INTERSPECIFIC MORPHOLOGIC VARIATION IN KANGAROO RATS (*DIPODOMYS*): DEGREE OF CONCORDANCE WITH GENIC VARIATION

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Abstract

Schnell, G. D. (Department of Zoology and Stovall Museum, University of Oklahoma, Norman, Oklahoma 73019), T. L. Best (Natural Sciences Research Institute, Natural History Museum, Eastern New Mexico University, Portales, New Mexico 88130), and M. L. Kennedy (Department of Biology, Memphis State University, Memphis, Tennessee 38152) 1978. Interspecific morphologic variation in kangaroo rats (Dipodomys): *degree of concordance with genic variation. Syst. Zool. 27:34–48.*—The 24 forms of kangaroo rats (*Dipodomys*) that have been recognized as species by one or more recent authors were studied using phenetic techniques. A total of 41 morphometric characters (4 skin, 16 skull, and 21 post-cranial) were measured for up to 10 males and 10 females of each species. The standardized average measurements were analyzed and then measurements were divided by principal component 1 projections based on unstandardized data to reduce the influence of overall size. Phenograms and three-dimensional principal component models were produced and the results compared with the findings of previous authors, including those from allozyme analyses. Several species pairs and groups involving a few species were stable throughout our studies and consistent with groups identified in phylogenetic, specialization, or other classificatory schemes. These include: *compactus* and *ordii*; *elephantinus* and *venustus*; *agilis*, *paralius*, *peninsularis*, and *antiquarius*; *nitratoides* and *merriami*; and *ornatus* and *phillipsii*. However, marked morphologic gaps (other than those based on size) are not present between many of the species groups and attempts to place species into such groups in classifications probably result in an indication of distinctness that goes beyond what is found in nature. In terms of interspecific comparisons, there was no association between phenetic groups based on morphologic data and those constructed using allozyme findings. When comparisons were made among previous classifications and our results, the allozyme data produced the most divergent classifications. Overall, the associations between our morphologic results and previous classifications were relatively weak, reflecting by and large the variance in arrangements of species groups, rather than major differences within groups. Given the relative indistinctness of morphologic groups, it seems unlikely that any one classification can accurately represent interspecific phenetic, cladistic, and or phylogenetic affinities within the genus. [Phenetics, taxonomic congruence, *Dipodomys*, kangaroo rats, morphometrics, allozymes.]*

Significant effort has been expended by a number of investigators studying evolutionary mechanisms to determine the extent of genic variation in local populations, among populations, and among closely related species (see Lewontin, 1974, and Powell, 1975, for general reviews; Selander and Johnson, 1973, summarized data for vertebrates). Workers have attempted to investigate and elucidate a fundamental aspect of evolutionary theory—that race formation and eventually speciation occur by the conversion of genetic variation within populations to variation among populations (Lewontin, 1967). Prakash (1969) emphasized that to understand the speciation process we not only should have a knowledge of genetic differences between closely related species (or populations within a species), but also of the correlation between genic differences and differences based on other characteristics, such as those describing various aspects of morphology, ecological preference, and behavior.

Relatively few studies have quantitatively compared interspecific differences in morphology against between species allozyme differences. Sokal (1973) indicated that allozyme variation is an unreliable indicator of classical morphologic (phenetic) variation, citing Sneath and

Sokal (1973, Section 5.12) for review of the literature; however, as is evident from their literature summary, few studies have addressed the problem.

Smith and Koehn (1971) conducted both phenetic and cladistic studies of morphologic and genic characters of *Catostomus* fishes; however, the character sets were analyzed simultaneously so that comparisons between morphologic and genic results were not the main emphasis. Gorman and Kim (1976) indicated that there was little correlation between electrophoretic and morphologic characters in *Anolis* lizards of the eastern Caribbean. Utter et al. (1973) stated that genetic relationships closely parallel anatomical relationships in eight species of trout and salmon. For Death Valley pupfish (*Cyprinodon*), Turner (1974) noted that, while considerable morphologic divergence had occurred between species, genetic divergence as measured by an electrophoretic survey of a number of proteins is lacking. Mickevich and Johnson (1976) analyzed the degree to which morphologic and allozyme data sets yield consistent phyletic interpretations for five nominal species of teleost fishes in the genus *Menidia*; they also discussed the degree of similarity in phenetic results and cited much of the relevant literature. A number of other papers include qualitative assessments of the concordance between similarities based on morphologic and genic characters. Most often, however, comparisons have involved only a few species.

In this paper, we have evaluated quantitatively the phenetic concordance in morphologic and genic traits for a number of kangaroo rat (*Dipodomys*) species. Johnson and Selander (1971) analyzed genic variation of 17 proteins in each of 11 species (see Fig. 1), and we obtained data on skeletal and external morphologic characters (although not from all of the same specimens). In addition, we procured specimens of the other species in the genus so that comparisons could be made of phenetic morphologic classifications and those of previous authors.

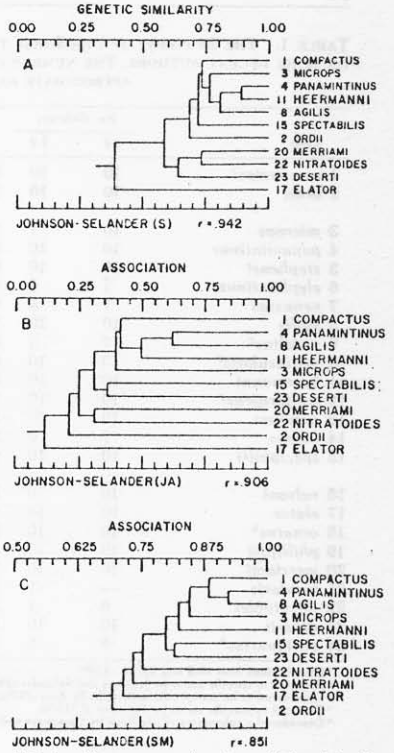

FIG. 1.—Phenograms showing relationships between species of *Dipodomys* based on the allozyme data of Johnson and Selander (1971). Species were clustered using UPGMA on (A) Roger's, (B) Jaccard's, and (C) simple matching similarity coefficients.

Kangaroo rats occupy arid and semiarid regions of western North America. The 24 forms (hereafter referred to as species) listed in Table 1 are thought or have until recently been thought to be distinct at the specific level. Taxonomically, *Dipodomys* has received considerable attention and a number of classifications have been proposed. Most authors have placed the species into "groups," which are essentially equivalent to the subgenera of other taxa. Grinnell (1921) divided *Dipodomys* into nine groups (Fig. 2A) and

TABLE 1. THE 24 FORMS OF *Dipodomys* THAT HAVE BEEN CLASSIFIED AS DISTINCT SPECIES BY ONE OR MORE RECENT AUTHORS. THE NUMBER OF SKELETAL SPECIMENS USED IN OUR ANALYSES AND THE APPROXIMATE RANGE OF EACH FORM ARE GIVEN.

Name	No. skeletons ♂♂	No. skeletons ♀♀	Distribution[1]
1 *compactus*[2]	10	10	Padre Island, Texas
2 *ordii*	10	10	S Alberta and Saskatchewan to Hidalgo; E California to central Oklahoma
3 *microps*	10	7	SE Oregon, Nevada, E California, W Uath
4 *panamintinus*	10	10	W Nevada, S California
5 *stephensi*	10	10	S California
6 *elephantinus*	7	6	W central California
7 *venustus*	7	8	W central California
8 *agilis*	10	10	S California, N Baja California
9 *paralius*[3]	7	3	W Baja California
10 *peninsularis*[3]	10	10	Central Baja California
11 *heermanni*	10	10	Central California
12 *californicus*[4]	10	10	N California, S Oregon
13 *gravipes*	10	10	NW Baja California
14 *ingens*	7	9	S central California
15 *spectabilis*	10	10	SE Arizona, New Mexico, W Texas, NE Sonora, Chihuahua, and SE Zacatecas
16 *nelsoni*	10	10	Big Bend of Rio Grande to S Nuevo Leon
17 *elator*	10	10	S Oklahoma and N central Texas
18 *ornatus*[5]	10	10	S Zacatecas and Aguascalientes
19 *phillipsii*	10	10	S Hidalgo to N Oaxaca
20 *merriami*	10	10	N Nevada to San Luis Potosi; Baja California to W Texas
21 *insularis*	—	1	San Jose Island, Baja California
22 *nitratoides*	6	4	S central California
23 *deserti*	10	10	Central Nevada to W Sonora
24 *antiquarius*[3]	8	5	San Juan Mine, Baja California

[1] Distributions from Hall and Kelson (1959).
[2] Elevated to specific status by Johnson and Selander (1971) and Schmidly and Hendricks (1976).
[3] Considered to be conspecific with *agilis* by Best (1978a).
[4] Elevated to specific status by Patton et al. (1976).
[5] Considered a subspecies of *phillipsii* by Genoways and Jones (1971).

treated in detail the forms occurring in California (Grinnell, 1922). Setzer (1949) recognized six groups, which were determined largely on the degree of specialization (Fig. 2B). Specialization was estimated using six different indices of osteological differences (appendage proportions, etc.), as well as one having to do with visceral arrangement. Lidicker (1960a) proposed a phylogenetic scheme involving six groups, with the Heermanni group divided into two subgroups (Fig. 2C). Mazrimas and Hatch (1972) did not construct a classification but showed a striking negative association between the amount of satellite DNA and the degree of specialization for 12 of the species. Stock (1974) analyzed mitotic chromosomes for 18 *Dipodomys* species and proposed a phylogenetic arrangement (Fig. 2D), and Best and Schnell (1974) constructed a specialized classification based on three bacular measurements (Fig. 3).

Given this history, we were interested in answering three questions. First, what are the phenetic affinities of the group based on a large suite of morphologic measurements? Second, how do these phenetic relationships compare with those suggested by previous authors, particularly relationships based on genic similarities? Finally, how similar are the other classifications to one another?

METHODS AND MATERIALS

For each of the 24 species, we attempted to obtain 10 male and 10 female skeletal specimens (Table 1); a total of 395 specimens was collected or borrowed

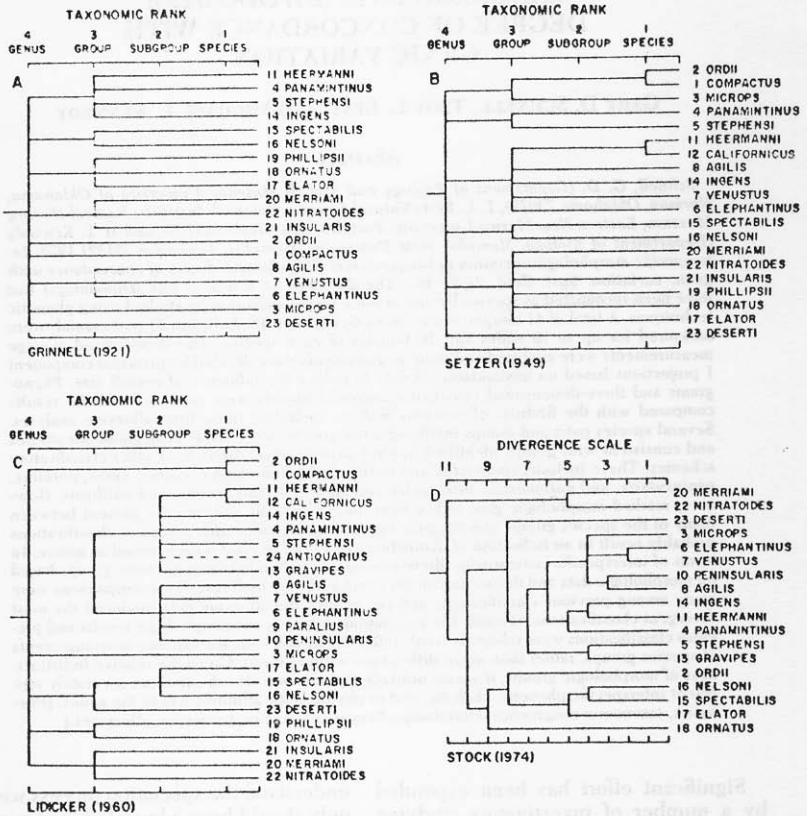

FIG. 2.—Dendrograms depicting *Dipodomys* classifications of (A) Grinnell (1921), (B) Setzer (1949), and (C) Lidicker (1960a), as well as (D) the divergence times estimated by Stock (1974).

from museum collections. We took 41 measurements, including 4 standard external characters, 16 from the skull and mandible, and 21 from the post-cranial skeleton (Table 2). External measurements were recorded from specimen tags, and skeletons were measured to the nearest 0.1 mm with dial calipers. Since sexual dimorphism has been shown for some species of *Dipodomys* (Lidicker, 1960a; Desha, 1967; Schmidly, 1971; Kennedy and Schnell, 1978; Schmidly and Hendricks, 1976; Best, 1978a), measurements for males and females were treated separately; thus, 82 characters were used. The means were calculated for each character in each sex for each species. For *D. insularis* only one complete skeleton was available—that of a female. In this case we also used its measurements as our best estimates for the male characters.

Phenetic similarities between species for morphologic characters are summarized in phenograms and three-dimensional models. NT-SYS (Numerical Tax-

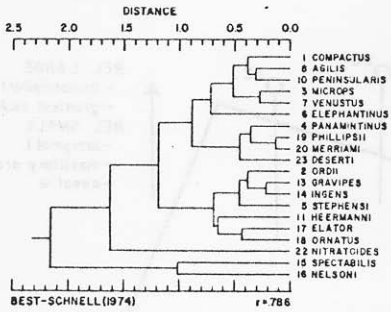

FIG. 3.—Phenetic similarities of kangaroo rats based on Best and Schnell's (1974) measurements of three bacular characters.

onomy System), a series of multivariate computer programs developed by F. James Rohlf, John Kishpaugh, and David Kirk, was used and characters were analyzed in two ways—one where the standardized average measurements (SKEL) were employed and the second where the average measurements were divided by unstandardized principal component I (SKEL/PC I).

In the first set of analyses, characters were standardized, so that each had a mean of zero and standard deviation of one among species. Product-moment correlation coefficients (CORR) and average distance coefficients (DIST) were calculated between all pairs of species (Sneath and Sokal, 1973). Correlations can range from +1 to −1 with high positive values indicating similarity. Distances are nonnegative and low values indicate similarity. Clusters were formed with the unweighted pair-group method using arithmetic averages (UPGMA; Sneath and Sokal, 1973) and summarized in phenograms. In the three-dimensional models, phenetic affinities were represented by projecting species with respect to the first three principal components extracted from a matrix of correlations among characters (Rohlf, 1968).

For the second set of analyses, where we wanted to reduce the influence of overall size, all characters (unstandardized) were divided by the species' projection on principal component I computed from unstandardized data. Data so modified were standardized and treated in the same way as the original measures.

For phenograms, the cophenetic correlation coefficient (r; Sokal and Rohlf, 1962) was computed between coefficients in the original similarity matrix and those implied in the phenogram. To obtain the cophenetic correlation coefficient of a principal component model, we calculated the correlation of the euclidian distance between each pair of species in the 3-D model with the respective average distance between each species pair in the multidimensional character space. Also, the proportion of the total variance explained by each component in the models was determined.

Several approaches were used to obtain comparative information from other authors. The genic data of Johnson and Selander (1971) were treated in three ways. First, we clustered species using UPGMA on a matrix of the unweighted mean coefficients of genic similarity (S, their Table 11) and obtained the phenogram in Fig. 1A. Next, each species was coded for the presence or absence of each allele at each locus (as summarized in their figs. 2 to 5). Using the resulting data matrix, we calculated the coefficient of Jaccard and the simple matching coefficient (Sneath and Sokal, 1973) for each species pair and clustered the species using UPGMA (Figs. 1B and C). For the former coefficient, negative matches are ignored (i.e., the absence of an allele in two species did not increase the similarity between them), while in the second both positive and negative matches influence similarity values.

In order to numerically depict similarities implied within the classifications of Grinnell (1921), Setzer (1949), and Lidicker (1960a; who summarized the other classifications, pages 132–134), we assigned specific values to represent the various levels of taxonomic similarity (see Fig. 2). When two forms were considered conspecific by a previous author,

TABLE 2. THE 41 MEASUREMENTS USED IN THIS STUDY.[1]

Skin
1 Body length
2 Tail length
3 Hind foot length
4 Ear length

Skull and Mandible
5 Basal skull length
6 Greatest skull length
7 Maxillary arch spread
8 Interorbital width
9 Nasal length
10 Intermaxillary width
11 Alveolar length
12 Lacrimal length
13 Maxillary arch width
14 Basioccipital length
15 Greatest skull depth
16 Greatest skull width
17 Zygomatic width
18 Nasal width
19 Mandible length
20 Mandible depth

Post-cranial Skeleton
21 Radius length
22 Ulna length
23 Humerus length
24 Humerus distal width
25 Humerus proximal width
26 Clavicle length
27 Scapula width
28 Scapula length
29 Scapula depth
30 Tibia length
31 Tibia distal width
32 Tibia proximal width
33 Femur length
34 Femur distal width
35 Femur proximal width
36 Pelvis length
37 Pelvis depth
38 Obturator foramen length
39 Obturator foramen width
40 Width fused vertebrae
41 Number fused vertebrae

[1] Figure 2 of Best (1978a) depicts how measurements were taken. Since his first measurement was not used in this study, the numbers assigned to our characters are always one less than those used by Best.

we assigned a similarity value of 1; if two species were represented as being in the same subgroup, similarity between them was considered to be 2; for two that were in the same group the similarity was 3; species within the genus but not associated at a lower level in a classification were assigned a similarity of 4. Thus, similarities between each pair of species could be delimited for each classification, with these values forming a triangular resemblance matrix. In Lidicker's (1960a) classification, *D. antiquarius* was added to his Heermanni group (dotted line in Fig. 2C), although it was described at a later date by Huey (1962).

In order to "quantify" Stock's (1974) dendrogram illustrating proposed phylogenetic relationships, we placed equally spaced, parallel, and horizontal lines across his fig. 6. The various degrees of relationship between species were represented with values from 2 to 11 (Fig. 2D). For comparisons with the results of Best and Schnell (1974), we used their phenogram and resemblance matrix based on three bacular measurements (Fig. 3).

We compared different phenograms with the coefficient of correlation of cophenetic values (Crovello, 1969). This is the correlation between sets of coefficients implied by the diagrams. Coefficients of correlation of similarity (i.e., resemblance) matrices—a correlation between the half matrices of two resemblance matrices, excluding the principal diagonal—were also calculated. We determined the correlations between each resemblance matrix (or phenogram) and each of the classifications (and its resemblance matrix if available) listed above. For comparisons involving a similarity against a dissimilarity matrix (or of phenograms based on them), the sign of the resulting correlation was changed so that similarity was represented by a positive correlation. In comparisons with and between other classifications, calculations were based only on species common to both analyses. The resulting similarity values between classifications were used in clustering with UPGMA to form a dendrogram that shows similarities between classifications.

RESULTS

Three-dimensional Models

In Fig. 4, the 24 species are projected onto the first three principal components based on the analysis of average measurements. These components explain 82.9, 3.6, and 3.2% (96.0% combined) of the total character variance. The cophenetic correlation of the model is 0.996, indicating that reducing the 82-dimensional character space to three dimensions results in essentially no distortion of the original distances.

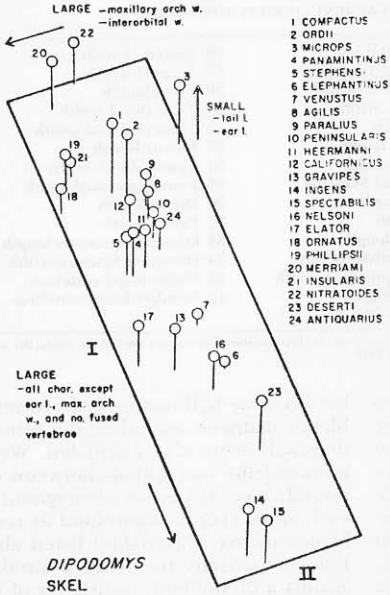

FIG. 4.—Projections of the 24 species of *Dipodomys* onto the first three principal components based on a matrix of correlations among average measurements. Characters with high positive or negative loadings on the three components are listed.

Principal component I is a size factor and separates our four groups: (1) the large *ingens* and *spectabilis* along with *deserti*; (2) the small *merriami* and *nitratoides*; (3) a medium-large sized group of *elator*, *gravipes*, *venustus*, *nelsoni*, and *elephantinus*; and (4) a medium-small sized group of the remaining species. This component has high positive loadings (0.69 or over) for all characters (both sexes) except ear length, maxillary arch width, and number of fused vertebrae. As for component II, *microps* has small maxillary arch and interorbital widths (loadings of 0.80 and 0.42 for males; 0.82 and 0.47 for females) and is separated from the other forms. Species such as *ornatus* and *elator* near the other edge of the diagram (Fig. 4) tend to be large for these characters. There were relatively high negative loadings on component III for tail and ear lengths (−0.79 and −0.56 for males; −0.49 and −0.81 for females). As implied by its name, *elephantinus* which is near the base of the model is large for ear length, as well as tail length; *compactus* and *ordii*, which have large projection values for III, are smaller for these characters than other species of about the same size.

In the analysis where characters were divided by projections of unstandardized principal component I, the species did not fall into particularly distinct groups in the model (Fig. 5). The first three components explain 31.4, 20.7, and 10.6% (62.2% combined) of the total character variance, and the cophenetic correlation coefficient of the model is 0.737. There are two sets of species that separate somewhat from the others: *ordii* and *compactus*; *gravipes*, *spectabilis*, and *ingens*. In addition, *merriami* and *nitratoides* are relatively similar and distinct from the other *Dipodomys*, as are *microps* and *deserti*.

The first component has high positive loadings (at least 0.70 for males and females, or 0.80 for one sex) for long bones and parts of the pelvic girdle (characters listed in Fig. 5). Relative to size (as estimated by unstandardized principal component I), animals with high values for projections onto principal component I, such as *ingens* have bigger humeri, tibiae, and femora, as well as relatively larger and wider pelvises. Species like *insularis* with low values are relatively small for these characteristics. Component II is a contrast between relative tail length and a number of other characters, particularly relative skull length measures (see list in Fig. 5). *D. ordii* and other species to the right of the diagram have relatively small tails and relatively long skulls, as well as relatively wide intermaxillaries and large ulnae (the latter most marked in females). Species at the other edge of the diagram—those with high values for projections on II such as *californicus* and *deserti*—exhibit the op-

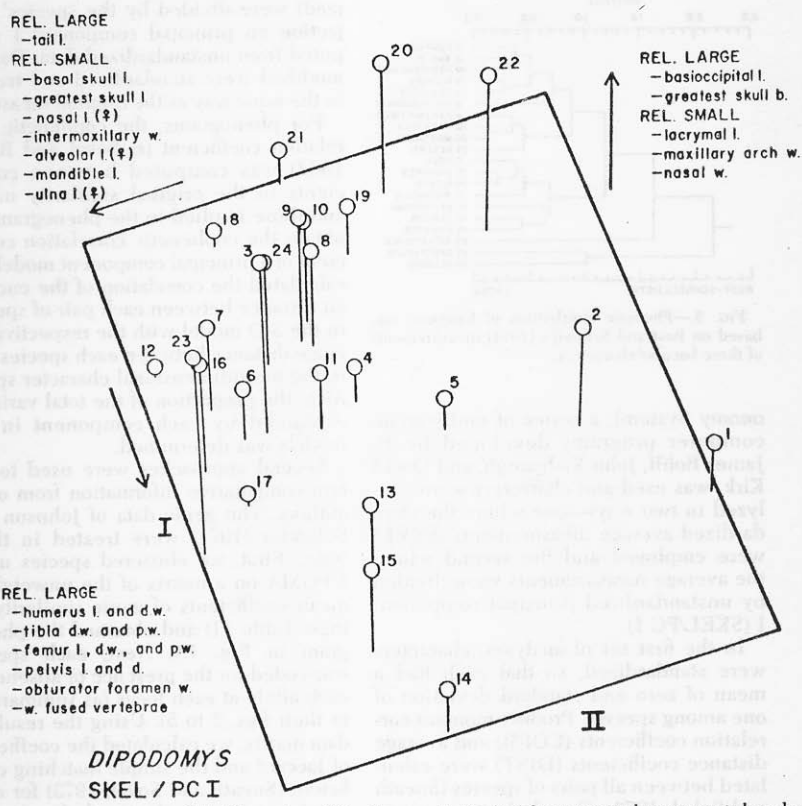

FIG. 5.—Projections of the 24 species of *Dipodomys* onto the first three principal components based on a matrix of correlations among average measurements divided by unstandardized principal component I. Characters with high positive or negative loadings on the three components are listed. Species numbers are the same as those indicated in Fig. 4.

posite condition. The third component is also a contrast. It has high positive correlations (0.50 for both sexes or 0.60 for one) with basioccipital length and greatest skull breadth and negative ones with lacrymal length as well as maxillary arch and nasal widths. *D. californicus* and *elator* which are near the base of the diagrams are—relative to their size—smaller for the former character group and larger for the latter group than other species. *D. microps*, *deserti*, and other *Dipodomys* with large projection values on III are larger for the former and smaller for the latter group of characters.

Phenograms

The four phenograms produced by our analyses are presented in Fig. 6. The one for distances based on average measurements (Fig. 6A) largely reflects the groupings outlined for the principal component model (Fig. 4). The four size groups separated by principal component I in

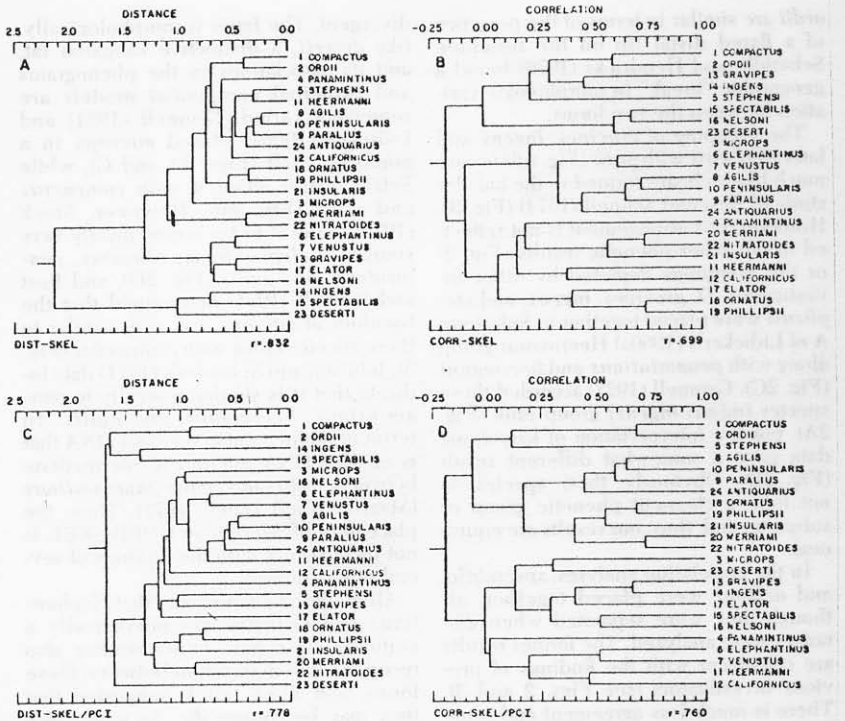

FIG. 6.—Phenograms based on 41 morphologic measures. The first two diagrams result from using average measurements, with resemblances being calculated as (A) average distance coefficients or (B) product-moment correlation coefficients. For the other two phenograms, average measurements were divided by unstandardized principal component I and resemblances were calculated with (C) average distance coefficients and (D) product moment correlation coefficients. The cophenetic correlation coefficient is given in the lower right corner of each diagram.

the model are evident in the phenogram, and *microps* (which is separated by II) is also shown in Fig. 6A to be somewhat distinct from the main group of species. The cophenetic correlation is 0.832 and indicates some distortion in terms of summarizing the distances with a phenogram.

The correlation phenogram for average measurements (Fig. 6B) is very different from the distance phenogram and the 3-D model. Several of the closely associated groups of species, such as *compactus* and *ordii* (or *agilis*, *peninsularis*, *paralius*, and *antiquarius*) are maintained. However, other new groups (such as *spectabilis*, *nelsoni*, and *deserti*) were formed. Four or five major divisions are indicated in the correlation phenogram, but the phenetic clusters are not particularly distinct. The lack of clear-cut groups is also reflected in the relatively low cophenetic correlation of 0.699.

Where the effect of size was modified, the phenograms (Figs. 6C and D) did not exhibit clusters that were any better defined—in fact less subdivision is evident. The distance phenogram (Fig. 6C)

grouped the outliers of the comparable 3-D model (Fig. 5) together (*compactus-ordii* and *ingens-spectabilis*). *D. deserti* is by itself at the bottom of the diagram and the remaining species are placed in two poorly defined groups. The cophenetic correlation was 0.778.

The CORR-SKEL/PC I phenogram (Fig. 6D) for the same data has one main subdivision and a total of four or five groups. Again, a number of small groups (e.g., *compactus* and *ordii*) are the same as those found in other phenograms. However, numerous differences, particularly in the arrangement of these small groups, are present. The relatively low cophenetic correlation of 0.760 is one reflection of the fact that the species groups are not distinctly separated, but rather tend to merge into one another.

Similarities Among Dendrograms and Among Resemblance Matrices

Correlations comparing the various previous classifications among themselves and with the phenograms and resemblance matrices from our studies are given in Table 3. Similarities range from −0.154 between Setzer's (1949) classification and the phenogram based on Johnson and Selander's (1971) genic data, where the simple matching coefficient was used, to 0.868 which results from the comparison of phenograms of the genic data where the simple matching coefficient and Jaccard's coefficient were employed (Table 3).

The similarities between resemblance matrices, which are the most appropriate to examine for comparisons between data sets, are further summarized in the dendrogram shown in Fig. 7A. Several groups are evident. The first includes the classifications of Grinnell (1921), Lidicker (1960a), Stock (1974), and Setzer (1949), with the latter being the most divergent. This group is joined to one containing the four phenograms of our study and then to the specialized bacular classification of Best and Schnell (1974). A substantial gap exists between these and the genic classifications based on the data of Johnson and Selander (1971).

TABLE 3. CORRELATIONS BETWEEN PAIRS OF RESEMBLANCE MATRICES (UPPER RIGHT) AND BETWEEN PAIRS OF DENDROGRAMS (LOWER LEFT). FOR GRINNELL (1922), SETZER (1949), LIDICKER (1960), AND STOCK (1974) THE VALUES IN THE RESEMBALANCE MATRIX AND THE COPEHNETIC MATRIX (I.E., THE SIMILARITIES IMPLIED BY A DENDROGRAM) ARE THE SAME.

	1 Grinnell (1921)	2 Setzer (1949)	3 Lidicker (1960)	4 Johnson-Selander (S)	5 Johnson-Selander (JA)	6 Johnson-Selander (SM)	7 Stock (1974)	8 Best-Schnell (1974)	9 CORR-SKEL	10 DIST-SKEL	11 CORR-SKEL/PC I	12 DIST-SKEL/PC I
1 Grinnell (1921)	X	.418	.648	.284	.279	.165	.530	.178	.418	.157	.373	.295
2 Setzer (1949)	.418	X	.539	.106	.001	−.032	.392	.182	.355	.214	.392	.279
3 Lidicker (1960)	.648	.539	X	.169	.171	.134	.734	.198	.335	.287	.298	.412
4 Johnson-Selander (S)	.301	.073	.136	X	.907	.649	.364	.134	.223	.159	.181	.246
5 Johnson-Selander (JA)	.244	−.039	.155	.857	X	.851	.462	.230	.170	.192	.066	.233
6 Johnson-Selander (SM)	.063	−.154	.020	.598	.868	X	.455	.248	.140	.141	.034	.088
7 Stock (1974)	.530	.392	.734	.413	.542	.534	X	.413	.297	.290	.269	.424
8 Best-Schnell (1974)	.200	.140	.184	−.018	.119	.122	.379	X	.233	.453	.225	.332
9 CORR-SKEL	.545	.449	.381	.059	.044	−.056	.355	.195	X	.395	.698	.499
10 DIST-SKEL	.086	.165	.163	.286	.291	.100	.088	.205	.210	X	.485	.668
11 CORR-SKEL/PC I	.251	.491	.237	−.009	−.061	−.099	.198	−.015	.456	.219	X	.622
12 DIST-SKEL/PC I	.239	.348	.430	.111	.183	.113	.398	.107	.428	.563	.289	X

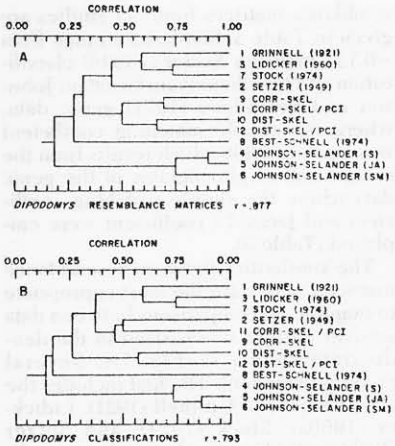

FIG. 7.—Dendrograms showing similarities among (A) resemblance matrices and (B) phenograms. Previous classifications are included in both sets of comparisons. The cophenetic correlation is indicated for each diagram.

The cluster analysis of phenograms (Fig. 7B) resulted in a slightly different arrangement. Setzer's (1949) classification grouped with CORR-SKEL/PC I, and these along with CORR-SKEL joined with the classifications of Grinnell (1921), Lidicker (1960a), and Stock (1974). These six classifications were then clustered with our two distance phenograms and then with the Best and Schnell (1974) classification. The genic dendrograms were separated from the others, with the treatments of Johnson and Selander's (1971) data with Jaccard's coefficient and the simple matching coefficient producing the most similar phenograms.

A number of species pairs or small species groups were stable throughout our studies and often these were consistent with groups identified in other classifications. These include: *compactus* and *ordii*; *elephantinus* and *venustus*; *agilis*, *paralius*, *peninsularis*, and *antiquarius*; *nitratoides* and *merriami*; and *ornatus* and *phillipsii*. Distinct breaks, however, were not necessarily evident between these various groups.

DISCUSSION

Phenetics and Species Groups

It is clear from Table 3 and Fig. 7 that previous classifications constructed to show phylogenetic relationships and/or degrees of specialization (those of Grinnell, 1921; Setzer, 1949; Lidicker, 1960a; and Stock, 1974) do not reflect well the degree of morphologic similarity between species as estimated primarily by skeletal measures (i.e., our phenograms and resemblance matrices). Such a statement could of course be made in reverse; both comments, however, refer only to the overall arrangement of all the species (which is what is measured by the calculated correlations) and not necessarily to arrangements within species groups of *Dipodomys*. The relatively low similarity values between these previous classifications, and our phenograms and resemblance in matrices in many cases reflect the different placement of a few species in the classfications being compared, rather than differences between classifications in the treatment of all forms.

In order to assess the degree of similarity in treatment of various species groups in the phenetic and other classifications, the groupings present in CORR-SKEL (Fig. 6B) will be analyzed in more detail. The placement of *compactus* and *ordii* in this and our other phenograms is as expected, since little question has been raised as to their close affinity by previous authors. Rather, comment has been directed at whether subspecies or closely related species are involved. Evidence as to their relationship has most recently been summarized and added to by Schmidly and Hendricks (1976) and Jannett (1976). Substantial differences in gene frequencies between *compactus* and *ordii* were noted by Johnson and Selander (1971) (see Fig. 1A); Best and Schnell (1974), who had only a small sample for *compactus*, found that on the basis of three bacular measurements the two were quite different, although Jannett (1976) showed that *compactus* and

ordii are similar in terms of the presence of a flared distal tip on the baculum. Schmidly and Hendricks (1976) found a geographic "break" in morphologic variation between the two forms.

The grouping of *gravipes*, *ingens* and later *stephensi* with *ordii* (Fig. 6B) is very much like a cluster formed in the bacular study of Best and Schnell (1974) (Fig. 3). However, this arrangement is not reflected in our other phenetic results (Fig. 6) or the groupings depicted by other investigators. *D. gravipes*, *ingens*, and *stephensi* were placed together in Subgroup A of Lidicker's (1960a) Heermanni group along with *panamintinus* and *heermanni* (Fig. 2C). Grinnell (1921) accorded these species (minus *ingens*) group rank (Fig. 2A), but the interpretation of karyotypic data gave a somewhat different result (Fig. 2D). Obviously, these species do not form a clear-cut phenetic group or subgroup and, thus, our results are equivocal.

In the correlation analyses, *spectabilis* and *nelsoni* were placed together, although they were separated when distances were analyzed. The former results are consistent with the findings of previous investigators (see Figs. 2 and 3). There is much less agreement and some puzzlement in terms of the appropriate placement of *deserti* in classificatory schemes, and its phenetic affinities do not clarify this situation. It is an outlier in terms of distances (see models in Figs. 4 and 5), and the location of *deserti* in each phenogram is different. Lidicker (1960a) placed *deserti* in a monotypic subgroup of his Spectabilis group (which included *elator*, *spectabilis* and *nelsoni*), while Grinnell (1921) and Setzer (1949) separated *deserti* into its own group. In contrast, Stock (1974) placed it in a monotypic subgroup of his Heermanni group. Considering only the presence and/or absence of alleles (Figs. 1B and C), genic data show the most similar species to *deserti* is *spectabilis*.

The next major cluster in CORR-SKEL contains seven species (species 3 to 24, inclusive), with *microps* being the most divergent. The latter is morphologically, like *deserti*, a distinctive kangaroo rat, and its associations in the phenograms and principal component models are somewhat varied. Grinnell (1921) and Lidicker (1960a) placed *microps* in a group by itself (Figs. 2A and C), while Setzer (1949) allied it with *compactus* and *ordii* (Fig. 2B). However, Stock (1974) found it to be karyotypically very similar to *elephantinus*, *venustus*, *peninsularis*, and *agilis* (Fig. 2D), and Best and Schnell (1974) determined that the baculum of *microps* was very similar to these species along with *compactus* (Fig. 3). Johnson and Selander's (1971) data indicate that it is similar genically to *panamintinus*, *heermanni*, and *agilis*. In terms of the percent of the total DNA that is satellite DNA, *microps* is intermediate between *ordii* and *agilis-panamintinus* (Mazrimas and Hatch, 1972). Thus, the placement of *microps* in CORR-SKEL is not inconsistent with the findings of several other studies.

All of our results indicate that *elephantinus* and *venustus* are phenetically a mutually close pair. Other studies also record a close association between these forms, and Stock (1974) suggested that they may be conspecific. As with these two forms, the allotment in CORR-SKEL of *agilis*, *paralius*, *peninsularis*, and *antiquarius* to one cluster is similar to other phenetic results. Their relationships are summarized by Best (1978a, b); our findings are consistent with his conclusion that these four forms are conspecific.

In CORR-SKEL, *panamintinus* is depicted as being only distantly associated with a cluster of *merriami*, *nitratoides*, and *insularis*. However, while *panamintinus* is shown as being rather distinctive, its closest phenetic affinities are with species usually placed in a Heermanni group (see Fig. 6). The latter treatment is consistent with the placement of and comments about this species by Lidicker (1960a) and Stock (1974). Clearly, *panamintinus* is phenetically an outlier in terms of any well-defined species group.

D. nitratoides and *merriami* are placed

together in all of our phenograms. While these two species have quite divergent bacula (Best and Schnell, 1974), most other types of data show close affinities between these two species (Grinnell, 1921; Lidicker, 1960a; Johnson and Selander, 1971; Stock, 1974). Also, the relatively unknown *insularis* is associated with these two species in all of our phenograms except DIST-SKEL, where size results in its being closer to *phillipsii* and *ornatus*. The former phenetic alignment is concordant with the treatment of this species by Grinnell (1921), Setzer (1949), and Lidicker (1960a) (Fig. 2).

The relatively close similarity of *heermanni* and *californicus* in CORR-SKEL is also indicated in CORR-SKEL/PC I (Fig. 2D). In the two distance phenograms, *californicus* is depicted as being loosely associated with a group of species that include *heermanni*. The morphologic similarity between *heermanni* and *californicus* is in agreement with the genic results and conclusions of Patton et al. (1976) and contrasts with Stock's (1974) suggestion that the latter is more closely related to *nitratoides*.

The last group in CORR-SKEL includes *elator*, *ornatus*, and *phillipsii*. The very close phenetic affinities between *ornatus* and *phillipsii* in all of our phenograms is supportive of the conclusion that the two forms are conspecific by Genoways and Jones (1971). *D. elator* does not show such a consistent phenetic pattern, however; it is closest to *gravipes* or a cluster containing this species in the other three phenograms (Figs. 2A, C, and D). Several authors have concluded that *elator* is most closely related to *ornatus* (Grinnell, 1921; Setzer, 1949; Best and Schnell, 1974), while Lidicker (1960a) and Stock (1974) indicated that the closest relatives of *elator* are *nelsoni* and *spectabilis*. Lidicker (1960b) suggested that *elator* probably was not particularly close to either the Spectabilis or the Phillipsii groups. Genically, *elator* was very different from other *Dipodomys* (see Fig. 1). Jannett (1976) felt that currently available data support the idea that *elator* is an early offshoot in the evolution of the genus and not merely a specialized form to be fitted into a Merriami or Spectabilis group.

As is evident from the previous discussion, a number of the phenetic, morphologic species groups that appear in our phenograms and principal component models are similar or identical to groups identified in phylogenetic, specialization, or other classificatory schemes. However, our morphologic results lead to the conclusion that distinct gaps—other than those based strictly on size—are not present between many of the groups of species. Thus, attempts to place species into well-defined and differentiated species groups (whether in a phenetic, phylogenetic, or other classification) will very likely result in an indication of distinctness that is greater than true of nature. Such a statement of course is not contrary to the fact that some species consistently group together. Also, it is clear that no single classification can accurately represent phenetic, cladistic, and phylogenetic affinities—as might be the case if clear-cut groups were present.

Genic and Other Similarities

Figure 7 shows that (taking all combinations simultaneously) interspecific similarities based on genic data are markedly different from those determined through other types of analyses. Johnson and Selander (1971) compared quantitatively their dendrogram based on genic data with Setzer's (1949) classification and obtained a correlation of 0.805; in addition, the comparison with Lidicker's (1960a) scheme yielded a 0.792. However, these measures involved comparisons of all populations sampled (as well as the inclusion of *Perognathus hispidus*), rather than just interspecific *Dipodomys* comparisons. When one eliminates intraspecific associations and those with *P. hispidus*, the correlations drop to only 0.073 and 0.136, respectively (Table 3)—values that indicate no association.

Also, essentially no correlation exists between morphologic and genic results.

The correlation values between resemblance matrices based on genic and our morphologic findings range from 0.066 between JOHNSON-SELANDER (SM) and DIST-SKEL/PC I to only 0.246 between the same genic matrix and CORR-SKEL (see Table 3). Thus, for kangaroo rats, it appears that protein and morphologic changes have proceeded in substantially different ways.

Mickevich and Johnson (1976) have discussed in some detail the congruence between morphologic and allozyme data. They stated that the impression of some authors has been that protein and morphologic characters have evolved concordantly, but that recently several studies have indicated a high degree of evolutionary independence of the two types of characters. Also, they appropriately emphasized that one should distinguish between methods of analysis and the types of characters. In our case (mentioned just above), comparisons are between phenetic results based on two different types of characters—allozyme and morphologic.

Their results, as do ours, show a relatively low degree of concordance between morphologic and genic data for *Menidia* when evaluated using phenetic methods of analysis. Mickevich and Johnson (1976) did find, however, close concordance when cladistic methods were employed to analyze the two character sets. They indicated that "The important point from our results is that the critical distinctions are those between methods of analysis rather than between types of characters." Whether cladistic methods will consistently give similar results from these two types of data sets remains to be demonstrated. Cladistic analyses of the two types of data for *Dipodomys* would be particularly interesting in light of the relative lack of phenetic morphologic separation of species groups, as well as the disparate phenetic results from morphologic and genic information. In addition, there are a number of previous classifications available for comparison.

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