EVOLUTIONARY RELATIONSHIPS OF KANGAROO MICE, GENUS *MICRODIPODOPS*

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ABSTRACT.—There is currently much controversy surrounding the issue as to whether kangaroo mice (*Microdipodops*) are more closely related to the kangaroo rats (genus *Dipodomys*; subfamily Dipodomyinae) or to the pocket mice (genus *Perognathus*; subfamily Perognathinae), or whether they represent a lineage distinct from both kangaroo rats and pocket mice. In an attempt to resolve this question, the two species of kangaroo mice were compared to seven other heteromyid taxa by means of cluster analyses based on a data matrix containing a broad spectrum of phenetic characters. The seven taxa selected for comparison with two species of *Microdipodops* include *Perognathus intermedius*, *P. hispidus*, *P. flavus*, *P. longimembris*, *Dipodomys merriami*, *D. ordii*, and *D. panamintinus*. Results of the analyses indicate clearly that *Microdipodops* is phenetically most similar to the silky pocket mice (subgenus *Perognathus*) as represented by *P. flavus* and *P. longimembris*. It is hypothesized that *Microdipodops* was derived from perognathine stock and evolved largely *in situ* in the Great Basin of North America during the Blancan age. That *Microdipodops* may represent the endpoint of a third lineage distinct from those giving rise to either *Perognathus* or *Dipodomys* is considered, but appears presently unanswerable in the absence of a fossil record of *Microdipodops*.

Kangaroo mice (genus *Microdipodops*) are members of the North American rodent family Heteromyidae and are restricted to extremely xeric, sandy habitats in the Great Basin Desert. The genus *Microdipodops*, known only from the Recent Epoch, is the poorest in terms of number of species (*M. megacephalus* and *M. pallidus*) and occupies the smallest geographic range of the five extant genera of heteromyids (*Perognathus*, *Dipodomys*, *Liomys*, and *Heteromys*). Though other genera of heteromyids have been studied intensively, comparatively little information is known about kangaroo mice.

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 Perognathinae (pocket mouse lineage) or the Dipodomyinae (kangaroo rat lineage) within the family? A third alternative to be considered is the possibility that *Microdipodops* represents a lineage distinct from both pocket mice and kangaroo rats. All authors agree that the mostly Neotropical subfamily Heteromyinae (*Liomys* and *Heteromys*) is clearly an evolutionarily independent lineage quite removed from the *Perognathus*, *Dipodomys*, and *Microdipodops* lineages (Wood, 1935; Reeder, 1956; Genoways, 1973). Merriam (1891) noted in the description of the genus that "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" (Fig. 1). Wood (1935) in his paleontological treatise on the evolutionary relationships of heteromyids likewise concluded that *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), employing mainly dental characters, performed an extensive review of both fossil and Recent heteromyids and placed *Microdipodops* in the subfamily Dipodomyinae. Thus, examination of the available fossil materials in two paleontological studies (Wood, 1935; Reeder, 1956) has led to opposite conclusions.

In an attempt to discern objectively the phyletic affinities of *Microdipodops*, cluster analyses based upon both correlation and distance matrices and a principal components analysis were employed. Forty characters were contained in the data matrix and

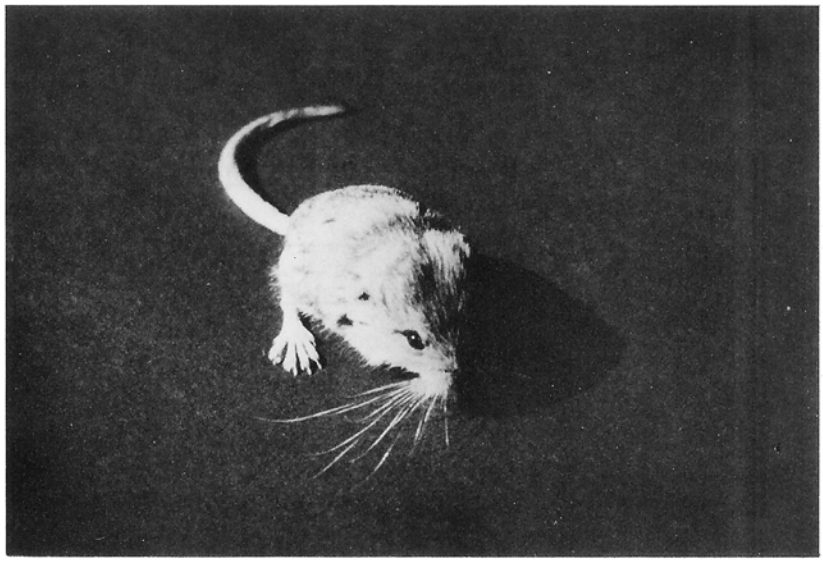

FIG. 1.—Photograph of *Microdipodops megacephalus* illustrating the large head, thickened middle of tail, and the long, furry hind feet.

used to determine the phenetic relationships of the taxa. The matrix represents a broad spectrum of characters including those derived from studies of phalli, bacula, spermatozoa, osteological features, chromosomes, and the pelage (Appendix A). Seven taxa were selected for comparison with the two species of *Microdipodops*, including *Perognathus intermedius* and *P. hispidus* of the subgenus *Chaetodipus*; *P. flavus* and *P. longimembris* of the subgenus *Perognathus*; and *Dipodomys merriami*, *D. ordii*, and *D. panamintinus*.

METHODS

Accounts and extensive descriptions of the characters for each of the nine species of heteromyids used in the study are given in my thesis (Hafner, 1976), and will not be detailed here. The characters used in the analyses, methods of scoring the characters, and the data matrix, though, are presented in Appendices A and B. Specimens used in this study are listed in Appendix C.

In the statistical analyses, OTU's (Operational Taxonomic Units) were the nine different species of heteromyids and the characters were mean values (see Appendices A and B). Using the 1974 version of the NTSYS program, an initial 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 40 characters (Appendix B). Cluster analyses, using UPGMA (unweighted pair-group method using arithmetic averages), were performed on the correlation and distance matrices producing correlation and distance phenograms. These procedures were performed on the IBM 370-145 computer at Texas Tech University.

Using a matrix of simple correlation among characters, once again, a partial correlation matrix was produced. The partial correlation matrix was then used as the basis for a principal components analysis. Both the partial correlation matrix and the principal components analysis were produced using the SPSS program on the CDC 6400 computer at the University of California, Berkeley. The partial correlation procedure removes the effects of one selected control variable from the relationships between the variables and is helpful in detecting and eliminating spurious relationships. Spurious correlations occur, for example, when the correlation between character X and Y is the result of the fact that character X varies along with another character Z, which is in fact, the true predictor of character Y. When the effects of this character (Z) are controlled or held constant by means of partial correlation, character Y may no longer vary with character X. Factors of size quite frequently create problems in the principal components analysis, inasmuch as they are heavily weighted along the first component and sometimes tend to obscure the true relationships among the OTU's. The partial correlation technique was utilized in this study, to

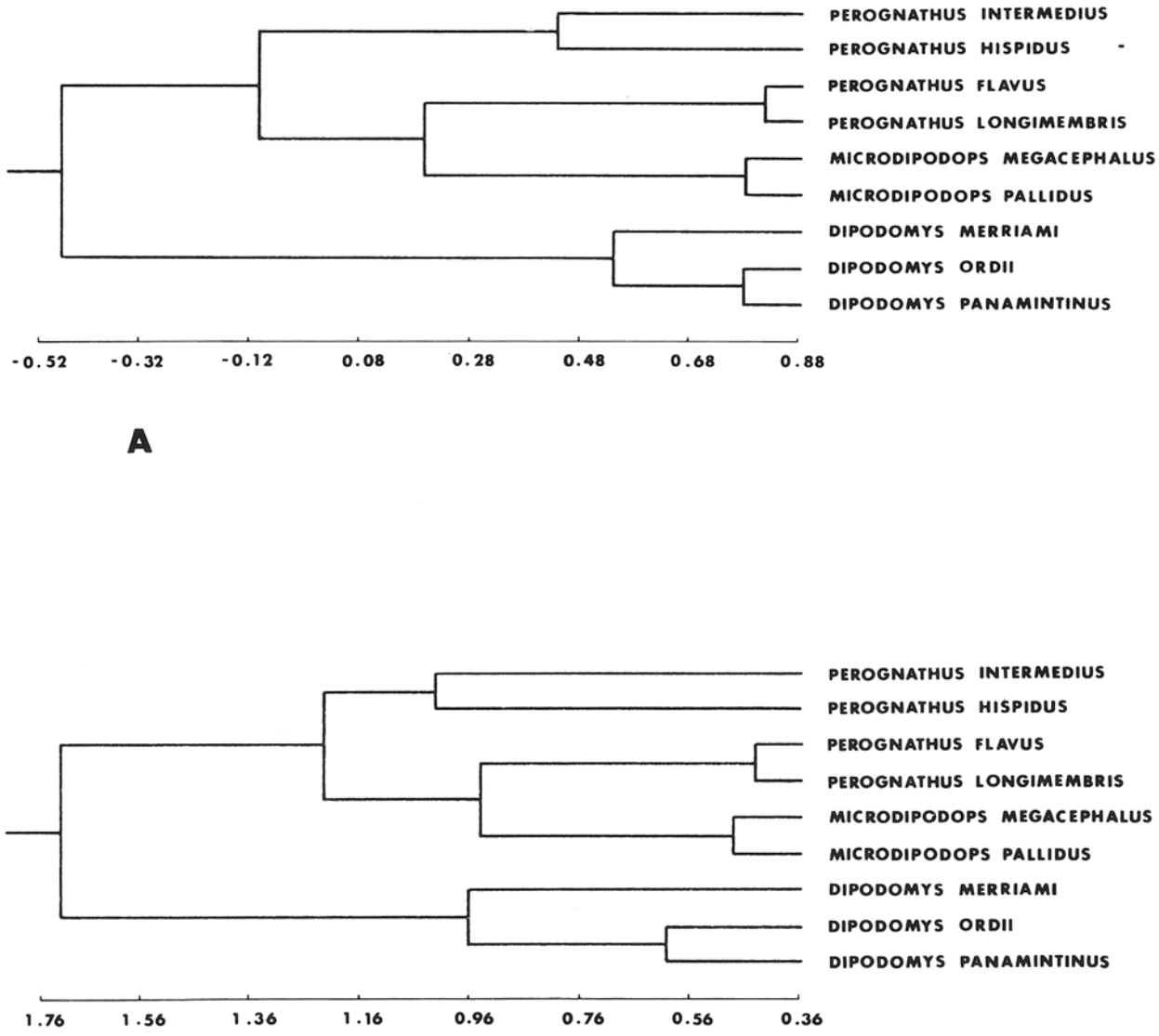

FIG. 2.—Phenograms illustrating the phenetic relationships among the nine taxa of heteromyids. A) correlation phenogram based upon the correlation matrix (cophenetic correlation coefficient is 0.976); B) distance phenogram derived from the distance matrix (cophenetic correlation coefficient is 0.961).

remove the "size" effect deemed to be manifested by several characters in the study. The matrix of partial correlation among characters was 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-orthographic paper. Discussion of the mechanics and theory of the clustering techniques are given by Sneath and Sokal (1973). The partial correlation procedure and the methods of clustering have been used in a similar fashion by Gould and Garwood (1969), Choate (1970), and Genoways (1973) among others.

RESULTS

In this study phyletic relationships are inferred on the basis of phenetic similarity and dissimilarity. The heteromyid taxa analyzed are doubtlessly closely related (in fact, the two subfamilies were considered one by Ellerman, 1940), yet some degree of morphological convergence is surely present. In order to minimize the effects of phenetic similarities resulting from morphological convergence, a wide variety of characters were examined so that, hopefully, a larger portion of the genome would be

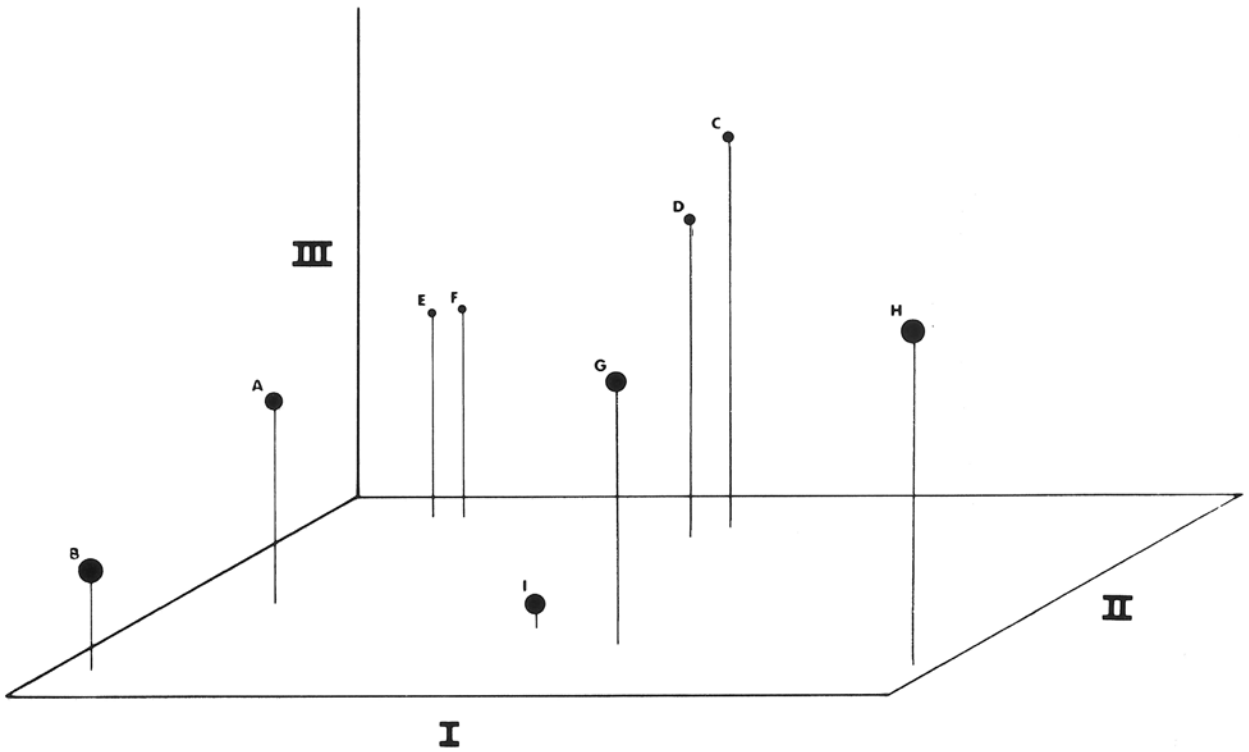

FIG. 3.—Three-dimensional projection of nine heteromyid taxa onto the first three principal components. Taxa are as follows: A) *Perognathus intermedius*; B) *P. hispidus*; C) *P. flavus*; D) *P. longimembris*; E) *Microdipodops megacephalus*; F) *M. pallidus*; G) *Dipodomys panamintinus*; H) *D. ordii*; I) *D. merriami*.

represented. Phenetic comparisons and evolutionary inferences thus were based on an assumed overall genotypic representation.

The correlation matrix (Table 1) and the correlation phenogram (Fig. 2) 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 only low correlation with the species of *Perognathus* and *Microdipodops* (all correlation coefficients less than −0.317). Not surprisingly, silky pocket mice (*P. flavus* and *P. longimembris*) proved to be the most 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 1) and the distance phenogram (Fig. 2) based upon it (cophenetic correlation coefficient is 0.961) reveal the same relation-

TABLE 1.—*Correlation matrix (above the diagonal) and distance matrix (below the diagonal) based upon 40 characters comparing nine species of heteromyids.*

Taxon	*P. intermedius*	*P. hispidus*	*P. flavus*	*P. longimembris*	*M. megacephalus*	*M. pallidus*	*D. merriami*	*D. ordii*	*D. panamintinus*
P. intermedius		0.445	0.096	0.036	−0.285	−0.218	−0.317	−0.365	−0.328
P. hispidus	1.023		−0.021	−0.018	−0.121	−0.205	−0.344	−0.466	−0.427
P. flavus	1.009	1.374		0.823	0.152	0.245	−0.605	−0.542	−0.589
P. longimembris	1.012	1.337	0.447		0.203	0.218	−0.523	−0.599	−0.605
M. megacephalus	1.223	1.441	1.042	0.970		0.783	−0.417	−0.373	−0.464
M. pallidus	1.087	1.374	0.907	0.876	0.483		−0.450	−0.465	−0.344
D. merriami	1.635	1.844	1.843	1.842	1.645	1.574		0.568	0.530
D. ordii	1.637	1.858	1.804	1.747	1.575	1.534	0.946		0.781
D. panamintinus	1.633	1.850	1.832	1.761	1.627	1.501	0.989	0.593	

TABLE 2.—*Factor matrix from correlation among 40 characters of nine species of heteromyids.*

Character	Component I	Component II	Component III
2	−0.073	0.946	0.006
3	−0.971	−0.170	0.094
4	−0.971	−0.170	0.094
5	0.826	0.172	0.453
6	0.710	0.319	0.276
7	0.816	0.140	0.157
8	−0.172	−0.859	−0.390
9	0.407	0.885	0.059
10	0.317	0.389	0.588
11	−0.210	−0.951	−0.108
12	0.586	0.175	0.047
13	0.407	0.885	0.059
14	−0.357	−0.276	−0.840
15	0.971	0.170	−0.094
16	0.140	0.984	0.005
17	0.540	−0.298	−0.024
18	0.971	0.170	−0.094
19	0.224	0.572	−0.294
20	0.179	0.883	−0.186
21	0.374	0.883	−0.105
22	−0.316	−0.597	0.658
23	0.185	−0.768	−0.561
24	−0.126	−0.345	0.166
25	−0.683	0.227	−0.152
26	−0.119	−0.021	−0.212
27	0.361	−0.594	−0.059
28	0.866	0.044	−0.234
29	−0.080	−0.992	0.042
30	0.057	−0.729	0.073
31	0.971	0.170	−0.094
32	−0.246	−0.336	0.110
33	0.971	0.170	−0.094
34	−0.708	0.689	0.001
35	0.971	0.170	−0.094
36	−0.971	−0.170	0.094
37	0.776	−0.460	−0.012
38	−0.338	−0.094	0.921
39	−0.459	−0.005	0.872
40	0.971	0.170	−0.094
Percent of variation explained	44.7	26.4	11.3

ships as did the correlation matrix and phenogram. Again, *Microdipodops* is most closely allied with the species of the subgenus *Perognathus*. *Microdipodops* and the species of *Perognathus* are only distantly associated with the species of *Dipodomys* (with all distance coefficients being greater than 1.501).

In the principal components analysis, the first seven factors explained 100% of the phenetic variation based upon the partial correlation matrix of correlation among 40 characters. The effects of size were minimized in the analysis by controlling for Character 1 (greatest skull length). The first three principal components explained 82.4% of the variation. It is evident from examination of the three-dimensional plot of the first three principal components (Fig. 3), that component I effectively separates the species of *Dipodomys* and the silky pocket mice from both *Microdipodops* and the chaetodipine pocket mice, and, in so doing, accounts for 44.7% of the total variation. Characters that contributed greatly to the separation of the groups along this compo-

nent (Table 2) were the following: 3, condition of lacrimals (negative value); 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); 31, presence or absence of tail stripes (positive); 33, wear patterns of molars (positive); 35, condition of caudal vertebrae (positive); 36, presence or absence of astragalus-cuboid contact (negative); 40, presence or absence of a white ring at the base of the tail (positive).

Component II, which explains 26.4% of the total phenetic variation, serves to distinguish the kangaroo mice and silky pocket mice from the chaetodipine pocket mice and the kangaroo rats. From examination of Fig. 3, it can be seen that the species of *Microdipodops* are phenetically nearest the silky pocket mice (*P. flavus* and *P. longimembris*) and clearly furthest from the kangaroo rats. Characters mostly responsible for separation along this axis (Table 2) were the following: 2, greatest skull breadth (positive); 11, length of baculum (negative); 16, soles of hind feet (positive); 29, greatest interparietal width (negative).

The third component serves to separate the congeneric species, particularly the chaetodipine pocket mice and the kangaroo rats. Component III explains 11.3% of the total phenetic variability. The characters with high weighting in this component were the following: 14, sperm tail length (negative); 38, number of digits on hind foot (positive); 39, hallux to heel measurement (positive).

Discussion

Phenetic Relationships

A thorough character by character examination of the variables listed in Appendix A (see Hafner, 1976) overwhelmingly shows that *Microdipodops* is not closely related to *Dipodomys*, but to *Perognathus*. The multivariate analyses presented here corroborate that conclusion. The results of the principal components analysis are in accord with the correlation and distance phenograms and clearly indicate that *Microdipodops* is most closely related, phenetically, to the silky pocket mice as represented in this study by *P. flavus* and *P. longimembris*, and should, in the absence of evidence suggesting an independent lineage, be considered to belong to the Perognathinae.

That kangaroo mice have been popularly allied with the kangaroo rat lineage is not difficult to understand. Following a superficial examination of skins and skulls of *Microdipodops*, *Dipodomys*, and *Perognathus*, one may conclude 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, would indicate that the above mentioned characters are convergent in nature inasmuch as they were virtually the only characteristics shared between the genera.

Elongation of the pes in heteromyid rodents is a consequence of adaptation to sandy desert soil and the ricochetal mode of locomotion. Comparative osteology of the hind foot in *Microdipodops* and *Dipodomys* indicates that elongation is the result of convergence. Structurally, the pes is quite different in each genus. In *Dipodomys* a marked tendency for atrophication of the hallux exists (see Character 39, hallux-heel measurement). In several species of *Dipodomys* the hallux is lost completely, leaving only four toes. But in *Perognathus* and *Microdipodops* there exists a different trend in that all five toes are retained and in no species is the hallux markedly reduced or absent (as in *Dipodomys*). Additionally, the tarsal elements (Character 36) are entirely different (Wood, 1935).

The degree of bullar inflation appears to reflect the ecological affinities of the species. Arid-adapted heteromyid species generally have relatively larger bullae than do the more mesic- and tropical-adapted taxa. The fact that *Microdipodops* and *Dipodomys* have greatly inflated bullae is, in itself, probably of no phyletic significance, because bullar inflation is known to be quite variable within the family as a whole.

Certainly those characters which are directly affected by the environment (such as degree of bullar inflation and length of hindfoot), are more "plastic" than others and, therefore, less reliable in determining phyletic relationships. It follows that characters dealing directly with aspects of reproduction would be rather conservative, and as such could serve as systematic tools. Examination and analysis of such characters (glans penis, spermatozoa, and baculum) clearly indicate a close relationship between silky pocket mice (subgenus *Perognathus*) and kangaroo mice. Additionally, preliminary studies of the accessory glands of the male reproductive tract of heteromyids (data not incorporated in this study) have shown *Microdipodops* to be structurally quite similar to the silky pocket mice and less so to both the chaetodipine pocket mice and the kangaroo rats (Mark S. Hafner, personal communication). A more complete and detailed account of similarities between kangaroo mice and pocket mice is presented elsewhere (Hafner, 1976).

Evolutionary Biogeography

Considering all available evidence, it appears that *Microdipodops* is a derivative of the pocket mouse lineage, though admittedly, it could be the sole surviving representative of one of the many lineages, distinct from either *Perognathus* or *Dipodomys*, that flourished during the late Tertiary of North America. In either event, the questions remain as to when, where, and under what circumstances such a specialized genus 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 trend was intimately associated with the general evolutionary events within the family Heteromyidae (Wood, 1935). The oldest known fossils of *Perognathus* date from the Miocene of western North America. During that period, the present Great Basin region and much of southwestern North America was subhumid to semiarid in climate. Climatic conditions at that time would appear inappropriate for an extremely arid-adapted group such as *Microdipodops*.

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 remove moisture from the generally eastward-moving oceanic air and allow little precipitation to reach the floor of the basin. Additionally, it was during the interpluvial periods of the Pleistocene that the large sand accumulations in the Great Basin were formed. It is postulated that the genus evolved largely *in situ* in early Pleistocene time, subsequent to the Sierra Nevada diastrophism.

The perognathine ancestor to *Microdipodops* was presumably adapted to semiarid grassland or subhumid scrub habitat. 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 particular desert environment to which kangaroo mice are so narrowly adapted 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. Simpson (1953), Downs (1956), and McLaren (1960) have associated tachytelic rates of evolution with such shifts in adaptive zones. The hypothesis of a fairly recent derivation of the genus is supported further by evidence from four sides: the lack of a fossil record; reconstruction of geological events; a restricted geographic distribution; and the fact that there

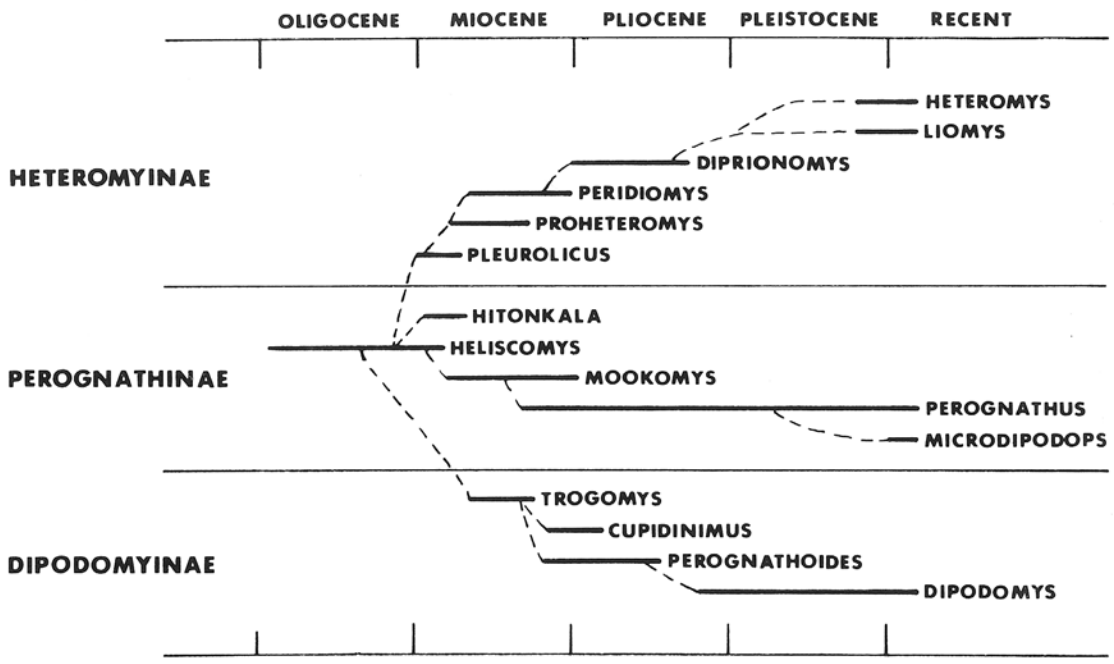

FIG. 4.—Phylogeny of the Heteromyidae showing the position of *Microdipodops* as evidenced by this study. Modified from Lindsay (1972).

are but two species referable to the genus. Although each line of evidence alone is refutable, the combined evidence constitutes strong supportive testimony to the recent evolution of the genus.

It is known that most of the basins in the Great Basin held pluvial lakes during glacial periods and these certainly must have had a profound effect on *Microdipodops*. But, as Morrison (1965) noted, lacustral intervals varied widely even during pluvial periods and major lakes of the Wisconsin period (including Lahonton, Mono, and Bonneville) actually withered to the point of desiccation. What effect the pluvial periods had on *Microdipodops* is speculative, but the distribution of the genus was doubtlessly compressed to the southern Great Basin, probably on hillsides and strandlines surrounding basins and lakes. I suspect that pluvial periods during the Pleistocene resulted in geographic isolation of kangaroo mouse populations, which subsequently allowed for a certain degree of evolutionary divergence (subspeciation).

Hall (1941) believed that the two species of *Microdipodops* hybridized at one locality (Penoyer Valley) in south-central Nevada. Based on Hall's work, the two species would be regarded, in a strict sense, as semispecies. The results of morphometric, genic, and chromosomal analyses (unpublished data) indicate clearly that the two nominal species are actually good biological species and that no hybridization occurs at the above locality.

Microdipodops megacephalus appears to be the more primitive (generalized) of the two species of *Microdipodops*. Morphologically, *M. megacephalus* is less specialized in terms of being adapted for desert existence, as it has smaller bullae and smaller hind feet than *M. pallidus*. It is the more generalized of the two ecologically, inasmuch as it inhabits both sparsely vegetated sand dune habitats (to which *M. pallidus* is restricted) and sandy soil overlaid with gravel in comparatively lush floral associations. *Microdipodops megacephalus* also occurs at higher elevations than does *M. pallidus* as well as on soils that would have been the last to be covered and the first to be exposed by fluctuations in pluvial lakes during the Pleistocene. Additionally, 12 subspecies have been described for the species *M. megacephalus*, whereas only four have been named for *M. pallidus*, suggesting that more time has been available for divergence in *M. megacephalus*.

Culminating this study of the evolutionary relationships of *Microdipodops*, I offer a phylogeny of the Heteromyidae (Fig. 4) based upon evidence presented in this analysis. Considering the high degree of phenetic similarity between species of *Microdipodops* and *Perognathus* and the absence of evidence suggesting that *Microdipodops* is representative of an independent heteromyid lineage, I presently refer *Microdipodops* to the subfamily Perognathinae.

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APPENDIX A

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

1 Greatest skull length (mensural data)
2 Greatest skull breadth (mensural data)
3 Lacrimals (hamular process joined, 1; free, 2)
4 Molars (nonrooted, 1; rooted, 2), data from Wood (1935)
5 2N (diploid number of chromosomes), includes data from Patton (1967*a*, 1967*b*), Genoways (1973), Stock (1974)
6 FN (fundamental number of chromosomes), includes data from Patton (1967*a*, 1967*b*), Genoways (1973), Stock (1974)
7 Morphology of Y chromosome (acrocentric to acrocentric-subtelocentric, 1; metacentric, 2), includes data from Patton (1967*a*, 1967*b*), Genoways (1973), Stock (1974)
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), Quay (1953)
16 Soles of hind feet (naked, 1; somewhat hairy, 2; fully haired, 3)
17 Crested tail (absence, 1; presence, 2)
18 Flank stripes (absence, 1; presence, 2)
19 Tail length/total length × 100 (mensural data)
20 Hind foot length/body length × 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 Average embryo count or litter size, data from Asdell (1964) except for that of *Perognathus intermedius* and *Dipodomys panamintinus*
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), data from Wood (1935)
36 Astragalus-cuboid articulation (absence, 1; presence, 2), data from Wood (1935)
37 Diameter of eye/body length × 100 (mensural data)
38 Number of digits on hind foot (four or five)
39 Hallux to heel (mensural data)
40 White ring at base of tail (absence, 1; presence, 2)

APPENDIX B

Matrix of characters (means in mm) used in the analyses of evolutionary relationships.

Character	*P. intermedius*	*P. hispidus*	*P. flavus*	*P. longimembris*	*M. megacephalus*	*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
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
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

APPENDIX C

Specimens of nine taxa of heteromyid rodents utilized in this study. The specimens are deposited at the following institutions: The Museum, Texas Tech University (TTU); Museum of Vertebrate Zoology, University of California (MVZ); Museum of Southwestern Biology, University of New Mexico (MSB); and some as yet uncatalogued material collected by the author (JCH) and Mark S. Hafner (MSH) to be deposited at The Museum, Texas Tech University and the Museum of Vertebrate Zoology, respectively.

Microdipodops megacephalus

Specimens examined (53).—CALIFORNIA: Mono Co.: 1.5 mi SW River Spring Lakes, Adobe Valley, 6,490 ft, 1 (TTU 24690). NEVADA: Mineral Co.: 0.5 mi SE Alkali Lake, Aurora Valley, 17.5 mi S, 6.5 mi W Hawthorne, 7,040 ft, 3 (TTU 24686–24688); Fletcher, 6,098 ft, 34 (MVZ 105488–105495, 107277–107279, 107281–107284, 107286–107290, 107293, 107294, 107296, 107297, 107300, 107301, 107303, 109699, 112005, 113398, 113399, 40435, 40436, 40440); 0.25 mi N Fletcher, 6,100 ft, 7 (MVZ 142184–142187, 142272, 142274, 142275); 2.5 mi NE Larkin Lake,

Alkali Valley, 21.5 mi S, 10.5 mi W Hawthorne, 6,860 ft, 7 (TTU 24652, 24654, 24658, 24662, 24671, 24677, 24680). Nye Co.: 7.5 mi E Cliff Spring, 5,900 ft, 1 (MVZ 52925).

Microdipodops pallidus

Specimens examined (31).—NEVADA: Churchill Co.: W end Soda Lake, 3,900 ft, 1 (MVZ 88091). Lyon Co.: 17 mi S, 5 mi E Yerington, 5,000 ft, 30 (TTU 24691–24716, 24645, 24832–24834).

Perognathus intermedius

Specimens examined (24).—ARIZONA: Mohave Co.: Willow Beach, Colorado River, 700 ft, 1 (MVZ 128157). Pima Co.: Black Mountain, 10 mi SW Tucson, 1 (MVZ 90347). Yuma Co.: 1.3 mi S, 5.6 mi E Ehrenberg, 4 (MVZ 147699, 147700, 147703, 147724); Tinajas Altas, 2 (MVZ 51787–51788). NEW MEXICO: Dona Ana Co.: Jornada Experimental Range, 1 (TTU 14794). Socorro Co.: 16 mi W, 1 mi N Bernardo, Ladron Mts., 7,500 ft, 1 (MSB 3768); 17 mi W Bernardo, Ladron Mts., 7,000 ft, 1 (MSB 3764); Lava Mesa, 2 mi SE San Marcial, 1 (MVZ 58700); 5 mi N, 2 mi W Socorro, 4,800 ft, 1 (TTU 24866). CHIHUAHUA: 5 mi N Cerro Campana, 5,350–5,600 ft, 3 (MVZ 124871, 124873, 124874); Llano de Las Carretas, 27 mi W Cuervo, 1 (MVZ 75628). SONORA: Ensenada del Perro, S end Tiburon Island, 1 (MVZ 75192); Pinacate Lava Flows, 2.7 mi W Los Vidrios, 1 (MVZ 148009); 2 mi E Punto Arenas, 500 ft, 75 mi W Hermosillo, 1 (MVZ 82705); 2 mi NNE Punta Chueca, 1 (MVZ 147731); Sierra Seri, 650 ft, 9 mi W Rancho San Javier, 70 mi W Hermosillo, 3 (MVZ 82711, 82733, 82734).

Perognathus hispidus

Specimens examined (3).—NEBRASKA: Dawes Co.: 5 mi S Chadron, 1 (TTU 7805). TEXAS: Garza Co.: 7 mi N Post, 1 (TTU 3903). Lubbock Co.: 3.5 mi S, 12 mi E Lubbock, 3,200 ft, 1 (TTU 24865).

Perognathus flavus

Specimens examined (4).—TEXAS: Deaf Smith Co.: 4.9 mi S, 4.8 mi E Glen Rio, 1 (TTU 7173). Jeff Davis Co.: 4.5 mi W Toyahvale, 3,700 ft, 1 (TTU 17285). Lubbock Co.: 3.5 mi S, 12 mi E Lubbock, 3,200 ft, 1 (JCH 846, to be catalogued at TTU); 4.5 mi S, 12 mi E Lubbock, 3,200 ft, 1 (TTU 24864).

Perognathus longimembris

Specimens examined (4).—CALIFORNIA: Los Angeles Co.: 5 mi NW Shoemaker, 3,400 ft, 1 (MVZ 42244). NEVADA: Humboldt Co.: 1.25 mi N Sulfur, 1 (MSB 15633). Lincoln Co.: 6 mi N, 31 mi W Hiko, 4,800 ft, 2 (TTU 24867, 24868).

Dipodomys merriami

Specimens examined (5).—ARIZONA: Cochise Co.: 6.2 mi SE Portal, Chiricahua Mtns., 1 (TTU 11608). CALIFORNIA: San Bernardino Co.: Barstow, 1 (MVZ 20928). NEVADA: Lyon Co.: 17 mi S, 5 mi E Yerington, 5,000 ft, 1 (TTU 24887). Mineral Co.: 0.25 mi N Fletcher, 6,100 ft, 1 (MVZ 142182). Washoe Co.: 6 mi S, 2.5 mi W Sutcliffe, 4,200 ft, 1 (JCH 838, to be catalogued at TTU).

Dipodomys ordii

Specimens examined (7).—NEBRASKA: Thomas Co.: Nebraska Nat. Forest, Bessey Div., 1 (TTU 4433). NEVADA: Lyon Co.: 17 mi S, 5 mi E Yerington, 5,000 ft, 1 (TTU 24900). NEW MEXICO: Chavez Co.: 10 mi W Caprock, 1 (TTU 5518). UTAH: Tooele Co.: 15 mi S, 11 mi W Dugway, 4,550 ft, 4 (TTU 24901, 24904, 24913, 24917).

Dipodomys panamintinus

Specimens examined (17).—CALIFORNIA: Kern Co.: Freeman Canyon, 2.6 mi E Walker Pass, 1 (MVZ 143970); Sand Canyon, 0.1 mi S Hwy 58, 3.1 mi ESE Monolith, 3,900 ft, T 32 S, R 34 E, NW ¼ Sec. 27, 5 (MSB 34935, 34938, 34939, 34941, 34942); Sand Canyon, 0.4 mi N Hwy 58, 2.9 mi E × S of Monolith, 3,949 ft, 8 (MSB 34912, 34917, 34920, 34927, 34929, 34930, 34896, 34897); 0.15 mi E Walker Pass Summit, 11.0 mi W Inyokern, 5,100 ft, 1 (MSH 294 to be catalogued at MVZ). San Bernardino Co.: 2 mi E Searles Station, 9 mi NNE Johannesburg, 3,200 ft, 2 (MSH 354 to be catalogued at MVZ, JCH 855 to be catalogued at TTU).