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SYSTEMATIC STATUS OF KANGAROO MICE, GENUS *MICRODIPODOPS*: MORPHOMETRIC, CHROMOSOMAL, AND PROTEIN ANALYSES

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ABSTRACT.—The systematic status of *Microdipodops megacephalus* and *M. pallidus* is investigated at the genic, karyotypic, and morphologic levels at a purported hybrid zone. Instances of hybridization are shown to be either nonexistent or present at extremely low levels (≤0.6%), and full specific status of the two taxa is affirmed. Amounts of genic variability and polymorphism are approximately equal for the species (H = 0.064) and fall well within the range observed for other vertebrate species. Estimates of the timing of the speciation event, based upon allozymic data, range from 1.2 to 6 million years before present. Possible means of ecological separation of the two sibling species in sympatry are suggested.

The systematic status of the two named species of kangaroo mice (*Microdipodops megacephalus* and *M. pallidus*) has been uncertain since the revision of the genus and subsequent comments by Hall (1941, 1946:380–382). On the basis of assumed hybridization between *M. megacephalus* and *M. pallidus* in Penoyer Valley in southern Nevada (three morphological hybrids were indicated), Hall (1941, 1946) considered the species to be in the process of diverging and not yet reproductively isolated at that locality. As such, the genus would comprise two semispecies of a superspecies complex (*sensu lato* Mayr, 1963). It is crucial, therefore, to establish the nature of genetic interaction between the two forms of *Microdipodops* at this locality in order to determine their systematic status. Determination of the relationship between the two forms has bearing not only on the current taxonomy of the group, but on the attendant historical biogeography of the genus. Based upon the assumption that hybridization occurred in Penoyer Valley, Hall (1946:381) postulated that this valley represented the center of differentiation of the two species. Alternative biogeographical interpretations hinge upon the presence or absence of hybridization and, more importantly, introgression at this locality.

Accordingly, *M. megacephalus* and *M. pallidus* in Penoyer Valley were examined at three levels of biological organization to determine the extent and significance of potential hybridization: 1) genic variability as assayed by starch-gel electrophoresis; 2) gene packaging as determined by non-preferentially stained karyotypes; and 3) phenotypic variability as assayed by external and cranial morphometrics and qualitative characters of the pelage.

MATERIALS AND METHODS

The area of sympatry studied covers approximately 130 ha on the southern border of an extensive playa in Penoyer Valley (6 mi N, 31 mi W Hiko, 4,800 ft., Lincoln Co., Nevada). From

our observations as well as those of Hall (field notes, 1932) and Ghiselin (1970), it appears that the area of actual sympatry skirts the distribution of the *Sarcobates*-dominated community that immediately surrounds the alkali flats. The two species are microsympatric (*sensu* Smith, 1955) along a narrow belt surrounding the dry lake, and differential habitat preferences are not apparent at this locality. Edaphically, this area is a fine-grained mixture of sandy and gravelly soils. The vegetation is a blend of the types that characterize the habitats of the two species throughout most of their respective ranges (Hall, 1941; personal observations).

Eighty-nine specimens (including 55 *M. pallidus* and 34 *M. megacephalus*) were collected from the zone of sympatry. Individuals were prepared as either skin-plus-skull, skin-plus-skeleton, or skeleton-only specimens and are deposited in either the Museum of Southwestern Biology, University of New Mexico, the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), or The Museum, Texas Tech University.

Forty of the 89 specimens, representing 20 of each species, were assayed for allozymic variability using starch-gel electrophoretic techniques as described by Selander et al. (1971). Samples of kidney and liver were frozen in either liquid nitrogen or dry ice immediately after collection. Only certain enzymes and other proteins occurring in an aqueous extract of the kidney were assayed in this analysis. Alleles were designated alphabetically in order of decreasing electromobility. From the remaining 49 individuals, non-preferentially stained karyotypes were prepared using a modification of the *in vivo* bone-marrow technique described by Patton (1967).

The 49 karyotyped specimens plus an additional 83 skin-plus-skull specimens collected from Penoyer Valley, largely in 1932, were used in the morphological analyses. The additional 83 specimens, deposited in the Museum of Vertebrate Zoology, included the three supposed hybrids reported by Hall (1941). Eleven cranial and three external measurements were taken for each of these specimens: greatest length of skull, basal length, greatest breadth, nasal length, maxillary breadth, least interorbital breadth, mandibular length, condylobasal length, length of upper tooth-row, width of first upper molar, angular bifurcation (a measure of the expansion of the wings of the angular process of the dentary; Fig. 1), total length, tail length, and hindfoot length. Cranial measurements were taken with dial calipers or craniometer and read to the nearest twentieth of a millimeter. The external measurements were read directly from the specimen tag. Only adult individuals, those showing substantial wear on the permanent fourth upper premolar, were used in the morphometric analyses. Sexes were pooled in these analyses, as Hall (1941), Schitoskey (1968), and Hafner (1976) all reported a lack of significant secondary sexual dimorphism in the characters under examination. The 14 variables were used in a series of stepwise discriminant function analyses using the BMD-07M program and the IBM 360 computer at the University of New Mexico.

Results

Genic Variability

Twenty-three presumptive loci encoding for 16 proteins were assayed. An additional protein, superoxide dismutase (SOD), was examined but could not be scored for all individuals and therefore was excluded from the analysis. Allelic variation across the 23 loci falls into three classes.

Monomorphic loci.—Loci at which the commonest allele was present at a frequency of > 0.95 were considered to be monomorphic. Eleven loci were monomorphic for the same allele in both species as follows: malate dehydrogenase-1 and -2 (MDH-1, -2), lactate dehydrogenase-1 and -2 (LDH-1, -2), isocitrate dehydrogenase-1 (IDH-1), glutamate dehydrogenase (GDH), sorbitol dehydrogenase (SDH), glutamic oxaloacetic transaminase-1 and -2 (GOT-1, -2), phosphoglucomutase-2 (PGM-2), and general protein amido black (AB).

Polytypic loci.—Three loci were fixed for different alleles in the two species: mannose phosphate isomerase-1 (MPI-1), alcohol dehydrogenase (ADH), and peptidase-1 (Pept-1).

Polymorphic loci.—The remaining nine loci were polymorphic in one or both species as follows: α-glycerophosphate dehydrogenase (αGPD), isocitrate dehydrogenase-2 (IDH-2), mannose phosphate isomerase-2 (MPI-2), adenosine deaminase

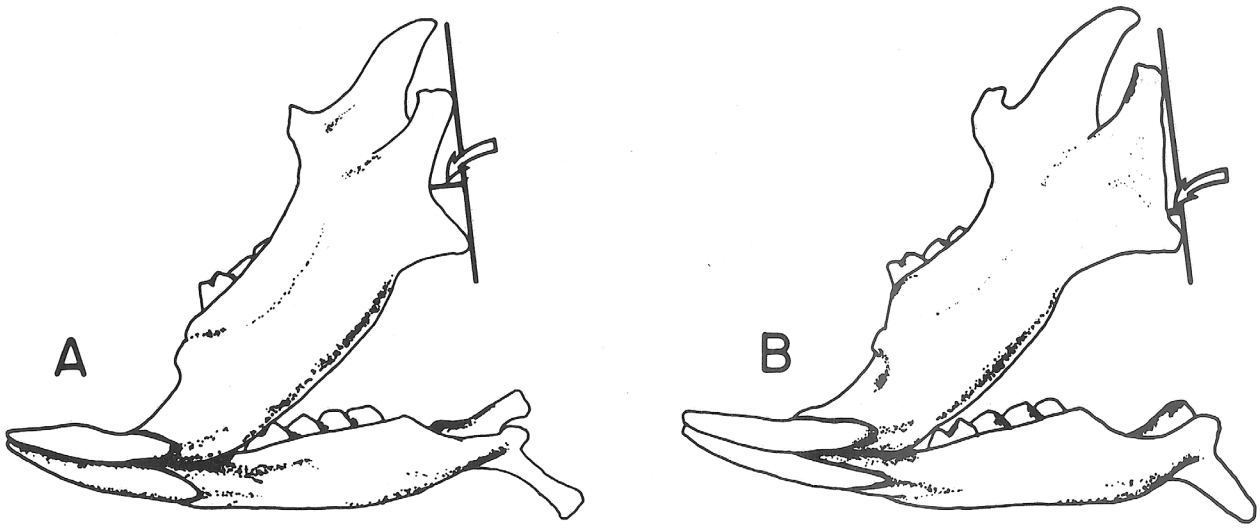

FIG. 1.—Angular bifurcation measure; dentaries viewed from ventro-lateral aspect (A = *Microdipodops pallidus*; B = *M. megacephalus*).

(ADA), 6-phosphogluconate dehydrogenase (6-PDG), phosphoglucose isomerase (PGI), phosphoglucomutase-1 (PGM-1), and esterase-1 and -2 (Est-1, -2).

Allele frequencies at eight polymorphic loci (excluding Est-1) are shown in Table 1. Because the high degree of variability seen at the Est-1 locus was extremely difficult to interpret, we have excluded this locus from all aspects of the analysis. Genic variability, H, as measured by the proportion of loci heterozygous per individual, and the proportion of polymorphic loci, P, are reported in Table 2. The values of 6.4% loci heterozygous per individual and 21.7% polymorphic loci for both species of *Microdipodops* are consistent with those values reported for most vertebrate species by Selander and Johnson (1973).

TABLE 1.—*Allelic frequencies at eight polymorphic loci in* Microdipodops.

Locus	Allele	Allelic frequencies	
		M. pallidus	*M. megacephalus*
∝GPD	a	0.45	
	b	0.55	0.68
	c		0.30
	d		0.02
IDH-2	a	0.25	1.0
	b	0.40	
	c	0.35	
MPI-2	a	0.40	1.0
	b	0.60	
ADA	a	0.12	
	b	0.88	1.0
6-PGD	a		0.08
	b	0.82	0.92
	c	0.18	
PGI	a	1.0	0.95
	b		0.05
PGM-1	a		0.53
	b	1.0	0.47
Est-2	a	1.0	0.62
	b		0.38

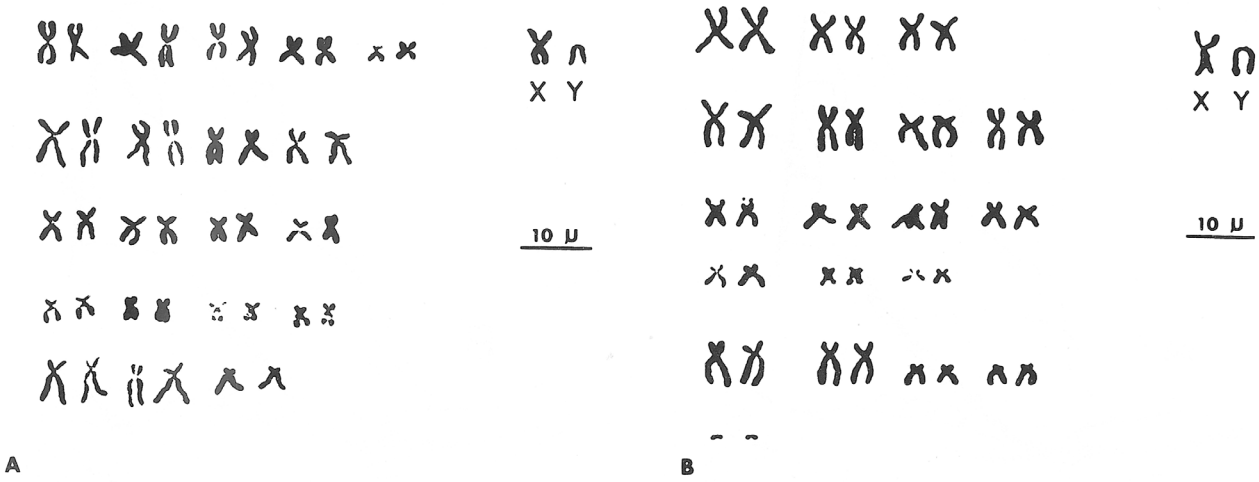

FIG. 2.—Karyotypes of *Microdipodops pallidus* (A) and *M. megacephalus* (B).

Chromosomal Analysis

Karyotypic survey of the genus *Microdipodops* demonstrated a consistent difference in diploid number (2n) between the two species: *M. pallidus* (Fig. 2a) has a diploid compliment of 42 chromosomes, while *M. megacephalus* (Fig. 2b) has 40. No intrapopulational karyotypic variation was observed. This difference in diploid number allowed for nonarbitrary taxonomic assignment of individuals at the study site and provided a means for detecting potential F_1 individuals (2n = 41). Of the 49 karyotyped specimens, 14 were assigned to *M. megacephalus* and 35 to *M. pallidus*. No chromosomal F_1 individual was found, and no variation in fundamental number (FN) was observed. Thus, all karyotyped individuals were positively assigned to one or the other species.

Morphometric Analysis

The fourteen variables (Table 3) were treated in three separate step-wise discriminant function analyses. The first involved karyotyped specimens only (specimens known chromosomally to be either *M. megacephalus* or *M. pallidus*). All individuals in this analysis were correctly identified with respect to karyotype (Fig. 3), each with a posterior probability of ≥ 0.999. Table 4 lists the discriminant rank and standardized canonical coefficients for each character in the first analysis. The standardized canonical coefficients indicate the relative contribution of each character to the first canon-

TABLE 2.—*Genic heterozygosity and polymorphism in* Microdipodops pallidus *and* M. megacephalus.

Locus	Genic Indices	Proportion of individuals heterozygous per locus (h)	
		M. pallidus	*M. megacephalus*
∝GPD		0.20	0.30
IDH-2		0.50	
MPI-2		0.40	
ADA		0.05	
6-PGD		0.25	0.15
PGI			0.10
PGM-1			0.32
Est-2			0.55
	H[a]	0.064	0.064
	P[b]	0.217	0.217

[a] H = Mean proportion of 22 loci (excluding Est-1) heterozygous per individual; [b] P = Proportion of 23 loci polymorphic.

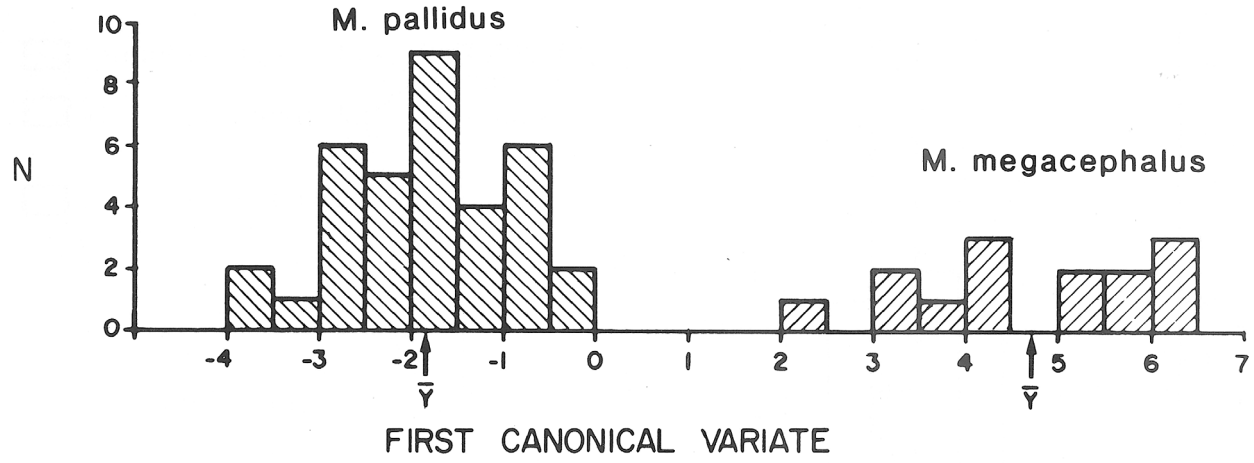

FIG. 3.—Frequency distribution for canonical variate scores: karyotyped specimens. $\bar{Y}$ indicates group mean.

ical variate; the discriminant rank orders the characters as to their relative discriminatory power (Baker et al., 1972). In all analyses, the same four characters were of highest discriminatory rank and 100% of the phenetic variation was explained by the first discriminant function.

In an attempt to determine the status of Hall's three presumed hybrid individuals, the 49 specimens of known karyotype were used as reference samples in a second discriminant function analysis. Eighty-two unkaryotyped specimens, including two of the three suspected hybrids, were included as a third, unknown, class. The discriminant function analysis assigned all but two specimens of the unknown class to one of the two species with a posterior probability of >0.95 (Fig. 4). Of these two individuals, one (MVZ 52672) was a presumed hybrid (Hall, 1941). The second of Hall's suspected hybrids (MVZ 52718) was classified as *M. pallidus* (p = 0.99). The third presumed hybrid was analyzed in a separate procedure based on only 13 variables, as the skull was partially damaged. It was classified as *M. megacephalus* with a posterior probability of 0.97.

TABLE 3.—*Summary of morphological variables of karyotyped reference samples of* Microdipodops pallidus *and* M. megacephalus *(Mean ± 2 standard errors).*

Variable	*M. pallidus* (N = 35)	*M. megacephalus* (N = 14)
External		
Total length	155.86 ± 1.83	148.79 ± 2.45
Tail length	88.97 ± 1.32	83.00 ± 1.88
Hind foot length	25.67 ± 0.21	25.00 ± 0.41
Cranial		
Greatest length	29.06 ± 0.16	28.38 ± 0.25
Basal length	18.77 ± 0.13	18.57 ± 0.16
Greatest breadth	20.10 ± 0.13	18.78 ± 0.25
Nasal length	9.80 ± 0.11	10.06 ± 0.14
Maxillary breadth	12.08 ± 0.09	11.31 ± 0.16
Least interorbital breadth	6.81 ± 0.06	6.32 ± 0.09
Mandibular length	10.90 ± 0.06	10.46 ± 0.10
Condylobasal length	20.89 ± 0.11	20.42 ± 0.20
Length of upper tooth row	2.65 ± 0.05	2.64 ± 0.07
Width of M^1	1.11 ± 0.02	1.03 ± 0.04
Angular bifurcation	0.42 ± 0.02	0.25 ± 0.04

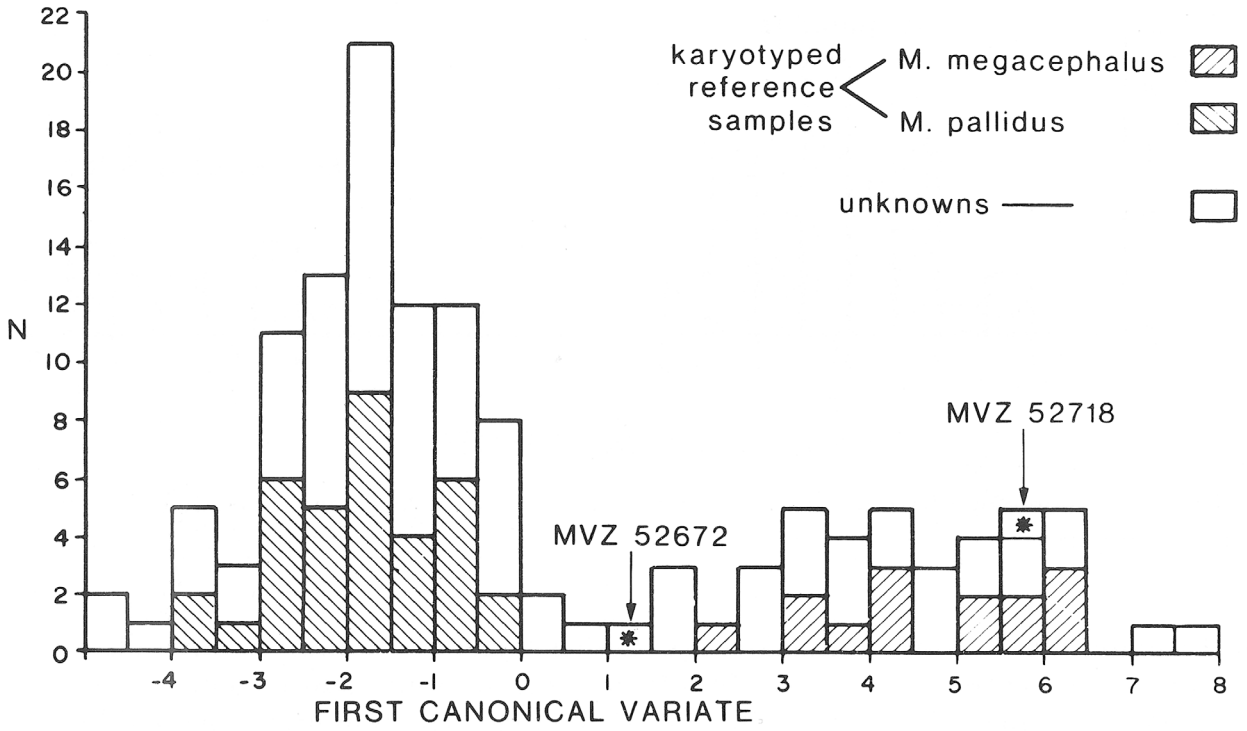

FIG. 4.—Frequency distribution for canonical variate scores. Suspected hybrid individuals (Hall, 1941) are indicated by asterisks.

In order to achieve assignment of all unknown individuals purely on morphometric grounds, a third analysis was undertaken. In this analysis, specimens classified with a posterior probability of >0.95 in the second procedure were combined with the original karyotyped reference samples and compared again with the two specimens that were not classified in the second analysis. Using the bolstered reference samples, these two specimens were classified as shown in Fig. 5, one to *M. megacephalus* and one to *M. pallidus*, each with posterior probabilities of >0.95.

All specimens were independently identified on the basis of three qualitative pelage characters. *M. megacephalus* is distinguishable from *M. pallidus* at this locality by terminal darkening of the tail, basal graying of the ventral pelage, and slightly buffy (versus white) post-auricular spots. Complete concordance was found between mor-

TABLE 4.—*Standardized canonical variate coefficients and discriminant rank for 14 mensural characters.*

Variable	Discriminant rank	Standardized coefficients
Greatest breadth	1	−0.5919
Angular bifurcation	2	−0.7073
Least interorbital breadth	3	−0.3554
Nasal length	4	0.3081
Hind foot length	5	−0.4154
Mandibular length	6	−0.2654
Greatest length	7	0.6251
Tail length	8	−0.3645
Basal length	9	0.6915
Total length	10	−0.2441
Condylobasal length	11	−0.3419
Width of M^1	12	−0.1179
Length of upper tooth row	13	0.1283
Maxillary breadth	14	−0.1027

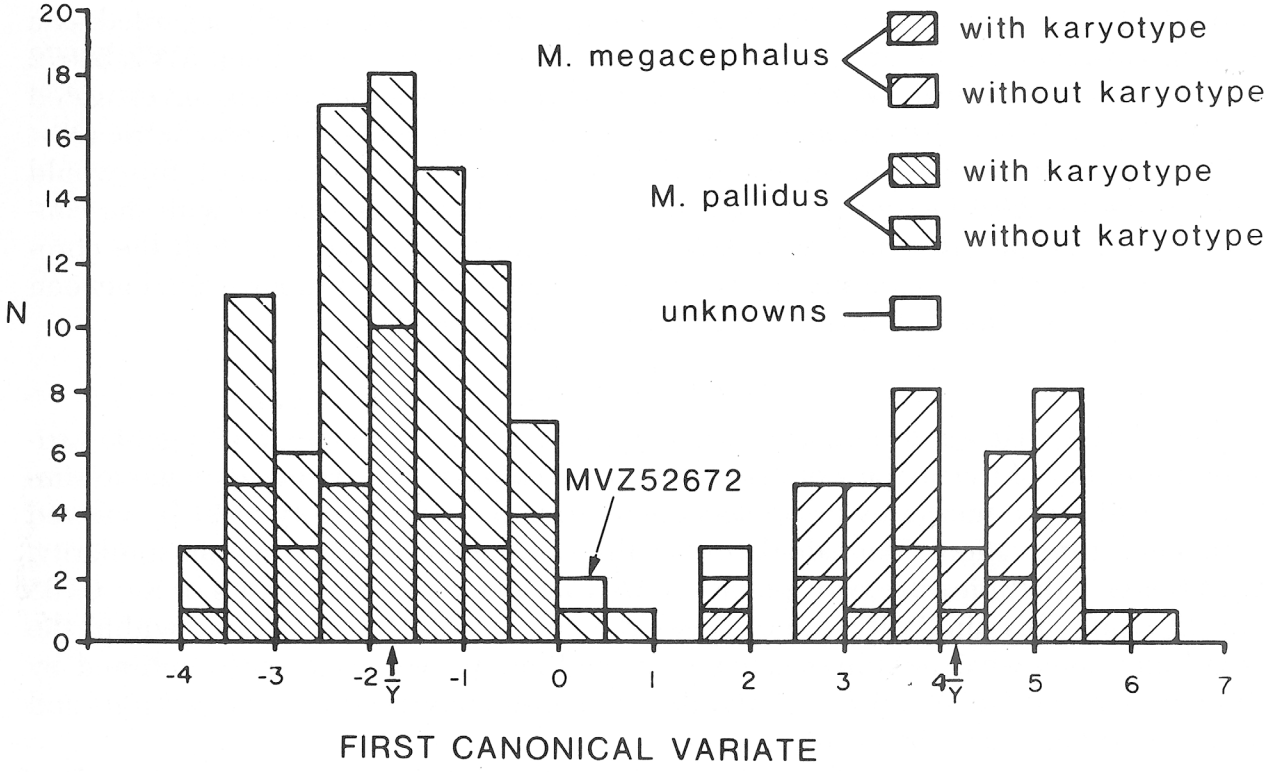

FIG. 5.—Frequency distribution for canonical variate scores. $\bar{Y}$ indicates group mean. The unknowns represent those specimens that were not classified in the previous analysis (Fig. 4).

phometric and pelage identification except in the case of one individual. Specimen MVZ 52672, one of Hall's presumed hybrids, which was classified morphometrically (in the third analysis; Fig. 5) as *M. pallidus*, exhibited all of the pelage features characteristic of *M. megacephalus*. In addition, the pterygoids and incisive foramina of this specimen, characters used by others in species identification (Hall, 1941; Hafner, 1976), are typical of the condition in *M. megacephalus*.

DISCUSSION

Systematic Status

In the electrophoretic analysis, the three polytypic and eight polymorphic loci display species markers, and hybrids, if present, should appear in the heterozygous form. Additionally, for the eight polymorphic loci analyzed, the two species were not found to share variant alleles. Five of the polymorphic loci (αGPD, ADA, 6-PGD, PGI, and Est-2) displayed the same major allele but had species specific minor alleles in one or both species. Three polymorphic loci (IDH-2, MPI-2, and PGM-1) displayed a species specific major allele for one of the two species (Table 1). No hybrid individuals were discerned at these loci among the 40 individuals examined.

Chromosomally, F_1 individuals would have of necessity a $2n = 41$ and backcross individuals would be expected to show variances in FN; neither was observed. In the morphologic analysis, only one individual (MVZ 52672) is of questionable hybrid status. From the above data, this specimen might be considered as either 1) a hybrid individual, as Hall (1941, 1946) believed, or 2) a morphological intermediate resulting purely from phenetic overlap. Patton (1973), among others, discussed the disadvantages of a purely exomorphological (versus chromosomally documented) approach to hybrid identification. Considering external phenetic variability, total reliance on morphological data might well lead to a classification of an individual into species "A" using certain characters and species "B" using others. A morphologically intermediate

individual, such as specimen MVZ 52672, might then be incorrectly regarded as a hybrid. However, in this instance, the proper classification of specimen MVZ 52672 is not absolutely critical. Of a total of 172 specimens of *Microdipodops* investigated using allozymic (N = 40 specimens), karyotypic (N = 49), and/or morphometric (N = 132) analyses, this specimen represents the only possible hybrid. At most, this would yield a low (≤0.6%) incidence of hybrid formation, a level consistent with the conclusion that *M. pallidus* and *M. megacephalus* are distinct species. Both the chromosomal and the electrophoretic analyses documented a lack of introgression between the two taxa, and thus full specific recognition is warrented.

Genic Similarity

Considering that we do not, as yet, know the range of interpopulational genic variation for either of the species of *Microdipodops*, comparisons based upon genic similarity or distance measures using specimens from a single locality must be viewed with some reservation. The calculation of the coefficient of overall genic similarity, S, of Rogers (1972) for the two species of *Microdipodops* yields a value of S = 0.733 (for 22 loci). This similarity value places the species of *Microdipodops* within the broad and somewhat nebulous category of sibling species as recently outlined by Zimmerman and Nejtek (1977). Certainly, on morphological criteria, *M. pallidus* and *M. megacephalus* are classic sibling species.

The measure of genetic differentiation (D) of Nei (1971) was also calculated (D = 0.247). This degree of genetic differentiation indicates that there have been approximately 24.7 allelic substitutions per 100 loci since the species diverged. Correlating genetic distance with time on the basis of two independent "molecular clock" theories yields quite different time estimates. The formula of Nei (1975) yields a time (t) since divergence of $t = 5 \times 10^6$ D = 1.24 million years (mid-Pleistocene). The formula of Sarich (1977), which is adjusted for differing rates of evolution in various protein classes, yields a time since divergence measure of approximately $t = 30 \times 10^6$ D = 7.4 million years (mid-late Pliocene). According to Sarich (1977), this formula applies when all assayed proteins are of the "slow-evolving" class. One of our 16 proteins was of the "fast-evolving" class (esterase), so perhaps a figure of ±6 million years would be more appropriate. Regardless, the span of time bracketed by the two estimates (1.24 million to 6 million years before present) allows for only a very rough time placement for the *M. megacephalus–M. pallidus* speciation event. Resolution as to the timing of this event awaits both a clearer understanding of rates of protein evolution and, hopefully, some degree of corroboration via the fossil record. To date, fossil material of *Microdipodops* is unknown.

Biogeographical and Ecological Considerations

Full reproductive isolation of the two species at Penoyer Valley has been demonstrated. Hence two lines of inquiry are immediately suggested: analyses of historic biogeography, and mechanisms of ecological separation between the species. If hybridization had indeed been documented at this locality, then Penoyer Valley would best be considered a zone of secondary contact between the species, with breakdown of reproductive isolating mechanisms. As no introgression and, probably, no hybridization is associated with the Penoyer Valley populations, there remains little reason to consider this locale as either an area of secondary contact with interbreeding between the forms, or as the center of divergence of the two taxa.

Hall (1941:381) hypothesized that ecological separation of the species, based on differential soil preferences and allied environmental parameters, resulted in physiological differentiation, as indicated by reproductive asynchrony. Ghiselin (1970), examining soil preferences of *Microdipodops* in Penoyer Valley, determined that *M.*

megacephalus preferred gravelly soils; he regarded *M. pallidus* as a substrate generalist. Ghiselin's results are in direct contradiction with the prevalent views on substrate specificity of the two taxa (Hall, 1941, 1946; Hafner, 1976; personal observations). Thus, while soil preferences may exist in Penoyer Valley, current data are conflicting and a resolution of the issue must await further study.

Our data on reproductive cycles of the two species indicate that the period of reproductive activity of *M. pallidus* is included within that of *M. megacephalus*; reproduction in *M. megacephalus* begins earlier and ends later than in *M. pallidus*. The significance, however, of this reproductive difference (and attendant physiological factors) and its potential bearing on the maintenance of reproductive isolation between the species has yet to be demonstrated.

Specific differences in the size and shape of the angular processes, pterygoids, and incisive foramina suggest a third means of ecological separation (Hafner, 1976): differential allocation of the food resource base. These characters are related to, or are direct components of, the masticatory apparatus, and it would appear that the functional significance of such noted differences between the species might be explained by differential food habits. The two qualitative characters, shape of incisive foramina and shape of pterygoids, were used to discriminate between the species by Hall (1941) and Hafner (1976). The third, a mensural character (angular bifurcation), was shown to be of high discriminatory power in this study (discriminant rank = 2). The incisive foramina are known to be passageways connecting the mouth with the vomeronasal organ (Jacobson's organ), which serves a chemosensory function. Thus, differences in size and shape of the incisive foramina could indicate differential ability to discriminate among food items or between species specific pheromones. The pterygoid bones and angular processes of the dentary serve as origin and insertion sites for the adductor muscles of the jaw, the *m. pterygoideus* and the *m. masseter*. Modification of these osseous elements may, again, be associated with divergence in masticatory habits. Although the dentition of *Microdipodops* has been given only cursory attention at the specific level, dental differences between the species appear slight.

The diet of kangaroo mice has not been studied thoroughly. The literature contains only brief statements detailing the cheekpouch contents of several individuals of each species (Hall and Linsdale, 1929; Bailey, 1936; Hall, 1941, 1946). A detailed analysis of food habits, reproductive cycles, and habitat preference of the two species is presently under investigation and should provide insight into the mechanisms of ecological separation.

Acknowledgments

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