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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 59

SAN FRANCISCO BAY AS A FACTOR INFLUENCING SPECIATION IN RODENTS

BY
EMMET T. HOOPER

ANN ARBOR
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FREDERICK M. GAIGE
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INTRODUCTION

JORDAN (1905, and elsewhere) focused the attention of biologists in North America on the role played by physical barriers in the speciation of plants and animals. Subsequently, many authors have reported studies which were concerned primarily with the effects of barriers in the evolution of species and races; collectively their studies treat several kinds of barriers and many different groups of organisms. Among those authors dealing recently with aquatic barriers to terrestrial North American mammals may be mentioned Grinnell (1914), Goldman (1937), Davis (1939), and Marshall (1940). Grinnell and Goldman were concerned with the effects of the Colorado River in the southwestern United States, Davis with the Snake River in Idaho, and Marshall with Great Salt Lake in Utah. Investigations of this sort, particularly if dealing extensively with data secured in the field, contribute largely to our knowledge of those factors in environments which limit the distribution of mammal kinds and, as well, probably influence the formation of new species.

The present study, an analysis of the native rodent fauna of a part of west-central California (Map 1), was designed primarily to determine the effects of San Francisco Bay and the lower part of the Sacramento River on the distribution and evolution of the rodent species. For the analysis I have attempted to sort out and present from field and laboratory notes information that would show: what kinds (species and subspecies) of indigenous rodents are present in the area, the characteristics of these kinds, for purposes of identification and for the analysis of the distributional problems involved, the nature of the environments in which each form lives, and some relationships of each of these environments. Finally, I have attempted to discuss and offer possible explanations for certain problems encountered, particularly those having to do with some effects of San Francisco Bay on the distribution and evolution of the rodents.

ACKNOWLEDGMENTS

Specimens used in this study are to be found in the Museum of Vertebrate Zoology, University of California; the California Academy of Sciences; and the Museum of Zoology, University of Michigan. All field notebooks, from which much information was obtained on range, habitat, and abundance of species, are deposited in the Museum of Vertebrate Zoology. For the use of these materials I am grateful to Alden H. Miller, Robert T. Orr, and the late J. Frank Daniel. I am particularly indebted to the late Joseph Grinnell, E. Raymond Hall, and Alden H. Miller, for reading parts of the manuscript critically and offering suggestions.

DESCRIPTION OF THE AREA

PHYSIOGRAPHY

The area which forms the basis for the present study is a section of west-central California, bounded on the west by the Pacific Ocean, and on the east, in general, by the Great Valley of California. The entire area, roughly rhomboid in shape, is about 130 miles long in a northwest-southeast direction, and seventy miles wide. The boundaries that define the area on the north, south, and east are the limits of all the counties, except Sacramento County, which touch on San Francisco, San Pablo, and Suisun bays. These counties, nine in number, have a total area of about seven thousand square miles.

A salient physiographic feature of the area is San Francisco Bay, a natural embayment which divides the area into approximate halves. This bay is a continuous water passage from the Pacific Ocean to the delta formed by the Sacramento and San Joaquin rivers. San Francisco Bay is considered locally to embrace only the central and the southern part of this water passage. The northern part is known as San Pablo Bay and the easterly embayment as Suisun Bay; the latter connects with San Pablo Bay by Carquinez Straits. In the present paper, however, the term San Francisco Bay, unless otherwise specified, refers to the entire water passage extending from the Sacramento River delta, near the east end of Suisun Bay, westward to the Pacific Ocean. Its total area amounts to about nine hundred square miles. The length of the main bay, exclusive of San Pablo and Suisun bays, is about fifty miles in a northwest-southeast line; the width varies from three to thirteen miles. Its area, at mean tide, is about four hundred square miles. The bay is connected with the Pacific Ocean by a narrow water passage, about six miles long and one to three miles in width, known as the Golden Gate. The closest approximation of the mainlands north and south of the bay is at Carquinez Straits. Here, bounded by precipitous cliffs several hundred feet in height, the water channel narrows to half a mile.

The waters of outer San Francisco and San Pablo bays occupy the central and lower parts of the valley of the Bay of San Francisco—one of three major longitudinal valleys which divide the coast ranges into outer and inner ranges. The remainder of this valley, not covered by water, extends northwesterly through Petaluma and Santa Rosa valleys to the head of the Russian River in Mendocino County, and southeasterly through the broad Santa Clara Valley to the headwaters of the San Benito River, a total distance of about 260 miles. Despite the length of the valley, the central part receives little drainage from the coast ranges. Instead, this central part receives the major runoff of the state, comprised in the combined flows of the Sacramento and San Joaquin rivers, which enter via Suisun Bay and Carquinez Straits. The runoff of the coast ranges in west-central California is principally by way of the Russian and San Benito rivers. North of the Golden Gate within the area studied, the outer coast ranges rise to a maximum height of 2604 feet on Mount Tamalpais, which is about ten miles northwest of the Golden Gate. About twenty miles north of Mount Tamalpais the stream-dissected mountain ridge of which Tamalpais is a part gives way to a series of rolling hills and shallow valleys. This rolling, grass-covered terrain, extending northward for about fifteen miles, almost to the Russian River, is that area herein referred to as the "Sonoma-Marin gap." It marks a break in the continuity of the flora and fauna of the humid coastal belt. Geologically, it is the remnant of an old peneplain (Holway, 1914: 109). North of the Russian River the country again is broken, and the ridges are mountainous much as they are near Mount Tamalpais. Southward from the Golden Gate, the ridges of the outer coast ranges increase in elevation to attain altitudes of about three thousand feet above sea level in the Santa Cruz Mountains in Santa Cruz and southern San Mateo counties.

The inner coast ranges rise abruptly to the east of the valley of the Bay of San Francisco and separate the more westerly hills and valleys from the plains of the Great Valley of California. Prominent as higher peaks are Mount St. Helena (4343 feet), Mount Diablo (3849 feet), and Mount Hamilton (4209 feet). Numerous sizable valleys, all now intensely cultivated, lie between the mountainous ridges.

CLIMATES

In general, the climate of the area is mild, relatively cool and dry in summer, and warm and wet during the winter. Precipitation is limited to the winter half of the year. Frosts are infrequent and snowfall in measurable amounts is rare.

As computed from data available from government weather stations (Bowie, 1934 *a* and *b*), the average annual temperature for the area is about 57° F. The average maximum temperature is 69°, and the average minimum about 46°. July, usually the hottest month, has an average temperature of about 66° and an average maximum of about 106°. January is the coldest month; the average maximum is 47° and the average minimum about 20°. The growing season (last killing frost to first killing frost) averages 276 days, varying from an average maximum of 362 days (at the Point Reyes weather station) to an average minimum of 180 days (at the station on the summit of Mount Hamilton). The annual precipitation decreases, in general, from north to south; the mean of the stations north of San Francisco Bay is about thirty-three inches, and the mean south of the bay about twenty inches; for the whole area it averages approximately twenty-seven inches. July and August are the driest months, with one-tenth or two-tenths of an inch a usual amount. January is the wettest month, with an average precipitation of about six inches—seven and one-half inches north of the bay and four and four-tenths south of it. The mean annual cloudiness averages between 50 and 60 per cent, ranging from over 70 per cent (along the coast in northern Sonoma County) to less than 40 per cent (in the inner coast ranges).

It is an area of local climates, one in which marked changes occur in short distances and where the air drainage system is modified by topography. Climatic conditions are influenced largely by elevations, sheltering influences of mountain ridges, and distances from the ocean. Because of local elevations, such as Mount St. Helena and Mount Diablo, areas of cool, relatively moist climate lie within a few miles of areas of warmer drier climates. For example, at the weather station on Mount St. Helena (elevation 2300 feet), the mean annual precipitation is 59.5 inches; ten miles to the south, at Calistoga (elevation 363 feet), the mean annual precipitation is 36.7 inches, 22.8 inches less than on St. Helena. Similarly, the mean annual precipitation in the Santa Clara Valley, at Campbell, is 15.3 inches; at Wright's, on the edge of the Santa Cruz Mountains, it is 44.8 inches, a difference of 29.5 inches in a distance of less than ten miles with an altitudinal difference of only 1383 feet. This mosaic of climates is accompanied by corresponding irregularities in the distribution of floras and faunas, as will be seen below.

An important effect of topographic features on the air drainage system is well illustrated at San Francisco Bay. In California, temperature, mean relative humidity, mean annual cloudiness, and mean annual precipitation isograms usually run north and south, conforming in general to the contours of the mountain ranges and the outline of the seacoast. This north-south trend is markedly disturbed at San Francisco Bay; the isograms are bowed abruptly eastward. Instead of being deflected by the coast ranges to parallel the seacoast, the cool, moisture-laden westerly winds, which prevail in these latitudes, continue almost unabated through the Golden Gate into the valley of San Francisco Bay; their ameliorating effect extends well into the Sacramento and San Joaquin valleys.

Fog and cloud cover, acting as screens which greatly reduce the amount of sunshine, are important factors in the climate of the region (Hovanitz, 1941). Their effect on temperature, rate of evaporation, and relative humidity is reflected in the kinds and numbers of terrestrial plants and animals living there. Fog and cloud cover appear to be necessary to some plants and of considerable importance to some mammals.

Byers (1930) has mapped the distribution of fogs of the central California coast for certain intervals during a summer day. Although representing only a single day and one in which the fog was perhaps more extensive than average, Byer's map illustrates fairly well the mean annual distribution of fog over the area and indicates the extent to which insolation is reduced by fog or clouds. The Santa Cruz Mountains, coastal San Mateo County, San Francisco County, the vicinity of Berkeley, and most of Marin County were foggy the entire day. Probably Sonoma County, north and west of the Russian River, not covered by Byer's survey, was also clouded all day. In extreme western Contra Costa and Alameda counties and northern Santa Clara County, fog remained at least until midday. It covered western San Mateo County and that part of Santa Clara County west of Mount Hamilton until 11 A.M. The remainder of the area west of Mount Hamilton, Mount Diablo, and Vaca Mountain was cleared by 9:30 A.M. That part of the area lying east of Hamilton, Diablo, and Vaca was free from fog the entire day.

GEOLOGIC HISTORY OF THE AREA

GEOMORPHOLOGY AND PHYSIOGRAPHY

There is no evidence from the fossil record that any of the rodent species now inhabiting west-central California occurred there prior to Pleistocene time. It is likely, therefore, that modern species became established in the bay area in Quaternary time, concurrent with the geomorphic changes which produced most of the present features of topography in the area.

By late Pliocene time the coastal part of California had been reduced approximately to a peneplain or series of peneplains. Numerous monadnocks, peaks, and ridges, however, rose above the general level. Some of those near the seacoast were surrounded by water, giving the coast the aspect of an archipelago. Peaks present then, but probably made more prominent features of the land by subsequent earth movements, were Mount St. Helena, Mount Diablo, and Mount Hamilton. The Great Valley was connected with the ocean by one of several straits, two of which are now known as Carquinez Straits (and the Golden Gate) and Pacheco Pass.

In late Pliocene or early Pleistocene there began a period of emergence, when the old peneplain was raised as much as fifteen hundred feet above sea level (Lawson, 1893: 157). Some streams antecedent to the emergence maintained their old courses by continued cutting of the rising land. Of prime importance among those streams is the Sacramento River. It continued to flow through the Carquinez Straits, between the Tiburon Peninsula and the land body that is now Angel Island, and out through the Golden Gate. The elevating of the coastal lands was accompanied by an emergence of the Great Valley; parts once under water, the present low foothills, for example, became dry land. All during this period of general elevation, which probably was accompanied by several local recessions of the terrain, particularly in Pleistocene, erosional forces wore down and dissected the land to its present early maturity (Osmont, 1904: 87).

In middle Pleistocene, movements occurred that separated the San Francisco-Marin block from the Berkeley Hills block, one result of which was the outlining by faulting of the valley system of San Francisco Bay (Lawson, 1914: 20). In this valley were deposited later Quaternary sediments derived, in large part, from erosion of the fronts of the bordering mountain blocks. Erosion of the blocks coupled with deposition and subsequent wave action on the valley floor flattened and broadened the valley, giving it a profile similar to that seen today.

Finally, as the most recent and indeed current change, came the submergence, to the extent of at least 378 feet in some parts, of the region about and including San Francisco Bay (Lawson, 1894: 271). This resulted in widening the expanse of water between the north and the south shores of the lower Sacramento River Valley and the flooding and drowning of other valleys to produce the topographic conditions now observable in the area. There is no physiographic evidence that any opening other than the Golden Gate has functioned as an outlet to the ocean for the Sacramento River during the present geomorphic cycle (Holway, 1914: 101–2). Throughout Quaternary time the course of the Sacramento River appears to have been, as it is now, through Carquinez Straits and the deep narrow canyon of the Golden Gate.

QUATERNARY CLIMATES

Since Pliocene the climates have been variable in the region of San Francisco Bay, with fluctuations that were probably closely correlated with oscillations from glacial to interglacial stages. It appears definite that cooler, temperate conditions extended much farther southward and inland over currently arid areas than they do at present. Also, there is some indication that tropical climatic conditions at times reached areas farther to the north than they do now. Probably the climates fluctuated from warm to cool and wet to dry several times in the Quaternary period.

Smith (1919), working with marine faunas, concluded that there were at least two major shifts in the climate of coastal California during Quaternary time. In early Pleistocene (Lower San Pedro beds), the entire coast of California was in the grip of a cold northern climate. Isotherms were shifted southward at least a thousand miles, and the temperature was generally lowered about 12° F. as far south as Los Angeles. This cooler period was interpreted as corresponding to the period of maximum glaciation in the Northern Hemisphere. A rebound took place in later Pleistocene (Upper San Pedro). Northern faunal species retreated northward and were replaced in the former southern parts of their ranges by tropical species from the south. These faunal movements indicated to Smith a minimum temperature at San Pedro of about 68° F., a rise of about 18° from Lower San Pedro. The amelioration of the climate extended as far north as Cape Nome, Alaska, and may have been synchronous with an interglacial or postglacial stage.

Chaney and Mason (1930: 24) found that the Willow Creek flora on Santa Cruz Island, probably of Pleistocene age, is closely similar to the forests now growing near Fort Bragg, Mendocino County, over four hundred miles to the northwest of Santa Cruz Island. This indicated to them climatic conditions on the island similar to those now obtaining at Fort Bragg. The Pleistocene flora at Carpinteria, San Luis Obispo County, points toward cool humid conditions similar to those present on the coast two hundred miles to the northwest (Chaney and Mason, 1933: 75).

From his studies of the Pleistocene avian faunas of the Carpinteria and McKittrick beds, Miller (1940: 809) concluded that "McKittrick and Carpinteria on opposite sides of the coast range were even more strongly contrasted in climate than they are now, the Carpinteria distinctly more humid with a Transition forest, the McKittrick possibly with closer approach spatially to cooler zones of plant life, but locally with arid, desert aspect no less extreme than that of today."

The identifications made in her study of the Pleistocene flora from near San Bruno, San Mateo County, suggested to Potbury (1932: 44) that the flora is comparable to that associated with the Douglas fir forests now on some of the eastern slopes in Marin County, north of San Francisco Bay. This may indicate a slight change in climate in the bay region.

Mason (1934: 110) concluded from his studies of the Pleistocene floras of the Tomales region, Marin County, that the "coastal region of central California during Pleistocene saw no such changes in the flora as are elsewhere apparent from glacial to interglacial epochs." Only the marginal flora near the limit of the tolerance ranges of its constituent species fluctuated in response to changing conditions. His analysis shows, however, that some fluctuations in climate in the coastal belt of this region did occur, as evidenced by the movements of some species to the north or south. His studies also indicate that no great change in climate is necessary to result in movements of a species, if the change applies to an extreme in the range of tolerance of the species for those climatic factors. A small change, thus, might result in a considerable widening inland and extension southward from its present limits of the ranges of the floras and faunas now closely restricted to the narrow fog belt along the seacoast.

The evidence derived from the studies mentioned above and from the discontinuous distribution of some species, for example, yellow pine and lodgepole pine (Munns, 1938: 19) and mountain beaver and jumping mice, is sufficient to indicate that in Cenozoic time and probably in Quaternary time in the bay area climatic conditions have fluctuated from those of the present time, and floras and faunas or parts thereof have moved northward, southward, and inland from their present range limits.

DISTRIBUTIONAL AREAS

Most rodent kinds do not range throughout the bay area; rather, each is restricted in its distribution to only a part of the area. Some species differentiate into geographic races, each of which has its own rather well-defined range. Such discontinuous distributions—the presence of some species and the absence of others in a particular area—and the differentiation of species into geographic races allow for recognition of certain distributional areas or faunal divisions (Map 1).

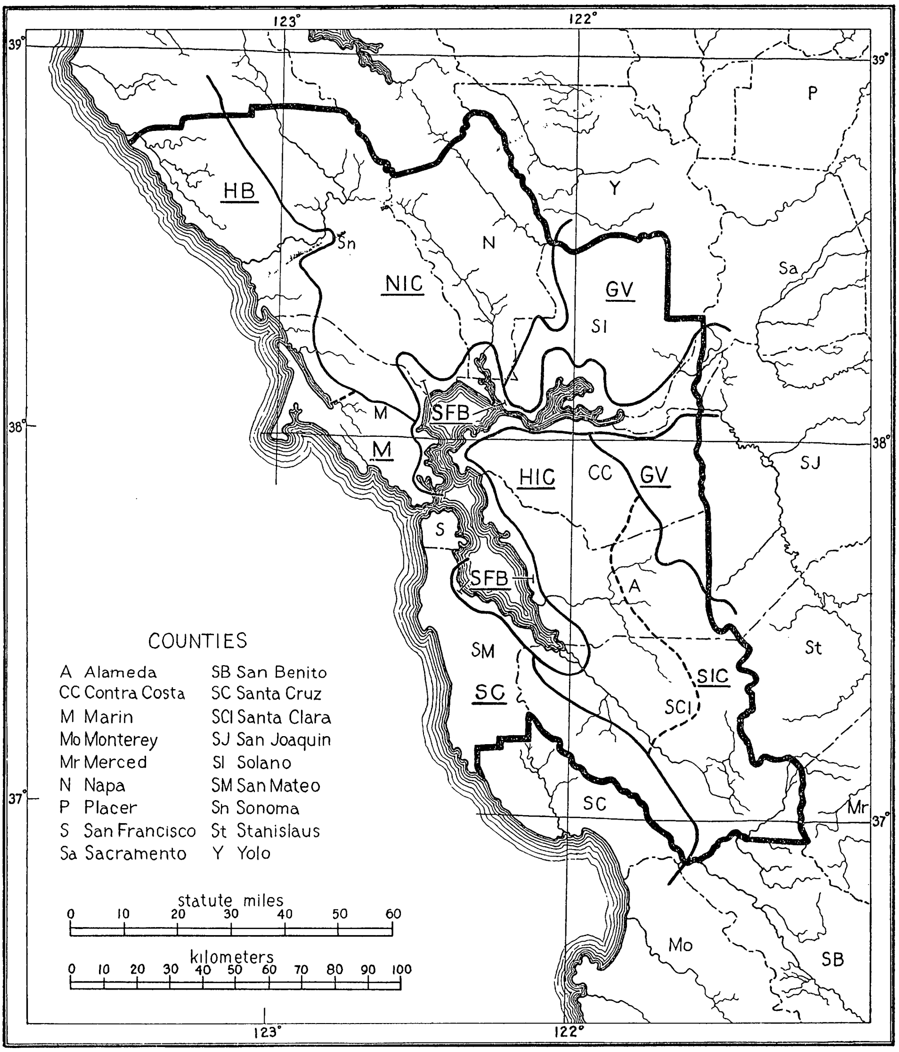
FAUNAL DIVISIONS

Faunal Area	Faunal Subarea	Faunal District
I. Humid coast	A. Northern humid coast	1. Humboldt Bay (HB)
		2. Marin (M)
	B. Southern humid coast	1. Santa Cruz (SC)
II. California	A. Inner coast	1. Northern inner coast (NIC)
		2. Southern inner coast (SIC)
		3. San Francisco Bay (SFB)
	B. Great Valley	1. Great Valley (GV)

The faunal classification employed here agrees closely with that outlined by Grinnell (1915: 12). It is based primarily on the distribution of native rodents rather than on birds, however, and for that reason, principally, the faunal divisions do not always agree. Two major faunal divisions or faunal areas are recognized in the area under consideration. Each of the faunal areas is divisible into areas of consecutively lesser rank designated as faunal subareas and faunal districts.

The present faunal units—faunal areas, faunal subareas, and faunal districts—are definable by geographic boundaries which correspond to the range limits in the bay area of several species or subspecies of indigenous rodents. A criterion for the recognition of each faunal unit was the restriction to it of at least one race or species of rodent. The area composed of western Alameda and Contra Costa counties and part of northern Santa Clara County (HIC, Map 1) is not treated as a separate faunal district because no race of rodent is peculiar to it, even though the aspect of the fauna, the aggregate of species and subspecies, is different from that seen elsewhere in the San Francisco Bay area. It is actually an intermediate area; it contains many of the kinds which are characteristic of either the Santa Cruz district or the southern inner coast district. Each faunal area occurs predominantly in one life zone.

The humid coast faunal area is an area of moderate, uniform temperature, high humidity, frequent fogs, and abundant rainfall. These factors make it one of luxuriant plant growth (Pl. V). Redwood (*Sequoia semper-*



MAP 1. The seven rodent faunal districts recognized in the San Francisco Bay area of west-central California. HB, Humboldt Bay; M, Marin; SC, Santa Cruz; NIC, northern inner coast; SIC, southern inner coast; SFB, San Francisco Bay; GV, Great Valley. The area immediately to the east of San Francisco Bay, indicated by the symbol HIC, is not treated as a separate district or included in one of the present districts for reasons given in the text. The size of the map necessitated a displacement inland of the lines bounding the San Francisco Bay district; as here shown they include more than the bayside marshes, which alone compose the district.

virens),[1] Douglas fir (*Pseudotsuga taxifolia*), tan oak (*Lithocarpus densiflora*), thimbleberry (*Rubus parviflorus*), and ninebark (*Physocarpus capitatus*) grow in dense stands in the more protected and humid places. Open grasslands, often studded with patches of Bishop pine (*Pinus muricata*), lowland fir (*Abies grandis*), and Sitka spruce (*Picea sitchensis*), replace the heavy forest growth on slopes and crests exposed to strong winds. In the Humboldt Bay and Marin districts and in the Santa Cruz Mountains in the Santa Cruz district, the average annual precipitation usually exceeds forty inches and in some places is greater than one hundred inches; the soils are gray-brown or blackish brown, medium acidic, rich in decaying organic matter, and chiefly of the Melbourne series (Kellogg, 1938: 1045). A Mediterranean type of climate is present in parts of the Santa Cruz district east of the outer coast ranges. Here the rainfall averages twelve to thirty inches annually; the summers are warm and dry and the winters moist; fogs are less frequent; the soils are dark brown, acidic, and principally of the Altamont series and related soils (Kellogg, 1938: 1053).

The humid climate, the looser, humus-filled dark soils, and the presence of distinctly northern species, such as lowland fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), western jumping mouse (*Zapus trinotatus*), and aplodontia (*Aplodontia rufa*), distinguish the northern humid coast faunal subarea from the southern humid coast faunal subarea (represented in the bay area by the Santa Cruz district). The occurrence of some northern species no farther south than southwestern Sonoma County differentiates the Humboldt Bay district from the Marin district. Sitka spruce, western red cedar (*Thuja plicata*), the California red-backed vole (*Clethrionomys californicus*), and the Douglas red squirrel (*Tamiasciurus douglasii*) are limited to areas north of the Marin district.

On the whole, a Mediterranean type of climate is characteristic of that part of the California faunal area within the geographic limits of the area studied. The summers are warm and dry, the winters mild and moist. Snow is comparatively rare and fogs common, particularly during the winter months. The annual rainfall generally averages about twelve to thirty inches. These factors are conducive to the growth of hardy perennials and early-flowering annuals that can mature and reproduce during the short, moist spring season. The hills, typically "bald," are clothed with grass, annual vegetation, and a few coast live oaks (*Quercus agrifolia*) (Pls. III and IV). Denser growths are limited to protected canyons and the higher mountainous areas. In such situations coyote brush (*Baccharis pilularis*), poison oak (*Rhus diversiloba*), ceanothus (*Ceanothus cuneatus*), chamise (*Adenostoma fasciculatum*), digger pine (*Pinus sabiniana*), and Coulter pine (*Pinus coulteri*) become common.

[1] Scientific names of plants are after Jepson (1925).

The climate in the northern inner coast district is less equable than that in the southern inner coast district. The mean annual precipitation often exceeds twenty inches and in some places reaches fifty inches. The summers are long, dry, and fairly hot, and the winters comparatively wet, with snow on the more elevated areas. The soils, strongly leached, acidic, and low in organic matter, are principally of the Sites series and related soils (Kellogg, 1938: 1058).

In the southern inner coast district the annual rainfall averages twelve to twenty-five inches, and the climate as a whole is of the Mediterranean type. The soils in the northern part of the area are predominantly of the Diablo series (Kellogg, 1938: 1106–7), dark gray and containing much black organic matter. Those of the southern part, south from southern Alameda County, are predominantly the brown, compact soils of the Holland, Sierra series, or associated soils (Kellogg, 1938: 1097–98). A warmer, drier climate and the restriction to it of several species—Coulter pine, old-man sage (*Artemisia californica*), California mouse (*Peromyscus californicus*), and lepida wood rat (*Neotoma lepida*), for example—distinguish the southern inner coast from the northern inner coast district.

The San Francisco Bay district is characterized by a cool humid climate, peat and muck soils, and the rather close restriction to the district of certain marsh-inhabiting species (Pl. I), as, for example, salicornia (*Salicornia ambigua*) and the San Francisco harvest mouse (*Reithrodontomys raviventris*). The district does not include upland areas as shown on Map 1 (SFB); the small size of the map results in displacement inland of the boundary lines.

Hot dry summers and cool moist winters with frequent fogs are typical of the Great Valley faunal subarea. Alluvium predominates (Kellogg, 1938: 1135), and the native vegetation is sparse. Grasses, "weeds," and other annuals constitute most of the plant growth on the foothills and plains; cottonwood (*Populus fremontii*), willow (*Salix* sp.), button willow (*Cephalanthus occidentalis*), and other riparian plants are common along stream courses. The Great Valley pocket mouse (*Perognathus inornatus inornatus*) is restricted to the Great Valley faunal subarea.

The species and subspecies of rodents of the special area under consideration are arranged below by faunal areas. Those listed in a faunal area always occur predominantly within that area; usually they are entirely restricted to it. A rodent is listed under the heading of the most inclusive faunal division that it typifies. Thus, *Peromyscus maniculatus rubidus* is characteristic of the humid coast faunal area, and, of course, of its faunal subareas and faunal districts. *Phenacomys longicaudus,* on the other hand, lives only in the Humboldt Bay district. Those kinds which range over several faunal units and cannot well be considered characteristic of any one are listed under the heading "General"; all, however, occur chiefly in the California faunal area. *Microtus c. aestuarinus* is treated as a member of the Great Valley fauna, because outside the area studied it is present in the Great Valley. The Great Valley faunal subarea could be further divided into the Sacramento Valley district and the San Joaquin Valley district, but that has not seemed necessary here.

- I. Humid coast faunal area
  - *Peromyscus maniculatus rubidus*
  - A. Northern humid coast faunal subarea
    - *Thomomys bottae minor*
    - *Peromyscus truei sequoiensis*
    - *Neotoma fuscipes monochroura*
    - 1. Humboldt Bay faunal district
      - *Eutamias townsendii ochrogenys*
      - *Tamiasciurus douglasii molli-pilosus*
      - *Phenacomys longicaudus*
      - *Clethrionomys californicus californicus*
    - 2. Marin faunal district
      - *Eutamias sonomae alleni*
      - *Aplodontia rufa phaea*
      - *Zapus trinotatus orarius*
  - B. Southern humid coast faunal subarea
    - *Sciurus griseus nigripes*
    - *Peromyscus californicus parasiticus*
    - *Neotoma fuscipes annectens*
    - 1. Santa Cruz faunal district
      - *Eutamias merriami pricei*
      - *Dipodomys venustus venustus*
- II. California faunal area
  - *Peromyscus maniculatus gambelii*
  - A. Inner coast faunal subarea
    - 1. Northern inner coast faunal district
      - *Eutamias sonomae sonomae*
      - *Dipodomys heermanni californicus*
      - *Neotoma fuscipes fuscipes*
    - 2. Southern inner coast faunal district
      - *Thomomys bottae diaboli*
      - *Dipodomys heermanni berkeleyensis*
      - *Dipodomys heermanni goldmani*
      - *Peromyscus californicus benitoensis*
      - *Neotoma lepida californica*
      - *Neotoma fuscipes perplexa*
    - 3. San Francisco Bay faunal district
      - *Reithrodontomys raviventris raviventris*
      - *Reithrodontomys raviventris halicoetes*
      - *Microtus californicus paludicola*
  - B. Great Valley faunal subarea (and faunal district)
    - *Thomomys bottae agricolaris*

Perognathus inornatus inornatus
Dipodomys heermanni tularensis
Microtus californicus aestuarinus

III. General (predominantly in the California faunal area, but locally in the humid coast faunal area)

Citellus beecheyi beecheyi
Citellus beecheyi douglasii
Sciurus griseus griseus
Thomomys bottae bottae
Perognathus californicus californicus
Reithrodontomys megalotis longicaudus
Peromyscus boylii boylii
Peromyscus truei gilberti
Microtus californicus californicus
Microtus californicus eximius

ECOLOGIC ASSOCIATIONS

As employed here the phrase ecologic association refers to a special assemblage of plants and rodents as they exist together under the current conditions of environment. It implies a dependence of some of the rodents on at least some of the plants. The term "association" is not used from the point of view of order of succession as Clements (1936, and elsewhere) employed it. Each association apparently corresponds to a major association of Grinnell and Swarth (1913), a habitat of Grinnell, Dixon, and Linsdale (1930), and an association subtype of Clark (1937).

Plants, primarily, have been taken as the basis for the present classification of associations, but each association has closely restricted to it at least one rodent species. There is no attempt here to devise a complete classification of all plant and animal associations in the area studied. Only those which seem to be most important from the point of view of continued survival of the native rodent species have been recognized. None of the other biotic associations apparent to me offers a particular set of environmental conditions to which a rodent species is closely restricted in its distribution. For a more complete classification of the associations in the region see Clark (1937).

Salicornia-Marsh Association

A belt of marshland extends almost continuously around the border of San Francisco Bay (Pl. I). This littoral belt is largely confined between the levels of high and low tide. At the mouth of a creek or river the belt widens and extends inland to the limits of brackish water. The soil is peaty and is usually wet. The vegetation is dense, low-lying, and composed almost entirely of salicornia or pickleweed (*Salicornia ambigua*). In the area studied two races of harvest mouse (*Reithrodontomys raviventris raviventris* and *R. r. halicoetes*) and two races of vole (*Microtus californicus paludicola* and *M. c. aestuarinus*) are closely restricted to this association.

Bunch-Grass Meadow Association

This association is characterized by clumps or "bunches" of vegetation growing to a height of three or four feet and spaced so closely that the ground is usually well hidden. The ground is peaty, resilient when fairly dry, and boggy when wet. Springs, ground seepage, small ponds, or small shallow streams keep the ground moist, usually throughout the year. All of this association that I have seen in the area studied is in the climatically uniform, humid fog belt in the humid coast faunal area. The largest area seen, typical of the habitat, is on the Point Reyes road, two to four miles west of Inverness, Marin County (Pl. II, Fig. 1). The western jumping mouse (*Zapus trinotatus orarius*) and other species of mammals requiring moist situations around fresh water are closely restricted to this association. The typical vegetation includes rushes (*Juncus* sp.), sedges (*Carex* sp.), brachen (*Pteris aquilina*), sword fern (*Polystichum munitum*), Johnson grass (*Holcus halepensis*), poison hemlock (*Conium maculatum*), and monkey flower (*Mimulus* sp.).

Dry Grassland Association

Most lands which support a cover of grasses and in which the soils become dry and hard in summer are here classed as dry grassland. The terrain may be flat, rolling, or steep. Characteristic of this association are the extensive, rolling, grass-covered hills and valleys in Solano and Contra Costa counties (Pls. III and IV). This association occurs predominantly in the California faunal area, but also may be seen locally in the humid coast faunal area on the warmer, more exposed slopes and in warm, dry valleys. The rodents characteristic of the association live in burrows in the ground or in passageways in the denser growths of grass. Some kinds, the ground squirrel for example, probably rely on the openness of the plant growth to see approaching enemies in time to escape to burrows. Rodents commonly in this association are: Beechey ground squirrel (*Citellus beecheyi*), Botta pocket gopher (*Thomomys bottae*), Heermann kangaroo rat (*Dipodomys heermanni*), deer mouse (*Peromyscus maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), and California vole (*Microtus californicus*) Brome grasses (*Bromus rubens, B. rigidus,* and *B. hordeaceus*), wild oats (*Avena barbata*), fescue (*Festuca megalura*), wild barley (*Hordeum gussoneanum*), koeleria (*Koeleria cristata*), and bur clover (*Medicago hispida*) are typical of the association.

Soft Chaparral Association

The soft chaparral association, as defined by Jepson (1925: 8), is a shrub formation of the Transition life zone. It is composed principally of thimbleberry (*Rubus parviflorus*), ninebark (*Physocarpus capitatus*), huckleberry

(*Vaccinium ovatum*), cream bush (*Holodiscus discolor*), and snowberry (*Symphoricarpos albus*). These often are present in dense stands with ceanothus (*Ceanothus thyrsiflorus*) and salal (*Gaultheria shallon*) as a redwood-Douglas fir forest border growth or as a dense understory within second-growth conifer forests (Pl. V, Fig. 1). In many places, particularly on the outer borders of redwood and Douglas fir forests, this association becomes mixed with hard chaparral, described below. Throughout the cooler, more humid parts of San Mateo and Santa Clara counties, it is more usual to find the two intermixed than to find pure stands of soft chaparral. Soils typical of this association are moist, loose, and rich in humus. The climate is cool and humid, and rain or fog may be expected almost daily. The Townsend chipmunk (*Eutamias townsendii ochrogenys*) is closely restricted to this association. Of common but not exclusive occurrence here are races of the Sonoma chipmunk (*Eutamias sonomae alleni*), the piñon mouse (*Peromyscus truei sequoiensis*), and the deer mouse (*Peromyscus maniculatus rubidus*).

Hard Chaparral Association

Most of the brush-covered lands in the bay area are included in the hard chaparral association (Pl. III). This association is most extensive in the inner coast faunal subarea, but it is also found on warmer, drier slopes in the humid coast faunal area. Typically, the soil is well drained, dry, and sandy or rocky, and the climate is moderately warm and arid during the summer months. Many of the plants in the association exhibit structures adapted to the xerophytic conditions, as illustrated by their reduced leaf surface, thickened epidermis, and dense wood. As conceived by Jepson (1925: 6) and as employed here, hard or true chaparral is always a mixed growth. This is a feature probably of primary importance to the associated rodent kinds, because pure stands of some of the constituent plant species (for example, coyote brush, chamise, or yerba santa) always have fewer, and usually entirely lack some or all, of the rodent kinds restricted to brushy cover. The heavy cover, numerous niches, varied food plants, and dry, well-drained soils make this association suitable for a large number of kinds of rodents. The following are some of the species associated closely or exclusively with hard chaparral: Sonoma chipmunk (*Eutamias sonomae*), Merriam chipmunk (*E. merriami*), Santa Cruz kangaroo rat (*Dipodomys venustus*), California mouse (*Peromyscus californicus*), and piñon mouse (*Peromyscus truei*).

The following plant species are characteristic of the association: ceanothus (*Ceanothus cuneatus* and *C. sorediatus*), poison oak (*Rhus diversiloba*), chamise (*Adenostoma fasciculatum*), coffee berry (*Rhamnus californica*), toyon (*Photinia arbutifolia*), manzanita (*Arctostaphylos glandulosa* and *A. canescens*), mountain mahogany (*Cercocarpus betuloides*), coyote brush (*Baccharis pilularis*), yerba santa (*Eriodictyon californicum*), pea chaparral (*Pickeringia montana*), and bush poppy (*Dendromecon rigida*). This association often is mingled with the foothill woodland association.

Sage-Coyote Brush Association

Some ground that is predominantly rocky, dry, well-drained, and sparsely covered with short grass, old-man sage (*Artemisia californica*), coyote brush (*Baccharis pilularis*), and, occasionally, ceanothus (*Ceanothus cuneatus*) is here considered a distinct association. This association is found on hills at scattered intervals over the whole area studied, but is best developed in the southern inner coast faunal district. The surface of the ground is more exposed to climatic elements than is that of any other association here mentioned. The amount of solar radiation received is great. Rains quickly drain off and through the porous ground, removing most of the topsoil that may have accumulated. Two rodent species, the California pocket mouse (*Perognathus californicus*) and the Heermann kangaroo rat (*Dipodomys heermanni*), are closely restricted to the association. These species are adapted to xeric conditions and an open terrain. They live in burrows, need no free water, feed principally on seeds, and possess morphological structures which enable them to convey their food from the exposed foraging grounds to safer underground burrows.

Riparian Association

The thickets of vegetation that form a narrow, practically continuous band along many creeks and rivers, particularly those draining the inner coast ranges, characterize the riparian association. The plants are closely restricted to the moist soils bordering the streams; few of them occur in abundance on the drier soils away from the stream courses. Willow (*Salix* sp.), Oregon ash (*Fraxinus oregona*), sycamore (*Platanus racemosa*), elderberry (*Sambucus glauca*), big-leaf maple (*Acer macrophyllum*), wild rose (*Rosa californica*), alder (*Alnus rubra* and *A. rhombifolia*), and hazel (*Corylus rostrata*) are characteristic of the association. The dusky-footed wood rat (*Neotoma fuscipes*) and the piñon mouse (*Peromyscus truei*) are common in this association, but are not entirely restricted to it. From the point of view of the distribution of rodents, this association is important principally because it provides the right cover for some brush-requiring forms—a set of bushy avenues connecting areas of true chaparral.

Foothill Woodland Association

The present foothill woodland association is closely similar to the foothill woodland association of Clark (1937: 224) and is principally in the inner coast faunal subarea. The woodland consists typically of dense or semiopen stands of oaks (*Quercus agrifolia, Q. wislizenii, Q. chrysolepis, Q. kelloggii,* and *Q. douglasii*), madrone (*Arbutus menziesii*), California bay (*Umbellularia californica*), buckeye (*Aesculus californica*), digger pine (*Pinus sabiniana*), and Coulter pine (*P. coulteri*). It occurs in many canyons and on some foothills in the area studied (Pl. IV). It is a mixed growth; rarely are there pure stands of any one of the constituent plant species. The ground is often covered with leaf litter and sometimes is partly covered with grass. The western gray squirrel (*Sciurus griseus*) and Boyle mouse (*Peromyscus boylii*) are closely restricted to this association. In many places in it trees are mingled with shrubs of the hard or soft chaparral associations. In such situations rodents are abundant, both in kinds and in individuals. Brush-loving species occur with arboreal species and with species (the dusky-footed wood rat, *Neotoma fuscipes,* for example) which apparently prefer a mixture of brush and trees.

Redwood-Douglas Fir Association

The Redwood-Douglas fir association (Pl. V) occupies river flats and low hills and protected canyons and valleys near the seacoast and, thus, predominantly, the humid coast faunal areas. It is best developed in the narrow fog-drenched belt along the coast and is entirely absent from slopes swept by strong winds and from dry hills and valleys outside the fog belt. Often associated with the redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga taxifolia*) are tan oak (*Lithocarpus densiflora*), garry oak (*Quercus garryana*), madrone (*Arbutus menziesii*), and California bay (*Umbellularia californica*). Grand fir (*Abies grandis*) and western hemlock (*Tsuga heterophylla*) are now rare in the bay area; most of the few remaining trees are in northwestern Sonoma County. Douglas fir, the oaks, madrone, and California bay tolerate drier conditions than does the redwood, as attested by their abundance and more rapid rate of reproduction in drier situations. The soil is usually moist, loose, and rich in humus. Three rodent species are mainly in the association; the Douglas red squirrel (*Tamiasciurus douglasii*), the red tree vole (*Phenacomys longicaudus*), and the California red-backed vole (*Clethrionomys californicus*).

SPECIES ACCOUNTS

In each account below, the name of the species or subspecies is followed by a brief synopsis of geographic range in the special area under consideration, particularly with respect to the form's occurrence north or south of San Francisco Bay. Where more than one race of a species is recorded, the characters of skin and skull which distinguish one race from another are listed in the account of one of the races. For each species, under the heading "Habitat," are recorded certain features in an environment, food supply excepted, which appear to define the occurrence of that species in the particular part of the environment it occupies. Such a method actually amounts to defining the "microhabitat" or ecologic niche of each species. Where there are two or more races of a species, the habitat is discussed in the account of the first race listed, but always applies to all the races of the species in the bay area. Intraspecific ecologic differences, thus, are not involved here. The number of specimens examined is noted, and, when necessary, other pertinent remarks are included.

External and cranial measurements in millimeters are given when they have served as bases for statements made in the text. Measurements of total length, tail, hind foot, and ear (unless otherwise indicated) were recorded by the collector. All other measurements and computations were made by me in accordance with current methods in systematic mammalogy. A few measurements require brief descriptions.

Length of brain case.—Measured from right optic foramen to the right exoccipital bone at a point just dorsal to the right occipital condyle.

Breadth of brain case.—Greatest breadth of skull on nuchal line.

Cranial breadth.—Measured from depression on the mastoid process of the squamosal (between the zygomatic process and the nuchal line) to the comparable position on the opposite side of the skull.

Cranial depth.—Measured from basisphenoid and basioccipital to most dorsal point of the cranium; one jaw of calipers placed in the interpterygoid fossa, the other on the most dorsal point of the cranium.

Height of skull at bullae.—Measured with one jaw of calipers across most ventral point of each bulla and the other situated in depression on middorsal line just anterior to nuchal line.

Anterior breadth of zygomata.—The greatest spread of the zygomatic processes of the maxillae.

Posterior breadth of zygomata.—The greatest spread of the zygomatic arches posteriorly.

Measurements employed for kangaroo rats are described by Grinnell (1922: 4–7) and those for wood rats by Hooper (1938: 216).

The distribution maps of the species show present geographic ranges in the area studied. Almost all are based on specimens examined by me and on records available to me in field notebooks. The ranges of three species are established chiefly by published records; actual specimens of those forms were not available for study. On the distribution maps solid figures represent localities whence specimens were examined; open figures indicate published or manuscript records.

The data which form the basis for the accounts below are given in greater detail in the original manuscript of the present paper, now filed as a dissertation in the University of California Library. For practical purposes these data have not been published in full; the original manuscript, however, is available to anyone desiring more specific details.

Citellus beecheyi beecheyi Richardson
Beechey ground squirrel

Range.—Throughout area south of San Francisco Bay (Map 2), but uncommon in the San Francisco Bay faunal district.

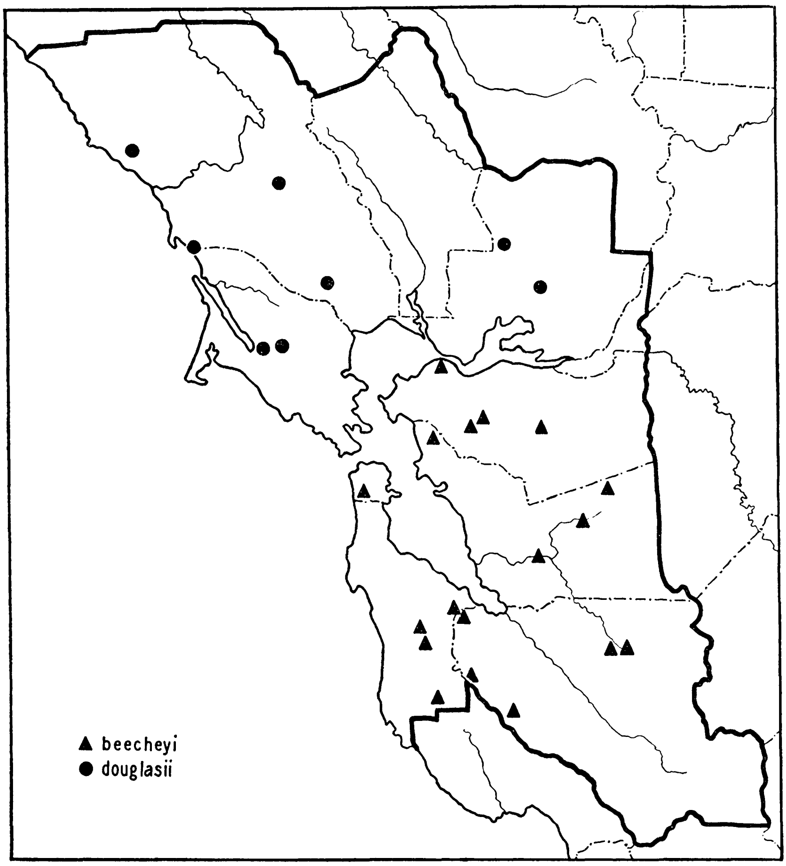
Habitat.—Open terrain, not woods or chaparral; grassland, with grasses not so high or rank as to obstruct the squirrel's field of vision for about fifty feet or more (Pl. III, Fig. 2); warm situations, slopes that receive much sunshine, particularly in spring and summer months; ground that is comparatively dry and well-drained, or at least safe from inundation during heavy rains; ground of a consistency that will permit tunneling by the squirrels and that will hold the shape of the tunnels after they are made, or rocky situations that provide well-protected crevices of sufficient size.

Remarks.—Fifty-nine specimens were examined. In his recent revision of the ground squirrels Howell (1938: 155) stated that intergradation of *beecheyi* with *fisheri* "occurs along the western side of San Joaquin Valley." The specimens I have examined from localities near the San Joaquin Valley, in eastern Alameda and Contra Costa counties, agree closely with near topotypes of *beecheyi*.

Citellus beecheyi douglasii Richardson

Range.—Throughout area north of San Francisco Bay, but less common in the north humid coast faunal subareas and the San Francisco Bay faunal district.

Comparisons.—From *C. b. beecheyi*, the only other race of ground squirrel in the bay area, *C. b. douglasii* differs in size (Table I), tail length (averaging 71 per cent of head and body length, as compared with 58 per cent in *beecheyi*), and characters of coloration and of cranium as follows: more pronounced dappling of dorsum; silvery white shoulders (dingy white in *beecheyi*); a well-defined dark brown, wedge-shaped area on nape between shoulders; palest bands of hairs of dorsal surface and of tail, silvery white (dingy white in *beecheyi*); gray ventral surface, with scant suffusion of cinnamon (usually strongly suffused with cinnamon in *beecheyi*); longer and narrower brain case.



MAP 2. Distribution of the subspecies of *Citellus beecheyi*, as established by specimens examined.

REMARKS.—Twenty-two specimens were examined. A specimen of *douglasii* in the collections of the California Academy of Sciences is labeled as collected at Martinez, a locality on the south side of San Francisco Bay, but I question the reliability of this record. I have collected several squirrels and seen many more in the area between Crockett and Avon, which includes Martinez; none was of the race *douglasii*.

The status of the *douglasii* squirrel with respect to the *beecheyi* squirrels appears to be remarkably similar to the relationships of certain species of kangaroo rats (Dale, 1939). The northern races of *Dipodomys heermanni* (*californicus, eximius,* and *saxatilis*) form a compact group allied to, but nevertheless uniformly differentiated from, the southern races (*heermanni, tularensis,* and others) of that species. A few specimens have been collected in areas between the previously known ranges of the two groups. These specimens are intermediate in all diagnostic characters except in the number of toes on the hind foot. The small first toe and claw is expressed as a unit without perceptible variation as to the amount of development; it is either present, as normally developed in the five-toed *heermanni* rats, or it is entirely absent. The intermediacy of the specimens in other respects, however, indicates that more complete intergradation is to be expected somewhere in the geographically intermediate area. *Citellus b. douglasii,* the geographic range of which in California conforms closely to that of the northern races of the kangaroo rats, meets the *beecheyi*-like *fisheri,* which, with *beecheyi,* ranges over the same areas as the southern races of *Dipodomys heermanni,* in the northern Sacramento Valley. Some squirrels from this area are intermediate in some characters between *douglasii* and *fisheri* and closely related races. Other specimens show no intermediacy, but are typical of one race or the other. In this instance, as with the kangaroo rats, more complete intergradation may be demonstrable when abundant material from geographically intermediate areas is at hand.

TABLE I

MEASUREMENTS OF ADULTS OF THE SUBSPECIES OF *Citellus beecheyi*

Examples are approximately one year of age and are from localities as follows: *beecheyi,* Berkeley, Alameda County; *douglasii,* coast region of northern California.

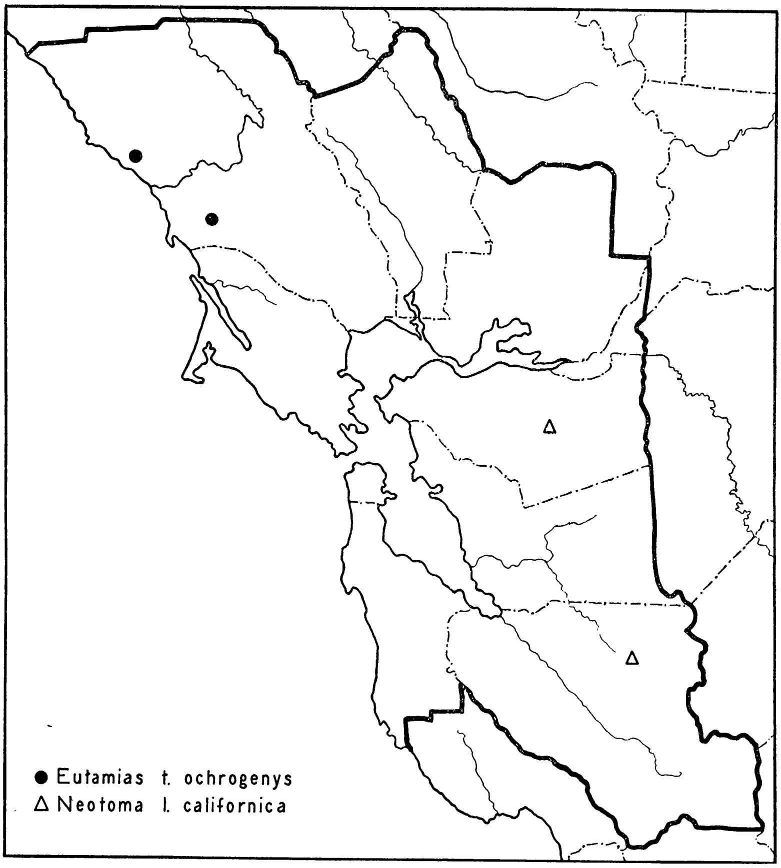
	beecheyi 3 ♀♀	*douglasii* 5 ♀♀
Total length	445 416–460	467 445–488
Tail	163 150–175	192 178–206
Hind foot	57 57–58	56 55–58
Body length	282 266–295	273 251–288
Basilar length	48.1 46.5–49.4	47.5 46.6–48.3
Zygomatic breadth	36.3 35.1–37.5	35.2 34.5–36.0
Nasal length	20.7 19.9–21.6	20.1 19.1–21.3
Length of brain case	24.3 23.8–24.6	24.1 23.5–25.0
Alveolar length of molar row	11.8 11.4–12.5	11.5 11.2–11.7
Ratio, tail length to body length (per cent)	58 56–62	71 62–77

Eutamias townsendii ochrogenys Merriam

Townsend chipmunk

RANGE.—Narrow belt along the seacoast in the Humboldt Bay faunal district; north from the vicinity of Freestone, Sonoma County (Map 3).

HABITAT.—Coniferous woods with an understory of brushy cover, or chaparral adjoining forests (Pl. V); cover offering protection near the ground and continuous, not interrupted by many open spaces; vantage points well above ground and protected skyward; situations protected from



MAP 3. Distribution of *Eutamias townsendii* and *Neotoma lepida,* as established by specimens examined (solid figures) and other records mentioned in the text (open figures).

strong cold winds; equable climate throughout the year, no freezing periods of lengthy duration; water, whether as fog drip or rain or as available in streams or pools; ground into which the chipmunk is able to dig.

REMARKS.—Twenty-four specimens were examined. The large size (Table II), relatively short tail (about 76 per cent of head and body length), dark and not well-contrasted coloration, sharply bicolored ears (in its summer pelage), broad spread of zygomata (over 21.2 mm.), and distinct postpalatal spine distinguish *ochrogenys* from the other kinds of chipmunks in the bay area. Its habitat preferences are also distinct. As C. Hart Merriam early pointed out (1897: 195), *ochrogenys* is a Boreal form, inhabiting coniferous forests and their bordering growths. *E. sonomae* and *E. merriami* are Sonoran kinds, living in chaparral and ranging inland farther from the seacoast. *E. s. alleni* and *E. merriami pricei* live within coniferous forests, but generally in Sonoran islands of chaparral or ''pseudo-chaparral,'' such as is simulated by the debris of fallen trees.

Eutamias sonomae sonomae Grinnell

Sonoma chipmunk

RANGE.—Mountainous areas north of San Francisco Bay; north from Freestone, Sonoma County, and from near Vacaville, Solano County (Map 4). Principally in the north inner coast faunal district, inland from the coastal belt occupied by *E. t. ochrogenys.*

HABITAT.—Much the same as for *E. townsendii,* but in heavier chaparral and warmer, drier situations, such as those occupied by the hard chaparral association (pp. 24–25).

REMARKS.—Thirty-seven specimens were examined. *E. sonomae* appears to be the ecologic counterpart of *E. merriami,* which occupies the comparatively warm, dry, chaparral-covered areas south of the bay. It is structurally and ecologically distinct from *E. townsendii,* the species occupying the humid coastal belt to the west but with which *sonomae* sometimes occurs locally. At each of two localities, Freestone and seven miles west of Cazadero, for example, the two kinds were collected; specimens of *sonomae* were taken principally in hard chaparral and those of *townsendii* among redwoods and soft chaparral. These two habitats occur side by side at these localities.

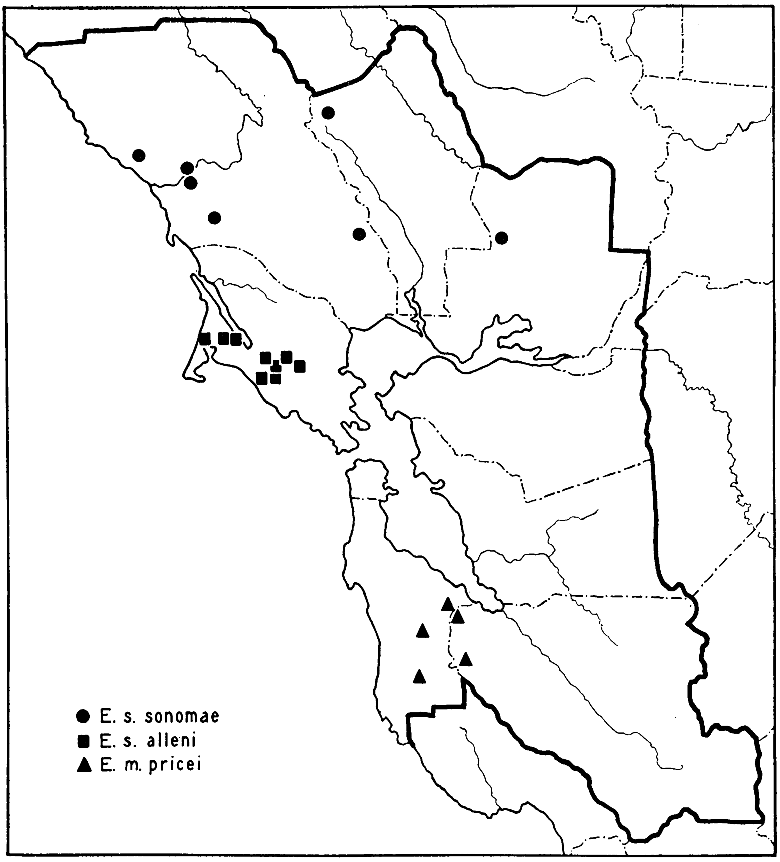
Eutamias sonomae alleni Howell

RANGE.—Range limits essentially those of the Marin faunal district; known from the triangular area extending from the vicinity of Muir Woods and San Rafael northwest to the base of the Tomales Peninsula, near Inverness.

COMPARISONS.—*Eutamias sonomae alleni* differs from *E. s. sonomae* in smaller size (well seen in total length, Table II); darker and more rufous dorsal coloration, particularly in the summer pelage; more extensive suffusion of cinnamon (less grayish) over the lighter parts of the pelage, particularly the dorsal and genal stripes and the belly; and shallower rostrum.

Compared with the other species of chipmunk in the bay area the species *sonomae,* including the races *sonomae* and *alleni,* is of medium to small size and of medium tail length (about 80 per cent of head and body length); it is brightly and contrastingly colored and has a short broad rostrum.

REMARKS.—Thirty-four specimens were examined. The forms *sonomae* and *alleni* in my opinion should be considered conspecific, even though the two are completely separated geographically and thus have no opportunity to interbreed. The two are similar in many characters of skin and skull; *alleni* is essentially a small *sonomae*. Evidence of complete intergradation,



MAP 4. Distribution of the subspecies of *Eutamias sonomae* and *Eutamias merriami*, as established by specimens examined.

now lacking, is to be expected from the study of a larger number of specimens.

Eutamias merriami pricei Allen

Merriam chipmunk

RANGE.—South of San Francisco Bay, within the Santa Cruz faunal district, in the bay area; specifically, south from the vicinity of Sierra Morena and Redwood City, San Mateo County (Map 4).

HABITAT.—Apparently the same as for *Eutamias sonomae.*

REMARKS.—Twenty-nine specimens were examined. *Eutamias merriami* is more closely related to *Eutamias sonomae* than to *Eutamias townsendii. Eutamias merriami pricei* and *Eutamias sonomae,* particularly the race *sonomae,* are similar in habitat preferences and many characteristics of skin and skull. *E. m. pricei* differs from *sonomae,* however, in the following characters: longer tail (Table II); grayer dorsum (less of tawny or cinnamon hues) in both summer and winter pelages, the light dorsal and cheek stripes whitish (in summer, at least, without a pronounced wash of reddish pigments) and less sharply contrasted with adjoining areas in the winter pelage; longer and narrower rostrum; and open, oval, or elliptical sphenopalatine vacuities.

From the species *Eutamias townsendii,* the subspecies *ochrogenys* in particular, *Eutamias merriami pricei* differs as follows: size smaller and tail longer; color lighter at all times of year; pale lines of back and cheeks whiter (not suffused with tawny or cinnamon); ears not so sharply bicolor; underparts whitish, with less of tawny suffusion; tail paler and edged with tan (not white); rostrum of skull narrower and longer, relative to the length

TABLE II

MEASUREMENTS OF ADULTS OF THE SUBSPECIES OF *Eutamias*

Localities represented are as follows: *E. townsendii ochrogenys,* western Sonoma County; *E. sonomae sonomae,* near Cazadero and Guerneville, Sonoma County; *E. s. alleni,* Marin County; *E. merriami pricei,* near Portola, San Mateo County.

	E. t. ochrogenys 3 ♀♀, 7 ♂♂	*E. s. sonomae* 3 ♀♀, 4 ♂♂	*E. s. alleni* 2 ♀♀, 5 ♂♂	*E. m. pricei* 5 ♀♀, 1 ♂
Total length	269 254–287	265 253–278	241 235–244	263 242–277
Tail	115 108–128	120 116–127	106 101–110	129 115–140
Hind foot	39 37–41	37 36–38	35 34–37	36 35–38
Body length	153 142–170	144 137–156	133 131–135	134 127–142
Greatest length of skull	40.0 38.9–41.6	38.9 38.2–39.6	37.6 36.6–39.1	38.2 36.9–38.9
Zygomatic breadth	22.1 21.2–22.6	20.8 20.2–21.3	20.5 20.3–21.0	20.4 19.6–20.9
Cranial breadth	17.5 17.0–18.1	17.0 16.6–17.5	16.7 16.3–17.2	17.1 16.9–17.4
Cranial depth	12.7 12.3–13.0	12.4 11.8–12.7	12.0 11.6–12.3	12.7 12.5–12.8
Nasal length	11.8 11.3–12.3	12.0 11.1–12.6	11.6 10.9–12.3	12.2 11.7–12.9
Depth of rostrum	6.4 6.1–6.7	6.3 5.9–6.4	6.1 5.8–6.3	6.2 6.0–6.3
Length of incisive foramen	2.8 2.6–2.9	2.4 2.1–2.7	2.4 2.1–2.7	2.6 2.5–2.8
Ratio, tail length to body length (per cent)	76 68–84	83 77–85	80 77–82	96 91–104

of the skull; zygomatic spread less; brain case relatively larger; nasals longer and notched more deeply terminally; palatine spine shorter; upper incisors more recurved; and sphenopalatine vacuities open.

The chipmunks south of San Francisco Bay (*E. merriami pricei*) are distinct from those north of the bay (*E. sonomae sonomae, E. s. alleni,* and *E. townsendii ochrogenys*) in at least three conspicuous features—two of skin and one of skull—namely, long tail (about 96 per cent of head and body length), buffy and gray coloration, and open sphenopalatine vacuities.

Tamiasciurus douglasii molli-pilosus Audubon and Bachman
Douglas red squirrel

RANGE.—Entirely north of San Francisco Bay and the Sonoma-Marin gap in the Humboldt Bay faunal district; north from the vicinity of Freestone, Sonoma County (Map 7).

HABITAT.—Broken or mixed woods and margins of heavy forests, but not highly open forests; redwoods, chiefly; woods of reproducing trees, not of immature saplings only; humid, cool situations protected from intense heat.

REMARKS.—Fifteen specimens were examined. The species is not abundant in the bay area. If numbers of individuals may be used as a criterion, the range of the species in Sonoma County may be considered marginal as regards requirements for red squirrel existence.

Sciurus griseus griseus Ord
Western gray squirrel

RANGE.—In mountains and wooded valleys north of San Francisco Bay; north from the vicinity of Muir Woods, Marin County, and near Vacaville, Solano County. Principally, in the Marin and northern inner coast districts, but also in drier parts of the Humboldt Bay district (Map 5).

HABITAT.—Trees, conifers, or hardwoods, in pure or mixed stands; open forests, with an open floor between the trees (Pl. IV); free water, whether from rain, dew, or other sources, within the home range of the squirrel.

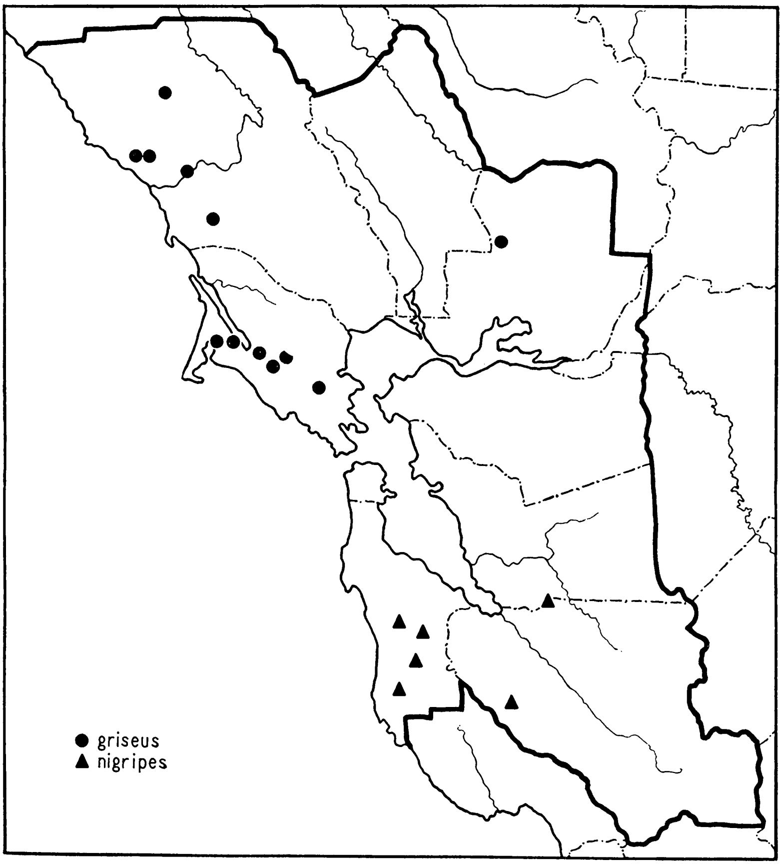
REMARKS.—Seventeen specimens were examined. A specimen from four miles west of Skaggs, Sonoma County, has the entire back surface of the ears as reddish brown as in *nigripes.*

Sciurus griseus nigripes Bryant

RANGE.—In mountains of the coast ranges south of San Francisco Bay; south from north-central San Mateo County. Principally in the southern humid coast faunal subarea, but also in the southern inner coast district, in the vicinity of Mount Hamilton, Santa Clara County.

COMPARISONS.—The following characters distinguish *nigripes* from *griseus:* smaller size (Table III); darker dorsum; reddish brown ears, foreback, and back of ears; black or blackish brown dorsal surface of feet (grizzled in *griseus*); a more distinct eye ring; narrower incisors (upper incisor at alveolus about 1.5 mm., compared with 1.8 mm. in *griseus*); shorter nasals (their length averages 34.6 per cent of total length of skull, 36 per cent in *griseus*); and relatively longer incisive foramen.

REMARKS.—Thirty-one specimens were examined. Specimens in juvenile



MAP 5. Distribution of the subspecies of *Sciurus griseus*, as established by specimens examined.

or faded, worn pelage of summer lack the reddish brown color on the back and ears. The single specimen examined from the Mount Hamilton range does not differ appreciably from specimens obtained in the Santa Cruz Mountains, which lie on the opposite side of the Santa Clara Valley from Mount Hamilton.

TABLE III

MEASUREMENTS OF ADULTS OF THE SUBSPECIES OF *Sciurus griseus*

The specimens of *griseus* are from the north-central coast of California; those of *nigripes* from San Mateo and western Santa Clara counties.

	griseus 9 ♀♀, 3 ♂♂	*nigripes* 5 ♀♀, 7 ♂♂
Total length	575 562–593	553 543–582
Tail	275 250–307	263 250–274
Hind foot	79 73–84	75 71–78
Body length	302 286–335	291 280–308
Greatest length of skull	66.4 64.7–69.1	64.2 62.1–66.9
Nasal length	24.1 22.8–25.2	22.2 21.5–23.5
Zygomatic breadth	37.9 36.5–39.5	36.2 35.2–38.1
Length of brain case	24.8 23.9–25.5	24.4 23.5–25.6
Breadth of brain case	27.0 26.3–28.1	25.7 24.8–26.8
Length of incisive foramen	3.8 3.4–4.3	4.0 3.7–4.5

Thomomys bottae bottae Eydoux and Gervais

Botta Pocket Gopher

RANGE.—Coastal part of area south of San Francisco Bay and principally west of the inner coast ranges (Map 6).

HABITAT.—Semiopen to open situations, not dense woods or chaparral; ground that is not water-soaked, not too rocky or adhesive to prohibit tunneling by the gopher, nor too sandy to fail to retain the shape of the burrow; ground supporting fleshy rootstocks.

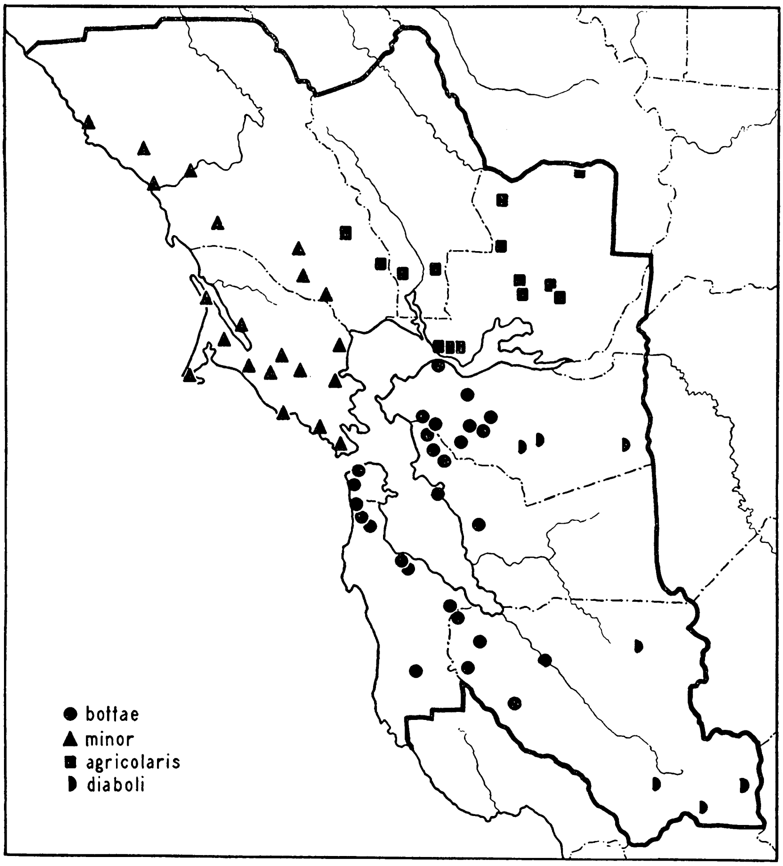
REMARKS.—Two hundred and ninety-six specimens were examined. Specimens from east of San Francisco Bay in the vicinity of Berkeley and Oakland, Alameda County, average larger and have broader zygomata, especially anteriorly, than those from the vicinity of San Francisco, San Francisco County, and Palo Alto, Santa Clara County. Specimens from Walnut Creek grade toward *diaboli* in characters of the rostrum and upper incisors.

Within the area studied, the gophers from north of San Francisco Bay (two races) have in common at least two features not seen in gophers from south of the bay (two races), namely, relatively weaker zygomata, without the broadly expanded maxilla, and pale yellow instead of dark yellow incisors.

Thomomys bottae minor Bailey

RANGE.—North of San Francisco Bay in the northern humid coast faunal subarea.

COMPARISON.—From the race *bottae, minor* differs in its smaller size (Tables IV and V); darker dorsal coloration; shallower and less angular skull; less rugged zygomata with much smaller zygomatic arm of the maxilla; broader interorbital space; more rounded occiput; broader nasals, anteriorly; and paler incisors. Compared with *agricolaris,* the geographic race into which it grades toward the east, *minor* is larger and is darker dor-



MAP 6. Distribution of the subspecies of *Thomomys bottae,* as established by specimens examined.

sally; it has less orange-cinnamon ventrally, a longer and narrower skull, well seen in the spread of the zygomata, breadth of the rostrum, and breadth of the brain case; shorter premaxillae, relative to the length of the nasals; and a more rounded occiput.

REMARKS.—One hundred and fifty-seven specimens were examined. The skulls of specimens from Marin County are more prominently ridged than are those from Fort Bragg, Mendocino County, the type locality of *minor*. In this respect they grade toward *bottae*.

Thomomys bottae agricolaris Grinnell

RANGE.—North of San Francisco Bay on the west side of the lower Sacramento Valley and on the slopes of the adjoining inner coast ranges; north from Carquinez Straits and east from the vicinity of Sonoma and Eldridge, Sonoma County, through southern Napa and Solano counties. Principally in the Great Valley district.

COMPARISONS.—From *bottae, agricolaris* differs in smaller size (Tables IV and V), paler (less blackish) dorsum, brighter, orange venter, shorter but proportionally broader brain case, larger bullae, and less recurved and paler upper incisors; the premaxillary tongues extend farther posteriorly beyond the nasals, the maxillary flange of the zygomatic arch is less developed, and the parietal ridges are slight and farther apart. The subspecies *agricolaris* is distinguishable from *diaboli* by the same characters, less pronounced, however, which separate *agricolaris* from *bottae*.

REMARKS.—Ninety specimens were examined. *T. b. agricolaris* is more distinct from *minor*, with which it intergrades toward the west, and *bottae* and *diaboli*, across San Francisco Bay, than it is from some neighboring races of *bottae—navus*, for example, in the Great Valley.

No specimens of pocket gophers from northern Napa County and northeastern Sonoma County are at hand. Examples from these areas may prove to be of the geographic race *acrirostratus* Grinnell (1935 *a:* 408), which may extend that far south in the coast ranges.

Thomomys bottae diaboli Grinnell

RANGE.—South of San Francisco Bay in the inner coast ranges; south and east from the vicinity of Mount Diablo, Contra Costa County; at the southern part of the range west to Gilroy, Santa Clara County. Principally in the southern inner coast faunal district.

COMPARISONS.—Specimens from the upper slopes of the inner coast ranges in Contra Costa and Santa Clara counties average slightly smaller and paler than do specimens of *bottae* from coastal areas; the nasals average slightly shorter, the rostrum narrower, the incisors more recurved, and the parietal ridges farther apart. From *minor, diaboli* differs in its paler coloration, less spread of zygomata, broadly expanded zygomatic process of maxilla, broader rostrum, and more recurved and brighter yellow, upper incisors.

REMARKS.—Sixty-seven specimens were examined. These pocket gophers to which the name *diaboli* is here applied are in varying degree intermediate in characters of skin and skull between *bottae* and *angularis*, the race occupy-

TABLE IV

MEASUREMENTS OF YOUNG ADULT FEMALES OF THE SUBSPECIES OF *Thomomys bottae**

The specimens are from localities as follows: *bottae,* Berkeley, Alameda County; *minor,* Muir Beach, Marin County; *agricolaris,* Denverton, Solano County; *diaboli,* Mount Diablo, Contra Costa County.

	bottae 8 ♀♀	*minor* 5 ♀♀	*agricolaris* 10 ♀♀	*diaboli* 9 ♀♀
Total length	197 185–204	203 193–208	194 177–201	201 193–216
Tail	62 55–68	59 57–61	55 49–61	57 50–65
Hind foot	28 26–30	28 25–29	26 25–27	27 25–28
Body length	135 125–141	145 135–151	138 126–143	144 137–151
Condylonasal length	36.6 35.3–37.9	35.7 35.2–36.5	34.8 33.8–35.6	35.4 34.6–36.3
Anterior breadth of zygomata	22.9 22.1–23.9	21.8 21.6–22.1	21.9 21.2–22.4	21.7 21.0–23.2
Posterior breadth of zygomata	23.4 22.3–24.5	22.9 22.4–23.3	23.2 22.6–23.6	22.8 21.8–24.4
Nasal length	12.0 11.3–12.8	11.1 10.7–11.8	11.4 10.4–12.1	11.2 10.6–12.1
Breadth of rostrum	7.1 6.7–7.5	6.8 6.7–6.9	6.7 6.3–7.1	6.8 6.2–7.1
Interorbital breadth	6.7 6.3–6.9	6.6 6.4–6.8	6.3 6.1–6.6	6.4 6.0–6.9
Breadth of brain case	19.3 18.5–20.1	18.3 18.0–18.6	18.6 18.2–19.4	18.6 18.0–19.6

* Two sets of measurements are given for each subspecies of *Thomomys bottae* present in the special area under consideration. The first set includes averages and extremes of females judged to be of young adult age, as determined by amount of closure of cranial sutures, degree of ridging of the skull, proximity and height of parietal ridges, and amount of wear on the molariform teeth. Animals of this age apparently make up the bulk of gophers in study collections. The greater numbers of specimens of one age allow for a selection of more satisfactory series for comparative purposes. The second set, measurements for a large, usually old, adult of each subspecies, is included to convey some concept of maximum size attained by females of each subspecies.

ing the western part of the San Joaquin Valley. Probably *diaboli* should be considered synonymous with *angularis,* and the gophers of central and eastern Contra Costa, Alameda, and Santa Clara counties referred to *bottae,* with the notation that they are grading toward *angularis.*

Perognathus inornatus inornatus Merriam
Great Valley pocket mouse

RANGE.—Great Valley faunal district. Known in the bay area only from remains in owl pellets collected on the north side of San Francisco Bay near Benicia, Solano County (Stoner, 1933: 204) and on the south side of the bay near Somersville, Contra Costa County (Map 7).

HABITAT.—"Dry, open, grassy or weedy ground, of fine-textured, usually sandy soil" (Grinnell, 1933: 149).

TABLE V

MEASUREMENTS OF AN OLD ADULT FEMALE OF EACH SUBSPECIES OF *Thomomys bottae**

The specimens are from localities as follows: *bottae,* Oakland, Alameda County; *minor,* near San Rafael, Marin County; *agricolaris,* Rio Vista Junction, Solano County; *diaboli,* Mount Diablo, Contra Costa County.

	bottae	*minor*	*agricolaris*	*diaboli*
Total length	227.0	211.0	195.0	233.0
Tail	62.0	61.0	48.0	67.0
Hind foot	30.0	31.0	28.0	30.0
Body length	165.0	150.0	147.0	166.0
Condylonasal length	40.8	38.9	35.8	39.2
Anterior breadth of zygomata	25.7	23.7	23.8	24.5
Posterior breadth of zygomata	26.2	25.2	25.2	25.1
Nasal length	14.5	12.7	11.0	12.8
Breadth of rostrum	7.9	7.4	7.0	7.3
Interorbital breadth	6.7	7.0	6.3	6.7
Breadth of brain case	21.8	20.6	19.8	20.4

* See note to Table IV.

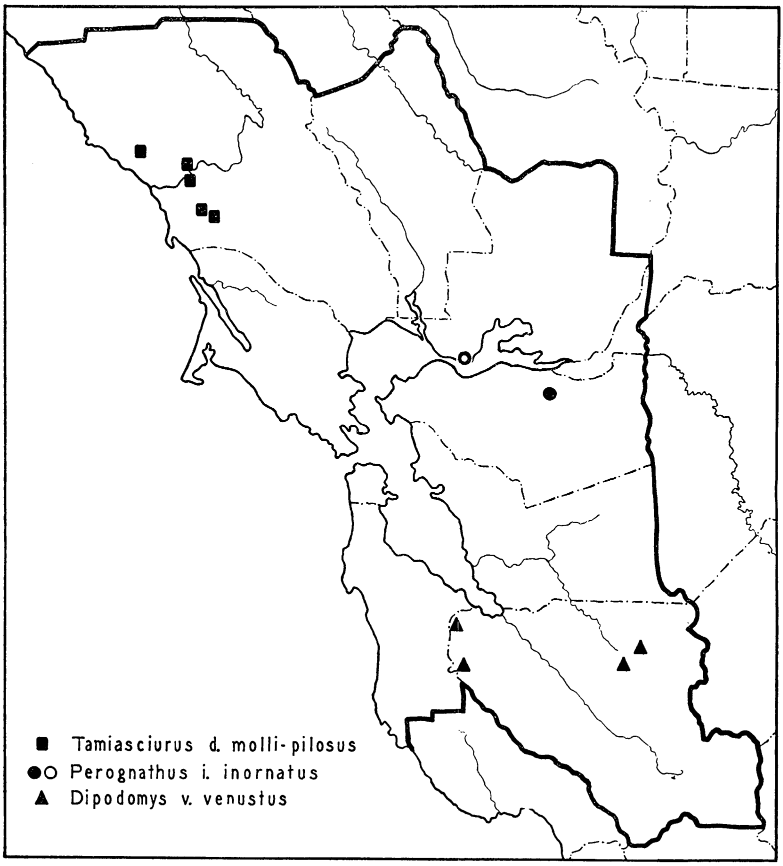
Perognathus californicus californicus Merriam
California pocket mouse

RANGE.—Mountains and foothills south of San Francisco Bay; south from northern San Mateo County and the vicinity of Sommersville, Contra Costa County (Map 8).

HABITAT.—Open to semiopen situation, not woods or heavy chaparral or ground densely covered with high herbaceous vegetation; ground that is rocky, hard, well drained, and dry, as on steep slopes (as that supporting *Artemisia californica*) exposed to abundant solar radiation, particularly during spring and summer months.

REMARKS.—One hundred and thirty specimens were examined. *Perognathus californicus dispar* may range into the extreme eastern part of the special area under consideration, but no specimens of that race have been examined. The species varies appreciably from place to place in the bay area. Specimens from the vicinity of Berkeley, the type locality of the race *californicus,* are unique in being small. They are intermediate in other characters between specimens from localities to the west (San Mateo and western Santa Clara counties) and east (vicinity of Mount Diablo). Specimens from Mount Diablo, the type locality of *Perognathus armatus* Merriam, differ slightly, on the average, from topotyes of *californicus* in larger size, larger ear, paler dorsum, and narrower brain case (relative to the greatest length of the skull). Specimens from San Mateo and western Santa Clara counties average larger than topotyes of *californicus,* the tail is longer (relative to the head and body length), and the skull is longer and broader (well seen in the longer and broader brain case, rostrum, and nasals).

There is some basis, thus, for recognizing three geographic races of pocket mice within the area presently ascribed to the race *californicus,* each characterized by peculiarities of skin and skull. Pending revision of the genus *Perognathus,* I refer all specimens of *Perognathus californicus* from the area studied to the race *californicus.*

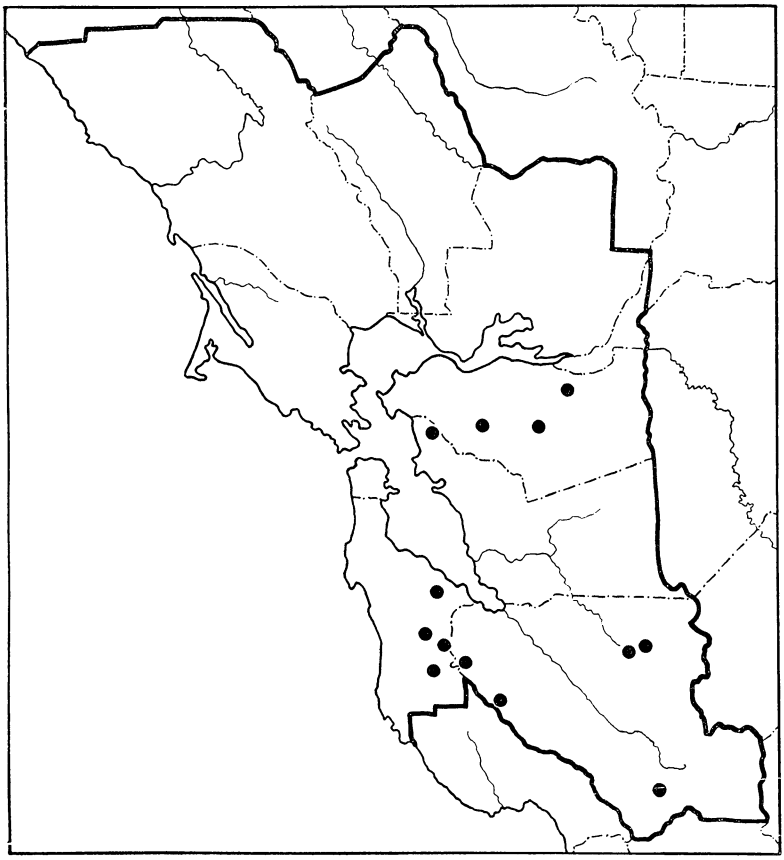


MAP 7. Distribution of *Tamiasciurus douglasii, Perognathus inornatus,* and *Dipodomys venustus,* as established by specimens examined (solid figures) and a published record (open figure).

Dipodomys heermanni californicus Merriam
Heermann kangaroo rat

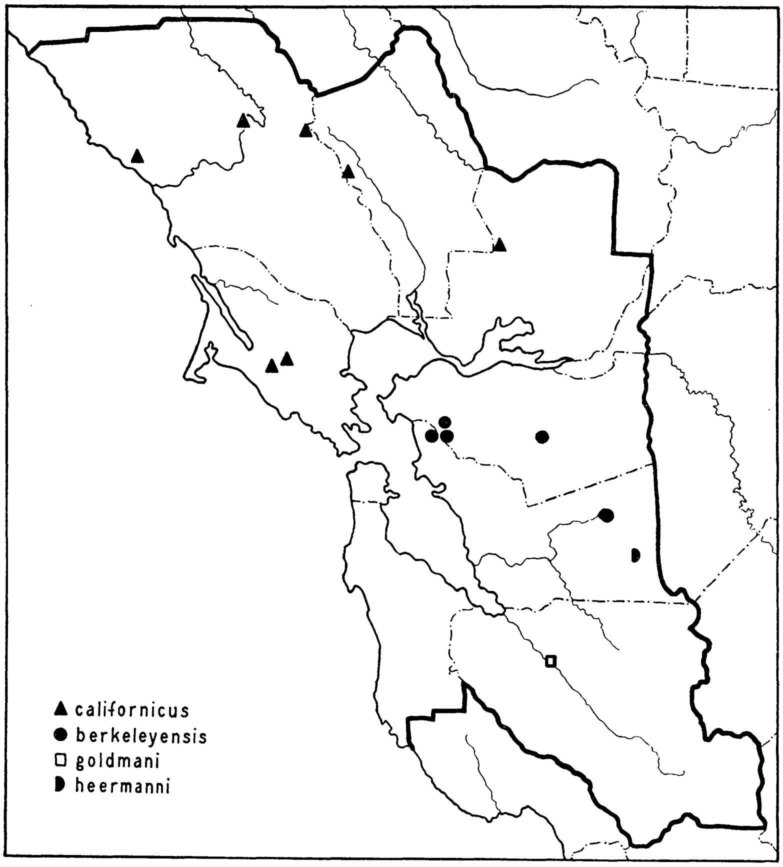
RANGE.—Throughout most of the area north of San Francisco Bay, but chiefly east of the humid belt along the seacoast and west of the Sacramento Valley. Known to occur as far south as the vicinity of Nicasio, Marin County, and east to near Vacaville, Solano County (Map 9).

HABITAT.—Open ground, whether treeless, sparsely covered with chaparral, or within a forest; grasses or some other growth of low vegetation, whether on hilltop, slope, or level, with plant growth not so high or dense as to prohibit free locomotion of the animal; ground that is gravelly, sandy, or that contains ready-made, kangaroo rat-size crevices or burrows; ground that receives considerable insolation, as on crests of hills and south-facing slopes.



MAP 8. Distribution of *Perognathus californicus,* as established by specimens examined.

REMARKS.—Seven specimens from the bay area were examined. Separated by San Francisco Bay from the other subspecies of *Dipodomys heermanni* in the bay area, *californicus* reflects well its isolation from those subspecies in its characteristics of skin and skull, of which large size, long white-tipped tail, four-toed hind feet, and broad supraoccipital and interparietal are particularly distinctive. The relationships of *californicus* with the more southern races of *Dipodomys heermanni* have been considered in some detail by Dale (1939) and summarized in the present paper under the account of *Citellus beecheyi douglasii* (p. 30). Probably, *californicus* should be treated as a race of *Dipodomys heermanni* and not as a separate species.



MAP 9. Distribution of the subspecies of *Dipodomys heermanni*, as established by specimens examined (solid figures) and a record (open figure).

Dipodomys heermanni berkeleyensis Grinnell

RANGE.—South of San Francisco Bay, from Berkeley, Alameda County, and Mount Diablo, Contra Costa County, south at least to the vicinity of Livermore, Contra Costa County.

COMPARISONS.—Closest affinity of *berkeleyensis* is with *goldmani*, whose known range lies a short distance to the south of that of *berkeleyensis*. The latter race, however, has a relatively shorter tail (Table VI), more decumbent upper incisors, slightly smaller auditory bullae, larger interparietal and supraoccipital, and less truncate posterior part of the brain case.

REMARKS.—Twenty specimens were examined. Little is known concerning the range of *berkeleyensis* and the variation correlated with geography occurring in that race. Specimens from Mount Diablo have a broader rostrum than do those from Berkeley; only two adult skulls from Berkeley are at hand. Two specimens examined from Livermore are intermediate in characters between *berkeleyensis* and *tularensis.*

Dipodomys heermanni goldmani Merriam

RANGE.—Known in the bay area only from the vicinity of San Jose, Santa Clara County, the northernmost record of occurrence of the subspecies. Probably lives principally in the southern inner coast faunal district.

COMPARISONS.—The race *goldmani* is smaller and darker than the race *tularensis,* the terminal tail hairs are shorter (longest hairs about 20 mm. in *goldmani* compared with 28 mm. in *tularensis*), the black tail stripes are more than twice the width of the white tail stripes, and the ear is slightly larger.

D. h. goldmani is more distinct from *californicus* than it is from *tularensis.* It is smaller and paler; the tail is shorter, much more scantily haired, and dark distally; five toes are present on the hind foot; the skull is relatively narrower across the temporal bullae, and the nasals are relatively shorter.

REMARKS.—The range of *goldmani* probably complements that of *venustus: goldmani* lives around the edges of valleys and on the adjoining lower slopes, whereas *venustus* occupies higher, cooler slopes and crests of ridges.

Dipodomys heermanni tularensis Merriam

RANGE.—Probably only extreme eastern Alameda County, in the special area under consideration.

COMPARISONS.—The race *tularensis* differs from *berkeleyensis* in the following characters: larger size (Table VI), smaller ear, longer tail tuft, narrower interparietal and supraoccipital, larger bullae, and more truncate posterior part of skull. The dorsal coloration is darker in tone; the dark facial, rump, and tail markings, as a result, contrast less with the adjoining areas.

D. h. tularensis is similar to *D. h. californicus* in size, but is much paler; the dark markings are less emphasized; the terminal tuft of the tail is longer and gray (not white); five toes are present on the hind foot; the nasals are shorter; the rostrum is more slender, and the maxillary arches are narrower (at the middle of the arch averaging 4.9 mm., as compared with 5.6 in *californicus*).

REMARKS.—Probably kangaroo rats that exhibit in full all the diagnostic characters of *tularensis* do not occur in the bay area. Two specimens at hand from near Livermore, Alameda County, are between *tularensis* and *berkeleyensis* in characters of skin and skull.

Dipodomys venustus venustus Merriam
Santa Cruz kangaroo rat

RANGE.—Coastal areas south of San Francisco Bay; chiefly in the outer coast ranges and the Santa Cruz faunal district but also recorded from the vicinity of Mount Hamilton, Santa Clara County, in the inner ranges and southern inner coast district (Map 7).

HABITAT.—Open to rather densely wooded lands supporting open to dense stands of chaparral and annuals; well-drained and friable soils, as on hilltops or slopes, not clay or extremely rocky soils; lands not cultivated annually; humid situations, where fogs or clouds are present almost daily.

REMARKS.—Twenty-five specimens were examined. *Dipodomys venustus* is, for the most part, ecologically separated from *D. heermanni*. The former

TABLE VI

MEASUREMENTS OF ADULTS OF THE SUBSPECIES OF *Dipodomys heermanni*

The specimens are from localities as follows: *californicus*, Mendocino County; *berkeleyensis*, Mount Diablo, Contra Costa County; *goldmani*, Seaside, Monterey County; *tularensis*, Tracy, San Joaquin County.

	californicus 6 ♀♀, 4 ♂♂	*berkeleyensis* 7 ♀♀, 4 ♂♂	*goldmani* 5 ♀♀, 5 ♂♂	*tularensis* 4 ♀♀, 6 ♂♂
Total length	319 298–340	289 280–302	291 276–305	301 272–313
Tail	198 183–217	173 166–182	178 169–188	184 161–193
Hind foot	45 43–47	42 39–45	42 40–44	44 42–46
Ear from notch (dry)	15 14–16	11 10–13	11 10–13	10 9–11
Body length	120 110–135	116 110–122	113 106–120	117 111–124
Greatest length of skull	39.9 38.9–41.2	38.3 36.7–39.6	39.1 37.8–41.1	39.8 37.9–40.8
Breadth of skull across bullae	24.3 23.2–24.9	23.6 22.1–24.5	24.0 23.3–24.8	24.6 23.4–25.5
Spread of maxillary arches	22.7 21.5–23.7	21.7 20.2–22.4	22.2 21.3–23.5	22.1 21.1–22.7
Nasal length	15.2 14.6–16.1	14.2 13.6–14.8	14.4 13.3–15.5	14.6 13.6–15.2
Greatest width of rostrum near end	4.2 3.5–4.6	3.7 3.4–4.0	3.9 3.4–4.3	3.9 3.7–4.1
Width of maxillary arch at middle	5.6 5.1–6.1	4.7 4.2–5.5	5.1 4.9–5.6	4.9 4.3–5.2
Length of longest hairs from tip of tail	22 17–25	20 17–24	20 16–23	28 22–34
Ratio, tail length to body length (per cent)	166 152–182	150 140–161	157 141–168	156 145–172

inhabits areas covered more or less heavily with chaparral and usually at higher elevations. The latter occupies the rocky or sandy lower slopes and valleys clothed with a rather sparse growth of grass and other low-growing annuals and perennials. Salient characters which distinguish the species *venustus* from the species *heermanni* are: large size (Table VI), dark dorsum, large ear, and narrow (both as regards their width and spread) maxillary arches.

Reithrodontomys megalotis longicaudus Baird
Western harvest mouse

RANGE.—Throughout area, both north and south of San Francisco Bay (Map 10).

HABITAT.—Open to semiopen ground, not continuous heavy chaparral or dense forest; growth of grass, low herbage, or low-lying bushes that provides cover, yet that is not so dense or high as to prohibit free movement of a harvest mouse (Pl. II, Fig. 2).

REMARKS.—One hundred and eighty-three specimens were examined. The ranges of *R. megalotis* and *R. raviventris* are complementary for the most part, but they overlap in some areas, as, for example, where relatively dry grasslands meet salicornia marshes. Specimens of each species were collected in the same trap line, in several instances in alternate traps, in the marshes near Avon and at the mouth of San Pablo Creek, Contra Costa County, and of Coyote Creek and Corte Madera Creek, Marin County.

There is some evidence that marsh-inhabiting individuals are more intensely pigmented than are individuals living on uplands. Two specimens from the head of Tomales Bay, four from Taylorville, and two from Nicasio, Marin County, are darker dorsally and more orange in tone ventrally than average. Three specimens from the marshes near Avon, Contra Costa County, are also darker than specimens from upland areas near by.

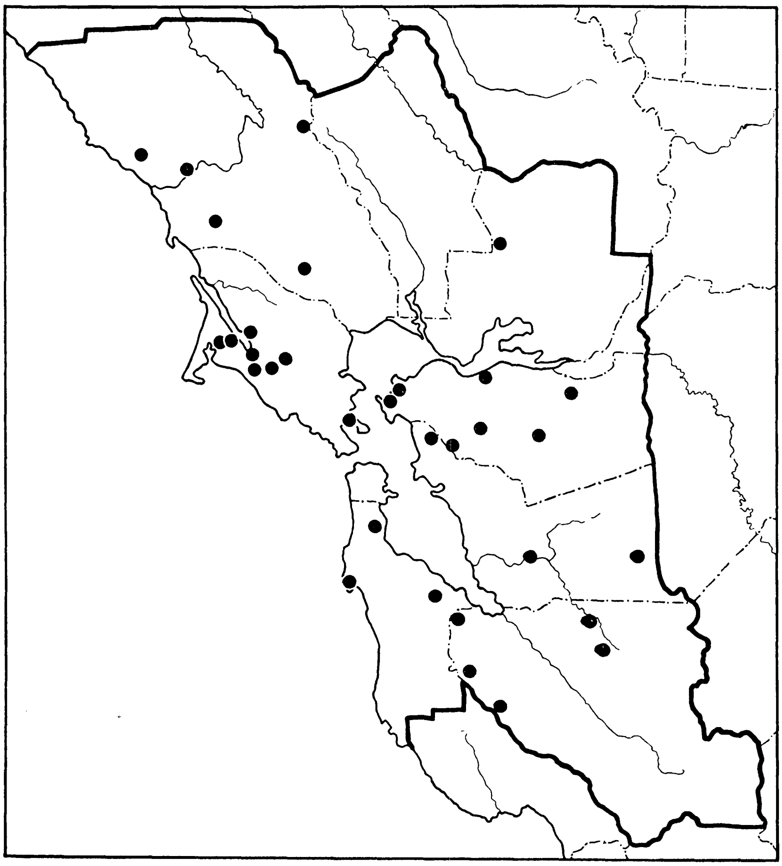
The specimens of *Reithrodontomys m. longicaudus* from the bay area differ from the specimens of *Reithrodontomys raviventris* at hand in the following characters: coarser, shorter fur of back and sides of body; paler, more grayish upper parts and white underparts; shorter brain case (Table VII); longer rostrum and nasals; and relatively longer incisive foramina.

Reithrodontomys raviventris raviventris Dixon
San Francisco harvest mouse

RANGE.—Both north and south of San Francisco Bay, entirely within the narrow belt of marshlands margining the bay; south from San Pablo Creek, Contra Costa County, around the south arm of San Francisco Bay to the vicinity of South San Francisco, San Mateo County; also in the bayside marshes in Marin County, at least as far north as Corte Madera. Confined to the San Francisco Bay faunal district (Map 11).

HABITAT.—Salt marshlands (Pl. I); marsh plants providing a dense mat a few inches above ground and a network of spaces on the ground; *Salicornia;* peat soils, continually moist; accessible elevated areas relatively safe from inundation and provided with the necessary cover.

REMARKS.—Forty-three specimens were examined. The presence of populations of *raviventris* north of San Francisco Bay in Marin County



MAP 10. Distribution of *Reithrodontomys megalotis,* as established by specimens examined.

that are completely isolated and yet are not perceptibly different from the populations south of the bay suggests that *raviventris* may have been transported to the north side during historical time. The transfer may have taken place in the latter part of the nineteenth century, when there was extensive commerce in hay, grain, and other products between many marsh-bordered ports within the bay. Petaluma and Alameda, for example, were then centers of shipping activity, ports of call for boats and barges from many other shipping points around the bay.

TABLE VII

MEASUREMENTS OF ADULTS OF SUBSPECIES OF *Reithrodontomys megalotis* AND *R. raviventris*

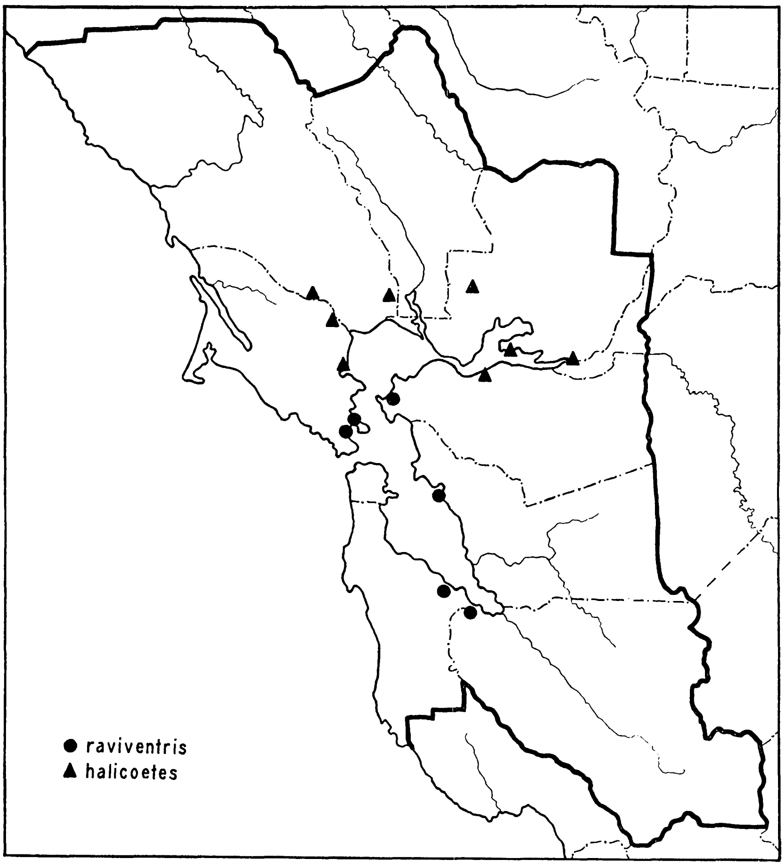
Examples are from localities as follows: *R. m. longicaudus*, Berkeley, Alameda County; *R. r. raviventris*, marshes along south arm of San Francisco Bay; *R. r. halicoetes*, Grizzly Island, Solano County.

	R. m. longicaudus 4 ♀♀, 13 ♂♂	*R. r. raviventris* 5 ♀♀, 10 ♂♂	*R. r. halicoetes* 7 ♀♀, 9 ♂♂
Total length	142 135–154	144 135–149	150 142–162
Tail	74 62–81	69 64–73	81 76–88
Hind foot	17 16–18	17 16–19	18 17–18
Body length	69 62–77	75 66–83 (5 spec.)	70 63–76
Greatest length of skull	20.7 20.2–21.1	21.0 20.2–21.4 (6 spec.)	20.8 19.8–21.5
Anterior breadth of zygomata	9.7 9.1–10.4	9.9 9.3–10.5 (6 spec.)	9.6 9.2–10.3
Posterior breadth of zygomata	10.4 9.8–10.8	10.6 10.2–10.9 (6 spec.)	10.7 10.2–10.9
Nasal length	7.7 7.3–8.1	7.5 7.1–7.9 (6 spec.)	7.4 6.9–7.8
Length of incisive foramen	4.4 4.2–4.6	4.3 4.0–4.6 (6 spec.)	4.0 3.5–4.3
Length of palatal bridge	3.2 3.0–3.5	3.4 3.0–3.6 (6 spec.)	3.3 3.0–3.5
Length of molar series	3.1 3.0–3.2	3.2 3.1–3.2 (5 spec.)	3.1 3.0–3.2
Depth of skull	7.8 7.4–8.1	8.1 7.9–8.3 (4 spec.)	8.1 7.8–8.5
Length of brain case	8.5 8.2–8.8	9.3 9.0–9.5	9.1 8.6–9.4
Ratio, tail length to body length (per cent)	107 83–121	93 77–104	116 104–127

Reithrodontomys raviventris halicoetes Dixon

RANGE.—Both north and south of San Francisco Bay, in bayside marshlands, and in the marshes of the lower part of the Sacramento River; west on the north side of the bay to five miles north of San Rafael, Marin County, and on the south side to the marshes near Avon, Contra Costa County, entirely east and north of the range of *raviventris*.

Comparisons.—*R. r. halicoetes* resembles *R. r. raviventris* in several features, of which size (Table VII), density and length of the fur, dorsal coloration, and length of the brain case are conspicuous. It differs from that race, however, in longer tail (averaging 81 mm., as compared with 69 mm. in *raviventris*), white venter (orange-cinnamon in *raviventris*),



Map 11. Distribution of the subspecies of *Reithrodontomys raviventris*, as established by specimens examined.

larger area of white on chin and throat, shorter incisive foramina, and narrower zygomata, anteriorly.

Remarks.—Seventy-six specimens were examined. Those from Grizzly Island, Solano County, exhibit more uniformly the characters of *halicoetes* than do topotypes from Petaluma.

The relationships of the forms *raviventris* and *halicoetes* have not been well understood. The specimens available to Howell (1914: 42) supplied but slight evidence of intergradation between the two forms, yet apparently the evidence was sufficient to indicate that more complete intergradation could be expected in specimens from areas geographically between the currently known ranges of those forms. Accordingly, he considered them to be conspecific. Grinnell (1933: 171) recognized each as a full species, because intergradation between the forms had not been demonstrated.

Several specimens at hand are intermediate between specimens of *raviventris* and *halicoetes* in the diagnostic characters of these forms; they are accordingly treated as subspecies. All but four of the twenty-four specimens of *halicoetes* from the Petaluma marshes, Sonoma County, are more or less suffused ventrally with the reddish orange of *raviventris;* some also have the short tail and broad zygomata of the latter race. A specimen from the Corte Madera marshes, Marin County, otherwise ''average'' *raviventris,* has the large white chin and throat area and long tail of *halicoetes.* Others from these marshes are variously between the two forms in characters of skin and skull.

Peromyscus californicus parasiticus Baird
California mouse

RANGE.—South of San Francisco Bay in the outer coast ranges and in that part of the inner ranges approximately east of the bay; chiefly in the Santa Cruz faunal district (Map 12).

HABITAT.—Chaparral or mixed chaparral and woods (not dense forests, grasslands, or pure stands of tall chamise) present continuously over relatively large areas (Pl. III), not as small isolated clumps; ground covered with litter, not grass-covered or bare, and well drained, as on hillsides.

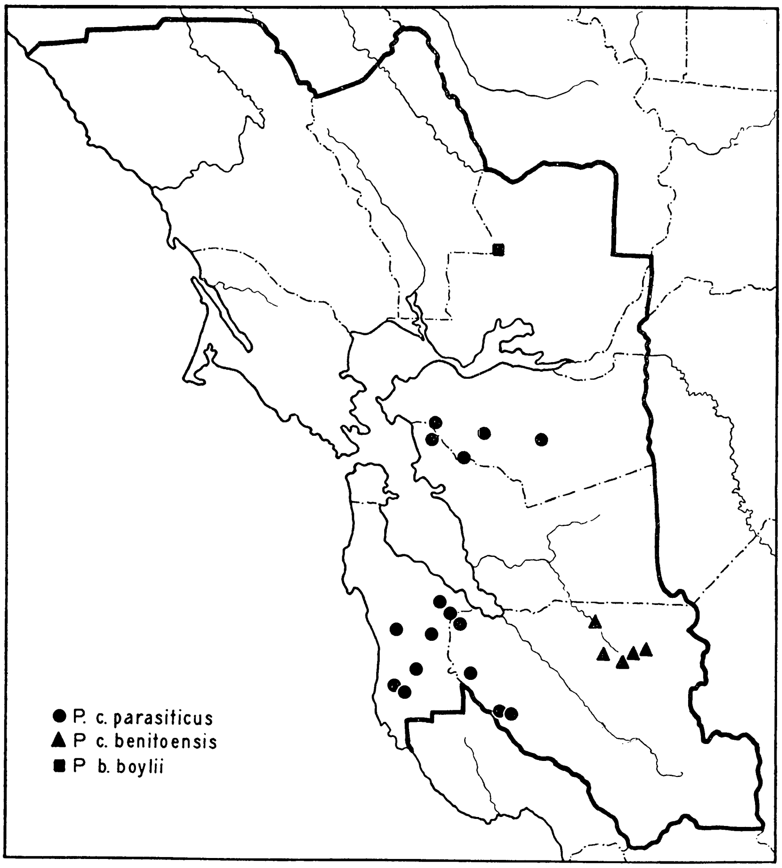
REMARKS.—One hundred and forty-six specimens were examined. Specimens from the vicinity of Berkeley, Alameda County, differ from topotypes of *parasiticus* and *benitoensis* almost as much as the topotypical series of each of these two races (from western Santa Clara County and Bear Valley, San Benito County, respectively) do from each other. Compared with them, Berkeley specimens have a longer skull (Table VIII), longer hard palate, and shorter incisive foramina. Their coloration is much as in topotypes of *parasiticus,* but darker gray dorsally (less cinnamon). The cinnamon-colored pectoral patch is smaller, and the tail is sharply bicolor.

Specimens from the vicinity of Mount Hamilton, Santa Clara County, are intermediate in characters of skin and skull between topotypes of *benitoensis* and *parasiticus,* but are nearer *benitoensis* in all characters except size of auditory bullae.

Peromyscus californicus benitoensis Grinnell and Orr

RANGE.—South of San Francisco Bay in the inner coast ranges and the southern inner coast faunal district; recorded north to Calaveras Valley, near Mount Hamilton, Santa Clara County.

COMPARISONS.—A study of the more complete material now available, obtained since Grinnell and Orr (1934) reviewed the species *Peromyscus californicus,* reveals that the following differences distinguish *benitoensis* from *parasiticus:* paler coloration, with less ventral pigmentation; shorter tail (Table VIII); slightly larger ear; broader brain case, relative to the greatest length of the skull; and larger auditory bullae.



MAP 12. Distribution of the subspecies of *Peromyscus californicus* and *Peromyscus boylii,* as established by specimens examined.

REMARKS.—Thirty-four specimens were examined, all from the vicinity of Mount Hamilton.

Peromyscus maniculatus gambelii Baird

Deer mouse

RANGE.—Throughout area, north and south of San Francisco Bay, but entirely inland from the humid belt along the seacoast (Map 13). Confined to the California faunal area.

HABITAT.—Ground provided with cover, whether that cover be ledges of rock, grass, chaparral, or forest (Pl. II, Fig. 2; Pls. III and IV), but not extremely wet areas or areas subject to frequent inundation, as those covered with *Salicornia* or other marsh plants.

REMARKS.—Ninety-three specimens were examined. *P. m. gambelii* grades into *P. m. rubidus* along the periphery of the coastal fog belt. In these geographically intermediate areas the mice vary in intermediacy in the characteristics of those two races; in a trap line one specimen may exhibit the characteristics of *gambelii*, another those of *rubidus*, and still others may be intermediate in one or more of the diagnostic characters of the two races. Specimens from nine miles northwest of Calistoga, Napa County, and from the marshes near Corte Madera and Manzanita, Marin County, for example, grade variously toward *rubidus*.

TABLE VIII

MEASUREMENTS OF ADULTS OF THE SUBSPECIES OF *Peromyscus californicus*

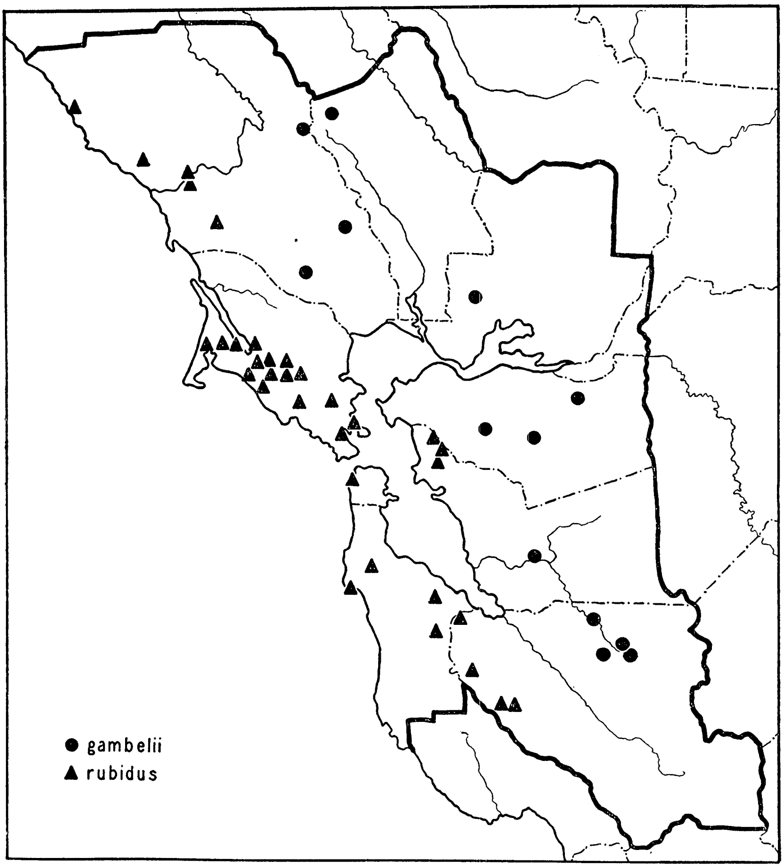
The measurements are of specimens from localities as follows: *parasiticus* (first column), Saratoga, Santa Clara County; *parasiticus* (second column), Berkeley, Alameda County; *benitoensis*, vicinity of San Benito and Hernandez, San Benito County.

	parasiticus 3 ♀♀, 3 ♂♂	*parasiticus* 6 ♀♀, 4 ♂♂	*benitoensis* 9 ♀♀, 5 ♂♂
Total length	257 250–265	253 248–258	253 242–260
Tail	136 128–144	134 127–140	133 125–139
Hind foot	27 26–28	28 25–32	27 26–28
Ear from notch (fresh)	24 23–26	....	26 25–28
Body length	120 115–122	118 108–126	119 114–125
Greatest length of skull	30.5 30.0–31.0	31.2 30.6–31.8	30.5 29.5–31.6
Basilar length	24.2 23.5–24.7	24.4 23.8–24.9	24.2 23.5–25.0
Nasal length	11.5 11.0–11.8	11.7 11.3–12.5	11.5 11.0–12.3
Zygomatic breadth	15.6 15.3–16.1	15.9 15.2–16.4	15.5 15.1–16.0
Length of incisive foramen	6.5 6.3–6.6	6.3 5.9–6.6	6.5 6.3–6.7
Length of palatal bridge	4.5 4.4–4.7	4.7 4.4–5.0	4.5 4.2–4.8
Interorbital breadth	5.0 4.8–5.1	4.8 4.5–5.0	5.1 4.8–5.3
Alveolar length of molar row	4.7 4.4–4.8	4.4 4.0–4.6	4.6 4.5–4.7
Ratio, tail length to body length (per cent)	113 105–119	112 101–130	111 105–115

Peromyscus maniculatus rubidus Osgood

RANGE.—Coastal belt both north and south of San Francisco Bay; confined to humid coast faunal area.

COMPARISONS.—The race *rubidus* differs from *gambelii* in larger size (Table IX); longer tail (averaging 94 per cent and 74 per cent, respectively, of head and body length); darker and more reddish coloration; narrower



MAP 13. Distribution of the subspecies of *Peromyscus maniculatus*, as established by specimens examined.

and longer brain case (its length about 98 per cent of its breadth, rather than 92 per cent as in *gambelii*); longer rostrum; and longer incisive foramina (averaging 5.5 mm. and 4.8 mm., respectively).

REMARKS.—One hundred and eighty-eight specimens were examined. The range of *rubidus* conforms, in general, to the distribution of the redwood-Douglas fir association. Factors controlling the distribution of this association may also influence the distribution of the large size, long tail, dark reddish coloration, and other characteristics of *rubidus*. In the bay area the characters of *rubidus* are best expressed in the populations in the coastal parts of Marin and Sonoma counties. Elsewhere the populations grade toward *gambelii*. Those south of San Francisco Bay in the humid coast faunal area and probably those in the vicinity of Berkeley, Alameda County, although obviously intermediate in character, may be included with *rubidus* because of their greater similarity to that race.

TABLE IX

MEASUREMENTS OF ADULTS OF THE SUBSPECIES OF *Peromyscus maniculatus*

The examples of *gambelii* are from near Antioch, Contra Costa County, and those of *rubidus* from Inverness, Marin County.

	gambelii 5 ♀ ♀, 7 ♂ ♂	*rubidus* 7 ♀ ♀, 3 ♂ ♂
Total length	153 144–166	184 172–196
Tail	65 58–67	89 79–96
Hind foot	19 18–20	22 21–23
Body length	88 85–92	95 85–104
Greatest length of skull	23.9 22.7–24.7	26.2 25.3–26.7
Zygomatic breadth	12.6 12.2–12.8	13.1 12.5–14.1
Breadth of brain case	10.5 10.1–11.1	10.9 10.6–11.1
Length of brain case	9.7 9.2–10.1	10.7 10.3–11.1
Nasal length	9.0 8.3–9.8	10.0 9.6–10.4
Length of palatal bridge	3.4 3.1–3.7	3.7 3.4–4.1
Length of incisive foramen	4.8 4.5–5.1	5.5 4.9–6.8
Alveolar length of molar row	3.5 3.3–3.7	3.9 3.7–4.1
Ratio, tail length to body length (per cent)	74 65–80	94 77–112

Peromyscus boylii boylii Baird

Boyle mouse

RANGE.—In the bay area known only from three specimens collected on Encinosa Creek, three miles west of Vacaville, Solano County (Pl. IV); the species probably ranges northwestwardly from Vacaville fairly continuously in the inner coast ranges, and in the northern inner coast faunal district (Map 12).

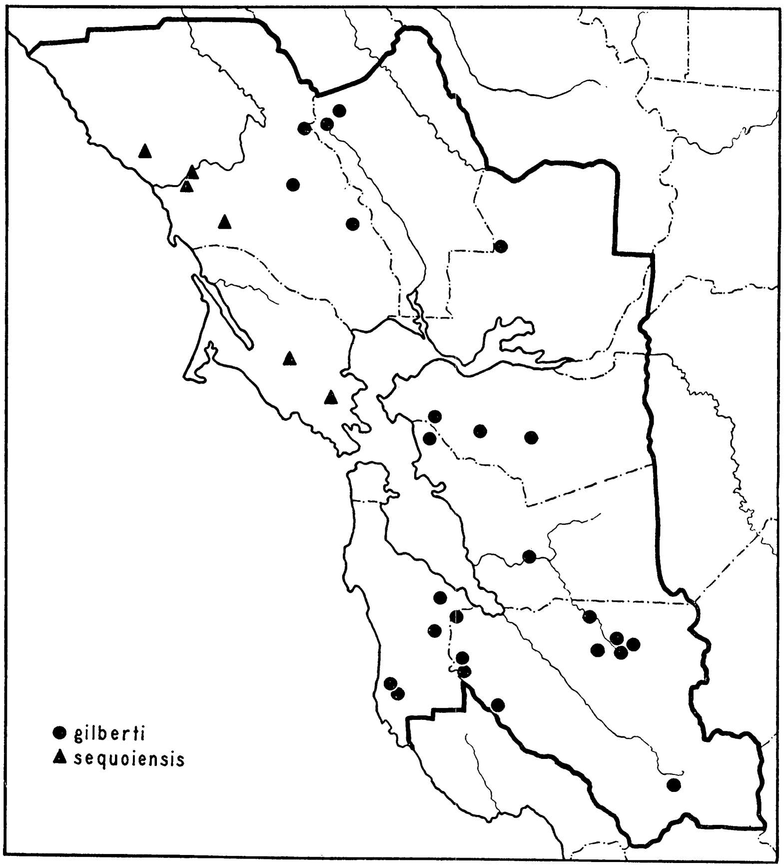
HABITAT.—"Wooded or brushy slopes, usually not far from water or at least seepages; perhaps commonest on cañon walls shaded by golden oaks" (Grinnell, 1933: 176).

Peromyscus truei gilberti Baird

Piñon mouse

RANGE.—Mountainous areas both north and south of San Francisco Bay, but interior to the coastal fog belt north of the bay (Map 14).

HABITAT.—Brushy or wooded areas or boulders (Pl. II, Fig. 2; Pl. III), not open grasslands, dense forests, pure stands of high-growing chamise, or



MAP 14. Distribution of the subspecies of *Peromyscus truei*, as established by specimens examined.

marshlands; ground that is comparatively dry, not subject to inundations; soil that the animal can dig into for refuges, or rocky situations suitable for refuges.

REMARKS.—Two hundred and forty-one specimens were examined. Specimens from San Mateo County and western Santa Clara County (west of the Santa Clara Valley) are slightly different from specimens collected farther inland (Mount Hamilton, Mount Diablo, and Berkeley). They average larger and darker, and the auditory bullae are more inflated.

Certain trends in variation observed in other rodents inhabiting the coastal region of California, in *Peromyscus maniculatus* and *Neotoma cinerea,* for example, also may be seen in *Peromyscus truei.* These trends are toward development of a darker color and a longer tail in humid areas near the seacoast. In *truei,* specimens from localities in the fog belt generally are darker and longer-tailed than specimens from inland and out of the fog belt. Differences in size, color, and tail length are apparent between coastal and inland populations. They are best seen in specimens from north of the bay, where a coastal race, *sequoiensis,* has been recognized (Hoffmeister, 1941: 129), but nevertheless are apparent in examples from farther to the south, as, for example, between specimens from Pescadero, San Mateo County, and Mount Hamilton, Santa Clara County.

TABLE X

MEASUREMENTS OF ADULTS OF THE SUBSPECIES OF *Peromyscus truei*

The examples of *gilberti* are from Mount Hamilton, Santa Clara County, and those of *sequoiensis* from the vicinity of Guerneville, Sonoma County (after Hoffmeister, 1941: 130).

	gilberti 6 ♀♀, 4 ♂♂	*sequoiensis* 4 ♀♀, 10 ♂♂
Total length	195 187–200	220 200–231
Tail	97 90–104	114 104–123
Hind foot	24 23–25	25 24–27
Greatest length of skull	28.2 27.4–29.0	29.7 28.3–30.7
Basilar length	21.3 20.5–22.7	22.2 20.9–23.1
Nasal length	10.7 10.1–11.2	11.0 10.3–11.3
Length of palatal bridge	4.2 3.9–4.5	4.5 4.3–5.0
Length of incisive foramen	5.7 5.4–6.0	6.0 5.6–6.2
Alveolar length of molar row	4.3 4.1–4.4	4.5 4.2–4.8

Certain differences are apparent between the populations of *gilberti* north and south of the bay. Specimens from the north (for example, near Mount St. Helena and Calistoga, Napa County) average darker and average larger in all measurements except length of nasals and incisive foramina than do specimens to the south (Mount Diablo, Contra Costa County, or Mount Hamilton, Santa Clara County). These differences are comparatively slight and do not warrant subspecific recognition.

Peromyscus truei sequoiensis Hoffmeister

RANGE.—North of San Francisco Bay in the humid, fog belt.

COMPARISONS.—Compared with *gilberti, sequoiensis* averages larger

(Table X), darker, and more reddish (less buffy) dorsally; the tail is actually and relatively longer; the palatal bridge is longer and more convex in outline at the interpterygoid fossa.

REMARKS.—Twenty-four specimens were examined, from Marin and western Sonoma counties. Specimens from certain localities in the fog belt south of the bay, on the periphery of the fog belt, or in humid islands inland are variously between *gilberti* and *sequoiensis* in characters. This is true, for example, of specimens from near Calistoga, Napa County, from Berkeley, Alameda County, and from several localities in San Mateo and western Santa Clara counties.

Neotoma lepida californica Price

Lepida wood rat

RANGE.—South of San Francisco Bay in the inner coast ranges (Map 3); known in the bay area from Mount Diablo, Contra Costa County (E. R. Hall, *in litt.*), and Mount Hamilton (von Bloeker, 1938: 202).

HABITAT.—Sparse chaparral, other bushy woody plants, or broken rock outcrops; wood debris, such as from fallen trees or jetsam along stream beds, that is accessible and is small enough to be carried by a rat to a nest site; dry, well-drained situations, such as on sunny south-facing slopes and canyon sides or on exposed, sandy flood plains.

REMARKS.—I have seen no specimens of *Neotoma lepida* collected in the bay area.

Neotoma fuscipes fuscipes Baird

Dusky-footed wood rat

RANGE.—North of San Francisco Bay in the inner coast ranges and the northern inner coast faunal district, principally west of the lower Sacramento Valley (known from the foothills near Vacaville, Solano County) and east of the humid coast belt (west and south as far as Petaluma, Sonoma County) (Map 15).

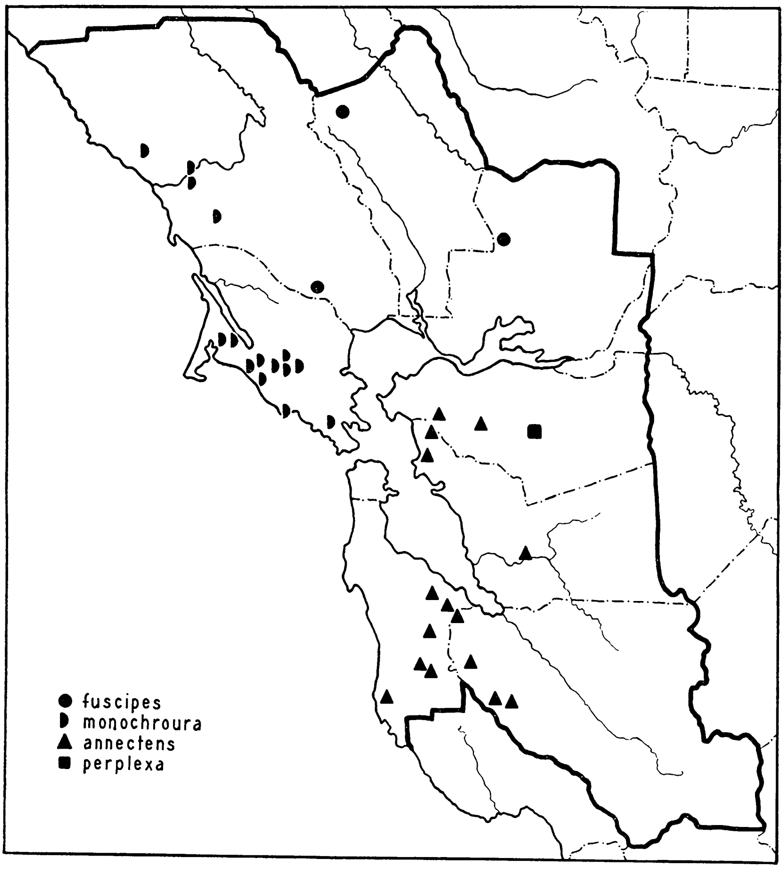
HABITAT.—Brushy or wooded areas (Pl. III) (not open grasslands or marshlands) or rocky situations near thickets of woody vegetation, where debris of a size suitable to the species is available for construction of nests, and where there are sites for retreats, such as trees, rock ledges, or ground into which the animal can dig to construct subsurface refuges.

REMARKS.—Thirteen specimens were examined. *N. f. fuscipes* is a pale race which inhabits the warmer and drier mountainous areas east of the cooler fog belt near the seacoast.

Neotoma fuscipes monochroura Rhoads

RANGE.—North of San Francisco Bay in the outer coast ranges; range limits, in the bay area, essentially those of the northern humid coast faunal subarea.

COMPARISONS.—The characters distinguishing *monochroura* from *fuscipes* are principally ones of coloration. *N. f. monochroura* is much darker dor-



MAP 15. Distribution of the subspecies of *Neotoma fuscipes*, as established by specimens examined.

sally (dark pinkish cinnamon as compared with pale cinnamon buff or grayish buff in *fuscipes*), the ventral surface is more extensively pigmented (not white), the hind feet are dusky above, and the tail is unicolored.

REMARKS.—Ninety-six specimens were examined. Specimens from Marin County, designated *splendens* by True (1894: 353), average slightly darker than do those from areas in Sonoma County north of the Sonoma-Marin gap.

Inland from the humid coastal belt the characters of *monochroura* grade gradually into those of *fuscipes.*

Most of the characters which distinguish *monochroura* from *fuscipes,* and, as well, *annectens* from *perplexa* (the coastal and interior races, respectively, south of the bay) are similar to those differentiating coastal from interior races in other species in the bay area. Coastal populations of *Peromyscus californicus, P. truei,* and *P. maniculatus* are more extensively pigmented than are interior populations.

TABLE XI

MEASUREMENTS OF ADULT FEMALES OF THE SUBSPECIES OF *Neotoma fuscipes*

Males average 3 to 7 per cent larger in each measurement. The examples are from localities as follows: *fuscipes,* Colusa and Glen counties; *monochroura,* seven miles west of Cazadero, Sonoma County; *annectens,* San Mateo and western Santa Clara counties; *perplexa,* Priest Valley, Monterey County.

	fuscipes 4 ♀♀	*monochroura* 7 ♀♀	*annectans* 10 ♀♀	*perplexa* 5 ♀♀
Total length	405 384–428	419 403–463	428 418–444	407 377–427
Tail	192 182–211	207 192–241	212 193–227	196 184–206
Hind foot	40 37–43	40 38–44	41 40–42	39 38–41
Ear from notch (dry)	27 26–29	25 24–27	28 26–29	29 28–30
Basilar length	40.0 38.4–41.1	39.4 38.7–40.8	40.5 38.7–42.7	39.2 37.9–40.9
Zygomatic breadth	25.0 23.7–25.7	25.3 24.3–26.1	25.8 24.9–26.4	25.2 24.6–26.0
Nasal length	19.0 18.0–20.1	18.2 17.4–19.1	18.8 18.0–19.9	18.5 18.0–18.8
Depth of skull	16.1 15.5–17.0	16.3 15.5–16.8	16.7 16.0–17.2	16.4 16.1–16.7
Breadth of rostrum	7.3 6.9–7.8	7.4 6.8–7.7	7.5 7.0–7.8	7.5 7.3–7.7
Depth of rostrum	7.5 7.2–7.8	7.5 7.1–7.9	7.8 7.3–8.1	7.8 7.3–8.4
Length of incisive foramen	10.8 10.4–11.1	10.4 9.8–11.3	10.7 10.0–11.1	10.2 9.6–11.0
Length of palatal bridge	8.6 8.3–8.8	8.9 8.3–9.5	9.1 8.6–10.0	8.5 8.2–8.9
Sum of foramen and bridge	19.4 18.7–19.9	19.3 18.5–20.8	19.8 19.2–20.9	18.7 18.0–19.4
Alveolar length of molar row	9.5 9.2–9.7	9.4 9.2–9.5	9.6 9.2–10.1	9.4 8.9–9.7
Breadth of bulla	8.0 7.9–8.2	7.5 7.1–8.2	8.2 7.7–8.5	8.6 8.3–8.7

Neotoma fuscipes annectens Elliot

RANGE.—Coastal belt south of San Francisco Bay, south from the Golden Gate and Carquinez Straits; at the northern part of the range east to the vicinity of Walnut Creek, Contra Costa County, and to Niles Canyon, Alameda County. Chiefly in the Santa Cruz faunal district.

COMPARISONS.—*N. f. annectens* differs from both *N. f. monochroura* and *N. f. fuscipes* in its narrower interpterygoid fossa, convex posterior border of palatal bridge, and larger bullae. It differs further from *monochroura* in smaller size, and from *fuscipes* in darker dorsal coloration, greater amount of pigmentation ventrally, dusky hind feet, and bicolored tail.

REMARKS.—One hundred and one specimens were examined. The characters of *annectens* are best developed in the mountains of Santa Cruz and San Mateo counties. Inland from these humid areas they grade into those of *perplexa.*

Neotoma fuscipes perplexa Hooper

RANGE.—South of San Francisco Bay in the inner coast ranges and the southern inner coast faunal district.

COMPARISONS.—The race *perplexa* differs from *annectens* as follows: distinctly brighter and more reddish dorsal coloration, less extensive duskiness of hind feet, larger ears, and proportionally larger bullae. Compared with both *monochroura* and *fuscipes,* it is slightly smaller, brighter, and more reddish and has a broader rostrum (relative to basilar length), larger bullae, and a convex posterior border of the palatal bridge. In addition, it is darker dorsally than *fuscipes,* the undersurface usually is not entirely white, and the hind feet are somewhat dusky.

REMARKS.—Seven specimens at hand from Mount Diablo, Contra Costa County, referred to the race *perplexa,* are the only specimens of the race I have examined from the bay area.

Clethrionomys californicus californicus Merriam
California red-backed vole

RANGE.—Northwestern Sonoma County in the Humboldt Bay faunal district (Map 16).

HABITAT.—Moist, log-strewn floors of coniferous forests.

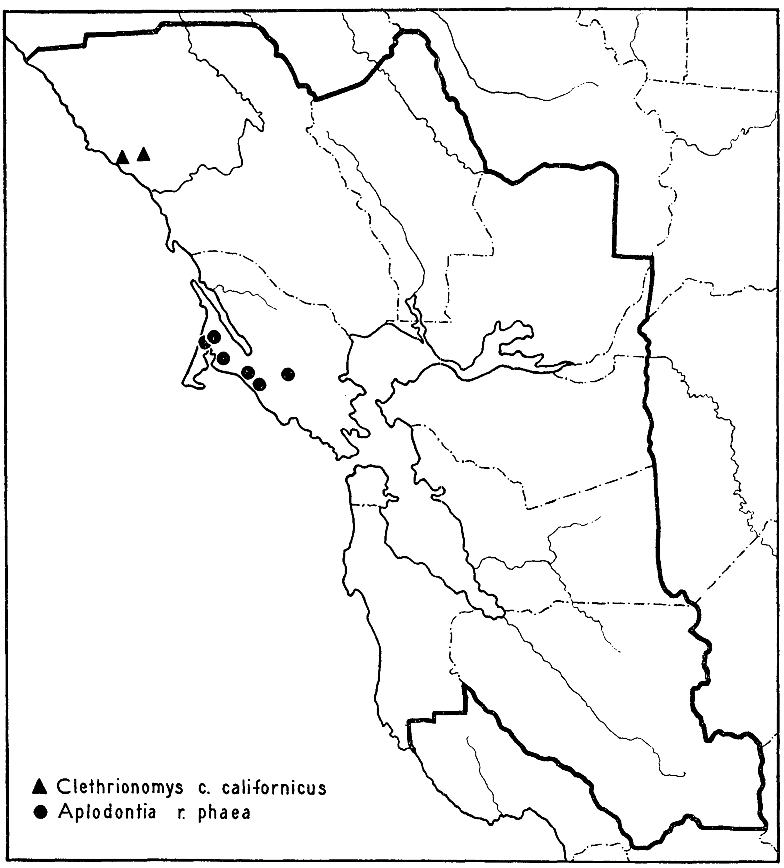
REMARKS.—The species is comparatively rare in the bay area. Extensive trapping in suitable habitat yielded only three specimens, one from two miles north of Fort Ross, and two from seven miles west of Cazadero, Sonoma County.

Phenacomys longicaudus True
Red tree vole

RANGE.—The narrow coastal fog belt in western Sonoma County, north from the vicinity of Occidental (Map 18). Confined to the Humboldt Bay faunal district.

HABITAT.—Douglas fir or grand fir, whether as a pure growth or mixed with other trees, in rather continuous stands, not isolated trees or small patches (conifers spaced sufficiently closely about a fir so that a tree vole can pass from one tree to the other without descending to the ground); cool situations, drenched almost daily by fog.

REMARKS.—Sixteen specimens were examined. In the bay areas, redwood and Douglas fir forests in less humid parts, fifteen or twenty miles from the coast, apparently are not inhabited by tree voles, nor has the species been collected in Marin and Santa Cruz counties, where habitat that should be suited to its needs is present.



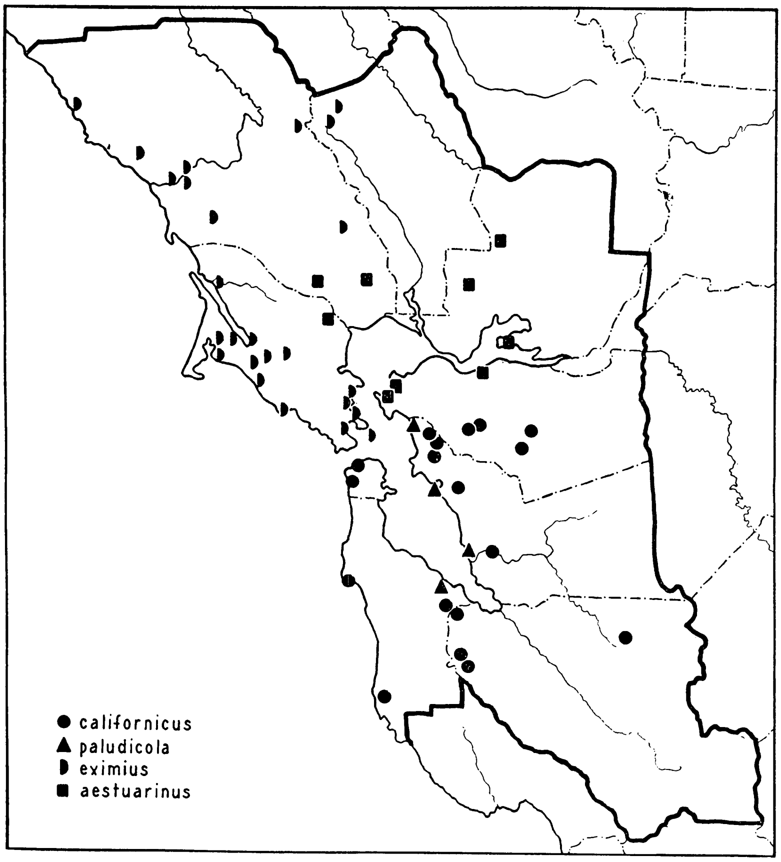
MAP 16. Distribution of *Clethrionomys californicus* and *Aplodontia rufa*, as established by specimens examined.

Microtus californicus californicus Peale
California vole

RANGE.—Throughout area south of San Francisco Bay, except the bayside marshes, the extreme eastern part of Contra Costa County, and the northeastern part of Alameda County (Map 17).

HABITAT.—Low-lying cover, forming a semiopen to dense mat near the ground, whether the cover be grass, herbs, shrubby vegetation, or debris and whether in marshes or on uplands; not dense forests, except in clearings where low-lying cover as that mentioned above is present.

REMARKS.—One hundred and fifty-nine specimens were examined. In



MAP 17. Distribution of the subspecies of *Microtus californicus*, as established by specimens examined.

the bay area the race *californicus* occurs predominantly on the uplands and in fresh-water marshes. Along the south arm of San Francisco Bay it grades into the slightly differentiated, marsh-inhabiting *paludicola*. In the marshes bordering Suisun Bay and in the Great Valley faunal district, it is replaced by the distinctly different *aestuarinus*.

Microtus californicus paludicola Hatfield

RANGE.—Salt marshes bordering the south arm of San Francisco Bay (Pl. I, Fig. 2); at the eastern side north to the vicinity of Albany, Alameda County, and at the west to northeastern San Mateo County. Confined to the San Francisco Bay faunal district.

COMPARISONS.—From *californicus, paludicola* shows average differences as follows: more reddish (less buffy) dorsum, narrower brain case (Table XII), longer rostrum and nasals (nasal length 29 per cent longer than molar row, as compared with 21 per cent in *californicus*), and a posterior internal loop of M^2.

The race *paludicola* is similar, particularly cranially, to *eximius,* north of San Francisco Bay; however, it averages smaller (total length 169 mm. as compared with 182 mm.), is less reddish dorsally, and the nasals and molar row are shorter.

REMARKS.—Fifty-six specimens were examined. The geographic range of *Microtus californicus paludicola,* as now known, is almost identical with that of *Reithrodontomys raviventris raviventris,* except that the range of the latter includes areas in Marin County north of the bay.

Microtus californicus eximius Kellogg

RANGE.—Coast region north of San Francisco Bay; north from the Golden Gate and Angel Island through most of Marin, Sonoma, and Napa counties, but excluding that part of Sonoma County lying south and east of Petaluma, the marshes near Burdell Station, Marin County, and the southern one-third of Napa County.

COMPARISONS.—Compared with *californicus, eximius* is larger and more reddish (less buffy and grayish) dorsally, the skull is relatively narrower, the nasals longer, the bullae less inflated, and the rostrum broader; a well-developed posterior internal loop is usually present in M^2.

From *aestuarinus, eximius* may be distinguished by its smaller size, paler, less blackish dorsum, narrower skull (well seen in the zygomatic breadth and the breadth of the brain case), and longer nasals (respectively, about 29 per cent and 17 per cent longer than molar row).

REMARKS.—One hundred and sixty-two specimens were examined. *M. c. eximius* intergrades with *M. c. aestuarinus* in the salt marshes of Marin County. Specimens from the marshes near Manzanita, Corte Madera, and San Rafael, for example, are intermediate in characters of skin and skull; all characters considered, however, the specimens are nearer *eximius.* Two specimens at hand from Bolinas, Marin County, are referred to *eximius* principally on the basis of coloration; cranially they do not permit a satisfactory identification. Kellogg (1918: 15) referred the specimens to *aestuarinus.*

Thirty-one specimens at hand from Angel Island in San Francisco Bay are, with some skepticism, referred to *eximius*. They resemble *eximius* in size and in most cranial characters, they are indistinguishable from *californicus* in coloration and the character of M^2, and they differ from all races herewith considered in the size of the brain case (Table XII). On the basis of the long, broad brain case alone, the populations of meadow mice on Angel Island might well warrant recognition as a distinct geographic race, but because they are variously similar to *eximius* and *californicus,* particularly the former, because they occupy an area geographically between those two races, and, finally, because occasional interchange of individuals from the mainland and island could occur (four specimens from Tiburon on the north mainland opposite the island also have the large brain case), it seems best to refer them to *eximius.*

Microtus californicus aestuarinus Kellogg

RANGE.—Salt marshes bordering the northern part of San Francisco Bay; at the northern side west to Burdell Station, Marin County, and Petaluma, Sonoma County, and at the south to San Pablo, Contra Costa County.

COMPARISONS.—The race *aestuarinus* differs from the race *californicus* in larger size (total length averages 190 mm., compared with 170 mm.), longer tail (43 per cent and 39 per cent of body length, respectively), much darker coloration, more angular skull, relatively shorter nasals (averaging 17 per cent more than length of molar row, compared with 21 per cent in *californicus*), longer molar row, broader rostrum, less recurved upper incisors, and smaller auditory bullae. A posterior internal loop also is usually present in M^2.

From *paludicola* with which it intergrades, *aestuarinus* differs in larger size (Table XII); longer tail; darker coloration; broader, more prominently ridged skull; more broadly spread and heavier zygomata; and shorter nasals (length 29 per cent greater than the length of the molar row in *paludicola*).

REMARKS.—One hundred and three specimens were examined. In the bay area, the characters of *aestuarinus* are best developed in specimens from the marshes bordering Suisun Bay. Westward from there the characters grade into those of *eximius* and *paludicola.* Specimens from the marshes near Giant and the mouth of San Pablo Creek, Contra Costa County, are intermediate in characters between *aestuarinus* and *paludicola,* but on the average slightly nearer the former. Specimens from the bayside marshes in Marin County, here referred to *eximius,* are between that race and *aestuarinus* in characters of skin and skull.

I find no characters which will distinguish the specimens of *aestuarinus* north of the bay from those south of the bay. This lack of differentiation may well be correlated with the incomplete isolation of the populations on the two sides. The marshlands abounding at the confluences of the Sacramento and San Joaquin rivers divide at Suisun Bay into two pincer-like arms that encompass most of San Francisco Bay and provide an almost continuous, marshy avenue for movements of the voles around the bay.

TABLE XII

MEASUREMENTS OF ADULTS OF THE SUBSPECIES OF *Microtus californicus*

The examples are from localities as follows: *californicus,* Berkeley, Alameda County; *paludicola,* marshes along southern arm of San Francisco Bay; *eximius* (first column), Sonoma and Mendocino counties and (second column) Angel Island, San Francisco Bay; *aestuarinus,* Grizzly Island, Solano County.

	californicus 3 ♀ ♀, 9 ♂ ♂	*paludicola* 2 ♀ ♀, 5 ♂ ♂	*eximius* 5 ♀ ♀, 8 ♂ ♂	*eximius* 1 ♀ ♀, 9 ♂ ♂	*aestuarinus* 2 ♀ ♀, 9 ♂ ♂
Total length	171 150–175	169 161–182	182 175–193	187 180–194	191 182–202
Tail	48 42–51	46 40–50	49 42–54	56 51–60	56 42–62
Hind foot	21 20–22	21 20–22	23 22–24	23 21–23	23 22–25
Body length	123 108–128	123 116–133	131 122–141	131 123–139	135 129–144
Basilar length	25.5 24.9–26.0	25.8 25.0–26.3	26.2 25.2–27.0	26.0 25.5–26.5	27.2 26.0–28.0
Zygomatic breadth	16.5 16.1–17.0	16.5 16.1–16.8	16.9 16.0–17.8	16.9 16.5–17.2	17.8 17.1–18.2
Nasal length	8.6 8.1–8.9	9.0 8.8–9.5	9.4 8.7–10.2	9.1 8.7–9.4	8.9 8.2–9.5
Length of brain case	13.7 13.1–14.2	13.8 13.4–14.2	14.1 13.4–14.9	14.2 13.7–14.9	14.6 13.8–15.1
Breadth of brain case	13.0 12.6–13.5	12.9 12.3–13.6	13.3 12.6–13.6	13.5 13.0–13.8	13.5 12.7–13.8
Height of skull at bullae	10.3 10.0–10.5	10.3 10.0–10.5	10.5 10.0–10.7	10.5 10.1–11.0	11.0 10.5–11.3
Alveolar length of molar row	7.1 6.7–7.5	7.0 6.7–7.4	7.3 6.8–7.7	7.2 6.8–7.6	7.6 7.2–8.0
Ratio, tail length to body length (per cent)	39 36–44	38 32–41	38 32–43	43 34–47	42 30–50

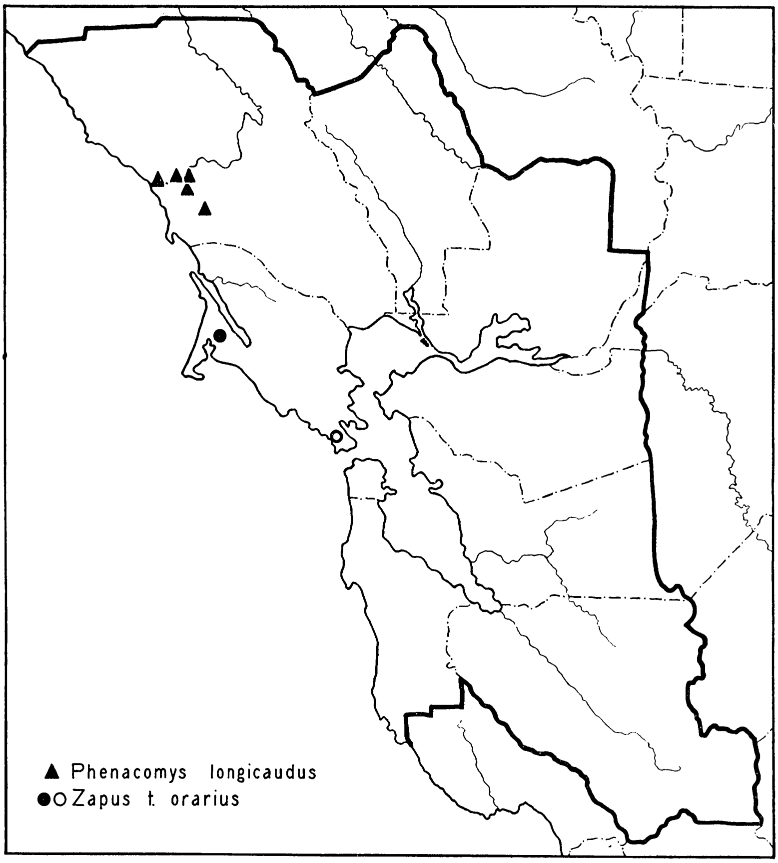
Aplodontia rufa phaea Merriam
Aplodontia

RANGE.—Southwestern half of Marin County, southeast from the vicinity of Inverness to near Olema, possibly to Mount Tamalpais (Map 16). Confined to the Marin faunal district.

HABITAT—Extensive and continuous heavy chaparral, or clumps of sword fern, growing in soil rich in humus, continually moist and easily excavated by an aplodontia; sloping ground, not flat; situations kept continually cool and moist by frequent fogs or rain.

REMARKS.—Twenty-five specimens were examined. *Aplodontia rufa phaea* is restricted to favorable situations within the southwestern half of

Marin County. Aplodontias, probably of the race *A. r. nigra,* may also be present in northwestern Sonoma County; *nigra* is known to range south in Mendocino County almost to the Sonoma County line. Interbreeding of *phaea* with *nigra* could not occur in the wild state, however, since, in the Sonoma-Marin gap, at least thirty-five or forty miles of country unsuitable for the species separate the populations of the two races. *A. rufa* appar-



MAP 18. Distribution of *Phenacomys longicaudus* and *Zapus trinotatus,* as established by specimens examined (solid figures) and a published record (open figure).

ently does not occur to the south of San Francisco Bay in the coast ranges, where habitat that should be suited to its needs is present (in San Mateo and Santa Cruz counties, for example).

Zapus trinotatus orarius Preble
Western jumping mouse

RANGE.—Southern and western Marin County (Map 18). Confined to the Marin faunal district.

HABITAT.—Meadows or marshlands; high growth of sedges or rushes (Pl. II, Fig. 1), or rather open, low-growing chaparral; ground that is moist yet safe from continuous inundation.

REMARKS.—In the bay region this species is known from only two areas, both in Marin County. I have examined sixteen specimens collected near Inverness (three to five miles west). Smith and Hopkins (1937: 191) recorded remains of individuals of *Zapus* in barn owl pellets collected in Elk Valley, near the extreme southern tip of the county.

Zapus orarius and *Zapus trinotatus eureka* may well be treated as subspecies of *Zapus trinotatus,* the earlier named form. They are similar in many characters of skin and skull, as A. B. Howell (1920: 231) indicated, and more complete intergradation between them may be expected when abundant material from geographically intermediate areas, northern Sonoma County, for example, is at hand. Interbreeding in the wild probably does not take place, for the two forms are separated by terrain unsuited to jumping mice (the Sonoma-Marin gap).

DISCUSSION

THE BAY AS A FACTOR IN RODENT DISTRIBUTION AND SPECIATION

San Francisco Bay influences in several important ways the distribution and evolution of the species and races of rodents present in the area. It supplies conditions suitable for the presence of extensive marshlands in which may have evolved species and races of rodents. It allows for the occurrence of humid, cool, coastal climates farther inland than usual in the region. Dark dorsal coloration and other characters which often are expressed in some species in humid coastal climates also occur inland with the humid climate. Finally, the bay is a barrier to the movements of individuals of all the rodent species. The ultimate northern or southern limits of the ranges of some species are the southern or northern shores, respectively, of the bay. Other species, occurring on both the north and south sides, differ subspecifically.

SPECIATION IN BAYSIDE MARSHES.—Three subspecies of two species live only in the salicornia-covered salt marshes that border San Francisco Bay and the lower Sacramento River. *Reithrodontomys raviventris raviventris* and *Microtus californicus paludicola* are restricted to the marshes around the main bay. *Reithrodontomys raviventris halicoetes* is found in the marshes adjoining San Pablo and Suisun bays and the lower part of the Sacramento River, as is also another race of *Microtus californicus—aestuarinus*—which, however, ranges well outside the bay area.

Salicornia-covered tidal marshes, similar in appearance to those bordering San Francisco Bay, are present elsewhere in west-central California, as, for example, around Tomales Bay, Marin County, and Halfmoon Bay, San Mateo County. In none of those marshes, so far as I am aware, are there endemic races or species of rodents. It would appear, then, that the San Francisco Bay marshes have provided at least one factor not present in the other marshes, a factor which has allowed for or caused the evolution of races in them alone.

The bay marshes are much larger than the other tidal marshes. Perhaps their greater size, which has effected partial isolation of the marsh-dwelling animals, has allowed the differentiation to take place. Size and isolation may not be the only differential factors involved, but they appear to be important ones. In the small marshes, genetic variability has not been allowed to become fixed in the marsh populations alone, but has continued to be distributed rather evenly among both the marsh and upland populations. In other words, the marsh and upland populations constitute one breeding population among which genetic variability and variations in gene frequencies tend to be spread equally. In the extensive San Francisco Bay marshes, on the other hand, the populations may be sufficiently large to have allowed genetic factors to become fixed in them alone, although they interbreed with the upland populations at the periphery of the marshes. If this be true, the rate of fixation must have exceeded the rate of dissipation brought about through interbreeding.

Prior to, or coincident with, the development of the external and cranial peculiarities of the species *R. raviventris,* there must have evolved a barrier of some sort, whether physical, physiological, or psychological, which now prevents free interbreeding between *R. raviventris* and *R. megalotis.* Both occur at the periphery of the marshes, but apparently do not interbreed.

The marsh species and races, as we see them now, may have evolved within Recent geological time. The flooded embayments and drowned valleys producing the San Francisco Bay marshes in their present extent result from the most recent geomorphic change in the bay area. Indeed, the submergence of the land, which resulted in the flooding of the low-lying shores, is occurring at the present time. The bases of certain Indian kitchen middens, once entirely above water, are now four feet below the ordinary high-tide mark (Osmont, 1904: 83). Extensive salt marshes probably were not present in the bay basin prior to Recent (possibly late Pleistocene) time, for the valley system of San Francisco Bay was not outlined until fairly late in Pleistocene (post-Alameda diastrophism, Lawson, 1914: 20), and the epoch (San Antonio) between the formation of that valley system and the beginning of the series of depressions (in late Pleistocene or Recent, Merritt and Temescal epoch, Lawson, 1914: 20) which have led to the formation of the present marshes is characterized by uplift, not recession. Any marshes then present must have decreased, not increased, in size and distribution. The current, extensive bayside marshes appear to have been developed in Recent time. It seems likely that those rodent forms that are endemic to the marshes and that apparently are so closely dependent upon the conditions supplied therein must also have evolved concomitantly in Recent time.

THE BAY AND THE DISTRIBUTION OF CLIMATES AND SOME CHARACTERS OF RODENTS.—San Francisco Bay acts as a highway over which cool, moisture-laden, onshore winds travel unimpeded inland and produce, over areas they reach, cool humid conditions similar to those present along the seacoast. In most places north and south of the bay the ridges of the outer coast ranges are sufficiently high in elevation to deflect those prevailing onshore winds and cause them to parallel the seacoast.

Grinnell (1935*a*: Pl. 3), on a map showing the distribution of life zones in California, indicated certain effects of the bay on the distribution of climates. Spread fanlike from Suisun Bay into the lower Sonoran zone (a belt characterized by warm, dry conditions, of the Sacramento and San Joaquin valleys) is a broad wedge of the cooler, more humid, upper Sonoran zone.

The apex of this wedge is Carquinez Straits, the narrow hill-bordered passage which constricts the flow of the onshore winds en route into the Great Valley. East of Carquinez Straits the terrain is comparatively flat, and winds, no longer checked by mountain ridges, spread out fanlike into the Great Valley. Opposite the Golden Gate, in the vicinity of Berkeley and Oakland, Alameda County, is an area of the cool, relatively humid Transition zone, an island, in effect, in upper Sonoran. Other similar islands occur elsewhere in the bay area. These ameliorating effects in inland climates are indirectly due to the bay.

There is a correlation between the distribution of these climatic conditions and that of certain morphological characters of some rodents. Several species are darker and more reddish dorsally and longer tailed in these cooler more humid areas than they are in warmer, drier areas. In dorsal coloration and tail length, for example, specimens of *Peromyscus maniculatus* from Berkeley and Oakland, a cool island of Transition zone in the warmer upper Sonoran, resemble specimens from coastal San Mateo County more than they do specimens from Sonoran areas ten or fifteen miles to the east. The same holds true, except for tail length, in the species *Peromyscus californicus* and *Neotoma fuscipes* (see accounts of these species).

THE BAY AS A BARRIER INFLUENCING DISTRIBUTION AND SPECIATION.—Arranged by families, genera, species, and subspecies the native rodent fauna of the area studied is distributed as follows with respect to San Francisco Bay:

North of Bay Only	*North and South of Bay*	*South of Bay Only*
	Families	
2	4	0
Aplodontiidae	Sciuridae	
Zapodidae	Geomyidae	
	Heteromyidae	
	Cricetidae	
	Genera	
5	10	0
Tamiasciurus	*Citellus*	
Clethrionomys	*Eutamias*	
Phenacomys	*Sciurus*	
Aplodontia	*Thomomys*	
Zapus	*Dipodomys*	
	Perognathus (?)	
	Reithrodontomys	
	Peromyscus	
	Neotoma	
	Microtus	
	Species	
8	11	5
Eutamias townsendii	*Citellus beecheyi*	*Eutamias merriami*
Eutamias sonomae	*Sciurus griseus*	*Perognathus californicus*

North of Bay Only	*North and South of Bay*	*South of Bay Only*
Tamiasciurus douglasii	*Thomomys bottae*	*Dipodomys venustus*
Peromyscus boylii	*Perognathus inornatus* (?)	*Peromyscus californicus*
Clethrionomys californicus	*Dipodomys heermanni*	*Neotoma lepida*
Phenacomys longicaudus	*Reithrodontomys megalotis*	
Aplodontia rufa	*Reithrodontomys raviventris*	
Zapus trinotatus	*Peromyscus maniculatus*	
	Peromyscus truei	
	Neotoma fuscipes	
	Microtus californicus	

Subspecies

18	8	17
C. b. douglasii		*C. b. beecheyi*
E. t. ochrogenys		
E. s. sonomae		*E. m. pricei*
E. s. alleni		
T. d. molli-pilosus		
S. g. griseus		*S. g. nigripes*
T. b. minor		*T. b. bottae*
T. b. agricolaris		*T. b. diaboli*
	P. i. inornatus (?)	*P. c. californicus*
D. h. californicus		*D. h. berkeleyensis*
		D. h. goldmani
		D. h. tularensis
		D. v. venustus
	R. m. longicaudus	
	R. r. raviventris	
	R. r. halicoetes	
		P. c. parasiticus
		P. c. benitoensis
	P. m. gambelii	
	P. m. rubidus	
P. b. boylii		
P. t. sequoiensis	*P. t. gilberti*	
N. f. fuscipes		*N. l. californicus*
N. f. monochroura		*N. f. perplexa*
C. c. californicus		*N. f. annectens*
P. l. longicaudus		*M. c. californicus*
M. c. eximius	*M. c. aestuarinus*	*M. c. paludicola*
A. r. phaea		
Z. t. orarius		

The bay is sufficiently large to check the geographic movements to north or south of the rodents native to the bay area, all of these rodents being terrestrial, not aquatic, in habit. At its narrowest place, Carquinez Straits, the bay is about half a mile wide between the north and south shores; elsewhere several miles of water separate the two shores. Strong tidal currents pass back and forth throughout the year.

That the bay actually is a barrier to most if not all of the species and that as a barrier it influences subspeciation and speciation in the rodent kinds is indicated by the distribution of the several species and subspecies with respect to the bay. Eight of the species north of the bay are absent from the south side. Of these, three (*Eutamias sonomae, Aplodontia rufa,* and *Zapus trinotatus*) range almost to the water's edge. Five species live to the south only; two of these (*Perognathus californicus* and *Peromyscus californicus*) are known to range near the south shores of the bay; others also may do so. That it is a barrier seems particularly obvious when one considers that suitable habitat on the opposite side of the bay, in some instances only a mile or two away, is unoccupied.

Further evidence of the effect of the bay, as a barrier, on speciation comes from the frequency of occurrence of distinct subspecies on each side of it. Different subspecies are recognized in all but four of the ten species known to occur both north and south of the bay. (*Perognathus inornatus* is omitted in this connection because the specimens at hand are too fragmentary for a satisfactory analysis of variation and because the records of the species in the bay area are subject to question; the species may not be present on both sides of the bay.) In one of the four species (*Peromyscus truei*) differentiation has occurred, but is not at a full subspecific level and separate races are not recognized. In another of the four (*Reithrodontomys raviventris*) the lack of differentiation might be expected, because the populations north and south of the bay are incompletely isolated from one another; the species inhabits the salt marshes which are nearly continuous around the bay. There remain, then, only two of the eight species, the populations of which apparently are isolated by the bay, which do not differentiate at that barrier.

As intimated above, some species mentioned herein do not range to the immediate shores of the bay and, thus, are not directly limited in their distribution by the bay. Some are checked in their southward or northward distribution by unsuitable habitat or other barriers, and range no closer than thirty miles from the bay. This is true particularly of boreal species, principally in northern coniferous forests and associated with northern conditions of climate. *Eutamias townsendii, Tamiasciurus douglasii, Clethrionomys californicus,* and *Phenacomys longicaudus,* all boreal kinds, do not occur south of the Sonoma-Marin gap, thirty miles north of the Golden Gate. Two Sonoran kinds, *Dipodomys venustus* and *Eutamias merriami,* likewise range only within fifteen or twenty miles of the bay, where they are checked by unsuitable conditions.

There is some evidence that at least two species, possibly four, are near limits of their tolerance. The distribution of *Aplodontia rufa* and *Zapus trinotatus* in the habitat available to them is spotted and discontinuous, giving the impression that they are "relics" from a time when environmental conditions were more widely favorable to them. More than that, they are represented by only a few individuals; they do not appear to be thriving, a condition markedly contrasted with that usually seen where the same species is supplied with conditions that are nearer optimum for its existence. That two other species, *Peromyscus californicus* and *Eutamias merriami,* may be approximating tolerance limits in the bay region is suggested by the limits of their distribution elsewhere in California. Both species range northward on the western slopes of the Sierra Nevada only to Mariposa County—about the latitude of San Francisco Bay. Factors associated with latitude may define the northern limits of those species in both the coast ranges and the Sierra Nevada.

DIFFERENTIATION UNDER ESSENTIALLY CONTINUOUS AND DISCONTINUOUS DISTRIBUTION

The coastal and interior parts of central and northern California stand in sharp contrast in environmental conditions. The coastal part is characterized by frequent fogs, relatively high humidity, moderate and comparatively constant temperatures, and low insolation—qualities which have led to the production of dark rich humus-filled soils and luxuriant plant growths. Interior to the narrow coastwise belt more xeric conditions prevail. Fogs are infrequent, the relative humidity is considerably lower, the amount of insolation is higher, and the temperatures are more extreme. Soils are usually paler and well leached, and the growth of vegetation is less profuse and more xeric in character. These environmental contrasts are definite and clear cut.

The northern and southern parts of the bay area (i.e., north and south of the bay) exhibit no such strong and consistent contrasts of environmental conditions. It is true that the northern part has a higher annual precipitation and lower annual temperature on the average (see account of climates, p. 11) and, in general, harbors cooler, more temperate climates than does the southern part. These conditions, however, are not continuously distributed. The northern and southern parts are not so sharply and consistently different in environmental conditions as are the coastal and inland belts.

The type of differentiation involved in the coastal and inland belts seems to be unlike that on the two sides of the bay. In the former type, where the environmental contrasts are rather clear cut, the differential characters parallel the environmental gradients. Where the bay has introduced isolation between areas not consistently different in such environmental features as distinguish the coastal and inland belts, parallel differentiation is mostly lacking and is replaced by differentiation in which there is little or no correspondence of morphological characters in the differentiating forms.

The differential characters distinguishing the coastal and inland subspecies appear to be comparatively simple adaptations to the differing environments and seem to have been evolved in response to some selective force which governed the direction of their evolution, since parallel clines tend to be established in each of the differentiating species. The characters distinguishing the coastal from the inland forms are mainly ones of coloration and general size. Compared with the inland forms, the coastal subspecies usually show larger size, a relatively longer and monocolored tail, increased pigmentation, particularly dorsally, darker color tones, and perhaps longer incisive foramina and a shorter hard palate. The distributions of the various characters are closely correlated with the distributions of the environmental gradients. This is well demonstrated in the coastal and interior races of *Peromyscus maniculatus, P. californicus, P. truei, Neotoma fuscipes,* and *Thomomys bottae.*

The differential characters distinguishing subspecies isolated from each other by the bay are complex. On the whole, they do not appear to be the simpler type of environmental response indicated above and commonly shown by many kinds of mammals and birds. If they are adaptive at all, they probably involve life ways or some other patterns now appearing more complex than simple environmental correlations. At present, most of the characters have no apparent adaptive significance and, in the absence of genetic data, no known genetic correlation with physiologic differences that may convey an adaptive advantage. Nor are gradients apparent in the differentiations; each species seems to have responded in its own way to the effects of isolation. The evolution of most of the differential characters apparently has rested mainly on chance fixation, proceeding possibly at variance to environmental forces, other than isolation, and to selective pressures which may have been active.

Thus, the bay-separated forms are variously identical or different in size, tail length, hues and patterns of coloration, and variously similar or dissimilar in number of homologous meristic parts and in shapes and sizes of various parts of the skull. The bay-separated populations of *Neotoma fuscipes* exhibit differences in the shape of the interpterygoid fossa and the posterior border of the hard palate. The subspecies of *Thomomys bottae* differ in the form of the zygomatic process of the maxilla and the color of the upper incisors. In *Sciurus griseus,* the races differ in size, in several characters involving the pattern and hue, in the width of the upper incisors, and in the length of the incisive foramina. In *Citellus beecheyi* the pattern of coloration is similar, but there are differences in hue and tone, in length of the tail, and in the length and breadth of the brain case. The bay-separated populations of *Dipodomys heermanni* differ in size, in tail length, in number of toes on the hind foot, in several characters of coloration, and in proportional sizes of certain parts of the skull.

The differentiation of the bay-separated forms, although at the present time involving chiefly subspecific levels, is of a sort which, more readily than the differentiation of inland and coastal forms, it seems to me, might be expected to transcend limitations and lead to full speciation. All of the bay-separated forms need not, and indeed probably will not, become specifically distinct, but most of them, particularly those that have evolved marked differences and that may not completely intergrade in geographically intermediate areas outside the bay area, appear to be well on the way toward species. The isolation imposed on them by the bay favors the complete differentiation of these forms.

SPECIFIC AND SUBSPECIFIC LEVELS OF DIFFERENTIATION

In the taxonomic analysis of the rodent fauna of the bay area, I have referred to two main levels of differentiation within a genus, namely the specific and the subspecific, and, in addition, have pointed out lesser geographic variants when such have been apparent. This procedure accords with current practice in mammalogy. Such an arrangement implies that species are sharply demarked from subspecies which are, in turn, sharply separated from any variants within a subspecies. Actually, the forms are not sharply separable, certainly not on the basis of amount of difference and probably not on the basis of intergradation or interbreeding. The differences between species and subspecies in the rodents of the bay area appear to be of degree, not kind. The specific level grades into the subspecific, which merges with that of lesser categories.

The representative forms (species or subspecies) which occur on both sides of the bay are listed below in order of decreasing distinction as regards relative amount of difference between the representative populations north and south of the bay. This scale was arrived at in the following way. Each form was rated numerically on the basis of total differences, in characters of skin and skull, which were observed between the populations on the two sides of the bay. The rating of a form determined its position in the scale; those of high rating were placed near the top, those of low rating toward the bottom. The weight given a character was based on my estimation of the stability of that character and its value in taxonomy, as determined by my experience with it in studies of the particular species involved, and the amount of difference shown in a structure in a species as compared with the amount shown in the homologous structure in another species. Body size was given a maximum weight of 3; relative difference in size of an external part, 4; presence or absence of a part, 10; differences in hue, 3; and of pattern of coloration, 8; difference in shape of parts of the skull, 6; and of relative size of parts of the skull, 4. The rating for the total differences noted in a form between bay-separated populations was secured by adding together the values set on each of the above characters. The actual totals for each species were of use only for determining the relative position of the species in the list and are not given here:

Dipodomys heermanni (*californicus* vs. *berkeleyensis* and *heermanni*)—strong subspecies, but likely to be regarded as separate species
Eutamias sonomae (vs. *E. merriami*)—here regarded as separate species
Sciurus griseus (*griseus* vs. *nigripes*)—strong subspecies
Citellus beecheyi (*douglasii* vs. *beecheyi*)—strong subspecies, regarded as full species by some
Neotoma fuscipes (*fuscipes* or *monochroura* vs. *perplexa* or *annectens*)—moderate subspecies
Thomomys bottae (*minor* or *agricolaris* vs. *bottae* or *diaboli*)—moderate subspecies
Microtus californicus (*eximius* vs. *californicus*)—moderate subspecies
Peromyscus truei—separation of populations possible on average features, but not deemed sufficient for recognition of subspecies
Peromyscus maniculatus—
Reithrodontomys raviventris—
Reithrodontomys megalotis—
} apparently complete identity of populations in each species

In each of three species, as here interpreted, the bay-separated populations are indistinguishable in characters of skin and skull. In one species the populations are separable on the basis of slight average characters, which, however, are not deemed sufficient for erection of separate subspecies. In the remaining seven representative forms, varying amounts of distinction are apparent, allowing for recognition, on the basis of extent of difference, of the general categories moderate and strong subspecies and full species.

To demonstrate essentially full intergradation of characters of two forms on the one hand and apparently complete purity of the separate forms at the opposite extreme is comparatively easy. The characters of some forms in the bay area grade into those of other forms in areas geographically between their population centers. Other forms in the same area maintain their separate identities, giving no evidence of intergradation in diagnostic characters or of interbreeding. To demonstrate with examples various stages between these two extremes is difficult and subject to qualifications. None of the species in the bay area, or elsewhere in California, has been studied in sufficient detail to enable one to state with certainty that the varying degrees of intergradation and of interbreeding, which are indicated, accurately represent conditions as they actually occur, and instead are not artificialities resulting from the lack of sufficient materials and study. That the latter may be true cannot be denied; however, present data indicate that degrees of intermediacy in intergradation and interbreeding among the rodent fauna of the bay area are recognizable. In the present study, intermediacy or intermixture of the characters of two similar forms I have taken to mean intergradation. Intergradation of two forms in geographically intermediate areas to me indicates interbreeding of the forms. Intergradation does not always indicate current interbreeding, however; morphologically similar, apparently closely related forms that are geographically isolated from one another may intergrade, but as now distributed obviously cannot interbreed. Their intermediacy may date from a former interbreeding, prior to present separation of ranges.

As examples of forms which exhibit essentially complete intergradation, and, it may be inferred, free interbreeding, the geographically complementary, coastal and inland subspecies of *Thomomys bottae, Peromyscus californicus, P. truei, P. maniculatus,* and *Neotoma fuscipes,* may be mentioned. The characters of the inland subspecies in each of these species grade into those of the coastal races toward the inner border of a humid belt which parallels the seacoast. The identity of each race is established by average differences which are best developed near the seacoast and inland, respectively. In geographically intermediate areas, intermediacy in morphological characters is attained.

The subspecies of the species *Eutamias sonomae, Aplodontia rufa,* and *Zapus trinotatus* illustrate intergradation through individual variation of geographically isolated forms. The races *E. s. alleni, A. r. phaea,* and *Z. t. orarius,* in Marin County, are geographically isolated by inhospitable terrain from the races *E. s. sonomae, A. r. nigra,* and *Z. t. eureka,* found twenty-five or fifty miles to the north in Sonoma and Mendocino counties. Actual interbreeding between the representative races appears to be impossible at the present time. There is, however, overlap in the range of variation of one or all of the diagnostic characters of each subspecies, and the two may be said to intergrade.

The species *Citellus beecheyi* and *Dipodomys heermanni* exemplify incomplete intergradation and, perhaps, incomplete interbreeding. Each of these species is divisible into what are here regarded as two subspecies groups (see accounts of *Citellus b. beecheyi* and *Dipodomys h. californicus* in the present paper), one of which occupies northwestern California, the other more southern and eastern parts of the state. Each of these groups exhibits certain characters that are not matched in the other group; there is but slight intergradation by individual variation. The ranges of the groups within each species apparently are isolated from one another over much of their extent, but they are known to merge in some areas (the ground squirrels in Butte County, Howell, 1938: 152, and the kangaroo rats in Eldorado County, Dale, 1939: 729). In each of these areas, complete, full intergradation, such as can be demonstrated between the coastal and inland races mentioned above, has not yet been observed, and the frequency of occurrence of animals more or less intermediate morphologically appears to be low. Further studies in these areas may show that interbreeding takes place at a normal rate, as indicated by the numerous individuals intermediate in morphological characters. On the other hand, and this I believe likely, it is possible that interbreeding between the two groups within each species is comparatively uncommon, whether due merely to scarcity of individuals in what are perhaps to them unfavorable areas or to some partial physical or psychological barrier to interbreeding.

Complete lack (as far as now known) of interbreeding and intergradation in important characters between two forms is exemplified by the kinds listed below. Each can with assurance be accorded full specific status. Each occurs with the other species of the genus that are mentioned below and completely maintains its identity. The kinds follow: *Eutamias townsendii* and *E. sonomae; Dipodomys heermanni* and *D. venustus; Reithrodontomys megalotis* and *R. raviventris; Peromyscus californicus, P. truei,* and *P. maniculatus;* and *Neotoma lepida* and *N. fuscipes.*

In the rodents of the bay area, then, the amount of difference and the completeness of intergradation and perhaps of interbreeding between two forms vary. Differences between species and races appear to be of degree rather than of kind, and an almost complete gradation can be demonstrated between the markedly different and apparently sexually isolated forms and the essentially identical, freely interbreeding, and intergrading forms. If evidence of intergradation or interbreeding is absent—the one definite criterion the mammal systematist has at present for distinguishing species from subspecies—the taxonomic status of a form, whether it is to be treated as a species, subspecies, or a member of some lesser category, usually depends, in final analysis, on the interpretation of the taxonomist.

The data in the present paper, though less significant than the evidence which might be presented by a geneticist or a physiologist, are out of harmony with the view, recently championed by Goldschmidt (1940), that "microevolution" and "macroevolution" are unrelated processes. The highly critical work of that author has led him to conclude: (1) that the processes involved in the formation of species are different in kind from those which have to do with the evolution of subspecies; (2) that the saltatory breaks between species are of a different sort, involving differences in the "reaction system" and in chromosome mechanism; (3) that fertility between species is lacking or, at most, highly incomplete; (4) that morphologic differences between true species tend to be large, in comparison, and, if adaptive at all, probably involve complex adjustments in the physiology of the animal. Subspecies, to Goldschmidt, are ephemeral stages in evolution, destined eventually to pass out of the evolutionary picture without evolving into distinct species. "Good species" arise, he thinks, only through sudden, drastic, yet perhaps subtle, organismal changes.

It has been shown in preceding pages, on the basis of morphologic differences, that no sharply marked distinctions are apparent between species and subspecies (as these categories are represented by the mammals of the region under study). The so-called specific level of distinction does not mark a sharply increased degree of differentiation. In magnitude, as well as in kind, some of the differences between the subspecies are like those which separate the full species. The species grade into the subspecies, which in turn merge with the lesser variants. Interfertility within a kind, too, appears to vary. To judge from the intergradational phenomena observed, some of the forms are completely interfertile and interbreed freely where they come together; others apparently are only partly fertile or fail completely to interbreed. It should be pointed out again, however, that data on interbreeding of the forms in the bay area are few and highly incomplete and need bolstering by experimental matings.

It seems probable that the subspecies which have been subject to isolation by the waters of the bay and have developed marked differences are more likely to become specifically distinct than are the representative subspecies in the coastal and inland belts. Perhaps their reaction systems and chromosomal complexes are at present sufficiently distinct for some or all of the bay-separated forms to be treated as full species. But even so, the distinctions in those systems and complexes would appear to be of degree, not of kind, in order to account for the gradation in characters, and concomitantly in systems and complexes, between the bay-separated forms through geographically intermediate populations outside the bay area.

HISTORY OF THE RODENT FAUNA

The history of the rodent fauna of the bay area that is given below is based chiefly on the study of the present distribution of species, both inside and outside the area, and, to a lesser extent, on the morphological affinities and the geographic distribution of races within the species. The fossil record contributed little. A highly discontinuous distribution of a species is taken to indicate, usually, a long-continued occupancy of its range. A continuous geographic range of a species, on the other hand, suggests a more recent immigration. A cue to the direction from which immigration took place is supplied by the geographic location of the entire range of a species. Thus, a species now predominantly Sonoran in occurrence usually is thought to have moved from the south into any boreal areas it now occupies. Similarly, a boreal species in the south is considered usually to be an emigrant from the north. The study of the affinities and differences of races within a species has contributed some information on the geographic movements of the species. A major difficulty with such studies, however, lies in determining actual affinities of races. Similarities may not indicate immediate kinship, but instead may be the result of parallel developments under similar environments.

The fossil record, for the part of California involved here, is so incomplete as to be of little use. It does show, however, that some species present in the bay area in Pliocene are now extinct and that species now living in the bay area existed elsewhere in California, if not also in the bay area, in Pleistocene. One species, a beaver, described from Pliocene deposits near Berkeley (J. C. Merriam, 1896), is now extinct. No modern rodent kinds have been recorded from deposits in the bay area; however, modern species, or kinds very similar to those now living, have been recorded from Pleistocene deposits elsewhere in California. Remains recovered from beds near Carpinteria and at Rancho La Brea, in southern California, include species of *Eutamias, Sciurus, Citellus, Thomomys, Perognathus, Dipodomys, Reithrodontomys, Peromyscus, Neotoma,* and *Microtus* (Dice, 1925, and Wilson, 1933)—all genera now represented in the bay area. More than that, the species of most of these genera appear to be the same as those now living both in southern California and in the bay area.

The study of the present distributions of the species and of apparent affinities of races within the several species throws more light on the history of the rodent fauna of the bay area. It indicates that the species comprising the present fauna probably did not become established in the bay area at the same time, but instead moved in at different times and from different directions. At least one species may have evolved in the bay area (see above section "Speciation in bayside marshes").

Aplodontia rufa and *Zapus trinotatus* are probably among the earliest of the modern occupants of the bay area. Both species are predominantly boreal in distribution at the present time, occupying comparatively cool, humid areas in the northwestern United States and in the higher mountains of California in the southern part of their ranges. It is logical to believe that both species, or their progenitors, originally from the north immigrated to the southern extreme of their ranges, perhaps to the areas they now occupy in Marin County. Environmental conditions probably were different then, because to reach Marin County the species crossed areas which now are unsuitable for them, for example the region which now separates the Marin and the Humboldt Bay districts. Habitat suitable for them in Marin County is local in occurrence, and their entire distribution is correspondingly discontinuous. Neither are they as abundant in much of that habitat (probably because the habitat is less developed toward their needs) as they are in more northern areas, where conditions appear to be more nearly optimum. The whole aspect of the distribution of each suggests early emigration from the north, when environmental conditions were more extensively suited to its needs, and a subsequent restriction of its range to the local isolated areas the species now occupies.

The present discontinuous distribution and differentiation of *Phenacomys* likewise suggests a comparatively long-time occupancy by *Phenacomys longicaudus* of the habitat it now possesses in the bay area. Throughout its entire known range the species apparently is local in occurrence, occupying only part of the redwood-Douglas fir forests, to which it is entirely restricted. The known facts of its habits and its distribution indicate that it is unable to withstand strong competition and marked changes in its environment. Also like *Aplodontia rufa* and *Zapus trinotatus,* it probably is of northern origin.

The species mentioned above are examples of boreal kinds which, by reason of their discontinuous distribution, differentiation, and apparently narrow tolerances, are judged to be early residents in the bay area. Other species of the modern rodent fauna may have become established in the bay area concurrently with them, as for example *Thomomys bottae,* a Sonoran species which by reason of its relatively sedentary habits and differentiation into many geographic races may be considered an early resident. Most of the kinds, however, appear to be more recent immigrants.

The ranges of *Tamiasciurus douglasii, Clethrionomys californicus,* and *Eutamias townsendii* are entirely north of the Sonoma-Marin gap, a belt of country in southern Sonoma and northern Marin counties which is unsuited to the needs of those species. This distribution pattern, with the predominantly boreal distribution of the species outside the bay area, indicates that they are emigrants from the north that moved into the bay area after the gap became impassable to them and, by the same reasoning, after the boreal species south of the gap in Marin County had moved in and become established.

The habits and present distribution of *Citellus beecheyi, Sciurus griseus, Eutamias sonomae, Dipodomys heermanni,* and *Neotoma fuscipes* indicate that each may have evolved in that part of the Pacific coast region west of the arid deserts from southern ancestral stock. Their more extensive and continuous distribution in California and the occurrence of at least three of these northward well into Oregon argue for their establishment in the bay area later than *Aplodontia* and *Zapus* and probably later than *Phenacomys* and *Thomomys.* The trenchancy of the intraspecific differences (interspecific differences between *Eutamias sonomae* and its ecologic counterpart, *E. merriami*) in morphologic characters which distinguish the bay-separated populations, however, indicate the establishment and semi-isolation of the populations in the north coast ranges before certain other Sonoran species, mentioned below, came in.

The most recent immigrants into the bay area are probably those Sonoran kinds which are either widely distributed in western North America and break up into few geographic races or, restricted in their occurrence principally to California, are found only south of the bay. *Peromyscus maniculatus, Reithrodontomys megalotis, Perognathus californicus, Dipodomys venustus, Peromyscus californicus,* and *Neotoma lepida* may belong in this category. The first two species are widely distributed in North America and are adaptable, comparatively quick to invade areas in northern regions made available and suitable to them by changes in the environment. *Perognathus californicus* and *N. lepida* are unknown from the north side of the bay where habitat suited to their respective needs, and situated only a mile or so away, is unoccupied by ecologically complementary kinds. This fact becomes all the more significant when the occurrence of many Sonoran kinds on the north side of the bay is noted, and it suggests that each of the kinds mentioned above is a recent emigrant from the south, which found the bay a barrier to further extension of range toward the north. It does not necessarily imply, however, that those Sonoran species well established on both sides of the bay and those Sonoran species represented by an ecologically similar counterpart on the opposite side (such as *Eutamias merriami* and *E. sonomae*) reached the areas presently occupied from contiguous areas immediately to the south or that they moved into the bay area before the bay barred their spread northward. There are avenues of habitat suitable for those species (and indeed in most instances, presently occupied by them) around the bay—via the San Joaquin and Sacramento valleys and adjoining hills for kinds requiring open situations and via the Sierra Nevada and coast ranges north of the bay for brush- or woods-requiring species. In fact, it seems to me highly probable that such a roundabout route to the north side of the bay was the route of immigration of some Sonoran species. Evidence for this pincer-like movement is derived from the present distribution of certain species, the manner in which their races meet adjoining races in the Sierra Nevada and the northern part of the Sacramento Valley, and the distribution of their intraspecific characters.

For example, the species *Peromyscus boylii* is an inhabitant of Sonoran areas of southwestern United States and Mexico and probably is of Sonoran origin. In California, its known range extends from the boundary of Mexico northward through the coast ranges and through the lower elevations on the western slopes of the Sierra Nevada. North of the Tehachapi Mountains its range is essentially continuous around the Great Valley of California except for a hiatus of about one hundred miles in the coast ranges bordering San Francisco Bay. The species is not known from that part of the bay area bounded by Solano County on the north and Monterey County on the south. If this area has remained free of *boylii*, and there is reason for believing that at least that part covered by the combined flows of the Sacramento and San Joaquin rivers has been devoid of the species since Pliocene, and the area now occupied by the waters of the bay uninhabited by the species since late Pleistocene or early Recent time (Lawson, 1914: 20), the populations in the coast ranges north of the bay may have reached there by way of the Sierra Nevada and not across the bay from the southern coast ranges. Further credence to this hypothesis may be afforded by the distribution of the intraspecific characters. The characters exhibited by specimens north of the bay, of the race *boylii,* are also held by those from the northern part of the Sierra Nevada. They differ from those in the coast ranges south of the bay and from those in the southern and central Sierra Nevada, race *rowleyi.*

Citellus beecheyi, Sciurus griseus, Dipodomys heermanni, and *Neotoma fuscipes,* all Sonoran species now established north and south of the bay, may have moved into the areas they now occupy by a route similar to that possibly followed by *Peromyscus boylii.* As for that species, the range is essentially continuous around the bay, and intraspecific affinities appear to be distributed via that route rather than directly across the bay; stated in another way, differences are greater across the bay than by a circuitous route around that barrier. Within each species the race or complex of races north of the bay stands apart from the race or group of races to the south of that barrier, giving evidence of long isolation, but nevertheless connecting by way of the "intermediate" races in the Sierra Nevada.

SUMMARY

A study was made of the distribution of the native rodents in a specially selected section of west-central California around San Francisco Bay. Forty-three kinds, species and subspecies, are recorded. Each is treated as to characters of skin and skull and geographic and ecologic distribution in the special area studied. Two rodent faunal areas, four faunal subareas, seven districts, and nine ecologic associations are recognized. Each faunal division has two or more rodent kinds and a set of environmental conditions peculiar to it. The ecologic associations are those which appear to be particularly important from the point of view of survival of the rodent species; they do not represent an exhaustive classification, by associations, of the flora and fauna of the area.

San Francisco Bay has had an important influence on the distribution and evolution of the rodents. It provides extensive marshlands to which at least three subspecies of rodents are restricted and in which they may have evolved, possibly entirely within Recent time. It allows for the occurrence inland of coastal climates, with which are correlated certain morphologic features of rodents. It is a physical barrier to the geographic movements of the rodents. Eighteen subspecies live north of the bay and seventeen south of it.

To judge from the highly discontinuous distributions, scanty populations, and, in some instances, limits of ranges outside the bay area, San Francisco Bay may mark approximately the northern or southern limits in the coast ranges of some species. The bay has served only to limit abruptly the ranges of certain species which perhaps would not occur much farther to the north or south if the barrier were absent.

In environmentally different coastal and inland belts in the bay area, the intraspecific differential characters of at least five species of rodents parallel the environmental gradients which are apparent as between those coastal and inland areas. The differential characters are principally of size and color and appear to have evolved in response to some selective force in the environment that governed the direction of their evolution. Where the bay has introduced isolation between areas not consistently different in such environmental features as distinguish the coastal and inland belts, parallel differentiation is mostly lacking. Character gradients in the several differentiating species are not apparent. Each species has responded in its own way to the effects of isolation; the evolution of most of the intraspecific differential characters appears to have rested on chance fixation alone, which may have preceded contrary to any selective pressures that may have been active. It seems likely that the differentiation of the bay-separated forms,

although now involving chiefly subspecific levels, is of a sort which, more readily than the differentiation of inland and coastal forms, might be expected to lead to full speciation.

No sharply marked distinctions are apparent between species and subspecies (as these categories are represented by the rodents in the bay area). The so-called specific level of distinction does not necessarily mark a much greater extent of differentiation. In magnitude, as well as in kind, some of the differences between subspecies are like those which separate full species. The species grade into the subspecies, which in turn merge with the lesser variants. Interbreeding within a kind, too, appears to vary from essentially complete to highly incomplete interbreeding; data on this phenomenon are incomplete. Speciation and subspeciation, to judge from the data in the present paper, are closely related processes, differing in degree not kind. This does not accord with the view recently championed by Goldschmidt (1940).

The rodent fauna of the bay area has changed in the geologic past and probably is changing now. It consists of elements which have moved in at different times and from different directions. The bay has influenced the present distribution of the faunal elements, the recent immigrants especially.

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PLATE I

FIG. 1. Salicornia-marsh association, as illustrated by the salt marshes at Morro Bay, San Luis Obispo County, November 7, 1918. Similar marshes border San Francisco Bay. (Photograph No. 2870, Mus. Vert. Zool.)

FIG. 2. View of salt marshes at low tide. Northeast from near Alviso, Santa Clara County, toward the mountainous ridges bounding the valley of San Francisco Bay on the east. October 29, 1938. (Photograph by Frederick H. Test.)

PLATE I

FIG. 1

FIG. 2

PLATE II

FIG. 1. View of marshy, bunch-grass meadow association as seen near Inverness, Marin County, June 7, 1913. (Photograph No. 994, Mus. Vert. Zool.)

FIG. 2. Ravine on north side of Strawberry Canyon, Berkeley, Alameda County. Woods composed chiefly of Coast live oak and California bay, bordered by old-man sage, coyote brush, and grasses. Grove of trees in upper right is of the nonnative eucalyptus. April, 1938. (Photograph by Frederick H. Test.)

PLATE II

Fig. 1

Fig. 2

PLATE III

FIG. 1. View west toward an enveloping fog bank on the flanks of Mount Diablo, Contra Costa County, July 23, 1912. Dry grassland, hard chaparral, and a few scattered oaks and digger or Counter pines are shown. (Photograph No. 853, Mus. Vert. Zool.)

FIG. 2. Fog-covered hillside near Walnut Creek, Contra Costa County, showing dry grassland, hard chaparral, and (poorly developed) foothill woodland associations. Burrows in grasslands in left center made by Beechey ground squirrels. August 15, 1918. (Photograph No. 2783, Mus. Vert. Zool.)

PLATE III

FIG. 1

FIG. 2

PLATE IV

FIG. 1. Foothill woodland and dry grassland associations as developed on the upper reaches of Encinosa Creek, west of Vacaville, Solano County, July 10, 1912. (Photograph No. 848, Mus. Vert. Zool.)

FIG. 2. A different view at the same locality, July 8, 1912. (Photograph No. 845, Mus. Vert. Zool.)

PLATE IV

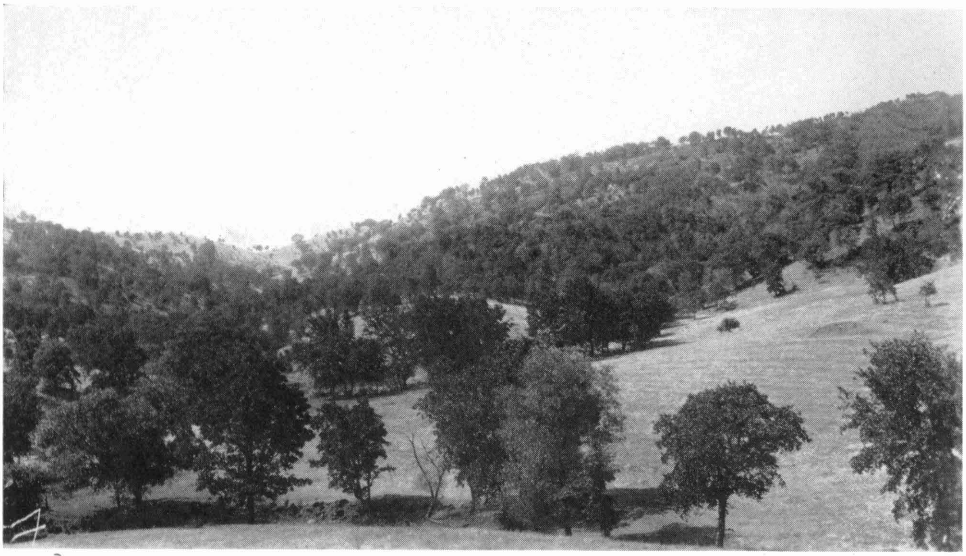

FIG. 1

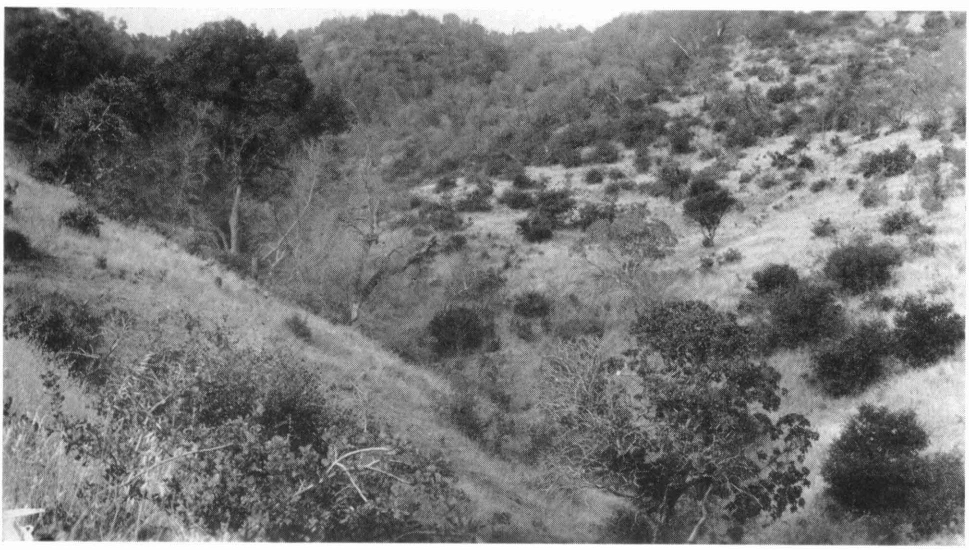

FIG. 2

PLATE V

FIG. 1. Second-growth redwoods, Douglas fir, and tan oak, interspersed with some soft chaparral at McEwen's Mill, Sonoma County, June 24, 1913. (Photograph No. 1001, Mus. Vert. Zool.)

FIG. 2. The redwood-Douglas fir association as developed on a slope near Freestone, Sonoma County, June 18, 1913. (Photograph No. 995, Mus. Vert. Zool.)

PLATE V

FIG. 1

FIG. 2

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