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A TERTIARY VERTEBRATE FAUNA FROM THE
UPPER CUYAMA DRAINAGE BASIN, CALIFORNIA

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With four plates and five text-figures

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INTRODUCTION

The discovery of Tertiary mammalian remains in the vicinity of Apache Canyon, in the upper Cuyama drainage basin, Ventura County, California, was made by Mr. John B. Stevens, geologist of the Associated Oil Company. Further collecting in this region has furnished a fauna of considerable stratigraphic and biologic significance. An investigation of the geologic features of the area and of the vertebrate collection was undertaken primarily with a view to establishing the position and relationships of the fossil assemblage in the sequence of Tertiary faunas known from the Pacific Coast and Great Basin provinces. A geologic study of the area in which the mammal-bearing beds occur and of the adjacent Lockwood Valley region to the east is still in progress.

The present study was suggested by Doctor Chester Stock, of the California Institute of Technology, to whom the author is greatly indebted for valuable advice during the progress of the investigation and patient criticism of the manuscript. The author wishes also to acknowledge the courtesy extended by Mr. Donald R. Dickey and his staff at the California Institute of Technology in allowing unreserved use of their excellent library and collection of recent mammals. The drawings were made by Mr. John L. Ridgway.

LOCATION AND PREVIOUS STUDIES OF REGION

The fossiliferous beds, indicated in figure 1, occur in the upper part of the Cuyama drainage system, west of Mount Pinos and south of the San Andreas Rift. Latitude 34° 50' N. and longitude 119° 20' W. intersect in a point near the vicinity of the fossil occurrences. The latter lie immediately south of the northern boundary of Ventura County, California.

During the period 1854-5, the Cuyama Valley was visited by one of the Pacific Railroad Survey parties and the geological features of the region were described by Thomas Antisell (1857, 53-57). Fairbanks (1894, 493-526) made a reconnaissance survey of the northern part of Ventura County and of several counties to the west and northwest, and later (1895, 273-300) described an analcite diabase on the northern side of Cuyama Valley. The report by A. C. Lawson (1908, 22 and 42) on the California Earthquake of 1906 includes a discussion of the principal physiographic features of the area. In the same publication Fairbanks described the San Andreas

Rift, which traverses the region to the north of the mammal-bearing beds. In studies relating to the occurrence of borax deposits, H. S. Gale (1914, 434-456) discussed the geology of the basin of Lockwood Valley immediately east of the upper Cuyama drainage. W. A. English (1916, 191-215) published a detailed description of the geology of Cuyama Valley, including a map of the formations involved in the structure of parts of both sides of the valley to the west of the fossil localities. The region north of the San Andreas Rift, in the vicinity of San Emigdio Mountain, has been described by R. W. Pack (1920, 1-179), and later by C. M. Wagner and K. H. Schilling (1923, 235-276). W. S. W. Kew (1919, 1-21) and R. N. Nelson (1925, 327-396) investigated the geology of portions of the upper Santa Ynez drainage basin lying to the southwest of Cuyama Valley.

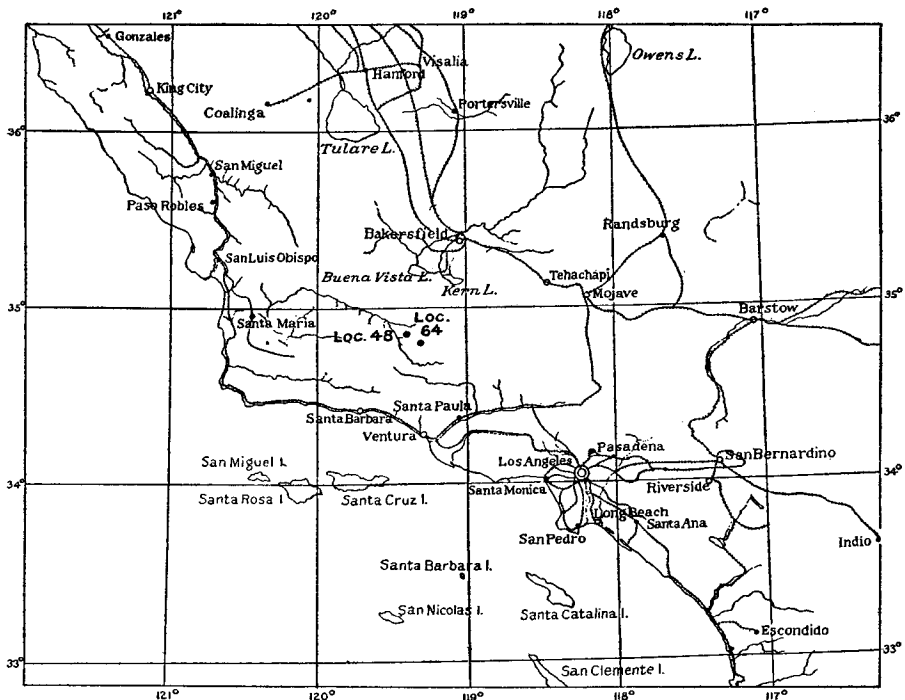


FIG. 1.—Index map of a portion of southern California showing location of Cuyama Valley fossil vertebrate occurrences.

STRATIGRAPHIC SUCCESSION

The formations identified by W. A. English as occurring on the southwest side of the Cuyama Valley are as follows: (1) a series of pre-Monterey shales, (2) the Monterey group, consisting of the Maricopa and Vaqueros members, (3) the Santa Margarita sandstones and shales, (4) the Cuyama Pliocene(?), (5) the Pleistocene

terrace sands and gravels, and (6) Recent alluvium. The stratigraphic succession in the vicinity of the fossil beds includes: (1) a large block of gneissoid granite to the east (Mount Pinos) with several scattered granite inliers in the sedimentary basin; (2) an extensive series of highly colored non-marine beds, considered by English as being approximately the equivalent of the Monterey; (3) the Santa Margarita(?) in the broad application of the name; and (4) Quaternary terrace and alluvial deposits.

OCCURRENCE OF FAUNA

The occurrence of Tertiary vertebrates in Apache Canyon is located approximately eight miles up this canyon, northwest of the Apache Canyon potrero. Parallel to and north of Apache Canyon is Quatal Canyon which has cut through the same horizon six or seven miles from Cuyama Valley.

The deposits in which the vertebrate fossils were found lie near the top of the formation tentatively recognized as the Monterey. The material is scattered through these upper beds from the bottom of a very conspicuous dark brown gypsiferous clay stratum to a level at least several hundred feet lower. The occurrence of fossil remains is not sharply limited to a definite horizon, but apparently becomes less frequent near the upper and lower limits of the section. The fossils are very scattered in the lowest levels exposed in the ravines adjacent to the northern portion of Apache Canyon, and the still lower horizons present in the northeastern part of Quatal Canyon have not been productive.

AGE AND RELATIONSHIPS OF THE CUYAMA FAUNA

The following is a faunal list of the types represented in the fossil collection from Cuyama Valley:

Testudinate remains

Avian remains

Carnivora

Canid ? sp.

Rodentia

Citellus (*Protospermophilus*) *quatalensis* n. subgen. and sp.

Perognathus furlongi n. sp.

Hypolagus ? *apachensis* n. sp.

Proboscidea

Mastodont sp.

Perissodactyla

Merychippus sumani Merriam

Protohippus sp.

Hipparion ? sp.

Artiodactyla

Oreodont sp.

Camelid sp.

Merycodus sp.

In an attempt to reach a satisfactory age determination of the rather incomplete fauna listed above, evidence can be secured not only from a comparative study of several of the individual forms

occurring in the assemblage, but also from a consideration of the stratigraphic position and structural relations of the mammal-bearing beds in the Cuyama region. It is important furthermore to recognize the relationship of the vertebrate horizon to deposits in which marine invertebrate faunas have been found.

W. A. English (1916, 191-215) correlated the Tertiary formations on the east and west sides of Cuyama Valley on the basis of regional structure. The broad portion of Cuyama Valley in which the Cuyama Ranch is located appears to be a synclinal basin, the axis of which leaves the valley on its east side between Ballinger and Quatal Canyons. The vertebrate horizon on the northeast flank of the syncline apparently occupies a stratigraphic position equivalent to that occupied by upper beds of the Monterey group on the southwest flank in Santa Barbara Canyon. In referring to the Monterey the formation containing the mammalian remains, a difficulty is encountered in that the lithology of this deposit is noticeably different from that of the Monterey on the west side of the valley. Moreover the lack of vertebrate fossils in the Monterey on the west side and the scarcity of invertebrate remains on the east side preclude the possibility of a satisfactory correlation of the two sets of beds on a basis furnished by paleontological data. Further evidence tending to support a correlation of the deposits occurring on the two sides of the valley rests on the presence of a basalt flow in the upper portion of the mammal-bearing beds as exposed north of Quatal Canyon. Basalt flows, according to English, are rather characteristic of this horizon at a number of localities, particularly in the Caliente Range to the north of Cuyama Valley where they are associated with upper beds of the Maricopa shales. It should be noted, however, that an earlier period of extrusion of perhaps Vaqueros age is recorded in the area north of Lockwood Valley, where flows are found in association with a colemanite deposit.

The following Tertiary invertebrate assemblages are recorded by English from the Cuyama region:

- (1) From close to the base of the white sandstone of the Vaqueros near Santa Barbara Canyon:

<i>Pecten magnolia</i>	<i>Pecten voleformis</i>
<i>Pecten bowersi</i>	<i>Turritella inezana</i>

- (2) From near the top of the Vaqueros southeast of Caliente Range:

<i>Chione panzana</i>	<i>Calyptrea</i>
<i>Chione</i> n. sp., near <i>diabloana</i>	<i>Murex vaquerosensis</i> new var.
<i>Mytilus mathewsoni</i> var. <i>expansus</i>	<i>Trophosyon</i> sp. ?
<i>Panopea estrellanus</i>	<i>Turritella ocoyana</i>
<i>Pecten crassicardo</i>	

- (3) From the upper part of the Monterey group south of Cuyama Valley:

<i>Scutella norrisi</i>	<i>Phacoides acutilineatus</i>
<i>Chione securis</i>	<i>Venus pertenuis</i>
<i>Ostrea veatchii</i> ?	<i>Turritella ocoyana</i>
<i>Pecten andersoni</i>	

(4) From the Whiterock Bluff shale (middle) member of the Santa Margarita formation:

<i>Astrodapsis antiselli</i>	<i>Venus pertenuis</i>
<i>Astrodapsis tumidus</i>	<i>Agasoma sinuatum</i>
<i>Ostrea titan</i>	<i>Turritella carisaensis</i>
<i>Pecten crassicardo</i>	<i>Turritella ocoyana</i> new var.?
<i>Trophon gabbianum</i> ?	<i>Tamiosoma gregaria</i>

The stratigraphic position of the mammal-bearing beds appears to be approximately equivalent to the deposits from which the invertebrates given in the third list above are recorded, and occurs apparently within the limits of the range of *Turritella ocoyana*. This position would place the vertebrate stage in close time relation with the stratigraphic or faunal unit commonly called the Temblor and currently considered as middle Miocene in age. *Ostrea titan* and *Pecten crassicardo* are unfortunately the only mollusks found in the marine deposits, which English considered Santa Margarita, that overlie the mammal horizon in Quatal Canyon.

CORRELATION OF FAUNA

PACIFIC COAST PROVINCE

Occurrences of Miocene mammal-bearing beds in the Coast Ranges of California are apparently infrequent, due to the dominance of marine formations in this region. Extensive transgressions of the sea were presumably characteristic of this period, and it becomes apparent that in the marginal transition zones lying between the coastal province and the Great Basin, where an interfingering of terrestrial accumulations representing temporary recessions of the sea may occur, were conditions most opportune for a record of land mammals. The significance of these occurrences in Tertiary correlation studies involving the Pacific Coast and the continental region to the east has been fully appreciated.

In the Coast Ranges north of Cuyama Valley the "Big Blue" or "Rainbow" beds of the North Coalinga region (J. C. Merriam, 1915) seemingly correspond stratigraphically to the Cuyama faunal horizon, particularly with regard to its relation to the overlying "Santa Margarita." At the former locality the *Merychippus* zone lies below the "Big Blue" in beds recognized as Temblor. The mammalian fauna of the *Merychippus* zone includes relatively few forms and is chiefly characterized by the presence of *Merychippus californicus*. On the basis of evidence furnished by a comparison of the stages of development in the merychippine group, *Merychippus sumani* occurring in the Cuyama fauna appears to be somewhat more advanced than *M. californicus*. This is suggested by the greater size, heavier cementation and more prominent styles of the upper cheek-teeth in the former species. This evidence might indicate a later age for the Cuyama assemblage, but it is not conclusive, inasmuch as primi-

tive forms may be contemporaneous with more advanced types. Certainly a consideration of the relative ages of the two horizons should take into account more than a single species. Unfortunately, in the present instance, mammalian types occurring in the one fauna are absent in the other, and this with the incomplete preservation of the materials from both horizons do not furnish an adequate basis for comparison.

Tertiary mammalian remains have been recorded by Chester Stock (1920, 267-276) from the Tecuya beds of Tecuya Canyon at the southern end of the San Joaquin Valley. It is interesting to note that the Tecuya beds are not far removed geographically from the deposits in the Cuyama region. These red beds are presumed to underlie conformably a marine series considered as the Monterey group. The fauna includes an hypertragulid, rhinoceros, and a sciurid. Although the direct comparisons which can be made between the Cuyama and Tecuya faunas are extremely limited, the presence of an hypertragulid in the latter assemblage is suggestive of an earlier stage. The difference in stratigraphic position of the two horizons with reference to the Monterey series is further evidence in support of this view.

The Mint Canyon fauna, from the Mint Canyon deposits in Los Angeles County, investigated by Mr. J. H. Maxson, is a Miocene assemblage exhibiting apparently some resemblance to the Cuyama. The following is a comparative list of the faunas from the Cuyama and Mint Canyon:

CUYAMA VALLEY:

Testudinate remains
 Avian remains
 Canid ? sp.
 Citellus (Protospermophilus)
 quatalensis n. subgen. and sp.
 Perognathus furlongi n. sp.
 Hypolagus ? apachensis n. sp.
 Mastodont sp.

Merychippus sumani Merriam

Protohippus sp.

Hipparion ? sp .

Camelid sp.
 Oreodont sp.
 Merycodus sp.

MINT CANYON:*

Testudinate remains
 Avian remains
 Aelurodon sp.

Hypolagus ? apachensis
 Trilophodon sp.
 Rhinocerotid, indet.
 Parahippus (Archeohippus) near
 mourningi Merriam
 Merychippus sp.
 Merychippus sumani Merriam
 Merychippus (Protohippus)
 intermontanus Merriam
 Protohippus sp.
 Hipparion ? near mohavense callodonte
 Merriam
 Hipparion ? sp.
 Prosthennops ? sp.
 Miolabis, new form
 Alticamelus ? sp.
 Oreodon, cf. Merychys
 Merycodus near necatus
 Large Antilocaprid indet.

* Faunal list furnished by J. H. Maxson.

The Mint Canyon beds lie stratigraphically below marine strata recognized by W. P. Woodring (1930) as being approximately equivalent to the Cierbo division of the San Pablo group. The stratigraphic positions of the Cuyama and Mint Canyon beds as at present determined do not prevent them from possessing nearly the same age. Furthermore, there prevails some faunal similarity between the two horizons. The equine species, *Merychippus sumani* Merriam, is present in both assemblages.

While the Cuyama fauna is too incompletely known to permit a satisfactory determination of exact time relationships to the Mint Canyon, it appears possible that the former is slightly older than the latter or occupies perhaps an early stage in the longer period represented by the entire Mint Canyon assemblage.

GREAT BASIN PROVINCE

The Cuyama fauna compares most favorably with the Barstow Miocene of the better-known Tertiary faunas of the Great Basin region. All the more important larger mammals of the Cuyama fauna are known from the Barstow, although specific comparisons are not always possible. The species *Merychippus sumani* was originally described from the Barstow by J. C. Merriam. Unfortunately the rodents from the latter horizon have not been as yet fully investigated.

The Cache Peak fauna (Buwalda, 1916, 75-85) described from deposits exposed in the Tehachapi Pass region not far to the east of the Cuyama locality may be somewhat less advanced than the Cuyama fauna, and the Phillips Ranch occurrence, from which is recorded a very primitive species of *Merychippus*, is probably much earlier.

DESCRIPTION OF MATERIAL

TESTUDINATE REMAINS

Tortoises are represented in the collection by a nearly complete limb bone and a number of fragments of the exoskeleton.

AVIAN REMAINS

An incomplete sacrum from the Cuyama beds has been identified by Dr. Hildegard Howard of the Los Angeles Museum as belonging to a bird.

CARNIVORA

Canid ? sp.

Remains of carnivores are almost totally lacking in the Cuyama assemblage. Fragments of a right and a left ramus comprise the only material available and represent a small canid-like form, approximating the recent fox in size. The right ramus, No. 64, is without teeth. The posterior root of P3, and roots of P4, and the anterior part of M1 are present in the jaw. Left ramus, No. 65, carries a partially preserved P4 and root portions of M1.

RODENTIA

Citellus (Protospermophilus) quatalensis n. subgen. and sp.

Type specimen—No. 30 C. I. T. Coll. Vert. Pale., a skull including superior dentition and lower jaw from locality 48 in Quatal Canyon, eight miles east of Cuyama Valley.

Paratypes—Left ramii, Nos. 31 and 32.

Subgeneric characters—Skull robust. Muzzle broad and vertically compressed with strong dorso-lateral ridges parallel to alveolar portion of incisors. Lower jaw shallow but strong. Superior surface of lower jaw between I and P₄ not greatly depressed. Upper and lower cheek teeth small, quadrate, low cusped and shallow basined. P₃ much reduced. Internal cusp partially divided on superior teeth. Trigonid ridge undeveloped in lower molars.

Specific characters—Superior and inferior diastemata between incisors and premolars relatively short. Palate wide in proportion to length of tooth row. Fossæ posterior to incisors and antero-lateral to anterior palatine foramina prominent. Lower tooth row long in proportion to depth of jaw. Masseteric fossa strong and terminates anteriorly beneath M₁. Lower teeth with postero-internal ridge terminating anteriorly in the entoconid which is disconnected from the paraconid. Very small accessory cuspule or cuspules between outer cusps on upper and lower cheek teeth.

Material—This species is represented in the collections of the California Institute by a series of eight specimens. Specimen No. 30 consists of the anterior part of the skull with the larger portion of the superior dentition and both ramii of the lower jaw which were found in immediate association with the skull. No. 34 is a more fragmentary skull than No. 30 and without teeth. Nos. 31 to 33 inclusive are lower jaw fragments carrying from two to four teeth apiece.

Description—The skull is characterized by an extremely broad muzzle with the premaxillaries forming a considerable portion of the dorsal surface well toward the anterior end. A strong dorso-lateral ridge extends parallel to the alveolar portion of the incisor from the zygoma to the nasal opening. In the living forms this ridge is not nearly so conspicuous. The width of the ventral surface of the skull is also very pronounced in the vicinity of the anterior palatine foramina. The fossæ posterior to the incisors and antero-lateral to the anterior palatine foramina are large as in many living ground squirrels. The ventro-lateral margins of the infra-orbital foramina are developed much as in Recent species referred to *Otospermophilus*.

The lower jaw has a rather short diastema between incisor and P₄. The superior margin of the jaw in this region is not much depressed below the level of the tooth-row. The depth of the mandible below the grinding teeth is small, this being rather characteristic of terrestrial forms and apparently an adaptive feature. The masseteric fossa is deep and the ridge along the lower margin in the anterior part is very prominent, indicating a strong masseter muscle.

P₃ is very small and simple, much as in *Sciurus*. In modern ground squirrels, particularly in the true citellids, this tooth is rather well developed and often bicuspid. The superior grinding teeth are quadrate in shape, rather low cusped and shallow basined as in both *Sciurus* and the otosper-

mophilid ground squirrels, and differ somewhat in these characters from the comparable teeth in the typical citellids. Moreover, the teeth are noticeably small in proportion to the size of the skull. The posterior ridge running transversely inward from the postero-lateral cusp (metacone) in teeth present in No. 30 is formed by the metacone and protocone and a small intermediate cusp. Also, it is noticeable that one or two intermediate cusps are present on the outer rim between the paracone and metacone in several of the teeth. The most characteristic feature in the upper dentition, however, lies in the division of the internal cusp in each tooth into two equal and closely appressed cusps, adding to the rectangular appearance of the teeth. These cusps are completely united in all Recent genera. The division of the cusps is a primitive character and is commonly found in the Eocene and early Oligocene Ischyromyidae, which family is regarded as ancestral to the Sciuridae (W. D. Matthew, 1910, 64).

The lower teeth increase in size from P4 to M2 and are rudely rectangular in shape, except P4 which is somewhat triangular due to the appressed character of the two anterior cusps. In this respect No. 30 corresponds more closely to *Otospermophilus* than to the typical citellids. The teeth have low, well-defined cusps and rather shallow basins. The postero-internal ridge is separated from the paraconid and carries a rather well-developed entoconid which is more like that in *Sciurus* than in any of the citellids. The paraconid is only slightly higher than the remaining, nearly equally elevated cusps, and in this respect approaches *Sciurus* and to a less extent *Otospermophilus*. The paraconid and protoconid do not tend to form a high trigonid ridge, as they do in typical *Citellus*.

Relationship—On the basis of available material, *Citellus* (*Protospermophilus*) *quatalensis* appears to resemble the Recent genus or subgenus *Otospermophilus* more nearly than it does any of the other sciurids. Moreover, the new form presents an association of primitive characters which suggests that the dentition possessed by the modern otospermophilids is more primitive than that exhibited by the typical citellids. This is also indicated by the development of the premolars which in the case of typical *Citellus* appear to have taken on more completely the characters of the molar teeth. From this consideration it seems probable that species of *Citellus* may have been derived from an *Otospermophilus*-like ancestor, probably later than the stage represented by *C. (P.) quatalensis*, assuming this form to be in or near the line of descent of the ground squirrels.

The ground squirrel stock may then have branched from the *Sciurus* line in post-Eocene time and prior to the upper Miocene. Moreover, existing groups of citellids are perhaps a result of post-Miocene specialization from a common ground-dwelling form and not in themselves culminating stages from a development along separate branches from the main sciurid stock. In arriving at this conclusion emphasis is placed particularly on the modification of the skull and lower jaw resulting from a semi-fossorial habitat. On the other hand, the dentition reflects to a certain extent the stage to which specialization has progressed in the different groups, the dentition of *Sciurus* having apparently retained the greatest association of primitive characters.

No. 30 differs from the type of *O. gidleyi*, described by Merriam, Stock and Moody (1925, 68-69) from the Rattlesnake Pliocene, in much shallower depth of mandible in proportion to length of tooth-row, in less elevation of the paraconid, and possibly in greater development of the entoconid. In

dentition *O. gidleyi* is more advanced than *C. (P.) quatalensis* and shows characters closer to the modern forms.

Measurements in millimeters

	C. (P.) quatalensis	S. griseus*	O. beecheyi*	C. richardsonii*
Depth of muzzle immediately in front of maxillaries.....	10.3	15.6	11.3	10.0
Width of muzzle.....	14.7	12.7	11.6	9.9
Length of diastema between I and P ₃	11.4	15.7	15.3	12.5
Width of palate between first molars	8.2	8.1	8.2	7.6
Length of palate from incisors to post-palatal notch.....	24.9	30.7	28.3	25.2
P ₃ -M ₃ , greatest length.....	a 10.5	11.6	11.2	10.6
I, anteroposterior diameter...	a 3.4	3.6	2.8	2.0
I, transverse diameter.....	1.9	2.0	1.8	1.6
P ₄ , anteroposterior diameter.....	2.0	2.3	2.0	1.9
P ₄ , transverse diameter.....	2.5	2.7	2.7	2.7
M ₁ , anteroposterior diameter.....	2.2	2.9	2.3	2.0
M ₁ , transverse diameter.....	2.6	3.3	3.2	3.0
M ₂ , anteroposterior diameter.....	2.3	3.1	2.5	2.0
M ₂ , transverse diameter.....	2.7	3.6	3.2	3.0
M ₃ , anteroposterior diameter.....	3.3	2.7	2.7
M ₃ , transverse diameter.....	3.3	3.0	2.8
Depth of ramus under M ₁	7.3	10.5	8.0	7.5
Length of diastema between I and P ₄	6.6	8.2	9.6	8.0
P ₄ -M ₃ , greatest length.....	10.0	12.0	11.0	9.5
I, anteroposterior diameter...	3.1	3.8	2.6	2.2
I, transverse diameter.....	1.6	1.4	1.6	1.5
P ₄ , anteroposterior diameter.....	1.9	2.2	2.1	1.9
P ₄ , transverse diameter.....	1.8	2.4	2.5	2.4
M ₁ , anteroposterior diameter.....	2.0	2.8	2.3	2.0
M ₁ , transverse diameter.....	2.3	3.3	3.1	2.6
M ₂ , anteroposterior diameter.....	2.4	3.0	2.8	2.2
M ₂ , transverse diameter.....	2.7	3.5	3.3	3.0
M ₃ , anteroposterior diameter.....	3.2	3.6	3.4	3.3
M ₃ , transverse diameter.....	2.7	3.2	3.1	2.8

a approximate

* Recent skulls from Donald R. Dickey Collection.

Perognathus furlongi n. sp.

Type specimen—No. 35 C. I. T. Coll. Vert. Pale., a fragmentary skull including superior dentition, from locality 64 in a ravine adjacent to Apache Canyon, eight miles northeast of Cuyama Valley.

Specific characters—Dorsal surface of the muzzle is broad with the naso-frontal suture anterior to the suture between premaxillary and frontal. Maxillary broad between the tooth-rows and diastema rather long. The tooth-row is not straight but tends to be convex outward. Teeth are convex externally in a vertical profile and the enamel is deeply infolded, slightly more so from the outer side than from the inner.

Comparison—Compared with the Recent species, *P. longimembris* and *P. californicus*, the teeth of the Cuyama form are somewhat less prismatic, each having a strongly convex external surface. The infolding of the enamel

in M₁ and M₂ is deeper in No. 35 than in the Recent species, making due allowance for differences arising from the inequality of wear in these teeth. The fold in both M₁ and M₂ is impressed well through the convexity of the outer side, giving the very base of the tooth at the alveolar border an indented outline.

The paleontological record of the pocket mice is very incompletely known. Dr. L. R. Dice (1925, 125) notes the presence in the Rancho La Brea Pleistocene of forms referable to the Recent subspecies *P. californicus californicus* Merriam. Matthew (1924, 85) has described the type *Peridomys rusticus* from the Miocene lower Snake Creek beds of Nebraska and places the genus in the family Heteromyidæ. *Peridomys* appears to be closely related to *Perognathus* but unfortunately no comparison can be made with the Cuyama specimen, inasmuch as Matthew's description was based on a lower jaw.

Perognathus furlongi is surprisingly similar to living species of the genus, considering the wide separation in time. Although the type is somewhat more primitive in dental characters than the Recent forms, there is notable correspondence in the general appearance. This species furnishes apparently another example of the stability of structural characters exhibited by groups of rodents in their evolution during the later Cenozoic.

Measurements in millimeters of specimen No. 35

Width of muzzle dorsally.....	4.9
Width of palate at anterior palatine foramina.....	2.7
Length of diastema between incisor and P ₄	7.1
Depth of muzzle above median point in diastema.....	6.2
Width of palate between first molars.....	2.8
Length from anterior end of P ₄ to posterior end of M ₃	4.1
I, anteroposterior diameter.....	1.4
I, transverse diameter.....	0.9
P ₄ , anteroposterior diameter.....	1.6
P ₄ , transverse diameter.....	1.2
M ₁ , anteroposterior diameter.....	0.9
M ₁ , transverse diameter.....	1.3
M ₂ , anteroposterior diameter.....	0.8
M ₂ , transverse diameter.....	1.2
M ₃ , anteroposterior diameter.....	0.7
M ₃ , transverse diameter.....	0.9

Hypolagus ? apachensis n. sp.

Type specimen—No. 36 C. I. T. Coll. Vert. Pale., a left ramus of the mandible including inferior dentition without incisor, from locality 64 in a ravine adjacent to Apache Canyon, eight miles northeast of Cuyama Valley.

Paratype—No. 39, a maxillary fragment including P₂ to M₃.

Specific characters—Size smaller than in other known species referred to *Hypolagus*. Masseteric fossa weak. Anteroposterior and transverse diameters of lower molariform teeth are nearly equal. P₃ is elongate anteroposteriorly with postero-external re-entrant fold simple and extending nearly halfway to internal margin, and antero-external re-entrant fold shallow and V-shaped. External surface of P₃ may show one or two slight longitudinal grooves. P₂ is fairly broad with one prominent and one less conspicuous anterior enamel fold.

Material—*H.?* *apachensis* is represented by approximately fifteen lower jaw fragments, retaining each from one tooth to a full set of grinding teeth. One fragment, No. 63, consists of the anterior portion of the ramus with the base of the incisor and P $\bar{3}$. In the collection are several maxillary fragments in various stages of preservation; No. 39 possesses a complete cheek-tooth series. A few incomplete limb elements are also present.

Description—*Hypolagus?* *apachensis* compares favorably in dimensions of lower jaw, as far as known, with living species of *Sylvilagus*. Each of the lower cheek-teeth from P $\bar{4}$ to M $\bar{2}$ inclusive exhibits a fairly simple external enamel fold extending practically to the internal margin. This fold divides each tooth into two adjoining columns. The internal surface of P $\bar{3}$ may not be evenly rounded, but may have a slight yet definite groove throughout the length of the tooth. In one of the jaw fragments, No. 38, C. I. T. Coll., P $\bar{3}$ is more elongated anteroposteriorly than is the case in specimen No. 36 and shows two such flexures. M $\bar{3}$ is a double columned tooth with the fission taking place as a result of the extension of the re-entrant fold from the external surface toward the inner margin of the tooth. The masseteric fossa is apparently weak and terminates anteriorly at a point directly beneath M $\bar{3}$.

In the complete upper series, No. 39, P $\bar{2}$ is elongated laterally and shows a pronounced anterior fold with a second and incipient fold external to it. P $\bar{3}$ to M $\bar{2}$ inclusive are simple teeth with an internal, feebly crenulated re-entrant fold extending slightly past the middle of each tooth. The crenulations are not so well defined as in modern species of rabbits from California and are more like those in *H. vetus*. The external surfaces of these teeth are folded inward, but not deeply.

Comparison—The Cuyama form differs from the type species, *Hypolagus vetus* (Kellogg) (1910, 436-437, and see also L. R. Dice, 1917, 181-182) from the Thousand Creek Pliocene of Nevada in smaller size and in the character of the teeth. P $\bar{3}$ is narrower, has a less triangular shape, a more convex anterior surface, and a slightly less sharp and shallower antero-external re-entrant fold than in *H. vetus*. Usually the groove or grooves on the inner surface of this tooth are not noticeably developed in *H. vetus*, but instead this portion of the tooth is abruptly flexed, giving the triangular cross-section. P $\bar{4}$ to M $\bar{2}$ are broader anteroposteriorly in proportion to their transverse width than in *H. vetus*. Also the upper teeth have a simpler, less serate internal fold than in the type species.

H.? *apachensis* differs from *H. edensis* Frick (1921, 348) of the lower Pliocene Eden beds in having a considerably shallower antero-external re-entrant fold in P $\bar{3}$ and a more posterior position of this infolding. In *H. edensis* the fold is more nearly on the anterior surface of the tooth and has in consequence changed materially the whole aspect of the tooth, giving it an appearance somewhat like that in modern forms.

The Cuyama species differs from *Lepus macrocephalus* Matthew (1907, 214-216) from the Upper Rosebud of South Dakota in possessing a larger diastema and shorter tooth row in proportion to depth of jaw. Also, *L. macrocephalus* is a distinctly larger form, although not much larger than *H. vetus*. Matthew in a later paper (1924, 86-87) refers this species and *L. primigenius* tentatively to the genus *Archæolagus*.

H.? *apachensis* approaches *Archæolagus ennisianus* (Cope) (1882, 385-386; see also Dice, 1917, 180-181) in size and in weakness of the lower jaw. Although the form is close to *Archæolagus* it appears to be

more advanced in most characters. P $\bar{3}$, though elongate, is not so elongate as in *A. ennisianus* and the antero-external re-entrant fold is sharp and more pronounced than in the latter type. P $\bar{2}$ has two instead of one anterior infold in *H. ? apachensis*, and the internal re-entrant fold in each of the upper molariform teeth extends beyond the middle of the tooth and possesses crenulations, which is not the case in *A. ennisianus*.

In some characters *H. ? apachensis* appears to be transitional between *A. ennisianus* and *H. vetus*, as may be inferred from the two comparisons. However, it is possible that *H. ? apachensis* is not at all in the line of *Lepus* and the genus or subgenus *Hypolagus*, but rather in a more primitive line derived from *Archæolagus*, and possibly leading to such forms as *Sylvilagus* as indicated by the rather uniform small size of the jaw in *H. ? apachensis*.

Measurements in millimeters

	H ? apachensis	H. vetus	H. edensis
Depth of lower jaw below P $\bar{4}$	No. 36 9.6	12.8
Length of diastema of lower jaw between I and P $\bar{3}$	No. 63 12.2	14.1
P $\bar{2}$ -M $\bar{3}$, greatest length.....	No. 39 11.0
P $\bar{2}$, anteroposterior diameter.....	1.1
P $\bar{2}$, transverse diameter.....	2.1
P $\bar{3}$, anteroposterior diameter.....	1.5
P $\bar{3}$, transverse diameter.....	3.2
P $\bar{4}$, anteroposterior diameter.....	1.8
P $\bar{4}$, transverse diameter.....	3.0
M $\bar{1}$, anteroposterior diameter.....	1.7
M $\bar{1}$, transverse diameter.....	2.8
M $\bar{2}$, anteroposterior diameter.....	1.6
M $\bar{2}$, transverse diameter.....	2.3
M $\bar{3}$, anteroposterior diameter.....	1.0
M $\bar{3}$, transverse diameter.....	1.6
P $\bar{3}$ -M $\bar{3}$, greatest length.....	No. 38 11.0
I, anteroposterior diameter.....	No. 63 1.5	1.9
I, transverse diameter.....	2.0	2.5
P $\bar{3}$, anteroposterior diameter.....	No. 36 2.3	2.9	2.4
P $\bar{3}$, transverse diameter.....	2.0	2.8	2.1
P $\bar{4}$, anteroposterior diameter.....	2.1	2.7
P $\bar{4}$, transverse diameter.....	2.2	3.2
M $\bar{1}$, anteroposterior diameter.....	2.0	2.4	2.0
M $\bar{1}$, transverse diameter.....	2.1	3.1	2.2
M $\bar{2}$, anteroposterior diameter.....	2.0	2.6	2.1
M $\bar{2}$, transverse diameter.....	2.1	2.8	2.2
M $\bar{3}$, anteroposterior diameter.....	No. 38 1.5
M $\bar{3}$, transverse diameter.....	1.6

PROBOSCIDEA

Several tooth fragments have been collected which undoubtedly belong to the mastodon group. The material is, however, too fragmentary to permit even a generic determination.

PERISSODACTYLA

Merychippus sumani Merriam

An incomplete upper and lower dentition, No. 41, Calif. Inst. Tech. Coll. Vert. Pale., from locality 48 in Quatal Canyon and a single upper cheek-tooth, No. 29, from locality 64 in Apache Canyon constitute the more im-

portant materials representing this genus and species. A number of scattered limb fragments are tentatively referred to the same type. Specimen No. 41 includes three upper cheek-teeth of the right side, a portion each of left P_4 and M_1 , several lower teeth and the posterior portions of the two rami.

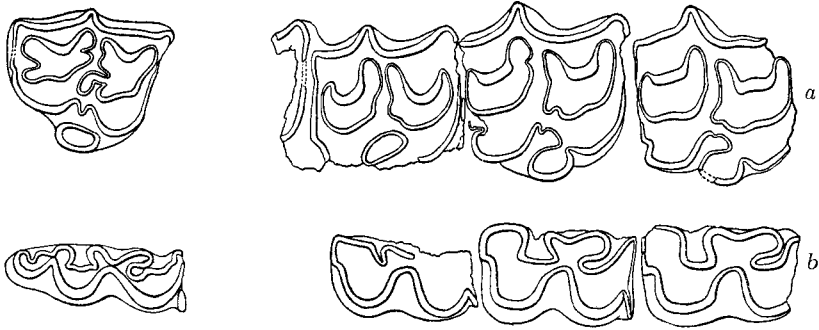


FIG. 2, *a* and *b*—*Merychippus sumani* Merriam. Superior and inferior cheek-teeth, No. 41, C.I.T. Coll.; *a*, occlusal view, P_3 , P_4 , M_1 (reversed from left side), and M_3 ; *b*, occlusal view, P_3 , P_4 , M_1 (reversed from left side), and M_3 ; x 1.0. Cuyama Valley Miocene, California.

Upper Cheek-Teeth—The upper teeth are well cemented and show a simple enamel pattern in an advanced stage of wear. The crowns of the teeth are nearly rectangular in cross-section, the anteroposterior length being slightly less than the transverse width in P_3 , P_4 and M_1 . The styles are prominent, especially the mesostyle as in the associated *Protohippus* material. The protocone is united with the protoconule in P_3 , but completely isolated in M_3 . P_4 shows a stage of wear in which the protocone has just united with the protoconule, but the isthmus is still very narrow. In M_1 the protocone has united with the hypocone as well as the protoconule. The hypocone is large in P_3 and M_1 with only a slight development of the posthypoconal valley. In P_4 the posthypoconal valley forms a somewhat deeper indentation. The fossettes are moderately broad, covering a large part of the crown area. M_3 shows greater relative complication of the enamel borders of the fossettes than in the preceding teeth, which is in accordance with their different crown heights.

M_3 exhibits a pli-caballin, a slight bifurcation of the pli-protoconule, a double pli-prefossette, and a single pli-hypostyle and pli-postfossette. In P_4 the pli-caballin and pli-protoconule are still prominent, but the pli-prefossette and pli-postfossette are nearly gone, and the pli-hypostyle is entirely absent. In P_3 and M_1 only a slight enamel plication exists in the region of the protoconule, representing the pli-protoconule.

Lower Cheek-Teeth—The inferior molars and premolars are relatively short anteroposteriorly and broad transversely. These teeth are well cemented and exhibit a simple enamel pattern as in the superior dentition. The protoconid and hypoconid are convex externally and the intervening enamel fold is of moderate depth, but very open. The metaconid-metastylid columns formed by an open anterior and a compressed posterior fold are strong and rounded, where wear has not proceeded too far. The groove between these two columns is particularly shallow. A prominent antero-external ridge on the protoconid is noticeable in P_4 and M_1 .

Comparison—The characters exhibited by the teeth of the Quatal Canyon specimen are similar to those found in the dentition of species of *Merychippus* from the Barstow Upper Miocene. No. 41 differs from *M. californicus* Merriam of the North Coalinga Region in greater cross-section of upper teeth, and in the presence of more prominent styles and a heavier deposit of cement in these teeth. The fossette borders show a less complicated enamel pattern than in the Coalinga species. This difference prevails even when comparison is made with well-worn teeth of the latter form. The Cuyama species appears to be more advanced than *M. californicus* in size and in the presence of stronger styles and of a heavier deposit of cement in the cheek-teeth.

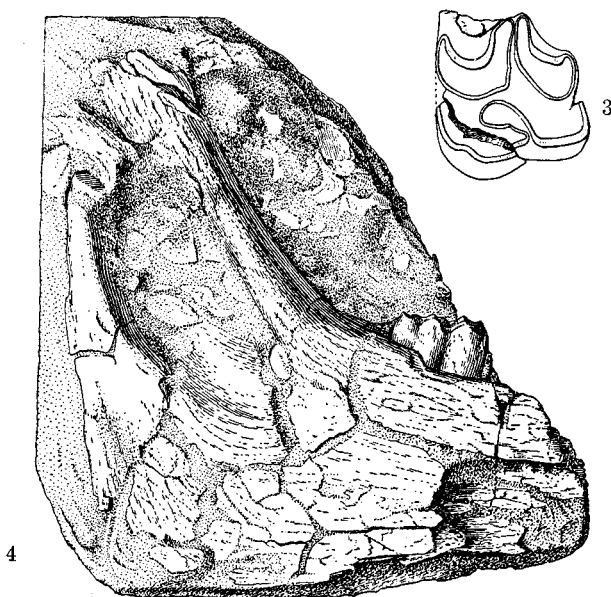


FIG. 3—*Merychippus sumani* Merriam. Upper cheek-tooth, No. 29 C.I.T. Coll., occlusal view; x 1.0. Cuyama Valley Miocene, California.

FIG. 4—*Merychippus sumani* Merriam. Posterior portion of right ramus of mandible with M $\bar{3}$, No. 41 C.I.T. Coll., lateral view; x 0.50. Cuyama Valley Miocene, California.

Upper teeth belonging to species of *Merychippus* from the Barstow Miocene of the Mohave Desert show considerable variation in size, in complication of enamel borders of the fossettes, and in degree of union of the protocone and protoconule. Dr. J. C. Merriam (1919) recognized in the equine assemblage from this locality three distinct but apparently related merychippine species. The largest of these, *M. intermontanus*, approaches *Protohippus* in size, cementation and simplicity of enamel pattern of the teeth. A somewhat smaller form is *M. calamarius stylodontus*, approaching *M. calamarius* in size and in the proportions of the teeth but with a less complicated enamel pattern. *M. c. stylodontus* differs from *M. intermontanus* in shortness of crown, separation of protocone from protoconule for considerable length of the tooth crown, as well as in size. The third species, *M. sumani*, has smaller teeth than in *M. intermontanus* and *M. c. stylodontus* and exhibits greater complication of the enamel lake

borders and more nearly complete isolation of the protocone except in very advanced stages of wear of upper cheek-teeth.

Presumably a somewhat similar example of variation in dental characters is seen in the merychippine forms recorded from the lower Snake Creek beds of Nebraska. Dr. W. D. Matthew (1924, 159-162) has concluded from a study of this material that a single species, *Merychippus paniensis* Cope is represented.

The Quatal Canyon specimen resembles rather closely the larger forms of *Merychippus* from the Barstow, particularly *M. calamarius stylodontus*, in simplicity of enamel pattern of the upper cheek-teeth. However, when teeth of the same stage of wear are compared, the Cuyama form is seen to resemble very closely specimen No. 21401, U. of C. Coll., referred to *M. sumani* Merriam. In the lower teeth the anteroexternal ridge of the protoconid is similar to that in *M. sumani*.

Should the several types of merychippine horses known from the Bartow be regarded as variants of a single form, as inferred by Merriam in 1915 (a, page 9; b, page 50) and as suggested by Matthew in 1924 (161-162) it may be found desirable to refer the Cuyama form to *M. calamarius sumani*.

Measurements in millimeters of dentitions of No. 41, Calif. Inst. Tech. Coll.

	Right	Left
P3, anteroposterior diameter.....	a21.0
P3, transverse diameter.....	23.0
P4, anteroposterior diameter.....	a22.0	a20.0
P4, transverse diameter.....	23.0
M1, anteroposterior diameter.....	20.0
M1, transverse diameter.....
M3, anteroposterior diameter.....	18.5
M3, transverse diameter.....	18.0
P3, anteroposterior diameter.....	a21.0
P3, transverse diameter.....	12.0
P4, anteroposterior diameter.....	21.0	21.5
P4, transverse diameter.....	11.5	12.0
M1, anteroposterior diameter.....	a19.0
M1, transverse diameter.....	9.0
M3, anteroposterior diameter.....	23.0
M3, transverse diameter.....	8.0

a, approximate

Protohippus sp.

The material referred to *Protohippus* includes several upper and lower teeth and a number of incomplete skeletal elements.

Unfortunately in most of the upper teeth only portions of the crowns are preserved, making specific determination difficult. These teeth resemble *Protohippus* and differ apparently from *Merychippus* in size and shape. They are characterized by a heavy deposit of cement. The limb fragments available suggest a type intermediate in size between the merychippine forms of the middle Miocene and the equid species of the Pleistocene.

The Cuyama form resembles somewhat the *P. perditus* group of the Great Plains region (Osborn, H. F., 1918, 127-130) except for the cross-section of the upper teeth, which is somewhat larger in the former than in the latter. A rather advanced stage in the development of the protohippine

horses from the Cuyama Miocene may be indicated by the size of the teeth, in which respect an approach is made to the genus *Pliohippus*.

Measurements in millimeters of the protohippine teeth

	Transverse width	Anteroposterior length	Height of crown
Left upper molar, No. 19	31	27	35
Left upper molar, No. 20	a 25	a 26	33
Left upper molar or premolar, No. 21	27 ?	29	42
Left P2 (?) No. 22.....	a 22	28	43
Right upper molar, No. 23.....	a 29	a 27	31
Right upper premolar, No. 25.....	a 26	29	53
Left lower tooth, No. 26.....	a 16	a 26	30
Right lower tooth, No. 27.....	12	26	45
Right lower tooth, No. 28.....	13	a 26	35

a, approximate

Hipparion ? sp.

A well-worn cheek-tooth, No. 24, from the Apache Canyon locality No. 64, exhibits characters suggestive of the genus *Hipparion*. The tooth is badly weathered, but the preserved portion of the crown exhibits a size of cross-section and a complication of the enamel pattern, particularly of the fossette borders, as in *Hipparion*.

The occurrence of the genus *Hipparion* in association with *Merychippus* is infrequent, and questionable in this case.

Measurements in millimeters of right upper cheek-tooth No. 24

Anteroposterior length	(?) 28
Transverse width	25
Height of crown	12-20

ARTIODACTYLA

Oreodont sp.

The presence of an oreodon in the Cuyama fauna is suggested by the posterior portion of a mandible with the roots of teeth remaining. This group of mammals may be further represented in the collection by several fragments of teeth and limb elements. The jaw fragment, No. 56, resembles in size No. 21487, U.C.C., from the Barstow, described as *Merycochaerus ? buwaldi* by J. C. Merriam. The Cuyama specimen is not generically determinable.

Camelid sp.

A fragment of the symphyseal region of a lower jaw, two astragali, and several incomplete fragments of limb elements represent the occurrence of a comparatively large camel. In so far as comparison can be made, this material corresponds favorably with comparable camel elements from the Barstow Miocene. At least two fragments of proximal phalanges suggest the presence of a smaller form related perhaps to *Procamelus*.

Merycodus sp.

The merycodont antelopes are among the more common types represented in the fauna. The material consists for the most part of scattered teeth

and jaw fragments, parts of limb bones, carpal and tarsal elements, vertebræ, and many small fragments of horns. A partially complete skull, specimen No. 59, C.I.T. Coll., with the right ramus of the lower jaw and several associated parts of the skeleton belonging to the same individual were collected at locality 64 in Apache Canyon.

While the skull of this specimen is small, the individual represented is presumably not a particularly young animal for the sutures are all indistinct, the teeth well worn, and the epiphyses completely fused with the shafts in the limb bones. A noteworthy feature of this specimen is the absence of horns, for the supra-orbital portion of the surface of the frontals is quite smooth. The margin of the left orbit has been crushed and the occipital region is also damaged. The right upper tooth row is complete, but the left series is entirely missing. $M\bar{3}$ is a two-lobed tooth with a third incipient posterior lobe. $M\bar{3}$ is a simple three-lobed tooth.

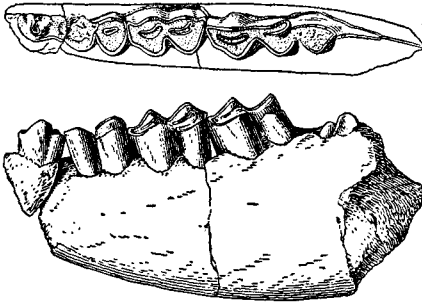


FIG. 5—*Merycodus* sp. Fragment of left ramus of mandible with $P\bar{4}$ to $M\bar{3}$ inclusive; No. 60 C.I.T. Coll.; lateral and occlusal views. \times 1.0. Cuyama Valley Miocene, California.

It is difficult to reach a specific determination of the Cuyama form based on this material, inasmuch as the proportions and attitude of the horns have played a large part in distinguishing the various species described from the later Tertiary. The position of the cranial sutures and the unquestionable hypsodonty of the posterior molars in No. 59 clearly indicate an individual belonging to the merycodont group of antelopes. The absence of horns in the Cuyama specimen may perhaps be attributed to a difference in sex, but it is noteworthy that hornless forms of the genus *Merycodus* have not been found as frequently as the horned types.

The detached pieces of horn which have been found are too fragmentary to be of value in approaching a conclusion as to specific relationship. Apparently skeletal proportions are not sufficiently reliable to be of diagnostic importance as a number of the recognized species can not be distinguished safely on characters other than horn structure.

Measurements in millimeters of specimens No. 59 and No. 60.

	Specimen No. 59	Specimen No. 60
Total length of skull.....	a132	
Approximate distance between orbital rims.....	60	
Length of upper tooth row, $P\bar{2}$ to $M\bar{3}$ inclusive.....	45	
Length of lower tooth row, $P\bar{2}$ to $M\bar{3}$ inclusive.....	48	43
Depth of mandible below $M\bar{3}$	15	($P\bar{4}$ to $M\bar{3}$ inclusive)
a, approximate		

LIST OF LOCALITIES

Monterey Miocene of Cuyama Valley, Ventura County, California:

Locality 48—Cliff sections and badlands in Quatal Canyon 2.5 miles east of Matthew's ranch house.

E. $\frac{1}{2}$ sec. 34 and S $\frac{1}{2}$ sec. 27, T. 9 N., R. 23 W., S. B. M.

Locality 64—Ravine off north side of Apache Canyon, approximately 8 miles northeast of Cuyama Valley and immediately northwest of the potrero at the head of Apache Canyon. Sec. 2 and portions of adjoining sections, T. 8 N., R. 23 W., S. B. M. U. S. G. S. Quadrangle, Mount Pinos.

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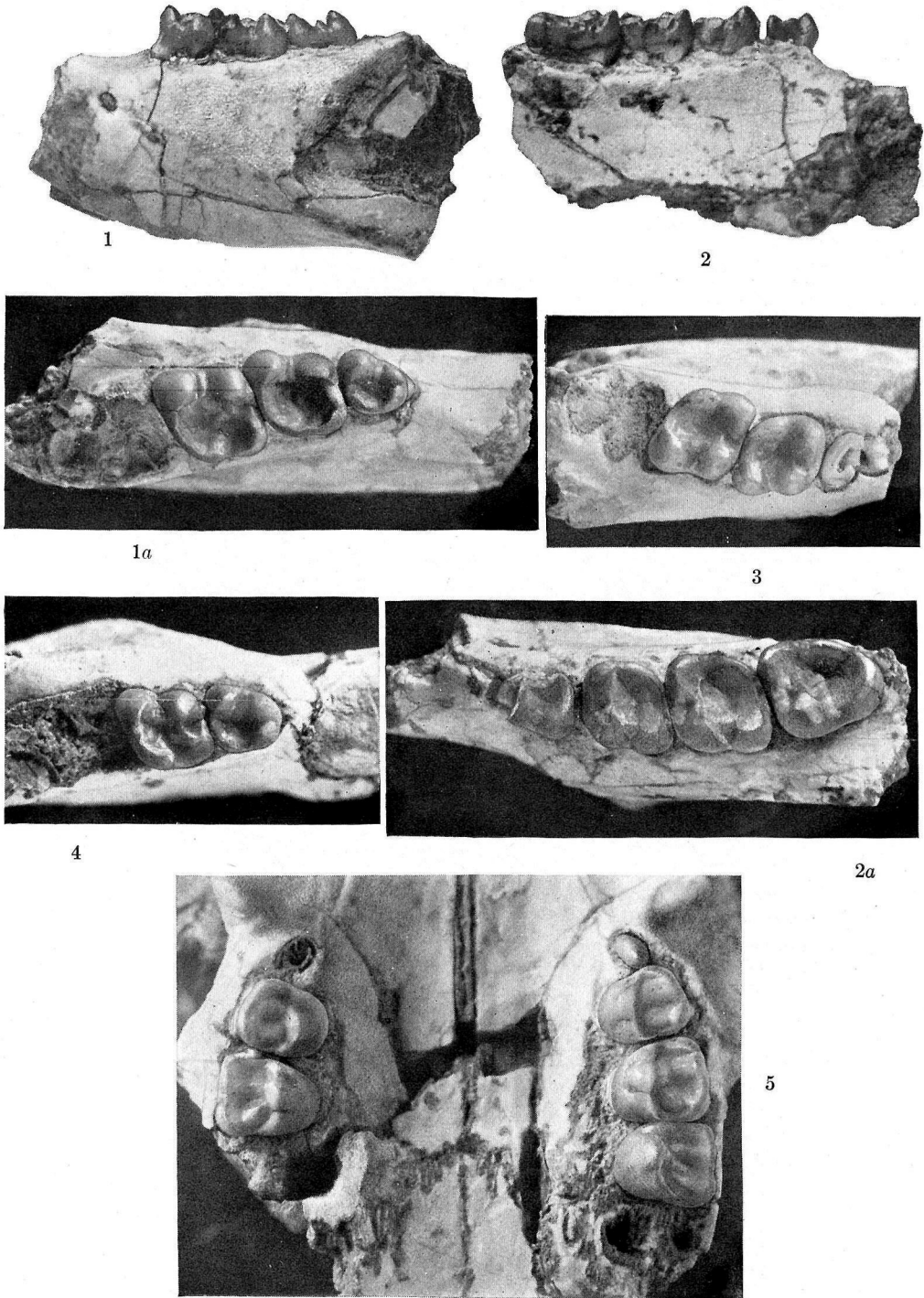
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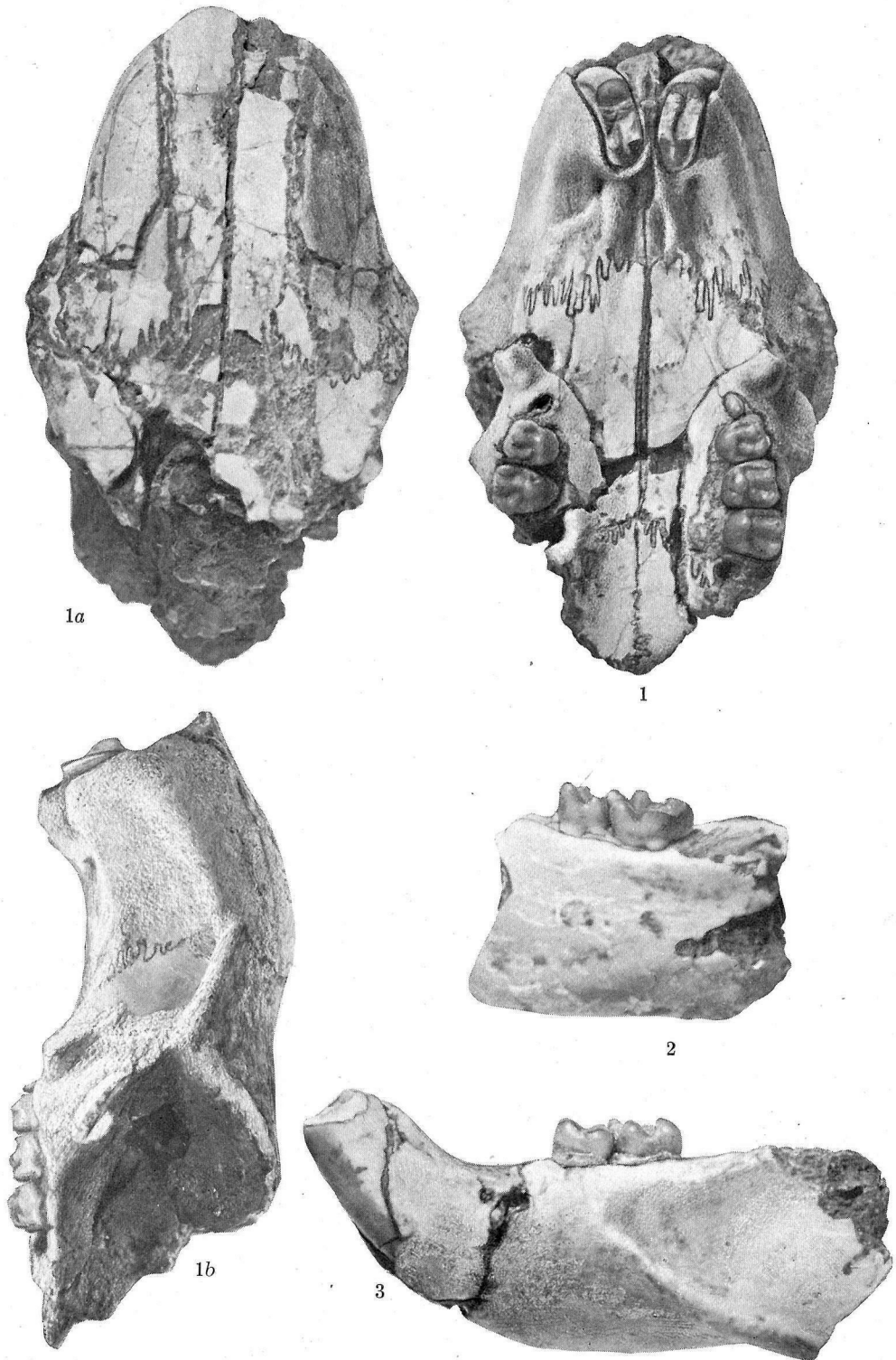
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Citellus (Protospermophilus) quatalensis n. subgen. and sp.

Fig. 1, ramus of mandible, No. 31 C.I.T. Col., lateral view, x 4.0; fig. 1a, occlusal view, x 5.0. Fig. 2, ramus of mandible, No. 32, C.I.T. Coll., lateral view, x 4.0; 2a, occlusal view, x 5.0. Fig. 3, right ramus of mandible, No. 30 C.I.T. Coll., occlusal view, x 5.0. Fig. 4, left ramus of mandible, No. 30 C.I.T. Coll., occlusal view, x 5.0. Fig. 5, superior dentition, No. 30 C.I.T. Coll., occlusal view, x 5.0. Cuyama Valley Miocene, California.



Citellus (Protospermophilus) quatalensis n. subgen. and sp.

Figs. 1, 1a, 1b, skull, No. 30 C.I.T. Coll.; fig. 1, ventral view; fig. 1a, dorsal view; fig. 1b, lateral view; x 3.0. Fig. 2, right ramus of mandible, No. 30 C.I.T. Coll., lateral view, x 4.0. Fig. 3, left ramus of mandible, No. 30 C.I.T., lateral view, x 4.0. Cuyama Valley Miocene, California.

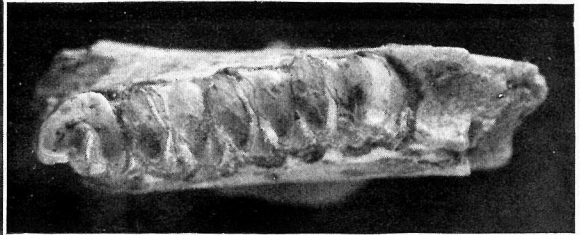
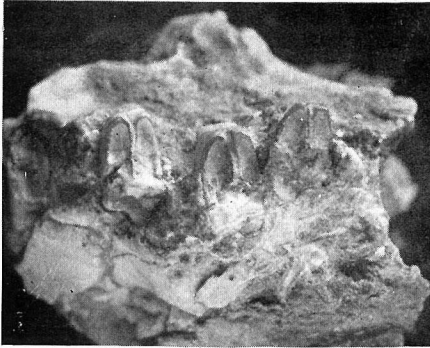
Hypolagus? apachensis n. sp.

Fig. 1, maxillary fragment, No. 37 C.I.T. Coll., occlusal view, x 5.0. Fig. 2, ramus of mandible, No. 36 C.I.T. Coll., lateral view, x 4.0; fig. 2a, occlusal view; x 5.0. Fig. 3, P₃, No. 32 C.I.T. Coll., occlusal view, x 5.0. Fig. 4, ramus of mandible, No. 38 C.I.T. Coll., occlusal view, x 5.0.

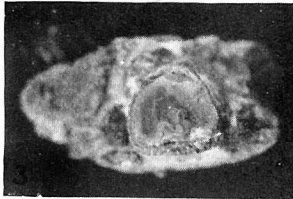
Perognathus furlongi n. sp.

Figs. 5, 5a, skull, No. 35 C.I.T. Coll.; fig. 5, lateral view; fig. 5a, dorsal view; x 4.0. Fig. 6, superior dentition, No. 35 C.I.T. Coll., occlusal view, x 10.0. Cuyama Valley Miocene, California.

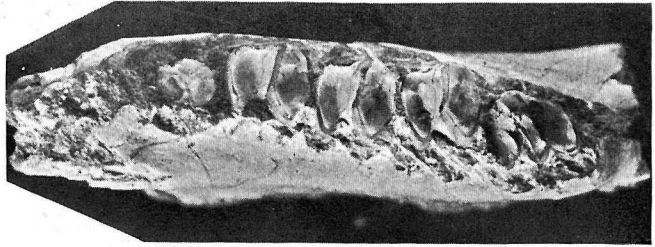
1



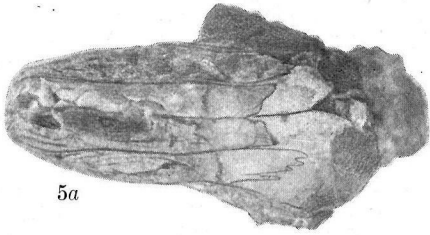
2a



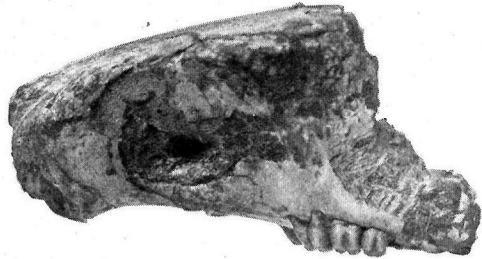
3



4

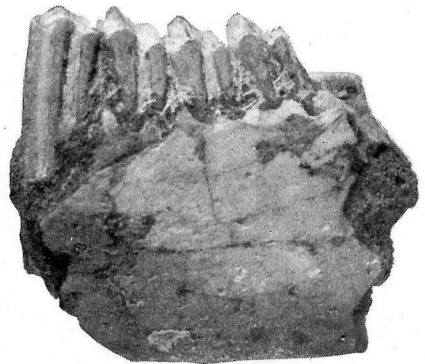
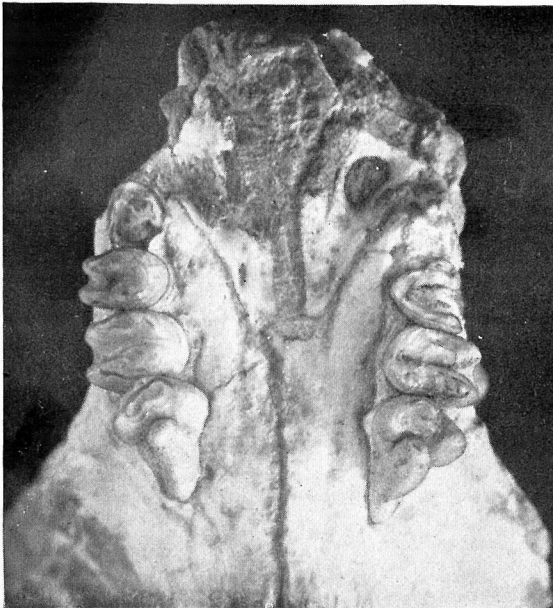


5a

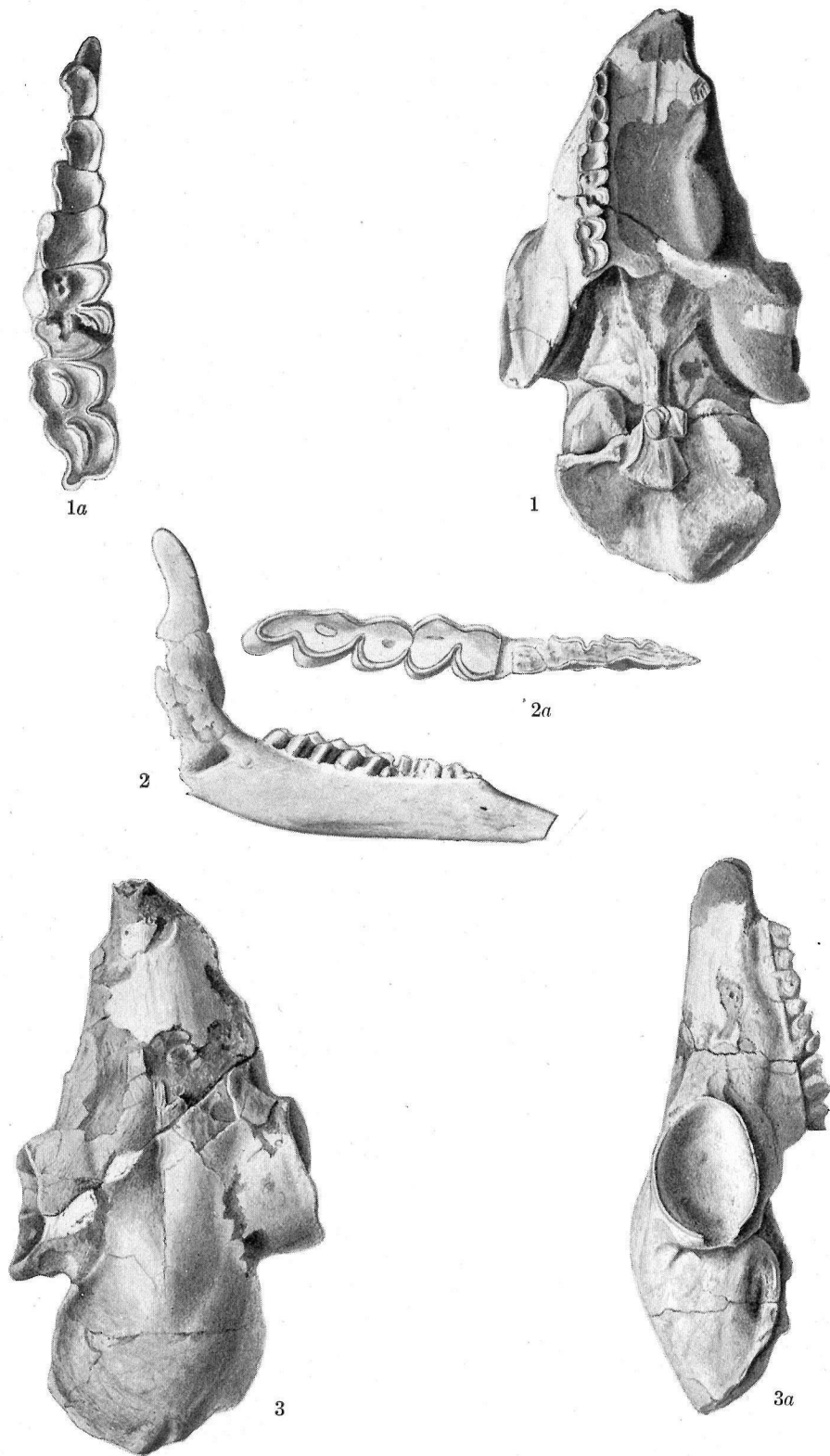


5

6



2



Merycodus sp.

Fig. 1, skull, No. 59 C.I.T. Coll., ventral view, x 0.66; fig. 1a, P₂ to M₃ inclusive, occlusal view, x 1.33. Fig. 2, ramus of mandible, No. 59 C.I.T. Coll., lateral view, x 0.66; fig. 2a, P₂ to M₃ inclusive, occlusal view, x 1.33. Figs. 3, 3a, skull, No. 59 C.I.T. Coll.; fig. 3, dorsal view; fig. 3a, lateral view; x 0.66. Cuyama Valley Miocene, California.