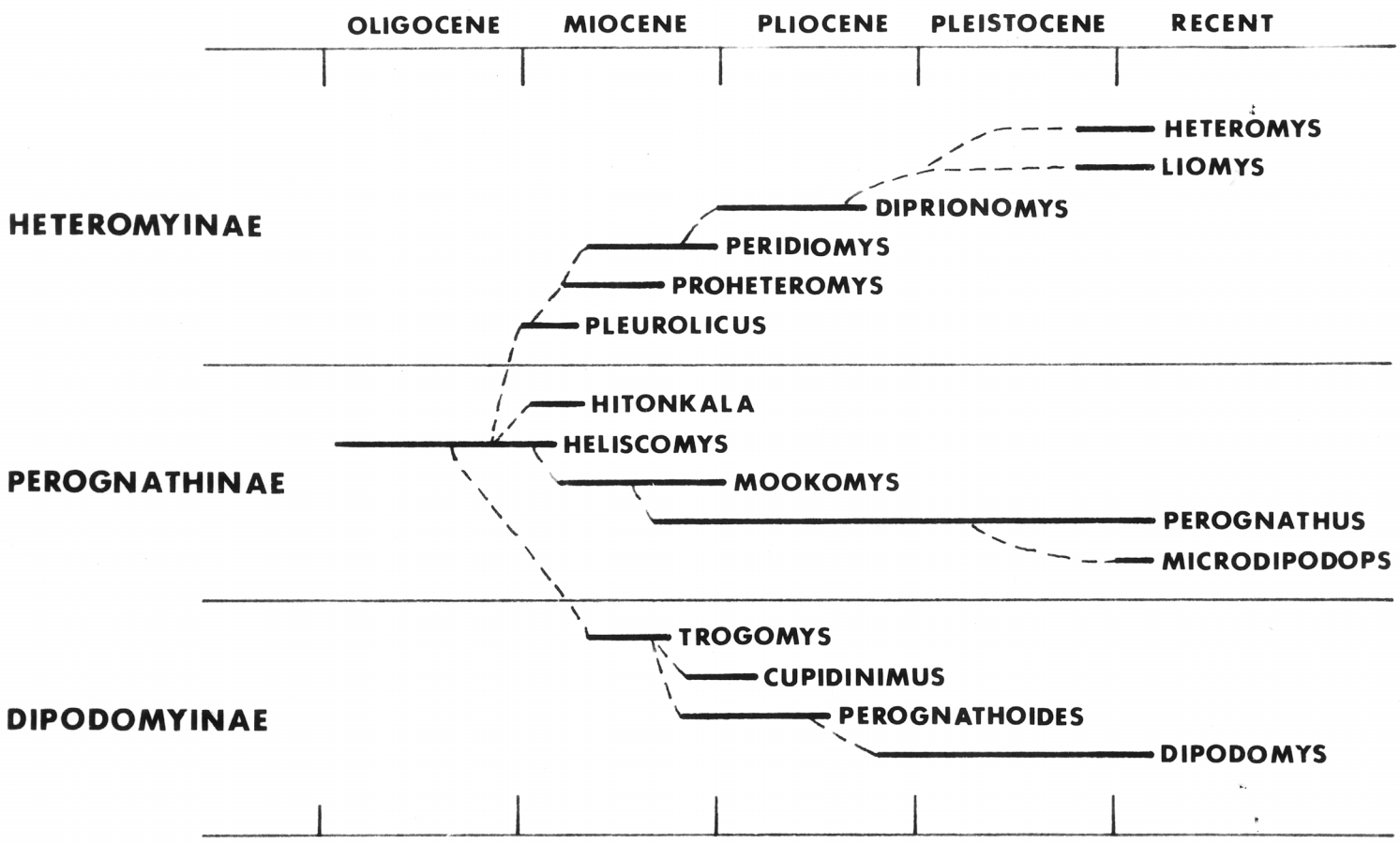
Fig. 21.--The great Basin region showing A, pluvial lakes during their maximum height during the Wisconsin and B, the distribution of the lakes today (after Morrison, 1965) Scale at center equals 100 kilometers.

A



B

Fig. 22.--Phylogeny of the Heteromyidae (excluding the Geomyinae and the Entoptychinae) showing the position of Microdipodops as evidenced by this study. Modified from Lindsay (1972).


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

at that particular locality mentioned.

M. megacephalus appears to be the more primitive of the two species of Microdipodops. Morphologically, M. megacephalus is less specialized in that it has smaller bullae and smaller hind feet than does M. pallidus. It is the more generalized of the two ecologically, because it inhabits both sparsely vegetated sand dune habitats (to which M. pallidus is restricted) and sandy soil overlaid with gravel in comparitively lush floral areas. Also, it occurs at higher elevations than does M. pallidus and on the soils that would have been the last to be covered and the first to be exposed by pluvial lakes during the Pleistocene. Most convincing of all, is the fact that 12 subspecies have been described for the species M. megacephalus, whereas only four have been named for M. pallidus, indicating that more time has been available for divergence in M. megacephalus.

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APPENDIX A

Additional specimens examined in the section of Evolutionary Relationships which were not cited previously.

Microdipodops megacephalus.--7.5 mi. E Cliff Spring, 5900 ft., Nye Co., Nevada, 1 (MVZ).

Microdipodops pallidus.--W end Soda Lake, 3900 ft., Churchill Co., Nevada, 1 (MVZ).

Perognathus flavus.--4.9 mi. S, 4.8 mi. E Glen Rio, Deaf Smith Co., Texas, 1 (TTU); 4.5 mi. W Toyahvale, 3700 ft., in Jeff Davis Co., Texas, 1 (TTU).

Perognathus longimembris.--5 mi. NW Shoemaker, 3400 ft., Los Angeles Co., California; 1 (MVZ); 1¼ mi. N Sulfur, Humboldt Co., Nevada, 1 (MSB).

Perognathus hispidus.--7 mi. N Post, Garza Co., Texas, 1 (TTU); 5 mi. S Chadron, Dawes Co., Nebraska, 1 (TTU).

Perognathus intermedius.--Jornada Experimenta Range, Dona Ana Co., New Mexico, 1 (TTU); 17 mi. W Bernardo, Ladron Mts., 7000 ft., Socorro Co., New Mexico, 1 (MSB); 16 mi. W, 1 mi. N Bernardo, Ladron Mts., 7500 ft., Socorro Co., New Mexico, 1 (MSB).

Dipodomys merriami.--Barstow, San Bernardino Co., California, 1 (MVZ); ¼ mi. N Fletcher, 6100 ft., Mineral Co., Nevada, 1 (MVZ); 6.2 mi. SE Portal, Chiricahua Mtns, Cochise Co., Arizona, 1 (TTU).

Dipodomys ordii.--10 mi. W Caprock, Chavez Co., New Mexico, 1 (TTU); Nebraska Nat. Forest, Bessey Div., Thomas Co., Nebraska, 1 (TTU).

APPENDIX A (CONTINUED)

D. panamintinus.--Freeman Canyon, 2.6 mi. E Walker Pass, Kern Co., California, 1 (MVZ); Sand Canyon, 0.4 mi. N Hwy 58, 2.9 mi. EXS of Monolith, 3949 ft., Kern Co., California, 8 (MSB); Sand Canyon, 0.1 mi. S Hwy 58, 3.1 mi. ESE Monolith, 3900 ft., T 32 S, R 34 E, NW ¼ Sec. 27, Kern Co., California, 5 (MSB).

APPENDIX B

Forty characters used in analyses of evolutionary relationships and methods of scoring the characters.

Characters and methods of scoring

1 Greatest skull length (mensural data)

2 Greatest skull breadth (mensural data)

3 Lacremals (hamular process joined, 1; free, 2)

4 Molars (nonrooted, 1; rooted, 2)

5 2N (diploid number of chromosomes)

6 FN (fundamental number of chromosomes)

7 Morphology of Y chromosome (acrocentric to acrocentric-subtelocentric, 1; metacentric, 2)

8 Length of glans penis (mensural data)

9 Urethral lappets (absence, 1; presence, 2)

10 Dorsal groove on glans penis (groove absence, 1; single groove, 2; double groove, 3)

11 Length of baculum (mensural data)

12 Morphology of baculum tip (straight or trifid, 1; moderately upturned, 2; sharply upturned, 3)

13 Pelage characteristics (harsh, 1; silky, 2)

14 Sperm tail length (mensural data)

15 Mid-dorsal gland (absence, 1; presence, 2)

16 Soles of hind feet (naked, 1; somewhat hairy, 2; fully haired, 3)

17 Crested tail (absence, 1; presence, 2)

APPENDIX B (CONTINUED)

18 Flank stripes (absence, 1; presence, 2)

19 Tail length/total length X 100 (mensural data)

20 Hind foot length/body length X 100 (mensural data)

21 Locomotion (quadrupedal, 1; partially bipedal, 2; bipedal, 3)

22 Width of glans penis (mensural data)

23 Length of tip of glans penis (mensural data)

24 Height of glans penis (mensural data)

25 Sperm head length (mensural data)

26 Sperm head width (mensural data)

27 Total length (mensural data)

28 Greatest width of maxillary arm of zygoma (mensural data)

29 Greatest interparietal width (mensural data)

30 Nasal length (mensural data)

31 White side stripes on tail (absence, 1; presence, 2)

32 Reproduction (average embryo count or litter size)

33 Molar wear patterns (dentine surrounded by enamel, 1; enamel limited to anterior and posterior plates, 2)

34 Tail greater diameter in middle than at base or tip (absence, 1; presence, 2)

35 Median ventral foramina in caudal vertebrae (absence, 1; presence, 2)

37 Diameter of eye/body length X 100 (mensural data)

38 Number of digits on hind foot (four or five)

39 Halux to heel (mensural data)

40 White ring at base of tail (absence, 1; presence, 2)

APPENDIX C

Matrix of characters used in the analyses of evolutionary relationships.

Character	*P. intermedius*	*P. hispidus*	*P. flavus*	*P. longimembris*	*M. megacepahlus*	*M. pallidus*	*D. merriami*	*D. ordii*	*D. panamintinus*
1	25.06	30.95	20.65	21.72	28.07	28.66	36.02	38.34	39.08
2	13.31	16.10	11.66	12.28	18.57	19.35	22.65	24.49	23.87
3	2.00	2.00	2.00	2.00	2.00	2.00	1.00	1.00	1.00
4	2.00	2.00	2.00	2.00	2.00	2.00	1.00	1.00	1.00
5	46.00	34.00	50.00	56.00	40.00	42.00	52.00	72.00	64.00
6	58.00	64.00	86.00	88.00	74.00	78.00	100.00	140.00	96.00
7	1.00	1.00	2.00	2.00	1.00	1.00	1.00	1.00	1.00
8	6.41	8.43	4.73	4.24	3.93	4.93	6.96	5.54	5.77
9	1.00	1.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
10	2.00	1.00	2.00	1.00	2.00	2.00	2.00	3.00	3.00
11	11.20	16.40	6.80	5.20	6.18	6.55	10.78	11.47	10.38
12	3.00	1.00	2.00	2.00	2.00	2.00	3.00	3.00	3.00
13	1.00	1.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
14	129.20	154.00	96.80	116.40	133.28	134.88	171.60	146.40	137.20
15	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00
16	1.00	1.00	2.00	2.00	3.00	3.00	3.00	3.00	3.00
17	2.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00
18	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00

APPENDIX C (CONTINUED)

Character	P. intermedius	P. hispidus	P. flavus	P. longimembris	M. megacephalus	M. pallidus	D. merriami	D. ordii	D. panamintinus
19	54.07	48.07	48.42	53.71	54.57	55.15	59.45	54.81	59.34
20	29.11	24.75	27.63	31.28	34.82	36.65	39.27	35.65	38.96
21	1.00	1.00	1.00	1.00	2.00	2.00	3.00	3.00	3.00
22	1.50	2.01	1.23	1.23	1.45	1.48	1.44	2.01	2.19
23	1.16	1.79	0.87	1.01	0.47	0.59	1.71	0.98	1.06
24	1.29	1.80	1.09	1.11	1.43	1.46	1.87	1.91	2.34
25	4.37	5.45	4.75	4.50	6.16	5.17	4.70	4.84	4.01
26	2.60	3.02	2.30	2.75	3.34	2.41	3.14	3.35	2.81
27	172.00	194.50	110.50	131.25	154.95	156.69	235.50	239.00	270.80
28	1.90	1.81	1.39	0.89	1.61	1.54	5.23	4.62	5.23
29	7.70	8.22	3.68	4.03	0.80	0.88	1.78	2.94	2.03
30	9.25	12.24	7.57	8.20	9.98	9.91	13.10	13.87	14.90
31	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00
32	3.43	5.50	4.50	5.00	3.90	3.90	3.10	3.00	4.14
33	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00
34	1.00	1.00	1.00	1.00	2.00	2.00	1.00	1.00	1.00
35	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00
36	2.00	2.00	2.00	2.00	2.00	2.00	1.00	1.00	1.00
37	5.23	4.75	4.50	4.58	3.99	4.31	5.81	6.13	5.62
38	5.00	5.00	5.00	5.00	5.00	5.00	4.00	5.00	5.00

APPENDIX C (CONTINUED)

Character	P. intermedius	P. hispidus	P. flavus	P. longimembris	M. megacephalus	M. pallidus	D. merriami	D. ordii	D. panamintinus
39	14.28	16.89	9.92	10.67	17.24	17.89	0.00	20.31	23.33
40	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00