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ABSTRACT: Bacular variation in 20 species (397 specimens) of *Dipodomys* was analyzed. No definite trend was apparent in the relationship between body size and bacular size. Comparisons based on three bacular measurements yielded phenetic classifications that showed marked similarities to the interspecific groupings of several previous investigators, although differences exist as well. Our resulting classifications differ significantly from those obtained using morphologic or genic information, but are similar to that suggested from karyotypic data. Significant age variation was evident in *D. ordii* in shape and size, with elongation occurring and essentially all growth taking place at the proximal end.

INTRODUCTION

Kangaroo rats (genus *Dipodomys*) occupy arid and semiarid regions of western North America from southern Canada through most of Mexico (Hall and Kelson, 1959). Some species have been studied extensively by classical taxonomic methods (Hall and Dale, 1939; Setzer, 1949; Lidicker, 1960a; Lackey, 1967; Genoways and Jones, 1971) and several classifications have been proposed (Grinnell, 1921, 1922; Wood, 1935; Burt, 1936; Setzer, 1949; Lidicker, 1960a; Johnson and Selander, 1971; Stock, 1974), but numerous problems regarding species limits and other aspects of relationships within the genus remain unresolved.

Bacula of adult kangaroo rats differ from other related heteromyids —*Perognathus, Liomys* and *Microdipodops*—in being more robust and generally larger. Geomyid bacula are similar in size and appearance, but are heavier and more rounded at the tip. Adult *Dipodomys* bacula have large, hollow, bulbous bases (Lidicker, 1960b), with species differing in the size of the bulbous base, length of the baculum, curvature of the shaft, and degree of upturn of the tip.

There are scattered descriptions of the bacula of some *Dipodomys* species (Boulware, 1943; Blair, 1954; Lackey, 1967; Genoways and Jones, 1971). However, only Burt (1936, 1960) and Lidicker (1960b) have made systematic comparisons of bacula for more than two or three species. At the time of their comparisons, information was available on only about one-half of the *Dipodomys* species and for many there were only small samples. The purpose of our study is to use the

more complete bacula data now available and examine: (1) age variation in bacular shape and size; (2) the degree of interspecific variation in bacula; (3) the relationship between body size and bacular size; and (4) phenetic affinities based upon bacular measurements.

MATERIALS AND METHODS

From 1966 to 1971 bacula were collected (from fresh specimens and standard museum study skins), prepared and stored in glycerin as outlined by Lidicker (1960b). Measurements were taken to the nearest 0.1 mm under a binocular microscope with dial calipers. Except for specimens of *D. ordii* studied for age variation, we used only fully adult specimens.

For studies of age variation, we analyzed 211 specimens of *D. ordii* collected near Norman, Okla. These were divided into age classes (juveniles, subadults and adults) on the following criteria: (1) completeness of dentition; (2) tooth wear; (3) translucence of auditory bullae; and (4) convexity of cranium. Adults have complete permanent dentition, subadults show evidence of the recent acquisition of some teeth, and the permanent dentition of juveniles may be absent or incomplete. The premolar and molars show some wear in adults, subadults have unworn to sightly worn premolar and molars, and wear is not evident in juveniles. We classed animals with translucent and smooth-surfaced bullae as adults; subadults have bullae that are at most only partially translucent, and the bullae of juveniles are opaque and rough in texture. A skull is viewed laterally to evaluate cranial convexity. In juveniles there is marked convexity in the dorsal surface of the cranium near the articulation between the frontal and parietal bones. The upper surface of the skull is convex in subadults, and this convexity is barely evident in adults. The first three criteria are modified slightly from those used by Lidicker (1960a) to age *D. merriami*.

To present a relatively complete picture of bacular variation within the genus, we combined our measurements with those of previous authors (Table 1). Measurement variation due to differences in technique between various authors is probably minimal, since all measurements are easily taken. Burt's (1936, 1960) measurements for *D. microps* and Genoways and Jones' (1971) for two specimens (KU19384 and 48987) of *D. phillipsii* were not included since their specimens appear immature. All drawings were made from photographs taken through a stereomicroscope.

Of the 21 *Dipodomys* species listed by Hall and Kelson (1959), bacular data are available on 19. No information was obtained for *D. antiquarius* (described by Huey, 1962), *D. paralius* and *D. insularis* —all found in Baja California. However, data for *D. compactus* were included, since Johnson and Selander (1971) suggested it should be given specific status. Species were assigned numbers (Table 1) according to the sequence of Hall and Kelson (1959).

The means of three measurements—bacular length, width, and height—for each species were analyzed as described below; then, to compare relative size, the logs of the three measurements were divided by the log of the mean body length for the appropriate species. This allows one to look at the *relative* change in the size of bacula in that body length is, in effect, "held constant" over all species. Clearly, it would have been desirable to calculate the ratios on each individual specimen and then average results; however, the nature of the data available (*i.e.*, information from the numerous sources) precluded using this approach. The rationale for using logs is detailed in Lewontin (1966) and Sokal and Rohlf (1969); for our data, analyses completed but not reported in this paper indicate that no major changes resulted because of the use of this transformation.

Clustering techniques were used to analyze differences between species and group them phenetically. Characters were standardized so that each would have a mean of zero and a standard deviation of one; average distance coefficients were calculated for all species pairs; and species were then clustered with the unweighted pair-group method using arithmetic averages. A further explanation of these techniques, plus the rationale for their use, is given in Sokal and Sneath (1963).

Generally, for numerical taxonomic studies, the use of only three characters is considered inadequate. However, mammalogists usually take only three measurements from *Dipodomys* bacula and have used these in constructing classifications. By undertaking this study, we do not mean to imply that our resulting phenograms should be interpreted as general classifications; rather, they estimate phenetic similarity of a very specialized structure.

If one wishes to determine species clusters based on only three characters, use of a clustering algorithmn should be less arbitrary than doing it by eye. However, one must be cautious in interpreting the clusters formed—just as one should always use care in drawing conclusions for clusters based on a small number of characters.

RESULTS

There is significant intraspecific age variation in bacula, as depicted for *D. ordii* (Fig. 1). Specimens were grouped into three categories using skull criteria and, then, within each were arranged in an age sequence. In the adults sequencing was very difficult, and the bacula figured are a random sample from all specimens. We were able to age subadults and juveniles quite accurately. The 17 juvenile specimens were sequenced according to age, and the bacula of specimens 4, 9 and 14 are diagrammed. For the 39 subadults sequenced, specimens 7, 20 and 32 are drawn.

Figure 1 shows the change in the shape and size of the bacula with age. Marked elongation occurs; in fact, essentially all additional growth occurs at the proximal end. The base increases greatly in size, while the curved distal end remains approximately the same size

TABLE 1.—Bacular measurements (mm)) and body lengths of 20 species of kangaroo rats (*Dipodomys*)

	Length						Width					
	Present			Previous		Combined	Present			Previous		Combined
Species	mean	(st. dev.;	n)	mean	(n)	mean (n)	mean	(st. dev.;	n)	mean	(n)	mean (n)
1. *ordii*	11.52	(0.70;	70)	11.31	(20)[a,b]	11.47 (90)	1.93	(0.29;	71)	1.68	(20)[a,b]	1.88 (91)
2. *microps*	10.87	(0.59;	6)			10.87 (6)	1.52	(0.28;	6)			1.52 (6)
3. *panamintinus*	9.73	(0.56;	6)	10.68	(13)[a,b]	10.38 (19)	0.88	(0.31;	6)	1.32	(13)[a,b]	1.18 (19)
4. *stephensi*	11.82	(0.16;	6)	11.67	(46)[c]	11.69 (52)	1.95	(0.29;	6)			1.95 (6)
5. *elephantinus*	9.60	(..... ;	1)			9.60 (1)	1.80	(..... ;	1)			1.80 (1)
6. *venustus*	10.35	(0.81;	6)			10.35 (6)	1.38	(0.04;	6)			1.38 (6)
7. *agilis*	9.37	(0.62;	11)	9.85 9.89 9.70	(2)[d] (11)[c] (11)[a,b]	9.66 (35)	1.67	(0.29;	11)	1.31	(11)[a,b]	1.49 (22)
8. *peninsularis*	9.18	(0.59;	4)			9.18 (4)	1.33	(0.28;	4)			1.33 (4)
9. *heermanni*	11.58	(0.55;	6)	11.57 11.44	(3)[d] (8)[a,b]	11.51 (17)	1.47	(0.18;	6)	1.49	(8)[a,b]	1.48 (14)
10. *gravipes*	12.45	(0.24;	4)	13.30	(1)[c]	12.62 (5)	1.83	(0.21;	4)	1.27	(1)[c]	1.72 (5)
11. *ingens*				12.34	(5)[a,b]	12.34 (5)				1.84	(5)[a,b]	1.84 (5)
12. *spectabilis*	17.11	(1.03;	13)	15.60	(5)[b]	16.69 (18)	2.52	(0.46;	13)	1.70	(5)[b]	2.29 (18)
13. *nelsoni*	15.00	(0.86;	4)			15.00 (4)	2.00	(0.44;	4)			2.00 (4)
14. *elator*	13.08	(0.26;	4)			13.08 (4)	1.73	(0.10;	4)			1.73 (4)
15. *ornatus*	10.85	(0.07;	2)	11.30 12.22	(4)[e] (5)[f]	11.73 (11)	1.55	(0.07;	2)	1.63 1.64	(4)[e] (5)[f]	1.62 (11)
16. *phillipsii*				10.50	(1)[b]	10.50 (1)				1.20	(1)[b]	1.20 (1)
17. *merriami*	11.13	(0.48;	20)	10.67	(65)[a,b]	10.78 (85)	1.44	(0.29;	20)	1.06	(65)[a,b]	1.15 (85)
18. *nitratoides*				13.34	(14)[a,b]	13.34 (14)				0.93	(14)[a,b]	0.93 (14)
19. *deserti*	9.56	(0.66;	13)	9.30	(5)[a,b]	9.49 (18)	1.09	(0.10;	13)	0.91	(5)[a,b]	1.04 (18)
20. *compactus*	9.75	(0.78;	2)			9.75 (2)	1.40	(0.14;	2)			1.40 (2)

[a] Burt (1936) [b] Burt (1960) [c] Lackey (1967) [d] Boulware (1943) [e] Genoways and Jones (1971) [f] Lidicker (1960b) [g] Hall and Kelson (1959) [h] males and females combined from Chalchicomula, Puebla, Mexico (Genoways and Jones, 1971) [i] Davis (1942)

TABLE 1.—(continued)

Species	Height: Present mean	Height: Present (st. dev.; n)	Height: Previous mean (n)	Height: Combined mean (n)	Body length: mean	Body length: (st. dev.; n)
1. *ordii*	2.18	(0.23; 71)	2.00 (20)[a,b]	2.14 (91)	119.42	(5.55; 77)
2. *microps*	1.55	(0.14; 6)		1.55 (6)	119.82	(5.67; 11)
3. *panamintinus*	1.18	(0.19; 6)	1.64 (13)[a,b]	1.49 (19)	119.85	(5.97; 13)
4. *stephensi*	1.87	(0.20; 6)		1.87 (6)	114.30	(5.57; 20)
5. *elephantinus*	1.80	(.....; 1)		1.80 (1)	124.00	(.....; ....)[g]
6. *venustus*	1.55	(0.14; 6)		1.55 (6)	124.00	(.....; ....)[g]
7. *agilis*	1.71	(0.25; 11)	1.60 (11)[a,b]	1.66 (22)	115.46	(5.70; 68)
8. *peninsularis*	1.73	(0.36; 4)		1.73 (4)	114.16	(7.59; 69)
9. *heermanni*	1.90	(0.22; 6)	2.01 (8)[a,b]	1.96 (14)	123.50	(0.71; 2)
10. *gravipes*	2.18	(0.19; 4)	1.58 (1)[c]	2.06 (5)	128.67	(6.60; 61)
11. *ingens*			2.02 (5)[a,b]	2.02 (5)	147.00	(.....; 2)[a]
12. *spectabilis*	2.70	(0.40; 13)	2.20 (5)[b]	2.56 (18)	144.81	(10.96; 27)
13. *nelsoni*	2.10	(0.41; 4)		2.10 (4)	130.75	(8.06; 4)
14. *elator*	1.70	(0.18; 4)		1.70 (4)	122.92	(5.45; 12)
15. *ornatus*	1.65	(0.21; 2)	1.75 (4)[e] 1.86 (5)[f]	1.65 (2)	102.92	(4.27; 12)
16. *phillipsii*			1.30 (1)[b]	1.30 (1)	104.03	(.....; 30)[h]
17. *merriami*		(0.27; 20)	1.19 (65)[a,b]	1.26 (85)	100.74	(4.82; 7)
18. *nitratoides*	1.50		1.13 (14)[a,b]	1.13 (14)	102.00	(.....; 7)[a]
19. *deserti*	1.28	(0.16; 13)	1.16 (5)[a,b]	1.25 (18)	141.89	(7.98; 9)
20. *compactus*	1.90	(0.00; 2)		1.90 (2)	117.00	(.....; ....)[i]

and shape. Changes due to age would affect all three standard measurements usually taken on bacula.

For interspecific comparisons the bacula of 20 species of *Dipodomys* have been drawn to the same scale (Fig. 2). Bacular measurements and body length for each species are given in Table 1. Differences in shape are evident. The *D. nitratoides* bacula is elongated, and bacula of *D. spectabilis* and *D. nelsoni* are notably more robust than those of other species. *D. deserti,* a large species, has one of the smallest bacula.

Figure 3 includes two three-dimensional models, one plot of the three bacular measurements and the other of logs of these measures relative to body length. The diagrams are very similar, indicating that differences in bacular size between species are essentially unrelated to the overall size of those animals. This is further demonstrated by the phenograms depicted in Figure 4, since only one marked difference is evident. When analyzing actual measurements (Fig. 4A), the cluster of *D. spectabilis* and *D. nelsoni* was the most distinct and *D. nitratoides* is separated from the majority of species. For relative measurements (Fig. 4B) the positions of the latter cluster and the *D. nitratoides* stem are reversed.

The cophenetic correlation coefficient (Sokal and Rohlf, 1962) is one measure of the degree to which a dendrogram accurately reflects values in its original similarity matrix. Cophenetic values of 0.786 and 0.774 for A and B, respectively, imply that some distortion has occurred in the representation of the original distances between species.

The coefficient of correlation of cophenetic values (Crovello, 1969)—a measure of overall similarity between two phenograms—is 0.790. The difference of this value from 1.000 (which would indicate that phenograms were identical) is mainly due to the switching of the two outer stems.

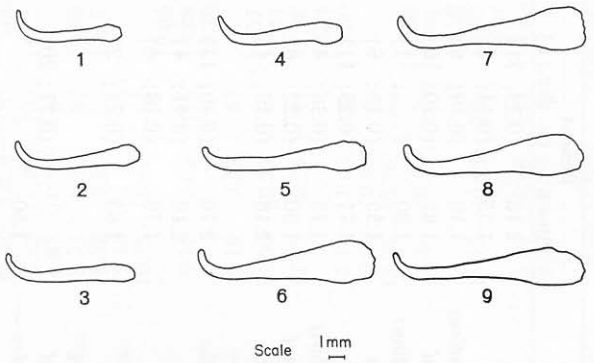

Fig. 1.—Representative specimens of bacula from *D. ordii,* showing variation in size and shape with age. Specimens 1, 2, and 3 are from juveniles (TLB specimen nos. 5035, 5258, 4516); 4, 5 and 6 are from subadults (4344, 5228, 3919); and 7, 8 and 9 are from adult specimens (3923, 4930, 4960). All were collected near Norman, Oklahoma

DISCUSSION

Age variation in bacular shape and size has been studied in several species of mammals. The growth pattern we observed in *D. ordii* is similar to most of those previously described. Friley (1949a) demonstrated that length is added primarily at the proximal end in *Lutra c. canadensis*, and an identical growth pattern is implied in similar investigations of *Castor canadensis* (Friley, 1949b) and *Mustela vison* (Elder, 1951). Conversely, Zimmerman (1972) noted that the prominent toothlike structures on the bacula of *Spermophilus tridecemlineatus* became more developed distally with increasing age. Age variation affects the three standard measurements on bacula of kangaroo rats, and the general form of the bone is greatly altered. For example,

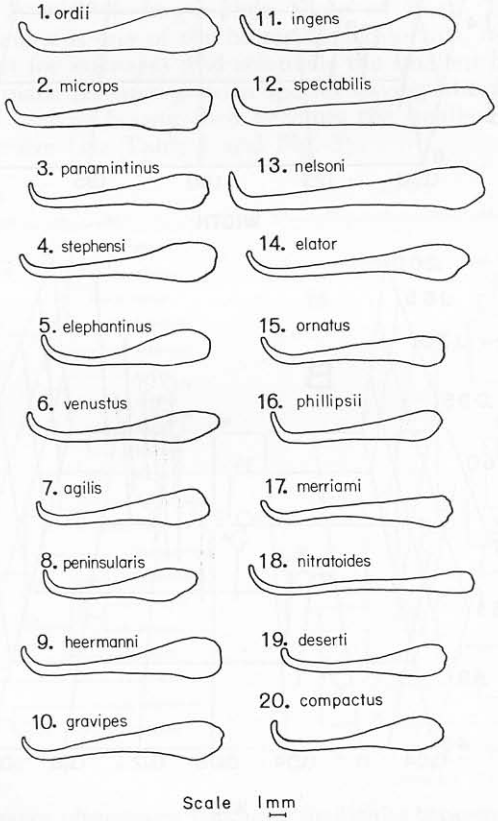

Fig. 2.—Bacula of 20 species of *Dipodomys* drawn to the same scale. All sketches are original, except for *D. ingens, D. phillipsii* and *D. nitratoides,* which are re-drawn from Burt (1960). Specimen numbers: 1, TLB4930; 2, TLB4190; 3, TLB4156; 4, OU5764; 5, OU7619; 6, MVZ97962; 7, TLB4187; 8, TLB4196; 9, OU7618; 10, TLB4188; 12, TLB4199; 13, ADS1869; 14, OU7622; 15, OU6225; 17, TLB2841; 19, TLB2400; 20, TLB5441

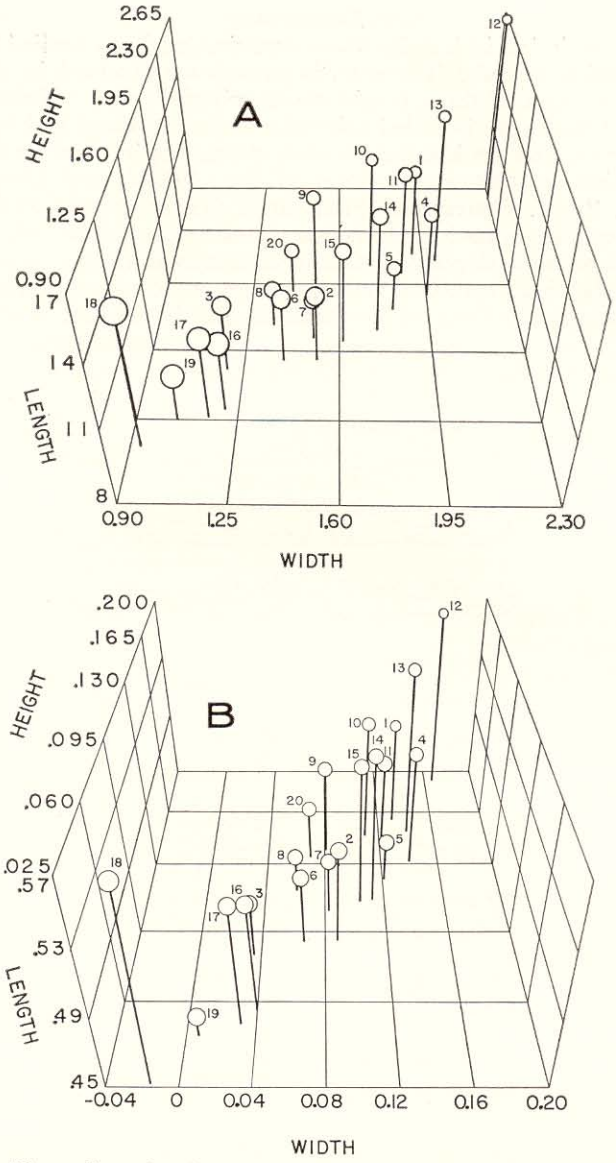

Fig. 3.—Three dimensional plots of bacular measurements of each of the 20 species of *Dipodomys*. Diagram A was constructed by plotting the average length, width and height of bacula. In diagram B the relative lengths, widths and heights of bacula are depicted. For B the natural log of each measurement was taken and this divided by the log of body length of the particular species. Species numbers are given in Table 1

Lackey's (1967) observations during a study of the *heermanni* group indicate "that the baculum base remains relatively small until the animal reaches full adult size." One should, therefore, interpret information from nonadult animals such as presented for *D. phillipsii* by Genoways and Jones (1971) and for *D. microps* by Burt (1960), with extreme care. The single *D. phillipsii* bacula figured by Burt may be somewhat aberrant or may represent an immature individual. Unfortunately, we have been unable to obtain additional material for comparison and, therefore, were compelled to use his measurements.

Burt (1960) noted for *D. microps* that "unless the four specimens available are all young, the baculum is the smallest and most delicate in the genus." For six adult specimens of this species, our measurements are at least 35% larger than those of Burt. He said that although *D. deserti* is one of the larger kangaroo rats, its baculum is actually (except for *microps*) and relatively the smallest he examined. Our measures place *D. microps* with species having intermediate-sized bacula, and *D. deserti* bacula then becomes the smallest in actual as well as relative size (*see* Table 1 and Fig. 3).

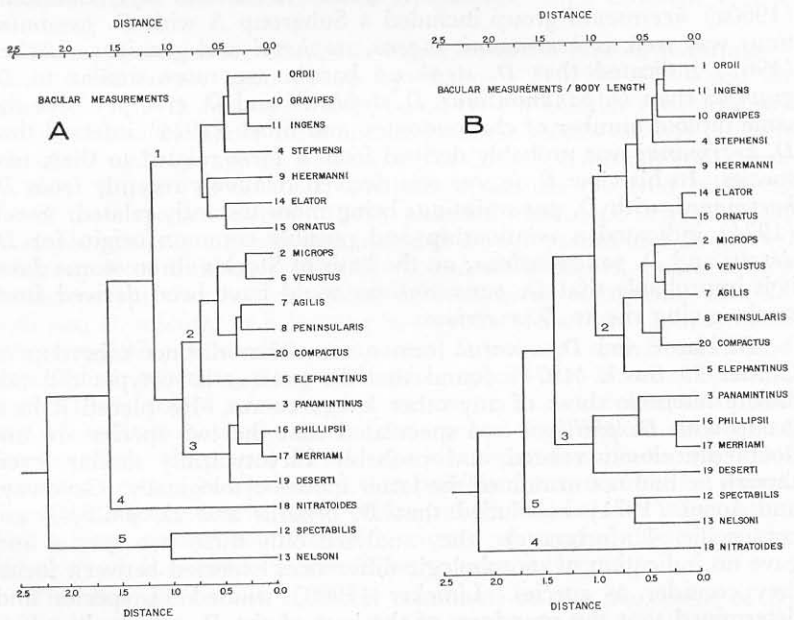

Fig. 4.—Distance phenograms indicating similarities between the 20 species of *Dipodomys* based on: (A) the three bacular measurements; and (B) the logs of the three bacular measurements divided by the log of the body length. The unweighted pair-group method using arithmetic averages (UPGMA) was used in clustering. The cophenetic correlation coefficients for A and B are 0.786 and 0.774, respectively. Numbers on branches of the tree delineate clusters mentioned in the discussion

Our analyses yielded five main clusters (Fig. 4). Although these groups are based entirely on bacular measurements, and as such represent a very specialized type of classification, it is still of interest to determine the similarities between our groupings and those of others. No other authors have placed all of the species of our Cluster 1 in one group. For instance, *D. ordii* is often isolated in its own group (Grinnell, 1922; Lidicker, 1960a; Stock, 1974) and was not similar biochemically to any of the other species studied by Johnson and Selander (1971).

Setzer (1949) placed *D. microps* in his *ordii* group, and Burt (1960) added *D. deserti* and *D. agilis*. Burt (1936) included five other species with *D. ordii—heermanni, panamintinus, stephensi, ingens* and *agilis*. Of these, *D. panamintinus* and *D. agilis* are not included in Cluster 1; *D. agilis* is discussed below. Our classifications show *D. panamintinus* to have closer affinities with species in Cluster 3; Burt (1936) did not have bacula from the three other species of Cluster 1. In Johnson and Selander's (1971) genic analysis, *D. panamintinus* was the species most similar to *D. heermanni* (although they did not study most of the species in Cluster 1). Lidicker's (1960a) *heermanni* group included a Subgroup A with *D. panamintinus* was well as *heermanni, ingens, stephensi* and *gravipes*. Lackey (1967) indicated that *D. stephensi* bacula are more similar to *D. gravipes* than *D. panamintinus*. *D. stephensi* and *D. gravipes* have the same diploid number of chromosomes, and Stock (1974) inferred that *D. heermanni* was probably derived from a form related to these two species. In his view *D. ingens* was derived relatively recently from *D. heermanni*, with *D. panamintinus* being more distantly related. Stock (1974) indicated a relationship and possibly common origin for *D. deserti* and *D. panamintinus;* on the basis of Stock's chromosome data, it is improbable that *D. panamintinus* could have been derived from stocks giving rise to *D. merriami*.

D. elator and *D. ornatus* form a somewhat distinct subgroup of Cluster 1. Stock (1974) found that *D. ornatus* karyotypes did not closely resemble those of any other kangaroo rat. He placed it in a group with *D. phillipsii* and speculated that the two species are undoubtedly closely related and probably karyotypically similar, even though he had not examined the latter species cytologically. Genoways and Jones (1971) concluded that *D. ornatus* and *D. phillipsii* are conspecific. Unfortunately, they analyzed only these two species and gave no indication of morphologic differences expected between forms they consider as species. Lidicker (1960) studied 11 species and determined that the roundness of the base of the *D. ornatus* baculum is similar only to that of *D. ingens* and is particularly unlike *D. spectabilis*. He found the robustness to be most like that of *D. ordii* and members of the *heermanni* group (*heermanni, panamintinus, agilis,* etc.), and "unlike *merriami, nitratoides, spectabilis, deserti* and *microps*."

Lidicker (1960b) pointed out the baffling question of the relation-

ship of *D. elator* to the other kangaroo rats and indicated a lack of information for the species. Most workers have suggested that *D. elator* is either closely related to the *phillipsii* group (Grinnell, 1922; Setzer, 1949) or to the *spectabilis* group (Davis, 1942; Lidicker, 1960a). Stock's 1974) karyotypic data allied *D. elator* with *D. spectabilis.* By protein variation analysis, Johnson and Selander (1971) demonstrated that *D. elator* is quite dissimilar to the 10 other species studied (including *D. spectabilis*); however, they did not have material from *D. phillipsii* or *D. ornatus.* Blair (1954), from one baculum of *D. elator,* indicated that it was more similar to that of *D. merriami* than *D. spectabilis,* suggesting to Lidicker (1960b) that *D. elator* is not especially close to either the *phillipsii* or the *spectabilis* groups, an interpretation supported by our results. Setzer (1949) merged Grinnell's *phillipsii* and *merriami* groups and placed *D. elator* next to *D. ornatus* and *D. phillipsii.* Finally, Dalquest and Collier (1964) considered *D. elator* most closely related to *D. ornatus.* While our bacula data clearly indicate close similarity between these two species, the continued lack of adequate bacular samples for *D. phillipsii* makes our placement of *D. phillipsii* in a different cluster tentative.

Three species in our Cluster 2—*agilis, venustus* and *elephantinus*—were placed in an *agilis* group by Grinnell (1922). He listed *D. compactus* and *D. microps* which, based on our bacular measures, are very similar to the above three species in single-species clusters on each side of the *agilis* group. *D. peninsularis* of Cluster 2 was not considered by him. Burt's (1936, 1960) analyses of bacula involved relatively few of these species. Setzer (1949) placed *D. agilis, D. venustus,* and *D. elephantinus* in a group that included *D. heermanni* and *D. ingens.* Subgroup B of Lidicker's (1960a) *heermanni* group is similar to our cluster, except that he considered *D. compactus* conspecific with *D. ordii* and *D. microps* as belonging in a group of its own. Johnson and Selander (1971) studied *D. compactus, D. microps* and *D. agilis* and placed them together, along with other species not in our Cluster 2. Stock (1974) found *microps, elephantinus, venustus, peninsularis,* and part of *agilis* to have the same fundamental and diploid number of chromosomes. He placed *D. microps* in a separate subgrouping of his *heermanni* group, but indicated that possibly the two could be joined. Thus, the interpretations based on karyotypic and bacular information give a very similar result in this cluster of species. Data on the karyology of *D. compactus* should prove most interesting.

The discussion above included comments on the placement of *D. phillipsii,* which we clustered with *D. merriami.* Setzer (1949) considered them closely related on the basis of visceral anatomy and skeletal characters.

D. deserti was placed alone by Grinnell (1922) and Davis (1942), while Lidicker (1960a) and Stock (1974) placed it by itself in a subgroup of their *spectabilis* and *heermanni* groups, respectively. Burt (1936) included it with *D. spectabilis* and *D. microps; D. merriami*

was in a separate cluster. Johnson and Selander (1971) showed *D. deserti* to be most similar genically to *D. merriami* and *D. nitratoides*. *D. deserti* was the most divergent species in Cluster 3, being somewhat between the other species in this cluster and *D. nitratoides* (Figs. 3 and 4).

Most opinions concerning *D. nitratoides* link it to *D. merriami* (Grinnell, 1922; Burt, 1936, 1960; Lidicker, 1960a; Johnson and Selander, 1971; Stock, 1974). Its long thin baculum (Fig. 2) is very different, but *D. nitratoides* clearly has its closest affinities with Cluster 3 which contains *D. merriami* (Fig. 3).

Most workers consider *D. spectabilis* and *D. nelsoni* of our Cluster 5 to be closely related. Heretofore, bacula of *D. nelsoni* have not been available. These two species have the largest bacula and have sometimes been allied with *D. elator* (Davis, 1942; Stock, 1974) or *D. deserti* (Lidicker, 1960a). *D. elator* does have a relatively elongated baculum (Fig. 3B), but close affinities of *D. spectabilis* and *D. nelsoni* with it are not indicated from our study.

Phenetic affinities indicated by our studies show similarities to those of Grinnell (1922) and Lidicker (1960a), although some differences exist. Affinities implied in our analyses differ markedly from those suggested by Setzer (1949) and Johnson and Selander (1971). Some of our results vary with bacular interpretations by Burt (1936, 1960) and Lidicker (1960b), but in part these differences reflect the current availability of more data. Our groupings conform very well to those suggested from karyotypic data by Stock (1974). The bacular analyses suggest several interpretations of karyologic data that might be profitably re-evaluated, although a certain degree of difference in the affinities indicated is to be expected, since two different character sets are being examined (*i.e.*, the hypothesis of nonspecificity usually holds only in part; Farris, 1971).

We have shown significant age variation of bacula exists within a species of kangaroo rat, a fact alluded to but given only passing attention by previous authors. That such variation could significantly affect interpretations of phenetic similarity between species is evident. Less clear is the importance of individual and geographic variation. To our knowledge, this type of variation has not been considered in detail, and only with the accumulation of relatively large samples has this become a problem that could and should be investigated in the future. A subjective analysis of limited data indicates that since differences between are considerably greater than within species, similarities between species would not be markedly changed by more detailed sampling.

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