San Fernando Valley State College

INTERRELATIONSHIPS OF FIVE SPECIES OF KANGAROO RATS (GENUS DIPODOMYS) IN SOUTHERN CALIFORNIA

A thesis submitted in partial satisfaction of the requirements for the degree of Master of Science in

Biology

by

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ABSTRACT

INTERRELATIONSHIPS OF FIVE SPECIES OF KANGAROO RATS (GENUS DIPODOMYS) IN SOUTHERN CALIFORNIA

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Karyotypes were prepared for five species of kangaroo rats (genus Dipodomys) from Southern California. Slides were obtained using bone marrow preparations from animals previously injected with colchicine. A total of eight subspecies were examined: D. agilis agilis and D. a. perplexus (2n=62); D. panamintinus mohavensis (2n=64); D. heermanni morroensis, D. h. arenae, and D. h. goldmani (2n=64); D. microps microps (2n=60); and D. merriami merriami (2n=52). The karyotype was used as a systematic tool to clarify the distribution and interrelations of these species.

The karyotypic distinctness of the morphologically similar D. panamintinus and D. agilis enabled me to demonstrate the presence of D. panamintinus associated with the Pinyon-Juniper Woodland within the supposed range of D. agilis agilis in the San Gabriel Mountains. D. microps was discovered in an Alkali Sink habitat near Lancaster. These localities represent range extensions for D. panamintinus and D. microps. Habitat is considered as a factor in determining distribution. That portion of the range of D. agilis perplexus which extends across the floor of the Antelope Valley as

depicted in Hall and Kelson (1959) should be deleted.

The similarity of the karyotypes of the broad-faced D. heermanni and D. panamintinus, and the difference of their karyotypes from that of the narrow-faced D. agilis, supports the current division of the heermanni group into broad-faced and narrow-faced subgroups.

INTRODUCTION

The genus Dipodomys, the kangaroo rats of the family Heteromyidae, contains twenty-one currently recognized species (Lidicker, 1960), twelve of which occur in California. The genus has been divided into "natural" groups most recently by Lidicker (1960). Location east or west of the Sierra Nevada-Tehachapi-Southern Coast Range Mountains is the criterion used by Hall and Kelson (1959) to separate D. heermanni and D. agilis from D. panamintinus. Although morphological characteristics are given by Grinnell (1922) and have been relied upon by most workers, there is overlap between ranges of measurements and individuals may not be separable on the basis of external morphology. One then depends upon existing range maps and classifies the animal on the basis of locality.

The morphology of the chromosomal complement of an organism, the karyotype, yields data at another level which are often helpful in systematic problems. If the external morphology is insufficiently different between two species for positive identification, morphology at the cellular level may solve the problem, provided that karyotypic evolution has not been identical for the species involved. Individuals can then be assigned to one or another of the possible species on the basis of this additional character.

In the last decade many workers have used the karyotype as a guide to intrageneric relationships in mammals. Nadler and Block (1962), Bender and Chu (1963), Nadler (1964, 1966), Baker and Patton (1967), Patton (1967a, b), Patton and Dingman (1968),

and Wahrman, Goitein, and Nevo (1969), among others, have used this character extensively in their analyses of problems in mammalian systematics. My purpose in this study is to clarify distributional and evolutionary relationships between some morphologically similar and closely related kangaroo rats, particularly of the heermanni group, in Southern California utilizing the karyotype as a systematic tool. Speculations concerning the ecological and phylogenetic relationships of these rodents are also advanced.

MATERIALS AND METHODS

The animals used in this study were taken with Sherman live-traps (10"x3"x3") using wild bird seed as bait. Oats were placed inside the traps to provide food for the captured animals. Specimens were kept alive in the laboratory until ready for use. Chromosome slides were prepared from bone marrow samples by the method of Ford and Hammerton (1956) as modified by Patton (1967a). Conventional museum study skins were prepared and have been deposited in the collection of the Los Angeles County Museum of Natural History. A list of the specimens examined together with trapping localities is contained in Appendix I. The morphological data gathered are summarized in Tables 2 and 3. Specimens were initially identified to species by morphological characteristics and to subspecies by location in reference to previously published ranges, with the exception of those specimens of D. panamintinus which represent an extension of the species range. My data were compared with the descriptions given in Grinnell (1922). The specimen of D. heermanni arenae was compared with the description of Boulware (1943). The specimen of D. heermanni goldmani was identified by Thomas S. Kelly, using the resources of the Museum of Vertebrate Zoology, University of California, Berkeley.

Slides prepared for karyotyping were scanned at 150X for well spread metaphase figures. Cells were not used if other chromosomes were in the vicinity, if there were overlaps which obscured chromosome morphology, or if the cell appeared to have been spread ex-

cessively. Cells were counted at 500X with the aid of a camera lucida. Counts of 20 cells per individual were made to determine the diploid number for the individual, except in the cases of D. microps and D. merriami, where poor preparations made this impossible. In these cases the diploid number was determined from counts of 13 cells for D. microps and 7 cells for D. merriami. For each individual the two best cells were selected for the preparation of karyotypes. Selected cells were photographed at 500X on 35mm Kodak High Contrast Copy film using a Zeiss Neofluar 40/0.75 objective. Enlargements of six to eight diameters were made for the determination of karyotypes.

In the construction of karyotypes it should be recognized that a chromosome is not necessarily paired with its homolog, even though every attempt was made to achieve the best pairing possible. In only a few cases was the morphology of every chromosome of a karyotype clear enough to yield indisputable results. All the karyotypes available for a species were compared with one another and with microscopic observations of chromosome spreads to arrive at the karyotype for the species. In no case was the assignment of a questionable pair of chromosomes to one or another group the basis of a taxonomic decision.

Karyotypes were analyzed using the nomenclature of Bender and Chu (1963). Chromosomes were considered metacentric if they had a median centromere and the ratio of arms was from 1:1 to 1:1.9. Chromosomes were considered submetacentric if they had a submedian centromere and the ratio of arms was from 1:2.0 to 1:4.9. Chromo-

somes were termed acrocentric if they had a terminal or nearly terminal centromere and the ratio of arms was 1:5.0 or greater. In determining the number of major arms, N.A. (equivalent to the "Fundamental Number" of Matthey, 1951), each metacentric and submetacentric autosome was scored as two, each acrocentric autosome was scored as one. When a questionable pair of chromosomes was encountered, it was placed in the group it most closely resembled. When both sexes were available for a species, the heteromorphic pair of chromosomes in the male was designated as the pair of sex chromosomes. This system of analysis is necessarily arbitrary, but until further refinements in technique make more exact determinations possible, this system seems best suited to the material and allows comparison with results published by other investigators.

RESULTS

The results of the karyotypic analysis are summarized in Table 1. Representative karyotypes are illustrated in Figs. 2-9. In order to facilitate comparison of karyotypes of the various species studied, the chromosome pairs in the figures were divided into bi-armed and uni-armed groups, arranged in order of decreasing size within each group. A total of 605 cells were counted: 78% of the counts agreed with the diploid number assigned to the species in question. Cells with a different number were considered to have had their chromosome complement altered in preparation. A description of each subspecies examined follows.

Dipodomys agilis agilis Gambel, Gambel Kangaroo Rat. Three individuals from two localities had a diploid number of 62 and a N.A. of 116. The karyotype contained 22 pairs of metacentrics, 6 pairs of submetacentrics, and 2 pairs of acrocentrics (Fig. 2). The sex chromosomes consisted of a metacentric X and an acrocentric Y.

Dipodomys agilis perplexus (Merriam), Walker Basin Kangaroo Rat. Three individuals from one locality had the same karyotype as D. a. agilis. The diploid number was 62, and the N.A. was 116. The karyotype consisted of 22 pairs of metacentrics, 6 pairs of submetacentrics, and 2 pairs of acrocentrics (Fig. 3). The sex chromosomes consisted of a metacentric X and an acrocentric Y.

Dipodomys panamintinus mohavensis (Grinnell), Mohave Kangaroo Rat. Seventeen specimens from four localities had a diploid number

of 64 and a N.A. of 94. The karyotype consisted of 14 pairs of metacentrics, 2 pairs of submetacentrics, and 15 pairs of acrocentrics (Fig. 4). The sex chromosomes consisted of a metacentric X and a small submetacentric Y.

This species represents my largest sample from the greatest number of localities. The geographic extremes, Mojave and Acton, are 45 miles apart. Every individual examined had the same karyotype. My observations indicate that all the trapping sites are joined by habitats suitable for D. panamintinus, with no interruption by natural barriers of any kind. It appears that isolation of populations has not taken place in this area, or if there has been isolation, no population which I sampled has developed a distinctive karyotype.

Dipodomys heermanni morroensis (Merriam), Morro Bay Kangaroo Rat. Three specimens from one locality were examined and had a diploid number of 64 and a N.A. of 90. The karyotype contained 14 pairs of metacentrics and 17 pairs of acrocentrics plus a metacentric X and a small submetacentric Y (Fig. 5).

One of the medium size pairs of metacentrics possessed satellites at the ends of the arms. Dipodomys h. goldmani shared this character, but the quality of slide preparation for D. h. arenae was such that the presence of satellites in this subspecies could not be confirmed.

Dipodomys heermanni arenae Boulware, Santa Barbara Kangaroo Rat. The single female examined had a diploid number of 64 and a N.A. of 90. The karyotype consisted of 14 pairs of metacentrics

and 17 pairs of acrocentrics (Fig. 6). No male was examined, but it is assumed that the sex chromosomes would be metacentric, as in D. h. morroensis.

Dipodomys heermanni goldmani (Merriam), Salinas Kangaroo Rat. The one female examined had a karyotype identical to that of the other subspecies of D. heermanni described above. The diploid number was 64 and the N.A. was 90. The karyotype consisted of 14 pairs of metacentrics and 17 pairs of acrocentrics (Fig. 7). No male was examined, but the sex chromosomes are assumed to be metacentric, as found in D. h. morroensis.

Dipodomys microps microps (Merriam), Small-Faced Kangaroo Rat. One female was examined and had a diploid number of 60 and a N.A. of 116. The karyotype consisted of 14 pairs of metacentrics and 16 pairs of submetacentrics (Fig. 8). There were no acrocentrics. No male of this species was examined, but the selection of any pair as sex chromosomes would not alter the N.A. of 116.

Dipodomys merriami merriami Mearns, Merriam Kangaroo Rat. The one female examined had a diploid number of 52 and a N.A. of 100. The karyotype consisted of 18 pairs of metacentrics and 8 pairs of submetacentrics (Fig. 9). No acrocentrics were found. No male of this species was examined, but the designation of any pair as sex chromosomes would not change the N.A. of 100.

Cross (1931) reported the diploid number of D. merriami merriami to be 86± based on one cell from one individual. My D. m. merriami has a diploid number of 52, which agrees with the figure given by James L. Patton (pers. comm.) for this species.

LOCALITIES AND HABITATS

The kangaroo rats used in this study were trapped at the sites indicated in Fig. 1. Trapping sites represented major differences in habitat. Photographs were taken of the trapping sites (Figs. 11-18) and plant samples were gathered for identification. Plants were identified initially with the aid of Munz and Keck (1959) and later compared with specimens in the San Fernando Valley State College Herbarium when they were available. All plant community designations follow Munz and Keck (1959).

Aliso Canyon (Fig. 11). Major plant: Eurotia lanta (Pursh) Moq. This wash bottom was trapped near its confluence with the Santa Clara River, near the junction of Santiago Road and Soledad Canyon Road, two miles east of Acton. The habitat differs from the surrounding Pinyon-Juniper Woodland by virtue of its location in a dry stream bed. Fourteen traps were set here on the night of September 25, 1968. Four D. panamintinus and two Peromyscus sp. were captured.

Santiago Road (Fig. 12). Major plants:

Juniperus californica Carr.	Eriogonum fasciculatum Benth.
Yucca Whipplei Torr.	Tetradymia axillaris A. Nels.
Ephedra viridis Cov.	Salazaria mexicana Torr.

This trapping site, two miles east of Acton, is typical of the Pinyon-Juniper Woodland which extends westward through the San Gabriel Mountains along the course of the Santa Clara River. Sixty traps were set on the night of September 25, 1968, at the bases of

junipers lining the sides of a wash. Seven D. panamintinus and three Peromyscus sp. were captured in this locality.

Avenue N, Palmdale (Fig. 13). Major plants:

Yucca brevifolia Englem. Tetradymia axillaris A. Nels.

Ephedra viridis Cov. Grayia spinosa (Hook.) Moq.

This locality, two and one-half miles north of Palmdale, supported a Joshua Tree Woodland community. There was no creosote bush, Larrea divaricata, in evidence. Seventy-four traps were set on the night of December 19, 1968. Seven D. panamintinus and six D. merriami were captured.

Avenue C, Lancaster (Fig. 14). Major plants:

Atriplex lentiformis (Torr.) Wats.

Atriplex Parryi Wats.

This locality is typical of the Alkali Sink community covering localized areas of the Antelope Valley. The soil surface was impregnated with salts and had formed a crust. Rodents were captured near holes in small mounds of sand which had accumulated around clumps of brush. The saltbush, represented by several species of Atriplex, was the only plant found in the immediate vicinity. Seventy-four traps were set on the night of November 24, 1968. Seven D. merriami, one D. microps, and one D. panamintinus were taken. Two Peromyscus sp. and one Ammospermophilus leucurus were captured in the same trap line.

Mojave (Fig. 15). Major plants:

Yucca brevifolia Englem. Grayia spinosa (Hook.) Moq.

Larrea divaricata Cav. Haplopappus acradenius (Green) Blake

This area represents a transition between Joshua Tree Woodland and Creosote Bush Scrub in the foothills of the Tehachapi Mountains. This is the type locality for D. panamintinus mohavensis. Seventy-four traps were set on the night of February 22, 1969. Thirty-five D. panamintinus, two D. merriami, two Neotoma lepida, and five Peromyscus sp. were captured. Dipodomys panamintinus was by far the most abundant rodent in this locality. Measurements (Table 2) from 24 specimens from this locality agree with those given by Grinnell (1918) and suggest that this series approximates the type for the species.

Frazier Park (hillside) (Fig. 16). Major plants:

Artemisia tridentata Nutt. Quercus dumosa Nutt.

Chrysothamnus nauseosus (Pall.) Britton

This habitat is similar to that described for D. agilis perplexus by Carpenter (1966). It is Sagebrush Scrub, with the basin sagebrush, Artemisia tridentata, covering most of the ground. This habitat proved unproductive at the time of year trapped (February 13, 1969). Patches of snow still remained on the ground. Out of 54 traps set only one D. a. perplexus was captured. No other rodents were taken.

Frazier Park (road) (Fig. 17). Major plants:

Ephedra viridis Cov. Ceanothus cuneatus (Hook.) Nutt.

Artemisia tridentata Nutt.

This was a disturbed environment between Sagebrush Scrub and patches of Yellow Pine Forest. Twenty traps were set parallel to the road

on February 13, 1969. Two D. a. perplexus and three Peromyscus truei were captured.

Mulholland Highway (Fig 18). Major plants:

Adenostoma fasciculatum H. & A. Quercus dumosa Nutt.

Artemisia californica Iess.

This locality was typical of the Chaparral community. Tall, dense growth on moderate to steep slopes characterized the trapping area. Twenty traps were set along a trail through the brush paralleling the highway, and 14 more were set on a flat, sandy plateau at the base of a hill on the night of October 10, 1968. Each of these areas yielded one D. agilis agilis.

DISCUSSION

The Karyotype as a Systematic Tool

Baker and Patton (1967) have pointed out that due to the variability of mammalian karyotypes it is necessary to evaluate intra- and interspecific karyotypic variation in each group under study before use of the karyotype as a taxonomic and phylogenetic tool is justified. There is no karyotypic variation between the species of the genus Myotis which have been examined (Baker and Patton, 1967). In this case the karyotype merely confirms the existence of a close relationship between the species of the genus. In contrast, Patton and Dingman (1968) found seven different karyotypes in isolated populations of Thomomys bottae. Here no one karyotype is diagnostic for the species. The kangaroo rats studied here appear to parallel the situation in the closely related genus Perognathus, in which each species usually has a characteristic karyotype (Patton, 1967a, b). The only variations from this one karyotype-one species rule thus far reported within the genus are in the species Perognathus amplus (Patton, 1967b) and Perognathus goldmani (Patton, unpub.). A consideration of the usefulness of the karyotype as a taxonomic tool within the species of Dipodomys studied here seems warranted.

Chromosome polymorphism.- Chromosome polymorphism, the variation of the karyotype within a population, is a relatively rare occurrence in the Mammalia (Blanks and Shellhammer, 1968; Ford, Hammerton, and Sharman, 1957). In the harvest mouse, Reithrodontomys megalotis (Blanks and Shellhammer, 1968), and the silver fox,

Vulpes vulpes (Gustavsson and Sundt, 1967) chromosome polymorphism involves microchromosomes which vary in number. A constant complement of chromosomes of normal size is found in both species. Gustavsson and Sundt (1967) have suggested that these microchromosomes represent a stage in the elimination of genetically inert material from the karyotype. If these microchromosomes carried any significant genes, it would be difficult to see how a polymorphic population could survive.

Karyotypic variation within an interbreeding population is apparently extremely rare, and has never been reported in sciuromorph rodents. The absence of microchromosomes and of any intraspecific variation in karyotype suggests that chromosome polymorphism does not occur in the kangaroo rats I have sampled.

Chromosome polytypy.- Chromosome polytypy, the variation of the karyotype between populations, demes, or subspecies of the same species, is a frequent occurrence among rodents. In spite of the great amount of polytypy in the pocket gophers studied by Patton and Dingman (1968), there was no intra-populational variation (polymorphism) of the karyotype. Evidence thus far available indicates that, with the infrequent exception of chromosomal polymorphism, intra-populational variation of karyotype does not occur in mammals. If this is the case, then even one specimen would be valid for determining karyotype of a given population. Evidence of polytypy must be sought by sampling other populations of the same species. Indeed, due to lack of material, many species have been described karyotypically on the basis of one specimen. In

such cases the possibility of polymorphism or of polytypy cannot be eliminated without further study. Even well-sampled species may have isolated populations in which karyotypic evolution has taken place. Only future studies on hybrids can clarify the significance of karyotypic differences in relation to the biology of the species involved.

As large a sample as possible is desirable in establishing the karyotype of a population. Hybrids between populations of a polytypic species do yield intermediate karyotypes (Patton and Dingman, 1968; Wharman et al., 1969), and if such a specimen provides the only karyotype available for a species, erroneous conclusions can be drawn. Sampling in this study is sufficiently broad to suggest that the conclusions presented here are generally valid. I have examined five specimens of D. heermanni from three localities, six of D. agilis from three localities, and seventeen of D. panamintinus from four localities. Each animal had the karyotype characteristic of its species. Extreme ranges for the samples are 106 miles for D. heermanni, 50 miles for D. agilis, and 45 miles for D. panamintinus. The evidence indicates an absence of polytypy within the area studied. This does not exclude the possibility that more distant representatives of these species would yield different karyotypes, but the use of the karyotype as a taxonomic tool in the area I have considered appears to be valid. Lester (pers. comm.) has reported polytypy in D. microps, as has Patton (pers. comm.) in D. spectabilis; therefore future reports of polytypy in the

species I have studied would not be surprising in view of their extensive geographic range.

The kangaroo rats from Southern California seem to be conservative with respect to karyotype. Each species displays a distinctive and constant karyotype which is useful in clarifying the distributional and evolutionary relationships between them.

Comparison of D. a. agilis and D. panamintinus

Routine identification of these two species has been based upon, and no doubt will continue to be based upon, external morphology. Overlap does exist in the diagnostic characters, and in these cases one must resort to other information. Within the genus the shape of the maxillary arch is used extensively as a taxonomic character (Grinnell, 1922). However the morphology of the maxillary arch is variable within a population and it cannot be relied upon as a distinguishing feature. Pelage color of the southern-most representatives of D. panamintinus is as dark as that of lighter specimens of D. agilis. Age and environmental differences lead to variations in the measurements which mask the identity of specimens. The karyotype offers a character which is more consistent for a species than morphological data.

Since the karyotype of D. agilis consists of almost all bi-armed pairs, whereas that of D. panamintinus contains one-half uni-armed pairs, it may be used as a positive means of differentiating these two species.

Distributional Considerations

Utilizing the karyotype I was able to verify the conclusion

suggested by morphological data; the kangaroo rats I trapped in Soledad Canyon were D. panamintinus rather than D. agilis, as current range maps imply. This population represents an extension of the previously known range of this species seven miles southward into the San Gabriel Mountains (Fig. 1). This trapping site does not represent the farthest extension of the Pinyon-Juniper Woodland into these mountains. This habitat continues westward along the course of the Santa Clara River beyond Solemint Junction. Thomas S. Kelly has taken a specimen of Dipodomys (No. 746, Vertebrate Collection, San Fernando Valley State College) from Rye Canyon, 1.2 miles east of the Bakersfield Freeway, near Castaic Junction, in a similar habitat even farther down the Santa Clara River. Measurements place this specimen into the species D. panamintinus, although it is some 20 miles from the nearest known record of D. panamintinus. Since this specimen is identical in coloration and skull morphology to my specimens from Santiago Road, I consider it to be D. panamintinus. Therefore, D. panamintinus probably occurs in the vicinity of Castaic Junction, farther west in the Pinyon-Juniper Woodland than my trapping sites indicate.

The desert wash habitat in the bed of the river and the Pinyon-Juniper Woodland on the surrounding slopes provide a habitat atypical for D. agilis agilis, but one which has been reported elsewhere (Vaughn, 1954) for D. panamintinus. The presence of this habitat and the absence of competition have allowed occupation of this area by D. panamintinus as far southwest as Acton, and probably as far west as Castaic Junction. This habitat has become an avenue of

penetration for D. panamintinus into areas considered the exclusive range of D. agilis agilis.

D. agilis agilis: Ecological Considerations

D. agilis agilis is characteristic of ground "clothed with an open type of chaparral," and "lives, in places, on sandy flats without any bushes, sometimes in open washes," and is found on both steep slopes and open ground (Grinnell, 1933:163). As mapped by Grinnell (1922), and Hall and Kelson (1959), this subspecies occurs in the coastal ranges of Southern California from Santa Barbara County southwest to Orange County, and extends inland to the extreme western parts of San Bernardino and Riverside Counties. A comparison with the map of natural vegetation of California presented by Burcham (1957) shows that this range coincides with the range of the Chaparral and Coastal Sage Scrub communities within the latitudinal limits of the subspecies. MacMillen (1964) has reported that D. a. agilis occurs in open areas in dense vegetation in eastern Los Angeles County. MacMillen's trapping area was a mixture of Chaparral and Coastal Sage Scrub communities. This subspecies has a home range of 0.82 acres (MacMillen, 1964) but this can vary with habitat. The limited power of digging in the kangaroo rats limits them to areas of loose soils (Grinnell, 1922:31), and as a result their burrows are often located in sandy areas within the Chaparral community.

D. agilis agilis is, therefore, an animal occurring primarily in the more hydric Chaparral of the coastal mountains of Southern California. Its absence from the Pinyon-Juniper Woodland along the

Santa Clara River can be attributed to the absence of a suitable habitat. The limitation of this subspecies by the Basin Sagebrush community of the Tehachapi Mountains can similarily be explained. In the latter case the habitat with a dense cover of tall shrubs is similar enough to have allowed occupation by another subspecies of Dipodomys agilis.

D. agilis perplexus: Distributional Considerations

The distribution ranges on the map (Fig. 2) were taken from Grinnell (1922) and are identical to those given in Hall and Kelson (1959), except for the range of D. agilis perplexus. The range of the eastern population of D. a. perplexus was determined from the locations given by Vaughn (1954). Hall and Kelson (1959) illustrate a corridor linking the population of D. a. perplexus in the Tehachapi Mountains to that in the San Gabriel and San Bernardino Mountains. Since the northern-most extension of the range of D. a. agilis in Los Angeles County is about 15 miles northeast of the site at Elizabeth Lake, 3,400 ft, any connection between the two populations of D. a. perplexus through the western San Gabriel Mountains is precluded. The corridor linking the two populations of D. a. perplexus must then include the towns of Pearblossom, Palmdale, Lancaster, and Willow Springs; i.e., it must comprise a path twelve miles wide through the center of the Antelope Valley.

According to Grinnell (1933:163) this subspecies "inhabits gravelly slopes clothed with chaparral." Vaughn (1954) found D. a. perplexus common in stands of basin sagebrush, often surrounded by unsuitable habitat. Vaughn states that this subspecies did not

penetrate nearby patches of Chaparral; i.e., Chaparral in the sense of Munz and Keck (1949). No D. a. perplexus has ever been reported from the Antelope Valley. My observations of the habitat available on the floor of this valley while trapping in the area lead me to conclude that the occurrence of D. agilis perplexus in the Antelope Valley is extremely improbable. Therefore, there can be no connection between the eastern and western populations reported for D. agilis perplexus. The range of this subspecies is incorrect in Hall and Kelson (1959) and the connection between the two populations should be deleted.

D. agilis perplexus: Ecological Considerations

Both Vaughn (1954) and Carpenter (1966) report that D. a. perplexus inhabits stands of basin sagebrush or brush-covered areas within the Yellow Pine Forest at higher elevations. I visited the type locality for D. a. perplexus, Walker Basin, Kern Co., and found the unaltered land around the edge of the basin covered with rabbit-brush (Chrysothamnus nauseosus var. consimilis) which led into a Yellow Pine Forest. Munz and Keck (1959) describe this variety of rabbit-brush as a Great Basin plant of the Sagebrush Scrub community. The Sagebrush Scrub community characterized my trapping site for this subspecies. This subspecies of D. agilis is adapted to a cooler, more hydric environment supporting a westward expansion of Sagebrush Scrub at lower elevations and mixed with Yellow Pine Forest at higher elevations. In contrast, D. agilis agilis is adapted to the warmer, more xeric Chaparral of the southern coastal mountains. Hence present information suggests that these subspecies

of D. agilis have different ecological requirements.

Vaughn (1954) reports intergradation between D. agilis agilis and D. agilis perplexus in the region of Devore, San Bernardino Co. It may be possible that his D. a. perplexus population is in reality a variant of D. a. agilis not related to the D. a. perplexus population of the Tehachapi Mountains. Since the reported populations of D. a. perplexus seem to be ecologically distinct from D. a. agilis (according to Vaughn), then two possibilities exist: 1) the eastern population represents an isolated segment of the currently named D. agilis perplexus which was formerly connected with the Tehachapi population, but due to a change in habitat is now restricted to the higher elevations of the San Bernardino Mountains; 2) the eastern population represents a population derived from D. agilis agilis which has become adapted to a habitat different from that of D. a. agilis and similar to that of D. a. perplexus of the Tehachapi Mountains, and has responded morphologically to this habitat in a manner parallel to that of D. a. perplexus. In this latter case Vaughn's specimens may have to be considered a new subspecies. This situation deserves further study.

Distribution of Dipodomys microps

A specimen of a five-toed kangaroo rat taken from the floor of the Antelope Valley had a diploid number of 60 and a karyotype entirely of bi-armed chromosomes. This animal proved to be Dipodomys microps. The only previous report of D. microps south of Olancha, Inyo Co., was an isolated population at Victorville represented by seven specimens (Grinnell, 1922). This new locality for D. microps

represents a westward extension of the range of this species of about 50 miles. I do not consider my trapping site the limit of the range of this species. Grinnell (1933:164) states that this species "inhabits dry sandy ground, sparsely grown to desert shrubbery such as saltbush." In the Alkali Sink where I trapped the specimen the ubiquitous plant was Atriplex, the saltbush. These alkali flats extend a few miles westward beyond Highway 14. It would not be surprising if D. microps were found wherever the alkaline conditions of the soil limited the vegetation to saltbush. The occurrence of this habitat appears to determine the distribution of this species of kangaroo rat.

Lan A. Lester (Los Angeles County Museum of Natural History) has taken D. microps near Randsburg, 50 miles northeast of my site and between the two previously reported marginal records for the species. His specimens were also taken in an Alkali Sink habitat dominated by Atriplex. Lester has also prepared chromosome slides of two specimens of D. microps from widely separated localities. One animal had a karyotype identical to that of my specimen, consisting of 60 bi-armed chromosomes, whereas the other had a diploid number of 60 but a karyotype containing approximately twelve pairs of acrocentric chromosomes. The latter animal was taken from a habitat different from that typical of D. microps, and in view of its karyotype, it may represent an evolutionarily distinct population. Further studies by Lester should clarify the systematic position of these specimens.

It seems reasonable to suppose that in the recent geologic past

both the population at Victorville and that represented by my Lancaster specimen were continuous with the population in the Owens Valley. Dipodomys microps persists in those low-lying areas where the Alkali Sink community remains. The dispersal of a species with a discontinuous distribution, such as D. microps or D. deserti (Grinnell, 1933), requires suitable habitats to support intervening- if only transitory- populations during periods of dispersal. Hence, the presence of D. microps in the Antelope Valley requires previous connections with the population of the Owens Valley through areas characterized at some time by an Alkali Sink habitat.

Evolutionary Implications

Although the data presented here are insufficient for the presentation of any detailed evolutionary scheme within Dipodomys, they do allow some speculation about intergroup relations. Lidicker (1960) recently revised the groups within the genus, recognizing the following groups: ordii, heermanni, microps, spectabilis, philipsi, and merriami. The largest of these, the heermanni group, contains 10 of the 21 species recognized by Lidicker. Lidicker further divides the heermanni group into two subgroups: a broad-faced Subgroup A, which includes the species heermanni, ingens, gravipes, panamintinus, and stephensi; and a narrow-faced Subgroup B, which includes the species agilis, venustus, elephantinus, paralius, and peninsularis. The broad-faced character is a result of greater spread of the maxillary arches, greater width of the maxillary arch, greater lateral projection of the maxillary arch, and sharper postero-external angle of the maxillary arch when compared to

narrow-faced individuals. Two extremes are illustrated in Fig. 10.

Heermanni Subgroup A.- D. heermanni and D. panamintinus, considered closely related on morphological grounds, are characterized by a karyotype consisting of about half bi-armed and half uni-armed chromosomes (Figs. 4-7). Close relationship between these two species is confirmed by karyotypic evidence.

Although this project was primarily concerned with clarifying the distributional relationships of D. agilis and D. panamintinus in the southwestern Antelope Valley, I also had an opportunity to examine specimens of three subspecies of D. heermanni. Karyotypes were identical for all. One subspecies examined, D. heermanni morroensis, was formerly considered specifically distinct (D. morroensis). While possession of the same karyotype as other subspecies of D. heermanni does not exclude the possibility that this restricted population is a separate species, those who would resurrect D. morroensis will find no support for their case in karyotypic data.

Heermanni Subgroup B.- The karyotype of D. agilis differs markedly from those of D. heermanni and D. panamintinus in that it has only two pairs of uni-armed chromosomes (Figs. 2, 3). This agrees with the accepted view, which considers D. agilis less closely related to D. heermanni and D. panamintinus than these two are to one another.

Significance of intrageneric groups.- The arrangement of the species of Dipodomys into "natural" groups has no current taxonomic standing; it merely reflects possible evolutionary relationships as interpreted by various investigators. Opinions have differed

regarding the closeness of the relationship between the narrow-faced and broad-faced members of the heermanni group. These subgroups may be as distinct from one another as the group is from other groups within the genus. Since the narrow-faced character is employed to separate other groups from one another, my view is that the narrow-faced members of the heermanni group should be recognized as a separate group. However, the problem of nomenclature is not so important as is the recognition of the relationships as they exist in nature. Both the division of the heermanni group into subgroups and the establishment of a separate narrow-faced group serve to recognize the existing divergence and differ only in emphasis.

Lackey (1967) considers the narrow-faced group to have arisen from heermanni stock in Baja California, and from there to have spread north to the present limit of San Francisco Bay. At present insufficient karyotypes of species within this group are available to speculate on this subject. I hope that information will become available in the future which will clarify the evolutionary history of this group of rodents.

Distribution and Habitat

It seems advisable to consider more carefully the habitat occupied by a species as well as the marginal records when attempting to determine the range of that species. It is not unusual to find a species occurring many miles from its known range if a suitable habitat exists and if, at some time, the species has had access to that habitat. The mapped range of a species should not include vast areas obviously unsuitable for that species.

Since Southern California is a physiographically complex region, it is not surprising that the mammalian fauna should be diverse. Hall and Kelson (1959: Vol. I, xxviii) point out that the high degree of relief in the southwestern United States "has resulted in a larger number of subspecies than any other continental area of equal size in the world." The physiography and climate of Southern California quite literally place mountains, desert, and seashore adjacent to one another. Thus a great variety of habitats are found in a restricted geographic area, and this has led to interdigitation of species' ranges and discontinuous distributions. For example, the valley of the Santa Clara River provides an avenue of penetration for D. panamintinus westward from its usual range. Likewise, other species may be expected to occur far from their known ranges along similar avenues of suitable habitat. It is hoped that the application of new systematic tools will help to clarify the distribution of the flora and fauna of this complex region.

CONCLUSIONS

1. The karyotype can successfully be used as a systematic tool for identifying closely related species if those species possess karyotypes distinct from one another, and if the karyotype within a species is constant over the range considered.

2. The range of D. panamintinus mohavensis should be extended from its current limit of the floor of the Antelope Valley southward to the vicinity of Acton. The range assigned to this species in this area should be restricted to semi-desert habitats and Pinyon-Juniper Woodland. Material in the collection of San Fernando Valley State College suggests that D. panamintinus may occur farther down the course of the Santa Clara River, possibly as far as Castaic Junction.

3. The range of D. microps should be extended westward to at least the region of the intersection of Sierra Highway and Avenue C, north of Lancaster, Los Angeles County. The range of D. microps should be limited to areas of Alkali Sink habitat, of which this species is characteristic.

4. The connection between the eastern and western populations of D. agilis perplexus across the floor of the Antelope Valley should be deleted.

5. Evidence from this study supports the current division of the heermanni group of Dipodomys into Subgroups A and B. This study adds karyotypic evidence to the cranial evidence already supporting this division.

6. Observed habitat differences seem to account for the distribu-

tion of the forms of kangaroo rats studied here. Future considerations of range should therefore be correlated with the availability of a suitable habitat for the animal involved.

Table 1. Karyotypic analysis of eight subspecies of Dipodomys. The number under the word autosomes refers to the number of homologous pairs. M = metacentric, SM = submetacentric, A = acrocentric, and N.A. = number of major arms.

Table 1. Karyotypic Analysis

Species	♂	♀	2n	Autosomes M	Autosomes SM	Autosomes A	Sex X	Sex Y	N.A.
heermanni group									
Subgroup A									
Dipodomys heermanni morroensis	2	1	64	14	-	17	M	SM	90
Dipodomys heermanni arenae	-	1	64	14	-	17	M	-	90
Dipodomys heermanni goldmani	-	1	64	14	-	17	M	-	90
Dipodomys panamintinus mohavensis	5	12	64	14	2	15	M	SM	94
Subgroup B									
Dipodomys agilis agilis	2	1	62	22	6	2	M	A	116
Dipodomys agilis perplexus	1	2	62	22	6	2	M	A	116
microps group									
Dipodomys microps microps	-	1	60	14	16	-	?	?	116
merriami group									
Dipodomys merriami merriami	-	1	52	18	8	-	?	?	100

Table 2. Summary of morphological data gathered for Dipodomys agilis agilis, Dipodomys agilis perplexus, Dipodomys panamintinus mohavensis (Santiago Road), Dipodomys panamintinus mohavensis (Palmdale), D. panamintinus mohavensis (Lancaster), and Dipodomys panamintinus mohavensis (Mojave).

Table 2. Summary of Morphological Data

Character	*D. a. agilis* 13 specimens		*D. a. perplexus* 3 specimens		*D. p. mohavensis* Santiago Rd. 11 specimens	
	Range	Mean	Range	Mean	Range	Mean
Total length	273-316	289	272-300	291	276-300	286
Head and body length	97-129	114	120	120	110-134	120
Tail length	162-189	175	152-180	169	157-177	168
Hind foot length	40-45	41.8	41-46	44.3	42-46	44.0
Ear length from notch	15-19	16.5	17-18	17	13-16	14.3
Ear length from crown	-	-	15-16	15	13-14	13.2
Greatest length of skull	37.9-40.2	39.5	38.2-40.6	39.7	38.9-41.5	39.7
Greatest breadth of skull	23.9-24.8	24.1	23.5-24.5	23.9	23.8-24.6	24.1
Spread of maxillary arches	19.7-21.4	20.7	20.6-21.3	21.0	21.9-24.0	22.9
Width of maxillary arch	4.4-4.9	4.6	4.6-4.8	4.7	4.9-5.7	5.2
Nasal length	13.0-14.8	14.1	14.4-14.9	14.6	14.5-15.9	15.0
Nasal width	3.5-4.2	3.8	3.8-3.9	3.8	3.5-4.2	3.9

Character	*D. p. mohavensis* Palmdale 7 specimens		*D. p. mohavensis* Lancaster 1 specimen	*D. p. mohavensis* Mojave 24 specimens	
	Range	Mean		Range	Mean
Total length	272-299	277	266	268-307	284
Head and body length	111-127	119	110	100-129	114
Tail length	157-178	164	156	162-178	171
Hind foot length	40-45	42.0	39	42-45	43.4
Ear length from notch	14-15	14.5	14	14-16	14.3
Ear length from crown	12-13	12.8	12	11-13	11.9
Greatest length of skull	38.4-40.8	38.8	35.7	38.5-41.2	39.7
Greatest breadth of skull	23.1-24.5	23.8	22.0	23.4-25.0	24.0
Spread of maxillary arches	21.0-24.0	22.2	21.2	22.0-23.6	22.9
Width of maxillary arch	5.1-5.8	5.3	4.8	4.8-5.6	5.2
Nasal length	14.5-15.7	14.8	13.6	14.7-16.0	15.2
Nasal width	3.6-4.0	3.7	3.5	3.3-4.2	3.8

Table 3. Summary of morphological data gathered for Dipodomys panamintinus mohavensis (composite), Dipodomys heermanni morroensis, Dipodomys heermanni arenae, Dipodomys microps microps, and Dipodomys merriami merriami.

Table 3. Summary of Morphological Data

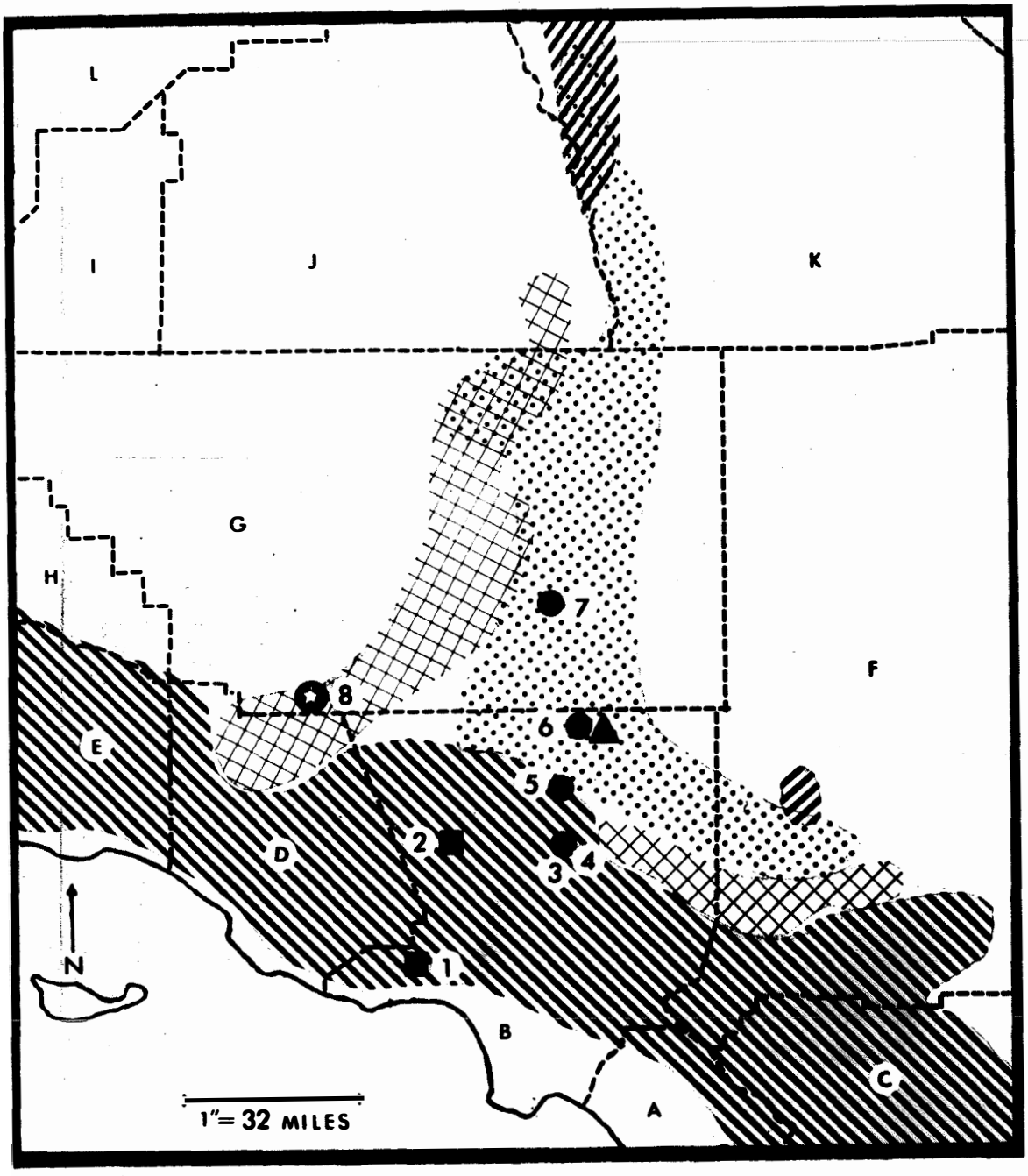
Character	D. p. mohavensis composite 43 specimens		D. h. morroensis 3 specimens		D. h. arenae 1 specimen
	Range	Mean	Range	Mean	
Total length	266-307	283	267-305	282	298
Head and body length	100-134	116	108-128	115	116
Tail length	156-178	169	158-177	167	182
Hind foot length	39-46	43.2	40-42	40.6	43
Ear length from notch	13-16	14.3	14-17	15.3	15
Ear length from crown	11-14	12.6	12	12	13
Greatest length of skull	35.7-41.2	39.4	36.6-39.1	37.9	38.8
Greatest breadth of skull	22.0-25.0	23.8	22.2-23.3	22.9	23.8
Spread of maxillary arches	21.0-24.0	22.8	21.0-22.6	21.7	21.7
Width of maxillary arch	4.8-5.8	5.2	4.7-5.6	5.0	5.1
Nasal length	13.6-16.0	15.0	13.6-14.3	14.0	14.2
Nasal width	3.3-4.2	3.8	3.8-4.0	3.9	3.9

Character	D. m. microps 1 specimen	D. m. merriami 1 specimen
Total length	267	242
Head and body length	111	95
Tail length	156	147
Hind foot length	39	38
Ear length from notch	13	13
Ear length from crown	11	11
Greatest length of skull	35.7	35.5
Greatest breadth of skull	22.5	22.5
Spread of maxillary arches	17.9	18.6
Width of maxillary arch	3.4	4.5
Nasal length	12.2	13.0
Nasal width	3.5	3.0

Fig. 1. Ranges for the kangaroo rats studied from Southern California are indicated by cross-hatching and stippling. All ranges are taken from Grinnell (1922) except for the eastern division of the range of D. agilis perplexus, which is taken from Vaughn (1954). Trapping localities are indicated by symbols. In the index given below the letters refer to counties and the numbers refer to trapping sites.

A. Orange County
B. Los Angeles County
C. Riverside County
D. Ventura County
E. Santa Barbara County
F. San Bernardino County
G. Kern County
H. San Luis Obispo County
I. Kings County
J. Tulare County
K. Inyo County
L. Fresno County

1. Near Mulholland Highway
2. Near Saugus
3. In Aliso Canyon
4. On Santiago Road
5. At Avenue N, Palmdale
6. At Avenue C, Lancaster
7. Near Mojave
8. Near Frazier Park



■ Dipodomys agilis agilis

★ Dipodomys agilis perplexus

● Dipodomys panamintinus mohavensis

▲ Dipodomys microps microps

Fig. 2. Karyotype of Dipodomys agilis agilis (female, BAC 51).

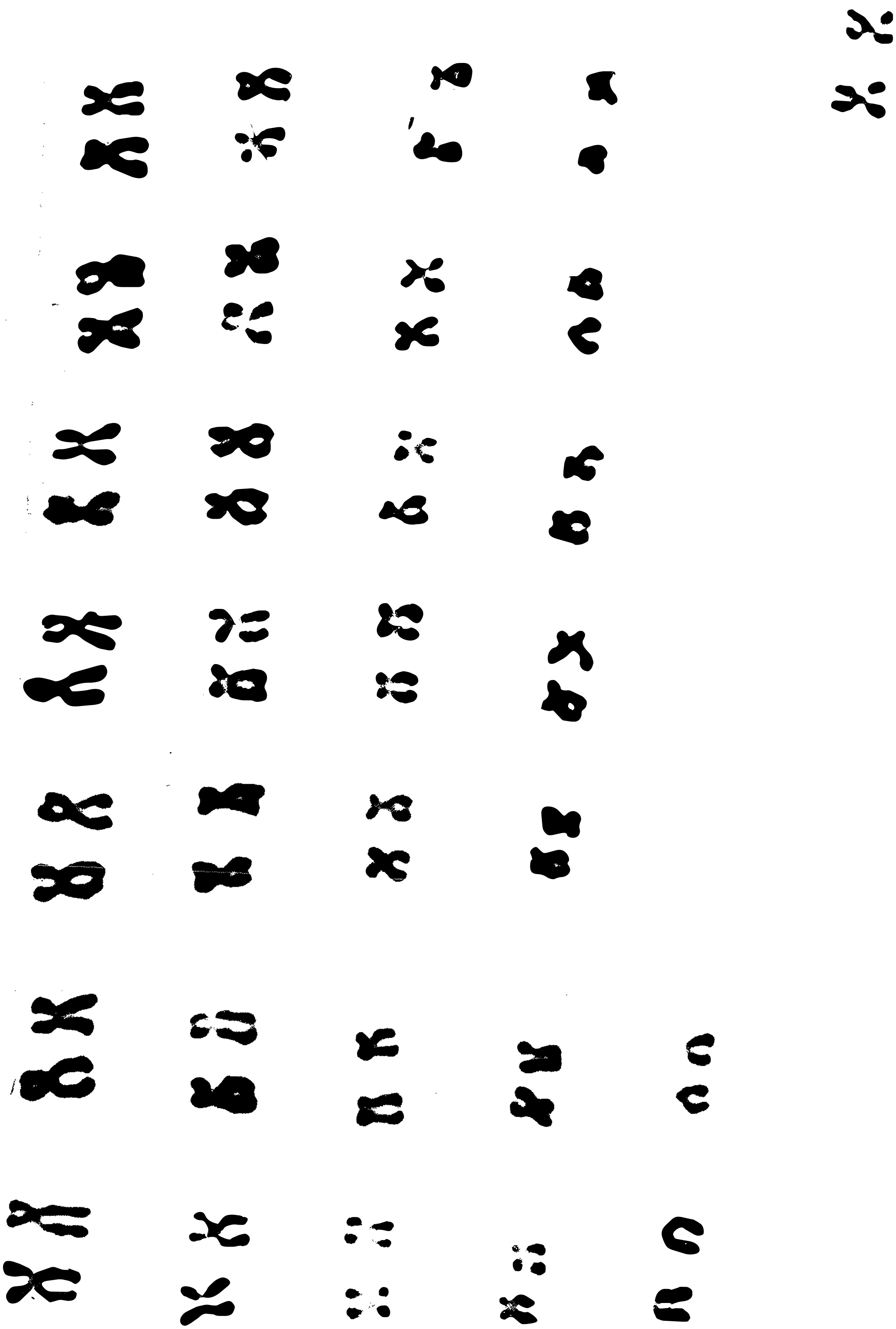


Fig. 3. Karyotype of Dipodomys agilis perplexus (male, BAC 56).

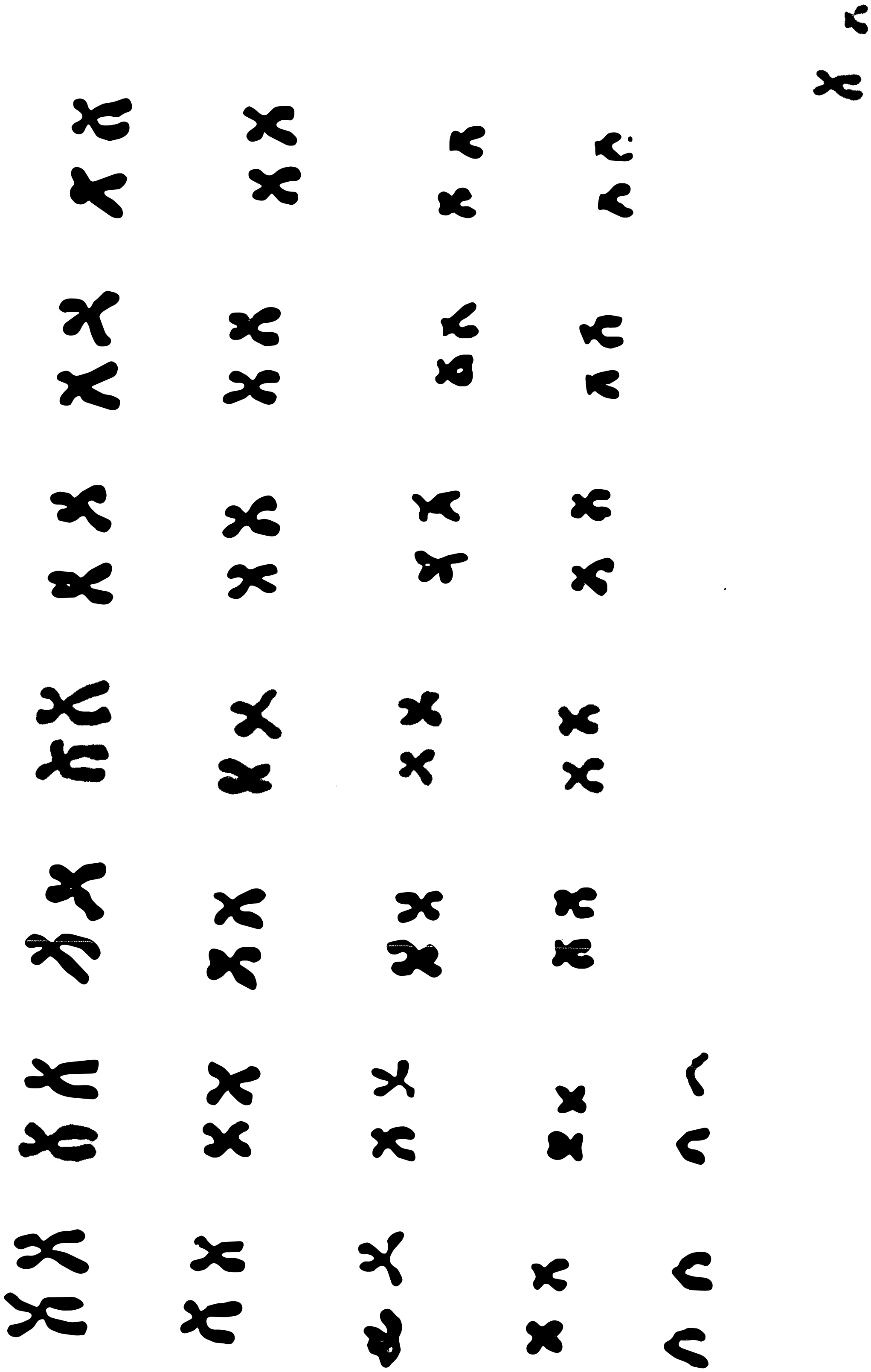


Fig. 4. Karyotype of Dipodomys panamintinus mohavensis (male, BAC 45).

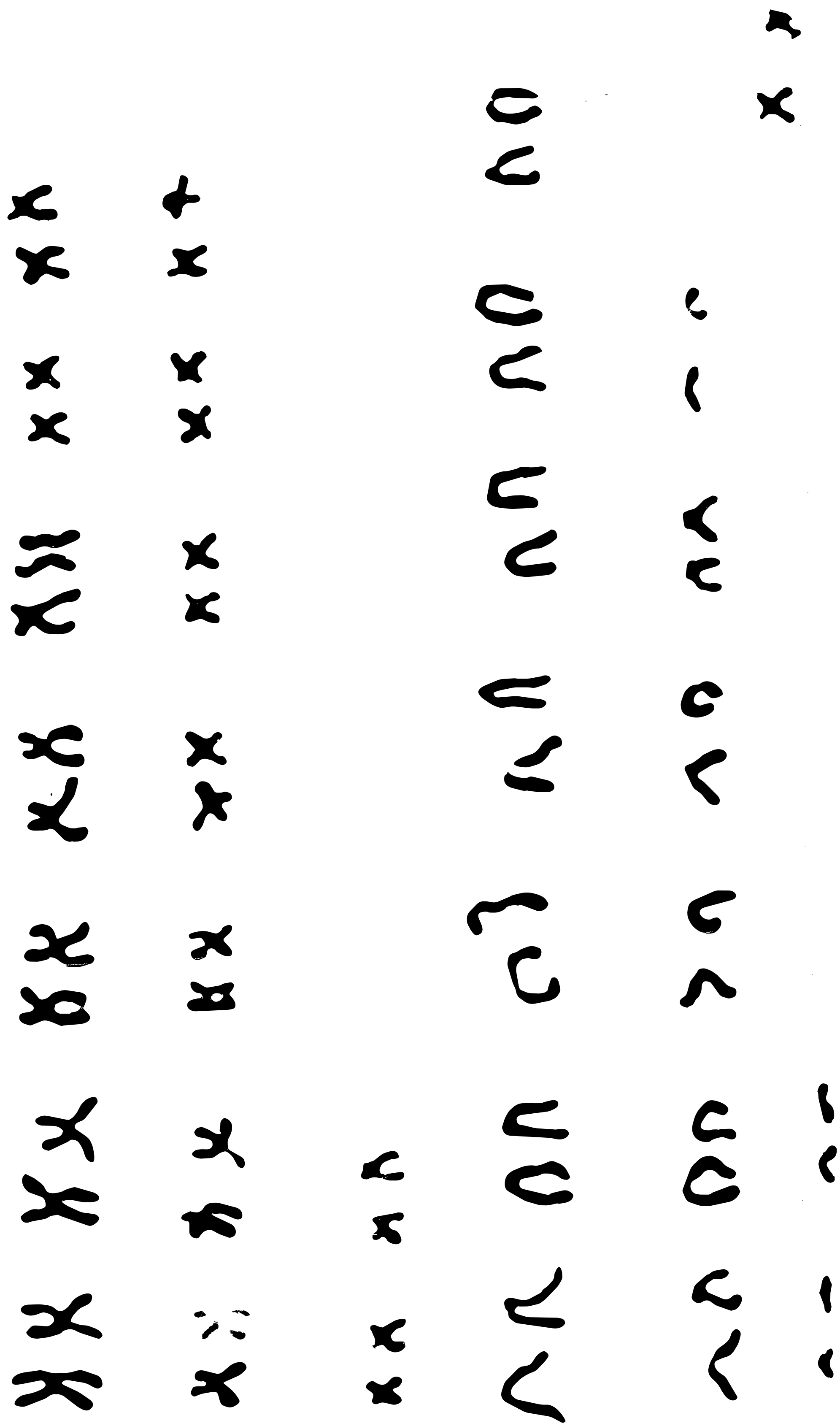


Fig. 5. Karyotype of Dipodomys heermanni morroensis (female, BAC 36).

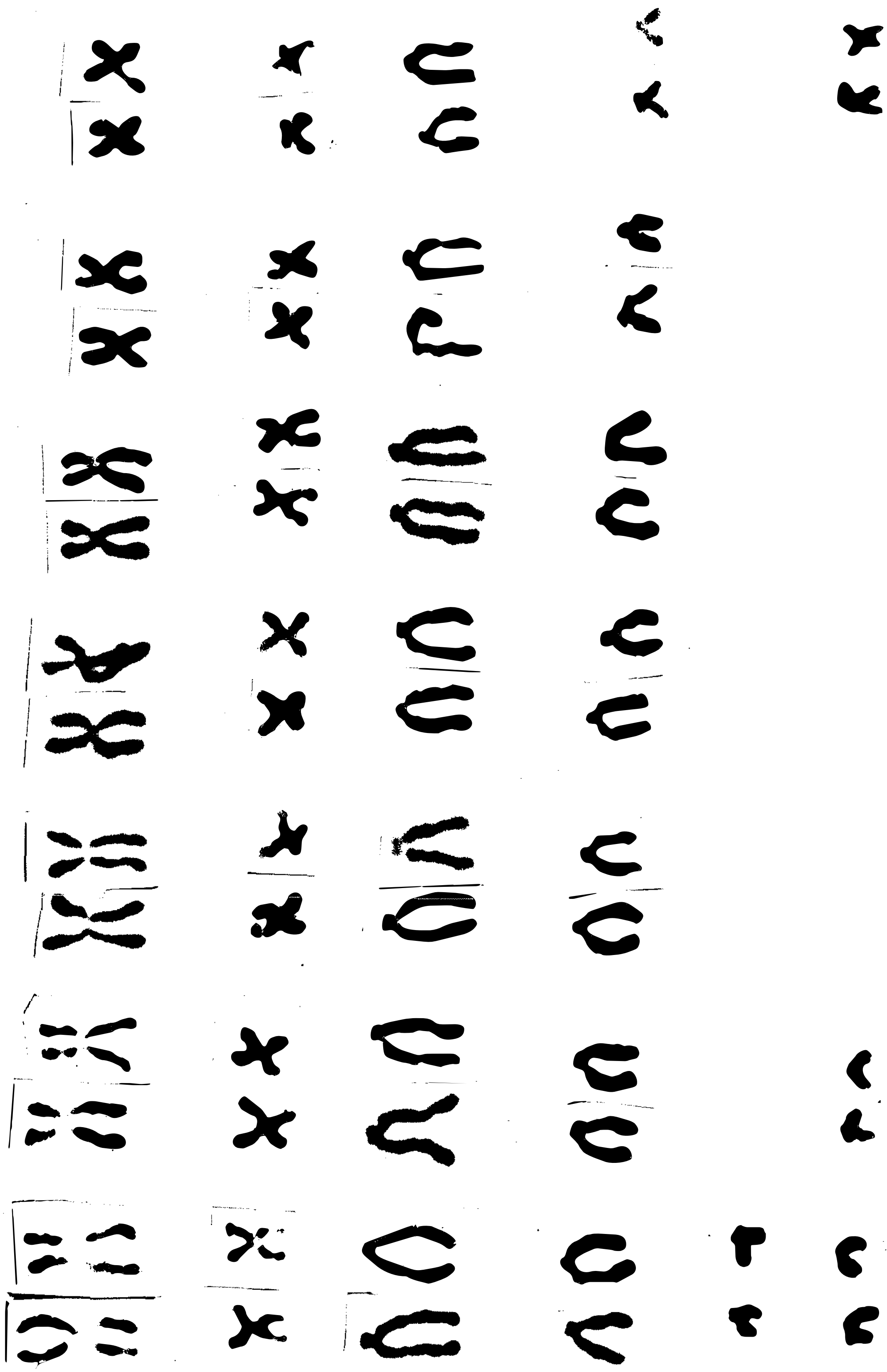


Fig. 6. Karyotype of Dipodomys heermanni arenae (female, BAC 54).

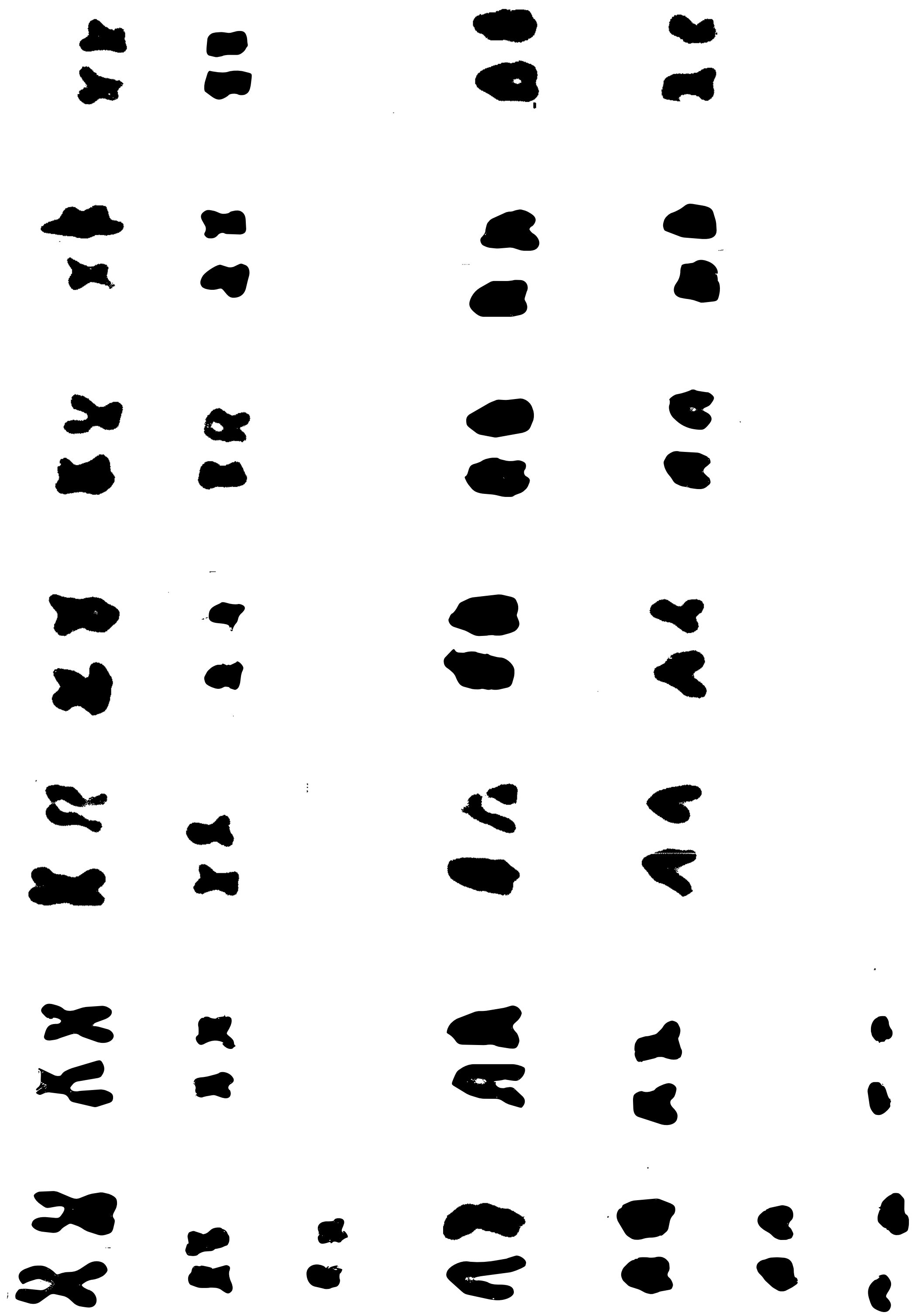


Fig. 7. Karyotype of Dipodomys heermanni goldmani (female TK 182).

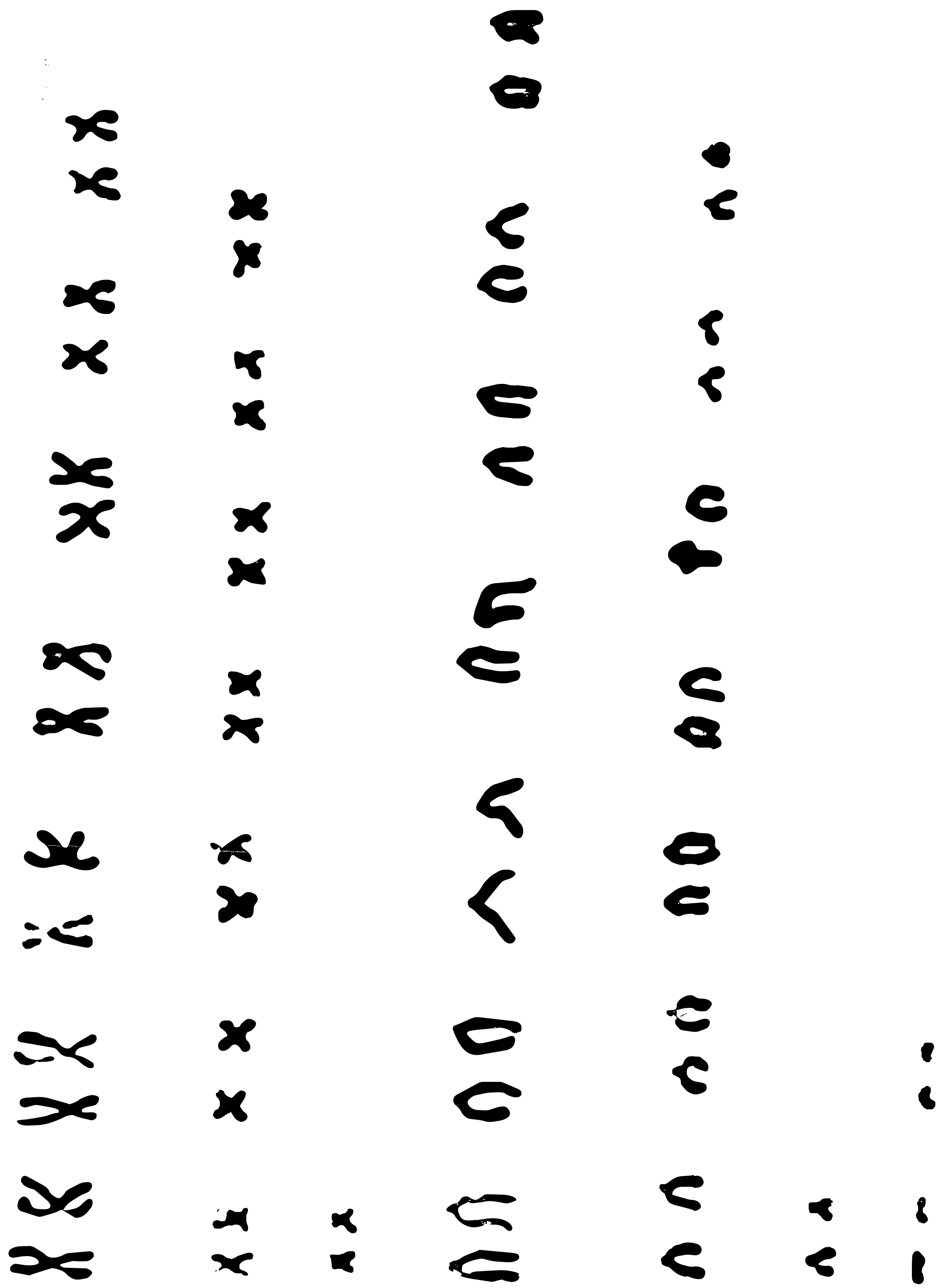


Fig. 8. Karyotype of Dipodomys microps microps (female, BAC 41).

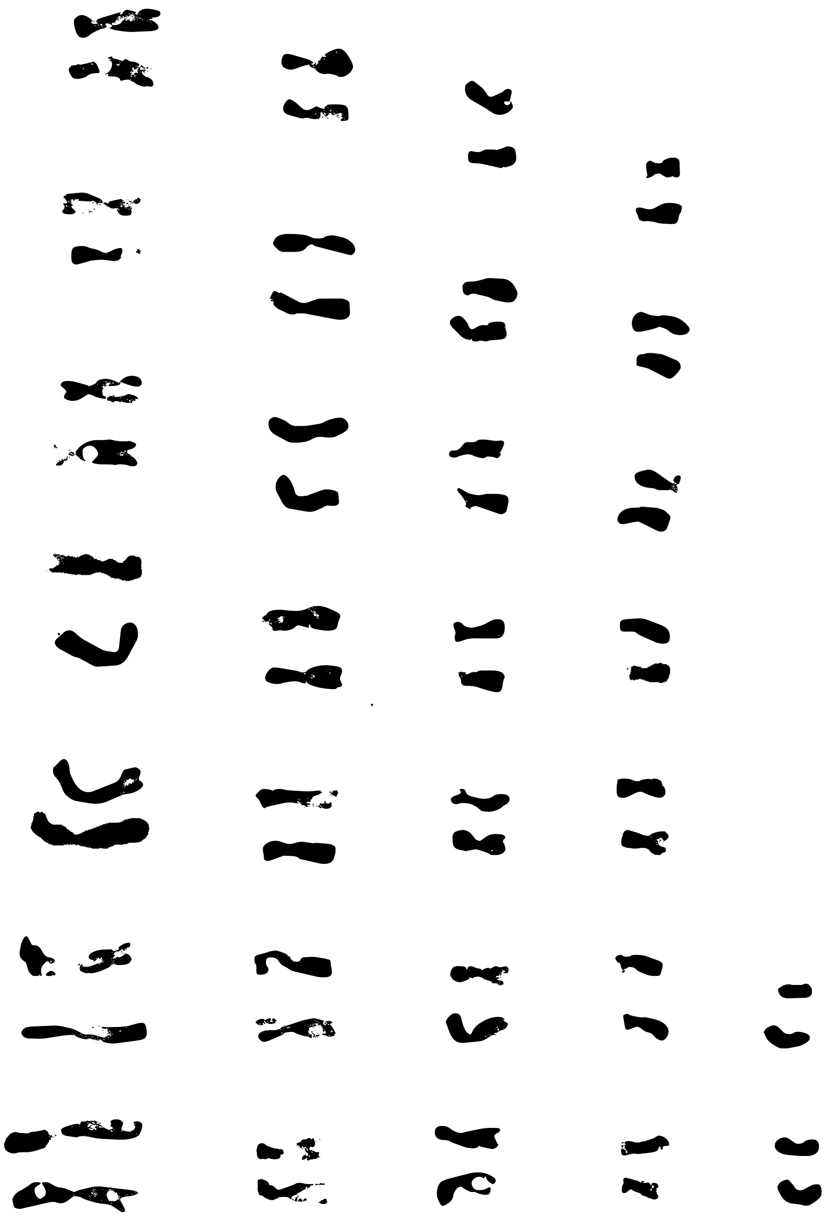


Fig. 9. Karyotype of Dipodomys merriami merriami (female, BAC 39).

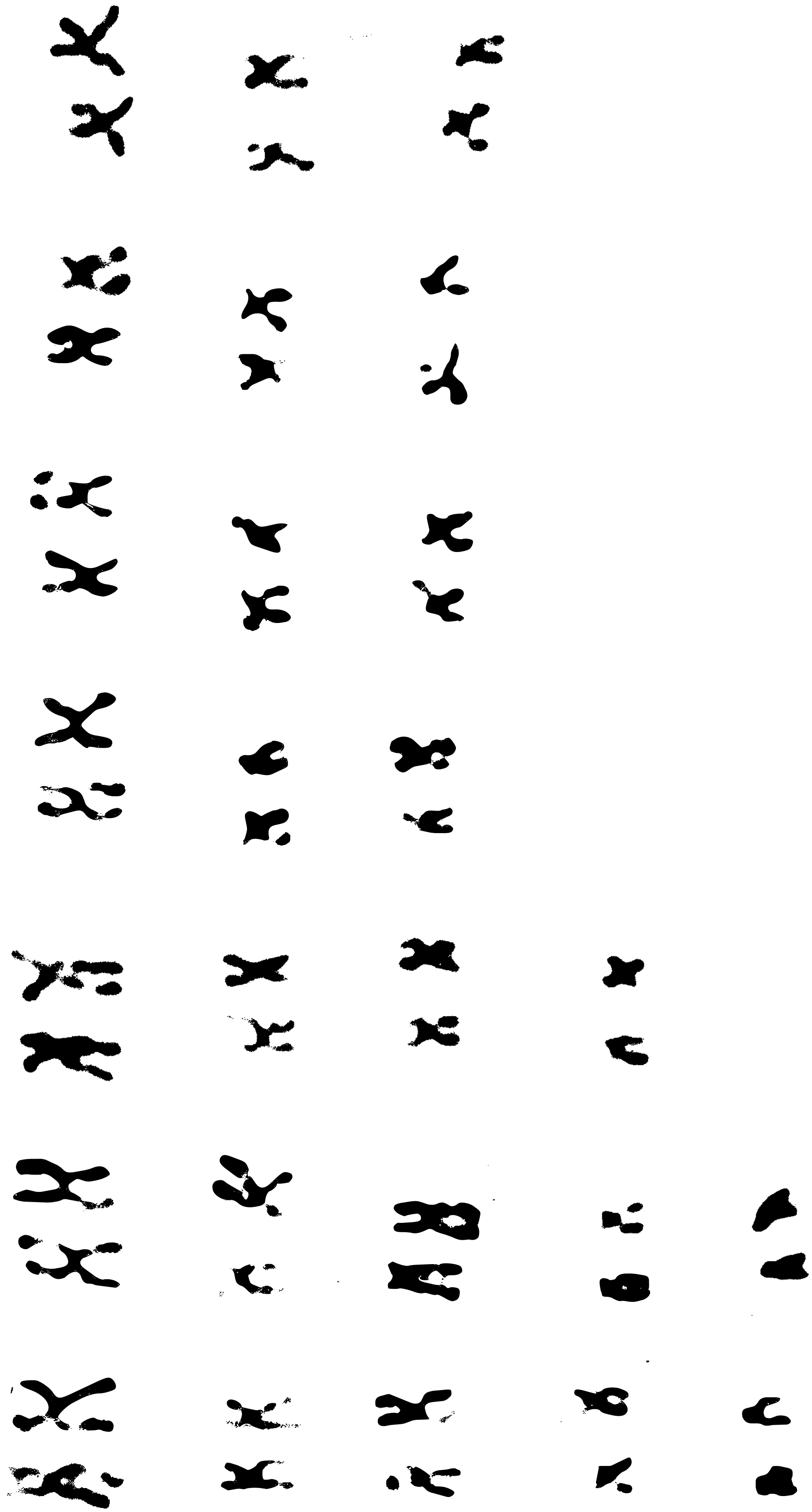


Fig. 10. Illustration of broad-faced and narrow-faced kangaroo rat skulls.

Top.- Skull of D. merriami merriami (BAC 39) illustrating the broad-faced character. Arrow indicates the width of the maxillary arch at middle.

Bottom.- Skull of D. microps microps (BAC 41) illustrating the narrow-faced character. Arrow indicates the width of the maxillary arch at middle.

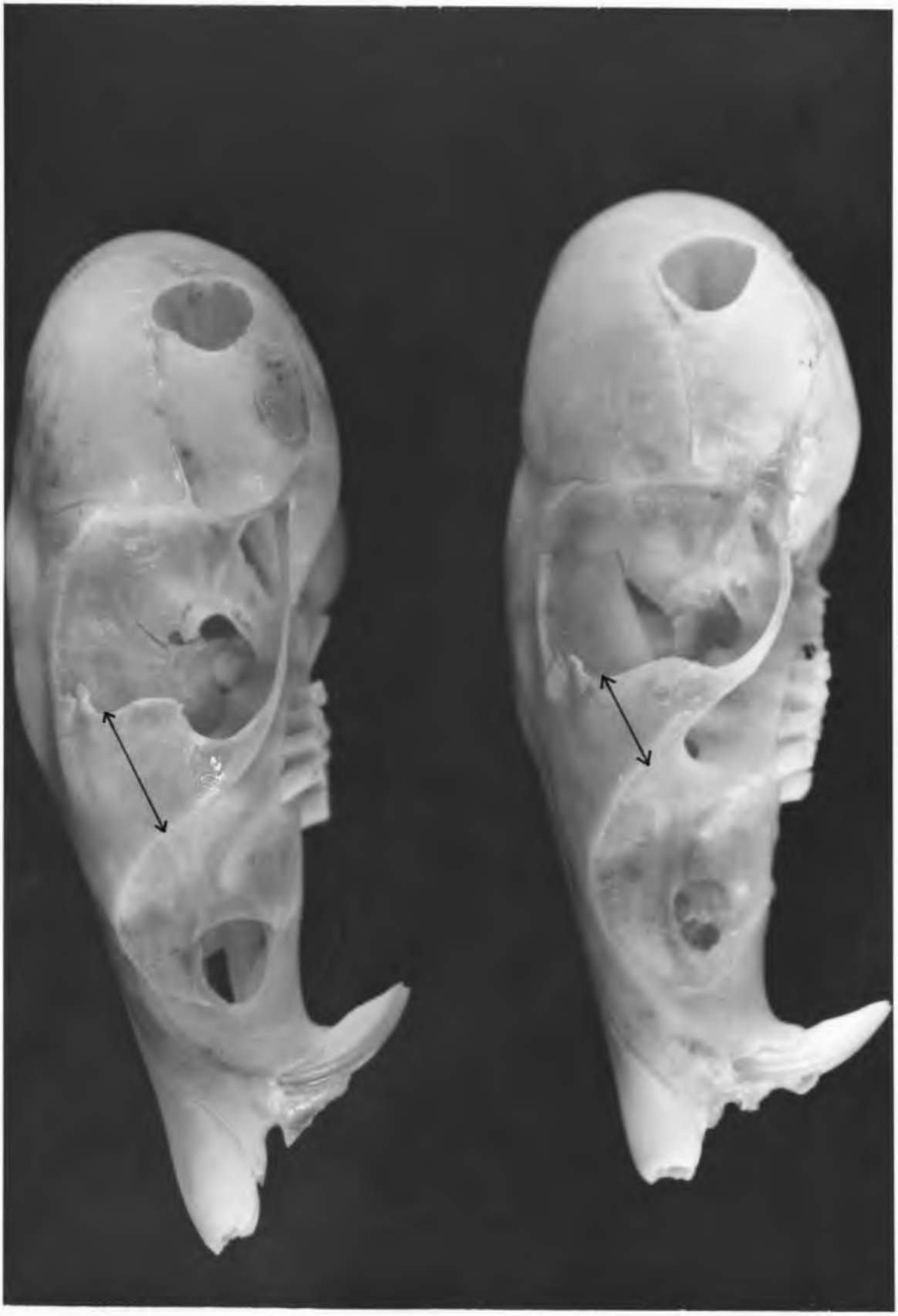


Fig. 11. Trapping site at Aliso Canyon. Desert wash habitat of Dipodomys panamintinus.

Fig. 12. Trapping site on Santiago Road. Pinyon-Juniper Woodland habitat of Dipodomys panamintinus.

Fig. 13. Trapping site at Avenue N, Palmdale. Joshua Tree Woodland habitat of Dipodomys panamintinus and Dipodomys merriami.

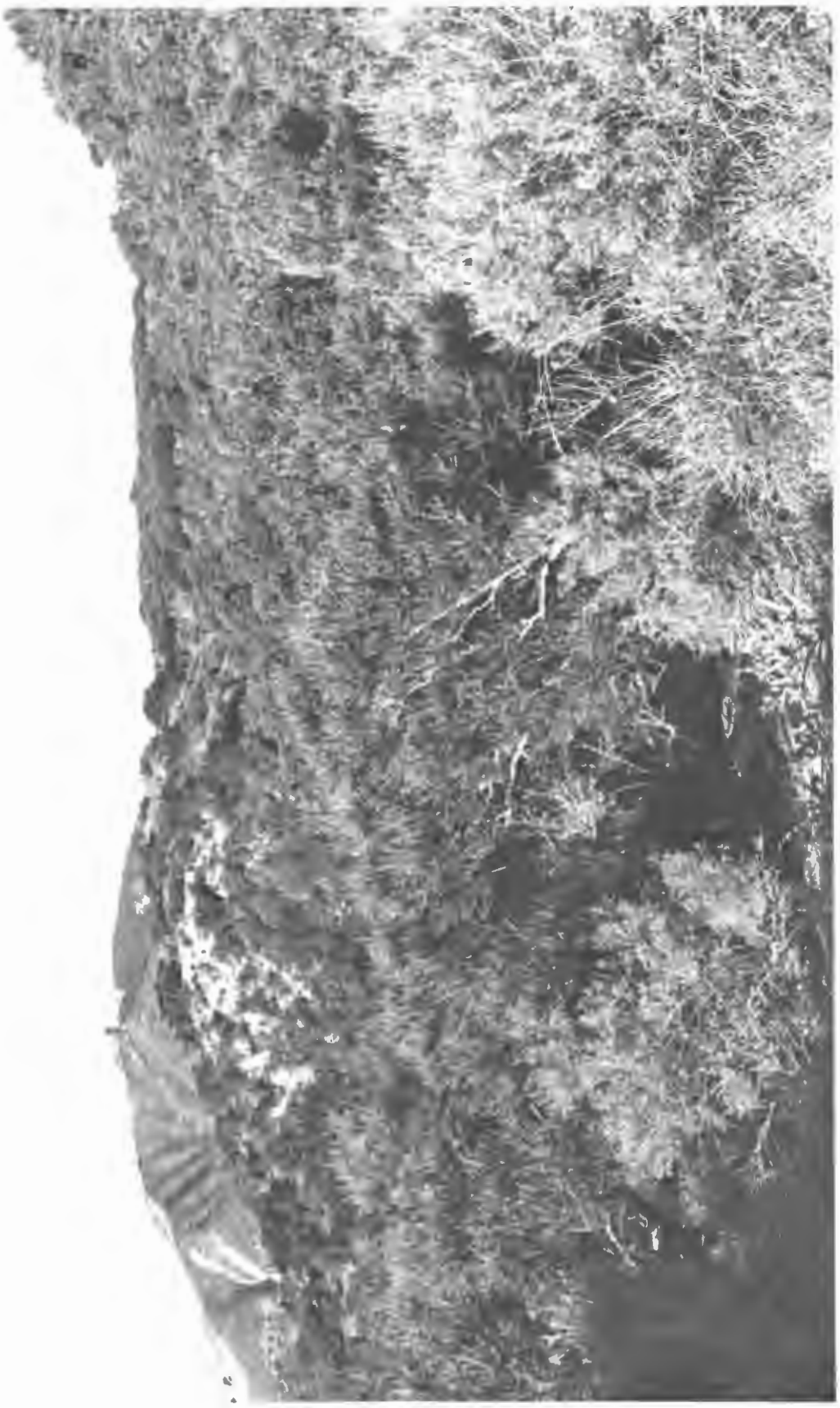
Fig. 14. Trapping site at Avenue C, Lancaster. Alkali Sink habitat of Dipodomys merriami. Dipodomys microps, and Dipodomys panamintinus.

Fig. 15. Trapping site near Warren Station, north of Mojave. This Joshua Tree Woodland-Creosote Bush Scrub is the habitat of Dipodomys panamintinus and Dipodomys merriami. This is the type locality for Dipodomys panamintinus mohavensis.

Fig. 16. Trapping site at Frazier Park (hillside). Sagebrush Scrub habitat of Dipodomys agilis perplexus.

Fig. 17. Trapping site at Frazier Park (road). A disturbed Sagebrush Scrub-Yellow Pine Forest habitat. Dipodomys agilis perplexus was taken here.

Fig. 18. Trapping site near Mulholland Highway. Chaparral habitat of Dipodomys agilis agilis.



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APPENDIX I

Specimens Examined

Specimens with numbers preceded by BAC are in my personal collection and have been deposited in the Los Angeles County Museum of Natural History. The specimen whose number is preceded by TK is in the collection of Mr. Thomas S. Kelly and has also been deposited at the Los Angeles County Museum of Natural History. The specimen whose number is preceded by the letters VSC is in the collection of San Fernando Valley State College.

Dipodomys agilis agilis.- Los Angeles County: Cold Creek-Stone Canyon Road, 200 yards west of junction with Mulholland Highway, 1 (BAC 50); Cold Creek-Stone Canyon Road, 0.7 mi. west of junction with Mulholland Highway, 1 (BAC 51); San Francisquito Canyon Road, Saugus, 1 (BAC 52).

Dipodomys agilis perplexus.- Kern County: South side of Mt. Pinos Road, 1.0 mi. west of Kern Co. Fire Dept. Station, Frazier Park, 5,000 ft, 3 (BAC 55, 56, 58).

Dipodomys panamintinus mohavensis.- Los Angeles County: Aliso Canyon Road, 0.5 mi. south of junction with Soledad Canyon Road, 4 (BAC 26-29); east side of Santiago Road, 0.5 mi. south of Antelope Valley Freeway, 7 (BAC 31-33, 35, 37-38, 42); 1.0 mi. south of Avenue N, 0.25 mi. west of Sierra Highway, Palmdale, 7 (BAC 40, 44-49); 0.25 mi. southeast of corner of Avenue C and Sierra Highway, Lancaster, 1 (BAC 57); 1.2 mi. east of Bakersfield Freeway, off Rye Canyon, Castaic Junction, 1 (VSC 746). Kern County: 0.5 mi. east

of railway station at Warren, about 5.0 mi. north of Mojave, 24 (BAC 59-82).

Dipodomys heermanni morroensis.- San Luis Obispo County: 1.0 mi. east of Los Osos, 3 (BAC 30, 36, 53).

Dipodomys heermanni arenae.- Santa Barbara County: 2.0 mi. NNW Lompoc, 1 (BAC 54).

Dipodomys heermanni goldmani.- San Benito County: 1.0 mi. west of Pinnacles National Monument (=2.5 mi. west of Little Pinnacles Ranger Station), 1 (TK 182).

Dipodomys microps microps.- Los Angeles County: 0.25 mi. southeast of corner of Avenue C and Sierra Highway, Lancaster, 1 (BAC 41).

Dipodomys merriami merriami.- Los Angeles County: 1.0 mi. south of Avenue N, 0.25 mi. west of Sierra Highway, Palmdale, 1 (BAC 39).