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Biosystematics of the HEERMANNI Subgroup A of the Genus DIPODOMYS (Rodentia: Heteromyidae)

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BIOSYSTEMATICS OF THE HEERMANNI SUBGROUP A OF THE GENUS DIPODOMYS (RODENTIA: HETEROMYIDAE)

by

Anthony G. Futcher

A Dissertation in Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy in the Field of Biology

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Each person whose signature appears below certifies that he has read this dissertation and, that in his opinion it is adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Leonard R. Brand, Associate Professor and Chairman of Biology

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Charles E. Winter, Professor and Chairman of Microbiology

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INTRODUCTION

The genus Dipodomys was described in 1841 based on the species D. phillipii Gray, 1841(=phillipsii). Since 1841 many additional species have been described and arranged in several groups. (Grinnell, 1921; Burt, 1936; Setzer, 1949). The most recent work on the taxonomy of Dipodomys (Lidicker, 1960) lists 21 species in 6 groups. Two new species have been described since 1960. They are D. antiquarius Huey, 1962 and D. cascus Huey, 1962. D. cascus has since been placed in synonymy with D. stephensi (Merriam, 1904), (Lackey, 1967), leaving a total of 22 species in the genus.

I am here presenting evidence supporting the separation of the northern four-toed subspecies of D. heermanni Le Conte, 1853 from the southern five-toed subspecies of D. heermanni. The three northern populations I recognize as a separate species under the name D. californicus Merriam, 1890. This gives a total of 23 species in the genus at the present.

This study is concerned with subgroup A of the heermanni group of the genus Dipodomys, which includes the following species.

D. heermanni Le Conte, 1853
D. californicus Merriam, 1890
D. ingens (Merriam, 1904)
D. panamintinus (Merriam, 1894)
D. stephensi (Merriam, 1907)
D. gravipes Huey, 1925

Dipodomys gravipes was not included in this study.

I was not successful in trapping any specimens of the Dipodomys cascus population after several attempts at Lackey's sites.

Unfortunately the areas he describes are being developed, and the population may have been extirpated.

The principal range of Dipodomys heermanni is northwest of the Tehachapi Mountains, and west of the Sierra Nevada Range, extending north to the vicinity of San Francisco Bay on the west, and Amador County in the east (Fig. 1).

Dipodomys californicus ranges from San Francisco Bay and Amador County north beyond the Oregon border. At the north end of the Sierra Nevada Range, this species crosses to the east as far as the Susanville area.

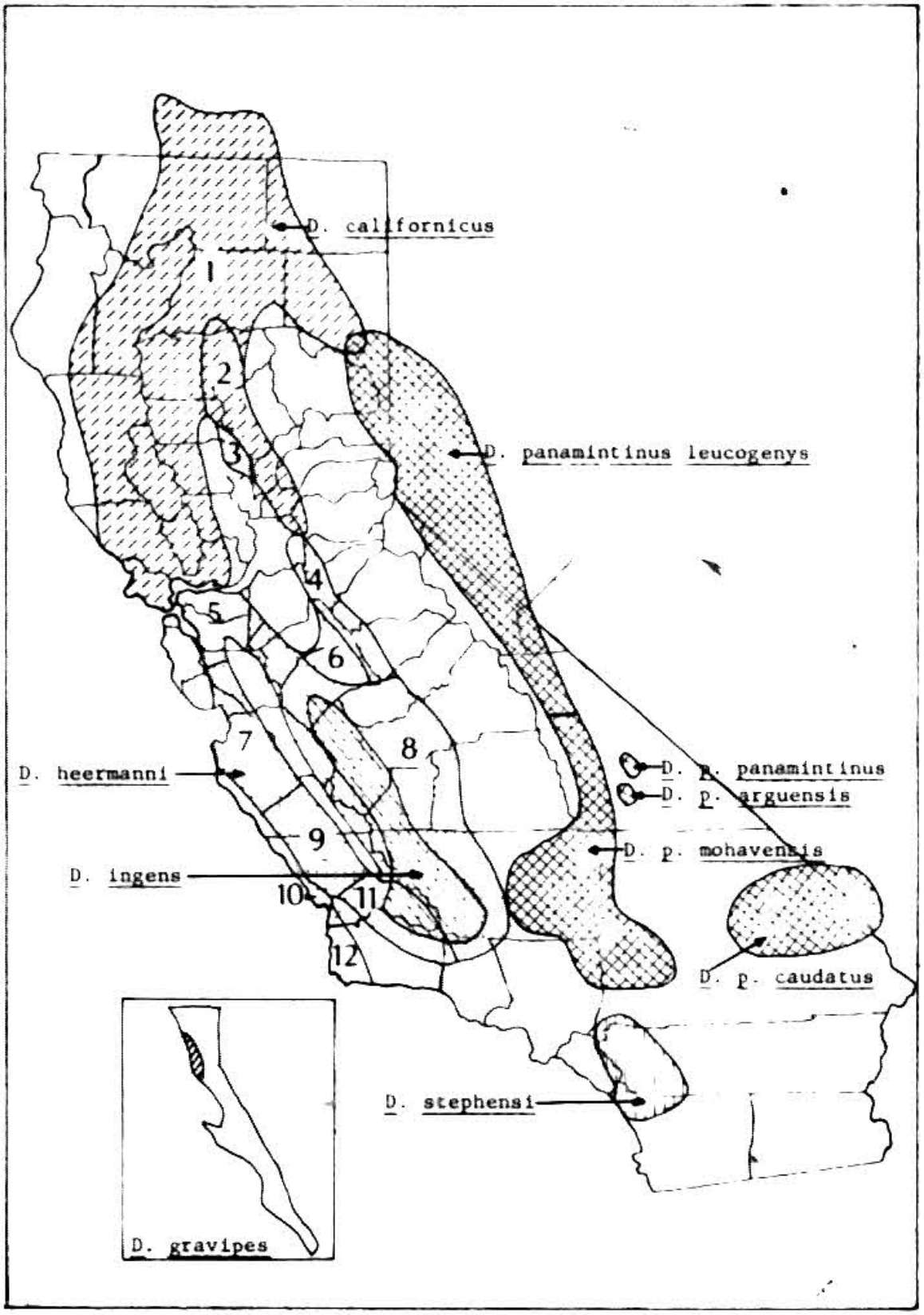
Dipodomys panamintinus ranges from the Mojave Desert north of the San Bernardino and San Gabriel Mountains, through the Owens Valley, between the Sierra Nevada Range and the White Mountains, around Mono Lake, east of Lake Tahoe, and north to Honey and Pyramid Lakes. In addition, there are three isolated populations--D. p. panamintinus (Merriam, 1894) in a limited area of the Panamint Range, D. p. arguensis Huey, 1945 from the Argus Mountains, and D. p. caudatus Hall, 1946 in the eastern part of the Mojave Desert.

Dipodomys stephensi is known only from southwestern San Bernardino County south of the San Bernardino Mountains, western Riverside County between the Santa Ana and San Jacinto Mountains, and northwestern San Diego County along the San Luis Rey River valley. The population from the San Luis Rey River valley is the population described as D. cascus by Huey (1962), and later placed in synonymy with D. stephensi by Lackey (1967).

Dipodomys ingens is found chiefly in the Carrizo Plains and

Figure 1. Distribution of the heermanni subgroup A species of the genus Dipodomys.

1. Dipodomys c. californicus
2. Dipodomys californicus saxatilis
3. Dipodomys californicus eximus
4. Dipodomys h. heermanni
5. Dipodomys heermanni berkeleyensis
6. Dipodomys heermanni dixoni
7. Dipodomys heermanni goldmani
8. Dipodomys heermanni tularensis
9. Dipodomys heermanni jolonensis
10. Dipodomys heermanni morroensis
11. Dipodomys heermanni swarthi
12. Dipodomys heermanni arenae


D. californicus
1
2
3
D. panamintinus leucogenys
4
5
6
7
8
D. heermanni
D. p. panamintinus
D. p. arguensis
9
D. p. mohavensis
D. ingens
10
11
12
D. p. caudatus
D. stephensi
D. gravipes

through the San Joaquin Valley.

Dipodomys gravipes is restricted to a small area of northwestern Baja California.

These ranges were determined from Hall and Kelson (1959), and Grinnell (1922), and from specimens in the Museum of Comparative Zoology, University of California, from the San Diego Natural History Museum, and from specimens collected in the course of this study.

The specific status of Dipodomys stephensi has been questioned by a number of authors, including Hall and Kelson (1959), who suggest that D. stephensi is only subspecifically distinct from the allopatric but adjacent species, D. panamintinus. Lackey (1967) demonstrated that D. stephensi seems to be more closely allied to D. heermanni than to D. panamintinus. My study presents evidence concerning the taxonomic status of D. stephensi and other species of the heermanni subgroup A in California.

Several methods of approaching the problem were considered. One of these was hybridization of supposed species. This was attempted, then rejected because of the great difficulty in breeding kangaroo rats in captivity. Chew (1958), Buttersworth (1961) and Eisenberg (1963) had success breeding some species, but my attempts over a period of two years were unsuccessful.

Previous to my work only three karyological studies had been made with Dipodomys, and all were with D. merriami Mearns, 1890 (Cross, 1931; Matthey, 1949, 1956). Karyology has proved to be a useful tool in clarifying some systematic problems (Nadler and Block, 1962; Nadler, 1964; Patton, 1967a, 1967b; Patton and Dingman, 1968; Sutton and Nadler,

1969). Two recent studies (Csuti, 1971; Fashing, 1973) reported on the karyotypes of four species of Dipodomys, including D. panamintinus and D. heermanni. Csuti's work indicates a close relationship between these two species. Fashing describes the karyotypes of the northern forms of D. heermanni, which I recognize as a distinct species, and contrasts them with the karyotypes of the southern forms of D. heermanni as reported by Csuti, and an unpublished work of A. D. Stock.

Another useful tool in systematics is serum protein electrophoresis. It has proved useful in mammals (Johnson and Wicks, 1959; Johnson, 1968; Brand and Ryckman, 1969), in birds (Beckman and Nilson, 1965), amphibians and reptiles (Dessauer and Fox, 1956). In addition, hemolymph of insects has proven to be of similar value (Brodie and Ryckman, 1967).

An extensive study of protein variation in Dipodomys (Johnson and Selander, 1971) shows a close relationship between D. panamintinus and D. heermanni. This concurs with Csuti's karyological analysis (Csuti, 1971).

MATERIALS AND METHODS

Specimens of kangaroo rats were collected in Sherman live traps baited with oatmeal, between February 1964 and July 1970. In areas where there was a good concentration of kangaroo rats, 75-100 percent of the traps had animals in them, and most of the animals captured were kangaroo rats.

An alternate method of capturing live animals was that of riding the rear bumper of a Volkswagen while traveling over desert trails. One or preferably two people riding on the bumper were armed with flashlights and butterfly nets. When an animal was seen in the beam of the headlights, the driver slowed down, while the potential captors moved quickly toward the kangaroo rat in an attempt to net it before it escaped down a burrow or into thick brush. This method proved to be efficient when the population density and weather were favorable. In windy, cold or wet weather, the kangaroo rats were either in or close to their burrows, and capture was much more difficult. If plant cover was dense, this method was not satisfactory.

One species--Dipodomys ingens--proved difficult to capture by this method, even under ideal conditions. This species was extremely wary. Animals immediately ran to their burrows, where they could be seen bobbing up and down in a manner reminiscent of burrowing owls. Any close approach would cause them to run deeper into the burrow, where capture was impossible. Fortunately, this species, along with all the other Dipodomys, readily entered the Sherman live traps.

One of the major problems of an extensive summer trip was that

of keeping the animals cool. They are quite heat-sensitive and on several occasions we lost a number of animals even though they were in an air-conditioned car.

In the laboratory, the animals were maintained in wire animal cages, or in plastic flower planters. Pine wood shavings were placed in the cages in such a way that the animal could dig into them and be partially hidden from sight. When the coat of the animal became disheveled, the animal was placed overnight in a box with sand covering the floor. This gave the animal ample time to restore the normal sleek appearance of the fur. The food consisted of a mixture of wheat, crushed oats, wild bird seed, and sunflower seeds. Lettuce regularly supplemented the diet. Some animals were maintained in this way for more than 18 months.

Serum electrophoresis

Animals were bled from the ventral caudal vein. Approximately two thirds of a capillary tube of blood was removed. The empty end of the tube was sealed by heating in a bunsen burner until the glass was annealed. The capillary tube was then placed in a centrifuge tube with the closed end down. The tubes were centrifuged at approximately 2500 rpm for 15-20 minutes in an International Clinical Centrifuge with an inclined head.

Sepraphore III cellulose acetate strips were soaked in Gelman High-resolution Buffer overnight or for at least three hours before using. The centrifuge capillary tubes were scored just above the compacted formed elements, and broken, so that only serum remained in

the tube. The serum was then loaded onto a Gelman Serum Applicator, and applied to the Sepraphore strip. The strip was then placed in the electrophoresis chamber. A constant voltage of 360 v with an amperage between 1.5 and 2.5 ma per strip was applied for 90 minutes. The strips were stained in Ponceau S stain fixitive solution and cleared in an alcoholic 10% acetic acid solution, after which they were placed on glass strips and gently dried in an incubator. (For detailed instructions on electrophoresis, see Gelman Procedures, Techniques and Apparatus for Electrophoresis, from Gelman Instrument Co., Ann Arbor, Mich.) Dried, cleared Sepraphore strips were scanned on a Densicord Recording Electrophoresis Densitometer and Integraph. The resulting tracings were examined and all peaks located. Three measurements were recorded for each peak, except those labeled peak 7 and peak 8. These measurements were a) migration distance, b) height of peak, and c) number of Integraph "blips" per peak. The latter measurement is a direct indication of the area of the peak as determined by the Integraph. Peaks 7 and 8 were of such low magnitude that it was not significant to try to score them for anything but migration distance.

Because of the variations within samples, even from the same animal at the same time, the following standardizations were made:

1. Distance of migration.

The albumin band of Dipodomys heermanni and D. panamintinus have the same migration distance (Johnson and Selander, 1971). Dipodomys ingens, D. stephensi and D. californicus were not reported by Johnson and Selander, but I assume the albumin migration distances for these three cases to be the same or similar to those reported. This assumption is based on the fact that a wide range of species of Dipodomys were

assayed by Johnson and Selander, and there was very little variation in albumin migration distance in the genus. Thus I do not believe any significant error would be introduced by assuming a constant migration distance for species which I assayed.

To standardize the data, I set the migration distance for all albumin bands at 100. All other bands were given as a percentage of the migration distance of the albumin.

2. Height of peak.

The height of the peak depends upon the density of the stain, which in turn is dependent in part upon the concentration of the protein. Since variations occur in the amount of sample applied to the strip, and also in the clearing of the strip, the albumin peak was assigned a height of 100. Each of the other peaks on a strip was then standardized by the same factor which gave the albumin peak a height of 100.

These data were punched on IBM computer cards, with the following data for each individual:

1. Distance of migration (standardized).
2. Height of peak (standardized).
3. Number of Integraph "blips".
4. Number of "blips" divided by height of peak.
5. Number of "blips" multipled by height of peak.

Comparison of the migration distance of the bands in all populations showed a total of 9 possible bands. These were numbered 1-8, with the ninth band being labeled "albumin". Where more than one tracing was available for one animal, the data were averaged, to give

a single set of figures for each animal.

From these data it was determined which bands were present in each population. Bands 4 and 5 are very close, and in 4 populations in which only one of these bands was present, I was unable to determine positively whether the band was 4 or 5. For this reason, two decks of cards were punched. In deck 1, the band was treated as band 4, and in deck 2, the band was treated as band 5. These decks were then subjected to Stepwise Discriminant Function Analysis (BMD07M - Revised July 24, 1969.) Dixon, 1967.

As a check on accuracy, the data decks were fed back into the computer as unknowns, and the computer was instructed to identify the unknowns into the populations of the original data.

Chromosomal analysis

A. Preparation of chromosomes.

Chromosomes were prepared by the colchicine-hypotonic citrate method of Ford and Hammerton (1956) as modified by Patton (1967a) with further modification of my own.

Reagents

1. Colchicine: 0.05% w/v (aqueous). Use 0.01 ml/g body weight.
2. Sodium citrate: 0.8% (aqueous).
3. Fixative: 3 parts absolute methanol to 1 part glacial acetic acid. Must be made fresh for each run.
4. Giemsa blood stain: 10% (aqueous). Must be made fresh for each run.

Procedure

1. Live animals were weighed, and injected intraperitoneally

with the appropriate volume of colchicine.

2. After 4-5 hours, the animals were euthanized. The femora were quickly removed, the epiphyses cut off, and the marrow flushed out by forcing warm (37°C) sodium citrate through the central marrow cavity with a syringe.
3. The syringe was then used to vigorously aspirate the marrow with sodium citrate in order to disperse and suspend the cells. The suspended cells were then incubated in a water bath at 37°C for 20 minutes.
4. The cells were filtered through cheesecloth prior to centrifugation at 1200 rpm in an International Clinical Centrifuge with an inclined head.
5. The supernatant was carefully poured off, and 3 ml fixative added gently so as not to disturb the button of cells. The cells were fixed for at least 30 minutes.
6. The button of cells was dispersed in the fixative by gentle agitation and aspiration with a Pasteur pipette, and then the suspension was centrifuged 5 minutes at 1000 rpm.
7. The supernatant was poured off, 1 ml fixative added, and the button resuspended.

Steps 6 and 7 were repeated twice. After the final wash and resuspension, the material was ready to mount.

8. Labeled, clean microscope slides were placed into ice cold distilled water. A cold slide was removed, and in rapid sequence, the excess water was shaken off, the bottom wiped on a paper towel, and 3-4 drops of cell suspension dropped

onto the slide from a height of approximately 30 cm.

9. The slide was tilted from side to side to spread the fixitive and cells, then dried by the ignition method of Shertz (1962).

10. As soon as the flame was extinguished, the slide was rapidly shaken to remove any remaining water droplets, and to hasten cooling, and then set aside to finish drying.

11. When the slides were dry, they were stained in Giemsa for 15 minutes, then very gently rinsed in distilled water, and set aside to dry.

12. The dried slides were immersed in toluene for about 30 seconds after which they were mounted in toluene-based Permount using a number 1 1/2 24x50 mm glass cover slip. (The number 1 1/2 thickness provides the ideal range of thickness for photography. Kodak Scientific and Technical Data Book P-2. Photography Through the Microscope. 4th Edition, 1966.)

B. Photography of chromosomes.

The prepared slides were systematically scanned under low power (100X) for good chromosome spreads. The microscope was equipped with a graduated mechanical stage, and coordinates for each spread were noted so that they could be readily relocated for photography. After 40 or more of the best spreads had been located, they were photographed using 35mm Kodak High Contrast Copy Film. A Wrattan No. 58 dark green filter was used to increase the viewing and photographic contrast. The film was developed in Kodak Microdol-X Developer for 6-7 minutes at 21°C (70°F). The negatives were printed on 4x5 inch Kodak Kodabromide F-5 single weight paper. These prints were used for counting the

chromosomes. The best negatives were enlarged to 8x10 inches for use in arranging the karyotype.

C. Counting and arranging the chromosomes.

The 4x5 prints were divided into segments and the number of chromosomes carefully counted. The number recorded was either an exact number, or if distortion or overlap prevented determination of an exact number, a number plus one with a question mark. (Nadler and Block, 1962).

There are several classification systems for chromosomes based on size, and relative lengths of biarmed chromosomes (Bender and Chu, 1963: Nadler and Block, 1962; Levan, Fredga, and Sandberg, 1964).

According to Csuti (1971),

> "Due to high diploid numbers and gradation in size and morphology of biarmed elements, designation of the X-chromosome can be only tentative without autoradiographic data. For similar reasons only two groups of chromosomes are recognized: metacentric--chromosomes distinctly biarmed; and acrocentric--chromosomes with second arms minute or absent (Lee and Zimmerman, 1969)."

I concur with his findings and use the same system. However, even this simplified system is difficult to apply in some cases. This is especially true in the case of Dipodomys stephensi, which has many chromosomes with minute or small arms or "rabbit ears". These could be interpreted as metacentric or acrocentric, depending upon the experimenter's concept of the terms "distinctly biarmed" and "minute".

Determination of X and Y chromosomes is very difficult in most

cases. However, in a few cases, a small metacentric chromosome found only in the males, can be positively identified as the Y chromosome.

For determination of the fundamental number (FN) ("Nombre Fundamental" after Matthey, 1951), I assumed all sex chromosomes to be metacentric, or biarmed. The rationale for this assumption is:

1. Acrocentric X chromosomes are rare in rodents, and when present, most or all of the karyotype is composed of acrocentric chromosomes.
2. In all previous work on Dipodomys, and in all cases in this study, all positively or tentatively identified sex chromosomes are metacentric.
3. If the X is metacentric and the Y is acrocentric, the number of acrocentric and metacentric chromosomes in the karyotypes of male and female animals should differ by one. This is not the case in any population I have studied.

For these reasons, I believe I have a reasonable basis for my assumption that X and Y chromosomes are metacentric in the animals studied.

RESULTS

Serum electrophoresis

The electrophoretic methods used revealed a potential 9 bands of protein in the populations studied. In no population were all 9 bands actually present. Bands 4 and 5 are very close, and in 4 populations where only one of these bands was present, I was unable to determine if it was band 4 or band 5. The data were analyzed twice, treating the bands as 4, then as 5. Bands 7 and 8 are very small, and were not included in the analysis. The distribution of bands in each population is shown in Table I, and representative tracings are shown in Figs. 2 and 3.

It will be seen that band 1 is unique to Dipodomys panamintinus caudatus. When stepwise discriminant function analysis was applied, this population was plotted at a great distance from the other 10 populations, which in turn were clumped in a very small area. (Fig. 4)

In order to get a better spread of the 10 other populations, the information about band 1 was suppressed, and only bands 2-6 and albumin were used. This resulted in a much better spread of the populations. (Fig. 4,5.) When looking at these figures, however, it must be remembered that band 1 has been suppressed, and that the actual position of Dipodomys panamintinus caudatus is well above the top of the graph.

Table 1. Protein Bands Present in Each Population.

Population	Band number								
	1	2	3	4	5	6	7	8	9(= albumin)
A. *Dipodomys ingens*		X	X	X	X	X	X		X
B. *Dipodomys stephensi*		X	X	X	X	X	X	X	X
C. *Dipodomys h. heermanni*		X	X		X	X		X	X
D. *Dipodomys heermanni arenae*		X	X	? or ?		X	X	X	X
E. *Dipodomys heermanni swarthi*		X	X	X	X	X	X		X
F. *Dipodomys panamintinus caudatus*	X	X	X	X	X	X	X		X
G. *Dipodomys panamintinus leucogenys*			X	? or ?		X	X	X	X
H. *Dipodomys panamintinus mohavensis*		X	X	X	X	X			X
I. *Dipodomys p. panamintinus*			X		X	X		X	X
J. *Dipodomys c. californicus*			X	? or ?		X		X	X
K. *Dipodomys californicus saxatilis*			X	? or ?		X		X	X

Figure 2. Representative tracings of serum electrophoresis patterns for *Dipodomys*.

A. *Dipodomys ingens*
B. *Dipodomys stephensi*
C. *Dipodomys h. heermanni*
D. *Dipodomys heermanni arenae*
E. *Dipodomys heermanni swarthi*

These tracings show raw data which have not been standardized.

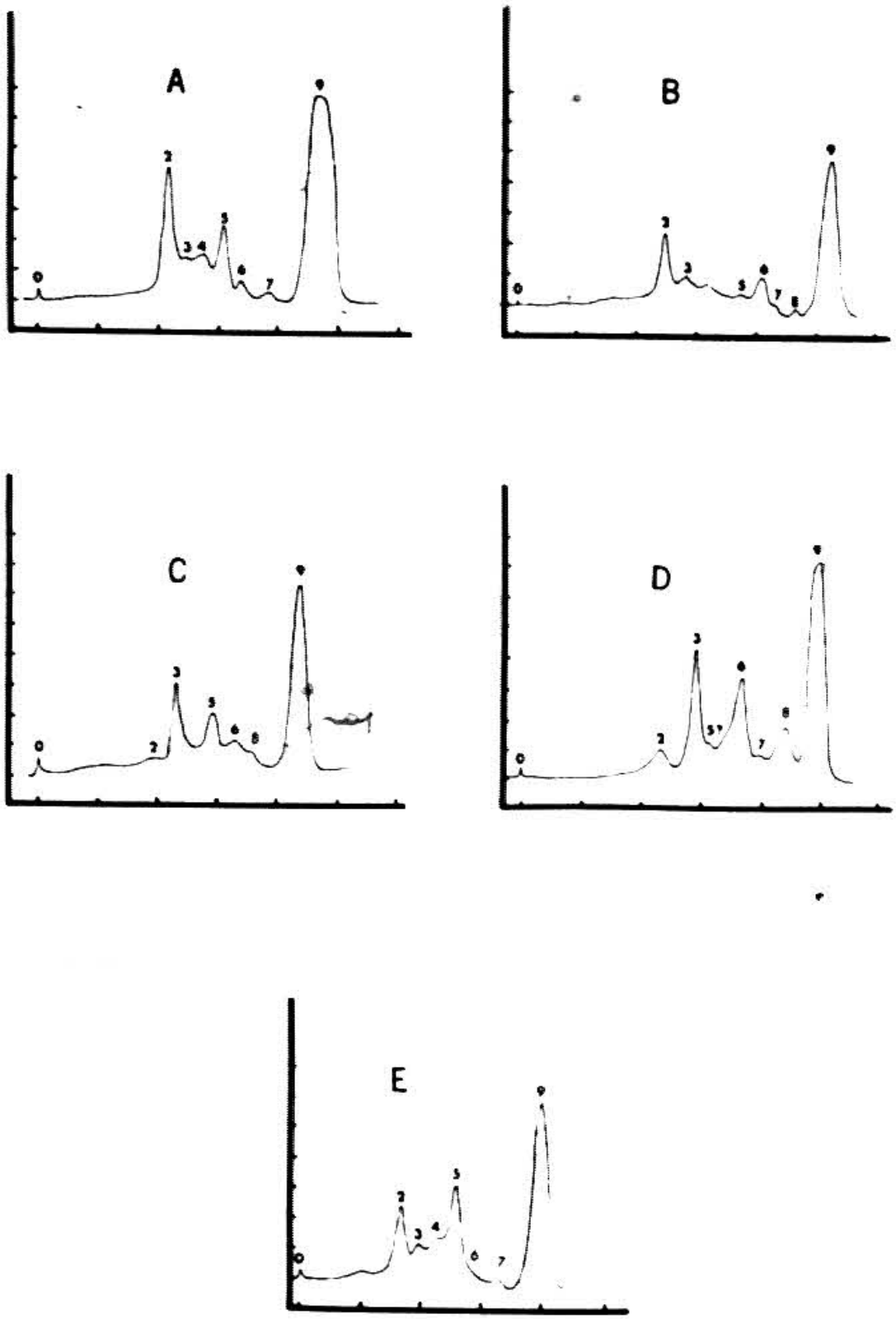
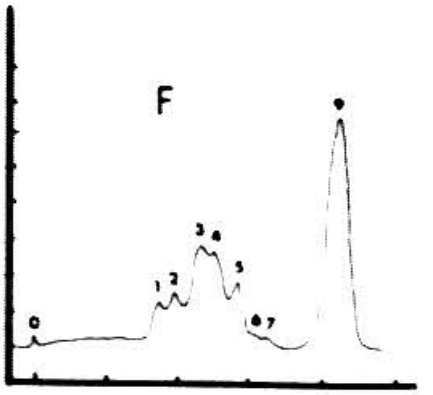

A
B
C
D
E

Figure 3. Representative tracings of serum electrophoresis patterns for *Dipodomys* (continued).

F. *Dipodomys panamintinus caudatus*
G. *Dipodomys panamintinus leucogenys*
H. *Dipodomys panamintinus mohavensis*
I. *Dipodomys p. panamintinus*
J. *Dipodomys c. californicus*
K. *Dipodomys californicus saxatilis*

These tracings show raw data which have not been standardized.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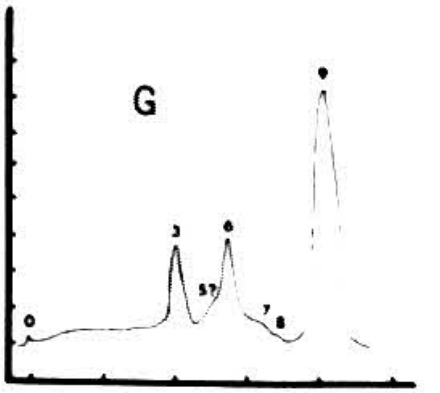
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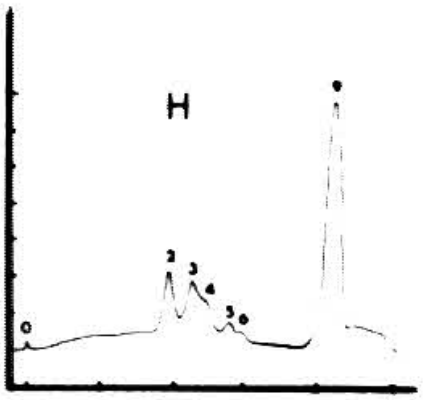
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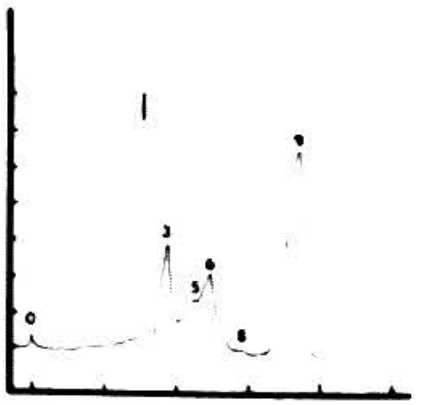
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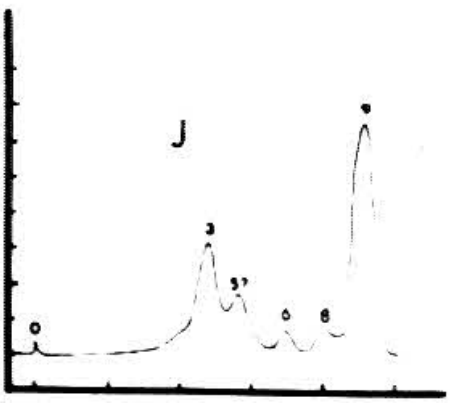
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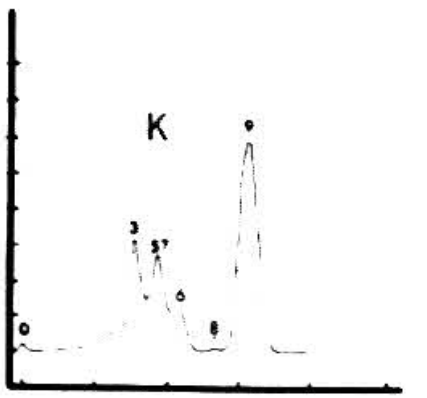

K

Figure 4. Scattergram of population means resulting from stepwise discriminant function analysis of electropherograms. (Individuals not plotted.)

A. *Dipodomys ingens*
B. *Dipodomys stephensi*
C. *Dipodomys h. heermanni*
D. *Dipodomys heermanni arenae*
E. *Dipodomys heermanni swarthi*
F. *Dipodomys panamintinus caudatus*
G. *Dipodomys panamintinus leucogenys*
H. *Dipodomys panamintinus mohavensis*
I. *Dipodomys p. panamintinus*
J. *Dipodomys c. californicus*
K. *Dipodomys californicus saxatilis*

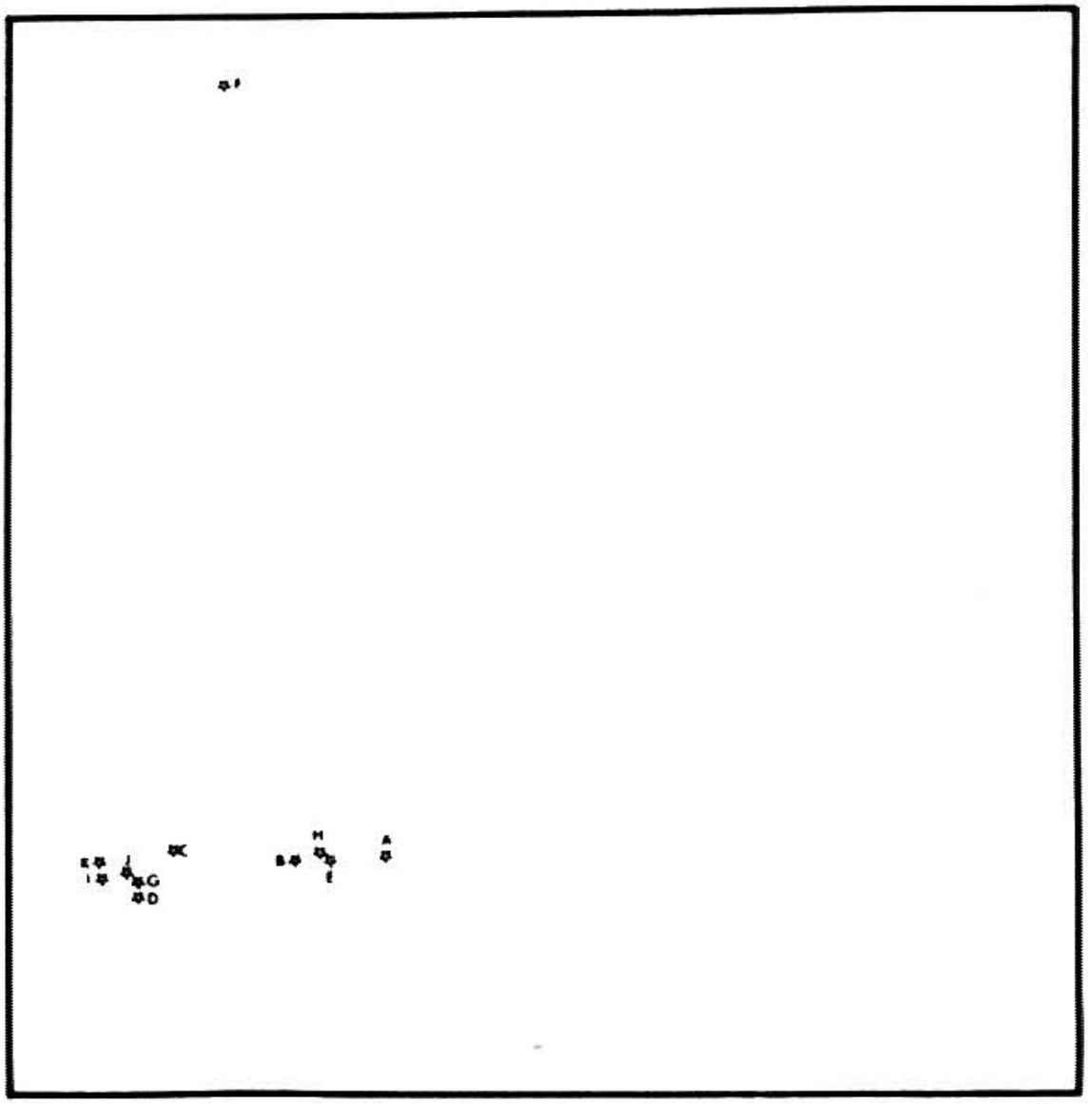

H
A
I
G
D

Figure 5. Scattergram resulting from stepwise discriminant function analysis of electropherograms, using card deck 1 (see text).

* = population mean.

A. *Dipodomys ingens*
B. *Dipodomys stephensi*
C. *Dipodomys h. heermanni*
D. *Dipodomys heermanni arenae*
E. *Dipodomys heermanni swarthi*
F. *Dipodomys panamintinus caudatus*
G. *Dipodomys panamintinus leucogenys*
H. *Dipodomys panamintinus mohavensis*
I. *Dipodomys p. panamintinus*
J. *Dipodomys c. californicus*
K. *Dipodomys californicus saxatilis*

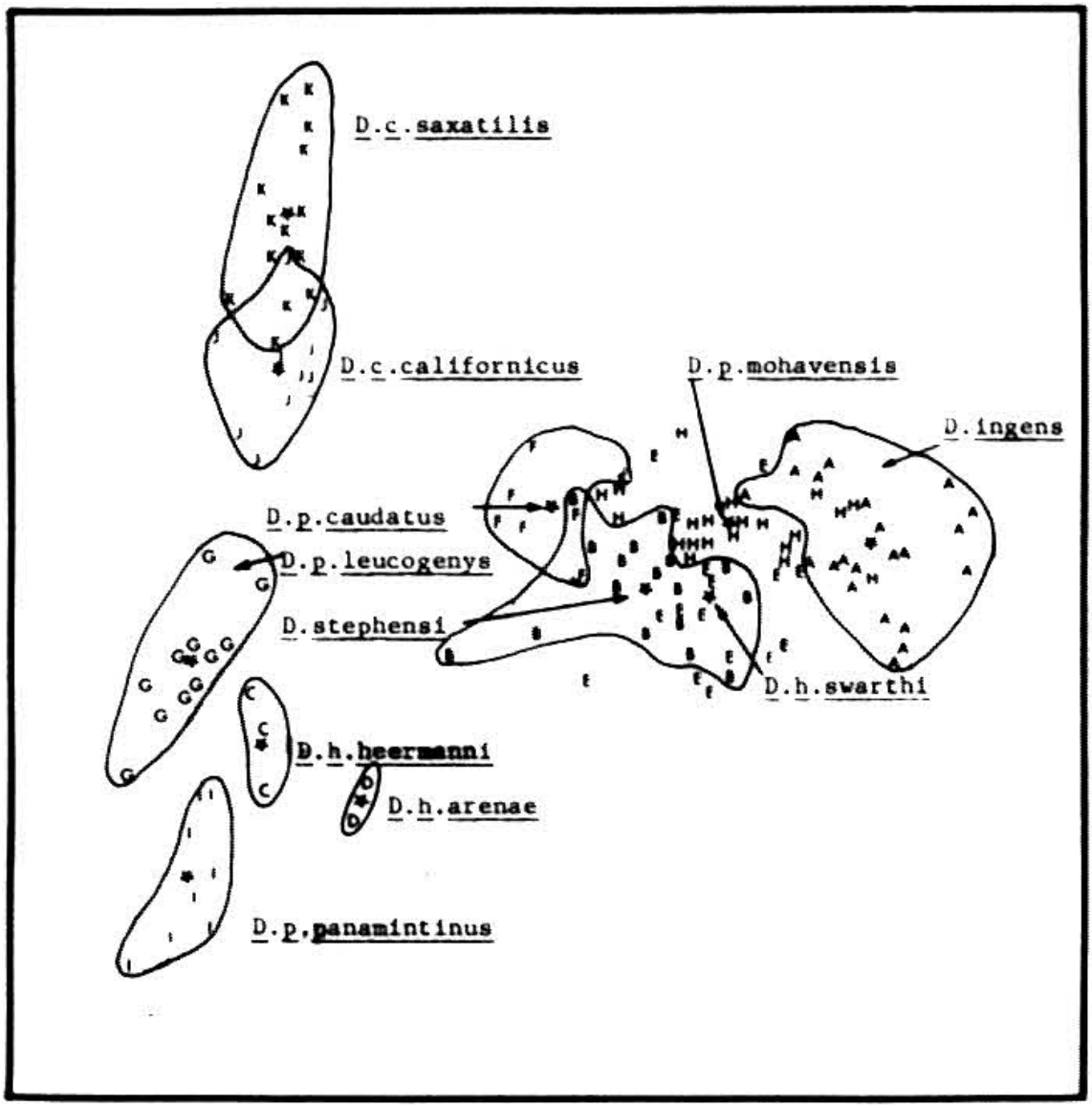
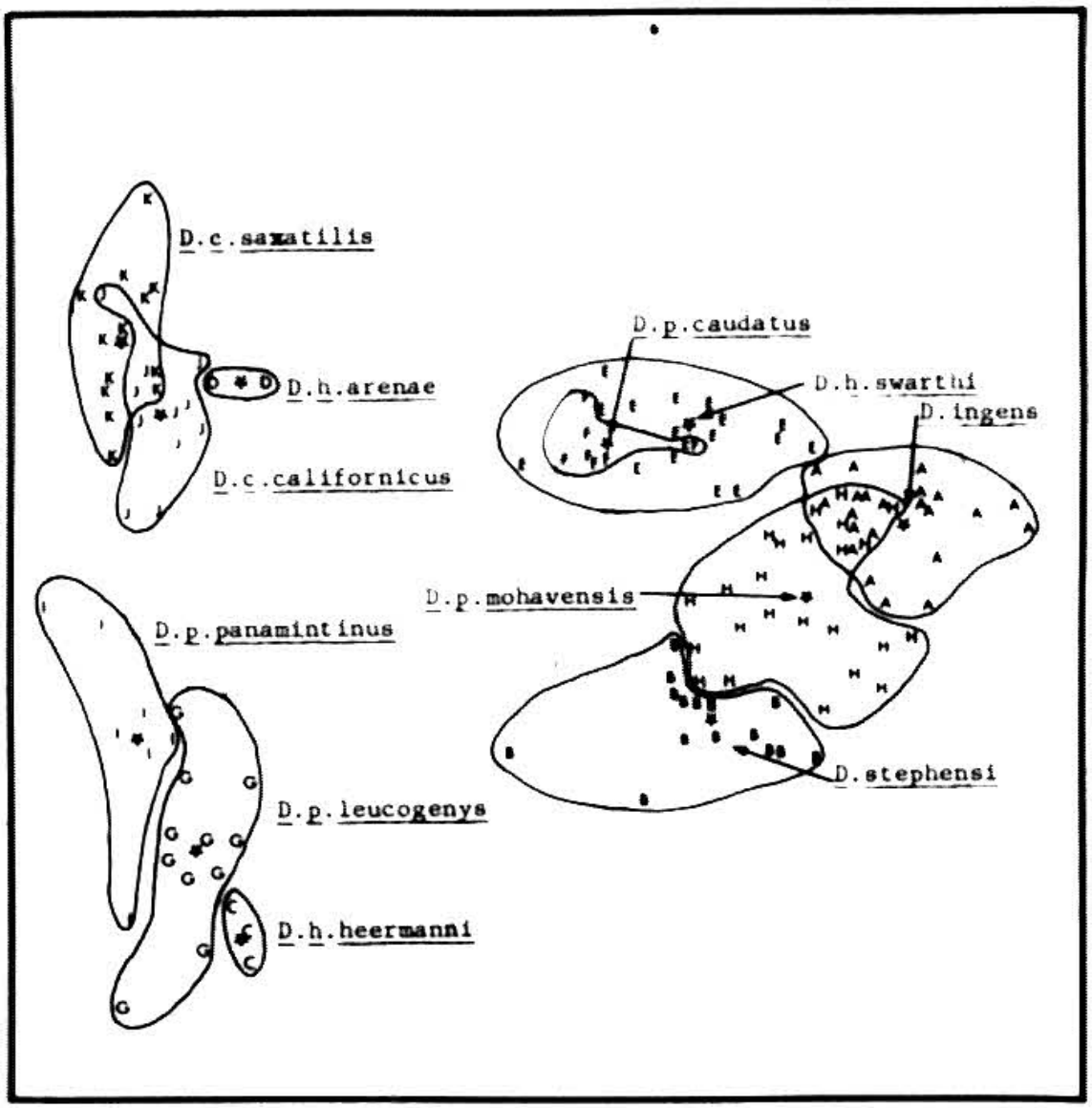

D.c.saxatilis
D.c.californicus
D.p.mohavensis
D.ingens
D.p.caudatus
D.p.leucogenys
D.stephensi
D.h.swarthi
D.h.heermanni
D.h.arenae
D.p.panamintinus

Figure 6. Scattergram resulting from stepwise discriminant function analysis of electropherograms, using deck 2 (see text).

* = population mean.

A. *Dipodomys ingens*
B. *Dipodomys stephensi*
C. *Dipodomys h. heermanni*
D. *Dipodomys heermanni arenae*
E. *Dipodomys heermanni swarthi*
F. *Dipodomys panamintinus caudatus*
G. *Dipodomys panamintinus leucogenys*
H. *Dipodomys panamintinus mohavensis*
I. *Dipodomys p. panamintinus*
J. *Dipodomys c. californicus*
K. *Dipodomys californicus saxatilis*


D.c.saxatilis
D.h.arenae
D.c.californicus
D.p.caudatus
D.h.swarthi
D.ingens
D.p.mohavensis
D.p.panamintinus
D.stephensi
D.p.leucogenys
D.h.heermanni

The only population which showed a major change in position between decks 1 and 2 is Dipodomys h. heermanni. Because of the small size of the population--only two individuals--I cannot determine the correct location on the scattergram.

The two Dipodomys californicus populations are far removed from the other populations, but are close to one another. When the data on these two populations were treated as unknowns, the computer misidentified 3 D. californicus saxatilis Grinnell and Linsdale, 1929 as D. c. californicus.

Another distinctly separated pair is Dipodomys p. panamintinus and D. p. leucogenys (Grinnell, 1919a). There is little overlap of these two populations and they are quite distant from all other populations except the two small populations D. h. heermanni and D. h. arenae Boulware, 1943 whose precise locations on the scattergram are uncertain. When the data are treated as unknowns, there are no misidentifications in deck 1, while deck 2 misidentifies one D. p. panamintinus as D. p. leucogenys, and one D. p. leucogenys as D. p. panamintinus.

Four of the remaining populations seem to clump around Dipodomys panamintinus mohavensis (Grinnell, 1918). Deck 1 shows them to be closely clumped, while deck 2 separates them slightly.

Dipodomys ingens and D. stephensi do not overlap at all, and when they are treated as unknowns, one is not misidentified as the other.

Dipodomys panamintinus mohavensis lies between, and overlaps both of the previous populations. When the data are treated as unknowns, two individuals are misidentified as D. ingens and one as D. stephensi.

Conversely, two D. ingens are misidentified as D. panamintinus mohavensis, and in deck 1 only, one D. stephensi is misidentified as D. panamintinus mohavensis.

In deck 1, Dipodomys heermanni swarthi Grinnell, 1919a overlaps D. ingens, D. stephensi, and D. p. mohavensis. In deck 2, there is no overlap of D. heermanni swarthi with the other three. There is only one misidentification when the data are treated as unknowns--in deck 1, one D. ingens is misidentified as D. heermanni swarthi.

Karyology

In subgroup A of the heermanni group of Dipodomys, I found four distinct types of karyotypes:

1. The D. ingens type.
2. The D. stephensi type
3. The D. heermanni-panamintinus type
4. The D. californicus type.

Dipodomys stephensi and D. ingens are monotypic species, but D. heermanni, D. panamintinus and D. californicus are polytypic species. There is slight variation in the D. heermanni-panamintinus karyotype, but the two populations of D. californicus which I sampled have identical karyotypes. The features of each population sampled are discussed below, and summarized in Table II.

1. The Dipodomys ingens karyotype. (Fig. 7)

This species has the highest chromosome count and highest FN of any species in the heermanni subgroup A. Although the 2n count of 72 is close to that of Dipodomys stephensi (2n=70), the morphology of the

Figure 7. Karyotype of *Dipodomys ingens*. A. Male. B. Female.

A

B

Table II. Summary of Karyotypes.

M = metacentric, A = acrocentric, FN = fundamental number. Figures or letters indicated by an asterisk (*) have not been positively determined. For a discussion of each case, see text. Populations indicated with double asterisks (**) are from Fashing's paper. (Fashing 1973.)

Population	2n	Autosomes M	Autosomes A	X	Y	FN	♂	♀
Dipodomys ingens	72	42	28	M*	M	112	2	4
Dipodomys stephensi	70	10-42*	58-26*	M*	M*	78-110*	3	1
Dipodomys h. heermanni	64*	34	26-28*	M*	-	96*	-	2
Dipodomys heermanni arenae	64	34	28	M*	M*	96	1	-
Dipodomys heermanni goldmani**	64	32	30	M	A	94	3	2
Dipodomys heermanni goldmani**	64	28	34	M	-	90	-	1
Dipodomys heermanni jolonensis**	64	32	30	M	A	94	1	-
Dipodomys heermanni morroensis**	64	28	34	M	M	90	2	1
Dipodomys heermanni swarthi	64	34	28	M*	M*	96	3	3
Dipodomys heermanni tularensis**	64	32	30	M	A	94	4	1
Dipodomys panamintinus arguensis	64*	34*	28*	M*	-	96*	-	1
Dipodomys panamintinus caudatus	64	32	30	M*	M*	94	3	4
Dipodomys panamintinus leucogenys	64	36	26	M*	M*	98	1	1
Dipodomys panamintinus mohavensis	64	34	28	M*	M*	96	3	1
Dipodomys p. panamintinus	64	36	26	M*	M*	98	1	2
Dipodomys c. californicus	52	50	-	M	M	100	3	1
Dipodomys californicus saxatilis	52	50	-	M	M	100	2	2

karyotype is markedly different. There are at least 40, but no more than 46 metacentric chromosomes. The majority of cells counted showed 44 metacentrics and 28 acrocentrics. However, one specimen appeared to have 42 metacentrics and 30 acrocentrics, while another had a substantial number of cells showing 45-46 metacentrics and 27-26 acrocentrics. The best overall picture of the karyotype is 44 metacentrics and 28 acrocentrics.

The Y chromosome of Dipodomys ingens can be identified. It is the smallest metacentric chromosome of the male karyotype, and is not present in any of the female karyotypes. The X chromosome has not been identified, but it is certainly a metacentric, since the male and female karyotypes show the same array of acrocentric chromosomes. These data show the FN of D. ingens to be 110.

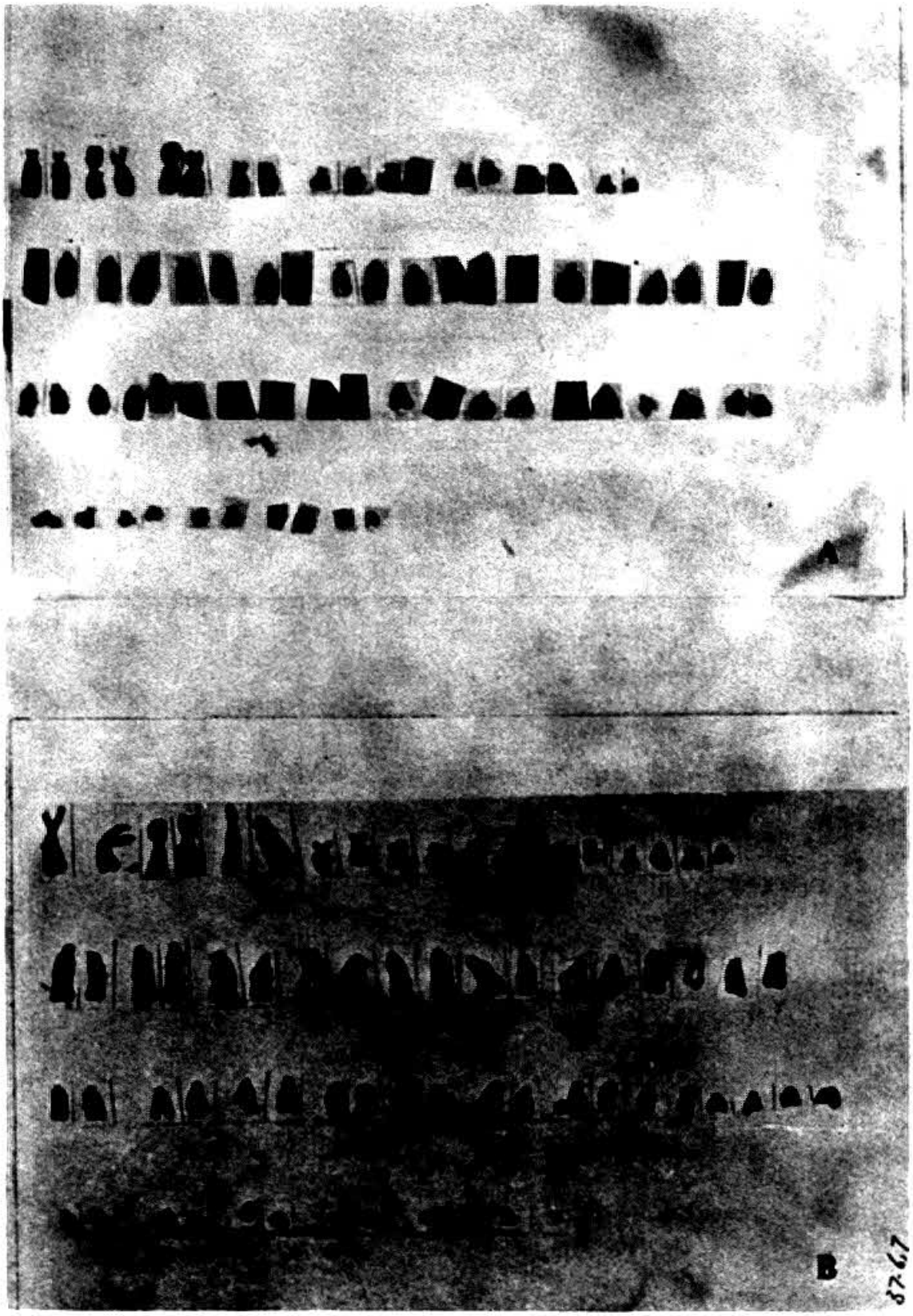
2. The Dipodomys stephensi karyotype. (Fig. 8)

The karyotype of this species is distinct. There are 12 chromosomes which are definitely metacentric, and 26 which are clearly acrocentric. The remaining 32 chromosomes have short or minute arms ("rabbit ears"), and it is a highly subjective decision whether they are acrocentric or metacentric. In the karyotypes selected for illustration, I have called 18 chromosomes metacentric, and left the remaining 52 as acrocentrics. This gives a FN of 84. The sex chromosomes have not been identified, but are assumed to metacentric.

3. The Dipodomys heermanni-panamintinus karyotype.

The "basic" karyotype has 64 chromosomes in all cases with the possible exception of D. h. heermanni, which seems to have as many

Figure 8. Karyotype of Dipodomys stephensi. A. Male. B. Female.


A
B
8767

cells with 62 chromosomes as with 64 chromosomes. The sex chromosomes have not been positively identified in any case, but all tentative identifications show them to be metacentric. The "basic" karyotype is further characterized by having 36 metacentric and 28 acrocentric chromosomes, giving a FN of 96. The 36 metacentrics can be rather arbitrarily divided into two groups--14 larger chromosomes, and 22 smaller ones. The division between the two groups is not well marked, but does seem to be valid. The 28 acrocentric chromosomes consist of 22 large to medium-sized chromosomes and 6 small ones. The larger acrocentrics seem to divide into subgroups, but because of the clinal change in size, no consistent subgroups could be set up.

The variations from this "basic" type will be described in the discussion of the karyotype of each population sampled.

Dipodomys h. heermanni. (Fig. 9)

Only two specimens of this important population were captured, and both were females. The chromosome preparations were unfortunately poor. There seemed to be a bimodal distribution of chromosome numbers in both specimens. This was observed after counting about 30 cells from each animal. In an attempt to clarify the problem, additional cells were photographed and counted, but the result was unchanged. The 2n count was almost evenly divided between 2n = 62 and 2n = 64.

The majority of cells in both specimens showed either 36 or 35 plus one questionable metacentric chromosome, so the discrepancy in 2n number appears to be in the number of acrocentrics. The cells showing 62 chromosomes could be incomplete karyotypes due to loss of chromosomes in preparation of the slides, although I do not know why only this

Figure 9. Karyotype of Dipodomys h. heermanni. A, B. Incomplete female karyotypes.

[illegible]

population would be so affected, or why only two chromosomes would be lost. Chromosomes could be obscured by cell debris, but the same two questions raised above apply to this explanation. The likelihood of genetic mosaicism seems to me to be exceedingly remote. I strongly suspect that this bimodality is an artifact and not a true phenomenon of the population, although I have no satisfactory explanation for it.

Assuming the diploid number to be 64, and the sex chromosomes to be metacentric, Dipodomys h. heermanni has a FN of 96, and a karyotype typical of the other two subspecies of D. heermanni which I sampled, with the exception that two of the six small acrocentric chromosomes of the "basic" D. heermanni-panamintinus karyotype are large enough to be included with the 22 large to medium chromosomes. Thus there are 24 large-medium acrocentrics and 4 small acrocentrics.

Dipodomys heermanni arenae. (Fig. 10A)

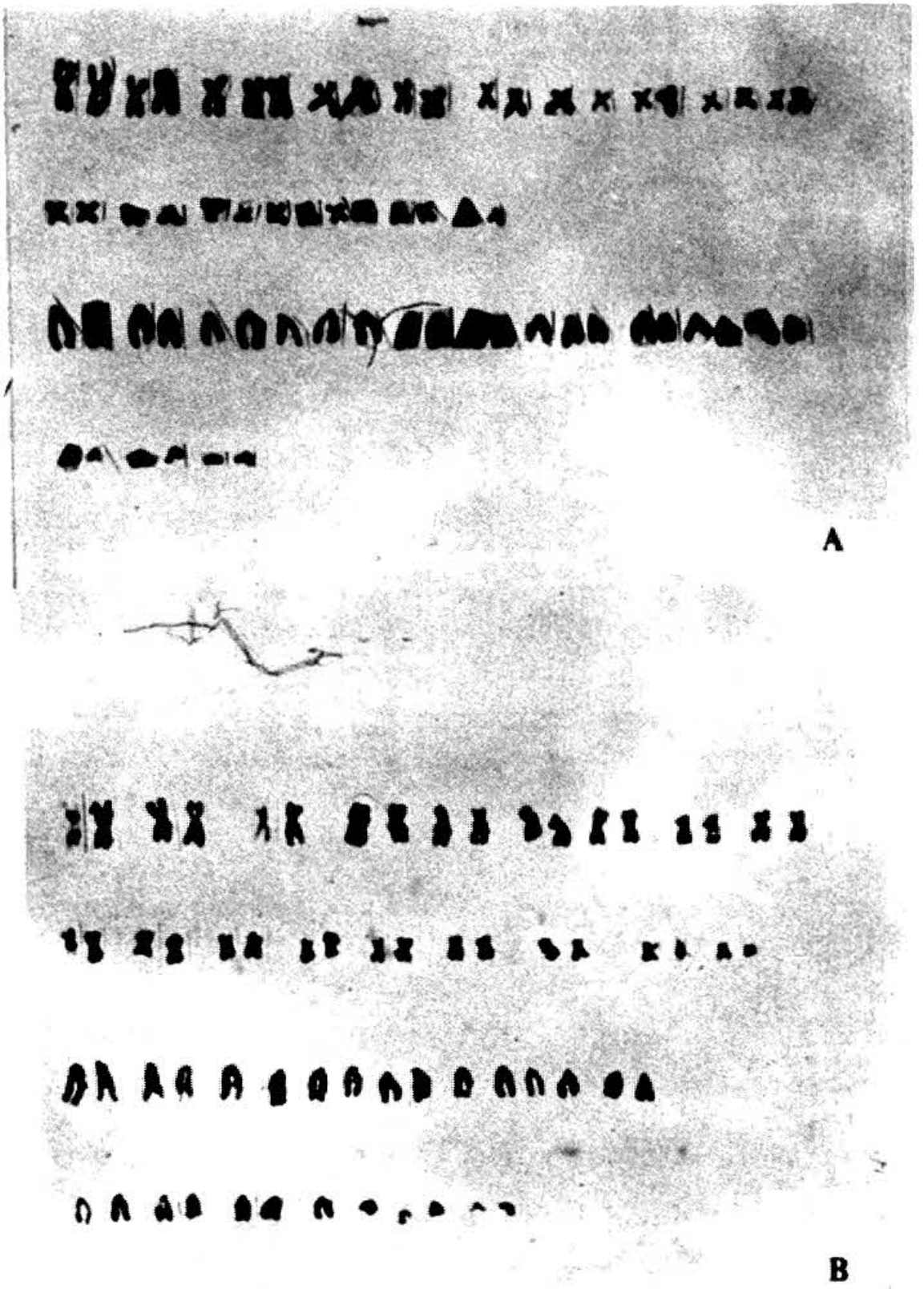
Csuti (1971) reported the karyotype of Dipodomys h. arenae, based on one female, to consist of 64 chromosomes, with 30 metacentric and 34 acrocentric chromosomes, and a FN of 90.

I had one male specimen, and my interpretation of the karyotype shows 2n = 64 with 36 metacentrics and 28 acrocentrics, and FN = 96. This interpretation is consistent with the "basic" Dipodomys heermanni-panamintinus karyotype.

The discrepancy between Csuti's results and my results arises in the interpretation of arm length of the smaller chromosomes, some of which I consider to be distinctly biarmed, while Csuti determines them to be acrocentric.

It is my observation that the photographic process may tend to

Figure 10. A. Karyotype of male Dipodomys heermanni arenae.
B. Karyotype of female Dipodomys panamintinus arguensis.



A

B

obscure short distinct arms, because of loss of resolution due to the extreme magnifications used. Therefore if there is a questionable chromosome, I prefer to place it in the metacentric category. This is especially true of small chromosomes, since a short arm makes up a relatively greater proportion of the total length of the chromosome, and thus it tends more to the metacentric class.

An additional reason for treating questionable chromosomes as metacentric comes from my observation of some spreads of chromosomes which were in late prophase or early metaphase, and so had not reached their maximum coiling and density. In these spreads, chromosomes which might show only a small knob on an acrocentric chromosome, or only minute arms, could be seen to have short but distinct arms beyond the centromere. While such spreads were not suitable for karyotypic analysis due to the considerable contortion and overlaps present, they did serve to demonstrate that questionable chromosomes often have distinct arms which may not be obvious at maximum coiling.

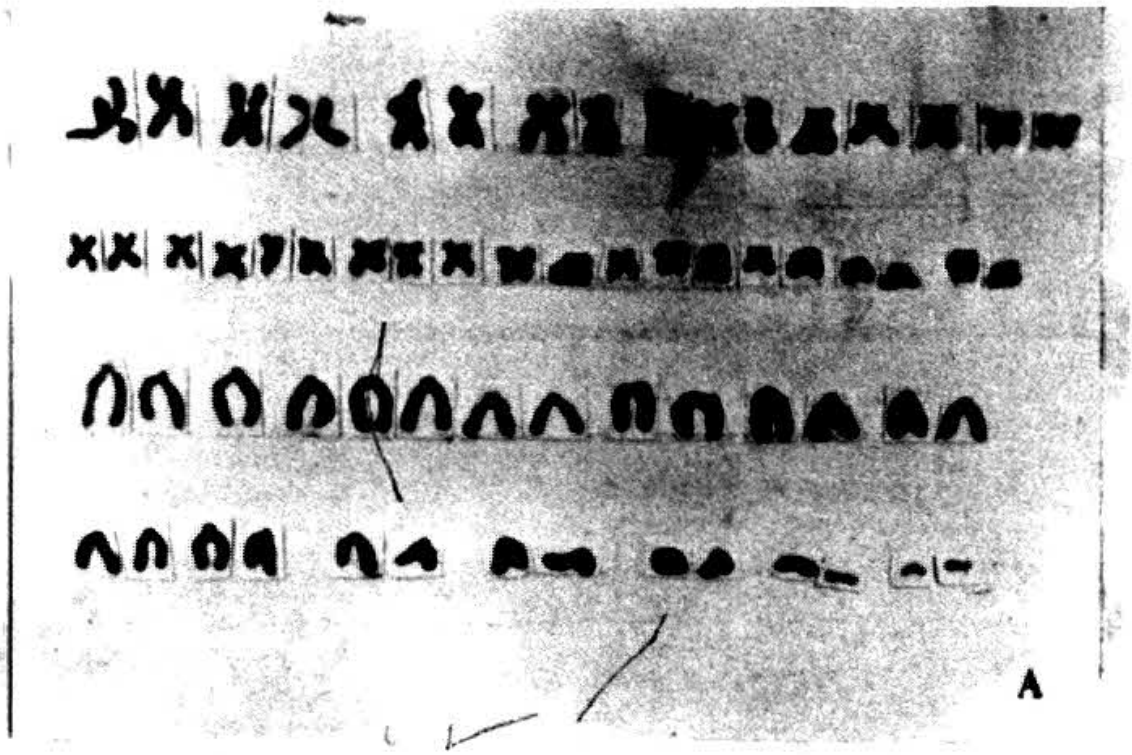
Dipodomys heermanni swarthi. (Fig. 11)

The karyotype of this population fits the "basic" karyotype, with 36 metacentrics, 28 acrocentrics, and, assuming metacentric sex chromosomes, a FN of 96.

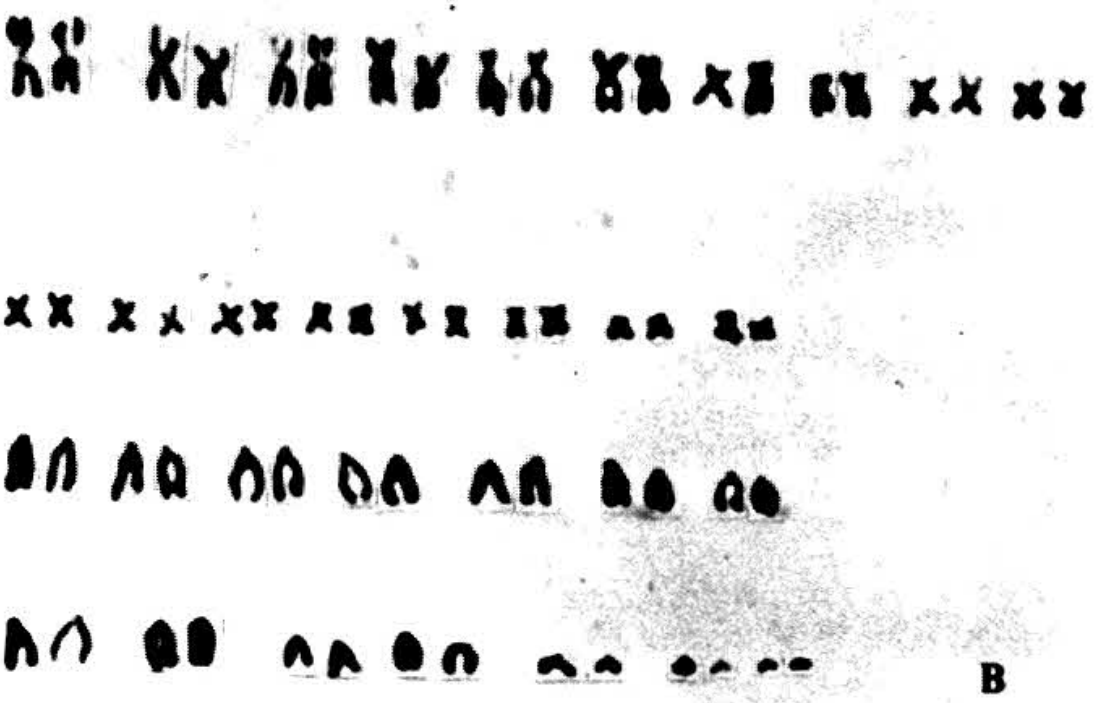
Dipodomys panamintinus arguensis. (Fig. 10B)

Only one specimen of this subspecies was captured, and as so often happened, chromosomes from the rare specimen turned out poorly! Only two really satisfactory spreads were found, so I report the karyotype of this population only in a tentative manner.

Figure 11. Karyotype of Dipodomys heermanni swarthi.
A. Male. B. Female.



A



B

The 2n number appears to be 64, as in all other subspecies of Dipodomys panamintinus. The two good spreads show 36 metacentrics and 28 acrocentrics, with a FN of 96. Some less satisfactory spreads appear to show 38 metacentrics and 26 acrocentrics, FN = 98. If FN = 96, the karyotype would be essentially the same as D. p. mohavensis, but if FN = 98, D. p. arguensis would have a karyotype more like D. p. leucogenys and D. p. panamintinus.

Presumably the sex chromosomes are metacentric.

The illustrated spreads are of the Dipodomys p. mohavensis type, and fit the "basic" D. heermanni-panamintinus karyotype.

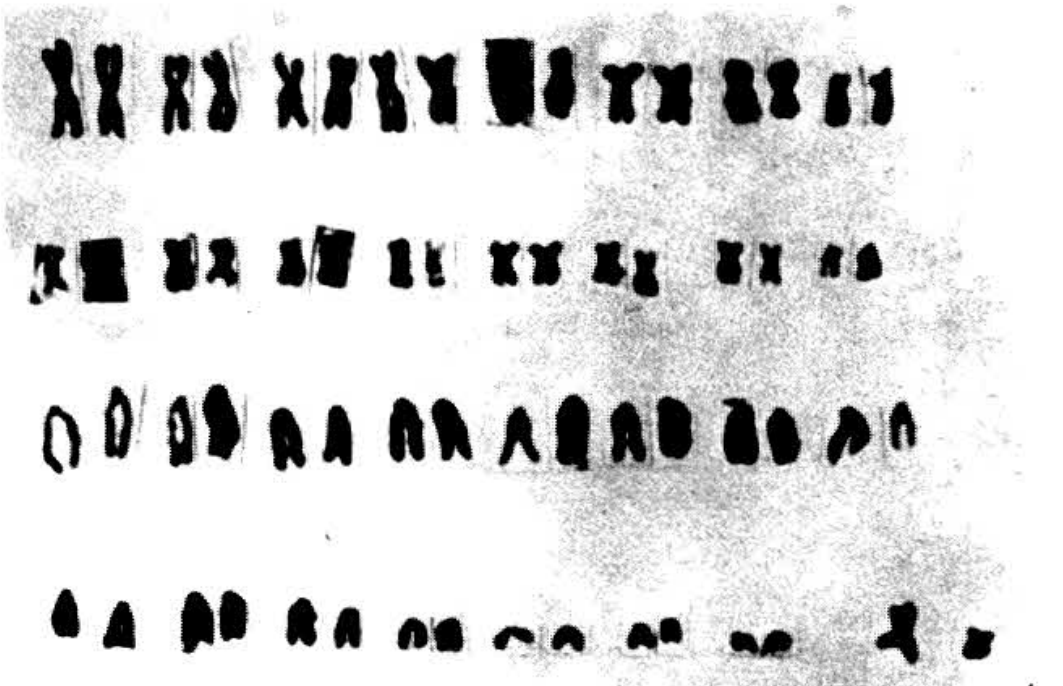
Dipodomys panamintinus caudatus. (Fig. 12)

Geographically speaking, this is the most isolated population of D. panamintinus. Its karyotype differs slightly from all other subspecies, and from the "basic" D. heermanni-panamintinus karyotype. There are 64 chromosomes, but only 34 metacentrics and 30 acrocentrics, with a FN of 94, assuming the sex chromosomes to be metacentric.

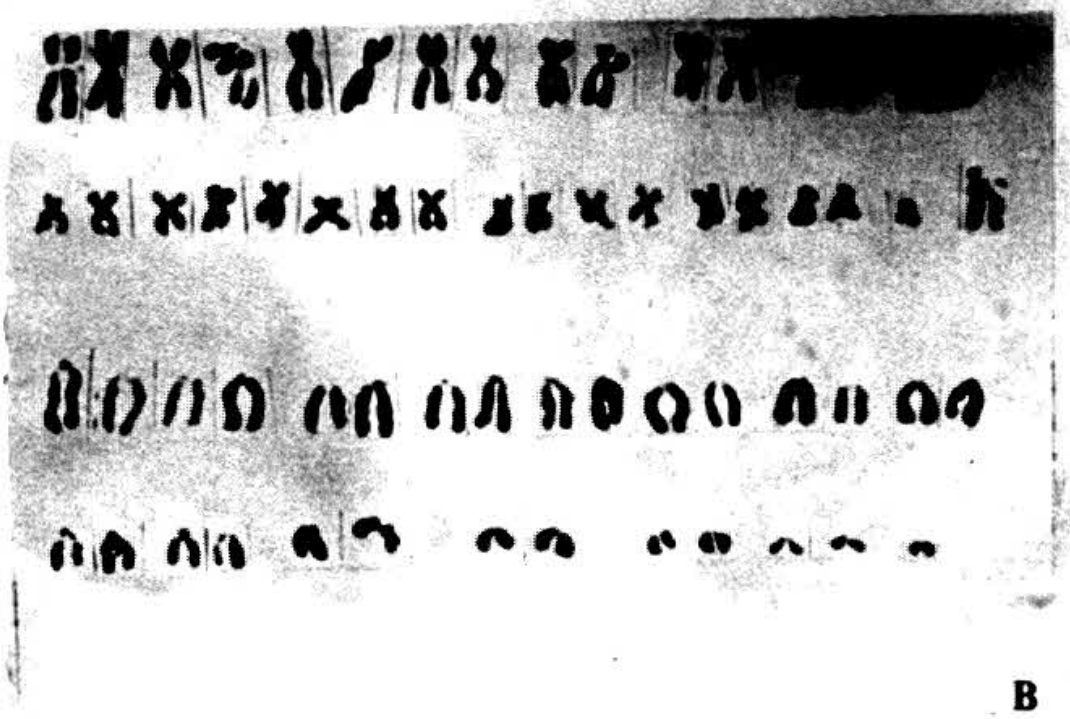
One male appeared to have but 30 metacentrics and 34 acrocentrics, based on a limited number of cells, and one female appeared to have 32 metacentrics and 32 acrocentrics. The best overall picture, however, shows 34 metacentrics and 30 acrocentrics.

This differs from the "basic" Dipodomys heermanni-panamintinus karyotype in the following way. There are 14-15 large metacentrics and 19-20 medium-small metacentrics, and 24 large-medium acrocentrics and 6 small acrocentrics. Thus it appears two medium-small metacentrics are replaced by two large-medium acrocentrics. This change could easily be accounted for by a pericentric inversion.

Figure 12. Karyotype of Dipodomys panamintinus caudatus.
A. Male. B. Female.



A



B

Dipodomys panamintinus leucogenys. (Fig. 13)

This subspecies differs from the "basic" heermanni-panamintinus karyotype. It has 38 metacentric and only 26 acrocentric chromosomes. One pair of the very small acrocentric chromosomes is absent, and an additional pair of metacentrics is present.

The sex chromosomes have not been identified, but are assumed to be metacentric, giving FN = 98. This pattern is essentially identical to that of Dipodomys p. panamintinus.

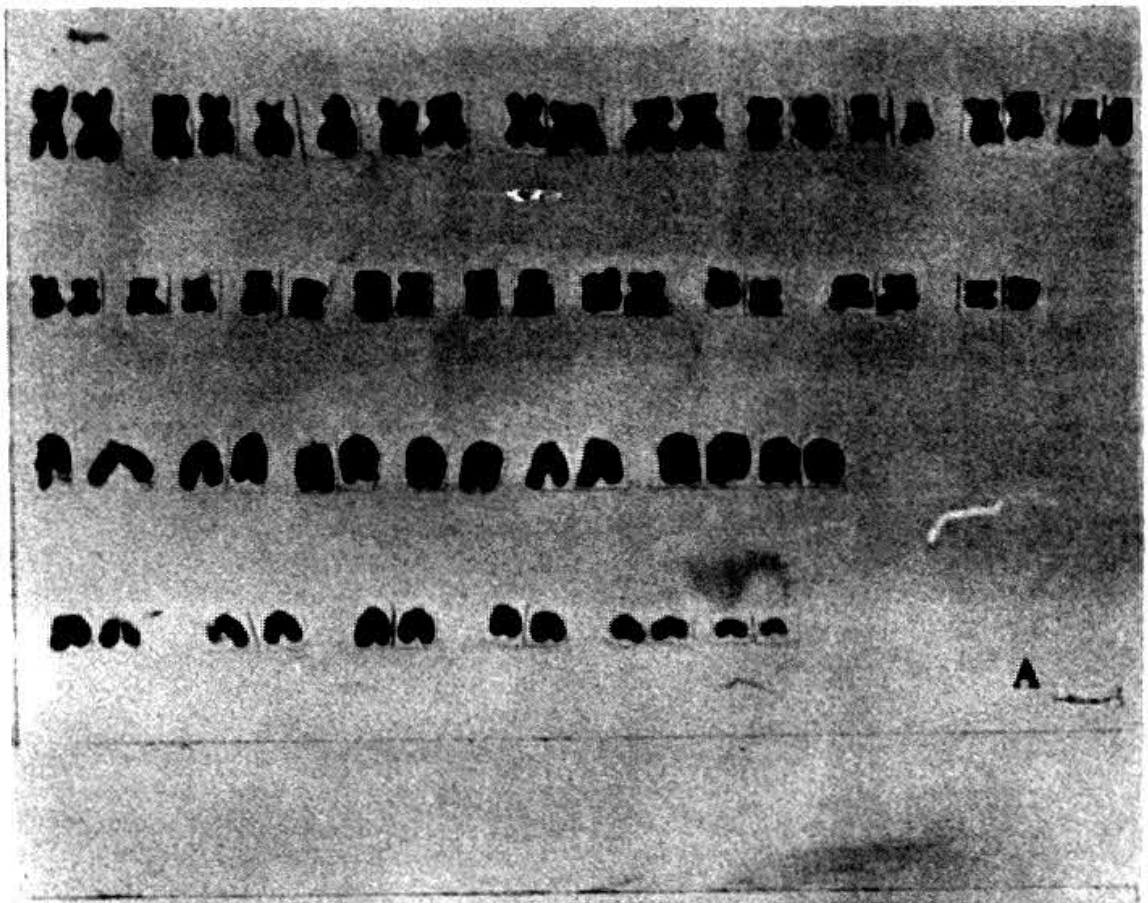
Dipodomys panamintinus mohavensis. (Fig. 14)

This subspecies exhibits the "basic" heermanni-panamintinus karyotype.

Dipodomys p. panamintinus. (Fig. 15)

The karyotype of this subspecies cannot be distinguished from that of Dipodomys p. leocogenys.

Figure 13. Karyotype of Dipodomys panamintinus leucogenys. A. Male. B. Female.


A

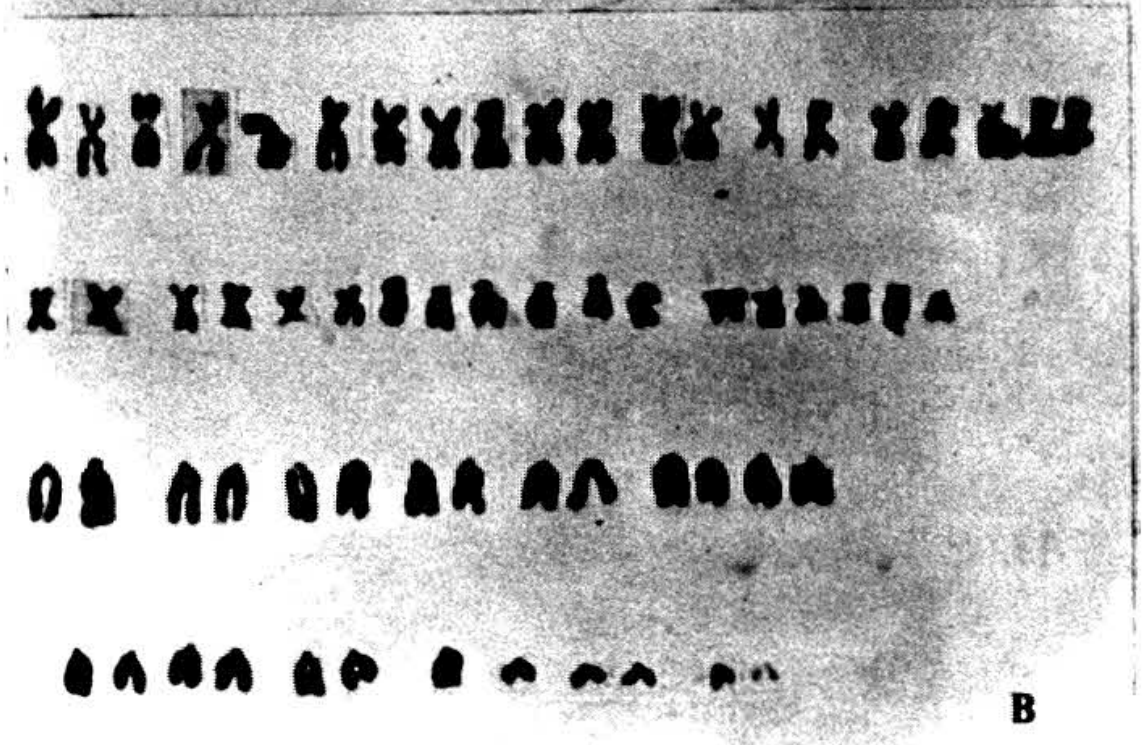
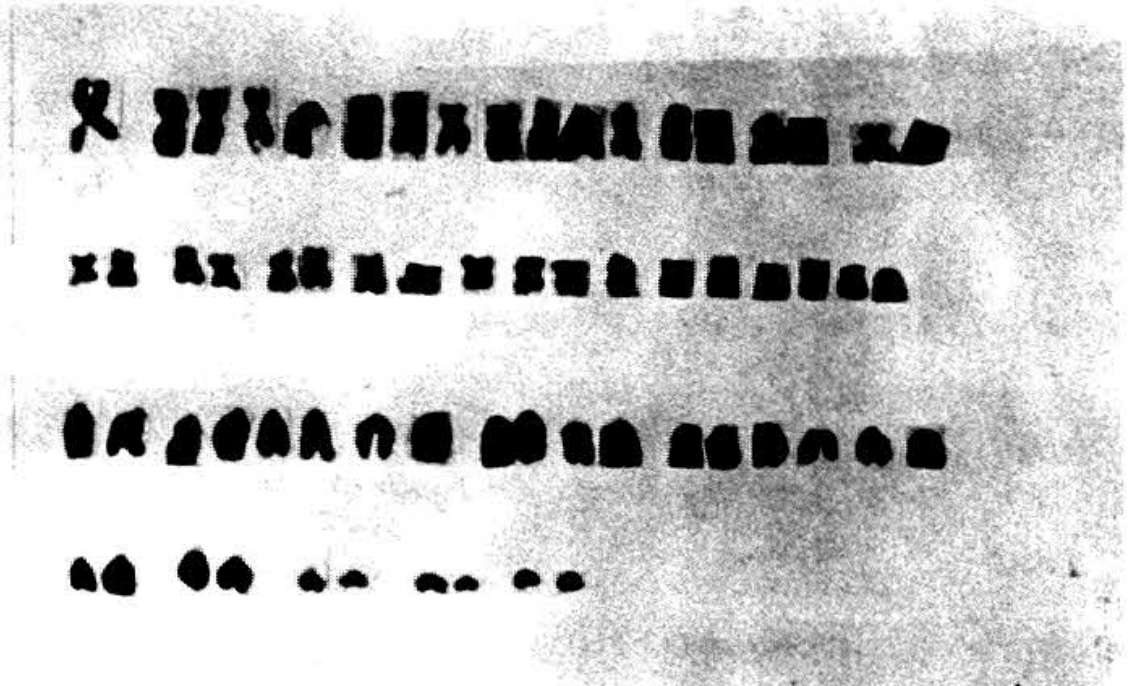
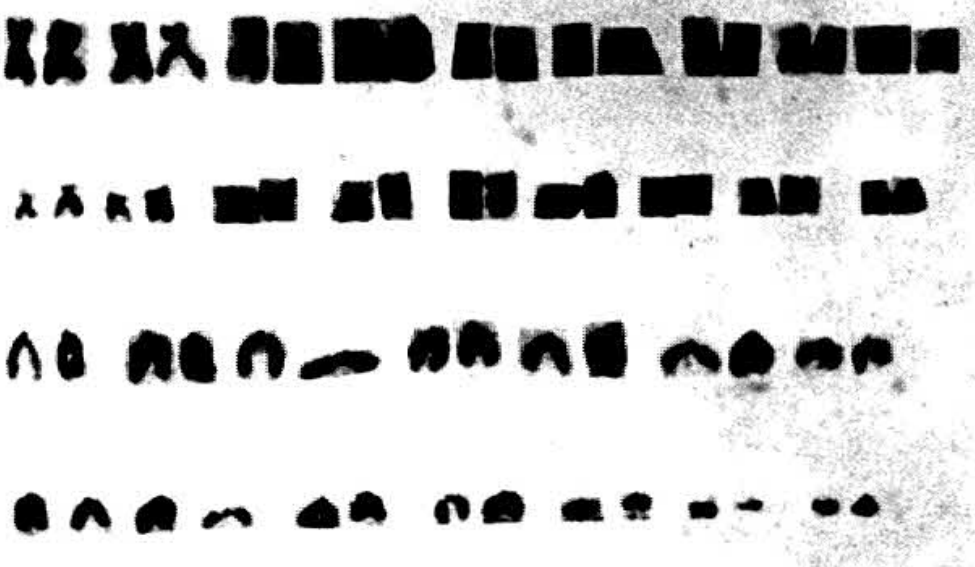

B

Figure 14. Karyotype of Dipodomys panamintinus mohavensis.
A. Male. B. Female.

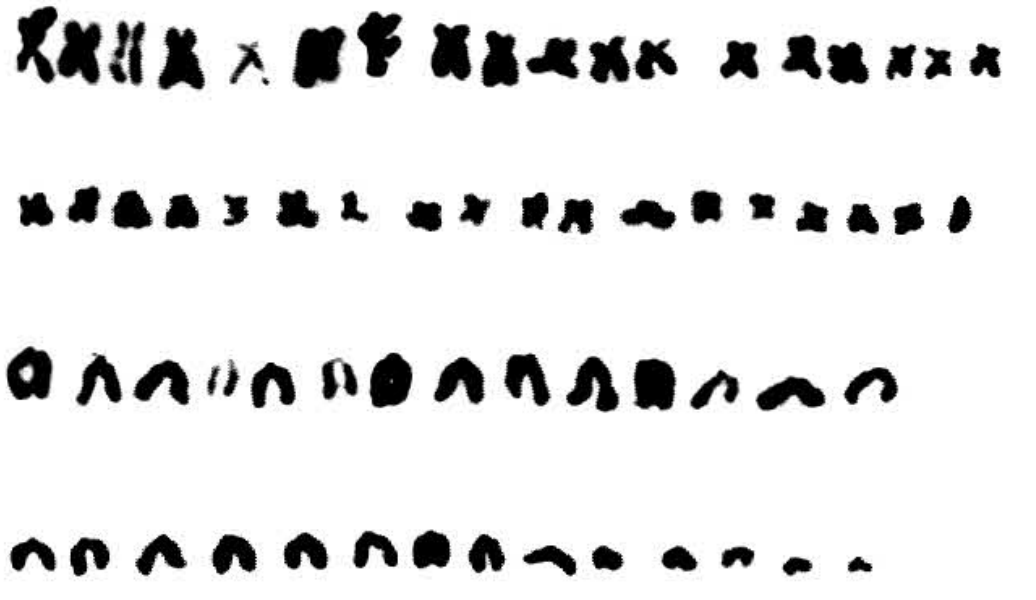


A

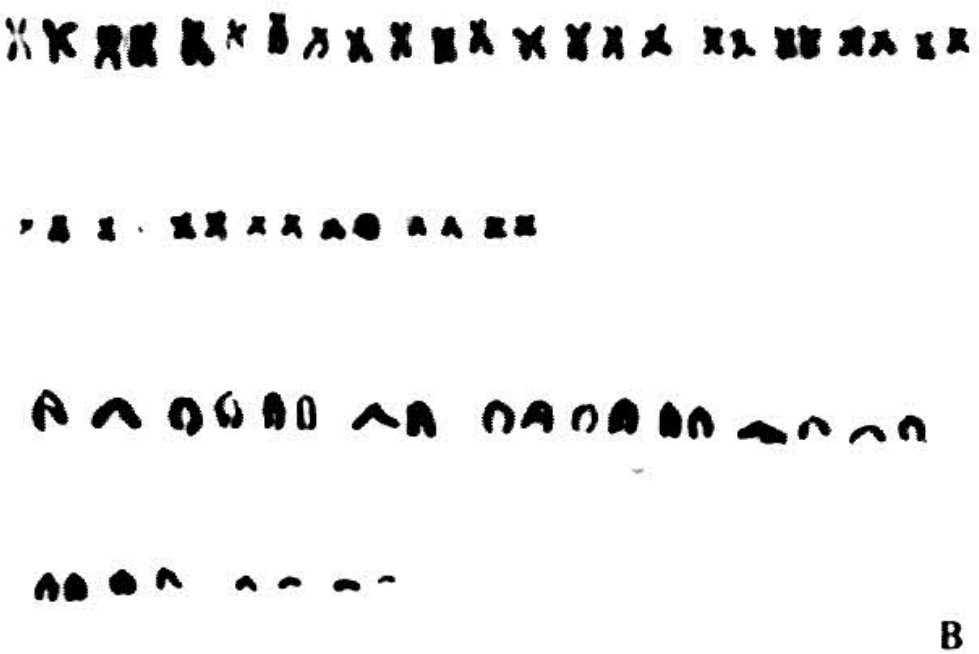


B

Figure 15. Karyotype of Dipodomys p. panamintinus.
A. Male. B. Female.



A



B

4. The Dipodomys californicus karyotype.

Perhaps the most surprising karyotype in subgroup A of the heermanni group is that of the northern four-toed populations of D. heermanni. Fashing (1973) reports a karyotype of 52 chromosomes, all but four of which are metacentric. My samples show the same karyotype, but I interpret all chromosomes as metacentrics. Both Fashing's and my pictures show short but distinct arms on the four chromosomes he interprets as acrocentrics. Thus I consider all 52 chromosomes to be metacentric, and the FN to be 100. This karyotype is completely different from all the others in subgroup A, and in fact is very similar to D. merriami which I sampled during my preliminary work.

It is this great difference in karyotypes which makes it clear to me that the four-toed populations of Dipodomys heermanni should be given full specific distinction from the southern five-toed forms, and thus be known as D. californicus Merriam.

D. c. californicus. (Fig. 16)

The Y chromosome of this population can be clearly identified as the smallest chromosome in the male karyotype. This chromosome is not represented in the female karyotype. The X chromosome is not positively identified, but obviously is metacentric.

D. c. saxatilis. (Fig. 17)

The karyotype of this population is indistinguishable from that of D. c. californicus.

Figure 16. Karyotype of *Dipodomys c. californicus*.
A. Male. B. Female.

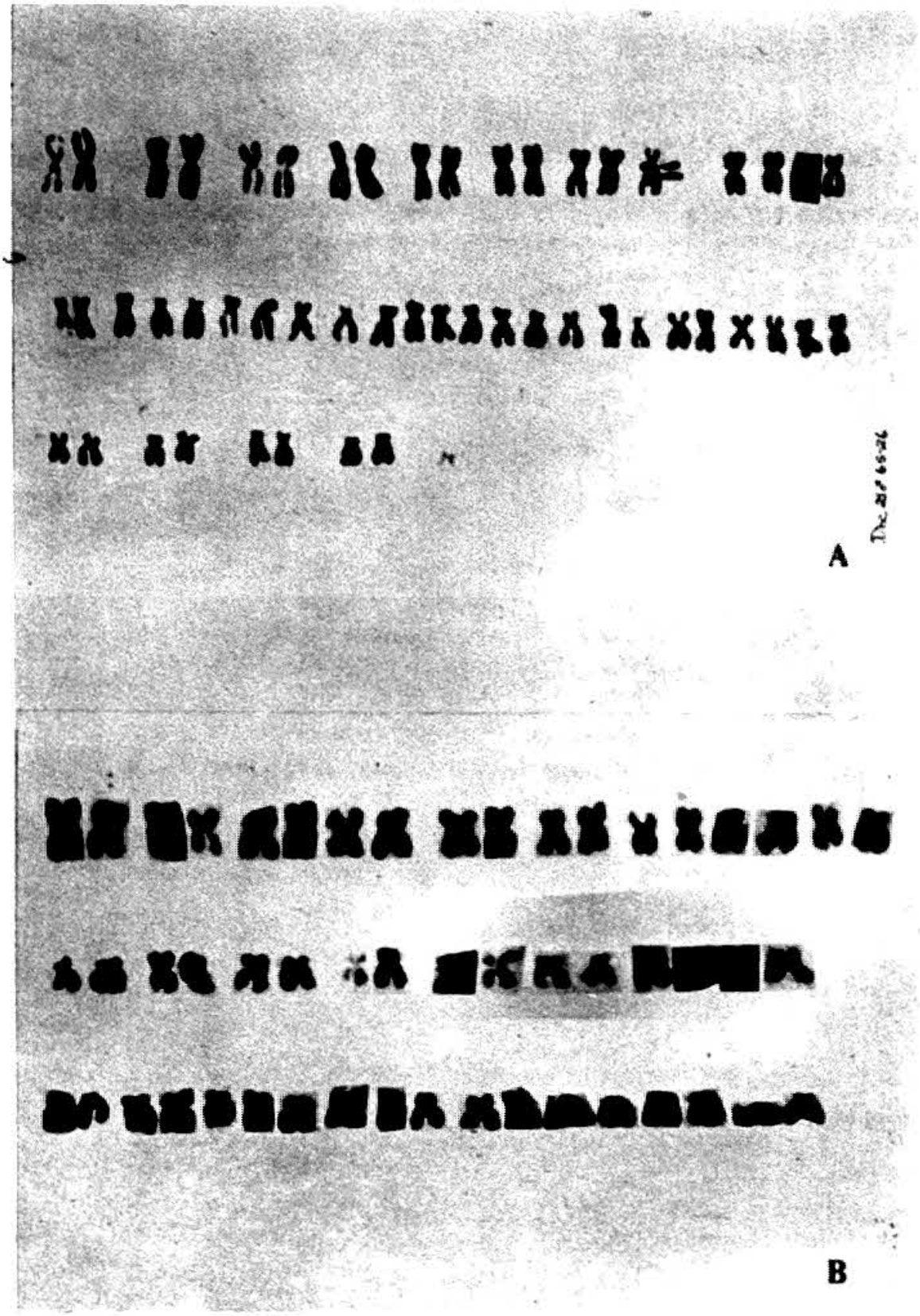
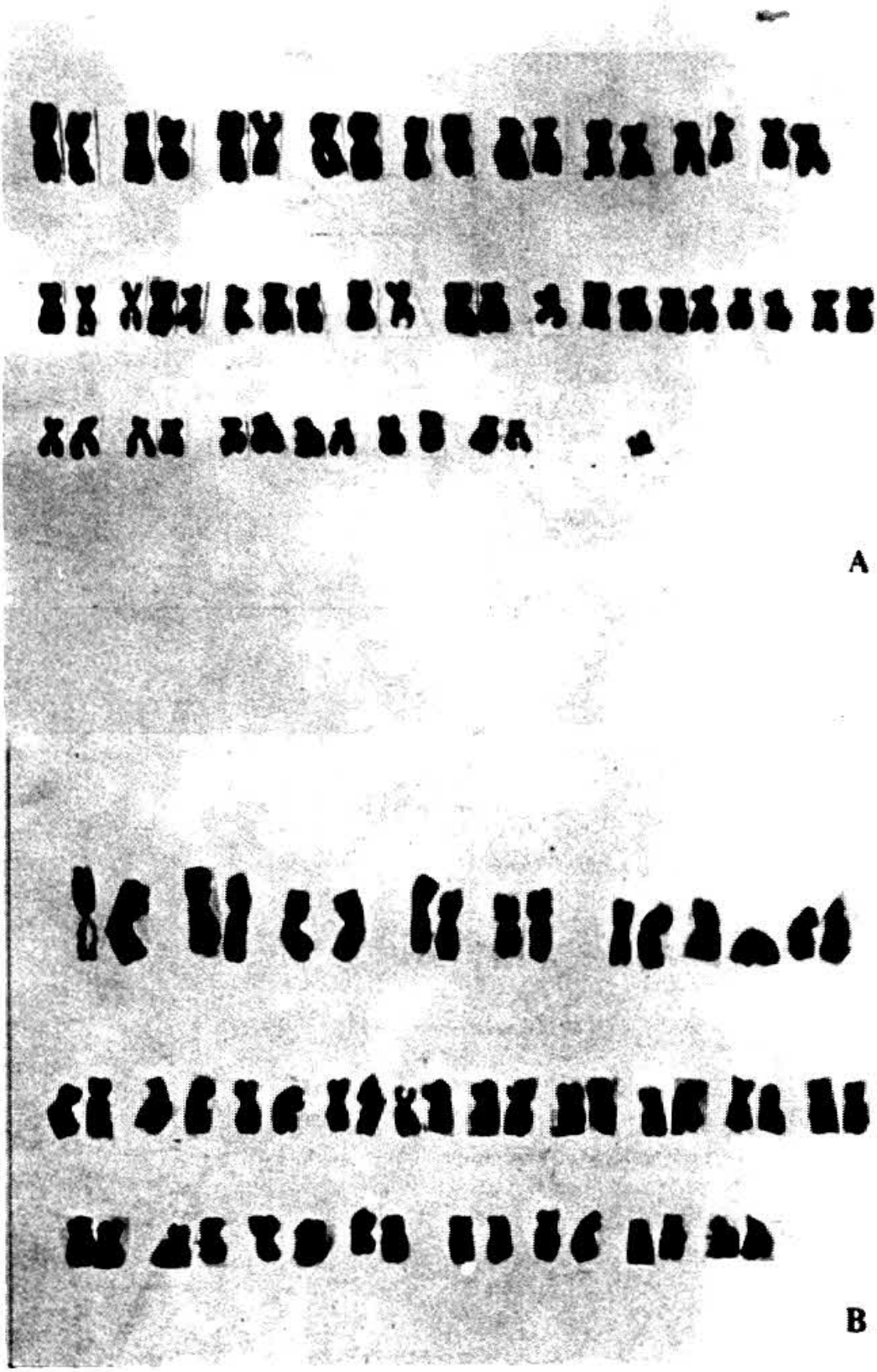

A
B

Figure 17. Karyotype of Dipodomys californicus saxatilis.
A. Male. B. Female.



A

B

DISCUSSION

The results of electrophoresis and karyology show rather good correlation in most cases. Of the two methods, I consider the karyological data to be more significant, since it is less subject to qualitative variations than the electrophoresis results. For example, the presence of band 1 in Dipodomys panamintinus caudatus resulted in its being plotted at a much greater distance from all other populations (Fig. 4), including other subspecies of D. panamintinus, than the distance between D. californicus and D. stephensi or D. ingens, which are certainly much more distantly related to one another than are the subspecies of D. panamintinus. The electrophoresis data do contribute useful information, which, in combination with karyology, contribute to determining relationships in subgroup A of the heermanni group of Dipodomys.

There can be little doubt about the specific status of D. californicus. Its karyotype and its serum pattern are both remarkably distinct (Figs. 5, 6, 16, 17). The two sampled subspecies are essentially identical in karyotype, and are close in serum pattern. The similarity of the karyotypes of this species and D. merriami raise the question as to whether or not it belongs in the heermanni group at all.

Dipodomys h. heermanni appears to approach D. californicus in serum pattern (Figs. 5, 6), but is distinctly different in its chromosomal complement (Figs. 9, 16, 17).

The two monotypic species, Dipodomys stephensi and D. ingens are distinct from each other on the basis of karyotype (Figs. 7, 8),

and of serum pattern (Figs. 5, 6). The position of these populations in the electropherogram brackets D. panamintinus mohavensis, which makes it tempting to speculate that they are isolates of the D. heermanni-panamintinus complex. However, the chromosomal evidence does not support this idea, nor does gross morphological data.

The Dipodomys heermanni-panamintinus group show some interesting relationships. My results suggest that this group may be a single highly variable species, or a cluster of several closely related species fitting Mayr's definition of a superspecies (Mayr, 1963, 1969).

The Dipodomys p. panamintinus and D. p. leucogenys pair shows close relationship in both electrophoretic and karyological data (Figs. 5, 6, 12, 15), and also in geographical data (Fig. 1).

Dipodomys panamintinus mohavensis and D. heermanni swarthi have similar or identical chromosomal complements (Figs. 11, 14), and are similar in electrophoretic patterns (Figs. 5, 6). Further study of these populations and other subspecies of D. heermanni not included in this study should prove enlightening concerning the status of D panamintinus and D. heermanni.

Dipodomys panamintinus caudatus is remotely related when judged by the electrophoretic results (Fig. 4), and the chromosomal analysis indicates that this population is somewhat different from other members of the group (Fig. 12). These data raise a question about the specific status of D. p. caudatus, and further investigation may show that complete speciation has occurred.

Dipodomys heermanni arenae shows a chromosomal complement similar to D. h. swarthi and D. panamintinus mohavensis (Figs. 10A, 11, 14), but its position on the electropherogram in Fig. 5 is close to D. p. panamintinus and D. p. leucogenys. The chromosomal data are more reliable in this group, since only three specimens were available for electrophoretic analysis, while the chromosomes were independently studied by Csuti (1971).

Dipodomys h. heermanni is hard to characterize. There were only two individuals available for study, and both chromosomal and electrophoretic data have proved inconclusive.

Dipodomys panamintinus arguensis, a rare form, was represented by only one individual. The chromosome preparations were poor, and show only that this population is consistent with others in the D. heermanni-panamintinus complex. No useable electropherograms were obtained.

As a result of the data presented in this paper, I have arranged the species of the heermanni subgroup A of the genus Dipodomys in the following manner, beginning with those of highest chromosome number, and proceeding to those with the lowest number. I have not included D. gravipes in this list, since I have no data on this species. Subspecies are listed alphabetically, except in D. panamintinus where there are three different groups of karyotypes represented. Synonymies are given for D. stephensi and D. californicus. All other synonymies are presented in Hall and Kelson, 1959.

Dipodomys ingens (Merriam, 1904)

Dipodomys stephensi (Merriam, 1907)

Synonym: D. cascus Huey, 1962

Dipodomys heermanni Le Conte, 1853

D. h. arenae Boulware, 1943

D. h. berkeleyensis Grinnell, 1919

D. h. dixoni Grinnell, 1919

D. h. goldmani (Merriam, 1904)

D. h. heermanni Le Conte, 1853

D. h. jolonensis Grinnell, 1919

D. h. morroensis (Merriam, 1907)

D. h. swarthi Grinnell, 1919

D. h. tularensis (Merriam, 1904)

Dipodomys panamintinus (Merriam, 1894)

D. p. mohavensis (Grinnell, 1918)

D. p. arguensis Huey, 1945

D. p. leucogenys (Grinnell, 1919)

D. p. panamintinus (Merriam, 1894)

D. p. caudatus Hall, 1946

Dipodomys californicus Merriam, 1890

D. c. californicus Merriam, 1890

Synonyms: D. c. pallidulus Bangs, 1899

D. c. trinitatus L. Kellogg, 1916

D. heermanni californicus Merriam, 1890: Grinnell, 1921

D. h. gabrielsoni Goldman, 1925

D. c. **eximius** Grinnell, 1919

Synonym: D. **heermanni eximius** Grinnell, 1919: Grinnell, 1921

D. c. **saxatilis** Grinnell and Linsdale, 1929

Synonym: D. **heermanni saxatilis** Grinnell and Linsdale, 1929

CONCLUSIONS

As a result of this study, I have arrived at the following conclusions:

1. The northern four-toed populations of Dipodomys heermanni represent a distinct species of kangaroo rats which should be known as Dipodomys californicus Merriam. This species include the following populations:

D. c. californicus Merriam, 1890

D. c. eximius Grinnell, 1919

D. c. saxatilis Grinnell and Linsdale, 1929

The position of Dipodomys californicus in the heermanni group should be reevaluated. Both karyotypic and some morphological data suggest a closer relationship with D. merriami. (Compare Fashing, 1973.)

2. Dipodomys stephensi is a distinct, well differentiated species, and is not immediately related to D. heermanni or D. panamintinus as has been suggested by several authors.

3. The specific status of Dipodomys heermanni and D. panamintinus merits further investigation, since the adjacently allopatric subspecies of both species show close similarity in karyotype and in position in the electropherogram.

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BIOSYSTEMATICS OF THE *HEERMANNI* SUBGROUP A OF THE GENUS *DIPODOMYS* (RODENTIA: HETEROMYIDAE)

by

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An Abstract of

a Dissertation in Partial Fulfillment

of the Requirements for the Degree

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ABSTRACT

This study investigates the taxonomic status of members of the heermanni subgroup of the genus Dipodomys.

Karyotypes were prepared for 12 populations of this subgroup, using in vivo cultures of bone marrow prepared by a modified colchicine-hypotonic citrate method. The 2n ranges from 52 - 72.

Electropherograms were prepared for 11 populations, and data derived from the tracings were subjected to stepwise discriminant function analysis, resulting in scattergrams which were used to indicate closeness of relationship between populations.

These data show that: a) Dipodomys stephensi (Merriam) and Dipodomys ingens (Merriam) are well defined species with 2n = 70 for D. stephensi and 2n = 72 for D. ingens.

b) the populations known as Dipodomys heermanni comprise two species--the southern five-toed forms (2n = 64), which retain the name D. heermanii Le Conte, and the northern four-toed forms (2n = 52), which take the name Dipodomys californicus Merriam.

c) the 5 subspecies of Dipodomys panamintinus (Merriam) (2n = 64) fall into three groups showing small differences in karyotype, and significant differences in serum patterns. D. panamintinus mohavensis (Grinnell) is very closely related to D. heermanni, and in fact many be conspecific with it. The entire D. heermanni-panamintinus complex appears to form a superspecies.