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LATE CENOZOIC VERTEBRATES OF THE SAN FRANCISCO BAY REGION

BY
DONALD E. SAVAGE

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LATE CENOZOIC VERTEBRATES OF THE SAN FRANCISCO BAY REGION

BY

DONALD E. SAVAGE

(A contribution from the University of California Museum of Paleontology)

ABSTRACT

A SURVEY of the vertebrate faunas from the nonmarine late Cenozoic deposits of the San Francisco Bay region has led to the conclusion that the expanse of time represented by these faunas may be subdivided into three parts. The nomenclature of these subdivisions is made correlative with the provincial age designations for the continental Tertiary which were proposed by the Wood Committee (1941). The provincial ages used for the Bay region are: "Blancan," the name proposed by the Wood Committee for the late Pliocene subepoch; "Irvingtonian," a new name for earlier Pleistocene typified by the Irvington fauna; "Rancholabrean," a new name for later Pleistocene typified by the Rancho La Brea fauna.

The vertebrate fossils of Blancan age from the San Francisco Bay region are few in number but support a proposed post-Pliocene (post-Blancan) date for the intense folding of at least part of the Coast Ranges. A concept of vertebrate land life in earlier Pleistocene time is well portrayed by the Irvington fauna. A logical and practical nomenclature of the horse (*Equus*) and the camelid (*Camelops*) of the Irvington fauna necessitates that many of the proposed species of these two genera be designated as indeterminate names. The fact that the beds which contain the Irvington fauna are only slightly tilted supports a pre-Pleistocene dating of the last intense folding of the Coast Ranges in this area. The later Pleistocene is represented by fossil materials from twelve or more sites in the San Francisco Bay region. The faunas are dated as later Pleistocene when they contain *Bison*. Discovery of fossil vertebrates beneath the present level of San Francisco Bay supports the idea that this submerged area was above sea level throughout much of Pleistocene time.

It is emphasized that the present knowledge of the phylogeny and ecology of land vertebrate species of the San Francisco Bay region within the post-Blancan to pre-Recent epoch (Pleistocene) warrants only a twofold chronological subdivision.

INTRODUCTION

THIS MONOGRAPH is an attempt to carry on the work of description of the fossil vertebrates of the San Francisco Bay region. The late Cenozoic terrestrial vertebrate faunas are now complete enough to enable us to date some of the containing strata. Especial attention has been given to the Irvington fauna because it is the best-known sample of earlier Pleistocene land life in the western United States. It is intended that the student of field stratigraphy and paleontology may use this paper as a supplement to Stirton's (1939*d*) study.

Many stratigraphic problems still exist in this area despite the fact that these problems have at times received the attention of competent geologists and paleontologists. No solution is offered for most of these questions, but recent fossil discoveries have given some evidence on the chronology and sequence of some of the beds. A continued reconnaissance is expected to produce other significant materials. Bit by bit, then, we may expect much of the geologic history of this region to be revealed by the discovery of fossil vertebrates.

ACKNOWLEDGMENTS

I am particularly grateful to the Boy Paleontologists of Hayward, California,¹ and to their director, Mr. Wesley Gordon, for collecting and preparing the main part of the Irvington fauna. They have made available their entire collections for scientific study. This boys' organization has set a pattern in the scientific curation of natural history specimens that even a nominally more professional group will find difficult to equal. The efforts of Mr. Gordon and others to establish an Alameda County natural history museum designed to serve particularly the scientific interests of young people are to be highly commended and should be assisted by all who are in a position to lend support.

I am also very much indebted to Mr. Stanley L. Bell and Mrs. Anna L. Bell, present owners and operators of the excavations from which most of the Irvington fauna has been obtained. Mrs. Bell has saved all specimens that have been discovered in the pits and has generously donated these materials to the Hayward Boy Paleontologists and to the University of California for study.

The research was done under the direction of Dr. R. A. Stirton, who has offered many guiding suggestions and criticisms. Dr. G. D. Louderback, Dr. Howel Williams, and Dr. J. W. Durham have read the manuscript and have made helpful criticisms. All recent comparative materials used in the study were made available by Dr. S. B. Benson of the Museum of Vertebrate Zoölogy, University of California.

All drawings accompanying this paper are by Mr. Owen J. Poe, Staff Artist in the Museum of Paleontology, University of California.

METHOD OF BIBLIOGRAPHIC CITATION, TEXT ABBREVIATIONS,
AND TECHNIQUE OF MENSURATION

The dates of all references cited in this study are alphabetized according to the listing of these references in the bibliographies of fossil vertebrates of North America. The bibliographies followed are Hay (1902*a*), Hay (1929 and 1930), Camp and VanderHoof (1940), Camp, Taylor, and Welles (1942), and Camp, Welles, and Green (1949).

The University of California Museum of Paleontology will be abbreviated U.C.M.P.; the University of California Museum of Vertebrate Zoölogy will be abbreviated U.C.M.V.Z.

All dental measurements in the systematic descriptions are made from the tooth enamel unless otherwise specified. All measurements listed in this paper are in millimeters.

BLANCAN

DESCRIPTION OF LOCALITIES

V4017. Willow Pass. In highway cut excavated in 1940; SE $\frac{1}{4}$ of SW $\frac{1}{4}$, Sec. 17, R. 1 W, T. 2 N; SW corner of Antioch quadrangle; locality on N side of highway about 380 ft. from

¹ Charter members of this organization are Lester Kent, Roy Kent, Bill Seaver, Bob Seaver, Phil Gordon, Wesley Gordon, Jr., Billy Gordon, Byron Lewis, Danny Hennigan, Leonard Hennigan, Jay Broadwell, David Pendergast, James Pendergast, James Ward, Sammy Harwood, Ralph Rosenblatt, and Jack Linnell. Honorary members are Mr. and Mrs. Stanley L. Bell, Mrs. Helen Silver, and Mr. Joseph Stephensen.

E edge of large road cut for highway leading from Willow Pass junction toward Muir Station (Concord to Pittsburg), about 4 ft. above level of pavement; fossil-bearing deposit a pebbly sandstone lentil of a series of predominantly grayish, loosely cemented conglomerates, pebbly sandstones, sandstones, and mudstones; some beds are reddish and greenish; rocks seen in conglomerates include chert pebbles (mostly jasper) probably derived from Franciscan, black chert, and black quartzite pebbles, highly altered igneous pebbles, sandstone pebbles from Franciscan or Cretaceous, a few dark limestone pebbles possibly derived from Cretaceous; beds nearly vertical at fossil site. (Weaver, 1949—Markley sandstone.) *Equus cf. simplicidens*—Blancan. Fig. 36.

V0301. Pittsburg. Described and located by Stirton (1939d, pp. 389–390). (Jenkins, 1941—Los Medanos formation; in his compilation, Jenkins was apparently informed that Weaver would name the formation “Los Medanos.”) (Weaver, 1949—Wolfskill formation.) *Borophagus pachyodon* (Merriam), *Testudo*, proboscidean—Blancan. Fig. 36.

DESCRIPTION OF MATERIAL

Equus cf. simplicidens (Cope)

(Figs. 1, a, b)

Locality V4017. Willow Pass. U.C.M.P. no. 35998, incomplete right lower jaw containing permanent cheek-tooth series; equivalent in size and enamel configuration in cheek teeth to mandible identified as *E. shoshonensis* (Gidley), U.C.M.P. no. 34036, from Hagerman, Idaho. Hagerman teeth in almost identical stage of wear; labial border of flexids of P_2 and P_3 of Idaho specimen more plicated than in California jaw, but this can be demonstrated as a variable character; molar flexids in Hagerman specimen less plicated than in jaw from Willow Pass. Individual teeth of *E. simplicidens* (Cope) from Mount Blanco, Texas, in University of California collection inseparable from corresponding teeth in Willow Pass jaw. Willow Pass teeth differ from teeth identified as *E. francescana* (Frick, 1921a, p. 325), including referred materials from Coso Mountains (J. R. Schultz, 1936), in possession of strong pli caballinid, by greater flattening of labial border of protoconid and hypoconid, and in possession of abruptly sharpened and deepened labial apex in metaconid-metastylid groove.

Discussion.—The differences listed above may not be constant, for, in miscellaneous teeth from Hagerman, all these characters are shown to be present or absent. These characters are present or absent in *E. simplicidens* also.

I believe that *E. shoshonensis*, *E. idahoensis* (Merriam), *E. proversus* (Merriam), and *E. francescana* may be, at most, racial subdivisions which can be referred to *E. simplicidens*. This opinion is based on the wide range of variation in dental pattern and skull proportions seen within Recent wild species of *Equus*. Relatively wide geographic separation is not necessarily a justification for speciation within the genus. It seems reasonably well established that the areas of the western United States represented by the known Blancan faunas were favored with an equable climate which was probably more moist than at present (Evans and Meade, 1944; Hibbard, 1941b; Gazin, 1936a). *Equus*, a wide-ranging animal, would find no climatic or ecological barrier to dispersal from one of these areas to another. It is also probable that mountain chains such as the Sierra Nevada did not form the obstruction to east-west dispersal in Blancan time that they do at



Fig. 1. *Equus cf. simplicidens*, U.C.M.P. no. 35998, loc. V4017: a, occlusal view of right lower jaw with P_1 to M_1 inclusive; b, lingual view. $\times \frac{1}{2}$.

present. There is strong reason to believe, then, that *E. simplicidens* was free to roam the western United States.

Plesippus Matthew (this is *Hippotigris* if McGrew and others are followed) is a category of subgeneric rank at most. It seems tenable that if various proposed genera for later equids—*Asinus*, *Plesippus*, *Hemionus*—are recognized, a much greater “splitting” of the Tertiary genera would be necessitated as a corollary. Stirton (1948, oral communication) has pointed out that such a classification is in keeping with the presently accepted categorical distinction between subgenera and genera of equids.

E. occidentalis Leidy, as the name is applied in this monograph (see discussion, p. 246), probably represents a consistently smaller animal with a more simple enamel pattern and a more caballine protocone than in *E. simplicidens*, and will be regarded as a distinct species extant in the Blancan of North America.

EARLIER PLEISTOCENE

DESCRIPTION OF IRVINGTON LOCALITY AND FAUNA

Geology.—The Irvington fauna has been obtained from three different sites south-east of the town of Irvington. Each site has been given a Museum of Paleontology locality number:

V3602. Irvington, site 1. Excavation of Garcia Sand and Gravel Co.; forms most prominent man-made scar on W flank of line of hills in this area; 1.3 mi. on bearing S 50° E from intersection of State Highway 17 with paved road to Mission San Jose; intersection taken as center of town of Irvington; progressive grid coordinates for V3602, 909,100–1,638,800, Pleasanton quadrangle (1943 ed.). Fig. 37.

V3604. Irvington, site 2. Excavation known by variety of names: Silva Gravel Pits, Hirsch Gravel Pits, Irvington Sand and Gravel Co.; now known as Bell Sand and Gravel Co.; approximate center of site 0.8 mi. on a bearing S 64° E from center of Irvington; prog. grid coord. 908,600–1,639,600, Pleasanton quadrangle (1943 ed.); most of fossil vertebrates of Irvington fauna obtained from this excavation. Fig. 37.

V3605. Irvington, site 3. Excavation was exploited for short time only; between V3602 and V3604, 1 mi. on a bearing S 55° E from center of Irvington; prog. grid coord. 908,800–1,639,200, Pleasanton quadrangle (1943 ed.). Fig. 37.

Discussion.—The fossil-bearing beds have been exposed by quarrying operations in a dissected physiographic bench formed at the foot of Mission Peak and other hills of the Mount Hamilton range. This feature will be referred to as the Irvington–Mission San Jose bench. It is terminated rather abruptly to the north by the alluvium-filled Mission Creek valley and is formed into a prominent fault scarp on its west flank by the Hayward rift. Figure 37 shows the Irvington locality sites.

The deposits at the fossil locations consist of stream-deposited sandy clays, sands, and gravels. Some beds are indurated to the degree that they should perhaps be termed mudstones or sandstones, but all are relatively soft and friable. A sample columnar section was taken from northeast to southwest across the Bell Sand and Gravel Company quarry, locality V3604, to illustrate the various textures and intraformational structures. It must be emphasized that the beds are extremely lenticular, and no one bed or lentil has been found to extend through the exposed

area of bedrock. For convenience, the series of beds can be divided into two units, although demarcation between these units is not definite:

1. Uppermost unit of finer clastics—mudstones and fine- to medium-grained sandstones, poorly indurated, cross-bedded, "punky" beds. Mean thickness about 70 feet. No fossil vertebrates have been recovered from this unit.

2. Lowermost unit of mixed coarse and fine clastics—cobble gravels and conglomerates to mudstones, all lenticular, cross-laminated, channeled, and poorly sorted. Exposed section approaches 200 feet in mean thickness. Fossil vertebrates are found scattered throughout this unit.

Pockets of brownish-red gravels have been exposed at times by the excavators. These gravels are channeled into both of the series of beds described above. These youngest gravels might have been derived from the red-colored terrestrial late Tertiary deposits (usually called Orinda formation) exposed in the Mount Hamilton range to the east.

The fossil-bearing beds, together with the overlying unit of finer clastics, dip to the northeast at an angle of approximately 20°. Small normal faults have been observed in these beds. The faults trend northwest-southeast and are downthrown on their west side. No fault with a vertical displacement of over 10 feet was seen.

COLUMNAR SECTION NORTHEAST TO SOUTHWEST ACROSS BELL SAND AND
GRAVEL COMPANY, U.C. LOC. V3604

<i>Lithology</i>	<i>Thickness (ft.)</i>
Soil mantle and top of exposed section	
Medium- to fine-grained sandstones and mudstones; buff tan with some brownish-red mottling; soft, massive, with some cross-bedding	50-90
Sandy cobble gravel, poorly sorted; bone fragments	30-65
Soft, massive, gray cross-bedded sandstone; with <i>Mammuthus</i> , <i>Equus</i> , <i>Camelops</i>	15-30
Pebbly and gritty sands, cross-bedded with conspicuous channeling. One complete stream channel fill exposed; with <i>Mammuthus</i> , <i>Tetrameryx</i> , <i>Camelops</i> , <i>Equus</i>	20±
Soft, gray sandstone	10±
Loose, medium-grained, gray-green sand; with rodents	1±
Soft, gray sandstone with carbonized and limonitized wood fragments	7±
Loose, coarse, gray-green sand; with <i>Camelops</i> , <i>Equus</i> , <i>Tetrameryx</i> , rodents, turtle	2±
Tough, brownish-yellow to gray argillaceous sand with scattered pebbles and poorly sorted pebble lenses; grades downward into tougher barren sandstone. Contains all Irvington mammals except some rodents; limonitized and carbonized imprints of twigs and leaves; goose, fresh-water gastropods and pelecypods; turtle, anurans	20±
Pebble-cobble gravel with coarse sand lenses; with <i>Mammuthus</i> and <i>Camelops</i>	10
Greenish-gray mudstone	8
Gray friable sandstone	15
Cobble gravel	4- 6
Tough gray sand	7- 9
Sandy pebble-cobble gravel; with <i>Mammuthus</i>	8-12
Tough gray sand; with <i>Mammuthus</i>	9-13
Bottom of exposed section	
Total thickness	270±

An interesting and varied suite of rocks is represented by the cobbles and pebbles at Irvington. The following have been determined by megascopic analysis:

1. Concretionary, calcite-cemented nodules of Pliocene sandstone. Pebbles and cobbles of this type with bone fragments preserved in same manner as terrestrial Pliocene vertebrates from other localities in Bay region.

2. Pebble-cobble conglomerate. These rock fragments possibly derived from some late Tertiary conglomerate because rocks are friable as compared to Cretaceous sandstone pebbles; rock fragments within these cobbles predominantly quartzite in specimens examined.

3. Chert—varicolored, greenish, red, gray, brown, black; probably derived from Franciscan.

4. Chert—yellowish brown or buff, finely laminated, tends to be blocky and in subangular fragments; probably derived from siliceous shales of Monterey formation.

5. Limestone—gray, bearing unidentifiable fragments of marine shells; probably of Tertiary age.

6. Limestone—nodules highly weathered and completely stained yellow brown except for clear or white veins of calcite; limestones of this type in Monterey formation of Berkeley Hills and Coast Ranges east of San Jose, but possibility not precluded of derivation from older beds.

7. Quartzose sandstone—brownish green, very hard and resistant, cemented with silica, some of contained quartz grains fracture when rock is chipped, contains abundant dark minerals and (or) rock chips; such cobbles invariably well-rounded; their primary origin thought to be from a Cretaceous sandstone; Max Crittenden (oral communication, 1948) points out that brown biotite flakes in these rocks are suggestive of a Cretaceous source.

8. Quartzose sandstone—reddish brown, has hardness and induration of greenish-brown sandstones; red color seems to be due to abundance of red orthoclase grains; probably from Cretaceous.

9. Sandstone—gray, moderately indurated, medium-grained; probably from Tertiary.

10. Sandstone—brownish green, less quartzose but similar to Cretaceous pebbles except for presence of muscovite mica flakes; Franciscan. (Presence of muscovite tends to separate Franciscan sandstones from Cretaceous sandstones, according to Max Crittenden.)

11. Silica-carbonate rock—brownish, limonitized calcareous material veined with silica; similar rocks common in Franciscan.

12. Porphyry—light grayish green; glassy ground mass, small phenocrysts or grains of glassy material; Tertiary.

13. Altered basalt—reddish-brown fragments, extremely altered, friable, impregnated with iron stain; some evidence of former porphyritic texture in some fragments; masses of this type known from Franciscan.

14. Pink granite—pink or salmon orthoclase and clear quartz with noticeably few accessory minerals; no plagioclase detected in several hand specimens, but may be present; relatively small amount of original ferromagnesian minerals probably leached out of rock.

Bedrock of this exact type is not exposed in or near the San Francisco Bay region today; although the gray granitics of the San Francisco–Marin block or the Montara–Santa Cruz mountain granitics could possibly have pink-colored phases from which the Irvington fragments were derived. It might be concluded that the granite cobbles were derived directly from a parent granite mass, since contained minerals are fresh and unweathered in appearance; but the rounding and polishing of the fragments and the leaching of the ferromagnesian minerals contradicts such a conclusion. The possibility should not be excluded that these rocks could have been brought from the pre-Franciscan Santa Lucia granitic body of the Hollister area. This body of granites and quartz diorites is about 60 miles south-southeast of Irvington. For a description of a Santa Lucia granite see I. F. Wilson (1943). It seems most likely, however, that a preëxisting conglomerate contributed these rocks to the Irvington deposits. Although this rock conforms to the megascopic description of a granite, there is a distinct possibility that it represents only a local, coarser-grained phase of the pink porphyry described below.

15. Porphyry—pink to buff; phenocrysts of orthoclase and quartz; possibly textural differentiate of pink granite described above; age could be pre-Franciscan.

16. †Granodiorite or †quartz diorite—gray, coarse-grained granitic cobbles, some with deep external weathering or alteration zone; plagioclase, orthoclase, quartz, biotite, and hornblende identifiable in unaltered portion of such rocks; dark accessory minerals in relatively great abundance.

Quartz diorite has been described from the Santa Lucia granitics of the San Juan Bautista quadrangle by Allen (1946, p. 21); this is 50 miles south of Irvington. Such rock is also found at Montara Mountain. (See Lawson, 1914, p. 4.) The rounding and alteration of these pebbles, however, indicate that they may have been derived from preëxisting conglomerate.

17. Altered serpentine—abundant green mineral in one specimen identified as probably talc by Max Crittenden (oral communication, 1948); such rocks probably derived from Franciscan.

It is emphasized that the great degree of rounding and polishing of the resistant cobbles at Irvington has two possible interpretations: (1) these cobbles were derived from older conglomerates; (2) the cobbles, if not derived from older conglomerates, have been transported from a distant source. It seems evident from cursory examination of the rock types present that the greatest amount of material was derived in its present physical character from the Cretaceous and Franciscan. The Franciscan varicolored cherts and the Cretaceous sandstones, combined, make up the bulk of the Irvington gravels.

The Irvington gravels differ markedly in the assemblage of rock types from the Recent and †late Pleistocene gravels in the alluvial fans formed by streams draining from the Mount Hamilton range. All such fan materials in the Niles–Mission San Jose–Milpitas region have a much greater proportion of Franciscan schists, virtually no cherts, and no pink granite pebbles. It is concluded that the bulk of materials in the Irvington beds were not derived from an eastern source. Cursory examination of the alluvial materials along the east flank of the Santa Cruz range has shown that they differ from those of Irvington in much the same manner, namely, in their lack of varicolored cherts and pink granitic pebbles.

Study of the cross-bedding in the deposits at Irvington has shown that there is no regular pattern, but most of the cross beds, particularly those of largest scale, dip to the northwest, north, and northeast. Although the evidence from cross-bedding is not conclusive in sediments formed by a braided, distributary system of streams in which the direction of water flow can almost reverse the general trend, it is nevertheless believed that the prevailing dip of the cross beds suggests that the waters were flowing generally from south to north. The criterion of cross-bedding, together with the dissimilarity of Irvington materials to bedrock and gravels of the adjacent mountains, lead me to believe that at least a large part of the Irvington materials was obtained from areas to the south. It must be admitted that these gravels could have been derived from such formations as the Cretaceous Oakland conglomerate exposed at the mouth of Alum Rock Canyon east of San Jose. Professor Louderback (oral communication, 1949) has emphasized that alluvial deposits like the beds at Irvington may be entirely of local origin. If so, it would be concluded that most of the pre-Tertiary rocks at Irvington have been derived from previously exposed, near-by hills of the Oakland conglomerate. The beds at Irvington might therefore be of the same type of genesis as the lower part

of the San Antonio formation. Lawson (1914, p. 15) noted that the lower San Antonio formation was composed of fragments derived from the front of the Berkeley Hills and does not bear chert debris from the Monterey formation which is exposed farther back in the hills. The occurrence of granitic rocks in the Irvington gravels is particularly interesting because the pink granites were apparently not obtained from any of the known phanocrystallines of the San Francisco Bay area.

LeConte (1891, p. 326) thought that the drainage of the Great Valley had formerly emptied into the Pacific Ocean at Monterey Bay by way of the present San Francisco Bay and Santa Clara Valley and that the Golden Gate was a postglacial development. Lawson (1893, p. 152) concluded that just the opposite had happened as far as the Santa Clara Valley is concerned. He thought that the San Benito-Santa Clara-San Francisco Bay physiographic trough represented, in late Tertiary time, an integrated drainage, and that materials from the higher, southern region of this drainage were transported northward and deposited as a delta. Lawson's theory had been objected to because of the high elevation (approx. 350 ft.) in the floor of this trough at Madrone, California. The Madrone area is a watershed at present. From this region waters drain north through Coyote Creek to San Francisco Bay and south through Pajaro River to Monterey Bay. It must be proposed that an upwarping of the valley in the vicinity of Madrone has taken place since the time of through drainage from San Benito to San Francisco Bay, if Lawson's concept is followed. It seemed for a time that the presence of the same fresh-water fish fauna in waters of the Sacramento River, Coyote Creek, and Pajaro River was evidence favoring LeConte's idea, but Branner (1907, pp. 1-10) rejected LeConte's hypothesis. Branner stated (p. 10) :

The mingling of the fish faunas of streams flowing into the Bay of Monterey with those of streams entering the Bay of San Francisco is explained by the fact that Coyote Creek, descending into the Santa Clara Valley from the Mount Hamilton range at the crest of the watershed between the San Francisco Bay and the Bay of Monterey, formed an alluvial cone and swung from side to side, emptying part of the time into the Pajaro and part of the time into the Coyote. The passage of fishes between the various streams entering the Bay of San Francisco must have taken place at a time when the coast stood enough higher than it does at present to have emptied the Bay of San Francisco, and thus to have permitted fishes to descend from the Sacramento and ascend the Coyote and other streams without entering salt water.

Of interest in this respect is Lawson's recent report (1948, p. 200) that almost immediately under the Golden Gate Bridge there exists a sharp V-shaped gorge cut in rock. Lawson concludes that this gorge was stream-cut when the sea level was much lower than it now is. At such a time, all the area of the present San Francisco Bay would presumably have been above sea level.

Allen (1946) has determined from terrace deposits that a Pleistocene San Benito River extended westward from San Juan Bautista and emptied into the deep (now submarine) Monterey Bay canyon. Superficially, Allen's data would seem to be contrary to Lawson's theory; but according to the physiographic data as outlined by Allen, the Monterey Bay embouchure of the San Benito River was not developed until later Pleistocene time. The mild diastrophism which tilted the Irvington beds and must have elevated parts of the same formation to the

southwest and south could be responsible for an elevation of the Madrone area to its present watershed height. This could have terminated the through drainage from San Benito to San Francisco and caused a diversion of the San Benito and Pajaro rivers into Monterey Bay.

It appears, then, that deductions on the probable source area of the Irvington sediments must remain hypothetical. The possibility is strongly suggested, however, that some of the Irvington rocks were derived from the area of San Juan Bautista-Hollister-San Benito and that during the early Pleistocene there was an integrated drainage straight through from the San Benito Valley to San Francisco Bay, as Lawson proposed. Negative evidence for this hypothesis consists of the possible local derivation of much of the material from Cretaceous conglomerate now largely covered up by later sediments.

The following sequence of events, based on the physiographic, lithologic, and structural data, seems to apply to the Irvington locality:

1. Deposition of earlier Pleistocene clays, sands, and gravels, with their contained vertebrate fauna, by streams or anastomosing branches of one stream flowing from south.
2. Reduction in elevation of drainage basin of stream, accompanied by reduction in grade of stream, resulting in interval of deposition of finer clastics at Irvington.
3. Mild diastrophism, tilting of beds northeastward by 20°-25°.
4. Base-leveling of entire Irvington area probably by lateral planation of stream or streams which had previously deposited the beds. This developed bench surface now seen atop Irvington sediments. During this interval, later gravels which truncate earlier Pleistocene beds were probably deposited and then partly removed.
5. Movement of Hayward fault, resulting in downthrow of beds on west at least 300 feet. Straight alignment of steep west flank of bench leads to belief that a true fault scarp is represented.
6. Rejuvenation of Mission Creek, with downcutting and removal of earlier Pleistocene beds. These beds may have extended farther north than at present. Initiation of headward erosion by small streams into fault-scarp front of Irvington-Mission San Jose bench.
7. Base-leveling and then alluviation of San Francisco Bay plain and valley of Mission Creek adjacent to Irvington-Mission San Jose bench, with continued dissection of this bench by small streams initiated during stage 6.
8. Later movement along Hayward fault, possibly with both horizontal and vertical displacements, resulting in formation of fault-origin lakes, The Lagoon, and Tule Pond,^a north of Irvington, and normal faults in Irvington beds bordering Hayward fault escarpment.

THE SANTA CLARA FORMATION

Lawson (1893, p. 152) first noted the presence of continental deposits in the northern end of Santa Clara Valley. He thought that these beds were most probably delta deposits laid down in a south extension of the present San Francisco Bay by a stream or streams draining from the south. Lawson gave no formational name to these beds. Cooper (1894, p. 171) called these deposits the "Santa Clara Lake beds" and assigned to them a Pliocene age on the basis of the contained invertebrates. Branner, Newsome, and Arnold (1909) described these beds as gravels, sands, and clays laid down in fresh-water lakes during a late Pliocene-early Pleistocene interval. The Santa Clara formation (their terminology) was thought to be contemporaneous with at least a part of the Merced (marine) formation.

^a W. O. Clark (1924, p. 17) noted that these lakes had originated from faulting.

Professor Louderback has informed me (oral communication, 1949) that Branner and associates thought that the beds at Irvington were exposures of the Santa Clara formation. W. O. Clark (1924) briefly discussed these beds and mapped them under the divisions "older alluvium" and "younger alluvium." The Irvington localities were included in the outcrop of Clark's older alluvium.

Hannibal (1911) and Dorf (1930) described fossil plants from the "Santa Clara" beds. Dorf gave a description of the deposits in Calabazas Canyon, 1.5 miles N 10° W of Saratoga, California:

The observed section consists of alternating beds of massive, fine, buff-colored conglomerates; sandy to shaly, blue or buff-colored sandstones; and thin layers of bluish shale; the series strikes north 25° west and dips 50° northeast and is overlain unconformably by horizontal gravels of valley alluvium. The rocks, particularly the shales and shaly sandstones, are considerably shattered and slickensided by local movements.

The beds of the Calabazas Canyon section differ from the Irvington beds in their greater consolidation and greater deformation. The Calabazas Canyon deposits may have been laid down earlier than the Irvington beds, but an age assignment is futile until more detailed field work can be accomplished. It is of course possible that the Santa Clara, as exemplified at Calabazas Canyon, and the beds at Irvington were laid down in one basin of deposition and that the Irvington materials simply represent a later continuation of this deposition. Dorf (1930) assigned an Upper Pliocene age to the Santa Clara flora. If this age is corroborated by all the evidence, the diastrophism affecting the Calabazas Canyon beds must have antedated the deposition of the beds at Irvington and would then be about contemporaneous with the post-Blancan disturbance of the Coast Ranges at Pittsburg, California.

The lower part of the San Antonio formation of Lawson (1914) may be of the same age as the beds at Irvington. A correlation is suggested by the similarity of general stratigraphic and physiographic position of the two formations. Louderback (oral communication, 1949) has pointed out that the vertebrates listed by Lawson from the San Antonio actually were collected north of the San Francisco quadrangle (probably in the vicinity of Rodeo, California) and should not be used to date the San Antonio formation.

The term "Santa Clara" has become a catchall which is applied to all alluvial deposits at the north end of the Santa Clara Valley. Deposits of several different types, different methods of genesis, and different age are now included under this name. It seems impossible to resolve the problem of nomenclature unless a precise type locality and type columnar section for the formation is selected. Because of the uncertainties of nomenclature at present, I employ no formational name for the deposits at Irvington.

SYSTEMATIC DESCRIPTION OF THE FAUNA

Class PISCES

Abundance of spines, vertebral centra, and isolated skull elements; at least two types of fish represented; obtained from loose sands along with remains of rodents.

Class AMPHIBIA

Order ANURA, Frogs and toads

Coracoid and probable shaft of a femur tentatively identified as anuran; coracoid, U.C.M.P. no. 38812, most similar to corresponding element in *Rana*; femoral shaft, U.C.M.P. no. 38813, femur of *Bufo*.

Class REPTILIA

Order CHELONIA

Fragments of turtle shell present but not common; material recovered now includes complete shell of an emyd, U.C.M.P. no. 39062.

Class AVES

Branta canadensis, Canada goose

Complete left humerus, U.C.M.P. no. 38336; slightly more robust at distal end than in Canada goose, otherwise virtually inseparable in all details from humerus of Recent bird in U.C.M.V.Z collection.

Discussion.—Miller and DeMay (1942, p. 82) have noted that this species is one of the most widely distributed of America's fossil birds, and in California it is already known from five or six different Pleistocene localities. In the light of Miller and DeMay's discussion of the variability of osteological characters in Pleistocene geese, it is concluded that the characters and size of the Irvington bone fall well within the range of variability of *Branta canadensis*.

Class MAMMALIA

Order EDENTATA

Megalonyx Harlan, ground sloth

(Fig. 2, *a*, *b*)

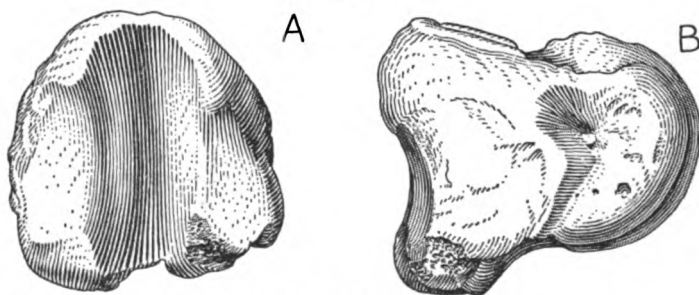


Fig. 2. *Megalonyx*, U.C.M.P. no. 38337, loc. V3604: *a*, proximal view of co-ossified proximal and median phalanx, digit III of pes; *b*, external view. $\times \frac{2}{3}$.

Co-ossified proximal and median phalanges of digit III in hind foot, U.C.M.P. no. 38337. Bone one-third shorter and relatively stockier than in *M. jeffersonii* (Desmarest) figured and described by Leidy (1855*b*, p. 44, Pl. XIII, figs. 17–18).

Discussion.—It may be assumed that the Irvington *Megalonyx* was a smaller, shorter-limbed animal than *M. jeffersonii*, although this must be a tentative conclusion because of incomplete data.

Megalonychidae

Incomplete thoracic vertebra, U.C.M.P. no. 38337A, megalonychid in character and referable to either *Megalonyx* or *Nothrotherium*; looks much like Stock's (1925a, pl. 5, fig. 5, and pl. 18, figs. 5–6) figures of posterior thoracic vertebra of *Nothrotherium shastense* Sinclair and of *Megalonyx jeffersonii californicus* Stock; relatively small size of Irvington specimen possibly favors its reference to *Nothrotherium*.

Fragment of vertebral centrum, U.C.M.P. no. 38337B, possibly referable to *Megalonyx*; larger than specimen no. 38337A.

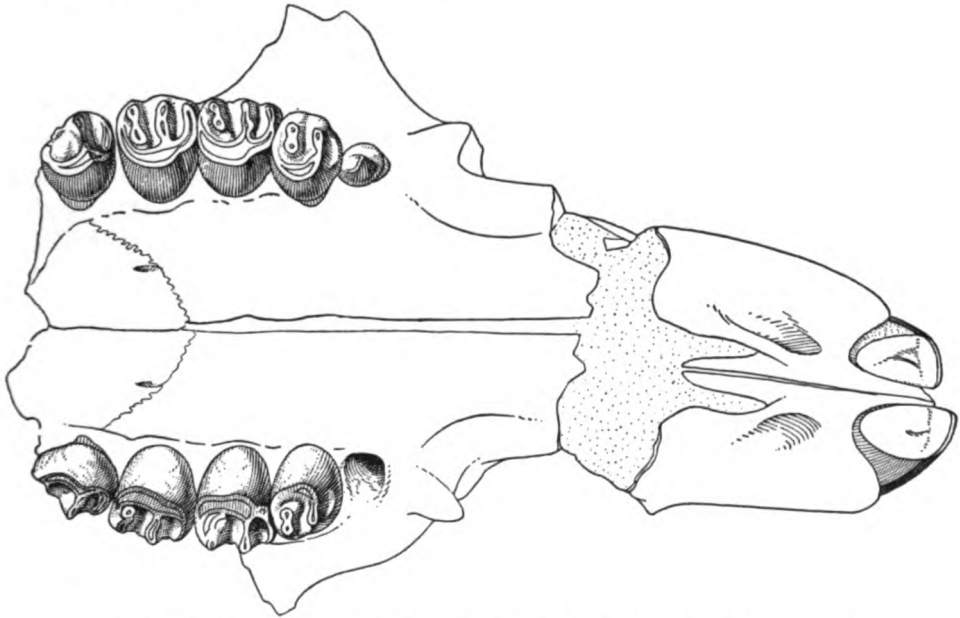


Fig. 3. *Citellus bensoni*, oclusal view of palate, U.C.M.P. no. 39187, loc. V3604. $\times 4$.

Order RODENTIA

Citellus (Otospermophilus) bensoni Gidley, ground squirrel

(Fig. 3)

Palate of young adult with complete dentition except for left P^3 , U.C.M.P. no. 39187. M^3 with small talon and resultant area of oclusal surface about equal to or smaller than area of M^2 ; mesostyles of all cheek teeth absent or megascopically not detectable; metaconule clearly separated from protocone until old age, close to metacone in young adult stage, evidently conical in unworn condition.

Discussion.—The Irvington specimen may be slightly larger than the types of *C. bensoni*; but other than this possible size difference, there is morphological identity of the materials. *C. bensoni* is from the Blancan of Arizona. Evidently,

there is noteworthy temporal as well as geographic separation between the specimens from Irvington and Arizona. It is quite possible that these two citellid populations would be classified as discrete species (or at least subspecies) if the complete data available to the student of Recent mammals could be applied. However, the only objective data are those based on morphology; it would be impractical and misleading to base classification on theoretical possibilities.

An examination of about 200 *Citellus* skulls in the University of California Museum of Vertebrate Zoology has shown that the subspecies *C. beecheyi beecheyi* (Richardson), *C. beecheyi fisheri* Merriam, and *C. variegatus grammurus* (Say) include animals which are quite close to *C. bensoni* from Irvington in general appearance of the teeth. There is never, to my knowledge, identity with the diagnostic characters of *C. bensoni*. Individuals with a somewhat reduced M^3 bear a relatively prominent mesostyle on at least one of the cheek teeth. In many individuals, P^4 to M^2 inclusively possess mesostyles. Most individuals of these Recent subspecies differ markedly from *C. bensoni* by their relatively large M^3 .

Thomomys Maximilian, pocket gopher

Four fragmentary lower jaws, U.C.M.P. no. 38811, containing incomplete cheek-tooth series; P_4 bears relatively wide lateral median inflections, this configuration cited as one of characters of *Thomomys* in contrast to *Geomys* Rafinesque; Irvington specimens of same size as Recent *Thomomys bottae bottae* (Eydoux and Gervais) including *T. bottae* from Rancho La Brea.

Perognathus Maximilian, pocket mouse

(Fig. 4)



Fig. 4. *Perognathus*, occlusal view of right P_4 , U.C.M.P. no. 38809, loc. V3604. $\times 20$.

Anterior portion of right jaw containing P_4 , U.C.M.P. no. 38809; P_4 differs from compared specimens of Recent *Perognathus californicus californicus* Merriam, and also differs in smaller size from Rancho La Brea series and in possessing posteromedian cusp; more material from Irvington desirable for species assignment.

Microtus Schrank, meadow vole

Two right lower molars, U.C.M.P. no. 38808, do not differ in size or character from corresponding teeth in jaws of Recent *Microtus californicus californicus* (Peale).

Peromyscus (*Haplomylomys*) *irvingtonensis* Savage n. sp.

(Fig. 5)

Holotype.—Incomplete right lower jaw with M_1 and M_2 , U.C.M.P. no. 38781.

Type locality.—V3604, Irvington, site 2. Large aggregates quarry of Bell Sand and Gravel Co.; 0.8 mi. SE of Irvington, California; progressive grid coordinates 908,600–1,639,600, Pleasanton quadrangle (1943 ed.). Loc. HV2U of Hayward Boy Paleontologists.

Diagnosis.—Length of cheek-tooth row (5.2 mm.) intermediate between *P. californicus californicus* (Gambel) and *P. nesodytes* Wilson; teeth relatively massive when compared with all

species of subgenus *Haplomylomys* except *P. antiquus* Kellogg, *P. pliocenicus* Wilson, and *P. nesodytes*; M_3 relatively large (anteroposterior diameter 1.4 mm.) as compared to other species except *P. antiquus* and possibly *P. pliocenicus*; M_3 slightly more reduced relative to other cheek teeth than in type of *P. antiquus*.

Description and comparisons.—Young adult; enamel capping of cusps worn away enough to expose only relatively small area of dentine.

Irvington jaw compared with approximately 70 jaws of Recent *P. californicus*

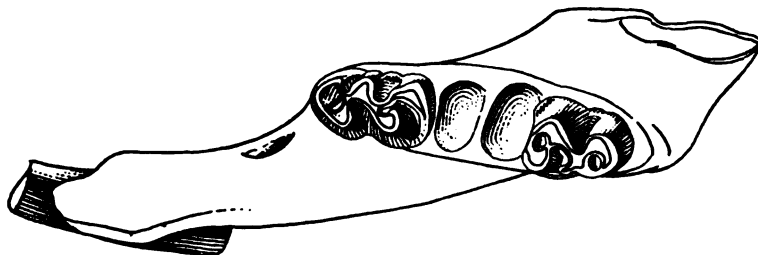


Fig. 5. *Peromyscus irvingtonensis* Savage, n. sp., holotype, occlusal view of right lower jaw with M_1 and M_3 , U.C.M.P. no. 38781, loc. V3604. $\times 8$.

californicus from Monterey and San Luis Obispo counties, California. *P. californicus californicus* largest of present-day subspecies north of Mexico; apparently same size, but teeth of fossil more massive and M_3 much less reduced than in Recent animals.

Irvington specimen in same size group as *P. antiquus* Kellogg (1910a), but is much smaller than *P. pliocenicus* and slightly smaller than *P. nesodytes*; *P. irving-*

COMPARATIVE MEASUREMENTS IN SAME STAGE OF WEAR

	<i>P. irvingtonensis</i>	<i>P. californicus</i>
Length of tooth row (M_1 – M_3)	5.2	4.5
Anteroposterior diameter, M_1	2.0	1.8
Greatest transverse diameter, M_1	1.3	1.1
Anteroposterior diameter, M_3	1.4	0.9
Greatest transverse diameter, M_3	1.2	0.8

tonensis larger than such proposed species as *P. kansasensis* Hibbard, *P. longidens* Hall, *P. dentalis* Hall, *P. brachygnathus* Gidley, *P. arizonae* (Gidley), *P. loxodon* (Cope), *P. eremicus* (Baird), and others.

Differs from *P. antiquus* in relatively wider teeth and greater reduction in size of M_3 relative to other cheek teeth.

P. nesodytes (Wilson, 1936b) characterized by partially bipartite anteromedian cusp in M_3 as compared to parallel-sided valley in some specimens of *P. californicus*, also larger than *P. californicus*; internal lake in anterointernal median cusp also present in some individuals of *P. californicus* when anterior and posterior walls of inflection unite internally with wear (Wilson, 1936b).

Discussion.—When *P. californicus* jaws were being compared with the Irvington specimen, a check was also made on the presence or absence of an anterointernal inflection on M_1 in the Recent assemblage. A tabulation was also made on the character of this groove in *Peromyscus* (*Peromyscus*) *eremicus fraterculus* (Miller) from Los Angeles, Orange, and Riverside counties, California. This tabulation indicates that there is more variation in *P. californicus* than in *P. fraterculus*. The variation in *P. californicus* is due partly to change with wear, as Wilson pointed out, but not entirely. The variation in *P. fraterculus* seems to be more directly attributable to change with wear. It was observed on both subspecies that

VARIATION IN THE ANTERIOINTERNAL GROOVE

	<i>P. c.</i> <i>californicus</i> (per cent)	<i>P. e.</i> <i>fraterculus</i> (per cent)
Fully developed anterointernal inflection.....	48	61
With disconnected internal lake and shallow groove.....	28	0
With shallow groove only.....	17	36
With internal lake only.....	3	0
With no indication of inflection.....	3	3

all degrees of depth of this inflection are present; consequently, the percentages listed in the table are undoubtedly somewhat biased.

The demonstrable variation in *P. californicus* makes it seem most likely that individuals of both *P. nesodytes* and *P. irvingtonensis* may be either with or without this inflection. The inflections in these two fossils could be "primitively" V-shaped (when present) in contrast to *P. californicus*. It follows, then, that the main distinctions are size and reduction of the third molar. Wilson noted that the cheek teeth of *P. nesodytes* are comparable in relative size to those of living members of the genus. The Irvington specimen, therefore, differs from both *P. nesodytes* and *P. californicus* by its unreduced M_3 .

It might be concluded that lack of reduction of the third lower molar is an unadvanced character of chronological significance were it not for the fact that a *Peromyscus* jaw from the Smiths Valley fauna, Middle Pliocene (near *P. antiquus* according to Wilson, 1936a), shows an M_3 as reduced as in the Recent species.

Order CARNIVORA

Canis cf. *dirus* (Leidy), dire wolf

(Fig. 6)

Miscellaneous broken parts of skeleton apparently from one individual, U.C.M.P. no. 38784; fragment of left lower jaw, no. 38749; distal half of tibia, no. 38525; right metacarpal, no. 38785; lumbar vertebra, no. 38786.

Jaw fragment contains complete M_2 , broken M_1 , small fragment of posterior root of P_4 and alveolus for M_3 ; border of ascending ramus immediately posterior and external to alveolus for M_3 shows exostosis; diseased condition evidently de-

veloped in and around bony socket for tooth; teeth well worn and of old animal; same size and character as *Canis dirus* (Leidy) from Rancho La Brea.

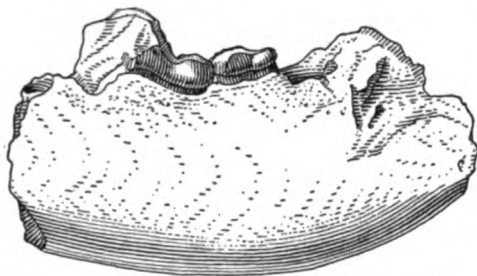


Fig. 6. *Canis* cf. *dirus*, labial view of left lower jaw fragment with M_1 and M_2 , U.C.M.P. no. 38749, loc. V3604. $\times \frac{2}{3}$.

Distal half of tibia with fused mid-section of fibular shaft; fused condition not seen on comparable tibias from Rancho La Brea in University of California collection but quite likely appears on some bones, of no taxonomic significance. Same size as Rancho La Brea bones but narrower transversely through distal articular surface; difference may be due to growth or to sexual or individual variation.

Metacarpal II indistinguishable from corresponding element in Rancho La Brea dire wolves.

Femoral shaft of no. 38784 is suggestive of being shorter and stockier than at least some of Rancho La Brea individuals.

Canidae, fox

(Fig. 7)

Broken fragment of right lower jaw bearing roots of P_3 and P_4 , and alveoli for P_2 and P_1 . U.C.M.P. no. 38783; small tibia, no. 39066, probably is same genus as jaw fragment.

Canis irvingtonensis Savage n. sp.

(Figs. 8, a, b, 9, a, b, 10)

Holotype.—Incomplete right lower jaw containing P_3 – M_2 inclusive, U.C.M.P. no. 38805.

Paratypes.—Left radius, U.C.M.P. no. 38804 and incomplete left lower jaw containing P_3 – M_2 inclusive, no. 38748.

Type locality.—V3604, Irvington, site 2. Large aggregates quarry of Bell Sand and Gravel Co.; 0.8 mi. SE of Irvington, California; progressive grid coordinates 908,600–1,639,600, Pleasanton quadrangle (1943 ed.). Loc. HV2T of Hayward Boy Paleontologists.

Diagnosis.—Small, relatively stocky coyote; jaw equal in length to that in *Canis latrans estor* Merriam but with deeper horizontal ramus; lower premolars no longer but relatively wider and more massive than in all other described species and subspecies of coyotes; premolars more closely spaced than *C. latrans lestes* Merriam, *C. l. ochropus* Eschscholtz and other subspecies, usually more closely spaced than in *C. l. estor*; smaller and relatively stockier animal than *C. lepophagus* Johnston.

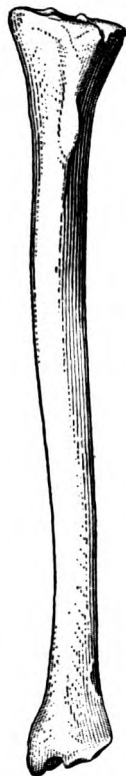
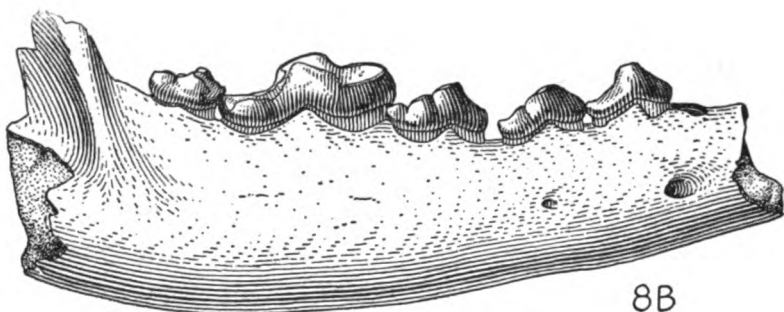


Fig. 7. Canidae, fox, anterior view of tibia, U.C.M.P. no. 39066, loc. V3604. $\times 1$.



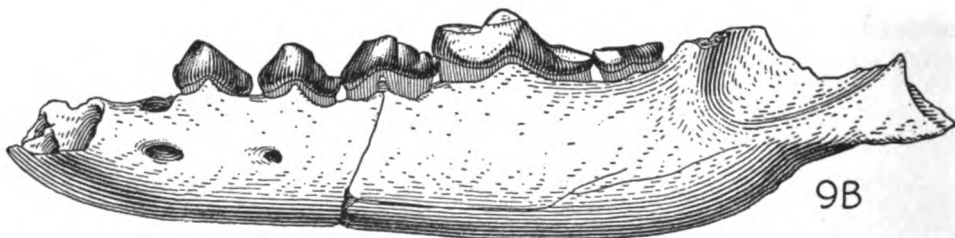
8A



8B



9A



9B

Fig. 8. *Canis irvingtonensis* Savage, n. sp., holotype, U.C.M.P. no. 38805, loc. V3604: a, occlusal view of right lower jaw with P_2 to M_2 inclusive; b, labial view. $\times 1$.

Fig. 9. *Canis irvingtonensis* Savage, n. sp., paratype, U.C.M.P. no. 38748, loc. V3604: a, occlusal view of left lower jaw with P_2 to M_2 inclusive; b, labial view. $\times 1$.

Comparisons.—The jaws from Irvington have been compared to a series of 30 specimens of *C. latrans ochropus* Recent specimens from San Mateo and Santa Clara counties, to a series of 9 jaws of *C. latrans lestes* (Recent) from Tuolumne County, to 40 jaws of *C. l. estor* (Recent) from California and Nevada, and to approximately 30 jaws of *C. l. ochropus* (Pleistocene) from Rancho La Brea. The Irvington jaw was found to differ from all the specimens listed above by its rela-

tively broad and closely appressed premolars and its shorter cheek-tooth series. One jaw from the La Brea series, U.C.M.P. no. 29134, does match the paratype Irvington jaw in these details, but M_1 on the La Brea jaw is noticeably larger and the ventral border of the La Brea jaw is more sharply curved posteriorly. The range of variation of these lower-jaw characters in the La Brea species possibly overlaps the range of characters in the Irvington animal, but this is not demonstrated in the materials available for study. In its proportions, the paratype Irvington jaw is closest to a modal *C. l. estor*, but the holotype of *C. irvingtonensis* is much more robust than any compared specimen. The length of the cheek-tooth series in *C. l. estor* ranges from less to more than that of *C. irvingtonensis* and in

MEASUREMENTS OF CANIS IRVINGTONENSIS SAVAGE

	Holotype no. 38805	Paratype no. 38748
Distance, P_3 - M_3 inclusive.....	70.6	66.2
Anteroposterior diameter, P_3	11.6	10.4
Greatest transverse diameter, P_3	5.1	4.9
Anteroposterior diameter, P_4	12.1	11.5
Greatest transverse diameter, P_4	5.1	5.1
Anteroposterior diameter, P_4	13.8	13.1
Greatest transverse diameter, P_4	6.6	6.4
Anteroposterior diameter, M_1	23.9	21.5
Greatest transverse diameter, M_1	10.2	8.7
Anteroposterior diameter, M_3	10.0	9.6
Greatest transverse diameter, M_3	7.6	7.0

some specimens the Recent subspecies shows as much crowding of premolars; but in none of the *C. l. estor* specimens do the premolars have the relatively great transverse diameter that is evinced on the Irvington coyote.* The depth of the horizontal ramus (vertical diameter) is much greater in *C. irvingtonensis* than in the *C. l. estor* jaws.

A coyote-like canid from the Fossil Lake fauna of Oregon, U.C.M.P. no. 2972, is even shorter-jawed and smaller than the Irvington coyote. Johnston (1938b, p. 389) noted that *C. lepophagus* Johnston from the Cita Canyon fauna (Blancan) had mandibles which "are deeper and stronger, and the premolars tend to have a greater anteroposterior diameter with a corresponding reduction in the spaces between them than is true of modern coyotes." Although *C. irvingtonensis* resembles *C. lepophagus*, the appression is not brought about by a relatively greater length of premolars. The premolars of *C. irvingtonensis* are no longer than in the other species.

The radius of *Tomarctus robustus* Green (1948) from the Ricardo fauna is the

* It is noted that in some specimens of *Canis latrans estor* the spacing of premolars was as great and the jaw was as long as in *C. l. lestes* and *C. l. ochropus*; but most of *C. l. estor* jaws were smaller than the other two Recent subspecies. One could hypothesize from this situation that the frequency for the gene (following Dobzhansky, 1941) promoting short jaw length and more closely spaced premolars was great in subspecies *C. l. estor* but that there is no absolute barrier to intermixture of genes from other subspecies. Thus, infrequently, a character in *C. l. lestes* or *C. l. ochropus* can appear within a *C. l. estor* population.

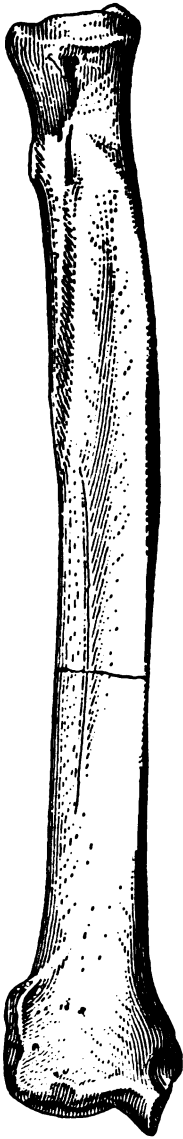


Fig. 10. *Canis irvingtonensis* Savage, n. sp., paratype, posterior view of left radius, U.C.M.P. no. 38804, loc. V3604. $\times 1$.

same length as in *C. irvingtonensis* but is less flattened anteroposteriorly. Also, the proximal and distal expansions of the Pliocene bone are relatively larger in respect to the shaft than they are in *C. irvingtonensis*.

The Irvington radius is 10 to 20 mm. shorter than six radii of *Osteoborus cynoides* (Martin) from the Hemphill fauna. *C. irvingtonensis* is more flattened anteroposteriorly, noticeably less stocky, and much less marked by prominences and rugosities. If the characters of massiveness and rugosity are indicative of a hyaenoid habitus, *C. irvingtonensis* certainly shows little or no tendency toward such an adaptation. In all characters, this limb bone is coyote-like, i.e., canine rather than borophagine.

From the evidence of the jaw and the radius it may be visualized that this shorter-jawed, shorter-limbed, stockier animal from Irvington was a coyote with a habitus tending to be somewhat different from known coyotes and perhaps resembling in some respects the foxes. It seems possible that *C. irvingtonensis* was adapted to living in a brush country and did not run for long distances as compared to the longer-limbed plains and plains-border coyotes. It seems unlikely that *C. irvingtonensis* is an annectant between the Blancan *C. lepophagus* and the later Pleistocene and Recent species. *C. lepophagus* is actually closer to the living *C. latrans* Say.

Machairodontinae, saber-toothed cat

(Fig. 11)

Two crania, U.C.M.P. nos. 38338 and 39228, with machairodont characters: broadly rounded occiput, relatively short distance between glenoidal fossae, broad and massive mastoid processes extending forward, close to postglenoid process, relatively flattened tympanic bullae, and extremely high and rugose sagittal and lambdoidal crests; smaller than most crania of *Smilodon californicus* Bovard; no. 39228 with P^4 and alveoli for C, P^3 and M^1 preserved; P^4 without protocone and without root underlying protoconal area, relatively long and narrow; C more compressed laterally and smaller than in *S. californicus*; P^3 relatively and actually smaller than in *S. californicus*, almost single-rooted; M^1 vestigial.

Discussion.—The Irvington cat is more specialized than *Smilodon californicus* in the reduction of P^3 and complete loss of protocone on P^4 . At the present time there appears to be good reason to refer this cat to *Dinobastis serus* Cope, thus substantiating a genus which has for a long time been considered a synonym of *Smilodon* Lund. There is also a distinct possibility that *Dinobastis* and the Irving-

ton material may be congeneric with *Ischyrosmilus* Merriam. After the necessary comparative materials are obtained, a complete treatment of the Irvington machairodont will be published in an addition to the description of the Irvington fauna. In the meantime, I refer this cat only to the subfamily.

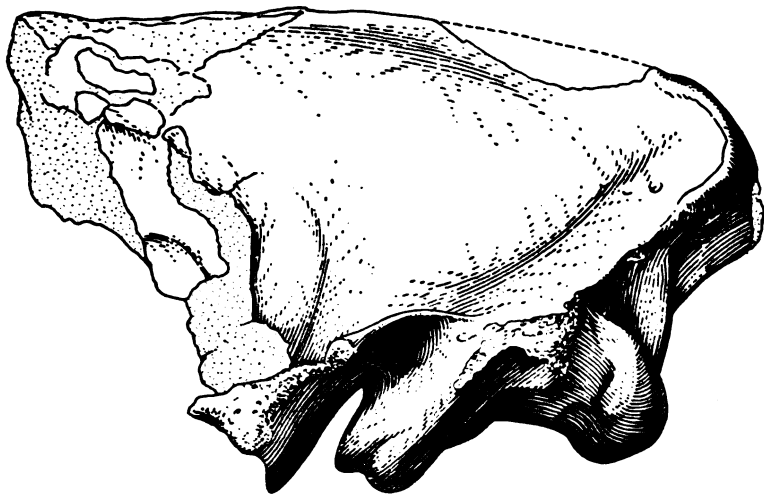


Fig. 11. Machairodontinae, view of left side of cranium, U.C.M.P. no. 38338, loc. V3604. $\times \frac{1}{2}$.

Order PROBOSCIDEA

Mammuthus columbi (Falconer), mammoth

(Fig. 12, a, b)

A palate containing left and right M^1 , U.C.M.P. no. 39180; M^2 lacking one-half of anterior ridge plate, U.C.M.P. no. 38803; parts of other teeth and miscellaneous appendicular elements.

M^1 —10 or 11 ridge plates worn, 8 or 9 unworn; maximum transverse diameter 79.5 mm.; enamel with approximate mean thickness of 3 mm.; 6–7 ridge plates in 100 mm. along occlusal surface, 7–7½ ridge plates in 100 mm. perpendicular to general plane of ridge plates; ridge plates as widely spaced at root of tooth as at crown.

M^2 —complete except for one-half of anterior ridge plate; 9 ridge plates exposed to occlusal surface; probably 11 total ridge plates; maximum transverse diameter measured on enamel 78 mm.; exterior layer of cement opposite midpoint of antero-posterior length of tooth, 0.5–2 mm. thick; mean thickness of enamel plates about 2 mm.; 5½–6 ridge plates in 100 mm.*

Discussion.—It was mentioned in the geological discussion of the Irvington localities that mammoth remains, all seemingly of one species, are found from

* On this tooth the occlusal surface is almost perpendicular to the general plane of the ridge plates.

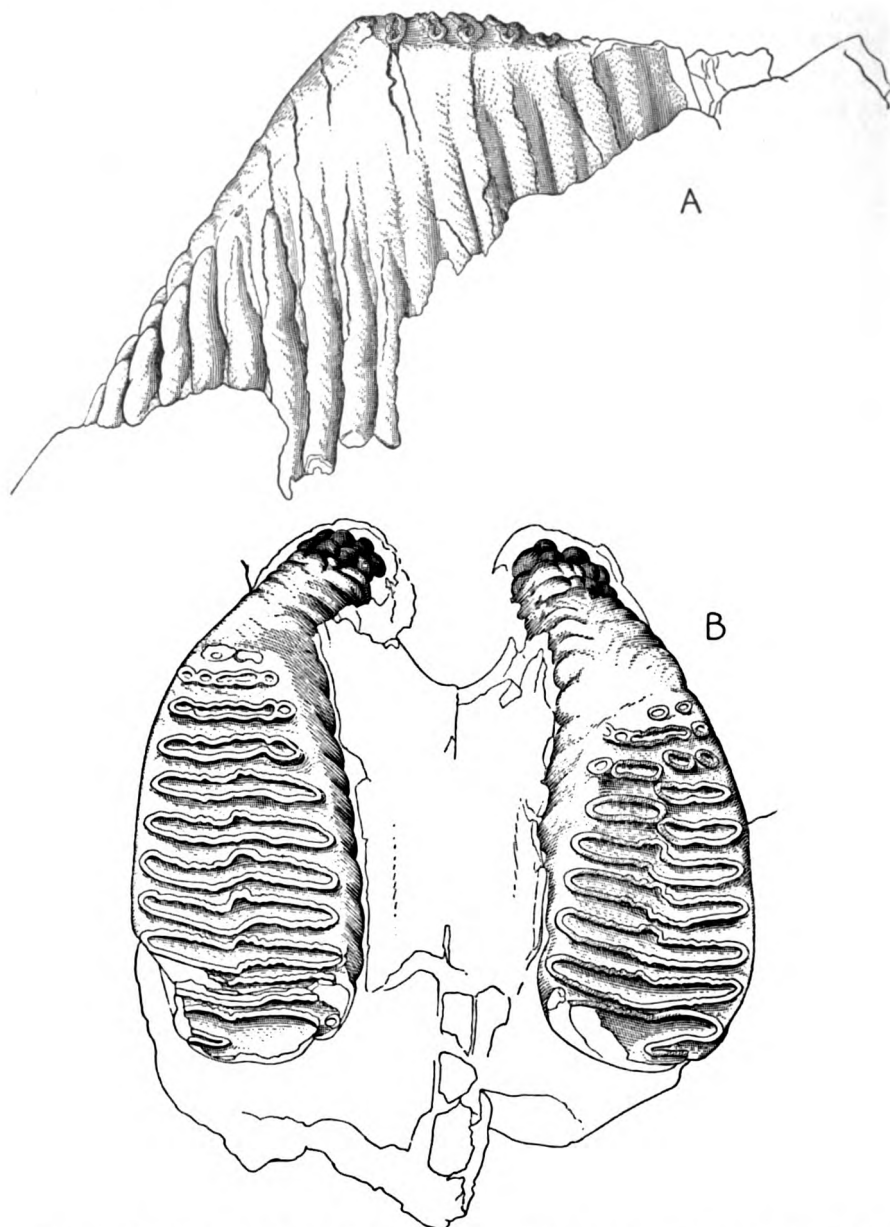


Fig. 12. *Mammuthus columbi*, U.C.M.P. no. 39180, loc. V3604: a, labial view of left M_1 ; b, occlusal view of palate with right and left M_1 . $\times \frac{1}{8}$.

bottom to top of the fossil-bearing beds. These mammoths offer some of the best evidence for assignment of a Pleistocene age to Irvington, since the Elephantidae are still unknown in the Blancan and pre-Blancan of the Western Hemisphere.

Osborn (1942) has compiled a prodigious amount of information pertaining to all proposed species of the Elephantidae. Reference to his work is essential. The

alacrity with which some paleontologists identify species of mammoth would make it seem that a species assignment for the Irvington animal should entail no uncertainty; yet this is not so. Identification from published diagnoses proves to be a highly subjective process. Osborn stated (p. 929) that in the mammoth, "the number, compression and elevation of the ridge-plates increase in all generic phyla, as the primitive browsing habit develops into a grazing habit." We could expect to find as a practical corollary, then, that the relative primitiveness of a species is inversely proportional to the number, compression, and elevation of the ridge plates in the cheek teeth. Generally, with the exception of the loxodonts, this corollary seems to be tenable. *Mammuthus planifrons* (Falconer and Cautley) from the Pinjor (= Villafranchian = Blancan) is regarded as the earliest and most primitive elephantid. It is characterized by a relatively small number of widely spaced ridge plates and by lower-crowned teeth as compared to later forms. *M. meridionalis* (Nesti) from the Val d'Arno and other Villafranchian units has essentially the same characters as *M. planifrons*. *M. primigenius* (Blumenbach), which is at the culmination of the mammuthine line, has many tightly appressed and highly elevated plates. These extremes are distinct; but structurally intermediate forms, such as the Irvington animal, are much more difficult to identify. Osborn (pp. 997-998) finally concluded that a progressive *M. (Archidiskodon) meridionalis* type of Eurasia migrated to North America and gave rise to *M. (Archidiskodon) imperator* (Leidy). Osborn derived *M. (Parelephas) columbi* (Falconer) of North America from a separate line of species beginning with *M. (Parelephas) trogontherioides* (Zuffardi) of the Villafranchian.

Osborn distinguished *M. columbi* from *M. imperator* by the narrower grinding teeth, thinner enamel ridge plates, thin cement outer coating, and ridge plates widely separated or arcuate at base and more convergent at summit of *M. columbi*. The ridge-plate formula for M^3 of the two species is nondistinctive. These dental distinctions are made to seem much more substantial when supported by size difference in the teeth and in the skeleton.

Osborn (p. 996) attempted a stratigraphic distinction between *M. columbi* and *M. imperator*, asserting that *M. imperator* is limited to Nebraskan and Aftonian (following Hay, 1923a, p. 15); and that *M. columbi* is a later Pleistocene species. I know of no tenable stratigraphic data to support such a distinction. The type of *M. imperator* was from somewhere in Thomas County, Nebraska, as nearly as can be determined (see Hay, 1924d, p. 100), and was evidently from a nonglacial deposit. The type of *M. columbi* was from Georgia; hence a stratigraphic comparison of the two occurrences and a correlation with the glacial sequence are matters of uncertainty. Perhaps *M. imperator* is an earlier structural stage in Osborn's plan of elephantid cheek-tooth evolution; but the materials from Irvington show that a "*columbi*" structural stage did exist in the pre-Bison, earlier Pleistocene of the Pacific Coast.

The isolated teeth from Irvington are about the same size and the individual enamel plates are as thin as in *Mammuthus jeffersonii* (Osborn); but their ridge plates are consistently more widely spaced than in *M. jeffersonii*. For the same reason, the Irvington animal is distinct from *M. progressus* Osborn and *M. primigenius* (Blumenbach).

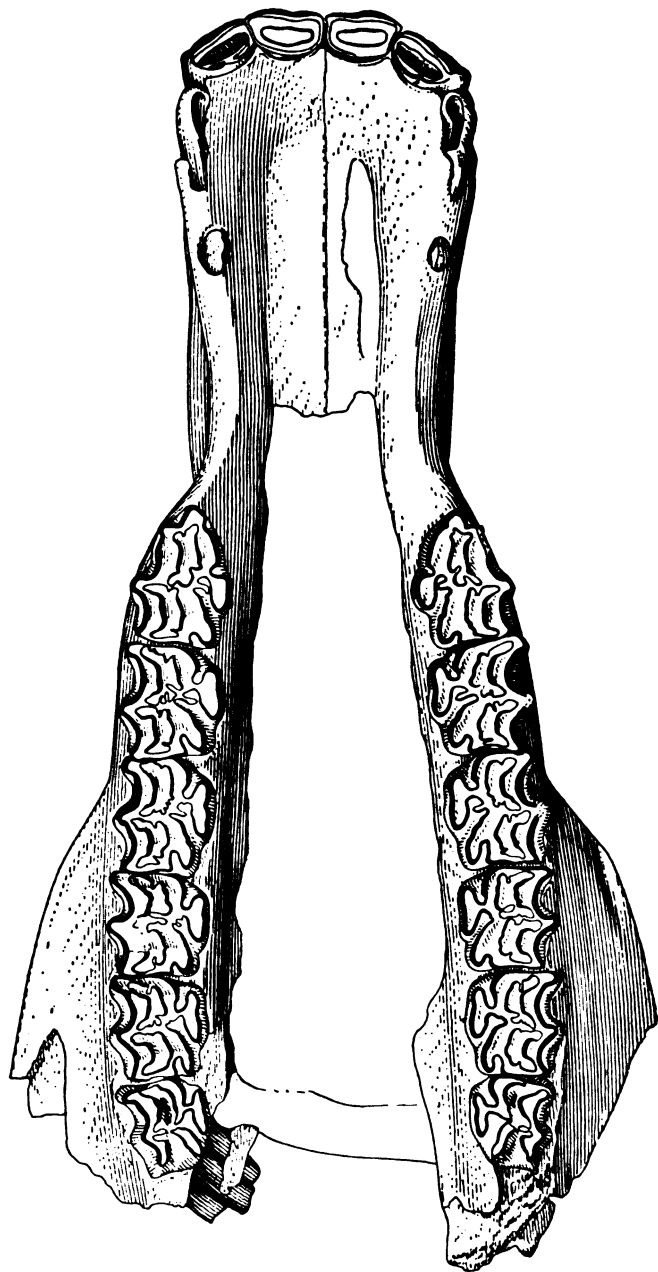


Fig. 13. *Equus* cf. *caballus*, occlusal view of palate with complete dentition, U.C.M.P. no. 38571, loc. V3604. $\times \frac{1}{2}$.

Order PERISSODACTYLA

Equus cf. *caballus* Linnaeus, horse

(Figs. 13, 14, 15, 16)

Stirton (1939*d*, pp. 294–298) noted the occurrence of the genus *Equus* in the Irvington fauna and described a broken skull, part of a lower jaw, a lower cheek tooth, and a cannon bone. This previous description of the Irvington horse can now be supplemented. A palate, maxillary fragments, many lower jaws (juvenile to old age), an abundance of dissociated upper and lower teeth, cannon bones, phalanges, vertebrae, carpals, and tarsals have been obtained. The complete palate, U.C.M.P. no. 38571, is from a young adult and shows characters which were somewhat obscure in the old-age skull described by Stirton.

Description.—No trace of P^1 in materials collected; P^2 widest of cheek-tooth series in young adult (about 27 mm.), P^4 widest in old adult (27.6 mm., Stirton)

VARIATION IN GREATEST TRANSVERSE DIAMETER OF UPPER CHEEK TEETH

	38571	38716	38573	33579
P^2	25.4		25.2	24.4
P^3	27.2		25.8	25.2
P^4	25.3		27.8	27.7
M^1	26.7	25.0	26.5	26.0
M^2	24.8	24.3		25.7
M^3	22.4	22.7		22.5
Estimated age.....	Young adult	Mature	Late mature	Old age

and in late maturity; height of crown in young adult measured on mid-vertical line along external surface, P^2 = 67 mm., P^3 = 79 mm., P^4 = 86 mm., M^1 indeterminate but about same as P^4 , M^2 = 94 mm., M^3 = 92 mm.

Protocones increase in transverse diameter from young adulthood to old age, relatively large and long, but triangular to ovoid on P^2 ; faint to moderately strong lingual groove usually present on protocones but may be absent on posterior premolars and third molar in early stage of wear, this groove directly opposite isthmus from protocone to protoselene on all specimens studied; lingual groove usually much fainter than on type teeth of *E. occidentalis* Leidy; heel of protocone strong on all teeth except P^2 ; isthmus remains narrow (except in old age) and of consistent width in a single cheek-tooth series; postprotoconal valley narrow in all stages of wear, extends almost to center of tooth in P^2 of young adult, but not deeply extended in all other teeth (different stages of wear were examined); pli caballin absent on all molars studied and on all premolars from maturity to old age inclusive, but only 3 mm. outpocketing of enamel border on P^2 to P^4 of a young adult; hypoconal groove open to base of tooth; fossettes with relatively simple enamel borders as in *E. excelsus* Leidy, *E. occidentalis* Leidy, and in contrast to strongly plicated borders in *E. pectinatus* Cope, *E. leidy* Hay, *E. yunnanensis* Colbert, and other proposed species; parastyle and mesostyle relatively rounded with wear, mesostyle somewhat V-shaped in young adult.

Depth of matured lower jaws beneath P_2 , 68.5 mm. (no. 32865, measured by Stirton), 70 mm. (no. 38582) to an estimated 80–85 mm. (no. 38573); depth of mature jaws beneath M_3 , 108 mm. (no. 38570) to 115 mm. (no. 38573); lower teeth rectangular in appearance due to flattening and frequent emargination of the external borders of protoconid and hypoconid; enamel lines usually simple and unplicated as noted by Stirton, although labial border of entoflexid on specimen

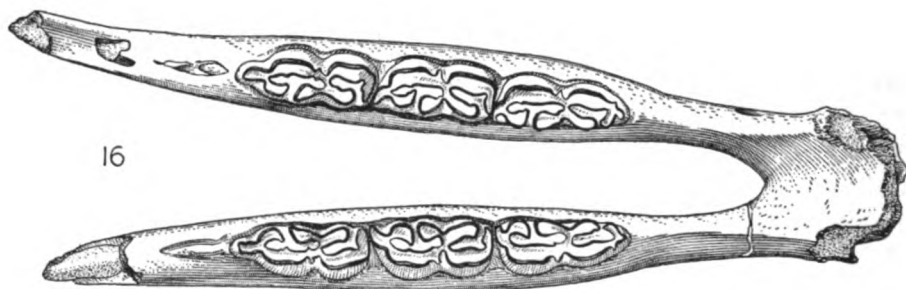


Fig. 14. *Equus* cf. *caballus*, occlusal view of left lower jaw with P_2 to M_3 inclusive, U.C.M.P. no. 38582, loc. V3604. $\times \frac{1}{2}$.

Fig. 15. *Equus* cf. *caballus*, occlusal view of left lower jaw with P_2 to M_3 inclusive, U.C.M.P. no. 38573, loc. V3604. $\times \frac{1}{2}$.

Fig. 16. *Equus* cf. *caballus*, occlusal view of mandible with complete deciduous cheek-tooth series, U.C.M.P. no. 38581, loc. V3604. $\times \frac{1}{2}$.

no. 38577 is strongly plicate; metaconid rounded and most metastylids with sharp angle to inner corner, configuration of metaconid and metastylid nondistinct from *E. caballus* Linnaeus or from *Equus* of Rancho La Brea; entoconid ovoid to almost square in outline and usually larger than metastylid; no trace of parastylid or hypostylid in any teeth available for study; metaconid and metastylid separated to base of tooth by groove usually U-shaped but approaching V shape on some teeth; hypoflexid extends inward to line of metaflexid and entoflexid on some teeth but not on more than one or two teeth in a given series from one animal; pli caballinid absent or present but not strong when present.

Deciduous upper dentition represented by isolated teeth; evidently with marked extreme in hypsodonty between DP^2 and DP^4 , DP^4 approximately one-third higher-crowned than DP^2 at equivalent stage of wear; protocone becomes progressively longer and narrower transversely and with more sharply defined heel from DP^2 to DP^4 as in other species of *Equus*; lingual indentation of protocone progressively broader and deeper from DP^2 to DP^4 , may be missing entirely on DP^2 ; prefossette opens into postprotoconal valley only in very early stage of wear; cross section of parastyle and mesostyle in deciduous premolars relatively longer in anteroposterior dimension and more rectangular in outline than corresponding styles of permanent cheek teeth.

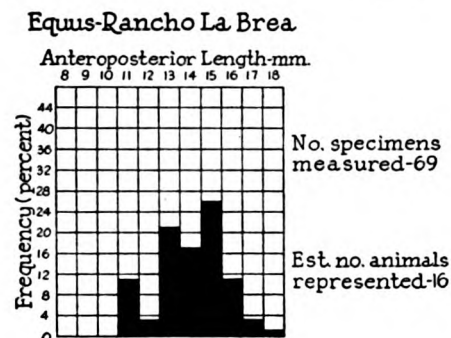
Lower deciduous cheek teeth resemble permanent dentition in simplicity of the enamel lines and general rectangularity of pattern; metastylid more angular in outline than metaconid as in permanent teeth; paralophid and hypoconulid more prominent than in permanent teeth; no trace of parastylid or hypostylid.

Discussion.—The relatively wide, U-shaped valley between the metaconid and metastylid and absence of hypostylid and parastylid in both milk and permanent teeth are the characters of the Irvington horse which make it conform to McGrew's (1944, p. 61) characterization of the caballine horses. It may be concluded that the Irvington horse is not closely akin to the subgenus *Plesippus* Matthew. McGrew's thesis that the plesippine species of North America suffered extinction at the close of Blancan time and that the Pleistocene of North America witnessed an immigration of caballines from Eurasia is judged to be logical after consideration of known evidence. It is noted, however, that the Rancho La Brea horse approaches plesippines in many of its characters.

Is the Irvington horse primitive? What is primitive in species of *Equus*? It is improbable that representatives of *Equus* can be classified as primitive or non-primitive by a system applicable to the entire world. Particularly in the Old World, where *Equus* has been continuously existent since Villafranchian time and has evolved into the caballines, zebras, asses, and half-asses, many of the characters evinced in the earliest forms are still retained by the Recent survivors. In North America certain characters seem to have a chronological implication. It is strongly affirmed, though, that these characters are applied to horse populations or to whatever concept there can be of horse populations as represented by the meager fossil remains; and the dating of a Pleistocene stratum by means of a contained single tooth or a few isolated teeth (particularly upper teeth) is insupportable and often fallacious.

Example. Character of the protocone.—In the North American Blancan to late Pleistocene species respectively, there is a general tendency, except in P^3 , for the protocone to become relatively more elongate, relatively thinner transversely, and for its long axis to become aligned more nearly parallel to the anteroposterior diameter of the tooth. Also, the protocones of the premolars are relatively shorter in comparison to those of the molars in the Blancan species which tend to have elongate molar protocones. Notable exceptions to these tendencies occur; some of the Blancan plesippines have long axes of protocones aligned parallel. (See J. R. Schultz, 1936, fig. 1.) The alignment of the protocone cannot be measured accurately; accordingly, the conclusion above is purely a matter of personal judgment.

A series of histograms showing anteroposterior diameters of protocones of adult upper teeth is shown on fig. 17. All the available upper cheek teeth were used except P^2 . No more than one series of P^3-M^3 from one animal was measured, so



Histograms of Length of Protocones. P^3-M^3 Inclusive.

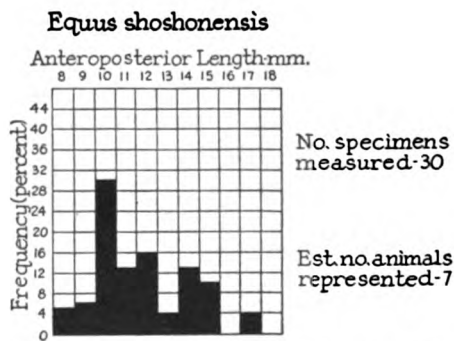
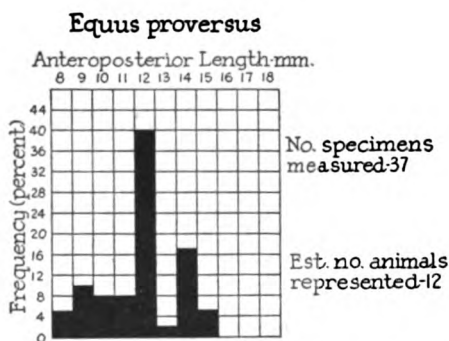
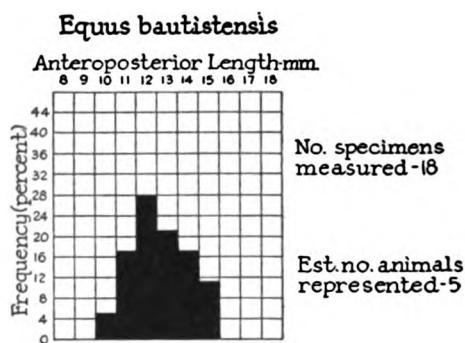
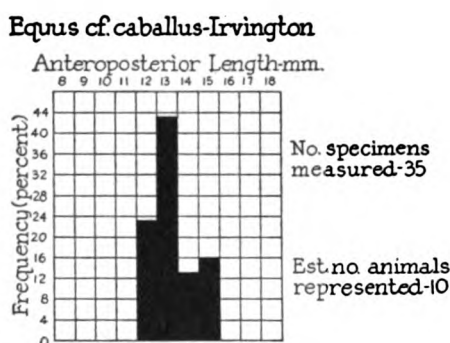


Fig. 17. Histograms of length of protocones in certain species of *Equus*. Lengths taken from P^3 to M^3 inclusive.

far as could be determined. The extremes of variation of the anteroposterior length of the protocone of a given cheek tooth were never farther apart than 2 mm. from the time the tooth is first worn to a normal occlusal surface until extreme old age. Since this variation with wear is relatively slight, teeth of all stages of wear through maturity were used. No attempt is made to establish the arithmetic mean or standard deviation in the manner suggested by Simpson and Roe (1939), but certain

interesting relationships are shown. Complete overlap by all the species in protocone lengths from 11.6 to 15.5, with all but *E. shoshonensis* having predominant numbers of protocones in this range, is evident. The two Blancan species probably have a wider range of variation than any of the later species, particularly in Blancan forms which tend to have elongate molar protocones. Note that in *E. shoshonensis* the variation extremes almost equal the entire range of variation of all the other species, lacking only 2 mm. This chart shows that a protocone between 9.6 and 17.5 mm. in anteroposterior diameter has no time-evolutionary significance.

The horse from Irvington belongs in a group with *E. lambei* Hay, *E. niobrarensis alaskae* Hay, and the horse which Tscherski (1892a) described from Liakhof Island, Siberia, as *E. caballus* Linnaeus. To this group I apply the designation *Equus* cf. *caballus*.

EVALUATION OF PROPOSED SPECIES OF EQUUS

An attempt to compare the Irvington horse to the proposed species of caballine *Equus* in North America is an almost hopeless task. Stirton (1939d, p. 395) has aptly summarized the obstacles which are inherent in this problem. A beginning student of speciation in *Equus* is completely overwhelmed by the multitude of presumably diagnostic species characters which have been used; he is even more confused to find that most of the proposed distinctions collapse into minor variations within a species when a large number of specimens are available from one locality. So many of the species names now carried in the literature are superfluous that an evaluation is demanded.

Any appraisal of fossil species of *Equus* in North America must be grounded on Gidley's excellent study (1901a). Some of his observations are erroneous in the light of present data; but his method of approach to the variation dilemma and his general treatment of species at that time were certainly a tribute to the author.

Hay's discussion (1915a, pp. 549-568) and review of the European species and subspecies merit praise also. Many of his conclusions are indeed perspicacious and judicial. Hay questioned the advisability of using the various kinds of present-day *Equus caballus* for comparison with fossil forms, since the present caballine has been so greatly affected by domestication and controlled breeding. He further recommended that the various skull and dental indices should first be tested on unmixed and undomesticated species. Of particular interest were Hay's conclusions:

Not all species can be distinguished by craniometrical methods. . . . Not too much dependence should be placed in any one measurement or in any single index. . . . all other characters ought to be considered in coming to a conclusion. . . . It is difficult to say which measurements and which indices are of the most importance. . . . In the application of these to special cases sometimes one index may be of special value; in other cases another index may be decisive.

One difference has often been emphasized in support of a species distinction when the similarities could be even more important. The species diagnoses have often been nothing more than characterizations of the genus. A notorious example is the presentation of relative size of the cheek teeth and complexity of the enamel folding of their fossettes as the diagnosis. So many of the species have proved to be "moderately large with moderate complications of the enamel" that there is no

longer any diagnostic or descriptive value in such a statement. Lurking among the maze of irrelevant descriptions and comparisons are the really important criteria with which lineages within this puzzling genus are to be compounded. At any time the recognition of a truly consistent difference may be more important than a multitude of similarities, particularly if any acceptable history of speciation or subspeciation is to be divulged.

It seems practical that if Pleistocene caballine materials in North America are ever to be employed with any certainty in stratigraphic problems, a very strict appraisal of the types is necessitated. Only when types are accompanied by sufficient materials to give at least some indication of infraspecific variation can there be a justification for the proposal of a new species among the equines. No objective comparisons may ever be formulated when reference of a specimen from one locality to a species from another locality is based on disparate material.

If one follows these tenets he is forced to utilize only four to eight Pleistocene caballine species names in North America. Such a drastic revision will not be universally accepted. This is true in part because of the lack of complete objectivity and conclusiveness on the part of the reviser, and in part because of established usage of poorly founded names.

Equus achates Hay and Cook (1930) was described from an upper molar collected near Frederick, Oklahoma. Species distinction was made because the writers knew of "no described molar so high, slender, and strongly curved." The diameters of the tooth place it in the size group of *E. tau* Owen. Although the tooth is indeed long as compared to many teeth which have been referred to other species, I believe that its relative length is not excessive. The photograph of the lateral view of this tooth permits no further comparisons. The species *E. achates* will be regarded as a *nomen vanum*.⁵

Equus calobatus Troxell (1915a) was established on an assembly of thin limb bones from Rock Creek, Texas. Troxell showed by various indices that *E. calobatus* possessed a slenderer cannon bone than specimens of *E. asinus* Frisch, *E. caballus*, and *E. scotti* Gidley. Troxell's conclusion that this is a very slender-limbed horse is acceptable, but a separate taxonomic category based on these limb elements was not warranted, since comparisons could not be made with species which had been described previously from Rock Creek. Cope (1893a), for example, based his species *E. semiplicatus* on material from Rock Creek. It seems much more logical that the equid remains from this locality, with the exception of *E. scotti* Gidley, should pertain to only one species. I regard *E. calobatus* as a *nomen vanum*.

Equus francisi Hay (1915a) is based on a skull and parts of a skeleton from the Lissie formation of Wharton County, Texas. Hay indicates that this horse is of the size and general character of *E. tau* Owen, but gave it a separate name because, unlike *E. tau*, the last premolar and the anterior two molars are wider than long.

⁵ *Nomen vanum* is the term proposed by Simpson (1945, p. 27). This phrase bears the general implication of the word "indeterminate," which was used by many earlier writers. Simpson (1947, p. 31) has added further explanation of his use of this term: "There are, as it happens, some names . . . the validity of which can hardly be judged one way or the other at present. Such names are not now known to be valid, and they cannot be applied to any specimens other than the type or syntypes. . . . It would be misleading to list these names and to use them on the same basis as names of reasonably established status . . . they are not technically homonyms, synonyms, or *nomina nuda*, and they maintain a standing in nomenclature although they have none in zoölogy."

Hay made no statement regarding the stage of wear of *E. francisi* teeth compared to the type of *E. tau*; but in a later publication (1917f, p. 439) he mentions that it is known "as the upper teeth are worn down the fore-and-aft length of the crown diminishes more rapidly than the width." Gidley (1901a, p. 99) had previously pointed out this characteristic. The teeth in a series of zebra skulls in the Museum of Paleontology, University of California, were examined to see if variations in the ratio of length to width of crown occur in specimens at about the same stage of wear. It was found that ratios in the same stage of wear were quite constant but that there is apparently a marked change in this ratio between early adult and mid-adult levels. A young adult specimen exhibits proportions not unlike *E. tau*, whereas a middle-aged adult specimen is like *E. francisi*. I believe, therefore, that Hay's species *E. francisi* should be referred to *E. tau*.

Hay stated that it was possible that this Texas horse actually belongs with *E. tau* but said that there were certain features which appear to mark the animal as being more primitive than Owen's species. He did not, however, designate the characters which were considered primitive. The characters of *E. tau* and *E. "francisi"* (= *E. tau*) suggest that this species might be a Blancan plesippine with a uniquely advanced protocone, or that it is a somewhat divergent Pleistocene caballine with characters in the lower dentition which approach Blancan plesippines. It is of interest to see that Gromova (1946, pp. 347-350) has found isolated upper and lower cheek teeth of a large horse in "latest Pleistocene" of Samarkand. Gromova named this horse *E. valeriani*. The proposed distinction of this species is its combination of a typical stenonian (hippotigrine or plesippine) metaconid-metastylid column with an elongate protocone. *E. valeriani* would seem to be, then, a structural annectant between stenonines and caballines persisting until a late time. The occurrence of a structural annectant between plesippines and caballines in North America, as is suggested by *E. tau*, might be interpreted as evidence that the containing deposit was either late Blancan or early to middle Pleistocene were it not for contradictory data such as Gromova has presented. Such evidence also opposes the generic separation of the zebras and horses and supports the contention that these two groups did not arise independently from different species of *Pliohippus*.

Equus holmesi Hay (1920b) was based on four upper cheek teeth from the Pleistocene of northeastern Oklahoma. The species diagnosis states (p. 119): "Teeth large. Enamel of fossettes with only medium complication; styles unusually broad." Hay stated that these teeth are the same size as *E. scotti* Gidley. He thought *E. scotti* was probably synonymous with *E. complicatus* Leidy. These teeth resemble figured specimens of both *E. scotti* and *E. complicatus*. *E. holmesi* Hay is a *nomen vanum*.

Equus jubatus Hay (1927d) was described from four well-worn associated upper cheek teeth collected at Cameron, Texas. These teeth, like an old individual (U.C.M.P. no. 38572) from the Irvington fauna, show relatively thick enamel. They could be referred to any Pleistocene species of equivalent size. *E. jubatus* is a *nomen vanum*.

Equus leidy Hay (1913b) was based on an upper molar from Peace Creek, Florida. Hay gave as characterization of the species: ". . . teeth of medium size, the length of the grinding surface of the first molar being about 25 mm., the width

about 24 mm., excluding the cement. Enamel surrounding the lakes rather strongly folded. Type tooth moderately curved."

This tooth and other teeth which Hay has referred to this species greatly resemble teeth which have been referred to *E. complicatus* Leidy, *E. holmesi* Hay (*nomen vanum*), and other proposed species. I regard *E. leidyi* as a *nomen vanum*.

Equus littoralis Hay (1913b) is based on an upper cheek tooth, also from Peace Creek, Florida. The enamel pattern is like that in the *E. complicatus*-*E. fraternus* Leidy group, but the tooth is small enough to compare with *E. tau*. This may be logically regarded as a small individual of the probable one species represented at Peace Creek. *E. littoralis* is a *nomen vanum* so far as this study is concerned.

Equus nevadanus Hay (1927d) is based on an upper cheek-tooth series from Manhattan, Nevada. Comparisons were made only with *E. laurentius* Hay. This could be one of several previously described species of moderate size. *E. nevadanus* will be regarded as a *nomen vanum*.

Hippotherium princeps Leidy (1890a) was formulated from a large upper cheek tooth found at Peace Creek, Florida. It is of the size of some of the larger species of *Equus*. Uniquely, the protocone is separated from the protoselene in a fashion resembling *Neohipparion*, even though the tooth has been abraded to a flat occlusal surface. Hay (1902a) thought this tooth belonged with *E. complicatus*. It has an anomalous enamel pattern, and the species is indeterminate. *H. princeps* is a *nomen vanum*.

Equus occidentalis Leidy (1865c) was based on an upper cheek tooth from the "Pleistocene auriferous gravels" in Tuolumne County, California, and two upper cheek teeth from an asphalt bed near Buena Vista Lake in Kern County, California. The latter locality is now usually called Asphalto. These teeth are all characterized by a simple and somewhat rectilinear enamel pattern and a broad lingual groove on the protocone. It is impossible to get topotypes of the Tuolumne County specimen, because the exact locality was never specified; it may or may not be Pleistocene in age. Stirton (oral communication, 1948) has called to my attention that topotypal lower cheek teeth from Asphalto bear the plesippine V-shaped groove between the metaconid and metastylid. Merriam (1913f) referred the abundant horse material from Rancho La Brea to *E. occidentalis*. Although there is remarkable identity in characters between the Rancho La Brea horse and the types of *E. occidentalis*, the La Brea horse is a true caballine (this is demonstrated by the character of its deciduous dentition) and must be referred to some other species. *E. occidentalis* is believed to be a valid species of plesippine affinity. It is singularly advanced over *E. simplicidens* (Cope), *E. shoshonensis* (Gidley), *E. francescana* Frick, *E. idahoensis* Merriam, and *E. proversus* (Merriam) in its development of a wide and prominent lingual groove on the protocone. The Blancan age assignment for this species is supported by the recovery of *Ischyrosmilus* and *Borophagus* from Asphalto. In a doctoral thesis for the University of Oklahoma, which is to be published posthumously, C. S. Johnston referred the *Equus* from the Cita Canyon fauna (Blancan) to *E. occidentalis*. Johnston came to this conclusion when the characters of the topotypes of *E. occidentalis* were pointed out to him by Stirton in an oral communication.

Equus fraternus Leidy (1860b).—This proposed species has had a complicated nomenclatural history. It was described by Leidy from material obtained near Charleston, South Carolina; but the name was a *nomen nudum*, since Leidy gave no precise description and designated no type. Cope (1896h, p. 467) chose to validate the species under Leidy's authorship and selected a tooth from Leidy's material to be the type. Gidley (1901a, p. 111) believed that the tooth Cope selected was not described by Leidy at all; so Gidley chose another tooth as Leidy's type. Hay (1913b, pp. 569–570) refuted Gidley's correction and reaffirmed Cope's selection of the type. These revisers indicated that *E. fraternus* is separable from *E. complicatus* Leidy only by a slight size difference. *E. fraternus* is the smaller of the two species in the descriptions of these writers, but the larger teeth of *E. fraternus* are indistinguishable from *E. complicatus*. There seems to be no adequate data for a differentiation. I believe that all the teeth from this locality should be referred to one species. *E. fraternus* will be employed only as a *nomen vanum*.

Equus complicatus Leidy (1858c) was based on a second upper molar. Paratypes were two posterior upper molars. The specimens were collected near Natchez, Mississippi. It would indeed be fortunate if this name could be retained for practical use, since this is the first proposed fossil *Equus* species from North America and many other subsequently described species are probably referable to this category. As Gidley (1901a, pp. 109–110) pointed out, however, *E. complicatus* itself is imperfectly characterized except in size. Although many teeth from different localities have been referred to it, there is no assurance in regard to such reference. The type indicates that *E. complicatus* was of medium to large size and with moderate to strong plication of the enamel borders of the fossettes, but these characters are certainly not unique in *Equus*. *E. complicatus* will be treated as a *nomen vanum*.

Equus excelsus Leidy (1858e) is a fragmentary right maxilla with P⁴ to M³. The specimen was collected somewhere along the Pawnee Loup branch of the Platte River in Nebraska. It is a moderately large horse. Although Hay (1913b, p. 592) continued to distinguish this species from *E. niobrarensis* Hay and other species on small differences in enamel configuration, Gidley (1901a, p. 113) thought that the species could not be clearly defined. Again, as with *E. complicatus* Leidy (*nomen vanum*) there seems to be no possibility of finding topotypes. *E. excelsus* will be set aside as a *nomen vanum* in this study.

Equus semiplicatus Cope (1893a) is an upper molar from Rock Creek, Texas. This specimen is insufficient for the construction of definitive species characters. It is known, though, that much topotypal material has been collected. In view of this fact, it seems possible that eventually this species may be established satisfactorily. It will be treated as a *nomen vanum* at this time. Cope's designation of the teeth from San Diego, Texas, as paratypes is not acceptable. So far as the referred skull and teeth are concerned, this seems to be a medium-sized *Equus* with simple tooth pattern.

Equus tau Owen (1870b) is an upper cheek-tooth series, lacking P², from the Valley of Mexico. It is characterized by the very small size of the teeth. Owen gave the relatively long anteroposterior diameter of the premolars as a character, but this diameter has been shown to vary markedly with wear of the teeth and probably

COMPARISON OF SPECIES OF EQUUS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	<i>R. hutchins</i>	<i>R. nioberrensis</i>	<i>R. scottii</i> ^a	Extremes of variation between <i>R. hutchins</i> and <i>R. nioberrensis</i>	Extremes of variation between either <i>R. hutchins</i> or <i>R. nioberrensis</i> and <i>R. scottii</i> ^b	<i>R. przewalskii</i> , 5216, Salenky ^c	<i>R. przewalskii</i> , 512, Tschernak ^c	Extremes of variation in 9 skulls of <i>R. przewalskii</i> ^b	<i>R. przew.</i> , U.S.N.M. 103338 ^b	<i>R. przew.</i> , U.S.N.M. 183020 ^b	Extremes of variation in 8 skulls of <i>R. przew.</i> ^b	Extremes of variation in 8 small domestic horses ^b	Extremes of variation in 8 large domestic horses ^b	Extremes of variation in all 16 domestic horses ^b
Basal length.....	552	530	530 ^a	22.0	22.0	495	440	55	557	525	33	26	49	159
Cephalic index.....	42.6	45.3	43.5	2.7	1.8	42.2	42.6	2.5	37.7	39.0	3.1	3.9	4.7	7.0
Craniocephalic index.....	35.3	34.3	37.8	1.0	3.5	34.1	34.1	2.3	34.1	36.2	2.5	1.8	4.6	6.1
Faciocephalic index.....	74.8	75.3	77.5	0.5	2.7	76.2	76.1	2.6	76.8	77.7	2.1	5.3	4.6	7.7
Vertex length.....	615	582	610 ^a	33.0	28.0	547	488	62	627	595	42	36	59	164
Ratio: Length of upper premolars to length of cheek-tooth series.....	51.3	54.2	55	2.9	3.0									

^a Measurements taken from young adult skull of *R. scottii*, U.C.M.P. no. 10608.

^b Taken from Hay (1916).

^c Approximate measurement to within 5 mm.

is not diagnostic. No other fossil species described in North America has been demonstrated to grade completely into the *E. tau* teeth on the basis of size, except *E. "francisi"* Hay (synonym of *E. tau* in this paper).

Equus pectinatus Cope (1899a) was based on nine upper premolars and molars probably from one animal. These were collected in cave deposits at Port Kennedy, Pennsylvania. The species was distinguished by its relatively small protocones and by the complicated enamel plication of the lakes. The teeth indicate that it is a large horse. I prefer to regard *E. pectinatus* as a valid category until it can be demonstrated that previously named species include the range of characters it portrays. This associated series of teeth at least shows what may be expected in variation of pattern and proportion between teeth in the same animal.

Equus giganteus Gidley (1901a) is based on a single upper cheek tooth from southwest Texas. It was distinguished by its very great size and relatively small fossettes. No individuals of other species of *Equus* have yet been described which attain the size of this tooth. In general appearance *E. giganteus* is not unlike certain teeth seen in *E. scotti*, *E. shoshonensis*, or *E. idahoensis*. It seems possible that this tooth might represent an unusually large individual of *E. scotti*. Among the teeth in the University of California collection, the plesippine from the Wichman fauna of Nevada, the large caballine from Fossil Lake, Oregon, and the large horse from Rancho La Brea and McKittrick most nearly attain the size of *E. giganteus*. I believe that *E. giganteus* is a valid species, possibly of plesippine affinity.

Equus niobrarensis Hay (1913b) and *Equus hatcheri* Hay (1915a).—*E. niobrarensis* was based on a complete skull (broken and restored to shape); *E. hatcheri* was based on a complete skull and lower jaw. Both types were collected from the Hay Springs quarry near Grayson, Nebraska. Hay very carefully compared *E. hatcheri* to *E. niobrarensis* and found that *E. hatcheri* had a longer and narrower skull, a shorter and broader face, and a straighter dorsal profile of skull. Irrespective of the differences which Hay itemized, the two types may be referred to the same species. The variation shown is due to a possible difference in sex between the two types, or is attributable to individual variation. *E. niobrarensis*, the smaller skull, has no canines; whereas *E. hatcheri*, the larger, has canines. This is not conclusive datum, but it suggests that *E. hatcheri* may have been male, and *E. niobrarensis* female. It seems necessary to compare the variation between the two specimens with the variation exhibited in nondomesticated strains of Recent equids. To do this, tables presented by Hay (1915a) may be used. (See the accompanying table.) It is believed that this tabulation demonstrates how practical conclusions can be formulated from Hay's data which are directly opposed to Hay's own conclusions. All linear measurements are in millimeters, and all measurements and indices are based on adult skulls. *E. hatcheri*, *E. niobrarensis*, and *E. scotti* are compared with two skulls of *E. przewalskii* and with two skulls of *E. grevyi* which were selected on account of extreme in basilar length. The fossil skulls are also compared to a series of skulls of *E. przewalskii*, *E. grevyi*, and a series of large and small domestic horses.

In the table it can be seen that the extremes of variation in indices and lengths are usually found in the domestic horses, even when these domestics are divided into groups of similar size. This supports Hay's conclusion (1915a, p. 552) that it

is inadvisable to use present-day *E. caballus* Linnaeus for comparison with fossil forms, since the domestic horse has been greatly affected by controlled breeding. Column 4 of this chart shows that (1) the difference in basal length between *E. hatcheri* and *E. niobrarensis* can be less than this difference within *E. przewalskii*, *E. grevyi*, and the domestic horse; (2) the difference in cephalic index between *E. hatcheri* and *E. niobrarensis* is greater than in the represented individuals of *E. przewalskii*, but can be less than with *E. grevyi* and the domestic horse; (3) the difference in craniocephalic and faciocephalic indices between *E. hatcheri* and *E. niobrarensis* can be much less than within any of the compared species; (4) the difference in vertex length can be less than within the compared species. In only one comparison out of ten, then, does a difference in index or length between *E. niobrarensis* and *E. hatcheri* exceed the difference that may be demonstrated among individuals within one Recent wild species. To be sure, this analysis does not attempt to put greater or lesser weight upon any given index or length; nor does it appraise the fact that differences in indices may or may not represent greater physical variation than do the differences in linear measurements. Is the cephalic index more important than the craniocephalic index or the faciocephalic index? If the cephalic index is most important in this example, will it be most important in comparisons of other species of *Equus*? I cannot even attempt to answer such questions. It seems, however, that by sheer weight of numbers of differences which are less extreme than within one compared species, there is no justification for a specific separation between the two Hay Springs horses on the basis of skull characters.

Hay (1915a, pp. 531-533) pointed out differences between the individual teeth of *E. hatcheri* and *E. niobrarensis*: *E. hatcheri* with all teeth longer anteroposteriorly, wider transversely, different in configuration of parastyle of P^3 and P^4 , lacks distinct lingual groove of protocone. He did not, however, give any of these differences any particular weight in the speciation: "It is probable that not all of the differences observed among these horses will prove to be of specific importance, but it seems to be proper to note them in order that the important character may in due time be discovered." In referring to the shape of parastyles of P^3 and P^4 , Hay states, "Probably in each species there is in this character a good deal of individual variation." It is here concluded that the differences in dentition are no more severe than the previously reviewed differences in skull characters and that all may be easily contained in the realm of individual variation.

Certain possibilities of error in the figures of the chart should not be disregarded. Considerable tolerance must be allowed when evaluating the linear measurements, even though these lengths were presumably all made by the same man. For example, the vertex length is specified as the distance from the incisive border to the middle of the occipital crest. Was this length measured along the line of curvature of the dorsal profile or was it measured as the straight-line distance between the two points? If either the incisive border or the middle of the occipital crest is incomplete, as it often is, what method was used in the estimation of vertex length? Such questions must, for the most part, remain unanswered for the student of horse skulls. Simpson and Roe (1939) have clearly outlined some of the uncertainties of interpretation of measurements which now exist in the literature.

A cursory examination led to the conclusion that these two Nebraska horses greatly resemble *Equus scotti* Gidley. Hay made no comparisons of *E. niobrarensis* and *E. hatcheri* with the previously described *E. scotti*. Column 3 of the table^a on page 248 shows that *E. scotti* (1) is in the general length of skull range of the Hay Springs horses, (2) is intermediate in cephalic index between *E. niobrarensis* and *E. hatcheri*, and (3) has a greater craniocephalic index than either of the Nebraska horses. Whether the index differences balance, underbalance, or overbalance the index and linear measurement similarities is purely a matter of personal interpretation. I feel that the general similarity in dentition, particularly between *E. hatcheri* and *E. scotti*, together with the skull similarities, is sufficient to throw *E. niobrarensis* and *E. hatcheri* into synonymy with *E. scotti*, with no more than a racial difference separating the Texas horse from the Nebraska forms. This conclusion is based purely on the published evidence; a detailed study of the skeletal topotypal material from the Hay Springs quarries in comparison with the numerous *E. scotti* skeletons may prove that the Nebraska horses differed in body proportions from the huge-skulled, medium-build Texas horse.

Equus scotti Gidley (1900a) was described from a nearly complete skeleton, including skull and lower jaws, from Rock Creek, Texas. *E. scotti* might represent the same species as *E. complicatus* Leidy (*nomen vanum*) and has been referred to that proposed species (Hay, 1920b). Since the type of *E. complicatus* (*nomen vanum*) is indeterminate and its referred materials (see, for example, Gidley, 1901a, Pl. XVIII) cannot qualify as topotypes, *E. scotti* remains a valid species.

Equus bautistensis Frick (1921a) was based on three associated upper premolars and referred topotypal upper and lower cheek teeth, incisors, and limb elements collected near Valle Vista, California. All except two of the sixteen lower cheek teeth, including two incomplete cheek-tooth series in jaw fragments, differ from the Irvington horse and others by the asymmetrical U-shaped groove between the metaconid and metastylid. This groove approaches a V shape in several specimens and is close to the pattern seen in some teeth of *E. simplicidens* and *E. shoshonenensis* of the Blancan. This character, therefore, might be regarded as primitive. Approximately ten of the eighteen upper cheek teeth of *E. bautistensis* are larger than any of the uppers which have been collected at Irvington. This suggests a probable mean size difference between the two horse populations. A consistent mean size difference, together with a difference in an enamel character, could represent either species distinction or infraspecific distinction so far as the criteria of neozoölogical speciation are concerned. Because of the appearance of the possibly primitive character in the lower cheek teeth, I prefer to treat *E. bautistensis* as a valid species.

Equus pacificus Leidy (1868d) was a large P³ from Martinez, California. Leidy stated that the tooth was not different from the Recent horse on its triturating surface and that it showed a more complex folding of the enamel borders of the fossettes than *E. excelsus* Leidy (*nomen vanum*). Gidley (1901a, pp. 116-117) thought the large horse from Fossil Lake, Oregon, belonged with this species. No

^a The measurements and indices given in the chart for *E. scotti* were taken from the skull of a young adult, U.C.M.P. no. 10608. Gidley (1901a) gave no measurements for the type of *E. scotti*.

one can say that Gidley's reference is wrong, yet the type tooth bears no definitive characters. Leidy's type is not considered determinate, and *E. pacificus* will be utilized only as a *nomen vanum*.

Equus laurentius Hay (1913b) was proposed on the basis of a remarkably well-preserved skull and mandible found on a sand bar of the Kansas River near Lawrence, Kansas. Hay compared this specimen with *E. caballus*, *E. niobrarensis* (synonym of *E. scotti* in this paper), and *E. excelsus* Leidy (*nomen vanum*). Matthew (1926c, p. 180) made a parenthetical statement in the bibliography accompanying his paper that *E. laurentius* was based on a Recent skull which was mistakenly supposed by the author to be of Pleistocene age. Hay (1927a) offered a rebuttal to Matthew's comment and reaffirmed that the type was actually a fossil. Hay at this time compared *E. laurentius* to an Arizona "Indian Pony" but could find differences only in the postprotoconal valleys and in the fossettes. I shall regard *E. laurentius* as a synonym of *E. caballus*. It seems likely that this was a feral horse, trapped in river quicksand and subsequently permineralized in a relatively short time.

Equus lambei Hay (1917f) was established from a complete skull and lower jaw from Gold Run Creek, Klondike region, Yukon Territory. The specimen is among the smaller, broad-skulled horses; the teeth appear to be unusually broad, with simple enamel lines and long protocones. The upper cheek teeth are similar to many of the teeth of the Irvington horse. Although this species was differentiated from *E. caballus*, there are no justifiable criteria for this distinction when the range of variation of a Recent wild species is compared. I believe that this specimen should be identified as *E. cf. caballus* on the basis of its type material.

I conclude that there are not more than seven species names of caballine *Equus* in the late Cenozoic of North America which should be given zoölogical usage at this time. These species are:

Equus pectinatus Cope—Port Kennedy, Pennsylvania

E. scotti Gidley—Rock Creek, Texas

E. bautistensis Frick—Valle Vista, California

E. tau Owen (this may be a plesippine)—Valley of Mexico

E. giganteus Gidley (this may be a plesippine)—Southwestern Texas

E. cf. caballus Linnaeus

The Rancho La Brea—McKittrick horse (probably a distinct species)

Order ARTIODACTYLA

Tayassuidae, peccary

(Fig. 18, a, b)

Maxillary fragment containing base of left upper canine tooth, U.C.M.P. no. 38533; possibly referable to *Platygonus* LeConte because of its large size and particularly because of large upper canine tooth; *Mylohyus* reported to have weakly developed upper canine; much larger than a specimen of *Platygonus leptorhinus* Williston, U.C.M.P. no. 26639; deep indentation of palate to accommodate tip of lower canine,

pit much deeper and wider in Irvington animal than in *P. leptorhinus* specimen; animal about same size or slightly smaller than large *P. cumberlandensis* Gidley from Maryland. (See Gidley and Gazin, 1938.)

	MEASUREMENTS	
	No. 38533	<i>P. leptorhinus</i> No. 26639
Anteroposterior diameter of C ² at base of tooth.....	19	14
Transverse diameter of C ² at base of tooth.....	12	8

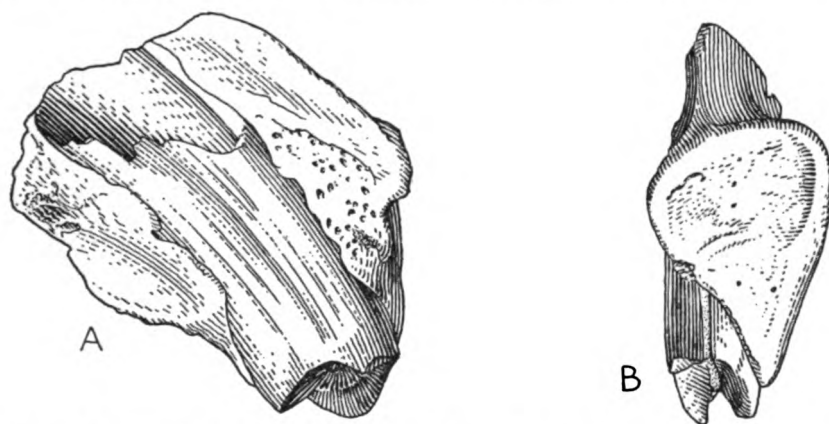


Fig. 18. Tayassuidae, U.C.M.P. no. 38533, loc. V3604: a, medial view of fragment of left maxilla with base of canine tooth; b, anterior view. $\times 1$.

Camelops minidokae Hay

(Figs. 19, 20, 21, 22, 23)

In the Irvington fauna are numerous lower jaw fragments, isolated teeth, limb bones, vertebrae, girdle bones, ribs, and two crushed skulls of *Camelops*. This species is more slender, and only slightly smaller than a specimen of the Recent *Camelus bactrianus* (U.C.M.V.Z. no. 74673). The Irvington *Camelops* belongs in the smaller size group of Pleistocene species and is inseparable from the type of *C. minidokae* on the basis of size.

Cranium.—Crushed palate with complete permanent cheek-tooth series, U.C.M.P. no. 38447, and crushed skull with DP²—M¹ inclusive, U.C.M.P. no. 38446.

Taper of rostrum indeterminable; character of frontal indeterminable; anterior border of orbit above M¹ in juvenile skull (anterior border of orbit above posterior portion of M³ in mature *C. hesternus* Leidy from Rancho La Brea); basicranial and basifacial axes apparently nearly parallel; nasals indeterminable; maxillary fossa not preserved in our specimens; anterior end of zygomatic process of squamosal as heavy as in *C. hesternus* and extends beneath posterior border of orbit; jugal border of orbit relatively as heavy as in *C. hesternus*; upper cheek-tooth series evidently more parallel to each other than in *Camelus*; character of internal choanae, sphenoids, glenoid fossa, paroccipital process, mastoid, occiput, anterior palatine foramina, and top of skull indeterminate.

Permanent dentition.—I³ and C not preserved in Irvington specimens; P³ relatively and actually smaller than in *C. hesternus*; but of same construction



Fig. 19. *Camelops minidokaensis*, occlusal view of incomplete skull with left DP₃ to M₁ inclusive and right DP₃ to M₁ inclusive, U.C.M.P. no. 38446, loc. V3604. x 1/2.

except for less prominent development of posterointernal heel; P^4 smaller than in *C. hesternus*, but quadrate, submolariform, and with two selenes as in *C. hesternus*; upper permanent molar teeth with styles less conspicuous than in specimens of *C. hesternus* available for comparison; M^1 with stronger mesostyle than parastyle and with ribs less prominent than in *C. hesternus*, general proportion of tooth equal to that in *C. hesternus*; M^2 with anterior lobe of greater transverse diameter than posterior lobe, mesostyle much stronger than parastyle in contrast to *C. hes-*

COMPARATIVE MEASUREMENTS OF *CAMELOPS MINIDOKAE*

Dimensions, following Hay's terminology	Paratypes	Holotype	Irvington specimens
Anteroposterior diameter, P_1 , at base.....		6.5 ?	No P_1
Transverse diameter, P_1 , at base.....		8.0 ?	No P_1
Depth of jaw at rear of M_3		58	62, 66, 72, 74, 75, 83*
Length of symphysis.....	102, 118		87, 94
Width of symphysis just behind canines.....	45, 46		30, 40
Length P_1 - M_3 inclusive, along grinding surface.....		147	135, 140, 142, 150
Height in front, inner face, P_1	27	28	23, 24, 26
Length at summit, P_1	24.5	23	20, 23, 23, 24
Greatest thickness, P_1	13	13	11, 12, 12, 13
Height in front, M_1	20	20	12, 14, 22
Length at summit, M_1	24	25	26, 26, 27, 33
Greatest thickness, M_1	17±	18	17, 18, 18, 19
Height in front, M_2	33±	50	30, 32, 35
Length at summit, M_2	40.5	40	33, 38, 39, 40, 47
Greatest thickness, M_2	20	20	18, 18, 19, 20, 21
Height in front, M_3	65	68	35, 52
Length at summit, M_3	55	56	36, 48, 51, 53, 54
Greatest thickness, M_3	19.6	20	17, 17, 18, 19, 20
Distance, base of fossette to summit of front lobe, M^3	64	..	72
Length at base of fossettes, M^3	49	..	35 approx.
Thickness through front lobe at base of fossettes, M^3	27	..	28

* As many of the specimens as were available from Irvington were measured and these measurements are listed serially.

ternus, anterior rib stronger than posterior rib; M^3 with parastyle about equal or slightly weaker than mesostyle in contrast to *C. hesternus*; metastyle inconspicuous.

Deciduous dentition.— DP^2 peglike, quadrangular in cross section, approximately 5 mm. in anteroposterior diameter; DP^2 shorter-crowned than permanent premolars, mesostyle strongest of styles, posterior lobe with much greater transverse diameter than anterior lobe; DP^4 shorter-crowned than permanent premolars, mesostyle strongest but parastyle and metastyle conspicuous, anterior and posterior lobes of about equal transverse diameter.

Mandible.—Left jaw fragments with complete cheek-tooth series, U.C.M.P. nos. 32923 and 38449; portion of mandible with complete right cheek-tooth series and symphysis, including caniniform teeth and incisors, U.C.M.P. no. 38448; left and right juvenile rami, U.C.M.P. nos. 38451 and 38450.

Length of mandibular symphysis about 90 mm. on each specimen; ratio of length

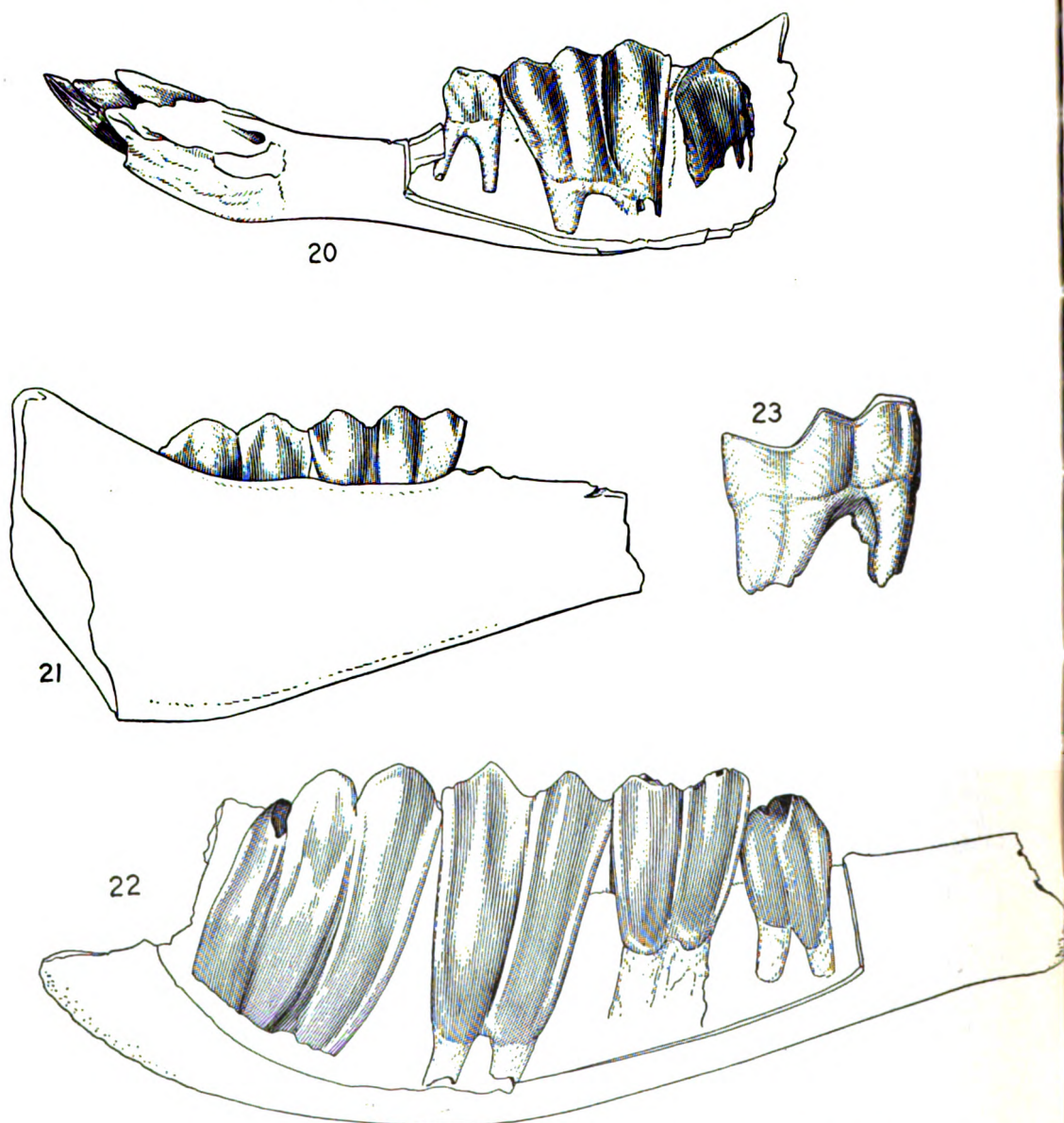


Fig. 20. *Camelops minidokae*, lingual view of right lower jaw with DI₁ to DI₃ and DP₃ to M₁ inclusive, U.C.M.P. no. 38450, loc. V3604. $\times \frac{1}{2}$.

Fig. 21. *Camelops minidokae*, lingual view of left lower jaw with DP₁ to M₁ inclusive, U.C.M.P. no. 38453, loc. V3604. $\times \frac{1}{2}$.

Fig. 22. *Camelops minidokae*, lingual view of left lower jaw with P₁ to M₃ inclusive, U.C.M.P. no. 38449, loc. V3604. $\times \frac{1}{2}$.

Fig. 23. *Camelops minidokae*, lingual view of left M₃, U.C.M.P. no. 38461, loc. V3604. $\times \frac{1}{2}$.

of symphysis to estimated total length of mandible is 1:4.5, a ratio found also in *C. hesternus*; ventral border of ramus as convex as *C. hesternus*; lower incisors subtriangular in cross section, blunt internally and tapering to sharper edge externally, arranged in echelon with I_3 slightly overlapping posterointernal surface of I_1 and I_3 abutting posterointernal surface of I_2 ; lower caniniform tooth more internal to line from P_4 to I_3 than in *C. hesternus*; P_4 wedge-shaped as in other species of *Camelops* and with deep posterior enamel fold in earlier stages of wear which completely disappears in later stages of wear, with one or two shallow lingual inflections; M_1 and M_2 with rather sharp median groove on lingual surface bordered anteriorly by an almost equally sharp pillar; other internal stylids and ribs inconspicuous as in *C. hesternus*; M_2 and M_3 without anteroexternal pillars as in other species of *Camelops*; general structure and alignment of molars not distinct from other species; DI_{1-3} distinguished from permanent incisors only by smaller size and lighter construction; alveolus for milk caniniform tooth present but this tooth not contained in youthful jaws thus far recovered; DP_3 in many respects a small copy of P_4 , with deeper posterior fold in early stages of wear which, with wear, forms a lake posteriorly, which eventually disappears; DP_4 three-lobed, somewhat resembling M_3 , from front to rear lobes become progressively greater in anteroposterior and transverse diameter in contrast to M_3 , lobes of about equal crown height in contrast to M_3 ; DP_4 much smaller than M_3 and much less hypsodont.

Discussion.—The Irvington camelid is of a size range which encompasses the type material of *C. minidokae* Hay. The Irvington material consistently exhibits a median lingual groove on M_1 and M_2 which is bounded anteriorly by a stylid and thus agrees with *C. minidokae* in the enamel pattern of the lower dentition. This configuration is admittedly not conclusive evidence of species relationship, since it is approached by certain specimens of *C. hesternus*. The type of *C. minidokae* possesses a small P_3 . This tooth has not been reported from any of the other jaws which have been referred to *Camelops* and does not appear among the Irvington specimens. I believe that the presence of this tooth on the type is of no taxonomic significance. The trend of evolution in camelids leading to a climax in the genus *Camelops* has been marked by a reduction in premolars. An atavism, such as sporadic recurrence of a premolar, may be expected infrequently in later members of a phyletic chain. Such a "wolf" tooth is known to appear anomalously among the Recent and fossil horses, and probably also among the Recent camels.

The cranium and mandibles of *C. minidokae* from Irvington are distinguished from *C. hesternus* by their persistently smaller size in all measurements and by the presence of a prominent internal median groove bordered anteriorly by a stylid in M_1 and M_2 . Needless to say, certain individual specimens from Irvington fall very close to the size and character range of *C. hesternus* from Rancho La Brea.

Appendicular skeleton.—The skeleton of *C. minidokae* from Irvington and *C. hesternus* from Rancho La Brea were studied with the intention of obtaining distinct characters applicable to the genus *Camelops*. Comparisons were made with *Paracamelus* (syn. *Megatylopus*) materials from the Higgins, Hemphill, and Rattlesnake faunas and with the published descriptions of *Gigantocamelus* and

Titanotylopus materials from Blancan faunas in Nebraska and Texas. Comparisons were made also with *Pliauchenia* from the Hemphill fauna and with camelids from the Mount Eden and Thousand Creek faunas.

Bones of *Camelops minidokae* smaller than the Hemphillian and Blancan bones of *Paracamelus*; *Camelops hesternus* elements fall within the size limits of *Paracamelus*. Bones of *Camelops minidokae* somewhat lighter than *C. hesternus* and *Camelus bactrianus* and little if any stockier than in *Pliauchenia* from Hemphill; *C. hesternus* approximately equal in stockiness to *Paracamelus* from Hemphill.

Discussion.—A statistical evaluation of the late Tertiary and Quaternary camelids, based on a master accumulation of materials from various institutions in the United States (following Simpson and Roe's formulae), would undoubtedly be enlightening; but such an endeavor is beyond the scope of the present study. It may be stated as a generalization that there are very few characters of the appendicular skeleton of *Camelops* which are peculiar to this genus. On all genera the articular areas, tuberosities, and other characters are of nondistinctive orientation and configuration.

Humerus.—*C. minidokae* equal in stockiness to *C. hesternus* but much smaller; *C. hesternus* much smaller than published measurements of *Gigantocamelus*; no character difference other than size between *C. minidokae* and *C. hesternus*.

TOTAL LENGTH OF HUMERI

<i>C. minidokae</i> , U.C.M.P. no. 38502.....	350
<i>C. hesternus</i>	420
<i>Gigantocamelus spatula</i> ^a (3 specimens)	427-550
<i>G. fricki</i> ^b	497

^a From Meade (1945).

^b From Barbour and Schultz (1939).

Metacarpals.—North American genera considered to differ from *Camelus bactrianus* by lesser divergence between unfused distal third and fourth metacarpal eminences and by relatively smaller transverse diameter at proximal end.

Carpals.—*Paracamelus* from Hemphill fauna differs in minor detail and proportion from both *C. hesternus* and *C. minidokae*, but amount of variation within any of species concerned is unknown; paracamelid carpals at hand invariably larger than those in *C. hesternus* and almost one-half larger than *C. minidokae*; unciform and pisiform differ most between the species; unciform of *Paracamelus* more elongate anteroposteriorly and less triangular in outline from proximal or distal view; posterior eminence of unciform of *Paracamelus* more constricted from remainder of bone than in species of *Camelops*; pisiform of *Paracamelus* more nearly square in outline from lateral view, much thicker on its dorsoposterior border.

Femur and tibia.—*C. minidokae* same proportion as *C. hesternus* but smaller. *C. minidokae* with longer and relatively stockier tibia than *Pliauchenia* from Hemphill.

TOTAL LENGTH OF FEMUR

<i>C. minidokae</i> , U.C.M.P. no. 38507.....	500±
<i>C. hesternus</i>	630
<i>Gigantocamelus spatula</i> ^a	628
<i>G. fricki</i> ^b	563

^a From Meade (1945).

^b From Barbour and Schultz (1939).

TOTAL LENGTH OF TIBIA

<i>C. minidokae</i> , U.C.M.P. no. 38510	470
<i>C. hesternus</i>	530
<i>Gigantocamelus spatula</i> ^a	585
<i>G. fricki</i> ^b	477
<i>Pliauchenia</i> , U.C.M.P. no. 31091	395

^a From Meade (1945).^b From Barbour and Schultz (1939).

Tarsals, metatarsals, and phalanges.—Calcaneum of *Camelops*, particularly *C. hesternus*, tends to be relatively shorter and stockier than in *Paracamelus*, *Pliauchenia*, and *Procamelus*; calcaneum, astragalus, and other tarsals of *C. minidokae* intermediate in size between *C. hesternus* and *Pliauchenia*, or between *Paracamelus* and *Procamelus*; articular facets of tarsals show no generic or specific peculiarities; phalanges of *C. minidokae* undifferentiated as to front or hind feet.

TOTAL LENGTH OF METATARSALS

<i>C. minidokae</i> , U.C.M.P. no. 38465	370
<i>C. hesternus</i>	395
<i>Gigantocamelus spatula</i> ^a (5 specimens)	402-438
<i>G. fricki</i> ^b	404

^a From Meade (1945).^b From Barbour and Schultz (1939).

STATUS OF THE GENUS CAMELOPS

The genotypic species of *Camelops* is *C. kansanus* Leidy (1854f). The species was based on a left premaxillary-maxillary fragment containing the base of the third incisor and the anterior border of the alveolus for the canine. The specimen was discovered "in the gravel drift of Kansas territory" (Leidy, p. 172). The type was subsequently figured by Merriam (1913b, p. 317, fig. 10, a, b). Differentiation of the Kansas specimen from the llama and true camel was based on a relatively great distance between the two alveoli represented.

Most of the species referred to the genus date from a very early time in the history of North American paleontological writings. Hay (1927d) was apparently the last writer to propose a new species, although hundreds, perhaps thousands, of specimens have been found in the last twenty years. *Eschatius conidens* Cope (1884g) probably belongs in the genus *Camelops*. Troxell (1915a) and Riggs (1945) have referred deciduous *Camelops* dentitions to "*Eschatius*." *Camelus maximus* Hay (1921a) and *Camelus arctoamericanus* Hay (1921a) are referable to *Camelops*. *C. maximus* and *C. arctoamericanus* were each based on an isolated first phalanx. These two bones are broader than many *Camelops* phalanges, but the proximal phalanges of *Camelops hesternus* from Rancho La Brea (U.C. 2051, 7-C-18') are of the same proportions. There are no characters, such as posteroproximal extension of the distal articular surface (one of Hay's main diagnostic criteria), which can be justifiably used to distinguish *Camelus* from *Camelops* by phalanges alone. I cannot agree with Hay either that these two bones merit a species separation or that they rate even a species designation, although they are of somewhat differing proportion and came from widely separated localities. The other North American

record of *Camelus* (*Camelus americanus* Wortman, 1898a), which was also listed by Hay (1930a), has been shown to be *Tanupolama* by Stock (1928c, p. 37).

The type of the genotypic species is so devoid of diagnostic characters that no specimen found can be referred to it with any certainty. Selection of topotypes is impossible because the locality of *C. kansanus* is indeterminable. It is therefore proposed to relegate the species name *kansanus* to the position of a *nomen vanum*.¹

The large camelid from Rancho La Brea is represented by an abundance of material in varying stages of growth and is unexcelled in quality of preservation. This camelid will serve admirably as a standard of reference to generic characters within the genus *Camelops*. Merriam (1913b, pp. 320-321) chose to refer the camelid from Rancho La Brea to *Camelops hesternus* (Leidy) on the basis of very close similarities in dentition with the type of that species. He noted that *C. hesternus* might be synonymous with the previously described *Auchenia californica* Leidy, but recognized the name *C. hesternus* as specifically distinct because of the supposed Tertiary occurrence of *Auchenia californica* (= *Camelops californicus* according to most authors). In the light of present data on "*A.*" *californica*, the question of synonymy of the two species must remain unanswered. Merriam (1913b, p. 318) has stated that there might be uncertainty whether or not the lower teeth of the type of *C. hesternus* all belong to one individual; but he concluded that only one individual was represented. A left jaw of *C. minidokae* from Irvington, U.C.M.P. no. 38449, which is in the same stage of wear as the type of *C. hesternus*, was dissected in order to show the complete aspect of the four cheek teeth. (See fig. 23.) Comparison of the Irvington jaw with Leidy's figure shows that the general appearance of the teeth and, in particular, the relative height of the crown of the teeth in both jaws is about the same. Merriam's conclusion is therefore supported.

I incorporate an expanded description of the cranium and mandible of *Camelops hesternus*, hoping that such a description will be of use to future workers who may recover isolated camelid material from the terrestrial Pleistocene of North America.

Camelops hesternus (Leidy 1873b)

Type.—Left lower cheek-tooth series from one individual and an upper molar thought to be from same individual.

Type locality.—Livermore Valley, California.

Referred specimens.—Complete skull and almost complete mandible, U.C.M.P. no. 20040, Rancho La Brea, Pleistocene. Complete skull and mandible, U.C.M.P. no. 20028, Rancho La Brea, Pleistocene. Front and hind leg assembly, U.C.M.P. no. 22263, Rancho La Brea, Pleistocene.

Description.—Modified after Leidy (1873b) and Merriam (1913b).

Cranium and mandible.—Rostrum tapers less abruptly toward anterior end than in *Camelus*, similar to *Lama*; frontal convex transversely with no median depres-

¹ A paramount objection to this treatment will be that such a revision cannot be allowed if the holotype still exists. It will be argued that a generic name must remain with the type of the genotypic species and, if the type species is indeterminate, the genus also is indeterminate. If the rules were so rigidly applied, the name *Camelops*, as well as most of the other names in vertebrate paleontology, would have to be set aside. There seems adequate reason to believe that all the materials which have been referred to *Camelops* in the literature are indeed congeneric. It is highly desirable to retain the well-known name *Camelops* because of the established usage of this name. I propose therefore to make *Camelops* an example wherein the type of a genotypic species shows distinct generic character but is not a distinct species.

sion; orbit relatively far toward posterior, with anterior border above M^2 ; basi-cranial and basifacial axes nearly parallel; nasals long and narrow, separated posteriorly by a wedge of frontals, in broad contact with premaxillaries anteriorly; large and deep fossa near upper margin of each maxillary above P^4 , inferior portion of this fossa not sharply marked, upper wall abrupt or formed into sharp overhanging ridge; lachrymal vacuities large and subtriangular in outline; anterior end of zygomatic process of squamosal heavy and of relatively great vertical dimension as in *Lama* and in contrast to *Camelus*; upper cheek-tooth series more parallel to each other than in *Camelus*; internal choanal opening V-shaped and relatively attenuated; basisphenoid and presphenoid form more distinct ridge than in *Camelus*; ventral projections of alisphenoids less divergent than in *Camelus*; glenoid fossa of same form as in *Lama* and without the ventroexternal projections seen in *Camelus*; paroccipital process relatively long and thin and with pronounced anteriorly directed hook; less separation of paroccipital and mastoid plates than in *Lama* or *Camelus*; occiput resembles *Camelus* and lacks strong median crest on supraoccipital region seen on *Lama*; lateral foramina of occiput lie in large and deep fossa, which notches lateral margin of occiput; frontal foramina relatively far apart but with only faint indication of channels which lead anteriorly from these foramina on *Lama*; infraorbital and supraorbital foramina nondistinctive in size and position; incisive foramina extend through distance from I^3 to C, being relatively longer than in *Camelus* or *Lama*; palatine portion of maxillaries extends as far anteriorly as front border of incisive foramina; length of mandibular symphysis about 120 mm. on three specimens, shorter than in *Camelus*, approximately one-fourth to one-fifth total length of jaw as in *Lama*, in contrast to approximately one-third ratio of *Camelus*; ventral border of horizontal ramus convex as in *Lama*; posteroventral border of jaw more rounded than in *Camelus*. For measurements of skull see Merriam (1913b, p. 313).

Dentition.— $I \frac{1}{3}$; $C \frac{1}{1}$; $P \frac{2}{1}$; $M \frac{3}{3}$.

P^1 does not protrude through palate, but causes development of bony papilla on diastem at point approximately one-third of distance from caniniform tooth to P^3 ; I^3 larger than C, laterally compressed, curved posteriorly, lanceolate; C less lanceolate than I^3 ; P^3 with narrow bladeliike crown and with small heel-like cusp or ridge posterointernally; P^4 quadrate, submolariform, with two selenes, more hypsodont than in *Lama*; upper molars with less prominent styles and external ribs than *Lama* but more prominent parastyles and ribs than *Camelus*; mesostyles tend to reflect anteriorly in contrast to *Camelus*^{*}; M^1 more hypsodont than in *Lama*, anterior lobe with somewhat greater transverse diameter than posterior lobe, parastyle less prominent than mesostyle, metastyle inconspicuous, anterior rib stronger

^{*} I am not sure that either of the canine teeth of this formula are actually canines. Stock (1928c) demonstrated that the tooth in this position in *Tanupolama* is an anterior premolar. A *Camelus bactrianus* jaw in the University of California collection also has an incisiform canine and a caniniform premolar. Meade (1945, pp. 537-538) noted, however, that in a specimen of *Camelops* from the Blanco there is a small caniniform premolar posterior to the main caniniform tooth. A papilla representing a rudimentary premolar lies posterior to the lower caniniform tooth on certain of the *Camelops* jaws from Rancho La Brea, but there is no evidence of an incisiform canine on any of these jaws.

^{*} This character was demonstrated by Lull (1921b, p. 170).

than posterior rib; M^2 with anterior lobe of greater transverse diameter than posterior lobe, parastyle about as strong as mesostyle, metastyle conspicuous; anterior rib stronger than posterior rib; M^3 of same general proportions as in *Lama* and *Camelus*, parastyle stronger than mesostyle, metastyle may be drawn out into prominent wing, anterior rib slightly more prominent than posterior rib. Lakes of upper cheek teeth apparently well filled with cement at time teeth are approximately one-third worn down. Lower incisors about like *Lama* except I_3 as large as, or only slightly smaller than, I_1 and I_2 ; lower C laterally compressed, lanceolate; P_4 wedge-shaped and approximates form of P_4 in *Lama*, with deep enamel fold posteriorly but medial side without deep folds seen in *Lama*; M_1 and M_2 with inner vertical groove between anterior and posterior lobes intermediate in depth between deep groove of *Lama* and shallow groove of *Camelus*; stylids and inner ribs of lower molars very inconspicuous as compared to either *Lama* or *Camelus*, M_2 and M_3 without any indication of anteroexternal pillar of *Lama* and *Tanupolama*; M_3 with posterior lobe aligned in anteroposterior axis with anterior lobes in contrast to *Camelus*, and relatively less constricted from middle lobe than in *Lama*. For detailed measurements see Merriam (1913b, p. 316).

EVALUATION OF PROPOSED SPECIES OF CAMELOPS

Camelops huerfanensis (Cragin, 1892a) was described from part of a palate and mandible, part of the occiput, fragments of the brain case, distal ends of a metapodial, and one proximal phalanx. The material was collected from beds of volcanic ash on a tributary of the Huerfano River, Huerfano County, Colorado. Hay (1913d, pp. 267-278) added appreciably to the description of this species. In general, *C. huerfanensis* is of the size and proportion of *C. hesternus*. Differentiation of the two species has been based on the following points:

Nasal border of premaxilla strongly concave in *C. huerfanensis* (Hay, 1913d); posterior palatine foramina opposite M^1 in *C. huerfanensis* instead of opposite P^2 or P^4 as in *C. hesternus* (Hay, 1913d); metastyle of M^3 bent strongly mesiad in contrast to *C. hesternus* (Hay, 1913d); upper canine emerges immediately behind incisor in *C. huerfanensis*²⁰ (Hay, 1913d); lower border of mandible from symphysis to point below last molar nearly straight in *C. huerfanensis*, strongly convex in *C. hesternus* (Hay, 1927d, pp. 87-88).

C. huerfanensis will be regarded as a distinct species which is rather closely related to *C. hesternus*. These two camelids, both of "gigantocamelid" dimension, are the largest of the described Pleistocene tylopods.

Camelops huerfanensis dallasi Lull (1921b) was described from three separate portions of a skull with an almost complete dentition. The type material, along with appendicular elements, was obtained from sands and gravels bordering the Trinity River (Lagow sand pit), East Dallas, Texas. Most of Lull's description was a comparison of his specimen with *Camelus* and *Lama*, and no attention was given to relationships with previously described species of *Camelops*, other than

²⁰ If this character is valid, *C. huerfanensis* is certainly unique among the known materials representing *Camelops*. Stirton (oral communication, 1948) has pointed out that if two teeth did emerge in juxtaposition in this specimen, they may represent the anomalous twinning of a single tooth bud in an early stage of development. A twinned condition of this sort is exhibited in a mandible of a Recent *Camelus* (U.C.M.P. no. 22849).

C. huerfanensis. The Dallas specimen is a large camel, falling into the size group of *C. huerfanensis* and *C. hesternus*. It was separated from *C. huerfanensis* because of differences in details of the occiput, the presence of diastemata between I^3 and the canines, and in the larger size of the metastyle of M^3 . The description of this subspecies, as published by Lull, could very well apply to *C. hesternus*; but since I have not examined the material I shall follow Lull's reference of the specimen to *C. huerfanensis*.

Camelops sulcatus (Cope, 1893a) was described as "*Holomeniscus*." The type is a left lower jaw fragment with a complete cheek-tooth series which was obtained from Pleistocene deposits in Austin County, Texas. This is a smaller *Camelops*; it falls into the lower size range of known specimens of *C. hesternus* Leidy from Rancho La Brea and is much smaller than known materials of *C. huerfanensis*. It differs from published figures of other species in its broadly rounded yet deep grooves on the inner faces of M_1 and M_2 , although it is approached in this character by a specimen of *C. hesternus* (U.C.M.P. no. 20028). The type of *C. minidokae* and the *C. minidokae* materials from Irvington are in the same size group, but differ from this Texas specimen in having a sharp groove bordered anteriorly by a ridge on the internal face of the first and second molars. Hay (1927d, p. 93) noted this distinction in his comparison of *C. minidokae* to *C. sulcatus*. *C. sulcatus* is outside the demonstrable limits of variation of the known materials representing other species and will be regarded as a separate and valid species.

Camelops minidokae Hay (1927d) was designated from a fragment of lower jaw with cheek-tooth series taken from a bed of gravel overlain by a lava flow, near Minidoka, Idaho. Hay referred the bones and teeth from at least four individuals to the species. In an earlier publication he had identified this material as *C. huerfanensis*, but the fact that it was consistently smaller in size than the type of *C. huerfanensis* finally convinced him that the Minidoka camelid was a new species. *C. minidokae* was distinguished from *C. sulcatus* by the presence of a median groove on the internal face of the lower molars which is bordered anteriorly by a styloid. It can be demonstrated with a series of jaws from the Irvington fauna that this character is somewhat variable, but the fact remains that *C. minidokae* may have been consistently distinct from *C. sulcatus*, *C. huerfanensis*, and *C. hesternus* in this configuration.

?*Camelops arenarum* Hay (1927d) was described on the inner part of the trochlea of the left humerus and the scaphoid and lunar bones of the right side. Material was collected from the Idaho formation at Froman Ferry, Canyon County, Idaho. Hay (p. 105) states that he would have referred this material to his "*Camelus maximus*" if it had been found in a deposit of unquestionable Pleistocene age. Evidently, Hay himself did not feel that there was any diagnostic morphology of the type. He attempted no definition of the species other than measurements, and these measurements are bracketed by the dimensions of like elements of the Rancho La Brea camelid. The name *C. arenarum* is therefore considered a *nomen vanum*.

Camelops aransas Hay (1926c) was described from a fragment of the right lower jaw containing the three molars. The material was collected in San Patricio County, Texas. The teeth are well worn; fossettes are obliterated. The broadly rounded outer lobes separated by relatively narrow valleys and the relatively flat inner

faces of these teeth were the characters used to distinguish this specimen from other species. Hay again noted that the specimen might belong to the genus *Camelus*.

Flatness of the inner face of the molars and lack of prominent styles are definitely not peculiar to this specimen. *C. hesternus* is typically of this conformation. Broadness or roundness of the outline of the outer lobes is to a large degree a function of tooth wear. All the lobes appear to become most rounded at about one-half of the total crown height. *C. aransas* Hay can be referred to either *C. huerfanensis* or *C. hesternus*, although it may have been smaller than modal individuals of either species. *C. aransas* is considered to be a *nomen vanum*.

Camelops nevadanus Hay (1927d) was described from materials collected in the canyon of the Walker River, 8 miles north of Schurz, Mineral County, Nevada. Hay's description is confusing. A dorsal vertebra, ulnoradius, sternal bones, and proximal end of a right metatarsal are designated as the type material for the species; yet he states that a fragment of a second lower molar which was found 1 mile south of the type locality determines the species as new.

This Nevada camelid is in the *C. hesternus*-*C. huerfanensis* size group and can be compared favorably with either species. The lack of diagnostic characters of any less than generic magnitude on the described material makes it requisite to designate *C. nevadanus* as a *nomen vanum*.

Camelops niobrarensis (Leidy, 1858e) was based upon two lower molars in a jaw fragment. Leidy himself noted (1869a, p. 161) that ". . . the grounds of its distinction are of a meagre character." This was apparently a large camelid comparable in size and in attributes of isolated teeth to either *C. hesternus* or *C. huerfanensis*. The lack of any character which might be consistently distinct makes *C. niobrarensis* another *nomen vanum*.

Camelops nitidus Hay (1920b) was proposed for a M_1 from near Afton, Oklahoma. His diagnosis of the species was (p. 123): "An animal of medium size. First lower molar as in *Auchenia*, except that the anterior outer style is missing." This diagnosis applies to any medium-sized *Camelops* M_1 . Hay's figure is no more definitive than is his description. *C. nitidus* can only be regarded as a *nomen vanum*.

Camelops vacondae Hay (1927d).—Hay decided that a first lower molar which had formed part of the type of *Megalomeryx niobrarensis* Leidy (1858e) was worthy of a separate specific status, *C. vacondae*. He noted that the inner face of this tooth showed feeble or no styles and that the outer faces of the lobes were broadly rounded. He also stated that this tooth might really be a *Camelus*. As is evident from Hay's discussion, there is nothing distinctive about the tooth. It is simply a large *Camelops* of the *C. hesternus*-*C. huerfanensis* group so far as the evident characters are concerned. I regard *C. vacondae* as a *nomen vanum*.

It is concluded that the genus *Camelops*, as known at this time, should include the following species which may be given zoological usage:

- C. kansanus* Leidy (type of the genus)—Species is a *nomen vanum*. "Kansas Territory"
- C. hesternus* (Leidy)—Livermore Valley, California
- C. huerfanensis* (Cragin)—Huerfano County, Colorado
- C. sulcatus* (Cope)—Austin County, Texas
- C. minidoka* Hay—Minidoka, Idaho

The species of *Camelops* seem divisible into two groups. These groups are separable mainly on a difference in size; but this size difference is supported by a dental character, or characters, peculiar to each of the species. The *C. hesternus*—*C. huerfanensis* group contains the larger-sized individuals; the *C. sulcatus*—*C. minidokae* group evinces smaller individuals. As would be expected, and even with the relatively poor representation available from the fossil record, there is no sharp boundary of size and dental character between these groups or between any two species. Any attempt to refer an isolated skeletal part or tooth to one of these species is insupportable in the light of our present knowledge about the genus.

Tanupolama Stock, slender camelid

(Fig. 24)

Right maxillary bone, U.C.M.P. no. 38511, with somewhat broken M^2 and M^3 and complete M^1 ; two metatarsal bones of juveniles, U.C.M.P. nos. 38512 and 38513; distal end of another metapodial.

Discussion.—The genotypic species *T. stevensi* (Merriam and Stock) is based on materials which are, rather uniquely, the best specimens representing the genus. Stock (1928c) believed that *Camelus americanus* Wortman (1898a) from the Hay Springs quarry of Grayson, Nebraska, belonged in the genus *Tanupolama*. Schultz and Stout (1948, p. 566) follow Stock's proposal and refer to the materials from the Hay Springs and Rushville localities as *Tanupolama americanus* (sic). *T. americana* seems clearly distinct from the genotypic species in its proportions and in the curvature of the mandible. Simpson (1929h, pp. 593–596) distinguished the species *T. mirifica* Simpson from Pinellas County, Florida, on characters of the associated lower and upper cheek teeth.

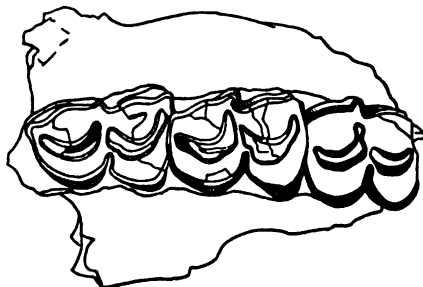


Fig. 24. *Tanupolama*, occlusal view of fragment of right maxilla with M^1 to M^3 inclusive, U.C.M.P. no. 38511, loc. V3604. $\times \frac{3}{8}$.

Cope's (1893a, pp. 85–86) *Holomeniscus macrocephalus* from Texas is equal in size and similar in proportions to *T. americana*; but the anteroexternal stylids of M_2 and M_3 are missing or were so small as to be overlooked by Cope in his illustration. *Auchenia vitakeriana* Cope (1878h) is referable to *Tanupolama* on the basis of its size, but Cope's meager description permits no adequate comparisons and there is no figure of the type.

The Irvington *Tanupolama* cannot be compared with *T. americana* because the type of *T. americana* is a lower jaw and no topotypal material from Hay Springs has yet been described. The Irvington material does show generic identity with *T. stevensi* and with *T. mirifica*. In these species the external ribs and styles on the upper molars are less pronounced than in *Lama*. Part of Simpson's (1929h) differentiation of *T. mirifica* from *T. stevensi* is the more sharply folded external surfaces of the upper molars from Florida. There is too much broken away from the outside in the M^1 from Irvington for an evaluation of this character, but the

external surfaces of M^1 and M^2 are as flat as in *T. stevensi*, if not flatter. The ribs, particularly, are less pronounced than in *T. mirifica*, although this is explained in part by a marked decrease in sharpness of external folding near the base of the molars in *Tanupolama*, and the Irvington teeth are more worn than the *mirifica* teeth. Simpson observes that the maximum length (anteroposterior diameter) and breadth (transverse diameter) on the *T. mirifica* upper molars are about equal. Except for M^3 , this is probably a generic character which is common to all the species. Stock's measurements of two specimens show that the breadth may actually exceed the length in late stages of wear in M^1 and M^2 but is noticeably less than the length on three specimens of M^3 . *Tanupolama* from Irvington shows the relatively greatest transverse diameter on M^1 , but all the molars are longer than wide. Simpson gives no measurements, but his figures show that the Florida molars are somewhat smaller in all diameters than the Irvington teeth.

COMPARATIVE MEASUREMENTS

	<i>T. stevensi</i>			<i>Tanupolama</i> Irvington
	No. 3	No. 4	No. 5	No. 38511
M^1 , greatest anteroposterior diameter....		23.0	19.4	22
M^1 , greatest transverse diameter.....		21.0	25.8	21
M^2 , greatest anteroposterior diameter....	29.7	28.7	23.9	27
M^2 , greatest transverse diameter.....	17.0	19.0	25.3	26
M^3 , greatest anteroposterior diameter....	31.4	27.7	31.3	29
M^3 , greatest transverse diameter.....	15.5	15.8	23.9	19
Apparent age of individual.....	Very young	Mature	Old	Mature

Measurements of the Irvington molars, as compared to Stock's measurements of *T. stevensi*, show that the two are about the same size. A comparison of the metatarsal from Irvington with Stock's figured specimen (an adult), and with an adult metatarsal from McKittrick, in the University of California collection, is not particularly revealing, since the Irvington material is juvenile. Such comparison shows, however, that there is great variation in the metapodials of *Tanupolama* in all the faunas.

?*Lama hollomani* was described by Hay and Cook (1930, pp. 21-23) on the basis of a broken metatarsal from the Pleistocene fauna near Frederick, Oklahoma. Referred to this species was a fragmentary lower jaw. Hay and Cook estimated the restored length of the metatarsal at 262 mm., equaling the length of *Lama*. This bone could have been much longer; the entire center section is missing. It seems very unlikely, moreover, that the South American genus would appear only at Frederick and in no other locality in the United States. I believe that ?*Lama hollomani* is referable to *Tanupolama* and that the species name is a *nomen vanum*; for the Frederick bone displays no definitive characters.

Interesting complications have arisen in regard to the nomenclature of Blaccan representatives of the genus *Tanupolama*. Gazin (1942b) has attempted to substantiate the species *T. longurio* (Hay) from Anita, Arizona, by reference of more complete material from a stratigraphically and geographically related locality

(Curtis Ranch) to this species. Hay's species was based on "a right hinder cannon bone, lacking the lower split end" and Gazin's materials were lower jaws and a maxillary; until more material is available from Hay's locality, no direct comparisons could or can be made. Hay's cannon bone offers no traits worthy of a species diagnosis, and *T. longurio* should be considered a *nomen vanum*. If the Curtis Ranch jaw is distinct from the other species (Gazin tentatively distinguished it from *T. stevensi*, *T. americana*, and *T. mirifica*), I believe a new name is necessary for it.

Meade (1945) described a new species, *T. blancoensis*, from the Blanco fauna. Types of this species were parts of lower jaws and a maxillary. Meade made no comparisons with the Blancan mandible that Gazin had described from Arizona. The figures indicate that the Arizona jaw is more like *Lama* in the prominence and sharpness of the anteroexternal and anterointernal styliids of M_3 .

It seems quite likely that there is much synonymy among the species of *Tanupolama*. If there is individual variation in *Tanupolama* as in *Camelops*, which is demonstrated in *C. minidokae* from Irvington and *C. hesternus* from Rancho La Brea, very little speciation is justified. Until such a probable variability is demonstrated by a series from one species in a given fauna, nothing is to be gained by a lumping of the proposed names.

ANCESTRY OF TANUPOLAMA, LAMA, AND CAMELOPS

Conclusions about the ancestry of *Camelops* are little more than possible combinations of unknowns and variables and, in this sense, are hardly worthy of formulation; yet the perplexing problem has attracted and probably will attract the attention of paleontologists in the ensuing years. *Camelops*, *Lama*, and *Tanupolama* have been considered to be more closely related to each other than to *Camelus*; although, admittedly, *Tanupolama* forms a uniquely long-limbed member and *Lama* a very small member of this otherwise closely knit group. This llama-like group from the Blancan and Pleistocene of the Americas is set apart from the species of *Camelus* of the Pinjor to Recent in Eurasia-Africa on the basis of elongate skull proportions, peculiar dental traits (in which *Camelops* bridges the gap between *Camelus* and *Lama*), obliquity of the posterior outline of the lower jaw, and perhaps nonuniformly less transverse expansion of the distal extremity of the metapodials.

The fossil record indicates that all the camelids of the late Pliocene, Pleistocene, and Recent must have come from North American earlier Pliocene ancestry. The search for an ancestral type for *Lama* and *Tanupolama* among the known Hemphillian and Clarendonian assemblages proves to be fruitless if one wishes to find a small, slender-limbed, pre-llama type of animal. Hemphillian materials which have been referred to *Pliauchenia* serve admirably for a structural type ancestral to both *Camelops* and *Camelus* but are unsuitable as ancestors for *Lama* and *Tanupolama*, unless one assumes a great and sudden reduction in massiveness and a sudden decrease in length of leg bones. Although it is established that an increase in size is not a universal tendency of evolution—dwarf faunas are known—it seems unlikely that the evolutionary trend of increase in size would completely reverse itself at this time.

There seems very little to favor either *Pliauchenia* or *Procamelus* of the Clarendonian assemblages as the likely ancestor for *Camelops*. Gregory (1942b) has demonstrated that both *Procamelus* and *Pliauchenia* at that time can have an unreduced premolar formula, although one of the diagnostic characters of *Pliauchenia* is its relatively reduced formula. The relationship of the Middle Pliocene camelids which have been called *Pliauchenia* to the Lower Pliocene forms is uncertain. It is even possible that *Procamelus* of the Lower Pliocene underwent a reduction of premolars paralleling *Pliauchenia* and that both genera are now included under the latter name in Hemphillian faunas. *Pliauchenia magnifontis* Gregory is, however, a suitable prototype for the Hemphillian species of *Pliauchenia*. It seems best at the present time to let the Hemphillian *Pliauchenia* be represented by dentitions with reduced premolar formulas. This *Pliauchenia* is distinct from materials now called *Paracamelus* only by a smaller modal size. Some of the jaws from the Clarendonian and Hemphillian which have been identified as *Paracamelus* or *Alticamelus* could also be ancestral to *Camelops*.²¹ Very little evolutionary change is required, however, to produce either *Camelops* or *Camelus* from the medium-sized Hemphillian *Pliauchenia*. If this phyletic sequence is actually true, it must be deduced that *Camelops* is similar to *Lama* and *Tanupolama* only by parallel development of similar structures. In like fashion, *Tanupolama* may resemble *Lama* only through parallelism.

The opinion might be offered that the relatively small, long-limbed, and brachydont camelids which have at times been called "*Altomeryx*" or "*Leptotylopus*"²² could be in a phyletic grouping with *Tanupolama* and *Lama*. There is scarcely enough material from this slender-limbed group to sustain conclusions. The brachydont dentitions, which might have stemmed from *Miolabis* of the Clarendonian, are not definitely associated with elongate skeletal elements.

Odocoileus Rafinesque, deer

(Fig. 25)

Basal portion of right antler with attached fragment of frontal bone, U.C.M.P. no. 38590; as in *Odocoileus hemionus* (Rafinesque), U.C.M.P. no. 10992, Irvington bone with knobbed portion of frontal forming base of antler and part of orbital vacuity formed by frontal immediately anteroventral to antler base; Irvington antler oval in cross section at base, flattened anteroposteriorly; approximately 60 mm. above point of union with frontal, antler bears medially projecting tine; distal tip of tine broken off.

Tetrameryx irvingtonensis Stirton, antilocaprid

(Figs. 26, 27, 28, 29, 30, 31, 32)

The type of Stirton's species, *T. irvingtonensis*, is a portion of a right horn core,

²¹ For an expansion of this concept and a critical review of the validity of the name *Paracamelus* see Macdonald (1951), Pliocene Mammalian Faunas of West Central Nevada (in press).

²² I am informed (Stirton, oral communication, 1948) that Matthew was thinking of the *Pliauchenia*-like camelid with hypsodont teeth from Hemphill when he listed the name "*Leptotylopus*." Meade (1945) is not justified in applying this name to the slender-limbed form from the Blanco fauna. Both "*Altomeryx*" and "*Leptotylopus*" are *nomina nuda*. Hibbard and Riggs (1949, p. 855) have already corrected Meade's usage of "*Leptotylopus*."

including the "basal two-thirds of anterior tine, part of posterior tine, and part of orbit." Paratypes were part of another right horn core, part of a left horn core, and two-thirds of a left metatarsal. Since Stirton's publication (1939*d*), a more complete assembly of bones representing this species has been obtained and further



Fig. 25. *Odocoileus*, anterior view of fragment of right antler, U.C.M.P. no. 38590, loc. V3604. $\times \frac{2}{3}$.

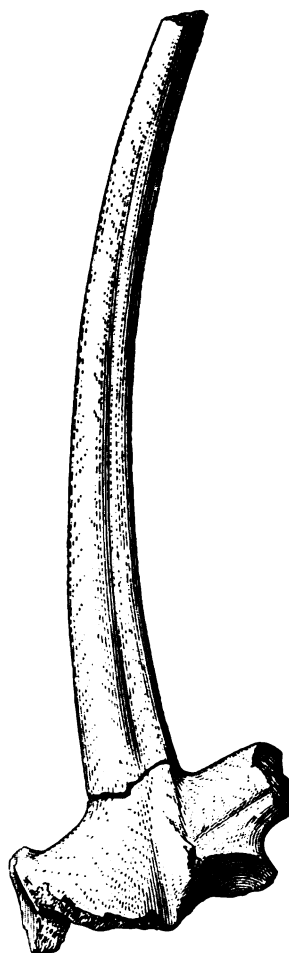


Fig. 26. *Tetrameryx irvingtonensis*, view of right side of cranial fragment including almost complete posterior tine, U.C.M.P. no. 39061, loc. V3604. $\times \frac{1}{4}$.

details may be added. Topotypal material now available for study includes a left maxilla with complete cheek-tooth series, three skulls (brain-case region only), several frontal bones and basal horn core fragments, two lower jaws with cheek-tooth series, a complete right metatarsal, fragments of metapodials, proximal part of a tibia, and a lumbar vertebra.

Description.—Angle of bifurcation between anterior and posterior tine ranges from 55° to 70° (U.C.M.P. nos. 38527, 38334, 37730), this angle only 25° on cast

COMPARATIVE MEASUREMENTS OF HORN CORES^a

	<i>T. irvingtonensis</i>							<i>T. shufeldti</i>
	Holotype no. 32872	No. 32871	No. 38515	No. 38334	No. 38328	No. 37730	No. 38327	
Anteroposterior diameter at base of anterior tine...	40	32	41	37	39	39	37	30
Transverse diameter at base of anterior tine.....	25	22	24	25	21	24	24	17
Anteroposterior diameter at base of posterior tine.	44	..	40	36	38	40	38	30
Transverse diameter at base of posterior tine.....	26	..	27	28	24	27	28	(from cast) 24

^a These measurements will probably vary from 3 to 6 mm. depending on the exact orientation of the measurements. An attempt has been made to take all measurements in the exact anteroposterior direction and in transverse direction in respect to the long axis of the skull, at a level on the line opposite the dorsal line of union of the two tines, parallel to the plane of the snout.

of type of *T. shuleri* Lull; anterior tines of mature animal (U.C.M.P. no. 37730), at least as long as, and perhaps slightly longer than, in Stirton's restoration (1939d, figs. 80, 81); upper tips of all tines of *T. irvingtonensis* broken off before or during deposition; but restorations based on decrease in diameter allowing for more abrupt taper at tips indicate posterior tines 13 inches (approx. 300 mm.) long and anterior tines at least 10 inches (approx. 230 mm.) long; no other described antilocaprids of Pleistocene approach *T. irvingtonensis* in length of horns, particularly in development of anterior tines; in *T. shuleri*, posterior tine groove begins in external position at base, spirals to anterior position near mid-length, and becomes external again at tip; *T. irvingtonensis* groove like that in *T. shuleri*, but never attains a comparable degree of anterior position; sulcus on anterior horn cores of *T. irvingtonensis* lies slightly to posterior as it approaches tip of tine; stockiness of *T.*

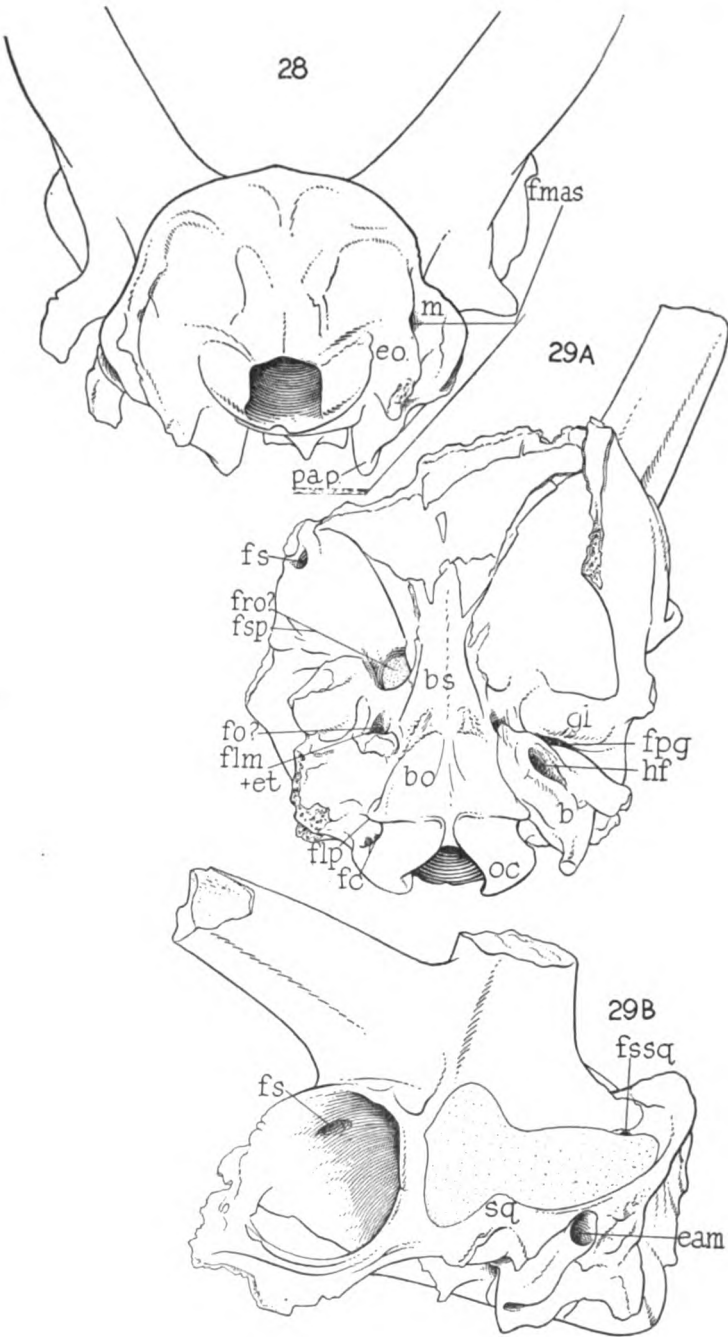


Fig. 27. *Tetrameryx irvingtonensis*, occlusal view of right maxilla with P³ to M³ inclusive, U.C.M.P. no. 38514, loc. V3604. $\times 1$.

irvingtonensis horn cores remains very constant; see comparative measurements of horn cores of *T. irvingtonensis* and *T. shuleri*.

Observation by Stirton that both anterior and posterior tines bear oval cross section at base and gradually change to circular cross section toward tips is corroborated by examination of about twenty incomplete horn cores; both anterior and posterior tines curve slightly toward median line of skull and toward anterior; posterior tines more erect, pointing almost dorsally from skull cap; anterior tines diverge more toward sides of skull and point anterolaterally; entire orientation and curvature of horn cores in *T. irvingtonensis* is quite different from *T. shuleri*; distance between two anterior tines at a distance of 110 mm. from orbital rim (length of anterior horn cores of *T. shuleri*) approximately 200 mm., whereas width between tips of anterior tines of *T. shuleri* is 178 mm.; distance between posterior tines at a length corresponding to length of posterior tines of *T. shuleri* is about 300 mm. (based on the restoration), about 275 mm. in *T. shuleri*.

Tooth-bearing right maxillary, U.C.M.P. no. 38514, shows same cheek-tooth formula as in *T. shuleri* and *Antilocapra americana* Ord: P = 3, M = 3; Lull noted on *T. shuleri* that M¹ was same size as in *A. americana*, but molars of fossil progressively larger and premolars progressively smaller than in Recent genus; *T. irvingtonensis* with much longer M¹ and M² but with M³ about equal or slightly less in anteroposterior diameter than *A. americana* (U.C.M.V.Z. no. 19321); posterior lobe of M³ in *T. irvingtonensis* relatively shorter than in *A. americana*, though this may be in part a result of greater wear on Recent tooth; premolars as large as



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A. americana or larger, and seem to reduce in size progressively to anterior at equal rate to that in Recent antilocaprid; Lull reported mesostyle on M^3 of *T. shuleri* more pronounced than in *Antilocapra*, but mesostyle on Irvington specimens less pronounced than in Recent genus; *T. shuleri* with external styles on premolars less conspicuous than in *Antilocapra*, *T. irvingtonensis* with premolar styles as prominent as in Recent genus.

Discussion.—Colbert and Chaffee (1939, p. 8) found that the teeth of *Tetrameryx onusrosagris* (synonym of *T. conklingi* Stock, 1930d?) differed little from the Recent *Antilocapra*. Upper dentitions of the Pleistocene and Recent genera do not seem to be a suitable medium for comparative study, with the possible exception of consistently and nonintergrading size difference.

In order that a more complete picture of *Tetrameryx* may be obtained, it is advisable to make a detailed comparison of the brain-case region of *T. irvingtonensis* with corresponding areas of *Merycodus furcatus* (Leidy), U.C.M.P. no. 32308, from the Pliocene Big Spring Canyon fauna, and with *Antilocapra americana* (U.C.M.V.Z. no. 19231). Gregory (1942b, p. 404) has compared *Merycodus* with *Antilocapra* and has shown that the bulla in *Merycodus* suggests that this genus is not far removed from the common ancestry of the Bovidae and Antilocapridae.

Comparisons.—Occiput of *T. irvingtonensis* with smooth margin like *Antilocapra* in contrast to *Merycodus* but more broadly rounded on laterodorsal borders than Recent or Pliocene genus; supraoccipital extends relatively higher above occipital condyles than on other two genera, with *M. furcatus* intermediate in this respect; mastoid process of periotic with semblance of being more completely fused to exoccipital in *Antilocapra*; fossil genera with dorsoventral slitlike groove at union of mastoid and exoccipital making lateral margins of occiput appear as though exoccipital had been pressed outward over mastoid; ridge on exoccipital that internally borders mastoid-exoccipital groove continuous ventrally with paroccipital process; *Antilocapra* with this ridge, but ridge bordered externally by relatively shallow and broad groove; mastoid foramen at dorsal end of this groove in *Merycodus* and *Antilocapra*, but more ventrally situated in *T. irvingtonensis*; paroccipital process shorter and heavier than in either *Merycodus* or *Antilocapra*, extending downward only as far as ventral border of occipital condyles (U.C.M.P. no. 38334); both *T. irvingtonensis* and *A. americana* with separate condylar or condyloid foramen in contrast to *M. furcatus*; posteriorly directed

Fig. 28. *Tetrameryx irvingtonensis*, posterior view of cranium, U.C.M.P. no. 38515, loc. V3604. $\times \frac{1}{2}$.

eo	exoccipital	m	mastoid
f. mas.	mastoid foramen	pa. p.	paroccipital process

Fig. 29. *Tetrameryx irvingtonensis*, U.C.M.P. no. 38334, loc. V3604. $\times \frac{1}{2}$.

a, ventral view of cranium:

b	bulla	flm	medial lacerate foramen	fpg	postglenoid foramen
bo	basioccipital	flp	posterior lacerate foramen	fsp	sphenorbital foramen
bs	basisphenoid	fo	foramen ovale	gl	glenoid fossa
et	eustachian tube	fro	foramen rotundum	hf	hyoid fossa
fc	condyloid foramina	fs	supraorbital foramen	oc	occipital condyle

b, view of left side of cranium:

eam	external auditory meatus	fssq	suprasquamosal foramen
fs	supraorbital foramen	sq	squamosal

foramen lacerum posterius bridged ventrally by exoccipital, this foramen an open groove in *A. americana* and *M. furcatus*; bulla similar to that in *A. americana* and less inflated than in *M. furcatus*; hyoid fossa of bulla longer and deeper pit than in *A. americana*; basioccipital plus basisphenoid element slightly more triangular in outline than in *Antilocapra* and *Merycodus* and marked by a sharper ventral keel in region of union of these two bones; stylomastoid foramen, foramen ovale, foramen lacerum anterius (? and foramen rotundum?), postglenoid fora-

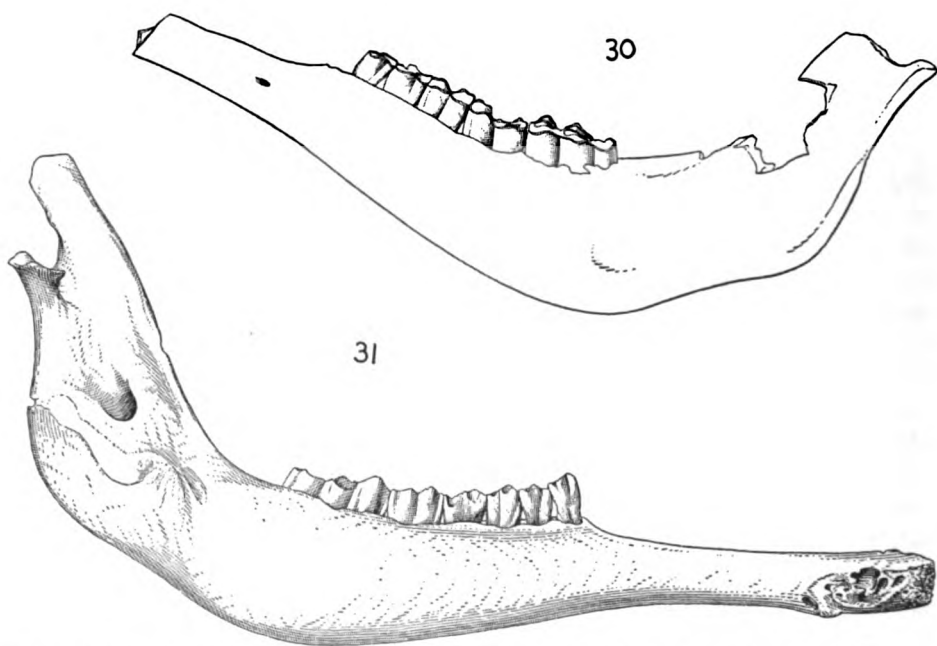


Fig. 30. *Tetrameryx irvingtonensis*, labial view of left lower jaw with P_1 to M_3 inclusive, U.C.M.P. no. 38520, loc. V3604. $\times \frac{1}{2}$.

Fig. 31. *Tetrameryx irvingtonensis*, lingual view of left lower jaw with P_1 to M_3 inclusive, U.C.M.P. no. 39078, loc. V3604. $\times \frac{1}{2}$.

men, suprasquamosal foramen, and optic foramen about same in all three genera; *T. irvingtonensis* unique by its greatly expanded, ventrolaterally projecting process of zygomatic arch located at union of jugal and squamosal; zygomatic process of squamosal with strong inverted V shape when viewed laterally in contrast to moderate outline of other genera; jugal below orbit deeply concave and jugal border of orbit thickened by ridge which ventrally borders rim of orbit in *T. irvingtonensis*.

Discussion.—There are more minor points of similarity in the occiput and basicranium between *Merycodus furcatus* and *Antilocapra americana* than between *M. furcatus* and *Tetrameryx irvingtonensis*. Reduced inflation of the bulla and seemingly minor changes in the zygoma would suffice to make the brain case of *Merycodus* a miniature of either of the later genera.

Mandible.—Heavier and deeper in *T. irvingtonensis* than in *A. americana*, heaviness particularly noticeable in region ventral to M_3 ; process for muscle attachment in mid-region of external jaw surface posterior to M_3 feebly developed as compared with *Antilocapra*; angle more deeply indented than in any compared specimens; M_3 shorter and stockier than in *Antilocapra*, stockiness caused by absence of pointed elongate posterior extension of posterior lobe; external grooves between lobes of M_3 relatively broad and almost U-shaped, axial plane nearly parallel to transverse vertical plane through jaw; in *Antilocapra* these grooves have oblique antero-internal to posteroexternal axial plane; median grooves of internal faces of molars deeper than in *Antilocapra*.

Discussion.—Colbert and Chaffee (1939, p. 8) stated that the lower teeth of *Tetrameryx onusrosagris* Roosevelt and Burden are in general narrower than those of *Antilocapra*, noting that there is considerable range in size of the fossil species resulting in the largest individuals being larger than the pronghorn. The two jaws of *T. irvingtonensis* constitute, for the most part, an exception to Colbert and Chaffee's characterization of the genus *Tetrameryx*. The Irvington jaws have cheek-tooth series which are slightly longer than a compared *Antilocapra*; but within this series some teeth are narrower, some wider, some larger, and some shorter than the correlative teeth in the Recent genus. I feel that differences in antilocaprid lower-jaw dentition make insecure criteria for taxonomic differentiation. The complete right metatarsal, U.C.M.P. no. 38521, here referred to *T. irvingtonensis*, indicates that the Irvington antilocaprid was as long-limbed and as slender as *Antilocapra*. *T. irvingtonensis* was therefore a normally built type with an "overspecialized" set of horns. Here again we are confronted with the possibility that a specialization may have actually been disadvantageous to survival of the species. *Tetrameryx*, *sensu lato*, and *Antilocapra* must have diverged from each other at the end of Hemphillian time or in an interval between Hemphillian and Blancan, since *Tetrameryx* is known from Blancan faunas.

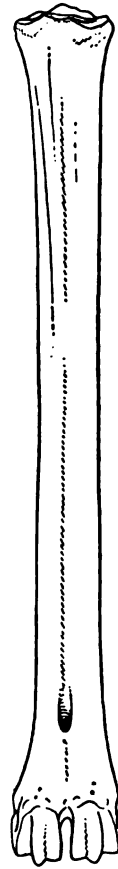


Fig. 32. *Tetrameryx irvingtonensis*, anterior view of right metatarsal, U.C.M.P. no. 38521, loc. V 3604. $\times \frac{1}{2}$.

Euceratherium Sinclair and Furlong

(Fig. 33)

Basal half of horn core, U.C.M.P. no. 34804; slightly larger than comparable element in *E. sinclairi* (Furlong, 1905a); distinguished from flat-horned bisons such as *Bison chaneyi* Cook, but smaller size and greater curvature; horn core flattened on anterior surface; orientation of horn evidently like that of other members of genus; proximal one-third directed posterolaterally and somewhat dorsally; distal two-thirds curves anteroventrally, then elevates anterodorsally to tip.

AGE OF THE IRVINGTON FAUNA

BIOLOGICAL CRITERIA

The conclusions on the chronological significance of various genera and species are obviously fixed upon the presently known geologic range of these animals.

Camelops minidokae Hay.—There is no morphological detail which prevents this species being considered ancestral to *Camelops hesternus* from Rancho La Brea. The evidence as indicated by the fossil species recognized in this paper might demonstrate that the evolutionary sequence within this genus was toward an increase in size, were it not for the occurrence of a large species of *Camelops* in Blancan faunas.

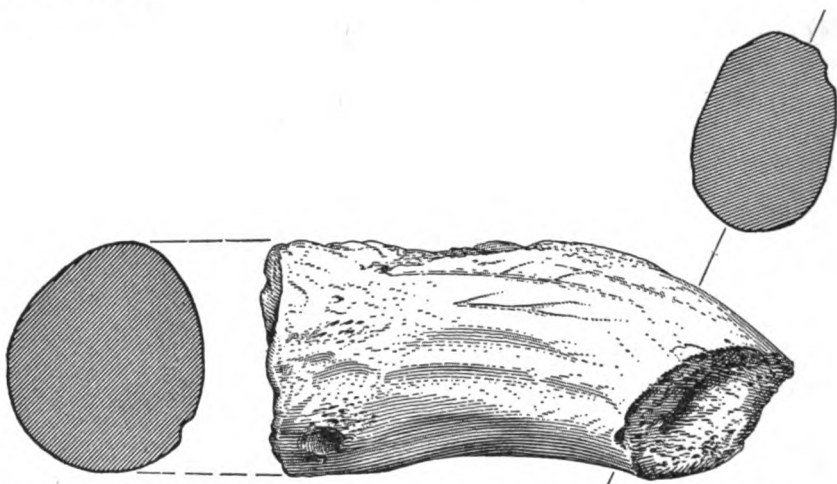


Fig. 33. *Euceratherium*, anterior view of left horn core, U.C.M.P. no. 34804, loc. V3604. $\times \frac{1}{2}$.

Equus cf. *caballus* Linnaeus.—Under the discussion of the recognition of primitive versus advanced attributes in the North American species of *Equus*, it is shown that the combination of the following characters tends to separate the Irvington horse from earlier, Blancan species: (1) U-shaped, lingually concave, metaconid-metastylid groove; (2) absence of hypostylid and parastylid in the milk and permanent teeth; (3) persistent combination of rather elongate, flattened protocone with strong lingual groove; (4) possible smaller head size in comparison to body size; (5) possible smaller occlusal diameters of cheek teeth (perhaps not as compared with *E. occidentalis*). These characters do not, in any sense, separate the Irvington horse from other Pleistocene species or from the Recent *E. caballus*.

Tanupolama.—This genus ranges from Blancan into later Pleistocene, and the species are not well enough known and differentiated to have a refined chronological value.

Tetrameryx irvingtonensis Stirton.—This species is at present known only from the Irvington fauna. It may well prove to be a characteristic earlier Pleistocene form of the San Francisco Bay region or of the Pacific Coast. Absence of the peculiar horn cores in such later Pleistocene faunas as Lone Tree Point is sug-

gestive, since the horn cores are abundant at Irvington, yet lacking at Lone Tree Point where smaller and more fragile elements of antilocaprids are known. It can at least be stated that *T. irvingtonensis* has been found only in pre-Bison deposits of the Bay area. Stirton (1939d, p. 399) has previously called attention to the occurrence of some badly weathered horn core fragments of the Bautista fauna which might be referable to this species.

Significant absence of *Bison*.—*Bison* is not represented in the Irvington fauna. In view of this fact it may seem rather strange that this genus should enter into a discussion of the age of the assemblage. I believe, however, that the dating of the Irvington and all other terrestrial Pleistocene vertebrate faunas in the Bay region must hinge on the presence or absence of this genus. Perhaps the absence of a fossil type can never be utilized as infallibly conclusive evidence; yet explanations such as accidents of preservation or a restricted habitat representation cannot suitably account for the lack of *Bison* remains in the Irvington assemblage. A relatively large fossil sample has been obtained. In abundance of material collected at earlier Pleistocene localities, the Irvington is probably exceeded only by the combined Hay Springs fauna of Nebraska. Animals, both large and small, which occupied and now occupy essentially the same general habitat as *Bison* are abundantly represented. No convincing reason can be formulated why the bison should be absent among all his ecological "cousins" except to conclude that the bison had not yet arrived in this area. I conclude that the Irvington fauna is definitely pre-Bison in age.

Schultz and Frankforter (1946) have formulated a plan for the sequence of species of *Bison* on the Great Plains. Schultz and Stout (1948) have reemphasized this plan. These writers have concluded that there has been a gradual diminution in the size of the bison since the first migrants arrived in the Great Plains during Kansan time. *Bison latifrons* (Harlan) is regarded as the oldest form and is believed to have appeared before the middle of the Pleistocene. The *B. latifrons* materials of Nebraska have been obtained from scattered exposures referred to the Grand Island gravels, which are considered to be late Kansan or early Yarmouth age by Nebraska geologists and paleontologists. Skinner and Kaisen (1947) have also expressed the belief that the larger and longer-horned bisons were among the first arrivals in North America and that certain of these forms evolved into the shorter-horned types leading into the late Pleistocene *Bison antiquus* Leidy. Skinner and Kaisen differ from the general plan of Schultz and associates in believing that a second wave of *Bison* species reached North America in the following interglacial and that this second wave included direct ancestors of the living *Bison bison* (Linnaeus). Skinner and Kaisen note (p. 155) also that there "is . . . some suggestion that *B. latifrons* was able to survive until late Pleistocene in Florida."

Of particular interest is the lack of bison remains in the Hay Springs-Rushville-Gordon fauna. (See Schultz and Stout, 1948.) It has been stated that the Upland formation of Lugen (1935a), which contains this fauna, is essentially contemporaneous with the Grand Island gravels. Why, then, is not *Bison latifrons* or one of the other large species present at Hay Springs? Answers to this question which revolve around possible peculiarity or isolation of habitat of *B. latifrons*, relative scarcity of individuals, or accidents of preservation do not suffice to explain away

this striking absence. *B. latifrons* is a normal component of mammalian assemblages at other localities. (See, for example, Simpson, 1930a, and VanderHoof, 1942b.) It seems most tenable, therefore, that the Hay Springs fauna should be regarded as pre-*Bison*.

Euceratherium.—This ruminant is now known from both earlier and later Pleistocene occurrences.

Odocoileus.—The genus is known from Blancan to Recent. Speciation in the fossil forms is at best uncertain.

Megalonyx.—The Irvington bones seemingly represent a larger form than is known from Blancan faunas; but the Irvington material is inseparable from late Pleistocene members of the genus.

Machairodontinae.—The sabertooth is not well enough known at present to have chronological import. There is a suggestion that it may represent an early Pleistocene continuance of a highly specialized line which first became distinct in Blancan time.

Mammuthus columbi.—This species Osborn has relegated to the later Pleistocene. I believe that the data thus far compiled are not precise enough to allow chronologic correlation within the family Elephantidae to lesser magnitude than epoch. The occurrences of *M. columbi* are too widespread, isolated, and diverse to merit correlation on as fine a scale as a subdivision of Pleistocene. The evidence of the combined fauna at Irvington demonstrates that *M. columbi* was present in the earlier as well as the later Pleistocene of North America.

Neotoma.—No significance in North American Pleistocene chronology.

Peromyscus irvingtonensis.—This species may lack advancement by its retention of a relatively unreduced third lower molar; but the present representation of the genus in the fossil record is so incomplete that such an observation may be only tentative. This animal appears less advanced than all late Pleistocene and Recent species, but it also appears less advanced than some Blancan and earlier forms as well. There is no effort made, therefore, to correlate this evolutionary stage with the earlier subepoch of Pleistocene time.

Citellus bensoni.—The specimen from Irvington is inseparable from the Blancan holotype and supports the concept of the antiquity of this fauna. It is distinct from all known late Pleistocene and Recent forms. The species characters may, however, represent a primitiveness carrying on in a divergent line, because more "advanced" characters are known in earlier forms.

Canidae, fox. —No significance in North American Pleistocene chronology.

Canis irvingtonensis.—This species shows lack of advancement toward the longer limbs and longer jaw with more widely spaced premolars of the Recent and late Pleistocene coyotes. Again, as with *Peromyscus irvingtonensis*, the evolutionary stage is not useful in chronology. The known Blancan coyotes seem closer to the late Pleistocene and Recent forms than does the Irvington animal.

Canis cf. *dirus*.—This animal helps distinguish the Irvington fauna from Blancan assemblages, but is inseparable from late Pleistocene forms.

Perognathus.—No significance in North American Pleistocene chronology.

Microtus.—This genus denotes the Irvington as post-Blancan, but is indistinguishable from the later Pleistocene and Recent animals.

Thomomys.—No significance in North American Pleistocene chronology.

Tayassuidae.—The family has no significance in North American Pleistocene chronology.

CHRONOLOGICAL CHART OF IRVINGTON MAMMALS

Chronology	Animal
Indeterminate	<i>Tayassuidae</i>
Probably post-Blancan through earlier Pleistocene	<i>Tetrameryx irvingtonensis</i> <i>Peromyscus irvingtonensis</i> <i>Canis irvingtonensis</i>
Post-Blancan through late Pleistocene	<i>Euceratherium</i> <i>Mammuthus columbi</i> <i>Canis cf. dirus</i> <i>Camelops minidokae</i>
Post-Blancan to Recent	<i>Equus cf. caballus</i> <i>Microtus</i>
Blancan through early Pleistocene	<i>Citellus bensaoni</i>
Blancan through late Pleistocene	<i>Tanupolama</i> <i>Megalonyx</i>
Blancan to Recent	<i>Odocoileus</i> <i>Neotoma</i>
Pre-Blancan through late Pleistocene	<i>Machairodontinae</i>
Pre-Blancan to Recent	<i>Canidae, fox</i> <i>Thomomys</i> <i>Perognathus</i>

Of the eighteen different mammals which have been identified, about 50 per cent are extinct, and about 40 per cent could possibly have a living representative referable to the same species. All the animals in this fauna which are also known from Blancan faunas, except *Odocoileus*, prove to be types of even greater chronologic range than would be thus indicated.

GEOLOGICAL CRITERIA

The structure of the deposits at Irvington suggests an antiquity for these beds when they are compared to other Quaternary sediments in the San Francisco Bay region. The fact that these beds have suffered a definite broad-scale tilting tends to distinguish them from the flat-lying sediments which have been termed later Pleistocene.

It is concluded that the Irvington fauna is earlier Pleistocene in age. "Earlier" is used to connote a time interval on the Pacific Coast of North America which is post-Blancan and before the time of existence of such faunas as Rancho La Brea.

CORRELATION OF THE IRVINGTON FAUNA

The Irvington fauna seems most closely contemporaneous with the Hay Springs-Rushville-Gordon assemblages of Nebraska (including the original Hay Springs quarry near Grayson), the Rock Creek of Texas, and the Bautista of southern California. The Borchers fauna of Kansas may be of equivalent age, but there are not enough genera known from the Borchers to make definite correlation. These conclusions are based in large degree on the absence of *Bison* in all the faunas; and it must be admitted that, aside from this one factor, any correlation between the Pacific Coast faunas and the Great Plains faunas is somewhat dogmatic.

The published lists of the Hay Springs fauna (Matthew, 1918a; Schultz and Stout, 1948) indicate that there is only a chance for significant comparison of the *Peromyscus*, coyote, horses, and *Camelops* with their counterparts in the Irvington fauna. The evolutionary "pattern" within the limits of Pleistocene time is not known for any of these genera. There is an intriguing suggestion that *Hayoceros* of Hay Springs and *Tetrameryx* of Irvington are equivalent, though divergent, structural stages of two branches of antilocaprids aberrant to the lineage of *Antilocapra*. The Nebraska material referred to *Equus calobatus nebrascensis* Frick (*E. calobatus* Troxell = *nomen vanum*, and the subspecies *nebrascensis* must be a *nomen nudum*) might be comparable to the Irvington horse. Regardless of species reference, however, there seem to be no available criteria for determining advancement among these equines. The reference of the Nebraska *Camelops* material to *C. kansanus* Leidy is not justified in my opinion (see previous discussion of *Camelops* in this paper). Even if the Hay Springs and Irvington camelids are different species, there still appears to be no justification for implying a chronological difference.

The Rock Creek fauna compares with Irvington in about the same manner as does the Nebraska assemblage. The *Equus semiplicatus* Cope (*nomen vanum*) and *E. calobatus* (*nomen vanum*) specimens may be about the same as the Irvington horse, but *E. scotti* is quite dissimilar. Evidently a dire wolf, a wolf, a coyote, and a fox are represented at Rock Creek; but none of these may be compared closely with the dire wolf, coyote, and fox from Irvington.

In all the faunal materials that may be compared, the Bautista appears to contain a group of animals identical or very similar to the Irvington assemblage. Unfortunately, everything but the horse material from Bautista is fragmentary. Frick (1921a) noted that the camelid from Bautista is a smaller form than the Rancho La Brea *Camelops*; therefore the Bautista animal may be the same species as the Irvington animal. The horses from the two faunas are very similar, although there is a size difference. It may be possible that *Tetrameryx irvingtonensis* is represented at Bautista. (See Frick, 1921a, figs. 17-18, p. 301.)

A direct correlation of the Irvington fauna with any of the European assemblies can be accomplished only after vigorous exercise of one's imagination. Probably the only means of approaching such a correlation is by use of the mammoths. It is judged that the Irvington mammoth represents a very early *Mammuthus trogontherii* (Pohlig) or a late *M. trogontherioides* (Zuffardi) stage in the general European sequence. On this basis the Irvington might be approximately the same age

as the antepenultimate interglacial faunas of the series arranged by Zeuner (1945, chap. x). These faunas are believed by Zeuner to be the first datable appearance of *Mammuthus* cf. *trogotherii*, and he believes they represent a time 490,000 years ago.

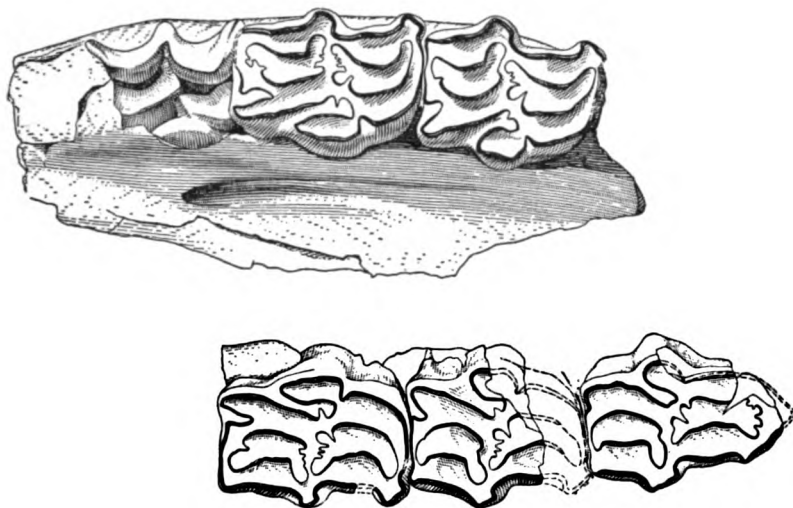


Fig. 34. *Equus*, occlusal view of right maxilla with DP² to M¹ and left DP² to DP⁴, U.C.M.P. no. 38226, loc. V4703. $\times \frac{3}{4}$.

LATER AND UNDIFFERENTIATED PLEISTOCENE LOCALITIES

DESCRIPTION OF LOCALITIES

V4703. Livorna Heights. Fine-grained, buff tan, silty, friable sandstone; exposure restricted, dip and strike not certainly determinable, but faint laminations and orientation of rock particles indicate approximately flat-lying beds; exposures of same lithology 100 yds. N and 200 yds. S also flat-lying; beds may extend northward past N end of Sugarloaf Hill, may connect with beds of same general lithology and form at least part of floor of Walnut Creek Valley; E central part of Concord quadrangle in valley between Sugarloaf Hill and foothills of Mount Diablo, approximately 3 mi. SE of geographic center of Walnut Creek; from basement of B. T. Murry house; prog. grid coörs. (1943 map ed.) 901,100–1,680,900. (U.S. Geol. Surv. Folio 193—Orinda formation; beds of same lithology as Temescal formation in Walnut Creek Valley as shown on Folio 193.) *Equus*—Pleistocene. Figs. 34 and 38.

V4719. Heidorn. Fine-grained, buff-colored, flat-lying sandstone, grading upward uniformly into a 3-ft. soil capping; 4 mi. SE of Antioch; 0.5 mi. WSW of Lone Tree School; in NE part of Mount Diablo quadrangle; from East Bay Municipal Utilities Dept. Mokelumne Aqueduct no. 2 on property of F. H. Heidorn, Jr.; prog. grid coörs. (1943 map ed.) 927,400–1,691,800. (Beds continuous with Montezuma formation of Weaver, 1949.) *Equus*—Pleistocene. Fig. 41.

V4018. Mussel Rock. Complete description of locality published by Peabody (1945). *Bison*, *Equus*, *Paramylodon*—later Pleistocene. Fig. 46.

V3505. Mussel Rock beach terrace. Fossil from raised terrace 75 ft. above beach due E of Mussel Rock, San Mateo County; "...large Proboscidean tusk seen in place but not collected," entered on U.C.M.P. locality card, August 14, 1935; prog. grid coörs. 855,500–1,657,100, San Mateo quadrangle (1943 ed.). *Bison*, proboscidean—later Pleistocene. Fig. 46.

Discussion.—The relationship of this locality to V4018 was not discussed by Peabody (1945) in his treatment of the latter site. The bison tooth from V3505 may have been transported downslope from the 200-foot elevation of V4018; the quality of preservation and coloration of this tooth is the same as the bison and horse material from the higher locality. However, the presence of a proboscidean tusk in place at the lower level is strong evidence that V3505 is truly a late Pleistocene deposit also. If both of these sites are later Pleistocene, as is indicated, there is available an incomplete gauge of the fluctuation of sea level here in late Pleistocene. At the time of deposition of V4018 (higher level) the coastline was farther to the west and either higher or lower than the level of V3505. Following terrestrial deposition at the upper level, the coastline quickly migrated eastward, either by relative elevation of sea level or rapid landward erosion, or both, and terraced the V3505 site. Subsequently, the sea level was again depressed some 75 feet to its present position.

LOCALITIES IN CATALOGUE OF MUSEUM OF PALEONTOLOGY,
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V3428. Union Oil tank farm. This locality shown by Stirton (1939d, fig. 85). *Mammuthus*—Pleistocene. Fig. 47.

V3609. Charles Hill (divide between Lafayette and Bryant). This locality shown by Stirton (1939d, fig. 93). Unit of flat-lying clays, sands, and pebble conglomerates in highway cut on main divide between Lafayette and Orinda; prog. grid coörds. 887,600–1,684,150, Concord quadrangle (1943 ed.). *Bison*, turtle—later Pleistocene. Fig. 39.

V3901. Fleishhacker beach. In sand and gravel opposite underpass leading from ocean beach to SW corner of Fleishhacker Pool, San Francisco; collected by Mr. David McC. McKell. *Mammuthus*, *Mammut cf. americanum*, *Equus*, mineralized wood fragments—Pleistocene. Fig. 46.

V3606. Seven Mile Beach. Alluvium exposed in small precipitous gully 30 ft. below top of sea cliff 950 ft. S of Mussel Rock, San Mateo County; prog. grid coörds. 855,750–1,656,100, San Mateo quadrangle (1943 ed.). Fossils from lenticular conglomerates and sandstones overlying Franciscan diabase and basalt and underlying Recent sand dunes; rock fragments of conglomerate derived from underlying Franciscan; discovery and geologic reconnaissance by Mr. Rodman K. Cross, Geology Department, Stanford University. Fossil level about 70 ft. above present sea level, hence corresponds with U.C. loc. V3505, Mussel Rock beach terrace. *Bison*—later Pleistocene. Fig. 46.

V2841. Harrison St. tunnel (Posey Tube). Fossil from 80 ft. below tide level in California Bridge and Tunnel Co. excavation for Harrison St. tunnel under Oakland Estuary; prog. grid coörds., approx. site, 877,400–1,672,000, San Francisco quadrangle (1942 ed.). *Mammuthus cf. columbi*—Pleistocene. Fig. 48.

V3411. Bay Bridge. Fossil from 180 ft. below surface of San Francisco Bay at Pier E-5 of Bay Bridge, about 1,000 ft. W of Key System (electric railroad) mole. *Mammuthus cf. columbi*—Pleistocene. Fig. 48.

V3933. Montclair playground. Fossil from yellow sandy clay; prog. grid coörds. 883,650–1,676,400, Concord quadrangle (1943 ed.). *Mammuthus*—Pleistocene. Fig. 40.

V3613. Berkeley Municipal Wharf. Fossils from sands and clays, obtained by dredging operations on Bay floor 25–45 ft. below water surface; near Berkeley Wharf, exact locality unknown. *Mammuthus cf. columbi*—Pleistocene. Fig. 48.

V3406. Mount Diablo summit road. Fossils from ferruginous sands and silts in excavation of first curve W of tollhouse on road from Danville to summit of Mount Diablo; in SW $\frac{1}{4}$, Sec. 14, T. 1 S, R. 1 W; prog. grid coörds. 908,950–1,677,750, Mount Diablo quadrangle (1943 ed.). *Bison latifrons*, *Equus*, *Mammuthus*—later Pleistocene. (See VanderHoof, 1942, for description of *Bison latifrons* materials.) Fig. 42.

1076.¹² North entrance to Southern Pacific tunnel 4. Fossil from clay, 600 ft. from N portal of

¹² Numbers not preceded by "V" are old Museum of Paleontology locality numbers which were listed consecutively as they were acquired.

tunnel and about 35 ft. below surface; presumably tunnel referred to is Bay Park (coörds. 865,200-1,663,000) or Roman (coörds. 865,000-1,665,400) in San Francisco. See San Mateo quadrangle (1943 ed.). *Mammut cf. americanum*—Pleistocene.

1082. North of Livermore. Alluvial deposit on N side of Livermore Valley, 1-2 mi. N of town of Livermore; might be same as U.C. loc. V4103. Reported fossil mammals—possibly Pleistocene.

1363. Bulls Head Point. Listed as being 0.75 mi. E of Martinez, California; could be type locality for *Equus pacificus* Leidy (*nomen vanum*). *Equus*—Pleistocene.

1375. Island at Union Oil Co. Unknown materials from gravels of small island at Union Oil works, presumably along shore at Oleum, California. Age possibly Pleistocene.

3023. McGrew's Ranch. Bluish clay overlain by gravels and unconformably overlying a greenish sandstone possibly of the Franciscan; approximately 7 mi. NW of Petaluma, California, and 0.75 mi. SE of W. McGrew's ranch house. *Paramylodon cf. harlani*—Pleistocene.

V0302. Hercules. Sand bed on landward side of Southern Pacific Railroad track, Sec. 22, R. 4 W, T. 2 N, 0.25 mi. N of old powder works at Pinole, California; 45 ft. above sea level; collected by Prof. A. C. Lawson. (Weaver, 1949—Montezuma formation.) *Bison*—later Pleistocene. Fig. 47.

V1201. Lone Tree Point 1. Usually called "Pecten Point" by University of California personnel who conduct class field trips to this area. Alluvial sands and gravels overlying Pinole tuff; often called "Rodeo beds" but this name preoccupied; N side Lone Tree Point, 200 yds. W of Southern Pacific Railroad station, Rodeo, California; prog. grid coörds. 878,200-1,701,950, Mare Island quadrangle (1942 ed.). Not mapped on general area of Pinole tuff, Weaver (1949), but would undoubtedly be considered his Montezuma formation. *Equus*, *Camelops*, small antilocaprid comparable to *Breameryx minor* (Taylor), large antilocaprid about size of *Antilocapra*, *Megalonox*, *Mammuthus cf. columbi*, *Bison*—later Pleistocene. Fig. 47.

V4014. Lone Tree Point 2. Not separated geographically from V1201, although sometimes considered southern and central part of Lone Tree Point. Later Pleistocene.

V2703. Near Suisun Slough. In tributary of Suisun Slough, somewhere between Suisun and Rio Vista, California. *Equus*—?Pleistocene.

V2842. San Antonio Creek. About 1 mi. from Bodega Bay on San Antonio Creek, Marin County. *Bison*, *Mammuthus cf. columbi*, *Mammut cf. americanum*—later Pleistocene. Fig. 49.

V3646. Eureka school. Gravelly blue clay; approx. 1.5 mi. NW of Eureka school, 5.5 mi. E and slightly N of Petaluma; prog. grid coörds. 852,150-1,727,700, Petaluma quadrangle (1942 ed.). (Weaver, 1949—Petaluma formation.) *Equus*, *Bison*—later Pleistocene. Fig. 50.

V3719. Collinsville. In excavation for beet cellar on BB Ranch, approx. 0.66 mi. N and slightly W of Collinsville, Solano County; SE $\frac{1}{4}$, SW $\frac{1}{4}$, Sec. 22, T. 1 E, T. 3 N, Antioch quadrangle. (Weaver, 1949—Recent younger valley alluvium.) *Mammuthus cf. columbi*, *Equus*—Pleistocene. Fig. 45.

V3937. Calaveras Dam. Museum notes report that fossil was in base of bluish-black sands overlying 1-5 ft. of cobble gravel which, in turn, overlies ?Franciscan serpentine; W bank of Calaveras Dam spillway, 12 mi. NNW of San Jose; prog. grid coörds. 920,700-1,635,500, San Jose quadrangle (1943 ed.). *Mammut cf. americanum*—Pleistocene. Fig. 51.

V4007. Aquatic Park. Containing deposit not exposed; center of S border Aquatic Park lake, Berkeley; prog. grid coörds. 875,150-1,679,200, San Francisco quadrangle (1942 ed.). *Bison*—later Pleistocene. Fig. 48.

V4008. Antioch. Blue clay below about 125 ft. of river sands and gravels; on S side San Joaquin River near convergence with Sacramento River. *Bison*, *Equus*, camelid, *Paramylodon*, *Mammuthus*—later Pleistocene.

V4045. Eighty-first Ave., Oakland. Under a blue clay in excavation for Sunshine Biscuit Co. plant on 81st Ave., between San Leandro Blvd. and East 14th St., Oakland. *Mammuthus*—Pleistocene.

V4047. Burke Ranch. Blue-gray clays and sands overlying steeply tilted beds of Tassajara formation; W valley wall Alamo Creek, 2.7 mi. NE of Dublin, California; prog. grid coörds. of sample exposure 912,000-1,664,350, Pleasanton quadrangle (1943 ed.); collected by Mr. Wesley Gordon and Hayward Boy Paleontologists. *Bison*, *Mammuthus*, *Equus*—later Pleistocene. Fig. 43.

V4103. Doolan Canyon. Clays of stream bank of Cottonwood Creek in Doolan Canyon, 3.75

mi. NW of Livermore; prog. grid coörds. 920,750-1,662,200, Pleasanton quadrangle (1943 ed.). *Mammut cf. americanum*, *Paramylodon cf. harlani*, *Bison cf. antiquus*, *Equus*—later Pleistocene. Fig. 44.

V4404. Alamo Creek, site 2. Alluvial sands and gravels in bank of Alamo Creek near juncture of old road along creek and newer paved highway; 6.5 mi. SE of Danville, California; prog. grid coörds. 912,300-1,677,550, Mount Diablo quadrangle (1943 ed.). *Citellus*, ground sloth—Pleistocene. Fig. 42.

V4505. Port Chicago. "Clay pit" S of Port Chicago. *Tapirus*, *Equus*—Pleistocene.

V4701. Pleasant Hill. Soft, buff-colored sandstone unconformably overlying tilted Tertiary beds, contains grit lenses and streaks of carbonized material; in excavation for East Bay Municipal Utilities Dept. Mokelumne Aqueduct no. 2, near Larkey Lane and 2d Ave., 10 ft. below ground surface; prog. grid coörds. 896,300-1,687,400, Concord quadrangle (1943 ed.). *Mammut americanum*—Pleistocene. Fig. 38.

V4901. Positas. Tilted sands and gravels exposed by highway excavations for Livermore bypass, U.S. Highway 50; prog. grid coörds. 927,400-1,660,500, Pleasanton quadrangle (1943 ed.). *Mammothus*, *Mammut cf. americanum*, *Equus*, camelid, anatis (duck), turtle—Pleistocene. San Jose State College and Montezuma School of Los Gatos also have obtained fossil vertebrate material from this site. Fig. 44.

V4921. San Miguel. From 3-ft. soil layer overlying buff-colored soft sandstone; 1 mi. (approx.) SE of intersection of State Highways 21 and 24 in Walnut Creek, on series of low hills 0.75 mi. N of N end of Sugarloaf Hill; prog. grid coörds. 899,650-1,683,550, Concord quadrangle (1943 ed.). *Bison cf. latifrons*—later Pleistocene. Fig. 38.

UNNUMBERED LOCALITIES KNOWN FROM THE RECORDS OF THE MUSEUM OF PALEONTOLOGY, UNIVERSITY OF CALIFORNIA

Near Antioch. Precise location of recovery site unknown. *Mammut cf. americanum*—Pleistocene.

University Ave., Berkeley. Printed statement by a Mr. Eastland which accompanies the specimen reflects some interesting though highly fanciful conclusions: "Part of a tooth of a *Mastodon* found at the junction of University Avenue and the railroad at Berkeley. This tooth is interesting on account of its showing evidence of glacial striation. This is not to be greatly wondered at seeing that a great deal of the land in Berkeley, in proximity to the foothills is made up of terminal moraine material." *Mammut cf. americanum*—Pleistocene.

At Sunol, California. Specimen reported to have been found 25 ft. below ground surface at Sunol; donated to Museum by a Miss Matthews. *Mammut cf. americanum*—Pleistocene.

Alameda County:

1. From one of Oakland-San Francisco Bay Bridge caissons. *Equus*.

2. Localities of Hayward Boy Paleontologists. Loc. HV1—On San Lorenzo Creek at Hayward High School; prog. grid coörds. 895,700-1,657,900, Hayward quadrangle (1942 ed.). *Equus*. Loc. HV1A—Approx. 400 ft. SE of 14th St. bridge over San Lorenzo Creek; prog. grid coörds. 894,200-1,658,800, Hayward quadrangle (1942 ed.). *Equus*. Loc. HV4A—Stream float in Crow Canyon, vicinity of Edenvale school; prog. grid coörds. 900,800-1,666,800, Concord quadrangle (1943 ed.). *Equus*, *Camelops*. Loc. HV4B—In Crow Canyon, region 1 mi. upstream from HV4A; prog. grid coörds. 902,100-1,668,600, Concord quadrangle (1943 ed.). *Equus*. Loc. HV4C—Stream float in Bolinas Creek; prog. grid coörds. 900,500-1,668,500, Concord quadrangle (1943 ed.). *Equus*—Pleistocene.

3. Gravels of Livermore Valley. Type of *Canis dirus* (Leidy) and *Camelops hesternus* (Leidy) reported to have come from these deposits.

Contra Costa County:

1. On Las Trampas Creek between Lafayette and Saranap. Bluish, sandy clay with gravel lenses lying unconformably on gray-brown marine sandstone; prog. grid coörds. 895,700-1,683,250, Concord quadrangle (1943 ed.). Proboscidean.

2. In Lafayette. Proboscidean scapula.

3. Near Rodeo, 0.2 mi. W of U.S. Highway 40 and 0.3 mi. SW of S point of town of Rodeo. Proboscidean.

4. Near Pittsburg. From East Bay Municipal Utilities Dept. Mokelumne Aqueduct no. 2, in cross-bedded sands and gravels; prog. grid coörds. 919,300–1,696,500, Mount Diablo quadrangle (1943 ed.). (Weaver, 1949—Montezuma formation.) Fossil retained by Artukovich Construction Co., contractor for East Bay M.U.D. in area. *Mammut cf. americanum*.

Marin County. Millerton Head. Gummy clay; prog. grid coörds. 822,600–1,711,500, Point Reyes quadrangle (1940 ed.); material collected by personnel from Marin College and now housed in that institution. (Weaver, 1949—Millerton formation.) *Bison*.

San Francisco County:

1. Bay Bridge excavation, Pier E-3, 180 ft. E of Goat Island. *Bison*.

2. Treasure Island, 45 ft. below level of Bay. *Mammuthus*.

3. Ocean beach, 0.25 mi. S of Fleishhacker Pool. *Mammut cf. americanum*.

San Mateo County:

1. Millbrae, 0.5 mi. N of Millbrae, 75 yds. E of Southern Pacific Railroad right-of-way. In dark blue sandy clay; material now at San Mateo Junior College. *Mammuthus cf. columbi* or *M. jeffersonii*. F. M. Stanger (1945, pp. 559–561) reported that 21 teeth and 10 tusks of the mammoth, as well as an *Equus* tooth, insects, and 68 "varieties" of plants were recovered from this locality.

2. Menlo Park station. Blackwelder (1929) reported discovery of mastodon remains from 2.3 mi. W of Menlo Park station and 28 mi. SE of San Francisco; material at Stanford University. Probably *Mammut*.

Solano County: Carquinez Strait, N shore, 3 mi. E of Carquinez highway bridge, U. S. Highway 40, on old McKay tannery property. *Mammut*.

Sonoma County: Griffeth Park, 8.5 mi. (by Monte Rio highway) W by N of Santa Rosa, California; material at Santa Rosa Junior College. Proboscidean.

For additional records of occurrences of late Cenozoic vertebrates in the San Francisco Bay region, see O. P. Hay (1927d).

CONCLUSIONS

LATE CENOZOIC CHRONOLOGY, PLIOCENE-PLEISTOCENE BOUNDARY

Flint (1948, pp. 546–547) believes that the best general basis for separating Pleistocene from Pliocene and also for subdivision of Pleistocene is climate. He grants that the initiation of glaciation was not contemporaneous on all parts of the earth, but he believes that this probability does not lessen the value of climatic fluctuation as a basis for correlation. He concludes that in keeping with geological principles and practices, the unconformity at the base of the earliest glacial deposits should be treated as the marker for the beginning of a new stratigraphic unit; hence this stratigraphic break logically marks the beginning of the Pleistocene.

The stratigraphic unity and uniqueness of glacial deposits are indisputable and serve admirably to set aside such a lithogenetic unit from underlying nonglacial beds in glaciated areas. The results of glacial climate, effective in higher latitudes during the Pleistocene, are peculiar; but the results of glacial climate vary with change in altitude, latitude, or longitude. It seems indisputable, therefore, that a "climatic unconformity" may be of different geologic age with change in geographic position, or with change in altitude. Any attempt to apply Pleistocene chronology based on glacial events and climates to terrestrial sequences in nonglaciated areas is particularly confusing.

Elias (1948, pp. 609–612) maintains that the Ogallala formation provides a prominent, widespread, and "easily recognizable geologic and physiographic datum,

which bears the marks of momentous events at the closing of the Tertiary and initiation of Quaternary time." Blancan beds, according to Elias, overlie the Ogallala caliche "cap rock" in the Texas Panhandle and other places throughout the High Plains. Yet it is known that the cap-rock caliche *overlies* beds containing the Cita Canyon fauna (Blancan) in the Texas Panhandle. Thus the stratigraphic relationships of Elias' cap-rock datum to the Blancan deposits is exactly reversed at Cita Canyon. Elias further states (p. 620) that in the area of the Great Plains the final basis for correlation and for definition of the beginning of the Pleistocene is diastrophism, "... try to recognize a major earth movement as the real indication of the beginning of the Pleistocene." He is supported in this general thesis by Bevan (1948, p. 620), and by Lugin (1948, p. 625). The presence of an unconformity has always been a powerful tool for the field worker who desires a natural dividing line to fit a scheme of stratigraphic classification, but this unconformity invariably turns out to be of chronologic adaptability only in the area wherein it may be observed and mapped.

Is strict adherence to typology the solution? Kleinpell (1948) has reemphasized that any deliverance from chaos in time-stratigraphic problems must be accomplished by constant reference to the type section or the type time-stratigraphic unit as governed by the law of priority in definition. Schultz and Stout (1948, p. 571) note that any consideration of the terms "Pleistocene" and "Pliocene" must involve correlation with the type sections in Italy. Unfortunately, as Kleinpell (1948) pointed out, Lyell's designation of type sections in Italy involves units of no less magnitude than a series-epoch, and the refinement of Lyell's definitions is still a controversial subject.

Lyell (1933) first designated the Sub-Apennine strata of northern Italy as the type section of his "Older Pliocene." This area includes Plaisancian, Astian, and Villafranchian-Calabrian sediments; and it is a moot question whether Lyell's concept of the Sub-Apennine strata did or did not include the Villafranchian beds. The type localities of Lyell's "Newer Pliocene" = Pleistocene are Ischia and Val di Noto (Naples area); this area contains Calabrian equivalents. Villafranchian-Calabrian sediments are thus exposed in both type areas. If the interpretation of Gignoux (1910), Schultz and Stout (1948), and others is followed, the Villafranchian may logically be regarded as Pleistocene by definition; if the interpretation of Pilgrim (1944), Zeuner (1946), Stirton (1948), and others is followed, the Villafranchian is Pliocene by definition.

Movius (1949, pp. 380-413) has prepared an excellent summary of Villafranchian stratigraphy and has offered many criteria supporting the contemporaneity of terrestrial Villafranchian deposits and their marine equivalents with the beginning of glaciation. He states (p. 404):

In other words, the stratigraphic evidence clearly indicates that the Villafranchian sediments of southern and southwestern Europe were accumulated during the first major glacial episode of late Cenozoic time. On this basis the Villafranchian is regarded by definition as marking the base of the Pleistocene rather than as representing the final stage of the Pliocene.

Movius is content to follow, without discussion, certain previous writers in the interpretation of priority and the definition of the terms "Pliocene" and "Pleistocene."

Moore (1949, pp. 1276–1280) supports basal Pleistocene assignment for the Villafranchian with a compilation of the data presented by the International Geological Congress and International Congress Pliocene-Pleistocene Commission. Moore notes in his review of the history of the terms “Pliocene” and “Pleistocene” (p. 1278) that the type locality of Pliocene rocks contains Plaisancian and Astian overlain by Calabrian and Villafranchian and that the type locality of Pleistocene rocks contains Epomeo marls, equivalent to Calabrian. He concludes, following these statements, that the relegation of Villafranchian-Calabrian to Pleistocene is in accord with Lyell’s definition. Yet Moore, too, ignores the fact that Lyell made no subdivision of the rocks in the type locality of the Pliocene and that a strict following of Lyell’s definition can only result in the designation of Plaisancian, Astian, *and* Villafranchian-Calabrian as typical Pliocene.

The entire question resolves itself, then: Shall priority in definition be utilized as a tool in stratigraphy and geochronology? Or shall consensus of opinion, based on climatological, orogenic, or paleobiological considerations be the criterion?

I believe that principles analogous to the International Rules of Zoölogical Nomenclature are applicable to stratigraphic problems of this sort. Priority of definition should be followed, except possibly in long-established usage of a concept or a name. When the original definition is somewhat obscure—as it is with many genera of mammals, for example—established usage then forms a useful substitute tool. The Villafranchian has appeared in many texts and charts as a stage representing late Pliocene time. I do not believe that good cause has yet been presented why there should be deviation from this established usage. If it be desired that a subdivision of the time-stratigraphic column be delimited by a marked diastrophic movement coupled with a noteworthy change in faunal composition, then there are evident in the San Francisco Bay region excellent criteria for designating Blancan as Upper Pliocene. The San Francisco Bay region is, however, a very small province and the late Cenozoic rocks of the area have singular structural characteristics.

Although I have used the Blancan as a unit of pre-Pleistocene time throughout this monograph, I express no adamant preference for such usage. It seems unimportant whether Blancan is called Pliocene or Pleistocene so long as it is recognized as a time of distinct faunal assemblage.

Zeuner’s attempts to establish a reliable chronology by means of a combination of astronomical and paleoclimatological methods (1945 and 1946) must be regarded as a notable contribution to our knowledge about the Pleistocene epoch. Certain conclusions which he presented were of especial interest. He noted (1945, p. 274) that the attempt to place an absolute chronology on the rate of evolution of various species or subdivisions thereof is made difficult by the uncertainties of nomenclature pertaining to these categories:

The difficulty of nomenclature comes in here. It is difficult to design a satisfactory nomenclature for Recent geographical races. With fossil forms it is even worse, partly because of the practice of paleontologists to treat races, subspecies and ecological varieties as taxonomic species, and partly because the time-element cannot be expressed in our present trinomial nomenclature.

Zeuner (1945, pp. 274–275) has compiled some lineages showing species succession and evolution throughout the Pleistocene. His concepts were based in part

on the earlier works of Stehlin, Pilgrim, Soergel, and others. The groups which he considered well enough represented in each deposit to account for individual and geographical variation and well enough established in the time-stratigraphic succession to be used as examples were the brown bears, cave bears, striped hyaenas, spotted hyaenas, voles, dicerorhine rhinoceroses, giant deer, straight-tusked elephants, and mammoths. An example: "(9) *Mammoth*.—*Elephas meridionalis* (Villafr., low. Pleist. to ApG1₁) → *trogontherii* (low. and mid. Pleist.) → *primigenius* (LG1). Teste Soergel (1912)." Zeuner himself has indirectly outlined a major objection to his proposed lineages (p. 275) in discussing Osborn's contrasting views on phylogeny of the elephants:

A different view is held by Osborn (1942), who regards the straight-tusked elephant and the mammoth as descendants of less closely related stocks of elephants. It is possible to defend this view if one restricts the species to typical material of *E. meridionalis*, *antiquus*, and *primigenius*. If one considers, however, the whole material of many thousands of specimens—many of them transitional—which are available in European collections, one finds that—

We must infer, therefore, that Zeuner has depended on popular concept of just what each species should be without too critical an appraisal of the reference of these better materials to the usually poor and incomplete types. There can, however, be no refutation of Zeuner's lineages without an exhaustive reëxamination of all the types and referred materials. The paramount object of such a study would be to bring a concept based on "thousands of specimens" into harmony with the Rules of Nomenclature.

The final result of Zeuner's application of his absolute chronology to the commonly approved phyletic sequence of certain species was his "cautious suggestion" (p. 278) that the evidence from several groups of mammals and from some insects indicates that 500,000 years are required for the evolution of a new species. If, in future, it can be proved to the satisfaction of all that Zeuner's premises are essentially correct, in spite of the many uncertainties which are inherent in the great mass of compiled data he has organized, then it must be admitted that the work on the Pleistocene sequence in Europe is far advanced over such work in the Western Hemisphere.

DATING AND CORRELATION OF THE TERRESTRIAL LATE CENOZOIC OF THE SAN FRANCISCO BAY REGION

It is concluded that only two divisions of Pleistocene time—provincial ages—may be recognized in the San Francisco Bay region on the basis of fossil vertebrate assemblages. A nomenclature is here applied that is correlative with the terminology of the Wood Committee (1941) in its classification of the North American continental Tertiary. The use of "biochronology" and "biostratigraphy" is avoided in this treatment since the evidence from land vertebrate-bearing deposits can seldom, if ever, meet the requirements of prior definitions of such terms. It is emphasized that these proposed provincial age names are based on faunal names and on the animals within these faunas. This nomenclature is, then, entirely separate from rock, formational names.¹⁴

¹⁴ It is noted that the Wood Committee has employed some provincial age names which have been utilized as formational names (e.g., Arikareean) and some names which have been used only with faunas (e.g., Clarendonian).

The later Pleistocene provincial age is named "Rancholabrean" and is typified by the Rancho La Brea fauna. The Rancholabrean is represented by several assemblages in the San Francisco Bay region, but all these assemblages combined are not so complete as the type fauna. Perhaps the use of this name will be protested because the Rancho La Brea assemblage is not a normal sedimentary accumulation; but actually, the selection of this term serves to accentuate the fact that this nomenclature is proposed on the concept of chronology as indicated exclusively by the evidence from fossil vertebrates. Rancholabrean faunas are denoted by their possession of the remains of *Bison* and by the presence of many mammalian species, particularly in the Carnivora and Rodentia, which are inseparable from Recent inhabitants of the same area. The component of the larger mammals in Rancholabrean faunas—*Mammuthus*, *Mammut*, *Camelops*, *Equus*, *Bison*, *Megalonychidae*, *Smilodon*, and others—consists of extinct species. The beds of rock containing Rancholabrean faunas in the San Francisco Bay region may often be distinguished from earlier deposits by a relatively flat-lying attitude.

The earlier Pleistocene provincial age (post-Blancan to pre-Rancholabrean) is named "Irvingtonian," and is typified by the Irvington fauna. The Irvington assemblage contains some mammalian species which appear to be unadvanced as compared to the most nearly related forms from the Rancholabrean and Recent. The Irvingtonian is marked by the absence of *Bison*. In contrast with the sediments containing Rancholabrean faunas in the San Francisco Bay region, the beds containing Irvingtonian fossils have been slightly tilted. There is now available criteria from the vertebrate fossils that deposits of Blancan age were involved in the orogeny of the Coast Ranges of this region. Statements by certain writers that this orogeny probably happened near the end of Pliocene time are therefore corroborated if the Blancan is regarded as the upper provincial age of the Pliocene.

It might be suggested that the relative abundance of Pleistocene vertebrates which have been dredged from various depths beneath the present level of San Francisco Bay indicates that this area was above sea level at the time of their accumulation. Upon this hypothesis could then be built the additional hypothesis that these vertebrates were deposited in streams or lakes in the San Francisco Bay valley at one of the times of maximum continental glaciation. This concept is in accord with Lawson's (1948, p. 200) statement that the drowned river gorge under the Golden Gate "may be dated hypothetically at the maximum glaciation of the Glacial period, when sea level was at its lowest for that period." We could visualize, then, these vertebrates being deposited in the lower reaches of the combined Coyote and other streams flowing from the south, just before this stream system emptied into the Sacramento-San Joaquin river drainage, flowing through Golden Gate Canyon to the sea. In my opinion, direct correlation of the present submarine canyons and submarine land vertebrate sites of the Pacific Coast with the maxima of glaciation remains conjectural. Lawson (1948, p. 201) has shown that the rise and fall of various sections of the California coast due to deformation of the earth's crust must not be disregarded.

MAPS

(Figs. 35–51)

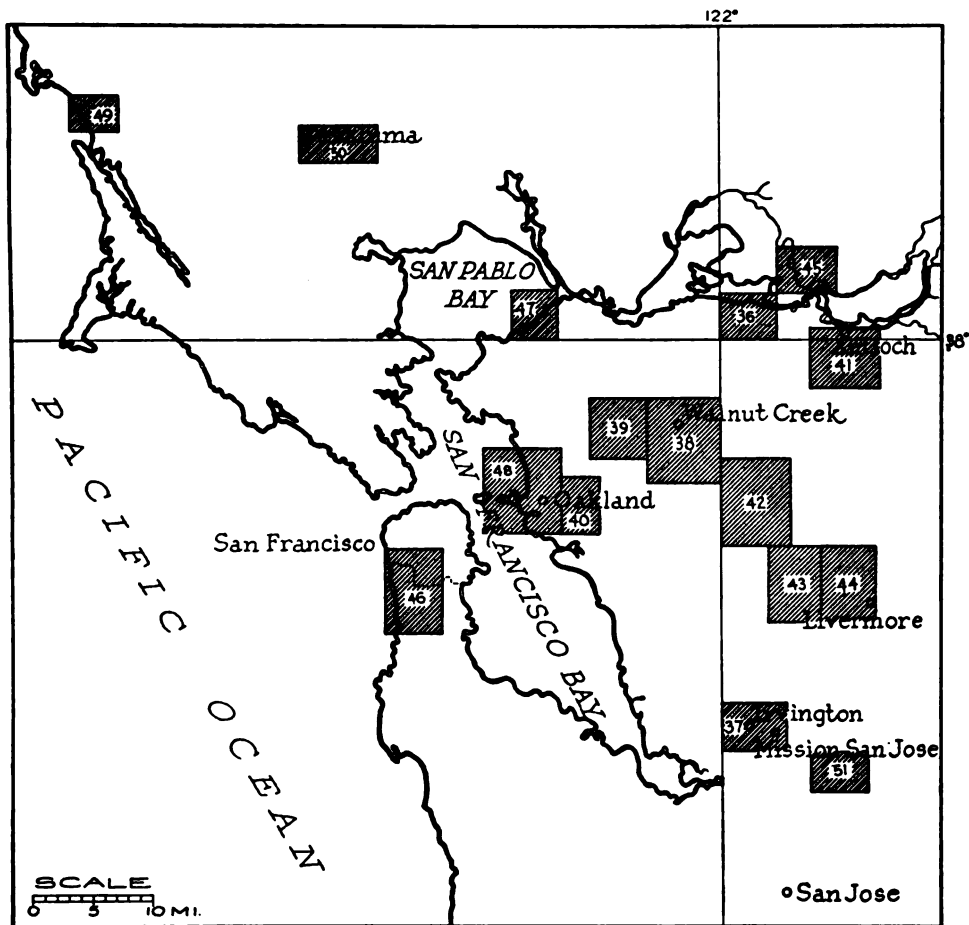


Fig. 35. Key map of San Francisco Bay region showing locations of extracts from U. S. Geological Survey quadrangles.

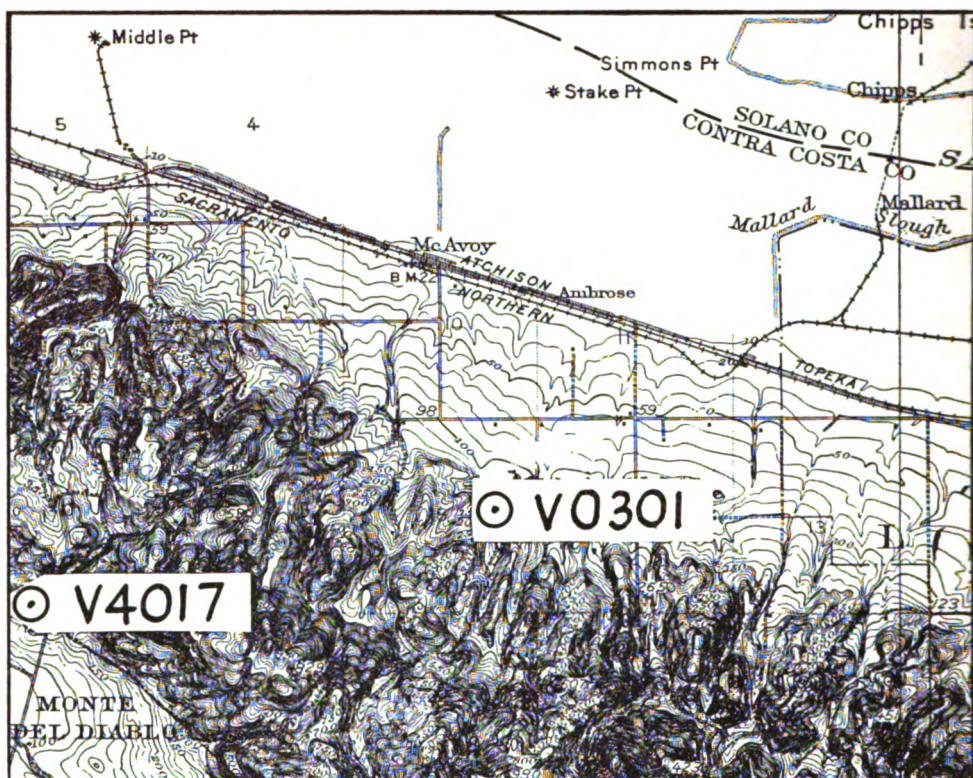


Fig. 36. Antioch quadrangle, edition of 1943. Contour interval, 10 feet.
Scale of this extract, 1: 62,500.

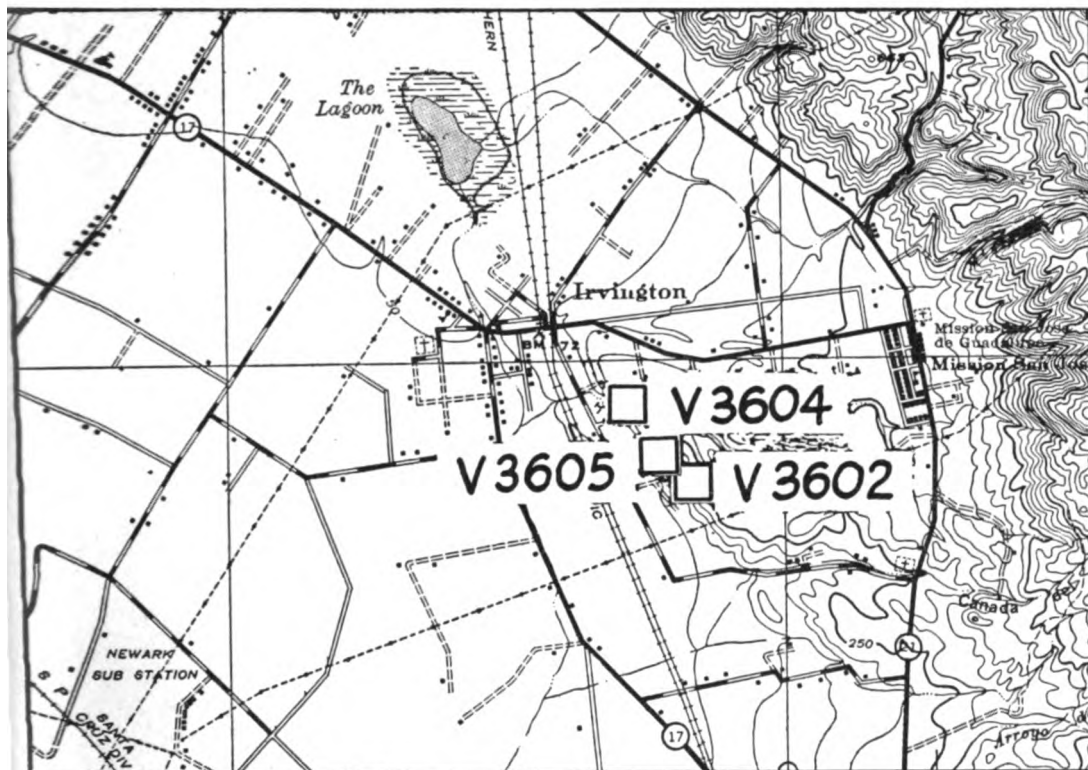


Fig. 37. Pleasanton quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

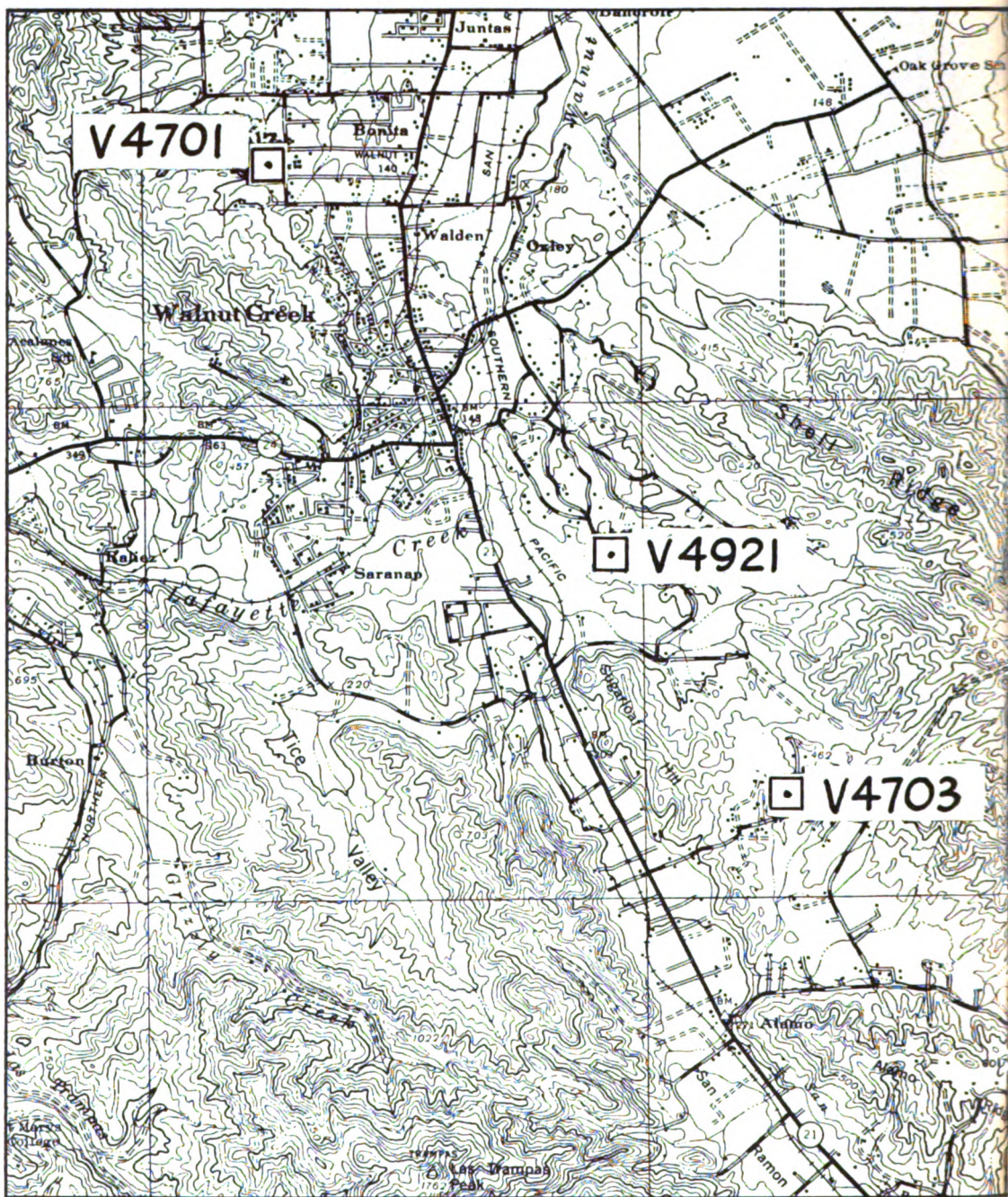


Fig. 38. Concord quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.



Fig. 39. Concord quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

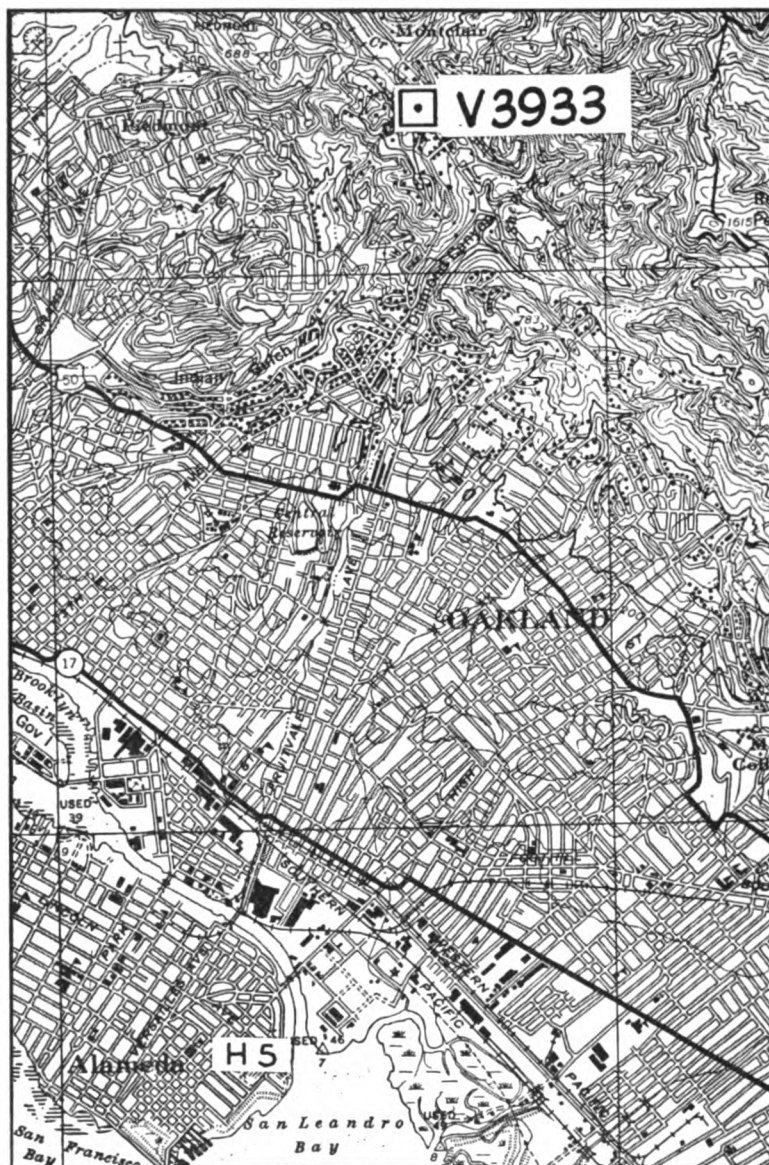


Fig. 40. Concord quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

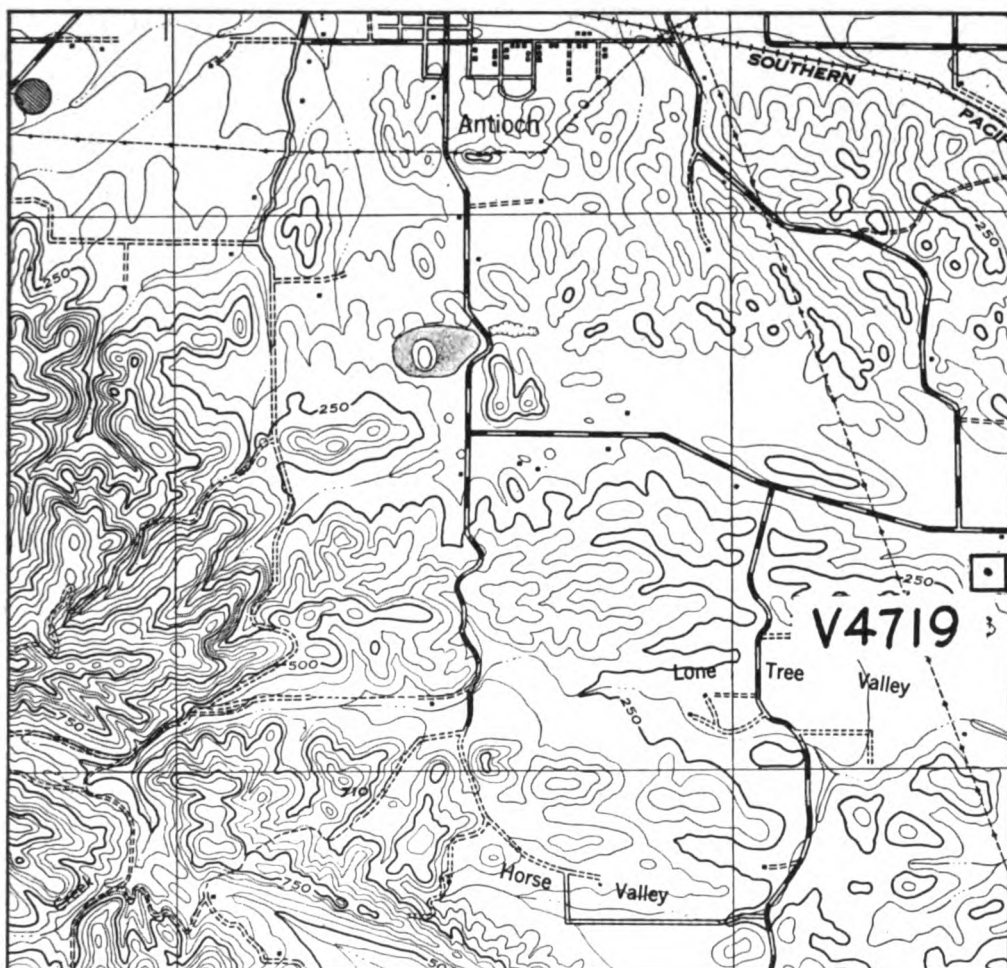


Fig. 41. Mount Diablo quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

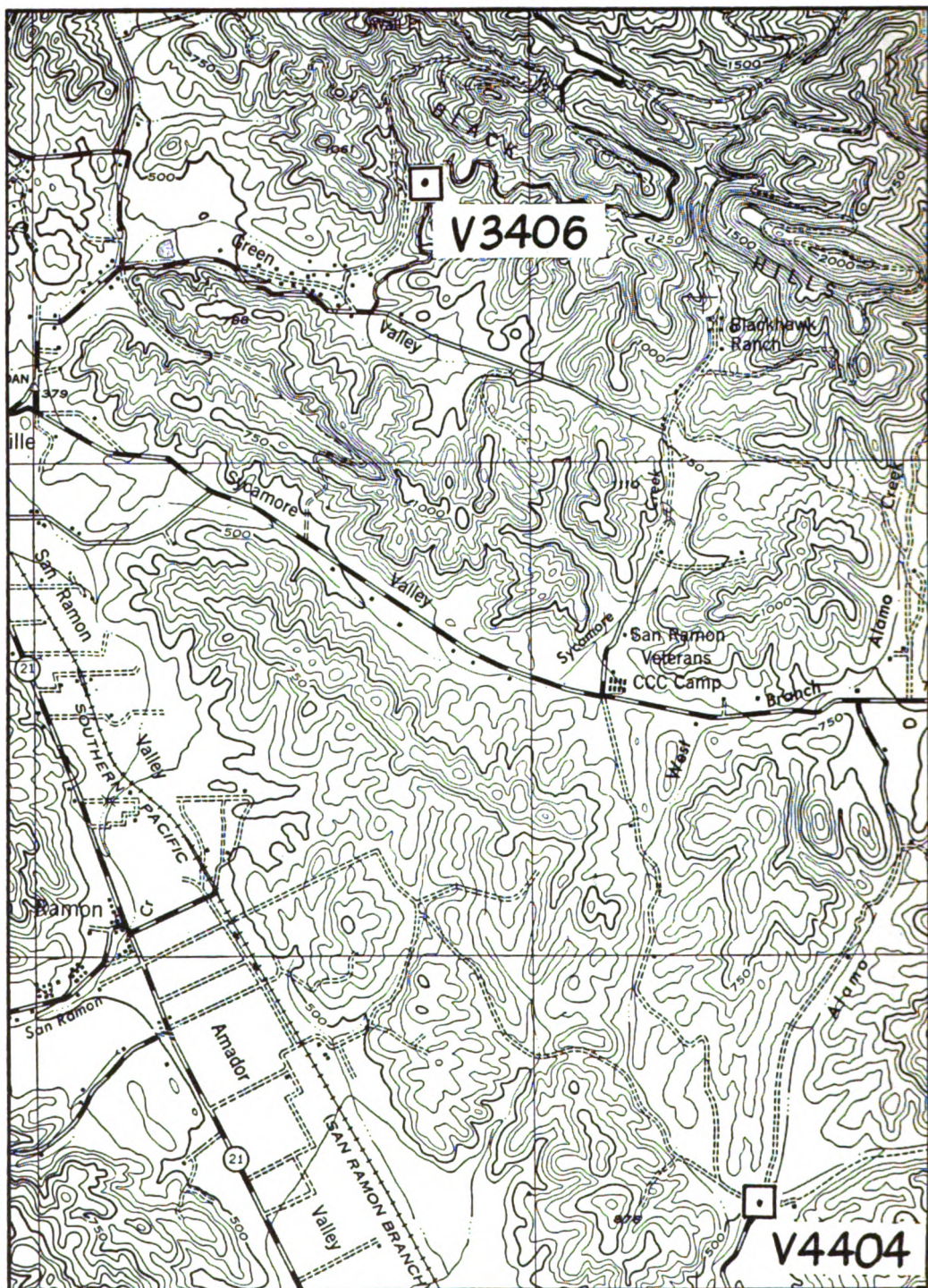


Fig. 42. Mount Diablo quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

[300]

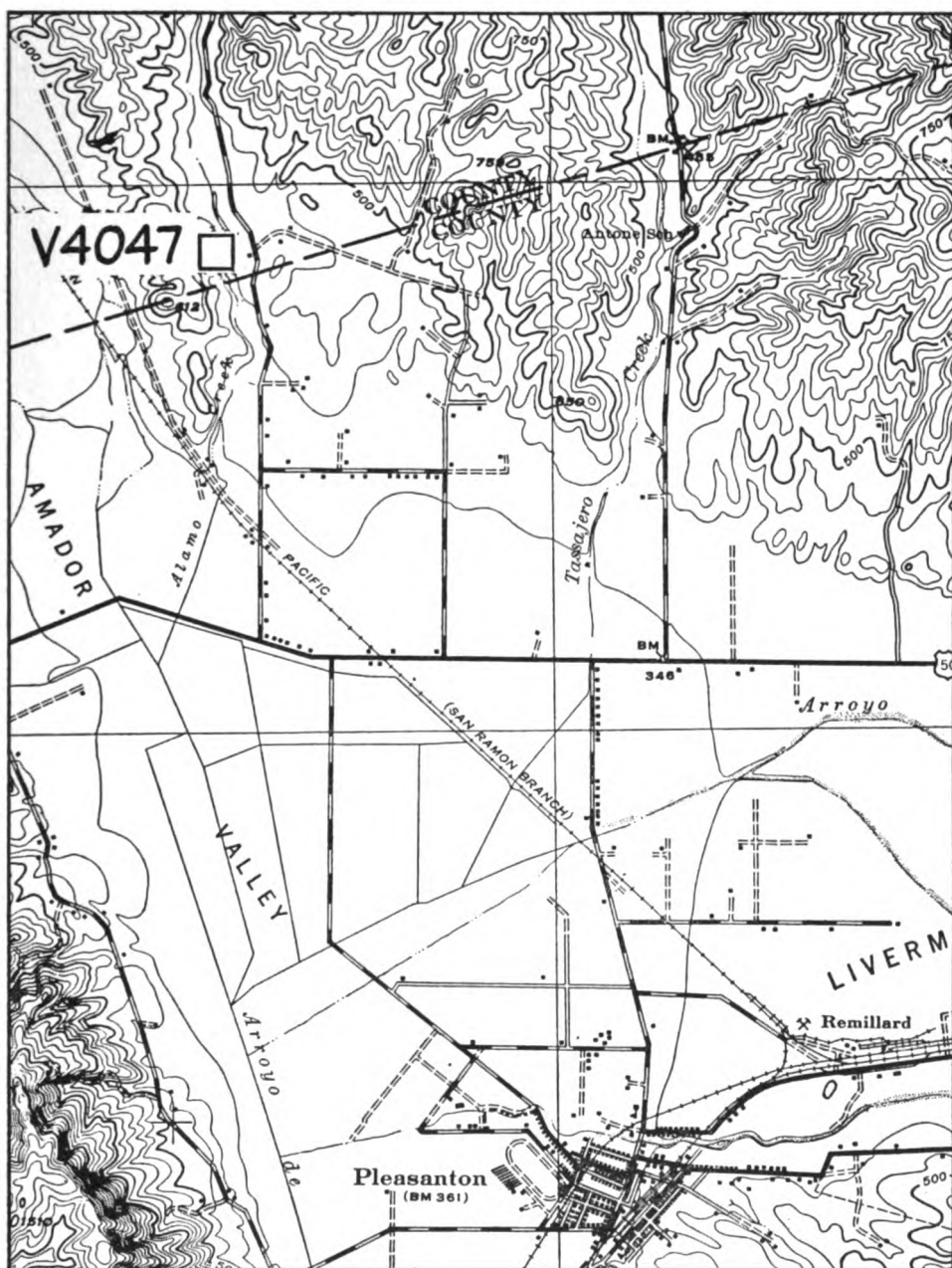


Fig. 43. Pleasanton quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

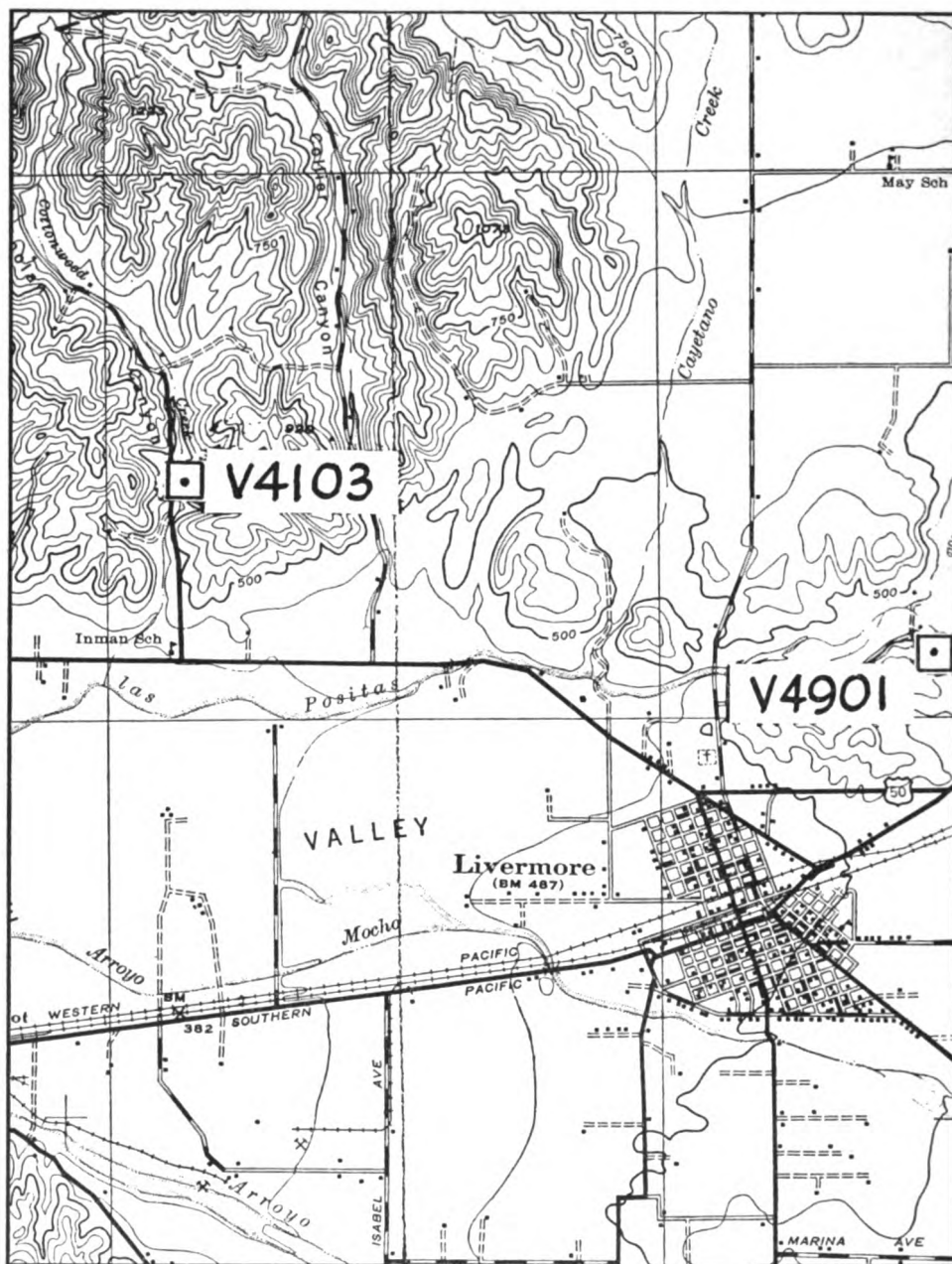


Fig. 44. Pleasanton quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

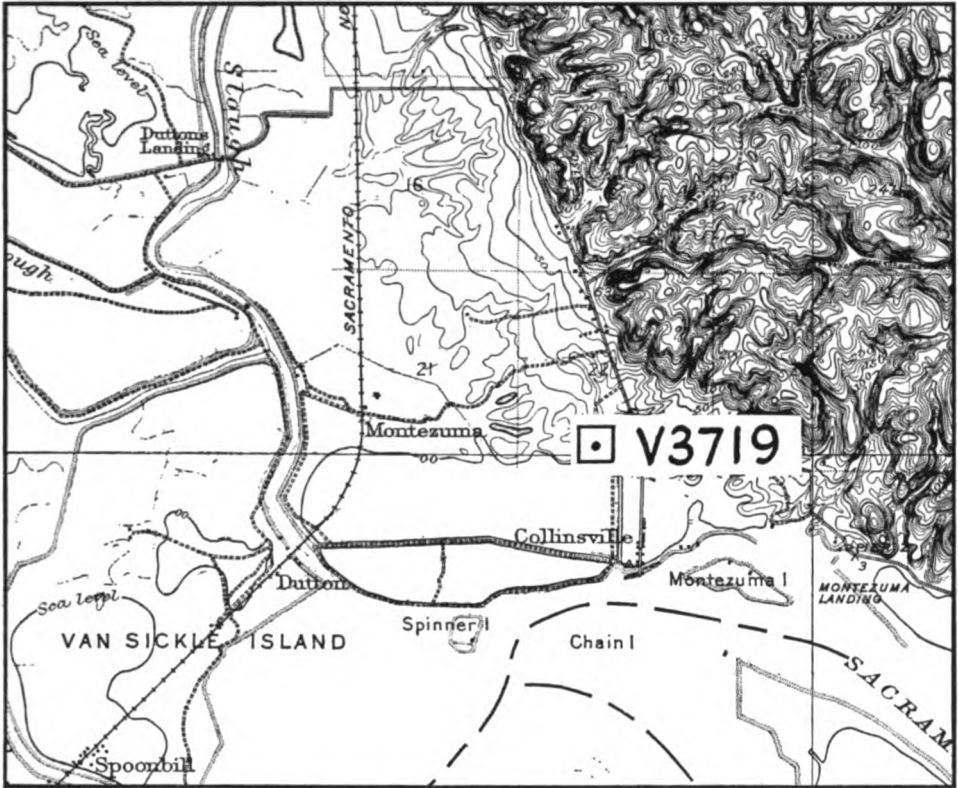


Fig. 45. Antioch quadrangle, edition of 1943. Contour interval, 10 feet.
Scale of this extract, 1: 62,500.



Fig. 46. San Mateo quadrangle, edition of 1943. Contour interval, 50 feet.
 Scale of this extract, 1: 62,500.

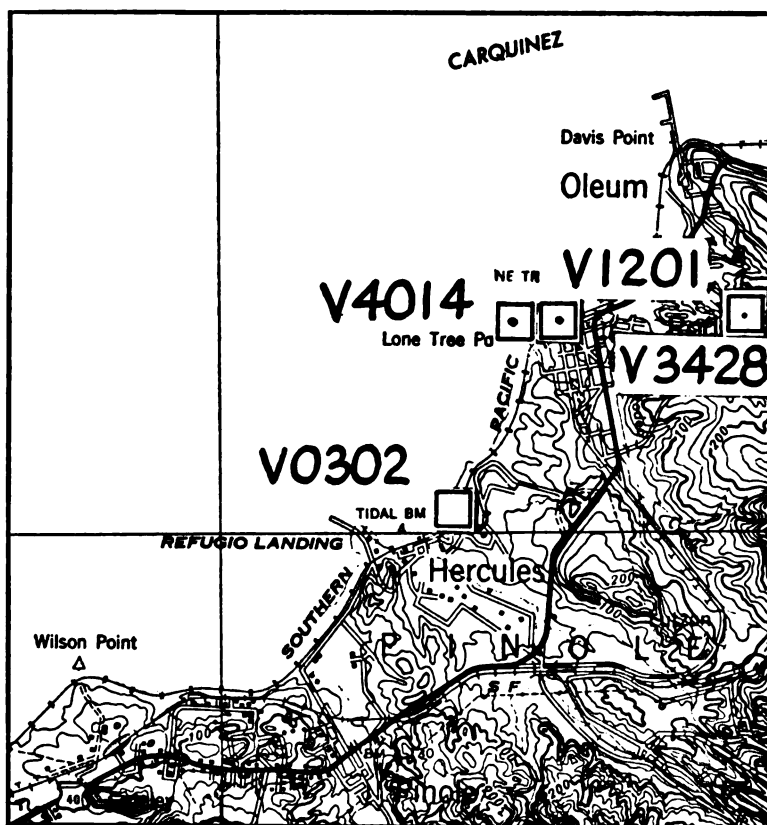


Fig. 47. Mare Island quadrangle, edition of 1942. Contour interval, 25 feet.
Scale of this extract, 1: 62,500.

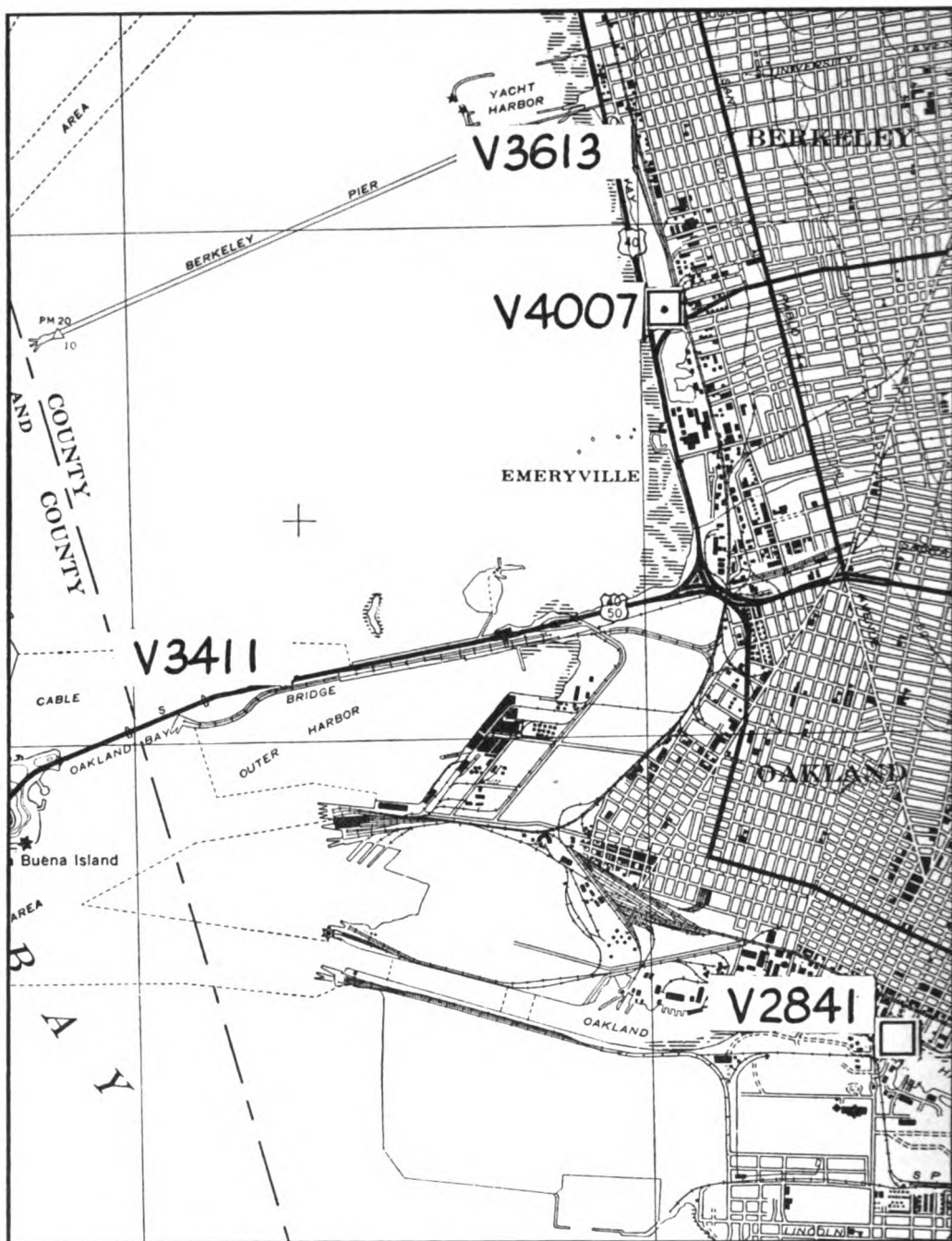


Fig. 48. San Francisco quadrangle, edition of 1942. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

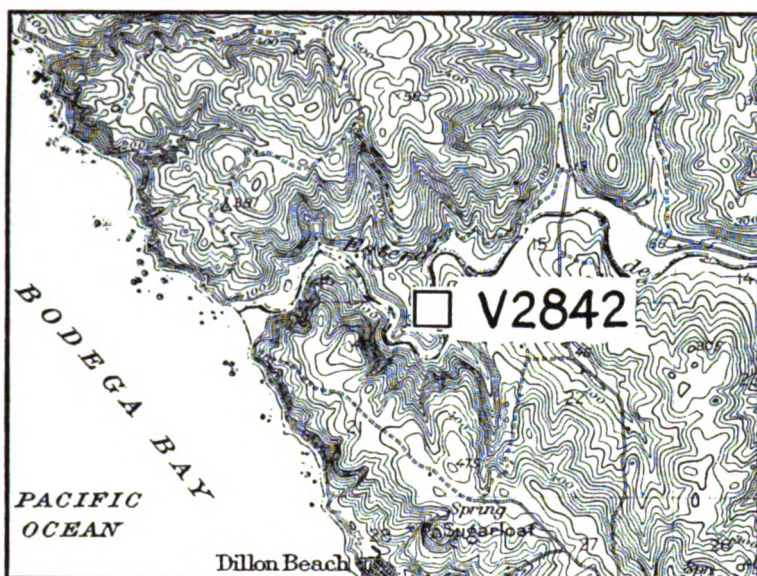


Fig. 49. Sebastopol quadrangle, edition of 1942. Contour interval, 25 feet.
Scale of this extract, 1: 62,500.

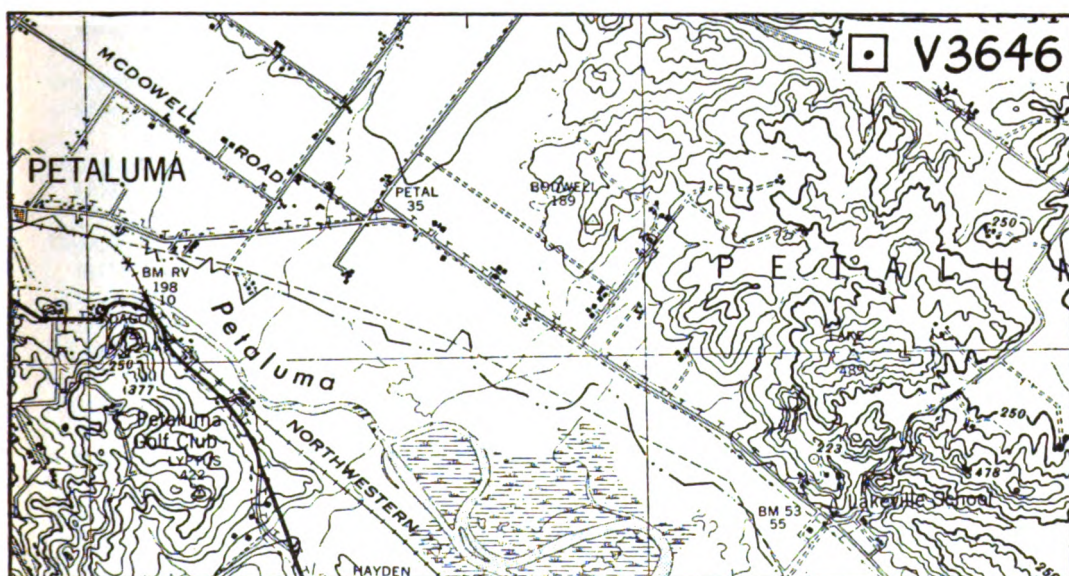


Fig. 50. Petaluma quadrangle, edition of 1942. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

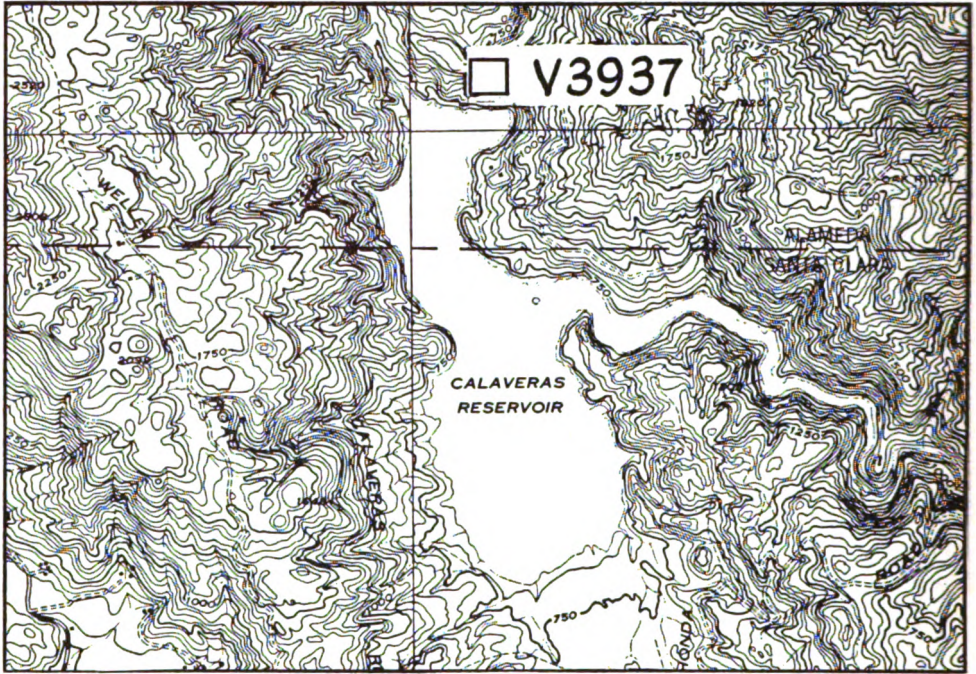


Fig. 51. San Jose quadrangle, edition of 1943. Contour interval, 50 feet.
Scale of this extract, 1: 62,500.

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